Stock-recruitment relationships of shortfin mako, *Isurus* oxyrinchus, in the North Pacific¹

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1 Abstract

2 This working paper provides estimates of steepness, which represents a fraction of the unfished 3 recruitment when spawning stock biomass is 20% of the unfished spawning stock biomass, for 4 the stock assessment of North Pacific shortfin mako (Isurus oxyrinchus) in 2024. The author 5 applied an existing age-structured model considering reproductive ecology of elasmobranchs. A 6 suite of values of steepness for North Pacific shortfin mako were estimated using numerical 7 simulations with multiple combinations of life history parameters such as updated growth curve, 8 natural mortality, reproductive cycle, and fecundity. The mean value and standard deviation of 9 steepness with the Beverton-Holt model for 17 scenarios of biological parameters were 0.228 and 10 0.086. These results suggested that the stock-recruitment relationship in the North Pacific shortfin 11 make remains little density-dependent and that its productivity is much lower than that of shortfin 12 mako in the Atlantic Ocean. The author therefore recommends reconsidering the selection of 13 key biological parameters such as growth, natural mortality, and reproductive cycle for the 14 stock assessment, and/or to do down-weight (or remove) such unreasonable low productivity 15 scenarios from the assessment.

16

17 Introduction

18 The stock-recruitment relationship is one of the most important factors needed to understand the 19 population dynamics of marine organisms and effectively manage populations exploited by 20 fisheries (Hilborn and Walters, 1992). The relationship between parental stock abundance and 21 subsequent recruitment is conventionally expressed by the Beverton-Holt model (Beverton and 22 Holt, 1957) and Ricker model (Ricker, 1954). If both unfished spawning biomass and recruitment 23 at that spawning biomass are given, the stock-recruitment relationships are determined using a 24 parameter (i.e. steepness) that represents a fraction of the unfished recruitment when spawning 25 stock biomass is 20% of the unfished spawning biomass (Mace and Doonan, 1988). This steepness 26 for the Beverton-Holt model is commonly used in stock assessment for pelagic sharks (e.g., ISC 27 2022). Direct estimation of stock-recruitment relationships in the assessment model were 28 attempted for several coastal and pelagic sharks, however, such challenges didn't work due to 29 insufficient available data (Walker, 1994; Gedamake et al., 2009). Stock-recruitment relationships 30 of blue sharks (Prionace glauca) and shortfin mako (Isurus oxyrinchus) in the North Pacific Ocean 31 were estimated outside the assessment model using an age-structured model for the reproductive 32 ecology of elasmobranchs with available biological parameters (Kai and Fujinami, 2018; Kai 33 2020). 34 Benchmark stock assessment of shortfin mako in the North Pacific is scheduled to conduct

35 in spring 2024 using a stock synthesis (SS) (Method and Wetzel, 2013). Key biological parameters

36 such as growth curve, natural mortality, reproductive cycle, and fecundity for this stock were

37 updated at the data preparatory meeting convened in January 2024 (ISC, 2024). The main objective

38 of this working paper is to estimate a suite of values of steepness using numerical simulations with

39 multiple combinations of biological parameters which were updated for the stock assessment of

- 40 North Pacific shortfin mako in 2024.
- 41

42 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).

46 To elucidate the magnitude of uncertainties in the estimates of stock recruitment 47 relationships in the North Pacific shortfin mako, a wide range of biological parameters for females 48 updated in the data preparatory meeting in January 2024 were used. The values of two growth 49 curves (JP approach with 1 band per year: US approach with 2 band per year until 5 years old then 50 1 band per year), two natural mortality rates (JP approach: US approach), three assumptions of 51 fecundity (constant, linear and power functions), and two reproductive cycles were treated as 52 uncertainty parameters. Other parameters such as longevity (i.e., maximum age), length-weight 53 relationships, and length at 50 % maturity were fixed to a constant value. All combinations of these 54 parameters were used to estimate steepness. The values of all parameters are summarized in Table 55 1. The author conducted the same numerical simulations as used for the North Pacific shortfin 56 mako (kai, 2020) to incorporate uncertainties in the natural mortality and produced the variance of 57 steepness. The computation of the numerical simulation was implemented using a code based on 58 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.

63

64 **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

- 67 that (h=0.317) used in the previous assessment in 2018 (ISC, 2018). The difference of the value of
- 68 steepness were caused by the different biological parameters and the different estimation method.
- 69 In 2018 assessment, the best available value of steepness (h=0.317) was estimated from a little
- faster growth curve (L_{∞} = 293.1 cm PCL; k=0.128), lower natural mortality (0.128) and 2-year

71 reproductive cycle (ISC, 2018). On the other hand, the mean value of steepness was estimated 72 from all combinations of biological parameters (17 scenarios) in consideration of uncertainties in 73 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 74 75 (Teo et al., 2024) were updated, and two scenarios of fecundity (linear and power functions) and 76 one scenario of reproductive cycle (3-year) were added to the estimation of steepness. Overall, the 77 results of this study indicated that the estimated values of steepness were much smaller than the 78 value of steepness in 2018 (see Table 2). Probably the new growth curves (JP approach and US 79 approach) had a large effect to the lower value of steepness because the new growth curves, 80 compared to the previous one (Takahashi et al., 2017) used in the stock assessment in 2018, that 81 resulted in the increase of the maturity at age from 10-11 year to 12 year for the JP-approach and 82 to 13 year for the US-approach.

83 Steepness of shortfin mako in the North and South Atlantic were computed based on the 84 biological information using a dual life table/Leslie matrix approach (Cortés, 2017). The estimated 85 steepness ranged from 0.34 to 0.52 for the North Atlantic and from 0.44 to 0.72 for the South 86 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 87 88 were quite lower (constant values of 0.081 for immature female and lower than the value for the 89 mature female) than that (0.133 or 0.139) of North Pacific shortfin mako in addition to the different 90 biological parameters such as growth curves for North Atlantic shortfin make (e.g. L_{∞} =350.6 and 91 k=0.064). In summary, these results suggested that the stock-recruitment relationship in the North 92 Pacific shortfin make remains little density-dependent and that its productivity is quite lower than 93 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.

101 The author concerns about the low value of steepness close to 0.2. The low productivity 102 may not account for the increase trends in the abundance (e.g. CPUE of Kinkai shallow longline 103 fishery and CPUE of US Hawaii deep set longline fishery). This may cause the difficulty in the 104 conditioning of SS modeling due to the inconsistency of the biological parameters with fishery 105 data. In addition, several combinations of biological parameters may not be suitable for North 106 Pacific shortfin make because this stock has been sustaining for several decades under the high

107 fishing pressure. The author therefore recommends reconsidering the selection of key

- 108 biological parameters such as growth, natural mortality, and reproductive cycle for the stock
- 109 assessment, and/or to do down-weight (or remove) such unreasonable low productivity
- 110 scenarios from the assessment.
- 111

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175 **Table 1.** Summary of biological parameters on the female shortfin mako and other sources. The176 symbol follows Kai (2020).

No. Function name 1 von-Bertalanffy growth curve (JP Parameter name Symbol Unit Value Reference 305.5 Kinney et al. (2024) Asymptotic size L_{∞} cm in PCL Growth rate k 0.101 approach¹) year-1 Length at age0 65.1 Length=L0+(Linf-L0)(1-exp(-k*age)) L_0 year 2 US approach² cm in PCL 272.4 L_{∞} -1 0.128

			year	01120
		L_0	year	65.2
3 Weight-length relationship		<i>c</i> ₁		3.4 Su et al. (2017)
Weight=c1*(10^(-5))*Length^c2		C 2		2.84
4 Length-based maturity ogives		<i>C</i> ₃		34.23 Semba and Liu (2017)
$Maturity=1/[1+exp{c3+c4*PCL}]$		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		С7		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	$a_{\rm max}$	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	у	2	2 Semba et al. (2011)
		у		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: TL(cm) was converted to the PCL(cm) using the equation: PCL=0.84 x TL-2.13 (Semba et al., 2009)

4: Median value based on empirical equations of maximum age, growpth parameters and maturity at age

177 178

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

182 the beta distribution to the estimated values of steepness due to skewness to the lower boundary

183 (i.e., h=0.2).

Scenario	Growth	Natural	Fecundity	Reproducti	Mean	SD
		mortality		ve cycle		
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

188 Appendix

189

190 Table A1. Estimates of mean and standard deviation of steepness for all 24 scenarios. The

- 191 estimates of steepness smaller than 0.2 were allowed to fit the beta distribution to the estimated
- 192 values of steepness. Red figures indicate the mean value of steepness is smaller than 0.2.
- 193

Scenario	Growth	Natural	Fecundity	Reproductive	Mean	SD
		mortality		cycle		
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
S 8	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).



199

200 **Figure A2**. Sample survival trajectories (n=20) created by assuming a family of probability

201 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

210 beta distribution for the Beverton-Holt stock–recruitment relationship model from 24 empirical

211 data (see **table A1**) plus scenario (S0) in 2018 assessment (ISC 2018), for which the mean (filled

212 circles) and their standard deviations (vertical bars) are shown for the empirical distribution.



217

Figure A5. Estimates of the North Pacific shortfin mako stock-recruitment relationship for the 218 219 Beverton-Holt stock-recruitment relationship model from 24 scenarios (see table A1) based on 220 different combinations of biological parameters plus scenario (S0) in 2018 assessment (ISC 2018). 221 Effect of four key biological parameters (i.e., growth curve, natural mortality, fecundity, and 222 reproductive cycle) to the estimation of steepness were compared. Shaded areas denote 95% 223 confidence intervals. Relative recruits indicate recruitment (R)/unfished recruitment (R0), and 224 relative biomass indicates biomass (B)/unfished biomass (B0).