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Cold-water coral mounds and reefs off Mauritania and associated megafauna

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This study presents the megafauna related to coral mounds (coral remains) and cold-water coral (CWC) reefs off Mauritania. The mound-specific megafauna was documented by comparing 47 trawl catches from coral mounds with 47 catches from off-mound areas, sampled from 1982 to 2022. Coral reef megafauna were described from eleven ROV dives conducted during two surveys held in 2020 and 2021. The mound and reef environment were documented using data from 2159 CTD profiles collected between 1995 and 2022. A detailed annotation of the ROV recorded videos was undertaken, and megafauna habitat relations were identified using multivariate statistics. The coral ecosystems that supported a rich megafauna were situated in the oxygen minimum zone at depths of 400 to 650 meters, with an average temperature of 10.55°C. The coral mound hosted 31% more species than adjacent off-mound areas, and fish contributed 66% of the taxa of five groups, followed by crustaceans contributing with 20%. The five most common species were *Helicolenus dactylopterus*, *Laemonema laureysi*, *Merluccius polli*, *Malacocephalus occidentalis* and *Hoplostethus cadenati*. The CWC reefs hosted 120 taxa representing 11 different faunal groups, with fish as the most species rich group, contributing 39% of the recorded taxa, followed by cnidarians represented by several corals (18 taxa) and crustaceans (17 taxa). The most abundant taxa on the reefs, in addition to the reef-building coral *Desmophyllum pertusum*, were the anemone *Synarachnactis* cf. *lloydii*, the corals *Acanthogorgia* cf. *hirsuta* and *Swiftia phaeton*, the crustaceans *Nematocarcinus africanus* and *Eumunida bella*, the fish *H. dactylopterus*, the bivalve *Acesta excavata* and the sponge *Cladorhiza corallophila*. Live coral, sand and mud were environmental drivers of species distribution on the reefs, and separate communities were related to different reef habitats. This study provides the first comprehensive description of the megafauna related to the cold-water coral mounds and reefs off Mauritania. The rich megafauna associated with these ecosystems highlights the urgent need for conservation measures, particularly in light of increasing pressures from oil and gas activities, deep-sea fishing, and the impact of climate change.

KEYWORDS

cold water corals (CWC), coral mounds, coral reefs, megafauna associated, Mauritania

1 Introduction

Cold-water corals (CWC) are widely distributed on continental margins and seamounts across most oceanic regions of the world, mainly at depths of 200–1500 m (Roberts et al., 2006, Roberts et al., 2009). In southwest Africa, they occur along the Angolan margin (Hebbeln et al., 2020; Le Guilloux et al., 2009), on the Angolan and Namibian margins (Hanz et al., 2019), on the Namibian shelf (Tamborrino et al., 2019), in the Gulf of Guinea (Buhl-Mortensen et al., 2017), along the Mauritania margin (Colman et al., 2005; Moctar et al., 2024; Ramos et al., 2017; Westphal et al., 2014; Wienberg et al., 2018), north of Senegal (Moctar et al., 2024), and south of Morocco (Buhl-Mortensen et al., 2024; Hebbeln et al., 2019). The recent discoveries of the different CWC reefs and mound provinces reveal that the West African margin is a coral hotspot area in the Atlantic Ocean (Wienberg et al., 2023). The habitat complexity and heterogeneity provided by CWC support a high diversity of benthic species and may also act as shelter and nurseries for many species, providing a wide range of habitats for invertebrates and fishes (Buhl-Mortensen et al., 2010; Capezzuto et al., 2018; Costello et al., 2005; D'Onghia et al., 2012; El Vadhel et al., 2024; Kutti et al., 2013; Mortensen & Fosså, 2006; Ross and Quattrini, 2007). Due to this important ecological role, CWC reef habitats are considered biodiversity hotspots in the deep sea (Henry and Roberts, 2017). Both live and dead coral structures can play an important role in increasing three-dimensionality and they provide a hard substratum in the deep sea that will add habitats for many species in an otherwise relatively homogeneous setting (Bongiorni et al., 2010; Buhl-Mortensen et al., 2010). Interestingly, the coral associated fauna is richer in the older and dead parts than in the live parts of actively growing reefs, and many reef organisms can be supported by the complex microhabitat provided by rubble, often with a clear role in ecosystem functioning (Mortensen et al., 1995; Wolfe et al., 2021).

Mauritanian waters (from 20°46'N to 16°04'N) are located in North Atlantic Africa at the meeting point of temperate and subtropical oceanic ecosystems and belong to the Canary Upwelling Current (CUC), making them one of the most productive areas worldwide (Camp et al., 1991; Carr and Kearns, 2003; Hagen, 2001). They support one of the oldest and most important West African fisheries (Brahim et al., 2021) that target pelagic and demersal resources, including deep fishing from 200 m to 1000 m depth. Marine biological studies in the Mauritanian waters have mainly focused on fish stocks of commercial interest on the continental shelf (< 200 m) (e.g., Braham et al., 2014; Braham, 2013; Meissa et al., 2013; Gascuel et al., 2007; Meissa and Gascuel, 2015). Since 2006, several scientific surveys have been conducted by German, Spanish, and Norwegian vessels in the deep waters (>200 m) with the aim of describing and characterizing the marine ecosystem with a focus on geology, fish communities, and more recently corals (Bridges et al., 2023; Eisele et al., 2011; Krastel et al., 2006; Ramos et al., 2017; Sanz et al., 2017; Westphal et al., 2014; Wienberg et al., 2018, Wienberg et al., 2023; Wienberg and Titschack, 2015; Buhl-Mortensen et al., 2024; Moctar et al., 2024). These scientific surveys and studies related to hydrocarbon exploration have greatly enhanced our understanding of the Mauritanian seabed and its diverse habitats. Among the most significant deep-sea ecosystems discovered in Mauritania waters are cold water corals (CWC) occurring as mounds (framework of coral remains) and active and live reefs. Coral mounds result from an interplay between coral growth, sediment input, and processes on the adjacent (off-mound) seafloor. The mounds are created by the framework-forming scleractinian *Desmophyllum pertusum* (formerly known as *L. pertusa*; see Addamo et al., 2016) and, to some degree, *Madrepora oculata* (Hebbeln et al., 2016; Wienberg and Titschack, 2015). Along the Mauritanian coast, coral mounds form an extensive ridge (~400 km long) at 400–550 m composed of coral remains with occasional live colonies (Wienberg et al., 2018, Wienberg et al., 2023). Large and actively growing CWC reefs have been documented in the region at 430–650 m as recently as in 2020 and 2021 (Buhl-Mortensen et al., 2024; Moctar et al., 2024). Both coral habitats occur within the prevailing oxygen minimum zone off Mauritania (Buhl-Mortensen et al., 2024; Moctar et al., 2024; Ramos et al., 2017; Westphal et al., 2014; Wienberg et al., 2018, Wienberg et al., 2023). Despite the progress made in recent years to study the deep-sea habitats off Mauritania, the available information on the fauna associated with CWC ecosystems is limited. Colman et al. (2005) and Westphal et al. (2014) published the first visual data on the coral habitat, using a Remotely Operated Vehicle (ROV). They reported the presence of some colonies of live CWC, mainly *Desmophyllum pertusum* and *Madrepora oculata*, associated with some benthic organisms (e.g., sponges, gorgonians, crustaceans, sea pens, fishes, molluscs etc.). Other studies have described new species associated with CWC habitats off Mauritania (e.g., Göcke et al., 2016; Hoffman et al., 2019; Sampaio et al., 2022). The relationship between *Helicolenus dactylopterus* and cold-water corals in Northwest Africa was described in detail (El Vadhel et al., 2024).

Despite these studies, there is still no comprehensive investigation of the megafauna associated with CWC reefs and mounds in Mauritanian waters and their contribution to ecosystem functioning and diversity. Our main objective is to describe the associated megafauna of two different CWC ecosystems occurring off Mauritania: the chain of coral mounds and the live coral reefs. The megafauna inhabiting coral mounds is characterized through a comparative analysis of trawl catches from coral mounds and those from adjacent off-mound areas conducted from 1982 to 2022 by four research vessels. The megafauna associated with CWC reef habitats is described through the analysis of videos from ROV dives undertaken as part of two seafloor habitat mapping surveys conducted by the R/V Dr. Fridtjof Nansen off Mauritania in 2020 and 2021. The results provide insight into the importance of these CWC habitats to the Mauritanian deep-sea ecosystem, information that is essential for the development of a national management plan for the use of marine resources and their ecosystems.

2 Materials and methods

2.1 Environmental setting

2.1.1 Oceanography

Situated within the Canary Current Large Marine Ecosystem (CCLME), the currents in Mauritanian waters represent one of the most complex transition systems in the world. This region serves as a convergence zone for subtropical water masses from the north and tropical water masses from the south (Peña-Izquierdo et al., 2015). The main water masses identified within the Mauritanian Exclusive Economic Zone (EEZ) include (i) surface waters within the mixed layer at depths ≤ 50 m, (ii) the North Atlantic and South Atlantic Central Waters (NACW, SACW), which occupy a permanent layer down to 600 m (Cianca et al., 2009), (iii) Antarctic Intermediate Waters (AAIW) found between 600 and 1000 m (Emery, 2001), and (iv) the North Atlantic Deep Waters (NADW), located between 1000 and 1600 m in depth (Tomczak and Godfrey, 1994).

The primary surface currents in this region are the Canary Current (CC) and the Mauritania Current (MC) (Zenk et al., 1991). The dominant current between 100 m and 300 m within the water column is the Poleward Undercurrent (PUC), responsible for the northward transport of the South Atlantic Central Waters (SACW) (Pelegrí et al., 2017). These relatively cold and less saline SACW are separated from the North Atlantic Central Waters (NACW) by the Cape Verde Frontal Zone (CVFZ), which shifts between 21°N and 16°N latitude (Peña-Izquierdo et al., 2015).

Mauritanian waters are influenced by the presence of oxygen minimum zones (OMZs), characterized by extremely low dissolved oxygen concentrations. Two well-known OMZs can be observed in the region. The Upper OMZ (~100 m deep) is primarily caused by intense biological productivity, which is driven by nutrient upwelling. The decomposition of sinking organic matter further depletes oxygen levels in the water. The Lower OMZ (~400 m deep) associated with advection of the anoxic South Atlantic Central Waters (SACW) by the Polar Undercurrent (PUC), which exacerbates the anoxic conditions.

2.2 CWC study sites

The study sites encompass mounds and reef areas at depths ranging from 400 to 650 m (Figure 1). The coral mounds extend from Cap Timiris to the border with Senegal, while the coral reefs are located north and south of the mounds. The southern reef site is composed of eight reefs, and the northern reef site comprises three reefs (Figure 1).

Here we discriminate between the coral mounds that are the remnants of former live coral reefs that in the region form a long barrier-like ridge. This old and basically dead structure formed by corals can host some live colonies. In contrast, a coral reef represents a single, well-defined structure built by the corals that have recently been actively growing, and reefs normally have actively growing parts.

2.2.1 The coral mounds

Colman et al. (2005) discovered a 190 km long succession of 100 m high coral mounds at 450–550 m depth, which later triggered several scientific surveys (Bridges et al., 2023; Eisele et al., 2011; Krastel et al., 2006; Ramos et al., 2017; Sanz et al., 2017; Westphal et al., 2014; Wienberg et al., 2018, Wienberg et al., 2023; Wienberg and Titschack, 2015). These coral mounds developed during the last 120,000 years, have an overall extension of ~400 km, and range between Cap Timiris (19°N) and the Senegalese border (16°N) (Ramos et al., 2017; Wienberg et al., 2018) (Figure 2). The mounds are cut by numerous canyons and submarine landslides. In some places, the mounds run in two parallel chains (Krastel et al., 2006; Sanz et al., 2017). The mounds are in a dormant state, with only scarce living coral colonies (Wienberg et al., 2018).

2.2.2 The coral reefs

Previous studies on CWC reported mainly fossil corals based on sediment cores (Colman et al., 2005; Wienberg et al., 2018) and dredge samplings (Ramos et al., 2017), whereas ROV surveys reported only a few live colonies (Colman et al., 2005; Westphal et al., 2014).

However, recent investigations have recorded several healthy *D. pertusum* reefs in both the northern (Buhl-Mortensen et al., 2024) and southern regions of Mauritania (Moctar et al., 2024). Additionally, 13 (CWC) reefs were discovered, in the study area at the border between Mauritania and Senegal; six of these were healthy, with areas having 15%–50% cover of live colonies, and some reefs, such as the "Khairidine reef", was approximately 70 m tall and 600 m long (Moctar et al., 2024).

2.3 Data sets

2.3.1 Oceanographic data

To describe the oceanographic setting of the CWC ecosystems, data from 2159 CTD profiles conducted within the Mauritanian EEZ were used. The profiles were conducted by 7 research vessels between 1995 and 2022 (Table 1) and were taken at depths between 0 and 1000 m, and 262 were from 400 to 650 m depth and positioned over the two CWC ecosystems. Data quality control and standardization were carried out using a Python script, which generated a standardized database of NetCDF files: (https://github.com/cmunozmas/nansen_pbgc_processing)

2.3.2 Data from the coral mound

Data from deep trawling surveys were used to describe the megafauna inhabiting the coral mounds. The surveys were conducted by four research vessels (RV. N'Diago, RV. Al-Awam, R.V Vizconde de Eza and R.V Fridtjof Nansen) between 1982 and 2022 along the Mauritanian continental slope (>200 m). For selection of relevant trawl catches, trawling stations were plotted using QGIS software (version 3.26). Trawl stations starting on the mound but ending off the mound were excluded from the analysis to avoid mixing habitats. In total, 47 trawl stations were conducted at 400–600 m depth on the coral mounds and could be included in

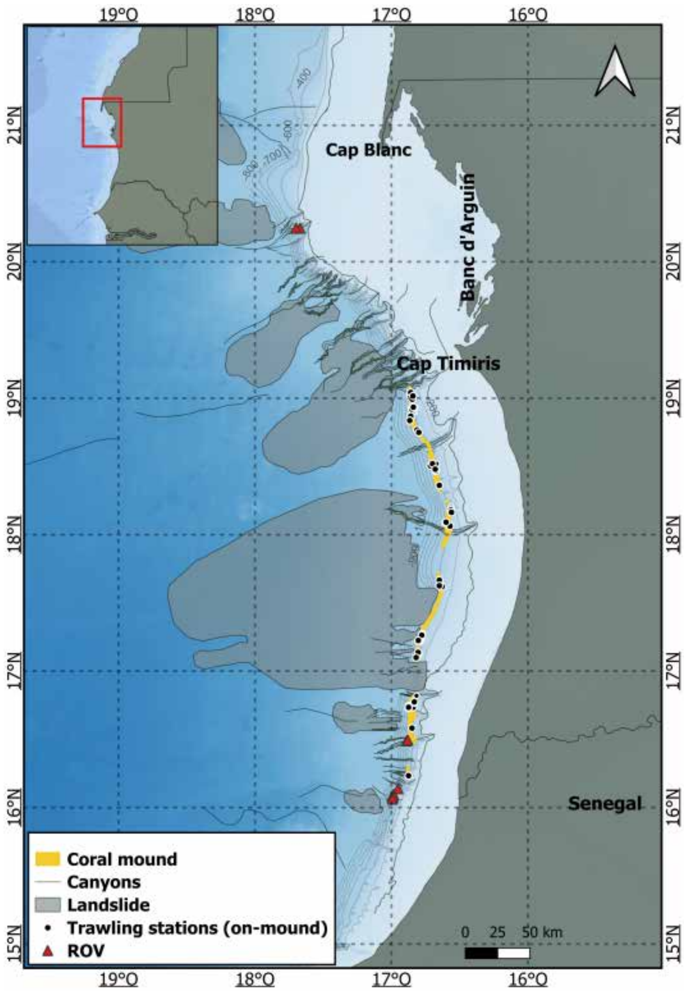

FIGURE 1
Map of the study area illustrating the distribution of coral mounds, canyons, and landslides along the Mauritian margins after (based on data from Colman et al., 2005; Ramos et al., 2017; Sanz et al., 2017; Westphal et al., 2014). The two CWC reef areas that were mapped and surveyed during 11 ROV dives are marked with red triangles. The 47 trawl surveys conducted in the coral mound zone are designated by black dots.

the analysis. For megafauna comparison, 47 off-mound trawl catches were selected adjacent to the mound barrier with a distance of at least 1.6 nautical miles from the mound to ensure habitat separation (Figure 3).

The two Mauritanian research vessels, R/V Al Awam and R/V N'Diago, were using an "Irish-type" trawl with an average horizontal opening of 17 m and a vertical opening ranging from 2.8 to 3.5 m. The mesh size was 60 mm in the front part and 45 mm in the cod-end (pocket). The Spanish vessel R/V Vizconde de Eza used "Lofoten bottom trawl" during scientific surveys with a horizontal opening of 17.70 m and a vertical opening of 5.5 m, and a 35 mm mesh size at the codend (Ramos et al., 2017). The R.V Fridtjof Nansen used a "Gisund super demersal" for trawling, with a horizontal opening of about 18 m and a vertical opening of around 5.5 m, and a 20 mm mesh size in the codend and a 10 mm mesh size in the inner net.

Fauna data from the trawl catches included information on taxon name, latitude and longitude, depth, collection date, and number and weight of each specimen. Trawling times were 30 min for the three vessels (RV. N'Diago, RV. Al-Awam, R.V Fridtjof Nansen) and 60 min for the R.V Vizconde de Eza. However, due to the uneven and complex nature of the seabed, especially in the coral mound area, some trawling stations could not reach the standard trawling duration used by vessels (60 min for Vizconde de Eza and 30 min for the other three vessels). This was primarily due to obstacles such as coral structures and steep topography, which limited trawling efficiency. To ensure comparability, all trawling data were standardized by time. The number of trawling stations per vessel and zone (on-mound and off-mound) is the same (47 trawling stations) (Table 2).

2.3.3 Data from coral reefs

Video data from ROV surveys were collected as part of two habitat mapping surveys conducted by the R/V Dr. Fridtjof Nansen in the framework of the EAF-Nansen Programme. The first survey took place in 2020, in the northern part of Mauritania, while the second survey was carried out in 2021 in the southern part, at the border between Mauritanian and Senegal. The main objectives of

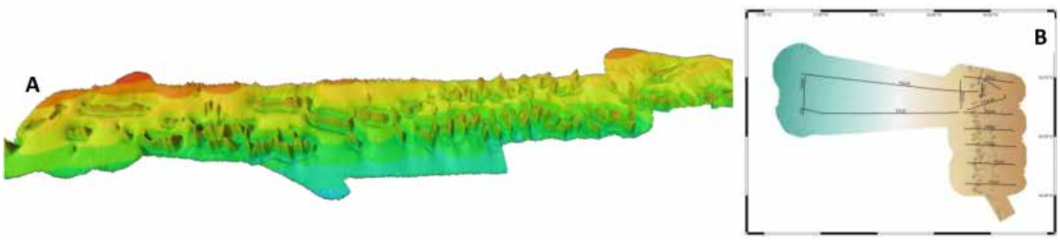

FIGURE 2
Bathymetric map showing the Mauritanian cold-water corals, **(A)** oblique view from W to E on a 30-nm-long strip off Cap Timiris coral mounds according to Freiwald et al. (2014), **(B)** Parasound profile of the Timiris mound complex (source: Bickert, T. and Shipboard Scientific Party of MSM127 (2024), unpublished data). Note that the two mound chains were developed.

both surveys were to document vulnerable seafloor habitats and their fauna, including CWC reefs, in this region (Table 3).

The Video Assisted Multi-Sampler (VAMS), developed by the Institute of Marine Research (IMR), was used to map the distribution of vulnerable ecosystems on the seafloor. It includes an ROV with a high-resolution video camera and two lasers mounted 5 cm apart, serving as a measuring scale, in addition it is equipped with five hydraulic operated grabs with a sampling area of 0.1 m^2 (For description see Buhl-Mortensen et al., 2017). During transects, the VAMS was tethered by the vessel at a speed of approximately 0.3 knots with the ROV flying in front. A total of 11 dives were conducted during the two surveys, with 3 dives in the north and 8 in the south. The total area surveyed was approximately 6800 m^2, covering a depth range of 440 m to 650 m.

2.4 Data analysis

2.4.1 Oceanography

A python script was used to process, analyse, and visualize oceanographic data to create profiles for the three environment parameters (temperature, salinity, and dissolved oxygen) in depth ranges between 0 to 1000 m. The analysis focused in particular on the depth zone of the two CWC ecosystems (400 to 650 m).

2.4.2 Fauna analysis

Data from trawls (94 stations) and ROV dives (11 videos) were organized separately in two different databases. We used the WoRMS Taxon Match Tool (available from https://www.marinespecies.org) to check the valid scientific name and complete the taxonomic classification for each taxon (e.g., phylum, class, order, family, etc.). For ROV data, species identification was based on videos and images. Taxonomists were consulted to confirm the identification of certain species (see Acknowledgments).

CWC Mounds: We analyzed the species diversity for on-mound and off-mound megafauna trawl catches. To describe and compare the diversity of both areas, species richness, Simpson index, Shannon-Weiner index, species accumulation curves, and Venn diagrams were calculated and drawn using the vegan package (Oksanen et al., 2022) in R software (version 4.2.1).

CWC Reefs: For the video analysis, we used the VideoNavigator software developed by the Institute of Marine Research (IMR) to identify, document and analyze the megafauna inhabiting the coral

TABLE 1 Number of CTDs by depth and research vessel from 1995 to 2022.

Depth (m)	Atlantida	Al Awam	Maria S. Merian	Atlantniro	Poseidon	Fridtjof Nansen	Vizconde de Eza	Total
0-100	47	740	5	15	4	447	20	1278
101-200	3	119	7	4	1	145	22	301
201-300	2	54	5	7	3	52	12	135
301-400	3	19	0	1	0	48	12	83
401-500	7	16	2	2	0	139	14	180
501-600	6	11	5	0	2	51	7	82
601-700	0	1	2	1	0	9	7	20
701-800	0	0	3	3	6	9	8	29
801-900	0	0	0	2	0	4	5	11
901-1000	1	0	0	3	0	15	21	40
Total	69	960	29	38	16	919	128	2159

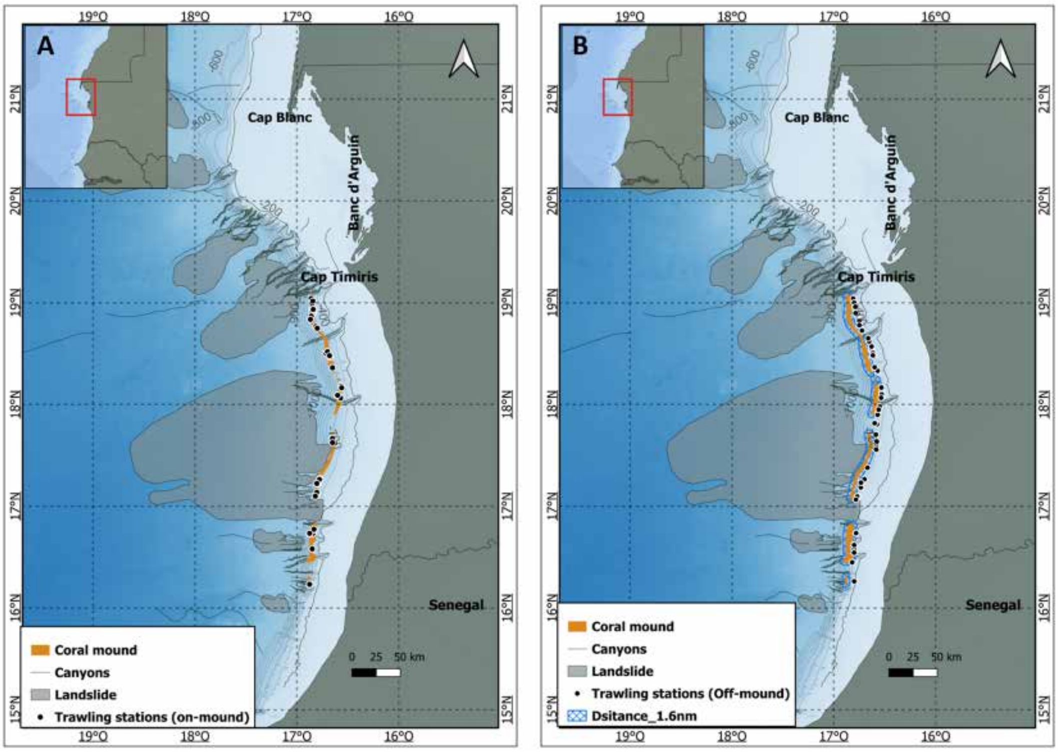

FIGURE 3
Map **(A)** shows the trawling stations conducted on-mound, and map **(B)** shows the trawling stations carried out in the off-mound area. The buffer zone of 1.6 nautical mile is indicated in blue.

reef habitat. The software provides output files containing date, time, geographical position, depths, species names, abundances, substrate type, as well as observation of human impact (e.g., trawl marks, litter, etc.). In total, 7 substrates were listed (live coral: when live CWC represents more than 25%, coral rubble, rubble and live, coral block, sandy mud, sandy gravel, and bedrock).

For identification of community patterns and their relationship with environmental variables, the multivariate analysis Detrended Correspondence Analysis (DCA) and cluster analysis were performed using the PC-ORD software: Multivariate Analysis of Ecological Data version 5 (McCune and Mefford, 1999). This was conducted using a species composition matrix and an environmental variable matrix.

Before analysis, the 11 annotated video transects were divided into subsamples based on the dominant substrate (>50% cover). To maintain relatively equal sample sizes, subsamples were divided into equal lengths based on the length/record-time of the video sub-samples. Only taxa that occurred in three subsamples or more, and only subsamples that recorded at least two taxa, were retained in the input matrix for analysis. This resulted in a final dataset of 50 subsamples and 69 taxa and to reduce the influence of highly abundant species, data were square-root transformed before analysis.

After an initial run of DCA, only four categories of substratum were selected to ensure better representation of environmental relations: Live coral present (if live coral covers more than 5%), coral skeleton (coral rubble combined with blocks), sand & mud and gravel & bedrock if they cover > 50% of the substratum. Other environmental variables included were rugosity with three levels (low: flat seafloor, medium: thick rubble and some coral colonies, and high: high-relief areas with many coral blocks and live coral), depth, and site position (degrees north and south).

A correlation matrix in R was used to investigate the correlation between the main CWC reef building species (*D. pertusum, M. oculata)* and the other species in the reef community, and a heatmap was generated using the ggplot2 package in R (Wickham, 2016) to illustrate the relative abundance of species across different substrate types. For spatial distribution of *D. pertusum*, we used the QGIS software (version 3.26) to show the occurrence of this species in the study area. This was based on data from the two surveys conducted in 2020 and 2021, as well as literature available on the presence of live *D. pertusum* in Mauritanian waters (Westphal et al., 2014).

3 Results

3.1 Oceanographic environment

The analysis of 2159 CTD vertical profiles shows the properties of water masses, the Figure 4 presents three profiles of temperature (°C), salinity (PSU), and dissolved oxygen (ML/L) plotted as functions of depth from 0 to 1000 m in the Mauritanian Exclusive Economic Zone (EEZ). These profiles are based on all the historical CTD data collected from 1995 to 2022.

TABLE 2 Number of trawling stations by zone (on-mound and off-mound) and vessels.

Zone	Depth range	Al-Awam	N'Diago	Vizconde de Eza	Fridtjof Nansen	Total
On-mound	400–600 m	31	6	3	7	47
Off-mound	200–350 m	31	6	3	7	47
Total		62	12	6	14	94

3.1.1 Temperature profile

The temperature profile demonstrates a typical thermocline structure, with warm surface waters reaching an average temperature of 22°C. Below this surface layer, temperatures decrease sharply through the thermocline, which spans from the surface to 100 m, with temperatures dropping to around 10°C at 500 m, beyond this depth, the temperature decline is more gradual, reaching around an average temperature of 5°C at 1000 m.

3.1.2 Salinity profile

Salinity remained relatively constant throughout the water column, ranging between 35 and 36 PSU, suggesting minimal variation and offering a consistent environment that can support marine life.

3.1.3 Dissolved oxygen profile

The dissolved oxygen profile reveals two prominent Oxygen Minimum Zones (OMZs): a shallow one at around 100 m and a deeper one near 400 m. The shallow OMZ exhibits a rapid drop in average oxygen concentrations from surface levels of approximately 4–5 ml L^{-1} to below 1 ml L^{-1}at 100 m. After that, the oxygen content levels out, averaging between 1 and 1.5 ml L^{-1}down to around 300 m, followed by a second, more pronounced decline at 400 m, where oxygen reaches its lowest average concentration. This depth corresponds to the onset of two CWC ecosystems. Below 400 m, average oxygen levels start to increase in the intermediate layer, reaching over 2.5 ml L^{-1} at 1000 m.

A focus on the area of occurrence of coral mounds and CWC reefs (400–650 m) through the analysis of more than 260 CTDs carried out in this depth range shows that the CWC ecosystems occur in waters characterized by an average temperature of 10.55°C, an average salinity of 35.28 PSU and an average dissolved oxygen of 1.24 ml L^{-1}. At this depth, dissolved oxygen concentrations could reach a minimum of 0.77 ml L^{-1} and the temperature could be as low as 7.58°C. (Table 4).

3.2 Trawling data analysis

The analysis of 47 trawl catches from coral mounds revealed a rich megafauna, including 282 recorded taxa belonging to the 5 taxonomic groups: Fish (187), Crustacea (56), Mollusca (31), Cnidaria (5) and Echinodermata (3).

The most common fish species was the blackbelly rosefish *Helicolenus dactylopterus* recorded in 41 out of 47 trawl catches. Other frequently reported species (found in more than 26 stations) included the guinean codling (*Laemonema laureysi)*, black hake (*Merluccius polli)*, western softhead grenadier (*Malacocephalus occidentalis)*, black slimehead (*Hoplostethus cadenati)*, Darwin's slimehead (*Gephyroberyx darwini)*, Blackbellied angler (*Lophius*

TABLE 3 Information on 11 ROV dives (A6–1 consists of 2 videos) including depth, position, transect length, duration, temperature, and observed % cover of live reef.

Surveys	Video	Depth (m)	Latitude and longitude		Transect length (m)	Duration	Reef health status
2020	A6-1	480-650	20°14'47"N	17°40'12"W	1218	3:27:05	0-30% live reef
	A6-2	525-591	20°14'47"N	17°42'00"W	371	1:03:57	0-1% live reef
2021	T2B-V1	545-648	16°29'38"N	16°53'36"W	330	2:09:52	Dead, few live reef
	T2B-V2	518-579	16°29'69"N	16°52'87"W	430	1:17:22	Dead, few live reef
	T3B-V1	530-566	16°04'83"N	16°59'83"W	220	0:52:53	0-15% live reef
	T3B-V2	504-518	16°04'73"N	16°59'93"W	300	1:10:09	0-15% live reef
	T3B-V4	520-603	16°05'79"N	16°59'22"W	260	1:10:34	0-15% live reef
	T3B-V6	505-580	16°05'85"N	16°59'12"W	280	0:52:53	0-5% live reef
	T3B-V7	580-644	16°03'75"N	16°59'53"W	530	1:25:37	0-15% live reef
	T3B-V11	439-517	16°08'33"N	16°57'09"W	600	1:15:41	0-30% live reef

The area covered (in percentage) by live coral colonies along the conducted transects was estimated using VideoNavigator Software.

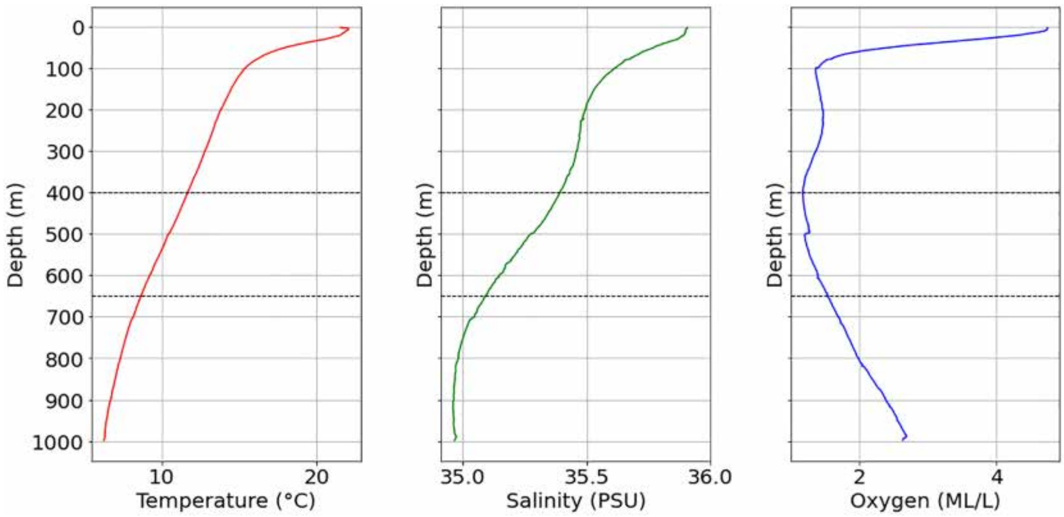

FIGURE 4
Temperature, salinity, and dissolved oxygen profiles of the CTD deployment in the Mauritanian EEZ between 1995 and 2022. The depth zone of mounds and reefs (400–650 m) is indicated by the dotted lines.

budegassa), Senegalese hake *(Merluccius senegalensis)*, and pink frogmouth (*Chaunax pictus)*. The most common of the crustaceans was the box crab, *Paromola cuvieri* occurring in 16 trawl catches, followed by the deep-water pink shrimp *Parapenaeus longirostris* and the African mud shrimp *Solenocera africana*, both encountered in more than 10 trawl catches.

The Mollusca group was dominated by the European flying squid *Todarodes sagittatus*, this species was reported in 21 trawl stations, followed by the shortfin squid *Illex coindetii* with 14 observations. The last two taxonomic groups (Cnidaria and Echinodermata) were poorly represented in data from demersal trawling surveys.

For the 30 most common species in both habitats, *H. dactylopterus* comes first in on-mound areas and second in off-mound adjacent areas. Other commercial species were also abundant in both areas (e.g., *M. polli, Parapenaeus longirostris, M. senegalensis, I. coindetii and L. budegassa*). (Table 5)

The diversity of species that inhabit the coral mound area (400 to 600 m) was compared to the adjacent off-mound habitat (200 to 350 m). Species richness was higher on-mound than off-mound (282 versus 216 taxa; Shannon index 1.87 versus 1.5; Simpson index 0.72 versus 0.64). Abundance (i.e., number of individuals, total catch) was more than two times higher off-mound than on-mound.

TABLE 4 Temperature, salinity and dissolved oxygen CTD profiles (400 to 650 m).

CTD profiles: 400–650 m	Min	Max	Mean
Temperature (°C)	7.58	13.19	10.55
Salinity (PSU)	34.96	35.63	35.28
Dissolved oxygen (ml L^{-1})	0.77	2.07	1.24

3.2.1 Diversity by family

The diversity of the megafauna on the mounds is high on family level, with 116 families representing 282 taxa found on coral mounds. The top 16 families are illustrated in Figure 5.

In terms of species richness, the most represented family is the deep-sea fish family Macrouridae, with 13 species, followed by the Soleidae family of flatfishes and the Centrophoridae family of squaliform sharks, each with 9 species. The Congridae family, which includes conger and garden eels, and the Pandalidae family of pandalid shrimps both have 8 species.

When considering the total catch, the Sebastidae family, which is represented by two fish species (*H. dactylopterus* and *Trachyscorpia cristulata*) account for more than 20%. The Merlucciidae family, including both species of black hake (*M. polli* and *M. senegalensis*), is second with over 15%. The Lophiidae family, which contains *L. budegassa*, *Lophius vaillanti* and *Lophius* sp., contributes more than 9%. Moreover, the Moridae family, which includes *Gadella imberbis*, *Gadella Maraldi*, *L. laureysi* and *Laemonema yarellii* as well as the Macrouridae family, which includes many species (*Bathygadus macrops*, *Coelorinchus braueri*, *Coelorinchus caelorhincus*, *Coryphaenoides* sp., *Hymenocephalus italicus*, *Malacocephalus laevis*, *Malacocephalus occidentalis*, *Malacocephalus* sp.,*Nezumia aequalis*, *Nezumia micronychodon*, *Nezumia* sp., *Trachyrincus scabrus*, *Trachyrincus* sp.) also contribute notably to the total catch on mound, with 8% and 7%, respectively.

3.2.2 Diversity between the on-mound and off-mound

A total of 349 species were identified from 94 trawls carried out in on-mound and off- mound sites. Of these species, 42% occurred in both habitats (overlapping circle), and over one third (38%) are found only on-mound (Figure 6). These results confirm the notable specific richness observed in the on-mound habitat.

3.2.3 Species accumulation curves

Species accumulation curves do not reach an asymptote, suggesting both sites are under sampled. However, the rate of species detection with increasing area sampled was faster on-mound than off-mound, thus highlighting that species richness is higher on-mound compared to off-mound habitat (Figure 7).

3.3 ROV dives data analysis

3.3.1 Presence of live CWC

Eight species of CWC were identified. These included the numerically dominant *Acanthogorgia* cf. *hirsuta* followed by *D. pertusum*, *Swiftia phaeton, Thesea talismani, M. oculata, Tanacetipathes cf.* spinescens, *Anthomastus* cf. *grandifloras* and *Clavularia borealis*. The highest concentration of living CWC was found in the far north (20°N), where *D. pertusum* predominated, and in the south, at the boundary between Mauritania and Senegal, where *D. pertusum* and *M. oculata* together formed reef structures (Figure 8).

3.3.2 Megafauna associated with CWC

The reefs offer habitat for many species. A total of 120 taxa belonging to 68 families were identified and divided into 11 groups. Fishes were diverse with 47 taxa, followed by Cnidaria (18 taxa), Crustacea (17 taxa), Mollusca and Echinodermata with 11 taxa for each group, and Porifera with 7 taxa. *H. dactylopterus* was the most observed fish species, with over 371 individuals. Cnidarians were dominated by *Synarachnactis cf. lloydii* (> 13000 individuals). While *Nematocarcinus africanus* was the most common crustacean (>900 individuals). Among mollusks, the bivalve *Gigantidas mauritanicus* was most frequent, with more than 1800 individuals. And the sponge *Cladorhiza corallophila* was prevalent among porifera (Table 6).

Overall, the reef areas supported a rich megafauna associated with the CWC coral reef. Figure 9 shows images of several common species found on the CWC reefs.

3.3.3 Heatmap analysis of species abundance across substrate types

To make a heatmap that displays the relative abundance of the 25 most abundant species across different substrate types, five species were selected from each type of substrate (Figure 10).

Species that demand more stable and substantial foundations, such as the bivalve *G. mauritanicus* and the deep-water-dwelling eel *C. cadenati*, are supported by bedrock substrates. *C. cadenati* uses rock crevices and bedrock formations as refuges. Notably, bacterial mats were frequently linked to the high abundance of *G. mauritanicus*. Species such as the fish *H. dactylopterus*, the crab *E. bella*, and the sea anemone *S. cf. lloydii* are common on coral blocks, indicating a predilection for intricate structures that provide food and refuge for these species. It is important to note that *S. cf. lloydii* was prevalent on all seven substrate types, demonstrating its broad range, habitat preference, and adaptability.

Coral rubble hosts a diverse range of species, underscoring the importance of this habitat type. The most abundant species included *S. cf. lloydii*, *A. cf. hirsuta*, and *B. piperitus*. Live coral is primarily inhabited by two CWC species, the gorgonian *A. cf. hirsuta* and the stony coral *D. pertusum*, along with *S. cf. lloydii*, which are the most dominant in this habitat. Similar species, including *A. cf. hirsuta*, *S. cf. lloydii*, and *S. phaeton*, also dominate in the combination of rubble and live coral, indicating that these species require hard substrate for survival.

The fish *H. dactylopterus*, the CWC species *D. pertusum*, and the *S. phaeton* have a slight presence in the sandy gravel substrate. Finally, sandy mud is dominated by two shrimp species, *N. africanus* and *Solenocera* sp., as well as *S. cf. lloydii*, indicating that softer, muddier substrates support a distinct species assemblage when compared to more solid or rocky settings.

3.3.4 Species-by-species correlation matrix

A correlation matrix between the 40 most frequent species is provided (Figure 11) to detect positive (in blue) and negative (in red) correlations between species in terms of occurrence (ranging from -1 to 1). A focus on the main reef building CWC *D. pertusum and M. oculata* shows that for *D. pertusum*, four species showed a strong positive correlation (0.9) with this species: *E. bella*, *P. placenta*, *Lophius* sp, and *C. borealis*. This was followed by a group of species with a correlation greater than 0.7: *A. excavata*, *M. oculata*, *P. cuvieri*, *A. cf. hirsuta*, *S. phaeton*, *H. dactylopterus*, *H. mediterraneus* and *C. corallophila*. For *M. oculata*, three species showed a strong positive correlation (greater than 0.9): *Acesta excavata*, *Lophius* sp., and *H. mediterraneus*, followed by *D. pertusum* (0.8), *P. placenta*, and *E. bella* (0.7).

3.3.5 Community patterns

The cluster analysis identified seven groups of organisms inhabiting CWC reefs, with one additional group (8) isolated from the arrangement (Figure 12).

Group 1 is characterized by the sea anemone *S.*cf. *lloydii* and two CWC species, *D. pertusum* and *S. phaeton*. The predominant substrates in this group are a mixture of different substrata (coral skeleton (37%), gravel & bedrock (28%), live coral present (19%), and Sand & mud (16%).

Group 2 shares similarities in terms of substratum with group 1 (49% of coral skeleton, 34% of sand and mud and 17% live coral present), it is also dominated by the sea anemone *S.*cf. *lloydii*, with the gorgonian *A.* cf. *hirsuta* and the sea fan *T. talismani*.Group 3 composed mainly of sand and mud (52%) with live coral present (48%), is dominated by the sea anemone *S. cf. lloydii* and crustaceans such as shrimps, *N. africanus.*

Group 4 has the highest diversity and abundance of species and features the sea anemone *S.* cf. *lloydii* and CWC species such as *A. cf. hirsuta*, *D. pertusum*, *S. phaeton*, *T. talismani*, and the crustacean *E. bella* along with the fish *H. dactylopterus*. This group is dominated by live coral substratum (60%) and coral skeleton (40%).

Group 5 is characterized by CWC species such as *A. cf. hirsuta*, *D. pertusum*, *M. oculata, T. talismani*, and the crustacean *E. bella*

TABLE 5 Species diversity and most common species in trawl catches from coral mound and off-mound environment.

Diversity index	Coral-mound	Off-mound
Number of species	282	216
Number of individuals	190415	441640
Total catch (kg)	8453	22295
Shannon-index	1.87	1.5
Simpson-index	0.72	0.64
The 30 most common species	*Helicolenus dactylopterus*	*Chlorophthalmus atlanticus*
	Laemonema laureysi	*Helicolenus dactylopterus*
	Merluccius polli	*Parapenaeus longirostris*
	Malacocephalus occidentalis	*Synagrops microlepis*
	Hoplostethus cadenati	*Pontinus kuhlii*
	Gephyroberyx darwinii	*Zenopsis conchifer*
	Todarodes sagittatus	*Merluccius polli*
	Lophius budegassa	*Merluccius senegalensis*
	Merluccius senegalensis	*Raja straeleni*
	Chaunax pictus	*Pterothrissus belloci*
	Coelorinchus coelorhincus	*Brotula barbata*
	Nezumia aequalis	*Malacocephalus occidentalis*
	Galeus polli	*Coelorinchus coelorhincus*
	Hoplostethus mediterraneus	*Scorpaena elongata*
	Malacocephalus laevis	*Illex coindetii*
	Lophius vaillanti	*Capros aper*
	Paramola cuvieri	*Gephyroberyx darwinii*
	Trigla lyra	*Hoplostethus mediterraneus*
	Galeus melastomus	*Malacocephalus laevis*
	Raja straeleni	*Todaropsis eblanae*
	Epigonus telescopus	*Scyliorhinus canicula*
	Parapenaeus longirostris	*Palinurus mauritanicus*
	Acanthocarpus brevispinus	*Monolene microstoma*
	Guentherus altivela	*Bembrops greyi*
	Chlorophthalmus atlanticus	*Trichiurus lepturus*
	Yarrella blackfordi	*Octopus vulgaris*
	Coelorhincus coelorinchus	*Myctophidae*
	Solenocera africana	*Lophius budegassa*
	Illex coindetii	*Synchiropus phaeton*
	Centrophorus granulosus	*Holothuroidae* spp.

Species are ordered based on abundance in total catch, with the most common on top.

the bivalve *A. excavata*. The substrate is primarily live coral present (100%).

Group 6 is dominated by sand and mud (76%) with 24% of coral skeleton. This group is characterized by *S. cf. lloydii*, and crustaceans inhabiting soft substrates such as *N. africanus*, *E. bella* and *B. piperitus*, the fish *H. dactylopterus and T. scabrus.*

Group 7 is characterized by shrimp's species such as *N. africanus* and *Solenocera* sp, sea anemone *S. cf. lloydii* and the sea

TABLE 6 A list of all taxa by group with the number of individuals annotated for the 11 ROV dives in the study area.

Groups	Species	Number of individuals
Cnidaria	*Synarachnactis cf. lloydii*	13780
	Acanthogorgia cf. hirsuta	3594
	Desmophyllum pertusum	1822
	Swiftia phaeton	692
	Thesea talismani	662
	Madrepora oculata	479
	Tanacetipathes cf. spinescens	397
	Desmophyllum sp	166
	Virgularia sp	66
	Hydrozoa	41
	Actiniaria	27
	Zoanthidae	26
	Epizoanthus sp	20
	Anthomastus cf. grandifloras	15
	Clavularia borealis	14
	Virgularia mirabilis	3
	Caryophyllia sp	2
	Funiculina quadrangularis	2
Crustacea	*Nematocarcinus africanus*	969
	Eumunida bella	823
	Solenocera sp	385
	Bathynectes piperitus	364
	Natantia	47
	Chaceon maritae	46
	Paromola cuvieri	34
	Paguroidea	7
	Cronius ruber	5
	Iridonida speciosa	5
	Plesionika sp	5
	Munidae	3
	Brachyura	2
	Macropodia sp	2
	Mysidae	2
	Aristeus sp	1
	Plesionika longicauda	1
Echinodermata	*Cidaris cidaris*	219
	Gracilechinus acutus	85

(Continued)

TABLE 6 Continued

Groups	Species	Number of individuals
	Peltaster placenta	22
	Echinoidea	10
	Brisingidae	6
	Asteroidea	5
	Coronaster briareus	5
	Asterias rubens	2
	Gracilechinus sp	2
	Henricia sp	1
	Holothuria arguinensis	1
Fish	*Helicolenus dactylopterus*	371
	Guentherus altivela	87
	Coloconger cadenati	84
	Trachyrincus scabrus	80
	Hoplostethus mediterraneus	59
	Nezumia sp	56
	Malacocephalus sp	43
	Merluccius polli	32
	Moridae	29
	Hoplostethus cadenati	22
	Lophius budegassa	21
	Halosaurus cf. ovenii	17
	Lophius sp	16
	Phycis blennoides	16
	Macrouridae	14
	Deania sp	11
	Synaphobranchus kaupii	10
	Trachyscorpia cristulata	8
	Galeus polli	5
	Anguilliformes	4
	Microchirus variegatus	4
	Scorpaena sp	4
	Teleostei	4
	Dalatias licha	3
	Deania calceus	3
	Gaidropsarus mauritanicus	3
	Merluccius sp	3
	Soleidae	3
	Centrophorus granulosus	2

(Continued)

TABLE 6 Continued

Groups	Species	Number of individuals
	Conger conger	2
	Galeus atlanticus	2
	Hoplostethus sp	2
	Muraena sp	2
	Myctophidae	2
	Raja sp	2
	Symphurus sp	2
	Centrophorus sp	1
	Chlorophthalmus agassizi	1
	Coloconger sp	1
	Coryphaenoides cf. rupestris	1
	Dibranchus atlanticus	1
	Gephyroberyx darwinii	1
	Leucoraja leucosticta	1
	Ophidiidae	1
	Oxynotus paradoxus	1
	Trachyscorpia echinata	1
	Triglidae	1
Mollusca	*Gigantidas mauritanicus*	1845
	Acesta excavata	379
	Gastropoda	24
	Xenophora sp	9
	Loligo vulgaris	5
	Sceptrulophora	4
	Prosobranchia	3
	Eledone cirrhosa	2
	Octopus vulgaris	2
	Polyplacophora	1
	Sepiola rossiaeformis	1
Polychaeta	*Sabellidae*	99
	Bonellia sp	12
	Polychaeta	6
	Eunice norvegica	1
	Terebellidae	1
Porifera	*Porifera*	576
	Cladorhiza corallophila	220
	Aphrocallistes sp	32
	Mellonympha mortenseni	17
	Asconema sp	15
	Polymastiidae	13
	Porifera encrusting	1
Foraminifera	*Pelosina arborescens*	168
Bryozoa	*Reteporella*	8
Chordata	*Ascidiacea*	62
Bacteria	Bacterial mats	27

pen *Virgularia* sp, which dominate this soft substrate community. This group is dominated by sand and mud (100%), (Table 7).

The DCA analysis considered seven environmental variables, including substrate types, rugosity levels, depth, and site (north and south). The DCA graph illustrates species distribution patterns in relation to key environmental gradients (Figure 13).

Axis 1 of the DCA shows a clear substrate gradient, with living coral habitats on the left and soft substrate habitats (sand and mud) on the right. Axis 2 appears to have a lesser association with depth. These major environmental variables, denoted by black arrows, shed light on how environmental gradients influence different species compositions, as seen in the spatial clustering of species groups. The groups on the left side of the plot are substantially influenced by live corals, implying that these species benefit from the structural complexity of coral ecosystems. In contrast, species groups on the right side of the plot are mostly influenced by sand and mud, showing a preference for places dominated by soft sediments.

The DCA indicated that the depth environmental gradient may exert a weaker influence on species distribution compared to other variables. The DCA analysis did not show any patterns for the other environmental variables, such as rugosity and site.

Species in groups 1, 4 and 5, are all associated with the presence of live coral. Group 1 is strongly associated with live coral presence, while group 4 lies between the live coral presence and depth gradient, suggesting that transitional species benefit from coral habitats and are tolerant of deeper conditions. Although Group 5 is not directly overlapping with the live coral presence cluster, its special placement and species composition indicate that live coral may still play a role in shaping its distribution. In terms of common species in different groups, it is worth noting that *S.* cf. *lloydii* was abundant across the seven substrate types, indicating a broad distribution. Common species in these groups (Groups 1, 4, and 5) include several coral species such as *D. pertusum, M. oculata*, *A.* cf. *hirsuta*, *S. phaeton*, *T. talismani, the* crustacean *E. bella*, and the fish *H. dactylopterus*, suggesting a preference for complex structures provided by coral habitat that offer shelter and food for these species.

The sandy mud arrow points aligns with Group 3, 6 and 7, indicating an influence on species distribution. Group 6 shows the strongest association with this substrate, suggesting a preference for

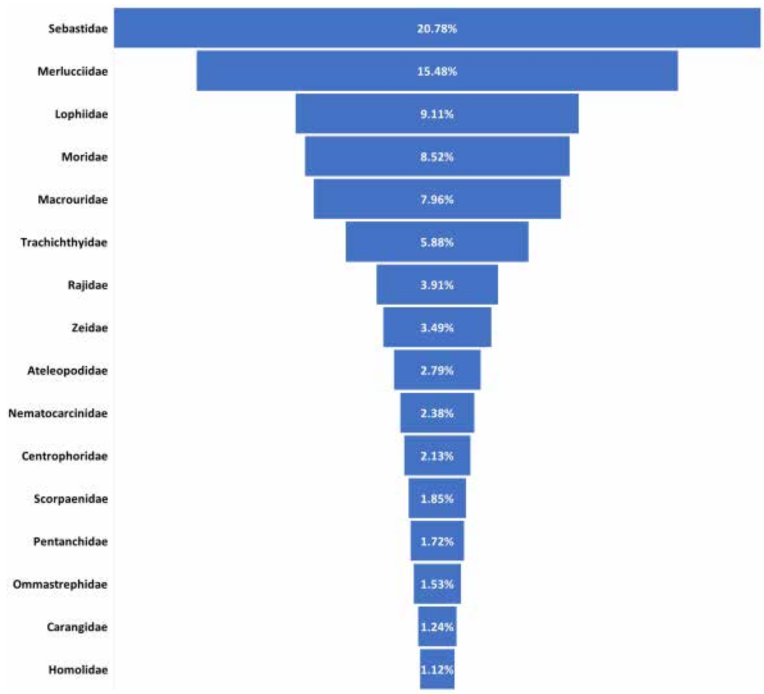

FIGURE 5
The sixty families of species that contribute significantly to the total catch on the mound.

soft sediments. Although Group 3 is situated near live coral, slightly away from the live coral presence gradient, this Groupe includes species that are commonly associated with the structural complexity provided by live coral. Their presence in areas where coral declines and transition into sandy mud suggests a degree of tolerance to soft sediments.

Group 7 is located close to the depth gradient but shows some affinity for sandy mud substrates. Its species distributions suggested a potential influence for both depth and soft sediment. These groups (2,3 and 7) are dominated by species typically found on soft substrates, such as shrimp species, *N. africanus* and *Solenocera* sp., and sea pen *Virgularia* sp., and the fish *T. scabrus*.

Group 2 is located in the central part of the DCA, close to the transition zone between different habitats. It aligns moderately with the depth gradient. This position suggests that species of this group tolerate deeper conditions compared to live coral groups (e.g.,

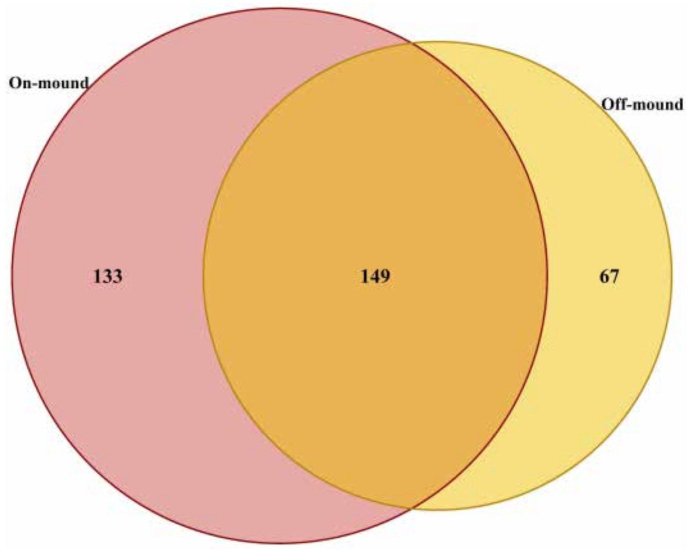

FIGURE 6
Venn diagram illustrates the number of shared and unique species between on- and off-mound areas.

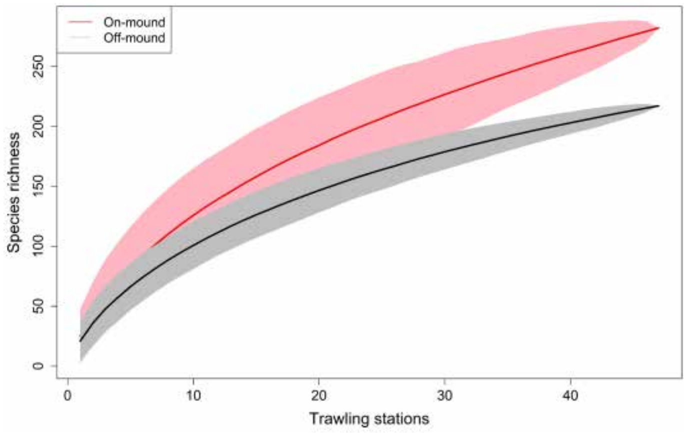

FIGURE 7
Species accumulation curves considering species richness per trawling stations: on-mound in pink and off-mound in gray.

Group 1), although they are not strict deep-water specialists. The two dominant species of this group are *S. cf. lloydii* and *N. africanus*.

One subsample (8) does not belong to a group and constitutes a single outlier sample. It contains very fewer species and doesn't represent a specific affinity.

Overall, the DCA highlights that the two substrate types (live coral presence and sand and mud) appear to be the most important drivers of species distribution, while the depth gradient exerts a weaker influence on species distribution compared to other variables. The absence of some other environmental variables (e.g., site) from the DCA results may indicate that the site variable (north and south) does not influence the distribution of species groups, suggesting that the two reefs zone show similarities in their species communities. This is supported by the fact that the northern reef video samples (A6) are mixed with the southern samples (T2B and T3B) in the cluster dendrograms (Figure 12).

The correlation matrix for the environmental variables (Table 8) shows that live coral is positively related to rugosity (0.60) and negatively related to sand & mud (-0.47). The strong correlation between live coral and rugosity may explain why the

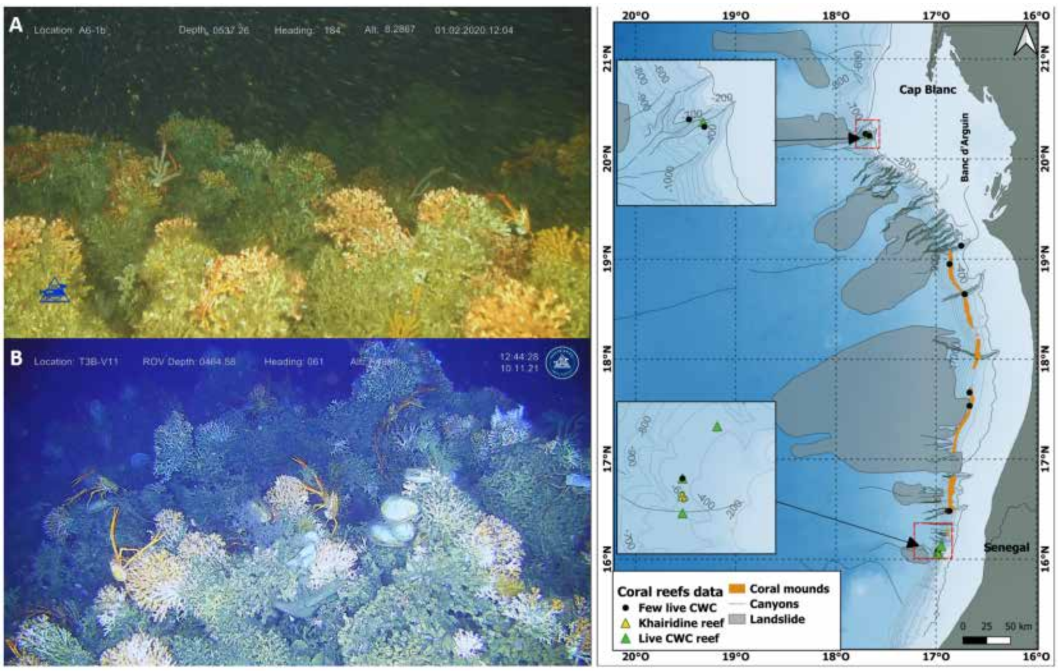

FIGURE 8
Map showing the presence of live CWC along the Mauritanian margin at the two CWC reef areas: **(A)** Northern reefs are constituted mainly by *D. pertusum* and, **(B)** southern reefs, which are constructed by *D. pertusum* and, to a lesser degree, by *M. oculata*, the bivalve *Acesta excavata* and the squat lobster *Eumunida bella* were abundant among the reef community, where they find food and shelter. Between the two reefs, few living corals are indicated (black dots) according to Westphal et al., 2014.

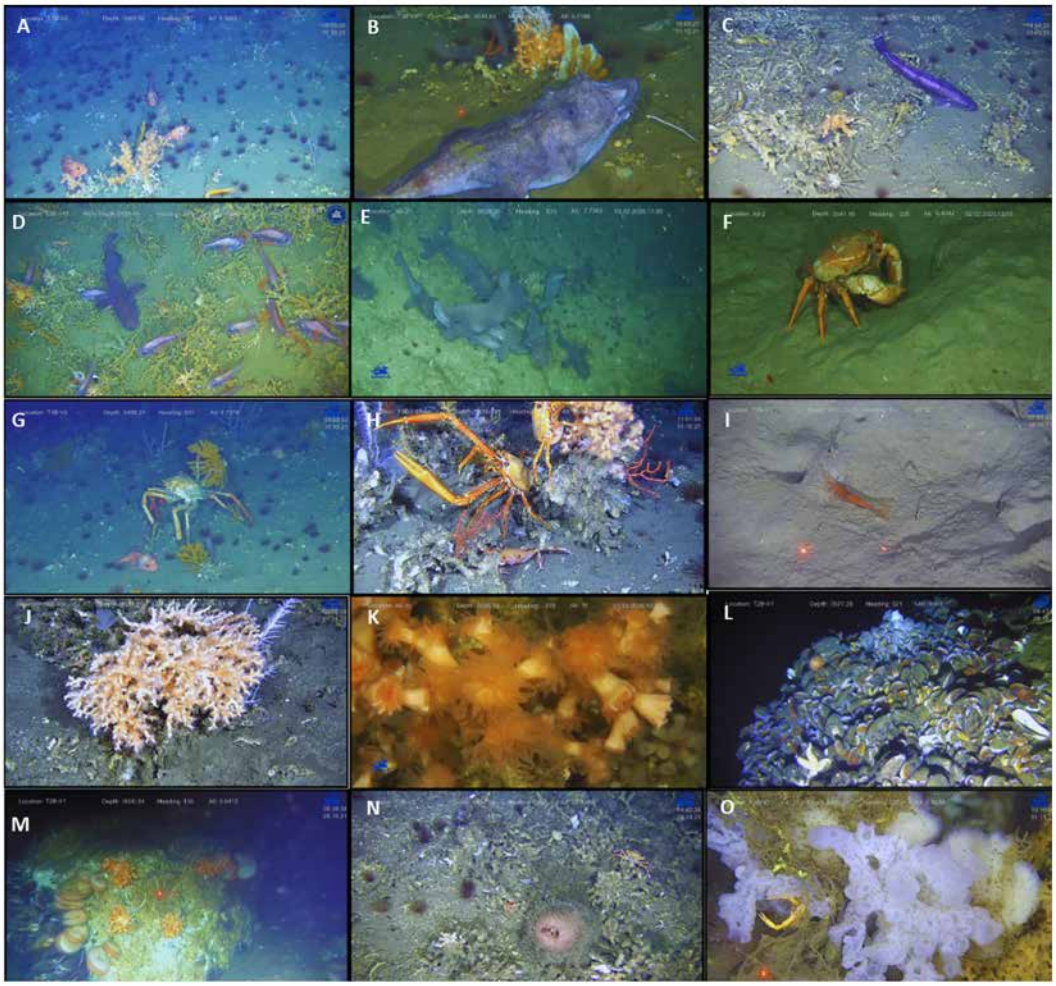

FIGURE 9
Representative ROV images of common species in the CWC reefs off Mauritania across the different taxonomic groups. **(A)** three specimens of *H. dactylopterus* with live *D. pertusum* in high densities of *S. lloydii*. **(B)** *L. budegassa* with live *D. pertusum*, *T. spinescens*, *S. phaeton, A. hirsuta, C. corallophila* and unidentified sponge. **(C)** *M. polli* and *C. cidaris* with mainly dead corals. **(D)** several individuals of the Mediterranean slimehead *H. mediterraneus*. **(E)** a school of jellynose fish (*G. altivela*) at the edge of the reef; this species is red-listed by the (IUCN). **(F)** a large West African geryon *C. maritae* resting in sandy mud sediment. **(G)** the large crab *P. cuvieri*. **(H)** tow specimens of the spring crab *E. bella* with *B. piperitus*. **(I)** the African spider shrimp *N. africanus*. **(J)** *M. oculata*. **(K)** a close-up of *D. pertusum* polyps. **(L)** intense presence of the bivalve *G. mauritanicus*, on top of bacteria mats with evidence of methane seep. **(M)** *A. excavata* attached to hard substrata with *D. pertusum*. **(N)** the sponge *M. mortenseni*. **(O)** the sponge *Aphrocallistes* sp.

rugosity was excluded from the DCA as a key environmental variable. Skeleton is positively related to live coral (0.33) and negatively related to sand and mud (-0.44), which is positively related to depth (0.25).

4 Discussion

4.1 Methodology

To compare coral mound megafauna with areas without mounds, we used data from trawls with a mesh size ranging from 20 to 45 mm, depending on the vessels, which cannot provide representative samples of smaller taxa (< 2 cm). This limitation was evident in the low representation of certain taxa within Cnidaria and Echinodermata, and the diversity of the communities was underestimated. We compared the mound community occurring at 400 to 600 meters depth with off-mound communities at 200 to 350 meters. Thus, in addition to the differences in the presence of coral mounds, they also differed in depth-related environmental settings (e.g.; temperature, salinity, and dissolved oxygen). In the study area, the difference in oceanographic settings within the depth zone covered is not pronounced, which makes the presence of coral mounds with their effect on terrain, substratum, currents, etc., the main driver behind the observed faunal differences.

The megafauna associated with CWC reefs were studied using 11 ROV video transects, covering approximately, 6800 m^2. Three transects were from the northern parts of the region and eight from the south. That is a few and disparate transects. The statistical analysis showed that the rich megafauna associated with the

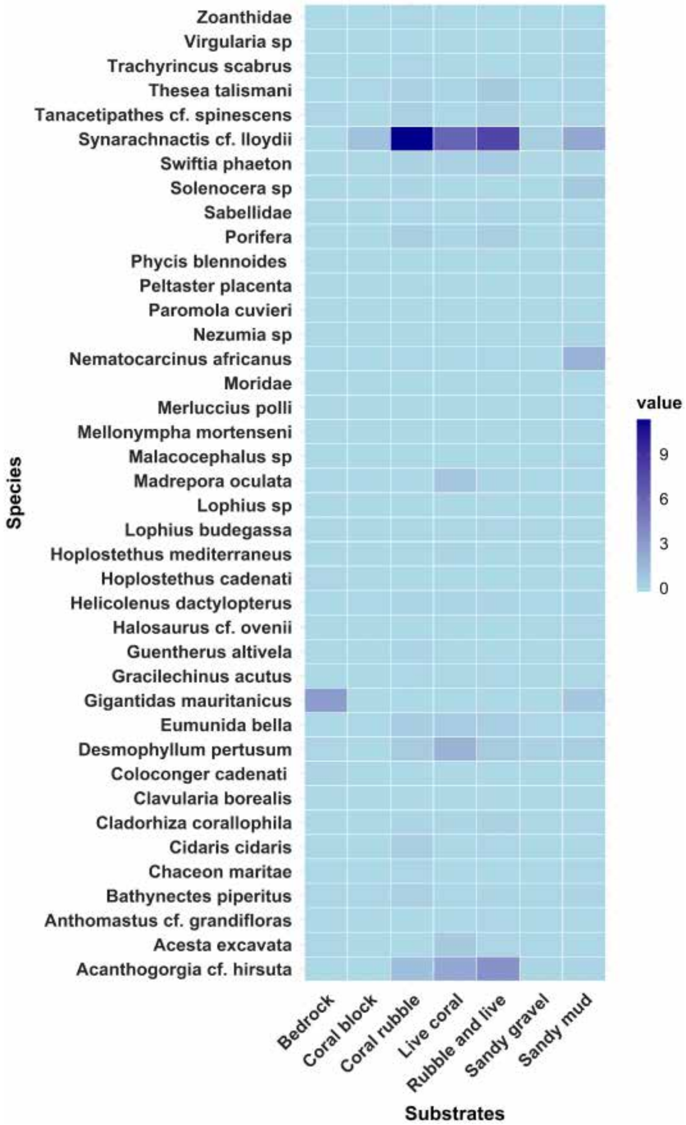

FIGURE 10
The heatmap shows species abundance across different substrates, the blue color gradients in this heatmap visually show the various levels of species abundance in relation to the seven substrates with dark blue indicating a high presence of the species on each substrate.

Mauritanian coral reefs is not different for reefs in the north and south. Even though the material is limited to 11 reef sites, the length of each transect ensures that the megafauna is well documented, and in addition, the present study is based on more ROV transects compared to the two previous studies of coral fauna in the region (Colman et al., 2005; Westphal et al., 2014).

4.2 Oceanography

Our results show the presence of two prominent oxygen minimum zones (OMZs): a shallower one at around 100 meters and a deeper, more pronounced one, near 400 meters. The deeper minimum zone coincides with the depth zone (400–650 m) in which coral mounds and CWC reefs occur in Mauritanian waters. In the depth zone of the CWC reefs, the recorded temperature ranged from 8.66 to 11.56°C, measured salinities ranged from 35.09 to 35.38 PSU, and oxygen concentration was from 1.17 to 1.53 ml L^{-1}. This is in line with other studies of CWC mound off Mauritania; Ramos et al., 2017; Westphal et al., 2014). On the West African continental margin, cold water coral mounds, typically having only coral skeletons or a few living colonies, have been reported from areas with low oxygen concentrations (<1.5 mL L^{-1}) off Angola and Namibia (Hanz et al., 2019; Le Guilloux et al., 2009).

Our study shows that a rich megafauna is associated with CWC mounds and reefs in the OMZ that clearly can tolerate the low oxygen concentrations. Recently, other studies have discovered live and healthy reefs at oxygen concentrations between 1.0 and 1.2 ml L^{-1} (Buhl-Mortensen et al., 2024) concluding that low oxygen concentrations are not hindering the growth of CWC reefs. The first alive and large CWC reef off Ghana was recorded from within

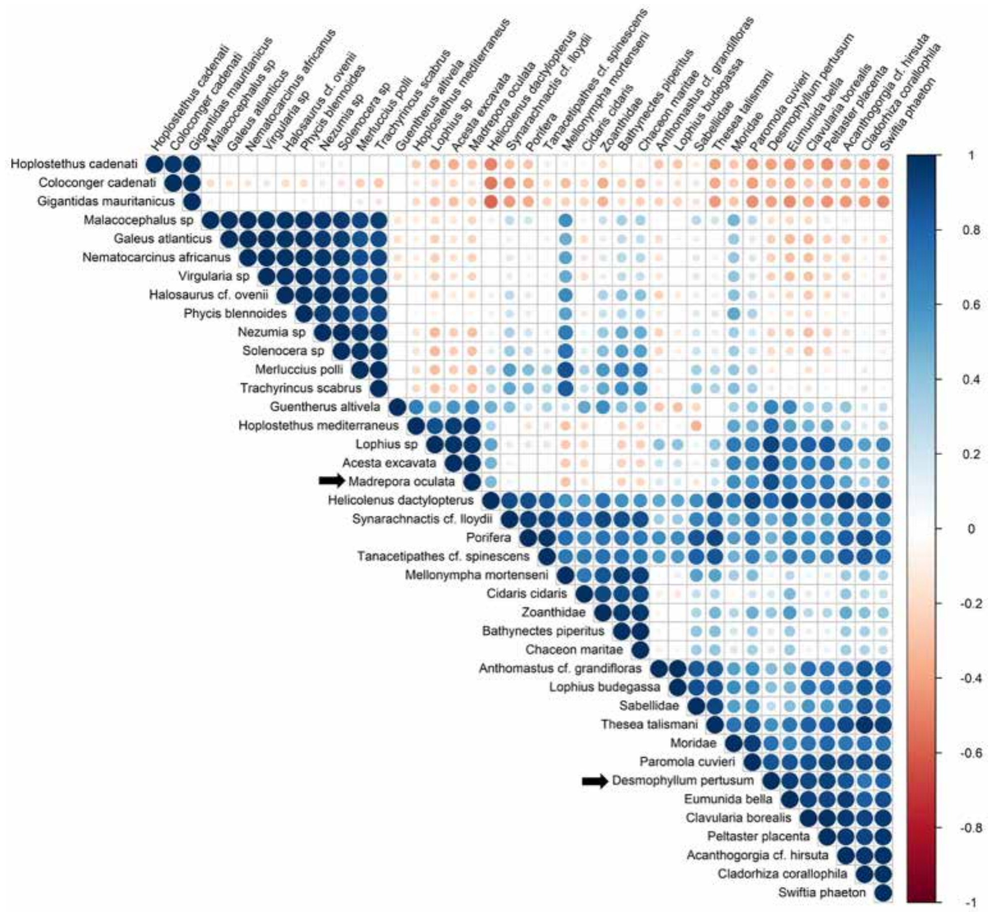

FIGURE 11
The correlation matrix of the different species associated with CWC. The legend color shows the correlation gradient from -1 (negative correlations) to 1 (positive correlations). The size of the circles and color intensity are proportional to the correlation coefficients. The main CWC species, *D. pertusum* and M. oculata are indicated by the black arrow.

the OMZ zone (Buhl-Mortensen et al., 2017), and live reefs from the Angola have been reported from the OMZ there (Hanz et al., 2019). Recently, healthy reefs were recorded in OMZ at the border between Mauritania and Senegal (Moctar et al., 2024). Our study shows that a rich megafauna is associated with CWC mounds and reefs in the OMZ that clearly also can tolerate low oxygen concentrations. Hebbeln et al. (2020) speculate that CWC thrive under these extreme conditions because they have developed certain adaptive metabolic strategies and that the negative effects of hypoxia could be compensated by the availability of enhanced food supply. On the other hand, Portilho-Ramos et al. (2022) demonstrated that low oxygen concentrations in deep waters can act as an additional stressor, while the food supply exerts the strongest effect on coral vitality.

4.3 Megafauna associated with CWC habitats

In this study, we use data from demersal trawling surveys to describe the species diversity related to coral mounds off Mauritania; this has not been done earlier in the region. Ramos et al. (2017) described the fauna colonizing coral mounds based on dredged material (13 rock dredge samplings), which cannot be compared directly with our observations due to the difference in methodology.

Diversity, as indicated by species richness, Shannon and Simpson indexes, and species accumulation curves, shows a richer community on the CWC mounds compared to the off-mound zone, and our results show a high-diversity community inhabiting coral mound including 282 taxa. The fish fauna on the coral mounds was dominated by the blackbelly rosefish *H. dactylopterus*, a species that is known to thrive in CWC habitats, and both juveniles and adults are frequently observed in CWC habitats in Northwest Africa (El Vadhel et al., 2024). Our observation confirms this relation to CWC, and other abundant fish species on the mound were *L. laureysi*, *M. polli*, *C. caelorhincus*, *H. cadenati*, *M. occidentalis*, *G. darwinii* and *H. mediterraneu*, of which several are known to be associated with CWC reefs (e.g., Capezzuto et al., 2018; Costello et al., 2005; Milligan et al., 2016).

In contrast to diversity, the biomass (total catch) and abundance (number of individuals) were twice as high in the off-mound zone compared to the mounds. The lower values obtained on-mound could be related to the coral mound structure acting as

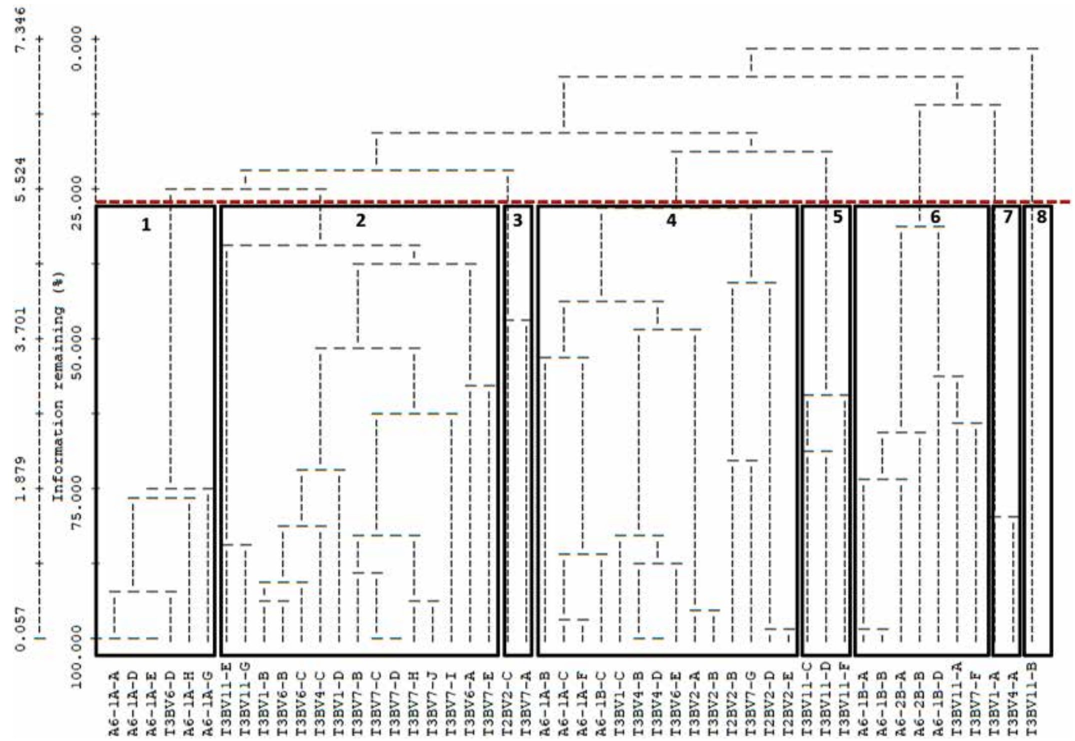

FIGURE 12
A dendrogram generated from hierarchical clustering based on species composition illustrates the similarities between samples, with eight primary community groups highlighted in different colors at a ~ 28% similarity levels.

an obstacle that negatively affects the catch efficiency of the fishing gear. Another reason could be that in the non-coral zone, the species have gregarious behavior, which facilitates their capture by trawling in significant quantities.

The ROV transects documented that the CWC reefs had a rich associated megafauna of 120 taxa, belonging to 11 fauna groups. The most abundant species on the reef by group were: fish (*H. dactylopterus*, *G. altivela*, *C. cadenati*, *T. scabrus*, *H. mediterraneus*, *Nezumia* sp, *Malacocephalus* sp, *M. polli*, *Moridae*, *H. cadenati*, and *L. budegassa*), Cnidaria (*S. cf. lloydii*, *A. cf. hirsuta*, *D. pertusum*, *S. phaeton*, *T. talismani*, *M. oculata* and *T. cf.* spinescens), Crustacea (*N. africanus*, *E. bella*, *Solenocera* sp, *B. piperitus* and *C. maritae*), Mollusca, (*G. mauritanicus* and *A. excavata*), Echinodermata (*C. cidaris*, *G. acutus*), and Porifera (*C. corallophila*, *Aphrocallistes* sp, and *M. mortenseni*).

In comparison, Westphal et al. (2014) reported from the same region a total of 39 taxa belonging to 7 fauna groups (Fish (16), Crustacea (9), Cnidaria (6), Mollusca (5), Polychaeta, Echinodermata and Annelida were represented by 1 taxon each). More than 22 taxa (56%) from this study were also documented in the present study. The most common fishes documented by Westphal et al. (2014) (*T. scabrus*, *Hoplostethus* sp., *H. dactylopterus*, *L. budegassa*) were also common in our study. And a highlight observation was an aggregation of the *G. altivela*, the gregarious behavior of this species near CWC was observed also in the present study. Some other species reported by Westphal et al. (2014) that were also common in our study include the crustaceans (*P. cuvieri*, *B. piperitus*, *E. bella*, *C. maritae*), mollusks (*A. excavata*).

Westphal et al. (2014) recorded several coral species off Mauritania, mainly *D. pertusum* and *M. oculata*, *Dendrophyllia cornigera* and *Acanthogorgia* sp., of these, *D. cornigera* was not observed in this study, however, we recorded in addition the corals; *S. phaeton*, *T. talismani*, *T.* cf. *spinescens*, *A.* cf. *grandifloras* and *C. borealis*.

Many of the recorded species are known to be associated with CWCs from other studies (e.g., Buhl-Mortensen et al., 2017; Costello et al., 2005; Henry and Roberts, 2017). It is interesting that even when the studied reefs are in an oxygen minimum zone, they still host many of the same associates.

Our study has documented species that are new to the region from CWC reefs; an example is *Cladorhiza corallophila*, a carnivorous sponge species that was described by Göcke et al. (2016). This sponge was common in association with *D. pertusa* and *M. oculata* in our study. The octocoral Swiftia (*Swiftia phaeton*) was described by Sampaio et al. (2022) from the upper bathyal off Mauritania. This species was in the present study very common and the fourth most recorded species. Finally, specimens of a new fish of Gadiformes (*Gaidropsarus mauritanicus*) that was discovered by Knorrn et al. (2024) were recorded three times in our study (Figure 14).

Our results reveal that both CWC mounds and reefs share several common species, despite the use of different sampling methods. These species, such as the fish *H. dactylopterus*, *M. polli*, *H. cadenati*, *G. darwinii*, *L. budegassa*, *H. mediterraneus*, and *G. altivela*, as well as the

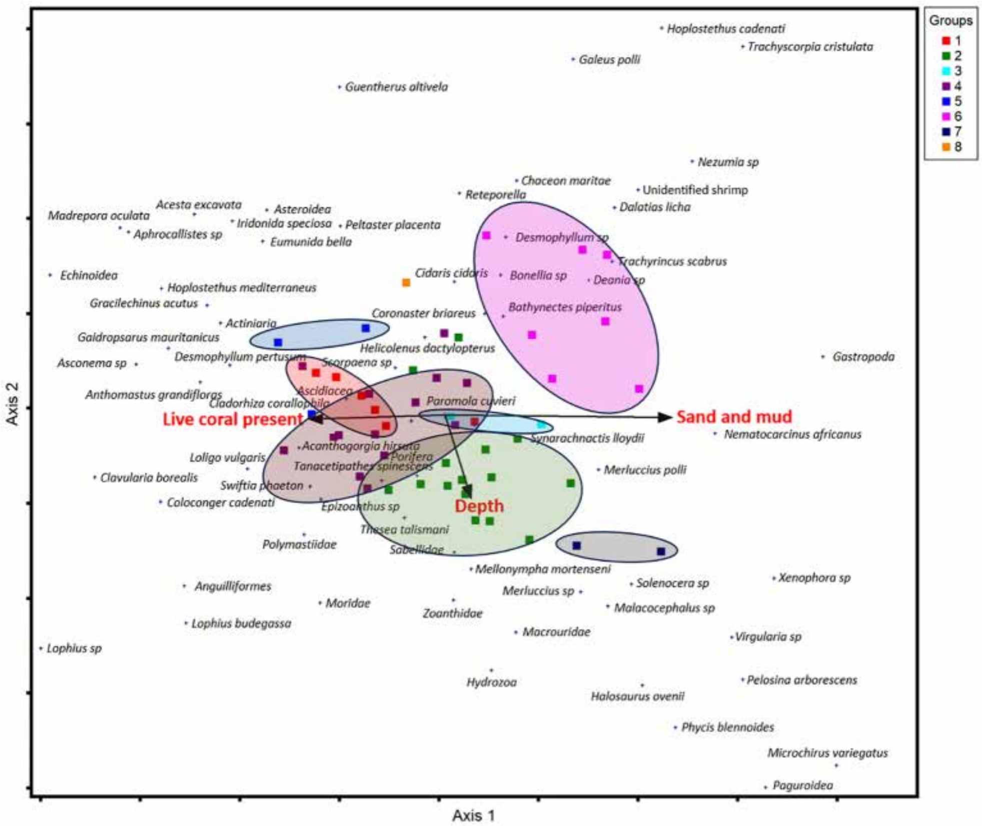

FIGURE 13
DCA ordination results for both axes (1 and 2), displaying the species community groups (1 to 7) colored according to the cluster results (Figure 12). The black line indicates the main environmental variables (live coral present, sandy mud and depth) related to the community composition.

FIGURE 14
ROV images showing the 3 species new to science recently discovered in the deep sea off Mauritania: **(A)** *C. corallophila* associated with *D. pertusum* and the fish *T. scabrus*, **(B)** *S. phaeton*, **(C)** *G. mauritanicus* with *A. cf. hirsuta*.

crustaceans *P. cuvieri* and *S. africana* occurred in both habitats. This overlap in species composition suggests that CWC mounds and reefs are ecologically linked and could act as a continuous essential habitat for some of the associated megafauna they have in common.

The megafauna associated with CWC is found in different sub habitats, including the coral related sub habitats (live coral, coral rubble, rubble and live), soft substrate (sandy mud) and hard substrate (bedrock, coral blocks, sandy gravel). Our results highlight the importance of coral substrates (coral rubble, rubble and live) for diversity. Indeed, more than 56% of the megafauna associated with CWC have been reported in this substrate. These results agree with Mortensen et al. (1995) and Wolfe et al. (2021), who found that the coral associated fauna is more abundant in the older and dead areas than in the live parts

TABLE 7 The main features of the seven groups include 10 common species, the number of species, individuals, the average of species and individuals by subsamples, the number of subsamples, and substrate types (%).

Species groups	1	2	3	4	5	6	7
Number of subsamples	6	15	2	14	3	7	2
Number of species	27	50	19	71	40	49	34
Min of species	9	11	11	14	22	10	23
Max of species	14	23	15	31	26	22	25
Average of species	12	17	13	22.5	24	16	24
Number of individuals	1737	6844	993	19465	4092	4040	1349
Min of individuals	161	232	366	513	972	235	544
Max of individuals	425	697	627	2904	1538	1601	805
Average of individuals	293	465	497	1709	1255	918	675
10 most common taxa	*S. cf. lloydii*	*S. cf. lloydii*	*S. cf. lloydii*	*S. cf. lloydii*	*A. cf. hirsuta*	*S. cf. lloydii*	*N. africanus*
	D. pertusum	*A. cf. hirsuta*	*N. africanus*	*A. cf. hirsuta*	*E. bella*	*N. africanus*	*S. cf. lloydii*
	S.phaeton	*T. talismani*	*A. cf. hirsuta*	*D. pertusum*	*D. pertusum*	*H. dactylopterus*	*Solenocera* sp
	A. cf. hirsuta	*S.phaeton*	*T. cf. spinescens*	*S. phaeton*	*M. oculata*	*T. scabrus*	*Virgularia* sp
	E. bella	*Porifera*	*C. cidaris*	*H. dactylopterus*	*T. talismani*	*E. bella*	*T. talismani*
	B. piperitus	*T. cf. spinescens*	*B. piperitus*	*E. bella*	*A. excavata*	*B. piperitus*	*P. arborescens*
	H. dactylopterus	*B. piperitus*	*D. pertusum*	*T. talismani*	*S. phaeton*	*Nezumia* sp	*Malacocephalus* sp
	T. talismani	*Solenocera* sp	*Malacocephalus* sp	*B. piperitus*	*G. acutus*	*D. pertusum*	*B. piperitus*
	C. corallophila	*D. pertusum*	*Solenocera* sp	*T. cf. spinescens*	*H. dactylopterus*	*Virgularia* sp	*Porifera*
	Porifera	*N. africanus*	*Desmophyllum* sp	*Porifera*	*C. corallophila*	*Gastropoda*	*H. dactylopterus*
Live coral present	19%	16%	48%	60%	100%	0%	0%
Coral skeleton	37%	50%	0%	40%	0%	25%	0%
Gravel & bedrock	28%	0%	0%	0%	0%	0%	0%
Sand & mud	16%	34%	52%	0%	0%	75%	100%

TABLE 8 Correlation table for environmental variables with the Pearson correlation coefficient.

	Coral skeleton	Gravel & bedrock	Live coral present	Sand & mud	Depth	Rugosity
Coral skeleton	1					
Gravel & bedrock	-0.16	1				
Live coral present	0.33	-0.13	1			
Sand & mud	-0.44	-0.15	-0.47	1		
Depth	0.07	0.1	-0.13	0.25	1	
Rugosity	0.08	-0.2	0.6	-0.63	-0.48	1

of actively growing reefs, where coral rubble creates complex microhabitats supporting diverse reef organisms.

The heatmap analysis of species abundance across the different substrate types, as well as the species-by-species correlation matrix, further reinforces the importance of habitat heterogeneity in structuring benthic communities on the CWC reefs off Mauritania. Species such as the fish *H. dactylopterus*, the crab *E. bella* and the bivalve *A. excavata* exhibited a strong preference for coral blocks and live corals, suggesting that these structures provide critical habitat complexity and refuge for these species (Buhl-

Mortensen et al., 2010). Our results further showed the functional importance of the frameworks of the two corals, *D. pertusum* and *M. oculata*, in sustaining a range of faunal assemblages. The species-by-species correlation matrix showed strong correlations between these important reef-building corals and the megafauna that they are linked with. Overall, these findings emphasize the critical role of various substrate types in supporting a wide range of species, emphasizing the importance of preserving diverse substrate types in order to maintain biodiversity and ecosystem function.

According to the diversity-by-family analysis, the majority of total catches (61%) on coral mounds are found in the families Sebastidae, Merlucciidae, Lophiidae, Moridae, and Macrouridae, which include many commercially important species like *M. polli*, *M. senegalensis*, *L. budegassa*, *L. vaillanti*, *H. dactylopterus*, and others. This is in line with the findings of Fernandez-Peralta and Gonzalez (2017), who examined the demersal ichthyofaunal assemblages in Mauritanian deep waters (80 to 1860 m) and discovered that Sebastidae and Merlucciidae are among the main demersal fish families in biomasses, contributing significantly to the total catch with over 25%.

The detrended correspondence analysis (DCA) revealed that the main factors influencing species distribution in CWC reefs are the presence of live coral colonies and sandy mud substrate. The DCA highlighted the importance of habitat complexity provided by live corals in shaping species composition; this is aligning with (Buhl-Mortensen et al., 2010), who emphasized how species diversity is impacted by coral structure. This finding is further supported by De Haast et al. (2024), who highlighted that the live coral substratum has an impact on taxa assemblages and is the most important factor in determining species distributions, further supporting this finding.

Our study generally revealed a rich and diverse megafauna inhabiting the two CWC ecosystems off Mauritania: the chain of mounds and the live reefs. These valuable and vulnerable habitats are facing various challenges, including deep-sea trawling and hydrocarbon exploitation, in addition to the impacts of climate change. The southern reefs, located on the border between Mauritania and Senegal (Moctar et al., 2024), support a remarkable biodiversity, including a significant presence of live *D. pertusum* in an area of gas resource development and exploitation. This situation requires special attention to protect this rich and vulnerable habitat.

5 Conclusion

This study provides, for the first time, a comprehensive description of the megafauna associated with cold-water coral (CWC) reefs and mounds off Mauritania. The data used include demersal trawling surveys conducted over four decades on board research vessels in the Mauritanian deep sea, as well as ROV video dives conducted as part of two seafloor habitat mapping surveys in 2020 and 2021. Our study documented a rich diversity of species associated with these CWC ecosystems. The megafauna inhabiting coral mounds consists of 282 taxa from five species groups, dominated by fishes. This megafauna is more diverse compared to the off-mound area. The CWC reefs provide habitat for many species (120 taxa) divided into 11 groups, including certain species recently discovered in the deep sea off Mauritania, such as *Cladorhiza corallophila*, *Swiftia phaeton*, and *Gaidropsarus mauritanicus*, which are relatively new to science.

The most notable observation is that the two CWC ecosystems thrive in the extreme environmental condition of the oxygen minimum zone, yet they still offer habitat for several taxa, many of which are globally associated with CWC ecosystems in other regions. Characteristic species of CWC habitats include the corals *Acanthogorgia cf. hirsuta*, *Desmophyllum pertusum*, *Swiftia phaeton*, *Thesea talismani*, *Madrepora oculata*, *Tanacetipathes cf. spinescens*, the sea anemone *Synarachnactis cf. lloydii*, the fish *Helicolenus dactylopterus*, *Laemonema laureysi*, *Merluccius polli*, *Hoplostethus cadenati*, *Trachyrincus scabrus*, *Hoplostethus mediterraneus* and *Gephyroberyx darwinii*, the crustaceans *Nematocarcinus africanus*, *Eumunida bella*, *Bathynectes piperitus*, the echinoderm *Cidaris cidaris*, the mollusks *Gigantidas mauritanicus* and *Acesta excavata* and the poriferan *Cladorhiza corallophila*.

Our findings underscore the ecological significance of CWC habitats off Mauritania and offer essential insights for developing a national marine resource management plan. Given rising anthropogenic pressures such as oil and gas exploration, deep-sea fishing, and climate change, these ecosystems require urgent conservation efforts.

Author's note

The views expressed in this publication are those of the author(s) and do not necessarily reflect the views or policies of the Food and Agriculture Organization of the United Nations and the Institute of Marine Research.

Data availability statement

The data underlying our findings are available upon request to FAO and the Mauritanian Institute of Oceanographic Research and Fisheries (IMROP).

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because the study is based on existing datasets.

Author contributions

HE: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. LB-M: Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing. MM: Data curation, Formal analysis, Methodology, Writing – review & editing. YE: Data curation, Formal analysis, Methodology, Writing – review & editing. BM: Conceptualization, Writing – review & editing. FL: Supervision, Writing – review & editing. LM:

Conceptualization, Formal analysis, Methodology, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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