



# Estimation of the population status of smooth hammerhead shark (*Sphyrna zygaena*) and scalloped hammerhead shark (*Sphyrna lewini*) in the Northwest Pacific Ocean: A data-limited approach

Hoang Huy Huynh<sup>a,b,c</sup>, Wen-Pei Tsai<sup>b,\*</sup>

<sup>a</sup> Institute of Aquatic Science and Technology, National Kaohsiung University of Science and Technology, Kaohsiung City 81157, Taiwan

<sup>b</sup> Department of Fisheries Technology and Management, National Kaohsiung University of Science and Technology, Kaohsiung City 81157, Taiwan

<sup>c</sup> Research Institute for Aquaculture No.2, Ho Chi Minh City 710000, Viet Nam

## ARTICLE INFO

### Keywords:

Demographic matrix model  
Hammerhead sharks  
Information limited-fisheries  
Uncertainty

## ABSTRACT

While data on fisheries, in general, may be limited, demographic models provide a valuable tool for gaining insights into population dynamics when a more comprehensive understanding is not feasible. Demographic models may be used in the study of population dynamics because they only require life history parameters. We performed a quantitative population projection on the basis of expert knowledge, estimated mortality, and published information on the life history of two hammerhead shark species, smooth hammerhead (*Sphyrna zygaena*) and scalloped hammerhead (*Sphyrna lewini*), and we conducted an elasticity analysis determine the sensitivity of each life stage to the population growth rate. This study highlights the overexploitation challenges faced by these two ecologically important and vulnerable species and emphasizes the need to reduce fishing mortality is crucial to achieving population growth. To increase the accuracy of demographic estimates for these species, it is necessary to conduct further investigations into their natural mortality and reproductive traits. The approach used in this study can be applied to other shark species across a diverse range of taxa with limited data on catch and effort. Moreover, this method is easy to use and interpret and can be used to predict future population size for data-limited species.

## 1. Introduction

The Chondrichthyes (sharks, rays, and chimeras) are assessed as a high-risk group due to their biology and exploitation. According to [Dulvy et al. \(2021\)](#), approximately 37.5% of chondrichthyan are estimated to be threatened. Furthermore, [Sherman et al. \(2023\)](#) found that out of the 134 coral-reef-associated shark and ray species, around two-thirds (59%) are threatened with extinction. With the increasing depletion of oceanic shark species worldwide, shark conservation and management have become increasingly crucial ([Gross, 2023](#); [Pacoureau et al., 2023](#); [Sherman et al., 2023](#)). Numerous shark species have been categorized as endangered or vulnerable in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Moreover, sharks, as a subclass of elasmobranchii, are the most vulnerable class of marine vertebrates ([Cardenosa et al., 2022](#); [Dulvy et al., 2021](#); [Talwar et al., 2022](#)). The majority of sharks are vital apex predators that help maintain the balance in marine ecosystems, and they serve as an

indicator of ocean health ([Booth and Gupta, 2023](#); [de Azevedo Menna et al., 2022](#)). Consequently, maintaining these roles requires the conservation of these apex predators.

Smooth hammerhead sharks (*Sphyrna zygaena*) and scalloped hammerhead sharks (*Sphyrna lewini*) are globally distributed in coastal, pelagic, and semi-oceanic waters throughout the world, particularly in tropical and warm-temperate ([Casper et al., 2005](#); [Compagno, 1984](#); [Compagno et al., 2005](#); [Daly-Engel et al., 2012](#)). One of the major threats to hammerhead sharks is overharvesting ([Baum and Blanchard, 2010](#); [Clarke et al., 2006](#); [Hayes et al., 2009](#); [Reid et al., 2011](#)). As a relatively late-maturing pelagic sharks grow slowly, reproduce late in life, and are slow to recover from population decline ([Camhi, 1998](#); [Stevens et al., 2000](#)). These species are commercially fished in oceanic waters off of Taiwan, specifically in the western North Pacific, with fishing ports located in the northeastern (Nanfngao fishing port) and southeastern (Hsinkang fishing port) regions ([Liu et al., 2022](#)), by Taiwanese and other vessels. At a global level, overexploitation, higher sensitivity to

\* Corresponding author.

E-mail address: [wptsai@nkust.edu.tw](mailto:wptsai@nkust.edu.tw) (W.-P. Tsai).

<https://doi.org/10.1016/j.seares.2023.102434>

Received 24 April 2023; Received in revised form 15 July 2023; Accepted 10 August 2023

Available online 14 August 2023

1385-1101/© 2023 The Authors. 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/>).

capture, and habitat loss have resulted in population declines (Drymon and Wells, 2017; Gallagher et al., 2014; Gulak et al., 2015). As a result, *S. zygaena* is categorized as “Vulnerable,” and *S. lewini* as “Critically Endangered” in the IUCN Red List of Threatened Species (Rigby et al., 2019), and both species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2013) in the Northwest Pacific. Additionally, the difficulties in identifying species have led to the grouping of large hammerheads (*Sphyrna* spp.) together in fisheries logbook records, leading to inaccuracies in species-specific catch records (Camhi et al., 2009). Data on the biological characteristics and conservation of smooth and scalloped hammerhead shark populations are limited (Gallagher and Klimley, 2018). Some studies have indicated a decline in the populations of these species in the northwest Pacific Ocean due to overexploitation (Liu and Chen, 1999; Tsai et al., 2018). However, studies are needed to further investigate the current population status of these species and determine whether conservation measures are necessary.

A comprehensive understanding of population dynamics, recruitment, growth, and mortality is essential for effective fishery management and improving stock evaluation (Maunder et al., 2023; Mildenerger et al., 2022). Obtaining sustainable yields of fish stock requires knowledge of fishing pressure and stock biomass levels relative to biological reference levels, which is crucial for formulating management strategies (Ludwig et al., 1993). Traditional methods such as statistical catch-at-age models, surplus production models, and several management measures have been increasingly applied in fishery management and sustainability (Goethel et al., 2022; Liu et al., 2016; Methot Jr and Wetzel, 2013; Punt, 2023); however, the applicability of these methods depends on the amount, quality, and type of available data (Carruthers et al., 2014; Dowling et al., 2019; Omori et al., 2016). Moreover, qualitative methods such as demographic projection models enable quantitative assessments of resiliency, extinction risk, and associated uncertainties, especially when data on the species' life history and ecology are limited (Tucker et al., 2021). Quantitative projections, which are based on basic biological data such as the survival rate, age at maturity, litter size, and longevity, have been increasingly employed in single-species demographic models, including those for sharks in the Northwest Pacific (Chang and Liu, 2018; Liu and Chen, 1999; Tsai et al., 2020; Tsai et al., 2010; Tsai et al., 2014; Tsai et al., 2019; Tsai and Huang, 2022). These methods provide primary outputs for subsequent demographic analyses, such as the analysis of the intrinsic rate of population growth (Caswell, 1989; Mollet and Cailliet, 2002; Simpfendorfer, 2005), the results of which can be used as a reference to derive evidence-based conservation and management measures.

The objectives of the present study were fourfold. First, we investigated the demographic dynamics of the two hammerhead shark species and developed conservation strategies based on size limits. In addition, we constructed a two-sex matrix-based population model by using Monte Carlo simulations to evaluate the effectiveness of conservation strategies for both hammerhead shark species. Several studies have reported sexual and size segregation in smooth and scalloped hammerhead sharks (Bejarano-Álvarez et al., 2011; Chin et al., 2017; Klimley, 1987). Building upon this knowledge, second, we used a variety of methods to derive the best available life history parameters, to help overcome data limitations when estimating fishing mortality and population growth rates of these shark species in the Northwest Pacific. As the third aim, we performed an elasticity analysis to determine the relative impact of different life history parameters on the population growth rate in these shark species. Finally, our findings contribute to the existing knowledge on these ecologically important and vulnerable species by providing a basis for viable management recommendations, considering different conservation strategies. Additionally, the approach used in this study may be applied to study the population dynamics of other shark species with limited data.

## 2. Materials and methods

### 2.1. Study area, species and data collection

The research was mainly conducted in the Northwest Pacific Ocean, a known traditional fishing ground for Taiwanese coastal and offshore longline fishing vessels with a gross tonnage of <100 (as shown in Fig. 1). The data used in this study were collected from a subsample of 2195 smooth hammerhead sharks (1329 females and 866 males) and 3339 scalloped hammerhead sharks (2132 females and 1207 males), recorded by observers, covering the period from January 2015 to December 2022 in the Nanfangao fish market located in eastern Taiwan. These data encompassed valuable details such as fork length (*FL*, cm), individual weight (kg), and specific information on the sex of these sharks.

### 2.2. Stock assessment metrics

#### 2.2.1. Life history characteristics

Data on the life history characteristics were obtained mainly from previous studies in the Northwest Pacific/Pacific Ocean. These data were used as the foundation for computing survival rates in demographic analyses (Table 1).

#### 2.2.2. Length–weight and length–length relationships

The fork lengths and body weights of smooth and scalloped hammerhead shark specimens from the subsample were measured to the nearest centimeter and kilogram, respectively, and the length–weight relationship was calculated using the power function given by Le Cren (1951), as performed by Keyombe et al. (2015) and Chandrvanshi et al. (2019) which was expressed as:  $W = aL^b$  (\*), where *W* is the total weight (kg), *L* is the fork length (cm), and  $\alpha$  and  $\beta$  are the scaling coefficient and exponent, respectively.  $\alpha$  and  $\beta$  represent the change in *L* relative to the weight. The analysis was conducted through nonlinear regression in R software (R Development Core, 2022). R software is freely available from the Comprehensive R Archive Network (CRAN) website (<https://cran.r-project.org/>). Fork length (*FL*) was converted to total length (*TL*) by using the length–length relationship to be able to apply the life history parameters to standardized data. The *FL* to *TL* conversion equation for smooth hammerhead sharks (Chou, 2004) is given as  $FL = 0.817TL - 7.0834$ , whereas that for scalloped hammerhead sharks (Shr, 2020) is given as  $TL = 1.253FL + 6.7554$ .

#### 2.2.3. Mortality rate estimation

Natural mortality ( $M_s$ ) is a vital component of understanding population dynamics and fisheries dynamics. According to Kenchington (2014),  $M_s$  is derived as follows:  $N_{t+1,j+1} = N_{t,j}e^{-Z_s} = N_{t,j}e^{-(F_s+M_s)}$ , where  $N_{t,j}$  is the number of individuals in the year class *j* of the population at time *t*. The total mortality rate ( $Z_s$ ) indicates the overall death rate, whereas the fishing mortality rate ( $F_s$ ) represents the variation in  $Z_s$  proportional to the fishing effort. Owing to the difficulty in obtaining accurate estimates of  $M_s$  for sharks, including hammerheads, various indirect methods of estimation have been used to estimate  $M_s$  as followings:

$$M_s = e^{0.42\ln(k_s)-0.83}, \text{ Frisk et al. (2001) (Frisk1)}$$

$$M_s = \frac{1}{0.44a_{max,s}+1.87}, \text{ Frisk et al. (2001) (Frisk2)}$$

$$M_s = 1.65/a_{mat,s}, \text{ Hisano et al. (2011) (Hisano1)}$$

$$M_s = 1.65/(a_{mat,s} - t_0), \text{ Hisano et al. (2011) (Hisano2)}$$

$$M_s = 4.899a_{max,s}^{-0.916}, \text{ Then et al. (2015) (Then1)}$$

$$M_s = 4.118k_s^{0.73}L_{\infty,s}^{-0.33}, \text{ Then et al. (2015) (Then2)}$$

$$M_s = e^{[1.583-1.087\ln(a_{max,s})]}, \text{ Dureuil et al. (2021) (Dureuil1)}$$

$$M_s = -\ln(0.0178/a_{max,s}), \text{ Dureuil et al. (2021) (Dureuil2)}$$

$$M_s = 1.92 \times W_a^{-0.250}, \text{ Peterson and Wroblewski (1984)}$$

$$M_s = 3W_a^{-0.288}, \text{ Lorenzen (1996)}$$

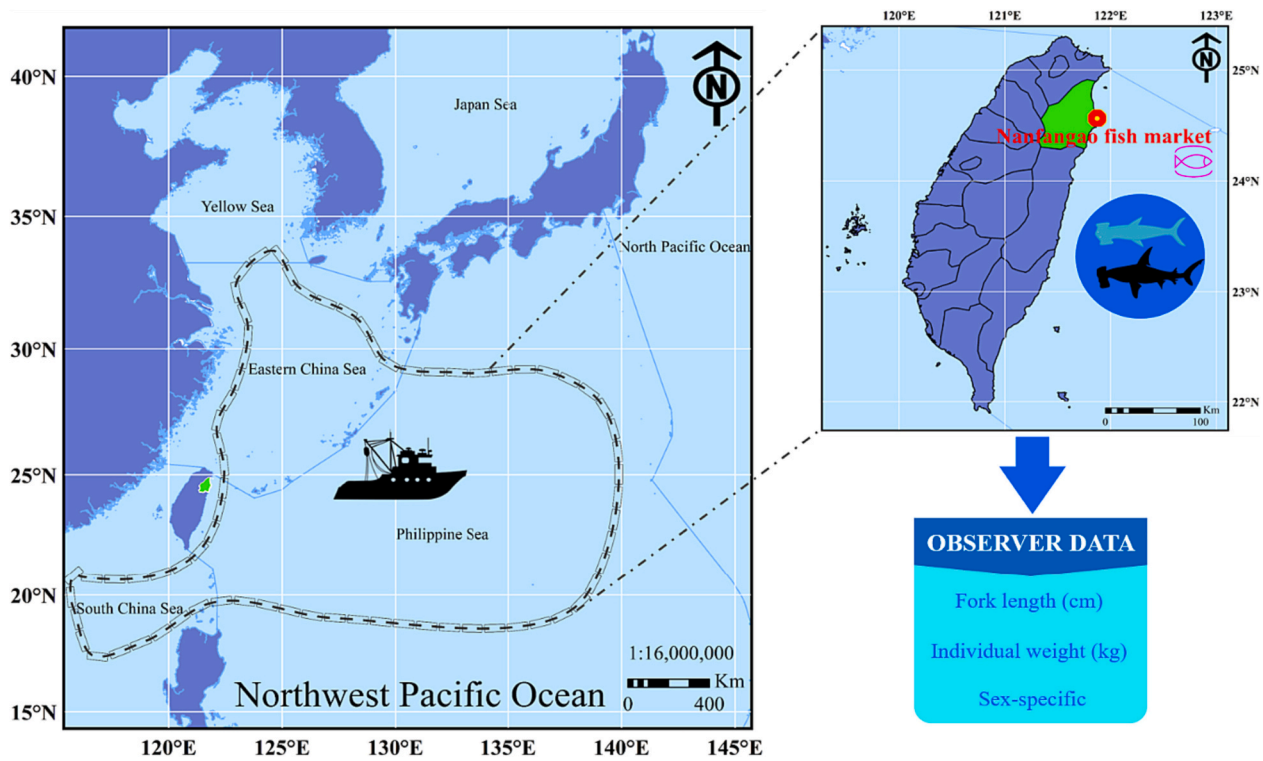


Fig. 1. Map of the study area highlighting the fishing grounds for Taiwanese coastal and offshore longline fishing vessels operating within the delineated net-around areas.

$$M_s = \frac{\beta k_s}{e^{k_s(0.302 \times a_{max,s}) - t_{0,s}} - 1}, \text{ Zhang and Megrey (2006) (Zhang \& Megrey 1)}$$

$$M_s = \frac{\beta k_s}{e^{k_s(a_{mat,s} - t_{0,s})} - 1}, \text{ Zhang and Megrey (2006) (Zhang \& Megrey 2)}$$

where  $a_{max}$  = longevity of smooth sharks was set at 21–33 years for female sharks and 18–28 years for male sharks and that for scalloped sharks was set as 24–46 years for female sharks and 21–25 years for male sharks (See Table 2 for more details –  $a_{max}$ ),  $a_{mat}$  = age at maturity for smooth and scalloped sharks was determined to be 9–11 years and 11–14 years for female and 7–9 years and 6–10 years for male sharks, respectively,  $\beta$  = exponent of the length/weight relationship was estimated from equation (\*) for smooth and scalloped sharks;  $L_\infty$ ,  $t_0$ , and  $k$  for both species were derived from data obtained through the Von Bertalanffy Growth Equation (VBGE) (Table 1).

$Z_s$  was estimated through the length-converted catch curve (LCCC) analysis. A regression approach was applied to capture data beyond the smallest length ( $L$ ), with a capture probability of 1, which is consistent with the previously reported method (Gayanilo and Sparre, 2005; Pauly, 1984). The slope of the regression line was used to estimate the overall mortality rate as follows:  $\ln\left(\frac{N_i}{\Delta t}\right) = a - Z_s t_i$ , where  $\Delta t$  is the time interval for fish to grow through each length group  $i$ ,  $N_i$  is the number of fish in each length group,  $a$  is a constant, and  $t_i$  is the corresponding fish ages relative to the mid-length of class  $i$ .  $\Delta t$  and  $t_i$  were calculated as follows:  $\Delta t = -\left(\frac{1}{k}\right) \times \ln\left[\frac{(L_\infty - L_{i+1})}{(L_\infty - L_i)}\right] \pi r^2$  and  $t_i = \left(\frac{1}{k}\right) \times \ln\left(1 - \frac{L_i}{L_\infty}\right) + t_0$ , where  $t_0$  represents the theoretical age at which a fish would attain a length of zero, and  $L_i$  represents the midpoint of the length class  $i$ . Finally, by subtracting  $Z_s$  from  $M_s$ , we obtained fishing mortality rates ( $F_s$ ) (Sparre and Venema, 1998):  $F_s = Z_s - M_s$ .

### 2.3. Development of demographic model

#### 2.3.1. Classification of developmental stages of smooth and scalloped hammerhead sharks

Mollet and Cailliet (2002) developed a life history matrix by utilizing

life history tables. Additionally, Liu (2002) observed sexual dimorphism in these hammerhead sharks, with females exhibiting longer body lengths and reaching sexual maturity later than males. Therefore, the life cycle of female smooth and scalloped hammerhead sharks is divided into six stages: neonates, juveniles, subadults, pregnant adults, and parturient adults. By contrast, the life cycle of male smooth and scalloped hammerhead sharks is divided into four stages: neonates, juveniles, subadults, and adults; as shown in Fig. 2.

#### 2.3.2. Stage-structured flexible two-sex matrix model

By using the life history diagram (Fig. 3), we developed a flexible two-sex stage-based Leslie matrix population projection model for smooth and scalloped hammerhead sharks. Based on their life cycle, the individuals were divided into stages by using the basic demographic formula:  $N_{t+1} = A_t N_t$ , at each time step the number of sharks in each stage class ( $N_t$ ) was multiplied by the life-history projection matrix ( $A_t$ ) to calculate the number of individuals in each stage class at the next time step ( $N_{t+1}$ ). The life-history projection matrix included survival and fecundity rates for each stage at that particular time (Caswell, 2000; Simpfendorfer, 2005). To ensure an equal offspring sex ratio, the sex ratio at birth (denoted by  $\rho$ ) was set to 0.5, consistent with previous studies (Chen, 1988; Krebs, 1985; Stevens, 1984; Stevens and Lyle, 1989). The fertility coefficient  $\bar{f}_i$  was the product of the stage-specific per-capita fecundity and the stage-specific survival rate ( $\sigma_i$ ), following the approach described by Caswell (2000)  $\bar{f}_i = \bar{f}_i \times \sigma_i$ . To assess the impact of the sex ratio on mating success, we used a modified harmonized mean

$$\text{birth function developed by Caswell (2000): } f_{i,s}(n) = \begin{cases} \frac{kn_s}{n_f + n_m} (s = m) \\ \frac{kn_s}{n_f + n_m} (s = f) \end{cases},$$

where  $k$  denotes litter size,  $n_m$  and  $n_f$  are the densities of male and female sharks that are capable of reproducing, respectively. We computed  $G_{i,s}$  as the product of the probability for each sex by multiplying the survival probability of an individual in stage  $i$  surviving

**Table 1**

Life history parameters, their estimates and references for smooth and scalloped hammerhead shark used in the study.  $a_{mat}$ : age at maturity,  $a_{max}$ : longevity,  $L_0$ : length at birth (cm).\*

Type/Species	Parameter	Female	Male	References
<b>Smooth hammerhead shark</b>				
Growth	$L_\infty$ (cm)	375.2	358.8	Chou (2004)
	$k$ (year <sup>-1</sup> )	0.111	0.128	Chou (2004)
	$t_0$ (years)	-1.306	-0.721	Chou (2004)
	$L_0$ (cm)	55	55	Liu (2002)
	$a_{max}$ (years)	25	24	Chou (2004)
		21	18	Coelho et al. (2011)
Fecundity	$a_{mat}$ (years)	11	7	Chou (2004) and Liu (2002)
		9	9	Cortés et al. (2010)
	Litter size	13–37	13–37	Liu (2002)
		mean 30	mean 30	
	Gestation period (months)	10		Liu (2002)
	Reproductive cycle (years)	2	2	Liu (2002)
<b>Scalloped hammerhead shark</b>				
Growth	$L_\infty$ (cm)	367.9	317.7	Shr (2020)
	$k$ (year <sup>-1</sup> )	0.142	0.165	Shr (2020)
	$t_0$ (years)	-0.380	-0.899*	Pauly (1980) and Shr (2020)
	$L_0$ (cm)	48.5	48.5	Chen (1988)
	$a_{max}$ (years)	24.41	21.10	Shr (2020)
		35	19	Drew et al. (2015)
Fecundity	$a_{mat}$ (years)	28	22	Chen et al. (1990) and Harry et al. (2011)
		-	21	Harry et al. (2011)
		13.15 (11–14)	8.92 (6–10)	Drew et al. (2015)
	Litter size	12–38	12–38	Chen (1988)
		mean 25.8	mean 25.8	
	Gestation period (months)	10		Chen (1988)
Reproductive cycle (years)	2	2	Chen (1988), Liu and Chen (1999) and White et al. (2008)	

\* Age at zero length ( $t_0$ ) is determined using the following empirical equation Pauly (1983):  $\log_{10}(-t_0) = -0.3922 - 0.275\log_{10}L_\infty - 1.038\log_{10}k$

**Table 2**

Uncertainties used in the stochastic simulations.

Species/ Uncertainty contributors	Female	Male	Presumed distribution
<b>Smooth hammerhead shark</b>			
$M_s$	In (mean, SD)	In (mean, SD)	Lognormal
$a_{mat}$	U [9–11] years	U [7–9] years	Uniform
Fecundity	Tri [13, 30, 37]	Tri [13, 30, 37]	Triangular distribution
$a_{max}$	Tri [21, 25, 33] years	Tri [18, 24, 28] years	Triangular distribution
<b>Scalloped hammerhead shark</b>			
$M_s$	In (mean, SD)	In (mean, SD)	Lognormal
$a_{mat}$	U [11–14] years	U [6–10] years	Uniform
Fecundity	Tri [12, 25.8, 38]	Tri [12, 25.8, 38]	Triangular distribution
$a_{max}$	Tri [24, 28, 46] years	Tri [21, 22, 25] years	Triangular distribution

( $\sigma_{i,s}$ ) with the probability of transitioning to another stage ( $\gamma_{i,s}$ ):  $G_{i,s} = \sigma_{i,s} \times \gamma_{i,s}$ . Moreover, the survival probability of an individual in its current stage is represented by  $p_{i,s}$ , as described by Brewster-Geisz and Miller (2000) and is given as follows:  $p_{i,s} = \sigma_{i,s} \times$

$$\gamma_{i,s} \text{ and } \begin{cases} \sigma_{i,s} = e^{-(M_{i,s}+F_{i,s})} \\ \gamma_{i,s} = \frac{(\sigma_{i,s}/\lambda_{init})^{T_{i,s}} - (\sigma_{i,s}/\lambda_{init})^{T_{i,s}-1}}{(\sigma_{i,s}/\lambda_{init})^{T_{i,s}} - 1} = \frac{(\sigma_{i,s})^{T_{i,s}} - (\sigma_{i,s})^{T_{i,s}-1}}{(\sigma_{i,s})^{T_{i,s}} - 1}, \end{cases}$$

where  $\lambda_{init}$  is the initial population growth rate (=1), and  $T_{i,s}$  is the duration of each stage for each sex. The finite population growth rate ( $\lambda$ ) can be obtained by solving the equation:  $|A - \lambda I| = 0$ , where  $I$  is the identity matrix (Caswell, 2000) and  $\lambda$  for each sex can be calculated separately by partitioning matrix  $A$  into female and male matrices. The calculation of the intrinsic rate of population increase (e.g.,  $r = \ln \lambda$ ) can be derived from the population growth rate  $\lambda$ . With  $\lambda$  value, a stable population growth occurs when  $\lambda = 1$ , while decreasing and increasing population growth are indicated by  $\lambda < 1$  and  $\lambda > 1$ , respectively.

The net reproductive rate ( $R_0$ ) is a measure of population growth rate from one generation to the next, which is calculated as the average number of offspring produced by an individual over its lifetime (Caswell, 2001 using matrix algebra). Finally, the generation time ( $G$ ) (Coale, 2015) was estimated as the time needed for the population to grow by a factor of  $R_0$  and is calculated using the following formula:  $G = \frac{\ln R_0}{\ln \lambda}$ .

**2.3.3. Elasticity analysis**

An elasticity analysis was performed to understand the effect of changes in reproductive and survival rates on population growth rates ( $\lambda$ ), and this result can be useful for devising conservation and management strategies (Simpfendorfer, 2005). Elasticities were calculated as the proportionate changes in individual matrix elements, while the other elements were kept constant, by using the formula:  $e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{(w \cdot v)}$ , where  $a_{ij}$  = matrix element located in row  $i$  and column  $j$ ,  $v_i$  = value of row  $i$  in the reproductive value vector  $v$ ,  $w_j$  = value of column  $j$  in the stable stage distribution vector  $w$  and let  $\langle w, v \rangle \geq$  scalar product of the two vectors. Individual elasticities for each stage can be added together to estimate the contribution of that stage to  $\lambda$  and that the sum of all matrix element elasticities is equal to 1 (Caswell, 2000; de Kroon et al., 1986; Ebert, 1999; Heppell et al., 1999).

**2.3.4. Incorporation of uncertainty in life history**

We used Monte Carlo simulations to incorporate uncertainty into matrix projections and demographic parameters, as recommended previously (Cortes, 1999; Cortés, 2002, 2008). With various indirect techniques for each sex and stage to derive mean and standard deviation (SD) values for a lognormal distribution, which was employed to estimate the uncertainty in  $M_s$ . For age at maturity, we employed a uniform probability distribution approach with appropriate lower and upper bounds of 9–11 years (female) and 7–9 years (male) for smooth hammerhead sharks and 11–14 years (female) and 6–10 years (male) for scalloped hammerhead sharks to account for uncertainty. Fecundity was assumed to follow a triangular distribution, with the mean litter size of 30 for smooth hammerhead sharks and 25.8 for scalloped hammerhead sharks (Liu, 2002; Chen, 1988).

The Von Bertalanffy Growth Equation (VBGE) described by Chou (2004) can be parameterized using the Gompertz (1825) function as:

$$T_{max,s} = \frac{1}{k_s} \ln \left[ \frac{\ln(L_{0,s}/L_{\infty,s})}{\ln(x)} \right],$$

where the growth parameters including  $k_s$ ,  $L_{\infty,s}$  and  $L_{0,s}$  are derived from the VBGE data (Table 1). The estimation of the potential maximum ages ( $T_{max,s}$ ) for female and male smooth hammerheads exceeding 33 and 28 years, respectively, was based on the assumption that the proportion of  $L_{\infty,s}$  attained at  $T_{max,s}$  is 0.95 (Ricker, 1979; Taylor, 1958), represented by  $x$ . The maximum observed ages ( $O_{max,s}$ ) were used to estimate  $T_{max,s}$ , following the equation:  $T_{max,s} = O_{max,s} \times 1.3$  (Cortés, 2002), which were 46 and 25 years for female and male scalloped hammerheads, respectively. Establishing the range of



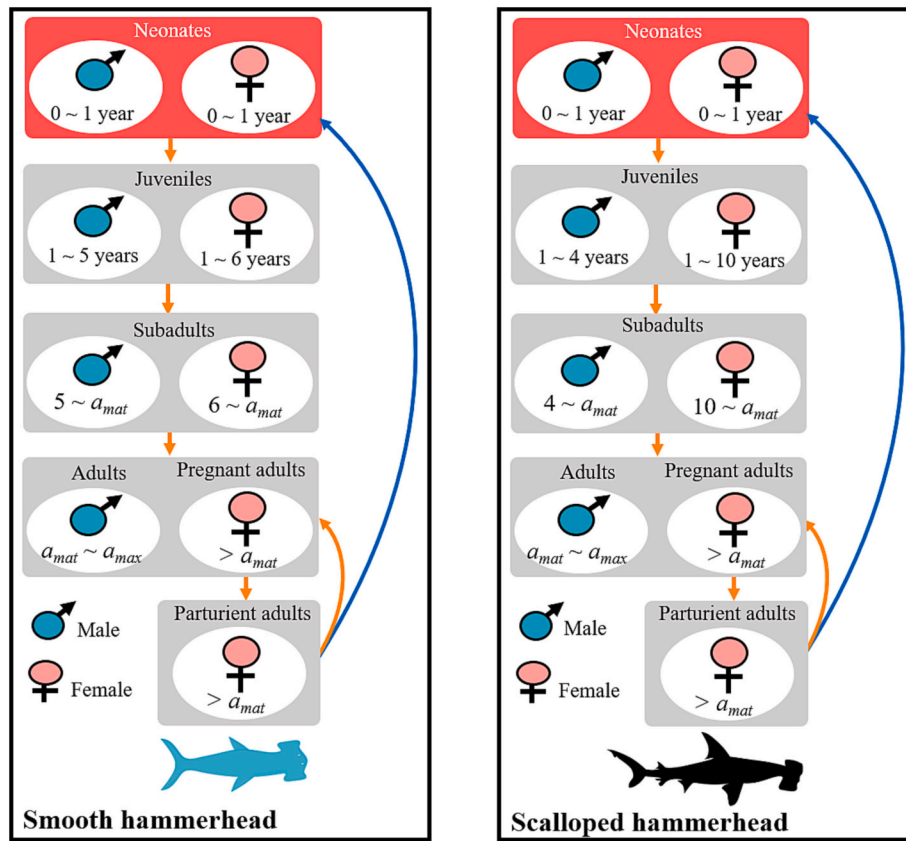


Fig. 2. Diagram of the life cycle of smooth and scalloped hammerhead sharks in the Northwest Pacific Ocean, including arrows that show the survival and growth of individuals between stages or their survival in the same stage ( $a_{max}$ : 18–28 years and 21–25 years for male sharks and 21–32 years and 24–46 years for female sharks and  $a_{mat}$ : 7–9 years and 6–10 years for male sharks and 9–11 years and 11–14 years for female sharks of smooth and scalloped hammerhead sharks, respectively).

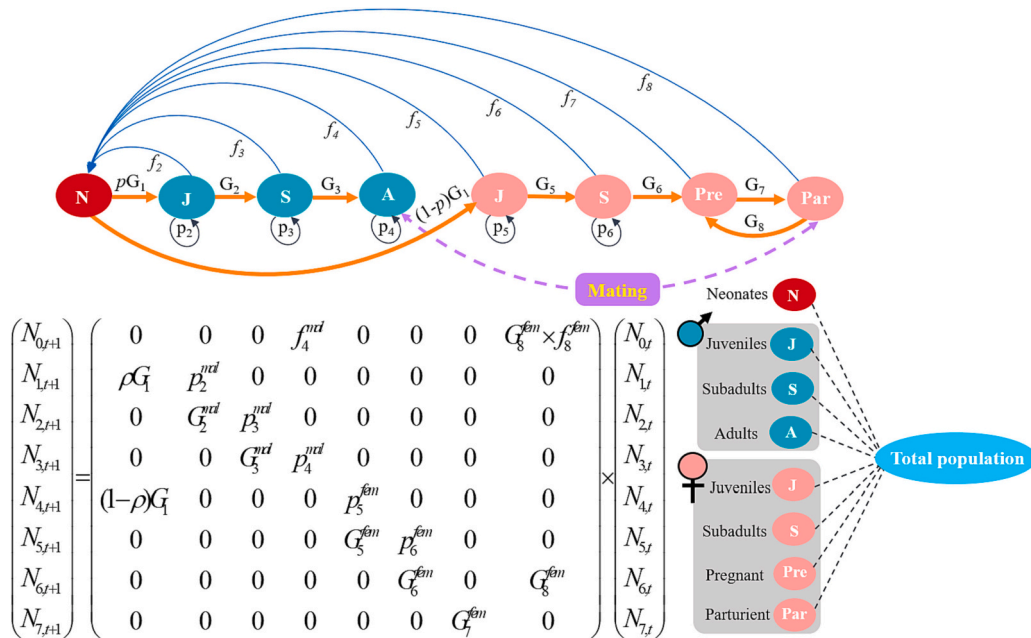


Fig. 3. Life cycle stages and flexible two-sex matrix model for smooth and scalloped hammerhead sharks considering their 2-year reproductive cycles under a monogamous mating system (male sharks and female sharks in the matrix are represented as  $ma^l$  and  $fm^l$ , respectively).

potential  $a_{max}$ , we integrated estimates with previous studies (refer to Table 1) and computed the lower and upper limits of a discrete triangular distribution. Our assumptions, including those for uncertainties of

$M_s$ ,  $a_{mat}$ , fecundity, and  $a_{max}$  for both species, are detailed in Table 2.

2.3.5. Assessment of stock status and management scenarios

To ensure the long-term sustainability of smooth and scalloped hammerhead sharks in the Northwest Pacific Ocean, management strategies should be developed by considering various aspects of fishing activities. However, managing fishery stocks is challenging due to the complex interaction of multiple factors within the ecosystem, and hinders our ability to predict and understand the overall impacts of fishing activities on the ecosystem. Therefore, we evaluated the effectiveness of various management strategies by conducting simulations as outlined in Fig. 4. These strategies included analyzing the natural condition (Scenario 1); status quo (Scenario 2); reducing the current fishing mortality (i.e., 60% and 50% of  $F_{cur}$  by stage as in Scenarios 3 and 4); and protecting immature and mature individuals (Scenarios 5 and 6).

We used Monte Carlo simulations to estimate  $\lambda$  and  $r$  for each scenario (as detailed in Table 2), taking into account uncertainties in  $M_s$ ,  $a_{mat}$ , fecundity, and  $a_{max}$ . The values of parameters were computed as means of 10,000 replicates, with 95% confidence intervals (CIs) determined from the 2.5th and 97.5th percentiles. All demographic analyses performed by the software PopTools (Hood, 2010), along with ggplot2 (Wickham et al., 2016) packages were used for graphical outputs within the R platform (R Development Core, 2022).

3. Results

3.1. Size distribution

The smooth hammerheads included in the sample had FLs of 140–200 cm (female sharks) and 150–180 cm (male sharks), whereas the majority of the scalloped hammerheads had FLs of 130–250 cm (female sharks) and 140–200 cm (male sharks; Fig. 5). Notably, our sample comprised several large individuals of both species, with the largest smooth hammerhead having FLs of 270 cm (female sharks) and 283 cm (male sharks) and the smallest having FLs of 111 cm (female sharks) and 99 cm (male sharks). Among scalloped hammerheads, the largest female collected had an FL of 289 cm, and the largest male had an FL of 292 cm, whereas the smallest female collected had an FL of 68 cm FL, and the smallest male had an FL of 97 cm.

3.2. Length-weight relationship

The length–weight relationship for smooth hammerheads yielded the following coefficients:  $\alpha = 1.888e^{-5}$  and  $\beta = 2.874$  for female sharks and  $\alpha = 2.541e^{-5}$  and  $\beta = 2.812$  for male sharks. Similarly, for scalloped hammerheads, the length–weight relationship yielded the coefficient values  $\alpha = 2.617e^{-6}$  and  $\beta = 3.276$  for female sharks and  $\alpha = 6.933e^{-6}$

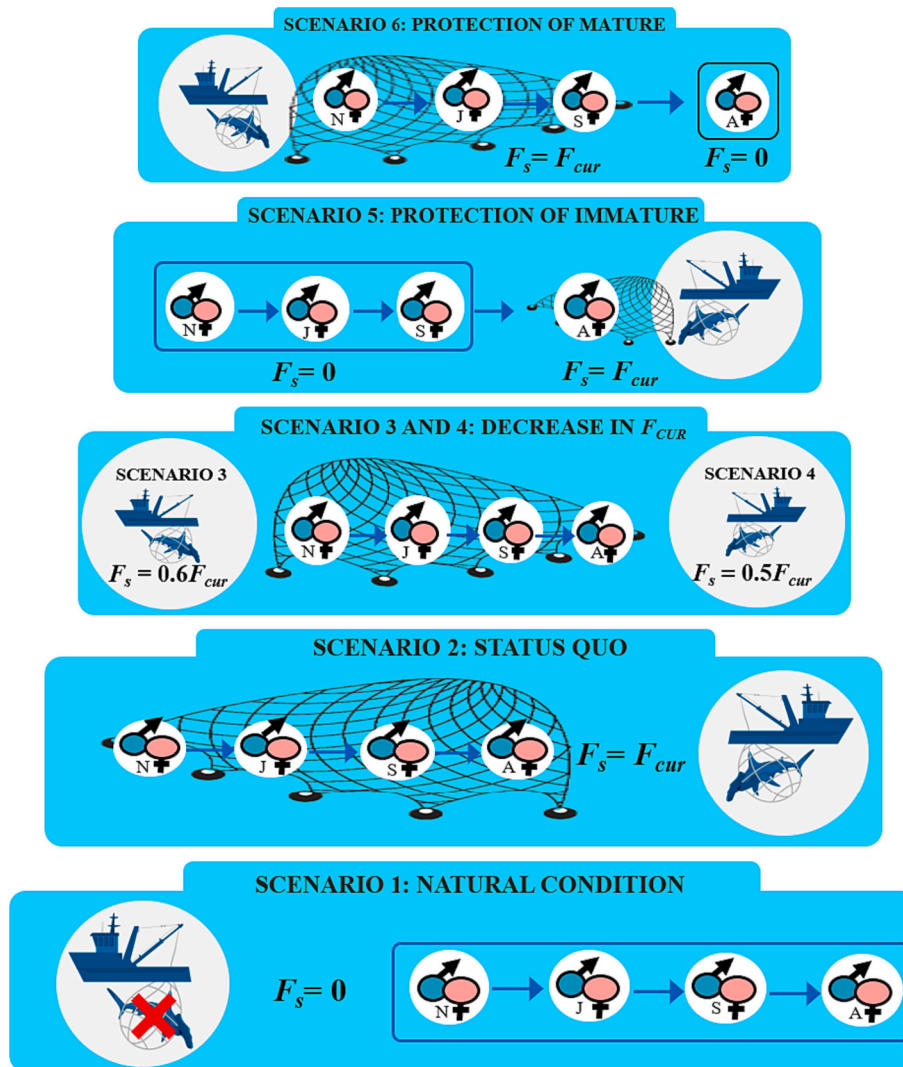


Fig. 4. Flowchart of the simulation framework employed in this study. The framework comprises six scenario models (where N = neonates, J = juveniles, S = subadults, A = adults).

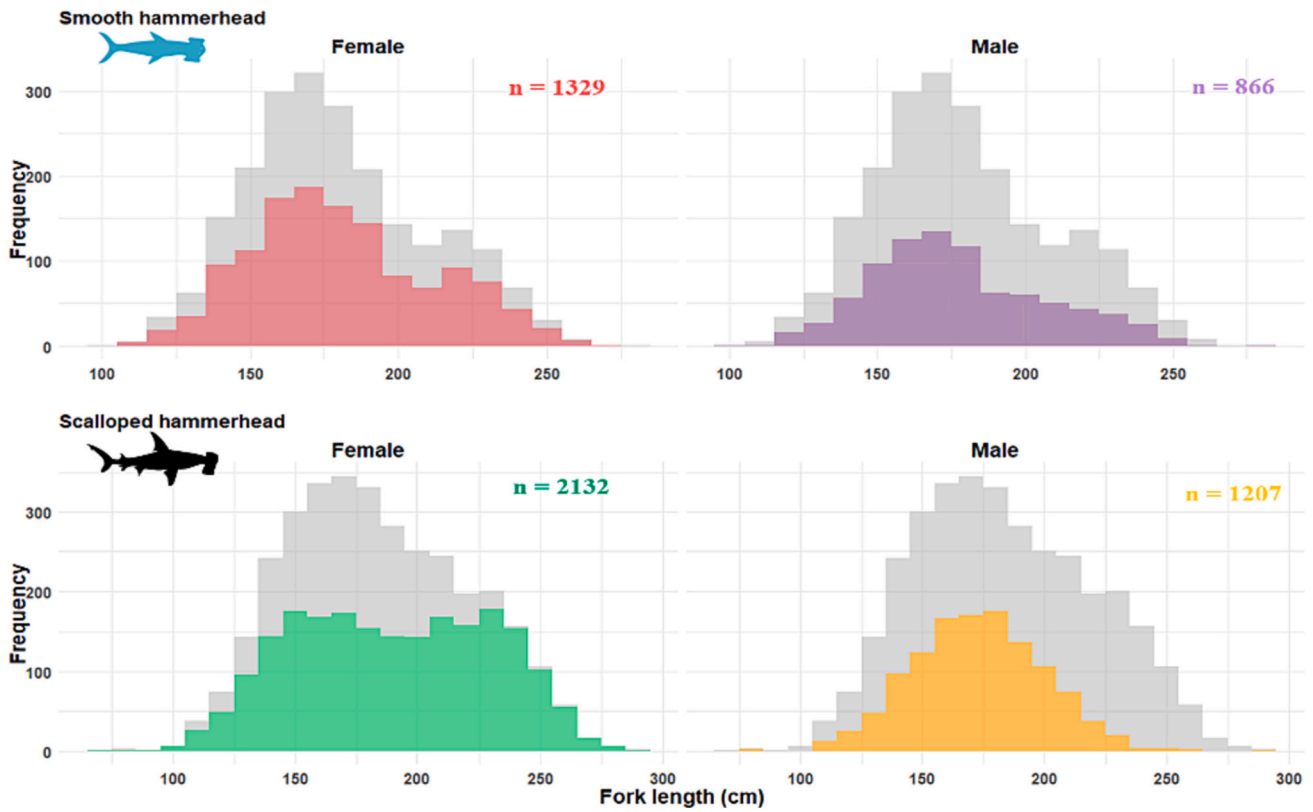


Fig. 5. Distribution of shark sizes of the smooth and scalloped hammerheads by sex in the Northwest Pacific Ocean from 2015 to 2022, in which the grey bars represent the combined length frequency.

and  $\beta = 3.081$  for male sharks, as shown in Fig. 6. These values were subsequently used as input parameters in the estimation of natural mortality by using the method by Zhang and Megrey (2006), as described by empirical equations Zhang & Megrey 1 and Zhang & Megrey 2.

### 3.3. Mortality rate estimation

We evaluated the  $M_s$  using various methods, as shown in Table 3. In line with expectations, our results consistently showed higher  $M_s$  values in male sharks than in female sharks for both species, which can be attributed to the observed shorter longevity of males necessitating

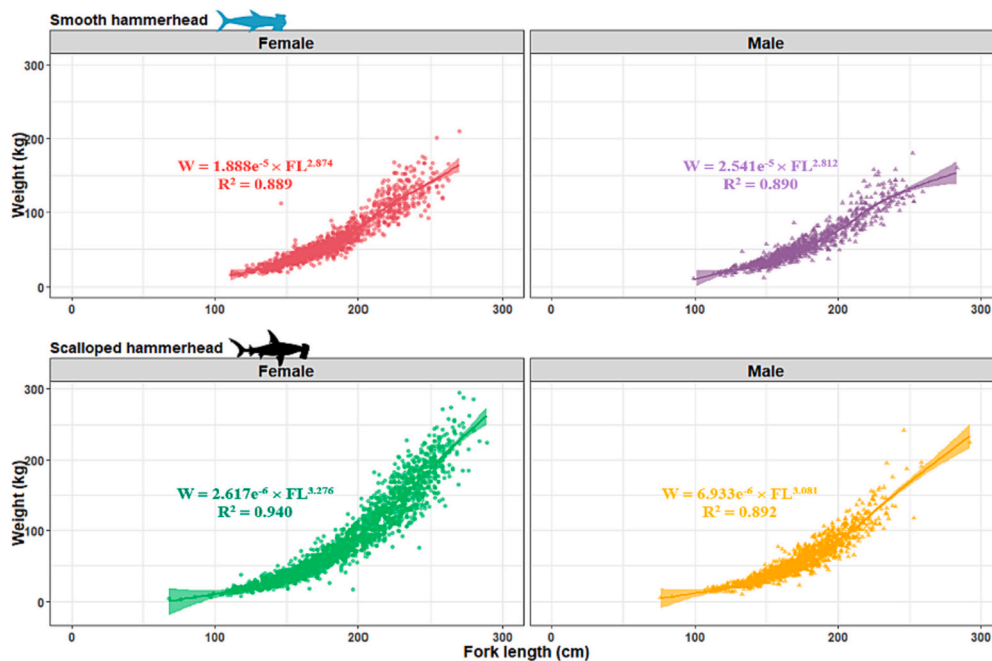


Fig. 6. Length–weight relationship for smooth and scalloped hammerhead sharks in the Northwest Pacific Ocean.

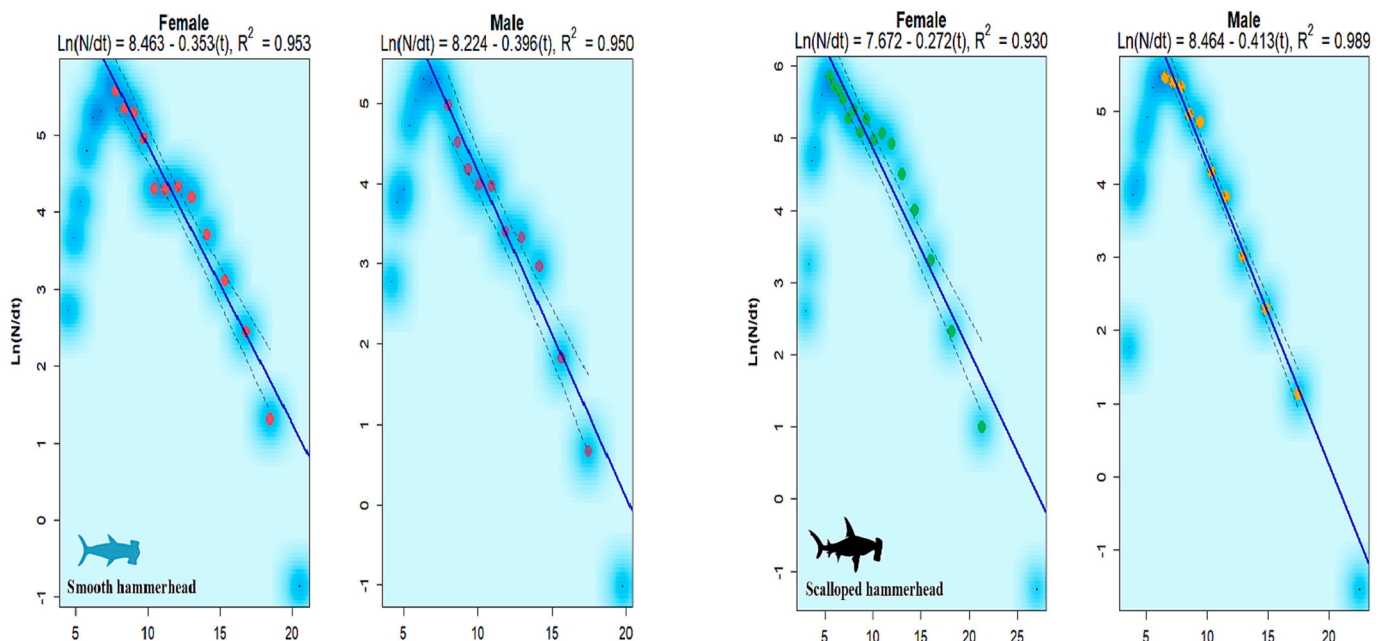
**Table 3**  
Estimated mortality rates, including  $M_s$ ,  $Z_s$  and  $F_s$  ( $\text{year}^{-1}$ ) for smooth and scalloped hammerhead sharks in the North Pacific Ocean.

Mortality	Species/ Method	Female ( $\text{year}^{-1}$ )	Male ( $\text{year}^{-1}$ )
Smooth hammerhead shark			
Natural mortality ( $M_s$ )	Frisk1	0.173	0.184
	Frisk2	0.117	0.132
	Hisano1	0.166	0.208
	Hisano2	0.146	0.185
	Then1	0.247	0.275
	Then2	0.117	0.132
	Dureuil1	0.140	0.160
	Dureuil2	0.154	0.174
	Peterson and Wroblewski (1984)	0.112	0.128
	Lorenzen (1996)	0.114	0.132
	Zhang & Megrey 1	0.188	0.214
	Zhang & Megrey 2	0.138	0.180
	Median	0.151	0.175
Total mortality ( $Z_s$ )	LCCC	0.353	0.396
Fishing mortality ( $F_s$ )	$Z_s - F_s$	0.202	0.221
Scalloped hammerhead shark			
Natural mortality ( $M_s$ )	Frisk1	0.192	0.205
	Frisk2	0.141	0.165
	Hisano1	0.133	0.213
	Hisano2	0.125	0.185
	Then1	0.205	0.281
	Then2	0.141	0.165
	Dureuil1	0.113	0.164
	Dureuil2	0.126	0.178
	Peterson and Wroblewski (1984)	0.091	0.117
	Lorenzen (1996)	0.090	0.120
	Zhang & Megrey 1	0.148	0.197
	Zhang & Megrey 2	0.118	0.179
	Median	0.135	0.181
Total mortality ( $Z_s$ )	LCCC	0.272	0.413
Fishing mortality ( $F_s$ )	$Z_s - F_s$	0.137	0.232

higher natural mortality rates ( $M_s$ ). The male and female smooth hammerheads had median  $M_s$  values of 0.175 and 0.151  $\text{year}^{-1}$ , respectively, while the male and female scalloped hammerheads had median  $M_s$  values of 0.181 and 0.135  $\text{year}^{-1}$ , respectively, as determined by our analysis. The mortality rate for each sex  $Z_s$  was estimated using a length-converted catch curve with a corresponding linear regression (Fig. 7). The data points in the middle of the graph corresponded to size/age groups that were the most vulnerable to capture by fishing gear and were used in our regression analysis. Male and female smooth hammerheads exhibited  $Z_s$  values of 0.396 and 0.353  $\text{year}^{-1}$ , respectively, while male and female scalloped hammerheads showed  $Z_s$  values of 0.413 and 0.272  $\text{year}^{-1}$ , respectively (Fig. 7). During the study period,  $F_s$  values of 0.221 and 0.202  $\text{year}^{-1}$  were obtained for male and female smooth hammerheads, and 0.232 and 0.137  $\text{year}^{-1}$  for male and female scalloped hammerheads, respectively, by subtracting  $M_s$  from  $Z_s$ , as shown in Table 3.

### 3.4. Demographic analyses

The results of the demographic analyses of smooth and scalloped hammerhead sharks are presented in Table S1. Table S2 presents the estimated life history matrix elements for both species under natural and current conditions. Under natural conditions, both species demonstrated population growth, with similar growth rates,  $\lambda = 1.198$  and 1.190  $\text{year}^{-1}$  for smooth and scalloped hammerheads, respectively. However, an analysis using the flexible two-sex matrix model showed a decrease in population growth rates under current fishing mortality levels. For the total population, the growth rates were  $\lambda = 0.918$  and 0.934  $\text{year}^{-1}$  for smooth and scalloped hammerheads, respectively; the sex-specific values were  $\lambda = 0.944$  and 0.890  $\text{year}^{-1}$  for male and female smooth hammerheads and 0.928 and 0.934  $\text{year}^{-1}$  for male and female scalloped hammerheads, respectively. These findings suggest a decline in the populations of both species under current fishing conditions as well as a further decline in female smooth hammerhead populations. Slight differences in the net reproduction rate ( $R_0$ ) were observed between the two species due to differences in the duration of the adult stages. The generation time  $G$  was estimated to be slightly longer for scalloped hammerheads than for smooth hammerheads (Table S1). Moreover, the results of the Monte Carlo simulations of key demographic parameters



**Fig. 7.** Estimates of  $Z_s$  for smooth and scalloped hammerhead sharks in the Northwest Pacific Ocean between 2015 and 2022, as derived through the length-converted catch curve method. The color scheme in the figure represents the density of data points, with darker-shaded areas indicating higher data density.



( $\lambda$ ,  $R_0$ , and  $T$ ; **Table S1**) provide a representation of the variability observed across the 10,000 simulations. These results highlight the importance of conducting species-specific demographic analyses and incorporating sex-specific values in two-sex stage-based models for planning conservation measures.

### 3.5. Elasticity analyses

The analysis of shark population elasticity highlights the need to prioritize the protection of immature smooth and scalloped hammerhead sharks, including neonates, juveniles, and subadults, in order to sustain their populations in the long run. The results, as shown in **Fig. 8**, indicate that immature individuals have higher elasticity than mature adults, which means they are more responsive to changes in natural and current conditions. Moreover, the analysis revealed that male hammerhead sharks of both species exhibited greater changes in  $\lambda$  than their female counterparts. It is important to note that female scalloped hammerhead sharks are more vulnerable to fishing pressure than natural mortality, as suggested by their higher elasticity compared to males. Hence, reducing fishing pressure is crucial, especially since fishing affects male and female scalloped hammerheads differently. In addition, the higher density of immature individuals in the population, as seen in the density plot (also **Fig. 8**), further emphasizes the importance of protecting them to ensure the long-term conservation of these sharks. Therefore, it is necessary to prioritize the protection of both male and female individuals, with particular emphasis on safeguarding immature sharks.

### 3.6. Current stock status and different management scenarios

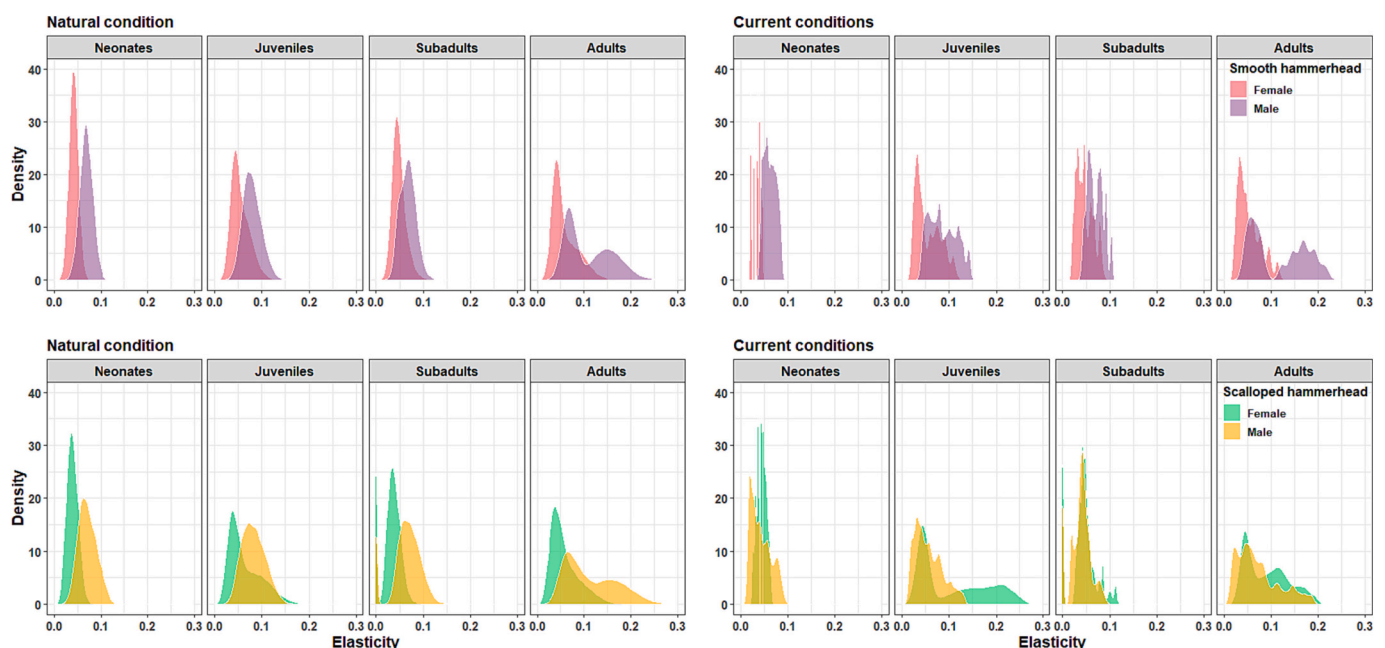
The  $\lambda$  values varied significantly between smooth and scalloped hammerhead sharks across different management scenarios in the demographic models (**Table S1**, **Fig. 9**). Our analysis revealed that when fishing mortality was absent (Scenario 1), the population growth increased for both species. Conversely, under current fishing pressure (Scenario 2), a negative growth rate was observed, indicating a predicted decline in the population. The population growth rates decreased to  $<1$  under moderate levels of fishing pressure for both species, which indicated unsustainable harvesting. However, decreasing the fishing mortality to 50% (Scenario 4) and 60% (Scenario 3) of the current levels

resulted in population growth rates ( $\lambda$ ) exceeding 1 for both male and female individuals of smooth and scalloped hammerhead sharks, respectively. The simulation results revealed that protecting immature individuals (Scenario 5) led to a high probability of  $\lambda > 1$  for both species. When protecting immature individuals (Scenario 5) was prioritized over protecting mature individuals (Scenario 6), we observed a clear population growth was observed in both male sharks and female sharks. Overall, our findings suggest that effective management measures are necessary to ensure the sustainable harvest of these shark species.

## 4. Discussion

### 4.1. Demographic analyses for shark stock assessment and fishery management

Demographic projection models have been widely used for assessing shark population stocks, which provide information vital for establishing relevant policies. The finite population growth rate ( $\lambda$ ) is a common measure of the population growth rate in demographic analyses. Studies have determined  $\lambda$  for various shark species by using population projection matrices (Au and Smith, 1997; Cailliet, 1992; Chen and Yuan, 2006; Cortés, 1995; Cortés and Parsons, 1996; Geng et al., 2021; Liu and Chen, 1999; Liu et al., 2021; Takeuchi et al., 2005; Tsai et al., 2020; Tsai et al., 2014; Tsai and Huang, 2022). Herewith, we employed the flexible two-sex matrix model population to conduct population biology and demographic analyses for smooth and scalloped hammerhead sharks, which considered sex-specific and dimorphic vital rates. Our results revealed that to achieve positive population growth for these sharks, the fishing mortality must be reduced considerably (50% and 60% of the current levels for smooth and scalloped hammerhead sharks, respectively). The mean population growth rate estimates for smooth and scalloped hammerhead sharks were  $\lambda = 1.198$  and  $1.190 \text{ year}^{-1}$ , respectively moderately differ from those reported in previous studies, possibly due to the differences in model types and study regions. This difference may be attributed to the variation in life history among species in different oceans; we found that species in the Northwest Pacific Ocean had later maturity ages and greater longevity than those in other oceans, as reported in previous studies (**Table S3**). Additionally, fishing had a considerable impact on both male and female hammerhead shark



**Fig. 8.** Elasticity distributions of smooth and scalloped hammerhead sharks in each stage in the Northwest Pacific Ocean.

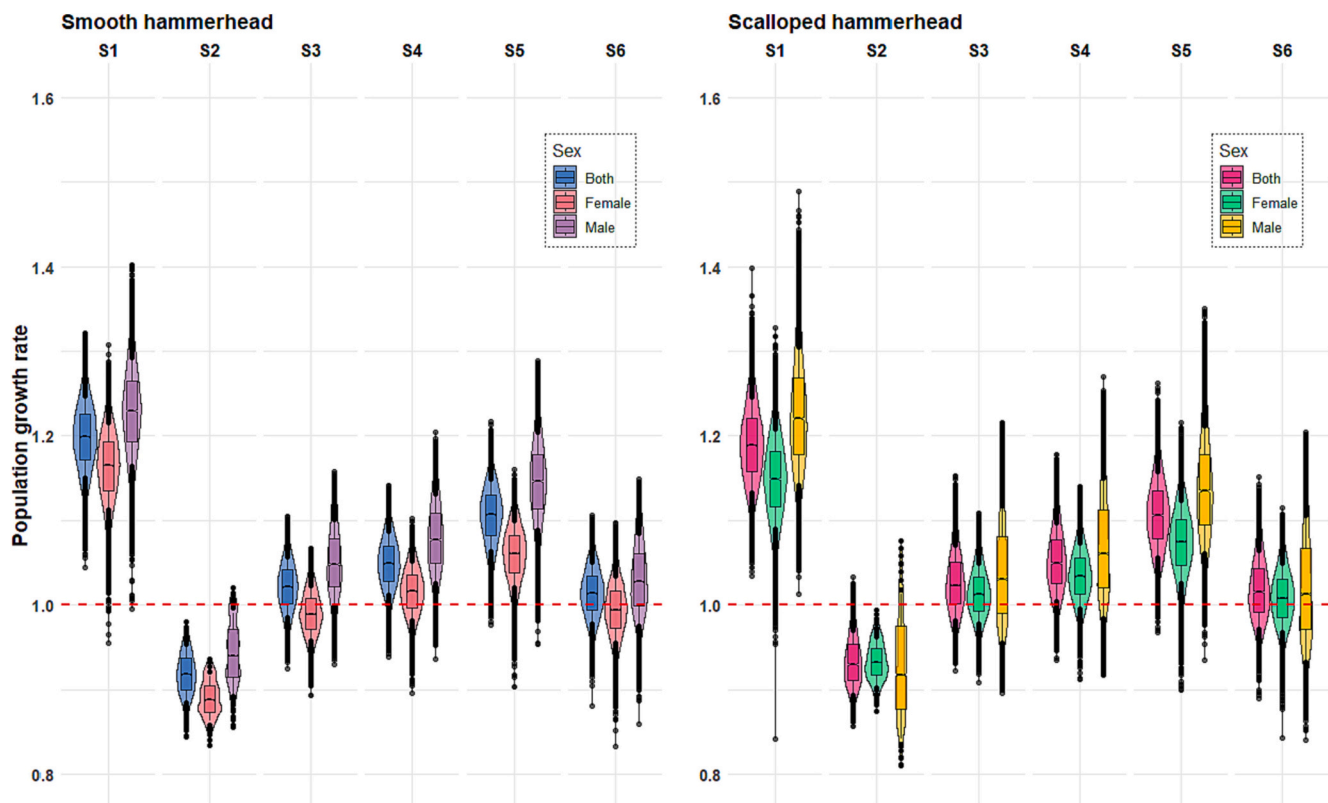


Fig. 9. Box plots illustrating the growth rate in smooth and scalloped hammerhead shark populations under various scenarios, with a red dashed line indicating population stability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

populations in our analysis; specifically, higher fishing mortality in males compared to females for smooth hammerhead sharks (Table 3), indicating fishing activities disproportionately impacted male hammerhead sharks, but the effect on female populations was more severe, which resulted in a lower  $\lambda$  for female sharks than for male sharks (Scenario 2, Table S1). Therefore, reducing the fishing mortality rates for both sexes is crucial to ensuring the long-term sustainability of these species.

Incorporating sexual dimorphism in population models is crucial for accurately assessing the stock status of species with sexual dimorphism. Sex-specific and dimorphic vital rates have been observed in various marine species, including some hammerhead sharks (Benavides et al., 2021; Estupiñán-Montaño et al., 2019; Klimley, 1987; Semba, 2018) and other shark species such as shortfin mako shark (*Isurus oxyrinchus*) (Semba et al., 2011; Semba et al., 2009; Tsai et al., 2015) and silky shark (*Carcharhinus falciformis*) (Clarke et al., 2011) as well as in nonshark species such as boarfish (*Capros aper*) (Hüsey et al., 2012), electric knifefish (*Gymnorhamphichthys rondoni*) (García and Zuanon, 2019), and European sea bass (*Dicentrarchus labrax* L.) (Faggion et al., 2021). Ignoring sex-specific differences can lead to inaccurate decline risk estimates and stock status evaluations (Caswell and Weeks, 1986; Kokko and Rankin, 2006; Miller and Inouye, 2011; Tsai et al., 2015; Tsai et al., 2014). In this study, Monte Carlo simulations were employed to assess the stock status of hammerhead sharks, revealing the significance of accounting for sexual dimorphism in population modeling, particularly in relation to the variability observed in  $\lambda$  (Table S1). The model revealed moderate differences in population growth rates when sex was considered, suggesting that such simulations can be used to evaluate the stock status of other shark species with sexual dimorphism or with limited life history data. Thus, accounting for sexual dimorphism is crucial for obtaining accurate decline risk estimates and for developing suitable management strategies. Indeed, the implementation of a two-sex matrix model, as demonstrated by Tsai et al. (2015), allows for a

more accurate assessment of population dynamics by considering other demographic parameters between males and females. Additionally, nonlinear two-sex models, discussed by Jenouvrier et al. (2010), provide insights into the direct and indirect effects of vital rates on population growth and structure, making them applicable to ecological and evolutionary studies across species.

In the field of stock assessment, model application software packages like Stock Synthesis, CASAL, MULTIFAN-CL, GADGET, and SAM are commonly used [refer to (Punt et al., 2020) for more details on their synthetic features]. Applying these methods to shark species, however, is challenging due to limited catch and effort data. Chen (2020) also utilized two-sex demographic models based on full sales records from the Nanfangao fish market. However, due to a lack of individual sex and length information in the sales records, a subsample of two hammerhead sharks was randomly collected from the landings to obtain sex-specific length frequency in our analyses. Undoubtedly, this assumes that enough of the fish have been captured for growth, length frequency, and relative weight sample size requirements. In addition, possible factors contributing to biased data collection for males or larger fish include gear selectivity, determining the sex of sharks difficult when external characteristics are not easily distinguishable, sampling effort, and observer coverage. The aim of our study was to explore whether data-limited methods could yield similar assessment results compared to more complex conventional stock assessment approaches. Thus, our methods were not specifically designed to account for fishery complexities such as sex ratio or gear selectivity. Although the full daily records data was not utilized in this study, our conclusion remains consistent with previous demographic analyses conducted for smooth hammerhead sharks (Chen, 2020). Consequently, we believe that the major conclusions of our analysis remain valid. Nevertheless, these results may still reflect a partial stock status in the Northwest Pacific Ocean, but the spatial coverage may not be adequate to fully evaluate the entire stock status.

Elasticity analysis is a useful tool for assessing the impact of different life stages on population growth, and the results can be used as predictors for corresponding outcomes in stochastic models (Caswell, 2001). According to the elasticity analysis, the population growth rate in both hammerhead shark species is related to the survival rates during the immature stage because small changes in these rates can significantly affect population growth, which is consistent with previous trends for other long-living vertebrates (Gallucci et al., 2006; Heppell et al., 2000; Heppell et al., 1999; Simpfendorfer, 2005). Therefore, management efforts should be prioritized for the individuals in the immature stage, including neonates, juveniles, and subadults as highlighted by the consistent outcomes in protecting immature individuals (Scenario 5) compared to other scenarios, to achieve the sustainable conservation of both hammerhead shark populations (Gallucci et al., 2006).

The findings of the present study are in line with those of previous studies, highlighting the problems of overexploitation of hammerhead shark populations, especially the smooth hammerhead species in the Northwest Pacific (Chen, 2020; Tsai et al., 2018), and the susceptibility of immature scalloped hammerhead sharks to long-term exploitation (Liu and Chen, 1999; Wu, 2019). Through this study, we gain a better understanding of the population dynamics of these shark species, which enables a more complete picture of their ecological status.

#### 4.2. Considering uncertainty in simulations

Our modeling method enables the exploration of multiple population scenarios; however, the projections are approximate estimates, and actual long-term population dynamics may differ from these projections. Indeed, there remains considerable uncertainty in vital parameters such as  $M_s$ ,  $a_{mat}$  and  $a_{max}$ , and fecundity for elasmobranch species (Geng et al., 2021; Grant et al., 2020; Tsai and Huang, 2022). Demographic analyses are largely dependent on these factors; therefore, the accurate determination of life history traits is crucial for successful fisheries conservation and management.

Reliable estimates of  $M_s$  are difficult to obtain because of the migration and varied distribution of marine animals, including sharks.  $M_s$  has a significant impact on stock productivity and reference points for fisheries management (Maunders et al., 2023; Punt et al., 2021). Although tagging data research is a promising method for studying the movement and behavior of sharks, it may not be feasible for most shark species, and even in data-rich cases, the reliability of  $M_s$  estimates from tagging data is debated (Regular et al., 2022; Rose and Walters, 2019). Demographic analyses of shark populations have employed various indirect mortality approaches to estimate various parameters including population size, growth rates, and survival rates; however, the accuracy of these approaches may be affected by various sources of bias such as the four biases mainly mentioned in Table 2 (Geng et al., 2021; Huynh et al., 2022; Liu et al., 2015; Smart et al., 2017; Tsai et al., 2010; Tsai and Huang, 2022). Therefore, this study employed empirical methods to estimate  $M_s$  in smooth and scalloped hammerhead sharks. We considered the range of empirical methods commonly used for elasmobranchs to capture the range of uncertainty in  $M_s$ , which may overcome the shortcomings of using a specific estimator derived from uncertain life history data. For both species, the  $M_s$  estimated using different approaches varied, and therefore, this vital rate had the highest uncertainty. Accurate estimation of  $M_s$  is critical because both target biomass and  $F_s$  depend on it, which leads to a “doubling” effect on allowable catches, as reported in many groundfish stocks (Punt et al., 2008). Therefore,  $M_s$  must be carefully considered in stock assessments. However, it is important to exercise caution in interpreting the results of this study until more definitive estimates of  $M_s$  are available for both species.

The uncertainty in life history parameters, including  $a_{mat}$  and  $a_{max}$ , is attributable to the limited sample sizes in studies (Chen et al., 1990; Chou, 2004; Liu, 2002; Shr, 2020). Yokoi et al. (2017) highlighted that to estimate the population growth rates for pelagic sharks, reliable aging

validation techniques must be employed. The use of a stochastic approach that accounts for annual fluctuations in  $a_{mat}$  for each sex allows better captures of the range of potential population growth rate estimates compared with the use of the conventional approach of using a fixed  $a_{mat}$  (Caswell, 2001; Cortés, 2002) and is more consistent with shark life history, where maturity does not occur at a fixed age. The findings of this study underscore the importance of accounting for sex-specific differences in  $a_{mat}$  when estimating population growth rates, especially in the context of fishing mortality. The observed variations in population growth rates between males and females underscore their different responses to fishing pressure, and this characteristic would not be captured from a combined estimate of population growth of two hammerhead sharks. The accurate estimation of  $a_{max}$  of shark populations is crucial for demographic analyses; however, it is challenging due to the uncertainties caused by natural variation, historical exploitation, and varying aging techniques (Chen and Yuan, 2006; Yokoi et al., 2017). The age estimation accuracy for sharks can be affected by the varying periodicity of band pair deposition during different life stages (Chen et al., 1990; Chou, 2004; Harry et al., 2011; Klimley, 1987). To overcome this challenge, we used a stochastic methodology that incorporated previously reported equations and a triangular distribution to assign the most likely age value between the minimum and maximum limits. We also highlighted the potential impact of low maximum age estimations from previous studies and estimated the theoretical  $a_{max}$  of the species based on growth parameter estimates. Using our approach, we found that the scalloped hammerhead is a long-living fish with a maximum longevity estimate of 55 years (Kotas et al., 2011), which demonstrates the importance of the potential range of  $a_{max}$  estimates that should be considered in conservation management strategies. Using a single (low) value for  $a_{max}$  may not fully capture the demographic characteristics of the population. Overall, our study highlighted the importance of obtaining reliable  $a_{max}$  data, avoiding assumptions solely based on theoretical estimates, conducting accurate demographic analyses and devising conservation management strategies. Uncertainty in fecundity is common, and fecundity may be underestimated due to the loss of embryos during capture, leading to an underestimation of litter size (Liu et al., 2015). As such, the improvement of stock assessments in future research requires the collection of more reliable litter size data through onboard observation, also through non-invasive techniques like ultrasound (Hammerschlag and Sulikowski, 2011).

The present study has limitations including uncertainties related to unit stock, density-dependent compensatory mechanisms, and assumptions regarding equilibrium dynamics. Future studies should refine their methods to address these limitations. In this study, we used stage-based models to estimate the populations of two hammerhead shark species in the Northwest Pacific, which was based on the hypothesis that the two species constitute a single unit stock. However, studies supporting or contradicting this hypothesis are currently few, and the genetic structure of these species in the Northwest Pacific remains poorly understood (Shan-Hui et al., 2020). Further, changes in life history parameters can have a significant impact on population dynamics, especially the population growth rate (Benton and Grant, 1999; Sæther et al., 2013). To address this problem, further research should employ molecular techniques for stock identification. Having separate demographic models for each stock would enable a deeper understanding of the population dynamics of these species.

The concept of compensatory density dependence has long been a debated topic in population dynamics, as it plays a crucial role in effective fisheries management (Macaluso, 1999; Rose et al., 2001). However, the mechanisms underlying the population responses of many species, especially elasmobranchs, to increased density remain poorly understood (Carlson et al., 2003; Cortés, 2007). To project demographic outcomes, we considered density dependence as a simple ceiling function, given its limitations in capturing the complexity of density-dependent responses in reality. However, based on their life history traits, elasmobranchs can be expected to exhibit minimal density-



dependent responses (Brewster-Geisz and Miller, 2000; Cortés, 1998). We assumed equilibrium dynamics in our demographic analyses, which may be reasonable for species with slow life histories that are less susceptible to large perturbations to their most productive individuals (Caswell, 2001). Incorporating the transient matrix model proposed allows for a better understanding of the stage structure, which is crucial for devising effective conservation strategies for species with slow life histories. By considering the dynamics and transitions between different life stages, conservation efforts can be tailored to target specific vulnerable stages and promote population persistence.

In our study, we recognize the importance of comprehending the range and movement patterns of the study species in the Northwest Pacific to ensure accurate stock assessment. These species possess contrasting characteristics, with scalloped hammerhead sharks, for instance, having combined traits of oceanic habitat, which promotes high dispersal, with potential fidelity to specific nursery grounds, especially for reproductive females (Duncan and Holland, 2006). Comparative analysis with other globally distributed sharks, such as the shortfin mako (*Isurus oxyrinchus*) and the soupfin (*Galeorhinus galeus*), revealed a less distinct population structure in comparison to the scalloped hammerhead (Ward and Gardner, 1997; Schrey and Heist, 2003). Consequently, conducting long-term studies is crucial to further understanding their movement patterns and population dynamics, leading to the development of more effective management strategies.

#### 4.3. Outlook

This study highlighted the problem of overexploitation of smooth and scalloped hammerhead shark populations in the Northwest Pacific and suggested that appropriate management can help in the sustainable fishing of these species. Future life history studies should use rigorous methodologies such as sampling from a wide size range and investigating key parameters such as litter size and growth. Additionally, comparable and reliable methodologies should be employed to determine aging, length-at-age modeling, maturity, and longevity to reduce ambiguity in the estimation of regional parameters and enhance population projections. In particular, a direct estimation of the vital rate  $M_x$  is crucial, which was found to be the most uncertain and influential in matrix analyses. Thus, the use of rigorous and consistent methods can provide more thorough understanding of the population dynamics of smooth and scalloped hammerhead sharks and help in the development of effective conservation and management strategies to ensure their long-term sustainability in the Northwest Pacific.

#### Funding

This study received financial support from the National Science Council of the Republic of China under Contract Nos NSC106–2611-M-992 -301 and NSC107–2611-M-992 -001.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

No data was used for the research described in the article.

#### Acknowledgements

The authors would like to express their gratitude to the three anonymous reviewers for their constructive comments and editorial suggestions, which greatly improved this manuscript. The authors also thank the Overseas Fisheries Development Council, Taiwan for providing

shark length and weight data of longline fisheries.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2023.102434>.

#### References

- Au, D.W., Smith, S.E., 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Can. J. Fish. Aquat. Sci.* 54 (2), 415–420.
- Baum, J.K., Blanchard, W., 2010. Inferring shark population trends from generalized linear mixed models of pelagic longline catch and effort data. *Fish. Res.* 102 (3), 229–239.
- Bejarano-Álvarez, M., Galvan-Magana, F., Ochoa-Baez, R.I., 2011. Reproductive biology of the scalloped hammerhead shark *Sphyrna lewini* (Chondrichthyes: Sphyrnidae) off south-West Mexico. *Aqua: international. J. Ichthyol.* 17 (1), 11–23.
- Benavides, M.T., Fodrie, F.J., Fegley, S.R., Bargione, G., 2021. Size changes within a southeastern United States coastal shark assemblage: 1975–2018. *Marine Coastal Fish.* 13 (3), 228–239.
- Benton, T.G., Grant, A., 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Ecol. Evol.* 14 (12), 467–471.
- Booth, H., Gupta, T., 2023. Shark fishing and shark finning. In: *The Ocean and us*. Springer, pp. 89–99.
- Brewster-Geisz, K., Miller, T., 2000. Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. *Fish. Bull.* 2.
- Cailliet, G.M., 1992. Demography of the Central California population of the leopard shark (*Triakis semifasciata*). *Mar. Freshw. Res.* 43 (1), 183–193.
- Camhi, M., 1998. Sharks and their Relatives: Ecology and Conservation. IUCN.
- Camhi, M.D., Valenti, S.V., Fordham, S.V., Fowler, S.L., Gibson, C., 2009. The Conservation Status of Pelagic Sharks and Rays. IUCN Species Survival Commission Shark Specialist Group, Newbury, p. 78.
- Cardena, D., Shea, S.K., Zhang, H., Fischer, G.A., Simpfendorfer, C.A., Chapman, D.D., 2022. Two thirds of species in a global shark fin trade hub are threatened with extinction: conservation potential of international trade regulations for coastal sharks. *Conserv. Lett.* 15 (5), e12910.
- Carlson, J.K., Cortés, E., Bethea, D.M., 2003. Life History and Population Dynamics of the Finetooth Shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico.
- Carruthers, T.R., Punt, A.E., Walters, C.J., MacCall, A., McAllister, M.K., Dick, E.J., Cope, J., 2014. Evaluating methods for setting catch limits in data-limited fisheries. *Fish. Res.* 153, 48–68.
- Casper, B., Domingo, A., Gaibor, N., Heupel, M., Kotas, E., Lamónaca, A., Pérez-Jiménez, J., Simpfendorfer, C., Smith, W., Stevens, J., 2005. *Sphyrna zygaena*. The IUCN Red List of Threatened Species.
- Caswell, H., 1989. Matrix population models: Construction. *Analys. Interpret.* 255.
- Caswell, H., 2000. Matrix Population Models, vol. 1. Sinauer Sunderland, MA.
- Caswell, H., 2001. Construction, analysis, and interpretation. Sunderland: Sinauer 585, 258–277.
- Caswell, H., Weeks, D.E., 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. *Am. Nat.* 128 (5), 707–735.
- Chandrvanshi, R., Uraon, R., Sarang, N., Vardia, H., 2019. Studies on length-weight relationship (LWR) and condition factor of *Labeo rohita* and *Cirrhinus mrigala* in sutiapat reservoir, Kabirdham, Chhattisgarh, India. *J. Entomol. Zool. Stud.* 7, 420–424.
- Chang, J.-H., Liu, K.-M., 2018. Demographic analysis of the shortfin Mako shark, *Isurus oxyrinchus* in the western North Pacific using stage-based models. *J. Fish. Soc. Taiwan* 45 (3), 153–172.
- Chen, C., 1988. Notes on reproduction in the scalloped hammerhead, *Sphyrna lewini*, in Taiwan waters. *Fish. Bull.* 86, 389–393.
- Chen, X.C., 2020. Mortality Estimates and Demographic Analysis for the Smooth Hammerhead Shark (*Sphyrna zygaena*) in the Northwest Pacific Ocean. Department of Production and Management, National Kaohsiung University of Science and Technology, Master Thesis.
- Chen, P., Yuan, W., 2006. Demographic analysis based on the growth parameter of sharks. *Fish. Res.* 78 (2–3), 374–379.
- Chen, C., Leu, T., Joung, S., Lo, N., 1990. Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. *Pac. Sci.* 44 (2), 156–170.
- Chin, A., Simpfendorfer, C., White, W., Johnson, G., McAuley, R., Heupel, M., 2017. Crossing lines: a multidisciplinary framework for assessing connectivity of hammerhead sharks across jurisdictional boundaries. *Sci. Rep.* 7 (1), 46061.
- Chou, Y.T., 2004. Studies on Age and Growth of Smooth Hammerhead, *Sphyrna zygaena* in Northeastern Taiwan Waters. Master Thesis, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University.
- CITES, 2013. Notification to the Parties No. 2013/012 Geneva, 19 April 2013, Concerning: Amendments to Appendices I And II of the Convention Adopted by the Conference of the Parties at its 16th Meeting, Bangkok (Thailand), 3–14 March 2013. <https://www.cites.org/sites/default/files/eng/notif/2013/E-Notif-2013-012.pdf>.
- Clarke, S.C., Magnussen, J.E., Abercrombie, D.L., McAllister, M.K., Shivji, M.S., 2006. Identification of shark species composition and proportion in the Hong Kong shark fin market based on molecular genetics and trade records. *Conserv. Biol.* 20 (1), 201–211.



- Clarke, C., Lea, J., Ormond, R., 2011. Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. *Mar. Freshw. Res.* 62 (6), 668–675.
- Coale, A.J., 2015. Growth and Structure of Human Populations: A Mathematical Investigation, vol. 1333. Princeton University Press.
- Coelho, R., Fernandez-Carvalho, J., Amorim, S., Santos, M.N., 2011. Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the eastern equatorial Atlantic Ocean, using vertebral sections. *Aquat. Living Resour.* 24 (4), 351–357. <https://doi.org/10.1051/alr/2011145>.
- Compagno, L., 1984. Sharks of the world. An annotated and illustrated catalogue of shark species to date. In: Part II (Carcharhiniformes). FAO Fisheries Synopsis. FAO Rome.
- Compagno, L., Dando, M., Fowler, S., 2005. Princeton Field Guides: Sharks of the World, vol. 2. Princeton University Press. Princeton, New Jersey.
- Cortés, E., 1995. Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico. *Oceanogr. Lit. Rev.* 9 (42), 788.
- Cortés, E., 1998. Demographic analysis as an aid in shark stock assessment and management. *Fish. Res.* 39 (2), 199–208.
- Cortés, E., 1999. A stochastic stage-based population model of the sandbar shark in the western North Atlantic. *Am. Fish. Soc. Symp.* 23, 115–136.
- Cortés, E., 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conserv. Biol.* 16 (4), 1048–1062.
- Cortés, E., 2007. Chondrichthyan demographic modelling: an essay on its use, abuse and future. *Mar. Freshw. Res.* 58 (1), 4–6.
- Cortés, E., 2008. Comparative life history and demography of pelagic sharks. *Sharks Open Ocean: Biol., Fish. Conservat.* 309–322.
- Cortés, E., Parsons, G.R., 1996. Comparative demography of two populations of the bonnethead shark (*Sphyrna tiburo*). *Can. J. Fish. Aquat. Sci.* 53 (4), 709–718.
- Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F., Domingo, A., Heupel, M., Holzhausen, H., Santos, M.N., Ribera, M., Simpfendorfer, C., 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquat. Living Resour.* 23 (1), 25–34. <https://doi.org/10.1051/alr/2009044>.
- Daly-Engel, T.S., Seraphin, K.D., Holland, K.N., Coffey, J.P., Nance, H.A., Toonen, R.J., Bowen, B.W., 2012. Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (*Sphyrna lewini*). *PLoS One* 7 (1), e29986.
- de Azevedo Menna, D.S., Graham, J., Garcés-García, K.C., Kuguru, G., 2022. Elasmobranch ecology and evolution. In: Minorities in Shark Sciences. CRC Press, pp. 35–70.
- de Kroon, H., Plaisier, A., van Groenendael, J., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67 (5), 1427–1431.
- Dowling, N.A., Smith, A.D., Smith, D.C., Parma, A.M., Dichmont, C.M., Sainsbury, K., Wilson, J.R., Dougherty, D.T., Cope, J.M., 2019. Generic solutions for data-limited fishery assessments are not so simple. *Fish. Fish.* 20 (1), 174–188.
- Drew, M., White, W.T., Dharmadi, Harry, A. V., Huvener, C., 2015. Age, growth and maturity of the pelagic thresher *Alopias pelagicus* and the scalloped hammerhead *Sphyrna lewini*. *J. Fish Biol.* 86 (1), 333–354. <https://doi.org/10.1111/jfb.12586>.
- Drymon, J.M., Wells, R.D., 2017. Double tagging clarifies post-release fate of great hammerheads (*Sphyrna mokarran*). *Animal Biotelemet.* 5, 1–7.
- Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Curr. Biol.* 31 (21), 4773–4787 (e4778).
- Duncan, K.M., Holland, K.N., 2006. Habitat use, growth rates, and dispersal patterns of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in a nursery habitat. *Mar. Ecol. Prog. Ser.* 312, 211–221.
- 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. *Mar. Ecol. Prog. Ser.* 667, 113–129.
- Ebert, T.A., 1999. Plant and Animal Populations. Academic Press San Diego, California.
- Estupiñán-Montaña, C., Cedeño-Figueroa, L., Estupiñán-Ortiz, J.F., Galván-Magaña, F., Sandoval-Londoño, A., Castañeda-Suarez, D., Polo-Silva, C.J., 2019. Feeding habits and trophic level of the smooth hammerhead shark, *Sphyrna zygaena* (Carcharhiniformes: Sphyrnidae), off Ecuador. *J. Mar. Biol. Assoc. U. K.* 99 (3), 673–680.
- Faggion, S., Vandeputte, M., Vergnet, A., Clota, F., Blanc, M.-O., Sanchez, P., Ruelle, F., Allal, F., 2021. Sex dimorphism in European sea bass (*Dicentrarchus labrax* L.): new insights into sex-related growth patterns during very early life stages. *PLoS One* 16 (4), e0239791.
- Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Can. J. Fish. Aquat. Sci.* 58 (5), 969–981.
- Gallagher, A.J., Klimley, A.P., 2018. The biology and conservation status of the large hammerhead shark complex: the great, scalloped, and smooth hammerheads. *Rev. Fish Biol. Fish.* 28 (4), 777–794.
- Gallagher, A.J., Hammerschlag, N., Shiffman, D.S., Giery, S.T., 2014. Evolved for extinction: the cost and conservation implications of specialization in hammerhead sharks. *Bioscience* 64 (7), 619–624.
- Gallucci, V.F., Taylor, I.G., Erzini, K., 2006. Conservation and management of exploited shark populations based on reproductive value. *Can. J. Fish. Aquat. Sci.* 63 (4), 931–942.
- García, E.Q., Zuanon, J., 2019. Sexual dimorphism in the electric knifefish, *Gymnorhamphichthys rondoni* (Rhamphichthyidae: Gymnotiformes). *Acta Amazon.* 49, 213–220.
- Gayaniño, F.C., Sparre, P., 2005. FAO-ICLARM Stock Assessment Tools II: User's Guide. Food & Agriculture Org.
- Geng, Z., Wang, Y., Kindong, R., Zhu, J., Dai, X., 2021. Demographic and harvest analysis for blue shark (*Prionace glauca*) in the Indian Ocean. *Reg. Stud. Mar. Sci.* 41, 101583.
- Goethel, D.R., Omori, K.L., Punt, A.E., Lynch, P.D., Berger, A.M., de Moor, C.L., Plagányi, É.E., Cope, J.M., Dowling, N.A., McGarvey, R., 2022. Oceans of plenty? Challenges, advancements, and future directions for the provision of evidence-based fisheries management advice. *Rev. Fish Biol. Fish.* 1–36.
- Gompertz, B., 1825. XXIV. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. In a letter to Francis Baily. *Esq. FRS & C. Philos. Trans. R. Soc. Lond.* 115, 513–583.
- Grant, M.I., Smart, J.J., Rigby, C.L., White, W.T., Chin, A., Baje, L., Simpfendorfer, C.A., 2020. Intraspecific demography of the silky shark (*Carcharhinus falciformis*): implications for fisheries management. *ICES J. Mar. Sci.* 77 (1), 241–255.
- Gross, M., 2023. Sharks face the jaws of extinction. *Curr. Biol.* 33 (3), R85–R87.
- Gulak, S., de Ron Santiago, A., Carlson, J., 2015. Hooking mortality of scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. *Afr. J. Mar. Sci.* 37 (2), 267–273.
- Hammerschlag, N., Sulikowski, J., 2011. Killing for conservation: the need for alternatives to lethal sampling of apex predatory sharks. *Endanger. Species Res.* 14 (2), 135–140.
- Harry, A.V., Macbeth, W.G., Gutteridge, A.N., Simpfendorfer, C.A., 2011. The life histories of endangered hammerhead sharks (*Carcharhiniformes*, *Sphyrnidae*) from the east coast of Australia. *J. Fish Biol.* 78 (7), 2026–2051. <https://doi.org/10.1111/j.1095-8649.2011.02992.x>.
- Hayes, C.G., Jiao, Y., Cortés, E., 2009. Stock assessment of scalloped hammerheads in the western North Atlantic Ocean and Gulf of Mexico. *N. Am. J. Fish Manag.* 29 (5), 1406–1417.
- Heppell, S.S., Crowder, L.B., Menzel, T.R., Musick, J., 1999. Life table analysis of long-lived marine species with implications for conservation and management. *Am. Fish. Soc. Symp.* 23, 137–148.
- Heppell, S., Pfister, C., de Kroon, H., 2000. Elasticity analysis in population biology: methods and applications [1]. *Ecology* 81 (3), 605.
- 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 (9), e25028.
- Hood, G., 2010. PopTools, Version 3.2.3. <http://www.poptools.org>.
- Hüssy, K., Coad, J.O., Farrell, E.D., Clausen, L.W., Clarke, M.W., 2012. Sexual dimorphism in size, age, maturation, and growth characteristics of boarfish (*Capros aper*) in the Northeast Atlantic. *ICES J. Mar. Sci.* 69 (10), 1729–1735.
- Huynh, H.H., Hung, C.-Y., Tsai, W.-P., 2022. Demographic analysis of shortfin mako shark (*Isurus oxyrinchus*) in the South Pacific Ocean. *Animals* 12 (22), 3229.
- Jenouvrier, S., Caswell, H., Barbraud, C., Weimerskirch, H., 2010. Mating behavior, population growth, and the operational sex ratio: a periodic two-sex model approach. *Am. Nat.* 175 (6), 739–752.
- Kenchington, T.J., 2014. Natural mortality estimators for information-limited fisheries. *Fish. Fish.* 15 (4), 533–562. <https://doi.org/10.1111/faf.12027>.
- Keyombe, J.L., Waitthaka, E., Obegi, B., 2015. Length–weight relationship and condition factor of *Clarias gariepinus* in Lake Naivasha, Kenya. *Int. J. Fish. Aquat. Stud.* 2 (6), 382–385.
- Klimley, A.P., 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environ. Biol. Fish.* 18, 27–40.
- Kokko, H., Rankin, D.J., 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosoph. Trans. Royal Soc. B: Biol. Sci.* 361 (1466), 319–334.
- Kotas, J.E., Mastrochirico, V., Petrere Junior, M., 2011. Age and growth of the scalloped hammerhead shark, *Sphyrna lewini* (Griffith and Smith, 1834), from the southern Brazilian coast. *Braz. J. Biol.* 71 (3), 755–761. <https://doi.org/10.1590/s1519-69842011000400022>.
- Krebs, C.J., 1985. Ecology; the Experimental Analysis of Distribution and Abundance.
- Le Cren, E.D., 1951. The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.* 201–219.
- Liu, S.T., 2002. Reproductive Biology of the Smooth Hammerhead, *Sphyrna zygaena*, in Northeastern Taiwanese Waters. Master Thesis, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University.
- Liu, K.-M., Chen, C.-T., 1999. Demographic analysis of the scalloped hammerhead, *Sphyrna lewini*, in the northwestern Pacific. *Fish. Sci.* 65 (2), 218–223.
- 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>.
- Liu, O.R., Thomas, L.R., Clemence, M., Fujita, R., Kritzer, J.P., McDonald, G., Szuwalski, C., 2016. An evaluation of harvest control methods for fishery management. *Rev. Fish. Sci. Aquacult.* 24 (3), 244–263.
- Liu, K.M., Huang, L.H., Su, K.Y., Joung, S.J., 2021. Vulnerability assessment of pelagic sharks in the Western North Pacific by using an integrated ecological risk assessment. *Animals (Basel)* 11 (8). <https://doi.org/10.3390/ani11082161>.
- Liu, K.-M., Huang, L.-H., Su, K.-Y., 2022. Assessment of the impact on 20 pelagic fish species by the Taiwanese small-scale longline fishery in the Western North Pacific using ecological risk assessment. *Animals* 12 (16), 2124.
- 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.
- Ludwig, D., Hilborn, R., Walters, C., 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260 (5104), 17–36.
- Macaluso, J., 1999. Red snapper season offered. *Advocate* 14.
- Mauder, M.N., Hamel, O.S., Lee, H.-H., Piner, K.R., Cope, J.M., Punt, A.E., Ianelli, J.N., Castillo-Jordan, C., Kapur, M.S., Method, R.D., 2023. A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. *Fish. Res.* 257, 106489.

- Method Jr., R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fish. Res.* 142, 86–99.
- Mildenberger, T.K., Berg, C.W., Kokkalis, A., Hordyk, A.R., Wetzel, C., Jacobsen, N.S., Punt, A.E., Nielsen, J.R., 2022. Implementing the precautionary approach into fisheries management: biomass reference points and uncertainty buffers. *Fish. Fish.* 23 (1), 73–92.
- Miller, T.E., Inouye, B.D., 2011. Confronting two-sex demographic models with data. *Ecology* 92 (11), 2141–2151.
- Mollet, H., Cailliet, G., 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Mar. Freshw. Res.* 53 (2), 503–515.
- Omori, K.L., Hoenig, J.M., Luehring, M.A., Baier-Lockhart, K., 2016. Effects of overestimating catch and effort on surplus production models. *Fish. Res.* 183, 138–145.
- Pacoureau, N., Carlson, J.K., Kindsvater, H.K., Rigby, C.L., Winker, H., Simpfendorfer, C.A., Charvet, P., Pollom, R.A., Barreto, R., Sherman, C.S., 2023. Conservation successes and challenges for wide-ranging sharks and rays. *Proc. Natl. Acad. Sci.* 120 (5), e2216891120.
- 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.
- Pauly, D., 1983. Some Simple Methods for the Assessment of Tropical Fish Stocks, vol. No. 234. FAO, Rome, Italy.
- Pauly, D., 1984. Fish Population Dynamics in Tropical Waters: A Manual for Use with Programmable Calculators, vol. 8. WorldFish.
- Peterson, I., Wroblewski, J., 1984. Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41 (7), 1117–1120.
- Punt, A.E., 2023. Those who fail to learn from history are condemned to repeat it: A perspective on current stock assessment good practices and the consequences of not following them. *Fish. Res.* 261, 106642.
- Punt, A.E., Cope, J.M., Haltuch, M.A., 2008. Reference Points and Decision Rules in US Federal Fisheries: West Coast Groundfish Experiences. American Fisheries Society Symposium.
- Punt, A.E., Dunn, A., Elvarsson, B.P., Hampton, J., Hoyle, S.D., Maunder, M.N., Methot, R.D., Nielsen, A., 2020. Essential features of the next-generation integrated fisheries stock assessment package: a perspective. *Fish. Res.* 229, 105617.
- Punt, A.E., Castillo-Jordán, C., Hamel, O.S., Cope, J.M., Maunder, M.N., Ianelli, J.N., 2021. Consequences of error in natural mortality and its estimation in stock assessment models. *Fish. Res.* 233, 105759.
- R Development Core, 2022. A Language and Environment for Statistical Computing.** <http://www.R-project.org>.
- Regular, P.M., Buren, A.D., Dwyer, K.S., Cadigan, N.G., Gregory, R.S., Koen-Alonso, M., Rideout, R.M., Robertson, G.J., Robertson, M.D., Stenson, G.B., 2022. Indexing starvation mortality to assess its role in the population regulation of northern cod. *Fish. Res.* 247, 106180.
- Reid, D., Robbins, W., Peddemors, V., 2011. Decadal trends in shark catches and effort from the New South Wales, Australia, shark meshing program 1950–2010. *Mar. Freshw. Res.* 62 (6), 676–693.
- Ricker, W., 1979. Growth rates and models. *Fish. Physiol.* 677–744.
- Rigby, C.L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Herman, K., Jabado, R.W., Liu, K.M., Marshall, A., et al., 2019. *Sphyrna mokarran*; the IUCN red list of threatened species 2019: e.T39386A2920499. In: International Union for Conservation of Nature and Natural Resources: Gland, Switzerland, 2019.
- Rose, G.A., Walters, C.J., 2019. The state of Canada's iconic northern cod: a second opinion. *Fish. Res.* 219, 105314.
- Rose, K.A., Cowan Jr., J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish. Fish.* 2 (4), 293–327.
- Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K.B., Barbraud, C., Becker, P.H., Blumstein, D.T., Dobson, F.S., 2013. How life history influences population dynamics in fluctuating environments. *Am. Nat.* 182 (6), 743–759.
- Schrey, A.W., Heist, E.J., 2003. Microsatellite analysis of population structure in the shortfin mako (*Isurus oxyrinchus*). *Can. J. Fish. Aquat. Sci.* 60, 670–675.
- Semba, Y., 2018. Significance of sex-specific ecological and life history traits on the sustainable exploitation of sharks. *Fish. Populat. Dynam., Monit., Manag.: Sustain. Fish. Etern. Ocean* 77–104.
- Semba, Y., Nakano, H., Aoki, I., 2009. Age and growth analysis of the shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific Ocean. *Environ. Biol. Fish.* 84, 377–391.
- Semba, Y., Aoki, I., Yokawa, K., 2011. Size at maturity and reproductive traits of shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific. *Mar. Freshw. Res.* 62 (1), 20–29.
- Shan-Hui, S., Liu, S.-Y.V., Liu, K.M., Tsai, W.P., 2020. Development and characterization of novel microsatellite loci for an endangered hammerhead shark *Sphyrna lewini* by using shotgun sequencing. *Taiwania* 65 (2).
- Sherman, C.S., Simpfendorfer, C.A., Pacoureau, N., Matsushiba, J.H., Yan, H.F., Walls, R. H., Rigby, C.L., VanderWright, W.J., Jabado, R.W., Pollom, R.A., 2023. Half a century of rising extinction risk of coral reef sharks and rays. *Nat. Commun.* 14 (1), 15.
- Shr, J.L., 2020. Age and Growth of Scalloped Hammerhead (*Sphyrna lewini*) in the Northeastern Taiwan Waters. Master Thesis, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University.
- Simpfendorfer, C.A., 2005. 9. Demographic models: life. *Manag. Techniq. Elasmobranch Fisher.* 474, 143.
- 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. *Fish. Res.* 191, 95–107.
- Sparre, P., Venema, S., 1998. Introduction to tropical fish stock assessment (1998) manual. FAO Fish. Tech. Pap. 306 (1), 1–440.
- Stevens, J., 1984. Biological observations on sharks caught by sport fisherman of New South Wales. *Mar. Freshw. Res.* 35 (5), 573–590.
- Stevens, J., Lyle, J., 1989. Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from northern Australia. *Mar. Freshw. Res.* 40 (2), 129–146.
- Stevens, J., Bonfil, R., Dulvy, N.K., Walker, P., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* 57 (3), 476–494.
- Takeuchi, Y., Senba, Y., Nakano, H., 2005. Demographic analysis on Atlantic blue and shortfin mako sharks. *Collect. Vol. Sci. Pap. ICCAT* 58 (3), 1157–1165.
- Talwar, B.S., Anderson, B., Avalos-Castillo, C.G., del Pilar Blanco-Parra, M., Briones, A., Cardena, D., Carlson, J.K., Charvet, P., Cotton, C.F., Cryslar, Z., 2022. Extinction risk, reconstructed catches and management of chondrichthyan fishes in the Western Central Atlantic Ocean. *Fish. Fish.* 23 (5), 1150–1179.
- Taylor, C.C., 1958. Cod growth and temperature. *ICES J. Mar. Sci.* 23 (3), 366–370.
- Then, A.Y., Hoenig, J.M., Hall, N.G., Hewitt, D.A., Jardim, H.E.E., 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES J. Mar. Sci.* 72 (1), 82–92.
- Tsai, W.P., Huang, C.H., 2022. Data-limited approach to the management and conservation of the pelagic thresher shark in the Northwest Pacific. *Conserv. Sci. Practice* 4 (6), e12682.
- Tsai, W.-P., Liu, K.-M., Joung, S.-J., 2010. Demographic analysis of the pelagic thresher shark, *Alopias pelagicus*, in the North-Western Pacific using a stochastic stage-based model. *Mar. Freshw. Res.* 61 (9), 1056–1066.
- Tsai, W.-P., Sun, C.-L., Punt, A.E., Liu, K.-M., 2014. Demographic analysis of the shortfin mako shark, *Isurus paucus*, in the Northwest Pacific using a two-sex stage-based matrix model. *ICES J. Mar. Sci.* 71 (7), 1604–1618.
- Tsai, W.-P., Liu, K.-M., Punt, A.E., Sun, C.-L., 2015. Assessing the potential biases of ignoring sexual dimorphism and mating mechanism in using a single-sex demographic model: the shortfin mako shark as a case study. *ICES J. Mar. Sci.* 72 (3), 793–803.
- Tsai, W.-P., Wu, J.-R., Yan, M.-Z., Liu, K.-M., 2018. Assessment of biological reference points for management of the smooth hammerhead shark, *Sphyrna zygaena*, in the Northwest Pacific Ocean. *J. Fish. Soc. Taiwan* 45 (1), 29–41.
- Tsai, W.P., Chang, Y.J., Liu, K.M., 2019. Development and testing of a Bayesian population model for the bigeye thresher shark, *Alopias superciliosus*, in an area subset of the western North Pacific. *Fish. Manag. Ecol.* 26 (3), 269–294.
- 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* 12 (20), 8646.
- Tucker, A.M., McGowan, C.P., Mulero Oliveras, E.S., Angeli, N.F., Zegarra, J.P., 2021. A demographic projection model to support conservation decision making for an endangered snake with limited monitoring data. *Anim. Conserv.* 24 (2), 291–301. <https://doi.org/10.1111/acv.12641>.
- Ward, R.D., Gardner, M.G., 1997. Stock Structure and Species Identification of School and Gummy Shark in Australian Waters. CSIRO, Hobart, Tasmania.
- White, W.T., Bartron, C., Potter, I.C., 2008. Catch composition and reproductive biology of *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes, Sphyrnidae) in Indonesian waters. *J. Fish Biol.* 72 (7), 1675–1689. <https://doi.org/10.1111/j.1095-8649.2008.01843.x>.
- Wickham, H., Chang, W., Wickham, M.H., 2016. Package 'ggplot2'. Create Elegant Data Visualisations Using the Grammar of Graphics. Version, 2 (1), pp. 1–189.
- Wu, J.R., 2019. Demographic Analysis and Risk Assessment of the Scalloped Hammerhead Shark (*Sphyrna lewini*) in the Pacific Ocean. Department of Production and Management, National Kaohsiung University of Science and Technology, Master Thesis.
- Yokoi, H., Ijima, H., Ohshimo, S., Yokawa, K., 2017. Impact of biology knowledge on the conservation and management of large pelagic sharks. *Sci. Rep.* 7 (1), 10619.
- Zhang, C.-I., Megrey, B.A., 2006. A revised Alvenson and carney model for estimating the instantaneous rate of natural mortality. *Trans. Am. Fish. Soc.* 135 (3), 620–633.