

Volume 24 | Issue 2

Article 31

LENGTH-BASED ESTIMATES OF GROWTH AND NATURAL MORTALITY FOR BLUE MARLIN (Makaira nigricans) IN THE NORTHWEST PACIFIC OCEAN

Nan-Jay Su

Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C. Current address: Department of Environmental Biology and FisheriesScience, Nat ional Taiwan Ocean University, Keelung, Taiwan, R.O.C.

Chi-Lu Sun

Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung, Taiwan, R.O.C., chilu@ntu.edu.tw

Chuan-Yuan Tai Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C

Su-Zan Yeh

Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C. 2 Current address: Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan, R.O.C

Follow this and additional works at: https://jmstt.ntou.edu.tw/journal

Part of the Aquaculture and Fisheries Commons

Recommended Citation

Su, Nan-Jay; Sun, Chi-Lu; Tai, Chuan-Yuan; and Yeh, Su-Zan (2016) "LENGTH-BASED ESTIMATES OF GROWTH AND NATURAL MORTALITY FOR BLUE MARLIN (Makaira nigricans) IN THE NORTHWEST PACIFIC OCEAN," *Journal of Marine Science and Technology*: Vol. 24: Iss. 2, Article 31.

DOI: 10.6119/JMST-015-0728-1

Available at: https://jmstt.ntou.edu.tw/journal/vol24/iss2/31

This Research Article is brought to you for free and open access by Journal of Marine Science and Technology. It has been accepted for inclusion in Journal of Marine Science and Technology by an authorized editor of Journal of Marine Science and Technology.

LENGTH-BASED ESTIMATES OF GROWTH AND NATURAL MORTALITY FOR BLUE MARLIN (Makaira nigricans) IN THE NORTHWEST PACIFIC OCEAN

Acknowledgements

We thank two anonymous referees for their constructive comments and suggestions. This study was funded partially by the Fisheries Agency and the Ministry of Science and Technology (the former National Science Council) of Taiwan through the research grants 90AS-1.4.5-FA-F2(3) and NSC89- 2316-B- 002-038 to Chi-Lu Sun.

LENGTH-BASED ESTIMATES OF GROWTH AND NATURAL MORTALITY FOR BLUE MARLIN (*Makaira nigricans*) IN THE NORTHWEST PACIFIC OCEAN

Nan-Jay Su^{1, 2}, Chi-Lu Sun^{1, 3}, Chuan-Yuan Tai¹, and Su-Zan Yeh^{1, 2}

Key words: sexual dimorphism, catch-at-size data, length-frequency analysis, life history parameters.

ABSTRACT

Blue marlin is an important resource for commercial and recreational fisheries. However, several life history parameters needed for stock assessments of this species are poorly determined. Sex-specific catch-at-size data (eye fork length, EFL) for blue marlin were collected from the Taiwanese offshore longline fishery in the northwest Pacific Ocean, and analyzed using the MULTIFAN, a length-frequency analysis, to derive growth parameters. The von Bertalanffy growth parameters of blue marlin were estimated to be different between sexes. The best model for the females included 11 age-classes in the lengthfrequency data sets (asymptotic length L_{∞} = 312.5 cm EFL, growth coefficient k = 0.111 yr⁻¹, and theoretical age at zero length $t_0 = -2.42$ yr), while 9 age-classes were identified for the males ($L_{\infty} = 232.8$ cm EFL, k = 0.131 yr⁻¹, and $t_0 = -3.58$ yr). Natural mortality rates, based on empirical equations, were estimated to be 0.258 yr⁻¹ for the males and 0.213 yr⁻¹ for the females, respectively. The estimates of growth parameters and mortality rates derived from this study could be used in stock assessments for blue marlin, and contribute towards the fisheries management of the species.

I. INTRODUCTION

Blue marlin *Makaira nigricans* are the largest of the billfishes, attaining up to 500 cm total length, and are a highly migratory species distributed throughout tropical, subtropical, and tem-



Fig. 1. Landings of blue marlin caught by the Taiwanese offshore and coastal fisheries from the northwest Pacific Ocean for 2001-2013. "Others" includes all the other offshore and coastal fisheries such as set-nets.

perate oceans between 45°N and 45°S (Molony, 2008). They have been consolidated into a single species worldwide from two species in the Indo-Pacific and Atlantic Oceans based on analyses of genetic divergence (Collette et al., 2006). A single stock of blue marlin in the Pacific Ocean has been assumed based on genetic analyses (Graves and McDowell, 2003) and fishery catch-rates (Kleiber et al., 2003). This assumption is also supported by the results of tagging experiments that have demonstrated that blue marlin migrate a long distance, with trans-basin and trans-oceanic (e.g., Pacific to Indian Ocean) movements (Hinton, 2001).

Blue marlin are important commercially and recreationally in the Pacific Ocean. They are caught primarily in pelagic longline fisheries targeting tuna (*Thunnus* spp.) and swordfish (*Xiphias gladius*), while small catches of blue marlin are also taken using surface gears, such as gillnets and harpoons, as well as by purse seine and baitboat fisheries (Molony, 2008). They are the most popular gamefish because of their large size and fighting ability (Hinton, 2001; Su et al., 2011). Landings of blue marlin caught by the Taiwanese offshore and coastal fisheries from the northwest Pacific Ocean varied between 1836

Paper submitted 04/09/14; revised 01/25/15; accepted 07/28/15. Author for correspondence: Chi-Lu Sun (e-mail: chilu@ntu.edu.tw).

¹ Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C. ² Current address: Department of Environmental Biology and Fisheries

Science, National Taiwan Ocean University, Keelung, Taiwan, R.O.C. ³Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung, Taiwan, R.O.C.

and 2746 mt during 2001-2013, but showed a slightly decreasing trend after 2005 (Fig. 1). Most of blue marlin were caught by offshore longliners (> 95%), and only a small proportion of blue marlin catch were taken by all the other offshore and coastal fisheries such as gillnets and harpoons.

Maximum size of blue marlin exhibits sexual dimorphism. Males usually reach a maximum size of about 160 kg, while females grow to much more than this (Wilson et al., 1991). The sizes-at-maturity of blue marlin also differ between the sexes (Sun et al., 2009). Several explanations have been proposed to explain the sexual dimorphism of this species, including sexspecific growth and mortality rates (Hill et al., 1989).

Several stock assessments have been conducted for blue marlin in the Pacific Ocean. The assessments concluded that this population is fully- or over-exploited (Kleiber et al., 2003; Su et al., 2012). Simulation studies have demonstrated that assessments of billfish stocks are sensitive to the values assumed for life history parameters (Wang et al., 2005; Su et al., 2011). However, biological parameters, such as growth rates, are lacking for blue marlin inter alia because of the ageing difficulties outlined above. This lack could lead to high uncertainty in stock assessment results, which may inhibit effective management (Hinton, 2001; Kleiber et al., 2003).

Growth models have been developed for several species of billfishes, but not for blue marlin across their entire life span (Kopf et al., 2010). Billfishes, including blue marlin, grow exceptionally rapidly when young (Drew et al., 2006). The otolith microstructure analysis has been used to develop a growth model for juvenile blue marlin (Prince et al., 1991). However, this ageing method is invalid when applied to adults because the individual increments are too close together to distinguish. It is also challenging to age adult blue marlin using the growth bands in fin spines owing to the vascularized core in spine sections (Hill et al., 1989). Vertebrae are also not a feasible ageing tool for blue marlin because there are numerous non-age related growth checks (Hill et al., 1989). It is also difficult to determine the growth rate of highly migratory species using tagging data due to extremely low recapture rates (Drew et al., 2006).

Fish in tropical areas sometimes carry no easily-deciphered birth certificates on their scales or otoliths, which leads to various length-based approaches that have been developed to deal with the difficulty or inability in ageing fish (Pauly and Morgan, 1987). For example, modal progression analysis can be used to estimate growth parameters successfully if age classes of fish can be followed clearly to separate the modes in lengthfrequency distributions. One of major advantages of lengthbased methods is that the size data are relatively easy to obtain and that the analytical procedures can be routinely used to derive vital parameters of fish population dynamics from distributions of size data (Gulland and Rosenberg, 1992).

The objectives of this study were to model the growth of blue marlin in the northwest Pacific Ocean by applying a lengthbased method, the MULTIFAN (Otter Research, 1992), to length-frequency data, and then to estimate the mortality rates for this population based on the derived growth information.



Fig. 2. Sampling area (shaded) of blue marlin in this study from the northwestern Pacific Ocean. Solid points show the locations of offshore longline operations as querying the fishermen.

Growth parameters and mortality rates were estimated by sex to assess if they differ between males and females, which could be used when modeling the population dynamics of this species by sex.

II. MATERIALS AND METHODS

Eye fork length (EFL, in cm) and whole weight (W, in kg) of the blue marlin caught by the Taiwanese offshore (small-scale) longline vessels (< 100 gross register tons) in the northwest Pacific Ocean were randomly collected on a monthly basis at the largest offshore longline fishing port, Tungkang, in southern Taiwan in 2001 (Fig. 2). Sex was determined by examining the gonads. Sex ratio was estimated as the number of females to the total number over sexes. EFL measurements were used in this study because measurements of lower jaw fork length were not available for all sampled animals due to fishermen removing the bills and jaws of some blue marlin at sea. The relationship between EFL and W was described, assuming lognormal errors, using the allometric equation: $W = a EFL^{b}$, where a and b are parameters. EFL-W relationships were derived to test, using the likelihood ratio test (Wang et al., 2006), for differences between the sexes, and to make conversions between different measurements if there was a need for this.

The MULTIFAN (Fournier et al., 1991; Otter Research, 1992) is a computer package, which can be used to analyze multiple length-frequency data sets simultaneously to estimate growth parameters. This is a likelihood-based method that uses the mixture of distributions approach, with consideration of biological constraints to enhance the reliability and accuracy of growth parameter estimates. The main assumptions underlying the MULTIFAN are: 1) recruitment occurs in seasonal pulses; 2) mean lengths-at-age lie on or are near the von Bertalanffy growth curve; 3) lengths of fish of each age are nor mally distributed; and 4) the standard deviation of the length-at-

Table I.	Monthly size ranges and sex ratios of blue marlin le	ength samples collected from the Taiwai	nese offshore longline
	fishery in the northwestern Pacific Ocean in 2001.	The sex ratio is expressed as the numb	per of females to total
	numbers over sexes.		

	Female		Male			
Month	n	Range of EFL (cm)	n	Range of EFL (cm)	Sex ratio	Total
January	65	100~248	75	100~232	0.464	140
February	47	157~226	44	121~209	0.516	91
March	52	107~275	74	125~187	0.413	126
April	54	126~259	123	130~190	0.305	177
May	41	116~243	109	129~191	0.273	150
June	59	122~237	97	128~219	0.378	156
July	82	124~238	142	121~183	0.366	224
August	80	104~247	195	120~190	0.291	275
September	79	101~275	98	101~192	0.446	177
October	49	104~245	48	105~198	0.505	97
November	102	100~230	50	102~190	0.671	152
December	25	100~219	21	104~178	0.543	46
Total	735	100~275	1076	100~232	0.406	1811

age is a linear function of mean length-at-age. The MULTIFAN provides a structured and relatively objective means to evaluate alternative factors that might affect observed length-frequency distributions, including growth rates, the number of notable age-classes, and gear selectivity on younger age-classes. The mathematical basis of this method and further details regarding the version of the MULTIFAN used for the analyses in this paper can be found in the MULTIFAN User's Manual (Otter Research, 1992).

Parameters of the von Bertalanffy growth curve can be obtained with systematic search in the MULTIFAN. Initial values for the following parameters are required to apply the MULTIFAN including: 1) number of age-classes, 2) the von Bertalanffy growth coefficient k, 3) the mean length of the youngest age-class, 4) the standard deviation of a distinct mode, and 5) the month in which the smallest animals enter the fishery. Based on annual increments in spine sections (Hill et al., 1989), the number of age-classes was assumed to be in the range 8-15, while initial k values from 0.1 to 0.2 yr⁻¹ (in steps of 0.02) for both sexes (Kleiber et al., 2003) were explored. For each given value of k, the model was tested with increasing numbers of cohorts, until adding an extra cohort does not improve the fit to the data.

September was designated in our cases as the month in which the youngest fish recruit to the fishery, because a group of the smallest individuals was observed in the lengthfrequencies during this month and because the major spawning season of blue marlin is from May to September (Sun et al., 2009), so that the length samples were renumbered in the MULTIFAN according to this. Estimates of growth parameters may be biased if the month was not selected correctly. Constraints on mean lengths-at-age were applied in length samples of blue marlin to allow for flexibility in the model fit when observed length frequency patterns are not very consistent with what would be expected.

The initial value for the standard deviation of an age-class was set to 20 cm (Hill et al., 1989), while the mean length of the voungest age-class was set to 115 cm EFL for both sexes given the results of the otolith analysis for young fish (Prince et al., 1991). Additional runs with the MULTIFAN were made to test for whether there is a linear trend in the standard deviation of length-at-age with age or the standard deviations of length-at-age are identical for all age-groups. This is because the proportions at age of the animals in the length-frequency samples might reflect a biased sample of the population due to age-dependent gear selectivity (Fournier et al., 1991). Additional MULTIFAN tests were therefore performed to examine whether younger age-groups in the model are subject to sampling bias and whether there is a case of seasonality for the growth of blue marlin. The most parsimonious model structure was determined using a χ^2 test based on likelihood values. The likelihood ratio test was used to test for the difference in growth parameters between the sexes.

Owing to that the estimate for theoretical age at zero length (t_0) was not provided by MULTIFAN, this parameter was thus estimated using the equation: $t_0 = t_1 + \ln(1-L_1/L_{\infty})/k$, where L_1 and t_1 are mean length and age of the first age-group estimated by the MULTIFAN. The Kolmogorov-Smirnov (K-S) test was used to examine differences in age-composition and length-frequency between the sexes.

Natural mortality rates (*M*) of blue marlin were estimated using Pauly's (1980) empirical relationship: $\ln(M) = -0.0152 - 0.279 \ln(L_{\infty}) + 0.6543 \ln(k) + 0.4634 \ln(T)$, where L_{∞} and *k* are the growth parameters and *T* is the temperature at which the species occurs (assumed to be 26°C according to Hinton (2001) and Pine et al. (2008)). Pauly's formula was initially developed for tropical fish species of 175 stocks, and therefore has given reasonable estimates for blue marlin (Pine et al., 2008). However, given that blue marlin are widely distributed in tropical waters, a range of temperature from 26~30°C was examined Table 2. Sex-specific mean lengths-at-age and standard deviation of blue marlin in the northwest Pacific Ocean esti-

	mated by the MULTIFA	N.		
	Female		Male	
Age	Mean length (cm)	Standard deviation	Mean length (cm)	Standard deviation
1	98.5	7.8	105.0	4.8
2	120.9	7.1	120.7	4.6
3	141.0	6.6	134.4	4.5
4	159.0	6.2	146.5	4.3
5	175.1	5.9	157.1	4.2
6	189.5	5.6	166.4	4.1
7	202.4	5.3	174.5	4.0
8	213.9	5.1	181.7	3.9
9	224.3	4.9	187.9	3.9
10	233.5	4.7		
11	241.8	4.6		



Fig. 3. Length-frequency distributions for blue marlin caught by the Taiwanese offshore longline fishery from the northwest Pacific Ocean.

based on previous studies on their habitats (Su et al., 2011). Natural mortality rates of blue marlin were also estimated based on equations developed by Murphy and Sakagawa: M = 1.879 k (Murphy and Sakagawa, 1977), Jensen: M = 1.6 k (Jensen, 1996) and Hoenig: $\ln(M) = 1.46 - 1.01 \ln(t_{max})$ (Hoenig, 1983), where t_{max} assumed to be 18 and 27 yrs for males and females, respectively, based on Hill et al. (1989), to examine the sensitivity of using alternative methods on estimating M.

III. RESULTS

The collected blue marlins of this study were from the north-western Pacific Ocean, including the South China Sea, as querying the fishermen about the locations of offshore longline operations (Fig. 2). A total of 1076 males and 735 females were sampled with mean lengths of 153.6 cm and 184.3 cm EFL, respectively. The sex ratio of sampled blue marlin catch was 0.406 for whole year, but varied from 0.273 to 0.671 among months.

The sample sizes, size ranges, and sex ratios of blue marlin length samples from the Taiwanese offshore longline fishery in the northwestern Pacific Ocean for each month were shown



Fig. 4. Relationships between eye fork length (EFL) and weight (W) for blue marlin in the northwest Pacific Ocean.

in Table 1. The largest fish were 275 cm and 232 cm EFL for females and males, respectively, while the smallest individuals were 100 cm EFL for both sexes. Sexual dimorphism in size is evident from the length-frequency distributions which differ significantly between the sexes (K-S test, P < 0.05; Fig. 3). The relationships between EFL and W differed significantly between the sexes based on the likelihood ratio test (P < 0.01), so sex-specific equations were reported for blue marlin (Fig. 4).

The best-fitting MULTIFAN model for both sexes was when no sampling bias for younger age-groups was included but the age-dependent trend in the standard deviation in length at age was estimated in the model (Table 2). In the best fits of



Fig. 5. Length-frequency distributions (bars) for female blue marlin and the results of the best fit from MULTIFAN (lines). The lines inside represent the normal distributions of length at a given age, and the outer lines represent the length-frequencies estimated by MULTIFAN. Broken vertical lines indicate the estimated mean lengths-at-age. Horizontal lines are constraints on mean lengths-at-age applied in the size samples.



Fig. 6. Length-frequency distributions (bars) for male blue marlin and the results of the best fit from MULTIFAN (lines). The lines inside represent the normal distributions of length at a given age, and the outer lines represent the length-frequencies estimated by MULTIFAN. Broken vertical lines indicate the estimated mean lengths-at-age. Horizontal lines are constraints on mean lengths-at-age applied in the size samples.

 Table 3. Estimates of growth parameters and natural mortality rates for blue marlin in the northwest Pacific Ocean.

 Values in the parenthesis represent standard deviations for the estimates.

Female	Male
312.5 (1.8)	232.8 (1.6)
0.111 (0.001)	0.131 (0.003)
-2.42 (0.03)	-3.58 (0.04)
0.213~0.228*	0.258~0.275*
	Female 312.5 (1.8) 0.111 (0.001) -2.42 (0.03) 0.213~0.228*

*Natural mortality rates were estimated based on sea surface temperature from 26~30°C.



Fig. 7. Growth curves (lines) and mean lengths-at-age (points) for blue marlin estimated by Skillman and Young (1976), Hill et al. (1989), and this study. Shaded areas indicate 95% confidence intervals.



Fig. 8. Age-compositions of blue marlin caught by the Taiwanese longline fishery from the northwest Pacific Ocean.

the MULTIFAN, 9 and 11 age-classes were identified in the length-frequency samples for males and females, respectively. The seasonality in growth of blue marlin was, as expected, not suggested by the MULTIFAN based on the χ^2 tests in the initial search because blue marlin is considered a tropical fish species. The estimated modes from the MULTIFAN (lines) generally follow the observed length-frequency data (bars), as revealed by visual inspection for both sexes (Figs. 5 and 6).

Sex-specific von Bertalanffy growth curves are presented (Fig. 7) because the growth parameters differed between the sexes, based on the likelihood ratio test (P < 0.01). The estimates for asymptotic length $L_{\infty} = 312.5$ cm EFL, growth coefficient

 $k = 0.111 \text{ yr}^{-1}$, and theoretical age at zero length $t_0 = -2.42 \text{ yr}$ for females, and $L_{\infty} = 232.8 \text{ cm EFL}$, $k = 0.131 \text{ yr}^{-1}$, and $t_0 = -3.58$ yr for males. However, the estimate of L_{∞} for females is much larger than the maximum observed size 275 cm EFL, but that for males is almost the same as the maximum observed length 232 cm EFL (Table 1). This could be expected because adult males seem to stop their growth while females continue to grow after 200 cm EFL (Fig. 7). The dominant age-classes were 3-5 and 5-7 yrs for males and females, comprising 70% and 67% of the length samples, respectively (Fig. 8).

Based on a range of temperature from $26 \sim 30^{\circ}$ C, *M* of blue marlin were estimated to be $0.213 \sim 0.228$ yr⁻¹ for females and $0.258 \sim 0.275$ yr⁻¹ for males, respectively (Table 3). All of the estimates for *M* using alternative equations produced similar results for blue marlin between sexes, except for a lower *M* for females estimated based on the method of Hoenig (1983). In general, the estimates of *M* differed between males (0.154-0.213 yr⁻¹) and females (0.210-0.258 yr⁻¹), further suggesting that male blue marlin have a larger *M* than females (Table 4).

IV. DISCUSSION

Age-structured related research for blue marlin is limited due to the difficulties on age determination for the fish (Molony, 2008). An alternative method to model the growth parameters of this species is through the use of length-frequency data, because length-frequency samples over time often contain useful information on growth, mortality, and recruitment (Hilborn and Walters, 1992). A strong seasonality in the spawning period could help to identify the modes clearly (Fournier et al., 1991). However, for tropical species, continuous recruitment may happen and prevent such identification of modes in lengthfrequency distributions, but this seems not the case for blue marlin. In some cases, however, length data from port sampling might be less than ideal for modeling the growth of a fish population. For example, small fish might be discarded by fish ermen at sea. However, being a valuable bycatch species, almost all blue marlin, including juveniles, are retained by fishers (Wang et al., 2006).

Skillman and Yong (1976) estimated the parameters of the von Bertalanffy growth function for blue marlin in the central North Pacific Ocean by modeling the progression of age-class in length-frequency distributions. However, their estimates were not biologically reasonable (e.g., an incredibly large estimate, over 1000 cm, for L_{∞}), primarily because they under-

	Female	Male	Unsexed	Reference
$k (yr^{-1})$	0.111	0.131		This study, based on MULTIFAN
	0.102	0.145		This study, based on mean lengths-at-age in Hill et al. (1989)
	0.10	0.15		Su et al. (2013)
			0.12	Salcedo-Bojorquez and Arreguin-Sanchez (2011)
			0.28	Goodyear (2003) and Pine et al. (2008)
			0.2	Kleiber et al. (2003)
$M(\mathrm{yr}^{-1})$	0.213	0.258		This study, based on Pauly (1980) with 26°C
	0.178	0.210		This study, based on Jensen (1996)
	0.154	0.232		This study, based on Hoenig (1983)
	0.209	0.246		This study, based on Murphy and Sakagawa (1977)
			0.41	Pine et al. (2008)
			0.38	Kleiber et al. (2003)
			0.15	Goodyear (2003)
	0.18	0.38		Hinton (2001), based on Pauly (1980)
	0.21	0.53		Hinton (2001), based on Boggs (1989)

Table 4. Comparison of estimates for von Bertalanffy growth coefficient (k) and natural mortality rates (M) of blue marlin from the previous studies.

estimated the number of age-classes in their samples (e.g., only 5 age-classes for males) (Fig. 7). The mean lengths of the oldest blue marlin aged using annual increments in fin spine sections were 345 cm (n = 2) for females and 213 cm (n = 1) for males in Hill et al. (1989) (in Molony, 2008). Although large individuals are rare, these observations of maximum length are comparable with the L_{∞} estimates for both sexes from this study, in which females are much larger that males. However, it is very valuable to collect length samples of blue marlin from other fisheries such as the Taiwanese distant-water longliners or other international fleets for comparison of growth parameter estimates based on data from various fisheries.

The range of growth rates for blue marlin reported in the literature illustrates that this parameter was not well known, and k is usually assumed to the same for both sexes. For example, a growth rate of 0.28 yr⁻¹ was estimated for both sexes by Goodyear (2003) and Pine et al. (2008) based on daily otolith rings of juveniles from Prince et al. (1991), while $k = 0.12 \text{ yr}^{-1}$ was assumed in Salcedo-Bojorquez and Arreguin-Sanchez (2011). Kleiber et al. (2003) reported that the growth rate of blue marlin cannot be determined well by sex in MULTIFAN-CL owing to the strong sexual dimorphism in growth and the lack of sex-specific catch-at-size data, and they assumed a value of 0.2 yr^{-1} for the assessment of this stock. Hill et al. (1989) did not provide growth rates for blue marlin owing to the difficulty in ageing larger fish, while sex-specific growth parameters were estimated by Su et al. (2013) based on empirical equations ($k = 0.10 \text{ yr}^{-1}$ for females and 0.15 yr⁻¹ for males). The growth patterns derived from this study are consistent with the mean lengths-at-age from Hill et al. (1989) and the growth parameters from Su et al. (2013) for both sexes (see summary for estimates of growth parameters in Table 4 and growth curves in Fig. 7).

The estimated sex-specific growth functions illustrate the sexual dimorphism in blue marlin (Fig. 7). It is unlikely that male blue marlin grow much larger than those sampled in the Taiwanese longline fisheries given the spatial and temporal coverage of data reported in the literature (Skillman and Yong, 1976; Wilson et al., 1991; Molony, 2008). This pattern, females achieving a larger size than males, occurs in other species of billfishes, as shown in Fig. 4 of Wang et al. (2006). However, sexual dimorphism in billfishes differs from most other fishes. In many species, including tunas, females invest more energy, compared with males, in maturation, and consequently have lower growth rates and maximum sizes (Schaefer, 1996). However, Wilson et al. (1991) concluded that sexual dimorphism in blue marlin was a result of different growth rates between the sexes, as those revealed in this study (Fig. 7), rather than different behavior, longevity, or other factors for billfish species.

It is often difficult to estimate M for exploited fish populations directly even through a designed field study, although Mmight be estimable using stock assessment models in few cases (Lee et al., 2011; Francis, 2012). Therefore, the published empirical relationships between M and life history parameters are frequently used to infer this parameter, even though in some cases, the relationships are inapplicable to certain species resulting unreasonable estimates for M. Among those approaches, the equation developed by Pauly (1980) is commonly used for marine teleost fish, including blue marlin. The estimates of M for blue marlin based on this equation were similar with those using the equation develop by Murphy and Sakagawa (1977) ($M = 0.246 \text{ yr}^{-1}$ for males and 0.209 yr⁻¹ for females). However, a large variation for M estimates was found (0.154-0.178 yr⁻¹ and 0.210-0.232 yr⁻¹ for females and males, respectively) when approaches of Jensen (1996) and Hoenig (1983) were applied to this population. The published *M* estimates for blue marlin also varied from 0.15 to 0.53 yr⁻¹ (Hinton, 2001; Goodyear, 2003; Pine et al., 2008), while a value of 0.38 yr⁻¹ was estimated within an assessment model for both sexes by Kleiber et al. (2003). Natural mortality rates were found to differ between the sexes, which re-emphasizes the need to take sexual dimorphism into account in stock assessments for sexually dimorphic species through, for example, the use of sex-specific life history parameters related to population process such as growth and natural mortality.

This study provides a quantitative account of growth and mortality rates for blue marlin in the northwest Pacific Ocean, and contributes substantially to the research of this species globally. The estimates of growth parameters and mortality rates by sex derived from in this study could be used to conduct sex-specific stock assessments for this species. However, age determination using other techniques within broad size ranges (such as the sampling of small fish) and larger sample sizes from this fishery or fisheries in other areas of the Pacific Ocean to fit growth functions by sex is also needed.

ACKNOWLEDGMENTS

We thank two anonymous referees for their constructive comments and suggestions. This study was funded partially by the Fisheries Agency and the Ministry of Science and Technology (the former National Science Council) of Taiwan through the research grants 90AS-1.4.5-FA-F2(3) and NSC89-2316-B- 002-038 to Chi-Lu Sun.

REFERENCES

- Boggs, C. H. (1989). Vital rate statistics for billfish stock assessment. Proceedings of the Second International Billfish Symposium, Kailua-Kona, Hawaii, USA, 225-233.
- Collette, B. B., J. R. McDowell and J. E. Graves (2006). Phylogeny of recent billfishes (Xiphioidei). Bulletin of Marine Science 79, 455-468.
- Drew, K., D. Die and F. Arocha (2006). Current efforts to develop an age and growth model of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*). Collective Volume of Scientific papers ICCAT 59, 274-281.
- Fournier, D. A., J. R. Sibert and M. Terceiro (1991). Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method. Canadian Journal of Fisheries and Aquatic Sciences 48, 591-598.
- Francis, R. I. C. C. (2012). The reliability of estimates of natural mortality from stock assessment models. Fisheries Research 119-120, 133-134.
- Goodyear, C. P. (2003). Blue marlin mean length: simulated response to increasing fishing mortality. Marine and Freshwater Research 54, 401-408.
- Graves, J. E. and J. R. McDowell (2003). Stock structure of the world's istiophorid billfishes: a genetic perspective. Marine and Freshwater Research 54, 287-298.
- Gulland, J. A. and A. A. Rosenberg (1992). A review of length-based approaches to assessing fish stocks. FAO Fisheries Technical Paper 323, Rome, Italy.
- Hill, K. T., G. M. Cailliet and R. L. Radtke (1989). A comparative analysis of growth zones in four calcified structures of Pacific blue marlin, *Makaira nigricans*. Fishery Bulletin 87, 829-843.
- Hilborn, R. and C. J. Walters (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, USA, pp. 410-433.
- Hinton, M. G. (2001). Status of blue marlin in the Pacific Ocean. Stock As-

sessment Report 1, IATTC, La Jolla, CA, USA.

- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 81, 898-903.
- Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53, 820-822.
- Kleiber, P., M. G. Hinton and Y. Uozumi (2003). Stock assessment of blue marlin (*Makaira nigricans*) in the Pacific using MUNTIFAN-CL. Marine and Freshwater Research 54, 349-360.
- Kopf, R. K., K. Drew and R. L. Humphreys (2010). Age estimation of billfishes (*Kajikia* spp.) using fin spine cross-sections: the need for an international code of practice. Aquatic Living Resources 23, 13-23.
- Lee, H. H., M. N. Maunder, K. R. Piner and R. D. Methot (2011). Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fisheries Research 109, 89-94.
- Molony, B. (2008). Fisheries biology and ecology of highly migratory species that commonly interact with industrialised longline and purse-seine fisheries in the western and central Pacific Ocean. Working Paper EB-IP-6, 4th Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission, Port Moresby, Papua New Guinea.
- Murphy, T. C. and G. T. Sakagawa (1997). A review and evaluation of estimates of natural mortality rates of tunas. Collective Volume of Scientific papers ICCAT 6, 117-123.
- Otter Research (1992). MULTIFAN 3 User's Guide and Reference Manual. Otter Research Ltd., Nanaimo, Canada.
- Pauly, D. (1980). On the interrelationships between natural morality, growth parameters and mean environmental temperatures in 175 fish stocks. Journal du Conseil international pour l'Exploration de la Mer 39, 175-192.
- Pauly, D. and G. R. Morgan (1987). Length-based methods in fisheries research. ICLARM Conference Proceedings 13, Manila, Philippines.
- Pine, W. E., S. J. D. Martell, O. P. Jensen, C. J. Walters and J. F. Kitchell (2008). Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of postrelease survival in effective policy design. Canadian Journal of Fisheries and Aquatic Sciences 65, 975-988.
- Prince, E. D., D. W. Lee, J. R. Zweifel and E. B. Brothers (1991). Estimating age and growth of young Atlantic blue marlin *Makaira nigricans* from otolith microstructure. Fishery Bulletin 89, 441-459.
- Salcedo-Bojorquez, S. and F. Arreguin-Sanchez (2011). An exploratory analysis to identify reproductive strategies of billfishes. Journal of Fisheries and Aquatic Science 6, 578-591.
- Schaefer, K. M. (1996). Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. Fishery Bulletin 94, 98-112.
- Skillman, R. A. and M. Y. Y. Yong (1976). von Bertalanffy growth curves for striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, in the central North Pacific Ocean. Fishery Bulletin 74, 553-566.
- Su, N. J., C. L. Sun, A. E. Punt, S. Z. Yeh and G. DiNardo (2011). Evaluation of a spatially sex-specific assessment method incorporating a habitat preference model for blue marlin (*Makaira nigricans*) in the Pacific Ocean. Fisheries Oceanography 20, 415-433.
- Su, N. J., C. L. Sun, A. E. Punt, S. Z. Yeh and G. DiNardo (2012). Incorporating habitat preference into the stock assessment and management of blue marlin (*Makaira nigricans*) in the Pacific Ocean. Marine and Freshwater Research 63, 565-575.
- Su, N. J., C. L. Sun, A. E. Punt, S. Z. Yeh, W. C. Chiang, Y. J. Chang and H. Y. Chang (2013). Effects of sexual dimorphism on population parameters and exploitation ratios of blue marlin (*Makaira nigricans*) in the northwest Pacific Ocean. Aquatic Living Resources 26, 19-24.
- Sun, C. L., Y. J. Chang, C. C. Tszeng, S. Z. Yeh and N. J. Su (2009). Reproductive biology of blue marlin (*Makaira nigricans*) in the western Pacific Ocean. Fishery Bulletin 107, 420-432.
- Wang, S. P., C. L. Sun, A. E. Punt and S. Z. Yeh (2005). Evaluation of a sexspecific age-structured assessment method for the swordfish, *Xiphias gladius*, in the North Pacific Ocean. Fisheries Research 73, 79-97.
- Wang, S. P., C. L. Sun, S. Z. Yeh, W. C. Chiang, N. J. Su, Y. J. Chang and C. H.

Liu (2006). Length distributions, weight-length relationships, and sex ratios at lengths for the billfishes in Taiwan waters. Bulletin of Marine Science 79, 865-869.

Wilson, C. A., J. M. Dean, E. D. Prince and D. W. Lee (1991). An examination

of sexual dimorphism in Atlantic and Pacific blue marlin using body weight, sagittae weight, and age estimates. Journal of Experimental Marine Biology and Ecology 151, 209-225.