Deep–Sea Research I 225 (2025) 104604

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri

Deep-sea biotope classification using opportunistic sampling: insights for future management

Heidy Q. Dias [a], Kerstin Kröger [a], Andrew J. Wheeler [b,c], Riccardo Arosio [b], Audrey Recouvreur [b], Tim P. Le Bas [d], Isobel A. Yeo [d], Patrick C. Collins [a,*]

[a] School of Biological Sciences, Queen's University, Northern Ireland, Belfast, UK
[b] School of Biological, Earth & Environmental Sciences/Environmental Research Institute, University College Cork, Cork, Ireland
[c] Research Ireland Centre in Applied Geosciences (iCRAG)/Research Ireland Centre for Energy, Climate & Marine (MaREI), University College Cork, Cork, Ireland
[d] National Oceanography Centre Southampton, Southampton, UK

ARTICLE INFO

Keywords:
Top-down
Bottom-up
Transect
Vulnerable marine ecosystems
Tropic seamount

ABSTRACT

An iterative approach to optimise deep-sea biotope classification using a combination of acoustic data and Remotely Operated Vehicle (ROV) video footage was developed and tested at the Tropic Seamount site in the Northeast Atlantic. Two methods for biotope classification were compared: a top-down approach based on acoustic substrate classification followed by biological characterisation, and a bottom-up approach using multivariate analysis of biological assemblages only. Video transects were analysed at two spatial resolutions (200 m and 50 m segments) to assess scale effects on biotope delineation. Biotopes were classified using a combination of geological and biological data with each biotope representing a distinct combination of substrate types and their associated benthic assemblages. The bottom-up approach using 50 m segments identified 12 distinct biotopes with stronger environmental correlations compared to broader classifications at 200 m scale. This study demonstrates that shorter transects (50 m) combined with bottom-up sampling approaches are preferable for capturing the ecological heterogeneity characteristic of deep-sea seamount environments, with important implications for vulnerable marine ecosystem identification and spatial management.

1. Introduction

Seamounts are submarine mountains that rise to at least 1000 m above the seafloor and often feature complex geology, including planar sedimentary surfaces and steep rocky flanks (Auster et al., 2005). Owing to this complexity, seamounts often provide high habitat heterogeneity. Seamounts often host distinct faunal assemblages with high species richness and thereby contribute significantly to marine biodiversity (Morgan et al., 2019). Seamounts are important sites for the extraction of living marine resources, supporting populations of commercially valuable species, which underscores the need for their sustainable management (Kerry et al., 2022). The importance of managing these habitats has been recognised globally with the United Nations' introduction of the concept of Vulnerable Marine Ecosystems (VMEs) (United Nations General Assembly (UNGA), 2007). In waters of EU member states, the European Habitats Directive (Council Directive 92/43/EEC) specifically requires the protection of 'reef' habitats (Annex I, habitat type 1170), which cover both geogenic and biogenic reefs including those found on seamounts. In the future, given that seamounts are potential targets for deep-sea mineral extraction, it seems pertinent to define variability scales of the biological communities of seamounts before such activities will occur to minimise environmental risk (Christiansen et al., 2020).

Classifying and mapping the biology of seamounts can be informative for marine spatial planning and biodiversity conservation (Howell et al., 2015). Benthic communities on seamounts are structured by environmental gradients, with depth and substrate being major factors (Duffy et al., 2013; Quattrini et al., 2014). An important outcome of this relationship is the identification of distinct assemblages of a biotope, which can serve as a proxy valuable tool for assessing environmental risks from both natural and human-induced disturbances. Essentially, the biotope acts as a baseline status with any measured changes in biotopes (both over space and time) indicative of changes (Boschen et al., 2015). When combined with a beyond-BACI (Before-After-Control-Impact) survey approach (Green, 1979; Underwood, 1991) i.e., an approach that extends traditional BACI designs through using multiple

* Corresponding author.
E-mail address: Patrick.Collins@qub.ac.uk (P.C. Collins).

https://doi.org/10.1016/j.dsr.2025.104604
Received 25 June 2025; Received in revised form 25 September 2025; Accepted 5 October 2025
Available online 8 October 2025

controls and employing longer time series, using the initial biotope status which provides a powerful tool to distinguish between natural and anthropogenically induced biological variability (Chatzievangelou et al., 2023). Biotope classification can be used to identify management units for high conservation interest targets, inform environmental risk assessments and support best practices and precautionary approaches to deep-sea environmental management (Henry et al., 2014). Biotope maps can also support the prediction of similar spatially constrained units in unsampled areas, thereby supporting the development of economic large-scale management frameworks (although some ground truthing is needed).

Deep-sea seamounts present challenges for biotope classification because of their pronounced spatial heterogeneity, such as variations in depth, substrate composition, and environmental conditions, creating a mosaic of distinct habitats (Clark et al., 2010). Anthropogenic activities such as bottom trawling or deep-sea mining can result in direct impacts (e.g., removal of habitats) and indirect effects (e.g., plumes) on fragile assemblages dominated by sponges and corals (Kaikkonen et al., 2018). The classification of biotopes at these deep-sea seamounts can support both the monitoring and management of these changes and inform risk mitigation strategies where applicable. Biotope classification is of relevance because it transforms complex ecological information into a structured, accessible format that is essential for effective marine policy and the sustainable management of our oceans. It is also important for implementing conservation frameworks such as the European Habitats Directive (92/43/EEC). For EU member states, the identification of deep-sea reef habitats (Annex I habitat type 1170), including biogenic reefs formed by cold-water corals and sponge aggregations, within their national jurisdiction is essential for meeting conservation obligations under this Directive. Because of the high habitat heterogeneity at seamounts, fine-scale information on seabed type and faunal assemblages is essential for appropriate biotope mapping (Buhl-Mortensen et al., 2012; Morgan et al., 2019). Within this context, the resolution scale of the data (i.e., length of video transects) may significantly influence the results, particularly for questions concerning biotic–abiotic relationships (La France et al., 2014). In terms of transect lengths, a 200 m distance segment seems to be commonly applied in deep-sea biotope mapping (Buhl-Mortensen et al., 2015; Kuhnz et al., 2022).

Beyond issues of scale, two analytical approaches are commonly applied for biotope classification: a top-down approach and a bottom-up approach. The classification, spatially discrete management units, produced from each will be different; hence, any inferences based on the classification will also likely differ (Swanborn et al., 2022). The top-down approach is based on geological dissimilarity, i.e., dissimilar geological features host dissimilar and distinct biological assemblages (Hewitt et al., 2004; La France et al., 2014). In the context of deep-sea sites where hard sampling of both biology and substrate data is challenging, this approach can involve the use of acoustic data to classify the seafloor based on substrate type, followed by the integration of biological information from ground-truth video data (Shumchenia and King, 2010; La France et al., 2014). The bottom-up approach delineates habitats on the basis of biological similarity in assemblages and uses multivariate statistics to identify significant relationships with environmental parameters (Shumchenia and King, 2010; La France et al., 2014).

Tropic Seamount, located in the Northeast Atlantic off the coast of western Sahara, NW Africa, is geologically well mapped guyot, with numerous dedicated scientific surveys (Palomino et al., 2016; Yeo et al., 2018, 2019; Ramiro-Sánchez et al., 2019). Owing to the competitively rich data landscape for a deep-sea site, this offers a rare opportunity to test and compare biotope classification methodologies at a fine spatial resolution. Previous studies on the Tropic Seamount have focused on its geological composition, volcanic origin (Schmincke and Graf, 2000; van den Bogaard, 2013), ferromanganese crusts (Lusty and Murton, 2018; Yeo et al., 2018; Josso et al., 2019), and different lithologies (Yeo et al., 2019). Biological studies have focused on deep-sea corals (Schmincke and Graf, 2000; Vázquez et al., 2011) and VME indicator sponges (Ramiro-Sánchez et al., 2019) found on Tropic Seamount, but detailed information on their biological assemblages and distributions is scarce. However, fine-scale (<100 m) biotope data for isolated guyots are scarce, yet such data are urgently needed for designating high-seas marine-protected area (Goode et al., 2021). Existing continental slope studies in Norway (Buhl-Mortensen et al., 2020) and the Bay of Biscay (Meyer et al., 2023) reveal striking small-scale heterogeneity, but their spatial context and sampling density differ markedly. Fine-scale biotope data from isolated seamounts are important for guiding management planning in areas beyond national jurisdiction.

Here, we address the following knowledge gaps: 1) Do top-down and bottom-up workflows converge on the same suite of biotopes at the seamount scale? (2) How sensitive are those classifications to transect length? (3) What ecological insight is gained by integrating both perspectives?

2. Materials and methods

2.1. Study area

Tropic Seamount, a star-shaped guyot in the Northeast Atlantic Ocean approximately 100 km from the coast of Western Sahara, spans an area of 50 km in length and 37 km in width (Fig. 1). The seamount has a flat top at a depth of 1000 m, with its base at 4200 m in water depth (Palomino et al., 2016). The formation of its four 10–13 km long spurs is attributed to the gravitational collapse of the flanks (Mitchell, 2001; Palomino et al., 2016). Originally an oceanic island, the seamount eroded and subsided to its current depth (Yeo et al., 2018). Wave erosion during subsidence has led to its current shape, which is covered by subsequent reef growth and sedimentation (Schmincke and Graf, 2000). Surface waters are influenced by the Canary Current, which flows southwestward along the African coast and joins the North Equatorial Current, transporting upwelled, nutrient-rich waters (Wooster et al., 1976; Pelegrí and Peña-Izquierdo, 2015). The seamount features rocky outcrops, sandy sediments with and without polymetallic nodules and carbonate and ferromanganese crusts.

2.2. Data collection and processing

All the data used in this study were collected during research cruise JC142 on the *RSS James Cook* from October to December 2016. During the survey, the entire seamount was mapped via a hull-mounted Kongsberg EM120 multibeam echo-sounder with a 90° swath angle and equidistant beam spacing at a speed of 5 kt. A total of 28 video dives were conducted via the ROV Isis (Murton et al., 2017).

2.2.1. Environmental data

Seven high-resolution dive transects from the Seamount plateau were selected for detailed analysis, covering approximately 26.7 km across different geological zones including summit areas (Fig. 1; Table 1). An AUV was deployed to map the seamount plateau and the tops of the spurs along preselected transect locations, and high-resolution bathymetry and backscatter data were collected via a Kongsberg EM2040 multibeam echosounder. Only the EM2040 data were used for habitat mapping and were processed via CARIS HIPS and SIPS v9.0 software with a defined vessel configuration and calibration values, gridded at 5 m resolution. The semi-automated methods offered by the CoMMa Toolbox (Arosio et al., 2024) were applied to repair artifacts, and gaps in the bathymetry dataset were filled using mean "Focal statistics" over a 5 × 5 neighbourhood, where each missing value was replaced by the average of its 25 surrounding cells. The algorithm was looped 12 times to ensure complete filling, and the external boundary of the dataset was reclipped (with some degree of simplification to remove irregular fringes) to remove boundary spreading. The EM2040 backscatter data were processed via the QPS FM Geocoder toolbox v7.6.3-bit

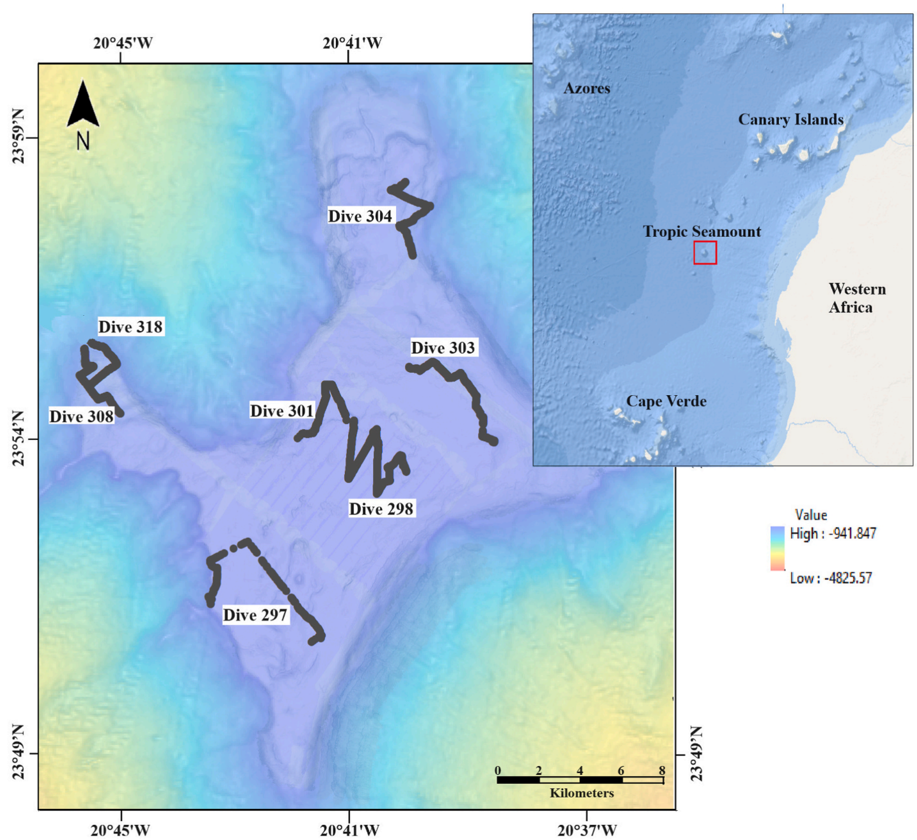

Fig. 1. Map of ROV dive locations at the Tropic Seamount.

Table 1
Summary of the ROV video dive transects taken at the Tropic Seamount.

Dive transects	Start Latitude Longitude	End Latitude Longitude	Location	Area covered (km^2)	Depth range (m)	No. of samples (200 m)	No. of samples (50 m)
297	23°50′23.72″ N 20°43′0.60″ W	23°51′0.24″ N 20°44′36.31″ W	Summit	5.70	954–1030	29	116
298	23°53′32.69″ N 20°42′18.10″ W	23°53′0.26″ N 20°41′30.21″ W	Summit	6.45	992–999	32	128
301	23°53′27.51″ N 20°43′7.96″ W	23°53′44.14″ N 20°42′25.90″ W	NE summit	2.75	995–1011	14	56
303	23°54′26.61″ N 20°41′24.89″ W	23°53′19.36″ N 20°40′3.21″ W	NE summit	4.00	972–1039	20	80
304	23°56′4.85″ N 20°41′21.12″ W	23°57′8.66″ N 20°41′28.94″ W	NW plateau	3.55	1061–1200	18	72
308	23°54′43.16″ N 20°46′37.19″ W	23°53′46.66″ N 20°46′3.95″ W	W summit	2.75	1145–1342	14	56
318	23°54′38.27″ N 20°46′13.58″ W	23°54′12.34″ N 20°46′29.85″ W	W summit	1.45	1210–1239	6	24

Edition Build 262 and gridded at 0.5 m. Variables such as slope (degrees of inclination) and rugosity (measure of topographic unevenness) were derived from the bathymetry, and together with the backscatter (measure of seafloor acoustics), a map of terrain classes was created via the Marine tools RSOBIA add-in (Le Bas, 2016) within ArcGIS 10.7.1 (ESRI, 2019). The different substrate types (sediment, debris, nodules, pavement, carbonate and lobate pavement) were derived from an extrapolation of the substrates observed in the ROV video data. Of these, pavement, carbonate, and lobate pavement substrates represent hard bottoms that would qualify as ’reef’ habitat (type 1170) under the European Habitats Directive, while areas with stable nodule fields may also support reef-associated communities. A substrate map (Fig. A3) was created and processed in ArcGIS Pro v3.1 (ESRI, 2023). We extracted five seafloor predictors (depth, bathymetric position index, acoustic backscatter, slope, and rugosity) for use in statistical analyses to identify environmental drivers of biotope distribution.

2.2.2. *Biological data*

Video data for faunal analysis were collected via the ROV Isis, which was equipped with a mini-Zeus HD video and a SCORPIO digital still camera (Murton et al., 2017). The ROV maintained an altitude of 2–3 m above the seabed, ensuring a consistent field of view of approximately 4–9 m width depending on camera angle. While this introduces some variance in transect width, the standardised altitude protocol minimised systematic bias in faunal detection across different substrate types. For quantitative analyses, we used presence-absence data rather than abundance counts to account for any remaining field-of-view variations. Synchronisation of the ROV video footage and navigation files was achieved via the Ocean Floor Observation Protocol (OFOP) v3.3.9 to generate georeferenced files, facilitating precise location referencing. A total of seven high-resolution video transects corresponding to 103 h of recording from the Seamount Plateau were analysed (Fig. 1). At each dive, the latitude and longitude, depth, area and location of the start and end of the drive were recorded (Table 1). Megabenthic fauna were identified from the video transects to the lowest possible taxonomic level via the available literature and identification keys. Motile species were recorded but were not included in the final analyses.

2.3. Data analysis

To derive biotopes, the video transects were subdivided into 200-m-long and 50-m-long analysis units (or samples) to compare the effects of using different transect lengths on the effectiveness of the mapping approaches used. The 200 m and 50 m transect lengths were selected based on: (1) 200 m representing the commonly applied standard in deep-sea biotope mapping (Buhl-Mortensen et al., 2015; Kuhnz et al., 2022), and (2) 50 m providing a finer resolution to test whether shorter segments better capture the spatial heterogeneity typical of seamount environments. These specific lengths balance ecological relevance with statistical robustness, ensuring sufficient sample sizes for multivariate analyses. This comparison directly addresses the knowledge gap regarding optimal sampling scales for biotope classification. The 50 m and 200 m biotope classifications were derived from the same dataset, segmented at different spatial resolutions and analysed separately but using identical methods. This allowed us to compare how transect length affects the detection of ecological patterns. A total of 133 (200 m) and 532 (50 m) samples were analysed, which covered approximately 26.7 km of the seamount (Table 1). While this represents only a small fraction of the total area (~0.000023 of 6850 km^2), the transects were strategically selected to capture representative spatial and environmental variability, ensuring that the sampled portion provides meaningful insights into seamount characteristics. The focus of this targeted sampling approach was to maximise the ecological information captured, following established protocols for deep-sea biotope mapping where comprehensive coverage is logistically unfeasible. For each sample, the presence of taxa was recorded. The faunal data thus obtained were analysed via the PERMANOVA + function (Anderson, 2008) as part of the PRIMER v7 software package (Clarke and Gorley, 2015). To identify significant differences in the biological dataset between substrates, an unrestricted Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2008) test was carried out. The effects of location and substrate type nested within the Tropic seamount were assessed via PERMANOVA, with Type III (partial) sums of squares, permutations of residuals under a mixed model and 999 permutations.

2.3.1. Top-down approach

Two approaches, top-down and bottom-up, were adopted to derive biotopes with distinct assemblages. In the top-down approach, the first step is to establish geological units on the bathymetry map of the seamount to define the distribution and extent of the habitat map units (La France et al., 2014) on the basis of the acoustic data. Substrate type descriptors were included as factors per sample. The presence−absence megafaunal data were transformed, and a Bray−Curtis resemblance matrix was created. Next, significant differences between sites and substrate types were identified via unrestricted PERMANOVA, which was permuted 999 times at a significance level of $p < 0.05$. The groupings were visualised via nonmetric multidimensional scaling (nMDS) analysis, which was based on a Bray−Curtis similarity matrix of faunal data from each individual sample. A similarity percentage analysis (SIMPER) with a 60 % cut-off for low contributions was carried out (Clarke and Gorley, 2006) to characterise the biological assemblages for substrate types and to obtain individual taxa contributions within each group of samples. The 60 % cut-off was selected based on established practices in deep-sea biotope studies (Howell et al., 2015; Davies et al., 2014) and represents a balance between capturing the dominant characterising taxa while avoiding noise from rare species that contribute minimally to assemblage definition. The SIMPER groups (hereafter referred to as biotopes) were further analysed for transects by assigning a centroid position that was the average position of all the transects within each biotope. For each biotope, the average of the environmental variables, such as depth, slope, rugosity and backscatter, was calculated to describe the seafloor environment. To explain the role of environmental variables in supporting biotopes, we conducted distance-based multivariate multiple regression (DistLM) marginal tests using the Akaike information criterion (AIC) (stepwise selection) to assess probabilities, and distance-based redundancy analysis (dbRDA) plots were obtained using the Bray−Curtis resemblance matrix for biotopes and a Euclidean distance resemblance matrix on normalised environmental data. All statistical analyses were performed independently on the datasets from the 200 m and the 50 m transects. This was done to determine whether the length of the transect affected the results, by comparing outcomes from the two different transect lengths.

2.3.2. Bottom-up approach

This approach is largely based on multivariate statistical analyses. The presence−absence biological data were transformed, and a Bray−Curtis resemblance matrix was derived. Significant differences across sites and substrate types were analysed using unrestricted PERMANOVA permuted 999 times at a significance level of $p < 0.05$. Hierarchical cluster analysis (CLUSTER) analysis was performed on the Bray−Curtis matrix to reveal similarities between biological assemblages. These groupings were visualised via nMDS analysis, which was based on a Bray−Curtis similarity matrix of faunal data using individual samples. The main taxa characterising each group were determined via a similarity profile (SIMPROF) test ($p < 0.05$) (Clarke et al., 2008). SIMPROF is used to identify significant clusters, as it creates biological assemblage groups in the absence of structure (substrate types) (Kuhnz et al., 2022). SIMPER was used to identify the characterising taxa in each SIMPROF assemblage group with 60 % cut-off criteria following deep-sea biotope practices to capture key taxa (as mentioned above). The frequency of substrate types was assigned for each biotope to describe the seafloor environment. Furthermore, a stepwise DistLM test was conducted using the AIC to discern the influencing environmental variables on the biotopes. Additionally, dbRDA plots were constructed via the Bray−Curtis resemblance matrix for biotopes and a Euclidean distance resemblance matrix for normalised environmental data. All the tests were conducted separately for the 200 m and 50 m transects for comparison. The best fit for biotope derivation identified by SIMPROF was further plotted on a map using ArcGIS Pro v3.1 (ESRI, 2023) to show the presence of biological assemblages.

2.4. Habitat classification

To marry biotopes with habitats and ensure consistency with European and international reporting standards, we applied a combination of the European Nature Information System (EUNIS) habitat classification scheme (European Environment Agency, 2022) and the Joint Nature Conservation Committee (JNCC) Marine Habitat Classification for Britain and Ireland (JNCC, 2022). EUNIS provides a hierarchical system for habitat description, comprising five major levels for biotope assignment: (1) environment (marine), (2) biological zone & substratum, (3) regional sea areas, (4) assemblage/community, and (5) facies/associations. This framework was used to establish the broad context of the surveyed areas within the deep-sea environment (Level 2: A6 Deep-sea bed).

However, recognising the need for a more detailed classification within the specific Atlantic mid-bathyal zone investigated, the dedicated deep-sea section of the JNCC marine habitat classification, which offers finer resolution, was also incorporated (Parry et al., 2015; Parry, 2019; JNCC, 2022). This allowed for the characterisation of specific habitats within the mid-bathyal region, thereby providing a more precise representation of the benthic communities. By integrating the EUNIS framework with the regional detail offered by JNCC, a comprehensive habitat classification was achieved. Of the two approaches evaluated (top-down and bottom-up), we selected the most suitable method to identify biotopes across varying transect lengths. This is further detailed by the use of megafaunal taxa, which contribute over 60 % to group similarity, based on presence−absence data. To characterise the biotopes identified in our study, the substrate types - sediment, debris, nodules, pavement, carbonate and lobate pavement were assigned on the basis of their frequency within each biotope. This allowed for the definition of distinct habitats associated with each biotope identified on the Tropic Seamount.

3. Results

3.1. Geological characteristics and megafaunal community structure

From the 200 m transects, six distinct substrate types were identified: sediment, debris, pavement, nodules, lobate pavement and mixed substrates. Of these, sediment and mixed substrates accounted for the largest proportion of the area, with 30 % coverage, followed by nodules at 16 % coverage (Fig. A1). Using the 50 m transects, a total of seven substrate types were observed, which included the abovementioned six substrate types, with the addition of carbonate substrates (Fig. A1). Sediment was the predominant substrate, covering 33 % of the area, followed by mixed substrates at 22.5 % and nodules at 18 %. In summary, both analyses revealed the seabed to be primarily composed of soft substrate (sediment) followed by mixed substrates that included both soft and hard materials. A more comprehensive understanding of the environmental variables was achieved by incorporating depth, slope, rugosity, and backscatter.

A total of 87 benthic megafaunal taxa were identified from 103 h of ROV footage captured across the seamount, representing six distinct phyla: Foraminifera, Porifera, Cnidaria, Echinodermata, Annelida and Arthropoda. The most dominant taxa included the protozoans Xenophyophoroidea sp., the hexactinellid sponges *Pheronema carpenteri* and *Aphrocallistes beatrix*, the black coral *Stichopathes* sp., the octocoral *Acanella arbuscula,* the cold-water coral *Solenosmilia variabilis* and the caridean shrimp Nematocarcinidae sp. These taxa were predominantly sessile (except Nematocarcinidae sp.) and were associated mainly with hard substrates and were also present in mixed substrates.

3.2. Biotope classification: top-down vs bottom-up

3.2.1. Top-down classification (200 m)

At 200 m resolution, the top-down approach identified 6 biotopes on the basis of substrate (Table A1). The nMDS plots revealed moderate clustering with some overlap (Fig. 2a). SIMPER analysis revealed eight dominant taxa characterising these biotopes (Table A1). PERMANOVA revealed significant differences in assemblage structure across locations and substrates (Table 2). distLM explained 92.5 % of the assemblage variation, with backscatter explaining a large amount of the variation in the substrate-based classes (Table 3; Fig. 3a).

3.2.2. Bottom-up classification (200 m)

Using hierarchical clustering, eight biotopes were delineated (Fig. 4a), characterised by 15 taxa (Table A2). Biotope 'b', dominated by Xenophyophoroidea sp. and Nematocarcinidae sp., was distinct and somewhat similar to the top-down sediment-based classes. The assemblages were broadly distributed across the mixed substrates (Fig. A2). PERMANOVA revealed significant variation across all factors (Table 2), although the pairwise differences were not statistically significant. distLM explained 67.2 % of the assemblage variation, with backscatter

Table 2
Results of PERMANOVA for the effects of substrates derived via top-down and bottom-up approaches on the Bray−Curtis similarity of megafaunal presence−absence data. For each approach, megafaunal data were analysed at different spatial scales (200 m and 50 m). Significant results ($p < 0.05$) are presented in bold.

		df	MS	Pseudo-F	*p* (perm)
	Top-down				
200 m	Location	3	23110.0	22.683	**0.001**
	Substrate	5	6356.8	4.778	**0.001**
	Location x substrate	9	961.8	1.154	0.225
50 m	Location	3	73020.0	45.782	**0.001**
	Substrate	6	9182.5	4.785	**0.001**
	Location x Substrate	17	1977.2	1.464	**0.001**
	Bottom-up				
200 m	Location	3	20841.0	21.135	**0.001**
	Substrate	5	5780.0	4.506	**0.001**
	Location x Substrate	9	906.5	1.051	0.357
50 m	Location	3	71134.0	45.076	**0.001**
	Substrate	6	9139.1	4.821	**0.001**
	Location x Substrate	17	1922.4	1.437	**0.002**

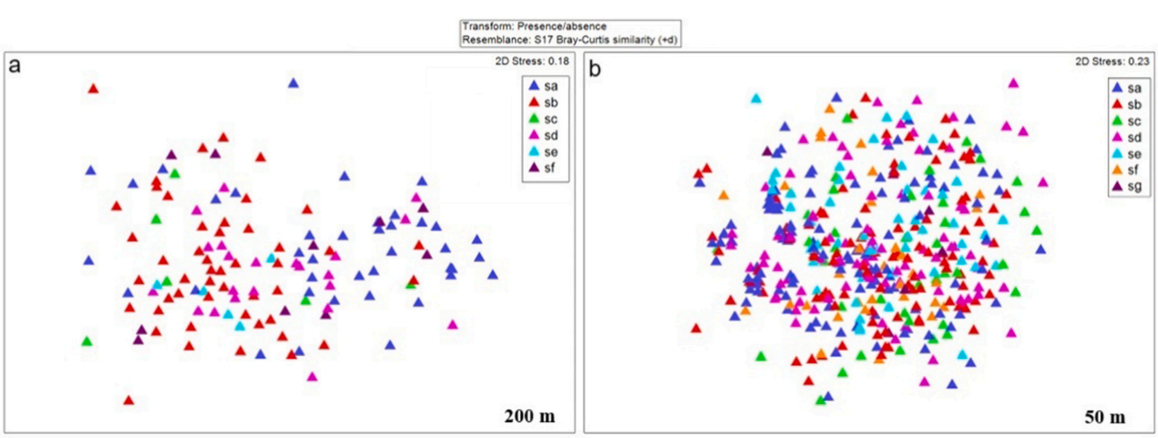

Fig. 2. Non-metric multidimensional scaling (nMDS) ordinations using Bray-Curtis similarities of transformed megafaunal presence-absence data. The biotope groupings are derived via the top-down approach for (a) the substrate on a 200 m-long transect and (b) the substrate on a 50 m-long transect. For the coloured biotope codes, refer to Table A1.

Table 3
Results of the distance-based linear model for the top-down approach at 200 m and 50 m transect lengths. Significant results ($p < 0.05$) are presented in bold.

Variable	SS (trace)	Pseudo-F	Significance *p*	Prop.
Based on substrate types for 200 m transects				
Depth	214.0	0.805	0.453	0.1675
Rugosity	477.2	2.385	0.172	0.3735
Slope	313.7	1.302	0.337	0.2456
Backscatter	937.5	11.025	**0.005**	0.7338
Based on substrate types for 50 m transects				
Depth	480.5	5.533	**0.010**	0.5253
Rugosity	256.6	1.949	0.140	0.2805
Slope	254.9	1.932	0.160	0.2787
Backscatter	342.1	2.987	0.057	0.3740

being the strongest predictor and slope being negatively correlated (Table 4; Fig. 5a).

3.2.3. Top-down classification (50 m)

At 50 m resolution, the top-down approach produced 7 biotopes for the substrate (Table A1). nMDS plots revealed clearer segregation among classes (Fig. 2b). SIMPER identified five dominant taxa (Table A2). PERMANOVA revealed significant differences across all factors and pairwise groups (Table 2). distLM explained 69.7 % of the variation in the substrate-based assemblages with depth (Table 3; Fig. 3b).

3.2.4. Bottom-up classification (50 m)

Twelve biotopes were identified through cluster analysis (Fig. 4b), described by 17 taxa (Table A2). Biotope 'j', dominated by Xenophyophoroidea sp. and Nematocarcinidae sp., matched a similar group at 200 m. Spatial associations were more distinct at 50 m, with specific biotopes linked to nodules and sediment (Fig. A2). PERMANOVA revealed strong and significant differences across all variables and pairwise combinations (Table 2). distLM explained 47.2 % of the total variation, with depth, slope, and backscatter all strongly correlated (Table 4; Fig. 5b).

3.3. Comparison between sampling resolutions

The finer 50 m resolution resulted in a greater number of more narrowly defined biotopes, reflecting increased ecological detail. Although some biotopes were consistent across scales, especially sediment-dominated groups with Xenophyophoroidea sp., the 50 m classifications presented stronger environmental associations and greater sensitivity to local habitat variability. The assemblage patterns were more diffuse and generalised at 200 m, supporting the use of shorter transects for detecting fine-scale ecological heterogeneity.

Table 4
Results of the distance-based linear model for the bottom-up approach at 200 m and 50 m transect lengths. Significant results ($p < 0.05$) are presented in bold.

Variable	SS (trace)	Pseudo-F	Significance *p*	Prop.
Based on biotopes for 200 m transects				
Depth	3644.4	3.372	**0.002**	0.2522
Rugosity	3252.5	2.904	**0.011**	0.2250
Slope	4106.8	3.969	**0.001**	0.2842
Backscatter	4600.9	4.670	**0.001**	0.3183
Based on biotopes for 50 m transects				
Depth	5226.7	3.812	**0.001**	0.2140
Rugosity	1894.7	1.177	0.323	0.0776
Slope	4776.5	3.404	**0.001**	0.1956
Backscatter	3276.5	2.169	**0.023**	0.1341

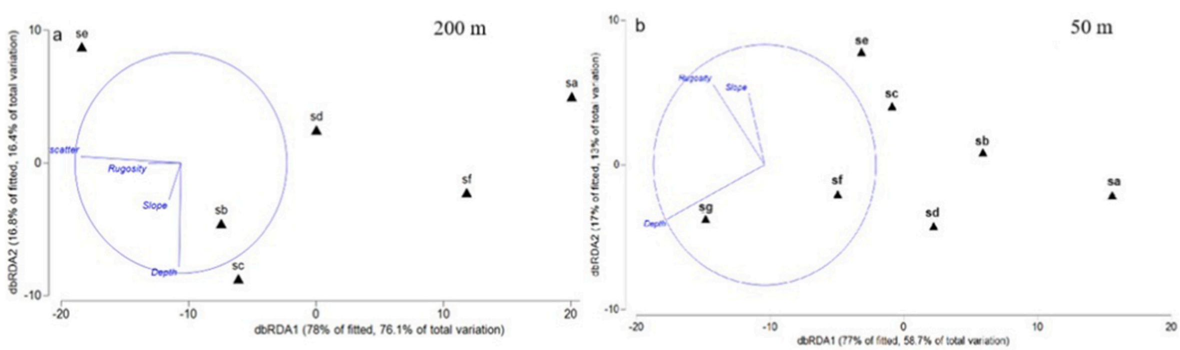

Fig. 3. Distance-based redundancy analysis (dbRDA) plots for the top-down approach based on 200 m transects for (a) the substrate and 50 m transects for (b) the substrate. The symbols represent biotopes (see Table A1 for codes).

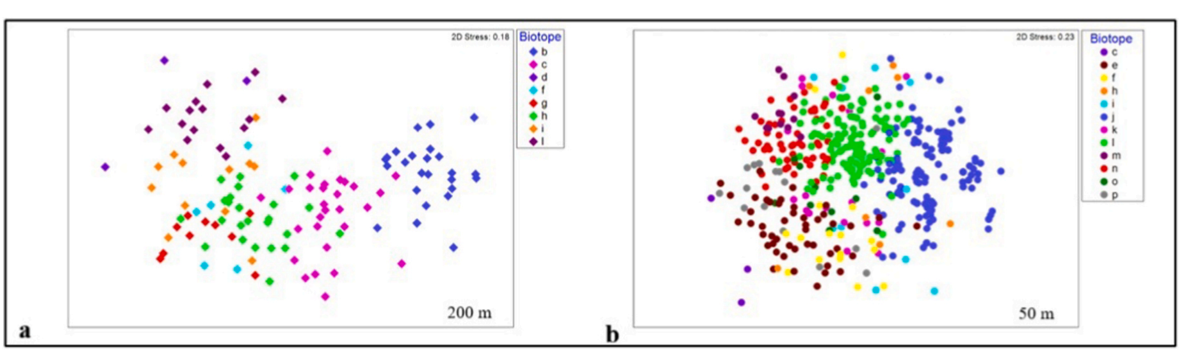

Fig. 4. Non-metric multidimensional scaling (nMDS) plots (bottom) based on the bottom-up approach for (a) 200 m and (b) 50 m transect lengths. For the biotope codes, refer to Table 5.

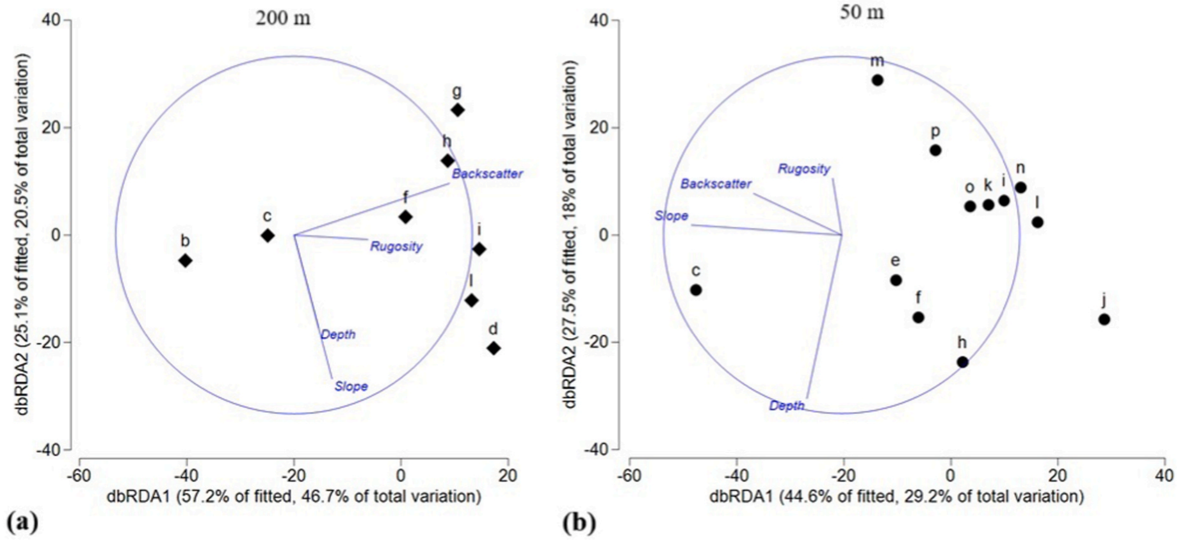

Fig. 5. Distance-based redundancy analysis (dbRDA) plots for the bottom-up approach based on (a) 200 m and (b) 50 m transect lengths. The symbols represent biotopes (see Table 5 for codes).

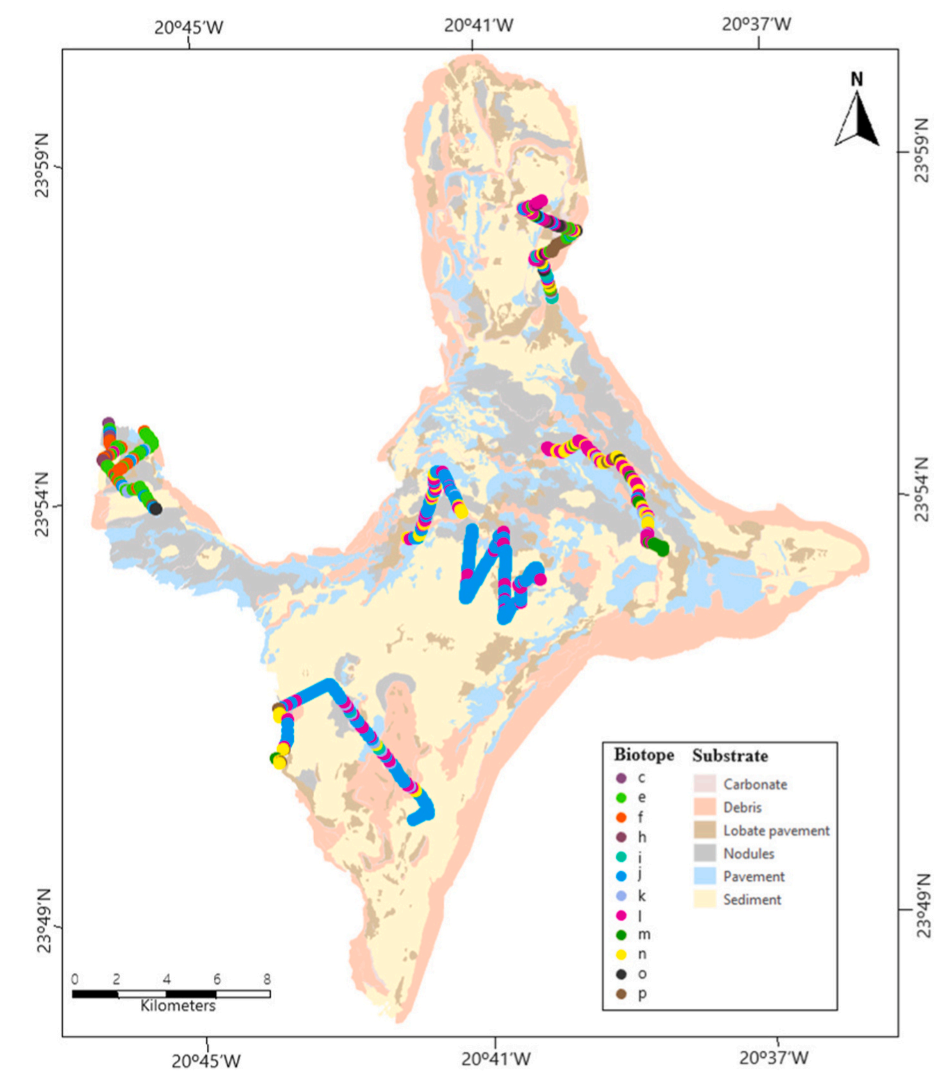

Fig. 6. Biotope distribution on the Tropic Seamount based on the bottom-up approach for biotope mapping and the use of 50 m video transects.

3.4. Biotope distribution on the Tropic Seamount

Compared with the top-down approach, the application of the bottom-up approach to the 50 m transects yielded more detailed results in terms of the biological assemblage groupings applied to both the 200 and 50 m transect lengths. This approach identified 12 distinct biotopes across the Tropic Seamount, with each biotope associated with a specific substrate type (Fig. 6). In the summit areas, biotope 'j', characterised by Xenophyophoroidea sp. and Nematocarcinidae sp. (Table 5), was dominant, particularly in locations with soft sediment, whereas the remaining biotopes were distributed across mixed substrates. Biotopes 'l' and 'n' were predominantly found at the northeast summit and were also associated with mixed substrates. The northwest plateau presented nearly all biotopes, mostly on mixed substrates. In the western summit area, biotope 'e', characterised by taxa such as *Solenosmilia variabilis*, *Chrysogorgia* sp., *Pheronema carpenteri*, and *Narella* sp., was dominant. Despite the wide distribution of different biotopes across various dive sites on the seamount, some biotopes were found only in specific areas. For example, biotope 'c' was found only on the west summit, biotope 'm' was found on the northwest summit, and biotope 'o' was found on the northwest plateau. This distribution pattern of the biotopes highlights the efficacy of the bottom-up approach at the 50 m scale in capturing the biological assemblages in relation to their geological context on the seamount.

Table 5
Biological assemblages (biotopes) identified via the bottom-up approach with 50 m transects. The species assemblage groupings were derived from the SIMPER analyses.

Group	Substrate type	Biotope code	Species assemblages	EUNIS classification
c	nodules	Sol.End	*Solenosmilia variabilis* *Chrysogorgia* sp. Paranthipathes sp. *Endoxocrinus* sp. Cladorhiza sp.	Cold-water corals, black corals and crinoid fields on Atlantic mid-bathyal nodule substratum
e	sediment	Sol.Chr	*Solenosmilia variabilis* *Chrysogorgia* sp. *Pheronema carpenteri* *Narella* sp.	Cold-water corals, gold corals and hexactinellid sponge assemblage on Atlantic mid-bathyal sand
f	nodules	Phe.Ker	*Pheronema carpenteri* *Keratoisis* sp. *Sticopathes* sp.	Hexactinellid sponges and black corals on Atlantic mid-bathyal nodule substratum
h	sediment	Xen.Chr	Xenophyophoroidea sp. *Chrysogorgia* sp. *Sticopathes* sp. Caryophyllidae sp. 2	Xenophyophores and mixed coral assemblage on Atlantic mid-bathyal sand
i	mixed	Sti	*Sticopathes* sp.	Black corals on Atlantic mid-bathyal mixed substratum
j	sediment	Xen. Nem	Xenophyophoroidea sp. Nematocarcinidae sp.	Xenophyophores on Atlantic mid-bathyal sand
k	nodules	Sti.Phe	*Sticopathes* sp. *Pheronema carpenteri*	Black corals and hexactinellid sponge assemblage on Atlantic mid-bathyal nodule substratum
l	mixed	Sti.Xen	*Sticopathes* sp. Xenophyophoroidea sp. Nematocarcinidae sp. *Aphrocallistes beatrix*	Black corals, xenophyophores, caridean shrimp and sponge assemblages on Atlantic mid-bathyal mixed substratum
`m	sediment	Aca.Aph	*Acanella arbuscula* *Aphrocallistes beatrix* Nematocarcinidae sp. *Paranthipathes* sp.	Coral dominated sponge and caridean shrimp assemblage on Atlantic mid-bathyal sand
n	mixed	Aph.Sti	*Aphrocallistes beatrix* *Sticopathes* sp. *Swiftia* sp.	Sponge dominated coral assemblage on Atlantic mis-bathyal mixed substratum
o	mixed	Aph.Phe	*Aphrocallistes beatrix* *Pheronema carpenteri* Xenophyophoroidea sp. *Hertwigia falcifera*	Sponge garden and xenophyophore fields on Atlantic mid-bathyal mixed substratum
p	mixed	Pha.Phe	*Phakellia* sp. *Pheronema carpenteri* *Solenosmilia variabilis*	Sponge grounds and cold-water coral assemblage on Atlantic mid-bathyal mixed substratum

4. Discussion

The present study has demonstrated that both the choice of analytical approach and the spatial resolution at which video data are assessed significantly influence biotope classification outcomes in deep-sea environments. The resolution of transect segmentation, particularly at 50 m versus 200 m scales, plays a critical role in determining the granularity and ecological accuracy of the resulting habitat maps. This finding is particularly relevant to the classification of seamount habitats, which are characterised by high environmental heterogeneity and patchy faunal distributions.

The bottom-up approach, which was applied at the finer 50 m scale, facilitated the identification of a greater number of biotopes and captured more subtle ecological patterns. This approach enables the delineation of distinct biological assemblages closely associated with specific geological features, suggesting that a resolution of 50 m is better suited for capturing the spatial complexity typical of seamount environments. The associations of distinct biotopes with polymetallic nodules, sloping rocky surfaces, and mixed sediments support the view that habitat heterogeneity is a principal driver of megafaunal assemblage structure on seamounts. The biological assemblages reflected the inherent heterogeneity associated with different substrate types; for example, habitats characterised by polymetallic nodules supported more than one distinct community, as evidenced by biotope 'f' (Phe. Ker) and biotope 'k' (Sti. Phe) on nodular habitats. These findings corroborate literature highlighting the importance of substrate composition and local geomorphology as key environmental drivers (de la Torriente et al., 2018; Ramiro-Sánchez et al., 2019; Corrêa et al., 2022; Kuhnz et al., 2022; Grinyó et al., 2022).

In contrast, the top-down approach produced broader biotope classifications, with fewer assemblages identified and greater compositional overlap between substrate types. While this approach was more efficient and yielded interpretable links between substrate classes and faunal composition at the 200 m scale, its coarser resolution appeared insufficient to capture the full ecological diversity of the seamount. The top-down method may thus be more appropriate for large-scale, initial mapping exercises in relatively homogeneous deep-sea settings, such as abyssal plains, where subtle habitat transitions are less pronounced (La France et al., 2014; Smith et al., 2015). Its reliance on predefined geological categories also presents limitations in systems where biological variation may not align neatly with acoustic classifications (Hewitt et al., 2004; Shumchenia and King, 2010; La France et al., 2014).

The observed divergence in biotope maps generated by the two approaches underscores the importance of methodological consideration in benthic habitat classification. Both approaches offer distinct benefits and challenges when applied to the complex and variable environments of seamounts, where accurate biotope classification is essential. Where spatial management decisions and conservation assessments are to be made, the analytical method employed can shape the understanding of ecosystem boundaries and the identification of vulnerable marine ecosystems (Davies et al., 2014; Chimienti et al., 2018). Given the current international emphasis on safeguarding deep-sea biodiversity, particularly in areas beyond national jurisdiction, these findings support the adoption of bottom-up classification strategies at fine spatial scales to improve the ecological relevance of derived management units. The use of finer transect lengths also appears advantageous in areas of known or suspected habitat heterogeneity. Shorter video segments enhanced the detection of associations between specific taxa and their preferred substrates, as exemplified by the identification of cold-water coral and crinoid assemblages associated with nodule-strewn slopes. While our results favour 50 m transects for heterogeneous seamount environments, 200 m transects may be preferable for: (1) initial reconnaissance surveys where broad habitat categories are sufficient, (2) relatively homogeneous environments such as abyssal plains, or (3) studies with time or resource constraints where maximising spatial coverage takes priority over fine-scale resolution. It is therefore recommended that transect segmentation of 50 m be employed in future biotope mapping efforts where high-resolution habitat characterisation is needed. In contrast, the 200 m segment frequently masked ecological variability, potentially leading to underestimation of biotope diversity and associated conservation value. Habitat maps based on the use of a finer resolution scale in the analysis can increase modelling efforts, as the predictive ability is influenced by the sample numbers (number of analysis units an overall transect video is split into) within a biotope (Buhl-Mortensen et al., 2020). The optimal transect length likely depends on the inherent spatial scale of biological patchiness in the target ecosystem, with 50 m appearing optimal for seamount environments characterised by moderate-scale (10–100m) habitat heterogeneity. For highly heterogeneous rocky reefs, even finer scales (10–25 m) might reveal additional ecological patterns, though this would require substantially more analytical effort. Future studies could employ multiscale analysis or sliding-window approaches to empirically determine optimal scales for specific environments.

Our findings also have implications for environmental baseline studies and impact assessments associated with emerging industries such as deep-sea mining. Seamounts are often considered potential sites for mineral extraction that support assemblages that are both unique and highly sensitive to physical disturbance (Azevedo et al., 2024). The identification of biotopes associated with polymetallic nodule fields in this study illustrates the need to account for within-substrate variability when evaluating potential impacts. Moreover, the strong influence of location on biological structure, likely reflecting factors such as current flow, sedimentation regime, and food availability, reinforces the need for spatially explicit environmental modelling when planning industrial activities (Bruneel et al., 2022). The biotopes identified in this study, particularly those dominated by *Solenosmilia variabilis*, may qualify as 'reef' habitats under the European Habitats Directive (habitat type 1170). This has important implications for conservation planning, as these habitats require protection under European legislation when found within European waters or areas of European interest.

From a management perspective, biotope maps developed through bottom-up approaches are likely to offer greater utility in defining conservation priorities and monitoring indicators. Their capacity to reflect true biological variability makes them valuable tools for spatial planning, VME identification, and the establishment of ecologically or biologically significant areas (EBSAs) (Clark et al., 2014; Corrêa et al., 2022; Baco et al., 2023). However, such approaches are more data- and resource-intensive and may not be feasible across large-scale survey regions without targeted sampling and computational capacity. The suitability of the Tropic Seamount for this methodological comparison is notable, given its relatively well-documented geological structure and history of dedicated biological and geophysical investigations. The findings derived here are likely to be of broader relevance to other isolated guyots and undersampled seamounts across the global ocean, particularly in high-seas regions where conservation planning is currently hindered by data scarcity. While it is not suggested that the applied methods are optimised for areas under immediate mining exploration, the approach is highly applicable to seamounts not yet formally evaluated and for which management guidance is needed.

In summary, the findings demonstrate that classification outcomes are highly sensitive to both the spatial resolution of the data and the analytical framework employed. Finer-scale, bottom-up approaches have been shown to more effectively capture ecological variability across complex seamount terrains, whereas broader, top-down methods, although operationally efficient, risk oversimplifying ecological patterns in heterogeneous environments. A limitation of our study is the relatively small proportion of the seamount surveyed. However, this sampling intensity is typical for deep-sea environments where ROV operations are time-consuming and costly. Our stratified sampling across different habitats and depths aimed to maximise ecological representativeness despite limited spatial coverage. These results underscore the importance of methodological transparency to ensure that biotope maps are accurately interpreted and appropriately applied in marine spatial planning and conservation decision-making. Future studies would benefit from increased sampling density, particularly in under studied habitats. These insights support the continued development of standardised, resolution-sensitive approaches for deep-sea habitat classification and underscore the importance of high-resolution biological and geological data for sustainable ocean management.

5. Conclusions

A total of 12 biotopes were identified on the Tropic Seamount by applying the bottom-up approach to biotope mapping on the basis of 50 m video transect segments. Our study underlines the critical importance of choosing the appropriate mapping approach for the ecosystem to be mapped. We mapped an area of high habitat heterogeneity, Tropic Seamount, for which the bottom-up approach using video transects 50 m in length proved to be better at capturing the ecological complexity inherent in this and typical of most seamounts. The bottom-up approach was superior in identifying distinct biotopes and their associations with specific environmental features. This ability makes this approach particularly suitable for mapping areas that are potentially of high conservation value. High-resolution geological and biological data provide the understanding required to develop measures for the sustainable management and protection of these unique marine ecosystems. Continued research and monitoring are essential to ensure the resilience and conservation of seamount biodiversity in the context of increasing human impacts.

CRediT authorship contribution statement

Heidy Q. Dias: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Kerstin Kröger:** Writing – review & editing, Validation. **Andrew J. Wheeler:** Writing – review & editing. **Riccardo Arosio:** Writing – review & editing, Validation, Software, Formal analysis. **Audrey Recouvreur:** Writing – review & editing. **Tim P. Le Bas:** Writing – review & editing, Validation, Software, Methodology. **Isobel A. Yeo:** Writing – review & editing. **Patrick C. Collins:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Ethics approval

This article does not contain any experiments with animals performed by any of the authors.

Funding

This work was developed under the TRIDENT project, a European project funded by the European Union's Horizon Europe research and innovation programme (Grant Agreement No 101091959). HQD and KK are supported by the UKRI Horizon Europe Guarantee (Grant Agreement No 100591963). AR was supported by the TRIDENT project, and RA was funded by the Cullen Postdoctoral Fellowship Grant No. PDOC 19/08/03 by the Marine Institute of Ireland.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The multibeam echosounder data and ROV imagery were provided courtesy of the National Oceanography Centre, Southampton, and were collected on the RSS James Cook (Cruise JC142) under the MarineE-Tech Project funded by NERC (NE/MO1151/1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2025.104604.

Data availability

Data will be made available on request.

References

Anderson, M.J., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. Primer-E Limited.

Arosio, R., Gafeira, J., De Clippele, L.H., Wheeler, A.J., Huvenne, V.A.I., Sacchetti, F., Conti, L.A., Lim, A., 2024. CoMMa toolbox: a GIS geomorphometry instrument to map and measure confined landforms. Geomorphology 458, 109227.

Auster, P.J., Moore, J., Heinonen, K.B., Watling, L., 2005. A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. In: Friewald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer-Verlag, New York, NY, pp. 761–769.

Azevedo, A., Guerra, A., Martins, I., 2024. Seamounts ecological modelling: a comprehensive review and assessment of modelling suitability to emergent challenges. Ocean Coast Manag. 251, 107050.

Baco, A.R., Ross, R., Althaus, F., Amon, D., Bridges, A.E., Brix, S., Buhl-Mortensen, P., Colaco, A., Carreiro-Silva, M., Clark, M.R., Du Preez, C., 2023. Towards a scientific community consensus on designating vulnerable marine ecosystems from imagery. PeerJ 11, e16024.

Boschen, R.E., Rowden, A.A., Clark, M.R., Barton, S.J., Pallentin, A., Gardner, J.P.A., 2015. Megabenthic assemblage structure on three New Zealand seamounts: implications for seafloor massive sulfide mining. Mar. Ecol. Prog. Ser. 523, 1–14.

Bruneel, S., Ho, L., Van Echelpoel, W., Schoeters, A., Raat, H., Moens, T., Bermudez, R., Luca, S., Goethals, P., 2022. Sampling errors and variability in video transects for assessment of reef fish assemblage structure and diversity. PLoS One 17 (7), e0271043.

Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M.F.J., 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.

Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M.J.F., Gonzalez-Mirelis, G., 2015. Habitat mapping as a tool for conservation and sustainable use of marine resources: some perspectives from the MAREANO programme, Norway. J. Sea Res. 100, 46–61.

Buhl-Mortensen, P., Dolan, M.F., Ross, R.E., Gonzalez-Mirelis, G., Buhl-Mortensen, L., Bjarnadóttir, L.R., Albretsen, J., 2020. Classification and mapping of benthic biotopes in arctic and sub-arctic Norwegian waters. Front. Mar. Sci. 7, 271.

Chatzievangelou, D., Robinson, N.J., Floegel, S., Bongiorni, L., Stefanni, S., Aguzzi, J., 2023. Data acquisition and processing strategies for the development of ecological indicators in the exploration and monitoring of deep-sea ecosystems under natural and anthropogenic changes. Front. Mar. Sci. 10, 1228891.

Chimienti, G., Angeletti, L., Rizzo, L., Tursi, A., Mastrototaro, F., 2018. ROV vs trawling approaches in the study of benthic communities: the case of Pennatula rubra (cnidaria: Pennatulacea). J. Mar. Biol. Assoc. U. K. 98 (8), 1859–1869.

Christiansen, B., Denda, A., Christiansen, S., 2020. Potential effects of deep seabed mining on pelagic and benthopelagic biota. Mar. Pol. 114, 103442.

Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J.M., 2010. The ecology of seamounts: structure, function, and human impacts. Ann. Rev. Mar. Sci 2, 253–278.

Clark, M.R., Rowden, A.A., Schlacher, T.A., Guinotte, J., Dunstan, P.K., Williams, A., O'Hara, T.D., Watling, L., Niklitschek, E., Tsuchida, S., 2014. Identifying ecologically or biologically significant areas (EBSA): a systematic method and its application to seamounts in the south Pacific Ocean. Ocean Coast Manag. 91, 65–79.

Clarke, K.R., Gorley, R.N., 2006. User manual/tutorial, vol. 93. Primer-E Ltd., Plymouth.

Clarke, K.R., Gorley, R.N., 2015. Primer v7 User Manual/Tutorial. PRIMER-E, Auckland, New Zealand.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J. Exp. Mar. Biol. Ecol. 366 (1–2), 56–69.

Corrêa, P.V.F., Jovane, L., Murton, B.J., Sumida, P.Y.G., 2022. Benthic megafauna habitats, community structure and environmental drivers at rio grande rise (SW Atlantic). Deep-Sea Res. Part I Oceanogr. Res. Pap. 186, 103811.

Davies, J.S., Howell, K.L., Stewart, H.A., Guinan, J., Golding, N., 2014. Defining biological assemblages (biotopes) of conservation interest in the submarine canyons of the southwest approaches (offshore United Kingdom) for use in marine habitat mapping. Deep Sea Res. Part II Top. Stud. Oceanogr. 104, 208–229.

De la Torriente, A., Serrano, A., Fernández-Salas, L.M., García, M., Aguilar, R., 2018. Identifying epibenthic habitats on the Seco de los Olivos Seamount: species assemblages and environmental characteristics. Deep-Sea Res. Part I Oceanogr. Res. Pap. 135, 9–22.

Duffy, J.E., Amaral-Zettler, L.A., Fautin, D.G., Paulay, G., Rynearson, T.A., Sosik, H.M., Stachowicz, J.J., 2013. Envisioning a marine biodiversity observation network. Biosci 63 (5), 350–361.

Environmental Systems Research Institute (ESRI), 2019. Arcgis Release 10.7.1. Redlands, CA: ESRI.

Environmental Systems Research Institute (ESRI), 2023. Arcgis Pro. ESRI, Inc, Redlands, CA [Software], Version 3.1. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

European Environment Agency (EEA), 2022. EUNIS Marine Habitat Classification Review 2019. European Environment Agency. Available at: https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification-1/eunis-marine-habitat-classification-review-2022.

Green, R.H., 1979. Sampling Design and Statistical Methods for Environmental Biologists. Wiley, New York, 978-0471327322.

Goode, S.L., Rowden, A.A., Bowden, D.A., Clark, M.R., Stephenson, F., 2021. Fine-scale mapping of mega-epibenthic communities and their patch characteristics on two New Zealand seamounts. Front. Mar. Sci. 8, 765407.

Grinyó, J., Francescangeli, M., Santín, A., Ercilla, G., Estrada, F., Mecho, A., Fanelli, E., Costa, C., Danovaro, R., Company, J.B., Sobrino, I., 2022. Megafaunal assemblages in deep-sea ecosystems of the Gulf of Cadiz, northeast Atlantic ocean. Deep-Sea Res. Part I Oceanogr. Res. Pap. 183, 103738.

Henry, L.A., Roberts, J.M., 2014. Recommendations for best practice in deep-sea habitat classification: bullimore et al. as a case study. ICES J. Mar. Sci. 71 (4), 895–898.

Hewitt, J.E., Thrush, S.F., Legendre, P., Funnell, G.A., Ellis, J., Morrison, M., 2004. Mapping of marine soft-sediment communities: integrated sampling for ecological interpretation. Ecol. Appl. 14 (4), 1203–1216.

Howell, K.L., Mowles, S.L., Foggo, A., 2015. Mounting evidence: near-seamount biology and the case for seamount conservation. Mar. Ecol. 36 (1), 278–285.

Joint Nature Conservation Committee (JNCC), 2022. The marine habitat classification for britain and Ireland version 22.04 [10/07/2024]. https://mhc.jncc.gov.uk/.

Josso, P., Parkinson, I., Horstwood, M., Lusty, P., Chenery, S., Murton, B., 2019. Improving confidence in ferromanganese crust age models: a composite geochemical approach. Chem. Geol. 513, 108–119.

Kaikkonen, L., Venesjärvi, R., Nygård, H., Kuikka, S., 2018. Assessing the impacts of seabed mineral extraction in the deep sea and coastal marine environments: current methods and recommendations for environmental risk assessment. Mar. Pollut. Bull. 135, 1183–1197.

Kerry, C.R., Exeter, O.M., Witt, M.J., 2022. Monitoring global fishing activity in proximity to seamounts using automatic identification systems. Fish Fish. 23 (3), 733–749.

Kuhnz, L.A., Gilbane, L., Cochrane, G.R., Paull, C.K., 2022. Multifactor biotopes as a method for detailed site characterisation in diverse benthic megafaunal communities and habitats in deep-water off morro Bay, California. Deep-Sea Res. I: Oceanogr. Res. Pap. 190, 103872.

La France, M., King, J.W., Oakley, B.A., Pratt, S., 2014. A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Cont. Shelf Res. 83, 24–44.

Le Bas, T., 2016. RSOBIA—A new OBIA toolbar and toolbox in ArcMap 10.x for segmentation and classification. In: Kerle, N., Gerke, M., Lefevre, S. (Eds.), GEOBIA 2016: Solutions and Synergies, vol. 4. University of Twente Faculty of Geo-Information and Earth Observation, Twente.

Lusty, P.A., Murton, B.J., 2018. Deep-ocean mineral deposits: metal resources and windows into earth processes. Elements: An Int. Magazine of Mineralogy, Geochem. Petrology 14 (5), 301–306.

Meyer, H.K., Davies, A.J., Roberts, E.M., Xavier, J.R., Ribeiro, P.A., Glenner, H., Birkely, S.R., Rapp, H.T., 2023. Beyond the tip of the seamount: distinct megabenthic communities found beyond the charismatic summit sponge ground on an arctic seamount (schulz bank, arctic mid-ocean ridge). Deep-Sea Res. I: Oceanogr. Res. Pap. 191, 103920.

Mitchell, N.C., 2001. Transition from circular to stellate forms of submarine volcanoes. J. Geophys. Res. Solid Earth 106 (B2), 1987–2003.

Morgan, N.B., Goode, S., Roark, E.B., Baco, A.R., 2019. Fine scale assemblage structure of benthic invertebrate megafauna on the north Pacific seamount mokumanamana. Front. Mar. Sci. 6, 715.

Murton, B.J., Lusty, P., Yeo, I.A., Howarth, S., 2017. Detailed description of FeMn crusts at tropic seamount. In: Proceedings of the American Geophysical Union, Fall Meeting 2017 abstract #OS34A-05. (Washington, DC: American Geophysical Union).

Palomino, D., López-González, N., Vázquez, J.T., Fernández-Salas, L.M., Rueda, J.L., Sánchez-Leal, R., Díaz-del-Río, V., 2016. Multidisciplinary study of mud volcanoes and diapirs and their relationship to seepages and bottom currents in the Gulf of Cádiz Continental slope (northeastern sector). Mar. Geol. 378, 196–212.

Parry, M., Howell, K.L., Narayanaswamy, B., Bett, B., Jones, D.O., Hughes, D., Piechaud, N., Nickell, T., Ellwood, H., Askew, N., Jenkins, C., 2015. A deep-sea section for the marine habitat classification of britain and Ireland. In A Deep-sea Section for the Marine Habitat Classification of Britain and Ireland. ISSN 0963 8901. In: JNCC (2022) the Marine Habitat Classification for Britain and Ireland Version 22.04 [10/06/2024]. https://mhc.jncc.gov.uk/resources#version1503.

Parry, M.E.V., 2019. Guidance on assigning benthic biotopes using EUNIS or the marine habitat classification of britain and Ireland (revised 2019), JNCC report no. 546. JNCC. Peterborough. ISSN 0963-8091.

Pelegrí, J.L., Peña-Izquierdo, J., 2015. Eastern boundary currents off north-west Africa. In: Valdés, L., Déniz-González, I. (Eds.), Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem. IOC-UNESCO, Paris, pp. 81–92. IOC Technical Series, No. 115.

Quattrini, A.M., Etnoyer, P.J., Doughty, C., English, L., Falco, R., Remon, N., Rittinghouse, M., Cordes, E.E., 2014. A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. Deep-Sea Res. Pt. II Top. Stud. Oceanogr. 99, 92–102.

Ramiro-Sánchez, B., González-Irusta, J.M., Henry, L.A., Cleland, J., Yeo, I., Xavier, J.R., Carreiro-Silva, M., Sampaio, Í., Spearman, J., Victorero, L., Messing, C.G., 2019. Characterization and mapping of a deep-sea sponge ground on the tropic seamount (northeast tropical atlantic): implications for spatial management in the high seas. Front. Mar. Sci. 6, 278.

Schmincke, H.-U., Graf, G., 2000. DECOS/OMEX II, Cruise No. 43, 25 November 1998-1914 January 1999. Hamburg: Leitstelle METEOR.

Shumchenia, E.J., King, J.W., 2010. Comparison of methods for integrating biological and physical data for marine habitat mapping and classification. Cont. Shelf Res. 30 (16), 1717–1729.

Smith, J., O'Brien, P.E., Stark, J.S., Johnstone, G.J., Riddle, M.J., 2015. Integrating multibeam sonar and underwater video data to map benthic habitats in an east antarctic nearshore environment. Estuar. Coast Shelf Sci. 164, 520–536.

Swanborn, D.J., Huvenne, V.A., Pittman, S.J., Woodall, L.C., 2022. Bringing seascape ecology to the deep seabed: a review and framework for its application. Limnol. Oceanogr. 67 (1), 66–88.

United Nations General Assembly (UNGA), 2007. UNGA Resolution on Sustainable Fishing (A/61/105). United Nations General Assembly.

Underwood, A.J., 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Aust. J. Mar. Freshw. Res. 42 (5), 569–587.

van den Bogaard, P., 2013. The origin of the canary island seamount province - new ages of old seamounts. Sci. Rep. 3, 2107.

Vázquez, J.T., Somoza-Losada, L., Rengel, J.A., Medialdea, T., Millán, A., Alcalá, C., González, F.J., Jiménez, P., León, R., López-González, N., Palomino, D., 2011. Informe científico-técnico de la campaña oceanográfica DRAGO 0511. Ampliación de la plataforma continental de España al oeste de las islas Canarias. ROV vs trawling approaches in the study of benthic communities: the case of Pennatula rubra (Cnidaria: Pennatulacea). J. Mar. Biol. Assoc. U. K. 98 (8), 1859–1869.

Wooster, W.S., Bakun, A., Mclain, D.R., 1976. Seasonal upwelling cycle along eastern boundary of north Atlantic. J. Mar. Res. 34, 131–141.

Yeo, I.A., Dobson, K., Josso, P., Pearce, R.B., Howarth, S.A., Lusty, P.A., Le Bas, T.P., Murton, B.J., 2018. Assessment of the mineral resource potential of Atlantic ferromanganese crusts based on their growth history, microstructure, and texture. Minerals 8 (8), 327.

Yeo, I.A., Howarth, S.A., Spearman, J., Cooper, A., Crossouard, N., Taylor, J., Turnbull, M., Murton, B.J., 2019. Distribution of and hydrographic controls on ferromanganese crusts: Tropic seamount, Atlantic. Ore Geol. Rev. 114, 103131.