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ORIGINAL ARTICLE

Estimates of life history parameters of the oceanic whitetip shark, *Carcharhinus longimanus*, in the Western North Pacific Ocean

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ABSTRACT
The age, growth and reproduction of the oceanic whitetip shark, *Carcharhinus longimanus*, in the western North Pacific Ocean were estimated based on 188 specimens (89 females and 99 males) collected before the prohibition of retaining on board for commercial use by the Western and Central Pacific Fisheries Commission (from November 2002 to January 2006) at the Nanfanao fish market in north-eastern Taiwan. The relationship between body weight (W) and total length (TL) for both sexes combined was estimated as follows: $W = 1.66 \times 10^{-5}\mathrm{TL}^{2.891}$ ($n = 188$, $P < 0.01$). The relationship between TL and the pre-caudal vertebral centrum radius (R) for sexes-combined data was described using the following equation: $TL = 29.98 + 20.99R$ ($n = 112$, $P < 0.05$). The opaque bands in pre-caudal vertebrae are formed once annually between June and September based on a marginal increment ratio analysis. The maximum number of growth band pairs was 12 for both sexes in this study. The two-parameter von Bertalanffy growth function best fits the length-at-age data, and the growth parameters (sexes combined) were estimated as follows: asymptotic length (L_∞) = 309.4 cm TL and growth coefficient (k) = 0.085/yr with the size at birth set as 64 cm TL ($n = 112$, $P < 0.01$). The litter size was 10–11, and the size at birth was at least 64 cm TL. The sizes at first and 50% maturity were 190 cm and 193.4 ± 0.97 cm TL for females and 172 cm and 194.4 ± 6.57 cm TL for males. These corresponded to 8.5 yr and 8.8 yr for females and 6.8 yr and 8.9 yr for males.

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Introduction

The oceanic whitetip shark, *Carcharhinus longimanus* (Poey, 1861), is a large pelagic shark that inhabits tropical and warm-temperate continental seas worldwide (Compagno 1984). It can be easily identified among *Carcharhinus* species by its long, white-tipped, rounded first dorsal and pectoral fins. Some aspects of biological information on the oceanic whitetip sharks have been described, i.e. the taxonomy, morphometry, distribution and biology (Garrick 1982); the distribution, general biological and ecological information (Compagno 1984); the reproduction in Australian waters (Stevens 1984; Last & Stevens 1994); the distribution, morphology and reproduction in the western Pacific Ocean (Saika & Yoshimura 1985); the age, growth and reproduction of populations in the western and central Pacific Ocean (WCPO) (Seki et al. 1998); the age, growth, morphometry and stock structure in the south-western equatorial Atlantic Ocean (Lessa et al. 1999a, 1999b); the general biological and ecological information (Bonfil et al. 2008); and the reproduction in the south-western equatorial Atlantic Ocean (Coelho et al. 2009). Recently, Howey-Jordan et al. (2013) described the movement and depth range of the oceanic whitetip sharks in the western North Atlantic using pop-up satellite archive tagging. However, biological information regarding this species is still lacking in the western North Pacific, especially in Taiwanese waters.

This species has been listed as vulnerable on the IUCN Red List of Threatened Species (Version 2014.3) and listed on Appendix II at the CITES CoP16 meeting due to the severe decline in population size in certain waters. The regional fisheries management organizations (RFMOs), such as the International Commission of Conservation on Atlantic Tunas (ICCAT), the Indian Ocean Tuna Commission (IOTC) and the Western and Central Pacific Fisheries Commission (WCPFC), have prohibited the retention of this species on board for commercial use (IOTC 2010; ICCAT 2011; WCPFC 2012). The CITES listing and the RFMO management

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measures on this species make the collection and transportation of biological samples of this species more difficult and complicated. Although a stock assessment of this species in the Pacific Ocean has been conducted (Rice & Harley 2012), its life history information is still limited, particularly for populations in the western North Pacific Ocean. To provide life history information towards stock recovery estimates for the oceanic whitetip sharks in this region, the objective of this study was to estimate the age, growth and reproduction of oceanic whitetip sharks in the western North Pacific Ocean based on the data collected before the prohibition of retaining on board for commercial use in this region.

Materials and methods

Source of data

The oceanic whitetip sharks caught in the western North Pacific Ocean (Figure 1) by the Taiwanese coastal and offshore longline vessels were landed at the Nanfanao fish market in north-eastern Taiwan. These sharks were caught primarily by small-scale longline fishing vessels (< 50 tons), which operate 7–14 days per trip, and some were caught by larger fishing vessels (50–100 tons) operating more than 30 days per trip (Liu et al. 2001). Most of these longline vessels target sharks from October to March and switch to dolphin fish, billfish and tunas from April to September (Liu et al. 2001). Only a few vessels target sharks year round. Each longline set includes 1000–1200 hooks with 4–5 hooks per basket at the depth of 80–120 m. All sharks were stored in chilled form on board and landed at the fish market without processing. These sharks were weighed before being auctioned and processed (heading, finning and eviscerating), enabling us to obtain accurate catch statistics (numbers) and individual body (whole) weights (W, in kg) from sales records.

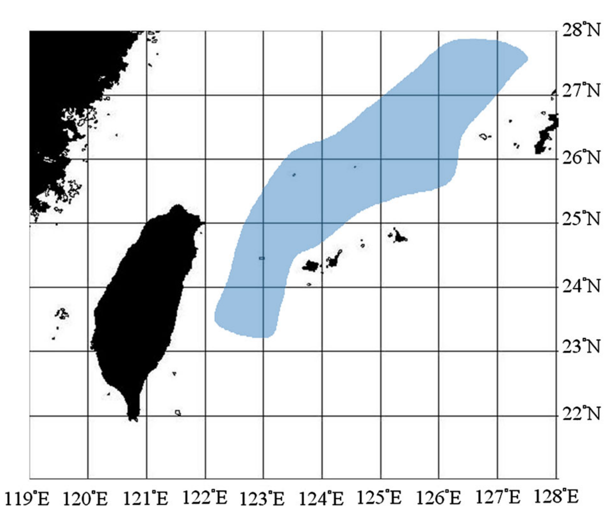

Figure 1. Sampling area of the oceanic whitetip sharks in the western North Pacific Ocean.

Specimens opportunistically collected at the Nanfanao fish market between November 2002 and January 2006 were used for age estimations and reproduction analyses. Measurements on the total length in natural form (TL, in cm), fork length (FL) and pre-caudal length (PCL) of these sharks were taken following the protocol described by Branstetter & Stiles (1987). Total length was used throughout this study. The sex of each specimen was identified. Pre-caudal vertebrae, the only vertebrae available from the fish market, were removed for the purposes of age determination. To facilitate comparisons with other studies that used different measurements (other than TL), a linear regression was used for conversion between the measurements. To determine the reproductive status of oceanic whitetip sharks, clasper lengths (CL) were measured, and the uteri condition, ova diameter and number of ova of pregnant females were examined and measured. The embryos of pregnant females were counted, sexed and measured (TL in cm).

Sexual maturity and size at birth

Sexual maturity for males was judged by the following criteria: (1) an abrupt change in the relationship between clasper length and total length; (2) the clasper and rhipidon being fully formed and spread open on fresh specimens; (3) the base of the clasper rotating easily such that the clasper can be directed anteriorly; and (4) stem cartilages becoming hardened or calcified (Spinger 1960; Clark & von Schmidt 1965; Holden & Raitt 1974; Pratt 1979). Sexual maturity for females was judged based on the following criteria: (1) immature – ovaries thin and of homogeneous cellular appearance throughout the gonad; follicles relatively indistinct from the oviducts; (2) mature – uteri well developed; a large ovary with fertilized ova or embryos found in the uteri; or the uteri being loose after parturition.

The size at birth was estimated from the observed maximum size of embryos and the minimum size of captured free-swimming individuals. The size at first maturity was estimated based on the observed smallest mature specimen. The size at 50% maturity (L_{50}) was estimated by a logistic model as follows: $P = 1/e^{-r(TL-L_{50})}$ where P is the proportion of mature fish in each length interval, and r and L_{50} are the parameters to be estimated. The 95% confidence interval (CI) of L_{50} can be estimated by $L_{50} \pm t_{0.975}$ SE.

Age estimation

Entire vertebral columns from two specimens (a 268 cm TL male and a 149 cm TL female) were used to compare the variations in band pair patterns on vertebral centra from different locations along the vertebral column of the specimens. The coefficient of variation (V) of the diameter of the vertebral centrum (D) was calculated for groups of 10 consecutive vertebrae using the formula: $V = (S/\bar{X}) \times 100\%$ where S is the standard deviation of the diameters of 10 consecutive vertebral centra and $\bar{X}$ is the mean diameter of 10 consecutive vertebral centra. The analysis revealed that the same band pair counts were found in both the pre-caudal vertebrae and the vertebrae located elsewhere. In addition, the smallest coefficient of variation was found for the vertebrae in the pre-caudal region and those below the first dorsal fin. Thus, pre-caudal vertebrae from 64 female and 77 male oceanic whitetip sharks were used for age determination.

The vertebrae were rinsed in 10% KOH for 5–60 minutes to remove connective tissue and then rinsed with running water for 24 h and air dried (Joung et al. 2004). After being soaked in ethyl alcohol and t-butyl alcohol, the vertebrae were embedded in paraffin to prevent shrinkage and deformation. The vertebral centra were then cut into two pieces along the lateral plane with an Isomet low-speed saw (Buehler, Lake Bluff, IL).

A Rigaku Industrial X-ray Apparatus was used to take radiographs of the vertebral centra (Liu et al. 1998) under the conditions of 0.2–3.2 mA and 40–45 KV for 3–4 minutes, depending on the size of the vertebral centra. Growth band pairs (defined as one translucent and one opaque band) were counted without prior knowledge of the size of the specimens from which they came. The first opaque band was assumed to be the birth mark (Figure 2). All vertebrae were read twice by the same reader, and counts were accepted only if both readings were in agreement. Following the protocol of previous studies (Chen et al. 1990; Joung et al. 2004), counts that differed by two or more band pairs were rejected. If the estimated number of band pairs differed by one, then the centra were recounted; the final count was accepted if it agreed with one of the previous counts. As the elapsed time between the birth date and birth mark deposition was unknown and the sampling date was not exactly the same as the time at opaque band formation, the age (years) of each specimen was estimated by the number of band pairs after birth mark plus 0.5 yr. The radius of each vertebral centrum (R) was measured on a line from the focus through the centre of the intermedialia to the ultimate centrum margin. The relationship between TL and the centrum radius was estimated using a simple linear regression analysis.

Figure 2. X-ray radiograph showing growth band pairs on the vertebral centrum of a 175 cm TL female oceanic whitetip shark. B, birth mark; R, centrum radius.

Marginal increment ratio analysis

The time of band formation was determined using the monthly changes in marginal increment ratio (MIR) (Cailliet & Goldman 2004). The MIR was estimated using the following formula: $MIR = (R - r_n)/(r_n - r_{n-1})$ where R is the centrum radius, and r_n and r_{n-1} are the radii of the ultimate and penultimate opaque bands, respectively.

Growth functions

Four growth functions were used to fit the length-at-age data. The size at birth (L_0) was set at 64 cm TL, which was the size of the largest full-term embryo observed in this study. The non-linear (NLIN) procedure of the statistical package SAS V. 9.0 (SAS Institute Inc. 2008, Cary, NC) was used to estimate the parameters of each function. The four growth functions used were as follows:

(1) von Bertalanffy growth function (VBGF; Beverton 1954)

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

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

(2) Two-parameter VBGF (Fabens 1965)

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt},$$

where L_0 was set as 64 cm.

(3) Robertson (Logistic) growth function (Robertson 1923)

$$L_t = \frac{L_\infty}{1 + e^{(b_R - k_R t)}},$$

where b_R and k_R represent the parameter to be estimated and the growth coefficient of the Robertson function, respectively.

(4) Gompertz growth function (Gompertz 1825)

$$L_t = L_\infty e^{-e^{(c - k_G t)}},$$

where k_G is the growth coefficient of the Gompertz function and c is the parameter to be estimated.

The goodness of fit of the four growth functions was compared based on the corrected Akaike's information criterion (AIC_c), AIC_c difference (ΔAIC_c) and AIC_c weight (w_i) (Burnham & Anderson 2002). AIC_c was expressed as:

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1},$$

$$AIC = n \times \ln(MSE) + 2K$$

(Akaike 1973), where n is the total sample size, MSE is the mean square of the residuals, and K is the number of parameters estimated in the growth function. The AIC_c difference (ΔAIC_c) of each model was calculated as the difference between $AIC_{c,i}$ and the lowest observed AIC_c value. The Akaike weight (w_i) is expressed as $w_i = \exp(-0.5\Delta_i)/\sum_{m=1}^{4}\exp(-0.5\Delta_m)$ where m is the number of growth functions being analysed. AIC weights with higher values indicated a better fit. A maximum likelihood ratio test (Kimura 1980) was used to examine the difference in growth between the sexes. A multi-model averaged asymptotic length $\bar{L}_\infty$ was estimated by the summation of L_∞ estimated by each growth function multiplied by its corresponding Akaike weight (Katsanevakis 2006; Katsanevakis & Maravelias 2008).

The age at maturity was estimated by substituting the size at 50% maturity derived from this study into the best growth function being selected. The relationship between body weight and total length was also determined for both males and females. An analysis of covariance (ANCOVA) (Zar 2010) was used to compare meristic relationships between the sexes while the maximum likelihood ratio test (Kimura 1980) was used to compare the weight-length relationship and growth functions between the sexes.

Results

In total, 188 specimens (89 females and 99 males) of oceanic whitetip sharks collected at the Nanfanao fish market between November 2002 and January 2006 were used for age estimations, maturity analyses and reproduction analyses (Table I). Among the female specimens, 16 were mature and 73 were immature, while 27 and 72 of the male specimens were mature and immature, respectively. The sex ratio was not significantly different from 1:1. Among the specimens, females ranged from 107 cm to 246 cm TL, and males ranged from 88 to 268 cm TL (Table I). Most sharks were in the range from 150 cm to 200 cm TL with the mode of 170–180 cm TL (Figure 3).

Meristic relationships

No significant difference was found for the sex-specific W-TL relationship. Thus, the relationship between W and TL (sexes combined) was described as follows: $W = 1.66 \times 10^{-5} TL^{2.819}$ ($r^2 = 0.90$, $n = 188$, $P < 0.05$). There were no significant differences between males

Table I. Sampling date, size range, and sex of the specimens of oceanic whitetip sharks used in this study.

Sampling date	Female		Male		
	N	Range of TL (cm)	N	Range of TL (cm)	Sum
November 2002	1	183	-	-	1
January 2003	2	186–213	-	-	2
February 2003	-	-	1	172	1
March 2003	3	173–188	1	168	4
April 2003	3	184–220	1	168	4
May 2003	4	165–246	2	156–157	6
June 2003	4	167–183	3	149–247	7
July 2003	8	153–195	8	145–227	16
August 2003	13	107–232	15	111–238	28
September 2003	-	-	1	88	1
October 2003	-	-	4	192–214	4
September 2004	-	-	1	93	1
December 2004	5	182–214	1	145	6
January 2005	3	148–187	6	148–233	9
March 2005	2	176–188	1	167	3
April 2005	4	154–210	14	115–191	18
May 2005	3	115–180	2	182–219	5
June 2005	9	140–175	10	121–236	19
July 2005	7	127–190	5	151–202	12
August 2005	4	151–189	5	169–182	9
September 2005	1	222	4	132–171	5
October 2005	3	167–203	7	169–244	10
November 2005	6	140–229	2	170–193	8
December 2005	3	156–217	1	268	4
January 2006	1	194	4	177–226	5
Total	89	107–246	99	88–268	188

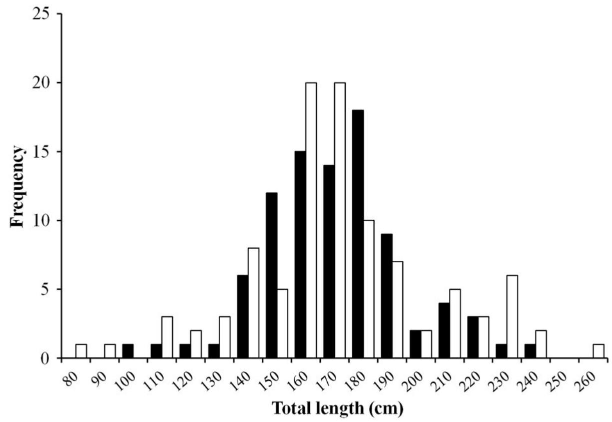

Figure 3. Total length frequency distribution of the oceanic whitetip sharks used in this study. Black, females; white, males.

and females in terms of meristic relationships (ANCOVA, $P > 0.05$). Thus, the relationships (sexes combined) between total length, fork length and precaudal length were estimated as follows:

$$\mathrm{FL} = -1.875 + 0.817TL\ (r^2 = 0.97, n = 188, P < 0.01)$$

and

$$\mathrm{PCL} = -6.019 + 0.755TL\ (r^2 = 0.97, n = 188, P < 0.01).$$

Size at maturity and size at birth

The onset of sexual maturity in male oceanic whitetip sharks appears to occur at ~185 cm TL, when the length of the claspers increased abruptly from 13 to 17 cm for specimens in the range 185–205 cm TL. The rate of increase in clasper length decreased in specimens > 205 cm TL (Figure 4). The males < 185 cm TL had soft claspers and straight vasa deferentia, and they were considered immature. Meanwhile, the specimens > 210 cm TL had rigid claspers and tightly coiled vasa deferentia, and they were considered mature (Figure 4). An individual (172 cm TL) having calcified claspers of 21.2 cm was considered as the smallest mature male while an individual (202 cm TL) with soft claspers of 12 cm was regarded as the largest immature male. The logistic curve describing the relationship between proportion of maturity (P) and TL was estimated to be $P = 1/e^{-0.0934(\mathrm{TL}-194.4)}$ ($n = 99$, $P < 0.05$) (Figure 5a). The size at 50% maturity with 95% CI was estimated to be 194.4 ± 6.57 cm TL for males.

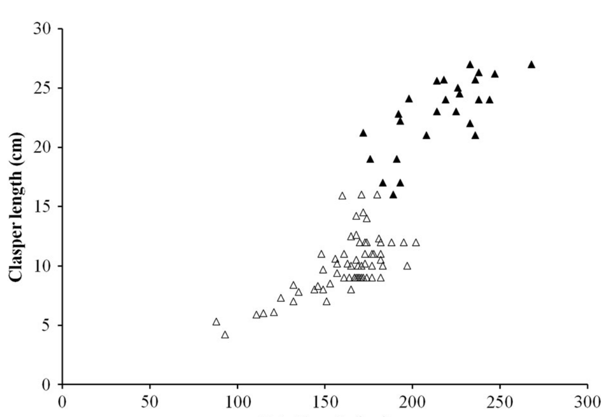

Figure 4. Relationship between total length and clasper length for male oceanic whitetip sharks in the western North Pacific Ocean. ▲, immature ($n = 70$); Δ, mature ($n = 29$).

All female specimens less than 180 cm TL with thin ovaries, threadlike uteri and oviduct were considered immature. The onset of sexual maturity in females appears to occur at a TL of 185 cm TL. The smallest mature female specimen was found in April 2005, and was 190 cm TL and 43 kg in weight. The specimens greater than > 200 cm TL had well-developed uteri and were considered mature. The logistic curve describing the relationship between P and TL was estimated to be $P = 1/e^{-0.3213(\mathrm{TL}-193.4)}$ ($n = 89$, $P < 0.05$) (Figure 5b). The size at 50% maturity with 95% CI was estimated to be 193.4 ± 0.97 cm TL for females.

Only two pregnant females were examined in detail in this study. A pregnant female collected in September 2005 (222 cm TL, 86 kg) had 10 embryos (five for each uterus, 56–64 cm TL, 1600–2600 g) and 10 unfertilized ova (0.4–0.8 mm ($n = 6$), and 10–11 mm ($n = 4$)) in the ovary. Another pregnant female (217 cm TL, 70 kg) collected in December 2005 had 11 embryos (five and six for left and right uterus, respectively, 19.5–22.3 cm TL, 88–148 g) and six unfertilized ova in the ovary. One mature but non-pregnant female (198 cm TL, 47 kg) also collected in December 2005 had 14 ova ranging from 0.8 to 24 mm in diameter with the majority being 8–14 mm ($n = 10$). The largest embryo (64 cm TL) with teeth and similar morphology to the free-swimming individual was considered to be a near-term embryo. The umbilical scar on the smallest free-swimming individual (93 cm TL) was healed, suggesting it was not a newly born individual. Hence, the size at birth of the oceanic whitetip shark was suggested to be at least 64 cm TL based on our observations.

TL–R relationship

Linear relationships between TL and R were found to be significant for both sexes, and no significant

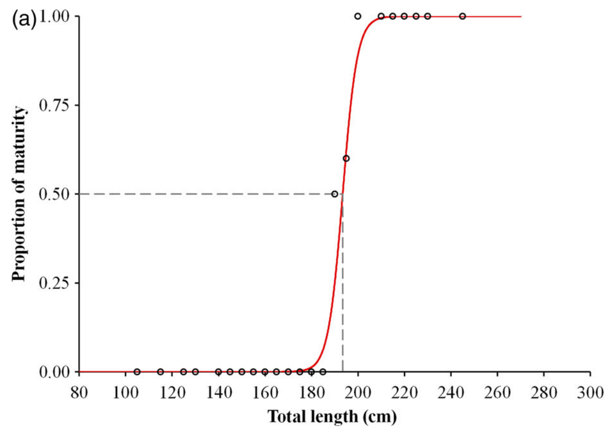

Figure 5. Relationship between proportion of maturity (P) and TL of male (a) and female (b) oceanic whitetip sharks in the western North Pacific Ocean.

difference was detected between the sexes. Thus, the relationship between TL and R for both sexes combined was described as follows:

$$TL = 29.98 + 20.99R\,(r^2 = 0.88,\ n = 112,\ P < 0.05).$$

The monthly changes in MIR for sexes-combined data indicated that the MIR began to increase in April, peaked in June, and decreased thereafter to the lowest value in September, suggesting that an opaque band forms once a year between June and September (Figure 6). In total, 29 (20%) of the 141 vertebrae were discarded due to the inconsistency in band pair readings. Maximum numbers of band pairs counted were 12 for females and males based on 112 vertebrae.

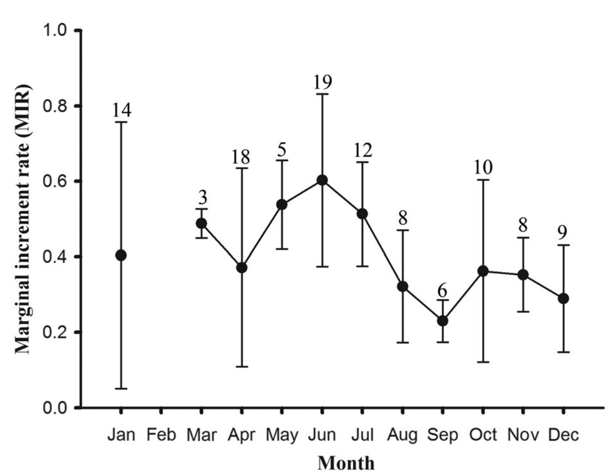

Figure 6. Monthly frequency changes in marginal increment ratio of vertebral centrum for the oceanic whitetip sharks. Numbers indicate sample sizes and vertical bars indicate mean ± 2SE.

Growth parameters

The four growth functions between the sexes were not significantly different at the 5% level based on the maximum likelihood ratio test. The estimated parameters of the four growth functions for sexes-combined data are shown in Table II. The L_∞ derived from the Robertson function was smaller than the observed maximum size (268 cm TL), suggesting that the Robertson function did not provide the best fit for the oceanic whitetip sharks. The two-parameter growth function had the smallest AIC_c (Table II), but the VBGF was supported equally well ($\Delta AIC_c < 2$). However, the L_∞ derived from the VBGF (347.3 cm TL) was much larger than the observed maximum size, indicating that the VBGF might not be the best function for this species. In addition, the highest w_i indicated that the 2VBGF is

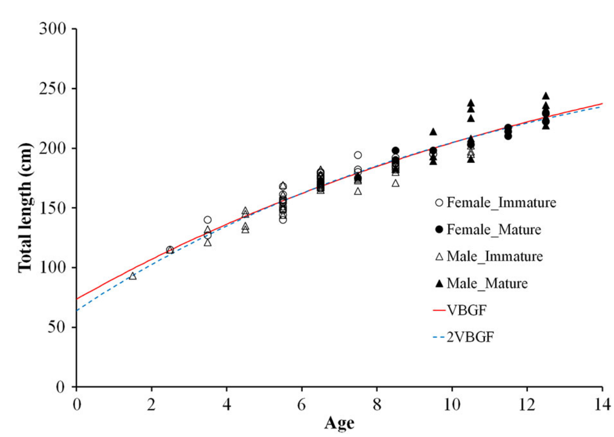

Figure 7. The sexes-combined 2VBGF (black solid line), and VBGF (black dotted line) growth curves for the oceanic whitetip sharks. ○, immature females; ●, mature females. Δ, immature males; ▲, mature males. 2VBGF, two-parameter von Bertalanffy growth function; VBGF, von Bertalanffy growth function.

Table II. Estimates of growth parameters and goodness of fit for four growth functions fitted to observed size-at-age data (sexes-combined) of the oceanic whitetip sharks.

Model	Parameters						
	L_∞	Growth coefficient	t_0	b_R/C	AIC_c	ΔAIC_c	w_i
VBGF	347.3	0.065	−3.645	–	481.3	0.79	0.334
VBGF with L_0	309.4	0.085	–	–	480.5	0.00	0.495
Robertson	266.8	0.193	–	0.730	485.4	4.88	0.043
Gompertz	289.3	0.130	–	0.238	483.2	2.71	0.128

Note: L_∞, the asymptotic length; t_0, the theoretical age at length 0; b_R, parameter to be estimated of the Robertson function; c, the parameter to be estimated of the Gompertz function; AIC_c, the corrected Akaike's information criterion; ΔAIC_c, AIC_c difference; w_i, AIC_c weight.

the best model for fitting the length-at-age data for the oceanic whitetip sharks. The parameters of the sexes-combined 2VBGF for the oceanic whitetip sharks were estimated as follows: $L_\infty = 309.4$ cm TL, $k = 0.085$ yr^{-1} ($n = 112$, $P < 0.01$) (Figure 7). The multi-model averaged L_∞ was estimated to be 317.7 cm TL.

The sizes at 50% maturity of oceanic whitetip sharks in the waters of north-eastern Taiwan were 193.4 cm TL and 194.4 cm TL for females and males, respectively, based on the maturity ogives (Figure 5). These values correspond to 8.8 yr for females and 8.9 yr for males based on the two-parameter von Bertalanffy growth equation mentioned above. The sizes at first maturity were 190 cm and 172 cm TL for females and males corresponding to 8.5 yr and 6.8 yr, respectively.

Discussion

Individuals smaller than 88 cm TL and larger than size at birth (64 cm TL) were not captured by the longline fishery in the western North Pacific, possibly because this species mainly inhabits the open sea, and its pupping ground is beyond the fishing ground of the Taiwanese offshore longline fishery. Seki et al. (1998) documented that small neonates and pregnant females with large embryos were found in the tropical waters in the central North Pacific. Their findings support our assumption that the sampling area in this study is not the major pupping or nursery ground of this species. In addition to the sampling area, the gear selection including hook depths (80–120 m) and hook size may also prevent the capture of small individuals.

The observed maximum size in this study (268 cm TL) was comparable with those (250–272 cm TL) in studies from the 1980s and 1990s (Table III). This value was also comparable with those reported in previous years in various waters. For example, Backus et al. (1956) reported a maximum size of 257 cm TL in the western North Atlantic, Strasburg (1958) documented a 246 cm TL female in the central Pacific, and Bass et al. (1973) documented a 270 cm TL female in the waters of southern Africa. These results suggested that the observed maximum size of oceanic whitetip sharks has been stable in recent decades.

The size at 50% maturity of the females derived from this study (193.4 cm TL) is comparable with the size at maturity found in different waters, i.e. 194 cm TL in eastern South African waters (Bass et al. 1973), 125–135 cm PCL (corresponding to 175–189 cm TL) in the central and western Pacific Ocean (Seki et al. 1998), 180–190 cm TL in the south-western equatorial Atlantic Ocean (Lessa et al. 1999a) and 200 cm TL in the south-western Pacific Ocean (Stevens 1984). The size at 50% maturity of males (194.4 cm TL) is comparable with those in the central and western Pacific (168–196 cm TL) (Seki et al. 1998) and in South African waters (194 cm TL) (Bass et al. 1973), but is larger than that in the West Pacific (170–180 cm TL) (Saika & Yoshimura 1985) (Table IV). The sizes at first maturity observed in this study (190 cm and 172 cm TL, for females and males, respectively) are comparable with other studies (Table IV). Seki et al. (1998) noted that the size at maturity should be slightly larger than 170–180 cm TL, as Saika & Yoshimura's (1985) estimate was not based on the criterion of calcification of the clasper. Our estimate based on a larger sample size and wider size range is believed to be more robust.

The size at birth estimated in the present study (at least 64 cm TL) is comparable with those in South African (Bass et al. 1973) and Australian waters (Stevens 1984) but smaller than those in the south-western equatorial Atlantic (Lessa et al. 1999a) and in the North Atlantic (Bigelow & Schroeder 1948) (Table IV). Our estimate also falls in the range reported by Seki et al. (1998) of 55–77 cm TL.

The mating season varies from late spring to early summer in the northern hemisphere (Backus et al. 1956; Bass et al. 1973; Seki et al. 1998) to autumn in the southern hemisphere (Stevens 1984; Coelho et al. 2009). As only two of 89 female specimens were found to be pregnant in this study, the mating season and parturition period could not be determined. However, the mature females and males mainly found from April to

Table III. Comparison of age and growth parameters of the VBGF for oceanic whitetip sharks from different studies.

Area	L_∞ (cm TL)	L_{max} (cm TL)	t_0	k	n	Authors
West Pacific	–	250	–	0.040–0.090	13	Saika and Yoshimura (1985)**
North Pacific	341.7	272	−2.698	0.103	225	Seki et al. (1998)**
Equatorial Atlantic	325.4	250	−3.342	0.075	106	Lessa et al. (1999a)*
	284.9	250	3.391	0.099		Lessa et al. (1999a)**
Western North Pacific	309.4	268	–	0.085	112	This study**,***

Note: From back-calculated data (*), and observed length-at-age data (**); ***, two-parameter VBGF.

July and October to December in this study supported the mating season proposed by previous studies. Saika & Yoshimura (1985) documented that the parturition season of oceanic whitetip sharks was May–June based on eight pregnant females collected at the same fishing market as in this study. A similar finding was not observed in this study because only one pregnant female with near-term embryos was found in September. The high percentage of immature females (> 80%) suggested a spatial size segregation for this population. Similar phenomena were found in the West Pacific (Saika & Yoshimura 1985) and in the South-west equatorial Atlantic (Coelho et al. 2009).

Two pregnant females in this study having 10 and 11 pups each is comparable with that in the South-west equatorial Atlantic (9.6, Coelho et al. 2009) but is larger than those in other waters (5.5 in the North-west Atlantic, 6.8 in the South-west Pacific and 7.0 in the South-west Indian Ocean) (Table IV). Saika & Yoshimura (1985) noted that the litter size was 3–14 (mean = 8.5) and that the litter size increases with the size of pregnant females.

The lack of very young or very old specimens may result in an overestimate of L_∞ (Cailliet & Goldman 2004). Our estimate of L_∞ (309.4 cm TL) using the 2VBGF is much larger than the maximum observed size (268 cm TL). Similar results were found for other studies in the North Pacific (Seki et al. 1998) and equatorial Atlantic (Lessa et al. 1999a) (Table III). The overestimate of L_∞ in this study may have resulted from this sampling bias. To improve the accuracy of parameter estimation, the collection of very young and very old specimens is urgently needed. However, the CITES listing and current management measure (prohibition of retention on board for commercial use) taken by the WCPFC on this species make the collection of specimens difficult in the future. One alternative to the collection of very young specimens is to use back-calculation techniques. However, this approach could not be used in this study because only the radii of the ultimate and penultimate opaque bands on each vertebral centrum were measured.

In this study, we used MIR to verify the periodicity of band-pair formation in this study and concluded that a single growth band pair was formed annually. Although uncertainty may occur in the measurements of the radii of the ultimate and penultimate bands when using MIR analysis, annual band pair deposition was also reported by other researchers studying oceanic whitetip sharks in other waters, including the WCPO (Seki et al. 1998) and the south-western Atlantic Ocean (Lessa et al. 1999a). The MIR analysis indicated that the opaque band on vertebral centra was formed in June to September. However, Seki et al. (1998) found that the opaque bands were deposited from March to May for oceanic whitetip sharks in the WCPO; Lessa et al. (1999a) concluded that the opaque bands were formed from July to August in the South-western equatorial Atlantic. Food availability among these sampling waters may account for the disparity in the time of band deposition observed in these studies.

Table IV. Comparison of reproductive parameters of oceanic whitetip sharks from different studies.

Area	Size at maturity (cm TL)		Size at birth (cm TL)	Litter size	Mating period	Parturition period	Authors
	Female	Male					
West Pacific	171	170–180	–	–	–	May–June	Saika and Yoshimura (1985)
North Pacific	175–189	168–196	63–77	1–14	June–July	February–July	Seki et al. (1998)
South Pacific	–	–	–	–	–	November	Seki et al. (1998)
North Atlantic	–	–	65–70	–	–	–	Bigelow and Schroeder (1948)
Southwestern Equatorial Atlantic	180–190		70	–	–	Late spring–summer	Lessa et al. (1999a, 1999b)
Southwestern Equatorial Atlantic	181–203	160–196	–	–	–	Possibly in January	Coelho et al. (2009)
South Africa	180–190	185–198	60–65	6–8	Early summer	Early summer	Bass et al. (1973)
Southwest Pacific	200	–	60–65	4–8	March–May	January–March	Stevens (1984)
Western North Pacific	190* 193.4**	172* 194.4**	>64	10–11	–	–	This study

Note: Size at maturity was from observed data except ** which is size at 50% maturity estimated from maturity ogive; *, size at first maturity.

To verify whether the birth mark was correctly assumed on the vertebral centra of the oceanic whitetip sharks, the mean radius length of the birth mark was substituted in the TL–R equation; the theoretical length at the time of birth mark formation was 65.3 cm, which was close to the observed size at birth of 64 cm. This estimate indicated that our assumption of a birth mark in the vertebral centra is reasonable.

Natanson et al. (2013) used the bomb radiocarbon dating technique to validate ageing, and they concluded that the vertebral band counting method underestimated the true age of dusky sharks older than 11 years in the North-western Atlantic Ocean. Whether a similar phenomenon occurs in oceanic whitetip sharks and results in an underestimation of the true age of this species in the western North Pacific Ocean requires further investigation.

The estimated L_∞ of the 2VBGF (309.4 cm TL) of the combined sexes was much larger than the maximum observed size of 246 cm TL for females and 268 cm TL for males. This value is smaller than those in the WCPO of 341.7 cm (Seki et al. 1998) and in the South-western equatorial Atlantic Ocean of 325.4 cm TL based on back-calculated data (Lessa et al. 1999a) (Table III). The growth curves derived from the 2VBGF and the VBGF were very similar except for a slight discrepancy before age 5 (Figure 7). The 2VBGF in this study predicted similar sizes at a certain age as those in the South-western equatorial Atlantic Ocean (Lessa et al. 1999a). However, the sizes at a certain age predicted from these two studies are much smaller than those by Seki et al. (1998) from the WCPO (Figure 8). This may be due to the difference in ocean water temperature because temperature plays an important role in determining the growth rates of sharks (Simpfendorfer et al. 2002). The specimens used in this study were primarily from subtropical waters (25–30°N), whereas the specimens examined by Seki et al. (1998) were primarily collected from tropical waters (0–20°N).

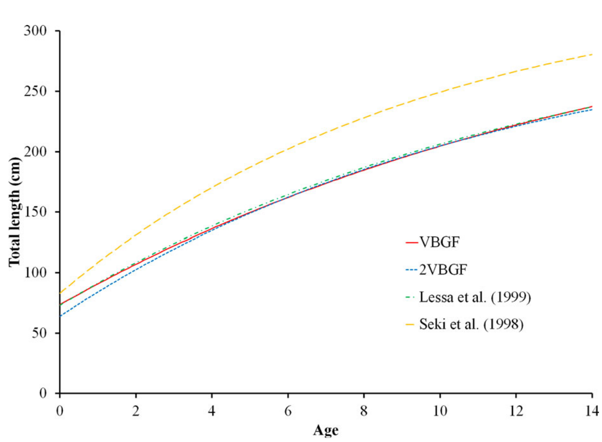

Figure 8. Comparison of the growth curves of oceanic whitetip sharks in different regions, from Seki et al. (1998), Lessa et al. (1999a) and the current study. 2VBGF was only used in the present study and VBGF was used in the other studies.

Katsanevakis (2006) and Katsanevakis & Maravelias (2008) concluded that multi-model inference should be used to produce a weighted L_∞ from among the growth functions. In this study, an averaged L_∞ was estimated following the method proposed by the above studies. However, the weighted growth coefficient cannot be estimated using a similar approach as k has different meaning among growth functions. Future work should focus on developing a model for estimating the weighted average of k.

Although this study was based on a limited sample size and a limited range of specimen sizes ($n = 188$, 88–268 cm TL), we believe that our results accurately depict the age, growth and reproduction of oceanic whitetip sharks in the western North Pacific Ocean. The characteristics of slow growth ($k = 0.085$/yr), late maturity (8.8 yr and 8.9 yr for females and males, respectively), and few offspring (10–11 / litter) render this population susceptible to overfishing. Given the prohibition on retaining oceanic whitetip sharks on board for commercial use in the Pacific Ocean implemented by the WCPFC since 2013, it is necessary to continue collecting discard and live release data to enable us to estimate the post-release mortality and to evaluate the effectiveness of this management measure in the future.

Disclosure statement

No potential conflict of interest was reported by the authors.

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