# Age and growth analysis of the shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific Ocean

**Yasuko Semba · Hideki Nakano · Ichiro Aoki**

**Abstract** We determined the age and growth rates of male and female shortfin makos, (*Isurus oxyrinchus*), from the western and central North Pacific Ocean. Growth band pairs were counted on half-cut vertebral centra using a shadowing method. In this method, we focused on the ridges on the surface of the centra, consisting of a convex and concave structure. After comparing four enhancing methods, we decided on the use of shadowing method for aging. Vertebrae from 128 males and 147 females were examined. The centrum edge analysis suggested annual band pair formation. Von Bertalanffy growth curves were fitted separately to the length-at-age data for males and females with birth length fixed. Until approximately 7 years of age, both sexes showed similar growth rates; thereafter, males showed a significantly slower growth rate compared to females. It was suggested males and females mature at approximately 6 years and 16 years, respectively. These life-history characteristics suggest relatively low productivity for this species, which agrees with reports on populations in other geographic regions.

**Keywords** Shortfin mako · Annual growth band pair deposition · Centrum edge analysis

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## Introduction

Sharks are one of the top predators in marine ecosystems. In general, sharks are long-lived and have life history characteristics that are quite different from those of teleosts, including slow growth, large adult size, late reproduction, and the live-birth of only a few, well-formed neonates. These characters make sharks especially susceptible to overfishing (Hoenig and Gruber 1990; Stevens et al. 2000), although some species are much more vulnerable than others. Smith et al. (1998) showed obvious pattern along the productivity continuum with regard to adult shark size and certain life-history traits. Specifically, medium to large sized coastal species tend to have lower recovery capacities compared to large pelagic species and coastal smaller species. The collection of species-specific

information is necessary for the understanding of life-history strategy of each species, which directly leads to assessment of the species-specific vulnerability and effective management.

The shortfin mako, Isurus oxyrinchus, is widely distributed in the tropical and warm-temperate oceans worldwide. It is a common, extremely active, and highly migratory species, with occasional inshore movements (Compagno 2001). According to Casey and Kohler (1992), this species prefers temperatures of 17 to 22°C and migrates according to changes in water temperature. As endotherms, shortfin makos maintain a body temperature higher than that of the ambient environment (Carey and Teal 1969; Carey et al. 1981). These characteristics enable the shortfin mako to migrate both horizontally and vertically on a large scale, in a short period of time (Holts and Bedford 1993; Sepulveda et al. 2004). In addition, the spatial segregation between sexes and among ontogenetic stages appears to occur in this species as indicated in many elasmobranch species (Springer 1967); for example, large adult females are rarely observed in the same location as juveniles.

Such wide distribution, migration, and sexual/ontogenetic stage segregation make the collection of sufficient data difficult, and thus information on the biology of this species is limited. However, recent technological advances and intensive studies have clarified many aspects of shortfin mako biology, including reproduction (Mollet et al. 2000; Duffy and Francis 2001; Francis and Duffy 2005; Joung and Hsu 2005), trophic level (Estrada et al. 2003), population structure (Schrey and Heist 2003), and vertical and horizontal migration (Klimley et al. 2002; Sepulveda et al. 2004). Although these reports have advanced our understanding of the ecological aspects of this species, the basic understanding of its life history is still insufficient.

Previous studies on the growth of the shortfin mako in the North Pacific and the northwest Atlantic produced conflicting results with regards to growth band pair deposition. However, this conflict has been settled by recent studies using bomb radiocarbon and tetracycline injection in individuals from the Atlantic Ocean (Campana et al. 2002; Natanson et al. 2006; Ardizzone et al. 2006). These results confirmed that one growth band pair is formed annually in individuals from both the Pacific and the Atlantic oceans. In the North Pacific, Ribot-Carballal et al. (2005) used the centrum edge analysis of the vertebra stained with silver nitrate to show that one band pair is deposited annually in individuals captured off the coast of Baja California. However, little information is available on the growth of the shortfin makos in the western and central North Pacific.

The recent and rapid collapse of large predatory fish populations is a global concern (Myers and Worm 2003, 2005). Baum et al. (2003) and Baum and Myers (2004) warned of a rapid decline in sharks in the northwest Atlantic. Burgess et al. (2005) disagreed with the magnitude of this decline and expressed doubt concerning the potential extinction of some species, suggesting that such inferences were based on inappropriate and limited data. However, Burgess et al. (2005) acknowledged that the populations of some shark species in the northwest Atlantic and the Gulf of Mexico have declined. Given this controversy, various approaches have been taken to assess the current status of sharks and to predict changes in population abundance under various situations (Cortés 2004). To do so, information on life history parameters derived from age and growth analyses plays an integral role. Age determination is an important component of population analyses and thus it is necessary to develop a growth equation that adequately describes the average growth rate of individuals in the population.

The aim of this study was to verify the periodicity of growth band pair formation, and to estimate age and growth parameters for shortfin makos inhabiting the western and central North Pacific. In addition, the growth curves generated in this study were compared to those for populations in other geographic regions.

## Materials and methods

### Sample collection

Vertebral samples were collected between 1992 and 2005 by the crews on board Japanese research vessels and tuna longline training vessels in the North Pacific; also included were five samples of neonate and juvenile sharks from the East China Sea. Additional samples were collected from the commercial longline vessels operating in the North Pacific between 2001 and 2005 (Fig. 1). Samples were collected year-round.

The precaudal length (PCL) was measured to the nearest cm in the straight line and was used as the

**Fig. 1** Sampling locations for the shortfin mako (*Isurus oxyrinchus*) in the western and central North Pacific Ocean. Each point denotes a position where samples were collected
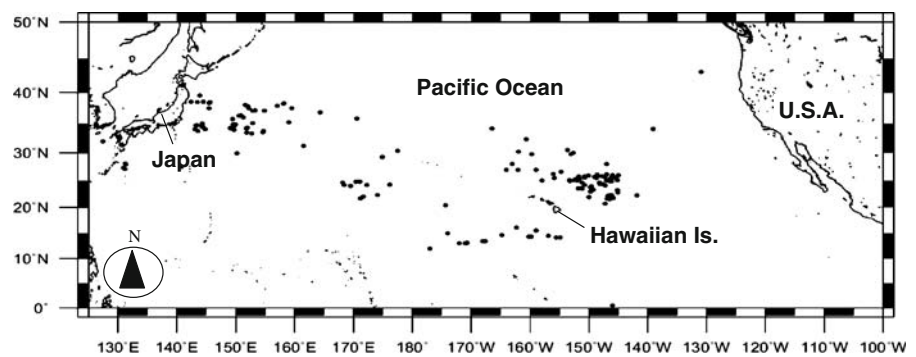
measure of body length throughout this paper. Vertebrae from 275 individuals (128 males and 147 females) were examined (Fig. 2). After sex determination and measurement of the PCL, a section of the vertebral column above the gill slits was excised and frozen at −40°C.

Because the head and viscera had been removed from the samples obtained from the commercial fishing vessels, the dorsal length (DL: distance between the origin of the first dorsal fin and that of the second dorsal fin) was measured to the nearest 0.1 cm and then converted to PCL using the equation below,

Males $\quad PCL = 2.04DL + 12.1 (n = 55, \ r^2 = 0.97)$

Females $\quad PCL = 2.18DL + 7.79 (n = 76, \ r^2 = 0.99)$

In this relationship, F-test indicated statistically significant difference between sexes ($P<0.05$;

$\lambda = 3.40 > F_{2,127}^{0.05} = 3.07$). The relationship between PCL and DL was derived from measurements of 131 intact individuals (PCL: 57.2 to 186.5 cm) collected by the research vessels. For this measurement, length was measured to the nearest 0.1 cm in the laboratory.

To compare the present measurements with previous data expressed as total length (TL) or fork length (FL), we used the following equations to convert the values into the equivalent PCL:

$$PCL = 0.84 \ TL - 2.13 (n = 131, \ r^2 = 0.99),$$

$$PCL = 0.91 \ FL - 0.95 (n = 130, \ r^2 = 1.00),$$

As there was no statistically significant difference between sexes for these two equations, (for both equations, $P>0.05$, F-test), the sexes were combined. TL and FL were measured to the nearest 0.1 cm in a

**Fig. 2** Length frequency of the specimen used for the analysis
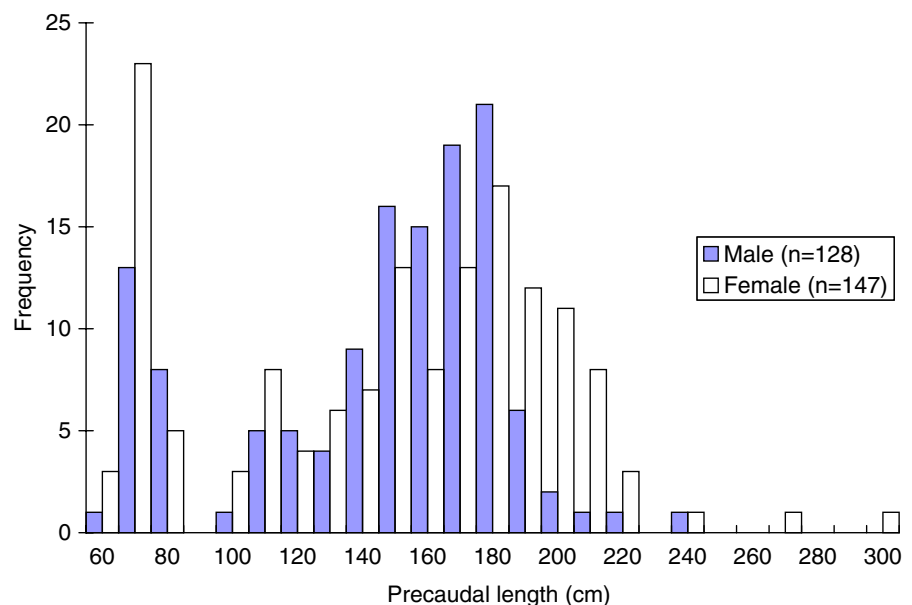
straight line with the tail in the natural position from 131 (PCL: 57.2 to 186.5 cm) and 130 (PCL: 57.2 to 186.5 cm) intact individuals, respectively, which were collected by the research vessels.

Vertebral processing and age determination

In the laboratory, the vertebrae were boiled to remove connective tissue and then stored in 70% ethanol until analysis. A single centrum was cut off, soaked in 6N sodium hydroxide solution, and scrubbed with a polishing buff (8-inch buff micro-cloth) to remove intervertebral cartilage from the surface of the vertebral centra. After drying, each centrum was cut into two longitudinal sections using a diamond saw (Mini-lab-cutter MC110; Maruto Co., Hiroshima, Japan) with the focus slightly to one side. The half-cut centra with the focus were used for analysis after washing away the bone particle and drying for 1 day.

Prior to final age determination, we tested four techniques to enhance vertebral growth bands: shadowing (half-cut centra), alizarin staining (section; Berry et al. 1977), silver nitrate staining (whole centra; Stevens 1975), and soft X-radiography (whole or half-cut centra; Cailliet et al. 1983). The shadowing method is derived from the method described by Francis and Maolagáin (2000), which visualizes the surface bands by oblique lateral illumination (reflected light) with fibre-optic light sources. We modified this method by cutting the centra into half and enhanced the microtopography of the three-dimensional structure on the surface of the centra after removal of the connective tissue and weakly calcified cartilage. We compared these four methods and checked the correspondence of three-dimensional structures observed in the shadowing method to the characters observed in the other three methods. The advantages of this method are simplicity, visual clarity, relative abundance of information amount and less time-consuming process. The three-dimensional structure visualized by shadowing method is observed as consecutive in relatively large area compared to planar sectioning method. In addition, the half-cut centra provide more information to interpret the growth bands not only from the surface of the centra (three-dimensional structure) but also from the corpus calcareum and intermedialia. This means our method

provides additional information to assist to distinguish checks or split bands occurring in the corpus calcareum, the intermedialia or both. This is the reason why we chose the shadowing method based on the check of correspondence among methods.

As we focused on the three-dimensional structure consisting of concave and convex structure, enhancement of the contrast of these two structures was necessary for accurate count of growth band pair. The shadowing method illuminates the regularly formed three-dimensional structures and thus creates light and dark contrasting features on the surface of the vertebral centra.

After bleaching and cleaning the centra, regular and alternate concave and convex concentric circles were observed on each centrum. We regarded a pair of these structures as a growth band pair (annulus) and counted the number of convex structures assuming this structure is an indicator of annulus. These band pairs were visually enhanced by shining reflected light from opposite sides using a fiber-optic light source (Fig. 3).

In this way, the convex and concave structures were observed as light and dark regions, respectively. These structures correspond to the opaque (convex) and translucent (concave) regions observed in the sagittal section. Additional information that is useful for interpreting these growth bands can be obtained from the corpus calcareum and intermedalia of the cutting plane of the half-cut centra.

To verify the periodicity of these structures, the most peripheral structure on each centrum was classified as either concave or convex and we used these data to determine the frequency of peripheral convex structures throughout the year. Classification was performed by a reader without knowledge of the collection date. The vertebrae of neonates, which displayed only a birthmark, were excluded from this analysis.

The centrum radius (CR) is the distance from the focus to the edge of the centrum perpendicular to the direction of the cutting plane. The CR was measured to the nearest 0.01 mm using a digital HF microscope (VH-8000; Keyence Corporation, Osaka, Japan). The relationship between the CR and PCL was examined separately for males and females using the nonlinear least-squares method. Solver (an add-in tool of
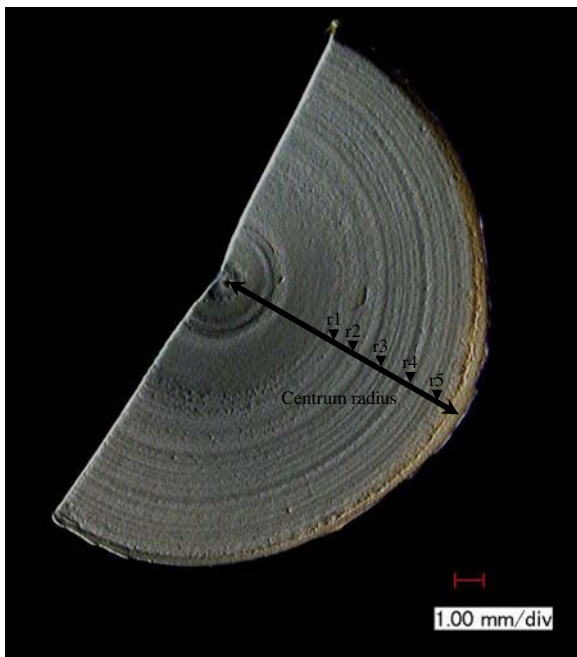
**Fig. 3** Half of a vertebral centrum with lateral illumination from fiber-optic sources. The triangles indicate a convex structure or growth band. This example is from a 137 cm PCL female, with a vertebral centrum radius of 9.5 cm, and an estimated age of 4.6 years

Microsoft Excel) was applied to the CR and PCL data for each individual. We used the likelihood ratio test developed by Cerrato (1990) to test for a significant difference in the coefficients of allometric equations between males and females. We tested the null hypothesis, $H_0$, no difference between sexes, versus the alternative hypothesis, $H_a$, significant difference between sexes. We defined $\widehat{\theta}$ as the least-squares estimate and $S\left(\widehat{\theta}\right)$ as the sum of the squares of residuals obtained under the null ($\omega$) and alternative ($\Omega$) hypotheses, respectively. The null hypothesis was rejected if

$$\lambda = \frac{\left(S\left(\widehat{\theta}_{1\omega}, \widehat{\theta}_{2\omega}\right) - S\left(\widehat{\theta}_{1\Omega}, \widehat{\theta}_{2\Omega}\right)\right)\big/q}{S\left(\widehat{\theta}_{1\Omega}, \widehat{\theta}_{2\Omega}\right)\big/(f_1 + f_2)} > F_{q, f_1 + f_2}^{0.05}$$

at a significance level of 0.05, where the subscripts 1 and 2 denote males and females, respectively, $q$ is the linear constraint of the form, $f_i = n_i - p$ $(i = 1, 2)$, in which $n_i$ is the sample size, and $p$ is the number of

parameters estimated in each equation (e.g., two for the allometric relationship and two for the alternative von Bertalanffy growth equation with size at birth fitted). $F_{q, f_1+f_2}^{\alpha}$ is the $100(1-\alpha)$ percentile of an F distribution with $q$ and $f_1 + f_2$ degrees of freedom.

For each growth band pair, the distance between the focus and the end of the convex structure was measured to the nearest 0.01 mm under a digital HF microscope (Fig. 3). The same reader counted the number of convex structures on each sample twice at different times (approximately 6 months apart) without knowledge of the individual body size, sex, or previous count. Then we calculated percent agreement (PA= [No. agreed/No. read]*100), and percent agreement plus or minus 1 year (PA= [±1 yr]) for length groups of 10 cm to evaluate precision. For the individuals above 220 cm, data was combined. In order to determine whether differences within reader was systematic (biased) or random, we conducted chi-square tests of symmetry suggested by Hoenig et al. (1995) as well as using age-bias plot. In addition, we calculated mean coefficient of variation (CV) for all the counts.

As the results of these analyses of precision and bias were acceptable, a third count was conducted whenever the first and second counts differed. If the third count was the same as either the first or second count, the count with two consentience was used in the analysis. If the third count did not agree with either of the former counts, the sample was excluded from the analysis.

Mollet et al. (2000) reported that shortfin makos give birth between March and June in the Northern Hemisphere. Because we frequently found neonates ranging from 57 to 75 cm PCL between May and June, age was estimated based on a tentative birth date of 1 May. As discussed later, the first band (birthmark) is formed after parturition and subsequent annuli (convex structures) formation occurs during the winter. Assuming that annuli (convex structures) are formed soon before or after 1 December, age in years was calculated as follows:

$$age = (x - 1) + \frac{(y - 5)}{12} \quad (x \geq 1, \ 1 \leq y \leq 12),$$

where $x$ is the number of convex structure and $y$ is the month when the individual was caught ($1 \leq y \leq 12$).

A modified form of the von Bertalanffy growth equation was fitted to the length-at-age data independently for males and females to ensure that the curve passed through the known size at birth (Simpfendorfer et al. 2002, Chidlow et al. 2007):

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

where $L_t$ = PCL at time $t$ (cm); $L_0$ = size at birth (cm) (74 cm TL) given by Joung and Hsu (2005); $L_\infty$ = asymptotic length (cm); and $k$ = brody growth constant (year$^{-1}$).

The nonlinear least-squares method was used to estimate this modified von Bertalanffy growth equation for each sex (Haddon 2001). Solver was applied to the length-at-age data for each individual to estimate parameters of growth equations. To calculate standard error (S.E.), we assumed normal error distribution (NED) as the error structure. The difference in the growth curves between sexes was tested following the method described by Cerrato (1990).

Growth curves were compared to those of other studies after converting the values for body length (i.e., TL or FL) into PCL. Additionally, we revised the growth curves described by Pratt and Casey (1983) to reflect the annual deposition of one growth band pair, thus allowing comparison with our curves.

## Results

The PCL of samples ranged from 53 to 240 cm for males and 57 to 300 cm for females (Fig. 2). The CR showed an allometric relationship with PCL for both sexes, indicating that the vertebral centrum is an appro-
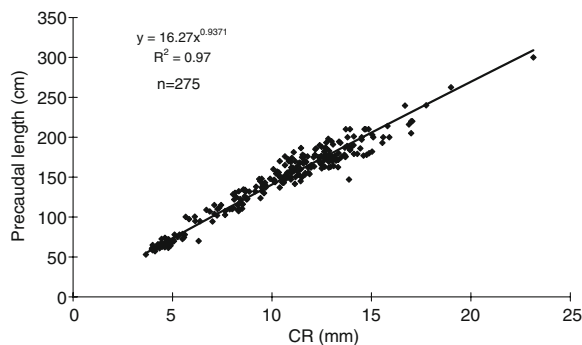
Fig. 4 Relationship between the vertebral centrum radius (CR) and precaudal length (PCL) in shortfin mako
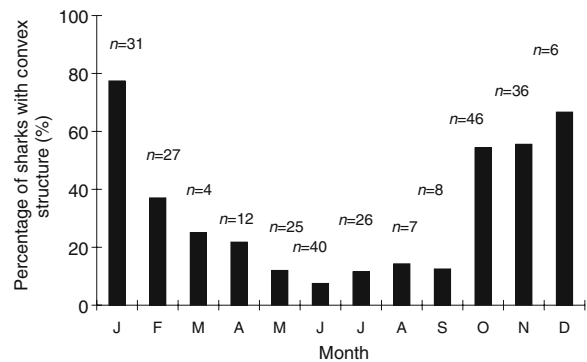
Fig. 5 Monthly changes in the percent presence of peripheral convex structures from vertebral centra of shortfin mako. The numbers above each bar indicate sample size

priate indicator of growth. There was no significant statistical difference in the PCL-CR relationship between sexes ($P > 0.05$, $\lambda = 0.57 < F_{2,271}^{0.05} = 3.03$); thus, we fitted a curve to the pooled data (Fig. 4), as follows:

$$PCL = 16.3 CR^{0.94} \left(n = 275, r^2 = 0.97\right),$$

We used the allometric equation for regression analysis because it displayed a better fit than the linear equation (error sum of squares: 28076.65 versus 28607.94, $r^2$: 0.97 versus 0.95, respectively).

We observed a marked difference in the frequency of peripheral convex structures throughout the year (Fig. 5). The frequency of the convex structures was low from March to September (summer) and high from October to January (winter). In contrast, the occurrence of the concave structure was high in the summer and low in the winter. This suggests that one pair of concave and convex structures is formed every year. December was tentatively identified as the month of annuli formation since a statistical model based on a circular distribution indicated the peak in December (Okamura and Semba, unpublished manuscript). They validated the periodicity of growth band pair formation by fitting the data in the present study (shown in Fig. 5) for three models; model with no band periodicity (model N), model with annual periodicity (model A), model with biannual periodicity (model B) and calculated AIC for each model. As a result, model with annual periodicity (model A) was selected with the lowest AIC among three models (AIC: 312.44 for model N, 271.89 for model A and 316.24 for model B) and they statistically confirmed the peak of convex structure in December from the model.

In many species of sharks, birthmark deposition occurs at or shortly after parturition (Branstetter and Stiles 1987; Simpfendorfer 1993; Loefer and Sedberry 2003). The shortfin mako is born at 70–74 cm TL (56–60 cm PCL; Stevens 1983; Mollet et al. 2000; Joung and Hsu 2005). No birthmarks were observed on individuals between 53 and 62 cm collected in May and June, except for two specimens of 60 and 61 cm that each displayed one band pair. The birth band corresponded to an angle change observed in the sagittal section. However, all neonates larger than 62 cm captured in the same month had one band pair, and all those larger than 70 cm displayed regularly deposited band pairs. The first band (convex structure) was therefore regarded as the birthmark (age = 0) and all the subsequent annuli (convex structures) i.e., winter marks, were deposited annually.

The number of annuli counted ranged from 0 to 20. The maximum number of annuli was 14 for a male of 240 cm PCL and 20 for a female of 300 cm PCL. Appendix (a) and Appendix (b) indicate mean radii of each band (convex structure) for each group with same number of band pairs for males and females, respectively. The percent agreement (PA) for all sample was 70.2% and percent agreement ± 1 (PA[±1]) was 95.3%. When grouped by 10-cm length increments, PA for individuals <150 cm PCL was relatively high (mean: 75%) and PA [±1] was above 90% for individuals <190 cm PCL (Table 1). Comparison of the first count with the second count indicated no systematic bias (Fig. 6). The mean CV was 3.7% and this value is close to the value by Natanson et al. (2006). The chi-square tests of symmetry gave no indication that differences within readers were systematic rather than due to random error ($\chi^2$ test, df= 22, $P>0.05$).

The estimated growth equations are as follows:

Males   $L_t = 60 + 171.3\{1 - \exp(-0.156t)\}$   $(n = 128)$,

Females   $L_t = 60 + 248.6\{1 - \exp(-0.090t)\}$   $(n = 147)$,

where $t$ is age (years). The likelihood ratio test of these growth curves (Cerrato 1990) indicated a significant difference between sexes within the size range of individuals used in the present study ($P<0.05$, $\lambda = 6.87 > F_{2,271}^{0.05} = 3.03$). The estimated S.E. of $L_\infty$ for females was larger than that for males, while S. E. of K for males was larger than for females (Table 2).

Growth rate was similar in both sexes until approximately 7 years of age, after which females out-grew than males of the same age (Fig. 7). The estimated growth curves were compared to those from other geographical regions (Fig. 8a, b).

The shortfin mako in the eastern North Pacific (Cailliet and Bedford 1983; Ribot-Carballal et al. 2005) grew at a slower rate than that in the western and central North Pacific. The growth curve estimated by Ribot-Carballal et al. (2005) was more similar to ours than that of Cailliet and Bedford (1983), especially for males. The growth curve estimated in the South Pacific (Bishop et al. 2006) and North Atlantic (Natanson et al. 2006) showed a slower growth rate than those indicated by our results.

For Atlantic shortfin mako, the annual formation of one growth band pair was validated by bomb radiocarbon experiment (Campana et al. 2002; Ardizzone et al. 2006) and by OTC-injection experiment (Natanson et al. 2006), therefore, we revised the growth curves reported by Pratt and Casey (1983) to reflect annual, instead of biannual, band pair deposition. The revised curves yielded a faster growth rate for both sexes than are suggested by our data.

## Discussion

Method of age determination

Growth band pairs were counted on half-cut vertebral centra using the shadowing method, which elucidates the three-dimensional convex and concave structures on the surface of the vertebral centra. This simple procedure provides a clear view and allows for relatively easy examination of the periphery of the centra. Francis and Maolagáin (2000) and Parsons (1983) used a similar method to examine growth bands in *Mustelus lenticulatus* and *Rhizoprionodon terraenovae*, respectively. We performed preliminary tests to compare the shadowing method with three other techniques, including sagittal sections stained with alizarin red, whole centra stained with silver nitrate and enhanced by soft X-radiography. In the soft X-radiographic method, the translucent and opaque regions of the centra corresponded to convex and concave structures, respectively. In the alizarin red and silver nitrate staining methods, the lightly

**Table 1** Percent aggreement (PA) and PA ± 1 year for the shortfin mako (*Isurus oxyrinchus*) in the western and central North Pacific Ocean for 10-cm precaudal length groups. The individuals above 220 cm were combined

| PCL (cm) | Total no. read | No. agreed upon | No. agreed upon ±1 | PA | PA ± 1 |
|---|---|---|---|---|---|
| 50–59 | 3 | 2 | 1 | 66.7 | 100 |
| 60–69 | 36 | 36 | 0 | 100.0 | 100.0 |
| 70–79 | 14 | 10 | 4 | 71.4 | 100 |
| 90–99 | 4 | 4 | 0 | 100 | 100 |
| 100–109 | 11 | 8 | 3 | 72.7 | 100 |
| 110–119 | 11 | 7 | 4 | 63.6 | 100 |
| 120–129 | 9 | 9 | 0 | 100 | 100 |
| 130–139 | 16 | 11 | 5 | 68.8 | 100 |
| 140–149 | 23 | 17 | 6 | 73.9 | 100 |
| 150–159 | 23 | 18 | 4 | 78.3 | 95.7 |
| 160–169 | 29 | 19 | 10 | 65.5 | 100 |
| 170–179 | 38 | 26 | 10 | 68.4 | 94.7 |
| 180–189 | 26 | 17 | 7 | 65.4 | 92.3 |
| 190–199 | 9 | 5 | 4 | 55.6 | 100 |
| 200–209 | 9 | 2 | 5 | 22.2 | 77.8 |
| 210–219 | 9 | 2 | 3 | 22.2 | 55.6 |
| >220 | 5 | 0 | 3 | 0.0 | 60 |
| Total | 275 | 193 | 69 | - | - |
| Mean | - | - | - | 70.2 | 95.3 |

stained (opaque) and deeply stained (translucent) regions corresponded to convex and concave structures, respectively. These observations suggest that concave structures are much more mineralized (calcium-rich) than convex structures (calcium-poor). These results also confirm that the three-dimensional structures visualized by the shadowing method are equivalent to the characters observed by traditional methods.

As a result of comparison, the fine structures enhanced by the X-radiography tend to cause overestimation of age because of counting checks or rings other than growth band. The shadowing method not only provides clear views but also allows the researcher to combine views from the surface of the centra and cutting planes, thus providing more information than other techniques, such as the planar (two dimensional) sectioning method or method using



**Fig. 6** Age-bias plot of 275 shortfin mako vertebral counts from two independent readings by the first author. The open and solid mark indicate the observed counts and the mean counts assigned by the second count for all fish which was assigned a given count in the first count up to 12, respectively. The vertical bars for the solid mark up to the first count of 11 indicate the 95% confidence interval. The one to one equivalence line is also represented
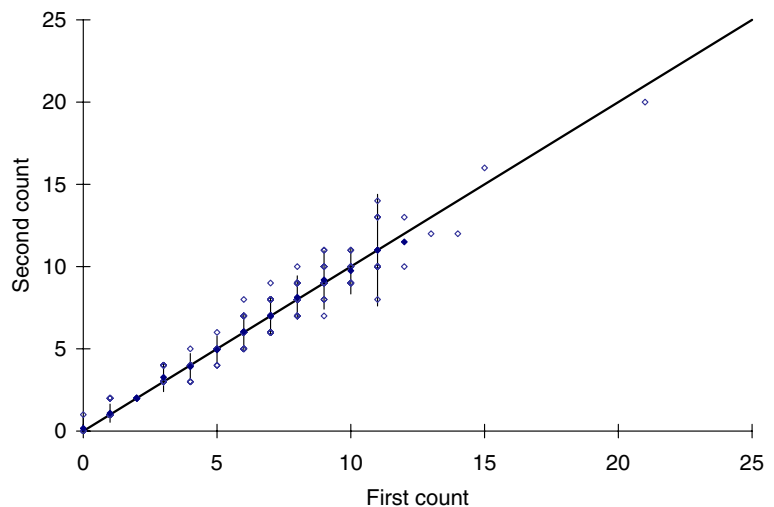
**Table 2** Von Bertalanffy growth parameter estimates and standard errors (S.E.) for male and female shortfin mako in the western and central North Pacific Ocean. $L_0$ was cited from the estimate by Joung and Hsu (2005)

|  | Sample size |  | $L_\infty$ (cm) | K (year$^{-1}$) | $L_0$ (cm) |
|---|---|---|---|---|---|
| Males | 128 | Estimate | 231.0 | 0.16 | 59.7 |
|  |  | S.E. | 15.5 | 0.0175 | - |
| Females | 147 | Estimate | 308.3 | 0.090 | 59.7 |
|  |  | S.E. | 21.7 | 0.0091 | - |

whole centra. From the precision and bias estimates, we believe that the view provided by the shadowing method is enough clear to obtain reproducible counts. However, counting growth band pair on vertebrae from large individuals is as difficult with the shadowing methods as with other methods. For this problem, simultaneous use of sectioned vertebrae will help to interpret the growth bands accurately. The concurrent use of a laser displacement sensor capable of measuring three-dimensional structures may make this method more efficient.
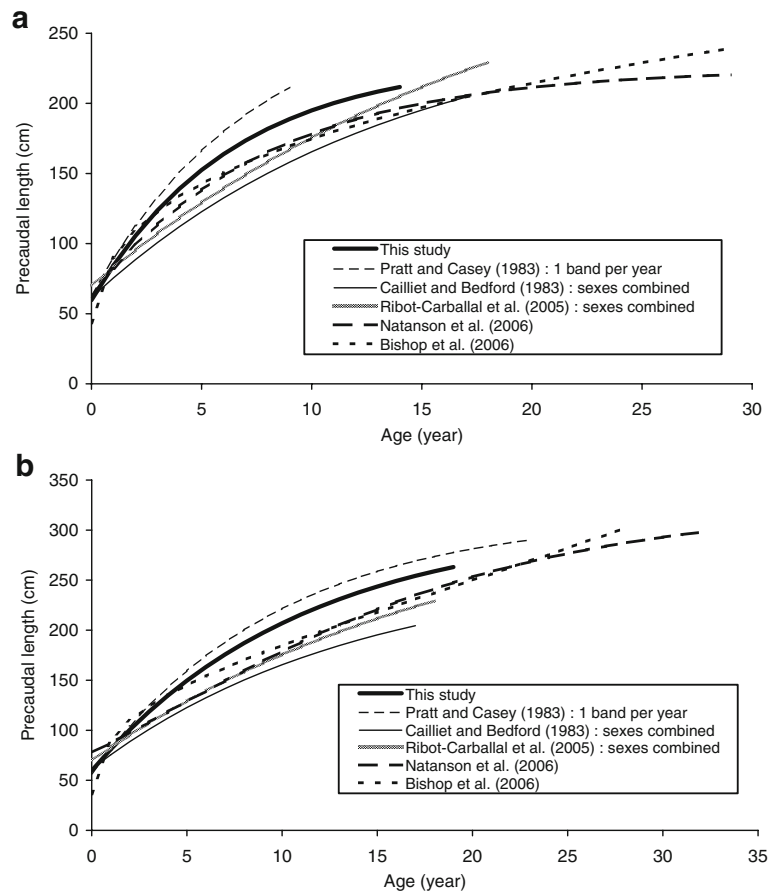
Growth

We estimated a theoretical maximum length in females of 308 cm PCL, which corresponds to 370 cm TL. Although this estimate is smaller than the estimated world maximum length of a shortfin mako, which is approximately 400 cm TL (Compagno 2001), it is suggested this estimate is acceptable considering the regional difference (337 cm TL for the Nansei Islands of Japan [Uchida et al. 1987], 350.7 cm TL for the southern California, 373.8 cm TL for New Zealand [Applegate 1977] and 380 cm TL for the east Indian Ocean [Gubanov 1974]).

Very few samples were obtained from large specimens (>200 cm); as a result, the growth curve is most reliable up to an age of 10 years; caution is advisable when estimating the growth of sharks more than 10 years old. Despite this disadvantage, our samples showed statistically significant sex-dependent differences in growth parameters. Until approximately 7 years of age, males and females grew at similar rates; after this point, the growth rate of males slowed in comparison to that of females. Although our small sample size for large sharks could have caused this discrepancy, previous studies have also reported similar sex-dependent differences in growth rate (Pratt and Casey 1983; Bishop et al. 2006; Natanson et al. 2006), suggesting that this is a general characteristic of this species. This difference may be attributable to differences in energy partitioning between males and females. According to Francis and Duffy (2005), males attain sexual maturity at 183 cm FL, whereas females are not sexually mature until they reach 280 cm FL. These body lengths correspond to ages of approximately 7 to 9 and 19 to 21 years, respectively (Bishop et al. 2006). It is possible that males devote their energy to reproduction including maturing process, rather than somatic growth toward their maturity, resulting in such marked sexual differences in size and age of maturity.



**Fig. 7** Estimated von Bertalanffy growth curves for female and male shortfin mako in the western and central North Pacific Ocean
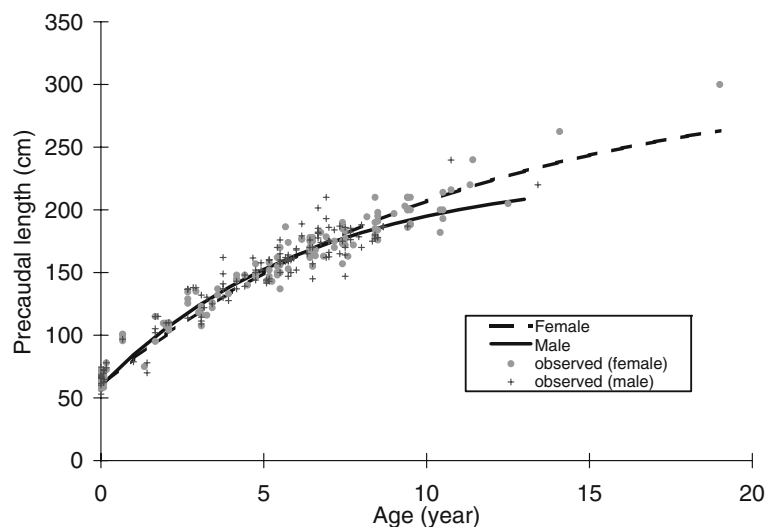
**Fig. 8** Comparison of growth curves to those reported in previous studies for **a** males and **b** females. The curves reported by Pratt and Casey (1983) were recalculated assuming one growth band pair formation per year



Growth band formation

The examination of vertebrae from neonates captured in May and June suggested that the formation of the first convex concentric structure (birthmark) occurs after parturition. The examination of vertebrae from older individuals suggested that subsequent convex concentric structures are formed every winter. In *Carcharhinus limbatus*, Branstetter (1987) proposed that the growth increment bordered by the birth annulus and the first postnatal annulus represented approximately 6 months of growth, and that the subsequent growth increments between annuli (i.e., after the second annulus) represented a full year. Based on the seasonality of parturition and annuli formation, we determined that the growth increment between the birthmark and the second annulus is approximately 7 months. Therefore, our results may differ from previous studies using methods that assume a growth increment of 1 year between the first and second annulus.

In this study, the result of the centrum edge analysis showed a clear annual trend with convex dominant in the winter and concave dominant in the summer. This result supports the annual growth band pair formation for the population in the western and central North Pacific Ocean, which is consistent with the results in the eastern Pacific Ocean. This supports the hypothesis that the periodicity of growth band pair formation for this species is same between the Pacific and the Atlantic.

Growth comparisons among geographical regions

Our results differ slightly from the results estimated in other regions. In the eastern North Pacific, two growth equations have been reported for the shortfin mako (Cailliet and Bedford 1983; Ribot-Carballal et al. 2005). These studies examined 44 and 109 vertebrae, respectively, and data from males and females were pooled. The growth curve estimated by Ribot-Carballal et al. (2005) showed a faster growth rate than that reported by Cailliet and Bedford (1983),

which was attributed to a larger sample size ($n=109$) and broader size range studied by Ribot-Carballal et al. (2005). The small sample size and paucity of samples from large individuals may have caused the difference between these results. In contrast, our sample size ($n=275$) is nearly twice as large and we measured a greater number of large individuals (>160 cm) than these previous studies. In addition, considering the sex-dependent difference in growth rate, a bias in the number of male and female specimens in each length class may have also led to biased age estimates. However, some difference between the eastern Pacific and the western and central North Pacific are to be expected as a result of regional factors related to population or environment. For example, the individuals sampled in the eastern Pacific were found in the coastal waters around the southern or Baja California, whereas our samples were collected in the offshore pelagic waters. Further research is required to address these regional differences.

In the Atlantic, the growth curves estimated by Pratt and Casey (1983) yielded a faster growth rate than those indicated by our data (especially for males), even after revising the curves for annual band pair formation. The size distribution of their samples and their original counts of band pair were relatively similar to ours; therefore, the difference in growth curves may be attributable to different manners of assigning length-at-age or the different growth model to fit the data. On the other hand, the growth curves estimated by Natanson et al. (2006) showed a slower growth rate than our estimates.

Growth curves estimated by Bishop et al. (2006) for sharks in the South Pacific also represented a slower growth rate than our estimates, but growth rate during the first 5 years was relatively similar. Despite these differences, we suggest that the variation in growth rates between the Pacific and the Atlantic oceans might be smaller than once thought.

The latter two studies [Natanson et al. (2006) and Bishop et al. (2006)] used different models to fit the length-at-age data, compared to the modified von Bertalanffy growth equation used in our study. They collected vertebral samples from a wide range of body lengths; therefore, discrepancies in growth curves may be attributable mainly to factors other than sampling bias, such as differences in the fit of models, counting criteria, or the calculation of length-at-age.

These discrepancies between this study and other studies may also be the result of different readers. If we assume the growth band pairs correspond in both the shadowing method and conventional methods based on the result of the preliminary analysis, the difference in reader's baseline for identification may occur, causing discrepancies in the interpretation of growth bands. We compared our counting method with the photographed examples provided by Ribot-Carballal et al. (2005; Fig. 4 in their text). In this specific case, their counts agreed with ours. This problem could be resolved by collecting a wide size range of OTC-injected tag-recapture samples for use as references, or by developing criteria for band identification based on cross-readings among readers using a unified method.

## Conclusion

We estimated a representative growth curve for the shortfin mako in the western and central North Pacific by collecting samples across a wide size range and then incorporating information on the seasonality of parturition and annuli formation.

Because numerous factors impact the estimation of growth curves, our results cannot be used to confirm regional differences in growth rates. However, such differences may be small or negligible. Our data from the western and central Pacific Ocean indicate that shortfin makos in this area grow slowly and mature late, and our results provide insight into the population structure. A better understanding of the age structure in a unified regional framework will allow us to construct effective guidelines for the assessment and management of the shortfin mako population.

**Appendix.** Mean radii of each band (convex structure) with (±) standard deviation for each group with same number of band pairs for *Isurus oxyrinchus* in the western and central North Pacific Ocean for (a) male and (b) female

(a)

| No. of band pair | Number of specimens | N th band | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| 0 | 3 | | | | | | | | | | | | | | |
| 1 | 17 | 4.04 (±0.10) | | | | | | | | | | | | | |
| 2 | 3 | 4.07 (±0.14) | 4.98 (±0.21) | | | | | | | | | | | | |
| 3 | 6 | 4.03 (±0.063) | 5.13 (±0.073) | 6.40 (±0.075) | | | | | | | | | | | |
| 4 | 12 | 4.05 (±0.14) | 5.10 (±0.14) | 6.45 (±0.13) | 7.48 (±0.17) | | | | | | | | | | |
| 5 | 10 | 4.02 (±0.08) | 5.14 (±0.11) | 6.46 (±0.10) | 7.60 (±0.11) | 8.59 (±0.10) | | | | | | | | | |
| 6 | 20 | 4.01 (±0.11) | 5.12 (±0.12) | 6.48 (±0.12) | 7.58 (±0.13) | 8.61 (±0.13) | 9.56 (±0.14) | | | | | | | | |
| 7 | 20 | 4.04 (±0.13) | 5.07 (±0.13) | 6.42 (±0.12) | 7.51 (±0.14) | 8.56 (±0.15) | 9.53 (±0.16) | 10.45 (±0.18) | | | | | | | |
| 8 | 23 | 3.98 (±0.12) | 5.04 (±0.13) | 6.43 (±0.14) | 7.54 (±0.12) | 8.55 (±0.14) | 9.56 (±0.13) | 10.54 (±0.15) | 11.49 (±0.15) | | | | | | |
| 9 | 9 | 4.05 (±0.17) | 5.05 (±0.08) | 6.53 (±0.41) | 7.54 (±0.15) | 8.54 (±0.06) | 9.50 (±0.12) | 10.44 (±0.14) | 11.37 (±0.16) | 12.25 (±0.20) | | | | | |
| 10 | 3 | 4.11 (±0.04) | 5.06 (±0.06) | 6.29 (±0.09) | 7.35 (±0.18) | 8.36 (±0.20) | 9.44 (±0.13) | 10.41 (±0.06) | 11.30 (±0.10) | 12.30 (±0.04) | 13.15 (±0.11) | | | | |
| 12 | 1 | 3.94 (-) | 4.92 (-) | 6.40 (-) | 7.45 (-) | 8.45 (-) | 9.32 (-) | 10.42 (-) | 11.37 (-) | 12.30 (-) | 13.30 (-) | 14.23 (-) | 15.17 | | |
| 14 | 1 | 4.18 (-) | 5.08 (-) | 6.42 (-) | 7.69 (-) | 8.83 (-) | 9.79 (-) | 10.56 (-) | 11.48 (-) | 12.27 (-) | 13.21 (-) | 14.05 (-) | 14.92 (-) | 15.68 (-) | 16.48 (-) |
| Average | | 4.03 | 5.08 | 6.44 | 7.54 | 8.56 | 9.54 | 10.48 | 11.44 | 12.27 | 13.19 | 14.14 | 15.04 | 15.68 | 16.48 |

**(b)**

| No. of band pair | Number of specimens | \(N\) th band 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 3 | | | | | | | | | | | | | | | | | | | | |
| 1 | 27 | 4.04 (±0.13) | | | | | | | | | | | | | | | | | | | |
| 2 | 5 | 3.92 (±0.029) | 5.00 (±0.040) | | | | | | | | | | | | | | | | | | |
| 3 | 7 | 4.01 (±0.081) | 5.08 (±0.064) | 6.38 (±0.081) | | | | | | | | | | | | | | | | | |
| 4 | 14 | 4.08 (±0.16) | 5.10 (±0.10) | 6.33 (±0.16) | 7.43 (±0.15) | | | | | | | | | | | | | | | | |
| 5 | 7 | 4.00 (±0.13) | 5.08 (±0.11) | 6.42 (±0.14) | 7.59 (±0.12) | 8.62 (±0.11) | | | | | | | | | | | | | | | |
| 6 | 16 | 4.00 (±0.13) | 5.09 (±0.12) | 6.40 (±0.11) | 7.55 (±0.08) | 8.57 (±0.11) | 9.52 (±0.13) | | | | | | | | | | | | | | |
| 7 | 19 | 4.03 (±0.16) | 5.12 (±0.12) | 6.43 (±0.13) | 7.53 (±0.13) | 8.55 (±0.11) | 9.52 (±0.10) | 10.47 (±0.13) | | | | | | | | | | | | | |
| 8 | 13 | 4.02 (±0.13) | 5.07 (±0.12) | 6.41 (±0.09) | 7.51 (±0.08) | 8.55 (±0.13) | 9.50 (±0.15) | 10.46 (±0.15) | 11.46 (±0.17) | | | | | | | | | | | | |
| 9 | 12 | 4.04 (±0.09) | 5.05 (±0.07) | 6.37 (±0.10) | 7.54 (±0.12) | 8.57 (±0.17) | 9.57 (±0.17) | 10.52 (±0.17) | 11.44 (±0.20) | 12.39 (±0.20) | | | | | | | | | | | |
| 10 | 13 | 4.02 (±0.20) | 5.10 (±0.16) | 6.44 (±0.16) | 7.56 (±0.15) | 8.65 (±0.12) | 9.64 (±0.15) | 10.60 (±0.14) | 11.49 (±0.19) | 12.36 (±0.24) | 13.20 (±0.27) | | | | | | | | | | |
| 11 | 5 | 4.08 (±0.10) | 5.11 (±0.22) | 6.48 (±0.17) | 7.59 (±0.19) | 8.72 (±0.17) | 9.67 (±0.13) | 10.60 (±0.10) | 11.45 (±0.06) | 12.44 (±0.07) | 13.47 (±0.16) | 14.21 (±0.21) | | | | | | | | | |
| 12 | 3 | 3.90 (±0.10) | 4.98 (±0.18) | 6.23 (±0.11) | 7.34 (±0.13) | 8.36 (±0.16) | 9.37 (±0.08) | 10.48 (±0.15) | 11.58 (±0.17) | 12.48 (±0.13) | 13.49 (±0.14) | 14.43 (±0.10) | 15.31 (±0.06) | | | | | | | | |
| 13 | 1 | 3.94 (-) | 4.94 (-) | 6.29 (-) | 7.44 (-) | 8.45 (-) | 9.46 (-) | 10.37 (-) | 11.40 (-) | 12.16 (-) | 13.12 (-) | 14.09 (-) | 15.14 (-) | 15.90 (-) | | | | | | | |
| 16 | 1 | 4.28 (-) | 5.14 (-) | 6.40 (-) | 7.50 (-) | 8.56 (-) | 9.58 (-) | 10.50 (-) | 11.57 (-) | 12.58 (-) | 13.61 (-) | 14.43 (-) | 15.35 (-) | 16.25 (-) | 17.00 (-) | 17.71 (-) | | | | | |
| 20 | 1 | 3.98 (-) | 5.22 (-) | 6.55 (-) | 7.63 (-) | 8.73 (-) | 9.86 (-) | 10.85 (-) | 11.89 (-) | 12.92 (-) | 13.62 (-) | 14.52 (-) | 15.34 (-) | 16.02 (-) | 16.76 (-) | 17.48 (-) | 18.3 (-) | 18.86 (-) | 19.60 (-) | 20.20 (-) | 20.93 (-) |
| Average | | 4.03 | 5.08 | 6.40 | 7.52 | 8.58 | 9.55 | 10.52 | 11.48 | 12.41 | 13.32 | 14.31 | 15.29 | 16.06 | 16.88 | 17.59 | 18.30 | 18.86 | 19.60 | 20.20 | 20.93 |

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