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A Review of Life History Parameters of the Pacific Blue Marlin[1]

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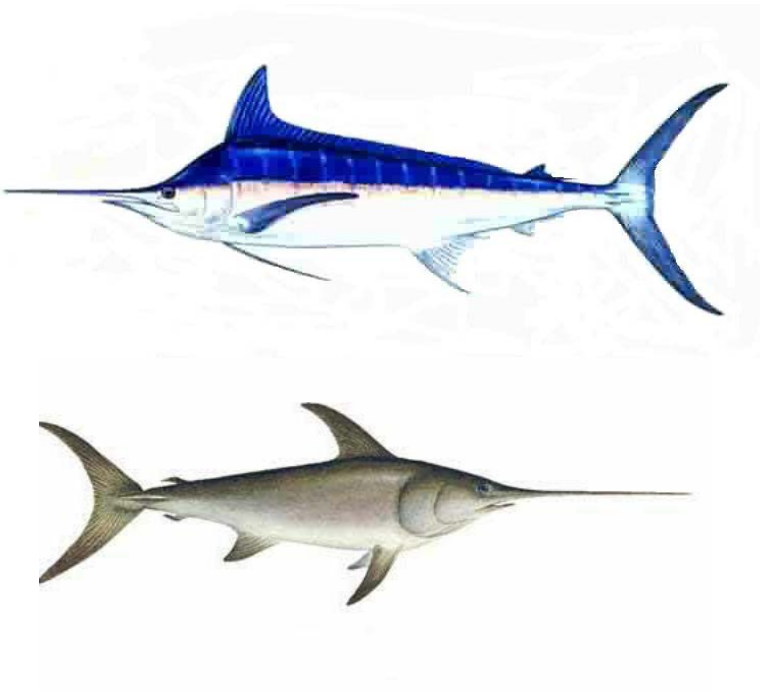

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A review of life history parameters of the Pacific blue marlin[*]

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Abstract

Our understanding of the biology of blue marlin (*Makaira nigricans*) in the Pacific Ocean has increased in the last three decades, and the progress is attributed to the development and application of a variety of novel tools. In this study, we provided a comprehensive examination of available data on the life history parameters of the Pacific blue marlin by re-examining current databases and literature. The present review provides a detailed synthesis on the growth, reproductive biology, mortality, and stock-recruitment relationship to the ISC billfish working group for possible application in stock assessments of the Pacific blue marlin. Knowledge of *M. nigricans* stock structure and environmental preference are also discussed.

1. Introduction

Blue marlin, *Makaira nigricans*, is a highly migratory cosmopolitan species distributed throughout tropical, subtropical, and temperate waters between 45 °N and 45 °S (Nakamura, 1985). They have been consolidated into a single species from two species in the Indo-Pacific and Atlantic Oceans, based on analyses of genetic divergence (Maguire et al., 2006). Fishery catch rates, as well as molecular analyses (Graves and McDowell, 2003), suggest a single stock of blue marlin in the Pacific Ocean (Kleiber et al., 2003). This assumption is also supported by the results of tagging experiments that have demonstrated that blue marlin migrate throughout the Pacific Ocean (Hinton, 2001).

Life history data for *M. nigricans* in different regions of the Pacific Ocean have been supplied by scientists during the last three decades, and an improved

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understanding of the basic biological parameters (e.g., growth, age at maturity, fecundity) is beginning to emerge. Recent advances in tagging studies are allowing researchers to elucidate the range and individual behavior of blue marlin (Holland et al., 1990; Block et al., 1992; Hinton, 2001). The preferences of this species for particular habitat-related factors may affect its distribution and vulnerability to being caught (Molony, 2005; Boyce et al., 2008). Various oceanographic and biological variables have been hypothesized to predict the density and distribution of blue marlin, such as water temperature, ocean fronts, current speed, oxygen content, prey availability, and zooplankton abundance (Boyce et al., 2008), and chlorophyll *a* concentration, mixed layer depth, and sea surface height anomaly (Su et al., 2008; 2011*a*).

Combined with past information, new findings have significantly enhanced our understanding of biology of *M. nigricans* in the Pacific Ocean and reduced the degree of uncertainty in modeling efforts to manage this valuable species. The purpose of this review is to comprehensively examine life history parameters of *M. nigricans* in the Pacific Ocean by examining existing data bases, included the recent studies that take advantage of novel approaches (e.g., histological technique), as well as taking a meta-analysis approach with published data from various sources. In addition, the aim of this review is to provide a list of input life history parameters to the ISC billfish working group for possible application in stock assessments of the Pacific blue marlin rather than trying to choose the best parameters.

2. Age and growth

Preliminary work has been done for the Pacific blue marlin based on the length-frequency data (Skillman and Yong, 1976). In this study, the growth of blue marlin, *M. nigricans*, was described by fitting von Bertalanffy growth curves (model 1 = an assumed age model; model 2 = a length-increment model, Fabens (1965)) to the progression of age-groups separated by the computer program ENORMSEP (Yong and Skillman, 1975), by quarters, through the Hawaiian longline fishery from 1960 to 1970. The sexes grew at about the same rate until 250 cm total fork length (TL) (188 cm eye to fork length, EFL) (see the definitions of length measurements in Fig. 1). Above this length, the growth rate of males declined and an asymptotic maximum length of 298.8 ~ 368.0 cm TL (226 ~ 280 cm EFL) was predicted. For females above 250 cm TL, the growth continued at a rapid rate; exhibiting little tendency toward an asymptote over the range of ages available to the study. The female L_∞ were estimated at 626.6 and 540.2 cm TL (466 and 402 cm EFL) for models 1 and 2, respectively, or approximately1,729 and 1,060 kg, respectively (Table 1). However, the authors suggested that there are not enough older age-groups to include in the regressions to obtain valid estimates of L_∞ or K.

Effort has been done evaluating hardparts (otoliths, vertebrae, dorsal spines, and anal spines) of blue marlin (sampled from four billfishing tournaments in Hawaii, 1982 ~ 1984) for use in age and growth studies (Hill, 1986; 1989); research found otoliths, and dorsal and anal fin spines sections all contained growth zones which were interpreted as annual events, and the number of growth zones increase with the size of the fish. Vertebrae contained some type of weekly or bi-weekly events, and no “annual” events were apparent. Mean length-at-estimated age values were similar for otolith, and dorsal and anal fin spines. Growth of females does not level off until a much later age than males (Fig. 2). The oldest male and female was estimated to be 18 years at 193.8 cm EFL and 26 years at 398.8 cm EFL, respectively (Table 2).

Age and growth of blue marlin were also examined from the second spines of the first anal fins (Chen, 2001) and the monthly length-frequency data (Dai, 2002) collected, respectively, from April 1999 to March 2000 and 2001 in the Tunkang fish market (southwestern coast of Taiwan). Trends in the monthly mean marginal increment ratio indicated that growth rings in the sections of anal spines are formed once a year. The maximum ages of the sampled fish were 9 (determined by spines) and 11 years (by the MULTIFAN method, Fournier et al., 1990) for males, and 11 and 14 years for females.

A comprehensive comparison of the age-length relationships for the Pacific blue marlin (Skillman and Yong, 1976; Hill, 1986; 1989; Chen, 2001; Dai, 2002) was shown in figure 2. The study of Skillman and Yong (1976) likely underestimated age and overestimated growth rate when their results are compared with those of other more recent studies. A significant larger size-at-age for ages 1 ~ 3 blue marlin were reported from the studies of Chen (2001) and Dai (2002). However, the predicted size-at-age after age 4 by Chen (2001) and Dai (2002) were general in agreement with the observations of Hill (1986). In addition, estimates of size-at-age of young blue marlin derived from otoliths were available in the Atlantic Ocean (Prince et al., 1991). Ages of 18 larvae ranged from 5 ~ 10 mm LJFL was estimated at 9 ~ 12 days while the estimated ages of juveniles, young adults, and adult (4.3 ~ 212 cm LJFL) was ranged from 21 to 495 days. This study suggested that otolith microstructure analysis could not be applied with confidence to blue marlin older than 1.4 years. Based on the these findings we are likely to conclude that blue marlin display rapid growth rates and most fish exceed 140 cm EFL within 3-4 years. Blue marlin are relatively long-lived with a longevity of more than 20 years (Hill, 1986; Wilson et al., 1991). However, the maximum ages of female and male blue marlin found in Hill (1986) were significantly larger than other studies. The differentials in the maximum age among studies could be due to the spatial differences in growth, size range of the collected samples, and/or the overestimation of the otolith increments for larger fish.

3. Length-weight relationships and conversion factors

A list of the sex-specific length-weight relationships of the Pacific blue marlin derived from various studies were shown in table 3. Most of the equations found to date seem to indicate that there is significant difference between sexes, so they are applied in separately. Other size-weight relationships can be used to obtain better estimates of catches in round weight from landed and processed catches. These include Kume and Joseph (1969) and Shimose (2009) that relates the gutted weight with EFL and the processed weight (without bill, caudal fin, gills, and viscera) with lower jaw to fork length (LJFL), respectively. A series of different conversions have also been carried such as that of Hill (1986) in the Hawaii waters and Dai (2002) in the Taiwan waters, making it possible to convert between different types of measurements (Table 4).

4. Reproductive biology

The spatio-temporal variation of the sexual maturity of blue marlin in the eastern Pacific Ocean has been evaluated by Shiohama (1969), Kume and Joseph (1969), Shingu et al. (1974), and Miyabe and Bayliff (1987), Nakano and Bayliff (1992), and Uosaki and Bayliff, (1999) based on the data from the Japanese longline fishery. In addition, Howard and Ueyanagi (1965), Matsumoto and Kazama (1974), and Nishikwawa et al. (1978 and 1985) have studied the distribution of blue marlin larvae and juvenile, and suggested that the occurrence of larvae and juvenile between 20 °N ~ 20 °S west of 130 °W. Patterns of the Pacific blue marlin reproduction in Hawaiian waters have described by Hopper (1990). Numerous studies examined the sexual maturity and spawning activity for the Pacific blue marlin. Nevertheless, none of those studies provided detailed information on ovarian development. The biological parameters are poorly understood for the blue marlin in the western Pacific area. More recently, Sun et al. (2009) provided a detail evaluation of the reproductive dynamics of blue marlin based on the histological assessment of gonad samples caught in the waters off Taiwan from September 2000 to December 2001. A similar study by Shimose et al. (2009) also presented the information of spawning seasonality and gonadal development of blue marlin specimens captured around the Yonaguni Island in southwestern Japan from February 2003 and February 2006.

4.1 Sex ratio

Sun at al. (2009) suggested that the overall sex ratio of the blue marlin catch was approximately 1:1 during the sampling period. In contrast, females outnumbered males at the waters of Yonaguni Island throughout the study period was found in Shimose et al. (2009). Both studies suggested blue marlin are sexually dimorphic; females are larger than males. The relationships between the female proportion (P_f) and *EFL* (Sun et al., 2009) and *LJFL* (Shimose et al., 2009) were described by the logistic functions (Fig. 3):

$$P_f = 1/\left\{1+e^{-\ln(19)[(EFL-175.16)/23.59]}\right\}, \text{ and}$$

$$P_f = 1/\left[e^{-0.17\times(LJFL-206)}\right]$$

Shung (1975) also noticed that the differential of sex ratios for blue marlin in the South China Sea (Pratas Islands). For the eastern Pacific Ocean, reproductively active male blue marlin are often smaller than 220 cm EFL, but all animals 230 cm EFL and larger are female (Kume and Joseph, 1969).

4.2 Size-at-maturity

Shiohama (1969) and Kume and Joseph (1969) considered female blue marlin with gonad indices of 3.1 or greater to be mature, and this convention is followed in the reports of Shingu et al. (1974), and Miyabe and Bayliff (1987), Nakano and Bayliff (1992), and Uosaki and Bayliff (1999). The reported size-at-first-maturity (SAFM) of blue marlin appears to vary across different regions of the Pacific Ocean. For example, the SAFM for female blue marlin was 157.8 cm EFL in the waters off Taiwan (Sun et al., 2009), 180 cm EFL around Yonaguni Island (Shimose et al. 2009), and 180 cm EFL (Miyabe and Bayliff, 1987; Uosaki and Bayliff, 1999) and 155 cm EFL (Nakano and Bayliff, 1992) in the eastern Pacific Ocean.

That value of size-at-first maturity is equivalent to the minimum size individual, sampled from a population, observed to be sexually mature. Studies have argued that reporting only the size at first maturity is useless, and even misleading (e.g., Schaefer, 2001). More recently, the relationship between the fraction mature (P_m) and size described by a logistic curve becomes ready as reported by Sun et al. (2009) (Fig. 4):

$$P_m = 1/\left\{1+e^{-\ln(19)[(EFL-179.76)/(194.2-179.76)]}\right\} \text{ for females, and}$$

$$P_m = 1/\left\{1+e^{-\ln(19)[(EFL-130)/(130.13-130)]}\right\} \text{ for males}$$

Sun et al. (2009) suggested that there was considerable uncertainty regarding the size-at-50% maturity for males owing to a lack of samples in the size range when male blue marlin are maturing (i.e., within the transition from immature to mature). However, males of blue marlin larger than 131 cm EFL (i.e., size-at-first-maturity) were all mature. Similar estimates of SAFM for males were also reported in western Pacific Ocean (130 ~ 140 cm EFL, Nakamura, 1985) and Yonaguni Island (140 cm EFL, Shimose et al. 2009).

4.3 Fecundity

Batch fecundity, estimated for the 26 mature ovaries (composed of the most advanced yolked, migratory nucleus and hydrated oocytes) with no early postovulatory follicles, ranged from 2.11 to 13.50 million eggs (6.94 ± 0.54; mean ± SE) was reported by Sun et al. (2009). This study suggested that the batch fecundity of blue marlin was size related, and fecundity increased nonlinearly with body size. The relationship between batch fecundity (BF) and EFL was $BF = 3.29 \times 10^{-12}\ EFL^{5.31}$ ($r^2 = 0.70$) (Fig. 5). Based on the same method, the batch fecundities of blue marlin was also estimated for 11 females (177 ~ 214 cm EFL) from 1.89 to 16.54 million eggs by counting the number of tertiary yolk oocytes and hydrated oocytes combined, and for 3 females (195 ~ 207 cm EFL) from 0.98 ~ 5.85 million eggs by counting the number of hydrated oocytes only in the study of Shimose et al. (2009).

5. Natural mortality

Natural mortality (M) is one of the most important parameters in assessing populations but is also one of the most difficult to estimate. Currently, tagging data of blue marlin are insufficient for estimating M. In practice, values of M of blue marlin in the Pacific Ocean have estimated by the indirect methods (Table 5). Boggs (1989) used the growth parameter $K = 0.285$ and 0.116 yr^{-1} (Skillman and Yong, 1976) to estimate M at 0.53 and 0.21 yr^{-1} for males and females, respectively, based on the method of Murphy and Sakagawa (1977). The method of Pauly (1980) was used with a set of growth parameters (Skillman and Yong, 1976) and a mean temperature estimate of 26 °C to calculate M values at 0.38, 0.41, 0.63, 0.81 yr^{-1} for males and 0.08, 0.14, 0.18, 0.19, 0.25 yr^{-1} for females by Hinton (2001). Dai (2002) also used the same method with a mean temperature 25°C to calculate M at 0.253 and 0.259 yr^{-1} for males and females, respectively. In addition, the M value (sex combined) was estimated at 0.38 yr^{-1} (approx. 95% confidence interval 0.30 ~ 0.45 yr^{-1}) from the MULTIFAN-CL model in Kleiber et al. (2003). In the study of Pine et al. (2008), the sex combined M of 0.41 yr^{-1} was also obtained by using the Pauly (1980)'s method with a mean temperature of 26 °C and the von Bertalanffy growth parameter (L_∞ = 244 cm LJFL, $K = 0.28\ \text{yr}^{-1}$) derived from the size-at-age data of Prince et al. (1991) and Wilson (1984).

6. Stock-recruitment relationship

Information of the stock recruitment relationship for the blue marlin is very limited. The Beverton-Hot stock recruitment curve was set up to fit the estimate of recruitment (age 2) and adult biomass (ages 2 ~ 21^+) of the Pacific blue marlin inside the stock assessment model MULTIFAN-CL of Kleiber et al. (2003). Steepness (*h*) is used to specify the stock-recruitment relationship (Francis, 1992). Su et al. (2011*b*) suggested that it seems inappropriate to assume a high value of *h* for blue marlin in the Pacific Ocean because substantial drops in recruitment of this population have been observed at low adult abundance (Molony, 2005; Kitchell et al., 2006). Therefore, the value of 0.5 was assumed in the base-case analysis to represent a compromise between no compensation and no reduction in recruitment (age 0) when biomass drops below 20% of the virgin biomass.

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Table 1. Overview of age and growth studies conducted on the Pacific blue marlin (*Makaira nigricans*). For Skillman and Yong (1976), case 1 = all age-groups, case 2= age-groups with > 2 individuals, 3 = same age-groups as for males with >2 individuals; numbers in the parentheses were estimates from the Fabens' (1965) method. For Chen (2001), case 1 = linear function for back-calculation, case 2 = power function. VBGF = von Bertalanffy growth function, Richard = Richards function (Richards, 1959), M = male, F = female, TL = total fork length, EFL = eye to fork length.

Sources	Skillman and Yong (1976)					Chen (2001)								Dai (2002)			
Data source	Hawaii longline fishery					Taiwanese inshore tuna longline fishery								Taiwanese inshore tuna longline fishery			
Growth model	VBGF	VBGF	VBGF	VBGF	VBGF	VBGF	VBGF	Richard	Richard	VBGF	VBGF	Richard	Richard	VBGF	VBGF	VBGF	VBGF
Fitting method	Modal analysis of length frequency + nonlinear-least squares (NLS)					NLS	NLS	NLS	NLS	NLS	NLS	NLS	NLS	MULTIFAN	ELEFAN I	MULTIFAN	ELEFAN I
Sex	M	M	F	F	F	M	M	M	M	F	F	F	F	M	M	F	F
Length (cm)	TL	TL	TL	TL	TL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL
Case	1	2	1	2	3	1	2	1	2	1	2	1	2				
L∞ (cm)	371.1 (282.3)	368.0 (298.8)	659.1 (807.8)	626.6 (540.2)	1248.1 (875.2)	338	229.7	346.9	333.4	420.7	283.2	501.8	421.8	232.8	215	312.5	309
K (yr^{-1})	0.285 (0.815)	0.315 (0.560)	0.116 (0.091)	0.123 (0.175)	0.048 (0.086)	0.04	0.11	0.02	0.01	0.03	0.09	0.03	0.01	0.13	0.17	0.11	0.15
t_0 (yr)	0.106	0.39	-0.161	-0.202	-0.674	-10.42	-5.21	-6.96	-1.78	-9.92	-4.65	-9.11	-1.76	-3.58		-2.42	
m								-0.56	-1.65			-0.11	-1.15				

Table 2. Overview of the calculated mean lengths (cm) at ages as determined by the modal analysis, otoliths, dorsal spines, and anal spines band counts for the Pacific blue marlin (*Makaira nigricans*). For Skillman and Yong (1976), the mean lengths at ages are only for the first quarter (years combined). For the Hill (1986), the statistics denote the mean ± 95% confidence interval. For Chen (2001), mean lengths at ages were from the linear back-calculation model, and the power function in parentheses. For Dai (2002), numbers in the parentheses denote the standard deviations. M = male, F = female, TL = total fork length, EFL = eye to fork length, LJFL = lower jaw to fork length.

Sources	Skillman and Yong (1976)			Hill (1986)						Chen (2001)		Dai (2002)	
Sex	M	F		M	M	M	F	F	F	M	F	M	F
Method	Modal analysis (ENORMSEP)			Otoliths	Dorsal spines	Anal spines	Otoliths	Dorsal spines	Anal spines	Anal spines + back-calculation		Modal analysis (MULTIFAN)	
Age	TL	TL	Age	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	LJFL	LJFL
0.71		55.5	1							125.77 (111.51)	129.23(110.70)	123.37 (4.8)	116.27 (7.75)
1.71	123	145.9	2							136.66 (124.91)	135.53(121.83)	140.38 (4.61)	140.63 (7.14)
2.71	172.7	190.5	3			95.4				146.37 (137.52)	146.71(138.19)	155.30 (4.45)	162.43 (6.63)
3.71	225	232.8	4			131.3±11.5	151.4			154.99 (146.58)	156.51(150.58)	168.40 (4.31)	181.94 (6.21)
4.71	240.5	286.8	5	174.9±33.1		155.9±5.68	141	141	141	161.91 (153.75)	165.33(162.00)	179.89 (4.2)	199.41 (5.85)
5.71	281.8	333.5	6	162.7±13.7	164.2±22.0	176.6±6.66	193.1±28.8		178.4	169.41 (159.25)	171.56(172.10)	189.97 (4.1)	215.04 (5.55)
6.71		366.1	7	176.3±7.17	171.1±6.08	176.2±3.14	193.6		206.7	176.90 (169.41)	179.06(179.76)	198.80 (4.01)	229.04 (5.29)
7.71		415.5	8	168.6±8.93	178.0±5.29	178.7±3.14	208.1±1.37		203.9±10.3	183.76 (177.52)	185.75(188.26)	206.57 (3.94)	241.57 (5.07)
			9	181.8±7.99	181.8±5.19	185.9±3.53	230.5±18.0	197	191.7±18.7	191.53 (185.98)	190.66(193.11)	213.37 (3.88)	252.79 (4.89)
			10	176.0±14.5	185.7±3.16	185.9±3.53	223.0±24.9	191.6	211.8±16.5	194.75 (192.37)	197.64(200.53)		262.83 (4.72)

Table 2. Overview of the calculated mean lengths at ages as determined by the modal analysis, otoliths, dorsal spines, and anal spines band counts for the Pacific blue marlin (*Makaira nigricans*). **(*Continued*)**

Sources	Skillman and Yong (1976)			Hill (1986)						Chen (2001)		Dai (2002)	
Sex	M	F		M	M	M	F	F	F	M	F	M	F
Method	Modal analysis (ENORMSEP)			Otoliths	Dorsal spines	Anal spines	Otoliths	Dorsal spines	Anal spines	Anal spines + back-calculation		Modal analysis (MULTIFAN)	
Age	TL	TL	Age	EFL	EFL	EFL	EFL	EFL	EFL	EFL	EFL	LJFL	LJFL
			11	186.4±8.48	192.1±14.9	190.7±7.74	216.4±15.3	206.0±7.83	217.3±22.6	202.52 (191.58)	206.88(213.45)		271.82 (4.58)
			12	196.4±5.10	189.6±14.9	184.5±10.8	247.1±28.4	217.8±20.1	216.3±17.8		214.12(219.29)		
			13	195.9±4.76		182.2±16.1	218.7±28.0	208.8	227.3±16.8		216.03(230.61)		
			14	194.2±11.1			237.6±10.2	297	248.9±31.4		224.76(235.74)		
			15				251.5±20.6	233.4±14.0	234.7±14.8				
			16	184.0±9.80			255.5±14.2	240.5±10.5	223.4±44.5				
			17				270.8	246.2	252.4				
			18			193.8	256.9	275.5±48.0					
			19						262.8±2.88				
			20					287.4	269.2±35.7				
			21										
			22				398.8						
			23				323.5						
			24				299.2	299.2					
			25						290.8±16.5				
			26					361.2±73.8	323.5				

Table 3. Length (cm) -weight (Kg) relationships for the Pacific blue marlin (*Makaira nigricans*). W = body weight, GW = body weight after gilled and gutted, PW = body weight without bill, caudal fin, gills, and viscera. EFL = eye to fork length, TL = total fork length, $LJFL$ = lower jaw to fork length. C = sex combined, F = females, M = males.

Sources	Sex	Equations	Sample size	Size range (cm)
Kume and Joseph (1969)	C	$W = 5.5565 \times 10^{-6}\ EFL^{3.0888}$	11	167 ~ 270
	C	$GW = 1.0242 \times 10^{-5} EFL^{2.9749}$	24	98 ~ 234
Wares and Sakagawa (1974)	C	$W = 2.0417 \times 10^{-6}\ EFL^{3.318}$	57	154 ~ 265
	C	$W = 2.8642 \times 10^{-8}\ TL^{3.905}$	20	221 ~ 347
Skillman and Yong (1974)	C	$W = 5.0048 \times 10^{-6} TL^{3.0214}$	453	135 ~ 457
Skillman and Yong (1976)	F	$TL = 65.4502\ W^{0.3030}$		
	M	$TL = 56.8780\ W^{0.3218}$		
Hill (1986)	F	$W = 7.129\ e^{0.013EFL}$ ($r^2 = 0.872$)	105	120 ~ 350
	M	$W = 4.354\ e^{0.016EFL}$ ($r^2 = 0.884$)	213	80 ~ 230
Chen (2001)	F	$W = 1 \times 10^{-5} EFL^{2.996}$ ($r^2 = 0.945$)	926	100 ~ 275
	M	$W = 2 \times 10^{-5} EFL^{2.883}$ ($r^2 = 0.9$)	666	100 ~ 220
Dai (2002)	F	$W = 6 \times 10^{-5} EFL^{2.7002}$ ($r^2 = 0.864$)	257	110 ~ 250
	M	$W = 1 \times 10^{-5} EFL^{2.9763}$ ($r^2 = 0.890$)	418	100 ~ 195
Uchiyama and Kazama (2003)	C	$W = 1.3 \times 10^{-6} EFL^{3.43}$ ($r^2 = 0.985$)	32	110 ~ 303
Shimose (2009)	C	$PW = 4.70 \times 10^{-6}\ LJFL^{3.11}$ ($r^2 = 0.936$)	1305	

Table 4. Conversion factors for the Pacific blue marlin (*Makaira nigricans*). *EFL* = eye to fork length, *TL* = total fork length, *LJFL* = lower jaw to fork length. C = sex combined, F = females, M = males

Sources	Sex	Equations	Sample size	Size range (cm)
Wares and Sakagawa (1974)	C	$EFL = TL \times 0.810 - 15.785$ ($r^2 = 0.997$)	21	221 ~ 347
	C	$EFL = LJFL \times 0.893 - 5.105$ ($r^2 = 0.979$)	22	194 ~ 297
Hill (1986)	F	$TL = 1.353 \times EFL - 4.836$ ($r^2 = 0.987$)	52	100 ~ 425
	M	$TL = 1.299 \times EFL + 4.105$ ($r^2 = 0.929$)	120	125 ~ 240
	F	$LJFL = 1.094 \times EFL + 9.512$ ($r^2 = 0.997$)	52	100 ~ 425
	M	$LJFL = 1.080 \times EFL + 11.780$ ($r^2 = 0.975$)	120	125 ~ 240
	F	$LJFL = 0.800 \times TL + 15.964$ ($r^2 = 0.989$)	52	110 ~ 570
	M	$LJFL = 0.786 \times TL + 18.951$ ($r^2 = 0.940$)	119	160 ~ 320
Dai (2002)	F	$LJFL = 1.071 \times EFL + 11.767$ ($r^2 = 0.959$)	64	
	M	$LJFL = 1.088 \times EFL + 8.894$ ($r^2 = 0.985$)	65	

Table 5.Overview of the natural mortality estimates for the Pacific blue marlin (*Makaira nigricans*). M = males, F = females, C = sex combined, SST = sea surface temperature. [a] in total fork length, [b] in eye to fork length, [c] in lower jaw to fork length.

Sources	Sex	Method	L_{∞}	K (yr^{-1})	Mean SST (°C)	Natural mortality (yr^{-1})
Boggs (1989)	M	Murphy and Sakagawa (1977)		0.285		0.53
	F			0.116		0.21
Hinton (2001)	M	Pauly (1980)	371.1[a]	0.285	26	0.38
	M		282.3	0.815		0.81
	M		368	0.315		0.41
	M		298.8	0.560		0.63
	F		659.1	0.116		0.18
	F		807.8~~0~~	0.091		0.14
	F		626.6	0.123		0.19
	F		540.2	0.175		0.25
	F		1248.1	0.048		0.08
	F		875.2	0.086		0.14
Dai (2002)	M	Pauly (1980)	232.8[b]	0.131	25	0.253
	F		312.5	0.111		0.209
Kleiber et al. (2003)	C	MULTIFAN-CL				0.38
Pine et al. (2008)	C	Pauly (1980)	244[c]	0.28	26	0.41

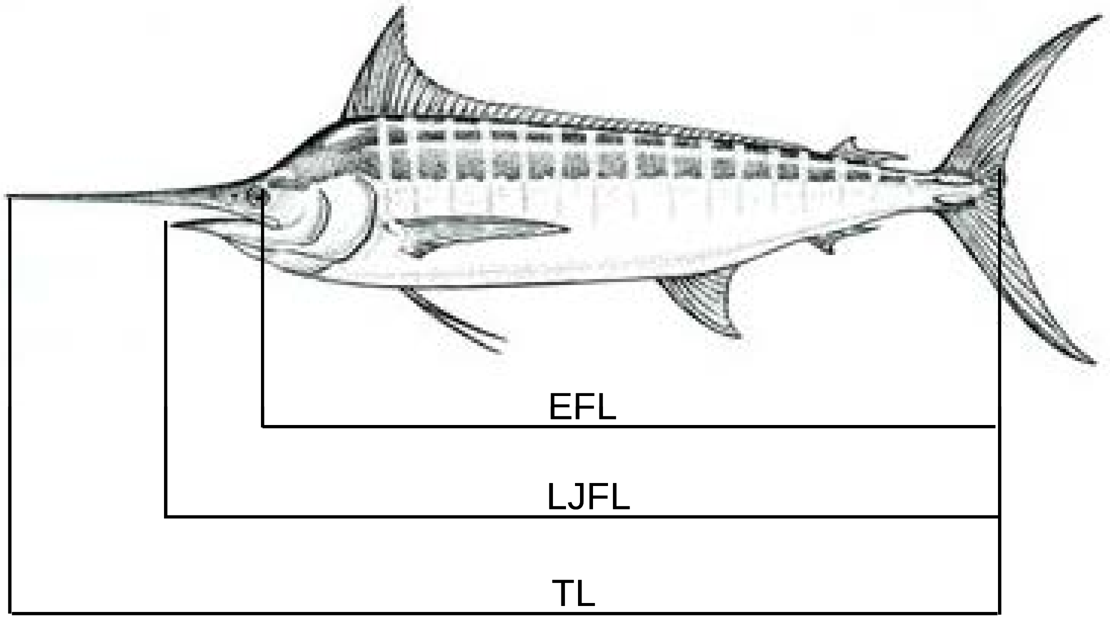

Figure 1. Measurements of the total fork length (TL), lower jaw to fork length (LJFL), and eye to fork length (EFL) of blue marlin (*Makaira nigricans*).

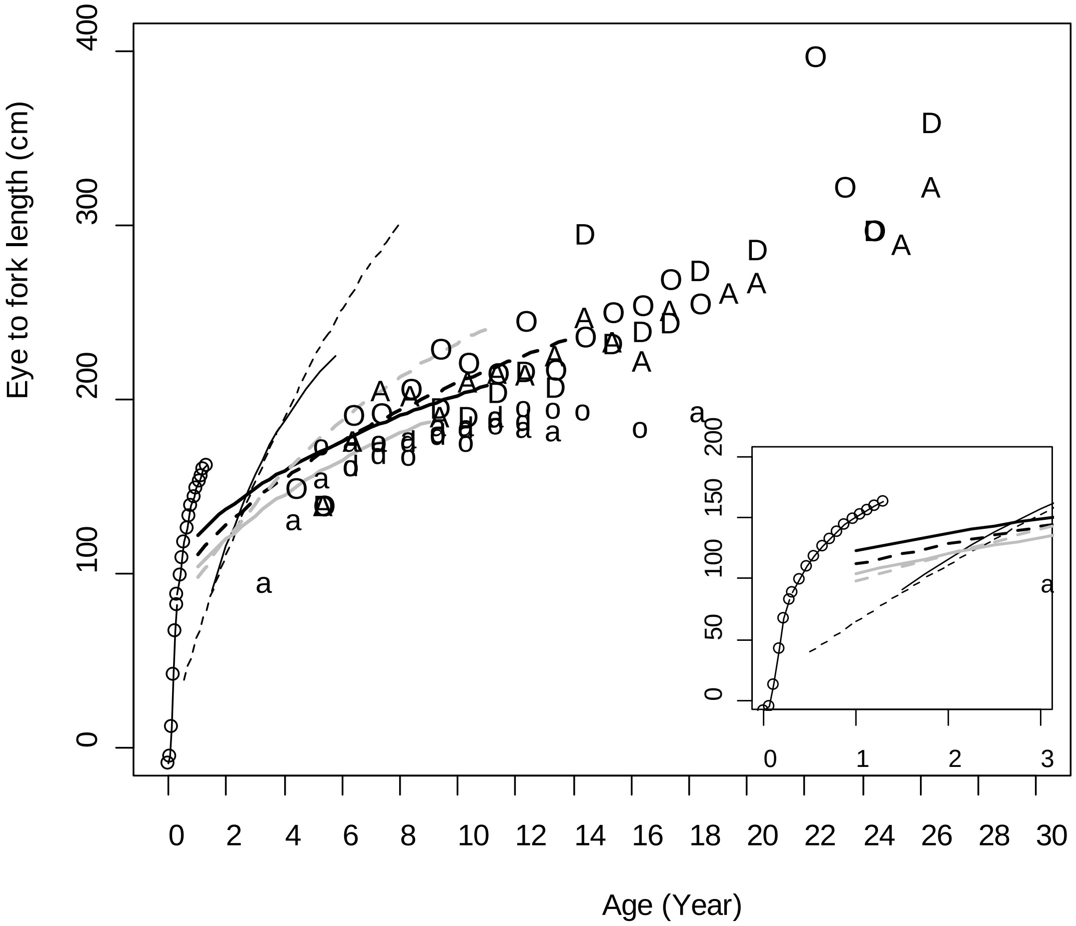

Figure 2. A comparison of the von Bertalanffy growth curves (VBGC) for blue marlin (*Makaira nigricans*) estimated by different authors. Dashed lines = females, solid lines = males. The thin lines, thick lines and gray lines represent the Pacific blue marlin studies of Skillman and Yong (1976), Chen (2001) and Dai (2002), respectively. The capital letters denote the mean lengths at ages as determined by the otoliths (O), dorsal spines (D), and anal spines (A) for females of Hill (1986). The lower case letters denote males. The circle-line denotes the predicted length-at-age for young Atlantic blue marlin by Prince et al. (1991).

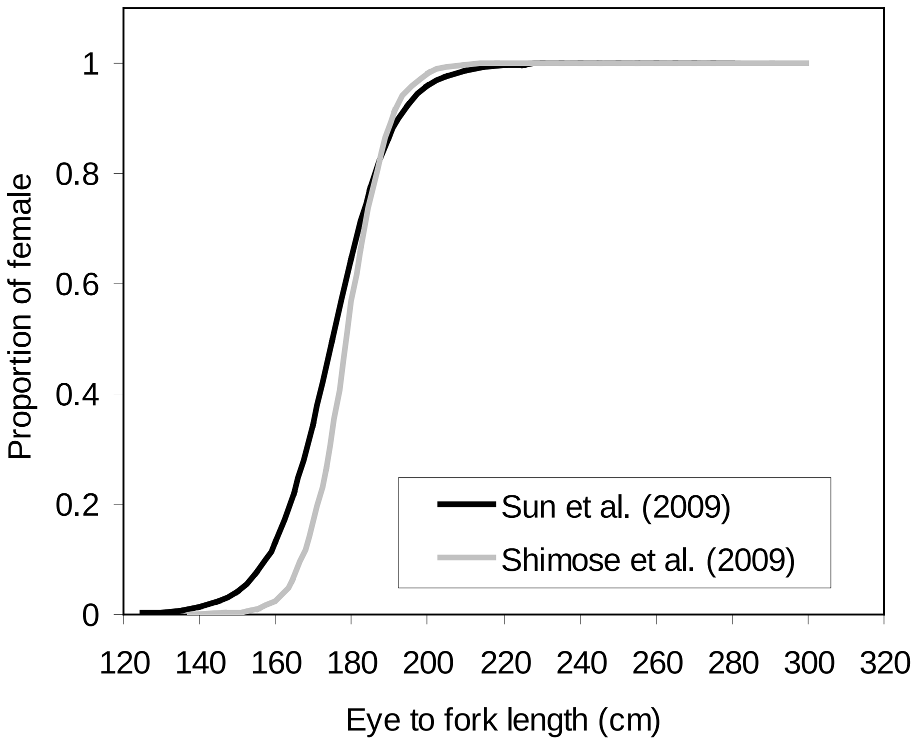

Figure 3. Proportion of female blue marlin (*Makaira nigricans*) plotted as functions of eye to fork length by different studies.

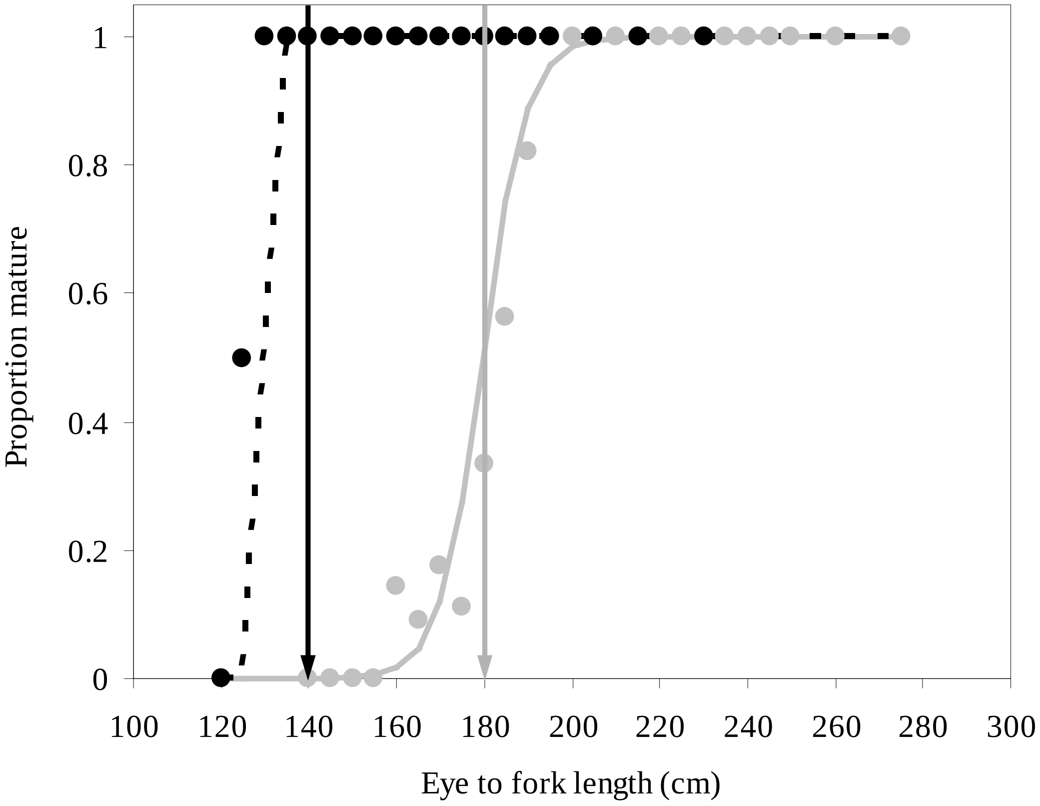

Figure 4. Percentages of mature blue marlin (*Makaira nigricans*) plotted as functions of eye to fork length reported by Sun et al. (2009). The solid circles represent the observed proportions mature-at-age (aggregated to 5 cm intervals). The arrows denote the estimates of size-at-first maturity by Shimose et al. (2009). Black color = males, gray color = females.

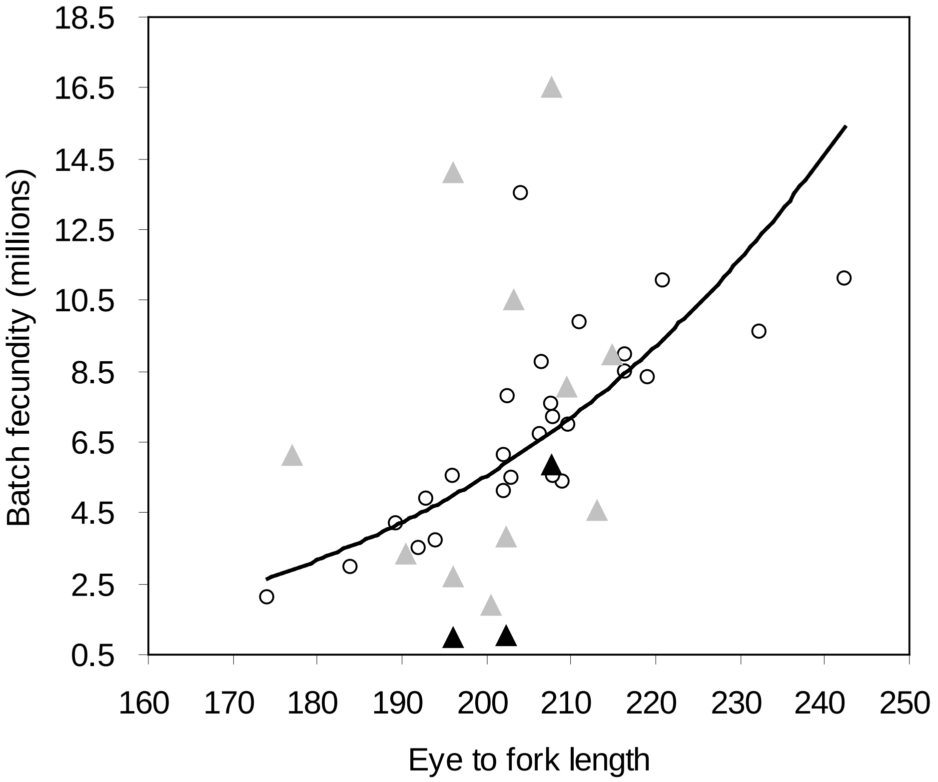

Figure 5. Predicted fecundity as a function of eye to fork length for blue marlin (*Makaira nigricans*) reported by Sun et al. (2009). The circles denote the observed data. The gray and black triangles, respectively, denote the number of tertiary yolk oocytes and hydrated oocytes combined and the number of hydrated oocytes only, from Shimose et al. (2009).