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The trophic relationships of two hake species (*Merluccius capensis* and *M. paradoxus*) and three shark species (*Centrophorus squamosus*, *Deania calcea* and *D. profundorum*) were investigated using nitrogen and carbon stable isotope signatures (δ^{15}N and δ^{13}C) of their muscle tissues. The sharks were more enriched in ^{15}N than the hake, an indication of the apex predator status of sharks. Among the sharks considered, *C. squamosus* occupied the highest trophic level and fed primarily on benthic prey. The two species of shark from the genus *Deania* were not different based on δ^{15}N or δ^{13}C, so they had similar diets. The δ^{13}C signatures indicated that *M. capensis* and sharks fed on prey derived from similar basal resources. However, there was a significant difference in δ^{13}C between *M. paradoxus* and all other species examined, suggesting that they occupied different feeding niches. Isotope-based population metrics showed narrower trophic ranges in sharks than *M. capensis*. Carbon and nitrogen ranges indicated that hake fed on a more diverse pool of carbon sources and had generally more enhanced trophic diversity in their feeding patterns than sharks. Among the species considered, *C. squamosus* occupied a unique isotopic space. Our results supported the hypothesis there are trophic overlaps among these species, but some interesting differentiation was revealed.

Keywords: diet, ecological role, food web, stable isotopes, standard ellipse area, trophic niche, top predators

Introduction

Trophic relationships play major roles in the structuring of aquatic systems (Vander Zanden et al. 2000; Heithaus et al. 2008; Laroche et al. 2008). Understanding the trophic relationships among different marine species is necessary for researchers to gain insights into how they influence food web structure (Pethybridge et al. 2011). The marine waters off Namibia have very high levels of upwelling-based primary production that support a large biomass of marine species, resulting in complex trophic linkages (Hutchings et al. 2009). Hake (*Merluccius capensis* and *M. paradoxus*) are important secondary and tertiary consumers in the Benguela Current ecosystem (Roel and Macpherson 1988; Heymans et al. 2004). Sharks such as *Centrophorus squamosus* (Bonnaterre, 1788)*, Deania calcea* (Lowe, 1839) and *Deania profundorum* (Smith & Radcliffe, 1912) have overlapping depth distributions with hake (Bianchi et al. 1999; Burmeister 2001). Shark species are considered top predators (Cortes 1999; Rogers et al. 2012) that feed on a variety of fish (Ebert 1991, 1994; Barnett et al. 2012), pinnipeds and cetaceans (Pethybridge et al. 2011). Stomach content analyses of *C. squamosus*, *D. calcea* and *D. profundorum* have indicated that they feed on hake (Yano 1991; Ebert et al. 1992; Ebert 1994) and other prey common with hake (Payne et al. 1987; Roel and Macpherson 1988)**.** However, the degree and nature of any trophic overlaps between hake (*M.*

capensis and *M. paradoxus*) and sharks (*C. squamosus*, *D. calcea* and *D. profundorum)* in Namibian waters have not been assessed.

Fisheries management is moving towards an ecosystem-based approach (Roux and Shannon 2004; Cochrane et al. 2009) that requires a more thorough understanding of trophic interactions among syntopic species (Shannon et al. 2006). Our study contributes towards recent research efforts that consider trophic dynamics as important determinants of fisheries management decisions. For example, several researchers have used stable isotope techniques to assess the trophic roles of sharks in different regions of the world (Davenport and Bax 2002; Estrada et al. 2003; Domi et al. 2005).

Given the common prey in their diets (Roel and Macpherson 1988; Yano 1991; Ebert 1994) and the overlapping depth distributions for sharks and hake (Macpherson and Roel 1987; Bianchi et al. 1999; Burmeister 2001), we hypothesised that their isotopic niches overlap substantially. Isotopic niche width correlates positively with diet breadth of a species (Cummings et al. 2012), and therefore it can be used to make inferences about a population's trophic niche width (Syväranta et al. 2013). Our study represents the first comparative investigation of the trophic relationships of sharks and hake in the northern Benguela Current ecosystem (Namibia) using stable isotope analysis.

Materials and methods

Field sampling

Fish were collected during hake biomass surveys (12 January–24 February 2011) in Namibian waters onboard *MV Blue Sea I*. The primary aim of the survey was to estimate the biomass and size composition of the hake stock off Namibia, hence sampling followed a predetermined schedule and route confined between the borders of Angola (latitude 17°12′ S) and South Africa (29°30′ S) at a depth range of 90–700 m (Figure 1). Sampling was done using a Gisund Super two-panel bottom trawl (head length 31 m, footrope 47 m, and vertical net opening 4.5–5.5 m). Trawling speed averaged 3.0 knots, and trawling time was 30 min except during interruptions arising from large catches, or a rocky or muddy bottom. The hake survey had a systematic transects design, with a semi-random distribution of stations along transects (Kainge et al. 2011). Sampling per station was done with the general goal of obtaining a wide size distribution of each species. At each sampling station, individual fish (up to 10 specimens when available) were chosen from the largest, intermediate and smallest size groups. After identification, each fish was measured (total length), and a small section of white muscle was removed from the anterior-dorsal region of each specimen (hake and sharks). Skin was removed from the muscle, and the muscle was immediately wrapped in aluminium foil and frozen at −20 °C on the ship.

Laboratory analysis

Tissue samples were dried for 48 h at 60 °C, ground to a fine powder using a mortar and pestle, and placed in polyethylene vials for storage. All samples collected were analysed at IsoEnvironmental CC (Grahamstown, South Africa) using a Europa Scientific elemental analyser coupled to a 20-20 isotope ratio mass spectrometer. Beet sugar, ammonium sulfate and casein were used as in-house standards calibrated against International Atomic Energy Agency (IAEA) standards CH-6 and N-1. The $^{12}C/^{13}C$ and $^{14}N/^{15}N$ isotope measurements were expressed in the delta notation relative to the levels of ^{13}C in Pee Dee Belemnite and ^{15}N in atmospheric nitrogen (N_2), according to the following equation:

$$\delta X = \{(R_{sample}/R_{standard}) - 1\} \times 1\,000$$

where X is ^{13}C or ^{15}N, and R is the ratio of the heavy to light isotope for the sample (R_{sample}) and standard ($R_{standard}$) in units of parts per thousand (‰).

Because carbon isotope ratios can be altered by changes in lipids irrespective of the carbon source (McConnaughey and McRoy 1979), measurements were mathematically corrected for lipid variations using a normalisation equation from Post et al. (2007):

$$\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$$

where $\delta^{13}C_{untreated}$ was the $\delta^{13}C$ of non-lipid extracted tissue. The $\delta^{13}C$ of samples having C:N ratios <3.5 do not benefit from lipid normalisation (Post et al. 2007), therefore only samples expressing C:N ratios >3.5 were lipid normalised.
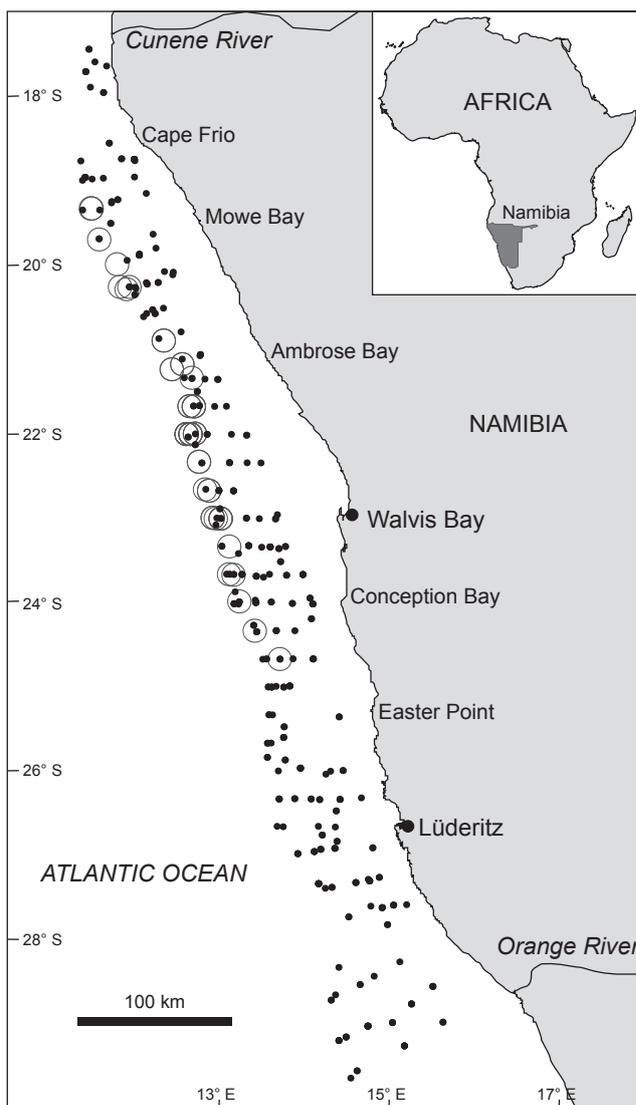
Figure 1: Map of the coast of Namibia showing the sample collection sites (empty circles)

Lipid extraction was not performed as it can alter $\delta^{15}N$ values, requiring separate analyses of $\delta^{13}C$ and $\delta^{15}N$ (Sweeting et al. 2006). The mathematical lipid correction method has worked successfully for lipid correction of $\delta^{13}C$ in deep-sea fishes (Hoffman and Sutton 2010).

To calculate the relative trophic level (TL) of each species, the following equation was used:

$$TL = [(\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta\delta^{15}N] + 2.0$$

where $\delta^{15}N_{consumer}$ is the signature of the consumer, $\delta^{15}N_{base}$ is the baseline value of the food web, $\Delta\delta^{15}N$ is the trophic enrichment factor, and the value 2.0 indicates the trophic level of the organism used to establish the $\delta^{15}N_{base}$ (in this case, bivalves *Choromytilus meridionalis* collected from Lüderitz [south coast, $n = 6$], Swakopmund [central coast, $n = 6$] and Henties Bay [northern coast, $n = 6$] during the same time frame; mean of 9.8‰). The mytilid bivalves

(TL = 2.0) were used as the base level because bivalves are primary consumers that have protracted isotopic turnover rates that can integrate seasonal variability (Lorrain et al. 2002; Fukumori et al. 2008). The trophic enrichment factor was set at 3.4‰ per trophic level (Minagawa and Wada 1984; Post 2002).

Statistical analysis

Differences in the $\delta^{15}N$ and $\delta^{13}C$ values among hake and shark species were determined using one-way permutational analysis of variance (PERMANOVA; 9 999 iterations using a Euclidean matrix) together with associated pairwise tests. The relationships between size (total length) and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) were evaluated using Spearman's rank correlation analysis. Isotope-based metrics calculated included $\delta^{15}N$ range (NR), an indicator of trophic diversity; $\delta^{13}C$ range (CR), representing the niche diversification at the base of a food web; and total area (TA) of the convex hull, which represented niche area occupied by a population (Layman et al. 2007). The convex hulls showed how individuals were dispersed in isotope niche space (Jackson et al. 2012). Because convex hull area increases with sample size (Jackson et al. 2011), total areas of convex hulls are not comparable between populations with different sample sizes. As such, the standard ellipse area, corrected for small sample sizes (SEA$_c$), was calculated to account for variation in sample size (Jackson et al. 2011). Statistical analyses were done using the SIAR package in R (R Core Team 2012) or PAST 3.0 (Hammer et al. 2001).

Results

Isotopic characteristics of hake and sharks

A total of 147 samples representing hake (*M. capensis* and *M. paradoxus)* and sharks *(D. profundorum, D. calcea* and *C. squamosus)* was analysed to derive $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures (Table 1)*. Centrophorus squamosus* had the highest mean $\delta^{15}N$ (15.1‰) and $\delta^{13}C$ values (−15.8‰). *Merluccius capensis* expressed the lowest mean $\delta^{15}N$ value (13.0‰), whereas *M. paradoxus* had the lowest mean $\delta^{13}C$ value (−16.6‰; Table 1). *Centrophorus squamosus* had the highest average trophic level of 3.5, whereas *M. capensis* had the lowest trophic level of 2.9 (Table 1).

Total length of the species considered ranged from 22 to 65 cm for *M. paradoxus*, 16 to 69 cm for *M. capensis*, 50 to 88 cm for *D. profundorum*, 43 to 121 cm for *C. squamosus* and 49 to 110 cm for *D. calcea. Deania calcea*, *M. capensis* and *M. paradoxus* showed significant correlations between

total length and $\delta^{15}N$, whereas *C. squamosus* and *D. profundorum* did not (Table 1, Figure 2a). *Merluccius paradoxus* was the only population that showed no significant correlation between length and $\delta^{13}C$ (Table 1, Figure 2b). Visual plots (Figure 2) and correlations clearly showed that the relationships between body length and isotopic signatures were different for each isotope and species and, although most of the relationships were linear, the relationship between $\delta^{13}C$ and body length of *M. capensis* was curvilinear (shown as a linear line in Figure 2b for consistency).

There was a significant difference in $\delta^{15}N$ values among the populations (one-way PERMANOVA, *F*-value = 38.77, df = 4, $p < 0.05$). Pairwise comparisons indicated that there were no significant differences between $\delta^{15}N$
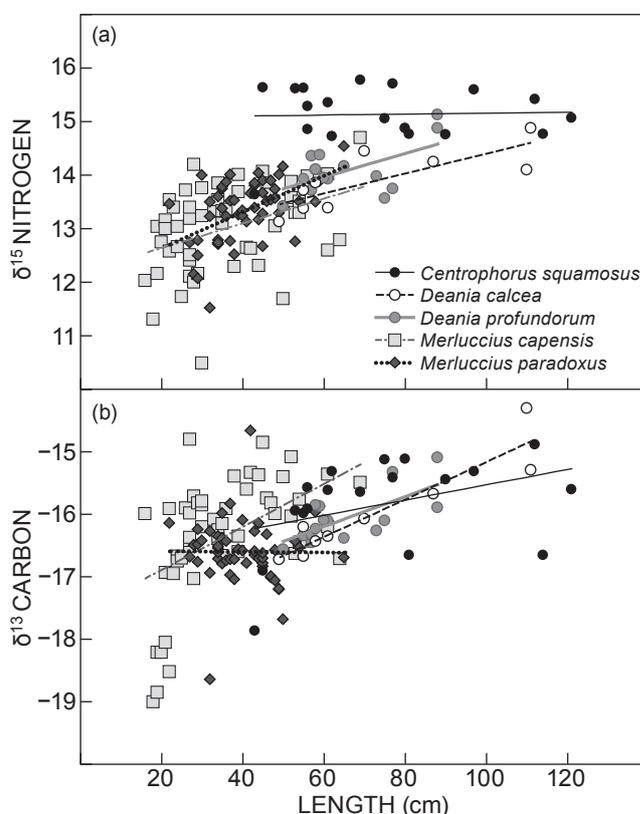
Figure 2: Isotopic values of (a) $\delta^{15}N$ and (b) $\delta^{13}C$ (‰) in sharks (*Centrophorus squamosus*, *Deania calcea* and *D. profundorum*) and hake (*Merluccius capensis* and *M. paradoxus*) relative to body length (cm). Lines represent correlation analyses

Table 1: Mean (SD) values of stable nitrogen and carbon isotope ratios for sharks and hake, together with sample sizes (*n*), trophic level (TL), C:N ratios and correlation results (*r* and *p*-values)

Species	n	TL	$\delta^{15}N$	$\delta^{13}C$	C:N	$\delta^{15}N$ vs Length		$\delta^{13}C$ vs Length	
						r	p-value	r	p-value
C. squamosus	18	3.56 (0.16)	15.11 (0.53)	−15.83 (0.78)	2.60 (0.21)	−0.14	0.57	0.48	0.04
D. calcea	9	3.19 (0.16)	13.90 (0.57)	−15.98 (0.78)	2.61 (0.05)	0.87	0.004	0.91	<0.01
D. profundorum	15	3.24 (0.13)	14.08 (0.46)	−16.07 (0.41)	2.61 (0.07)	0.36	0.19	0.65	0.009
M. capensis	54	2.93 (0.24)	13.02 (0.81)	−16.31 (0.94)	3.21 (0.07)	0.41	0.003	0.51	<0.001
M. paradoxus	52	3.10 (1.70)	13.32 (0.59)	−16.60 (0.53)	3.26 (0.17)	0.49	<0.001	−0.16	0.25

in *D. profundorum* and *D. calcea* (*p* = 0.39*)*, but all other pairs were significantly different (*p* < 0.05). There was a significant difference in δ¹³C values (*F*-value = 4.74, df = 4, *p* < 0.05) among populations, and the pairwise comparisons showed that the difference occurred between *M. paradoxus* and all other populations (*p* < 0.05).

Trophic niches

Isotope-based population metrics indicated that *M. capensis* had the widest δ¹⁵N (largest difference = 4.2‰) and δ¹³C ranges (4.2‰), whereas *D. profundorum* had the narrowest δ¹⁵N (1.7‰) and δ¹³C ranges (1.5‰). *Merluccius capensis* had the largest convex hull (TA; 10.52), with *D. profundorum* having the smallest (1.65; Table 2). *Merluccius capensis* had the largest SEAc (2.35), whereas *D. profundorum* had the smallest (0.56; Table 2, Figure 3). The trophic niches of *Deania* sharks overlapped with those of both hake populations (Figure 3).

Discussion

We investigated the trophic relationships of two hake species (*M. capensis* and *M. paradoxus*) and three sharks (*C. squamosus*, *D. calcea* and *D. profundorum)* off Namibia using stable isotopes. The shark populations had higher δ¹⁵N signatures than hake, but they all had mostly similar δ¹³C signatures. The general similarities in δ¹³C signatures (except for *M. paradoxus*) indicated that almost all of the predator populations we analysed fed on prey having similar δ¹³C signatures. The distinction of δ¹³C values in *M. paradoxus* compared with the other hake was not expected, but indicated some measurable differences in the prey fields of this population. Isotope-based population metrics (δ¹⁵N range and δ¹³C range) indicated that the hake populations had greater diversification in their feeding habits than the shark populations.

Centrophorus squamosus fed at the highest trophic level compared with the other species analysed (mean δ¹⁵N 15.1‰, trophic level 3.5), with their nitrogen isotope values significantly different from all of the other shark and hake populations. The two sharks from the *Deania* genus (*D. profundorum* and *D. calcea*) were not significantly different from each other in terms of δ¹⁵N values, an indication that they fed on prey from similar trophic levels. *Merluccius capensis* and *M. paradoxus* also differed from one another, and from the sharks, in terms of δ¹⁵N values, although we had expected substantial similarities between the two hake populations. However, the overall isotopic niche similarities between the hake species (Figure 3)

confirmed stomach content findings from previous studies, which indicated that they had similar prey in their diets (Roel and Macpherson 1988). Differences in diet relative to ontogenic development have been identified in the two hake species inhabiting the marine waters off Namibia (Iitembu et al. 2012), but because the size ranges of the two populations in our study were similar, differences in ontogeny between species probably were not important. *Merluccius capensis*, with the lowest δ¹⁵N values (mean 13.0‰; TL = 2.93), fed at the lowest trophic level compared with all of the other populations, possibly because it fed on prey with lower δ¹⁵N values inhabiting the continental shelf (Yoshii et al. 1999) since it inhabits shallower depths than *M. paradoxus* (Burmeister 2001). The prey base of *D. calcea* overlapped with that of *M. paradoxus* and *M. capensis* (shown from the overlaps in isotopic niche space; Figure 3), but the isotopic niches of the other sharks were quite distinct from the hake, showing clear partitioning of the prey available in the region.

The shark *C. squamosus* had the highest δ¹³C values (mean −15.8‰), an indication of its possible dependence on benthic prey, which are generally more enriched in ¹³C than pelagic prey (France 1995; Davenport and Bax 2002; Le Loc'h et al. 2008). Studies using stomach content analyses have also indicated that C. *squamosus* is a benthic foraging shark (Dunn et al. 2013). However, the only significant difference in δ¹³C was between *M. paradoxus* and all of the other populations, so *M. paradoxus* fed on prey that differed in carbon sources. *Merluccius paradoxus*, which had the lowest δ¹³C (mean −16.6‰), probably had increased proportions of pelagic prey in its diet. The relatively higher δ¹³C values in benthic species occur because of their dependence on organic carbon modified through degradation and microbial recycling processes (Fry and Wainright 1991; Hobson et al. 1995). Although measuring the strength of trophic interactions between species is difficult (Wootton and Emmerson 2005), the isotopic information we have collected from the Benguela Current region indicated that the trophic interactions between all of the species were relatively and surprisingly weak, apart from the two *Deania* sharks.
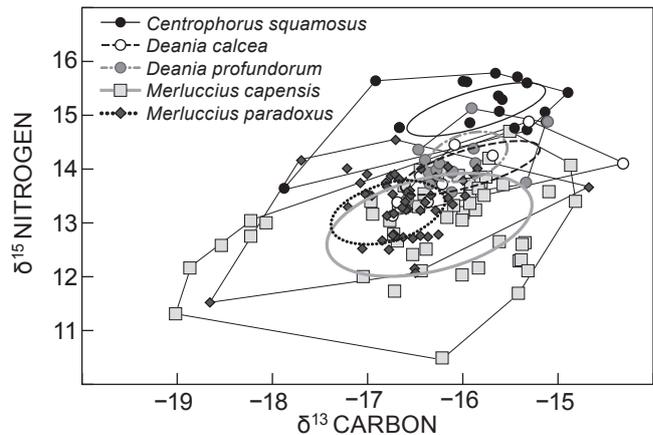
Figure 3: Isotopic niches of *Centrophorus squamosus*, *Deania calcea*, *D. profundorum*, *Merluccius capensis* and *M. paradoxus* as depicted by convex hull (polygons) and SEAc (ellipses)

Table 2: Carbon ranges (δ¹³C *R*), nitrogen ranges (δ¹⁵N *R*), total convex hull areas (TA) and standard ellipse areas (SEAc) of hake and shark populations. The number of individuals used to calculate the metrics are shown in parentheses

Species	δ¹⁵N *R*	δ¹³C *R*	TA	SEAc
C. squamosus (18)	2.14	2.98	3.36	1.21
D. calcea (9)	1.76	2.43	1.86	1.22
D. profundorum (15)	1.71	1.48	1.65	0.56
M. capensis (54)	4.21	4.20	10.52	2.35
M. paradoxus (52)	3.02	3.97	6.26	0.97

The populations of hake and the shark *D. calcea* had significant positive correlations between total length and $\delta^{15}N$ values, an indication of ontogenetic shifts in their feeding habits (Araújo et al. 2011). Positive correlations between total length and $\delta^{15}N$ are common in many marine organisms (Deudero et al. 2004), including hake (Iitembu et al. 2012) and sharks (Estrada et al. 2006). The absence of a significant correlation between body size and $\delta^{15}N$ values in *C. squamosus* was probably because we did not sample any very small individuals from that population (all sharks collected were >40 cm), and the lack of a significant relationship in *D. profundorum* was probably an effect of the small sample size ($n = 15$). *Merluccius paradoxus* did not have a significant relationship between $\delta^{13}C$ values and total length, indicating some degree of specialisation in this species. While fish can feed on a wide range of available prey, the community biomass may be largely reliant on only a few relatively abundant prey taxa (Al-Habsi et al. 2008). However, conclusions on specialisation cannot be based on isotope data only, and we recommend additional stomach content analyses be conducted on sharks and hake at different stages of their life cycles.

Merluccius capensis, which had wider $\delta^{15}N$ and $\delta^{13}C$ ranges than the other species, possibly fed on prey from various trophic levels and multiple basal resources. All of the sharks expressed narrower $\delta^{15}N$ and $\delta^{13}C$ ranges than the hake, an indication of narrow feeding ranges in the sharks. The total isotopic area (TA), which represents the total amount of niche area occupied by a species (Layman et al. 2007), was also narrower for the sharks compared with the hake. In term of SEA$_c$, that of *M. paradoxus* was less than those of C. *squamosus* and *D. profundorum.* Although top predators such as sharks are often assumed to be dietary generalists, there is evidence that *s*ome shark species such as tiger sharks (*Galeocerdo cuvier*) exhibit some form of specialised feeding (Taylor and Bennett 2008; Matich et al. 2011). The variations in isotopic niche areas of our species of interest can also be an indication of their varying levels of specialisation. Our data on three shark populations from the Benguela Current region indicated that *C. squamosus* occupied a unique isotopic niche area (Figure 3). The similarities between the diets of *D. profundorum* and *D. calcea* (see SEA$_c$ in Figure 3) are probably related to the morphological similarities in their body forms and feeding structures (Bianchi et al. 1999; Ferry-Graham et al. 2002). The overlapping isotopic niche areas in these two shark populations indicated that they probably had similar diets, and the separate niche area for *C. squamosus* indicated that it had a more specialised diet distinct from the other sharks (Figure 3). Fatty acid profiling and gut content analyses of dogfish have indicated that sharks occupying a broad depth and bathymetric distribution were recognised as generalist feeders, whilst other species occupying upper-slopes had dietary selectivity for crustaceans (Pethybridge et al. 2011). A study using fatty acid and stomach content analyses is recommended to investigate the factors driving the differences in diet among the three shark populations from the Benguela Current region.

The three shark populations occupied relatively small areas of isotopic niche space relative to *M. capensis*. Narrower isotopic niches in the sharks can indicate feeding specialisation that reduced competition with *M. capensis*; however, the individual variability in isotopic values showed some degree of overlap among these predators. Our study carries limitations inherent in the use of stable isotopes in ecological studies, such as the potential errors involved in using average trophic fractionation factors of 3.4‰ for $\delta^{15}N$ and 0.39‰ for $\delta^{13}C$ (Post 2002). Experimental work has demonstrated that fractionation can vary among consumers (Vanderklift and Ponsard 2003; Caut et al. 2009). Future studies should therefore focus on measuring species-specific trophic fractionation factors. While our data allowed for some inferences on the trophic relationships of several predators, we recommend additional studies with increased sample sizes of predators and prey across different temporal and spatial scales. The increase in sample size can increase the precision of population-level isotopic niche calculations (Syväranta et al. 2013), and it will cover a wider distribution range of these predators' populations. We found interesting differences in isotopic niche among most of our species of interest, so a next step is to obtain more detailed information about the temporal changes in the distribution of the populations in the Benguela region so that we may infer how these trophically similar populations are partitioning their environment.

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