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Age and growth of sandbar shark, *Carcharhinus plumbeus*, in northeastern Taiwan waters

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Abstract

Age and growth of the sandbar shark, *Carcharhinus plumbeus*, the important and abundant shark resource for Taiwanese inshore fishery caught by longline in northeastern Taiwan waters from 1989 to 1992, were determined from vertebrae growth band counts from 448 individuals. Translucent and opaque bands on vertebral centra were formed once a year. The parameters for von Bertalanffy growth curves were based on age and observed length and were L_∞ = 210.0 cm TL, K = 0.17 year^{-1}, t_0 = −2.3 year for both sexes (n = 362, ranges 82–219 cm TL). Mean growth rate calculated from observed data by using the von Bertalanffy growth equations was 22.2 cm/year (0–1 year), 18.7–11.2 cm/year (2–5 year), 9.5–4.8 cm/year (6–10 year), and 4.1–2.1 cm/year (11–15 year). Calculated age at maturity was about 7.5–8.2 year for females and 8.2 year for males. The oldest individuals we have aged were 19.8 year (187 cm TL) and 20.8 year (210 cm TL) for male and female, respectively. The sandbar shark in northeastern Taiwan waters showed an increasing growth rate during the juvenile stage suggesting that the population of this species is seriously vulnerable to heavy fishing.

Keywords: Age and growth; Sandbar shark; Taiwan

1. Introduction

The sandbar shark (*Carcharhinus plumbeus*) is widely distributed in tropical and subtropical regions of the Pacific Ocean, the Indian Ocean, the Atlantic Ocean and the Mediterranean (Bigelow and Schröder, 1948; Taniuchi, 1971; Bass et al., 1973). Garrick (1982) and Compagno (1984) have provided details on the distribution and taxonomy of *C. plumbeus* in their revisions of this genus.

The sandbar shark is commonly found in northeastern Taiwan waters, and is one of the most abundant species contributing to the commercial shark fishery of the northeastern Taiwanese waters (Chen et al., 1996). Based on data from the fish market in Nan-Fan-Ao

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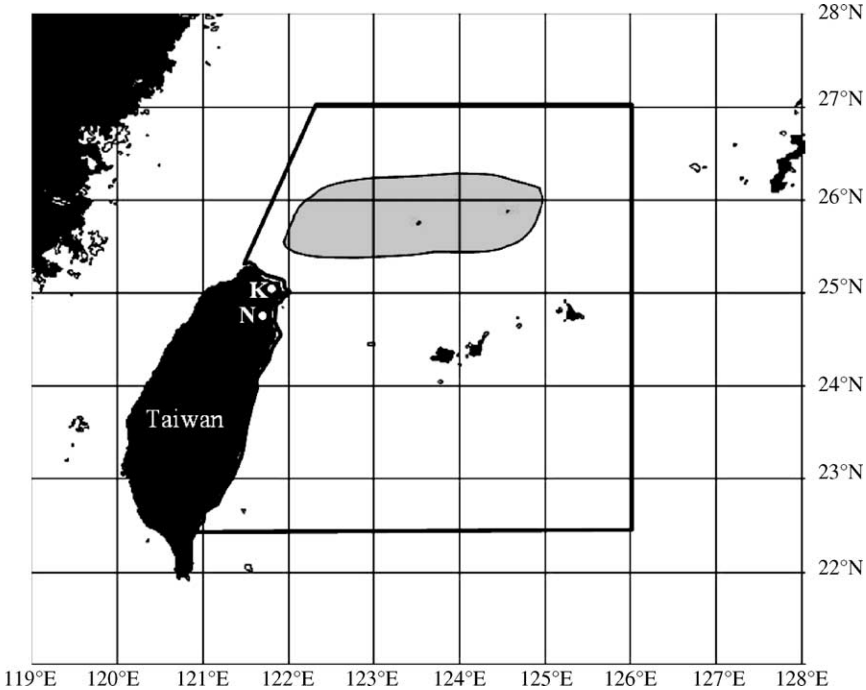

Fig. 1. Sampling area of *C. plumbeus* off eastern and northeastern Taiwan. The shadow represents fishing area for longline fisheries. The dark represents main sampling area. K: Keelung; N: Nan-Fan-Ao.

(Fig. 1), located in northeastern Taiwan, over 170 t of sandbar shark have been landed annually for a decade, representing 10% of the total catch in weight of sharks in this area and makes it second among shark species caught (unpublished data). The wholesale price of the sandbar shark at auction is valued at U.S.$ 350,000 per year. However, the catches of this species have declined in recent years due to high fishing mortality. The catches of sandbar shark landed at Nan-Fan-Ao fish market show a trend of decreasing in mean total weight from 1991 to 2002. The mean total weight is 41.3 kg in 1991, then down to 34.2 kg in 2002 (personal communication). Therefore, a feasible management seems to be necessary for this and other shark species in this area.

Lack of accurate age information on sharks has been a major stumbling block to fisheries research. The topic of "shark ageing" has received increasing attention since it started in the mid 1970's. Growth rings on the face of vertebral centra consist of calcified opaque bands adjacent to less calcified translucent bands, and have long been though to represent seasonal growth patterns (Jagerskiold, 1915; Ridewood, 1921; Jones and Geen, 1977; Radtke and Cailliet, 1984; Cailliet, 1990). Several studies have verified that the calcified bands represent annual summer growth, and several carcharhinid shark species have been aged using this assumption (Natanson et al., 1999, 2002; Allen and Wintner, 2002; Simpfendorfer et al., 2002; Wintner et al., 2002).

Despite several authors reporting on ages of the sandbar shark in some areas (Springer, 1960; Wass, 1973), nothing is known about ages of sandbar sharks in Taiwanese waters as none of these publications dealt with this area. Springer discussed the possibility of rapid growth to maturity (150 cm fork length) in 2–3 years based on length-frequency data. Wass (1973) reported age at maturity to be between 3 and 13 years old for Hawaiian specimens, and Casey et al. (1985) were the first to attempt to verify the annual formation of growth rings in the sandbar shark from the western North Atlantic. Casey and Natanson (1992) revised their earlier conclusions and suggested that the sandbar shark may grow much slower than their previously reported. Sminkey and Musick (1995) indicated that the sandbar shark population in western Atlantic along the coast of the United States showed a small increase in juvenile growth rate after population depletion. Because of their generally low reproductive rate and the direct relationship between stock size and recruitment, shark populations are extremely susceptible to overfishing (Holden, 1974). Based on demographic simulations, Sminkey and Musick (1995) also suggested that the sandbar shark populations could be depleted under high fishing mortality on mature fish or by any substantial fishing mortality on immature ages. These results implied that the sandbar shark population is vulnerable to intense fishing activities.

At present, development of a management plan for sharks is difficult in many countries because of a lack of adequate biological data, especially accurate age and growth information on the commonly caught shark species. This study is aimed to provide detailed information of the age and growth of the sandbar shark from northeastern Taiwan waters, based on the examination of vertebral rings.

2. Materials and methods

Specimens examined were from commercial longline fishery catches off northeastern Taiwan between 1989 and 1992 (Fig. 1). The fishing depth varied from 30 to 120 m. All the samples in this study were collected from Nan-Fan-Ao fish market with random sampling each month but the all landed sandbar sharks at each sampling day were collected as possible.

All measurements were taken in a straight line between perpendiculars with the caudal fin placed in a natural position (Branstetter, 1986; Branstetter and Stiles, 1987). Total lengths (TL) are used throughout this paper, and for comparison with other literature, which has reported length as fork length (FL) or precaudal length (PCL). The relationships between total length and fork length, precaudal length were calculated. Since two or more smaller sharks of similar size are sometimes weighed together in Taiwanese markets, we usually use this weight dividing the total numbers as the "mean weight" for one individual's body weight.

Table 1
The specimens used for age and growth analysis in this study

Month	Female		Male	
	N	Range of TL (cm)	*N*	Range of TL (cm)
November 1989	11	162–219	2	180–198
December 1989	25	146–219	21	144–207
February 1990	10	169–200	3	162–209
March 1990	9	180–205	–	–
July 1990	–	–	8	179–197
August 1990	15	17–212	5	125–190
September 1990	1	167	5	169–193
October 1990	–	–	7	188–197
November 1990	24	157–206	14	160–196
December 1990	6	144–217	11	133–201
January 1991	24	182–210	17	86–195
February 1991	9	126–186	19	121–169
March 1991	12	172–216	11	132–194
April 1991	4	175-207	5	167–180
May 1991	8	18–207	20	173–199
June 1991	3	182–195	4	178–190
November 1991	8	182–210	4	171–186
December 1991	8	161–200	10	163–194
January 1992	3	161–21	18	153–201
March 1992	1	185	15	170–200
June 1992	1	182	2	185–190
July 1992	1	200	2	188–209
August 1992	2	197–199	–	–
Total	215	82–219	233	86–209

Reproductive development and maturity determinations followed guidelines developed elsewhere (Clark and von Schmidt, 1965; Branstetter, 1981; Branstetter and Stiles, 1987). Males were considered mature when the claspers' siphon sacs were fully developed. Presence of sperm did not constitute a maturity criterion (Clark and von Schmidt, 1965). Females were considered mature based on uterine development, the presence of developing or ripe ovarian eggs, or the presence of uterine eggs or embryos.

Vertebrae located just under the first dorsal fin or branchial chamber are usually used for shark analysis,

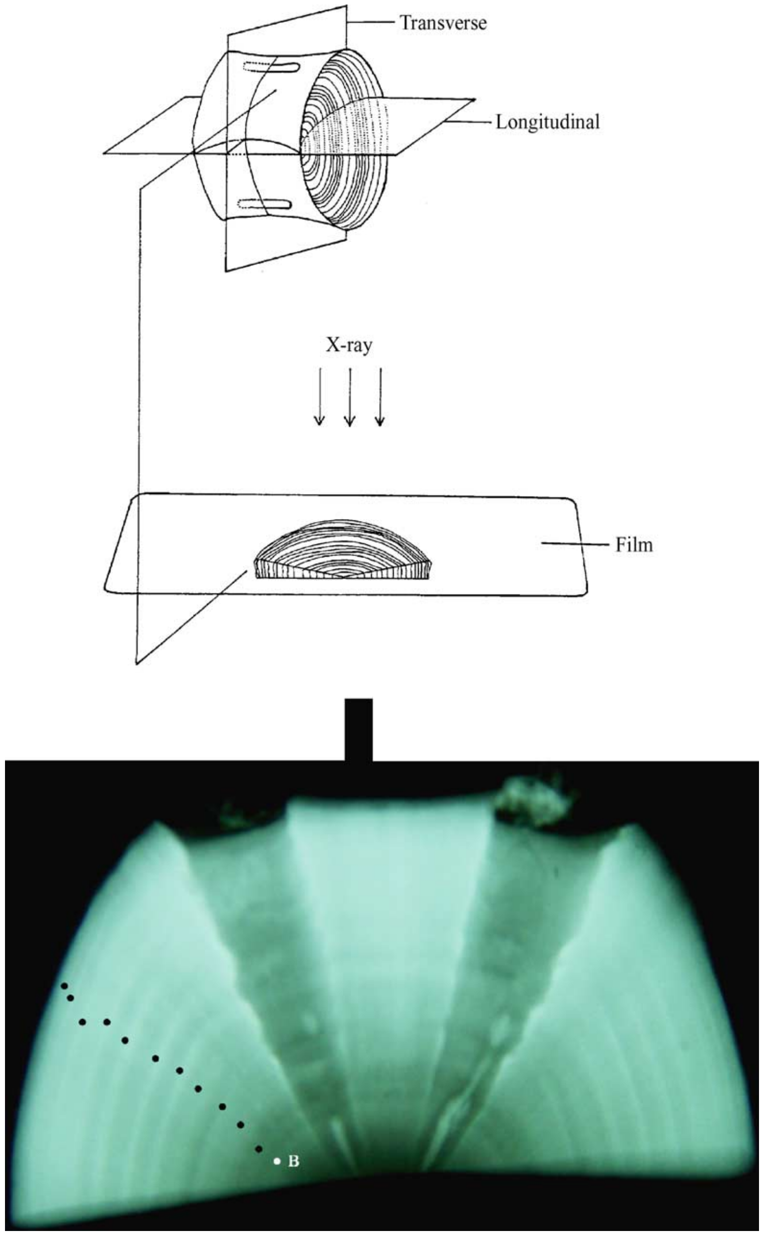

Fig. 2. Caudal peduncle vertebra and diagram of centrum showing the two sectioning plane used.

as the vertebrae from this position are relatively homogeneous and possess a large radius and clearer growth bands (Cailliet et al., 1983a, 1983b; Pratt and Casey, 1983; Branstetter, 1987a, 1987b). The vertebrae of five specimens had been taken from the caudal peduncle and branchial chamber for comparison with earlier experiments, and we found no difference of growth bands counts between these two positions. Although vertebrae from the caudal peduncle were smaller than those from under the first dorsal fin, they also possess clear growth bands and are suitable for age analysis in this species.

For age and growth analysis, vertebrae from the caudal peduncle were removed from 233 males (86–209 cm) and 215 females (82–219 cm) and were frozen (Table 1).

Clean centra were sectioned both along the transverse and longitudinal plane (Fig. 2) to prepare them for several band-enhancement techniques. To facilitate cutting, centra were paraffin-impregnated for 12 h prior to sectioning, and were held in place with a bone chuck while cutting. Several techniques were used to elucidate bands clearly. Eosin and hematoxylin staining did not distinguish peripheral bands. The most successful technique was X-radiography, which has also been tried on vertebrae of *Mustelus henlei* by Yudin and Cailliet (1990).

X-radiographs were taken using a Rigaku Industrial X-ray Apparatus (Model: Radioflex 90 GSB) with FUJI industrial X-ray film (Fine Grain and High Contrast). One growth zone was defined as a combination of an opaque and a translucent band. Opaque bands are more heavily mineralized than translucent bands hence more electrons can penetrate translucent bands (Cailliet and Radtke, 1987). On an X-radiograph, opaque bands appear white and translucent bands appear dark. X-radiographs were viewed through a light box at 10× magnification using transmitted light and growth bands were counted.

Numbers of bands were counted without prior knowledge of the length of specimens. Counts are accepted if both counts by two different readers are in agreement. If the estimated number of bands differed by one band, then the centrum was recounted and the final count then accepted as the agreed age. Following previous studies, counts that differed by two or more bands were rejected (Chen et al., 1990). Distance from the focus to the outer edge of each band, and the dorsal radius were measured in a straight line through the center of the intermedialia.

The time of growth band formation was estimated from monthly changes in marginal increment rate (MIR), using the following equation:

$$\mathrm{MIR} = \frac{R - r_n}{r_n - r_{n-1})}$$

where R is the centrum radius and r_n and r_{n-1} are radius of the ultimate and penultimate bands, respectively.

The relationship between the centrum radius (R) and TL was estimated using linear regression analysis. Each complete band pair was measured and these values were inserted into the regression equation to back-calculate the TL of a shark at completion of formation of each band.

Growth curves were fitted using the von Bertalanffy growth equation (VBGE). The nonlinear regression PAR BMDP statistical package (Dixon et al., 1985) was used to obtain estimates of parameters of VBGE as follows:

$$L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$$

where L_t is length at age t, L_∞ the asymptotic length, K the growth coefficient, t is age (years from birth), and t_0 is the age at length zero.

All growth rates were calculated using the VBGE based on observed length-at-age and back-calculated values. The relationship of body weight (W) and length was also examined. An analysis of covariance (ANCOVA) was used to compare R–TL relationships between sexes. The VBGE of both sexes were compared by analysis of residual sum of squares (ARSS) test (Chen et al., 1992), and the relationships of W-TL of both sexes were compared by likelihood test (Kimura, 1980).

3. Results

3.1. Relationship between total length (TL; in cm), fork length (FL; in cm) and precaudal length (PCL; in cm)

For comparison with other literature, TL was calculated from our data with the following formulae:

- Female: FL = 0.6547 + 0.8105TL (n = 97; r^2 = 0.94)
- PCL = −5.0554 + 0.7681TL (n = 189; r^2 = 0.95)
- Male: FL = −2.6411 + 0.8232TL (n = 66; r^2 = 0.94)
- PCL = −0.4908 + 0.7391TL (n = 210; r^2 = 0.94)

3.2. Relationship between centrum radius (R) and total length (TL)

A significant linear relationship (Fig. 3) was found between the R (in cm) and TL (in cm). An analysis of covariance was used to compare the homogeneity of R–TL relationships between sexes, indicating that the two equations are significantly different in slopes (ANCOVA, $P < 0.05$). The R–TL relationships for 176 females and 186 males as follows:

- Female: TL = 173.0R + 61.3 (n = 176; r^2 = 0.72)
- Male: TL = 134.7R + 84.0 (n = 186; r^2 = 0.54)

3.3. Time of annulus formation

Marginal increment rate (MIR) analysis (Fig. 4) showed a trend of increasing marginal increment widths from spring to autumn. The highest MIR means occurred in September for both sexes, and then showed a trend of decreasing MIR. Thus an opaque band deposited once a year. We assumed that the opaque band represented a 1-year annulus which formed in December. The standard deviations of monthly samples were large because annulus growth for each individual or age groups was different, even in the same month (Chen et al., 1990).

No annulus was found in the centra of the largest embryo (60 cm), which was collected during February. Although no juveniles bearing a single annulus were captured, several juveniles about 90 cm TL that were caught in November exhibited two annuli. It is therefore reasonable to assume that the first annulus is formed on 1st December after birth (birth in February, see Joung and Chen, 1995). Hence the age at first annulus formation was 0.8 year, the second at 1.8 year, the third at 2.8 year, and so on.

3.4. Back-calculated length at time of annulus formation

Vertebrae from the caudal peduncle were removed from 448 individuals. 32 (7.1%) were rejected as being deformed and 54 (12.1%) because of bands counts disagreement. In total, 362 (176 females and 186 males) (80.8%) samples were used for back-calculation.

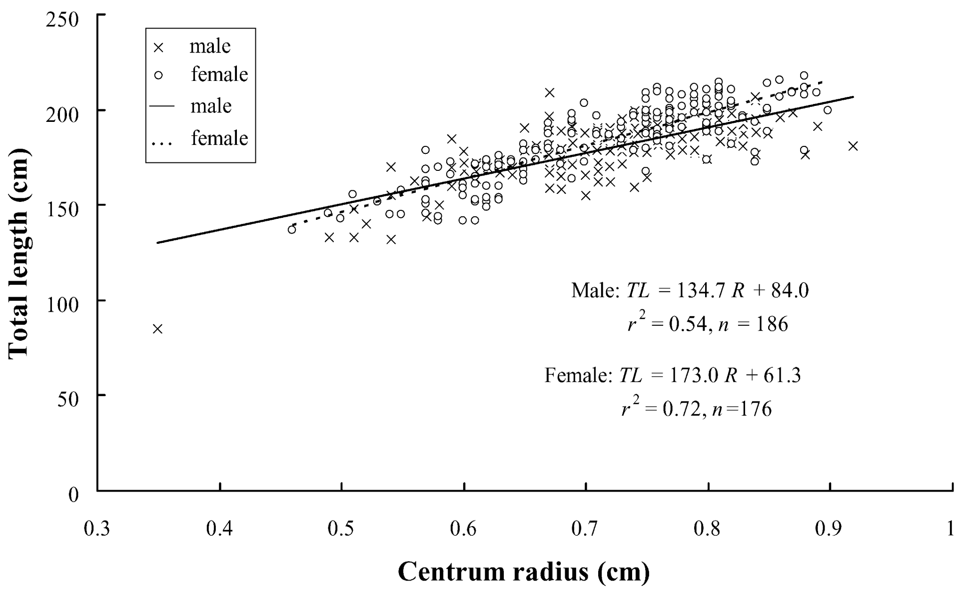

Fig. 3. Relationship between total length and centrum radius in *C. plumbeus* from Taiwan.

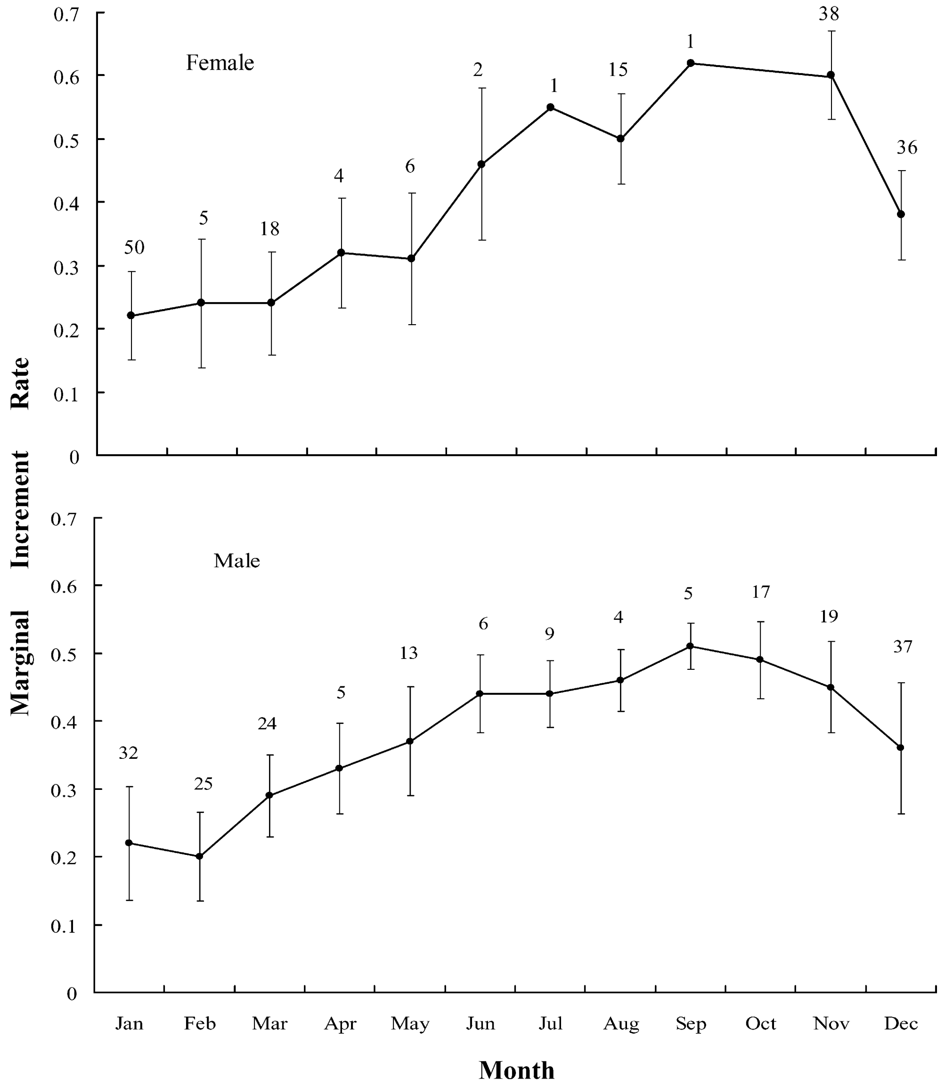

Fig. 4. Monthly change of marginal increment ratio of *C. plumbeus* from Taiwan. Vertical lines indicates ± 1S.E. Top: female; bottom: male.

A mean annulus radius was calculated for each sex. Mean radii for each annulus were summed. It is obvious that Lee's phenomenon (the differences between calculated length and true length at earlier annuli is greater at younger ages (Lee, 1912; Ricker, 1958) does exist in the sandbar shark. By putting those annuli radii values into TL-R linear equations, back-calculated total lengths at the time of annulus formation were calculated and are presented in Tables 2 and 3.

3.5. Estimation of parameters in the von Bertalanffy growth equation (VBGE)

Observed lengths at different ages were used to calculate the VBGE predicted lengths. The VBGE of both sexes were compared by ARSS-test, indicating that the two equations are not significantly different ($F = 1.85$, $P > 0.05$). The parameter of VBGE estimates were $K = 0.17\ \text{year}^{-1}$, $L_\infty = 210.0$ cm, and $t_0 = -2.3$ year for both

Table 2
Back-calculated total length at time of annulus formation for male *C. plumbeus* from Taiwan

Annulus	*N*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	0																				
2	1	112.3	128.5																		
3	2	117.7	133.8	148.7																	
4	3	115.0	129.8	141.9	147.3																
5	5	112.3	125.8	139.2	150.0	155.4															
6	10	113.6	127.1	139.2	150.0	160.8	170.2														
7	16	109.6	123.1	135.2	146.0	155.4	162.1	170.2													
8	14	108.2	120.4	131.1	140.6	148.7	158.1	166.2	172.9												
9	15	108.2	120.4	131.1	141.9	150.0	158.1	166.2	172.9	179.6											
10	16	106.9	117.7	127.1	136.5	144.6	151.4	158.1	166.2	172.9	178.3										
11	24	108.2	119.0	127.1	136.5	143.3	151.4	159.4	164.8	171.6	176.9	182.3									
12	17	108.2	119.0	127.1	135.2	143.3	150.0	156.7	163.5	170.2	175.6	182.3	186.4								
13	17	108.2	117.7	125.8	132.5	139.2	144.6	151.4	156.7	163.5	168.9	175.6	179.6	185.0							
14	16	108.2	116.3	123.1	129.8	137.9	143.3	150.0	155.4	160.8	167.5	172.9	176.9	181.0	186.4						
15	10	106.9	117.7	125.8	131.1	136.5	141.9	147.3	152.7	156.7	162.1	167.5	172.9	176.9	181.0	186.4					
16	11	106.9	116.3	124.4	132.5	137.9	144.6	148.7	154.0	159.4	167.5	170.2	174.2	179.6	183.7	186.4	190.4				
17	5	104.2	113.6	120.4	124.4	131.1	137.9	143.3	148.7	152.7	158.1	162.1	166.2	171.6	175.6	179.6	183.7	187.7			
18	2	105.6	113.6	123.1	128.5	135.2	141.9	146.0	150.0	154.0	159.4	163.5	166.2	172.9	175.6	178.3	182.3	185.0	187.7		
19	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
20	2	109.6	119.0	125.8	131.1	135.2	139.2	144.6	148.7	152.7	156.7	159.4	162.1	164.8	168.9	171.6	175.6	178.3	182.3	186.4	189.1

Table 3
Back-calculated total length at time of annulus formation for female *C. plumbeus* from Taiwan

Annulus	*N*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	0	–																			
2	0	–	–																		
3	0	–	–	–																	
4	3	95.9	114.9	128.8	142.6																
5	7	94.2	108.0	121.9	137.4	151.3															
6	15	92.4	108.0	123.6	137.4	151.3	161.6														
7	16	92.4	106.3	121.9	134.0	147.8	156.5	165.1													
8	17	90.7	104.6	116.7	128.8	139.2	149.5	158.2	166.8												
9	12	92.4	106.3	118.4	132.2	142.6	153.0	163.4	172.0	178.9											
10	13	90.7	102.8	114.9	127.0	137.4	147.8	156.5	163.4	172.0	178.9										
11	19	90.7	104.6	116.7	127.0	139.2	147.8	158.2	166.8	173.8	182.4	189.3									
12	18	90.7	104.6	116.7	125.3	135.7	144.3	151.3	161.6	170.3	177.2	184.1	191.1								
13	11	90.7	102.8	114.9	123.6	132.2	139.2	147.8	154.7	163.4	170.3	177.2	185.9	192.8							
14	15	90.7	102.8	113.2	121.9	130.5	139.2	147.8	156.5	163.4	170.3	175.5	180.7	187.6	194.5						
15	8	89.0	102.8	113.2	123.6	130.5	139.2	146.1	153.0	159.9	165.1	172.0	180.7	187.6	194.5	201.4					
16	13	87.3	99.4	109.7	120.1	128.8	135.7	142.6	151.3	156.5	163.4	170.3	175.5	182.4	187.6	194.5	199.7				
17	4	89.0	102.8	113.2	121.9	130.5	139.2	146.1	151.3	158.2	165.1	172.0	178.9	184.1	189.3	192.8	196.2	201.4			
18	3	87.3	99.4	111.5	123.6	130.5	135.7	142.6	149.5	156.5	163.4	168.6	175.5	178.9	184.1	189.3	192.8	198.0	203.2		
19	1	90.7	102.8	113.2	123.6	130.5	137.4	144.3	149.5	154.7	159.9	165.1	170.3	178.9	185.9	191.1	194.5	199.7	203.2	206.6	
20	1	89.0	104.6	113.2	116.7	121.9	128.8	134.0	139.2	147.8	153.0	158.2	163.4	173.8	180.7	185.9	189.3	196.2	203.2	208.4	213.5

sexes. The von Bertalantty growth curves for both sexes fit the observed data relatively well (Fig. 5). The growth rate during the first year was estimated to be 22.2 cm, then 18.7–11.2 cm/year for years 2–5, 9.5–4.8 cm/year for years 6–10, and 4.1–2.1 cm/year for years 11–15 (Table 4).

Back-calculated lengths for ultimate annulus formation at different ages were also used to calculate the predicted lengths of VBGE. The ARSS-test indicating that the VBGE of both sexes was significantly different ($F = 24.67$, $P < 0.05$). The parameter estimates were $K = 0.10$ year^{-1}, $L_\infty = 223.0$ cm, and $t_0 = -4.5$ year for females and $K = 0.14$ year^{-1}, $L_\infty = 200.0$ cm, and $t_0 = -4.0$ year for males. Von Bertalanffy curves produced from back-calculated data were close to the observed data curve (Fig. 5). Length at birth was calculated to be 80.8 cm for females and 85.8 cm for males. Typical observed lengths of embryos at birth were about 60–65 cm (Joung and Chen, 1995). Growth during the first year was estimated to be 13.5 cm for females and 14.9 cm for males, then 12.3–9.1 cm/year for females and 13.0–8.6 cm/year for males for years 2–5, and 8.2–5.5 cm/year for females and 7.4–4.2 cm/year for males for years 6–10, and 5.0–3.4 cm/year for females and 3.7-2.1 cm/year for males for years 11–15 (Table 4).

Length at sexual maturity for the sandbar shark was about 170–175 cm in females and 175 cm in males (Joung and Chen, 1995). Age at maturity in the present study was calculated to be about 7.5–8.2 year for females and 8.2 year for males, based on the VBGE from observed data, and 9.9–10.9 year for females and 10.9 year for males from back-calculated data. The oldest individuals we have aged were 19.8 year (187 cm TL) and 20.8 year (210 cm TL) for male and female, respectively.

3.6. Relationship between body weight and total length

The general length–weight relationships (Fig. 6) of both sexes were compared by likelihood ratio test, indicating that two equations are not significantly different ($x^2 = 0.72$, $P > 0.05$). The sexes combined length–weight relationship represented as follows: $W = 1.89 \times 10^{-6}\ \mathrm{TL}^{3.23}$ ($n = 400$; $r^2 = 0.98$)

4. Discussion

For fisheries management, determination of age and growth patterns is essential and is particularly

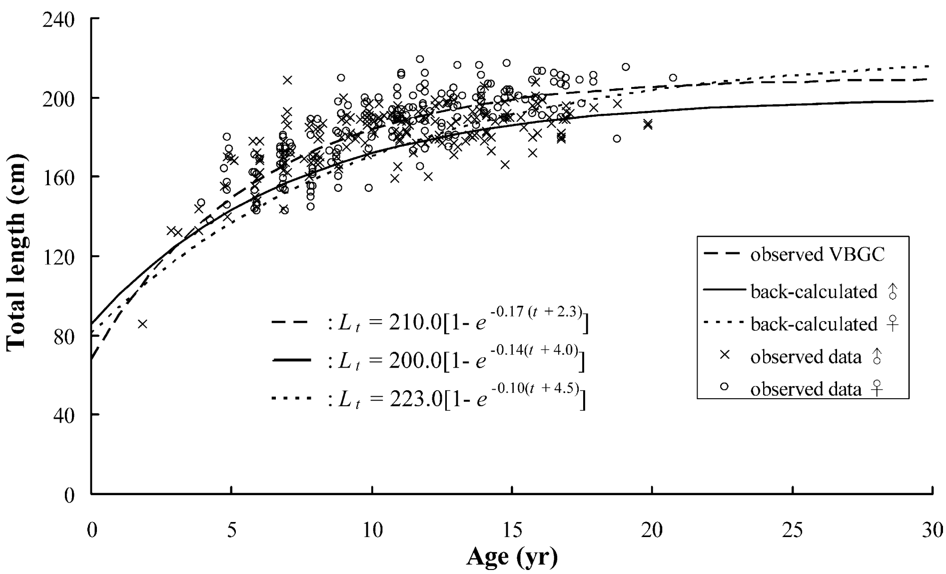

Fig. 5. von Bertalanffy growth curves of *C. plumbeus*.

Table 4
Annuli growth rate (cm/year) calculated from VBGC based on observed length-at age and back-calculated values

Age	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15
Growth rate (observed data)	22.2	18.7	15.8	13.3	11.2	9.5	8.0	6.8	5.7	4.8	4.1	3.4	2.9	2.4	2.1
Growth rate (back-calculated)															
Female	13.5	12.3	11.1	10.0	9.1	8.2	7.4	6.7	6.1	5.5	5.0	4.5	4.0	3.7	3.4
Male	14.9	13.0	11.2	9.8	8.6	7.4	6.4	5.6	4.9	4.2	3.7	3.2	2.8	2.4	2.1

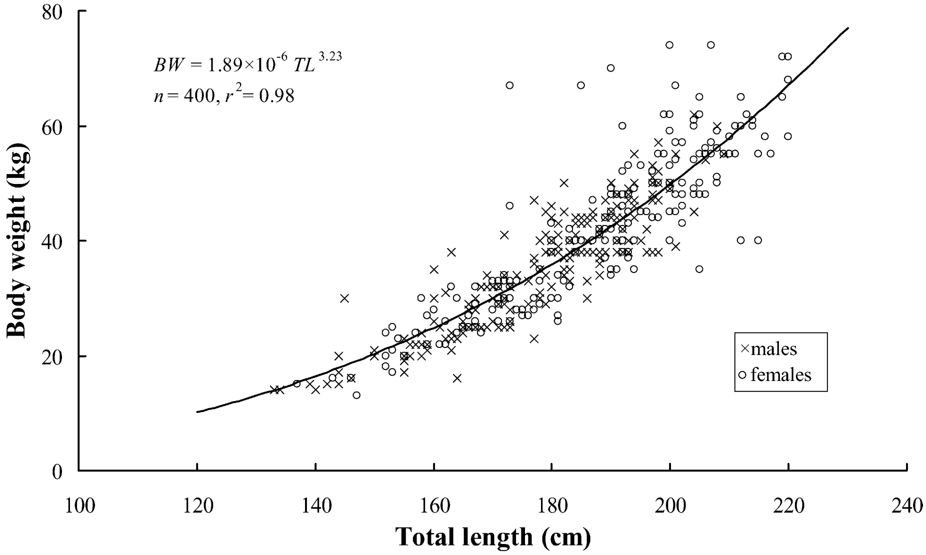

Fig. 6. Relationship between body weight and total length of *C. plumbeus* from Taiwan.

important to those species that are vulnerable to high fishing effort. But many problems could arise in estimating age and growth patterns of large size and long longevity fish species. With sharks, it could be difficult to obtain sufficient individuals of all size and age classes, due to the high cost, fishing method and time involved (Brothers, 1983). Although sandbar sharks can be found in northeastern Taiwan waters throughout the year, during May through July most fishermen from this area change their fishing gear or fishing ground to target high value species (e.g., *Makaira mazara*, *Tetrapterus audax*, *Thunnus albacares*, *T. thynnus*, *Coryphaena hippurus*). This situation is the major reason for the increased difficulty of obtaining the sufficient sample sizes during the summer season. Moreover, in Taiwan because two or more sharks of similar size are often weighed together in markets, furthermore, market fish are often piled on each other after weighing, causing difficulty in taking length measurements accurately. Thus the regression curves in this study showed relatively low correlations.

According to fishermen, juvenile sandbar shark (<120 cm, calculated age 3) can be caught either by longline or bottom trawler below depths of 20–30 m. Immature (especially <150 cm, calculated age 5) specimens were rarely collected. We conclude that the pups of sandbar sharks were not born at the fishing grounds.

Casey et al. (1985) used analysis of growth zones in vertebrae, growth of aquarium specimens, length–frequencies and tag returns to study the age and growth of sandbar sharks from the western North Atlantic, and provided compelling evidence showing close agreement of age and growth estimates. Casey and Natanson (1992) indicated that the growth rate could be much slower than the results obtained from the above methods based on their tagging experiments. Therefore, Casey et al. (1985) may have bias in the use of any one method as the sole means of ageing large sharks.

Of the 448 vertebrae examined, 32 (7.1%) were rejected as being deformed. This may be a shortcoming of taking the vertebrae from the caudal peduncle. Centra of the caudal peduncle are weakest when the shark is young, and the irregular vertebrae may be caused by attacks from predators. No obvious differences were found in these sharks compared to normal specimens and no specimen was collected with all its vertebrae irregularly shaped. Thus we inferred that these events happened when the fish were young.

One possible source of error in reading vertebrae is in distinguishing between the birth annulus and the first annulus (formed in December). Not all the vertebrae we observed had a distinct birth annulus; the first annulus may have been mistaken as a birthmark. The back-calculated length at birth was 80.5 and 85.8 cm for females and males, higher than the mean length (60–65 cm) of the embryos that were near full term.

Vertebral rings occur systematically as length increases. Their formation is probably more directly related to factors other than size (Pratt and Casey, 1983). In several age studies, year marks form in summer (Allen and Wintner, 2002; Natanson et al., 1999; Simpfendorfer et al., 2002; Wintner et al., 2002). Our analysis indicates that the year marks are deposited once a year in mid-winter. This phenomenon was also found in many carcharhinid species such as *Carcharhinus brevipinna* (Branstetter, 1987a), *C. falciformis* (Branstetter, 1987b), *C. leucas* (Branstetter and Stiles, 1987), *C. limbatus* (Branstetter, 1987a) and *Sphyearna lewini* (Branstetter, 1987b). Casey et al. (1985) set January as the midpoint of band deposition for *C. plumbeus*, which coincided with opaque band deposition in from the western North Atlantic and two studies cite “spring” as the time of opaque band deposition in *Mustelus manazo* (Tanaka and Mizue, 1979) and *Prionace glauca* (Stevens, 1975).

As in this study, most work on age and growth verification of sharks has indicated one opaque band and one translucent band formed annually in the centra (Cailliet et al., 1986). However, some species may produce two band pairs annually (e.g., *Cetorhinus maximus*; Parker and Stott, 1965) and Natanson (unpubl.) has found no regular periodicity for band formation in *Squatina californica*. Moreover, the same species captured from different areas may show different band formation. For example, *S. lewini*, from North Carolina and the northeastern Gulf of Mexico deposit one band annually in the centra (Branstetter, 1987b; Schwartz, 1983) but the same species captured in northeastern Taiwan waters produce two band pairs annually (Chen et al., 1990).

Factors that mediate temporal periodicity of calcium deposition in elasmobranch centra are not known. Change in temperature and diet and stress-related activity such as migration have been suggested (Stevens, 1975; Pratt and Casey, 1983). In northern Taiwanese waters the lowest water temperatures (c.18 °C) occur from December to February, so annulus formation in December may be correlated with that lower temperature.

Estimates by Casey et al. (1985) of K values for *C. plumbeus* were 0.05 year^{-1} (female) and 0.04 year^{-1} (male), which are substantially lower than our estimates of 0.17 year^{-1} based on observed data. These K values represent Taiwanese sandbar shark have a faster growth rate, while those from the western North Atlantic are relatively slow growing. The higher temperature in Taiwan waters might be the major explanation on the faster growth rate of Taiwanese sandbar shark compared with the North Atlantic one.

Young sharks are more susceptible to predation than old ones, and depending on the habitat used by the young, early growth rates may have a large effect on survival. The estimated K value derived from VBGE in this study is similar to many other carcharinids. New borns of both sexes increase in length by approximately 1/4 from length at birth in the first year of life. This relatively rapid growth would increase swimming efficiency and speed, thus increasing survival chances (Thompson and Simanek, 1977). More coastal and slow growing species, such as *S. lewini* grows very slowly (K = 0.07), produces numerous young (>30) which may help to offset high mortality rates (Branstetter, 1987b). The sandbar shark in this study showed a moderate K value but give birth to relativity large young (60–65 cm). Hence, this species produces on average only 7.4 pups per gestation (Joung and Chen, 1995), but the neonates may bear a relatively lower mortality.

The growth rate for Taiwan-caught sandbar shark was 22.2 cm/year in the first year, 18.7–11.2 cm/year for ages 2–5, and 9.5–4.8 cm/year for ages 6–10 were recorded. Casey’s specimens from the western North Atlantic seem to grow slower than those in Taiwanese waters, and have demonstrated average growth rates of 20, 10–6 and 9–7 cm/year, respectively (Casey et al., 1985).

The L_∞ values estimated from observed and back-calculated data was 210.0 cm, which was smaller than the 250.0 cm TL of Casey et al. (1985). Age at sexual maturity for Taiwanese sandbar shark is also younger than that reported for Casey's specimens from the western North Atlantic, where males matured at 13 year and females at 12 year.

The data indicate that the sandbar shark is long-lived with a relatively low fecundity, and natural mortality of the young may be high. As with many other elasmobranchs this combination of *K*-selection characteristic may result in an overexploitation of this species under increased recreational and commercial fishing pressure (Musick and Colvocoresses, 1986). The catches of sandbar sharks and their sizes have decreased in northeastern Taiwan waters in last few years (Chen et al., 1996). Therefore, the phenomenon of increasing growth rate in sandbar shark at juvenile ages, which happened in the western North Atlantic after population depletion (Sminkey and Musick, 1995), may also occur in Taiwanese sandbar shark in the future.

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