



# Environmental drivers of upper mesopelagic fish assemblages in the Benguela Upwelling System

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**ABSTRACT:** The Benguela upwelling system is one of the most productive marine ecosystems in the world; however, little is known about the community structure of mesopelagic fishes in its northern (nBUS) and southern (sBUS) subsystems. We analyzed around 1900 specimens from 13 stations in the nBUS and 11 stations in the sBUS during the austral summer and found 88 species and 24 families of mesopelagic fishes. Seven distinct assemblages characterized by water mass, oxygen concentration in the surface layer, and chlorophyll concentrations between 50 and 100 m were identified. The stations belonging to the nBUS shelf assemblage were low in oxygen concentration, had a mean abundance of 0.064 ind. 10 m<sup>-2</sup>, and were represented exclusively by *Diaphus dumerilii*. The sBUS shelf assemblage had a mean abundance of 15.00 ind. 10 m<sup>-2</sup> and *Maurolicus walvisensis* dominated. Two sBUS offshore assemblages had a mean abundance of 1.12 and 9.48 ind. 10 m<sup>-2</sup>. The most abundant taxa within the groups were *Hygophum hanseni*, *Cyclothone* spp., and *D. meadi*. Three nBUS offshore clusters had an abundance of 10.21, 11.88, and 14.19 ind. 10 m<sup>-2</sup>, and *D. hudsoni* prevailed in 2 groups, while *M. walvisensis* dominated the third group. Our study provides insight into the environmental factors that drive the composition of mesopelagic fishes on the shelf and in the upper pelagic zone in these highly productive subsystems. Possible future changes in these subsystems, such as an expansion of the oxygen minimum zone, can thus be expected to affect certain mesopelagic taxa that are essential for the food web of the subsystems.

**KEY WORDS:** Myctophidae · Sternoptychidae · Stomiidae · Water mass · Community composition · Biodiversity · Eastern boundary currents

## 1. INTRODUCTION

With an estimated biomass of up to 15 Gt in the global oceans, mesopelagic fishes play an important role in marine food webs and the transfer of organic matter (Van de Putte et al. 2006, Irigoien et al. 2014). Mesopelagic fishes also contribute to the ocean's carbon pump through pronounced diel vertical migrations: they ascend to the surface at night to feed and return to greater depths, where excretion takes place (Davison et al. 2013). Consequently, carbon and organic matter are actively transported to the mesopelagic layer (200–1000 m), where they can remain

suspended, sink further, or be re-mineralized by bacteria (Irigoien et al. 2014).

Many environmental factors can influence the abundance and composition of mesopelagic fishes in the world's oceans. The depth of the deep scattering layer, which is partly made up of mesopelagic fishes, is influenced by environmental factors such as oxygen concentration, turbidity, wind stress, mixed layer depth, surface chlorophyll, as well as the temperature in this layer (Bianchi et al. 2013, Klevjer et al. 2016, Aksnes et al. 2017, Proud et al. 2017, 2019). Oceanic fronts can also affect mesopelagic assemblages, as reported from the California Current eco-

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system and the eastern Central and North Atlantic, where frontal zones may act as a distributional barrier for mesopelagic larvae (Netburn & Koslow 2018, Dove et al. 2021).

The Benguela upwelling system (BUS) is located on the western coast of southern Africa between 19 and 34° S. It represents one of the 4 major eastern boundary currents of the world (Hutchings et al. 2009), in which nutrient upwelling supports extraordinarily productive food webs. It is dominated by the Benguela Current to the west and influenced by the warm Angola Current in the north and the warm Agulhas Current in the south (Rae 2005, Lett et al. 2007). The Benguela system is divided into 2 subsystems, the northern and southern Benguela (nBUS and sBUS), which are separated by the perennial Lüderitz upwelling cell (26° S), one of the most intense upwelling cells in the world (Rae 2005, Kirkman et al. 2016). Typical features of the sBUS are seasonal wind-driven upwelling and high productivity (Hutchings et al. 2009). While upwelling is continuous throughout the year in the central Benguela at the Lüderitz cell, winds, upwelling intensity, and phytoplankton biomass peak during austral summer and fall (December–May) in the sBUS and in late winter and spring (June–November) in the nBUS (Rae 2005, Hutchings et al. 2009). The nBUS and sBUS are influenced by different water masses. The sBUS is dominated by nutrient-poor Eastern South Atlantic Central Water (ESACW). In the nBUS, ESACW prevails on the shelf during the main upwelling season in austral winter and spring, while nutrient-rich South Atlantic Central Water (SACW) is transported to the nBUS during the austral summer (Mohrholz et al. 2008, Flohr et al. 2014, Tim et al. 2018). These waters also differ in their oxygen content; SACW has low oxygen concentrations with some hypoxic layers (values  $<1.4 \text{ ml l}^{-1} \text{ O}_2$ ) whereas ESACW is oxygen-rich (Mohrholz et al. 2008).

Differing water masses and biogeochemical processes can lead to changes in primary productivity and may also affect higher trophic levels (Wasmund et al. 2016, Ekau et al. 2018). Both the nBUS and sBUS have seen strong changes in their commercial small pelagic fish stocks, with a collapse in both regions in the 1960s and 1970s due to high fishery exploitation and changes in environmental conditions leading to low recruitment (Schwartzlose et al. 1999, Cury & Shannon 2004). While pelagic fish stocks have recovered in the sBUS, this has not been the case in the nBUS (van der Lingen et al. 2006). Currently, fishing pressure on mesopelagic fishes is not strong; however, there is potential for exploitation due to their high unexploited biomass (St. John

et al. 2016). Mesopelagic fishes are vital for the pelagic food web; they feed mostly on zooplankton as well as other mesopelagic fishes and are preyed upon by predatory fish such as hake (Punt & Leslie 1995, Pillar & Barange 1997, Durholtz et al. 2015) and sharks (Carrassón et al. 1992, Filmalter et al. 2017) as well as seals (Naito et al. 2013). Despite their important role in the food web, little is known about mesopelagic fish assemblages in the BUS and potential differences in their abundance and community composition between the subsystems.

So far, studies of mesopelagic fishes in the BUS have mostly focused on the southern subsystem with an emphasis on lanternfishes (Myctophidae) (Hulley & Prosch 1987, Hulley & Lutjeharms 1989, Hulley 1992). Less attention has been given to other species-rich families such as dragonfishes (Stomiidae), bristlemouths (Gonostomatidae), and hatchetfishes (Sternoptychidae, except for *Mauroliticus walvisensis*). In the sBUS, the most abundant species of mesopelagics are the myctophid *Lampanyctodes hectoris* Günther, 1876 and the sternoptychid *M. walvisensis* (Hulley & Prosch 1987, Parin & Kobylansky 1993), formerly identified as *M. muelleri* Gmelin, 1789 in the BUS. The estimated density of *M. walvisensis* on the sBUS shelf was assessed at 4–10 t km<sup>-2</sup> in a study during the 1980s (Armstrong & Prosch 1991). The density of *L. hectoris* has also been described for both eggs and larvae, with estimates of 11–500 larvae m<sup>-2</sup> in the west of Cape Agulhas and offshore on the West Coast, with maxima off the 200 m isobath (Prosch 1991). The latter 2 species occupy the upper slope and shelf and are found at the continental shelf break. Up to 10% of the pelagic purse seine catches during the 1970s and 1980s in South Africa consisted of *L. hectoris* (Hulley & Prosch 1987). In the nBUS, studies on mesopelagic fishes also focused on the Family Myctophidae (Rubiés 1985). Two communities were examined in this study; namely, the Valdivia Bank community, which is about 400 miles (645 km) off the coast and not highly influenced by the Benguela Current, and the Benguela Current community, with species occupying the shelf and slope. The Benguela Current community was dominated by pseudoceanic species (Hulley 1981) that depend on coastal ecosystems such as *L. hectoris* and warm-water species such as *Diaphus dumerilii* or *D. taaningi*.

As the world's oceans face increasing temperatures, expanding oxygen minimum zones (OMZs), and higher demand for new fisheries resources (Gjøsaeter & Kawaguchi 1980), it is important to gain more insight into this large and understudied group of fishes. The aim of this study was to assess the

assemblage structure of slope and shelf mesopelagic fish communities in the southern and northern subsystems of the Benguela and to elucidate which environmental factors determine species composition in the austral summer season.

## 2. MATERIALS AND METHODS

### 2.1. Sampling and species identification

Sampling took place on board the R/V 'Meteor' (cruise M153) in the BUS during austral summer (February and March) of 2019 (Ekau 2019). Data on salinity, temperature, oxygen concentration, and chlorophyll concentration were collected using a CTD (Sea Bird Scientific, PLUS SBE 9) at each sampling station before the nets were deployed, as well as at further stations in each subsystem. In total, 48 stations were sampled in the nBUS, 43 in the sBUS, and 2 in the Lüderitz cell (see Fig. 1). Mesopelagic fishes were collected using an open-system rectangular midwater trawl (RMT 8) with an 8 m<sup>2</sup> opening, a mesh size of

4000 µm, and a net bucket cod-end with a mesh size of 1000 µm (Baker et al. 1973). The effective tow duration of each haul was about 30 min with a ship speed of 2.5–3.0 knots. The RMT was deployed to a water depth of 101–601 m (depending on the depth of the station) and was hauled at an oblique angle (Table 1). In this study, we sampled on the shelf at depths shallower than the mesopelagic zone, since abundant mesopelagic species such as *Lampanyctodes hectoris* and *Maurolicus walvisensis* may also occupy the shelf region of the Benguela (Hulley & Prosch 1987, Armstrong & Prosch 1991). It must also be noted that mesopelagic species that live below 500 m and do not perform vertical migration, such as some species of the families Melamphidae and Bathylagidae, may have been missed in this study (Sutton et al. 2008). The depth meter attached to the RMT worked at the beginning of the cruise, but became defective and was not used for the majority of stations. When the depth meter was functional, the ratio of the wire length to sampling depth was about 1.5 due to the oblique angle of the net. A typical haul had a wire length of 750 m at an estimated sampling depth of

Table 1. Data of stations where the rectangular midwater trawl (RMT 8) was used on cruise M153 in the southern (sBUS; Stns 8–26) and northern (nBUS; Stns 31–53) Benguela Upwelling Systems. Stns 18 and 39 were sampled repeatedly over a 48 h period, yet, because the distance between trawls was at least 3 km or over 12 h apart, the respective samples were assumed to be independent. (\*) sampling depths calculated when the depth meter was not functioning. T: twilight; N: night; D: day; M: month

Region	Stn No.	Latitude (°S)	Longitude (°E)	Bottom depth (m)	Sampling depth (m)	Cable length (m)	Date (dd.mm) (2019)	Time (UTC)	Time of day	
sBUS	8	31.022	15.992	337	317*	650	19.02	22:05	N	
	15	32.027	16.414	397	377*	675	21.02	16:41	D	
	16	32.029	15.998	800	550	752	22.02	00:13	N	
	18-6	31.116	15.204	1270	500*	752	24.02	04:15	N	
	18-8	31.077	15.190	1270	500*	750	24.02	16:22	D	
	18-9-1	31.018	15.134	1270	500*	750	24.02	23:01	N	
	18-9-2	31.042	15.081	1270	101*	151	25.02	00:24	N	
	22	30.035	16.427	186	166*	271	26.02	21:22	N	
	24	30.093	14.667	537	500*	701	27.02	15:59	D	
	25	30.036	14.327	1088	500*	752	28.02	00:11	N	
	26	29.910	14.320	1111	601*	901	28.02	02:35	N	
	nBUS	31	23.057	13.968	143	124	210	02.03	22:15	N
		32	22.941	13.563	154	115	226	03.03	01:04	N
		34	23.060	12.660	1229	390	751	03.03	19:15	N
35		23.015	12.250	2286	400	751	04.03	22:12	N	
38		21.055	11.497	1895	500*	751	06.03	18:04	N	
39-1		21.007	11.998	1025	500*	750	07.03	02:14	N	
39-3		21.041	12.016	1004	500*	750	07.03	17:12	D	
39-4		21.002	11.999	1015	500*	750	07.03	22:47	N	
45		20.025	11.831	427	330	601	09.03	17:53	T	
46		19.913	11.417	2619	500*	750	09.03	21:28	N	
49		21.686	12.587	590	400	751	10.03	22:42	N	
52		22.227	12.748	533	450	597	11.03	18:34	N	
53		22.168	13.389	188	130	270	12.03	02:09	N	

500 m. We used these hauls as references to calculate the filtered volume of water (and abundance of fishes) for subsequent hauls without depth measurements. We used the size of the net opening ( $8 \text{ m}^2$ ) and the distance traveled with the following equation, assuming that the track can be approximated by the sum of the hypotenuse of 2 equal right triangles, to calculate the abundance for species  $i$ :

$$n_i = \frac{c_{i,s}}{V_s} = \frac{c_{i,s}}{2 \times d_s \times A} \quad (1)$$

where  $c_{i,s}$  represents the count of individuals of a given species  $i$  in the sample  $s$ ,  $V_s$  represents the volume of water,  $d_s$  represents the distance that the net traveled to a given depth (which is doubled to account for descent and ascent), and  $A$  represents the area of the net opening. The respective abundance per unit area is obtained by multiplying the  $n_i$  by water depth. In shallower areas, while the speed of the haul was relatively constant, changes in currents may have changed the angle of the net at some stations, leading to sampling depths that were deeper than the bottom depth. Because we did not reach the bottom (which could be verified from the catch), we assumed the sampling depth was 20 m above the seafloor and used this sampling depth in calculations of filtered water volume. Sampling was mostly done at night and conducted along transects perpendicular to the coast, so that sampling effort could take place along the shelf, slope, and offshore. Upon removal of the net buckets, samples were flushed from the cod-ends and stored in a phosphate-buffered 3.6% formalin solution.

Species identification was performed by using several taxonomic references (Nafpaktitis et al. 1977, Smith & Heemstra 2003, Richards 2005, Sutton et al. 2020). Organisms were identified to the lowest taxonomic level, usually species. Specimens of the genus *Cyclothone* were pooled as *Cyclothone* spp. because many specimens were too damaged for identification to species level. The most abundant *Cyclothone* species was *C. braueri*, but it is highly likely that more species were present in the samples. Juvenile fishes were determined to the lowest taxonomic level possible and included in the species list; however, all larvae and juveniles were excluded from all analyses unless otherwise stated.

## 2.2. Hydrography

Depth profiles, potential temperature–salinity (T–S) plots, satellite images of sea surface temperature and

chl  $a$  concentration, and vertical transects were created in Ocean Data View (ODV) v.5.2.1 (Schlitzer 2018) in order to identify patterns of chl  $a$ , temperature, salinity, and oxygen and to identify water masses. Two separate water masses were identified by comparing our T–S plots to the values of salinity, temperature, and oxygen described in Poole & Tomczak (1999), Rae (2005), Mohrholz et al. (2008), and Flohr et al. (2014). SACW water has previously been defined by salinity of 34.72–35.636, temperature of 8.00–16.00°C, and oxygen concentration of 22.43–68.48  $\mu\text{mol l}^{-1}$ . ESACW has been characterized by salinity of 34.41–35.30, temperature of 5.95–14.41°C, and oxygen concentration of 249.34–300.06  $\mu\text{mol l}^{-1}$  (Poole & Tomczak 1999, Mohrholz et al. 2008). ESACW and SACW assignments were used to compare differences in mesopelagic fish assemblages between the 2 subsystems in order to test the hypothesis that differing water masses are associated with differing assemblage structures. Hydrographic data for multivariate statistics were analyzed with the ‘oce’ package (v.1.2.0; Kelley & Richards 2021) in R. Satellite data for sea surface temperature Level 4 (JPL MUR MEaSUREs Project 2015) and chl  $a$  concentration at resolutions of 0.01 km and 4 km, respectively, were extracted for February in the sBUS and March in the nBUS (NASA Goddard Space Flight Center et al. 2018). Data was visualized in ODV.

## 2.3. Assemblage structure

Species compositional data were analyzed in the ‘vegan’ (v.2.5.6; Oksanen et al. 2020) and ‘clustsig’ (v.1.1; Whitaker & Christman 2015) packages of R v.1.3.1073 (R Core Team 2013). To evaluate if the sampling effort was sufficient and to predict the number of species in each subsystem, species accumulation curves were created. Rarefaction curves were also used to determine the richness and expected number of species at each individual station. When the asymptote was not reached, it was an indication that more species were expected to be present at a station. Abundance data ( $\text{ind. } 10 \text{ m}^{-2}$ ) by species were used to calculate total species richness, Shannon’s diversity index (Shannon & Weaver 1963) and Pielou’s evenness index (Pielou 1975) for each station and subsystem. To test for significant differences in abundance between subsystems, a Mann-Whitney  $U$ -test used for non-parametric data was performed.

Species that occurred at only one station were removed to avoid zero-inflated data and the possible misinterpretation of results, which resulted in 51 species that were included in all multivariate analyses

(Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m688p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m688p133_supp.pdf)). Stns 53 and 31 were excluded from the analysis because they only contained species that were either only present at the respective station or were not mesopelagic species. These were 4 unidentified individuals of the Family Gobiidae and one unidentified *Stomias* sp. at Stn 53 as well as one unidentified individual of the family Gobiidae and 3 *Scomberesox* sp. (*Scomberesocidae*) specimens at Stn 31. In order to reduce the skew of the data, abundance data were transformed using the Hellinger transformation, which gives low weight to species with low counts and many zeros, as was the case in our data (Legendre & Gallagher 2001).

The Bray-Curtis (Field et al. 1982) similarity matrix was calculated based on our species and station table. We used non-metric multidimensional scaling (NMDS) analysis to visualize community characteristics (Field et al. 1982). In order to identify significant clusters, we used the similarity profile procedure SIMPROF (Clarke et al. 2008), where the group average linkage method was applied (1000 permutations). A similarity percentage analysis (SIMPER) (Clarke & Warwick 1994) test was performed to identify the species that best explained differences between communities.

To determine how environmental factors contributed to patterns in mesopelagic fish communities, we used a forward selection procedure to select environmental variables. Based on the depth profiles, the temperature, salinity, chl *a*, and oxygen concentrations showed large changes in the first 50 m of the water column and little change at greater depths. Every 10 m, the mean concentrations were calculated down to 100 m. Correlation plots were then used to select groups of variables whose depths had a correlation <0.70 (Fig. S2) in order to avoid collinearity (Dormann et al. 2013) and overparameterization. As a result, the factors included in forward selection were mean temperature between 3–40, 40–100, and 100–200 m; mean salinity between 3–30, 30–100, and 100–200 m; mean chl *a* concentration between 2–50, 50–100, and 100–200 m; and mean oxygen concentration between 3–10, 10–30, 40–100, and 100–200 m, as well as the depth of the oxycline (defined as the depth at the point of the maximum gradient), bottom depth, mixed layer depth, and water mass affiliation. The forward-selection procedure resulted in a model that included water mass, oxygen at 3–10 m, and chl *a* at 50–100 m, which was confirmed with the lowest Akaike's information criterion (AIC) score when compared to all models produced by the analysis. To test if these variables were significant, the Monte-Carlo permu-

tation test was performed. To make sure that variables were not significant due to collinearity, the variance inflation factor (VIF) was determined. Since all were below the threshold of 10 (Dormann et al. 2013), the analysis confirmed that these variables were independently significant. Redundancy analysis (RDA) was then used to visualize the differences in mesopelagic fish assemblages among the environmental factors. Stn 26 was excluded from the RDA analysis because CTD data were not available for this station.

#### 2.4. Zoogeographic and habitat assignment

Based on the species that contributed the most to the dissimilarity between clusters (see Table 3) and the species that were overall the most abundant (see Table 4), we used QGIS (QGIS Development Team 2014) to visualize species distributions within the BUS. Distributions were then compared with the zoogeographic affiliation of selected species and to the distribution and zoogeographic patterns described in Rubiés (1985) and Hulley (1992). Hulley (1981) described various distributional groups of myctophids characterized as 'high oceanic' and 'pseudoceanic', with many sub-patterns within. Pseudoceanic species are those distributed over the shelf and slope of land masses or oceanic islands and high oceanic species, which have a widespread pattern or are grouped by warm-water or cold-water patterns. Species descriptions were accompanied by the weighted mean bottom depth (MBD) at sampling stations. The MBD for a species was determined as:

$$MBD_s = \sum_i \frac{n_{i,s}}{N_s} \times D_i \quad (2)$$

where  $n_{i,s}$  is the abundance of species  $s$  at each station  $i$  divided by the total abundance of that species from all stations ( $N_s$ ), and  $D_i$  is the bottom depth of the station.

### 3. RESULTS

#### 3.1. Oceanographic conditions

The T–S plot of sampling stations from both regions revealed a clear distinction between water masses from the nBUS and sBUS (Fig. 1). One CTD station in the Lüderitz upwelling cell showed intermediate water properties, which mark a boundary between the nBUS and sBUS (Fig. 2a). The nBUS



was mostly composed of SACW, with ranges of salinity and temperature as described in Mohrholz et al. (2008) as Angola Gyre Water. In the upper 100 m, there was an influence of ESACW in the nBUS, and surface waters were composed of Modified Upwelled Water (MUW) (Rae 2005). At temperatures  $>15^{\circ}\text{C}$  and salinity  $>35.5$ , Oceanic Surface Water (OSW) was present in the nBUS (Rae 2005). The sBUS was composed of mostly ESACW. In the upper 50 m, MUW was present in the sBUS resembling characteristics of the Lüderitz upwelling water. Depth profiles revealed that throughout the water column, oxygen levels were lower in the nBUS than in the sBUS (Fig. 2), especially at stations on the shelf (Stns 31, 32, and 5). Chl *a* patterns showed that Stns 22, 18-9, and 18-8 had the highest concentrations above 50 m, while Stns 24 and 8 had higher concentrations between 50 and 100 m. Transects showed that oxygen concentrations were lower in the nBUS than in the sBUS. While the sBUS had concentrations below  $2\text{ mg l}^{-1}$  near the coast, concentrations of less than  $2\text{ mg l}^{-1}$  and lower extended far off the slope in the nBUS (Fig. 3). Satellite images obtained during the study showed upwelling with associated cold temperatures at the Lüderitz cell, between the nBUS and the sBUS (Fig. 4). In general, sea surface temperatures were lower on the shelf of the nBUS than on the sBUS shelf. Chl *a* concentrations were highest close to the shore on the shelf of both the nBUS and the sBUS.

### 3.2. Mesopelagic fish assemblages

A total of 1853 fish specimens were analyzed from 13 stations in the nBUS and 11 in the sBUS. We found a total of 88 species and 24 families of mesopelagic fishes in the subsystems (Table S1). Families with the highest numbers of species were Myctophidae (35 species), Stomiidae (10 species), and Sternoptychidae (8 species). The nBUS had 17 families, dominated by Myctophidae (66%) and followed by Sternoptychidae (13.3%), Stomiidae (5.8%), Gonostomatidae (4.5%), and Bathylagidae (3.5%). The dominant species overall were *Diaphus hudsoni* (25.1%), *Maurolicus walvisensis* (12.0%), and *Lampanyctus australis* (11.3%). Myctophidae in the nBUS consisted mainly of *D. hudsoni* (37.8%), *L. australis* (17.0%), *Symbolophorus boops* (7.4%), and *D. dumerilii* (6.5%). In the sBUS, mesopelagic fishes of 10 mesopelagic families were caught. The dominant families were Sternoptychidae (48.9%), Myctophidae (24.8%), and Gonostomatidae (19.0%). The prevailing species were *M. walvisensis* (42.3%), *Cyclothone* spp. (18.9%), and *D. meadi* (9.1%). Within the Myctophidae, *D. meadi* contributed 35.6%, *Lampanyctodes hectoris* 13.9%, *Hygophum hanseni* 11.4%, and *D. hudsoni* 10.7%.

Abundances were not significantly different between the 2 subsystems, with a mean of 10.14 ind.  $10\text{ m}^{-2}$  in the nBUS and 8.77 ind.  $10\text{ m}^{-2}$  in the sBUS ( $p = 0.91$ ). Mean diversity and evenness in the nBUS

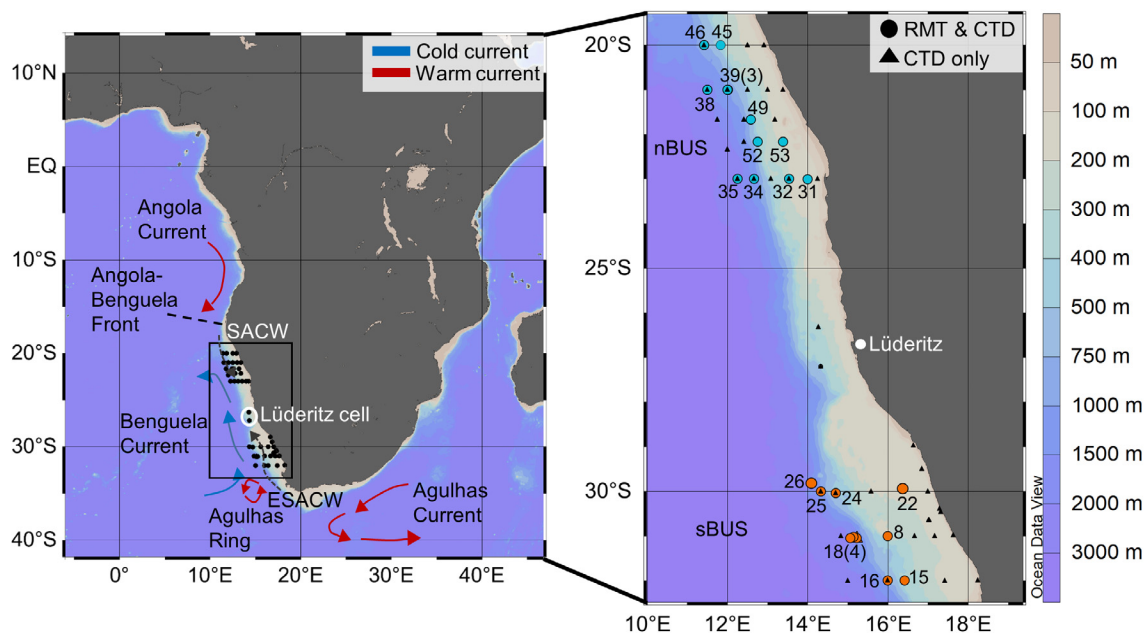


Fig. 1. Rectangular midwater trawl (RMT) stations in the northern (nBUS) and southern (sBUS) subsystems of the Benguela Current, where hydrographic data and sampling of mesopelagic fishes took place. SACW: South Atlantic Central Water; ESACW: Eastern South Atlantic Central Water

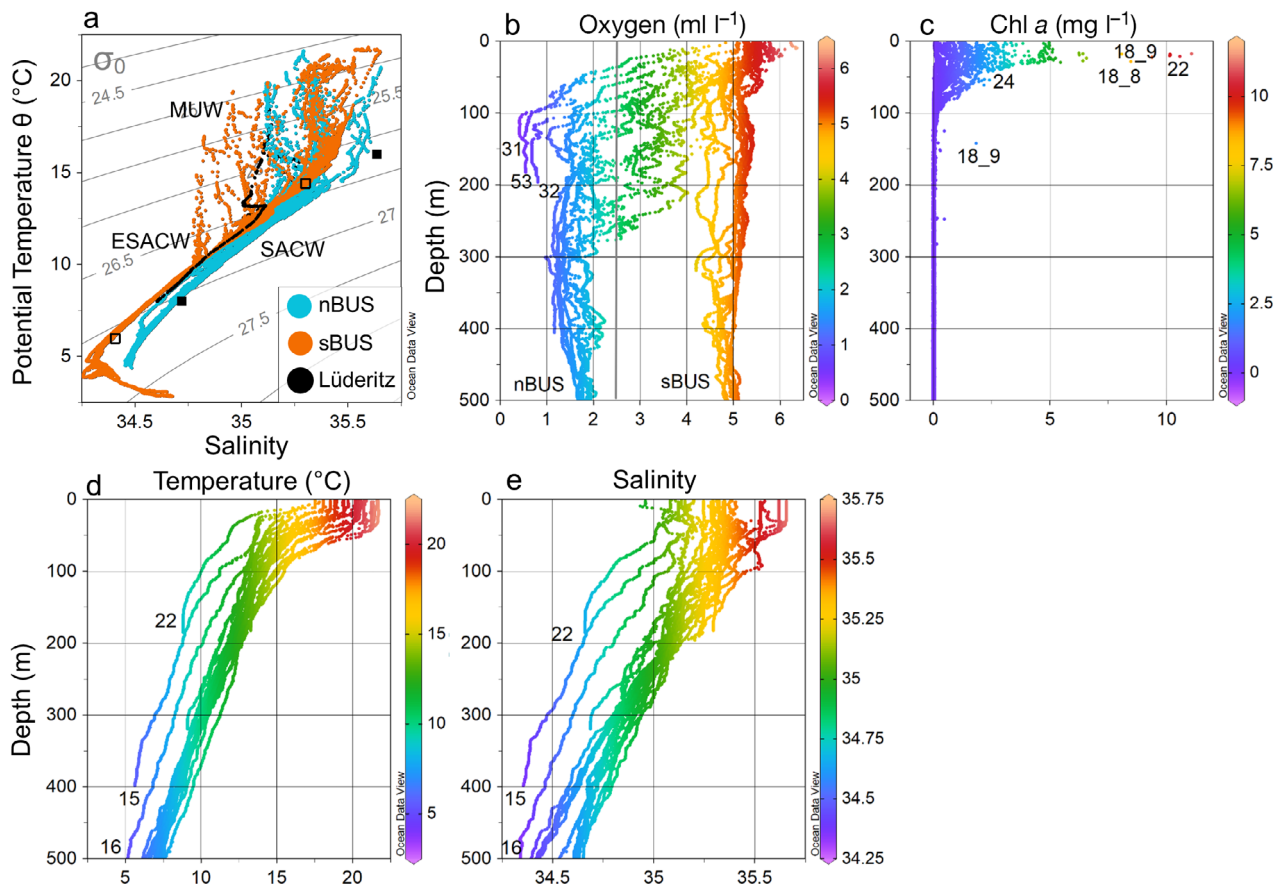


Fig. 2. (a) Potential temperature–salinity (T–S) plots showing identified water masses, and depth profiles of (b) oxygen concentration, (c) chl *a* concentration, (d) temperature, and (e) salinity. Numbers in (b–e) are station numbers. Squares in the T–S plot represent the minimum and maximum temperature and salinity for Eastern South Atlantic Central Water (ESACW) (open) and South Atlantic Central Water (SACW) (closed) as previously described in Poole & Tomczak (1999), Rae (2005), Mohrholz et al. (2008), and Flohr et al. (2014). MUW: Modified Upwelled Water

were 1.65 and 0.21, respectively, and 1.40 and 0.26, respectively, in the sBUS (Table S2). It should be noted, however, that at Stn 31, a high number of *Aequorea* spp. hydromedusae were caught in the net, which may have biased the sampling of fish. This station was not considered in statistical analyses, since its species were not classified as mesopelagic.

The species accumulation curves suggest a larger total number of species in the nBUS compared to the sBUS (Fig. 5). However, for both regions, the asymptote of the accumulation curve was not reached, demonstrating that there are more species present in each subsystem than were collected in our study. Rarefaction curves are very steep for the majority of stations in the nBUS as well as in the sBUS (e.g. Stns 18-9-1, 16, and 25) (Fig. 5). An asymptote was again not reached, indicating that these stations also had the potential for higher species richness. While the species accumulation curves seem to indicate that

the nBUS and sBUS communities were homogeneous in species richness, rarefaction curves revealed that there is high variation within each subsystem.

### 3.3. Assemblage structure and environmental drivers

The analysis of similarities (ANOSIM) showed that there was no difference between communities that were sampled during the day, night, dawn/dusk ( $R = -0.102$ ,  $p = 0.822$ ). NMDS revealed a clear separation in community composition of mesopelagic fishes between stations in the nBUS and sBUS (Fig. 6). The SIMPROF procedure revealed 7 significant clusters of mesopelagic fish assemblages (Fig. 7). Stations in the sBUS shelf break were affiliated with the ESACW and those of the nBUS shelf break were associated with the SACW. Stations from the nBUS

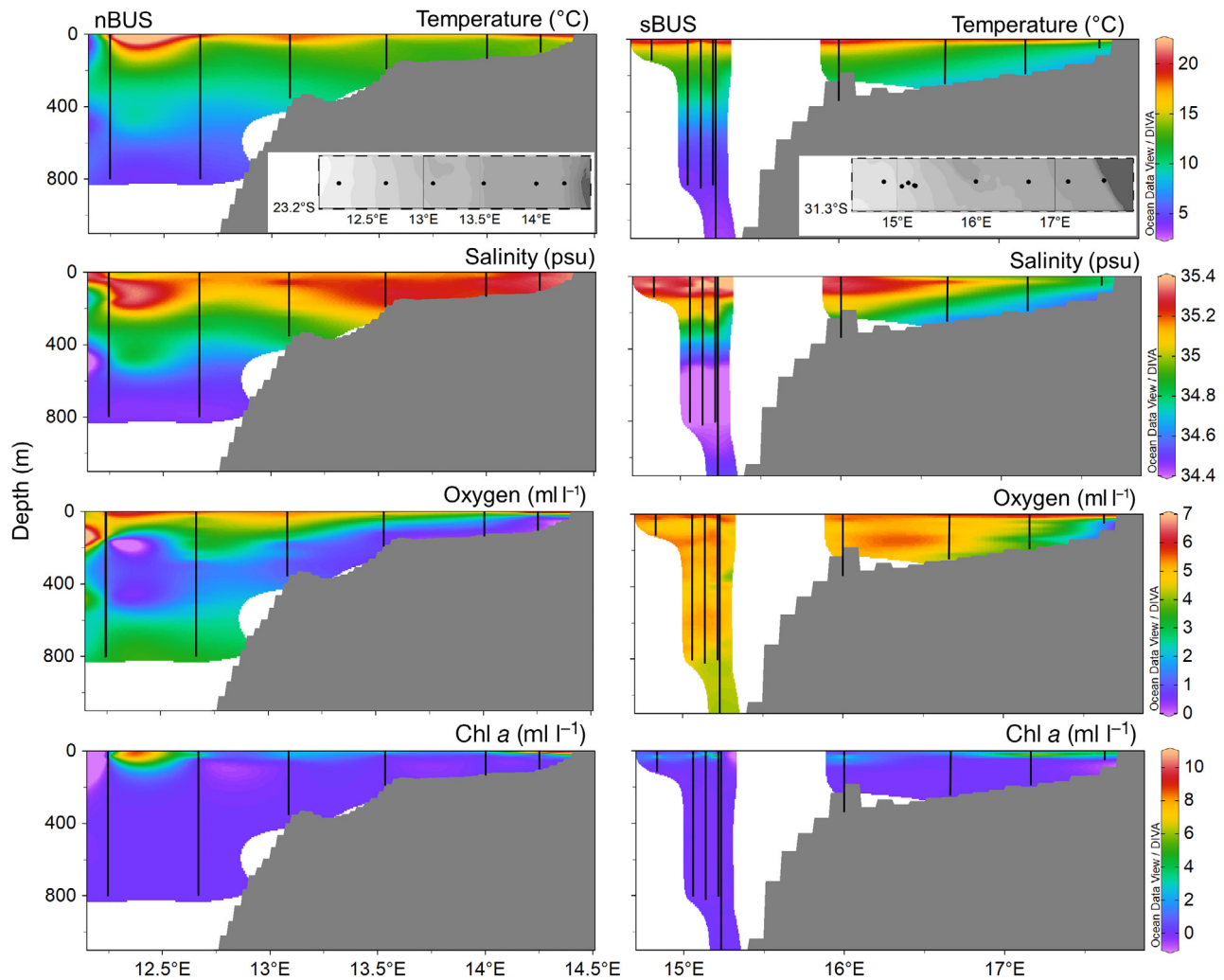


Fig. 3. Vertical transects of temperature, salinity, oxygen, and chl a concentrations for the northern (nBUS, left) and southern (sBUS, right) Benguela Upwelling Systems. Transects used are shown in the temperature profile windows. Vertical black lines: positions of CTD casts where the parameters were measured

formed a 'nBUS shelf' group, which consisted only of Stn 32 as well as 3 offshore groups ('nBUS offshore N1', 'offshore N2', and 'offshore N3') (Fig. 7). Similarly, stations from the sBUS formed a 'sBUS shelf' group (Stns 8, 22, 24) as well as 2 offshore groups ('sBUS offshore S1', 'offshore S2', however, 'sBUS offshore S1' only contained one group, which was Stn 18-9-2). Over 96% of the species that made up the sBUS shelf cluster were *M. walvisensis* and *L. hectoris*. The nBUS shelf cluster was also composed only of *D. dumerilii* as well as the epipelagic species *Scorpaenopsis* sp., which was not included in the analysis but was present at the stations in this cluster. The offshore S1 cluster consisted of 64.0% *H. hanseni*, followed by *D. meadi* (12.0%) and 6 other species all contributing to less than 5% of the fishes in this cluster. The offshore S2 cluster was dominated

by *Cyclothone* spp. (31.2%), followed by *D. meadi* (15.5%), and *M. walvisensis* (12.0%); 33 other species contributed less than 50% to the total proportion of fishes in the assemblage. The offshore N1 assemblage comprised 28 species, dominated by *D. hudsoni* (25.3%), *Lampanyctus australis* (17.5%), and *D. dumerilii* (13.7%). The offshore N2 assemblage was made up of 39 species; *D. hudsoni* prevailed (44.2%), followed by *L. australis* (7.2%), and *Cyclothone* spp. (5.2%). Offshore N3 cluster comprised 29 species; the most dominant were *M. walvisensis* (36.5%), *S. boops* (13.9%), and *L. australis* (12.4%) (Table 2).

SIMPER was used to determine which species contributed most to the differences between the communities (Table S3). The species most responsible for differences in mesopelagic fish assemblages be-



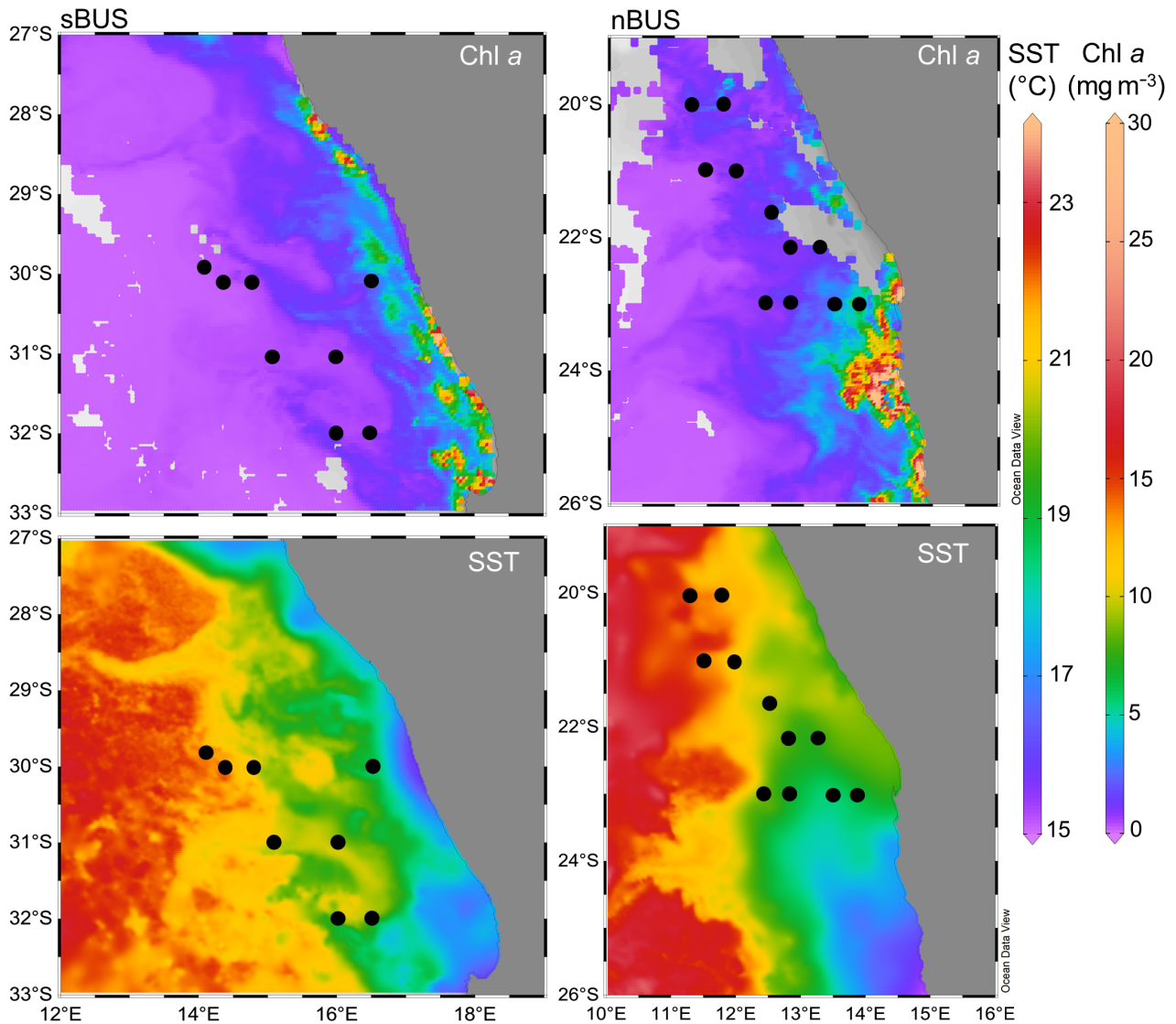


Fig. 4. Satellite images of chl *a* concentration and sea surface temperature (SST) in the southern (sBUS) and northern (nBUS) Benguela Upwelling Systems. Satellite images of the SST are from February 20 (sBUS) and March 3 (nBUS) and chl *a* data are a composite of 8 days from February 18–25 (sBUS) and March 6–13 (nBUS)

tween the nBUS shelf and nBUS offshore groups was *D. dumerilii* for all offshore groups (20.3% offshore N1; 25.9% N2; 24.3% N3) (Table S3), although these were not always the most abundant species. The species that prevailed offshore in the nBUS was *D. hudsoni* in communities N1 and N2, with an abundance of 9.21 and 20.98 ind.  $10\text{ m}^{-2}$ , respectively. In the offshore N3 assemblage, the most abundant species was *M. walvisensis*, with an abundance of 15.03 ind.  $10\text{ m}^{-2}$  (Table 2). Species that contributed to the greatest differences within the offshore communities of the nBUS clusters were *S. boops* (offshore N2 vs. N3), *D. dumerilii* (offshore N1 vs. N2), and *M. walvisensis* (offshore N1 vs. N3). Differences be-

tween the sBUS shelf and sBUS offshore communities were mostly attributed to *M. walvisensis* for both offshore groups. The proportion, abundance, and group-wise comparisons from the SIMPER analysis can be found in Tables 2 & S3, respectively. The mean total abundance of stations within assigned clusters and the total abundance of species within a given cluster are presented in Table 2. See Table S1 for a full species list of fishes observed in the nBUS and sBUS.

The Monte Carlo permutation test revealed that the first 2 RDA axes were significant ( $p \leq 0.001$ ) and explained 33% of the variance (20 and 13%, respectively). Significant environmental factors were water

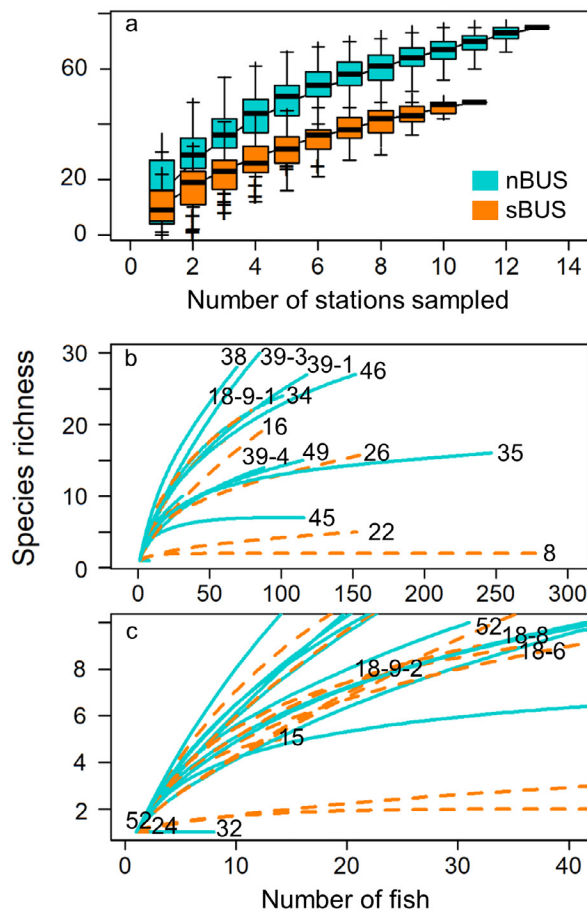


Fig. 5. (a) Species accumulation curve and (b,c) rarefaction curves of mesopelagic fishes sampled in the northern (nBUS) and southern (sBUS) Benguela subsystems. Boxplots of the species accumulation curve represent the median, quartiles, and the minimum and maximum number of species. Outliers are marked with '+'. Rarefaction curves show the total number of individual fish that were sampled and the species richness at each station

mass ( $p \leq 0.001$ ), chl *a* concentration from 50–100 m ( $p = 0.001$ ), and oxygen concentration at the surface from 3–10 m ( $p = 0.004$ ) (Table 3). RDA was used for better visualization of the relationships between species, stations, and environmental factors (Fig. 8). The RDA revealed that *M. walvisensis* was highly associated with the sBUS shelf assemblage and chl *a* concentration from 50–100 m. *Valencienellus tripunctulatus*, *D. meadi*, *H. hanseni*, *Argyropelecus hemigymnus*, and *Cyclothone* spp. were linked to the sBUS offshore S2 assemblage, and arrows in the plot show that oxygen at 3–10 m was a main driver of these communities. Species that were associated with the offshore N1 assemblage such as *D. hudsoni* and *L. australis* were not strongly associated with environmental parameters.

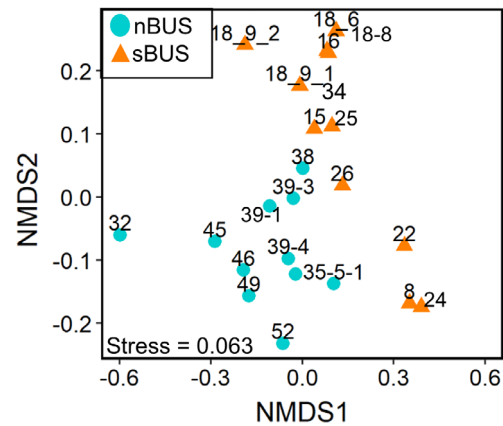


Fig. 6. Non-metric multidimensional scaling (NMDS) plot for stations (symbols with station numbers) with mesopelagic fish communities of the northern (nBUS) and southern (sBUS) Benguela subsystems, based on Bray-Curtis dissimilarity matrix for Hellinger-transformed fish abundance data

### 3.4. Zoogeography

We used the results of the SIMPER analysis, abundance data, and RDA analysis to describe the zoogeographic patterns of species that were (1) highly influential within groups (SIMPER), (2) abundant, and/or (3) strongly associated with station groups and environmental factors (RDA) (Table 4). *D. hudsoni* had a weighted MBD of 1361 m and *L. australis* of 997 m. Both species were mostly found in the nBUS and further offshore and occurred in low abundances in the sBUS, showing oceanic warm-water distribution patterns (Fig. 9). In contrast, *D. meadi* was much more abundant in the sBUS than in the nBUS. Based on their MBD of 202 and 805 m, species such as *Lampantodes hectoris* and *M. walvisensis* would be classified as shelf and partially pseudo-oceanic species, respectively, due to their dominance at stations such as Stns 22 and 8, but they were also collected on the shelf break (Fig. 9). The MBD of *M. walvisensis* was deeper than the shelf depth due to its high abundance at Stn 35-5, which was 2286 m deep. *Cyclothone* spp. occurred in the nBUS and the sBUS, showing a broad distribution range. It is important to note that these samples were collected during austral summer, and the distribution of mesopelagic fishes may differ seasonally.

## 4. DISCUSSION

### 4.1. Mesopelagic fish assemblages

While the overall abundance of mesopelagic fishes did not differ between nBUS and sBUS, 7 different

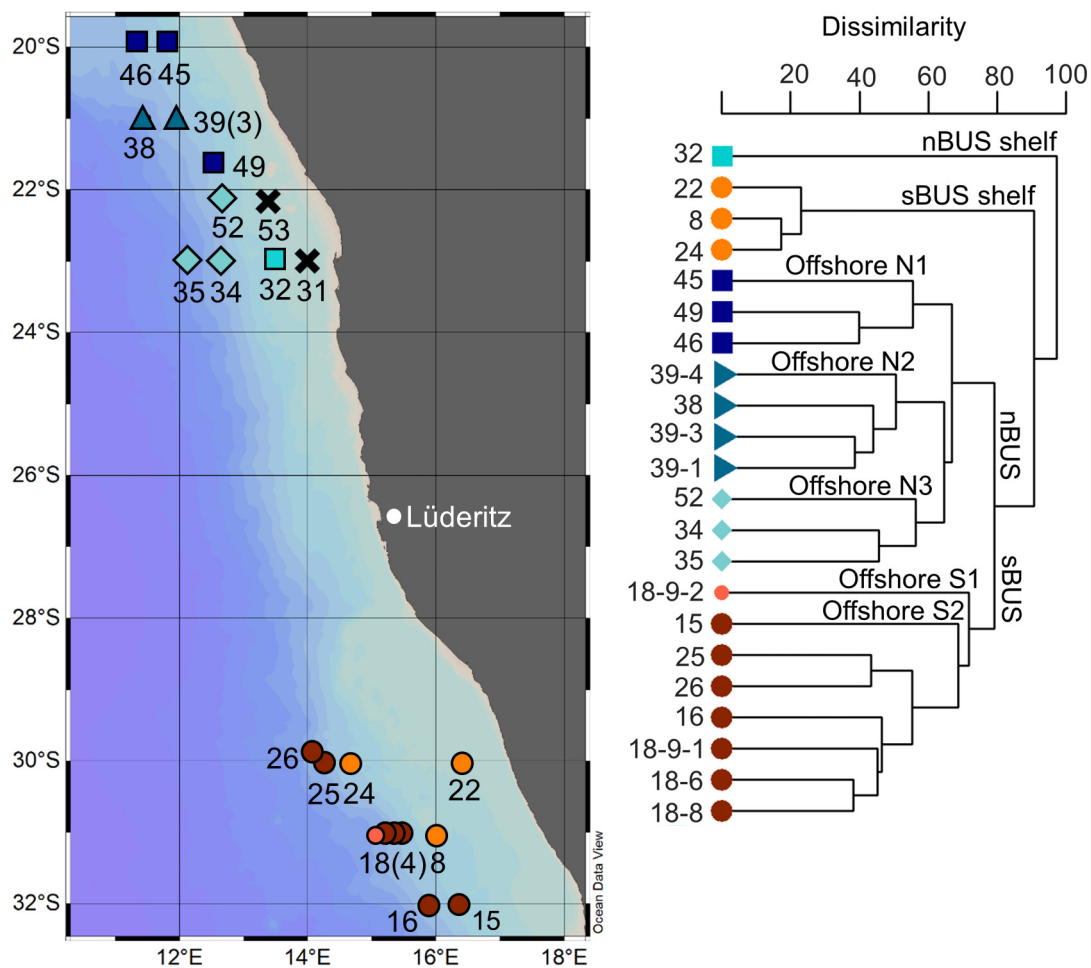


Fig. 7. Station map (left), with clusters of mesopelagic fish communities based on hierarchical cluster analysis (right) using the complete linkage method on Bray-Curtis dissimilarity matrix for Hellinger-transformed abundance data. '✱' represents stations that were removed from the analysis due to low frequency of occurrence (<2)

assemblages were identified between the 2 subsystems. In these assemblages, clusters of similar community composition indicated a clear distinction between the southern and northern Benguela subsystems as well as stations on the shelf and offshore. Previous studies have shown that nBUS contains a mix of tropical species, most likely due to the intrusion of Angolan Current water (Rubiés 1985), as well as more temperate and cold-water species such as *Lampanyctus australis* and *Diaphus hudsoni*. In the current study, we found the shelf and slope of the nBUS to be composed of SACW, with properties described by Mohrholz et al. (2008) as Angola Gyre water. For these reasons, we may have also seen higher species richness in offshore stations in the nBUS than the sBUS, since there are species typical of the cold-water Benguela Current as well as warm tropical Angolan Current waters (Rubiés 1985). In the nBUS there are also seasonal differences in water

masses: in the austral summer, SACW dominates, while in the austral winter, ESACW spreads further north (Mohrholz et al. 2008). These influences of Benguela Current water masses as well as SACW and ESACW may explain the high diversity in the offshore stations of the nBUS.

While species richness was greater in the offshore stations of the nBUS than on the shelf or in the sBUS, species accumulation curves revealed that there was most likely greater richness and species that we did not catch. This was also confirmed by the rarefaction curves, suggesting that individual stations in both subsystems had the potential for greater species richness. A possible explanation for this is that the RMT 8 net has a rather small opening and therefore net avoidance by larger or faster species of mesopelagic fishes may have occurred. Through a combination of net sampling and acoustics, Kaartvedt et al. (2012) found that net avoidance of the myctophid *Bentho-*

Table 2. Total abundance and percentage of each mesopelagic fish species within each assigned cluster in the northern (nBUS) and southern (sBUS) Benguela Upwelling System. Note that mean total abundance refers to the total number of fish in a cluster corrected by the number of stations representative of each cluster, while species abundance is the total abundance within a cluster. Only species contributing  $\geq 3\%$  are presented

Region	Species	Proportion (%)	Abundance (ind. $10\text{ m}^{-2}$ )
sBUS shelf (3)	<i>Maurolicus walvisensis</i>	89.8	40.40
	<i>Lampanyctodes hectoris</i>	7.5	3.38
	Mean total abundance (all species)		15.00
nBUS shelf (1)	<i>Diaphus dumerilii</i>	100.0	0.64
	Mean total abundance (all species)		0.64
Offshore S1 (1)	<i>Hygophum hanseni</i>	64.0	0.71
	<i>Diaphus meadi</i>	12.0	0.13
	<i>Chauliodus sloani</i>	4.0	0.04
	<i>Diaphus meadi</i>	4.0	0.04
	<i>Diogenichthys atlanticus</i>	4.0	0.04
	<i>Lobianchia gemellarii</i>	4.0	0.04
	<i>Notolychnus valdiviae</i>	4.0	0.04
	<i>Symbolophorus barnardi</i>	4.0	0.04
	Mean total abundance (all species)		1.11
Offshore S2 (7)	<i>Cyclothone</i> spp.	31.2	20.68
	<i>Diaphus meadi</i>	15.5	10.26
	<i>Maurolicus walvisensis</i>	12.0	7.97
	<i>Argyropelecus hemigymnus</i>	6.4	4.25
	<i>Vinciguerria attenuata</i>	5.7	3.77
	<i>Valenciennellus tripunctulatus</i>	4.9	3.24
	<i>Diaphus hudsoni</i>	4.5	3.01
	<i>Hygophum hanseni</i>	3.7	2.52
	<i>Lobianchia dofleini</i>	3.6	2.40
	Mean total abundance (all species)		9.48
Offshore N1 (3)	<i>Diaphus hudsoni</i>	25.3	9.21
	<i>Lampanyctus australis</i>	17.5	6.37
	<i>Diaphus dumerilii</i>	13.7	4.97
	<i>Symbolophorus barnardi</i>	11.9	4.34
	<i>Diaphus taaningi</i>	7.1	2.58
	<i>Melanolagus bericoides</i>	5.1	2.09
	<i>Stomias boa</i>	5.0	1.82
	<i>Hoplostethus melanopus</i>	3.1	1.13
Mean total abundance (all species)		10.21	
Offshore N2 (4)	<i>Diaphus hudsoni</i>	44.2	20.98
	<i>Lampanyctus australis</i>	7.2	3.41
	<i>Cyclothone</i> spp.	5.2	2.47
	<i>Diaphus meadi</i>	4.7	2.23
	<i>Lobianchia dofleini</i>	3.7	1.75
	<i>Scopelopsis multipunctatus</i>	3.4	1.59
	Mean total abundance (all species)		11.88
Offshore N3 (3)	<i>Maurolicus walvisensis</i>	36.5	15.54
	<i>Symbolophorus boops</i>	13.9	5.92
	<i>Lampanyctus australis</i>	12.4	5.28
	<i>Diaphus hudsoni</i>	7.7	3.28
	<i>Cyclothone</i> spp.	7.2	3.08
	<i>Melanolagus bericoides</i>	4.9	2.07
	<i>Stomias boa</i>	4.4	1.87
	Mean total abundance (all species)		14.19

*sema glaciale* led to the underestimation of abundances. For these reasons, it is important to take into account that we may have lower abundances of reported species than are actually present in the ecosystem and that some species present in the environment are not reported in our findings. Another important caveat to consider is seasonality. Our samples are representative of austral summer; however, during winter, communities may differ, as there are also many differences in water masses and upwelling intensity in the Benguela region during austral winter (Mohrholz et al. 2008, Hutchings et al. 2009). For future studies, we recommend greater sampling effort and the combined use of trawls and acoustics as well as sampling during multiple seasons and years.

Species composition differed between subsystems as well as between stations on the shelf and offshore. The shelf group of the sBUS was mostly dominated by *Maurolicus walvisensis* and *Lampanyctodes hectoris*, which are both known as slope- and shelf-associated species (Hulley & Prosch 1987). *L. hectoris* has previously been classified as one of the few shelf-associated species of lanternfish (Hulley 1981). We collected this species during our study in austral summer; however, it may show seasonal differences in its distribution (Rubiés 1985, Hulley & Lutjeharms 1989). *L. hectoris* has been classified as a pseudo-oceanic species, also inhabiting colder waters particularly during spawning times from late winter to early summer with peaks in spring (Prosch 1991). Spawning takes place off the coast of South Africa, where the greatest egg densities were found offshore of the 200 m isobath of Cape Canyon and Good Hope Valley (Prosch 1991). Stn 15 was closest to these spawning areas and had the second highest abundance of *L. hectoris*, while the highest abundance was detected further north at Stn 8 on the shelf. However, because our sampling took place in late austral summer, it is



Table 3. Redundancy analysis (RDA) describing environmental factors that affect fish communities at each station. Table shows adjusted  $R^2$  value describing portion of total variance explained by the environmental variables and test statistics of the Monte-Carlo permutation test, when testing the global model, the RDA axis, and each environmental factor. Model selected was defined as species matrix ~ water mass + oxygen 3–10 m + chl a 50–100 m.  $F$  is the  $F$ -statistic (999 permutations); \* $p < 0.05$ . Variance inflation factors (VIF) confirmed that factors were not collinear and could be kept in the model

Test	Adjusted $R^2$	df	Variance	$F$	p	VIF
Model	0.27	4	0.27	3.44	0.001*	
Residuals		17	0.44			
Water mass		1	0.13	4.93	0.001*	1.17
Oxygen 3–10 m		1	0.07	2.68	0.004*	1.59
Chl a 50–100 m		1	0.09	3.41	0.001*	1.78
Residuals		15	0.40			
RDA1		1	0.20	5.42	0.001*	
RDA2		1	0.13	3.50	0.009*	
RDA3		1	0.04	1.40	0.185	
Residuals		17	0.44			

likely that most *L. hectoris* were not in the spawning grounds but instead in other areas of the shelf and slope.

The shelf assemblage in the nBUS had very low abundance and richness compared to the other

assemblages. The species that contributed most to the difference between the nBUS shelf and other groups was *Diaphus dumerilii*; however, its abundance was low compared to species that best described other groups, such as *D. meadi* or *M. walvisensis*. *D. dumerilii* occurred on the shelf as well as at offshore stations, suggesting pseudo-oceanic warm-water patterns, as also described by Hulley (1981). One factor that may have influenced the community composition at the stations on the nBUS shelf was the presence of jellyfishes, which were not included in the analysis, although there was a higher biomass of *Aequorea* spp. than fishes at Stns 53 and 31 (authors' unpubl. data). Although there was a higher biomass of jellyfishes than fishes, their volume was less than that

of the cod-end, thus they are unlikely to have altered the catching efficacy of the net. Jellyfishes can impact trophic interactions, as they occupy a similar trophic level as small pelagic fishes, feeding on zooplankton such as copepods and euphausiid eggs,

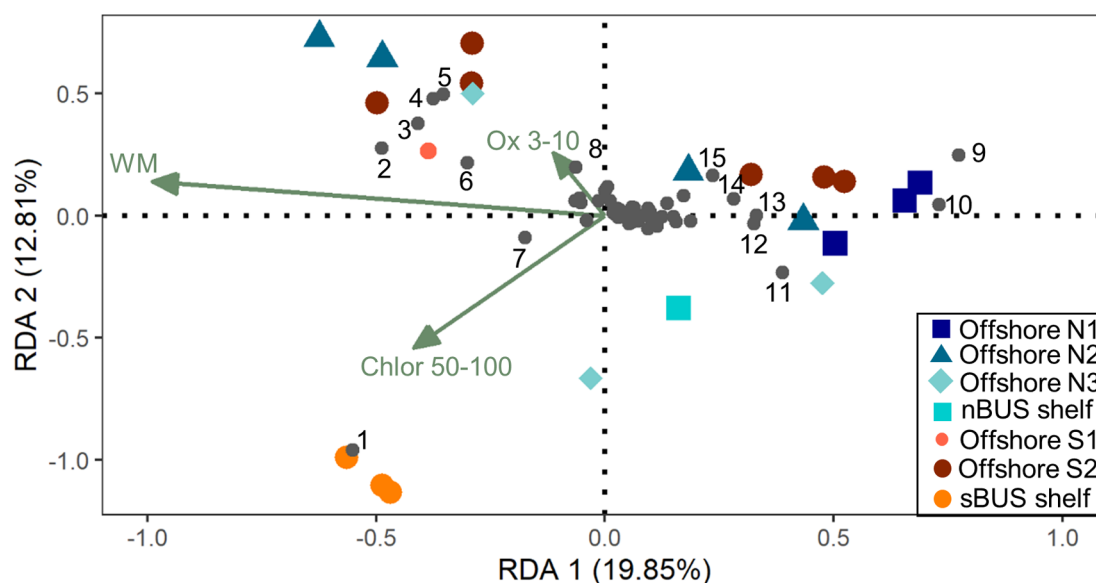


Fig. 8. Redundancy analysis (RDA) ordination between mesopelagic fish assemblages and environmental variables at stations in the northern (nBUS) and southern (sBUS) Benguela Upwelling subsystems. Arrows represent environmental drivers of community composition ( $p < 0.001$ ), which are mean chl a concentration 50–100 m, mean oxygen concentration 3–10 m, and water mass (WM). Colored dots represent the 7 clusters identified by the SIMPROF routine ( $p < 0.001$ ), which are made up of nBUS shelf, sBUS shelf, and offshore communities of the nBUS (offshore N1, N2, N3) and sBUS (offshore S1, S2). Small dots with numbers represent individual species: 1: *Maurolicus walvisensis*; 2: *Cyclothone* spp.; 3: *Hygophum hanseni*; 4: *Argyropelecus hemigymnus*; 5: *Diaphus meadi*; 6: *Valencienellus tripunctulatus*; 7: *Lampanyctodes hectoris*; 8: *D. diadematus*; 9: *D. hudsoni*; 10: *Lampanyctus australis*; 11: *D. dumerilii*; 12: *Symbolophorus boops*; 13: *Stomias boa*; 14: *Melanolagus bericoides*; 15: *Symbolophorus barnardi*



Table 4. Assignment of zoogeographic patterns for mesopelagic fishes in the Benguela Upwelling Systems (north: nBUS; south: sBUS) during the austral summer, based on the present study as well as those previously described. Weighted mean bottom depth (MBD) for the current study has been calculated for each species. Species were selected based on their abundance, contribution to community composition as indicated by SIMPER analysis, or they were strongly associated with environmental variables as indicated in the RDA. (–) indicates that the species has not been reported in a previous study. The subsystem listed in column 'present study' indicates the subsystem where that given species was most abundant. Species may still be present in both subsystems

	Hulley (1981, 1992)	Rubiés (1985) <sup>a</sup>	Present study	MBD (m)
Bathylagidae				
<i>Melanolagus bericoides</i>	–	–	nBUS, high oceanic,	2010
Gonostomatidae				
<i>Cyclothone</i> spp.	–	–	sBUS, high oceanic	2025
Myctophidae				
<i>Diaphus dumerilii</i>	Oceanic zone, tropical pattern	Pseudo-oceanic, warm-water species	nBUS, broad pattern with pseudo-oceanic, warm-water species	508
<i>Diaphus hudsoni</i>	Subantarctic pattern, semi-subantarctic pattern	Northern limit to 18° 01' S, truly oceanic, subantarctic pattern	nBUS, pseudo-oceanic and oceanic, warm-water species	1361
<i>Diaphus meadi</i>	South temperate pattern, convergence sub-pattern	Truly oceanic species, temperate pattern	sBUS, broad, temperate pattern	1140
<i>Diaphus taaningi</i>	Pseudo-oceanic, warm water, slope-water lanternfish	Pseudo-oceanic, warm-water species	nBUS, pseudo-oceanic, warm-water species	595
<i>Hygophum hansenii</i>	South temperate pattern, convergence sub-pattern	Truly oceanic species, temperate pattern	sBUS, broad, temperate pattern	1231
<i>Lampanyctus australis</i>	South temperate pattern, convergence sub-pattern	Truly oceanic species, subantarctic pattern	nBUS high oceanic and broad, warm-water species	997
<i>Notoscopelus resplendens</i>	Broadly tropical pattern	Truly oceanic species, subtropical–tropical pattern	nBUS offshore, warm-water species	1548
<i>Lampanyctodes hectoris</i>	Pseudo-oceanic zone, cold-water Benguela pattern, upper slope and shelf break	Pseudo-oceanic, cold-water pattern, shelf species	sBUS, pseudo-oceanic and shelf pattern	202
<i>Symbolophorus barnardi</i>	Sub-tropical pattern	Truly oceanic species, subtropical pattern	nBUS shelf break, warm-water species	1293
<i>Symbolophorus boops</i>	Semi-subantarctic, pattern of Argentine and Brazilian coast in Malvinas confluence, where mix of subtropical and Antarctic waters present	Truly oceanic species, subantarctic pattern	nBUS shelf break, the presence in the Lüderitz cell (unpubl. data) shows temperate–subantarctic patterns	1541
Sternoptychidae				
<i>Argyroteleus hemigymnus</i>	–	–	sBUS pseudo-oceanic, distributed near land masses or oceanic islands and sea mounts and associated with shelf edge <sup>b</sup>	805
<i>Maurollicus walvisensis</i>	Pseudo-oceanic	–	sBUS shelf (and some pseudo-oceanic) species	1165
<i>Valenciennellus tripunctulatus</i>	–	–	sBUS pseudo-oceanic, distributed near land masses or oceanic islands and sea mounts <sup>b</sup>	1128
Stomiidae				
<i>Stomias boa</i>	–	–	nBUS pseudo-oceanic and oceanic, widespread pattern	1110

<sup>a</sup>Rubiés 1985 as well as literature within Wisner (1976), Backus et al. (1977), Hulley (1981), Bekker (1983); <sup>b</sup>Fock et al. (2004), Pusch et al. (2004a), Olivar et al. (2017)

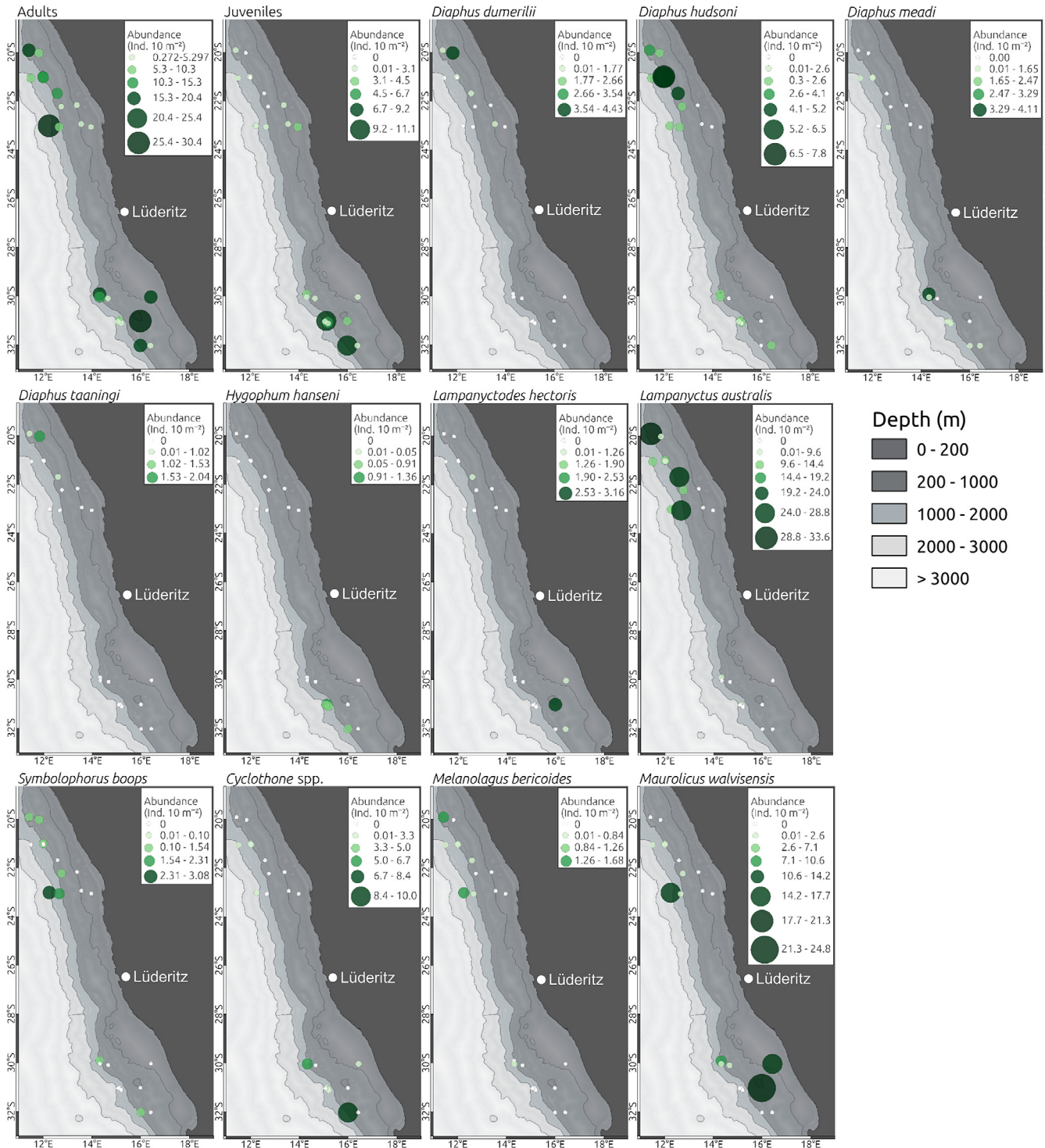


Fig. 9. Abundance and distribution of dominant and/or highly typical species of mesopelagic fishes in the Benguela Upwelling Systems. For adults and juveniles, all mesopelagic fish species have been pooled

among other taxa (Brodeur et al. 2008). While stocks of small pelagics have recovered in the sBUS over recent decades, this has not been the case in the nBUS (van der Lingen et al. 2006). Instead, large populations of jellyfishes such as *Aequorea* sp., but

also the gobies *Sufflogobius* sp. have taken their place (Sparks et al. 2001, Roux et al. 2013). Jellyfishes may be able to outcompete mesopelagic fishes that frequently inhabit the shelf similar to *M. walvisensis* and *L. hectoris*. *Aequorea* sp. and *Sufflo-*

*gobius* sp. co-occurred at Stns 31 and 53, but *D. dumerilii* was only found at Stn 32, where jellies were rare (however, *Sufflogobius* sp. was present). In contrast, we did not find high numbers of *Aequorea* sp. or other jellyfishes on the shelf of the sBUS.

The myctophid species *D. hudsoni* and *Lampanyctus australis* commonly occur in the nBUS area as well as further offshore at the Valdivia Bank (Rubiés 1985). Our study identified 3 offshore communities in the nBUS, similar to the findings of Rubiés (1985). The most dominant species was *D. hudsoni* in 2 groups, followed by *L. australis* at offshore communities N1 and N2. The myctophid species *D. hudsoni* and *L. australis* commonly occur in the nBUS area as well as further offshore at the Valdivia Bank (Rubiés 1985). In our study, *D. hudsoni* was usually found with higher abundances in the nBUS than in the sBUS, possibly because spawning takes place around 20° S, near the Orange River mouth at depths below 400 m (Olivar 1987). *D. hudsoni* is also distributed in the area of the Subtropical Convergence, but is limited between the 5–15°C isotherms at 200 m (Hulley 1981). *L. australis* has been associated with convergence zones and was collected in the Atlantic at the Subtropical Convergence (Hulley 1981). Data from Hulley (1981) showed that the upper limit of *L. australis* may be the 12–13°C isotherms at 200 m, and the lower limit for the species may be the 6–7°C isotherms at 200 m.

Two offshore groups were identified in the sBUS; however, group offshore S1 only consisted of Stn 18-9-2, hence, conclusions cannot be made about this assemblage. This station consisted of a high abundance of *Hygophum hanseni* compared to all other sBUS offshore stations. In the offshore S2 assemblage, *Cyclothone* spp. prevailed, and *D. hudsoni*, the dominant species in the nBUS offshore stations, was replaced by a dominance of *D. meadi*, which share very similar morphologies. This may be a good example of niche partitioning, where each species plays a similar role in its specific habitat. Each of these species can be found in both subsystems, but only one species is more abundant than the other in a subsystem. In addition, the Lüderitz upwelling cell may create a biological barrier, separating populations on both sides of the front (Kirkman et al. 2016). Isolation leading to morphological differences was reported for *L. australis*. The species has higher numbers of gill rakers in the upwelling area than populations outside upwelling areas (Rubiés 1985). This may lead to species differentiation and utilization of different food sources, where fishes with a higher number of gill rakers may be able to feed on smaller

organisms (Rubiés 1985). *Diaphus* spp. belong to a very species-rich myctophid genus, and this group has diversified at a greater rate than other genera in the family (Davis et al. 2014, Martin & Davis 2016). Rubiés (1985) classified *D. meadi* as a truly oceanic species with temperate patterns, and according to Koubbi (1993), *D. meadi* was grouped with taxa present in subtropical areas as well as in frontal transition zones, with the Subantarctic Front as the southern limit.

#### 4.2. Environmental drivers of assemblage structure

The environmental factors that could best explain the composition of mesopelagic fish communities were local water masses as well as certain conditions in the upper water column; specifically, chl *a* concentration between 50–100 m and oxygen concentration between 3–10 m. Previous studies have shown that water masses and the frontal zones between them can influence the composition of mesopelagic fish assemblages (Fock et al. 2004, Fock 2009, Netburn & Koslow 2018, Tiedemann et al. 2018, Dove et al. 2021). *D. dumerilii*, previously classified as having pseudo-oceanic and warm-water patterns (Rubiés 1985), occurred at a station on the shelf of the nBUS, which is influenced by warm Angolan water. In contrast, species such as *D. meadi* had a much wider distribution. Although *D. meadi* dominated at the offshore stations of the sBUS, it occurred frequently in all areas of the nBUS and the sBUS. Although this species has previously been classified as having an oceanic and temperate pattern, it was distributed in areas influenced by both cold- and warm-water fronts in the nBUS and the sBUS.

Stations in the Offshore S2 group were a mix of myctophids previously characterized with cold-water, temperate, and subtropical patterns (cold water: *Lampanyctodes hectoris*; subantarctic: *Metelectrona ventralis*, *S. boops*, *D. hudsoni*; temperate: *Lampanyctus intricarius*, *D. meadi*; subtropical: *S. barnardi*) (Rubiés 1985) as well as the sternoptychids *A. hemigymnus* and *Valencienellus tripunctulatus*. This may be due to seasonal intrusions of differing water masses such as seasonal Agulhas Current water coming up the South African coast and transporting species from different water masses, which then establish populations in the BUS systems (Hulley & Lutjeharms 1995). For instance, *D. diadematus* is characterized as having what is defined as an extended Agulhas Current pattern but was found at 3 stations in the sBUS as well as 2 stations in the nBUS (Hulley 1981, Hulley &

Prosch 1987). Species that were influenced by the Angola Current and are typical of tropical waters were *D. dumerilii* and *D. taaningi* (Rubiés 1985). *D. dumerilii* was found at most stations in the North, not only at those near the Angola Benguela Frontal Zone, demonstrating that there is influence of tropical waters throughout the entire northern Benguela as shown by our hydrographic data. The distribution also coincides with that of Hulley (1981). *D. taaningi* was only found at stations in the nBUS, and this species has previously been described as a species typical of warm waters and most likely of Angola Current influence (Rubiés 1985).

The passing of taxa between fronts can be either prevented or promoted, depending on the presence of a vertical or horizontal convergence zone (Koubbi 1993). When there is a convergence zone that acts as a vertical front, many organisms cannot pass because it acts as a barrier. In contrast, horizontal convergence zones can be passed by mesopelagic fishes because during their vertical migration they eventually reach a depth layer where there is no longer a physical or chemical boundary and where they can cross (Lutjeharms et al. 1985, Koubbi 1993). This may help explain why some species which typically have an Agulhas Current pattern are also present in small numbers in the nBUS, influenced by other water masses, such as *D. diadematus*.

Throughout the water column, lower oxygen concentrations occurred in the nBUS than in the sBUS. In the nBUS, an OMZ was present between 50 and 100 m on the shelf, and these low oxygen levels can extend towards the shelf edge (Mohrholz et al. 2008, Ekau et al. 2018). In our study, the bathydemersal bonefish *Nemoopsis belloci* (Albulidae) was present at Stn 53 on the nBUS shelf, a species typical of low-oxygen environments, along with horse mackerel *Trachurus t. capensis* and the goby *Sufflogobius bibarbatus* (Mas-Riera et al. 1990, Gallo & Levin 2016). Certain species are better adapted to these low-oxygen conditions and, for instance, copepods of the families Eucalanidae and Metridinidae may dominate the OMZ (Teuber et al. 2013). These copepods have lower metabolic rates and are often vertical migrators, adaptations that help them to exist in these deoxygenated zones (Teuber et al. 2013). The ability to survive in the OMZ has also been reported for some species of non-migrating mesopelagic fishes, such as *Cyclothone* spp., as well as the myctophid *D. vanhoeffeni* (Olivar et al. 2017). However, we did not find mesopelagic species that are tolerant to OMZs in low-oxygenated areas, only non-mesopelagic species.

While there was very low species richness and overall abundance of mesopelagic fishes on the shelf, richness was higher in the nBUS than in the sBUS, despite lower oxygen concentrations. One possible explanation is that the OMZ can serve as a short-term refuge for migrating species since many predatory fish avoid regions with low oxygen. The higher diversity in the nBUS compared to the sBUS may also be explained by habitats composed of a 'mosaic' structure. Heterogeneity in the environment can provide many niches and thus increase species richness, as has been confirmed for benthic communities (Switzer et al. 2016). This may result in a variety of species: those well adapted to low-oxygen conditions and others that cannot cope with OMZs. Such an overall higher diversity would include species very specific to one type of environment as well as opportunistic species adapted to either environment. Should OMZs intensify and expand to greater depths in the future, this may result in a shift in the diversity and evenness of fishes present in the area today.

Chl *a* concentration also showed trends toward environmental drivers of assemblage structure. Areas with higher chl *a* concentrations (or primary productivity) have been positively correlated with zooplankton abundance and affected mesopelagic fish assemblages (Fock et al. 2004, Lebourges-Dhaussy et al. 2009, Godet et al. 2020, Dove et al. 2021). At night, zooplankton such as copepods migrate to these areas rich in chlorophyll (Lebourges-Dhaussy et al. 2009). Many mesopelagic fishes, e.g. myctophids, follow their prey and feed on zooplankton such as copepods and euphausiids in these layers (Pusch et al. 2004b, Bernal et al. 2015). This may lead to differences in composition and abundance of mesopelagic fishes in these areas with higher prey abundances. Consequently, other fishes that feed on myctophids, such as stomiids, may forage in upper layers at night for small mesopelagic fishes as well as for euphausiids (Sutton & Hopkins 1996).

In the present study, we show that there are 7 distinct mesopelagic fish assemblages in the upper mesopelagic zone and the shelf of the BUS during the austral summer. These assemblages differ in both composition and abundance between the nBUS and sBUS, as well as on the shelf versus further offshore. This study elucidates that environmental drivers of mesopelagic fish assemblages in the BUS are chl *a* concentration, oxygen concentration, and water mass during the austral summer. Because these environmental factors can change seasonally and annually in this highly dynamic ecosystem, there is a need for long-term monitoring of mesopelagic fish com-



munities in the area. If OMZs expand further as predicted by climate models (Stramma et al. 2010), our results may have severe implications, as oxygen was a main driver of assemblage structure in the BUS.

Follow-up questions which arise from these observations of differences in species assemblages between the BUS subsystems can be summarized as follows. How do the upper mesopelagic and shelf mesopelagic communities sampled in this study compare with communities further offshore in the Benguela Current? What are the effects of community composition on food webs and trophic efficiency in the BUS? Although mesopelagic fishes are not yet heavily exploited, they are classified as one of the largest fisheries resources in the global oceans (Gjøsaeter & Kawaguchi 1980, Irigoien et al. 2014, Standal & Grimaldo 2020), and their exploitation could affect further trophic levels. Due to their high biomass and the differences in assemblages between subsystems in the BUS, it may lead to changes in the trophic transfer efficiency between these highly productive subsystems.

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