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A Bayesian Hierarchical Meta-Analysis of Blue Marlin (*Makaira nigricans*) Growth in the Pacific Ocean[1]

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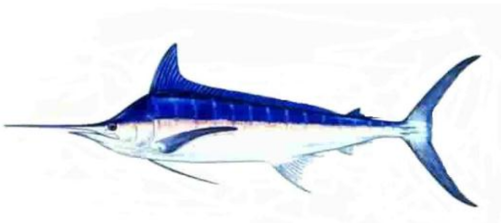

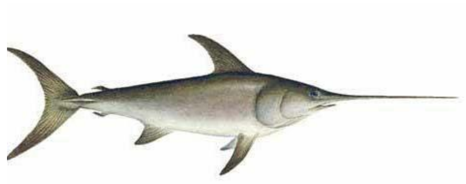

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A Bayesian hierarchical meta-analysis of blue marlin (*Makaira nigricans*) growth in the Pacific Ocean

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Abstract

Growth characteristics of the Pacific blue marlin, *Makaira nigricans*, a highly migratory species of economic importance for the commercial and recreational fishery, are incomplete and inconsistent among various ageing studies across its geographical range. In this study, Bayesian hierarchical meta-analysis was used to describe variability in growth rates with age studies treated as a random effect. The Bayesian hierarchical model was found to fit the data better than the models with no hierarchical structure for ageing studies based on the deviance information criterion. According to the fast growth rate for juvenile Pacific blue marlin identified by the otolith microstructure counts, the von Bertalanffy growth parameters estimated for the *M. nigricans* population and their standard errors ($\pm\sigma$) were L_∞ = 316.08 (cm, eye-to-fork length) (49.13), K = 0.11 (year^{-1}) (0.06), and t_0 = -4.71 (1.06) for females and L_∞ = 210.54 (17.99), K = 0.21 (0.07), and t_0 = -3.50 (0.02) for males. We suggest that the posterior probability distributions of the hyperparameters from this analysis can provide plausible input for future implementation of population dynamics models to make precautionary management decisions.

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1. Introduction

The biological relationship between age and length is fundamental to many fisheries population dynamics models used to establish sustainable levels of exploitation (Beverton and Holt, 1957). For example, growth is essential in the determination of lifespan, age-at-recruitment, age-at-first capture, age-at-maturity, cohort identification, and is related to life history traits such as natural mortality (Charnov, 1993; Jensen, 1998). Modeling growth is an intrinsic component of almost all quantitative fisheries stock assessment approaches (*e.g.*, size- and age-structured stock assessment models, Quinn and Deriso, 1999; yield calculations, Beverton and Holt, 1957; Gulland, 1983).

There are a number of approaches to modeling growth. The von Bertalanffy growth function (VBGF; von Bertalanffy, 1938) is the most widely used in fisheries and its parameters are particularly useful in describing general fish growth (Chen *et al.*,1992; Quinn and Deriso, 1999) and deriving fisheries reference points (Clark, 1991). Although the common applications of the VBGF are descriptions of average size-at-age, many studies have quantified variation in size-at-age due to either environmental or individual characteristics (Wang and Thomas, 1995; Prajneshu and Venugopalan, 1999). Temperature, food availability, and population density are considered to be dominant factors in the variability of estimated age and growth parameters among year classes of a population (Krohn *et al.*, 1997) or across its geographical range (Helser and Lai, 2004; Escati-Peñaloza *et al.*, 2010). Other factors that can cause variation in growth include size-selective mortality (Myers, 1989) or measurement error (Campana, 2001; Cope and Punt, 2007).

Preliminary estimates of age and growth of Pacific blue marlin have been made based on length-frequency data (Skillman and Yong, 1976). Additional ageing research has been done evaluating hardparts (otoliths, vertebrae, dorsal-, and anal- spines) of blue marlin caught in Hawaiian waters for the use in age and growth studies (Hill, 1986; 1989). Age and growth of blue marlin have also been examined based on the second spine of the first anal fin (Chen, 2001) and also based on monthly length-frequency data (Dai, 2002) sampled from April 1999 to March 2000 and 2001 in the offshore waters of Taiwan. Age determination based on the dorsal fin of blue marlin sampled in the waters of Yonaguni Island (Japan) was also recently carried out by Shimose (2008). These studies produced different predicted growth curves for *M. nigricans* (see Fig. 2 of ISC, 2012), which has been an ongoing problem in the development of reliable growth parameters for a Pacific blue marlin stock assessment. In addition, uncertainty in the growth parameters can lead to uncertainty in the estimation of life history parameters such as natural mortality and age- or length-at-maturity, which implies greater uncertainty in the determination of stock status (Chang *et al*., 2009).

Hierarchical meta-analysis and Bayesian methods have widely used in the fisheries as desirable tools for estimating and quantifying uncertainty in population parameters under study (Punt and Hilborn, 1997; Liermann and Hilborn, 1997; Michielsens and McAllister, 2004). For example, Helser and Lai (2004) use a hierarchical meta-analysis to estimate expected growth of fish among geographically distinct populations of a fish species in North America. Zhang *et al*. (2009) developed Bayesian hierarchical models to incorporate the individual growth variation into the estimation of the growth parameters of northern abalone, *Haliotis kamtschatkana*, using tag-recapture data. The Bayesian hierarchical models were developed to describe temporal variation in growth rates for the Johnsons Lee red abalone (*Haliotis rufescens*) population by Jiao *et al*. (2010). Forrest *et al*. (2010) developed a hierarchical Bayesian meta-analysis to improve estimates of stock–recruit parameters, characterize management-related parameters (*e.g.*, optimal harvest rate) Pacific rockfishes (*Sebastes spp.*).

In this study, we use a hierarchical approach with multilevel priors to address the problem of describing female and male blue marlin growth rates and their associated uncertainty when substantial variability in estimates of growth exists among multiple published studies. Parameters of a VBGF for the Pacific blue marlin were estimated using a Bayesian hierarchical approach in which “study (/method)” was treated as a random effect (Andrews *et al*., 2012). The estimated hyperparameters, the parameters that further specify the priors of the parameters in the model, characterized the variation in size at age from the multiple studies and provided a more comprehensive representation of important variation in growth. To evaluate the potential benefits of the hierarchical modeling approach, the goodness-of-fit of alternative hierarchical and non-hierarchical models was compared using the deviance information criterion (DIC) and other model diagnostics. Furthermore, the assumption of unequal variances among various ageing studies was also evaluated. Ultimately, the objective of this study was to construct VBGF models to describe the overall growth dynamics of blue marlin and to provide input parameters for stock assessment.

2. Materials and methods

2.1. Data collection

Substantial data for the blue marlin growth in mean length-at-age has been compiled for numerous studies in Pacific Ocean. In this study, the VBGFs were estimated using the most reliable age data, which included the selected mean length-at-age data from Hill (1986), Chen (2001), Dai(2002), and Shimose (2008) (Table 1). The study of Skillman and Yong (1976) was taken out of our analysis because a lack of older age-groups in the mode analysis to estimate the valid values of growth parameters. The combined data set consisted of a total of 50 and 39 mean length-at-age samples for females and males, respectively, with lengths ranging from 95 ~ 325 and 95 ~ 200 cm EFL and the maximum identified ages of 18 and 26 years. In this case, we treated the predicted mean length at age for each study as an observed data point to be predicted in the hierarchical Bayes and non-hierarchical models.

2.2. von Bertalanffy growth function

Blue marlin growth was assumed to follow the von Bertalanffy model:

(1) $\hat{L}_t = L_\infty(1 - e^{-K\times t - t_0})$

where $\hat{L}_t$ is the expected length at age t, L_∞ is the asymptotic length and K is the Brody growth rate parameters, t is age in years, and t_0 is the theoretical age at which the length is zero. We assumed that each aging study was expected to have its own von Bertalanffy curve. Parameters of the VBGFs for *M. nigricans* in the Pacific Ocean were estimated using a Bayesian hierarchical approach (*e.g.*, Helser and Lai, 2004; Jiao *et al.*, 2010; Andrews *et al.*,

2012) with ageing studies treated as a random effect. Each of the ageing studies was treated separately because it was expected that each would produce different amounts of observation error in length-at-age data. The base-case hierarchical growth model (HB) for estimating the expected length of the *i*th fish aged with the *j*th ageing method under the von Bertalanffy growth curve was modeled as (Gelman *et al.*, 2004):

$$(2)\ \ \hat{L}_{i,j} = L_{\infty,j}(1 - e^{-K_j \times t_{i,j} - t_0})$$

where fish age was $t_{i,j}$, $L_{\infty,j}$ and K_j were the asymptotic length and Brody growth rate parameters, respectively, measured by the *j*th ageing studies. The observation model for length of the ith fish aged with the *j*th age reading method ($L_{i,j}$) as a function of expected length under the von Bertalanffy growth curve and observation error ε_j for the *j*th age reading method was

$$(3)\ \ L_{i,j} = \hat{L}_{i,j} + \varepsilon_j \qquad \text{where} \quad \varepsilon_j \sim N(0, \sigma_j^2)$$

A Bayesian hierarchical growth model assigns priors of hyperparameters to yield the joint posterior using Bayes' theorem can be written as:

$$p(\theta = L_{\infty,j}, K_j, \mu_\infty, \mu_K, t_0, \sigma_\infty, \sigma_K \,|\, L) = \frac{\prod_j f(L_j \,|\, L_{\infty,j}, K_j, t_0)\pi_1(L_{\infty,j} \,|\, \mu_\infty, \sigma_\infty)u_1(\mu_\infty)v_1(\sigma_\infty)\pi_2(K_j \,|\, \mu_K, \sigma_K)u_2(\mu_K)v_2(\sigma_K)\pi_3(t_0)}{\int_{-\infty}^{+\infty}\prod_j f(L_j \,|\, L_{\infty,j}, K_j, t_0)\pi_1(L_{\infty,j} \,|\, \mu_\infty, \sigma_\infty)u_1(\mu_\infty)v_1(\sigma_\infty)\pi_2(K_j \,|\, \mu_K, \sigma_K)u_2(\mu_K)v_2(\sigma_K)\pi_3(t_0)d\theta}$$

where $f(L_j|\theta)$ is the probability density function (*p.d.f.*) of mean size-at-age L_j on parameter vector θ; u_1( ), v_2( ), u_2( ), v_2( ), and π_3 are the *p.d.f.* of μ_∞, σ_∞, μ_K , σ_K, and t_0, respectively.

In this study, the hierarchical structure is implemented in the model through a multilevel prior of study-specific growth parameters (*i.e.*, the subscript *j*). Prior distributions for the $L_{\infty,j}$ and K_j parameters were assumed to came from normal distributions of $L_{\infty,j} \sim N(\mu_\infty, \sigma^2_{L_\infty})$ and $K_j \sim N(\mu_K, \sigma^2_K)$, respectively. The hyperparameters, μ_∞ and μ_K, are the population mean values for L_∞ and *K*, respectively. The hyperparameters, $\sigma_{L_\infty}^2$ and σ_K^2, are between-studies variances in L_∞ and *K*, respectively. Because the lack of size-at-age measurements for the younger fish, we simplified the model structure and estimated a common t_0 parameter for each of the ageing studies (Andrews *et al*., 2012). More specifically, the t_0 parameter was a diffuse normal distribution centered at zero [*i.e.*, $t_0 \sim N(0,10)$]. Furthermore, the observation errors (ε_j) are normally distributed with zero mean and a study-specific length-at-age variance (σ_j^2). As a result, any potential heterogeneity in the variance of length-at-age estimates among the ageing studies was directly incorporated into the sample likelihood for each method.

Bayesian model requires specification of prior distributions on all unobserved quantities. Uninformative priors were used for both the population hyperparameters and the observation error variances. In particular, the prior for the population mean asymptotic length was set to be a diffuse normal distribution, and the prior for the mean Brody growth rate parameter was set to be a diffuse beta distribution (Zhang *et al*., 2009; Andrews *et al*., 2012):

$$\begin{aligned} \mu_\infty &\sim N(300,100) \\ \mu_K &\sim \text{Beta}(1,1) \end{aligned} \quad (4)$$

The priors for the parameter variances and the observation error variances were all set to be diffuse inverse gamma distributions (Zhang *et al*., 2009; Andrews *et al*., 2012), because this distribution is the conjugate prior for the unknown variance of a normally distributed mean (e.g., Ntzoufras, 2009)

$$\begin{aligned} \frac{1}{\sigma_\infty^2} &\sim Gamma(0.01,0.01) \\ \frac{1}{\sigma_K^2} &\sim Gamma(0.01,0.01) \\ \frac{1}{\sigma_j^2} &\sim Gamma(0.3,0.3) \end{aligned} \quad (5)$$

To compare the performance of the hierarchically structured model with other VBGFs, another three hierarchical models were developed (Table 2). The first alternative model was identical to the base-case hierarchical model but assumed a single common error variance σ^2 for all ageing studies. This hierarchical model with homogeneous variance (HBHV model) was included to evaluate whether the assumption of unequal variances among studies was justifiable given the observed length-at-age data. The second alternative was a simple Bayesian model (SB model) with no hierarchical structure for ageing study, but the observation error was study-specific. In this approach, there was a single prior for the asymptotic length L_∞ and growth parameter *K*, respectively, given by Eq. 4. The third alternative was a SB model with common observation error variance (SBHV model).

2.3. Diagnostics

The WinBUGS software program (Spiegelhalter *et al*., 2003) was used for the Bayesian analyses. The estimates of parameters were evaluated based on 1,000,000 samples after 10,000 burn-in samples, thinning to one draw every 1,000th sample, from MCMC simulation of the joint posterior distribution. We monitored auto-correlation at various lags to assess whether adequate burn-in and stationarity of the mean had been achieved (Geweke, 1992; Gelman *et al*., 2004). Three chains were used with different initial values for the convergence test by the Gelman–Rubin diagnostics (Gelman and Rubin, 1992) as implemented in the R language (R Development Core Team 2008) and the CODA package (Plummer *et al*., 2006). Evidence of convergence was warranted by this test, as the three independent chains virtually overlapped with each other after the burn-in period.

The goodness-of-fit of the alternative and base-case models to the observed data were evaluated using the deviance information criterion (DIC; Spiegelhalter *et al*., 2002), a Bayesian analog of the Akaike Information Criterion. In this context, the VBGF model with the minimum DIC value would be judged to provide the best predictive model fit to the data with the caveat that differences of less than two units of deviance indicated that there was no substantial difference between model fits and that differences of more than seven units were substantial (e.g., Spiegelhalter *et al*., 2002). Following conventional practice, the root mean squared error (RMSE) and the mean absolute percentage error (MAPE) was also used to assess the goodness-of-fit. We also calculated the Bayesian *p*-value, which is the probability that the “ideal” data could be as extreme or more extreme than the observed data (Meng, 1994). Bayesian *p*-values of around 0.5 indicate the model is right for the data, whereas extreme *p*-values near 0 or 1 indicate conflict between data and some attributes of the model under investigation. To obtain the “ideal” data sets, one replicate data set was assembled using the same model that was fit to the actual data set at each MCMC iteration using the values of the current parameter values.

3. Results and Discussion

3.1. Diagnostics

The Gelman and Rubin statistics for all of the parameters, including all variance terms, were equal to unity, which indicated convergence of the Markov chains. We evaluated convergence of the MCMC simulation to the target distribution and model goodness-of-fit using predictive posterior checks. Independent chain sequences from starting the MCMC simulation at different initial parameter values showed highly coherent trace plots and nearly indistinguishable kernel densities (Fig. A1). These results are illustrated for the hyperparameters, μ_∞ and μ_K, but all other model parameters showed qualitatively the same convergence properties. Autocorrelation within the chain sequence diminished after a lag of about 3 (Fig. A2). Further evidence of convergence was shown by the Geweke (1992) test statistics. All diagnostics indicated that the posterior distribution of the model parameters was adequately sampled by the MCMC simulations.

3.2. von Bertalanffy growth function

The mean Bayesian *p*-values were around 0.5 for all models, which suggested that the fitted models were generally adequate for the blue marlin mean size-at-age data. The expected lengths at age for the *M. nigricans* population in the Pacific Ocean were derived from the posterior means of the VBGF parameters estimated with four VBGF models (Figure 1).

The goodness-of-fit comparison of the base-case hierarchical model (HB) and the three alternative models indicated that there was a substantial difference in the quality of model fits (Table 2). Although the unequal variances among various ageing studies was not justifiable for the female hierarchical model according to the RMSE, models with multilevel priors for the growth parameters generally performed better than the simple Bayes models (*i.e.*, SB and SBHV model). Among the 4 models, SBHV model, the model with no hierarchical structure and a common observation error variance resulted in the largest DIC value for both sexes. The DIC differences (ΔDIC) for the HBHV model relative to the HB model were substantial with ΔDIC = 95.48 and 129.10 for females and males, respectively. Substantial ΔDIC was also found for SBHV model relative the SB model (ΔDIC = 58.65 for females and 43.90 for males). These results indicated that the unequal variances among age reading methods were justifiable given the observed length-at-age data.

Substantial differences in DIC values existed between the SB model and HB model for females (ΔDIC = 131.42) and males (ΔDIC = 96.91). The HB model, hierarchical model with heterogeneous variances for the ageing studies, had the lowest DIC value (246.89 for females and 159.42 for males), which indicated that there was large variation in growth estimates among studies and that the hierarchical model produced the best fit to the five size-at-age data sets. For the HB model, comparisons of estimated standard deviations of μ_∞ (31.03 and 17.99 for females and males, respectively) and μ_K (0.08 and 0.07) with means of estimated σ_∞ (61.51 and 32.14) and σ_K (0.15 and 0.13) also indicated the substantial variability in the asymptotic length and growth rate coefficient among studies. Furthermore, comparisons of estimated σ_∞/μ_∞ (0.22 and 0.15 for females and males, respectively) with σ_K/μ_K (0.77 and 0.64) indicated that the inclusion of hierarchical structure for aging studies had a stronger effect on the estimate of the Brody growth coefficient than on the estimate of the asymptotic length. As a result, we suggested that the hierarchical model was useful in incorporating the growth variation among various studies and to determine a single growth curve for the *M. nigricans* in the Pacific Ocean.

The growth pattern between females and males are different, with means of μ_∞ and L_∞ of females was much larger than males for all models. Furthermore, the means of μ_K and K of females was smaller than males for all models. For the HB model, the estimated CV of μ_∞ were much larger in females than males, which implied the sex-specific variability in mean growth for the population. The between-studies variances in L_∞ and *K*, the hyperparameters of σ_∞ and σ_K, were also found to be different between females and males. For example, the mean σ_∞ and σ_K of females (61.51 and 0.15) was larger than males (32.14 and 0.13), respectively (Table 3). As a result, blue marlin population exhibits sexual dimorphism in mean growth and variability. The between studies errors and observation errors were also different between females and males, thus the sex-specific VBGF may need to be used in any future stock assessment.

4. Discussion

The fast growth rate of juvenile Atlantic blue marlin was demonstrated by otolith microstructure counts reported by Prince *et al*. (1991) and a similar pattern of rapid growth was found forjuvenile Pacific blue marlin by Shimose (unpublished data). By comparing the estimated size at age 1 derived from the otolith counts to the predicted values from different VGBFs (Fig. 1), it was evident that the female HBHV model and male HB model produced predictions of juvenile size at age 1 that were most consistent with the growth studies of Shimose (unpublished data) and Prince *et al*. (1991). Furthermore, the estimated values of asymptotic length from the female HBHV model and the male HB model were relatively higher, which was consistent with the observations of large fish in the Japanese fisheries (Kimoto and Yokawa, 2012). We suggest that the parameters of female HBHV model and male HB model are appropriate for use in stock assessment modeling. We also suggest that more research be conducted on juvenile growth rates in order to derive a more reliable growth curve for Pacific blue marlin.

The relative performance of the hierarchical and non-hierarchical models was, of course, contingent on the particular dataset used in this study. It should be noted that the Bayesian hierarchical growth model may not always make better prediction than the simple Bayesian growth model when the number of data sets is small. Nevertheless, the results of our study provide clear evidence that the Bayesian hierarchical model is capable of improving the quality of growth predictions for blue marlin and is also able to address the problem of describing growth rates and their associated uncertainty when data from alternative ageing studies indicate substantial variability in growth. Ultimately, growth models that address such variation are likely the most useful for describing the overall population dynamics of blue marlin for stock assessment.

In this study, independent normal distributions of each one of parameters were assumed as priors. Some other modeling approaches, such as using multivariate normal distributions for priors (as suggested by Pilling *et al*., 2002; Helser and Lai, 2004) may be considered in the future based on the known correlations among growth parameters for the blue marlin populations. Furthermore, the base-case hierarchical growth model considered is the von Bertalanffy curve. Although the VBGF is the most widely used in fisheries (Chen *et al*., 1992; Quinn and Deriso, 1999), other growth curves can perform better and are worth exploring in the future. For example, the variability in the individual growth of the rudimentary hermaphrodite (*Diplodus annularis*) was described using a 5-parameter Bayesian model which accounted for a singular change in the growth rate of this species (Alós *et al*., 2010).

In conclusion, Bayesian hierarchical analysis was used to describe the variability in growth rate among various studies and to determine a single growth curve. The hierarchical model was shown to be capable of making more accurate predictions than the simple Bayes model through successfully accommodating growth variability, using the hierarchical structure mean size-at-age data sets. Growth differed significantly between the sexes; females reached larger sizes, but approached their asymptotic size slower than did males. The mean VBGF parameters estimated for the Pacific blue marlin population and their standard errors ($\pm\sigma$) were: L_∞ = 316.08 (49.13), K = 0.11 (0.06), and t_0 = -4.71 (1.06) for females and L_∞ = 210.54 (17.99), K = 0.21 (0.07), and t_0 = -3.50 (0.02) for males.

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Table 1. Source of age information used in the meta-analysis of blue marlin (*Makaira nigricans*) growth in the Pacific Ocean.

Region	Sex	N of ages	[a] Range of mean size-at-age	Ageing method	Year	Source
Hawaii waters	F	26	140-325	Anal spine	1982-1984	Hill (1986)
Hawaii waters	M	18	95-195	Anal spine	1982-1984	Hill (1986)
Taiwan waters	F	14	130-225	[b] Anal spine	1999-2000	Chen (2001)
Taiwan waters	M	11	125-200	[b] Anal spine	1999-2000	Chen (2001)
Taiwan waters	F	11	95-240	Size frequency	2001	Dai (2002)
Taiwan waters	M	9	100-190	Size frequency	2001	Dai (2002)
Yonaguni Island, Japan	F	9	190-215	[b] Dorsal spine	2003-2006	Shimose (2008)
Yonaguni Island, Japan	M	8	160-175	[b] Dorsal spine	2003-2006	Shimose (2008)

[a] Eye-to-fork length; [b] back-calculation

Table 2. Model comparison among hierarchical and nonhierarchical growth models of blue marlin (*Makaira nigricans*).

Measurement	Female				Male			
	HB model	HBHV model	SB model	SBHV model	HB model	HBHV model	SB model	SBHV model
Bayesian *p*-value	0.556	0.480	0.539	0.504	0.515	0.511	0.546	0.497
RMSE	10.839	10.373	28.111	21.827	8.456	9.281	14.062	12.125
MAPE	0.173	0.233	0.462	0.517	0.954	0.927	1.009	1.274
DIC	246.892	342.368	378.315	436.966	159.420	288.513	256.325	300.225

HB model: Bayesian hierarchical model with heterogeneous observation variance;
HBHV model: Bayesian hierarchical model with homogeneous observation variance;
SB model: Simple Bayesian model with heterogeneous observation variance;
SBHV model: Simple Bayesian model with homogeneous observation variance.

Table 3. Estimated posterior distributions of parameters in the hierarchical and nonhierarchical growth models for blue marlin (*Makaira nigricans*).

Model	Sex	Asymptotic length (cm EFL)							K (year^{-1})							t_0					
			Mean	SD	CV	2.50%	Median	97.50%		Mean	SD	CV	2.50%	Median	97.50%	Mean	SD	CV	2.50%	Median	97.50%
HB	Female	μ_∞	274.446	31.033	0.113	214.200	273.500	338.855	μ_K	0.192	0.081	0.423	0.053	0.184	0.381	-2.412	0.006	0.003	-2.417	-2.414	-2.394
		σ_∞	61.514	35.972	0.585	25.228	51.450	157.110	σ_K	0.147	0.100	0.677	0.060	0.123	0.377						
HBHV		μ_∞	316.082	49.130	0.155	223.886	312.700	420.965	μ_K	0.107	0.055	0.514	0.026	0.100	0.231	-4.708	1.059	0.225	-7.061	-4.614	-2.918
		σ_∞	94.308	87.449	0.927	2.512	72.465	305.882	σ_K	0.080	0.067	0.837	0.025	0.065	0.218						
SB		L_∞	309.602	1.765	0.006	306.000	309.700	313.000	K	0.111	0.002	0.014	0.108	0.111	0.114	-2.411	0.033	0.014	-2.472	-2.412	-2.344
SBHV		L_∞	354.280	51.263	0.145	279.072	346.450	478.527	K	0.054	0.019	0.359	0.025	0.051	0.101	-9.158	2.395	0.262	-14.351	-8.992	-4.963
HB	Male	μ_∞	210.543	17.990	0.085	177.890	209.200	250.782	μ_K	0.205	0.070	0.343	0.068	0.202	0.366	-3.503	0.018	0.005	-3.514	-3.507	-3.458
		σ_∞	32.142	24.532	0.763	12.749	26.270	88.667	σ_K	0.131	0.081	0.616	0.052	0.110	0.352						
HBHV		μ_∞	204.270	10.475	0.051	187.300	203.200	227.100	μ_K	0.211	0.065	0.308	0.107	0.203	0.362	-3.052	0.846	0.277	-4.960	-2.955	-1.658
		σ_∞	4.328	8.064	1.863	0.035	1.048	27.139	σ_K	0.069	0.057	0.831	0.022	0.052	0.232						
SB		L_∞	231.443	2.471	0.011	226.500	231.400	236.400	K	0.131	0.004	0.031	0.123	0.131	0.140	-3.504	0.089	0.026	-3.682	-3.504	-3.317
SBHV		L_∞	213.918	19.119	0.089	191.400	209.900	260.537	K	0.154	0.047	0.302	0.069	0.153	0.251	-4.770	1.679	0.352	-8.741	-4.460	-2.408

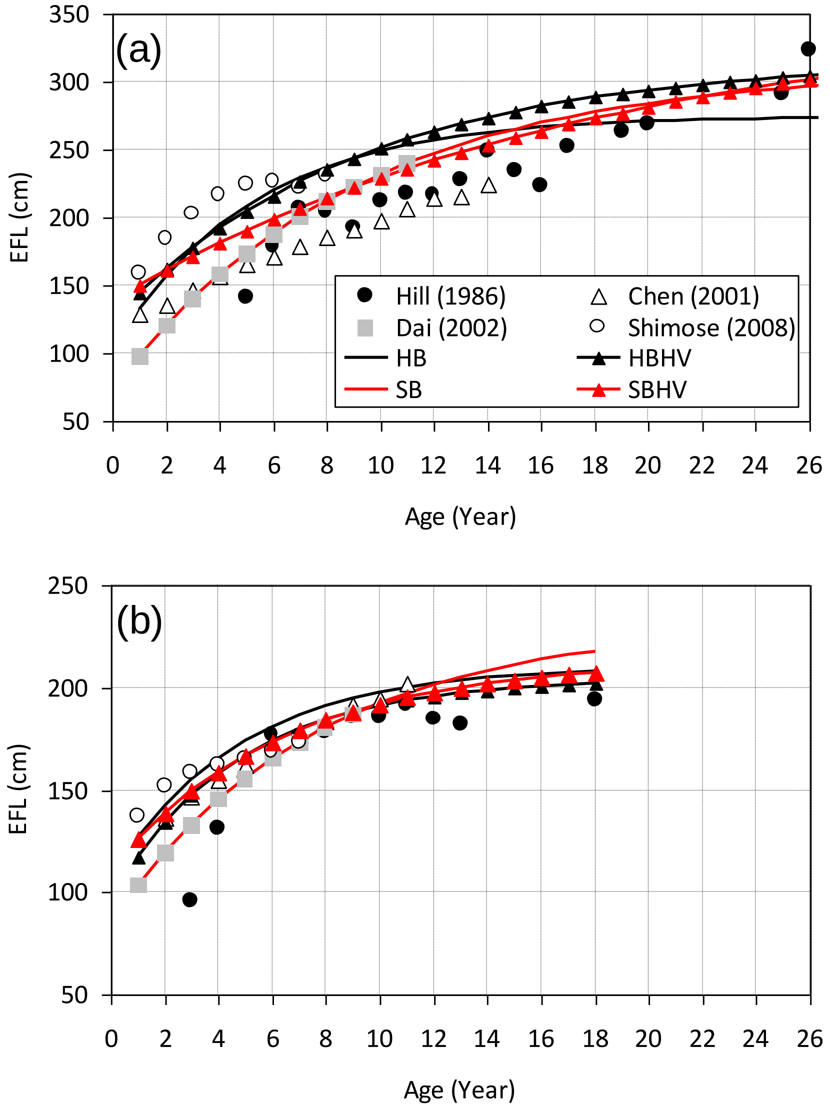

Figure 1. Female (a) and male (b) von Bertalanffy growth curves derived from 4 different growth models (defined in Table 2) plotted with mean size-at-age data considered reliable for blue marlin (*Makaira nigricans*) in the Pacific Ocean.

[1] Working document submitted to the ISC Billfish Working Group Workshop, 16-23 January 2013, Honolulu, USA. Document not to be cited without author's written permission.

Appendix

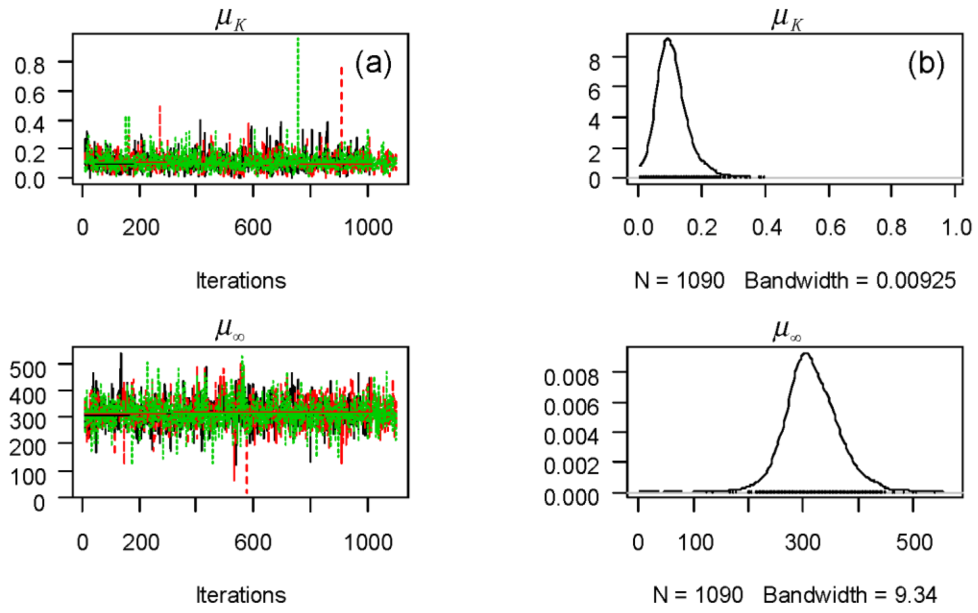

Figure A1.Trace (a) and kernel density (b) plots for the von Bertalanffy growth parameters μ_∞ and μ_K for female blue marlin (*Makaira nigricans*) drawn from 10,000 MCMC samples of the base-case hierarchical growth model (HB model). Trace and kernel density plots shown are based on three independent chain sequences from starting the MCMC simulation at different initial parameter values.

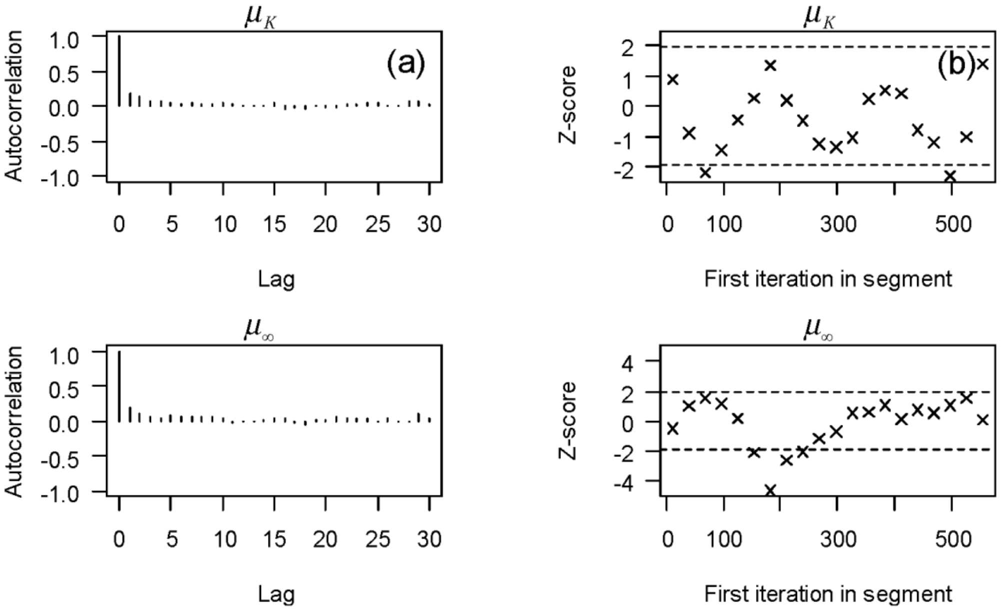

Figure A2. Autocorrelation function plots (a) and Geweke statistics (b) of parameters μ_∞ and μ_K for female blue marlin (*Makaira nigricans*) based on the base-case hierarchical model (HB model). A large number of Z-scores falling in the horizontal dotted lines (Z = ±1.96) suggests convergence.