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The influence of the cape canyon on the food web structure of the southern Benguela upwelling system

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ABSTRACT

Submarine canyons are heterogeneous environments known to support a variety of benthic organisms and they are considered biodiversity hotspots. The peculiar hydrographic conditions that characterize these systems, including the high level of organic matter accumulation and transport, can lead to intense resuspension that can influence the food available to the benthos. The Cape Canyon is the largest South African canyon located off the western margin of the country. It has a unique structure that connects the coastline to deep-sea environments, and it is also extremely productive being under the influence of upwelling. Here we aim to characterize the role of hydrography in influencing the food availability to the benthos, comparing stations within the Cape Canyon and from adjacent areas. Samples were collected in March 2017 and data were acquired to describe the physical environment (temperature, salinity, oxygen) in relation to the benthic invertebrate specimens used for stable isotope analyses. The $\delta^{15}N$ of suspended particulate matter (SPM) did not vary between canyon and non-canyon regions, but it increased with depth, most likely as the result of particle bacterial remineralization. In contrast, the $\delta^{13}C_{SPM}$ changed as a function of canyon. Such effects were only partially reflected in the $\delta^{15}N$ and $\delta^{13}C$ of the trophic groups identified, which generally did not vary between canyon and non-canyon stations. This information increases our understanding of the ecological function of the benthos in and around the Cape Canyon, which is essential for the ongoing marine spatial planning efforts.

1. Introduction

Submarine canyons are steep-walled incisions in the continental slope, and they are known to be important conduits of sediment from land to offshore environments (Vetter et al., 2010; Moors-Murphy, 2014; Muñoz et al., 2017; Santora et al., 2018; Pearman et al., 2023). The peculiar topography of canyons alters the direction of currents and promotes upwelling, enhancing productivity relative to the surrounding regions (Allen et al., 2001; Saldías and Allen, 2020). Canyons exhibit diverse substrate types that contribute to habitat heterogeneity and serve key ecological functions, including acting as nursery and feeding grounds. They also enhance fisheries productivity (Brodeur, 2001) and function as hotspots for biomass and biodiversity (De Leo et al., 2010; Santora et al., 2018). The unique nature of canyons is seen when they are compared to adjacent non-canyon habitats. It has been shown that locations within canyons harboured higher fish and crustacean biomass (De Leo et al., 2010; Sardà et al., 1994), fish diversity (De Leo et al., 2014) and invertebrate richness (Filander et al., 2022) compared to non-canyon locations. However, similarities between canyon and non-canyon areas have been observed for a wide spectrum of organisms from marine megafauna (Vetter et al., 2010) to amphipods assemblages (Soliman et al., 2022). Additionally, species richness and diversity in canyons are not consistently higher than adjacent slopes, a pattern that has been linked to the influence of several factors including oxygen availability (De Leo et al., 2014), substratum type (Filander et al., 2022) or habitat disturbance (Paterson et al., 2011).

In offshore deep-sea environments, benthic communities rely largely on sinking particulate organic matter produced by phytoplankton at the surface as their primary source of food (Gage and Tyler, 1991; Klages et al., 2003). The magnitude and quality of this food source depends on

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several factors as, for instance, rates of primary production and bacterial degradation, grazer activities and particle sinking velocity (Kiørboe, 2001; Riley et al., 2012; Puccinelli et al., 2018; Koski et al., 2020; Puccinelli et al., 2020). As a result, only a small part of this sinking material generally reaches the seafloor, and deep-sea environments are thus recognised as food limited (De La Rocha and Passow, 2007; Gooday and Rathburn, 1999). The morphological structure of marine canyons can favour the channelling of organic matter to the seafloor, with canyons being identified as hotspots of food availability to the benthos (Demopoulos et al., 2017). The food input to canyons can enhance the productivity of the benthic environment leading to a higher diversity and biomass in the canyon region in comparison to adjacent areas (De Leo et al., 2010; Romero-Romero et al., 2016; Stefanescu et al., 1994; Vetter and Dayton, 1999; Vetter and Dayton, 1998). However, canyons may be subjected to variable current flow and turbulence, which can lead to partitioning of food within the canyon (accumulation of food in some parts of the canyon and a flow through food system in others). Different substratum types within canyons can ultimately affect the availability of food resources and the diversity of the benthic community (Cartes et al., 2010; Masson et al., 2010; Papiol et al., 2013).

Stable isotope analyses of nitrogen (N, δ^{15}N) and carbon (C, δ^{13}C) have been extensively used to study marine food webs (e.g., Peterson and Fry, 1987; Fry, 1988; Hansson et al., 1997). The δ^{15}N of organic matter is often used to evaluate the trophic position of consumers in the food chain, with the δ^{15}N of organisms at higher trophic levels progressively increasing (Peterson and Fry, 1987). The δ^{13}C of organic matter provides insights into the food source assimilated by a consumer, with phytoplankton being the main food source for primary consumers in the open ocean (Descolas-Gros and Fontungne, 1990; Burkhardt et al., 1999). The δ^{15}N and δ^{13}C variability of the primary producers are propagated through the food web and reflected in the δ^{13}C and δ^{15}N of primary consumers and higher trophic levels (Montoya et al., 2002). The magnitude of the δ^{13}C and δ^{15}N increase from one trophic level to the next (i.e., trophic enrichment factor) has been estimated to be 1‰ and 2.3‰ for δ^{13}C and δ^{15}N, respectively (McCutchan et al., 2003).

The Cape Canyon is the largest South African bathymetric feature located on the western continental shelf of the country (de Wet and Compton, 2021). It is characterized by a four kilometres (km) wide head that incises the narrow continental shelf off St Helena Bay (Wigley and Compton, 2006; Fig. 1). This geomorphological feature extends for a distance of 200 km offshore and can be traced in the abyss, forming a connection between the coastline and deep-sea environments. The Cape Canyon is an extremely productive region being under the influence of the southern Benguela upwelling system, and supports economically relevant fisheries (Crawford, 2007; Hutchings et al., 2009; Kirkman et al., 2016). Due its ecological functions, the head of the canyon (see Fig. 1) is an offshore Marine Protected Area (MPA) since 2019 (DEA, 2019; Filander et al., 2022). The canyon has been well-studied in terms of geology (e.g., Compton et al., 2004; Dingle, 1980; Wigley and Compton, 2007), and recent papers have provided the first description of the deep-sea benthic community (Filander et al., 2022; Samaai et al., 2020). However, knowledge on the food web connections in the system and relevance of the benthic community for higher trophic levels is still absent.

This study aims to provide the first information about the benthic trophic food web of the Cape Canyon, by looking at differences in δ^{13}C

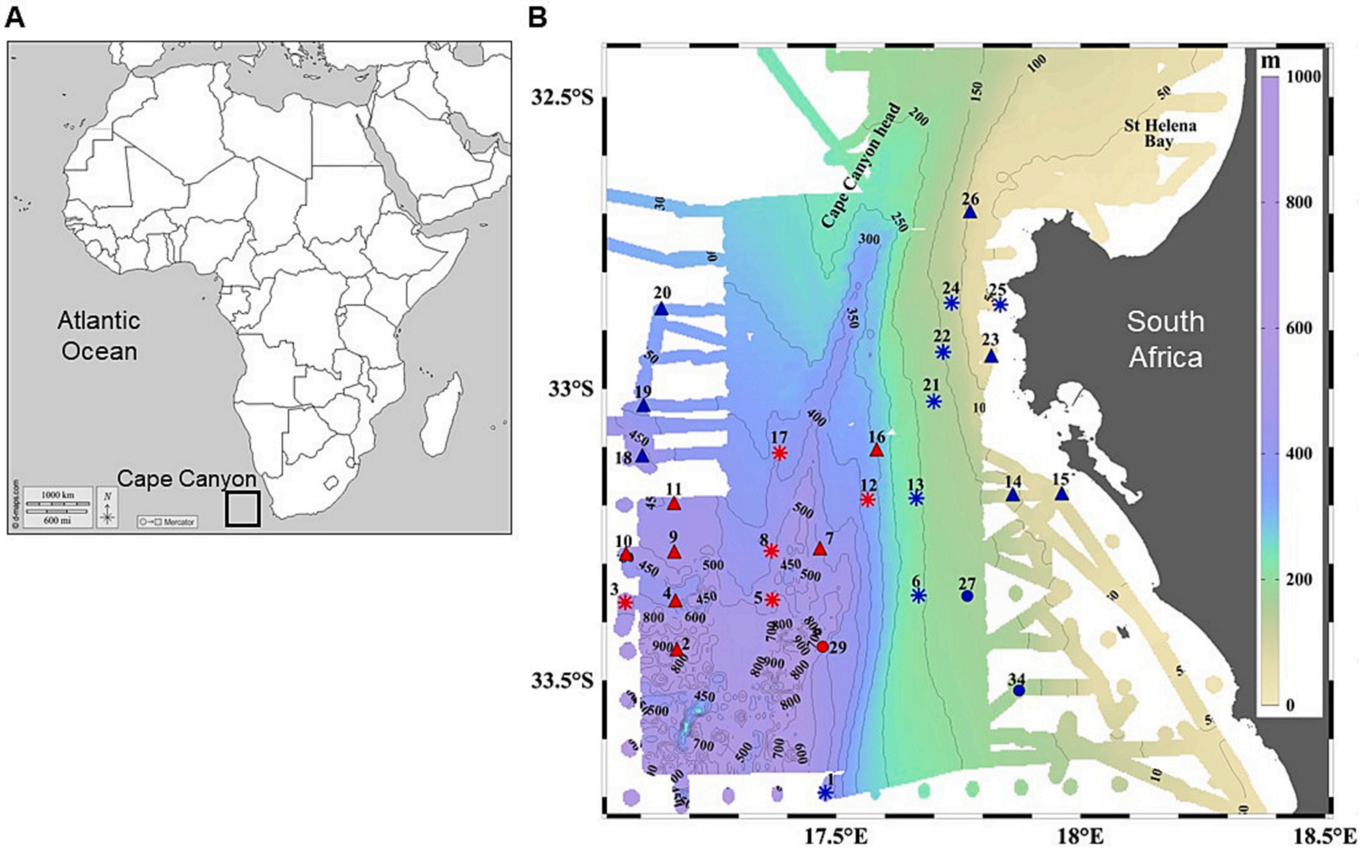

Fig. 1. Map of the study region (A) indicating the location of the Cape Canyon (black box); and zoom in (B) showing stations where samples of suspended particulate matter (SPM, triangles) and SPM + benthic invertebrate samples (asterisks) were collected in canyon (red colour) and non-canyon (blue colour) regions in 2017. Only benthic invertebrate samples were collected at stations 27, 29 and 34 (circles). Bathymetry data were obtained compiling data collected in the region in 2016, 2017 and 2018 as described in Filander et al. (2022). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and $\delta^{15}N$ values a) in the suspended particulate matter (SPM) considered the main food source available to the benthos, and b) of the benthic community, within and outside the canyon.

2. Material and methods

2.1. Study area and sample collection

Samples were collected onboard the RS *Algoa* (Voyage 236) in March 2017 at 29 stations in the Cape Canyon region (Fig. 1). The SPM samples were collected from 26 stations, and benthos samples were concurrently collected at 12 of these stations. Benthos was collected from three additional stations (stations 27, 29 and 34; Fig. 1). Of the 26 SPM stations, 14 were non-canyon stations (208 ± 146 m depth) and 12 were canyon stations (491 ± 110 m depth); while among the 15 benthos stations, nine were non-canyon stations (198 ± 110 m depth), and six were canyon stations (485 ± 107 m depth) (Fig. 1). Canyon and non-canyon stations were defined following Filander et al. (2022) and were based on the geo-morphology characteristics of the study area (Compton et al., 2004; Palan, 2017; Wigley and Compton, 2007).

The physical environment was sampled using a SeaBird SBE911 conductivity-temperature-depth (CTD) profiler. Temperature, salinity, and dissolved oxygen were measured using the CTD. Dissolved oxygen concentrations of discrete seawater samples from selected depths were also determined by Winkler titrations, to calibrate the dissolved oxygen profiles.

At each SPM station, seawater was collected in opaque high-density polyethylene bottles at the surface, thermocline and bottom (three replicates of 4 L from each depth), using remotely-fired Niskin bottles. Seawater samples were shaken to ensure homogeneity, then filtered gently (< 5 cm Hg vacuum) onto pre-combusted (450 °C for 5 h) GF/F filters (0.7 μm nominal pore size, 47 mm diameter).

Benthic sampling was conducted using a customized dredge with a dimension of 30 cm × 100 cm and mesh size of 1 cm^2. At each station, the dredge was towed at 1 knot for 15–20 min. Detailed descriptions of the benthic community composition at the sampled stations is available in Filander et al. (2022), and thus it was not repeated here. Up to five individuals from each taxon were collected for stable isotope analysis. Taxa were identified and dissected following Puccinelli et al. (2020, 2018). Benthic samples were rinsed with filtered seawater to remove pieces of shell, epiphytes and other exogenous material.

The SPM and the animal samples were placed in pre-combusted foil and stored frozen at −80 °C until laboratory analyses.

2.2. Laboratory analyses

In the laboratory, SPM and animal tissue samples were dried at 60 °C for 48 h. SPM subsamples were cored with a 20 mm punch and folded into tin foil cups. Heavily-carbonated animal species were decalcified following Fry (1988) and Cloern et al. (2002) by adding 2 N hydrochloric acid (HCl) drop-by-drop until CO_2 release stopped. Samples were then re-dried at 60 °C without rinsing to minimize loss of dissolved organic matter. Because decalcification can affect tissue $\delta^{13}C$ values (Mateo et al., 2008), we applied HCl only to the calcium carbonate-containing animal samples, namely Asteroidea, Anthozoa and Ophiuroidea. Samples without a calcium carbonate component were not treated with HCl. Tissue samples prepared for $\delta^{15}N$ analysis were not subjected to acidification. Thus, for Asteroidea, Anthozoa and Ophiuroidea only, we analysed two samples for each specimen: one that was decalcified and measured for $\delta^{13}C$ and another non-decalcified sample measured for $\delta^{15}N$. Once dried, animal samples were ground to a fine powder in a ball mill and 1 mg subsamples were weighed into tin foil capsules. SPM and animal samples were analysed for the stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) using a Flash EA 1112 Series coupled to a Delta V Plus IRMS housed in the Stable Isotope Laboratory of the Archaeology Department of the University of Cape Town. A laboratory running standard (Merck Gel: $\delta^{13}C = -20.57‰$, $\delta^{15}N = 6.8‰$, C % = 43.83, N % = 14.64) and in the case of the GF/F samples, blanks (pre-combusted unused GF/F filters), were run after every 10–20 samples. All results are referenced to Vienna Pee-Dee Belemnite (VPBD) for carbon isotope ratios and to N_2 in air for nitrogen isotope ratios. Analytical precision was <0.2‰ for $\delta^{13}C$ and < 0.1‰ for $\delta^{15}N$. Results are expressed in standard unit notation as follows:

$$X\ (‰) = \frac{(Rsample - Rstandard)}{Rstandard} \times 1000 \tag{1}$$

where X is $\delta^{13}C$ or $\delta^{15}N$ and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

The trophic level of each taxon was calculated according to Eq. (2) following DeNiro and Epstein (1981):

$$TL = \frac{([\delta^{15}N_{consumer} - \delta^{15}N_{SPM}])}{2.3} + 1 \tag{2}$$

where TL represents the trophic position of the target species, $\delta^{15}N_{consumer}$ refers to the $\delta^{15}N$ of the target species, $\delta^{15}N_{SPM}$ refers to the $\delta^{15}N$ of the SPM collected from the bottom sample of the corresponding station, and 2.3 refers to the trophic enrichment factor which was derived empirically from the meta analyses conducted by McCutchan et al. (2003).

Some studies have proposed the use of primary consumers (rather than SPM) as the baseline for trophic level assessment as their isotopic composition integrates over more appropriate timescales (one to several months vs. days for SPM) (Vander Zanden and Rasmussen, 1999; Puccinelli et al., 2018, 2020). While using this second approach to compute benthic organism trophic levels could be beneficial, we could not identify a suitable primary consumer present at most stations and with generally low $\delta^{15}N$ values. For this reason, this approach was not used.

2.3. Statistical analyses

In order to investigate the effects of depth and canyon on the $\delta^{13}C$ and $\delta^{15}N$ values of SPM, we used an analysis of variance (ANOVA) with a factorial design consisting of the following factors: *Water Column Depth* (surface, thermocline, bottom), *Canyon* (canyon, non-canyon) and *Station* (random, nested in *Canyon*). In the event of significant results, Tukey HSD post hoc tests were conducted.

A similar approach was used to investigate variation in the stable isotope composition of the benthos but given that a different number of replicates and species were collected at each station, we evaluated the effect of factors *Canyon* and *Station* on the trophic composition of trophic groups instead of on individual species. Benthic invertebrates were assigned to a feeding group based on their mechanism and the type of food ingestion, as described in Puccinelli et al. (2018, 2020). Five trophic groups were identified as follows: Deposit feeders (Df)- feeding on suspended organic matter; Deposit feeders-Scavengers (Df-Sc)- feeding on organic matter (suspended), bacteria, carrion and detritus on the seafloor; Predators (Pr)- feeding on live prey; Deposit feeders -Scavengers-Predator (Df-Sc-Pr)- feeding on a combination of sources used by Df-Sc and Pr; Suspension/Filter feeders (Sf)- feeding on suspended organic matter and plankton in the water column. Here, we used an ANOVA with a factorial design consisting of the factors: *Canyon* (canyon, non-canyon), *Station* (random, nested in *Canyon*) and *Trophic Group* (Df, Df-Sc, Pr, Df-Sc-Pr, Sf).

Pearson correlation analysis were performed to investigate possible relationships between the $\delta^{13}C$ and $\delta^{15}N$ of the trophic groups with the environmental variables, including bottom temperature and oxygen concentrations.

Analyses were performed using R version 4.3.0. Figures were created in ArcGis 10.6.1, R and Sigma Plot.

3. Results

3.1. Physical environment

Horizontal distributions of temperature and dissolved oxygen concentrations at the surface and bottom (within 5–10 m from the seafloor) are illustrated in Fig. 2. At the surface, nearshore regions (shoreward of the 100 m isobath) were characterized by cooler (<14 °C) recently upwelled waters, with the most recently upwelled water (<12 °C) associated with generally lower dissolved oxygen concentrations (<3 mL L^{-1}). In the south-eastern part of the sampled region, there was an area of elevated (<10 mL L^{-1}) dissolved oxygen at the surface between the coast and the 100 m isobath. Further offshore, surface waters were much warmer, exceeding 17 °C eastward of the 300 m isobath. At the bottom of the water column, temperatures ranged from 10.4 °C in the nearshore regions to about 4 °C at the deepest sampled stations, with the coldest water located within the canyon. The opposite gradient was observed for dissolved oxygen, with the lowest concentrations in the nearshore regions.

3.2. Suspended particulate matter

The SPM $\delta^{15}N$ and $\delta^{13}C$ values varied with depth and among stations, but with different effects of the factor *Canyon* ($p > 0.05$).

The $\delta^{15}N_{SPM}$ varied significantly as a function of *Water Column Depth*, with bottom samples having a higher $\delta^{15}N_{SPM}$ than surface and thermocline samples (7.4 ± 0.2‰ vs. 4.4 ± 0.2‰), the latter two being not significantly different (Tables 1 and 2). This pattern was observed at all

Table 1
Significant and non-significant effects of the factor *Canyon* on the $\delta^{15}N$, $\delta^{13}C$ and C:N of suspended particulate matter (SPM) and benthic trophic groups. Deposit feeders/Scavengers (Df/Sc), Deposit feeders (Df), Predators/Scavengers/Deposit feeders (Pr/Sc/Df), Suspension feeders (Sf) and Predators (Pr).

	Canyon		
	$\delta^{15}N$	$\delta^{13}C$	C:N
SPM	no	yes $p < 0.01$	yes $p < 0.01$
Df-Sc	no	yes $p < 0.01$	no
Df	no	no	no
Df-Sc-Pr	no	no	no
Sf	no	no	no
Pr	no	yes $p < 0.05$	no

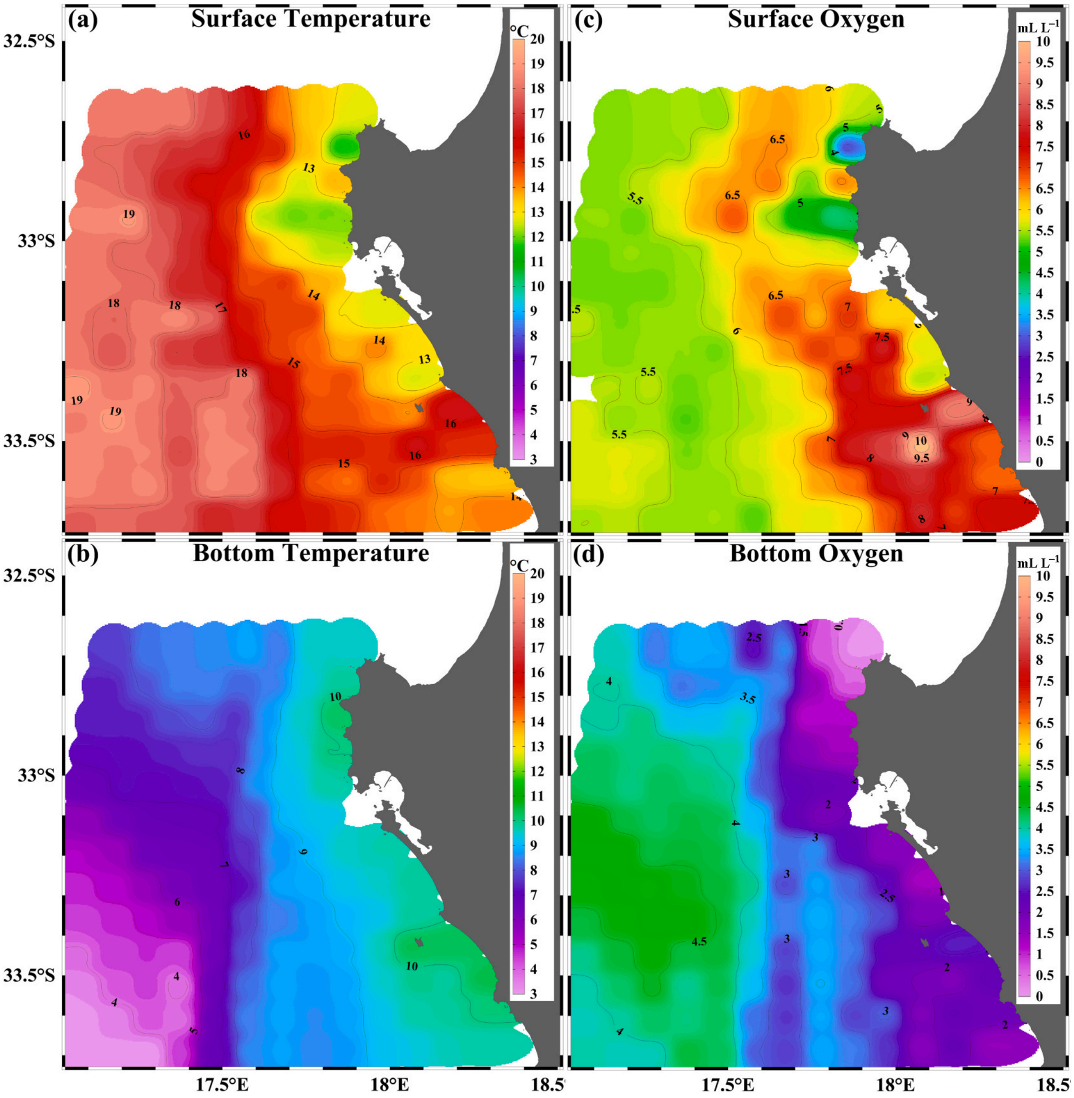

Fig. 2. Surface and bottom (within 5–10 m from the seafloor) distributions of temperature (a and c) and dissolved oxygen (b and d), measured in the Cape Canyon region in 2017.

Table 2
δ^{15}N, δ^{13}C and C:N (mean ± standard deviation) of suspended particulate matter (SPM) collected at canyon and non-canyon stations from three depth (surface, thermocline and bottom) in the Cape Canyon region in 2017. See Fig. 1 for station locations.

Station#	Depth collection	Canyon	δ^{15}N (‰)			δ^{13}C (‰)			C:N		
1	Bottom – 449 m	non-canyon	7.73	±	0.43	−20.51	±	0.92	9.67	±	0.58
1	Surface	non-canyon	5.00	±	0.32	−19.39	±	0.03	6.13	±	0.09
1	Thermocline – 16 m	non-canyon	1.61	±	0.87	−19.06	±	0.16	6.57	±	0.07
2	Bottom – 656 m	canyon	7.34	±	0.15	−18.44	±	0.30	11.13	±	0.58
2	Surface	canyon	4.34	±	0.34	−20.25	±	0.49	8.10	±	0.20
2	Thermocline – 34 m	canyon	5.04	±	0.36	−20.25	±	0.39	7.80	±	0.06
3	Bottom – 553 m	canyon	7.46	±	0.70	−18.47	±	0.24	13.50	±	0.92
3	Surface	canyon	5.60	±	0.10	−20.67	±	0.45	8.23	±	0.35
3	Thermocline – 23 m	canyon	2.34	±	0.00	−20.14	±	0.19	7.27	±	0.27
4	Bottom – 549 m	canyon	6.98	±	0.12	−20.47	±	0.34	12.70	±	0.15
4	Surface	canyon	3.52	±	0.07	−20.42	±	0.07	6.90	±	0.12
4	Thermocline – 23 m	canyon	3.04	±	0.67	−21.57	±	0.14	7.20	±	0.25
5	Bottom – 498 m	canyon	7.35	±	0.15	−19.23	±	0.16	12.00	±	0.21
5	Surface	canyon	3.27	±	0.04	−20.97	±	0.07	6.33	±	0.09
5	Thermocline – 63 m	canyon	4.85	±	0.05	−21.50	±	0.13	6.43	±	0.12
6	Bottom – 200 m	non-canyon	8.34	±	0.11	−18.24	±	0.33	9.67	±	0.48
6	Surface	non-canyon	4.35	±	0.02	−19.12	±	0.07	6.23	±	0.09
6	Thermocline – 20 m	non-canyon	4.50	±	0.50	−19.19	±	0.01	6.07	±	0.03
7	Bottom – 449 m	canyon	8.82	±	0.19	−19.50	±	0.25	10.63	±	0.29
7	Surface	canyon	4.03	±	0.04	−19.24	±	0.05	6.17	±	0.07
7	Thermocline – 42 m	canyon	7.55	±	0.51	−21.34	±	0.10	7.17	±	0.22
8	Bottom – 482 m	canyon	7.55	±	0.20	−19.43	±	0.16	11.37	±	0.73
8	Surface	canyon	3.62	±	0.12	−20.06	±	0.10	6.43	±	0.07
8	Thermocline – 39 m	canyon	5.72	±	0.51	−21.43	±	0.07	7.33	±	0.07
9	Bottom – 488 m	canyon	7.25	±	0.27	−17.63	±	0.33	10.57	±	0.30
9	Surface	canyon	3.37	±	0.04	−20.12	±	0.07	6.30	±	0.10
9	Thermocline – 40 m	canyon	3.26	±	0.07	−19.79	±	0.20	6.03	±	0.07
10	Bottom – 540 m	canyon	7.19	±	0.18	−16.81	±	0.53	11.77	±	0.62
10	Surface	canyon	3.94	±	0.05	−20.36	±	0.09	6.93	±	0.12
10	Thermocline – 29 m	canyon	4.02	±	0.16	−20.32	±	0.08	6.33	±	0.07
11	Bottom – 451 m	canyon	7.11	±	0.25	−20.48	±	0.39	10.47	±	0.86
11	Surface	canyon	3.16	±	0.37	−20.63	±	0.05	6.40	±	0.06
11	Thermocline – 27 m	canyon	3.44	±	0.15	−21.09	±	0.34	6.63	±	0.44
12	Bottom – 326 m	canyon	7.75	±	0.52	−18.06	±	0.23	8.67	±	0.23
12	Surface	canyon	5.68	±	0.04	−16.94	±	0.02	6.93	±	0.07
12	Thermocline – 45 m	canyon	4.84	±	0.06	−18.20	±	0.09	5.97	±	0.03
13	Bottom – 207 m	non-canyon	6.58	±	0.49	−17.71	±	0.64	7.40	±	0.25
13	Surface	non-canyon	4.51	±	0.05	−18.03	±	0.06	7.67	±	0.03
13	Thermocline – 12 m	non-canyon	3.88	±	0.06	−18.23	±	0.07	6.80	±	0.06
14	Bottom – 102 m	non-canyon	8.97	±	0.12	−16.88	±	0.17	7.30	±	0.06
14	Surface	non-canyon	3.31	±	0.04	−18.68	±	0.07	5.93	±	0.03
14	Thermocline – 20 m	non-canyon	4.72	±	0.07	−19.41	±	0.08	5.63	±	0.07
15	Bottom – 74 m	non-canyon	8.05	±	0.06	−17.49	±	0.08	7.40	±	0.45
15	Surface	non-canyon	3.56	±	0.15	−20.38	±	0.12	5.73	±	0.03
15	Thermocline – 9 m	non-canyon	5.12	±	0.10	−21.36	±	0.09	5.60	±	0.06
16	Bottom – 294 m	canyon	8.58	±	0.10	−17.65	±	0.25	8.67	±	0.19
16	Surface	canyon	3.77	±	0.04	−18.51	±	0.10	6.40	±	0.06
16	Thermocline – 96 m	canyon	4.27	±	0.06	−18.93	±	0.03	6.00	±	0.06
17	Bottom – 406 m	canyon	8.35	±	0.20	−17.51	±	0.20	10.17	±	0.27
17	Surface	canyon	3.02	±	0.07	−18.68	±	0.05	5.67	±	0.09
17	Thermocline – 67 m	canyon	3.96	±	0.11	−19.52	±	0.02	5.90	±	0.06
18	Bottom – 450 m	non-canyon	8.15	±	0.15	−18.10	±	0.24	9.50	±	0.76
18	Surface	non-canyon	5.17	±	0.13	−20.71	±	0.08	6.37	±	0.17
18	Thermocline – 40 m	non-canyon	4.50	±	0.05	−20.35	±	0.17	6.17	±	0.03
19	Bottom – 402 m	non-canyon	8.52	±	0.08	−17.27	±	0.30	9.40	±	0.40
19	Surface	non-canyon	4.12	±	0.07	−20.69	±	0.07	6.43	±	0.07
19	Thermocline – 42 m	non-canyon	4.61	±	0.09	−21.50	±	0.17	6.50	±	0.10
20	Bottom – 330 m	non-canyon	8.38	±	0.02	−15.70	±	0.35	10.27	±	0.15
20	Surface	non-canyon	3.73	±	0.09	−20.86	±	0.09	6.46	±	0.15
20	Thermocline – 42 m	non-canyon	4.85	±	0.17	−22.13	±	0.20	7.29	±	0.11
21	Bottom – 162 m	non-canyon	8.26	±	0.05	−17.73	±	0.05	8.83	±	0.12
21	Surface	non-canyon	3.38	±	0.01	−19.05	±	0.06	6.31	±	0.08
21	Thermocline – 20 m	non-canyon	2.95	±	0.42	−19.21	±	0.09	6.36	±	0.09
22	Bottom – 144 m	non-canyon	8.85	±	0.04	−17.26	±	0.26	8.20	±	0.17
22	Surface	non-canyon	3.00	±	0.01	−20.23	±	0.10	6.40	±	0.06
22	Thermocline – 34 m	non-canyon	6.06	±	0.02	−19.00	±	0.21	6.93	±	0.29
23	Bottom – 58 m	non-canyon	1.63	±	0.26	−21.43	±	0.12	5.07	±	0.07
23	Surface	non-canyon	3.42	±	0.07	−21.62	±	0.06	5.53	±	0.09
23	Thermocline – 30 m	non-canyon	6.75	±	0.06	−16.94	±	0.13	6.80	±	0.10
24	Bottom – 128 m	non-canyon	3.99	±	0.11	−20.41	±	0.10	5.03	±	0.03
24	Surface	non-canyon	5.87	±	0.12	−20.63	±	0.26	5.20	±	0.06
24	Thermocline – 28 m	non-canyon	8.72	±	0.14	−17.95	±	0.35	6.60	±	0.30
25	Bottom – 35 m	non-canyon	6.78	±	0.09	−19.96	±	0.24	5.03	±	0.07

(*continued on next page*)

Table 2 (*continued*)

Station#	Depth collection	Canyon	δ^{15}N (‰)			δ^{13}C (‰)			C:N		
25	Surface	non-canyon	4.22	±	0.16	−20.55	±	0.12	4.90	±	0.00
25	Thermocline – 9 m	non-canyon	7.37	±	0.11	−18.67	±	0.10	5.43	±	0.17
26	Surface	non-canyon	6.02	±	0.05	−20.27	±	0.11	4.83	±	0.03
26	Thermocline – 22 m	non-canyon	8.00	±	0.03	−16.78	±	0.08	6.00	±	0.00

stations, regardless of their maximum (max) depth (Fig. 3). While the highest $\delta^{15}N_{SPM}$ were recorded for bottom samples of the deepest stations (max 660 m), the closest inshore stations which had a relative shallow max depth (<100 m; e.g., stations 14, 15, 24, 25) also showed relatively high $\delta^{15}N_{SPM}$ (3.8–9.2‰). The inshore station 23 (depth 54 m) showed an outstanding pattern having low bottom $\delta^{15}N_{SPM}$ of 1.6 ± 0.4‰, which was statistically different from the other stations ($p < 0.01$).

The results of the $\delta^{13}C_{SPM}$ showed significant effects of the factors *Canyon* ($p < 0.05$), *Water Column Depth* ($p < 0.001$) as well as their interaction ($p < 0.01$), with $\delta^{13}C_{SPM}$ progressively increasing with depth (surface −19.9 ± 0.2‰ vs. bottom −18.5 ± 0.2‰; Table 1). Surface samples had the lowest $\delta^{13}C_{SPM}$ (−19.9 ± 0.2‰) followed by thermocline (−19.8 ± 0.2‰) and bottom samples (−18.5 ± 0.2‰). $\delta^{13}C_{SPM}$ of the thermocline varied as a function of the factor *Canyon* ($p < 0.01$), with non-canyon stations having a lower $\delta^{13}C_{SPM}$ than canyon stations (−20.3 ± 0.2‰ vs. −19.3 ± 0.2‰; Fig. 3).

The C:N ratio of SPM changed again with depth and between canyon and non-canyon stations, with bottom samples from canyon stations having the highest C:N (11.0 ± 0.2), followed by bottom samples of non-canyon stations (7.9 ± 0.2), and thermocline/surface samples which did not differ from each other (6.6 ± 0.2).

3.3. Benthos

The trophic groups showed variable δ^{15}N and δ^{13}C values, with Df-Sc having the largest stable isotope range (δ^{15}N, 7.9–15.8‰; δ^{13}C, −11.2 to −20.0‰) and being the most abundant group across the study region (present at eight out of the 15 stations), followed by Df (δ^{15}N, 8.9–12.6‰; δ^{13}C, −12.3 to −20.4‰; present at four stations), Df-Sc-Pr (δ^{15}N, 8.3–16.3‰; δ^{13}C −12.4 – −20.3‰; present at five stations), Sf (δ^{15}N, 9.7–16.1‰; δ^{13}C, −14.6 to −19.6‰; present at six stations), and Pr that had the most limited range (δ^{15}N, 7.2–14.9‰; δ^{13}C, −14.7 to −16.7‰; present at six stations) (Fig. 4, Tables 1 and 3). δ^{15}N, δ^{13}C and C:N were not significantly correlated with bottom temperature and oxygen concentrations ($r = 0.15$, 0.13 and 0.11 for temperature, $r = -0.01$, −0.06 and − 0.18 for oxygen).

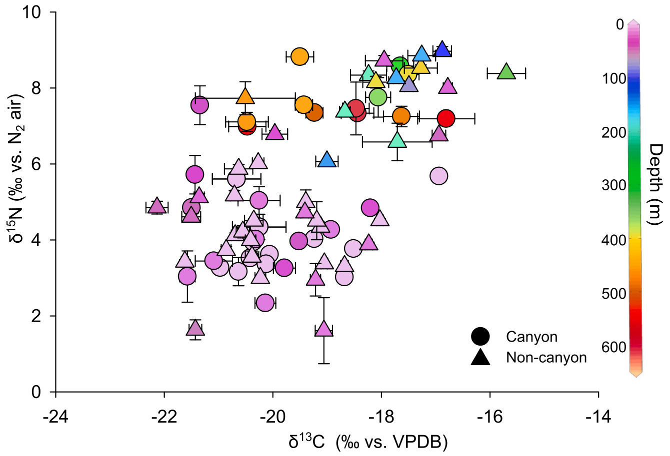

Fig. 3. Stable isotope composition (δ^{13}C and δ^{15}N mean ± standard error) of suspended particulate matter (SPM) collected from different depths (indicated by the colours) at canyon (circle) and non-canyon (triangle) stations in the Cape Canyon region in 2017.

Because of the large overlapping stable isotope values (Fig. S.1), we decided to investigate the effects of the factor *Canyon* on each trophic group separately.

Df-Sc did not show effects of *Canyon* on the specimens δ^{15}N, but there was variability among stations, with specimens from the canyon station 5 having significant lower δ^{15}N values in comparison to the other canyon stations ($p < 0.01$) which did not differ from each other (9.9 ± 0.6‰ vs. 12.0 ± 0.7‰). In contrast, the δ^{13}C composition of Df-Sc significantly changed as a function of *Canyon*, generally with specimens from canyon stations having lower δ^{13}C values than non-canyon stations (−16.9 ± 0.4‰ vs. −15.4 ± 0.6), although there was variability among stations (Fig. 4 a). There were no effects on the C:N of Df-Sc.

Although Df were represented by a limited number of specimens and stations (Fig. 4 b), there was no effect of *Canyon* on either the δ^{15}N, δ^{13}C or C:N.

In the case of Df-Sc-Pr, specimens δ^{15}N did not change as a function of the factor *Canyon* (Fig. 4 c), however there was variability among stations, with the canyon station 3 having lower δ^{15}N values than the other canyon stations (8.4 ± 0.9‰ vs. 13.2 ± 0.4‰). We also recorded δ^{15}N variability among non-canyon stations, with station 1 having higher δ^{15}N values than station 17 (14.3 ± 0.7‰ vs. 11.1 ± 0.6‰; $p < 0.05$). The δ^{13}C values of Df-Sc-Pr also did not differ between canyon and non-canyon stations, but there was variability among stations, with station 3 having a lower δ^{13}C value than any other stations (−19.4 ± 1.1‰ vs. −16.4 ± 1.9‰). C:N did not change as a function of *Canyon*.

The δ^{15}N values of Sf changed significantly as a function of the factor *Canyon* ($p < 0.01$), however with large variability among stations ($p < 0.001$), with samples from the canyon stations 5 and 13 having a lower δ^{15}N in comparison to the other stations (10.8 ± 0.7‰ vs. 13.3 ± 1.0‰) (Fig. 4 d). In contrast, δ^{13}C values of Sf were not affected by any factor, as well as the C:N, although stations 6 and 13 had the highest C:N ratio (5.2 ± 1.6).

The δ^{15}N values of Pr were not affected by the factor *Canyon*, but there was a significant effect of *Station* (nested in Canyon) with the canyon station 22 having higher δ^{15}N values than station 34 (Fig. 4 e). Generally, stations 5 and 22 had the highest δ^{15}N values across the study area (13.2 ± 2.1‰ vs. 9.9 ± 1.2‰). In contrast, the δ^{13}C values of Pr changed significantly in relation to *Canyon* ($p < 0.05$), with specimens from non-canyon stations having a slightly lower δ^{13}C value than Pr from canyon stations (−16.1 ± 0.2‰ vs. −15.3 ± 0.3‰). There were no effects of *Canyon* on the C:N of Pr (3.8 ± 0.3).

The TL of each specimen investigated was approximately three levels higher than SPM, with averages between 2.7 and 3.3. Pr had the widest range of TL (0.5–4.3), followed by Df-Sc-Pr (1.4–4.7), Df-Sc (1.3–4.3), Sf (2.0–4.6) and Df (2.0–3.4). However, there was considerable spatial variability among the specimens investigated, such that it was not possible to attribute a particular trophic group to a specific TL (Table 3).

4. Discussion

This study aimed to investigate the trophic food web of the Cape Canyon and to assess possible variability in the stable isotope composition of SPM, representing the main food source to the benthos, and trophic groups inhabiting the canyon and the nearby non-canyon regions. The $\delta^{15}N_{SPM}$ did not vary as a function of canyon, while $\delta^{13}C_{SPM}$ showed a variable pattern. Similar results were observed for the stable

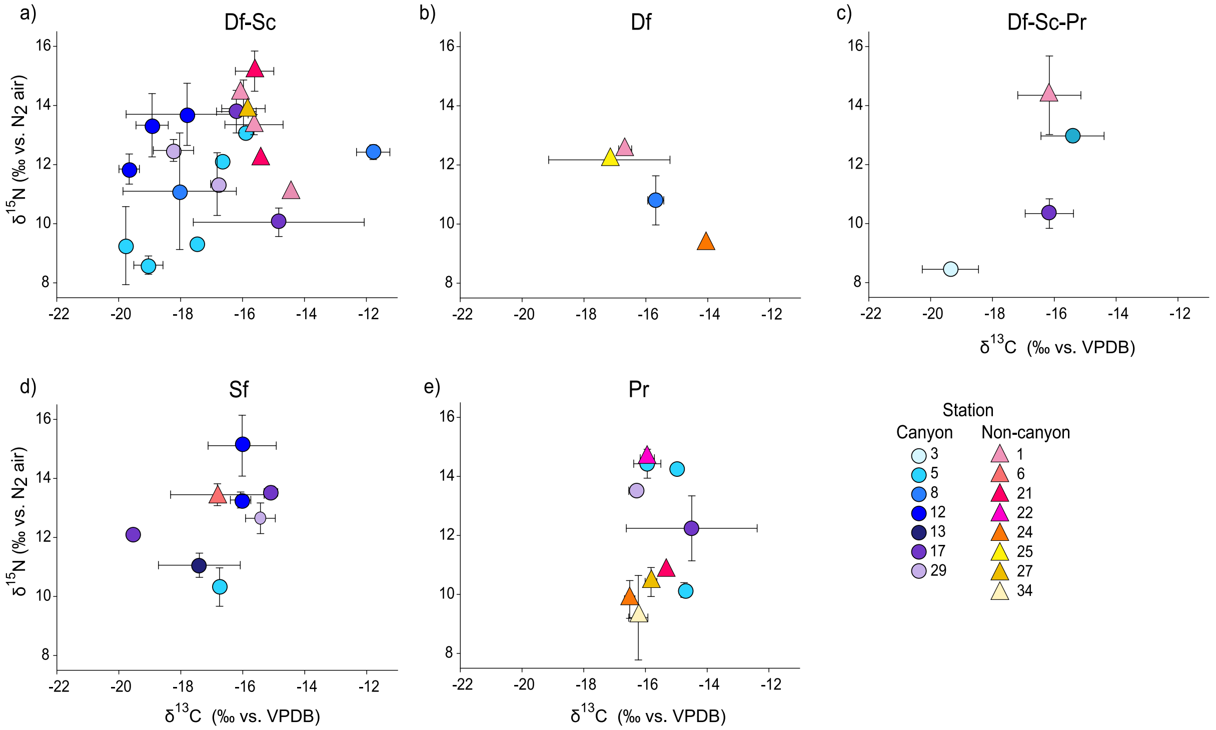

Fig. 4. Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$, mean ± standard error) of benthic trophic groups collected at canyon (circle) and non-canyon (tringle) stations in the Cape Canyon region in 2017. a) deposit feeders – scavengers (Df-Sc), b) Df, c) Df – Sc – predators (Pr), d) suspension feeders (Sf), and e) Pr.

isotope composition of the benthic trophic groups investigated, which did not show significant effects of the factor canyon.

Offshore benthic species receive the majority of their food in the form of organic particles sinking from the euphotic zone which is modified in the water column before it reaches the seafloor (Mintenbeck et al., 2007). At the seafloor, organic matter can either be directly assimilated through filtration, or following partial bacterial degradation before it is assimilated (Saino and Hattori, 1980; Wada, 1980; Macko and Estep, 1984). The $\delta^{15}N_{SPM}$ is controlled by a) the $\delta^{15}N$ of both new and recycled N sources (Minagawa and Wada, 1984; Altabet, 1988; Fawcett et al., 2011, 2014; Treibergs et al., 2014), which in the Cape Canyon region are influenced by upwelling and the Benguela current (Flynn et al., 2018, 2020), b) the extent of phytoplankton consumption (Altabet and Francois, 1994; Sigman et al., 1999) and c) the isotopic fractionation during oxidative degradation of SPM by bacteria, which rises the $\delta^{15}N$ of the particle pool (Wada, 1980; Macko and Estep, 1984; Altabet et al., 1999; Möbius, 2013). In this study, we observed a rise in the $\delta^{15}N_{SPM}$ with depth at every station (from 4.4 ± 0.2‰ at the surface to 7.4 ± 0.2‰ bottom), which can be attributed to isotopic fractionation during bacterial remineralization. This effect was observed regardless of the maximum depth of the stations and whether they were located inside or outside the canyon.

While we did not directly assess an effect of depth on the $\delta^{15}N$ of the trophic groups investigated, canyon stations were generally deeper than non-canyon stations (491 ± 110 m vs. 208 ± 146 m), which should have resulted in a higher $\delta^{15}N$ of the taxa located in the canyon in comparison to co-trophic groups from adjacent regions. This effect should have been linked to remineralization-driven increases in $\delta^{15}N_{SPM}$ with depth, for at least trophic groups that feed directly on SPM (i.e., Sf) (Mintenbeck et al., 2007; Puccinelli et al., 2018, 2020). However, this was not the case, with none of the trophic groups investigated showing an effect of canyon. Additionally, the trophic groups that feed on SPM (e.g., Sf) had a higher $\delta^{15}N$ value and trophic level than trophic groups such as Pr, which are higher in the food chain, and are thus known to have the highest $\delta^{15}N$ values and trophic level in a benthic food web (Denda et al., 2017; Puccinelli et al., 2020). The discrepancy between the $\delta^{15}N$ values of SPM and trophic groups, and the lack of a canyon effect on the $\delta^{15}N$ of the latter, could be due to a few factors. The SPM collected during this investigation represents a short-term record of conditions prior the sampling, while the $\delta^{15}N$ of trophic groups reflects an integrated isotopic composition of their assimilated food over a period of days to months, depending on a few factors including species, tissue type or specimen size (Kaufman et al., 2008; McMahon et al., 2006). Consequently, the SPM collected on the same day as the benthic invertebrates does not necessarily represent the average diet of the taxa investigated. The stable isotope turnover rate of benthic organisms are taxon-dependent (Kaufman et al., 2008), thus it can change as a function of the diet of the taxa, with organisms feeding on a mixed diet having a more variable $\delta^{15}N$ (Gamboa-Delgado et al., 2013; Iken et al., 2001). The stable isotope turnover rate also depends on the specimen ontogenetic stage, as juveniles and adults can differ in $\delta^{15}N$ due to shifts in trophic niche during body development (Pakhomov et al., 2003). Additionally, only a selection of trophic groups investigated here feed directly on SPM (e.g., Sf), while the others feed on particles present in the sediment such as detritus or live prey, suggesting that SPM is not necessarily the most accurate trophic baseline to use, and other potential food sources (i.e., sediment) should have been accounted for (Parzanini et al., 2019; Reid et al., 2012). This result was also supported by the estimated benthos trophic levels, which were on average between 2 and 3, rather large for specimens feeding on SPM alone. Some studies have proposed the use of primary consumers (rather than SPM) as the baseline for trophic level assessment as their isotopic composition integrates over more appropriate timescales (one to several months) (Vander Zanden and Rasmussen, 1999; Puccinelli et al., 2018). However, this approach was not possible to use in this study because we did not collect a widespread taxon across all sampled stations, feeding on SPM and with generally low $\delta^{15}N$ that could be used as baseline. The Cape Canyon is located within the Benguela upwelling system, and upwelling is known to play a major role in shaping marine food webs (e.g., Puccinelli et al., 2016a, 2016b; Laiz-Carrión et al., 2022; Couret et al., 2023). There were some evidences of channelling of colder waters within the canyon (Fig. 2), in agreement with early studies which have also demonstrated some

Table 3
Stable nitrogen and carbon isotope ratios and trophic level of benthic taxa (mean ± standard error) collected in the Cape Canyon region in 2017. Trophic level was calculated using suspended particulate matter as baseline food source. See Fig. 1 for station locations. Pr = predator, Sc = scavenger, Df = deposit feeder, Sf = suspension feeder, and n = number of samples analysed.

Canyon	Taxonomic group/Species		Station #	n	$\delta^{15}N$ (‰ vs. N_2) air)	$\delta^{13}C$ (‰ vs. VPDB)	C:N	Trophic Group	TL
Canyon	Annelida								
	Polychaeta	Polychaeta sp. 1	5	2	10.32 ± 0.65	−16.75 ± 0.02	4.01 ± 0.57	Sf	1.9
		Polychaeta sp. 2	27	3	13.89 ± 0.97	−15.97 ± 0.7	4.2 ± 0.15	Df-Sc	2.6
		Echiura sp	8	2	10.8 ± 0.83	−15.68 ± 0.26	5.58 ± 0.52	Df	2
	Arthropoda								
	Malacostraca	*Merhippolyte agulhasensis*	3	2	8.45 ± 0.1	−19.36 ± 0.91	3.22 ± 0.12	Df-Sc-Pr	1.3
			5	2	12.97 ± 0.22	−15.41 ± 1.02	3.38 ± 0.06	Df-Sc-Pr	2.7
		Neopilumnoplax heterochir	29	2	13.51 ± 0.13	−16.34 ± 0.2	3.38 ± 0.09	Pr-Sc	2.8
		Parapagurus bouvieri	5	2	9.26 ± 1.32	−19.77 ± 0.1	5.57 ± 1.41	Df-Sc	1.6
		Pterygosquilla capensis	21	1	10.84	−15.38	3.38	Pr	1.8
		Sympagurus dimorphus	5	1	9.34	−17.47	3.78	Df-Sc	1.6
	Cnidaria								
	Anthozoa	Anthozoa sp	12	2	15.11 ± 1.03	−16.02 ± 1.1	3.6 ± 0.26	Sf	3.2
		Virgularia sp	13	3	11.06 ± 0.41	−17.4 ± 1.32	4.63 ± 0.32	Sf	3
	Echinodermarta								
	Asteriodea	*Crossaster penicillatus*	5	1	12.13	−16.65	3.32	Df-Sc	2.4
	Ophiuroidea	*Ophiocten affinis simulans*	5	1	13.1	−15.91	3.36	Df-Sc	2.7
			8	2	12.42 ± 0.25	−11.78 ± 0.54	4.92 ± 0.4	Df-Sc	2.4
			29	5	12.48 ± 0.37	−18.23 ± 0.65	3.89 ± 0.31	Df-Sc	2.5
		Ophiolycus dentatus	29	3	11.34 ± 1.06	−16.82 ± 0.21	3.08 ± 0.1	Df-Sc	2.2
			12	2	13.7 ± 1.05	−17.79 ± 1.97	3.58 ± 0.58	Df-Sc	2.7
		Ophiothamnus remotus remotus	12	2	13.33 ± 1.07	−18.92 ± 0.52	4.91 ± 0.15	Df-Sc	2.6
		Ophiothrix aristulata	8	2	11.1 ± 1.97	−18.03 ± 1.83	3.84 ± 0.4	Df-Sc	2
		Ophiura (Ophiura) trimeni	5	2	8.6 ± 0.31	−19.04 ± 0.47	3.73 ± 0.25	Df-Sc	1.4
			12	2	11.85 ± 0.51	−19.66 ± 0.33	3.43 ± 0.18	Df-Sc	2.2
	Mollusca								
	Gastropoda	*Athleta abyssicola*	5	2	14.43 ± 0.49	−15.94 ± 0.44	3.59 ± 0.05	Pr	3.1
		Coluzea sp	5	2	10.15 ± 0.25	−14.75 ± 0.02	3.63 ± 0.1	Pr	1.8
		Fusivoluta pyrrhostoma	5	1	14.24	−15.03	3.6	Pr	3
	Bivalvia	*Limopsis chuni*	12	3	13.27 ± 0.27	−16.07 ± 0.33	3.61 ± 0.09	Sf	2.6
			29	3	12.65 ± 0.52	−15.43 ± 0.48	3.83 ± 0.14	Sf	2.6
Non-canyon	Annelida								
	Polychaeta	Polychaeta sp. 2	1	1	11.11	−14.43	3.28	Df-Sc	2
			21	1	12.22	−15.37	3.59	Df-Sc	2.2
		Polychaeta sp. 3	1	3	13.35 ± 0.34	−15.63 ± 0.94	3.73 ± 0.19	Df-Sc	2.7
			17	3	13.79 ± 0.72	−16.2 ± 0.64	3.33 ± 0.19	Df-Sc	2.6
		Echiura sp	1	2	12.52 ± 0.13	−16.67 ± 0.21	3.83 ± 0.11	Df	2.4
	Clitellata	*Hirudinea sp*	25	3	12.17 ± 0.09	−17.18 ± 1.96	4.92 ± 1.01	Df	2.6
	Arthropoda								
	Malacostraca	*Merhippolyte agulhasensis*	17	3	10.34 ± 0.5	−16.16 ± 0.78	3.78 ± 0.13	Df-Sc-Pr	1.6
		Neopilumnoplax heterochir	17	2	12.24 ± 1.1	−14.5 ± 2.12	4.42 ± 1.08	Pr-Sc	2.1
		Pterygosquilla capensis	21	1	10.84	−15.38	3.38	Pr	1.8
			24	3	9.83 ± 0.64	−16.51 ± 0.17	4.31 ± 0.08	Pr	2.7
			27	3	10.42 ± 0.49	−15.82 ± 0.19	3.63 ± 0.13	Pr	1.6
			34	3	9.21 ± 1.43	−16.23 ± 0.31	4.1 ± 0.2	Pr	1.3
	Ostracoda	*Ostracid sp*	1	3	14.35 ± 1.33	−16.16 ± 1.02	4.24 ± 0.38	Df-Sc-Pr	2.9
	Cnidaria								
	Anthozoa	Virgularia sp	13	3	11.06 ± 0.41	−17.4 ± 1.32	4.63 ± 0.32	Sf	3
		Anthozoa sp	17	3	13.53 ± 0.21	−15.09 ± 0.22	3.32 ± 0.06	Sf	2.5
		Thouarella sp	17	2	12.09 ± 0.07	−19.53 ± 0.06	4.1 ± 0.11	Sf	2.1
	Echinodermarta								
	Asteriodea	Asteriodea sp	22	2	14.61 ± 0.16	−15.94 ± 0.23	3.65 ± 0.14	Pr	2.7
	Holothuroidea	*Hemiocnus insolens*	24	1	8.95	−12.35	4.68	Df	2.5
	Ophiuroidea	*Ophiolycus dentatus*	17	4	10.05 ± 0.48	−14.83 ± 2.76	3.9 ± 0.52	Df-Sc	0.8
	Mollusca								
		Limopsis chuni	6	4	13.45 ± 0.37	−16.82 ± 1.51	5.57 ± 1.54	Sf	2.5
	Sipuncula								
		Sipuncula sp	1	1	14.45	−16.05	5.23	Df-Sc	3
	Phascolosomatidea	Phascolosomatidea sp	21	2	15.16 ± 0.68	−15.61 ± 0.62	3.75 ± 0.24	Df-Sc	3

localised upwelling within the canyon (Nelson and Polito, 1987; Shannon et al., 1981). However, these hydrographic conditions did not differ significantly from those at the surrounding non-canyon locations and there was no significant correlation between bottom temperature and oxygen with the stable isotope composition of the trophic groups. This pattern suggests that the entire region is subjected to approximately similar environmental conditions (Filander et al., 2022; Lamont et al., 2018), and thus the effects of upwelling differences for the benthos $\delta^{15}N$ from canyon vs. non-canyon locations would be difficult to disentangle. These results are in contrast with studies conducted in other canyons, where benthos isotopic compositions differed between canyon and adjacent slope environments due different depositional mechanisms of organic matter in canyon and non-canyon linked to topography and regional hydrography (Demopoulos et al., 2017); or different degradation pathways or organic matter between the two regions (Dell'Anno et al., 2013).

While the effect of the factor *Canyon* on the $\delta^{15}N$ of trophic groups was non-significant, most of them showed variability among stations. In most cases this variation did not follow a clear pattern, apart from the canyon station 5 where Df-Sc and Sf had a significantly lower δ^{15}N and Pr a significantly higher δ^{15}N than co-trophic groups from the other canyon stations. Within trophic group variability presumably reflects selection of a particular fraction of organic matter (Baker and Levinton, 2003; Lovvorn et al., 2005), or the inability to discriminate among filtered particles (Mincks et al., 2005). Additionally, isotopic differences are also observed among species that feed on the same food sources, linked to variation in physiological mechanisms and metabolism which are characteristics of each species (Puccinelli et al., 2018, 2020). Although during the sampling we aimed to collect the same species across stations, species were not equally present across them. Species distribution vary as a function for instance of depth, substratum type, sedimentary processes or food availability (Haley et al., 2017; Long and Baco, 2014; Puccinelli et al., 2018; Robertson et al., 2020; von der Meden et al., 2017), resulting in some species being more abundant in some areas than others. Additionally, before it became an MPA in 2019, the Cape Canyon had been subjected to bottom trawling, with no baseline benthic data available before demersal fishing operations took place. Demersal fishing is a primary activity influencing benthic community composition and habitats (Atkinson et al., 2011), with varying trawling intensities resulting in different communities in the affected areas (Fleddum et al., 2013), and with species showing different recovery rates to trawling activities (Hiddink et al., 2019). Together these factors can thus further shape species distribution.

The result of δ^{13}C contrasted with the δ^{15}N, showing significant effects of the factor *Canyon* on the $\delta^{13}C_{SPM}$ and on the δ^{13}C of selected trophic groups, although there was large spatial variability among stations and no clear consistency among trophic groups. The $\delta^{13}C_{SPM}$ between canyon and non-canyon stations differed only for thermocline samples, while $\delta^{13}C_{SPM}$ of surface and bottom samples did not change as a function of *Canyon*. However, $\delta^{13}C_{SPM}$ increased with depth, regardless of the presence of canyon, as it was observed for $\delta^{15}N_{SPM}$. The δ^{13}C of phytoplankton biomass depends on several factors including phytoplankton community composition, temperature and nutrient availability, which leads to water masses with different physical and biological properties generally being characterized by variable δ^{13}C (Wong and Sackett, 1978; Descolas-Gros and Fontungne, 1990; Burkhardt et al., 1999). The Cape Canyon region is mostly supported by cold, nutrient-rich Central Waters, which is a mixture of South Atlantic Central Water, South Atlantic Subtropical Mode Water, and Subantarctic Mode Water (SAMW), all of which have different source regions (Lamont et al., 2015; Flynn et al., 2020). Although these water masses may differ in their δ^{13}C values from their source regions, the strong mixing that typically occurs in the Cape Basin (Kersalé et al., 2018) likely smears out these differences to some extent, resulting in the larger range and more variable δ^{13}C values observed.

While the oceanographic conditions in the immediate vicinity of the Cape Canyon would be influenced by recently-upwelled surface waters advected into the region from the coast, such waters are also expected to be advected along the continental shelf and slope from the south-eastern part of the upwelling system (Hutchings et al., 2009; Lamont et al., 2015). Event-scale variability resulting in changes in phytoplankton community composition over a few days are commonly observed in the near-shore regions (Hutchings et al., 2009), much further inshore than our area of interest. Lamont et al. (2018) have demonstrated that the entire shelf region of the Benguela upwelling system is largely dominated by microphytoplankton at seasonal timescales. Thus, even if shelf waters are advected into the Cape Canyon region from further east or south, we do not expect that this will result in significant changes in the phytoplankton assemblages that form the basis of the sampled SPM in the region.

Among the trophic groups investigated, only Df-Sc and Pr showed variation in relation to *Canyon*, with specimens of Df-Sc from canyon stations having a lower δ^{13}C than non-canyon stations, while Pr showed the opposite pattern with higher δ^{13}C at canyon stations. The δ^{13}C of the other trophic groups was not affected by any factors, however there was variability among stations. Accounting for 1‰ trophic enrichment between trophic levels, benthos had δ^{13}C values higher than what was expected by feeding on SPM alone. This was the case for trophic groups feeding directly on SPM, such as Sf, and others (e.g., Pr) that should have a trophic level of 2 or 3. The explanation for the discrepancy between the δ^{13}C of consumers and SPM has very similar explanations to what reported for the δ^{15}N, including different stable isotope turnover rates between SPM and consumers (Kaufman et al., 2008; McMahon et al., 2006), or in the benthos feeding behaviour. For instance, some species can selectively feed on the most nutritious food once available (Legeżyńska et al., 2014), or others can have a mixed diet, feeding on a variety of food sources including live prey and fresh/decomposing organic matter, with their diet changing as a function of time (Macdonald et al., 2010; McTigue and Dunton, 2014).

The C:N ratios are commonly used to estimate the relative proportion of terrestrial and marine SPM into a system (Meyers, 1994), with C:N of marine SPM being in the range of ~6 and freshwater sources of ~12 (Harmelin-Vivien et al., 2008; Savoye et al., 2003; Ricciardelli et al., 2017). In this study the C:N ratios were < 12 indicating the predominance of a marine source, which is expected given the offshore location of the stations sampled, however the $C:N_{SPM}$ values of bottom samples were significantly higher than thermocline/surface samples (11.0 ± 0.2 vs. < 8). Given that the canyon connects the coastline to the deep-sea environment, we could have expected to observe a terrestrial signal, at least within the canyon itself. This effect was not seen in the canyon surface layers, probably because of strong persistent wind mixing that typically occurs in upwelling regions (Hutchings et al., 2009; Kirkman et al., 2016; Lamont et al., 2015). However a terrestrial input could explain the high C:N values of bottom canyon stations we observed. The Cape Canyon is located at the proximity to the west coast of South Africa, an area that is known to bring freshwater and terrestrial inputs to the surrounding marine system (Herrmann et al., 2016).

In summary, while the stable isotope composition of benthic organisms in the Cape Canyon did not differ significantly from nearby limitrophe non-canyon stations, it is essential to recognize that other factors such as depth or proximity to land might mask potential canyon effects within the system.

Understanding abiotic and biotic trophic interactions provides valuable insights into the functionality of deep-sea ecosystems (Demopoulos et al., 2017; Gontikaki et al., 2011; Parzanini et al., 2019; Vilas et al., 2020) and supports robust management plans, especially in the context of environmental change (Stowasser et al., 2012; Van Audenhaege et al., 2019). This paper presents data from the Cape Canyon region outside the gazetted Cape Canyon head MPA, which currently stands as the sole protected submarine canyon in the Southern Benguela region. The lower areas of the Cape Canyon, as stated in the National Biodiversity Assessment report (Sink et al., 2019), lack protection and are vulnerable to extensive bottom trawling activities. The spatial prioritization analysis conducted by Harris et al. (2022) also reached a similar conclusion, providing a strong basis for future planning to prioritize biodiversity areas for additional MPAs. The novel trophic estimates presented in this study, along with the Filander et al. (2022) findings, may provide a data-driven basis towards identifying potential areas for expanding protection efforts in the Southern Benguela. Further investigations considering temporal and spatial variability, particularly within the Cape Canyon head MPA, can enhance our understanding of the benthic food web structure in this extensive underwater feature, which may additionally contribute to South Africa's Marine Spatial Planning zoning plans.

CRediT authorship contribution statement

Eleonora Puccinelli: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Zoleka Filander:** Conceptualization, Funding

acquisition, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing, Resources. **Tarron Lamont:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data generated from this study are available on the public repository of the South African Marine Information Management System (MIMS) with the following DOIs: 10.15493/DEA.MIMS.12642023, 10.15493/DEA.MIMS.12652023

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2024.103965.

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