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Age and Growth Estimates of the Whitespotted Bamboo Shark, *Chiloscyllium plagiosum*, in the Northern Waters of Taiwan

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Wei-Ke Chen, Po-Chuan Chen, Kwang-Ming Liu, and Shyh-Bin Wang (2007) Age and growth estimates of the whitespotted bamboo shark, *Chiloscyllium plagiosum*, in the northern waters of Taiwan. *Zoological Studies* **46**(1): 92-102. Age and growth rates of the whitespotted bamboo shark, *Chiloscyllium plagiosum*, were described from 481 specimens (313 females and 168 males, 35.5-85.0 cm in total length) collected from Feb. 2002 to Feb. 2003 in waters off northern Taiwan on bottom longlines or lobster trap nets. The sex-specific relationships between weight (W) and total length (TL) significantly differed and could be expressed as: $W = 1.64 \times 10^{-3}\ TL^{3.15}$ ($n = 313$, $p < 0.05$) for females and $W = 5.09 \times 10^{-3}\ TL^{2.87}$ ($n = 168$, $p < 0.05$) for males. Age was determined using vertebral banding patterns. A single growth band (comprising translucent and opaque zones) is formed each year, with up to 7 bands observed for both sexes. A marginal increment ratio analysis indicated that the translucent zone formed from June to Sept. Four growth functions, the traditional von Bertalanffy (VBGF), VBGF with a fixed size-at-birth (L_0), Gompertz, and Robertson functions were used to model the observed length-at-age data. The sex-specific growth equations significantly differed. The traditional VBGF, based on observed length-at-age data, predicted an asymptotic length (L_∞) of 95.9 cm TL, a growth coefficient (k) of 0.205, a theoretical age at zero length (t_0) of -0.95 yr for females; and an L_∞ of 100.9 cm TL, k of 0.198, t_0 of -0.90 yr for males. The parameters of VBGF with L_0 set to 15.0 cm were estimated to be an of L_∞ 93.2 cm TL and k of 0.224 for females; and an of L_∞ 98.5 cm TL and k of 0.212 for males. Akaike's information criterion showed that the VBGF with L_0 had the best fit. Ages at maturity estimated from the VBGF with L_0 were 4.5 and 4.4 yr for females and males, respectively. http://zoolstud.sinica.edu.tw/Journals/46.1/92.pdf

Key words: Age and growth, *Chiloscyllium plagiosum*, von Bertalanffy growth equation, Northern Taiwan.

In Taiwan, shark catch statistics are categorized into (1) large pelagic sharks and (2) small demersal sharks in the *Fisheries Statistics Yearbook Taiwan*. Annual yields of small sharks in Taiwan declined dramatically from 5699 tn in 1993 to 1176 tn in 2003, which implied that these stocks, mainly caught by trawlers and longliners in coastal waters off Taiwan, have experienced heavy exploitation in recent years. Huang (1996) mentioned that the spotted shark, *Mustelus manazo*, once a very common species, had almost completely disappeared from central and southwestern Taiwanese waters. Chen et al. (1996) also described severe declines in several demersal shark species such as the sawfish, *Anoxypristis cuspidata*, and members of the Centrophoridae. Fisheries-related biological information, essential for fisheries management, is urgently needed to ensure sustainable utilization of demersal shark stocks.

The whitespotted bamboo shark, *Chiloscyllium plagiosum*, is a small, demersal species that inhabits tropical and subtropical coastal waters of the Indo-Pacific region. This species is broadly distributed off Madagascar, India, Sri Lanka, Thailand, Indonesia, Vietnam, Malaysia, Singapore, the Philippines, China, Taiwan, and Japan (Compagno 2001). However, very little is known about its stock structure. In Taiwan, this species is found in the coastal waters of western

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and northern Taiwan and is one of the most important small shark species in terms of catch biomass. According to our survey from 2002 to 2003, the unit price of this species was US$8-10/kg at Fugi fishing port, northern Taiwan. Unfortunately, catch statistics for this species are not available because it is not sold through the regular fish market system.

Biological information on the whitespotted bamboo shark is very limited although there has been some work on its captive biology. Mating, spawning, hatching, and embryo development have been described from specimens held in aquaria (Masuda and Teshima 1994, Miki 1994, Masuda 1998). The female reproductive system (Chen et al. 2002) and the functional morphology of the pectoral fins have also been described (Wilga and Lauder 2001). Chen and Liu (2006) indicated that the mating season was from Dec. to Jan., the ovulation season was estimated to occur from Mar. to May, and hatching occurred from June to Aug. Age, growth rates, and estimates of the age at maturity, which are important for stock assessment and fisheries management, are, however, lacking for this species.

The objective of this study was to provide the first detailed information on the age and growth of *C. plagiosum* in waters off northern Taiwan, which can be used in stock evaluations in this region.

MATERIALS AND METHODS

Whitespotted bamboo sharks were collected monthly from the Fugi fish market, Taipei County, northern Taiwan (Table 1). All specimens were caught by commercial longline or lobster trap net fisheries in the waters off northern Taiwan between Feb. 2002 and Feb. 2003 (Fig. 1). Measurements were taken of total length (TL in cm) and body weight (W in g), and the sex was identified and recorded. The Chi-square test was used to examine the homogeneity of the sex ratio. The relationship between body weight and total length was described by the allometric equation $W = a \times TL^b$, where a and b are parameters. An analysis of covariance was used to compare the weight-length relationships between sexes.

Vertebrae of the sharks were used for age determination. Samples from 4 specimens (74 and 78 cm *TL* for 2 females and 77 and 79 cm *TL* for 2 males) were used to compare variations in banding patterns on the vertebral centra from different locations within specimens. Since the 11th to the 20th vertebrae were the largest and exhibited the same band counts as those vertebrae in other locations, these vertebrae were used for age analysis in this study. Vertebrae were rinsed in 5% KOH for 2-4 h to remove connective tissue, washed in running water for 24 h, and then rinsed

Table 1. Numbers and size ranges of female and male whitespotted bamboo sharks used for the age and growth analyses in this study

Month year	Female		Male		Sex ratio	
	n	Range of *TL* (cm)	*n*	Range of *TL* (cm)	(F/M)	Total
Feb. 2002	4	55.5-79.0	5	71.0-85.0	0.80	9
Mar. 2002	16	54.1-82.5	10	57.2-82.0	1.60	26
Apr. 2002	37	56.4-85.0	23	55.0-84.0	1.61	60
May 2002	29	35.5-81.5	4	58.2-76.5	7.25*	33
June 2002	20	56.0-76.8	7	51.3-69.5	2.86*	27
July 2002	16	55.4-79.0	23	55.5-79.5	0.70	39
Aug. 2002	31	37.5-77.5	21	38.6-73.0	1.48	52
Sept. 2002	33	38.7-77.0	12	43.0-76.0	2.75*	45
Oct. 2002	31	40.5-66.0	11	41.7-66.6	2.82*	42
Nov. 2002	30	47.5-74.0	9	49.4-67.5	3.33*	39
Dec. 2002	26	49.0-70.0	12	50.0-70.0	2.17*	38
Jan. 2003	30	52.0-80.3	22	51.0-79.3	1.36	52
Feb. 2003	10	57.0-84.0	9	58.0-83.0	1.11	19
Total	313	35.5-85.0	168	38.6-85.0	1.86*	481

*Significant at the 5% level.

in glycerol for 1-4 days. Cleaned centra were examined under a microscope (Zeiss Stemi SV6, Hamburg, Germany) and images were captured by an attached CCD camera (Q-IMAGING QICAM FAST 1394, Burnaby, Canada). These images were processed by an image process system (Auto-Montage Essentials, Frederick, USA). The software is designed to overcome the problems traditionally associated with an inadequate depth of field for imaging 3-dimensional specimens, by allowing a composite, perfectly focused image to be produced. This is achieved by combining the focused parts from a series of images focused at different heights on the specimen to form an in-focus composite. Growth bands (comprising translucent and opaque zones, which were interpreted under conditions of reflected light) were counted without prior knowledge of the sex or length of the specimens. Counts were accepted only if both counts by 2 readers were in agreement. If the estimated numbers of bands differed, the centrum was recounted and the final count was accepted as the agreed number. If the 3rd count did not reach a consensus with one of the previous 2 counts, the sample was discarded. The diameter of each centrum (D) was measured to the nearest 0.1 mm. Distances from the focus to the outer edge of the last 2 bands (r_n, r_{n-1}), and to the lateral radius (R), as well as marginal increments, were measured on a line across the corpus to the centrum edge (Fig. 2). The angle change along the centrum face of all vertebrae was regarded as the birth mark (Goldman 2004).

A marginal increment ratio (MIR) analysis was performed to determine the time of band formation using the following equation (Liu et al. 1998):

$MIR = (R-r_n)/(r_n-r_{n-1})$;

where R is the centrum radius, and r_n and r_{n-1} are the radii of the ultimate and penultimate bands, respectively. One-factor analysis of variance (ANOVA) was used to test the homogeneity of the MIR among months. Tukey's post hoc comparison test was used to conduct pair-wise comparisons. The relationship between the centrum diameter and TL was estimated using a linear regression analysis. The periodicity of band formation was validated based on a captive specimen that had hatched in a Taitung aquarium.

The index of the average percentage error (IAPE) (Beamish and Fournier 1981) was calculated to compare reproducibility of the age determination between 2 readings:

$$\text{IAPE} = \frac{1}{N}\left(\frac{1}{N}\sum_{i=1}^{R}\left(\frac{X_{ij}-X_j}{X_j}\right)\right)\text{x}100;$$

where N is the number of fish aged, R is the number of readings, X_{ij} is the i^{th} age determination of the j^{th} fish, and X_j is the mean age calculated for the j^{th} fish.

Four growth functions were used to model the observed length at age, the length at birth (L_0), and the length data of 31 one-month-old individuals (16 females and 15 males) of the whitespotted bamboo shark. L_0 was estimated from the mean size

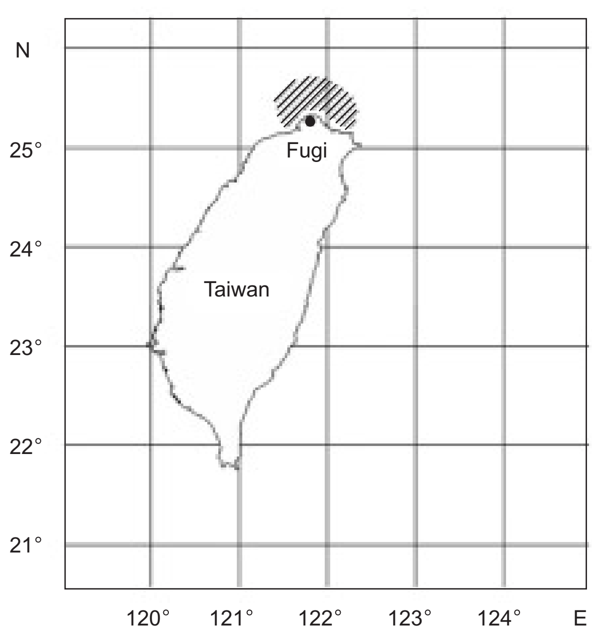

Fig. 1. Sampling area (shaded) of *Chiloscyllium plagiosum* in this study.

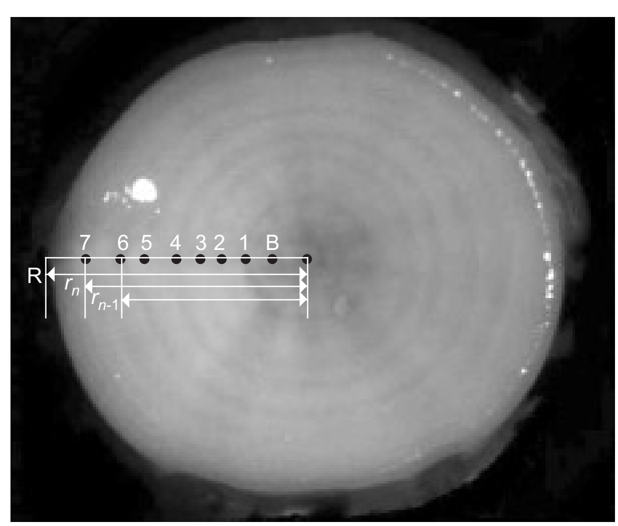

Fig. 2. Growth bands formed on the vertebral centrum of *Chiloscyllium plagiosum*. B, birth mark.

at birth of 16 individuals (10 females and 6 males), which were hatched from eggs deposited by captive females in the laboratory. The NLIN procedure of the statistical package SAS vers. 8.2 (SAS Institute, 2001, Cary, NC, USA) was used to estimate the parameters of each function. The 4 growth functions are described as follows.

(1) Traditional VBGF (von Bertalanffy 1938):

$L_t = \{L_\infty(1-e^{-k(t-t_0)})\}$;

where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth coefficient, t is the age (year from birth), and t_0 is the age at length 0.

(2) VBGF with L_0 (Fabens 1965):

$L_t = L_\infty(1-be^{-kt}\}$;

where $b = (L_\infty - L_0)/L_\infty$ and L_0 is the length at birth and was set to 15.0 cm.

(3) Robertson (1923) growth function:

$L_t = L_\infty/(1+e^{-k(t-t_0)}\}$.

(4) Gompertz (1825) growth function:

$L_t = L_\infty e^{-e^{-k(t-t_0)}}$.

The goodness of fit of the 4 growth functions was compared based on Akaike's information criterion (AIC, Haddor 2001). AIC was expressed as:

$AIC = n\text{xln}(MSE)+2k$;

where n is the total sample size, MSE is the mean square of residuals, and k is the number of parameters estimated in the growth function.

RESULTS

In total, 481 (313 females and 168 males) specimens were collected. Females ranged from 35.5 to 85.0 cm *TL* and males from 38.6 to 85.0 cm *TL* (Table 1). The sex ratio, 1.86, of all specimens significantly differed from 1.0 (Chi-square test $p < 0.05$). Significant differences in the sex ratio were also recorded in May, June, and Sept. to Dec. (Table 1).

Relationships between body weight (W) and total length (TL) were described as follows:

Females: $W = 1.64 \times 10^{-3}\ TL^{3.15}$ ($n = 313$, $r^2 = 0.98$, $p < 0.01$) (Fig. 3); and

Males: $W = 5.09 \times 10^{-3}\ TL^{2.87}$ ($n = 168$, $r^2 = 0.99$, $p < 0.01$) (Fig. 3).

An analysis of the covariance of the logarithmic weight and total length suggested that the relationship between sexes significantly differed at the 5% level. However, no significant difference in the relationship between gutted weight (GW) and TL was found between sexes, and the equation describing the relationship for the sexes was combined as follows:

$GW = 1.6 \times 10^{-6}\ TL^{3.13}$ ($n = 481$, $r^2 = 0.98$, $p < 0.01$) (Fig. 3).

Significant linear relationships were found between the centrum diameter (D) and TL for 313 females and 168 males (ANCOVA, $p < 0.05$):

Females: $TL = 15.93 + 7.184D$ ($n = 313$, $r^2 = 0.86$, $p < 0.01$) (Fig. 4); and

Males: $TL = 14.73 + 7.477D$ ($n = 168$, $r^2 = 0.87$, $p < 0.01$) (Fig. 4).

Age estimates ranging from 1+ to 7+ for both sexes were based on 449 (293 females and 156 males) of the 481 vertebral centra examined. In total, 32 vertebral centra (6.7%) were rejected because the 3rd band counts differed from the previous 2 counts. The precision estimation provided an average IAPE of 4.2% for the overall sample. Percent agreement between examiners was 77.9% total agreement, 92% for 1 band, and 97.3% for 2 bands. Percent agreement by size category also indicated good precision over most size classes (Table 2).

Monthly changes in the vertebral MIR of females and males appeared to peak at 0.89 and 0.80 in June followed by an abrupt decrease to

Table 2. Percent agreement (PA) of the age determinations for *Chiloscyllium plagiosum* by size classes

Total length classes (cm)	*n*	Agree	Agree ± 1	PA	PA ± 1
20-29	1	1	1	100	100
30-39	7	7	7	100	100
40-49	44	36	44	82	100
50-59	167	142	164	85	98
60-69	113	87	105	77	93
70-79	97	66	77	68	79
80-89	20	11	15	55	75
Total	449	350	413		
Mean PA				81	92.1

0.47 and 0.31 in Sept., respectively (Fig. 5). Significant differences were found in the MIR among months for both sexes (one-way ANOVA, $p < 0.05$). Tukey's post hoc pair-wise comparisons revealed that the MIR in Sept. significantly differed from those in June and July ($p < 0.05$). These results suggest that translucent zones form once a year between June and Sept. in both sexes.

The whitespotted bamboo shark is oviparous, its ovulation season is from Mar. to May, and eggs hatch between June and Aug. (Chen and Liu 2006). The time of birth corresponds to that of band formation. It is therefore reasonable to assume that each age at band formation corresponds to a year. Three bands in the vertebral centrum were counted in a 30-month-old captive specimen (61 cm *TL*) indicating the existence of a birth mark. A birth mark was found on every vertebral centrum. The maximum size and age observed were 85 cm *TL* and 7 yr for both sexes (Tables 3, 4).

The parameters of the 4 growth models were estimated as follows.

(1) Traditional VBGF:

Female: $L_t = 95.9(1-e^{-0.05(t+0.95)})$ (n = 309, r^2 = 0.99, $p < 0.01$) (Fig. 6); and

Male: $L_t = 100.9(1-e^{-0.198(t+0.90)})$ (n = 171, r^2 = 0.99, $p < 0.01$) (Fig. 6).

(2) VBGF with L_0:

Female: $L_t = 93.2(1-0.837e^{-0.224t})$ (n = 309, r^2 = 0.99, $p < 0.01$) (Fig. 6); and

Male: $L_t = 98.5(1-0.848e^{-0.212t})$ (n = 171, r^2 = 0.99, $p < 0.01$) (Fig. 6).

(3) Robertson growth function:

Female: $L_t = 79.5/(1+e^{-0.569(t-1.83)})$ (n = 309,

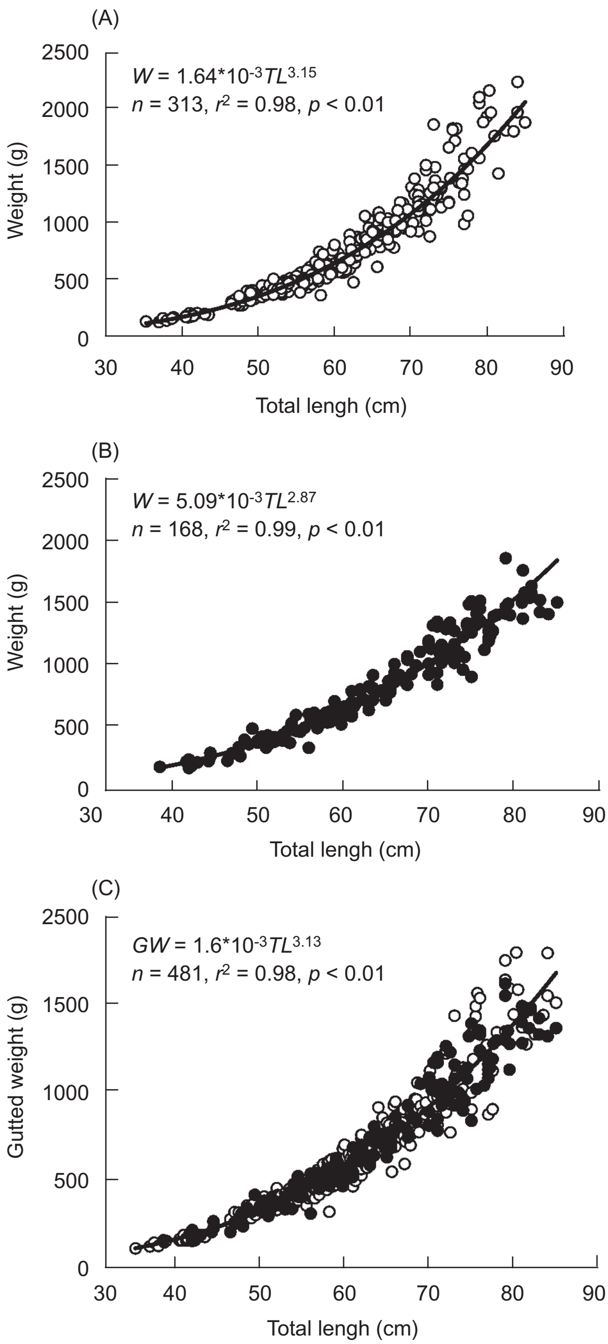

Fig. 3. Relationship between body weight (W) and total length (TL) of *Chiloscyllium plagiosum*. (A) Female; (B) male; (C) sexes combined (○, female; ●, male).

Table 3. Size-at-age of female whitespotted bamboo sharks

Female	Age (yr)						
TL (cm)	1	2	3	4	5	6	7
20-24	1						
25-29							
30-34							
35-39	3	3					
40-44		7	4				
45-49	1	2	13	1			
50-54	1	4	32	7			
55-59	1	10	43	25			
60-64			21	21	2		
65-69			3	22	4	2	
70-74			5	5	15	7	
75-79			1	2	5	10	
80-84				2	3	1	4
n	7	26	122	85	29	20	4
Mean	41.4	49.4	56.6	62.8	73.0	74.5	80.8
SE	3.1	0.6	0.1	0.2	0.4	0.4	0.6

$r^2 = 0.99$, $p < 0.01$) (Fig. 6); and

Male: $L_t = 81.0/(1+e^{-0.608(t-1.91)})$ ($n = 171$, $r^2 = 0.99$, $p < 0.01$) (Fig. 6).

(4) Gompertz growth function:

Female: $L_t = 84.0e^{-e^{-0.390(t-1.02)}}$ ($n = 309$, $r^2 = 0.99$, $p < 0.01$) (Fig. 6); and

Male: $L_t = 86.3e^{-e^{-0.402(t-1.13)}}$ ($n = 171$, $r^2 = 0.99$, $p < 0.01$) (Fig. 6).

Cailliet et al. (1992) mentioned that the longevity of sharks can be estimated as the age at which 95% of the L_∞ is reached. The longevity of whitespotted bamboo sharks was estimated to be 13.7 and 14.2 yr based on the traditional VBGF and 12.6 and 13.4 yr from VBGF with L_0 for females and males, respectively.

Although the VBGF with L_0 produced similar growth parameters as the traditional VBGF, it had the smallest AIC and SE among the 4 growth functions (Table 5) and is likely the best model to describe the growth of whitespotted bamboo sharks.

The mean size at maturity for females and males was estimated to be 64.9 and 65.6 cm *TL*, respectively, based on the relationship between mature percentage and total length (Chen and Liu 2006), which corresponds to ages of 4.5 and 4.4 yr, respectively, when substituted into the VBGF with L_0.

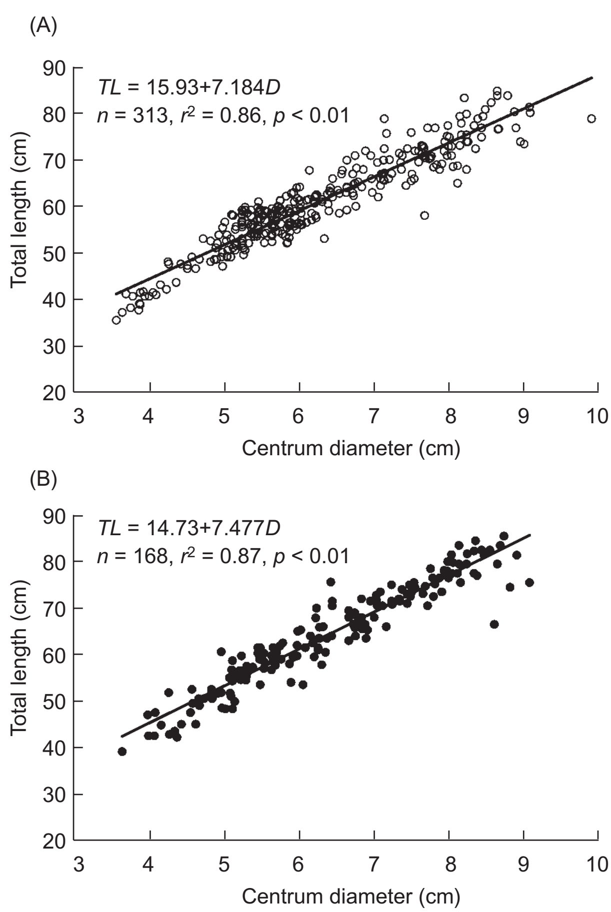

Fig. 4. Relationship between total length (TL) and centrum diameter (D) of *Chiloscyllium plagiosum*. (A) Female; (B) male.

DISCUSSION

Whitespotted bamboo sharks can be caught year round in the coastal waters off northern Taiwan. The longline fishery rarely captures individuals smaller than 40 cm *TL*, possibly because smaller individuals prefer shallower inshore waters. Size-specific gear selectivity may be another possible factor. The sex ratio of the total captured specimens was 1.86 (313 females: 168 males), but varied from month to month. Significant ($p < 0.05$) sex ratio differences from 1: 1 were found in May, June, and Sept. to Dec. Springer (1960) noted that sexes of the sandbar shark, *Carcharhinus plumbeus*, often segregated, except during courtship and mating. This type of sexual segregation might account for deviations in the sex ratio during the course of the year.

In this study, we found that the *W*-*TL* relation-

Table 4. Size-at-age of male whitespotted bamboo sharks

Male	Age (yr)						
TL (cm)	1	2	3	4	5	6	7
20-24							
25-29							
30-34							
35-39	1						
40-44		4	4				
45-49		2	5	1			
50-54		3	12	3			
55-59		3	16	6		1	
60-64			6	15			
65-69		1	1	11	4		
70-74			2	9	13	3	
75-79			1	5	9	5	
80-84				2	1	6	
85-89							1
n	1	13	47	52	27	15	1
Mean	38.6	50.8	55.7	65.8	73.2	77.1	85.0
SE		1.2	0.3	0.3	0.3	0.9	

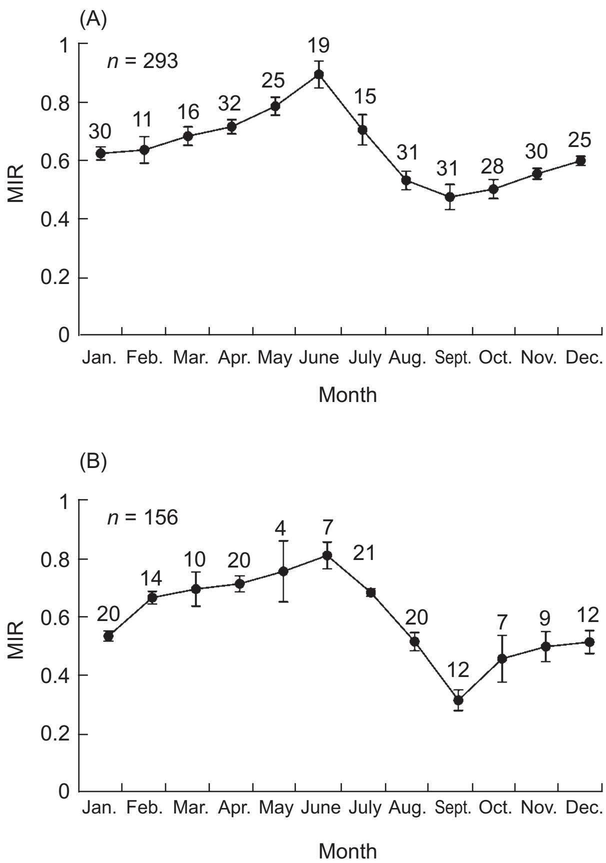

Fig. 5. Monthly changes in the marginal increment ratio of *Chiloscyllium plagiosum*. (A) Female; (B) male. Numbers indicate the sample size, and vertical bars indicate ± 1 SE.

ship significantly differed between sexes; however, no significant difference in the *GW-TL* relationship between sexes was found. This suggests that the larger liver (*t*-test, $p < 0.05$) and ovaries (*t*-test, $p < 0.05$) of mature females might result in the difference in the *W-TL* relationship between sexes.

Several techniques have been used in an attempt to increase the clarity of bands in vertebral centra. Staining sectioned centra with hematoxylin and eosin did not distinguish peripheral bands of whitespotted bamboo sharks. X-radiography, which was used successfully on vertebrae of *Mustelus henlei* (Yudin and Cailliet 1990), was also tried but did not provide usable results. We found that a useful way to enhance centrum bands was to rinse the vertebrae with glycerol. Image processing resulted in clear images extending from the centrum focus to the centrum edge, thereby facilitating band counting. This simple and efficient technique enhanced vertebral bands in *C. plagiosum* and may prove suitable for similar assessments in other species.

Cailliet and Goldman (2004) mentioned that there has been an increase in the use of both verification and validation methodologies in chondrichthyan growth studies, such as marginal increment analysis, centrum edge analysis, size mode analysis, tag-recapture analysis, captive growth analysis, OTC marking, and bomb carbon. Using

Table 5. Estimated growth parameters and Akaike's information criterion (AIC) values of 4 growth functions. Values in parentheses indicate the SE

Growth function	Sex	L_∞ (cm)	k (yr^{-1})	t_0 (yr)	AIC	r^2	n
VBGF	F	95.9 (5.0)	0.205 (0.023)	-0.95 (0.14)	1113.9	0.99	309
	M	100.9 (7.2)	0.198 (0.030)	-0.90 (0.15)	639.2	0.99	171
VBGF with L_0	F	93.2 (3.8)	0.224 (0.019)		1112.4	0.99	309
	M	98.5 (5.9)	0.212 (0.025)		636.9	0.99	171
Robertson	F	79.5 (1.9)	0.569 (0.037)	1.83 (0.10)	1133.6	0.99	309
	M	81.0 (2.2)	0.608 (0.047)	1.91 (0.13)	650.2	0.99	171
Gompertz	F	84.0 (2.7)	0.390 (0.030)	1.02 (0.10)	1122.8	0.99	309
	M	86.3 (3.4)	0.402 (0.037)	1.13 (0.13)	643.8	0.99	171

combinations of verification and validation approaches is most likely to produce convincing results. We used MIR and captive specimens to validate growth data. The former suggested that 1 band was formed per year for the whitespotted bamboo shark. Although no tagging or tetracycline labeling was employed to validate this result, we used a captive specimen to verify our findings. Three bands (1 birth mark and 2 growth bands) on the vertebral centrum were counted in this specimen, supporting our assumption of the existence of a birth mark and the addition of 1 band per year.

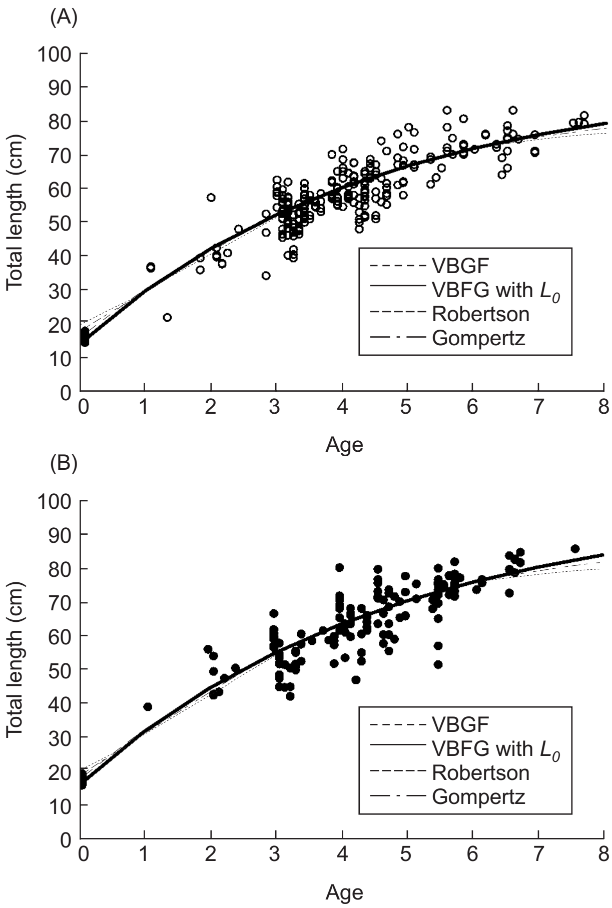

Fig. 6. VBGF, VBGF with L_0, Robertson, and Gompertz growth curves of *Chiloscyllium plagiosum* in this study. (A) Female; (B) male.

As in this study, most work on age and growth verification in sharks supports 1 growth band being formed per year on the centra. Examples include the spotted shark, *Mustelus manazo* (Tanaka and Mizue 1979, Yamaguchi et al. 1996), smooth dogfish, *M. griseus* (Wang and Chen 1982), bigeye thresher, *Alopias superciliosus* (Liu et al. 1998), and bull shark, *Carcharhinus leucas* (Wintner et al. 2002). However, it has been suggested that some species produce 2 bands annually (e.g., basking shark, *Cetorhinus maximus* (Parker and Stott 1965) and shortfin mako, *Isurus oxyrinchus* (Pratt and Casey 1983)). The Pacific angel shark, *Squatina californica*, deposits growth bands irregularly (Natanson 1984).

There are several possible explanations for band formation. A shortage of food, food deprivation caused by migration and spawning, and changing temperatures may all be factors affecting their formation (Stevens 1973, Wang and Chen 1982, Campana 1983, Pratt and Casey 1983), but there are insufficient data to verify any specific cause in this study. Although the timing of deposition of the translucent zones (slow growth) was contrary to the majority of studies on elasmobranchs (Cailliet and Goldman 2004), Loefer and

Table 6. Comparison of growth parameters of small sharks reported by different authors

Species	Region	Sex	L_∞ (cm)	k (yr^{-1})	t_0 (yr)	Authors
Chiloscyllium plagiosum	Northern Taiwan	Female	93.1	0.224		Current study
		Male	98.4	0.213		
Furgaleus macki	Southwestern Australia	Female	120.7	0.369	-0.544	Simpfendorfer et al. (2000)
		Male	121.5	0.423	-0.472	
Mustelus canis	Northwest Atlantic	Female	123.6	0.292	-1.943	Conrath et al. (2002)
		Male	105.2	0.439	-1.524	
Mustelus californicus	California, USA	Female	142.4	0.22	-1.03	Yudin and Cailliet (1990)
		Male	101.8	0.35	-1.00	
Mustelus henlei	California, USA	Female	97.6	0.225	-1.38	Yudin and Cailliet (1990)
		Male	86.1	0.285	-1.09	
Mustelus manazo	Nagasaki, Japan	Female	99.9	0.20	-2.88	Cailliet et al. (1990)
		Male	84.6	0.22	-3.69	

Sedberry (2003) and Simpfendorfer (1993) reported summer deposition of the translucent zone for 2 species of sharpnose sharks, *Rhizoprionodon terraenovae* and *R. acutus*. Simpfendorfer (1993) suggested that stress during the breeding season was a possible explanation for band deposition. The correspondence of translucent zone formation and hatching season (June to Aug.) suggests that band formation in the bamboo shark might be correlated to spawning behavior. However, the underlying mechanisms governing band deposition still need to be determined.

Branstetter (1987) categorized the k values as 0.05-0.10/yr for slowly growing species, 0.10-0.20/yr for species with moderate growth, and 0.20-0.50/yr for rapidly growing species. Based on these criteria, whitespotted bamboo sharks in Taiwan waters have a rapid growth rate. Similar patterns were also reported for other small sharks i.e., the whiskery shark, *Furgaleus macki* (k = 0.29-0.42, Simpfendorfer et al. 2000); smooth dogfish, *Mustelus canis* (k = 0.21-0.53, Francis 1981; k = 0.29-0.44, Conrath et al. 2002); Japanese dogfish, *M. manazo* (k = 0.2-0.22, Cailliet et al. 1990); brown smoothhound, *M. henlei* (k = 0.23-0.28, Yudin and Cailliet 1990); and gray smoothhound, *M. californicus* (k = 0.22-0.35, Yudin and Cailliet 1990) (Table 6).

In recent years, IAPE has commonly been used to estimate variations in different readings or to estimate the reading error of different examiners (Beamish and Fournier 1981, Simpfendorfer et al. 2000). However, the IAPE can vary by study. The IAPE was estimated to be 13.0% for the blacktip shark, *Carcharhinus limbatus* (Wintner and Cliff 1995) but only 3.0% for the oceanic whitetip shark, *C. longimanus* (Lessa et al. 1999). Although the IAPE was used as an index of the precision of the age determination, it could not indicate the source of variation and could not account for differences among processing procedures (Hoenig et al. 1995). Cailliet and Goldman (2004) suggested that a comparison of the IAPE is only useful for the same species in the same waters. As no similar work has been done in Taiwanese waters, the small value of IAPE (4.2%) in the current study suggests that the age determination was reliable.

The traditional VBGF has been used to describe the growth of most elasmobranchs, either from observed length-at-age or from back-calculated length data. However, the VBGF does not fit all shark species. Mollet et al. (2002) noted that the Gompertz growth model better fit growth in the pelagic stingray, *Dasyatis violacea* than did the VBGF. Neer and Cailliet (2001) found similar results in the Pacific electric ray, *Torpedo californica*. In this study, L_∞ values estimated from the Gompertz and Robertson growth functions for both sexes were smaller than the maximum observed length (L_{max}) at 85 cm *TL*. The biologically unrealistic results implied that these 2 functions are not suitable to describe the growth of whitespotted bamboo sharks. On the other hand, L_∞ values estimated with the traditional VBGF and the VBGF with L_0 were greater than 85 cm *TL* (the maximum observed data), and the maximum reported size was 98 cm *TL* in males (Miki 1994), which are believed to be more biologically realistic.

Goosen and Smale (1997) found that the VBGF with a fixed size at birth better describes the growth of sharks if the estimated size at birth data are available. Neer et al. (2005) used a Monte-Carlo simulation incorporating variability in L_0 (ranging from 45 to 65 cm) and obtained similar results to the VBGF with a fixed L_0. Although variability in L_0 was not included in our model, we believe that the VBGF with a fixed L_0 used in this study correctly described the growth of whitespotted bamboo sharks.

Cailliet and Goldman (2004) reported that growth model estimates are greatly affected by the lack of very young or old individuals. Joung et al. (2004) found that size at birth estimated by the traditional VBGF was less than the size of full-term embryos. Conversely, Liu et al. (1999) found that L_0 was overestimated by the traditional VBGF for the pelagic thresher shark. We found similar results in the whitespotted bamboo shark where L_0 with the estimated traditional VBGF was 17.0 and 16.5 cm for females and males, respectively, and were thus larger than the observed L_0 of 15.0 cm. Since both the observed L_0 and newly hatched length were used in parameter estimation, we believe that the VBGF with L_0 used in this study correctly described the growth of this species. Overall, the results we obtained using the VBGF with L_0 produced more biologically realistic parameters than did the traditional VBGF.

In conclusion, this study provides the first detailed estimates of age and growth for the whitespotted bamboo shark, which can be used as biological input parameters in further stock evaluations in this region. However, additional validation of the size composition and stock structure is needed for future studies.

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