[Original Article]

Ontogenetic growth pattern of the extant smalltooth sandtiger shark, *Odontaspis ferox* (Lamniformes: Odontaspididae) —application from and to paleontology

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Abstract

The smalltooth sandtiger shark, *Odontaspis ferox* (Risso 1810), is an enigmatic modern lamniform shark. In this study, a 'single-sample' paleontological technique previously used to examine the growth patterns of some fossil sharks is applied to a specimen of extant *O. ferox* of an unknown sex that measured 297 cm in total length (TL). Growth increments presumably deposited annually identified in its vertebrae suggest that the *O. ferox* individual was 14 years old at the time of its capture. The von Bertalanffy growth function experimentally fitted to the data gives the following growth parameters: L_0 = 93.850 cm TL, L_∞ = 315.206 cm TL, and k = 0.183 yr^{-1}. The L_∞ value strongly suggests that the specimen must have been a male, and the size at birth and size at maturity based on our study agree well with published field-based observations on *O. ferox*. Where *O. ferox* occurs in the fossil record as far back as in the early Miocene, this study also presents a method to infer the TL from an isolated tooth for *O. ferox*, useful for paleoecological reconstruction.

Key words: Elasmobranchii, growth, Lamniformes, Odontaspididae, ontogeny

Introduction

The growth pattern and life history traits of large marine predatory species, such as sharks, are important parameters to understand the population dynamics of many marine organisms because those predators greatly affect the community in which they inhabit (e.g., Cailliet et al. 2006; Goldman et al. 2012). To this end, the von Bertalanffy growth function (VBGF) is the most common quantitative method used to describe the growth of modern fishes, especially sharks and rays (Chondrichthyes: Elasmobranchii) based on growth bands on calcified structures such as vertebral centra (e.g., Cailliet and Goldman 2004; Goldman 2004), and the technique has also been applied to some extinct sharks (e.g., Shimada 2008; Cook et al. 2011; Newbrey et al. 2015). Whereas conventional VBGF studies on modern elasmobranchs require a large sample size from a population for a rigorous growth analysis (e.g., Cailliet et al. 1983; Liu et al. 1998, 1999; Wintner and Cliff 1999; Natanson et al. 2002), Shimada (2008) in particular demonstrated that the ontogenetic growth pattern of an extinct elasmobranch can be elucidated from a single individual if the fossil specimen preserves presumed annually deposited growth increments in

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its vertebral centra and if the size of the individual (e.g., total length, TL) is known such as based on a complete or nearly complete skeleton.

In this paper, we demonstrate that Shimada's (2008) 'single-sample' paleontological technique using VBGF can be applied to extant species in which the application is especially useful for a rare taxon. We examine the growth pattern of the extant smalltooth sandtiger shark, *Odontaspis ferox* (Risso 1810) (Lamniformes: Odontaspididae), for this demonstration based on one of only a few known preserved specimens in the United States. Our study sheds some new light into the life history strategies of *O. ferox* that is elusive and has an exceptionally spotty distribution (Compagno 2001). Whereas this study shows an application of paleontological technique to an extant taxon, we also demonstrate that the generated data can then be applied to paleontology, notably to assess the TL of extinct odontaspidids from the size of a fossil odontaspidid tooth.

Methods and Methods

The specimen of *Odontaspis ferox* used in this study, BPBM 9335, is a head of an individual caught in bottom-set gillnet off the coast of Oahu, Hawaii, in 1969, and belongs to Bernice P. Bishop Museum in Honolulu, Hawaii, USA (Fig. 1A). The individual measured 297 cm TL according to the museum catalog card. However, it does not accompany its sex record.

The skeletal components of BPBM 9335 were examined using a computed tomography (CT) scanner, and generated CT images showed that a total of eight vertebrae are preserved in the specimen (Fig. 1B). We then removed three of the eight vertebrae using a scalpel, two of which (seventh and eighth vertebrae) were sectioned to examine incremental bands whereas the other vertebra (sixth vertebra) has been kept intact (note: the sixth vertebra was illustrated by Hansen et al. 2013, fig. 5B-F, along with its x-ray image). After removing the bulk of connective tissues, the vertebrae were left to dry completely in a ventilated hood for 24-36 h. The seventh and eighth vertebrae

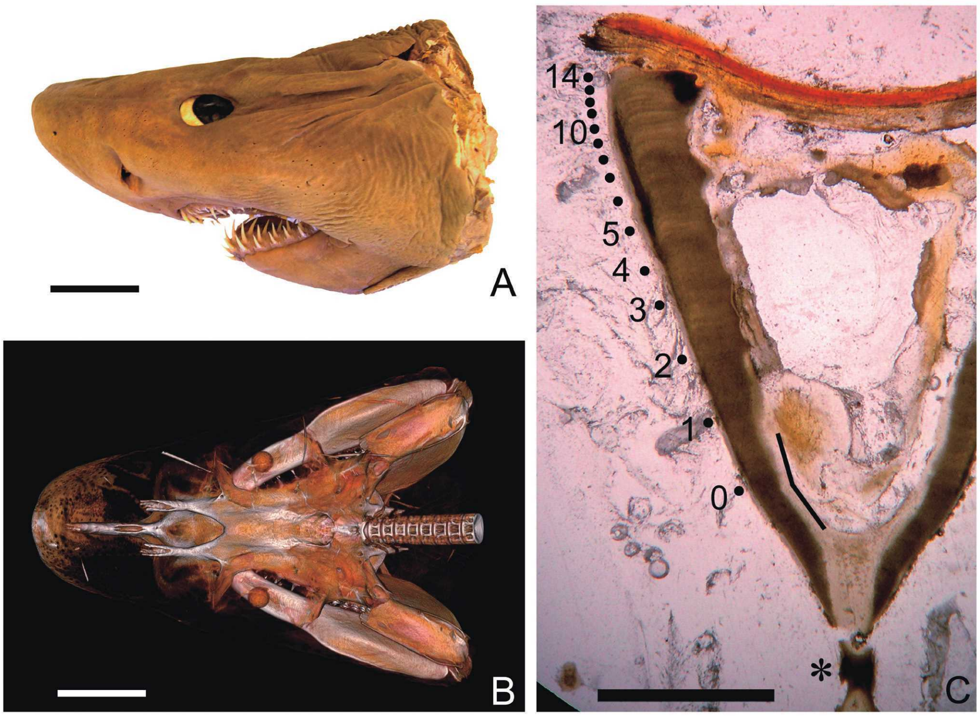

Fig. 1. Examined specimen of smalltooth sandtiger shark, *Odontaspis ferox* (BPBM 9335). A, photograph of entire head specimen in left lateral view; B, CT image in dorsal view showing string of eight vertebrae to the right; C, close-up view of sectioned vertebra under dissecting microscope with identified bands and their numbers (asterisk = focus, or center, of centra; 0 = band at birth, that also accompanies 'angle change' indicated by bent line). Bar scale: A, B = 10 cm; C = 5 mm.

were sanded with grade 60 and grade 120 sandpapers until their focus (midpoint). The sanded side of each vertebra was then mounted to a glass slide using the mounting medium, Permount™, secured with a clamp to avoid warping of the vertebrae, and they were left in ventilated hood for at least 24 h until the mounted medium became completely dry. Each of the vertebrae was then further sanded using successively finer grades of sand paper (grades 60, 120, 220, and 600) to a thickness of approximately 0.2-0.4 mm. A dissecting microscope with transmitted light was shined behind each sectioned vertebra and a high-resolution digital photograph with a millimeter scale was taken for image analysis. After confirming that both sectioned vertebrae have an identical growth band pattern, the brightness and contrast of the photographic image for one of them (i.e., the seventh vertebra) were manipulated using graphic software to enhance the visibility of the bands adequate to collect band number (BN; i.e. equivalent to the number of years, or 'ontogenetic age') and centrum radius (CR; in millimeters) measurements.

The BN and CR data formed the basis of our VBGF analysis. One VBGF takes a form of $L_{(t)} = L_\infty - (L_\infty - L_0)e^{-kt}$ (von Bertalanffy 1938), where t is time (= 'age' in year), L_0 the length at birth, L_∞ the estimate of asymptotic (= maximum) length, and k the rate constant with units of reciprocal time. The VBGF parameters for *Odontaspis ferox* were obtained using Microsoft Excel with the Solver Add-in. Strictly speaking, data for the VBGF analysis must be for independent measurements taken from multiple specimens that are randomly sampled from a population. Measurements taken from one vertebra here provide dependent measurements, so the statistical operations in our study must be viewed experimental with a hypothetical supposition that each BN-TL pair (including BN 0) was obtained from a randomly sampled individual of a population. With this supposition, the VBGF was experimentally fitted to the data to correlate the BN values with TL values.

Results

Both sectioned vertebrae exhibit a total BN of 14 (excluding the band at birth that is BN = 0) with no perceivable differences in CR values between the two sectioned samples. Table 1 shows each CR at each BN, each band interval (BI) from one band to its successive band, percent centrum radius (pCR) at each BN by treating BN of 14 as 100%, and each extrapolated TL from each pCR at each BN by considering the TL of 297 cm at capture as 100%. The VBGF experimentally fitted to the data to correlate the BN values with TL values (Table 1) is statistically significant (non-linear regression: R^2 = 99.8%). Figure 2A shows the relationship between BN and TL based on data in Table 1, and the quantitative relationships between the BN and TL yield the following VBGF parameters: L_0 = 93.850 cm TL, L_∞ = 315.206 cm TL, and k = 0.183 yr^{-1}.

Table 1. Raw measurements (BN, CR, and BI) and derived measurements (pCR, TL, and CH) based on sectioned vertebrae of *Odontaspis ferox* (BPBM 9335; Fig. 1C). Abbreviations: BN, band number; CR, centrum radius; BI, band interval; pCR, percent centrum radius from center of vertebra; TL, total length of entire shark; CH of tallest (lower second anterior) tooth, maximum vertical crown height.

BN	CR (mm)	BI (mm)	pCR (%)	TL (cm)	CH (mm)
0	5.3	-	32.7	97.2	8.5
1	7.1	1.8	43.8	130.2	11.4
2	8.7	1.6	53.7	159.5	14.0
3	9.9	1.2	61.1	181.5	15.9
4	11.3	1.4	69.8	207.2	18.1
5	12.4	1.1	76.5	227.3	19.9
6	13.3	0.9	82.1	243.8	21.3
7	14.0	0.7	86.4	256.7	22.5
8	14.6	0.6	90.1	267.7	23.4
9	15.0	0.4	92.6	275.0	24.1
10	15.3	0.3	94.4	280.5	24.5
11	15.5	0.2	95.7	284.2	24.9
12	15.7	0.2	96.9	287.8	25.2
13	16.0	0.3	98.8	293.3	25.7
14	16.2	0.2	100.0	297.0	26.0

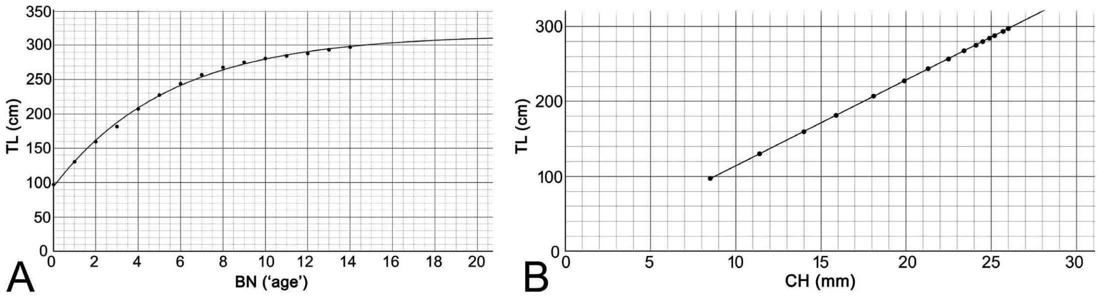

Fig. 2. Growth models of smalltooth sandtiger shark, *Odontaspis ferox* based on BPBM 9335 (Fig. 1; Table 1). A, von Bertalanffy growth function (VBGF) fitted to data points that show relationship of number of vertebral growth bands (BN, or 'age' of individual in years) with total length (TL); B, linear function fitted to data points that show relationship of CH with TL.

Discussion

Ontogeny and life history strategies

Fergusson et al. (2007) conducted a comprehensive review of global occurrence records of *Odontaspis ferox*, and based on the smallest individuals ever captured, they suggested that the size at birth must be approximately 100 cm TL. Our back-calculation based on BPBM 9335 gives the size at birth to be about 97 cm TL (Table 1), and our VBGF analysis gives L_0 of approximately 94 cm TL. Although the size at birth may be around 95 cm TL, our study broadly agrees with Fergusson et al.'s (2007) estimation of about 100 cm TL at birth for the species.

The largest individual of *Odontaspis ferox* on record is a female that measured 450 cm TL, whereas the largest male on record is 344 cm TL (Fergusson et al. 2007). The L_∞ of about 315 cm TL based on BPBM 9335 is intriguing because it is closer to the largest recorded male than to the largest recorded female. Fergusson et al.'s (2007) review of global occurrence records of *O. ferox* consisted of 62 captures of which 21 were males, 28 were females, and the remaining records unknown sex (note: BPBM 9335 is listed as one of the capture records with an unknown sex). Of the 21 males in Fergusson et al.'s (2007) data, 20 of them accompany TL data, but only one of them, the 344-cm-TL individual, exceeds our L_∞ value. This is in striking contrast with the 28 reported females in which 14 individuals exceeded our L_∞ of 315 cm TL. Assuming that our analytical method and VBGF parameters are reasonable, our study along with Fergusson et al.'s (2007) data strongly suggests that BPBM 9335 must have been a male. If so, whereas our VBGF (Fig. 2A) is considered to be a male-specific curve, BPBM 9335 would represent the fourth largest captured male on record based on Fergusson et al.'s (2007, table 1) tabulation and subsequent reports on the occurrences of *O. ferox* (e.g., Garla and Garcia 2008; Acuña-Marrero et al. 2013; Long et al. 2014; Estupiñán-Montaño et al. 2016). It should be noted that an estimated asymptotic length expressed by L_∞ does not represent the maximum possible length but rather the average length-at-age (i.e., some individuals may be larger or smaller than the calculated L_∞ value: Francis 1988); therefore, the presence of the 344-cm-TL individual that exceeds our L_∞ value does not necessarily discredit our VBGF analysis. Rather, our interpretation is compelling considering the fact that 19 of the 20 reported males with recorded TL in Fergusson et al.'s (2007) compilation are under our L_∞ value in which the second and third largest males to the 344-cm-TL male measure 310 and 304 cm TL, respectively.

The BN of 14 in our study (Fig. 1C; Table 1) suggests that the individual represented by BPBM 9335 is assumed to have died at age 14. Natanson et al. (2006) presented the equation for the estimated age at 95% of L_∞ as $Longevity = (1/k)\,ln\{(L_\infty - L_0)/[L_\infty(1 - x)]\}$ with $x = L_{(t)}/L_\infty = 0.95$, and in fact, the calculation yields an estimated longevity of 14.439 years for *Odontaspis ferox*. Given that BPBM 9335 is interpreted to be the fourth largest male individual ever captured (see above) and that its TL of 297 cm is quite close to the obtained L_∞ of 315 cm TL, we do not necessarily consider the average longevity of 14 or 15 years for male *O. ferox* to be unreasonable. The exact age for the largest 344-cm-TL male reported by Fergusson et al. (2007) is uncertain, but it must have been a ripe old age for a male *O. ferox*, that likely easily exceeded 15 years old in age. This interpretation is particularly possible given that recent studies have shown that vertebra-based age assessments on extant elasmobranchs have a tendency of underestimation (Passerotti et al.

2014; Harry et al. 2017).

Our data indicate that the shark individual represented by BPBM 9335 doubled in size (compared to its size at birth) within the first four years of its life (Table 1). Furthermore, our data (Table 1) also suggest that more than 75% of its total growth was completed within the first five years of its life with the TL of roughly 227 cm. This observation is quite intriguing considering the fact that size at maturity in *O. ferox* is suggested to be around 200-250 cm TL for males (vs. 300-350 cm TL for females: Fergusson et al. 2007). In other words, the onset of a major decrease in its growth rate at about age 5 corresponds well to the timing of sexual maturity for males suggested by Fergusson et al. (2007).

The known depth range for *Odontaspis ferox* is 10-1,015 m (Weigmann 2016, p. 852). However, Fergusson et al. (2007) found that juveniles are generally caught at water depths between 200 and 600 m, whereas larger specimens (>200 cm TL) are caught across the entire depth range. Most of the juvenile samples included in Fergusson et al.'s (2007, table 1) study measured ≤160 cm TL, and this observation would mean that those small individuals must be generally no older than 2 years old based on our data (Table 1).

Paleontological application

Whereas the genus *Odontaspis* is known in the fossil record from the Late Cretaceous (Campanian) (Cappetta 2012), the fossil record of *O. ferox* is spotty but does exist, including the early Miocene of central Chile (Saurez et al. 2006) and the late Miocene-early Pliocene of Venezuela (Aguilera and De Aguilera 2001). However, they are so far all represented by isolated teeth. Here, we present a method to extrapolate the TL of an individual from an isolated tooth based on BPBM 9335.

In BPBM 9335, the tallest tooth is the lower second anterior tooth (sensu Shimada 2002), measuring 26.0 mm in maximum vertical crown (= enameloid) height (CH). Similar to the way we derived each of our TL value for each BN (Table 1), we extrapolated each CH value from each pCR for each BN by considering the CH of 26.0 mm at capture as 100%. The CH of 26.0 mm and all the extrapolated CH values are given on the far right side of Table 1, and Figure 2B illustrates the relationships between the CH and TL with a linear function of $y = 11.425x - 0.024$, where x = CH and y = TL. The data points in Figure 2B show a perfect linear relationship because each plot represents a theoretical CH value and a theoretical TL value based on their respective pCR value, which itself represents an extrapolated value, with the assumption that BN 14 corresponds to 297 cm TL based on BPBM 9335.

Although subtle differences are present among them, upper and lower anterior teeth of *Odontaspis ferox* consist of the tallest teeth in its dentition and are characterized by tall slender crown (Shimada 2002). For example, a fossil tooth of *O. ferox* illustrated by Aguilera and De Aguilera (2001, fig. 5.18, 5.19) and one of two fossil teeth of *O. ferox* described by Saurez et al. (2006, fig. 4j) have a tall slender crown and thus identified as anterior teeth. Based on the figures, they have a CH of about 17 mm and 12 mm, respectively. When the CH values are applied to the linear equation $y = 11.425x - 0.024$, the fossil teeth are estimated to have come from individuals that measured about 194 cm TL and 137 cm TL, respectively. It must be noted that these fossil teeth may not have been represented the largest tooth in each respective shark's mouth in life, but because the linear equation is based on the largest tooth in BPBM 9335, one can state that the shark likely measured 'at least' about 194 cm TL and 137 cm TL, respectively. Furthermore, their respective estimated TL in Table 1 can be used to suggest that the former and latter individuals were at least 3 years old (BN = 3) and 1 year old (BN = 1), respectively.

Because the linear equation is for anterior teeth, smaller teeth from other positions of the dentition (e.g., symphysial, intermediate, or lateral) cannot be applied to it for their TL estimations. In addition, it should be noted that the equation is assumed to be for male individuals, and there is no guarantee that the fossil population had the same growth pattern as in the modern population. Nevertheless, the linear equation for anterior teeth presented here gives the best estimate for *Odontaspis ferox* in the fossil record at the present time. Appendix 1 lists the CH and crown width (CW) of the labial-most complete functional tooth in each tooth type on the right side of BPBM 9335. Because not all fossil specimens are anterior teeth, and because the crown may be incomplete, measurements in Appendix 1 allow one to employ the same method used to generate CH values or CW values for each tooth type at each age (i.e., each BN) through back calculation by using the pCR and by considering each measurement in

Appendix 1 to be 100%.

Concluding Remarks

Age and growth estimates are essential for constructing age-structured population dynamic models for conservation of any given elasmobranch species (Cailliet et al. 2006). Because very little is known about the growth pattern of *Odontaspis ferox*, any new growth-related data, such as our present study, give insight into the life history strategies of this enigmatic shark. This is particularly important considering the fact that *O. ferox* is assumed to regulate local populations of prey species, such as squid, prawns, bony fishes, and other small elasmobranchs as a large predator, and that it is regarded as a "vulnerable" species globally (see Fergusson et al. 2007). Where *O. ferox* has a long geologic record (at least for 20 million years since the early Miocene: Suarez et al. 2006), this present study also offers a method to extrapolate the TL of extinct individuals of *O. ferox* from fossil teeth that would be useful for paleoecological reconstruction of ancient oceans in which *O. ferox* inhabited.

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Appendix 1. Crown height (first number) and crown width (second number) of each tooth type measured from complete labial-most functional tooth on right side of BPBM 9335 (some distal-most lateral teeth not measurable due to deep positions in mouth). Abbreviations (uppercase = upper tooth; lowercase = lower tooth: see Shimada, 2002): ‘A’ or ‘a’ = anterior tooth; ‘I’ or ‘i’ = intermediate tooth; ‘L’ or ‘l’ = lateral teeth; ‘S’ or ‘s’ = symphysial tooth.

BPBM 9335: S1 = 8.6, 4.8; A1 = 22.1, 12.0; A2 = 19.2, 12.0; I1 = 8.3, 5.5; I2 = 7.4, 5.2; I3 = 7.3, 7.3; I4 = 7.8, 4.9; L1 = 12.7, 11.0; L2 = 15.0, 12.6; L3 = 14.6, 12.6; L4 = 14.3, 12.6; L5 = 12.4, 11.2; L6 = 11.1, 10.3; L7 = 9.8, 8.8; L8 = 8.6, 7.9; L9 = 7.0, 7.0; s1 = 11.4, 4.1; a1 = 24.2, 9.9; a2 = 26.0, 12.5; i1 = 21.8, 12.0; l1 = 16.2, 11.1; l2 = 15.3, 10.9; l3 = 13.8, 10.8; l4 = 13.3, 9.8; l5, 11.0, 8.6; l6 = 10.5, 8.4; l7 = 9.3, 8.2.