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Characterising the trophic relationships between cuttlefishes, myctophids and round herring in the Northern Benguela

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Abstract

Round herrings, myctophids, and cuttlefishes are a crucial part of the trophic interactions in the northern Benguela, as they form important trophic linkages between macrozooplankton and predators like hake, horse mackerel, and monk. The main objective of this study was to understand their trophic relationships using stable isotope measurements of their tissues. Tissues from round herring [*Etrumeus whiteheadi*], Myctophid species [*Symbolophorus boops*, *Lampanyctodes hectoris, Diaphus hudsoni*, *Lampanyctus australis, Diaphus meadi*], and cuttlefishes [*Sepia australis* and *Sepia elegans]* specimens were collected off Namibia. There were little variations in nitrogen stable isotopes ($\delta^{15}N$) values among these species, an indication that they fed at similar trophic positions. The trophic levels ranged from 2.51 to 3.00, an indication of their zooplanktivorous feeding habits. Among these species *S. boops* fed at a relatively higher trophic level, while *L. hectoris* fed at the lowest trophic level. *Diaphus hudsoni* had the lowest carbon stable isotope ($\delta^{13}C$) values and *E. whiteheadi* the highest. Significant differences were observed in $\delta^{13}C$ values between most species, suggesting significant variations in their carbon sources. Isotope-based metrics showed overlapping trophic niches, with *S. boops* having a significantly broader niche. Our observations support the hypothesis that although these forage species have overlapping trophic niches, there are pronounced differences in the carbon sources of their prey.

Keywords: Cuttlefishes, Myctophids, Northern Benguela, round herring, trophic interactions.

1. Introduction

The marine waters off Namibia are highly productive as a result of the Benguela upwelling phenomenon along the southwest coast of Africa (Hutchings et al., 2009). The bases of most marine food webs consist of phytoplankton, with zooplankton being the major link between primary producers and higher trophic levels (García-Isarch, Millán, & Ramos, 2012). Many marine ecosystems have large numbers of species at the lower trophic levels, and a substantial numbers of predatory fishes that feed at the apex or near-apex levels, and a crucial intermediate trophic level of plankton-feeding pelagic fishes (Bakun, 2006; Cury et al., 2011). Round herring, myctophids, and cuttlefish species are part of the intermediate trophic level of plankton-feeding fish species in the Northern Benguela (Pakhomov, Perissinotto, & McQuaid, 1996; Hutchings et al., 2009). They are important prey of predators like hake species (*Merluccius paradoxus* and *M. capensis*) (Roel & Macpherson, 1988), horse mackerel (*Trachurus capensis*) (Macpherson & Roel 1987) and Monkfish (*Lophius*

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vomerinus) (Walmsley, Leslie, & Sauer, 2005), and therefore form important trophic linkages between primary consumers and these predators.

Cuttlefishes [*Sepia elegans* (Blainville, 1827) and *Sepia australis* (Quoy and Gaimard, 1832)] are found from 30 m to 459 m depth (Bianchi et al., 1999) and feed on zooplankton and fish (Mqoqi, Lipiński, & Salvanes, 2007). The myctophids [(*Symbolophorus boops* (Richardson, 1845), *Lampanyctodes hectoris* (Günther, 1876), *Diaphus hudsoni* (Zurbrigg & Scott, 1976), *Lampanyctus australis* (Tåning, 1932) and *Diaphus meadi* (Nafpaktitis, 1978)] occur at depths of 250 to 500 m (Bianchi et al., 1999) and are significant predators of zooplankton (Connan, Mayzaud, Duhamel, Bonnevie, & Cherel, 2010). Round herring (*Etrumeus whiteheadi*) occurs at a depth of about 200 m (Bianchi et al., 1999; Sumaila & Steinshamn, 2004), its food items consist of mainly zooplankton (James, 1988).

Food webs consist of a network of organisms connected by their trophic interactions, with differences in the relative strength and importance of these interactions. Assessing these trophic relationships is a daunting task, especially when considering that year-round sampling of different components of the food web is highly problematic (Cortés, 1999). Understanding trophic relationships among marine species is however crucial to managing our marine ecosystem with higher certainty (Mueter & Megrey, 2006; Yodzis, 1994), and through management approaches that consider multi-species trophic interactions (Garcia & Cochrane, 2005; Cochrane et al., 2009). Stable isotope analysis is now increasingly used in ecological research (Post et al., 2007; Iitembu, Miller, Ohmori, Kanime, & Wells, 2012). Stable isotope method is based on the principle that carbon and nitrogen isotope ratios in animals' tissues closely reflect that of their diet (Vander Zanden, Hulshof, Ridgway, & Rasmussen, 1998; Post, 2002).

This study aimed at understanding trophic interactions of cuttlefishes (*S. elegans* and *S. australis*); myctophids (*S. boops*, *L. hectoris, D. hudsoni*, *L. australis, and D. meadi*) and round herring (*Etrumeus whiteheadi*) in the Northern Benguela using stable isotope (δ^{13}C & δ^{15}N) measurements. It was hypothesised that these species have overlapping trophic niches as they have common prey and overlapping depth distributions. This study contributes towards understanding trophic interactions in Namibian marine waters, which could lead become relevant in ecosystem management decisions. The results could also contribute towards the construction of ecosystem models of the Northern Benguela current ecosystem.

2. Material and Methods

2.1 Field sampling

This study was conducted off the coast of Namibia, from 29° S to 17° S (Fig 1). Sampling was done during the annual hake (January and February 2013 and 2014), monkfish (November 2012 and 2013) and horse mackerel (September, October and March 2012–2014) biomass surveys on board the *FV Blue Sea* I and *R.V. Welwitchia*. A Gisund Super two-panel bottom trawl net was used for hake surveys, albatross bottom trawl net was used for monkfish survey while Carmen midwater trawl net was used in horse mackerel surveys. Because of the nature of the main surveying work, the sampling followed survey pre-determined stations. A maximum of five individuals per species were collected when available in the trawling net. After the identification of each fish; their length and weight measurements were recorded. The samples were stored in ziplock bags and frozen at about -20 °C.

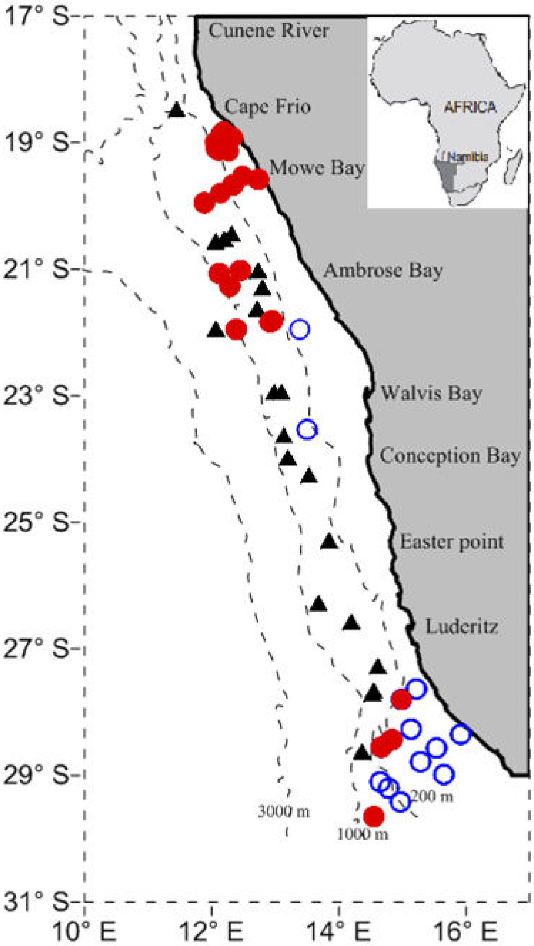

Figure 1: Geographical positions where samples for *Etrumeus whiteheadi* (red closed circle), myctophids (black triangle) and Sepia sp (blue open circle) were collected off Namibia.

2.2 Laboratory analyses

A tissue (about 0.05 g) was cut from the anterior-dorsal region of each fish and from each cephalopod. The muscle tissue was dried in an oven for 48 h, at 60 °C and ground into a fine powder. Isotope analysis was done using a Europa Scientific Elemental Analyzer coupled to a 20–20 Isotope Ratio Mass Spectrometer (IRMS) (Rhodes University, South Africa). 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 ^{14}N in atmospheric nitrogen (N_2) as parts per thousand (‰).

No lipid extraction was done, and because carbon isotope ratios can be altered by changes in lipids irrespective of the carbon source (McConnaughey & McRoy, 1979), all $\delta^{13}C$ of samples were lipid normalised using the normalisation equation from Post et al. (2007):

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

where $\delta^{13}C_{\text{untreated}}$ is the $\delta^{13}C$ of non-lipid extracted tissue, $C{:}\ N$ is the mass ratio of carbon and nitrogen. The mathematical correction was done for the $\delta^{13}C$ of samples having C: N ratios < 3.5 do not benefit from lipid normalization (Post et al., 2007) and were not lipid corrected.

2.3 Statistical analysis

Data was examined for normality and homogeneity of variance using the Shapiro-Wilk and Levene tests, respectively. Analysis of variance (ANOVA) was used to test for significant differences in $\delta^{15}N$ and $\delta^{13}C$ of the analysed species. Where there were statistically significant differences, a post-hoc comparison was done by a Tukey HSD (Tukey Honest Significant Difference) test.

The trophic level (TL) of each species, was calculated by the following equation:

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

where $\delta^{15}N_{consumer}$ is the isotope value of the consumer, $\delta^{15}N_{base}$ is the baseline value, $\Delta\ \delta^{15}N$ is the trophic enrichment factor, which was set at 3.4‰ in $\delta^{15}N$ (Minagawa & Wada, 1984; Post, 2002), the value 2.0 indicates the TL of the organism used to establish the $\delta^{15}N_{base}$. The mean $\delta^{15}N_{base}$ was 9.2‰, obtained from two mytilid bivalve species (*Choromytilus meridionalis* and *Mytilis galloprovincialis*) measured in (Iitembu et al., 2012). The bivalve species were chosen because they are primary consumers that have protracted isotopic turnover rates that can integrate seasonal variability (Lorrain et al., 2002; Fukumori et al., 2008). Nitrogen stable isotopes ($\delta^{15}N$) range (NR), an indicator of trophic diversity; Carbon ($\delta^{13}C$) range (CR), signifying 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 were calculated following (Layman, Quattrochi, Peyer, & Allgeier, 2007). The convex hulls indicated how individuals were dispersed in isotope niche space (Jackson et al., 2012). The total areas of the convex hull are affected by variation in sample size, (Jackson, Inger, Parnell, & Bearhop, 2011); hence a standard ellipse area (SEAc), was used compare the species trophic niche. All statistical tests were performed using R (R Core Team, 2018, Vienna, Austria).

Table 1: Mean (SD) values of $\delta^{15}N$ and $\delta^{13}C$, together with sample sizes (n), total length (cm), depth range, trophic level (TL) and C: N ratios of sampled fish species

Species	Total Length (cm)	Depth range (m)	$\delta^{15}N$	$\delta^{13}C$	C:N	TL
S. boops (66)	6.01 -1.6	214-574	10.94(±0.97)	-17.44(±0.83)	4.13	2.51
D. hudsoni (11)	6.50-8.19	28-306	11.12(±0.25)	-17.72(±0.53)	5.33	2.57
E. whiteheadi (117)	5.51-23.00	17-511	11.09(±1.77)	-16.86(±1.15)	3.49	2.67
D. meadi (21)	5.40-9.92	18-378	11.73(±1.19)	-17.24(±0.82)	4.93	2.75
S. australis (64)	5.00-10.00	87-236	11.74(±0.64)	-17.36(±0.46)	3.58	2.75
S. elegans (7)	7.03-10.00	56-286	11.75(±1.18)	-17.16(±0.74)	3.59	2.75
L. australis (28)	4.53-14.70	30-478	11.80(±1.16)	-16.99(±0.79)	4.61	2.77
L. hectoris(20)	4.92-8.21	111-428	12.61(±0.73)	-17.24(±0.72)	4.61	3.00

3. Results

3.1 Species isotopic characteristics

A total of 334 samples representing round herring, myctophids species and cuttlefishes was analysed to derive $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures (Table 1). *Symbolophorus boops* had the lowest mean $\delta^{15}N$ values (10.94‰) while *L. hectoris* had the highest mean $\delta^{15}N$ (12.61‰) values. *Diaphus hudsoni* had the lowest mean $\delta^{13}C$ (-17.72‰) values, while *E. whiteheadi* had the highest mean $\delta^{13}C$ (-16.86 ‰). Mean trophic levels estimated using $\delta^{15}N$ data was lowest (TL = 2.51) for *S. boops* and highest (TL = 3.0) for *L. hectoris* (Table 1). ANOVA results indicated significant differences in $\delta^{13}C$ values ($P < 0.01$, F = 6.16) and $\delta^{15}N$ values ($P < 0.01$, F = 2.74) among species.

Pairwise Tukey HSD post hoc test results for $\delta^{13}C$ indicated that *D. hudsoni* was significantly different from all the species analysed (Table 2). *Etrumeus whiteheadi* was also significantly different from most of the species, except *S. australis* (Table 2). Pairwise Tukey HSD post hoc test results for $\delta^{15}N$ indicated that most species were not significant different from each other. However, significant differences were found between the following species: *L. hectoris* was significantly different from *D. hudsoni*; *E. whiteheadi* and from *S. boops; Sepia australis* was significantly different from *E. whiteheadi* and *S. boops* (Table 2).

Table 2: Tukey multiple comparisons of means of $\delta^{13}C$ (Degree of freedom = 6.16) and $\delta^{15}N$ (Degree of freedom = 2.74)

Prey species compared	$\delta^{13}C$	$\delta^{15}N$
D. hudsoni - *L. hectoris*	p = 0.04	P = 0.004
D. hudsoni - *L. australis*	p = 0.02	
D. hudsoni - *E. whiteheadi*	p= 0.00	
D. hudsoni - S. *boops*	p = 0.00	
D. hudsoni - *S. elegans*	p = 0.00	
D. hudsoni - *S. australis*	p = 0.00	
E. whiteheadi - *S. boops*	p = 0.00	
E. whiteheadi - *L. australis*	p = 0.00	
E. whiteheadi - *L. hectoris*	p = 0.00	P = 0.00
E. whiteheadi - *S. australis*	p = 0.00	P = 0.02
E. whiteheadi - *D. meadi*	p = 0.00	
S. australis - *S. boops*	p = 0.01	P = 0.01
S. australis - *L. hectoris*	p = 0.01	
S. australis - *D. meadi*	p = 0.00	
S. elegans - *D. meadi*	p = 0.04	
L. hectoris - *S. boops*		P = 0.00

The *P*-values shown are only for species that were significantly different from each other in $\delta^{15}N$ or $\delta^{13}C$.

Table 3: Carbon range ($\delta^{13}C'R$), nitrogen range ($\delta^{15}NR$), the total area of the convex hull (TA) and standard ellipse area (SEAc) of species in this study

Species	δ^{15} NR	δ^{13} C' R	SEAc	TA
Etrumeus whiteheadi (117)	4.73	8.64	3.01	15.37
Diaphus hudsoni (11)	0.76	1.74	0.58	1.08
Diaphus meadi (21)	4.27	3.59	3.57	8.1
Lampanyctus australis (28)	3.61	3.6	3.42	9.57
Lampanyctodes hectoris (20)	3.31	2.96	1.32	4.01
Symbolophorus boops(66)	4.82	3.66	3.35	15.68
Sepia elegans (7)	3.39	4.91	2.61	3.6
Sepia australis (64)	3.66	2.17	0.68	4.37

The number of individuals used to calculate the metrics is shown in parentheses.

3.2 Trophic niches

Isotope-based population metrics indicated that the trophic niche (TA) of *S. boops* was the widest (15.68), whereas for *D. hudsoni* (1.08) was the narrowest (Fig. 2, Table 3). The trophic niches of *S. australis* and *S. boops* overlapped with all species analysed (Fig. 2). The trophic niches of *D. hudsoni, L. australis* and *E. whiteheadi* overlapped with the rest of the species analysed with exemption of *D. meadi* and *S. elegans* (Fig. 2). The trophic niches of *L. hectoris* did not overlap with that of *D. meadi* but overlapped with the rest of the analysed species (Fig. 2). *Sepia elegans* only overlapped with *S. australis*, *S. boops* and *L. hectoris*. While *D. meadi* only overlapped with *S. boops* and *S. australis* (Fig. 2). *Symbolophorus boops* had the highest NR (4.82), while *D. hudsoni* had the lowest $\delta^{15}NR$ (0.76) (Table 3). The $\delta^{13}CR$ was lowest for *D. hudsoni* (1.74), and highest for *E. whiteheadi* (8.64). *Diaphus meadi* had the largest standard ellipse area (SEAc) (3.57), while *D. hudsoni* had the smallest (0.58) (Table 3).

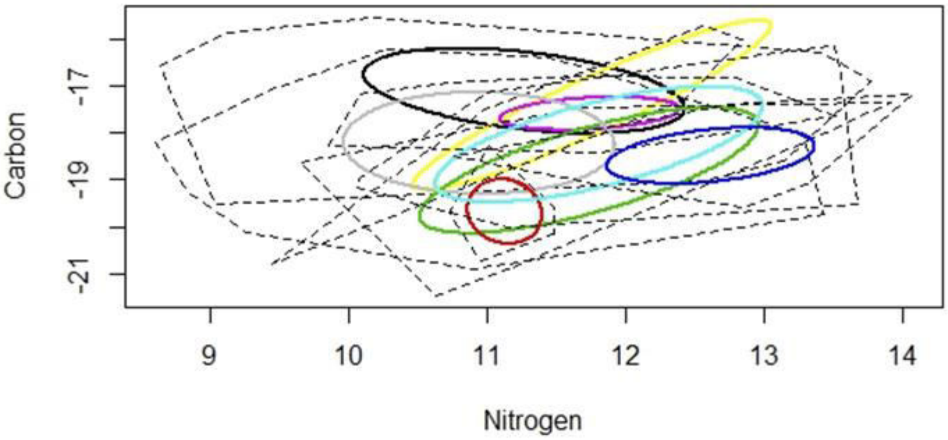

Figure 2: Trophic niche comparisons of *Etrumeus whiteheadi* (black circle), *Symbolophorus boops* (light blue circle), *Lampanyctus australis* (yellow circle), *Lampanyctodes hectoris* (grey circle), *Diaphus meadi* (dark blue circle), *Diaphus hudsoni* (pink circle), *Sepia australis* (green circle) and *Sepia elegans* (red circle) as portrayed by convex hull (polygons) and SEAc (ellipses).

4. Discussion

This study aimed at understanding the trophic relationships between various round herring, myctophids and cuttlefishes species off Namibia, using stable isotope values extracted from their muscle tissues. There were little variations is nitrogen ($\delta^{15}N$) values, while significant differences were observed in carbon ($\delta^{13}C$) values. The above is an indication that while these species fed at similar trophic levels, there were significant differences in carbon sources of their prey. All the species appeared to be predominantly zooplanktivorous as their trophic level (TL) ranged from 2.51–3.00. These species also had overlapping feeding ranges based on their overlapping isotopic niches. There were, however, differences in niche sizes, with *S. boops* (myctophids species) having a significantly wider trophic niche.

Most myctophids fed at a secondary trophic level, supporting the findings from (Connan et al., 2010) and (Pakhomov et al., 1996) that observed that diet of myctophids consisted of mainly of copepods. The cuttlefishes were also found to be feeding at a secondary trophic level, which is consistent with the findings from Mqoqi et al. (2007), who indicated that their diet consisted of primary consumers (euphausiids, mysids, and megalopae). Round herring (*Etrumeus whiteheadi*) had TL of 2.67, an indication that it fed on primary consumers. The TL of Round herring in this study is similar to what is reported in Iitembu et al. (2012). Round herring (*E. whiteheadi)* was also reported to feed at 3.64 TL (Van Der Lingen & Miller, 2014) in the southern Benguela ecosystem, a possible result of the biogeographic differences in isotopic baseline between northern and southern Benguela ecosystems. The isotopic baseline used to calculate the trophic positions (Post, 2002) are known to differ between geographic regions due to differences in local biogeochemical processes or prey availability (Espinoza, Munroe, Clarke, Fisk, & Wehrtmann, 2015).

Species-specific results showed that *Diaphus meadi, S. australis* and *S. elegans* fed on prey with similar $\delta^{15}N$ signatures. *Lampanyctodes hectoris* fed at the highest TL (3.00), indicating that it fed on preys with higher $\delta^{15}N$ measurements. Gaskett, Bulman, He, and Goldsworthy (2001) have observed remains of small fish in a diet of a myctophid species (*Elecrona carlsbergis*), and it is possible that *L. hectoris* fed on small fish which influenced its TL. *Symbolophorus boops* fed at the lowest TL (2.51), in comparison to other species considered in this study.

The $\delta^{15}N$ values of the species under this study were higher (10.94‰–12.61‰) than that of two mytilid bivalve species (*C. meridionalis* and *M. galloprovincialis*) (Kohler et al., 2011) which are primary consumers collected off Namibia (9.2 ‰). The above indicates that the species in this study are secondary consumers.

Most species were not significantly different from each other in term of δ^{15}N values (Table 2), which indicate they fed on prey with similar trophic positions. This is consistent with the fact that most of these species are documented as feeding on zooplanktons (Pakhomov et al., 1996; Bianchi et al., 1999). Some significant differences observed in δ^{15}N values were between *L. hectoris,* which was significantly different from *D. hudsoni*, *E. whiteheadi* and *S. boops*; *Sepia australis* significantly different from *E. whiteheadi* and *S. boops*. Differences in δ^{15}N values show that these species are dependent on different dietary resources which may be from different feeding positions. In terms of NR, an indicator of trophic diversity (Layman et al., 2007), a high NR was reported for *S. boops* (4.82‰) (Table 3). The above suggests that *S. boops* had high trophic diversity in its diet, while its feeding activities were directed at low trophic as shown by it having the lowest δ^{15}N values (10.94‰). The lowest NR (0.76‰) was observed for *D. hudsoni*, suggesting low trophic diversity in its feeding habits. Low trophic diversity of *D. hudsoni* is supported by results in Pakhomov et al. (1996) that observed that its stomach contents were dominated by *Pleuromamma* spp. (a copepod) in the southern Benguela ecosystem.

All species showed low δ^{13}C (-17.72‰ to -16.86‰, Table 1), when compared with primary consumers (-18.90‰) observed in (Kohler et al., 2011). This suggests that most species fed more offshore (Kurle et al., 2011) than the primary consumers in Kohler et al. (2011). Variations in δ^{13}C values of organisms in a marine trophic system, as displayed in some species analysed in this study (Table 1 & 2), may be mainly due to habitat-related carbon source (phytoplankton vs. benthic primary production) in the food webs (Peterson & Fry, 1987). The differences in δ^{13}C have also been attributed to differences in the foraging area (Hobson, 2005), which in this study can be as results depth-related differences of their distribution (Fig. 1). There is also evidence that the movement of organisms between deep water to shallower water can cause variation in their δ^{13}C signatures (Kurle & Worthy, 2001). *Diaphus hudsoni* had the lowest δ^{13}C values (-17.72‰) (Table 1), which could be a result of off-shore feeding activities. Most species were significantly different from each other terms of δ^{13}C (Table 3). The differences in δ^{13}C suggest that there are significant differences in local biogeochemical processes (Espinoza et al., 2015). The difference can also be an indication that the northern Benguela ecosystem is more dynamic, resulting in a heterogeneous mixture of food sources available to the various prey.

In terms of CR, *Diaphus hudsoni* had the lowest CR (Table 3) an indication of less diverse basal resource (Layman et al., 2007). *Etrumeus whiteheadi* had the highest CR (8.64‰) (Table 3), suggesting multiple basal resources in its diet, and the highest δ^{13}C values (-16.86‰) (Table 1). Van Der Lingen and Miller (2011) suggested that *E. whiteheadi* feeds on large zooplankton, the species may be dependent on pelagic phytoplankton driven-primary production as variations in δ^{13}C are known to occur between benthic-pelagic production (Nam, Miller, Huan, Tang, & Omori, 2011)

In terms of isotopic niches, *D. meadi* and *S. boops* had the widest than other species analysed (sea SEAc in Table 3). The above suggests that this species possibly have generalised feeding habits, which is highly influenced by prey availability and abundance. In contrast, *D. hudsoni* occupied a narrower isotopic niche (sea SEAc in Table 3) which can indicate some forms of feeding specialization (Young & Blaber, 1986). The isotopic niche (Fig. 2) of the species analysed, suggest that they had overlapping trophic niches, which is consistent with findings these species feed on from Gibbons (1999) and Mqoqi et al. (2007). The overlapping trophic niches could also be an indication that these species have little dietary specialisation (Young & Blaber, 1986). The trophic niche for *S. australis* overlapped with those of all the species analysed, while that of *D. meadi* only overlapped with those of *S. autralis* and *S. boops*. The above suggests that *D. meadi* had a diet that is different from most species considered in this study (Fig. 2). Our observations of the isotopic niche in this study support the hypothesis that these species have an overlapping trophic niche, although some specific differences were observed.

This study characterised the trophic relationships among cuttlefish, myctophids and round herring species in northern Benguela. The study also showed that the trophic relationships in Northern Benguela are highly complex and may be driven by various factors like local biochemical processes which are still not well understood. There is, therefore, a need for long term studies on these species which integrate small scale as well as large-scale temporal and spatial sampling of the ecosystem, to improve our understanding of trophic interactions within the northern Benguela ecosystem.

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