


ARTICLE

Is restricting catch to young sharks only more sustainable? Exploring a controversial management strategy for bull, tiger, blue and bonnethead sharks

Matheus Souza Ferreira de Barros^{1,2}  | Cícero Diogo Lins de Oliveira³  |
Vandick da Silva Batista³ 

¹Dauphin Island Sea Lab, Dauphin Island, Alabama, USA

²School of Marine and Environmental Sciences, University of South Alabama, Mobile, Alabama, USA

³Laboratório de Conservação e Manejo de Recursos Naturais Renováveis (LACOM) da Universidade Federal de Alagoas (UFAL), Instituto de Ciências Biológicas e da Saúde (ICBS), Maceió, Brazil

Correspondence

Matheus Souza Ferreira de Barros, Dauphin Island Sea Lab, Department of Marine Sciences of the University of South Alabama, Dauphin Island Alabama, USA.

Email: matheus.barrosteu@gmail.com

Abstract

Proper management of shark populations is an immediate concern due to their high vulnerability. In this study, we applied stochastic demographic models for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*) to test how population growth behaved under different exploitation scenarios, such as the exclusion of older sharks from fisheries. Populations grew at considerably slow rates when unfished, except for *P. glauca*. When fisheries targeted all individuals, populations started to decline at generally very low fishing mortality and harvest rates. Conversely, when adult individuals were excluded from fisheries, population resiliency increased despite higher fishing pressures, with no negative growth rates even if harvest levels were doubled. This study indicates that conservation of these species may benefit from protecting adult stocks.

KEYWORDS

Chondrichthyes, elasmobranchs, fisheries, management, population ecology

1 | INTRODUCTION

Sharks are widespread predators in the subclass Elasmobranchii that perform a diverse array of functions that contribute to ecosystem stability and resilience (Camhi et al., 2009; Chapman, 2017). Current evidence suggests that sharks generally act as crucial mesopredators that support strong food web interactions, thereby making biological communities more resilient to external perturbations (Bascompte et al., 2005; Ferretti et al., 2010). In addition, sharks also participate in nutrient cycling (Williams et al., 2018), and even create or modify important habitats for fish (Fallows et al., 2013).

Shark species are targeted or accidentally caught by unmanaged multi-specific, targeted fisheries or as by-catch in fisheries virtually all over the world. As a result, catches have decreased substantially and reduced probabilities of capturing larger individuals due to augmented effort in recent years (Barousse et al., 2014;

Davidson et al., 2016; Jordaan et al., 2020; Roff et al., 2018). This situation may be even worse because catches are usually underestimated, with evidence pointing that the exploited biomass to supply the international fin trade is roughly three to four times higher than that reported in the only global database (Clarke et al., 2006). In fact, widespread underestimation of shark captures hinders stock assessments and implementation of management strategies (Cashion et al., 2019). As a result, many shark populations have decline around the world (Baum & Myers, 2004; Lawson et al., 2020; Lessa et al., 2016; Santana et al., 2020; Santander-Neto et al., 2021), with significant increases in extinction risk being estimated (Dulvy et al., 2014). Currently, ~75% of shark species are threatened to some level (Pacoureaux et al., 2021).

Widespread declines are because most elasmobranchs have life histories that make them less resilient to fishing mortality than teleost fish (Dulvy et al., 2008; Pacoureaux et al., 2021). Slow growth

rates, large asymptotic sizes, low fecundity and late maturations cause shark populations to grow at remarkably slow rates even when unexploited (Schindler et al., 2002; Cortés, 2008; Dulvy et al., 2008; Field et al., 2009; Smart et al., 2017; Grant et al., 2018, 2020; Erhardt & Weder, 2020). Consequently, even low levels of fishing mortality can lead to disturbances in population dynamics such as decreased recruitment strengths and cause declines (Schindler et al., 2002; Smart et al., 2017; Santana et al., 2020; Tsai et al., 2020). In addition, there is only scant evidence pointing to compensatory effects of exploitation on shark population parameters such as increased fecundities and earlier maturation (Frisk et al., 2005).

Despite the high vulnerability and widespread declines in sharks, traditional fishery-dependent comprehensive marine shark stock assessments are absent in much of the world, thereby undermining the potential to implement reliable empirical evidence-based management advice (Bradshaw et al., 2018). In the face of this data-poor situation, demographic modelling has emerged as an alternative tool to provide and evaluate potential management measures by determining important quantitative population parameters and identifying the most vulnerable life stages (Cortés, 1998; Simpfendorfer, 2004; Cortés et al., 2015). Demographic modelling does not require extensive catch and effort data, but rather uses basic life-history information that is easier to obtain and more readily available, such as growth parameters, fecundities and estimated mortalities to project population growth rates and other important demographic parameters (Bradshaw et al., 2018; Caswell, 2018; Santana et al., 2020; Smart et al., 2017). In addition, incorporation of the random effects of environmental stochasticity and variation in life-history traits in demographic models enables measurement of uncertainty (McAuley et al., 2007; Smart et al., 2017).

Implementation of length-based limits in fisheries is one of the most common output control alternatives to catch limits (Camhi et al., 2009; King, 2013), especially in tropical and subtropical fisheries, where fishing fleets are usually artisanal to semi-artisanal and difficult to monitor (King, 2013). Current discussions and analyses address the feasibility of implementing maximum harvestable age (MHA) policies as an alternative to sustainably manage shark fisheries, where an optimum age-at-last capture is set to maximise yield while still maintaining stable populations (Grant et al., 2020; Smart

et al., 2020; Smart et al., 2017). Despite being counterintuitive, MHA harvest policies assume that protecting older, larger reproducing sharks, while harvesting juveniles, may maintain population stability by replacing high natural mortality rates commonly experienced by juveniles with fishing mortality (Prince, 2005; Smart et al., 2017). MPA harvest policies require species-specific testing because shark life histories and responses to fishing and management policies are highly variable (Cortés, 2002; Liu et al., 2015; Grant et al., 2020).

The objective of this study was to determine whether populations of four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*) can withstand fishing in a more sustainable manner if harvest was focused on juvenile age classes only. To achieve this objective, we simulated how population growth rates of each species responded to different management strategies using static, age-structured and stochastic life tables relying on published life-history parameters.

2 | MATERIALS AND METHODS

2.1 | Life-history information

Life history parameters were extracted from the literature (Tables 1 and 2), as the foundation for demographic calculations in subsequent analysis. The von Bertalanffy growth parameters were sampled from studies that modelled age and growth using vertebral analysis only, rather than from indirect methods such as length frequency analysis (Neer et al., 2005 for *C. leucas*, Emmons et al., 2021 for *G. cuvier*, Andrade et al., 2019 for *P. glauca* and Frazier et al., 2014 for *S. tiburo*). When possible, estimates of age at 50% maturity (A_{50}) were also obtained from the same age and growth study to minimise parameter discrepancies due to spatial variation, although this was only available for *S. tiburo*. Similarly, mean litter sizes were also obtained from other studies, while standard errors were assumed to be equal to one third of the mean (Cortés, 2002). Ages at first reproduction were defined as ages at 50% maturity (A_{50}) added to 1-year gestation periods (Mollet & Cailliet, 2002; Smart et al., 2017).

Parameter	<i>C. leucas</i>	<i>G. cuvier</i>	<i>P. glauca</i>	<i>S. tiburo</i>
K (year ⁻¹)	0.089 (0.007) ^a	0.061 (0.002) ^d	0.116 (0.006) ^f	0.18 (0.007) ^h
L_{∞} (cm)	229.92 (80.7) ^a	386.6 (48.57) ^d	290.6 (6.9) ^f	103.6* (4.66) ^h
L_0 (cm)	65.66 (48.45) ^a	67.4 (16.2) ^d	39.5 (0) ^f	52.73* (0.57) ^h
t_{\max}	29 ^a	31 ^d	25 ^f	25 ^h
A_{50}	10 ^b	11 ^e	6 ^g	6.7 (0.17) ^h
Litter size	8.7 (2.8) ^c	26 (14) ^e	35.5 (10.65) ^g	10 (3.33) ⁱ

Note: Life-history parameters include K = instantaneous growth rate; L_{∞} = asymptotic length; L_0 = length-at-age zero; t_{\max} = maximum age; A_{50} = age at first maturity; and litter size = number of pups. References include ^aNeer et al. (2005); ^bCruz-Martínez (2005); ^cCliff and Dudley (2010); ^dEmmons et al. (2021); ^eHolmes et al. (2015); ^fAndrade et al. (2019); ^gFrazier et al. (2014); ^hLombardi-Carlson et al. (2003). L_{∞} and L_0 for *S. tiburo* are in fork length (FL).

TABLE 1 Life-history parameters (standard errors) for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)



TABLE 2 Equations used to estimate natural mortality from life-history parameters for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Reference	Equation
Dureuil et al. (2021)	$M = e^{(1.583-1.087\ln[t_{\max}])}$
Dureuil et al. (2021)	$M = -\ln[0.0178] / t_{\max}$
Frisk et al. (2001)	$M = e^{(0.42\ln[K]-0.83)}$
Frisk et al. (2001)	$M = \frac{1}{(0.44 \cdot A_{50} + 1.87)}$
Hisano et al. (2011)	$M = \frac{1.65}{A_{50}}$

Note: Life-history parameters include t_{\max} = maximum age; K = instantaneous growth rate, A_{50} = age at first maturity.

2.2 | Mortality and survival rates

Natural mortality (M) was estimated using regression equations specifically developed for elasmobranchs from life-history parameters such as maximum age, age at maturity and growth rate and natural mortality (Frisk et al., 2001; Dureuil et al., 2021). Normal distributions for all estimators were based on means and standard deviations of relevant life-history parameters to incorporate uncertainty into further analysis (Quintero et al., 2017). For validation, resulting population growth distributions for each natural mortality estimator were verified to fall within reasonable ranges in prior testing according to the criteria from Grant et al. (2020). Following this criterion, no M estimator was excluded for any species from further analysis. The maximum age (t_{\max}), included in some of the estimators, was estimated by the inverse of the von Bertalanffy growth equation with the assumption that 1% of the population survived to attain the asymptotic length (Dureuil et al., 2021).

2.3 | Demographic analysis

A static demographic analysis was executed with a single-sex, post-breeding census using stochastic age-structured life tables (R code available as Supporting Information S1). This method utilises age-specific survivorship and fertility-at-age to estimate parameters that describe population dynamics such as growth rates per year and generation time (Caswell, 2018; Rockwood, 2015), based on the Euler-Lotka equation:

$$\sum_{x=1}^{t_{\max}} (l_x)(m_x)(e^{-rx}) = 1$$

where t_{\max} is the maximum attainable age, l_x is the probability of a shark being alive at the “beginning” of the age class x , m_x is the age-specific fecundity or the annual number of female pups produced by females at age x (obtained by multiplying average litter size by l_x [Smart et al., 2017; Caswell, 2018]), and r is the intrinsic population

growth rate. The parameter l_x was calculated with the following equation:

$$l_x = e^{(-Mx)}$$

where M is the natural mortality rate (yr^{-1}) estimated by regression from life-history parameters described above.

The net reproductive rate (R_0) represents the potential increase in the population per generation or the average female offspring bred by each female in a generation, while the generation time (G) is defined as the average amount of time that passes between the reproductive onset of two consecutive generations (Rockwood, 2015):

$$R_0 = \sum l_x m_x \quad (1)$$

$$G = \frac{(\sum x l_x m_x)}{R_0} \quad (2)$$

The finite rate of population increase (λ) was then calculated as the following (Rockwood, 2015):

$$\lambda = e^{\left(\frac{\ln[R_0]}{G}\right)}$$

2.4 | Simulations and stochasticity

Uncertainty of life-history parameters is related to the inherent stochasticity of dynamic ecological systems (Haddon, 2011). Therefore, demographic analysis that aims to project important population features must incorporate variability in life-history traits utilised as inputs (Cortés, 2002; Simpfendorfer, 2004; McAuley et al., 2007; Smart et al., 2017; Caswell, 2018). For that, the “stochastic.LT” function was used (R code available in the Supporting Information S1) to execute Monte Carlo simulations with 10,000 iterations with random, pre-specified variation (mean and standard errors) for each life-history parameter and a fixed random seed value. For each iteration, one life table replicate and subsequent parameters were outputted and incorporated in normal distributions derived from random variation of parameter inputs.

Natural mortality was treated in two ways: random equal-probability selection for each estimator in each Monte Carlo run (between-estimator selection; Smart et al., 2017; Oliveira et al., 2021), and from normal distributions built from means and standard deviations of relevant life-history parameters (within-estimator selection). In addition, other vital rates that were reported as single values only, such as age at first maturity and consequently age at first reproduction, were varied using triangular distributions (deviation of 1 year) (Cortés, 2002; Oliveira et al., 2021). Maximum ages (t_{\max}) were fixed and chosen as the highest value after comparing observed values from the literature (Table 1) and estimates from the inverse von Bertalanffy equation (Dureuil et al., 2021). Furthermore, model outputs were described as mean and 95% confidence intervals (defined as the 25th and 975th percentiles of posterior distributions).

2.5 | Elasticity analysis

Elasticity analysis was used to assess proportional contributions of each element in the life table on resulting population growth estimate (i.e. the influence of changes in individual parameters on model outputs, to identify conservation priorities or parameters to target for improved estimation; Caswell, 2018). For that, the life table was transformed into a Leslie Matrix (Wang et al., 2017) by incorporating fertility-at-age (f_x) and probability of surviving to the next age class (p_x):

$$p_x = \frac{(l_x + l_{x+1})}{2}$$

$$f_x = (l_{x-1})(m_x)$$

$$A = \begin{matrix} & f_1 & f_2 & f_3 & f_4 & f_x \\ p_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_x & 0 \end{matrix}$$

in which λ is the dominant eigenvalue of A , and f_x is fertility-at-age, which incorporates survival at age 0. Elasticities of matrix elements (e_{ij}) were then calculated using the R package "popbio" (Stubben et al., 2020):

$$e_{ij} = \frac{\delta \log[\lambda]}{\delta \log[a_{ij}]}$$

where a_{ij} is the element in row i and column j of matrix A .

2.6 | Exploitation scenarios

Simulations with survival rates calculated by natural mortality only (no-fishery hypothetical scenario) were used to estimate expected demographic parameters in the absence of exploitation. Two exploitation scenarios in which fishing mortality was applied differently to each age class for all species: (1) all age classes were equally vulnerable to capture, with fishing mortality F constant across age classes; and (2) application of a maximum harvestable size (MHS) policy, where F was only applied to age classes younger than the age limit (Prince, 2005; Smart et al., 2017). Survival rates l_x in the MLS scenario were calculated as follows:

$$l_x = \begin{cases} e^{-(M+F)}, & \text{age} < \text{MHS} \\ e^{-M}, & \text{age} \geq \text{MHS} \end{cases}$$

Critical levels of fishing mortality (F_{critical}) for the first scenario were determined for all species by iteratively increasing F and recording the

resulting λ distributions for each increase in $F = 0.01$. Then, simple linear models using F as the explanatory variable and λ as the response variable were fitted for all species to estimate the value of F that corresponded to a population growth rate equal to unity (F_{critical}). This is equivalent to the maximum level of fishing effort that can be applied without causing a population decline (Smart et al., 2017). In addition, slopes of the regression lines were reported in order to compare the rate of response of each population to increases in fishing pressure. We assumed that differences between slopes indicate different responses of population growth to fishing mortality.

To evaluate MHS harvest policies, similar procedures were used. Both F and MHA were systematically increased, for use in a regression analysis of F_{critical} values in relation to each MHA. To compare scenarios, relative yield and harvest rates were used instead of fishing mortality, because the same F applied to the entire population or only a few age classes would correspond to drastically different harvest rates. Therefore, the U_{critical} equation was adapted from Smart et al. (2017) to account for the harvested proportion of the population (P_{HARVEST}):

$$P_{\text{harvest}}(\%) = \left[(1 - e^{-F_{\text{critical}}}) \times \sum \text{SAD}_{i < \text{MHA}} \right] \times 100$$

$$\text{SAD}_x = \frac{[l_x e^{-rx}]}{\sum l_x e^{-rx}}$$

This equation incorporates age-specific stable age distributions (SAD) to obtain the proportion of the whole population that would be harvested at a specific level of fishing mortality when a maximum age policy was applied through summing the mean stable age values for each age $<$ MHA. For example, for an MHA of age 3, proportions of the stable age distribution from age 0 to age 2 sharks were summed to quantify the exploited segment of the population. We assumed that the most suitable harvest strategy maintained the highest harvest without causing the population to decline (Prince, 2005; Smart et al., 2020, 2017).

3 | RESULTS

Based on the means and standard errors of life-history parameters, five normally distributed natural mortality estimates were generated for each species. The species *C. leucas* and *G. cuvier* generally had the lowest M , with smaller M for both being estimated from maximum age (Dureuil et al., 2021) and the highest estimated from maturity (Hisano et al., 2011). Similarly, species with the highest M (*S. tiburo* and *P. glauca*) had smaller M estimated from maximum age (Dureuil et al., 2021; Table 3).

Slower-growing *C. leucas* and *G. cuvier* had higher survival than faster growing, shorter-lived *P. glauca* and *S. tiburo* (Figures 1 and 2, Tables S1–S4). Generation time for *G. cuvier* was longest (about 14 years), whereas *P. glauca* was the shortest (only 8 years). Conversely, *P. glauca* had the highest net reproductive rate (almost 15 average pups per female), whereas *C. leucas* was lowest (around 2 pups per female).

TABLE 3 Natural mortality (M) estimates ($\pm 95\%$ confidence intervals) for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Method/study	<i>C. leucas</i>	<i>G. cuvier</i>	<i>P. glauca</i>	<i>S. tiburo</i>
Dureuil et al. (2021)	0.141 (0.137–0.158)	0.112 (0.106–0.119)	0.146 (0.137–0.158)	0.147 (0.125–0.178)
Dureuil et al. (2021)	0.158 (0.151–0.172)	0.126 (0.11–0.141)	0.154 (0.147–0.165)	0.161 (0.137–0.190)
Frisk O1 (Frisk et al., 2001)	0.157 (0.149–0.166)	0.134 (0.127–0.142)	0.176 (0.169–0.182)	0.212 (0.206–0.218)
Frisk O2 (Frisk et al., 2001)	0.159 (0.143–0.181)	0.148 (0.12–0.2)	0.22 (0.191–0.3)	0.207 (0.195–0.221)
Hisano et al. (2011)	0.165 (0.141–0.197)	0.15 (0.109–0.21)	NA	0.235 (0.214–0.26)

FIGURE 1 Mean survival curves ($\pm 95\%$ confidence intervals) derived from the stochastic Monte Carlo simulations for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*).

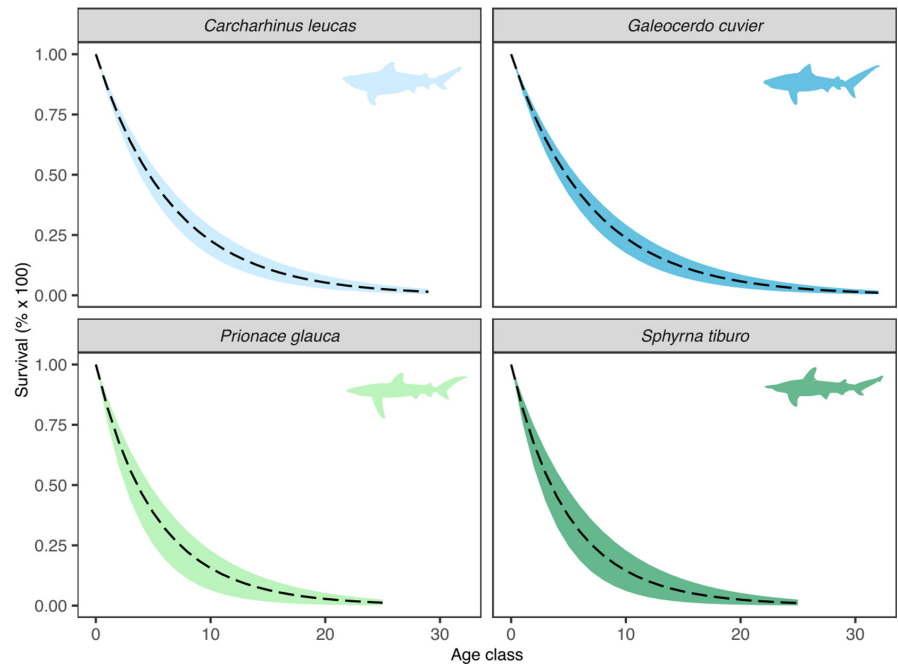
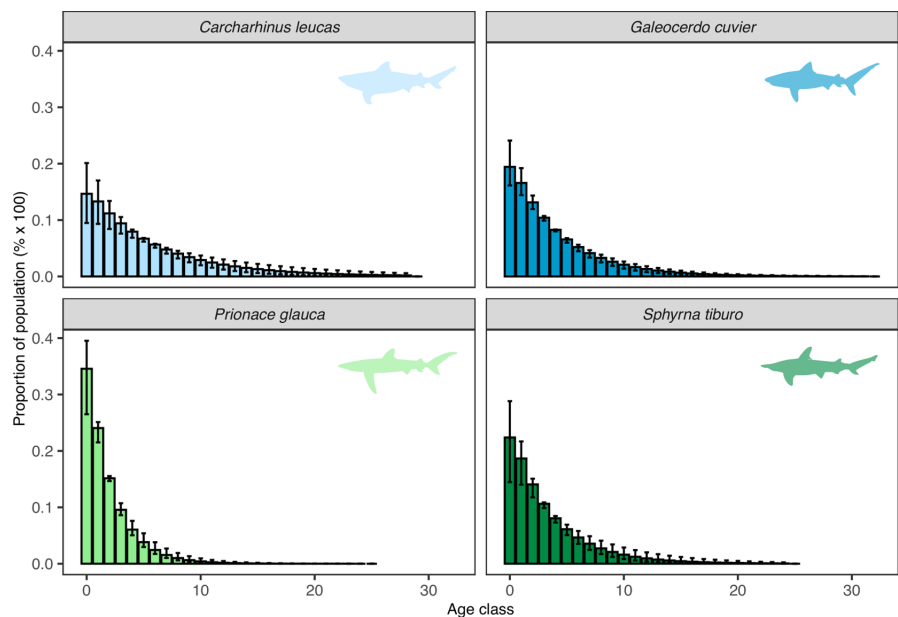


FIGURE 2 Mean stable age distributions ($\pm 95\%$ confidence intervals) derived from the stochastic Monte Carlo simulations for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*).



Population growth rate was fastest for *P. glauca* (up to 35% per generation; mean $\lambda = 1.35$), slowest for *C. leucas* (2% each year; mean $\lambda = 1.019$) and intermediate for *G. cuvier* and *S. tiburo* (mean λ of 1.08 and 1.098, respectively) (Table 4 and Figure 3). Juvenile survival was

the most influential parameter on λ for all species, followed by fecundity and adult survival (Table 5).

When fishing mortality was the same for all ages, population growth rates of all four species were remarkably sensible

TABLE 4 Generation time (G), net reproductive rate (R_0) and finite rate of increase (λ) derived from Monte Carlo posterior distributions (mean and 95% confidence intervals) for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Species	G	R_0	λ
<i>C. leucas</i>	13.337 (11.26–15.56)	1.503 (0.56–3.87)	1.019 (0.96–1.111)
<i>G. cuvier</i>	14.47 (12.95–16.09)	3.54 (1.9–6.22)	1.08 (1.04–1.15)
<i>P. glauca</i>	8.43 (7.78–8.85)	14.86 (5.4–26.6)	1.35 (1.23–1.44)
<i>S. tiburo</i>	9.37 (8.84–9.83)	2.77 (0.8–5.82)	1.098 (0.98–1.19)

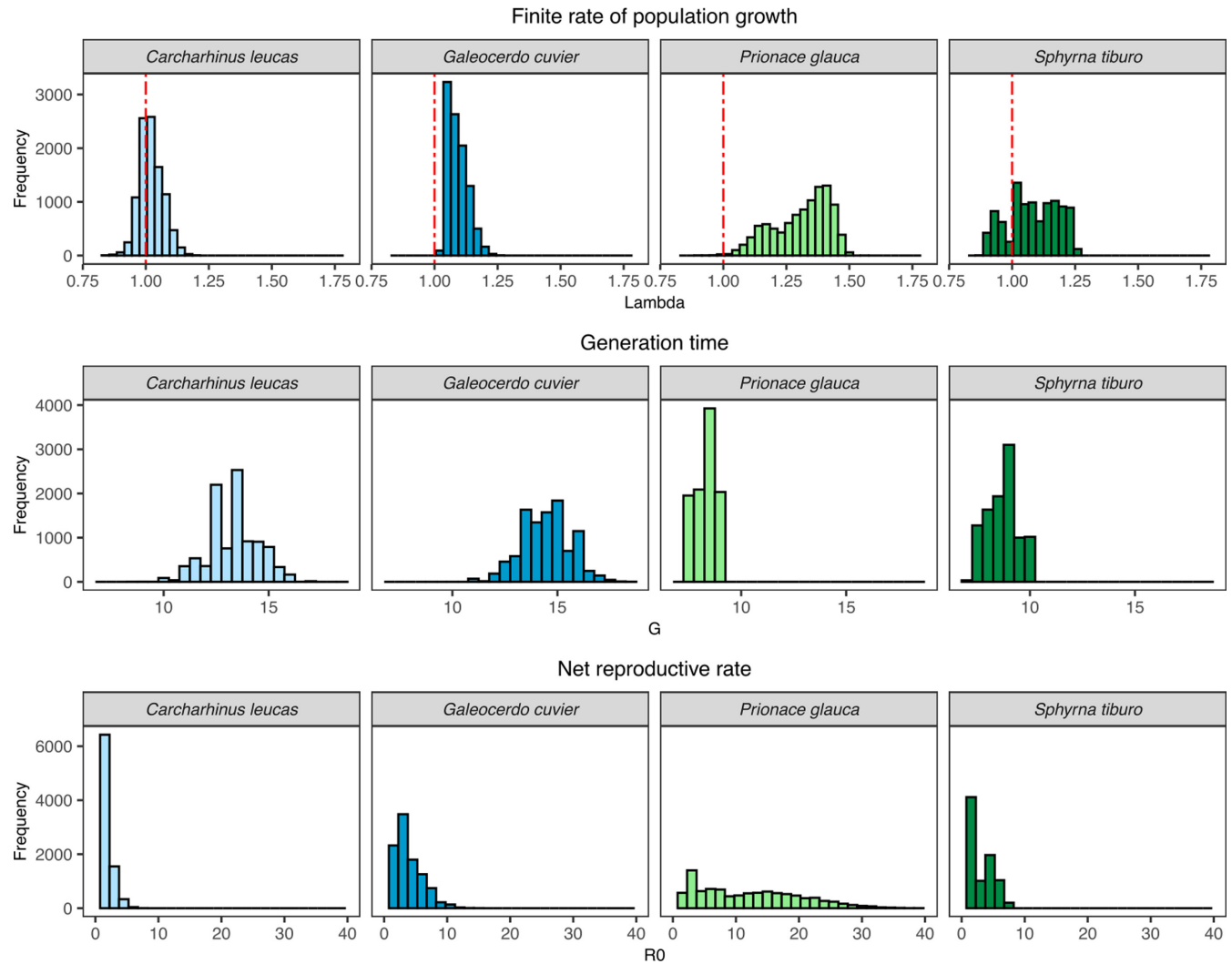


FIGURE 3 Distributions of finite rate of population growth (λ), generation time (G) and net reproductive rate (R_0) derived from Monte Carlo posterior distributions for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*).

TABLE 5 Elasticity values for Leslie matrix input parameters (juvenile survival, adult survival and fertility) for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Variable	<i>C. leucas</i>	<i>G. cuvier</i>	<i>P. glauca</i>	<i>S. tiburo</i>
Juvenile survival	0.81	0.83	0.59	0.68
Adult survival	0.06	0.05	0.04	0.15
Fertility	0.13	0.12	0.26	0.17

to increases in fishing mortality. Populations of *C. leucas*, *G. cuvier* and *S. tiburo* started declining at more than 10% per year for $F > 0.1 \text{ year}^{-1}$ (which corresponds to a harvest rate of about 9.52% of the whole population), while the population of *P. glauca* declined at about 5% for $F > 0.15$ (harvest rate of 13.9%). Critical levels of fishing mortality (F_{critical}) were 0.027 year^{-1} (harvest level = 2.6%) for *C. leucas*, 0.041 year^{-1} (4.0%) for *G. cuvier*, 0.141 year^{-1} (13.1%) for *P. glauca* and 0.053 year^{-1} (5.2%) for *S. tiburo* (Figure 4). The studied

FIGURE 4 Linear regressions between fishing mortality (F) and simulated finite rates of increase (λ) for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*). The dashed red line represents $\lambda = 1$ (stable population growth rate).

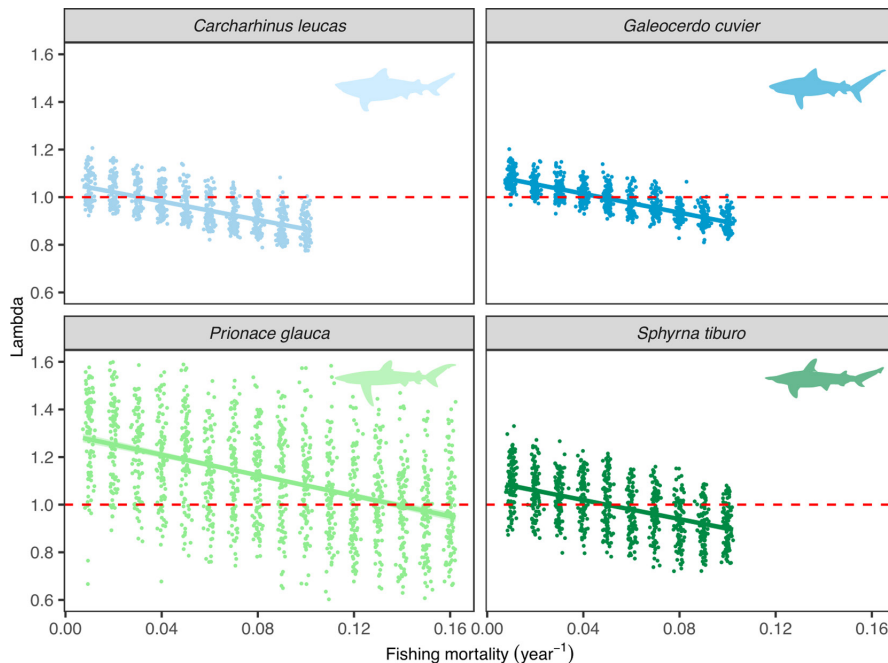


TABLE 6 Parameters (slopes and intercepts) of linear regression models between fishing mortality (F) as the explanatory variable and the finite rate of population increase (λ) as the response variable, among four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Coefficient	<i>C. leucas</i>		<i>G. cuvier</i>		<i>P. glauca</i>		<i>S. tiburo</i>	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept (a)	1.091	0.0044	1.122	0.0029	1.488	0.016	1.165	0.007
Slope (b)	-1.94	0.07	-2.005	0.048	-2.253	0.17	-1.844	0.127

species appear to respond differently to increases in fishing mortality (Table 6).

When fishing mortality was limited to ages 0–1, fishing mortality F could increase up to 0.227 year^{-1} for *C. leucas* (20.3% of ages 0–1 and 7.5% of the whole population), 0.347 year^{-1} for *G. cuvier* (29.3% of ages 0–1 and 11.7% of the whole population) and 0.428 year^{-1} for *P. glauca* (42.8% of ages 0–1 and 22.2% of the whole population). For *S. tiburo*, harvest levels could be increased to $F = 0.161 \text{ year}^{-1}$ (7.9% for the whole population) when age 1–2 sharks are fished. Based on growth parameters used in this study, size limits would be 80 cm for *C. leucas*, 86 cm for *G. cuvier*, 67 cm for *P. glauca* and 68 cm for *S. tiburo*. Increasing the MHA by 1 would allow fishing for larger individuals while maintaining similar harvest levels (Table 7).

4 | DISCUSSION

Demographic analyses are an important tool for assessing elasmobranch and other age-structured population dynamics by allowing the estimation of productivity and potential consequences of alternative management strategies in the absence of comprehensive catch data of information-limited species (Cortés, 1998; Chen & Yuan, 2006; Smart et al., 2017; Oliveira et al., 2021). Our models indicated that the shark species studied herein are particularly vulnerable

to indiscriminate fishing pressure, except for *P. glauca*. Specifically, we found that the simulated populations may decline sharply at relatively low levels of unrestricted fishing pressure (more than 10% per generation at fishing mortalities higher than 0.05 for some species). Additionally, we provided evidence that restricting harvest of older age classes may be a useful management strategy for allowing populations to be more resilient to increased fishing pressure.

Despite using elasmobranch-specific equations to estimate natural mortality M as recommended by Zhou et al. (2022), estimates of M we used in this study varied considerably within species. Because M values were used to estimate survival and fecundity-at-age in life tables, most of the uncertainty and variation in demographic parameter estimates arose from M . This was confirmed by elasticity analysis that showed substantial influence of survival on population growth rates for all species. Still, our estimates of M were within published ranges for species, including female bull sharks *C. leucas* in the Northeastern Gulf of Mexico ($0.11\text{--}0.17 \text{ year}^{-1}$, Heupel & Simpfendorfer, 2011); tiger shark *G. cuvier* in the western North Atlantic Ocean ($0.08\text{--}0.22 \text{ year}^{-1}$, Driggers et al., 2008); and female blue shark *P. glauca* in Japanese seas ($0.089\text{--}0.35 \text{ year}^{-1}$, Semba & Yokoi, 2014), while no reliable growth parameters to estimate M were available for bonnethead *S. tiburo*.

Demographic parameters estimated in this study fell within the expected ranges for the studied species. For example, simulated

TABLE 7 Critical levels of fishing mortality (F_{critical}) for each maximum harvestable ages 1–5 (MHA), annual fishing mortality rate (harvested proportion of age classes within the limit) and harvested proportion of the whole population (P_{harvest}) for each age limit for four shark species (bull shark *Carcharhinus leucas*, tiger shark *Galeocerdo cuvier*, blue shark *Prionace glauca* and bonnethead *Sphyrna tiburo*)

Species	MHA	F_{critical} (year ⁻¹)	Annual F (%)	P_{harvest} (%)
<i>C. leucas</i>	1	0.227	0.203	0.075*
	2	0.152	0.141	0.072
	3	0.118	0.111	0.069
	4	0.0981	0.093	0.066
	5	0.0806	0.077	0.059
<i>G. cuvier</i>	1	0.347	0.293	0.117*
	2	0.235	0.209	0.113
	3	0.181	0.165	0.106
	4	0.147	0.136	0.099
	5	0.124	0.116	0.09
<i>P. glauca</i>	1	0.428	0.348	0.222*
	2	0.304	0.262	0.204
	3	0.24	0.213	0.186
	4	0.201	0.183	0.167
	5	0.185	0.169	0.16
<i>S. tiburo</i>	1	0.194	0.176	0.068
	2	0.161	0.149	0.079*
	3	0.123	0.116	0.074
	4	0.107	0.102	0.073
	5	0.0856	0.083	0.065

Note: For MHA = 2, harvested age classes are <2 or age 0 + age 1. Asterisks (*) represent the highest attainable harvested proportion for each species.

productivity of bull shark *C. leucas* was similarly low (mean $\lambda = 0.998$, Cortés, 2002; compared with mean λ of 1.019 for our unfished scenario), with the difference likely due to the use of different age-at-maturity estimates (18 years, Cortés, 2002; 11 years in our study) that also resulted in different generation times (21 years, Cortés, 2002; 14 years in our study). Similarly, the simulated finite rate of population growth of tiger shark *G. cuvier* was higher (1.24, Cortés, 2002; 1.08 in this study), again likely due to differences in age-at-maturity and fecundity, whereas generation times were similar. The population growth rate we estimated for blue shark *P. glauca* (around 35% per generation), one of the most productive shark species, was similar to several other studies (Chen & Yuan, 2006; Geng et al., 2021; Takeuchi et al., 2005).

Correctly selecting and capturing input parameter distributions is crucial before running demographic models, along with the influence of geographic variation in life-history traits on local rates of population growth (Cortés, 2002). For example, there was more than 30% of variation among estimates of population growth for scalloped hammerhead *S. lewini* between the Northwestern Gulf of

Mexico and Western Pacific (Cortés, 2002). Consequently, demographic models have been proposed as *a priori* additions to traditional stock assessments to inform potential regional differences in population parameters and to set priors for distributions of population parameters in Bayesian frameworks (Grant et al., 2020; McAllister et al., 2011).

Our simulations with constant fishing mortality among age classes suggest that *C. leucas*, *G. cuvier* and *S. tiburo* are particularly vulnerable to fishing pressure, with their populations starting to decline at F of only 0.05 year⁻¹. Conversely, the blue shark *P. glauca* was more tolerant of higher F , with population decline at more than triple the level of fishing mortality that caused other species to decline. Nevertheless, such levels of F correspond to only 5% (*C. leucas*, *G. cuvier* and *S. tiburo*) and 15% (*P. glauca*) harvest rates of the whole population. In fact, a substantial amount of studies also demonstrated that sharks with similar life-histories are also not able to withstand low/moderate fishing. For example, slow-growing *Heterodontus portusjacksoni* ($K < 0.1$) in Australia started declining if F exceeded 0.07 year⁻¹ (Powter & Gladstone, 2008) and slow-growing *Carcharhinus limbatus* and *C. albimarginatus* declined more than 4% per year when F was smaller than 0.1 year⁻¹ (Smart et al., 2017). Similarly, *C. falciformis* ($K = 0.066$ –0.15 year⁻¹) tolerated no more than $F = 0.08$ year⁻¹ (Grant et al., 2020). Slow-growing ($K < 0.1$) Elasmobranchs of medium-to-large maximum sizes and late ages-at-maturity (e.g. *C. leucas* and *G. cuvier*) are among the most vulnerable species and have the slowest recovery potentials, in some cases requiring decades to recover from even moderate levels of exploitation (Frisk et al., 2001; Smith et al., 1998). We also showed that those species are particularly sensitive to low fishing mortality ($F < 0.045$ year⁻¹). Nevertheless, the bonnethead *S. tiburo* is also vulnerable to exploitation, although not extremely slow-growing, because its relatively low fecundity and large body size contributes to its low resilience.

We found that the application of a MHA to age 0 and age 1 sharks enabled harvest levels to be more than doubled without causing and of the four species to decline. Similarly, restricting harvest only to juveniles allowed a higher level of effort without causing population declines for two *Carcharhinus* spp. (Smart et al., 2017). Furthermore, harvesting juvenile silky shark *C. falciformis* may be sustainable at higher fishing mortality (Grant et al., 2020). The concept of a “gauntlet” fishery, where reproductive individuals are excluded from harvest, emerged as a tool for harvesting long-lived species, based on the assumption that adults are protected from harvest so they can replace harvested juveniles (Prince, 2005). The proposed mechanism that makes such a strategy an effective option for managing elasmobranch fisheries is due to their particular stock–recruitment relationship, wherein recruitment strongly depends on breeding stock size due to their relatively low fecundity and long gestation times, as opposed to other teleost fishes where recruitment still occurs when adult stock sizes are low (Schindler et al., 2002; Taylor et al., 2013). Consequently, removal of adults has a large impact on population growth rates because of increased weak recruitment (Kinney & Simpfendorfer, 2009; Simpfendorfer, 1999), along



with the fact that juvenile sharks can usually withstand more fishing pressure because of higher natural mortality and abundance (Kinney & Simpfendorfer, 2009), as we found for the MHA harvest scenarios (this study). Also, despite the general influence of juvenile survival on population growth rate, this parameter has much less proportional influence when based on neonates or YOY (Gallucci et al., 2011). In conclusion, management measures based on “gauntlet” fisheries should set narrow size limits for harvest because of the effect of variability in length-at-age on the target age limit (Smart et al., 2017). Others have also concluded that capturing neonates only may be a feasible option as an output control (Cortés, 1999; Simpfendorfer, 1999).

Because many shark species have bipartite life cycles and exhibit habit shifts between early and late life stages, concentrating effort in major nursery areas can be used to limit capture of adults (Kinney & Simpfendorfer 2009). However, such nurseries often contribute proportionately more to recruitment for a population (Beck et al., 2001; Lefcheck et al., 2019). Therefore, potential management measures must focus on a priori determination of the relative recruitment value of different target nurseries for a stock (Kinney & Simpfendorfer, 2009) by using elasmobranch-focused nursery concepts (Heupel et al., 2007; Heupel & Simpfendorfer, 2011) to avoid overharvesting crucial nurseries. Alternatively, adopting particularly size-selective fishing gear, such as gillnets (Carlson and Cortés, 2003; Hamley, 2011), can be an option when juveniles and adults occupy the same area, such as coastal shark species (Carlson et al., 2008; Heupel et al., 2019). In theory, size-selective gear will capture proportionately more small individuals in small mesh sizes that saturate with juveniles faster (Simpfendorfer, 1999).

Another advantage of restricting harvest to juvenile sharks relates to human health concerns, because high-trophic level, long-lived predators, like sharks, are high in mercury and other heavy metals (Rumbold et al., 2014; Rodríguez-Gutiérrez et al., 2020; Amezcua et al., 2022). Such harmful substances often exceed safe concentrations for human consumption, particularly for larger individuals of long-lived species (Amezcua et al., 2022; Garcia Barcia et al., 2020; Maurice et al., 2021; Rodríguez-Gutiérrez et al., 2020). By contrast, smaller sharks are more likely to have lower concentrations of heavy metals than their larger counterparts (Pethybridge et al., 2010; Rodríguez-Gutiérrez et al., 2020; Lara et al., 2022).

5 | CONCLUSION

We provided novel estimates of demographic parameters, along with intrinsic uncertainty, for *C. leucas*, *G. cuvier*, *P. glauca* and *S. tiburo*, by using an updated framework to run stochastic life table-based models and project the effects of increased fishing pressure under different harvest strategies for shark species. We demonstrated that four shark species were vulnerable to low–moderate levels of fishing mortality when no output control was in place. Conversely, simulations indicated that harvest could be increased in a sustainable

manner if maximum size limits were implemented, thereby contributing to growing evidence that such a management strategy can be effectively applied to sharks.

Because shark fisheries must be based on the precautionary principle to avoid worsening an already deteriorating situation (Barker, 2005; Momigliano et al., 2014; Shiffman et al., 2016), we recommend considering an age limit on harvest of neonates or age 1 sharks of *C. leucas*, *G. cuvier*, *P. glauca* and *S. tiburo*, because at least three of the four species studied here should not be exploited in the absence of conservation or mitigation measures (Shiffman et al., 2016). In addition, rather than increasing harvest of these species under a MHA strategy, we urge the protection of adult stocks of all four species and the adoption of an MHA strategy to increase resilience of harvested populations.

ACKNOWLEDGEMENTS

The first author would like to thank all fellows from the Laboratory of Ecology, Fish and Fisheries, and the Laboratory of Conservation and Management of Renewable Resources for the help with basic demographic model theory and useful comments.

CONFLICT OF INTEREST

The authors declare that there is no relevant conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The dataset used in this article will be made available upon reasonable request to the corresponding author.

ORCID

Matheus Souza Ferreira de Barros  <https://orcid.org/0000-0002-8829-1417>

Cícero Diogo Lins de Oliveira  <https://orcid.org/0000-0003-3779-023X>

Vandick da Silva Batista  <https://orcid.org/0000-0002-1183-1067>

REFERENCES

- Amezcua, F., Ruelas-Inzunza, J., Coiraton, C., Spanopoulos-Zarco, P. & Páez-Osuna, F. (2022) A global review of cadmium, mercury, and selenium in sharks: geographical patterns, baseline levels and human health implications. *Reviews of Environmental Contamination and Toxicology*, 260(1), 1–13. <https://doi.org/10.1007/S44169-021-00006-2>
- Andrade, I., Rosa, D., Muñoz-Lechuga, R. & Coelho, R. (2019) Age and growth of the blue shark (*Prionace glauca*) in the Indian Ocean. *Fisheries Research*, 211, 238–246. <https://doi.org/10.1016/J.FISHRES.2018.11.019>
- Barausse, A., Correale, V., Curkovic, A., Finotto, L., Riginella, E., Visentin, E. et al. (2014) The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. *ICES Journal of Marine Science*, 71, 1593–1603. <https://doi.org/10.1093/icesjms/fst222>
- Barker, M.J. & Schluessel, V. (2005) Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15, 325–347. <https://doi.org/10.1002/aqc.660>

- Bascompte, J., Melián, C.J. & Sala, E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102, 5443–5447. <https://doi.org/10.1073/PNAS.0501562102>
- Baum, J.K. & Myers, R.A. (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*, 7, 135–145. <https://doi.org/10.1111/J.1461-0248.2003.00564.X>
- Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M. et al. (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*, 51, 633–641. <https://doi.org/10.1641/0006-3568>
- Bradshaw, C.J.A., Prowse, T.A.A., Drew, M., Gillanders, B.M., Donnellan, S.C. & Huvaneers, C. (2018) Predicting sustainable shark harvests when stock assessments are lacking. *ICES Journal of Marine Science*, 75, 1591–1601. <https://doi.org/10.1093/ICESJMS/FSY031>
- Camhi, M.D., Pikitch, E.K. & Babcock, E.A. (2009) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Oxford, UK: Blackwell Publishing Ltd, pp. 1–502. <https://doi.org/10.1002/978144302516>
- Carlson, J.K. & Cortés, E. (2003) Gillnet selectivity of small coastal sharks off the southeastern United States. *Fisheries Research*, 60, 405–414. [https://doi.org/10.1016/S0165-7836\(02\)00135-2](https://doi.org/10.1016/S0165-7836(02)00135-2)
- Carlson, J.K., Heupel, M.R., Bethea, D.M. & Hollensead, L.D. (2008) Coastal habitat use and residency of juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*). *Estuaries and Coasts*, 31, 931–940. <https://doi.org/10.1007/S12237>
- Cashion, M.S., Bailly, N. & Pauly, D. (2019) Official catch data underrepresent shark and ray taxa caught in Mediterranean and Black Sea fisheries. *Marine Policy*, 105, 1–9. <https://doi.org/10.1016/J.MARPOL.2019.02.041>
- Caswell, H. (2018). Matrix population models: construction, analysis and interpretation, 722.
- Chapman, B. (2017). Shark Attacks: Myths, Misunderstandings and Human Fear - Blake Chapman - Google Livros.
- Chen, P. & Yuan, W. (2006) Demographic analysis based on the growth parameter of sharks. *Fisheries Research*, 78, 374–379. <https://doi.org/10.1016/J.FISHRES.2006.01.007>
- Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J. et al. (2006) Global estimates of shark catches using trade records from commercial markets. *Ecology Letters*, 9, 1115–1126. <https://doi.org/10.1111/J.1461-0248.2006.00968.X>
- Cliff, G. & Dudley, S.F. (2010) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. *South African Journal of Marine Science*, 10, 253–270. <https://doi.org/10.2989/02577619109504636>
- Cortés, E. (1998) Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research*, 39, 199–208. [https://doi.org/10.1016/S0165-7836\(98\)00183-0](https://doi.org/10.1016/S0165-7836(98)00183-0)
- Cortés, E. (1999) A stochastic stage-based population model of the sandbar shark in the Western North Atlantic. *American Fisheries Society Symposium*, 23, 115–136.
- Cortés, E. (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology*, 16, 1048–1062. <https://doi.org/10.1046/J.1523-1739.2002.00423.X>
- Cortés, E. (2008) Life history patterns and correlations in sharks. *Reviews in Fisheries Science*, 8, 299–344. <https://doi.org/10.1080/10408340308951115>
- Cortés, E., Brooks, E.N. & Shertz, K.W. (2015) Risk assessment of cartilaginous fish populations. *ICES Journal of Marine Science*, 72, 1057–1068. <https://doi.org/10.1093/ICESJMS/FSU157>
- Cruz-Martinez, A. (2005) Age and growth of the bull shark *Carcharhinus leucas* from southern Gulf of Mexico. *Journal of Northwest Atlantic Fishery Science*, 35, 367–374. <https://doi.org/10.2960/J.v35.m481>
- Davidson, L.N.K., Krawchuk, M.A. & Dulvy, N.K. (2016) Why have global shark and ray landings declined: improved management or overfishing? *Fish and Fisheries*, 17, 438–458. <https://doi.org/10.1111/FAF.12119>
- Driggers, W.B., Ingram, G.W., Grace, M.A., Gledhill, C.T., Henwood, T.A., Horton, C.N. et al. (2008) Pupping areas and mortality rates of young tiger sharks *Galeocerdo cuvier* in the western North Atlantic Ocean. *Aquatic Biology*, 2, 161–170. <https://doi.org/10.3354/AB00045>
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A. et al. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, 459–482. <https://doi.org/10.1002/AQC.975>
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R. et al. (2014) Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590. <https://doi.org/10.7554/ELIFE.00590>
- Dureuil, M., Aeberhard, W.H., Burnett, K.A., Hueter, R.E., Tyminski, J.P. & Worm, B. (2021) Unified natural mortality estimation for teleosts and elasmobranchs. *Marine Ecology Progress Series*, 667, 113–129. <https://doi.org/10.3354/MEPS13704>
- Emmons, S.M., D'Alberty, B.M., Smart, J.J., Simpfendorfer, C.A., Emmons, S.M., D'Alberty, B.M. et al. (2021) Age and growth of tiger shark (*Galeocerdo cuvier*) from Western Australia. *Marine and Freshwater Research*, 72, 950–963. <https://doi.org/10.1071/MF20291>
- Erhardt, T. & Weder, R. (2020) Shark hunting: on the vulnerability of resources with heterogeneous species. *Resource and Energy Economics*, 61, 101181.
- Fallows, C., Gallagher, A.J. & Hammerschlag, N. (2013) White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PLoS One*, 8, e60797. <https://doi.org/10.1371/JOURNAL.PONE.0060797>
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13, 1055–1071. <https://doi.org/10.1111/J.1461-0248.2010.01489.X>
- Field, I.C., Meekan, M.G., Buckworth, R.C. & Bradshaw, C.J.A. (2009) Chapter 4 susceptibility of sharks, rays and chimaeras to global extinction. *Advances in Marine Biology*, 56, 275–363. [https://doi.org/10.1016/S0065-2881\(09\)56004-X](https://doi.org/10.1016/S0065-2881(09)56004-X)
- Frazier, B.S., Driggers, W.B., Adams, D.H., Jones, C.M. & Loefer, J.K. (2014) Validated age, growth and maturity of the bonnethead *Sphyrna tiburo* in the western North Atlantic Ocean. *Journal of Fish Biology*, 85, 688–712. <https://doi.org/10.1111/JFB.12450>
- Frisk, M.G., Miller, T.J. & Dulvy, N.K. (2005) Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *Journal of Northwest Atlantic Fishery Science*, 35, 27–45. <https://doi.org/10.2960/J.v35.m514>
- Frisk, M.G., Miller, T.J. & Fogarty, M.J. (2001) Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 969–981. <https://doi.org/10.1139/F01-051/ASSET/IMAGES/INFIN.GIF>
- Gallucci, V.F., Taylor, I.G. & Erzini, K. (2011) Conservation and management of exploited shark populations based on reproductive value. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 931–942. <https://doi.org/10.1139/f05-267>
- Garcia Barcia, L., Argiro, J., Babcock, E.A., Cai, Y., Shea, S.K.H. & Chapman, D.D. (2020) Mercury and arsenic in processed fins from nine of the most traded shark species in the Hong Kong and China dried seafood markets: the potential health risks of shark fin soup. *Marine Pollution Bulletin*, 157, 111281. <https://doi.org/10.1016/J.MARPOLBUL.2020.111281>
- Geng, Z., Wang, Y., Kindong, R., Zhu, J. & Dai, X. (2021) Demographic and harvest analysis for blue shark (*Prionace glauca*) in the Indian



- Ocean. *Regional Studies in Marine Science*, 41, 101583. <https://doi.org/10.1016/J.RSMA.2020.101583>
- Grant, M.I., Smart, J.J., Rigby, C.L., White, W.T., Chin, A., Baje, L. et al. (2020) Intraspecific demography of the silky shark (*Carcharhinus falciformis*): implications for fisheries management. *ICES Journal of Marine Science*, 77, 241–255. <https://doi.org/10.1093/ICESJMS/FSZ196>
- Grant, M.I., Smart, J.J., White, W.T., Chin, A., Baje, L., Simpfendorfer, C.A. et al. (2018) Life history characteristics of the silky shark *Carcharhinus falciformis* from the central West Pacific. *Marine and Freshwater Research*, 69, 562–573. <https://doi.org/10.1071/MF17163>
- Haddon, M., (2011). Modelling and quantitative methods in fisheries – 2nd Edition – Malcol.
- Hamley, J.M. (2011) Review of Gillnet Selectivity. *Journal of the Fisheries Research Board of Canada*, 32, 1943–1969. <https://doi.org/10.1139/f75-233>
- Heupel, M.R., Carlson, J.K. & Simpfendorfer, C.A. (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, 337, 287–297. <https://doi.org/10.3354/MEPS337287>
- Heupel, M.R., Munroe, S.E.M., Lédée, E.J.I., Chin, A. & Simpfendorfer, C.A. (2019) Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. *Marine Biology*, 166, 1–17. <https://doi.org/10.1007/S00227-019-3511-7/TABLES/5>
- Heupel, M.R. & Simpfendorfer, C.A. (2011) Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. *Marine Ecology Progress Series*, 433, 237–244. <https://doi.org/10.3354/MEPS09191>
- Hisano, M., Connolly, S.R. & Robbins, W.D. (2011) Population growth rates of reef sharks with and without fishing on the great barrier reef: robust estimation with multiple models. *PLoS One*, 6, e25028. <https://doi.org/10.1371/JOURNAL.PONE.0025028>
- Holmes, B.J., Peddemors, V.M., Gutteridge, A.N., Geraghty, P.T., Chan, R.W.K., Tibbetts, I.R. et al. (2015). Age and growth of the tiger shark *Galeocerdo cuvier* off the east coast of Australia. *Journal of Fish Biology*, 87(2), 422–448.
- Jordaan, G.L., Santos, J. & Groeneveld, J.C. (2020) Shark discards in selective and mixed-species pelagic longline fisheries. *PLoS One*, 15, e0238595. <https://doi.org/10.1371/JOURNAL.PONE.0238595>
- King, M. (2013) *Fisheries biology, assessment and management*, 2nd edition. Oxford, UK: Wiley-Blackwell Publishing. <https://doi.org/10.1002/9781118688038>
- Kinney, M.J. & Simpfendorfer, C.A. (2009) Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters*, 2, 53–60. <https://doi.org/10.1111/J.1755-263X.2008.00046.X>
- Lara, A., Galván-Magaña, F., Elorriaga-Verplancken, F.R., Marmolejo-Rodríguez, A.J., González-Armas, R., Arreola-Mendoza, L. et al. (2022) Mercury, selenium and cadmium in juvenile blue (*Prionace glauca*) and smooth hammerhead (*Sphyrna zygaena*) sharks from the northwest Mexican Pacific coast. *Marine Pollution Bulletin*, 175, 113311. <https://doi.org/10.1016/J.MARPOLBUL.2021.113311>
- Lawson, J.M., Pollom, R.A., Gordon, C.A., Barker, J., Meyers, E.K.M., Zidowitz, H. et al. (2020) Extinction risk and conservation of critically endangered angel sharks in the eastern Atlantic and Mediterranean Sea. *ICES Journal of Marine Science*, 77, 12–29. <https://doi.org/10.1093/ICESJMS/FSZ222>
- Lefcheck, J.S., Hughes, B.B., Johnson, A.J., Pfirmann, B.W., Rasher, D.B., Smyth, A.R. et al. (2019) Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, 12, e12645. <https://doi.org/10.1111/CONL.12645>
- Lessa, R., Batista, V.S. & Santana, F.M. (2016) Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrinchus*) off Brazil. *Global Ecology and Conservation*, 7, 70–81. <https://doi.org/10.1016/J.GECCO.2016.04.003>
- Liu, K.M., Chin, C.P., Chen, C.H. & Chang, J.H. (2015) Estimating finite rate of population increase for sharks based on vital parameters. *PLoS One*, 10(11), e0143008. <https://doi.org/10.1371/JOURNAL.PONE.0143008>
- Lombardi-Carlson, L.A., Cortés, E.B., Parsons, G.R. & Manire, C.C.A. (2003) Related papers Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Marine and Freshwater Research*, 54, 875–883. <https://doi.org/10.1071/MF03023>
- Maurice, L., Croizier, G., Morales, G., Carpintero, N., Guayasamin, J.M., Sonke, J. et al. (2021) Concentrations and stable isotopes of mercury in sharks of the Galapagos marine reserve: Human health concerns and feeding patterns. *Ecotoxicology and Environmental Safety*, 215, 112122. <https://doi.org/10.1016/J.ECOENV.2021.112122>
- McAllister, M.K., Pikitch, E.K. & Babcock, E.A. (2011) Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1871–1890. <https://doi.org/10.1139/f01-114>
- McAuley, R.B., Simpfendorfer, C.A. & Hall, N.G. (2007) A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two long-lived shark stocks. *ICES Journal of Marine Science*, 64, 1710–1722. <https://doi.org/10.1093/ICESJMS/FSM146>
- Mollet, H.F. & Cailliet, G.M. (2002) Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Marine and Freshwater Research*, 53, 503–516. <https://doi.org/10.1071/MF01803>
- Momigliano, P., Jaiteh, V.F. & Speed, C. (2014) Predators in danger: shark conservation and management in Australia, New Zealand and their neighbours. In: *Austral Ark: The State of Wildlife in Australia and New Zealand*. Cambridge, UK: Cambridge University Press, pp. 467–491. <https://doi.org/10.1017/CBO9781139519960.024>
- Neer, J.A., Thompson, B.A. & Carlson, J.K. (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. *Journal of Fish Biology*, 67, 370–383. <https://doi.org/10.1111/J.0022-1112.2005.00743.X>
- Oliveira, C.D.L., Oliveira, C.Y.B., Camilo, J.P.G. & da Silva Batista, V. (2021) Demographic analysis reveals a population decline of the longnose stingray *Hypanus guttatus* in northeastern Brazil. *Regional Studies in Marine Science*, 41, 101554. <https://doi.org/10.1016/J.RSMA.2020.101554>
- Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K. et al. (2021) Half a century of global decline in oceanic sharks and rays. *Nature*, 589, 567–571. <https://doi.org/10.1038/s41586-020-03173-9>
- Pethybridge, H., Cossa, D. & Butler, E.C.V. (2010) Mercury in 16 demersal sharks from Southeast Australia: biotic and abiotic sources of variation and consumer health implications. *Marine Environmental Research*, 69, 18–26. <https://doi.org/10.1016/J.MARENRES.2009.07.006>
- Powter, D.M. & Gladstone, W. (2008) The reproductive biology and ecology of the Port Jackson shark *Heterodontus portusjacksoni* in the coastal waters of eastern Australia. *Journal of Fish Biology*, 72(10), 2615–2633. <https://doi.org/10.1111/j.1095-8649.2008.01878.x>
- Prince, J.D. (2005) Gauntlet fisheries for elasmobranchs - the secret of sustainable shark fisheries. *Journal of Northwest Atlantic Fishery Science*, 35, 407–416. <https://doi.org/10.2960/J.V35.M520>
- Quintero, F.O.L., Contreras-Reyes, J.E. & Wiff, R. (2017) Incorporating uncertainty into a length-based estimator of natural mortality in fish populations. *Fishery Bulletin*, 115, 355–364.
- Rockwood, L. (2015) Introduction to population ecology. *Austral Ecology*, 31, 907–908. <https://doi.org/10.1111/j.1442-9993.2006.01674.x>
- Wiley.
- Rodríguez-Gutiérrez, J., Galván-Magaña, F., Jacobo-Estrada, T., Arreola-Mendoza, L., Sujitha, S.B. & Jonathan, M.P. (2020) Mercury-selenium

- concentrations in silky sharks (*Carcharhinus falciformis*) and their toxicological concerns in the southern Mexican Pacific. *Marine Pollution Bulletin*, 153, 111011. <https://doi.org/10.1016/J.MARPOLBUL.2020.111011>
- Roff, G., Brown, C.J., Priest, M.A. & Mumby, P.J. (2018) Decline of coastal apex shark populations over the past half century. *Communications Biology*, 1, 1–11. <https://doi.org/10.1038/s42003-018-0233-1>
- Rumbold, D., Wasno, R., Hammerschlag, N. & Volety, A. (2014) Mercury accumulation in sharks from the coastal waters of Southwest Florida. *Archives of Environmental Contamination and Toxicology*, 67, 402–412. <https://doi.org/10.1007/S00244-014-0050-6/FIGURES/3>
- Santana, F.M., Feitosa, L.M. & Lessa, R.P. (2020) From plentiful to critically endangered: demographic evidence of the artisanal fisheries impact on the smalltail shark (*Carcharhinus porosus*) from northern Brazil. *PLoS One*, 15, e0236146. <https://doi.org/10.1371/JOURNAL.PONE.0236146>
- Santander-Neto, J., Barreto, R., Santana, F.M. & Lessa, R.P.T. (2021) Age, growth and demography of the silky shark *Carcharhinus falciformis* from the southwestern Atlantic. *Endangered Species Research*, 45, 237–249. <https://doi.org/10.3354/ESR01131>
- Schindler, D.E., Essington, T.E., Kitchell, J.F., Boggs, C. & Hilborn, R. (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecological Applications*, 12, 735–748. [https://doi.org/10.1890/1051-0761\(2002\)012](https://doi.org/10.1890/1051-0761(2002)012)
- Semba, Y., Yokoi, H., 2014. Update of age and sex specific natural mortality of the blue shark (*Prionace glauca*) in the North Pacific Ocean. ISC Working Group Workshop. National Taiwan Ocean University.
- Shiffman, D.S., Hammerschlag, N., Shiffman, D. & Abess, J. (2016) Shark conservation and management policy: a review and primer for non-specialists. *Animal Conservation*, 19, 401–412. <https://doi.org/10.1111/ACV.12265>
- Simpfendorfer, C.A. (1999) Demographic analysis of the dusky shark fishery in southwestern Australia – ScienceBase-catalog. *American Fisheries Society*, 23, 149–160.
- Simpfendorfer, C.A. (2004) Demographic models: life tables, matrix models and rebound potential. In: *Management Techniques for Elasmobranch Fisheries*. Rome, Italy: Food and Agriculture Organization (FAO), pp. 187–204.
- Smart, J.J., Chin, A., Tobin, A.J., White, W.T., Kumasi, B. & Simpfendorfer, C.A. (2017) Stochastic demographic analyses of the silvertip shark (*Carcharhinus albimarginatus*) and the common blacktip shark (*Carcharhinus limbatus*) from the Indo-Pacific. *Fisheries Research*, 191, 95–107. <https://doi.org/10.1016/J.FISHRES.2017.03.002>
- Smart, J.J., White, W.T., Baje, L., Chin, A., D'Alberto, B.M., Grant, M.I. et al. (2020) Can multi-species shark longline fisheries be managed sustainably using size limits? Theoretically, yes. Realistically, no. *Journal of Applied Ecology*, 57, 1847–1860. <https://doi.org/10.1111/1365-2664.13659>
- Smith, S.E., Au, D.W. & Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, 49, 663–678. <https://doi.org/10.1071/MF97135>
- Stubben, C., Milligan, B., Nantel, P. (2020). CRAN - Package popbio. <https://cran.r-project.org/web/packages/popbio/index.html> (Accessed 8.9.21).
- Takeuchi, Y., Senba, Y. & Nakano, H. (2005) Demographic analysis on Atlantic blue and shortfin mako sharks. *Collective Volumes of Scientific Papers - ICCAT*, 58, 1157–1165.
- Taylor, I.G., Gertseva, V., Methot, R.D. & Maunder, M.N. (2013) A stock-recruitment relationship based on pre-recruit survival, illustrated with application to spiny dogfish shark. *Fisheries Research*, 142, 15–21.
- Tsai, W.P., Liu, K.M. & Chang, Y.J. (2020) Evaluation of biological reference points for conservation and management of the bigeye thresher shark, *Alopias superciliosus*, in the Northwest Pacific. *Sustainability (Switzerland)*, 12, 1–29. <https://doi.org/10.3390/SU12208646>
- Wang, T., Gao, X., Jakovlić, I. & Liu, H.Z. (2017) Life tables and elasticity analyses of Yangtze River fish species with implications for conservation and management. *Reviews in Fish Biology and Fisheries*, 27, 255–266. <https://doi.org/10.1007/S11160-016-9464-8/FIGURES/2>
- Williams, J.J., Papastamatiou, Y.P., Caselle, J.E., Bradley, D. & Jacoby, D.M.P. (2018) Mobile marine predators: an understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172456. <https://doi.org/10.1098/RSPB.2017.2456>
- Zhou, S., Deng, R.A., Dunn, M.R., Hoyle, S.D., Lei, Y. & Williams, A.J. (2022) Evaluating methods for estimating shark natural mortality rate and management reference points using life-history parameters. *Fish and Fisheries*, 23, 462–477. <https://doi.org/10.1111/FAF.12627>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: de Barros, M. S. F., de Oliveira, C. D. L. & da Silva Batista, V. (2022). Is restricting catch to young sharks only more sustainable? Exploring a controversial management strategy for bull, tiger, blue and bonnethead sharks. *Fisheries Management and Ecology*, 29, 921–932. <https://doi.org/10.1111/fme.12593>