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# Demographic and harvest analysis for blue shark (*Prionace glauca*) in the Indian Ocean

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ABSTRACT

An estimate of the population growth rate ($\gamma$) is an essential biological information that can be input into stock assessment models to estimate management quantities for commercial fisheries. Demographic analysis conducted using the Leslie matrix method was used to estimate $\gamma$ for Indian Ocean blue shark (*Prionace glauca*), with Monte Carlo simulation used to quantify uncertainty. A harvest analysis was conducted with various selectivity patterns. The results indicated that the productivity of the blue shark was high, with $\gamma = 0.26$–$0.32\ \text{y}^{-1}$ under the assumption of a one-year reproductive cycle. The steepness of the Beverton–Holt stock-recruitment model was estimated to be 0.72 (0.24–0.87) when the Castro and Mejuto fecundity formular was assumed, and 0.80 (0.65–0.88) when the Fujinami et al. fecundity formular was assumed. Harvest analysis with tuna longline selectivity led to lower sustainable harvest rates, but a higher proportion of biomass removed compared to the selectivity patterns for other fisheries. This study provides crucial prior information on the population growth rate and steepness parameters, which can be incorporated into stock assessments for blue shark. Besides, harvest analysis could be a supplement for data-poor stock assessment and risk analysis, to evaluate a tradeoff among different fisheries when considering a management strategy.

## 1. Introduction

Blue shark (*Prionace glauca*; BSH) is one of the most common bycatch species in pelagic tuna and swordfish longline fisheries (Nakano and Stevens, 2008; Bustamante and Bennett, 2013). It was globally assessed as "Near Threatened" in the last IUCN (International Union for Conservation of Nature) assessment. The catch of blue shark decreased during the early 1990s due to the worldwide ban of high-seas drift gillnet fisheries, and there has been no significant increase in catches in the Pacific or Atlantic Oceans thereafter (ICCAT, 2015; ISC, 2017). Blue sharks were found to be neither overfished nor subject to overfishing in previous stock assessments in the Pacific (Takeuchi et al., 2016; ISC, 2017) and Atlantic Oceans (ICCAT, 2015).

Blue shark in the Indian Ocean was not being overfished but may be experiencing overfishing based on the last stock assessment by the Indian Ocean Tuna Commission (IOTC) in 2017 (Rice, 2017; IOTC, 2017). However, the Indian Ocean blue shark (IO BSH) has experienced high fishing pressure in recent years, and current catch risk might deplete the stock to overfished status relatively quickly (IOTC, 2017). Catches of IO BSH have been recorded since 1950"- in the IOTC database (https://www.iotc.org/node/4108) and increased steadily from 1950–2019.

The IOTC scientific committee (SC) has suggested using multiple assessment methods (e.g., biomass dynamics models and age-structured assessment models) to compare estimates of stock status for IO BSH and provide more comprehensive management advice. Biomass dynamics models (e.g., Bayesian biomass dynamics model) rely on a prior distribution for the intrinsic rate of population increase ($\gamma$), which needs to be estimated outside the assessment model. Age structured assessment models (e.g., Stock Synthesis) often require values for the steepness ($h$) of the stock-recruitment relationship (the expected proportion of unfished recruitment for a stock depleted to 20% of its unfished spawning biomass) as an input parameter, which is also difficult to estimate inside a stock assessment model (Zhu et al., 2012). Geng et al. (2020) have incorporated life history information into Bayesian surplus production model to describe the performance and consequence for generating the informative prior from a basic demographic analysis where some biological parameter (e.g. pups survival rate) were collected from operating model of their simulation not life history information. The aim of their research was not to present a detailed demographic analysis, and female-only analysis might not reflect size and sexual dimorphism for IO BSH. The parameters of $\gamma$ and $h$ have not been estimated for the IO BSH. Therefore, it is important to

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estimate these parameters to improve the assessment of IO BSH and develop management advice.

Steepness is a biological parameter defining the productivity of a population when the spawning size decreases. Therefore, theoretically, it can be estimated from life-history information, including maximum recruitment per spawning biomass and the slope of the unfished stock-recruitment relationship curve (Myers et al., 1999). Demographic analysis tends to perform better for long-lived and slow-growing shark species (Tribuzio and Kruse, 2011). Demographic analysis with only life history information (growth curve, fecundity, and survival at age) was used to estimate the intrinsic rate of population increase and steepness of elasmobranch species in the Pacific and the Atlantic Oceans (e.g., Takeuchi et al., 2005; Chen and Yuan, 2006; Tsai et al., 2010; Cortés, 2016). However, no demographic model has been developed for IO BSH to estimate $\gamma$ and related parameters.

The objectives of this study were to (1) estimate $\gamma$ and quantify the uncertainty of the estimate, (2) estimate steepness; and (3) investigate the influence of harvesting scenarios on achieving a stationary population trajectory for IO BSH. Uncertainty about the estimate of natural motility ($M$), a parameter of the demographic model, is a major source of uncertainty in this study. Therefore, we used several empirical methods to estimate $M$ and accounted for the uncertainty in the resulting estimates in the analyses.

## 2. Material and methods

### 2.1. Demographic method

Demographic analysis can be conducted using age- or size-structured population dynamics models and can be either female-only or for both sexes (Tsai et al., 2014). A two-sex Leslie population projection matrix (Caswell, 2006; Yokoi et al., 2017) was used to represent the demography of the IO BSH:

$$N_{t+1} = \mathbf{MH}N_t \tag{1}$$

where $N_t$ is the vector of numbers at each age in year t, and **H** is the harvest (or exploitation) matrix. For demographic analysis, **H** equal to 1 means unfished status; And for harvest analysis, H can be represented by the harvest survival rate (proportions of individuals surviving harvest). The matrix **M** is a Leslie population projection matrix:

$$\mathbf{M} = \begin{bmatrix} F_{0,m} & F_{1,m} & \dots & F_{max-1,m} & F_{0,f} & F_{1,f} & \dots & F_{max-1,f} & 0 \\ pS_{0,m} & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & S_{1,m} & \dots & 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & S_{max-1,m} & 0 & 0 & \dots & 0 & 0 \\ (1-p)S_{0,f} & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & S_{1,f} & \dots & 0 & 0 \\ \vdots & \vdots & \dots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & 0 & 0 & 0 & \dots & S_{max-1,f} & 0 \end{bmatrix} \tag{2}$$

where $S_x$ is the annual natural survivorship of age $x$ for male ($m$) and female ($f$). The $F_x$ elements represent the age-specific per-capita fecundity rates. The $p$ is the sex ratio in out study, and equal to 0.5 for the Indian Ocean blue shark (Coelho et al., 2018). A birth-pulse population and a post-breeding census were assumed (Caswell, 2006). Accordingly, the first age class (age 0) is represented by the newborn pups, and the fecundity ($F_x$) terms include the probability that a pregnant female survives and delivers pups at the end of the year (e.g, $F_x = L_x S_x$, where $L_x$ is the average number of female pups per female or male). The values for the $L_x$ were calculated as the number of pups per individual, which was then divided by the length of the reproductive cycle in years.

$L_x$ can be calculated by Eqs. (3) and (4) (Caswell, 2006; Yokoi et al., 2017), and we assumed monogamy and an equal litter size for both sexes (Tsai et al., 2014):

$$L_{x,sex} = \begin{cases} \dfrac{k_x R_f}{R_f + R_m} & sex = f \\ \dfrac{k_x R_m}{R_f + R_m} & sex = m \end{cases} \tag{3}$$

$$R_{sex} = \sum_{x=1}^{x_{max}} Mat_x n_{x,sex} \tag{4}$$

where $Mat_x$ is an knife-cut value(0 or 1) for maturation age and age-at-delivery of male and female respectively (e.g., if the age exceed maturation age, $Mat_x = 1$; else $Mat_x = 0$), $k_x$ is the litter size at age x, and $n_{x,sex}$ is the relative number of individuals of age x and $sex$ when population achieved stable stage. We generated the initial population of vector given by uniform random numbers $n_{x,sex} \sim$U[0,1], and calculated 3000 times stable projection matrix by repeated multiplication. More detail about how to calculated $n_{x,sex}$ can be found by Yokoi et al. research (2017).

According to matrix algebra $\mathbf{M}N_t = \lambda N_t$, where $\lambda$ is the eigenvalue of matrix **M.** Therefore, $\lambda$ is the finite rate of population increase, and $\gamma = \ln\lambda$ is the intrinsic rate of population increase. The value of $\lambda$ is determined by finding the dominant eigenvalue of **M** (Simpfendorfer et al., 2005). The underlying assumption of the matrix model (Equations and 2) is that the population will grow exponentially and reach a stable age distribution (*sad*) (Caswell, 2006). Therefore, to estimate $\gamma$ and its uncertainty, several biological parameters (e.g., growth and longevity) and their uncertainty need to be estimated, as described in the following sections.

The Beverton–Holt (B–H) and Ricker models are two conventional stock-recruitment relationships. The B–H model is based on the assumption of density-dependent mortality rather than abundance-dependent mortality. Based on Kai and Fujinami (2018) and previous stock assessments (Rice, 2017), it is reasonable to select the B–H model to estimate recruitment for blue shark. We follow Myers et al. (1999) and calculate the steepness $h$ of the B–H stock-recruit model using parameters from the demographic analysis:

$$\hat{\alpha} = \alpha \cdot SPR_{F=0} \tag{5}$$

$$h = \frac{\hat{\alpha}}{4 + \hat{\alpha}} \tag{6}$$

where represents the number of spawners produced by each spawner over its lifetime, $SPR_{F=0}$ is the spawning biomass-per-recruit at unfished equilibrium population size(obtained from $R_0$), and is the slope of the population at the origin(extremely low population size). For the B–H stock-recruitment curve, the also referred to the maximum density-independent survival, and could be derived from recruits and spawners (or pups). Therefore, Brooks et al. (2010) showed that for sharks where eggs could be counted, is equivalent to first-year (pups) survival. More theoretical and analytical details about estimation of steepness could be found in researches of Myers et al. (1999) and Brooks et al. (2010). All demographic and simulation analyses were coded in the R language for statistical computing.

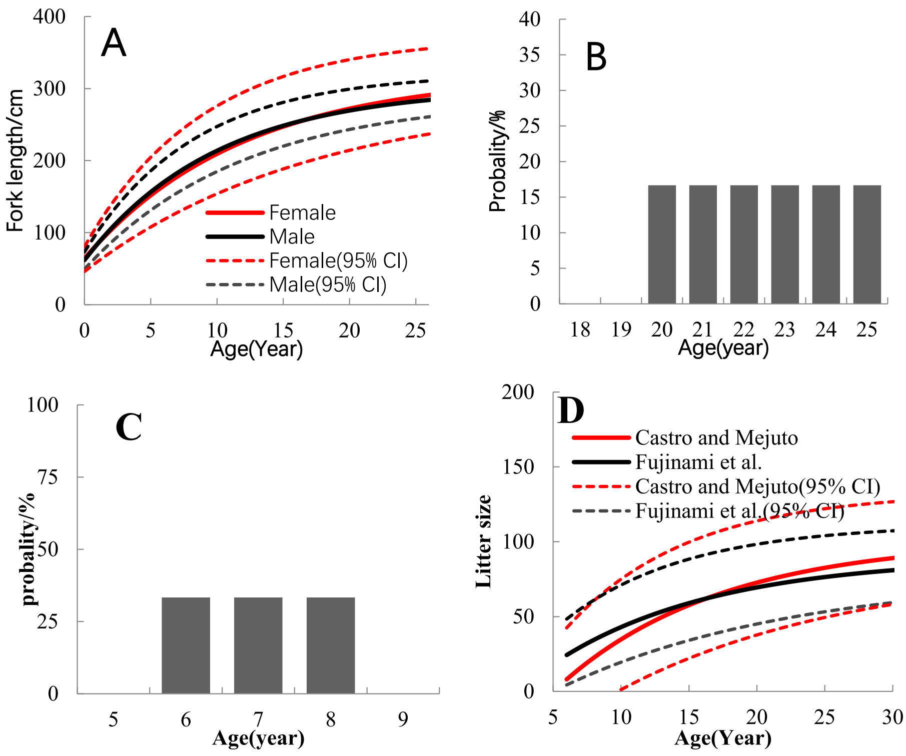

**Fig. 1.** Uncertainty in the life-history parameters (best estimates of 95% confidence intervals) for Indian Ocean blue shark: A, Length-at-age; B, Longevity; C, Age-at-delivery; D, Fecundity-at-age (Litter Size-Age model).

## 2.2. *Life-history parameters and uncertainty*

### 2.2.1. *Growth and longevity*

Few studies focused on the age and growth of IO BSH. Andrade et al. (2019) and Jolly et al. (2013) estimated the parameters of the von Bertalanffy growth model for this stock, with the latter being based on samples from the coastal areas of South Africa, which are unlikely to be representative of the entire IO BSH population.

Therefore, the growth parameter (and 95% CI) estimates for females and males from Andrade et al. (2019) (Fig. 1A) were used in this study: $L_\infty = 319.7$ (291.1–371.8) cm, $k = 0.084$ (0.058–0.111) $y^{-1}$, and $L_0 = 64.1$ (46.1–80.5) cm for female; $L_\infty = 302.0$ (287.6–321.2) cm, $k = 0.1$ (0.084–0.121) $y^{-1}$, and $L_0 = 61.9$ (49.4–73.3) cm for male.

Nakano and Stevens (2008) provided an estimate of longevity ($t_{max}$) of 20 yr for IO BSH. However, Andrade et al. (2017) reported the oldest individual was 25 years in the Indian Ocean. To integrate the uncertainty about longevity, we assumed a discrete uniform distribution of $U$ [20, 25] for $t_{\max}$ (Fig. 1B).

The weight ($W$, kg) and fork length ($FL$, cm) relationship for female blue sharks was assumed to follow that of Romanov and Romanova (2009) (Eq. (7)) :

$$W = 0.835 \times 10^{-5} \times FL^{2.972} \tag{7}$$

### 2.2.2. *Maturity and reproduction*

Pratt (1979) found that female blue sharks generally first become pregnant before five years of age and full sexual maturity is achieved at a 185 cm fork length (FL), which translates to 6 or 7 years using juvenile growth curves (Aires-da-Silva and Gallucci, 2007; Henderson et al., 2001). Sexual maturity is attained at about 4 - 7 years for males (Nakano, 1994; Jolly et al., 2013). In this study, age-at-maturity was replaced by age-at-delivery, which represents the age at which females first produce pups, i.e. the age-at-maturity plus the gestation period (∼12 months for this species). Reproduction studies in the Atlantic Ocean all favor an annual reproductive cycle ($RC$), both for the re-examined North Atlantic (Pratt, 1979) and the South Atlantic (Hazin et al., 1994; Montealegre-Quijano, 2007) and the Pacific Ocean (Fujinami et al., 2017; Nakano and Stevens, 2008). We thus assumed a one-year $RC$ in this study. We assumed a discrete uniform distribution of $U$ (6, 8) for the age-at-delivery of females (Fig. 1C), and U[4, 7] for the age-at-maturity of males. Fecundity is an essential parameter for demographic analysis. Castro and Mejuto (1995) found a positive linear relationship between fecundity (litter size, $LS$) and fork length for blue shark, i.e.:

$$LS = -91.97 + 0.6052 \times FL \tag{8}$$

To cover more uncertainty of the life history information for blue shark, another fecundity formula (Eq. (9)) was included in this study (Fujinami et al., 2017).

$$LS = -45.64 + 0.4232 \times FL \tag{9}$$

We used Eqs. (8) and (9), and the growth function of Andrade et al. (2017) to generate a relationship between litter size and age (hereafter litter size-age model; Fig. 1D). The sex ratio at birth was assumed to be 1:1, as suggested by several studies (e.g., Hazin et al., 1994; Castro and Mejuto, 1995). Input life history information and their references were list in Table 1.

### 2.2.3. *Natural mortality and survival rate*

Age-specific survival rate ($S_t$) is defined as:

$$S_t = e^{-Mt} \tag{10}$$

where $M_t$ is the (instantaneous) natural morality for age t. Natural mortality is often difficult to estimate so it is often the primary source of uncertainty in population dynamics modeling. Consequently, we considered four empirical methods to estimate $M$:

(1) The Then et al. (2015) method, which updated Hoenig's (1983) method, i.e., $M = 4.899{t_{max}}^{-0.916}$;

**Table 1**
Input life history information of the Indian Ocena blue shark.

| Parameter | Value | | Reference |
|---|---|---|---|
| | Female | Male | |
| $L_\infty$(cm) | 319.7 (291.1–371.8) | 302.0 (287.6–321.2) | Andrade et al. (2017) |
| $k$ ( $y^{-1}$) | 0.084 (0.058–0.111) | 0.1 (0.084–0.121) | Andrade et al. (2017) |
| $L_0$ (cm) | 64.1 (46.1–80.5) | 61.9 (49.4–73.3) | Andrade et al. (2017) |
| Longevity (yr) | U[20, 26] | | Andrade et al. (2017) |
| Weight (kg)-at-length (cm) | $W = 0.835 \times 10^{-5} \times FL^{2.972}$ | | Romanov and Romanova (2009) |
| Age-at-delivery (yr) | U[6, 8] | NA | Pratt (1979) |
| Age-at-maturity (yr) | NA | U[4, 7] | Pratt (1979), Hazin et al. (1994) and Montealegre-Quijano (2007) |
| Fecundity (litter size) | $LS = -91.97 + 0.6052 \times FL$<br>$LS = -45.64 + 0.4232 \times FL$ | | Castro and Mejuto (1995)<br>Fujinami et al. (2017) |
| Reproductive cycle | One-year | | Henderson et al. (2001)<br>Aires-da-Silva and Gallucci (2007)<br>Fujinami et al. (2017) |

(2) The Jensen (1996) method, which estimates $M$ based on the age-at-maturity($t_{mat}$; the age-at-delivery less gestation period), i.e., $M = \frac{1.65}{t_{mat}}$;

(3) The Chen and Watanabe's (1989) method, which estimates $M$ based on a relationship between $M$ and the growth parameters (including their uncertainty) and age at maturity.

Methods (1) - (2) calculates an age-independent value for $M$ while method (3) calculate age-specific $M$ values.

### 2.2.4. Accounting for uncertainty

The consequences of uncertainty regarding the life-history parameters were captured using Monte Carlo simulation. This involves estimating the distribution of $M$ (age-invariant or age-specific) for each method from the sampling of life history parameters (e.g. $L_{inf}$, $L_0$, age-at-maturity, longevity, etc.) in their distribution, each set of $M$ being calculated from once sampling. A total of 4000 vectors of $M$-at-age (referred to as "ALL methods") were obtained based on 1000 vectors for each method. Except estimation of each set of $M$ mimic the uncertainty from the life history, and $n_{x,sex}$, an vector parameter for calculating the fecundity per age by sex, would be influenced by this sampling as well.

Triangular distribution (probability density functions, *pdf*) was assumed for annual survival at age (Caswell, 2006). The triangular distribution can be used to represent the uncertainty in life-history parameters before stochastic demographic analysis is conducted (Cortés, 2002, 2008). This distribution is particularly convenient because it allows a lower and upper bound for the parameter and the assignment of a most likely value between this range(Aires-da-Silva and Gallucci, 2007). Although lognorm distribution had been selected as an alternative distribution in some study, it usually lead to a similar result, especially for the measures of central tendency (Cortés, 2002; Aires-da-Silva and Gallucci, 2007). Therefore, only triangular distribution was used in this study.

For each age, the lowest and highest estimates of survival rates derived from the above 4,000 $M$ estimates were taken as the bounds, and the mean value was assumed as the most likely value in the triangular distributions. The *pdfs* calculated was used as the survival rates in this demographic analysis. Beside, scenario one and two used fecundity formulas of Castro and Mejuto (1995) and Fujinami et al. (2017) to reflect uncertainty respectively.

### 2.2.5. Scenarios of demographic analysis

The key output of the demographic analysis is the intrinsic rate of population increase ($\gamma$). The uncertainty of $\gamma$ arises from the uncertainties in the life-history parameters. In this study, two scenarios were developed to investigate the impacts of uncertainty about survivorship on the estimates of $\gamma$, i.e., the triangular distribution for scenario one and lognormal distribution for scenario two. For each scenario, 10,000 Monte Carlo simulations were run by sampling from the generated life-history parameters and hence maturity-at-age, fecundity-at-age, maximum age, and age-at-maturity Distributions for four demographic parameters, i.e., the intrinsic rate of population increase ($\gamma$), net reproductive rate ($R_0$), generation time ($G$), and population doubling time ($t_{x2}$) were estimated based on the methods and definitions in Aires-da-Silva and Gallucci (2007).

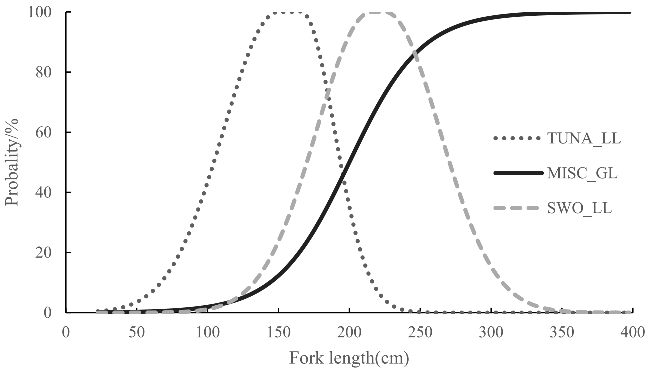

**Fig. 2.** Selectivity curves for Indian Ocean blue shark.

### 2.2.6. Harvest analysis

Demographic analysis is different from traditional full stock assessment since the input is only biological information and it cannot make the harvest control rule or total annual catch directly. However, harvest analysis can be used to investigate the influence of the different management strategy. The principle is changing harvest survival rate based on different management strategy, and finding a maximum harvest rate ($H_{\mathrm{MSY}}$) leading to a $\lambda$ equal to one where the stock can be sustained. Given the actual harvest rate by age is the product of the $H_{\mathrm{MSY}}$ and selectivity per age, $H_{\mathrm{MSY}}$ might exceed 100% for some fisheries, however actual harvest rate per age would be limited to a value lower than 1.

Demographic analysis commonly assumes knife-edged selectivity at an age-at-first-capture ($t_c$) when conducting projections (e.g. Aires-da-Silva and Gallucci, 2007). Such selectivity curves might be appropriate for gillnet (when catching small pelagic fish) and trawl fisheries. However, for longline fisheries, a key source of mortality for IO BSH, are often assumed to have dome-shaped selection patterns. According to the latest assessment of IO BSH (Rice, 2017) and IOTC annual report (IOTC, 2017), three fleets, pelagic longline targeting swordfish (SWO_LL) and tuna

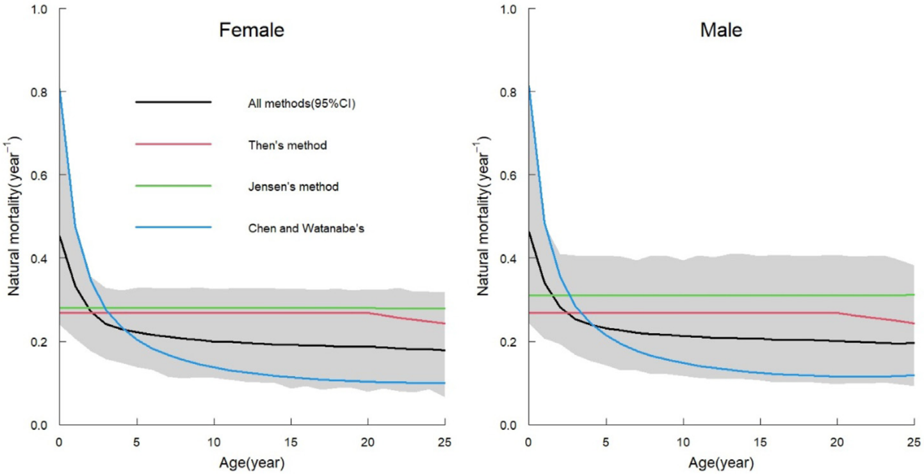

**Fig. 3.** The mean of survivorship by sex (thick line) estimated by different methods with 95% confidence intervals (the gray area represents uncertainty around “All methods”).

(TUNA_LL), and coastal gillnet (refer to MISC_GL), has generally been considered as major fisheries for IO BSH. In this study, selectivity for these three fleets was based on Rice (2017) (Fig. 2).

Narrow selectivity patterns such as TUNA_LL might result in extremely high harvest rates for full-selected animals. It is appropriate to include an alternative to evaluating the influence of fishing on the entire population size an adjusted stationary harvest (proportion removed, *PR*) was computed (Breen and Cook, 2002),

$$PR_j = \sum_{a=1}^{t_{max}} Sel_{a,j} * us_{a,j} * sad_{a,j} \qquad (11)$$

where $Sel_{a,j}$ is the percentage of selectivity of fleet $j$ at age $a$, and *sad* is the percentage of age structure under stationary harvest.

## 3. Results

### 3.1. Natural mortality estimate

The natural mortality estimates from different methods are shown in Fig. 3. The methods of Chen and Watanabe lead to higher estimates of natural mortality for younger individuals. The range of the mean (overage) of $M$ from various methods was 0.11–0.28 $y^{-1}$ and 0.12–0.32 $y^{-1}$ for female and male respectively (animals older than five years). The natural mortality rate for females of age 0 ($M_0$) estimated using the “Chen and Watanabe” and “ALL methods” were 0.80 $y^{-1}$ and 0.45 $y^{-1}$, and for male were 0.81 $y^{-1}$ and 0.46 $y^{-1}$ respectively. For the uncertainty around “All methods”, males have higher uncertainty than female, especially for the larger upper bound of the 95% confidence intervals.

Fig. 3 showed the probability distribution of survivorship at ages 0 to 5 years, and 24 to 25 years estimated from “ALL methods”, suggesting there is no noticeable change with increasing age above age 3(Fig. 3). For both sex, the greatest variance was the same for ages zero, and the least variance was the same for age two as well.

### 3.2. Demographic analysis

The estimates of demographic parameters for IO BSH are listed in Table 2. It is interesting to note that when assuming the Castro and Mejuto (1995) fecundity formular (scenario one), the net reproductive rate ($R_0$) and $\gamma$ were significantly lower than those in scenario two, equal to 21.16 and 0.26, respectively. When Fujinami et al. (2017). fecundity formular was assumed, $G$ and $t_{x2}$ increased and decreased, respectively. The distribution of $\gamma$ for each scenario is shown in Fig. 4. Scenario 2 will lead to a higher and more narrow distribution for $\gamma$; the most probable values for $\gamma$ were 0.26 and 0.33 estimated by scenario 1 and 2, respectively.

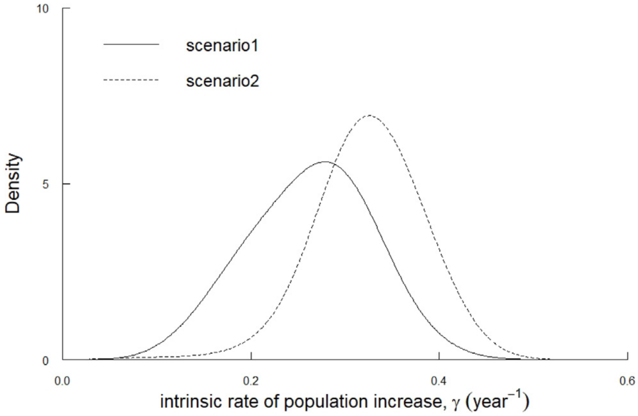

**Fig. 4.** Probability distributions of $\gamma$ in different scenarios.

**Table 2**
Result of demographic parameters for Indian Ocean blue shark.

| Parameters | Scenario 1 | | | Scenario 2 | | |
|---|---|---|---|---|---|---|
| | Mean | Lower | Upper | Mean | Lower | Upper |
| $\gamma$ | 0.26 | 0.14 | 0.38 | 0.33 | 0.22 | 0.43 |
| $R_0$ | 21.16 | 2.08 | 42.44 | 28.24 | 12.37 | 45.24 |
| $G$ | 11.04 | 3.17 | 14.98 | 10.23 | 8.67 | 11.96 |
| $t_{x2}$ | 2.82 | 1.83 | 5.04 | 2.21 | 1.65 | 3.20 |

Lower and Upper denote the lower and upper bounds of the 95% confidence interval respectively.

The estimated steepness (95% CI) was 0.72(0.24–0.87) for scenario 1 and 0.80 (0.65–0.88) for scenario 2. The Fujinami et al. (2017) fecundity formular would lead to an obvious increase in steepness estimates (Fig. 5).

### 3.3. Harvest analysis

The distribution of stationary harvest rates and the proportion removed associated with each fishery are shown in Figs. 6–7,

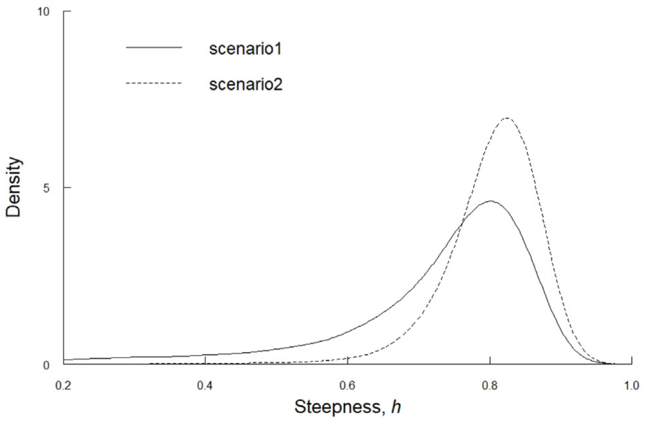

**Fig. 5.** Probability distributions of steepness *h* from different scenarios.

respectively. Scenario 2 can lead to higher estimation than the scenario 1, but due to the similar trend between them and just different magnitude, we only describe the results based on Scenario 1 here and more detailed result can be found in Table 3. For scenario 1, the highest stationary harvest rate (mean = 0.75; 95% CI: 0.31–1.35) was obtained by fishery MISC_GL. TUNA_LL (mean = 0.39; 95% CI: 0.24–0.49) and SWO_LL (mean = 0.83; 95% CI: 0.30 – 1.83) had similar mean values, however, the former had a more narrow range of value.

Comparing the proportion removed of the number of blue shark when fleets operated at their harvest rate, the TUNA_LL captured significantly more (mean = 0.13; 95% CI: 0.09–0.16) than MISC_GL (mean = 0.09, 95% CI: 0.05–0.12) or SWO_LL (mean = 0.05, 95% CI: 0.03–0.08), which were similar and had upper limits less than 0.1.

## 4. Discussion

### 4.1. Natural mortality

As for many aquatic species, estimation of natural mortality for blue shark relies on empirical methods. The estimates of $M$ (across age and maturity status) for adult female IO BSH were 0.11–0.28 $\text{y}^{-1}$ and for adult male were 0.12–0.32 $\text{y}^{-1}$, close to the estimates in other areas. For example, Nakano (1994) estimated the $M$ for blue shark in the North Pacific Ocean to be 0.17–0.21 $\text{y}^{-1}$, while, the $M$ was estimated at 0.20 $\text{y}^{-1}$ by Takeuchi et al. (2005) and 0.24 $\text{y}^{-1}$ by Chen and Yuan (2006) for blue shark in the Atlantic.

Branstetter (1990) showed that young blue sharks tend to have higher natural mortality than older animals; therefore, the assumption of age-independent $M$ may not be realistic. The methods of Chen and Watanabe (1989) produced quite a different estimate of $M$ for young blue sharks, e.g., $M_0 = 0.80\ \text{y}^{-1}$ and 0.81 $\text{y}^{-1}$ for female and male, respectively. Integrating three methods for estimating $M$ led an average value of 0.45–0.46 $\text{y}^{-1}$, higher than that estimated by Aires-da-Silva and Gallucci (2007) (0.4 $\text{y}^{-1}$) for blue shark the North Atlantic.

### 4.2. Population growth rate and steepness

This study is the first to estimate the population growth rate for IO BSH using a demographic method. Geng et al. (2020) has conducted a demographic analysis for IO BSH to make a simulation test, however them get the pups survival rate from steepness through know operating model not indirectly from the real life history information. IO BSH was found to be relatively productive, with an intrinsic rate of population increase of 0.26–0.33. As $\gamma$ is equal to $\lambda$ (finite rate of population increase) after log-transformation (Caswell, 2006), $\lambda$ of the IO BSH was estimated to be 1.30–1.39. Using the demographic approach, Takeuchi et al. (2005) and Chen and Yuan (2006) estimated $\gamma$ for blue shark in the North Atlantic Ocean to be 0.34 $\text{y}^{-1}$ and 0.35 $\text{y}^{-1}$, respectively. Aires-da-Silva and Gallucci (2007) considered a scenario with a two age-stage(juvenile and adult) $M$ similar to this study, resulting in a lower $\gamma$. The demographic analysis was used to estimate that the $\lambda$ of shortfin Mako (1.05–1.08) and pelagic thresher shark (1.06) in the northwest Pacific (Tsai et al., 2010, 2014) was lower than the $\lambda$ of blue shark in this study.

The difference in estimates for Atlantic blue shark may relate to growth parameters, i.e., $h = 0.73$ for North Atlantic blue shark with $L_\infty = 310.8$ cm and $h = 0.53$ for South Atlantic blue shark with $L_\infty = 246.0$ cm (Cortés, 2016). A higher growth rate tends to lead to a greater steepness. Rosa and Coelho (2016) also found that steepness was higher when assuming a uniform distribution of litter size ($U$ [36.7–37.1]) than when using Equation 5 of Castro and Mejuto (1995) method. The best estimate of steepness occurred at $h = 0.5$ in the most recent stock assessment for IO BSH, which was based on the Stock Synthesis model(Rice, 2017). Kleiber et al. (2009) assumed a low steepness of 0.70 in assessing the North Pacific blue shark using MULTI FAN-CL and Takeuchi et al. (2016) assumed steepness values of 0.4–0.8 when assessing the blue shark of the western and central Pacific Ocean.

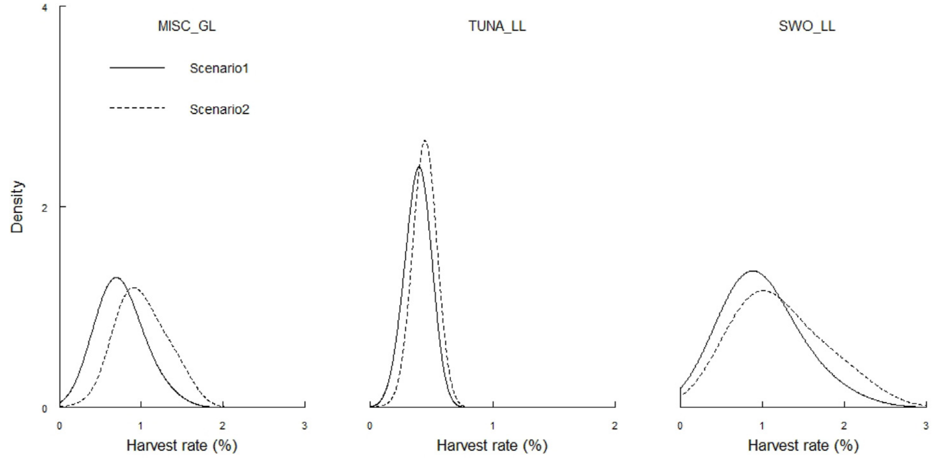

**Fig. 6.** Probability distributions of stationary harvest rate by fishery.

**Table 3**
Result of harvest analysis for the Indian Ocean blue shark.

| Parameter | Fleets | Scenario 1 | | | Scenario 2 | | |
|---|---|---|---|---|---|---|---|
| | | Mean | Lower | Upper | Mean | Lower | Upper |
| Harvest rate | MISC_GL | 0.75 | 0.31 | 1.35 | 1.01 | 0.55 | 1.56 |
| | TUNA_LL | 0.39 | 0.24 | 0.49 | 0.44 | 0.34 | 0.52 |
| | SWO_LL | 0.83 | 0.30 | 1.83 | 1.18 | 0.55 | 2.16 |
| Proportion removed | MISC_GL | 0.09 | 0.05 | 0.12 | 0.10 | 0.07 | 0.14 |
| | TUNA_LL | 0.13 | 0.09 | 0.16 | 0.14 | 0.12 | 0.16 |
| | SWO_LL | 0.05 | 0.03 | 0.08 | 0.07 | 0.05 | 0.09 |

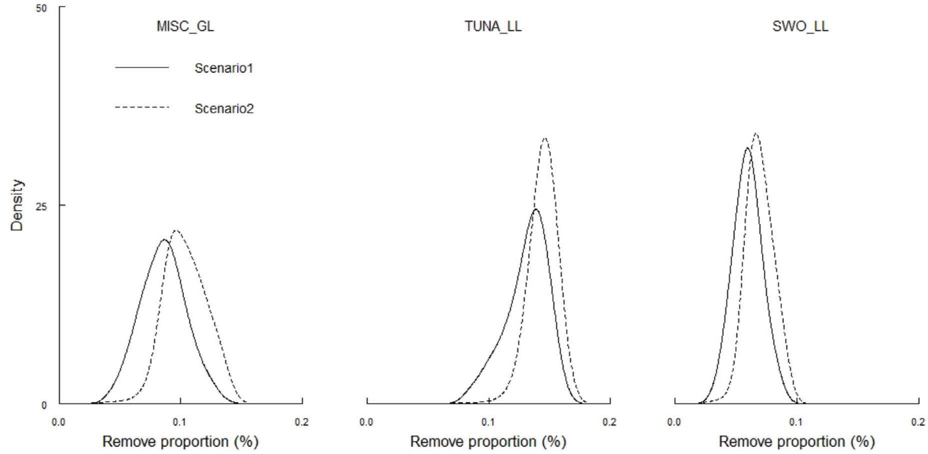

**Fig. 7.** Probability distributions of proportion removed with a stationary harvest rate.

The mean steepness obtained in the current study was 0.72 for Castro and Mejuto (1995) method and $h = 0.80$ for Fujinami et al. (2017) methods. This study suggests that demographic analysis can provide an alternative way to estimate steepness, which is often difficult to estimate with formal stock assessment models. It should also be noted that the uncertainty around estimates needs to be further investigated using ground-truth based simulation studies.

### *4.3. Demographic method in support of stock assessment*

We found that tuna longline fisheries (TUNA_LL), which are more selective for juvenile blue sharks than the other fisheries, can lead to a lower $H_{\mathrm{MSY}}$. This implies that fishing with longline fishery only leads to a lower fishing mortality corresponding to MSY, compared with other fisheries. Afterword, we used selectivity and its reflected stable age structure to calculate the actual proportion removed of the stock (Fig. 7). This revealed that the tuna longline can keep stock stable with the highest proportion removed. The harvest analysis indicated that the survival of the juvenile segment (0–4 years) is the key factor driving productivity for long-lived species, especially for sharks (Cortés, 2002). Although pelagic longline fisheries which mostly target tuna would lead to relative high fishing pressure on juveniles, their narrow selectivity could still maintain productivity due to their low selectivity for matured biomass.

Along with elasticity analysis, the demographic method can provide supporting information for fishery management and conservation measures (e.g., setting size limits of capture and annual harvest rates; (Tsai et al., 2014). However, in most situations, it is not possible to make use of fishery-dependent data directly (e.g., catch data, tagging data) without the stock assessment model. Fortunately, the demographic method can be used to develop the prior distribution for critical parameters of a stock assessment (e.g., the intrinsic rate of population increase), which are necessary for Bayesian stock assessment (McAllister et al., 2001). Biomass dynamics models and related data-poor approaches such as the Catch-MSY model (Martell and Froese, 2013) and stock reduction analysis (Kimura et al., 1984) can also integrate biological information with demography.

## CRediT authorship contribution statement

**Zhe Geng:** Conception and design of study, Acquisition of data, Analysis and/or interpretation of data, Writing - original draft. **Yang Wang:** Acquisition of data. **Richard Kindong:** Writing - review & editing. **Jiangfeng Zhu:** Conception and design of study. **Xiaojie Dai:** Acquisition of data, Writing - original draft.

## 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.

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