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Marked spatial heterogeneity of macro-benthic communities along a shallow-mesophotic depth gradient in Reunion Island

Ludovic Hoarau[1,2,3], François Guilhaumon[1], Sophie Bureau[1,3], Perrine Mangion[1], Priscille Labarrère[2], Lionel Bigot[1,3], Pascale Chabanet[1,3], Lucie Penin[1,3] & Mehdi Adjeroud[3,4,5]

Mesophotic coral ecosystems (MCEs) have gained considerable attention this last decade but the paucity of knowledge on these ecosystems is pronounced, particularly in the Southwestern Indian Ocean region. We explore the spatial variation in macro-benthic and scleractinian communities along a wide depth gradient (15–95 m) and among contrasted sites around Reunion Island. Values for percent

vertical zonation of communities. We recorded a transition of light-dependent communities towards heterotrophic organisms between shallow and upper mesophotic zones at 30–45 m, and a community shift in the lower mesophotic zone at 75 m. Despite overlaps in scleractinian genera distribution along the depth gradient, predominant genera of shallow depths were in low abundance in MCEs (> 30 m).

habitats and harboring abundant cnidarian-habitat forming organisms. Supporting the 'Deep Reef Refuge Hypothesis', 56% of scleractinian genera spanned shallow to mesophotic depths, while one-third were depth specialists, either shallow or mesophotic. This highlights the limited refuge potential of mesophotic reefs for Southwestern Indian Ocean coral communities.
data for monitoring and conserving Reunion Island's MCEs.

Keywords Mesophotic coral ecosystems, Benthic communities, Community shift, Deep refuge hypothesis, Reunion Island, Southwestern Indian Ocean

Current coral reef assessment and temporal monitoring are mostly restricted to euphotic zones (reef flats, lagoon patch reefs, shallow fore reef, and outer slope) not exceeding 30 m depths (hereafter shallow zones). The limit of 30 m is widely, but arbitrarily, considered as the starting depth horizon of mesophotic coral ecosystems (MCEs), defined as 'middle-light' ecosystems of tropical and sub-tropical, light-dependent macro-benthic communities[1] MCEs are traditionally divided into an upper zone that starts around 30–40 m depth, and a lower zone from ~ 60–80 down to ~ 150 m depth. The largest surfaces covered by reef corals and other reef ecosystem engineers are distributed along this depth 'twilight' horizon[2,3]. Hence, MCEs would represent the "invisible" submerged part of the coral ecosystem iceberg, covering more than 3/4 of coral dominated habitat extent[4,5]. There is therefore an urgent need for assessing the diversity and distribution of these ecosystems and understanding the environmental factors and anthropogenic stressors responsible for structural and functional community changes, especially in the context of global degradation of coral reefs and other marine habitats worldwide[6–10].

Studying MCEs is challenging due to financial and technical constraints[11–13]. However, the development of non-destructive, deep-sea observation technologies, including mixed-gas and closed or semi-closed-circuit rebreathers[14,15] has led to increased scientific attention to these ecosystems[16–18]. Further, MCEs are of greater interest due to their unique biodiversity[19] and their potential role as refuges for shallow-water species[20–23]. The "Deep Reef Refugia Hypothesis (DRRH)"[20,24] assumes sufficient vertical connectivity between populations[25]

[1]UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de Nouvelle-Calédonie), Saint-Denis, La Réunion, France. [2]Grand Port Maritime De La Réunion, Le Port, La Réunion, France. [3]Laboratoire d'Excellence CORAIL, Paris, France. [4]UMR ENTROPIE (IRD, Université de La Réunion, CNRS, IFREMER, Université de Nouvelle-Calédonie), Perpignan, France. [5]PSL Université Paris, UAR 3278 CRIOBE - EPHE-UPVD-CNRS, 66860 Perpignan, France. email: ludovic.remy.hoarau@gmail.com

and relative preservation of mesophotic habitats from disturbances (i.e., depth refuge[23]). However, the DRRH is largely debated[26] and may be context-dependent, varying by region, species and the depth range considered[27]. For example, the ability of mesophotic populations to replenish their shallow-water counterparts varies among species[28] and is particularly limited for species with reduced reproductive performances[29]. Several studies suggest that MCE populations may be genetically distinct from shallow reefs[30,31] or lack vertical connectivity[19,28,32–35]. While the DRRH implies that mesophotic habitats are relatively preserved from large-scale disturbances such as cyclones, thermal bleaching events, or outbreaks of coral predators such as the sea star *Acanthaster* spp., MCEs have been shown to be impacted by environmental and anthropogenic disturbances and, in some cases, are threatened as much as their shallow counterparts[36–42].

From the information available, it appears that macro-benthic communities shift towards a distinct zonation of communities along the bathymetric gradient[3,43–47]. The gradients of environmental conditions with increasing depth, including temperature and light[48,49], are the main drivers of this zonation[50,51]. The lower mesophotic zone hosts depth-specialist species adapted to deep environment conditions[47,52–54], which can unexpectedly present high coral cover[55–57], biodiversity and rate of endemism[58–60]. However, the ecological division of mesophotic zones is based on a limited number of studies and regions, preventing generalizations about biogeographic patterns and changes in macro-benthic community structure along a bathymetric gradient[53]. Regional environmental differences can lead to significant variations in organism composition at these depths[21], resulting in distinct communities[61]. Furthermore, community overlap between shallow zones and MCEs can vary by region and taxon[62–64]. For example, the proportion of species present in both shallow zones and MCEs varies geographically and taxonomically between 26 and 97%[65]. The depth limits of MCEs exhibit even greater variability, as illustrated by the identification of new species[66] and extension of horizontal and vertical distribution[67–70].

Quantitative studies over a large depth gradient in MCEs are limited in the Indian Ocean[5,65], with previous reports only in Seychelles[71,72], Tanzania[73] and the Chagos Archipelago[74]. Moreover, studies have rarely resulted in coral reef conservation plans, and if so are often designed for shallow zones[75,76]. Reunion Island is part of Mascarene Islands, an ecoregion of the Western Indian Ocean recently categorized as 'critically endangered' facing the highest levels of risk of coral reef ecosystems collapses in the region[77]. Several local studies have been conducted on the benthic communities at shallow coral reefs and lava flows[78–83]. Moreover, the mesophotic zone of Reunion Island, represents roughly 70% of the coastal habitats between 0 and 150 m depth[4,5], underscoring the importance of increasing our knowledge of MCEs. Confronted with multiple disturbances from various origins, a better understanding of the ecological characteristics of deeper ecosystems is required to support adequate conservation strategies for coral reef ecosystems[84,85]. Identifying key habitats and community structures of MCEs, and monitoring any changes that occur, is a necessary step before addressing the ecological processes and the function of deep habitats as refuges[17,44,86,87]. Having this knowledge will enable the identification of the various threats that these MCEs are facing, the characterization of potential community changes, and the development of appropriate management and conservation strategies[73,88,89].

Benthic communities in Reunion Island are distributed along a narrow insular shelf that extends up to 5 km from the coast. Hitherto, cover and diversity of scleractinian corals from the shallow reef flat up to 40 m was poorly studied and only on the western coral reef[90,91]. Recent explorations into the lower mesophotic zone using closed-circuit rebreathers have led to the discovery of localized, distinct deep cnidarian compositions and high coral cover[57,92]. Quantifying the spatial patterns of macro-benthic communities across various island locations and along the full shallow-mesophotic gradient can help identify specific and unique habitats, as well as those that provide potential spatial or temporal refuge for biodiversity under environmental changes and anthropogenic stressors (but see[19]).

In this study, we provide the first quantitative information of MCEs around Reunion Island, examining the spatial patterns of sessile macro-benthic community structure, with a focus on diversity of scleractinian corals across various locations and depths (15–95 m). In this context, we addressed the following questions: How does composition, cover and abundance of sessile macro-benthic communities vary among locations (horizontal variation) and depths (vertical variation)? What are the implications of our results for the DRRH and the consequences for the management and conservation of MCEs in Reunion Island?

Materials and methods

Study sites

Reunion Island is a small volcanic island (ca. ~ 3500 km^2) of the Mascarene Archipelago (along with Mauritius and Rodrigues islands) in the Southwestern Indian Ocean (SWIO) located 700 km east of Madagascar. The coast of Reunion Island extends for 150 km and features a narrow, 25 km long fringing coral reef (~ 12 km^2 area) off the western and southwestern parts of the island. The southeastern coast is characterized by volcanic lava flows from modern eruptive events, with several eruptions that flowed into the ocean over the last two decades, such as those in 2007[93,94]. The northern part of Reunion Island has manmade concrete artificial blocks and patch reefs dominated by unconsolidated substrates and is consistently influenced from watershed flows and coastline shoreline modification. The coastline of Reunion Island is distinguished by the extremely narrow island shelf and steep slopes. To account for these contrasting coastlines and provide a comprehensive understanding of the island's ecological characteristics, four representative locations were investigated between September 2021 and September 2023: the fringing coral reef on the leeward western coast (Fig. 1a), the extended insular shelf (Fig. 1b), the island's main commercial and maritime port, on the northwestern coast (Fig. 1c), and the volcanic lava flow location on the windward southeastern coast (Fig. 1d). Ten sites dominated by hard substrates across the four locations of the island were selected: three coral reef sites (R1, R2 and R3), three port sites (P1, P2 and P3), three volcanic lava flow sites (V1, V2 and V3) and a single site on the most extended insular shelf (S) along the island's coast. At each site, six depths horizons (i.e., 15, 30, 45, 60, 75, and 95 m) were surveyed (Fig. 1), thus representing a total of 60 stations. Sites within each location were located at least 2 km away from each

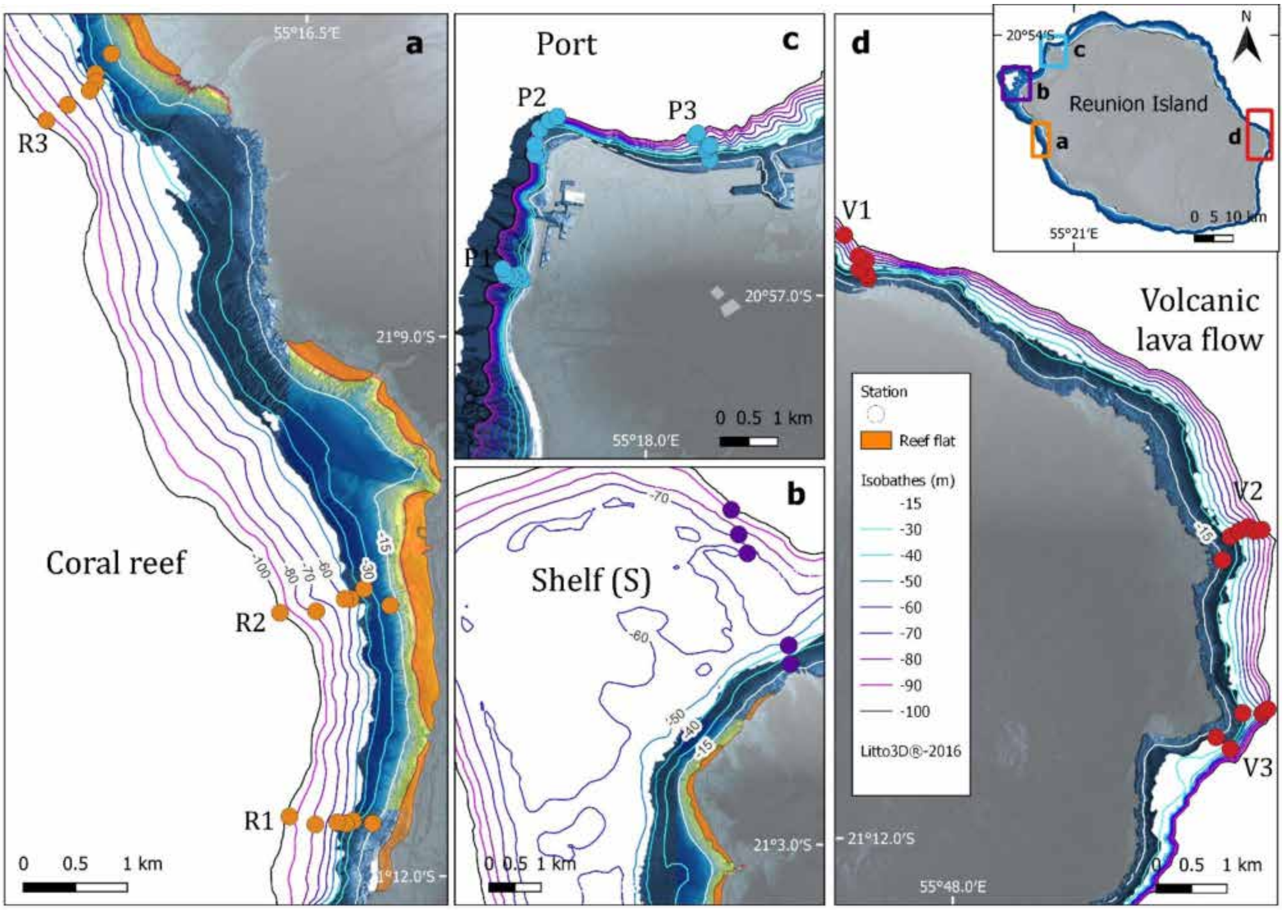

Fig. 1. Location of the 60 stations among the 10 sites at four locations around Reunion Island: (**a**) coral reef (insert in yellow), (**b**) shelf (in purple), (**c**) port (in blue) and (**d**) volcanic lava flow (in red). At each site, stations were disposed at six depths: 15, 30, 45, 60, 75, and 95 m.

other and were selected according to the likelihood of presence of hard-bottom habitats based on knowledge from previous habitat mapping and bottom drop-camera inspections revealing seabed types and sedimentary forms (CARTOMAR project of sedimentological mapping of the coastal seabed of Reunion Island from − 20 to − 100 m deep).

Sampling of macro-benthic communities

Stations were surveyed by technical SCUBA and closed-circuit rebreathers using TRIMIX below 50 m depth. Given the technical diving constraints and the framework of our objectives, we selected the photo-quadrat method as the best sampling protocol for studying macro-benthic community structure of MCEs. At each station, 40 photo-quadrats (50 × 50 cm, covering a total area of 10 m^2 per station) were randomly placed along each isobath, avoiding overlap in the photo-quadrats by taking pictures every alternate meter. These were performed by divers using a Sony α7C camera in a Nauticam Housing, with a 28 mm lens, 24.2-Megapixel high-definition resolution and two Sea & Sea YS-D2J lights mounted to a 0.85 m high steel fabricated monopod, which permitted a consistent angle and orthogonal height above the substrate for all photos. The 40 photo-quadrats from each station were used as replicates to calculate the mean percent cover and densities of macro-benthic community organisms. All 2400 photo-quadrats were analyzed by a single and same observer to limit potential biases.

Cover (%) of macro-benthic organisms was estimated using Coral Point Count with Excel Extension software (CPCe)[95] based on 50 randomly distributed points per image. Nine categories of major macro-benthic organisms were considered: scleractinians, antipatharians, octocorals, hydrozoans (macro-benthic hydrozoan colonies > 1 cm in height for the following genera: *Zygophylax*, *Sertularia*, *Sertularella*, *Macrorhynchia,* and *Antenella*, and those forming a calcareous skeleton: *Millepora*, *Stylaster* and *Distichopora*), crustose coralline algae (CCA), turf algae, macroalgae (including *Dictyota*, *Lobophora* and *Halimeda)*, sponges, other sessile macro-benthic invertebrates (i.e., actiniarians, ascidians, corallimorpharians, foraminifers, bryozoans and zoanthids).

Photo-quadrats provided a quantitative method to assess coral communities at depths of up to 95 m, albeit with the constraint of limiting data collection to the genus level. This compromise in taxonomic resolution was considered acceptable, given the challenges of accurately identifying corals to the species level in the field, even during direct observation. Moreover, generic diversity indices have been successfully applied in previous studies to explore scleractinian diversity across depth gradients, demonstrating their value in informing conservation and management strategies[9,47,96]. Scleractinian corals were identified by experts to the genus level based on the identification guides and the updated taxonomic classification of scleractinians[97–100]. Family identification for octocorals was done following identification guides and from the lists of locally identified and described species[78,101–104] and based on the last revised classification of octocorals[105]. For antipatharian and hydrozoan corals, family identification was done following identification guides and from previous works on these specific taxa in the region[92,106,107]. Cnidarian taxa was verified with World Register of Marine Species (WORMS). To quantify cnidaria density (colonies.m^{-2}), we counted every scleractinian (juveniles $<$ 5 cm in colony diameter, and adults $\geq$ 5 cm), antipatharian, octocoral and hydrozoan corals (only colonies forming a calcareous skeleton: *Millepora*, *Stylaster* and *Distichopora*) using ImageJ software[108].

Environmental variables

Temperature was measured during seven months (between September 2022 and April 2023, therefore capturing two austral winter months followed by five summer months) with a 15 min interval with HOBO Water Temperature Pro v2 Data loggers. These environmental parameter loggers were deployed at 15, 45 and 75 m depths at 3 sites (coral reef R2, port P3 and volcanic lava flow V2), thus encompassing nine stations. Photosynthetically active radiation (PAR) was also measured during seven months (between September 2022 and April 2023) with a 15 min interval with DEFI2-L JFE Advantech light-irradiance loggers. Only the first 15 days of light records were considered in winter and in summer when loggers were fixed because of the potential effects biofouling on the logger over a longer period. As for temperature loggers, light loggers were deployed at 15, 45 and 75 m depths at the same as above nine stations. Since temperature and light were not recorded at all stations, these parameters were not considered in the statistical analyses but were used for data interpretation (Supplementary Figs. S1–S4).

Statistical analyses

We analyzed the spatial variation of all macro-benthic categories cover at the four locations and among depths using linear models (LM). Linear models were preferred over linear-mixed models and generalized linear (mixed) models (site within location as a random factor) since, when comparing the full models, LM produced the lowest corrected Akaike's information criterion (AICc[109]) and avoided overdispersion (function *testDispersion* of 'DHARMa' R package). All statistical analyses were conducted using R version v4.3.0 (R Development Core Team 4.3.0, 2023). The full model considered was: depth + depth^2 + location + depth:location + depth^2:location. A parabolic relationship with depth (i.e., a quadratic term of depth) was included in the models to account for potential hump-shaped relationships between depth on macro-benthic cover and coral richness[110]. The most parsimonious combinations of fixed effects were found using model selection based on AICc (models fitted using maximum likelihood). We used the function *dredge* of 'MuMIn' package to fit a complete set of models with all possible combinations of the explanatory variables. We then determined the subset of 'best models' as the ones with ΔAICc value $<$ 2 (the difference between each model's AICc and the AICc of the best model). In addition, we used Akaike weights derived from the AICc (wAICc) to evaluate the relative likelihood of each model, given the dataset and the set of models taken into account, and to assess the relative importance of each variable by summing these wAICc across the models in which they were included. Akaike weights were directly interpreted in terms of each model's probability of being the best at explaining the data[109].

To visualize dissimilarities in horizontal (across locations along Reunion Island coasts) and vertical (along the depth gradient) composition of sessile macro-benthic and scleractinian assemblages, we used non-metric multidimensional scaling (NMDS) based on Bray–Curtis distances calculated on percent cover data. NMDS were performed using the function *metaMDS* of the 'vegan' package[111]. The function *envfit* was used to obtain the fitted correlation vector scores for different macro-benthic categories and scleractinian genera. Macro-benthic categories and scleractinian genera that exhibited significant correlations ($p < 0.05$) were then visualized using a biplot created with the 'ggplot2' R package[112].

To test for vertical and horizontal differences between macro-benthic, cnidarian and scleractinian communities, we conducted distance-based permutational multivariate analysis of variance (PERMANOVA[113]). All models were run with 9999 permutations using the R 'vegan' package with *vegdist* and *adonis2* functions[111]. If the PERMANOVA results were significant, a post hoc multilevel pairwise analysis was performed using the *pairwise.adonis* function in the 'Pairwise-adonis' package with Benjamini and Hochberg-corrected *p* values[114]. Homogeneity of variance was tested using the *betadisper* and *permutest* functions to check for the effect of within-group dispersion[115].

Results

Environmental variables

Temperature values decreased with increasing depth across the three locations (i.e., coral reef, port and volcanic lava flow) and seasonality was substantial. Temperature values exhibited significant variability during the summer, with pronounced differences observed between depths throughout the season (Supplementary Fig. S1). During the recorded period (September 2022 to April 2023) at 15 m depth, the average daily temperature was 26.2 ± 1.8 °C (mean ± standard deviation) on the coral reef, 26.2 ± 1.7 °C at port, and 25.7 ± 1.6 °C on volcanic lava flow. At 45 m, daily temperature averaged 25.4 ± 1.4 °C, 25.3 ± 1.3 °C and 24.9 ± 1.3 °C, at the three locations respectively. At 75 m, we recorded 24.1 ± 0.8 °C, 23.7 ± 0.6 °C and 23.7 ± 0.6 °C, respectively. In winter 2022 (September–October 2022), temperature differences between depths were minimal at all three locations, with mean daily temperature ranging between 23.2 and 23.7 °C, across depths and locations. In summer (November 2022–April 2023), daily temperatures averaged 27.0 ± 1.2 °C at 15 m, 26.0 ± 1.1 °C at 45 m, and 24.4 ± 0.8 °C at 75 m on the coral reef; 27.0 ± 1.2 °C at 15 m, 25.8 ± 1.0 °C at 45 m, and 23.9 ± 0.6 °C at 75 m at port; and 26.3 ± 2.3 °C at 15 m, 25.3 ± 2.3 °C at 45 m, and 23.7 ± 2.0 °C at 75 m on lava flow.

PAR is highly dependent on location, time of the day and season (Supplementary Figs. S2–S4). The median of these peak values representing typical exposure recorded over the entire period shows that the 10% of surface PAR was recorded between 41 and 55 m depth across the three locations. The 1% and 0.1% surface PAR values were measured between 82 and 109 m, and between 124 and 164 m depth, respectively.

Macro-benthic cover and cnidarian abundance

Overall (all stations pooled), macro-benthic communities of hard substrates were dominated by turf algae (37.7 ± 2.6%, mean ± SE), CCA (16.5 ± 1.8%,), scleractinians (9.8 ± 1.6%,), and sponges (6.9 ± 1.3%). We found low covers of macroalgae (3.6 ± 0.6%), hydrozoans (2.7 ± 0.7%), octocorals (1.8 ± 0.4%), antipatharians (0.4 ± 0.1%) and other sessile macro-benthic organisms (0.1 ± 0.3%). Mean percent cover of benthic communities showed contrasted patterns among depths and locations (Fig. 2, Supplementary Figs. S5–S8).

According to the AICc-based model selection procedure, the variation in scleractinian cover was best explained by location and depth (Table 1). Location was included in all best models and therefore had the maximum value of relative importance (1.00). Depth was included in two models and had a value of importance of 0.73. The depths 15 m and 60 m presented on average the highest scleractinian cover (mean ± SE: 14.0 ± 2.9% and 13.0 ± 4.3%, respectively; Supplementary Fig. S7) and 95 m the lowest (1.6 ± 3.3%). Volcanic lava flow harbored higher scleractinian cover (15.8 ± 3.8%) than port stations (3.3 ± 1.1%; Supplementary Fig. S6). The highest values of scleractinian percent cover occurred on lava flow at V2 at 75 m and 60 m (59.4 ± 1.8% and 46.1 ± 2.5%, respectively) and on coral reef at R2 at 45 m (43.4 ± 3.1%) (see Fig. 2). Likewise, depth and location were important to explain the variation of octocorals and antipatharians cover (Table 1). The quadratic term of depth and the interaction of depth and location weakly predicted the percent cover of octocorals and antipatharians. Cover of antipatharians were the highest for several stations at 75 m (1.1 ± 0.6%) and 95 m (0.6 ± 0.2%) in comparison with stations at 15 m and 30 m depth where antipatharians were nearly absent (0.01 ± 0.01%; Supplementary Fig. S6). The highest percent cover of octocorals was found at port (mean ± SE = 3.0 ± 0.9%; range at 45–95 m depth: 7.5–12.5%). Depth and locations had also a strong influence on hydrozoans percent cover (relative importance of 0.53 and 1 respectively) while depth^2 has a weak influence (0.18). The highest percent cover of hydrozoans was found at volcanic lava flows (5.4 ± 2.1%; Fig. 2).

For CCA cover, depth and depth^2 had the maximum relative importance of 1.00, and location with 0.61. Intermediate depths (45 and 60 m) presented the highest cover of CCA (24.5 ± 4.0% and 22.4 ± 4.6%, respectively) while at 15 m there was the lowest cover of CCA (8.8 ± 1.9%). Port presented the lowest cover of CCA (10.7 ± 2.3%) while volcanic lava flow showed the highest value (22.1 ± 3.7%). Depth and location were important factors explaining the variation of turf algae cover that was the highest at the shallowest depths, 15 m (59.3 ± 3.8%) and 30 m (49.4 ± 5.9%), with the lowest values recorded at 95 m depth (14.0 ± 3.0%). Port presented the highest turf algae cover (44.1 ± 4.6%) while volcanic lava flow showed the lowest ones (30.0 ± 4.7%). For macroalgae cover, only location was included in the model. Overall, macroalgae was the highest at volcanic lava flows (5.8 ± 1.3%).

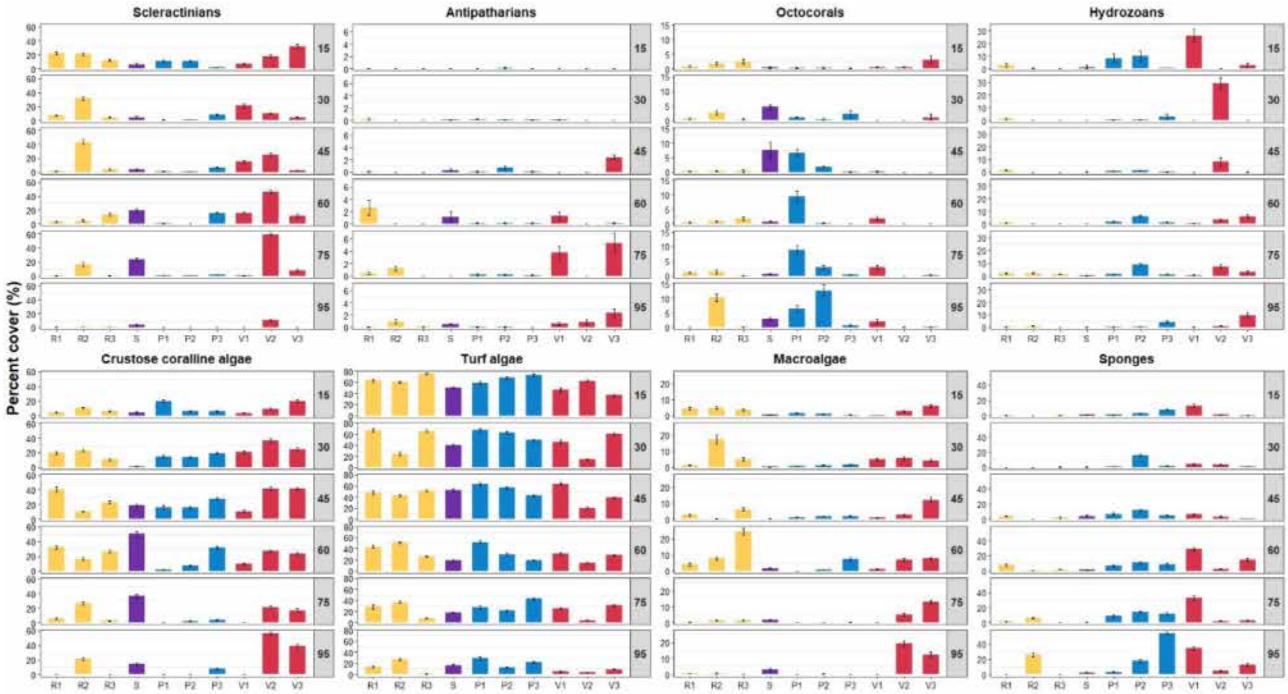

Fig. 2. Mean percent cover of eight sessile macro-benthic categories at the 60 stations, disposed across the 10 sites (with coral reef sites in yellow, shelf in purple, port in blue, and volcanic lava flow in red) and the 6 depths (15, 30, 45, 60, 75, and 95 m). Error bars indicate ± SE.

Variables	**Intercept**	**Depth**	**Depth^2**	**Location**	**Depth:Location**	**Depth^2:Location**	***df***	***logLik***	***AICc***	***ΔAICc***	***wAICc***
Scleractinians	15.680	− 0.103	NI	+	NI	NI	6	− 229.524	472.6	0	0.477
	10.170	NI	NI	+	NI	NI	5	− 231.349	473.8	1.18	0.265
	9.884	0.175	− 0.0025	+	NI	NI	7	− 228.856	473.9	1.23	0.258
Importance		**0.735**	**0.258**	**1**							
Coefficient		**− 0.005**	**− 0.0025**		**0**	**0**					
Octocorals	1.407	0.027	NI	+	NI	NI	6	− 141.141	295.9	0	0.352
	3.376	− 0.010	NI	+	+	NI	9	− 137.281	296.2	0.30	0.304
	0.400	0.027	NI	NI	NI	NI	3	− 145.265	297.0	1.09	0.204
	2.379	− 0.020	0.0004	+	NI	NI	7	− 140.786	297.7	1.86	0.139
Importance		**1**	**0.14**	**0.8**	**0.3**						
Coefficient		**0.009**	**0.0004**								
Antipatharians	− 0.227	0.011	NI	+	NI	NI	6	− 76.095	165.8	0	0.366
	− 0.121	0.011	NI	NI	NI	NI	3	− 80.108	166.6	0.87	0.237
	0.029	0.006	NI	+	+	NI	9	− 72.594	166.8	1.01	0.220
	− 0.638	0.030	− 0.0002	+	NI	NI	7	− 75.537	167.2	1.45	0.177
Importance		**1**	**0.18**	**0.76**	**0.22**						
Coefficient		**0.013**	**− 0.0002**								
Hydrozoans	0.300	NI	NI	+	NI	NI	5	− 181.177	373.5	0	0.464
	2.068	− 0.033	NI	+	NI	NI	6	− 180.191	374.0	0.50	0.361
	4.417	− 0.146	0.001	+	NI	NI	7	− 179.624	375.4	1.94	0.176
Importance		**0.54**	**0.18**	**1**							
Coefficient		**− 0.070**	**0.001**								
CCA	5.528	0.731	− 0.007	+	NI	NI	7	− 234.797	485.7	0	0.611
	1.279	0.731	− 0.007	NI	NI	NI	4	− 238.960	486.6	0.9	0.389
Importance		**1**	**1**	**0.61**							
Coefficient		**0.731**	**− 0.007**								
Turf algae	63.25	− 0.578	NI	+	NI	NI	6	− 231.526	476.6	0	1
Importance		**1**		**1**							
Coefficient		**− 0.578**									
Macroalgae	1.217	NI	NI	+	NI	NI	5	− 175.732	362.6	0	1
Importance				**1**							
Coefficient											
Sponges	− 6.788	0.156	NI	+	NI	NI	6	− 212.806	439.2	0	0.652
	− 2.432	− 0.053	0.002	+	NI	NI	7	− 212.147	440.4	1.25	0.348
Importance		**1**	**0.35**	**1**							
Coefficient		**0.083**	**0.002**								
Others sessile	0.799	− 0.019	0.0002	+	NI	+	10	− 101.492	227.5	0	0.692
	− 1.106	0.066	− 0.0005	+	+	+	13	− 97.591	229.1	1.62	0.308
Importance		**1**	**1**	**1**	**0.31**	**1**					
Coefficient		**0.034**	**< 0.0001**								

Table 1. Summary of best linear models used to describe variation of macro-benthic cover. The importance of each variable is estimated by summing, for each combination of variable, the Akaike weights of the models in which it was included. NI indicates that the variable was not included in the model. CCA: crustose coralline algae. Significant values are in [bold].

The percent cover of sponges was strongly influence by depth and location (both having a relative importance of 1.00) with the highest cover recorded at 95 m (15.6 ± 5.7%), and the lowest at 15 m (2.7 ± 1.3%). Thus, coral reef and shelf displayed the lowest mean sponge cover (2.8 ± 1.5% and 1.6 ± 0.6% respectively) while volcanic lava flows and port displayed in comparison higher value (9.3 ± 2.7% and 10.4 ± 2.8% respectively). Other sessile macro-benthic cover was the highest at the greatest depths, 60 m (1.82 ± 0.6%), 75 m (1.02 ± 0.2%) and 95 m (3.5 ± 1.0%), in comparison with 15 m (0.02 ± 0.01%) and 30 m (0.07 ± 0.03%) (Supplementary Fig. S8).

Cnidarian density showed contrasted patterns among depths and locations (Fig. 3; Supplementary Figs. S9 and S10). For scleractinian, octocoral and antipatharian densities, depth had the maximum relative importance of 1.00. Location also had a strong influence on scleractinian and hydrozoan densities (relative importance of 0.73 and 1.00, respectively). Depth^2 was only considered significantly important for scleractinians but had a weak influence on their densities (0.22). Location also had a relatively weak influence on octocoral and antipatharian densities (relative importance of 0.38 and 0.42 respectively) (Table 2).

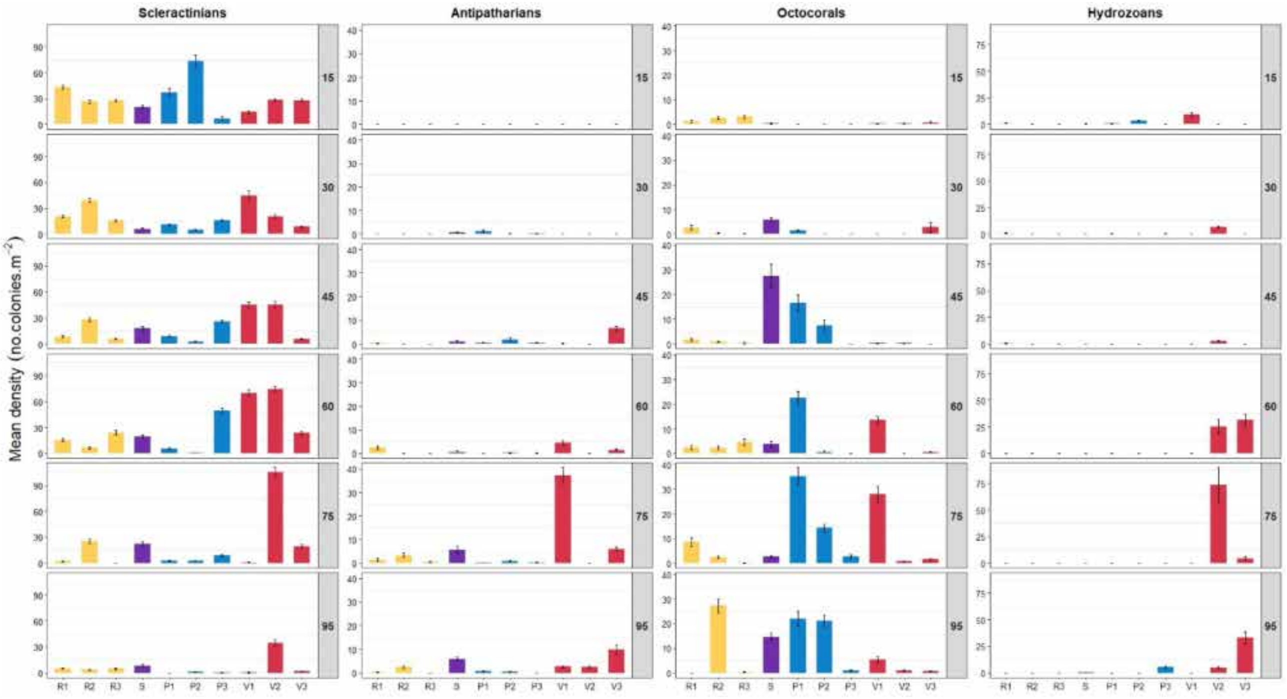

Fig. 3. Mean density (number of colonies.m^{-2}) of cnidarian (scleractinians, octocorals, antipatharians and hydrozoans) at the 60 stations disposed across the 10 sites (with coral reef sites in yellow, shelf in purple, port in blue, and volcanic lava flow in red) and 6 depths (15, 30, 45, 60, 75, and 95 m). Error bars indicate ± S.E.

Variables	Intercept	Depth	Depth^2	Location	Depth:Location	Depth^2:Location	*df*	*logLik*	*AICc*	*ΔAICc*	*wAICc*
Scleractinians	27.94	− 0.21	NI	+	NI	NI	6	− 262.391	538.4	0	0.514
	31.54	− 0.21	NI	NI	NI	NI	3	− 266.611	539.6	1.28	0.270
	20.01	0.171	− 0.0035	+	NI	NI	7	− 261.974	540.1	1.74	0.216
Importance		**1**	**0.22**	**0.73**							
Coefficient		**− 0.128**	**− 0.0035**								
Octocorals	-1.116	0.12	NI	NI	NI	NI	3	− 209.971	426.4	0	0.618
	-3.024	0.12	NI	+	NI	NI	6	− 206.873	427.3	0.96	0.382
Importance		**1**		**0.38**							
Coefficient		**0.12**									
Antipatharians	-0.913	0.049	NI	NI	NI	NI	3	− 179.969	366.4	0	0.581
	-2.033	0.049	NI	+	NI	NI	6	− 176.718	367.0	0.66	0.419
Importance		**1**		**0.42**	**0.22**						
Coefficient		**0.049**									
Hydrozoans	0.161	NI	NI	+	NI	NI	5	− 224.871	460.9	0	0.547
	-3.616	− 0.071	NI	+	NI	NI	6	− 223.822	461.2	0.38	0.453
Importance		**0.45**		**1**							
Coefficient		**− 0.071**									

Table 2. Summary of best linear models used to describe variation of cnidarian density. The importance of each variable is estimated by summing, for each combination of variable, the Akaike weights of the models in which it was included. NI indicates that the variable was not included in the model. Significant values are in [bold].

Macro-benthic communities and scleractinian assemblages

The macro-benthic community structure varied significantly among depths ($R^2 = 0.21$, pseudo-F = 18.78, $p = 0.0001$; *betadisper*, pseudo-F = 6.47, $p = 0.001$; Supplementary Table S1A). The NMDS illustrates that the assemblage structure of sessile macro-benthic categories at 15 m is distinct from the assemblage structure at all other depths, except for the 30 m depth. Likewise, there are also clear separations of macro-benthic assemblages between 30–45 m and 75–95 m (Fig. 4a). These distinctions (depth zonation) were confirmed through the pairwise comparisons of macro-macro-benthic community structures along the depth gradient (Supplementary Table S6B). The location also has a significant effect on the assemblage structure ($R^2 = 0.127$, $F = 3.746$, $p = 0.0001$, Supplementary Table S1A), and no significance within-group dispersions was detected (*betadisper*, pseudo-$F = 0.598$, $p = 0.594$; Fig. 4b). Pairwise comparisons showed significant differences between port and all other locations as well as between coral reef and volcanic lava flow (Supplementary Table S1C).

We also found a significant interaction between depth and location (Supplementary Table S6) suggesting divergent vertical patterns of variability in the composition of sessile macro-benthic assemblages among locations. The NMDS (Fig. 4a,b) and PERMANOVA results suggested that depth had a greater influence on macro-benthic community structure than location. The highest variability in macro-benthic community structure was recorded at the greatest depths (*betadisper* $p = 0.001$, average distance to centroids at 60 m, 75 m and 95 m depths of 0.27, 0.36 and 0.44 respectively; Supplementary Fig. S11a). The variability of macro-benthic community structure was the lowest at 15 m depth (average distance to centroid 0.16; Fig. 4a). Variation in macro-benthic assemblage structure was mainly driven by scleractinians, turf algae, CCA and sponges (Supplementary Fig. S12).

A total of 39 scleractinian genera from 16 families were identified across all the study stations. A depth distribution analysis revealed that most of these genera were distributed in the mesophotic zone below 30 m depth (Fig. 5). The scleractinian generic richness was the highest at 45 m depth (33 genera) and the lowest at 95 m depth (10 genera) (Supplementary Fig. S13). While most of genera were found along a large depth gradient from 15 to 60 m depths (depth-generalist), several genera were found along the entire studied depth gradient (i.e., *Montipora*, *Echinophyllia*, *Pachyseris* and *Leptoseris*), four genera were found to be restricted to shallow sites ≤ 30 m depth (i.e., shallow-specialist: *Psammocora*, *Galaxea*, *Platygyra* and *Herpolitha*) and nine genera

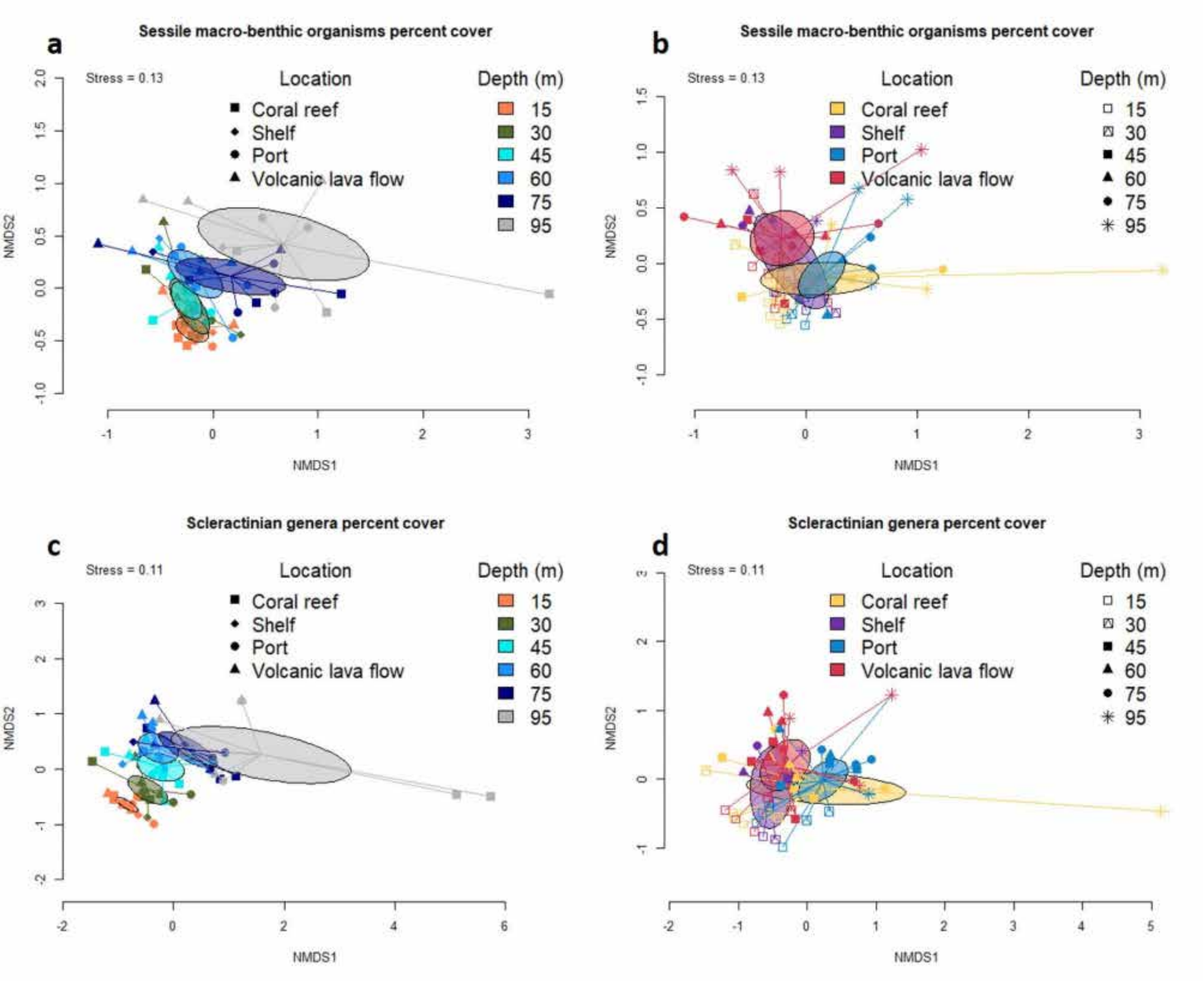

Fig. 4. Non-metric multidimensional scaling (NMDS) of percent cover of sessile macro-benthic (**a** and **b**) and scleractinian (**c** and **d**) communities based on untransformed Bray–Curtis dissimilarity distance matrix. Different symbols represent locations and ellipses the standard error with 95% confidence limit of depth centroid (**a** and **c**). Different symbols represent depths and ellipses the standard error with 95% confidence limit of location centroid (**b** and **d**).

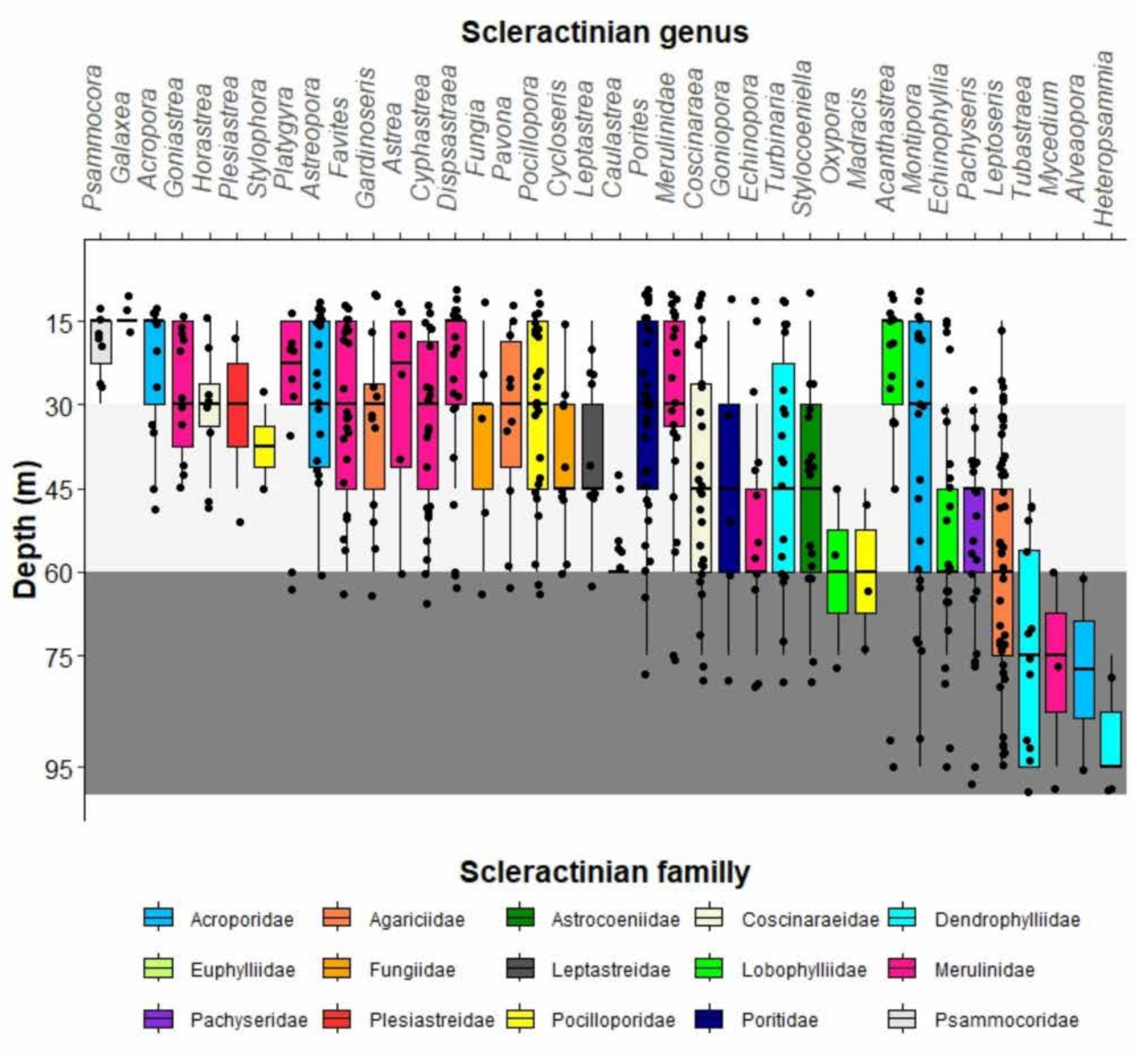

Fig. 5. Depth distribution of the different genera pooled for the ten study sites of Reunion Island. Different colors represent different scleractinian families. Boxplots show presence–absence of scleractinian genera at 15, 30, 45, 60, 75 and 95 m depths. The changes from white to grey shading backgrounds highlight shallow depths (< 30 m), upper (30–60 m), and lower (> 60 m) mesophotic depths respectively, as commonly delimited. Note that two genera *Herpolitha* (Fungiidae) and *Scolymia* (Faviidae) are not displayed as they were found at only one station at 30 m and 75 m, respectively.

occurred almost exclusively in the deepest sites (e.g., depth-specialist mainly found below 45 m depth: *Caulastrea*, *Oxypora*, *Madracis*, *Echinophyllia*, *Pachyseris*, *Tubastraea*, *Mycedium*, *Alveopora* and *Heteropsammia*).

Composition of scleractinian assemblages varied significantly among depths (Fig. 4c; $R^2 = 0.13$, pseudo-F = 9.192, $p = 0.0001$; *betadisper*, pseudo-F = 2.957, $p = 0.017$) and among locations (Fig. 4d; $R^2 = 0.08$, pseudo-F = 1.841, $p = 0.0031$; *betadisper*, pseudo-F = 1.623, $p = 0.187$; Supplementary Table S2A). Pairwise comparisons among the six depth zones revealed significant differences between 15 m and all others depths. As with macro-benthic communities, composition of scleractinian assemblages varied significantly between depths at 30 and 45 m compared to 75 and 95 m, and between 60 and 95 m (Supplementary Table S2A). A significant variation in the composition of scleractinian assemblages was found between port and volcanic lava flow (Supplementary Table S2B). The highest variability in scleractinian community structure was recorded at 95 m and at 45 m depths, while the shallowest depth displayed the lowest variability (Fig. 4c, Supplementary Fig. S11b).

Variation in the composition of scleractinian assemblages was significantly driven by *Heteropsammia*, *Tubastrea* and *Leptoseris* in the deepest sites, and *Porites*, *Astreopora*, *Dipsastraea*, *Psammocora*, *Favites* and

Pocillopora in the shallowest sites (Supplementary Fig. S14). Some were dominant across sites (Supplementary Figs. S15 and S16). For instance, *Leptoseris*, *Pachyseris* and *Montipora* were dominant below 45 m depth, while *Pocillopora*, *Porites* and *Astreopora* were found in all locations but mostly in shallow depths at 15–30 m. *Pocillopora* dominated coral assemblages in all but one stations at 15 m (dominance of *Porites* at R2-15 m).

Likewise, they were substantial variations with depth and sites in the composition of antipatharian, octocoral and hydrozoan families (Supplementary Figs. S17 and S19).

Discussion

Our findings shed light on the depth zonation patterns observed in sessile macro-benthic, cnidarian and scleractinian communities, highlighting contrasted habitats within MCEs in Reunion Island. We point out a well-defined ecological zonation, characterized by a shift in both macro-benthic and scleractinian assemblages at 30–45 m and at 60–75 m. These changes indicate a clear distinction between shallow and upper mesophotic communities, as well as between upper and lower mesophotic communities respectively. Mesophotic macro-benthic communities around the island are clearly distinct from their shallow counterparts, as recently shown in studies in the region, in the Seychelles and the Chagos Archipelago[72,74]. Shallow benthic communities, dominated by autotrophic organisms such as algae and scleractinians, extend into the upper mesophotic zone. Here, the community composition overlaps with those of their shallow counterparts, and representing a transition zone between shallow and mesophotic community structure[16,27]. A significant cnidarian community shift was observed at 75 m with a clear change towards a decline in scleractinian densities but denser octocorals and antipatharians from this depth limit. The lower mesophotic macro-benthic communities are dominated by sponges, octocorals, antipatharians and other sessile organisms such as bryozoans and ascidians. This shift towards mixotrophic and/or heterotrophic dominated communities in the lower mesophotic zone at 60–80 m depth is congruent with other studies around the world, and is likely to represent a global pattern[17,27,45,48].

These boundaries of MCEs were further emphasized by our analyses on scleractinian assemblages and match previously established boundaries across other geographical regions, also occurring between 30 and 40 m[43,47] and from 60 m[46,47,96]. Scleractinian assemblages distinctly change with depth. *Pocillopora*, *Porites*, *Astreopora*, *Dipsastraea*, *Favites* and *Psammocora* are strongly associated with shallow scleractinian assemblages. Nine genera were mesophotic-depth specialists as they were recorded almost exclusively in the mesophotic zone (e.g., *Oxypora*, *Pachyseris*). Thus, our study specifically underscores the dominance of a few scleractinian genera at mesophotic depths, such as *Leptoseris*, *Pachyseris,* and *Montipora*. The dominance by these three genera was reported in MCEs across the Red Sea[47,116] and various Indo-Pacific regions[117,118], in French-Polynesia[119], in Hawaii[53], on the Great Barrier Reef[58] and in the central Indian Ocean[74]. Their vertical distribution is likely to reflect a host–symbiont depth specialization[120–122], and depth morphological, photo-acclimatization and photosynthetic adaptations[123–128]. Some hard corals may also be capable of increasing heterotrophic reliance to other resource allocations with increasing depth and decreasing light[123,124,129,130].

Our study shows that PAR (i.e., light) and temperature are important drivers of the structure of mesophotic macro-benthic and scleractinian communities at Reunion Island. Values of light and temperature decreased with depth, with a marked difference between shallow and mesophotic depths and a higher variability during summer. The 10% and 1% surface PAR values, representing the midpoint and endpoint of the euphotic zone where it is hypothesized that symbiont photosynthesis balances coral respiration[84], align with the NMDS sessile macro-benthic and scleractinian community separations (Fig. 4). The 10% surface PAR was recorded between 41 and 54 m. This suggests that 45 m represents the upper limit of MCEs across locations in Reunion Island. Roughly 1% surface PAR, often considered as the lower limit of the mesophotic zone[45], was found between 82 and 109 m depending on location. In the PERMANOVA analyses of macro-benthic and scleractinian assemblages, the 75–95 m depths displayed a significant separation from shallower depths ≤ 45 m (see Supplementary Tables S1 and S2), suggesting 75 m as the lower limit of MCEs in Reunion Island. Although irradiance values measured in this study are consistent with those close from the western Indian Ocean in the Chagos Archipelago[131], they can display important spatial and temporal variations. There are limitations in our data to indicate what depth zones at 1% or 0.1% surface PAR (based on the maximum depth of light-dependent benthic organisms as suggested by Laverick et al.[46]) are the most suitable boundary to be defined as the lower mesophotic zone. As our sampling did not extend beyond 95 m, it is unclear whether scleractinians and other light-dependent organisms are present at greater depths. Depth-related temperature variations are frequently identified as key drivers of MCEs[72,74,132]. These fluctuations arise from physical processes such as water column stratification, upwellings, and internal waves, which might change the thermocline, the pycnocline and nutrient availability[1,21,27]. In addition, seasonal high temperature with depth, can substantially affect mesophotic scleractinian coral mortality, as recently documented in the Chagos Archipelago[42]. Cold-water bleaching of a mesophotic coral reef was also recently documented in the Eastern Tropical Pacific at Clipperton Atoll[133]. Temperature therefore plays a key role in the structure of mesophotic communities and the regulation of their demographic processes.

In addition to the distinctness of MCEs from shallow habitats, our results highlight a strong spatial heterogeneity in MCEs macro-benthic and scleractinian assemblages among the four locations surveyed around Reunion Island. Cover and composition of both macro-benthic and scleractinian assemblages were highly variable among locations, specifically in MCEs. Scleractinian generic richness peaks at 45 m depth which could be attributed to a mid-domain effect (as in[96]). Pinehiro et al.[134] suggested intermediate levels of disturbance for shallow reefs[135] to explain the maintenance of long term scleractinian diversity in MCEs. Similarly to Pérez-Rosales et al.[96], the variation in composition between scleractinian communities increases with depth (i.e., beta-diversity[136,137]) and are the highest in MCEs. This highlights the uniqueness of mesophotic environments when comparing sites particularly across lower mesophotic sites (but see[138]). In contrast, shallow sites exhibit a greater similarity to each other.

Of the 39 scleractinian genera recorded in this study, 74% were observed at shallow depths (15–30 m) with only four genera restricted to these depths (Fig. 5). The majority of observed scleractinian genera (56%) have a large depth distribution extending from 15 m down to 60 m depths. Although these genera were often recorded in low abundance through the mesophotic zone, our findings suggest that upper mesophotic habitats (45–60 m) in Reunion Island may serve as a suitable space for the growth of these depth-generalist genera. In particular, *Pocillopora* and *Porites*, two ubiquitous and ecologically important reef building scleractinian corals dominating shallow depths, were found to be thriving in the upper mesophotic zone, which should encourage future research efforts to build on these genera with genetic and morphological analyses for species-level resolution, as the presence of these coral genera along a large depth gradient does not necessarily indicate that the same species are present. In other words, a coral genus found over a large depth gradient may likely be constituted of several species[139]. *Pocillopora* and *Porites* as for other scleractinian genera may exhibit generalist characteristics, yet comprises distinct species experiencing genetic isolation with subtle morphological differences[140] and a wealth of undescribed diversity within species, driving to taxonomic challenges[118,141–144]. On the other hand, the coral genera identified exclusively at a particular depth (Fig. 5) suggest the presence of distinct species adapted to that environment (e.g., *Madracis* exclusively found in the lower mesophotic zone). Our results highlight that 10% and 23% of recorded scleractinian genera were distributed at depths ≤ 30 m (shallow specialists) and > 30 m (mesophotic specialists), respectively. As a result, the first postulate of the DRRH implying a 'reseeding' potential of shallow habitat is unlikely for one third of these scleractinian genera and their corresponding pool of species. Therefore, although our results raise hope for the DRRH potential for a substantial proportion of scleractinian genera (56%), the validity of the DRRH at the whole reef community level is unlikely to hold under such ecological distinctness[19,145], particularly considering the lower MCEs communities[54]. The reproductive sources of MCEs species after disturbance or their active 'reseeding' potential of shallow habitat should be specifically evaluated[20,28]. Studies on the reproductive potential of mesophotic corals across extensive depth gradients are still limited. This scarcity hampers our ability to delineate trends within scleractinian species, thereby restricting our understanding of connectivity at the ecosystem scale. While some species, such as *Porites astreoides*, retain reproductive capacity at mesophotic depths[146], others show significant reductions in fecundity, oocyte size, or altered reproductive timing, limiting their potential to replenish shallow reefs[29]. For example, *Paramontastraea peresi* produces smaller and fewer oocytes in mesophotic habitats, likely due to energetic constraints from reduced light availability[147]. These findings further emphasize the need for species-specific studies to accurately assess the reseeding potential of MCEs for shallow reef recovery. In addition, the second DRRH postulate implies relative immunity of MCEs facing natural disturbances and anthropogenic stressors[20]. As in many MCEs in the world[148], discarded fishing lines and plastic debris entangled in habitat-forming taxa were observed at all locations in MCEs (Supplementary Fig. S20). This underlines the impact of anthropogenic pollutions on Reunion Island MCEs and the subsequent need for protection and consideration in the planning of marine protected areas.

The upper mesophotic zone also presents the highest percent cover of CCA. These algae components may be important contributors to the overall stability of coral ecosystems in the mesophotic environments[149]. In shallow reefs, CCA display a significant role in stabilizing sand and carbonate particles and participate in reef growth and carbonate production[150]. Some species can provide settlement cues for coral larvae, thus contributing significantly to coral larval settlement and survival in shallow habitats[151–153]. Moreover, CCA are known to contribute to the overall reef resilience[154]. However, their function role particularly in mesophotic ecosystems, might be more nuanced as the stabilizing function of CCA in the deeper environments could vary and may not be as prominent as in shallow reefs. This suggests that while CCA might support long-term persistence of reef communities (i.e., depth resilience areas sensu[23]), identifying CCA at species level and their impact in mesophotic ecosystems requires further examination.

We found that overall, scleractinian cover decreases with depth. This trend is expected for light-dependent organisms beyond scleractinians[43,46,48,58,155] (Supplementary Figs. S2–S4). However, several MCEs stations exhibited high scleractinian cover (40–60%). These results underline the unique biological nature and ecological value of mesophotic habitats, favorable for the survival and growth of corals at several locations. Mesophotic depths may indeed offer suitable refuge for locally high scleractinian cover (> 40% cover) as documented in various regions, for instance in the Caribbean Sea at Curaçao[56], the Pacific Ocean in Hawaii[50,53], in French Polynesia[119], on the Great Barrier Reef[156], at Lord Howe Island[55] and in the western Indian Ocean in Reunion Island[57]. While MCEs sites with high scleractinian cover have been neglected in spatial marine protected areas, prioritizing them in conservation strategies would help in preserving these unique and ecologically valuable habitats.

Our findings show that MCEs at Reunion Island harbor distinct communities. Particularly, the lower mesophotic zone has an important potential spatial refuge for other important tridimensional benthic structuring habitat organisms. These eco-engineering species supporting a wide diversity of marine organisms[157] including sponges, octocorals, antipatharians and hydrozoans. Overall sponge cover at 95 m was fivefold higher than at 15 m depth. Increasing cover/biomass of sponges along the shallow-mesophotic gradient is likely a common pattern across tropical regions and is supported here for the SWIO. The sponge cover in Eilat's MCEs is sixfold higher than of the shallow counterparts[149]. This 'sponge increase with depth hypothesis' remains the subject of an ongoing debate[158–160] even though it was previously documented throughout the Caribbean[161,162], and in the Pacific Ocean in Palau and Chuuk[163]. Poorly studied but important MCE habitat-forming taxa, the antipatharians[164] also become steadily more abundant deeper in MCEs, as described across disparate biogeographic tropical regions (Hawaii[50], Australia[55], Japan[155], Seychelles[72]; Indonesia[165]). Octocorals also exhibit distinct patterns in abundance along the depth gradient[103,166,167]. Increasing abundance and diversity of octocorals across the shallow-mesophotic gradient was documented in other coral reefs[58,168,169], and even across a relatively small depth range in the shallow zones (5–15 m[170]).

Information on the abundance and diversity of organisms in MCEs also provides valuable insights into regional biodiversity trends. Patterns observed in these deeper zones help clarify the distribution of reef species and their ecological functions. Copus et al.[171] has recently highlighted through the 'habitat persistence hypothesis'[23] how species inhabiting MCEs might exhibit distinct biogeographical patterns compared to shallow-reef organisms. Specifically, species restricted to deep (mesophotic) reefs generally have smaller geographical ranges and higher levels of endemism, as opposed to shallow-reef species, which are more widespread (e.g.,[59,132,172,173]). Moreover, the traditional pattern of high diversity in the Indo-Australian Archipelago, which diminishes eastward across the tropical Pacific, does not appear to hold for MCE organisms, indicating that deep-reef biodiversity may follow different regional trends compared to shallow reefs[5]. In the Caribbean Sea, the dominance of a few ecological generalists and relatively low diversity could suggest that mesophotic reefs may not function as refugia as effectively as those in biodiversity hotspots like the Coral Triangle. Further studies combining ecological surveys with genetic analyses are essential to explore the depth-specific dynamics of reef biodiversity and improve our understanding of the role of MCEs in coral reef resilience and conservation.

In Reunion Island, hydrozoans of the shallow depths were mostly composed of *Millepora* spp. that dominated benthic assemblages (i.e., volcanic sites V1 and V2 at 15 m and 30 m depth, respectively). As in other reef sites worldwide, they were generally found in low cover[174] although they may be locally abundant and even dominate shallow communities[175,176]. Hydrozoans at mesophotic depths below 45 m on volcanic lava flows were dominated by fragile calcareous hydrozoans *Stylaster* cf. *flabelliformis*[57] and *Distichopora* spp. These stylasterids mostly inhabit deep zones with few known species that have colonized waters shallower than 50 m[177,178]. Several large colonies of *Stylaster* cf. *flabilliformis* colonies (> 30 cm width) were recorded colonizing the wall at one site in the port at 95 m depth. This extends the horizontal distribution of this endemic and rare species at the island scale, as, to our knowledge, *Stylaster* had only been reported on the eastern volcanic coast in Reunion Island[57,92].

In this study, we highlighted heterogeneous seascapes of MCEs in Reunion Island (as illustrated in Supplementary Fig. S5). MCEs contain a high diversity of mesophotic scleractinian corals, antipatharian, gorgonian and hydrozoan forests and sponge aggregations, all important and forming distinct communities and unique seascapes. The high scleractinian cover recorded at some sites in Reunion Island MCEs, together with the high densities of other important habitat-forming taxa, are encouraging insights for MCEs conservation. However, the current Reunion Island MPA (Réserve Naturelle Marine de La Réunion) located on the western coral reef does not encompass the majority of MCEs, as no-take zones only extend to the 40 m bathymetric limit at the deepest points. No specific protection exists at other island locations. Therefore, the conservation of Reunion Island MCEs requires adjusting the current MPA with updated management objectives specifically focusing on MCEs and expanding the MPA, in particular the no-take zones, to more accurately reflect the mesophotic gradient. At other locations, establishing MPAs should aim to protect vulnerable MCEs and regulate anthropogenic activities that harm these ecosystems[179]. For instance, the reinforcement of the management of fishing activities or the implementation of specific measures, such as those to avoid fishing line entanglements, particularly in areas supporting large tridimensional habitat forming taxa or vulnerable animal forests, is of paramount importance. In addition, actions should be taken to reduce the negative effects of freshwater and nutrient inputs from terrestrial run-off and watersheds[180,181]. Finally, before implementing area-based conservation measures or planning reserve networks, it is essential to study both vertical and horizontal genetic connectivity to effectively guide biodiversity conservation decisions[182–184] and ensure the long-term health and resilience of these unique and still largely unknown ecosystems.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. Most of data generated and analyzed during this study are included in this published article (and its Supplementary Information file).

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Author contributions

Conceptualization: L.H., L.P., M.A.; Data curation: L.H., P.M.; Formal analysis: L.H., F.G.; Funding acquisition: L.H., L.P., P.L., P.C., M.A.; Investigation: L.H., S.B., L.B.; Methodology: L.H., L.P., F.G., M.A.; Project administration: L.P., P.L., P.C., M.A.; Resources/Software: L.H.; Supervision: L.P., P.L., M.A.; Validation: L.H., L.P., P.L., M.A.; Visualization: L.H., F.G.; Writing—original draft: L.H.; Writing—review and editing: L.H., L.P., F.G., M.A.; All authors contributed to the article and approved the submitted version.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to L.H.

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