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The relationship between the tooth size and total body length in the white shark, *Carcharodon carcharias* (Lamniformes: Lamnidae)

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Abstract

The relationship between the height of tooth crown (CH) and total body length (TL) in the modern great white shark, *Carcharodon carcharias* (Linnaeus) (Lamniformes: Lamnidae) is examined using regression analyses. The results suggest: 1) that an increase in the CH of each tooth through replacement is proportional to the increase in the TL, 2) that the CH can be used to predict the TL, and 3) that distally located teeth develop faster through replacement compared to mesially located teeth. A comparison with previous data suggests that the "growth rate" between the crown and root is perhaps not isometric. These data can be applied to paleontological practices.

Key words: dentition, elasmobranch, growth, lamnoid, morphology, variation

Introduction

The presence of intraspecific variation in tooth morphology is known in various elasmobranchs. Common examples (other than pathologic or abnormal teeth: e.g., Gudger, 1937) include ones caused by sexual differences (e.g., Springer, 1966; Kajiura and Tricas, 1996) and ones by ontogeny (e.g., Reif, 1976; Shimada, 2002b). However, data on morphological variation are still scarce for most elasmobranchs. Some have examined intraspecific variation of one or a few selected teeth quantitatively, but none of them evaluated the dental homology critically (e.g., Applegate, 1965; Randall, 1973). Indeed, the inability to recognize homologous teeth across conspecific individuals has hampered investigators to conduct rigorous analyses on

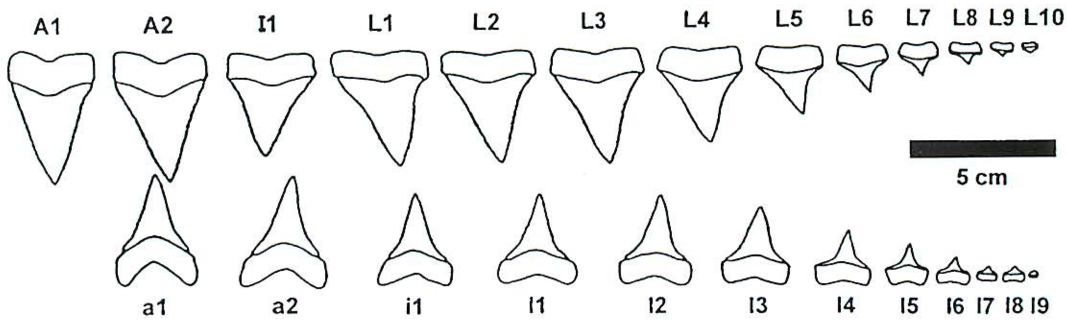

Fig.1. Representative upper and lower dental series of modern great white shark, *Carcharodon carcharias* (mesial to the left; labial view). Tooth types: A, upper anterior tooth; a, lower anterior tooth; I, upper intermediate tooth; i, lower intermediate tooth; L, upper lateral tooth; l, lower lateral tooth. Illustration traced from Uyeno and Matsushima (1979, fig. 2); tooth type identification based on Shimada (2002a).

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such variations.

The recognition of homologous teeth across macrophagous lamniforms and among individuals of each macrophagous lamniform species (Shimada, 2002a) has opened up a new avenue to examine their teeth quantitatively. Here, I focus on the dentition of the modern great white shark, *Carcharodon carcharias* (Linnaeus). Equipped with large, triangular, serrated teeth (Fig. 1), *C. carcharias* (Lamniformes: Lamnidae) is the largest modern macropredatory shark, which is cosmopolitan in temperate and tropical seas (Compagno, 1984). The objective of this study is to examine the ontogenetic relationship between the tooth size and body size in *C. carcharias*.

2. Materials and methods

Dental measurements were taken from 12 jaw samples of non-embryonic *Carcharodon carcharias*, each with a known total length (TL: Appendix 1). Ten of them are a part of Gordon Hubbell collection (GH: JAWS International, Gainesville, Florida). The other two samples are housed in the Natural History Museum of Los Angeles County (LACM), California, and Scripps Institution of Oceanography (SIO), La Jolla, California. The height of tooth crown (CH = the maximum vertical enameloid height on the labial side) of 12 upper teeth (A1-A2, I1, and L1-L9) and 11 lower teeth (a1-a2, i1, and l1-l8) in each sample was measured (Appendix 1; for tooth types, see Fig. 1; for additional dental data of these samples, see Shimada, 2002a). Then, the relationship between the CH and TL was examined using regression analysis (least squares method; simple linear regression, $y = a + bx$, where a is the constant and b is the slope of the line; x = CH in mm; y = TL in cm; $\alpha = 0.05$; for statistics, see Zar, 1996). The null hypothesis is: The CH does not predict the TL.

3. Results

Table 1 lists the results of the regression analyses (see also Fig.2). All regression lines show a positive correlation. The slope of the lines generally increases from mesially located teeth to distally located teeth for both upper and lower dental series. All lines have a high correlation coefficient ($r > 0.914$) and a high statistical significance ($p < 0.001$).

4. Discussion

Interpretation of results

A high r-value and a low p-value for each regression analysis (Table 1) suggest that, in *Carcharodon carcharias*, the CH of any tooth can be used to predict the TL (but see also Mollet *et al.* [1996] for discussion on morphometric variability in white sharks). A positive correlation in each regression line indicates that an increase in the CH of each tooth through replacement is proportional to the increase in the TL. The general increase in the slope of regression lines from mesially located teeth to distally located teeth suggests that the "growth rate" (through replacement) of

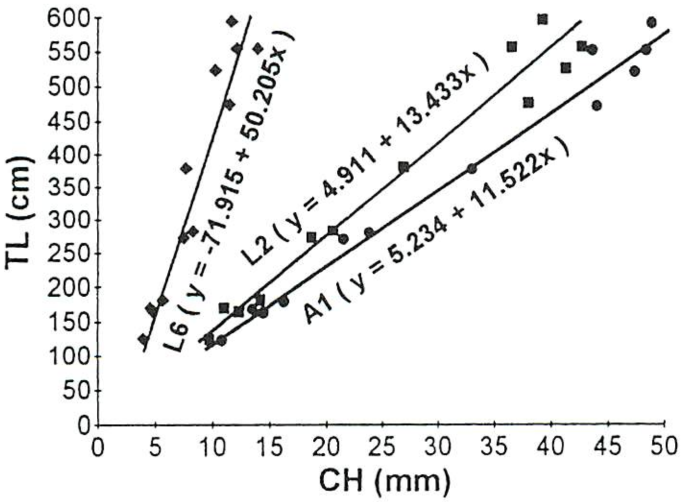

Fig.2. Bivariate scatter with regression line between crown height (CH) and total body length (TL) for the first upper anterior tooth (A1: circle), second upper lateral tooth (L2: square), and sixth upper lateral tooth (L6: diamond) in *Carcharodon carcharias* (n=12; for measurements, see Appendix 1; for statistics of regression lines, see Table 1).

Table 1. Regression analyses between tooth crown height (CH) and total body length (TL) among 12 individuals of *Carcharodon carcharias* (x = CH in mm [for tooth types, see Fig. 1]; y = TL in cm; degrees of freedom = 1,10). Statistical notations: r, correlation coefficient; p, probability of estimates; s.e., standard error of estimates.

x	Regression equation	r	F-ratio	p	s.e.
Upper teeth					
A1 TL	y= 5.234 +11.522x	0.992	581.542	0.000	24.150
A2 TL	y= -2.160 +12.103x	0.993	716.006	0.000	21.799
I1 TL	y= 19.162 +15.738x	0.978	215.284	0.000	39.132
L1 TL	y= 5.540 +14.197x	0.986	352.591	0.000	30.846
L2 TL	y= 4.911 +13.433x	0.983	285.552	0.000	34.165
L3 TL	y= 0.464 +14.550x	0.986	338.746	0.000	31.452
L4 TL	y= 5.569 +17.658x	0.982	277.245	0.000	34.656
L5 TL	y= -5.778 +26.381x	0.954	101.940	0.000	55.515
L6 TL	y= -71.915 +50.205x	0.956	106.109	0.000	54.509
L7 TL	y= -48.696 +69.292x	0.934	68.243	0.000	66.402
L8 TL	y= -84.781+104.968x	0.942	79.184	0.000	62.196
L9 TL	y= -62.050+142.142x	0.926	60.387	0.000	70.009
Lower teeth					
a1 TL	y= -8.216 +14.895x	0.978	222.406	0.000	38.528
a2 TL	y= -7.643 +13.597x	0.962	123.423	0.000	50.849
i1 TL	y= -10.765 +17.616x	0.961	120.402	0.000	51.435
l1 TL	y= 9.962 +17.437x	0.963	127.474	0.000	50.095
l2 TL	y= 1.131 +19.204x	0.967	145.119	0.000	47.160
l3 TL	y= -30.947 +25.132x	0.967	143.141	0.000	47.463
l4 TL	y= -51.765 +35.210x	0.959	114.572	0.000	52.625
l5 TL	y= -73.120 +55.262x	0.958	110.696	0.000	53.463
l6 TL	y= -117.456 +96.971x	0.914	50.428	0.000	75.559
l7 TL	y= -64.732+138.350x	0.921	55.910	0.000	72.348
l8 TL	y= -137.593+231.411x	0.958	110.284	0.000	53.555

distally located teeth is greater than that of mesially located teeth. It is intriguing to note that the exact same trend is seen in the modern shortfin mako, *Isurus oxyrinchus* Rafinesque, which is another lamnid species (Shimada, 2002c).

Gottfried *et al.* (1996) studied the relationship between the TL and tooth height (crown + root) of the A2 in *Carcharodon carcharias*, although they did not evaluate the dental homology rigorously. They gave the regression equation of TL = -22.000 + 9.600x, where x referred to the tooth height of the A2 in mm and TL expressed in cm (n = 73; range = 127-600 cm TL; r = 0.980). The fact that the slope in my study (b = 12.103; Table 1) is slightly steeper than that in the study by Gottfried *et al.* (1996; b = 9.600) may suggest that the growth rate (through replacement) between the crown and root is not isometric, but rather the root may develop slightly faster than its crown. If so, at least in the A2, the root may be more robust in larger individuals than in small individuals. The increase in root height may increase the surface area for the tooth to attach to the jaw cartilage.

Paleontological Applications

Lamniforms are common in the fossil record, but they are represented chiefly by isolated teeth (e.g., Cappetta, 1987). One of the extinct lamniforms is the "megatooth" shark, "*C.*" *megalodon* (Agassiz), which is characterized by gigantic, massive teeth with serrated cutting edges. Its generic assignment has been controversial, some placing the taxon into the genus *Carcharodon* Müller and Henle (e.g., Applegate and Espinosa-Arrubarrena, 1996; Gottfried *et al.*, 1996; Purdy *et al.*, 2001), while others into the genus *Carcharocles* Jordan and Hannibal (e.g., Cappetta, 1987; Goto, 1989; Yabe and Hirayama, 1998). The discussion of its taxonomy is beyond the scope of this paper. Thus, the taxon is here referred simply as "*C.*" *megalodon*. Where its teeth reach 168 mm in total height (i.e., crown + root; Applegate and Espinosa-Arrubarrena, 1996), the TL of "*C.*" *megalodon* has been scrutinized for a long time (e.g., Randall, 1973). Using the total tooth height of 168 mm, Gottfried *et al.* (1996) estimated the TL of the "*C.*" *megalodon* as 1590 cm based on their regression equation for the A2 of the modern *Carcharodon carcharias* (see above).

Regardless of its taxonomic placement, using the modern *C. carcharias* as a model to infer the TL of "*C.*" *megalodon* is logical, because *C. carcharias* is the largest extant macrophagous lamniform and the only extant lamniform with serrated teeth. Applegate and Espinosa-Arrubarrena's (1996) illustration of a large "*C.*" *megalodon* tooth, which is 168 mm in total height, suggests that its CH measures approximately 125 mm. Based on two assumptions, a conservative TL estimation is possible for "*C.*" *megalodon* that carried the gigantic tooth: 1) that it represents the largest tooth on the jaws (the A1 or A2); and 2) that the CH of the tooth has the same size relation to the TL as the CH-TL relationships in modern *C. carcharias*. When the CH of 125 mm is applied to the regression equation for the A1 and A2 (Table 1), the TL of "*C.*" *megalodon* with such a tooth is estimated to be about 1445 cm and 1511 cm, respectively. My estimates are slightly lower than the estimated TL of Gottfried *et al.* (1996; 1590 cm TL). This may be due to the possible difference in the "growth rate" between the CH and root height (see above). Nevertheless, my result and that by Gottfried et al. (1996) suggest that large "*C.*" *megalodon* measured approximately 14-16 m TL.

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Appendix 1

Examined specimens (with TL, sex, and locality data) and crown height of each tooth (in mm; for tooth types, see Fig. 1; value in parenthesis = estimated measurement).

LACM 39474-1 (165 cm TL; male; California, U.S.A.), right dental series: A1, 14.5; A2, 14.8; I1, 10.0; L1, 12.3; L2, 12.5; L3, 11.9; L4, 9.8; L5, 7.1; L6, 4.8; L7, 3.3; L8, 2.3; L9, 1.3; a1, 13.2; a2, (13.7); i1, (10.5); l1, 10.1; l2, 9.8; l3, 8.6; l4, 6.9; l5, 4.8; l6, 2.7; l7, 1.5; l8, 1.2.

SIO 55-95g (181 cm TL; female; California, U.S.A.), right dental series: A1, (16.3); A2, (16.4); I1, 11.2; L1, 13.4; L2, (14.4); L3, 13.3; L4, (10.8); L5, 8.8; L6, 5.7; L7, 4.2; L8, 3.0; L9, 2.3; L10, 1.6; a1, (13.0); a2, (15.5); i1, (12.3); l1, 11.0; l2, 10.7; l3, 9.9; l4, 7.4; l5, 5.3; l6, 3.4; l7, 2.5; l8, 1.7.

GH-Car1-01 (272 cm TL; male; California, U.S.A.), left dental series: A1, 21.5; A2, 22.3; I1, 14.6; L1, 18.5; L2, 18.9; L3, 17.9; L4, 14.2; L5, 11.3; L6, 7.5; L7, 5.2; L8, 3.5; L9, 2.4; L10, 1.3; a1, 18.2; a2, 20.4; i1, 15.8; l1, 14.3; l2, (12.4); l3, 10.5; l4, 8.4; l5, 5.7; l6, 4.3; l7, 2.2; l8, 1.7.

GH-Car1-02 (170 cm TL; male; California, U.S.A.), right dental series: A1, 13.5; A2, (13.5); I1, 9.5; L1, 10.9; L2, 11.2; L3, 10.5; L4, 8.7; L5, 6.3; L6, 4.6; L7, 3.2; L8, 2.3; L9, 1.6; L10, 1.3; a1, 12.8; a2, 13.3; i1, 10.2; l1, 9.4; l2, 9.2; l3, 7.7; l4, 6.3; l5, 4.6; l6, 3.3; l7, 1.9; l8, 1.4; l9, 0.8; l10, 0.5.

GH-Car1-06 (125 cm TL; male; California, U.S.A.), right dental series: A1, 10.8; A2, 10.2; I1, 7.1; L1, 8.5; L2, 9.9; L3, 9.7; L4, 7.2; L5, 5.7; L6, 4.0; L7, 2.7; L8, 2.1; L9, 1.6; L10, 1.5; a1, 7.9; a2, 10.1; i1, 7.9; l1, 6.8; l2, 7.0; l3, 6.8; l4, 5.6; l5, 3.5; l6, 2.4; l7, 1.5; l8, 1.0; l9, 0.5.

GH-Car1-08 (523 cm TL; female; California, U.S.A.), left dental series: A1, 47.3; A2, 44.5; I1, 33.8; L1, 38.0; L2, 41.5; L3, 38.0; L4, 31.7; L5, 23.6; L6, 10.3; L7, 8.5; L8, 5.8; L9, 3.3; L10, 1.6; a1, 33.2; a2, 34.3; i1, 28.4; l1, 28.4; l2, 27.8; l3, 22.3; l4, 16.2; l5, 10.7; l6, 6.2; l7, 4.8; l8, 2.8; l9, 2.8.

GH-Car1-09 (282 cm TL; female; Florida, U.S.A.), right dental series: A1, 23.8; A2, 22.5; I1, 17.2; L1, 18.5; L2, 20.8; L3, 19.6; L4, 16.5; L5, 11.1; L6, 8.3; L7, 5.1; L8, 3.9; L9, 2.6; a1, 20.3; a2, 21.7; i1, 16.3; l1, 15.6; l2, 13.4; l3, 12.4; l4, 9.5; l5, 6.6; l6, 4.7; l7, 2.2; l8, 1.8.

GH-Car1-11 (474 cm TL; male; Florida, U.S.A.), right dental series: A1, 44.0; A2, 42.7; I1, 33.7; L1, 35.7; L2, 38.2; L3, 35.5; L4, 29.7; L5, 19.4; L6, 11.5; L7, 6.7; L8, 5.6; L9, 4.2; a1, 36.7; a2, 42.3; i1, 32.4; l1, 31.9; l2, 29.3; l3, 23.3; l4, 17.5; l5, 12.1; l6, 7.6; l7, 3.9; l8, 2.8; l9, 2.0; l10, 1.5.

GH-Car1-13 (379 cm TL; male; Florida, U.S.A.), right dental series: A1, 33.0; A2, 31.3; I1, 22.4; L1, 26.3; L2, 27.1; L3, 24.9; L4, 19.3; L5, 11.6; L6, 7.7; L7, 5.4; L8, 4.5; L9, 3.3; a1, 25.6; a2, 28.5; i1, 23.5; l1, 21.0; l2, 19.8; l3, 16.2; l4, 11.6; l5, 7.6; l6, 5.5; l7, 4.0; l8, 2.7; l9, 1.7.

GH-Car1-14 (554 cm TL; female; Australia), right dental series: A1, 48.3; A2, 46.6; I1, 34.7; L1, 41.3; L2, 42.9; L3, 40.0; L4, 31.5; L5, 21.1; L6, 14.0; L7, 10.4; L8, 5.9; L9, 4.9; a1, 41.3; a2, 45.5; i1, 35.2; l1, 34.1; l2, 30.1; l3, 24.8; l4, 18.7; l5, 11.3; l6, 6.5; l7, 4.1; l8, 2.7; l9, 1.9.

GH-Car1-15 (554 cm TL; female; Australia), right dental series: A1, 43.6; A2, 42.2; I1, 29.6; L1, 35.7; L2, 36.8; L3, 34.0; L4, 28.5; L5, 19.6; L6, 12.2; L7, 7.8; L8, 5.4; L9, 3.8; L10, 3.6; a1, 34.7; a2, 36.2; i1, 27.3; l1, 27.0; l2, 25.8; l3, 20.0; l4, 14.6; l5, 10.4; l6, 6.0; l7, 3.9; l8, 2.8; l9, 1.0.

GH-Car1-19 (594 cm TL; female; Australia), right dental series: A1, 48.8; A2, 48.2; I1, 33.1; L1, 37.2; L2, 39.5; L3, 38.0; L4, 30.3; L5, 19.0; L6, 11.7; L7, 7.6; L8, 5.1; L9, 4.0; L10, 1.8; a1, 36.6; a2, 39.5; i1, 29.8; l1, 28.6; l2, 26.5; l3, 22.3; l4, 16.3; l5, 10.6; l6, 6.0; l7, 4.0; l8, 3.0; l9, 2.0.