

## CHAPTER 3

# Size-Based Analysis of Diet and Trophic Position of the White Shark (*Carcharodon carcharias*) in South African Waters

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## ABSTRACT

Understanding the diet and trophic ecology of apex predators is critical for effective ecosystem management, but analysis is generally restricted by their low abundance, threatened status, and, hence, available data. To address this knowledge gap for the White Shark (*Carcharodon carcharias*), we examined stomach content data ( $n = 225$ ) and undertook preliminary stable isotope

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analysis ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of muscle tissue ( $n = 21$ ) of sharks sampled from KwaZulu-Natal, South Africa. Summarized stomach content analysis (SCA) data identified a size-based transition in diet, an increase in mammalian prey, and a corresponding decrease in teleost and elasmobranch prey with increasing size of shark. Multivariate analysis of SCA data by size class was significant, but a high degree of overlap of functional prey groups across size classes was observed. The smallest sharks containing whale and seal prey were 194 and 209 cm precaudal length (PCL), respectively. Trophic position calculated from SCA data ( $\text{TP}_{\text{SCA}}$ ) ranged from 4.2 to 5.0 with sharks feeding across 0.8 trophic levels. Although  $\text{TP}_{\text{SCA}}$  data were highly variable, there was a significant linear relationship with increasing size of shark. Similarly, there was a significant increase in  $\delta^{15}\text{N}$  of muscle tissue with size of shark and feeding across 1.4 trophic levels was predicted. Sharks >200 cm PCL had highly variable  $\delta^{15}\text{N}$  muscle tissue values (minimum, 14.7; maximum, 16.8), possibly indicating multiple feeding strategies. For  $\delta^{13}\text{C}$ , the two smallest animals (124 and 134 cm PCL) had lower  $\delta^{13}\text{C}$  values relative to all other sharks except the largest individual. Because these sharks are newborn animals, this suggests interference of the maternal signature and may indicate that large individuals, including pregnant females, switch forage base and/or remain offshore for extended periods of time.

## INTRODUCTION

With the advent of industrial fishing and the initial absence of multispecies management directives, stocks of marine predators have undergone drastic declines (Myers and Worm, 2003, 2005; Hutchings and Baum, 2005). For terrestrial systems, “top-down” effects of predator removal have been historically documented (Elton, 1927; Leopold et al., 1947; Paine, 1980), but our understanding of equivalent processes in marine systems has been limited (Baum and Worm, 2009). Recent work, however, has started to recognize the need to define the role of predators to better understand the processes maintaining ecosystem function, stability, and resilience and to determine the consequences of continued overexploitation (Stevens et al., 2000; Myers et al., 2007; Heithaus et al., 2008; Baum and Worm, 2009).

Quantifying diet provides an important tool to examine the role of an organism within the system it inhabits and the influence it exerts on potential prey populations (Cortés and Gruber, 1990; Wetherbee et al., 1990). Diet data are also required to estimate trophic position and to generate size-based trophic profiles (Pauly et al., 1998; Cortés, 1999). These baseline data are required to develop predictive frameworks for monitoring prey or predator removal and/or population fluctuations (Pace et al., 1999; Myers et al., 2007; Heithaus et al., 2008). Traditionally, SCA has been used to examine diet/trophic interactions through providing insights into the type of prey consumed and the diversity of prey consumed and enabling the calculation of standardized trophic position (Cortés, 1997 and 1999). Importantly, SCA can be used to determine how these parameters vary with sex and size (Lowe et al., 1996). More recently, chemical tracers, for example the stable isotopes of nitrogen and carbon ( $^{15}\text{N}$  and  $^{13}\text{C}$ ), have been employed as a complementary tool to SCA (Vander Zanden et al., 1997; Fisk et al., 2002). Stable isotopes of a predator’s muscle tissue reflect that of the prey consumed and foraging location and are generally long-term integrated measures (MacNeil et al., 2005; Hussey et al., 2011). Nitrogen isotopes are viewed as the most reliable measure of trophic position (Post, 2002), whereas carbon isotopes typically reflect variation in baseline producers and therefore the foraging habitat of the predator (DeNiro and Epstein, 1978).

The White Shark (*Carcharodon carcharias*) is one of the largest of all extant marine predators, attaining a maximum recorded total length of 6 m (see Chapter 7, this volume). It is distributed throughout temperate waters but is reported from both tropical and temperate regions (Compagno, 2002). It is principally an epipelagic predator inhabiting coastal waters but is also known to reside

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in oceanic waters (Weng et al., 2007a; Nasby-Lucas, 2009; Jorgenson et al., 2010; Chapters 11 and 21, this volume) and undertake large-scale migrations (Bonfil et al., 2005, 2010; Chapter 21, this volume). With concerns over localized depletions of this species, the White Shark was afforded protection in South Africa, Australia, and the United States. It is listed as vulnerable by the International Union for Conservation of Nature and Natural Resources and included on Appendix II of the Convention on International Trade in Endangered Species, to restrict international trade in body parts.

Because large predatory sharks can influence prey population dynamics and their range encompasses different management subareas and fishing pressures, regional White Shark populations can potentially exert significant control across multiple components of the marine ecosystem (Hussey et al., 2011). To date, most research focused on the diet of White Sharks has either examined limited stomach content data (Bass et al., 1975; Klimley, 1985) or the localized feeding patterns and predatory behavior at seal colonies (Klimley et al., 1992, 1996, 2001; Martin et al., 2005; Laroche et al., 2008; Chapter 9, this volume). Our knowledge of general diet and size-based diet/trophic position has remained limited with the exception of stomach content data presented by Tricas and McCosker (1984) and Cliff et al. (1989) and more recently nitrogen stable-isotope profiles reported by Estrada et al. (2006). This is not surprising considering the logistical difficulties of studying free-ranging marine predators and the low natural abundance, threatened status, and, hence, available data for White Sharks (Tricas and McCosker, 1984; Malcolm et al., 2001). The objectives of this study were as follows:

1. Examine size-based diet shifts and calculate ontogenetic trophic profiles using a comprehensive archived stomach content data set.
2. Compare ontogenetic trophic profiles generated from stomach content data with those from nitrogen stable-isotope data ( $\delta^{15}\text{N}$ ) of white muscle tissue.
3. Investigate size-based switches in foraging location using carbon stable isotope data ( $\delta^{13}\text{C}$ ).

This study was focused on the White Shark population off the coast of Southern Africa.

## MATERIALS AND METHODS

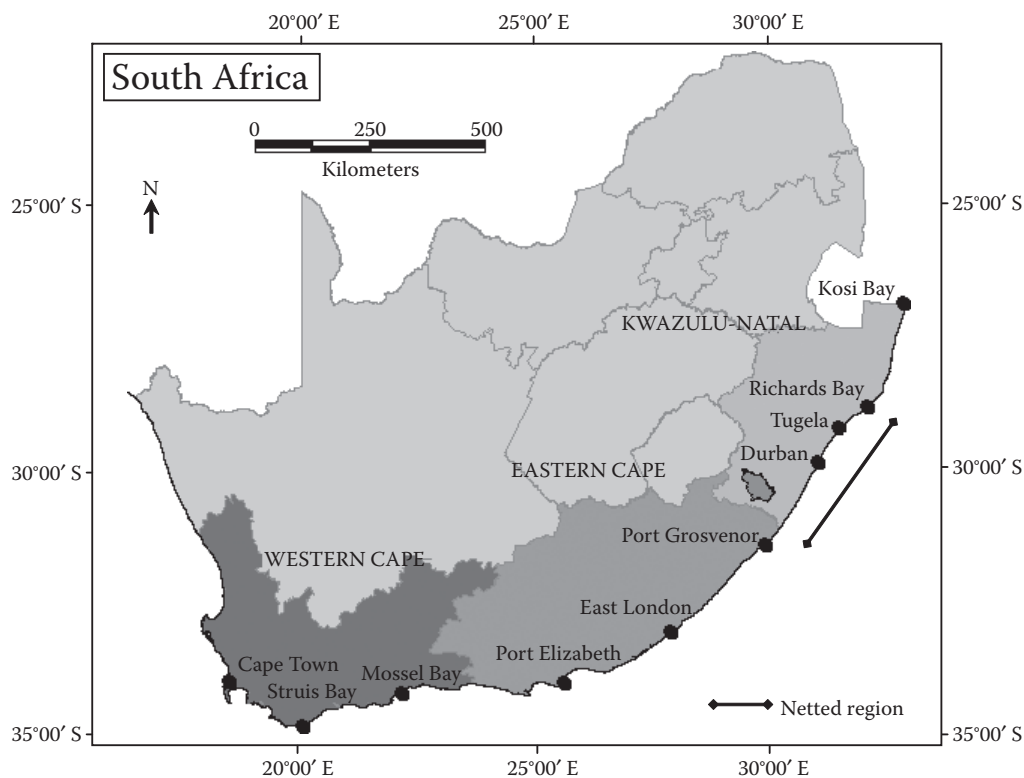
### Stomach Content Sampling

Samples (225 sharks with reliable stomach content data) were obtained from White Sharks incidentally caught in beach protection nets set at popular bathing beaches along the coast of KwaZulu-Natal (KZN), South Africa between 1978 and 2009 (Figure 3.1). The nets were set approximately 300–500 m parallel to the beach in water 10–14 m deep (Dudley et al., 2005). For specific details regarding net-servicing operations, refer to Cliff et al. (1988).

PCL was measured as the straight-line distance from the tip of the snout to the precaudal notch as defined by Dudley et al. (2005). Maturity stage was determined by the state of the reproductive organs according to Cliff et al. (1989). Stomach contents were sorted; prey was identified to the lowest possible taxonomic level, counted, and weighed to the nearest 0.1 g. Suspected scavenging of prey items was documented.

### Diet Composition

Cumulative prey curves were used to assess the sample size sufficiency for accurately describing total diet and diet by size class. The order of stomachs sampled was randomized 999 times, and the mean cumulative exponential of new prey items was plotted as a function of sample size. Diet is considered to be adequately described when the curve approaches an asymptote (Ferry and Cailliet,



**Figure 3.1** Map of South Africa showing the KwaZulu-Natal coastline where White Sharks were incidentally sampled from KwaZulu-Natal Sharks Board beach protection nets.

1996). To standardize our results with previous elasmobranch-diet studies, diet composition was calculated as percentage number (%N), percentage mass (%M), percentage occurrence (%O), and percentage index of relative importance (%IRI) (Hyslop, 1980; Cortés, 1997).

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For statistical analysis, prey were grouped according to functional prey categories defined by family and habitat (Table 3.1). All analysis was conducted with data for both sexes pooled, because a one-way analysis of similarities (ANOSIM) found no significant difference in overall diet composition between sexes ( $R = 0.023$ ,  $p = 0.122$ ).

### Size-Based Diet Shift

To examine whether White Sharks undergo a size-based diet shift, we evaluated differences in dietary composition of sharks in four successive size classes; <185 cm, 185–234.9 cm, 235–284.9 cm, and >285 cm. Sizes were defined to provide maximum resolution to examine size-based diet shifts, while maintaining sample numbers per size class. Division by maturity was deemed unsuitable because of limited catches of mature sharks. Each dietary index, %N, %M, %F, and %IRI size class data were subjected to nonmetric multidimensional scaling based on a Bray-Curtis similarity coefficient and one-way ANOSIM (White et al., 2004; Huveneers et al., 2007). Accepting that individual stomachs of large sharks typically contain only one or a few of the many identified prey items, dietary data for groups of three to five individual sharks were pooled per size class prior to the above analyses, herein referred to as dietary samples (Platell and Potter, 2001; White et al., 2004). Similarity percentage analysis was used to explore the dietary categories that contributed most to dissimilarity in diet between size classes (Clarke and Warwick, 2001).

**Table 3.1** Percentage Number (%N), Percentage Mass (%M), Percentage Frequency (%F), and Percentage Index of Relative Importance (%IRI) of Functional Prey Groups, Identified to Species Level Where Possible, in the Diet of Successive Size Classes of White Shark Sampled from South African Waters

	1 (<185 cm PCL)				2 (185–234.9 cm PCL)				3 (235–284.9 cm PCL)				4 (≥285 cm PCL)			
	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI
Elasmobranch	38.33	71.81	44.44	67.72	7.23	46.31	37.21	34.59	3.36	44.88	36.17	29.92	28.57	24.18	33.33	1784
Squaliformes																
Dogfish, <i>Squalus</i> sp.	13.33	2.48	2.78	1.98	0	0	0	0	0	0	0	0	0	0	0	0
Orectolobiformes																
Whale shark, <i>Rhincodon typus</i>	0	0	0	0	0	0	0	0	0	0	0	0	4.76	0.1	8.33	1.16
Carcharhiniformes																
Requiem sharks, unidentified Carcharhinidae	0	0	0	0	0.11	0.94	0.78	0.08	0.35	1.01	4.26	0.39	0	0	0	0
Dusky, <i>Carcharhinus obscurus</i> *	3.33	13.16	5.56	4.14	2.63	18.14	10.85	20.89	1.06	10.57	10.64	8.27	0	0	0	0
Sandbar, <i>Carcharhinus plumbeus</i>	0	0	0	0	0.11	1.94	0.78	0.15	0	0	0	0	0	0	0	0
Milk, <i>Rhizoprionodon acutus</i>	0	0	0	0	0.33	2.52	2.33	0.61	0	0	0	0	0	0	0	0
Copper, <i>Carcharhinus brachyurus</i> *	0	0	0	0	0	0	0	0	0.18	13.92	2.13	2.01	0	0	0	0
Hammerhead sharks, unidentified sphyrnid spp.	0	0	0	0	0.11	1.14	0.78	0.09	0.18	6.28	2.13	0.92	4.76	9.48	8.33	3.4
Lamniformes																
Thresher, unidentified Alopiidae	0	0	0	0	0.11	1.63	0.78	0.13	0	0	0	0	0	0	0	0
Spotted ragged tooth, <i>Carcharias taurus</i>	0	0	0	0	0	0	0	0	0.35	6.16	4.26	1.85	0	0	0	0
Unidentified shark																
Unidentified shark	3.33	3.56	5.56	1.73	0.22	2.33	1.55	0.37	0.35	3.26	4.26	1.03	4.76	10.38	8.33	3.61
Unidentified small shark	11.67	34.47	19.44	40.51	2.3	2.14	15.5	6.38	0.18	0.02	2.13	0.03	4.76	1.96	8.33	1.61
Unidentified large shark*	1.67	14.83	2.78	2.07	0.55	11.22	3.88	4.23	0.18	3.14	2.13	0.47	4.76	2.24	8.33	1.67
Benthic rajiformes																
Guitarfishes, unidentified Rhinobatidae	0	0	0	0	0.11	0.06	0.78	0.01	0.18	0.49	2.13	0.10	0	0	0	0

*continued*

**Table 3.1** Percentage Number (%N), Percentage Mass (%M), Percentage Frequency (%F), and Percentage Index of Relative Importance (%IRI) of Functional Prey Groups, Identified to Species Level Where Possible, in the Diet of Successive Size Classes of White Shark Sampled from South African Waters (Continued)

	1 (<185 cm PCL)				2 (185–234.9 cm PCL)				3 (235–284.9 cm PCL)				4 (≥285 cm PCL)			
	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI
Giant guitarfish, <i>Rhynchobatus djiddensis</i>	0	0	0	0	0.11	0.78	0.78	0.06	0	0	0	0	0	0	0	0
Stingray, unidentified	1.67	0.16	2.78	0.23	0	0	0	0	0.18	<0.01	2.13	0.03	0	0	0	0
Dasyatidae																
Benthopelagic rajiformes																
Spotted eagle ray, <i>Aetobatus narinari</i>	0	0	0	0	0.11	3.23	0.78	0.24	0	0	0	0	0	0	0	0
Bull ray, <i>Pteromyiaeus bovinus</i>	0	0	0	0	0.11	0.01	0.78	0.01	0	0	0	0	0	0	0	0
Manta ray, <i>Manta birostris</i>	1.67	2.5	2.78	0.52	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified ray	0	0	0	0	0.11	0.16	0.78	0.02	0	0	0	0	0	0	0	0
Unidentified batoid																
Unidentified elasmobranch	1.67	0.65	2.78	0.29	0.22	0.07	1.55	0.04	0.18	<0.01	2.13	0.03	4.76	0.02	8.33	1.14
Unidentified elasmobranch	1.67	6.49	2.78	0.31	4.82	24.54	33.33	16.99	3.36	29.14	40.43	22.66	47.62	70.19	66.67	79.67
Mammal																
Pinnipedia																
Unidentified seal	0	0	0	0	0.99	5.4	6.98	4.13	2.12	14.86	25.53	28.97	19.05	21.13	33.33	38.38
Odontoceti																
Unidentified dolphin*	0	0	0	0	2.74	11	19.38	24.67	0.88	7.64	8.51	4.85	4.76	0.01	8.33	1.14
Bottlenose dolphin, <i>Tursiops aduncus</i> *	0	0	0	0	0.11	0.53	0.78	0.05	0.18	0.10	2.13	0.04	4.76	12.83	8.33	4.2
Common dolphin, <i>Delphinus delphis</i> *	1.67	6.49	2.78	1.02	0.11	5.45	0.78	0.4	0	0	0	0	4.76	1.39	8.33	1.47
Risso's dolphin, <i>Grampus griseus</i>	0	0	0	0	0	0	0	0	0.18	3.72	2.13	0.55	0	0	0	0
Mysticeti																
Unidentified whale	0	0	0	0	0.33	0.15	2.33	0.1	0.18	2.83	2.13	0.43	14.29	34.83	25	35.19
Unidentified mammal																
Cetacean	0	0	0	0	0.11	1.56	0.78	0.12	0	0	0	0	0	0	0	0
Mammal	0	0	0	0	0.33	0.44	2.33	0.17	0	0	0	0	0	0	0	0

Unidentified land animal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teleost	25	21.25	30.56	19.55	82.04	29	0.01	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0
Reef																						
Herrings, Clupeidae	0	0	0	0	0	0	0	0	0	0.18	0.03	2.13	0.03	0	0	0	0	0	0	0	0	0
Halfmoon rockcod, <i>Epinephelus rivulatus</i>	0	0	0	0	0.11	0.25	0.78	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spotted grunter, <i>Pomadasys commersonii</i>	0	0	0	0	1.75	0.08	0.78	0.13	0	0	0	0	0	19.05	5.55	8.33	5.87					
Santer, <i>Cheilimerius nufar</i>	0	0	0	0	0.11	0.16	0.78	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Englishman, <i>Chrysoblephus anglicus</i>	0	0	0	0	0.11	0.03	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eels, Anguilliformes	0	0	0	0	0.11	0.04	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelagic																						
South African pilchard, <i>Sardinops ocellatus</i>	0	0	0	0	76.89	23.65	3.1	28.89	88.87	19.21	6.38	46.10	0	0	0	0	0	0	0	0	0	0
Tunas, Scombridae	0	0	0	0	0.22	0.45	1.55	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chub mackerel, <i>Scomber japonicus</i>	5	1.04	2.78	0.76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Benthic																						
Seacatfishes, Ariidae	0	0	0	0	0.11	0.03	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sea breams, Sparidae	3.33	1.05	5.56	1.1	0.11	0.11	0.78	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White musselcracker (brusher), <i>Sparodon durbanensis</i>	0	0	0	0	0.33	1.35	1.55	0.24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slinger, <i>Chrysoblephus puniceus</i>	0	0	0	0	0	0	0	0	0.18	0.04	2.13	0.03	0	0	0	0	0	0	0	0	0	0
Bronze bream, <i>Pachymetopon grande</i>	0	0	0	0	0.11	0.48	0.78	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Red tior-tior, <i>Pagellus natalensis</i>	0	0	0	0	0.11	0.01	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karenteen, <i>Sarpa salpa</i>	0	0	0	0	0.11	0.02	0.78	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kob, <i>Argyrosomus hololepidotus</i>	0	0	0	0	0.11	0.21	0.78	0.02	0.18	5.76	2.13	0.84	0	0	0	0	0	0	0	0	0	0
Geelbek, <i>Atractoscion aequidens</i>	1.67	3.73	2.78	0.68	0.22	0.3	0.78	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0	0

continued

continued

**Table 3.1** Percentage Number (%N), Percentage Mass (%M), Percentage Frequency (%F), and Percentage Index of Relative Importance (%IRI) of Functional Prey Groups, Identified to Species Level Where Possible, in the Diet of Successive Size Classes of White Shark Sampled from South African Waters (Continued)

	1 (<185 cm PCL)				2 (185–234.9 cm PCL)				3 (235–284.9 cm PCL)				4 (≥285 cm PCL)			
	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI
Unidentified teleost	15	15.43	22.22	30.53	1.53	1.83	10.08	3.14	1.24	0.94	14.89	2.16	0	0	0	0
Cephalopod	28.33	0.43	30.56	12.16	5.81	0.15	20.16	2.08	2.47	<0.01	14.89	0.63	4.76	0.08	8.33	0.41
Octopodiformes																
Unidentified octopus	0	0	0	0	0.33	<0.01	2.33	0.07	0.35	0	4.26	0.10	0	0	0	0
Decapodiformes, teuthida																
Unidentified squid	13.33	0	11.11	6.69	3.4	<0.01	8.53	2.69	0.71	<0.01	6.38	0.30	0	0	0	0
Loligo squids, Loligo spp.	5	0.11	5.56	1.28	0.55	<0.01	2.33	0.12	0.53	<0.01	2.13	0.08	0	0	0	0
Chiroteuthid squids, Chiroteuthidae	0	0	0	0	0	0	0	0	0.18	<0.01	2.13	0.03	0	0	0	0
Decapodiformes, sepiida																
Unidentified cuttlefish	8.33	0.31	13.89	5.42	1.53	0.14	9.3	1.45	0	0	0	0	4.76	0.08	8.33	1.16
Unidentified cephalopods	1.67	<0.01	2.78	0.21	0	0	0	0	0.71	<0.01	2.13	0.10	0	0	0	0
Mollusk	6.67	0.02	2.78	0.26	0.11	<0.01	0.78	0	0	0	0	0	0	0	0	0
Unidentified bivalves	6.67	0.02	2.78	0.84	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified invertebrate	0	0	0	0	0.11	<0.01	0.78	0.01	0	0	0	0	0	0	0	0

\* Evidence for prey items scavenged by White Sharks.



## Stable Isotope Sampling and Analysis

Muscle tissue was sampled from sharks caught in beach protection nets between 2005 and 2008 ( $n = 21$ ). All sharks were removed from nets, transported to the KwaZulu-Natal Sharks Board main laboratory, and stored frozen until public dissection. White muscle tissue (~5 g) was excised anterior to the first dorsal fin adjacent to the vertebral column and stored frozen. Prior to stable isotope analysis, the muscle tissue was freeze dried and homogenized using a SPEX CertiPrep 8000-D ball milling unit (SPEX CertiPrep, Metuchen, NJ). Accepting the known effect of lipid content on  $\delta^{13}\text{C}$  values (DeNiro and Epstein, 1977), all muscle tissue samples were lipid extracted following the technique detailed by Hussey et al. (2010a). Between 400 and 600  $\mu\text{g}$  of both nonlipid-extracted (BULK) and lipid-extracted (LE) tissue per individual shark were weighed into tin capsules, and stable carbon and nitrogen isotope ratios were provided from a continuous flow isotope ratio mass spectrometer (Finnigan MAT Delta<sup>plus</sup>; Thermo Finnigan, San Jose, CA, USA).

Stable isotope abundances are expressed in  $\delta$  values as the deviation from standards in parts per thousand (‰) using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (3.1)$$

where  $X$  is  $^{15}\text{N}$  or  $^{13}\text{C}$ , and  $R$  is the ratio  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ . The standard reference material was atmospheric nitrogen for  $\text{N}_2$  and Pee Dee Belemnite carbonate for  $\text{CO}_2$ . The analytical precision (standard deviation) based on two standards ( $n = 59$  for each standard): NIST 8414 and internal lab fish muscle were 0.11‰ and 0.19‰, respectively, for  $\delta^{15}\text{N}$  and were 0.05‰ and 0.06‰, respectively, for  $\delta^{13}\text{C}$ . Paired  $t$  tests were used to examine directional changes in  $\delta^{15}\text{N}$ , ‰N,  $\delta^{13}\text{C}$ , ‰C, and C:N ratio between BULK and LE muscle tissue.

## Size-Based Trophic Profile

Trophic position of White Sharks using stomach content data ( $\text{TP}_{\text{SCA}}$ ) was calculated following Cortés (1999),

$$\text{TP}_{\text{SCA}} = 1 + \left( \sum_{i=1}^7 p_i \times \text{TP}_i \right) \quad (3.2) \quad \text{AQ6}$$

where  $\text{TP}_{\text{SCA}}$  is diet-calculated trophic position per dietary sample,  $p_i$  is the proportion of each prey category in the total diet (expressed as %M), and  $\text{TP}_i$  is the trophic position for each functional prey category. The trophic positions of functional prey categories were defined as: elasmobranch (3.65), teleost (3.24), cephalopod (3.2), crustacean (2.52), mollusk (2.1), bird (3.87), and mammal (4.02) based on Cortés (1999). The miscellaneous functional prey group was excluded from all trophic position calculations.

Both  $\text{TP}_{\text{SCA}}$  for all dietary samples within the four defined size classes and mean  $\text{TP}_{\text{SCA}}$  ( $\pm$  S.D.) per size class were calculated. Accepting that dietary samples consisted of consecutive increasing size animals, the mean PCL for each dietary sample was also calculated and plotted against the  $\text{TP}_{\text{SCA}}$  estimate.

To examine  $\delta^{15}\text{N}$  ontogenetic trophic shifts and to facilitate a comparison with  $\text{TP}_{\text{SCA}}$ ,  $\delta^{15}\text{N}$  data were plotted versus PCL for each shark, and mean ( $\pm$  S.D.) data were presented per size class. A trophic level was defined as 2.29‰  $\delta^{15}\text{N}$  according to Hussey et al. (2010a, 2010b) based on a semicontrolled experiment on large sharks.

Size-based  $\delta^{13}\text{C}$  profiles were examined to explore possible switches in foraging location/base with increasing size of shark. This was undertaken based on reported gradients in  $\delta^{13}\text{C}$  in the marine environment off southern Africa (Hill et al., 2006; Hill and McQuaid, 2008):

1. An increase in  $\delta^{13}\text{C}$  moving from KZN to the Western Cape
2. Depleted  $\delta^{13}\text{C}$  values in offshore waters compared with coastal waters

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## RESULTS

### Stomach Content Data

#### Diet Composition

The cumulative prey curve for all sharks combined indicated that the data were describing a general asymptotic relationship but stabilization was not achieved (Figure 3.2a). Cumulative prey curves for data divided by size class did not approach an asymptote. This indicated that more individuals would be required to provide a more accurate representation of diet by size class, particularly for size class 4 animals (>285 cm PCL; Figure 3.2b–e).

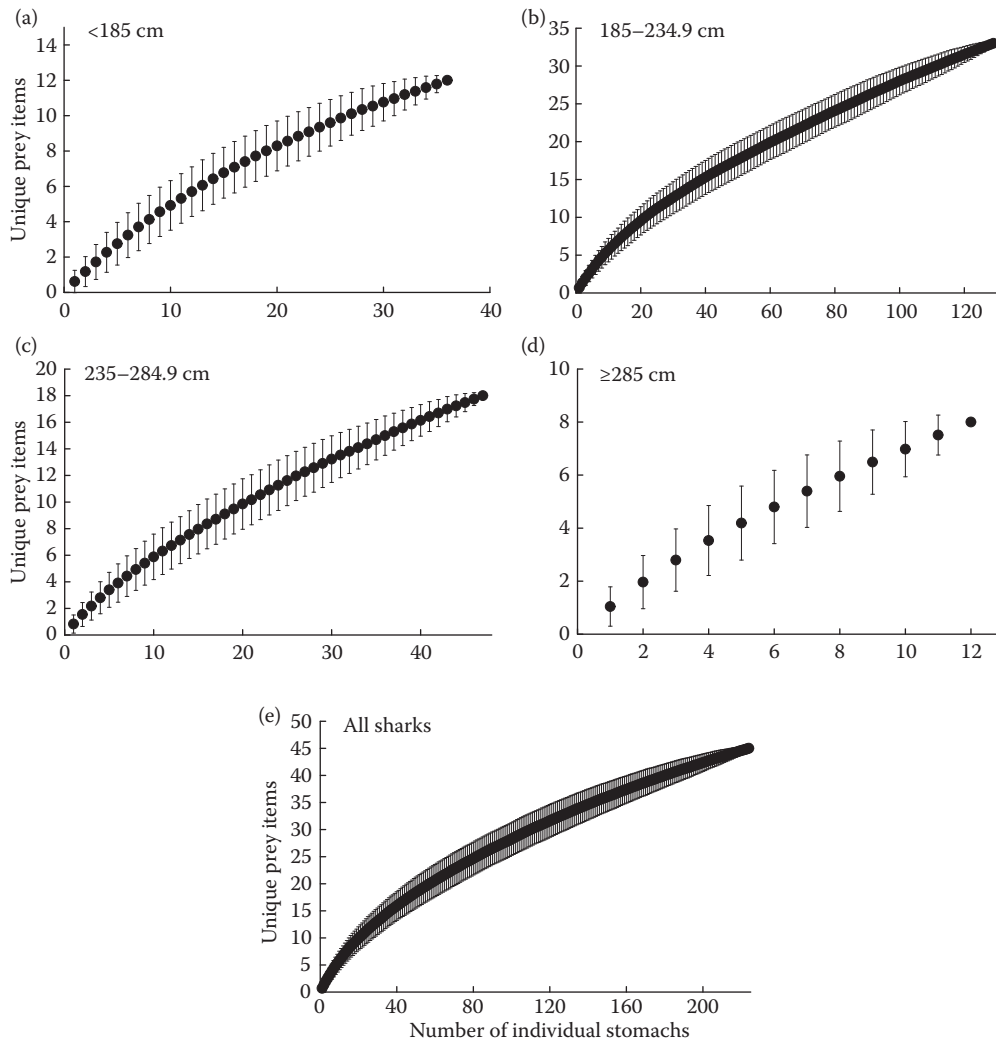
A diverse range of prey items were consumed within the main functional prey groups: elasmobranch ( $n = 14$ ), mammal ( $n = 5$ ), teleost ( $n = 18$ ), and cephalopod ( $n = 4$ ) (Table 3.1 and Figure 3.3). Identified prey items were of varying size, ranging from large unidentified whale (mysticeti) and whale shark (*Rhincodon typus*) to small loligo squids, South African pilchards (*Sardinops ocellatus*), and unidentified bivalves (Table 3.1).

In terms of %M, %F, and %IRI, elasmobranchs were the principal diet component of the smallest White Sharks followed by teleost prey. Elasmobranch prey was dominated by the dusky shark (*Carcharhinus obscurus*), whereas teleost prey consisted of chub mackerel (*Scomber japonicus*) and sea breams (Sparidae) (Table 3.1). When considering %N, %F, and %IRI, cephalopods were also important to the diet of small sharks, specifically unidentified squids (Figure 3.4a and Table 3.1). With increasing size class of White Shark, there was a marked increase in mammal prey for all calculated diet indices and a corresponding decrease in teleost, elasmobranch, and cephalopod prey (Figure 3.4; cephalopods for %N, %F, and %IRI only). Of the elasmobranch prey, dusky sharks remained the most important prey item of size class 2 and 3 sharks, but overall elasmobranch prey diversity increased (Table 3.1). Size class 2 White Sharks (185–234.9 cm) consumed the most diverse range of reef, pelagic, and benthic teleosts (Table 3.1). Within the diet of the large White Sharks (>285 cm), seal was the most numerous mammal prey item (%N), whereas whale contributed the most by mass (%M) (Figure 3.4, a and b).

#### Size-Based Diet Shift

For all of the diet indices examined, White Sharks underwent a significant size-based shift in diet (Figure 3.5). Multidimensional scaling ordination of the data showed a level of diet separation between size class 1 and 4 sharks, but a high degree of overlap between all size class sharks was evident as indicated by the low global  $R$  statistic values (Figure 3.5). Pairwise comparisons found that the diet of size class 1 sharks was significantly different from all other size classes for all calculated indices (Figure 3.5). Similarity percentage analysis found that mammal prey was the principal dietary component driving this diet separation.

Shark and cephalopod prey principally occurred in the diet of sharks between 140 and 270 cm PCL (Figure 3.6). All of the main functional prey groups occurred in the diet of sharks measuring ~200 and 250 cm PCL. Of the marine-mammal prey, dolphin was first consumed by a shark of 177 cm



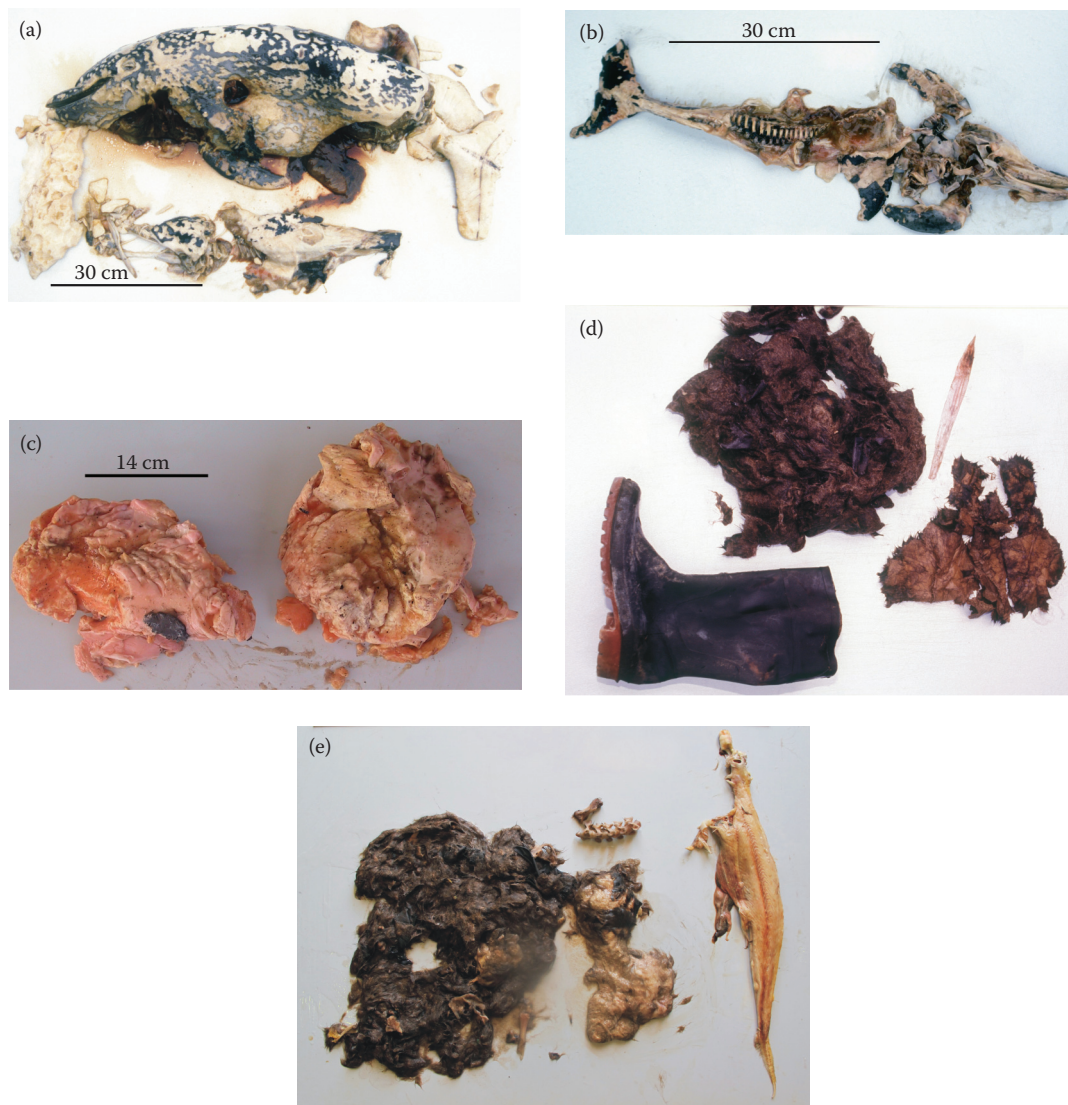
**Figure 3.2** Randomized cumulative prey curve for White Sharks sampled from beach protection nets. (a) Size class 1 (<185 cm PCL). (b) Size class 2 (185–234.9 cm PCL). (c) Size class 3 (235–284.9 cm PCL). (d) Size class 4 (≥285 cm PCL). (e) All White Sharks combined.

PCL, seal by a shark of 194 cm PCL, and whale by a shark measuring 208 cm PCL (Figure 3.6). Seal and whale were the dominant prey, occurring in the diet of sharks >300 cm PCL (Figure 3.6).

## Ontogenetic Trophic Profile

### Stomach Content Data ( $TP_{SCA}$ )

Stomach content-calculated trophic position ( $TP_{SCA}$ ) varied from 4.2 to 5.0 (Figure 3.7a). Although  $TP_{SCA}$  estimates were highly variable across the size range of animals examined (Figure 3.7a), there was a significant increase in  $TP_{SCA}$  with PCL (linear regression:  $r^2 = 11.7\%$ ;  $F_{1,75} = 11.05$ ,  $p = 0.001$ ). Overall  $TP_{SCA}$  predicted White Sharks of all sizes feeding across 0.8 trophic levels. Mean size class  $TP_{SCA}$  values predicted feeding across 0.3 trophic levels (Figure 3.7a).



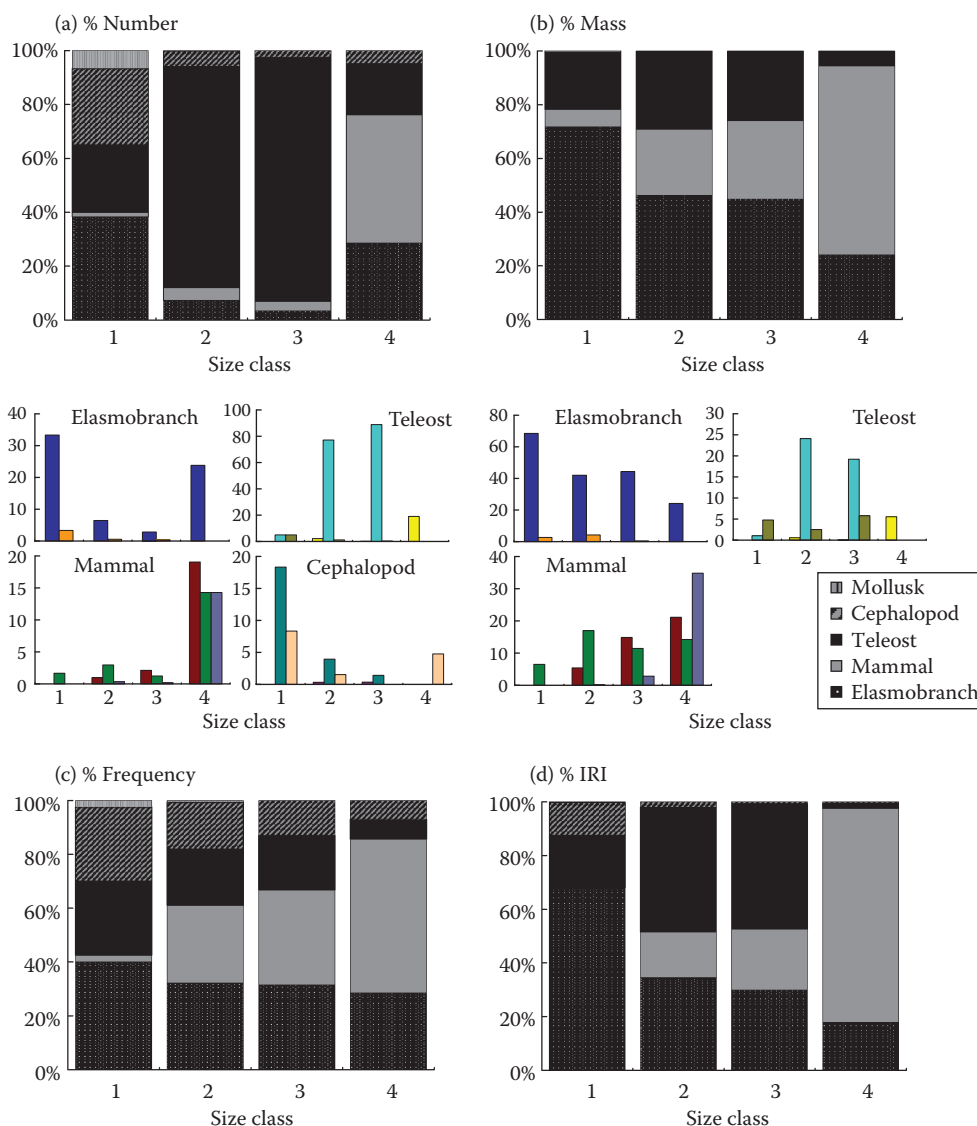
**Figure 3.3** Stomach contents retrieved from White Sharks incidentally caught in beach protection nets in KwaZulu-Natal, South Africa. (a) Unidentified whale blubber and unidentified dolphin (302-cm PCL female). (b) Unidentified dolphin (177-cm PCL female). (c) Unidentified whale blubber (325-cm PCL female). (d) Unidentified seal and rubber boot (235-cm PCL male). (e) Unidentified seal and milk shark (*Rhizoprionodon acutus*) (231-cm PCL female). PCL, precaudal length of the dissected shark.

### **Stable Isotopes ( $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ): Lipid Extraction Effects**

Lipid extraction of White Shark muscle tissue resulted in a significant increase in  $\delta^{13}\text{C}$ , %C, and C:N ratio, a significant decrease in %N, and no change in  $\delta^{15}\text{N}$  values (Figure 3.8). Because lipid extraction resulted in a significant increase in  $\delta^{13}\text{C}$ , LE data were used in all subsequent analysis.

### **Stable Isotope Data ( $TP_{SIA}$ )**

The values of  $\delta^{15}\text{N}$  increased from 13.4‰ to ~15.4‰ between animals of 124–200 cm PCL (Figure 3.7b). For animals >200 cm PCL,  $\delta^{15}\text{N}$  were variable, ranging between 14.9‰ and 16.6‰

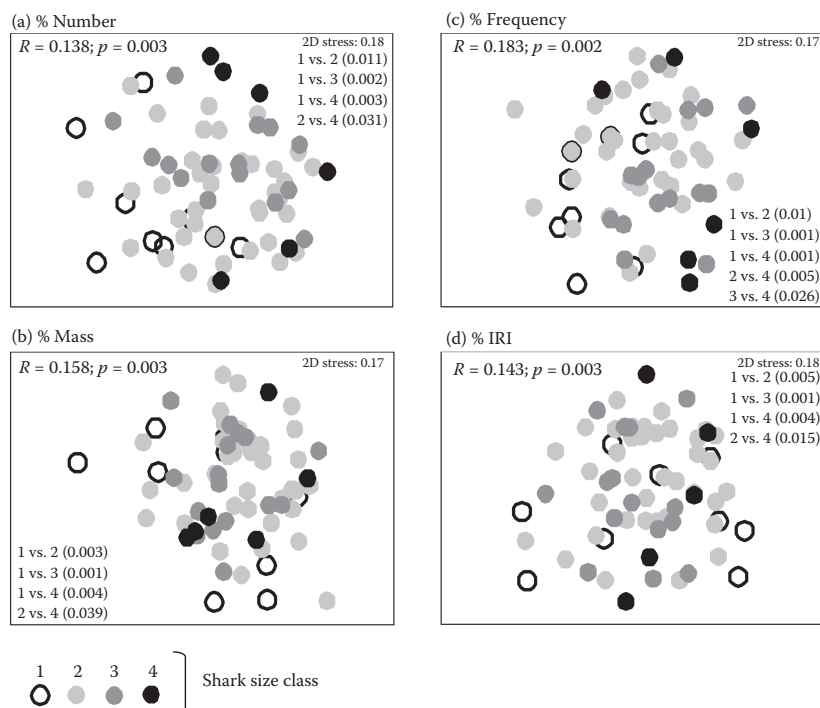


**Figure 3.4** Graphic summary of White Shark stomach content data. Percentage number (%N) (a) and percentage mass (%M) (b) contribution to total diet of each size class of shark, including detailed breakdown of main functional prey groups: elasmobranch (shark ■, ray ■), teleost (reef ■, pelagic ■), benthic ■, mammal (dolphin ■, seal ■, whale ■), and cephalopod (octopus ■, squid ■, cuttlefish ■). (c and d) Percentage frequency (%F) (c) and percentage index of relative importance (%IRI) (d).

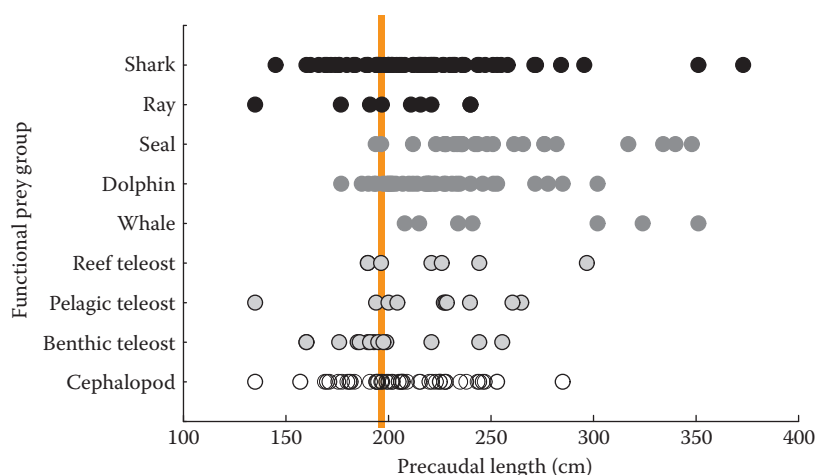
(Figure 3.7b). Overall there was a significant linear increase in  $\delta^{15}\text{N}$  with PCL ( $r^2 = 24.6\%$ ;  $F_{1,19} = 7.51$ ,  $p = 0.013$ ). Nitrogen stable isotopes predicted that White Sharks of all sizes were feeding across 1.4 trophic levels. Mean size class  $\delta^{15}\text{N}$  values predicted feeding across 0.7 trophic levels.

### Foraging Location ( $\delta^{13}\text{C}$ )

The  $\delta^{13}\text{C}$  values of the two smallest White Sharks, a female of 124.0 cm PCL ( $-16.76\text{‰}$ ) and a male of 134.0 cm PCL ( $-15.99\text{‰}$ ), were depleted and similar to the value for the largest animal,

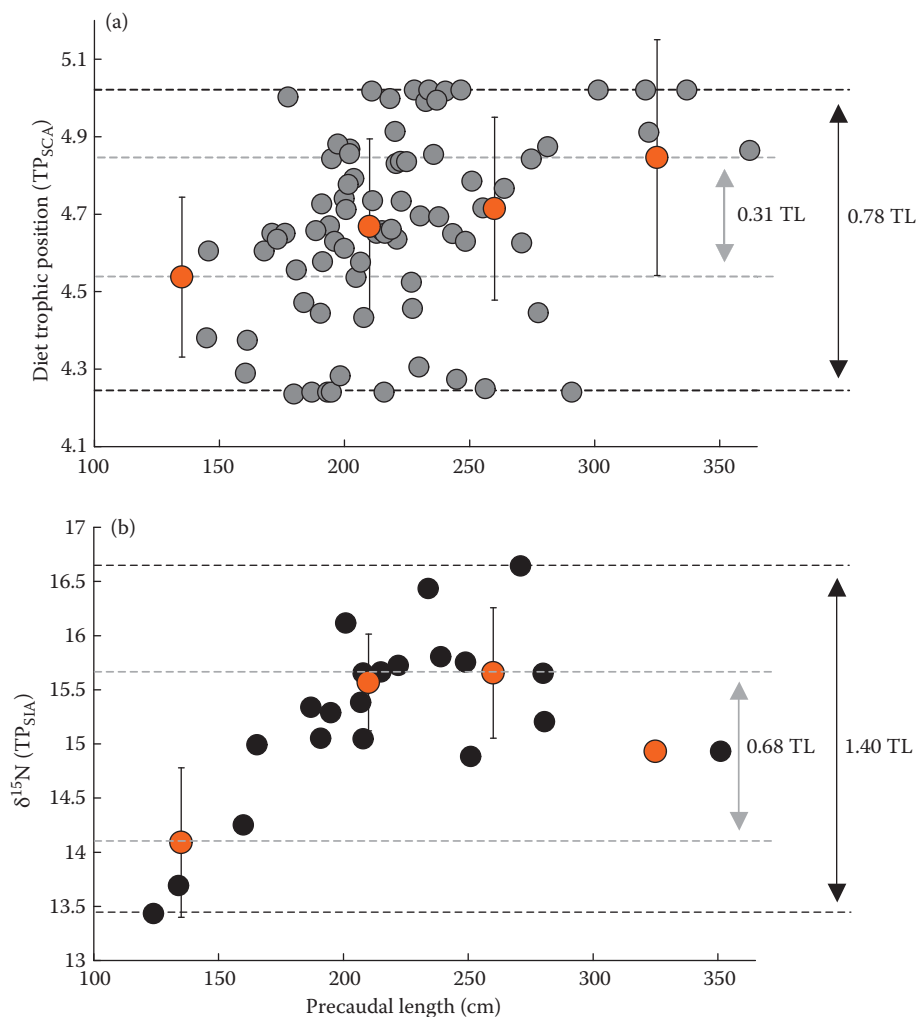


**Figure 3.5** Nonmetric multidimensional scaling of the White Shark stomach content data by size class for each diet index. (a) Percentage number (%N). (b) Percentage mass (%M). (c) Percentage frequency (%F). (d) Percentage index of relative importance (%IRI).  $R$ , ANOSIM global  $R$  statistic and associated  $p$  value. Significant pairwise tests (with  $p$  value in brackets) are detailed in each figure. The level of statistical significance was set at  $\alpha = 0.05$ .



**Figure 3.6** The relationship between White Shark length and occurrence of the functional prey groups. The vertical orange line indicates the smallest Australian/American White Shark with pinniped stomach content remains according to Tricas and McCosker (1984) [240 cm TL = ~198 cm PCL according to Cliff et al. (1989)].



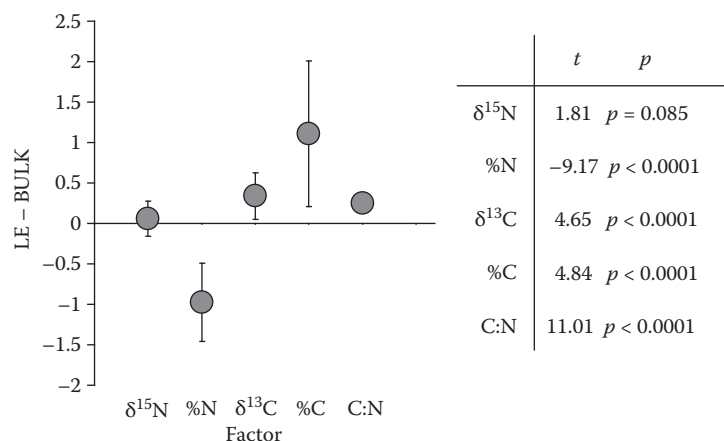


**Figure 3.7** The relationship between diet calculated trophic position ( $TP_{SCA}$ ) (a) and  $\delta^{15}N$  ( $TP_{SIA}$ ) trophic position (b) with increasing size of White Shark. The grey dots in (a) are the calculated  $TP_{SCA}$  for each dietary sample, and the black dots in (b) are  $\delta^{15}N$  values ( $TP_{SIA}$ ) for individual White Sharks. Mean ( $\pm$ SD)  $TP_{SCA}$  and  $\delta^{15}N$  ( $TP_{SIA}$ ) per size class are shown (orange dots). The arrows indicate the trophic range of the White Shark for individual animals and for mean size-class data.

which measured 351.2 cm PCL (male shark:  $-16.00\text{‰}$ ) (Figure 3.9). Overall, the data followed a parabolic shape, with a rapid increase in  $\delta^{13}C$  with size, followed by a plateau, with evidence for a decline in the largest animal (Figure 3.9). Sharks measuring between 160.0 and 280.0 cm PCL had a mean ( $\pm$ SD)  $\delta^{13}C$  value of  $-14.66\text{‰} \pm 0.43$  with a minimum and maximum of  $-15.28\text{‰}$  and  $-14.02\text{‰}$ , respectively.

## DISCUSSION

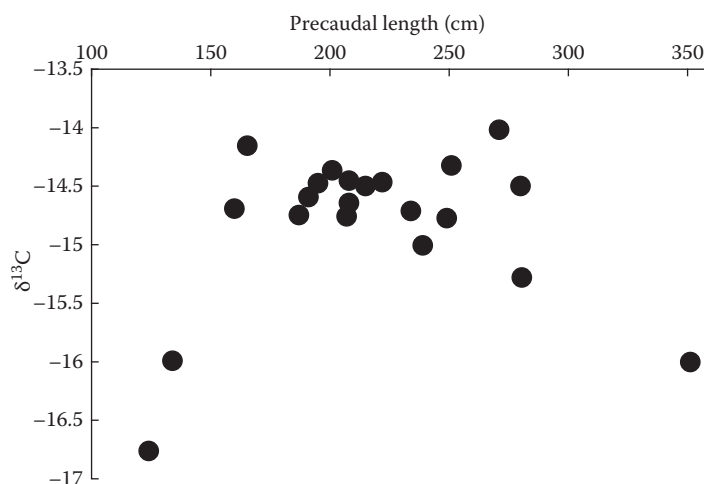
By analyzing the most comprehensive archival stomach content data available combined with preliminary stable isotope data, it was possible to define size-based diet shifts and to generate ontogenetic trophic profiles of South African White Sharks. These data complement previous



**Figure 3.8** The effect of the lipid extraction process on  $\delta^{15}\text{N}$ , total percentage of nitrogen (%N),  $\delta^{13}\text{C}$ , total percentage of carbon (%C), and C:N ratio of muscle tissue of White Sharks. LE, values for lipid-extracted tissue; BULK, values for nonlipid-extracted tissue.

stomach content data from South Africa (Bass et al., 1975; Cliff et al., 1989, 1996; the data presented in this study amalgamates that in the latter two studies) and other geographic localities (Tricas and McCosker, 1984; Bruce, 1992; Fergusson et al., 2000; Malcolm et al., 2001) and stable isotope data for the eastern North Atlantic (Estrada et al., 2006) and Pacific Oceans (Kerr et al., 2006).

Diet data derived from stomach contents for White Sharks has typically been restricted by sample numbers (Bass et al., 1975; Tricas and McCosker, 1984; Bruce, 1992) and the occurrence of empty or everted stomachs (Bass et al., 1975; Cliff et al., 1989). Cumulative prey curves indicated that the overall data set provided a reasonable indication of the total diet of the White Shark but that diet by size class will require further investigation. As with many large predatory sharks, the White Shark exhibited generalist feeding behavior, incorporating a large number of prey items from several functional prey categories. This type of feeding is reported for other closely related lamnids



**Figure 3.9** The relationship between  $\delta^{13}\text{C}$  and increasing size of White Shark as an indicator of size-based shifts in foraging location.



(Stillwell and Kohler, 1982; Joyce et al., 2002) and for many large carcharhinids (Wetherbee et al., 1990; Simpfendorfer et al., 2001). Within the functional prey categories, prey diversity in terms of habitat of occurrence was also high; for example, the teleost group included reef, pelagic, and demersal species. This suggests that White Sharks forage in a number of habitats and/or opportunistically forage if prey is abundant or easily available. Both Tricas and McCosker (1984) and Klimley (1985) reported near-shore pelagic and demersal teleost species in the stomachs of White Sharks. Furthermore, diving behavior documented from pop-up archival satellite tags indicates that White Sharks adopt various foraging modes, including feeding in the surface mixed layer, on the seabed, and at depth (Dewar et al., 2004; Weng et al., 2007a, 2007b; Nasby-Lucas, 2009; Chapter 22, this volume). The generalist feeding strategy of White Sharks is likely related to the availability of preferred prey, seasonal prey abundance, and/or the energetic requirements of an individual related to life stage.

Typical of large predatory fish (Scharf et al., 2000), the White Shark demonstrated asymmetric feeding behavior, whereby larger prey were consumed with increasing predator size, but small prey items were retained in the diet. Squid, loligo squid, chiroteuthid squid, and cuttlefish, for example, were found in the stomachs of sharks >244 cm PCL, as well as those of smaller animals. The fact that the diet of small White Sharks is a subset of the diet of larger individuals was a principal factor contributing to the high degree of overlap of functional prey categories across size classes. The occurrence of small prey in the diet of large sharks, however, may indicate that abundant small fish such as the South African sardine, *Sardinops sagax*, may be energetically viable prey when compared with the energetic costs of chase down, manipulation, handling, and the probability of prey capture associated with marine-mammal prey. The stomachs of three White Sharks, measuring, 227.8, 228.5, and 239.8 cm PCL contained 300, 300, and 477 sardines each. These feeding events are linked to the annual sardine run off the South African coast (Cliff et al., 1996; Dudley and Cliff, 2010).

A clear size-based shift in diet was evident, even when considering the high degree of overlap in functional prey categories across size classes. The diet of the smallest White Sharks was focused on elasmobranchs and teleosts, and the first evidence for foraging on seals was an individual measuring 194 cm PCL. This is in agreement with Tricas and McCosker (1984) for the size of White Sharks first feeding on seal off Australia and the United States. Tricas and McCosker (1984) postulated that an ontogenetic development in dentition at approximately 3 m TL may account for the shift in predatory behavior. Whale and seal were the dominant prey occurring in the diet of White Sharks >3 m in this study, in agreement with Tricas and McCosker (1984) and Casey and Pratt (1985). Further comparative study into the dentition of White Sharks off California relative to South Africa and other geographically separated populations and how this relates to diet is required. The occurrence of seals in the diet of White Sharks >200 cm PCL is in agreement with observations on White Shark-seal predation events in the western cape (Martin et al., 2005; Chapter 9, this volume) and supports the hypothesis of White Sharks showing preference for marine mammals with increasing size (Tricas and McCosker, 1984; Casey and Pratt, 1985; Klimley, 1985). It is important to note, however, that White Sharks feeding on whale prey are typically scavenging events (McCosker, 1985; Long and Jones, 1996; Dudley et al., 2000) and are therefore opportunistic in nature in contrast to directed predation on pinnipeds (Martin et al., 2005; Chapter 9, this volume). Stomach content data therefore indicate that White Sharks are opportunist, generalist predators similar to many large sharks (Ebert, 1994) but show size-based preference for large-bodied, energetically valuable prey. The abundance of seal prey (i.e., seal colonies) influences the movement and residency pattern of White Sharks >200 cm PCL, but when considering the diverse habitats occupied by prey identified from stomach contents, it does not constrain movement (Bruce et al., 2006; Chapters 11 and 21, this volume).

As would be expected, there was an increase in diet-calculated trophic position ( $TP_{SCA}$ ) and  $\delta^{15}N$  ( $TP_{SIA}$ ) with increasing size of shark, correlated with the size-based shift to mammal

prey.  $TP_{SCA}$  calculated from dietary samples was highly variable across the size range of sharks sampled, similar to the findings of Cortés (1999). This was likely a result of the high degree of overlap of functional prey groups across size classes. For  $\delta^{15}N$  and accepting the small sample size, the initial increase in  $TP_{SIA}$  was fairly rapid in contrast to  $TP_{SCA}$ . Midsize range sharks, however, had variable  $\delta^{15}N$  values. Because  $\delta^{15}N$  values of muscle tissue represent long term integrated dietary signatures (MacNeil et al., 2005), this could correspond to variable feeding strategies, whereby some sharks selectively feed on marine mammals, whereas other individuals roam between shelf and oceanic waters. Variation in habitat therefore drives differences in foraging behavior. This is supported by variable residency rates for individual White Sharks at seal colonies (Bonfil et al., 2005). Alternatively, the observed variation in  $\delta^{15}N$  values could be an indication of individual foraging success. Certain White Sharks may be more skilled and able to feed on seals, whereas other less successful individuals incorporate other prey within their diet to meet energetic requirements. Intrapopulation variation in foraging success is well documented across a broad range of species. We cannot rule out, however, that elevated  $\delta^{15}N$  signatures or the observed  $\delta^{15}N$  variation of the midsize sharks may be a result of a cessation of feeding. It is well documented that the tissues of animals that cease feeding for extended periods of time increase in  $^{15}N$  (Hobson et al., 1993). Previously, Carey et al. (1982) estimated that a White Shark could survive for 1.5 months on 30 kg of whale blubber. When considering the documented transoceanic migration speed of a White Shark (Bonfil et al., 2005), it is also possible that feeding is limited during these long-distance movements. Consequently, the observed  $\delta^{15}N$  variation may be a result of interval based feeding patterns or sharks that have returned from a migration and/or are in poor condition.

Habitat partitioning between small and large animals may also contribute to the observed size-based shifts in diet and associated trophic position. Weng et al. (2007b) reported that small White Sharks off the coast of California occupied coastal nursery regions that were partially separated from the habitat occupied by larger individuals and were not characterized by large seal populations. Based on catches of small individuals (Bass et al., 1975; Cliff et al., 1989) and a scavenging event (Dicken, 2008), the suggested nursery region for White Sharks off southern Africa is in eastern cape waters. Larger White Sharks are known to transit through this area (Bonfil et al., 2005) but are more commonly sighted in the vicinity of highly productive seal colonies in the western cape (Martin et al., 2005). Size-based habitat partitioning and associated diet separation is widely reported in sharks (Simpfendorfer et al., 2005). Furthermore, the eastern cape and KwaZulu-Natal provide highly productive nursery habitat for numerous carcharhinid species, including the dusky shark (Hussey et al., 2009). This may explain the high incidence of elasmobranch prey, particularly the dusky shark, in the diet of White Sharks. The  $\delta^{13}C$  data, however, are contradictory to this proposed size-based habitat model because the two smallest animals had the most depleted  $\delta^{13}C$  values, indicative of offshore foraging (Schell et al., 1998). The smallest sharks, however, were estimated to be only a few months old, and their isotope values were most probably confounded by the maternal signature (Olin et al., 2011).

White sharks >4 m PCL are not commonly reported from the coastal waters of the cape region or from captures in beach protection nets in KZN (Cliff et al., 1989, 1996). In the eastern Pacific Ocean, large White Sharks are known to be seasonal residents during the elephant seal (*Mirounga angustirostris*) pupping season (Weng et al., 2007b; Jorgenson et al., 2010) but then move offshore (Weng et al., 2007b; Domeier and Nasby-Lucas, 2008; Chapter 11, this volume), with large females remaining resident in offshore waters for extended periods of time (Jorgenson et al., 2010; Chapter 11, this volume). The largest animal included in this diet analysis was 373 cm PCL, and therefore we have limited data to comment on the prey of large mature White Sharks. The data for the largest size class would suggest that whale and seal are primary dietary components, but stomach content data may be inaccurate if these sharks inhabit offshore waters for extended periods of time, because oceanic prey may be digested and therefore not detected when the animal returns inshore. The fact

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that the  $\delta^{13}\text{C}$  value of the largest shark and the smallest shark were depleted relative to all the mid-size sharks may indicate that large animals in South African waters, including pregnant females, are foraging in offshore waters and remain offshore. Malcolm et al. (2001) found that White Sharks >5 m TL contained only teleosts and elasmobranchs, and Smale and Cliff (Chapter 4, this volume), using cephalopod beaks from this stomach content data, suggested that oceanic cephalopods may be an important diet component of the largest White Sharks. Considering the abundance of large cephalopods in oceanic waters and their importance in the diet of carnivorous whales (Fiscus et al., 1989), cephalopods in conjunction with pelagic teleosts may be an underestimated component in the diet of large White Sharks.

In conclusion, the White Shark off Southern Africa is an opportunist, generalist predator that shows size-based preference for marine-mammal prey, similar to observations on the diet and feeding behavior of this species in other geographic localities. Both stomach content and stable isotope data ( $\delta^{15}\text{N}$ ), however, showed that White Sharks >200 cm PCL may not all feed exclusively on marine mammals, indicating (1) individual specialization within a generalist population and (2) interindividual foraging success.

Further work, including coupling genetic and stable isotope analyses, is required to examine these points. The White Shark is an apex predator that exerts influence across multiple components of marine ecosystems. Considering the inability of such large predatory sharks to sustain exploitation even at moderate levels (Garcia et al., 2008), understanding and documenting the diet and trophic ecology of this species is a requirement for ecosystem- and fisheries-management and conservation initiatives.

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