



# Highly conserved tooth morphology in allopatric elasmobranch populations despite contrasting diets—a case of *Triakis megalopterus* in southern Africa

M. Soekoe · M. J. Smale · W. M. Potts

Received: 19 August 2021 / Accepted: 8 June 2022 / Published online: 30 June 2022  
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

**Abstract** The role dentition plays in shaping feeding patterns has significant consequences for understanding the evolution of shark feeding. Despite this, research has generally failed to compare tooth morphology and feeding ecology in elasmobranchs. For this reason, the diet and dentition of 120 *Triakis megalopterus* were examined from three study sites in southern Africa. Teleosts and crustaceans dominated the prey categories of *T. megalopterus* in Angola, and the Eastern Cape, respectively. Individuals from the Western Cape, however, fed almost exclusively on *Jasus lalandii* (%N > 98.1). This suggests that *T. megalopterus* may employ flexible foraging tactics to exploit abundant prey. Despite substantial dietary differences by region, the dentition of *T. megalopterus* remained remarkably similar amongst populations. This species possesses an anterior plate-like dentition with posterior teeth that rise into a short but sharp cusp, consistent with a trophic generalist. It is

hypothesized that *T. megalopterus* employs a suction feeding mechanism while depressing and rotating these cusps, forming a plate-like grasping surface, thus avoiding tooth damage when feeding on crustaceans. Despite regional dental homology, a strong correlation exists between the feeding habits and dental divergence of this species throughout ontogeny. Small *T. megalopterus* have dorsoventrally flattened, more molariform lateral teeth which increase in area and width from small to large specimens, while the medial-inferior and medial-superior teeth lengthen producing a single cusp. The ontogenetic variation in dietary composition (increasing importance of cephalopods with size) appeared to be facilitated by this cusp development for grasping and/or manipulating soft-bodied prey.

**Keywords** *Triakis megalopterus* · Spotted gully · Elasmobranch · Feeding ecology · Tooth morphology · Ontogeny

M. Soekoe (✉) · W. M. Potts  
Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown 6140, South Africa  
e-mail: mich@reelsci.org

M. Soekoe  
Reel Science Co, Postnet Suite 294, Private Bag X29,  
Somerset West 7129, South Africa

M. J. Smale  
Department of Zoology, Institute for Coastal and Marine Research, Nelson Mandela University, PO Box 77000,  
Port Elizabeth, South Africa

## Introduction

While ontogenetic changes in tooth morphology (Cullen and Marshall 2019; Berio et al. 2020) may suggest that the feeding morphology of chondrichthyans could be adaptive (Moss 1977), the true extent of adaptation and selection of these structures can be better assessed by examining allopatric populations. Allopatric populations inhabit different geographic

regions (Ayala 1982) where they are subject to contrasting environmental conditions, habitat, resource availability, exploitation, and predation. These types of selective pressures have the potential to alter the phenotype of individuals by changes to basic biological parameters (Bakun 2010), fitness, and behaviour (Shiu and Borevitz 2008). Since these types of selective pressures are the driving force of natural selection and evolution (Schaffner and Sabeti 2008), feeding can have a major impact on the phenotypic and genotypic expression in populations. Unfortunately, up to now, few studies have contrasted the tooth morphology of different populations of chondrichthyans (except Lucifora et al. 2003). This presents a major gap in our understanding of the evolution of chondrichthyan feeding.

Understanding the relationships between morphology and performance is necessary to explore patterns of adaptation and selection (Wainwright 1996), specifically as the feeding morphology of an organism is the basis for its fitness and survival (Whitenack and Motta 2010). Several studies have examined the feeding morphology of teleosts (e.g. Stoner and Livingstone 1984; Eggold and Motta 1992; Ward-Campbell and Beamish 2005; Cassemiro et al. 2008; Richardson et al. 2011; Winkler et al. 2014) and it is evident that prey preference and feeding behaviour are strongly influenced by head morphology, jaw mechanics, and dentition (Wainwright and Richard 1995; Grubich et al. 2008). However, few studies have compared dentition and feeding in sharks. The feeding morphology of chondrichthyans has largely focused on the morphology of the chondrocranium and functional feeding mechanisms (Moss 1977; Maisey 1985; Waller and Baranes 1991; Motta et al. 1997, 2008; Wilga and Motta 1998; Motta and Wilga 1999; Wilga et al. 2001; Dean and Motta 2004; Ramsay and Wilga 2007), mechanics of biting, bite force and puncture/draw mechanics (Huber et al. 2005, 2006, 2009; Whitenack and Motta 2010; Ferrara et al. 2011; Habegger et al. 2012; Corn et al. 2016; Ballell and Ferrón 2021), ontogenetic shifts (Summers et al. 2004; Lowry 2005; Gutteridge and Bennett 2014; Wilga et al. 2016; Estupiñán-Montaña et al. 2019; Berio et al. 2020; Di Lorenzo et al. 2020), dental sexual dimorphism (Kajiura and Tricas 1996; Berio et al. 2020), structure and composition of teeth (Enax et al. 2012; Tian et al. 2019), tooth homology (Shimada

2002), and heterodonty (Litvinov and Laptikhovsky 2005).

There appear to be no studies comparing the tooth morphology and diets of allopatric shark populations despite the proposal by Motta and Wilga (2001) that there is an ecomorphological association between diet, feeding behaviour, and dental morphology in sharks. While it is relatively easy to study how ontogenetic shifts in diet are reflected in present-day tooth morphology, comparing the tooth morphology, of separate populations, that have different diets, throughout the species' distribution, is relatively unexplored.

The spotted gully shark, *Triakis megalopterus* (Smith 1849), is found in the temperate continental waters of the western Indian and south-eastern Atlantic oceans, in southern Angola, Namibia, and South Africa (Smale and Goosen 1999). Southern Angola is a warm-temperate zone (Potts et al. 2015) that forms part of the Namib ecoregion in the northern Benguela province (Spalding et al. 2009) where the intertidal zone is dominated by sandy beaches, sandstone rocky outcrops, and a continental shelf approximately 36 km wide (Duarte et al. 2005). In the Cunene River mouth and Baia dos Tigres, the seafloor on the continental shelf is lined by coarse sand and clay/silt ocean floors, respectively (Bianchi 1992). The South African waters differ between the Western and Eastern Provinces. The Western Cape falls within the cool-temperate zone (Potts et al. 2015) in the Agulhas province and the Agulhas Bank ecoregion (Spalding et al. 2009) where the nearshore habitat is characterized by rocky patches with large sandy sections and kelp forests (Turpie et al. 2009). The Eastern Cape falls within the warm-temperate zone (Potts et al. 2015) of the Agulhas province and Agulhas Bank ecoregion (Spalding et al. 2009) and dominated by mixed sand and rocky reef surf zones (Hutchings and Clark 2012).

To date, only one study has examined the feeding of *T. megalopterus*, in the Eastern Cape of South Africa (Smale and Goosen 1999). The authors suggested that *T. megalopterus* appears to be a nocturnal generalist predator, with a diet consisting of crustaceans, cephalopods, teleosts, and small elasmobranchs. There is currently no information on the diet of *T. megalopterus* from the rest of South Africa (i.e. Western Cape) or southern Angola.

At present, there is also no information available regarding the tooth morphology of *T. megalopterus*. Bass et al. (1975) suggested no sexual dimorphism in the tooth morphology of this species. However, the author's sample size only consisted of two males (140 and 143 cm) and three females (82–147 cm). In a figure published by the same authors, one can derive a tooth width and cusp height of approximately 2.5 mm and 2.2 mm, respectively, though the figure only represented 12 teeth, from the centre of the upper jaw, of a single male specimen (140 cm TOT). Correspondingly, Smale and Goosen (1999) only described the teeth of *T. megalopterus* as small and pointed, giving no further reference to tooth morphology.

Comparative tooth morphology has been recorded for the family Triakidae (Herman et al. 1988). These authors found the tooth morphology of *Triakis scyllium* and *Triakis semifasciata* to be similar. Both species possess relatively compressed principal cusps that lean toward the commissure; weakly developed secondary cusplets; crowns lacking true basal median apron or median uvula and fine elongate striae present on the outer and inner crown. However, *Triakis maculata* and *Triakis acutipinna* differ from the above in that they possess suberect and squatina-like principal crown; an absence of secondary cusplets; vague median apron and a basal median uvula; and strong basal costule on both outer and inner crown. Unfortunately, Herman et al. (1988) did not examine *T. megalopterus*.

Genetic analyses of *T. megalopterus*, using both mitochondrial and microsatellite DNA, revealed that the population structure of this species conforms to a transoceanic arrangement, Atlantic (Angola, Western Cape) versus Indian Ocean (Eastern Cape) populations (Soekoe 2016). The separation of the EC clade seemed to be predominantly due to the historical isolation of populations, owing to the exposure of the Agulhas Bank, during the Pleistocene and extended periods of a reduction of the reef habitat of *T. megalopterus* during the Last Glacial Maximum. This makes *T. megalopterus* an ideal species to assess possible allopatric variations in the feeding and tooth morphology of elasmobranchs.

This study aimed to gain a better understanding of the dietary composition and tooth morphology of *T. megalopterus* and to further establish if dietary differences amongst allopatric populations may influence the tooth morphology of this species. To do this, the

stomach contents and tooth morphology information from specimens in southern Angola, the Western Cape, and the Eastern Cape of South Africa were collected and analyzed.

# Material and methods

## Data collection and diet description

Sampling took place over 3 years, beginning in November 2011 and ending in February 2013. A total of 120 specimens of *T. megalopterus* (see Table 1) were collected using standard angling techniques.

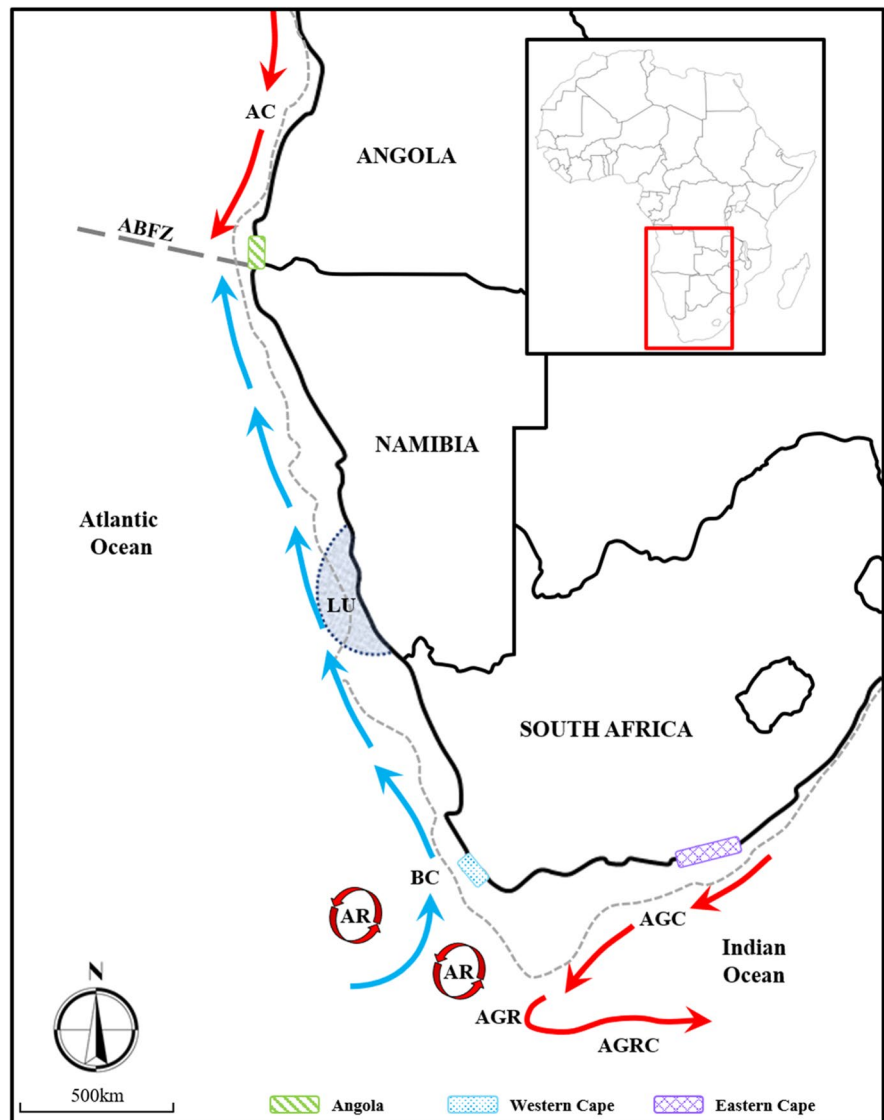
Sampling took place across three geographic locations and two oceanic regions (the southeast Atlantic and southwest Indian Ocean, see Fig. 1). The southeast Atlantic Ocean samples are from Angola (AN;  $n=43$ ) and the Western Cape (WC;  $n=33$ ). The southwest Indian Ocean samples are from the Eastern Cape (EC;  $n=46$ ).

Specimens were sacrificed by severing the spinal cord. Stomachs were removed by cutting the oesophagus and the start of the spiral valve intestine. Where possible, stomach contents were analyzed fresh. If stomachs had to be preserved for later analysis, the otoliths in the contents were removed, dried, and stored in Eppendorf tubes. Cephalopod beaks were cleaned of excess tissue and stored in 70% ethanol. The remainder of the contents was stored in 10% formalin. Freshly processed stomachs were weighed whole, cut open, and the contents removed. Bait was

**Table 1** Sample size breakdown of *Triakis megalopterus* sampled throughout southern Africa

	Angola (AN)	Western Cape (WC)	Eastern Cape (EC)
Small (<999 mm)	<b>11</b>	<b>1</b>	<b>28</b>
Females	3	0	14
Males	8	1	14
Medium (1000–1399 mm)	<b>7</b>	<b>4</b>	<b>7</b>
Females	5	4	7
Males	2	0	0
Large (> 1400 mm)	<b>25</b>	<b>28</b>	<b>9</b>
Females	21	20	7
Males	4	8	2

**Fig. 1** Map of sampling sites and oceanographic features surrounding southern Africa; AC—Angola Current, ABFZ—Angola-Benguela Frontal Zone, LU—Lüderitz Upwelling Cell, AR—Agulhas Rings, BC—Benguela Current, WAB—Western Agulhas Bank, AGR—Agulhas Retroflection, AGRC—Agulhas Return Current, AGC—Agulhas Current (adapted from Shannon et al. 2006; Coetzee et al. 2008; Von der Heyden et al. 2011)



immediately removed and excluded from subsequent analysis. Prey were sorted, enumerated, and identified to the lowest taxonomic level possible. If prey items were not whole, the numerical estimates were based on countable parts, such as claws and legs for crustaceans, otoliths for fishes, and beaks for cephalopods. Stomach contents were sieved to drain excess fluid and weighed to the nearest 0.01 g. Unidentifiable matter was weighed separately. All prey items were also measured. Total length (TL) for teleosts, carapace width (CW) and length (CL) for crustaceans, and mantle width (MW) and length (ML) for cephalopods, henceforth termed as “prey size”.

#### Diet quantification

Prey items were quantified using a range of common indices (Hyslop 1980). These included percent frequency of occurrence (%O), which is the number of stomachs containing a specific prey item divided by the total number of stomachs containing prey. This index reflects the proportion of predators utilizing a prey resource, or the homogeneity of the hunting method (Cortés 1997) and was calculated as:

$$%O_i = \frac{J_i}{P} \times 100$$

where:

$J_i$  = number of fish containing prey item  $i$ .

$P$  = number of fish with food in their stomach.

Percent abundance or number (%N) is the total number of prey items within each category divided by the total number of individual prey items. Although this index generally provides information on the feeding behaviour of a population (Zacharia 2004), no allowance is made for the size differences between food items. Percent number (%N) was calculated as:

$$\%N_i = \frac{N_i}{\sum_{i=1}^Q N_i}$$

where:

$N_i$  = number of food category  $i$ .

The percent gravimetric index (%W) is the weight of a prey category divided by the total weight of all prey items. This method generally provides information on the nutritional importance of the different dietary items (Zacharia 2004); however, digestion makes this method difficult, as prey items are not always whole. Percentage weight was calculated as:

$$\%W_i = \frac{W_i}{\sum_{i=1}^Q W_i}$$

where:

$W_i$  = number of food category  $i$ .

Each of these three measures (%O, %N, and %W) provides a different insight into the feeding habits of the organism in question (Cortés 1997). When considered separately, these three indices reflect a bias toward highly abundant prey (%O), small/digested prey (%N), or infrequent, large, non-digested prey (%W). Factors such as prey type, meal size, and evacuation rates (Bush and Holland 2002) may also obscure prey importance.

Thus, it is suggested that a compound index of all the above indices be used, the most popular of these being the index of relative prey importance (IRI; Pinkas et al. 1971):

$$IRI_i = (\%N_i + \%W_i)\%O_i$$

The IRI value was converted into a percentage, for ease of comparison among food types, using the following equation (Cortés 1997):

$$\%IRI = \frac{100IRI_i}{\sum_{i=1}^n IRI_i}$$

where:

$n$  = total number of food categories at a given taxonomic level.

There is, however, much controversy regarding the accuracy of these types of compound indices. Not only do they use average values from different measures, they also combine the variation and errors associated with them (Hyslop 1980). Thus, %W, %O, and %IRI (see Tables 5 and 6 in the Appendix) were solely included as supplementary material to enable direct comparison with other studies. For this study, %N is presented to be directly comparable to the previous work by Smale and Goosen (1999).

### Diet ontogenetic shift

Sharks collected were placed into three size classes: small (<999 mm), medium (1000–1399 mm), and large (>1400 mm) following Smale and Goosen (1999). The %N, %W, %O, and %IRI for each prey category and size class were calculated. The %N data were standardized, square root transformed, and subjected to Bray–Curtis similarity analyses (Bray and Curtis 1957), group averaged clustering, and multidimensional scaling (MDS; Clarke and Warwick 2001) ordination using Primer v6. The MDS was included as the data are not forced into a hierarchy as with the cluster analysis; thus, MDS is less constraining (Shepard 1980). For the MDS, minimum stress of 0.01 and 25 restarts were used and agglomerative cluster analysis based on the Bray–Curtis similarity coefficients was calculated. Significant differences of size classes were tested using the one-way analysis of similarity (ANOSIM) in Primer v6. Differences between sites were considered significant at  $p < 0.05$ . The extent of significant differences was determined by the  $R$ -statistic (Clarke and Green 1988), which ranges between zero (no similarity) and one (100% similarity); thus, the  $R$ -value indicates no similarity and 100% resemblance respectively. All dietary data were analyzed at the level of family.

### Diet seasonality

Sampling in AN only took place in summer (November/December 2011) and winter (June/July 2012). For



this reason, and direct comparison, only data from summer (December–February) and winter (March–August) samples were included in the seasonal analysis. The %N, %W, %O, and %IRI for each prey category, in each season (summer and winter), were calculated. Data for %N was standardized, square root transformed, and subjected to Bray–Curtis similarity analyses (Bray and Curtis 1957), group averaged clustering, and two-dimensional non-metric multidimensional scaling (MDS; Clarke and Warwick 2001) ordination. Independent *t*-tests were used to test the seasonal differences within each locality.

### Tooth morphology

All jaws ( $n=120$ ) were placed in hot water ( $\sim 60$ – $90$  °C) for approximately 5 min or until the connective tissue was soft. Teeth were extracted, from four positions, using forceps, from only the right-hand side of each jaw. The tooth form of individuals varied according to the jaw quadrants. Thus, three sequential teeth were removed from the exact same location, for each individual (Fig. 2).

The four different sets of teeth removed include the lateral-superior (Fig. 3a), medial-superior (Fig. 3b), lateral-inferior (Fig. 3c), and medial-inferior (Fig. 3d), of each specimen.

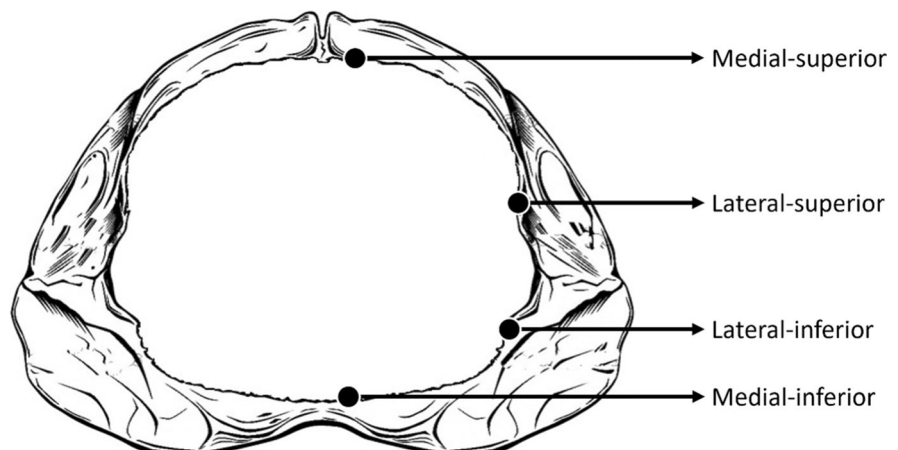
To minimize bias due to polyphyodonty, teeth were removed from the third lingual row to avoid underdeveloped or worn/damaged teeth. This area was chosen as it was evident that the teeth were fully developed, yet still protected by a thin covering of connective tissue. The most pristine (no damage from feeding or removal) tooth from each of the three duplicates was selected

and fixed onto microscope slides. The labial face of the teeth was photographed using a Leica DMC2900 microscope camera at a magnification of  $40\times$ . Photos were imported into SigmaScan Pro 5 software where four landmarks: the maximum mesial width (LM1); maximum height (LM2); maximum distal width (LM3); and crown tip (LM4) were marked. The length (L, distance from LM4 to LM2) and width (W, distance from LM1 to LM3) were measured (Fig. 3e). Landmarks were connected with straight lines to yield a box truss (Fig. 3f) measuring four diagonal length measurements (D1–D4) and four angles (A1–A4). To add quantitative measurements of shape, two of SigmaScan's built-in parameters were also incorporated into the analysis. Shape factor (S) calculates how circular an object is where a straight line has a shape factor approaching zero, and a perfect circle has a shape factor of one. Compactness (C) is a measure of elongation, where values are larger for objects of elongated shape, and  $4\pi$  ( $\approx 12.57$ ) for a perfect circle (Matusiewicz et al. 2007).

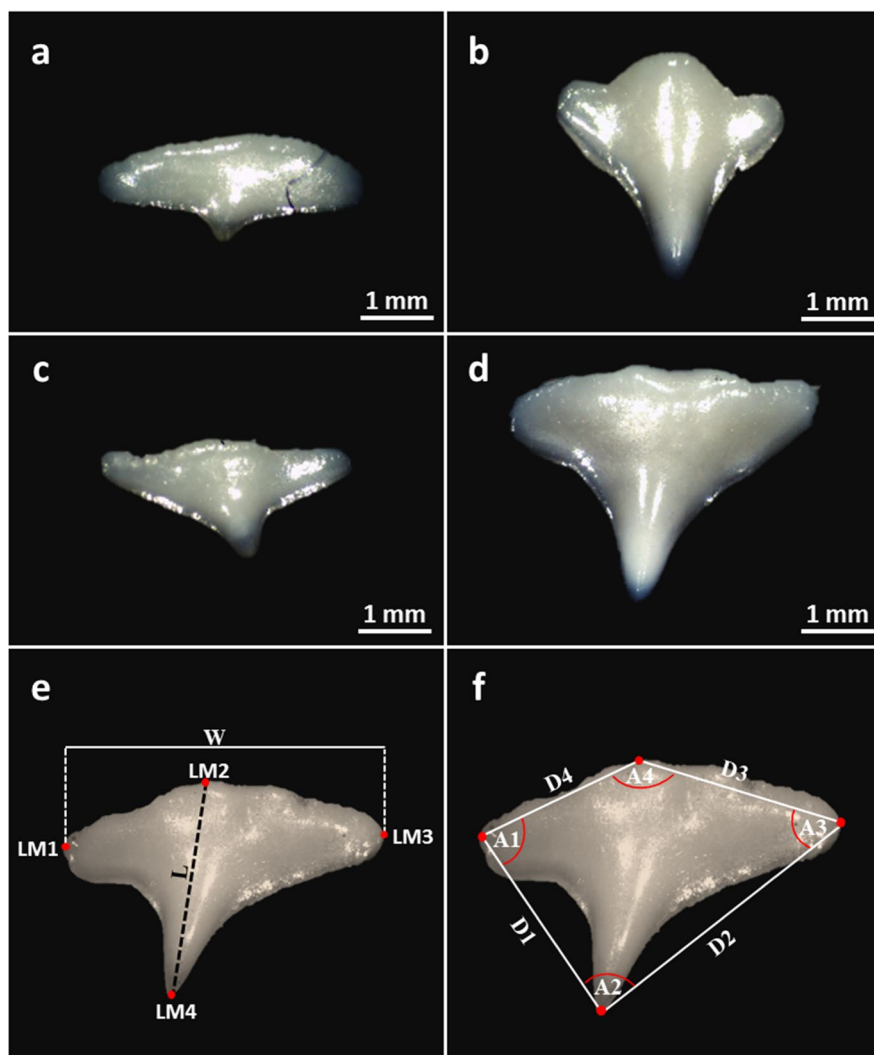
### Tooth morphology transformation of absolute measurements

Since allometric shifts in growth are common amongst elasmobranch fishes (Lowry 2005; Frisk and Miller 2006; Lowry et al. 2007; Reiss and Bonnan 2010; Irschick and Hammerschlag 2015), absolute morphological measurements were transformed to size-independent measurements before the tooth morphology analysis. Although a popular choice when it comes to size correction in data, the use of ratios has been known to result in false approximations of shape differences (Brookstein et al. 1985), to be indifferent

**Fig. 2** Front view of a jaw showing the four positions where consecutive teeth were extracted



**Fig. 3** Labial view of *T. megalopterus* teeth depicting (a) lateral-superior, (b) medial-superior, (c) lateral-inferior, (d) medial-inferior, and (e, f) the four landmarks and associated box truss used to infer morphological differences amongst size and locations; LM1—maximum mesial width, LM2—maximum height, LM3—maximum distal width, LM4—crown tip, W—width, L—length, A1–A4—angle measurements, D1–D4—diagonal measurements



to allometric variances (Parsons et al. 2003), and to reduce statistical power (Atchley et al. 1976). For this reason, all morphometric characters were adjusted to an overall mean total length of = 1205 mm according to the following equation (Simon et al. 2010):

$$Y_{ij}' = \log Y_{ij} - b_j (\log TOT_i - \log \overline{TOT})$$

where:

$Y_{ij}'$  = is the adjusted value of character  $j$  for individual  $i$ .

$Y_{ij}$  = is the original value.

$b_j$  = is the pooled regression coefficient of  $\log Y$  on  $\log TOT$ .

$TOT_i$  = is the total length of individual  $i$ .

$\overline{TOT}$  = overall mean total length.

Because all morphometric measurements were adjusted to an overall mean total length, the effect of size differences between sexes should have been removed. Therefore, combined sex data were used for the initial analyses. However, when significant ( $p < 0.05$ ) differences were found between populations, separate ANOVAs were run for sex, using only the significantly different variables, to ensure the differences were not sex-based. If significant differences

were found between sexes within a comparison, paired sample *t*-tests were run to determine exactly where the significance lay.

### Tooth morphology data analysis

Variations amongst populations were tested using ANOVA after a Levene's median test confirmed equal/unequal variance. If variances were equal ( $p > 0.05$ ), Fisher's least significant difference (LSD) procedure was used to identify homogenous groups. If variances were not equal ( $p < 0.05$ ), data were analyzed using the Games-Howell post hoc test. All statistical analyses were done using Statistica v10 (StatSoft 2011) and IBM SPSS Statistics v28 (IBM Corporation 2021). Variables were considered to be significantly different if  $p < 0.05$ .

### Tooth shape analysis

To assess ontogenetic change in shape, SHAPE 1.3 (Iwata and Ukai 2001) was used to evaluate and illustrate the growth of the teeth of *T. megalopterus* from EC as this population had the best distribution of individuals in each size class. Photos of all teeth were loaded into the SHAPE software, no measurements were manually taken, and no data was entered. SHAPE software is made up of four different applications. ChainCoder converts the uploaded images into black and white before extracting and delineating the information into chain code (Freeman 1974). Chc2Nef uses the chain code data to calculate the elliptic Fourier descriptors (EFD; Kuhl and Giardina 1982) from which a principal component analysis (PCA) is performed within PrinComp. Thereafter, the shape variations of the principal components are illustrated (Furuta et al. 1995).

## Results

Of the 120 stomachs that were examined, nine were empty. Only one small (470 mm) individual was caught in WC and this one had an empty stomach. For this reason, small sharks in WC could not be included in the analyses.

A total of 19 prey species belonging to seven families of teleost, eight families of crustaceans, and three mollusc families were recorded (Table 2). This may be an underestimate because there was a large amount of digested and unidentifiable prey in the stomachs of

AN and EC specimens. Miscellaneous items such as a small black stone and a piece of aquatic plant (Phaeophyceae) were considered accidental ingestions, thus not included in the discussion.

### Ontogenetic shift

There were significant differences in the mean size of teleost (ANOVA,  $F(2,27)=29.12$ ,  $p < 0.01$ ) and crustacean (ANOVA,  $F(2,27)=12.44$ ,  $p < 0.01$ ) in the diet of small, medium, and large *T. megalopterus* (Fig. 4). A Tukey post hoc test revealed that teleosts in the diet of the smaller size class were significantly smaller than in the medium ( $p < 0.01$ ) and large ( $p < 0.01$ ) size classes. Crustaceans were significantly larger in the large size class when compared with the small size class (Tukey post hoc test,  $p < 0.01$ ). There was no significant difference in the size of the molluscan prey between the size classes (ANOVA,  $F(2,27)=0.68$ ,  $p=0.54$ ).

Prey diversity for all size classes (Table 1) increased from WC to EC and AN with three, seven, and 17 species present, respectively. Besides one *Octopus vulgaris* beak, no miscellaneous items or unidentifiable material was found in WC. The highest quantities of unidentifiable material were in EC (%N=6.7 to 7.1) followed by AN (%N=3.6 to 6.1).

Crustaceans were present in the diet of *T. megalopterus* from all size classes and at all locations, although they were most prominent in WC (%N=98.1 to 100) and EC (%N=53.3 to 86.7) populations. The Cape rock lobster (*Jasus lalandii*) dominated the diet of WC individuals (%N>98.1) with no teleosts observed. Besides *J. lalandii*, only one species/specimen of crustacean (*Plagusia chabrui*, %N=1.9) and mollusc (*O. vulgaris*, %N=1.9) were identified.

Crustaceans were the most prominent prey in the diet of EC specimens of all sizes although the %N of crustaceans ingested decreased from small (%N=86.7) to large (%N=46.7) specimens. Interestingly, only large sharks (EC, %N=13.3) fed on the bigger and noxious *Galeichthys feliceps*. In conjunction with a decrease in crustaceans with increasing size class, there was an increase in the ingestion of molluscs (medium, %N=14.3 and large, %N=13.3) which comprised *O. vulgaris* and *Haliotis midae* (Table 1).

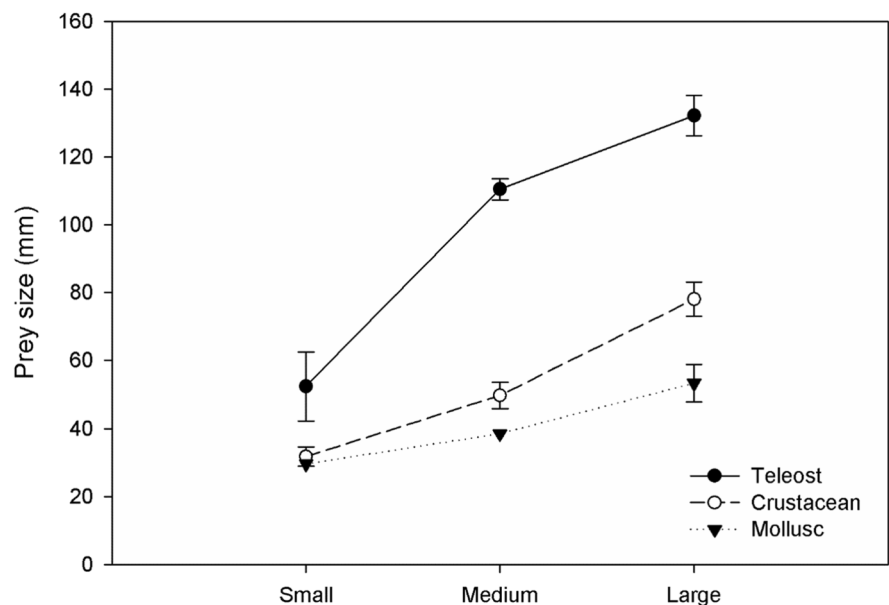


**Table 2** Percent abundance or number (%N) for small, medium, and large *T. megalopterus* from Western Cape, Eastern Cape, and Angola

	Western Cape		Eastern Cape			Angola		
	Medium	Large	Small	Medium	Large	Small	Medium	Large
Teleost					20.00	70.73	67.86	49.49
Ariidae								
<i>Galeichthys</i> sp.					13.33			16.16
Sparidae								
<i>Diplodus sargus capensis</i>								3.03
Clupeidae								
<i>Sardinella aurita</i>						14.63	7.14	7.07
Bleniidae								
<i>Parablennius pili-cornis</i>						17.07		
Sciaenidae								
<i>Atractoscion aequidens</i>								1.01
Haemulidae								
<i>Pomadasys olivaceum</i>								1.01
Ammodytidae								
<i>Ammodytes</i> sp.						2.44	3.57	1.01
Unidentified Teleost					6.67	36.59	57.14	20.20
Elasmobranchs								2.02
Squalidae								
<i>Squalus</i> sp.								2.02
Crustaceans	100.00	98.11	86.67	71.43	53.33	17.07	21.43	15.15
Polybiidae								
<i>Ovalipes trimaculatus</i>							3.57	4.04
Squillidae								
<i>Pterygosquilla</i> sp.								2.02
Cancridae								
<i>Metacarcinus magister</i>						4.88	14.29	1.01
Scyllaridae								
<i>Scyllarides elisabethae</i>					6.67			
Caridea			4.44				3.57	1.01
Xanthidae								
<i>Atergatis roseus</i>								2.02
Plagusiidae								
<i>Plagusia chabrus</i>		1.89	73.33	64.29	13.33	7.32		
Palinuridae								
<i>Jasus lalandii</i>	100.00	96.23	2.22		20.00			1.01
Tetraclitidae								
<i>Tetraclita serrata</i>				7.14	6.67			1.01
Unidentified Crustacean			6.67		6.67	4.88		3.03
Molluscs		1.89		14.29	13.33	7.32	7.14	27.27
Cephalopods								
Octopodidae								

**Table 2** (continued)

	Western Cape		Eastern Cape			Angola		
	Medium	Large	Small	Medium	Large	Small	Medium	Large
<i>Octopus vulgaris</i>		1.89			6.67	7.32	3.57	23.23
Loliginidae								
<i>Loligo vulgaris reynaudii</i>							3.57	3.03
Gastropods								
Haliotidae								
<i>Haliotis midae</i>				14.29	6.67			
Muricidae								
<i>Urosalpinx subsinuatus</i>								1.01
Miscellaneous			13.33	14.29	13.33	4.88	3.57	6.06
Unidentified material			6.67	7.14	6.67	4.88	3.57	6.06
Black Stone			2.22					
Phaeophyceae			4.44	7.14	6.67			

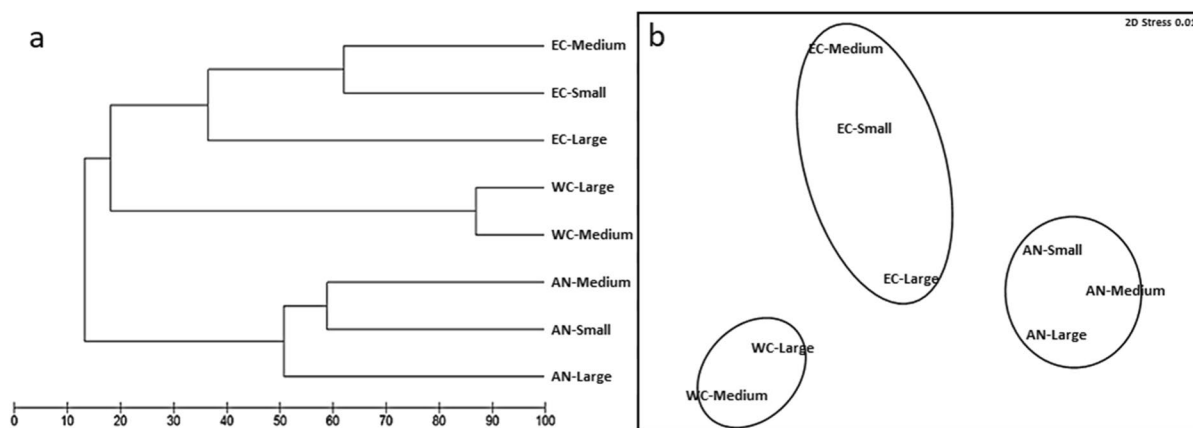
**Fig. 4** Relation between predator size class and prey size (teleost—TL, crustacean—CW, and mollusc—MW); TL—total length, CW—carapace width, ML—mantle length, error bars represent standard error

In AN, teleosts were commonly observed in the stomachs of all size classes although their importance decreased from small (%N=17.1) to large (%N=15.2) individuals. Correspondingly, the importance of molluscs increased from small (%N=7.3) to large (%N=27.3) specimens. Molluscs comprised both the common octopus (*O. vulgaris*) and the Cape Hope squid (*Loligo vulgaris reynaudii*). Only large

sharks from AN (%N=16.2) and EC (%N=13.3) fed on *G. feliceps*.

#### Regional differences

Dietary differences were clear in terms of regions and size as depicted in the Bray–Curtis similarity matrix-based cluster analysis (Fig. 5a) and MDS plot



**Fig. 5** Size class analysis for the %N of prey family similarity displaying the (a) Bray–Curtis similarity matrix-based cluster analysis and (b) a two-dimensional representation of the MDS

plot depicting a 30% resemblance level; %N—percent number, AN—Angola, EC—Eastern Cape, WC—Western Cape, MDS—multidimensional scaling

(Fig. 5b) using %N. The diet of *T. megalopterus* was significantly different in all three populations and their size classes (ANOSIM,  $R = -0.32$ ,  $p = 0.94$ ).

Cluster analysis of %N indicated an 18.2% similarity between WC and EC and 13.3% similarity between the South African and AN populations. The highest similarity was in WC-medium and WC-large (87.0%), where both size classes predominantly fed on *J. lalandii*. In EC, the diet of small and medium specimens was 62.1% similar with large quantities of *P. chabrus* included in the diet of both size classes. The diets of EC-large specimens, however, were only 36.5% similar to the combined small and medium classes, indicative of the diet expansion of large individuals to include teleosts, *O. vulgaris* and *H. midae*. The diets of AN specimens were comparable in all size classes with a similarity of AN-large (50.8%) compared to small and medium (59.0%), as all size classes in this population preyed upon all prey categories with only the prey diversity increasing.

Additional cluster analyses, where the three size classes were compared amongst locations, revealed that small specimens from EC and AN (no data for WC-small was available) showed a 24.1% similarity. Though both populations of small specimens fed on Plagusiidae, the quantity thereof was tenfold larger in EC (%N=73.3) than in AN (%N=7.3). The dominant diet of individuals from AN, WC, and EC was unidentified teleosts (%N=57.1), Palinuridae (%N=100.0), and Plagusiidae (%N=64.3), respectively, and there ANOSIM found no (0%)

similarity in the diet between these populations. Large individuals from AN and EC grouped with 40.7%, whereas both populations only showed a 24.4% similarity with WC.

#### Diet seasonality

*Jasus lalandii* dominated the diet of individuals in the WC throughout the year, with no apparent seasonal pattern (Table 3). In contrast, seasonal changes were evident in EC and AN. In EC, no teleosts or molluscs were recorded in winter. Crustacean ingestion, particularly that of *P. chabrus*, increased from summer (%N=51.1) to winter (%N=72.4). Caridea (%N=6.9) were only recorded in winter samples. Several prey items including *J. lalandii* (%N=8.9), *Galeichthys* sp. (%N=4.4), *Scyllarides elisabethae* (%N=2.2), *O. vulgaris* (%N=2.2), and *H. midae* (%N=6.7) were only present in the diet of EC *T. megalopterus* in summer.

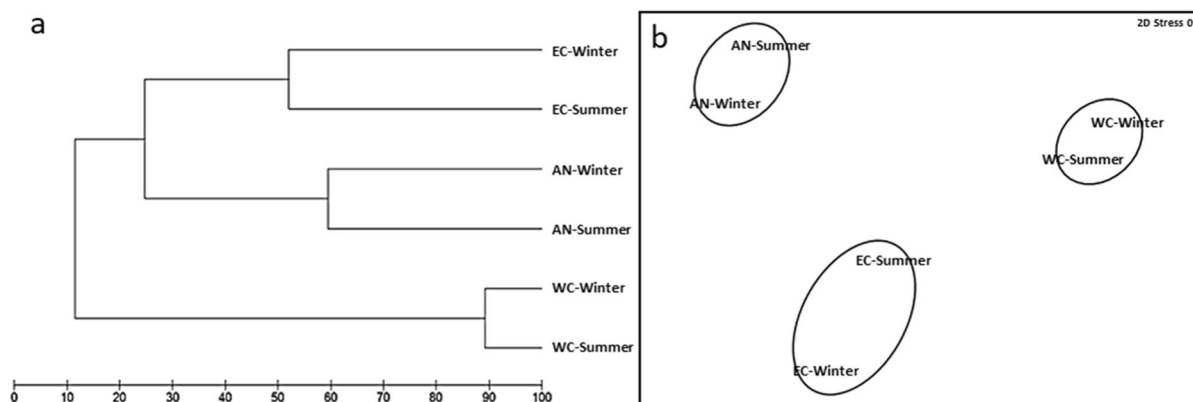
In AN, *T. megalopterus* fed on teleosts, crustaceans, and molluscs in similar quantities in both summer and winter. The largest change in diet of AN specimens was a %N=7.9 increase in mollusc intake during summer. Unlike in EC, *Galeichthys* sp. were present in AN during both seasons, although their numbers doubled in summer (%N=11.1). Both *Parablennius pilicornis* (%N=13.5) and *Ammodytes* sp. (%N=5.8) were only present in summer diets of *T. megalopterus*, while *Atractoscion aequidens* (%N=0.9), *Diplodus capensis* (%N=2.6), and

**Table 3** Percent abundance or number (%N) separated by summer and winter from individuals of the Western Cape, Eastern Cape, and Angola

	Western Cape		Eastern Cape		Angola	
	Summer	Winter	Summer	Winter	Summer	Winter
Teleost			<b>4.44</b>		<b>57.26</b>	<b>57.69</b>
Ariidae						
<i>Galeichthys</i> sp.			2.22		11.11	5.77
Sparidae						
<i>Diplodus sargus capensis</i>					2.56	
Clupeidae						
<i>Sardinella aurita</i>					6.84	13.46
Bleniidae						
<i>Parablennius pilicornis</i>						13.46
Sciaenidae						
<i>Atractoscion aequidens</i>					0.85	
Haemulidae						
<i>Pomadasys olivaceum</i>					0.85	
Ammodytidae						
<i>Ammodytes</i> sp.						5.77
Unidentified Teleost			2.22		35.04	19.23
Elasmobranchs						<b>3.85</b>
Squalidae						
<i>Squalus</i> sp.						3.85
Crustaceans	<b>100.00</b>	<b>100.00</b>	<b>73.33</b>	<b>86.21</b>	<b>15.38</b>	<b>21.15</b>
Polybiidae						
<i>Ovalipes trimaculatus</i>					0.85	7.69
Squillidae						
<i>Pterygosquilla</i> sp.					1.71	
Cancridae						
<i>Metacarcinus magister</i>					5.13	1.92
Scyllaridae						
<i>Scyllarides elisabethae</i>			2.22			
Caridea				6.90	1.71	
Xanthidae						
<i>Atergatis roseus</i>					1.71	
Plagusiidae						
<i>Plagusia chabrus</i>	4.55		51.11	72.41	1.71	3.85
Palinuridae						
<i>Jasus lalandii</i>	95.45	100.00	8.89		0.85	
Tetraclitidae						
<i>Tetraclita serrata</i>			8.89			1.92
Unidentified Crustacean			2.22	6.90	1.71	5.77
Molluscs			<b>8.89</b>		<b>21.37</b>	<b>13.46</b>
Cephalopods						
Octopodidae						
<i>Octopus vulgaris</i>			2.22		18.80	9.62
Loliginidae						
<i>Loligo vulgaris reynaudii</i>					2.56	1.92

**Table 3** (continued)

	Western Cape		Eastern Cape		Angola	
	Summer	Winter	Summer	Winter	Summer	Winter
Gastropods						
Haliotidae						
<i>Haliotis midae</i>			6.67			
Muricidae						
<i>Urosalpinx subsinuatus</i>						1.92
Miscellaneous			<b>13.33</b>	<b>13.79</b>	<b>5.98</b>	<b>3.85</b>
Unidentified material			8.89	3.45	5.98	3.85
Black Stone				3.45		
Phaeophyceae			4.44	6.90		

**Fig. 6** Seasonal analysis for %N of prey family similarity displaying the (a) Bray–Curtis similarity matrix-based cluster analysis and (b) a two-dimensional representation of the MDS

plot depicting a resemblance level of 25%; %N—percent number, AN—Angola, EC—Eastern Cape, WC—Western Cape, MDS—multidimensional scaling

*Pomadasys olivaceum* (%N=0.9) were only present in the winter diets of AN specimens.

Seasonal differences in the feeding of *T. megalopterus* showed significant separation of all populations and seasons (ANOSIM,  $R = -0.4$ ,  $p = 1.0$ ). The seasonal cluster analysis (Fig. 6a) showed the similarity of summer and winter diets of *T. megalopterus* were 52.0%, 59.5%, and 89.2% for EC, AN, and WC, respectively. The MDS plot (Fig. 6b) clearly showed a split between all three populations at the 25% resemblance level. This, as with the ontogeny, showed the differences to be more related to location rather than season.

Only one specimen of *T. megalopterus* was captured in the WC during winter and its stomach contents, which comprised *J. lalandii*, were like those captured in spring ( $n = 12$ ) and autumn ( $n = 7$ ). Therefore, although limited in data availability, it is

unlikely that the diet during winter would change in this region. Besides *J. lalandii*, only one *P. chabrus* was present in the stomach contents of a summer-sampled specimen and one *O. vulgaris* in a spring-sampled specimen. Unfortunately, spring samples were not included in the analysis. The largest seasonal change was in EC, where no teleosts or molluscs were found in the winter diet.

#### Tooth morphology

The tooth morphology analysis revealed comparable results for all four teeth from the three populations (Table 4). Of the 52 variables analyzed, only three variables showed significant ( $p < 0.05$ ) differences, all between AN and EC. This indicates that the medial-superior teeth of AN specimens are shorter in length (L) and both the medial-superior



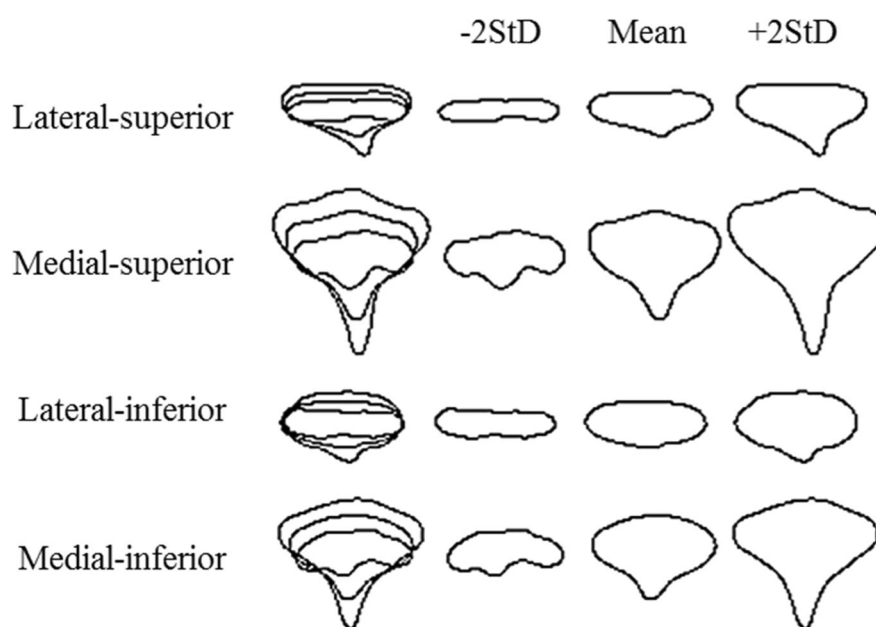
**Table 4** Results of ANOVAs of tooth data for *T. megalopterus* from Angola (AN), Western Cape (WC), and Eastern Cape (EC); *F*—Levene's *F* statistic, *p*—Levene's significance, \**p* < 0.05 indicating unequal variance, \*\*significance at the 5% nominal level, size-independent measurements given in millimeters except for the angles (A1–A4) given in degrees

	Levene's test for equality of variance		Least significant difference (LSD)/ Games-Howell ( <i>p</i> )			Population means (size-independent measurements)		
	<i>F</i>	<i>p</i>	AN-EC	AN-WC	EC-WC	AN	EC	WC
<b>Lateral-superior</b>								
W	0.483	0.619	0.188	0.491	0.559	0.657	0.705	0.739
L	0.567	0.570	0.184	0.131	0.684	−0.396	−0.231	−0.267
A1	5.844	<b>0.004*</b>	0.779	0.831	0.980	4.763	4.813	4.820
A2	1.125	0.330	0.508	0.725	0.776	3.790	3.757	3.734
A3	2.682	0.075	0.999	0.713	0.655	5.030	5.022	5.030
A4	4.299	<b>0.017*</b>	0.862	0.123	0.094	4.082	4.407	4.114
D1	0.929	0.399	0.132	0.357	0.611	0.155	0.234	0.270
D2	1.223	0.300	0.226	0.342	0.880	−0.031	0.041	0.051
D3	1.316	0.274	0.085	0.134	0.966	−0.004	0.114	0.117
D4	0.689	0.505	0.552	0.606	0.210	−0.005	−0.043	0.034
S	1.925	0.153	0.696	0.237	0.311	−0.886	−0.815	−0.865
C	1.808	0.171	0.699	0.225	0.291	3.417	3.345	3.397
<b>Medial-superior</b>								
W	1.775	0.176	0.213	0.867	0.257	0.778	0.786	0.829
L	0.027	0.973	<b>0.043**</b>	0.806	0.061	0.611	0.627	0.727
A1	3.443	<b>0.037*</b>	0.141	0.449	0.503	4.354	4.320	4.294
A2	1.766	0.178	0.197	0.753	0.314	4.316	4.330	4.369
A3	1.646	0.199	0.196	0.698	0.357	4.890	4.879	4.858
A4	6.696	<b>0.002*</b>	0.699	0.914	0.404	4.464	4.516	4.347
D1	0.351	0.705	0.165	0.830	0.082	0.614	0.604	0.676
D2	0.147	0.863	0.076	0.685	0.157	0.548	0.571	0.636
D3	1.051	0.355	<b>0.008**</b>	0.158	0.228	0.143	0.209	0.255
D4	0.330	0.720	0.710	0.361	0.135	0.207	0.160	0.223
S	0.353	0.703	0.120	0.400	0.510	−0.473	−0.455	−0.443
C	0.426	0.654	0.137	0.456	0.483	3.003	2.987	2.975
<b>Lateral-inferior</b>								
W	0.273	0.762	0.586	0.433	0.128	0.637	0.682	0.608
L	3.434	<b>0.037*</b>	0.345	0.703	0.143	−0.347	−0.316	−0.416
A1	3.813	<b>0.026*</b>	0.439	0.381	0.817	4.879	4.912	4.905
A2	1.365	0.261	0.146	0.319	0.720	3.750	3.685	3.665
A3	2.198	0.118	0.176	0.677	0.342	4.939	4.947	4.963
A4	2.153	0.123	0.173	0.805	0.080	4.515	4.558	4.307
D1	0.689	0.505	0.853	0.200	0.082	0.001	0.077	−0.008
D2	0.901	0.410	0.490	0.599	0.172	0.046	0.078	0.008
D3	0.230	0.795	0.923	0.184	0.089	−0.005	0.078	−0.010
D4	0.596	0.553	0.202	0.897	0.129	0.024	0.032	−0.050
S	3.933	<b>0.024*</b>	0.414	0.763	0.609	−0.804	−0.818	−0.839
C	3.540	<b>0.034*</b>	0.414	0.779	0.591	3.335	3.349	3.370
<b>Medial-inferior</b>								
W	0.320	0.727	0.381	0.894	0.273	1.011	1.005	1.042
L	0.989	0.376	0.064	0.398	0.327	0.706	0.752	0.797
A1	1.610	0.206	0.737	0.979	0.744	4.417	4.416	4.408
A2	2.248	0.112	0.086	0.193	0.783	4.168	4.229	4.240

**Table 4** (continued)

	Levene's test for equality of variance		Least significant difference (LSD)/ Games-Howell ( $p$ )			Population means (size-independent measurements)		
	$F$	$p$	AN-EC	AN-WC	EC-WC	AN	EC	WC
A3	0.139	0.870	0.461	0.868	0.556	4.898	4.894	4.883
A4	1.582	0.212	0.170	0.600	0.399	4.622	4.526	4.397
D1	0.444	0.643	0.063	0.266	0.509	0.635	0.686	0.711
D2	0.241	0.787	0.607	0.927	0.509	0.775	0.770	0.802
D3	4.343	<b>0.016*</b>	0.651	0.054	0.065	0.438	0.343	0.419
D4	0.038	0.963	<b>0.041**</b>	0.092	0.868	0.359	0.449	0.457
S	2.676	0.075	0.660	0.643	0.304	−0.462	−0.471	−0.455
C	3.189	<b>0.047*</b>	0.705	0.623	0.319	2.991	3.001	2.985

**Fig. 7** Shape variation of *Triakis megalopterus* teeth from Eastern Cape. Super-imposed outlines in the first column represent all the shape variations per tooth type. Each column shows the case where the score takes  $-2\text{StD}$  (standard deviation), mean, or  $+2\text{StD}$ , as labelled



(D3) and medial-inferior (D4) teeth from AN have a narrower base. These three variables showed no significant ( $p > 0.05$ ) differences between males and females for the medial-superior L (ANOVA,  $F(46.99) = 0.45$ ,  $p = 0.77$ ), medial-superior D3 (ANOVA,  $F(46.29) = 0.06$ ,  $p = 0.29$ ), and medial-inferior D4 (ANOVA,  $F(54.03) = 0.62$ ,  $p = 0.77$ ).

#### Ontogenetic shifts on tooth shape

As only three tooth morphology variables showed significant differences between AN and EC, the shape analysis (Fig. 7) was only performed using the EC sample subset as this population had the best

distribution of individuals in each size class. The shape analysis showed the teeth of *T. megalopterus* increased in length with ontogeny. Small specimens had dorsoventrally flattened and more molariform lateral teeth, while the teeth of larger specimens were broader at their base and lengthened to produce a single cusp. This cusp was more evident in the teeth positioned in the medial parts of the jaw.

#### Discussion

Much like *T. semifasciata* (Ackerman 1971; Talent 1976; Kao 2000), *T. megalopterus* is a trophic

generalist that feeds in the benthic and pelagic environments on a wide range of prey including teleosts, crustaceans, and molluscs. Generally, the diets of *T. megalopterus* from AN and EC comprised teleosts, crustaceans, and molluscs. In the WC, however, this species preys almost exclusively on Cape rock lobster (*J. lalandii*).

Geographical differences in shark diets have been observed for many species, including *Negaprion brevirostris* (Cortés and Gruber 1990), *Prionace glauca* (McCord and Campana 2003), *Mustelus manazo* (Yamaguchi and Taniuchi 2000), *R. terraenovae* (Bethea et al. 2006), *C. plumbeus* (Ellis and Musick 2006), and *G. cuvier* (Dicken et al. 2017). These studies have highlighted various factors contributing to this trend, factors that all emphasize differences in the living biotic environment (Yamaguchi and Taniuchi 2000), e.g. habitat differences (Bethea et al. 2007), relative prey abundance (McCord and Campana 2003), and increased species richness toward the tropics (Rohde 2014). According to Reusch (2014), the ocean environment is partitioned by latitudinal and longitudinal gradients caused by combinations of numerous abiotic factors (i.e. light, turbulence, oxygen, pressure, temperature) that are affected by seasons and the diurnal cycle. All these factors will affect species diversity and thus prey availability in different ecosystems. Because AN is closest to the equator and WC is furthest away, this pattern of species richness conforms to the latitudinal diversity gradient theory (Roy et al. 1998; Mittelbach et al. 2007; Ekau and Verheye 2010; Sanders 2014) and the related temperature hypothesis (Tittensor et al. 2010) which suggests that the slow metabolic rates associated with lower temperatures lead to lower speciation rates and thus lower species diversity (Rohde 2014). With mean annual sea surface temperatures of 20.4 °C for AN (Richardson 2010), 18.0 °C for EC (Karczmarski et al. 1999), and 16.5 °C for WC (Dufois and Rouault 2012), these results also support the temperature hypothesis. Furthermore, Angola has a poorly developed economy and as a result, the absolute biodiversity loss has been relatively small in comparison to its natural resource base (Biggs et al. 2008). Though both the WC and EC sample sites are situated on the Agulhas bank (the western and eastern sides, respectively), EC had double the prey diversity of WC. Many taxa show a trend of increasing species richness from the west to east coasts of South Africa (Branch

and Griffiths 1988; Bustamante et al. 1997; Awad et al. 2002). This is perhaps because of the warmer, more productive, and well-oxygenated water associated with the EC region, compared with the cold, low oxygen, and low productivity (Hutchings et al. 2009) waters characteristic of the WC study area. According to Watson et al. (2005), overexploitation has the highest impact on the biodiversity of marine ecosystems. Correspondingly, overfishing in the Western Cape during the twentieth century severely depleted South African linefish populations (Griffiths 2000), which is evident from the 80% drop in commercial catch per unit effort (CPUE) already reported almost two decades ago between Cape Hangklip and Walker Bay (Attwood and Farquhar 1999). Although the east coast of South Africa has fewer and smaller commercial fisheries than that of the west coast, the east coast has a high human population density resulting in overexploitation of coastal fish as the recreational and subsistence fishers take advantage of inshore resources (Griffiths et al. 2010).

Interestingly, approximately 80% of all Cape rock lobsters found in the stomach contents of medium (1000–1399 mm) and large (> 1400 mm) *T. megalopterus* sharks were light in colour and had soft exoskeletons. This indicates that the lobsters had recently undergone ecdysis (Cockcroft and Goosen 1995), making them immobile and more vulnerable to predation (Stein 2013). This condition-dependent risk-taking (Wirsing and Ripple 2010) maximizes energy gain (Pulliam 1974; Macarthur and Pianka 2014; Huber et al. 2019) ensuring optimal foraging by the predator. A precise prediction of the optimal foraging theory (OFT; Hugie and Dill 1994) and its basic prey model (BPM), which states a predator should choose its prey by its profitability especially when the prey is highly abundant (Gill 2003), and a predator should concentrate on this prey instead of broadening its diet (Dill 1983). The shift in diet to the most plentiful prey in the system indicates a flexible foraging tactic (Newman 2003) and opportunistic predation (Huber et al. 2019) in *T. megalopterus* as has been found in other shark species such as *N. brevirostris* (Newman et al. 2012).

Despite environmental changes in the WC between seasons, there was limited evidence for corresponding dietary variation, with the Cape rock lobster remaining dominant in the diets of *T. megalopterus* throughout the year. This is most likely due to its year-round

abundance and the general lack of teleost prey in the WC. In EC, no teleosts or molluscs were recorded in winter samples although there was an increase in crustacean ingestions in this season. The reductions in teleosts in the diets are most likely a reflection of the seasonal abundance of this prey in EC as seasonal variation in the feeding habits of elasmobranchs are generally due to changes in the abundance and distribution of prey (Braccini and Perez 2005). Baremore et al. (2010) found similar patterning in *Squatina dumeril* where medium and large size specimens showed seasonal-related differences in their diets by feeding predominantly on squid in autumn and teleosts in spring. These authors proposed that this variation was due to a seasonal change in the demersal fish community, natural variation in the diet, and/or a broadening of niche breadth with season. Contrary to EC, the AN population fed on teleosts and crustaceans all year round with a slight increase in mollusc ingestion during the summer months. This shows that despite the warm Angola Current migrating southward into the study region during summer; this distinct seasonal signal does not appear to have a major impact on the feeding of *T. megalopterus*.

The tooth morphology of *T. megalopterus* consists of a plate-like dentition where the anterior teeth are molar-like while the posterior teeth rise into a short but sharp, non-serrated cusp. Secondary cusplets are not present. In comparison to other Triakidae (Herman et al. 1988), the teeth of *T. megalopterus* lack the true basal median apron, median uvula, and weakly developed secondary cusplets as seen in *T. scyllium* and *T. semifasciata*. The teeth of *T. megalopterus* resemble that of *T. maculata* and *T. acutipinna*.

The plate-like dentition could suggest a crushing feeding mechanism and a durophagous diet (Moss 1977), while the short cusps enable the shark to penetrate (Huber et al. 2009) grasp, restrain, and/or manipulate soft-bodied prey such as teleosts and molluscs (Ramsay and Wilga 2007). This dentition appears to directly correlate with the feeding of *T. megalopterus*; however, there was no sign that this species was using the plate-like dentition to crush prey. In the WC particularly, stomach contents were whole and showed no sign of bite marks. The only evidence that teeth were used in the feeding strategy of *T. megalopterus* was the fact that some of the Cape rock lobster antennae were severed at the base of their heads. This may be attributed to the bite force of the plate-like teeth

that sever the antennae when the mouth closes. The absence of bite marks on whole prey items indicates that *T. megalopterus* may make use of a suction feeding technique which is common in Triakidae and reported for *Mustelus mustelus* (Wilga et al. 2016), *T. semifasciata* (Ferry-Graham 1998), *Mustelus higmani* (Tagliafico et al. 2015), and *Mustelus canis* (Wilga et al. 2016). The lack of evidence for the use of their plate-like dentition may suggest that there may be functional redundancy in the morphology of this species. This may promote the evolution of phenotypic diversity. However, one must be cognisant that different morphological structures can yield equivalent functions (many-to-one mapping, Alfaro et al. 2005) and thus it is possible that the present tooth morphology of the species may render it capable of utilising a much wider range of food types than observed in this study and this should be explored further.

Interestingly, despite the large differences in diet amongst populations, particularly in the WC, this difference does not correlate to the tooth morphology of this population. One would expect that with a predominantly durophagous diet in WC, this population's dentition would have evolved to a molariform tooth lacking the sharp cusp. However, only three tooth morphology variables (medial-superior base width, medial-superior length, and medial-inferior base width) differed significantly, and these differences were evident between AN and EC. This may be because *T. megalopterus* are mostly suction feeders that only use their teeth for limited grasping/manipulation of prey. Therefore, their teeth do not need to or have not had enough time to, evolve to suit their method of feeding. Another explanation may be that to not damage the sharp cusps when gripping hard exoskeletons, *T. megalopterus* may depress and rotate these cusps inwards leaving the broader labial face of the teeth to form a plate-like grasping surface. This depression and rotation are not uncommon in chondrichthyans (see Ramsay and Wilga 2007). Alternatively, as the increased population sizes of *J. lalandii* east of Cape Hangklip only occurred in the 1990s (Tarr et al. 1996; Turpie et al. 2003; Cockcroft et al. 2008; Blamey and Branch 2012), the altered prey preference in WC may not have occurred long enough ago to have had an effect of the evolution of the tooth morphology of this population.

Despite minimal differences between the tooth morphology of the various populations, there was a change in dentition with ontogeny. In the subset analysis of EC

dentition, small *T. megalopterus* have dorsoventrally flattened and more molariform lateral teeth. These lateral teeth have no cusps, only small, coarse serrations which would be more suited for a durophagous diet where crushing or grinding of hard-bodied prey is required. As *T. megalopterus* grow, so do their teeth grow and change shape. There is an increase in the area and width of the teeth from small to large specimens where the medial-inferior and medial-superior broaden at their base and lengthen to produce a single cusp. The development of this cusp may enable larger specimens to grasp/clutch and manipulate softer-bodied prey to inhibit their escape (Ramsay and Wilga 2007). Therefore, the ontogenetic development of this cusp may be indicative of a diet expansion to include softer-bodied prey species with increasing size. In one of the few statistical studies to incorporate feeding and dental morphology throughout ontogeny (Powter et al. 2010), *Heterodontus portusjacksoni* showed a similar, although opposite pattern to that observed for *T. megalopterus*. Juvenile *H. portusjacksoni* have the sharp, cuspidate anterior teeth needed to grasp soft-bodied benthic invertebrates, while the adults had more molariform teeth suited to their durophagous diet.

Despite the historical separation of the EC population, and the differences observed in the feeding habits of the same, teeth morphology showed no significant differences. This may either be attributed to the hypothesized suction feeding employed by this species or show that the separation of the population has just not been enough time to show evidence of evolution. This comes as no surprise as chondrichthyans have existed for at least 450 million years (Hoenig and Gruber 1990), thus demonstrating remarkable historic endurance (Grogan et al. 2012) with evolutionary rates estimated to be six times slower than in mammals and up to eight times slower than in primates and ungulates (Martin et al. 1992; Martin and Palumbi 1993).

## Conclusions

The feeding of *T. megalopterus* was predominantly influenced by temperature and overexploitation through the impacts these factors had on prey diversity. This species has shown the ability to employ flexible foraging tactics, which include fast swimming to capture pelagic prey (as is the case for the AN population) and the ability to navigate high relief areas to capture crustaceans in rocky habitats (South African populations). This broad trophic

adaptability could be one of the key features that have allowed the elasmobranch species to remain relatively unchanged through time. The differences in feeding of *T. megalopterus* in the three populations suggest that this species has broad trophic adaptability, afforded to them by a molariform and cuspidate tooth morphology which favours generalist feeding.

Ontogenetic change in tooth morphology is evident in *T. megalopterus*. Small sharks have dorsoventrally flattened, more molariform lateral teeth with no cusps, only small, coarse serrations, more suited for a durophagous diet. Large sharks show an increase in the area and width of the teeth where the medial-inferior and medial-superior broaden at their base and lengthen to produce a single cusp. The development of this cusp enables larger specimens to grasp/clutch and manipulate softer-bodied prey to inhibit their escape. Thus, the ontogenetic change in tooth morphology may be indicative of a diet expansion to include softer-bodied prey species with increasing size. There is no evidence of sexual dental dimorphism and virtually no difference amongst populations, despite differences in feeding amongst *T. megalopterus* populations, particularly in the WC.

Although feeding biology is now better understood for *T. megalopterus*, information on methods of prey detection and an understanding of the feeding mechanisms are still needed for a more comprehensive understanding of the feeding strategy of this species. Small sample sizes and an uneven spread of sex and size classes hampered the assessment of ontogenetic and seasonal feeding differences. Further analysis with larger sample sizes is required to accurately assess ontogenetic and seasonal feeding differences. This analysis should also include tooth and row counts for *T. megalopterus* as this did not form part of the current research.

**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

## Declarations

**Conflict of interest** The authors declare no competing interests.



**Table 5** Frequency of occurrence (%O), gravimetric index (%W) and index of relative prey importance (%IRI) for small, medium, and large *T. megalopterus* from Western Cape, Eastern Cape, and Angola

	Western Cape						Eastern Cape						Angola											
	Medium			Large			Small			Medium			Large			Small			Medium			Large		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
Teleost	31.82 21.43 24.51 65.37 45.45 74.59 53.83 60.00 88.84 34.41 40.54 34.52																							
Ariidae																								
<i>Galeichthys</i> sp.	10.24 14.29 15.33																							
Sparidae																								
<i>Diplodus sargus capensis</i>	22.78 16.22 21.98																							
Clupeidae																								
<i>Sardinella aurita</i>	0.07 4.05 0.44																							
Bleniidae																								
<i>Parablennius pilicornis</i>	20.88 9.09 11.49 10.77 13.33 5.10 6.94 5.41 2.64																							
Sciaenidae	17.04 9.09 11.04																							
<i>Attractoscion aequidens</i>	0.01 1.35 0.05																							
Haemulidae																								
<i>Pomadasys olivaceum</i>	0.00 1.35 0.05																							
Ammodytidae																								
<i>Ammodytes</i> sp.	0.25 4.55 0.44 3.41 6.67 0.99 0.04 1.35 0.05																							
Unidentified Teleost	21.58 7.14 9.18 27.20 22.73 51.62 39.66 40.00 82.75 4.58 10.81 9.32																							
Elasmobranchs	0.08 2.70 0.20																							
Scyliorhinidae																								

Table 5 (continued)

	Western Cape						Eastern Cape						Angola					
	Medium			Large			Small			Medium			Small			Medium		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
<i>Scyltorhinus</i> sp.																0.08	2.70	0.20
<b>Crustacea</b>	100.00	100.00	100.00	99.87	96.43	99.96	97.87	83.78	99.12	87.55	55.56	90.62	59.49	50.00	64.00	23.72	36.36	17.93
<b>ceans</b>																20.00	6.65	10.76
Polybidae																		
<i>Ovalipes tri-</i>																21.11	6.67	3.52
<i>maculatus</i>																	4.28	5.41
Squillidae																		1.57
<i>Pterygos-</i>																		
<i>quilla</i> sp.																0.89	2.70	0.27
Cancridae																		
<i>Metacar-</i>																1.05	9.09	1.92
<i>cinus</i>																3.65	6.67	2.56
<i>magister</i>																		
Scyllaridae																		
<i>Scyllarides</i>																		
<i>elisa-</i>																27.67	7.14	11.16
<i>bethae</i>																		
Caridea																		
Xanthidae																0.51	6.67	0.58
<i>Atergatis</i>																		
<i>roseus</i>																	1.94	2.70
Plagusidae																		
<i>Plagusia</i>				0.58	3.57	0.05	92.69	67.57	98.08	87.55	44.44	89.56	9.46	7.14	7.41	7.27	18.18	9.45
<i>chabrus</i>																		
Palinuridae																		
<i>Jasus lalan-</i>	100.00	100.00	100.00	99.28	92.86	99.91	1.02	2.70	0.08							22.03	21.43	40.99
<i>dii</i>																	1.06	1.35
Tetraclitidae																		0.10

**Table 5** (continued)

	Western Cape						Eastern Cape						Angola					
	Medium			Large			Small			Medium			Small			Medium		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
<i>Tetracilita serrata</i>																0.00	1.35	0.05
Unidentified Crustacean							3.46	8.11	0.72							0.33	7.14	2.27
<b>Molluscs</b>				<b>0.13</b>	<b>3.57</b>	<b>0.04</b>				<b>8.32</b>	<b>22.22</b>	<b>6.67</b>	<b>6.49</b>	<b>14.29</b>	<b>6.44</b>	<b>8.27</b>	<b>9.09</b>	<b>5.05</b>
Cephalopods																		
Octopodidae																		
<i>Octopus vulgaris</i>				0.13	3.57	0.04							0.00	7.14	2.17	8.27	9.09	5.05
Loliginidae																		
<i>Loligo vulgaris reynaudii</i>																13.06	6.67	2.37
Gastropods																		
Haliotidae																		
<i>Haliotis midae</i>																		
Muricidae																		
<i>Urosalpinx subsinuatus</i>																	0.04	1.35
<b>Miscellaneous</b>																		
Unidentified material							2.01	8.11	0.61				2.01	8.11	0.61			
Black Stone							0.12	2.70	0.06									
Phaeophyceae							0.00	5.41	0.21				0.00	5.41	0.21			

**Table 6** Frequency of occurrence (%O), gravimetric index (%W) and index of relative prey importance (%IRI) for summer and winter *T. megalopterus* stomach contents from the Western Cape, Eastern Cape, and Angola

	Western Cape			Eastern Cape			Angola		
	Summer			Summer			Summer		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
<b>Teleost</b>				<b>16.63</b>	<b>5.88</b>	<b>1.31</b>	<b>54.07</b>	<b>46.75</b>	<b>61.22</b>
Ariidae									
<i>Galeichthys</i> sp.				4.76	2.94	0.43	28.42	11.69	17.00
Sparidae									
<i>Diplodus sargus capensis</i>							0.12	3.90	0.39
Clupeidae									
<i>Sardinella aurita</i>							9.40	7.79	4.65
Bleniidae									
<i>Parablennius pilicornis</i>									
Sciaenidae									
<i>Atractoscion aequidens</i>							0.01	1.30	0.04
Haemulidae									
<i>Pomadasys olivaceum</i>							0.00	1.30	0.04
Ammodyti- dae									
<i>Ammodytes</i> sp.									
Unidentified Teleost				11.87	2.94	0.88	16.10	20.78	39.10
<b>Elasmo- branchs</b>									
Scyliorhini- dae							<b>0.13</b>	<b>6.06</b>	<b>1.28</b>

Table 6 (continued)

	Western Cape						Eastern Cape						Angola					
	Summer			Winter			Summer			Winter			Summer			Winter		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
<i>Scyllorhinus</i> sp.																0.13	6.06	1.28
<b>Crustaceans</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>74.33</b>	<b>64.71</b>	<b>92.69</b>	<b>99.53</b>	<b>83.33</b>	<b>99.22</b>	<b>14.60</b>	<b>19.48</b>	<b>2.97</b>	<b>10.47</b>	<b>30.30</b>	<b>15.19</b>
Polybiidae																		
<i>Ovalipes trimaculatus</i>													2.02	1.30	0.14	8.35	12.12	10.31
Squillidae																		
<i>Pterygosquilla</i> sp.													1.65	2.60	0.32			
Canceridae																		
<i>Metacarcinus</i>													2.83	3.90	1.14	0.09	3.03	0.32
<i>magister</i>																		
Scyllaridae																		
<i>Scyllarides elisabethae</i>							15.23	2.94	1.09									
Caridea										1.38	8.33	0.61	0.08	2.60	0.17			
Xanthidae													3.60	2.60	0.51			
<i>Atergatis roseus</i>																		
Plagusidae																		
<i>Plagusia chabrus</i>	1.81	10.00	0.36				46.48	41.18	85.03	93.43	66.67	97.75	0.28	2.60	0.19	0.37	3.03	0.68
Palinuridae																		
<i>Jasus lalandii</i>	98.19	90.00	99.64	100.00	100.00	100.00	12.45	11.76	5.31				1.97	1.30	0.14			
Tetracelitidae																		
<i>Tetracelita serrata</i>							0.00	5.88	1.11							0.00	3.03	0.31



Table 6 (continued)

	Western Cape			Eastern Cape			Angola		
	Summer			Summer			Summer		
	%W	%O	%IRI	%W	%O	%IRI	%W	%O	%IRI
Unidentified Crustacean	0.18	2.94	0.15	4.73	8.33	0.86	2.17	2.60	0.37
<b>Molluscs</b>									
Cephalopods	6.00	11.76	2.50				25.49	24.68	31.85
Octopodidae									
<i>Octopus vulgaris</i>	0.00	2.94	0.14				21.67	20.78	30.94
Loliginidae									
<i>Loligo vulgaris reynaudii</i>							3.82	3.90	0.92
Gastropods									
Haliotidae									
<i>Haliotis midae</i>	6.00	8.82	2.37						
Muricidae									
<i>Urosalpinx subsinuatus</i>									
<b>Miscellaneous</b>									
Unidentified material	3.03	17.65	3.49	0.47	16.67	0.78	5.84	9.09	3.95
Black Stone	2.82	11.76	2.92	0.23	4.17	0.14	5.84	9.09	3.95
Phaeophyceae	0.21	5.88	0.58	0.00	8.33	0.51			

**Table 7** Results of ANOVAs of tooth data for *T. megalopterus* from Angola (AN), Western Cape (WC) and Eastern Cape (EC) with absolute population means; *F*—Levene's *F* statistic, *p*—Levene's significance, \**p* < 0.05 indicating unequal variance, \*\*significance at the 5% nominal level, absolute measurement given in mm except for the angles (A1–A4) given in degrees

	Levene's Test for Equality of Variance		Least Significant Difference (LSD)/ Games-Howell ( <i>p</i> )			Population Means (absolute measurement)		
	<i>F</i>	<i>p</i>	AN-EC	AN-WC	EC-WC	AN	EC	WC
<b>Lateral-superior</b>								
W	0.483	0.619	0.188	0.491	0.559	2.449	1.616	2.593
L	0.567	0.570	0.184	0.131	0.684	1.014	0.599	1.160
A1	5.844	<b>0.004*</b>	0.779	0.831	0.980	115.919	137.120	117.416
A2	1.125	0.330	0.508	0.725	0.776	54.368	37.842	48.881
A3	2.682	0.075	0.999	0.713	0.655	142.789	150.545	152.806
A4	4.299	<b>0.017*</b>	0.862	0.123	0.094	77.484	84.745	83.806
D1	0.929	0.399	0.132	0.357	0.611	1.599	0.989	1.759
D2	1.223	0.300	0.226	0.342	0.880	1.227	0.837	1.315
D3	1.316	0.274	0.085	0.134	0.966	1.261	0.874	1.452
D4	0.689	0.505	0.552	0.606	0.210	1.264	0.814	1.219
S	1.925	0.153	0.696	0.237	0.311	0.443	0.400	0.473
C	1.808	0.171	0.699	0.225	0.291	29.313	33.592	27.122
<b>Medial-superior</b>								
W	1.775	0.176	0.213	0.867	0.257	2.621	1.861	2.672
L	0.027	0.973	<b>0.043**</b>	0.806	0.061	2.387	1.541	2.441
A1	3.443	<b>0.037*</b>	0.141	0.449	0.503	75.468	84.828	72.279
A2	1.766	0.178	0.197	0.753	0.314	78.136	73.611	78.729
A3	1.646	0.199	0.196	0.698	0.357	133.482	131.262	131.821
A4	6.696	<b>0.002*</b>	0.699	0.914	0.404	94.682	91.282	96.772
D1	0.351	0.705	0.165	0.830	0.082	2.331	1.512	2.339
D2	0.147	0.863	0.076	0.685	0.157	2.209	1.430	2.277
D3	1.051	0.355	<b>0.008**</b>	0.158	0.228	1.390	1.050	1.501
D4	0.330	0.720	0.710	0.361	0.135	1.472	1.009	1.426
S	0.353	0.703	0.120	0.400	0.510	0.624	0.631	0.633
C	0.426	0.654	0.137	0.456	0.483	20.279	20.247	19.926
<b>Lateral-inferior</b>								
W	0.273	0.762	0.586	0.433	0.128	2.287	1.509	2.431
L	3.434	<b>0.037*</b>	0.345	0.703	0.143	0.915	0.620	0.989
A1	3.813	<b>0.026*</b>	0.439	0.381	0.817	130.013	136.625	133.507
A2	1.365	0.261	0.146	0.319	0.720	46.238	39.187	43.195
A3	2.198	0.118	0.176	0.677	0.342	138.474	144.357	139.814
A4	2.153	0.123	0.173	0.805	0.080	93.357	90.539	98.656
D1	0.689	0.505	0.853	0.200	0.082	1.223	0.867	1.350
D2	0.901	0.410	0.490	0.599	0.172	1.274	0.875	1.352
D3	0.230	0.795	0.923	0.184	0.089	1.204	0.832	1.322
D4	0.596	0.553	0.202	0.897	0.129	1.244	0.775	1.281
S	3.933	<b>0.024*</b>	0.414	0.763	0.609	0.469	0.427	0.465
C	3.540	<b>0.034*</b>	0.414	0.779	0.591	27.165	30.413	27.789
<b>Medial-inferior</b>								
W	0.320	0.727	0.381	0.894	0.273	3.308	2.245	3.315
L	0.989	0.376	0.064	0.398	0.327	2.649	1.672	2.760
A1	1.610	0.206	0.737	0.979	0.744	77.041	95.521	77.431
A2	2.248	0.112	0.086	0.193	0.783	67.582	65.865	72.094
A3	0.139	0.870	0.461	0.868	0.556	136.289	129.243	135.824

**Table 7** (continued)

	Levene's Test for Equality of Variance		Least Significant Difference (LSD)/ Games-Howell ( <i>p</i> )			Population Means (absolute measurement)		
	<i>F</i>	<i>p</i>	AN-EC	AN-WC	EC-WC	AN	EC	WC
A4	1.582	0.212	0.170	0.600	0.399	109.416	90.529	99.657
D1	0.444	0.643	0.063	0.266	0.509	2.404	1.555	2.550
D2	0.241	0.787	0.607	0.927	0.509	2.813	1.681	2.802
D3	4.343	<b>0.016*</b>	0.651	0.054	0.065	1.848	1.229	1.677
D4	0.038	0.963	<b>0.041**</b>	0.092	0.868	1.722	1.264	1.908
S	2.676	0.075	0.660	0.643	0.304	0.639	0.623	0.633
C	3.189	<b>0.047*</b>	0.705	0.623	0.319	19.710	20.279	19.902

**Table 5****Table 6****Table 7**

## References

- Ackerman LT (1971) Contributions to the biology of the leopard shark, *Triakis semifasciata* (Girard) in Elkhorn Slough, Monterey Bay, California. Master's Thesis. Sacramento State College. Retrieved from: <https://scholarworks.calstate.edu/downloads/8w32rb26n>
- Alfaro ME, Bolnick DI, Wainwright PC (2005) Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. *Am Nat* 165:140–154. <https://doi.org/10.1086/429564>
- Atchley WR, Gaskins CT, Anderson D (1976) Statistical properties of ratios. I Empirical Results *Syst Biol* 25:137–148. <https://doi.org/10.2307/2412740>
- Attwood CG, Farquhar M (1999) Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. *South African J Mar Sci* 21:415–432. <https://doi.org/10.2989/025776199784126150>
- Awad AA, Griffiths CL, Turpie JK (2002) Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. *Divers Distrib* 8:129–145
- Ayala FJ (1982) Population and evolutionary genetics: a primer. The Benjamin/Cummings Publishing Co., California
- Bakun A (2010) Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: Conceptual templates and schematic constructs. *J Mar Syst* 79:361–373. <https://doi.org/10.1016/j.jmarsys.2008.12.008>
- Ballell A, Ferrón HG (2021) Biomechanical insights into the dentition of megatooth sharks (Lamniformes: Otodontidae). *Sci Rep* 11:1–9. <https://doi.org/10.1038/s41598-020-80323-z>
- Baremore IE, Murie DJ, Carlson JK (2010) Seasonal and size-related differences in diet of the Atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. *Aquat Biol* 8:125–136. <https://doi.org/10.3354/ab00214>
- Bass AJ, D'Aubrey JD, Kistnasamy N (1975) Sharks of the east coast of Southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. *South African Assoc Mar Biol Res Investig Rep* 38:100
- Berio F, Evin A, Goudemand N, Debiais-Thibaud M (2020) The intraspecific diversity of tooth morphology in the large-spotted catshark *Scyliorhinus stellaris*: insights into the ontogenetic cues driving sexual dimorphism. *J Anat* 237:960–978. <https://doi.org/10.1111/joa.13257>
- Bethea DM, Carlson JK, Buckel JA, Satterwhite M (2006) Ontogenetic and site-related trends in the diet of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* from the northeast Gulf of Mexico. *Bull Mar Sci* 78:287–307
- Bethea DM, Hale L, Carlson JK et al (2007) Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. *Int J Life Ocean Coast Waters* 152:1009–1020
- Bianchi G (1992) Demersal assemblages of the continental shelf and upper slope of Angola. *Mar Ecol Prog Ser* 81:101–120
- Biggs R, Simons H, Bakkenes M et al (2008) Scenarios of biodiversity loss in southern Africa in the 21st century. *Glob Environ Chang* 18:296–309. <https://doi.org/10.1016/j.gloenvcha.2008.02.001>
- Blamey LK, Branch GM (2012) Regime shift of a kelp-forest benthic community induced by an 'invasion' of the rock lobster *Jasus lalandii*. *J Exp Mar Bio Ecol* 420:33–47
- Braccini JM, Perez JE (2005) Feeding habits of the sand skate *Psammobatis extenta* (Garman, 1913): Sources of variation in dietary composition. *Mar Freshw Res* 56:395–403
- Branch GM, Griffiths CL (1988) The Benguela ecosystem: the coastal zone. In: Barnes M (ed) *Oceanography and Marine Biology*. University Press, Aberdeen, An Annual Review, pp 395–486
- Bray JR, Curtis TJ (1957) An ordination of upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Brookstein FL, Chernoff B, Elder RL et al (1985) Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. *Acad Nat Sci Philadelphia* 15:1–277

- Bush A, Holland K (2002) Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kane'ohe Bay, O'ahu. *Hawaii J Exp Biol Ecol* 278:157–178
- Bustamante R, Branch GM, Eekhout S (1997) The influence of physical factors on the distribution and zonation patterns of South African rocky shore communities. *South African J* 18:119–136
- Cassemiro FAS, Rangel TFLVB, Pelicice FM, Hahn NS (2008) Allometric and ontogenetic patterns related to feeding of a neotropical fish, *Satanoperca pappaterra* (Perciformes, Cichlidae). *Ecol Freshw Fish* 17:155–164. <https://doi.org/10.1111/j.1600-0633.2007.00270.x>
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E Ltd, Plymouth, United Kingdom, pp 1–176
- Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effect' study. *Mar Ecol Prog Ser* 46:213–226
- Cockcroft AC, Goosen PC (1995) Shrinkage at moulting in the rock lobster *Jasus lalandii* and associated changes in reproductive parameters. *South African J Mar Sci* 16:195–203
- Cockcroft AC, van Zyl D, Hutchings L (2008) Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. *African J Mar Sci* 30:149–159
- Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP (2008) Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES J Mar Sci* 65:1676–1688. <https://doi.org/10.1093/icesjms/fsn184>
- Corn KA, Farina SC, Brash J, Summers AP (2016) Modelling tooth–prey interactions in sharks: the importance of dynamic testing. *R Soc Open Sci* 3:160141. <https://doi.org/10.1098/rsos.160141>
- Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Can J Fish Aquat Sci* 54:726–738
- Cortés E, Gruber SH (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia* 1:204–218
- Cullen JA, Marshall CD (2019) Do sharks exhibit heterodonty by tooth position and over ontogeny? A comparison using elliptic Fourier analysis. *J Morphol* 280:687–700. <https://doi.org/10.1002/jmor.20975>
- Dean MN, Motta PJ (2004) Anatomy and functional morphology of the feeding apparatus of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea). *J Morphol* 262:462–483. <https://doi.org/10.1002/jmor.10245>
- Di Lorenzo M, Vizzini S, Signa G et al (2020) Ontogenetic trophic segregation between two threatened smooth-hound sharks in the Central Mediterranean Sea. *Sci Rep* 10:1–15. <https://doi.org/10.1038/s41598-020-67858-x>
- Dicken ML, Hussey NE, Christiansen HM, Smale MJ, Nkabi N, Cliff G, Wintner SP (2017) Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. *PLoS One* 12:1–25. <https://doi.org/10.1371/journal.pone.0177897>
- Dill LM (1983) Adaptive flexibility in the foraging behavior of fishes. *Can J Fish Aquat Sci* 40:398–408
- Duarte A, Fielding P, Sowman M, Bergh M (2005) Overview and analysis of socio-economic and fisheries information to promote the management of artisanal fisheries in the Benguela Current Large Marine Ecosystem (BCLME) region (Angola). Final report and recommendations no. LMR/AFSE/03/01/B. <http://hdl.handle.net/11070/3124>
- Dufois F, Rouault M (2012) Sea surface temperature in False Bay (South Africa): Towards a better understanding of its seasonal and inter-annual variability. *Cont Shelf Res* 43:24–35. <https://doi.org/10.1016/j.csr.2012.04.009>
- Eggold BT, Motta PJ (1992) Ontogenetic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*. *Environ Biol Fishes* 34:139–158. <https://doi.org/10.1007/BF00002390>
- Ekau W, Verheye HM (2010) Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. *African J Mar Sci* 27:629–639. <https://doi.org/10.2989/18142320509504123>
- Ellis JK, Musick JA (2006) Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. *Environ Biol Fishes* 80:51–67. <https://doi.org/10.1007/s10641-006-9116-2>
- Enax J, Prymak O, Raabe D, Epple M (2012) Structure, composition, and mechanical properties of shark teeth. *J Struct Biol* 178:290–299
- Estupiñán-Montaño C, Galván-Magaña F, Sánchez-González A et al (2019) Dietary ontogeny of the blue shark, *Prionace glauca*, based on the analysis of  $\delta^{13}C$  and  $\delta^{15}N$  in vertebrae. *Mar Biol* 166:1–13. <https://doi.org/10.1007/s00227-019-3550-0>
- Ferrara TL, Clausen P, Huber DR et al (2011) Mechanics of biting in great white and sandtiger sharks. *J Biomech* 44:430–435. <https://doi.org/10.1016/j.jbiomech.2010.09.028>
- Ferry-Graham LA (1998) Effects of prey size and mobility on prey-capture kinematics in leopard sharks *Triakis semifasciata*. *J Exp Biol* 201:2433–2444
- Freeman H (1974) Computer processing of line drawing images. *ACM Comput Surv* 6:57–97
- Frisk MG, Miller TJ (2006) Age, growth, and latitudinal patterns of two Rajidae species in the northwestern Atlantic: Little skate (*Leucoraja erinacea*) and winter skate (*Leucoraja ocellata*). *Can J Fish Aquat Sci* 63:1078–1091. <https://doi.org/10.1139/f06-005>
- Furuta N, Ninomiya S, Takahashi S et al (1995) Quantitative evaluation of soybean (*Glycine max* L., Merr.) leaflet shape by principal component scores based on elliptic Fourier descriptor. *Breed Sci* 45:315–320
- Gill AB (2003) The dynamics of prey choice in fish: the importance of prey size and satiation. *J Fish Biol* 63:105–116
- Griffiths MH (2000) Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *South African J Mar Sci* 22:81–110. <https://doi.org/10.2989/025776100784125663>
- Griffiths CL, Robinson TB, Lange L, Mead A (2010) Marine biodiversity in South Africa: an evaluation of current

- states of knowledge. PLoS ONE 5:e12008. <https://doi.org/10.1371/journal.pone.0012008>
- Grogan ED, Lund R, Greenfest-Allen E (2012) The origin and relationships of early Chondrichthyan. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of Sharks and Their Relatives, 2nd edn. CRC Press, Florida, USA, pp 453–485
- Grubich JR, Rice AN, Westneat MW (2008) Functional morphology of bite mechanics in the great barracuda (*Sphyraena barracuda*). Zoology 111:16–29
- Gutteridge AN, Bennett MB (2014) Functional implications of ontogenetically and sexually dimorphic dentition in the eastern shovelnose ray, *Aptychotrema rostrata*. J Exp Biol 217:192–200. <https://doi.org/10.1242/jeb.089326>
- Habegger M, Motta P, Huber D, Dean M (2012) Feeding biomechanics and theoretical calculations of bite force in bull sharks (*Carcharhinus leucas*) during ontogeny. Eff Grain Boundaries Paraconductivity YBCO 115:354–364
- Herman J, Hovestadt-Euler M, Hovestadt D (1988) Contributions to the study of the comparative morphology of teeth and other relevant ichthyodolites in living supraspecific taxa of Chondrichthyan fishes Part A : Selachii. No. 2a : Order : Carcharhiniformes - Family : Triakidae. Bull R Belgian Inst Nat Sci 58:99–126
- Hoening JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Tech Rep NMFS 90:1–16
- Huber DR, Eason TG, Hueter RE, Motta PJ (2005) Analysis of the bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci*. J Exp Biol 208:3553–3571. <https://doi.org/10.1242/jeb.01816>
- Huber DR, Weggelaar CL, Motta PJ (2006) Scaling of bite force in the blacktip shark *Carcharhinus limbatus*. Zoology 109:109–119
- Huber DR, Claes JM, Mallefet J, Herrel A (2009) Is extreme bite performance associated with extreme morphologies in sharks? Physiol Biochem Zool 82:20–28. <https://doi.org/10.1086/588177>
- Huber D, Wilga C, Dean M et al (2019) Feeding in cartilaginous fishes: an interdisciplinary synthesis. Springer, Cham, pp 231–295. [https://doi.org/10.1007/978-3-030-13739-7\\_8](https://doi.org/10.1007/978-3-030-13739-7_8)
- Hugie DM, Dill LM (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. J Fish Biol 45:151–169
- Hutchings L, van der Lingen CD, Shannon LJ et al (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15–32. <https://doi.org/10.1016/j.pocean.2009.07.046>
- Hutchings K, Clark BM (2012) Marine specialist report and impact assessment for the proposed brackish water reverse osmosis desalination plant discharge at Port Alfred. prepared for Coastal Environmental Services and the Amathole Water Board. Cape Town, South Africa
- Hyslop EJ (1980) Stomach contents analysis: a review of methods and their application. J Fish Biol 17:411–429
- IBM Corporation (2021) IBM SPSS Statistics for Windows, Version 27.0. IBM Corp, Armonk, NY
- Irschick DJ, Hammerschlag N (2015) Morphological scaling of body form in four shark species differing in ecology and life history. Biol J Linn Soc 114:126–135. <https://doi.org/10.1111/bij.12404>
- Iwata H, Ukai Y (2001) SHAPE: A computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. J Hered 93:384–385
- Kajiura S, Tricas T (1996) Seasonal dynamics of dental sexual dimorphism in the Atlantic stingray *Dasyatis sabina*. J Exp Biol 199:2297–2306
- Kao SJ (2000) Diet, daily ration and gastric evacuation of the leopard shark (*Triakis semifasciata*). California State University Hayward and Moss Landing Marine Laboratories
- Karczmarski L, Cockcroft VG, McLachlan A (1999) Group size and seasonal pattern of occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. South African J Mar Sci 21:89–97. <https://doi.org/10.2989/025776199784126024>
- Kuhl FP, Giardina CR (1982) Elliptic Fourier features of a closed contour. Comput Graph Image Process 18:236–258
- Litvinov FF, Laptikhovsky VV (2005) Methods of investigations of shark heterodonty and dental formulae's variability with the blue shark, *Prionace glauca* taken as an example. ICES CM 27:15
- Lowry DC (2005) The early ontogeny of feeding in two shark species: developmental aspects of morphology, behavior, and performance. PhD Thesis. University of South Florida, pp 1–114. <http://scholarcommons.usf.edu/etd/749>
- Lowry D, Motta PJ, Hueter RE (2007) The ontogeny of feeding behavior and cranial morphology in the leopard shark *Triakis semifasciata* (Girard 1854): a longitudinal perspective. J Exp Mar Bio Ecol 341:153–167. <https://doi.org/10.1016/j.jembe.2006.07.018>
- Lucifora LO, Cione AL, Menni RC, Escalante AH (2003) Tooth row counts, vicariance, and the distribution of the sand tiger shark *Carcharias taurus*. Ecography (cop) 26:567–572
- Macarthur RH, Pianka ER (2014) On optimal use of a patchy environment. Am Nat 100:603–609
- Maisey JG (1985) Cranial morphology of the fossil elasmobranch *Synechodus dubrisiensis*. Am Museum Novit 2804:1–28
- Martin AP, Palumbi SR (1993) Body size, metabolic rate, generation time, and the molecular clock. Proc Natl Acad Sci U S A 90:4087–4091. <https://doi.org/10.1073/pnas.90.9.4087>
- Martin A, Naylor GJP, Palumbi SR (1992) Rates of mitochondrial DNA evolution in sharks are slow compared with mammals. Lett to Nat 357:153–155
- Matusiewicz P, Czarski A, Adrian H (2007) Estimation of materials microstructure parameters using computer program SigmaScan Pro. Metall Foundry Eng 33:33–40. <https://doi.org/10.7494/mafe.2007.33.1.33>
- McCord ME, Campana SE (2003) A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. J Northwest Atl Fish Sci 32:57–63
- Mittelbach GG, Schemske DW, Cornell HV et al (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol Lett 10:315–331. <https://doi.org/10.1111/J.1461-0248.2007.01020.X>

- Moss SA (1977) Feeding Mechanisms in Sharks. *Am Zool* 17:355–364
- Motta PJ, Wilga CD (1999) Anatomy of the feeding apparatus of the nurse shark, *Ginglymostoma cirratum*. *J Morphol* 241:33–60
- Motta PJ, Wilga CD (2001) Advances in the study of feeding behaviors, mechanisms and mechanics of sharks. *Environ Biol Fishes* 60:131–156
- Motta PJ, Tricas TC, Hueter RE, Summers AP (1997) Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *J Exp Biol* 200:2765–2780
- Motta PJ, Hueter RE, Tricas TC et al (2008) Functional morphology of the feeding apparatus, feeding constraints, and suction performance in the nurse shark *Ginglymostoma cirratum*. *J Morphol* 269:1041–1055. <https://doi.org/10.1002/jmor.10626>
- Newman SP (2003) Spatial and temporal variation in diet and prey preference of nursery-bound juvenile lemon sharks (*Negaprion brevirostris*) at Bimini. University of Plymouth, Bahamas
- Newman SP, Handy RD, Gruber SH (2012) Ontogenetic diet shifts and prey selection in nursery bound lemon sharks, *Negaprion brevirostris*, indicate a flexible foraging tactic. *Environ Biol Fishes* 95:115–126. <https://doi.org/10.1007/s10641-011-9828-9>
- Parsons KJ, Robinson BW, Hrbek T (2003) Getting into shape: an empirical comparison of traditional truss-based morphometric methods with a newer geometric method applied to New World cichlids. *Environ Biol Fishes* 67(4):417–431
- Pinkas L, Oliphant S, Iverson I (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif Fish Game* 152:1–105
- Potts WM, Gotz A, James N (2015) Review of the projected impacts of climate change on coastal fishes in southern Africa. *Rev Fish Biol Fish* 25(4):603–630. <https://doi.org/10.1007/s10745-006-9094-1>
- Powter DM, Gladstone W, Platell M (2010) The influence of sex and maturity on the diet, mouth morphology and dentition of the Port Jackson shark, *Heterodontus portusjacksoni*. *Mar Freshw Res* 61:74–85. <https://doi.org/10.1071/mf09021>
- Pulliam HR (1974) On the theory of optimal diets. *Am Nat* 108:59–75
- Ramsay JB, Wilga CD (2007) Morphology and mechanics of the teeth and jaws of the white-spotted bamboo sharks (*Chiloscyllium plagiosum*). *Jouornal Morphol* 268:664–682. <https://doi.org/10.1002/jmor>
- Reiss KL, Bonnan MF (2010) Ontogenetic scaling of caudal fin shape in *Squalus acanthias* (Chondrichthyes, Elasmobranchii): a geometric morphometric analysis with implications for caudal fin functional morphology. *Anat Rec (hoboken)* 293:1184–1191. <https://doi.org/10.1002/ar.21155>
- Reusch TBH (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evol Appl* 7:104–122. <https://doi.org/10.1111/eva.12109>
- Richardson TJ (2010) The taxonomy, life-history and population dynamics of blacktail, *diplodus capensis* (perciformes: sparidae), in southern Angola. MSc Thesis, Rhodes University
- Richardson TJ, Potts WM, Santos CV, Sauer WHH (2011) Ontogenetic dietary shift and morphological correlates for *Diplodus capensis* (Teleostei: Sparidae) in southern Angola. *African Zool* 46:280–287
- Rohde K (2014) Latitudinal gradients in species the search for the diversity: primary cause. *Oikos* 65:514–527
- Roy K, Jablonski D, Valentine JW, Rosenberg G (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc Natl Acad Sci U S A* 95:3699–3702
- Sanders HL (2014) Marine benthic diversity: a comparative study. *Am Nat* 102:243–282
- Schaffner S, Sabeti P (2008) Evolutionary adaptation in the human lineage. *Nat Educ* 1:1–14
- Shannon VH, Hempel G, Malanotte-Rizzoli P, Moloney P, Woods JD (2006) Benguela: predicting a large marine ecosystem, First. Elsevier, Amsterdam, The Netherlands
- Shepard RN (1980) Multidimensional scaling, trends in ecology and evolution-fitting, and clustering. *Science* (80-) 210:390–398
- Shimada K (2002) Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). *J Morphol* 251:38–72. <https://doi.org/10.1002/jmor.1073>
- Shiu S-H, Borevitz JO (2008) The next generation of microarray research: applications in evolutionary and ecological genomics. *Heredity (edinb)* 100:141–149. <https://doi.org/10.1038/sj.hdy.6800916>
- Simon KD, Bakar Y, Temple SE, Mazlan AG (2010) Morphometric and meristic variation in two congeneric archer fishes *Toxotes chatareus* (Hamilton 1822) and *Toxotes jaculatrix* (Pallas 1767) inhabiting Malaysian coastal waters. *J Zhejiang Univ Sci B (Biomed Biotechnol)* 11:871–879. <https://doi.org/10.1631/jzus.B1000054>
- Smale MJ, Goosen AJ (1999) Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fish Bull* 97:987–998
- Soekoe M (2016) Adaptations in allopatric populations of *Triakis megalopterus* isolated by the Benguela Current. Rhodes University, Steps towards understanding evolutionary processes affecting regional biodiversity
- Spalding MD, Fox HE, Allen GR et al (2009) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Am Inst Biol Sci* 57:573–583
- StatSoft Inc. (2011) STATISTICA (Data Analysis Software System), Version 10. <http://www.statsoft.com>
- Stein RA (2013) Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecol Soc Am* 58:1237–1253
- Stoner A, Livingstone R (1984) Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1:174–187
- Summers AP, Ketcham RA, Rowe T (2004) Structure and function of the horn shark (*Heterodontus francisci*) cranium through ontogeny: development of a hard prey specialist. *J Morphol* 260:1–12. <https://doi.org/10.1002/jmor.10141>
- Tagliafico A, Hernández-Ávila I, Rangel S, Rago N (2015) Size of catch, reproduction and feeding of the small-eye smooth-hound, *Mustelus higmani* (Carcharhiniformes: Triakidae), in Margarita Isand, Venezuela. *Sci Mar* 79:443–452



- Talent LG (1976) Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. *Calif Fish Game* 62:286–298
- Tarr RJQ, Williams PVG, Mackenzie AJ (1996) Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. *South African J Mar Sci* 17:319–323
- Tian J, Zeng H, Ping H, Ji W, Xie J, Chi W, Xie H, Zhengyi F (2019) Microstructure and composition characterization of teeth from different species. In: *Proceeding of the 42nd international conference on advanced ceramics and composites: ceramic engineering and science proceedings* 39(3):233–241
- Tittensor DP, Mora C, Jetz W et al (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101. <https://doi.org/10.1038/nature09329>
- Turpie JK, Heydenrych BJ, Lamberth SJ (2003) Economic value of terrestrial and marine biodiversity in the Cape Floristic Region: implications for defining effective and socially optimal conservation strategies. *Biol Conserv* 112:233–251. [https://doi.org/10.1016/S0006-3207\(02\)00398-1](https://doi.org/10.1016/S0006-3207(02)00398-1)
- Turpie JK, Clark BM, Hutchings K, Orr KK, De Wet J (2009) Ecology, value and management of the Kogelberg coast. Cape Town
- Von der Heyden S, Bowie RCK, Prochazka K et al (2011) Phylogeographic patterns and cryptic speciation across oceanographic barriers in South African intertidal fishes. *J Evol Biol* 24:2505–2519. <https://doi.org/10.1111/j.1420-9101.2011.02382.x>
- Wainwright PC (1996) Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* 77:1336–1343. <https://doi.org/10.2307/2265531>
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environ Biol Fishes* 44:97–113
- Waller GNH, Baranes A (1991) Chondrocranium morphology of northern Red Sea triakid sharks and relationships to feeding habits. *J Fish Biol* 38:715–730
- Ward-Campbell BMS, Beamish FWH (2005) Ontogenetic changes in morphology and diet in the snakehead, *Channa limbata*, a predatory fish in western Thailand. *Environ Biol Fishes* 72:251–257. <https://doi.org/10.1007/s10641-004-1744-9>
- Watson RT, Rosswall T, Steiner A, Töpfer K, Arico S, Bridge-water P (2005) Ecosystems and human well-being: biodiversity synthesis. A Report of the Millennium Ecosystem Assessment. World Resources Institute, Washington, DC
- Whitenack LB, Motta PJ (2010) Performance of shark teeth during puncture and draw: implications for the mechanics of cutting. *Biol J Linn Soc* 100:271–286. <https://doi.org/10.1111/j.1095-8312.2010.01421.x>
- Wilga CD, Motta PJ (1998) Feeding mechanism of the Atlantic guitarfish *Rhinobatos lentiginosus*: Modulation of kinematic and motor activity. *J Exp Biol* 201:3167–3184
- Wilga CD, Heuter RE, Wainwright PC, Motta PJ (2001) Evolution of upper jaw protrusion mechanisms in elasmobranchs. *Am Zool* 41:1248–1257
- Wilga CD, Diniz SE, Steele PR et al (2016) Ontogeny of feeding mechanics in smoothhound sharks: morphology and cartilage stiffness. *Integr Comp Biol* 56:1–7. <https://doi.org/10.1093/icb/icw078>
- Winkler A, Santos C, Potts W (2014) Diagnosing the sexual pattern of *Diplodus cervinus hottentotus* (Pisces: Sparidae) from southern Angola. *African J Mar Sci* 1–8. <https://doi.org/10.2989/1814232X.2014.969771>
- Wirsing AJ, Ripple WJ (2010) A comparison of shark and wolf research reveals similar behavioral responses by prey. *Front Ecol Environ* 9:335–341. <https://doi.org/10.1890/090226>
- Yamaguchi A, Taniuchi T (2000) Food variations and ontogenetic dietary shift of the star-spotted-dogfish *Mustelus manazo* at five locations in Japan and Taiwan. *Fish Sci* 66:1039–1048. <https://doi.org/10.1046/j.1444-2906.2000.00166.x>
- Zacharia PU (2004) Trophodynamics and review of methods for stomach content analysis of fishes. Demersal Fisheries Division Central Marine Fisheries Research Institute, Kochi

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Reproduced with permission of copyright owner. Further reproduction prohibited without permission.