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

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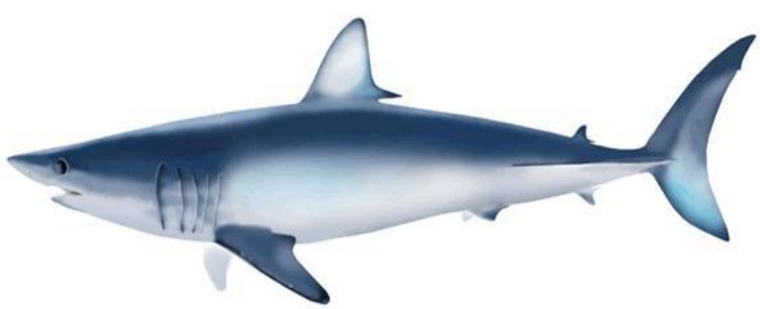

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Abstract

This document is a discussion paper for considering a potential method that effectively utilizes all age and growth data provided by the ISC Shark Working Group members to estimate a growth curve for shortfin mako sharks in the North Pacific Ocean. A possible method of meta-analysis to estimate a growth curve is reviewed and usefulness of this method is briefly examined using simulated age and growth data for hypothetical fish species. Characteristics of the raw age and growth data currently compiled and shared are also overviewed, and points/issues to be considered or resolved for applying the method to these data are raised.

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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, 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, Bishop et al., 2006, Natanson et al. 2006, Rivot-Carball al et al. 2006, Cerna and Licandeo 2009, Semba et al. 2009, Wells et al. 2013, Dono et al. 2015, Kai et al. 2015). Among these growth rate estimates, Wells et al. (2013) and Kai et al. (2015) are for juvenile shortfin mako in the North Pacific. Cailliet and Bedford (1983), Rivot-Carball al et al. (2006), and Semba et al. (2009) analyzed the growth rates of both juvenile and adult shortfin mako in the North Pacific. These estimates, however, have shown considerably different growth rates of shortfin mako in the North Pacific. These differences have partly come from the fact that the use of information about the vertebrae 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). 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 raw data from their age and growth studies for working collaboratively on meta-analyses to try to come up with the most parsimonious conclusions about growth of shortfin mako in the North Pacific (ISC 2015). Currently some of these raw age and growth data have been compiled and shared among the members.

This document is a discussion paper for considering a potential method that effectively utilizes all the age and growth data provided by the SHARKWG members to estimate a growth curve for shortfin mako sharks in the North Pacific. First, a possible method of meta-analysis to estimate a growth curve is reviewed. Then usefulness of this method is briefly examined using simulated age and growth data for hypothetical fish species. Finally, characteristics of the raw age and growth data currently compiled and shared are overviewed, and points/issues to be considered or resolved for applying the method to these data are raised.

2. A potential 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 is assumed to follow a VBG model and each growth study by the ISC members is treated as a random effect, then, for the North Pacific shortfin mako, Bayesian hierarchical meta-analysis can also be applied to the age and growth data, which were collected from the ISC members, in the similar way in Andrews et al. (2012) and Chang et al. (2013). Andrews et al. (2012) and Chang et al. (2013) used this analytic approach to examine growth rates and their associated uncertainties for tropical deepwater snapper and Pacific blue marlin, respectively. 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 ISC member's study (or with j-th ageing method used by each ISC member) under the VBG ($E[L_{i,j}]$) is written as:

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$$E[L_{i,j}] = L_{\infty,j}\left\{1 - \exp\left(-K_j(t_{i,j} - t_0)\right)\right\} \quad (1)$$

where $t_{i,j}$ and t_0 are fish age in years and the theoretical age at which the length is zero, respectively. $L_{\infty,j}$ and K_j are the asymptotic length and Brody growth rate parameters, respectively.

An observation for length of the i-th shortfin mako aged in the j-th ISC 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 ISC 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 $L_{\infty,j}$, K_j, and t_0 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.

Among parameters $L_{\infty,j}$, K_j, and t_0 in equation 1, only t_0 is not modeled with a random effect (not study-specific) and a common t_0 parameter value for all of members' studies is estimated in this approach because the t_0 parameter is often imprecisely estimated when there is a lack of length-at-age data for younger fish (Andrews et al. 2012). Thus, the prior for t_0 is assumed to follow a diffuse normal distribution centered at zero such as:

$$t_0 \sim N(0, 100) \quad (5)$$

Posterior distributions of the parameters of the model above (μ_∞, μ_K, σ_∞, σ_K, t_0, and σ_j) are estimated by Markov chain Monte Carlo (MCMC) method setting appropriate priors for these parameters.

3. Example analysis using simulated age and growth data

In this section, usefulness of the method reviewed in previous section is briefly examined using simulated age and growth data for hypothetical fish species.

The growth rate for this hypothetical fish species was assumed to follow a VBG curve of which parameters L_∞ and K had normal distributions (true distributions) with the population means (μ_∞ and μ_K) of 675 mm and 0.24, the standard deviations (σ_∞ and σ_K) of 18 and 0.057, and with fixed t_0 to -0.29, respectively. We assumed that there were five studies (the subscript j) in which 50, 65, 75, 85, and 100 data (the subscript i) were collected, respectively. Then, setting μ_∞ = 675, μ_K = 0.24, σ_∞ = 18, σ_K = 0.057, t_0 = -0.29, and σ_j = (15, 20, 25, 30, 35), age and growth data ($L_{i,j}$) were generated according to equations 1 to 4 (Fig. 1).

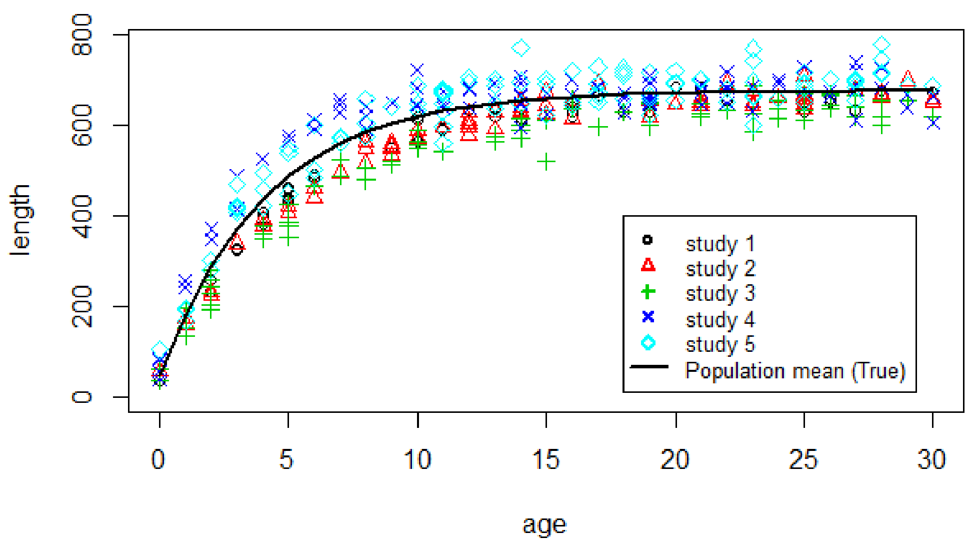

Fig. 1. Simulated age and growth data for hypothetical fish species. The symbols with different colors represent the data from different studies. The solid line is the VBG curve (true) drawn using the assumed population means (μ_∞ and μ_K) of distributions for L_∞ and K, and assumed t_0.

To analyze these simulated data using the method described in previous section, the priors for the population mean asymptotic length (μ_∞) and for the Brody growth rate parameter (μ_K) were set as below (Andrews et al. 2012):

$$\mu_\infty \sim N(100, 10000) \qquad (6)$$

$$\mu_K \sim \text{Beta}(1, 1) \qquad (7)$$

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 (Andrews et al. 2012):

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$$\frac{1}{\sigma_{\infty}^{2}} \sim \text{Gamma}(10^{-4}, 10^{-4}) \quad (8)$$

$$\frac{1}{\sigma_{K}^{2}} \sim \text{Gamma}(10^{-4}, 10^{-4}) \quad (9)$$

$$\frac{1}{\sigma_{j}^{2}} \sim \text{Gamma}(10^{-4}, 10^{-4}) \quad (10)$$

Posterior distributions of the parameters of the VBG model were estimated by 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 275000 iterations sampled with a thinning rate of 1/25 and a burn-in period of 25000 iterations for a total of 30000 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.

Results are shown in Table 1 and Fig. 2. The true value of parameters in the hierarchical VBG model for the hypothetical fish species are all within 95% credible limits of estimated posterior distributions (Table 1). Although there is almost no difference visually appeared between two growth curves based on estimated posterior median and true population mean parameter values, respectively (Fig. 2), estimates of μ_{∞} and t_0 are somewhat different from the true values (Table 1).

Overall, parameters in the hierarchical VBG model and their associated uncertainties are adequately estimated. The Bayesian hierarchical modeling approach reviewed in previous section is considered as a sensible way for conducting meta-analysis of North Pacific shortfin mako shark growth data.

Table 1. Estimated posterior distributions of parameters in the hierarchical VBG model for the hypothetical fish species. True values set when example data were generated through simulations are also shown.

Parameter	2.50%	median	97.50%	True
μ_{∞}	644	667.9	689.7	675
μ_K	0.1541	0.2336	0.3145	0.242
σ_{∞}	9.746	19.3	52.39	18
σ_K	0.03683	0.06939	0.1862	0.057
t_0	-0.459	-0.362	-0.2699	-0.29
σ_1	14.05	16.94	21.04	15
σ_2	15.61	18.4	22.14	20
σ_3	22.82	26.64	31.69	25
σ_4	24.42	28.27	33.15	30
σ_5	31.88	36.44	42.24	35

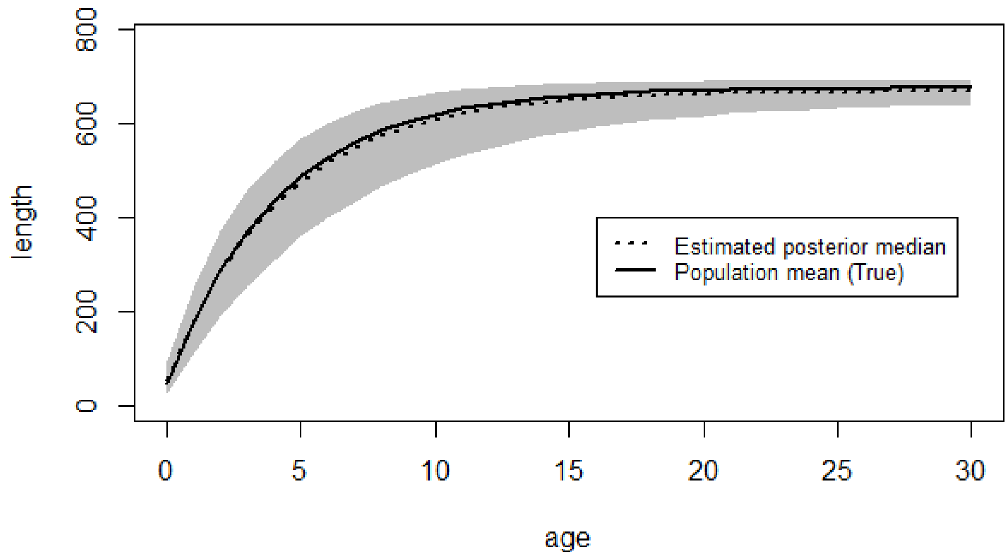


Fig. 2. Comparison between two VBG curves based on estimated posterior median and true population mean parameter values of the VBG model for the hypothetical fish species. The dotted and solid lines represent the curves based on estimated posterior median and true population mean parameters values, respectively. The shaded area is the estimated 95% credible envelope.

4. Available age and growth data compiled: an overview

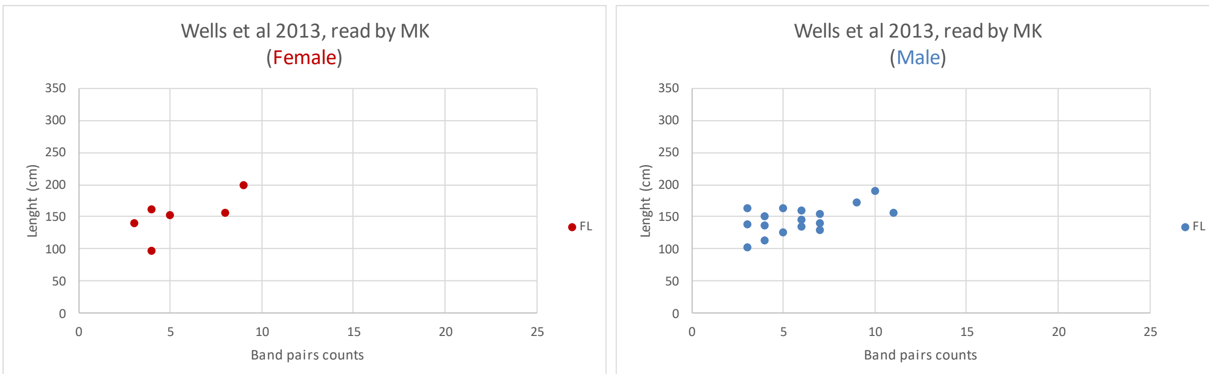
The US, Japan, and Mexico had submitted raw data of their age and growth studies for North Pacific shortfin mako shark to the ISC SHARKWG chair (S. Kohin). These raw data have been provided by the WG chair in the MS-excel format[1] and shared among the WG member scientists. In this section, characteristics of these raw are overviewed.

[1] Excel file names for these raw data are 'Mako length vs BP count data template adopted (With US data).xlsx', 'Mako length vs BP count data template adopted (Japan).xlsx', and 'Mako length vs BP count data template MEXICO FINAL.xlsx.'

(1) The US data

Raw data submitted from the US (Wells et al. 2013) are visually summarized in Fig. 3. For the US data, there are two datasets originated from the same vertebra samples, namely 'Read by MK' and 'Read by Wells and co-authors'. The study location is 'southern California'. The laboratory method for processing vertebrae used is 'Sectioned/Hard X-ray'. The length type used is 'FL (Fork length)'.

(a) 'Read by MK' data



(b) 'Read by Wells and co-authors' data (Average band counts were plotted)

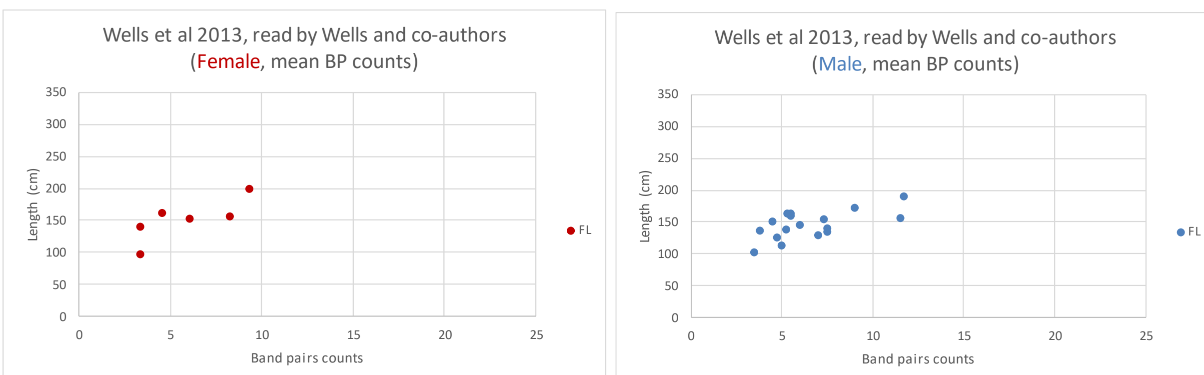


Fig. 3. Raw age and growth data submitted from the US (Wells et al. 2013).

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(2) Japan data

Raw data submitted from Japan (Semba et al. 2009) are visually summarized in Fig. 4. The study location is 'western and central North Pacific'. The laboratory method for processing vertebrae used is 'Shadowing' applied for the half-cut centrum. The length type used is 'PCL (Pre-caudal length)'.

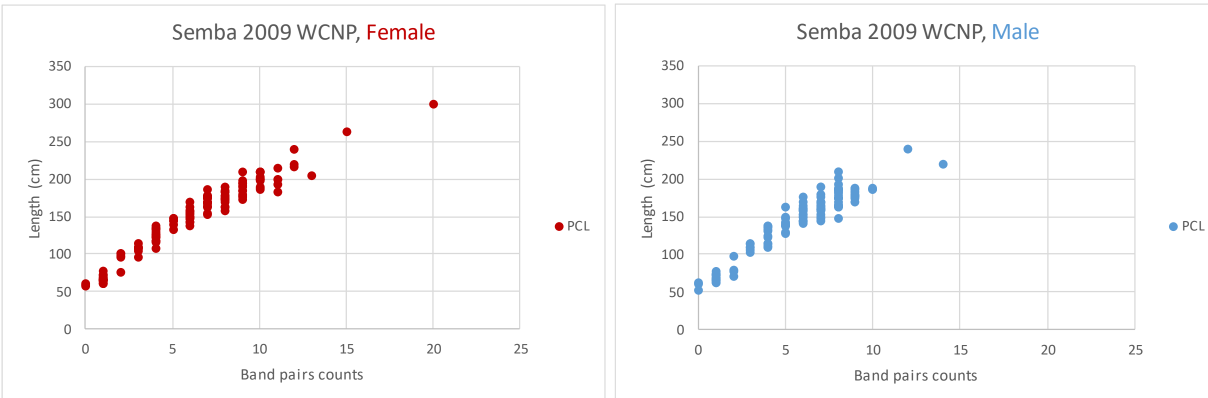

Fig. 4. Raw age and growth data submitted from Japan (Semba et al. 2009).

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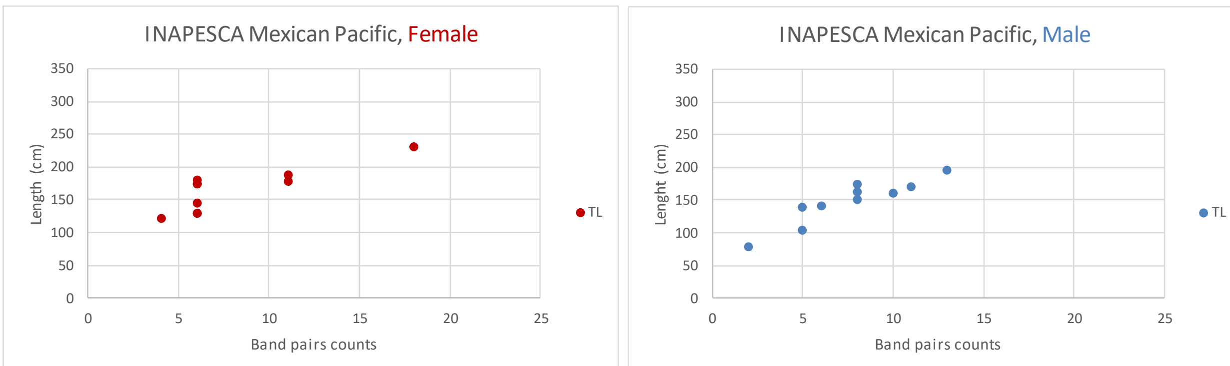
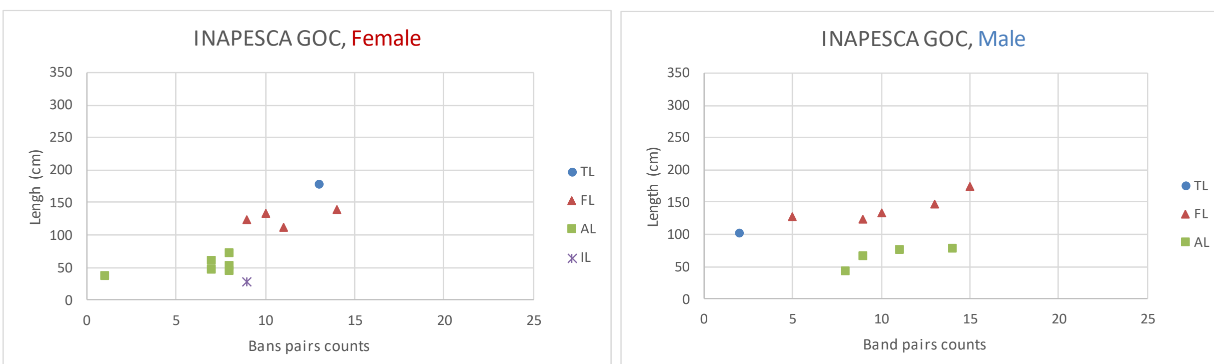
(3) Mexico data

Raw data submitted from Mexico are visually summarized in Fig. 5. There are two data origins (institutions) for Mexico data, namely 'INAPESCA 2014' and 'UAS 2014'. For the 'INAPESCA 2014' data, there are two study locations, 'Mexican Pacific' and 'Gulf of California (GOC)'. The study location for 'UAS 2014' data is 'GOC'. Laboratory method for processing vertebrae used is 'Sectioned/transmitted light'. The length types used are 'TL (Total length)' for 'INAPESCA 2014/Mexican Pacific', 'TL', 'FL', 'AL (Alternative length)', and 'IL (Inter-dorsal length)' for 'INAPESCA 2014/GOC', 'TL', 'FL', and 'AL' for 'UAS 2014/GOC'.

(a) 'INAPESCA 2014' data / 'Mexican Pacific'



(b) 'INAPESCA 2014' data / 'Gulf of California (GOC)'



(c) 'UAS 2014' data / 'GOC'

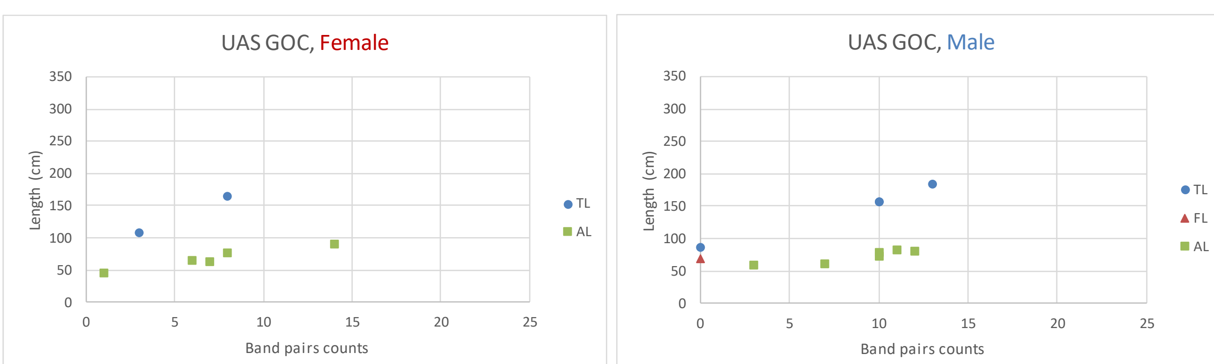


Fig. 5. Raw age and growth data submitted from Mexico.

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5. Points/issues to be considered or resolved for analysis

In this section, some points/issues to be considered or resolved for applying the meta-analysis method reviewed in previous section to the data are raised.

- Length types used are different depending upon member nations (Figs. 3 to 5). The US and Japan used FL and PCL, respectively, while there were mixed uses of multiple length types (TL, FL, AL, and IL) in the Mexico dataset. Can all measurements in TL, FL, and AL be converted to PCL using the following equations? : PCL = (TL x 0.816) + 0.784; TL = (FL + 0.397) / 0.913; FL = (AL x 2.402) + 9.996 (Sippel et al 2015). How can IL (Inter-dorsal length) be converted to PCL? If IL and AL are same as DL (distance between the origin of the first dorsal fin and that of the second dorsal fin), then can the following equations be used? : PCL = 2.04DL + 12.1 for male, PCL = 2.18DL + 7.79 for female (Semba et al. 2009).

- How are numbers of band pairs converted to ages? For the first band (birthmark), can it be assumed that age = (the number of band pairs) – 1? For subsequent annuli (convex structures), in Semba et al. (2009), assuming that birth month is May and annuli are formed soon before or after 1 December, age in years is calculated as follow: age = $(x - 1) + (y - 5) / 12$ ($x \geq 1$, $1 \leq y \leq 12$) where x is the number of convex structure and y is the month when the individual was caught.

  For other members' studies (the US and Mexico), it needs to be checked how birth month and timing of annuli formation are treated. It also needs to be checked whether it can be assumed that age = (the number of band - 1) / 2 in a case considering that two bands are formed per year.

- For the US data, which are band pairs data to be used in analysis, 'Read by MK' or 'Read by Wells and co-authors' data? If 'Read by Wells and co-authors' data is to be used, then are the average values to be used for band pairs data? Or the average of 'Read by MK' and 'Read by Wells and co-authors' data must be used?

- In dealing with the Mexico data, even though the laboratory method used is same 'Sectioned/transmitted light' for all the samples, how are these data to be treated/classified as a "study"? As combined all Mexico data (treated as one study), as classified according to institutions (treated as two studies), as classified according to study locations (treated as two studies), or as classified according to each institution/study location combination treated as (three studies)?

  It needs to be checked whether samples used in analysis are different between 'INAPESCA 2014' / 'Gulf of California (GOC)' data and 'UAS 2014' / 'GOC' data. If samples are different between the two institutions and the study location is same, then can the data from the two institutions be aggregated? If samples are of the same individuals between the two institutions, then can the data be averaged?

- Except the Japan data, there are only a few data available for younger (< age 3) shark (Figs. 3 to 5). Kai et al. (2015) estimated a VBG curve for juvenile shortfin mako shark in the North Pacific. Is there any way to incorporate this VBG curve for juveniles into meta-analysis of the VBG curve for whole age spectrum?

  One possible way is that, using the mean and variance of growth curve (for ≤ age 2) estimated from length data, samples of age-length pair are randomly generated by simulation, then these simulated data are added to the existing age and growth datasets of the North Pacific shortfin mako and are utilized in meta-analysis.

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