The tooth, the whole tooth and nothing but the tooth: tooth shape and ontogenetic shift dynamics in the white shark

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Abstract

Ontogenetic dietary shifts are widespread across the animal kingdom, and often involve associated morphological changes in foraging phenotype. These changes may differ between sexes or vary between individuals, and are important factors in the ecology of species. While such factors have received much attention in terrestrial systems, they are much less well understood in marine taxa. The white shark *Carcharodon carcharias* is a marine apex predator that is accepted to provide a classic example of an ontogenetic dietary shift, with an associated change in tooth morphology from cuspidate to broad. Our results however, which include measurements obtained using a novel photographic method, reveal significant differences between the sexes in the relationship between tooth cuspidity and shark total length (TL), and a novel ontogenetic change in male tooth shape. Males exhibit broader upper first teeth and increased distal inclination of upper third teeth with increasing length, while females do not present a consistent morphological change. Substantial individual variation, with implications for pace of life syndrome, was present in males, and tooth polymorphism was suggested in females. Sexual differences and individual variation may play major roles in ontogenetic changes in tooth morphology in white sharks, with potential implications for their foraging biology. Such individual and sexual differences should be included in studies of ontogenetic shift dynamics in other species and systems.

Keywords: apex predator, *Carcharodon carcharias*, individual variation, ontogenetic dietary shift, phenotypic polymorphism, sexual variation

Introduction

Ontogenetic shifts in ecological niche are widespread across the animal kingdom, and represent changes in resource use with size, from birth/hatching to maximum size (Werner & Gilliam, 1984). In some species, ontogenetic shifts in diet are generally characterized by a change from smaller size classes consuming a limited range of relatively small prey species, to larger size classes consuming a wider range of prey items with a larger mean body size (Wilson, 1975). Such shifts in diet can be accompanied, or even made possible, by allometric scaling of morphological features, in which one morphological feature changes disproportionately to general body growth. In some species, there may be phenotypic polymorphism in the ontogenetic change in morphology and diet, resulting in trophic polymorphism (Hutchinson, 1957; Van Valen, 1965; Meyer, 1989, 1990).

The ecological importance of ontogenetic dietary shifts and associated morphological changes, and of sexual or individual variation in them, may be particularly significant in marine apex predators such as sharks because of their often keystone ecology and vulnerable conservation status (Matich & Heithaus, 2015). It is becoming increasingly clear that sharks exhibit sexual and individual differences in diet and habitat use, and allometric scaling of morphological features through ontogeny. For example, bull sharks *Carcharhinus leucus* (Müller & Henle, 1839), tiger sharks *Galeocerdo cuvier* (Péron & Lesueur, 1822), and other large pelagic sharks show individual variation in diet (Heithaus et al., 2002, Matich et al., 2011, Kiszka et al., 2015), and female scalloped hammerheads *Sphyrna lewini* (Griffith & Smith, 1834) shift to offshore habitats at a smaller size than males, where access to pelagic prey and improved foraging success allow them to grow faster than their male counterparts (Klimley, 1987). Bull, tiger, blacktip *Carcharhinus limbatus* (Müller &

Henle, 1839), and horn sharks *Heterodontus francisci* (Girard, 1855) show allometric changes in head shape and musculature (Huber et al., 2006; Kolmann & Huber, 2009; Habegger et al., 2012; Fu et al., 2016), and bull, tiger and white *Carcharodon carcharias* (Linnaeus 1758) sharks show this with caudal-fin shape (Lingham-Soliar, 2005; Irschick & Hammerschlag, 2014). Allometric scaling of mouth length and width is also evident in the viper dogfish *Trigonognathus kabeyai* (Mochizuki & Fumio, 1990) (Yano et al., 2003).

Individual variation in tooth morphology, a mechanistic facilitator of shark diet (Frazzetta, 1988; Compagno, 1990) has been reported for sand tiger *Carcharias taurus*, blue *Prionace glauca* (Linnaeus 1758), and porbeagle *Lamna nasus* (Bonnaterre, 1788) sharks (Litvinov, 1983; Shimada, 2002a; Lucifora et al., 2003; Litvinov & Laptikhovsky, 2005). Sexual dimorphism in tooth shape has been linked to different diets (Litvinov & Laptikhovsky, 2005), but can also be an adaptation that gives males greater purchase when holding on to females during copulation (Kajiura & Tricas, 1996). Quantifying ontogenetic change is logistically challenging in large pelagic elasmobranchs due to their intolerance of captivity, cryptic habitat use, wide-ranging movements, relatively low abundance and handling difficulty. As such, many ontogeny studies have been limited to dead specimens.

The white shark is a classic example of a morphological, diet-related change through ontogeny. White sharks are a member of the Lamniformes, an order for which tooth morphology is an informative defining character (Compagno, 1990). It is widely accepted that white sharks undergo an ontogenetic shift in prey preference (Cliff et al., 1989; Bruce, 1992; Compagno, 2001; Estrada et al., 2006; Hussey et al., 2012). Stomach content and stable isotope analyses indicate that this shift constitutes a change in trophic level, from a predominantly piscivorous diet when young, to marine mammals making up the major component of diet when older (Tricas & McCosker, 1984; Klimley, 1985; Cliff et al., 1989; Estrada et al., 2006; Hussey et al., 2012). The estimated length at which they undergo this dietary shift varies between 2 m and 3.4 m body length (Cliff et al., 1989; Bruce, 1992; Compagno, 2001; Malcolm et al., 2001; Bruce, 2006; Estrada et al., 2006; Hussey et al., 2012), and is generally considered to occur in both sexes at the same size, despite the fact that white sharks are sexually dimorphic, with males reaching maturity at approximately 3.5 m and females at 4.5 m in length (Francis, 1996; Pratt, 1996; Compagno, 2001; Bruce & Bradford, 2012). This dietary shift is widely accepted to be facilitated by a change in tooth morphology, from relatively pointed (cuspidate) teeth with serrational cusplets adapted to puncturing piscivorous prey, to broader teeth lacking serrational cusplets that are better suited to handling mammalian prey (Tricas & McCosker, 1984; Frazzetta, 1988; Hubbell, 1996; Whitenack & Motta, 2010; Bemis et al., 2015) (Figure 1). However, the primary reliance of adult white sharks on marine mammal prey is arguably overstated (Fergusson et al., 2009), and there is mounting evidence of individual dietary variation that does not appear to be related to sex or age (Estrada et al., 2006; Hussey et al., 2012; Carlisle et al., 2012; Kim et al., 2012; Hamady et al., 2014; Pethybridge et al., 2014; Christiansen et al., 2015; Towner et al., 2016). Individual and sexual differences in foraging strategy have been found (Huveneers et al., 2015; Towner et al., 2016), and there are questions over whether it occurs at all for some individuals (Estrada et al., 2006; Hussey et al., 2012). Tooth shape in adult white sharks has also been reported as highly variable, with some large sharks retaining the more cuspidate tooth shape of juveniles (Hubbell, 1996; Castro, 2012). However, the only previous explicit investigations of tooth morphometrics in relation to sex and body length included only tooth height (Randall, 1973, 1987; Mollet et al., 1996; Shimada, 2002b), a metric which does not capture tooth cuspidity. As tooth cuspidity is considered to play an important role in the ontogenetic dietary shift, this leaves a substantial gap in our understanding of the dynamics of this shift, including within and between the sexes.

Morphological changes through ontogeny are difficult to measure in wild animals, especially those inhabiting marine environments, and even more so in wide-ranging apex predators. White sharks provide an excellent opportunity to study these changes because their predictable aggregation at certain pinniped colonies, and the ease with which they can be lured to boats and photographed, makes photographic analysis of live sharks a potentially valuable source of information on tooth morphology. Here we examine the ontogenetic change in tooth cuspidity by integrating published data and tooth measurements from jaws of dead sharks with a new non-invasive method of quantifying tooth morphology for live sharks from photographs, and examine how the ontogenetic change in tooth morphology differs between sexes and individuals.

Materials and Methods

TOOTH CUSPIDITY

Teeth are described as per the system detailed by Moyer et al., (2015) and Bemis et al., (2015), in which teeth are given a code based on their location in the left or right side of the jaw (L and R, respectively), in Meckel's or palatoquadrate cartilage (M and P, respectively), and then numbered distally to medially, relative to the appropriate symphysis (Figure 2A, 3A). We used measurements of tooth crown height and width, as described in Hubbell, (1996), to calculate tooth cuspidity, dividing the crown height by the crown width to produce what we have termed the tooth index value (Figure 2B). The presence of serrational cusplets are not mentioned in the published datasets, and were not observed in any of the specimens that we measured. For analyses of the relationship between tooth cuspidity and shark length, all tooth measurements were taken from RP1 or LP1 teeth (Figure 2). We included P1 data from 23 live sharks in Gansbaai, South Africa (34.5805° S, 19.3518° E), using a novel photographic method and ImageJ software (Abramoff et al., 2004) described below. We included measurements taken manually from teeth of 50 jaws in the jaw collection held by the KwaZulu-Natal Sharks Board (KZNSB) South Africa, and P1 crown height and width data from 55 sharks, published by Hubbell, (1996), and Mollet et al., (1996; where in the latter, crown height was termed “UA1E2” and crown width “UA1W”). KZNSB sharks were caught as part of a bather safety program, and jaws either dried or frozen at time of measurement. The Gansbaai and KZNSB sharks both came from the same South Africa population. The sharks in Hubbell (1996) and Mollet et al., (1996) came from multiple populations (Australia-New Zealand, South Africa, Northeast Pacific, Northwest Atlantic).

TOOTH ANGLE

The intermediate upper tooth (R/LP3, Figure 3A, B, C, D) is markedly different in shape from the P1 and P2 teeth, in that it typically displays asymmetry, and an approximately straight medial edge (Applegate & Espinosa-Arrubarrena, 1996; Hubbell, 1996). The angle of the tip of the crown in comparison to the tooth midpoint shows greater variation in this tooth than the equivalent angles of the P1 and P2 teeth (Hubbell, 1996), and was thus selected as another potential metric for analysing relationships between tooth morphology and shark length (Figure 3B, D). One P3 tooth per shark was selected, and ImageJ software was used to measure the angle (lateral or medial) of the tip of the tooth crown in relation to the midpoint of the tooth base (Hubbell (1996), Figure 3B, D). Medial inclinations were denoted by positive angles, and distal inclinations as negative (Figure 3B). We combined P3 angle measurements derived from photographs of live sharks (see below), and photographs of jaws held by the KZNSB, with data published by Hubbell, (1996).

SHARK LENGTH

Shark lengths (total length) were directly measured for sharks in the KZNSB and published datasets. For live sharks in Gansbaai, lengths were estimated in the field by visually comparing the free-swimming sharks to an object of known length (a 4.7 m length cage diving cage), fixed to the side of the boat, as has been done in many previous studies (Kock et al., 2013; Towner et al., 2013a, 2016).

PHOTOGRAPHIC METHOD

We took measurements of crown height, width, and angle from photographs of both live sharks and KZNSB jaws (Figures 2C, D, 3, 4). Live sharks were photographed from a cage diving vessel operated by Marine Dynamics, based in Gansbaai, South Africa. The photographs were taken when sharks were interacting with stimuli (salmon head bait and a wooden seal decoy), during three field trips: August-October 2014, February-April 2015, and June 2015. Sharks were individually identified using photographs of the first dorsal fin and DARWIN ID software, with digital traces of the outline of the fin being matched by the software and confirmed by eye (Stanley, 1995; Towner et al., 2013b). We gave tooth images a quality score rating of 1–6, based on their resolution, clarity and angle relative to the camera, and only images with a score of four or above were included in analyses, based on the results of the repeatability of the method, described below. These images were imported into ImageJ software where measurements of crown height, crown width and tooth angle were taken in pixels. Height and width measurements were taken three times, and averages used in the calculation of tooth index values.

Statistical Analyses

To investigate scaling relationships between shark length and P1 tooth index, both variables were $\log_{10}$ transformed, sorted into male and female datasets, and analysed with linear regression. Log_{10} transformations are typically used to increase linearity of allometric relationships, which tend to form curves as they are a power function, e.g. (Huber et al., 2006; Kolmann & Huber, 2009; Habegger et al., 2012). If the predicted isometric slope of 1 fell outside of the 95% confidence intervals of the regression slope, the relationship was considered allometric (Sokal & Rohlf, 1995). To identify discrete tooth index groupings (e.g. pre- and post-ontogenetic shift and/or polymorphs) in P1 teeth, hierarchical cluster analyses were applied to P1 tooth index data. The NbClust function in R statistical software (version 3.2.4.) (R Core Team, 2016) was used to identify the optimal number of clusters with which to perform the cluster analyses *a priori*. A Mann-Whitney U test and one-way ANOVA were applied to data from males and females, respectively, to test for differences in shark length between tooth clusters (male data were non-normal; female data had more than two clusters). Linear regression analyses were further applied separately to male and female P3 tooth angle and shark length data, and an isometric slope of 1 used to determine allometry. Log_{10} transformations were not used for these data, as they included negative and positive values.

We conducted tests of both accuracy and repeatability to determine the robustness of the photographic methodology (Jeffreys et al., 2013). We used the white shark jaw collection held by the KZNSB to assess the accuracy of our photographic method for measuring tooth cuspidity (Figure 2A, B). We measured LM1 and LM2 teeth of 35 jaws using a tape measure in situ, and used photographs of the same jaws to measure the same teeth digitally, in pixels, using ImageJ software. We used linear regression to compare the tooth index values produced from manual and digital measurements. We further compared digital measurements, obtained from multiple photographs of the same teeth of live Gansbaai sharks, to assess the repeatability of our photographic method (Figure 4). This dataset included teeth from both the upper and lower jaw, in any position visible, provided the quality of the image met the requirements described above. The teeth of eleven individual sharks, totalling 12 unique teeth, each measured at least twice, were included in a repeatability calculation described by Lessells & Boag, (1987). This calculation uses the mean square values produced by a one way analysis of variance (ANOVA) (IBM SPSS v22) (MS_W = within group variance, MS_A = among group variance) as such; Repeatability (r) = $S^2_A / S^2 + S^2_A$, where $S^2 = MS_W$, $S^2_A = (MS_A - MS_W)/n_0$, $n_0 = [1/(a-1)] * [\sum ni - \sum ni^2 / \sum ni)$, a = number of groups, and n_i = sample size of the ith group. Two repeatability scores were calculated: using teeth with a quality score of three and above (n=46), or four and above (n=25).

Results

P1 tooth index in male white sharks was significantly related to body length (linear regression, $F_{1,55} = 20.6$, $P < 0.001$, 95% confidence interval on slope -0.17 and -0.07, $r^2 = 0.25$), and was negatively allometric, with the predicted isometric slope of 1 being outside the 95% confidence intervals of the regression slope (Figure 5A). Tooth index in female sharks also decreased significantly with body length (linear regression, $F_{1, 61} = 4.0$, $P = 0.05$, 95% confidence interval on slope -0.14 and -1.23, $r^2 = 0.05$), but showed isometry (predicted isometric slope of 1 was inside of the 95% confidence intervals) (Figure 5B). Additionally, there was much greater variability in the relationship for females than for males ($r^2 = 0.05$ and $r^2 = 0.25$, respectively) (Figure 4B).

The angle of the P3 tooth was significantly related to shark length in male sharks (linear regression, $F = 6.85$, $P = 0.019$; 95% confidence interval on slope -0.94 and -0.1, $r^2 = 0.31$) in an isometric relationship, as the predicted isometric slope was 1 (Figure 5C). In female sharks, the angle of the P3 tooth was not related to shark length (linear regression, $F = 2.62$, $P = 0.146$, 95% confidence interval on slope -4.35 and 0.69, $r^2 = 0.05$) (Figure 5D). The P1 teeth of male sharks formed two clusters; one where teeth were relatively cuspidate, and another where teeth were broader (Figure 5A). The lengths of sharks in the two tooth clusters were significantly different (Mann-Whitney U test, $U = 191$, $P < 0.001$). Female P1 teeth separated into three clusters that represented cuspidate, intermediate and broad teeth (Figure 5B), and shark length did not significantly differ between these clusters (one way ANOVA, $F_{1, 62} = 0.234$, $P = 0.63$, 95% confidence interval on slope -0.14 and 0.22, $r^2 = 0.01$).

There was a significant, positive relationship between the measurements taken directly from teeth and from photographs (P1 and P2: linear regression, $F_{1,34} = 43.02$, $P < 0.001$, 95% confidence interval: 0.57 - 1.08, $r^2 = 0.57$; P1 only: linear regression, $F_{1,16} = 61.0$, $P < 0.001$, 95% confidence interval: 0.73 - 1.27, $r^2 = 0.8$) (Figure 6A and B, respectively). Digital images of only the P1 tooth were therefore substantially more accurate than those of the P2 tooth. Tooth measurements showed high repeatability, which was substantially greater when using images ranked four or more (Table I), and therefore only those were considered in analyses of tooth index and shark length.

Discussion

The results show that white sharks exhibit an ontogenetic shift in tooth shape, but that this relationship differs between sexes, and shows substantial individual variation. Males showed a distinct increase in P1 tooth breadth with length, and a change in angle of the P3 tooth, both of which were far less pronounced in females. Measurements taken from photos were accurate and repeatable, suggesting that use of photos of live sharks could be a valuable source of data for future studies.

The results confirm that male white sharks undergo an ontogenetic shift in tooth shape. Upper first teeth of male sharks become significantly more broad with increasing shark length, showing negative allometry, and male sharks clustered into cuspidate and broad-toothed groups that significantly differed in shark length, with the more cuspidate group containing smaller sharks than the broad group. These two clusters likely represent pre- and post-ontogenetic shift individuals. This ontogenetic change in white sharks is commonly believed to facilitate the inclusion of marine mammals into their diet (Tricas & McCosker, 1984; Klimley, 1985; Frazzetta, 1988; Cliff et al., 1989; Hubbell, 1996; Estrada et al., 2006; Hussey et al., 2012). The medial angle of the P3 tooth was also found to scale significantly with shark length in males, in an isometric relationship. This tooth has been hypothesised to be a specialised tool for inflicting large, disabling wounds on pinniped prey due to its shape and location on the strongest part of the jaw (Martin et al., 2005). An increase in the distal inclination of the tooth tip, as evidenced in males, could be a further adaptation for handling and despatching marine mammals. Alternatively, this change in angle could assist in the handling of females during copulation, during which male sharks bite females in the gill, head, and pectoral regions (Kajiura & Tricas, 1996; Pratt & Carrier, 2001).

Although shark lengths in the cuspidate and broad clusters of males were significantly different, providing further evidence of a distinct change in tooth shape through ontogeny, there was significant variation and overlap in size. This indicates that there may be individual variation in the length at which male sharks undergo the ontogenetic shift. Males reach sexual maturity at a similar size to that at which they undergo the ontogenetic shift in tooth morphology (Cliff et al., 1989). This suggests that the ontogenetic shifts in diet and tooth shape are intrinsically linked to sexual maturity. In animals, individual variation in life history traits such as the onset of maturity, coupled with behavioural changes such as changes in habitat use and diet, can be components of a pace-of-life syndrome, in which life-history trade-offs produce consistent behavioural differences in areas such as activity level, movement patterns, boldness and aggressiveness (Ricklefs & Wikelski, 2002; Stamps, 2007; Wolf et al., 2007; Biro & Stamps, 2008; Réale et al., 2010). For example, in the house mouse *Mus musculus* (Linnaeus 1758), size and age at maturity is linked to activity level, growth rate, fecundity, adult body size, and longevity, with ‘fast paced’ mice being more active, faster growing, and reach maturity at a smaller size and younger age than ‘slow paced’ mice (Wirth-Dzieciolowska et al., 1996; Wirth-Dzieçiołowska & Czumińska, 2000; Wirth-Dzięciołowska et al., 2005). The higher energetic needs of individuals which mature more quickly, require morphological and physiological adaptations that enable them to consume the necessary volume or type of sustenance (Biro & Stamps, 2008). In the case of white sharks, this could pertain to broader teeth facilitating the incorporation of energy rich marine mammals into their diet. White sharks exhibit sexual and individual differences in migratory behaviour (Weng et al., 2007; Block et al., 2011; Domeier & Nasby-Lucas, 2012; Kock et al., 2013), that will affect the water temperatures individuals inhabit and, because white sharks are endothermic (Carey et al., 1982) therefore the energetic demands of thermoregulation, producing individual variation in energetic demands that may influence pace-of-life strategies. Elevated hunger and activity levels increase risk of fishing mortality, and can lead to rapid depletion of fast paced genotypes (Young et al., 2006; Biro & Post, 2008; Mittelbach et al., 2014; Härkönen et al., 2014).

Female white shark teeth were found to scale with isometry in relation to shark length, and the observed level of variation made any overall relationship very weak. Additionally, the facts that the angle of the intermediate tooth did not scale with shark length and that the cluster analysis suggested three tooth groups as opposed to the two groups in males, demonstrate that ontogenetic shifts in tooth shape differ between males and females. That these tooth types were independent of shark length, suggests that female white sharks may exhibit phenotypic polymorphism. Stable isotope analyses suggest that some females do not undergo an ontogenetic dietary shift, and can show consistent dietary specialisation instead (Estrada et al., 2006; Hussey et al., 2012; Kim et al., 2012; Pethybridge et al., 2014; Christiansen et al., 2015). However, the mechanism behind such specialisation has not been elucidated. Tooth polymorphism facilitates niche polymorphism in sympatric populations of some fish species (Meyer, 1990), and has been linked to dietary specialisation in other shark species (Litvinov, 1983; Litvinov & Laptikhovsky, 2005). As tooth shape is generally accepted to relate to the exploitation of different prey types in white sharks (Tricas & McCosker, 1984; Frazzetta, 1988; Hubbell, 1996), it is reasonable to suggest that sharks with cuspidate, intermediate or broad teeth feed preferentially on different prey, constituting trophic polymorphism in females. Potential consequences of specialisation in white shark diets include altered food web structure if changes in resource availability affect tooth morphs differently (Christiansen et al., 2015), and differing levels of bioaccumulation of toxins (Young et al., 2006; Biro & Post, 2008; Mittelbach et al., 2014; Härkönen et al., 2014), an issue already known to pose a significant threat to white sharks generally (Schlenk et al., 2005; Mull et al., 2012; Lyons et al., 2013; Marsilli et al., 2016). While we cannot rule out geographic variation in female shark tooth shape, it seems less likely as no such variation was evident in male teeth.

One of the major limitations in establishing the ontogenetic relationships between morphology, diet and maturity, especially in threatened species, is sample size. For sharks, the majority of tooth data currently available is from a limited number of jaw collections, harvested from dead specimens. Our study shows that our novel photographic method produces accurate and repeatable tooth shape data of live white sharks in the field, providing that image quality is controlled, and these data can be used to study the ontogenetic dietary shift. The increase in accuracy when comparing digital and manual measurements of P1 teeth and pooled P1 and P2 teeth is likely due to parallax error, induced by P2 teeth not being exactly front on to the camera due to their position in the jaw. This highlights the importance of ensuring that the position of the tooth relative to the camera is directly parallel.

We have developed a non-lethal research method that can be used to provide sample sizes that better elucidate the onset and occurrence of ontogenetic shifts within and between populations, in addition to individual variation, sexual dimorphism and polymorphism in white sharks, and potentially other sharks as well. Ontogenetic shift dynamics are a major component of elasmobranch life history. Consideration of sexual and individual variation in ontogenetic shift dynamics will therefore be important both for understanding the ecology of a species, and for the development of effective management strategies.

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Tables

Table I: Repeatability of tooth index values obtained from photographs of teeth, with image quality of ≥ 3 and ≥ 4 Image quality score, number of images (n), group means, degrees of freedom (df), coefficient of variation (CV), 95% confidence intervals (CI), repeatability (R) and P values.

Quality Score	n	Group Mean	df	CV (%)	95% CI	R	P
≥3	46	1.09	45	0.092	1.17	0.57	<0.001
≥4	25	1.10	24	1.32	0.57	0.86	<0.001

Figures

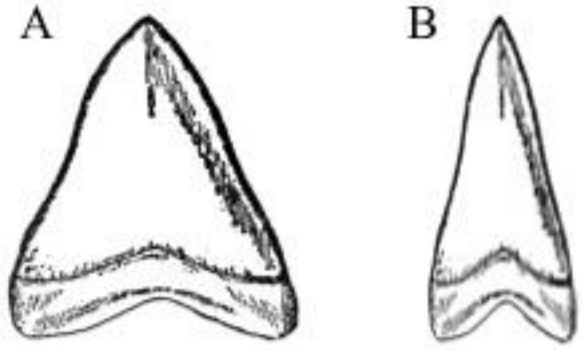

Fig. 1. Illustrations of variation in white shark tooth breadth and cuspidity; A) broad tooth, B) cuspidate tooth.

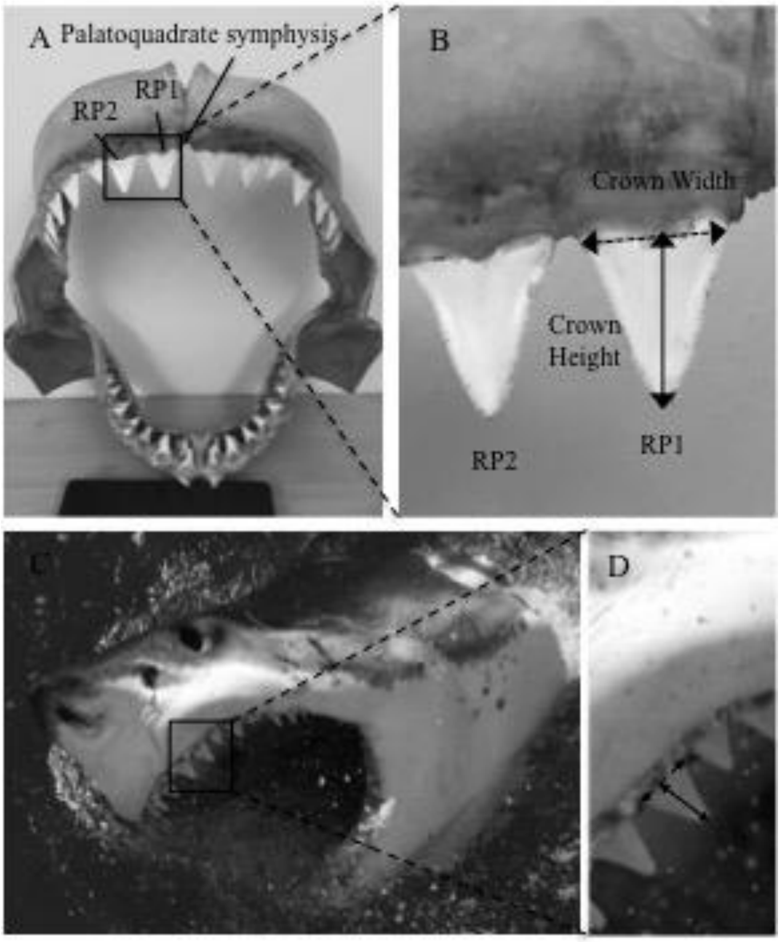

Fig. 2. A) Diagram showing position of white shark teeth used in the study; A) photograph of a jaw held in the KwaZulu-Natal Sharks Board jaw collection, indicating the position of RP1 and RP2 teeth, B) close up view of RP1 and RP2 teeth depicted in A, with crown height and base length measurements indicated on the RP1

tooth, C) example photograph of an RP1 and RP2 tooth of a live shark, taken on board the Marine Dynamics cage diving vessel in Gansbaai, South Africa, D) close up view of the teeth depicted in C, with crown height and base length measurements of the LP2 tooth indicated.

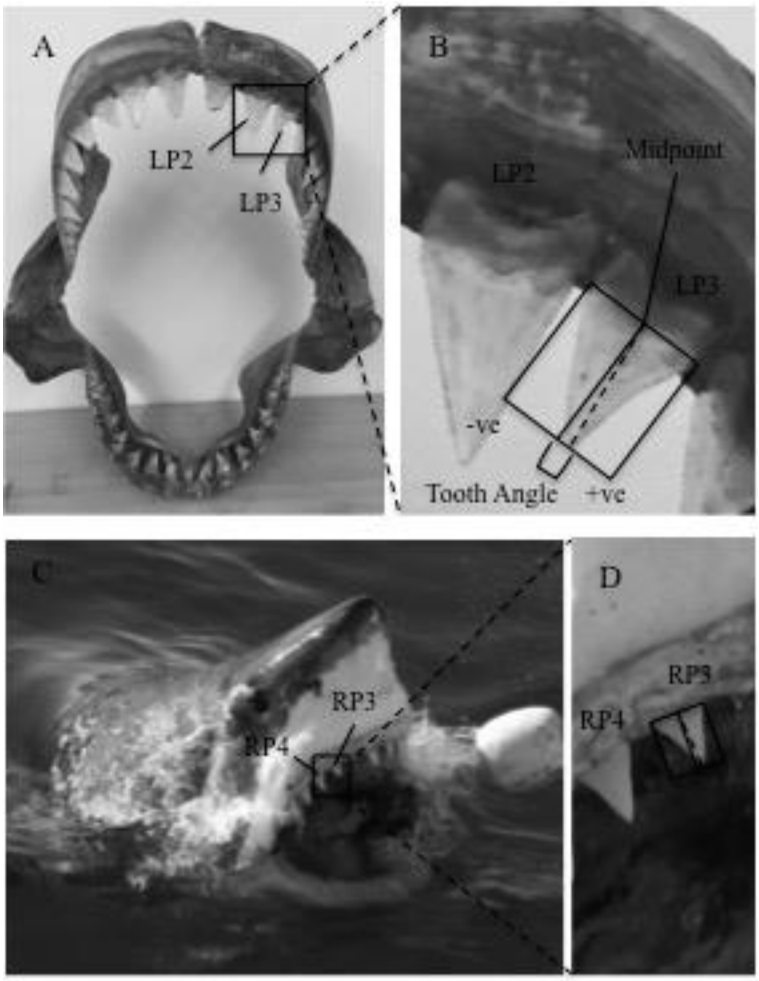

Fig. 3 Derivation of tooth angle from the P3 tooth from; A) photograph of a jaw held in the KwaZulu-Natal Sharks Board jaw collection, indicating the position of LP2 and LP3 teeth, B) close up view of LP2 and LP3 teeth depicted in A, with tooth midpoint and tooth angle indicated on the LP3 tooth C) example photograph of an RP3 and RP4 tooth of a live shark, taken on board the Marine Dynamics cage diving vessel in

Gansbaai, South Africa, D) close-up view of the teeth depicted in C, with tooth angle measurement of the LP3 tooth indicated.

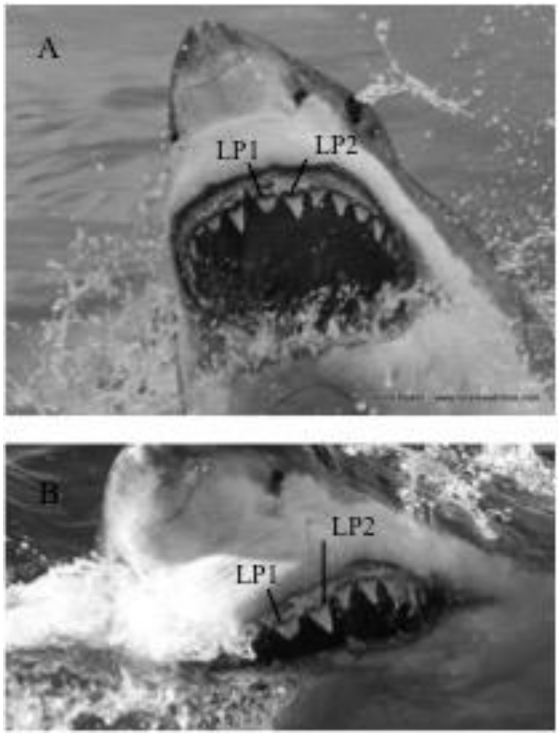

Fig. 4 Photographs of the P2 teeth of an individually identified white shark “Rosie” used in the repeatability test of the photographic method. Image A was taken on 15/03/2015 © Kelly Baker www.sharkwatch.sa, image B was taken on 24/03/2015.

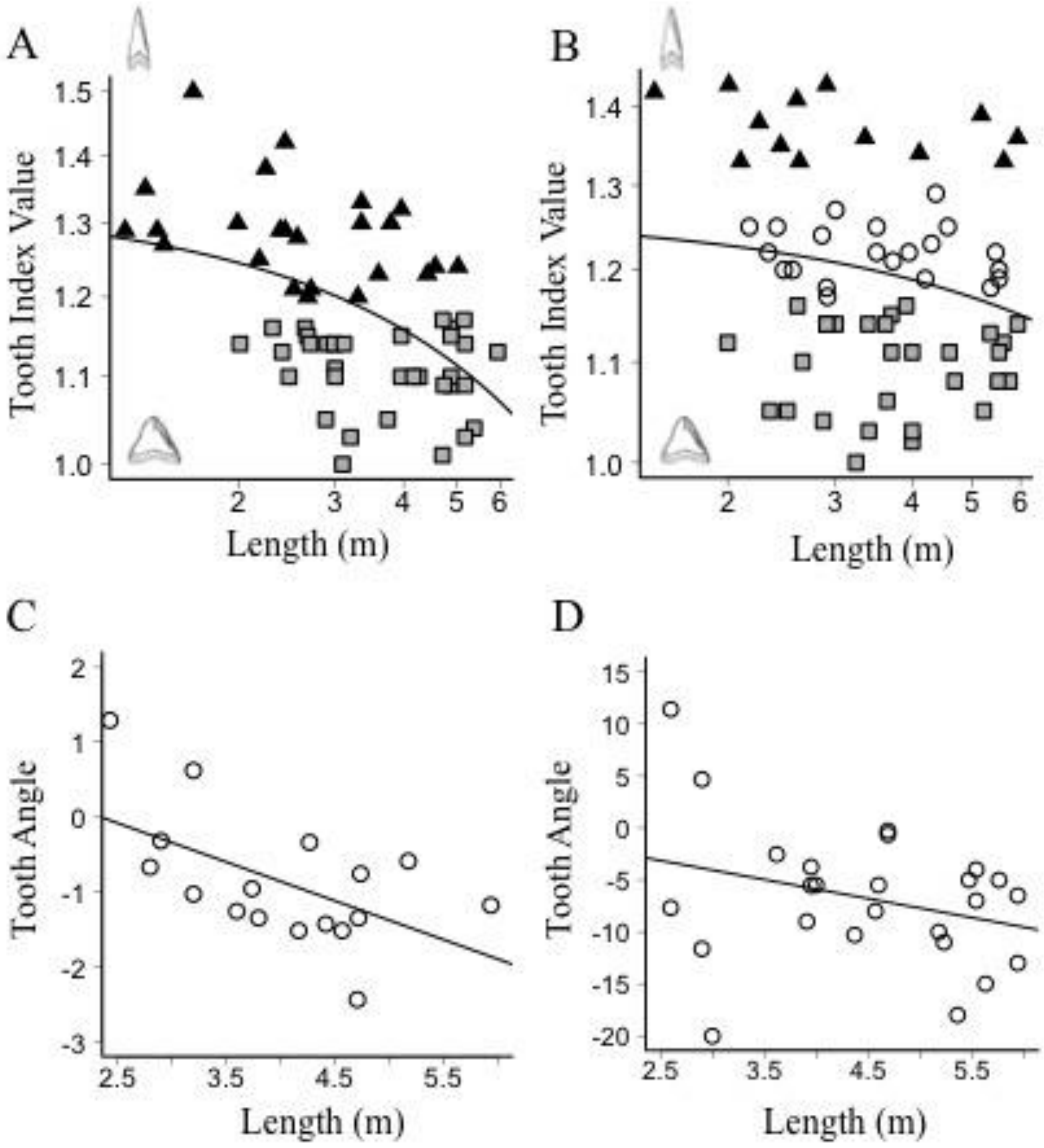

Fig. 5. Relationship between $\log_{10}$ P1 tooth index and $\log_{10}$ body length (m) for A) male white sharks ($y = -0.119x + 0.131$; $r^2 = 0.25$; $n = 57$), and B) female white sharks ($y = -0.0226x + 1.28$; $r^2 = 0.085$; $n = 71$). Broad and cuspidate tooth types are illustrated on the y-axes. Males formed two clusters, with teeth that were relatively cuspidate (triangles) or relatively broad (squares); females formed three clusters, with teeth that were relatively cuspidate (triangles), intermediate (circles) or relatively broad (squares). Also shown are the relationships between the angle of the P3 tooth

and body length (m) for C) male white sharks (*y* = -3.075*x* + 7.205; r^2 = 0.31; n = 17), and D) female white sharks (*y* = -0.617*x* + -5.1663; r^2 = 0.09; n = 22).

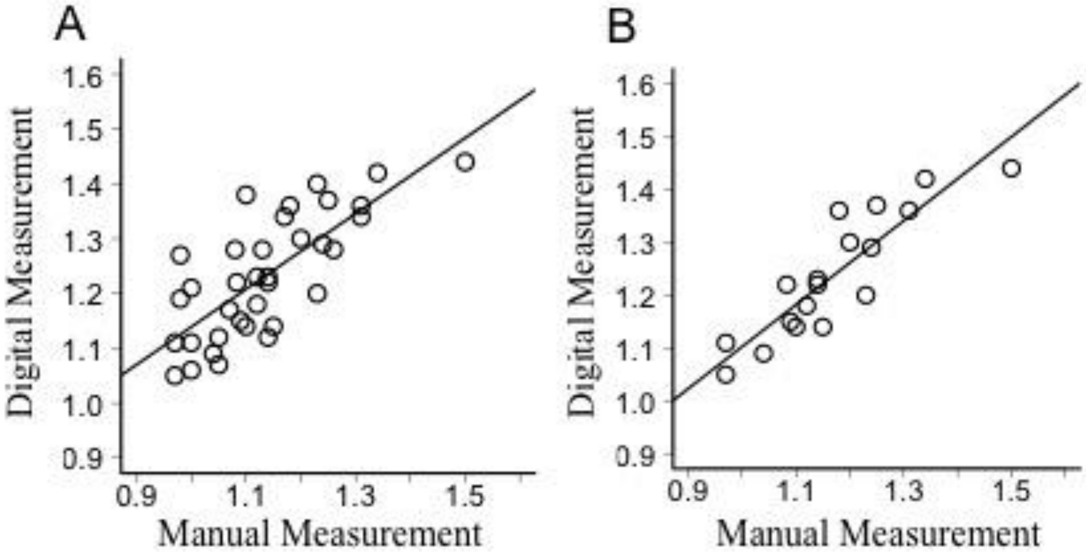

Fig. 6. Relationship between index value measurements of teeth taken directly, and from photographs, for jaws of white sharks caught by the KwaZulu-Natal Sharks Board. A) P1 and P2 teeth (*y* = 0.6928*x* + 0.4457; r^2 = 0.57; n = 35; B) P1 teeth only (*y* = 0.8009*x* + 0.2996; r^2 = 0.8; n = 18).