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Cold-water coral assemblages on vertical walls from the Northeast Atlantic

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Abstract

Aim: In this study, we assess patterns of cold-water coral assemblages observed on deep-sea vertical walls. Similar to their shallow-water counterparts, vertical and overhanging walls in the deep sea can host highly diverse communities, but because of their geometry, these habitats are generally overlooked and remain poorly known. These vertical habitats are however of particular interest, because they can protect vulnerable coral ecosystems from trawling activities. As such, it is important to understand their ecology and assess their global importance.

Location: Vertical walls on complex geomorphic features, in particular walls of the Rockall Bank Slope Failure Escarpment, Whittard and Explorer Canyons, Northeast Atlantic.

Methods: Video analysis of remotely operated vehicle transects carried out at five sites is used to investigate differences in species composition and diversity across walls and to compare those to nearby cold-water coral sites on flat terrain. A high-resolution photogrammetric reconstruction is further employed to examine whether wall complexity plays a role in promoting niche differentiation at very fine spatial scales.

Results: The investigated walls showed differences in species assemblage both across walls and in comparison to flat sites, with the fine-scale heterogeneity engendered by walls allowing niche differentiation between closely related taxa.

Main Conclusions: Vertical walls represent an important cold-water coral habitat with differences in species composition across walls within a region, illustrating their role in driving diversity patterns. Based on publicly available bathymetric datasets and a catalogue of broad-scale terrain features, globally over 8,000 features are likely to have vertical walls and cold-water corals, which highlight the need to consider deep-sea vertical habitats in current conservation efforts.

KEYWORDS

cold-water corals, deep sea, distribution, diversity, niche differentiation, spatial patterns, vertical walls

1 | INTRODUCTION

In order to address conservation needs in the deep sea, we need to understand better the spatial distribution of ecologically important habitats, and this can be facilitated by identifying the factors that play significant roles in shaping biological spatial patterns. The relative importance of these variables are expected to change across habitats and scale, with environmental factors most likely to explain species coexistence patterns at broader spatial scales and biotic processes at finer scales (Tamme, Hiiesalu, Laanisto, Szava-Kovats, & Pärtel, 2010). From a conservation perspective, identifying the drivers behind biodiversity patterns can help shape approaches to marine spatial planning (Economo, 2011). For example, when environmental controls are most important, maximizing representation might be favoured, while when biotic controls are most relevant, protection of specific features may be optimal. Along the same line, niche theory suggests that each species exploits its environment differently (i.e., niche differentiation) and communities arise from heterogeneity in environmental conditions and limited resources (Hutchinson, 1957). This hypothesis implies that more complex environments, which provide increased niche differentiation, may act as biodiversity hotspots of particular conservation value. The main issue in the deep sea is that most habitats are poorly studied, with rarer ones still being discovered.

In shallow waters, the slope of the seabed has long been identified as an important structuring component of benthic communities (Witman & Dayton, 2001). When comparing vertical and horizontal substrata, predation (by fish and urchins, for example), sunlight intensity, sedimentation rates and wave action may all be structuring factors (Miller & Etter, 2008; Sebens, 1986). This can often lead to horizontal substrata being dominated by macroalgae and vertical sites being colonized by epifaunal suspension feeders (Miller & Etter, 2011). In tropical coral reefs, corals are often more abundant on vertical surfaces, where competition with algae and sedimentation rates may be reduced (Birkeland, 1977; Rogers, Fitz, Gilnack, Beets, & Hardin, 1984; Sheppard, 1982). Rich and abundant communities of suspension feeders on vertical walls have also been reported for deeper waters (Haedrich & Gagnon, 1991), but it is only in recent years that technological advances, particularly the increasing use of remotely operated vehicles (ROV), have allowed for more detailed descriptions of such environments (Bell, Alt, & Jones, 2016; Huvenne et al., 2011; Johnson et al., 2013) As a result, large vertical reefs of overhanging scleractinians (Brooke & Ross, 2014; Fabri et al., 2014; Huvenne et al., 2011; Van den Beld et al., 2017) and walls inhabited by Alcyonacea (Brooke et al., 2017; Edinger et al., 2011; Quattrini et al., 2015) or dominated by other community types such as bivalves (Johnson et al., 2013; Ludvigsen, Sortland, Johnsen, & Singh, 2007) and sponges (Bell et al., 2016; Brooke et al., 2017; Genin, Paull, & Dillon, 1992) are being discovered. Some of these steep walls have been reported as harbouring the highest abundances of corals or bivalves in the area (Gasbarro, Wan, & Tunnicliffe, 2018; Johnson et al., 2013; Morris, Tyler, Masson, Huvenne, & Rogers, 2013) with high numbers of other associated species also observed (Robert, Jones, Tyler, Rooij, & Huvenne, 2015).

Cold-water corals are currently at risk from both environmental changes and direct anthropogenic impacts (e.g., trawl fisheries) (Freiwald, Helge Fosså, Grehan, Koslow, & Roberts, 2004) and are the subject of targeted conservation strategies (Huvenne, Bett, Masson, Bas, & Wheeler, 2016; Ross & Howell, 2013). The general association between cold-water corals and seafloor slope is well established and has successfully been employed to inform management (Lo Iacono et al., 2018; Rengstorf, Yesson, Brown, & Grehan, 2013), but vertical walls are of particular interest as they can provide natural protection against bottom trawling. Larval dispersal from these refuges may also help recolonize damaged habitats. However, despite their likely significance, the diversity, abundance and uniqueness of such habitats along the continental slope are not known as the lower resolution bathymetric maps generally available for the deep-sea underestimate slope, while sampling techniques such as trawls and towed cameras are not suited to vertical habitats.

In this paper, we examine the spatial patterns of coral assemblages observed on deep-sea vertical walls at local and regional scales in the Northeast Atlantic and examine implications for management and conservation. The objective is to identify whether cold-water coral assemblages on verticals walls harbour different species assemblages than corals on flat terrain. We use video analysis of ROV transects carried out at five sites in the Northeast Atlantic to investigate species assemblage, diversity and niche differentiation.

2 | METHODS

We investigated composition of vertical cold-water coral communities through case studies in the Northeast Atlantic. These case studies included a landslide escarpment and four sites in two submarine canyons (Table 1, Figure 1). During the "Slope Collapses on Rockall Bank and Escarpment Habitats" (SORBEH) cruise in July 2014 (*RV Celtic Explorer*-14011), the *ROV Holland I* was employed to survey a submarine landslide headwall scarp (Georgiopoulou, Shannon, Sacchetti, Haughton, & Benetti, 2013; Figure 1a). As part of the "Complex Deep-sea Environments: Mapping habitat heterogeneity As Proxy for biodiversity" (CODEMAP) project (cruise *RRS James Cook*-125), two branches of Whittard Canyon, with walls on both sides, were surveyed using the *ROV Isis* (Figure 1b). Another wall was surveyed in the nearby Explorer Canyon (Figure 1b,c). In addition, two ROV dives completed during a previous cruise (JC-036) in Whittard Canyon were also included in this analysis. For each of these dives, sections of videos recorded with the ROVs moving vertically from the base to the top of the walls were separated into transects for analysis (18 in total). To assess differences in species assemblages, we included an additional 10 video transects (from CE-14011, JC-125, JC-036 and another older Whittard Canyon expedition, JC-010) where cold-water corals on flat ground were observed at comparable depths. Dive locations and geological settings are summarized in Table 1.

Remotely operated vehicle positioning was obtained using an ultra-short baseline system (USBL) with an accuracy of 1% of

TABLE 1 List of cruises, vehicles and general environmental characteristics for each dive. Location names for Whittard Canyon based on Amaro et al. (2016)

Cruise	ROV	Dive	Camera system (resolution)	No. of transects	Depth (min–max)	Ave. transect length x width (m)	Location	Orientation	Geology
CE-14011	*Holland I*	D10	OE 14366 (1,920 × 1,080)	3	1,530–1,400 m	450 × 2.6	Rockall Escarpment	Southwest–Northeast	Volcanic rocks and hardened layered yellowish sedimentary rocks
CE-14011	*Holland I*	D07	OE 14366 (1,920 × 1,080)	2	930–950 m 1,000–1,030 m	185 × 4.3	Rockall Escarpment	Flat	Mix of sediment and coral patches with rocky outcrops of extrusive volcanic rock and indurated bioclastic sediments
CE-14011	*Holland I*	D08	OE 14366 (1,920 × 1,080)	2	820–850 m 1,000–1,010 m	180 × 5.2	Rockall Escarpment	Flat	Mix of sediment and coral patches with rocky outcrops
JC-010	*ISIS*	D065	Pegasus Insite Tritech (768 × 576)	1	950–875 m	150 × 2.1	Whittard Canyon Eastern Branch	Flat	Rippled soft sediments and coral rubble
JC-036	*ISIS*	D109	Pegasus Insite Tritech (768 × 576)	1	1,650–1,510 m	230 × 3.5	Whittard Canyon Western Branch	West	Friable, less competent thickly bedded light orange to greyish white sedimentary units
JC-036	*ISIS*	D114	Pegasus Insite Tritech (768 × 576)	2	1,390–1,350 m 1,610–1,570 m	300 × 2.4	Whittard Canyon Eastern Branch	Flat	Outcrop of indurated sediment with manganese coating
JC-036	*ISIS*	D116	Pegasus Insite Tritech (768 × 576)	2	1,360–1,290 m	490 × 2.5	Whittard Canyon Eastern Branch	Northeast	Alternations of strong and weak, thinly bedded sedimentary units
JC-036	*ISIS*	D117	Pegasus Insite Tritech (768 × 576)	1	1,815–1,810 m	135 × 3.0	Whittard Canyon Eastern Branch	Flat	Soft sediment and coral rubble
JC-125	*ISIS*	D246	Insite Super Scorpio (1,920 × 1,080)	2	805–800 m 850–830 m	230 × 2.1	Explorer Canyon	Flat	Soft Sediments and coral rubble
JC-125	*ISIS*	D249	Insite Super Scorpio (1,920 × 1,080)	3	1,340–1,290 m	120 × NA	Whittard Canyon Eastern Branch	Northeast	Alternations of strong and weak, thinly bedded sedimentary units
JC-125	*ISIS*	D254	Insite Super Scorpio (1,920 × 1,080)	1	1,050–1,030 m	260 × 3.5	Explorer Canyon	Northwest	Weak thinly bedded sedimentary units
JC-125	*ISIS*	D255	Insite Super Scorpio (1,920 × 1,080)	5	740–560 m	510 × 2.9	Whittard Canyon Western Middle Branch	Northwest	Friable, less competent thickly bedded light orange to greyish white sedimentary units
JC-125	*ISIS*	D256	Insite Super Scorpio (1,920 × 1,080)	1	820–650 m	280 × 5.1	Whittard Canyon Western Middle Branch	Southeast	Friable, less competent thickly bedded light orange to greyish white sedimentary units
JC-125	*ISIS*	D263	Insite Super Scorpio (1,920 × 1,080)	2	1,420–1,260 m	350 × 4.3	Whittard Canyon Eastern Branch	Southwest	Brown to orange lithology resistant to erosion and less competent dark grey one

depth. Laser beams separated by 100 mm were present for scaling. Overlapping frames were extracted and imported to form a "stack" in the freely available software ImageJ (National Institutes of Health, https://imagej.nih.gov/ij/). Each organism larger than 20 mm was identified, marked and its pixel position recorded to avoid risks of double counting using the "Cell Counter" plugin. A single observer made the species identifications using imagery catalogues available for the area (Howell & Davies, 2010; Howell, Davies, & Beld, 2017; Jones et al., 2009) or used morphospecies (also known as operational taxonomic unit) when species-level identification could not be achieved (ophiuroids, hydroids and brachiopods were not included as reliable counts could not be obtained). Use of morphospecies enables the differentiation of taxa below the lowest taxonomic level to which an organism can be identified based on imagery alone, using features such as colour, growth form, branching pattern, ecological information (e.g., depth), etc. (Howell et al., 2019). As this approach complicates comparison between research groups or reuse of data, a reference image for each morphospecies (as well as the species matrix) is provided as Supporting Information. Differences in species composition were investigated using non-metric dimensional scaling carried out on a Bray–Curtis resemblance matrix computed on the Hellinger-transformed (Legendre & Gallagher, 2001) species matrix. Alpha (i.e., within-sample) diversity was evaluated using rarefaction curves. To investigate the composition of associated species, reef-building coral colonies were not included in these analyses.

To further establish how vertical walls may provide different habitats, we investigated the spatial distribution of three Alcyonacea species at local scales. These were three of the most commonly observed morphospecies on Whittard Canyon's northeast facing wall in the Eastern branch (~500 m^2, Figure 2a). Owing to the difficulties of sampling on a vertical wall with the ROV hovering, no specimen of these morphospecies was collected during the expeditions. Based on the "CATAMI Classification Scheme for scoring marine biota and substrata in underwater imagery classification," these three taxa would fall under the Black & Octocorals Non-fleshy: Arborescent (red species), Black & Octocorals Non-fleshy: Bushy (pink species) and Black & Octocorals Fan: Rigid (yellow species; Figure 2c). On this wall, the *ROV Isis* carried out video surveys of overlapping horizontal lines, which we employed for ultra-high-resolution photogrammetric reconstructions (Figure 2a and Video S1). Structure-from-Motion techniques allow for scaled and georeferenced 3D reconstructions to be achieved from a single camera moving around a scene (Ullman, 1979). The commercial software AGISOFT PHOTOSCAN professional edition (v1.2.4) was used. One frame every 3 s was extracted (representing 2,587 images) from the Insite Pacific Scorpio video data (1,920 × 1,080 pixels, Figure 2b), and the detailed procedure presented in Robert et al. (2017) was followed. The point cloud processing software CloudCompare (v2.6.1) was used to compute local terrain descriptors (slope and aspect converted to eastness and northness) at a scale of 0.05 m, and Gaussian roughness also derived at 0.02 and 0.1 m.

A marker was set within the point cloud in AGISOFT PHOTOSCAN to locally position each individual. Markers were exported as xyz files and, for each, terrain descriptors were assigned by computing the mean of the ten nearest points. In addition, at each point, the presence of dead or live coral framework was assessed. As our aim was to determine whether there was a difference in environmental conditions between the localities where a species occurs from those generally available in the area (e.g., background), rather than to model species–environment relationships, we opted for an ordination technique. Ordination techniques allow for direct comparisons of environmental space and are less likely to overestimate niche overlap (Broennimann et al., 2012). To determine whether the investigated species' niche differed from the average conditions available in the background, the approach created by Dolédec, Chessel, and Gimaret-Carpentier (2000) was applied, using the "niche" function of the "ade4" R package (Dray & Dufour, 2007). We first carried out a principal component analysis (PCA) based on a matrix composed of the environmental conditions at all locations where the three species were present as well as at 10,000 randomly drawn background points (Broennimann et al., 2012; Di Cola et al., 2017). For each species, a centre of gravity was calculated in PCA space based on the rows representing each species' presences. From this centre of gravity, the square distance to the PCA centre, called the outlying mean index (also termed marginality), represents the level of difference between the average habitat conditions used by that species and the average conditions available in the background.

To examine niche overlap, the environmental space, as represented by the first two axes of the PCA, was divided into a 100 × 100 grid and a kernel density function was applied to obtain the smoothed density of occurrence of the chosen species in each grid cell (Broennimann et al., 2012). Niche overlap between species *x* and *y* was calculated using the metric D as presented in Warren, Glor, and Turelli (2008),

$$D = 1 - 0.5 \sum_i |px_i - py_i|$$

where *p* is the occupancy as obtained from the kernel density function for each cell *i*. *D* varies from 0, when there is no overlap, to 1, when there is complete overlap. Permutation tests (using 999 permutations) were employed to assess test significance.

3 | RESULTS

Based on the video transects, a total of 38,720 individuals/colonies from 112 morphospecies (of which 26 were cold-water coral morphospecies) were encountered on the walls of the Rockall Bank Escarpment, Whittard and Explorer Canyons (Tables S1 and S2), with cold-water corals (Scleractinia, Alcyonacea and Antipatharia) forming the overall largest component (Figure S1, Figure 3). However, sponges were more prevalent on the walls of the Rockall Escarpment while bivalves (the deep-sea oyster *Neopycnodonte zibrowii* and the limid clam *Acesta* sp.) were much more numerous on Whittard Canyon's western middle branch walls. The Rockall Escarpment showed the highest species richness, followed by the southwest

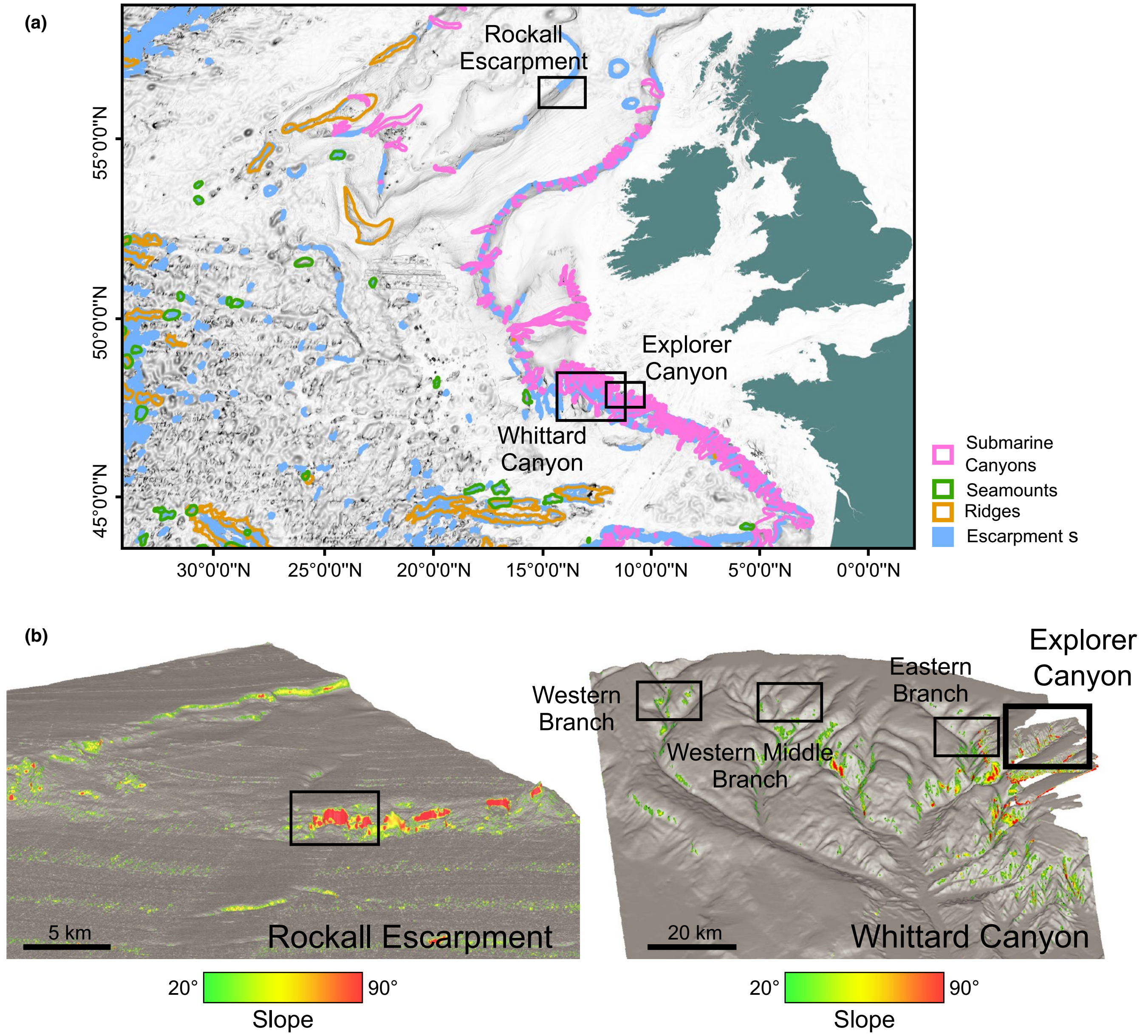

FIGURE 1 Location of study sites (the Rockall Escarpment as well as Whittard and Explorer Canyons) in the Northeast Atlantic overlaid with (a) broad geomorphic features as identified by Harris et al. (2014). (b) Bathymetry for the Rockall Escarpment, Whittard Canyon (INFOMAR, http://www.infomar.ie/) and Explorer Canyon (MESH Atlantic, http://www.meshatlantic.eu/), showing high slope areas where walls are likely to occur (displayed with four times vertical exaggeration)

facing transect of Whittard Canyon's eastern branch. In Whittard Canyon, corals were mostly composed of *Desmophyllum pertusum* (previously *Lophelia pertusa* (Addamo et al., 2016)) and solitary cup corals *Desmophyllum* sp., but occurrences of *Solenosmilia variabilis* and *Madrepora oculata* as well as 13 morphotypes of Alcyonacea were also encountered. On Whittard Canyon's western wall and in Explorer Canyon, *Primnoa* sp. colonies were also numerous. Corals on the Rockall Escarpment were mainly composed of *S. variabilis* and solitary cup corals *Desmophyllum* sp., but the black coral *Stichopathes* sp. was also common.

The sites assessed showed slightly higher richness at flat locations, but differences in species assemblages occurred between most sites as well as between flat and vertical sites (Figure 4). One notable exception is Whittard Canyon's dive 065, which clusters closer to transects from the western middle branch. It is, however, important to note that this particular transect occurs at shallower depths (950–875 m) than the other eastern branch transects, with western middle branch transects also being shallower. As sites across branches varied in depth, it is currently not possible to determine whether the pattern observed is the result of differences in species composition across branches or differences across depth. The fact that transects from Explorer Canyon and Whittard Canyon's western middle branch still cluster together despite the geographical distance would suggest the latter.

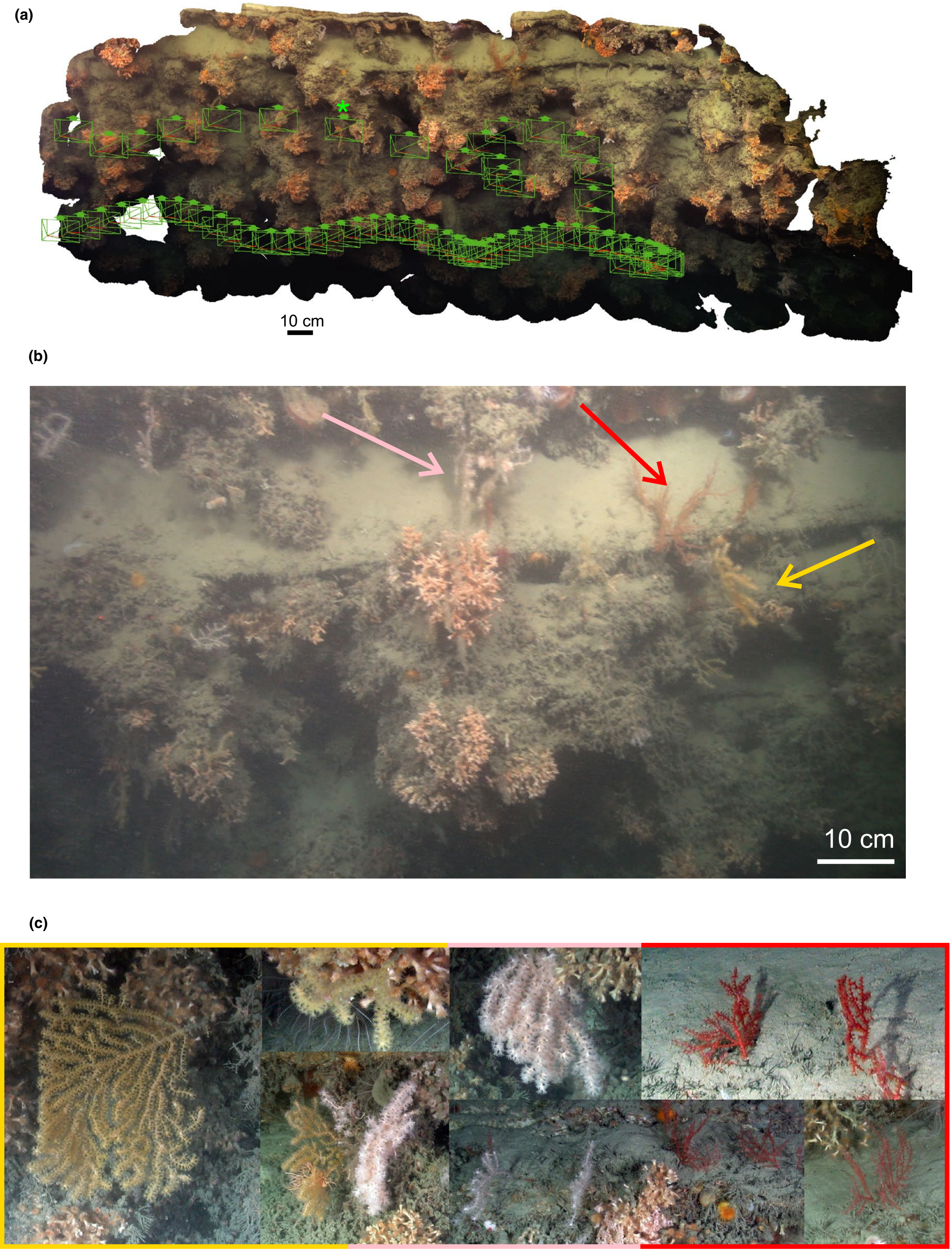

FIGURE 2 (a) Photogrammetry (Structure-from-Motion) reconstruction of a section of wall in Whittard Canyon's Eastern branch. The ROV camera locations used to build this reconstruction are shown in green. Video S1, provided as supporting information, shows a fly-through animation of this section of wall. The * shows the position of the image shown in (b). The three Alcyonacea morphospecies used for the local analysis are identified by arrows and shown in more details in (c)

Within the space of the reconstructed wall, 421, 303 and 542 individuals of the yellow (likely *Ancanthogorgia* sp.), pink (likely Primnoidea sp) and red (possibly Plexauridae sp.) morphospecies of Alcyonacea respectively, were identified. Permutation tests revealed that the average habitat conditions used by each species was different (*p*-value: .001) from the average conditions available in the

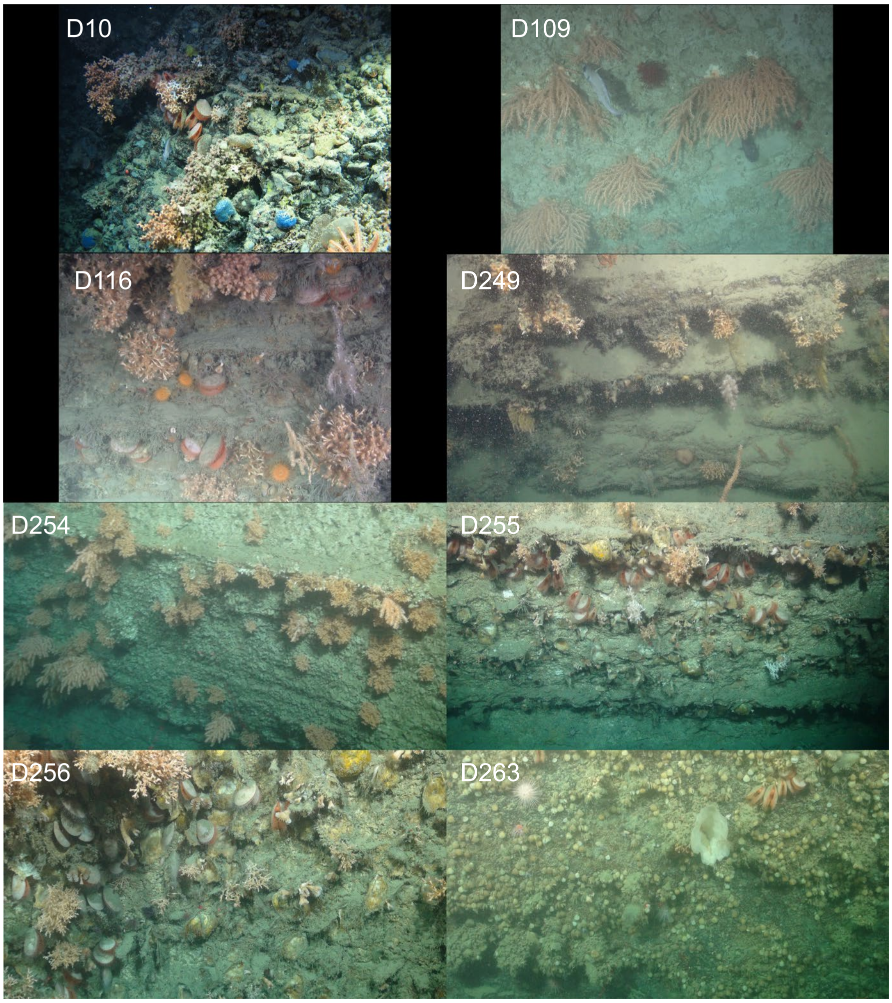

FIGURE 3 Example of digital still images for each of the walls surveyed. Dive numbers as listed in Table 1

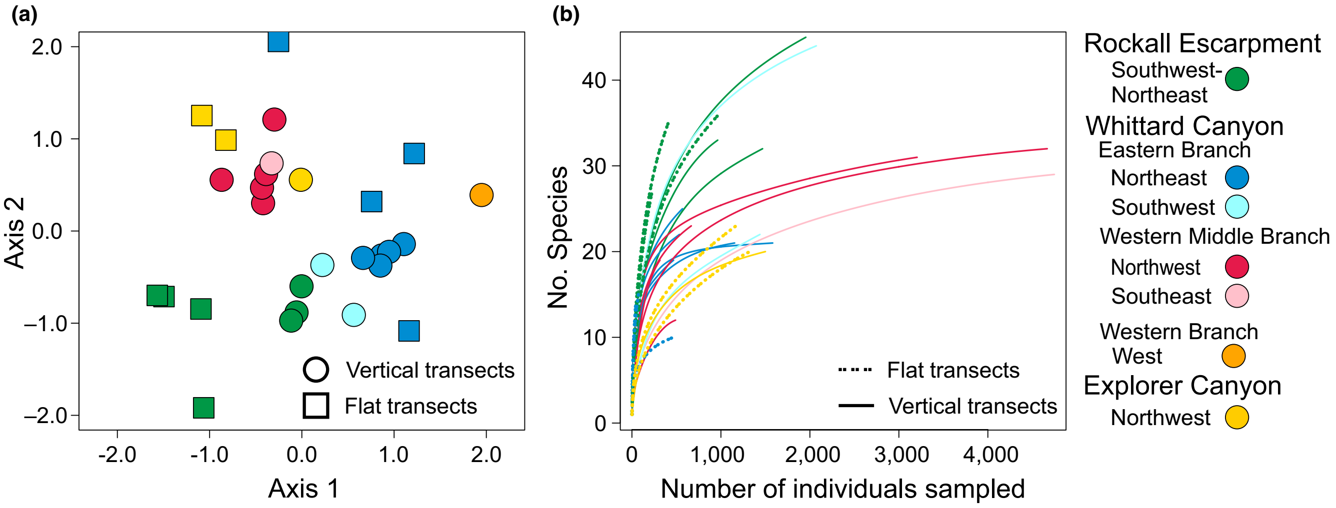

FIGURE 4 (a) Non-metric dimensional scaling (Stress = 0.18) of the megabenthic species (not including reef-building coral species) observed in video transects carried out on the Rockall Escarpment, as well as in Whittard and Explorer Canyons (b) Rarefaction curves

background (Figure 5). However, the outlying mean index (yellow: 1.25, pink: 1.70 and red: 0.914) indicated that these differences were relatively small. Asthe PCA's first two axes only represented 36.8% of the variation in environmental parameters, we expect that the addition of other environmental parameters would improve differentiation ability. Comparison of niche overlap showed that all three Alcyonacea morphospecies' niches shared some of the same environmental conditions (*D* values for yellow–pink: 0.702, red–yellow: 0.674 and red–pink: 0.660), but that niche overlap with the red morphospecies was still less than could be expected by chance (*p*-value for yellow–pink: .179, red–yellow: .003 and red–pink: .007). The yellow and pink morphospecies of Alcyonacea were frequently found attached to both dead and living (though likely not attached to live tissue) coral framework of *D. pertusum*, associated with higher rugosity values, while the red morphospecies tended to be observed on ledges where sediment had accumulated.

4 | DISCUSSION

Within the Northeast Atlantic region examined here, species assemblages differed between most of the walls investigated as well as between vertical and horizontal habitats, although many species co-occurred. Differences in habitat use between certain species were demonstrated at the scale of a single wall, with the fine-scale structural complexity provided by vertical habitats likely providing additional niche space exploited by certain species.

4.1 | Drivers of cold-water coral assemblages

Many studies have found a range of environmental variables to be useful in explaining cold-water coral taxa spatial patterns (Table 2), with clear trends apparent in the scale at which particular environmental variables are significant. However, this may also reflect the lack of information regarding the spatial variability of certain predictors at specific scales. For example, variables such as substrate type become significant at finer resolutions, but are not often available for global assessment. Similarly, other variables, such as current speed or productivity levels, are available only at broader scales, even if finer-scale variations are also likely to be important.

Our results suggested that the differences in species assemblages observed between sites were, at least in part, depth related. Increases in depth correlated with decreases in measured temperatures, with the wall on the Rockall Escarpment being the coldest (4.7°C), followed by Whittard Canyon's western branch (5.6°C), eastern branch (6.9°C), middle western branch (10.8°C) and Explorer Canyon (11.7°C). Although some cold-water coral species co-occurred across walls, one species was usually dominant. For example, the deepest and coldest wall, Rockall Escarpment, was dominated by *S. variabilis* and various taxa of Antipatharians. *Solenosmilia variabilis* globally tends to occur in deeper and colder waters than *D. pertusum* and *M. oculata* (Davies & Guinotte, 2011; Roberts, Wheeler, Freiwald, & Cairns, 2009) while Isididae and Antipathidae also have deeper mean depths than other deep-sea coral families (Etnoyer & Morgan, 2005). In the eastern branch of Whittard Canyon, isopycnal displacement caused by internal tides could lead to daily changes of up to 1°C in temperature (Hall, Aslam, & Huvenne, 2017), and the wider temperature tolerance window or stronger physiological capacity for adjustment to temperature fluctuations of *D. pertusum* when compared to *M. oculata* (Naumann, Orejas, & Ferrier-Pagès, 2014) could be another reason for observed differences in abundance across branches.

Comparing walls of similar depth on opposite sides of Whittard Canyon's western middle branch, we found a very high similarity in species composition and diversity. However, in the case of the eastern branch, differences were clearly apparent and were almost as large as differences with the transects on flat terrain. Differences in the geology of these two walls could in part explain this pattern. Walls in Whittard Canyon were generally composed of friable, less competent sedimentary units of varying thickness (Carter et al., 2018; Robert et al., 2017), but one notable exception is the southwest facing wall in Whittard Canyon's eastern branch. This wall was composed of two lithologies, including a harder rock that seemed resistant to erosion. More competent, resistant rocks were also found along the Rockall Escarpment, and both walls appeared more hospitable to other colonizing organisms (mainly brachiopods, sessile holothurians and sponges), which led to higher diversity. Soft sediments dominated the surroundings of most coral patches at flat sites, and the inclusion of soft sediment associated fauna, occurring between coral patches, increased diversity. Despite differences in species composition between horizontal and vertical sites, flat terrain transects were more similar to their same-site similar-depth vertical counterparts than to each other. Within sites, the higher variability observed at flat sites is likely linked to the greater separation in transect locations. It may be that high dispersal rates increase the number of shared species, while environmental conditions play a role in regulating their relative abundance.

Differences in species dominance could also arise as a result of the first species to colonize, with the established species outcompeting the others for space, leading to possible alternate states (Sutherland, 1974). In shallower coral reefs, competition with faster growing organisms, such as barnacles, tunicates and bryozoans, can reduce coral recruitment (Birkeland, 1977). However, once established, large colonial organisms reduce exposed substrate and overgrow adjacent individuals, potentially limiting the occurrence of certain species (Jackson, 1977; Sebens, 1986), while the additional structural complexity may favour colonization by other taxa. Although the lower competition rates occurring in deeper waters may diminish the importance of such mechanisms, this could potentially explain the lower number of species observed on the northeast facing wall of the eastern branch, where *D. pertusum* completely covered the wall in certain areas. On the other hand, for species occurring on coral framework away from the wall (such as the yellow and pink morphospecies of Alcyonanceans), this apparently small change in location likely influenced the hydrodynamic regime encountered and the ability of an individual to capture food (Gori, Reynaud, Orejas, & Ferrier-Pagès, 2015; Orejas et al., 2016; Purser, Orejas, Moje, & Thomsen, 2014). One could also expect that on highly friable rock, coral colonies may be size/weight limited and less able to overgrow and limit the space available for colonization by other organisms, possibly explaining bivalve dominance in the western middle branch. On the northwest facing wall of the eastern branch, bed-scale variations in rock strength and friability also led to the formation of ledges through preferential erosion where

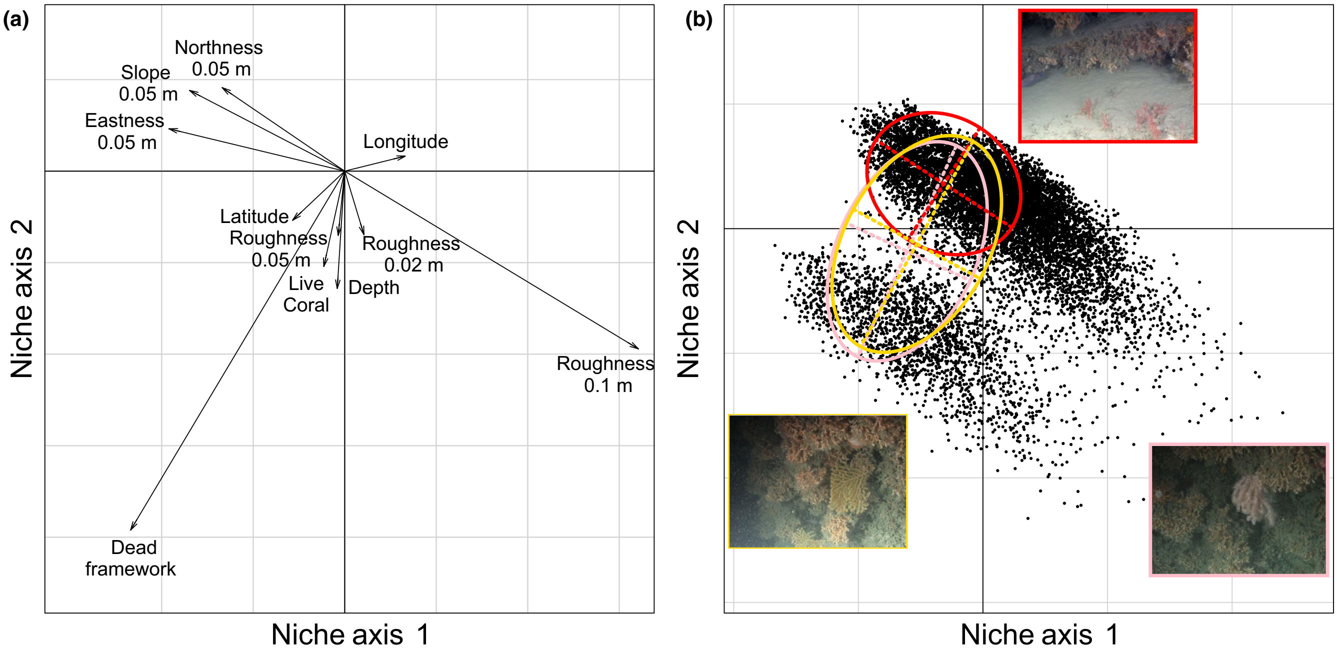

FIGURE 5 Outlying mean index analysis two-dimensional plots showing (a) the environmental variables and (b) all data points (black dots, all coral locations and background points on vertical wall) and species niche (ellipse) for three morphospecies of Alcyonacea (red, yellow and pink). The centre of the dashed lines shows the species centre of gravity while the ellipse represents 1.5 x the standard deviation

sediment accumulated, contributing to fine-scale heterogeneity and niche separation.

Resource availability may further play a role in determining whether colonies of smaller fast-growing organisms establish first and outcompete the larvae of slower growing species or whether these slower growing organisms can develop enough to eventually become dominant (Birkeland, 1977; Kneitel & Chase, 2004; Lavorel & Garnier, 2002). For example, owing to greater filtering capacities, bivalves may be better able to handle less regular food supply than corals (Johnson et al., 2013). Modelling studies of internal tides within Whittard Canyon have found high energy levels, with some particularly high near-bottom velocities in the eastern and western branches (Amaro et al., 2016; Aslam, Hall, & Dye, 2018). Depending on the orientation of individual walls to the oncoming current, the hydrodynamic regime created may trap food particles and increase food availability in certain areas while nearby areas in the lee side of the wall experience a different regime. Nepheloid layers have been recorded in proximity to the investigated walls in Whittard Canyon (Huvenne et al., 2011; Johnson et al., 2013; Wilson, Raine, Raine, Mohn, & White, 2015). Such benthic nepheloid layers were particularly rich in fresh and labile organic matter, but showed differences in content across branches (Huvenne et al., 2011; Wilson, 2016).

4.2 | Conservation Importance

Based on currently available global bathymetric maps, estimating the area potentially represented by vertical walls is very difficult. For example, based on the 15 arc second resolution of the SRTM15_PLUS global satellite bathymetry grid (Olson, Becker, & Sandwell, 2016), the highest slope value calculated for Whittard Canyon, an area known to harbour vertical walls, is 53° (Figure 6). As such, if areas with slopes >20° are taken as representing areas of potential very steep topography in specific deep-sea features with complex topographies such as canyon systems, seamounts, ridges and escarpments as compiled in the global seafloor geomorphic features catalogue by Harris, Macmillan-Lawler, Rupp, and Baker (2014) (Figure 1a), this could add up to 421,000 km^2 (with an additional 682,000 km^2 on escarpment, which can overlap with other features). Of course, not all walls would occur in broadly suitable cold-water coral habitats, but 6,000 km^2 (with an additional 12,000 km^2 on escarpment) of these potential walls occurred in regions predicted to be suitable for cold-water corals based on the modelling of Davies and Guinotte (2011) (for five common reef-forming cold-water scleractinian species: *D. pertusum*, *M. oculata*, *S. variabilis*, *Enallopsammia rostrata* and *Goniocorella dumosa*) (Figure 7). However, even with regions broadly suitable for cold-water coral presence, not all walls can be expected to harbour communities of particular significance.

As our results demonstrated differences in species assemblages between most walls investigated, from a global conservation perspective, this potentially represents up to 18,000 km^2 of vertical cold-water coral habitat across over 8,000 complex geomorphic features. Considering the bathymetric resolution available, it is to be expected that not all areas with slopes greater than 20° are likely to represent vertical or overhanging walls, but these first estimates are obtained using a plan view, with the true surface area represented by vertical structures remaining underestimated. In addition, many smaller features, or

TABLE 2 Environmental variables found to be important drivers of cold-water coral spatial patterns from species distribution model studies

Scale	Environmental controls	Studies
Global (1,000's km)	Depth[1,2] Aragonite Saturation[1,2,3] Calcite Saturation[4] Oxygen level[1,2,3,4] Productivity[1,2 ,3,4] Temperature[1,2,4] Salinity[1,2] Dissolved inorganic carbon[3] Nutrient concentrations*[3] Topography[4]	1. Davies, Wisshak, Orr, and Murray Roberts (2008) (1 deg) 2. Davies and Guinotte (2011) (30 arc sec) 3. Tittensor et al. (2009) (2 min) 4. Yesson et al. (2012) (30 arc sec)
Regions (100's–10's km)	Depth[1,6,10,11,12] Hydrodynamics**[1,5,6,7,10] Productivity***[1,6,8,9,10] Temperature[1,5,6,7,8,9,10,12] Salinity[1,8,12] Topography****[5,6,7,8,9,10,11,12] Substrate Type[7] Aragonite Saturation[9] Oxygen level[9] Nutrient concentrations[9] Geomorphology[10]	1. Davies et al. (2008) (0.5 deg) 5. Rengstorf et al. (2013) (200 m) 6. Bryan and Metaxas (2007) (2–5 min) 7. Leverette and Metaxas (2005) (9 km) 8. Anderson, Guinotte, Rowden, Clark, et al. (2016) (250 m) 9. Anderson, Guinotte, Rowden, Clark, et al. (2016) (30 arc sec) 10. Tracey, Rowden, Mackay, and Compton (2011) (250 m) 11. Ross and Howell (2013) (30 arc sec) 12. Guijarro et al. (2016) (0.015 deg)
Local (10's km–100's m)	Depth[13,15,17,18] Backscatter[14,18] Topography****[13,14,15,16,17,18,19] Geomorphology[13] Substrate Type[13] Hydrodynamics**[18,20]	13. Howell, Holt, Endrino, and Stewart (2011) (200 m, 25 m) 14. Robert et al. (2015) (50 m) 15. Dolan, Grehan, Guinan, and Brown (2008) (0.5 m) 16. Guinan, Brown, Dolan, and Grehan (2009) (550 m, 30 m) 17. Woodby, Carlile, and Hulbert (2009) (15–50 m) 18. de Clippele et al. (2017) (2 m) 19. Lo Iacono et al. (2018) (5 m) 20. Bargain et al. (2018) (20 m)

Note: Certain environmental variables were grouped (indicated by asterisks) and listed studies may have found one or more of these variables as significant. The resolution employed in each study is indicated in parenthesis.

Supercript numbers refer to the studies listed in the right-hand side column.

*Silica, phosphate, nitrate concentrations.

**Current speed/direction, orbital speed, bottom shear stress.

***Surface level chlorophyll a, particulate organic carbon export/flux, dissolved organic matter.

****Slope, standard deviation of slope, aspect, rugosity, bathymetric position index, fractal dimension.

steep walls in other geomorphic categories, would add to these estimates. Although overlapping modelled coral habitat suitability distributions with potential occurrences of vertical walls can only provide very coarse estimates, it allows us to examine the conservation importance of these features until global initiatives such as GEBCO Seabed2030 can provide higher resolution global bathymetric datasets (Mayer et al., 2018). To put these estimates into perspective, a world-wide assessment of shallow tropical coral reefs, based on 500 m resolution data, estimated that they covered 212,340 km^2 (Burke, Reytar, Spalding, & Perry, 2011). A similar assessment is not available for cold-water coral reefs, but our estimates indicate a surface area equivalent to 8% of the estimated surface area of shallow coral reefs is covered by currently overlooked vertical cold-water coral habitat. Although only 508 of the geomorphic features have at least one OBIS (Ocean Biogeographic Information System) record for any of the five previously listed species (Figure 7), this small number illustrates how little we know of the global spatial distribution of cold-water coral species, with many areas of the world remaining greatly under-sampled and poorly mapped. In particular, coral samples from vertical walls would be especially underrepresented in the OBIS records because of the associated sampling difficulties. Most records available would result from traditional sampling techniques (e.g., trawls and dredges), which would have purposefully avoided high profile structures. Collections on vertical walls would require ROV or manned-submersible, and even so, sampling while hovering remains problematic for most vehicles. Recent developments in the use of underwater hyperspectral imagery may help counteract such difficulties by reducing the need for samples for species identification and improving automated quantification of live coral cover for monitoring (Dumke, Nornes, et al., 2018; Dumke, Purser, et al., 2018).

Until very recently (see Davies et al. (2017)), hierarchical classification schemes aimed at informing ecosystem-based

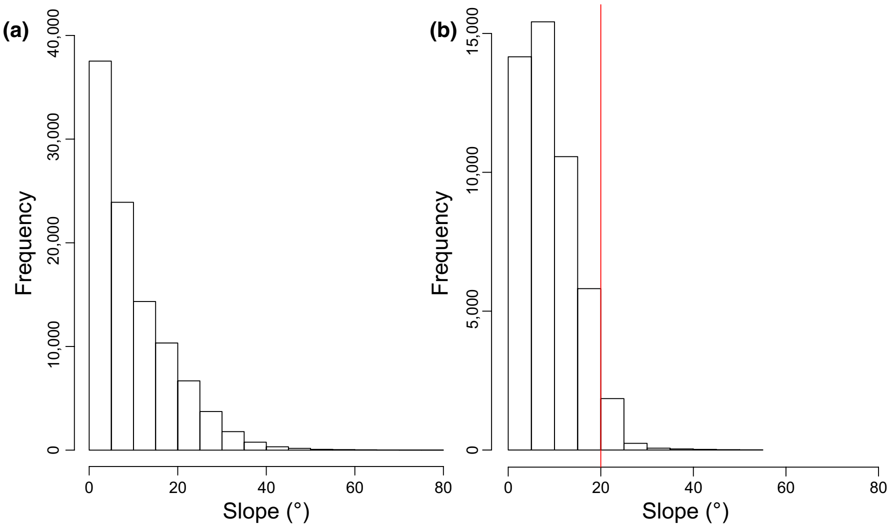

FIGURE 6 (a) Histogram based on ship-borne multibeam bathymetry (50 m resolution) of Whittard Canyon, showing the existence of steep walls (maximum slope 88°). (b) Histogram based on the SRTM15_PLUS global satellite bathymetry grid (15 s resolution, ~500 m) for Whittard Canyon illustrating the smoothing effect of lower resolution data (maximum slope 53°)

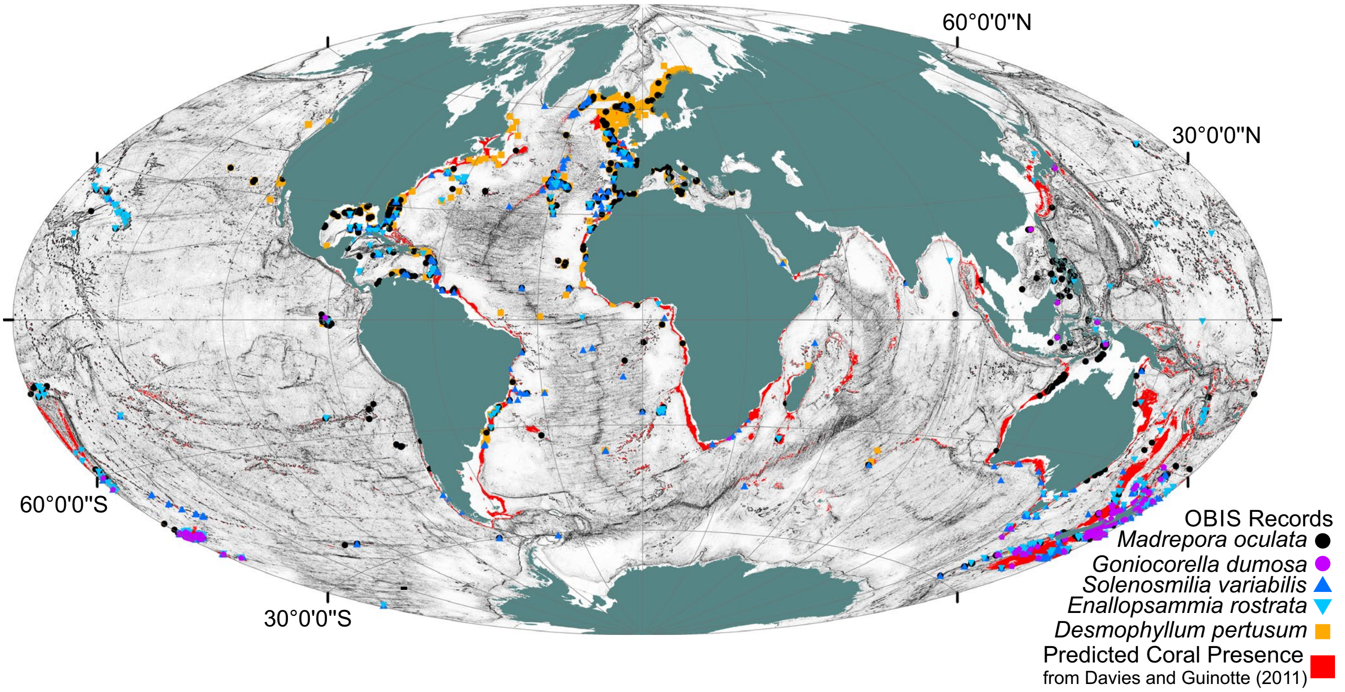

FIGURE 7 Global slope map (Aitoff world projection), OBIS presence records for five species of reef-building cold-water corals (*Desmophyllum pertusum*, *Madrepora oculata*, *Solenosmilia variabilis*, *Enallopsammia rostrata* and *Goniocorella dumosa)* and areas of predicted cold-water coral presence as produced by Davies and Guinotte (2011)

management in deep waters did not specifically consider vertical habitats. Yet, such walls likely play an important role in supplying larvae to surrounding areas (Smith & Witman, 1999), especially considering that *D. pertusum* larvae could possibly survive for more than three weeks (Brooke & Ross, 2014; Larsson et al., 2014). In addition, the rough topography can also protect these vulnerable cold-water coral ecosystems from threats such as commercial bottom trawling. However, such activities also lead to other effects, such as increased suspended particulate matter and change in organic content (Puig et al., 2012; Wilson, Kiriakoulakis, et al., 2015). Although many CWC are tolerant of moderate to high sedimentation rates (Brooke, Holmes, & Young, 2009), it has been suggested that reduced sediment accumulation on vertical walls could be beneficial for feeding ability and larvae survival (Brooke & Ross, 2014; Brooke et al., 2017), and anthropogenic changes to such processes could have unknown effects on vertical wall assemblages. As the temporal variability of most environmental factors, and their influence on spatial patterns, remains mostly unknown, cold-water corals on rocky walls will continue to be vulnerable to the current changes in ocean conditions, while acute disturbances are likely to arise following increasing anthropogenic activities in the deep sea.

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DATA AVAILABILITY STATEMENT

The datasets generated during the production of the current study are available from the corresponding author upon reasonable request.

REFERENCES

Addamo, A. M., Vertino, A., Stolarski, J., García-Jiménez, R., Taviani, M., & Machordom, A. (2016). Merging scleractinian genera: The overwhelming genetic similarity between solitary Desmophyllum and colonial Lophelia. *BMC Evolutionary Biology*, *16*, 108. https://doi.org/10.1186/s12862-016-0654-8

Amaro, T., Huvenne, V. A. I., Allcock, A. L., Aslam, T., Davies, J. S., Danovaro, R., … Wilson, A. M. (2016). The Whittard Canyon – A case study of submarine canyon processes. *Progress in Oceanography*, *146*, 38–57. https://doi.org/10.1016/j.pocean.2016.06.003

Anderson, O. F., Guinotte, J. M., Rowden, A. A., Clark, M. R., Mormede, S., Davies, A. J., & Bowden, D. A. (2016). Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. *Ocean & Coastal Management*, *120*, 110–126. https://doi.org/10.1016/j.ocecoaman.2015.11.025

Aslam, T., Hall, R. A., & Dye, S. R. (2018). Internal tides in a dendritic submarine canyon. *Progress in Oceanography*, *169*, 20–32. https://doi.org/10.1016/j.pocean.2017.10.005

Bargain, A., Foglini, F., Pairaud, I., Bonaldo, D., Carniel, S., Angeletti, L., … Fabri, M. (2018). Predictive habitat modeling in two Mediterranean canyons including hydrodynamic variables. *Progress in Oceanography*, *169*, 151–168. https://doi.org/10.1016/j.pocean.2018.02.015

Bell, J. B., Alt, C. H., & Jones, D. O. (2016). Benthic megafauna on steep slopes at the Northern Mid-Atlantic Ridge. *Marine Ecology*, *37*, 1290–1302. https://doi.org/10.1111/maec.12319

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the surviva; of coral recruits. *Third International Coral Reef Symposium*.

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., … Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Brooke, S., Holmes, M., & Young, C. (2009). Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. *Marine Ecology Progress Series*, *390*, 137–144. https://doi.org/10.3354/meps08191

Brooke, S., & Ross, S. W. (2014). First observations of the cold-water coral *Lophelia pertusa* in mid-Atlantic canyons of the USA. *Deep Sea Research Part II: Topical Studies in Oceanography*, *104*, 245–251. https://doi.org/10.1016/j.dsr2.2013.06.011

Brooke, S., Watts, M., Heil, A., Rhode, M., Mienis, F., Duineveld, G., … Ross, S. (2017). Distributions and habitat associations of deep-water corals in Norfolk and Baltimore Canyons, Mid-Atlantic Bight, USA. *Deep Sea Research Part II: Topical Studies in Oceanography*, *137*, 131–147. https://doi.org/10.1016/j.dsr2.2016.05.008

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2011). *Reefs at risk revisited*. Washington, DC: World Resources Institute.

Byan, T. L., & Metaxas, A. (2007). Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. *Marine Ecology Progress Series*, *330*, 113–126. https://doi.org/10.3354/meps330113

Carter, G. D., Huvenne, V. A., Gales, J. A., Lo Iacono, C., Marsh, L., Ougier-Simonin, A., … Wynn, R. B. (2018). Ongoing evolution of submarine canyon rockwalls; examples from the Whittard Canyon, Celtic Margin (NE Atlantic). *Progress in Oceanography*, *69*, 79–88. https://doi.org/10.1016/j.pocean.2018.02.001

Davies, A. J., & Guinotte, J. M. (2011). Global habitat suitability for framework-forming cold-water corals. *PLoS ONE*, *6*, e18483. https://doi.org/10.1371/journal.pone.0018483

Davies, A. J., Wisshak, M., Orr, J. C., & Murray Roberts, J. (2008). Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep Sea Research Part I: Oceanographic Research Papers*, *55*, 1048–1062. https://doi.org/10.1016/j.dsr.2008.04.010

Davies, J. S., Guillaumont, B., Tempera, F., Vertino, A., Beuck, L., Ólafsdóttir, S. H., … Grehan, A. (2017). A new classification scheme of European cold-water coral habitats: Implications for ecosystem-based management of the deep sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *145*, 102–109. https://doi.org/10.1016/j.dsr2.2017.04.014

De Clippele, L., Gafeira, J., Robert, K., Hennige, S., Lavaleye, M., Duineveld, G., … Roberts, J. (2017). Using novel acoustic and visual mapping tools to predict the small-scale spatial distribution of live biogenic reef framework in cold-water coral habitats. *Coral Reefs*, *36*, 255–268. https://doi.org/10.1007/s00338-016-1519-8

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., … Guisan, A. (2017). ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*, 774–787. https://doi.org/10.1111/ecog.02671

Dolan, M. F. J., 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 Research Part I: Oceanographic Research Papers*, *55*, 1564–1579.

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

Dray, S., & Dufour, A. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Dumke, I., Nornes, S. M., Purser, A., Marcon, Y., Ludvigsen, M., Ellefmo, S. L., … Søreide, F. (2018). First hyperspectral imaging survey of the deep seafloor: High-resolution mapping of manganese nodules. *Remote Sensing of Environment*, *209*, 19–30. https://doi.org/10.1016/j.rse.2018.02.024

Dumke, I., Purser, A., Marcon, Y., Nornes, S. M., Johnsen, G., Ludvigsen, M., & Søreide, F. (2018). Underwater hyperspectral imaging as an in situ taxonomic tool for deep-sea megafauna. *Scientific Reports*, *8*, 12860. https://doi.org/10.1038/s41598-018-31261-4

Economo, E. P. (2011). Biodiversity conservation in metacommunity networks: Linking pattern and persistence. *The American Naturalist*, *177*, E167–E180. https://doi.org/10.1086/659946

Edinger, E. N., Sherwood, O. A., Piper, D. J., Wareham, V. E., Baker, K. D., Gilkinson, K. D., & Scott, D. B. (2011). Geological features supporting deep-sea coral habitat in Atlantic Canada. *Continental Shelf Research*, *31*, S69–S84. https://doi.org/10.1016/j.csr.2010.07.004

Etnoyer, P., & Morgan, L. E. (2005). Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In A. Freiwald, & J. M. Roberts (Eds.), *Cold-water corals and ecosystems* (pp. 331–343). Berlin, Heidelberg, Germany: Springer Berlin Heidelberg.

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 Research Part II: Topical Studies in Oceanography*, *104*, 184–207. https://doi.org/10.1016/j.dsr2.2013.06.016

Freiwald, A., Helge Fosså, J., Grehan, A., Koslow, T., & Roberts, J. M. (2004). *Cold-water coral reefs* (84 pp.). UNEP-WCMC Biodiversity Series, 22. Cambridge, UK:UNEP-WCMC.

Gasbarro, R., Wan, D., & Tunnicliffe, V. (2018). Composition and functional diversity of macrofaunal assemblages on vertical walls of a deep northeast Pacific fjord. *Marine Ecology Progress Series*, *597*, 47–64. https://doi.org/10.3354/meps12599

Genin, A., Paull, C. K., & Dillon, W. P. (1992). Anomalous abundances of deep-sea fauna on a rocky bottom exposed to strong currents. *Deep Sea Research Part A. Oceanographic Research Papers*, *39*, 293–302. https://doi.org/10.1016/0198-0149(92)90110-F

Georgiopoulou, A., Shannon, P. M., Sacchetti, F., Haughton, P. D. W., & Benetti, S. (2013). Basement-controlled multiple slope collapses, Rockall Bank Slide Complex, NE Atlantic. *Marine Geology*, *336*, 198–214. https://doi.org/10.1016/j.margeo.2012.12.003

Gori, A., Reynaud, S., Orejas, C., & Ferrier-Pagès, C. (2015). The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. *Journal of Experimental Marine Biology and Ecology*, *466*, 92–97. https://doi.org/10.1016/j.jembe.2015.02.004

Guijarro, J., Beazley, L., Lirette, C., Kenchington, E., Wareham, V., Gilkinson, K., … Murillo, F. J. (2016). *Species distribution modelling of corals and sponges from research vessel survey data in the Newfoundland and Labrador region for use in the identification of significant benthic areas*. Dartmouth, NS: Fisheries and Oceans Canada, Bedford Institute of Oceanography.

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

Haedrich, R. L., & Gagnon, J. (1991). Rock wall fauna in a deep Newfoundland fiord. *Continental Shelf Research*, *11*, 1199–1207. https://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 Research Part I: Oceanographic Research Papers*, *126*, 73–84. https://doi.org/10.1016/j.dsr.2017.05.015

Harris, P. T., Macmillan-Lawler, M., Rupp, J., & Baker, E. K. (2014). Geomorphology of the oceans. *Marine Geology*, *352*, 4–24. https://doi.org/10.1016/j.margeo.2014.01.011

Howell, K. L., & Davies, J. S. (2010). *Deep-sea species image catalogue*. Plymouth, UK: Marine Biology and Ecology Research Centre, Marine Institute at the University of Plymouth. https://deepseacru.org/2016/12/16/deep-sea-species-image-catalogue/

Howell, K. L., Davies, J. S., Allcock, A. L., Braga-Henriques, A., Buhl-Mortensen, P., Carreiro-Silva, M., … Game, C. A. (2019). A framework for the development of a global standardised marine taxon reference image database (SMarTaR-ID) to support image-based analyses. *BioRxiv*, 670786. https://doi.org/10.1101/670786

Howell, K. L., Davies, J. S., & van den Beld, I. (2017). *Deep-sea species image catalogue*. University of Plymouth, Ifremer, NOAA. http://www.deepseacatalogue.fr/

Howell, K. L., Holt, R., Endrino, I. P., & Stewart, H. (2011). When the species is also a habitat: Comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. *Biological Conservation*, *144*, 2656–2665. https://doi.org/10.1016/j.biocon.2011.07.025

Hutchinson, G. E. (1957). The multivariate niche. *Cold Spring Harbor Symposium on Quantitative Biology*, *22*, 415–421.

Huvenne, V. A. I., Bett, B., Masson, D., Le Bas, T., & Wheeler, A. (2016). Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. *Biological Conservation*, *200*, 60–69. https://doi.org/10.1016/j.biocon.2016.05.030

Huvenne, V. A. I., Tyler, P. A., Masson, D. G., Fisher, E. H., Hauton, C., Hühnerbach, V., … Wolff, G. A. (2011). A picture on the wall: Innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS ONE*, *6*, e28755. https://doi.org/10.1371/journal.pone.0028755

Jackson, J. B. C. (1977). Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *The American Naturalist*, *111*, 743–767. https://doi.org/10.1086/283203

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*, e79917. https://doi.org/10.1371/journal.pone.0079917

Jones, D., Gates, A., Curry, R., Thomson, M., Pile, A., & Benfield, M. (2009). *Media database archive*. SERPENT Project. Retrieved from http://archive.serpentproject.com/

Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecology Letters*, *7*, 69–80. https://doi.org/10.1046/j.1461-0248.2003.00551.x

Larsson, A. I., Järnegren, J., Strömberg, S. M., Dahl, M. P., Lundälv, T., & Brooke, S. (2014). Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. *PLoS ONE*, *9*, e102222. https://doi.org/10.1371/journal.pone.0102222

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legendre, P., & Gallagher, E. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280. https://doi.org/10.1007/s004420100716

Leverette, T. L., & Metaxas, A. (2005). Predicting habitat for two species of deep-water coral on the Canadian Atlantic continental shelf and slope. In A. Freiwald, & J. M. Roberts (Eds.), *Cold-water corals and ecosystems* (pp. 467–479). Berlin, Heidelberg, Germany: Springer Berlin Heidelberg.

Lo Iacono, C., Robert, K., Gonzalez-Villanueva, R., Gori, A., Gili, J., & Orejas, C. (2018). Predicting cold-water coral distribution in the Cap de Creus Canyon (NW Mediterranean): Implications for marine conservation planning. *Progress in Oceanography*, *69*, 169–180. https://doi.org/10.1016/j.pocean.2018.02.012

Ludvigsen, M., Sortland, B., Johnsen, G., & Singh, H. (2007). Applications of geo-referenced underwater photo mosaics in marine biology and archaeology. *Oceanography*, *20*, 140–149. https://doi.org/10.5670/oceanog.2007.14

Mayer, L., Jakobsson, M., Allen, G., Dorschel, B., Falconer, R., Ferrini, V., … Weatherall, P. (2018). The Nippon Foundation—GEBCO seabed 2030 project: The quest to see the world's oceans completely mapped by 2030. *Geosciences*, *8*, 63. https://doi.org/10.3390/geosciences8020063

Miller, R. J., & Etter, R. J. (2008). Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. *Ecology*, *89*, 452–462. https://doi.org/10.1890/06-1099.1

Miller, R. J., & Etter, R. J. (2011). Rock walls: Small-scale diversity hotspots in the subtidal Gulf of Maine. *Marine Ecology Progress Series*, *425*, 153–165. https://doi.org/10.3354/meps09025

Morris, K. J., Tyler, P. A., Masson, D. G., Huvenne, V. I. A., & Rogers, A. D. (2013). Distribution of cold-water corals in the Whittard Canyon, NE Atlantic Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *92*, 136–144. https://doi.org/10.1016/j.dsr2.2013.03.036

Naumann, M. S., Orejas, C., & Ferrier-Pagès, C. (2014). Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. *Deep Sea Research Part II: Topical Studies in Oceanography*, *99*, 36–41. https://doi.org/10.1016/j.dsr2.2013.05.025

Olson, C. J., Becker, J. J., & Sandwell, D. T. (2016). *SRTM15_PLUS: Data fusion of Shuttle Radar Topography Mission (SRTM) land topography with measured and estimated seafloor topography (NCEI Accession 0150537). Version 1.1*.

Orejas, C., Gori, A., Rad-Menéndez, C., Last, K. S., Davies, A. J., Beveridge, C. M., … Roberts, J. M. (2016). The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*. *Journal of Experimental Marine Biology and Ecology*, *481*, 34–40. https://doi.org/10.1016/j.jembe.2016.04.002

Puig, P., Canals, M., Company, J. B., Martin, J., Amblas, D., Lastras, G., … Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature*, *489*, 286–289. https://doi.org/10.1038/nature11410

Purser, A., Orejas, C., Moje, A., & Thomsen, L. (2014). The influence of flow velocity and suspended particulate concentration on net prey capture rates by the scleractinian coral *Balanophyllia europaea* (Scleractinia: Dendrophylliidae). *Journal of the Marine Biological Association of the United Kingdom*, *94*, 687–696.

Quattrini, A. M., Nizinski, M. S., Chaytor, J. D., Demopoulos, A. W. J., Roark, E. B., France, S. C., … Shank, T. M. (2015). Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic habitats and diverse communities. *PLoS ONE*, *10*, e0139904. https://doi.org/10.1371/journal.pone.0139904

Rengstorf, A. M., Yesson, C., Brown, C., & Grehan, A. J. (2013). High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. *Journal of Biogeography*, *40*, 1702–1714. https://doi.org/10.1111/jbi.12123

Robert, K., Huvenne, V. A., Georgiopoulou, A., Jones, D. O., Marsh, L., Carter, G., & Chaumillon, L. (2017). New approaches to high-resolution mapping of marine vertical structures. *Scientific Reports*, *7*, 9005. https://doi.org/10.1038/s41598-017-09382-z

Robert, K., Jones, D. O., Tyler, P. A., Van Rooij, D., & Huvenne, V. A. (2015). Finding the hotspots within a biodiversity hotspot: Fine-scale biological predictions within a submarine canyon using high-resolution acoustic mapping techniques. *Marine Ecology*, *36*, 1256–1276. https://doi.org/10.1111/maec.12228

Roberts, J. M., Wheeler, A. J., Freiwald, A., & Cairns, S. D. (2009). *Cold-water corals: The biology and geology of deep-sea coral habitats*. Cambridge, UK: Cambridge University Press.

Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J., & Hardin, J. (1984). Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S. *Virgin Islands*. *Coral Reefs*, *3*, 69–76. https://doi.org/10.1007/BF00263756

Ross, R. E., & Howell, K. L. (2013). Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. *Diversity and Distributions*, *19*, 433–445. https://doi.org/10.1111/ddi.12010

Sebens, K. P. (1986). Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs*, *56*, 73–96. https://doi.org/10.2307/2937271

Sheppard, C. (1982). Coral populations on reef slopes and their major controls. *Marine Ecology Progress Series*, *7*, 83–115. https://doi.org/10.3354/meps007083

Smith, F., & Witman, J. D. (1999). Species diversity in subtidal landscapes: Maintenance by physical processes and larval recruitment. *Ecology*, *80*, 51–69. https://doi.org/10.1890/0012-9658(1999)080[0051:SDISLM]2.0.CO;2

Sutherland, J. P. (1974). Multiple stable points in natural communities. *The American Naturalist*, *108*, 859–873. https://doi.org/10.1086/282961

Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., & Pärtel, M. (2010). Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, *21*, 796–801. https://doi.org/10.1111/j.1654-1103.2010.01185.x

Tittensor, D. P., Baco, A. R., Brewin, P. E., Clark, M. R., Consalvey, M., Hall-Spencer, J., … Rogers, A. D. (2009). Predicting global habitat suitability for stony corals on seamounts. *Journal of Biogeography*, *36*, 1111–1128. https://doi.org/10.1111/j.1365-2699.2008.02062.x

Tracey, D. M., Rowden, A. A., Mackay, K. A., & Compton, T. (2011). Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. *Marine Ecology Progress Series*, *430*, 1–22. https://doi.org/10.3354/meps09164

Ullman, S. (1979). The interpretation of structure from motion. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *203*(1153), 405–426.

Van den Beld, I., Bourillet, J., Arnaud-Haond, S., de Chambure, L., Davies, J. S., Guillaumont, B., … Menot, L. (2017). Cold-water coral habitats in submarine canyons of the Bay of Biscay. *Frontiers in Marine Science*, *4*, 118. https://doi.org/10.3389/fmars.2017.00118

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution*, *62*, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Wilson, A. M. (2016). *Lateral transport of suspended particulate matter in nepheloid layers along the Irish continental margin – A case study of the Whittard Canyon, North-East Atlantic Ocean*. Ph.D. thesis, National University of Ireland Galway, 303.

Wilson, A. M., Kiriakoulakis, K., Raine, R., Gerritsen, H. D., Blackbird, S., Allcock, A. L., & White, M. (2015). Anthropogenic influence on sediment transport in the Whittard Canyon, NE Atlantic. *Marine Pollution Bulletin*, *101*, 320–329. https://doi.org/10.1016/j.marpolbul.2015.10.067

Wilson, A. M., Raine, R., Mohn, C., & White, M. (2015). Nepheloid layer distribution in the Whittard Canyon, NE Atlantic margin. *Marine Geology*, *367*, 130–142. https://doi.org/10.1016/j.margeo.2015.06.002

Witman, J. D., & Dayton, P. K. (2001). Rocky subtidal communities. In M. Bertness, S. Gaines, & M. Hay (Eds.), *Marine community ecology* (pp. 339–366). Sunderland, MA: Sinauer Associates, Inc.

Woodby, D., Carlile, D., & Hulbert, L. (2009). Predictive modeling of coral distribution in the Central Aleutian Islands, USA. *Marine Ecology Progress Series*, *397*, 227–240. https://doi.org/10.3354/meps08358

Yesson, C., Taylor, M. L., Tittensor, D. P., Davies, A. J., Guinotte, J., Baco, A., … Rogers, A. D. (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography*, *39*, 1278–1292. https://doi.org/10.1111/j.1365-2699.2011.02681.x

BIOSKETCH

K. Robert works on seafloor and habitat mapping, with a particular focus on deep-sea habitats and research interests in quantifying 3D heterogeneity and the effects of scale. Authors of this study formed a multi-disciplinary team and collaborated on projects (e.g., CODEMAP: http://www.codemap.eu/ and SORBEH: http://scientistsatsea.blogspot.co.uk/2014/07/) aimed at developing new techniques to map complex deep-sea habitats in order to characterize further their ecological and geological components.

KR carried out video and statistical analyses, wrote the manuscript and prepared the figures. VAIH and AG were chief scientists for the research expeditions during which the datasets were collected, and contributed to interpretation of results and writing of manuscript. DOBJ provided ecological insights and contributed to the writing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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