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Marine habitat mapping of the deep seabed between Madeira and the Desertas Islands

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Abstract

Benthic habitat mapping is essential for improving our understanding and management of the deep sea. Imaging systems play a crucial role in obtaining data of this remote environment, allowing for better analysis and comprehension. During the cruise MSM126 “Jellyweb Madeira”, four dives were conducted to survey the deeper zone of the ridge between Madeira and the Desertas Islands, using a remotely operated vehicle (ROV) and an ocean floor observation system (XOFOS) to describe and identify the macrofaunal benthic organisms and assess the occurrence of benthic habitats of conservation concern. Through the annotation of morphotypes and the application of non-parametric multivariate analysis techniques, ten distinct habitats were identified: four were categorized as “coral gardens”, four as “deep-sea sponge aggregations”, and one was characterized by the presence of both corals and sponges. Additionally, one habitat was noted for its potential significance to biodiversity. The classification of these habitats as Vulnerable Marine Ecosystems (VMEs) was conducted based on criteria established by organizations such as FAO, OSPAR and ICES. Furthermore, the effects of environmental variables on site composition were investigated, with depth identified as the primary driver. Further analysis didn’t find a correlation between habitat presence and mobile fauna. Observed signs of human impact on the seafloor highlight the need to protect these habitats. We discovered a diverse deep benthic fauna on the deep seabed between Madeira and the Desertas Islands, including VME indicators, at previously unstudied depths in this area.

Introduction

Vulnerable habitats under the sea

Oceans cover more than 70% of the Earth's surface and have an indispensable role for the health of the planet and the survival of its inhabitants, including our own species. The deep sea, defined as the waters and seafloor below 200 m, forms the largest existing ecosystem, covering 90% of the total ocean (Gage & Tyler, 1991; Klemmer & Rolf, 2024; Thurber et al., 2014). Fisheries, metal extraction, tourism and energy production are partially sustained by the deep sea, contributing to economy and society development (Mayer et al., 2018; Mejjad & Rovere, 2021). The deep sea performs numerous critical functions, including absorbing and storing carbon emissions from human activities, which helps mitigate climate change (Sabine et al., 2004). These functions are examples of ecosystem services, a rapidly growing field which is progressively revealing the environment's immense potential and economic value. The deep sea is crucial for sustaining life on Earth, but it is increasingly facing severe threats. Marine pollution, with 6.4 million tons of litter entering the ocean yearly, accumulates in the waters and on the deep seabed (Mejjad & Rovere, 2021; UNEP, 2009) and increasing ocean acidification endangers marine life, disrupts the food web, alters the distribution of marine species and threatens the vital services provided by the oceans (Hogg et al., 2016; Thurber et al., 2014).

The deep seabed is home to benthic communities, which can form three-dimensional structures that shape the surrounding environment by affecting hydrodynamic regimes, organic matter distribution, and sediment resuspension, contributing to the formation of biogenic habitats (Beaumont et al., 2007). By providing hard substrates, food sources, and protection from predators, these habitats create favorable conditions for various deep-sea organisms (Beaumont et al., 2007). They foster biodiversity and can serve as nurseries and feeding grounds for commercially targeted fish (Beaumont et al., 2007; Costello et al., 2005; Husebø et al., 2002; Thurber et al., 2014). The organisms that form these habitats are often "ecosystem engineers", being capable of modifying the surrounding environment, modulating directly or indirectly the availability of resources used by other organisms (Jones et al., 1994). Biogenic habitats are important to various organisms and thus cover a crucial role as biodiversity hotspot, paramount for the ocean functioning (Gray, 1997; Henry & Roberts, 2007; Des Roches et al., 2018; Van Oevelen et al., 2009). Other than increasing biodiversity, they are renowned for the provision of many other ecosystem services, such as carbon sequestration and nutrient cycling (Beaumont et al., 2007; Cathalot et al., 2015; Coppari et al., 2016; Grehan et al., 2003; Soetaert et al., 2016). Sponge aggregations represent one of the most known types of biogenic habitats in the deep sea. Sponges play a crucial role in biogeochemical processes, particularly in benthopelagic coupling, by facilitating the flow of matter and energy between the two domains. Their activities, such as excretion, recycling, and the provisioning of nutrients, are fundamental to the ocean's functioning (Cathalot et al., 2015; Coppari et al., 2016). In cold (4-14 °C) and deep parts of the oceans, some particular types of benthic communities are present; they are referred to as the cold water coral (CWC) reefs: unlike the reefs found in the photic zone, they don't exhibit symbiosis with microalgae and feed exclusively by heterotrophy (Mullineaux & Mills, 2005; Roberts et al., 2006). Their distribution is primarily influenced by cold water currents, providing them with food, rather than depth itself (Buhl-Mortensen et al., 2010). Thus, zones with topographic relief that accelerate currents, such as seamounts or guyots, favor thriving of these communities (Roberts et al., 2006). Cold-water corals encompass a diverse range of species, including hard corals (scleractinians), octocorals (such as gorgonians), and hydrocorals (Roberts et al., 2006). Black coral gardens are particularly important for conservation due to their role in providing food and shelter for various species, witnessed by the presence of epibionts and found association with megafauna (Chimienti et al., 2020; Gibson et al., 2006). Black corals, scientifically known as Antipatharia, predominantly constitute these formations and are seldom found in association with other coral species like *Paramuricea clavata* and *Eunicella cavolini* (Chimienti et al., 2020). They need hard substrates to fix to the seabed, being devoid of structures to engage in the softer substrates. They are filter feeders, and some species serve with mucus to catch prey, mainly belonging to zooplankton, captured through nematocysts (Wagner et al., 2012). Benthic communities are essential for the ocean functioning, but they are increasingly facing severe threats. Ocean acidification, caused by the increase of atmospheric CO_2, represents one of the main threats for cold water corals: it compromises their calcification process and therefore their growth

(Roberts et al., 2006). Furthermore, model predictions suggest that the aragonite (a form of calcium carbonate) dissolution depth could progressively decrease, hindering the CWCs from thriving in the areas where they are now found (Roberts et al., 2006). Another impact caused by humans is bottom trawling: this fishing practice directly damages and removes deep-sea organisms, characterized by long lifespans and slow growth rates, that translate into longer times needed to recover from the impacts (Althaus et al., 2009; Kaiser et al., 2006; Mejjad & Rovere, 2021; Puig et al., 2012). Bottom trawling has many more impacts on the environment, such as the disruption of infaunal communities, the modification of substrate characteristics, and the alteration of the nutrient content: these factors alter the environment and prevent a community from returning to its pristine state (Puig et al., 2012). Other fisheries techniques, such as longlines, can have meaningful impacts on the environment. Although these gears are considered less impactful, they can be transported by the currents and compromise the three-dimensional structure of animal aggregations, hindering some of their ecological functions (Chimienti et al., 2020). Biogenic habitats possess a remarkable ability to withstand natural disturbances. However, when factors such as global climate change and human exploitation act in combination or occur more frequently, these ecosystems cannot sustain themselves and end up collapsing (Rossi et al., 2017). The slow recovery capacity of the species involved can make short term recovery impossible (Kaiser et al., 2006). The resilience of marine ecosystems is decreasing with the loss of biodiversity, linked to their ability to recover more rapidly from stress, therefore protecting biodiversity is crucial for preserving marine habitats (Peterson et al., 1998; Reusch et al., 2008).

Vulnerability is a key concept when discussing and assessing habitat characteristics, especially related to the influence of human activities. The Food and Agriculture Association (FAO) defines vulnerability as the likelihood that a population, community, or habitat will suffer significant harm from short-term or long-term disturbances. It also considers the time it takes to recover and the chances of successful recovery. (FAO, 2009). To delineate easily applicable standards, the expression “Vulnerable Marine Ecosystems” (VMEs) was introduced at the United Nations General Assembly (UNGA). The first aim of the VME concept was to identify habitats subject to fishery activities and that therefore needed protection

(FAO, 2024a). VMEs are defined as “groups of species, communities, or habitats that may be vulnerable to impacts from fishing activities” (FAO, 2009; FAO, 2017). The impacts’ scope has been broadened in 2016 to encompass a wider range of human activities; these new areas of interest include seabed mining, oil and gas exploration, shipping, cable and pipeline installation, and bioprospecting. Emerging activities, including ocean energy and carbon injection, were also added to this list (FAO, 2016). FAO provides a list of characteristics to help with the identification of these ecosystems, presenting 5 criteria that can be expanded based on new evidence or particularities of the studied region (FAO, 2009). They correspond to uniqueness or rarity, functional significance of the habitat, fragility, life-history traits of component species that make recovery difficult, and structural complexity. Their description helps to identify ecosystems that host particular species and/or play fundamental ecological roles and are particularly vulnerable to human impact. Intrinsic characteristics alone are insufficient to evaluate VMEs: "significant adverse impacts" must also be considered. These impacts can severely compromise the structure or functioning of ecosystems, including preventing populations from reproducing or causing biodiversity loss. Their evaluation requires to consider both their interaction and cumulative effects (FAO, 2009). Therefore, the overall impact of a disturbance of an ecosystem results from a complex interplay between the disturbance’s characteristics and the ecosystem’s traits that increase its vulnerability (FAO, 2009). A similar habitat classification, also following the concept of habitats of emerging attention and protection, was developed by the Commission for the Protection of the Marine Environment of the North-East Atlantic (OSPAR). This international organization works to protect and conserve marine ecosystems and biodiversity in the North-East Atlantic region. It was developed after the Oslo-Paris Convention in 1992 for the safeguarding of the North-East Atlantic marine environment and the sustainable removal of decommissioned offshore oil platforms (OSPAR, 2010). OSPAR has assessed several criteria that help recognize species and habitats in need of protection and has formulated a “List of Threatened and/or Declining Species & Habitats”, contributing to the protection of the most vulnerable marine organisms and ecosystems (OSPAR, 2024a).

The concept of VME was also taken into account by ICES, The International Council for the Exploration of the Sea (ICES, 2024a). It is a global scientific organization, composed of representatives from various governments, dedicated to conducting and coordinating marine research. The aim of this council is to provide impartial, science-based advice to governments and other stakeholders to support the sustainable use and conservation of marine ecosystems (FAO, 2016). Similarly to OSPAR and FAO, ICES has established a list of habitats of concern; although not all the OSPAR habitats fall into the categorization of Vulnerable Marine Ecosystems, they still require consideration, keeping in mind that they provide essential information for biodiversity description and protection (Table 1).

OSPAR	ICES	FAO
Carbonate Mounds	**Cold-water coral reef**	**Cold-water coral reef**
Coral Gardens	*Lophelia pertusa/Madrepora oculata* reef	*Lophelia pertusa* reef
***Cymodocea* Meadows**	*Solenosmilia variabilis* reef	*Solenosmilia variabilis* reef
Deep-Sea Sponge Aggregations	**Coral garden**	**Coral garden**
Haploops	Hard-bottom coral garden	Hard bottom garden
Intertidal Mudflats	Hard-bottom gorgonian and black coral gardens	Hard bottom gorgonian and black coral gardens
Intertidal Mytilus edulis Beds	Colonial scleractinians on rocky out-crops	Colonial scleractinians on rocky outcrops
Kelp Forest	Non-reefal scleractinian aggregations	Non-reefal scleractinian aggregations
Littoral Chalk Communities	Stylasterid corals on hard substrata	Soft-bottom coral gardens
***Lophelia pertusa* Reefs**	Soft-bottom coral garden	Soft-bottom gorgonian and black coral gardens
Maerl Beds	Soft-bottom gorgonian and black coral gardens	Cup-coral fields
***Modiolus modiolus* Beds**	Cup-coral fields	Cauliflower coral fields
Oceanic Ridges with Hydrothermal Vents	Cauliflower Coral Fields	**Deep-sea sponge aggregations**
***Ostrea edulis* Beds**	**Deep-sea sponge aggregations**	Other sponge aggregations
***Sabellaria spinulosa* Reefs**	Soft-bottom sponge aggregations	Hard-bottom sponge gardens

Seamounts	Hard-bottom sponge aggregations	Glass sponge communities
Sea Pen & Burrowing Megafauna	**Sea-pen fields**	**Seapen fields**
Zostera Beds	**Anemone aggregations**	**Tube-dwelling anemone patches**
	Soft-bottom anemone aggregations	**Mud- and sand-emergent fauna**
	Hard-bottom anemone aggregations	**Bryozoan patches**
	Mud and sand emergent fauna	
	Bryozoan patches	
	Hydrothermal vents/fields	
	Cold seeps	

Table 1: *Comparison of the three classifications (OSPAR, ICES, FAO) of habitats of conservation concern. The main categories of habitats are written in bold and their subgroups are underlined, while the sub- subgroups are written in gray. Furthermore, habitats shared among the three classifications are represented with the same color background, to facilitate the comparison (FAO, 2024b; ICES, 2024b; OSPAR, 2024b).*

Benthic habitat mapping

Because of their ecological importance, it is essential to learn more about deep benthic habitats. A valuable tool for studying their distribution, abundance, and monitor changes over time is benthic habitat mapping. It is defined as the "spatially continuous prediction of biological patterns on the seafloor" (Misiuk & Brown, 2024). A habitat is the combination of both biological and physical features (Verfaillie et al., 2009), therefore, habitat mapping involves the acquisition of abiotic data like information about substrate, along with a biological component, regarding the composition, abundance and distribution of the biological communities. Water significantly hinders data transmission in marine mapping compared to terrestrial mapping. Satellite imagery provides a broad overview of large-scale information such as tectonics and primary productivity, but its resolution is insufficient for detailed habitat structure analysis (Mayer et al., 2018). Gravitational information loses resolution as it rises through water; this distortion is referred to as "upward continuation" and, combined with the distance between satellites and the seafloor, it limits the accuracy of seabed topography mapping based on satellite methods (Mayer et al., 2018). More precise methods have been developed for a more detailed understanding of the seafloor's structure. Widely used tools are multibeam echosounders (MBES), which produce detailed bathymetric maps by ensonifying the seafloor with a swath of sonar pings across the vessel's survey track and detecting the bottom echo. Obtained bathymetric data provide information regarding seafloor depth, while backscatter can provide information about seafloor composition and roughness. (Pickrill & Todd, 2003; Swanborn et al., 2022). These physical data are then complemented by distribution and abundance data of benthic organisms, acquired by, e.g., in situ observations. These observations can be recorded using relatively low-invasive tools, such as remotely operated vehicles (ROVs) (de Mendonça & Metaxas, 2021). They have the advantage of being piloted, allowing operators to adjust their course as needed, and they can be equipped with additional gear, such as a mechanical arm for sample collection (McLean et al., 2020). Moreover, ROVs facilitate image acquisition in deep and morphologically complex environments, like vertical walls, which are challenging to sample with other methods (Robert et al., 2015). These tools have also been utilized in multiple benthic habitat mapping studies (e.g., Nestorowicz et al., 2021; Innangi et al., 2019). Towed cameras, which are tethered and towed behind a ship, usually maintain a set height above the seafloor without making contact (de Mendonça & Metaxas, 2021). These have been applied in both mobile fauna assessments (e.g., Drazen et al., 2019; Ilich et al., 2021) and habitat mapping studies (e.g., Hanafi-Portier, 2024; Ilich et al., 2021). Other methods that are used in marine habitat mapping include drop cameras, deployed from a vessel and lowered to the seabed, and autonomous underwater vehicles (AUVs). The latter, unlike the other tools, are untethered and can conduct imagery transects near the seafloor, potentially reducing noise and discontinuous lighting and offering greater opportunities for Artificial Intelligence image analysis (Morris et al., 2014; QinYuan He et al., 2023). The combination of abiotic data and biological ground-truthing data allows to fit and train predictive models about the spatial distribution of benthic habitats (Misiuk & Brown, 2024).

Seabed mapping has many important applications, from managing human activities like fishing or shipping to protecting marine environments. It’s especially useful in combining these aspects, as it connects human interests with a better understanding of the environment, helping to manage both in a more balanced way. Notable examples of the application of habitat mapping includes a study from Browns Bank in Canada where a high-resolution multibeam echosounder was used to map scallop distribution. The results led to optimized scallop harvesting, reducing trawling time by 75%. The reduction in trawling not only improved resource management, but also had positive environmental effects by minimizing disturbance and preserving the habitats of other commercial species, thereby increasing their availability (Pickrill & Todd, 2003). Recent advances in remote sensing and mapping technologies have improved the ability to quantify and analyze marine landscapes, for example detecting ecological differences between protected and unprotected areas (Huntington et al., 2010). The increasing establishment of MPAs in the last years reflects a rising effort towards protection and conservation of marine environments, in which benthic habitat mapping proves helpful especially in the least accessible regions, where biological and geological sample collection is challenging (Hogg et al., 2016; Hogg et al., 2018).Benthic habitat mapping offers significant benefits for understanding and conserving endangered habitats. It allows the identification of VMEs, such as areas containing corals, sponges, and other delicate organisms, enhancing knowledge of these ecosystems (Ardron et al., 2014; Nestorowicz et al., 2021). Furthermore, it supports the planning of fishing activities to minimize harmful effects on marine ecosystems, contributing to the development of protocols and potentially leading to protective measures, such as enclosures (Althaus et al., 2009; FAO, 2009). A key innovation involving mapping introduced in the North-East Atlantic in 2014 concerns the mandatory requirement to accurately map the seabed before and during exploratory fishing activities. This is carried out using seabed maps, precisely identifying areas where VMEs are or could be present (FAO, 2016). In essence, it is necessary to implement preventive and corrective measures to protect Vulnerable Marine Ecosystems, through the management of fishing areas, the report of vulnerable habitats, and the employment of the best available information. (FAO, 2009). For this purpose, seabed mapping represents a critical tool for understanding and conserving vulnerable marine habitats.

Madeira and the Island Mass Effect

The northeastern Central Atlantic Ocean basin is a vast expanse of water bordered by the Azores-Gibraltar fracture zone to the north, the Mid-Atlantic Ridge to the west, the African coast to the east, and the equator to the south (Carracedo & Troll, 2020). Madeira is an archipelago located in this oceanic area and together with Cape Verde, the Azores, and the Canary Islands, forms the biogeographical region known as Macaronesia. All four Macaronesian archipelagos share many natural features, including climate, flora, fauna, and seafloor characteristics, and have a common volcanic origin (Carracedo & Troll, 2020). Madeira’s water circulation and characteristics are influenced by the features of wind circulation and the island's presence, that is a key factor in the Island Mass Effect (IME): the northeast trade winds, originating from the Azores subtropical high-pressure system, blow towards the island, while the island's mountainous formation shelters its southern part from the force of these winds (Caldeira et al., 2002; Campuzano et al., 2010). This creates a calmer and colder environment on the leeward side of the island, with water temperatures approximately 3°C lower than the rest of the island (Campuzano et al., 2010). There are eddies, fronts and upwelling phenomena around the coast of Madeira that bring up cold water, boosting primary production and thus influencing organism’s growth and distribution (Caldeira et al., 2002; Campuzano et al., 2010). An upwelling phenomenon is observed in the region between the island of Madeira and the Desertas Islands, part of Madeiran archipelago, where water dynamics and characteristics are influenced by the presence of a submarine oceanic crest (Campuzano et al., 2010). More precisely, it is an underwater ridge, formed from a collapsed volcanic crater, rising steeply from the deep ocean (1000 to 200 meters). Interacting with local currents, it hinders circulation, causing notable upwelling of cold waters rich in nutrients in that zone (Caldeira et al., 2002; Campuzano et al., 2010). Previous studies have investigated the Madeiran seabed to identify habitats requiring protection. Braga-Henriques et al. (2022) focused on the southern side of the Madeira-Desertas Ridge, identifying biotopes (as termed in their study) including mixed coral and sponge aggregations, various coral gardens, and other habitats reported by OSPAR in shallower areas, such as maërl beds and kelp forests. Another study from Ribeiro and Neves (2020) conducted in shallower parts of the Madeiran marine park of Cabo Girão also reported the presence of habitats of conservation concern and fish species including 18 important for fisheries and 3 included in the IUCN list of threatened species (Ribeiro & Neves, 2020). These findings suggest that Madeira, despite lacking reports from OSPAR and FAO, may be a significant biodiversity hotspot in need of protection.

Objectives

1. To identify and quantify the diversity of deep seabed communities found on the ridge between Madeira and the Desertas Islands, with a particular emphasis on the ones that are significant from a conservation perspective. Before starting annotation, guides and studies on the NE Atlantic were reviewed, leading to the hypothesis that similar fauna would be found off Madeira and across the NE Atlantic. Supplementary Material provides details on observed morphotypes, comparing them with the species reported in the studies (Suppl. Material 1,3).
2. To group the studied sites into diverse habitat types, then classify them as VMEs, and study their composition, spatial distribution, and relationship with environmental factors. We expect to observe clear zonation, as reported in a study conducted in the same region (Braga-Henriques et al., 2022).
3. To study the environmental differences between the studied sites and their influence on biological composition.
4. To assess whether the presence of benthic habitats influences the occurrence of mobile fauna. Numerous studies (e.g., Costello et al., 2005; Miller et al., 2012) report associations between mobile fauna, particularly fish, and benthic formations. We expect similar findings.

Focus and terminology

This study primarily focuses on the biological aspects that determine habitat classifications according to FAO, ICES, and OSPAR. The identification of communities of organisms in various sites is therefore a key step. Each site will be characterized by its dominant biological component, leading to its classification into a specific habitat, as a combination of its physical features and its biological component. Biogenic habitats are characterized by extensive three-dimensional structures created by organisms themselves (Thurber et al., 2014). Therefore, the focus will be initially on the identification of organisms that contribute to this three-dimensionality and then characterize the sites that host them. A crucial step in this study will be the creation of a map illustrating the distribution of these habitats along the surveyed transects. This map will be based on the presence of the organisms investigated at specific locations along the sampled transects. In this study, the terms "habitat" and "ecosystem" (specifically in the context of VMEs) are used interchangeably to describe these biologically and structurally distinct areas.

Materials and Methods

Study area

The Madeira archipelago consists of three main islands, located between latitudes 32º22'20"N and 33º7'50"N, and longitudes 16º16'30"W and 17º16'38"W (Campuzano et al., 2010) (Figure 1). It is connected to mainland Portugal by a chain of seamounts, which have been studied for their role as biodiversity hotspots (Wienberg, 2013; Carracedo & Troll 2020). The investigated area lies between Madeira and the Desertas Islands, which form a single volcanic system consisting of two rift arms (Geldmacher & Hoernle, 2000), dated to 5.6 million years ago (Carracedo & Troll, 2020).

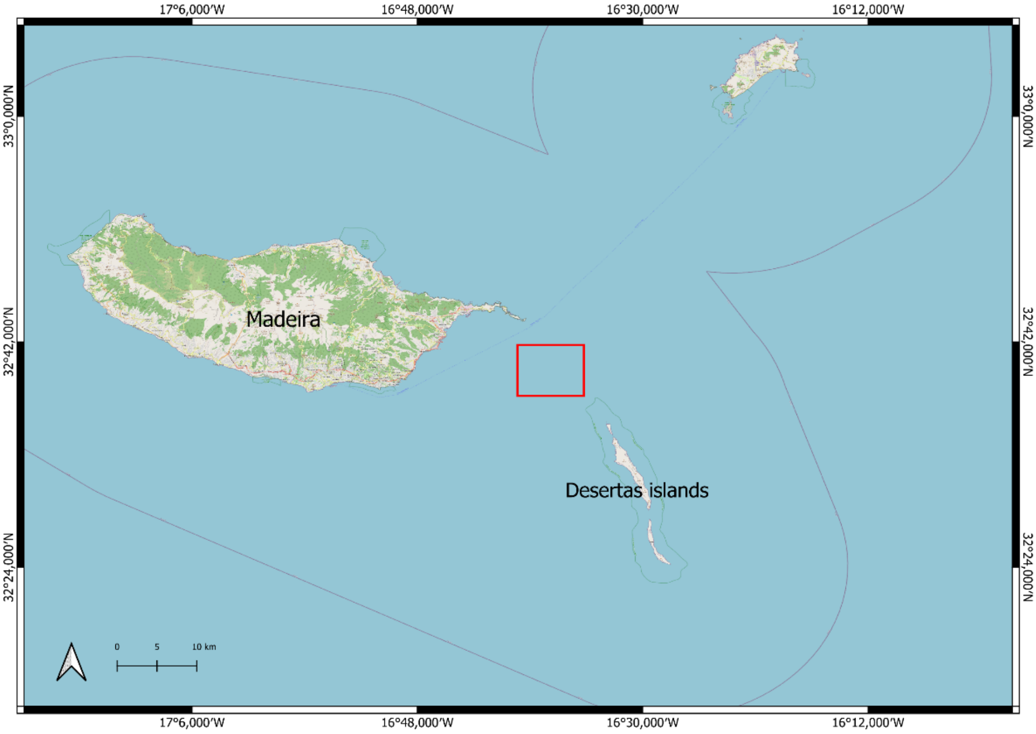

Figure 1: *Map showing the Madeira archipelago with the study region depicted as a red rectangle. Base map and data from OpenStreetMap and OpenStreetMap Foundation (CC-BY-SA). © https://www.openstreetmap.org and contributors.*

Data acquisition

The image and video data used in this study were collected during the cruise MSM126 “Jellyweb Madeira” in February 2024. Two different optical systems were deployed during MSM126 to record the deep seafloor of the Madeiran slopes. The towed camera systems XOFOS (X Ocean Floor Observation System) was used to make continuous downslope transects and the remotely operated vehicle ROV PHOCA was used to make more detailed recordings of interesting areas, being piloted upslope or along the slope. A total of eight XOFOS and six benthic ROV dives were conducted during MSM126 of which two XOFOS and two ROV dives were analyzed in this study (Figure 2). Further details are provided in Table 2. XOFOS was towed very closely over the seafloor (ca. 4 m) at 0.5-0.7 knots. Video data from ROV PHOCA was recorded using an Imenco HD-SDI Bullshark camera (Abegg & Linke, 2017) and divided into 20-minute video files. XOFOS (Ocean Floor Observing System) is a towed camera system consisting of a metal cage housing three cameras: the first is oriented forward, for navigation purposes; the second is a downward looking Sony 4k camera for seafloor observations and the third, looking downward too, is called OIS (Ocean Imaging System). For the purposes of this study, the photos, taken from the OIS at 10-seconds intervals, were primarily used for detailed analysis, while the videos coming from the Sony camera served for verification. The tool was also equipped with two sizing lasers and telemetry. An optical fiber connection to the ship enabled real-time transmission of images and data. Both the ROV and XOFOS were equipped with a CTD, recording conductivity, water temperature and depth. A Sonardyne USBL system was provided by the ship and the two systems were equipped with an USBL beacon, allowing georeferencing of the image and video data. In addition to that, both systems were equipped with sensors recording speed, motion, heading and distance to the seafloor. The latter was obtained thanks to a Doppler Velocity Log (DVL). Metadata of the systems were collected using OFOP (Ocean Floor Observation Protocol).

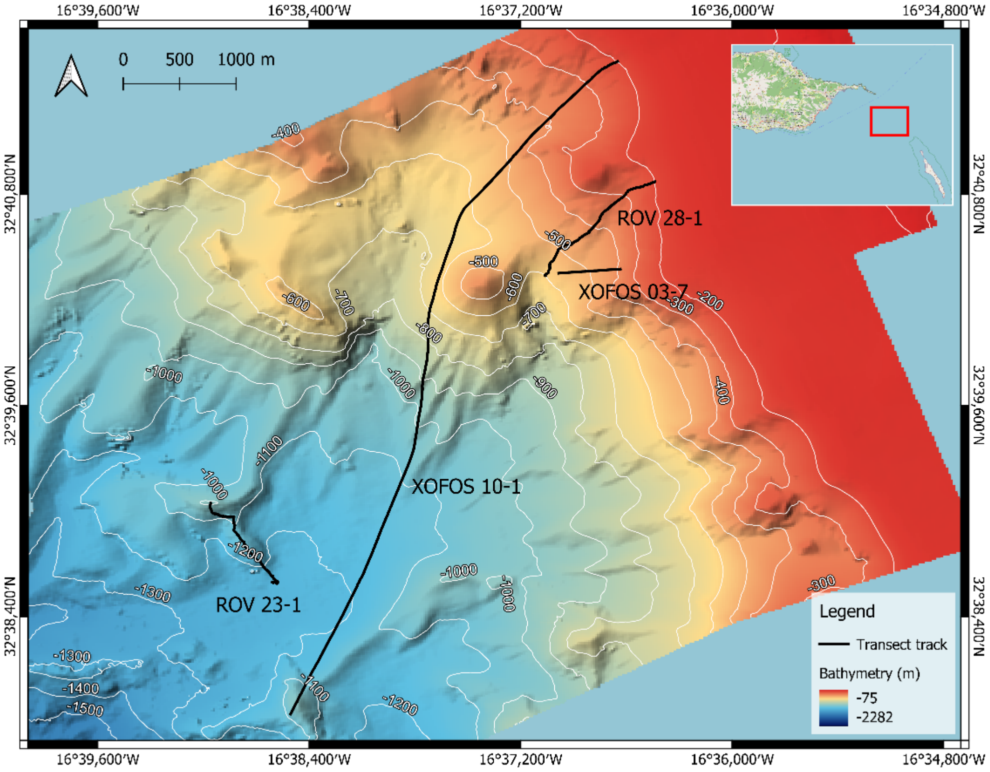

Figure 2: *Map displaying bathymetry of the surveyed area and track of transects. Their names (ROV 23-1, ROV 28-1, XOFOS 03-7, XOFOS 10-1) were assigned based on the system used, the deployment station, and the dive number. Bathymetry was generated using ship-based MBES systems during MSM126. Base map and data from OpenStreetMap and OpenStreetMap Foundation (CC-BY-SA). © https://www.openstreetmap.org and contributors.*

	XOFOS 10-1	**XOFOS 03-7**	**ROV 23-1**	**ROV 28-1**
Data type	Images	Images	Videos	Videos
Transect length (m)	7740	553	ca. 1200	ca. 1500
Data amount	2242 images	214 images	4 hours, 41 minutes and 52 seconds*	3 hours, 39 minutes and 7 seconds
Number of annotations	12540	4848	1186	1895
Start time	2024-02-12 21:49:54	2024-02-10 17:33:51	2024-02-15 10:56:24	2024-02-16 09:25:39
End time	2024-02-13 04:03:24	2024-02-10 18:09:21	2024-02-15 16:29:13	2024-02-16 13:04:46
Min. depth (m)	196.3	355.0	997.8	199.9
Max. depth (m)	1207.1	543.9	1248.8	601.4
Gear	Towed camera system XOFOS	Towed camera system XOFOS	ROV PHOCA	ROV PHOCA

Table 2: *Overview of the imagery and video data analyzed in this study. These XOFOS and ROV dives were conducted during MSM126. Start and end times refer to the moments of first arrival at the seafloor and final departure from it. *here, total time differs from the difference between start and end time due to a significant off-bottom interval.*

Annotations

The annotation process was entirely conducted on BIIGLE (BIIGLE, 2024). This platform allows users to label organisms and report any type of feature in videos and images, through the generation of different types of annotations (Langenkämper et al., 2017). As concerns XOFOS transects, for each image the substrate type was indicated to facilitate further analysis. The approach used was as follows: if the area was fully covered by sand or mud, the substrate was classified as soft; if it was rocky, composed of boulders, or in any way hard, it was classified as hard substrate. When one of these two substrate types clearly dominated, that label was applied. In cases where both were equally present (commonly, patches of rock scattered on sand), a third label, corresponding to mixed substrate, was assigned. As for video footage belonging to ROV transects, the same method was applied, using whole-frame annotations: continuous segments of the video displaying a specific substrate type were marked accordingly. Concerning organisms, the following approach was applied to both videos and images in the same way. All labels were point-annotations, and a label tree was developed and continuously updated. The structure began with easily distinguishable phyla (e.g., Cnidaria, Porifera (Sponges), Echinoderms) or general taxonomic groups (e.g., Fish, Ascidians). Categories based primarily on morphological characteristics were then created to further classify the organisms. Additionally, the labels "Unknown" and "Human trace" were introduced to report organisms (or supposed organisms) with high uncertainty and to document human-related items, such as bottles or plastic pieces. Since the study relied on imagery data and not physical samples, the classification of organisms focused on morphotypes. The use of morphotypes when there is uncertainty about identification is supported by other studies on benthic habitat mapping (egg., Howell et al., 2010; Ramos et al., 2016; Uhlenkott et al., 2022). Mobile organisms such as fish and crustaceans were labeled too, to study their relationship with the presence of habitats. The approach consisted of annotating single organisms, or single colonies in the case of cnidarians. The main challenge was identifying encrusting sponges, therefore points where they were most prominent in color were marked. Several guides and online platforms were used for identification (CCALMR, 2009; Howell et al., 2017; NOAA, 2024; Oliveira et al., 2017; Tracey, 2014; WoRMS, 2024a).

Data analysis

Data was analyzed using RStudio (Posit team, 2024). The habitat analysis only considered sessile organisms, while certain mobile fauna was used for further correlation analyses. Only morphotypes clearly assignable to a phylum were chosen, to avoid incorrect outcomes. Finally, a selection was made based on the abundance of each morphotype. In studies similar to this, it is common to exclude some species (or morphotypes, in this case) because they may generate noise in the data, compromising the clearness of the study (Park et al., 2006). For example, it is possible to put a threshold based on the number of taxa present in a sample (Braga-Henriques et al., 2022) or select species that appear over a selected threshold (Dufrêne & Legendre, 1997). In this study, for each transect, we only considered morphotypes occurring more than 10 times per transect. Structurally and functionally similar morphotypes were grouped together. For instance, single and spread sponges were put together due to the difficulty in assigning them to a specific category. This choice was supported by the fact that sponges are typically grouped together in FAO, OSPAR and ICES habitat classifications, in "Deep-sea sponge aggregations". However, lollipop and laminar sponges, with their distinct shape, were considered separately. A similar approach was applied to corals: they were mainly grouped based on their general morphology and distinctions were made on color or if they exhibited a clearly different body organization, that could reflect a different ecological role.

Non-parametric multivariate analysis

Non-parametric multivariate analysis refers to a set of statistical techniques used to analyze datasets with multiple variables without assuming an underlying distribution of the data. This approach is frequently adopted in studies involving the presence of multiple species at various sites and has been documented in marine research, where specific strategies for analyzing such data have been outlined (Clarke, 1993; Field et al., 1982). Clustering is a multidimensional analysis technique that groups a collection of objects based on their similarities. This method helps to identify patterns or structures within a dataset by bringing similar items together (Legendre & Legendre, 1998). In this study, the objects corresponded to sites, since the goal was to group them through cluster analysis based on similarities in biological composition. To combine the ROV video and the XOFOS image data into one cluster analysis, the transects were partitioned into sites of equal lengths of 10 meters, following the example of Nestorowicz et al. (2021), who demonstrated clear results using 10-meter lengths as a standard. In the ROV videos, a script based on ROV's position divided the footage into sites by successively adding up distances between consecutive USBL positions until reaching 10 m. Assuming a constant vessel speed, a similar division was applied to the XOFOS tracks. By measuring the total transect length and the number of images, the distance between each image was calculated, allowing for the selection of 3 images for the XOFOS 10-1 transect and 4 for the XOFOS 03-7 transect. In addition to the previously described exclusions, further organism selection was implemented to reduce noise in the data. For each site, only morphotypes occurring at least 5 times were kept. Empty sites were excluded from the analysis.

Data handling and cluster analysis

When studying communities, especially in marine environment, the presence of highly abundant species or groups of organisms (in this case, sponges) can overshadow the presence of relevantly abundant species, so it is common to use data transformation (Field et al., 1982). Here we applied root-root transformation, used in diverse ecology studies (e.g., Field et al., 1982; Stephenson & Burgess, 1980). Bray-Curtis index (Bray & Curtis, 1957) is considered suitable for community composition data and was used to build the distance matrix. It considers absolute species abundances in the samples and was used in several ecological studies even applied to marine benthic communities (Bae & Park, 2020; Clarke, 1993; Field et al., 1982; Krawczyk et al., 2021; Lacharité & Brown, 2019; Lee et al., 2018; Nestorowicz et al., 2021; Pabis et al., 2020). The aim of cluster analysis is to segregate groups with similar traits and assign them into clusters. In hierarchical polythetic agglomerative cluster analysis, each sample is considered as a single cluster and then it is grouped with other samples to form bigger groups (Bakker, 2024). In this case, the clusters will contain sites that are considered similar based on the analysis of the distance coefficient previously calculated. The algorithm chosen is the "average linkage" method (also known as the "unweighted pair-group arithmetic average", UPGMA): each sample joins the group to which it has the lowest average distance (Legendre & Legendre, 1998). It has largely been used in ecology studies (e.g., Field et al., 1982; Lacharité & Brown, 2019; Nestorowicz et al., 2021; Pabis et al., 2020). Several algorithms have been developed to determine the optimal number of clusters (k). In this study, the Calinski-Harabasz index was applied. It is based on the ratio of between-cluster dispersion to within-cluster dispersion (Calinski & Harabasz, 1974) and has been identified as the most effective k-choice criterion among 30 indices (Milligan & Cooper, 1985). This index has also been used for cluster analysis in marine studies (e.g., Verfaillie et al., 2009). Non-Metric Multidimensional Scaling (NMDS) is a commonly employed method for visually representing community relationships in ecological studies (Clarke, 1993). It is a non-parametric technique that transforms multidimensional data into a lower-dimensional space while keeping the rank order of the distances between samples (Borcard et al., 2018). As a consequence, samples that are more similar to each other in the original dataset are placed closer together in the NMDS plot, while those that are more different are positioned further apart (Legendre & Legendre, 1998). This method facilitates the visualization of distances among sites after being assigned to different clusters. NMDS aims to represent objects in fewer dimensions by arranging them based on their differences. It does this by minimizing a "stress" value, which measures how well the distances between objects in the reduced space match their original dissimilarities. A lower stress value means the reduced dimension space is a good representation of the original distances (Clarke, 1993; Legendre & Legendre, 1998). A Shepard diagram compares the dissimilarities among objects in the ordination plot with the original dissimilarities (Borcard et al., 2018). The final step of this analysis is to display the clusters on a map, displaying the geographical positioning of habitats along the transects. Its realization is performed through RStudio (Posit team, 2024) and QGIS (QGIS.org, 2024).

Cluster description

For each cluster, the percentages of the morphotypes with highest transformed abundance and substrate types were calculated. Additionally, an indicator species analysis (ISA) was performed to provide ecological meaning to the groups of sites (Bakker, 2024; Dufrêne & Legendre, 1997). This index reaches its maximum when all individuals of a species are found within a single group of sites and when that species is present in all sites of that group (Dufrêne and Legendre, 1997). This type of analysis has been utilized in several studies (Bae & Park, 2020; Lacharité & Brown, 2019; Lee et al., 2018; Verfaillie et al., 2009), to understand ecological relationships among species and their habitats.

It is represented as

$$\mathbf{IndVal_{ij} = A_{ij}} \times \mathbf{B_{ij}} \times \mathbf{100}$$

With:

Specificity (A_{ij}): This is calculated as $\text{Nindividuals}_{ij}/\text{Nindividuals}_{i}$, representing the mean abundance of species i in the sites of group j compared to all groups in the study. A_{ij} is maximal when species i is exclusively present in cluster j.

Fidelity (B_{ij}): This is determined using $\text{Nsites}_{ij}/\text{Nsites}_{i}$, which indicates the relative frequency of occurrence of species i in the sites of group j. B_{ij} reaches its maximum when species i is found in all sites of cluster j.

In this study, species were replaced with morphotypes. Morphotypes with a statistically significant IndVal higher than 25% and a p-value less than 0.05 were selected as indicator morphotypes. The statistical significance of indicator value indices is calculated by randomly reassigning sites to different clusters 999 times. The ISA was conducted using the indval function in the R package labdsv (Posit team, 2024).

Environmental differences

The average values of depth, temperature, salinity, slope, roughness and aspect for each site were analyzed and plotted to determine if there were significant differences between clusters. Depth, temperature and salinity data were obtained from the CTDs. Depth measurements were calculated by adding the altitude provided by the DVL to the CTD water depth. As for the XOFOS 03-7 transect, DVL altitude data was missing, so the average altitude recorded in the XOFOS 10-1 transect was added to the depth measurement provided by CTD. Slope, roughness and aspect were extracted from the Digital Elevation Model (DEM) grid obtained during the cruise. The bathymetry data was collected using the ship-based Kongsberg EM712 and EM122 MBES systems. Initial cleaning was performed with QPS Qimera and the data was exported as a DEM with a cell size of 20 by 20 meters. Due to only crude cleaning, extracted derivatives like slope and roughness may contain errors. A Kruskal-Wallis test was employed to assess the differences among clusters; this test was suggested by Field et al. (1982) and employed by Pabis et al. (2021) and Waheed et al. (2022) in ecological studies. For each environmental variable, the null hypothesis (H_0) stated that there is no significant difference in the variable across the clusters. The alternative hypothesis (H_a) stated that there is a significant difference in the variable among the clusters. A Canonical Correspondence Analysis (CCA) was chosen to investigate the relationship between biological composition and environmental variables. This method is frequently used in aquatic studies (e.g., Fierro et al., 2019) characterized by both constrained and unconstrained datasets, often containing a high proportion of zeros (Myers et al., 2021; ter Braak & Verdonschot, 1995). Detrended Correspondence Analysis (DCA) was performed to test if a unimodal ordination method was applicable, checking the length of the first DCA axis. A Spearman's Rank Correlation provided further information revealing multicollinearity among the environmental variables; for each pair of environmental variables, the null hypothesis (H_0) stated that there is no significant correlation between the variables. The alternative hypothesis (H_a) stated that there is a significant correlation between the variables. In case of covarying variables, only one of them was taken in the CCA. Environmental variables considered were depth, temperature, salinity, slope, roughness, aspect (continuous variables), and substrate type (categorical). A permutation test evaluated significance generating p-values for each CCA's axis to indicate whether the variation it explains is statistically significant.

Mobile fauna association

The aim of this analysis was to determine if there is a connection between the presence of mobile fauna and habitat clusters. To investigate this relationship, a Wilcoxon rank-sum test was used. This non-parametric test compares two groups of sites: those that are part of a habitat cluster and those that are not. By looking at the average presence of mobile fauna in each group, the test can determine if there is a significant difference between them. The following hypotheses were tested: H_0 (null hypothesis): There is no significant difference in the presence of mobile fauna between sites that are part of a habitat cluster and those that are not. H_a (alternative hypothesis): There is a significant difference in the presence of mobile fauna between sites that are part of a habitat cluster and those that are not.

Results

Annotations

A total amount of 20469 labels were obtained from the annotation of the four transects. The amount of habitat-forming morphotypes considered in the analysis was 15. The Supplementary Material section contains further information regarding the identification criteria (Suppl. Material 1). The annotations also included 37 human-made items, such as glass bottles, food packaging, and plastic products.

Cluster analysis and NMDS

The Calinski-Harabasz index reached its maximum at 10 clusters, identifying this as the optimal number of clusters (k), with a score of 61.8, the highest value within the range of 2 to 15 clusters. Therefore, the sites were divided into 10 groups. The dendrogram (Figure 3) visually represents this division, where each node corresponds to a division into smaller clusters and different colors are used for each cluster (habitat). The NMDS analysis stopped at a stress value of 0.075. The Shepard plot (Figure 5) displays the model's goodness of fit.

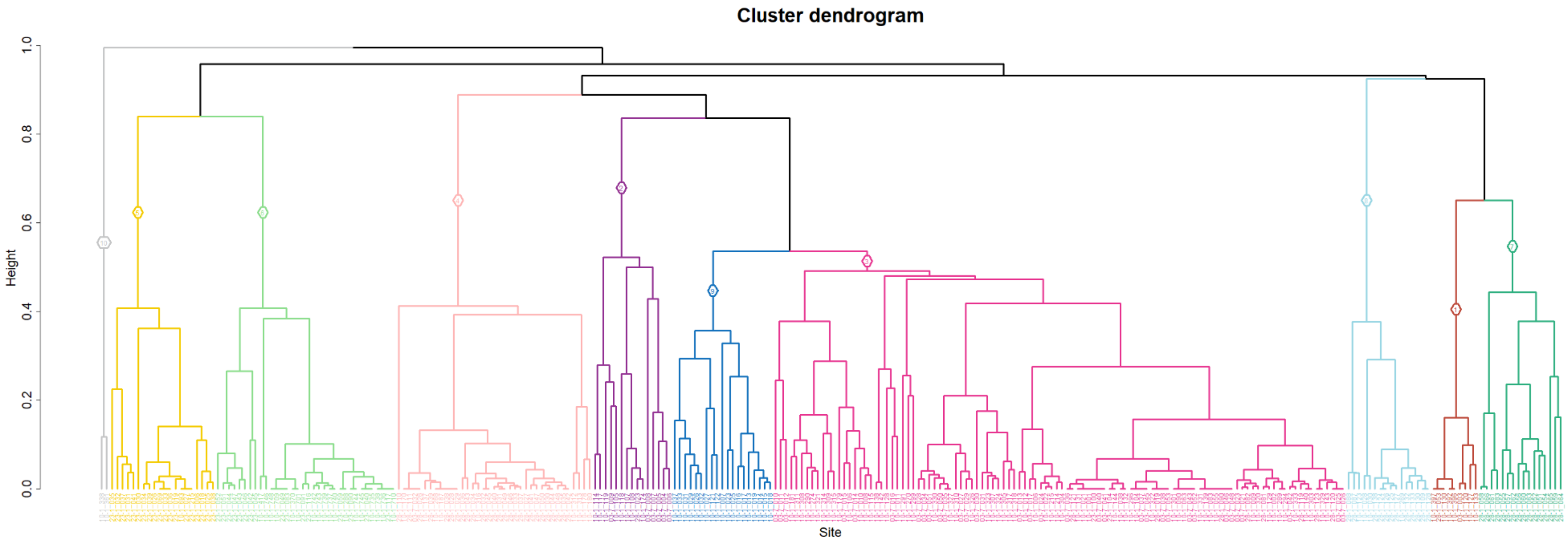

Figure 3: *Dendrogram illustrating the site clustering, obtained using average linkage clustering (UPGMA) on a Bray-Curtis distance matrix based on the biological composition of sites. Sites belonging to the same cluster (habitat type) are characterized by a different color and its number is reported in the tree.*

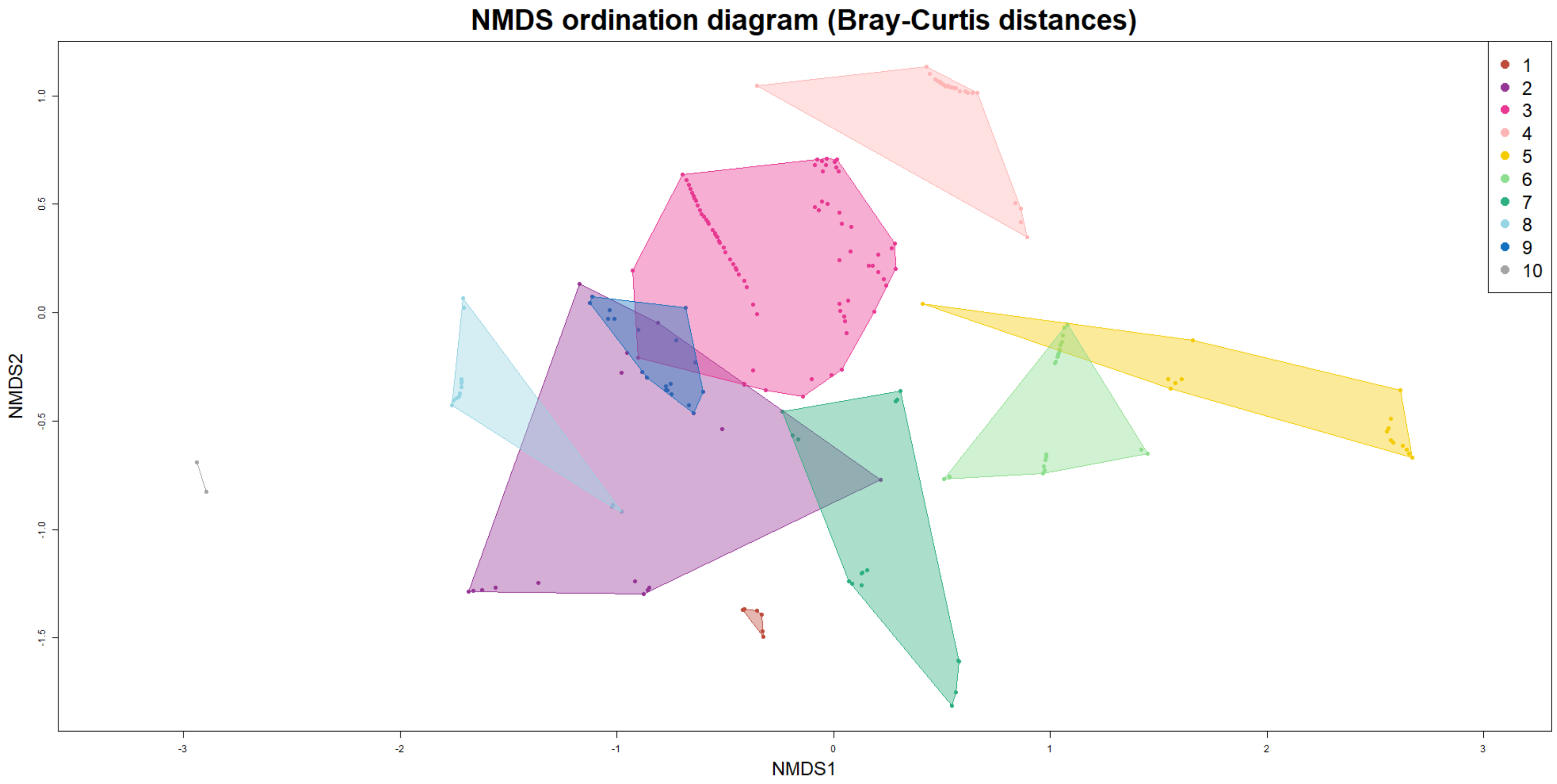

Figure 4: *Non-Metric Multidimensional Scaling (NMDS) plot. Sites belonging to the same group are colored the same and connected to each other.*

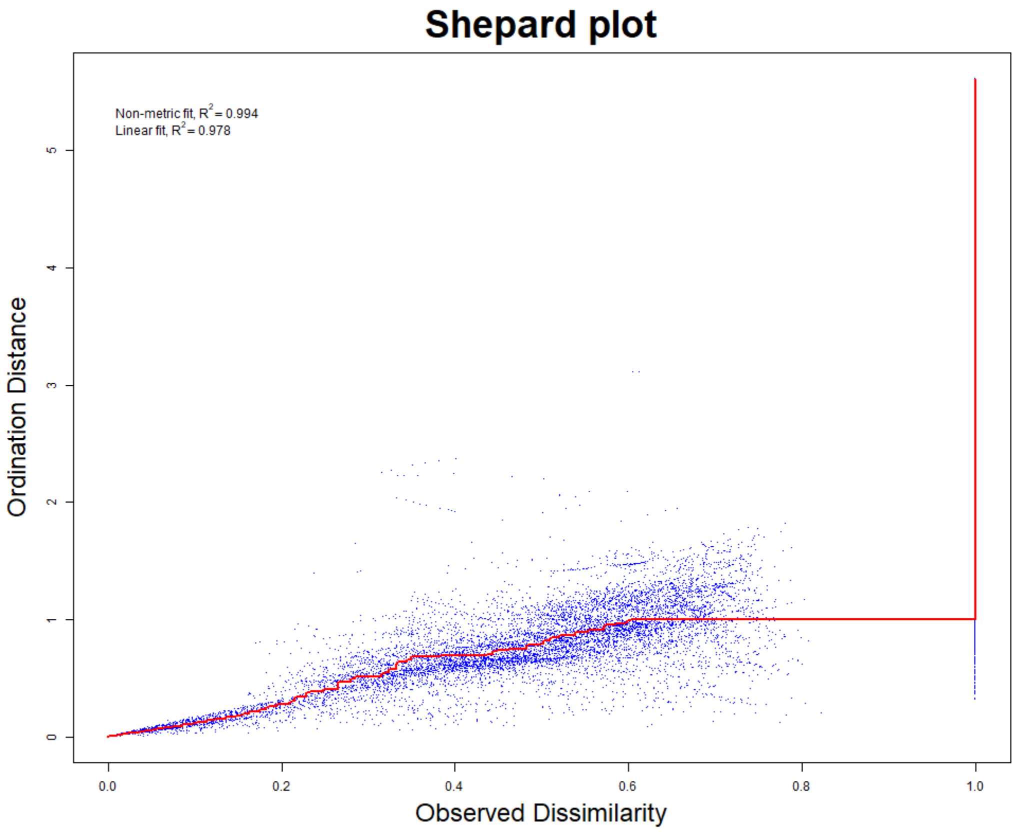

Figure 5: *The Shepard plot shows the distances among sites in the ordination plot against their original distances. The* R^2 *values obtained from the regression between these two sets of distances measures the goodness of fit of the NMDS ordination.*

Cluster description

Each habitat identified through the cluster analysis is described in detail below. The habitats are named after their indicator morphotype, except for the third habitat, which lacks a specific indicator according to the analysis. Instead, this habitat is named based on the most frequently occurring morphotype. All analyses were conducted using transformed abundance data (double square root) and, since the clustering was based on these transformed values, all subsequent analyses also utilize the transformed data to maintain consistency. The following text reports the main findings for each habitat. Representative images are in Figure 6, while Figure 7 displays their distribution along the transects. Complete tables containing abundance percentages, IndVal, A and B scores are put in the Supplementary Material (Suppl. Material 5).

	XOFOS 10-1	**XOFOS 03-7**	**ROV 23-1**	**ROV 28-1**	**Total**
Habitat 1	7	1	0	1	**9**
Habitat 2	8	6	0	1	**15**
Habitat 3	64	34	2	8	**108**
Habitat 4	9	1	0	27	**37**
Habitat 5	1	0	19	0	**20**
Habitat 6	18	0	16	0	**34**
Habitat 7	0	0	0	16	**16**
Habitat 8	4	0	0	12	**16**
Habitat 9	19	0	0	0	**19**
Habitat 10	2	0	0	0	**2**

Table 3: *For each habitat, the number of sites is shown, the total of which accounts for 276.*

Biogenic habitat 1 - Whip corals

Hard substrate constitutes 74% of this first habitat. Whip corals are the only one morphotype identified in the sites belonging to this habitat. The indicator species analysis assigned whip corals a score of 39%, which is equal to the Specificity value (A).

Biogenic habitat 2 - Rounded laminar sponges

This habitat is mainly composed of laminar sponges which are characterized by their round shape, making up 58% of the community. They are followed by whip corals at 18% and non-laminar sponges at 16%. The indicator morphotype for this cluster corresponds to the rounded laminar sponges, with an IndVal score of 98.7%. B is equal to 1, therefore A is equal to IndVal. The substrate in this habitat is primarily hard, accounting for 89% of the total.

Biogenic habitat 3 - Non-laminar sponges

This habitat constitutes an exception, as the ISA does not identify any morphotype with significant confidence. However, it is primarily composed of non-laminar sponges (69%), followed by lollipop sponges (15%) and white branched corals (10%). These species are likely not highlighted in the ISA because they are distributed across sites in other habitats. This habitat is the most widespread, occurring in 108 sites out of 276. Sites with at least 5 non-laminar sponges are present in 5 out of 10 habitat types. The substrate composition includes 49% hard substrate, 18% mixed substrate, and 32% soft substrate.

Biogenic habitat 4 - Lollipop sponges

This habitat is primarily characterized by the presence of lollipop sponges, which form 90% of the community. It is mainly found in ROV 28-1 transect. The ISA assigned this morphotype a score of 70.8%, with a B value of 1, indicating that lollipop sponges are represented in every site within this habitat, which is composed of 92% soft substrate.

Biogenic habitat 5 - Golden corals

This biogenic habitat is dominated by golden corals (Chrysogorgiidae), with a 75% abundance and a IndVal of 93,5%. It is mainly composed of hard substrate (80%) Except for one site from XOFOS 10-1 transect, the others belong to ROV 23-1 transect.

Biogenic habitat 6 - White branched corals

This habitat is characterized by white branched corals, accounting for 75.3% of the biodiversity within this cluster (IndVal corresponds to 64%). The second most common morphotype in this habitat corresponds to the pink fan-shaped corals (16%). They were only observed in ROV 23-1 transect and have an Indicator Value of 24% (with p-value > 0.05). Hard substrate accounts for 97% of the total.

Biogenic habitat 7 - Laminar white corals

This habitat is primarily composed of laminar white corals (52.7%) and whip corals (30.0%). Only the former obtained a significant IndVal of 100%, the highest possible, while whip corals' IndVal score remained at 18% due to low Specificity (0.26), despite a relatively high Fidelity of 0.69. This habitat is exclusively found in ROV 28-1 transect. The substrate for this habitat consists of 56% hard substrate and 44% soft substrate.

Biogenic habitat 8 - Convoluted laminar sponges

This habitat, mainly composed of hard substrate (86%), is characterized by the presence of convoluted laminar sponges, making up 86% of the abundance. Whip corals are the second most common, accounting for 16%. Convoluted laminar sponges occur in sites of other clusters (with a Specificity of 0.45) and are present in all sites of this cluster (Fidelity equal to 1), achieving a final IndVal score of 45%.

Biogenic habitat 9 - Non-laminar sponges and branched black corals

The most occurring morphotypes are non-laminar sponges (46%), convoluted laminar sponges (34%) and branched black corals (14%). Only the first and the last morphotypes obtained a significant p-value, despite all having IndVal scores higher than 40%. The substrate is entirely hard.

Biogenic habitat 10 - Crinoids

This habitat is particularly notable because it consists of only two sites. It is dominated by crinoids, which are the indicator morphotypes with an IndVal score close to the maximum (97%) and 100% occurrence in these sites (B = 1). The substrate composition is reported as 17% hard, 17% mixed, and the rest soft.

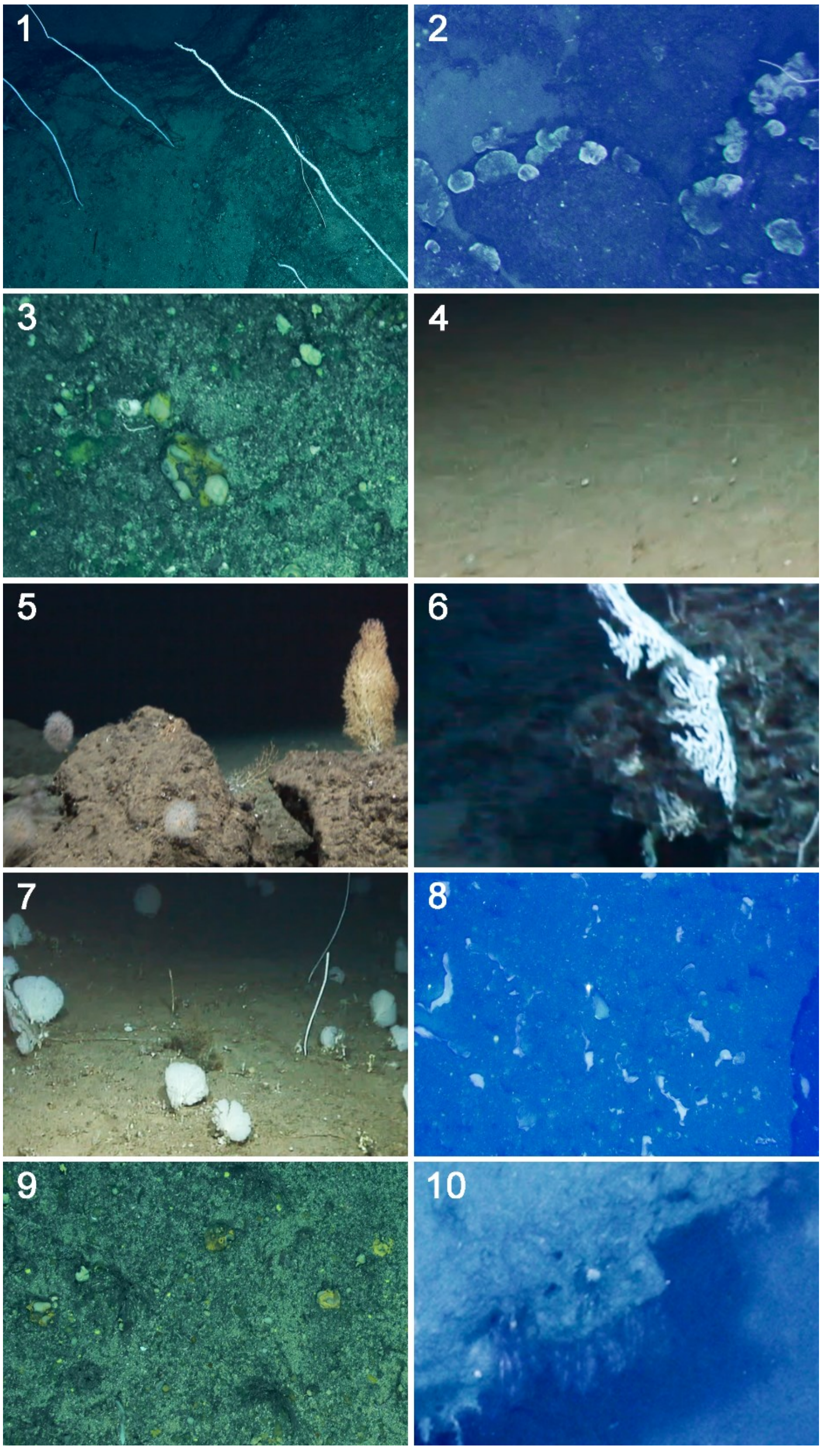

Figure 6: *Collection of representative images for each habitat type, named after the indicator morphotypes (except for the third). 1) Whip corals 2) Rounded laminar sponges 3) Non-laminar sponges 4) Lollipop sponges 5) Golden corals 6) White branched corals 7) Laminar white corals 8) Convoluted laminar sponges 9) Non-laminar sponges and branched black corals 10) Crinoids*

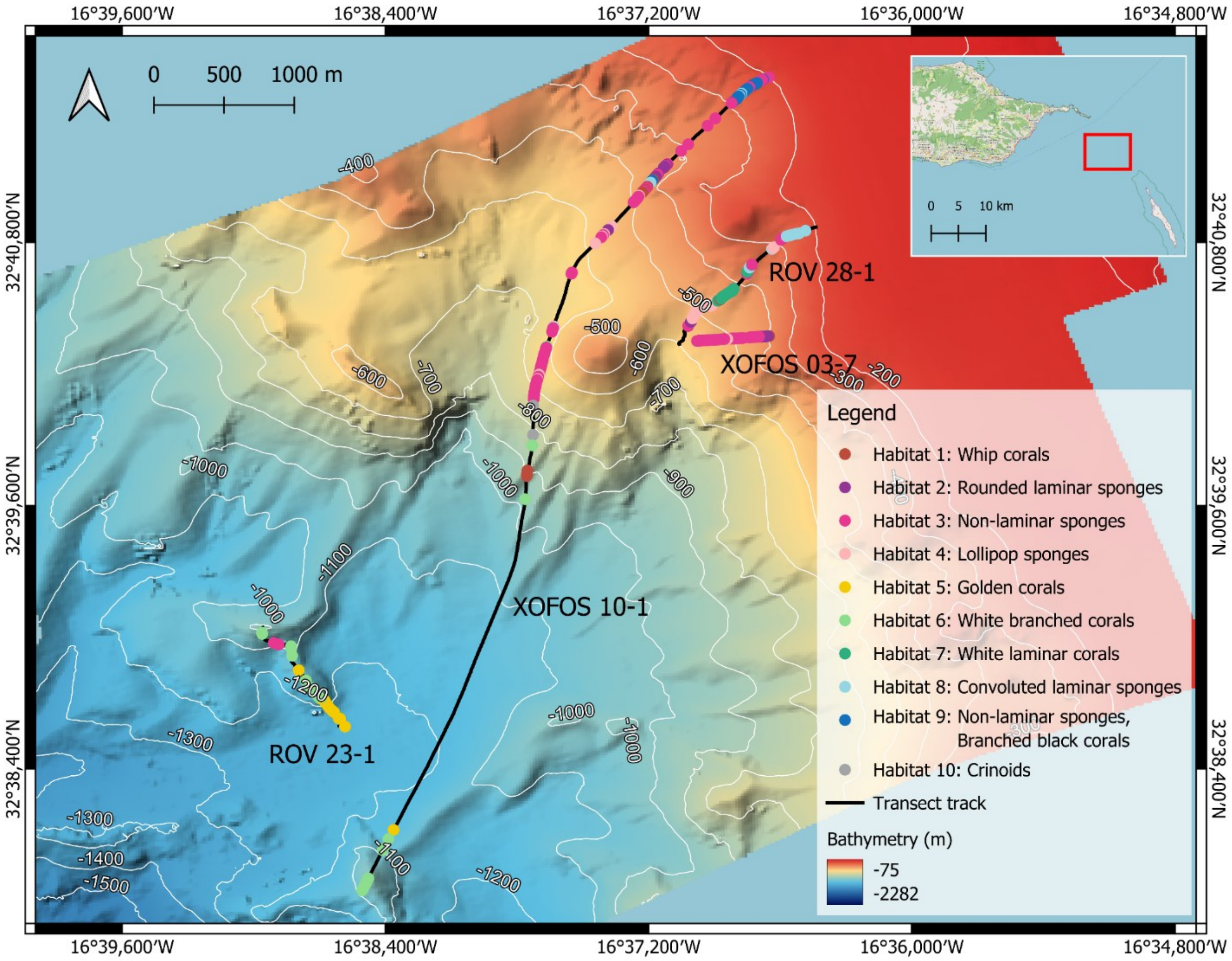

Figure 7: *Map illustrating the distribution of the 10 habitats along the transects. Bathymetry was generated using ship-based MBES systems during MSM126. Base map and data from OpenStreetMap and OpenStreetMap Foundation (CC-BY-SA). © https://www.openstreetmap.org and contributors.*

Environmental differences

Differences across clusters

A Kruskal-Wallis test indicated that there was a significant difference in depth across the clusters, χ^2 (9, N = 276) = 179.9, p < 2.2e-16. Similarly, there was a significant difference in temperature across the clusters, χ^2 (9, N = 276) = 171.16, p < 2.2e-16. There was also a significant difference in salinity across the clusters, χ^2 (9, N = 276) = 92.347, p = 5.499e-16. A Kruskal-Wallis test indicated that there was a significant difference in slope across the clusters, χ^2 (9, N = 276) = 43.56, p = 1.7e-06. There was also a significant difference in roughness across the clusters, χ^2 (9, N = 276) = 46.63, p = 4.61e-07. Furthermore, there was also a significant difference in aspect across the clusters, χ^2 (9, N = 276) = 97.12, p < 2.2e-16.

For each environmental variable, a p-value <0.05 leads us to reject the null hypothesis (H_0).

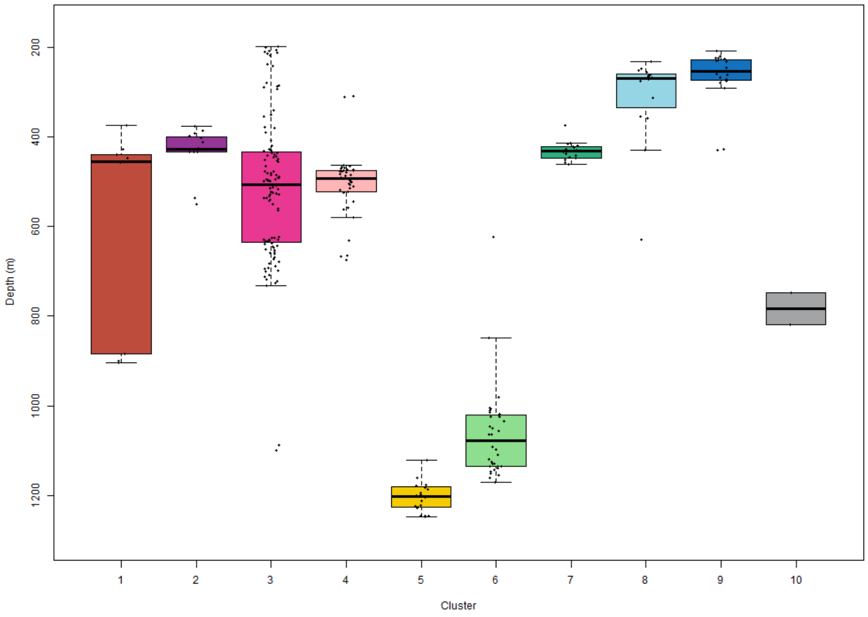

Figure 8: *Boxplots of clusters of sites against depth showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

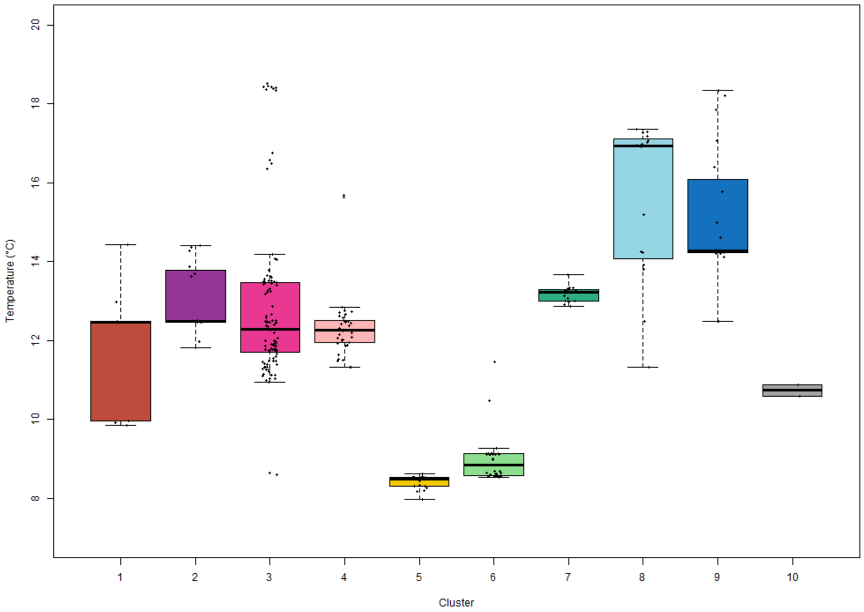

Figure 9: *Boxplots of clusters of sites against temperature showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

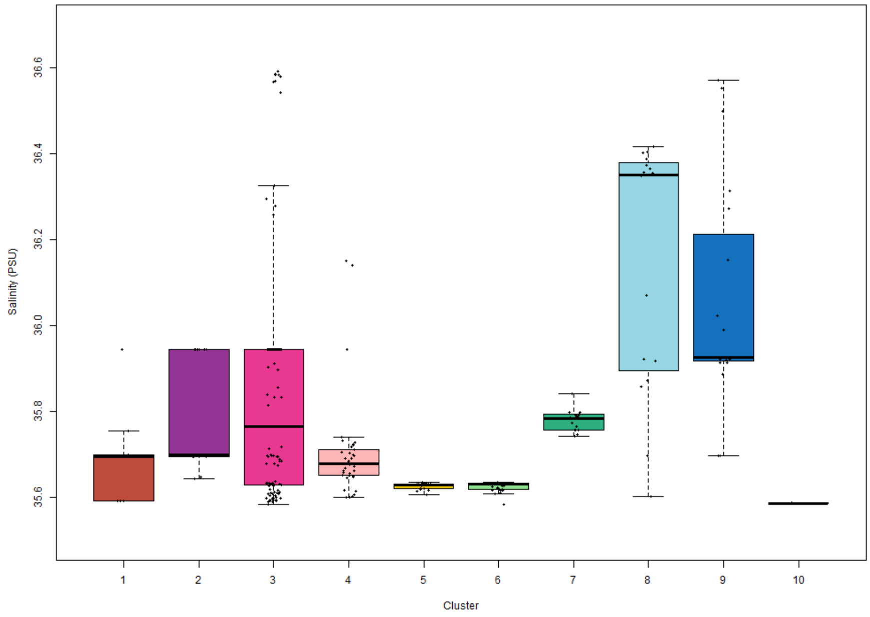

Figure 10: *Boxplots of clusters of sites against salinity showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

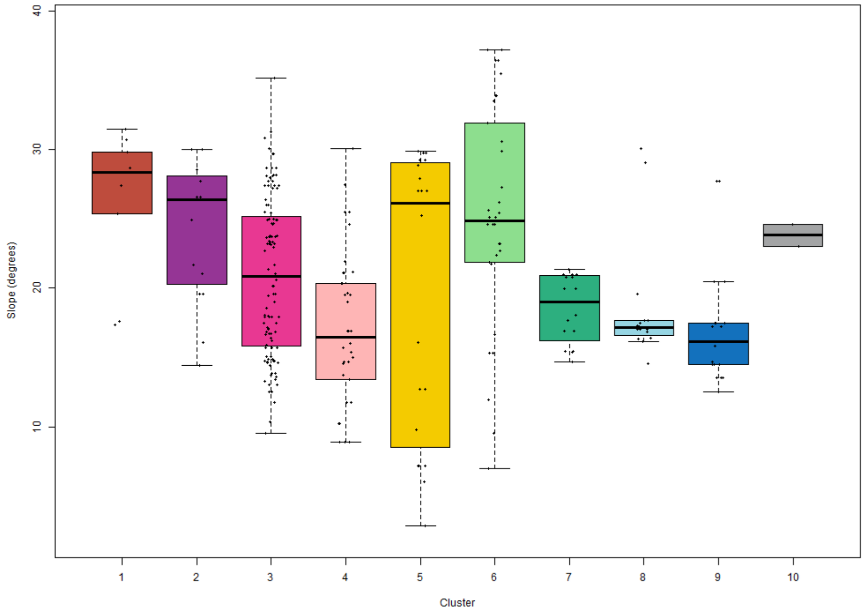

Figure 11: *Boxplots of clusters of sites against slope showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

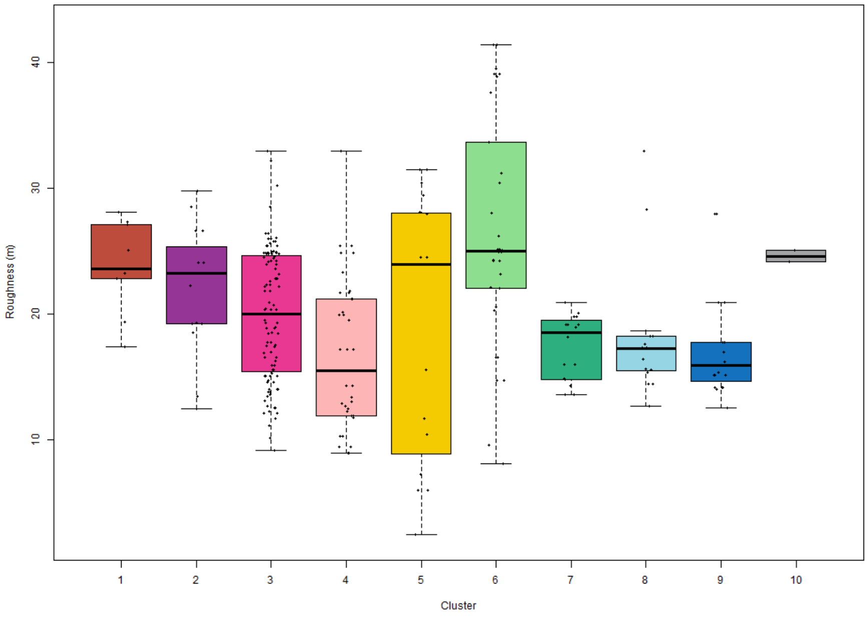

Figure 12: *Boxplots of clusters of sites against roughness showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

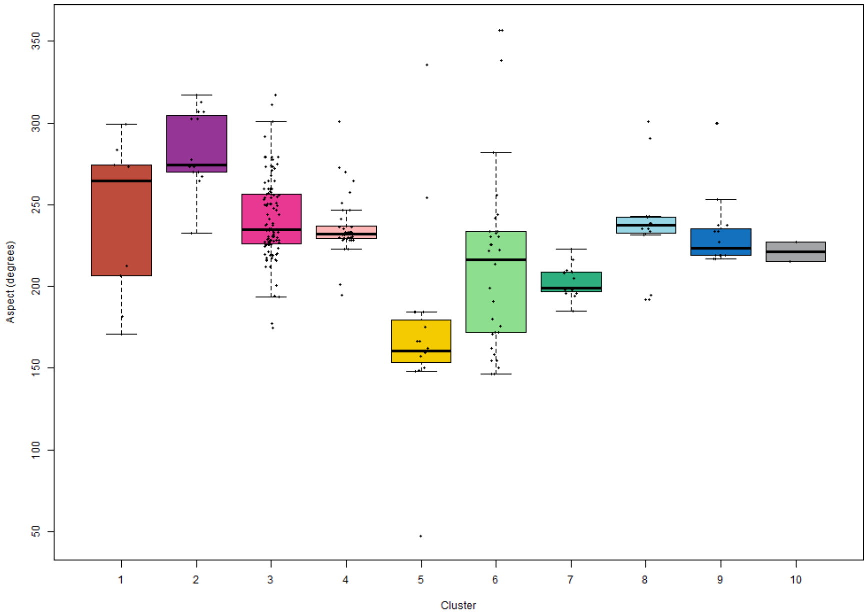

Figure 13: *Boxplots of clusters of sites against aspect showing the median, quartiles, and whiskers. The lower whisker extends to the smallest point within 1.5 times the interquartile range (IQR) below the first quartile, while the upper whisker extends to the largest point within 1.5 times the IQR above the third quartile.*

DCA results

A DCA was run based on site composition data. The DCA1 axis length is 6.21, which is greater than 3. This suggests a unimodal relationship, which means Canonical Correspondence Analysis (CCA) would be the more appropriate method.

Correlation

A Spearman's correlation analysis was conducted to evaluate the relationship between each environmental variable. Table 4 reports the r_s values. Excluding correlations of each variable with itself, cells with significant p-values are highlighted in blue, while non-significant ones are in yellow. Darker blue cells contain r_s values that show strong correlations (< -0.8 or > 0.8) and were selected for further analysis: depth was retained to also represent temperature and salinity, and slope to represent roughness.

	Depth	**Temperature**	**Salinity**	**Slope**	**Roughness**	**Aspect**
Depth	1					
Temperature	-0.976	1				
Salinity	-0.811	0.860	1			
Slope	0.334	-0.358	-0.442	1		
Roughness	0.393	-0.424	-0.479	0.947	1	
Aspect	-0.204	0.175	-0.042	0.279	0.203	1

Table 4: *Spearman's correlation (r_s) between environmental variables. Cells colored in blue indicate significant p-values, with darker blue representing strong correlations (< -0.8 or > 0.8), while yellow indicates non-significant values.*

CCA

Each of the axes from the first to the fourth has a significant p-value (0.001), meaning that they explain a statistically significant amount of variation in the composition data. The proportion of variation explained by each axis gradually decreases; the first axis (CCA1) explains 68% of the variance while the second (CCA2) explains the 24%. CCA1 is primarily driven by depth, which shows a strong positive correlation (0.967) with biological composition. In contrast, aspect has a notable negative correlation (-0.519), while slope contributes moderately (0.135). As for CCA2, the variable slope exhibits a moderate positive correlation

(0.310). Additionally, aspect also shows a positive association (0.418). Conversely, hard substrate has a significant negative correlation (-0.666).

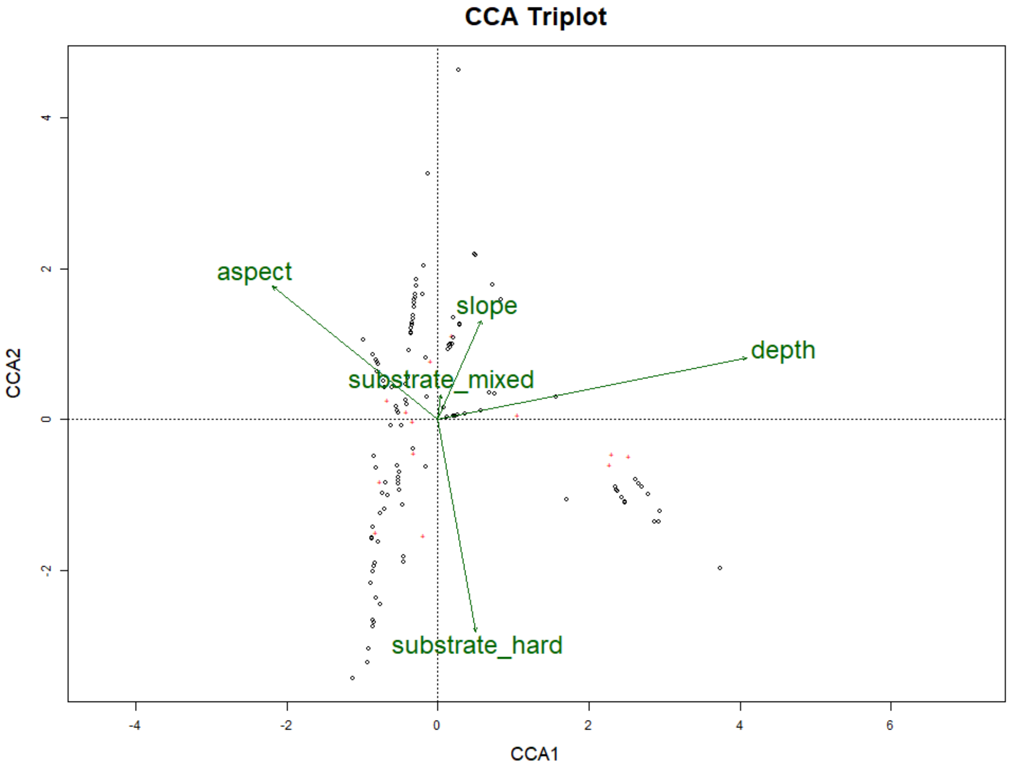

Figure 14: *CCA triplot that displays how the communities are organized with respect to the environmental variables.*

Mobile fauna association

A Wilcoxon rank-sum test was performed to evaluate whether mobile fauna presence differed by site type. The results indicated that there was no significant difference between the mobile fauna presence in sites that belong to a habitat and sites that don't belong to a habitat, U = 100864, p = 0.3637. A p-value > 0.05 indicates that we fail to accept the null hypothesis (H_0).

Discussion

This study focused on exploring the deeper zone of the ridge between Madeira and the Desertas Islands, aiming primarily to study the diversity and distribution of benthic macrofaunal communities and classify the habitats they form as Vulnerable Marine Ecosystems (VMEs). Identification was based on morphotypes, with 15 considered in the analysis, revealing 10 distinct habitats, each characterized by unique compositions and environmental features. Additionally, the study investigated the relationship between faunal composition and environmental variables and assessed whether mobile fauna is associated with the identified habitats. The discussion highlights the main findings and discusses the challenges encountered throughout the process.

Fauna Identification

The primary objective was to identify and quantify organisms, focusing on classification by morphotype. Without physical samples, it was challenging to assign species-specific labels, so a more generalized approach was adopted, focusing on the morphology and function of individuals. While clear separations were often possible, they were sometimes impeded by differences in image and video quality. This study focused on sessile macrofauna, with sponges and corals being the main organisms of interest, as they are part of OSPAR concern habitats, such as "Coral Gardens" and "Deep-Sea Sponge Aggregations." Sponges play an ecological role as filter feeders and nutrient recyclers (Cathalot et al., 2015; Coppari et al., 2016), and four morphotypes were detected as habitat indicators. Rounded laminar sponges exhibited a clearly distinguishable shape compared to convoluted laminar sponges, which also showed different aggregation patterns. Lollipop sponges, with their spherical stalked shape, were relatively simple to distinguish. Non-laminar sponges included encrusting and single-form sponges, which were grouped together due to resolution limitations. The second main group was corals, which form "Coral Gardens" and other types of VMEs. Various coral morphologies were identified and grouped, though analysis considered general features like morphology or color. Habitat-indicative coral morphotypes included branched black corals, primarily observed in the shallower areas of the XOFOS 10-1 transect, and "golden corals", corresponding to Chrysogorgiidae with their characteristic bottle-brush shape. As their names suggest, the black color of the former and the ochre tint of the latter aided in their identification. Other indicator morphotypes included whip corals, identifiable by long, stiff white structures; "white branched corals", which grouped corals with similar branching structures; "pink fan corals", distinct for their pink color and shape; and "white laminar corals", notable for their visible branching despite a laminar structure. Crinoids represented another indicator morphotype, clearly distinguishable from other organisms thanks to their feathery appearance and often banded coloring. Additional details regarding morphotype identification, including descriptions of excluded morphotypes, are provided in the Supplementary Material (Suppl. Material 1, 2, 3). Furthermore, the supplementary material includes a detailed label tree with all subdivisions for each group (Suppl. Material 4). A challenge across all categories was the limited availability of regional identification guides. The primary guide used refers to another NE Atlantic zone (Oliveira et al., 2017), while other resources have a global scope with few images per species, and sometimes it was not feasible to find images related to species listed in studies or databases.

Clustering results

The cluster analysis identified 10 habitat types, that likely reflect what was observed while completing the annotation process. NMDS was selected to best visualize site composition differences, and, since it carries risks of suboptimal solutions (Borcard et al., 2018), multiple runs help verify that the lowest stress value is achieved consistently (Clarke, 1993). A stress value of 0.075 corresponds to a good ordination, being less than 0.1 (Clarke, 1993). The Shepard plot further confirmed that robustness was achieved: the final NMDS ordination explains 99.4% of variance in dissimilarity ranks, suggesting an accurate reflection of original rank-order relationships, while the high linear fit confirms that distances in the ordination space closely match the original distances, and it is visually confirmed that the sites representation align with the clustering analysis results.

Habitat description

Five out of ten habitats fell within the classification of coral gardens, comprising various coral types displaying diverse morphologies. Habitat 1, characterized by whip corals as indicator morphotype, contained sites only hosting these organisms, indicating that the cluster analysis effectively separated sites based solely on the presence of whip corals from other habitats. The ISA assigned whip corals a Specificity score (A) of 0.39, reflecting that, although they are found at each site of this habitat type (Fidelity is equal to 1), these corals also appear in sites of other habitat types. Indeed, this morphotype frequently occurs across multiple sites and is often associated with other aggregations, forming a consistent component of the fauna. A clear example is Habitat 7, characterized by white laminar corals as the indicator morphotype. Whip corals were commonly found here, but their non-indicator status is likely due to their presence across various sites; therefore, while the cluster analysis grouped whip coral-dominated sites without other phyla (Habitat 1), whip corals did not achieve a significant indicator score where they appeared alongside other morphotypes. Golden corals were easy to identify visually, and subsequently clustered. These corals, belonging to the family Chrysogorgiidae, shape the surrounding environment, forming dense, intricate branches that could potentially support various life forms. Cluster analysis grouped sites hosting these corals in Habitat 5, where they were the main morphotype. Habitat 6, meanwhile, was named after white branched corals. The second most common morphotype (16%) in this habitat was represented by the pink fan-shaped corals, notable for their distinctive shape and color. They were only observed in ROV 23-1 transect; thus, they did not represent all sites in the cluster, reaching an Indicator Value of 0.24, characterized by a Specificity (A) of 1. Clustering them with branched corals was reasonable given the structural similarities. Probably, they could have obtained a clustering separation using higher k values. The final coral-including habitat was Habitat 9, where branched black corals were one of two indicator morphotypes and ranked third in abundance. It is noteworthy that, although black corals were abundant above 200 m (unpublished data from MSM126 cruise), as concerns deep sea they only appeared grouped in the shallower parts of the XOFOS 10-1 transect. Although less abundant than non-laminar sponges (the other indicator morphotype), data transformations probably helped smoothen this difference, allowing for recognition of their ecological significance. Sponges were observed at all depths and across all transects, but the habitats predominantly composed of them were found in shallower areas compared to others (Figure 8). The first mainly sponge-based habitat identified by the cluster analysis is Habitat 2, with rounded laminar sponges as the indicator morphotype. Their unique structure made them easy to be classified and distinguished. However, a common challenge with this phylum, not only concerning this habitat, was species identification, thus further classification beyond Demospongiae wasn't feasible. These sponges were observed to form large banks, either closely distributed or packed, providing a three-dimensional environment that creates potential shelters. They show high Specificity and Fidelity to this cluster, appearing in all its sites and being rarely found in sites of other clusters. On the other hand, Habitat 8 is represented by convoluted laminar sponges. They have a Specificity score of 0.45, meaning that 55% of these sponges are found in sites belonging to a different habitat. However, within this habitat, these sponges appear in distinct assemblages, close together but not stacked. Their unique morphology adds three-dimensionality to the substrate, providing shelter and space for other life forms. Habitat 4 features lollipop sponges as the indicator morphotype. This habitat mainly corresponds to a section of the ROV 28-1 dive, where a sandy area scattered with these sponges was observed. Lollipop sponges also appear in other habitats, exhibiting a Specificity to habitat 4 of 0.71. Non-laminar sponges characterize Habitat 9 as indicator morphotype, alongside branched black corals. These are widespread, but likely represent multiple species, grouped here due to their similar function and appearance. This habitat also has a high presence of convoluted laminar sponges, which, though excluded from the indicator species analysis, are the second most frequent morphotype (34%). One of the most interesting cases is Habitat 3, where non-laminar sponges are dominant (69%) but do not appear as indicators in the ISA. This omission reduces their perceived ecological relevance; however, it's important to note that this habitat type is the most widespread and deserves recognition. This suggests that ISA shouldn't be the only descriptor for each cluster. If percentage abundance and human observations are not considered, valuable data on some groups of organisms in the surveyed area could be missed.

Despite the remaining habitat, corresponding to the tenth, was only found in two sites, it was included in the analysis since it is hosting organisms with potential conservation value, contributing to distinct three-dimensional structures. Crinoids are the indicator morphotype of this habitat and were found on patchy hard substrate in areas otherwise dominated by sand. This case highlights the importance of being familiar with the dataset alongside data analysis. Crinoids are associated with areas of high fish abundance (Colloca et al., 2004) and, while not classified as a vulnerable habitat, studies in the NE Atlantic (e.g., Nestorowicz et al., 2021; Fonseca et al., 2014) document the presence of their aggregations as crinoid beds. However, ICES lists them among VME indicators, focusing only on stalked individuals (ICES, 2024b), and FAO considers them as VME indicators, but only in the northwestern Atlantic (FAO, 2024b). This indicates that, despite existing research, there is still limited awareness and concern regarding their ecological significance. As with other habitats identified, crinoids are suspension feeders, that contribute to the formation of benthic biogenic habitats by aggregating. Forming aggregations is especially beneficial, as higher organism density enhances water movement around them, bringing more food; greater water flow enhances their feeding efficiency, enabling faster growth rates and achieving larger sizes (Sebens, 1987). Cold water corals and sponges, which are the main composers of these habitats, create benthic structures that provide refuge, feeding grounds, and nursery areas for various commercially important fish species (Miller et al., 2012). These habitats not only boost fish production, but also offer significant human benefits, such as acting as carbon sinks and enhancing habitat resilience (Grehan et al., 2003; Soetaert et al., 2016). Numerous studies emphasize the role of cold water corals as ecological engineers, creating complex three-dimensional structures that offer shelter, support biodiversity, and contribute to nutrient cycling (Henry & Roberts, 2007; Jones et al., 1994; van Oevelen et al., 2009). Whip corals, for instance, have been shown to enhance fish abundance (Schweitzer & Stevens, 2019), while black corals play a critical role in forming habitats that support diverse associated fauna and serve as spawning, nursery, and feeding areas for many species (Bo et al., 2014; Chimienti et al., 2020). Furthermore, studies indicate that declines in coral cover are associated with reduced fish abundance (Wilson et al., 2006). Studies on coral-based habitats often focus on reef or mound formations created by reef-forming cold-water corals, such as *Lophelia pertusa* (Costello et al., 2005; Roberts et al., 2006; van Oevelen, 2009). In contrast, the coral habitats identified in this study are looser assemblages, yet they likely serve a similar ecological role to those described in earlier research. Therefore, the biogenic habitats discovered in the waters off Madeira highlight the area's ecological importance. Mapping these habitats is essential not only for protecting them and preserving their ecological functions but also for supporting regional biodiversity; this study, like similar ones (e.g., Braga-Henriques et al., 2022; Nestorowicz et al., 2021), lays the foundation for comprehensive habitat mapping that can result in a proper predictive habitat map (e.g., Krawczyk et al., 2021; Uhlenkott et al., 2022). Further research can expand to broader regions, collecting more data at multiple points or along different transects to enable modeling of adjacent zones and the completion of a predictive model that can result in a habitat map. However, despite offering a descriptive perspective, this study reports the presence of unique organisms and habitats, offering opportunities for further investigation into their distribution and ecological roles.

Environmental variables

Kruskall-Wallis tests revealed that each tested variable significantly differed across habitat clusters, suggesting that clustering based on biological composition also depicted variations in environmental variables. To further investigate this, a Canonical Correspondence Analysis (CCA) was applied to assess the influence of these environmental drivers. Depth demonstrated to be the main diver, while it is also important to consider substrate-related variables, namely aspect, slope and substrate type. Valuable insights emerged from habitats 4, 7, and 9. Habitat 4, identified by the presence of lollipop sponges, was consistently observed in transect ROV 28-1 within the 463-579 m depth range, though this range was also sampled in other transects. Habitat 7, with white laminar corals as indicators, was found between 414-431 m, being exclusive to ROV 28-1 transect despite that depth range was surveyed also in XOFOS 10-1 and XOFOS 03-7 transects. Additionally, Habitat 9, characterized by non-laminar sponges and branched black corals, only appeared in XOFOS 10-1 transect despite being within a depth range (207-291 m) also sampled in ROV 28-1 transect. These findings suggest that factors beyond depth may influence biological composition, indicating that depth should not be considered alone. Another interesting observation comes from Habitat 5, characterized by golden corals as indicators. It was consistently observed in ROV 23-1 transect (19 sites out of 20) and exhibited a depth range of 1121 to 1248 m. XOFOS 10-1 was the only other transect where this habitat type was found was, at a site within its depth range (1178 m), suggesting that depth is likely a main driver for these corals. Along with environmental variables, biological traits such as reproductive strategies, species-specific adaptations and connectivity may also influence habitat distribution (Coelho & Lasker, 2016), though these factors fall outside the scope of this study.

This type of analysis has also been conducted in other studies focused on documenting habitat presence across different zones of the NE Atlantic. For instance, Nestorowicz et al. (2021) investigated 8.8 km over three dives, while Braga-Henriques et al. (2022) surveyed a total of 3.8 km in a single transect. In the first study, depth was identified as the primary factor, while the second study found depth, temperature, and salinity to be the most influential on species composition; these variables are correlated, as shown in this study and generally understood. While depth appears to be a key factor, other parameters also play significant roles across all three studies. Given the amount and length of transects analyzed in this study (with ours covering the greatest length, approximately 11 km), it's important to consider that the limited number of transects and depth range may introduce bias. In our study and Nestorowicz's, certain depths were not sampled the same number of times, while Braga-Henriques surveyed only a single transect. An approach like that proposed by Ramos et al. (2016), which sampled the same depths across four transects, could be followed to obtain more reliable results. Furthermore, integrating additional sampled variables could enhance the study of environmental factors (Verfaillie et al., 2009). For example, currents have been shown to influence fauna distribution (e.g., Kaufmann et al., 1989); thus, future studies could benefit from including this variable.

Mobile fauna association

The Wilcoxon rank-sum test showed that there is not enough evidence to conclude a significant difference in fish presence between sites within habitats identified in this study and those outside these habitats. The widespread distribution of mobile fauna likely contributes to this result, as these animals can occasionally be found outside specific habitat zones. The results of this study might be explained by the equipment scaring off mobile animals. In the forward-facing XOFOS camera, fish were observed swimming away, meaning that they couldn't be captured in the view of the downward-looking camera. While scientific literature suggests a possible positive correlation (Des Roches et al., 2018; Gray, 1997; Henry & Roberts, 2007; Price et al., 2021; van Oevelen et al., 2009), most of the observed structures in our study were loose aggregations rather than dense forests, where higher densities might attract more mobile species. This could provide an explanation for the lack of correlation found in this study. A research from the same region of this study offers only descriptive insights, noting that fish aggregations were observed near habitats during their dives (Braga-Henriques et al., 2022).

Limitations, considerations and future improvements

The use of two different imaging systems leads to the need to standardize the data to account for sampling bias as much as possible. Several other studies (e.g., Schweitzer & Stevens, 2019) have been conducted merging data obtained through different methods. One issue arising from this was sample size consistency, which represented a challenge due to varying proximity to the substrate. Imagery from tools operating closer to the substrate inevitably captures fewer individuals than those operating at greater distances. The ROV, being closer to the substrate than the XOFOS, helped overcome this issue by often surveying in multiple directions to better capture the existing fauna.

A point that emerged during this study was the importance of accompanying analyses with an understanding of the data set. For example, morphotypes that were visually occurring were not counted as indicators in all habitats due to the algorithms used. Braga-Henriques et al. (2022) overcame this issue by accompanying indicator species with characteristic species, chosen based on different criteria. However, we decided to rely on indicators because they represented the habitats, reflecting the observations before the analysis. Still, it is important to underline the limits of this approach and specify if, when studying a habitat, some important and relevant species must be included, complementing the ISA. The field of non-parametric multivariate analysis is characterized by several types of choices regarding transformations, clustering, and distance matrix algorithms. Multiple tests are recommended to determine the best approach for the database used, with the main aim of representing reality and what was observed.

In addition to considering the aforementioned aspects, improvements can also be implemented in the annotation process; technological advancements, such as Artificial Intelligence image analysis, are increasingly being integrated into this field (Pavoni et al., 2021) and could be implemented in future studies. The annotations from this study can serve as a training data set for algorithms designed to assist with organism detection and identification in benthic habitat mapping studies.

Conservation outcomes

One core aim of this study, beyond descriptive exploration, was to assess the presence of habitats of conservation concern according to criteria from various organizations. OSPAR, a major authority on vulnerable habitat detection and protection, offers only broad definitions for habitats like coral gardens, described as "relatively dense aggregations of colonies or individuals of one or more coral species" (OSPAR, 2010). These aggregations can appear on either hard or soft substrates and specific density guidelines are lacking due to varying species characteristics. A study published by ICES attempted to establish some criteria (Bullimore et al., 2013), but they relied on specific analyses and methods that cannot always be implemented. Similarly, EUNIS classifications (EUNIS, 2024) for coral-based habitats are limited, especially for the Northeast Atlantic, offering only broad categories, which do not fully encompass the habitat diversity observed in this and similar studies (Nestorowicz et al., 2021; Ramos et al., 2016). For example, EUNIS classification ME123 defines "Mixed cold-water coral communities on Atlantic upper bathyal rock" as composed of *Lophelia pertusa* and, occasionally, *Madrepora oculata*, without considering other alternative species. This classification is underdeveloped for lower bathyal and upper bathyal sand habitats, like those identified in this study. The same applies to sponge-characterized habitats: OSPAR describes deep-sea sponge aggregations, providing environmental ranges without specific definitions, while EUNIS's ME122 description for “Sponge communities on Atlantic upper bathyal rock” specifies only two habitat types based on sponge species. To date, an official framework remains absent. Setting abundance or density threshold values to define habitats is challenging, given the broad range of densities and other features reported by OSPAR (OSPAR, 2010). Bullimore et al. (2013) concluded that current definitions are insufficient for accurately mapping "coral garden" habitats, as standard methods struggle to reliably distinguish them. To align with OSPAR’s goal of protecting dense coral aggregations, a clearer definition is necessary. Establishing a unique habitat assessment method, with defined abundance thresholds, could significantly enhance habitat mapping by allowing for updates as new habitats are identified, dynamically expanding its scope, and helping further habitat identification efforts representing a unique trusted reference. A practical approach could involve setting defined thresholds while also including zones with coral densities just below these thresholds, maintaining a precautionary approach to support conservation (Bullimore et al., 2013). Features that confer vulnerability to a habitat, based on FAO criteria (FAO, 2009) are not testable in this study since more details regarding single species and the assemblage they compose are needed. Since habitats found in this study can be ascribed to coral gardens and deep-sea sponge aggregations, they could be described as vulnerable. This is supported by the fact that FAO relies on OSPAR classification when describing and assessing habitat's conservation status (FAO, 2024c), and by the fact that sponges and corals (and, in some cases, crinoids) are considered as VME indicators (FAO, 2024b; ICES, 2024b).

Other studies conducted in the northeastern Atlantic identified habitats of conservation concern. For example, only one other study has been conducted in the zone between Madeira and the Desertas Islands, investigating depths and reporting a biotope dominated by alcyonacean gorgonians such as *Viminella flagellum*, along with a variety of sponges, at depths of 252-366 m. Another biotope was characterized by *Eunicella verrucosa* at depths of 173-252 m (Braga-Henriques et al., 2022). Compared to our study, the surveyed deep sea area was much smaller; nonetheless, a similarity can be observed in the habitats dominated by *Viminella flagellum*, a whip coral that can be ascribed to the indicator morphotype of Habitat 1 (Suppl. Material 1, 3). However, the depth interval where Habitat 1 was found (373-905 m) was not surveyed in the compared study. Additionally, the presence of *Eunicella verrucosa* in a biotope that also includes depths below 200 m confirms the presence of white branched corals. The other biotopes in that study were found at shallower depths, making our study the only one to describe the deeper areas of the region, exceeding depths of 1200 m and reporting unique habitats.

Although Madeira falls just outside OSPAR's Region V (OSPAR, 2024c), its proximity allows for applicable considerations, as OSPAR's 2022 reports rate coral and sponge habitats in "poor" status across all regions, highlighting an urgent need for protective measures even in the NE Atlantic (OSPAR, 2024d.). Studies off the Azores and Portugal coast reported the presence of deep-sea habitats composed by corals, similar to those observed in this study, such as whip corals and white branched corals; furthermore, deep-sea sponge aggregations and other interesting habitats are described in those areas (Braga-Henriques et al., 2022; Carreiro-Silva et al., 2017; Huvenne et al., 2012; Nestorowicz et al., 2021; Taranto et al., 2023). The OSPAR 2018 Quality Status Report for sponges and corals identifies fisheries as the primary threat to coral gardens and deep sea sponge aggregations (OSPAR, 2010), with several studies documenting the impact of this activity (Althaus et al., 2009; Kaiser et al., 2006; Mejjad & Rovere, 2021; Puig et al., 2012). A proposed solution is banning bottom trawling below 200 meters, a measure initially recommended to protect fish spawning grounds off Madeira (Delgado et al., 2018), but potentially beneficial for preserving benthic habitats as well. From a conservation perspective, the establishment of Marine Protected Areas (MPAs) offers a promising solution that is increasingly being implemented (Maestro et al., 2019) and has shown benefits for both habitat protection and resource production (Huntington et al., 2010). Additionally, the human-made items found during this study highlight the ongoing impact of human activities on the seafloor in the study region, further emphasizing the need for effective management and protection strategies.

Conclusions

This study identified ten distinct habitats, nine of which are classified as Vulnerable Marine Ecosystems according to FAO, OSPAR, and ICES criteria, while the remaining habitat contains organisms of particular interest. A comparison with a previous study conducted in the same region, the Madeira-Desertas Ridge, reveals some similarities in composition. However, this comparison is limited, as the previous study did not focus on deeper areas. Our study is the only one to describe the deeper parts of the region, exceeding depths of 1200 m and reporting unique habitats. Nine habitats can be categorized as deep sponge aggregations or coral gardens. However, the lack of clear classification criteria makes it difficult to assign specific labels to these habitats. The classification of deep-sea habitats remains underdeveloped (Bullimore et al., 2013; Nestorowicz et al., 2021; Ramos et al., 2016), highlighting the need for further research and data collection. The insights from this study contribute significantly to understanding the area's composition and biodiversity. Implementing broader surveys, rather than relying solely on transects, could enhance data collection by covering larger areas, which would contribute to the development of predictive habitat maps, similar to those generated in other studies (e.g., Krawycz et al., 2021; Uhlenkott et al., 2022). Incorporating biological samples for DNA analysis can further refine habitat classifications by confirming species identification, especially for commonly found or ambiguous organisms. Artificial Intelligence image analysis could further support and enhance imaging analyses like the one presented in this study. Currently, only 26.1% of the seafloor has been mapped, despite the Seabed 2030 project's goal of mapping the entire ocean by 2030 (Mayer et al., 2018; Seabed 2030-GEBCO, 2024). Benthic habitat mapping plays a key role in managing marine environments and addressing human activities (Pickrill & Todd, 2003; Hogg et al., 2016), and the recent Kunming-Montreal Global Biodiversity Framework (COP15, 2022) further emphasizes marine biodiversity's value. Therefore, the implementation of this method, focused on biological aspects, will be essential to pursue both conservation and human-related objectives. To generate valuable data and achieve more beneficial outcomes, collaborative, multidisciplinary efforts in seabed mapping are needed.

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Sincere thanks to my family and friends, who have always supported me throughout this journey. I would also like to dedicate a special thought to my grandfather Armido and my great-uncle Silvestro, whose presence I dearly miss, and who I wish could have been here to witness the completion of this path.

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Supplementary Material

S1. Considered morphotypes

	Description	**Proposed taxonomy**
Anemones	Black or orange in color, they exhibit tentacles and are sometimes found with a stem.	Actiniaria/Ceriantharia
Branched black corals	They present a thin branched structure and are dark-colored.	*Antipathes furcata*
Crinoids	Distinguishable by their feathery aspect. They are often banded alternating lighter and darker parts.	*Leptometra celtica*
Golden corals	Characterized by a "bottle-brush" structure, these organisms have a light color and a distinctive shape.	*Chrysogorgia sp.*
Convoluted laminar sponges	They present a white laminar structure that sometimes presents twists.	Demospongiae
Lollipop sponges	Their aspect is characterized by a clearly defined spherical shape sustained by a stalk attached to the substrate.	*Stylocordyla sp.*
Feathery black corals	A long stem with numerous closely spaced branches creates a fluffy appearance. The color is dark.	Antipatharia

Funnel-like laminar sponges	These organisms have a very large, hollow structure folded into itself, resembling a top hat.	*Asconema setubalense*
Non-laminar sponges	This group contains sponges with a morphology that does not fit into laminar or lollipop categories. They are white or yellow, either encrusting or single.	Demospongiae/ Hexactinellida
Rounded laminar sponges	They present a white laminar structure, with rounded edges. They are commonly found stacked against one other.	Demospongiae
Sea pens	Characterized by a feather-like, branching structure, resembling a quill pen. They typically have a central stalk with polyps arranged along the sides.	Pennatulacea
Whip corals	Their morphology clearly displays a sequence of polyps along a straight, either convoluted or stiff, rod-like structure.	*Viminella flagellum*
White branched corals	These organisms are colonies of polyps that form branch-like structures, likely ascribable to corals.	Anthozoa
White laminar corals	A branched structure is visible, but fused to form a foil-like shape. They are white.	Anthozoa

Pink fan corals	Hard corals that form large, pink, fan-like structures.	*Eunicella sp.*

Table S1: *This table displays the morphotypes that were considered in the analysis and the main characteristics that helped with their identification. Where feasible, it is reported the estimated species or the lower taxonomic group.*

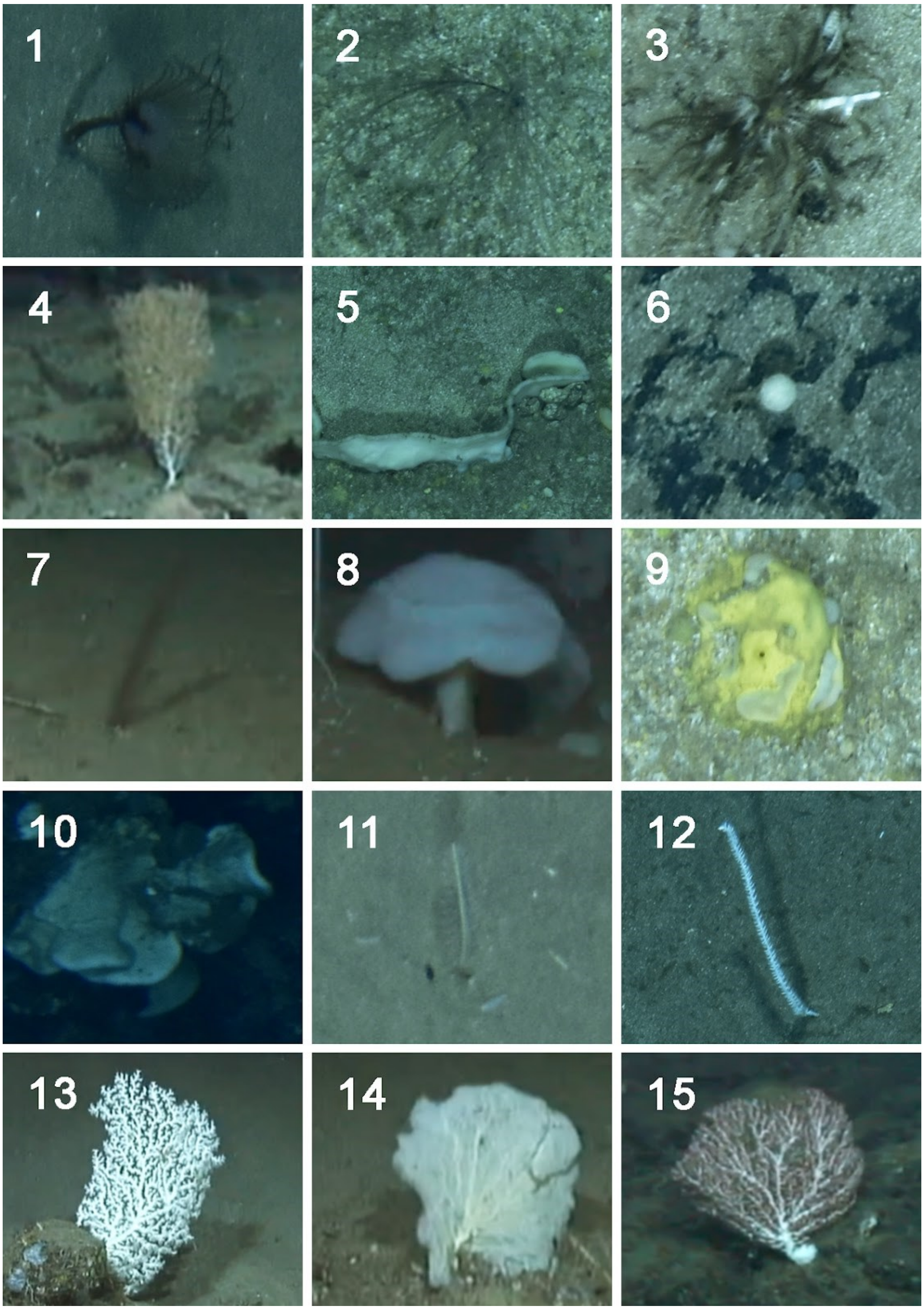


Figure S1: *Pictures of morphotypes considered in the analysis. 1) Anemones 2) Branched black corals 3) Crinoids 3) Golden corals 5) Convoluted laminar sponges 6) Lollipop sponges 7) Feathery black corals 8) Funnel-like laminar sponges 9) Non-laminar sponges 10) Rounded laminar sponges 11) Sea pens 12) Whip corals 13) White branched corals 14) White laminar corals 15) Pink fan corals*

S2. Excluded morphotypes

Among the unclassified organisms, four raised particular interest, leading to identification attempts. Although conclusive identification was not possible, some hypotheses are presented here.

Little white branched organisms

In the XOFOS 10-1 transect, several small, sparsely branched specimens were found aggregated, particularly on soft substrate. The challenge was represented by the lack of references to determine whether they were juvenile individuals of larger species or dead individuals. Their identification remained uncertain (if they were corals, bryozoans, or something else). Although they were significant due to their abundance, no feedback was received from experts.

Reef-forming corals

Similar challenges were encountered as with the others, but these specimens were somewhat more distinguishable, though identifying the phylum was still not possible. They exhibited highly varied morphologies and intricate structures, but their restricted distribution led to their exclusion from further consideration.

White foam

This morphotype was observed at several sites, but the resolution did not allow for distinguishing whether it is a bryozoan, cnidarian, or sponge. In the label tree, it is placed under cnidarians.

Protists-resembling

Found only in XOFOS 10-1, these resemble large protist formations, composed by Xenophyophores, enlisted among VME species indicators by ICES (ICES, 2024b). Their identification is uncertain, and with only six observations they were excluded from further analysis.

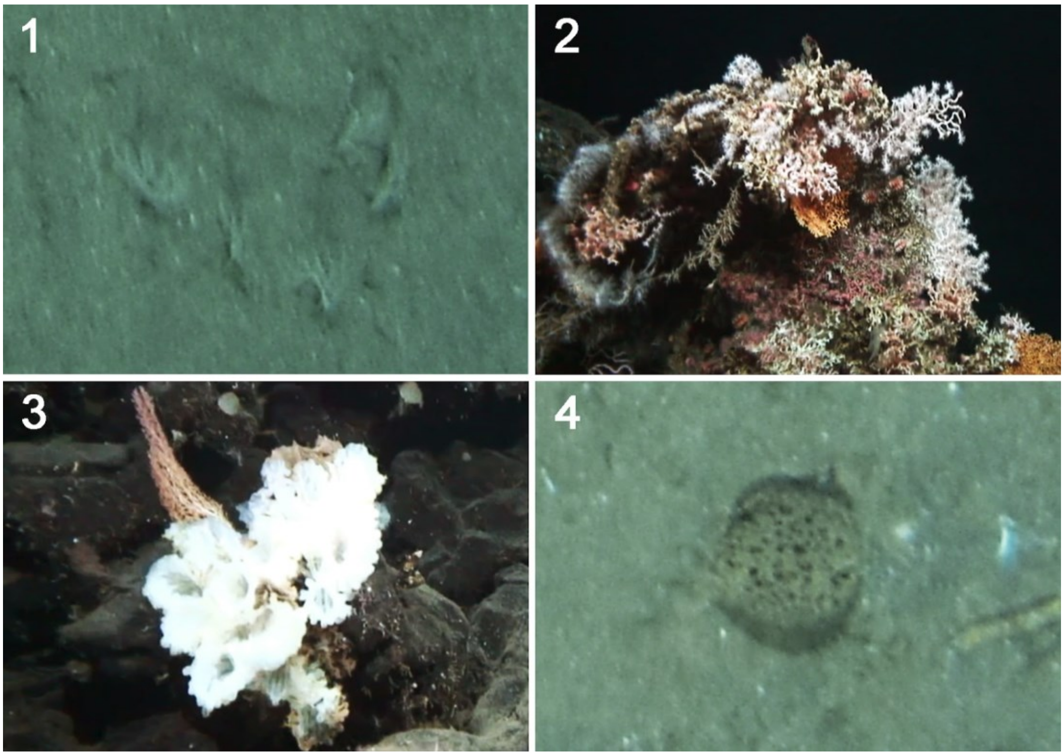


Figure S2: *Pictures of morphotypes excluded from the analysis. 1) Little white branched organisms 2) Reef-forming corals 3) White foam 4) Protists-resembling*

S3. Identification attempt

The aim of this study was not to identify organisms at the species level, but rather to classify them by morphotype. However, despite the lack of physical samples, it may still be both interesting and relevant to identify some of the observed organisms. Below is a list of the most likely identifications for each group, alongside some considerations regarding choices that were made.

Cnidaria

Whip corals, specifically *Viminella flagellum*, have been reported in NE Atlantic in several studies and guides (Braga-Henriques et al., 2013; Braga-Henriques et al., 2022; Oliveira et al., 2017; Taranto et al., 2023). According to WoRMS, its distribution is confirmed within the investigated area, and its diffusion would suggest that this species may correspond to the observed whip corals (WoRMS, 2024b). As for branched black corals, *Antipathes furcata* appears to be the most accurate identification. While several species of black corals have been recorded in the NE Atlantic (WoRMS, 2024a), this species is the one that most closely resembles the specimens observed in the transects. Golden corals have been reported in one study conducted in the NE Atlantic (Braga-Henriques et al., 2013), and their presence has been confirmed by online research (WoRMS, 2024c.). These specimens belong to the family Chrysogorgiidae, but an assessment of the species and genus is uncertain, with a more likely belonging to the genus *Chrysogorgia.* As for the white branched corals, multiple hypotheses have been considered. As previously mentioned, they certainly belong to different species and fall within this category because of their morphology. *Eunicella* is a genus of fan-shaped octocorals, reported in NE Atlantic by different studies (Braga-Henriques et al., 2013; Braga-Henriques et al., 2022; Nestorowicz et al., 2021). Its morphology resembles some of the fan-shaped white and pink corals, and specimens can be found in these two different colorations. Unfortunately, there are no tools to state if these two morphologies belong to the same species.

Echinoderms

Two morphotypes of sea urchins were observed. One is likely from the genus *Echinus*, though its identification is less significant due to its low occurrence. The other morphotype, which was much more common, is almost certainly *Cidaris*

cidaris, a species widely reported in several studies and field guides (e.g., Nestorowicz et al., 2021; Oliveira et al., 2017). Concerning Crinoidea, the resolution of the images makes it difficult to determine the exact species. Oliveira et al. (2017), Nestorowicz et al. (2021), and WoRMS (WoRMS, 2024d) all note the presence of *Leptometra celtica* in the NE Atlantic, and the observed individuals resemble this species. However, a definitive identification cannot be made. Based on current evidence, it is possible to assign these crinoids to the order Comatulida.

Crustaceans

The only organism that can be confidently identified is *Cerataspis monstrosus* (NOAA, 2024b; WoRMS, 2024e.). As for the other species, tentative identifications were made, but they are not reported as they do not play a significant role in habitat formation and the confidence is lower compared to *C. monstrosus*. Like other mobile species, they were included in the analysis to understand their distribution in relation to the presence of specific habitats.

Fish

The shark observed in the XOFOS 10-1 transect is probably belonging to the genus *Deania*. While the species identification is not certain and not crucial to the study, that annotation might be meaningful due to the vulnerability of sharks as K-selected species (Pacoureau et al., 2021). Frequent observations were attributed to grenadiers (order Gadiformes, family Macrouridae, subfamily Macrourinae) and Halosauridae, although species-level identification was not possible. However, clear identifications were made for *Laemonema yarrellii* and *Scorpaena maderensis*. They were both reported by Oliveira et al. (2017), with the latter being typical of Madeira, as its name suggests.

Porifera

This phylum posed the greatest challenge for identification, making a definitive classification impossible. However, some laminar sponges could potentially be assigned to *Asconema setubalense*, while certain spherical sponges resemble *Topsentia*. On the other hand, lollipop sponges were easier to identify due to their distinctive structure, and they were found in two colors: blue and white. For the blue specimens, Oliveira et al. (2017) suggest they likely belong to the genus *Stylocordyla*. The white lollipop sponges are also thought to be *Stylocordyla*, but they could belong to other genera as well. Oliveira et al. (2017) identify *Stylocordyla pellita* as a white species found in the studied region. Another species reported in the NE Atantic is *Stylocordyla borealis*. Oliveira also mentions *Podospongia lovenii* and *Sympagella delauzei*, which closely resemble the observed organisms. Due to the limited knowledge and the absence of complete image databases, this identification remains hypothetical and open to any other improvements. This uncertainty leads to the decision to refer to them collectively as lollipop sponges.

S4. Label tree

This is the label tree used on BIIGLE to label the organisms. The names of certain labels were changed during the analyses.

- algae_and_leaves
- ascidian
- bin
    - blackcoralbranches
    - compactdrybushes
    - deadwhitecorals
    - exwhitesinglesponges
    - exyellowsinglesponges
- cnidaria
    - anemones
        - anemones_generic
        - anemones_orange
    - blackcorals
        - blackcorals_branched
        - blackcorals_feathery
        - blackcorals_filiform
    - goldencorals
    - laminarwhitecorals
    - pennatulacea
    - pinkfancorals
    - redcorals
    - redorangetentacles
    - reefformingcorals
        - RF1
        - RF2
        - RF3
        - RF4
        - RF5
        - RF6
        - RF7
        - RF8
        - RF9

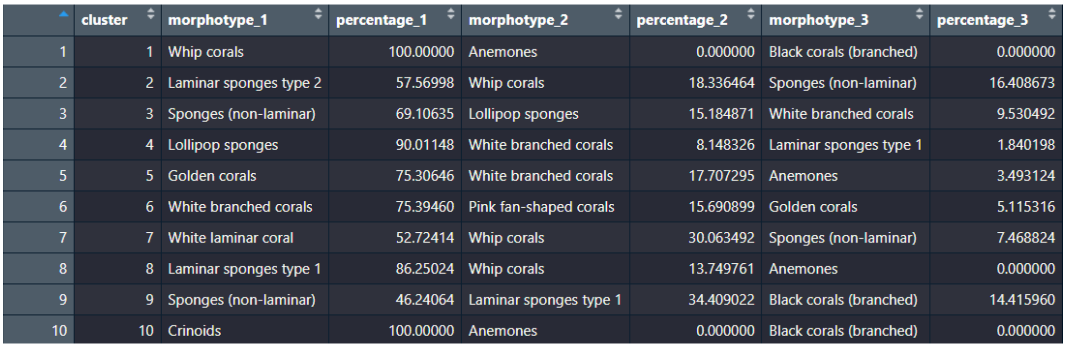
    - whipcorals
        - whipcorals_thick
        - whipcorals_thin
    - whitebranchedcorals
        - WB1_hand
        - WB2_leaf
        - WB3_fan
        - WB4_thunder
        - WB5_pearl
        - WB6_plant
        - WB7_tree
        - WB8_conic
        - WB9_thick
        - WB10_fluffy
        - WB11_greyfan
        - WB12_hexagon
        - WB13_fanlittle
        - WB14_cauliflower
        - WB15_v
        - WB16_long
        - WB17_irregular
        - WB18_compact
    - whitefoam
    - yellowfeathery
- crustacea
    - crustaceans_unident
    - decapoda
        - dendrobranchiata
            - penaeoidea
                - aristeidae
                    - aristeus_antennatus
                    - cerataspis_monstrosus
                - benthesicymidae
        - pleocyemata
            - anomura
                - chirostyloidea

            - galatheoidea
            - paguroidea
        - brachyura
        - caridea
            - longantennae
            - orangespottedshrimp
            - striped
- echinoderm
    - asteroidea
        - stars_bigger
        - stars_little
    - crinoidea
        - crinoidea_aggregating
        - crinoidea_orange
        - crinoidea_yellowforked
    - echinoidea
        - cidaris_cidaris
        - echinoidea_unidentified
        - spherical_echinus
    - ophiuroidea
- fish
    - chondrichthyes
    - teleosts
        - 1_bigbeast
        - F2_bluebrown
        - F3_blueblackbottomdweller
        - F4_blueeellike
        - F5_blueandwhitemustache
        - F6_chaunacidae
        - F7_congerlike
        - F8_darkfusiform
        - F9_flatfish
        - F10_forkedtail
        - F11_green
        - F12_halosauridae
        - F13_laemonemayarrellii

        - F14_macrourinae
        - F15_new
        - F16_orangebottomdweller
        - F17_fishable
        - F18_redred
        - F19_sardinelike
        - F20_scorpaenamaderensis
        - F21_striped
        - F22_stripedblue
        - F23_white
        - F24_whiteorange
        - F25_genericteleost
- humantrace
- mollusc
    - chiton_or_isopod
    - clam
    - squid
- porifera
    - laminarsponges
        - LS1_purelaminar
        - LS2_rounded
        - LS3_asconema_setubalense
        - LS4_largefoil
    - singlesponges
        - singlesponges_white
            - white_generic
            - white_spiny_topsentia
            - white_tubular
        - singlesponges_yellow
        - stylocordyla
            - stylocordyla_blue
            - stylocordyla_white
    - spreadsponges
        - spreadsponges_white
        - spreadsponges_yellow
- shell

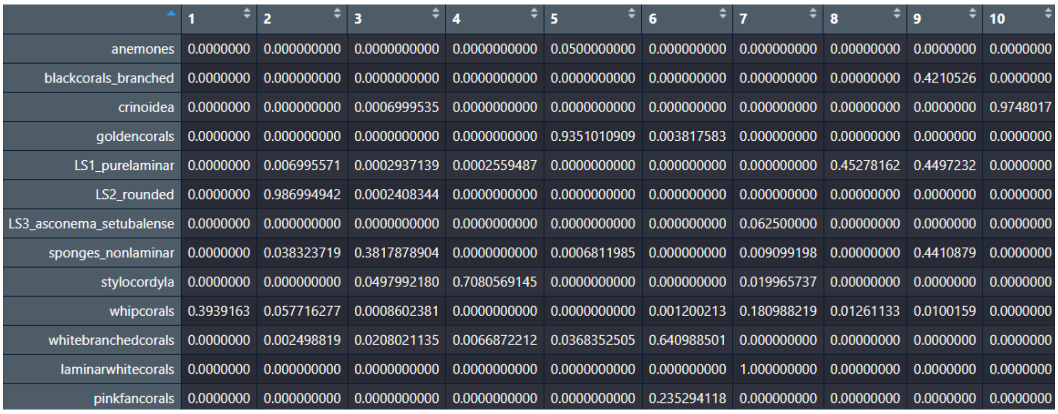
- unknown
    - anemonestructured
    - coralresembling
        - blackstiffrods
        - copper_maybeblack
        - generic_corallike
        - littlewhitebranched
        - triangles
    - crinoidlike
    - dead
    - floating
    - protist_macro
    - redbush
    - spongelike
    - temaki
    - veryunknown
    - wormy
- worm
    - longworm
    - platyhelminthes

S5. Habitat description: supplementary tables



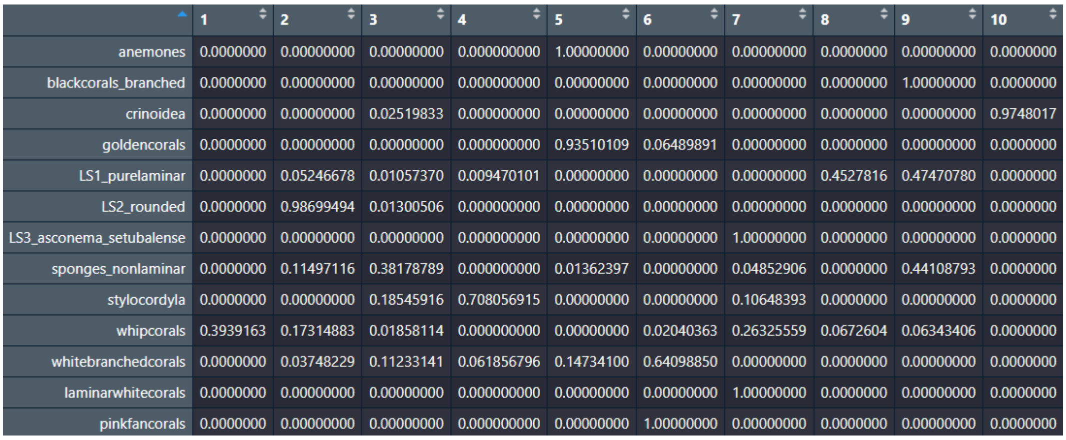
	cluster	morphotype_1	percentage_1	morphotype_2	percentage_2	morphotype_3	percentage_3
1	1	Whip corals	100.00000	Anemones	0.000000	Black corals (branched)	0.000000
2	2	Laminar sponges type 2	57.56998	Whip corals	18.336464	Sponges (non-laminar)	16.408673
3	3	Sponges (non-laminar)	69.10635	Lollipop sponges	15.184871	White branched corals	9.530492
4	4	Lollipop sponges	90.01148	White branched corals	8.148326	Laminar sponges type 1	1.840198
5	5	Golden corals	75.30646	White branched corals	17.707295	Anemones	3.493124
6	6	White branched corals	75.39460	Pink fan-shaped corals	15.690899	Golden corals	5.115316
7	7	White laminar coral	52.72414	Whip corals	30.063492	Sponges (non-laminar)	7.468824
8	8	Laminar sponges type 1	86.25024	Whip corals	13.749761	Anemones	0.000000
9	9	Sponges (non-laminar)	46.24064	Laminar sponges type 1	34.409022	Black corals (branched)	14.415960
10	10	Crinoids	100.00000	Anemones	0.000000	Black corals (branched)	0.000000

Table S2: *This table presents the percentages of the transformed abundance of the three most common morphotypes identified in each habitat.*



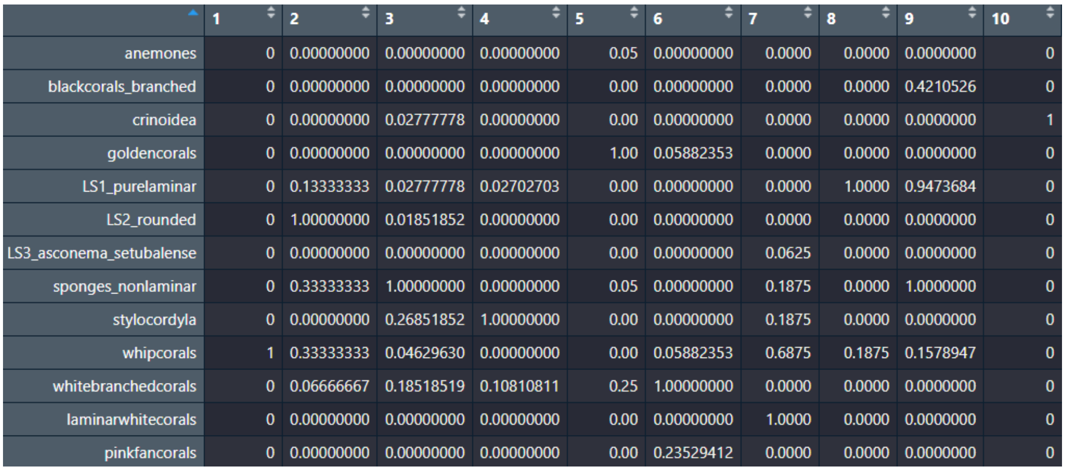
	1	2	3	4	5	6	7	8	9	10
anemones	0.0000000	0.000000000	0.0000000000	0.0000000000	0.0500000000	0.000000000	0.000000000	0.00000000	0.0000000	0.0000000
blackcorals_branched	0.0000000	0.000000000	0.0000000000	0.0000000000	0.0000000000	0.000000000	0.000000000	0.00000000	0.4210526	0.0000000
crinoidea	0.0000000	0.000000000	0.0006999535	0.0000000000	0.0000000000	0.000000000	0.000000000	0.00000000	0.0000000	0.9748017
goldencorals	0.0000000	0.000000000	0.0000000000	0.0000000000	0.9351010909	0.003817583	0.000000000	0.00000000	0.0000000	0.0000000
LS1_purelaminar	0.0000000	0.006995571	0.0002937139	0.0002559487	0.0000000000	0.000000000	0.000000000	0.45278162	0.4497232	0.0000000
LS2_rounded	0.0000000	0.986994942	0.0002408344	0.0000000000	0.0000000000	0.000000000	0.000000000	0.00000000	0.0000000	0.0000000
LS3_asconema_setubalense	0.0000000	0.000000000	0.0000000000	0.0000000000	0.0000000000	0.000000000	0.062500000	0.00000000	0.0000000	0.0000000
sponges_nonlaminar	0.0000000	0.038323719	0.3817878904	0.0000000000	0.0006811985	0.000000000	0.009099198	0.00000000	0.4410879	0.0000000
stylocordyla	0.0000000	0.000000000	0.0497992180	0.7080569145	0.0000000000	0.000000000	0.019965737	0.00000000	0.0000000	0.0000000
whipcorals	0.3939163	0.057716277	0.0008602381	0.0000000000	0.0000000000	0.001200213	0.180988219	0.01261133	0.0100159	0.0000000
whitebranchedcorals	0.0000000	0.002498819	0.0208021135	0.0066872212	0.0368352505	0.640988501	0.000000000	0.00000000	0.0000000	0.0000000
laminarwhitecorals	0.0000000	0.000000000	0.0000000000	0.0000000000	0.0000000000	0.000000000	1.000000000	0.00000000	0.0000000	0.0000000
pinkfancorals	0.0000000	0.000000000	0.0000000000	0.0000000000	0.0000000000	0.235294118	0.000000000	0.00000000	0.0000000	0.0000000

Table S3: *This table presents the IndVal scores of the morphotypes in each habitat.*



	1	2	3	4	5	6	7	8	9	10
anemones	0.0000000	0.00000000	0.00000000	0.000000000	1.00000000	0.00000000	0.00000000	0.0000000	0.00000000	0.0000000
blackcorals_branched	0.0000000	0.00000000	0.00000000	0.000000000	0.00000000	0.00000000	0.00000000	0.0000000	1.00000000	0.0000000
crinoidea	0.0000000	0.00000000	0.02519833	0.000000000	0.00000000	0.00000000	0.00000000	0.0000000	0.00000000	0.9748017
goldencorals	0.0000000	0.00000000	0.00000000	0.000000000	0.93510109	0.06489891	0.00000000	0.0000000	0.00000000	0.0000000
LS1_purelaminar	0.0000000	0.05246678	0.01057370	0.009470101	0.00000000	0.00000000	0.00000000	0.4527816	0.47470780	0.0000000
LS2_rounded	0.0000000	0.98699494	0.01300506	0.000000000	0.00000000	0.00000000	0.00000000	0.0000000	0.00000000	0.0000000
LS3_asconema_setubalense	0.0000000	0.00000000	0.00000000	0.000000000	0.00000000	0.00000000	1.00000000	0.0000000	0.00000000	0.0000000
sponges_nonlaminar	0.0000000	0.11497116	0.38178789	0.000000000	0.01362397	0.00000000	0.04852906	0.0000000	0.44108793	0.0000000
stylocordyla	0.0000000	0.00000000	0.18545916	0.708056915	0.00000000	0.00000000	0.10648393	0.0000000	0.00000000	0.0000000
whipcorals	0.3939163	0.17314883	0.01858114	0.000000000	0.00000000	0.02040363	0.26325559	0.0672604	0.06343406	0.0000000
whitebranchedcorals	0.0000000	0.03748229	0.11233141	0.061856796	0.14734100	0.64098850	0.00000000	0.0000000	0.00000000	0.0000000
laminarwhitecorals	0.0000000	0.00000000	0.00000000	0.000000000	0.00000000	0.00000000	1.00000000	0.0000000	0.00000000	0.0000000
pinkfancorals	0.0000000	0.00000000	0.00000000	0.000000000	0.00000000	1.00000000	0.00000000	0.0000000	0.00000000	0.0000000

Table S4: *This table presents the Specificity (A) values of the morphotypes in each habitat.*



	1	2	3	4	5	6	7	8	9	10
anemones	0	0.00000000	0.00000000	0.00000000	0.05	0.00000000	0.0000	0.0000	0.0000000	0
blackcorals_branched	0	0.00000000	0.00000000	0.00000000	0.00	0.00000000	0.0000	0.0000	0.4210526	0
crinoidea	0	0.00000000	0.02777778	0.00000000	0.00	0.00000000	0.0000	0.0000	0.0000000	1
goldencorals	0	0.00000000	0.00000000	0.00000000	1.00	0.05882353	0.0000	0.0000	0.0000000	0
LS1_purelaminar	0	0.13333333	0.02777778	0.02702703	0.00	0.00000000	0.0000	1.0000	0.9473684	0
LS2_rounded	0	1.00000000	0.01851852	0.00000000	0.00	0.00000000	0.0000	0.0000	0.0000000	0
LS3_asconema_setubalense	0	0.00000000	0.00000000	0.00000000	0.00	0.00000000	0.0625	0.0000	0.0000000	0
sponges_nonlaminar	0	0.33333333	1.00000000	0.00000000	0.05	0.00000000	0.1875	0.0000	1.0000000	0
stylocordyla	0	0.00000000	0.26851852	1.00000000	0.00	0.00000000	0.1875	0.0000	0.0000000	0
whipcorals	1	0.33333333	0.04629630	0.00000000	0.00	0.05882353	0.6875	0.1875	0.1578947	0
whitebranchedcorals	0	0.06666667	0.18518519	0.10810811	0.25	1.00000000	0.0000	0.0000	0.0000000	0
laminarwhitecorals	0	0.00000000	0.00000000	0.00000000	0.00	0.00000000	1.0000	0.0000	0.0000000	0
pinkfancorals	0	0.00000000	0.00000000	0.00000000	0.00	0.23529412	0.0000	0.0000	0.0000000	0

Table S5: *This table presents the Fidelity (B) values of the morphotypes in each habitat.*

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