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Age, Growth and Reproduction of the Oceanic Whitetip Shark from the Pacific Ocean

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We studied age, growth, and maturity of the oceanic whitetip shark *Carcharhinus longimanus* in the North Pacific, and the reproduction in the North and South Pacific, captured with tuna longline from Nov. 1967 to Oct. 1995. Vertebral rings were examined from 111 males (precaudal length: 54–172 cm) and 114 females (precaudal length: 50–195 cm). Minimum and maximum numbers of translucent rings were 0 and 11. Marginal increment analysis suggested annualus deposition occurs during spring. A growth difference between sexes was not found. A von Bertalanffy growth equation combining both sexes was as follows;

$$L_t = 244.58 \times \{1 - e^{-0.103 \times (t+2.698)}\}$$

L_t was expressed as precaudal length in cm at age t.

The reproductive condition was examined from 136 males and 85 females. Maturation was determined to be when precaudal length was between 125 and 135 cm for both sexes (4–5 years). The parturition period is extended over a long duration. The birth size was 45–55 cm and litter size varied from 1–14 with a mean of approximately six in the North Pacific.

Key words: Pacific, *Carcharhinus longimanus*, age, growth, reproduction, maturation

In recent years, fishery by-catch has been regarded as a threat to marine biodiversity. Elasmobranchs are especially vulnerable to fishing pressure because of their low abundance, late maturity and low fecundity.[1] On the other hand, elasmobranchs have been exploited as both food fish and medical materials. Historically, sharks were discarded because of their low commercial value, but in the latest years sharks have been considered a promising resource for anti-cancer treatment, artificial skin, and anti-blood coagulation medicine.[2]

Though biological information on shark resources is required for rational exploitation and fisheries knowledge, such information is limited for many species.[3] Particularly, basic information such as annual growth rate and maturity size is quite deficient for many oceanic species because of difficulty in sampling in the oceanic regions.

The oceanic whitetip shark *Carcharhinus longimanus* is a large species, attaining 3.5 m in total length, and widely distributed in the surface layer of warm waters far at sea.[4-10] Strasburg[6] suggested the oceanic whitetip shark is the second most abundant carcharinoid in the North Pacific. Bonfil[11] estimated annual catches of the oceanic whitetip shark in the North Pacific tuna longline fisheries to be more than 7,200 fishes based on the catch rates reported by Strasburg[6] and total fishing efforts (hooks) estimated by Nakano and Watanabe.[12] However, very little is known about the biology of the oceanic whitetip shark. Only one study[9] on the age and growth is available, based upon the centrum observation of 13 sharks. We report here age, growth and reproduction of the oceanic whitetip shark from the Pacific Ocean employing examination of vertebral rings and gonadal conditions.

Materials and Methods

Samples and biological data were collected from four researches aboard institutional tuna longline fishing vessels in the Pacific from November 1967 to October 1995 (Fig. 1, Table 1).

Age and growth of the oceanic whitetip shark were analyzed from vertebrae collected in the three researches

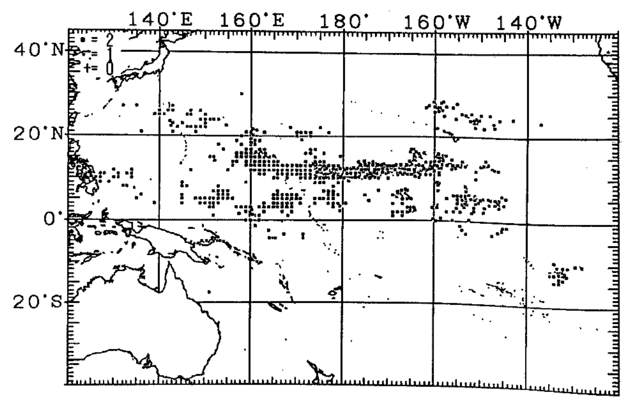

Fig. 1. Catch sites of the oceanic whitetip sharks in this study.

Table 1. Source of data used in this study

Research name	Authors' Research	Authors' Committal Research	NRIF By-catch Research	Committal Research of Univ. of Tokyo
Periods	1995.1–1995.3	1995.1–1995.10	1992.2–1995.3	1967.11–1971.2
No. of vessels	1	12	34	5
No. of researches	1	16	190	16
Shark catch No.	26	270	5028	>1575
Used shark No.				
the North Pacific				
total	26	270	120	34
male	18	129	39	
female	8	137	81	34
pregnant	1	15	65	34
embryo				
(litter:individual)	1:10	15:83	65:409	34:220
the South Pacific				
total	—	—	6	18
male	—	—		
female	—	—	6	18
pregnant	—	—	6	18
embryo	—	—		
(litter:individual)	—	—	5:25	18:109

(authors' research, authors' committal research and National Research Institute of Far Seas Fisheries (NRIFS) by catch research). The vertebrae were sampled from 143 males (139 free-swimming individuals ranging from 54–172 cm in precaudal length (PL; the distance from snout to precaudal pit); 4 embryos ranging from 26.4–47.6 cm PL), and 146 females (140 free-swimming individuals ranging from 47–195 cm PL; 6 embryos ranging from 26.0–53.4 cm PL) from the North Pacific. After measurement of precaudal length, centra were obtained from near gill slits. Vertebral samples were frozen at −40°C. They were boiled in our laboratory to remove the connective tissues from the centrum surface and stored in 70% alcohol for more than a month before processing.

Three observation methods (silver nitrate staining, soft-X-ray fluoroscopy and alizarin red S staining) were examined for six sets of whole and sectioned centra from different sizes. Silver nitrate staining followed Stevens[13] and the alizarin red S staining method of Berry *et al.*[14] was modified. Alizarin red S of thin centrum sections showed a distinct stain differently from the former method. The solution is the mixture of potassium hydroxide (15% in distilled water), glycerin (16% in distilled water) and alizarin stock solution by the ratio in 35:14:1. The alizarin stock solution is composed of the mixture of 2 g alizarin red S, 33 cc distilled water and 33 cc concentrated acetic acid.

Vertebrae were cut into longitudinal sections with a diamond band saw (EXAKT-cutting grinding system BS-3000 by EXAKR-Apparatebau). First, centra were cut in half through centrum focus. The focus of the section was determined by the presence of the notochordal remnant. The sectioned surface of the half-centrum was polished with wet 3,000 grit sandpaper and attached to transparent plastic board with an adhesive. Each centrum section was cut laterally again to produce an approximately 0.3 mm thin section, the exposed surface was polished, and the section was soaked in the staining solution for about 4–24 hours. After staining they were rinsed in running tap water for several minutes, and soaked into 100% ethanol. Finally, the section was packed with Euparal and cover glass.

Sections were observed and measured using a Nikon Profile Projector V-16E (Nippon Kogaku K.K.) with transmitted light. Centrum radius and ring radius were measured to the nearest 0.001 mm. The centra of carcharhinid sharks are well calcified, and concentric annuli are formed as concentric depressions on the centrum face (corpus calcareum). Furthermore, the annuli bordered with hard stained bands in corpus calcareum, and well stained stratified structures pass through the intermedialia, connecting both side of this mark. The centrum radius was measured as a perpendicular line from the notochordal remnant (focus) to the end of corpus calcareum (inner margin of the corpus calcareum. Fig. 2), and ring (annulus) radii are measured in the same way to each depression. In the case where wavy structures were not clear in the corpus calcareum, the measurement was made at the end of hard stained part in the corpus calcareum. All samples were counted for four times without knowledge of the length of the specimen, and only the data were used if the counts agreed three times.

Marginal increment analysis was performed to verify the periodicity of ring formation. Marginal increments were calculated by dividing absolute marginal increment widths by the width of the last fully formed ring. Obtained marginal increments were compared by month of capture. The centra of embryos and neonates were compared to determine when the birth ring forms. The estimated precaudal lengths at the time of annulus formation were back-calculated from mean values of each ring radius. A von Bertalanffy growth function was fitted using the Akamine's computer program by the least squares method.[15] The PL-at-age from the von Bertalanffy growth curve was compared with the observed PL-at-age at capture. Age at capture was determined based on the number of annuli and marginal increments.

The measurement data and clasper, testis, ovary (right

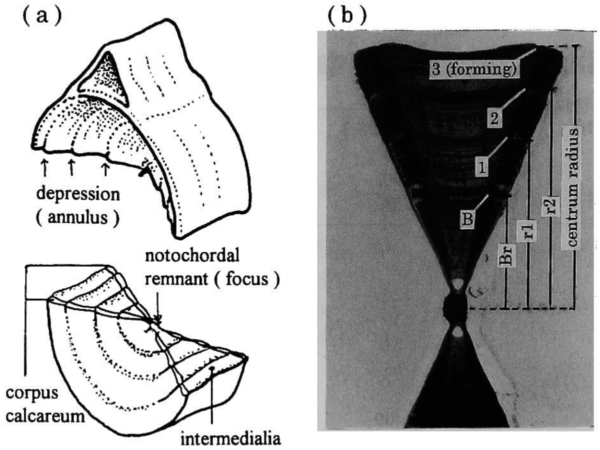

Fig. 2. Diagram of typical centrum showing the sectioning plane used (a), and alizarin red S stained centrum section obtained from a 114 cm PL male of the oceanic whitetip shark with a birth ring and three growth rings (b). "Br" is birth ring radius, "r1" and "r2" are radius of each growth ring.

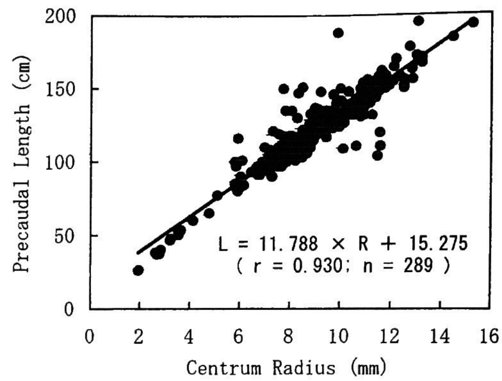

Fig. 3. Linear relationship between centrum radius and precaudal length for the oceanic whitetip sharks (n=289, the North Pacific Sample).

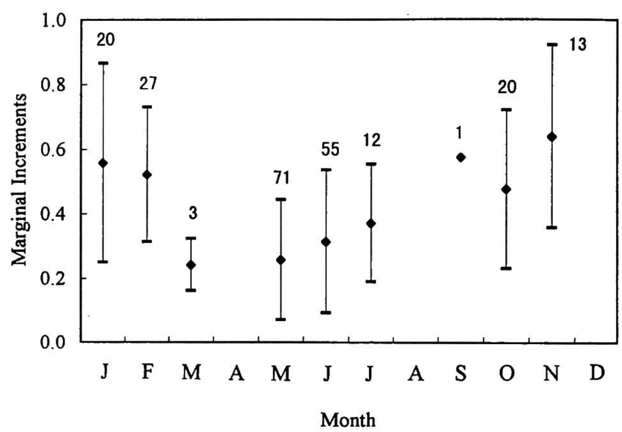

Fig. 4. Marginal increments for the oceanic whitetip shark centrum by each month (the North Pacific sample).

Plots and bars show the mean and the standard deviation respectively. The number above upper standard deviation plot indicates sample number.

only) samples were collected from January to July in 1995 (by authors' research and authors' committal research). Body weights were recorded for 133 males and 128 females. Clasper lengths were measured to the nearest 1 mm for 136 males. For 15 males, the degree of clasper calcification was judged by rigidity, and the existence of semen was judged from the presence of white mucus in the Wolffian duct, seminal vesicle and sperm sac. Testes of 102 males and ovaries of 145 females were sampled and frozen immediately at $-40°C$. These were defrosted and weighed to the nearest 0.1 g in the laboratory. The largest egg diameter for 81 females was measured with a caliper in the laboratory. Pregnancy was examined for 145 females. Precaudal length and body weight of embryos from 15 litters were obtained in the laboratory. Supplemental data (the captured position, litter size and precaudal length of pregnant females, neonates and embryos) from the two researches (NRIF by-catch research and the committal research of Univ. Tokyo) were included in this analysis.

We transformed precaudal length (PL) to total length (TL) using the data presented by Bass *et al.*[14] to enable comparison of our study with other reports. The equation was:

$$TL = 1.397 \times PL$$

Results

Age and Growth

A total of 225 samples (included 111 males and 114 females) were used for aging analysis. Centrum radius showed a liner relationship with precaudal length (Fig. 3). Sexes were combined because of no difference between sexes (ANCOVA: $F_0 = 0.011 \ll F_{(1,\infty)}\ (0.05)$). The equation obtained was:

$$L = 11.788 \times R + 15.275 \quad (r = 0.930)$$

Marginal increment analysis indicated annuli form in spring (Fig. 4). Marginal increments were small in March and May, and increase gradually thereafter. Age was assigned assuming an annual band formation. In this study, corroboration with comparisons to back-calculated lengths at each ring could not be conducted because samples were not enough for some months and age classes, but it is needed for more precise study.

There were no differences between sexes for the first to ninth ring radii (ANCOVA: $F_0 = 0.00005 \ll F_{(1,9)}\ (0.05)$); accordingly we concluded that the oceanic whitetip shark has no sexual difference in growth. Mean PL-at-age was back-calculated from mean ring radius data combined sexs (Table 2). The expected PL at formation of birth ring is 58 cm. No ring was seen in full-term embryos' centra, but all neonates had a ring either formed or forming, even in specimens smaller than near-term embryos. This indicates birth ring formed soon after birth. The von Bertalanffy growth function was:

$$L_t = 244.58 \times \{1 - e^{-0.103 \times (t + 2.698)}\}$$

The curve fit very well to back-calculated and observed PL (Fig. 5).

Table 2. Mean back-calculated precaudal lengths corresponding to centrum rings by age-class for 225 oceanic whitetip sharks, sexes combined

Age Class	Sample Size	Birth	Mean back-calculated precaudal length (cm) at ring for each age-class										
			1	2	3	4	5	6	7	8	9	10	11
Neonate	4	58.45											
1	11	55.99	78.07										
2	53	57.87	78.88	98.28									
3	59	58.14	77.39	95.30	109.41								
4	34	57.27	78.69	95.50	109.65	122.18							
5	28	58.46	75.73	94.15	109.72	122.79	135.11						
6	16	57.29	77.50	96.82	110.44	123.49	135.65	144.46					
7	12	58.10	78.64	95.70	109.72	120.91	133.62	144.18	152.72				
8	3	57.66	76.89	89.81	106.32	122.27	134.59	146.10	154.38	162.22			
9	2	61.50	78.16	94.29	108.88	123.46	135.88	145.20	157.46	161.78	169.40		
10	2	58.17	76.27	89.87	110.59	120.42	130.92	145.11	155.19	161.74	169.29	175.89	
11	1	57.87	78.21	94.42	109.77	119.94	131.88	147.82	155.38	162.27	170.09	180.52	188.83
Total	225	57.85	77.84	95.93	109.60	122.38	134.78	144.67	153.82	161.99	169.49	177.43	188.83

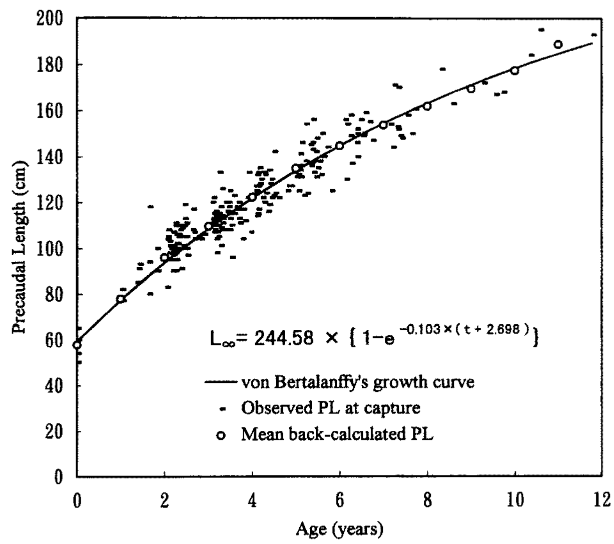

Fig. 5. The von Bertalanffy's growth curve fitted to mean back-calculated lengths at age for each age-class, sexes combined, based on centrum analysis for the oceanic whitetip shark from the North Pacific. The age at capture is the sum of number of annuli and marginal increments (neonate's age-at-capture is only the number of annuli).

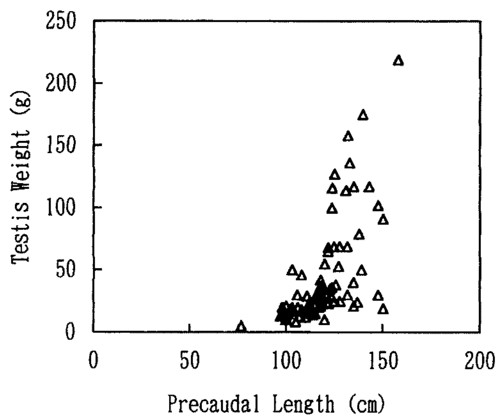

Fig. 6. The relationship between precaudal length and testis weight for 102 males of the oceanic whitetip shark in the North Pacific.

Reproduction

The relationship between precaudal length (PL) and body weight (BW) was different between sexes (ANCOVA, $F_0 = 14.738 < F_{(1,\infty)}$ (0.05)):

$$BW = 3.077 \times 10^{-5} \times PL^{2.860}$$

(133 males; r=0.937)

and

$$BW = 5.076 \times 10^{-5} \times PL^{2.761}$$

(128 females; r=0.941).

We determined that male maturity is reached at 120–140 cm PL. Testes weights between May and July increased with precaudal lengths, and showed rapid increase from 120 cm PL (Fig. 6). The beginning of testis ripeness seems to be 120 cm PL judging from the winding distribution of testes weight. Clasper length of 136 males increased rapidly between 100 and 140 cm PL (Fig. 7). Claspers longer than 180 mm were calcified, and specimens with them had semen (Fig. 7). Claspers over 180 mm were not seen in individuals less than 110 cm PL, but were observed at 112 cm PL. The percentages of such individuals were 35.7% in the 121–130 cm PL class, 78.9% in the 131–140 cm PL class and almost all males larger than 141 cm PL had claspers over 180 mm. Following Bass *et al.*[7] that males are considered mature when the claspers are fully grown with the rigid cartilage, our data indicate male maturity was reached completely when clasper lengths extended over 180 mm. Therefore, maturity occurs between 110 and 140 cm PL, and most males mature between 125 and 135 cm PL (175–189 cm TL). Male mature size in this study corresponds to the age between four to five years old in our growth curve.

The smallest pregnant female was 98 cm PL (Fig. 8). We could not obtain pregnancy ratio because pregnancy was not fully investigated, but until 130 cm PL, the frequency of occurrence of pregnant females was low. Ovary weights

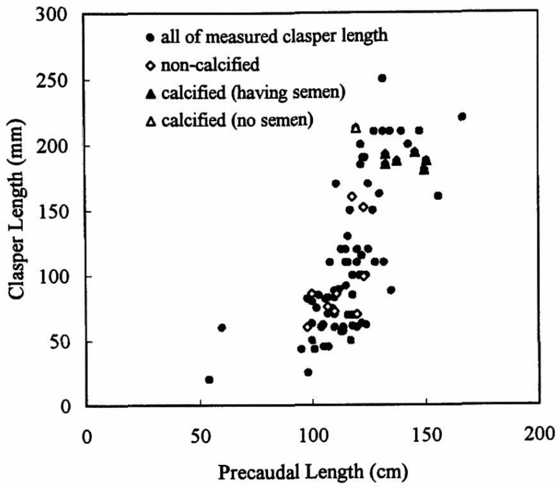

Fig. 7. The relationship between precaudal length and clasper length for 136 males of the oceanic whitetip shark in the North Pacific.

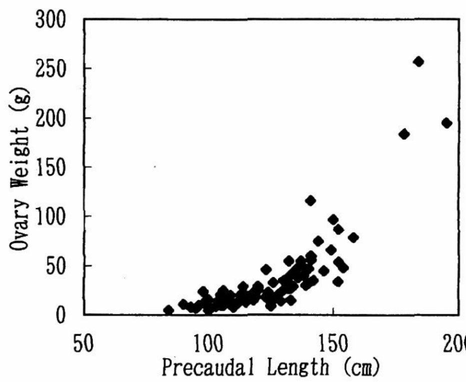

Fig. 8. The histogram of precaudal length in pregnant females of the oceanic whitetip shark.

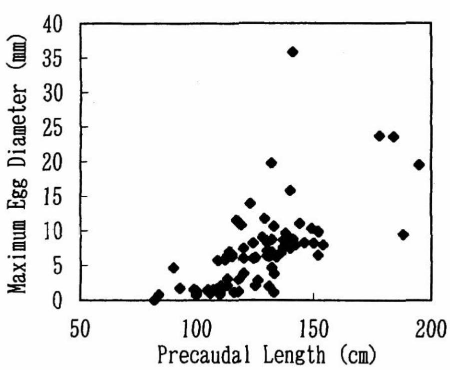

Fig. 9. The relationship between precaudal length and ovary weight for 85 females of the oceanic whitetip shark in the North Pacific.

(Fig. 9) and egg diameters (Fig. 10) increased with precaudal lengths, and the latter scattered suddenly from 121–130 cm PL class. The largest egg diameter within the smallest pregnant female was 6.3 mm. The ratio of females with eggs over 6.0 mm in diameter to all females within the

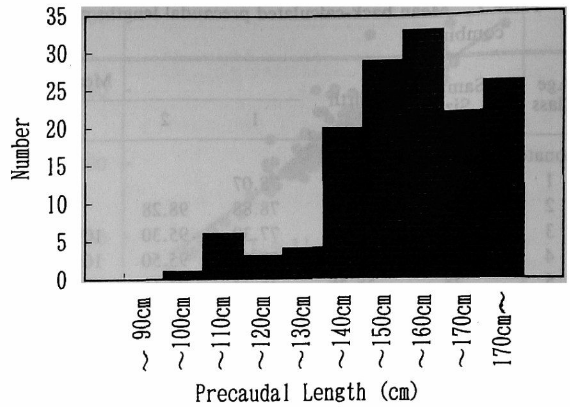

Fig. 10. The relationship between precaudal length and maximum egg diameter for 81 females of the oceanic whitetip shark in the North Pacific.

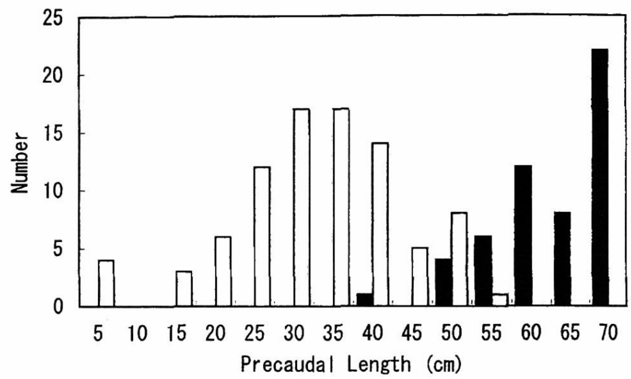

Fig. 11. The histogram of precaudal length in neonates (black) and average size of embryos within a litter (white).

same precaudal length class was 50% in 111–120 cm PL class, and all females over 141 cm PL had large eggs (Fig. 10). Most female maturity seems to be reached at 125–135 cm PL at the age of about four to five years old. The maximum egg size was 35 mm for non-pregnant females and 23 mm for pregnant females. The pregnant females do not seem to get pregnant again soon after parturition.

The size of embryos overlapped with the size of neonates at 40–55 cm (55–75 cm TL, Fig. 11), therefore this is the birth size. However, the 40 cm neonate is quite small in comparison with another neonates, suggesting that the neonate was premature. Therefore the usual birth size can be estimated between 45 and 55 cm PL. In the North Pacific, small embryos (less than 50 mm PL) were observed from June to July, mid-term embryos (50–200 mm PL) from July to January, large embryos (larger than 450 mm PL) from January to June, and small free swimming individuals (smaller than 600 mm PL) from February to July and November (Fig. 12). In the South Pacific, small to mid-term embryos were observed in November and large ones in February and September. Our data were not enough to support a well defined reproductive season but rather showed an extended period of parturition.

The litter sizes for 97 pregnant females from the North

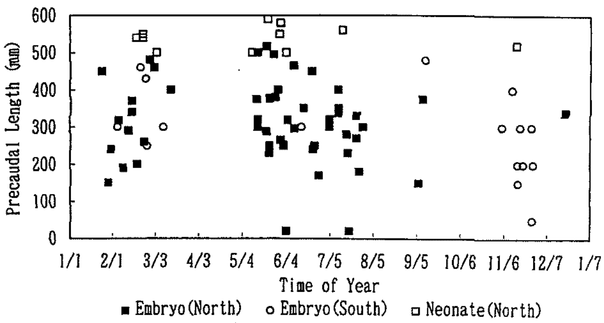

Fig. 12. The relationship between precaudal length and time of year for average size of embryos for each litter and neonates of the North and South Pacific.

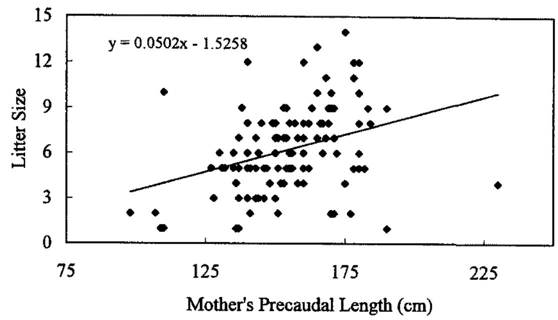

Fig. 13. The relationship between precaudal length of mother and litter size in the North Pacific.

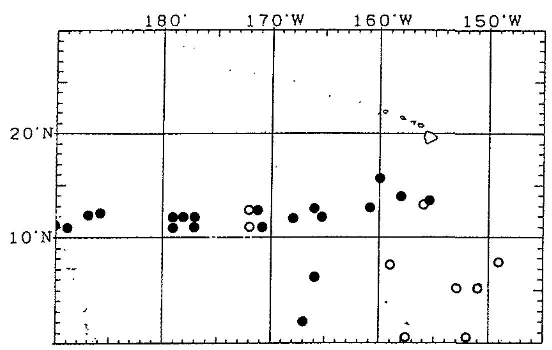

Fig. 14. The distribution of small neonates (smaller than 60 cm PL) and the pregnant females with large embryos over 45 cm PL averaged by each litter in the North Pacific. (●: neonates and ○: pregnant females with large embryos).

Pacific ranged from 1–14, with a mode of five and an average of 6.2. Sex ratio was 1:1 for each litter and total embryos (622 individuals, $\chi^2=0.890$, $p>0.05$). The relationship between mother's precaudal length and litter size was:

$$Y=0.0502X-1.52 \quad (r=0.391)$$

where X is mother's precaudal length and Y is litter size (Fig. 13). There was no significant relationship between mother's precaudal length and litter size in the South Pacific perhaps for too small sample size. The litter size in the South Pacific varied from 1–12 with an average of 5.5.

The nursery area in the North Pacific seems to be in the central Pacific judging from the distribution of neonates smaller than 60 cm PL and pregnant females with large embryos over 450 mm PL (Fig. 14).

Discussion

For the oceanic whitetip shark, vertebral rings from 13 individuals were examined by Saika and Yoshimura.[9] Almost none of our ring counts agreed with their results. They may have counted ancillary rings present in the intermediaria and the corpus calcareum. Our growth parameters did not agreed with the estimated range calculated by Branstetter[16] based on Bass *et al.*,[7] Backus *et al.*[5] and Saika and Yoshimura.[9] Branstetter[16] regarded the oceanic whitetip shark as a slow growth species (growth coefficient $K<0.10$) like the bull shark *Carcharhinus leucas* and the sandbar shark *Carcharhinus plumbeus*. Following his opinion, our estimation value of K ($K=0.103$) classifies the oceanic whitetip shark into the rapid growth species ($K>0.10$) like the silky shark *Carcharhinus falciformis* and the blue shark *Prionace glauca*.

The reported largest shark is 3.5 m TL (250 cm PL) which Bigelow and Schroeder[4] had an exact measurement. Bigelow and Schroeder[4] suggested the maximum size of 365–395 cm TL (261–283 cm PL), but Backus *et al.*[5] estimated smaller. Our result ($L_\infty=245$ cm PL) followed Backus *et al.*,[5] but the possibility of regional difference also needed to be considered.

Saika and Yoshimura[9] estimated testes ripened at 168 cm TL from the observation of testes tissue for seven males, and maturity was at 170–180 cm TL (121–128 cm PL) from clasper lengths for 14 males in the western Pacific. This is similar to our data. However, they did not investigate the body size at the clasper calcification. The calcification finishes at the full elongation, and hence, it is more appropriate to consider the mature size as a little larger than their estimates. Bass *et al.*[7] suggested 194 cm TL is a border line between mature and immature males in South African waters. This is larger than our estimate, and may be due to a regional difference in populations of this species.

Bass *et al.*[7] judged signs of maturity in females by distinct eggs in the ovary and expansion of the uterine, and estimated maturity size as 170–180 cm TL (122–129 cm PL). Saika and Yoshimura[9] reported the mature female of 171 cm TL (122 cm PL) from their observation on eggs and uteri. Uterine form was not investigated in this study; maturation was based on pregnant females, ovary weight and egg size. The occurrence of the 98 cm pregnant female is unusual because pregnant female less than 125–135 cm PL (175–189 cm TL) have rarely observed in the longline fisheries [Seki: unpubl. data]. Therefore females reach maturity at sizes over 125–135 cm PL. The estimated mature size of female is similar to other studies.[7,9] The very small pregnant female may suggest that we are dealing with some local sub-population which matures at a smaller size and does not attain as large as the maximum length.

Backus *et al.*[5] and Bass *et al.*[7] estimated parturition occurs from late spring to summer. Saika and Yoshimura[9] suggested protracted periods of parturition and mating. Our data on embryo size distribution do not show an apparent parturition period but a quite extended duration over the year. However, it is possible to estimate that conception occurs between June and July, and parturition occurs between February and July in the North Pacific. If it is the case, the gestation period may be considered to be 9–12 months, which agrees with the result of Backus *et al.*[5] On the other hand, conception seems to occur in November in the South Pacific, judging from embryo size distribution shown in Fig. 12. It is also possible to estimate that the oceanic whitetip shark does not have a well defined reproductive cycle because of embryo occurrence in almost every month when data were obtained. Since we have limited data on reproduction in time and space, further efforts for the collection of biological data, particularly in time between August and January and in the South Pacific region, are needed to clarify reproductive habits of the oceanic whitetip shark with wide distribution.

The result for birth size in this study, 40–55 cm PL (55–77 cm TL) indicates the wider range (of birth size) than the estimation by other studies.[5,7,9] The litter size, correlation between the length of the mother and the litter size and the sex ratio of embryos are similer to other reports.[7,9]

The oceanic whitetip shark has a nursery ground in the oceanic region. This tendency differs from that of some rapid growth oceanic species like the silky shark and the night shark *Carlcharhinus signatus*. Their neonates inhabit the deep reef areas along continental shelf edge to escape predation risk from large sharks.[16] The oceanic whitetip shark seems to have a different survival strategy from the above species. Rapid annual growth and rapid maturity may be necessary to survival strategy of the oceanic whitetip shark.

Backus *et al.*[5] discussed that pregnant females would not mate during the coming summer judging from the fact that pup-bearing females had much smaller eggs than non-pregnant females. Our measurement of egg size agrees with Backus *et al.*[5] Age and growth, age at maturity, litter size, gestation period and frequency of pregnancy are very important in the stock management of sharks. This study elucidated some of these important life-history parameters.

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References

1) R. Bonfil, R. Mena, and D. de Anda: Biological parameters of commercially exploited silky sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico. *U.S. Dep. Commer., NOAA Tech. Rep. NMFS*, **115**, 73-86 (1990).

2) V. G. Springer and J. P. Gold: Sharks in Question, The Smithsonian Answer Book, Smithsonian Institution Press, 1989, p. 187.

3) H. Nakano and T. Seki: Cruise report of the Japanese tuna longline fishery (central tropical Pacific: Ashumaru), National Research Institute of Far Seas Fisheries, 1994, p. 73.

4) H. B. Bigelow and W. C. Schroeder: Sharks, in "Fishes of the western North Atlantic, Part one" (ed. by A. E. Parr and Y. H. Olsen), *Sears Found. Mar. Res., Yale Univ. Mem.*, **1**, 59-546 (1948).

5) R. H. Backus, S. Springer, and E. L. Arnold: A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). *Deep Sea Res.*, **3**, 178-188 (1956).

6) D. W. Strasburg: Distribution, abundance, and habits of pelagic sharks in the Central Pacific Ocean. *Fish. Bull.*, **138**, 335-361 (1958).

7) A. J. Bass, J. D. D'Aubrey, and N. Kistnasamy: Sharks of the east coast of southern Africa. I.The genus *Carcharhinus* (Carcharhinidae). *S. Afr. Assoc. Mar. Biol. Res., Invest. Rep.*, **33**, 8–9 and 49–55 (1973).

8) Garrick, J. A. F.: Sharks of the Genus *Carcharhinus. U.S. Dep. Commer. NOAA Tech. Rep. NMFS Circular*, **445**, 1982, p. 194.

9) S. Saika and H. Yoshimura: Oceanic whitetip shark (*Carcharhinus longimanus*) in the western Pacific. *Reps. Japanese Society for Elasmobranch Studies*, **20**, 11-21 (1985).

10) T. Taniuchi: Some biological aspects of sharks caught by floating longline-1. Species, distribution, species composition and hook rates. *Reps. Japanese Society for Elasmobranchs Studies*, **31**, 1-12 (1994).

11) R. Bonfil: Overview of world elasmobranch fisheries, FAO Fish. Tech. Paper. 341., Food and Agriculture Organization of the United Nations. Rome, Italy, 1994, p. 119.

12) H. Nakano and Y. Watanabe: Effect of high seas driftnet fisheries on blue shark stock in the North Pacific, Compendium of documents submitted to the Scientific Review of North Pacific Highseas Driftnet Fisheries, Sidney, Vol. 1, 1991.

13) J. D. Stevens 1975: Vertebral rings as a means of age determination in the blue shark (*Prionace glauga* L.). *J. Mar. Biol. Assoc. U.K.*, **55**, 657-665 (1975).

14) F. H. Berry, D. W. Lee, and A. R. Bertolino: Age estimates in Atlantic bluefin tuna-an objective examination and an intuitive analysis of rhythmic markings on vertebrae and in otoliths, in "Collection volume of scientific papers" Vol. VI(2), Interntional commission for the conservation of Atlantic tunas, Madrid, 1977, pp. 306–316.

15) T. Akamine: Expansion of growth curve using periodic function and BASIC programs by Marquardt's method. *Bull. Jap. Sea Reg. Fish. Res. Lab.*, **36**, 77-107 (1986)

16) S. Branstetter: Early life-history implications of selected carcharhinoid and lamnoid sharks of the Northwest Atlantic. in "Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries" (ed. by H. L. Pratt, Jr., S. H. Gruber, and T. Taniuchi), U. S. Dep. Commer., *NOAA Tech. Rep. NMFS*, **90**, 17-28 (1990).