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Age and Growth of the Scalloped Hammerhead, *Sphyrna lewini*, in Northeastern Taiwan Waters[1]

C. T. CHEN,[2] T. C. LEU,[2] S. J. JOUNG,[2] and N. C. H. LO[3]

ABSTRACT: Age and growth of the scalloped hammerhead, *Sphyrna lewini*, caught mostly by longline and harpoon in northeastern Taiwan waters from December 1984 to November 1985, were determined from annulus counts from 325 individuals. Translucent and opaque zones on vertebral centra were formed twice a year, in June and December. The von Bertalanffy growth curve parameters obtained using a nonlinear regression based on age and observed length were as follows: asymptotic length (L_∞) = 319.72 cm total length (TL), growth coefficient (K) = 0.249, age at zero length (t_0) = − 0.413 yr for females; and L_∞ = 320.59 cm TL, K = 0.222, t_0 = − 0.746 yr for males. Growth was apparently fast and varied among individuals. Growth rates for females were estimated to be 63 cm for the first year, 23–50 cm/yr for years 2–5, and 3–19 cm/yr for years 6–13. Growth rates for males was 54 cm for the first year, 22–42 cm/yr for years 2–5, and 11–18 cm/yr for years 6–8. Holden's method was applied to estimate growth parameters for purposes of comparison. Estimated age at maturity was 4.1 yr (210 cm TL) for females and 3.8 yr (198 cm TL) for males, based on the von Bertalanffy growth equation from back-calculated data. The largest female (331 cm TL) whose age was determined in this study was 14.0 yr old; the largest male (301 cm TL) was 10.6 yr old.

THE SCALLOPED HAMMERHEAD shark, *Sphyrna lewini*, is common in coastal warm temperate and tropical seas throughout much of the world (Compagno 1984) and is found in Taiwan waters. Catches from areas west and south of Taiwan are smaller than those from areas to the east (Chen et al. 1988). This species is commonly found from Pung Chia Island to Guei Shan Island (Figure 1) and is one of the most abundant species contributing to the commercial shark fishery of the northeastern waters of Taiwan (Chen et al. 1988). Based on data from the fish market in Nan Fan Ao near Suao city, located in northeastern Taiwan, 500 tons of scalloped hammerheads are landed per year, representing 25% of the total catch of sharks in this area and ranking this species first among all shark species caught. The total catch of scalloped hammerheads is valued at (U.S.) 1 million dollars per year. Sharks are among the most valuable food resources in Taiwan. However, because of their low reproductive rate sharks are extremely susceptible to overfishing (Holden 1974, 1977).

To ensure the continued abundance of scalloped hammerheads as a food source, the life history of the shark must be understood before instituting any fishing management methods. Chen et al. (1988) investigated the reproductive biology of scalloped hammerheads captured off Nan Fan Ao, but not age and growth. Clarke (1971) examined the growth of scalloped hammerheads by using tag-recaptured neonatals in Hawaii. Schwartz (1983) and Branstetter (1987*a*) noted the age and growth of scalloped hammerheads from North Carolina and the Gulf of Mexico using analyses of vertebral rings. Ageing methods for sharks were summarized by Schwartz (1983), but he did not verify annual ring formation in scalloped hammerheads. Branstet-

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[2] Graduate School of Fisheries, National Taiwan Ocean University, Keelung, Taiwan, Republic of China.

[3] Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, California 92038.

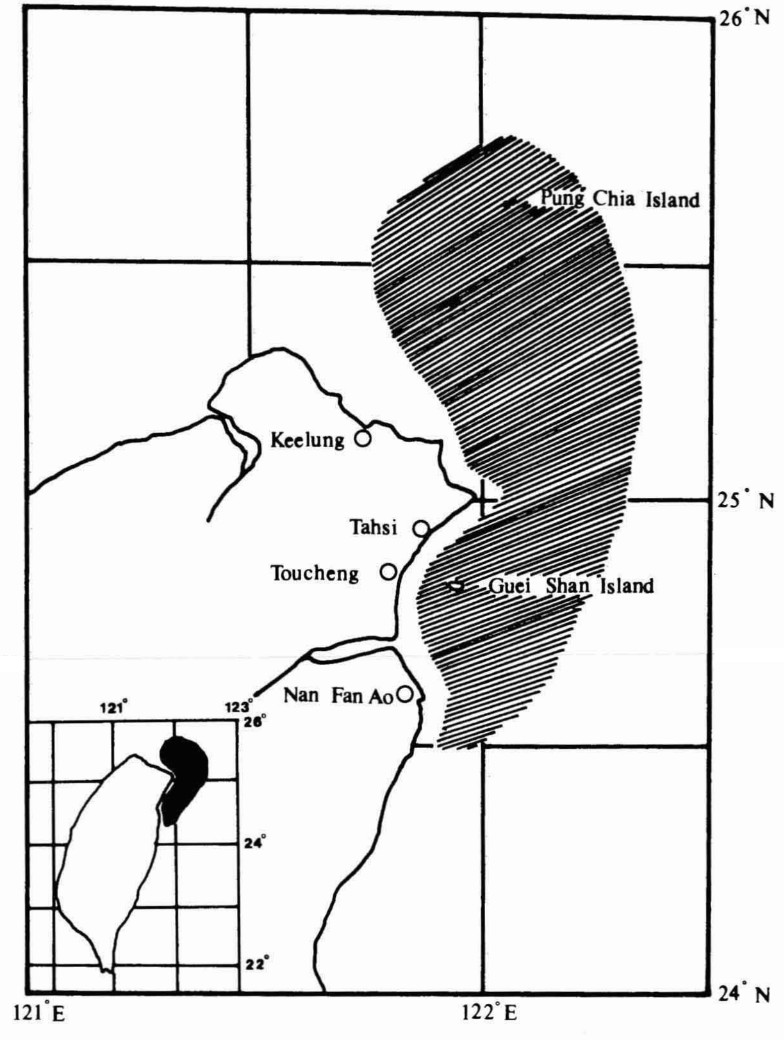

FIGURE 1. Sampling area of *S. lewini* off northeastern Taiwan.

ter (1987*a*) suggested annual formation of annuli for Gulf of Mexico specimens because of observations of increasing width in marginal increments along the centrum edge. Alternating opaque and translucent bands form in the vertebral centra of many elasmobranches during growth, and if a regular periodicity can be demonstrated for the formation of these bands throughout the life of the animal, they can be used to assess ages for individuals in the samples and to estimate growth rates for the population (Branstetter et al. 1987). Holden (1974) used reproductive data (i.e., maximum observed length, gestation period, and length at birth of embryo) to estimate the growth rate in elasmobranches. The vertebral rings (annuli) of Branstetter et al. (1987) and Holden's method (1974) were utilized in this study to analyze the age and growth of scalloped hammerheads captured in waters off northeastern Taiwan.

MATERIALS AND METHODS

Scalloped hammerheads (276 females and 49 males) were obtained from fish markets in Tashi and Nan Fan Ao between December

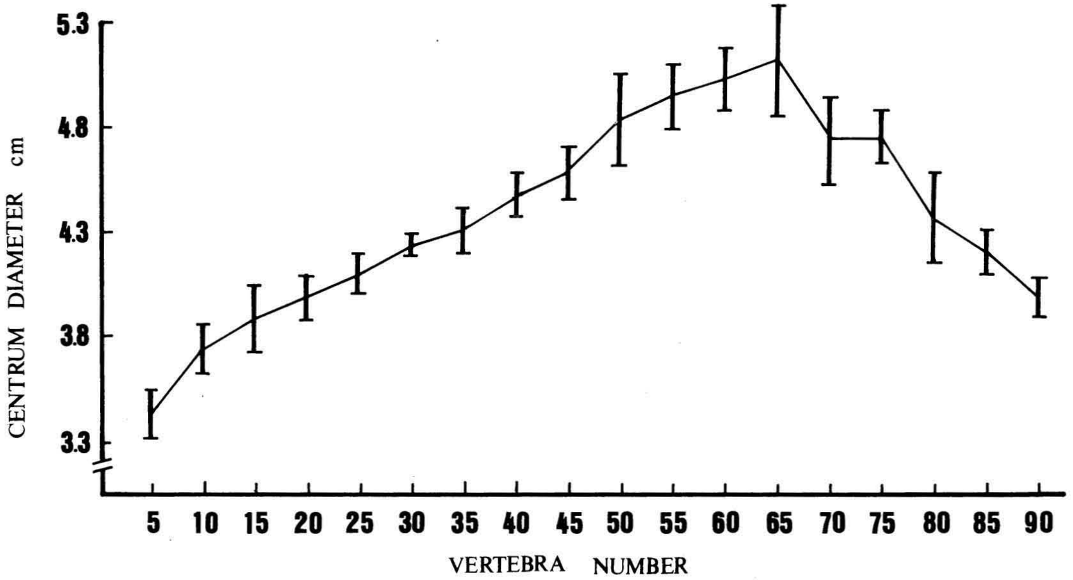

FIGURE 2. Average centrum diameter at different locations along the vertebral column of *S. lewini* from Taiwan. Four specimens were sampled: 47.2 cm, 49.2 cm, 49.5 cm, and 49.9 cm TL. Vertical bars indicate ± 1 SD.

1984 and November 1985. Larger sharks were captured mostly by longline and harpoon; small sharks were captured by trawl and longline. The primary fishing area was located off northeastern Taiwan (Figure 1). All sizes were included in the samples. Measurements were taken of total length (TL) (in cm) and weight (W) (in kg). Methods follow Chen et al. (1988). Total length is used throughout this report.

The 35th through 40th vertebrae, located just under the first dorsal fin, were sampled from each shark. These were the only vertebrae readily available in the market, and they are easy to locate under the first dorsal fin. Measurements of centra of the vertebrae just under the first dorsal fin were also used by Stevens (1975), Tanaka et al. (1978), and Wang and Chen (1982). To determine if these vertebral areas were suitable for age determination, four specimens of similar sizes were selected to compare variation in the radii of the centra. The size of the 35th through 40th vertebrae seems to be more stable (mean = 1.8, SE = 1.4, $n = 4$) (Figure 2) than that of vertebrae sampled elsewhere in the column. The vertebrae were prepared by (1) soaking the vertebrae for ca. 30 min in boiling water; (2) removing the connective tissue from the centrum; (3) sectioning along a longitudinal plane; (4) grinding along the central longitudinal axis until the centrum was ca. 0.2 mm thick; and (5) observing the section of centrum with a dissecting microscope at $10\times$ magnification by reflected light.

Measurements for back calculation were made with an ocular micrometer using transmitted light. Periodic marks appear to traverse the centra of the vertebrae of the scalloped hammerhead. These marks, viewed by transmitted light, are opaque. In this study they are termed annuli (annulus); they are analogous to the term "band" or "ring" used by other authors. Validation of annuli as time marks was not attempted. The radius of each centrum was measured from the focus to the outer margin (Figure 3). Measurements were made at least twice. Measurements were accepted if both measurements obtained were in agreement. If the estimated number of annuli differed by one annulus, then the centrum was remeasured. Measurements that differed by two or more annuli were rejected. Measurements of 57 of the 325 vertebrae were rejected.

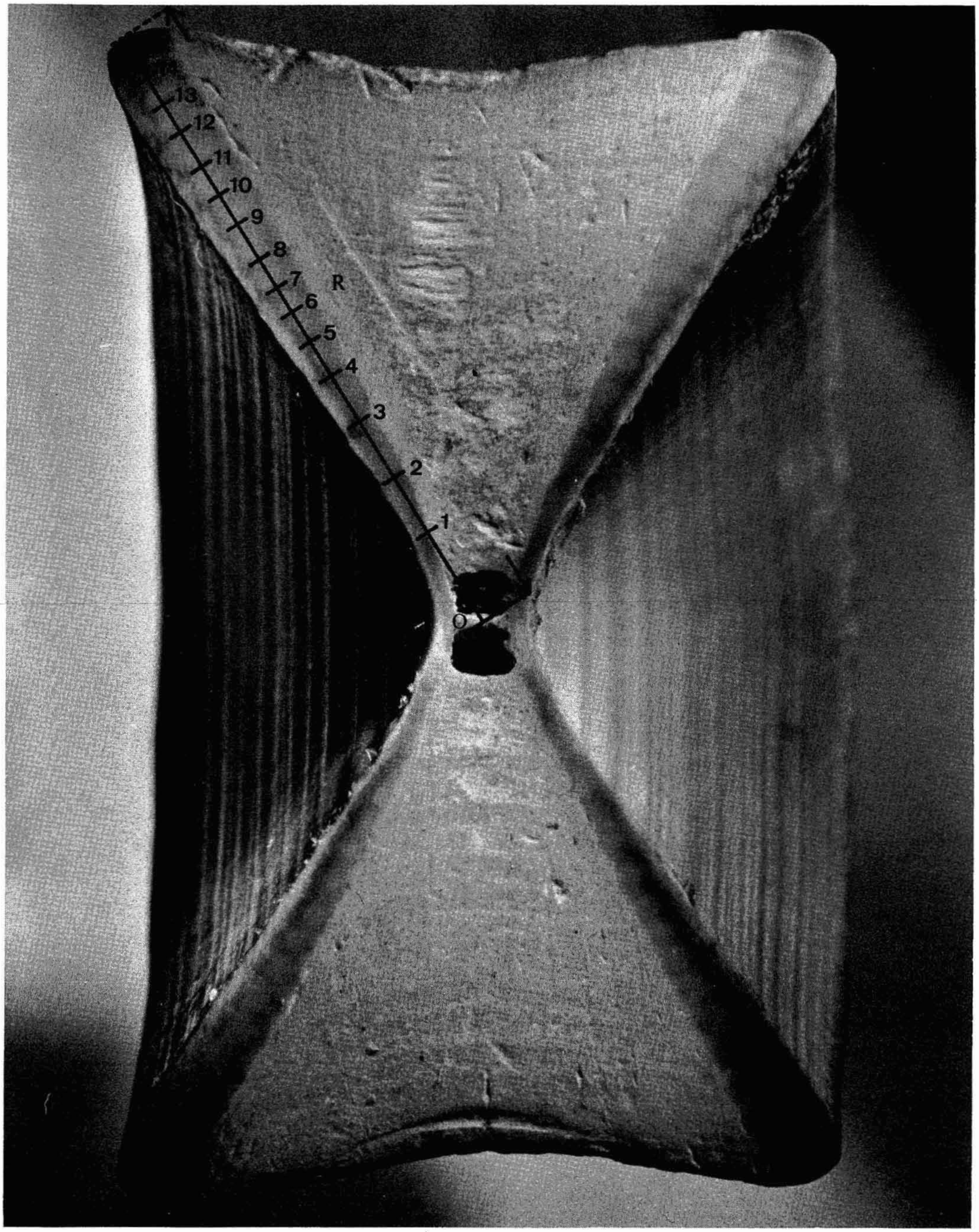

FIGURE 3. Longitudinal section of vertebra of *S. lewini* used for age determination. 1–14 = annulus marks; centrum radii were measured from focus (O) to outer margin of the vertebrae.

The time of annulus formation was estimated from monthly changes in the marginal increment (M.I.) using the following equation:

$$\text{M.I.} = (\text{R} - \text{r}_n)/(\text{r}_n - \text{r}_{n-1})$$

where R is the centrum radius and r_n and r_{n-1} are radii of the ultimate and penultimate annuli, respectively. The centrum radius and total length curvilinear equation were utilized to back calculate time of annulus formation.

The von Bertalanffy growth equation (VBGE) curve (Draper and Smith 1981) was selected as the growth model. The nonlinear regression PAR BMDP statistical package (Dixon et al. 1985) was used to obtain the parameter estimates of VBGE by using (1) observed length and age, and (2) the back-calculated length at the time of annulus formation and the age for each sex. The VBGE is as follows:

$$\text{L}_t = \text{L}_\infty \{1 - \exp[-K(t - t_0)]\}$$

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

In addition, Holden's method (1974) was used to obtain growth parameter estimates for comparative purposes. Holden's method requires the maximum observed length (L_{max}), gestation period (g) (= age at zero length), and length at birth (L_{g}) to estimate the growth coefficient K:

$$K = -\ln(1 - \text{L}_{\text{g}}/\text{L}_{\text{max}})/\text{g}$$

All of the growth rates were estimated from a computerized form of the VBGE.

The relationship of body weight and total length was also examined for males and females. An analysis of covariance was used to detect the possible difference in the weight-length relationship between the sexes.

RESULTS

Relationship between Centrum Radius and Total Length

A significant curvilinear relationship (Figure 4*a*,*b*) was found between the centrum radius (R) and total length (TL) for 226 females and 42 males: female: $\text{TL} = 18.833\ \text{R}^{0.9568}$ [$r = 0.984$, $n = 226$, 18.833 (SE = 0.1007), 0.9568 (SE = 0.0322)]; male: $\text{TL} = 20.361\ \text{R}^{0.9362}$ [$r = 0.993$, $n = 42$, 20.361 (SE = 0.1011), 0.9362 (SE = 0.049)]. Both curves pass through the origin. The curvilinear forms were probably related to slowing of vertebral growth in larger sharks.

Time of Annulus (Opaque Zone) Formation

The two smallest M.I. means for both immature and mature females occurred in June and in December (Figure 5). Thus an opaque zone for females occurred twice a year, the first in June and the second in December. We assumed that the opaque zone is a half-year annulus. Standard error was large because annulus growth for each individual was different, even in the same month. For example, in June some annuli were nearly formed (M.I. were large), and some had already been formed (M.I. were small). The time of annulus formation for males could be roughly estimated in spite of small sample size ($n = 42$) (Figure 5). As in females, males had two smaller M.I., in June and again in December, and we assumed that an opaque zone for males occurred twice a year.

No annulus was found in the centra of embryos during the breeding season (from May to July) (see Chen et al. 1988). Three juveniles (58 cm, 59 cm, and 60 cm) caught in October did, however, exhibit one annulus. It is therefore reasonable to assume that the first annulus is formed in June, immediately after birth. Hence the age of first annulus formation was at 0 yr, the second at 0.5 yr, the third at 1 yr, the fourth at 1.5 yr, and so on. Odd-numbered annuli formed between June and November, and even-numbered annuli formed between December and May (Table 1). This observation supports the conclusion that annuli form in June and December each year.

Back-calculated Length at Time of Annulus Formation

A mean annulus radius was calculated for each sex. Mean radii for each annulus were summed. It is obvious that Lee's (1912) phe-

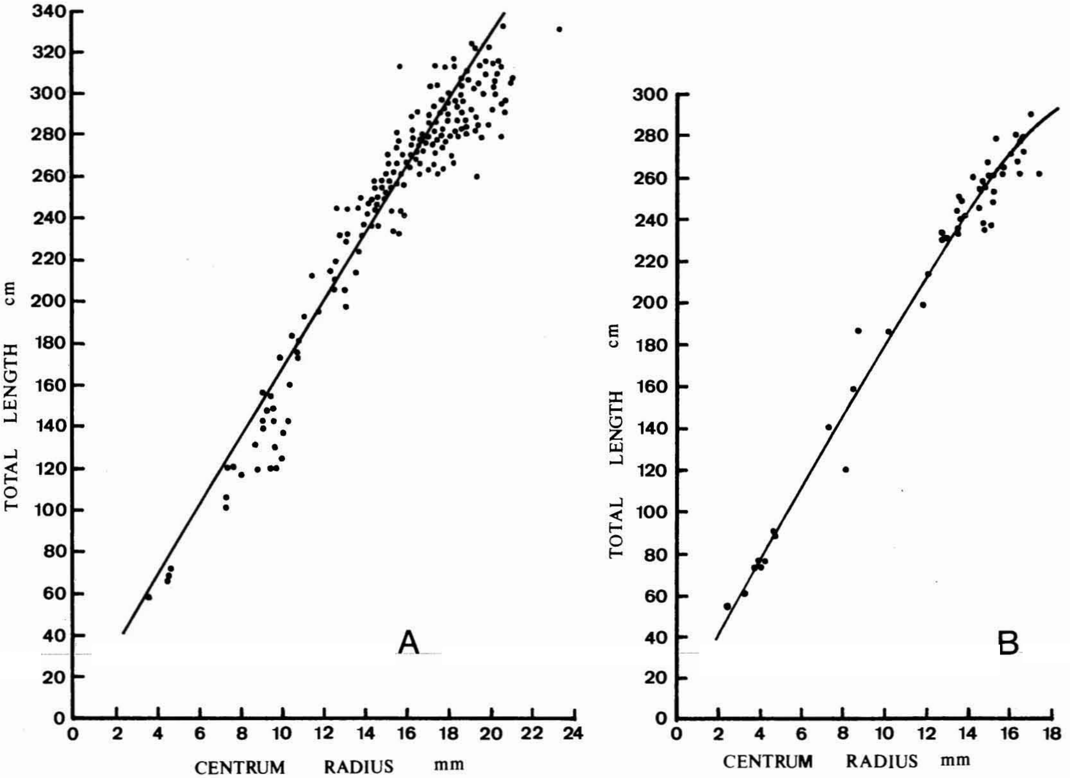

FIGURE 4. Relationship between total length (TL) and centrum radius (R) in *S. lewini* from Taiwan. *A*, females ($TL = 18.833R^{0.9568}$ [$r = 0.984$]); *B*, males ($TL = 20.361R^{0.9362}$ [$r = 0.993$]).

nomenon (the difference between calculated length and true length at earlier annuli is greater at younger ages [Rick 1958, 188]) does exist in the scalloped hammerhead. By putting those annuli radii values into TL-R curvilinear equations, back-calculated lengths at the time of annulus formation were calculated (Tables 2 and 3).

Estimation of Parameters in von Bertalanffy Growth Equations

NONLINEAR REGRESSION ESTIMATES. (1) Observed lengths at different ages were used to calculate the VBGE predicted lengths. The von Bertalanffy growth curves for both sexes fit the observed data relatively well (Figure 6), although some variations caused by few data and variable lengths at different ages were seen in young age groups. The parameter

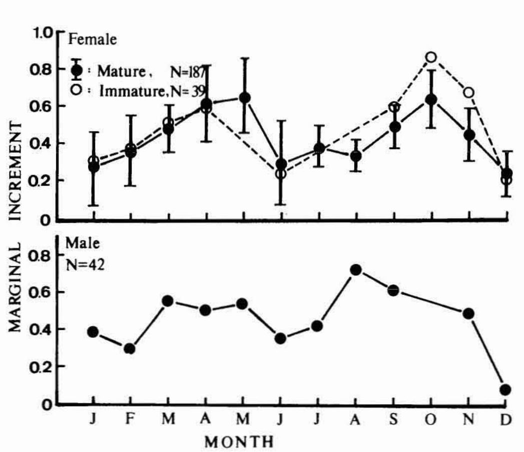

FIGURE 5. Monthly change of marginal increment of *S. lewini* from Taiwan. Vertical lines indicate ±1 SD. *Top*, females; *bottom*, males.

TABLE 1

NUMBER OF VISIBLE ANNULI OF *S. lewini* FROM TAIWAN (DOES NOT INCLUDE REJECTED VERTEBRAE) (*top*, FEMALE; *bottom*, MALE)

		ANNULUS GROUP																												
YEAR	MONTH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	TOTAL
1984	Dec						1					1	3				1						1							7
1985	Jan.			1	7	1	5		1		3	1	1		1				1		2		5		3					32
	Feb.		2												2		4		3		3		3		2		2			21
	Mar.		1		1										1		1		1		3		2				1			11
	Apr.												3		5		2		3		2		1		4		1			21
	May																3			2	4		3		1		2		1	16
	Jun.							1				2		4		1	1	3				1		2						15
	Jul.											2		4		4		2		4		1		1				1		19
	Aug.											3		7	1	2		5		1										19
	Sep.					1		1	4		1	1		3		3		1		4		1		1						21
	Oct.	1						1	2			1		3	1	4		3		1		2		3		1		1		24
	Nov.					1		1						3		4		3		3	1			2	1	1				20
Total		1	3	1	8	3	6	4	7	0	4	11	7	24	11	18	12	17	8	15	15	5	15	9	11	2	6	2	1	226

		ANNULUS GROUP																				
YEAR	MONTH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	TOTAL
1984	Dec.						1															1
1985	Jan.										1											1
	Feb.		2								1		1									4
	Mar.		1										1				1		2			5
	Apr.										1		1				1					3
	May														1		1				1	3
	Jun.										1	1		1	1			1				5
	Jul.		1	1					1				1	1		2		2				9
	Aug.									1		1										2
	Sep.							2				2										4
	Oct.	2										1										3
	Nov.					1				1												2
Total		2	4	1	—	1	1	2	1	2	4	5	4	2	2	2	3	3	2	—	1	42

TABLE 2

BACK-CALCULATED TOTAL LENGTH AT TIME OF ANNULUS FORMATION OF FEMALE *S. lewini* FROM TAIWAN

		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	22	23	24	25	26	27	28
1	1	45.3																											
2	3	52.2	72.1																										
3	1	53.9	66.7	76.9																									
4	8	69.9	95.9	112.7	134.9																								
5	3	55.3	79.9	103.7	123.7	141.8																							
6	6	69.1	92.2	108.6	126.0	141.7	155.6																						
7	4	62.4	82.1	101.6	121.9	142.3	163.3	184.5																					
8	1	74.3	105.1	121.4	138.0	154.0	173.8	189.7	206.2																				
9	6	57.5	74.3	91.0	106.1	123.4	139.5	157.9	176.4	192.6																			
10	4	63.3	86.2	98.4	117.1	137.7	159.6	177.8	194.9	210.3	225.3																		
11	11	61.4	80.6	99.1	117.1	133.9	149.2	165.3	181.7	198.5	213.0	226.7																	
12	7	61.8	85.0	104.7	121.9	140.5	158.9	175.2	193.8	211.2	227.2	241.2	255.6																
13	24	57.8	75.7	92.2	108.4	123.7	140.0	157.4	175.7	192.3	207.8	221.9	235.6	249.4															
14	11	68.4	87.3	102.9	119.5	135.4	151.9	168.5	185.6	200.7	216.6	230.6	242.8	254.7	265.9														
15	18	59.5	75.2	91.5	107.1	122.2	136.9	151.9	158.4	183.4	198.6	204.3	226.2	238.3	249.5	262.7													
16	12	65.2	81.9	99.2	115.6	131.9	146.6	163.6	178.6	193.8	209.1	224.0	237.2	249.4	259.8	269.9	280.1												
17	17	59.9	77.9	94.7	108.7	124.3	139.4	155.0	171.8	185.6	199.4	213.3	227.4	240.6	251.9	262.8	272.4	281.8											
18	8	65.5	79.4	94.7	109.1	123.9	137.1	151.5	166.9	181.6	195.4	209.3	223.3	235.6	248.3	259.6	272.3	283.4	292.8										
19	15	60.7	76.9	91.2	103.4	116.6	130.1	143.2	156.4	170.2	184.3	198.3	211.7	225.9	239.6	251.9	263.0	273.1	282.6	291.4									
20	15	63.0	79.9	94.4	108.4	122.4	136.9	150.7	166.1	180.1	194.1	207.8	221.2	234.0	245.9	256.0	265.7	276.0	284.4	292.4	200.5								
21	5	61.2	77.4	91.7	103.7	114.6	127.5	142.7	157.8	173.4	191.2	205.4	218.7	231.2	241.2	251.8	262.5	271.8	281.2	288.5	294.7	301.9							
22	15	66.2	82.8	97.6	111.2	122.4	134.8	148.1	161.4	176.0	189.5	203.0	215.9	228.0	240.1	251.8	262.2	272.6	282.5	290.9	299.4	307.8	315.6						
23	9	54.9	70.3	83.5	95.4	107.1	120.0	132.4	145.9	160.5	174.9	189.2	202.3	213.5	226.4	238.8	249.9	259.2	268.3	275.6	282.3	288.1	294.3	301.1					
24	11	58.3	74.9	88.7	102.2	114.7	127.3	140.0	152.8	166.3	179.8	192.6	205.3	217.2	228.0	239.1	246.7	260.3	270.2	278.8	287.3	295.2	302.9	310.8	317.0				
25	2	64.1	79.4	92.9	104.6	114.6	124.5	141.0	155.0	169.7	180.3	194.1	207.0	220.0	232.8	242.5	252.9	266.5	276.9	286.5	295.2	304.0	313.5	323.8	331.7	340.4			
26	6	61.1	78.2	90.0	104.2	116.2	127.8	140.7	152.8	165.3	178.3	190.3	204.1	217.1	230.4	242.0	251.0	264.4	274.0	282.8	290.0	296.3	303.2	310.6	317.9	324.6	331.3		
27	2	66.7	76.0	86.2	95.4	104.6	116.2	127.0	138.5	152.5	168.1	182.7	194.1	207.0	220.8	231.2	240.1	248.9	256.1	263.3	272.1	279.3	285.7	292.0	298.4	304.0	311.1	316.7	
28	1	55.8	71.3	86.2	98.1	107.9	119.5	132.6	146.3	157.3	169.2	180.4	194.9	203.0	210.9	219.1	227.5	235.7	243.3	252.1	259.6	269.1	272.9	276.1	279.8	282.0	285.5	289.7	293.0
Weighted mean		61.6	79.6	96.1	110.9	124.8	139.4	155.3	167.7	183.4	197.6	210.3	223.5	234.8	244.2	254.0	261.2	271.5	279.0	285.8	292.2	297.5	304.0	306.2	315.2	319.8	321.7	303.2	293.0

TABLE 3

BACK-CALCULATED TOTAL LENGTH AT TIME OF ANNULUS FORMATION OF MALE *S. lewini* FROM TAIWAN

		TOTAL LENGTH (cm)																	
ANNULUS	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	2	87.6																	
2	4	61.4	85.0																
3	1	65.8	83.2	95.3															
4	1	69.3	96.7	119.0	136.5														
5	1	56.9	79.8	97.0	109.0	125.9													
6	1	55.2	78.0	95.3	109.0	120.8	137.6												
7	2	58.7	79.8	105.6	122.5	136.0	149.3	164.2											
8	1	56.9	74.6	91.9	109.0	117.4	130.9	142.7	159.3										
9	2	59.6	78.9	98.7	115.8	132.6	145.2	161.8	179.9	200.4									
10	4	56.9	81.2	97.2	114.9	131.8	151.0	168.4	189.7	206.9	226.0								
11	5	51.2	71.4	89.5	107.6	125.5	142.0	160.6	178.4	196.1	211.1	226.7							
12	4	54.8	75.9	98.4	118.3	135.1	154.0	170.8	186.1	202.5	215.5	229.3	243.8						
13	2	70.2	88.4	103.0	121.7	138.5	161.8	177.4	194.7	208.5	224.7	239.3	252.9	269.0					
14	2	52.5	70.2	89.3	104.7	124.2	141.8	158.5	171.7	190.6	204.4	217.4	231.2	242.5	255.4				
15	2	43.5	62.3	78.9	94.4	109.0	125.9	144.3	160.9	179.1	193.0	204.5	219.1	231.2	244.9	257.8			
16	3	50.3	62.3	77.5	92.4	103.9	118.6	132.6	149.3	167.1	182.4	196.6	209.0	224.3	238.8	251.7	266.1		
17	3	48.6	62.3	77.5	88.9	104.4	116.3	130.4	144.8	157.1	171.3	188.9	206.4	218.7	231.2	243.6	257.0	271.8	
18	2	48.0	67.5	78.0	88.4	98.7	109.0	119.1	131.8	146.0	159.3	173.3	184.8	197.9	210.1	215.0	234.4	246.5	258.6
Weighted mean		56.8	74.9	91.4	107.6	122.0	138.1	154.1	170.0	187.6	201.8	211.8	222.1	229.4	235.9	243.1	254.7	261.8	258.6

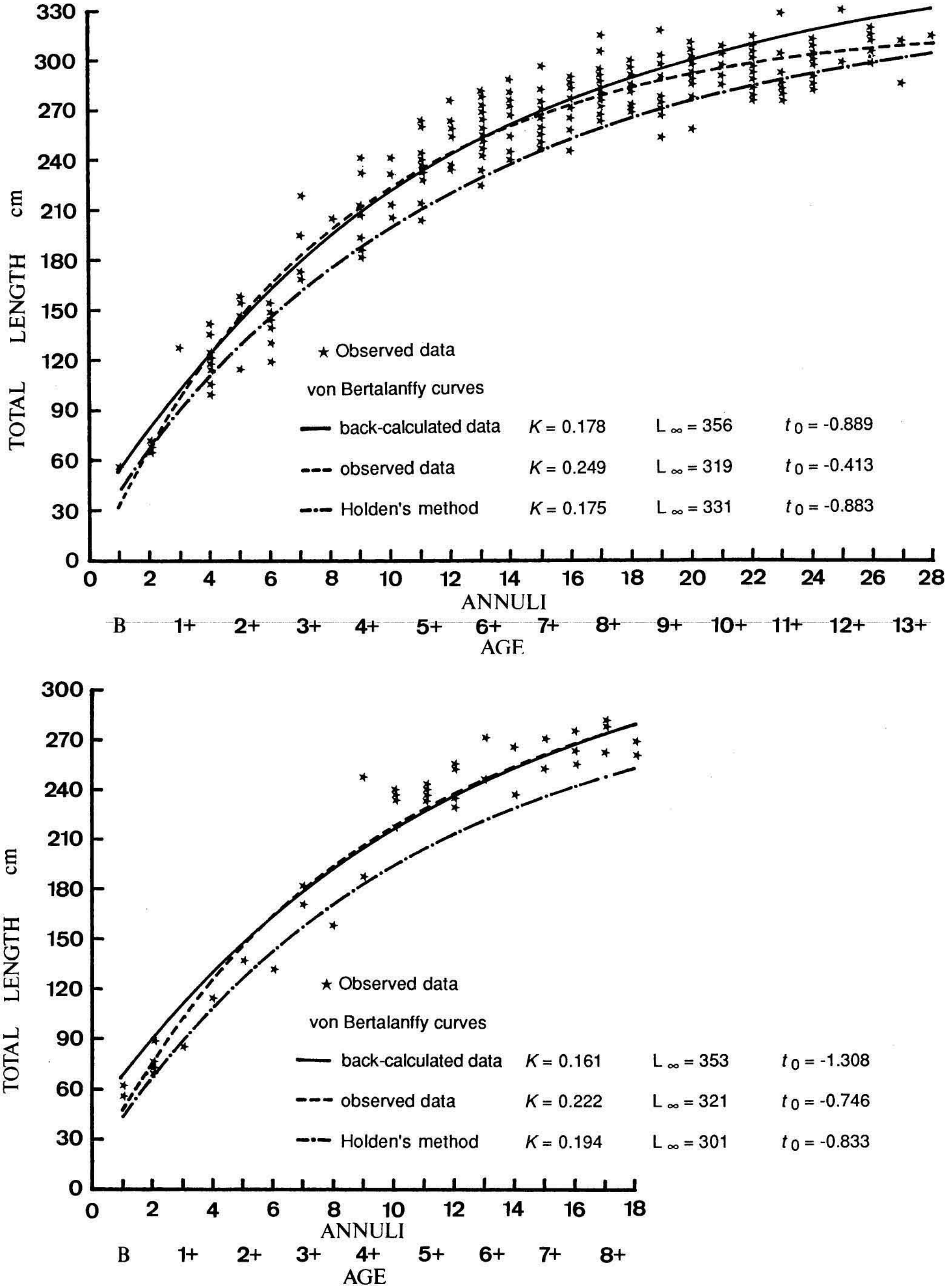

FIGURE 6. Von Bertalanffy growth curves for *S. lewini* from Taiwan. Individuals plotted by their annuli (time elapsed since the formation of the half-year annulus). B, birth mark. *Top*, females; *bottom*, males.

estimates were $K = 0.249$ (SE = 0.0122), $L_\infty = 319.72$ cm (SE = 3.7485), and $t_0 = -0.413$ yr (SE = 0.1031) for females and $K = 0.222$ (SE = 0.0389), $L_\infty = 320.59$ cm (SE = 21.4894), and $t_0 = -0.746$ yr (SE = 0.1998) for males. Length at birth was estimated to be 31.3 cm for females and 48.9 cm for males. Females are smaller at birth than the average length of embryos at birth (45 cm). The growth rate during the first year was estimated to be 63 cm for females and 54 cm for males, then 23–50 cm/yr for females and 22–42 cm/yr for males for years 2–5, and 3–19 cm/yr for females for years 6–13 and 11–18 cm/yr for males for years 6–8.

(2) Back-calculated lengths for ultimate annulus formation at different ages (diagonal column, Tables 2 and 3) are 45.3 cm at 0 yr, 72.1 cm at 0.5 yr, 76.9 cm at 1 yr, 134.9 cm at 1.5 yr, etc. In Table 2, these lengths were also used to calculate the predicted lengths of the VBGE. The parameter estimates were $K = 0.178$, $L_\infty = 355.75$ cm, and $t_0 = -0.889$ yr for females and $K = 0.161$, $L_\infty = 352.81$ cm, and $t_0 = -1.308$ yr for males. A von Bertalanffy curve produced from back-calculated length-at-different-ages data was close to the observed data curve (Figure 6) although there were small differences in length data in both young and older specimens.

The length at sexual maturity for the scalloped hammerhead was 210 cm TL in females and 198 cm TL in males (Chen et al. 1988). The age at maturity in the present study was 4.0 yr for females and 3.8 yr for males, based on the VBGE from back-calculated data. Using the back-calculated data, age at maximum size was 14.0 yr for females (331 cm TL) and 10.6 yr for males (301 cm TL).

HOLDEN'S METHOD. The gestation period (g) is 10 months (= 0.833 yr), which is equivalent to age at zero length. Length at birth for the embryo (L_g) is 45 cm, and maximum observed length (L_{max}) is 331 cm TL for females and 301 cm for males (Chen et al. 1988). Based on Holden's method, we obtained $K = 0.175$ for females and 0.194 for males. Thus VBGE (Figure 6) for both sexes were obtained as follows:

$$\text{females: } L_t = 331\,\{1 - \exp[-0.175\,(t + 0.833)]\}$$

$$\text{males: } L_t = 301\,\{1 - \exp[-0.194\,(t + 0.833)]\}$$

From these equations, the calculated length at age zero is 45 cm. This agrees well with the birth length of embryos from back calculation and observation. The first-year growth rate was estimated to be 45 cm for both sexes, then 22.8–38.6 cm/yr for females and 20.8–37.2 cm/yr for males for years 2–5, and 5.6–19.2 cm/yr for females and 4.4–17.1 cm/yr for males for years 6–13.

The predicted lengths using VBGE obtained from Holden's method were somewhat smaller than those from observed data and back-calculated data.

Relationship between Body Weight and Total Length

The general length-weight relationships (Figure 7) were as follows:

$$\text{females: } W = (2.82 \times 10^{-6})\,TL^{3.129} \quad (n = 276)$$

$$\text{males: } W = (1.35 \times 10^{-6})\,TL^{3.252} \quad (n = 49)$$

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

The weight-growth equations, transformed from the VBGE were as follows:

$$\text{females: } W = 293.56\,\{1 - \exp[-0.156\,(t + 1.053)]\}^{3.129}$$

$$\text{males: } W = 159.88\,\{1 - \exp[-0.238\,(t + 1.076)]\}^{3.252}$$

DISCUSSION

The disparity between the number of males and females was striking (Chen et al. 1988). We do not know whether scalloped hammer-

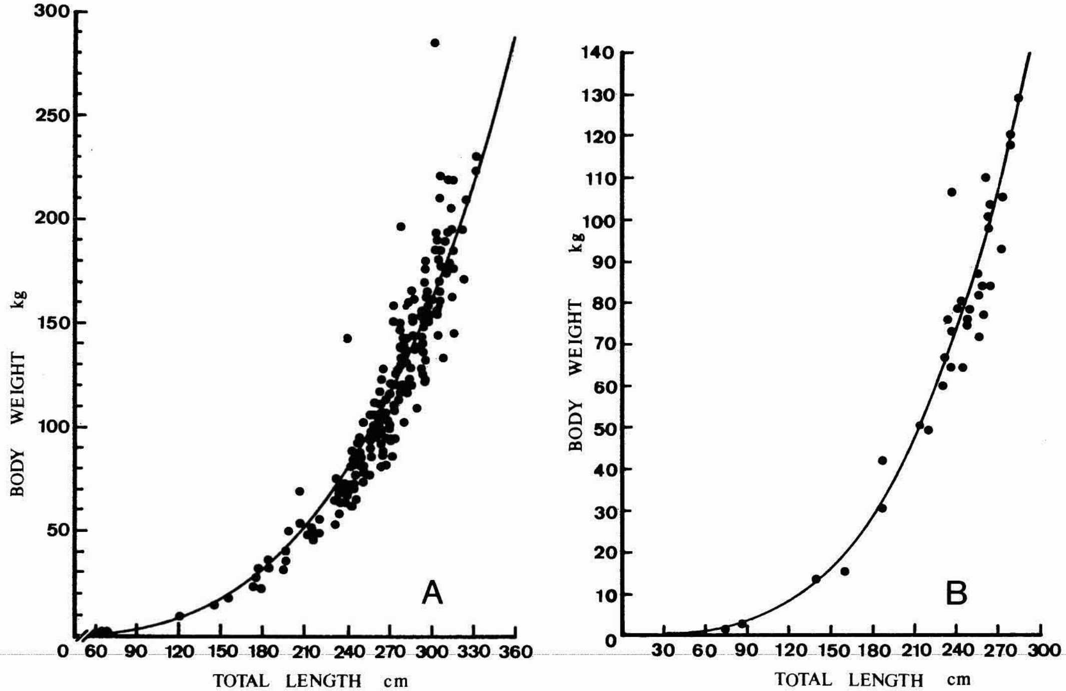

FIGURE 7. Relationship between body weight (W) and total length (TL) in *S. lewini* from Taiwan. *A*, females ($W = 2.82 \times 10^{-6} \times TL^{3.129}$); *B*, males ($W = 1.35 \times 10^{-6} \times TL^{3.252}$).

head females were more vulnerable to fishing gear than males or were simply more numerous in this area than in other areas. Perhaps males inhabit areas further off shore and were not well represented in our study area. Clarke (1971), Klimley (1981), and Branstetter (1987*a*) thought that females were associated more with oceanic waters than with shelf waters. Taiwanese hammerheads were caught primarily in coastal areas rather than oceanic waters. These differences in sex disparity need further investigation.

The relationship between centrum radius and total length seemed to be close to a curvilinear regression. The linear regression was also calculated, as follows: females: $TL = 16.25 + 152.33\ R$ ($r = 0.956$); males: $TL = 22.19 + 154.81\ R$ ($r = 0.982$). Although both curvilinear and linear regressions are significant, the curvilinear is more suitable than the linear.

There are several possible explanations for the first annulus formation in June for both sexes. Shortage of food supply, deprivation caused by migration, and changing temperatures may all be factors, but we have no available data to verify any specific cause. Lowest water temperatures (18°C) occur in northern Taiwan waters from December to February. Hence, the second half-year annulus formed in December may be correlated with that lower temperature. It is unlikely that apparent formation of two annuli per year is due to the migration of hammerheads into the study area from another population as was reported for *Carcharhinus acronotus* by Schwartz (1984). The existence of two rings per year has also been reported by Parker and Stott (1965) for the basking shark and by Pratt and Casey (1983) for shortfin makos.

Lee's phenomenon could arise from two sources. Most of our samples were taken by longline and harpoon employed at the sea surface, which are selective for large individuals. Smaller sharks were taken only by trawl near the bottom. Thus selective mortality of fast-growing young sharks could be responsible for the observed difference in annuli radii.

The VBGE parameter K, estimated from observed data, was 0.249 for females and 0.222 for males. These values are larger than those from the back-calculated data (0.178 for females and 0.161 for males). Conversely, L_∞ and t_0 estimated from observed data were smaller than those from back-calculated data (Figure 6). These differences in K, L_∞, and t_0 derived from observed data and back-calculated data could be caused by our limited data with great variation in length in the same age group for younger and older specimens. Holden's (1974) estimate of the K value for female *Sphyrna diplana* (= *S. lewini*) was 0.150, lower than our estimates based on Holden's method: 0.175 (females) and 0.194 (males). This difference in K estimated from various data may result from our use of a different gestation period (0.833 yr) rather than Holden's 1-yr period. Branstetter (1987*b*) categorized the K values as 0.05–0.10 for slow-growth species, 0.10–0.20 for average-growth species, and 0.21–0.50 for rapid-growth species. Based on these criteria, Taiwanese scalloped hammerheads have an average growth rate. However, scalloped hammerheads from the Gulf of Mexico were estimated to have a K of 0.073 by Branstetter (1987*a*), indicating a slow-growth species.

Holden's method is a quick way of obtaining K values and seems to be effective in dealing with the growth equation in scalloped hammerhead sharks. As Francis (1981) pointed out, Holden's method provides a mechanism for rapidly estimating elasmobranch growth rates. It is, however, not a substitute for growth rate analysis based on age determination and should only be used in the absence of actual data or as an interim measure, such as the initial value for nonlinear regression.

The growth rate for Taiwan-caught specimens was 63 cm for females and 54 cm for males in the first year and 23–50 cm/yr for females and 22–42 cm/yr for males for ages 2–5 yr. Growth increments of females of 3–19 cm/yr for ages 6–13 yr and of males of 3–15 cm/yr for ages 6–8 yr were recorded. Conversely, Branstetter's (1987*a*) specimens from the Gulf of Mexico demonstrated average growth rates of 15 cm, 10–15 cm, and 5–7 cm, respectively, which were much slower than those of Taiwanese specimens. Growth rates recorded by Schwartz (1983) were 10–15 cm/yr during the first 5 yr, decreasing from 10 cm/yr to 5 cm/yr for years 5–8. Thus, Taiwan hammerheads apparently grew at least twice as fast as those from the Gulf of Mexico and North Carolina. We attribute these geographic growth-rate differences to the formation of two annuli per year in Taiwanese specimens in contrast to the formation of one annulus per year found in Gulf of Mexico and North Carolina specimens. However, if two vertebral annuli are assumed to be formed each year in Gulf of Mexico sharks, then Branstetter's growth estimations would approach our results.

Pratt and Casey (1983) assumed that two centrum annuli were formed each year by shortfin makos from the northeastern Atlantic. This led them to conclude that shortfin mako growth was rapid when compared with growth in most other sharks. Their data indicated that growth rates for combined sexes of shortfin makos were 43–44 cm/yr for the first and second years and 9–29 cm/yr during the next 9 yr. These growth rates in a different species were somewhat similar to our results.

The predicted lengths at birth from nonlinear regression, based on observed data, were 31.3 cm for females and 48.9 cm for males. The estimates for females were smaller than the average length observed in full-term embryos (45 cm); the males were somewhat larger. The overestimated or underestimated length at birth was probably caused by the small sample size of young fish and the great variation in sharks of similar length but of different ages. Coincidentally, estimate of length at birth employing Holden's method was 44.9 cm, a length similar to that observed in full-term embryos.

The L_∞ values estimated from observed data were 319.72 cm for females and 320.59 cm for males, which were close to the maximum sizes we recorded: 331 cm for females and 301 cm for males. Likewise, the female L_∞ value of 331 cm was close to Branstetter's (1987*a*) observation (329 cm). However, using the back-calculated data, we calculated the L_∞ values as 355.75 cm for females and 352.81 cm for males, both values larger than observed maximum length.

Age at sexual maturity for Taiwan scalloped hammerheads is much younger than that reported for specimens from the Gulf of Mexico, where males matured at 10 yr (180 cm) and females at 15 yr (250 cm) (Branstetter 1987*a*).

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