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**Evaluation of harvest strategies for pelagic sharks taking
ecological characteristics into consideration: an example for
North Pacific blue shark**

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1 Evaluation of harvest strategies for pelagic sharks taking ecological
2 characteristics into consideration: an example for North Pacific blue shark
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12
13 **Abstract**

14 We have developed a population dynamics model that considers the spatial
15 segregation by sex and ontogenetic stages of pelagic sharks. The model was used to
16 evaluate the performance of harvest strategies based on ecological characteristics. We
17 proposed five harvest strategies for longline fisheries based on the ecological
18 characteristics of blue shark (*Prionace glauca*) in the North Pacific. Management
19 objectives for depleted populations are to increase yield to the level that provides
20 maximum sustainable yield (MSY) through increases in biomass without collapsing the
21 fishery. Deterministic and stochastic analyses were undertaken. We determined that the
22 harvest of male sharks was robust to uncertainty of environmental changes, reducing the
23 likelihood of fishery collapse and stabilizing yield and mean biomass. The harvest of
24 male sharks was also robust to the uncertainties of biological parameters such as natural

mortality and steepness. These results suggested that, if there was no sperm limitation or impact on the mating behavior of the species, the harvest of males would be the most appropriate harvest strategy for blue shark in the North Pacific.

Keywords: harvest strategy, pelagic shark, blue shark, population dynamics model, ecological characteristics

Introduction

Over the past few decades, many pelagic sharks have faced widespread declines in numbers due to fisheries expansion into the open ocean (Baum et al. 2003; Myers et al. 2007; Dulvy et al. 2008; Ferretti et al. 2008; Petersen et al. 2009; Clarke et al. 2013), although some stock assessments found no detectable decreases in the biomass of the North Pacific blue shark (*Prionace glauca*) (Sibert et al. 2006; Kleiber et al. 2009; Rice et al. 2014). In recent years, several tuna regional fisheries management organizations (RFMOs) have conducted stock assessments for the world's major pelagic sharks such as blue shark (ICCAT 2015; IOTC 2015; ISC 2014; Rice et al. 2014), oceanic whitetip shark (*Carcharhinus longimanus*) and silky shark (*Carcharhinus falciformis*) (Rice and Harley 2012, 2013), and shortfin mako (*Isurus oxyrinchus*) (ICCAT 2012). The stock status of the North Pacific blue shark from the most recent stock assessment indicated that the stock is not in an overfished state and that overfishing is not occurring (ISC 2014; Rice et al. 2014). These assessments can be problematic due to incomplete data, where sharks and other bycatch are not well recorded in commercial fisheries targeting high-value tuna (Walker 1988; Bonfil 1994). Nevertheless, it is well known that pelagic sharks are susceptible to overfishing due to their slow growth rate, late maturity at age, and low fecundity (Compagno 2001). These

49 life history parameters can be used in examining the demographic characteristics of
50 pelagic sharks and assessing ecological risks for the management and conservation of
51 these sharks (Cortés 2002; Aires-da-Silva and Gallucci 2007; Kirby and Hobday 2007;
52 Cortés et al. 2010; Tsai et al. 2014). For example, Cortés et al. (2010) conducted
53 ecological risk assessments on eleven pelagic elasmobranchs in the Atlantic Ocean and
54 indicated that most species had low productivity and varying levels of susceptibility to
55 pelagic longline gear. Kirby and Hobday (2007) also conducted ecological risk
56 assessments for the effects of fishing in the western and central Pacific Ocean and found
57 similar results.

58 Implementation of harvest strategies for pelagic sharks should ideally be
59 species-specific using the results of indicator analyses, stock assessments, or ecological
60 risk assessments. However, catch limits and other common harvest strategies for tunas
61 and billfishes may not be enough to reduce the catch of pelagic sharks, because sharks
62 are incidentally caught by longliners targeting tunas and billfish (Bonfil 1994; Stevens
63 et al. 2000). If there is little information on the stock status, precautionary harvest
64 strategies (FAO 1995) should be implemented for pelagic sharks, particularly those that
65 have low productivity and high susceptibility to fishing mortality. More conservative
66 harvest strategies based on the precautionary approach would make it possible to avoid
67 further stock declines.

68 Pelagic sharks often exhibit spatial segregation by sex, size, and age (Nakano
69 1994; Nakano and Seki 2003; Mucientes et al. 2009). This segregation arises from
70 differences in the spatial distribution of different cohorts, perhaps arising from
71 biological partitioning of available habitat. Such segregation is thought to reduce
72 intraspecific cannibalism and competition (Nakano 1994). Ecological characteristics

such as sex- and size-specific segregation could complicate management if fisheries operate at a specific time and area where specific size classes or sexes are found. However, the management of pelagic sharks is poorly developed and takes little consideration of spatial distribution (Mucientes et al. 2009).

Blue sharks are highly migratory cosmopolitan predators distributed throughout temperate and tropical waters of the world's oceans (Campagno 1984). They are the most abundant pelagic shark species around the world (Nakano 1994; Nakano and Seki 2003). Blue shark in the Pacific is thought to comprise two stocks, roughly separated north and south along the equator (ISC 2014). A recent genetic study supports the existence of a single population of blue shark in the North Pacific (King et al. 2015). Blue shark in the North Pacific is frequently caught as bycatch by pelagic longline fisheries targeting tuna and billfish (Nakano 1994; Nakano and Seki 2003).

A number of fisheries operating from Japan target blue shark. Fishery data from these fisheries supported the hypothesis of sex- and size-specific migration and distribution of blue shark in the North Pacific (Nakano 1994). Adults occur widely between 0° and 40°N. Mating occurs during early summer (April to May) in waters between 20° and 30°N. Pregnant females migrate to pupping grounds between 30° and 40°N during the Boreal summer in May to June. Sub-adult females aged 2 to 5 years generally move north of the pupping grounds, while sub-adult males aged 2 to 4 years generally move south of the pupping grounds. Blue shark are sexually dimorphic with males being larger than females; males reach maturity at 4 to 6 years and females at 5 to 7 years (Nakano 1994).

The aim of this study is to evaluate harvest strategies for pelagic sharks taking their ecological characteristics into consideration, with a focus on North Pacific blue

97 shark as an example.

98

99 **Materials and Methods**

100 This study constructs a mathematical model based on a two-sex stage-based
101 matrix model to evaluate harvest strategies for pelagic sharks. The model has a distinct
102 spatial segregation by sex and ontogenetic stages (i.e., immature male, immature
103 female, mature male, mature female, and pregnant female). We tested five harvest
104 strategies based on the ecological characteristics of blue shark in the North Pacific: (1)
105 harvest of juveniles (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks
106 (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).
107 Deterministic and stochastic analyses were undertaken to investigate whether the
108 harvest strategies could result in increased biomass and harvest at the level of maximum
109 sustainable yield (MSY). A stochastic framework that accounts for uncertainties in the
110 biological and environmental parameters was implemented using Monte Carlo
111 simulations. Several scenarios were used to evaluate the impact that these uncertainties
112 have on achieving the management objectives below. Although management objectives
113 for the North Pacific blue shark have not been determined at the Western and Central
114 Pacific Fisheries Commission (WCPFC) and the Inter-American Tropical Tuna
115 Commission (IATTC), in this study we used a tentative management objective for
116 depleted populations, which is to increase yield to a level that provides MSY through an
117 increase in biomass without collapsing the fishery.

118

119 *Population dynamics model*

120 We constructed a discrete population dynamics model for pelagic sharks. The

model accounted for spatial segregation by sex and ontogenetic stages. We assumed that mature and immature sharks segregated their habitat into northern and southern areas such as blue shark in the North Pacific (Fig. 1). The northern area comprises pupping and nursery grounds, while the southern area comprises mating and feeding grounds. Immature males and females move to the southern area every year after a constant proportion of immature sharks grows to the mature stage. The pregnancy rate is dependent on the ratio of the number of mature males to the total number of mature sharks. Pregnant females move to the northern area for parturition and immediately return to the southern area after pupping. Recruitment is dependent on the number of pregnant females. The survival rate varies with sex and ontogenetic stage. We developed the population dynamics model based on the assumptions described above. The model has five groups (i.e., variants):

$$\begin{aligned}
 (1) \quad x_{t+1} &= \gamma R(X_t^P) + S^x(1 - r^x)x_t \\
 (2) \quad y_{t+1} &= (1 - \gamma)R(X_t^P) + S^y(1 - r^y)y_t \\
 (3) \quad X_{t+1} &= S^X r^x x_t + S^X(1 - \beta(X_t, Y_t))X_t + S^X X_t^P \\
 (4) \quad Y_{t+1} &= S^Y r^y y_t + S^Y Y_t \\
 (5) \quad X_{t+1}^P &= S^{X^P} \beta(X_t, Y_t)X_t
 \end{aligned}$$

where t is the year; x and y are the number of immature females and males, respectively; X and Y are the number of mature females and males, respectively; X^P is the number of pregnant females; γ is the sex ratio of newly recruited immature sharks; R is a reproductive function that depends on X^P ; S is the annual survival rate; r is the proportion of immature sharks developing to maturity; and β is a pregnancy rate that depends on the ratio between mature males and females. The function R is replaced by the Beverton-Holt (BH) stock-recruitment model or the Ricker (RI) stock-recruitment

145 model to give

146 (6)
$$R(X^P) = \frac{aX^PW^X}{1+bX^PW^X} \exp\left(\xi - \frac{\sigma_R^2}{2}\right), \quad \xi \sim N(0, \sigma_R^2) \quad \text{for the BH model, and}$$

147 (7)
$$R(X^P) = aX^PW^Xe^{-bX^PW^X} \exp\left(\xi - \frac{\sigma_R^2}{2}\right) \quad \text{for the RI model,}$$

148 where a and b are constants, W is body weight, ξ is the normally distributed errors, and
 149 σ_R is the standard deviation of the process errors. The pregnancy rate β is replaced by
 150 the following function of male availability (Caswell 2001):

151 (8)
$$\beta(X, Y) = \frac{Y}{X+Y}.$$

152 The annual survival rate is given as

153 (9)
$$S^i = e^{-M^i - F^i},$$

154 where i is one of the five groups (e.g., x), M is the natural mortality rate, and F is the
 155 fishing mortality rate. The proportion of immature sharks developing to maturity is
 156 given as

157 (10)
$$r^i = \frac{(S^i)^{\tau^i} - (S^i)^{\tau^i - 1}}{(S^i)^{\tau^i} - 1},$$

158 where τ is the period of immaturity (Caswell 2001). Deterministic analyses based on the
 159 equations above showed that the population was able to exist in an equilibrium state
 160 (see Appendix A).

161 The parameters of the population dynamics model were estimated based on
 162 the biological data of blue sharks in the North Pacific. The value of M was estimated
 163 using a relationship between body weight and the natural mortality rate (Peterson and
 164 Wrobloski 1984). The value of W was estimated using the equation of length at age and
 165 body weight at length (Nakano 1994). The value of τ was given based on the age of

166 maturity, i.e., females aged 5 to 7 years and males aged 4 to 6 years (Nakano 1994). The
167 value of γ was given based on a one-to-one sex ratio (Nakano 1994). The value of
168 steepness (h), i.e., the fraction of unfished recruitment when spawning stock biomass is
169 20% of its unfished level (Mace and Doonan 1988), was arbitrarily given, because there
170 was no information on stock-recruitment relationships. The default values of all the
171 parameters (basecase) are shown in Appendix B. Since the basecase had an equilibrium
172 point under the situation of no exploitation, we regarded the total number of five groups
173 in the equilibrium state as the carrying capacity. Deterministic and stochastic numerical
174 simulations were conducted to examine whether the harvest strategies could achieve the
175 management objectives.

177 *Design of the simulation study*

178 The deterministic numerical simulation was carried out using the population
179 dynamics model in the equilibrium state. The performance of the harvest strategies was
180 evaluated using biological reference points (BRPs) based on the MSY. The model
181 provided the values of MSY (or Y_{msy}), F at MSY (F_{msy}), and biomass at MSY (B_{msy})
182 using the default parameters (Table A1). The fishing mortality rate (F) was changed
183 from low to high values to examine the relationships between F and quantitative values
184 (yield and biomass).

185 Sensitivity analyses were attempted based on the deterministic model to
186 examine the impact of uncertainties in the biological parameters on MSY and B_{msy} for
187 each harvest strategy. We focused on the uncertainties of natural mortality (M) and
188 steepness (h) in stock-recruitment relationships because we had no reliable information
189 on those parameters. Natural mortality rates for each group were changed from $0.5M$ to

190 1.5M in 0.01M increments, and steepness was changed from 0.21 to 0.99 in 0.0078
191 increments.

192 The stochastic numerical simulation was carried out using the stochastic
193 population dynamics model. The simulation period was 60 years. Simulation trials were
194 repeated 1000 times with different series of random numbers ($\sigma_R=0.3$). The value of σ_R
195 was arbitrarily given because our knowledge of the magnitude of errors was
196 insufficient. The initial population number at $t=1$, N_1 , was set to equal 20% of carrying
197 capacity under the assumption that the population had already been depleted before the
198 harvest strategies were started. The simulation was continued after the time series of the
199 population exceeded the threshold of the fishery's collapse (see Risk below for a
200 definition of the threshold).

201 Since regime shift changes the stock-recruitment relationships of marine
202 species (Kawasaki 2013), it was assumed that regime shifts could change the parameter
203 of a in the stock-recruitment relationships (see equations (6) and (7)). It was also
204 assumed that a low reproductive value ($a = 0.0245$) arose from a low-productivity
205 regime and that a high reproductive value ($a = 0.245$) arose from a high-productivity
206 regime, where high productivity refers to a current average productivity that allows
207 biomass to increase to the MSY level under a favorable fishing mortality rate (i.e.,
208 F_{msy}). For simplicity, the range of the reproductive value was scaled between 0 and 1,
209 where the reproductive rate gradually increases as the scaled value approaches 1 (Fig.
210 2). Fisheries with high exploitation would be sustainable when managed under a
211 high-productivity regime, while the risk of fishery collapse increases under a
212 low-productivity regime where a low reproductive rate increases the possibility that
213 stocks will be overfished. We therefore examined the risk of fishery collapse as regimes

214 shifted from high to low productivity and vice versa.

215 The mating mechanism basically influences the proportion of breeding
216 females, which has a large impact on the perceived population growth rate (Tsai et al.,
217 2015). Infrequent behavioral observations of mating in the field (Chapman et al. 2003)
218 and genetic studies (Feldheim et al. 2001; Chapman et al. 2004) provide evidence for
219 the mating mechanism of elasmobranchs. Fitzpatrick et al. (2012) reviewed genetic
220 studies supporting the evidence of polyandry (a female mating with multiple males in a
221 single breeding season), and multiple paternity was documented in 12 of 15
222 elasmobranchs. It has been shown that the blue shark has a high incidence of polyandry
223 (80.0%) based on microsatellite DNA analyses of litters (Fitzpatrick 2012). Since a
224 decrease in the number of males could jeopardize the success of mating, we also
225 examined the impact of blue shark polyandry on the performance statistics (see
226 Appendix D) and discussed the uncertainties.

227 Three different performance statistics were used to evaluate the impact of
228 uncertainties in stock-recruitment relationships on the achievement of management
229 objectives:

230 i) Risk (%):

231 The number of simulations in which the population number fell below 5% of carrying
232 capacity relative to the total number of 1000 simulations;

233 ii) Yield (tons)

234 The mean value of the estimated catch for the 1000 simulations where the estimated
235 catch is an average for a simulation period;

236 iii) Biomass (tons)

237 The mean value of the estimated biomass for the 1000 simulations where the

238 estimated biomass is an average for a simulation period.

239 For performance statistics (ii) and (iii), values relative to the MSY level (Y/Y_{msy} and

240 B/B_{msy}) were also used to compare performances among different strategies.

241 Four productivity scenarios were tested:

242 (I) Harvest using different harvest strategies under no regime shifts: a

243 high-productivity regime for 60 years;

244 (II) Harvest using different harvest strategies under no regime shifts: a

245 low-productivity regime for 60 years;

246 (III) Harvest using different harvest strategies under regime shifts: a high-productivity

247 regime for the first 30 years followed by a lower-productivity regime for the next

248 30 years;

249 (IV) Harvest using different harvest strategies under regime shifts: a lower-productivity

250 regime for the first 30 years followed by a high-productivity regime for the next

251 30 years.

252 For Scenarios (III) and (IV), the productivity rate under a lower-productivity regime

253 was gradually reduced from 1 to 0 in 0.033 steps, and performance statistics were

254 compared under ideal fishing pressure ($F=F_{\text{msy}}$).

255 These numerical simulations were carried out using an R package (R Core

256 Team, 2013).

257

258 Results

259 The relationships between fishing mortality rate (F) and quantitative values

260 (yield and biomass) are shown in Fig. 3. The yield curves are dome-shaped and the

261 biomass curves decrease continuously. The yield curves show that yield increased when

262 F increased from 0 to the level of MSY (Fig. 3a). The biomass curves show that the
263 trends in declines were different among the five harvest strategies (Fig. 3b): the harvest
264 of juvenile sharks (JU) resulted in the lowest MSY, while the harvest of adult sharks
265 (AD) had the highest MSY (Table 1); the harvest of all sharks (AL) had the lowest F_{msy} ,
266 while the harvest of juvenile sharks (JU) had the highest F_{msy} ; and the harvest of all
267 sharks (AL) had the lowest B_{msy} , while the harvest of female sharks (FE) had the highest
268 B_{msy} (Table 1).

269 The sensitivity of F_{msy} and MSY to the natural mortality rate (M) showed that
270 the variation in M had a small impact on the F_{msy} for all harvest strategies, while the
271 variation in M had a large impact on MSY, especially for AD, MA, and AL (Fig. 4a and
272 b). The magnitudes of M had a large impact on the mean body weight as well as the
273 survival rate, in particular for fast-growing mature males that accounted for the large
274 variation in yield for AD, MA, and AL. Steepness (h) had a large impact on F_{msy} as well
275 as MSY (Fig. 4c and d). The variation in F_{msy} estimates was large for JU and AD,
276 indicating that the high variation of F was caused by changes in the stock-recruitment
277 relationships (Fig. 4c). The variation in estimates of MSY was larger for AD and AL
278 but smaller for MA and FE (Fig. 4d). The magnitude of steepness had a large impact on
279 the stock-recruitment relationships, which resulted in the large variation in yield for AD
280 and AL. However, MA and FE were insensitive to the steepness. The variation in the
281 estimates of MSY for JU was small irrespective of the large variation in F_{msy} . These
282 results suggest that the impact of natural mortality was large for harvest strategies that
283 included the harvest of mature males, while the impact of steepness was small for
284 harvest strategies that harvested one sex. The magnitude of steepness as well as the
285 strength of density-dependent compensation had a large impact on the values of MSY,

286 especially for AD and AL, although the results from the Beverton-Holt and Ricker
287 models tended to be similar (see Appendix C).

288 We provided examples of annual changes in population size in the four
289 scenarios (Fig. 5). For Scenario (I), population numbers tended to increase gradually
290 and were stable near the equilibrium point with random fluctuations (Fig. 5a). As a
291 result, there was no risk of fishery collapse for any harvest strategies under the fishing
292 mortality rate at MSY. These results indicate that none of the harvest strategies presents
293 any risk unless a regime shift occurs. For Scenario (II), population numbers tended to
294 decrease constantly and fell below the threshold of fishery collapse. For Scenario (III),
295 population numbers tended to increase during the first 30 years and then decrease
296 sharply during the second 30 years under a low-productivity regime ($a = 0.0245$) even
297 though the fishing mortality rate was at the MSY level. As a result, population numbers
298 for AD and AL fell below the threshold (Fig. 5b). For Scenario (IV), population
299 numbers for all harvest strategies tended to decrease slightly during the first 30 years
300 and then increase during the second 30 years under a high-productivity regime
301 ($a=0.245$) with the fishing mortality rate at the MSY level. As a result, population
302 numbers for all harvest strategies except MA caused the fishery to collapse (Fig. 5c).
303 This result suggests that catching mature sharks was not a suitable method of avoiding
304 fishery collapse when the population was heavily depleted due to low reproductivity.

305 The risk of fishery collapse increased for the five harvest strategies as
306 follows: AD, AL, JU, FE, and then MA, in line with decreases in the reproductive rate
307 from 1 to 0. (Fig. 6a). Yield and biomass decreased for all harvest strategies as the
308 reproductive rate decreased from 1 to 0 under the lower-productivity regime in Scenario
309 (III) (Fig. 6b and c). The harvest of adult sharks (AD) had the highest risk of fishery

collapse, while the harvest of males (MA) had the lowest risk (Fig. 6d and e). The high risk of fishery collapse was caused by a decrease in reproductivity following the depletion of both male and female mature sharks, and the low risk was caused by the maintenance of reproductivity due to the high survival rate of mature female sharks. Male sharks, due to their rapid growth, also contributed significantly to productivity. The harvest of female sharks (FE) made it possible to maintain the highest mean biomass, while the harvest of all sharks (AL) resulted in the lowest mean biomass (Fig. 6d and f). High biomass could be maintained because FE was able to maintain the number of males, especially mature males, as they grow faster and larger than females. AL, on the other hand, caused both growth and recruitment overfishing (Hilborn and Walters 1992), which in turn decreased the number of immature and mature sharks. The harvest of adult sharks (AD) made it possible to maintain the highest mean yield, while the harvest of juvenile sharks (FE) resulted in the lowest mean yield (Fig. 6e and f). High mean yields could be maintained because AD could catch large-sized sharks while avoiding growth overfishing (Hilborn and Walters 1992). Low mean yields, however, were caused by JU due to growth overfishing.

Results similar to those in Scenario (III) were observed for the risk of fishery collapse in Scenario (IV) (Fig. 7a). However, the order of yield and biomass for each harvest strategy changed as the reproductive rate decreased from 1 toward 0 (Fig. 7b and c). The yield of AD and AL was particularly noteworthy because these harvest strategies harvested mature sharks while the reproductive rate was low (Fig. 7b). The biomass of FE was also noteworthy because this harvest strategy harvested female sharks while the reproductive rate was low. The very low reproductive rate decreased the recruitment of male sharks and resulted in a decrease of biomass (Fig. 7c). The

relationships among mean risk, mean yield, and mean biomass showed identical tendencies (Fig. 7d, e, and f).

Performances for the values relative to the MSY level in Scenarios (III) and (IV) were different (Fig. 8a and b): in Scenario (III), all harvest strategies could increase the population during the first 30 years, but in Scenario (IV), some harvest strategies had difficulty increasing the population after having become heavily depleted due to the low productivity (see Fig. 5c and d). Overall, the performance of MA was better than all other harvest strategies in both scenarios (Fig. 8a and b). The harvest of all sharks (AL) and juvenile sharks (JU) also resulted in a higher mean B/B_{msy} (Fig. 8a and b) due to the lower B_{msy} (Table 1), while the harvest of female sharks (FE) resulted in a lower mean B/B_{msy} due to the higher B_{msy} (Table 1). The harvest of all sharks (AL) and female sharks (FE) resulted in a higher mean Y/Y_{msy} in Scenario (III) (Fig. 8a), while in Scenario (IV) the higher mean Y/Y_{msy} resulted from the harvest of juvenile sharks (JU) (Fig. 8b). The harvest of adult sharks (AD), however, resulted in the lowest mean Y/Y_{msy} in both scenarios (Figs. 8a and b) due to the fact that it had the highest MSY (Table 1). These results suggested that the harvest strategies of AL and JU also had the potential to achieve increases in catch and biomass during regime shifts from high to low and low to high productivity, respectively.

Discussion

We have developed a population dynamics model that accounts for spatial segregation by sex and the ontogenetic stages of blue sharks, which can be used to evaluate the performance of harvest strategies based on ecological characteristics. This method may be useful in assessing other pelagic sharks that exhibit sexual dimorphism

or for which there is sexual segregation. The life history parameters of pelagic sharks that are selected are key factors in the evaluation of harvest strategies. These parameters of pelagic sharks are frequently insufficient and may have large uncertainties (Cortés 2000; Cortés 2002; Cortés et al. 2010; Liu et al. 2015). Improvement in the availability and reliability of life history parameters would play an important role in the appropriate management of pelagic sharks. For blue sharks, we were able to use life history parameters (e.g., growth curve, maturity at ages, and weight-length relationships, etc.), which were derived from a large data set collected across the North Pacific (Nakano 1994). Nevertheless, the natural mortality rate and stock recruitment relationships of blue sharks are major uncertainties. These parameters are very difficult to estimate because of the lack of sufficient information on their life history (Tsai et al. 2011). Furthermore, most methods for estimating those parameters were developed for teleost species, not sharks (e.g., Peterson and Wroblewski 1984; Mangel et al. 2010). In future work, large tagging studies in the western and central North Pacific will be necessary to enhance the accuracy of estimates for natural mortality, and inferences of steepness for sharks must also be developed for the reliable management of blue sharks in the North Pacific.

Taylor et al. (2013) developed a pre-recruit, survival-based stock-recruitment model for low-fecundity species. The model illustrated a more direct connection between spawning output and recruitment than species generating millions of eggs. However, the model was not applied in this study due to the lack of data for the parameter values and the fact that the model is more complex than traditional models such as the BH model.

The numerical simulations illustrated that the harvest of males (MA)

performed well with respect to the risk of fishery collapse, mean yield, and mean biomass as a whole under the regime shifts and fishing mortality at the MSY level. The favorable performance of MA is attributable to the ban on female catches and the high productivity of males. The ban on female catches increased the survival rate of mature females and resulted in high reproductivity. The high productivity of males was due to the higher survival rate, faster growth, and larger body mass of male sharks compared to the females. In addition, the sensitivity analysis indicated that MA was robust to the uncertainties of biological parameters such as natural mortality rate and steepness. These results suggested that MA was the most appropriate harvest strategy for pelagic sharks in the North Pacific such as the blue shark in efforts to achieve the management objectives of increasing yield by increasing biomass without collapsing the fishery. The harvest of immature sharks (JU), however, performed poorly as a whole (Figs. 6 and 7), although the relative values of catch and biomass performed well (Fig. 8b). The poor performance of JU was attributable to growth overfishing, which decreased the proportions of the mature sharks to all sharks and resulted in a low survival rate, small body mass, and low reproduction. Additionally, the sensitivity analysis indicated that JU was highly sensitive to changes in the biological parameters. These results suggest that the catch of juveniles should be avoided in the management of pelagic sharks.

It is possible to apply the harvest of males (MA) or the harvest of females (FE) to longline fisheries targeting pelagic sharks such as the blue shark, because longliners are not only able to identify the sex of the sharks from their external form – when they are not too large and active – but can also release the sharks easily (e.g., cut the line) without bringing them on deck. Longline fisheries also tend to have lower shark mortality rates for some species such as the blue shark and the tiger shark

(Gallagher et al. 2014). A recent study on the Canadian pelagic longline fishery showed that more than 85% of blue sharks survive after being hooked by a longline, and estimates of the post-release mortality rate of 109 blue shark individuals in a pop-up satellite tagging study was 9.8% (Campana et al. 2015). Unlike the mortality of blue sharks, the post-release mortality rate of two lamnid shark species (porbeagle and shortfin mako), at 27–31%, is considerably higher (Campana et al. 2015). These results suggest that the management of blue sharks has high potential for success when applied to longline fisheries. It is necessary to bear in mind, however, that hooking and post-release mortality can reduce the effectiveness of the catch-and-release of sharks when the harvest strategy is applied to longline fisheries targeting blue sharks.

The harvest of mature sharks (AD) is also a feasible harvest strategy that uses minimum catch lengths to protect immature sharks. Our study showed that AD performed well and allowed the highest mean yield, although the performances of relative values were poor due to the high values of MSY. AD had a high risk of fishery collapse (about 23%), considerably higher than MA (about 13%), and is thus not suitable for the management of pelagic sharks such as blue shark from the perspective of stock conservation. In general, regulations governing minimum catch lengths are expected to reduce growth overfishing and increase the catch as a result of increases in the biomass. AD, however, also caused recruitment overfishing that occurs when mature sharks including pregnant females are fished down to a point where recruitment (R) is substantially reduced or fails (Sissenwine and Shepherd 1987). AD would perform better if the harvest of pregnant females or mature females with no experience of parturition were prohibited. This may be difficult in reality, however, because it is not possible for fishermen to easily determine whether a shark is mature or pregnant.

430 In the western and central North Pacific, Japanese offshore longliners
431 occasionally target blue shark to harvest their valuable fins and meat (Ishimura and
432 Bailey 2013). The blue shark caught in those areas are mainly juveniles and sub-adults
433 but included adults (60–160 cm precaudal length, aged 0–6 years) (Nakano 1994). Since
434 the ages of maturity for blue sharks are 5–7 years for females and 4–6 years for males
435 (Nakano 1994), fairly large mature sharks are occasionally caught (or retained) by
436 Japanese longliners. Establishing a minimum catch length could therefore be an
437 effective way to protect immature sharks, especially juvenile sharks (aged 0–1 years).
438 Regulations governing minimum catch lengths for Japanese longline fisheries have the
439 potential to prevent growth and recruitment overfishing of blue sharks in the real world.

440 Time and area closure is another effective method for appropriately managing
441 the blue shark, because these sharks have sex-specific migration and distribution
442 patterns (Nakano 1994). It would thus be possible to avoid harvesting in waters
443 primarily inhabited by females. This method has the additional advantage of possibly
444 mitigating the impact of bycatch (Dunn et al. 2011; Cambie et al. 2013) and protecting
445 nursery and other grounds where vulnerable life history stages such as pupping and
446 mating occur (Kinney and Simpfendorfer 2009). Taking into account the spatiotemporal
447 distribution changes of pelagic sharks (Kai et al. 2015), a dynamic closure may be more
448 appropriate for the management of these sharks than a conventional static closure,
449 because it establishes marine protected areas corresponding to changes in the condition
450 of the ecosystem and/or population status (Game et al. 2009). However, we point out
451 that this will only work for fisheries targeting shark. Tuna fisheries will continue to
452 catch blue shark in the closed area and some of the sharks will die. As a result, the
453 effectiveness of the measure will be diluted by the tuna fisheries. Other forms of

454 mitigation measures on the tuna fisheries such as avoiding shark lines and wire traces
455 may mitigate the capture of sharks in the temporarily closed areas.

456 Regime shifts in physical oceanography are responsible for inter-decadal
457 change in marine biomass (Kawasaki 2013). Although we assumed that regime shifts
458 changed the reproductivity of the blue shark, these shifts can also change growth
459 production. Little is known of blue shark life history parameters such as the intrinsic
460 growth rate, which appears to vary greatly with regime shifts and other environmental
461 changes. Because the blue shark is long lived (about 16 years for males) and sexual
462 maturation occurs late (in 4–7 years), it is difficult to directly understand how climate
463 affects the abundance of blue sharks. Based on the Kuroshio/Oyashio ecosystem, Yatsu
464 et al. (2013) speculated that highly migratory transitional pelagic species such as the
465 blue shark might increase at the beginning of warming but would decrease as
466 temperatures continued to rise. Juvenile blue sharks are known to migrate into the high
467 Chl-a area of the western North Pacific (Ichii et al. 2004). Their utilization of this
468 productive area could therefore contribute to their high growth rate and the consequent
469 high productivity of the blue shark (Ichii et al. 2016). Mortality of sharks caused by
470 fisheries has been recognized as one of the main factors driving the decline in their
471 populations (Báez 2015). It could thus be important for shark conservation policies to
472 understand the relationships between declines in the population and regime shifts
473 (Worm et al. 2013).

474 The harvest of male sharks (MA) under the polyandrous mating mechanism
475 performed worse than the monogamous mating mechanism with respect to the risk of
476 fishery collapse, mean yield, and mean biomass as a whole, while the harvest of female
477 sharks (FE) under the polyandrous mating mechanism performed better than the

478 monogamous mechanism (Fig. A2). The differences in the mating mechanisms had a
479 small impact on the performance of other harvest strategies (JU, AL, and AD) (Fig. A2).
480 These results suggested that the polyandrous mating mechanism of blue shark can make
481 MA less effective, FE more effective, and other harvest strategies ineffective. Although
482 multiple paternity was revealed in the microsatellite DNA profiling of blue shark litters
483 (Fitzpatrick, 2012), the actual harem ratio of blue shark is unclear, because female
484 sharks can store spermatozoa in their oviducal gland until the female is ready for
485 fertilization, and they utilize internal fertilization (Pratt, 1979). Male sharks thus have
486 many opportunities to mate with other female sharks in a single breeding season after
487 mating with the first female. The promiscuous sexual behavior of blue shark can result
488 in a harem ratio of close to 1:1 on average. It is therefore essential to carefully monitor
489 changes in recruitment if either MA or FE is applied to the management of blue sharks.

490 Taking ecological characteristics such as spatial segregation by sex and
491 ontogenetic stages into consideration, the harvest of males (MA) had the lowest impact
492 on the overall reproductivity of blue shark in the North Pacific. In this simulation
493 analysis, the harvest of males only was estimated to increase to a level that resulted in
494 maximum sustainable yield (MSY) by increasing biomass without collapsing the
495 fishery. The performance of MA was also better than that of the harvest of all sharks
496 (AL), a common harvest strategy that does not consider the ecological characteristics of
497 pelagic sharks. MA is suitable for longline fisheries due to their characteristics and
498 ability to mostly identify sex by the sharks' external form and to release sharks without
499 considerable damage. However, it is essential to carefully monitor the recruitment, as
500 the sex ratio of MA biased toward females might reduce the pregnancy rate due to
501 uncertainties in the mating mechanism.

502

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508

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688

689 Table 1. Three biological reference points (MSY, maximum sustainable yield; B_{msy} ,
 690 biomass at MSY; F_{msy} , fishing mortality rate at MSY) in an equilibrium state under
 691 different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult
 692 sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and
 693 (5) harvest of all sharks (AL). Parameter values are set at default values (see Table A1).
 694

Harvest strategy	MSY (tons)	Bmsy (tons)	Fmsy (year ⁻¹)
JU	19.2	1037.8	0.151
AD	75.0	1004.2	0.103
MA	44.3	1404.6	0.086
FE	23.6	1601.2	0.066
AL	56.1	986.7	0.058

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699

700 Figure captions

701

702 Fig. 1. Schematic model of pelagic sharks such as blue shark in the North Pacific that
703 account for spatial segregation by sex and ontogenetic stages. A population was
704 separated into five groups based on sex, maturity, and pregnancy. Variables y , x , Y , X ,
705 and X^p denote the number of immature males, immature females, mature males, mature
706 females, and pregnant females, respectively; R is a reproduction function that depends
707 on the number of pregnant females; r denotes the proportion of the population shifting
708 to the mature stage; and β denotes the pregnancy rate, which depends on the ratio
709 between the number of adult males and females. The areas of distribution are based on
710 Nakano (1994).

711

712 Fig. 2. Relationships between pregnant females and recruitment that accounts for the
713 reproductive rate. A low reproductive value ($a = 0.0245$) arises from a low-productivity
714 regime (thin line), and a high reproductive value ($a = 0.245$) arises from a
715 high-productivity regime (thick line). The reproductive value is scaled between 0 and 1
716 (vertical dotted line).

717

718 Fig. 3. Yield and biomass in the equilibrium state versus changes in fishing mortality
719 rate (F) under different harvest strategies: (1) harvest of juvenile sharks (JU), (2)
720 harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female
721 sharks (FE), and (5) harvest of all sharks (AL). Parameter values are set at default
722 values (see Table A1).

723

Fig. 4. Sensitivity analyses of F_{msy} and MSY (maximum sustainable yield) to natural mortality rate (M) and steepness (h) of a stock-recruitment model (Beverton-Holt) under different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL). The boxplot denotes interquartile ranges of each value. M for each group was changed from $0.5M$ to $1.5M$ in $0.01M$ increments, and steepness was changed from 0.21 to 0.99 in 0.0078 increments. Other parameter values are set at default values (see Table A1).

Fig. 5. Examples of population dynamics for different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL), under different patterns of regime shifts. Panel (a) depicts Scenario (I): no regime shifts during 60 years of a high-productivity regime. Panel (b) depicts Scenario (II): no regime shifts during 60 years of a low-productivity regime. Panel (c) depicts Scenario (III): regime shifts with a high-productivity regime for the first 30 years and a lower-productivity regime for the next 30 years. Panel (d) depicts Scenario (IV): regime shifts with a lower-productivity regime for the first 30 years and a high-productivity regime for the next 30 years. Parameter- a for Scenarios (III) and (IV) was fixed under a lower-productivity regime. Dotted black line indicates the threshold of fishery collapse. Red lines of the population trajectory indicate incidences of fishery collapse.

Fig. 6. Risk of fishery collapse, mean yield, mean biomass versus changes in reproductive rate from 1 to 0 under a low-productivity regime (see Fig. 2), and

relationships between mean risk and mean biomass, mean risk and mean yield, and mean yield and mean biomass under the regime shifts of Scenario (III) and different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).

753

Fig. 7. Risk of fishery collapse, mean yield, and mean biomass versus changes in reproductive rate from 1 to 0 under a low-productivity regime, and relationships between mean risk and mean biomass, mean risk and mean yield, and mean yield and mean biomass under the regime shifts of Scenario (IV) and different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).

760

Fig. 8. Mean relative yield to MSY (Y/Y_{msy}) and mean relative biomass to biomass at MSY (B/B_{msy}) under the regime shifts of Scenarios (III) and (IV) and different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).

Fig.1

91x58mm (300 x 300 DPI)

Fig.2

203x135mm (300 x 300 DPI)

Fig.3

304x365mm (300 x 300 DPI)

Fig.4

203x162mm (300 x 300 DPI)

Fig.5

203x162mm (300 x 300 DPI)

Fig.6

304x365mm (300 x 300 DPI)

Fig.7

304x365mm (300 x 300 DPI)

Fig.8

127x63mm (300 x 300 DPI)

1 Appendices

2 Appendix A

3 A1. Equilibrium analysis

4 This analysis searches for a condition under which a population is sustainable
 5 by generating a positive equilibrium point. First, we search for the equilibrium state
 6 with no fishing ($x_{t+1} = x_t$, $y_{t+1} = y_t$, $X_{t+1} = X_t$, $Y_{t+1} = Y_t$, $X^P_{t+1} = X^P_t$) using Eqs. (1) to (5) as
 7 follows:

$$8 \quad x = \gamma R + S^x(1 - r^x)x, \quad (A.1)$$

$$9 \quad y = (1 - \gamma)R + S^y(1 - r^y)y, \quad (A.2)$$

$$10 \quad X = S^X r^x x + S^X \left(1 - \frac{Y}{X+Y}\right) X + S^X X^P, \quad (A.3)$$

$$11 \quad Y = S^Y r_y y + S^Y Y, \quad (A.4)$$

$$12 \quad X^P = S^{X^P} \frac{Y}{X+Y} X. \quad (A.5)$$

13 These equations can generate a positive equilibrium point:

$$14 \quad N^* = (x^*, y^*, X^*, Y^*, X^{P*})$$

15 where N represents a population number at the equilibrium state (*). From Eq. (A.1),

$$16 \quad x^* = \frac{\gamma}{1 - S^x(1 - r^x)} R^*. \quad (A.6)$$

17 From Eq. (A.2),

$$18 \quad y^* = \frac{1 - \gamma}{1 - S^y(1 - r^y)} R^*. \quad (A.7)$$

19 From Eq. (A.5), $\frac{XY}{X+Y} = \frac{X^P}{S^{X^P}}$. When this equation is substituted into Eq. (A.3), we obtain

$$20 \quad X^* = \frac{S^X r^x x}{(1 - S^x)} - \frac{S^X (1 - S^{X^P}) X^P}{(1 - S^x) S^{X^P}}. \quad (A.8)$$

21 From Eq. (A.4),

$$Y^* = \frac{S_Y r_Y y}{1 - S_Y} \quad (A.9)$$

Here, we replace the equations as follows: $A = \frac{\gamma}{1 - S^X(1 - r^X)}$, $B = \frac{1 - \gamma}{1 - S^Y(1 - r^Y)}$, $C = \frac{S^Y r^Y}{1 - S^Y}$,

$D = \frac{S^X r^X}{(1 - S^X)}$, $F = \frac{S^X(1 - S^X)}{(1 - S^X)S^{X^P}}$. The variables in the equilibrium state are then rewritten as

follows:

From Eq. (A.6),

$$x^* = AR^* \quad (A.10)$$

From Eq. (A.7),

$$y^* = BR^* \quad (A.11)$$

From Eq. (A.8),

$$X^* = Dx^* - FX^{P^*} \quad (A.12)$$

From Eq. (A.9),

$$Y^* = Cy^* \quad (A.13)$$

From Eq. (A.5),

$$X^{P^*} = S^{X^{P^*}} \left(\frac{Cy^*}{(Dx^* - FX^{P^*}) + Cy^*} \right) (Dx^* - FX^{P^*}) \quad (A.14)$$

Substitute Eqs. (A.10) to (A.13) to obtain Eq. (A.14), and rearrange the formula as

$$S^{X^P} ABCDR^{*2} - (S_{X^P} BCF + AD\delta^{-1} + BC)X^{P^*}R^* + FX^{P^*2} = 0 \quad (A.15)$$

Eq. (A.15) can be rewritten as

$$QR^{*2} - zX^{P^*}R^* + F\delta^{-1}X^{P^*2} = 0 \quad (A.16)$$

where $Q = S^{X^P} ABCD$, and $z = CB + AD\delta^{-1} + S^{X^P} CBFS$.

Divide both sides of Eq. (A.16) by R^2 to obtain

$$Q - z\frac{X^{P^*}}{R^*} + F\left(\frac{X^{P^*}}{R^*}\right)^2 = 0 \quad (A.17)$$

Accordingly, we can generate the spawning per recruit (SPR) by finding the solution of Eq. (A.17) in

$$SPR = \frac{X^{P^*} W^X}{R^*} = \left(\frac{z \pm \sqrt{z^2 - 4FQ}}{2F} \right) W^X, \quad (A.18)$$

where W is the body weight of an individual. Here, the function of recruitment is expressed by the Beverton-Holt (BH) stock-recruitment model:

$$R^* = \frac{aX^{P^*} W^X}{1 + bX^{P^*} W^X}. \quad (A.19)$$

Substitute Eq. (A.19) into Eq. (A.18) to obtain

$$X^{P^*} = \frac{aSPR - 1}{bW^X}. \quad (A.20)$$

If $X^* = Dx^* - FX^{P^*} > 0$ in Eqs. (A.12) and (A.14), N^* becomes a positive value.

Hence, the existence condition of the equilibrium point is

$$Dx^* - FX^{P^*} = DA \frac{aX^{P^*} W^X}{1 + bX^{P^*} W^X} - FX^{P^*} > 0. \quad (A.21)$$

Rearrange the equation and we can generate the existence condition:

$$\frac{ADaW^X - F}{bW^X F} > X^{P^*} > 0. \quad (A.22)$$

Next, the function of recruitment is expressed by the Ricker (RI) stock-recruitment model:

$$R^* = aX^{P^*} W^X e^{-bX^{P^*} W^X}. \quad (A.23)$$

Substitute Eq. (A.23) into Eq. (A.18) to obtain

$$X^{P^*} = \left(\frac{1}{bW^X} \right) \log(aSPR). \quad (A.24)$$

If $X^* = Dx^* - FX^{P^*} > 0$ in Eq. (A.12) and Eq. (A.14), N^* becomes a positive value.

Hence, the existence condition of the equilibrium point is

$$Dx^* - FX^{P^*} = DAaX^{P^*} W^X e^{-bX^{P^*} W^X} - FX^{P^*} > 0,$$

$$X^{P^*} (DAaW^X e^{-bX^{P^*}W^X} - F) > 0. \quad (\text{A.25})$$

Because $X^{P^*} > 0$, $DAaW^X e^{-bX^{P^*}W^X} - F > 0$ must be satisfied. Accordingly, we can generate the existence condition:

$$\left(\frac{1}{bW^X}\right) \log\left(\frac{DAaW^X}{F}\right) > X^{P^*} > 0. \quad (\text{A.26})$$

68

69 A2. Stock-recruitment (SR) relationships with steepness

70 Equations (A.19) and (A.23), rewritten using steepness (h), unfished

71 spawning stock biomass (X^{P^*}), recruits (R^*) of the SR relationship, and parameters a

72 and b , are expressed as follows:

$$\text{BH model: } hR^* = \frac{a0.2X^{P^*}W^X}{1+b0.2X^{P^*}W^X} \quad (\text{A.27})$$

74 Substitute Eq. (A.20), the unfished condition of recruitment, into Eq. (A.27) to obtain

$$h = \frac{0.2(1+bX^{P^*}W^X)}{1+0.2bX^{P^*}W^X} = \frac{1+bX^{P^*}W^X}{5+bX^{P^*}W^X}, \quad (\text{A.28})$$

$$\text{76 where } a = \frac{4h}{SPR(1-h)} \text{ and } b = \frac{5h-1}{X^{P^*}W^X(1-h)}.$$

$$\text{77 RI model: } hR^* = a0.2X^{P^*}W^X e^{-0.2bX^{P^*}W^X} \quad (\text{A.29})$$

78 Substitute Eq. (A.24), the unfished condition of recruitment, into Eq. (A.29) to obtain

$$\text{79 } h = 0.2e^{0.8bX^{P^*}W^X}, \quad (\text{A.30})$$

$$\text{80 where } a = \frac{(5h)^{1.25}}{SPR} \text{ and } b = \frac{5\log(5h)}{4X^{P^*}W^X}.$$

81

82 A3. Catch equations

83 Biomass, B , is given by the equation

$$\text{84 } B = xW^x + yW^y + XW^X + YW^Y + X^P W^X. \quad (\text{A.31})$$

85 Yield, Y , in biomass is given by the equation

$$86 \quad Y = B[1 - \exp(-F)], \quad (\text{A.32})$$

87 where F is the fishing mortality rate.

88

89 A4. Initial recruitment and biomass

90 Initial recruitment in number ($R_0 = 10,000$) at the unfished condition was
 91 arbitrarily given to calculate the quantities of MSY levels. The carrying capacity was
 92 estimated based on the initial recruitment using the stock-recruitment relationships at
 93 the unfished condition.

94

95 Appendix B

96 B1. Biological parameters

97 We used the following method to generate the biological parameters of blue
 98 shark in Table A1. Duration of the immature stage, τ , was derived from the median
 99 value of mature ages for male (aged 4–6 years) and females (aged 5–7 years) in the
 100 North Pacific (Nakano 1994). Maximum age, A , was derived from knowledge of blue
 101 shark in the North Pacific (Blanco-Parra et al. 2008). Length at age, L_a , was derived
 102 from knowledge of blue shark in the North Pacific (Nakano 1994):

$$103 \quad \text{Male: } L_a = 289.7[1 - \exp\{-0.129(a + 0.756)\}], \quad (\text{B.1})$$

$$104 \quad \text{Female: } L_a = 243.3[1 - \exp\{-0.144(a + 0.849)\}], \quad (\text{B.2})$$

105 where L is precaudal length (PCL, cm) and a is age. Weight (kg) at age, W_a , was derived
 106 from the weight-length relationships of blue shark in the North Pacific (Nakano 1994):

$$107 \quad \text{Male: } W_a = 5.388L_a^{3.102} \times 10^{-6}, \quad (\text{B.3})$$

108 Female: $W_a = 3.293L_a^{3.225} \times 10^{-6}$. (B.4)

109 Natural mortality rate at age, M_a , was derived from an empirical equation (Peterson and
110 Wrobloski 1984):

111 $M_a = 1.92(W_a \times 10^3)^{-0.25}$. (B.5)

112 Natural mortality rates of immature and mature sharks, male and female, were estimated
113 using the mean value of each duration. The natural mortality rate of pregnant females
114 was assumed to be the same as that of mature females. The mean body weight of
115 immature and mature sharks was estimated using the equation weighted by the natural
116 mortality rate and fishing mortality rate:

117 $\bar{W} = \sum_j \frac{W_j \exp\{-\sum_1^j (M_k + F_k)\}}{\sum_j \exp\{-\sum_1^j (M_k + F_k)\}}$, (B.6)

118 where j is the total number by age in each group, and k is the age of M and F for each
119 group.

121 B2. Several growth curves of North Pacific blue shark

122 In the North Pacific, several sex-specific growth curves of blue shark were
123 estimated using data collected at different areas with different size ranges. However we
124 used sex-specific growth curves estimated by Nakano (1994) because the data is
125 collected from across the North Pacific and a wide range of size classes from 30 to 220
126 cm PCL is used. On the other hand, three sex-specific growth curves were estimated
127 using data collected from limited areas: the northwest coast of Mexico (Blanco-parr et al.
128 2008), California waters (Cailliet and Bedford 1983), and offshore and coastal areas
129 around Taiwan (Hsu et al. 2011). Tanaka et al. (1990) estimated sex-specific growth
130 curves using data from the western Pacific off Japan and the eastern Pacific off

California; however, the data have no sizes smaller than 110 cm in total length and these data can therefore cause a large bias in the estimation of the parameter.

Appendix C

C1. Ricker model

The magnitude of biological reference points changed considerably, though the results in the Beverton-Holt and Ricker models tended to be similar except that the value of MSY for FE was larger than that for MA, and the value of B_{msy} for JU was smaller than that for AD (Table A2). The magnitude of steepness as well as the strength of the density-dependent compensation had a large impact on the values of MSY, especially for AD and AL, though the results in the Beverton-Holt and Ricker models tended to be similar (Fig. A1).

Appendix D

D1. Uncertainty in mating mechanism

The influence of sex ratio on mating success was modeled using the harmonic mean birth function (Caswell 2001):

$$\beta(X, Y) = \frac{Y}{X\delta^{-1} + Y}, \quad (D.1)$$

where δ is the harem size. When $\delta = 1$, Eq. (D.1) assumes monogamy (one female with one male in a single breeding season), where the pregnancy rate β is 0.5 under the female-male sex ratio of 1:1. When $\delta < 1$, Eq. (D.1) assumes polyandry (one female with multiple males in a single breeding season). Since there is no information about the harem size of blue shark, δ is assumed to be 1/3 and 1/9, where the pregnancy rate is 0.25 and 0.1, respectively, under the female-male sex ratio of 1:1. Basecase (default)

parameters in Table 1 are used for the simulation study. Scenarios (III) and (IV) are used to compare the performance statistics.

Appendix References

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174 Appendix Tables

175

176 Table A1. Default parameters based on biological data of blue shark.

Parameter name	Symbol	Unit	Stage	Sex	Value
Natural mortality	M^x	year ⁻¹	Juvenile	F	0.247
	M^X		Adult	F	0.119
	M^y		Juvenile	M	0.260
	M^Y		Adult	M	0.109
Body weight *	W^x	kg	Juvenile	F	9.51
	W^X		Adult	F	67.8
	W^y		Juvenile	M	8.52
	W^Y		Adult	M	93.0
Duration of immaturity	τ^x	year		M	6
	τ^y			F	5
Maximum age	A^x	year		M	16
	A^y			F	12
Sex ratio	γ	None			0.5
Mating relationships between male and female	δ	None			1
Steepness	h				0.6

177 * Values of body weights in this table were derived from Eq. (B6) with F=0 for all stages.

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181

182

183 Table A2. Biological reference points in the equilibrium state under different harvest
184 strategies in the case of Ricker stock-recruitment relationships. Biological reference
185 points (MSY, maximum sustainable yield; B_{msy} , biomass at MSY; F_{msy} , fishing
186 mortality rate at MSY) in the equilibrium state under different harvest strategies: (1)
187 harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male
188 sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).
189 Parameter values are set at default values except for the stock-recruitment relationships
190 (see Table A1).

191

Harvest strategy	MSY (tons)	B_{msy} (tons)	F_{msy} (year ⁻¹)
JU	72.1	1305.4	0.421
AD	289.8	1806.8	0.390
MA	83.2	2688.2	0.276
FE	91.1	5278.2	0.206
AL	228.6	1348.4	0.186

192

193

194

195 Appendix figure

196

197

198

199 Fig. A1. Sensitivity analyses of F_{MSY} and MSY (maximum sustainable yield) to natural
 200 mortality rate (M) and steepness (h) of the stock-recruitment model (Ricker) under
 201 different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult
 202 sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and
 203 (5) harvest of all sharks (AL). The boxplot denotes interquartile ranges of each value.
 204 Parameter values are set at default values (see Table A1).

205

Fig. A2. Relationships between mean risk and mean biomass, mean risk and mean yield, and mean yield and mean biomass, under the mating mechanisms of monogamy and polyandry where the ratios (e.g. 1:1) indicate the harem ratio of female to male, the regime shifts of Scenarios (III) and (IV), and different harvest strategies: (1) harvest of juvenile sharks (JU), (2) harvest of adult sharks (AD), (3) harvest of male sharks (MA), (4) harvest of female sharks (FE), and (5) harvest of all sharks (AL).