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The tooth, the whole tooth and nothing but the tooth: tooth shape and ontogenetic shift dynamics in the white shark *Carcharodon carcharias* — Source link

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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**

4

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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.

371

372

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378

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650

651 **Tables**

652

653 **Table I:** Repeatability of tooth index values obtained from photographs of teeth, with
654 image quality of ≥ 3 and ≥ 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
≥ 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

657

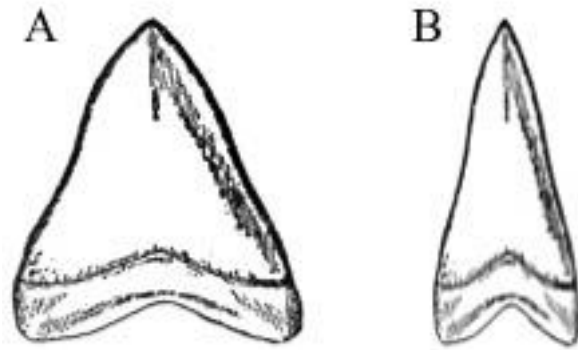
658

659 **Figures**

660

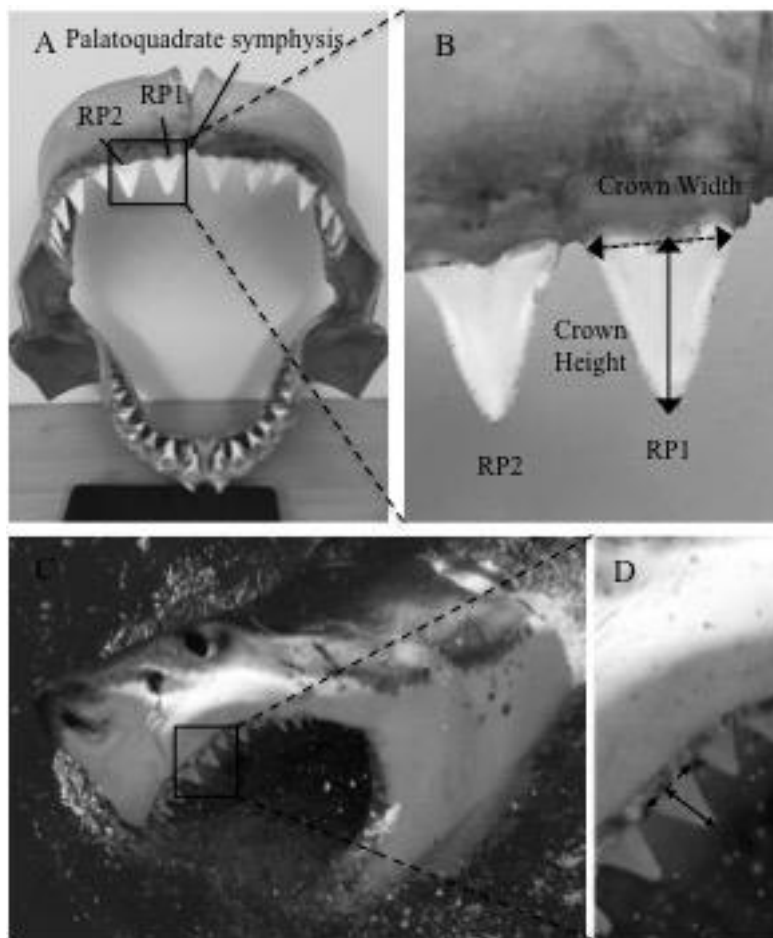
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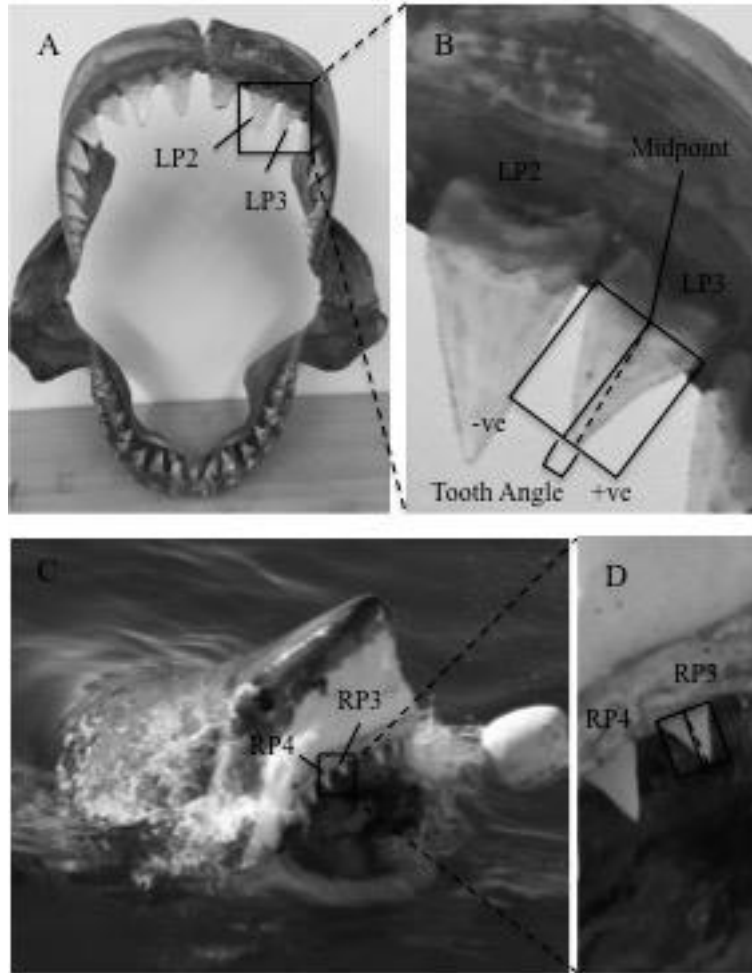
664 **Fig. 1.** Illustrations of variation in white shark tooth breadth and cuspidity; A) broad
665 tooth, B) cuspidate tooth.



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

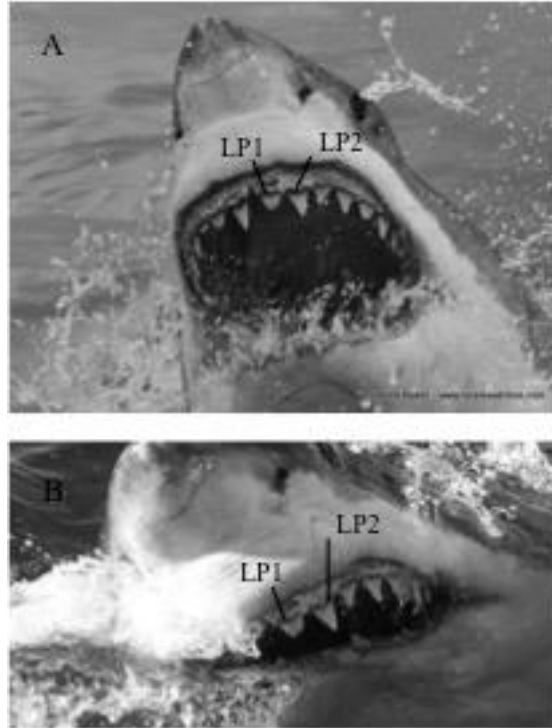
671 tooth, C) example photograph of an RP1 and RP2 tooth of a live shark, taken on board
672 the Marine Dynamics cage diving vessel in Gansbaai, South Africa, D) close up view
673 of the teeth depicted in C, with crown height and base length measurements of the
674 LP2 tooth indicated.
675



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.

684

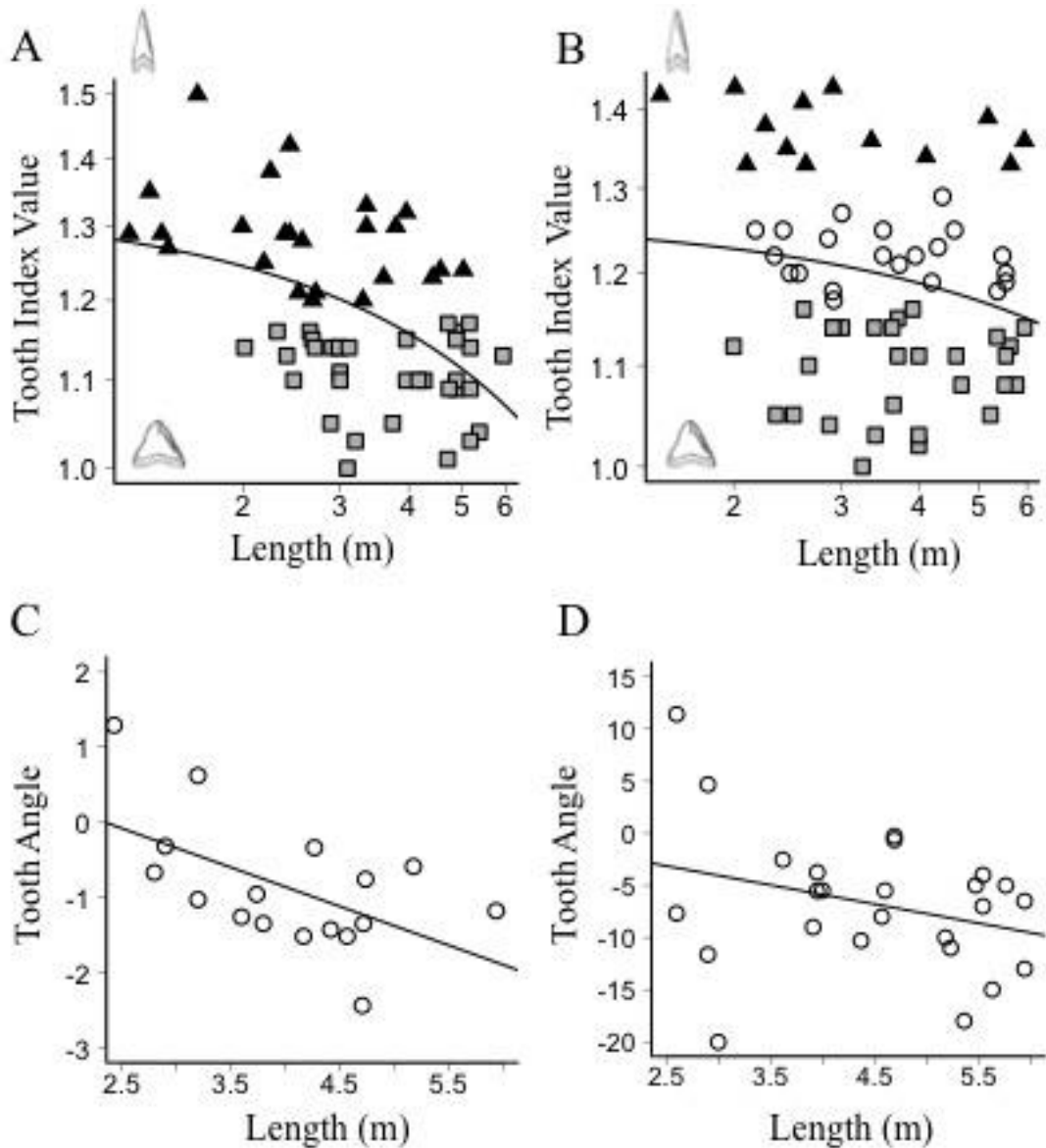


685

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, image B was taken on 24/03/2015.

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690



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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

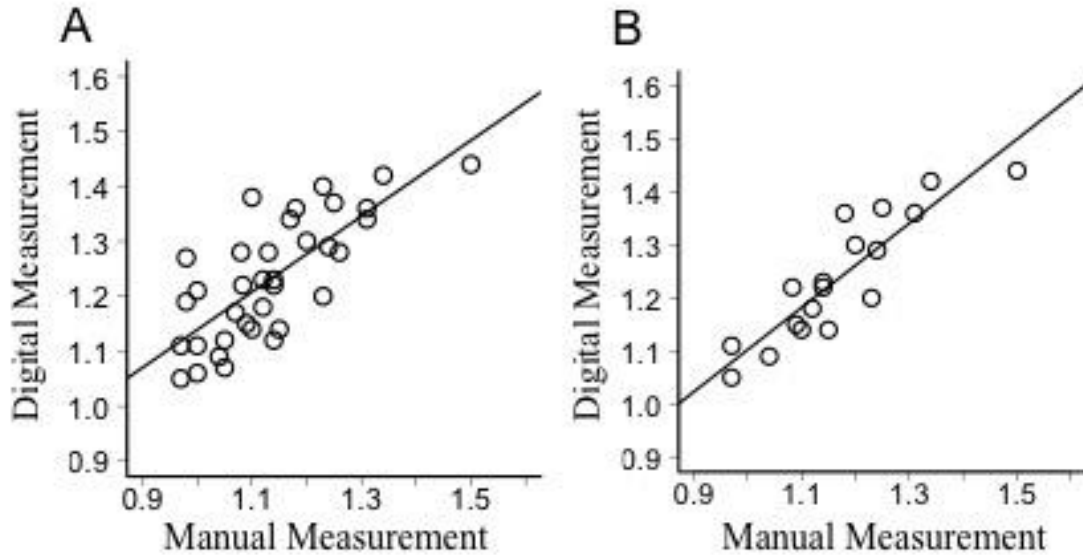
699 broad (squares). Also shown are the relationships between the angle of the P3 tooth

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

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