![NPFC North Pacific Fisheries Commission]

Summary of the possible ranges of the key parameters in the age-structured stock assessment models for Pacific saury

Shin-Ichiro NAKAYAMA, Taiki FUJI, Satoshi SUYAMA, Miyako NAYA, Hiroomi MIYAMOTO, Midori HASHIMOTO

Fisheries Research and Education Agency, Japan

Summary

We summarized the key parameters in the age-structured models for Pacific saury and their possible ranges to be considered, based on our best biological knowledge and discussion so far. The key parameters we focus on in this document are: 1. natural mortalities for age 0 and age 1 fish (M_0 and M_1, respectively), 2. the treatment of age 0 fish spawning, and 3. the steepness of the Beverton-Holt stock recruitment relationship (h). We recommend to consider [1.71, 2.75] and [0.5, 1] as the possible range of M_0 and M_1/M_0, respectively. We also recommend to consider [0.05, 0.2] as a possible range for a degree of relative contribution of age 0 to age 1 egg production, interpreted as the product of maturation rate, relative fecundity per weight, and relative times of spawning in a spawning season. We also created a prior distribution of steepness parameter based on our best knowledge on PS biology to present a possible range of the steepness to be considered. The 0.025, 0.5, 0.975 percentiles of the distribution of h were 0.26, 0.96, and 0.99, respectively, indicating that we should not ignore the possibility that the steepness of PS might be smaller than is estimated from phylogeny. We recommend to check model sensitivities inside these ranges when the parameters are fixed, or, if they are estimated, to check whether the estimated values are inside the ranges or not.

Introduction

The North Pacific Fisheries Commission (NPFC) Small Scientific Commission (SSC) for Pacific saury (PS) is developing the next generation age-structured stock assessment model. Because the behavior of the age-structured models largely depend on the biological assumptions, clarifying uncertain parameters and observing the sensitivity of the model behavior against the assumptions of the parameters are essential to identify on which point we should focus. In this document, we summarize the key parameters and their possible ranges to be considered, based on our best biological knowledge and discussion so far. The key parameters we focus on in this document are: 1. natural mortalities for age 0 and age 1 fish (M_0 and M_1, respectively), 2. the treatment of age 0 fish spawning, and 3. the steepness of the Beverton-Holt stock recruitment relationship (h).

1. Natural mortality

Natural mortality coefficient, denoted by M, is one of the key parameters in the age-structured models, because it affects the scaling, resilience, reference points, etc. of the stock. Since M is difficult to estimate inside the age-structured models, it is generally fixed at plausible levels that are estimated outside the models. For this purpose, many M estimators, which are able to be calculated from easily observable traits, are developed [reviewed in Kenchington et al. (2014)].

For PS, the NPFC SSC PS previously discussed how to treat natural mortality and some candidate M for the age-structured models (Nakayama et al., 2019 and 2021; Hsu et al., 2022). A member applied an age-specific M in a preliminary age-structured models for PS and concluded that fixing, or at least restricting M (fixing the ratio of M at age 1 and 0, for example) is recommended, rather than a free estimation (Nakayama et al. 2019). The member's age-specific M were fixed at $M_0 = 2.04$ and $M_1/M_0 = 0.772$, where M_0 and M_1 were the natural mortality coefficients for age 0 and 1 fish, respectively, based on a known natural mortality estimator (Charnov et al., 2013). In contrast, another member applied a fixed, common M (shared by age 0 and 1, $M = 2.18$) derived by Fishlife (Thorson et al., 2017), which statistically estimate many biological traits based on phylogeny relationships (Hsu et al., 2022). In conclusion, we recommend to consider [1.71, 2.75] as the possible range of M_0, since this range includes all of the candidate values introduced so far (Nakayama et al., 2019, Hsu et al., 2022). There are only two values of M_1/M_0, 0.772 and 1, introduced so far (Nakayama et al., 2019 and 2021, Hsu et al., 2022). The value of M_1/M_0 is not likely to exceed 1 since age 1 fish have larger body size, and might be lower than 0.772. Therefore we recommend to consider [0.5, 1] as the possible range of M_1/M_0. Note that M_1 here does not include the infinite mortality of age 1 fish after spawning (i.e. all age 1 fish die after spawning).

2. Age 0 fish spawning

It is known that not a negligible portion of age 0 fish take part in the spawning (Fuji et al. 2021). The degree of the age 0 fish contribution in the spawning activity might be one of the key parameters in the age-structured stock assessment models for PS. The degree of contribution is expressed by a product of three factors: the proportion of matured age 0 fish, the batch fecundity of age 0 fish relative to age 1 fish, and the times of spawning activities of age 0 fish, relative to age 1 fish, in a single spawning period. In spawning seasons, all age 1 fish are considered to spawn because it is the last spawning season of their lives. On the other hand, it is estimated that about 30% of the age-0 fish spawn (Fuji et al. 2021). Number of eggs spawned per fish per day during winter in average was 220 for age 0 fish and 740 for age 1 (Fuji et al. 2023). Given the difference in body weight between ages, number of eggs per day per body weight (g) was calculated as 6.9 for age 1 and 4.1 for age 0. Age-specific spawning period is unknown, however, Suyama (2013) confirmed age 0 population continued spawning for about four months in tank. Age 1 might spawn considerably more eggs per fish per spawning season than age 0 because in most batch-spawning species the older/larger females begin

spawning earlier in the season and continue for longer than younger and smaller females (Marshall, 2016).

Therefore, if one expresses the age 0 fish spawning activity by formulating spawning stock biomass calculation as

$$SSB = \gamma B_{age0} + SSB_{age1} \qquad (1),$$

where SSB, B_{age0}, SSB_{age1} denotes the total spawning stock biomass, total age 0 biomass, and total age 1 biomass, respectively, and γ is the degree of contribution of age 0 fish, which is a constant interpreted as the product of maturation rate, relative fecundity per weight, and relative times of spawning in a spawning season. γ should not be larger than 0.2; relative proportion of maturity and fecundity per weight of age 0 is 0.3 and 0.6 (4.1/6.9), respectively (Fuji et al. 2023), and thus γ is calculated to be 0.18 (0.3 times 0.6), assuming equal spawning periods between ages. In general, older fish are known to have a longer spawning season (Marshall 2016), so γ could be smaller than this value. From this information, we recommend to consider [0.05, 0.2] as a possible range for γ.

3. Steepness of the stock recruitment relationship

Steepness (h) is one of the key parameter in age-structured models that represents the degree of recruitment resilience against a decrease of spawning stock biomass (SSB). Steepness is defined as

$$h = \frac{R(0.2\,SSB_0)}{R(SSB_0)}, \qquad (2)$$

where SSB_0 denotes the SSB under absence of fishing pressure and $R(x)$ is a function that determines the amount of recruitment. This means when $h = 1$, then the amount of recruitment is independent from SSB (perfect resilience), and when $h = 0.2$, then the amount of recruitment is linearly dependent on SSB. Although steepness can be estimated inside stock assessment models, it is difficult in many cases. In such cases, steepness is fixed at plausible values, considering phylogenetic relationships and/or life history characteristics. However, steepness fixed at too large value might lead to a too aggressive stock management and thus a decrease or even collapse of the target stock. Therefore, we should be sensitive for the possibilities that the actual steepness might be smaller than we consider. In this document, we try to theoretically create a prior distribution of steepness for PS from biological characteristics, based on the argument in Mangel et al. (2010). Such prior distribution is used in Bayesian methods to represent our "belief" on the value of h, but still useful even if we do not use Bayesian methods, because it tells how likely an estimates of h or assumptions on h under consideration are.

With Beverton-Holt stock recruitment relationship

$$R = \frac{\alpha\,SSB}{1 + \beta SSB}, \qquad (3)$$

where α is the expected number of recruitment from an unit SSB under absence of exploitation and

density effect and β is the extent of the density effect, steepness is written as

$$h = \frac{\alpha SPR_0}{4 + \alpha SPR_0}, \tag{4}$$

where SPR_0 is expected number of unit SSB from a single recruitment, under absence of exploitation. Therefore, steepness is an increasing function of the product of α and SPR_0. The definitions of α and SPR_0 above indicates that the product of α and SPR_0 expresses the expected number of unit SSB from a unit of SSB in previous generation, under absence of exploitation and density effect. According to the assumptions of the age-structured model we previously proposed to NPFC (see Nakayama et al., 2021 for details), αSPR_0 is expressed as

$$\alpha SPR_0 = e^{-\frac{M_0}{2} - M_e} E_{age1} \left(\gamma \frac{W_0}{W_1} + e^{-M_1} \right), \tag{5}$$

where M_e, E_{age1}, W_a denote the mortality coefficient in the early life stage (from spawning to recruitment), number of egg production of an age 1 fish per spawning period, and wet weight of an age a fish in the spawning season, respectively. In short, steepness will be small when natural mortalities are high, number of eggs is low, and gamma is low. Obtaining eqs. 4 and 5, now it is able to calculate the point estimate of steepness, if we have certain information on the parameters. Now, we have relatively certain values for W_0 and W_1 (= 0.0536 and 0.107 kg, respectively): in other words, other parameters have very large uncertainty. Therefore, our goal here is evaluating the possible range which is likely to contain the true value of steepness, rather than obtaining a point estimate. We first summarized our best knowledge on the early life stage mortality (M_e), the egg production (E_{age1}), age-specific natural mortalities (M_0 and M_1), and the extent of the age 0 fish spawning (γ), although we already discussed age-specific natural mortalities and the extent of the age 0 fish spawning in the sections above. Then we set prior distributions for these parameters based on the knowledge and randomly generated many sets of these parameters (M_e, E_{age1}, M_0, M_1, and γ) according to the prior distributions. Finally, the parameter sets were substituted into eqs. 4 and 5 to obtain a prior distribution of steepness reflecting our knowledge on the biological characteristics of PS.

The early life stage mortality (M_e) is decomposed into the mortality of eggs, larvae (from hatch to 40mm), and juvenile (before recruitment). The eggs of PS are attached to the floating materials such as algae, meanwhile most of small pelagic fishes scatters the buoyant eggs into the ocean. Such unique spawning behavior of PS potentially hides/protects the eggs from predators (Akagawa 2010). Therefore, the eggs of PS are not likely to be massively predated as eggs of other small pelagic fishes. Thus we simply set a prior for egg mortality (M_{egg}) as an uniform distribution U(0.03, 0.22), based on the hatch rate observed in a preceding study (Hotta and Fukushima, 1963). Watanabe et al. (1997) reported the daily average mortalities of PS larvae and the durations of larvae period in several years and seasons. From this information, we set the prior distribution for the larvae mortality (M_{larva}) as a lognormal distribution with a mean and SD of 4.17 and 1.56, respectively. To

estimate the juvenile mortality ($M_{juvenile}$), we used known equations that convert fish's dry weight (W_d) to daily mortality, M_d (McGurk, 1987):

$$M_d = 2.2 \times 10^{-4} W_d^{-0.85}, \quad (W_d < 0.00504g)$$
$$M_d = 5.26 \times 10^{-3} W_d^{-0.25}, \quad (otherwise). \tag{6}$$

We used equations between the days after hatch (d) and the body length of PS juveniles (l) and between the body length and wet weight (W_w) to calculate the days after hatch dependent wet weight of PS juveniles:

$$l = 14.58 \exp[-exp(-0.02025d - 55.08)] \tag{7}$$
$$W_w = 0.0028l^{3.13}. \tag{8}$$

The dry weight of the fish was obtained by assuming 85% hydration (Kamler, 1992). We finally summed up M_d throughout the period from the day a fish becomes juvenile (d) to recruitment (180 days) to obtain the expect of $M_{juvenile}$ ($\widehat{M_{juvenile}}$):

$$\widehat{M_{juvenile}} = \sum_{d}^{180} M_d. \tag{9}$$

Here, d is the sum of the days from spawning to hatch and the days from hatch to becoming juveniles. From available knowledge (Hotta and Fukushima, 1963), we set a prior for the egg period as a lognormal distributions with mean and SD of 12 days and 1 day, respectively. We also set a prior for the larva period as a lognormal distributions with mean and SD of 52.35 days and 9.22 days, respectively (Watanabe et al., 1997). The sampled d was rounded to the closest integer before being substituted in eq. (9). The mortality estimation by eq. (6) seems to contain large uncertainty, therefore we set a lognormal distribution with mean and CV of $\widehat{M_{juvenile}}$ and 30%, respectively, as a prior distribution of $M_{juvenile}$. M_e, was calculated by summing M_{egg}, M_{larva}, and $M_{juvenile}$.

Although there are only few knowledge about per-spawning-season fecundity of age 1 PS, the number of eggs per age 1 individual per spawning season in the field was estimated to be 70800-116400 eggs for age 1 fish based on Fuji et al. (2023), assuming a spawning season of four months as in Suyama (2013). Reflecting this knowledge, we set an continuous uniform distribution U(50000, 200000) as the prior distribution for the number of eggs produced by an age 1 fish in a spawning season (E_{age1}). The upper boundary of the prior distribution is much larger than the empirically estimated number (116400). This is because the assumed duration of age 1 spawning in the estimation (four month) might be longer in reality.

According to the discussion on the natural mortality of PS after recruitment (Nakayama et al., 2019; Hsu et al., 2022) and the argument in the section above, we arbitrary set a lognormal distribution with a mean and SD of 2.1 and 0.3 as the primer distribution for the natural mortality of age 0 fish (M_0), so as to cover the values already discussed (1.71–2.75, Nakayama et al., 2019). We set a prior distribution for M_1/M_0, [U(0.5, 1)] rather than for M_1 itself, because the restriction of M_1 depends on the value of M_0.

Reflecting the argument in the section 2 in this document, we set an uniform distribution U(0.05, 0.2) as the prior distribution for γ

According to these prior distributions, we generated 10000 combinations of M_{egg}, M_{larva}, $M_{juvenile}$, E_{age1}, M_0, M_1, and γ, and calculated the steepness (h) for each of them (Fig. 1). The 0.025, 0.5, 0.975 percentiles of the distribution of h were 0.26, 0.96, and 0.99, respectively, and the mean was 0.88. The estimated mean h was close to the one estimated from phylogeny (= 0.86, Hsu et al., 2022). Nevertheless, the wide range of uncertainty observed here indicates that we should not ignore the possibility that the steepness of PS might be smaller than is estimated from phylogeny.

4. How to use the ranges shown above

If the key parameters are fixed at a certain values, the values should be inside the ranges proposed above, unless there are any biological reasons to consider values outside the ranges. On the other hand, when the key parameters are estimated inside the age-structured stock assessment models, we should check whether the estimated values are inside the proposed ranges or not.

References

Akagawa I (2010) Spawning and parental care. In: Tsukamoto K (eds) Basics of ecology in fishes. pp. 223-241. Koseisha-Koseikaku Tokyo

Charnov EL, Gislason H, Pope JG (2013) Evolutionary assembly rules for fish life histories. Fish and Fisheries 14: 213-224

Fuji T, Suyama S, Nakayama S, Hashimoto M, Oshima K (2019) A review of the biology for Pacific saury, *Cololabis saira* in the North Pacific Ocean. NPFC-2019-SSC PS05-WP13(Rev.1)

Fuji T, Suyama S, Miyamoto H, Nakayama S, Hashimoto M, Naya M, Kawabata A, Nakatsuka S (2021) Proportion of Pacific saury spawned during their first spawning season estimated by the histological observations of ovary tissues. NPFC-2021-SSC PS07-WP03

Fuji T, Nakayama S, Hashimoto M, Miyamoto H, Suyama S (2023) Age-specific fecundity of Pacific saury. NPFC-2023-SSC PS11-WP08

Hotta H.,and Fukushima S., (1967). FLUCTUATION IN THE ABUNDANCE OF SAURY ON THE NORTHEASTERN SEA OF JAPAN (II). Bulletin of Tohoku Regional Fisheries Research Laboratory, (23), 61-72.

Hsu, J., Chang, Y.J., Hsieh, C.H., Huang, W.B., Ching, T.H. (2022). Preliminary stock assessment model in Stock Synthesis 3.30 for the Pacific saury in Northwestern Pacific Ocean. NPFC-2022-SSC PS09-WP10.

Kamler, E. (1992) Early Life History of Fish. An Energetics Approach. Chapman and Hall, London and New York.

Kenchington TJ (2014) Natural mortality estimators for information-limited fisheries. Fish and

Fisheries 15: 533-562.

Mangel, M., Brodziak, J., & DiNardo, G. (2010). Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. Fish and Fisheries, 11(1), 89-104.

Marshall CT (2016) Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. In: Jakobsen T, Fogarty MJ, Megrey B, and Moksness E (eds) Fish reproductive biology: implications for assessment and management, second edition. John Wiley & Sons, Ltd.

McGurk, M. D. (1987). Natural mortality and spatial patchiness: Reply to Gulland. Marine ecology progress series. Oldendorf, 39(2), 201-206.

Nakayama, S-I., Suyama, S., Fuji, T., Hashimoto, M., and Oshima, K. (2019) A trial calculation of natural mortality estimators for Pacific saury. NPFC-2019-SSC PS05-WP18.

Nakayama S-I., Fuji T., Suyama S., Naya M., Miyamoto H., Hashimoto M., Oshima K., Kawabata A., and Nakatsuka S. (2021) An example state-space age-structured stock assessment model for Pacific saury NPFC-2021-SSC PS07-WP21.

Suyama S (2013) Spawning habits of Pacific saury *Cololabis saira* under tank experiments. In: Kurita Y, Kawabe R, Matsuyama M (eds) Studies on reproductive biology of fishery resources - progress by application of tank experiments and bio-logging pp. 92-106. Koseisha-Koseikaku Tokyo

Thorson JT, Munch SB, Cope JM, and Gao J (2017) Predicting life history parameters for all fishes worldwide. Ecological Applications, 27(8): 2262–227.

Watanabe Y., Oozeki Y., and Kitagawa D. (1997). Larval parameters determining preschooling juvenile production of Pacific saury (*Cololabis saira*) in the northwestern Pacific. Canadian Journal of Fisheries and Aquatic Sciences. 54(5): 1067-1076. https://doi.org/10.1139/f97-013
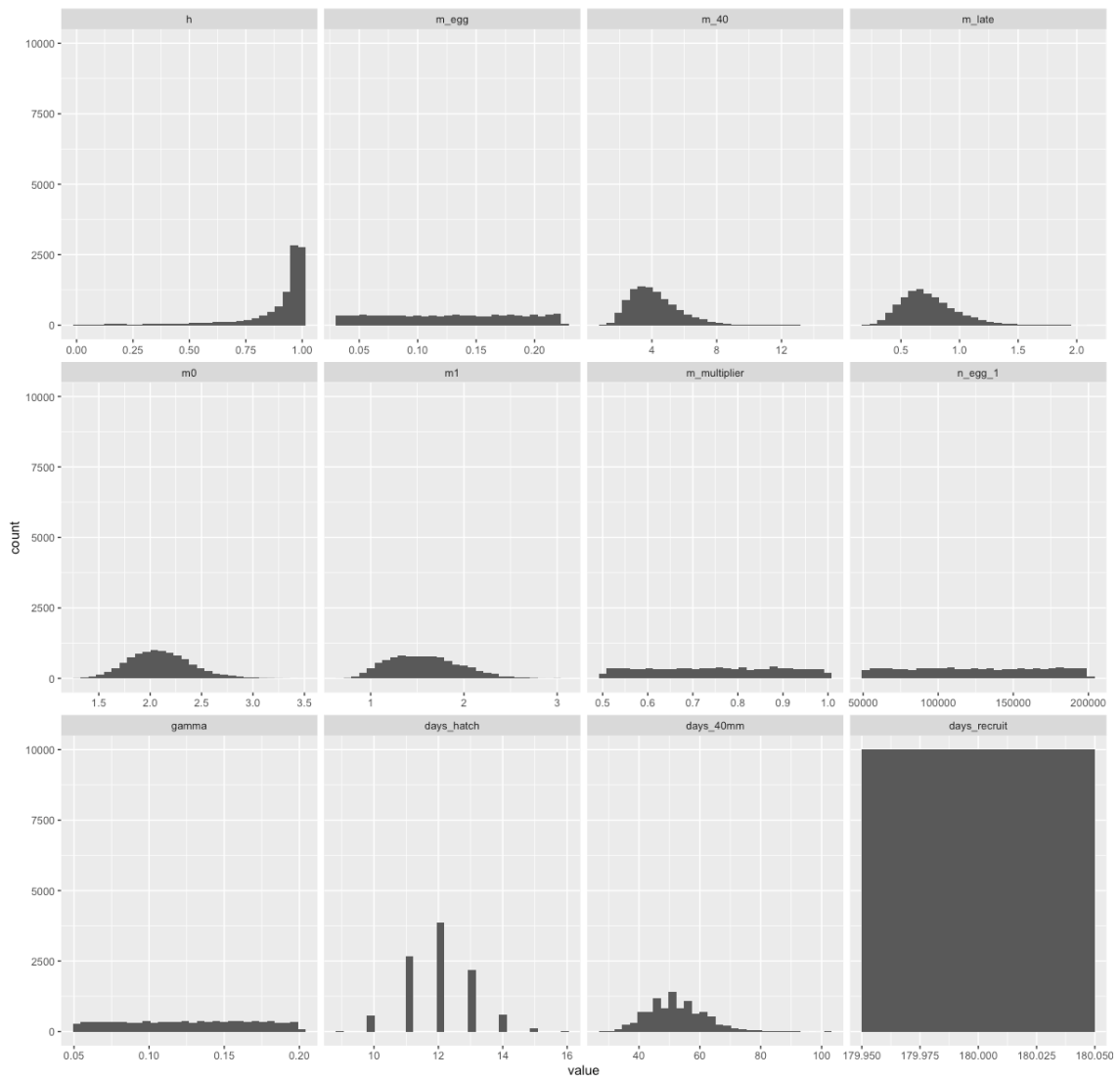
Figure 1. The prior distribution for each parameters.