



**Abstract**—Accurate estimation of growth parameters is vital for stock assessments and management of exploited species. To determine if changes in sex-specific growth parameters of the blue shark (*Prionace glauca*) have occurred in the North Pacific Ocean following population declines in the 1980s and 1990s, we analyzed data obtained from the vertebrae of 659 male and 620 female sharks that had precaudal lengths (PCLs) of 33.4–258.3 cm and were captured over a wide geographic area between 2010 and 2016. Maximum counts of growth bands were 18 for males and 17 for females. Significant ( $P < 0.001$ ) between-sex differences were detected in growth parameters. We estimated parameters of the von Bertalanffy growth function: for males, the theoretical asymptotic length ( $L_{\infty}$ ) was 284.9 cm PCL, the growth coefficient ( $k$ ) was 0.117/year, and the theoretical age at zero length ( $t_0$ ) was  $-1.35$  years, and, for females,  $L_{\infty}$  was 257.2 cm PCL,  $k$  was 0.146/year, and  $t_0$  was  $-0.97$  years. Sexual discrepancies in growth rates are likely a function of differences in energy allocation relating to reproduction between sexes. Given that no remarkable change in growth parameters was observed over 3 decades, life history parameters of this population do not appear to have been affected by shifts in stock abundance or environmental fluctuation.

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## Age determination and growth of the blue shark (*Prionace glauca*) in the western North Pacific Ocean

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The blue shark (*Prionace glauca*) is a large pelagic species found worldwide from temperate waters to the tropics, from 60°N to 50°S (Nakano and Stevens, 2008). This species is one of the most prolific and resilient of all sharks (Smith et al., 1998; Cortés et al., 2010) and the most abundant pelagic shark globally (Nakano and Stevens, 2008). Blue sharks are also a valuable fisheries resource that is commonly caught in pelagic longline fisheries both as a target species and as bycatch (Nakano and Stevens, 2008). Their meat, liver (oil), cartilage, and fins are used in many countries (Clarke et al., 2006; Camhi et al., 2008). Consequently, stock assessments of this species have been conducted by several regional fisheries management organizations to implement appropriate regional conservation and management strategies.

Accurate age and growth information is essential for sustainable management of exploited species. Such basic life history parameters are necessary to estimate population growth rates, age at recruitment, mortality rates, and longevity (Campana, 2001; Goldman et al., 2012; Yokoi et al.,

2017). Because sexual dimorphism is common in shark species—with females being typically larger than males (Sims, 2005)—life history parameters should be based on sex-specific growth equations for proper stock assessment and management (Punt and Walker, 1998; Chang and Liu, 2009). Estimates of parameters, such as “spawning biomass” (the term *spawning biomass* is used in stock assessment reports to represent the biomass of reproductive organisms), maximum sustainable yield, and fishing intensity, can be strongly biased when an assessment does not take sexual dimorphism into consideration (Wang et al., 2005).

Several studies have reported age and growth information for blue sharks of the North Pacific Ocean (Cailliet and Bedford, 1983; Tanaka et al., 1990; Nakano, 1994; Blanco-Parra et al., 2008). However, variation in growth parameters reported in these studies could be caused by differences in sample size and size range (e.g., Cailliet and Bedford, 1983; Henderson et al., 2001; Blanco-Parra et al., 2008) and in aging technique and precision (Tanaka et

al., 1990). Additionally, growth parameters of sharks can vary as a consequence of population density (e.g., Sminkey and Musick, 1995; Carlson and Baremore, 2003; Cassoff et al., 2007). Therefore, estimation of growth parameters requires that the effects of these sampling and technical biases be taken into consideration.

It has been considered that the growth parameters described by Nakano (1994), for blue sharks of the North Pacific Ocean, are representative of the life history of this species and for this population (ISC, 2017), given that a relatively large number of samples were collected over a wide area throughout the North Pacific Ocean in 1982 and 1983. However, stock biomass of blue sharks in the North Pacific Ocean decreased in the 1980s, reached their lowest level in the early 1990s, and increased from the mid-1990s to 2005 (Hiraoka et al., 2016; Ohshimo et al., 2016; ISC, 2017). Therefore, it is possible that life history parameters, such as growth rate and age at maturity, of this population had changed over these 3 decades because stock biomass fluctuated widely. Accordingly, our objectives were to determine 1) present-day sex-specific growth parameters of blue sharks in the western North Pacific Ocean, on the basis of analysis of vertebrae of a wide size range collected from a large geographic area throughout the year, and 2) if any change in growth rate had occurred over the last 3 decades.

## Materials and methods

### Sample collection

Blue sharks were captured between 2010 and 2016 by Japanese research vessels (longline, driftnet, and trawl) and by commercial longliners operating in the western North Pacific Ocean (Fig. 1A). Sex was determined by presence or absence of the male copulatory organs (claspers). Precaudal length (PCL), the distance from the tip of the snout to the precaudal pit, and dorsal length (DL), the distance from the origin of the first dorsal fin to the origin of the second dorsal fin, in a natural position were measured to the nearest centimeter for specimens collected by



**Figure 1**

(A) Map of sampling locations and (B) length-frequency distribution for blue sharks (*Prionace glauca*) captured between 2010 and 2016 in the western North Pacific Ocean. The letter *n* refers to the number of samples used for growth analysis.

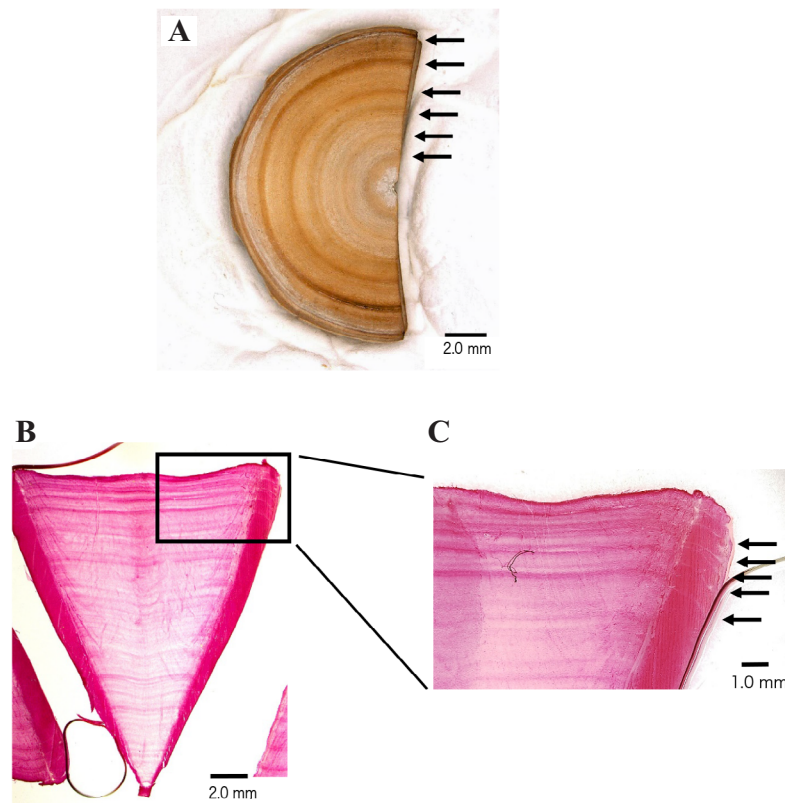
using a research vessel. Only DL was measured for sharks caught by commercial vessels because the head and viscera were removed prior to measurement; DL was converted to PCL following Fujinami et al. (2017).

### Age determination

Cervical vertebrae were excised from the region above the branchial chamber and stored frozen until processing. Vertebral centra were boiled for approximately 20 min to remove most connective tissue, then stored in 70% ethanol before being washed in running water, soaked in sodium hydroxide solution ( $5000 \text{ mol/m}^3 \text{ NaOH}$ ), and scrubbed with a polishing buff (20-cm microfiber cloth; Sankei Co.<sup>1</sup>, Tokyo, Japan) to remove residual connective tissue from their surfaces. After cleaning, centra were washed in running water, cut longitudinally into 2 sections by using a diamond saw (MC-110; Maruto Instrument Co., Tokyo, Japan) with the focus slightly to one side to avoid cutting the focus (Fig. 2A); each half-cut section was then air-dried for 24 h. The centrum radius (CR), from the focus to the edge of the centrum perpendicular to the direction of the cutting plane, was measured to the nearest 0.01 mm by using a digital microscope (VH-8000; Keyence Corp., Osaka, Japan). The CR to PCL relationship was estimated by using linear regression and was compared by sex by using analysis of covariance (ANCOVA).

For blue sharks, Fujinami et al. (2018a) recommended use of a burn method (for younger individuals) simultaneously with other methods, such as thin sectioning, bomb radiocarbon dating, or tag-recapture dating (for older individuals). Accordingly, we used a burn method, which is highly efficient and is accurate for aging of small- and medium-sized blue sharks (<200 cm PCL) (Fujinami et al., 2018a), and a thin-sectioning method, which is useful for aging older sharks (e.g., Matta et al., 2017).

Growth bands on vertebrae of specimens less than 200 cm PCL were enhanced by burning the centrum in accordance with Fujinami et al. (2018a). Vertebral centra were heated to 250°C in a drying oven (DO-300A; AS ONE Corp., Osaka, Japan) for 6–12 min (Fig. 2A). For larger specimens (>200 cm PCL), centra were sec-



**Figure 2**

Images of vertebrae from blue sharks (*Prionace glauca*) captured between 2010 and 2016 in the western North Pacific Ocean. Vertebra were treated to enhance growth bands by using (A) a burn method and (B and C) thin-sectioning after staining with alizarin red. Black arrows indicate observed growth bands for 2 sharks of different lengths, one less than and another greater than 200 cm in precaudal length (PCL): (A) 181.0 cm PCL and (B) 252.0 cm PCL. Panel C provides an enlarged image of the vertebra in panel B.

tioned (1.0 mm) by using a sliding microtome (Retortome REM-710; Yamato Kohki Industrial Co., Asaka, Japan) without embedding, after they were cleaned and cut in half as described previously. Sections were stained with alizarin red for 2 min in accordance with Berry et al. (1977) and rinsed in running tap water for approximately 10 min (Fig. 2B). Finally, stained sections were dehydrated through a graded ethanol series (70%, 80%, 90%, and 100%) and mounted on microscope slides.

Burned centra were observed by using the shadowing method (Francis and Maolagáin, 2000; Semba et al., 2009) with a digital microscope and fiber-optic light. Sections were observed by using an SZX7 stereo microscope (Olympus Corp., Tokyo, Japan) with reflected light. We defined a growth-band pair as one convex band (dark, narrow) and one concave band (light, broad) on the centrum surface when the burn method was used, and we defined a band pair as one

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

translucent band and one opaque band on the corpus calcareum when the thin-sectioning method was used. We counted the number of convex structures for the burn method and translucent bands for the sectioning method. A single reader (reader 1: senior author) twice counted bands at 2 different times without prior knowledge of specimen length. A third count was made if the first and second counts did not coincide. If the third count was the same as either the first or second count, the duplicated measure was used in analysis; if the third count did not agree, a sample was excluded from analysis. A random subsample of 200 individuals was read by a separate reader (reader 2: S. Tanaka) to ensure consensus in interpretation of growth bands. To evaluate inter- (both readers) and intrareader (reader 1) aging precision, an index of average percentage error (IAPE) (Beamish and Fournier, 1981) and mean coefficient of variation (CV) (Chang, 1982) were calculated. An age-bias plot also was constructed to test inter- and intrareader counts (Campana et al., 1995).

For age estimation, we assumed a tentative birth date of 1 June on the basis of the birth season estimated by Fujinami et al. (2017). The first band (birth band) was considered to be formed after parturition on the basis of the observation of vertebral centra of near-term embryos and neonates (see the “Results” section). In addition, we assumed subsequent growth bands formed annually, on 1 December (see the “Results” section); therefore, the age of each specimen was calculated as follows:

$$\text{Age} = (\alpha - 1) + \frac{(\beta - 6)}{12} \quad (\alpha \geq 1, 1 \leq \beta \leq 12), \quad (1)$$

where  $\alpha$  = the number of convex structures (translucent bands) deposited after the birth band; and  $\beta$  = the month when the individual was caught.

#### Age verification

To verify periodicity of growth-band formation, the most peripheral structure on each centrum was classified as either convex (translucent) or concave (opaque). We analyzed monthly changes in frequency of each band on the centrum edge throughout the year. The periodicity of growth-band pairs was verified by using a statistical model developed by Okamura and Semba (2009). Three models were constructed according to different periodicities of growth-band formation: an annual cycle, a biannual cycle, or no seasonal cycle. Okamura and Semba (2009) suggested that the model with the lowest Akaike's information criterion (Burnham and Anderson, 2002) is preferred because it is estimated to be closest to the unknown reality that generated the data. Vertebral centra with only one band (birth band) were excluded from analysis.

#### Growth analysis

The von Bertalanffy growth function (von Bertalanffy, 1938) was fitted to observed length-at-age data by using the maximum likelihood approach with the op-

tim function in R (vers. 3.3.0; R Core Team, 2016), as follows:

$$L_t = L_\infty (1 - e^{-k(t-t_0)}), \quad (2)$$

where  $L_t$  = the predicted length at age  $t$  (in years);

$L_\infty$  = the theoretical asymptotic length (in centimeters);

$k$  = the growth coefficient (per year); and

$t_0$  = the theoretical age at zero length.

We used Kimura's likelihood ratio to test for a significant difference in the growth parameters of males and females (Kimura, 1980). We tested the null hypothesis ( $H_0$ , all parameters are different between sexes) versus the alternative hypothesis ( $H_1$ – $H_3$ , the sex-specific growth model, in which one of the parameters is shared for each sex, and  $H_4$ , all parameters are shared between sexes). The 95% confidence intervals (95% CIs) of parameter estimates were derived from 2000 resampled data sets by using the bootstrap method.

Theoretical longevity ( $t_{\max}$ ) was estimated following methods of Taylor (1958) and Fabens (1965):

$$t_{\max} = t_0 - \frac{\ln(0.05)}{k} \quad (\text{Taylor, 1958}) \quad \text{and} \quad (3)$$

$$t_{\max} = 5 \frac{\ln_2}{k} \quad (\text{Fabens, 1965}). \quad (4)$$

#### Age at maturity and maternity

According to criteria described by Fujinami et al. (2017), sexual maturation in males was classified into 3 stages on the basis of calcification of the claspers and testis development (for details, see [Suppl. Table 1](#)): 1) immature juvenile, 2) maturing juvenile, and 3) mature adult. For females, sexual maturity was assessed on the basis of uterine width, ovarian development, and the presence of embryos or fertilized eggs, with 5 stages recognized (for details, see [Suppl. Table 1](#)): 1) immature juvenile, 2) maturing juvenile, 3) mature adult, 4) mature pregnant, and 5) mature postpartum. The maturation stage of each specimen was converted into binary data (immature=0, mature=1) at age intervals of 1 year for statistical analysis. A logistic regression model was fitted to the binomial maturity data, to determine ages at 50% maturity for both sexes, as follows:

$$Y = 1 / [1 + \exp\{-(\alpha + \beta\chi)\}], \quad (5)$$

where  $Y$  = the proportion of mature individuals of each age;

$\chi$  = age; and

$\alpha$  and  $\beta$  = coefficients.

A generalized linear model with a binomial error structure and logit-link function was used to estimate the  $\alpha$  and  $\beta$  coefficients by using R. Female maternity ogive also was determined by using maternal condition according to criteria described by Fujinami et al. (2017) (for details, see [Suppl. Table 1](#)). Data for maternal condition (pregnant or postpartum) or non-maternal con-



**Table 1**

Monthly numbers of vertebrae used for age determination of blue sharks (*Prionace glauca*) captured in 2010–2016 in the western North Pacific Ocean.

Sex	Month												Total
	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	
Male	51	31	25	66	107	74	39	15	29	65	85	72	659
Female	25	44	42	65	61	61	29	0	22	69	97	105	620
Total	76	75	67	131	168	135	68	15	51	134	182	177	1279

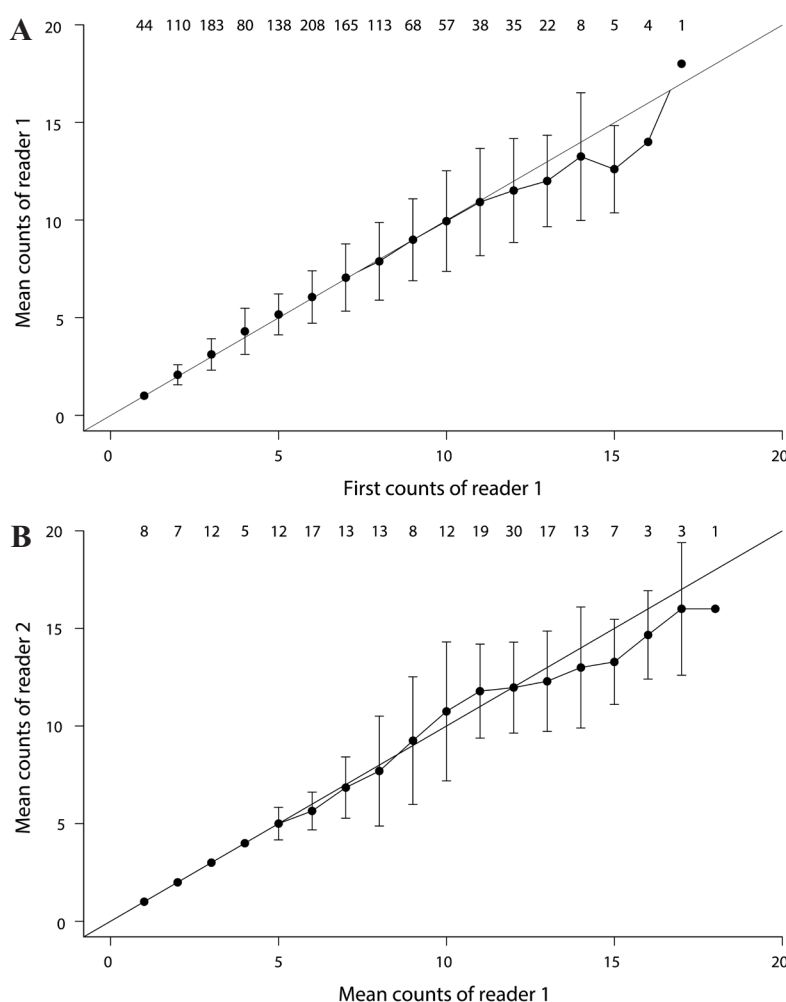
dition (immature or non-pregnant mature) were converted to binomial data (non-maternal condition=0, maternal condition=1). The logistic function was fitted to these data in the same way as it was fitted to the maturity data for estimating age at 50% maturity.

## Results

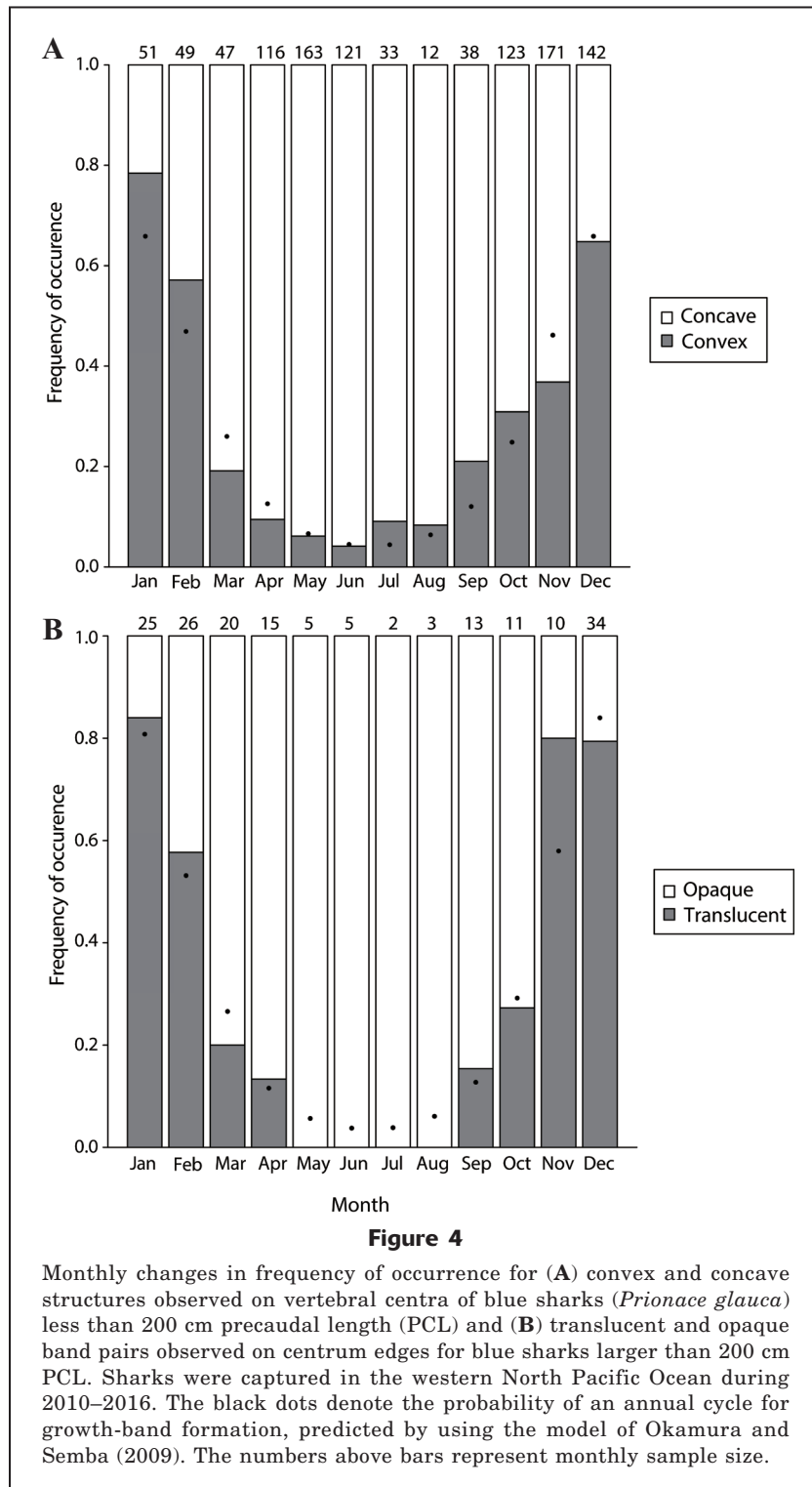
### Age determination and verification

Cervical vertebrae were collected from 1347 blue sharks (688 males, 645 females, and 14 sex undetermined). Of these sharks, for growth analysis, we used data for 1279 individuals (659 males and 620 females; Table 1), which had PCLs of 33.4–258.3 cm for males and 33.4–243.3 cm for females (Fig. 1B). The sex-specific relationship between CR and PCL trended in a linear fashion, with no significant difference between sexes (ANCOVA:  $F=3.70$ ,  $P=0.06$ ). The sex-combined equation for the relationship of CR and PCL was  $PCL=15.96CR+20.85$  (coefficient of determination [ $r^2$ ]=0.920,  $n=1279$ ).

Counts of growth bands were 1–18 for males and 1–17 for females. There was a high level of both inter- and intrareader agreement in band counts (Fig. 3, A and B). However, errors associated with age estimates of older sharks were larger than those associated with ages for younger sharks, although sample sizes were small. In repeat counts by reader 1, the counts for 710 samples (55.5%) agreed completely and the counts for 467 samples (36.5%) differed by one band. For inter-reader comparison of counts of 200 vertebrae, the counts for 86 sam-

**Figure 3**

Age-bias plots of pairwise comparison of vertebral counts (A) by reader 1 (intrareader: first counts versus mean counts) and (B) by separate readers (inter-reader: reader 1 versus reader 2) for blue sharks (*Prionace glauca*) captured between 2010 and 2016 in the western North Pacific Ocean. Error bars represent 95% confidence intervals. The diagonal line indicates 1:1 equivalence. Numbers at the top of the graph denote the sample sizes for each count.



ples (43.0%) agreed completely and the counts for 61 samples (30.5%) differed by only one band. For intra-reader (reader 1) and inter-reader (reader 1–2) evaluations of precision, the IAPE values were 3.7% and 5.3% and the CV values were 4.2% and 5.9%. No pre-birth band was apparent on near-term embryos captured in May, but

one growth (narrow) band was apparent on neonates captured in late June and July.

Monthly characterization of the centrum edge differed throughout the year both for specimens less than 200 cm PCL ( $n=1066$ ) and for specimens greater than 200 cm PCL ( $n=169$ ) (Fig. 4). The proportion of con-

**Table 2**

Comparison of goodness of fit for statistical models developed for 3 different periodicities of growth-band formation in blue sharks (*Prionace glauca*) of 2 size classes defined by precaudal length (PCL). The model with the lowest Akaike's information criterion (AIC) is preferred because it is estimated to be closest to the unknown reality that generated the data. The  $\Delta$ AIC statistic is the relative difference between the best model (which has an  $\Delta$ AIC of zero) and each of the other models in the set.

Size class	Periodicity of band formation	AIC	$\Delta$ AIC
Individuals <200 cm PCL	Annual cycle	1009.8	0.0
	Biannual cycle	1232.5	222.7
	No cycle	1283.7	273.9
Individuals >200 cm PCL	Annual cycle	169.0	0.0
	Biannual cycle	240.1	71.1
	No cycle	236.1	67.1

**Table 3**

Results from likelihood ratio tests (Kimura, 1980) for the von Bertalanffy growth model used to examine differences in growth parameters between male and female blue sharks (*Prionace glauca*) in the western North Pacific Ocean. The parameters of the von Bertalanffy growth model are the theoretical asymptotic length ( $L_{\infty}$ ), measured in centimeters in precaudal length; the annual growth coefficient ( $k$ ); and the theoretical age, measured in years, at zero length ( $t_0$ ).  $H_0$ =null hypothesis (all growth parameters differ by sex).

Test	Hypothesis	Male			Female			$\chi^2$	P-value
		$L_{\infty}$	$k$	$t_0$	$L_{\infty}$	$k$	$t_0$		
$H_0$ vs. $H_1$	$L_{\infty}$ (male) = $L_{\infty}$ (female)	267.4	0.134	-1.16	267.4	0.133	-1.10	16.36	<0.001
$H_0$ vs. $H_2$	$k$ (male) = $k$ (female)	268.6	0.133	-1.14	266.5	0.133	-1.12	14.94	<0.001
$H_0$ vs. $H_3$	$t_0$ (male) = $t_0$ (female)	273.4	0.130	-1.14	263.0	0.136	-1.14	12.37	<0.001
$H_0$ vs. $H_4$	All parameters same between sexes	267.1	0.134	-1.13	267.1	0.134	-1.13	21.66	<0.001

vex structures (Fig. 4A) and translucent bands (Fig. 4B) tended to increase from the boreal autumn to winter, peaking in January, and to be lowest in summer. In contrast, concave structures (Fig. 4A) and opaque bands (Fig. 4B) were prevalent in summer and least common in winter. The results of the statistical analysis of Okamura and Semba (2009) indicate that the annual cycle of band formation was most plausible because the model with that periodicity had the smallest Akaike's information criterion (Table 2).

#### Growth parameters

There was a significant difference between the sexes in estimates for parameters of the von Bertalanffy growth function (Table 3). Females had a higher growth coefficient ( $k=0.146/\text{year}$ ) than males ( $k=0.117/\text{year}$ ), but their theoretical asymptotic length ( $L_{\infty}=257.2$  cm PCL) was shorter than that for males ( $L_{\infty}=284.9$  cm PCL) (Table 4, Fig. 5). Growth rates of both sexes were similar until an age of approximately 7 years, after which

the female growth rate gradually decreased relative to that for males of the same age.

The maximum observed age was 17.3 years for males and 15.8 years for females. Theoretical longevity estimates, calculated by using methods of Taylor (1958) and Fabens (1965), were 24.3 and 29.6 years for males and 19.5 and 23.7 years for females. These values were greater than the maximum observed age for either sex.

#### Age at maturity and maternity

Maturity data were available for 414 males (33.4–252.0 cm PCL) and 365 females (33.4–238.0 cm PCL). The youngest mature individuals were 4.0 years old, and, for both sexes, the maximum age recorded for an immature individual was 7.0 years. The age at which 50% of males were mature was 5.9 years (95% CI: 5.3–6.4 years), and that of females was 5.3 years (95% CI: 4.7–5.7 years) (Fig. 6, A and B). Maternity condition data were available for 354 females (33.4–238.0 cm PCL); the age at which 50% of females were in maternal con-

**Table 4**

Estimates, with 95% confidence intervals (95% CIs), of the parameters for the von Bertalanffy growth model used to examine differences in growth parameters between sexes for blue sharks (*Prionace glauca*) in the western North Pacific Ocean. The parameters are the theoretical asymptotic length ( $L_{\infty}$ ), measured in centimeters in precaudal length; the annual growth coefficient ( $k$ ); and the theoretical age, measured in years, at zero length ( $t_0$ ).

Sex	Parameter	$L_{\infty}$	$k$	$t_0$
Male	Estimate	284.9	0.117	−1.35
	Lower 95% CI	258.0	0.109	−1.44
	Upper 95% CI	294.6	0.145	−0.90
Female	Estimate	257.2	0.146	−0.97
	Lower 95% CI	246.6	0.131	−1.17
	Upper 95% CI	267.6	0.163	−0.79

dition was 6.7 years (95% CI: 6.3–7.2 years) (Fig. 6C), an age that is 1.4 years older than the estimate of age at 50% maturity for females.

## Discussion

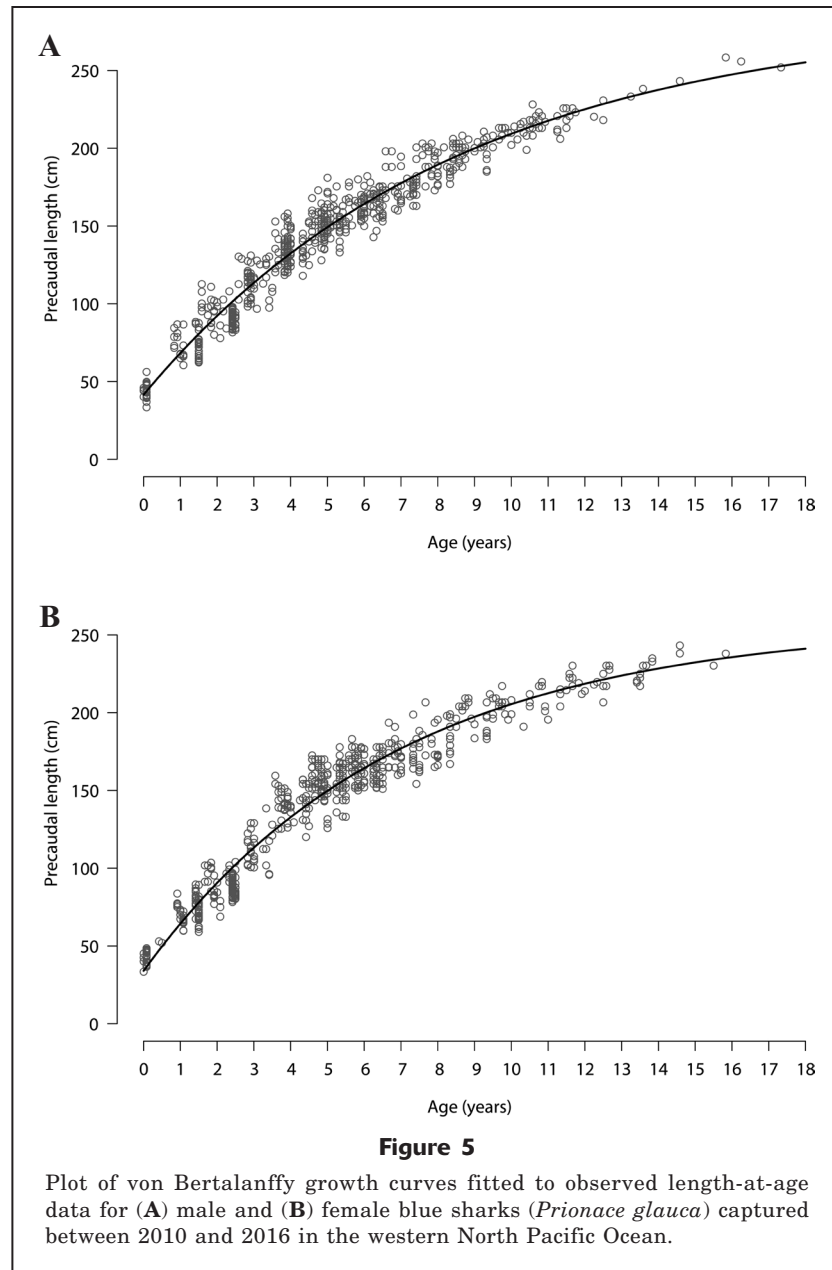
In this study, we simultaneously used a burn method (Fujinami et al., 2018a) for specimens less than 200 cm PCL and a thin-sectioning method (e.g., Matta et al., 2017) for individuals greater than 200 cm PCL. Ages of blue sharks of the North Pacific Ocean have been determined previously by using silver nitrate impregnation and thin-sectioning methods (Table 5). The convex and concave structures that we observed by using the burn method correspond with the translucent and opaque bands apparent in silver nitrate impregnation (Fujinami et al., 2018a) and sectioning with alizarin red for older specimens, respectively, indicating that our approach with simultaneous use of a burn method and sectioning provides comparable age estimates for the size range compared. The precision of ages estimated by using a burn method and silver nitrate impregnation was high for small- and medium-sized individuals (<200 cm PCL), particularly when the burn method was used, and the precision for both methods was lower for older specimens (Fujinami et al., 2018a). Use of the burn method tended to result in counts of fewer bands than the use of the thin-sectioning method when band counts exceeded 11, for a subsample ( $n=97$ ) of individuals exceeding 190 cm PCL (Suppl. Table 2). Shark vertebral growth and band-pair deposition are both tightly linked to somatic growth; therefore, vertebral growth decreases in older specimens (i.e., the vertebral edge narrows in older sharks) (Natanson et al., 2018). Such limited growth for older specimens is detectable in thin sections; however, it is much more

difficult to determine in intact vertebrae (Matta et al., 2017). Consequently, we believe that the simultaneous use of burn and thin-sectioning methods provides a more accurate estimate of age than the use of only a single method.

We observed banding patterns in blue sharks similar to those reported previously. Nakano (1994) suggested that the birth band of blue sharks of the North Pacific Ocean forms just after summer and that subsequent growth bands form annually in the boreal winter (on the basis of silver nitrate impregnation). Slow growth-zone formation from late autumn to winter and fast growth-zone formation during spring and summer also were reported by Wells et al. (2017) on the basis of research that involved analysis of vertebrae from blue sharks injected with oxytetracycline and tagged and recaptured in the eastern North Pacific Ocean. Our results, from the use of both burn and thin-sectioning methods, are similar to those of previous studies in the North Pacific Ocean: narrow bands (slow growth) are formed in the winter, and broad bands (fast growth) are formed in the summer. Therefore, we assert that growth-band deposition after the birth band in blue sharks of the North Pacific Ocean occurs annually, regardless of the aging technique and geographic area of sampling used to estimate ages. Consequently, the increment between the first and second bands represents about 6 months of growth (tentative birth period in June, subsequent band formation in December)—a result similar to that reported by Nakano (1994). Similar patterns also have been reported in other species, such as the blacktip shark (*Carcharhinus limbatus*) (Branstetter, 1987) and the shortfin mako (*Isurus oxyrinchus*) (Semba et al., 2009). Several triggers, such as environment experienced (e.g., water temperature), prey availability, physiological differences, and movement patterns, might be related to postnatal band formation (e.g., Natanson and Cailliet, 1990; Wells et al., 2017).

The asymptotic length of blue sharks in the eastern North Pacific Ocean (Cailliet and Bedford, 1983; Blanco-Parra et al., 2008) is much smaller than that of blue sharks in the western North Pacific Ocean (Tanaka et al., 1990; Nakano, 1994; and herein, see Table 5). To provide quantitative estimation for growth parameters, access to specimens from neonate to larger and older individuals is necessary because estimates of growth parameters generally are affected by small sample sizes of small or large specimens (Campana, 2001; Goldman et al., 2012). Growth parameters we report for this study differ from those reported for sharks in the eastern North Pacific Ocean (Cailliet and Bedford, 1983; Blanco-Parra et al., 2008), possibly because few larger and older specimens (most individuals were less than 200 cm PCL) were represented in samples in those studies. The size range of specimens reported from the central South Pacific Ocean by Joung et al. (2017) is similar to the range we report, as are estimates of growth parameters, especially asymptotic length (Table 5). However, our estimated female as-





ymptotic length is less than that reported for the North Atlantic Ocean (Skomal and Natanson, 2003; Table 5), possibly because a greater size range of individuals was examined in that study. Although we cannot discount the possibility of underestimation, we can assert that, at least for blue sharks in the North Pacific Ocean, our estimation of growth parameters used more specimens of a greater size range than that of any previous study.

Another possible reason for variation in growth parameters among studies could be differences in aging technique and precision (Tanaka et al., 1990). Whereas most previous studies on blue sharks of the North Pacific Ocean have used silver nitrate impregnation to age specimens (Table 5), we simultaneously used 2

complementary techniques (burn and thin-sectioning methods) to effectively age sharks of different lengths (Fujinami et al., 2018a). As discussed previously, growth bands apparent from the use of a burn method and silver nitrate impregnation are comparable; therefore, we consider any effect of technique to be slight. Furthermore, because we used the thin-sectioning method on older sharks, we minimized underestimation of age. The aging precision (IAPE and CV) that we achieved by combining techniques is comparable to that from the use of a single technique like thin sectioning (Lessa et al., 2004), silver nitrate impregnation (Blanco-Parra et al., 2008), or X-ray imaging (Joung et al., 2017; Joung et al., 2018). Consequently, our aging

Table 5

Estimates of growth parameters of the von Bertalanffy growth function for blue sharks (*Prionace glauca*) from previous studies. Total lengths (TLs) and fork lengths (FLs) from studies were converted to precaudal length (PCL) by using conversion factors of Fujinami et al. (2017). The parameters are the theoretical asymptotic length ( $L_{\infty}$ ), measured in centimeters; the annual growth coefficient ( $k$ ); and the theoretical age, measured in years, at zero length ( $t_0$ ).  $n$ =sample size used in the age determination.

Region	Sex	$n$	Size range (cm PCL)	$L_{\infty}$	$k$	$t_0$	Max. age	Aging method	Study citation
N Pacific	Male	43	–	284.8	0.10	–1.38	11	Stained thin section	Tanaka et al. (1990)
	Female	152	–	233.4	0.16	–1.01	8		
N Pacific	Male	148	–	289.7	0.13	–0.76	10	Silver nitrate staining	Nakano (1994)
	Female	123	–	243.3	0.14	–0.85	10		
NE Pacific	Male	38	18.1–192.9	226.6	0.18	–1.11	9	Silver nitrate staining	Cailliet and Bedford (1983)
	Female	88		184.9	0.25	–0.80	9		
NE Pacific	Male	122	59.4–206.9	230.1	0.10	–2.44	16	Silver nitrate staining	Blanco-Parra et al. (2008)
	Female	62	66.5–192.8	181.5	0.15	–2.15	12		
NW Pacific	Male	659	33.4–258.3	284.9	0.12	–1.35	17	Burn method and stained thin section	This study
	Female	620	33.4–243.3	257.2	0.15	–0.97	16		
Central S Pacific	Male	173	87.5–242.0	290.0	0.13	–1.48	15	X-ray image	Joung et al. (2018)
	Female	86	82.1–227.9	254.0	0.16	–1.29	11		
N Atlantic	Combined	411	44.9–286.8	263.6	0.17	–1.43	16	Thin section	Skomal and Natanson (2003)
	Male	287		259.5	0.18	–1.35	16		
	Female	119		285.7	0.13	–1.77	15		
NE Atlantic	Combined	159	46.2–174.1	289.9	0.12	–1.33	6	Unstained whole	Henderson et al. (2001)
S Atlantic	Combined	742	74.3–249.8	270.9	0.13	–1.31	15	X-ray image	Joung et al. (2017)
SW Atlantic	Combined	236	131.8–238.1	270.9	0.16	–1.01	12	Thin section	Lessa et al. (2004)

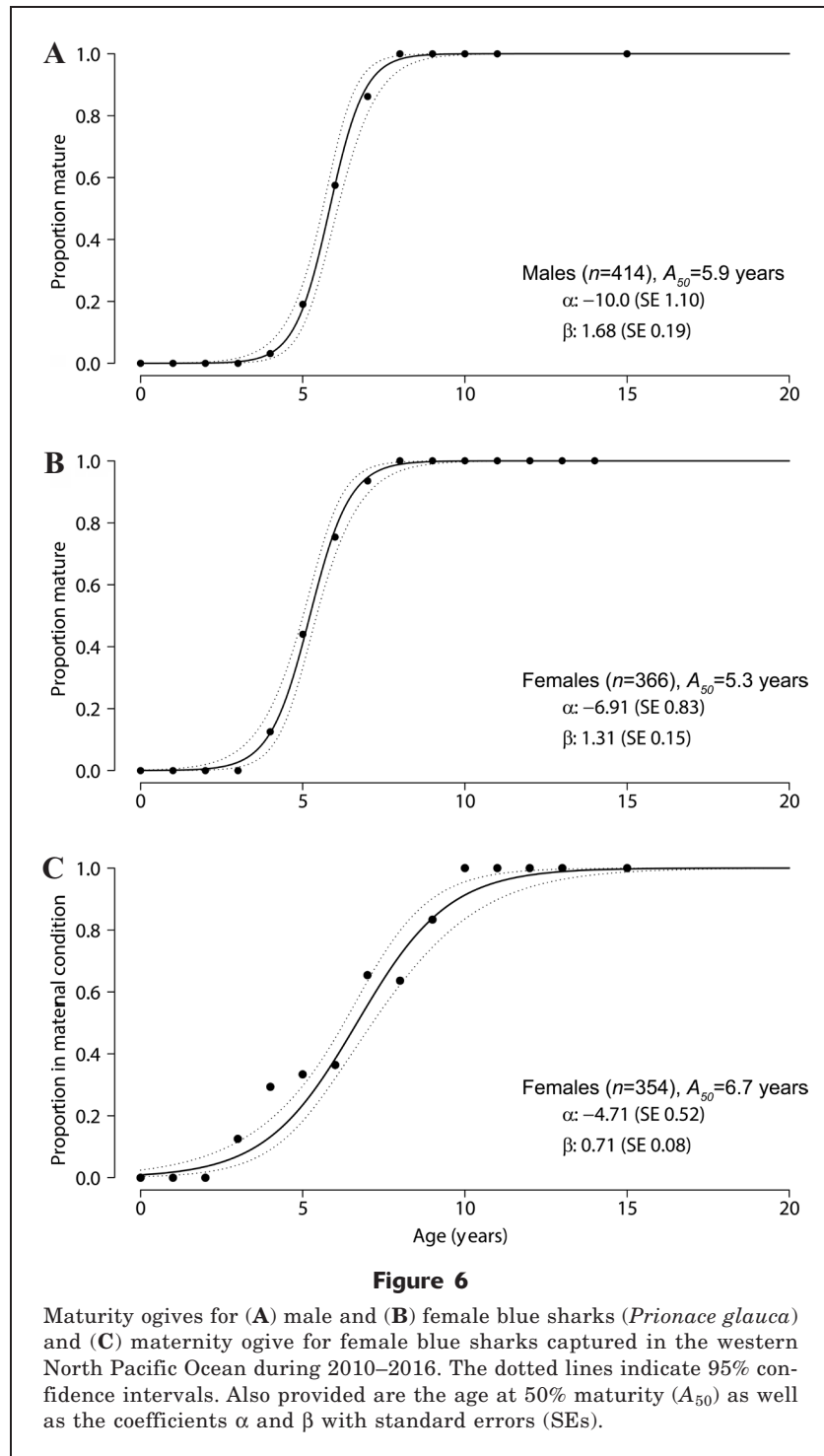
precision was greater than reference IAPE and CV values (Campana, 2001) that are considered acceptable.

Our findings indicate that male blue sharks grow larger than females and that the difference in growth rate occurs after females reproduce (after the age of approximately 7 years). This fact is widely supported by previous studies for blue sharks of the Pacific Ocean (Table 5). However, although the occurrence of sexual differences in growth is well known in elasmobranchs, females typically grow larger than males (e.g., Cortés, 2000). Skomal and Natanson (2003) provided the only previous report of female blue sharks growing larger than males, but they considered the extremely large female (286.8 cm in calculated PCL, Table 5) in their study to be very rare given natural mortality. Skomal and Natanson (2003) also reported that differences in female growth began at ~7 years of age. Therefore, sexual differences in growth rates of blue sharks are likely attributable to differential energy allocation between sexes, as has been reported for several other shark species (e.g., Semba et al., 2009; Joung et al., 2018). In general, the onset of maturity results in reduced energy allocation toward growth and in increased allocation toward reproduction (Jensen, 1985) because mating, gestation, and parturition in female sharks consumes considerable energy (Francis and Duffy, 2005). Blue sharks are one of the most productive (high fecundity and annual reproductive cycle) viviparous sharks (Fujinami et al., 2017), unlike others

in the family Carcharhinidae, indicating that females may expend more energy than males on reproduction (e.g., mating, gestation, pupping, and migration related to reproduction) and more energy on reproduction than on somatic growth following sexual maturation.

Whereas the male asymptotic length from our study is similar to that from Nakano (1994), the asymptotic length for females from our study is slightly greater (257.2 cm PCL, Table 5), possibly because we examined a greater number of large-sized females. Nevertheless, our growth parameters do not differ remarkably from those of Nakano (1994), indicating that shark growth rates have not changed demonstrably with shifts in stock abundance from the 1980s to the 2010s.

The most recent stock assessment of blue sharks in the North Pacific Ocean reported a prompt recovery of spawning biomass (ISC, 2017). Estimated female spawning biomass exceeded 300,000 metric tons (t) in the early 1980s, decreased to approximately 200,000 t in the 1990s, and began recovery from the late 1990s to reach 300,000 t in the 2010s. This upward population trend has been attributed to a decrease in fishing pressure following prohibition of high seas drift nets in 1992 and subsequent decrease in the numbers of long-line vessels (Hiraoka et al., 2016). Although the difference in spawning biomass of blue sharks from the North Pacific Ocean between the early 1980s (Nakano, 1994) and the 2010s (our study) is not great, the biomass in the intervening years fluctuated considerably.



One possible reason for the variation is that growth and sexual maturation may have changed concomitant with declines in shark abundance during the 1980s, but, along with a rebounding of this population during the mid-1990s and 2005, these parameters might have recovered to and reached values comparable to pre-decline levels of the 1980s. Alternatively, the rapid

stock fluctuation of the 1980s and 1990s might have had no effect on growth and maturation of blue sharks of the North Pacific Ocean. Reproductive parameters (e.g., size at maturity and gestation period) of sharks in the western North Pacific Ocean during 2010–2016 (Fujinami et al., 2017) differ little from those reported by Nakano (1994) for the period from 1978 to 1987.

Because a compensatory response can take a long time (e.g., Carlson and Baremore, 2003), the second of these explanations is more plausible.

Blue sharks have a considerable geographic range, from coastal to pelagic waters and from temperate regions to the tropics (Nakano and Stevens, 2008) in sea temperatures of 5.6–28.0°C (Nakano and Seki, 2003). This species is also an opportunistic feeder, with a diet that reflects abundance of local prey, such as fish and squid (e.g., Preti et al., 2012; Fujinami et al., 2018b). As such, blue sharks are likely tolerant of fluctuations in food resources, buffering the species from anthropogenic stress and changes in environmental conditions, such as water temperature (Levitus et al., 2005; Levitus et al., 2012) and prey abundance (Chavez et al., 2003). In addition to its high adaptability, this species' relatively fast growth and high productivity probably explain why it has been able to maintain high biomass levels, outnumbering other shark species in pelagic waters.

We establish that growth parameters of blue sharks of the North Pacific Ocean have not changed remarkably from levels observed from the 1980s to the present day, despite changes in stock abundance or environmental conditions. Because male blue sharks grew larger than females, and after the age of about 7 years had growth rates different from females, we believe a sex-specific approach for assessing stocks of blue sharks in the North Pacific Ocean is necessary. Given the number of samples in our study, their size range, and the accuracy of our aging technique, we believe the growth parameters that we report are appropriate for future stock assessments and management of blue sharks in the North Pacific Ocean. Bomb radiocarbon dating and tag-recapture techniques would further clarify growth rates of these sharks, given that current methods and structure-based aging techniques might underestimate age, especially for larger and older individuals (Harry, 2018; Natanson et al., 2018).

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## Supplementary Table 2

Cross-comparison of counts of growth-band pairs from the use of the burn and thin-sectioning methods for blue sharks (*Prionace glauca*)

captured between 2010 and 2016 in the western North Pacific Ocean.

		Number of band counts with burn method							
		9	10	11	12	13	14	15	16
Number of band counts with thin- sectioning method	9	1	0	0	0	0	0	0	0
	10	0	3	1	0	0	0	0	0
	11	0	3	13	1	0	0	0	0
	12	0	0	10	17	0	0	0	0
	13	0	0	3	5	12	0	0	0
	14	0	0	0	4	4	6	1	0
	15	0	0	0	0	1	4	1	0
	16	0	0	0	1	0	2	0	1
	17	0	0	0	0	0	1	1	0
	18	0	0	0	0	0	0	0	1

## Supplementary Table

The observed total lengths (TLs) from May 1995 through December 2013, the ratios of the clasper outer length to the pelvic inner length (CLO:P2I) from October 2005 through October 2013, and the plasma concentrations of testosterone (T) and progesterone (P4) from May 2008 through December 2013 in a male whale shark (*Rhincodon typus*) in captivity at the Okinawa Churaumi Aquarium in Japan. Also provided are water temperatures in the exhibition tank from May 2008 through December 2013.

Date	TL (cm)	CLO:P2I	T (ng/mL)	P4 (ng/mL)	Temp. (°C)
Mar. 1995	460				
Apr. 1996	470				
Jul. 2001	600				
Sep. 2002	660				
Aug. 2004	700				
Mar. 2005	744				
Oct. 2005		1.00			
Jul. 2006		1.02			
Sep. 2006	753				
Mar. 2007	777				
Sep. 2007	792	1.03			
May. 2008			3.27	0.11	23.6
Jun. 2008			5.80	0.42	28.1
Jul. 2008			6.05	1.20	27.7
Aug. 2008			7.64	1.42	29.7
Sep. 2008		1.03	8.04	1.15	28.4
Oct. 2008			9.17	0.85	27.6
Nov. 2008			3.43	0.16	24.6
Dec. 2008	807		3.80	0.07	23.0
Jan. 2009			3.89	0.36	22.1
Feb. 2009			3.08	0.52	22.3
Mar. 2009			5.23	0.62	22.6
Apr. 2010			4.07	0.56	22.3
Jun. 2009			4.25	0.00	23.9
Jul. 2009		1.04	8.26	0.10	29.1
Oct. 2009			7.51	0.57	25.7
Nov. 2009			9.43	0.80	24.8
Dec. 2009	832				



Date	TL (cm)	CLO:P2I	T (ng/mL)	P4 (ng/mL)	Temp. (°C)
Jan. 2010			3.61	0.33	21.6
Jun. 2010			7.40	1.13	24.0
Oct. 2010		1.05	5.78	0.05	27.1
Dec. 2010	841				
Jan. 2011			4.88	0.14	21.7
Feb. 2011			4.83	0.27	21.7
Mar. 2011			5.70	0.21	22.5
Apr. 2011			4.27	0.21	21.7
May. 2011			7.75	0.30	23.6
Jun. 2011			11.45	0.42	26.0
Jul. 2011			13.50	0.98	28.5
Aug. 2011		1.09	11.24	0.90	27.0
Oct. 2011		1.20	24.46	1.19	25.3
Nov. 2011		1.20			
Dec. 2011	853	1.37	18.36	0.35	23.4
Jan. 2012		1.37	14.73	0.26	21.9
Feb. 2012		1.38			
Mar. 2012		1.42			
Apr. 2012		1.44			
May. 2012		1.47	31.95	1.35	25.5
Jun. 2012		1.51	21.49	0.89	27.1
Jul. 2012		1.60	8.42	0.55	29.0
Aug. 2012		1.60	15.63	1.56	28.5
Sep. 2012		1.60	6.27	3.30	26.5
Oct. 2012		1.60	9.30	2.06	25.3
Nov. 2012		1.60	19.83	0.49	23.8
Dec. 2012	853	1.60	14.72	0.89	22.3
Jan. 2013		1.60	15.85	0.57	21.5
Feb. 2013		1.60			
Mar. 2013		1.60	14.18	0.13	21.7
Apr. 2013		1.60	118.04	2.84	22.4
May. 2013		1.60	90.30	1.69	22.4
Jun. 2013		1.60			
Jul. 2013		1.60	48.66	1.78	29.2
Aug. 2013		1.60	22.45	0.67	29.0
Sep. 2013		1.60	8.34	0.15	27.9
Oct. 2013		1.60	12.30	0.15	26.1
Nov. 2013			63.95	0.53	23.9
Dec. 2013	854		91.28	1.35	22.4

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