Working paper for

13th Working Party on Ecosystems and Bycatch (WPEB13)

Indian Ocean Tuna Commission (IOTC)

San Sebastián, Spain
4-8 September 2017

Estimating population growth rate for Indian Ocean blue shark (*Prionace glauca*) using demographic method

Document #: IOTC–2017–WPEB13–21 Rev_1

Zhe Geng, Jiangfeng Zhu*

*E-mail: jfzhu@shou.edu.cn

College of Marine Sciences, Shanghai Ocean University, 999 Hucheng Huan Road, Shanghai 201306, China;

Key Laboratory of Oceanic Fisheries Exploration, Ministry of Agriculture, 999 Hucheng Huan Road, Shanghai 201306, China

上海海洋大學

Estimating population growth rate for Indian Ocean blue shark (*Prionace glauca*) using demographic method

Summary

The study conducted demographic analysis to estimate population growth rate and steepness of stock-recruitment relationship by Leslie matrix method for the Indian Ocean blue shark (Prionace glauca). Monte Carlo simulation was used to integrate uncertainty of biological information. The results indicated that blue shark productivity was high, with the intrinsic rate of increase $\gamma=0.25\text{-}0.33\ y^{-1}$ *based on a one-year reproductive cycle (RC) assumption; However, the productivity was lower, with* $\gamma=0.19\text{-}0.20\ y^{-1}$ *based on a two-year RC assumption. The steepness of Beverton-Holt stock-recruitment model was estimated to be 0.76-0.81 in most scenarios, except for one scenario (steepness was 0.85) in which constant natural mortality at age was assumed.*

Blue shark (*Prionace glauca*) distributes widely in the tropical and temperate waters and is one of the main bycatch species in tuna longline fisheries (Nakano and Stevens, 2008). Blue shark was defined as "Near Threatened" species globally in the current IUCN species list of threat status (IOTC–WPEB12, 2016). Many of the shark species were difficult to be assessed using formal stock assessment models due to lack of reliable fishery data (Pilling et al., 2009).

There remains considerable uncertainties in the estimates of catch and size composition data over the past decade for the Indian Ocean blue shark (IO BSH), which resulted in the evaluation of stock status being highly uncertain (IOTC–WPEB12, 2016). Alternative methods to formal stock assessment models are thus needed for blue shark in the Indian Ocean. Data poor approaches have been used for providing scientific evidences of setting catch limit for many data poor fisheries (e.g., in the US; Newman, 2015). However, most of these approaches still relay on historical catch data (Rosenberg, 2014), which may not be reliably available for the IO BSH.

Demographic analysis relaying only on life-history parameters can serve as alternative population dynamic model for fish species (Simpfendorfer, 2005). The basic output from demographic analysis is the intrinsic rate of population increase, a measure of potential growth rate of population (Simpfendorfer, 2005). Demographic analysis tends to show better performance for long-live and slow-growing shark specie (Tribuzio and Kruse, 2011). This method has been applied for blue shark in the Atlantic Ocean (Aires-da-Silva and Gallucci, 2007).

The objective of this study is to (1) estimate the intrinsic rate of population increase and associated uncertainties by constructing an age-structured matrix population model and applying simulation approach to account for uncertainties in life history parameters; and (2) use the intrinsic rate of population increase to inform the estimate of steepness of spawner-recruitment relationship, a parameter which is hardly estimable within formal stock assessment models (Zhu et al., 2012). The results will provide important information in our understanding of the population dynamics and to develop management advice for IO BSH.

1 Material and methods

1.1 Demographic method

An age-structured matrix population model (Caswell 2001) was used to investigate the demography of the IO BSH:

$$N_{\mathrm{t}+1} = \mathbf{M} N_{\mathrm{t}} \tag{1}$$

where N_{t} is the vector with numbers at each age in year t. The matrix **M** is a Leslie population projection matrix:

$$\mathbf{M} = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_\mathrm{x} \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & \ldots & 0 & 0 \\ 0 & 0 & 0 & s_{\mathrm{x}-1} & 0 \end{bmatrix} \tag{2}$$

where the s_x element is the annual natural survivorship term for age x. The f_x elements represent the age-specific per-capita fecundity rates. A birth-pulse population and a post-breeding census were assumed (Caswell, 2001). Accordingly, the first age class (age 0) is represented by the new born pups and the fecundity (f_x) terms include the probability that a pregnant female survives and delivers the pups at the end of the year ($f_\mathrm{x} = s_\mathrm{x}\mathrm{M}_\mathrm{x}$, in which M_x is the average number of female pups per female).The M_x terms were calculated as the product of the number of pups per female and the female sex ratio of the litters, which was then divided by the length of the reproductive cycle in years. Thus, Equation 1 is a female population growth model (Aires-da-Silva and Gallucci, 2007).

According to matrix algebra, $AN_t = \lambda N_t$, where λ is called the eigenvalue of matrix *A***.**

Therefore, biologically λ is the finite rate of population increase and γ ($= \ln \lambda$) is defined as the intrinsic rate of population increase (Brewster-Geisz and Miller, 2000). The value of λ is determined by finding the dominant eigenvalue of *A* by using matrix algebra (Simpfendorfer, 2005). The underlying assumption of the matrix model (Equation 1) is that the population will grow exponentially and reach a stable age distribution with equilibrium (Caswell 2001).

1.2 Life-history parameter and uncertainty

1.2.1 Growth and longevity

The age and growth of IO BSH has not been intensively investigated. Rabehagasoa (2014) and Jolly (2013) provided two studies estimating growth model for this species, with the later sampling only from the coastal areas of South Africa, which might not be reprehensive for the IO BSH population. Therefore, the growth parameter estimates for the females from Inês (2017) was used in this study, i.e., L_∞=283.2, k=0.13 per year, and t_0= -1.31. The growth curve was shown in **Fig. 1a**.

Nakano (2008) provided an estimate of longevity (t_max) of 20 years for IO BSH. Combining the Cailliet's (1992) empirical formula (Equation 3) with growth parameters by Inês (2017) resulted in an longevity estimate of t_max=26years.

$$t_{max} = 5 \times (\ln 2)/k \tag{3}$$

To integrate the uncertainty of longevity, we assumed a discrete uniform distribution of *U* [20-26] for t_max (**Fig. 1b**).

The weight (W, kg) and fork length (FL, cm) relationship for female blue sharks follows **Romanov (2009)**(Equation 4):

$$W = 0.835 \times 10^{-5} \times FL^{2.972} \tag{4}$$

1.2.2 Maturity and reproduction

Pratt (1979) found that female blue sharks tend to be pregnant before 5 years old, even though they begin to mate in the earlier ages. To consider the uncertainty of mature age, we assumed a discrete uniform distribution of *U* (5, 7) for the mature age of the females, the same as the Atlantic blue shark (Aires-da-Silva and Gallucci, 2007) **(Fig. 1c)**.

Fecundity is an important parameter for demographic analysis. To address the uncertainty of fecundity, we considered two options for quantifying the fecundity. Castro (1995) found a linear relationship between fecundity (litter size, *LS*) and fork length for blue shark (Equation 5).

$$LS = -91.97 + 0.6052 \times FL \tag{5}$$

We used the Equation 5 and growth function of Inês (2017) to generate a relationship between litter size and age (termed as LS-Age model), as shown in **Fig. 1d**. As Mejuto (2005) we also assumed discrete uniform distribution of *U* (36.7-37.1) for litter size per reproductive cycle. The sex ratio at birth was assumed to be 1:1 as suggested by many studies (Hazin, 1994; Castro, 1995).

To consider the uncertainty of length of reproductive cycle (RC), we considered two options using information of blue shark in other oceans, i.e., a one-year *RC* based on Nakano (2008) for the Pacific blue shark and a two-year *RC* as in Aires-da-Silva and Gallucci (2007) for Atlantic blue shark.

1.2.3 Survival rate and natural mortality

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

$$S_t = e^{-Mt} \tag{6}$$

where M_t is the (instantaneous) natural morality. Thus, the estimate of survival rate is dependent on natural mortality. As natural mortality is often difficult to be estimated and is the main source of uncertainty in quantifying population dynamics. We considered five empirical methods to calculate M based on life-history information: (1) Hoenig’s (1983) method, i.e., $\ln(M) = 1.46 - 1.01\ln(t_{max})$; (2) Jensen’ (1996) method, i.e., $M = 1.5k$; (3) Hewett and Hoenig’s (2005) method, i.e., $M = 4.22/t_{max}$; (4) Peterson and Wroblewski’s (1984) method, i.e., $M_t = 1.92W_t^{-0.25}$; and (5) Chen and Watanabe’s (1989) method which estimates M based on its relationship with growth parameters and mature age. Each of methods (1)-(3) calculates a constant M value for all ages; while each of methods (4)-(5) calculates age-specific M values.

1.3 Scenarios of demographic analysis

The basic output of demographic analysis is the intrinsic rate of population increase (γ). The uncertainty of γ estimate results from the uncertainty in the life-history parameters. In this study, we considered **four scenarios** to address the uncertainties associated with **Fecundity (litter size), reproductive cycle, and natural mortality** (**Table 1**). The scenarios were developed to investigate the impacts of uncertainty of fecundity, reproductive cycle, and natural mortality on the estimates of γ.

For the two options of fecundity estimates, Scenarios 1-3 used age-specific litter size as the LS-Age model shown in **Fig. 1d**; while Scenario 4 used a discrete uniform distribution of U [36.7-37.1] (**Table 1**), in which a random litter size was drawn as the input of demographic analysis. For the two options of *RC* (one-year and two-year), a similar random sampling was applied for each scenario.

For the natural mortality, Scenario 1 included the three methods of calculating M which is constant over age classes; while Scenarios 2-4 included all the five methods ("all methods") of calculating M. In each scenario, one "M method" was simply randomly drawn with the M estimates to be the input of demographic analysis.

The triangular distribution can be used to represent the uncertainty in life-history parameters that precedes stochastic demographic work (Cortés, 2002, 2007). Survivorship, calculated from the estimates of M, can be quantified as triangular distribution or lognormal distribution (Caswell, 2001). For each scenario, we considered both triangular distribution and lognormal distribution for survivorship. The lowest and highest estimates of survival rates derived from 100 samplings of M estimates were taken as the bounds and the mean value was assumed as the most likely value in the triangular distributions. Similarly, the log-transformed mean and variance of survival rate estimates from 100 samplings of M estimates were used to create the lognormal distribution of survival rate. Then, for both triangular distribution and lognormal distribution of survival rates, 10,000 Monte Carlo simulations were run for each scenario by sampling from the survival rate and reproductive cycle distributions.

For each scenario, four demographic parameters, i.e., the intrinsic rate of population increase (γ), net reproductive rate (R_0), generation time (G), and population doubling time (t_{x2}) were estimated.

1.4 Estimating steepness of stock-recruitment model

The steepness parameter of the stock-recruitment relationship model is one of the most influential factors in integrated stock assessment modeling (Zhu et al., 2012). It is also one of the parameters that are difficult to be estimated inside stock assessment models. However, since steepness is a parameter biologically defining the productivity of a population when the spawning size decreases, theoretically it can be estimated from life history information. Here we follow the method of Myers et al. (1999) to estimate the steepness of Beverton-Holt stock-recruitment model based upon demographic information:

$$h = \frac{\alpha \cdot \mathrm{SPR}_{\mathrm{F=0}}}{4+\alpha \cdot \mathrm{SPR}_{\mathrm{F=0}}} \quad (7)$$

where α is the maximum number of recruits per spawning biomass (come from R0), $SPR_{F=0}$ is the spawning biomass per recruit at no fishing. The equation 7 can be expressed as equation 8(Simon, 2012):

$$l(a) = \prod_{t=1}^{a-1} S(t) \quad (8)$$

$$SPR_{F=0} = \sum_{a=1}^{A} l(a) \cdot W_a \cdot g(a) \cdot sr/RLC \quad (9)$$

where $S(t)$ is ratio of annual survival rate to annual fecundity at age *t*, $l(a)$ is the fraction of individuals surviving from recruitment (age 1) to age a, W_a is female individual weight at age *a*; $g(a)$ is the probability of maturity at age *a*; and *sr* is the sex ratio at birth. The uncertainties in the demographic parameters are transferred to the estimates of steepness. We assumed $g(a) = 0$ for fish younger than age at maturity and $g(a) = 1$ for fish older than age at maturity. All demographic and simulation analyses were coded in the R Language for Statistical Computing (R Core Team, 2016).

2 Results

2.1Natural mortality estimate

Fig. 2 showed the natural mortality at age estimated from “all methods” as listed in Table 1. The natural mortality estimates from lognormal distribution showed larger variation than from triangular distribution, and were lower for younger ages. Fig. 3 showed the natural mortality from different method options. Peterson and Wroblewski’s equation estimated higher natural mortalities for younger individuals. Chen's method provided similar trend, but estimated more high natural mortality for younger individuals. The range of M from different method options was 0.16-0.24 y^{-1}.The $M_{t=0}$ for females estimated by Chen's method, Peterson and Wroblewski’s method, and “all methods”, was 1.2 y^{-1}, 0.45 y^{-1}, and 0.54y^{-1}, respectively.

2.2 Intrinsic rate of population increase

Table 2 showed the results of demographic analysis for Indian Ocean blue shark. The net reproductive rate (R_0) was the highest in Scenario 1, and the lowest in Scenario 3. The lowest generation time (G) occurred in Scenario 4. The population generation time was estimated to be the longest in Scenario 3, and not obviously different among other scenarios. The estimates of γ and R_0 were higher, and the estimates of G and t_{x2} were lower when the survival rate followed lognormal distribution.

The distribution of estimate of γ for each scenario was shown in Fig. 4. The estimate of γ showed small variations both for lognormal and triangular distributions of survival rate in Scenario 1; however, the variation was much larger in Scenario 4. In all scenarios, the triangular distribution of survival rate led to lower estimate of γ than lognormal distribution.

2.3 Steepness estimate

The estimate of steepness was the highest in Scenario 1 (Table 3, Fig. 5), with no obvious differences among other scenarios. In Scenario 1, the steepness did not show obvious difference between triangular distribution and lognormal distribution of survival rate. In other scenarios, triangular distribution of survival rate led to a lower steepness estimate.

Scenario 1 resulted in the highest estimate of steepness; probably because this scenario neglected the change of M with age. Scenarios 2 and 3 produced almost the same steepness, indicating that reproductive cycle did not greatly impact the estimate of steepness. The steepness estimate from Scenario 4 was slightly higher than that from Scenario 2, owing to the difference in the estimate of litter size.

3. Discussion

3.1 Natural mortality estimate

There is lack of study for blue shark natural mortality worldwide. The empirical estimates of M for adult female IO BSH was 0.16-0.24 per year, close to the estimates of other areas, e.g., the M of blue shark in the North Pacific Ocean was estimated to be 0.17-0.21 per year by Nakano (1994) and 0.20-0.24 per year by Hsu et al. (2011). In the Atlantic, the M was estimated at 0.20 per year in Takeuchi (2005) and 0.24 per year in Chen (2006).

Previous study showed that young blue sharks tend to have higher natural mortality (Branstetter, 1990); therefore constant M may not reflect the real story of the population mortality. The method of Chen and Watanabe’s (1989) and Peterson and Wroblewski (1984) produced quite different M estimates for young blue sharks, i.e., $M_{t=0}$ =1.2 per year and 0.45 per year, respectively. A random sampling of the five methods in this study produced an average estimate of 0.54 per year, almost the same as the estimate by Nakano (1994), but higher than estimate by Aires-da-Silva and Gallucci (2007) ($M_{t=0}$=0.4 per year). Therefore, the “random sampling” method tended to produce more reliable estimates of M. The assumption of triangular distribution of M tended to result in M estimates with less variance (Fig. 3), consistent with the results in Aires-da-Silva and Gallucci (2007).

3.2 Demographic analysis

Demographic analysis showed that Scenario 3 had longer reproductive cycle and lower fecundity, therefore longer generation time and population doubling time, and lower population growth rate and net reproductive rate. Using demographic method, the γ estimate of blue shark in the north Atlantic Ocean was 0.34 y^{-1} and 0.35 y^{-1} by Takeuchi et al. (2005) and Chen and Yuan (2006). The study of Aires-da-Silva and Gallucci (2007) considered a scenario with age-specific M similar as in this study, resulting in a lower γ. A longer reproductive cycle would result in lower population growth rate.

3.3 Steepness estimate

Using demographic method, Rosa and Coelho (2016) obtained h=0.80 when the litter size followed a uniform distribution of U[36.7-37.1], and h=0.87 when the litter size was calculated using Nakano's equation. They used growth parameters estimated from coastal South Africa (L_∞=334.7 cm). The difference of estimates for Atlantic blue shark may also relate to growth parameters, i.e., h=0.73 for North Atlantic blue shark with L_∞=310.8 cm and h=0.53 for South Atlantic blue shark with L_∞=246.0 cm (Cortés et al., 2016). A higher growth rate tends to lead to a higher steepness. Rosa and Coelho (2016) also found that the steepness from assuming uniform distribution of litter size (U [36.7-37.1]) was higher than that from using Nakano's method (Equation 5).

In recent IO BSH stock assessments, the Stock Synthesis model got the best model fit with a steepness assumption of h=0.5 (Rice and Sharma, 2015). Kleiber (2009) assumed a mean steepness of 0.70 in assessing the North Pacific blue shark using MULTIFAN-CL. Takeuchi (2016) assumed steepness values of 0.4-0.8 in assessing the blue shark of western and central Pacific Ocean. Overall, the estimates of steepness in the current study are 0.76-0.81, except for the Scenario 1 which assumed a constant M.

Acknowledgements

We are grateful to Drs Alexandre Aires-Da-Silva and Carolina Minte-Vera (IATTC) and for their guidance and assistance with coding and analysis of the demographic analysis. This study was supported by the Project of GaoFeng Discipline of Fishery Science, National Natural Science Foundation of China (41676120), and National Engineering Research Center for Oceanic Fisheries at Shanghai Ocean University, China. The majority of work in this study was done when the senior author Z. Geng was visiting in IATTC headquarters.

Reference

Aires-da-Silva, A. M., Gallucci, V. F. 2007. Demographic and risk analyses applied to management and conservation of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Marine and Freshwater Research,58(6): 570-580.

Branstetter, S.1990. Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. NOAA Technical Report NMFS, 90: 17-28.

Booth, A. J., Foulis, A. J., Smale, M. J. 2011. Age validation, growth, mortality, and demographic modeling of spotted gully shark (*Triakis Megalopterus*) from the southeast coast of South Africa. Fishery Bulletin, 109(1): 101-112.

Cailliet, G. M., Mollet, H. F., Pittenger, G. G., et al. 1992. Growth and demography of the Pacific angle shark (*Squatina californica*), based upon tag returns off California. Marine and Freshwater Research, 43(5): 1313-1330.

Carlos, B., Michael, B. B. 2013. Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. Fisheries research, 143: 174-183.

Castro, J. A., Mejuto, J. 1995. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. Marine and Freshwater Research, 46(6): 967-973.

Caswell, H. 2001. Matrix population models. John Wiley & Sons, Ltd,1-3

Chen, S., Watanabe, S. 1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi, 55(2): 205–208.

Chen, P., Yuan, W. 2006. Demographic analysis based on the growth parameter of sharks. Fisheries research, 78(2): 374-379.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Conservation Biology 16, 1048–1062. doi:10.1046/J.1523-1739.2002.00423.X

Cortés, E. 2007. Comparative life-history and demography of pelagic sharks. In ‘Sharks of the Open Ocean’. Eds E. K. Pikitch and M. Camhi. Blackwell Scientific: Oxford.

Cortés, E. 2016. Estimates of maximum population growth rate and steepness for blue sharks in the North and South Atlantic Ocean. Collect. Vol. Sci. Pap. Iccat, 72(5): 1180-1185.

Rosa, D., Coelho, R. 2016. Estimates of intrinsic rate of population change and steepness for blue shark (*Prionace glauca*) in the Indian Ocean. IOTC–2016–WPEB12–18.

Gubanov, Y. P., Grigor’yev, V. N. 1975. Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. Journal of Ichthyology,15: 37-43.

Hazin, F. H. V., Kihara, K., Otsuka, K., et al. 1994. Reproduction of the blue shark Prionace glauca in the south-western equatorial Atlantic Ocean. Fisheries science,60(5): 487-491.

Hewitt, D. A., Hoenig, J. M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fishery Bulletin, 103(2): 433-437.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin, 82(1):898 - 903.

Hsu, H. H., Joung, S. J., Lyu, G. T. ,et al. 2017. Age and growth of the blue shark, *Prionace glauca*, in the northwest Pacific. ISC-11-SHARKWG-2-INFO02.

Inês, A., Daniela, R., Rúben, M-L, et al. 2017. Age and growth of the blue shark (Prionace glauca) in the Indian Ocean. IOTC-2017-WPEB13-20.

IOTC. 2015. Status of the Indian Ocean blue shark (BSH: *Prionace glauca*),IOTC-2015-SC18-ES17

IOTC. 2016. Blue Shark catches reported to the IOTC Secretariat, and a review of current estimation procedures, IOTC–2016–WPEB12–INFO4.

IOTC. 2016. Report of the 12th Session of the IOTC Working Party on Ecosystems and Bycatch. IOTC–2016–WPEB12–R

Jiao, Y., Cortés, E., Andrews, K., et al. 2011. Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach. Ecological Applications, 21(7): 2691-2708.

Jensen, A. L.1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences, 53(4): 820-822.

Jolly, K. A., Da-Silva, C., Attwood, C. G. 2013. Age, growth and reproductive biology of the blue shark *Prionace glauca* in South African waters. African Journal of Marine Science, 35(1): 99-109.

Kleiber, P., Clarke, S., Bigelow, K., et al. 2009. North Pacific blue shark stock assessment. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center.

Mejuto, J., García-Cortés, B. 2005. Reproductive and distribution parameters of the blue shark *Prionace glauca*, on the basis of on-board observations at sea in the Atlantic, Indian and Pacific Oceans. Collect Vol. Sci. Pap. ICCAT. 58: 951–973

Myers, R. A., Bowen, K. G., Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences, 56(12): 2404-2419.

Nakano, H.1994 Age, reproduction and migration of blue shark [Prionace] in the north Pacific Ocean. Bulletin-National Research Institute of Far Seas Fisheries (Japan).

Nakano, H., Stevens, J. D. 2008. The biology and ecology of the blue shark, *Prionace glauca*. Sharks of the Open Ocean: Biology, Fisheries and Conservation, p 140-151.

Newman, D., Berkson, J., Suatoni, L. 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. Fisheries Research, 164: 86-93.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil, 39(2): 175-192.

Pratt, H. L.1979. Reproduction in the blue shark, *Prionace glauca*. Fishery bulletin,77(2): 445-470.

Peterson, I., Wroblewski, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 41(7): 1117-1120.

Pilling, G. M., Apostolaki, P., Failler, P., et al. 2009. Assessment and management of data-poor fisheries. Advance in Fishery Science,50: 280-305.

Punt, A. E., Smith, D. C., Koopman, 99M. T. 2005. Using information for data-rich species to inform assessments of data-poor species through Bayesian stock assessment methods. Primary Industries Research Victoria.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rice, J., Semba, Y. 2014. Age and sex specific natural mortality of the blue shark (*Prionace glauca*) in the North Pacific Ocean. ISC/14/SHARKWG-1.

Rice, J., Harley, S., Maunder, M., et al. 2013. Stock assessment of blue shark in the north Pacific Ocean using Stock Synthesis. Western and Central Pacific Fisheries Commission Scientific Committee Ninth Regular Session, 6-14.

Rice, J., Sharma, R. 2015. Stock assessment blue shark (*Prionace glauca*) in the Indian Ocean using Stock Synthesis. IOTC–2015–WPEB11–28 Rev_1.

Rosa, D., Coelho, R. 2016. Estimates of intrinsic rate of population change and steepness For blue shark (*prionace glauca*) in the Indian Ocean. IOTC–2016–WPEB12–18.

Romanov, E., Romanova, N. 2009. Size distribution and length-weight relationships for some large pelagic sharks in the Indian Ocean. IOTC-2009-WPEB-06.

Rosenberg, A. A., Fogarty, M. J., Cooper, A. B., et al. 2014. Developing new approaches to global stock status assessment and fishery production potential of the seas. FAO.

Simon, M., Fromentin, J. M., Bonhommeau, S., et al. 2012. Effects of stochasticity in early life history on steepness and population growth rate estimates: An illustration on Atlantic bluefin tuna. PloS one, 2012, 7(10): e48583.

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.

Tsai, W. P., Sun, C. L., Punt, A. E., et al. 2014. Demographic analysis of the shortfin mako shark, *Isurus oxyrinchus*, in the Northwest Pacific using a two-sex stage-based matrix model. ICES Journal of Marine Science: Journal du Conseil, 71(7): 1604-1618.

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. Marine and Freshwater Research, 61(9): 1056-1066.

Takeuchi, Y., Tremblay-Boyer, L., Pilling, G.M., et al. 2016. Assessment of blue shark in the southwestern Pacific, WCPFC-SC12-2016/SA-WP-08 REV1

Tribuzio, C. A., Kruse, G. H. 2011. Demographic and risk analyses of spiny dogfish (*Squalus suckleyi*) in the Gulf of Alaska using age-and stage-based population models. Marine and Freshwater Research, 62(12): 1395-1406.

Zhu, J. F., Chen, Y., Dai, X. J., et al. 2012. Implications of uncertainty in the spawner–recruitment relationship for fisheries management: An illustration using bigeye tuna (*Thunnus obesus*) in the eastern Pacific Ocean. Fisheries Research, 119: 89-93.

Table.1 Scenarios of demographic analysis for Indian Ocean blue shark

Scenario	Litter size (LS)	Reproductive cycle (*RC*)	M method
1	LS-Age model	1	constant M for all ages (Hoenig 1983; Jensen, 1996; Hewett and Hoenig, 2005)
2	LS-Age model	1	all methods
3	LS-Age model	2	all methods
4	*U* [36.7-37.1]	1	all methods

Table 2. Mean of demographic parameters for Indian Ocean blue shark in each scenario with different survival rate distributions

Scenario	Triangular distribution				Lognormal distribution			
	γ	R_0	G	t_{x2}	γ	R_0	G	t_{x2}
1	0.30	28.58	11.33	2.36	0.30	29.66	11.35	2.34
2	0.25	20.67	11.90	2.76	0.27	24.05	11.73	2.64
3	0.19	10.36	12.32	3.72	0.20	12.06	12.14	3.55
4	0.31	21.13	9.85	2.28	0.33	25.06	9.73	2.17

Table 3. Estimates of steepness of Beverton-Holt spawner-recruitment relationship for the Indian Ocean blue shark

Scenario	Triangular distribution for survival rate				Lognormal distribution for survival rate			
	Mean	Median	Lower 90% CI	Upper 95% CI	Mean	Median	Lower 90% CI	Upper 95% CI
1	0.85	0.85	0.80	0.89	0.85	0.85	0.80	0.90
2	0.76	0.77	0.63	0.85	0.79	0.81	0.50	0.89
3	0.76	0.77	0.63	0.85	0.79	0.81	0.52	0.89
4	0.78	0.79	0.65	0.86	0.81	0.83	0.55	0.90

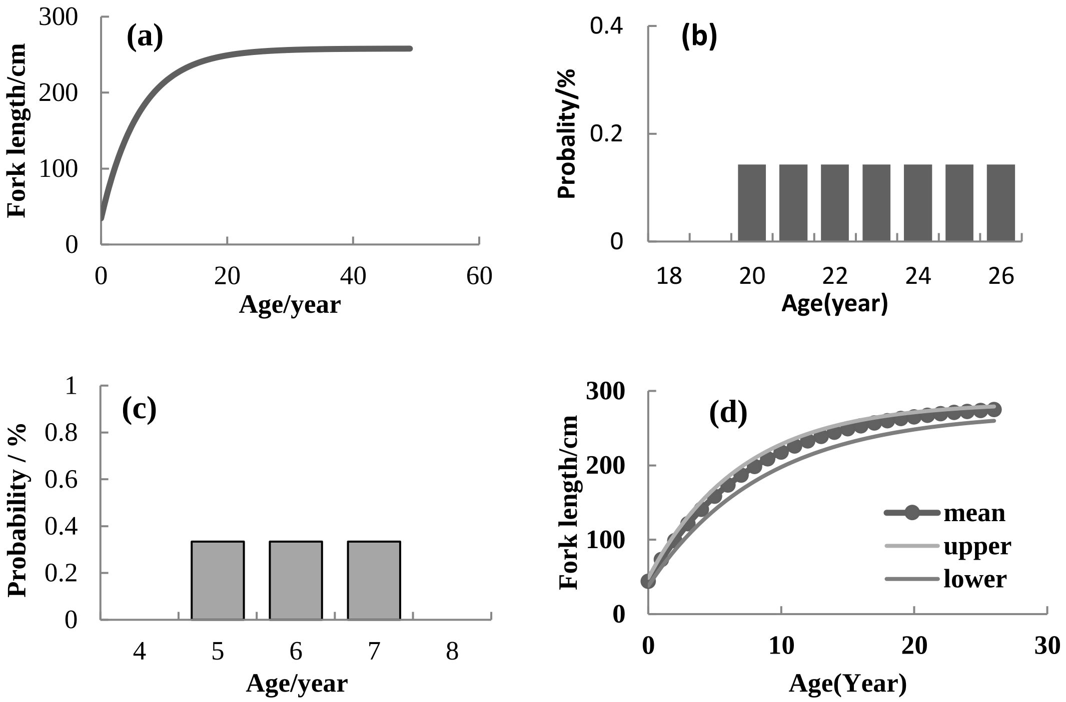

Fig. 1 Uncertainty in the life-history parameters of the Indian Ocean blue shark: (a) Length-at-age, (b) Longevity, (c) Age-at-maturity, (d) Fecundity-at-age (LS-Age model)

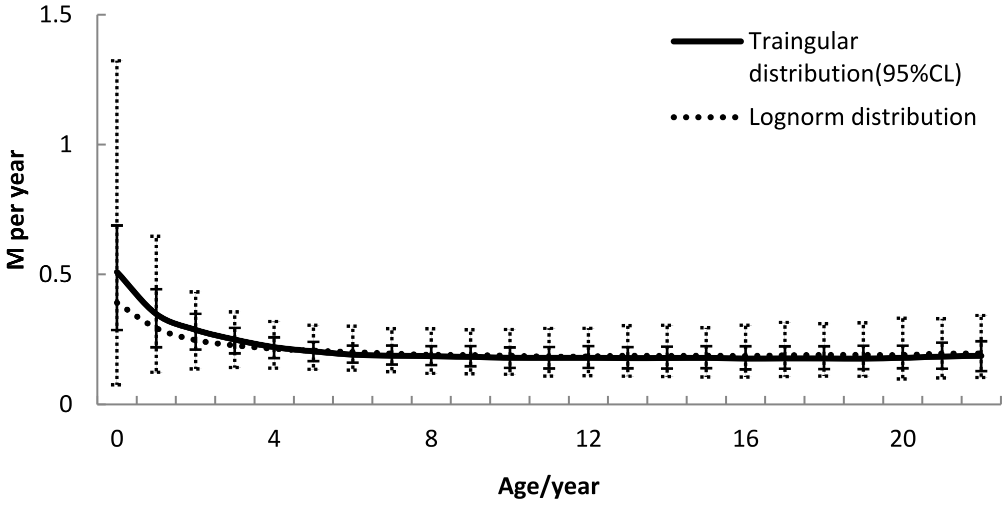

Fig. 2 Natural mortality estimates by “all methods”

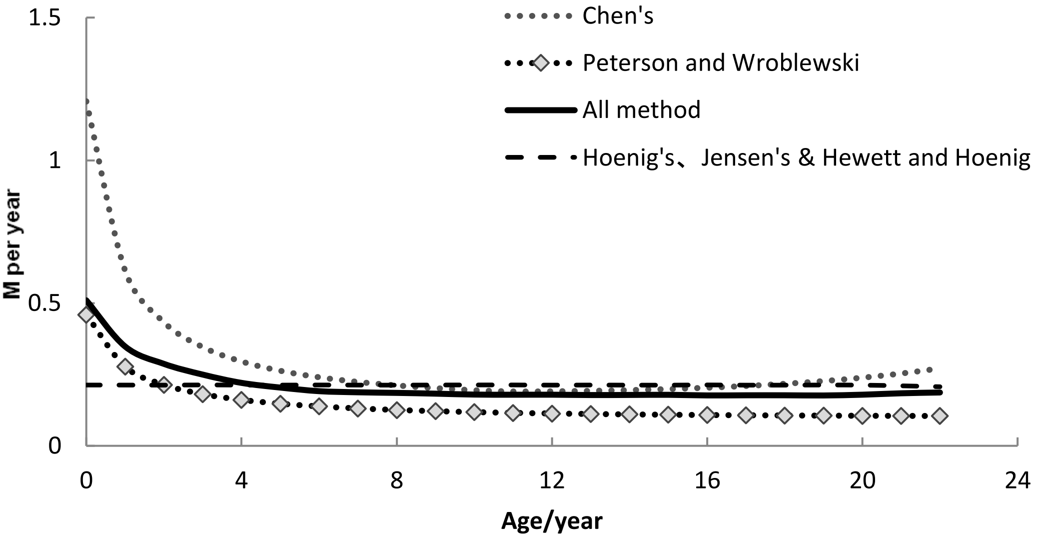

Fig. 3 Natural mortality estimates by different methods

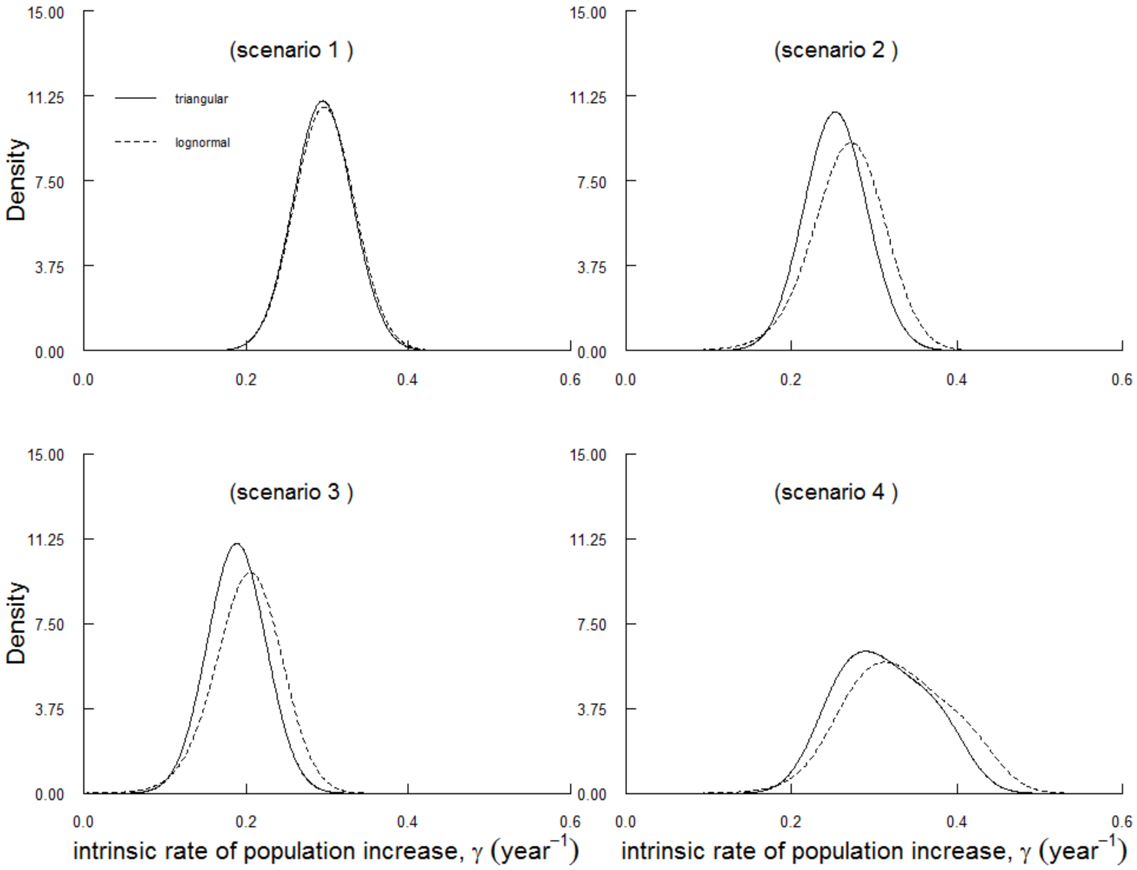

Fig. 4 Probability distributions of γ in different scenarios

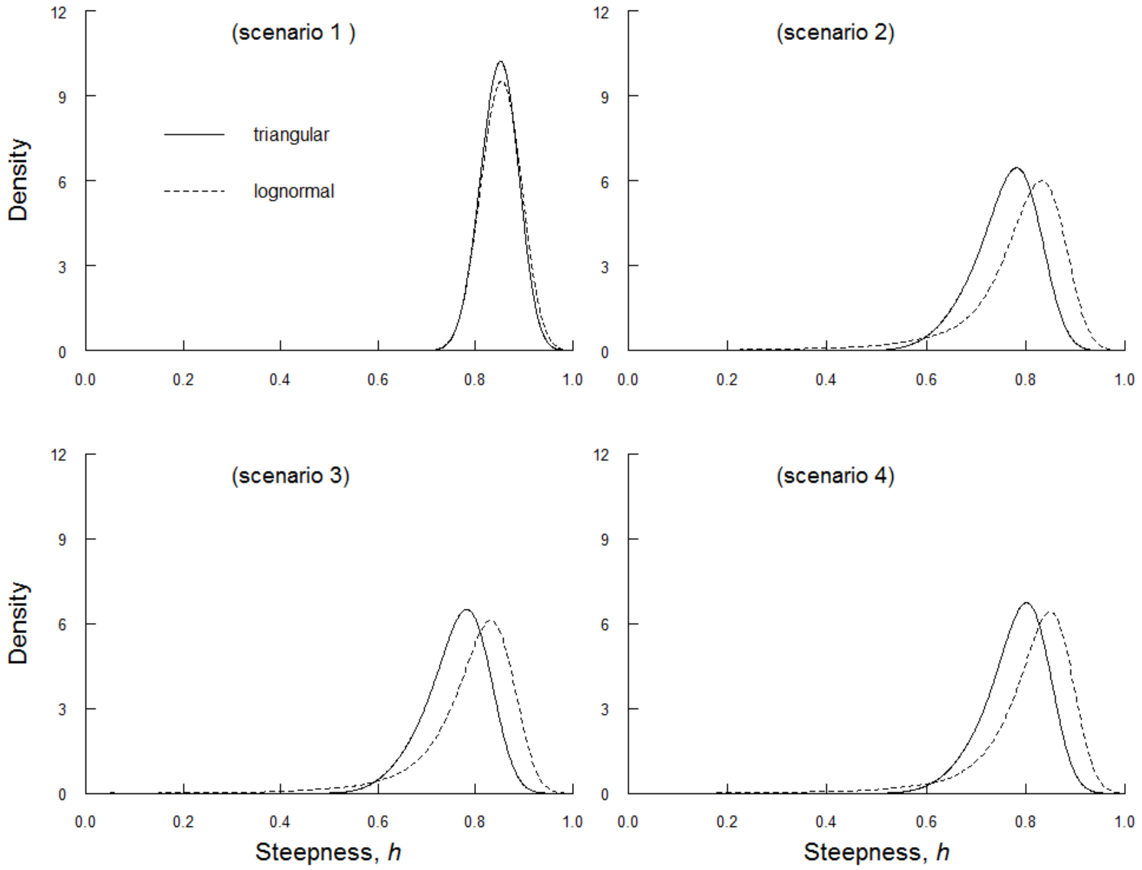

Fig. 5 Probability distributions of steepness with different survival rate distribution for each scenario