Abstract.–Age and growth of *Alopias superciliosus* in waters off northeastern Taiwan were determined from vertebral band counts on 321 specimens (214 females and 107 males) and verified with a length-frequency analysis of 821 specimens (491 females and 330 males). Growth bands formed once a year according to marginal increment analysis and numbered up to 21 and 20 bands for females and males, respectively. The parameters of von Bertalanffy growth equations estimated from vertebral readings were the following: asymptotic precaudal length (L_∞) = 224.6 cm, growth coefficient (K) = 0.092/yr, age at zero length (t_0) = –4.21 yr for females; and L_∞ = 218.8 cm, K = 0.088/yr, t_0 = –4.24 yr for males. The ages at maturity were estimated to be 12.3–13.4 yr for females, 9–10 yr for males. The largest female aged from vertebrae was 20 yr old, the largest male 19 yr old. Length-frequency analysis supported our vertebral ageing estimates.

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Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters

Kwang-Ming Liu
Po-Jen Chiang
Che-Tsung Chen
Department of Fishery Science
National Taiwan Ocean University
Keelung 20224, Taiwan
E-mail address (for K.-M. Liu): kmliu@ntou66.ntou.edu.tw

The bigeye thresher shark, *Alopias superciliosus* (Lowe), is circumtropical and subtropical in distribution (Compagno, 1984). It is found over the continental slope around Taiwan and is abundant at depths of 40–100 m in waters off northeastern Taiwan (Fig. 1). Based on daily catch data (1989–1994) from Nan Fan Ao fish market, near Suao, estimates of annual landings of bigeye threshers in number of fish are about 3300, and 220 metric tons (t) in weight, 13% of the total annual shark catch.

Biological information, particularly on reproduction, for bigeye thresher is abundant (Nakamura, 1935; Cadenat, 1956; Bass et al., 1975; Stillwell and Casey, 1976; Gruber and Compagno, 1981; Gilmore, 1983, 1993; Moreno and Moron, 1992; Chen et al., 1997) but little is known about age and growth. Other than Gruber and Compagno's (1981) preliminary estimation on the age and growth of bigeye threshers, no studies have been published. Accurate age structure of stocks is essential for stock assessment and fishery management. This study provides the first information concerning age and growth of bigeye threshers from waters off northeastern Taiwan. Age and growth, from vertebral band counts, were verified with length-frequency analysis.

Materials and methods

Thresher sharks caught in northeastern Taiwan waters by commercial longlines were sampled at Nan Fan Ao fish market, from September 1993 to October 1994.

Precaudal length (PCL), fork length (FL), and total length (TL) (in cm) were measured and weighed at the fish market. Because caudal fins of bigeye thresher sharks are often damaged, PCL is used throughout this paper, unless otherwise noted. After specimens were gutted, a total of 371 (245 females and 126 males) precaudal vertebrae were removed for age determination. Vertebrae located under the first dorsal fin are often used for age determination (Casey et al., 1985; Branstetter and Stiles, 1987; Chen et al., 1990); samples from two specimens (166 cm and 171 cm PCL) were used to compare variations in banding patterns from centra at different locations along the vertebral column. Precaudal vertebrae had the same band counts as those under the dorsal fin and were used for age analysis in this study because these are the only vertebrae readily available at market.

X-ray radiography (Cailliet et al., 1983; Cailliet, 1990; Joung, 1993) and staining of vertebrae (Stevens, 1975; Casey et al., 1985; Tanaka, 1991; Joung, 1993) are two methods commonly used to enhance the clarity of bands on vertebrae. The silver nitrate technique of Stevens (1975) was tried but no increase in clarity of bands was observed; hence, we did not use the technique. The x-ray method, which is simpler and yields better clarity of bands with a Java video image analysis system, was used.

A Rigaku industrial x-ray apparatus (model: radioflex 90 GSB) with Fuji industrial x-ray film (fine grain and high contrast) was used to take x-radiographs of vertebral centra. Banding patterns in every x-radiograph were counted three times by one of the authors during a three-month period; only those centra whose band counts were the same for at least two of the three readings were accepted for further analysis. Growth bands included fast-growth and slow-growth zones. The radii of each band and vertebrae were measured on a line from the nucleus (notochord) to the outer edge of each band and to the outer margin of each vertebrae with x-radiography and the Java video image analysis system (Fig. 2).

The time of band formation was estimated from monthly change of marginal increment (MI) with the following equation:

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

where R = the vertebral radius; and
r_n and r_{n-1} = radii of the ultimate and penultimate bands, respectively.

In addition, Tanaka and Mizue's (1979) method was used to identify the ultimate band on the basis of the following stages: opaque zone, narrow translucent zone (the width of translucent zone is smaller than half width of opaque zone), and wide translucent zone (the width of translucent zone is larger than half width of opaque zone).

The growth of bigeye thresher sharks was described with the von Bertalanffy growth equation (VBGE) as

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where L_t = the length at age t;
L_∞ = the asymptotic length;
K = the growth coefficient; and
t_0 = the theoretical age at zero length.

The parameters of VBGE were estimated from a Walford plot (Walford, 1946).

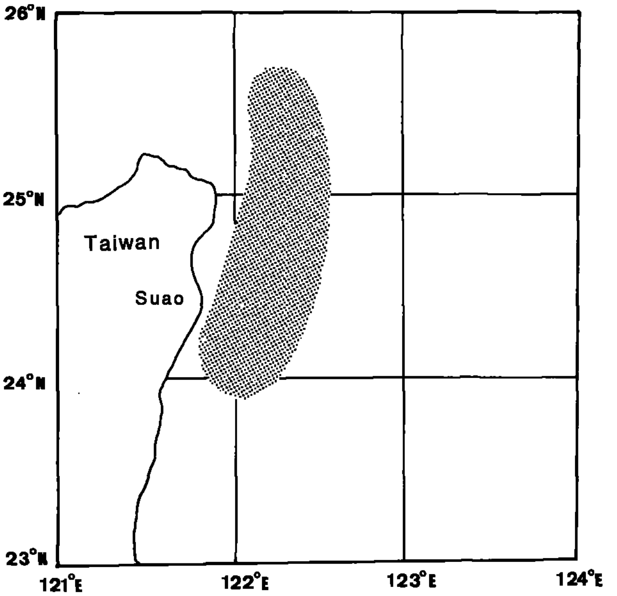

Figure 1

Sampling area for *Alopias superciliosus* in northeastern Taiwan waters.

The asymptotic weight was obtained by substituting L_∞ into the weight-length relationship; the VBGE on weight can be expressed as

$$W_t = W_\infty\left(1 - e^{-K(t-t_0)}\right)^b,$$

where W_t = the weight at age t;
W_∞ = the asymptotic weight; and
b = the exponent of the weight-length relationship.

Length-frequency distributions of 821 individuals (330 males, 491 females), grouped by season and sex, were analyzed with the computer package MULTIFAN (Fournier et al., 1990) to estimate the parameters of von Bertalanffy growth equations. Initial values of the L_∞ and K were adapted from those obtained in the previous section.

The relation between precaudal length and vertebral radius was tested with an F-test, and the difference in regression lines between sexes was tested with analysis of covariance.

Results

The relation between precaudal length and vertebral radius showed a slightly curved trend for both sexes (Fig. 3) and was statistically significant (P<0.05).

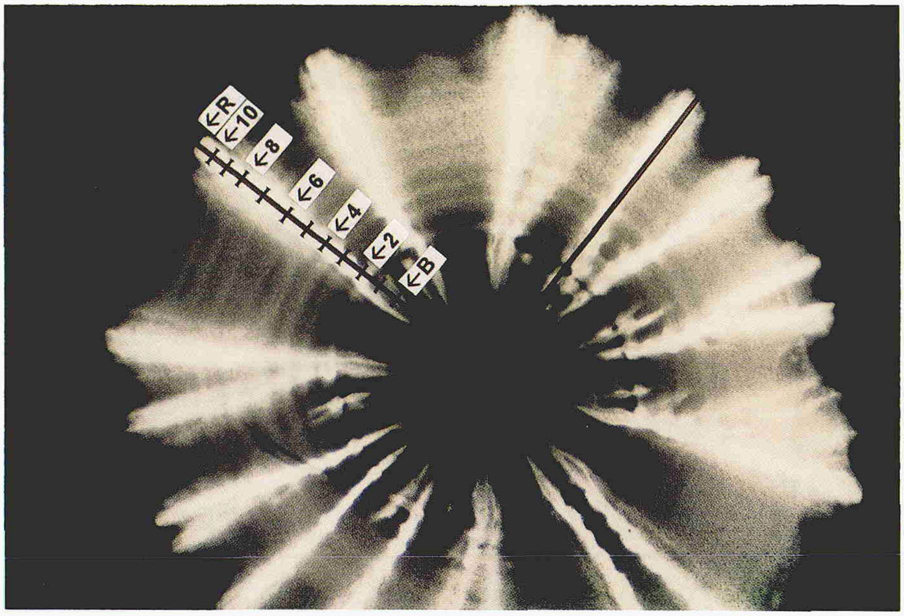

Figure 2

X-ray radiograph of *Alopias superciliosus* used for age determination. B = birth mark, R = vertebral centrum radius. Radiating bands are indicated in even years: 2,4,6,8, and 10.

Analysis of covariance indicated that there is significant difference in PCL-R relationships between female and male ($P<0.05$). Therefore, the PCL-R relationships were expressed by sex as follows:

female: $PCL = 50.84\ R^{0.494}$ $(r^2=0.75,\ n=214)$,
male: $PCL = 48.91\ R^{0.492}$ $(r^2=0.75,\ n=107)$.

Growth bands included two types of growth zones, as shown on the x-radiographs. These varied with season; usually a more calcified zone (translucent zones in Fig. 2) represented growth in summer (Casey et al., 1985; Cailliet et al., 1986; Branstetter and McEachran, 1986).

The vertebral bands numbered up to 21 and 20 for females and males, respectively. Owing to a lack of smaller specimens, the mean vertebral radii of bands I–III for females and I–V for males were interpolated from the relationship between vertebral radius and number of bands. The back-calculated length at band formation was able to be obtained by substituting the mean band radii (r_i) for R in the PCL-R relationship (Table 1).

The monthly change in vertebrae (MI) indicated that MI reached its peak in February, 0.60 for males, decreasing thereafter to its lowest value of 0.08 in June, and increasing thereafter (Fig. 4). This trend suggested that a vertebral band was formed once a year in the period April to July. A similar trend was found for females. Following Tanaka and Mizue's (1979) ageing criteria, we found that translucent zones (fast-growth zones) were formed between late spring and early summer, slow growth zones in winter, compa-

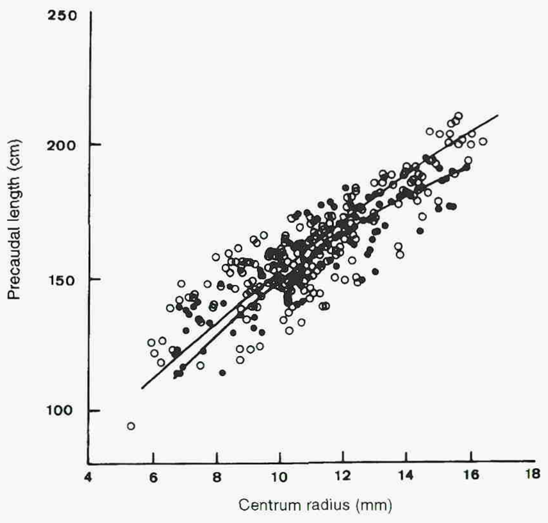

Figure 3

Relationship between precaudal length and centrum radius of *Alopias superciliosus*. ○ = female; ● = male.

Table 1

Back-calculated precaudal length at time of band formation of female *Alopias superciliosus*. *n* = sample size, B = birth.

		Precaudal length (mm)																				
Annulus	*n*	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
B	0	793.26																				
1	0	786.92	927.03																			
2	0	780.53	921.27	1075.37																		
3	1	752.31	920.31	1054.06	1153.59																	
4	3	769.59	910.14	1045.81	1146.52	1246.83																
5	8	759.50	877.17	1009.42	1152.07	1239.09	1322.33															
6	5	729.61	891.97	1023.99	1131.02	1232.82	1317.7	1396.33														
7	6	744.71	869.95	996.40	1146.30	1224.89	1310.77	1384.95	1463.29													
8	9	731.17	877.45	1024.23	1116.53	1210.93	1304.95	1378.55	1457.49	1532.69												
9	11	722.11	846.30	1006.05	1109.22	1212.38	1311.24	1372.12	1470.92	1526.92	1590.91											
10	18	705.61	862.39	987.33	1054.89	1205.66	1272.9	1365.65	1445.58	1521.05	1585.60	1643.49										
11	24	688.53	854.31	993.75	1110.68	1199.21	1286.75	1360.44	1418.36	1502.87	1580.65	1637.89	1683.24									
12	30	698.58	848.83	966.57	1089.96	1208.97	1166.43	1377.01	1420.21	1509.31	1567.64	1632.73	1684.05	1742.22								
13	23	657.63	821.34	981.02	1083.27	1189.05	1275.83	1349.21	1429.56	1520.97	1552.99	1612.15	1678.74	1737.38	1788.94							
14	24	691.83	838.97	976.53	1078.4	1151.75	1270.93	1344.77	1423.62	1499.39	1563.67	1622.13	1658.14	1719.16	1783.74	1832.89						
15	15	662.44	835.66	998.03	1074.09	1179.65	1259.09	1340.22	1419.59	1481.62	1559.21	1617.77	1667.62	1726.93	1778.81	1828.50	1870.77					
16	12	684.65	856.08	972.02	1088.92	1211.65	1262.65	1335.28	1410.00	1490.49	1570.17	1598.93	1662.70	1721.47	1789.36	1823.89	1865.81	1909.11				
17	9	700.93	829.29	966.96	1068.47	1171.35	1258.29	1315.52	1410.53	1486.23	1551.14	1608.45	1672.07	1717.29	1769.03	1818.86	1853.57	1904.25	1942.43			
18	10	680.38	827.47	964.23	1064.71	1169.11	1254.72	1326.47	1355.76	1481.87	1546.01	1603.51	1653.05	1712.52	1764.76	1829.31	1856.97	1899.38	1938.22	1966.23		
19	4	679.26	826.40	962.66	1062.00	1166.32	1252.12	1323.27	1402.74	1479.18	1542.23	1599.86	1649.74	1707.81	1760.82	1810.20	1852.30	1894.68	1933.50	1961.51	1981.34	
20	2	673.64	823.19	960.05	1058.21	1164.93	1252.12	1321.1	1401.32	1473.79	1538.35	1595.59	1646.88	1707.01	1759.62	1803.90	1822.67	1893.05	1931.90	1960.12	1980.59	2000.57
Weighted mean		696.35	848.46	985.32	1091.31	1195.33	1263.12	1355.48	1424.73	1504.99	1566.75	1622.46	1671.66	1727.71	1780.21	1826.51	1860.72	1902.87	1938.47	1964.29	1981.09	2000.57
SE		39.856	32.496	28.911	32.895	26.464	36.926	23.599	28.463	18.368	15.378	14.530	12.983	10.142	11.720	10.257	16.303	5.045	3.288	0.980	0.529	0.000

rable to the results from MI. This finding indicates that one band is formed per year by bigeye thresher sharks.

Chen et al. (1997) estimated PCL at birth for the bigeye thresher shark to be 73.7 cm, similar to our estimated mean length at the birth mark formation (69.6 cm). Because no growth band was found for embryos, the first band was assumed to be a birth mark.

For comparison with other literature that reported total length (TL), PCL and FL can be converted to TL with the following equations:

$$\begin{array}{lll} \text{female: } & TL = 15.3 + 1.81PCL & (r^2=0.90,\ n=177); \\ & TL = 13.3 + 1.69FL & (r^2=0.89,\ n=177); \\ \text{male: } & TL = 15.1 + 1.76PCL & (r^2=0.88,\ n=68); \\ & TL = 26.3 + 1.56FL & (r^2=0.81,\ n=68). \end{array}$$

The relations between body weight and total length, and body weight and precaudal length are described as follows:

$$\begin{array}{lll} \text{female: } & W = 6.87 \times 10^{-5} PCL^{2.769} & (r^2=0.88,\ n=421); \\ & W = 1.02 \times 10^{-5} TL^{2.78} & (r^2=0.90,\ n=175); \\ \text{male: } & W = 9.93 \times 10^{-5} PCL^{2.685} & (r^2=0.83,\ n=187); \\ & W = 3.73 \times 10^{-5} TL^{2.57} & (r^2=0.80,\ n=65). \end{array}$$

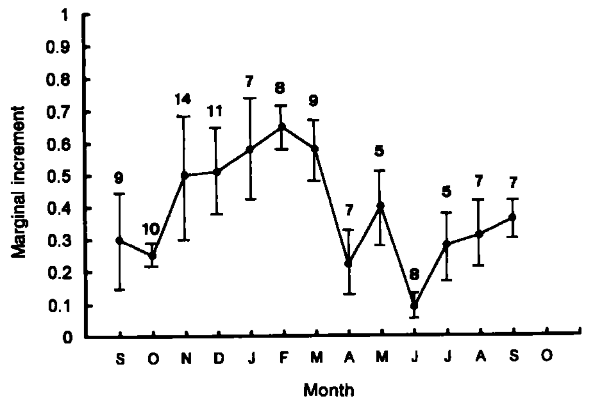

Figure 4

Monthly change of marginal increment of male *Alopias superciliosus*. Numbers indicate sample size and vertical bars indicate ±SE.

The parameters of VBGE estimated from band counts for females and males are given in Table 2 and the VBGE in PCL (cm) are

$$\begin{array}{ll} \text{female: } L_t = 224.6\,(1 - e^{-0.092(t+4.21)}); & \\ \text{male: } L_t = 218.8\,(1 - e^{-0.088(t+4.24)}) & \text{(Figs. 5, 6).} \end{array}$$

With the above equations, the asymptotic PCL can be converted to asymptotic TL as 422 cm for female, 385 cm for male. The VBGE in weight (kg) can be expressed as follows:

$$\begin{array}{l} \text{female: } W_t = 222.8\,(1-e^{-0.092(t+4.21)})^{2.769}; \\ \text{male: } W_t = 190.5\,(1-e^{-0.088(t+4.24)})^{2.685}. \end{array}$$

Female bigeye threshers are estimated to mature between 175 and 180 cm PCL (Chen et al., 1997), 78% and 80% of asymptotic length, and between 12.3 and 13.4 yr old. The largest immature female was 185 cm PCL, 14.6 yr.; the smallest mature female was 154 cm PCL, 8.4 yr. Males mature between 150 and 155 cm PCL (Chen et al., 1997), 69% and 70% of asymptotic length, and between 9 and 10 yr old. The largest immature male was 171 cm PCL, 13 yr; the smallest mature male was 138 PCL, 7 yr (Chen et al., 1997).

The length-frequency histograms for both sexes used in the analysis and results of the best data fits were plotted in Figures 7 and 8, females and males, respectively. In the best fits, age classes 18 and 20 were obtained for females and males, respectively. The estimated modes followed the length-frequency line closely and overlay the peaks well (Figs. 7 and 8). For estimated mean lengths at age of female and males see Table 3. The parameters of VBGE were estimated as $L_\infty = 230.5$ cm, $K = 0.092$/yr, $t_0 = -3.69$ for females, and $L_\infty = 224.4$ cm, $K = 0.087$/yr, $t_0 = -4.61$ for males; these parameters were similar to those from vertebral band counts (Table 2).

Table 2

Comparison of the von Bertalanffy parameters derived from vertebral band count and length-frequency analysis of *Alopias superciliosus*.

	Male				Female			
Parameters	L_∞	K	t_0	n	L_∞	K	t_0	n
Vertebral reading	218.8	0.088	−4.24	107	224.6	0.092	−4.21	214
Length-frequency	224.4	0.087	−4.61	330	230.5	0.092	−3.69	491

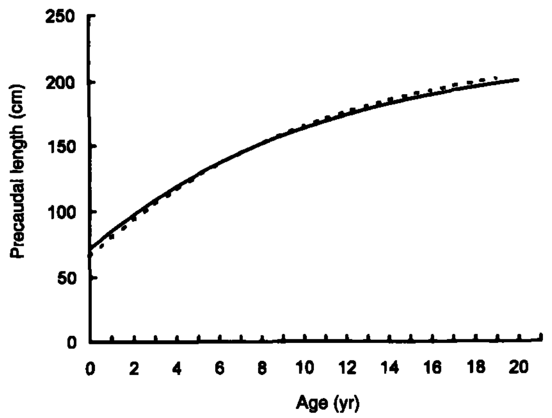

Figure 5

The von Bertalanffy growth curve for female *Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

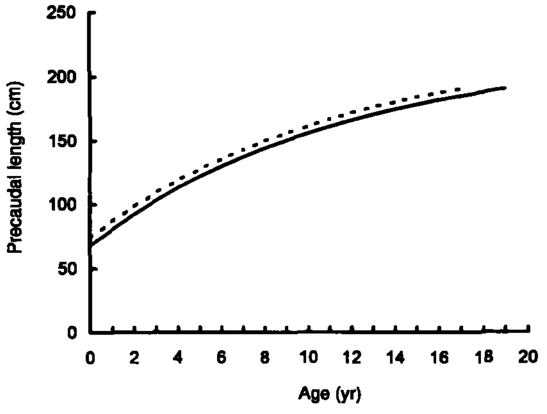

Figure 6

The von Bertalanffy growth curve for *male Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

Discussion

Joung (1993) noted that the ultimate band shown on the x-radiograph was difficult to read with a magnifier. In our study, an image processing system was used to solve this problem.

According to Branstetter (1990), growth coefficients (*K*) in VBGEs falling in the range of 0.05–0.10/yr is a slow-growing species; 0.1–0.2/yr is a moderate-growing species; and 0.2–0.5/yr is a fast-growing species. In this study, *K* was estimated as 0.092/yr for females, 0.088/yr for males; these are in the slow-growth category. Cailliet et al. (1983) estimated the growth rate of the California common thresher shark (*Alopias vulpinus*) to be 0.108/yr, comparable to our study. Other slow-growing species include the great white shark (*Carcharodon carcharias*) (*K*=0.058/yr, Cailliet et al., 1986), bull shark (*Carcharhinus leucas*)(*K*=0.039/yr, Hoenig, 1979), dusky shark (*C. obscurus*) (*K*=0.038–0.039/yr, Natanson et al., 1995), sandbar shark (*C. plumbeus*) (*K*=0.046/yr, Casey and Natanson, 1992, *K*=0.057–0.089/yr, Sminkey and Musick, 1995), scalloped hammerhead (*Sphyrna lewini*) (*K*=0.054/yr, Hoenig, 1979; *K*=0.073/yr, Branstetter, 1987), and *Squalus acanthias* (*K*=0.037/yr, Jones and Geen, 1977).

Most sharks form a vertebral band once each year i.e. *Triakis semifasciata* (Smith, 1984), *Carcharhinus limbatus*, *C. brevipinus* (Branstetter, 1987), *C. plumbeus* (Casey and Natanson, 1992), *C. falciformis*, *Rhizoprionodon terraenovae*, *Galeocerdo cuvieri* (Branstetter and Stiles, 1987), and *Carcharodon carcharias* (Cailliet et al., 1986). Some sharks form two vertebral bands per year, i.e. *Sphyrna lewini* (Chen et al., 1990), *Galeorhinus japonicus* (Tanaka and Mizue, 1978), *Isurus oxyrinchus* (Pratt and Casey, 1983), and *Cetorhinus maximus* (Parker and Stott, 1965). In the present study, although the time of band formation fell within a greater time range, the hypothesis of one band per year was validated by MI and Tanaka and Mizue's (1979) method. Similar results were reported for other species in Alopiidae, i.e. the common thresher sharks (Cailliet et al., 1983) and pelagic thresher sharks (Liao, 1996).

Formation of shark vertebral bands may be related to water temperature, change of prey (Steven, 1975), shark migration, and mating (Pratt and Casey, 1983). Because bigeye thresher sharks have no fixed spawning season, the band formation may not be closely related to mating. Elevated water temperatures in spring and summer are a possible factor in band formation. Jones and Geen (1977) documented that highly calcified bands represent summer growth of vertebral centra. The first vertebral band was assumed to be a birth mark in this study. Similar findings were reported for other species in Alopiidae, i.e. the common thresher sharks, *Alopias vulpinus*, (Cailliet et al., 1983) and pelagic thresher sharks, *A. pelagicus*, (Liao, 1996).

In the present study, ages at maturity were estimated to be 12.3–13.4 yr for females (332–341 cm TL), and 9–10 yr for males (270–288 cm TL). However, Gruber and Compagno (1981) reported younger ages at maturity but similar sizes in the Atlantic Ocean, 4.5 yr (356 cm TL) and 3.5 yr, females and males, respectively. Gruber and Compagno (1981) counted vertebral bands of a 287-cm-TL female and reported 8–11 bands, 2^+ yr. This length falls in the

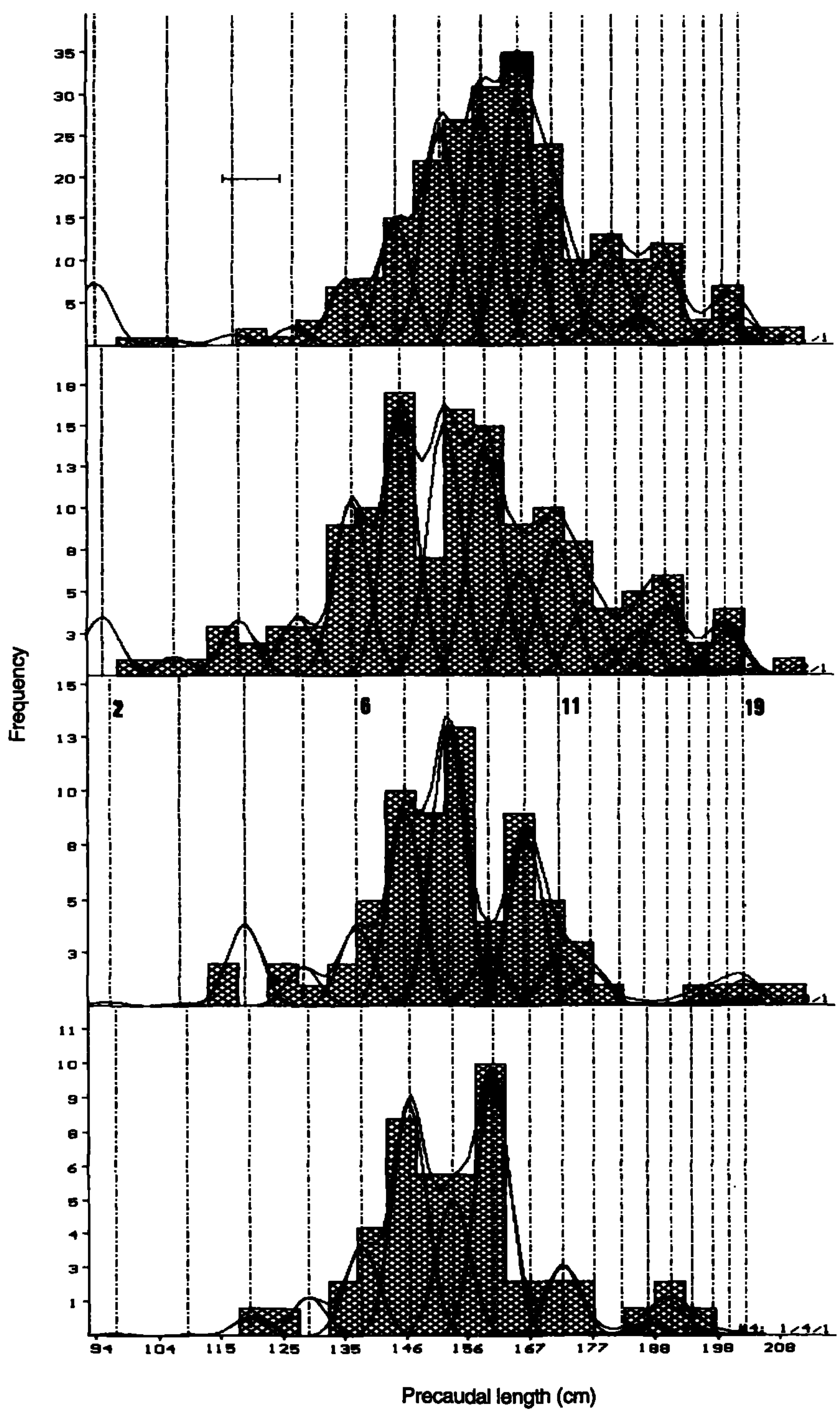

Figure 7

Length-frequency histograms for female *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

Table 3

Length (cm) at age estimates (yr) from length-frequency analysis of *Alpias superciliosus*. B = birth.

Sex	Age (yr)																			
	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Female	66.26	80.71	93.88	105.89	116.85	126.84	135.96	144.27	151.86	158.77	165.20	170.83	176.08	180.87	185.23	198.21	192.85	196.16	199.18	201.93
Male	74.12	86.68	98.19	108.75	118.42	127.28	135.40	142.84	149.66	155.91	161.64	166.89	171.70	176.11	180.15	183.86	187.25	190.36		

9–10 yr age class according to our estimations. We suggest that the results of Gruber and Compagno (1981), based on Holden's method (1974), may not be an accurate estimate; we believe ours to be more reasonable.

The size at maturity in different areas were similar, i.e. females matured at 332–341 cm TL in this area (Chen et al., 1997), 355 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 340 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Males matured at 270.1–287.9 cm TL in this area (Chen et al., 1997), 290–300 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 276 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Thus, size at maturity of the northwestern Pacific populations of *A. superciliosus* was very similar to those of populations elsewhere (Chen et al., 1997).

The maximum TL for female bigeye thresher sharks was 450 cm in Florida waters (Gilmore, 1983), 452 cm in Cuba (Guitart, 1975), 458 cm in New Zealand (Grey, 1928), and 422 cm and 357 cm, female and male, respectively, in this study. Possible reasons why this species is smaller in northeastern Taiwan than in other waters may be due to different environments, genes, gear selection, sampling bias, and fishing mortality.

Age and growth assessment of sharks from hard parts has been verified by length-frequency analysis to increase accuracy (Stevens, 1975; Pratt and Casey, 1983; Natanson et al., 1995). In this study, vertebral and

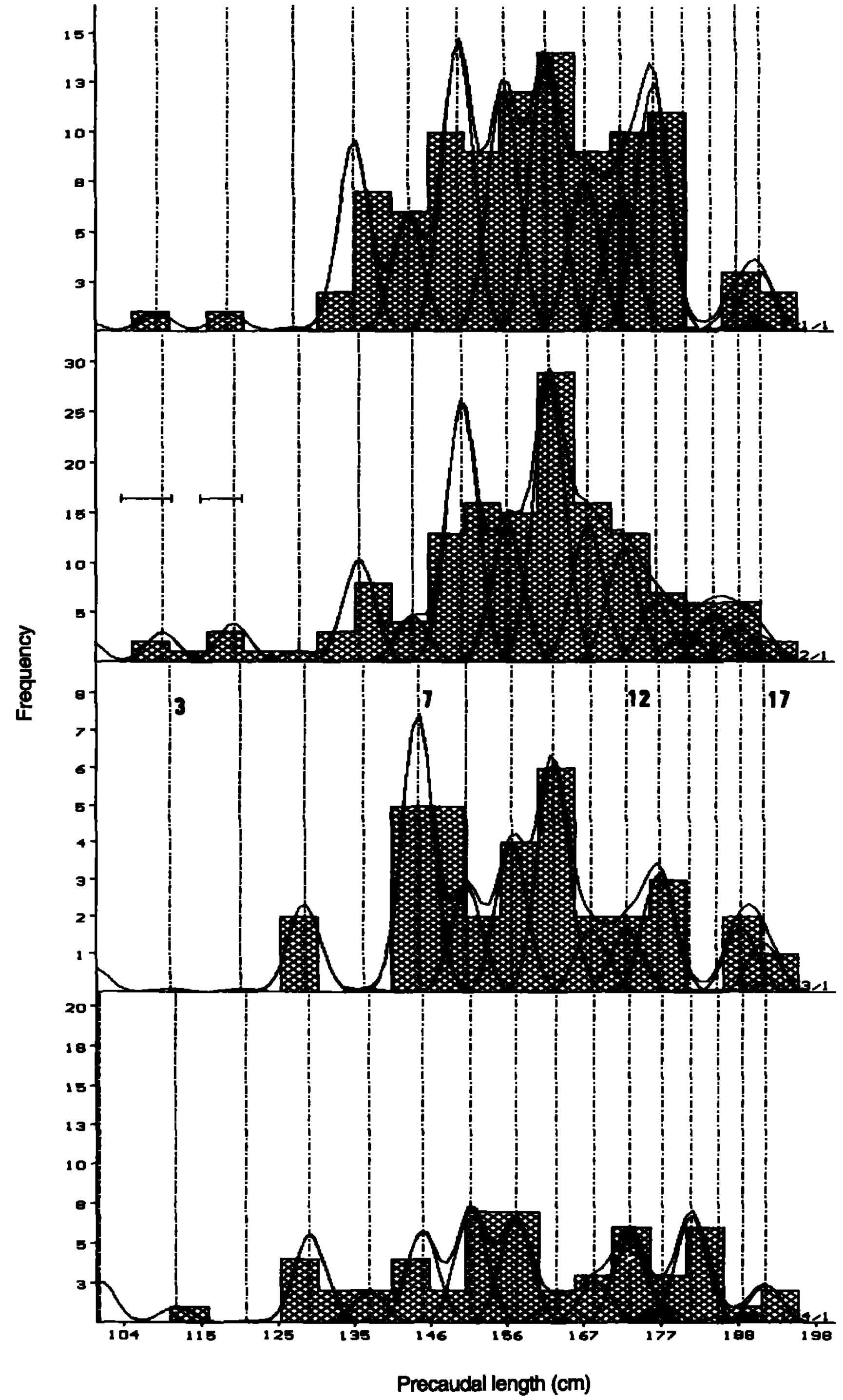

Figure 8

Length-frequency histograms for male *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

length-frequency data were analyzed independently to derive estimates of the von Bertalanffy growth parameters for the bigeye thresher shark. Parameter estimation with MULTIFAN was based on the maximum likelihood method which has been successfully applied to various marine animals (Fournier et al., 1990; Haist and Porter, 1993; Bigelow et al., 1995; Pagavino and Gaertner, 1995). Growth curves derived from MULTIFAN and vertebral band counts are in good agreement for females but the former method yields larger size at age than the latter for males (Figs. 5 and 6). In addition, the similar values of VBGE parameters derived from MULTIFAN and vertebral band counts suggest that the age and growth estimation for bigeye thresher sharks in this study is reliable. The age classes (20 and 18) sliced by MULTIFAN from length-frequency data are less than those from vertebral reading (21 and 20). Small sample size and overlapping lengths at older ages may obscure length modes (Ernizi, 1990), and length-frequency estimates may be somewhat biased because of limitations of data and properties of length-frequency methods (Majkowski et al., 1987; Shepherd et al., 1987; Natanson and Cailliet, 1990). Thus, the vertebral method is considered more robust and the length-frequency analysis is used for verification only.

Acknowledgments

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