



Seamount seascape composition and configuration shape Southwest Indian Ridge fish assemblages

D.J.B. Swanborn^{a,b,*}, V.A.I. Huvenne^c, T. Malpas^d, S.J. Pittman^{e,f}, A.D. Rogers^{a,g}, M.L. Taylor^h, L.C. Woodall^{a,b}

^a Department of Biology, University of Oxford, UK

^b Nekton, Oxford, UK

^c Ocean BioGeoSciences, National Oceanography Centre, Southampton, UK

^d School of Biosciences, University of Sheffield, UK

^e Oxford Seascape Ecology Lab, School of Geography and the Environment, Oxford, UK

^f Marine Institute, University of Plymouth, Plymouth, UK

^g REV Ocean, Lysaker, Norway

^h School of Life Sciences, University of Essex, Colchester, UK

ARTICLE INFO

Keywords:

Habitat mapping
Deep-water fish
Geomorphology
Seamounts
Seascape ecology
Southwest Indian Ridge

ABSTRACT

Seamounts are commercially important fishing grounds. Yet, little is known about their physical characteristics as fish habitat, important for informing conservation and ecosystem-based management.

This study examines how multiscale seabed spatial heterogeneity influences commercially important fish families at three Southwest Indian Ridge seamounts (Coral Seamount, Melville Bank and Atlantis Bank). We quantified seascape heterogeneity from bathymetry and geomorphological habitat maps and identified 15 focal fish families from video data. Fish-habitat associations were examined using spatial pattern metrics that measured terrain morphology, seascape composition (variety and relative abundance of patch types) and seascape configuration (spatial arrangement of patches). Broader seascape context was characterised by geographic location and water depth. Multivariate regression trees and random forests modelled fish-habitat associations and identified the most influential explanatory variables.

Assemblage characteristics and individual families were strongly influenced by geographic location and depth, and at finer scales (500 m buffers) seascape composition and configuration helped explain fish-habitat associations. Spatially continuous summit habitat and complex shaped ridge features supported high abundance and diversity of commercial fish families. Metrics of seascape composition and configuration (i.e., habitat size, shape and structural connectivity) had higher predictive power than the terrain metrics commonly used in developing proxies for deep-water fish species and biodiversity.

These outcomes indicate that seascape metrics, commonly applied on land and in shallow marine environments, are also relevant environmental predictors of fish distributions in deep-sea environments. We highlight strong context dependency and depth-specific associations that hinder attempts to draw wider generalisations on fish-seascape linkages for seamounts.

1. Introduction

Seamounts are elevated topographic features (>100 m) on the seabed (Yesson et al., 2011). They are recognised as hotspots of benthic and pelagic diversity and support a high abundance of demersal and benthopelagic fishes compared to the surrounding environment (Serrao Santos and Morato, 2008). Fish aggregations around these elevated

topographic features have also led to the establishment of deep-sea fisheries (Clark, 2009). These fisheries can have high catch-per-unit-effort ratios and large ecological impacts, exacerbated by the low growth and high mortality rates of many seamount-associated species (Pitcher et al., 2007). Despite the ecological and economic importance of seamount-associated fish, fish-habitat relationships around seamounts remain poorly understood, with only a fraction of

* Corresponding author. Department of Biology, University of Oxford, UK.

E-mail address: denise.swanborn@env-res.ox.ac.uk (D.J.B. Swanborn).

<https://doi.org/10.1016/j.dsr.2022.103921>

Received 24 June 2022; Received in revised form 1 November 2022; Accepted 2 November 2022

Available online 5 November 2022

0967-0637/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

total seamounts sampled (Kvile et al., 2014). Very few studies have measured multiscale heterogeneity in benthic seascape structure to examine its ecological relevance for mobile marine species. A better understanding of the linkages between seascape characteristics and fish assemblages may have significant implications for ecology, ecosystem-based fisheries management and biodiversity conservation (Leitner et al., 2021; Santos et al., 2021).

Environmental gradients and patchiness in abiotic and biotic conditions are characteristic of seamounts. Varying topography, substrate types, the overlying hydrodynamic regime and benthic cover create gradients and patchiness in a range of habitat types, influencing biological diversity at the seafloor (Goode et al., 2021; McClain and Schlacher, 2015). Heterogeneity can be represented and quantified in terms of patch mosaic composition (the variety and relative abundance of habitat types), spatial configuration (the arrangement of patches), and terrain surface morphology (Pittman et al., 2021; Wedding et al., 2011). Quantitative seascape ecology studies of the effect of seascape composition, configuration and terrain structure have yielded important insights into the fish communities of shallow marine systems including, for example, those exploring the importance of the type, size and shape of habitat features (Boström et al., 2011), their spatial configuration (Meynecke et al., 2008), and those including understanding the influence of spatial scale and context (Forman, 1995; Pittman et al., 2004).

Studies measuring deep-water fish-habitat associations, including at seamounts, have predominantly focused on depth and substrate characteristics, revealing that deep-water fishes use a range of habitat types over different scales (Auster et al., 2005; Quattrini et al., 2012). Fish may use biogenic features for shelter or food sources (Rogers et al., 2007), feeding aggregations are seen on larger features such as summits and crests (Leitner et al., 2021; Morato and Clark, 2007) and soft-sediment areas of low complexity can host significantly different assemblages compared to complex habitat types (Devine et al., 2020; Ross et al., 2015). The diversity of broad-scale habitat or patch types and their abundance (seascape composition) is therefore ecologically relevant for mobile species across depths (Anderson et al., 2009; Borland et al., 2021). Additionally, the spatial characteristics of the local and surrounding seabed environment (seascape configuration) appear to influence the distribution and abundance patterns of deep-water demersal fishes (Anderson et al., 2009).

Despite an increasing interest in studying the influence of habitat characteristics on deep-water fish (e.g. Leitner et al., 2021), key knowledge gaps remain on the importance of the spatial patterns of habitat patches, terrains and the surrounding seascape for seamount-associated fish, as well as on the transferability of theoretical frameworks developed on land to the deep sea (Swanborn et al., 2022b). Yet, similar questions, concepts and quantitative techniques for measuring heterogeneity in terrestrial landscapes and in shallow waters may provide insights into the importance of environmental heterogeneity for demersal fish associated with seamounts. Improved data quality and availability of *in-situ* biological survey data collected using remotely operated vehicles (ROVs), combined with high-resolution bathymetry and habitat mapping, provide unprecedented opportunities to explore the ecological relevance of benthic seascape patterns on biological assemblages (Swanborn et al., 2022b).

The Southwest Indian Ridge (SWIR) seamounts remain poorly studied, yet have been subject to intense deep-sea fishing activity over the past 40 years (Rogers et al., 2017; Woodall et al., 2015). Some seamount aggregating species such as orange roughy (*Hoplostethus atlanticus*), pelagic armourhead (Pentacerotidae), oreos (Oreosomatidae) and alfonso (Beryx sp.) are highly valued by commercial fisheries, leading to intense exploitation (Clark, 2009; Clark et al., 2007; Rogers, 2017). Although SWIR seamounts are known aggregation spots for commercially important species, little is known about the physical habitat characteristics that support them (Rogers, 2013). Knowledge on the potential function of seascape spatial patterns as a proxy for predicting fish assemblages can inform management, for example, by

identifying and characterising priority areas for conservation (Clark et al., 2012; Moore et al., 2016).

This study aims to identify commercially important demersal fish families at three SWIR seamounts and examine the ecological importance of seabed environmental heterogeneity at multiple spatial scales for these families by employing the theoretical framework of seascape ecology. To identify ecologically important seascape features, we assess 1) whether seamount assemblages differ between depth zones and seamounts; and whether seascape composition and configuration are key drivers of 2) assemblage characteristics (abundance, richness and diversity) and 3) individual fish families.

2. Methods

2.1. Study locations

Data used in this study were collected during the 2011 JC066 cruise aboard RRS *James Cook* (Rogers and Taylor, 2012). The considered seamounts, Coral Seamount (Fig. 1b), Melville Bank (Fig. 1c), and Atlantis Bank (Fig. 1d), are located along the ultra-slow spreading SWIR and characterised by varying morphologies and summit depths. They are positioned within different regional oceanographic conditions created by the Agulhas Return Current, the Sub-Tropical Front and the Sub-Antarctic Front, which influence the biodiversity these seamounts host (Fig. 1a) (Pollard and Read, 2017; Rogers et al., 2017).

2.2. ROV surveys

To survey demersal fish populations, upslope video transects were conducted with the ROV Kiel 6000 (Fig. 1). The ROV, where possible, was run at 1m above the seabed at approximately 0.2 kts and carried a CTD for *in-situ* oceanographic measurements. While the sampled depth ranges overlap across the three features, due to weather conditions and seamount morphology, sampling effort and average depth surveyed differed per site (Table 1). Dives at Melville Bank were conducted at the shallowest depths, Coral Seamount contained the majority of dives in the bathyal zone (>1000 m) and Atlantis Bank contained predominantly dives in the twilight zone (200–1000 m).

2.3. Biological data

Continuous annotation of underwater video data collected by the ROV was conducted with QuickTime Viewer (Apple Inc.), where a screenshot was taken for every fish sighting during the dive (Malpas, 2017). Every sighting was then identified to the lowest taxonomic level possible (Malpas, 2017) using a combination of reference books (Gon and Heemstra, 1990; Whitehead, 1985) and the online database Fish-Base (Froese and Pauly, 2020). A full list of species observed at the three seamounts, including those not analysed in this study, can be found in Appendix A. Substratum type (bedrock, boulders, cobbles, gravel, mud, rubble, cold-water coral reef, mesophotic coral reef) was also recorded from these screenshots according to the majority rule (the dominant cover determines the substratum type). When no substrate type was visible in the screenshot (e.g. as a result of camera orientation or bad visibility) substrate type was recorded as 'NA'. All sightings were linked to ROV track metadata using timestamps containing position (latitude, longitude, depth) and oceanographic data (temperature, salinity, pressure).

The continuous ROV dives were divided into separate transects to derive comparable sampling units. The appropriate transect length was determined by iteratively testing different transect lengths in steps of 25 m (the resolution of bathymetry) between 50 and 700 m. The transect length maximising both the number of samples (transects) and the number of individuals incorporated in the analysis was 250 m (Figure B1 in Appendix B). Identified transects were spaced a minimum of 100 m apart to create individual sampling units. Transects with fewer than

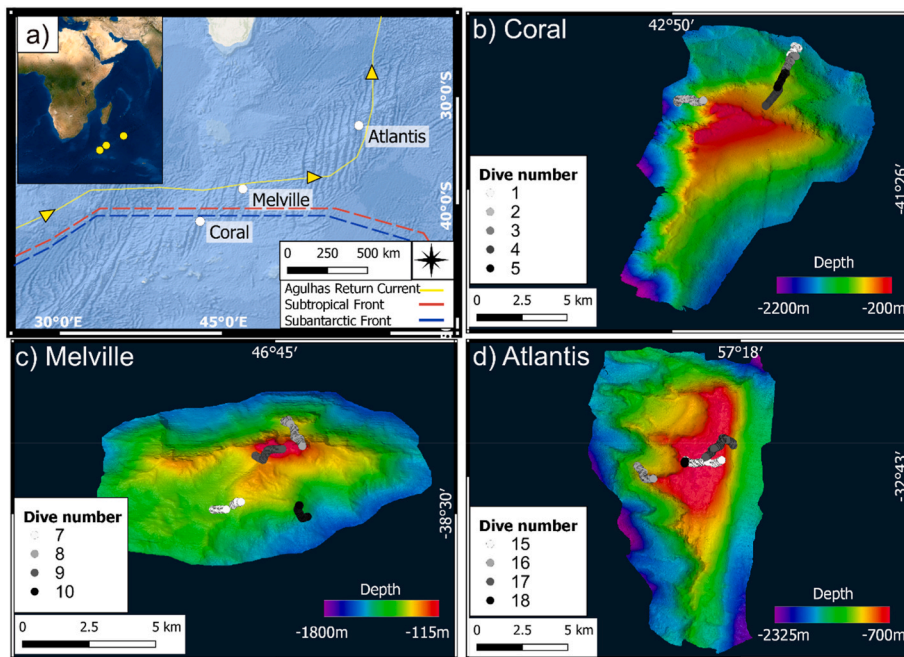


Fig. 1. Surveyed SWIR seamounts described in Rogers and Taylor (2012). Panel a indicates the location of the three surveyed seamounts and dominant influences on local oceanography. Subsequent panels show multibeam bathymetry and location of ROV dives at Coral (b), Melville (c) and Atlantis (d) (note different horizontal and vertical scales). Colour bars indicate seamount depth. Dives differed in depth range surveyed, dive time and distance covered. Dive 6 was a sample collection dive and therefore not included. Dive 11–14 were conducted at locations not considered in this study.

Table 1

Characteristics of conducted ROV dives (Rogers and Taylor, 2012). Dives were semi-randomly selected to cover different geomorphological features of each seamount and differed in depth range surveyed, dive time and distance covered.

Site	ROV Dive no.	Date	Depth range (m)	Dive time (min)	Distance (m)
Coral Seamount	1	12/11/2011	1400–1090	506	1533
	2	13/11/2011	1493–622	507	3518
	3	14/11/2011	1065–681	597	1870
	4	16/11/2011	745–510	270	2305
	5	20/11/2011	738–731	316	1025
Melville Bank	7	23/11/2011	900–671	442	1827
	8	24/11/2011	675–150	505	1946
	9	25/11/2011	380–125	414	1638
	10	26/11/2011	1295–970	334	972
Atlantis Bank	15	09/12/2011	720–748	640	2639
	16	10/12/2011	1100–825	385	1428
	17	13/12/2011	1000–720	519	3353
	18	14/12/2011	740–730	98	130
Total				6649	29672

three fish present were removed to enable subsequent statistical analysis. The final number of transects analysed in this study was 55 (17 at Coral; 19 at Melville; 19 at Atlantis). Fish from 20 commercially important families (Rogers et al., 2009, 2017) were recorded per transect (Table 2), and all analyses were conducted at family level. Families with fewer than three observations were removed from the analysis.

Observations were standardised by transect duration (obs/duration in hours) before calculating total abundance, richness (number of families), and Shannon diversity index (using the total number of

individuals and the number of individuals of each family) per transect. This was deemed appropriate because ROV speed differed across transects due to current-driven variations, and this study focuses on highly mobile species.

2.4. Environmental data

For each transect, we identified descriptive parameters (site, depth, substratum type and distance to nearest ridge feature, oceanographic parameters) and quantified variables describing terrain structure and seascape composition and configuration in three different sizes of area (250m, 500m, 1000m) surrounding transects, referred to as ‘buffer zone’ in the remainder of the paper (Table 3).

Terrain structure was extracted from bathymetric data at a raster cell resolution of 25 m × 25 m (Rogers and Taylor, 2012). Orientation, slope, terrain complexity (VRM, TRI) and curvature (including TPI) (Wilson et al., 2007) were quantified within a 3 × 3 moving window using R packages raster (Hijmans, 2017) and spatialEco (Evans, 2017) and the average value for each terrain derivative was recorded per transect (Table 3). Benthic seascape composition and configuration were measured using unsupervised seabed habitat maps (Swanborn et al., 2022a) at a raster cell resolution of 25 m × 25 m. To produce these maps, geomorphological habitat types were determined through K-means classification in R v3.6.3. Depth-normalised terrain characteristics from 5 SWIR seamounts, Coral Seamount, Melville Bank, Middle of What Seamount, Sapmer Bank and Atlantis Bank (using relative depth, slope, curvature, terrain complexity and aspect) formed the input for the analysis. Five habitat types were identified and mapped out: seamount summit, ridges, slopes, NW flanks and SE flanks. Habitat maps were used to identify seascape composition (proportion of habitat types, their size, abundance, richness and diversity) and configuration (spatial configuration of habitat types, full list of metrics in Table 3). These were quantified in multi-scale sample units extending 250 m, 500 m and 1000 m around each transect with Fragstats 4.2 (McGarigal et al., 2012) (Fig. 2). Fragstats is a spatial analysis program. It uses the areal extent and spatial distribution of patches (in this case, habitat types) from categorical maps of landscapes (in this case, seascapes) to obtain measures of landscape structure (Table 3).

Collinearity between derived variables was analysed using the

Table 2

Commercially important fish families observed at Coral, Melville and Atlantis, including species-level observations common name and ROV dives in which species from this family were observed. Families in bold font represent the 15 families that were retained in the analysis.

Family	Species	Common name	ROV Dive no.
Berycidae (alfonsinos)	<i>Beryx</i> sp., <i>Beryx splendens</i> <i>Centroberyx druzhinini</i>	Splendid alfonsino	4,5,7,15,17,18
Carangidae (amberjacks)	<i>Seriola lalandi</i>	Yellowtail amberjack	9
Centrolophidae (medusafishes)	<i>Centrolophus niger</i> <i>Hyperoglyphe antarctica</i>	Black ruff Bluenose warehouse	7, 10, 15, 17, 18
Cyttidae (dories)	<i>Cyttus traversi</i>	King dory	8, 15
Etmopteridae (lantern shark)	<i>Etmopterus</i> sp. <i>Etmopterus spinax</i>	Lantern shark Velvet belly lanternshark	3, 4, 7, 8, 10, 15, 17
Gempylidae (escalars)	<i>Promethichthys prometheus</i>	Roudi escolar	1, 7, 17
Hexanchidae (cow shark)	<i>Hexanchus griseus</i>	Blunt-nosed sixgill shark	2, 17
Latridae (trumpeter)	<i>Nemadactylus monodactylus</i>	St Paul's fingerfin	9, 17
Moridae (morid cod)	<i>Guttigadus kongi</i> <i>Mora moro</i>	Austral cod Common mora	1, 2, 3, 4, 5, 7, 8, 9, 10, 15, 16, 17
	<i>Guttigadus</i> sp. <i>Laemonema compressicauda</i> <i>Lepidion</i> sp. <i>Physiculus</i> sp. <i>Tripteryphycis</i> sp.	Morid cod Morid cod Morid cod	
Nototeniidae (Antarctic cod)	<i>Disotichus eleginoides</i>	Patagonian toothfish	1
Odontaspidae (sand shark)	<i>Odontaspis ferox</i>	Smalltooth sand tiger	9
Ophidiidae (cusk eel)	<i>Ophidiidae</i> sp.	Cusk eel	5
Oreosomatidae (oreos)	<i>Alloctytus niger</i> <i>Neocyttus rhomboidalis</i> <i>Oreosoma atlanticum</i> <i>Pseudocyttus maculatus</i>	Black oreo Spiky oreo Ox-eyed oreo Smooth oreo	1, 10, 15, 16, 17
Pentacerotidae (armourheads)	<i>Pentaceros richardsoni</i>	Pelagic armourhead	15, 16, 17, 18
Polyprionidae (wreckfish)	<i>Polyprion americanus</i> <i>Polyprion oxygeneios</i>	Atlantic wreckfish Hapuku wreckfish	2, 7, 8, 9, 15, 17
Scorpaenidae (scorpionfish)	<i>Scorpaenidae</i> sp. <i>Scorpaena</i> sp.	Scorpionfish	7, 8, 9, 10, 15, 17
Scyliorhinidae (catshark)	<i>Apisturus</i> sp. <i>Bythaelurus naylori</i>	Ghost catsharks Dusky snout catshark	10, 17
Sebastidae (rockfish)	<i>Heliconus dactylopterus</i> <i>Trachyscorpia</i> sp. <i>Sebastes norvegicus</i>	Blackbelly rosefish Rockfish Rosefish	2, 4, 7, 8, 9, 15, 17
Squalidae (dogfish shark)	<i>Squalus mitsukurii</i>	Shortspine spurdog	15, 17, 18
Trachichthyidae (slimehead)	<i>Hoplostethus atlanticus</i>	Orange roughy	2, 4, 10, 15, 16, 17, 18

Spearman correlation index. Of variable pairs with a correlation >0.7 , one variable was removed based on the variables' ease of interpretation. Measures of seascape composition and configuration were highly collinear between buffer sizes. The strength of associations between

biological metrics and the metrics extracted from the different buffer sizes were identified to identify the appropriate scale of analysis. Metrics extracted from 500 m buffers exhibited stronger correlation with family abundance, and were retained. A total of 18 variables describing environmental structure was used for analysis (Table 3).

2.5. Analysis

All modelling and analysis was conducted in R version 4.0.3.

2.5.1. Assemblage composition with site and depth

To assess whether seamount assemblages differ between depth zones and seamount (geographic location), a PERMANOVA (Permutational Multivariate Analysis of Variance) was conducted on the Bray-Curtis dissimilarity matrix over 999 permutations. The time-corrected abundance data matrix was fourth-root transformed before analysis to reduce the effect of dominant outliers such as abundant schooling fish (i.e. Polyprionidae, Oreosomatidae). Pairwise comparisons were performed post-hoc using the R package *pairwiseAdonis* (Martinez Arbizu, 2020). Additionally, indicator species analysis (Cáceres and Legendre, 2009) determined whether families exhibited significant associations with sites or depth classes. A nMDS (non-metric multidimensional scaling) plot was used to visualise compositional similarities in fish assemblages between transects.

2.5.2. Assemblage-level responses to seascape heterogeneity

Regression trees and random forests (Breiman, 2001) tested associations of assemblage characteristics (abundance, richness and diversity) with predictor variables. These approaches were chosen for their ability to explore potentially complex non-linear fish-seascape associations, including interactions between predictors (Knudby et al., 2010).

Binary regression trees, implemented through R package *rpart* v4.1.16 (Therneau and Atkinson, 2019) visualised the main structure of regression relationships. Trees for abundance, richness and diversity were fitted using 10-fold cross-validation. Tree size (number of splits) was controlled by optimising the complexity parameter (cp) value to maximise cross-validation accuracy with high R squared values.

Random forests, implemented using R package *RandomForestSRC* v3.1.1 (Ishwaran and Kogalur, 2021), assessed the importance and influence of predictor variables on assemblage characteristics. Models were implemented by bootstrapping without replacement and tuned to minimise the cross-validated prediction error (out-of-bag or OOB error). Tuning involved setting the optimum number of variables selected as candidates for splitting node (mtry) and the minimum size of the terminal node. The OOB data was used for a performance assessment using variance explained (R Squared) and the error rate. Confidence intervals evaluating the change in Mean Squared Error over 200 random permutations assessed variable importance, with significance tested at the $\alpha = 0.05$ level (Breiman, 2001). Partial dependence plots subsequently showed the response of assemblage characteristics to significant predictor variables. Variable interactions were tested using maximal subtree analysis (Ishwaran and Kogalur, 2007).

2.5.3. Fish family responses to heterogeneity

As individual fish families may have specific habitat associations (Moore et al., 2016), multivariate alternatives of regression trees and random forests were applied to test whether families are associated with particular combinations of environmental variables.

Multivariate regression trees (MRTs) (De'ath, 2002), implemented using R package *mvpart* v1.6–2 (De'ath, 2014), explored, explained and predicted relationships between multispecies data and environmental characteristics. They were constructed using 10-fold cross-validation, and the optimum tree size was chosen using the lowest value for the relative cross-validated error.

Multivariate random forests (MRFs) (Segal and Xiao, 2011), implemented using the package *RandomForestSRC* v3.1.1 (Ishwaran and

Table 3

Measures of environmental structure explored for use in models, including abbreviated names used in the analysis where applicable. The 18 variables retained are indicated.

Type	Metric	Description	Scales	Retained?
Descriptive	Site	Seamount name		Yes
	Depth	Continuous (m)	Transect	Yes
	Distance to ridge feature (RidgeDist)	The closer to a ridge the higher the likelihood of high productivity	average	Yes
Oceanography	Temperature	Temperature (°C)	Transect	No, highly collinear with depth
	Salinity	Salinity (g/kg)	average	No, highly collinear with site
	Pressure	Pressure (bar)		No, highly collinear with depth
Terrain structure	Slope	Slope angle (degrees)	Transect	Yes
	Slope of slope	The change of the slope gradient, acts as measure of terrain variability	average	No, highly collinear with VRM
	Vector Ruggedness Measure (VRM)	Measure of terrain complexity		Yes
	Terrain Ruggedness Index (TRI)	Local variation in seabed terrain, associated with changes in habitat complexity		No, highly collinear with slope and proportion of sloping habitat
	Curvature	The orientation and relative elevation of the surface		No, highly collinear with TPI
	Topographic Position Index (TPI)	Measure of curvature – indicates relative elevation		Yes
	Aspect (eastness and northness)	Measures of terrain orientation		Yes
Composition	Substratum type	Cold water coral, mesophotic reef, coral rubble, gravel, boulders, cobbles, bedrock and sediment veneer, mud	Transect average	Yes
	Proportion of habitat - summit (Summit_prop), slope, SE flanks (SE_prop), NW flanks (NW_prop), ridges (Ridge_prop)	Proportion of each patch type in surrounding environment	Buffers (250m, 500m, 1000m)	Yes x4 (500m buffer) – apart from proportion of sloping habitat (highly collinear with slope and TRI)
	Mean patch area (PatchArea)	Average size of patches in surrounding environment		Yes (500m buffer)
	Patch abundance and richness	Measures of the number of patches present and the number of different types		No, highly collinear with Shannon evenness and diversity, patch area, landscape shape index, interspersions and juxtaposition and division index
	Shannon Diversity in seascape structure	Diversity metrics incorporating the number of patch types and their relative abundance		No, highly collinear with Shannon evenness, landscape shape index and division index
Configuration	Shannon Evenness in seascape structure			No, highly collinear with Shannon diversity, landscape shape index and division index
	Contagion	Extent to which patch types are aggregated or clumped. Higher values indicate increased aggregation.	Buffers (250m, 500m, 1000m)	Yes (500m buffer)
	Mean Shape Index (PatchShape)	Quantifies average shape of patches by using a ratio of patch perimeter to patch surface area: higher values indicate more complex shapes.		Yes (500m buffer)
	Mean Euclidean Nearest Neighbour (ENN)	Measure of average proximity between patches. Lower values indicate more connected seascape.		Yes (500m buffer)
	Interspersion and Juxtaposition index (Interspersion)	Measure of intermixing.		Yes (500m buffer)
	Landscape shape index (LandscapeShape)	Measure of patch disaggregation. Higher values indicate more disaggregation and internal edge.		Yes (500m buffer)
	Division index (Division)	Measure of splitting. Higher values indicate a more subdivided landscape.		No, highly collinear with landscape shape index, Shannon diversity and evenness and patch richness

Kogalur, 2021), extended MRTs with subsampling techniques from random forests. MRFs were constructed using bootstrapping without replacement and tuned the number of candidates for splitting node (mtry) and the minimum size of the terminal node. Model performance was assessed using the mean OOB prediction error (standardised mean squared error) and average OOB variance. Ten model resamples repeating this process were created to assess precision.

For each family, the model resample with the lowest mean squared error was selected to calculate confidence intervals of variable importance over 200 random permutations, similar to traditional random forests. The five most important variables were recorded for each family and partial dependence plots showed fish family responses to these variables. The number of times each variable occurred as one of the five primary drivers was recorded to identify the relative importance of terrain structure, composition, and configuration metrics. Finally, variable interactions were tested using maximal subtree analysis (Ishwaran and Kogalur, 2007).

3. Results

3.1. Assemblage composition with site and depth

The final modelling dataset contained 1053 fish observations including at least 47 unique taxa from 15 commercially important families. The most abundant families were the Polyprionidae (wreckfish, $n = 270$), followed by the Moridae (morid cod, $n = 216$), Oreosomatidae (oreos, $n = 133$), Latridae (trumpeteers, $n = 124$), Squalidae (dogfish sharks, $n = 110$), and Pentacerotidae (armourheads, $n = 81$). The most widespread families, measured as the number of transects in which they were present, were the Moridae ($n = 44$), Scorpaenidae (scorpionfishes, $n = 20$), Sebastidae (rockfishes, $n = 18$) and Oreosomatidae ($n = 16$).

The PERMANOVA revealed significant differences in fish assemblages between depth zones (photoc, twilight and bathyal), sites, and interaction effects between site and depth, with the majority of variance attributed to site effects (40%) (Table C1 in Appendix C). Pairwise comparisons (Table C2) showed that assemblages differed significantly

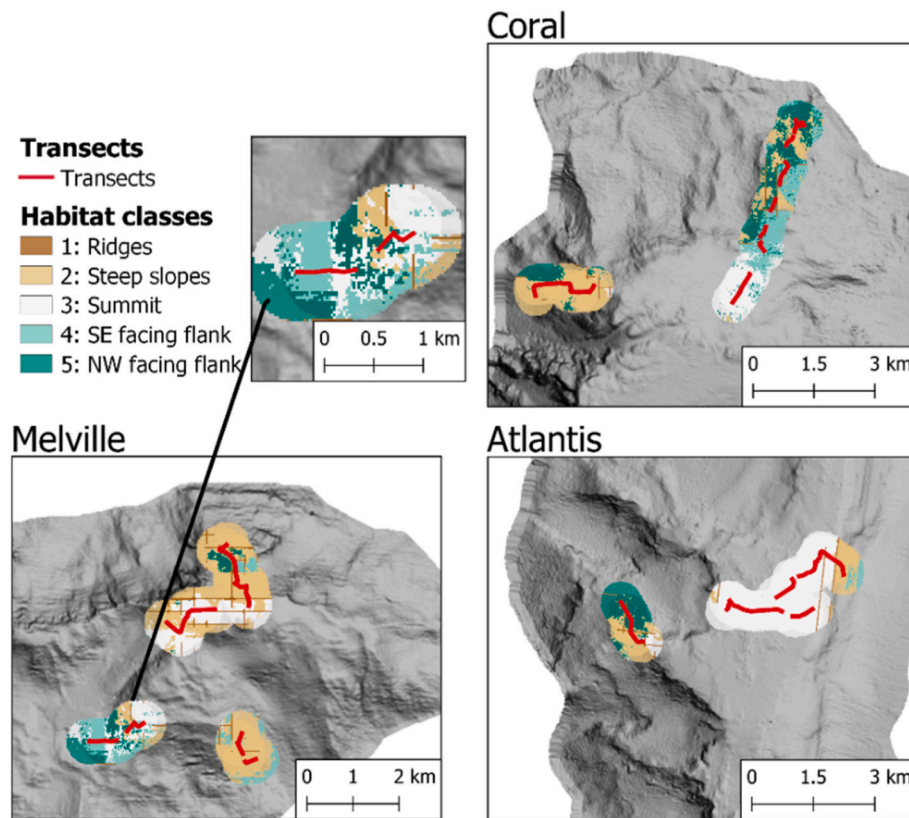


Fig. 2. Spatial visualisation of environmental data extraction. 500m buffers were created around the 250m transects (red lines) and used to quantify seascape composition and configuration using the occurrence and spatial distribution of habitat types (top left). Remaining panels show 500m habitat types in buffers and 250m transects plotted on hillshade maps of Coral, Melville and Atlantis.

between all sites ($p < 0.05$), with Coral Seamount most different from other sites. Further, pairwise comparisons between depth zones (Table C3) showed that assemblages differed significantly ($p < 0.05$) between the photic and bathyal zone and between the photic and twilight zone (defined in Table 4), but not between the twilight and bathyal zone. As photic transects were only found at Melville, the PERMANOVA was also run excluding these four transects. Site and depth class were still significant influences on assemblage characteristics (Table C4), but the importance of site effects was decreased (28.8%).

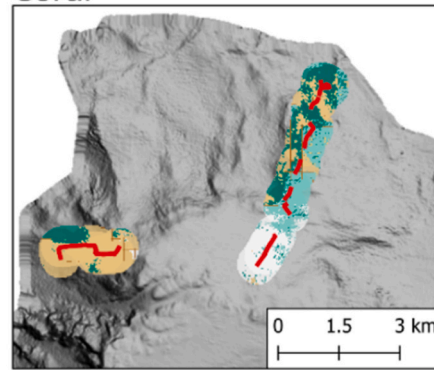
Indicator species showed that the majority of families (10 out of 15) in the modelling dataset were significantly ($p < 0.05$) associated with a site and/or a depth zone (Table 4). These findings were apparent in the nMDS (Fig. 3), which showed that fish abundance was driven by site and depth as well as family associations.

Table 4

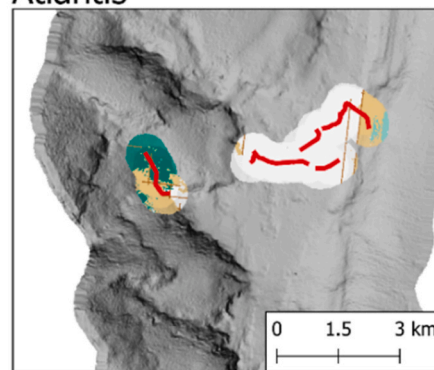
Associations of family occurrence with site and depth zone. Bold font and star indicate significant association.

Site	Families
Coral	Moridae*
Melville	Carangidae* , Etmopteridae, Latridae* , Polyprionidae* , Scorpaenidae* , Sebastidae*
Atlantis	Berycidae* , Centrolophidae, Gempylidae, Hexanchidae, Oreosomatidae* , Pentacerotidae* , Squalidae* , Trachichthyidae
Depth Range	Families
Photic zone (0–200m)	Carangidae* , Latridae* , Polyprionidae* , Scorpaenidae* , Sebastidae*
Twilight zone (200m–1000m)	Berycidae, Centrolophidae, Gempylidae, Pentacerotidae, Scorpaenidae, Sebastidae, Squalidae
Bathyal zone (>1000m)	Etmopteridae, Hexanchidae, Moridae, Oreosomatidae, Trachichthyidae*

Coral



Atlantis



3.2. Assemblage-level responses to heterogeneity

Regression trees (Fig. 4) explained 87% of variation in abundance and 77% of variation for both richness and diversity, but had cross-validated errors of over 50%. This indicates high explanatory power, but limited predictive power. The influence of the main splitting parameters was identified by random forests (Fig. 5), which explained 40.73% of variation in abundance, 42.3% of variation in richness and 52.75% of variation in diversity, but equally had higher error rates. The main driving variables of assemblage characteristics are depth, site, the proportion of summit and the proportion of ridge in surrounding buffers, patch shape and landscape shape.

Fish abundance (Fig. 4a) is strongly dependent on depth, with shallower areas (>400m) characterised by highest abundances. In the twilight and bathyal zones, more complex patch shapes support higher abundance. For simpler patch shapes substrate characteristics are important, and patches with gravel, rubble or cold-water coral host higher abundances than patches with boulders and sediment veneer or mud. Random Forests (Fig. 5a and b) confirmed a strong dependency of abundance on depth and a positive association with complex patch shapes and disaggregated seascapes. Some evidence of variable interactions were observed (Fig. D1 in Appendix D) between Depth and Patch Shape.

Family richness (Fig. 4b) is driven by site, and transects surveyed at Coral host lower richness than Atlantis and Melville. At Atlantis and Melville, areas with higher proportions of summit, high structural complexity and complex patch shape support highest richness. For transects with a lower proportion of summit, the proportion of ridge habitat in surrounding buffers positively influences richness. Random Forests (Fig. 5c and d) confirmed lowest richness at Coral, and positive associations with an increased proportion of summit and ridge habitat

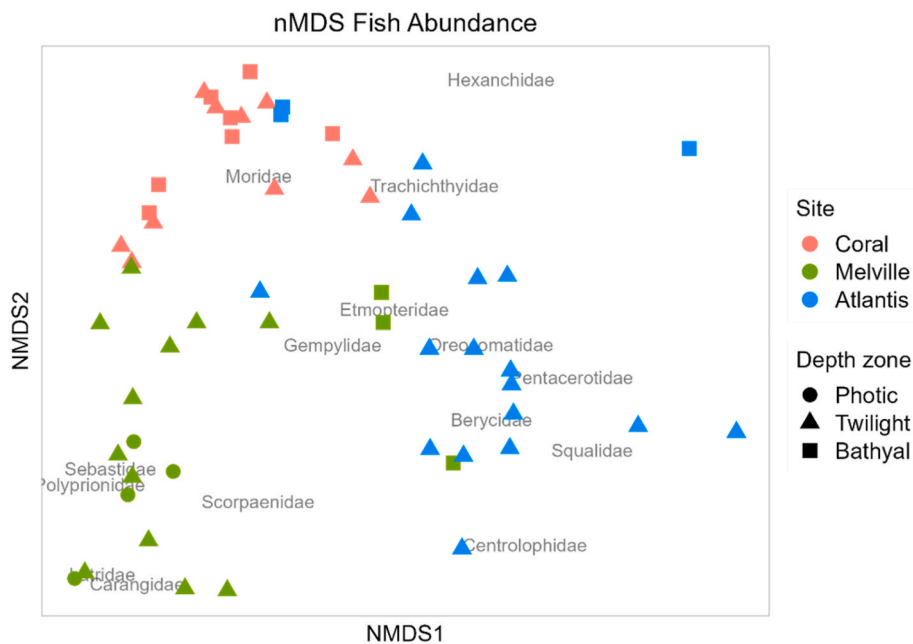


Fig. 3. nMDS (stress = 0.08) conducted on standardised fish abundance data confirming site- and depth driven separation of assemblages. Symbol colours denote the seamount, and symbol shapes denote the depth zone (photic: <200m, twilight: 200m–1000m, bathyal: >1000m).

and complex patch shapes. They additionally showed an effect of depth, with higher family richness in shallower transects. There was no evidence of interactions between variables included in the model (Fig. D2), apart from weak ties between Site and the proportion of summit.

Shannon diversity in assemblage structure (Fig. 4c) is equally site-dependent, with higher diversity in the transects surveyed at Atlantis and Melville than at Coral. At Atlantis and Melville, more aggregated landscapes with high structural complexity host highest diversity, followed by more diverse landscapes with small patch areas. At Coral, diversity is higher in more sloping areas. Random forests (Fig. 5e and f) revealed an additional effect of the proportion of summit habitat and a positive, but not significant, association with the proportion of ridge habitat. However, resampled variable importance confidence intervals revealed that only site, proportion of summit and landscape shape were significant ($p < 0.05$) drivers. No variable interactions were observed (Fig. D3), apart from weak ties between site and landscape shape (simpler landscape shapes at Atlantis).

3.3. Family-specific responses to heterogeneity

Multivariate regression trees on untransformed family abundance data (Fig. 6) explained 74% of variation, but, like the single regression trees, had low predictive power. Primary splits (depth, patch shape, proportion of ridge and summit and site) matched those obtained for the univariate variables.

Multivariate random forests modelled the effects of measures of heterogeneity on individual families. Across families, MRFs explained an average 34% of variance, but had low predictive power indicating results do not readily generalise. Model performance (Fig. 7) varied between families and depth zones. Overall, model performance was best (higher variance explained, lower error rate) for photic and twilight families occurring in higher abundances (Latridae, Carangidae, Polyprionidae, Pentacerotidae, Squalidae). Most families for which reduced model performance was observed (Etmopteridae, Centrolophidae, Hexanchidae, Gempylidae) were bathyal and had a lower number of observations in the modelling dataset. As fish occurrence is heavily influenced by heterogeneity of oceanographic parameters in addition to terrain parameters, family models with variance explained of over 30% were deemed acceptable (Berycidae, Carangidae, Latridae, Moridae,

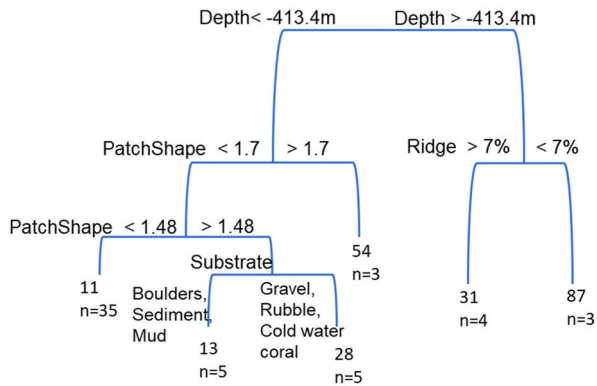
Oreosomatidae, Pentacerotidae, Polyprionidae, Sebastidae, Squalidae) following similar values in shallow reef studies (Costa et al., 2014; Pittman et al., 2009).

Associations with seascape composition, configuration and terrain structure were assessed per depth class. Families associated with the photic zone were Carangidae, Latridae, Polyprionidae, Scorpaenidae and Sebastidae (example of plots are given for Sebastidae in Fig. 8). Variable importance plots for these families (Fig. E1 in Appendix E) revealed a combined effect of site and depth. Melville Bank was the only site where the photic zone was surveyed as it was the shallowest seamount summit. Habitat composition also affected abundance, with the proportion of slope and ridge habitat positively driving abundance of Polyprionidae, Carangidae and Scorpaenidae, but Sebastidae showed negative associations with ridge habitat. Some families also showed weak associations with the proportion of summit (Latridae, Polyprionidae) or SE flanks (Latridae, Carangidae). For Latridae, substratum type (mesophotic reef) was important. Of the configuration metrics, patch shape was important for Sebastidae (Fig. 8), indicating a role of spatially simple patch types.

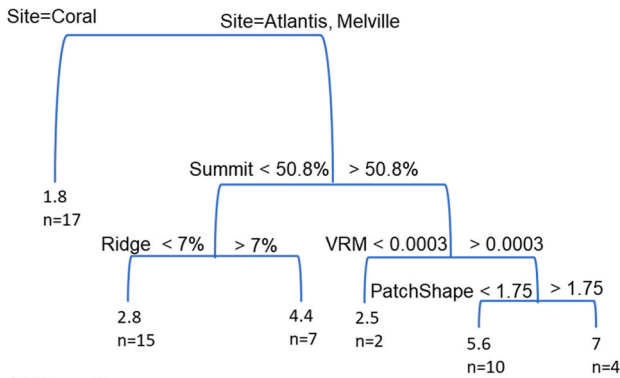
Families associated with the twilight zone were Pentacerotidae, Squalidae, Berycidae, Gempylidae and Centrolophidae (Fig. E2). Most of these families were affiliated with transects at Atlantis Bank and showed a positive association with the summit. There was a strong role for configuration metrics with abundance increasing with increased patch area (Pentacerotidae, Centrolophidae), complex patch shapes (Pentacerotidae, Squalidae) and aggregated landscape characteristics (Pentacerotidae, Squalidae, Berycidae, Centrolophidae). Some families (Pentacerotidae, Gempylidae) also appeared dependent on complex patch shapes.

Families associated with the bathyal zone were Etmopteridae, Hexanchidae, Moridae, Oreosomatidae and Trachichthyidae (Fig. E3). Only models for Oreosomatidae and Moridae had reliable performance. Across families there was a dependence on site and depth, with families at Atlantis Bank (Trachichthyidae, Oreosomatidae, Hexanchidae) associated with increased proportions of ridge habitat and/or reduced summit proportion. Effects of configuration metrics were mixed, but small patch areas (Oreosomatidae, Etmopteridae), increased contagion (Moridae, Etmopteridae), landscape clumping (Moridae, Hexanchidae) and complex patch shapes (Hexanchidae, Oreosomatidae) were

a) Abundance



b) Richness



c) Diversity

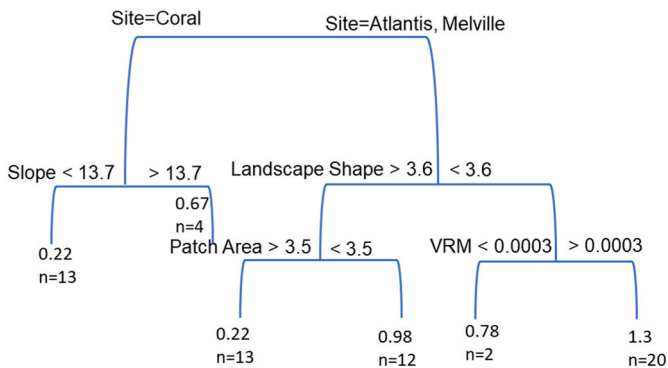


Fig. 4. Regression trees for a) Abundance, b) Richness and c) Shannon Diversity. Splits indicate important breaks in variable values, whereas end nodes indicate average abundance, richness and diversity values and the number of observations in that split.

influential.

Summing the times that each variable appeared in the main five predictor variables of each family (Fig. 9), key variables were site and depth, followed by configuration measures (landscape shape, patch shape and patch area), and composition measures (proportion of summit, ridge and flank). The importance of terrain metrics (VRM, TPI, northness and eastness) was reduced. Limited predictor interactions were found in the maximal subtree analysis (Fig. E4) for Depth, Landscape Shape and Patch Shape.

4. Discussion

4.1. Fish assemblages with site and depth

Assemblage composition differed between the transects surveyed on each seamount. Fish abundance, diversity and richness was lowest in the transects surveyed at Coral Seamount and few of the families found at other sites were found here. Melville Bank was the shallowest seamount surveyed, with a summit hosting a high abundance of predatory fish including amberjacks, wreck fishes and trumpeteers. The summit of Atlantis Bank was deepest, but transects surveyed at this site hosted high fish diversity, richness and abundance, including oreos, pelagic armourhead and orange roughy.

These differences in faunal composition may be explained by the highly dynamic and variable oceanographic conditions created by the Agulhas Return Current, the Subtropical Front, and the Sub-Antarctic Front (Rogers et al., 2017) influencing the geographic distribution of surveyed fish families. Oceanographic conditions including parameters like temperature, salinity, oxygen, water mass, and current strength at Coral Seamount, which are highly correlated with depth, were strongly different from the other sites. It was the only seamount located in cooler, more saline and oxygenated sub-Antarctic waters close to the Sub-Antarctic Front and south of the Agulhas Return Current and Sub-tropical Front (Pollard and Read, 2017). Melville Bank is located just north of the Subtropical front and Agulhas Return Current, and therefore exposed to dynamic conditions that can vary between Subtropical and Sub-Antarctic. Additionally, its summit extends into the photic zone and provides unusual and isolated shallow water habitat compared to the surrounding ocean, explaining the occurrence of mesophotic coral ecosystems and the high abundance of fish also found in shallow reef environments. Atlantis is located further northeast in the Subtropical Anticyclonic gyre. It experiences weak eddy currents and semi-diurnal upwelling creating varying productivity patterns (Read and Pollard, 2017) likely important for the high diversity of found fish communities. It is notable that observations on the biodiversity of pelagic species across the studied section of the Southwest Indian Ridge showed similar division of communities attributed to water mass variation from bacterioplankton to micronekton (midwater shrimps and gnathophausiids, cephalopods) and nekton (Djurhuus et al., 2017; Laptikhovskiy et al., 2017; Letessier et al., 2017). Knowing that survey depth is a major driver of deep-sea biodiversity and correlated with parameters as temperature and pressure (Table 3), the varying average site survey depth may further emphasise some of the broad-scale biological patterns found.

4.2. Responses to seascape heterogeneity

Fish-habitat associations were mainly driven by depth and site, but seascape metrics (composition and configuration) proved useful to describe habitat associations at studied locations in more detail.

4.2.1. Seascape composition

Seascape composition, the type and abundance of different broad-scale bathymetric habitat types (summit, ridge, slope, flanks), strongly influenced fish assemblages.

The proportion of summit habitat was particularly important. At Coral Seamount and Melville Bank, higher proportions of summit habitat were associated with higher richness and diversity - noting the summit of Coral Seamount was not as extensively surveyed as those of Melville and Atlantis- and at Atlantis the abundance of multiple families (Berycidae, Pentacerotidae, Squalidae) was dependent on the proportion of summit habitat. In other geographic areas, seamount summits have also been shown to host higher biological abundance, richness and diversity than other parts of the seamounts (González-Irusta et al., 2021; Porteiro et al., 2013). Processes operating on seamount summits are different from those on flanks, for example the exposure to topographically induced physical circulation. Although no evidence of Taylor

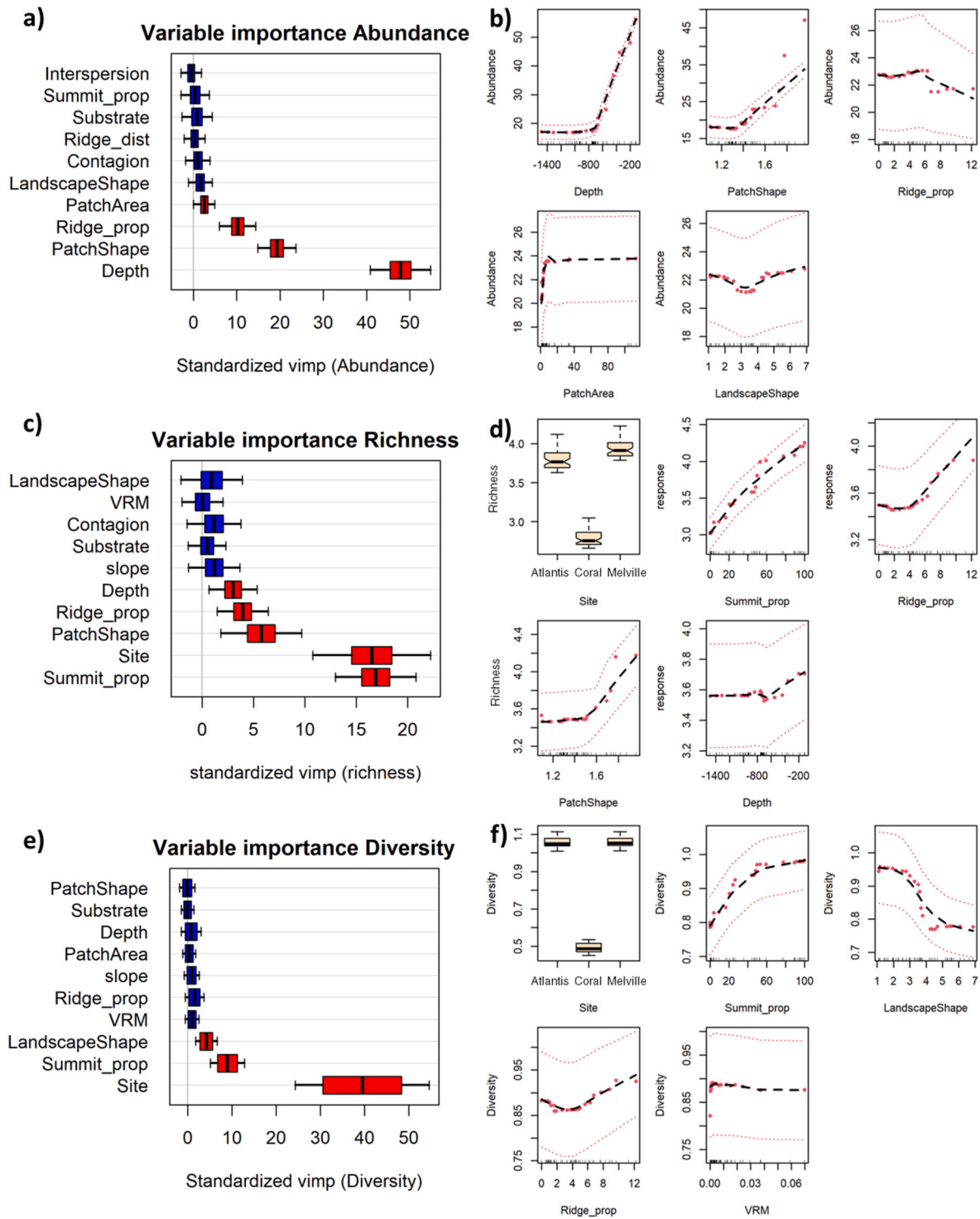


Fig. 5. Importance and effect of seascape heterogeneity on abundance (a,b), richness (c,d) and diversity (e,f). Left-hand panels indicate variable importance (vimp) of the 10 main variables obtained through resampling, with red colours indicating a significant ($p < 0.05$) effect. Right-hand plots show partial responses to the main 5 (including significant) parameters, where black dashed lines and red points indicate the partial values, and the dashed red lines indicate an error bar of two standard errors.

columns was found at these seamounts in a 2009 study, internal tide formation, tidal driven up and down welling and mixing was observed around seamount crests (Read and Pollard, 2017). These may influence nutrient and prey availability (Clark et al., 2011; White et al., 2007) potentially resulting in community differences as we found here.

The second important habitat type was the proportion of ridge features. Local topographic elevations such as ridges and crests have been

demonstrated to positively benefit fish biodiversity (Leitner et al., 2021), but our results only partly matched those observations. A higher proportion of ridge features was positively correlated with richness, but did not significantly affect abundance or diversity. However, ridges were a key determinant of the abundance of several individual families (Carangidae, Oreosomatidae, Scorpaenidae, Trachichthyidae). The partial effect of ridge habitat may be related to the fact that, as for

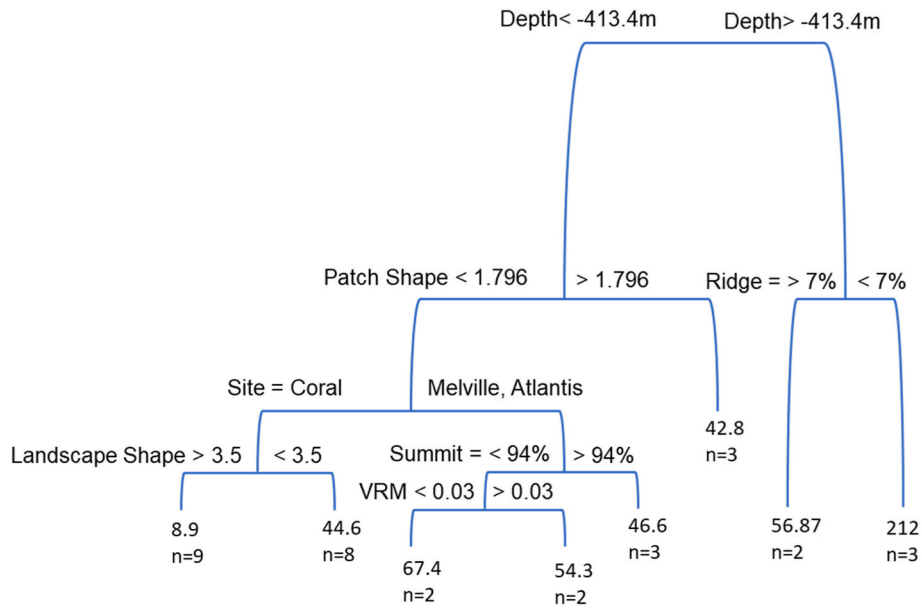


Fig. 6. Multivariate regression tree of fish family abundance. Splits indicate important breaks in variable values. End nodes indicate average abundance and the number of observations in that grouping.

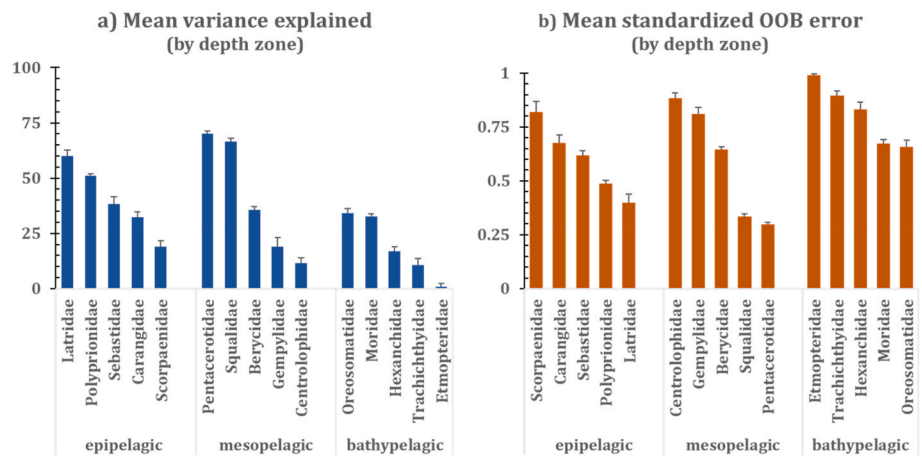


Fig. 7. Model performance of multivariate random forests measured by variance explained (a) and standardized out-of-bag error (b). Error bars represent standard deviations over 10 model resamples.

summit habitat, ridges did not receive equal survey effort across sites. Additionally, the broad spatial resolution at which habitat maps were produced may not be appropriate for all surveyed assemblages (Kendall et al., 2011).

Despite the importance of steeply sloping habitat for biodiversity through possible current amplification and effects on prey availability (see for example Leitner et al., 2021, in a shallower survey at 300–400m), the analysis did not reveal a clear effect of these features on demersal fish assemblages, apart from at Coral where steeper slope gradients were correlated with higher diversity. Similar to slope, the proportion of flank habitat did not appear to influence assemblage characteristics. When flank habitat occurred in the top five driving variables for families (Gempylidae, Carangidae, Latridae, Hexanchidae), abundance had a negative association with the proportion of flank habitat suggesting that flanks hosted lower abundances of fish. However, flank habitat was only extensively surveyed at Coral, where overall fish abundance, diversity and richness were lower than at the other sites. A more extensive survey of flank habitat at Melville Bank or Atlantis Bank might support a more reliable assessment of the importance of flank habitat. Assemblages on flanks may show high specificity and

diversity because of taxa only found at deeper depths (González-Irusta et al., 2021). Flank habitats are also more prone to trawling than other parts of the seamounts, which might further influence fish assemblages. Video observations confirmed historical or ongoing fishing activity at all three seamounts (Rogers and Taylor, 2012; Woodall et al., 2015).

It is important to recognise that habitat maps were created without ground-truthing benthic assemblage occurrence or substratum types and instead are based on geomorphological characteristics of the terrain. Although substratum types were captured as separate predictive variables in the analyses, incorporating ground-truthing in the production of habitat maps may provide a more detailed view on the effect of habitat composition and configuration on demersal fish.

4.2.2. Seascapes configuration

Incorporating configuration metrics helped assess the effects of patch area, patch shape and seascape aggregation on fish assemblages and individual families.

Larger patch sizes were expected to positively influence abundance. On land, many species have minimum patch size requirements (Godron, 1981), which also appear important for demersal fish species (Anderson

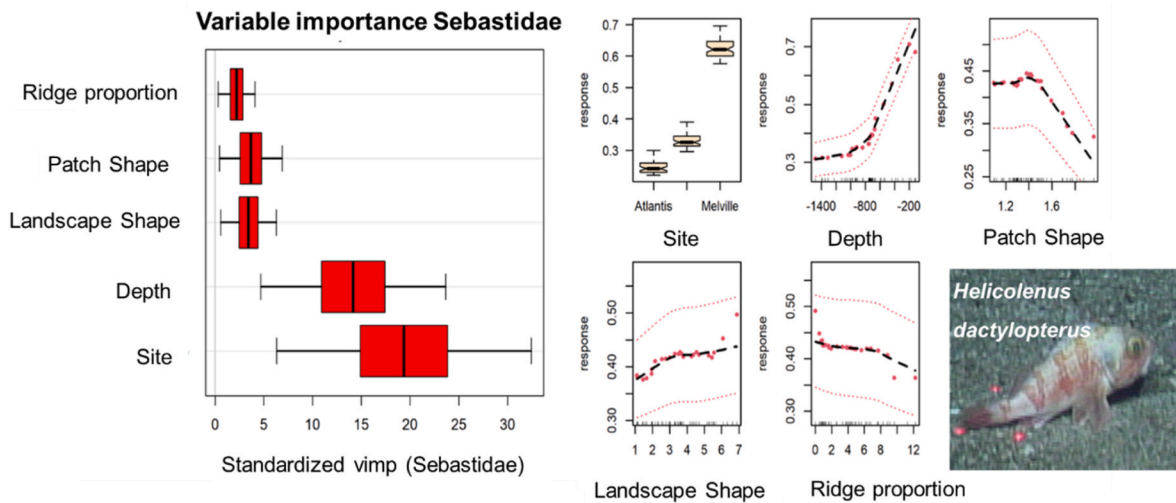


Fig. 8. Example output of variable importance (left panel) and effect of predictor variables (right panel) on the abundance of Sebastidae. Outputs for other families can be found in Appendix E.

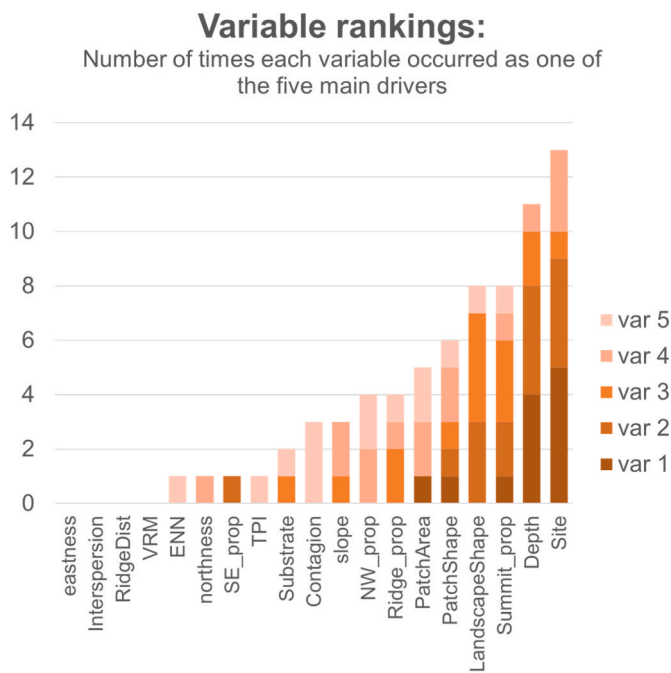


Fig. 9. Variable rankings (number of times each variable occurred as one of the five main drivers) obtained from multivariate regression trees.

et al., 2009). A positive relationship between patch area and abundance was found for some summit-associated aggregating fish families at Atlantis (Pentacerothidae, Centrolophidae). These larger patch areas indicate increased availability of spatially continuous summit habitat, and support larger feeding aggregations. In contrast, assemblage diversity and some bottom-dwelling twilight zone and bathyal families (Etmopteridae, Gempylidae) relate to small patch areas in more aggregated seascapes. These results fit the perspective of niche theory, which predicts more diverse and connected seabed environments support higher biological diversity (Harris, 2012; Ismail et al., 2018). This might be relevant for bottom-dwelling families that utilise their local environment for different activities (e.g. feeding, resting).

More complex patch shapes were expected to negatively influence fish assemblage characteristics due to edge effects: the abrupt changes in physical structure at the transition zones between patch types. Indeed,

away from the summit, rockfish and scorpionfish (Sebastidae, Scorpaenidae) were associated with simple patch shapes. These solitary fish are bottom-dwelling and have low activity levels, and therefore might depend on contiguous environmental conditions. In contrast, complex patch shapes positively influenced abundance and richness of several other families (e.g. Pentacerothidae, Oreosomatidae). This matches literature from coastal habitats, suggesting that fish biodiversity may show positive responses to edges (Boström et al., 2011). In seamount environments, complex patch shapes may, for example, be linked to the presence of complex shaped crest and ridge features. These complex features may be important demersal fish by protecting from predation, or enhancing foraging opportunities by concentrating food particles (Genin and Dower, 2008; Read and Pollard, 2017). Additionally, more complex patch shapes may create a more heterogeneous environment, that following niche theory, would be positively related to richness and diversity.

Aggregated landscape characteristics were expected to positively influence abundance because of structural connectivity provided by spatial continuity (Grober-Dunsmore et al., 2007). Indeed, spatial continuity, measured by the landscape shape index, was the main configuration metric influencing fish families and overall abundance and diversity. It is important to reiterate that the landscape shape index was highly collinear with landscape diversity, evenness, patch abundance and richness, and splitting index, and therefore also functions as a proxy of these metrics. The effect of landscape shape index varied between families, which also explains the non-linear relationship of landscape shape to overall fish abundance. Spatially contiguous seascapes appeared mainly important for the twilight zone associated fish families found at Atlantis (including Pentacerothidae, Squalidae, Berycidae, Centrolophidae). These families dwell over summits for feeding and/or hunting, and increased availability of spatially contiguous summit habitat might therefore support larger abundances of these families. In contrast, bottom-dwelling Sebastidae appeared correlated to higher values of the landscape shape index. These indicate increased patch richness, and bottom-dwelling families might benefit from multiple patch types in their direct surroundings to support their low activity levels. Similarly, higher values of contagion and nearest neighbour index were important for bottom-dwelling Moridae at Coral Seamount, that use multiple habitats and may benefit from increased proximity of these habitats.

Interpreting fish-habitat associations using seascape metrics requires consideration of scale-dependent responses. Broad-scale habitat maps were deemed appropriate as many of the fish families targeted for

fishing are highly mobile and use their environment over extended areas (Shotton, 2006). However, producing habitat maps at scales ecologically relevant for the fish families might further improve knowledge gained. For example, “summit” was classified as one feature, but within the broad-scale summit feature there can be features such as boulders that might be ecologically relevant for some species (Bo et al., 2021). Here, we did not account for such finer scale interactions, as the resolution of the input data did not allow to resolve such detail. However, “substrate type” was incorporated at a finer scale (average of photo frames within transects) as fine-scale substrate features have been shown to strongly influence deep-water fish communities (Quattrini et al., 2012; Ross and Quattrini, 2007) but was not a major predictive variable.

4.3. Final considerations

4.3.1. Importance

Conservation and fishery management of remote deep-sea ecosystems such as seamounts rely partly on proxies of habitat suitability to estimate ecologically important areas (Clark et al., 2012; Moore et al., 2016a). This study highlighted that the regional environment, predominantly seamount site and depth, determines the boundary conditions for more local effects of seascape composition, configuration and terrain structure on fish assemblages. A previous hierarchical biophysical classification of seamounts incorporating summit depth in the southern Indian Ocean already assigned Coral, Melville and Atlantis belonging to different biogeographic classes along the SWIR (Clark et al., 2011); see also Sutton et al. (2017) for the twilight zone). This is consistent with the findings of this study that commercial assemblages differed significantly between the studied seamounts and depth zones. These findings have implications for establishing representative benthic or marine protected areas in this region.

At the scale of individual seamounts, current frameworks in seamount management already recognise the importance of particular broad-scale habitats – seascape composition-such as the summit (Clark and Dunn, 2012). This study indicates the spatial characteristics and configuration of these habitats, in particular their shape and spatial continuity, are equally ecologically important. Considering spatial configuration could be valuable to achieve a representative network of protected areas incorporating seamounts varying in spatial characteristics of morphology (Clark et al., 2011).

Methodologically, this study also demonstrated that patch-based metrics provided a strategy to test new hypotheses related to species diversity in the deep sea, although this study did not provide conclusive results. Additionally, patch-based metrics had larger predictive power than continuous terrain metrics commonly used in developing proxies for deep-water biodiversity. The geomorphological habitat map from which composition and configuration metrics were derived in this study, was however constructed based on geomorphological characteristics, which incorporate terrain structure.

4.3.2. Study limitations

Although seascape composition, configuration and terrain structure proved useful to disentangle fish-habitat associations with different sets of environmental characteristics, they were derived from a limited number of observations and highly site-specific. This was indicated by the differences in performance of random forests and regression trees. Whereas both exhibited high explanatory power, predictive power was limited, limiting universal conclusions on the effect of seascape composition and configuration on seamount-associated fish. Additionally, there are biases associated with all fish sampling methods, including video transects conducted with ROVs (Sward et al., 2019). Specifically, conducting video transects using an ROV may result in avoidance or fleeing behaviour of fish (Stoner et al., 2008), and underwater vehicles could be less successful at recording fish species on steep slopes and hiding within crevices (Osuka et al., 2021), compromising the ability to record all individuals originally present at a

location.

Additionally, the lack of extensive surveys on all seamount habitats in this study limited the ability to identify assemblages and their drivers on seamount flanks. We envision future studies can expand on this knowledge and therefore recommend further adoption of seascape metrics. Further, finer-scale data, both in taxonomic resolution and spatial resolution might provide additional insight in characteristics important for individual species targeted by fisheries. Indeed, finer scale taxonomic data may be more accurate for deep-sea habitat suitability modelling (Bowden et al., 2021) and fish-habitat associations are dependent on spatial scale and environmental context (Anderson et al., 2009).

5. Conclusion

As few seamount ecosystems have been studied in detail, there remains a need to increase our understanding on how seamount habitat heterogeneity supports biology and ecology (Rogers, 2018). Using seascape ecology metrics rarely used in deep-water environments to study fish-habitat associations at SWIR seamounts, this study revealed:

- 1) Fish assemblages were primarily driven by depth and site, and seascape composition, configuration and terrain structure explained associations within sites and depth classes
- 2) Demersal fish responded to unique combinations of seascape composition, configuration and terrain structure depending on their traits, with some overlap between families found in the same sites and depth zones.
- 3) Broad-scale habitat features, specifically the summit and the proportion of ridge habitat, and their spatial continuity and shape, were main drivers of assemblage characteristics
- 4) Seascape composition and configuration metrics had higher explanatory power than commonly used terrain structure metrics.

Based on these findings, we recommend that future studies looking at habitat suitability over the full spectrum of seamount morphology continue to consider the spatial composition and configuration of seascapes.

Author contributions

DS- conceptualization, methodology, formal analysis, writing – original draft, writing-review & editing. TM: formal analysis (fish ID). ADR: Funding acquisition, field data collection, formal analysis (fish ID), writing-review & editing. VH, SP, LW: supervision, writing-review & editing. MT: Field data collection, writing-review & editing.

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.

Data availability

Biological dataset has been made available in the Supplementary Material. Environmental data is available upon request

Acknowledgements

This manuscript is part of the PhD research of DS. DS is funded by Natural Environment Research Council (NERC) Grant No NE/L002612/1, Nekton and an IMarEST Stanley Gray Fellowship. VH is funded by NERC Grant No NE/R000123/1 (ACCORD) and Grant No NE/R015953/1 (CLASS), and enjoyed a Fellowship from the Hanse-Wissenschaftskolleg Institute for Advanced Study during the final

preparation stages of this manuscript. LW is funded by Nekton. This is Nekton contribution 31. ADR acknowledges funding of REV Ocean and Nekton during the completion of this paper. MT was partially funded by Darwin Plus grant DPLUS089.

Many thanks to the captain, crew, technicians and scientists onboard RRS James Cook JC066 for data collection. The cruise was supported by NERC Grant NE/F005504/1 (“Benthic biodiversity of seamounts in the southwest Indian Ocean”), Lead PI AD Rogers, and was part of the IUCN Seamounts Project (FFEM-SWIO-P00917), funded by the GEF supported by UNDP. The funders had no roles in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2022.103921>.

References

- Anderson, T.J., Syms, C., Roberts, D.A., Howard, D.F., 2009. Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. *J. Exp. Mar. Biol. Ecol.* 379, 34–42. <https://doi.org/10.1016/j.jembe.2009.07.033>.
- 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: *Cold-Water Corals and Ecosystems*. Springer-Verlag, Berlin/Heidelberg, pp. 761–769. https://doi.org/10.1007/3-540-27673-4_40.
- Bo, M., Coppari, M., Betti, F., Enrichetti, F., Bertolino, M., Massa, F., Bava, S., Gay, G., Cattaneo-Vietti, R., Bavestrello, G., 2021. The high biodiversity and vulnerability of two Mediterranean bathyal seamounts support the need for creating offshore protected areas. *Aquat. Conserv.* 31, 543–566. <https://doi.org/10.1002/aqc.3456>.
- Borland, H.P., Gilby, B.L., Henderson, C.J., Leon, J.X., Schlacher, T.A., Connolly, R.M., Pittman, S.J., Sheaves, M., Olds, A.D., 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. *Fish. Fish.* 22, 707–734. <https://doi.org/10.1111/faf.12546>.
- Boström, C., Pittman, S., Simenstad, C., Kneib, R., 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Mar. Ecol. Prog. Ser.* 427, 191–217. <https://doi.org/10.3354/meps09051>.
- Bowden, D.A., Anderson, O.F., Rowden, A.A., Stephenson, F., Clark, M.R., 2021. Assessing habitat suitability models for the deep sea: is our ability to predict the distributions of seafloor fauna improving? *Front. Mar. Sci.* 8 <https://doi.org/10.3389/fmars.2021.632389>.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32. <https://doi.org/10.1023/A:1010933404324>.
- Cáceres, M. De, Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>.
- Clark, M.R., 2009. Deep sea seamount fisheries: a review of global status and future prospects. *Lat Am J Aquat Res* 37, 501–512. <https://doi.org/10.3856/vol37-issue3-fulltext-17>.
- Clark, M.R., Dunn, M.R., 2012. Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. *Environ. Conserv.* 39, 204–214. <https://doi.org/10.1017/S0376892912000021>.
- Clark, M.R., Schlacher, T.A., Rowden, A.A., Stocks, K.I., Consalvey, M., 2012. Science priorities for seamounts: research links to conservation and management. *PLoS One* 7, e29232. <https://doi.org/10.1371/journal.pone.0029232>.
- Clark, M.R., Vinnichenko, V.I., Gordon, J.D.M., Beck-Bulat, G.Z., Kukharev, N.N., Kakora, A.F., 2007. Large-scale distant-water trawl fisheries on seamounts. In: *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, Oxford, UK, pp. 361–399. <https://doi.org/10.1002/9780470691953.ch17>.
- Clark, M.R., Watling, L., Rowden, A.A., Guinotte, J.M., Smith, C.R., 2011. A global seamount classification to aid the scientific design of marine protected area networks. *Ocean Coast Manag.* 54, 19–36. <https://doi.org/10.1016/j.ocecoaman.2010.10.006>.
- Costa, B., Taylor, J.C., Kracker, L., Battista, T., Pittman, S., 2014. Mapping reef fish and the seascape: using acoustics and spatial modeling to guide coastal management. *PLoS One* 9, e85555. <https://doi.org/10.1371/journal.pone.0085555>.
- De'ath, G., 2014. mvpart: multivariate partitioning. <https://cran.r-project.org/package=mvpart>.
- De'ath, G., 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83, 1105–1117. [https://doi.org/10.1890/0012-9658\(2002\)083\[1105:MRTANT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2).
- Devine, B.M., Baker, K.D., Edinger, E.N., Fisher, J.A.D., 2020. Habitat associations and assemblage structure of demersal deep-sea fishes on the eastern Flemish Cap and Orphan Seamount. *Deep Sea Res 1 Oceanogr Res Pap* 157, 103210. <https://doi.org/10.1016/j.dsr.2019.103210>.
- Djurhuus, A., Read, J.F., Rogers, A.D., 2017. The spatial distribution of particulate organic carbon and microorganisms on seamounts of the South West Indian Ridge. *Deep Sea Res 2 Top Stud Oceanogr* 136, 73–84. <https://doi.org/10.1016/j.dsr.2015.11.015>.
- Evans, J.S., 2017. spatialEco. R package, version 0.0.1-7. <https://cran.r-project.org/package=spatialEco>.
- Forman, R.T.T., 1995. Some general principles of landscape and regional ecology. *Landscape Ecol.* 10, 133–142. <https://doi.org/10.1007/BF00133027>.
- Froese, R., Pauly, D., 2020. FishBase [WWW Document]. World Wide Web electronic publication. www.fishbase.org.
- Genin, A., Dower, J.F., 2008. Seamount plankton dynamics. *Seamounts: Ecol. Fish. Conserv.* 87–100. <https://doi.org/10.1002/9780470691953.ch5>.
- Godron, M., 1981. Patches and structural components for a landscape ecology. *Bioscience* 31, 733–740. <https://doi.org/10.2307/1308780>.
- Gon, O., Heemstra, P.C., 1990. *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown, RSA.
- González-Irusta, J., De la Torre, A., Punzón, A., Blanco, M., Arronte, J., Bañón, R., Cartes, J., Serrano, A., 2021. Living at the top. Connectivity limitations and summit depth drive fish diversity patterns in an isolated seamount. *Mar. Ecol. Prog. Ser.* 670, 121–137. <https://doi.org/10.3354/meps13766>.
- 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 <https://doi.org/10.3389/fmars.2021.765407>.
- Grober-Dunsmore, R., Frazer, T.K., Lindberg, W.J., Beets, J., 2007. Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs* 26, 201–216. <https://doi.org/10.1007/s00338-006-0180-z>.
- Harris, P.T., 2012. Surrogacy. In: Harris, P.T., Baker, E.K. (Eds.), *Seafloor Geomorphology as Benthic Habitat*. Elsevier, pp. 93–108. <https://doi.org/10.1016/B978-0-12-385140-6.00005-0>.
- Hijmans, R.J., 2017. Raster: Geographic Data Analysis and Modeling. R package version 2.6-7. <https://cran.r-project.org/package=raster>.
- Ishwaran, H., Kogalur, U., 2021. Fast Unified Random Forests for Survival, Regression, and Classification (RF-SRC). <https://cran.r-project.org/web/packages/randomForestSRC/index.html>.
- Ishwaran, H., Kogalur, U.B., 2007. Random survival forests for R. *R. News* 7, 25–31.
- Ismail, K., Huvenne, V., Robert, K., 2018. Quantifying spatial heterogeneity in submarine canyons. *Prog. Oceanogr.* 169, 181–198. <https://doi.org/10.1016/j.pocean.2018.03.006>.
- Kendall, M., Miller, T., Pittman, S., 2011. Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish. *Mar. Ecol. Prog. Ser.* 427, 259–274. <https://doi.org/10.3354/meps08945>.
- Knudby, A., Brenning, A., LeDrew, E., 2010. New approaches to modelling fish-habitat relationships. *Ecol. Model.* 221, 503–511. <https://doi.org/10.1016/j.ecolmodel.2009.11.008>.
- Kvile, K.O., Taranto, G.H., Pitcher, T.J., Morato, T., 2014. A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework. *Biol. Conserv.* 173, 108–120. <https://doi.org/10.1016/j.biocon.2013.10.002>.
- Lapikhovskiy, V., Boersch-Supan, P., Bolstad, K., Kemp, K., Letessier, T., Rogers, A.D., 2017. Cephalopods of the Southwest Indian Ocean Ridge: a hotspot of biological diversity and absence of endemism. *Deep Sea Res 2 Top Stud Oceanogr* 136, 98–107. <https://doi.org/10.1016/j.dsr.2015.07.002>.
- Leitner, A., Friedrich, T., Kelley, C., Travis, S., Partridge, D., Powell, B., Drazen, J., 2021. Biogeophysical influence of large-scale bathymetric habitat types on mesophotic and upper bathyal demersal fish assemblages: a Hawaiian case study. *Mar. Ecol. Prog. Ser.* 659, 219–236. <https://doi.org/10.3354/meps13581>.
- Letessier, T.B., De Grave, S., Boersch-Supan, P.H., Kemp, K.M., Brierley, A.S., Rogers, A.D., 2017. Seamount influences on mid-water shrimps (Decapoda) and gnathophausiids (Lophogastridea) of the South-West Indian Ridge. *Deep Sea Res 2 Top Stud Oceanogr* 136, 85–97. <https://doi.org/10.1016/j.dsr.2015.05.009>.
- Malpas, T., 2017. *Variation in Demersal Community Composition in the Indian Ocean*. University of Oxford.
- Martinez Arbizu, P., 2020. pairwiseAdonis: Pairwise Multilevel Comparison Using Adonis. R package version 0.4. <https://github.com/pmartinezarbizu/pairwiseAdonis>.
- McClain, C.R., Schlacher, T.A., 2015. On some hypotheses of diversity of animal life at great depths on the sea floor. *Mar. Ecol.* 36, 849–872. <https://doi.org/10.1111/maec.12288>.
- McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS V4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.
- Meynecke, J.-O., Lee, S.Y., Duke, N.C., 2008. Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. *Biol. Conserv.* 141, 981–996. <https://doi.org/10.1016/j.biocon.2008.01.018>.
- Moore, C., Drazen, J.C., Radford, B.T., Kelley, C., Newman, S.J., 2016. Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. *Mar. Pol.* 69, 32–41. <https://doi.org/10.1016/j.marpol.2016.03.021>.
- Morato, T., Clark, M.R., 2007. Seamount fishes: ecology and life histories. In: *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, Oxford, UK, pp. 170–188. <https://doi.org/10.1002/9780470691953.ch9>.
- Osuka, K.E., McClean, C., Stewart, B.D., Bett, B.J., Le Bas, T., Howe, J., Abernethy, C., Yahya, S., Obura, D., Samoilys, M., 2021. Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: implications for management and conservation. *Ocean Coast Manag.* 200, 105463. <https://doi.org/10.1016/j.ocecoaman.2020.105463>.
- Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S., 2007. *Seamounts: Ecology, Fisheries & Conservation*. Seamounts: Ecology, Fisheries & Conservation. <https://doi.org/10.1002/9780470691953>.

- Pittman, S., McAlpine, C., Pittman, K., 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. *Mar. Ecol. Prog. Ser.* 283, 233–254. <https://doi.org/10.3354/meps283233>.
- Pittman, S., Yates, K., Bouchet, P., Alvarez-Berastegui, D., Andréfouët, S., Bell, S., Berkström, C., Boström, C., Brown, C., Connolly, R., Devillers, R., Egleston, D., Gilby, B., Gullström, M., Halpern, B., Hidalgo, M., Holstein, D., Hovel, K., Huettmann, F., Jackson, E., James, W., Kellner, J., Kot, C., Lecours, V., Lepczyk, C., Nagelkerken, I., Nelson, J., Olds, A., Santos, R., Scales, K., Schneider, D., Schilling, H., Simenstad, C., Suthers, I., Trembl, E., Wedding, L., Yates, P., Young, M., 2021. Seascape ecology: identifying research priorities for an emerging ocean sustainability science. *Mar. Ecol. Prog. Ser.* 663, 1–29. <https://doi.org/10.3354/meps13661>.
- Pittman, S.J., Costa, B.M., Battista, T.A., 2009. Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *J. Coast Res.* 10053, 27–38. <https://doi.org/10.2112/si53-004.1>.
- Pollard, R., Read, J., 2017. Circulation, stratification and seamounts in the southwest Indian ocean. *Deep Sea Res 2 Top Stud Oceanogr* 136, 36–43. <https://doi.org/10.1016/j.dsr2.2015.02.018>.
- Porteiro, F.M., Gomes-Pereira, J.N., Pham, C.K., Tempera, F., Santos, R.S., 2013. Distribution and habitat association of benthic fish on the Condor seamount (NE Atlantic, Azores) from in situ observations. *Deep Sea Res 2 Top Stud Oceanogr* 98, 114–128. <https://doi.org/10.1016/j.dsr2.2013.09.015>.
- Quattrini, A.M., Ross, S.W., Carlson, M.C.T., Nizinski, M.S., 2012. Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. *Mar. Biol.* 159, 1079–1094. <https://doi.org/10.1007/s00227-012-1888-7>.
- Read, J., Pollard, R., 2017. An introduction to the physical oceanography of six seamounts in the southwest Indian Ocean. *Deep Sea Res 2 Top Stud Oceanogr* 136, 44–58. <https://doi.org/10.1016/j.dsr2.2015.06.022>.
- Rogers, A.D., 2018. The biology of seamounts: 25 Years on. In: *Advances in Marine Biology*, pp. 137–224. <https://doi.org/10.1016/bs.amb.2018.06.001>.
- Rogers, A.D., 2017. Pelagic ecology of the south west Indian ocean Ridge seamounts: introduction and overview. *Deep Sea Res 2 Top Stud Oceanogr* 136, 1–4. <https://doi.org/10.1016/j.dsr2.2016.12.009>.
- Rogers, A.D., 2013. Seamounts Project: an Ecosystem Approach to Management of Seamounts in the Southern Indian Ocean. IUCN. Gland, Switzerland.
- Rogers, A.D., Alvheim, O., Bemanaja, E., Benivary, D., Boersch-Supan, P., Bornman, T.G., Cedras, R., Du Plessis, N., Gotheil, S., Høines, A., Kemp, K., Kristiansen, J., Letessier, T., Mangar, V., Mazungula, N., Mørk, T., Pinet, P., Pollard, R., Read, J., Sonnekus, T., 2017. Pelagic communities of the south west Indian ocean seamounts: R/V dr Fridtjof nansen cruise 2009-410. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 136, 5–35. <https://doi.org/10.1016/j.dsr2.2016.12.010>.
- Rogers, A.D., Alvheim, O., Bemanaja, E., Benivary, D., Boersch-Supan, P.H., Bornman, T., Cedras, R., Du Plessis, N., 2009. Cruise Report “Dr. Fridtjof Nansen” Southern Indian Ocean Seamounts (IUCN/GEF/UNDP/ZSL/ASCLME/NERC/EAF Nansen Project/ECOMAR/ACEP 2009 Cruise 410), 1–182.
- Rogers, A.D., Baco, A., Griffiths, H., Hart, T., Hall-Spencer, J.M., 2007. Corals on seamounts. In: *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, Oxford, UK, pp. 141–169. <https://doi.org/10.1002/9780470691953.ch8>.
- Rogers, A.D., Taylor, M.L., 2012. Benthic Biodiversity of Seamounts in the Southwest Indian Ocean Cruise Report. R/V James Cook 066 Southwest Indian Ocean Seamounts expedition – November 7th – December 21st, 2011.
- Ross, S.W., Quattrini, A.M., 2007. The fish fauna associated with deep coral banks off the southeastern United States. *Deep Sea Res 1 Oceanogr Res Pap* 54, 975–1007. <https://doi.org/10.1016/j.dsr.2007.03.010>.
- Ross, S.W., Rhode, M., Quattrini, A.M., 2015. Demersal fish distribution and habitat use within and near Baltimore and Norfolk Canyons, U.S. middle Atlantic slope. *Deep Sea Res 1 Oceanogr Res Pap* 103, 137–154. <https://doi.org/10.1016/j.dsr.2015.06.004>.
- Santos, R., Medeiros-Leal, W., Novoa-Pabon, A., Silva, H., Pinho, M., 2021. Demersal fish assemblages on seamounts exploited by fishing in the Azores (NE Atlantic). *J. Appl. Ichthyol.* 37, 198–215. <https://doi.org/10.1111/jai.14165>.
- Segal, M., Xiao, Y., 2011. *Multivariate Random Forests*, vol. 1. Wiley Interdiscip Rev Data Min Knowl Discov, pp. 80–87. <https://doi.org/10.1002/widm.12>.
- Serra Santos, R., Morato, T., 2008. Conservation and utilization of biodiversity in seamounts & Telmo. In: *Norway/UN Conference on Ecosystems and People – Biodiversity for Development – the Road to 2010 and beyond*, pp. 162–169.
- Shotton, S., 2006. Management of Demersal Fisheries Resources of the Southern Indian Ocean. *FAO Fisheries Circular*, 2010.
- Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., Wakefield, W.W., 2008. Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Can. J. Fish. Aquat. Sci.* 65, 1230–1243. <https://doi.org/10.1139/F08-032>.
- Sutton, T.T., Clark, M.R., Dunn, D.C., Halpin, P.N., Rogers, A.D., Guinotte, J., Bograd, S. J., Angel, M.V., Perez, J.A.A., Wishner, K., Haedrich, R.L., Lindsay, D.J., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Blachowiak-Samolyk, K., Robison, B. H., Gjerde, K.M., Pierrot-Bults, A., Bernal, P., Reygondeau, G., Heino, M., 2017. A global biogeographic classification of the mesopelagic zone. *Deep Sea Res 1 Oceanogr Res Pap* 126, 85–102. <https://doi.org/10.1016/j.dsr.2017.05.006>.
- Swanborn, D.J.B., Huvenne, V.A.I., Pittman, S.J., Rogers, A.D., Taylor, M.L., Woodall, L. C., 2022a. Mapping, quantifying and comparing seascape heterogeneity of Southwest Indian Ridge seamounts. *Landsc. Ecol.* <https://doi.org/10.1007/s10980-022-01541-6>.
- Swanborn, D.J.B., Huvenne, V.A.I., Pittman, S.J., Woodall, L.C., 2022b. Bringing seascape ecology to the deep seabed: a review and framework for its application. *Limnol. Oceanogr.* 67, 66–88. <https://doi.org/10.1002/lno.11976>.
- Sward, D., Monk, J., Barrett, N., 2019. A systematic review of remotely operated vehicle surveys for visually assessing fish assemblages. *Front. Mar. Sci.* <https://doi.org/10.3389/fmars.2019.00134>.
- Therneau, T., Atkinson, B., 2019. Rpart: Recursive Partitioning and Regression Trees. <https://cran.r-project.org/package=rpart>.
- Wedding, L., Lepczyk, C., Pittman, S., Friedlander, A., Jorgensen, S., 2011. Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. *Mar. Ecol. Prog. Ser.* 427, 219–232. <https://doi.org/10.3354/meps09119>.
- White, M., Bashmachnikov, I., Arstegui, J., Martins, A., 2007. Physical processes and seamount productivity. In: *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, Oxford, UK, pp. 62–84. <https://doi.org/10.1002/9780470691953.ch4>.
- Whitehead, P.J.P., 1985. *FAO Species Catalogue*.
- Wilson, M.F.J., O’Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Mar. Geodes.* 30, 3–35. <https://doi.org/10.1080/01490410701295962>.
- Woodall, L.C., Robison, L.F., Rogers, A.D., Narayanaswamy, B.E., Paterson, G.L.J., 2015. Deep-sea litter: a comparison of seamounts, banks and a ridge in the Atlantic and Indian Oceans reveals both environmental and anthropogenic factors impact accumulation and composition. *Front. Mar. Sci.* 2, 1–10. <https://doi.org/10.3389/fmars.2015.00003>.
- Yesson, C., Clark, M.R., Taylor, M.L., Rogers, A.D., 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Res 1 Oceanogr Res Pap* 58, 442–453. <https://doi.org/10.1016/j.dsr.2011.02.004>.