

## Ontogenetic Shift Dynamics in White Sharks

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### 2 **The tooth, the whole tooth and nothing but the tooth: tooth shape** 3 **and ontogenetic shift dynamics in the white shark**

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18

19 **Abstract**

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

39

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

42 **Introduction**

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

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

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67 Henle, 1839), and horn sharks *Heterodontus francisci* (Girard, 1855) show allometric  
68 changes in head shape and musculature (Huber et al., 2006; Kolmann & Huber, 2009;  
69 Habegger et al., 2012; Fu et al., 2016), and bull, tiger and white *Carcharodon*  
70 *carcharias* (Linnaeus 1758) sharks show this with caudal-fin shape (Lingham-Soliar,  
71 2005; Irschick & Hammerschlag, 2014). Allometric scaling of mouth length and  
72 width is also evident in the viper dogfish *Trigonognathus kabeyai* (Mochizuki &  
73 Fumio, 1990) (Yano et al., 2003).

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

85 The white shark is a classic example of a morphological, diet-related change  
86 through ontogeny. White sharks are a member of the Lamniformes, an order for  
87 which tooth morphology is an informative defining character (Compagno, 1990). It is  
88 widely accepted that white sharks undergo an ontogenetic shift in prey preference  
89 (Cliff et al., 1989; Bruce, 1992; Compagno, 2001; Estrada et al., 2006; Hussey et al.,  
90 2012). Stomach content and stable isotope analyses indicate that this shift constitutes  
91 a change in trophic level, from a predominantly piscivorous diet when young, to

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92 marine mammals making up the major component of diet when older (Tricas &  
93 McCosker, 1984; Klimley, 1985; Cliff et al., 1989; Estrada et al., 2006; Hussey et al.,  
94 2012). The estimated length at which they undergo this dietary shift varies between 2  
95 m and 3.4 m body length (Cliff et al., 1989; Bruce, 1992; Compagno, 2001; Malcolm  
96 et al., 2001; Bruce, 2006; Estrada et al., 2006; Hussey et al., 2012), and is generally  
97 considered to occur in both sexes at the same size, despite the fact that white sharks  
98 are sexually dimorphic, with males reaching maturity at approximately 3.5 m and  
99 females at 4.5 m in length (Francis, 1996; Pratt, 1996; Compagno, 2001; Bruce &  
100 Bradford, 2012). This dietary shift is widely accepted to be facilitated by a change in  
101 tooth morphology, from relatively pointed (cuspidate) teeth with serrational cusplets  
102 adapted to puncturing piscivorous prey, to broader teeth lacking serrational cusplets  
103 that are better suited to handling mammalian prey (Tricas & McCosker, 1984;  
104 Frazzetta, 1988; Hubbell, 1996; Whitenack & Motta, 2010; Bemis et al., 2015)  
105 (Figure 1). However, the primary reliance of adult white sharks on marine mammal  
106 prey is arguably overstated (Fergusson et al., 2009), and there is mounting evidence of  
107 individual dietary variation that does not appear to be related to sex or age (Estrada et  
108 al., 2006; Hussey et al., 2012; Carlisle et al., 2012; Kim et al., 2012; Hamady et al.,  
109 2014; Pethybridge et al., 2014; Christiansen et al., 2015; Towner et al., 2016).  
110 Individual and sexual differences in foraging strategy have been found (Huveneers et  
111 al., 2015; Towner et al., 2016), and there are questions over whether it occurs at all  
112 for some individuals (Estrada et al., 2006; Hussey et al., 2012). Tooth shape in adult  
113 white sharks has also been reported as highly variable, with some large sharks  
114 retaining the more cuspidate tooth shape of juveniles (Hubbell, 1996; Castro, 2012).  
115 However, the only previous explicit investigations of tooth morphometrics in relation  
116 to sex and body length included only tooth height (Randall, 1973, 1987; Mollet et al.,

117 1996; Shimada, 2002b), a metric which does not capture tooth cuspidity. As tooth  
118 cuspidity is considered to play an important role in the ontogenetic dietary shift, this  
119 leaves a substantial gap in our understanding of the dynamics of this shift, including  
120 within and between the sexes.

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

132

133

## 134 **Materials and Methods**

### 135 TOOTH CUSPIDITY

136 Teeth are described as per the system detailed by Moyer et al., (2015) and Bemis et  
137 al., (2015), in which teeth are given a code based on their location in the left or right  
138 side of the jaw (L and R, respectively), in Meckel's or palatoquadrate cartilage (M  
139 and P, respectively), and then numbered distally to medially, relative to the  
140 appropriate symphysis (Figure 2A, 3A). We used measurements of tooth crown height  
141 and width, as described in Hubbell, (1996), to calculate tooth cuspidity, dividing the

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142 crown height by the crown width to produce what we have termed the tooth index  
143 value (Figure 2B). The presence of serrational cusplets are not mentioned in the  
144 published datasets, and were not observed in any of the specimens that we measured.  
145 For analyses of the relationship between tooth cuspidity and shark length, all tooth  
146 measurements were taken from RP1 or LP1 teeth (Figure 2). We included P1 data  
147 from 23 live sharks in Gansbaai, South Africa (34.5805° S, 19.3518° E), using a novel  
148 photographic method and ImageJ software (Abramoff et al., 2004) described below.  
149 We included measurements taken manually from teeth of 50 jaws in the jaw  
150 collection held by the KwaZulu-Natal Sharks Board (KZNSB) South Africa, and P1  
151 crown height and width data from 55 sharks, published by Hubbell, (1996), and  
152 Mollet et al., (1996; where in the latter, crown height was termed “UA1E2” and  
153 crown width “UA1W”). KZNSB sharks were caught as part of a bather safety  
154 program, and jaws either dried or frozen at time of measurement. The Gansbaai and  
155 KZNSB sharks both came from the same South Africa population. The sharks in  
156 Hubbell (1996) and Mollet et al., (1996) came from multiple populations (Australia-  
157 New Zealand, South Africa, Northeast Pacific, Northwest Atlantic).

158

### 159 TOOTH ANGLE

160 The intermediate upper tooth (R/LP3, Figure 3A, B, C, D) is markedly  
161 different in shape from the P1 and P2 teeth, in that it typically displays asymmetry,  
162 and an approximately straight medial edge (Applegate & Espinosa-Arrubarrena, 1996;  
163 Hubbell, 1996). The angle of the tip of the crown in comparison to the tooth midpoint  
164 shows greater variation in this tooth than the equivalent angles of the P1 and P2 teeth  
165 (Hubbell, 1996), and was thus selected as another potential metric for analysing  
166 relationships between tooth morphology and shark length (Figure 3B, D). One P3

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167 tooth per shark was selected, and ImageJ software was used to measure the angle  
168 (lateral or medial) of the tip of the tooth crown in relation to the midpoint of the tooth  
169 base (Hubbell (1996), Figure 3B, D). Medial inclinations were denoted by positive  
170 angles, and distal inclinations as negative (Figure 3B). We combined P3 angle  
171 measurements derived from photographs of live sharks (see below), and photographs  
172 of jaws held by the KZNSB, with data published by Hubbell, (1996).

173

### 174 SHARK LENGTH

175 Shark lengths (total length) were directly measured for sharks in the KZNSB  
176 and published datasets. For live sharks in Gansbaai, lengths were estimated in the  
177 field by visually comparing the free-swimming sharks to an object of known length (a  
178 4.7 m length cage diving cage), fixed to the side of the boat, as has been done in many  
179 previous studies (Kock et al., 2013; Towner et al., 2013a, 2016).

180

### 181 PHOTOGRAPHIC METHOD

182 We took measurements of crown height, width, and angle from photographs of  
183 both live sharks and KZNSB jaws (Figures 2C, D, 3, 4). Live sharks were  
184 photographed from a cage diving vessel operated by Marine Dynamics, based in  
185 Gansbaai, South Africa. The photographs were taken when sharks were interacting  
186 with stimuli (salmon head bait and a wooden seal decoy), during three field trips:  
187 August-October 2014, February-April 2015, and June 2015. Sharks were individually  
188 identified using photographs of the first dorsal fin and DARWIN ID software, with  
189 digital traces of the outline of the fin being matched by the software and confirmed by  
190 eye (Stanley, 1995; Towner et al., 2013b). We gave tooth images a quality score  
191 rating of 1–6, based on their resolution, clarity and angle relative to the camera, and



192 only images with a score of four or above were included in analyses, based on the  
193 results of the repeatability of the method, described below. These images were  
194 imported into ImageJ software where measurements of crown height, crown width  
195 and tooth angle were taken in pixels. Height and width measurements were taken  
196 three times, and averages used in the calculation of tooth index values.

197

### 198 **Statistical Analyses**

199 To investigate scaling relationships between shark length and P1 tooth index, both  
200 variables were  $\log_{10}$  transformed, sorted into male and female datasets, and analysed  
201 with linear regression.  $\log_{10}$  transformations are typically used to increase linearity  
202 of allometric relationships, which tend to form curves as they are a power function,  
203 e.g. (Huber et al., 2006; Kolmann & Huber, 2009; Habegger et al., 2012). If the  
204 predicted isometric slope of 1 fell outside of the 95% confidence intervals of the  
205 regression slope, the relationship was considered allometric (Sokal & Rohlf, 1995).

206 To identify discrete tooth index groupings (e.g. pre- and post-ontogenetic shift and/or  
207 polymorphs) in P1 teeth, hierarchical cluster analyses were applied to P1 tooth index  
208 data. The NbClust function in R statistical software (version 3.2.4.) (R Core Team,  
209 2016) was used to identify the optimal number of clusters with which to perform the  
210 cluster analyses *a priori*. A Mann-Whitney U test and one-way ANOVA were  
211 applied to data from males and females, respectively, to test for differences in shark  
212 length between tooth clusters (male data were non-normal; female data had more than  
213 two clusters). Linear regression analyses were further applied separately to male and  
214 female P3 tooth angle and shark length data, and an isometric slope of 1 used to  
215 determine allometry.  $\log_{10}$  transformations were not used for these data, as they  
216 included negative and positive values.

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

237

## 238 **Results**

239 P1 tooth index in male white sharks was significantly related to body length (linear  
 240 regression,  $F_{1,55} = 20.6$ ,  $P < 0.001$ , 95% confidence interval on slope -0.17 and -0.07,  
 241  $r^2 = 0.25$ ), and was negatively allometric, with the predicted isometric slope of 1

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242 being outside the 95% confidence intervals of the regression slope (Figure 5A). Tooth  
243 index in female sharks also decreased significantly with body length (linear  
244 regression,  $F_{1,61} = 4.0$ ,  $P = 0.05$ , 95% confidence interval on slope -0.14 and -1.23,  $r^2$   
245 = 0.05), but showed isometry (predicted isometric slope of 1 was inside of the 95%  
246 confidence intervals) (Figure 5B). Additionally, there was much greater variability in  
247 the relationship for females than for males ( $r^2 = 0.05$  and  $r^2 = 0.25$ , respectively)  
248 (Figure 4B).

249         The angle of the P3 tooth was significantly related to shark length in male  
250 sharks (linear regression,  $F = 6.85$ ,  $P = 0.019$ ; 95% confidence interval on slope -0.94  
251 and -0.1,  $r^2 = 0.31$ ) in an isometric relationship, as the predicted isometric slope was 1  
252 (Figure 5C). In female sharks, the angle of the P3 tooth was not related to shark length  
253 (linear regression,  $F = 2.62$ ,  $P = 0.146$ , 95% confidence interval on slope -4.35 and  
254 0.69,  $r^2 = 0.05$ ) (Figure 5D). The P1 teeth of male sharks formed two clusters; one  
255 where teeth were relatively cuspidate, and another where teeth were broader (Figure  
256 5A). The lengths of sharks in the two tooth clusters were significantly different  
257 (Mann-Whitney U test,  $U = 191$ ,  $P < 0.001$ ). Female P1 teeth separated into three  
258 clusters that represented cuspidate, intermediate and broad teeth (Figure 5B), and  
259 shark length did not significantly differ between these clusters (one way ANOVA,  $F_{1,62}$   
260 = 0.234,  $P = 0.63$ , 95% confidence interval on slope -0.14 and 0.22,  $r^2 = 0.01$ ).

261         There was a significant, positive relationship between the measurements taken  
262 directly from teeth and from photographs (P1 and P2: linear regression,  $F_{1,34} = 43.02$ ,  
263  $P < 0.001$ , 95% confidence interval: 0.57 - 1.08,  $r^2 = 0.57$ ; P1 only: linear regression,  
264  $F_{1,16} = 61.0$ ,  $P < 0.001$ , 95% confidence interval: 0.73 - 1.27,  $r^2 = 0.8$ ) (Figure 6A and  
265 B, respectively). Digital images of only the P1 tooth were therefore substantially more  
266 accurate than those of the P2 tooth. Tooth measurements showed high repeatability,

267 which was substantially greater when using images ranked four or more (Table I), and  
268 therefore only those were considered in analyses of tooth index and shark length.

269

270

## 271 **Discussion**

272 The results show that white sharks exhibit an ontogenetic shift in tooth shape, but that  
273 this relationship differs between sexes, and shows substantial individual variation.

274 Males showed a distinct increase in P1 tooth breadth with length, and a change in  
275 angle of the P3 tooth, both of which were far less pronounced in females.

276 Measurements taken from photos were accurate and repeatable, suggesting that use of  
277 photos of live sharks could be a valuable source of data for future studies.

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

292 handling and despatching marine mammals. Alternatively, this change in angle could  
293 assist in the handling of females during copulation, during which male sharks bite  
294 females in the gill, head, and pectoral regions (Kajiura & Tricas, 1996; Pratt &  
295 Carrier, 2001).

296         Although shark lengths in the cuspidate and broad clusters of males were  
297 significantly different, providing further evidence of a distinct change in tooth shape  
298 through ontogeny, there was significant variation and overlap in size. This indicates  
299 that there may be individual variation in the length at which male sharks undergo the  
300 ontogenetic shift. Males reach sexual maturity at a similar size to that at which they  
301 undergo the ontogenetic shift in tooth morphology (Cliff et al., 1989). This suggests  
302 that the ontogenetic shifts in diet and tooth shape are intrinsically linked to sexual  
303 maturity. In animals, individual variation in life history traits such as the onset of  
304 maturity, coupled with behavioural changes such as changes in habitat use and diet,  
305 can be components of a pace-of-life syndrome, in which life-history trade-offs  
306 produce consistent behavioural differences in areas such as activity level, movement  
307 patterns, boldness and aggressiveness (Ricklefs & Wikelski, 2002; Stamps, 2007;  
308 Wolf et al., 2007; Biro & Stamps, 2008; Réale et al., 2010). For example, in the house  
309 mouse *Mus musculus* (Linnaeus 1758), size and age at maturity is linked to activity  
310 level, growth rate, fecundity, adult body size, and longevity, with ‘fast paced’ mice  
311 being more active, faster growing, and reach maturity at a smaller size and younger  
312 age than ‘slow paced’ mice (Wirth-Dzieciolowska et al., 1996; Wirth-Dzięciółowska  
313 & Czumińska, 2000; Wirth-Dzięciółowska et al., 2005). The higher energetic needs of  
314 individuals which mature more quickly, require morphological and physiological  
315 adaptations that enable them to consume the necessary volume or type of sustenance  
316 (Biro & Stamps, 2008). In the case of white sharks, this could pertain to broader teeth

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317 facilitating the incorporation of energy rich marine mammals into their diet. White  
318 sharks exhibit sexual and individual differences in migratory behaviour (Weng et al.,  
319 2007; Block et al., 2011; Domeier & Nasby-Lucas, 2012; Kock et al., 2013), that will  
320 affect the water temperatures individuals inhabit and, because white sharks are  
321 endothermic (Carey et al., 1982) therefore the energetic demands of thermoregulation,  
322 producing individual variation in energetic demands that may influence pace-of-life  
323 strategies. Elevated hunger and activity levels increase risk of fishing mortality, and  
324 can lead to rapid depletion of fast paced genotypes (Young et al., 2006; Biro & Post,  
325 2008; Mittelbach et al., 2014; Härkönen et al., 2014).

326 Female white shark teeth were found to scale with isometry in relation to  
327 shark length, and the observed level of variation made any overall relationship very  
328 weak. Additionally, the facts that the angle of the intermediate tooth did not scale with  
329 shark length and that the cluster analysis suggested three tooth groups as opposed to  
330 the two groups in males, demonstrate that ontogenetic shifts in tooth shape differ  
331 between males and females. That these tooth types were independent of shark length,  
332 suggests that female white sharks may exhibit phenotypic polymorphism. Stable  
333 isotope analyses suggest that some females do not undergo an ontogenetic dietary  
334 shift, and can show consistent dietary specialisation instead (Estrada et al., 2006;  
335 Hussey et al., 2012; Kim et al., 2012; Pethybridge et al., 2014; Christiansen et al.,  
336 2015). However, the mechanism behind such specialisation has not been elucidated.  
337 Tooth polymorphism facilitates niche polymorphism in sympatric populations of  
338 some fish species (Meyer, 1990), and has been linked to dietary specialisation in other  
339 shark species (Litvinov, 1983; Litvinov & Laptikhovsky, 2005). As tooth shape is  
340 generally accepted to relate to the exploitation of different prey types in white sharks  
341 (Tricas & McCosker, 1984; Frazzetta, 1988; Hubbell, 1996), it is reasonable to

342 suggest that sharks with cuspidate, intermediate or broad teeth feed preferentially on  
343 different prey, constituting trophic polymorphism in females. Potential consequences  
344 of specialisation in white shark diets include altered food web structure if changes in  
345 resource availability affect tooth morphs differently (Christiansen et al., 2015), and  
346 differing levels of bioaccumulation of toxins (Young et al., 2006; Biro & Post, 2008;  
347 Mittelbach et al., 2014; Härkönen et al., 2014), an issue already known to pose a  
348 significant threat to white sharks generally (Schlenk et al., 2005; Mull et al., 2012;  
349 Lyons et al., 2013; Marsilli et al., 2016). While we cannot rule out geographic  
350 variation in female shark tooth shape, it seems less likely as no such variation was  
351 evident in male teeth.

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

363         We have developed a non-lethal research method that can be used to provide  
364 sample sizes that better elucidate the onset and occurrence of ontogenetic shifts within  
365 and between populations, in addition to individual variation, sexual dimorphism and  
366 polymorphism in white sharks, and potentially other sharks as well. Ontogenetic shift

367 dynamics are a major component of elasmobranch life history. Consideration of  
368 sexual and individual variation in ontogenetic shift dynamics will therefore be  
369 important both for understanding the ecology of a species, and for the development of  
370 effective management strategies.

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378

## 379 **References**

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### 651 **Tables**

652

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

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

657

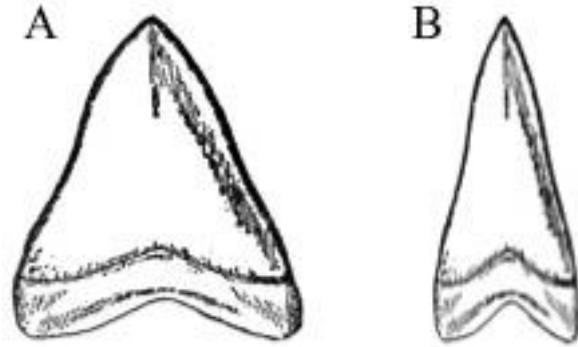
658

### 659 **Figures**

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661

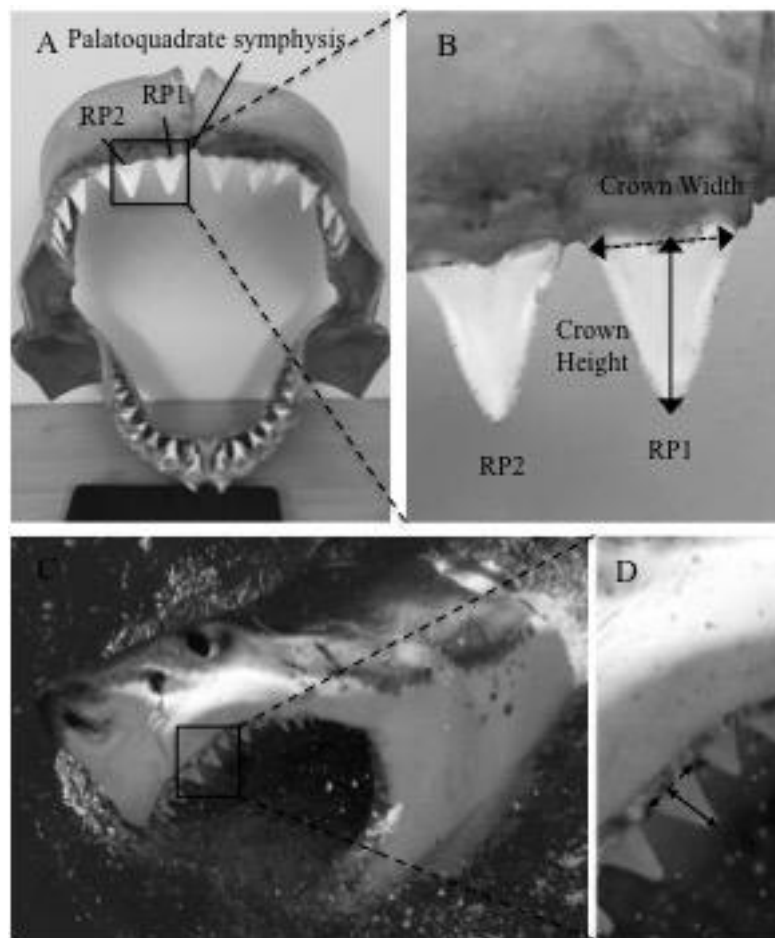
662



663

664 **Fig. 1.** Illustrations of variation in white shark tooth breadth and cuspidity; A) broad

665 tooth, B) cuspidate tooth.



666

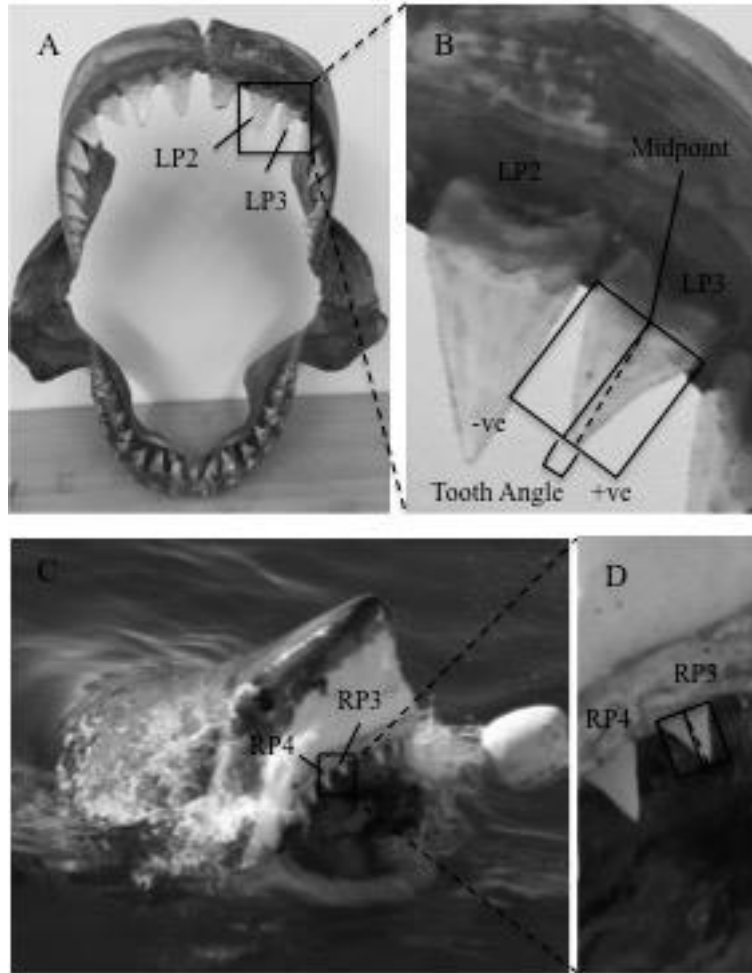
667 **Fig. 2.** A) Diagram showing position of white shark teeth used in the study; A)

668 photograph of a jaw held in the KwaZulu-Natal Sharks Board jaw collection,

669 indicating the position of RP1 and RP2 teeth, B) close up view of RP1 and RP2 teeth

670 depicted in A, with crown height and base length measurements indicated on the RP1

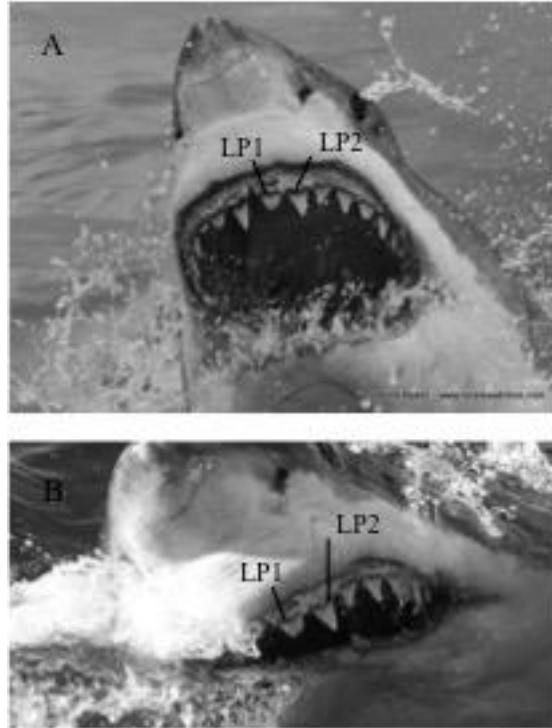
671 tooth, C) example photograph of an RP1 and RP2 tooth of a live shark, taken on board  
672 the Marine Dynamics cage diving vessel in Gansbaai, South Africa, D) close up view  
673 of the teeth depicted in C, with crown height and base length measurements of the  
674 LP2 tooth indicated.  
675



676  
677 **Fig. 3** Derivation of tooth angle from the P3 tooth from; A) photograph of a jaw held  
678 in the KwaZulu-Natal Sharks Board jaw collection, indicating the position of LP2 and  
679 LP3 teeth, B) close up view of LP2 and LP3 teeth depicted in A, with tooth midpoint  
680 and tooth angle indicated on the LP3 tooth C) example photograph of an RP3 and  
681 RP4 tooth of a live shark, taken on board the Marine Dynamics cage diving vessel in

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

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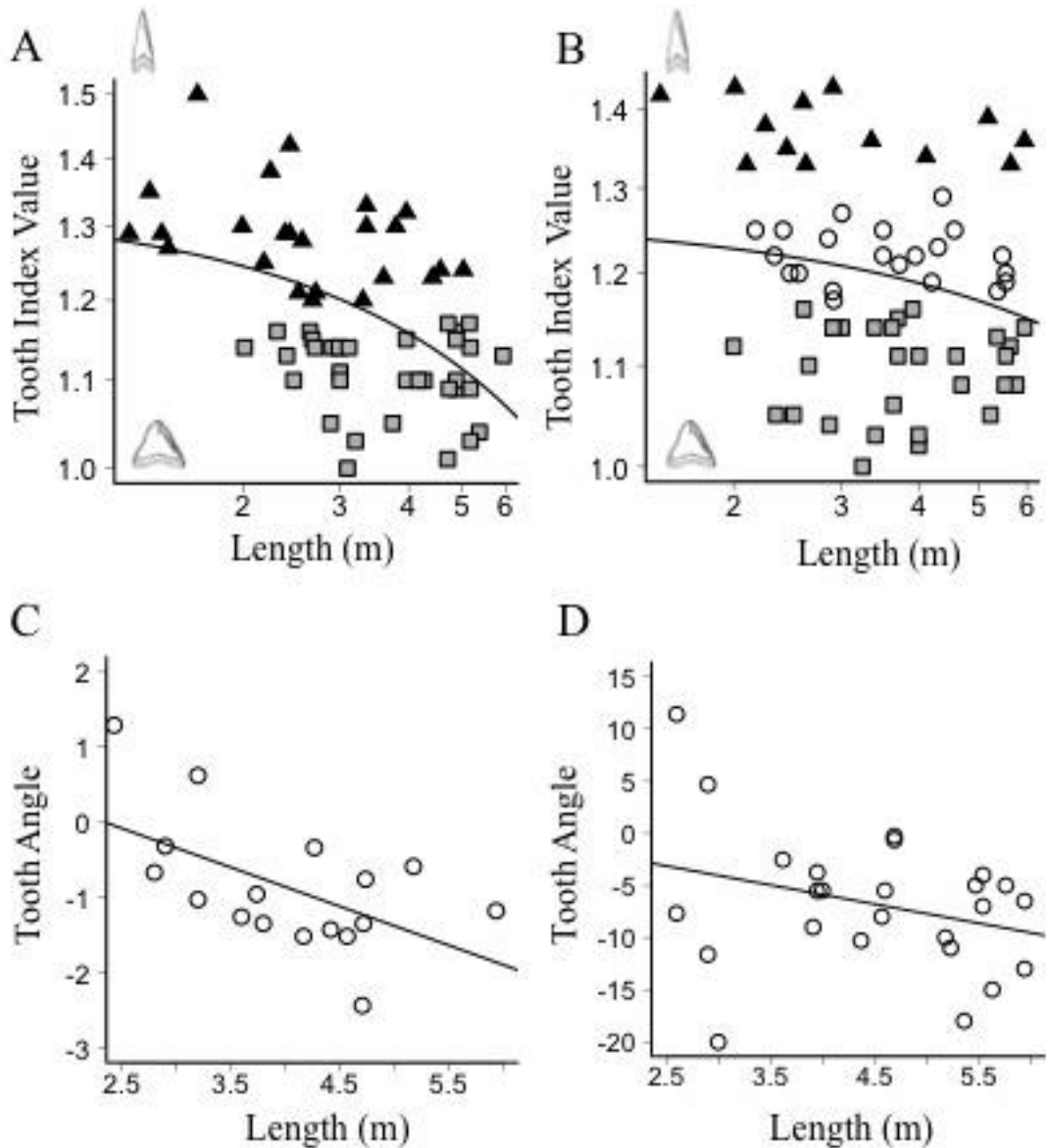
685

686 **Fig. 4** Photographs of the P2 teeth of an individually identified white shark “Rosie”  
687 used in the repeatability test of the photographic method. Image A was taken on  
688 15/03/2015 © Kelly Baker [www.sharkwatch.sa](http://www.sharkwatch.sa), image B was taken on 24/03/2015.

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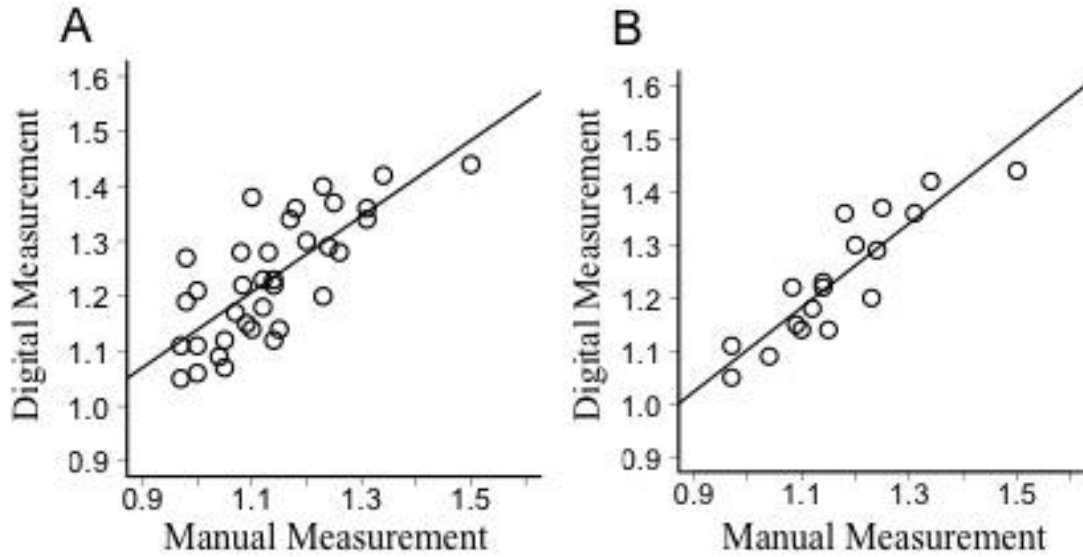
692

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

700 and body length (m) for C) male white sharks ( $y = -3.075x + 7.205$ ;  $r^2 = 0.31$ ;  $n = 17$ ),

701 and D) female white sharks ( $y = -0.617x + -5.1663$ ;  $r^2 = 0.09$ ;  $n = 22$ ).

702



703

704 **Fig. 6.** Relationship between index value measurements of teeth taken directly, and

705 from photographs, for jaws of white sharks caught by the KwaZulu-Natal Sharks

706 Board. A) P1 and P2 teeth ( $y = 0.6928x + 0.4457$ ;  $r^2 = 0.57$ ;  $n = 35$ ; B) P1 teeth only

707 ( $y = 0.8009x + 0.2996$ ;  $r^2 = 0.8$ ;  $n = 18$ ).

708