# Stock-recruitment relationships of shortfin mako, Isurus oxyrinchus, in the North Pacific ${ }^{1}$ 

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#### Abstract

This working paper provides estimates of steepness, which represents a fraction of the unfished recruitment when spawning stock biomass is $20 \%$ of the unfished spawning stock biomass, for the stock assessment of North Pacific shortfin mako (Isurus oxyrinchus) in 2024. The author applied an existing age-structured model considering reproductive ecology of elasmobranchs. A suite of values of steepness for North Pacific shortfin mako were estimated using numerical simulations with multiple combinations of life history parameters such as updated growth curve, natural mortality, reproductive cycle, and fecundity. The mean value and standard deviation of steepness with the Beverton-Holt model for 17 scenarios of biological parameters were 0.228 and 0.086 . These results suggested that the stock-recruitment relationship in the North Pacific shortfin mako remains little density-dependent and that its productivity is much lower than that of shortfin mako in the Atlantic Ocean. The author therefore recommends reconsidering the selection of key biological parameters such as growth, natural mortality, and reproductive cycle for the stock assessment, and/or to do down-weight (or remove) such unreasonable low productivity scenarios from the assessment.


## Introduction

The stock-recruitment relationship is one of the most important factors needed to understand the population dynamics of marine organisms and effectively manage populations exploited by fisheries (Hilborn and Walters, 1992). The relationship between parental stock abundance and subsequent recruitment is conventionally expressed by the Beverton-Holt model (Beverton and Holt, 1957) and Ricker model (Ricker, 1954). If both unfished spawning biomass and recruitment at that spawning biomass are given, the stock-recruitment relationships are determined using a parameter (i.e. steepness) that represents a fraction of the unfished recruitment when spawning stock biomass is $20 \%$ of the unfished spawning biomass (Mace and Doonan, 1988). This steepness for the Beverton-Holt model is commonly used in stock assessment for pelagic sharks (e.g., ISC 2022). Direct estimation of stock-recruitment relationships in the assessment model were attempted for several coastal and pelagic sharks, however, such challenges didn't work due to insufficient available data (Walker, 1994; Gedamake et al., 2009). Stock-recruitment relationships of blue sharks (Prionace glauca) and shortfin mako (Isurus oxyrinchus) in the North Pacific Ocean were estimated outside the assessment model using an age-structured model for the reproductive ecology of elasmobranchs with available biological parameters (Kai and Fujinami, 2018; Kai 2020).

Benchmark stock assessment of shortfin mako in the North Pacific is scheduled to conduct in spring 2024 using a stock synthesis (SS) (Method and Wetzel, 2013). Key biological parameters
such as growth curve, natural mortality, reproductive cycle, and fecundity for this stock were updated at the data preparatory meeting convened in January 2024 (ISC, 2024). The main objective of this working paper is to estimate a suite of values of steepness using numerical simulations with multiple combinations of biological parameters which were updated for the stock assessment of North Pacific shortfin mako in 2024.

## Materials and Methods

The author applied an existing numerical approach with age-structured model in consideration of the reproductive ecology of elasmobranchs (Kai and Fujinami, 2018; Kai 2020) to the North Pacific shortfin mako. The details of the age-structured model were described in Kai (2020).

To elucidate the magnitude of uncertainties in the estimates of stock recruitment relationships in the North Pacific shortfin mako, a wide range of biological parameters for females updated in the data preparatory meeting in January 2024 were used. The values of two growth curves (JP approach with 1 band per year: US approach with 2 band per year until 5 years old then 1 band per year), two natural mortality rates (JP approach: US approach), three assumptions of fecundity (constant, linear and power functions), and two reproductive cycles were treated as uncertainty parameters. Other parameters such as longevity (i.e., maximum age), length-weight relationships, and length at $50 \%$ maturity were fixed to a constant value. All combinations of these parameters were used to estimate steepness. The values of all parameters are summarized in Table 1. The author conducted the same numerical simulations as used for the North Pacific shortfin mako (kai, 2020) to incorporate uncertainties in the natural mortality and produced the variance of steepness. The computation of the numerical simulation was implemented using a code based on the R package (R Development Core Team, 2023).

Appendix table (Table A1) and figures (Figures A1-A5) are given, under that values of steepness smaller than 0.2 are allowed, to enhance the understanding of the effect of the biological parameters to the estimates of steepness and to find an unrealistic combination of biological parameters.

## Results and Discussion

The mean and standard deviation of steepness with the Beverton-Holt model for 17 combinations of biological parameters were 0.228 and 0.086 . The mean value of steepness was much lower than that ( $\mathrm{h}=0.317$ ) used in the previous assessment in 2018 (ISC, 2018). The difference of the value of steepness were caused by the different biological parameters and the different estimation method. In 2018 assessment, the best available value of steepness ( $\mathrm{h}=0.317$ ) was estimated from a little faster growth curve ( $\mathrm{L}_{\infty}=293.1 \mathrm{~cm}$ PCL; $\mathrm{k}=0.128$ ), lower natural mortality ( 0.128 ) and 2-year
reproductive cycle (ISC, 2018). On the other hand, the mean value of steepness was estimated from all combinations of biological parameters ( 17 scenarios) in consideration of uncertainties in the growth curve, natural mortality, fecundity, and reproductive cycle in this study. In addition, the key biological parameters such as growth curve (Kinney et al., 2024) and natural mortality (Teo et al., 2024) were updated, and two scenarios of fecundity (linear and power functions) and one scenario of reproductive cycle (3-year) were added to the estimation of steepness. Overall, the results of this study indicated that the estimated values of steepness were much smaller than the value of steepness in 2018 (see Table 2). Probably the new growth curves (JP approach and US approach) had a large effect to the lower value of steepness because the new growth curves, compared to the previous one (Takahashi et al., 2017) used in the stock assessment in 2018, that resulted in the increase of the maturity at age from 10-11 year to 12 year for the JP-approach and to 13 year for the US-approach.

Steepness of shortfin mako in the North and South Atlantic were computed based on the biological information using a dual life table/Leslie matrix approach (Cortés, 2017). The estimated steepness ranged from 0.34 to 0.52 for the North Atlantic and from 0.44 to 0.72 for the South Atlantic. These higher values in the Atlantic were largely different from the lower estimates of steepness in the North Pacific because the natural mortality schedules of Atlantic shortfin mako were quite lower (constant values of 0.081 for immature female and lower than the value for the mature female) than that ( 0.133 or 0.139 ) of North Pacific shortfin mako in addition to the different biological parameters such as growth curves for North Atlantic shortfin mako (e.g. $L_{\infty}=350.6$ and $k=0.064)$. In summary, these results suggested that the stock-recruitment relationship in the North Pacific shortfin mako remains little density-dependent and that its productivity is quite lower than that of shortfin mako in the Atlantic Ocean.

The mean value of steepness was estimated from all combinations ( 24 scenarios) of biological parameters except for the scenarios ( 7 scenarios), which were not able to estimate the parameters of beta distribution due to the skewed datasets of steepness to the lower bound (i.e., 0.2 ). These results suggested that several combinations of the biological parameters (e.g., the combination of growth curve of US approach and 3-year reproductive cycle) are unsuitable for the sustainable stocks such as a North Pacific shortfin mako under the fishing pressure because lower steepness closed to 0.2 means that there is no resilience even if the low population density.

The author concerns about the low value of steepness close to 0.2 . The low productivity may not account for the increase trends in the abundance (e.g. CPUE of Kinkai shallow longline fishery and CPUE of US Hawaii deep set longline fishery). This may cause the difficulty in the conditioning of SS modeling due to the inconsistency of the biological parameters with fishery data. In addition, several combinations of biological parameters may not be suitable for North

Pacific shortfin mako because this stock has been sustaining for several decades under the high fishing pressure. The author therefore recommends reconsidering the selection of key biological parameters such as growth, natural mortality, and reproductive cycle for the stock assessment, and/or to do down-weight (or remove) such unreasonable low productivity scenarios from the assessment.

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Table 1. Summary of biological parameters on the female shortfin mako and other sources. The symbol follows Kai (2020).

| No. Function name | Parameter name | Symbol | Unit | Value Reference |
| :---: | :---: | :---: | :---: | :---: |
| 1 von-Bertalanffy growth curve (JP | Asymptotic size | $L_{\infty}$ | cm in PCL | 305.5 Kinney et al. (2024) |
| approach ${ }^{1}$ ) | Growth rate | $k$ | year ${ }^{-1}$ | 0.101 |
| Length $=$ L0 $+($ Linf $-L 0)\left(1-\exp \left(-\mathrm{k}^{*}\right.\right.$ age $)$ ) | Length at age0 | $L_{0}$ | year | 65.1 |
| 2 US approach ${ }^{2}$ |  | $L_{\infty}$ | cm in PCL | 272.4 |
|  |  | $k$ | year ${ }^{-1}$ | 0.128 |
|  |  | $L_{0}$ | year | 65.2 |
| 3 Weight-length relationship |  | $c_{1}$ |  | 3.4 Su et al. (2017) |
| Weight $=\mathrm{c} 1 *\left(10^{\wedge}(-5)\right)^{*}$ Length ${ }^{\wedge}$ 2 |  | $c_{2}$ |  | 2.84 |
| 4 Length-based maturity ogives |  | $c_{3}$ |  | 34.23 Semba and Liu (2017) |
| Maturity $=1 /[1+\exp \{\mathrm{c} 3+\mathrm{c} 4 * \mathrm{PCL}\}]$ |  | $c_{4}$ |  | -0.146 |
| 5 Fecundity (constant*maturity rate) |  |  |  | 12 Mollet et al. (2000) |
| 6 Fecundity (linear equation*maturity rate) |  | $c_{5}$ |  | -12.4 Semba et al. (2011) |
| Litter=c5+c6*PCL |  | $c_{6}$ |  | 0.12 |
| 7 Fecundity (power function*maturity rate) ${ }^{3}$ |  | $c_{7}$ |  | 0.81 Mollet et al. (2000) |
| Litter=c7*TL^c8 |  | $c_{8}$ | TL:meter | 2.346 |
| 8 Natural mortality |  |  |  |  |
| Meta analysis ${ }^{4}$ (JP approach ${ }^{1}$ ) | Natural mortality (constant) | $M$ | year ${ }^{-1}$ | 0.139 Teo et al. (2024) |
| US approach ${ }^{2}$ |  | M | year ${ }^{-1}$ | 0.133 |
| 9 Gamma distribution |  | $v$ |  | 9.7 Kai (2020) |
| 10 | Maximum age | $a_{\text {max }}$ | year | 32 Natanson et al. (2006) |
| 11 | Sex ratio | $r$ |  | 0.5 Semba (2011); Joung and Hsu (2005) |
| 12 Pre-recruit survival |  |  |  |  |
|  | Survival at stage 0-2 | $S_{0-2}$ | year ${ }^{-1}$ | 1 Kai (2020) |
| 13 Theoretical equation (JP approach ${ }^{1}$ ) | Survival at stage 3 | $S_{3}$ | year ${ }^{-1}$ | 0.870 Teo et al. (2024) |
| US approach ${ }^{2}$ |  | $S_{3}$ | year ${ }^{-1}$ | 0.875 Teo et al. (2024) |
| 14 No function | Reproductive period | $y$ |  | 2 Semba et al. (2011) |
|  |  | $y$ |  | 3 Joung and Hsu (2005) |
| 15 | Days to recruit from partrition | $d$ | day ${ }^{-1}$ | 180 Kai et al. (2015) |

1: Assumption of aging with one band per year without length frequency data
2: Assumption of aging with two band per year until 5 year old then one band per year with length frequency data
3: $\mathrm{TL}(\mathrm{cm})$ was converted to the $\mathrm{PCL}(\mathrm{cm})$ using the equation: $\mathrm{PCL}=0.84 \times \mathrm{TL}-2.13$ (Semba et al., 2009)
4: Median value based on empirical equations of maximum age, growpth parameters and maturity at age

Table 2. Estimates of mean and standard deviation of steepness for different combinations of key biological parameters. Several scenarios could not estimate the values due to failure of the fitting the beta distribution to the estimated values of steepness due to skewness to the lower boundary (i.e., $\mathrm{h}=0.2$ ).

| Scenario | Growth | Natural <br> mortality | Fecundity | Reproducti <br> ve cycle | Mean | SD |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| S1 | JP approach | JP approach | Constant | 2 year | 0.247 | 0.068 |
| S2 | US approach | JP approach | Constant | 2 year | 0.209 | 0.022 |
| S3 | JP approach | US approach | Constant | 2 year | 0.274 | 0.076 |
| S4 | US approach | US approach | Constant | 2 year | 0.221 | 0.042 |
| S5 | JP approach | JP approach | Linear | 2 year | 0.242 | 0.065 |
| S6 | US approach | JP approach | Linear | 2 year |  |  |
| S7 | JP approach | US approach | Linear | 2 year | 0.268 | 0.076 |
| S8 | US approach | US approach | Linear | 2 year | 0.208 | 0.018 |
| S9 | JP approach | JP approach | Power | 2 year | 0.271 | 0.078 |
| S10 | US approach | JP approach | Power | 2 year | 0.210 | 0.024 |
| S11 | JP approach | US approach | Power | 2 year | 0.303 | 0.076 |
| S12 | US approach | US approach | Power | 2 year | 0.223 | 0.045 |
| S13 | JP approach | JP approach | Constant | 3 year | 0.208 | 0.019 |
| S14 | US approach | JP approach | Constant | 3 year |  |  |
| S15 | JP approach | US approach | Constant | 3 year | 0.218 | 0.036 |
| S16 | US approach | US approach | Constant | 3 year |  |  |
| S17 | JP approach | JP approach | Linear | 3 year | 0.206 | 0.015 |
| S18 | US approach | JP approach | Linear | 3 year |  |  |
| S19 | JP approach | US approach | Linear | 3 year | 0.215 | 0.032 |
| S20 | US approach | US approach | Linear | 3 year |  |  |
| S21 | JP approach | JP approach | Power | 3 year | 0.217 | 0.036 |
| S22 | US approach | JP approach | Power | 3 year |  |  |
| S23 | JP approach | US approach | Power | 3 year | 0.233 | 0.056 |
| S24 | US approach | US approach | Power | 3 year |  |  |
| Mean |  |  |  |  | 0.228 | 0.086 |

## Appendix

Table A1. Estimates of mean and standard deviation of steepness for all 24 scenarios. The estimates of steepness smaller than 0.2 were allowed to fit the beta distribution to the estimated values of steepness. Red figures indicate the mean value of steepness is smaller than 0.2.

| Scenario | Growth | Natural <br> mortality | Fecundity | Reproductive <br> cycle | Mean | SD |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| S1 | JP approach | JP approach | Constant | 2 year | 0.246 | 0.051 |
| S2 | US approach | JP approach | Constant | 2 year | 0.179 | 0.044 |
| S3 | JP approach | US approach | Constant | 2 year | 0.275 | 0.052 |
| S4 | US approach | US approach | Constant | 2 year | 0.205 | 0.046 |
| S5 | JP approach | JP approach | Linear | 2 year | 0.239 | 0.050 |
| S6 | US approach | JP approach | Linear | 2 year | 0.153 | 0.038 |
| S7 | JP approach | US approach | Linear | 2 year | 0.269 | 0.051 |
| S8 | US approach | US approach | Linear | 2 year | 0.176 | 0.041 |
| S9 | JP approach | JP approach | Power | 2 year | 0.272 | 0.053 |
| S10 | US approach | JP approach | Power | 2 year | 0.184 | 0.044 |
| S11 | JP approach | US approach | Power | 2 year | 0.305 | 0.054 |
| S12 | US approach | US approach | Power | 2 year | 0.210 | 0.046 |
| S13 | JP approach | JP approach | Constant | 3 year | 0.179 | 0.040 |
| S14 | US approach | JP approach | Constant | 3 year | 0.128 | 0.033 |
| S15 | JP approach | US approach | Constant | 3 year | 0.203 | 0.042 |
| S16 | US approach | US approach | Constant | 3 year | 0.148 | 0.036 |
| S17 | JP approach | JP approach | Linear | 3 year | 0.174 | 0.039 |
| S18 | US approach | JP approach | Linear | 3 year | 0.108 | 0.028 |
| S19 | JP approach | US approach | Linear | 3 year | 0.198 | 0.041 |
| S20 | US approach | US approach | Linear | 3 year | 0.126 | 0.031 |
| S21 | JP approach | JP approach | Power | 3 year | 0.201 | 0.043 |
| S22 | US approach | JP approach | Power | 3 year | 0.131 | 0.033 |
| S23 | JP approach | US approach | Power | 3 year | 0.227 | 0.045 |
| S24 | US approach | US approach | Power | 3 year | 0.151 | 0.036 |
| Mean |  |  |  |  | 0.195 | 0.042 |



Figure A1. Gamma distribution for a constant natural mortality rate for three mean values ( 0.128 black line, 0.139 blue line, and 0.133 red line) with a coefficient variation ( 0.32 ).


Figure A2. Sample survival trajectories ( $\mathrm{n}=20$ ) created by assuming a family of probability distribution for the rate of natural mortality dependent on age for three mean values ( 0.128 black line, 0.139 blue line, and 0.133 red line) with a coefficient variation ( 0.32 ).


Figure A3. Maturity at ages for three growth curves. Horizontal broken line denotes the maturity at size ( 233 cm PCL) estimated by Semba and Liu (2017).


Figure A4. Empirical frequency distributions of steepness and the fitted curves (solid line) by beta distribution for the Beverton-Holt stock-recruitment relationship model from 24 empirical data (see table A1) plus scenario (S0) in 2018 assessment (ISC 2018), for which the mean (filled circles) and their standard deviations (vertical bars) are shown for the empirical distribution.


Figure A5. Estimates of the North Pacific shortfin mako stock-recruitment relationship for the Beverton-Holt stock-recruitment relationship model from 24 scenarios (see table A1) based on different combinations of biological parameters plus scenario (S0) in 2018 assessment (ISC 2018). Effect of four key biological parameters (i.e., growth curve, natural mortality, fecundity, and reproductive cycle) to the estimation of steepness were compared. Shaded areas denote $95 \%$ confidence intervals. Relative recruits indicate recruitment (R)/unfished recruitment (R0), and relative biomass indicates biomass (B)/unfished biomass (B0).


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