Remote Sensing in Ecology and Conservation
Open Access
ZSL LET'S WORK FOR WILDLIFE

ORIGINAL RESEARCH

Structure-from-motion photogrammetry demonstrates that fine-scale seascape heterogeneity is essential in shaping mesophotic fish assemblages

Denise J. B. Swanborn[1,2,3], Paris V. Stefanoudis[1,3], Veerle A. I. Huvenne[4], Simon J. Pittman[5,6] & Lucy C. Woodall[1,3]

[1]Department of Zoology, University of Oxford, Oxford, UK
[2]Department of Earth Sciences, University of Oxford, Oxford, UK
[3]Nekton, Oxford, UK
[4]Ocean BioGeosciences, National Oceanography Centre (NOC), Southampton, UK
[5]Oxford Seascape Ecology Lab, School of Geography and the Environment, University of Oxford, Oxford, UK
[6]Marine Institute, University of Plymouth, Plymouth, UK

Keywords
Habitat heterogeneity, mesophotic coral ecosystems, seascape ecology, Seychelles, SfM photogrammetry, spatial pattern metrics

Correspondence
Denise J. B. Swanborn, Department of Zoology, University of Oxford, Oxford, UK.
Tel: +44 1865 (2) 71234; E-mail: denise.swanborn@env-res.ox.ac.uk

Funding Information
This work forms part of the PhD research of DS funded by the Natural Environment Research Council (NERC) Grant No NE/L002612/1, Nekton and a Stanley Gray Fellowship from the IMarEST. VH is funded by the 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 paper. LW and PS are funded by Nekton. This is Nekton contribution 30.

Editor: Kylie Scales
Associate Editor: Alice Jones

Received: 14 March 2022; Revised: 1 June 2022; Accepted: 20 June 2022

doi: 10.1002/rse2.290

Abstract

Benthic components of tropical mesophotic coral ecosystems (MCEs) are home to diverse fish assemblages, but the effect of multiscale spatial benthic characteristics on MCE fish is not well understood. To investigate the influence of fine-scale benthic seascape structure and broad-scale environmental characteristics on MCE fish, we surveyed fish assemblages in Seychelles at 30, 60 and 120 m depth using submersible video transects. Spatial pattern metrics from seascape ecology were applied to quantify fine-scale benthic seascape composition, configuration and terrain morphology from structure-from-motion photogrammetry and multibeam echosounder bathymetry and to explore seascape–fish associations. Hierarchical clustering using fish abundance and biomass data identified four distinct assemblages separated by the depth and geographic location, but also significantly influenced by variations in fine-scale seascape structure. Results further revealed variable responses of assemblage characteristics (fish biomass, abundance, trophic group richness, Shannon diversity) to seascape heterogeneity at different depths. Sites with steep slopes and high terrain complexity hosted higher fish abundance and biomass, with shallower fish assemblages (30–60 m) positively associated with aggregated patch mixtures of coral, rubble, sediment and macroalgae with variable patch shapes. Deeper fish assemblages (120 m) were positively associated with relief and structural complexity and local variability in the substratum and benthic cover. Our study demonstrates the potential of spatial pattern metrics quantifying benthic composition, configuration and terrain structure to delineate mesophotic fish–habitat associations. Furthermore, incorporating a finer-scale perspective proved valuable to explain the compositional patterns of MCE fish assemblages. As developments in marine surveying and monitoring of MCEs continue, we suggest that future studies incorporating spatial pattern metrics with multiscale remotely sensed data can provide insights will that are both ecologically meaningful to fish and operationally relevant to conservation strategies.

Introduction

Mesophotic coral ecosystems (MCEs), typically found in tropical and subtropical regions at water depths between 30 and 150 m (Hinderstein et al., 2010), form important fish habitats (Blyth-Skyrme et al., 2013; Lindfield et al., 2016; Rocha et al., 2018). Detailed characterisations of MCEs and their associated biodiversity remain rare

compared to shallow water reefs because of the technological, logistical and financial resources required to sample and survey them (Turner et al., 2019). Knowledge of the environmental drivers and habitat preferences of MCE fish species and assemblages is fundamental to informing monitoring and sustainable management strategies (Button et al., 2021; Weijerman et al., 2019).

Benthic habitat heterogeneity is a known driver of fish assemblages across depth. Fish respond to environmental heterogeneity at multiple spatial scales, and knowledge of these patterns might therefore provide ecologically important insights (Borland et al., 2021). Conceptual tools and quantitative methods from landscape ecology can be transferred to benthic marine systems to understand the effect of multiscale benthic habitat heterogeneity. Spatial pattern metrics have been developed to quantify seascape composition (the abundance and variety of patch types), configuration (the spatial arrangement of patch types) and terrain morphology (e.g. slope, structural complexity) from habitat maps or digital bathymetric models (Lecours et al., 2016; Swanborn, Huvenne, et al., 2022; Wedding et al., 2011). In shallow water reefs, these have, amongst others, provided new insights into seascape connectivity (McMahon et al., 2012), species-specific responses to environmental structure (Hitt et al., 2011), the importance of terrain complexity (Wedding et al., 2019) and scale-dependent responses (Kendall et al., 2011). Environmental heterogeneity in seascape composition, configuration and terrain structure equally influences fishes at greater depths (Anderson et al., 2009; Moore et al., 2011).

Yet, to date, no studies have quantified multiscale benthic habitat heterogeneity using spatial pattern metrics across MCE seascapes, leaving knowledge gaps about its ecological significance to MCE fish assemblages (Swanborn, Huvenne, et al., 2022). Instead, much MCE research has focused on exploring and characterising the effect of broad-scale environmental characteristics, with water depth (Lesser et al., 2019), geographical location (Fukunaga et al., 2017; Pinheiro et al., 2016; Quimpo et al., 2019) and site geomorphology (Osuka et al., 2021) recognised as key drivers of MCE fish distribution. Furthermore, rarely are spatial pattern metrics applied to very high-resolution (cm-m) maps and models of mesophotic seascape structure, even though cm-scale metrics quantified from models produced through structure-from-motion (SfM) photogrammetry are demonstrated predictors of shallow water and deep-sea (>200 m) coral reef fish (González-Rivero et al., 2017; Price et al., 2019).

This study aims to quantify and assess the combined effect of broader scale drivers (depth, geographic location) and fine-scale (cm-m) benthic habitat heterogeneity on MCE fish assemblages by focusing on MCEs from geographically separated coral atolls in Seychelles, Western Indian Ocean. Although knowledge and interest in MCE biodiversity and conservation are increasing globally (Holstein et al., 2019; Soares et al., 2020), MCEs in the Western Indian Ocean remain particularly understudied (Pyle & Copus, 2019). Using a combination of video-based fish transect surveys and high-resolution underwater photogrammetric reconstructions of benthic seascape structure, we investigated (1) groupings of Western Indian Ocean MCE reef fish assemblages and their composition, (2) the broader scale gradients (depth and location) and fine-scale seascape characteristics (terrain structure, composition and configuration) driving those groupings and (3) their effects on assemblage characteristics within these groupings.

Materials and Methods

Seychelles is an archipelagic state in the Western Indian Ocean. Seven research sites around six coral atolls of the Outer Islands were surveyed in March–April 2019 (Fig. 1) during the *First Descent: Seychelles* expedition (Woodall & Rivers, 2019). Aldabra, Astove, Alphonse and Desroches were located off the Amirantes Bank, although the latter was located close (16 km) to it, and St Joseph and Poivre were located on the Amirantes Bank. This study used fish and benthic data collected during submersible and remotely operated vehicle (ROV) stereo-video surveys conducted along 30, 60 and 120 m depth contours. Each survey was 250 m long, conducted with a speed of ~0.2 knots, and at a distance from the seabed of c. 1–2 m.

Remotely sensed data

At each site, 50 m transects for photogrammetric reconstructions (Fig. 2) were extracted from the 250 m video survey's Ultra-Short Baseline (USBL) tracks. This transect length was chosen to prevent cumulative positioning errors (see Price et al., 2019) and is consistent with transect lengths used in previous Western Indian Ocean fish surveys (Osuka et al., 2018; Samoilys et al., 2019). Photo frames were extracted from downward-facing video every 2 s using FreeVideotoJPG converter (DVDVideoSoft, 2018), linked to transect USBL position using timestamps and used to construct orthomosaics and digital bathymetric models (DBMs) using SfM photogrammetry in Agisoft Metashape Professional version 1.5.5 (Agisoft LLC, 2019) (steps and settings in Appendix S1). When transects were reconstructed using data from the same 250 m video survey, they were spaced at least 25 m apart to maintain independent sampling units (Fig. 2B). SfM reconstructions were cropped to a maximum width of 5 m before constructing DBMs and orthomosaics (Fig. 3) to ensure consistency with the belt transect area used for biological

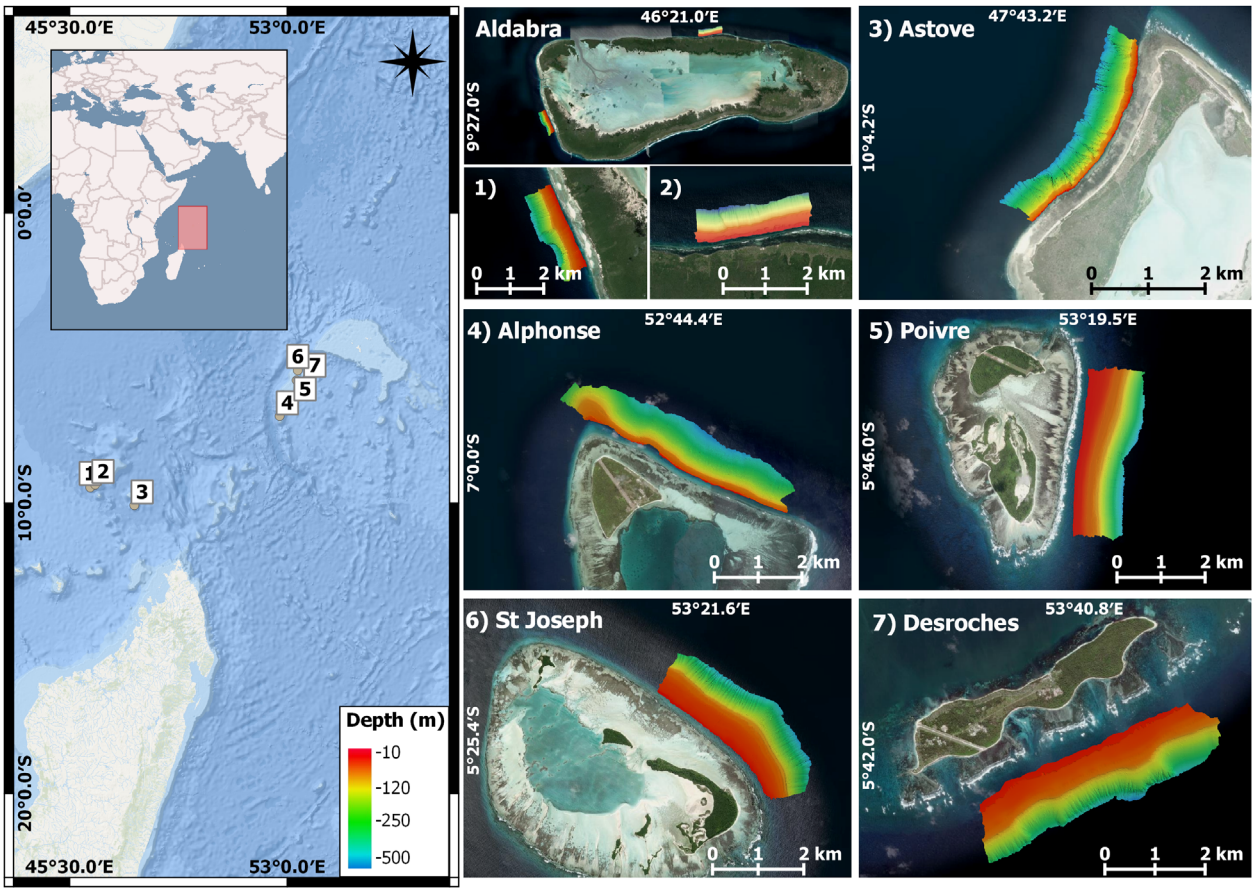

Figure 1. Map of locations surveyed during First Descent: Seychelles expedition in 2019. Swath bathymetry data collected at each site between 0 and 500 m were plotted to indicate the area in which video surveys were conducted.

data extraction (see 'Fish assemblage data' below), and models <40 m and >60 m long were removed to ensure consistent sampling units were used in the analysis. Although the internal, relative positioning of the 3D models was correct, owing to a lack of submersible attitude data (pitch, roll, heading), the absolute orientation of the models in space could not be determined. Hence, the resulting models were manually rotated in a horizontal plane, after which the orthomosaics and DBMs were exported at multiple resolutions, representing de-trended benthic features of multiple sizes (1, 5, 10, 15 and 20 cm), to evaluate any scale-dependent responses of fish assemblage composition to seascape structure.

Terrain structure

Terrain derivatives measuring orientation, curvature and topographic complexity were extracted from these multi-resolution DBMs with a focal window size of 3 × 3 pixels (Fig. 3B), using the R raster (Hijmans, 2017) and SpatialEco (Evans, 2017) packages (Table 1) and summarised with the mean value per transect. As the lack of attitude, data prohibited the calculation of absolute slope values from the DBMs, but the slope is an important variable for mesophotic fish assemblages (Osuka et al., 2021), the mean slope value for each transect was instead calculated from bathymetric data collected by multibeam echosounder and gridded at 2 × 2 m (Fig. 1, details about multibeam bathymetry data are presented in Swanborn,Fassbender, et al., 2022). Satellite data and bathymetry data (Fig. 1) were used to measure the distance to shore in QGIS 3.12.

Patch metrics: composition and configuration

Multiscale orthomosaics were imported into ArcMap 10.6 for maximum likelihood classification. Per orthomosaic, 80–120 training samples representing the different substrate types (sediment (incl. Sediment veneer), bedrock, coral rubble, live scleractinian coral, macroalgae/seagrass

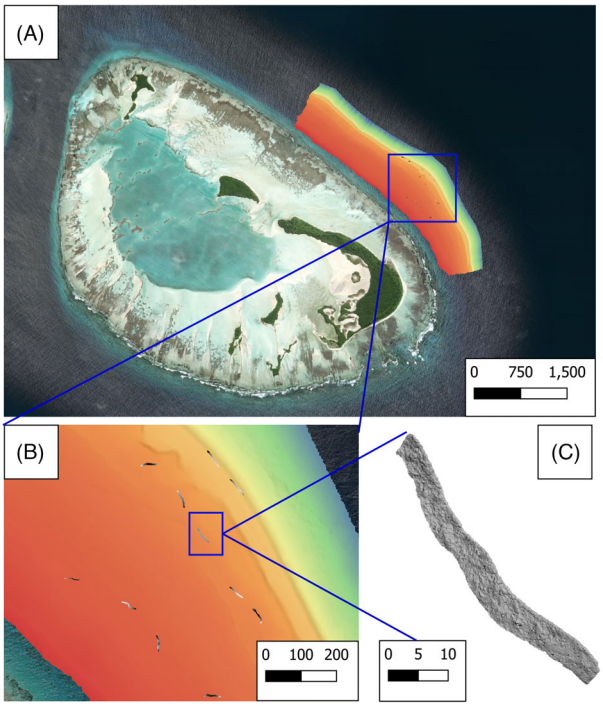

Figure 2. Example of photogrammetry transect reconstructions conducted at St Joseph. (A) shows an overview picture of the site, (B) shows transect locations at the three different depths (30, 60 and 120 m) plotted on the bathymetry, and (C) represents a close-up of a transect. The scale is in metres.

and octocoral/sponges) evenly divided amongst classes were manually created. Four heavily shaded transects were excluded as shading compromised the tool's ability to accurately identify substrate classes. Multiscale classified files (Fig. 3C) resulting from the maximum likelihood classification were imported into FragStats version 4.2.1 (McGarigal et al., 2012) to quantify seascape composition and configuration over the entire transect (Table 1).

Selection of predictor variables

Spearman correlation coefficients assessed the independence of predictor variables. When pairs of predictor variables were highly correlated ($|\rho| > 0.7$), metrics that had the strongest correlation with total fish abundance and biomass were retained (Table 1). As spatial pattern metrics exhibited a correlation between resolutions, Spearman correlation coefficients were calculated between multiscale spatial pattern metrics and assemblage characteristics. Only metrics at the resolution that had the strongest correlation with assemblage characteristics were retained for analysis. DBMs at 5 cm resolution were retained for terrain metrics, apart from TPI (15 cm). The patch metrics were obtained from orthomosaics extracted at 10 cm resolution. Other resolutions were removed from further analysis.

Fish assemblage data

Fish occurrence and total length were continuously recorded using EventMeasure (SeaGIS) software (Seager, 2014) from a forward-facing survey video (Stefanoudis et al., in review). Fish were identified at the lowest taxonomic level possible and subdivided into trophic groups (Appendix S2) as a proxy for their functional role (Osuka et al., 2018; Samoilys et al., 2019). Biomass was calculated using published length–weight relationships on FishBase (Froese & Pauly, 2020).

Fish observations at the locations of 50 m photogrammetric transect reconstructions were extracted from the overall 250 m video survey using time stamps. For the current analysis, three datasets were produced. The first dataset consisted of total abundance and biomass per transect. The second consisted of trophic group abundance and biomass per transect as a proxy for functional roles (Rincón-Díaz et al., 2018). The third contained transect-level descriptive data (total abundance, Shannon diversity, trophic group richness, biomass and assemblage size structure (binned fish length observations, 0–5, 5–10, 10–20, 20–30, 30–50 and >50 cm)). To enable statistical analysis, transects were excluded from the analysis when only unidentified fish were present or when fewer than three fish were observed. Unidentified fish, making up c. 4% of all observed fish, were included in abundance counts but excluded from trophic group richness, Shannon diversity and biomass counts.

Data analysis

The final dataset contained 91 transects from the seven sites (Fig. 1) of which there were 33 from 30 m, 27 from 60 m and 31 from 120 m. All analyses were conducted in RStudio v3.5.1. For Alphonse atoll, only transects at 30 m were available, due to malfunctioning of the USBL system during transects conducted at 60 and 120 m.

Categorising fish assemblage groupings

Ward's clustering analysis based on Bray Curtis distance on fourth-root transformed transect abundance and biomass data explored assemblage groupings. A univariate PERMANOVA ($n = 9999$) through the 'adonis' function in R package vegan (Oksanen et al., 2018) assessed the significance of obtained groupings. A pairwise PERMANOVA elaborated on significant differences using the package pairwiseAdonis (Martinez Arbizu, 2020). After clustering, the composition of each grouping was assessed

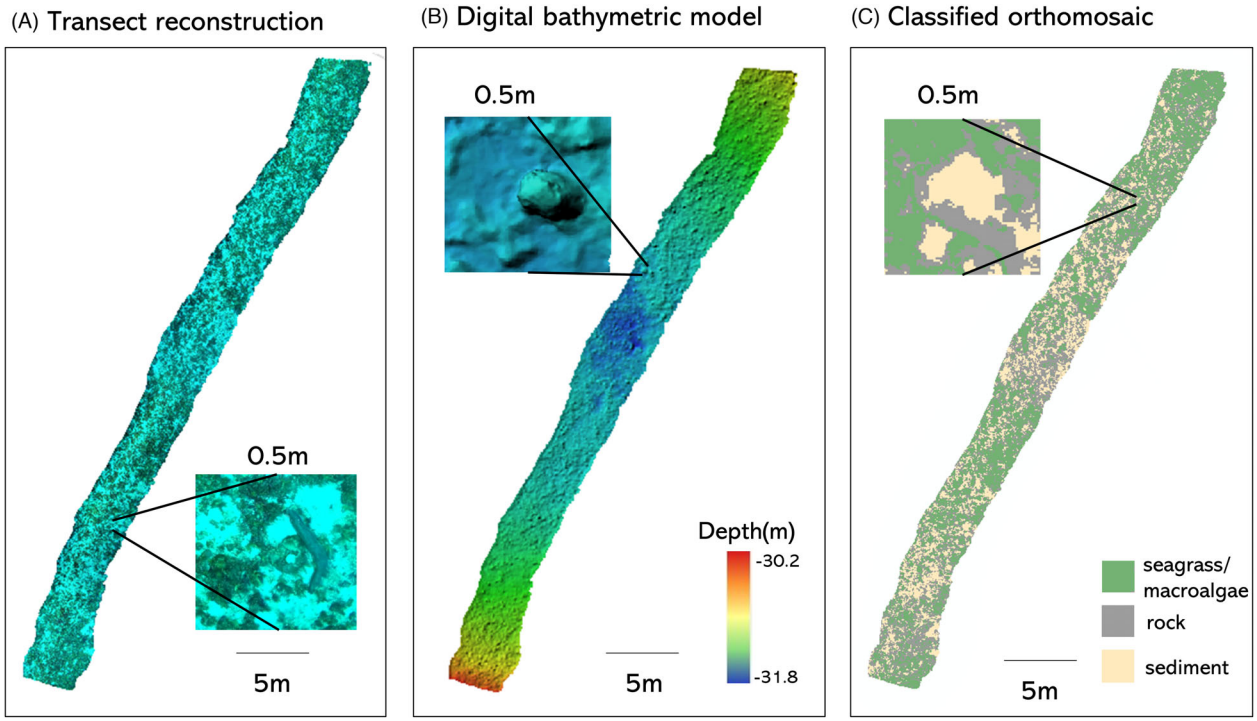

Figure 3. Outputs of benthic data extraction, demonstrated using an example from a transect at 30 m depth at Poivre. SfM photogrammetry produced a reconstruction of a transect (A), from which a digital bathymetric model (B) and an orthomosaic were exported. The orthomosaics were classified into major substrate types present (C).

using trophic group proportional abundance, biomass and the proportion of individuals in each binned length class, and differences in biomass and abundance were assessed using Kruskal–Wallis tests and Wilcoxon rank-sum test pairwise comparisons. Dufrene-Legendre Indicator species analysis (Dufrene & Legendre, 1997) aimed to identify what species are significantly ($P < 0.05$) associated with and characteristic of each grouping.

Environmental drivers of assemblage groupings

Distance-based Redundancy Analysis (dbRDA) (McArdle & Anderson, 2001) established which environmental parameters and species were driving patterns in fish assemblage structure using abundance and biomass. The environmental dataset was rescaled to zero mean and unit variance before running the dbRDA and 'site' was included as a categorical variable. A stepwise forward selection procedure using adjusted R^2 and P values produced the most parsimonious model to explain variation in fish assemblage structure. Permutation tests ($n = 999$) assessed the significance of each retained predictor variable and dbRDA axis. Associations between sites and environmental variables were visualised using biplots, where the length and direction of vectors indicate the strength and direction of the relationship, and normal confidence ordination ellipses indicated the different assemblages.

Group-level determinants of assemblage characteristics

A regression-based random forest (RF) algorithm (Breiman, 2001) was applied to model the association between environmental drivers and group-level metrics (abundance, biomass, Shannon diversity, trophic group richness) per identified assemblage (referred to as 'within-assemblage characteristics') As clusters contained transects from multiple sites and variable depths, depth and site were included in models.

Model building, training and performance assessment was implemented using R packages caret (Kuhn, 2018) and randomForest (Liaw & Wiener, 2002). Models were constructed using three repeats of 5-fold cross-validation to reduce overfitting. The number of trees and variables used for splitting at each node was optimised using the RMSE (root mean square error). Ten resamples of the final model were created for performance assessment using the mean and standard errors of R^2 and normalised MAE (Mean Absolute Error). Predictor variable

Table 1. Predictor variables considered for describing fish assemblage structure extracted from photogrammetric reconstructions, including metrics of continuous terrain structure, composition and configuration

	Type	Metric	Description	Retained?	Resolution retained
Environmental gradients		Mean depth (recorded as negative values)	Average distance from seabed to surface in m	Yes (correlated with % bedrock)	m
		Site	Surveyed atoll	Yes	NA
		Distance to shore	Geographic proxy for cross-shelf variation in oceanographic and environmental conditions	Yes	m
Continuous terrain structure (2.5D)	Orientation	Aspect Horn (1981) measured as eastness and northness	Orientation of the seabed	Yes (correlated with curvature)	5 cm
	Topographic complexity	Vector Ruggedness Measure (VRM) Sappington et al. (2007)	Variation in the three-dimensional orientation of grid cells within a neighbourhood	Yes (correlated with TRI and SAR)	5 cm
		Topographic Roughness Index (TRI) Riley et al. (1999)	Local variation in elevation of adjacent grid cells within a neighbourhood	No (correlated with VRM)	NA
		Surface area ratio (SAR)	Ratio between the three-dimensional surface area and the planar area	No (correlated with VRM)	NA
	Curvature	Total curvature Zevenbergen and Thorne (1987)	Surface orientation and relative elevation	No (correlated with aspect)	NA
		Topographic Position Index (TPI) Weiss (2001)	Indicates whether an area is part of an elevated or depressed feature of the surrounding terrain	Yes	15 cm
	Slope	Slope (degrees) Horn (1981)	Elevational change in the terrain	Yes	2 m, from bathymetry
Patch-based metrics (2D)	Composition	Patch richness	Number of different substrates and cover types	Yes	10 cm
		Relative proportion	Percentage cover of each substrate or cover type (sediment, bedrock, coral rubble, scleractinian coral, macroalgae and seagrass)	Yes (except bedrock, which was correlated with depth and %rubble)	10 cm
		Simpson diversity Simpson (1949)	Landscape diversity as a function of proportion and richness	No (correlated with contagion and % macroalgae)	NA
		Simpson evenness Simpson (1949)	Measures how evenly dispersed substrate classes are	No (correlated with contagion and % macroalgae)	NA
	Configuration	Shape index Patton (1975)	Average shape of a substrate patch based on edge length increases with the complexity	Yes	10 cm
		Proximity index Gustafson and Parker (1992)	Unitless measure of the average nearness of a patch of the same type increases with nearness	Yes	10 cm
		Division index Jaeger (2000)	Fragmentation of the seascape, increases with subdivision	Yes	10 cm
		Contagion Li and Reynolds (1993)	Measures patch type intermixing, as well as patch spatial distribution, increases with aggregation	Yes (correlated with diversity and evenness)	10 cm

Metrics were examined at multiple resolutions. The right column shows variables retained for analysis and at what resolution.

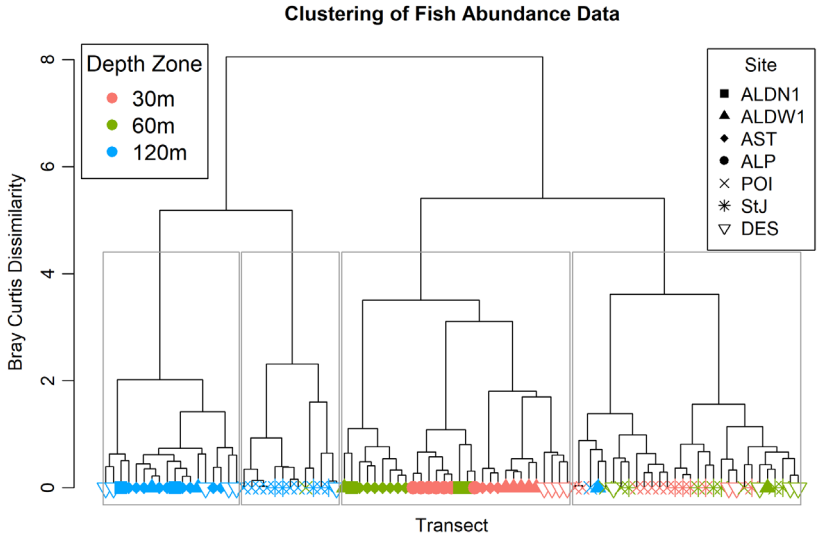

Figure 4. Clustering of fish abundance per transect where grey boxes delineate different clusters. Colours represent depth classes of observations. Symbols represent the site, with closed symbols representing off-bank islands (Aldabra, Astove and Alphonse) and open symbols representing sites on and next to the Amirantes bank (Poivre, St Joseph and Desroches).

contributions to the final random forest model are defined as the decrease in node impurity by splitting that variable, measured by the residual sum of squares, and scaled to a percentage. Partial dependence plots were interpreted to better understand the dependence between the response variables and the five most influential predictors.

Results

Assemblage groupings

The clustering analysis on transect fish abundance and biomass data revealed four distinct depth- and site-driven groupings (Fig. 4; Appendix S3). The PERMANOVA confirmed significant differences between groupings ($P < 0.001$), and subsequent pairwise comparisons indicated that all assemblage groupings differed from each other ($P < 0.05$).

The abundance observations (Fig. 4) split into two depth-driven groups as follows: the 120 m transects and a combination of the 30 and 60 m transects. Observations clustered by site within these depth groups, with islands on the Amirantes Bank (Poivre, St. Joseph) distinct from Aldabra, Astove and Alphonse (hereafter referred to as 'off- bank islands'). Transects at Desroches occurred across all clusters. Consequently, four assemblage clusters were delineated, representing the 30 and 60 m ('upper mesophotic', UM) observations of the off-bank islands (UM_OFF), the 120 m ('lower mesophotic', LM) observations of the off-bank islands (LM_OFF), the 30 and 60 m observations of the Amirantes bank (UM_AM) and the 120 m observations of the Amirantes bank (LM_AM). Clustering performed using biomass data found similar depth- and site-driven groupings (Appendix S3).

Subsequent assemblage characteristic comparisons provided further insight into the compositional differences between identified clusters (Fig. 5). Fish biomass per transect, but not abundance, was significantly ($P < 0.05$) higher in the 30–60 m clusters than in deeper 120 m clusters at the same location. Moreover, both abundance and biomass were significantly ($P < 0.05$) higher in UM_OFF than in UM_AM, but only biomass was higher in LM_OFF compared to LM_AM. In terms of trophic composition (Fig. 5A and B), planktivorous and invertivorous fish were numerically dominant across all clusters. However, the importance of planktivorous fish was reduced and replaced by higher contributions of piscivorous, carnivorous and omnivorous species when biomass data were used (Fig. 5C and D). This is reflected in the size distribution of fish with proportionately more large-bodied fish (>20 cm), that tend to be piscivorous or carnivorous, found in off-bank island clusters and a higher number of smaller individuals, typically planktivorous, dominating in shallower clusters (Fig. 5E and F).

Indicator species analysis revealed that 36 of the 76 species sampled were significantly associated with a specific cluster (Appendix S4). UM_OFF was the most species-rich, containing planktivores, piscivores, invertivores and herbivores, including species of commercial interest (e.g. *Caranx* spp., *Epinephelus* spp., *Lutjanus* spp., *Cephalopholis* spp). UM_AM showed associations with several piscivorous and invertivorous species, but few were significant. Lower mesophotic assemblages in both geographies were

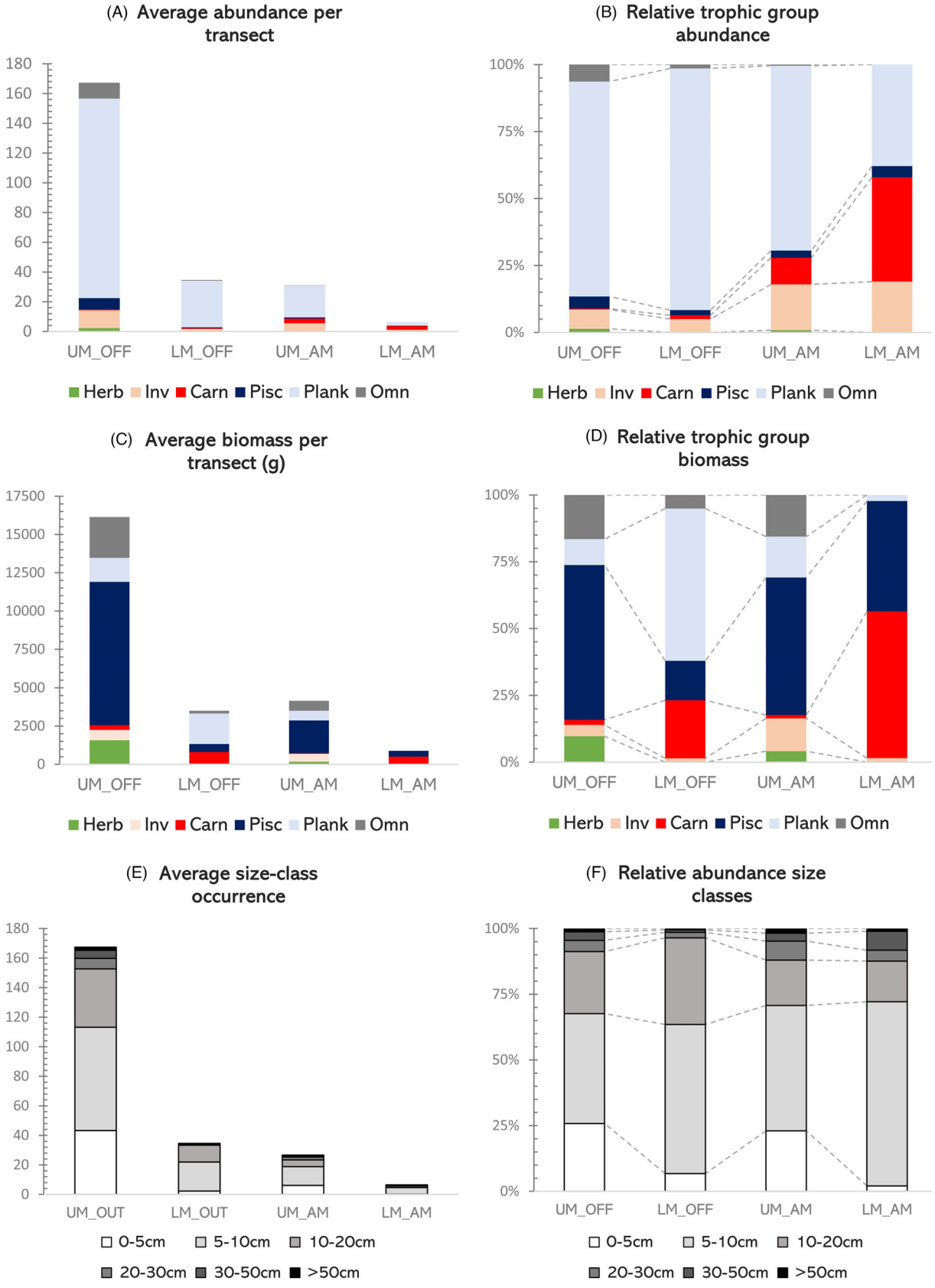

Figure 5. Composition of trophic groups in each of the four identified clusters, where UM_OFF and LM_OFF represent the 30–60 m observations, and 120 m observations of off-bank islands and UM_AM and LM_AM represent the 30–60 m observations and 120 m observations of the Amirantes bank. Upper panels show average group abundance per cluster (A) and the relative abundance of trophic groups per cluster (B). Middle panels show average group biomass per cluster (C) and the relative biomass of trophic groups per cluster (D). Bottom panels show the occurrence of size classes per cluster (E) and the relative abundance of size classes (F).

associated with distinct planktivorous and carnivorous fish species (e.g. *Pseudanthias* spp., *Scorpaenodes* spp.), with a higher number of planktivorous species associated with LM_OFF.

Drivers of assemblage groupings

In addition to broad-scale environmental drivers (depth and site) already identified (Fig. 4), fine-scale spatial terrain metrics describing habitat composition (substratum type), configuration (proximity index, contagion) and terrain structure (slope, VRM) were also statistically significant in explaining variation in assemblage abundance and biomass. Adjusted R^2 values showed that 46.9% and 39.7% of the variation in abundance-based and biomass-based fish datasets, respectively, could be attributed to the combined effects of broad-scale and fine-scale environmental variables included in the model.

The final selected models contained identical predictor variables for both datasets (abundance and biomass), with the additional inclusion of contagion, rubble and scleractinian coral cover in the abundance model, and distance to shore in the biomass model (Table 2). Permutational tests (n = 999) showed the significance of included variables (Table 2A). Depth and site were the largest contributors in both models, jointly explaining >35% of the total variation.

Table 2. Variables included in abundance (a) and biomass (b) dbRDA

	d.f.	Sum of squares	% total unadjusted variance explained	*P* value
(a) ANOVA abundance dbRDA				
Site*	6	8.987	24.13	<0.001
Depth*	1	5.295	14.22	<0.001
Vector Ruggedness measure*	1	1.5324	4.11	<0.001
Coral*	1	1.1785	3.16	<0.001
Sediment*	1	0.8818	2.37	<0.001
Macroalgae/ seagrass*	1	0.8243	2.21	<0.001
Proximity index*	1	0.7399	1.99	0.004
Slope*	1	0.5421	1.46	0.005
Rubble*	1	0.3973	1.07	0.033
Contagion	1	0.3892	1.05	0.051
Residual	75	16.475	55.76%	
(b) ANOVA biomass dbRDA				
Site*	6	8.675	23.81	<0.001
Depth*	1	4.3784	12.02	<0.001
Vector Ruggedness measure*	1	1.5089	4.14	<0.001
Macroalgae/ seagrass*	1	1.1707	3.21	<0.001
Sediment*	1	1.0414	2.86	<0.001
Proximity index*	1	0.7629	2.09	0.002
Slope*	1	0.5809	1.59	<0.001
Shoredist*	1	0.4893	1.34	0.012
Residual variance	77	19.8226	54.40%	

*Indicate a significant contribution to the variable.

Environmental influences

The ordination biplots displayed transect dissimilarity along the first and second dbRDA axes for both fish abundance (Fig. 6A) and biomass data (Fig. 6B). Environmental scores indicated which environmental variables each significant dbRDA axis represented (Appendix S5; Fig. 6). The first axis contained depth and slope, representing the shallow to deep gradient and transition from gently to steeper sloping environments. The second axis, comprising coral, VRM, slope and distance to shore, represented the gradient from structurally complex reef habitats near shore to more gently sloping environments further offshore, with site-specific gradations.

Transects were strongly separated by depth, proximity index and contagion (abundance only), with transects on the Amirantes bank (St. Joseph, Poivre) distinct from Aldabra, Astove and Alphonse across gradients of structural complexity (VRM), slope and the proportion of sediment. UM_OFF was found on sloping and complex terrain characterised by macroalgae/seagrass and live coral. LM_OFF was found on the terrain of similar structure, but on a more homogeneous substrate environment composed mainly of bedrock (associated with depth, Table 1). UM_AM was associated with less gradually sloping flats with sediment and coral rubble cover. Similar to LM_OFF, LM_AM was associated with homogeneous bedrock terrain (correlated with depth) of comparatively lower structural complexity and further

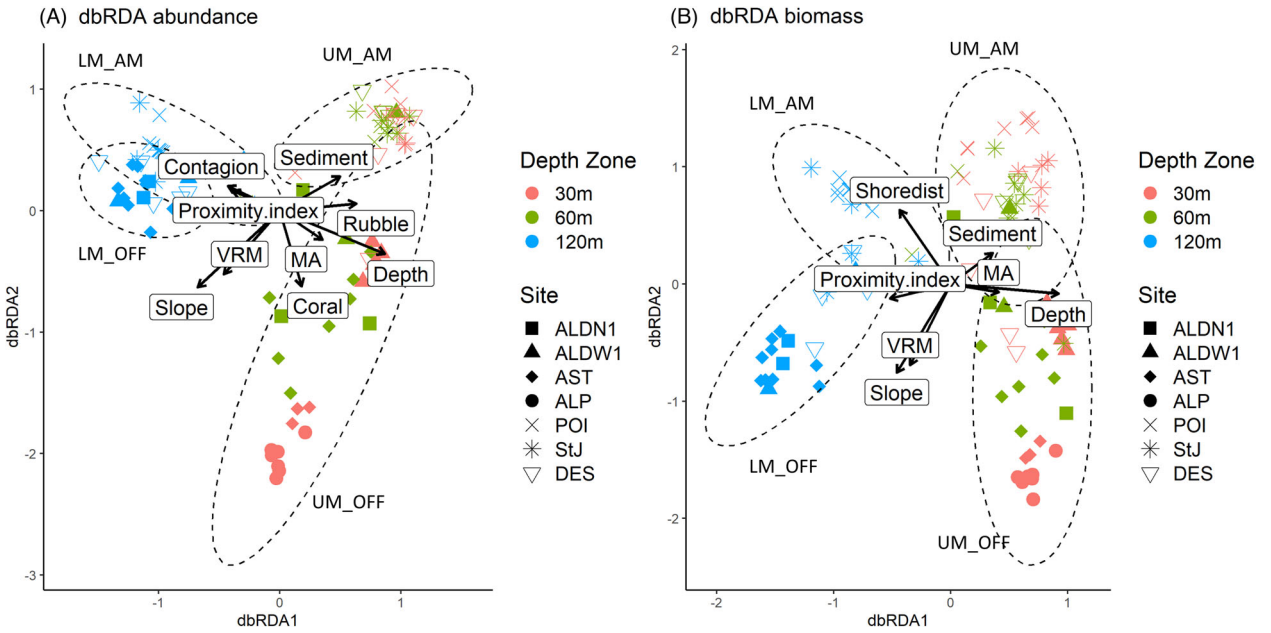

Figure 6. Ordination biplot of species abundance (A) and biomass (B) per transect as a function of dbRDA1 (17.72% variance abundance and 14.37% biomass) and dbRDA2 (10.94% variance abundance and 9.68% biomass). Point colours show the depth zones of transects, while point shapes show the site at which each transect was conducted. Continuous environmental variables included in the model have been superimposed as vectors displaying the strength (represented by vector length) and direction of their effect, with depth included as a negative variable. The site was included as a categorical variable. Ordination ellipses indicate identified assemblage clusters.

from shore. The contribution of substratum types (coral, macroalgae/seagrass, sediment and rubble) was larger for abundance than for biomass (only sediment and macroalgae/seagrass) and spread was larger for biomass.

Group-level drivers of assemblage characteristics

Model performance

Constructed RF models for fish assemblage structure (abundance, biomass, trophic group richness, Shannon diversity) as a function of benthic seascape characteristics explained a good but variable proportion of variance (mean 0.62, SD 0.07) (Appendix S6). MAE values (Appendix S6B–E) showed that predictive accuracy varied between variable and grouping. Mean normalised MAE was highest for abundance models (60.99%) and biomass models (65.29%) and shallow clusters (UM_OFF = 50.56% and UM_AM (62.41%)). Model performance based on benthic seascape characteristics was considered adequate as in similar shallow reef studies (Costa et al., 2014; Pittman et al., 2009), fish assemblages are also driven by the conditions of the overlying water column and wider benthic environment, which this study did not quantify.

Variable importance

Variable importance plots (Fig. 7) revealed that final models were composed of combinations of predictor variables, with no clear patterns across assemblage characteristics. Partial dependence plots (Appendix S7) showed the effects of the five most important variables on assemblage characteristics. Within UM_OFF (Fig. 6A, Appendix S7-1), composition metrics positively influenced abundance (coral), Shannon diversity and trophic group richness (sediment), and configuration metrics revealed more aggregated patch characteristics (contagion, proximity index) were associated with higher abundance, biomass and Shannon diversity. In the other 30–60 m grouping, UM_AM (Fig. 6C, Appendix S7-3), composition metrics equally showed positive effects of patch types on abundance (coral), biomass and Shannon diversity (sediment), and trophic group richness (rubble), while configuration metrics showed a positive relationship between complex patch shapes and Shannon diversity and richness. In both 120 m groupings (Fig. 6B and D, Appendix S7-2,4), structurally complex (high VRM) and elevated terrain (TPI) measured using terrain metrics drove fish abundance, Shannon diversity and trophic group richness. Additionally, fine-scale fragmentation (high division

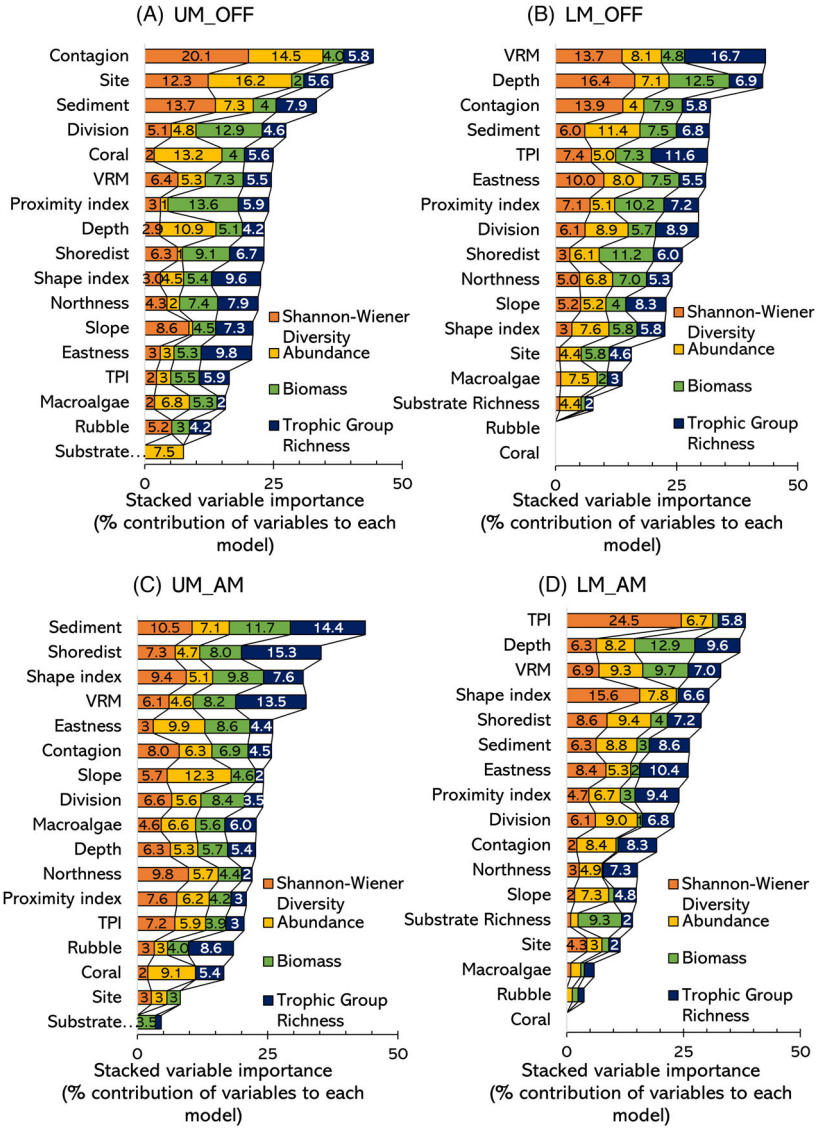

Figure 7. Variable contributions to model assemblage characteristics for the shallower assemblage of the off-bank islands (UM_OFF) (A), the deeper assemblage of the off-bank islands (LM_OFF) (B), the shallower assemblage of the Amirantes bank (UM_AM) (C) and the deeper assemblage of the Amirantes bank (LM_AM) (D). Variable contributions were standardised to a percentage of the overall assemblage descriptor model and stacked to evaluate variable importance across models.

index, high proximity index, reduced contagion) positively influenced abundance, Shannon diversity and trophic group richness at LM_OFF, but effects of composition and configuration were less clear at LM_AM.

Discussion

Understanding the multiscale environmental drivers of MCE fish assemblages is important to understand their ecology and functioning, and thus aid their conservation and management. Using the Seychelles atolls as a study system, this study revealed that broad-scale drivers of depth and location shape distinct grouping of mesophotic fish assemblages, and that these groupings exhibit variable responses to fine-scale terrain structure, seascape composition and configuration at mesophotic depths (30, 60 and 120 m). The findings highlight a need to develop research and monitoring programmes explicitly incorporating environmental data across spatial scales to improve insights into the ecological effect of mesophotic habitat heterogeneity.

Mesophotic fish–habitat associations

Broad-scale assemblage groupings

Assemblages were separated along gradients of depth, site and geomorphology.

Depth-dependent shifts in MCE fish abundance, biomass and taxonomic composition concur with previously reported effects of depth (Andradi-Brown et al., 2016; Kahng et al., 2014; Stefanoudis et al., 2019). The taxonomic distinctiveness of the 120 m assemblages from those at 30 and 60 m follows findings elsewhere (Button et al., 2021; Pinheiro et al., 2016) and might indicate a faunal break between these depths (Lesser et al., 2019). However, there was a lack of data between 60 and 120 m and therefore the transition of fish assemblages may also be gradual. Changes in the relative abundance and biomass of trophic groups with depth match those previously discussed in literature in other regions (Andradi-Brown et al., 2016; Kahng et al., 2010; Stefanoudis et al., 2019).

Fish assemblages vary across geographic locations because of regional differences in environmental conditions, connectivity and historical use patterns (e.g. fishing activity) (Samoilys et al., 2019). Regional differences in Western Indian Ocean oceanographic conditions mediated by the African mainland and the Mascarene Plateau (Obura, 2012) influence biogeography (McClanahan et al., 2014), likely resulting in compositional differences between the eastern and western sites. Study sites also differ in local geological settings (Fig. 1), particularly their distance to the Amirantes Bank (Mart, 1988). Sites on the Amirantes Bank (Poivre, St. Joseph) have different exposure to local circulation than sites off it (Aldabra, Astove, Alphonse, Desroches) (Hamylton et al., 2012). Desroches is off the Amirantes bank yet close (16 km) to it, which may explain the shared ecological characteristics with both Amirantes and off-bank sites. Further, geographic location may act as a proxy for historical use and protection. The lower abundance and biomass of commercially important omnivorous and piscivorous species (Lutjanidae, Lethrinidae, Carangidae, Serranidae) at the Amirantes sites compared to the off-bank islands is consistent with historical artisanal and subsistence fishing patterns, that traditionally dominated coastal domestic catch (Christ et al., 2020). Although Aldabra has also been afforded long-term marine protection, it is difficult to determine the absolute effect without appropriate baselines.

Furthermore, local site geomorphology differed between survey sites in the off-bank islands and sites on and next to the Amirantes bank. Amirantes sites featured extended gradually sloping sandy shelves, whereas the off-bank sites featured short reef ridges and steep slopes (captured in this study by slope and VRM). The slope is an important predictor of MCE fish biomass (Weijerman et al., 2019) and can influence hydrographic parameters that influence the dispersion of food particles such as upwelling (Osuka et al., 2021; Sherman et al., 2019), matching the higher abundance and biomass of planktivorous and piscivorous species found in the off-bank islands. Geomorphology also influences sediment dynamics (Sherman et al., 2016), and the Amirantes sites with lower slope gradients and rugosity sites featured higher sedimentation. This inhibits coral recruitment and growth (Smith et al., 2019) and is consistent with the lower abundance/biomass of reef-dependent fish.

Local assemblage structuring

Fine-scale variations in terrain structure, composition and configuration explained a substantial amount of variation in addition to the broad-scale drivers, especially given that fish assemblages are strongly driven by characteristics of the overlying water column.

Of the metrics describing terrain structure, fine-scale habitat complexity measured by VRM mainly influenced MCE fish, supporting results from other reef systems (Ferrari et al., 2016; Price et al., 2019). In the 30–60 m region, increased habitat complexity was linked to complex site geomorphology or hard coral in UM_OFF. In the 120 m assemblages, habitat complexity and TPI drove abundance, trophic group richness and Shannon-Wiener diversity, demonstrating that elevated, ridge-like features are important in supporting biodiverse assemblages. This is congruent with the lower mesophotic and subphotic habitat preferences previously reported in Hawaii (Weijerman et al., 2019).

Seascape composition was measured as the relative abundance of patch types and distinct substrates were associated with 30–60 m (sediment, coral, rubble and macroalgae) and 120 m (bedrock and sediment) mesophotic assemblages. The effects of coral and coral rubble on 30–60 m assemblage structure match reports of coral cover as key drivers of MCE assemblages (Quimpo et al., 2019), whereas the proportion of sediment supported trophic group richness, Shannon-Wiener diversity and biomass. The proportion of sediment also positively influenced LM_OFF mesophotic fish abundance in the otherwise homogeneous bedrock environment at 120 m. Previous shallow reef studies found that as fishes use multiple environments, patch mixtures including sediment can positively influence fish assemblages (Sievers et al., 2020). These results indicate that these effects extend into deeper reef systems.

Configuration metrics measured the spatial arrangements of patch types. At UM_OFF, assemblage abundance

and biomass increased with more aggregated and connected seascape characteristics. Aggregation could indicate structural connectivity, which has proven important in maintaining fish abundance and biomass in shallow water coral reefs (Grober-Dunsmore et al., 2007). Additionally, diversity and trophic group richness at UM_AM increased with complex patch structure, indicating that fine-scale spatial heterogeneity is important in maintaining diverse assemblages (Hewitt et al., 2005). In the lower mesophotic clusters, fine-scale fragmentation appeared to support fish abundance, functional group richness and Shannon diversity. This may reflect the patchiness of mesophotic benthic cover (octocorals and sponges) and sediment at 120 m, which tend to form more isolated patches on and between bedrock that are nevertheless beneficial for the resident fish fauna, whereas at 30–60 m ecologically important benthic cover and substratum patches tend to be more extended and well connected.

Methodological considerations

Although logistical challenges of obtaining MCE video surveys through underwater vehicles or technical diving remain, our ability to obtain high-resolution environmental and biological data beyond conventional SCUBA depth continues to increase. This study extended landscape ecology approaches developed on land and increasingly applied in shallow water environments to fine-scale remotely sensed data on MCEs. Spatial pattern metrics captured diverse aspects of seascape structure (composition, configuration and terrain structure) from SfM photogrammetry outputs to assess fine-scale (cm-m) MCE fish–habitat associations. Our findings indicate for the first time that fine-scale spatial pattern metrics explain mesophotic fish assemblage structure and habitat associations in addition to broad-scale drivers of depth and location. Outcomes also suggest the potential of this approach for similar research in other reef systems.

Although terrain metrics such as those employed here may act as a proxy for local hydrographic conditions (Wilson et al., 2007), uncaptured variations in the overlying water column (e.g. currents, primary productivity, or water chemistry) likely contribute to the unexplained variation and imperfect predictive power of Random Forest models. Developing and incorporating pelagic metrics of seascape structure remains an important focal point for seascape studies, particularly for deeper benthic systems (Kavanaugh et al., 2016; Swanborn, Huvenne, et al., 2022).

Additionally, seascape structure influences fish assemblages at multiple scales (Anderson et al., 2009; Pittman & Brown, 2011), including scales other than the cm-scale metrics captured in this study (Weijerman et al., 2019). Although home ranges of smaller fish might be within the spatial scale covered in this study, larger-bodied fish will have home ranges that greatly exceed the 50mx5m areas covered here, which might compromise the detection of accurate habitat relationships (Kendall et al., 2011). Further research investigating the influence of seascape structure around transects, for example derived from habitat maps, could provide key insights into the effects of the large-scale context and potential connectivity between habitats.

MCE monitoring and conservation

At present, few conservation and management efforts directly target deep reef habitats, despite their importance for ecosystem function and services (Soares et al., 2020). Areas of high MCE fish abundance and biomass includec sites with steep slopes and high terrain complexity, with upper and middle mesophotic habitats characterised by the coral cover and connected patch mixtures, and lower mesophotic habitats with fine-scale habitat heterogeneity in topography and substratum types. These areas should form important targets for future surveying and monitoring efforts as well as for fisheries. Monitoring programmes could benefit from incorporating spatial pattern metrics to identify where and when they change and to evaluate possible implications for associated species and habitats (Wedding et al., 2011). All findings on habitat associations of MCE fish at different depth zones uncovered in this study were shared with stakeholders from the region.

Acknowledgements

We would like to thank the captain and crew of the *R/V Ocean Zephyr* for their support during the First Descent: Seychelles Expedition in 2019, and the Seychelles government and partners, in particular members of the Ministry of Agriculture, Climate Change and Environment, for the approval to conduct work within Seychelles waters. The research permit for Seychelles was issued by the Seychelles Bureau of Standards (Permit Number: 524). We are also grateful to partners who made data collection possible, in particular the crew and technicians from Triton submersibles, Global SubDive and ROV Support for submersible and ROV video data acquisition. Further thanks to Mike Pownall for help with USBL tracking and data extraction, Sara Winter for initial annotations of the fish video data, Melita Samoilys for her help with fish identifications and Dave Price for initial discussions and ideas for the photogrammetry analysis. We are also grateful for the detailed and constructive feedback of two reviewers that have helped improve the paper.

This work forms part of the PhD research of DS funded by the Natural Environment Research Council (NERC) Grant No NE/L002612/, Nekton and a Stanley Gray Fellowship from the IMarEST. VH is funded by the 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 paper. LW and PS are funded by Nekton. This is Nekton contribution 30.

Authors' Contribution

DS conceptualised the study, conducted all statistical analyses and wrote the paper. PS calibrated, analysed and annotated the fish video data. LW created the video transect survey plan and ran the expedition. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

Agisoft LLC. (2019) Agisoft Metashape Professional. Available from: https://www.agisoft.com/downloads/installer/

Anderson, T.J., Syms, C., Roberts, D.A. & Howard, D.F. (2009) Multiscale fish–habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. *Journal of Experimental Marine Biology and Ecology*, **379**(1–2), 34–42. https://doi.org/10.1016/j.jembe.2009.07.033

Andradi-Brown, D.A., Gress, E., Wright, G., Exton, D.A. & Rogers, A.D. (2016) Reef fish community biomass and trophic structure changes across shallow to upper-mesophotic reefs in the Mesoamerican barrier reef, Caribbean. *PloS One*, **11**(6), e0156641. https://doi.org/10.1371/journal.pone.0156641

Blyth-Skyrme, V., Rooney, J.J.B., Parrish, F.A. & Boland, R.C. (2013) Mesophotic coral ecosystems — potential candidates as essential fish habitat and habitat areas of particular concern, *Pacific Islands Fishery Science Center, National Marine Fishery Science Center Administrative Report H-13-02*, (April), 53.

Borland, H.P., Gilby, B.L., Henderson, C.J., Leon, J.X., Schlacher, T.A., Connolly, R.M. et al. (2021) The influence of seafloor terrain on fish and fisheries: a global synthesis. *Fish and Fisheries*, **22**(4), 707–734. https://doi.org/10.1111/faf.12546

Breiman, L. (2001) Random forests. *Machine Learning*, **45**, 5–32. https://doi.org/10.1023/A:1010933404324

Button, R.E., Parker, D., Coetzee, V., Samaai, T., Palmer, R.M., Sink, K. et al. (2021) ROV assessment of mesophotic fish and associated habitats across the continental shelf of the Amathole region. *Scientific Reports*, **11**(1), 1–11. https://doi.org/10.1038/s41598-021-97369-2

Christ, H.J., White, R., Hood, L., Vianna, G. & Zeller, D. (2020) A baseline for the blue economy: catch and effort history in the Republic of Seychelles domestic fisheries. *Frontiers in Marine Science*, **7**(May), 1–13. https://doi.org/10.3389/fmars.2020.00269

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**(1), e85555. https://doi.org/10.1371/journal.pone.0085555

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**(3), 345. https://doi.org/10.2307/2963459

Evans, J. S. (2017) spatialEco. R package, version 0.0.1-7. Available from: https://cran.r-project.org/package=spatialEco

Ferrari, R., McKinnon, D., He, H., Smith, R.N., Corke, P., González-Rivero, M. et al. (2016) Quantifying multiscale habitat structural complexity: a cost-effective framework for underwater 3D modelling. *Remote Sensing*, **8**(2), 113. https://doi.org/10.3390/rs8020113

Froese, R. & Pauly, D. (2020) FishBase, world wide web electronic publication. Available from: www.fishbase.org

Fukunaga, A., Kosaki, R.K. & Wagner, D. (2017) Changes in mesophotic reef fish assemblages along depth and geographical gradients in the northwestern Hawaiian islands. *Coral Reefs*, **36**(3), 785–790. https://doi.org/10.1007/s00338-017-1569-6

González-Rivero, M., Harborne, A.R., Herrera-Reveles, A., Bozec, Y.M., Rogers, A., Friedman, A. et al. (2017) Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports*, **7** (June), 1–15. https://doi.org/10.1038/s41598-017-14272-5

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**(1), 201–216. https://doi.org/10.1007/s00338-006-0180-z

Gustafson, E.J. & Parker, G.R. (1992) Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology*, **7**(2), 101–110. https://doi.org/10.1007/BF02418941

Hamylton, S., Spencer, T. & Hagan, A.B. (2012) Coral reefs and reef islands of the amirantes archipelago, western Indian ocean. *Seafloor Geomorphology as Benthic Habitat*, 349–356. https://doi.org/10.1016/B978-0-12-385140-6.00022-0

Hewitt, J.E., Thrush, S.F., Halliday, J. & Duffy, C. (2005) The importance of small-scale habitat structure for maintaining beta diversity. *Ecology*, **86**(6), 1619–1626. https://doi.org/10.1890/04-1099

Hijmans, R. J. (2017) Raster: geographic data analysis and modeling. R package version 2.6-7. Available from: https://cran.r-project.org/package=raster

Hinderstein, L.M., Marr, J.C.A., Martinez, F.A., Dowgiallo, M.J., Puglise, K.A., Pyle, R.L. et al. (2010) Theme section on "mesophotic coral ecosystems: characterisation, ecology, and management". *Coral Reefs*, **29**(2), 247–251. https://doi.org/10.1007/s00338-010-0614-5

Hitt, S., Pittman, S. & Nemeth, R. (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series*, **427**, 275–291. https://doi.org/10.3354/meps09093

Holstein, D.M., Fletcher, P., Groves, S.H. & Smith, T.B. (2019) Ecosystem services of mesophotic coral ecosystems and a call for better accounting. In: *Mesophotic coral ecosystems*. Cham: Springer, pp. 943–956. https://doi.org/10.1007/978-3-319-92735-0_49

Horn, B.K.P. (1981) Hill shading and the reflectance map. *Proceedings of the IEEE*, **69**(1), 14–47. https://doi.org/10.1109/PROC.1981.11918

Jaeger, J.A. (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology*, **15**(2), 115–130. https://doi.org/10.1023/A:1008129329289

Kahng, S., Copus, J. & Wagner, D. (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, **7**(April), 72–81. https://doi.org/10.1016/j.cosust.2013.11.019

Kahng, S.E., Garcia-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E. et al. (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, **29**(2), 255–275. https://doi.org/10.1007/s00338-010-0593-6

Kavanaugh, M.T., Oliver, M.J., Chavez, F.P., Letelier, R.M., Muller-Karger, F.E., Doney, S.C. et al. (2016) Seascapes as a new vernacular for pelagic ocean monitoring, management and conservation. *ICES Journal of Marine Science*, **73**(7), 1839–1850. https://doi.org/10.1093/icesjms/fsw086

Kendall, M., Miller, T. & Pittman, S. (2011) Patterns of scale-dependency and the influence of map resolution on the seascape ecology of reef fish. *Marine Ecology Progress Series*, **427**, 259–274. https://doi.org/10.3354/meps08945

Kuhn, M. (2018) Caret: classification and regression training. R package version 6.0-80. Available from: https://cran.r-project.org/package=caret

Lecours, V., Brown, C.J., Devillers, R., Lucieer, V.L. & Edinger, E.N. (2016) Comparing selections of environmental variables for ecological studies: a focus on terrain attributes. *PLoS One*, **11**(12). https://doi.org/10.1371/journal.pone.0167128

Lesser, M.P., Slattery, M., Laverick, J.H., Macartney, K.J. & Bridge, T.C. (2019) Global community breaks at 60 m on mesophotic coral reefs. *Global Ecology and Biogeography*, **28**(10), 1403–1416. https://doi.org/10.1111/geb.12940

Li, H. & Reynolds, J.F. (1993) A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology*, **8**(3), 155–162. https://doi.org/10.1007/BF00125347

Liaw, A. and Wiener, M. (2002) Classification and regression by randomForest. R News, pp. 18–22. Available from: https://cran.r-project.org/doc/Rnews/

Lindfield, S.J., Harvey, E.S., Halford, A.R. & McIlwain, J.L. (2016) Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs*, **35**(1), 125–137. https://doi.org/10.1007/s00338-015-1386-8

Mart, Y. (1988) The tectonic setting of the Seychelles, Mascarene and Amirante plateaus in the western equatorial Indian Ocean. *Marine Geology*, **79**(3–4), 261–274. https://doi.org/10.1016/0025-3227(88)90042-4

Martinez Arbizu, P. (2020) pairwiseAdonis: pairwise multilevel comparison using Adonis. R package version 0.4. Available from: https://github.com/pmartinezarbizu/pairwiseAdonis

McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**(1), 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2

McClanahan, T.R., Ateweberhan, M., Darling, E.S., Graham, N.A. & Muthiga, N.A. (2014) Biogeography and change among regional coral communities across the western Indian Ocean. *PLoS One*, **9**(4), 1–9. https://doi.org/10.1371/journal.pone.0093385

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. Available from: http://www.umass.edu/landeco/research/fragstats/fragstats.html

McMahon, K. W., Berumen, M. L. and Thorrold, S. R. (2012) Linking habitat mosaics and connectivity in a coral reef seascape, *Proceedings of the National Academy of Sciences of the United States of America*, **109**(38), pp. 15372–15376. doi: 10.1073/pnas.1206378109.

Moore, C.H., Van Niel, K. & Harvey, E.S. (2011) The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography*, **34**(3), 425–435. https://doi.org/10.1111/j.1600-0587.2010.06436.x

Obura, D. (2012) The diversity and biogeography of Western Indian Ocean reef-building corals. *PLoS One*, **7**(9). https://doi.org/10.1371/journal.pone.0045013

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2018) Vegan: community ecology package. R package version 2.5-2. Available from: https://cran.r-project.org/package=vegan

Osuka, K., Kochzius, M., Vanreusel, A., Obura, D. & Samoilys, M. (2018) Linkage between fish functional groups and coral reef benthic habitat composition in the Western Indian Ocean. *Journal of the Marine Biological Association of the United Kingdom*, **98**(2), 387–400. https://doi.org/10.1017/S0025315416001399

Osuka, K.E., McClean, C., Stewart, B.D., Bett, B.J., Le Bas, T., Howe, J. et al. (2021) Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: implications for management and conservation. *Ocean and Coastal Management*, **200**, 105463. https://doi.org/10.1016/j.ocecoaman.2020.105463

Patton, D. R. (1975) A diversity index for quantifying habitat "edge". *Wildlife Society Bulletin*, **3**, pp. 171–173. Available from: https://www.jstor.org/stable/3781151

Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Shepherd, B., Chequer, A.D. & Rocha, L.A. (2016) Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, **35**(1), 139–151. https://doi.org/10.1007/s00338-015-1381-0

Pittman, S.J. & Brown, K.A. (2011) Multiscale approach for predicting fish species distributions across coral reef seascapes. *PLoS One*, **6**(5), e20583. https://doi.org/10.1371/journal.pone.0020583

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. *Journal of Coastal Research*, **10053**(10053), 27–38. https://doi.org/10.2112/SI53-004.1

Price, D.M., Robert, K., Callaway, A., Hall, R.A. & Huvenne, V.A. (2019) Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs*, **38**(5), 1007–1021. https://doi.org/10.1007/s00338-019-01827-3

Pyle, R.L. & Copus, J.M. (2019) Mesophotic coral ecosystems: introduction and overview. *Mesophotic Coral ecosystems*, 3–27. https://doi.org/10.1007/978-3-319-92735-0_1

Quimpo, T.J., Cabaitan, P.C., Olavides, R.D., Dumalagan, E.E., Jr., Munar, J. & Siringan, F.P. (2019) Spatial variability in reef-fish assemblages in shallow and upper mesophotic coral ecosystems in The Philippines. *Journal of Fish Biology*, **94**(1), 17–28. https://doi.org/10.1111/jfb.13848

Riley, S., DeGloria, S.D. & Elliot, R. (1999) A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, **5**(1–4), 23–27. Available from: http://download.osgeo.org/qgis/doc/reference-docs/Terrain_Ruggedness_Index.pdf

Rincón-Díaz, M.P., Pittman, S.J., Arismendi, I. & Heppell, S.S. (2018) Functional diversity metrics detect spatio-temporal changes in the fish communities of a Caribbean marine protected area. *Ecosphere*, **9**(10). https://doi.org/10.1002/ecs2.2433

Rocha, L.A., Pinheiro, H.T., Shepherd, B., Papastamatiou, Y.P., Luiz, O.J., Pyle, R.L. et al. (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*, **361**(6399), 281–284. https://doi.org/10.1126/science.aaq1614

Samoilys, M.A., Halford, A. & Osuka, K. (2019) Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecology and Evolution*, **9**(7), 4149–4167. https://doi.org/10.1002/ece3.5044

Sappington, J.M., Longshore, K.M. & Thompton, D.B. (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using Bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, **71**(5), 1419–1426. https://doi.org/10.2193/2005-723

Seager, J. (2014) *(SeaGIS) EventMeasure*. Available from: https://www.seagis.com.au/event.html

Sherman, C., Schmidt, W., Appeldoorn, R., Hutchinson, Y., Ruiz, H., Nemeth, M. et al. (2016) Sediment dynamics and their potential influence on insular-slope mesophotic coral ecosystems. *Continental Shelf Research*, **129**(September), 1–9. https://doi.org/10.1016/j.csr.2016.09.012

Sherman, C.E., Locker, S.D., Webster, J.M. & Weinstein, D.K. (2019) Geology and geomorphology. *Mesophotic Coral Ecosystems*, 849–878. https://doi.org/10.1007/978-3-319-92735-0_44

Sievers, K.T., McClure, E.C., Abesamis, R.A. & Russ, G.R. (2020) Non-reef habitats in a tropical seascape affect density and biomass of fishes on coral reefs. *Ecology and Evolution*, **10**(24), 13673–13686. https://doi.org/10.1002/ece3.6940

Simpson, E. H. (1949) Measurment of diversity, *Nature*, **688** (1943), p. 688. Available from: https://doi.org/10.1038/163688a0

Smith, T.B., Holstein, D.M. & Ennis, R.S. (2019) Disturbance in mesophotic coral ecosystems and linkages to conservation and management. In: Loya, Y., Puglise, K.A. & Bridge, T.C.L. (Eds.) *Mesophotic coral ecosystems*. Cham: Springer International Publishing, pp. 911–929. https://doi.org/10.1007/978-3-319-92735-0_47

Soares, M., Araújo, J., Ferreira, S., Santos, B., Boavida, J.R.H., Costantini, F. et al. (2020) Why do mesophotic coral ecosystems have to be protected? *Science of the Total Environment*, **726**, 138456. https://doi.org/10.1016/j.scitotenv.2020.138456

Stefanoudis, P.V., Gress, E., Pitt, J.M., Smith, S.R., Kincaid, T., Rivers, M. et al. (2019) Depth-dependent structuring of reef fish assemblages from the shallows to the rariphotic zone. *Frontiers in Marine Science*, **6**(JUN), 1–16. https://doi.org/10.3389/fmars.2019.00307

Swanborn, D.J., Huvenne, V.A., Pittman, S.J. & Woodall, L.C. (2022) Bringing seascape ecology to the deep seabed: a review and framework for its application. *Limnology and Oceanography*, **67**, 66–88. https://doi.org/10.1002/lno.11976

Swanborn, D.J.B., Fassbender, N., Huvenne, V.A.I., Stefanoudis, P.V. & Woodall, L.C. (2022) Geomorphological

drivers of deeper reef habitats around Seychelles. *Coral Reefs*. https://doi.org/10.1007/s00338-022-02281-4

Turner, J.A., Andradi-Brown, D.A., Gori, A., Bongaerts, P., Burdett, H.L., Ferrier-Pagès, C. et al. (2019) Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. In: Loya, Y., Puglise, K.A. & Bridge, T.C.L. (Eds.) *Mesophotic coral ecosystems*. Cham: Springer International Publishing, pp. 989–1003. https://doi.org/10.1007/978-3-319-92735-0_52

Wedding, L.M., Jorgensen, S., Lepczyk, C.A. & Friedlander, A.M. (2019) Remote sensing of three-dimensional coral reef structure enhances predictive modeling of fish assemblages. *Remote Sensing in Ecology and Conservation*, **5**(2), 150–159. https://doi.org/10.1002/rse2.115

Wedding, L.M., Lepczyk, C.A., Pittman, S.J., Friedlander, A.M. & Jorgensen, S. (2011) Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. *Marine Ecology Progress Series*, **427**, 219–232. https://doi.org/10.3354/meps09119

Weijerman, M., Grüss, A., Dove, D., Asher, J., Williams, I.D., Kelley, C. et al. (2019) Shining a light on the composition and distribution patterns of mesophotic and subphotic fish communities in Hawai'i. *Marine Ecology Progress Series*, **630**, 161–182. https://doi.org/10.3354/meps13135

Weiss, A. D. (2001) Topographic position and landforms analysis, in *poster presentation* ESRI User Conference, San Diego, CA. http://www.jennessent.com/downloads/TPI-poster-TNC_18x22.pdf

Wilson, M.F., O'Connell, B., Brown, C., Guinan, J.C. & Grehan, A.J. (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, **30**(1–2), 3–35. https://doi.org/10.1080/01490410701295962

Woodall, L. & Rivers, M. (2019) *First descent: Indian Ocean*. Seychelles Expedition Cruise Report. Available from: https://cdn.nektonmission.org/3_Docs/Seychelles_Nekton_Expedition_Cruise_Report_Final_2020.pdf.

Zevenbergen, L.W. & Thorne, C.R. (1987) Quantitative analysis of land surface topography. *Earth Surface Processes and Landforms*, **12**(1), 47–56. https://doi.org/10.1002/esp.3290120107

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Photogrammetric reconstruction parameters.
Appendix S2. Trophic groupings.
Appendix S3. Biomass plots.
Appendix S4. Species associated with each cluster.
Appendix S5. Significance of dbRDA axes and contributing variables.
Appendix S6. Model performance.
Appendix S7. Partial dependence plots.

