Meta-analysis of Growth Curve for Shortfin Mako Shark in the North Pacific*

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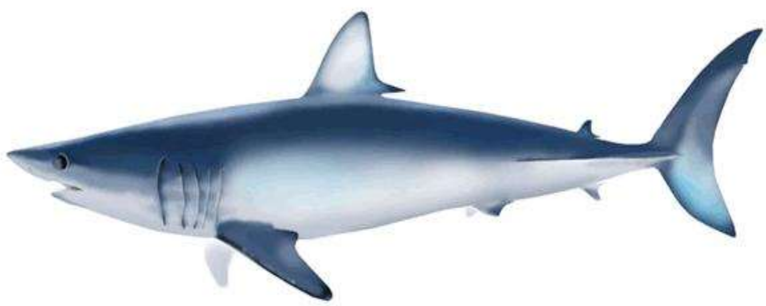

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Abstract

This document reports results of estimating a growth curve for shortfin mako sharks in the North Pacific by the proposed meta-analysis approach of Bayesian hierarchical model using the age and growth data provided by the ISC SHARKWG members (US, Mexico, Taiwan, and Japan). Seven data sets of length at age (5 from vertebrae observation and 2 from length frequency analysis) were compiled. Each data set represents a different individual age and growth study being conducted by each member, and were treated as random effect in the meta-analysis. Estimated medians and 95% credible interval (CI) of posterior distribution values of the parameters, μ_{∞} and μ_K (the mean of entire population for the asymptotic length and Brody growth rate parameters, L_{∞} and K) were 232.0 cm in precaudal length, PCL (CI: 224.6-257.3 cm PCL) and 0.174 year^{-1} (CI: 0.116-0.238 year^{-1}), respectively for male. Those for female were 293.1 cm PCL (CI: 255.2-335.9 cm PCL) and 0.128 year^{-1} (CI: 0.080-0.186 year^{-1}), respectively. In addition to the analysis using all the seven data sets, two analyses without data provided by Taiwan and without two sets of length frequency data provided by Japan and US were also conducted to examine impacts of these data on parameter estimates. Compared to the estimates of μ_K from the analysis using all the seven data sets, the estimates of μ_K were higher for both sexes in the case without Taiwan's data. In contrast, the estimates of μ_K were lower for male and female in the case without the length frequency data than in both cases of using all the seven data sets in the analysis and of excluding Taiwan's data.

1. Introduction

Upon a request from the Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean (WCPFC), the International Scientific Committee for tuna and tuna-like species in the North Pacific Ocean (ISC) Shark Working Group (SHARKWG) is in charge of conducting a stock assessment for shortfin mako shark, *Isurus oxyrinchus*, in the North Pacific Ocean. One of requirements when conducting the stock assessment is information of growth curve. For shortfin mako in the North Pacific, a variety of the age and growth rates estimated from vertebrae, tagging and body length information are available (Cailliet and Bedford 1983, Pratt and Casey 1983, Ribot-Carball al et al. 2006, Semba et al. 2009, Wells et al. 2013, Kai et al. 2015). Among these growth rate estimates, Wells et al. (2013) and Kai et al. (2015) are for juvenile north Pacific shortfin mako. Depending on the study, estimated growth of shortfin mako varies considerably within the North Pacific and the factors to cause the differences include enhancement methods for growth band count, different hypothesis for growth band deposition (annual or biannual), criteria and definition in band counting, different assumption made in estimation of age (i.e., type of growth equation, birth month, calculation of decimal ages etc.), type of data used (i.e., band count or length frequency), and sample size and range other than regional difference in growth rate. Given the complex factors above, it is difficult to select the most appropriate growth parameter which represents the growth of North Pacific population at present. Especially, it is suggested that the use of information about the vertebrae only is still immature because of controversial issues raised regarding the possibility of biannual band-pair deposition for the first few years (Wells et al. 2013, Kinney et al. 2016) and thus simultaneous use of growth estimates based on length frequency data is appropriate. For stock assessment, the most parsimonious results about growth of shortfin mako in the North Pacific for the whole age spectrum from juvenile to adult fish is desired.

The United States (US), Mexico, Taiwan, and Japan have independently been doing age and growth studies of shortfin mako sharks in the North Pacific based on vertebra band counts. At the ISC SHARKWG workshop in 2014, the SHARKWG members agreed to share data from their age and growth studies for working collaboratively on meta-analysis to try to come up with the most parsimonious conclusions about growth of shortfin mako in the North Pacific (ISC 2015). These age and growth data were presented by the members and reviewed at the third Shark Age and Growth workshop in October 2017 to be used in the meta-analysis (ISC 2017). Based on studies of Andrews et al. (2012) and Chang et al. (2013), Takahashi et al. (2016) have proposed a potential approach of meta-analysis that effectively utilizes all the age and growth data provided by the members to estimate a most parsimonious growth curve. This document reports results of estimating a growth curve for shortfin mako sharks in the North Pacific using the age and growth data provided by the SHARKWG members and the proposed meta-analysis approach. In addition to the analysis using all the seven data sets, two analyses without specific data were also conducted to examine impacts of the data on parameter estimates.

2. Materials and Methods

2.1. Data used

At the third Shark Age and Growth workshop in October 2017, shark ageing experts from Mexico, US, Taiwan, and Japan presented their age and growth data and reviewed characteristics of these data for use in the meta-analysis (ISC 2017). Description of the data is summarized in Table 1. There are seven studies (5 from vertebrae observation and 2 from length frequency analysis) consisting of female and male data sets. It was agreed at the workshop that the data from these seven studies would be used for potential inputs of the meta-analysis (ISC 2017). As a whole, age and size ranges of the data used are 0 to 30 years old and 49 to 310 cm in precaudal length (PCL), respectively.

For length at age data from vertebrae observation by Wells et al. (2013), Lyons et al. (2015), and Kinney et al. (2016), only a subset of these data was provided by US. For the ISC reference collection, only length at age data of US readings were used in the meta-analysis (one data record with no length information was removed). For length frequency data, subsets (randomly sampled 125 data for each study and sex) from Runcie et al. (2016) and from Kai et al. (2015) were used in the analysis because the amounts of these data were very large (over 1 000 data records for each study and sex) compared to those of other age and growth data. The length frequency data from Runcie et al. (2016) have no age information attached. Age information for these data were calculated using the following conversion equations and attached to data records: age = $(-1/K)\log(1-(PCL-L_0)/(L_\infty-L_0))$ (growth parameters, K=0.17, L_∞=228.5 cm PCL estimated by Kai et al. 2015 based on data in Wells et al. 2013, assuming the length at age 0, L_0=60 cm PCL agreed in the Workshop); PCL=0.91*$ForkLength$-0.95 (Semba et al. 2009).

In addition to the meta-analysis using all the seven data sets indicated in Table 1, two additional analyses using data excluding data provided by Taiwan and data excluding two sets of length frequency data (from Kai et al. 2015 and Runcie et al 2016) were also conducted to examine impacts of these data on results of parameter estimates. These types of data sets were chosen for this purpose because these data appeared to have different age and growth characteristics compared to other growth data.

2.2. Method of meta-analysis for age and growth data

The von Bertalanffy growth (VBG) model (von Bertalanffy 1938) is the most commonly used in fisheries to describe fish growth (Haddon 2011). If growth of shortfin mako shark in the North Pacific is assumed to follow a VBG model and each growth study by the ISC SHARKWG members is treated as a random effect, then, Bayesian hierarchical meta-analysis can also be applied to the age and growth data for this species, which were collected from the members, in the similar way in Andrews et al. (2012) and Chang et al. (2013). Takahashi et al. (2016) have proposed this meta-analysis approach for estimating a most parsimonious growth curve of north Pacific shortfin mako to be used in stock assessment and examined usefulness of the approach by simulation exercise. In this section, we review this approach of Bayesian hierarchical meta-analysis.

Suppose that the expected length of the i-th shortfin mako aged in the j-th member's study (or with j-th ageing method used by each member) under the VBG ($E[L_{i,j}]$) is written as:

$$E[L_{i,j}] = L_0 + (L_{\infty,j} - L_0)\{1 - \exp(-K_j t_{i,j})\} \quad (1)$$

where $t_{i,j}$ and L_0 are fish age in years and the length at age 0, respectively. $L_{\infty,j}$ and K_j are the asymptotic length and Brody growth rate parameters, respectively. This equation form is for the VBG model when the birth length, L_0, is known (Simpfendorfer et al. 2002).

An observation for length of the i-th shortfin mako aged in the j-th member's study is modeled as below using $E[L_{i,j}]$ and the observation error ε_j:

$$L_{i,j} = E[L_{i,j}] + \varepsilon_j \quad \text{where } \varepsilon_j \sim N(0, \sigma_j^2) \quad (2)$$

In equation 2, the observation errors are assumed to follow the normal distribution with zero mean and a study-specific (or method-specific) variance σ_j.

In this Bayesian hierarchical modeling, each member's study is assumed to have its own VBG curve that comes from the population of VBG curves (i.e., treated as random effects) and a hierarchical structure is implemented in the model by assigning multi-level priors of study-specific VBG parameters. This means that the VBG parameters $L_{\infty,j}$ and K_j are considered as drawn from the populations of each parameter which have prior distributions of certain types. Prior distributions for $L_{\infty,j}$ and K_j are assumed to follow normal distributions, respectively as below:

$$L_{\infty,j} \sim N(\mu_{\infty}, \sigma_{\infty}^2) \quad (3)$$

$$K_j \sim N(\mu_K, \sigma_K^2) \quad (4)$$

The hyperparameters μ_∞ and μ_K are the population mean for L_∞ and K, respectively. The hyperparameters σ^2_∞ and σ^2_K are the population variance (i.e., between-studies variance) for L_∞ and K, respectively.

Assuming that there was no auxiliary information on the population parameter values of the VBG model from previous studies of north Pacific shortfin mako, uninformative priors were used for both the population parameters and the observation error variances. The priors for the population mean asymptotic length (μ_∞) and for the Brody growth rate parameter (μ_K) were set using a normal distribution and a beta distribution as below:

$$\mu_\infty \sim N(100, 10000) \quad (5)$$

$$\mu_K \sim \mathrm{Beta}(1, 1) \quad (6)$$

The priors for the parameter variances (σ_∞ and σ_K) and the observation error variances (σ_j) were all assumed to have diffuse inverse gamma distributions as below, because this distribution is the conjugate prior for the unknown variance of a normally distributed mean:

$$\frac{1}{\sigma_\infty^2} \sim \mathrm{Gamma}(10^{-4}, 10^{-4}) \quad (7)$$

$$\frac{1}{\sigma_K^2} \sim \mathrm{Gamma}(10^{-4}, 10^{-4}) \quad (8)$$

$$\frac{1}{\sigma_j^2} \sim \mathrm{Gamma}(10^{-4}, 10^{-4}) \quad (9)$$

Posterior distributions of the parameters of the VBG model (μ_∞, μ_K, σ_∞, σ_K, and σ_j) were predicted by Markov chain Monte Carlo (MCMC) method using the WinBUGS software (version 1.4.3; Spiegelhalter et al. 2003) and related 'R2WinBUGS' package (Gelman et al. 2014) of R (R Core Team 2016). Three MCMC chains were simulated for each run. Each chain consisted of 2 750 000 iterations sampled with a thinning rate of 1/250 and a burn-in period of 250 000 iterations for a total of 30 000 MCMC samples. Convergence of the MCMC samples to posterior distribution was confirmed using Gelman and Rubin (1992) diagnostics. Autocorrelations were also monitored to check whether the MCMC samples were serially correlated.

Meta-analyses were conducted for male and female, separately, to estimate sex specific VBG model parameters.

3. Results and Discussion

3.1. Diagnostics

Whether the Markov chains have reached a stable equilibrium distribution was checked by inspecting the Brooks-Gelman-Rubin (BGR) diagnostic statistics. The BGR diagnostic statistics for all parameters estimated have values around 1 (less than 1.1), which indicated that Markov chains converged. Trace plots for three independent chain sequences of MCMC simulation starting from different initial parameter values showed highly stable coherence and resulting kernel densities were nearly indistinguishable (Fig. A1). Autocorrelation function plots showed that the chains were hardly autocorrelated (Fig. A2).

Although diagnostics of the results are explained here only for the hyperparameters μ_∞ and μ_K, all other parameters have qualitatively the similar convergence and autocorrelation properties to those for these two hyperparameters.

3.2. Statistics for estimated VBG curve parameters from posterior distributions

Statistics for estimated VBG curve parameters, μ_∞, μ_K, σ_∞, and σ_K, from posterior distribution using all the seven sets of age and growth data (Table 1) are summarized in Table 2. Medians and 95% credible interval (CI) of the distributions of μ_∞ and μ_K were 232.0 (CI: 224.6-257.3) and 0.174 (CI: 0.116-0.238), respectively for male. Those for female were 293.1 (CI: 255.2-335.9) and 0.128 (CI: 0.080-0.186), respectively. The median VBG curves and 95% CI drawn using these estimated parameter values are shown in Fig. 1. These results suggest that female shortfin mako shark has higher L_∞ and lower K values than male does as previously reported. Estimated parameters, L_∞ and K, from the seven individual studies are summarized in Table A1. Estimated medians of L_∞ for the individual studies ranged from -2% to +3% of the population estimate, μ_∞ for male and from -22% to +13% for female. Similarly, medians of K for the individual studies ranged from -48% to +67% of the population estimate, μ_K, for male and from -60% to +55% for female. These results indicate that ageing method (each data set or each member's ageing study) has a greater impact on the estimate of K than on the estimate of L_∞ for individual ageing study.

Statistics for estimated VBG curve parameters from posterior distribution using all the seven sets of age and growth data excluding data provided by Taiwan, and excluding two sets of length frequency data are summarized in Table 3 and 4, respectively.

For analysis without data provided by Taiwan, medians and 95% CI of the posterior distributions of μ_∞ and μ_K were 233.3 (CI: 219.7-268.0) and 0.186 (CI: 0.130-0.252), respectively for male. Those for female were 282.3 (CI: 243.8-329.9) and 0.144 (CI: 0.099-0.199). Compared to the estimates of μ_K from the analysis using all the seven data sets, the estimates of μ_K were higher for both sexes in this case. This result suggests that data provided by Taiwan have information of slower growth than other data. Estimated parameters of L_∞ and K from posterior distributions for individual six studies from the analysis without Taiwan's data are summarized in Table A2. Estimated medians of L_∞ for the individual studies ranged from -2% to +5% of the population estimate, μ_∞ for male and from -19% to +9% for female. Similarly, medians of K for the individual studies ranged from -23% to +54% of the population estimate, μ_K, for male and from -26% to +40% for female. Similar to the results from the analysis using all the seven data sets, in this case, too, ageing method has a stronger impact on the estimate of K than on the estimate of L_∞ for individual ageing study.

For analysis excluding both sets of length frequency data from Japan and US, medians and 95% CI of the posterior distributions of of μ_∞ and μ_K were 244.4 (CI: 228.7-272.3) and 0.139 (CI: 0.092-0.193), respectively for male (Table 4). Those for female were 315.5 (CI: 289.2-336.8) and 0.097 (CI: 0.060-0.140). The estimates of μ_K were lower for male and female in this case than in both cases where all the seven data sets were used in the analysis and where Taiwan's data were excluded. This result suggests that length frequency data from Japan and US would estimate faster growth than other data. Statistics for estimated parameters of L_∞ and K from the posterior distributions for five individual studies from the analysis excluding length frequency data are summarized in Table A3. Estimated medians of L_∞ for the individual studies ranged from -2% to +1% of the population estimate, μ_∞ for male and from -2% to +2% for female. Medians of K for the individual studies ranged from -40% to +28% of the population estimate, μ_K, for male and from -44% to +27% for female. Again, in this case, ageing method has also a stronger influence on the estimate of K than on the estimate of L_∞ for individual ageing study.

For comparison, three VBG curves drawn with estimated median parameter values from the meta-analyses using all the seven data sets, the six data sets without Taiwan's data, and the five data sets without two sets of length frequency data from Japan and US for male and female are plotted in Fig. 2. There are some differences seen, especially for female, in the shape of the growth curve between the curve for the case without Taiwan's data and those for the other two cases.

A sequence of meta-analyses we conducted using different combinations of compiled age and growth data sets indicates that parameter estimates of the VBG curve from posterior distribution, especially for K, are influenced by which data sets were chosen for the analysis. This is not unexpected thing because data from a different individual ageing study have its own information about the entire population of north Pacific shortfin mako shark. To estimate the VBG curve parameter values taking the meta-analysis approach for use in future stock assessment, we advise to utilize all the seven sets of age and growth data in the analysis. We iterate further that the seven data sets have been already agreed at the third Shark Age and Growth Workshop for inputs to meta-analysis (ISC 2017). However, if reconsideration of which sets of age and growth data are used in the analysis is needed, selection of the data sets should not be arbitrary and intentional for obtaining particular results.

References

Andrews AH, DeMartini EE, Brodziak J, Nichols RS, Humphreys RL (2012) A long-lived life history for tropical, deepwater snapper (*Pristipomoides filamentosus*): bomb radiocarbon and lead-radium dating as extensions of daily increment analysis in otoliths. Can J Fish Aquat Sci 69:1850-1869

Cailliet GM, Bedford D (1983) The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. Cal coop ocean fish Journal 24: 57–69

Chang Y-J, Brodziak J, Lee H-H, DiNardo G, Sun C-L (2013) A Bayesian hierarchical meta-analysis of blue marlin (*Makaira nigricans*) growth in the Pacific Ocean. ISC/13/BILLWG-1/02. Working document submitted to the ISC Billfish Working Group Workshop, 16–23 January 2013, Honolulu, Hawaii, USA

Gelman A, Rubin D (1992) Inference from iterative simulation using multiple sequences. Stat Sci 7:457-472

Gelman A, Sturtz S, Ligges U (2014) Package 'R2WinBUGS' manual, version 2.1-19

Haddon M (2011) Modelling and quantitative methods in fisheries, 2nd ed. Chapman & Hall/CRC, Boca Raton, Florida, USA

ISC (2015) Report of Shark Working Group Workshop. Annex 4 of the report of the fifteenth meeting of the International Scientific Committee for tuna and tuna-like species in the North Pacific Ocean, plenary session (ISC15), 15–20 July 2015, Kona, Hawaii, USA

ISC (2017) Report of the third Shark Age and Growth Workshop sponsored by the International Scientific Committee for tuna and tuna-like species in the North Pacific Ocean, 19–24 October 2017, Shizuoka, Japan

Kai M, Shozaki K, Ohshimo S, Yokawa, K (2015) Growth and spatiotemporal distribution of juvenile shortfin mako (*Isurus oxyrinchus*) in the western and central North Pacific. Mar Freshwater Res 66:1176–1190

Kinney MJ, Wells RJD, Kohin S (2016) Oxytetracycline age validation of an adult shortfin mako shark *Isurus oxyrinchus* after 6 years at liberty. J Fish Biol 89:1828–1833

Lyons K, Preti A, Madigan D.J, Wells RJD, Blasius ME, Snodgrass OE, Kacev D, Harris JD, Dewar H, Kohin S, MacKenzie K, Lowe CG (2015) Insights into the life history and ecology of a large shortfin mako shark (*Isurus oxyrinchus*) captured in southern California. J. Fish Biol. 87: 200–211. doi:10.1111/jfb.12709

Pratt HL, Casey JG (1983) Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can J Fish Aquat Sci 40**:** 1944–1957

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ribot-Carballal MC, Galván-Magana F, Quinonez-Velazquez C (2005) Age and growth of the shortfin mako shark, *Isurus oxyrinchus*, from the western coast of Baja California Sur, Mexico. Fish Res 75: 14–21

Rodríguez-Madrigala JA *et al* (2017) *Title*. ISC/17/SHARKWG-1/nn. Working document submitted to the ISC Shark Working Group Workshop, 28 November-4 December 2017, Shimizu, Shizuoka, Japan (to be submitted)

Runcie R, Holts D, Wraith J, Xu Y, Ramon D, Rasmussen R, Kohin S (2016) A fishery-independent survey of juvenile shortfin mako (*Isurus oxyrinchus*) and blue (*Prionace glauca*) sharks in the Southern California Bight, 1994-2013. Fish. Res. 183, 233–243.

Semba Y, Nakano H, Aoki I (2009) Age and growth analysis of the shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific Ocean. Environ Biol Fish 84:377–391

Semba Y *et al* (2017) *Title*. ISC/17/SHARKWG-1/nn. Working document submitted to the ISC Shark Working Group Workshop, 28 November-4 December 2017, Shimizu, Shizuoka, Japan (to be submitted)

Sippel T, Ohshimo S, Yokawa K, Kai M, Carvalho F, Liu K-M, Castillo-Geniz JL, Kohin S (2015) Spatial and temporal patterns of shortfin mako shark size and sex in the North Pacific Ocean. ISC/15/SHARKWG-1/04. Working document submitted to the ISC Shark Working Group Workshop, 9–17 March 2015, Shimizu, Shizuoka, Japan

Simpfendorfer CA, McAuley RB, Chidlow J, Unsworth P (2002) Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. Mar Freshwater Res 53: 567–573.

Spiegelhalter D, Thomas A, Best N, Lunn D (2003) WinBUGS user manual, Version 1.4.

Takahashi N, Kai M, Semba Y (2016) A potential method for meta-analysis of growth curve for shortfin mako shark in the North Pacific. ISC/16/SHARKWG-1/08. Working document submitted to the ISC Shark Working Group Workshop, 14–21 November 2016, Busan, Korea

von Bertalanffy L (1938) A quantitative theory of organic growth. Human Biol 10:181–213

Wells RJD, Smith SE, Kohin S, Freund E, Spear N, Ramon DA (2013) Age validation of juvenile Shortfin Mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California. Fish Bull 111: 147–160

Table 1. Description of age and growth data used in the meta-analysis of shortfin mako shark growth in the North Pacific Ocean.

Region in North Pacific	Sex	Age range	Size range (PCL cm)	Sample size	Ageing method	Source
Western & central	Male	0-13	53-240	181	Vertebrae (half-cut centrum, shadowing method)	Semba et al. 2017 (Japan)
Western & central	Female	0-19	57-300	209	Vertebrae (half-cut centrum, shadowing method)	Semba et al. 2017 (Japan)
Eastern	Male	0-11	59-215	114	Vertebrae (stained whole centrum and sectioned with transmitted light)	Rodríguez-Madrigala et al. 2017 (Mexico)
Eastern	Female	0-14	67-242	121	Vertebrae (stained whole centrum and sectioned with transmitted light)	Rodríguez-Madrigala et al. 2017 (Mexico)
Eastern	Male	1-10	93-195	18	Vertebrae (section, X-ray)	Wells et al. 2013, Kinney et al. 2016, Lyons et al. 2015 (US)
Eastern	Female	1-22	89-310	7	Vertebrae (section, X-ray)	Wells et al. 2013, Kinney et al. 2016, Lyons et al. 2015 (US)
Western & central	Male	0-23	66-229	170	Vertebrae (whole centrum, X-ray)	Provided by Taiwan (Unpublished)
Western & central	Female	0-30	65-301	167	Vertebrae (whole centrum, X-ray)	Provided by Taiwan (Unpublished)
Western, eastern, & central	Male	0-10	54-225	25	Vertebrae (section, X-ray)	ISC reference collection (US readings)
Western, eastern, & central	Female	0-15	49-279	32	Vertebrae (section, X-ray)	ISC reference collection (US readings)
Western & central	Male	0-2	63-148	125	Length frequency	Kai et al. 2015 (Japan)
Western & central	Female	0-2	67-150	125	Length frequency	Kai et al. 2015 (Japan)
Eastern	Male	0-2	62-108	125	Length frequency	Runcie et al. 2016 (US)
Eastern	Female	0-2	62-108	125	Length frequency	Runcie et al. 2016 (US)

Table 2. Summary of statistics from predicted posterior distributions of VBG curve parameters using all the seven age and growth data.

Sex	L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%		Mean	SD	2.5%	Median	97.5%
Male	μ_∞	234.9	9.1	224.6	232.0	257.3	μ_K	0.175	0.030	0.116	0.174	0.238
	σ_∞	9.74	11.22	0.02	6.57	37.84	σ_K	0.071	0.029	0.036	0.065	0.144
Female	μ_∞	293.8	20.3	255.2	293.1	335.9	μ_K	0.129	0.026	0.080	0.128	0.186
	σ_∞	44.29	18.34	22.52	40.14	89.81	σ_K	0.060	0.026	0.030	0.054	0.127

Table 3. Summary of statistics from predicted posterior distributions of VBG curve parameters using the age and growth data without data provided by Taiwan.

Sex	L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%		Mean	SD	2.5%	Median	97.5%
Male	μ_∞	236.9	12.6	219.7	233.3	268.0	μ_K	0.187	0.032	0.130	0.186	0.252
	σ_∞	14.83	16.14	0.02	11.26	53.89	σ_K	0.062	0.033	0.022	0.054	0.145
Female	μ_∞	283.5	21.8	243.8	282.3	329.9	μ_K	0.145	0.025	0.099	0.144	0.199
	σ_∞	41.51	21.49	17.92	36.52	94.72	σ_K	0.050	0.030	0.020	0.043	0.119

Table 4. Summary of statistics from predicted posterior distributions of VBG curve parameters using the age and growth data without two data sets of the length frequency data.

Sex	L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%		Mean	SD	2.5%	Median	97.5%
Male	μ_∞	245.7	11.5	228.7	244.4	272.3	μ_K	0.140	0.025	0.092	0.139	0.193
	σ_∞	9.80	14.87	0.01	2.98	48.54	σ_K	0.047	0.025	0.019	0.041	0.110
Female	μ_∞	314.9	12.3	289.2	315.5	336.8	μ_K	0.098	0.020	0.060	0.097	0.140
	σ_∞	12.86	15.97	0.02	8.54	50.59	σ_K	0.038	0.020	0.017	0.033	0.089

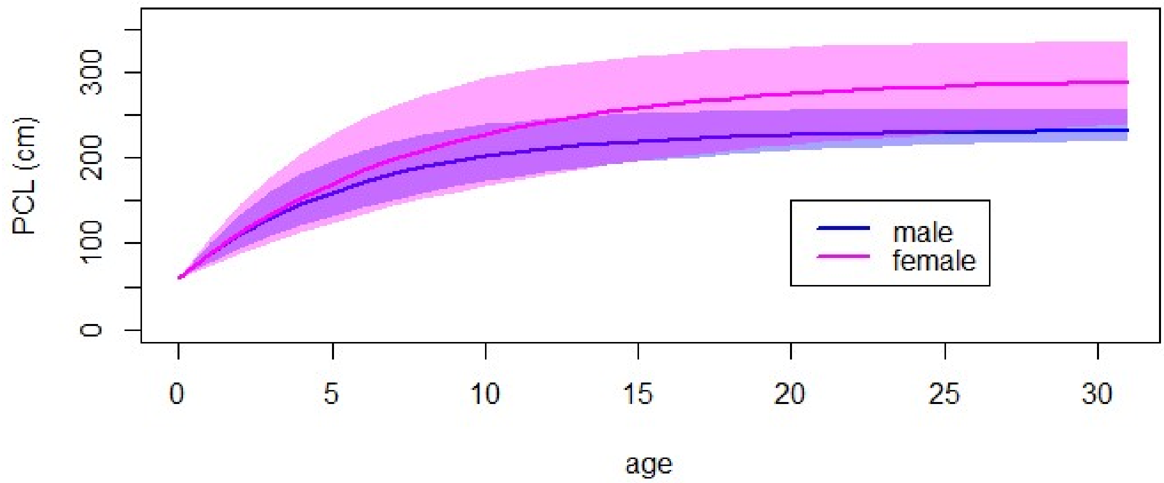


Fig. 1. Male and female VBG curves drawn with estimated parameter values from the meta-analysis using all the seven data sets in Table 1. Solid lines are medians and shades represent 95% credible interval.

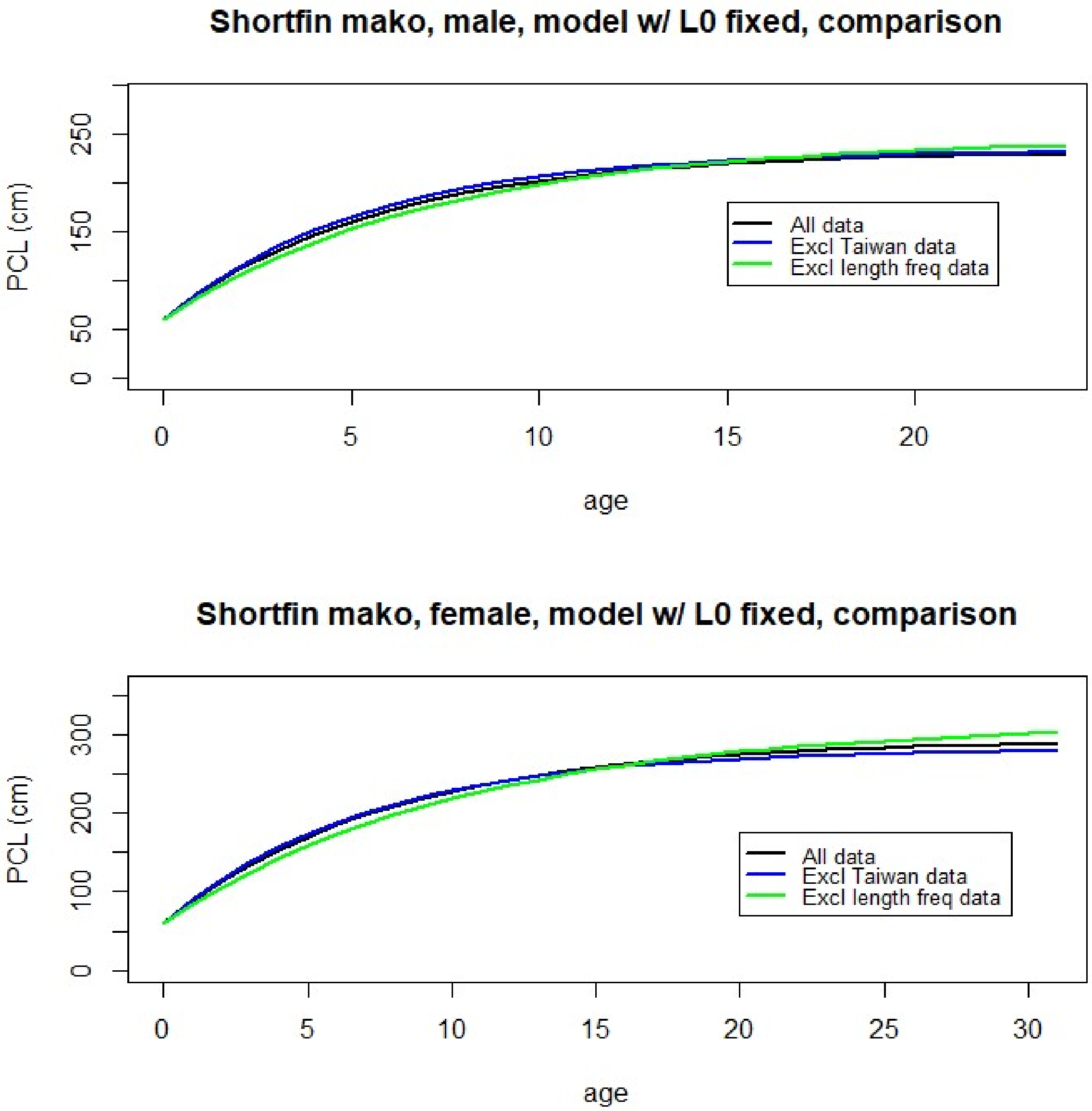
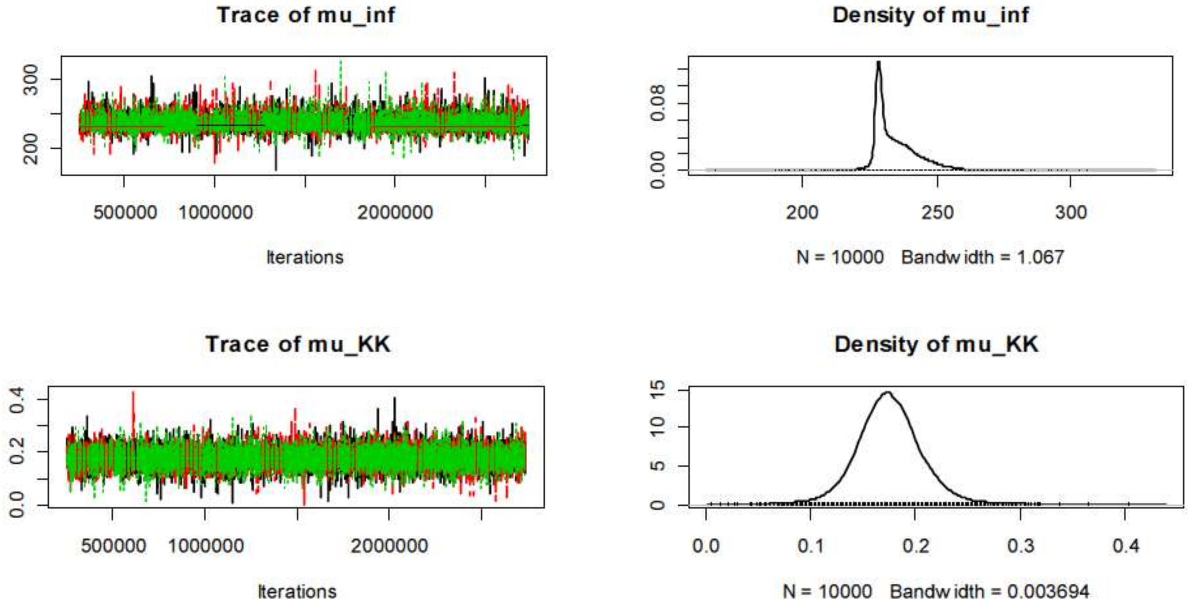


Fig. 2. Comparisons of VBG curves drawn with estimated median parameter values from the meta-analyses using all the seven data sets in Table 1, the six data sets without Taiwan's data, and the five data sets without two sets of length frequency data from Japan and US for male (upper panel) and female (lower panel).

Appendix

(a) Male



(b) Female

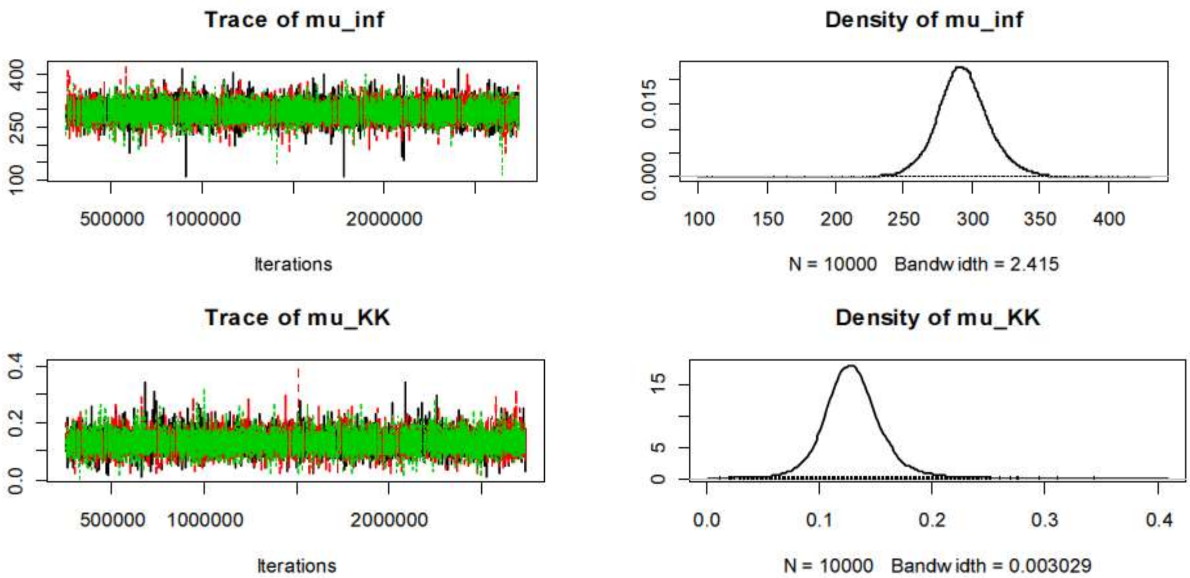


Fig. A1. Trace (left panel) and kernel density (right panel) plots for the VBG parameters, μ_∞ and μ_K (eq. 3 and 4) for male and female north Pacific shortfin mako shark drawn from 30 000 MCMC samples. Trace and kernel density plots are based on three independent MCMC chain sequences.

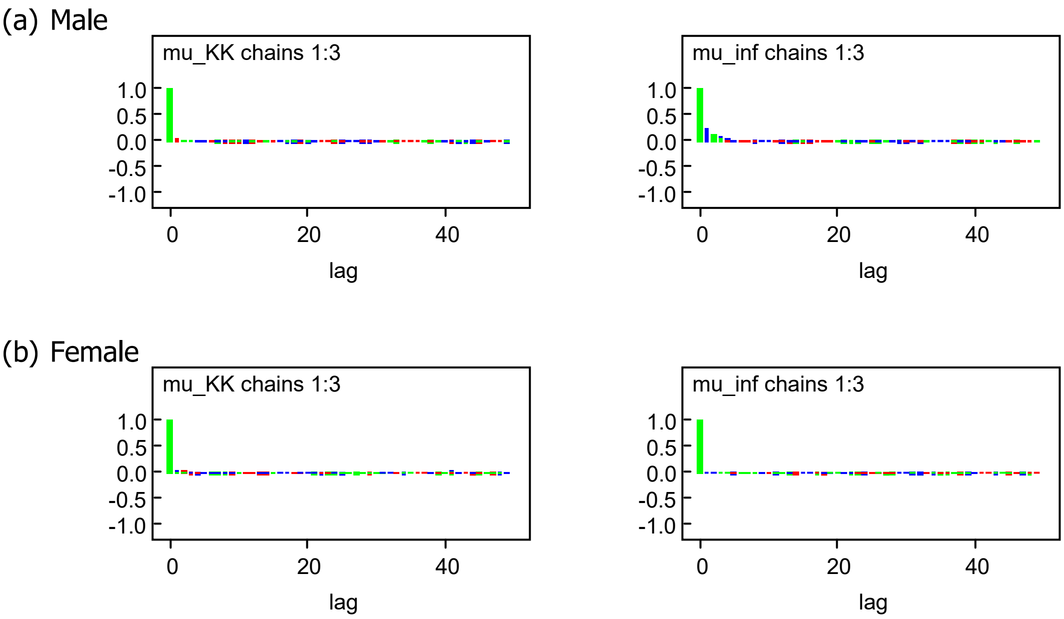


Fig. A2. Autocorrelation function plots of for the VBG parameters, μ_∞ and μ_K (eq. 3 and 4) for male and female north Pacific shortfin mako shark.

Table A1. Summary of statistics from predicted posterior distributions of VBG curve parameters for each member's ageing study using all the seven age and growth data. Percent of mu (% of μ) denotes a difference between overall mean and each mean value.

Sex		L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%	% of μ	Mean	SD	2.5%	Median	97.5%	% of μ
Male	μ (hyperparameter)	234.9	9.1	224.6	232.0	257.3	0%	0.175	0.030	0.116	0.174	0.238	0%
	Japan	232.3	7.3	220.6	229.8	250.2	-1%	0.157	0.011	0.133	0.159	0.177	-9%
	Mexico	242.9	15.5	227.7	238.8	279.0	+3%	0.146	0.015	0.114	0.149	0.166	-14%
	US	229.6	12.2	200.7	228.7	255.7	-1%	0.178	0.024	0.137	0.175	0.237	+1%
	Taiwan	233.6	6.4	225.2	231.6	248.6	0%	0.090	0.005	0.078	0.091	0.098	-48%
	ISC Ref	241.3	17.0	225.7	234.9	285.8	+1%	0.196	0.027	0.137	0.199	0.242	+15%
	Japan length freq	236.2	16.6	210.6	230.5	279.3	-1%	0.286	0.032	0.216	0.290	0.346	+67%
	US length freq	228.5	0.1	228.3	228.5	228.8	-2%	0.170	0.000	0.170	0.170	0.170	-2%
Female	μ (hyperparameter)	293.8	20.3	255.2	293.1	335.9	0%	0.129	0.026	0.080	0.128	0.186	0%
	Japan	283.4	13.1	260.1	282.5	311.5	-4%	0.106	0.009	0.089	0.106	0.126	-17%
	Mexico	296.2	14.7	269.6	295.4	327.4	+1%	0.104	0.008	0.088	0.104	0.121	-19%
	US	316.0	25.2	268.2	315.3	367.4	+8%	0.130	0.025	0.087	0.128	0.185	0%
	Taiwan	332.5	10.5	313.2	332.1	354.5	+13%	0.052	0.003	0.046	0.052	0.057	-60%
	ISC Ref	301.3	20.1	266.3	299.7	345.3	+2%	0.138	0.019	0.103	0.137	0.179	+7%
	Japan length freq	302.8	41.9	224.9	300.6	392.7	+3%	0.206	0.046	0.137	0.199	0.316	+55%
	US length freq	228.6	0.1	228.4	228.6	228.8	-22%	0.170	0.000	0.170	0.170	0.170	+33%

Table A2. Summary of statistics from predicted posterior distributions of VBG curve parameters for each member's ageing study using the age and growth data without data provided by Taiwan. Percent of mu (% of μ) denotes a difference between overall mean and each mean value.

Sex		L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%	% of μ	Mean	SD	2.5%	Median	97.5%	% of μ
Male	μ (hyperparameter)	236.9	12.8	219.7	233.3	268.0	0%	0.187	0.032	0.130	0.186	0.252	0%
	Japan	232.3	7.9	218.6	229.7	251.3	-2%	0.157	0.012	0.132	0.159	0.180	-14%
	Mexico	246.6	17.1	227.6	244.3	284.2	+5%	0.143	0.016	0.111	0.143	0.166	-23%
	US	227.8	14.7	193.7	228.5	258.6	-2%	0.182	0.029	0.135	0.178	0.255	-4%
	ISC Ref	245.8	20.2	225.4	240.0	296.0	+3%	0.190	0.030	0.129	0.193	0.241	+4%
	Japan length freq	241.4	24.9	202.7	232.8	308.6	0%	0.279	0.045	0.186	0.286	0.370	+54%
	US length freq	228.5	0.1	228.3	228.5	228.8	-2%	0.170	0.000	0.170	0.170	0.170	-8%
Female	μ (hyperparameter)	283.5	21.8	243.8	282.3	329.9	0%	0.145	0.025	0.099	0.144	0.199	0%
	Japan	280.2	12.5	257.9	279.4	306.8	-1%	0.109	0.009	0.091	0.109	0.128	-24%
	Mexico	292.1	14.3	266.4	291.3	322.6	+3%	0.107	0.008	0.090	0.107	0.124	-26%
	US	307.9	24.9	259.9	307.7	358.5	+9%	0.138	0.026	0.094	0.135	0.195	-6%
	ISC Ref	295.8	18.7	262.8	294.4	336.2	+4%	0.143	0.019	0.108	0.143	0.184	-1%
	Japan length freq	301.5	40.8	227.9	298.4	391.6	+6%	0.206	0.044	0.138	0.201	0.308	+40%
	US length freq	228.6	0.1	228.4	228.6	228.8	-19%	0.170	0.000	0.170	0.170	0.170	+18%

Table A3. Summary of statistics from predicted posterior distributions of VBG curve parameters for each member's ageing study using the age and growth data without two data sets of the length frequency data. Percent of mu (% of *μ*) denotes a difference between overall mean and each mean value.

Sex		L_∞ (cm PCL)						K (year^{-1})					
		Mean	SD	2.5%	Median	97.5%	% of *μ*	Mean	SD	2.5%	Median	97.5%	% of *μ*
Male	*μ* (hyperparameter)	245.7	11.5	228.7	244.4	272.3	0%	0.140	0.025	0.092	0.139	0.193	0%
	Japan	241.6	8.4	224.3	241.6	258.2	-1%	0.145	0.011	0.125	0.144	0.170	+3%
	Mexico	250.9	13.5	232.8	247.5	284.9	+1%	0.138	0.012	0.111	0.140	0.157	+1%
	US	242.6	13.7	211.8	242.5	272.0	-1%	0.158	0.021	0.121	0.156	0.208	+12%
	Taiwan	240.7	7.3	226.4	240.7	255.0	-2%	0.084	0.006	0.074	0.084	0.097	-40%
	ISC Ref	253.0	18.9	231.8	247.3	304.5	+1%	0.175	0.024	0.122	0.178	0.217	+28%
Female	*μ* (hyperparameter)	314.9	12.3	289.2	315.5	336.8	0%	0.098	0.020	0.060	0.097	0.140	0%
	Japan	305.5	16.1	271.3	308.6	330.5	-2%	0.093	0.010	0.080	0.090	0.115	-7%
	Mexico	310.3	13.3	280.9	312.1	332.6	-1%	0.097	0.007	0.086	0.095	0.113	-2%
	US	319.8	15.1	292.0	318.7	354.9	+1%	0.121	0.017	0.088	0.120	0.157	+24%
	Taiwan	324.0	10.3	306.6	323.0	346.7	+2%	0.054	0.003	0.048	0.054	0.060	-44%
	ISC Ref	315.4	13.8	285.8	315.9	343.1	0%	0.124	0.013	0.102	0.123	0.153	+27%