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Age, Growth, and Reproduction of the Spinner Shark, *Carcharhinus brevipinna*, in the Northeastern Waters of Taiwan

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Shoou-Jeng Joung, Yih-Yia Liao, Kwang-Ming Liu, Che-Tsung Chen, and Len-Chi Leu (2005) Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the northeastern waters of Taiwan. *Zoological Studies* **44**(1): 102-110. Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1938), are described from 383 specimens (193 females and 190 males) collected from Oct. 1995 to Sep. 1996 in waters off northeastern Taiwan. Annuli in precaudal vertebrae form once a year and numbered up to 21 and 17 for females and males, respectively. The von Bertalanffy growth parameters estimates, based on age and back-calculated length data, were as follows: asymptotic (L_∞) = 288.2 cm total length (TL), growth coefficient (k) = 0.151/yr, age at 0 length (t_0) = -1.988 yr for females; and L_∞= 257.4 cm TL, k = 0.203/yr, t_0 = -1.709 yr for males. The growth rate for females was estimated to be 29.9 cm for the 1st year, and then decreased from 25.7 to 16.3 cm/yr for years 2~5, from 14.0 to 7.7 cm/yr for years 6~10, and from 6.6 to 1.7 cm/yr for years 11~20. Growth rate for males was 33.4 cm/yr for the 1st year, then decreased from 27.3 to 14.8 cm/yr for years 2~5, from 12.1 to 5.4 cm/yr for years 6~10, and from 4.4 to 0.7 cm/yr for years 11~20. The mean total lengths at maturity were estimated to be 222.5 and 220.5 cm for females and males, which corresponded to 7.8 and 7.9 yr, respectively. Evidence suggested a 2 yr reproductive cycle in females, with a gestation period of 10~12 mo. *Carcharhinus brevipinna* is viviparous, with a yolk-sac placenta. The number of embryos per litter (N) was 3~14 (mean, 8.5), and it increased with the size of the mother (N = -45.06 + 0.198TL). TL at birth was estimated to be 65~70 cm , and the sex ratio of embryos was 1: 1.
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Key words: Age and growth, Reproduction, Spinner shark, Taiwan.

The spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1938) is common in coastal warm-temperate, subtropical, and tropical regions worldwide (Compagno 1984). It is found abundantly off northeastern Taiwan, representing an important species for the commercial shark fishery in this area. According to catch statistics from the Nanfangao fish market, the biggest landing port for the shark fishery in northeastern Taiwan, annual landing of this species is about 115 tons, and ranks 6th (6%) in weight among all shark species in the region. This species is caught mostly in Oct. to Apr. when waters are cooler in this region (Liu et al. 2001).

To date, biological information on the spinner shark is limited. Clark and von Schmidt (1965) documented the reproductive biology of this species in the Northwest Atlantic. Branstetter (1982) described the key characters of species identification for *C. brevipinna* and *C. limtatus*. Age, growth, and reproduction estimates are available for the northwestern Atlantic (Branstetter

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1987) and South Indian Ocean (Allen and Cliff 2000), but are lacking for the northwestern Pacific. Such life-history information is very important for stock assessment and fisheries management of this species. Estimates of size or age at maturity are essential information for age- and size-structured models, such as the spawner per recruit model (Katsukawa et al. 1999) and other size- or age-structured models (Deriso et al. 1985, Quinn II et al. 1990).

The objective of this study was to provide the 1st detailed information concerning aspects of the fisheries biology, including age, growth, size at maturity, sex ratio, reproductive season, and gestation period for the spinner shark in waters off northeastern Taiwan. The results of this study can be used as biological input parameters for further evaluation of the spinner stock in the western North Pacific.

MATERIALS AND METHODS

In total, 383 spinner sharks were examined for this study (Table 1). All specimens were caught by the commercial long-line fishery in the waters off northeastern Taiwan between Oct. 1995 and Sept. 1996 (Fig. 1).

Measurements (in cm) were taken of total length (TL), fork length (FL), and precaudal length (PCL). Methods follow Branstetter and Stiles (1987) and Joung and Chen (1995). Total length is used throughout this report. Fork length and precaudal length were estimated from those measurements to facilitate comparison with the literature using the following formulae (Liu et al. 1998):

in females,

TL = 19.27 + 1.21PCL (n = 111, r^2 = 0.96, p < 0.05), and

TL =13.30 + 1.69FL (n = 111, r^2 = 0.89, p < 0.05); and

in males,

TL =11.55 + 1.27PCL (n = 82, r^2 = 0.94, p < 0.05), and

TL = 26.30 + 1.56FL (n = 82, r^2 = 0.81, p < 0.05).

Body weight, reproductive status, clasper length (CL) measured from the cloaca to the tip of the clasper, the condition of the uteri, ovarian egg diameter, and the number of eggs were also recorded. When pregnant females were examined, embryos were counted, sexed, and measured for total length. In addition, precaudal vertebrae were removed for age determination.

Sexual maturity of males was judged using the following criteria: (1) the abrupt change in the relationship between CL and TL (Holden and Raitt 1974, Pratt 1979); (2) the clasper and rhipidon fully formed and spread open on a fresh specimen

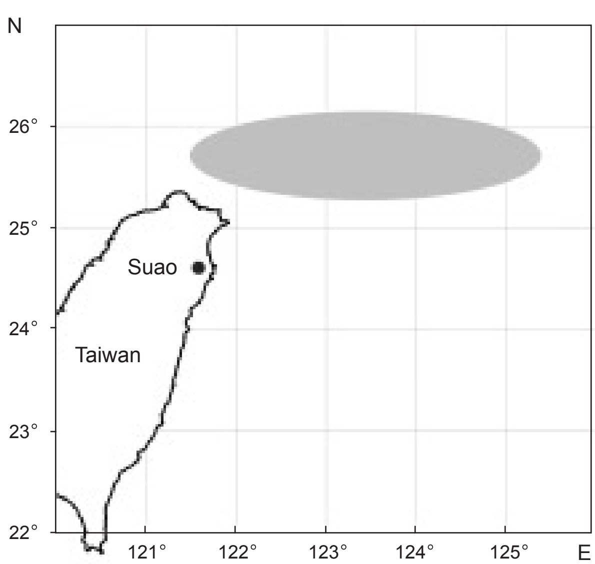

Fig. 1. Sampling area of *Carcharhinus brevipinna* in this study.

Table 1. Number of specimens of *Carcharhinus brevipinna* at different maturation stages in this study

TL of specimen (cm)	Female		Male	
	Immature	mature	immature	mature
110~120	2		1	
121~130	0		3	
131~140	6		6	
141~150	3		3	
151~160	12		2	
161~170	14		16	
171~180	17		9	
181~190	15		14	
191~200	13		13	
201~210	9		7	
211~220	6	1	8	4
221~230	3	6	6	12
231~240		14	2	24
241~250		12		28
251~260		17		24
261~270		17		5
271~280		12		1
281~290		5		0
291~300		8		1
301~310		1		1
Total	100	93	90	100

(Clark and von Schmidt 1965, Pratt 1979); (3) the base of the clasper easily rotated such that the clasper can be directed anteriorly (Clark and von Schmidt 1965); (4) stem cartilage having become hardened or calcified when mature (Springer 1960); and (5) the presence of male sexual products (Kauffman 1950). Sexual maturity of females was judged using the following criteria: (1) immature - ovaries thin and with a homogenous cellular appearance throughout the gonads, ova < 15 mm in diameter, uteri threadlike, flaccid and relatively indistinct from the oviducts; and (2) mature - ovary with large well-yolked eggs greater than 15 mm in diameter, uteri well developed, or embryos found in uteri (Liu et al. 1999).

The size at birth was estimated from the observed maximum size of embryos and the minimum size of captured free-swimming individuals. The mean size at 1st maturity was defined to be the length at which 50% of the individuals of each sex were mature. The logistic model, $Y = 1/(1 + e^{-(a + bX)})$ (King 1995) was used to describe the relationship between proportions of mature fish (Y) in each length interval and for each fork length (X) based on 193 and 190 specimens of females and males, respectively. Mean size at 1st maturity was then obtained by substituting $Y = 0.5$ in above equation. The X^2 test was used to examine the homogeneity of the sex ratio.

Vertebrae from 208 sharks (119 females and 89 males; Table 2) were used for age determination. Samples from 2 specimens (both 260 cm TL) were used to compare variations in banding patterns from vertebral centra at different locations within specimens. Precaudal vertebrae had the same annulus counts as did vertebrae located under the 1st dorsal fin; thus precaudal vertebrae were used for age analysis in this study because these vertebrae were readily available at the market. Vertebrae were rinsed in 8%~10% KOH for 8~12 h to remove connective tissue, washed in running water for another 24 h, and then air-dried.

Cleaned centra were sectioned along the longitudinal plane in 100 μm thicknesses with a low-speed saw. To facilitate cutting, centra were paraffin-impregnated for 12 h prior to sectioning, and were held with a crescent wrench while cutting.

Annuli were counted without prior knowledge of the length of the specimens. Counts were only accepted if both counts by 2 different readers were in agreement. If the estimated number of annuli differed by 1 annulus, then the centrum was recounted. Following previous studies, counts that differed by 2 or more annuli were rejected (Chen et al. 1990). Distances from the focus to the outer edge of each annulus, and to the dorsal radius, as well as marginal increments, were measured on a line from the focus through the center of the intermedialia to the centrum edge.

The time of annulus formation was estimated from monthly changes in the marginal increment (MI), using the following equation (Liu et al. 1998):

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

where R is the centrum radius, and r_n and r_{n-1} are the radius of the ultimate and penultimate annuli, respectively. The relationship between the centrum radius (R) and TL was estimated using a curvilinear regression analysis. The radius for

Table 2. Specimens used for the age and growth analyses in this study

Month Year	No. of specimens	Female Range of TL (cm)	No. of specimens	Male Range of TL (cm)
Oct. 1995	1	253	0	-
Nov. 1995	5	235~265	8	182~260
Dec. 1995	37	166~289	19	163~262
Jan. 1996	10	164~273	13	133~238
Feb. 1996	7	182~267	12	164~251
Mar. 1996	20	131~276	10	125~231
Apr. 1996	10	130~227	7	128~242
May 1996	16	225~295	5	178~261
June 1996	6	278~298	0	-
July 1996	4	153~265	0	-
Aug. 1996	3	170~213	3	221~265
Sept. 1996	5	169~299	12	178~304
Total	119	130~299	89	125~304

each complete band pair was then used to back-calculate the TL of a shark at each band.

The growth of spinner sharks was described using the von Bertalanffy growth equation (VBGE). The NLIN procedure of the statistical package, SAS (North Carolina, USA), was used to estimate the parameters of VBGE as follows (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.

The growth rates at different stages were estimated from the VBGE. The relationship between body weight (W) and total length was also determined for both males and females. An analysis of covariance was used to compare weight-length relationships between sexes.

RESULTS

The onset of sexual maturity in the male spinner shark appeared to occur at about 210~220 cm TL (Table 1). Of the 190 males examined, 82 of 86 specimens of < 220 cm TL with soft claspers were considered immature. Ninety-six of the 104 specimens of > 220 cm TL with rigid claspers were considered mature (Table 1). The logistic curve describing the relationship between the proportion of mature males (Y) in each length interval and TL was estimated to be $Y = 1/[1+e^{(37.68-0.171X)}]$ (n = 190, $p < 0.05$). The mean size at 1st maturity was estimated to be 220.5 cm TL when Y = 0.5 was substituted into the above equation.

The onset of sexual maturity in female spinner sharks appeared to occur at a TL of about 210~220 cm (Table 1). Of the 193 females examined, 97 of 98 specimens of < 220 cm TL with thin ovaries, threadlike uteri, and a flaccid oviduct were considered immature. Ninety-two of 95 specimens of > 220 cm TL with eggs > 15 mm in diameter and well-developed uteri thus were considered mature (Table 1). The logistic curve for mature females was estimated to be $Y = 1/[1+e^{(58.42-0.263X)}]$ (n = 193, $p < 0.05$). The mean size at 1st maturity was estimated to be 222.5 cm TL. In the females we examined, only the right ovary developed, whereas both uteri appeared functional.

The number of embryos per litter ranged from 3 to 14, with a mean of 8.5. The sex ratio was 1: 1 (89 for each sex) for 178 embryos found in 21 litters. The relationship between the total number of embryos (N) and total length of the mother could be described by the linear regression equation (Fig. 3): N = -45.062 + 0.198TL (n = 21). Although this suggests that the fecundity is related to the size of the mother, the relationship was not particularly strong (r^2 = 0.68).

No embryos were found in Oct., Nov., Dec., or Jan., although some mature sharks had fertilized eggs in their uteri in Dec. and Jan. After 10~12 mo of development, most embryos had reached a total length of around 65~70 cm, at which size they could readily be separated from the placenta, suggesting that they were full-term and ready to be born. As pups are usually born after Sept., we estimated the gestation period to be 10~12 mo (Fig. 3).

Significant curvilinear relationships were found between the centrum radius (R) and total length (TL) for 82 females and 111 males (Fig. 4): females TL = $33.78R^{0.778}$ (n = 82, r^2 = 0.84); males TL = $30.09R^{0.833}$ (n = 111, r^2 = 0.83). The curvilinear forms are probably related to the slowing of vertebral growth in the caudal region of larger

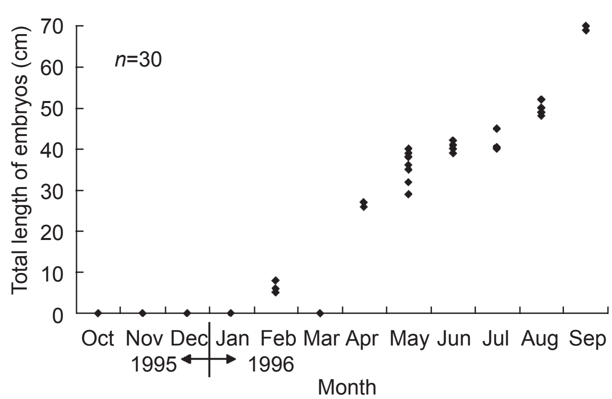

Fig. 2. Monthly growth of embryos in female *Carcharhinus brevipinna*.

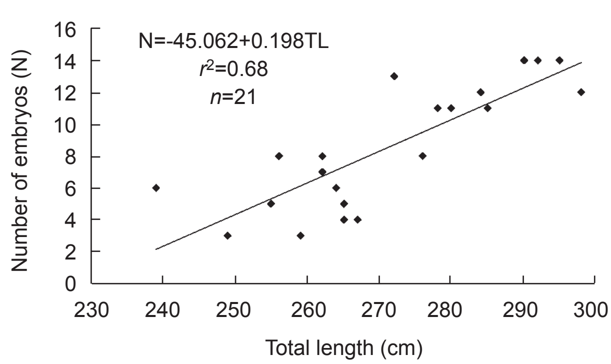

Fig. 3. Relationship between the number of embryos and the total length of *Carcharhinus brevipinna* females.

sharks.

Relationships between body weight (W) and total length were described as follows:
in females,
W = 3x10^{-6}TL$^{3.144}$ (n = 111, r^2 = 0.89) (Fig. 5), and
in males,
W = 8x10^{-6}TL$^{2.943}$ (n = 82, r^2 = 0.90).

An analysis of the covariance of the logarithmic weight and length suggested that the relationship between sexes significantly differed at the 5% level.

Monthly changes in vertebral MI appeared to peak at 0.96 in Nov. for females followed by an abrupt decrease to 0.21 in Jan. (Fig. 6). A similar trend was also shown for males, suggesting that an annulus formed once a year between Nov. and Jan. in both sexes.

No annulus was found in the centra of the largest embryo which was collected during Sep. Although no juveniles bearing a single annulus were captured, centra of several juveniles about 120~130 cm in TL caught between Jan. and Apr. did, however, exhibit 2 annuli. It is therefore reasonable to assume that the birth mark was formed in the 1st Dec. (0.167 yr) after birth (in Oct.), and the age at formation of the 1st annulus was 1.167 yr, the 2nd was 2.167 yr, the 3rd was 3.167 yr, and so on.

A mean annulus radius was calculated for each sex. Mean radii for each annulus were summed. Lee's phenomenon (Lee 1912) was exhibited by this spinner shark data set. These annulus radius values were used in TL-R curvilinear equations to back-calculate the lengths at the time of annulus formation (Table 3).

Back-calculated lengths for ultimate annulus formation at different ages (diagonal column, Table 3) were used to calculate the predicted lengths in the VBGE. The estimated parameters were k = 0.151/yr, L_∞= 288.2 cm, and t_0 = -1.998 yr for females, and k = 0.203/yr, L_∞= 257.4 cm, and t_0 = -1.709 yr for males. A von Bertalanffy curve obtained from back-calculated length-at-age data was close to the observed data (Fig. 7). Length at birth (L_0) was estimated to be 75 cm. Growth during the 1st year was estimated to be 29.9 cm for females and 33.4 cm for males, then it decreased from 25.7 to 16.3 cm/yr for females and from 27.3

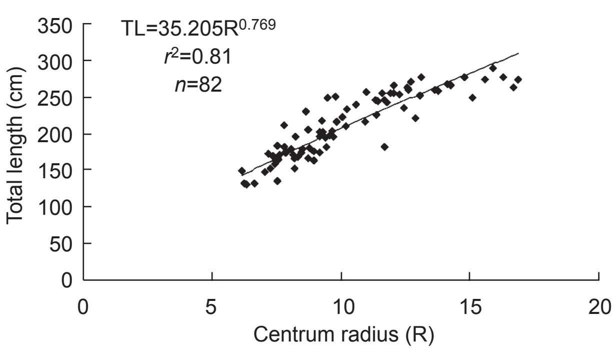

Fig. 4. Relationship between the total length (TL) and the centrum radius (R) of female *Carcharhinus brevipinna*.

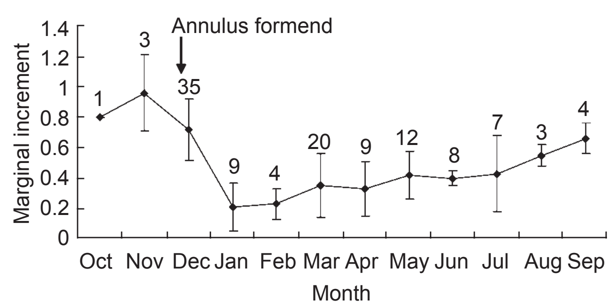

Fig. 6. Monthly changes in the marginal increments of *Carcharhinus brevipinna* females. Numbers above each mean indicate the sample size, and vertical bars indicate ± 1 SD.

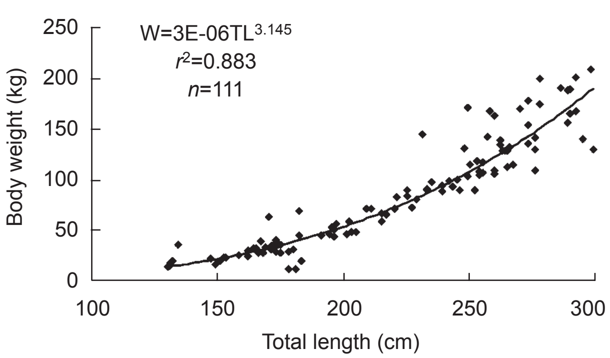

Fig. 5. Relationship between the body weight (W) and total length (TL) of *Carcharhinus brevipinna* females.

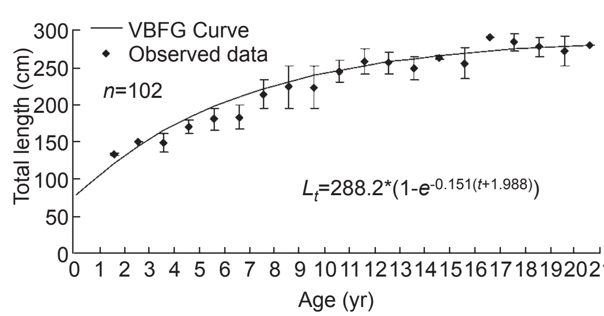

Fig. 7. von Bertalanffy growth curve for *Carcharhinus brevipinna* females in this study. Vertical bars indicate ± 1 SD.

Table 3. Back-calculated total length at time of annulus formation of *Carcharhinus brevipinna* females

		Total length (cm)																				
Annulus	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	0	81																				
2	4	81	117																			
3	6	77	102	129																		
4	12	83	113	134	159																	
5	10	80	110	131	150	170																
6	11	74	100	122	140	156	175															
7	10	81	108	131	151	168	185	204														
8	3	80	110	135	156	176	193	206	221													
9	7	71	98	120	140	158	174	188	202	219												
10	6	82	110	134	157	178	195	211	224	236	248											
11	4	74	98	118	141	161	178	191	211	227	240	253										
12	3	78	107	136	156	173	190	204	216	226	235	242	250									
13	6	77	105	126	147	164	182	195	206	216	225	232	239	246								
14	4	76	100	120	137	155	174	191	206	218	228	235	245	252	259							
15	2	74	103	136	144	166	183	197	208	219	227	233	239	245	251	261						
16	1	83	101	124	142	160	174	187	198	210	221	233	245	259	270	279	284					
17	3	67	97	120	139	157	174	187	200	211	223	234	245	254	261	267	272	278				
18	4	77	96	114	133	151	166	180	193	202	210	218	226	233	240	245	250	256	262			
19	4	66	86	103	119	134	147	161	174	185	194	205	215	224	233	240	247	253	259	265		
20	1	68	95	108	119	133	146	159	173	186	198	209	219	228	235	242	249	256	262	268	276	
21	1	67	80	99	118	137	149	162	177	188	200	210	220	227	234	242	248	255	260	265	270	274
Weighted	mean	76	102	123	142	159	174	188	201	211	221	228	234	241	248	254	258	260	261	266	273	274

to 14.8 cm/yr for males for years 2~5, from 14.0 to 7.7 cm/yr for females and from 12.1 to 5.4 cm/yr for males for years 6~10, and from 6.6 to 1.7 cm/yr for females and from 4.4 to 0.7 cm/yr for males for years 11~20.

The mean size at 1st maturity for females was estimated to be 222.5 cm TL, and this length corresponded to an age of 7.8 yr when substituted into the VBGE. Males matured at 220.5 cm TL which corresponded to 7.9 yr. The largest immature male was 238 cm TL and was aged at 11.0 yr, while the smallest mature male was 211 cm TL and was aged at 6.7 yr in this study.

DISCUSSION

In this study, we found that useful ways to assess maturity for spinner shark males were clasper morphology and hardness. Pratt (1979) and Joung and Chen (1995) also noted the utility of these features in assessing male sexual maturity for other shark species.

Ovarian eggs in *Carcharhinus brevipinna* do not continue to ripen during gestation. Joung and Chen (1995) and Tanaka et al. (1990) noted the same condition in the sandbar shark, *C. plumbeus*, and frilled shark, *Clamydoselachus anguineus*. Tanaka et al. (1990) suggested that in the case of the frilled shark, there was simply no room for ovarian eggs to develop, when all the available space was taken up by the liver, stomach, and developing embryos. Although this may hold for the frilled shark, it is not suitable for application to the spinner shark because the size of its fully developed ovarian eggs are considerably smaller (< 42 mm) than that of the frilled shark (100 mm). In general, egg size reflects the reproductive pattern of the species. For example, in *Scoliodon* and *Gymnura*, eggs are much smaller. Their developing embryos receive almost all of their nutrients via the placenta of trophonemata (Ranzi 1934). In *C. brevipinna*, developing embryos receive almost all of their nutrients via the placenta, as in other sharks of the genus *Carcharhinus* (Joung and Chen 1995).

Wourms (1977) categorized 3 basic types of reproductive cycles: (1) reproduction occurring throughout the year; (2) a partially defined annual cycle with 1 or 2 peaks during the year; and (3) a well-defined annual or biennial cycle. The 1st category consists of those species that are either reproductively active throughout the year or for most parts of the year. Several examples of this reproductive strategy were documented by Chen et al. (1996) for *Galeus sauteri* and Liu et al. (1999) for *Alopias pelagicus* from northeastern Taiwan, the latter of which appears to breed throughout the year. In this study, the spinner shark would appear to be an example of the 3rd type of reproductive pattern, in that it shows a distinct biennial cycle. A similar finding was also documented for the spinner shark in the southern Indian Ocean (Allen and Cliff 2000) and other *Carcharhinus* species such as *C. plumbeus* (Joung and Chen 1995) and *C. falciformis* (Oshitani et al. 2003). The gestation period of the spinner shark was herein estimated to be 10~12 mo. During the breeding season (Oct. to Dec.), we found that approximately 50% of mature females were pregnant. In other words, 2 distinct reproductive groups were apparent: the 1st group had full-term embryos in the uterus and undeveloped ovaries, whereas the 2nd group had no ripe ova with empty but expanded and flaccid uteri. This suggests that *C. brevipinna* has a resting stage for 1 yr of its 2 yr reproductive cycle. Although Allen and Cliff (2000) suggested a gestation period of 13~18 mo for spinner sharks in South Indian Ocean, they concluded that a 2 yr reproductive cycle exists in females. Similar findings were also reported for spinner sharks in the northwestern Atlantic (Branstetter 1987), the sandbar shark, *Carcharhinus plumbeus* (Springer 1960, Cliff et al. 1988), bull shark, *C. leucas* (Cliff and Dudley 1991), bronze whaler shark, *C. bradryurus* (Walter and Ebert 1991), and dusky shark, *C. obscurus* (Natason and Kohler 1996).

Spinner sharks are abundant in the coastal waters along northeastern Taiwan, especially between Nov. and May (Liu et al. 2001). The longline fishery rarely captures individuals smaller than 130 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: 1 (193: 190), although it varied from month to month. No significant difference from 1: 1 ($p > 0.05$) in the sex ratio was found in either the breeding (Oct. to Dec.) or non-breeding season (Jan. to Sept.). Springer (1960) noted that sexes are 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, the length observed in full-term embryos was 65~70 cm TL, which is comparable with that in the northwestern Atlantic of 60~70 cm

(Branstetter 1987), but is larger than that in the southern Indian Ocean at 50~60 cm (Allen and Cliff 2000). Many factors may have contributed to these discrepancies, and elucidation of the actual mechanisms requires further investigation.

Large neonates may benefit by enhanced prey capture and predator-escaping ability, thus increasing their survival chances after parturition (Branstetter 1990). Species with low fecundity always breed larger neonates, and the ratio of size at birth (L_b) and maximum observed length (L_{max}) are usually also high (Branstetter 1990). The L_b / L_{max} ratio in *Alopias superciliosus* is 0.32 (Chen et al. 1997) and 0.42~0.51 in *A. pelagicus* (Liu et al. 1999), which always has a litter size of 2, with 1 embryo in each uterus. In this study, the estimated litter size was 4~11 (mean = 8.5), which is close to that reported from the southern Indian Ocean with a mean of 9 (Allen and Cliff 2000). The L_b / L_{max} ratio for spinner sharks was estimated to be 0.22~0.23, which is comparable with that of *C. plumbeus* (0.27~0.31, Joung and Chen 1995) but smaller than those of *Alopias superciliosus* and *A. pelagicus*. Hence, the litter sizes of *C. brevipinna* and *C. plumbeus* are reasonably higher than those of thresher sharks because of smaller neonates and L_b / L_{max} ratios.

The size at sexual maturity of female spinner sharks as determined in this study is in keeping with Holden and Raitt's (1974) suggestion that the mean length at maturity (L_m) for female elasmobranches approximates 0.60~0.90 of the maximum observed length (L_{max}). The L_m / L_{max} ratio ranges from 0.5 to 0.95 for sharks, with most being between 0.65 and 0.8 (Holden 1974, Tanaka and Mizue 1979, Taniuchi et al. 1983). The L_m / L_{max} ratios were estimated to be 0.74~0.77 for females and 0.72~0.76 for males in this study, which were smaller than those reported in the northwestern Atlantic of 0.86 and 0.88 for females and males, respectively (Branstetter 1987). Nevertheless, the spinner shark falls in the category of a standard maturity pattern.

There are several possible explanations for annulus formation. A shortage of food, deprivation caused by migration, and changing temperatures may all be factors affecting its formation (Stevens 1973, Pratt and Casey 1983), but there are insufficient data to verify any specific cause in this study. However, the lowest water temperatures (18°C) occur in northern Taiwan waters from Dec. to the following Feb. Hence, the annulus being formed in Dec. suggests that it might be correlated with low water temperatures.

Branstetter (1987) categorized the *k* values as 0.05~0.10/yr for slowly growing species, 0.10~0.20/yr for species with average growth, and 0.20~0.50/yr for rapidly growing species. Based on these criteria, spinner sharks in Taiwan waters have a moderate growth rate. Similar patterns for *C. plumbeus* (k = 0.17/yr) and *C. falciformis* (k = 0.148/yr) in the Pacific Ocean were also reported (Oshitani et al. 2003, Joung et al. 2004 pers.). However, Branstetter (1987) reported that spinner sharks in the northwestern Atlantic have a fast growth rate (k = 0.212/yr). A small sample size (n = 14) and a lack of large specimens used by Branstetter (1987) may have led to an overestimation of k and underestimation of L_∞. Different environments could be another possible factor resulting in the differences.

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