Mesopelagic fish assemblages in the Mauritanian Upwelling System off Northwest Africa with oxygen as a major driving force

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ABSTRACT: The aims of this study were to determine the community composition and environmental drivers of mesopelagic fishes in the Mauritanian Upwelling System. Mesopelagic fish communities were sampled at 17 stations in August of 2016 off the coast of Senegal and Mauritania using a non-closing rectangular midwater trawl (RMT). This subregion is the most productive area of the Canary Current and has a pronounced and permanent oxygen minimum zone (OMZ). The sampling area was mainly composed of low-oxygenated South Atlantic Central Water, except for 1 station, where North Atlantic Central Water prevailed. Three distinct mesopelagic fish communities were identified. One community occurred in the vicinity of a coldwater eddy and was dominated by the myctophid *Benthosema glaciale*. In contrast, the gonostomatid genus *Cyclothone* prevailed in the other 2 communities and made up 62 and 51% of the total fish abundance. Our analyses revealed that the environmental factors that primarily influenced the composition of these mesopelagic fish assemblages were the oxygen concentrations at 10, 100, and 600 m depth. The present study shows that the mixing of water masses at frontal zones leads to communities representative of both water masses. In the case of the Mauritanian upwelling region, a high portion of the mesopelagic fish species were well adapted to OMZ conditions.

KEY WORDS: Eastern Boundary Upwelling System · Micronekton · *Cyclothone* · *Benthosema glaciale* · Myctophidae · Community composition · Oxygen minimum zone · OMZ

1. INTRODUCTION

The mesopelagic zone, roughly between 200 and 1000 m depth, holds the highest biomass of fishes in the world's oceans (Kaartvedt et al. 2012, Irigoien et al. 2014). This includes species-rich families such as Myctophidae, Sternoptychidae, Gonostomatidae, Stomiidae, and Phosichthyidae (Nafpaktitis 1977, Whitehead et al. 1984, Sutton et al. 2020). Mesopelagic fishes are well adapted to their low-light environments, with adaptations such as ventral light organs, enlarged and highly sensitive eyes, and reduced energetic requirements, to name a few (Childress & Seibel 1998, Levin 2003, Davis et al. 2014, de Busserolles & Marshall 2017). Many mesopelagic species are also well accustomed to low-oxygen concentrations and take refuge in the oxygen minimum zone (OMZ) (Childress & Seibel 1998, Levin 2003) that is often present in highly productive waters, especially in the mesopelagic layer (Stramma et al. 2012). In these areas, high primary production leads to the sinking and degradation of organic matter, reducing oxygen concentrations to levels below 0.5 ml l^{-1} (Levin 2003, Helly & Levin 2004). In OMZs, mesopelagic fishes may find refuge from predators with high metabolic rates, such as tuna or billfishes (Stramma et al. 2012).

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Although mesopelagic fishes are currently of minor economic importance, they are a vital component of the pelagic food web and major prey to various commercially important species (Werner et al. 2019, Valls et al. 2022). Many mesopelagic fishes, such as myctophids, perform diel vertical migrations (Pearcy & Laurs 1966, Davison et al. 2013, Klevjer et al. 2016); at dusk they ascend to the surface to feed on smaller organisms such as zooplankton, and at dawn they return to the twilight zone to avoid consumption by larger predators such as tuna (Valls et al. 2022), hake (Van der Lingen & Miller 2014, Durholtz et al. 2015), cod (Werner et al. 2019, Stoltenberg et al. 2021), sharks (Carrassón et al. 1992, Filmalter et al. 2017), and seals (Naito et al. 2013). Mesopelagic fishes also play an important role in the transport of organic matter and interlink epipelagic and mesopelagic layers (Gjøsaeter & Kawaguchi 1980, Klevjer et al. 2012, Irigoien et al. 2014, Eduardo et al. 2020b); in the California Current region, mesopelagic fishes transport up to 17% of the carbon from the epipelagic to mesopelagic layers through vertical migration (Davison et al. 2013). Respiration and excretion mainly take place at depth during the day, and carbon and organic matter are consequently stored in the mesopelagic layer (Davison et al. 2013, Irigoien et al. 2014, Eduardo et al. 2020b).

Along with the Benguela, Humboldt, and California Current Systems, the Canary Current is 1 of the 4 major Eastern Boundary Upwelling Systems (Carr & Kearns 2003). Despite making up only 2% of the global ocean's surface, these highly productive areas may yield 20% of global fisheries (Pauly & Christensen 1995), with the catches in the Canary Current Large Marine Ecosystem reaching 3.5 million t in 2017 (FAO 2020, Failler 2020). The Canary Current spans 12—43°N in latitude and is separated into 5 subregions: the Galician, Portuguese, Gulf of Cadiz, Moroccan, and Mauritanian—Senegalese subregions (Arístegui et al. 2009, Kämpf & Chapman 2016). They differ in their physical and biological properties due to differing geographical features, external inputs, seasonality, and many other factors (Dai & Trenberth 2002, Arístegui et al. 2009). The most productive of the 5 subregions is the southernmost Mauritanian—Senegalese subregion between 12 and 21°N. It is dominated by nutrient-rich South Atlantic Central Water (SACW) and has a pronounced OMZ, including hypoxic zones (Karstensen et al. 2008, Arístegui et al. 2009). This area is exposed to upwelling-favourable winds, and upwelling is most prominent during the winter (December—April) (Arístegui et al. 2009, Kämpf & Chapman 2016, Sylla et al. 2019).

Sutton et al. (2017) defined 33 mesopelagic ecoregions for the global ocean based on water mass characteristics, the presence of OMZs, temperature and primary production data, and data on the associated fish fauna and community composition. A proposed ecoregion called 'Mauritania/Cape Verde' showed unique features due to the presence of 'cool-water' taxa as well as endemic species and distinct fish communities (Sutton et al. 2017). This ecoregion is bounded to the north and west by the Central North Atlantic ecoregion and to the south by the Tropical and West Equatorial Atlantic ecoregion. The latter are in general more oligotrophic, except for distinct regions where upwelling occurs (Sutton et al. 2017). Few data on the composition and assemblage structure of adult mesopelagic fishes are available from the Mauritania/Cape Verde ecoregion (Olivar et al. 2017, Czudaj et al. 2021). These studies were part of a transect that spanned the tropical and equatorial Atlantic and included a few stations in the Mauritania—Senegalese subregion (Olivar et al. 2017) and stations from 13°N to the equator, but no stations north of Dakar (ca. 15°N). Depending on net size, the dominant species in the area from 13 to ~8°N were the myctophids *Lepidophanes guentheri, Diaphus vanhoeffeni, Notoscopelus replendens, Hygophum macrochir*, and *Ceratoscopelus warmingii*, as well as the lightfish *Vinciguerria nimbaria* (Phosichthyidae), which all contributed more than 10% to the total abundance (Czudaj et al. 2021). The species that prevailed in terms of biomass were *N. resplendens* and *L. guentheri* (Czudaj et al. 2021). Overall, when using the MOCNESS net, the most abundant taxon was the gonostomatid genus *Cyclothone*, with more than 60% of the total abundance north of the equator (Olivar et al. 2017). Other abundant taxa at the northern stations (near the Cape Verde Islands region) were the melamphaids (species pooled), the sternoptychids *Sternoptyx diaphana* and *Argyropelecus sladeni*, the stomiid *Chauliodus sloani*, the phosichthid *V. nimbaria*, and the myctophids *Notolychnus valdiviae* and *Lampanyctus alatus*, which together contributed about 15% to total abundance.

Because previous studies in the Central Atlantic were located more offshore, only a few samples were collected from this zone, where intense mixing of water masses occurs (Olivar et al. 2017, Czudaj et al. 2021). Samples of fish larvae have previously indicated their high dependence on local water mass distribution (John & Zelck 1997, Tiedemann et al. 2018), and in the present study, sampling was carried out in an area where North Atlantic Central Water (NACW)

and SACW mixed. Because of small-scale variation within the subregion, it was important to have a high resolution in the sampling scheme (i.e. many stations within a small area). The aims of this study were to determine the community composition of mesopelagic fishes in the Mauritanian—Senegalese subregion of the Canary Current Large Marine Ecosystem and to identify environmental factors that influence these communities. We hypothesized that species composition depends largely on water masses; hence, their differing physical and/or biological properties are reflected in the different fish communities, and we predicted more tropical species at stations that are dominated by SACW and more temperate species at stations dominated by NACW. Consequently, where mixing of water masses occurs, we expected species that are typical of both warmer SACW and colder NACW.

2. MATERIALS AND METHODS

2.1. Hydrography

Sampling took place from the RV 'Meteor' (cruise M129) in the Mauritanian—Senegalese subregion of the Canary Current (12.4—20.2° N) from 4 to 22 August 2016 (Fig. 1) (Ekau 2016). Hydrographic parameters such as temperature, salinity, oxygen, and chlorophyll *a* (chl *a*) concentration were recorded using a conductivity, temperature, and depth profiler (CTD) (Sea Bird Scientific, PLUS SBE 9) at each sampling station down to 1000—1500 m depth (0.5 m s^{-1} descent and 1 m s^{-1} ascent). Potential temperature—salinity (T-S) plots and depth profiles were produced in Ocean Data View ODV v. 5.2.1 (Schlitzer 2018). T-S plots were used to identify water masses based on the properties described by Tomczak (1981) and applied
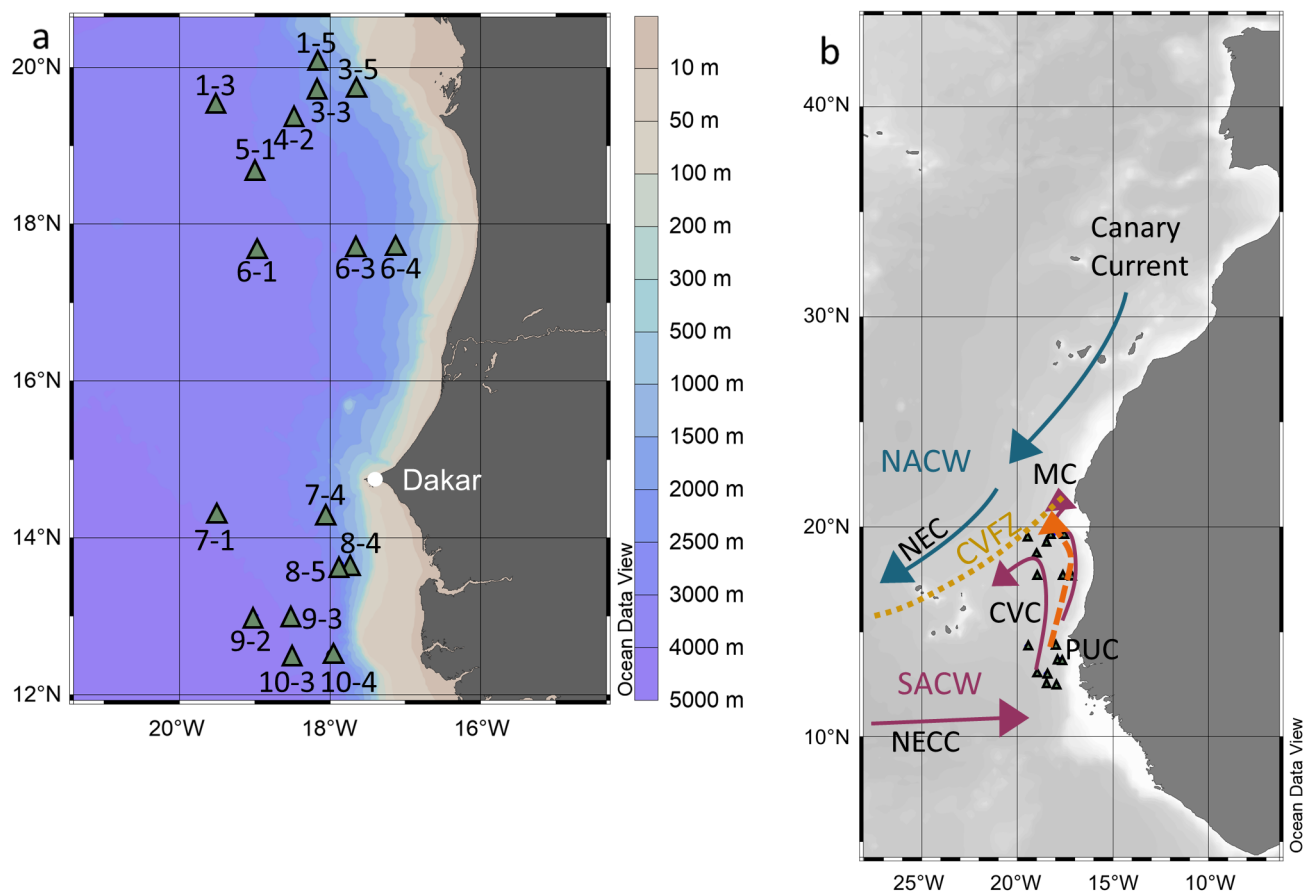

Fig. 1. Locations of (a) 17 sampling stations of mesopelagic fishes using the rectangular midwater trawl (RMT) and collection of hydrographic data in the Canary Current Upwelling System off the coast of Mauritania and Senegal and (b) major hydrographic features of the sampling region. Currents (black letters) in figure adapted from Arístegui et al. (2009) and Versteegh et al. (2022). Blue represents cold water and red warm water. Water masses: CVFZ: Cape Verde Frontal Zone, NACW: North Atlantic Central Water, SACW: South Atlantic Central Water, Currents: CVC: Cape Verde Current, MC: Mauritania Current, NEC: North Equatorial Current, NECC: North Equatorial Counter Current, PUC: Poleward Under Current

by Tiedemann et al. (2018). Water masses were defined as a line through specific points of temperature and salinity. If station points fell on the line, the station was dominated by the given water mass. More specifically, SACW was defined as a line through the points of 7.24°C, 34.95 and 16.00°C, 35.77, while NACW was defined by 2 lines, through 7.50°C, 35.05, 11.00°C, 35.47, and 18.65°C, 36.76. When reporting oxygen concentrations in the OMZ, mild hypoxia was defined as an oxygen concentration between 1.4 and 2 ml l^{-1} and intermediate hypoxia between 0.5 and 1.4 ml l^{-1} (Hofmann et al. 2011). Data for sea surface temperature (SST) satellite images at a resolution of 100 m were obtained through the JPL MUR MEaSUREs Project (2015). Satellite images were a composite of 8 d of data from 12–20 August 2016, as this was in the middle of the sampling period. Chl a data were obtained at a resolution of 4 km (NASA Goddard Space Flight Center et al. 2018). A composite of the data from the entire month of August 2016 was used, because shorter time periods contained many missing values and a patchy surface plot.

2.2. Sampling and species identification

A non-closing rectangular midwater trawl (Baker & Clarke 1973) with an 8 m^2 net opening (RMT 8) was deployed to approximately 560 m depth (wire length of ca. 1000 m) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m733p095_supp.pdf) as a double oblique tow, for approximately 60 min with a ship speed of 2–3 knots, at the same stations where the CTD was deployed (Table 1). The RMT we used was non-closing, so it was open from the surface to maximum sampling depth (and returned open, back to the surface). The net had a mesh size of 4.5 mm on the main panels and 1 mm at the cod-ends. Cod-ends were flushed, and the fish specimens were stored in a phosphate-buffered 3.6% formalin solution before further analysis. Fishes were identified to the lowest taxonomic level possible, which was usually species level, using Nafpaktitis (1977) and Whitehead et al. (1984). Only adult mesopelagic fishes were included in the analysis.

No depth meter or flowmeter was available, so sampling depth and consequently water volume were estimated based on known wire lengths and sampling depths from trawls in the Benguela region, using the same net and ship speed (Table S2). The ratio between wire length and sampling depth was 1.77 ± 0.26, hence a minimum and maximum sampling depth and water volume were also calculated (Table S1). To estimate the volume of water (V), we used the area of the net opening (8 m^2) (A), distance travelled (d), and estimated sampling depth (Table 1) of each haul assuming that the net followed the track of the hypotenuse of 2 equal right triangles:

$$V = 2 \times d \times A \tag{1}$$

The number of fishes m^{-3} was calculated. To determine the abundance per unit area, the number of

Table 1. Data of the rectangular midwater trawl (RMT) and conductivity–temperature–depth (CTD) stations in the Canary Current, where sampling of mesopelagic fishes took place and environmental data were recorded. Characterization for the time of day (dawn: DA, day: D) based on civil dawn, sunrise, sunset, and civil dusk in each specific location at time of midwater trawl

Stn no.	Date (2016; d/mo)	Time (UTC)	Latitude (°N)	Longitude (°W)	Wire length (m)	Distance travelled (km)	Estimated sampling depth (m)	Bottom depth (m)
1-3	04/08	14:50$_D$	19.495	19.506	1000	3.69	566	3203
1-5	05/08	07:50$_D$	20.108	18.170	1000	5.35	566	2233
3-3	08/08	07:05$_D$	19.688	18.189	1000	4.62	566	2270
3-5	08/08	17:26$_D$	19.636	17.620	800	4.70	453	1854
4-2	11/08	06:50$_{DA}$	19.328	18.523	1000	5.92	566	2714
5-1	11/08	16:34$_D$	18.695	18.999	1000	5.03	566	3035
6-4	14/08	09:07$_D$	17.685	17.175	1000	3.90	566	1990
6-3	14/08	16:13$_D$	17.681	17.666	1000	4.84	566	2610
6-1	15/08	07:36 $_D$	17.687	19.011	1000	3.37	566	3189
7-1	16/08	13:24 $_D$	14.283	19.471	1000	5.28	566	3825
7-4	17/08	08:39$_D$	14.355	18.073	1000	5.01	566	2240
8-5	19/08	06:55$_{DA}$	13.694	17.745	1000	5.57	566	1948
8-4	19/08	12:31$_D$	13.691	17.869	1000	4.07	566	2470
9-2	20/08	09:58$_D$	12.975	18.988	1000	4.71	566	4229
9-3	20/08	17:37$_D$	13.000	18.501	1000	3.48	566	3876
10-4	22/08	09:12$_D$	12.491	17.953	1000	4.20	566	2632
10-3	22/08	16:30$_D$	12.488	18.498	1000	2.84	566	4011

fishes m^{-3} was multiplied by the sampled depth range.

2.3. Statistical analysis

All data were analysed in the statistical software R (R Core Team 2013) using the packages 'vegan' (v.2.5.6; Oksanen et al. 2020) and 'oce' (v.1.2.0; Kelley & Richards 2021). In the present study, we conducted statistical analyses using a significance level (α) of 0.05. Environmental variables were standardized. For all multivariate statistics, species with a frequency of occurrence of <2 (occurred at less than 2 stations) were removed from all further analyses, which resulted in a total of 59 species analysed. The Hellinger transformation was performed on species data, which transforms the absolute abundance into relative abundance and then takes the square root of the values (Legendre & Gallagher 2001). This is ideal for species matrices with many low counts or zero values, as was the case in our data set. The Bray-Curtis similarity matrix was calculated for our species matrix. An analysis of similarities (ANOSIM) was used in order to test if the time of day of each haul influenced the community composition. To determine assemblage structure, the similarity profile (SIMPROF) routine analysis (Clarke et al. 2008) was performed to test for significant clusters of stations, based on the community composition with the average-linkage method and with 1000 permutations. Data were visualized with a dendrogram and nonmetric multi-dimensional scaling analysis (nMDS) (Field et al. 1982). Similarity percentage (SIMPER) analysis (Clarke & Warwick 1994) was then applied to determine which species best explained the differences between communities.

To test which environmental parameters influenced community composition, we included bottom depth, mixed-layer depth (MLD), and chl *a* concentration at 10 and 100 m, and oxygen concentration, temperature, and salinity at 10, 100, 200, 400, and 600 m, for a total of 19 variables (Table 2). In order to avoid multicollinearity between variables, we checked the correlation between all environmental variables and removed variables with a collinearity of ≥0.7 (Fig. S1) (Dormann et al. 2013). It has been recommended that the ecological relevance be taken into account when selecting variables (Dormann et al. 2013). For example, if oxygen at 600 m and temperature at 10 m had a correlation of ≥0.7, we would leave the parameter that may be more relevant for a mesopelagic community, i.e. that of oxygen at 600 m and remove tempera-

Table 2. Environmental variables included in the correlation matrix ('c' in the table) (see Fig. S1 in the Supplement) and variables used in the forward selection model after removal of highly correlated variables (≥ 0.7) ('f'). Mixed layer depth (m) and bottom depth (m) were also included in the correlation matrix and forward selection model

Depth (m)	Salinity (PSU)	Oxygen (ml l^{-1})	Temperature (°C)	Chlorophyll *a* (mg m^{-3})
10	c	c, f	c	c, f
100	c	c, f	c, f	c, f
200	c	c	c, f	
400	c, f	c, f	c, f	
600	c	c, f	c, f	

ture at 10 m. Based on the correlation matrices described above, 13 variables were included in the model (Table 2). Using these variables, a step-wise forward selection model using the 'ordistep' function of the 'vegan' package was used, and the significance of variables selected for the model were then tested using the Monte-Carlo permutation test. Furthermore, the variance inflation factor (VIF) was determined to ensure that the variables selected by the forward selection were not collinear (Dormann et al. 2013).

3. RESULTS

3.1. Hydrography

T-S plots showed that the water masses at the stations were mostly composed of SACW, except for Stn 1-3, which was dominated by NACW from about 120 to 500 m. Below 500 m, there was likely a mix of NACW and SACW, with little variation between water mass properties (Fig. 2a). Depth profiles revealed similar patterns of oxygen concentration, chl *a* concentration, temperature, and salinity, except for Stn 1-3, which stood out from the rest of the stations. Stn 1-3 had a higher oxygen concentration, especially between about 50 and 500 m depth, and it also had a higher salinity from 50 to 300 m. At all stations, the lowest oxygen concentration occurred between about 40 and 100 m and again at about 400 m (Fig. 2b; Fig. S2). At all stations, highest oxygen concentrations (4—6 ml l^{-1}) were found in the upper 40 m of the water column, with maxima between about 25 and 30 m. In general, the OMZ spanned 40—600 m, with intermediate hypoxic conditions and mild hypoxic conditions between 600 and 800 m (Fig. 2; Fig. S2). SST was 28°C at Stns 6-3 through 10-4,
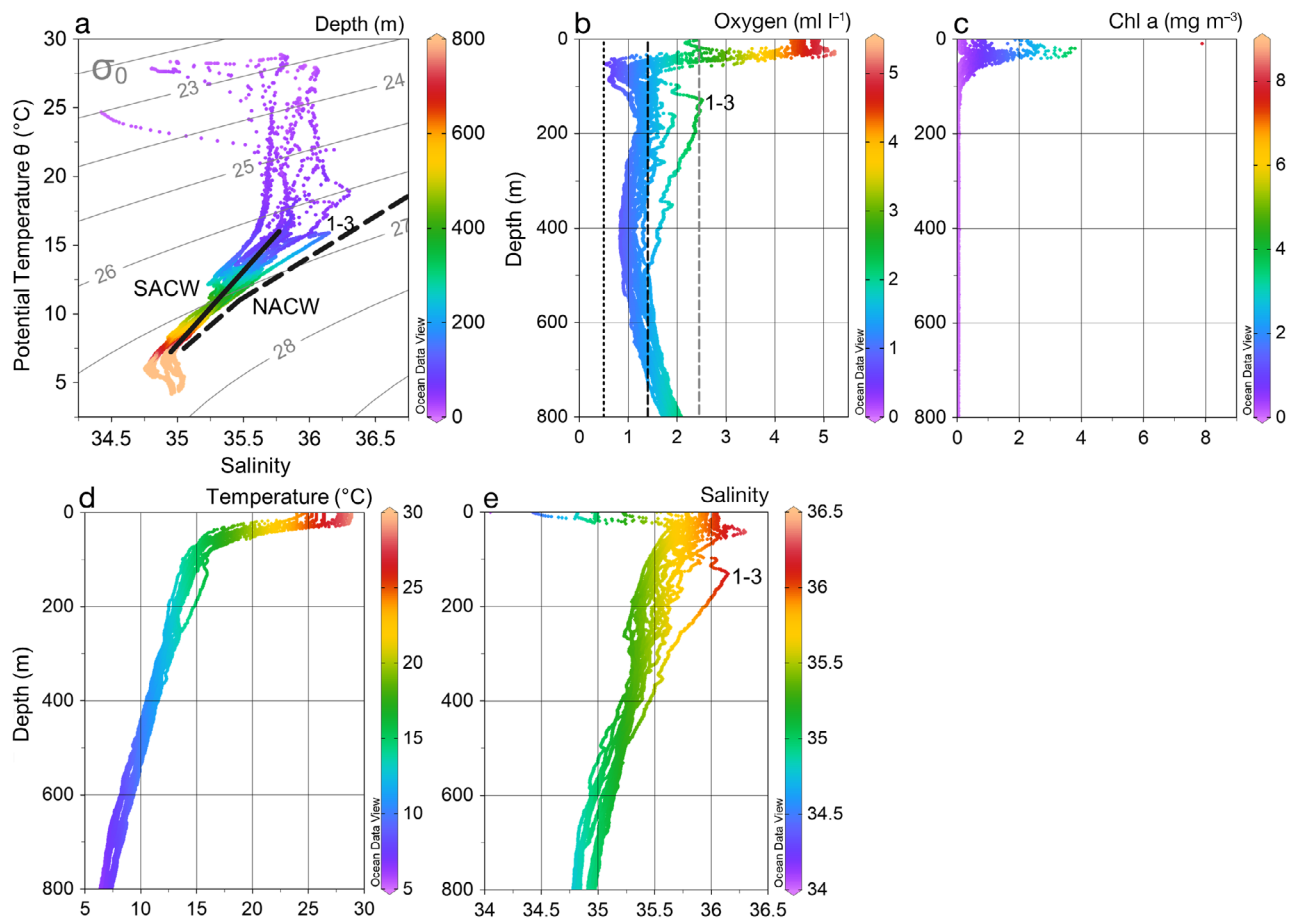
Fig. 2. (a) Potential temperature—salinity (T-S) plot showing the North Atlantic Central Water (NACW) mass and the South Atlantic Central Water (SACW) mass with isopycnals shown in grey. Depth profiles indicate (b) oxygen concentration, (c) chl *a* concentration, (d) temperature, and (e) salinity (PSU) of sampling stations in the Mauritanian—Senegalese subregion of the Canary Current. Depth range of CTD was from 1000 to 1500 m (we have focused here on the upper 800 m). Definitions of water masses are based on Tomczak (1981) as applied by Tiedemann et al. (2018). Numbers in (a), (b), and (e) indicate the station number (i.e. Stn 1-3). In (b), oxygen concentrations below 0.5 ml l⁻¹ (black dotted line) indicate severe hypoxia; concentrations of 0.5—1.4 ml l⁻¹ (black dashed line) indicate intermediate ('coastal') hypoxia, and 1.4—2.45 ml l⁻¹ (gray dashed line) reflect mild hypoxia (Hofmann et al. 2011)

whereas SST was cooler further north at Stns 1-3 through 6-1. Near Stns 1-5 and 3-5, there was a pocket with the lowest SST of about 24°C (Fig. 3). Chl *a* concentrations were similar at all stations, but highest in the area near Stns 1-5 and 3-5, where SST was lowest, probably due to local upwelling further north, near these stations (Fig. 3).

3.2. Species assemblages

We analysed a total of 1309 fish specimens, which resulted in 88 species from 24 families. The family Myctophidae showed the highest richness with 25 species, and the most dominant genus in terms of abundance was *Cyclothone*. Six species of *Cyclothone*

were identified, most frequently *C. livida*, which was present at all stations where individuals occurred. *Cyclothone* was overall the most abundant genus, and distribution maps show its presence in all sampling areas, with maxima at Stns 10-3 and 6-3 (Fig. 4). All species identified are listed in Table S3. A range of species abundances for each cluster can be found in Table S4 that were calculated based on the minimum and maximum water volumes. The ANOSIM showed no difference between communities that were sampled at differing times of the day (dawn and daytime in our case shown in Table 1) (R = 0.025, p = 0.398).

Three clusters were defined through cluster analysis (Fig. 5, Table 3). Cluster A consisted of the offshore Stns 1-3 and 5-1. The prevailing taxon was *Cyclothone* spp. (62.2%), followed by *Lobianchia dofleini* (4.2%)
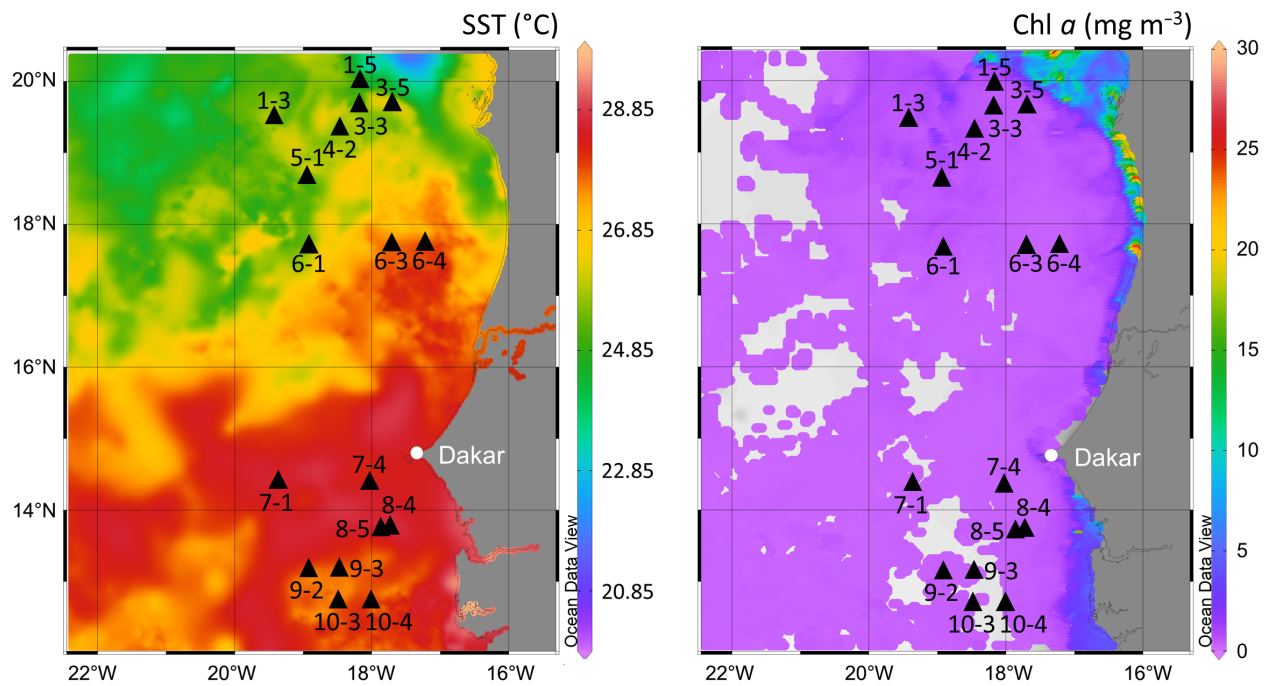
Fig. 3. Satellite images showing sea surface temperature (SST) and chl *a* concentrations in the Mauritanian—Senegalese subregion of the Canary Current. SST plot derived from 12 to 20 August 2016; chl *a* data represent a 1 mo composite for August 2016. Triangles: sampling stations

and *Argyropelecus hemigymnus* (4.2%), while 22 species contributed to the rest of the assemblage structure and 21 of those accounted for less than 3% of the total abundance. Cluster B consisted of stations on the slope (Stns 1-5, 3-3, and 4-2) dominated by *Benthosema glaciale* (31.7%) and *Cyclothone* spp. (25.3%). Other common species in this cluster were *Hygophum macrochir* (4.7%), *Vinciguerria nimbaria* (4.5%), *Diaphus vanhoeffeni* (3.6%), *Stomias boa* (3.4%), and *Myctophum affine* (3.0%). The rest of the cluster included 27 species, with less than 3% per species. Cluster C had the highest species richness, and included the majority of stations (Fig. 5). Stations in this cluster were influenced by SACW from about 50 to 800 m (Fig. 2a). Interestingly, Stn 3-5, which was much closer to all stations of Cluster B, was associated with Cluster C. The dominant taxon in Cluster C was *Cyclothone* spp. (51.4%), followed by *Polyipnus polli* (10.0%), and *D. vanhoeffeni* (5.3%). Additional species (n = 49) in this cluster contributed less than 4% to species richness.

SIMPER revealed the most influential species for differences between clusters (Table S5). Although *Cyclothone* spp. were present in each cluster, this genus still accounted for differences between the clusters. Interestingly, there was not one single species that explained most of the differences in assem-blages; instead, all species accounted for a very low percentage. *B. glaciale* (10.8%) and *Cyclothone* spp. (6.9%) were mainly responsible for the differences in assemblages between Clusters A and B, whereas between Clusters A and C, the most important species were *P. polli* (7.3%) and *D. vanhoeffeni* (6.1%). Between Clusters B and C, the species that accounted for the most dissimilarity were *B. glaciale* (14.0%) and *Cyclothone* spp. (6.4%). Distribution maps revealed that *B. glaciale* prevailed more at the northern stations (Stns 1-3 to 6-1) than in the south (Stns 7-1 to 10-4), with abundance maxima at Stns 1-5 and 4-2 and few individuals at Stn 3-3 (Cluster B stations) (Fig. 4).

3.3. Environmental drivers of mesopelagic fish communities

To test which environmental factors determined the assemblages of mesopelagic fishes, our model consisted of 13 environmental variables. Through forward selection, the final model identified oxygen at 10, 100, and 600 m as the most influential environmental factors. The Monte Carlo permutation test was significant for the selected model ($F = 2.6$, p = 0.001) (Table 4). The first and third RDA axes were significant, and the variance explained by the first 2 axes
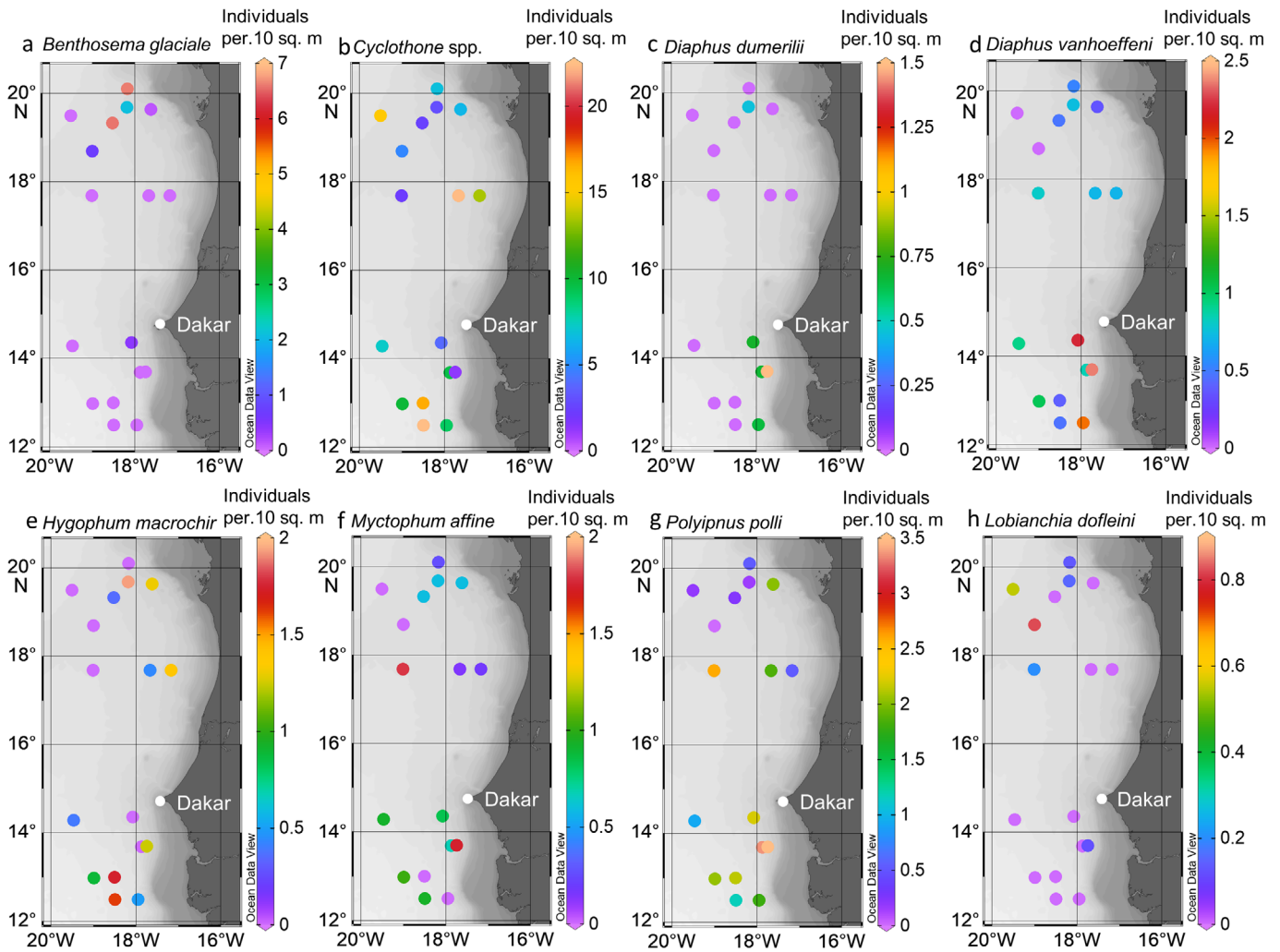
Fig. 4. Abundance (ind. 10 m^{-2}, note different scales) of most abundant or important mesopelagic fish species in the Mauritanian—Senegalese subregion of the Canary Current, as identified by SIMPER analysis

was 27.9% and that explained by the first and third axis was 27.0%. (Fig. 6, Table 4). The VIF was not above 3 for all 3 selected variables, signifying that there was no collinearity between the selected environmental variables. Visualization of the RDA analysis showed that cluster B, dominated by *B. glaciale*, was associated with the oxygen concentration at 600 m. Stn 1-3 (which was in Cluster A based on species composition) was also highly correlated with oxygen concentrations and was the station with the highest oxygen concentration throughout the water column and dominated by NACW (Fig. 6b). Cluster C was not strongly associated with any of the environmental variables (Fig. 6). Cluster A stations were associated with oxygen concentration at 10 and 100 m, as were the species *A. hemigymnus* and *L. dofleini*, and the genus *Cyclothone*.

4. DISCUSSION

4.1. Sampling constraints

We sampled mesopelagic fishes using a rectangular midwater trawl. Because the net opening was rather small and towed at low speeds, avoidance by larger fishes was likely. Active net avoidance has previously been verified through a combination of net sampling and hydroacoustic data. Net catches of the myctophid *Benthosema glaciale* resulted in a mean abundance of about 0.05 ± 0.01 ind. per 100 m^3, while assessments based on acoustics yielded 3.6 ± 0.05 ind. per 100 m^3 (Kaartvedt et al. 2012). The use of different net sizes can also influence the catch rate, size spectrum, and species composition of mesopelagic fishes (Czudaj et al. 2021). A combination of net
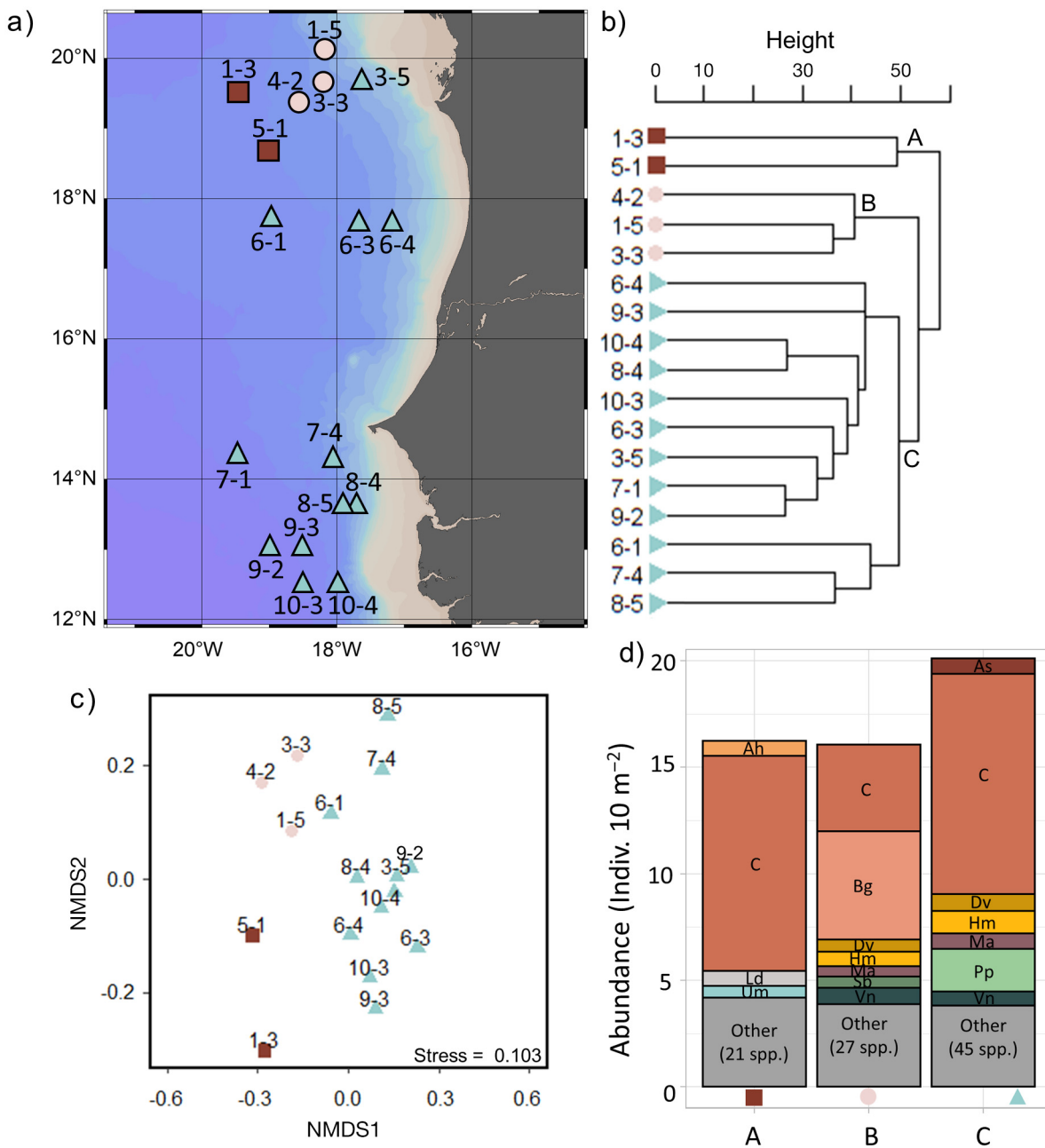
Fig. 5. (a) Distribution with (b) corresponding clusters of stations based on dendrogram results of Hellinger-transformed species data and Bray-Curtis distance matrix. (c) Non-metric multi-dimensional scaling plot with colours and symbols of clusters in (b). (d) Abundance of dominant species that contribute to Clusters A, B, and C. Taxa abbreviated in bars contribute at least 3% to total abundance ('Other': species <3%). Ah: *Argyropelecus hemigymnus*; As: *Argyropelecus sladeni*; Bg: *Benthosema glaciale*; C: *Cyclothone*; Dv: *Diaphus vanhoeffeni*; Hm: *Hygophum macrochir*; Ld: *Lobianchia dofleini*; Ma: *Myctophum affine*; Pp: *Polyipnus polli*; Sb: *Stomias boa*; Um: unidentified myctophid; Vn: *Vinciguerria nimbaria*

sizes as well as hydroacoustics would be the ideal approach to sample and obtain the best representation of species and size classes in a region.

The second constraint in the present study concerns the sampling depth, since no depth meter was present. The wire length was always available, so we assumed that the relation between wire length and sampling depth was similar between stations, although this may differ based on current speed and direction. For these reasons, we provided a range of

Table 3. Total and mean abundance (ind. $10 \, m^{-2}$) and relative abundance (%) of each mesopelagic fish species within each assigned cluster in the Mauritanian upwelling system. Total abundance refers to the total abundance within a cluster, and mean abundance has been corrected for the number of stations representative of each cluster, which is shown in the cluster column. Relative abundance is the portion of each species within a cluster. Only species that contributed >3% are represented here

Cluster	Species	Relative abundance (%)	Total abundance (ind. $10 \, m^{-2}$)	Mean abundance (ind. $10 \, m^{-2}$)
A (2 stations)	*Cyclothone* spp.	62.2	20.2	10.1
	Lobianchia dofleini	4.2	1.4	0.7
	Argyropelecus hemigymnus	4.2	1.4	0.7
	Unidentified myctophid	3.2	1.1	0.6
	Other (21 species)	26.1	8.4	4.2
B (3 stations)	*Benthosema glaciale*	31.7	15.2	5.1
	Cyclothone spp.	25.3	12.2	4.1
	Hygophum machrochir	4.7	2.3	0.8
	Vinciguerria nimbaria	4.5	2.1	0.7
	Diaphus vanhoeffeni	3.6	1.7	0.6
	Stomias boa	3.4	1.6	0.5
	Myctophum affine	3.0	1.4	0.5
	Other (27 species)	23.8	11.6	3.9
C (12 stations)	*Cyclothone* spp.	51.4	124.1	10.3
	Polyipnus polli	10.0	24.0	2.0
	Diaphus vanhoeffeni	5.3	12.7	1.1
	Hygophum machrochir	3.9	9.5	0.8
	Myctophum affine	3.6	8.8	0.7
	Argyropelecus sladeni	3.5	8.5	0.7
	Vinciguerria nimbaria	3.3	7.9	0.7
	Other (45 species)	19.0	45.8	3.8

Table 4. Results of the redundancy analysis (RDA) describing the environmental factors that best explain the variation in community composition of mesopelagic fishes of the Mauritanian–Senegalese subregion of the Canary Current. A Monte Carlo permutation test was used to select the best fit model with the lowest value of Akaike's information criterion (AIC) and the variance inflation factor (VIF), which showed no collinearity between environmental variables in the selected model. The number after oxygen indicates the depth (m) that was significant in the model. Significance is marked with an asterisk (*p < 0.05)

Test	Adjusted R^2	df	Variance	F	p	VIF and AIC
Model	0.38	3	0.12	2.64	0.001*	−21.2 (AIC)
Residuals		13	0.19			
Oxygen 600		1	0.05	3.08	0.002*	1.8 (VIF)
Oxygen 100		1	0.03	2.16	0.018*	1.5 (VIF)
Oxygen 10		1	0.03	2.23	0.006*	2.1 (VIF)
RDA1		1	0.05	3.56	0.003*	
RDA2		1	0.03	2.27	0.051	
RDA3		1	0.03	2.08	0.032*	
Residuals		13	0.19			

tion of the mesopelagic fish community in our catches with both migrating and non-migrating species.

4.2. Hydrography

The observed presence of both NACW and SACW could be expected, as the northernmost sampling stations were also located near the Cape Verde Frontal Zone (CVFZ), where NACW and SACW water masses merge (Arístegui et al. 2009). The presence of a coldwater eddy and the CVFZ to the north makes this a highly dynamic area, where stations are not strictly typical of SACW or NACW, but have properties of both water masses. While NACW is colder and more oxygen-rich, SACW is higher in nutrients, warmer, saltier, and lower in oxygen. SACW is an older water mass and becomes deoxygenated over time, because it is not in contact with the surface, resulting in its lower oxygen concentration (Fraga 1974, Ríos et al. 1992, Pastor et al. 2012, Olivar et al. 2016).
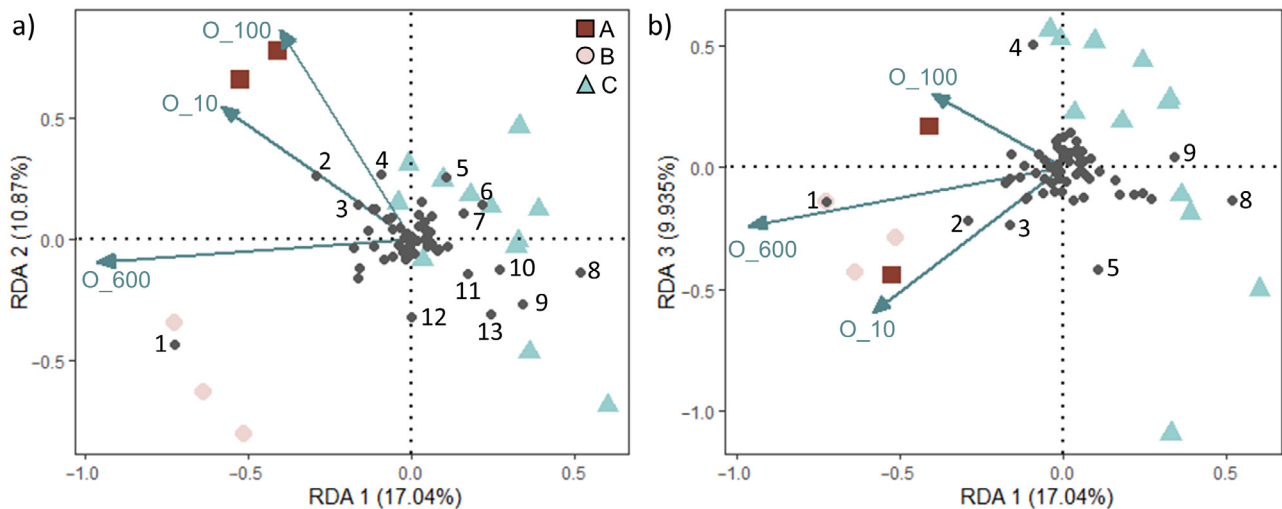
filtered volumes and species abundances. We caught mesopelagic species in all hauls, including several species of the genus *Cyclothone,* among others, that are non-migrating species. *Cyclothone* spp. occurred at almost all stations in the present study; therefore, we presume to have obtained an adequate representa-

Fig. 6. Visual results of the redundancy analysis (RDA), showing which environmental factors drive mesopelagic fish assemblages in the Mauritanian—Senegalese subregion of the Canary Current comparing (a) RDA1 and RDA 2 axes and (b) RDA 1 and RDA 3 axes. Colored symbols indicate stations based on Clusters A, B, and C defined by the SIMPROF analysis; black points with numbers indicate species. Species that are highly correlated to clusters and influenced by environmental factors are 1: *Benthosema glaciale*, 2: *Argyropelecus hemigymnus*, 3: *Lobianchia dofleini*, 4: *Cyclothone* spp., 5: *Lampanyctus isaacsi*, 6: *Sternoptyx diaphana*, 7: *Argyropelecus gigas*, 8: *Polyipnus polli*, 9: *Diaphus vanhoeffeni*, 10: *Vinciguerria nimbaria*, 11: *Myctophum affine*, 12: *Hygophum macrochir*, 13: *Diaphus dumerilii*

The frontal zone can act as both a barrier as well as a mixer with regard to faunal composition and distribution (Netburn & Koslow 2018). Due to the poleward undercurrent flowing north in the area between 18 and 23° N, the oxygen concentration between 100 and 300 m was previously recorded to be below 1.5 ml l^{-1} (Peña-Izquierdo et al. 2012), indicating an OMZ (Olivar et al. 2016). We also observed these patterns, with oxygen concentrations below 1.5 ml l^{-1}, in almost the entire upper water column, from ca. 40 to 600 m. In addition to the impact of the frontal zone, stations closer to the coast (Fig. 1) may also be influenced by the slope current flowing north (Aristegui et al. 2009). In contrast, the stations further offshore, such as Stns 6-1, 9-2, and 7-1, were probably dominated by the northerly Mauritania Current (Arístegui et al. 2009). Tiedemann et al. (2018) compared the hydrography of stations in the region (18—22° N), where stations partially overlapped with those in the present study. They found that stations south of 20° N were representative of SACW, except for 1 station in the same area as our Stn 3-5. We found all stations except for Stn 1-3 to be mostly composed of SACW (Fig. 2), however it is important to take seasonality into account. Stations in the present study were located further offshore than in the other study, and Tiedemann et al. (2018) collected their samples in March during strong upwelling from the north to 20° N.

4.3. Mesopelagic fish assemblages and distribution

In the present study, we identified 3 mesopelagic fish communities (Clusters A—C) in the Mauritanian—Senegalese subregion of the Canary Current. *Cyclothone* spp. was the most abundant taxon in 2 communities (Clusters A and C), which coincided with the results of Olivar et al. (2017), where *Cyclothone* was the most abundant genus at stations north of the equator. Olivar et al. (2017) found that at stations near Cape Blanc and the Canary Islands, *Cyclothone* spp. accounted for >60% of total fish biomass. Stations closer to the equator had a *Cyclothone* spp. abundance of 47%, with a mean of 6.9 ind. 10 m^{-2}. Our estimates were slightly higher, with mean abundances of 10.1 ind. 10 m^{-2} per station in Cluster A. At stations further south than our sampling stations, *Lobianchia dofleini* was more dominant (Olivar et al. 2017). This species has previously been associated with and exclusively found at stations composed of Eastern North Atlantic Central Water (ENACW) water (Olivar et al. 2017). However, in the present study, it was a component of Cluster A, including a station dominated by NACW and SACW. *L. dofleini* also occurred at other stations composed of SACW, although at lower abundances. Hulley (1981) recorded this species in the entire Canary Current area as well as in the northern Benguela subsystem. *Argyropelecus hemigymnus*, the third most abundant species in

Cluster A, has a circumglobal distribution in tropical and subtropical waters and offshore in the western tropical Atlantic (Eduardo et al. 2020a, Froese & Pauly 2021, Duncan et al. 2022).

Cluster B was composed of 3 stations in the northernmost sampling area, and the dominant species was *B. glaciale*, followed by *Cyclothone* spp., *Vinciguerria nimbaria*, and *Hygophum macrochir*. Recently, larvae of *V. nimbaria* and *H. macrochir* typical of warm water have been very dominant in this area (Dove et al. 2020). The Mauritanian region is known to host many adult *Cyclothone* spp., so it is not uncommon to find these species residing together (Dove et al. 2021). Similarly, Olivar et al. (2016) described a southern subgroup with adults of the tropically associated *V. nimbaria,* as well as sternoptychid larvae. According to Kinzer (1977) and Fock et al. (2004), *B. glaciale* occurs more typically in temperate latitudes with a 'subpolar—temperate' distribution pattern. However, it has been sporadically reported from the Canary Current area (Backus et al. 1977, Kinzer 1977, Badcock 1981), as a result of local upwelling and consequently lower temperatures. John & Zelck (1997) reported *B. glaciale* in the Mauritania upwelling region and described its zoogeographical pattern not as a coldwater myctophid, but as a 'central Mauritania province' species. Maximum abundances of this species occurred on the Mauritanian slope, along with *Myctophum punctatum*. The latter was described as a coldwater species and it was present in our samples, although at only 1 station (and was therefore excluded from further analyses). In fact, a single adult specimen of *M. punctatum* was identified at Stn 3-3, one of the northernmost stations. Large established populations of *M. punctatum* may not exist here, because the temperatures in the surrounding area are too warm.

Similar to Cluster A, Cluster C was dominated by *Cyclothone* (51.4% of total individuals). The stations in this cluster (specifically those below 16° N) overlapped with the sampling region of Czudaj et al. (2021). However, in the latter study, *Cyclothone* spp. were far less abundant and only reached 17% of total abundance in the communities where they were most abundant. *Polyipnus polli* was the second most abundant species in Cluster C, followed by *D. vanhoeffeni*. Both *P. polli* and *D. vanhoeffeni* were abundant species north of the equator, which agrees well with Olivar et al. (2017), who reported the same 3 dominant species. These species seem to be very typical of the tropical Atlantic, where SACW dominates, and Krefft (1974) suggested a tropical distribution within the Atlantic for these species.

4.4. Assemblages in relation to regional hydrography

Composition of mesopelagic fish communities depends on many biotic and abiotic factors such as primary production or chlorophyll concentration (Dove et al. 2020, Duncan et al. 2022), physical properties, e.g. water mass characteristics, temperature (Olivar et al. 2016, Tiedemann et al. 2018, Dove et al. 2021, Duncan et al. 2022), the presence of frontal zones (Netburn & Koslow 2018, Tiedemann et al. 2018), or hydrographic features such as seamounts (Fock et al. 2002). Our study in the Mauritanian upwelling region concentrated on adult individuals, which has not been carried out as frequently (Nafpaktitis 1977, Olivar et al. 2017, Czudaj et al. 2021). Most previous studies focused on larval communities (Olivar et al. 2016, Hsieh et al. 2017, Tiedemann et al. 2018, Dove et al. 2021, Olivar & Beckley 2022). Larvae can be considered good indicators of water masses because of their short stage duration, whereas adults may pass through different water masses by means of vertical and horizontal migration (Lutjeharms et al. 1985, Koubbi 1993, Olivar et al. 2016). Based on the species present in each community, community composition is representative of water mass properties. Between 18 and 20° N, there were probably 2 'transition communities' (Clusters A and B) adjacent to the permanent upwelling region of the Canary Current Upwelling System. This coincided with water mass properties that showed a mixing of NACW and SACW in the area. South of 18° N, the clustering based on species composition corresponded with SACW being the dominant water mass. For example, *B. glaciale* was not found in the SACW community but was found in the transition communities, and its occurrence is typical of temperate waters (Hulley 1981) and cold upwelling waters along the Mauritanian slope (John & Zelck 1997). Despite the prevalence of SACW in both the tropical Mauritanian Upwelling System and in the subtropical Benguela Upwelling System (Duncan et al. 2022), assemblage composition of mesopelagic fishes was different in both regions, except for the above mentioned *L. dofleini* and *A. hemigynmus* as well as *Stomias boa*. This indicates that the effect of water mass affiliation may be overridden at a larger scale by regional physical properties. Current speed of the Atlantic Thermohaline Circulation (THC) is slow (10—20 km yr^{-1}; see Webb 2019), while surface currents may move faster. Rühs et al. (2019) estimated surface passage times across the South Atlantic from the Agulhas Current to the entry point of the North Brazil Current in the North Atlantic to be around 12 yr.

This is on the same order of magnitude with regard to residence times for water masses at the transition between the North Atlantic and Arctic Ocean (Wefing et al. 2021). Thus, effects of seasonal and interannual changes in surface properties such as mixed layer depth, production regime, and temperature in conjunction with interference with the ambient community may override water mass effects for the duration of several generations considering a lifespan of 3–9 yr for mesopelagic fishes (Knorrn et al. 2024). This could explain that at regional scales, water mass properties prevail, whereas at the basin scale, additionally the modification of surface waters may determine the composition of mesopelagic assemblages. Hence, despite a relatively small number of distinct Atlantic intermediate water masses, this may lead to a significant biogeographical diversity (see Sutton et al. 2017).

Our analyses of specific environmental factors affecting mesopelagic fish communities showed that oxygen concentration from the surface to 600 m was the most influential environmental parameter for mesopelagic fish communities. In the eastern tropical North Atlantic, there is a permanent OMZ from about 300 to 600 m, and oxygen concentrations are expected to continue to decline (Karstensen et al. 2008, Stramma et al. 2009, Hauss et al. 2016). In the region, a weakening of the zonal jets has led to a decrease in ventilation and expansion of the OMZ (Brandt et al. 2010). Oxygen has often been described as an important factor shaping fish assemblages, from benthic (Gallo & Levin 2016) and reef-dwelling (Hughes et al. 2020, Johnson et al. 2021, Meyer-Gutbrod et al. 2021) to mesopelagic fishes (Levin 2003, Netburn & Koslow 2015, Gallo & Levin 2016, Koslow et al. 2019). We also detected this pronounced OMZ, which spanned from ~40 to ~600 m in the present study. This has strong implications on the fauna that is able to survive under hypoxic conditions in the water column, because oxygen concentrations even below 3 ml l^{-1} may act as a barrier for species, especially at larval stages (Ekau et al. 2010). Some organisms that are able to remain in the OMZ are the calanoid copepods *Rhincalanus nasutus* and *Pleuromamma* spp. (Teuber et al. 2013, Hauss et al. 2016) or the mesopelagic fishes *Cyclothone* spp. and *D. vanhoeffeni* (Olivar et al. 2017). Gelatinous zooplankton in the Eastern Tropical North Atlantic region have also shown vertical distribution patterns related to environmental factors including oxygen (Hoving et al. 2020). While some species remained in the OMZ, others resided above or below the OMZ or even migrated between layers, demonstrating that some species may be more tolerant to low oxygen levels than others (Hoving et al. 2020).

Some mesopelagic fishes are able to linger in the OMZ during the day but ascend to the epipelagic layer at night to make up for the oxygen deficit (Kinzer et al. 1993). One example is the myctophid *Diaphus arabicus* in the Arabian Sea, which resides in an OMZ with oxygen levels below 0.1 ml O_2 l^{-1} during the day and migrates to the oxygen-rich surface at night (Kinzer et al. 1993). Large predatory fishes are probably more affected by low oxygen concentrations due to their large size and consequently higher metabolic demands, whereas smaller organisms may be able to survive or even thrive in OMZs that may serve as refuge areas (Childress & Seibel 1998, Stramma et al. 2012, Olivar et al. 2017).

4.5. Conclusions and outlook

In the present study, we showed that in the Mauritanian upwelling region, (1) mesopelagic fish assemblages are related to water mass distribution, (2) areas with mixing of water masses probably have 'transition' communities with temperate and tropical species, (3) oxygen plays a major role in community composition, and (4) low oxygen environments are dominated by OMZ-tolerant taxa. This is reflected in the high abundance of *Cyclothone* spp. and small myctophids (*D. vanhoeffeni*, *H. macrochir*) in the OMZ. Over the last 5 decades, the Canary Current Upwelling System has experienced increased warming, which is expected to continue with climate change (Carson & Harrison 2008, Arístegui et al. 2009, Demarcq 2009). Due to increased stratification from warming, OMZs, especially in highly productive areas such as eastern boundary currents, are expanding both vertically and horizontally (Stramma et al. 2009, 2010). This reduces the available habitat for many oxygen-sensitive pelagic animals that may either escape, adapt, or not survive (Stramma et al. 2012). In the case of mesopelagic fishes, we know that small-sized taxa such as *Cyclothone* or *D. vanhoeffeni* are well adapted to hypoxia (Olivar et al. 2017), in contrast to larger species with higher metabolic needs (Stramma et al. 2012). In demersal fishes, it has been shown that gill surface area and metabolic enzyme activities are related to the OMZ (Friedman et al. 2012). Some active species have a larger gill surface area in order to take up more oxygen, while less active fishes like the rockfish *Sebastolobus* have small gills and low aerobic activity (Friedman et al. 2012).

We expect that mesopelagic fishes residing in the OMZ to also have physiological, behavioural, and morphological adaptations that help them balance

their oxygen demands with that available in the water column. Currently, little is known about the metabolic requirements of most mesopelagic fish species. When taxa such as *Cyclothone* do not migrate vertically, this may lead to a decrease in the active transport of carbon by fishes, compared to more oxygenated regions. For instance, the viperfish *Chauliodus sloani* migrates further into the epipelagic layer in temperate regions than in tropical regions due to lower temperatures, which may in turn change its contribution of carbon to the mesopelagic layer (Eduardo et al. 2020b). We may not only see behavioural changes within an individual species but shifts in species composition, for example a shift to smaller and non-migrating species in low-oxygenated regions, which may lead to a decrease in the exchange of nutrients (such as N and P) and carbon between the epipelagic and mesopelagic layer. As temperatures increase and OMZs expand, it is important to monitor meso- and epipelagic communities, since changes in abundance and diversity can have a strong impact on both the trophodynamics and the biological carbon pump in these pelagic systems.

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