Stock-recruitment relationships of the North Pacific blue shark [1]

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Abstract

This working paper provides stock-recruitment relationships of blue shark (*Prionace glauca*) in the North pacific. We developed a pre-recruit survival model for the early life history of blue sharks and combined it with an existing model for the reproductive ecology of teleost species. We used biological data collected from wide areas of the western North Pacific between 2010 and 2016 to estimate key biological parameters. The model provides a point estimate for steepness, which is a fraction of unfished recruitment when spawning stock biomass is 20% of the species' unfished spawning stock biomass. We conducted numerical simulations to incorporate uncertainties in the biological parameters. The mean values and their standard deviations for steepness were 0.68 (standard deviation = 0.073) for the Beverton-Holt model and 1.17 (standard deviation = 0.314) for the Ricker model. The curves showed a steep slope around the lower spawning biomass for both models and a slight decline of recruitment at high spawning stock biomass for the Ricker model. These results suggest that the stock-recruitment relationship in North Pacific blue shark was high density-dependent and that its productivity is higher than that of other pelagic sharks. We discuss the plausibility of the estimates as a stock-recruitment relationships of blue shark.

Introduction

The blue shark (*Prionace glauca*) is a large, highly migratory oceanic pelagic shark found throughout the world in tropical and temperate seas (Nakano and Stevens, 2008), and it is the world's most abundant pelagic shark species (Nakano, 1994; Nakano and Seki, 2003).

Stock assessment of North Pacific blue shark that was conducted in 2014 using a stock synthesis model with the function of a low-fecundity stock-recruitment relationship (LFSR) (Taylor et al., 2013). It was found that the parameters (i.e. shapes) of the LFSR had a large impact on the stock status concerning whether the stock biomass had become overfished or was being overfished (ISC, 2014). In particular, it is unclear how density dependence influences the relationships between spawning biomass and recruitment. It is therefore urgently essential to clarify the stock-recruitment relationships for North Pacific blue shark.

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Materials and Methods

We develop a pre-recruit survival model for the early life history of blue sharks and combine it with an existing model for the reproductive ecology of teleost species. Mangel *et al*. (2010) derived equations of steepness (*h*) from an age-structured model with Beverton-Holt and Ricker recruitments:

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$$h = \frac{\alpha_s(1-r)\overline{W_f}}{4+\alpha_s(1-r)\overline{W_f}} \quad \text{for the Beverton-Holt model} \tag{1}$$

and

$$h = 0.2(\alpha_s(1-r)\overline{W_f})^{0.8} \quad \text{for the Ricker model,} \tag{2}$$

where the unit of α_s is new individuals per spawning biomass, r is a sex ratio, and $\overline{W_f}$ is the expected surviving mature biomass per recruit. To find α_s, we consider a female fish of age a, with mass $W(a)$, length $L(a)$, and probability of being mature $p_{f,m}(a)$. If we suppose that $\psi(W(a))$ is the fecundity of this individual in a single spawning event, $S_l(d_l)$ is larval survival to recruited day d_l from spawning day, and s_f is the spawning frequency, and since the total number of eggs spawned by a female at a certain age contributes to new individuals after depletion, the number of new individuals per spawning biomass in this case would be

$$\alpha_s = \frac{\psi(W(a))S_l(d_l)s_f}{W(a)}. \tag{3}$$

The expected surviving mature biomass per recruit is defined as

$$\overline{W_f} = \sum_{a=1}^{a_{max}} S(a)W_f(a)p_{f,m}(a) \tag{4}$$

where $S(a)$ is survival from age 0 to age a and is derived from the natural mortality M, where

$$S(a) = \prod_{i=0}^{a-1} \exp(-M(i)) \tag{5}$$

and W_f is the body mass of female fish. It is assumed that $W(a)$ is allometrically related to length so that $W(a) = c_1 L(a)^{c_2}$ where c_1 and c_2 are constants and where

$$L(a) = L_\infty(1 - e^{-k(a-a_0)}) \tag{6}$$

where L_∞ is asymptotic size, k is the growth rate, and a_0 is the theoretical age at length 0.

The most significant difference between teleost species such as tunas and pelagic sharks is their reproductive strategy. The former produces eggs that hatch outside the body of the female, and the latter produces eggs that hatch inside the body and the female then gives birth to live young. We seek to develop a model that accounts for the pre-recruit survival of blue shark while accounting for differences in the survival rate at four distinct life history stages before recruitment: fertilized eggs (stage 0), embryos inside the body of female fish (stage 1), neonates immediately after pupping (stage 2), and pre-recruit neonates (stage 3). We use a product of the survival rates at each stage:

$$S_{pre} = S_0 S_1 S_2 S_3 \tag{7}$$

where S_{pre} is a pre-recruit survival rate and S_x is a survival rate at stage x (i.e. from 0 to 3). The survival rates at stages 0 and 1 are considered to be extremely high, because the survival is not dependent on competition, predation, or environmental influences. On the other hand, the survival rates of embryos at stages 2 and 3 are subject to the influences of an extreme environment that cause high natural mortality in these embryos. We suppose that the natural mortality of embryos at stage 3 is size (or age)-dependent, and we estimate the values using a modified equation proposed in the stock assessment of Atlantic yellowfin tuna (*Thunnus albacares*) in 2016. The Method II (Walters *et*

al., 2016) is defined as

$$M(a) = \frac{M_T(a_{max}-a_c)}{ln\left(\frac{L_c}{L_c+L_\infty(\exp(k(a_{max}-a_c))-1)}\right)} ln\left(\frac{L(a)}{L(a)+L_\infty(\exp(k)-1)}\right) \tag{8}$$

where M_T is a Target-M defined as a mean natural mortality from the age at first full recruitment (a_c) to maximum age, and L_c is the body length at a_c. Here, the definition of the "first full recruitment" is used as an alternative meaning of the first estimated age for the calculation of the Target-M (i.e. age 0). We used a value of 0.23 as the Target-M that estimated from the meta-analysis for the natural mortality of blue shark in the world oceans (Campana *et al.*, 2004). Justification for the use of the Equation (8) is described in Semba and Yokoi (2016). The age of an embryo in year a can be replaced by the age in days d_e using $a = d_e/365$.

We also modify the other parts of the model proposed by Mangel *et al.* (2010). New individuals per spawning biomass in Equation (3) is replaced by

$$\alpha_s = \frac{\psi(L(a))S_{pre}S_{cycle}}{W(a)} \tag{9}$$

where $\psi(L(a))$ is litter size and S_{cycle} is the frequency of reproduction in a year. In addition, viviparous elasmobranchs are commonly known to have a next gestation without a resting period after parturition (Castro, 2009). The frequency of reproduction is calculated from $S_{cycle} = 1/y$ where y is a reproductive period (gestation + ovulation + resting) in a year. For the maturity ogives of females in Equation (4), we use a length-based logistic curve:

$$p_{f,m}(L(a)) = \frac{1}{(1+\exp(c_3+c_4L(a)))} \tag{10}$$

where c_3 and c_4 are constants.

The parameters of the pre-recruitment model for blue shark were estimated based on the biological data. It is well known that embryo of blue shark occurs from the fertilized-eggs, and then the placenta is formed from the tissue of the embryo. Hence blue shark fundamentally has a same number of fertilized eggs, placenta, and embryos. The value of S_0 was estimated using the occurrence rate of embryos from fertilized eggs for blue shark. We assumed that the embryos of blue shark were almost immortal at stage 1 (i.e. $S_1 \cong 1$), because we found that the total number of embryos before parturition was the same as the number of placenta for all pregnant females of blue shark (n = 124) who had no physical damage. Instead, we assumed that the embryos at stage 2 incurred natural mortality due to abnormalities such as prematurity or deformation (Figure 1). The values of S_2 were therefore estimated using the proportion of abnormal embryos. The values of S_0 and S_2 were assumed to be a normal distribution with average rates and standard deviations (Figure 2). The value of S_3 and the natural mortality after recruitment for females was estimated using Equation (7). The default values of all parameters are shown in Table 1.

The biological parameters of blue shark in the North Pacific have been amply studied

(Cailliet and Bedford, 1983; Nakano, 1994; Nakano and Seki, 2003; Blanco-Parra *et al.*, 2008; Carrera-Fernández, *et al.*, 2010). Uncertainties associated with age at length, weight at length, age at maturity, longevity, and reproductive ecology for blue sharks are lower than those for any other pelagic shark due to the high quality and quantity of the data. For example, Japanese longline fisheries in the eastern parts of Japan frequently land blue shark throughout the year, and the capture ranges of size are wide, from juvenile to adult for both sexes. The reliability of estimates for the vital parameters is therefore high. One problem is the natural mortality rate after parturition, as it represents the highest uncertainty in the life table of blue shark in the North Pacific. To characterize variation in the rate of natural mortality, we use gamma density (Mangel, 2006; Mangel *et al.*, 2010) so that the probability density function for *M* is

$$f(m) = \frac{\lambda^v}{\Gamma(v)} \exp(-\lambda m) m^{v-1} dm \tag{11}$$

where v and λ are parameters. In this formulation, the expected value of *M* is $E(M) = \bar{M} = \frac{v}{\lambda}$ and the coefficient of variation is $CV(M) = \frac{1}{\sqrt{v}}$ We use the theoretical equation (8) as the means for the probability density in Equation (11) and assume the same value of v for all ages.

A numerical simulation was conducted to estimate the steepness in a manner similar to Mangel *et al.* (2010) where the variation in steepness was created from the variation in survival. Imagine that we sub-sample *K* populations of simulated fish, with *N* female fish in each of the samples. The purpose is to determine the age for each of *N* fish in the sub-sample of the *k*th population. The procedure is as follows:

(i) Calculate the survival rate at age *a* of the *n*th fish in the *k*th population: $\tilde{S}(a_{n,k})$ is arbitrarily given using a uniformly distributed random variable $\tilde{U}_{n,k}$, where $\tilde{S}(a_{n,k}) = \tilde{U}_{n,k}$ and $S(a)$ is calculated from Equation (5);

(ii) Each population *k* experiences a series of values of $m_0, m_1, \ldots m_{a-1}$, drawn from the age-specific gamma density in Equation (11);

(iii) A search is conducted for an age *j* that can satisfy the inequality $\sum_{a=0}^{j} M(a) < -\log(\tilde{U}_{n,k}) < \sum_{a=0}^{j+1} M(a)$; and

(iv) When the inequality $\sum_{a=0}^{j+1} M(a) + \log(\tilde{U}_{n,k}) > -\log(\tilde{U}_{n,k}) - \sum_{a=0}^{j} M(a)$ is satisfied, 1 is added to the age *j*.

The determination of the age of the shark specifies the length, weight, and probability of maturity. In other words, a consideration of uncertainty in the natural mortality in the framework of numerical simulation results in considerations of uncertainties in the other biological parameters. Since Equations (4) and (9) could be used to calculate the steepness in Equations (1) and (2), it was possible to generate a frequency distribution for steepness based on the *K* populations of *N* fish. The values of *K*=200 and *N*=200 were used for computation. To create the frequency distribution, values of steepness between 0.2 and 1.0 in increments of 0.013 were discretized for the Beverton-Holt

model and between 0.2 and 3.0 in increments of 0.045 for the Ricker model. Repeating the process described above made it possible to obtain multiple versions of the frequency distribution for steepness. The empirical distributions for the steepness were then fit to the beta density (Mangel, 2006; Mangel *et al*., 2010). The computation of the numerical simulation was implemented using a code based on the R package (R Core Team, 2013).

The stock-recruitment relationship based on pre-recruit survival is currently available within the stock synthesis assessment platform (Taylor, 2013). It is therefore crucial for future stock assessments of North Pacific blue shark to specify the parameters (z_{frac} and β) using the output of the stock-recruitment relationships for the Beverton-Holt and Ricker models in this study. The stock-recruitment relationships derived from the above models were both fit to the LFSR as:

$$R(t) = B(t)(\exp(-\log\left(\frac{R_0}{B_0}\right)\left(z_{frac}\left(1 - \left(\frac{B(t)}{B_0}\right)^{\beta}\right)\right) - 1)) \tag{12}$$

where R is the recruitment in year t, B is the spawning output in year t, R_0 is the recruitment at unfished equilibrium, B_0 is the spawning output at unfished equilibrium, and z_{frac} and β are parameters.

Results

The resulting probability densities of the natural mortality rate showed symmetric curves, and the ranges were wider for younger ages (Figure 3a). The age-dependent natural mortality rate generated variations in the survival ratio by age (Figure 3b). Under the large uncertainties in the survival ratio, empirical frequency distribution showed relatively narrow ranges of steepness for the Beverton-Holt model and wide ranges of steepness for the Ricker model (Figure 4). The mean and standard deviations obtained for 200 replicate runs showed wider ranges of error bars around the peak of the fitted curves (Figure 4). The mean values and their standard deviations (SD) for steepness were estimated using beta density, and those mean values were 0.68 (SD = 0.073) and 1.17 (SD = 0.31) for the Beverton-Holt model and the Ricker model, respectively (Figure 4). The curves showed a steep slope around the lower spawning biomass (Figure 5), and the Ricker model showed a slight decline of recruitment at the high spawning stock biomass. The z_{frac} and β of LFSR were 1.03 and 0.28, respectively, for the Beverton-Holt model, and 0.69 and 1.00 for the Ricker model. These results suggested that the stock-recruitment relationship of North Pacific blue shark was high density-dependent, and that productivity was higher than that of other pelagic sharks.

Discussion

Productivity (i.e. population growth rate λ) of pelagic sharks has been estimated using life tables and age-structured Leslie matrices (e.g. Cortés, 2002; Cortés *et al.*, 2010; Tsai *et al.*, 2014; Liu *et al*., 2015). Cortés (2002) and Cortés *et al*. (2010) showed that blue shark exhibited the highest

productivity (λ = 1.401 year^{-1} and λ = 1.331 year^{-1}, respectively) among the pelagic sharks. The stock-recruitment relationship (steepness: h) of blue shark, however, was unclear in the world's oceans except for the Atlantic Ocean. Cortés (2015) estimated the steepness of blue shark for the North and South Atlantic stocks using a method similar to that used in this study, but pre-recruit survival was not considered in the model. The estimates of steepness ranged from 0.73 to 0.93 for the North Atlantic stock and from 0.55 to 0.84 for the South Atlantic. In this paper, we first quantified the values of steepness— h = 0.68 for Beverton-Holt— h = 1.17 for Ricker — using the modeling of pre-recruit survival of pelagic sharks with reliable life history parameters. The value of BH model was lower than that of highly migratory tuna species such as Pacific bluefin tuna (*Thunnus orientalis*) (h = 0.999) (Mangel *et al*., 2010), while the estimates was relatively high compared to those of other pelagic sharks. Harley (2002) demonstrated wide ranges of steepness between 0.25 and 0.67 for different scenarios of natural mortality rate by growth stage using the statistical catch-at-length model for porbeagle shark (*Lamna nasus*) in the Northwest Atlantic. Cortés *et al*. (2006) estimated a low value of steepness (h = 0.29) in their stock assessment of dusky shark (*Carcharhinus obscurus*) in the U.S. Atlantic and the Gulf of Mexico. Taylor *et al.* (2013) also estimated low values of steepness (h < 0.29) from the model's application to spiny dogfish. For pelagic sharks, it is generally assumed that recruitment is directly related to spawning stock size due to their overall life history strategy of slow growth rates, maturity at a late age, and low fecundity (Compagno, 2001). Blue shark, however, has a significantly different strategy: fast growth rates, maturity at an early age, and high fecundity (Nakano, 1994). These distinct biological strategies resulted in a high compensation (Figure 5), and it supports the fact that blue shark is the most abundant pelagic shark (Nakano and Stevens, 2008).

We examined the impact of the changes in the longevity on the estimates of steepness because there is no direct evidence to prove the maximum age although we used an observed maximum age: 16 for female (Fujinami *et al*., 2016) as a default value. An alternative maximum age of 24 was estimated using the empirical relationships between growth rate k and maximum age: $a_{max} = 5\ln(2)/k$ (Fabens, 1965). The value of maximum age had a large impact on the estimates of steepness (Fig.6). A lower maximum age (16) gave a higher steepness (h=0.68 for Beverton-Holt model and h=1.17 for Ricker model), whereas a higher maximum age (24) gave a lower steepness (h=0.62, the z_{frac} and β of LFSR were 0.850 and 0.327 respectively for Beverton-Holt model and h=0.97 for Ricker model). Additional sensitivity runs were summarized in Appendix table.

Our study produced model estimates of steepness of 0.68 and 1.17 respectively from two different stock-recruitment functions (Beverton-Holt and Ricker). These estimates imply an extraordinary ability of blue shark populations to compensate for declines in adult abundance through improved recruitment of juveniles to the spawning stock: the Beverton-Holt estimate indicates a 3.4-fold increase (0.68/0.20) in recruits per spawner compared with a population having

no density-dependent compensation, and the Ricker estimate suggests a 5.9-fold increase (1.17/0.2). While some density-dependent compensation following loss of spawners is inevitable, compensation at these estimated levels is likely to be very high because most previous estimates of steepness for sharks were less than 0.3 as we mentioned above.

It is considered that two main factors: survivorships and fecundity have a large impact on the compensation due to the density dependent. Survival rate may have a strong relation with prey and predator. Fecundity will increase as the nutritional conditions of adult female is increased. An increase of the prior recruitment survivorships directly makes the recruitment increase. An increase of the juvenile survivorships also may increase the growth rate leading to an earlier age or size at maturity, thereby an extended period of reproductive competence and reduction in length of the gestation period leading to shorter reproductive cycles. However, survivorships of blue shark might not be increased due to the reduction in the competition of the food and space because blue shark is the most wide-ranging shark/fish on Earth and is an omnivorous fish. In addition, the compensation due to an increase of the survivorships may not have a large impact on the growth and maturity for blue sharks because those estimates are quite stable and there is no large difference among individuals (Fujinami et al. 2016a,b). Generally, prior recruitment survivorships for sharks could be increased due to a decrease of the food competition as well as a reduction in adult biomass that resulting in reduction of the cannibalism on juveniles. However, the compensation due to the cannibalism is very rare for blue shark because there is little evidence that the blue shark feed on each other from a study of the feeding habit (Hernández-Aguilar et al., 2016). On the other hand, an increase of the nutritional condition may lead the rapid increase of the fecundity because the ranges of the fecundity at each size classes for blue shark were quite large (Fujinami et al. 2016a). If the nutritional condition is changed due to the density dependence resulted from the changes in the spawner, the fecundity is changeable in the ranges at each size classes. Fujinami et al. (2016a) showed that the range of fecundity from minimum to maximum value at each size classes was 45.3 on average and the range was 45.12 – 45.30. These results indicated that the fecundity can largely change by the individuals. Probably, the fecundity is changed by the nutritional condition at the habitat. If there is a small density dependence for the spwner, it has a high potential to increase the recruitment due to an improvement of the nutritional condition of the adult females. Current good condition of the stock status (ISC 2014) also means that the fecundity may increase if the stock biomass is decreased to the depleted level. The combinations of the increases in the survivorships and fecundity could be more increase the recruitment than the increase of the single effects. The value of steepness: 3.4 for BH model is likely because of these mechanisms. However, the high compensation due to the increase of the spawner (i.e. Ricker) is unlikely for blue shark because the possibility of the cannibalism among blue shark is quite low and the impact of the predation by other pelagic sharks on the blue shark stock is not large because the abundance of blue shark is quite larger

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than those of any other pelagic sharks. Ohshimo et al. (2016) showed that the CPUE of blue shark was approximately more than 20 times compared to that of shortfin mako.

In summary, a significant change in the survivorships due to the compensation is unlikely, while the change in the fecundity due to the compensation is likely and the combinations of survivorships and fecundity are likely as well. Therefore, the steepness of 0.68 is applicable as a parameter in the stock assessment model for blue shark in the North Pacific.

Reference

Blanco-Parra, M. P., Galván-Magaña, F., and Farías, F. M. 2008. Age and growth of the blue shark, *Prionace glauca* Linnaeus, 1758, in the Northwest coast off Mexico. Revista de Biología Marina y Oceanografía, 43: 513–520.

Cailliet, G. M., Martin, L. K., Harvey, J. T., Kusher, D., and Welden, B. A. 1983. Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. NOAA Technical Report NMFS, 8: 179–188.

Campana, S. E., Marks, L., Joyce, W., and Kohler N. 2004. Catch, bycatch and indices of population status of blue shark (*Prionace glauca*) in the Canadian Atlantic. SCRS/2004/080.

Carrera-Fernández, M., Galván-Magaña, F., and Ceballos-Vazquez, B. P. 2010. Reproductive biology of the blue shark, *Prionace glauca* (Chondrichthyes: Carcharhindae) off Baja California Sur, Mexico. aqua, International Journal of Ichthyology, 16: 101–110.

Castro, J. I. (2009). Observations on the reproductive cycles of some viviparous North American sharks. *Aqua, International Journal of Ichthyology* 15, 205-222.

Compagno, L. J. V. 2001. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Vol. 2. Bullhead, mackerel and carpet sharks (*Heterodontiformes*, *Lamniformes* and *Orectolobiformes*). FAO Species Catalogue for Fishery Purposes. No. 1, Vol. 2. Rome, FAO.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conservation Biology, 16: 1048–1062.

Cortés, E., Brooks, E. N., Apostolaki, P., and Brown, C. A. 2006. Stock assessment of dusky shark in the U.S. Atlantic and Gulf of Mexico. http://www.fisheries.noaa.gov/sfa/hms/species/sharks/documents/2006_dusky_shark_assessment_for_distribution.pdf

Cortés, E. 2015. Estimates of maximum population growth rate and steepness for blue sharks in the North and South Atlantic Ocean. Collective Volume of Scientific Paper of ICCAT. 72: 1180–1185.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth. 29: 265–289.

Fujinami, Y., Semba, Y., Okamoto, H., Ohshimo, S., and Tanaka, S. 2016a. Reproductive biology of

the blue shark, *Prionace glauca*, in the western North Pacific Ocean. ISC/16/SHARKWG-1/01.

Fujinami, Y., Semba, Y., Ijima, H., and Tanaka, S. 2016b. Age and growth estimation of the blue shark, *Prionace glauca*, in the western North Pacific Ocean. ISC/16/SHARKWG-1/02.

Harley, S. J. 2002. Statistical catch-at-length model for porbeagle shark (*Lamna nasus*) in the Northwest Atlantic. Collective Volume of Scientific Paper of ICCAT. 54: 1314–1332.

Hernández-Aguilar, S.B., Escobar-Sánchz, O., Galván-Magana, F. and Abitia-Cárdenas, L.A. 2016. Trophic ecology of the blue shark (Prionace glauca) based on stable isotopes (δ13C and δ15N) and stomach content. Journal of the Marine Biological Association of the United Kingdom, in press DOI: 10.1017/S0025315415001393

ISC. 2014. Stock assessment and future projections of blue shark in the North Pacific Ocean. Report of the Shark Working Group.
http://isc.fra.go.jp/pdf/ISC14/Annex%2013%20%20BSH%20assessment%20report%208-26-14-final.pdf

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology, 49: 627–647.

Mangel, M., Brodziak, J., and Dinardo, G. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. Fish and Fisheries, 11: 89–104.

Nakano, H. 1994. Age, reproduction and migration of blue shark in the North Pacific Ocean. Bulletin of National Research Institute of Far Seas Fisheries, 31: 141−256.

Nakano, H., and Seki, M. P. 2003. Synopsis of biological data on the blue shark, *Prionace glauca* Linnaeus. Bulletin of Fisheries Research Agency, 6: 18−55.

Nakano, H., and Stevens, J. D. 2008. The biology and ecology of the blue shark, *Prionace glauca*. *In* Sharks of the open ocean: biology, fisheries and conservation, pp. 140–151. Ed. by Camhi, M. D., Pikitch, E. K., and Babcock, E. A. Blackwell Publishing Ltd., Oxford.

Ohshimo, S., Fujinami, Y., Shiozaki, K., Mikihiko, K., Semba, Y., Katsumata, N., Ochi, D., Matsunaga, H., Minami, H., Kiyota, M. and Yokawa, K. 2016. Distribution, body length, and abundance of blue shark and shortfin mako offshore of northeastern Japan, as determined from observed pelagic longline data, 2000-2014. *Fisheries Oceanography*, 25:259–276.doi: 10.1111/fog.12149

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
http://www.R-project.org.

Semba, Y., and Yokoi, H. 2016. Update of age and sex specific natural mortality of the blue shark (*Prionace glauca*) in the North Pacific Ocean. ISC/16/SHARKWG-1/06.

Snelson Jr, F. F., Burgess, G. H., and Roman, B. L. 2008. The reproductive biology of pelagic

elasmobranchs. *In* Sharks of the open ocean: biology, fisheries and conservation, pp. 24–53. Ed. by Camhi, M. D., Pikitch, E. K., and Babcock, E. A. Blackwell Publishing Ltd., Oxford.

Taylor, I. G., Gertseva, V., Methot, R. D., and Maunder, M. N. 2013. A stock- recruitment relationship based on pre-recruit survival, illustrated with application to spiny dogfish shark. Fisheries Research, 142: 15–21.

Tsai, W. P., Sun, C. L., Punt, A. E., and Liu, K. M. 2014. Demographic analysis of the shortfin mako shark, *Isurus oxyrinchus*, in the Northwest Pacific using a two-sex stage-based matrix model. ICES Journal of Marine Science, 71: 1604–1618.

Walter, J., Sharma, R., Cass-Calay, S., Ortiz, M., Brown, C. (2016) Scaling natural mortality rate as a function of length or weight with an application to yellowfin tuna. SCRS/2016/116.

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Table 1. Default parameters based on biological data of the female blue shark.

No.	Function name	Parameter name	Symbol	Unit	Value	Reference
1	von-Bertalanffy growth curve	Asymptotic size	L_∞	cm in PCI	256.3	Fujinami et al. (2016b)
		Growth rate	k	year^{-1}	0.147	
		Theoretical age at length at 0	a_0	year	0.97	
2	Weight-length relationship		c_1		5.859	Fujinami et al. (2016a)
			c_2		3.093	
3	Length-based maturity		c_3		24.52	Fujinami et al. (2016a)
			c_4		-0.16	
4	Littersize-length relationship		c_5		-45.54	Fujinami et al. (2016a)
			c_6		0.455	
5	Natural mortality					
	Theoretical equation		M	year^{-1}	Not shown	Semba and Yokoi (2016)
		Target M	M_T	year^{-1}	0.23	Campana et al. (2004)
			a_c	year	0	
	Gamma distribution		v		9.7	Mangel et al. (2010)
			λ		Not shown	
6	No function	Maximum age	a_{max}	year	16	Fujinami et al. (2016b)
7	No function	Sex ratio	r		0.5	Nakano (1994)
8	Pre-recruit survival					
	Normal distribution	Survival at stage 0	S_0	year^{-1}	0.965	Estimated in this paper
	No function	Survival at stage 1	S_1	year^{-1}	1	
	Normal distribution	Survival at stage 2	S_2	year^{-1}	0.993	Estimated in this paper
	Theoretical equation		M	year^{-1}	Not shown	Semba and Yokoi (2016a)
9	Reproductive cycle					
	No function	Reproductive period	y		1	Fujinami et al. (2016) and Nakano (1994)
		Days to recruit from partrition	d	day^{-1}	365	Estimated based on Nakano (1994)
10	Stock-recruitment relationship					
		Unfished recruitment	R_0	Number in 1000	1000	Arbitrarily given
		Unfished spawning biomass	B_0	tons	25000	Arbitrarily given

.

Figures

Figure 1. Examples of abnormal embryos inside the uterus of pregnant females, of which (a) has no mouth and (b)is premature and (c) is normal. The two embryos in (b) were found in a pregnant female. Length of the bamboo scale beside the embryos is 30 cm.
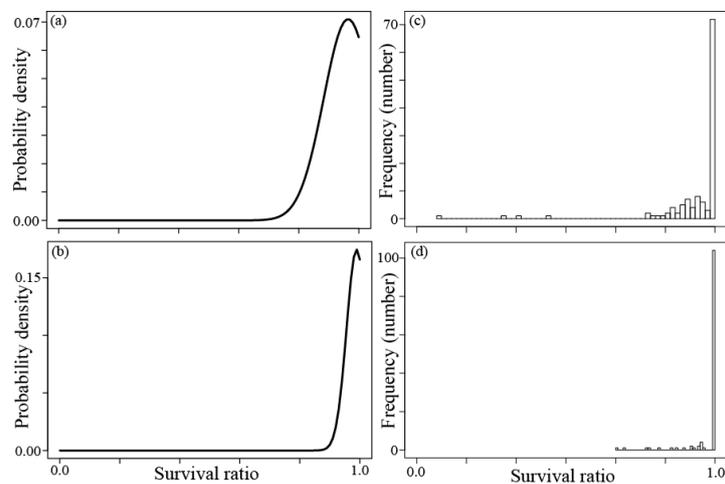

Figure 2. Probability density of survival ratio for (a) stage 0, fertilized eggs (mean and standard deviation: 0.965±0.081), and (b) stage 2, embryos immediately after parturition (mean and standard deviation: 0.993±0.026 cm). The mean and standard deviation of the normal distributions were given from the data of 122 females for (c) the frequency against the proportion of fertilized eggs that developed and (d) the frequency against the proportion of abnormal embryos to total embryos inside the uterus. The total observed numbers of normal, premature, and abnormal embryos were 4079, 22, and 19, respectively.
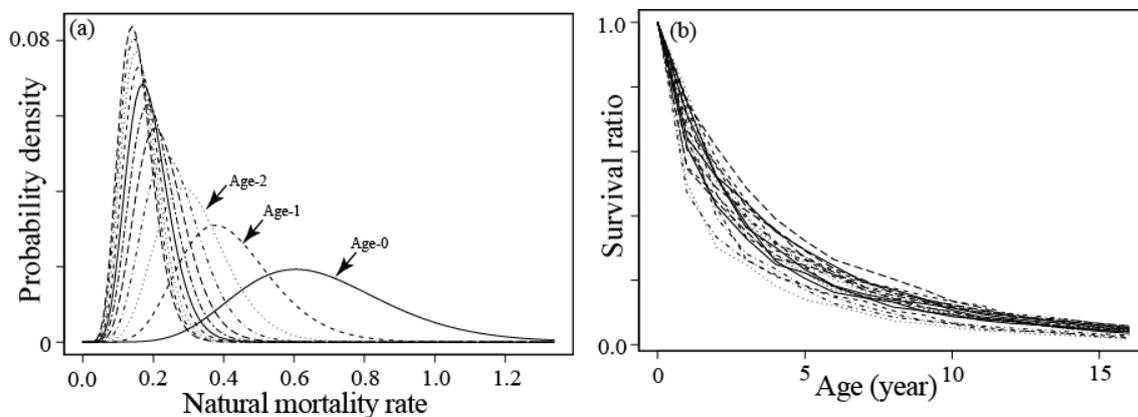
Figure 3. (a) Gamma distributions for age-dependent natural mortality rate and (b) sample survival trajectories (n=20) created by assuming a family of probability distributions for the rate of natural mortality dependent on age. Gamma distributions for ages older than 11 are not shown in (a).
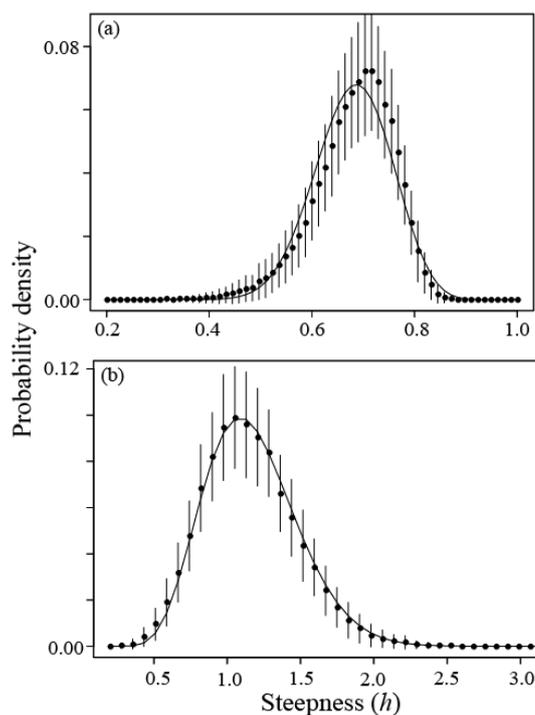

Figure 4. Empirical frequency distribution of steepness and the fitted curves (solid line) by beta distribution for (a) the Beverton-Holt model and (b) the Ricker model, for which the mean (filled circles) and its standard deviations (vertical bars) are shown for the empirical distribution.
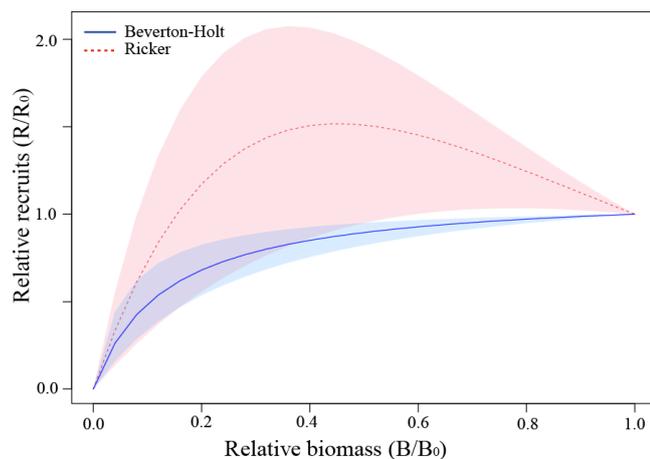

Figure 5. Estimates of North Pacific blue shark stock-recruitment relationship for the Beverton-Holt model (solid blue line) and the Ricker model (broken red line). Shaded blue and red areas denote 95% confidence intervals.
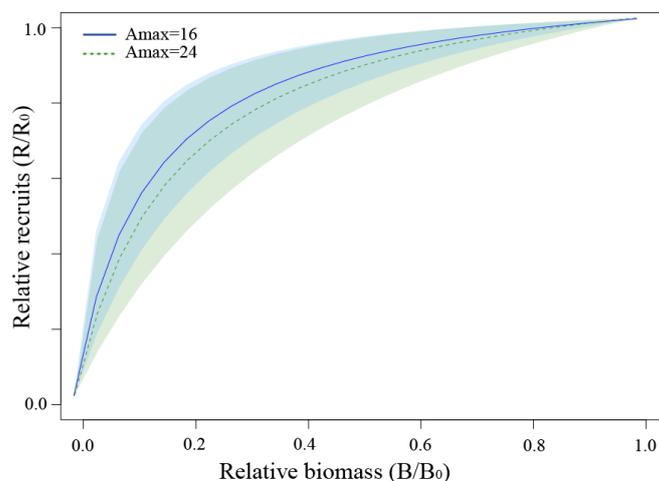

Figure 6. Impacts of the changes in the maximum age from 16 (solid blue line) to 24 (broken green line) on the estimates of North Pacific blue shark stock-recruitment relationship for the Beverton-Holt model.

Appendix

Table A1. Additional estimation of the steepness and parameters of the Low-Fecundity Stock-Recruitment function for eight scenarios with regards to the reproductive cycle and maximum ages. An empirical equation (Petersen and Wroblewski, 1984) and theoretical equation: Walter II (Walters et al. 2016) were used to estimate the natural mortality respectively and then steepness was estimated. Two reproductive cycles were used from Fujinami et al. (2016a) and Joung et al. (2011), and three maximum ages were calculated from the theoretical two equations (Fabens, 1965 and Chin and Liu, 2013). Growth, maturity, litter size were used from Fujinami et al. (2016a,b). Grey column shows the reference case in this study.

| | Empirical equation (Peterson and Wroblewski, 1984) | | Walter-II methods (Walter et al. 2016) based on the campana et al. (2004) | | | | | |
| | cycle=1 | cycle=2 | cycle=1 | cycle=2 | cycle=1 | cycle=2 | cycle=1 | cycle=2 |
			tmax=20	tmax=20	tmax=24	tmax=24	tmax=30	tmax=30
Steepness	0.942	0.890	0.657	0.495	0.623	0.459	0.565	0.406
Sfrac	1.000	1.000	0.954	0.546	0.850	0.473	0.699	0.371
Beta	0.389	0.370	0.299	0.446	0.327	0.485	0.378	0.552

Appendix references

Joung, S.J., Hsu, H.H., Liu, K.M., and Wu, T.Y. 2011. Reproductive biology of the blue shark, *Prionace glauca*, in the northwestern Pacific. ISC/11/SHARKWG-2/12.

Chin, C.P., and Liu, K.M. 2013. Estimate of the intrinsic rate of population increase for the blue shark in the North Pacific. ISC/13/SHARKWG-2/04.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth. 29: 265–289.

Fujinami, Y., Semba, Y., Okamoto, H., Ohshimo, S., and Tanaka, S. 2016a. Reproductive biology of the blue shark, *Prionace glauca*, in the western North Pacific Ocean. ISC/16/SHARKWG-1/01.

Fujinami, Y., Semba, Y., Ijima, H., and Tanaka, S. 2016b. Age and growth estimation of the blue shark, *Prionace glauca*, in the western North Pacific Ocean. ISC/16/SHARKWG-1/02.

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

Walter, J., Sharma, R., Cass-Calay, S., Ortiz, M., Brown, C. (2016) Scaling natural mortality rate as a function of length or weight with an application to yellowfin tuna. SCRS/2016/116.

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