Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Trouble in the trawls: Is bycatch in trawl fisheries preventing the recovery of sawfish? A case study using the US population of smalltooth sawfish, *Pristis pectinata*

John K. Carlson

NOAA Fisheries Service, Southeast Fisheries Science Center, Highly Migratory Species Branch, 3500 Delwood Beach Road, Panama City, FL 32408, USA

ARTICLE INFO

Keywords: Endangered Sawfishes Population viability model Population size Fishing mortality

ABSTRACT

All five species of sawfish (Family Pristidae), are among the most threatened families of elasmobranchs, and face significant threats from fishing, in particular trawl fisheries, and habitat loss. Unfortunately, there is little data on the level of sawfish taken in trawl fisheries outside Australia and the United States and case studies from these areas can provide a "risk analysis" for populations elsewhere. In the United States, bycatch risk for smalltooth sawfish is significantly higher for the southeast shrimp trawl fishery than all other fisheries assessed. Using new estimates of life history and population size, an updated population viability model was developed and trajectories using different scenarios of initial population sizes, fishery catches and post-release mortality were projected for 100 years. The simulated population trajectories for the assumed initial population sizes and fishing mortality ranged between population extinction, quasi-extinction, to a slight reduction in population size and in some cases the population continuing to recover. The most pessimistic scenarios were when the initial population was lowest and post-release mortality in the shrimp trawl fishery was highest. Quasi-extinction for some scenarios was between 6.9 and 22.8 years. While some scenarios suggest that smalltooth sawfish still can recover despite the potential for shrimp trawl fishing mortality, key input variables for these optimistic scenarios is the initial population size and the true level of fishing mortality. This uncertainty highlights the importance of improving our understanding of sawfish life history, captures in fisheries and their associated post-release mortality.

1. Introduction

The incidental capture or bycatch of non-targeted species in fishing gear is widely recognized as an important threat to the conservation status of many animal populations (Read et al., 2006; Gilman et al., 2010; Reeves et al., 2013). Bottom trawling is a relatively non-selective fishing method, and in many cases, bycatch often comprises a much higher proportion of the total catch than the target species (Saila, 1983; Andrew and Pepperell, 1992). Bottom trawl impacts on elasmobranchs have been widely documented globally in various fisheries and areas (see review in Molina and Cooke, 2012; Oliver et al., 2015). For example, elasmobranch bycatch in the shrimp trawl fishery in Pacific waters off Costa Rica comprised 25 species and 13 families (Clarke et al., 2016). In Australia's Northern Prawn Fishery, 56 species of elasmobranchs have been documented in this fishery and these species comprise around 4 % of the bycatch by weight (Stobutzki et al., 2001).

Globally, all five species of sawfish populations face significant threats from fishing and habitat loss. Sawfish are among the most threatened families of elasmobranchs (Dulvy et al., 2014, 2016). All species in the Family are now listed as Critically Endangered under

https://doi.org/10.1016/j.gecco.2023.e02745

Received 24 April 2023; Received in revised form 20 November 2023; Accepted 21 November 2023

Available online 29 November 2023

2351-9894/Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).







the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species with inferred or suspected population declines greater than 80 % over the last three generations (Harry et al., in press). The toothed rostra of sawfish make them highly susceptible to entanglement, particularly in trawls. The difficulty of removing and releasing them alive combined with the high value of their fins suggests there is a high likelihood of retention even though they are captured infrequently (Dulvy et al., 2014; Yan et al., 2021) and are prohibited under some national and international regulations (Fordham et al., 2018). Moreover, bycatch reduction devices in trawls such as turtle excluder devices (TEDs) and other similar designs with escape panels as option to reduce mortality of sawfish is unlikely to be successful because of their toothed rostra. As bycatch in trawls has been identified as a significant threat to the recovery of all sawfish species, conservation planning requires knowledge of the level of bycatch mortality populations can withstand while still increase in population size (Harrison and Dulvy, 2014). Unfortunately, there is little data on the number of sawfish captured in trawl fisheries outside Australia and the United States and case studies from these areas can provide a "risk analysis" for populations elsewhere on levels of bycatch these species can withstand to enable recovery as their biology is similar (Dulvy et al., 2014).

In the United States, smalltooth sawfish, *Pristis pectinata*, historically ranged from Texas to North Carolina, but the range has contracted to southwest Florida primarily due to habitat loss and bycatch in fisheries (Brame et al., 2019). The species was listed as Endangered under the US Endangered Species Act (ESA) in 2003. Despite some of the highest levels of protection afforded by the ESA, smalltooth sawfish are still captured as bycatch in commercial fisheries. In a recent study using smalltooth sawfish movement data with fisheries effort, Graham et al. (2022) determined bycatch risk associated with the US southeast shrimp trawl fishery was significantly higher than all other fisheries assessed, indicating that this fishery currently poses the greatest threat to recovery. Using population viability models and estimated levels of bycatch, Carlson and Simpfendorfer (2015) indicated that smalltooth sawfish in US waters have the ability to recover providing fishing-related mortality remained low. However, since that publication, levels of bycatch authorized in the shrimp trawl fishery have increased (NMFS, 2021), and it is currently uncertain if smalltooth sawfish can still recover given any increase in bycatch levels. In addition, new and updated information is available on smalltooth sawfish life history (e.g. Brame et al., 2019) and populations size determined through genetic analysis (Feldheim et al., 2017; Smith, 2021). As a case study for other sawfish species and as a potential measure of their ability to recovery, the goals of this study were to determine smalltooth sawfish's capability to recover under various scenarios of bycatch mortality, specifically from the US southeast shrimp trawl fishery, as well as other sources of bycatch.

2. Methods

The population viability model for female smalltooth sawfish developed by Carlson and Simpfendorfer (2015) was updated with new life history information. In the new model, I updated the original fecundity estimate of 7–17 offspring/female from Carlson and Simpfendorfer (2015) using the range (7–14 offspring/female) from Brame et al. (2019). A Monte Carlo simulation was used because Brame et al. (2019) did not provide a mean or standard deviation due to low sample sizes. The Monte Carlo simulation used 1000 random values derived from a uniform probability density function between 7 and 14 to obtain an estimate of the mean and standard deviation which was used as the inputs to the model. The sex ratio was assumed to be 1:1 and reproductive periodicity is assumed to be biennial. Female age-at-maturity was determined by fitting a logistic model to the binomial maturity data (immature=0, mature=1) from all current unpublished reproductive information collected through necropsies or hormone analysis (Poulakis, unpublished; Gelsleichter, unpublished, respectively). The age at maturity was determined by back-transforming the median length at maturity using estimates from the von Bertalanffy function in Scharer et al. (2012). Back-transforming the updated length at maturity (384 cm stretched total length) results in a median age of maturity of eight (8).

Carlson and Simpfendorfer (2015) estimated the instantaneous rate of natural mortality (converted to survivorship) through

Table 1

Female life history and baseline parameters used in development of smalltooth sawfish population viability model with a comparison of previous values used in Carlson and Simpfendorfer (2015). Values in parentheses represent standard deviations used as inputs to the age matrix.

Parameter	Value this study	Source	Previous value	Updated
Age-at-maturity	8 years	This study	7 and 11 years	Yes
Maximum age	30 years	Scharer et al. (2012)	30 years	No
Litter size (yr)	2.62 (0.504)	Brame et al. (2019)	3.1 (0.758)	Yes
		This study		
Survivorship				
Age 0	0.87 (0.208)	Carlson and Simpfendorfer (2015)	0.87 (0.131)	No
Age 1	0.87 (0.131)		0.89 (0.104)	
Age 2	0.89 (0.104)		0.90 (0.093)	
Age 3	0.90 (0.093)		0.91 (0.087)	
Age 4	0.91 (0.087)		0.92 (0.082)	
Age 5–6	0.92 (0.082)		0.93 (0.080)	
Age 7–11	0.93 (0.080)		0.94 (0.080)	
Age 12–30	0.94 (0.080)		0.87 (0.131)	
Initial total population size	8075 females	Ne/Nc: (Smith, 2021)	600 females	Yes
	2975 females	Ne/Nc ((Portnoy et al., 2009;Ahonen et al., 2009;Dudgeon and Ovenden, 2015).	2250 females	
	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 (2015)	45,000 females	No

multiple indirect life history methods to incorporate the range of mortality mechanisms (e.g. temperature, growth or maximum age). Carlson and Simpfendorfer (2015) derived natural mortality through a combination of the methods of Hoenig's (1983),Pauly (1980), Peterson and Wroblewski (1984) and Lorenzen (1996). As there are no new estimates of growth or maximum age, the instantaneous rate of natural mortality were retained from Carlson and Simpfendorfer (2015) (Table 1). The updated life history parameters were input into a post-breeding Leslie matrix following Caswell (2001). The parameters estimated through the Leslie matrix were the population finite growth rate (λ), the stable age-distribution vector (w), the age-specific reproductive value vector (ν), and the elasticities of the matrix elements (e_{ij}). Within this matrix formulation, λ was calculated as the dominant eigenvalue of the projection matrix. The vectors of the stable age distribution (w) and the age-specific reproductive value (ν) were given by the dominant right and left eigen vectors, respectively. The elasticities of each matrix element (e_{ij}) were calculated according to Caswell (2001).

2.1. Bycatch mortality

Estimates of fishing mortality by commercial shrimp trawlers were updated based on the information in the ESA Section 7 Consultation-Biological Opinion for the US Shrimp Fishery (NMFS, 2021). In the updated opinion based on an analysis by Carlson (2020), a total of 1806 smalltooth sawfish could be captured over any running 5 years, which equates to approximately 180 female sawfish per year assuming females and males are equally captured. Recognizing that there is no information on post release mortality, 4 scenarios were constructed assuming 100 %, 75 %, 50 %, and 25 % post release mortality (Table 2). An examination of the length information from smalltooth sawfish captured indicates most animals captured were > 360 cm STL, thus mortality was applied to ages 6–30.

Bycatch in the shrimp trawl fishery is not the only source of mortality for smalltooth sawfish and as bycatch impacts from other fisheries may be cumulative in impacting their recovery, two additional sources of bycatch mortality were included: the shark bottom longline and recreational rod and reel fishery. Bycatch in coastal gillnet fisheries could also occur, but since 1998 with observer coverage ranging up to 100 % (Baremore et al., 2007), there has been only one documented interaction (Kroetz et al., 2020) and as Graham et al. (2022) determined bycatch risk was currently low, no mortality from this fishery was included.

For the shark bottom longline fishery, an analysis of observer data from the fishery indicated 31.4 subadult and adult sawfish were caught from 2007 through 2010 (Carlson and Richards, 2011). While most animals captured in longline fisheries are released alive (Carlson, unpublished data), the current level of post release mortality is unknown. Given increases in blood lactate are associated with higher levels of stress and the increased chance of mortality (Skomal and Mandelman, 2012), lactate levels can be used as a proxy for estimating post-release mortality. Prohaska et al. (2018) determined blood lactate levels of smalltooth sawfish captured on bottom longlines was among the lowest of the species examined (mean= 2.54 mmol l^{-1}). For comparison, Prohaska et al. (2018) determined great hammerhead shark (*Sphyrna mokarran*) had among the highest levels of blood lactate (12.9 mmol l⁻¹). As part of stock assessment for great hammerhead, Courtney et al. (2021) determined a post release mortality rate for great hammerhead= 41.9 % of live releases from bottom longline gear. As the lactate levels were ~5 times lower in smalltooth sawfish, the mortality rate from great hammerhead shark was applied to the estimated captures of smalltooth sawfish in the shark bottom longline fishery with a reduction of 5 times to account for differences in lactate levels (8.2 % mortality rate for smalltooth sawfish) from Carlson and Richards (2011). This assumed the difference in lactate levels reflected a difference in post release mortality. Similar to shrimp trawls, mortality was applied to ages 6–30.

Recreational fishing bycatch was incorporated into the model as mortality by fishers using rod and line. It is not currently known how many smalltooth sawfish are captured in the recreational fishery and what percentage of those captures are female. Reported encounters in the US Sawfish Recovery Database suggest about 500 individuals are caught per year, which is likely an underestimate (Tonya Wiley, Havenworth Coastal Conservation, personal communication). A potential proxy for an estimate of recreational catches is the great hammerhead shark, as this species, like smalltooth sawfish, is caught in shallow water by Florida shore-based and inshore

Table	2
-------	---

Summary of population viability scenarios for fishing mortalities applied to smalltooth sawfish. Mortalities represent the number of animals.

Scenario	Initial population size	Recreational Fishing Mortality	Shark Bottom Longline Mortalities	Shrimp Trawl Mortalities
1	8075	11	1	45
2	8075	11	1	90
3	8075	11	1	135
4	8075	11	1	180
5	2975	11	1	45
6	2975	11	1	90
7	2975	11	1	135
8	2975	11	1	180
9	1255	11	1	45
10	1255	11	1	90
11	1255	11	1	135
12	1255	11	1	180
13	1695	11	1	45
14	1695	11	1	90
15	1695	11	1	135
16	1695	11	1	180

fishers and must be released alive (https://www.flrules.org/gateway/ChapterHome.asp?Chapter=68B-44). The average number of live releases of great hammerhead in Florida from 2018 to 2020 was 1013 sharks (Cortés and Baertlein, 2021). There are currently no estimates of blood lactate levels for shore-based caught great hammerheads by recreational fishers but estimates from blacktip shark (*Carcharhinus limbatus*) (Whitney et al., 2017) are 4.5 times higher than for smalltooth sawfish caught on rod and reel (Prohaska et al., 2018). Using the post release mortality rate for blacktip sharks from recreational fishers (9.7 %; Whitney et al., 2017) and applying a ratio to account for differences in lactate levels, a recreational post release mortality rate of 2.1 % was assumed for the estimated catches of smalltooth sawfish. Recreational fishing mortality scenarios were applied to ages 1–30.

2.2. Population projections

The revised Leslie matrix was used to update the model developed in RAMAS Metapopulation (Akçakaya, 2005) by Carlson and Simpfendorfer (2015) to project and examine population responses to conditions set in the models. This model implements a standard Leslie matrix (L) that provided 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:

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

Carlson and Simpfendorfer (2015) developed two initial population estimates using density information (Wiley and Simpfendorfer, 2010) applied to the hypothesized area of occupancy and the effective genetic population size (Ne) from Chapman et al. (2011). There is still no current census data available on the size of the smalltooth sawfish population in US waters. Therefore, initial population size was estimated using four approaches. Two recent genetic studies provide updates to the effective genetic population size estimated from Chapman et al. (2011) and alternately the current number of breeders in two of the major birthing areas and critical habitat units described in Norton et al. (2012).

Analysis of tissue samples collected between 2002 and 2008 initially showed Ne was 250–350 individuals (Chapman et al., 2011). However a new analysis with updated data from 2012 to 2015 found that Ne is much closer to 650 (95 % confidence limits 367–2358; Smith, 2021). For some elasmobranch populations, N_e has been reported to approximate the census population size (N_c) with the ratios of N_e/N_c to range from 0.84 for sandbar shark (*Carcharhinus plumbeus*), 0.71 for grey nurse (*Carcharias taurus*) and 0.82 for zebra sharks (Portnoy et al., 2009; Ahonen et al., 2009; Dudgeon and Ovenden, 2015). However, for the juvenile proportion of the population, Smith (2021) estimated an N_e/N_c ratio for smalltooth sawfish between 0.41 and 0.46. Thus, we assumed two scenarios to provide an estimate of current census population size using the mean of the estimates for sandbar, grey nurse and zebra shark and the median estimate from Smith (2021).

As part of determining N_e , Smith (2021) also estimated the number of breeders (N_B), or the number of breeding adults that produce a particular cohort (Waples et al., 2014) for the Ten Thousand Islands/Everglades Unit of critical habitat (Norton et al., 2012). Current estimates of N_B are 284 individuals (95% confidence limits; 1–1425). For the Charlotte Harbor Estuary Unit of critical habitat, which is smaller and more anthropogenically disturbed, NB was estimated at 28-78 individuals (Chapman, unpublished data referenced in Smith, 2021). As no mean or standard deviation was provided, a Monte Carlo simulation to obtain 1000 random values was derived from a uniform probability density function between 28 and 78 and the mean and standard deviation derived from that simulation. In addition to the two critical habitat units, an area outside the two critical habitat units that would also support a breeding population is the areas within the Florida Keys National Marine Sanctuary. An examination of sawfish encounter records reported by the public (U.S. Sawfish Recovery Database, unpublished data) indicates records of very small sawfish (<100 cm STL) in the lower Florida Keys with most records in the Key West, Great White Heron and Key Deer National Wildlife Refuges indicating sawfish give birth in these areas. While it is likely that the number of breeders in these areas is less than in the other Critical Habitat areas (Adam Brame, NOAA Fisheries Service, personal communication), it still represents a proportion of the population. As there is no estimate of N_B for that area, the average density of breeders (number/area) from the Charlotte Harbor Estuary Unit and Ten Thousand Islands/Everglades Unit was applied to the area of these three National Wildlife Refuges. This would be the most conservative approach to estimate the number of breeders in the lower Florida Keys as other areas in the Florida Keys could potentially also contribute to the population but these areas were excluded due to uncertainty.

In an alternate study using juvenile samples to reconstruct parental genotypes, Feldheim et al. (2017), determined that 55 females gave birth to the 349 juveniles sampled in the Charlotte Harbor Estuary between 2004 and 2015. Similarly, Smith et al. (2021) determined that 71 females contributed to the 310 juveniles sampled in the Ten Thousand Islands/Everglades Unit between 2000 and 2015. Again, as no estimate is available for the lower Florida Keys, the average density of adult females (number/area) from the Feldheim et al. (2017) and Smith et al. (2021) study was applied to the area of the National Wildlife Refuges. When constructing total population sizes for the 4 hypothesized initial population size scenarios, it was assumed the population was in a stable age distribution produced by the Leslie matrix.

Quasi-extinction rates were measured as the probability that less than a specific number of individuals survive to the next stage. Quasi-extinction threshold were set at 24 adult females (\sim 175 total females) based on the median of the lowest historical estimates (1887–2017) of N_e from Smith (2021). Carrying capacity for smalltooth sawfish was determined to be 45,000 females for the entire historical range of smalltooth sawfish (\sim North Carolina to Texas) based on Carlson and Simpfendorfer (2015).

The population was projected forward for 100 years (~5 generations based on IUCN Criteria; Carlson et al., 2022) for each scenario. 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



Fig. 1. Frequency distributions of the stable age distribution produced by the Leslie matrix, reproductive value (relative contribution of each age class to future generations), and elasticity values (i.e. the proportional sensitivities of the finite rate of increase to small changes in matrix elements of survivorship and reproduction).

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 in the Monte Carlo simulation (see previous). Fishing mortality is introduced as the number harvested from each of the designated ages proportional to its abundance at the current time step. Each time step was replicated 500 times. RAMAS introduced variation in carrying capacity (*K*) by randomly sampling a single deviate at each time step based on the estimated standard deviation given for *K*. Measurement error in the initial population size and harvest levels (i.e fishing mortality) was set by specifying a coefficient of variation (CV) of 0.3. 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) was the population growth rate at time t, Rmax was the maximum population increase rate, 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 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 Akcakaya (2005).

3. Results

Estimates of population growth (λ) when age-at-maturity was 8 years was 1.165 yr⁻¹. Age classes 8–20 years had the highest reproductive value. The elasticities obtained for smalltooth sawfish indicate that the population is more sensitive to changes in survival rates than to those in reproduction (Fig. 1).

The simulated population trajectories for the assumed initial population sizes and fishing mortality ranged between population extinction (number of females=0), quasi-extinction, to a slight reduction in population size and in some cases the population continuing to recover (see appendix 1 for all scenarios).

For the 100 % post-release mortality shrimp trawl scenarios, an initial population size of 1255 or 1695 females became extinct or had few females remaining after 12–15 years (Scenario 12 and 16). The scenario with moderate initial population sizes (2975 females) under 100 % mortality still showed moderate growth with the population increasing proportionally from its initial size by about 50 % (Fig. 3). For the largest initial population size, population was relatively unaffected, increasing to over 30,000 females in 100 years.

Out of the scenarios with 50–75 % post-release mortality shrimp trawl, one scenario (Scenario 11) resulted in the population declining by 94 % (Fig. 3). Scenarios 7 and 15 showed negligible population increases and five scenarios demonstrated population increases from 30 % to 280 % of initial size over the 100 years.

Quasi-extinction was found for six of the 16 scenarios (Fig. 4). The median time to quasi-extinction from all simulations within each scenario was between 6.9 and 22.8 years. Quasi-extinction was determined to occur with moderate fishing mortality and when the initial population size was the smallest.



Fig. 2. Simulated population projections of the smalltooth sawfish for scenarios 7, 12, 15 and 16. Blue circles=the mean abundance at time t. Solid lines represent the \pm 1 standard deviation of the population at time t.



Fig. 3. 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.

4. Discussion

Under baseline conditions, the smalltooth sawfish population's finite rate of population increase ($\lambda = 1.165$) was lower to that previously developed by Carlson and Simpfendorfer (2015) when assuming age at maturity was 8 but similar when age at maturity was 11 years ($\lambda = 1.150$). Since the publication of Carlson and Simpfendorfer (2015), it has been determined that it is likely that the larger litter size (17.5 individuals) determined by Bigelow and Schroeder (1953) was an overestimate and was excluded in Brame et al. (2019). The age of maturity used by Carlson and Simpfendorfer (2015) was also revised with new data as more research using data on plasma concentrations of sex hormones to characterize maturity and necropsied females, with the addition of fitting a logistic model to the data, has helped to refine the age of maturity. Yet, even with the lowered productivity levels, smalltooth sawfish still have among the higher levels of intrinsic rates of population growth (r) of large bodied elasmobranchs. Grant (2021) using updated life history information for largetooth sawfish, *Pristis pristis*, populations in Australia estimated population growth (λ) from 1.14 to 1.05 year⁻¹. Cortés (2016) considered species to be medium to fast growing when the intrinsic rate of growth using the Euler equation ranged from 0.074 to 0.237 year⁻¹. Assuming the finite rate of population growth follows $\lambda = \exp^r$, then values of r for smalltooth sawfish approximate 0.153 year⁻¹ and for largetooth sawfish 0.131-0.048 year⁻¹ While life history data for dwarf sawfish, Pristis clavata, and green sawfish, Pristis zijsron are highly uncertain (Grant et al., 2022; Harry et al., 2022; respectively), there is growing evidence that narrow sawfish (Anoxypristis cuspidate) reach sexual maturity early (2-3 yrs) and have intrinsic rates of population increase (r) greater then 0.27 yr⁻¹, making this species less susceptible to fishing pressure (D'Anastasi et al., 2013). This shows promise that some sawfish populations have the ability to recover despite suffering drastic population declines and range contractions through a significant portion of their range.

There were considerable differences among scenarios in population trajectories for the smalltooth sawfish population. Depending upon the combination of inputs, the projected population levels varied from increases with little impact from fishing mortality, to essentially no change in population abundance, moderate declines, and declines through to either quasi-extinction or complete extinction within a short period of time (~12 years). The most dramatic declining trends resulted largely from the impact on the initial population size from the highest assumed fishing mortalities (100 % and 75 % post release mortality). Scenarios where the population size was smallest were not able to successfully replace themselves despite the moderate level of productivity smalltooth sawfish possess. Scenarios where the initial population was highest approached carrying capacity within 20 years when the level of fishing mortality was moderate to low. Unfortunately, information on population size to make accurate predictions on recovery for sawfishes is rare. Outside this study, only Grant (2021) using information of density estimates for smalltooth sawfish in the US (Wiley and Simpfendorfer, 2010) estimated population sizes of 1353–2751 subadult and adult females for 3 areas in northern Australia. Similarly to this study, using a stage based matrix in a population viability model, Grant (2021) predicted populations of largetooth sawfish declined significantly and rapidly when initial population size was lowest.

With the lack of reliable data on census size, the use of the genetic effective population size (N_e) as an input into risk analysis and viability modeling is growing in popularity. N_e is the evolutionary analogue of N_c , defined as the number of theoretical 'ideal' individuals, where all have an equal likelihood of contributing their genes to the next generation (Waples, 2022). N_e determines the rate of inbreeding and the loss of genetic variation, and therefore, can predict the evolutionary potential of a population (Ferchaud et al., 2016). For ecological applications, N_e can be defined by the number of potential parents, and mean and variance in offspring number, which can be used to estimate the effect of genetic drift in the next generation (Waples, 2022). N_e is often smaller than N_c , and assumed N_e/N_c ratios can be useful in estimating historic population sizes in elasmobranchs, such as the southwest Australian population of white shark (*Carcharodon carcharias*) (see Braccini et al., 2017). Few reliable N_e estimates exist for elasmobranchs, partly because its



Fig. 4. Cumulative probability of quasi-extinction, the predicted number of years that will pass before the population falls below 24 adult females (~175 total females), depending on the scenario. Dashed lines are 95 % confidence intervals.

calculation is complicated in long-live, iteroparous species with overlapping generations (e.g., Waples et al., 2014). Another metric often used for such species is the number of breeders that produced a sampled cohort (N_b) (Waples, 2005). Regardless, reliable estimates of N_e and N_b are ultimately dependent upon the sampling regimes, number of loci (i.e., power of the data), and analytical approaches employed (Waples, 1989; Tallmon et al., 2004; Waples and Feutry, 2022). A promising approach for estimating N_e for

elasmobranchs has recently emerged which incorporates purposefully designed sampling regimes, data from 1000's of single nucleotide polymorphisms (SNPs), and a close-kin mark recapture analytical framework (CKMR, Bravington et al., 2016) (see Hillary et al., 2018; Delaval et al., 2022; Trenkel et al., 2022). CKMR approaches leveraging genomic datasets could lead to more precise estimates of N_e, a better understanding of the relationship between N_c and N_e and N_b, increasing the utility of these data in assessing and monitoring the status of populations.

The analyses in this study assumed that the main current sources of fishing mortality are from the southeast shrimp trawl fishery. While Graham et al. (2022) determined bycatch risk associated with the shrimp trawl fishery was significantly higher than other commercial fisheries, the associated level of take of smalltooth sawfish is still highly uncertain. However, this may not be the case elsewhere as all species of sawfish are subjected to mortality in other net fisheries, in particular gillnet fisheries (Dulvy et al., 2014). For the US population of smalltooth sawfish, unreliable estimates of the capture of smalltooth sawfish are due to low observer coverage combined with the lack of accurate total shrimp trawl effort data, resulting in annual bycatch estimates from 2007 to 2019 varying in the hundreds of animals, and a lack of post-release survival studies (Carlson, 2020). In addition to the level of take, the impact to which segment of the population is limited. Few smalltooth sawfish are actually measured by at-sea observers, as most lengths are estimated while the animal is being cut from the net often with limited visibility. Thus, fishing mortality was randomly applied to sub-adults through the adult proportion of the population (ages 6–30). If fishing mortality is more specific to adult females before they have a chance to breed, the overall impact on smalltooth sawfish recovery could be greater. Finally, while smalltooth sawfish appear to have among the lowest levels of stress related to capture among elasmobranchs (Prohaska et al., 2018), given shrimp trawl tow times for the Gulf of Mexico average 5.2 h (Scott-Denton et al., 2012) it is likely the higher estimates of post release mortality are more relevant to these simulations.

While this population viability model is an improvement over Carlson and Simpfendorfer (2015), there is still uncertainty in many parameters for smalltooth sawfish as well as all sawfishes. Fecundity is still based on small sample sizes and survivorship was obtained using indirect methods, most methods being based on life history parameters such as age and growth. Grant (2021), in his population viability model, suggested better information on the reproductive biology of largetooth sawfish should be a high priority for future research, as the reproductive periodicity (annual vs biennial) is still uncertain though has a large influence on recovery potential. This stochastic modeling approach has provided a useful framework for demonstrating how the current lack of reliable biological data, as well as fishing mortality levels, affects our knowledge of the recovery of sawfish. For example, scenarios that resulted in more optimistic population trajectories still contained replications within the scenario where the population was relatively stable or showed a slight decline. The further collection of life history and fisheries information for all sawfishes is therefore required for improved estimates of their productivity and ability to recover.

Some scenarios suggest that smalltooth sawfish in the US still can recover despite the potential for shrimp trawl fishing mortality, though scenarios show the rate of recovery will vary depending on the input variables. A recent Bayesian analysis (Sherley et al., 2020) of multiple indices of relative abundance from scientific surveys and commercial and recreational data suggests the US population is increasing (Carlson et al., 2022). This lends credibility to some of the more optimistic scenarios developed for this study. However, key input variables for these optimistic scenarios is the initial population size, life history, and the true level of removals by fishing and their associated uncertainty. This uncertainty, similarly to what was found by Grant (2021) for largetooth sawfish, highlights the importance of improving our understanding of life history and current population size not only for smalltooth sawfish but all species. A combination of emerging technologies, such as more advanced genetic techniques to determine population size and electronic monitoring for increasing observer coverage (e.g. Moncrief-Cox et al., 2020) could contribute to a reduction in uncertainty about population size, mortality rates, and trajectories.

Declaration of Competing Interest

I disclose as the sole author I do not have any financial and personal relationships with other people or organizations that could inappropriately influence (bias) this work. There is no conflict of interest elsewhere.

Data availability

Data will be made available on request.

Acknowledgements

Adam Brame and Colin Simpfendorfer provided comments on the initial draft of the manuscript. Nicole Philips and Demian Chapman were key in providing a better understanding of the nuances of using effective genetic population size as a proxy for initial populations size.

Appendix 1

Simulated population projections of the smalltooth sawfish population with various levels of fishing mortality and initial population size. Blue circles=the mean abundance at time t for scenarios 1, 5, 9 and 13, red circles=scenarios 2, 6, 10 and 14, green circles= 3, 7, 11 and 15 and yellow circles=scenarios 4, 8, 12 and 16. Solid lines represent the \pm 1 standard deviation of the population mean at time t with the colors corresponding to the mean abundance symbols.

J.K. Carlson



References

Ahonen, H., Harcourt, R.G., Stow, A.J., 2009. Nuclear and mitochondrial DNA reveals isolation of imperilled grey nurse shark populations (*Carcharias taurus*). Mol. Ecol. 18 (21), 4409–4421.

Akçakaya, H.R., 2005. RAMAS Metapop: Viability Analysis for Stage-Structured Metapopulations (version 5.0). Applied Biomathematics. Setauket, New York.

Andrew, N.L., Pepperell, J.G., 1992. The by-catch of shrimp trawl fisheries. Oceanography and Marine Biology: An Annual Review.

Baremore, I.E., Carlson, J.K., Hollensead, L.D., Bethea, D.M., 2007. Catch and bycatch in US southeast gillnet fisheries, 2007. NOAA Technical Memorandum NMFS SEFSC- 565, 19 p.

Bigelow, H.B., Schroeder, W.C., 1953. Fishes of the western North Atlantic, Part II. Sawfishes, guitarfishes, skates, rays, and chimaeroids. Mem Sears Found Mar Res. Yale University, New Haven, CT.

Braccini, M., Taylor, S., Bruce, B., McAuley, R., 2017. Modelling the population trajectory of West Australian white sharks. Ecol. Model. 360, 363–377.

Brame, A.B., Wiley, T.R., Carlson, J.K., Fordham, S.V., Grubbs, R.D., Osborne, J., Scharer, R.M., Bethea, D.M., Poulakis, G.R., 2019. Biology, ecology, and status of the smalltooth sawfish *Pristis pectinata* in the USA. Endangered Species Res. 39, 9–23.

Bravington, M.V., Skaug, H.J., Anderson, E.C., 2016. Close-Kin Mark-Recapture. Stat. Sci. 31 (2), 259–274.

Carlson, J.K. 2020. Estimated Incidental Take of Smalltooth Sawfish (Pristis pectinata) and Giant Manta Ray (Manta birostris) in the South Atlantic and Gulf of Mexico Shrimp Trawl Fishery. Panama City Laboratory Contribution Series 20–03.

Carlson, J.K., Richards, P.M., 2011. Takes of Protected Species in the Northwest Atlantic Ocean and Gulf of Mexico Shark Bottom Longline and Gillnet Fishery 2007-2010. Internal report, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, SFD Contribution PCB-11–13.

Carlson, J.K., Simpfendorfer, C.A., 2015. Recovery potential of smalltooth sawfish, *Pristis pectinata*, in the United States determined using population viability models. Aquat. Conserv.: Mar. Freshw. Ecosyst. 25 (2), 187–200.

Carlson, J.K., Blanco-Parra, M.P., Bonfil-Sanders, R., Charles, R., Charvet, P., Chevis, M., Dulvy, N.K., Espinoza, M., Faria, V., Ferretti, F., Fordham, S., Giovos, I., Graham, J., Grubbs, D., Pacoureau, N., Phillips, N.M. 2022. Pristis pectinata. The IUCN Red List of Threatened Species 2022: e.T18175A58298676. https://dx.doi. org/10.2305/IUCN.UK.2022-2.RLTS.T18175A58298676.en. Accessed on 13 March 2023.

Caswell, H., 2001. Matrix Population Models. Construction, Analysis, and Interpretation, 2nd edition. Sinauer, Sunderland, Massachusetts.

Chapman, D.D., Simpfendorfer, C.A., Wiley, T.R., Poulakis, G.R., Curtis, C., Tringali, M., Carlson, J.K., Feldheim, K.A., 2011. Genetic diversity despite population collapse in a critically endangered marine fish: the smalltooth sawfish (Pristis pectinata). J. Hered. 102 (6), 643–652.

Clarke, T.M., Espinoza, M., Ahrens, R., Wehrtmann, I.S., 2016. Elasmobranch bycatch associated with the shrimp trawl fishery off the Pacific coast of Costa Rica, Central America. Fish. Bull. 114 (1).

Cortés, E., 2016. Perspectives on the intrinsic rate of population growth. Methods Ecol. Evol. 7 (10), 1136-1145.

Cortés, E., Baertlein, H. 2021. Preliminary catches of hammerhead sharks in the U.S. Atlantic, Gulf of Mexico, and Caribbean. SEDAR77-DW04. SEDAR, North Charleston, SC. 88 pp.

Courtney, D., Mathers, A., Kroetz, A., 2021. An Updated Literature Review of Post-Release Live-Discard Mortality Rate Estimates in Sharks for use in SEDAR 77. SEDAR77-DW25. SEDAR, North Charleston, SC. 47 pp.

D'Anastasi, B., Simpfendorfer, C., van Herwerden, L. 2013. Anoxypristis cuspidata (errata version published in 2019). The IUCN Red List of Threatened Species 2013: e. T39389A141789456. https://dx.doi.org/10.2305/IUCN.UK.2013–1.RLTS.T39389A141789456.en.

Delaval, A., Bendall, V., Hetherington, S.J., Skaug, H.J., Frost, M., Jones, C.S., Noble, L.R., 2022. Evaluating the suitability of close-kin mark-recapture as a demographic modelling tool for a critically endangered elasmobranch population. Evolut. Appl.

Dudgeon, C.L., Ovenden, J.R., 2015. The relationship between abundance and genetic effective population size in elasmobranchs: an example from the globally threatened zebra shark Stegostoma fasciatum within its protected range. Conserv. Genet. 16, 1443–1454.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., 2014. Extinction risk and conservation of the world's sharks and rays. elife 3, e00590.

Dulvy, N.K., Davidson, L.N., Kyne, P.M., Simpfendorfer, C.A., Harrison, L.R., Carlson, J.K., Fordham, S.V., 2016. Ghosts of the coast: global extinction risk and conservation of sawfishes. Aquat. Conserv.: Mar. Freshw. Ecosyst. 26 (1), 134–153.

Feldheim, K.A., Fields, A.T., Chapman, D.D., Scharer, R.M., Poulakis, G.R., 2017. Insights into reproduction and behavior of the smalltooth sawfish *Pristis pectinata*. Endanger. Species Res. 34, 463–471.

Ferchaud, A.L., Perrier, C., April, J., Hernandez, C., Dionne, M., Bernatchez, L., 2016. Making sense of the relationships between Ne, Nb and Nc towards defining conservation thresholds in Atlantic salmon (Salmo salar). Heredity 117 (4), 268–278.

Fordham, S.V., Jabado, R., Kyne, P.M., Charvet, P., Dulvy, N.K., 2018. Saving sawfish: Progress and priorities. IUCN Shark Specialist Group, Vancouver.

Gilman, E., Gearhart, J., Price, B., Eckert, S., Milliken, H., Wang, J., Swimmer, Y., Shiode, D., Abe, O., Hoyt Peckham, S., Chaloupka, M., 2010. Mitigating sea turtle by-catch in coastal passive net fisheries. Fish and Fisheries 11 (1), 57–88.

Graham, J., Kroetz, A.M., Poulakis, G.R., Scharer, R.M., Carlson, J.K., Lowerre-Barbieri, S.K., Morley, D., Reyier, E.A., Grubbs, R.D., 2022. Commercial fishery bycatch risk for large juvenile and adult Smalltooth sawfish (*Pristis pectinata*) in Florida waters. Aquat. Conserv.: Mar. Freshw. Ecosyst. 32 (3), 401–416.

Grant, M.I., 2021. Conservation of non-marine elasmobranchs (Doctoral dissertation, James Cook University).

Grant, M.I., Charles, R., Fordham, S., Harry, A.V., Lear, K.O., Morgan, D.L., Phillips, N.M., Simeon, B., Wakhida, Y. and Wueringer, B.E. 2022. Pristis clavata. The IUCN Red List of Threatened Species 2022: e.T39390A68641215. https://dx.doi.org/10.2305/IUCN.UK.2022–2.RLTS.T39390A68641215.en.

Harrison, L.R., Dulvy, N.K., 2014. Sawfish: a global strategy for conservation, IUCN: International Union for Conservation of Nature. IUCN Species Survival Commission (SSC), Shark Specialist Group, IUCN, Species Programme, Zoological Society of London (ZSL), UK.

Harry, A.V., Carlson, J.K., Espinoza, M., Haque, A.B., Jabado, R.W., Rigby, C.L. in preparation. Sawfish move closer to extinction, but positive signs are emerging. Oryx.

Harry, A.V., Everett, B., Faria, V., Fordham, S., Grant, M.I., Haque, A.B., Ho, H., Jabado, R.W., Jones, G.C.A., Lear, K.O., Morgan, D.L., Phillips, N.M., Spaet, J.L.Y., Tanna, A. and Wueringer, B.E. 2022. *Pristis zijsron*. The IUCN Red List of Threatened Species 2022: e.T39393A58304631. https://dx.doi.org/10.2305/IUCN.UK. 2022–2.RLTS.T39393A58304631.en.

Hillary, R.M., Bravington, M.V., Patterson, T.A., Grewe, P., Bradford, R., Feutry, P., Gunasekera, R., Peddemors, V., Werry, J., Francis, M.P., Duffy, C.A.J., 2018. Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. Sci. Rep. 8 (1), 2661.

Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull., 81, pp.898-903.

Kroetz, A.M., Mathers, A.N., Carlson, J.K., 2020. Evaluating protected species bycatch in the US Southeast Gillnet Fishery. Fish. Res. 228, 105573.

Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish. Biol. 49 (4), 627–642.

Molina, J.M., Cooke, S.J., 2012. Trends in shark bycatch research: current status and research needs. Rev. Fish. Biol. Fish. 22, 719–737.

Moncrief-Cox, H.E., Carlson, J.K., Norris, G.S., Wealti, M.C., Deacy, B.M., Scott-Denton, E., 2020. Development of video electronic monitoring systems to record smalltooth sawfish, *Pristis pectinata*, interactions in the shrimp trawl fisheries of the southeastern United States, with application to other protected species and large bycatches. Mar. Fish. Rev. 82 (3–4), 1–8.

National Marine Fisheries Service (NMFS). 2021. Endangered Species Act (ESA) - Section 7 Consultation Biological Opinion. Reinitiation of Endangered Species Act (ESA) Section 7 Consultation on the Implementation of the Sea Turtle Conservation Regulations under the ESA and the Authorization of the Southeast U.S. Shrimp Fisheries in Federal Waters under the Magnuson-Stevens Fishery Management and Conservation Act (MSFMCA). SERO-2021–00087. 297 pp.

Norton, S.L., Wiley, T.R., Carlson, J.K., Frick, A.L., Poulakis, G.R., Simpfendorfer, C.A., 2012. Designating critical habitat for juvenile endangered smalltooth sawfish in the United States. Mar. Coast. Fish. 4 (1), 473–480.

Oliver, S., Braccini, M., Newman, S.J., Harvey, E.S., 2015. Global patterns in the bycatch of sharks and rays. Mar. Policy 54, 86–97.

J.K. Carlson

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES J. Mar. Sci. 39 (2), 175–192.

Peterson, I., Wroblewski, J.S., 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41 (7), 1117–1120.

Portnoy, D.S., McDowell, J.R., McCandless, C.T., Musick, J.A., Graves, J.E., 2009. Effective size closely approximates the census size in the heavily exploited western Atlantic population of the sandbar shark, Carcharhinus plumbeus. Conserv. Genet. 10, 1697–1705.

Prohaska, B.K., Bethea, D.M., Poulakis, G.R., Scharer, R.M., Knotek, R., Carlson, J.K., Grubbs, R.D., 2018. Physiological stress in the smalltooth sawfish: effects of ontogeny, capture method, and habitat quality. Endanger. Species Res. 36, 121–135.

Read, A.J., Drinker, P., Northridge, S., 2006. Bycatch of marine mammals in US and global fisheries. Conserv. Biol. 20 (1), 163-169.

Reeves, R.R., McClellan, K., Werner, T.B., 2013. Marine mammal bycatch in gillnet and other entangling net fisheries, 1990 to 2011. Endangered Species Research 20 (1), 71–97.

Saila, S.B., 1983. Importance and assessment of discards in commercial fisheries. Food and Agriculture Organization of the United Nations.

- Scharer, R.M., Patterson III, W.F., Carlson, J.K., Poulakis, G.R., 2012. Age and growth of endangered smalltooth sawfish (Pristis pectinata) verified with LA-ICP-MS analysis of vertebrae. Plos One. https://doi.org/10.1371/journal.pone.0047850.
- Scott-Denton, E., Cryer, P.F., Duffy, M.R., Gocke, J.P., Harrelson, M.R., Kinsella, D.L., Nance, J.M., Pulver, J.R., Smith, R.C., Williams, J.A., 2012. Characterization of the US Gulf of Mexico and South Atlantic penaeid and rock shrimp fisheries based on observer data. Mar. Fish. Rev. 74 (4), 1–27.
- Sherley, R.B., Winker, H., Rigby, C.L., Kyne, P.M., Pollom, R., Pacoureau, N., Herman, K., Carlson, J.K., Yin, J.S., Kindsvater, H.K., Dulvy, N.K., 2020. Estimating IUCN Red List population reduction: JARA—A decision-support tool applied to pelagic sharks. Conserv. Lett. 13 (2), e12688.
- Skomal, G.B., Mandelman, J.W., 2012. The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol. 162 (2), 146–155.
- Smith, K.L. 2021. Leveraging multiple data sources: How catch data, metadata, and genetic samples can aid the recovery of endangered smalltooth sawfish (Pristis pectinata). Dissertation. Louisiana State University-The School of Renewable Natural Resources.
- Smith, K.L., Feldheim, K., Carlson, J.K., Wiley, T.R., Taylor, S.S., 2021. Female philopatry in smalltooth sawfish Pristis pectinata: conservation and management implications. Endanger. Species Res. 45, 85–98.
- Stobutzki, I., Miller, M., Brewer, D., 2001. Sustainability of fishery bycatch: a process for assessing highly diverse and numerous bycatch. Environ. Conserv. 28 (2), 167–181.
- Tallmon, D.A., Luikart, G., Beaumont, M.A., 2004. Comparative evaluation of a new effective population size estimator based on approximate Bayesian computation. Genetics 167 (2), 977–988.
- Trenkel, V.M., Charrier, G., Lorance, P., Bravington, M.V., 2022. Close-kin mark-recapture abundance estimation: practical insights and lessons learned. ICES J. Mar. Sci. 79 (2), 413–422.
- Waples, R.S., 1989. A generalized approach for estimating effective population size from temporal changes in allele frequency. Genetics 121 (2), 379–391.
- Waples, R.S., 2005. Genetic estimates of contemporary effective population size: to what time periods do the estimates apply? Molecular Ecology 14 (11), 3335–3352. Waples, R.S., 2022. What is Ne, anyway? J. Hered. 113 (4), 371–379.

Waples, R.S., Feutry, P., 2022. Close-kin methods to estimate census size and effective population size. Fish Fish 23 (2), 273-293.

- Waples, R.S., Antao, T., Luikart, G., 2014. Effects of overlapping generations on linkage disequilibrium estimates of effective population size. Genetics 197 (2), 769–780.
- Whitney, N.M., White, C.F., Anderson, P.A., Hueter, R.E., Skomal, G.B., 2017. The physiological stress response, postrelease behavior, and mortality of blacktip sharks (*Carcharhinus limbatus*) caught on circle and J-hooks in the Florida recreational fishery. Fish. Bull. (4), 532–544.
- Wiley, T.R., Simpfendorfer, C.A., 2010. Using public encounter data to direct recovery efforts for the endangered smalltooth sawfish Pristis pectinata. Endanger. Species Res. 12 (3), 179–191.
- Yan, H.F., Kyne, P.M., Jabado, R.W., Leeney, R.H., Davidson, L.N., Derrick, D.H., Finucci, B., Freckleton, R.P., Fordham, S.V., Dulvy, N.K., 2021. Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. Sci. Adv. 7 (7), eabb6026.