Zoological Studies **50**(3): 284-295 (2011)

Zoological Studies

Age and Growth Estimates of the Blacktip Sawtail Catshark *Galeus sauteri* in Northeastern Waters of Taiwan

Kwang-Ming Liu[1], Chia-Ping Lin[1], Shoou-Jeng Joung[2], and Shyh-Bin Wang[1,*]

[1] *Institute of Marine Affairs and Resource Management, National Taiwan Ocean Univ., 2 Pei-Ning Road, Keelung 202, Taiwan*
[2] *Department of Environmental Biology and Fisheries Science, National Taiwan Ocean Univ., 2 Pei-Ning Road, Keelung 202, Taiwan*

(Accepted December 31, 2010)

Kwang-Ming Liu, Chia-Ping Lin, Shoou-Jeng Joung, and Shyh-Bin Wang (2011) Age and growth estimates of the blacktip sawtail catshark *Galeus sauteri* in northeastern waters of Taiwan. *Zoological Studies* **50**(3): 284-295. The blacktip sawtail catshark *Galeus sauteri* is a small, demersal species that inhabits tropical and subtropical coastal waters of the western Pacific region. It is one of the most important small shark species in terms of catch biomass for the trawl fishery in Taiwanese waters, but its stock status is poorly known. In this study, age and growth of this species were described from 739 specimens (388 females and 351 males, 8.5-49.8 cm in total length; TL) collected from Nov. 2007 to Oct. 2008 in waters off northeastern Taiwan by demersal or shrimp trawlers. Sex-specific relationships between the weight (TW) and TL significantly differed and could be expressed as: $TW = 2.09 \times 10^{-3} TL^{3.10}$ ($n = 1052$, $p < 0.05$) for females and $TW = 3.45 \times 10^{-3} TL^{2.94}$ ($n = 884$, $p < 0.05$) for males. Age was determined using band-pair reading of sectioned vertebrae. A single growth band pair (comprising translucent and opaque bands) is formed each year, and up to 14 and 12 band pairs were respectively observed for females and males. An edge analysis indicated that the translucent bands formed from July to Aug. Four growth functions, the traditional von Bertalanffy (VBGF), VBGF with a fixed size-at-birth (L_0), Gompertz, and Robertson (logistic) were used to model the observed length-at-age data. The sex-specific growth equations significantly differed. The logistic function had the best fit for both sexes, and the growth parameters including the 95% confidence intervals with a bootstrap method were estimated as follows: asymptotic length L_∞ = 48.30 (47.16-49.47) cm TL, and growth coefficient k = 0.374 (0.344-0.402) yr^{-1} for females, L_∞ = 44.29 (42.91-45.88) cm TL and k = 0.392 (0.356-0.429) yr^{-1} for males. The ages at maturity were respectively estimated to be 9.14 and 7.57 yr for females and males, by substituting the mean sizes at maturity into the Robertson growth equation. Longevities of females and males were respectively estimated to be 20.9 and 12.4 yr. http://zoolstud.sinica.edu.tw/Journals/50.3/284.pdf

Key words: Life history parameters, Vertebra, Robertson function, Bootstrap method, Longevity.

Sharks are the top predators and play important roles in marine ecosystems; however, their catch statistics are generally lacking due to the low economic value of their meat. This situation is even worse for small sharks, with species-specific catch data of such sharks generally unavailable. For example, the leafscale gulper shark *Centrophorus squamosus* and Portuguese dogfish *C. coelolepis* were recorded as the same species, *siki*, by the French demersal trawl fishery (Anon 2002, Figueiredo et al. 2005). Sharks smaller than 150 cm in total length (TL) are grouped as *cazon* in Mexico. In Taiwan, shark catch statistics are categorized into (1) large, pelagic sharks and (2) small, demersal sharks in the *Fisheries Statistics Yearbook Taiwan* (Anon 2009). The latter includes the young of large sharks such as scalloped hammerhead *Sphyrna lewini*, silky shark *Carcharhinus falciformis*, and small sharks, i.e., blacktip sawtail catshark *Galeus sauteri*, whitespotted bamboo shark *Chiloscyllium plagiosum*, and starspotted smoothhound *Mustelus*

---

[*] To whom correspondence and reprint requests should be addressed. Tel: 886-2-24622192 ext. 5602. Fax: 886-2-24635859. E-mail:sbwang@mail.ntou.edu.tw

manzao. Annual yields of small sharks in Taiwan declined dramatically from 5699 tons in 1993 to 510 tons in 2008, which implies that these stocks, mainly caught by trawlers and longliners in coastal waters off Taiwan, have experienced heavy exploitation in recent years. Huang (1996) mentioned that the starspotted smoothhound, once a very common species, had almost disappeared from central to southwestern Taiwan waters. Chen et al. (1996) also described a severe decline of several demersal shark species such as sawfish *Anoxypristis cuspidata* and some species of Centrophoridae. Fisheries-related biological information, essential to fishery management, is urgently needed to ensure sustainable utilization of demersal shark stocks.

The blacktip sawtail catshark is a small, demersal species that inhabits tropical and subtropical coastal waters of the western Pacific region. It is distributed off the Philippines, Taiwan, and southern Japan (Compagno 1984, Chen et al. 1996). In Taiwan, this species is found in coastal waters of western and northern Taiwan and is one of the most important small shark species in terms of catch. However, its stock status is poorly known. According to our survey in 2006-2008, this species is the most abundant elasmobranch bycatch of trawl fisheries in northeastern Taiwan. Unfortunately, catch statistics of this species are not available because only large individuals are sold, while small ones are regarded as trash fish (food for fish farms). Age and growth information of small sharks in Taiwanese waters are sporadic despite descriptions of spotless smoothhound *Mustelus griseus* (Wang and Chen 1982), starspotted smoothhound (Yamaguchi et al. 1996), and whitespotted bamboo shark (Chen et al. 2007). Biological information on the blacktip sawtail catshark is very limited. Liao (1992) suggested that the size at birth of this species is 6.7 cm in TL, and the size at free swimming is 7-8 cm in TL after an embryonic development period of at least 72 d. Chen et al. (1996) indicated that the blacktip sawtail shark is oviparous; a female can produce 2 egg capsules in each ovulation season. The maximum observed sizes were 45-47 cm in TL for females and 41-43 cm in TL for males with respective 50% sizes at maturity of 40-41 and 34-35 cm TL (Chen et al. 1996). Age, growth rates, and estimates of the age at maturity, which are important for stock assessment and fisheries management, are however lacking for this species.

Therefore, the objective of this study was to provide the 1st detailed information on the age and growth of the blacktip sawtail catshark in waters off northeastern Taiwan. It is hoped that the results derived from this study will be used as input parameters for further assessment of the stock in this region.

MATERIALS AND METHODS

Blacktip sawtail catsharks were collected monthly from the Tahsi Fish Market, Ilan County, northeastern Taiwan (Table 1). All specimens were caught by the commercial bottom trawl or shrimp trawl fishery in the waters off northeastern Taiwan between Nov. 2007 and Oct. 2008 (Fig. 1). Measurements were taken of TL (cm), precaudal length (PCL in cm), and TW (g), and the sex was determined. A Chi-squared test was used to examine the homogeneity of the sex ratio. The relationship between TW and TL was described by the allometric equation: $TW = a \times TL^b$, where a and b are parameters. A maximum-likelihood ratio test (Kimura 1980) was used to compare weight-length relationships between the sexes.

Vertebrae were used for age determination. Samples from 6 specimens (3 for each sex) were used to compare variations in band-pairing patterns on vertebral centra from different locations within specimens. The diameter of each centrum (DC) was measured on a line that crossed the corpus to the centrum edge with vernier calipers. As there are 218 vertebrae for this species, only the 1st 40 vertebrae were analyzed because of their large size. The coefficient of variation (CV) of the diameter of the vertebral centrum was calculated every 5 consecutive vertebrae as a group using the formula: $V = \frac{S}{\overline{X}} \times 100\%$ where S is standard deviation and $\overline{X}$ is the mean diameter of each 5 vertebrae. Since the 16th-20th vertebrae had the smallest CV and exhibited the same band-pair counts as vertebrae in other locations, these 5 vertebrae were used for the age analysis in this study.

Vertebrae were rinsed in 90°C water for 5 min to remove connective tissue, and decalcified with 100% decalcifying reagents (Shandon TBD-1, Pittsburgh, PA, USA) following Natanson et al. (2007), washed in running water for a few hours, and rinsed in a 95% alcohol solution. Cleaned vertebral centra were sectioned along the longitudinal plane at 60 μm in thickness with a low-speed saw (Rotary microtome, Leica RM2125, Nussloch, Germany). To facilitate cutting, centra were paraffin-impregnated for 12 h prior to sectioning, and were held with a crescent wrench while cutting. Sectioned vertebral centra were stained with hematoxylin, rinsed in glycerin, and then mounted (Natanson et al. 2007). These vertebral centra were examined using a digital microscope (ESPA IS47, ESPA Systems Co. Ltd., HsinChu City, Taiwan), and images were captured with an attached charge-coupled device (CCD) camera (ESPA Systems Co. Ltd., HsinChu City,

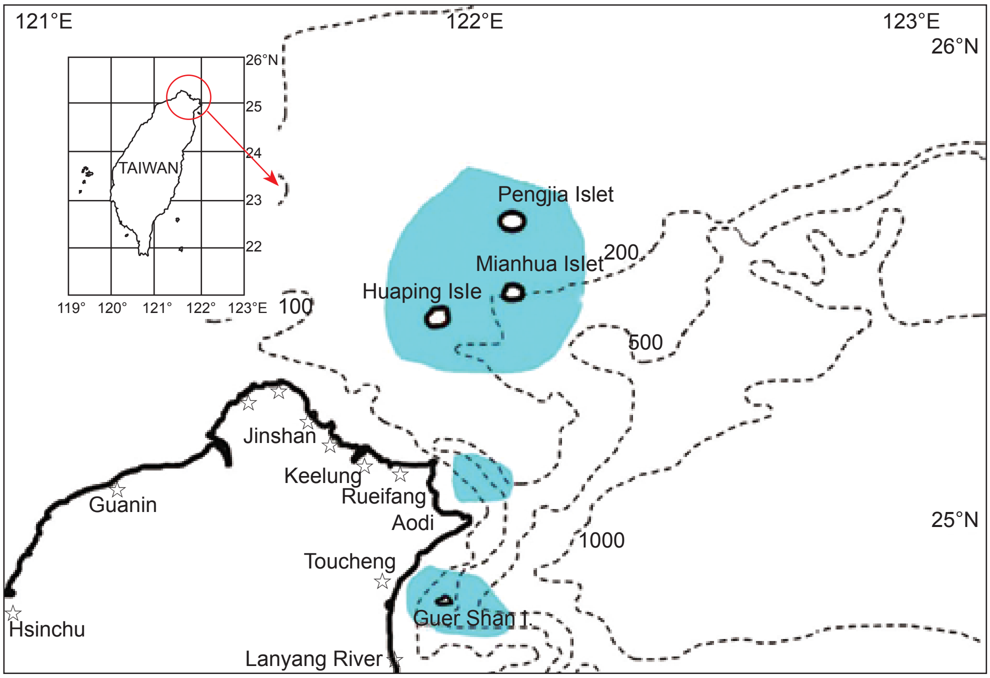

Fig. 1. Sampling area (shaded) of blacktip sawtail catsharks in this study.

Table 1. Total length (TL) and sample size of blacktip sawtail catshark used for the age and growth analysis in this study

Date of sampling	Females		Males		
	n	Range of TL (cm)	*n*	Range of TL (cm)	Total
Aug. 2007	58	11.4-47.8	53	11.1-42.3	111
Sept. 2007	129	10.1-47	73	9.8-40.4	202
Oct. 2007	69	10.8-45.1	50	9.3-40.2	119
Nov. 2007	48	11.2-45.4	23	12.5-40.7	71
Dec. 2007	94	10.7-47.8	114	14.5-42.3	208
Jan. 2008	61	9.1-46.4	60	8.5-41	121
Feb. 2008	125	10.2-46.6	78	8.3-43.2	203
Mar. 2008	88	9.6-46	45	9.1-40.8	133
Apr. 2008	57	9-46.6	59	8.8-41.9	116
May 2008	118	9-45.7	83	9.1-42.2	201
June 2008	102	9.7-45.5	115	8.6-40.5	217
July 2008	56	14.4-47.7	112	17.1-42.7	168
Aug. 2008	295	9.7-49.8	231	11-42.6	526
Sept. 2008	222	9.7-47	230	9-42.5	452
Oct. 2008	226	8.8-45.8	255	9.4-40.6	481
Nov. 2008	213	10.1-46.3	209	8.6-42.8	422
Dec. 2008	161	9.1-47.2	177	11.1-40	338
Total	2122	8.8-49.8	1967	8.3-43.2	4089

Taiwan). These images were processed with a MicroCap image process system (HsinChu City, Taiwan). Growth band pairs (comprising translucent and opaque bands, which were interpreted under conditions of reflected light) were counted without prior knowledge of the sex or length of the specimens (Fig. 2). Counts were accepted only if both counts by the same reader were in agreement. If the estimated numbers of band pairs differed, the centrum was recounted, and the final count was accepted as the agreed upon number. If a 3rd count had no consensus with one of the previous 2 counts, the sample was discarded. An edge analysis was performed to determine the time of band-pair formation using monthly changes in the frequency of the translucent and opaque edges on the vertebrae. Edge frequencies were correlated with the mean monthly sea surface temperature (SST) in northeastern Taiwan to determine whether growth-band pair formation coincided with environmental variations. The relationship between the centrum diameter and TL was estimated using a linear regression analysis. To facilitate comparisons with other work that reported their results in a measure other than TL, a linear regression was used to convert between TL and PCL. An analysis of covariance (ANCOVA) was used to compare the TL-DC and TL-PCL relationships between sexes.

The index of the average percentage error (IAPE) (Beamish and Fournier 1981), CV, and precision index (D) (Chang 1982, Campana 2001) were calculated along with the age-bias plot (Campana et al. 1995) to compare reproducibility of age determination between 2 readings:

$$IAPE = \frac{1}{N}\sum_{j=1}^{n}\left[\frac{1}{R}\sum_{i=1}^{R}\left[\frac{|X_{ij} - X_j|}{X_j}\right]\right] \times 100\%$$

$$CV = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij} - X_j)^2}{R - 1}}}{X_j}\right] \times 100\%$$

$$D = \frac{CV}{\sqrt{R}}$$

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

Four growth functions were used to model the observed length at age. Length at birth (L_0) was adapted from Liao (1992) estimated from the mean size at birth of 2 individuals (one of each sex), which hatched from eggs deposited by captive females in the laboratory. The NLIN procedure of the statistical package SAS vers. 9.0 (SAS Institute, 2008, Cary, NC, USA) was used to estimate the parameters of each function. The 4 growth functions are described as follows:

(1) von Bertalanffy growth function (VBGF, von Bertalanffy 1938)

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

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

(2) VBGF with L_0 (Fabens 1965)

$$L_t = L_0 + (L_\infty - L_0) \{1 - \exp [- kt] \}$$

where L_0 is the length at birth and was set to 6.7 cm (Liao 1992).

(3) Robertson (logistic) growth function (Robertson 1923)

$$L_t = \frac{L_\infty}{[1 + \exp (b - kt)]}$$

where b is the parameter to be estimated.

Fig. 2. Growth band pairs formed on a section of the vertebral centrum of blacktip sawtail catshark. Dots indicate opaque bands.

(4) Gompertz growth function (Gompertz 1825)

$$L_t = L_\infty \exp [-c \exp (-kt)]$$

where c is the parameter to be estimated.

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

$$AIC = n \times 1n (MSE) + 2k$$

where n is the total sample size, MSE is the mean square of residuals, and k is the number of parameters estimated in the growth function. The bias-corrected percentile confidence intervals (CIs) of the growth parameters for the best model were estimated using a bootstrap method with 1000 replicates (Efron and Tibshirani 1993). The age at maturity was estimated by substituting the mean size at maturity (Chen et al. 1996) into the best growth function selected. The longevity (T_{max}) was assumed to be the age at 99% of L_∞ using Fabens' (1965) equation: $T_{max} = 7 \times \frac{1n\ 2}{k}$.

RESULTS

In total, 739 (388 female and 351 male) specimens were collected for the age analysis. Females ranged 8.8-49.8 cm and males 8.5-43.2 cm in TL (Table 1). Relationships between the TW and TL were described as follows (Fig. 3):

Females: $TW = 2.09 \times 10^{-3}\ TL^{3.10}$ (n = 1052, $p < 0.01$) and

Males: $TW = 3.45 \times 10^{-3}\ TL^{2.94}$ (n = 884, $p < 0.01$).

The maximum likelihood ratio test of TW vs. TL suggested that the relationship between sexes significantly differed at the 1% level. However, no significant differences in the TL-PCL or TL-DC relationships between sexes were found (ANCOVA, $p > 0.05$), and the combined-sex equations were estimated to be (Fig. 4):

TL = 1.50 + 1.362 PCL (n = 3808, r^2 = 0.99, $p < 0.01$) and

TL = 5.28 + 12.273 (n = 673, r^2 = 0.97, $p < 0.01$).

Age estimates ranging from 0^+ to 14^+ for females and 0^+ to 12^+ for males were based on 511 (275 females and 236 males) of the 565 vertebral centra examined. In total, 54 vertebral centra (9.56%) were rejected because the 3rd band-pair count differed from the previous 2 counts. The precision estimate provided an average IAPE of 3.41%, a CV of 4.55%, and a D of 3.22% for the overall sample. The percent agreement between

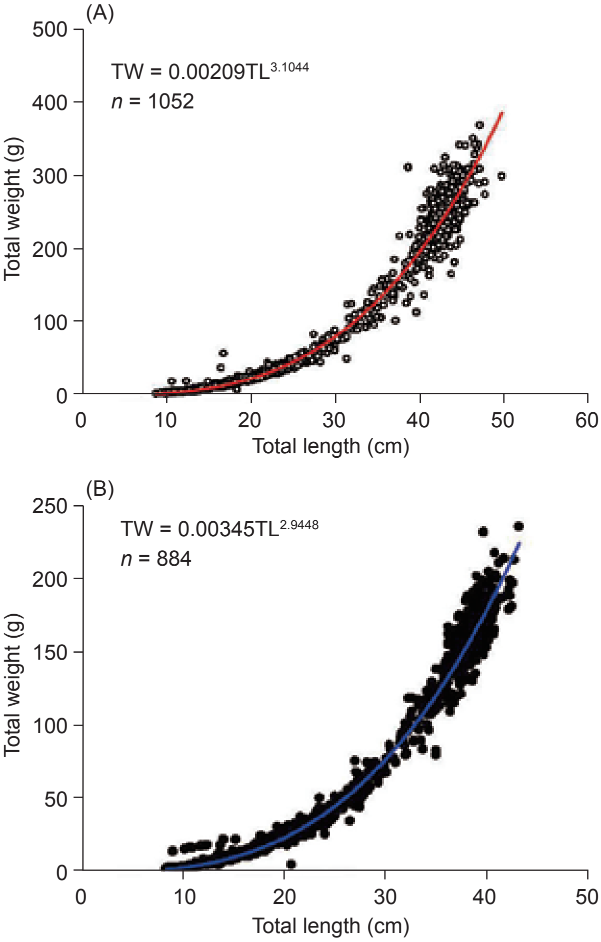

Fig. 3. Relationship between body weight (TW) and total length (TL) of blacktip sawtail catshark. (A) Females, (B) males.

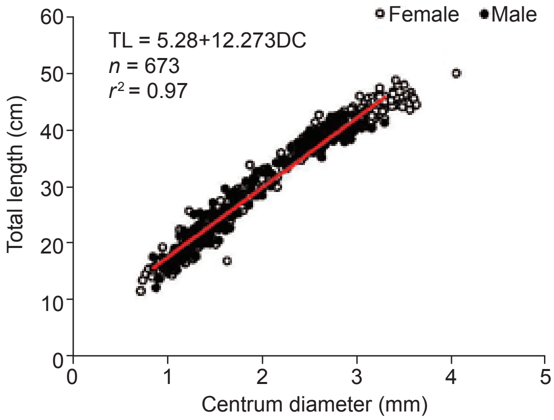

Fig. 4. Relationship between total length (TL) and centrum diameter (DC) of blacktip sawtail catshark.

the 2 readings was 62.3% total agreement and 90.4% within 1 band pair. The percent agreement by size category also indicated good precision over most size classes (Table 2).

Monthly frequency changes in translucent and opaque edges on vertebral centra for both sexes indicated that opaque bands mostly appeared from Feb. to July, while translucent bands dominated from Aug. to Jan. (Fig. 5). From these results, we suggest that a growth band pair formed once a year in both sexes.

The blacktip sawtail catshark is oviparous, and ovulation is found year round (Chen et al. 1996). As no birth mark was found on any vertebral centrum and the time lag between the birth and 1st band pair formation is difficult to estimate, it was assumed to be 0.5 yr in the present study. The age of each shark was then estimated based on (0.5 + (the number of band pairs - 1) + the time lag between the sampling date and opaque band formation (assumed to be 1 Aug.)) accordingly. The maximum size and age observed were 49.8 cm TL and 14 yr for females and 43.2 cm TL and 12 yr for males (Tables 3, 4).

The parameters of the 4 growth functions were estimated as follows (Fig. 6):

(1) VBGF

Female: $L_t = 69.8 \{1 - \exp[-0.089 (t + 0.307)]\}$ ($n = 275$, $p < 0.01$)

Male: $L_t = 70.1 \{1 - \exp[-0.081 (t + 0.527)]\}$ ($n = 236$, $p < 0.01$).

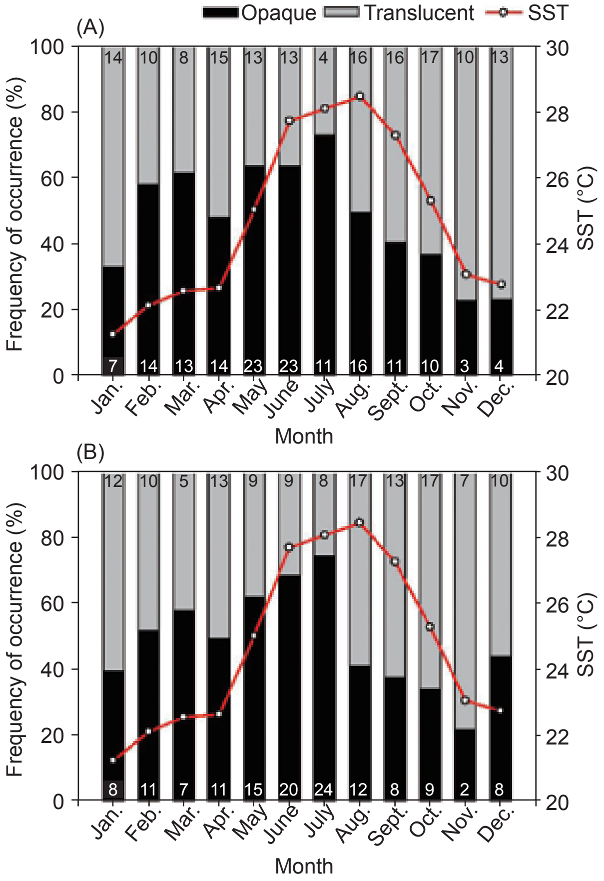

Fig. 5. Monthly frequency changes in band edges of the blacktip sawtail catshark related to the mean monthly sea surface temperature (SST). (A) Females, (B) males. Numbers indicate the sample sizes of translucent and opaque bands.

Table 2. Percent agreement (PA) of the age determination for blacktip sawtail catshark by age classes

Age class (yr)	Total no. read	No. that agreed	No. that agreed ± 1	PA	PA ± 1
1	17	17	17	100.00	100.00
2	33	33	33	100.00	100.00
3	26	23	26	88.46	100.00
4	50	34	49	68.00	98.00
5	42	29	41	69.05	97.62
6	38	30	37	78.95	97.37
7	44	24	40	54.55	90.91
8	46	20	36	43.48	78.26
9	79	45	70	56.96	88.61
10	94	60	85	63.83	90.43
11	55	26	49	47.27	89.09
12	24	8	17	33.33	70.83
13	13	3	10	23.08	76.92
14	3	0	1	0.00	33.33
Total	565	352	511	-	-
Mean	-	-	-	62.30	90.44

(2) VBGF with L_0

Female: $L_t = 6.7 + 101.6\ [1 - \exp(-0.046t)]$ ($n = 275$, $p < 0.01$)

Male: $L_t = 6.7 + 118.8\ [1 - \exp(-0.036t)]$ ($n = 236$, $p < 0.01$).

(3) Robertson (logistic) growth function

Female: $L_t = \dfrac{48.3}{[1 + \exp(1.77 - 0.374t)]}$ ($n = 275$, $p < 0.01$)

Male: $L_t = \dfrac{44.3}{[1 + \exp(1.71 - 0.392t)]}$ ($n = 236$, $p < 0.01$).

(4) Gompertz growth function

Female: $L_t = 52.8 \exp[-2.28 \exp(-0.232t)]$ ($n = 275$, $p < 0.01$)

Male: $L_t = 49.1 \exp[-2.20 \exp(-0.238t)]$ ($n = 236$, $p < 0.01$).

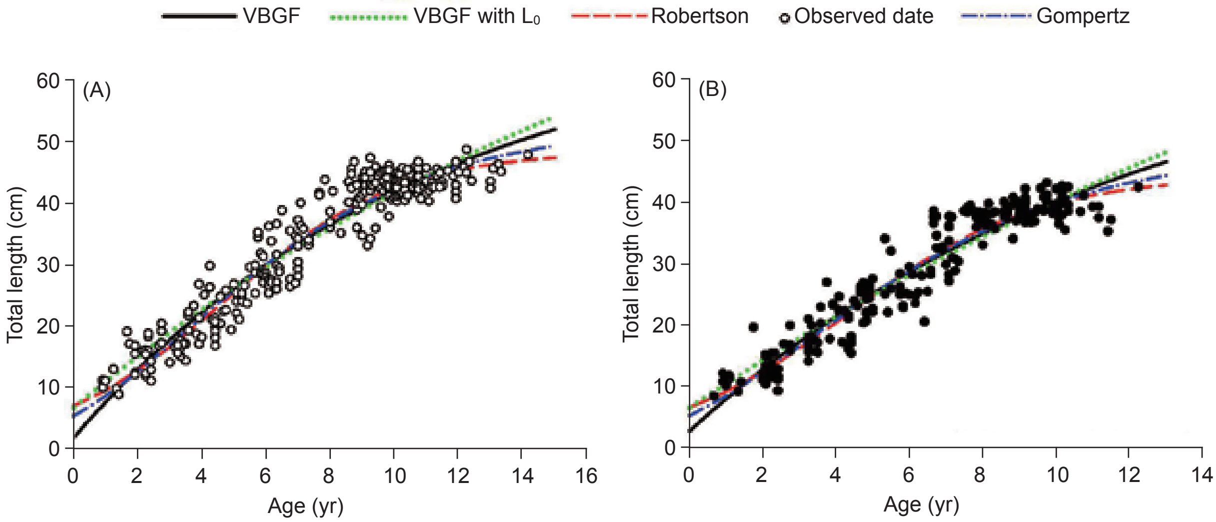

Fig. 6. von Bertalanffy growth function (VBGF), VBGF with a fixed size at birth (L_0), Robertson, and Gompertz growth curves of the blacktip sawtail catshark in this study. (A) Females (○), (B) males (●).

Table 3. Age-length key of the female blacktip sawtail catshark

	Age group (yr)														
Total length (cm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	*n*
8-11	3														3
11-14	4	6													10
14-17		7	7	2											16
17-20		4	6	9	1										20
20-23			1	7	5										13
23-26				2	8	3									13
26-29				2	2	12	4								20
29-32				1		7	2								10
32-35						2	5		3						10
35-38						3	4	3	2	1					13
38-41							2	1	8	6	3	1			21
41-44								4	14	34	22	5	2		81
44-47									8	14	10	7	3		42
47-50									1			1		1	3
n	7	17	14	23	16	27	17	8	36	55	35	14	5	1	275
Mean	10.63	14.96	16.94	20.67	23.59	29.54	32.92	39.31	41.61	42.71	43.23	44.38	44.48	47.70	
Standard deviation	1.32	2.57	1.58	3.63	2.19	3.22	4.21	3.19	3.45	1.70	1.57	2.14	1.60	-	

The Robertson function had the smallest AIC among the 4 growth functions (Table 5), and thus was selected as the best model to describe the growth of blacktip sawtail catsharks. The maximum-likelihood ratio test suggested a significant difference in growth between sexes ($\chi^2 = 40.90$, $p < 0.01$); thus, the growth equations were accordingly expressed by sex (Table 5). The bias-corrected 95% CIs of the growth parameters of the Robertson function were estimated as follows: $L_\infty = 48.30$ (47.16-49.47) cm TL, $k = 0.374$ (0.344-0.402) yr^{-1} for females, and $L_\infty = 44.29$ (42.91-45.88) cm TL, $k = 0.392$ (0.356-0.429) yr^{-1} for males.

Mean sizes at maturity for females and males were estimated to be 40.5 and 34.5 cm in TL, respectively, based on the relationship between the mature percentage and TL using the logistic model (Chen et al. 1996), which corresponded to the ages of 9.14 and 7.57 yr, respectively, when substituted into the Robertson growth equation derived in this study. The longevities of female and male blacktip sawtail catsharks were respectively estimated to be 20.9 and 12.4 yr.

DISCUSSION

Several techniques have been used in attempts to increase the clarity of band pairs in vertebral centra. X-radiography, which was successfully used on the vertebrae of brown smoothhound *Mustelus henlei* (Yudin and Cailliet 1990), failed to provide useful results in this study. Chen et al. (2007) suggested rinsing vertebrae with glycerol to enhance centrum band pairs of whitespotted bamboo shark. This method was also tried in the present study but failed to provide good results. We found that a useful way to enhance centrum band pairs is to decalcify the vertebrae with decalcifying reagents and then section them. Sectioned centra stained with glycerin, silver nitrate, cobalt nitrate, crystal violet, copper sulfate, and hematoxylin were examined in this study. We found that the best method is to stain vertebrae with hematoxylin which distinguished peripheral band pairs of blacktip sawtail catsharks. A similar finding was suggested by Natanson et al. (2007) for the smooth skate *Malacoraja senta*. They concluded that this method can reduce the occurrence of false band pairs and enhance the determination of peripheral band pairs. Image processing resulted in clear images extending from the centrum focus to the centrum edge, thereby facilitating band-pair counting. This technique enhanced vertebral band pairs in blacktip sawtail catshark and may prove suitable for similar assessments in other species.

Cailliet and Goldman (2004) mentioned that there were increases in the use of both verification and validation methodology in chondrichthyan growth studies, such as marginal increment analysis (MIA), centrum edge analysis, size mode analysis, tag-recapture analysis, captive growth analysis, tetracycline labeling, and bomb carbon. Using combinations of verification and validation

Table 4. Age-length key of the male blacktip sawtail catshark

	Age group (yr)												
Total length (cm)	1	2	3	4	5	6	7	8	9	10	11	12	*n*
8-11	6	2											8
11-14	4	12											16
14-17		4	8	3									15
17-20		1	6	7									14
20-23			3	8	7	2							20
23-26				4	10	8	1						23
26-29				1	4	5	4						14
29-32						1	5						6
32-35					1	1	6	1	1				10
35-38							8	10	8	4	2	1	33
38-41							1	10	23	30	3		67
41-44									1	7	1	1	10
n	10	19	17	23	22	17	25	21	33	41	6	2	236
Mean	10.71	13.16	17.35	20.30	24.63	25.87	33.02	37.44	38.87	39.52	39.55	39.85	
Standard deviation	1.15	2.34	1.76	3.22	2.92	2.76	3.93	1.57	1.68	1.46	1.10	3.75	

approaches is most likely to produce more-convincing results. When combined with additional techniques, such as MIA, an edge analysis can provide valuable corroborative evidence to validate the periodicity of band formation (Cailliet et al. 2006). Because of the uncertainty of measuring the radius of the ultimate band pair, instead of combining it with the MIA, we only used the edge analysis to validate the periodicity of band-pair formation in this study and found that 1 band pair is formed per year by the blacktip sawtail catshark. Chen et al. (2007) used a captive specimen to verify their findings on band-pair formation for the whitespotted bamboo shark. In the present study, no tagging or tetracycline labeling was employed to validate our results. Therefore, a captive study is needed in the future to further validate the periodicity of band-pair formation in this species.

As in this study, most work on age and growth verification in sharks supports 1 growth band pair being formed per year in the centra. Examples include the starspotted smoothhound (Tanaka and Mizue 1979, Yamaguchi et al. 1996), spotless smoothhound (Wang and Chen 1982), and white-spotted bamboo shark (Chen et al. 2007). However, it was suggested that some species produce 2 band pairs annually, e.g., shortfin mako *Isurus oxyrinchus* (Pratt and Casey 1983) and scalloped hammerhead shark (Chen et al. 1990). The Pacific angel shark *Squatina californica* deposits growth band pairs irregularly (Natanson 1984).

There are several possible explanations for band-pair formation. A shortage of food, deprivation caused by migration and spawning, and changing temperatures may all be factors affecting their formation (Stevens 1973, Wang and Chen 1982, Campana 1983, Pratt and Casey 1983), but there are insufficient data to verify any specific cause in this study. The timing of deposition of translucent bands (fast growth) in this study contradicted the majority of studies on elasmobranchs (Cailliet and Goldman 2004). Simpfendorfer (1993) and Loefer and Sedberry (2003) reported summer deposition of the translucent bands by the Australian sharpnose shark *Rhizoprionodon acutus* and Atlantic sharpnose shark *R. terraenovae*. They suggested that stress during the breeding season was a possible explanation for band-pair deposition. It is less likely that band-pair deposition for the blacktip sawtail catshark would correlate with breeding, as the spawning behavior was found to occur year round (Chen et al. 1996). Therefore, the underlying mechanisms governing band-pair deposition in this species still require further investigation.

Table 5. Comparison of parameters estimated with different functions based on the length-at-age data of the blacktip sawtail catshark

Sex	Growth function	L_∞ (cm)	k (yr^{-1})	MSE	AIC
Female	VBGF	69.8	0.089	10.48	652.2
	VBGF with L_0	101.6	0.046	11.24	669.4
	Robertson	48.3	0.374	8.60	597.9
	Gompertz	52.8	0.232	9.33	620.1
Male	VBGF	70.1	0.081	9.55	538.6
	VBGF with L_0	118.8	0.036	10.09	549.5
	Robertson	44.3	0.392	8.23	503.3
	Gompertz	49.1	0.238	8.74	517.6

VBGF, von Bertalanffy growth function; L_∞, asymptotic length ; *k*, growth coefficient; MSE, mean square of the residuals; AIC, Akaike's information criterion.

The reliability of aging can be evaluated by (1) the IAPE (Beamish and Fournier 1981), (2) the CV (Chang 1982), (3) the D (Chang 1982), and (4) the percent agreement (PA; Cailliet and Goldman 2004). Among them, the IAPE and CV are the 2 indices most commonly used. Campana (2001) suggested that a CV of < 5% is a reasonable estimate. Cailliet and Goldman (2004) suggested that comparisons of the IAPE are only useful for the same species in the same waters. As no similar work has been done in Taiwanese waters, small values of the IAPE (3.41%) and CV (4.55%) in the current study suggest that the age determination was reliable.

The traditional VBGF is used to describe the growth of most elasmobranchs, either from observed length-at-age or from back-calculated length data. However, the VBGF does not fit all shark species. Mollet et al. (2002) noted that the Gompertz growth model of growth in the pelagic stingray *Dasyatis violacea* fit better than the VBGF. Neer and Cailliet (2001) found similar results in the Pacific electric ray *Torpedo californica*. In this study, L_∞ estimated from the VBGF and the VBGF with L_0 (Table 5) were much larger than the L_{max} for both sexes (49.8 cm TL for females and 43.2 cm for males). On the other hand, L_∞ values estimated from the Robertson growth function for both sexes were close to L_{max}, and is thought to biologically be more realistic. In addition, the observed growth rates of blacktip sawtail catsharks increased with age, peaked at 4-8 yr old, and then decreased (Tables 3, 4) which corresponded to the age-specific growth rate curve derived from the

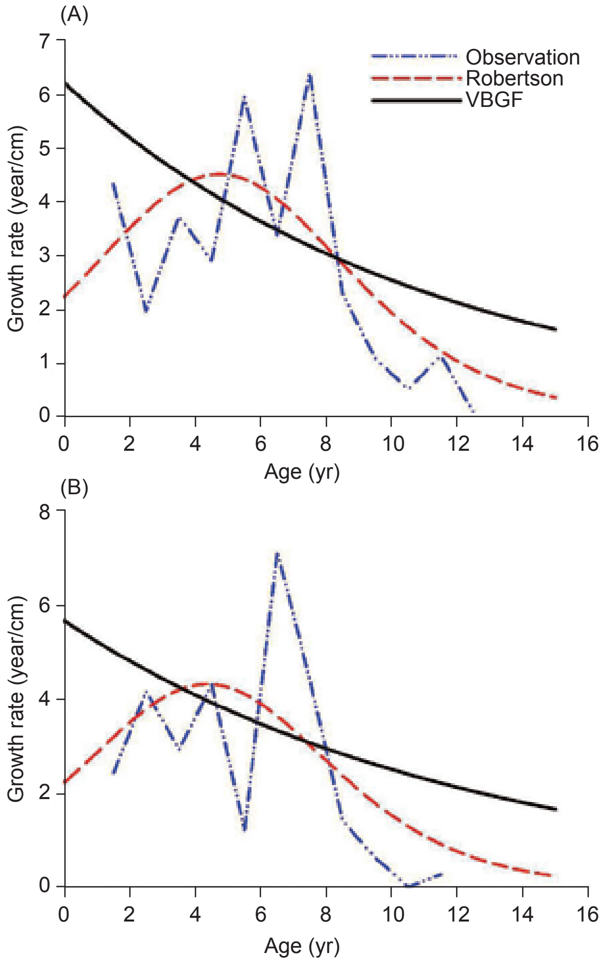

Fig. 7. Age-specific growth rate of blacktip sawtail catshark. (A) Females; –• •– : observation, – – – – : Roberson, ——— : von Bertalanffy growth function (VBGF); (B) Males, –• •–: observation, – – – – : Robertson, ——— : VBGF.

Robertson function (Fig. 7). Meanwhile, growth rates derived from the VBGF and VBGF with L_0 decreased exponentially with age, which does not correctly describe the growth rate of this species. The biologically unrealistic results imply that these 2 functions are unsuitable to describe the growth of blacktip sawtail catsharks. From an examination of the diet of blacktip sawtail catsharks, we found that the proportion of empty stomachs was as high as 73.7% for 0+ individuals, and it decreased to 40.6% for 1+ individuals (Lin unpubl. data). This suggests that the maximum growth rate of this species may not occur in the 1st year, as their swimming and feeding abilities are not fully developed. As a result, energy allocation may influence the growth rate of this species, which could explain why the Robertson function was the best growth model for this species.

The blacktip sawtail catsharks in Taiwanese waters fall into the rapid-growth group based on Branstetter's (1987) criteria. Similar patterns were also reported for other small sharks, i.e., whiskery shark *Furgaleus macki* (k = 0.29-0.42 yr^{-1}, Simpfendorfer et al. 2000); smooth dogfish *M. canis* (k = 0.21-0.53 yr^{-1}, Francis 1981, k = 0.29-0.44 yr^{-1}, Conrath et al. 2002); starspotted smoothhound (k = 0.2-0.22 yr^{-1}, Cailliet et al. 1990); brown smoothhound *M. henlei* (k = 0.23-0.28 yr^{-1}, Yudin and Cailliet 1990); gray smoothhound *M. californicus* (k = 0.22-0.35 yr^{-1}, Yudin and Cailliet 1990); and whitespotted bamboo shark (Chen et al. 2007) (Table 6).

The L_∞ of sharks might be correlated to the depth of their habitats. L_∞ values of the blacktip

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

Species	Region	Growth function	Sex	L_∞ (cm)	k	Authors
Chiloscyllium plagiosum	Northern Tai wan	VBGF with L_0	Female	93.1	0.224	Chen et al. (2007)
		VBGF with L_0	Male	98.4	0.213	
Furgaleus macki	Southwestern Australia	VBGF	Female	120.7	0.369	Simpfendorfer et al. (2000)
		VBGF	Male	121.5	0.423	
Mustelus canis	Northwest Atlantic	VBGF	Female	123.6	0.292	Conrath et al. (2002)
		VBGF	Male	105.2	0.439	
Mustelus californicus	California, USA	VBGF	Female	142.4	0.220	Yudin and Cailliet (1990)
		VBGF	Male	101.8	0.350	
Mustelus henlei	California, USA	VBGF	Female	97.6	0.225	Yudin and Cailliet (1990)
		VBGF	Male	86.1	0.285	
Mustelus manazo	Nagasaki, Japan	VBGF	Female	99.9	0.200	Cailliet et al. (1990)
		VBGF	Male	84.6	0.220	
Galeus sauteri	Northeastern Taiwan	Robertson	Female	48.3	0.374	Current study
		Robertson	Male	44.3	0.392	

L_∞, asymptotic length; k, growth coefficient; VGBF, von Bertalanffy growth function; L_0, fixed size at birth.

sawtail catshark estimated from this study were 48.3 and 44.3 cm in TL for females and males, respectively, which are similar to those of the lantern shark *Etmopterus spinax* (Coelho and Erzini 2008) and smooth lantern shark *E. pusillus* (Coelho and Erzini 2007). These sharks are demersal species which live at 100-300 m in depth. Other small sharks such as whitespotted bamboo shark, smooth dogfish, and smalltail shark *Carcharhinus porosus*, which live in shallower waters at 20-200 m have larger L_∞ values.

The ratio, L_m / L_∞, ranges 0.6-0.8 for sharks (Compagno 1984). In this study, the ratios were estimated to be 0.84 and 0.78 for females and males, respectively, which fall into the late- and moderate-maturing group, respectively (Joung 1993). The smalltail shark and whitespotted bamboo shark also fall into this group.

The blacktip sawtail catshark falls into the 2nd group with a characteristic of fast growth and a short lifespan based on the life-history parameters analysis of 39 species (62 stocks) (Chen 2007). Management measures of regular stock assessments, coupled with fishing seasons and fishing area closures, were recommended for these species (King and MacFarlane 2003).

In conclusion, this study provides the 1st detailed estimates of age and growth for the blacktip sawtail catshark, which can be used as biological input parameters for further stock evaluations in this region. Still, additional validation of the size composition and stock structure is needed in future studies.

Acknowledgments: We would like to thank 2 anonymous reviewers for their constructive help in greatly improving this manuscript. Financial support for this study was from the National Science Council, Taiwan, through grants NSC97-2313-B-019-002-MY2 and NSC98-2621-M-019-001.

REFERENCES

Anon. 2002. Report of the working group on the biology and assessment of deep-sea fisheries resources. Copenhagen, Denmark: ICES C.M. document no. ACFM 16.

Anon. 2009. Fisheries Statistics Year Book Taiwan. Fisheries Agency, Council of Agriculture, Republic of China, Taipei, Taiwan.

Beamish RJ, DA Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. **38:** 982-983.

Branstetter S. 1987. Age and growth estimates for blacktip, *Carcharhinus limbatus* and spinner, *C. brevipinna* sharks from the northwestern Gulf of Mexico. Copeia **1987:** 964-974.

Cailliet GM, KJ Goldman. 2004. Age determination and validation in chondrichthyan fishes. *In* JF Carrier, JA Musick, MR Heithaus, eds. The biology of sharks and their relatives. Boca Raton, FL: CRC Press, pp. 399-447.

Cailliet GM, KG Yudin, S Tanaka, T Taniuchi. 1990. Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral band pairs. *In* WS Pratt Jr, SH Gruber, T Taniuchi, eds. Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. Washington D.C.: National Oceanic and Atmospheric Administration Technical Report, pp. 167-176.

Cailliet GM, WD Smith, HF Mollet, KJ Goldman. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environ. Biol. Fish. **77:** 211-228.

Campana SE. 1983. Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Can. J. Zool. **61:** 1591-1597.

Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59:** 197-242.

Campana SE, MC Annand, JI McMillan. 1995. Graphical and statistical methods for determining consistency of age determinations. Trans. Am. Fish. Soc. **124:** 131-138.

Chang WYB. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. **39:** 1208-1210.

Chen CH. 2007. Shark management based on vital parameters analysis. MS thesis, National Taiwan Ocean Univ., Keelung, Taiwan, 131 pp.

Chen CT, TC Leu, SJ Joung, NCH Lo. 1990. Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. Pac. Sci. **44:** 156-170.

Chen CT, YY Liao, SJ Joung. 1996. Reproduction of the blacktip sawtail catshark, *Galeus sauteri*, in the waters off northeastern Taiwan. Ichthyol. Res. **43:** 231-237.

Chen WK, PC Chen, KM Liu, SB Wang. 2007. Age and growth estimates of the whitespotted bamboo shark, *Chiloscyllium plagiosum*, in the northern waters of Taiwan. Zool. Stud. **46:** 92-102.

Coelho R, K Erzini. 2008. Life history of a wide-ranging deepwater lantern shark in the north-east Atlantic, *Etmopterus spinax* (Chondrichthyes: Etmopteridae), with implications for conservation. J. Fish. Biol. **73:** 1419-1443.

Coelho R, K Erzini. 2007. Population parameters of the smooth lantern shark, *Etmopterus pusillus*, in southern Portugal (NE Atlantic). Fish. Res. **86:** 42-57.

Compagno LJV. 1984. FAO species catalogue. Vol. 4, Part 2: Sharks of the world. FAO Fish. Synop. **125:** 173.

Conrath CL, J Gelsleichter, JA Musick. 2002. Age and growth of the smooth dogfish (*Mustelus canis*) in the Northwest Atlantic Ocean. Fish. Bull. **100:** 674-682.

Efron B, RJ Tibshirani. 1993. An introduction to the bootstrap. London: Chapman and Hall.

Fabens AJ. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth **29:** 265-289.

Figueiredo I, PB Machado, LS Gordo. 2005. Deep-water sharks fisheries off the Portuguese continental coast. J. NW Atlantic Fish. Sci. **35:** 291-298.

Francis MP. 1981. Von Bertalanffy growth rates in species of *Mustelus* (Elasmobranchii: Triakidae). Copeia **1981:** 189-192.

Gompertz B. 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining life contingencies. Phil. Trans. Royal Soc. Lond. Ser. A **115:** 513-585.

Haddon M. 2001. Modelling and quantitative methods in fishes. London: Chapman and Hall/CRC Press.

Huang SY. 1996. Genetic variations of *Mustelus manazo* (Carcharhiniformes: Triakidae) between the populations from Taiwanese and Japanese waters. MS thesis, National Taiwan Ocean Univ., Keelung, Taiwan, 53 pp.

Joung SJ. 1993. Biology of the sandbar shark, *Carcharhinus plumbeus*, in northeastern waters of Taiwan. PhD dissertation, National Taiwan Ocean Univ., Keelung, Taiwan, 162 pp.

Kimura DK. 1980. Likelihood models for the von Bertalanffy growth curve. Fish. Bull. **77:** 765-767.

King JR, GA McFarlane. 2003. Marine fish life history strategies: applications to fishery management. Fish. Manag. Ecol. **10:** 249-264.

Liao YY. 1992. Reproduction of the blacktip sawtail catshark, *Galeus sauteri*, in Guei-Shan Island waters, northeastern Taiwan. MS thesis, National Taiwan Ocean Univ., Keelung, Taiwan, 87 pp.

Loefer JK, GR Sedberry. 2003. Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States. Fish. Bull. **101:** 75-88.

Mollet HF, JM Ezcurra, JB O'Sullivan. 2002. Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). Mar. Freshwater Res. **53:** 531-541.

Natanson LJ. 1984. Aspects of the age, growth, and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. MS thesis, San Jose State Univ., San Jose, CA, 71 pp.

Natanson LJ, JA Sulikowski, JR Kneebone, PC Tsang. 2007. Age and growth estimates for the smooth skate, *Malacoraja senta*, in the Gulf of Maine. Environ. Biol. Fish. **80:** 293-308.

Neer JA, GM Cailliet. 2001. Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia **2001:** 842-847.

Pratt HL Jr, JG Casey. 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. **40:** 1944-1957.

Robertson TB. 1923. The chemical basis of growth and senescence. Philadelphia, PA: JB Lippincott, 98 pp.

Simpfendorfer CA. 1993. Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. Environ. Biol. Fish. **36:** 233-241.

Simpfendorfer CA, J Chidlow, R McAuley, P Unsworth. 2000. Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia. Environ. Biol. Fish. **58:** 335-343.

Stevens JD. 1973. Stomach contents of the blue shark (*Prionace glauca* L.) off southwest England. J. Mar. Biol. Assoc. UK **53:** 357-361.

Tanaka S, K Mizue. 1979. Age and growth of Japanese dogfish, *Mustelus manazo* Bleeker, in the East China Sea. Bull. Jpn. Soc. Sci. Fish. **45:** 43-50.

von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. **10:** 181-213.

Wang TM, CT Chen. 1982. Age and growth of smooth dogfish, *Mustelus griseus*, in northwestern Taiwan waters. J. Fish. Soc. Taiwan **9:** 1-12.

Yamaguchi A, T Taniuchi, M Shimizu. 1996. Age and growth of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. Fish. Sci. **62:** 919-922.

Yudin KG, GM Cailliet. 1990. Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei*, sharks from central California. Copeia **1990:** 191-204.