RESEARCH ARTICLE

Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts

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Abstract

Context   Seamounts are abundant geomorphological features creating seabed spatial heterogeneity, a main driver of deep-sea biodiversity. Despite its ecological importance, substantial knowledge gaps exist on the character of seamount spatial heterogeneity.

Objectives   This study aimed to map, quantify and compare seamount seascapes to test whether individual habitats and seamounts differ in geomorphological structuring, and to identify spatial pattern metrics useful to discriminate between habitats and seamounts.

Methods   We mapped and classified geomorphological habitat using bathymetric data collected at five Southwest Indian Ridge seamounts. Spatial pattern metrics from landscape ecology are applied to quantify and compare seascape heterogeneity in composition and configuration represented in resulting habitat maps.

Results   Whilst part of the same regional geological feature, seamounts differed in seascape composition and configuration. Five geomorphological habitat types occurred across sites, which within seamounts differed in patch area, shape and clustering, with ridge habitat most dissimilar. Across seamounts, the spatial distribution of patches differed in number, shape, habitat aggregation and intermixing, and outcomes were used to score seamounts on a gradient from low to high spatial heterogeneity.

Conclusions   Although seamounts have been conceptualised as similar habitats, this study revealed quantitative differences in seascape spatial heterogeneity. As variations in relative proportion and spatial

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relationships of habitats within seamounts may influence ecological functioning, the proposed quantitative approach can generate insights into within-seamount characteristics and seamount types relevant for habitat mappers and marine managers focusing on representational ecosystem-based management of seamounts. Further research into associations of sessile and mobile seamount biodiversity with seascape composition and configuration at relevant spatial scales will help improve ecological interpretation of metrics, as will incorporating oceanographic parameters.

Keywords Habitat mapping · Geomorphology · Seamounts · Seascape ecology · Seabed · Southwest Indian Ridge

Introduction

Seamounts, typically defined as undersea mountains rising steeply from the seafloor, are some of the most prominent and widespread features of seabed topography globally (Yesson et al. 2011). They host distinct and vulnerable benthic communities forming complex biogenic habitats, and support mobile megafauna such as commercially important fish, marine mammals, and sea birds (Rogers 2018). Environmental heterogeneity, including variation in substrate type, topographic relief, and hydrodynamic exposure (McArthur et al. 2010) contribute to the ecological importance of seamounts and the high variability in faunal assemblages and distributions observed among and within individual seamounts (Rogers 2018).

Although seabed heterogeneity has long been recognised as a main driver of biodiversity in deep-sea environments (Thistle 1983), its spatial geometry is rarely quantified. Quantitative knowledge of environmental heterogeneity is key for a better understanding of seamount ecology, and could lead to insights into the potential ecological implications of spatial structuring of habitats that host and support seamount biodiversity (Clark et al. 2012; Swanborn et al. 2022). Addressing knowledge gaps around the character and consequences of benthic seascape heterogeneity is a priority because extensive physical disturbances change the spatial structure of seamount seascapes. Notably, trawling directly modifies benthic habitat mosaics with long-lasting effects due to low benthic recolonisation rates (Huvenne et al. 2016; Williams et al. 2020). A pattern-oriented approach facilitates comparisons between the structure of different seamounts, which can provide critical knowledge to classify seamount ecosystems for representational protection of their characteristics through marine protected area networks (Clark et al. 2011a).

Advances in mapping technologies and analysis techniques provide broad-scale maps from which environmental surrogates for biological communities in the deep sea can be derived (Howell et al. 2020). Measures of geomorphological structure (Wilson et al. 2007) and substrate types extracted from continuous bathymetry and backscatter acoustic maps are used as proxy for benthic communities' potential occurrence and distribution, and form input for benthic habitat maps (Brown et al. 2011). These segment and classify seascapes into areas of similar abiotic conditions that may be associated with a particular biological community. Land- and seascape ecologists have developed a wide range of analytical tools to quantify spatial heterogeneity from patch-mosaic representations as benthic habitat maps, focusing on the composition (patch types and their relative amount) and configuration (the spatial arrangement and orientation of patches) of seascapes (Wedding et al. 2011; Swanborn et al. 2022). Variations in composition and configuration influence assemblage make-up, biodiversity patterns and organism movement, and ultimately ecological processes across the seascape such as structural and functional connectivity (Pittman et al. 2021).

This study focuses on five seamounts on the Southwest Indian Ridge (SWIR). These are amongst the least scientifically studied globally, but are located in a geographic zone at high risk from fishing (Clark et al. 2011a) and have been targeted by industrial fisheries for decades (Rogers et al. 2017; Marsac et al. 2020). Data on these seamounts remain sparse, but global predictive modelling studies have linked the SWIR to potential habitat for vulnerable communities (Yesson et al. 2012) and indicate high vulnerability to human impacts (Clark and Tittensor 2010; Marsac et al. 2020). At present, knowledge gaps remain about the spatial patterns in terrain geomorphology (e.g., slope, topographic complexity) and patch-mosaic structure (i.e. seascape composition and configuration) of individual SWIR seamounts.

This study quantifies and compares spatial heterogeneity represented in geomorphological habitat maps from five SWIR seamounts varying in summit depths, shapes and sizes. The aims were to: (1) map and classify habitat types of SWIR seamounts based on geomorphological characteristics; (2) quantify and compare spatial environmental heterogeneity to test whether studied habitats and seamounts differ in geomorphological structuring; and (3) evaluate which metrics were most useful to discriminate spatial heterogeneity in composition and configuration within and between seamounts.

Methods

Data used in this study were collected during RRS *James Cook* NERC cruise JC066 in November and December 2011 (Rogers and Taylor 2012). Surveyed seamounts (Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Seamount and Atlantis Bank) vary in shape, size and summit depth (Figs. 1, 2), and are located in different water masses. More extensive morphological descriptions can be found in Muller (2017).

Study sites

Coral Seamount (41° 28′ S, 42° 53′ E) is situated east of the Discovery II Fracture Zone with a summit located at 200 m depth. The seamount is elongated from north to south over approximately 18 km. Coral is the only surveyed site located in cooler waters close to the Subantarctic Front.

Melville Bank (38° 28′ S, 42° 44′ E) is located on the eastern side of the Indomed Fracture Zone, 45 km north of the SWIR axial valley, and stretches from east to west over approximately 13.5 km. Extensive ridge features characterise the steep shallow (100 m) summit and the flanks show embayments, chutes and debris deposits.

Middle of What (MOW) Seamount (37° 59′ S, 50° 24′ E) is positioned 30 km south of the mid-axial rift valley on a rim flank uplift. It is the only surveyed location not associated with a transform fault. MOW seamount is small in height and extent, stretching over 12 km, and has a deeper summit (975 m, Fig. 2) than other surveyed sites.

Sapmer Seamount (36° 5′ S, 52° 6′ E) is located on the west flank of the Gallieni Fracture zone. The seamount is triangular-shaped and extends 17 km along the fracture zone. The summit is truncated at 250 m depth and features irregular, rough bathymetry (Fig. 2). Sapmer has volcanic ridges forming flank rift zones and slope failure processes characterise the flanks.

Atlantis Bank (32° 45′ S, 57° 16′ E) is an oceanic core complex created through fault action (Dick et al. 2019), stretching north to south 14 km along the Atlantis II Fracture Zone. The summit is flat at a depth of 700 m (Fig. 2). The western side features embayments created through mass wasting events.

Data collection

Swath bathymetry and backscatter data were acquired using a hull-mounted Kongsberg-Simrad EM120 multibeam echo sounder, operated at a frequency of 12 kHz and used with the maximum 191 beams, giving 150° coverage (Muller 2017). Any pings from beam angles greater than 120° were discounted to reduce errors. Adverse weather conditions, specifically rough sea states resulting in bubble entrainment, provided lower quality backscatter for Coral and Melville (Muller 2017, SI 1). Produced .all files incorporating navigation and sound velocity information were obtained from the British Oceanographic Data Centre (BODC) in September 2020, and Qimera 2.3.1 and FlederMaus GeocoderToolbox (FMGT) 7.9.5 (QPS) were used for further manual editing of swath bathymetry (removing spurious data points) and backscatter. Bathymetric models were gridded to a resolution of 25 m.

Analysis

The analysis consisted of three steps: (1) scale selection and terrain analysis; (2) classifying seamount seascapes in broad-scale geomorphological habitats or patch types; and (3) quantifying seascape composition and configuration represented in habitat maps. Steps 1 and 2 followed an objective unsupervised classification technique (Verfaillie et al. 2009; Ismail et al. 2015). Statistical analyses were conducted in RStudio using R v3.6.3.

The quantification of terrain morphology was conducted at two spatial resolutions: the spatial resolution of the digital bathymetric model (25 m) and a

Fig. 1 Surveyed seamounts on the Southwest Indian Ridge. Individual images show seamount topography, and insets show surrounding geological context (GEBCO). White dashed lines indicate locations of cross sections in Fig. 2
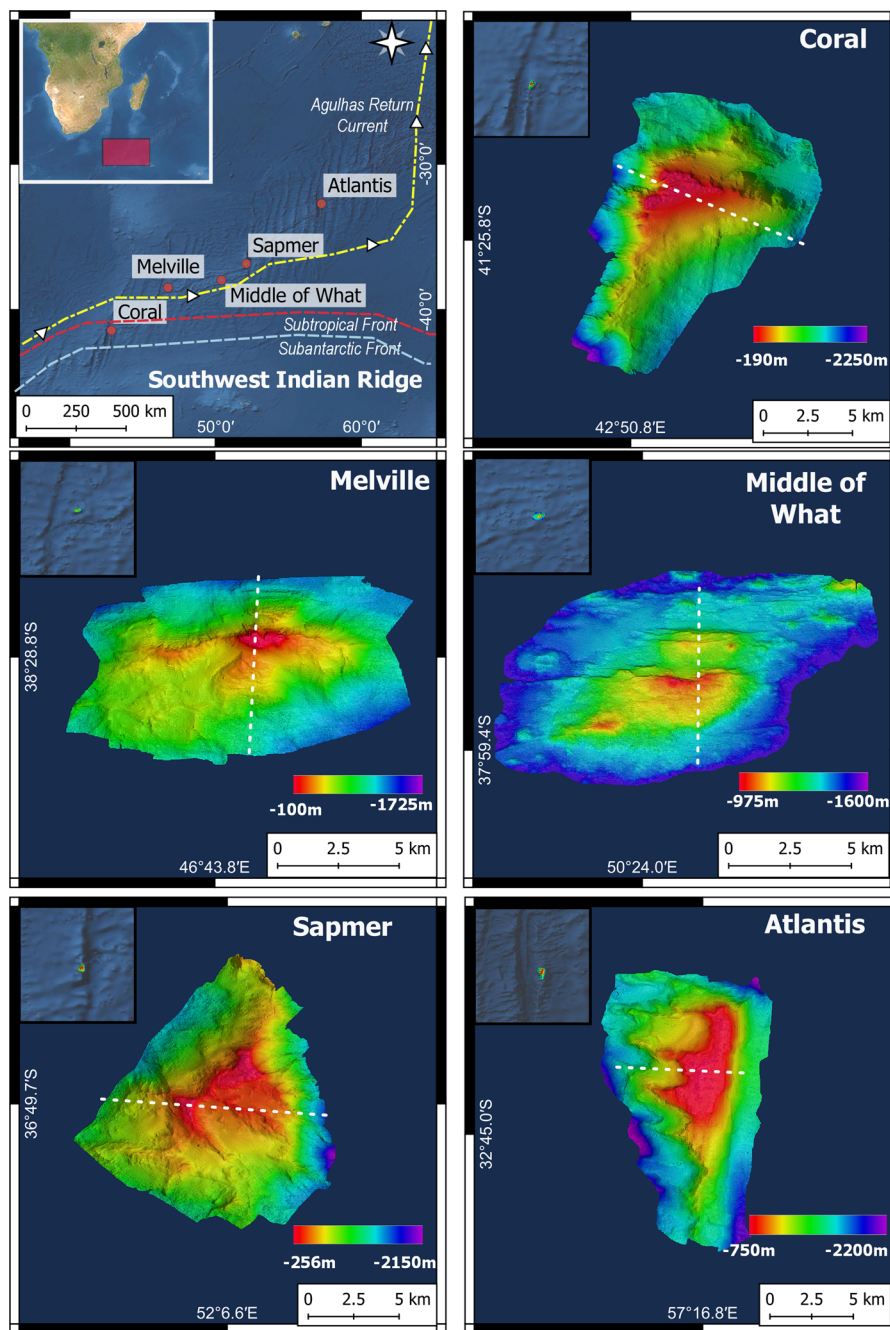
broader resolution (275 m) determined using the Estimation Scale Parameter technique (Drăguţ et al. 2010), applied in R. This multiscale approach detects the scale at which an abrupt rate of change occurs in local variance (ROC-LV) and considers this the appropriate resolution to resolve potentially important landscape features. LV was calculated as the average standard deviation within a 3×3 moving window over 25 m spatial scale increments on bathymetry data layers created through bilinear interpolation. A
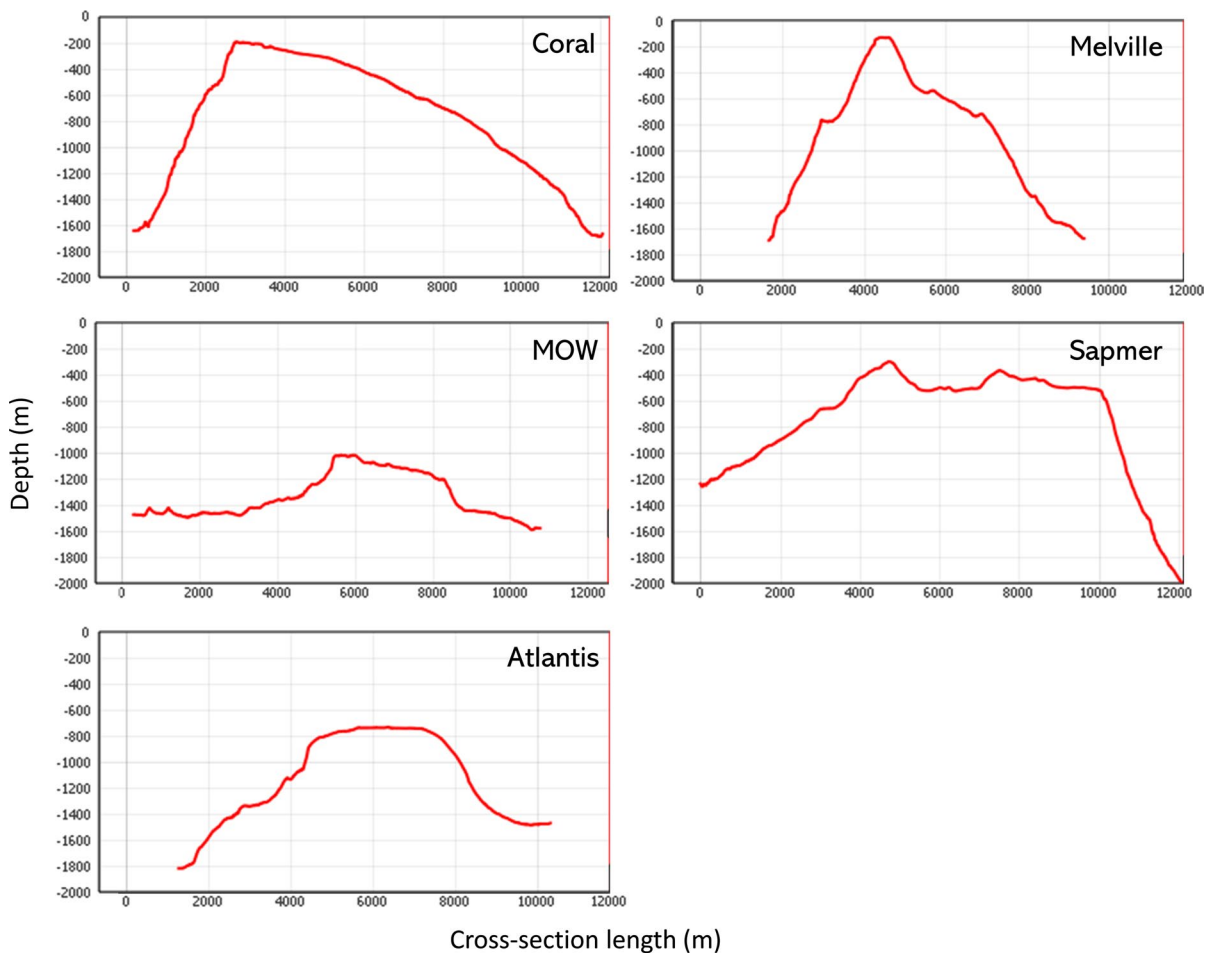
Fig. 2 Profile plots of seamounts between 0 and 2000 m depth. Locations of cross sections are indicated as white dashed lines in Fig. 1. Profiles were taken in west-north-west to east-south-east direction at Coral, west to east direction at Sapmer and Atlantis, and in north to south direction at Melville and MOW. X values represent the length of the cross-section in m (12 km)

combined ROC-LV curve (SI 2) was produced by considering its average value across scale levels to calculate the appropriate broad scale resolution across sites. A first break in the ROC-LV occurred at 275 m and was therefore taken as the resolution to calculate broad-scale predictors.

Multiple ecologically relevant variables measuring seamount geomorphology were quantified from bathymetry at the two focal spatial scales (25 m and 275 m) (Table 1). Individual seamount depth ranges were scaled and centred to correct for the absolute depth differences, thereby focusing on within-seamount geomorphological heterogeneity.

Unsupervised classification

The full dataset consisted of the values of terrain derivatives and depth at each pixel across sites, standardised to zero-mean and unit-variance to have equal weight in the analysis. The unsupervised classification consisted of two steps: Principal Component Analysis (PCA) and K-means clustering.

PCA was used to reduce data dimensionality and remove collinearity of input variables (Jolliffe and Cadima 2016). The Kaiser Harris criterion prioritised principal components (PCs) for subsequent analysis, retaining PCs with eigenvalues larger than 1. The PCs were subjected to K-means clustering (Hartigan

Table 1 Terrain metrics extracted from bathymetric data

	Terrain variable	Description	Produced in:
Terrain variables	Depth	Bathymetric surface representing depth	Qimera 2.3.1
	Slope (Horn 1981)	Rate of change of depth	R raster package
	Eastness (Horn 1981)	Direction of slope: orientation on east–west scale	R raster package, sin(aspect)
	Northness (Horn 1981)	Direction of slope: orientation on north–south scale	R raster package, cos(aspect)
	Total curvature (Zevenbergen and Thorne 1987)	Second derivative of seabed terrain, describes relative position of features	R spatialEco package, 3×3 neighbourhood
	Topographic Position Index (TPI) (De Reu et al. 2013)	Elevation of cells (positive or negative) compared to neighbouring cells using mean deviations	R spatialEco package, 3×3 neighbourhood
	Terrain Ruggedness Index (TRI) (Riley et al. 1999)	Local variation in seabed terrain around a central pixel	R spatialEco package, 3×3 neighbourhood
	Vector Ruggedness Measure (VRM) (Sappington et al. 2007)	Measure of ruggedness in three dimensions	R spatialEco package, 3×3 neighbourhood
	Slope of Slope	Rate of change of slope; measure of terrain complexity	R raster package
	Backscatter	Measure of reflectivity of seabed, corresponding to substrate type	FMGT 7.9.5

and Wong 1979), and elbow plots determined the optimum number of clusters. The bend in the plot at 5 clusters (SI 4), corresponding to a change in slope gradient, was chosen as the appropriate number of clusters. The K-means clustering algorithm, ran using 5 clusters and 500 random starting configurations, assigned each pixel of the input data a cluster membership. This final cluster solution was used to produce geomorphological habitat maps showing each pixel's cluster membership at each site. Boxplots were used to help characterise the environmental variables for each habitat.

Quantifying and comparing seascape structure

Spatial pattern metrics were applied using Fragstats v4.12 (McGarigal et al. 2012) to assess variability in seascape composition (amount and variety of patches) and configuration (spatial geometry of patches) from habitat maps (Table 2). Spatial pattern metrics can be calculated at multiple levels of analysis: the individual patch, the habitat class or patch type, and the overall seascape. We selected metrics at the class and

seascape level. Class-level metrics allow for comparing the composition and configuration of each identified habitat type across sites, whereas seascape-level metrics were applied to each seamount's entire habitat map to allow comparisons among locations. Class-level metrics were calculated using the mean value (sum of patch type metric values divided by the total number of patches), providing a patch-centric perspective. Seascape-level metrics were based on the area-weighted mean patch characteristics that correct for the relative size of habitat patches (McGarigal and Marks 1994).

One-way Analysis of Variance (ANOVA) with pair-wise comparisons were used to assess whether class-level characteristics differed significantly ($p < 0.05$) between habitats. Before conducting ANOVA, assumptions of normality and homogeneity of variance were checked using the Shapiro–Wilk test and Levene's test. Data were transformed using the Box-Cox family of transformations if assumptions were violated. At a seascape level, metrics with the largest variability were used to assess spatial heterogeneity between seamounts.

Table 2 Categorical spatial pattern metrics extracted from habitat maps. Metrics with separate references were developed for Fragstats with an ecological interpretation in mind, whereas metrics without references are existing concepts implemented in Fragstats

Group	Metric type	Fragstats metric and abbreviation	Description
Composition: type and abundance of patch types	*Area metrics*: basic metrics describing area composed by habitat patches	Percentage of landscape (PLAND)	Relative proportion of each patch
		Mean patch size (AREA)	Average size of individual habitat patches
	Diversity metrics: describe the compositional makeup of the landscape	Shannon diversity (SHDI)	Composite measure incorporating richness (number of different patch types) and evenness. Larger values indicate greater number of patch types and/or evenness
		Shannon evenness (SHEI)	Describes the distribution of area among patch types. Equals 1 when area is distributed evenly
Configuration: spatial arrangement of patch types	*Shape metrics*: unitless metrics describing geometric complexity of patch shapes	Shape index (SHAPE) (Patton 1975)	Perimeter area ratio corrected for patch size, where patch shape is compared to a square of the same size. Increases as patch shape becomes more complex
		Gyration (GYRATE)	Mean extent of patch. Higher indicates more elongated patch
		Contiguity index (CONTIG) (LaGro 1991)	Patch shape is assessed based on the spatial connectedness of patches. The CI increases with larger contiguous path shapes
	Isolation metrics: describe the degree of spatial isolation of patches	Euclidean Nearest Neighbour Distance (ENN)	Shortest straight-line distance between the centre of a focal patch and the centre of nearest neighbour of the same class
		ENN coefficient of variation (ENN_CV)	Measure of patch dispersion: the larger, the more irregular the spread of patches
	Subdivision metrics: describe the degree to which landscape is broken up in different patches	Number of patches (NP)	Number of different patches in landscape: the higher, the more fragmented
		Patch density (PD)	Number of patches per unit of area
		Splitting index (SPLIT) (Jaeger 2000)	Degree of subdivision; increases as the landscape is increasingly subdivided into smaller patches

Table 2 (continued)

Group	Metric type	Fragstats metric and abbreviation	Description
	Aggregation and interspersion metrics: describe the spatial distribution and intermixing of patch types	Contagion index (CONTAG) (Li and Reynolds 1993)	Measures the degree to which patch types are aggregated. Higher values indicate few large, contiguous patches with poor dispersion and interspersion, whereas lower values indicate higher dispersion and interspersion
		Clumpiness index (CLUMPY) (class only metric)	Dispersion index depicting the deviation from a random distribution. (0). Small values (-1) indicate maximal disaggregation whereas higher values (1) indicate greater clumping
		(normalised) Landscape shape index (LSI) (Patton 1975)	Ratio of total edge to area adjusted for landscape size. The larger its value, the larger internal edge and disaggregation is, whereas smaller values indicate a compact landscape. The normalised LSI is scaled between 0 and 1
		Interspersion and juxtaposition index (IJI) (McGarigal and Marks 1995)	Measures the degree to which patch types are intermixed. The higher, the more evenly interspersed patches are in a mixture of patch types
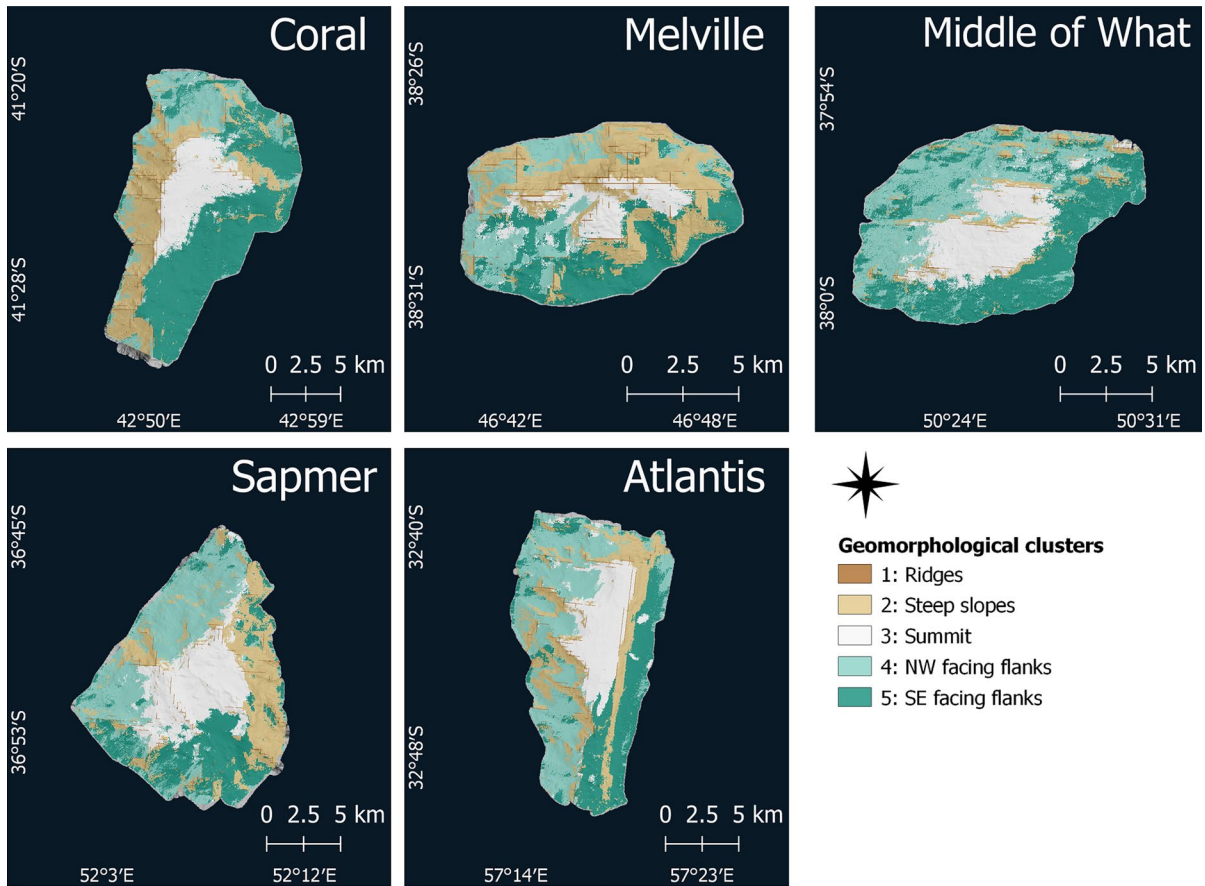
Fig. 3 Distribution of identified geomorphological clusters corresponding to habitat types at each surveyed seamount

Results

Habitat characteristics

The PCA procedure revealed nine significant (eigenvalue > 1) principal components that explained 90% of the total variance in predictor data (SI 3–1). Topographic ruggedness and slope contributed strongly to PC1, whereas PC2 consisted of depth, broad-scale curvature, and topographic position index (SI 3–2).

Habitat maps (Fig. 3) showed the distributions of five geomorphological habitat types (patch types) obtained through clustering the principal components. Maps were used in conjunction with boxplots (Fig. 4) to determine the character of identified

geomorphological habitats. These were mainly distinguished by variations in slope, complexity, depth, and orientation. Habitat 1 consisted of shallower areas associated with the summit of seamounts. The terrain was flat and of low structural complexity, with local relief at individual seamounts. Habitat 2 was highly sloping (> 20°), with elevated terrain complexity. Habitat 3 and 4 were both gently sloping flank habitats (5°–20°) and distinguished by orientation (habitat 3: south/south-east/east, habitat 4: north/north-west/west). At MOW and Melville, this included far-field habitat off the main seamount structure. Habitat 5 consists of highly structurally complex and sloping terrain, linked to local highs such as crests, ridges and scarps found on the tops of the seamounts and the edges of mass wasting features.
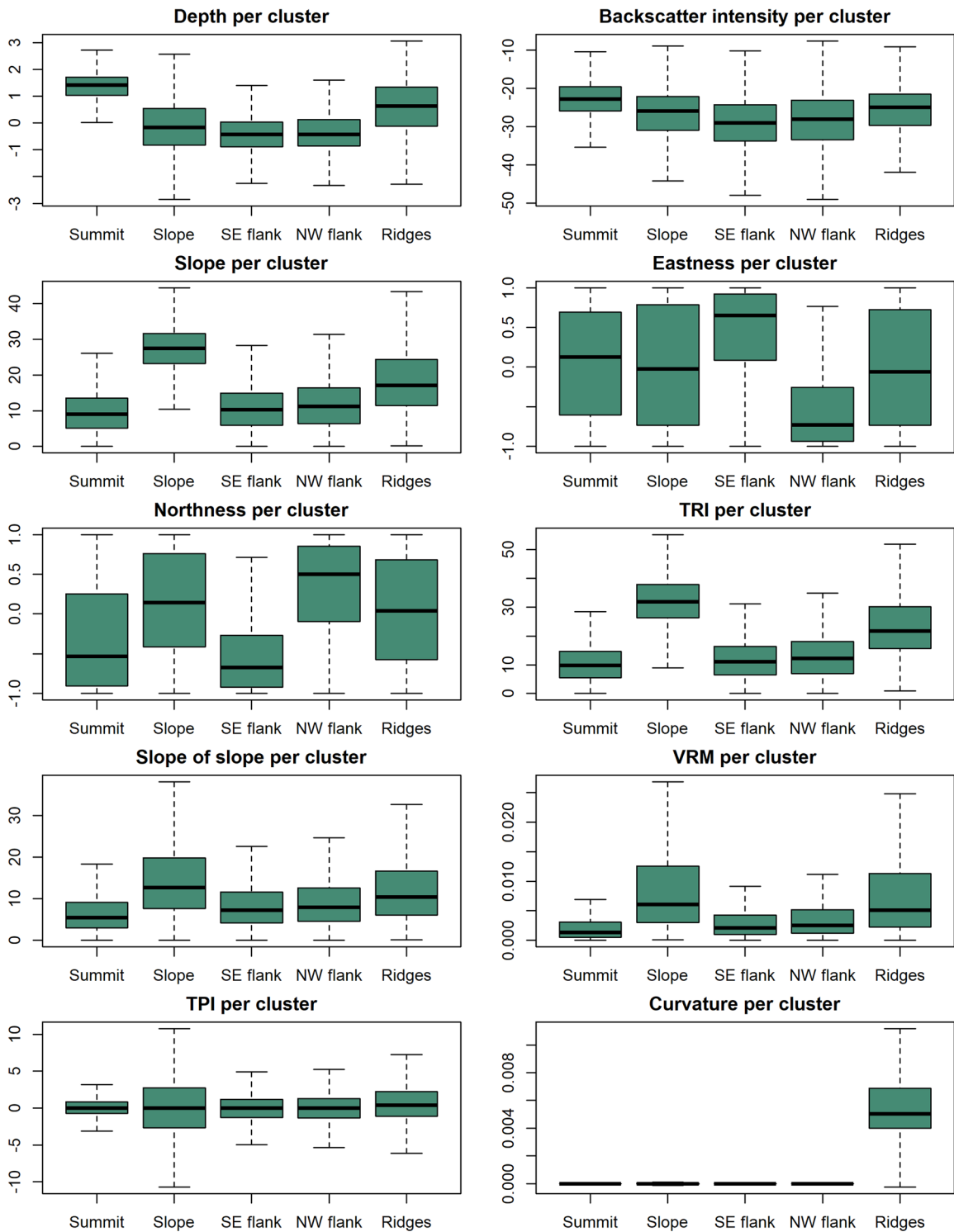
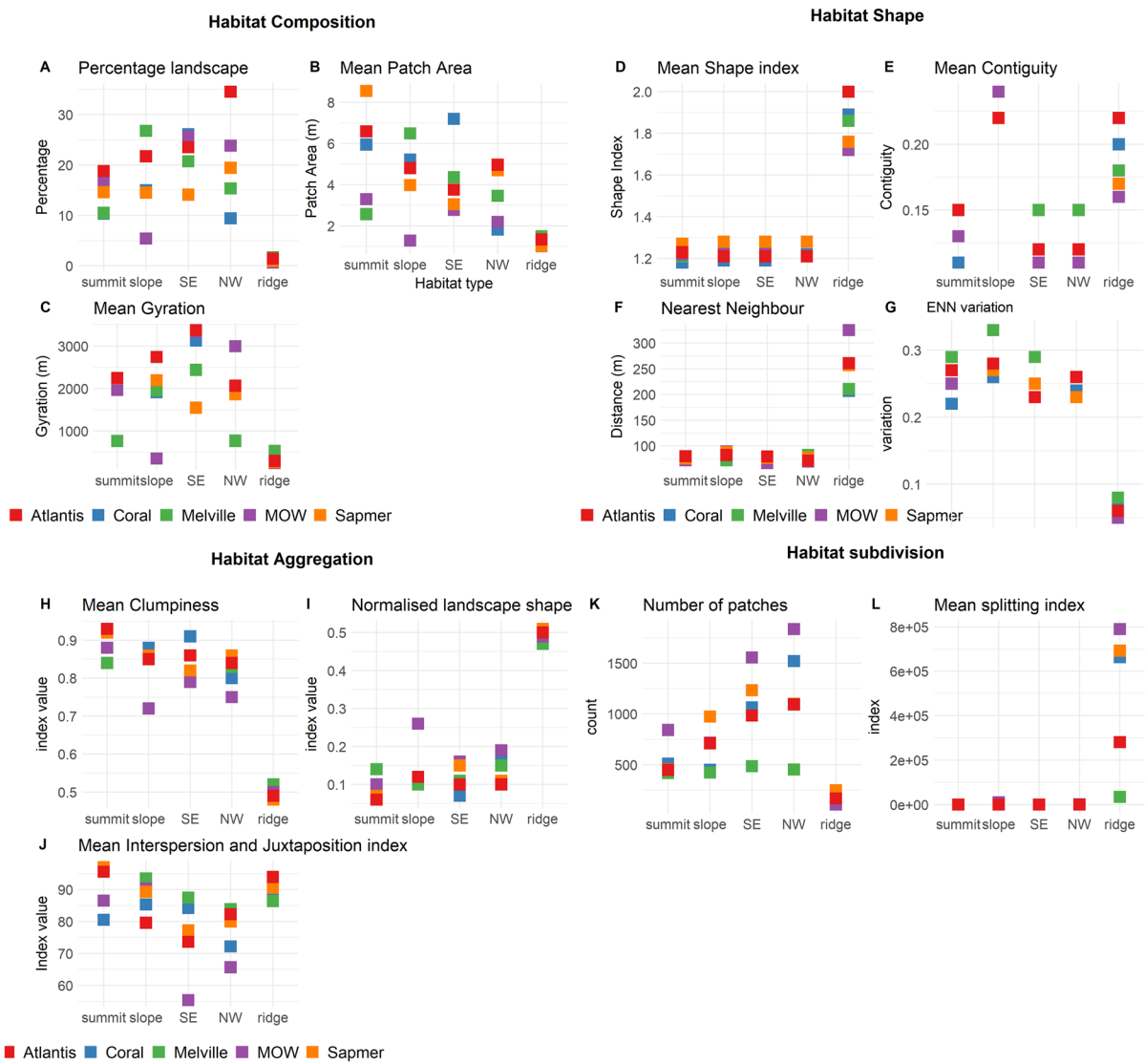**Fig. 4** Characteristics of each habitat

Fig. 5 Class-level metric values for each habitat type per site, arranged by metrics of habitat composition, shape, isolation, aggregation, subdivision and interspersion and juxtaposition

Structural comparison between sites

Class-level

Class level metrics (Fig. 5, SI 5–1) quantified the spatial characteristics of identified habitat types at each site, and ANOVA showed whether patch characteristics differed significantly between patch types (SI 6).

Habitat 1 Habitat 1 (summits) had larger proportional abundances, patch area and gyration at Atlantis,

Sapmer and MOW (Fig. 5A, B) and occurred in contiguous and simple shapes (Fig. 5D, E). The summits significantly differed from flanks and slopes in high aggregation and interspersion, and limited subdivision (Fig. 5H, J, L, SI 6). Summit habitat at Melville was however disaggregated (Fig. 5H, I), deviating from this pattern.

Habitat 2 The relative abundance, mean size and extent of slope Habitat 2 differed across sites (Fig. 5A, B, C), with the largest proportional abundance at Mel-

ville and a limited area and extent at MOW. It significantly differed from other habitat types in a higher degree of contiguity and dispersion (Fig. 5E, G, SI 6). Subdivision, aggregation and interspersion indices also showed reduced clumping and interspersion (Fig. 5H, I, J) at MOW.

Habitat 3 South-east facing flanks formed over 20% of seamount habitat at all sites apart from Sapmer (Fig. 5A) with largest patch size and extent at Coral and Atlantis (Fig. 5B, C). Aggregation and subdivision indices indicated an aggregated occurrence pattern with high clumping (Fig. 5H, I) and low splitting, but with reduced interspersion (Fig. 5J).

Habitat 4 Composition and configuration of northwest facing flanks was not significantly different from south-east facing flanks (SI 6). The relative abundance, mean size and extent of Habitat 4 were variable per site with largest proportional abundance and patch area at Atlantis (Fig. 5A, B). Like habitat 3, distribution indices showed an aggregated occurrence pattern with least intermixing.

Habitat 5 Highly complex ridges of Habitat 5 were significantly different from all other habitat types in both composition and configuration (SI 6). It occupied a smaller percentage of landscape with a small patch size and extent (Fig. 5A–C). Patches had more complex shapes (Fig. 5D) and occurred in multiple small, disaggregated patches (Fig. 5H, I) that were spatially isolated and more dispersed (Fig. 5F, L) across sites than other habitat types.

The metrics most useful to distinguish between habitat classes (measured by the number of significant differences) were the contiguity index, the variation in nearest neighbour distance, the number of patches and the clumpiness index (SI 6).

Seascape-level

Landscape-level metrics (Fig. 6, SI 5–2) compared overall seascape structure at each seamount. Composition-wise, sites differed in area (Fig. 6C, D), but not diversity metrics (Fig. 6A, B). Configuration-wise, sites differed in seascape shape (Fig. 6E, F), subdivision (Fig. 6I–K) and seascape aggregation (Fig. 6L–N). Seascape metrics were used to rank the seamounts from lowest spatial complexity

(large, contiguous patches and aggregated landscapes) to highest spatial complexity (small and complex patches, subdivided and intermixed seascapes) (Fig. 7).

At Coral, composition and shape metrics showed that mean patch size (Fig. 6C) and contiguity (Fig. 6F) were large compared to other sites. Patch shapes were relatively simple (Fig. 6E), and aggregation metrics confirmed a clumped seascape structure (Fig. 6L) with low patch density (Fig. 6J).

At Atlantis, patches exhibited relatively large spatial extent (Fig. 6D) and shape metrics suggest uniform patch characteristics. Subdivision metrics (Fig. 6J, K) indicate reduced seascape subdivision whilst aggregation and interspersion indices (Fig. 6L) suggest clumping.

Middle of What has smaller patch sizes (Fig. 6C), but with larger extent (Fig. 6D) and complex patch shapes (Fig. 6E, F). Subdivision and isolation metrics show many patches at high patch density (Fig. 6I, J) and close proximity (Fig. 6G). Aggregation indices confirmed high disaggregation (Fig. 6L, M) and limited patch intermixing (Fig. 6N). This indicates a high number of small patches in an extensive matrix of another patch type.

Patches at Sapmer were larger (Fig. 6C) and relatively contiguous. Subdivision and isolation metrics show increased isolation (Fig. 6G) and landscape splitting (Fig. 6K), which was matched by aggregation metrics confirming seascape disaggregation (Fig. 6M), reduced clumping (Fig. 6L) and, in contrast to Middle of What, intermixing of patch types (Fig. 6N).

Melville had the smallest mean patch size (Fig. 6C), and extent (Fig. 6D). Low contagion (Fig. 6L) and landscape shape (Fig. 6M) indicate limited clumping and high disaggregation, and dispersion and interspersion indices (Fig. 6N) show high intermixing of patch types.

Discussion

Geomorphological drivers of habitats

The unsupervised classification identified similar habitat types across seamounts, distinguished by variations in depth, slope, structural complexity and orientation. Depth is one of the primary determinants
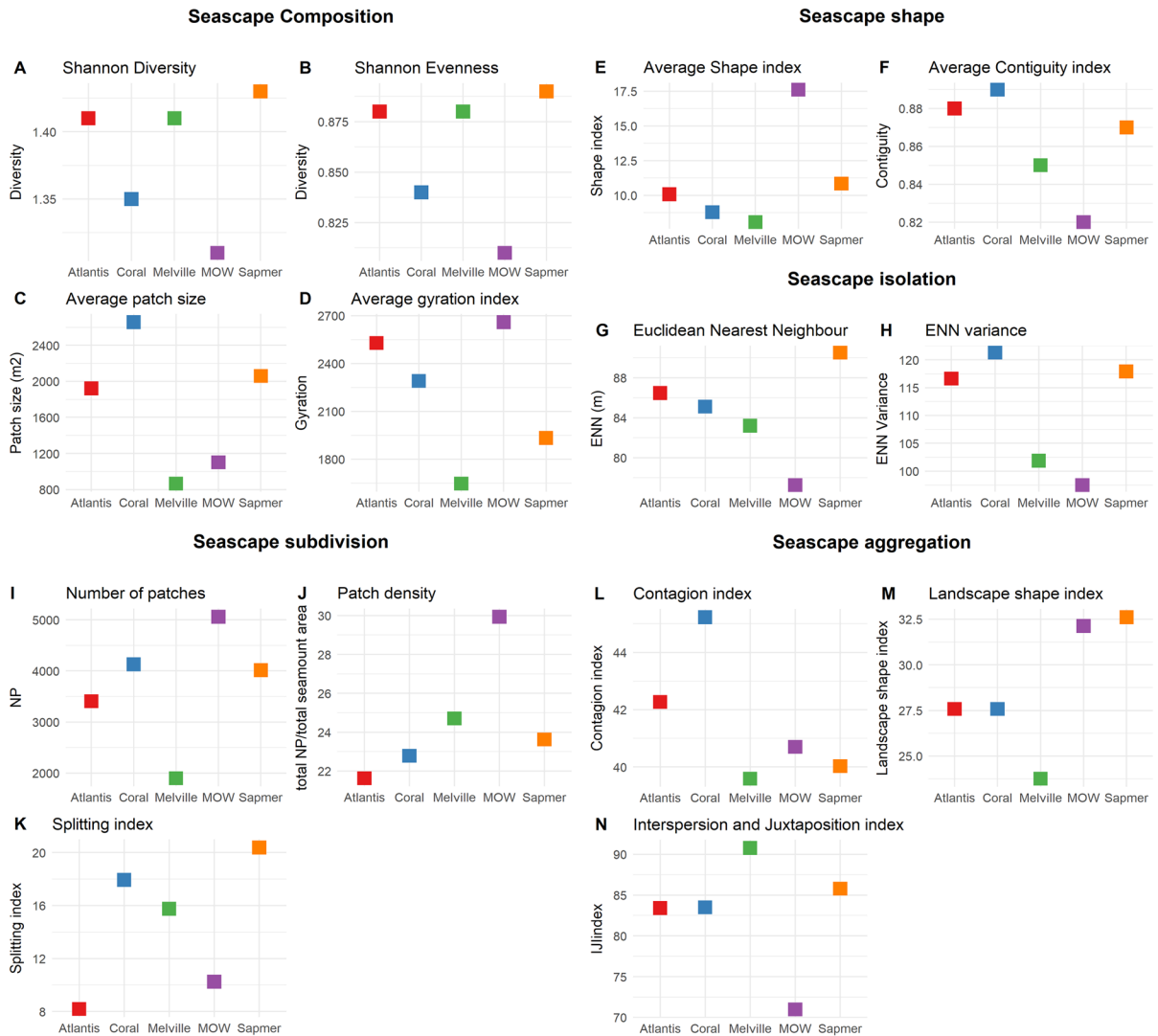
Fig. 6 Seascape-level metrics per site, arranged by metrics of seascape composition, patch shape, isolation, subdivision and aggregation

of marine biodiversity, including on seamounts, as it correlates with physical characteristics of the water column as temperature, oxygen, pressure, salinity, organic matter and light penetration. The classification established limited depth zonation within flanks and slopes. As a result of species replacement with depth these habitats likely host varying assemblages (Victorero et al. 2018), although they may be functionally similar by having comparable functional traits (de la Torriente et al. 2020). For example, steep slopes with rocky outcrops may host various

cold-water coral assemblages that differ in species composition, but all function as filter feeders.

Slope, structural complexity and orientation distinguished flank habitats, summit habitat and ridges. These variables may influence exposure to local hydrodynamic regime and the deposition of sediment and organic matter (Clark et al. 2010). Steep and structurally complex features experience reduced sedimentation, accelerate hydrodynamic flow, and can result in deep ocean mixing (White et al. 2007). Nutrient availability through such current amplification can positively promote the presence of coral

Fig. 7 Sites scored along a gradient of increasing spatial complexity. Coral and Atlantis were spatially less complex with large, contiguous patches, whereas MOW, Sapmer and Melville were more spatially complex with a larger number of patches and varying degrees of aggregation and interspersion
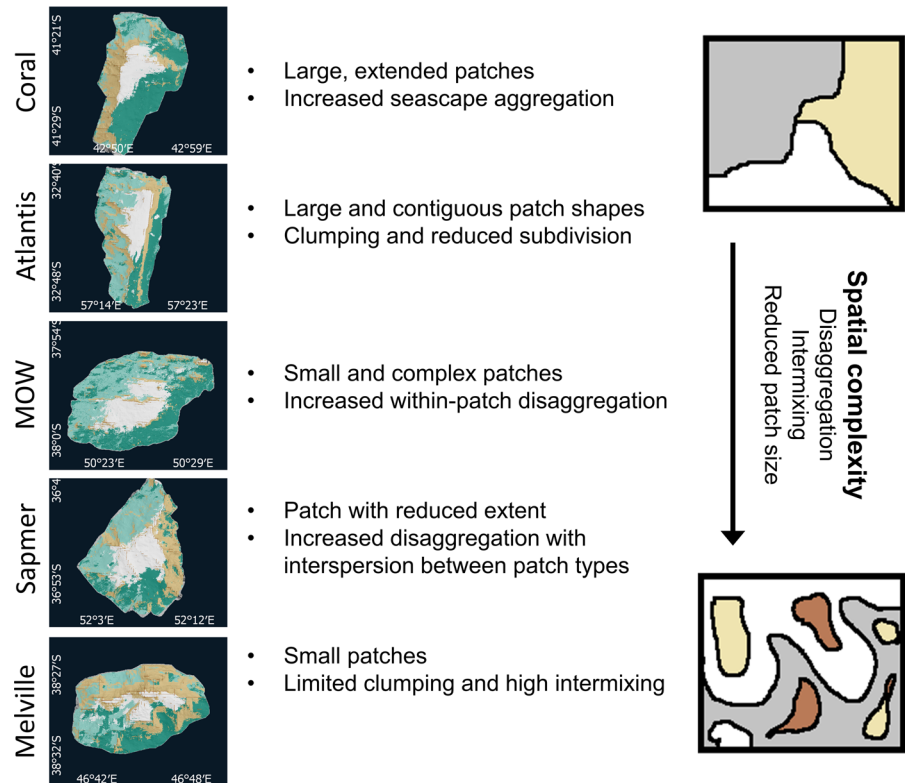
habitat (Quattrini et al. 2012) and seamount associated fish (Leitner et al. 2021). Orientation has been used as proxy for hydrodynamic flow and exposure to the prevailing currents. However, prevailing currents differ across surveyed seamounts because of regional processes (Pollard and Read 2017), and delineated flanks at seamounts might therefore not be directly comparable. Further research incorporating spatially explicit oceanographic parameters (Pearman et al. 2020) could help quantify environmental heterogeneity in current exposure.

Assessment of spatial heterogeneity

Habitat-level heterogeneity: differences between patches

Geomorphological characteristics of identified seamount habitats can function as predictors of benthic assemblage composition and distribution through biological associations with substratum types, structural complexity, hydrodynamic exposure and other environmental parameters (Brown et al. 2011). Metrics showed habitat types also differed in composition and configuration, with possible implications for ecology.

Flat-topped seamount summits, habitat 1, are often associated with particular substratum types, relevant for sediment-associated epifauna and infauna (Rogers 2018). The summits of Coral, Sapmer and Atlantis featured local relief as boulders, rocky outcrops, and carbonate pavement, providing attachment opportunities for sessile benthos (Rogers and Taylor 2012). This internal heterogeneity might also be ecologically relevant for certain mobile species, providing opportunities for different activities as feeding or shelter. Hydrodynamic mixing of deeper nutrient-rich water upward over the summit (White et al. 2007) may be pronounced at sites with complex summit shapes such as Melville (Read and Pollard 2017).

Highly sloping flanks of Habitat 2 are frequently associated with hard substrate for benthic settlement, and increased exposure to strong currents (Yesson et al. 2012). Video observations showed the steep western slope of Coral hosted a distinctive community of brachiopods, sponges, octocorals and black coral (Rogers and Taylor 2012). Habitat 2 was more spatially

contiguous than other habitat types. Spatial contiguity might indicate structural connectivity important for habitat-specific species (Meynecke et al. 2008). Additionally, the interspersion between other habitat types might be relevant for seamount fish and marine mammals using a wider range of environments.

Habitats 3 and 4 extended to greater depths. Backscatter data (SI 1) and limited video observations (SI 7, Rogers and Taylor 2012) indicated these flanks were covered in soft sediment patches important for benthic fauna (Durden et al. 2015) and mid- and deep water fish associated with soft substrate (Morato and Clark 2007). Flanks differed in their high spatial aggregation and large patch types, indicating extended core habitat availability but limited connection to other patch types. Combined with greater depth, these flanks are likely inhabited by specialised communities. Evidence of trawling and fishing-associated litter (Woodall et al. 2015) suggests that these large flank habitats with limited vertical relief to impede trawling (Clark et al. 2011b) are at risk of anthropogenic effects. Such disturbance can result in habitat fragmentation, impacting the highly aggregated character of these habitats.

The ridges and crests that compose Habitat 5 have high structural complexity and hard substrate, likely promoting exposure to flow. Evidence for such bathymetrically modified hydrodynamic features over ridges was observed at Coral, Melville and Sapmer (Read and Pollard 2017). Observations supported diverse biogenic habitats at ridges, with dense communities of coral, large sponges, anemones, stylasterids, black corals, octocorals and brachiopods (Rogers and Taylor 2012) which may also benefit fish assemblages (Quattrini et al. 2012; Leitner et al. 2021). The small size and fragmentation of ridge habitats show that they are typically limited and dispersed across seamount seascapes, possibly providing hotspots of highly diverse and productive benthic habitat interspersed between other habitat types.

Seascape-level heterogeneity: differences between seamounts

Composition The type and abundance of seabed habitat types influences biodiversity and ecosystem functioning (Zeppilli et al. 2016) and was measured by composition metrics. Although variable in proportional abundance, each seamount featured all five

identified habitat types resulting in limited variation in diversity metrics. However, area metrics varied across sites and showed Coral, Sapmer and Atlantis featured larger patch shapes. Under theoretical ecology, larger areas are predicted to host higher species richness (Turner and Gardner 2015). Species-area relationships apply to deep-sea sessile benthic diversity across depth bands and substratum types (Foster et al. 2013), and are therefore likely applicable to seamounts too. Deep-sea mobile megafauna may be habitat specialists and predictably associated with geomorphic habitat features (Quattrini et al. 2012). The occurrence and abundance of some habitat-specific mobile megafauna may be linked to minimum area requirements and influenced by the gyration index (extent), which was particularly large for MOW, Atlantis and Coral. However, as minimum area requirements are unknown for many deep sea species environments knowledge gaps remain the transferability of such concepts.

Configuration

Patch shape Patch metrics showed that seascapes differed in patch complexity. Complex patch shapes are thought to offer limited core area and increased edge, resulting in greater exposure to external environmental conditions (Ries et al. 2017). These edge effects alter the habitat quality of patch edges in different ways, depending on biological traits and the quality differences between adjacent habitat types. Average patch shapes at Coral and Atlantis were less spatially complex, suggesting increased availability of core habitat, whereas MOW featured more complex patch shapes. Edge effects are little studied in deep-sea benthic environments, but appear relevant in the context of physical disturbances (Harris 2012). Additionally, transitions between broad-scale benthic habitat types may be less discrete than on land (Lucieer and Lucieer 2009).

Aggregation and interspersion Seascapes differed in aggregation and interspersion characteristics with possible implications for structural connectivity across the seascape. Little is known about the influence of structural connectivity on benthic and demersal fauna associated with the deep seabed, especially as many species disperse larvae through the water column (Swanborn et al. 2022). Patch aggregation is likely important for mobile habitat-specific spe-

cies with limited dispersal ranges as they facilitate movement between patches of the same type. Coral and Atlantis featured more aggregated seascape characteristics, suggesting increased habitat connectivity. Conversely, the diversity in morphological features at Middle of What resulted in higher patch disaggregation and isolation. This has been linked to reduced connectivity in terrestrial habitats, which may impact metapopulation and community dynamics of mobile species. The intermixing of patch types, such as seen at Melville and Sapmer, meanwhile, may be ecologically relevant for migratory species as large predatory fish and marine mammals that use multiple habitat types across regions and depths of the seamount (e.g. feeding and shelter) (Holland and Grubbs 2007).

Importance and methodological considerations

Relevance approach

When prioritising seamounts for protected area establishment or incorporation in marine protected area networks, an important consideration is ensuring that representative physical and biological features are included (Clark et al. 2011a, 2014), also recognised in Aichi Biodiversity Target 11 (Rees et al. 2018). Previous biogeographic classifications of seamount environments based on representation have been conducted at broad scales and did not incorporate patterns of seabed structure (Clark et al. 2011a). We showed that seamounts differ in the proportional abundance and spatial characteristics of geomorphological habitats. Seamounts differed primarily in patch size and extent (composition) and in shape, aggregation and interspersion (configuration). As these variations are likely biologically meaningful, spatial metrics could be valuable additions to broad-scale physical variables as depth and oceanographic parameters to group seamounts with similar characteristics. Based on this limited study of SWIR seamounts, the degree of aggregation and interspersion and patch shape complexity appear important descriptors of spatial variation.

This study also showed that composition and configuration can differ within individual seamounts. Different habitat features could benefit from being incorporated in the case of protection of a subset of a single seamount. For example, a zoning plan focused on protecting a seamount summit might fail to incorporate spatial representation, as ridges, flanks, and steep slopes can host different biological communities with different vulnerabilities to impacts (Bo et al. 2021) but also have different spatial characteristics.

Transferability technique

This study used a top-down classification based on terrain derivatives to identify habitat types. However, proposed approach of quantifying environmental heterogeneity using spatial pattern metrics also extends to seabed and habitat maps produced using other methods (e.g. geomorphons, semi-automated and automated approaches, Janowski et al. 2022; Summers et al. 2021) Further mapping efforts incorporating other environmental data sources could help the representation of other sources of environmental heterogeneity. For example, oceanographic variables and different water masses strongly contribute to heterogeneity, mediated by the height of the seamount, its shape, size and fine-scale topography, and the strength of the current regime (Rogers 2018). Studied seamounts were located in different water masses (Coral close to the Subantarctic Front, Melville, Middle of What and Sapmer by the Subtropical and Agulhas Fronts, and Atlantis in the Sub-Tropical Anticyclonic Gyre). Therefore ecologically important oceanographic parameters such as temperature, current velocity, dissolved oxygen and salinity likely differ between seamounts. Dynamic models incorporating spatio-temporal changes in oceanography might further refine obtained insights within seamounts (Kavanaugh et al. 2016) as oceanographic conditions at the seabed were variable over tidal cycles (Read and Pollard 2017).

Scale-dependency and ground-truthing

Here we did not consider a specific phenomenon but instead focused on quantifying and comparing broad-scale features. Although generalities will emerge, resolving the ecological implications of heterogeneity in seascape characteristics requires consideration of thematic scale. What constitutes a suitable habitat depends on the life history traits, life style (i.e. benthic, infaunal, epifaunal) and mobility of the species or process under consideration (Levin 1992). As species-environment associations were not explicitly quantified

and incorporated to inform the classification, produced maps do not intend to predict the occurrence and distribution of biological communities. However, uncovered broad-scale habitat types exhibit internal heterogeneity that may be ecologically relevant for associated species. Hierarchical classification approaches using ecological validation could help reclassify broad-scale entities into finer-scale physical habitat types and test the accuracy of identified habitat types and their spatial characteristics for particular species (Hogg et al. 2018). Considerations of appropriate thematic scale for the phenomenon under consideration will also improve the relevance and interpretation of spatial pattern metrics (Pittman et al. 2021). Seamount-associated sessile and mobile benthos have different habitat requirements than mobile megafauna as fish or mammals due to mobility ranges and life history traits.

Metric interpretation

The study also highlighted some uncertainties in the transferability of interpretations of landscape ecology metrics to deep-sea habitats. Transitions between habitat types may be less discrete (edge effects), and organisms have different dispersal strategies (water column). Also, the interpretation of metrics for sessile benthic organisms is less clear cut. Therefore, we recommend further multiscale studies testing the ecological relevance of habitat composition and configuration on sessile and mobile seamount biota, for example, generating predictor variables for explaining distribution patterns. Such knowledge would help further the conceptual importance of spatial pattern metrics from landscape ecology in heterogeneous deep-sea environments at scales appropriate for the phenomenon under consideration.

Conclusions

Using a quantitative approach combining habitat mapping and spatial pattern metrics, this study found that (1) SWIR seamounts hosted five similar geomorphological habitat types (summit, slope, south-east facing and north-west facing flanks and ridges) despite varying morphology; (2) SWIR seamounts differed in spatial composition and configuration at class and seascape level; and (3) at class-level, metrics of contiguity, isolation

and clumping differentiated patch types, whereas at seascape-level patch area, intermixing and disaggregation distinguished seamounts. These variables allowed us to score seamounts on a gradient from low spatial heterogeneity (large, aggregated and isolated patches) to high spatial heterogeneity (small, disaggregated and highly interspersed patches).

Variations in spatial structure can have consequences for the biological communities, habitats and ecological processes on seamounts. The spatially-explicit approach presented here to quantify seabed heterogeneity is likely of interest to a broader community of seabed and habitat researchers, and important for considerations of representational protection of within-seamount characteristics and seamount types. To help improve ecological interpretation of metrics, we recommend further study of biodiversity associations at appropriate scales, and incorporating oceanographic parameters in mapping strategies.

Declarations

Competing interests The authors declare no competing interests.

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