Fine-scale variability in habitat selection and niche differentiation between sponges and cold-water corals on vertical walls of the Charlie-Gibbs Fracture Zone

Ana Belén Yánez-Suárez [a,b] [ID],[*], Loïc Van Audenhaege [c], Tyler D. Eddy [d], Katleen Robert [a]

[a] School of Ocean Technology, Fisheries and Marine Institute, Memorial University of Newfoundland and Labrador, Canada
[b] School of Fisheries, Fisheries and Marine Institute, Memorial University of Newfoundland and Labrador, Canada
[c] Ocean BioGeosciences, National Oceanography Centre, European Way, Southampton, United Kingdom
[d] Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute, Memorial University of Newfoundland and Labrador, Canada

ARTICLE INFO

ABSTRACT

Deep-sea vertical walls are characterized by enhanced hydrodynamics and hard substrates, making them particularly suitable habitats for suspension feeders, including vulnerable marine ecosystems (VMEs) indicator taxa, like cold-water corals (CWC) and sponges. These species enhance the complexity of the abiotic background and the retention of trophic resources increasing habitat availability for other organisms. While some areas of vertical walls present a high density of VMEs, others are mostly bare rock. However, the habitat characteristics that favor the presence of CWC and sponges within vertical walls at a fine-scale (under 1 m) are still poorly understood despite their ecological importance. Owing to technological limitations, fine-scale terrain variables (e.g., orientation, curvature, verticality, roughness, slope) have seldom been quantified in deep-sea habitats. These terrain variables can represent proxies of community structuring factors (e.g., hydrodynamics conveying food, sedimentation rates) important to understand habitat selection of VME indicator species. In this study, we investigate the fine-scale habitat selection and niche differentiation of CWC and sponges on vertical walls of the Charlie-Gibbs Fracture Zone. Structure-from-motion photogrammetry was employed to create high-resolution 3D models of three vertical walls based on remotely operated vehicle (ROV) videos (at 1060-1901 m depth). The 3D models were used to derive terrain variables at fine-scale and geotag corals and sponges. Using ecological niche factor analysis, we reveal that corals and sponges selected habitat features that significantly differ from the average habitat available. The corals and sponges studied showed large or complete niche partitioning. *Solenosmilia* sp. had total niche separation with *Geodia* spp. and globular sponges and partial separation with *Hertwigia* spp., while Scleralcyonacea showed partial niche separation with *Geodia* spp. and globular sponges. Conversely, the niches of closely related sponges were more similar. This research advances our understanding of the processes enabling species co-existence among these organisms and the factors influencing habitat preferences of VME indicator species on steep underwater landscapes.

1. Introduction

The deep sea harbors heterogeneous landscapes and resembles the complex topography observed on land (e.g., seamounts, cliffs, canyons) (Gage and Tyler, 1991). However, owing to past technological limitations like lower-resolution down-looking shipboard multibeam echosounders (Huvenne et al., 2011) and towed video systems (Robert et al., 2017), vertical walls, remain understudied (Robert et al., 2020). Only since the 1990s, when occupied submersibles (Haedrich and Gagnon, 1991) and remotely operated vehicles (ROV) became more common, did the study of vertical walls become achievable, as their full potential for hosting diverse communities was realized (Huvenne et al., 2011; Johnson et al., 2013; Van Audenhaege et al., 2021).

Deep-sea vertical walls can lead to complex hydrodynamic patterns (Hall et al., 2017; Harris and Whiteway, 2011; Zhu et al., 2019) due to the interaction of currents with the complex topography (Hall et al., 2017; Obelcz et al., 2014; Greiffenhagen et al., 2024). They are characterized by low sedimentation rates and hard substrates (Robert et al., 2020), making them suitable habitats for sessile filter feeders, including vulnerable marine ecosystem (VME) indicator taxa such as cold-water corals (CWC) and sponges (Huvenne et al., 2011; Robert

et al., 2020) important ecosystem engineers that provide habitat for other organisms. Although longlines and nets entangled with corals have been reported on deep-sea vertical walls (Fabri et al., 2014; Orejas et al., 2009), owing to their steep topography and high complexity, vertical walls are not targets of bottom trawling and may serve as a refuge (Huvenne et al., 2011; Robert et al., 2020). As a result, these walls may act as a source of larvae to recolonize surrounding impacted areas (Huvenne et al., 2011; Smith and Witman, 1999).

Highly heterogeneous structures such as vertical walls provide more micro-habitats to be used by diverse taxa (MacArthur, 1958; Robertson and Sheldon, 1979), enabling co-existence through a process known as niche differentiation (Williams, 1964; Zuppinger-Dingley et al., 2014). The ecological niche concept, developed by Grinnell (1917) and Elton (1927), explains species distribution and interactions within ecosystems. The Grinnellian niche focuses on the impact of geographical habitat and its biotic and abiotic components on species distribution, while the Eltonian niche emphasizes biotic interactions like food webs. Hutchinson (1957) expanded this by describing the ecological niche as an hypervolume in the multidimensional space defined by environmental variables where a species can be sustained (Hutchinson, 1957, 1978), and the realized niche is the actual subset of these conditions where the species lives, narrowed by external pressures (Colwell and Rangel, 2009). Niche overlap and niche separation based on the Hutchinson definition, can be quantified by examining habitat selection of CWC and sponges across a range of scales. At broader scales factors such as depth, water mass temperature, oceanic currents, may be more important while at finer scale components such as terrain variables and local currents may be more important (Amaro et al., 2016; Dolan et al., 2008; White and Dorschel, 2010), but all scales need to be characterized in order to delineate a species habitat preference (García and Ortiz-Pulido, 2004; Lecours et al., 2015).

Terrain variables capturing topographic complexity (e.g., slope, rugosity, orientation) can act as proxies for biotic and abiotic factors harder to quantify (e.g., food availability, wave action, sedimentation rates, local currents) (Dolan et al., 2008). Mega (1 to 10 s km) and meso (10s m to 1 km) scale (Greene et al., 1999) topographic variables can be used to develop coarse predictive habitat models to identify potential areas where species may be present (Guinan et al., 2009). However, environmental variables at mega and meso scales do not capture local habitat features, nor do biotic and abiotic processes at the scale experienced by megabenthic organisms. For example, fine-scale rugosity can capture the complexity of abiotic (e.g., small crevices formed between rocks) and biotic structures (e.g., hard coral complexity), while slope and orientation can serve as proxies for local currents and food. These variables have long been used in studying the ecology of shallow-water coral reefs (Kovalenko et al., 2012) as shallow waters coral larvae make important choices regarding habitat selection even at a millimetric scale (Price, 2010; Speare et al., 2023). Recent advancements in structure-from-motion (SfM) photogrammetry now enable the creation of 3D reconstructions from video, facilitating the extraction of fine-scale topographic information (Price et al., 2019; Robert et al., 2017, 2020).

In this study, we obtained fine-scale environmental variables using SfM photogrammetry in order to understand habitat preferences and niche differentiation of CWC and sponges on vertical walls, allowing us to examine how different VME-indicator taxa may partition environmental space within specific wall locations. This study will contribute to further our understanding of the role of vertical wall heterogeneity in promoting species co-existence in the deep sea.

2. Materials and methods

2.1. Study site

The Charlie-Gibbs Fracture Zone is a prominent geological and topographic feature that divides the Mid-Atlantic Ridge (Olivet et al.,

Table 1
Coordinates (UTM Zone 25N) and depth range for each vertical wall reconstruction created in Agisoft Metashape.

Wall	Easting Start	Northing Start	Easting End	Northing End	Depth range (m)
D7	605 387	5 801 196	605 388	5 801 216	1414–1430
D8	637 004	5 794 761	637 021	5 794 748	1060–1083
D9	621 983	5 794 055	621 995	5 794 083	1848–1901

1974), located approximately mid-way between Iceland and the Azores (Priede et al., 2013). Subtropical and subpolar waters meet in the CGFZ (Søiland et al., 2008), creating a high-nutrient convergence zone that promotes an abundance of zooplankton (Taylor and Ferrari, 2011) which supports a high biodiversity (Priede et al., 2013). Due to this high biodiversity (Mortensen et al., 2008; Gebruk and Krylova, 2013), the CGFZ was declared a marine protected area (The Charlie-Gibbs South High Seas MPA (OSPAR, 2010)), one of the first MPA established in international waters. Subsequently, in 2013, a second MPA was established to protect the north of the CGFZ where this study took place, but it only covers the water column (OSPAR, 2012).

2.2. Data collection

During the Tectonic Ocean Spreading at the Charlie-Gibbs Fracture Zone (TOSCA) expedition onboard the RV Celtic Explorer in May-June 2018 (CE18008 Cruise Report, 2018), video transects were conducted using the ROV Holland I equipped with a high-definition oblique-facing camera (Kongsberg Maritime OE14-502a HDTV, 1080i resolution, 25 frames per second) (Fig. 1). The ROV position was continuously recorded using Ultra Short Baseline (USBL) systems (IXSEA GAPS USBL and Sonardyne Ranger 2 USBL, with an accuracy of 1% of the depth). The ROV flew at 0.3 knots at an approximate altitude of 1.5 m above the seabed.

2.3. 3D reconstruction and taxa geotagging

Sections of vertical walls were identified from the video transects, and using the software Blender 2.92, one frame per second was extracted from these video sections and georeferenced based on USBL positioning. Applying structure-from-motion (SfM) photogrammetric techniques, three vertical walls, one in each of the dives 7, 8 and 9 (Table 1, Fig. 2A), were reconstructed using Agisoft Metashape (v.1.6.1). The SfM process consisted of frame alignment, followed by masking of visible ROV components or low light areas in individual frames. Subsequently, markers were set on the lasers (0.1 m distance) in individual frames to create scale bars used to optimize aligned frames and estimate the error between known laser separation and the reconstructed model (Robert et al., 2017). The absolute error in the reconstructed camera location was 10 to 20 m, in line with the known error for USBL navigation (1% of depth). However, within each 3D reconstruction, the relative geolocation errors for individual organisms were < 0.01 m. Dense point clouds were then created, selecting high-quality depth maps generation to obtain a more detailed and accurate geometry. Each dense point cloud was scrutinized to identify distortions and errors, then the dense cloud confidence was checked, and points with the lowest confidence values were deleted. The dense point cloud was exported as XYZ into CloudCompare (v.2.12.4).

2.4. Extraction of biological data

Sponge and coral colonies larger than 4 cm were identified and geotagged in the 3D reconstructions using markers in Agisoft Metashape (Fig. 2B) and exported as text files. The species catalogue produced by Keogh et al. (2022) was used together with the Standardized Marine Taxon Reference Image Database (SMarTaR-ID V1 Consortium 2022) for identifications. Organisms were identified to the highest taxonomic
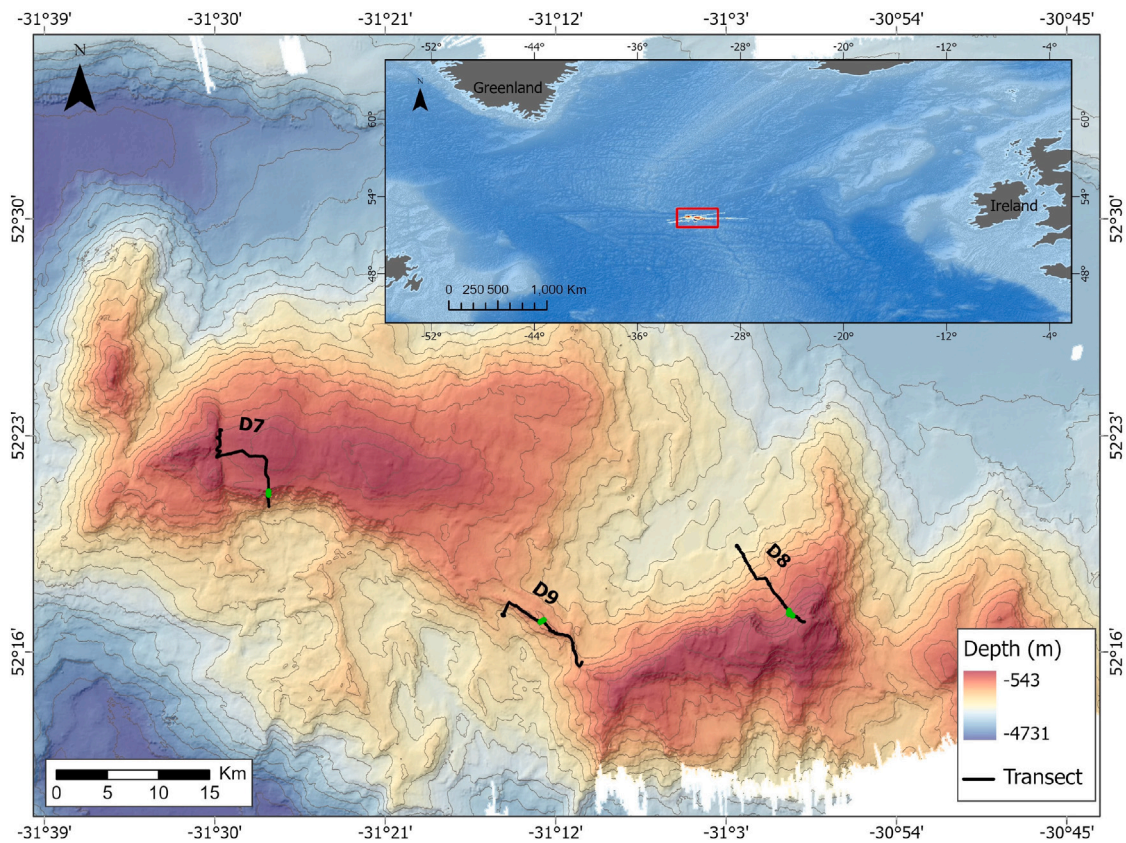
Fig. 1. Bathymetry of the Charlie-Gibbs Fracture Zone (CGFZ) and location of the three ROV transects (dives 7, 8 and 9) from the TOSCA survey in which 3D reconstructions were carried out (the green shapes highlight the position of the reconstructed vertical walls sections). Contour lines are at 200 m depth intervals. The Inset map showing the location of the CGFZ-TOSCA survey is highlighted in a red box. Bathymetry (UTM Zone 25N) from the GEBCO Compilation Group (2023) and world continent shapefile from ESRI.

level possible based on their morphologies and colors. When species-level identification could not be achieved due to the limitation of imagery analysis (Howell et al., 2019), organisms were classified as morphotaxa. For the phylum Porifera, it is common to categorize to morphological groups since most species cannot be identified without a specimen (Bell et al., 2006; Schönberg, 2021). For the analysis three genera (Scleractinian *Solenosmilia* sp., and Poriferans *Hertwigia* spp. and *Geodia* spp.) and two morphotaxa (containing more than one species) were studied. *Geodia* spp likely included three species of *Geodia* that due to lack of physical samples could not be confidently separated (cf. *Geodia* megastrella and two other similar *Geodia* sp.). Globular sponges (different from *Geodia* spp) identified to belong to the class Demospongiae were grouped as reliable distinction could not be achieved and these taxa are likely to be close functionally (Schönberg, 2021). Finally, fan-shaped Octocorals of the family Coralliidae (three morphotaxa) and one organism possibly belonging to the family Primnoidae were grouped by their order Scleralcyonacea. Identification of sponges and octocorals was confirmed by taxonomic experts (Supplementary material S1 Image catalogue). The organisms investigated in this study are considered vulnerable marine ecosystems (VME) indicator taxa (FAO, 2008) due to their uniqueness, functional significance, fragility, and structural complexity.

2.5. Extraction of habitat descriptors

For each dense cloud uploaded as an XYZ file in CloudCompare, normals (defined as vectors orthogonal to the plane) were calculated using a quadratic local model (previously called height function) and a local neighborhood radius or "Kernel radius", set to six different scales (0.02, 0.05, 0.1, 0.2, 0.3, 0.5 m) to capture a range of fine-scale topographic descriptors. Six terrain variables, in addition to depth,

were computed (Fig. 2C) at each scale. These terrain variables included slope, aspect later converted to northness and eastness in the R statistical software (v.3.6.3, R Core Team (2020)), roughness, mean curvature, and verticality, leading to 36 terrain variables (see Wilson et al. (2007) for descriptions). In order to improve subsequent analysis speed, the point clouds were sub-sampled to a minimum distance between points of 0.15 m in CloudCompare and exported as text files.

2.6. Statistical analysis

Text files of georeferenced VME indicator taxa and terrain variables were loaded in the R statistical software (v.3.6.3, R Core Team (2020)), where the K-nearest neighbor algorithm function "nn2" from the "RANN" package was applied (K=10) to compute the mean habitat conditions for each individual organism. The entire dataset of terrain variables was used to describe the background habitat for each wall.

To identify the niche and habitat selection of the target morphotaxa, we used Ecological Niche Factor Analysis (ENFA) and Outlying Mean Index (OMI) for each vertical wall (Chu et al., 2019; Husson et al., 2017). Conducting the analysis per wall ensured that the habitat selection was assessed in function of the local fine scale environmental conditions experienced by the species as opposed to broadening the range of conditions experienced across broader spatial scales. For instance, favorable local currents affecting one wall will not necessarily be the same on a wall several kilometers away, and merging multiple locations into the same analysis would likely lower our capability to disentangle fine-scale factors.

ENFA is a multivariate analysis built on Hutchinson's ecological niche concept (Hirzel et al., 2002). In practice, the ENFA approximates the niche hypervolume with a principal component analysis (PCA). ENFA is a presence-only analysis that compares where the focal
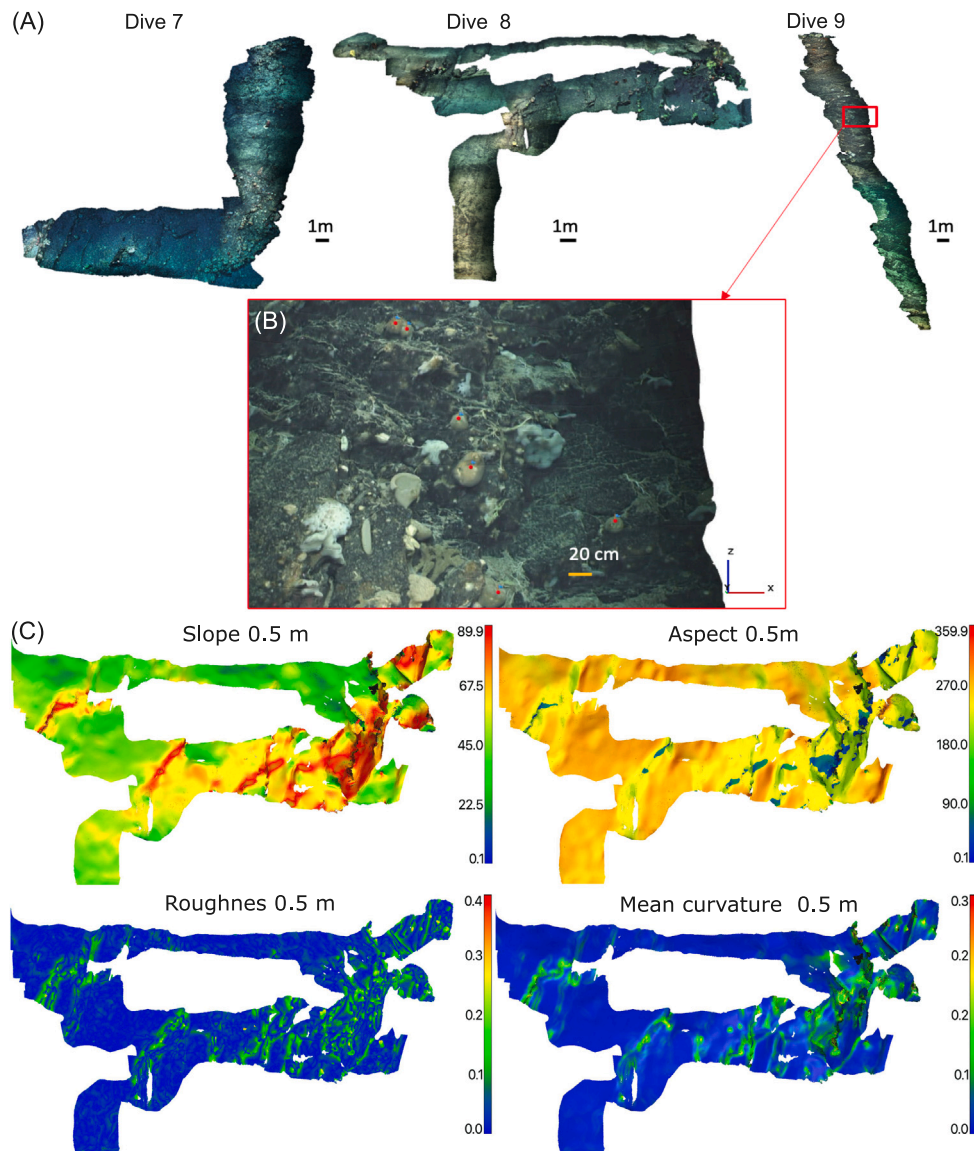
Fig. 2. (A) 3D point clouds of the vertical walls in Dive 7, Dive 8 and Dive 9. (B) Close-up showing taxa geotagged by red dots (*Geodia* spp.) and the resolution achieved in the 3D model. (C) Four of the terrain variables computed on dense point clouds using CloudCompare (scale 0.5 m).

species was observed to a reference set describing the entire study area (background habitat) (Hirzel et al., 2002). It provides a measure of the realized niche within available environmental conditions by computing two parameters: marginality and specialization. Marginality measures the departure of the niche (i.e. environment used) from the environment available (i.e. background), identifying the preference of the population or species for specific environmental conditions (Basille et al., 2008). It is a vector computed as the squared distance from the mean available environmental conditions to the mean used environmental conditions (Hirzel et al., 2002). Specialization represents the narrowness of the niche in comparison to the overall habitat conditions available to the species (Hirzel et al., 2002). The narrower the niche, the higher the specialization, indicating that the species is less tolerant to environmental variation (Basille et al., 2008). ENFA is helpful in answering where the organisms can establish (niche) and what they are searching for (habitat selection), as well as identifying which variables are the most important (Basille et al., 2008).

To compute ENFA, we used the "adehabitatHS" package (Calenge, 2022) in R statistical software (R Core Team, 2020) where the "enfa" function allows the projection of the niche on an orthogonal plane

where marginality corresponds to the X axis and specialization to the Y axis. Although ENFA is robust to collinearity (Sillero and Barbosa, 2021), before performing ENFA, environmental data collinearity was minimized by discarding the variable with lowest influence in marginality, from pairs of variables exhibiting a Pearson r > 0.5. Data frames containing habitat conditions used for each individual species (used habitat) and the background environmental condition (environment available) were combined in one environmental matrix (E) for each wall (E=NxP, where columns P correspond to the terrain variables, and *N* rows representing individual presences and background points) (Calenge, 2011). Considering the different extents of the 3D reconstructions, 5735 points were used as background for Dive 7 (D7); 13,538 points for Dive 8 (D8); and 11,749 points for Dive 9 (D9). The datasets were then normalized using square root transformation (Calenge, 2022). ENFA is robust to departure from normality, but it is optimal when the data is nearly symmetric (Basille et al., 2008). PCA was used on the described matrix (E=NxP) as a preliminary multivariate analysis calculated on the transformed environmental data using the function "dudi.pca" from the "ade4" package. Then ENFA was computed on the column-centered and standardized data (duality

diagram) produced by the PCA and a vector containing the utilization weights (ones for presences and zeros for background) associated with each coordinate of the point cloud. A permutation test based on random sampling and implemented in the "randtest" function in the package "adehabitat" (Monte Carlo 999 permutations) assessed the significance of the ENFA analysis for each morphotaxon on each wall.

The Outlying Mean Index (OMI) (Dolédec et al., 2000) was used to assess niche separation among morphotaxa and their environmental tolerance (Chu et al., 2019). OMI analysis identifies the separation of morphotaxa based on the differentiation of their niches using the marginality index. OMI quantifies the disparity between the mean habitat conditions utilized by different species (centroid of a species' realized niche) and the average background habitat conditions found within the sampled area (center of the OMI PCA) (Dolédec et al., 2000). By employing OMI analysis, species are positioned based on their mean OMI, maximizing the discrepancy in their niche compared to a reference. This reference is not characterized by the average or the most prevalent species but rather represents an imaginary ubiquitous species capable of thriving in the broadest range of habitat conditions (Chu et al., 2019; Dolédec et al., 2000). Taxa exhibiting OMI values close to zero are commonly found in habitat conditions that are representative of the study area (common habitats), whereas taxa displaying OMI values higher than zero are associated with habitats that diverge from the average background habitat conditions. OMI also provides a tolerance index that indicates whether a morphotaxon occurs across a narrow or a wide range of environmental conditions. In other words, it indicates whether a taxon is more specialist (low tolerance) or more generalist (high tolerance) (Dolédec et al., 2000). To run the OMI analysis, the habitat conditions utilized by the taxa and the background habitat conditions were merged for each wall, and a vector containing species presence for each data point was created. Then, a PCA was run on the environmental data. The duality diagram obtained from the PCA, together with species presence, was used in the OMI analysis performed in R statistical software using the package "ade4" (Dray and Dufour, 2007) function "niche". A Montecarlo test (999 permutations) was used to assess the significance of niche separation from the average habitat conditions.

3. Results

The three sections of vertical walls reconstructed (wall D7, wall D8, and wall D9) had an area of 132.48 m^2, 282.00 m^2, and 155.34 m^2, respectively, totaling 596.82 m^2. In these three sections of vertical walls, 459 organisms classified as *Solenosmilia* sp. ($n = 250$), Scleralcyonacea ($n = 22$), *Hertwigia* spp. ($n = 51$), globular sponges ($n = 90$) and *Geodia* spp. ($n = 46$) were georeferenced (Table 2).

3.1. Ecological Niche Factor Analysis (ENFA)

The variables defining each species' niche were chosen based on the highest observed marginality values. The species studied on each wall showed the most pronounced habitat selection for terrain variables at a scale of 0.5 m. Hence, only habitat selection observed at this scale was considered further (additional details on ENFA values at the other scales can be found in Supplementary material S2). ENFA analysis revealed significant habitat selection for each taxon (p-value < 0.05) (Table 2), indicating that the habitat used by these taxa significantly differed from the mean habitat conditions. *Solenosmilia* sp. showed the highest marginality (marginality coefficient 6.85 observed in Dive 8), and *Geodia* spp. showed the lowest (marginality coefficient = 0.64, observed in Dive 9).

The hard coral *Solenosmilia* sp. showed its highest marginality values for aspect (represented by northness and eastness), indicating a selection for wall faces with a specific orientation (Figs. 3A and 4A). *Solenosmilia* sp. also occurred in the steepest areas with higher verticality. When the wall had a large variety of overhangs and edges (as

was the case of D8), indirectly measured by mean curvature (Fig. 5), *Solenosmilia* sp. showed a preference for areas with high values of curvature. The ENFA specialization axis (Y-axis) for *Solenosmilia* sp. was mainly driven by high values of roughness.

Scleralcyonacea showed higher selectivity for the shallower areas of the vertical wall in D9 (the only wall where it was observed). Its specialization was defined by high values of roughness (Fig. 6A).

The glass sponge *Hertwigia* spp. preferred habitats with higher values of mean curvature, while orientation was less important for this species. *Hertwigia* spp. showed specialization for areas of high roughness and steep slopes (Fig. 4B).

The globular sponges morphotaxa showed selectivity for steep slopes and higher values of mean curvature. A higher marginality value for specific orientation was observed only in the wider 3D reconstruction where the taxa occurred (wall D7) but not in a narrower wall (wall D9). Deeper areas of the reconstructed sections of vertical walls were selected by this morphotaxon. Globular sponges' specialization was driven by high values of rugosity (Fig. 3B and 6B). *Geodia* spp. also showed higher habitat selectivity for higher values of mean curvature followed by orientation. Its specialization was driven by high values of roughness (Fig. 3C and 6C). Verticality also influenced *Geodia* spp. specialization in the 3D reconstruction that covered the wider vertical wall in D7; this pattern was not observed in the narrower 3D reconstruction of wall D9.

3.2. Outlying mean index (OMI)

The Outlying Mean Index identified varying levels of niche separation among the different species studied within each of the 3D reconstructed vertical walls. Monte Carlo tests (999 permutations) applied to OMI for each vertical wall yielded significant marginality values for each taxon (p-value < 0.05) (Table 3).

Complete niche separation was identified for wall D7, where *Solenosmilia's* marginality and tolerance significantly differed from those of *Geodia* spp. and globular sponges (Fig. 7A). *Solenosmilia's* realized niche was closer to the mean habitat conditions (OMI 1.84), indicating lower marginality than globular sponges and *Geodia* spp. (3.3 and 2.73, respectively). The ellipse of *Solenosmilia* sp. was wider, indicating higher tolerance (Tolerance 0.75) than the other two species (Tolerance 0.38, 0.08, respectively) (Fig. 7A). Conversely, in the second reconstruction where *Solenosmilia* sp. occurred (wall D8), a small section of its realized niche overlapped with the glass sponge *Hertwigia's* niche (Fig. 8A). The niche of *Solenosmilia* sp. was farther away from the mean habitat conditions (intersection of the x and y axes), showing higher marginality than *Hertwigia* spp. (Fig. 8A). *Hertwigia* spp. ellipse was wider and longer than the one of *Solenosmilia* sp., indicating that *Solenosmilia* sp. had a more restricted niche that deviated further from the typical conditions observed and had a lower tolerance to environmental variation than *Hertwigia* spp.

The soft coral morphotaxa Scleralcyonacea, showed low niche overlap with the other species studied on wall D9 (*Geodia* spp. and globular sponges, Fig. 9A). Scleralcyonacea's realized niche center was the farthest from the average habitat (OMI 1.21). This taxon presented a narrower ellipse, indicating lower tolerance (tolerance 0.48) than *Geodia* spp. and globular sponges (tolerance 1.4, 1.3 respectively). In the two wall sections where both globular sponges and *Geodia* spp. occurred, their niches overlapped, indicating similar habitat preferences and little niche differentiation for these related taxa.

4. Discussion

In the reconstructed sections of the vertical walls, the morphotaxa studied selected habitat characteristics that significantly differed from the background habitat available. Notably, corals and sponges showed large or complete niche partitioning, while the niches of more closely
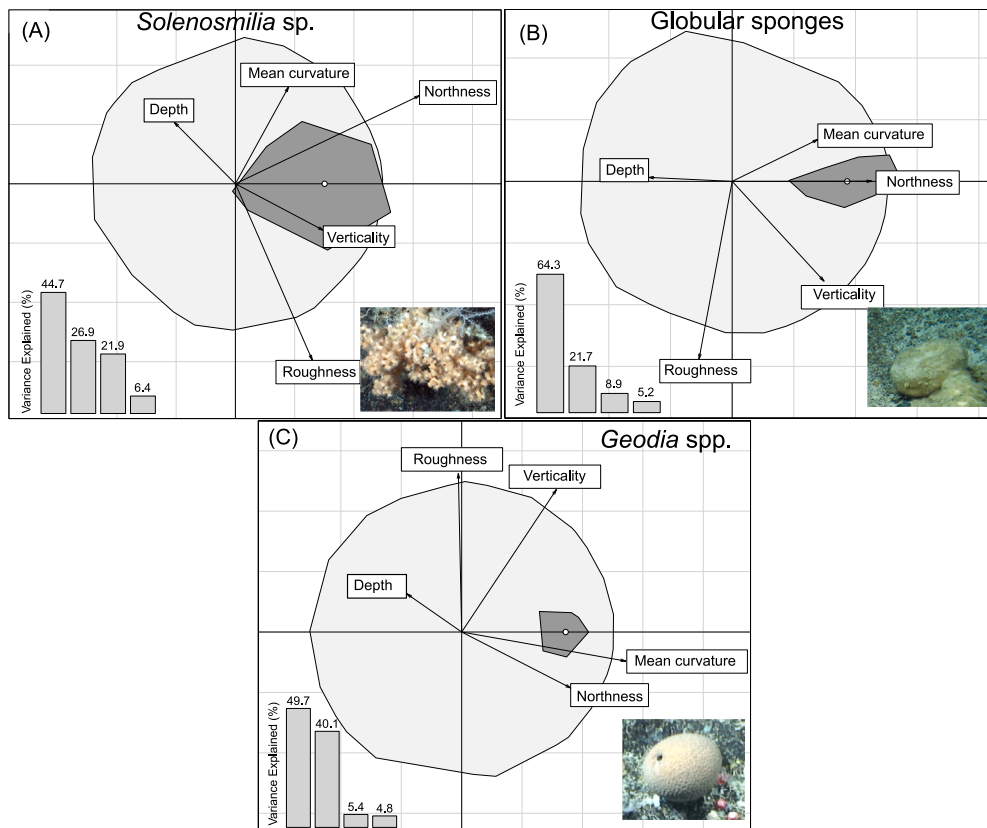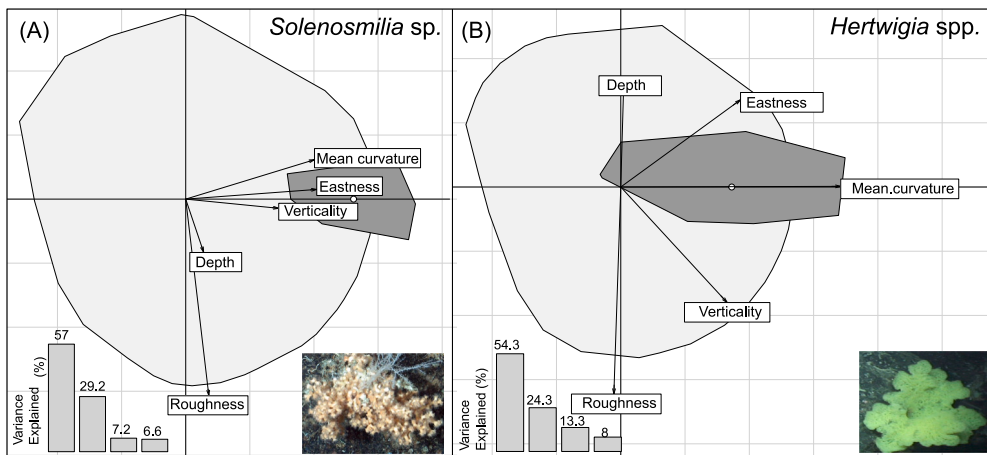
Fig. 3. Vertical wall of Dive 7 (wall D7) Ecological Niche Factor Analysis (ENFA) bi-plots, illustrating the marginality axis (*x*-axis) and the first specialization axis (*y*-axis) for (A) *Solenosmilia* sp., (B) globular sponges, and (C) *Geodia* spp. The light gray polygons represent available habitat, while dark gray polygons depict the habitat occupied by the respective species. Arrows denote projections of environmental variables (scale 0.5 m), and the white dot on the *x*-axis indicates the centroid of the habitat used.

Fig. 4. Vertical wall of Dive 8 (wall D8) Ecological Niche Factor Analysis (ENFA) bi-plots, illustrating the marginality axis (*x*-axis) and the first specialization axis (*y*-axis) for (A) *Solenosmilia* sp., (B) *Hertwigia* spp. The light gray polygons represent available habitat, while dark gray polygons depict the habitat occupied by the respective species. Arrows denote projections of environmental variables (scale 0.5 m), and the white dot on the *x*-axis indicates the centroid of the habitat used.

related (morphologically similar and taxonomic closer) sponges (globular sponges and *Geodia* spp.) were more similar. The most relevant variables for the species habitat selection were orientation, mean curvature and depth, with these topographic variables likely proxies for other environmental drivers such as currents, food exposure, wave action and sediment rates (Dolan et al., 2008). Morphotaxa selectivity may be related to differences in taxa physiology and morphology that influence differential food intake, and capacity to tolerate sediment exposure. This study helps explain how sessile filter feeders can cohabitate in complex vertical walls and highlights the importance of vertical walls

for VME indicator taxa. Although vertical walls are generally less impacted by human activities and our study was conducted within a marine protected area, a large net was found entangled with *Hertwigia* spp. on a steep slope (Supplementary material S3). This evidences that even these less affected areas require more comprehensive protection.

4.1. Habitat selection on vertical walls

Fine-scale orientation was an important factor in the habitat selection of *Solenosmilia* sp. on the two walls where it was present (in wall 7
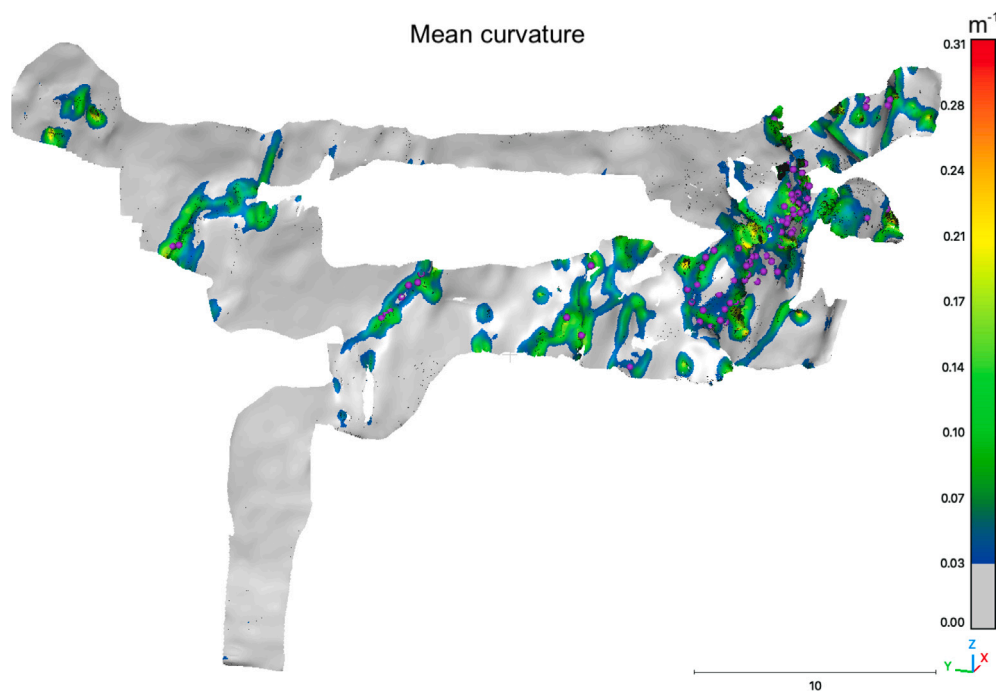
Fig. 5. 3D point cloud of the reconstructed section of the vertical wall of Dive 8 (wall D8) showing the areas where mean curvature is higher than 0.03 m⁻¹, coinciding with edges and overhangs and the locations of *Solenosmilia* sp. represented by purple dots (scale 0.5 m).

Table 2
Species marginality values obtained from Environmental Niche Factor Analysis (ENFA) at scale 0.5 m. Only variables with collinearity <0.5 were retained. Positive values of marginality mean that the morphotaxa selected locations with higher values of the corresponding environmental variable.

Wall	Taxa	Depth	Roughness	Mean curvature	Verticality	Northness	Eastness	Marginality coefficient	Count	p value
D7	*Solenosmilia* sp.	−0.39	0.49	0.34	0.57	1.19		2.26	136	<0.001
D7	Globular sponges	−0.75	−0.29	0.77	0.82	1.25		3.48	47	<0.001
D7	*Geodia* spp.	−0.42	−0.03	1.25	0.72	0.83		2.96	15	<0.001
D8	*Solenosmilia* sp.	0.23	0.29	1.62	1.17		1.65	6.85	114	<0.001
D8	*Hertwigia* spp.	0.02	−0.04	1.39	0.67		0.76	2.98	51	<0.001
D9	Scleralcyonacea	0.78	0.63	0.49	−0.20	−0.02		1.28	22	<0.001
D9	Globular sponges	−0.62	0.46	0.52	0.50	0.40		1.27	43	<0.001
D9	*Geodia* spp.	−0.07	0.30	0.22	0.64	0.64		0.64	31	<0.002

Table 3
Results of the OMI analysis and significance of permutation tests. Inertia is the weight sums of square distance to the origin of environmental axes; OMI is the outlying mean index based on marginality, it indicates whether the taxa occupy habitats that are markedly different from the typical habitat conditions; Tol is the tolerance index (values close to zero mean narrower niche, higher specialization); Rtol is the residual tolerance. Values in italics (*omi*, *tol*, *rtol*) represent the corresponding parameter's variability percentages.

Dive	Taxa	Inertia	OMI	Tol	Rtol	*omi*	*tol*	*rtol*	p value
D7	*Solenosmilia* sp.	4.76	1.84	0.75	2.17	38.80	15.70	45.50	<0.001
D7	Globular sponges	4.87	3.30	0.38	1.19	67.90	7.80	24.40	<0.001
D7	*Geodia* spp.	4.51	2.73	0.08	1.70	60.60	1.80	37.60	<0.001
D8	*Solenosmilia* sp.	9.37	6.95	0.63	1.79	74.20	6.70	19.10	<0.001
D8	*Hertwigia* spp.	7.07	2.99	2.25	1.82	42.30	31.90	25.80	<0.001
D9	Scleralcyonacea	3.88	1.11	0.46	2.31	28.50	11.80	59.60	<0.001
D9	Globular sponges	4.41	0.87	1.38	2.16	19.80	31.30	48.90	<0.002
D9	*Geodia* spp.	3.22	0.37	1.43	1.42	11.40	44.60	44.00	<0.052

Solenosmilia sp. selected northness and in wall 8 eastness). Orientation can provide a proxy for how much a location is exposed or sheltered from currents at the scale studied (Dolan et al., 2008). On a large scale, the deep bottom currents in the CGFZ flow westward (Priede et al., 2013). However, the complex topography of this region will affect the fine-scale flow of currents, and different preferences for orientation may represent different favorable fine-scale currents among walls (Hall et al., 2017). *Solenosmilia* sp. also showed significant selectivity for steep slopes and lower tolerance for flatter areas. Although vertical

walls can offer a hard substrate for species to settle to maintain a population, adequate food input and low exposure to sediment accumulation are also necessary. Habitat selectivity of corals for overhanging and specific orientation may favor exposure to food-rich currents (Bilan et al., 2023) through the interaction between topography and currents, whereby higher speed flows favor sediment removal (Orejas et al., 2009). A study in the Whittard Canyon, Northeast Atlantic, observed that the hard coral species *Desmophyllum pertusum* (also known as *Lophelia pertusa*) occurred on steeper slopes and edges, with some walls having denser communities than others (Huvenne et al., 2011; Morris et al., 2013).

The morphotaxa belonging to the Scleralcyonacea family had a narrower niche, showing a preference for shallower areas within the vertical wall (1848–1867 m). Depth is known as an important variable influencing species distribution (Buhl-Mortensen and Buhl-Mortensen, 2006; Schlacher et al., 2010) but is likely a proxy for other environmental drivers such as temperature and oxygen concentration (Chu et al., 2019). However, at the small scale investigated here, the preference for specific depth likely coincides with a zonation pattern explained by the level of exposure to sediments. The shallower areas of wall D9 farther from the seabed could be observed to have less sediment than deeper areas (Fig. 10). Exposed hard substrate is necessary for the anchoring of certain Scleralcyonacea species, such as *Paragorgia* (Buhl-Mortensen and Buhl-Mortensen, 2004), while accumulation of sediment may disturb these organisms (Bryan and Metaxas, 2007).
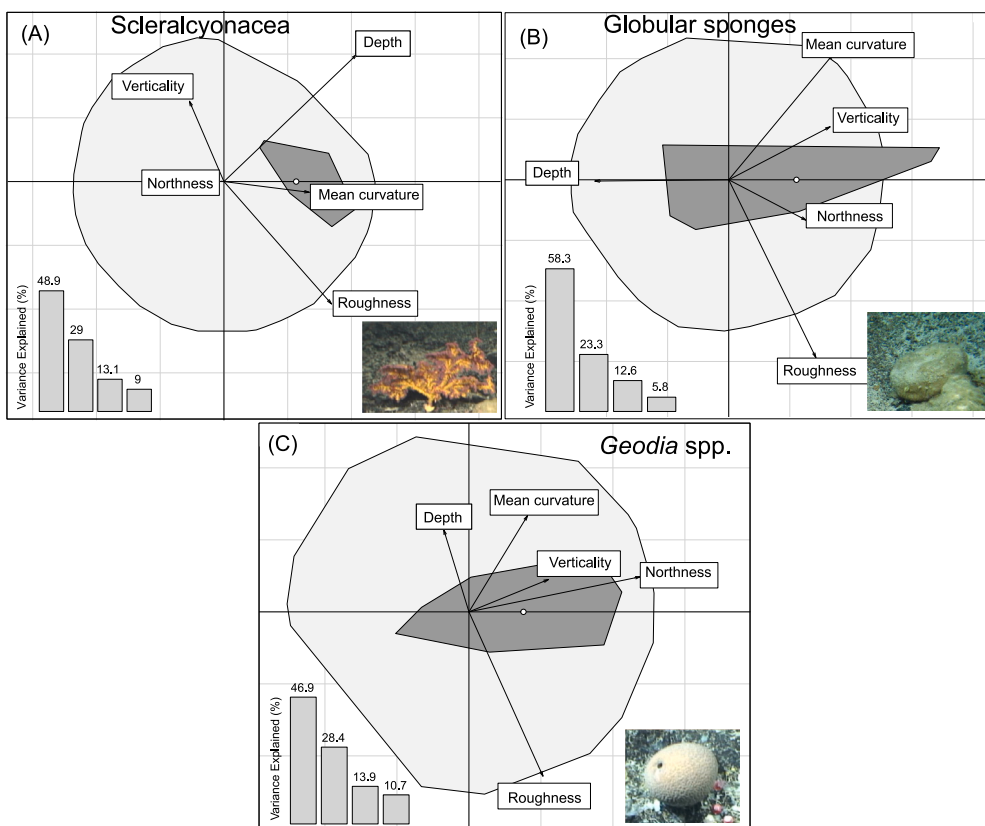
Fig. 6. Vertical wall of Dive 9 (wall D9). Ecological Niche Factor Analysis (ENFA) bi-plots, illustrating the marginality axis (*x*-axis) and the first specialization axis (*y*-axis) for (A) Scleralcyonacea, (B) globular sponges, and (C) *Geodia* spp. The light gray polygons represent available habitat, while dark gray polygons depict the habitat occupied by the respective species. Arrows denote projections of environmental variables (scale 0.5 m), and the white dot on the *x*-axis indicates the centroid of the habitat used.
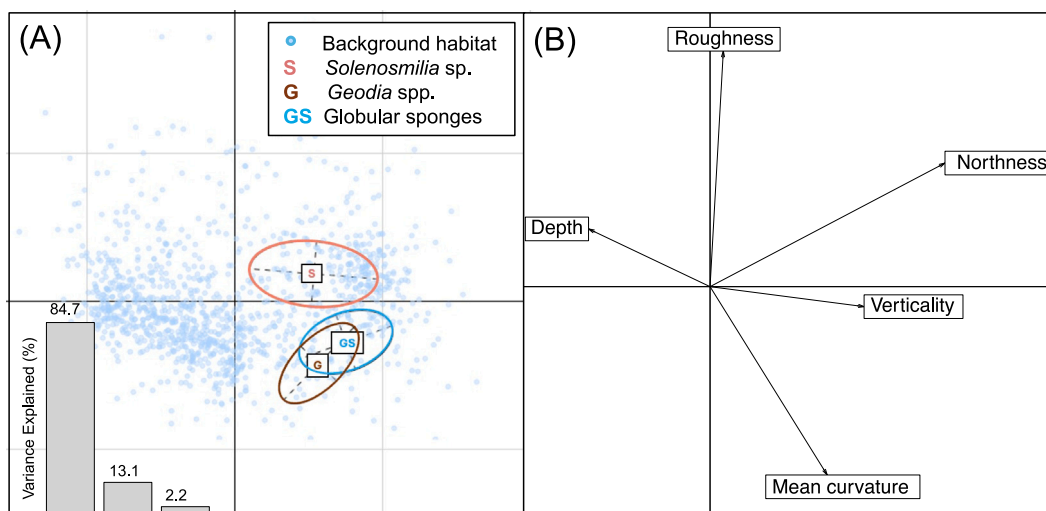
Fig. 7. Outlying Mean Index (OMI) analysis for the taxa investigated on the vertical wall of Dive 7 (D7) at a scale of 0.5 m, with collinearity under 0.5. (A) Ellipses illustrate the niches of *Solenosmilia* sp., globular sponges and *Geodia* spp. over the background habitat conditions (blue dots). (B) Arrows denote the contribution of the environmental variables employed in the analysis.

For example, Scleralcyonacea in Whittard Canyon did not occur in areas with accumulations of sediment (Morris et al., 2013). Although *Paragorgia arborea* has been shown to change growth direction to face orientation associated with currents and food (Mortensen and Buhl-Mortensen, 2005; Prado et al., 2019), we could not detect preferences for orientation. This may be due to the fact that the section of the reconstructed vertical wall D9 was narrow and did not encapsulate a broader range of orientation.

Globular sponges morphotaxa were the only sponges that showed high selectivity for deeper areas within the vertical wall (1891–1901 m). These deeper areas close to the flat terrain had higher sediment accumulation. Conversely, *Geodia* spp. did not show preferences for specific depth and occurred in areas with and without sediment accumulation. They also selected overhangs and had a low tolerance for slope variation, preferring very steep areas of the vertical wall.
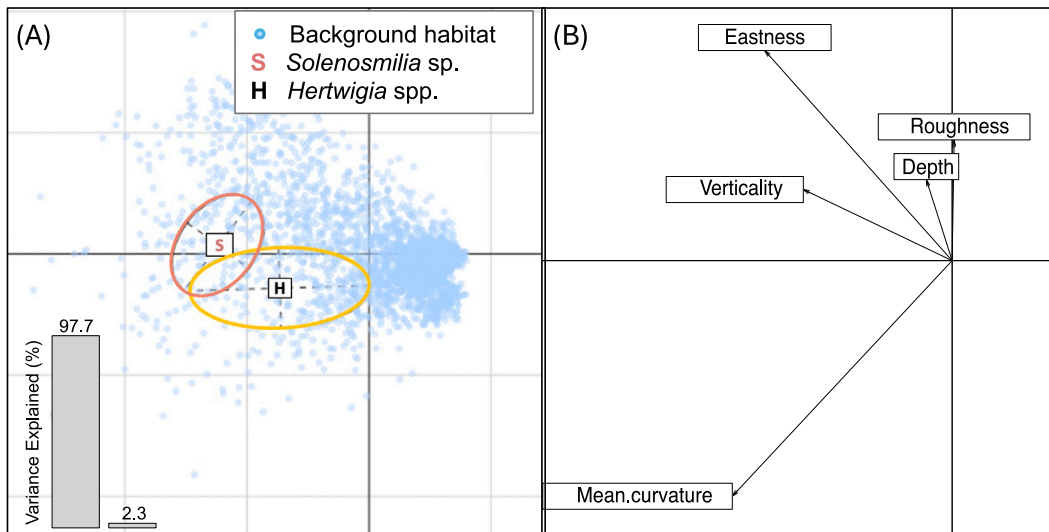
Fig. 8. Outlying Mean Index (OMI) analysis for the taxa investigated on the vertical wall of Dive 8 (D8) at a scale of 0.5 m, with collinearity under 0.5. (A) Ellipses illustrate the niches of *Solenosmilia* sp. and *Hertwigia* spp. over the background habitat conditions (blue dots). (B) Arrows denote the contribution of the environmental variables employed in the analysis.
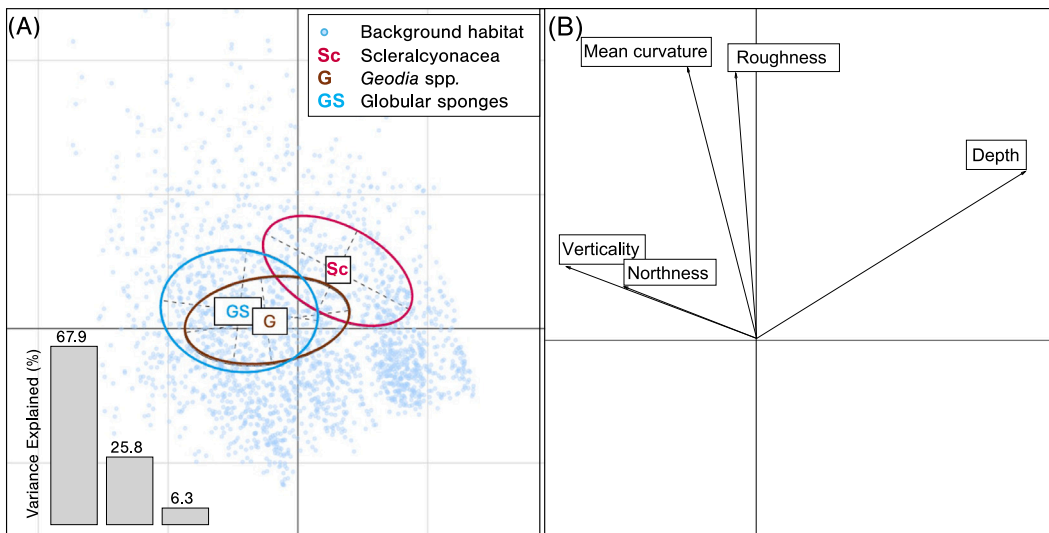

Fig. 9. Outlying Mean Index (OMI) analysis for the taxa investigated on the vertical wall of Dive 9 (D9) at a scale of 0.5 m, with collinearity under 0.5. (A) Ellipses illustrate the niches Of Scleralcyonacea, globular sponges, *Geodia* spp. over the background habitat conditions (blue dots). (B) Arrows denote the contribution of the environmental variables employed in the analysis.

Hertwigia spp., the only glass sponge studied here, strongly preferred higher values of mean curvature (proxy of overhanging) and to a lesser extent, verticality. This is in agreement with previous studies that found that glass sponges tend to occur on steep slopes, preferentially in areas free of sediments (Leys et al., 2004). Glass sponges have species-specific sediment tolerance and when exposed to excessive sediment, can stop feeding for short periods (Grant et al., 2018; Leys et al., 2007).

All the species showed high specialization for roughness. This observation should be interpreted carefully as each taxon contributed to the roughness at different scales. This problem was higher at smaller scales explored here (0.02–0.1), and why only the 0.5 m scale was included in the final model.

4.2. Niche differentiation

The largest niche difference was observed between corals and sponges. *Solenosmilia* sp. showed complete niche differentiation with globular sponges and *Geodia* spp., and partial separation with the

glass sponge *Hertwigia* spp. Scleralcyonacea showed considerable niche differentiation with globular sponges and *Geodia* spp. Mean curvature (a proxy of overhangs) influenced specialization for *Solenosmilia* sp., indicating that the species had a low tolerance for variation of this parameter, while for Demosponge (i.e., *Geodia* spp., and *Hertwigia* spp.), this factor did not influence their tolerance. Instead, mean curvature was only related to habitat preferences (marginality > 0.7).

The most important variable separating *Solenosmilia's* niche from the niches of *Geodia* spp., globular sponges and *Hertwigia* spp. was *Solenosmilia's* consistent and higher selectivity for a specific orientation. Specific orientation may favor the availability of zooplankton, zooplankton waste (faecal pellets and dead zooplankton) and phytodetritus (Duineveld et al., 2004, 2007; Naumann et al., 2015). In a food-limited deep-sea (Maier et al., 2020) favorable orientation may be crucial for corals. In contrast, sponges have high filtering capacity, feed mainly on bacteria, and can sustain their population in areas with intermittent food availability (Hanz et al., 2021; Leys et al., 2007).
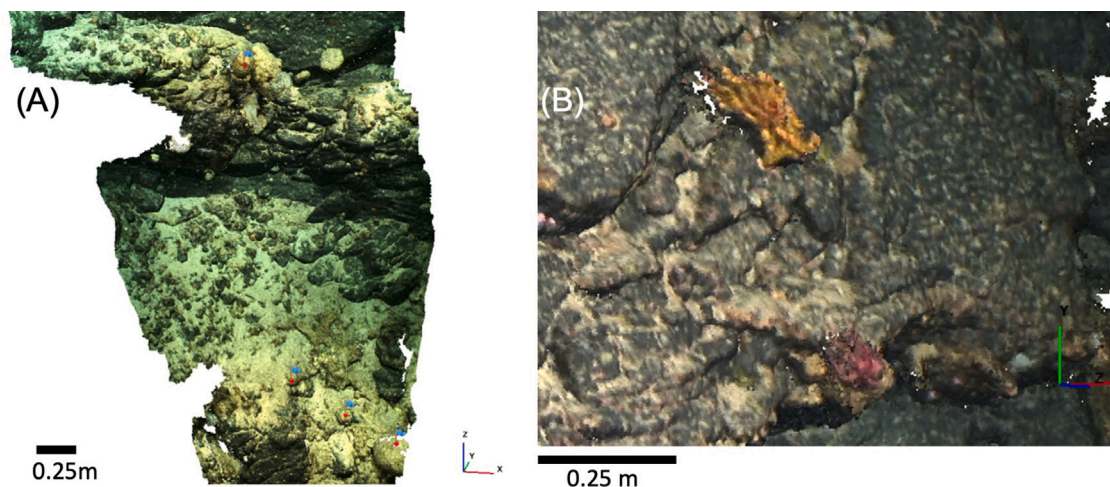
Fig. 10. 3D reconstruction of wall D9. (A) Accumulation of sediment in the deeper areas and location of globular sponges marked with red dots. (B) Shallower areas displaying lower accumulation of sediment and the presence of a yellow individual of the family Scleralcyonacea.

The partial separation of the Scleralcyonacea niche from globular sponges and *Geodia* spp. was Scleralcyonacea's preference for shallower areas possible due to the lower sediment exposure in the wall sections away from the seafloor. Some sponges are generally less affected by sedimentation due to their ability to efficiently contract and expel unwanted sediment particles (Grant et al., 2018; Leys et al., 2007); they can slow their respiration when exposed to high concentrations of suspended sediments (100 mg l-1) and are able to recover after exposure (Tjensvoll et al., 2013). Conversely, corals can be strongly affected as sediments can clog their polyps, causing higher mortality (Bilan et al., 2023; Carreiro-Silva et al., 2022).

The niches of the closely related morphotaxa, such as globular sponges and *Geodia* spp., exhibited high overlap. This overlap suggests that they occupy a similar habitat and may compete for the same resources. However, the taxonomic resolution of globular sponges is limited due to the constraints of video annotation, particularly affecting species within the phylum Porifera (Howell et al., 2019; Schönberg, 2021). The study of niche differentiation at a higher taxonomic resolution may reveal greater niche separation between these taxa. Therefore, for future studies, it is advisable to (a) increasing the coverage of image acquisition to capture more individuals and (b) collecting samples for taxonomic identification. Furthermore, to reduce intensive sampling needed to account for cryptic species, (c) environmental DNA (eDNA) could be used as a complementary tool to aid in taxonomy. Adopting these suggestions could enable a more detailed exploration of niche differentiation at finer taxonomic levels.

5. Conclusion

The terrain variables considered in this study represent a small part of the ecological niche of the species. Numerous biotic and abiotic factors, along with species interactions, may influence habitat selection on vertical walls. However, obtaining these data for deep-sea research is often challenging due to the substantial time and financial constraints associated with this type of in-situ studies. Here, we provided a partial reconstruction of the studied taxa niche, which focused on the recognized importance of terrain at fine scales (Buhl-Mortensen et al., 2012; Dolan et al., 2008; Van Audenhaege et al., 2021). Fine-scale terrain data based on structure-from-motion reconstructions can be derived from opportunistic surveys, allowing a further understanding of deep-sea spatial ecology at a relatively low cost.

This study enhances our understanding of the drivers influencing fine-scale diversity in vertical walls, as occurring through niche partitioning and habitat selection. Given that vertical walls host a variety of fine-scale habitats due to their topographic complexity, this research provides a mechanistic explanation of how vertical walls support higher biodiversity compared to flatter areas. This knowledge is necessary not only to better understand the ecology of these important species (Georgian et al., 2014) but also to promote the conservation of vertical wall environments. Furthermore, enhancing our understanding of cold-water corals habitat preferences at a fine-scale may have the potential to improve the success of restoration efforts (Bassett et al., 2023). Based on a niche understanding, species distribution modeling could be applied on larger-scale topographic maps of vertical walls to help decision-making on which areas to monitor and preserve. Presently, the North of the Charlie-Gibbs Fracture Zone (CGFC) is designated as a Marine Protected Area (MPA), but only the water column is protected, not its seabed (OSPAR Commission, 2012). This study provides evidence for the importance of vertical wall heterogeneity for vulnerable marine ecosystem indicators in the CGFZ and can help support further measures to ensure their conservation.

CRediT authorship contribution statement

Ana Belén Yáñez-Suárez: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Loïc Van Audenhaege:** Writing – review & editing, Investigation. **Tyler D. Eddy:** Writing – review & editing. **Katleen Robert:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization.

Ethical approval

No animal testing was performed during this study.

Sampling and field studies

All necessary permits for sampling and observational field studies have been obtained by the authors and expedition party. The study is compliant with CBD and Nagoya protocols.

Funding

Declaration of competing interest

Acknowledgments

Appendix A. Supplementary material

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.dsr2.2024.105437.

Data availability

Data will be made available on request.

References

Amaro, T., Huvenne, V.A., Allcock, A.L., Aslam, T., Davies, J.S., Danovaro, R., De Stigter, H.C., Duineveld, G.C., Gambi, C., Gooday, A.J., Gunton, L.M., Hall, R., Howell, K.L., Ingels, J., Kiriakoulakis, K., Kershaw, C.E., Lavaleye, M.S., Robert, K., Stewart, H., Van Rooij, D., White, M., Wilson, A.M., 2016. The Whittard Canyon - A case study of submarine canyon processes. Prog. Oceanogr. 146, 38–57. http://dx.doi.org/10.1016/j.pocean.2016.06.003.

Basille, M., Calenge, C., Marboutin, É., Andersen, R., Gaillard, J.M., 2008. Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecol. Model. 211 (1–2), 233–240. http://dx.doi.org/10.1016/j.ecolmodel.2007.09.006.

Bassett, R.J., Herting, J., Frometa, S., Sharuga, J., Howell, L., Siceloff, J., Bourque, M., Cromwell, K., Francis, R., Clark, A., Demopoulos, A., David, K., Benson, S.L., Harter, B., 2023. Comprehensive Inventory of Habitat Assessment and Evaluation Datasets to Support Deepwater Horizon Mesophotic and Deep-Sea Coral Restoration (Tech. Rep. No. February 2023). Tech. Rep. No. February 2023, National Oceanic and Atmospheric Administration, p. 68. http://dx.doi.org/10.25923/kz7t-4674.

Bell, J.J., Burton, M., Bullimore, B., Newman, P.B., Lock, K., 2006. Morphological monitoring of subtidal sponge assemblages. Mar. Ecol. Prog. Ser. 311, 79–91. http://dx.doi.org/10.3354/meps311079.

Bilan, M., Gori, A., Grinyó, J., Biel-Cabanelas, M., Puigcerver-Segarra, X., Santín, A., Piraino, S., Rossi, S., Puig, P., 2023. Vulnerability of six cold-water corals to sediment resuspension from bottom trawling fishing. Marine Poll. Bull. 196, http://dx.doi.org/10.1016/j.marpolbul.2023.115423.

Bryan, T.L., Metaxas, A., 2007. Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. Mar. Ecol. Prog. Ser. 330, 113–126. http://dx.doi.org/10.3354/meps330113.

Buhl-Mortensen, P., Buhl-Mortensen, L., 2004. Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Mar. Biol. 144 (6), 1223–1238. http://dx.doi.org/10.1007/s00227-003-1280-8.

Buhl-Mortensen, P., Buhl-Mortensen, L., 2006. Deep-water corals and their habitats in the gully, a submarine canyon off Atlantic Canada. Cold-Water Corals Ecosys. 247–277. http://dx.doi.org/10.1007/3-540-27673-4_12.

Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M., Dannheim, J., Bellec, V., Holte, B., 2012. Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685, 191–219.

Calenge, C., 2011. Exploratory analysis of the habitat selection by the wildlife in R : the adehabitatHS Package. R CRAN Proj. 1–60.

Calenge, C., 2022. Package ' adehabitatHS '. R CRAN Proj..

Carreiro-Silva, M., Martins, I., Riou, V., Raimundo, J., Caetano, M., Bettencourt, R., Rakka, M., Cerqueira, T., Godinho, A., Morato, T., Colaço, A., 2022. Mechanical and toxicological effects of deep-sea mining sediment plumes on a habitat-forming cold-water octocoral. Front. Mar. Sci. 9, http://dx.doi.org/10.3389/fmars.2022.915650.

Chu, J.W., Nephin, J., Georgian, S., Knudby, A., Rooper, C., Gale, K.S., 2019. Modelling the environmental niche space and distributions of cold-water corals and sponges in the Canadian Northeast Pacific Ocean. Deep Sea Res. Part I: Oceanogr. Res. Pap. 151, http://dx.doi.org/10.1016/j.dsr.2019.06.009.

Colwell, R.K., Rangel, T.F., 2009. Hutchinson's duality: The once and future niche. Proc. Natl. Acad. Sci. USA 106 (Suppl. 2), 19651–19658. http://dx.doi.org/10.1073/pnas.0901650106.

Dolan, M.F., Grehan, A.J., Guinan, J.C., Brown, C., 2008. Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data. Deep Sea Res. Part I: Oceanogr. Res. Pap. 55 (11), 1564–1579. http://dx.doi.org/10.1016/j.dsr.2008.06.010.

Dolédec, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: A new method. Ecology 81 (10), 2914–2927. http://dx.doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2.

Dray, S., Dufour, A.B., 2007. The ade4 package: Implementing the duality diagram for ecologists. J. Stat. Softw. 22 (4), 1–20. http://dx.doi.org/10.18637/jss.v022.i04.

Duineveld, G.C., Lavaleye, M.S., Berghuis, E.M., 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). Mar. Ecol. Prog. Ser. 277, 13–23. http://dx.doi.org/10.3354/meps277013.

Duineveld, G.C., Lavaleye, M.S., Bergman, M.J., De Stigter, H., Mienis, F., 2007. Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. Bull. Mar. Sci. 81 (3), 449–467, URL www.lophelia.org.

Elton, C.S., 1927. Animal ecology, by Charles Elton; With an Introduction By Julian S. Huxley. Macmillan Co, New York, pp. 1–256. http://dx.doi.org/10.5962/bhl.title.7435.

Fabri, M.C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., Freiwald, A., 2014. Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 104, 184–207. http://dx.doi.org/10.1016/j.dsr2.2013.06.016.

FAO, 2008. International guidelines for the management of deep-sea fisheries in the high seas. SPRFMO-VI-SWG-INF01 1–32, URL https://www.sprfmo.int/assets/Meetings/Meetings-before-2013/Scientific-Working-Group/SWG-06-2008/7e88751513/SPRFMO6-SWG-INF01-FAO-Deepwater-Guidelines-Final-Sep20.pdf.

Gage, J.D., Tyler, P.A., 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press.

García, D., Ortiz-Pulido, R., 2004. Patterns of resource tracking by avian frugivores at multiple spatial scales: Two case studies on discordance among scales. Ecography 27 (2), 187–196. http://dx.doi.org/10.1111/j.0906-7590.2004.03751.x.

Gebruk, A.V., Krylova, E.M., 2013. Megafauna of the Charlie-Gibbs Fracture Zone (northern Mid-Atlantic Ridge) based on video observations. J. Mar. Biol. Assoc. UK 93 (5), 1143–1150. http://dx.doi.org/10.1017/S0025315412001890.

Georgian, S.E., Shedd, W., Cordes, E.E., 2014. High-resolution ecological niche modelling of the cold-water coral Lophelia pertusa in the Gulf of Mexico. Mar. Ecol. Prog. Ser. 506, 145–161. http://dx.doi.org/10.3354/meps10816.

Grant, N., Matveev, E., Kahn, A.S., Leys, S.P., 2018. Suspended sediment causes feeding current arrests in situ in the glass sponge Aphrocallistes vastus. Mar. Environ. Res. 137, 111–120. http://dx.doi.org/10.1016/j.marenvres.2018.02.020.

Greene, H.G., Yoklavich, M.M., Starr, R.M., O'Connell, V.M., Wakefield, W.W., Sullivan, D.E., McRea, J.E., Cailliet, G.M., 1999. A classification scheme for deep seafloor habitats. Oceanol. Acta 22 (6), 663–678. http://dx.doi.org/10.1016/S0399-1784(00)88957-4.

Greiffenhagen, L., Kutti, T., Maier, S.R., De Clippele, L.H., 2024. Biomass mapping of fjordic cold-water coral reefs reveals distinct functional role of vertical wall habitat. Deep Sea Res. Part I: Oceanogr. Res. Pap. 211, 104350.

Grinnell, J., 1917. The Niche-Relationships of the California Thrasher. The Auk 34 (4), 427–433. http://dx.doi.org/10.2307/4072271.

Guinan, J., Brown, C., Dolan, M.F., Grehan, A.J., 2009. Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. Ecol. Inform. 4 (2), 83–92. http://dx.doi.org/10.1016/j.ecoinf.2009.01.004.

Haedrich, R.L., Gagnon, J.M., 1991. Rock wall fauna in a deep Newfoundland fiord. Cont. Shelf Res. 11 (8–10), 1199–1207. http://dx.doi.org/10.1016/0278-4343(91)90097-P.

Hall, R.A., Aslam, T., Huvenne, V.A., 2017. Partly standing internal tides in a dendritic submarine canyon observed by an ocean glider. Deep Sea Res. Part I: Oceanogr. Res. Pap. 126, 73–84. http://dx.doi.org/10.1016/j.dsr.2017.05.015.

Hanz, U., Roberts, E.M., Duineveld, G., Davies, A., van Haren, H., Rapp, H.T., Reichart, G.J., Mienis, F., 2021. Long-term observations reveal environmental conditions and food supply mechanisms at an Arctic deep-sea sponge ground. J. Geophys. Res.: Oceans 126 (3), http://dx.doi.org/10.1029/2020JC016776.

Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. Mar. Geol. 285 (1–4), 69–86. http://dx.doi.org/10.1016/j.margeo.2011.05.008, URL http://dx.doi.org/10.1016/j.margeo.2011.05.008.

Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology 83 (7), 2027. http://dx.doi.org/10.2307/3071784.

Howell, K.L., Davies, J.S., Allcock, A.L., Braga-Henriques, A., Buhl-Mortensen, P., Carreiro-Silva, M., Dominguez-Carrió, C., Durden, J.M., Foster, N.L., Game, C.A., Hitchin, B., Horton, T., Hosking, B., Jones, D.O., Mah, C., Marchais, C.L., Menot, L., Morato, T., Pearman, T.R., Piechaud, N., Ross, R.E., Ruhl, H.A., Saeedi, H., Stefanoudis, P.V., Taranto, G.H., Thompson, M.B., Taylor, J.R., Tyler, P., Vad, J., Victorero, L., Vieira, R.P., Woodall, L.C., Xavier, J.R., Wagner, D., 2019. A framework for the development of a global standardised marine taxon reference image database (SMarTaR-ID) to support imagebased analyses. PLoS ONE 14 (12), 1–25. http://dx.doi.org/10.1371/journal.pone.0218904.

Husson, B., Sarradin, P.M., Zeppilli, D., Sarrazin, J., 2017. Picturing thermal niches and biomass of hydrothermal vent species. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 137, 6–25. http://dx.doi.org/10.1016/j.dsr2.2016.05.028.

Hutchinson, G.E., 1957. Concluding Remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415–427. http://dx.doi.org/10.1101/SQB.1957.022.01.039.

Hutchinson, G.E., 1978. An Introduction to Population Ecology. Yale University, pp. 1–260.

Huvenne, V.A., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach, V., Bas, T.P., Wolff, G.A., 2011. A picture on the wall: Innovative mapping reveals cold-water coral refuge in submarine canyon. In: Roberts, J.M. (Ed.), PLoS ONE 6 (12), e28755. http://dx.doi.org/10.1371/journal.pone.0028755.

Johnson, M.P., White, M., Wilson, A., Würzberg, L., Schwabe, E., Folch, H., Allcock, A.L., 2013. A vertical wall dominated by Acesta excavata and Neopycnodonte zibrowii, part of an undersampled group of deep-sea habitats. PLoS ONE 8 (11), 1–9. http://dx.doi.org/10.1371/journal.pone.0079917.

Keogh, P., Command, R.J., Edinger, E., Georgiopoulou, A., Robert, K., 2022. Benthic megafaunal biodiversity of the Charlie-Gibbs Fracture Zone: spatial variation, potential drivers, and conservation status. Mar. Biodiversity 52 (5), http://dx.doi.org/10.1007/s12526-022-01285-1.

Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: Approaches and future directions. Hydrobiologia 685 (1), 1–17. http://dx.doi.org/10.1007/s10750-011-0974-z.

Lecours, V., Devillers, R., Schneider, D.C., Lucieer, V.L., Brown, C.J., Edinger, E.N., 2015. Spatial scale and geographic context in benthic habitat mapping: Review and future directions. Mar. Ecol. Prog. Ser. 535, 259–284. http://dx.doi.org/10.3354/meps11378.

Leys, S.P., Mackie, G.O., Reiswig, H.M., 2007. The biology of glass sponges. Adv. Mar. Biol. 52, 1–145. http://dx.doi.org/10.1016/S0065-2881(06)52001-2.

Leys, S.P., Wilson, K., Holeton, C., Reiswig, H.M., Austin, W.C., Tunnicliffe, V., 2004. Patterns of glass sponge (Porifera, Hexactinellida) distribution in coastal waters of British Columbia, Canada. Mar. Ecol. Prog. Ser. 283, 133–149. http://dx.doi.org/10.3354/meps283133.

MacArthur, R.H., 1958. Population Ecology of some warblers of Northeastern coniferous forests. Ecology 39 (4), 599–619. http://dx.doi.org/10.2307/1931600.

Maier, S.R., Kutti, T., Bannister, R.J., Fang, J.K.H., van Breugel, P., van Rijswijk, P., van Oevelen, D., 2020. Recycling pathways in cold-water coral reefs: Use of dissolved organic matter and bacteria by key suspension feeding taxa. Sci. Rep. 10 (1), 1–13. http://dx.doi.org/10.1038/s41598-020-66463-2.

Morris, K.J., Tyler, P.A., Masson, D.G., Huvenne, V.I., Rogers, A.D., 2013. Distribution of cold-water corals in the Whittard Canyon, NE Atlantic Ocean. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 92, 136–144.

Mortensen, P.B., Buhl-Mortensen, L., 2005. Morphology and growth of the deep-water gorgonians Primnoa resedaeformis and Paragorgia arborea. Mar. Biol. 147, 775–788.

Mortensen, P., Buhl-Mortensen, L., Gebruk, A., Krylova, E., 2008. Occurrence of deep-water corals on the mid-atlantic ridge based on MAR-eco data. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 55 (1–2), 142–152.

Naumann, M.S., Tolosa, I., Taviani, M., Grover, R., Ferrier-Pagès, C., 2015. Trophic ecology of two cold-water coral species from the Mediterranean Sea revealed by lipid biomarkers and compound-specific isotope analyses. Coral Reefs 34 (4), 1165–1175. http://dx.doi.org/10.1007/s00338-015-1325-8.

Obelcz, J., Brothers, D., Chaytor, J., ten Brink, U., Ross, S.W., Brooke, S., 2014. Geomorphic characterization of four shelf-sourced submarine canyons along the U.S. Mid-Atlantic continental margin. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 104, 106–119. http://dx.doi.org/10.1016/j.dsr2.2013.09.013.

Olivet, J.-L., Le Pichon, X., Monti, S., Sichler, B., 1974. Charlie-Gibbs fracture zone. J. Geophys. Res. 79 (14), 2059–2072. http://dx.doi.org/10.1029/jb079i014p02059.

Orejas, C., Gori, A., Lo Iacono, C., Puig, P., Gili, J.M., Dale, M.R., 2009. Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: Spatial distribution, density and anthropogenic impact. Mar. Ecol. Prog. Ser. 397, 37–51. http://dx.doi.org/10.3354/meps08314.

OSPAR, 2010. Background Document on the Charlie-Gibbs Fracture Zone Biodiversity Series. (ISBN 978-1-907390-64-7), OSPAR Commission.

OSPAR, 2012. Background Document on Charlie-Gibbs North High Seas MPA Biodiversity Series. (ISBN 978-1-907390-34-0), OSPAR Commission.

Prado, E., Sánchez, F., Rodríguez-Basalo, A., Altuna, Á., Cobo, A., 2019. Analysis of the population structure of a gorgonian forest (Placogorgia sp.) using a photogrammetric 3D modeling approach at Le Danois Bank, Cantabrian Sea. Deep-Sea Res. Part I: Oceanogr. Res. Pap. 153, http://dx.doi.org/10.1016/j.dsr.2019.103124.

Price, 2010. Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. Oecol. 163 (3), 747–758. http://dx.doi.org/10.1007/s00442-010-1578-4.

Price, D.M., Robert, K., Callaway, A., Lo Iacono, C., Hall, R.A., Huvenne, V.A., 2019. Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. Coral Reefs 38, 1007–1021.

Priede, I.G., Billett, D.S., Brierley, A.S., Hoelzel, A.R., Inall, M., Miller, P.I., Cousins, N.J., Shields, M.A., Fujii, T., 2013. The ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie-Gibbs Fracture Zone; ECO-MAR project strategy and description of the sampling programme 2007–2010. Deep-Sea Res. Part II: Top. Stud. Oceanogr. 98, 220–230. http://dx.doi.org/10.1016/j.dsr2.2013.06.012.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org/.

Robert, K., Huvenne, V.A., Georgiopoulou, A., Jones, D.O., Marsh, L., Carter, D.O., Chaumillon, L., 2017. New approaches to high-resolution mapping of marine vertical structures. Sci. Rep. 7 (1), 1–14. http://dx.doi.org/10.1038/s41598-017-09382-z.

Robert, K., Jones, D.O., Georgiopoulou, A., Huvenne, V.A., 2020. Cold-water coral assemblages on vertical walls from the Northeast Atlantic. In: Burns, K.C. (Ed.), Diversity and Distributions 26 (3), 284–298. http://dx.doi.org/10.1111/ddi.13011.

Robertson, D.R., Sheldon, J.M., 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. J. Exp. Mar. Biol. Ecol. 40 (3), 285–298. http://dx.doi.org/10.1016/0022-0981(79)90057-1.

Schlacher, T.A., Rowden, A.A., Dower, J.F., Consalvey, M., 2010. Seamount science scales undersea mountains: New research and outlook. Mar. Ecol. 31 (Suppl. 1), 1–13. http://dx.doi.org/10.1111/j.1439-0485.2010.00396.x.

Schönberg, C.H.L., 2021. No taxonomy needed: Sponge functional morphologies inform about environmental conditions. Ecol. Indic. 129, http://dx.doi.org/10.1016/j.ecolind.2021.107806.

Sillero, N., Barbosa, A.M., 2021. Common mistakes in ecological niche models. Biol. J. Linnean Soc. 35 (2), 213–226. http://dx.doi.org/10.1080/13658816.2020.1798968.

Smith, F., Witman, J.D., 1999. Species diversity in subtidal landscapes: Maintenance by physical processes and larval recruitment. Ecology 80 (1), 51–69. http://dx.doi.org/10.1890/0012-9658(1999)080[0051:SDISLM]2.0.CO;2, URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/0012-9658(1999)080%5B0051:SDISLM%5D2.0.CO%3B2.

Søiland, H., Budgell, W.P., Knutsen, O., 2008. The physical oceanographic conditions along the Mid-Atlantic Ridge north of the Azores in June-July 2004. Deep Sea Res. Part II: Top. Stud. Oceanogr. 55 (1–2), 29–44. http://dx.doi.org/10.1016/j.dsr2.2007.09.015.

Speare, K., Duran, A., Miller, M., Moeller, H., Burkepile, D., 2023. Small-scale habitat selection by larvae of a reef-building coral. Mar. Ecol. Prog. Ser. 724, 67–79. http://dx.doi.org/10.3354/meps14434.

Taylor, J.R., Ferrari, R., 2011. Ocean fronts trigger high latitude phytoplankton blooms. Geophys. Res. Lett. 38 (23), http://dx.doi.org/10.1029/2011GL049312.

Tjensvoll, I., Kutti, T., Fosså, J.H., Bannister, R., 2013. Rapid respiratory responses of the deep-water sponge Geodia barretti exposed to suspended sediments. Aquatic Biol. 19 (1), 65–73.

Van Audenhaege, L., Broad, E., Hendry, K.R., Huvenne, V.A.I., 2021. High-resolution vertical habitat mapping of a deep-sea cliff offshore greenland. Front. Mar. Sci. 8, 1–18. http://dx.doi.org/10.3389/fmars.2021.669372.

White, M., Dorschel, B., 2010. The importance of the permanent thermocline to the cold water coral carbonate mound distribution in the North East Atlantic. Earth Planet. Sci. Lett. 296 (3–4), 395–402.

Williams, C.B., 1964. Patterns in the Balance of Nature and Related Problems in Quantitative Ecology. vol. 3, (2), Academic Press, London and New York, p. 324. http://dx.doi.org/10.1002/IROH.19650500209.

Wilson, M.F., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the Continental Slope. vol. 30, (1–2), pp. 3–35. http://dx.doi.org/10.1080/01490410701295962.

Zhu, G., Ren, B., Wang, Y., Qiu, D., 2019. The influence of vertical-wall structure on monochromatic wave transformation characteristics over the platform reef. Zhongguo Kexue Jishu Kexue/Scientia Sinica Technologica 49 (8), 919–929. http://dx.doi.org/10.1360/N092018-00006.

Zuppinger-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., De Deyn, G.B., Flynn, D.F., 2014. Selection for niche differentiation in plant communities increases biodiversity effects. Nature 515 (7525), 108–111. http://dx.doi.org/10.1038/nature13869.