



# Age and growth of Black marlin (*Istiompax indica*) off eastern Taiwan



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## ABSTRACT

The age and growth characteristics of black marlin (*Istiompax indica*) off eastern Taiwan were studied using growth rings on cross sections of the third dorsal spine. Length and weight data, and first dorsal fins were collected monthly at Shinkang fish market in southeastern Taiwan from July 2004 to April 2006. In total, 923 dorsal fins were collected, of which 874 (95%) (187 males and 687 females) were aged successfully. Trends in monthly mean marginal increment ratios indicated that growth rings formed once a year. Two methods were used to back-calculate lengths of presumed ages, and growth was described using the standard and generalized von Bertalanffy growth functions. The most parsimonious description of growth assumed that length-at-age followed the standard von Bertalanffy function and that the relationship between spine radius and lower jaw fork length (LJFL) followed a power function. Growth differed between males and females. The growth parameters estimated for males were asymptotic length ( $L_{\infty}$ ) = 305.8 cm LJFL, growth coefficient ( $k$ ) = 0.125 yr<sup>-1</sup>, age at zero length ( $t_0$ ) = -2.27 yr, and those for females were  $L_{\infty}$  = 396.6 cm LJFL,  $k$  = 0.094 yr<sup>-1</sup>,  $t_0$  = -1.83 yr. Males were larger than females in the first four years of life, while females attained larger sizes by age 5 and lived much longer than males and consequently grew much larger. The maximum age observed in this study was 11 years for females and 5 years for males. The life span difference between males and females was most likely caused by sex-specific mortality (or differential longevity).

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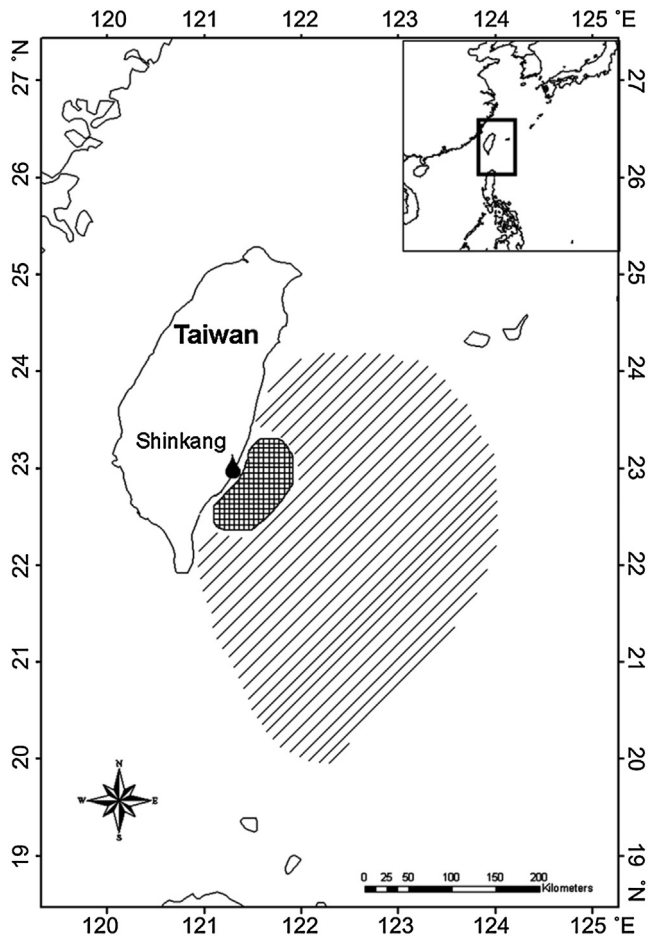
## 1. Introduction

Black marlin (*Istiompax indica*) is a commercially important species inhabiting the tropical and subtropical Pacific and Indian Oceans (Nakamura, 1985). In the Pacific, they usually occur between 45°S and 40°N, with highest densities in the North Pacific found in the warm Kuroshio Current and its branches (Nakamura, 1985). The annual landings of black marlin from offshore and coastal fisheries in Taiwan were around 1000 to 2100 mt between 1985 and 1994; though catches declined to around 500 mt during 1995 to 2002. The landings increased again gradually from 586 mt in 2003 and reached a maximum of 1323 mt in 2006. Since then, the annual landings have decreased steadily to 451 mt in 2012 (Anon, 2013). Off eastern Taiwan, black marlin are mainly harvested using gill nets during winter, occasionally taken by the harpoon fishery, and incidentally captured as bycatch in the offshore longline fishery. The Shinkang fish market processes most of Taiwan's black marlin landings from offshore and coastal fisheries:

72% (419 mt) in 2003, 88% (1159 mt) in 2006 and 54% (244 mt) in 2012.

Information on age and growth of fishes is a central element in population dynamics and fishery management (Brothers, 1983). Several studies on age and growth have been conducted for other billfishes, such as blue marlin (Wilson et al., 1991), sailfin (de Sylva, 1957; Farber, 1981; Chiang et al., 2004), striped marlin (Kopf et al., 2011), and swordfish (Esteves et al., 1995; Ehrhardt et al., 1996; Sun et al., 2002). However, almost no attempt has been made to age black marlin, except by Speare (2003) who evaluated and interpreted age and growth of black marlin in recreational fisheries off eastern Australia using otoliths (sagittae), and dorsal and anal fin spines. The objectives of this study were: (1) to estimate the age and growth of black marlin by counting growth rings on cross sections of the third spine of the first dorsal fin; and (2) to use this information to find the best growth model (standard or generalized von Bertalanffy growth function) for black marlin off eastern Taiwan. This information will allow the age composition of the catch to be determined, which in turn will allow the status of black marlin stock off eastern Taiwan to be assessed using yield-per-recruit or sequential population analysis techniques.

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**Fig. 1.** Commercial fishing grounds of the gillnet, harpoon (cross lines) and longline (oblique lines) fisheries based in the Shinkang fishing port (black dot).

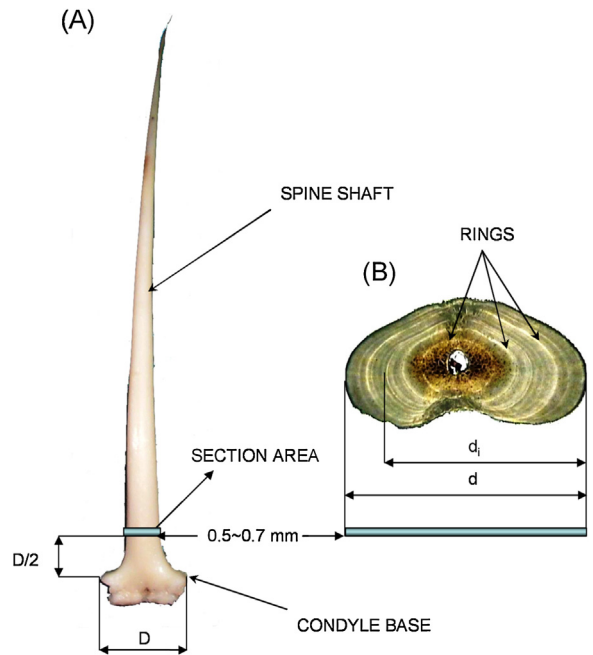
## 2. Materials and methods

### 2.1. Materials preparation and ring reading

Data on lower jaw fork length (LJFL), eye fork length (EFL) (measured to the nearest cm) and round weight (RW) (whole fish measured to the nearest 0.1 kg), and samples of the first dorsal fins of black marlin were collected monthly at the Shinkang fish market (Fig. 1) from July 2004 to April 2006. Sex was determined by inspection of macroscopic and microscopic characteristics of the gonads (Merrett, 1970, 1971; Sun et al., 2009; Kopf et al., 2012).

The dorsal fins were kept in cold storage until being boiled to remove tissue and to separate the third spine. Two cross sections of 0.5 and 0.7 mm in thickness were taken successively along the length of each spine with a low-speed "ISOMET" saw (model no. 11-1280) with diamond wafering blades, at a location equivalent to approximately half of the maximum width of the condyle base measured perpendicularly from the line of maximum condyle width (Fig. 2A; Ehrhardt et al., 1996). The sections were immersed in 95% ethanol for several minutes for cleaning, placed on disposable paper to air dry, and then stored in a labeled plastic case for later reading. Spine sections were examined with a binocular dissecting microscope (model: Leica-MZ6) under transmitted light at zoom magnifications of 10 to 20 $\times$  depending on the sizes of sections.

Growth rings were visible as alternating wide opaque and narrow translucent zones, and age estimates were assigned based on the total number of paired opaque and translucent zones (Kopf et al., 2011). The more visible of the two sections was read twice by



**Fig. 2.** (A) The third dorsal fin spine and the site of cross section and (B) cross section showing the measurements taken for age determination of black marlin, *Istiompax indica*. ( $D$ —width of condyle base;  $d$ , diameter of spine;  $d_i$ , diameter of ring).

the same reader, approximately two weeks apart. The section was read again when the two ring counts differed, and the spine was considered unreadable and discarded if the third ring count differed from both of the previous two ring counts. The precision of reading was evaluated using average percent error (APE) (Beamish and Fournier, 1981; Campana, 2001). Images of the cross sections were captured using the Image-Pro Image analysis software package (Media Cybernetics, Silver Spring MD, 1997), in combination with a dissecting microscope equipped with a charged coupled device camera (model: Toshiba IK-630) and a computer equipped with a high-resolution (800  $\times$  600 pixel) monitor.

The distance from the center of the spine section to the outer edge of each growth ring was measured in microns with the Image-Pro software package after calibration against an optical micrometer. The center of the spine section was estimated following Cayré and Diouf (1983) (Fig. 2B). The distances ( $d_i$ ) were then converted into radii ( $r_i$ ) using the equation  $r_i = d_i - (d/2)$  (Megalofonou, 2000; Sun et al., 2001) where  $r_i$  is the radius of ring  $i$ ;  $d_i$  is the distance from the outside edge of ring  $i$  to the opposite edge of the cross section; and  $d$  is diameter of the spine.

False growth rings were defined following Berkeley and Houde (1983), Tserpes and Tsimenides (1995), and Ehrhardt et al. (1996).

### 2.2. Accounting for missing early rings

The first several growth rings of larger specimens were sometimes obscured because of the large size of the vascularized core of the spine. The number of early but missing growth rings was therefore estimated using the replacement method of Hill et al. (1989) and Chiang et al. (2004). This involved first compiling ring radii statistics from younger specimens that had at least clearly visible first or second rings. Radii of the first four visible rings of the samples which had missing early rings were then compared with the data for younger specimens. When the radii of at least two successive rings of the first four visible rings in samples fit within one standard deviation of the mean radii of each of two or more rings from younger reference specimens, the number of missing rings

was computed as the difference between the ring counts for the matched radii.

### 2.3. Age validation

The marginal increment ratio (MIR) was used to indirectly validate or corroborate rings as annuli. It was estimated for each specimen using the equation  $MIR = (R - r_n) / (r_n - r_{n-1})$  (Hayashi, 1976; Prince et al., 1988) where  $R$  is the spine radius; and  $r_n$  and  $r_{n-1}$  are radius of rings  $n$  and  $n-1$ . The mean MIR and its standard error were computed monthly by sex.

### 2.4. Growth estimation

Growth of males and females was estimated by back-calculation of lengths at presumed ages using two methods. The Fraser–Lee method was based on the assumption that the relationship between spine radius ( $R$ ) and LJFL ( $L$ ) was linear, i.e.,  $L = a_1 + b_1 R$  (Berkeley and Houde, 1983; Sun et al., 2002), while the Monastyrsky method was based on the assumption of a power function, i.e.,  $L = a_2 R^{b_2}$  (Ehrhardt, 1992; Sun et al., 2002). The parameters of the relationships were estimated by maximum likelihood, assuming log-normally distributed errors.

The equations used to back-calculate the lengths at presumed ages were:

$$\text{Fraser – Lee method : } L_n = a_1 + \left(\frac{r_n}{R}\right) (L - a_1) \quad (1)$$

$$\text{Monastyrsky method : } L_n = \left(\frac{r_n}{R}\right)^{b_2} L \quad (2)$$

where  $L_n$  is the LJFL when ring  $n$  was formed;  $L$  is the LJFL at time of capture; and  $r_n$  is the radius of ring  $n$ .

The standard von Bertalanffy growth function (Standard VB; von Bertalanffy, 1938) and generalized von Bertalanffy growth function (Generalized VB; Richards, 1959) were then fitted to the mean back-calculated male and female lengths-at-age from the Fraser–Lee and Monastyrsky methods. Model parameters were estimated using a nonlinear least square procedure assuming additive error (Gauss–Newton method, NLIN of SAS Institute, 1990).

$$\text{Standard VB : } L_t = L_\infty (1 - \exp^{-k(t-t_0)}) \quad (3)$$

$$\text{Generalized VB : } L_t = L_\infty (1 - \exp^{-K(1-m)(t-t_0)})^{1/1-m} \quad (4)$$

where  $L_t$  is the mean LJFL at age  $t$ ;  $L_\infty$  is the asymptotic length;  $t_0$  is the hypothetical age at length zero;  $k$  and  $K$  are growth coefficients; and  $m$  is the fourth order growth-equation parameter.

An analysis of residual sum of squares (ARSS) was used to test whether the growth curves for the two sexes differed (Chen et al., 1992).

## 3. Results

### 3.1. Size distributions and sex ratios

Length and weight data for 4521 individuals (3799 females, 586 males, and 136 fish of unknown sex) were collected. The overall sex ratio (defined as the numbers of females relative to the total numbers of females and males) was 0.87. Females ranged from 151 to 368 cm LJFL (mean = 219.2, SD = 29.1,  $n = 3799$ ) or 31 to 469 kg RW (mean = 105.2, SD = 47.3), and males ranged from 147 to 262 cm LJFL (mean = 178.2, SD = 14.5,  $n = 586$ ) or 26 to 159 kg RW (mean = 52.1, SD = 15.3) (Fig. 3).

There was only one male fish larger than 250 cm LJFL. Further analysis (Fig. 4) indicated that 67% of the samples (i.e., 2533 female and 437 male fish, ranging from 151–329 cm LJFL for females and 151–262 cm LJFL for males, with a sex ratio of 0.85) were caught by

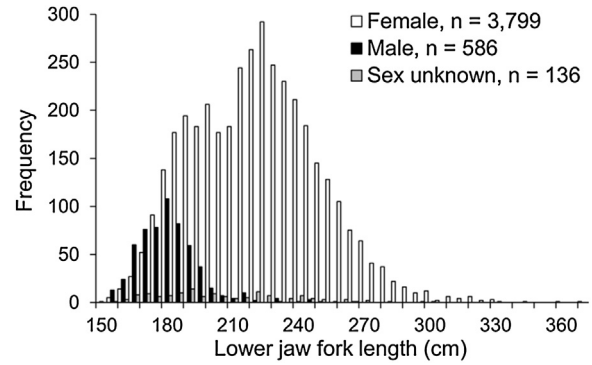


Fig. 3. Size frequency distribution (5 cm intervals) by sex for the black marlin, *Istiompax indica*, sampled at the Shinkang fish market, July 2004 to April 2006.

the gillnet fishery, and 26% (1010 female and 108 male fish, ranging from 152–360 cm LJFL for females and 152–243 cm LJFL for males, with a sex ratio of 0.90) from the harpoon fishery. The remaining 7% (256 female and 41 male fish, ranging from 167–368 cm LJFL for females and 147–245 cm LJFL for males, with a sex ratio of 0.86) were captured by the longline fishery.

Table 1 summarizes the relationships between LJFL and EFL and between LJFL and RW by sex. Both equations differed significantly between males and females (ANCOVA,  $F_{1,4383} = 11.87$ ,  $P < 0.05$  for LJFL–EFL, and  $F_{1,4383} = 33.00$ ,  $P < 0.05$  for LJFL–RW).

### 3.2. Age estimation

Of the 923 dorsal spines sampled, 874 (95%) (687 females and 187 males) were read successfully and the average percent error (APE) was 9.17% for females and 6.23% for males. The aged females ranged in size from 151 to 323 cm LJFL and 31 to 302 kg RW, and the aged males ranged from 152 to 214 cm LJFL and 26 to 85 kg RW.

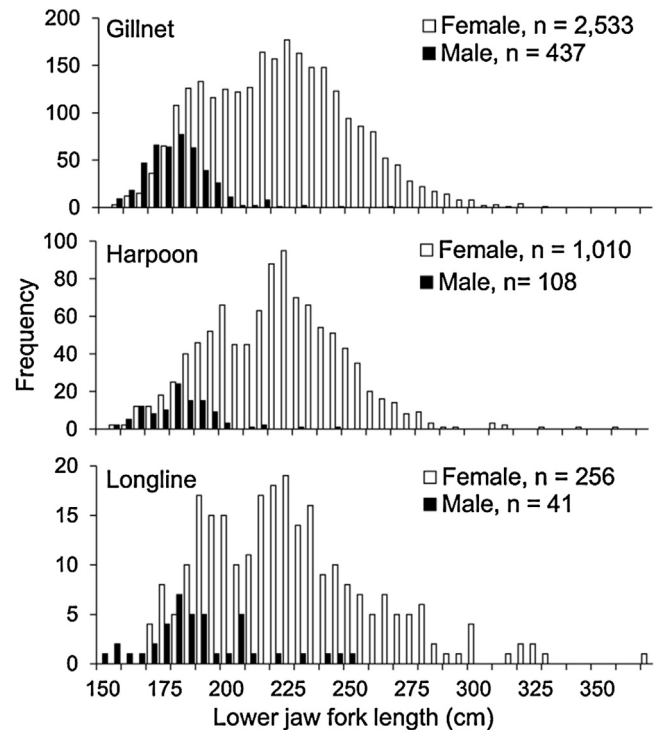
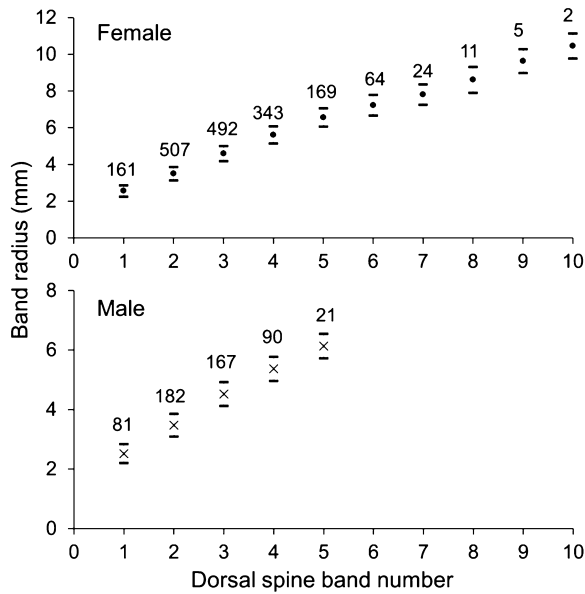


Fig. 4. Size-frequency distributions by different commercial fishing gears (gillnet, harpoon and longline) for the female and male black marlin, *Istiompax indica*, sampled at the Shinkang fish market.

**Table 1**

Linear relationships ( $Y = a + bX$ ) between lower jaw fork length (LJFL, cm) and eye fork length (EFL, cm), and the length–weight (round weight, RW (kg)) relationships ( $Y = a \times X^b$ ) for black marlin, *Istiompax indica*, off eastern Taiwan.

Y	X	a	b	n	LJFL range (cm)	RW range (kg)	r <sup>2</sup>
Male							
LJFL	EFL	9.51	1.0881	586	147–262		0.98
RW	LJFL	2.00E–05	2.8954	586	147–262	26–159	0.84
Female							
LJFL	EFL	4.6327	1.1204	3799	151–368		0.99
RW	LJFL	3.00E–06	3.1929	3799	151–368	31–469	0.93

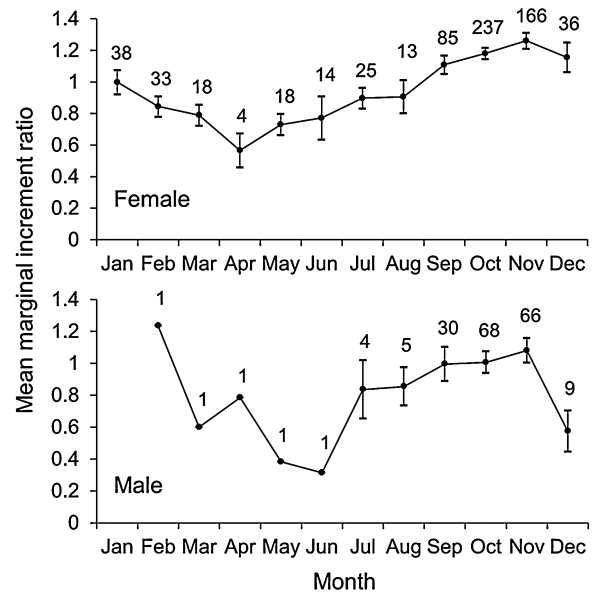


**Fig. 5.** Mean ( $\pm$ SD) ring radius for the female and male black marlin, *Istiompax indica*, collected from eastern Taiwan which had at least the first or second ring present. The numbers above the vertical bars are sample sizes.

Five-hundred and seven (74%) spines for females and 182 (97%) spines for males had at least the first or second rings visible and ring radii statistics by sex are summarized in Fig. 5. All other specimens were assigned inner rings and final age estimates based upon these voucher data. Mean ring radii by age group for males and females, after correction for missing early rings, are listed in Table 2. The maximum estimated ages of black marlin, before and after correction for missing early rings for females, were 8 years and 11 years, respectively, and for males was 5 years.

### 3.3. Age validation

Monthly mean marginal increment ratios (MIR) for females were highest during September–December but declined markedly after January and reached a minimum of 0.6 in April (Fig. 6) and did not differ significantly from May to August (Kruskal–Wallis test,  $H = 3.78$ ,  $df = 3$ ,  $P = 0.29$ ). However, mean MIRs in September through January were significantly higher than those in February through April (Kruskal–Wallis test,  $H = 26.51$ ,  $df = 1$ ,  $P < 0.01$ ). The trends in monthly mean MIRs were similar to those for all ages combined when the data were split into two age groups, i.e., ages 2–5 and ages 6–11. This analysis suggested that one growth ring was formed each year, most likely during February to April for female black marlin. Monthly mean MIRs for males; however, could not be validated due to unrepresentative and small sample sizes (no samples in January and only six samples (i.e., one sample per month) from February to June). We assumed one growth ring was formed each year for males given the results for females.



**Fig. 6.** Monthly mean marginal increment ratios for the female and male black marlin, *Istiompax indica*, collected from eastern Taiwan during July 2004 to April 2006. Vertical bars are  $\pm 1$  SE, numbers above the vertical bars are sample sizes.

### 3.4. Growth estimation

Sex-specific relationships between LJFL and spine radius based on the Fraser–Lee (linear regression) and Monastyrsky (power function) methods are shown in Fig. 7. Relationships for males and females based on the Fraser–Lee and Monastyrsky methods differed significantly ( $F_{1,872} = 5.15$ ,  $P < 0.01$  and  $F_{1,872} = 5.28$ ,  $P < 0.01$ ). According to Akaike's Information Criteria (Akaike, 1969), the Monastyrsky method (power function) provided a better fit to the data ( $\Delta AIC = 0.5197$  for males and 0.6411 for females). Therefore, as is common in istiophorid age and growth studies, the most parsimonious representation of the data was a power function with separate parameters for males and females.

The mean back-calculated lengths-at-age obtained from the Fraser–Lee and Monastyrsky methods are listed in Table 3. The estimated standard and generalized VB curves are shown in Fig. 8 by sex, and the corresponding parameter estimates are listed in Table 4. The growth curves for males differed significantly from those for females based on the ARSS (standard VB: Fraser–Lee:  $F_{3,3158} = 27.22$ ,  $P < 0.05$ ; Monastyrsky:  $F_{3,3158} = 35.65$ ,  $P < 0.05$ ; generalized VB: Fraser–Lee:  $F_{3,3158} = 20.89$ ,  $P < 0.05$ ; Monastyrsky:  $F_{3,3158} = 141.77$ ,  $P < 0.05$ ). Males were larger than females before age 4. However, females were significantly larger than males in the entire sample ( $t$ -test,  $P < 0.05$ ). After the first year of life, growth rates of both sexes of black marlin slowed down appreciably. However, females lived much longer than males, and consequently grew to a much larger sizes.

**Table 2**  
Mean radius of each ring for male and female black marlin, *Istiompax indica*, off eastern Taiwan. Roman numerals indicate the number of rings. Numbers in parentheses are the number of specimens for which the specified ring was readable. “—” means no data owing to vascularization at core area.

Age class	Sample size	Mean radius (mm) of each band										
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Male												
1												
2	15	2.5 (15)	3.90 (15)									
3	77	2.49 (40)	3.50 (77)	4.64 (77)								
4	72	2.47 (22)	3.33 (70)	4.39 (72)	5.38 (72)							
5	23	2.82 (4)	3.30 (21)	4.35 (23)	5.25 (23)	6.09 (23)						
Mean		2.52	3.45	4.49	5.34	6.05						
S.D.		0.32	0.38	0.40	0.40	0.40						
Growth increase			0.93	1.03	0.86	0.71						
Female												
1												
2	15	2.66 (15)	3.92 (15)									
3	149	2.44 (78)	3.53 (149)	4.74 (149)								
4	175	2.55 (49)	3.42 (174)	4.53 (175)	5.67 (175)							
5	149	2.6 (14)	3.46 (105)	4.48 (149)	5.56 (149)	6.69 (149)						
6	79	2.43 (5)	3.53 (40)	4.4 (77)	5.44 (77)	6.44 (79)	7.37 (79)					
7	48	–	3.54(13)	4.4 (44)	5.3 (48)	6.19 (48)	7.05 (48)	7.86 (48)				
8	52	–	3.52(6)	4.37 (41)	5.25 (52)	6.22 (51)	7.08 (52)	7.92 (52)	8.64 (52)			
9	11	–	3.36(3)	4.34 (8)	5.24 (10)	6.13 (11)	7.07 (11)	7.94 (11)	8.65 (11)	9.30 (11)		
10	5	–	3.71(2)	4.29 (5)	5.19 (5)	6.11 (5)	6.95 (5)	7.84 (5)	8.71 (5)	9.50 (5)	10.14 (5)	
11	4	–	–	–	5.33 (4)	6.35 (4)	7.31 (4)	8.18 (4)	9.08 (4)	9.78 (4)	10.57 (4)	11.22 (4)
Mean		2.56	3.49	4.53	5.51	6.46	7.19	7.90	8.67	9.45	10.33	11.22
S.D.		0.31	0.36	0.41	0.47	0.49	0.53	0.56	0.64	0.60	0.59	0.73
Growth increase			0.94	1.04	0.98	0.95	0.73	0.72	0.76	0.78	0.88	0.89



**Table 3**Mean back-calculated lower jaw fork lengths at age for black marlin, *Istiompax indica*, off eastern Taiwan.

Age (yr)	Back-calculated length (cm)			
	Fraser–Lee's method		Monastyrsky method	
	Male	Female	Male	Female
1	119.2936	107.7423	109.2784	94.12819
2	135.3948	127.117	130.7748	119.014
3	153.5658	148.385	152.1142	144.4171
4	170.6955	169.2439	170.567	167.6925
5	184.2668	189.6924	184.5573	189.543
6		205.4291		206.0252
7		220.5007		221.4928
8		236.4783		237.5686
9		253.5411		255.2987
10		267.1266		269.1556
11		286.8821		288.7749

## 4. Discussion

### 4.1. Size distributions and sex ratios

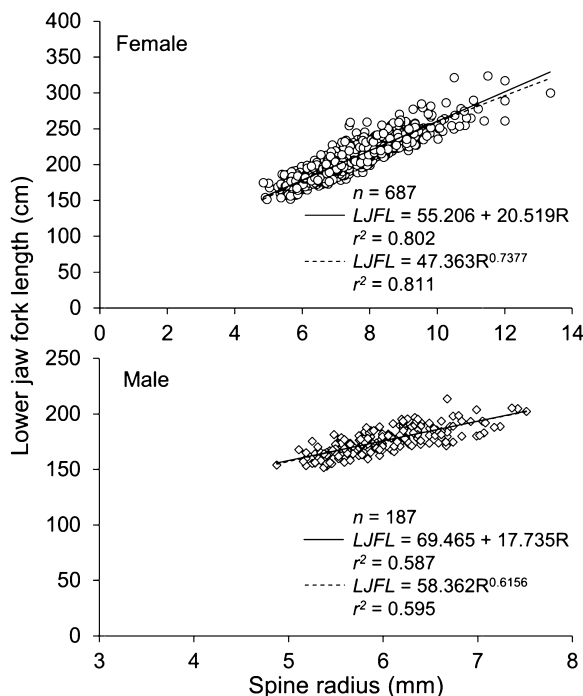
The maximum size measured in the fish market was 368 cm for females and 262 cm LJFL for males, and the overall sex ratio was 0.87, which deviated significantly from the expected 0.5. A preponderance of females in the larger size classes has been reported for several billfishes in Taiwan: blue marlin (Sun et al., 2009); sailfish (Chiang et al., 2004, 2006); and swordfish (Sun et al., 2002; Wang et al., 2003). Sexual dichotomy has been suggested to be due to differences in availability, growth and mortality (Schaefer, 1998, 2001; Sun et al., 2009). Gear selectivity can be ruled-out as a factor given the length distributions and sex ratios by different gears (Figs. 3 and 4). Differences in growth rates (Table 3) were not sufficient to lead to the disproportionate differences in sizes between sexes. The estimated maximum age was 5 years for male and 11 years for female black marlin, indicating both sexes were not equally long-lived. Accordingly, the most parsimonious

explanation for the near complete absence of larger (>262 cm LJFL) male black marlin seems to be differential mortality (or differential longevity). This is indirectly supported by the estimates of natural mortality for black marlin using Pauly's (1980) empirical equation assuming a yearly mean sea temperature of 26 °C ( $0.234 \text{ yr}^{-1}$  for males and  $0.180 \text{ yr}^{-1}$  for females).

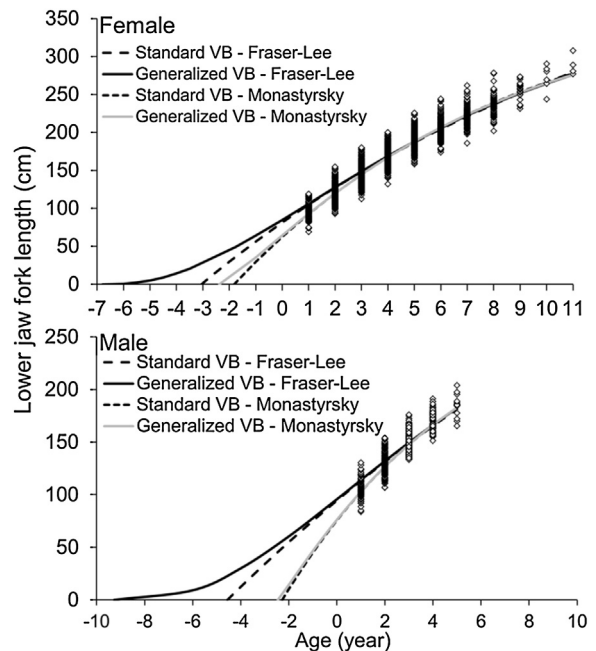
### 4.2. Age estimation

Dorsal-fin spines appear to be useful for aging black marlin as demonstrated in present study. They are easily sampled without reducing the economic value of the fish, and can also be read easily (i.e., growth rings stand out clearly). By contrast, otoliths are extremely small and fragile, and are often difficult to locate (Radtke, 1983). Reading and interpreting otoliths is also more time-consuming and expensive than reading spines (Compeán-Jimenez and Bard, 1983; Kopf et al., 2010).

The problems associated with using fin-spines for ageing are the possible existence of false rings and the vascularized core which can obscure early growth rings; especially in larger fish (Berkeley and Houde, 1983; Hedgepeth and Jolley, 1983; Tserpes and Tsimenides,



**Fig. 7.** Linear regression and power function relationships between lower jaw fork length and spine radius for the female and male black marlin, *Istiompax indica*, off eastern Taiwan.



**Fig. 8.** Standard and generalized von Bertalanffy growth curves estimated by the Fraser–Lee and Monastyrsky methods for the female and male black marlin, *Istiompax indica*, off eastern Taiwan.

**Table 4**  
Parameter estimates and standard errors (in parentheses) for the standard and generalized von Bertalanffy growth models for black marlin, *Istiompax indica*, off eastern Taiwan.  $L_{\infty}$  = asymptotic length;  $k$  and  $K$  = growth coefficients;  $t_0$  = hypothetical age at length zero; and  $m$  = the fourth order growth-equation parameter.

	Standard von Bertalanffy growth model				Generalized von Bertalanffy growth model			
	Fraser–Lee’s method		Monastyrsky method		Fraser–Lee’s method		Monastyrsky method	
	Male	Female	Male	Female	Male	Female	Male	Female
$L_{\infty}$	609.1 (9.7)	500.7 (4.5)	305.8 (9.4)	396.6 (1.3)	345.6 (7.0)	484.0 (7.0)	301.9 (7.1)	366.5 (7.1)
$k$	0.037 (0.030)	0.058 (0.006)	0.125 (0.038)	0.094 (0.006)				
$K$					0.390 (0.342)	0.346 (0.155)	0.142 (0.151)	0.147 (0.193)
$t_0$	−4.56 (0.82)	−3.06 (0.13)	−2.27 (0.44)	−1.83 (0.09)	−9.27 (1.87)	−6.79 (0.76)	−2.46 (1.03)	−2.38 (0.35)
$m$					0.691 (0.003)	0.631 (0.002)	0.069 (0.019)	0.193 (0.080)

1995; Megalofonou, 2000; Sun et al., 2001, 2002; Chiang et al., 2004). However, experienced readers can overcome problems of multiple rings by determining whether the rings are continuous around the circumference of the entire spine section and by measuring their distance from older and newer rings (Tserpes and Tsimenides, 1995; Megalofonou, 2000).

Missing early growth rings in larger specimens were accounted for by compiling ring radii statistics for younger specimens that had at least the first or second rings visible. Similar approaches for solving the problem of missing rings have also been used for Pacific blue marlin (Hill et al., 1989) and sailfish (Chiang et al., 2004).

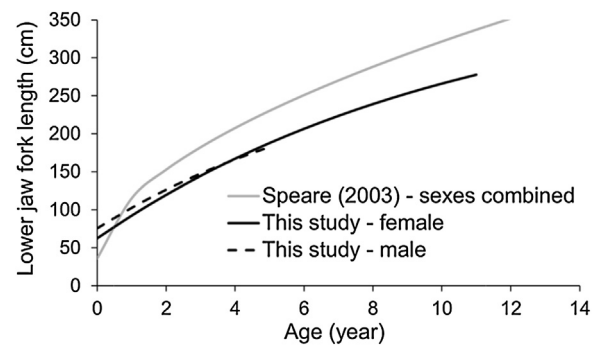
#### 4.3. Age validation

Marginal increment ratio analysis is the most commonly applied method for age validation (Campana, 2001), and this analysis suggested that one growth ring was formed each year during February to April for female black marlin. In addition to MIR, edge analysis could also be used for age validation. However, the MIR and edge analyses provide only partial, indirect age validation. Therefore, uncertainty remains in the age estimates since no direct age validation was performed in this study. Complete validation requires either mark-recapture data or known-age fish (Beamish and McFarlane, 1983; Prince et al., 1991), or the examination of daily micro-increments from otoliths of young individuals (Kopf et al., 2011). Speare (2003) suggested that age validation based on micro-increments in otoliths should be restricted to black marlin less than 160 cm LJFL; sizes which were unavailable in this study.

Billfish are difficult to keep in captivity and return rates of plastic tagged fish are extremely low (Ortiz et al., 2003). Speare (2003) showed, however, based on an oxytetracycline-injected and recaptured male black marlin, that growth of the spine radius from 3.50 mm to 4.34 mm was attained over at least 6 months, a growth rate which seems consistent with the results of this study.

#### 4.4. Selection of a growth equation

Although female black marlin are smaller than males before age 4, females can attain larger sizes than males by age 5 (Table 3) and live longer (11 years old). The length–weight relationships differed significantly between the sexes, and both the standard and generalized VB curves (based on either the Fraser–Lee or Monastyrsky method) appear to fit the black marlin data reasonably well (Fig. 7). However, the standard VB curve is commonly used to describe asymptotic growth in fish, and provides a more realistic description of the growth of age 0 fish (i.e., the length at age 0 was close to zero) (Fig. 9; Table 4). The power function provides a better overall fit to the LJFL versus spine radius data set. Therefore, parameter



**Fig. 9.** A comparison of the growth curves of Pacific black marlin estimated by the present study and Speare (2003). Data from Speare (2003) was taken from his Fig. 8 and was overlaid.

estimates and standard errors obtained from the standard VB fitted to Monastyrsky back-calculated lengths-at-age (i.e., for males: asymptotic length ( $L_{\infty}$ ) =  $305.8 \pm 9.4$  cm LJFL, growth coefficient ( $k$ ) =  $0.125 \pm 0.038$  yr<sup>−1</sup>, age at zero length ( $t_0$ ) =  $-2.27 \pm 0.44$  yr; and for females:  $L_{\infty}$  =  $396.6 \pm 1.3$  cm LJFL,  $k$  =  $0.094 \pm 0.006$  yr<sup>−1</sup>,  $t_0$  =  $-1.83 \pm 0.09$  yr) are recommended as the most credible for determining the age composition of black marlin off eastern Taiwan.

Age and growth for black marlin, using dorsal fin spines for ageing, was reported from the east coast of Australia (Speare, 2003). The maximum ages found in our study, 11 years for females and 5 years for males, are close to the maximum ages of 12 years for females and 6 years for males obtained by Speare (2003). However, the growth curve for black marlin reported by Speare (2003) exhibited much higher growth rates at age <1 and thus much larger sizes-at-age (>120 cm LJFL) than the present study (Fig. 9). This might be due to differences in the primary size range of samples between the present study (160 to 250 cm LJFL) and Speare's (120 to 200 cm LJFL), and also due to the fact that Speare's estimate for growth combined both sexes.

In summary, results of this study are considered essential information for the conservation of black marlin populations in the Western Pacific and the data will be used as input parameters for further stock assessments using yield-per-recruit or sequential population analyses.

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