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„A study of the community structure and zonation of hard and soft corals through the use of photo-transects at two offshore reefs in the central Red Sea“

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Table of contents

Abstract: The Red Sea holds the highest hard coral diversity in the Indian Ocean, but the central and southern Red Sea remain poorly studied. The aim of this study was to assess the community composition and zonation of hard and soft corals at two offshore Sudanese reefs: Merlot and Sha'ab Rumi. 22 photo transects were surveyed at 0 - 21 m depth, encompassing three habitats: reef edge, vertical wall and reef slope; only the latter occurs at both sites. 104 and 89 hard coral taxa were found at each study site, respectively. Most previous studies from the north and central Red Sea report lower richness, indicating these reefs are particularly diverse. Comparisons with previous studies indicate both sites are healthy. Distinct coral communities characterize the reef edge, the vertical wall, and the two reef slope habitats. They are similar to previously described communities, but important discrepancies regarding dominant groups and indicator species exist. These could be due to methodological differences, insufficient study of Sudanese reefs, or community shifts caused by bleaching events. Only the reef slope communities were comparable between sites, with the one at Sha'ab Rumi being overall more diverse. The diversity of hard corals increased with depth, possibly due to the interaction between the variation in environmental disturbances and light availability. Photo transects proved effective to study multiple aspects of coral reef ecology. The utilization of additional close-up images for the identification of certain groups would aid in increasing the achievable taxonomic resolution.

1. INTRODUCTION

The Red Sea is a narrow body of water stretching for 2000 km in between the Arabian Peninsula and continental Africa. It is the northernmost tropical sea and the only enclosed coral sea in the world, and so it is widely recognized as a unique marine environment (Berumen et al., 2019; Klaus, 2015). Red Sea reefs hold the highest diversity of hard corals in the entire Indian ocean, and notably possess a high degree of endemism among scleractinians and other multiple well-studied groups (Berumen et al., 2019). As a result, the Red Sea has been commonly referred to as a "center of evolution" (DeVantier et al., 2000; Sheppard & Sheppard, 1991; Spalding et al., 2007). It is also notable for possessing a strong latitudinal environmental gradient, as it extends from 12.5°, bordering the Gulf of Aden, to almost 30° N at the Gulf of Suez, which hosts some of the northernmost hermatypic coral growth in the world (Berumen et al., 2019; Sheppard & Sheppard, 1991). The northern Red Sea is highly oligotrophic and saline, and hosts very diverse coral reefs despite strong annual temperature variation (Churchill et al., 2019; Moustafa & Hallock, 2008). Here the difference in sea surface temperature between summer and winter can be over 14 °C, and on occasion, water temperatures can surpass both the usual low and high temperature thresholds for coral growth (Churchill et al., 2019; Moustafa & Hallock, 2008). In contrast, the southern Red Sea is richer in nutrients and has higher sediment input, resulting in mostly turbid, lower diversity, and sometimes algae-dominated reefs (Klaus, 2015; Sheppard & Sheppard, 1991). Furthermore, it also tends to experience constant high daily sea surface temperatures (Churchill et al., 2019; Klaus, 2015). Such high environmental variation has resulted in the Red Sea being viewed as a sort of "natural laboratory" to study how extreme conditions shape the development of coral reefs.

Due to the strong environmental gradient, the partition of the Red Sea into various eco-regions has been proposed on multiple occasions (Ormond et al., 1984; Sheppard & Sheppard, 1991; Veron, 1995). Two subregions are currently accepted, north-central and southern, with the limit between them somewhere close to 20° N (Spalding et al., 2007). This separation was based on differing dominant taxa and species composition of benthic reef organisms and other well studied groups, despite both eco-regions sharing most of the same species pool (Berumen et al., 2019; Sheppard et al., 1992). Although the north and central parts of the Red Sea are considered to form a single eco-region, the central Red Sea coasts of Saudi Arabia and Sudan possess a wide variety of reef types, such as

fringing, barrier, patch, platform and even atoll-like structures (Klaus, 2015; Rowlands & Purkis, 2015; Sheppard & Sheppard, 1991), that host a wide variety of unique habitats not found further north, where short fringing reefs that end in steep drop-offs tend to dominate (DeVantier et al., 2000; Sheppard & Sheppard, 1991). A wider array of available habitats in the central Red Sea results in the development of unique reef communities which are not found elsewhere in the region (Klaus, 2015; Sheppard & Sheppard, 1991). The central Red Sea thus represents a distinct marine environment, with a wider variety of reef habitats than the northern Red Sea, and distinct environmental conditions that shape reef development differently than in the southern Red Sea.

Despite being well studied, much of the recent work on extant Red Sea coral reefs has focused on the northernmost areas, such as the Gulf of Aqaba, with the central and southern regions lagging behind (Klaus, 2015; Klaus et al., 2008b). Though the establishment of the Red Sea Research Center at King Abdullah University of Science and Technology in 2009 has increased the amount of recent publications from the Arabian coast, areas in the western central Red Sea, such as the coast of Sudan, remain understudied, and only few studies have been published in the past two decades (e.g.: DeCarlo et al., 2020; Elamin et al., 2014; Hussey et al., 2013; Kattan et al., 2017; Reinicke et al., 2003; Rezzolla et al., 2014; Spiridonov & Neumann, 2008). Of these, just a handful deal with coral diversity and ecology. Although multiple extensive surveys and expeditions of the Sudanese coast took place in the early 2000's, these were carried out to inform coastal management and conservation decisions and so only technical reports were produced as a result (Kotb et al., 2004, 2008; PERSGA, 2003, 2010). These unfortunately lack crucial ecological information such as hard and soft coral community composition and depth zonation, diversity indices, detailed methodological information, and comparisons through statistical testing, and only include general information such as percentage cover of mayor groups (e.g.: live hard corals, soft corals, dead corals, algae, etc.). Other more seemingly thorough reports, such as those of the African Parks Foundation (2006), Klaus et al. (2008a) and Chekchak & Klaus (2013), were never published, and their results are only mentioned in the works of Klaus et al. (2008b), Klaus (2015) and Nasr (2015). Furthermore, many of these reports cite hard and soft coral species richness numbers based on early studies such as Schuhmacher & Mergner (1985), Sheppard & Sheppard (1991), Schuhmacher et al. (1995) and Reinicke et al. (2003). This is troublesome as many advancements on Red Sea coral diversity have been made in

recent years with the ranges of multiple species being expanded, with significant changes in nomenclature, and with new species descriptions (Arrigoni, Benzoni, Huang, et al., 2016; Arrigoni, Benzoni, Terraneo, et al., 2016; Arrigoni, Berumen, et al., 2016; Arrigoni et al., 2017, 2018, 2020; Benzoni et al., 2012; Bouwmeester et al., 2015; Haverkort-Yeh et al., 2013; McFadden et al., 2017; Terraneo et al., 2014; Terraneo, Benzoni, et al., 2019; Veron, 2000). As a result, the information currently available on Sudanese coral diversity may be largely outdated. This has consequences for the planning and management of conservation strategies on Sudanese coral reefs, as it is likely there are many species which remain unseen due to out-of-date taxonomic references or simply due to insufficient sampling.

The use of photo-transects through the quadrats photography has been widely adopted worldwide as a cost-effective way to obtain reliable data on community composition and diversity of benthic communities (Flower et al., 2017; Jokiel et al., 2015; Morrison et al., 2012; Pante & Dustan, 2012). Though several variations of the method exist, depending on the software used and implemented sampling technique (e.g.: points counts vs area estimates) (Roelfsema et al., 2006), the main advantages are the same for all: fast acquirement of large amounts of benthic cover data with relatively little effort and resources. Even though the subsequent analysis of the photoquadrats can often be time-consuming, this is offset by the significant reduction on fieldwork required, which in turn saves time and costs. This method has successfully been implemented to study multiple aspect of benthic coral reef ecology in the northern Red Sea (Alexandroff et al., 2016; Eyal-Shaham et al., 2016; Eyal et al., 2016; Feldman et al., 2018; Moustafa & Hallock, 2008; Wielgus et al., 2004; Wooster et al., 2019), but to this study's best knowledge, it has yet to be implemented in the central Red Sea. It is therefore the aim of this work to study the community composition and depth zonation of hard and soft corals at two Sudanese off-shore coral reefs, through the implementation of photo-transects. Special care will be given to incorporate recent changes to coral taxonomy to ensure the results obtained are in line with our most current understanding of Red Sea coral diversity. As this is likely the first implementation of the photo-transect method in Sudanese reefs, attention will be given to this technique's effectiveness for sampling and recording the diversity of hard corals, and so pitfalls and potential improvements will be discussed.

2. MATERIALS & METHODS

2.1 Description of study sites

Fieldwork was carried out at the Merlot and Sha'ab Rumi reefs, located off the coast of Sudan. Both are categorized as off-shore platform reefs (Klaus, 2015), based on Rowlands & Purkis (2015) reef type classification system. Merlot reef (20°50'35.94"N, 37°25'6.80"E) is found within the Dungonab Bay and Mukkawar Island National Park (Klaus, 2015; Rezzolla et al., 2014), approximately 15 km E of the northern tip of Mukkawar island. It is approximately 1.15 km long by 0.5 km wide, of oblong shape, with its long axis roughly positioned on an E – W orientation (Figs. 1a & 1c). Sha'ab Rumi reef (19°56'22.91"N, 37°24'13.05"E) lays further south, 15 km NE of Port Sudan and 20 km offshore (Hussey et al., 2013). It is a semi-enclosed atoll-like structure, approximately 3.8 km long by 1 km wide (Hussey et al., 2013; Klaus, 2015) (Fig. 1b). The reef is more or less spindle-shaped and oriented N – S (Hussey et al., 2013; Rezzolla et al., 2014) (Fig. 1b). Both the northern and southern areas of Sha'ab Rumi house a plateau, with the southern one being longer and more slender (Hussey et al., 2013) (Fig. 1b). Water currents in the study area flow towards the north along the coast of Sudan, following the water circulation pattern caused by a permanent large eddy system (Sofianos & Johns, 2003). However, surface water movement is mainly driven by local wind patterns, which generally blows from the NW to the SE (Klaus, 2015).

The study sites were located at the outer faces of both reefs (Fig. 1). The Merlot locality possessed multiple crevices and caves, and the slope steepness varied greatly with depth. Being located on the southern area of the reef (Fig. 1), the Merlot study site seems well protected from wind-driven waves and surface currents. The perceived water clarity was low, and the site seems to experience high levels of sedimentation. In comparison, the study site at Sha'ab Rumi is more exposed to surface currents, as it is located on the south-western part of the reef (Fig. 1) and so the predominant surface currents flow parallel to the reef structure.

2.2 Fieldwork

Through SCUBA diving, 14 photoquadrat-transects were laid out at Merlot and eight at Sha'ab Rumi (Table 1). The transects were demarcated using a measuring tape, and had an approximate length of 20 m. At Merlot, these covered a depth range from 1-2 to 20 m, while at Sha'ab Rumi the sampled depth range varied from 3 to 21 m (Table 1).

Photographs were taken with an Olympus Tough TG-5 DSLR camera with an underwater Olympus PT-058 housing, and attached by a metal frame to a 50 × 50 cm quadrat. The quadrat was positioned on the surface of the benthos, and photographs were taken all along the transect. Although in theory only 40 quadrats are needed to cover the full length of each 20 m transect, the number of photoquadrats which were required to realize this goal varied from transect to transect, due to variations in the three-dimensional structure of the reef and in the level of overlap between adjacent quadrats (Table 1). For the transects laid out at 3 – 5 and 8 – 10 m depth (See table 1), additional line-intersect transects were also performed (data not included in this study). In these cases, most corals were identified *in situ*, but detailed close-up photographs of coral colonies of uncertain identity were taken for subsequent species verification. In some instances, these images also aided in coral identification for the photoquadrats.

2.3 Photoquadrat analysis

The photoquadrats we processed using the image-editing software GNU Image Manipulation Program (GIMP) 2.10.24, where the quadrat was centered and the images corrected for lens distortion. Taxon identification and acquirement of abundance data was performed using the software Coral Point Count with Excel extensions (CPCe) 4.1 (Kohler & Gill, 2006). In addition, the software ImageJ (Abràmoff et al., 2004) was used for taking morphological measurements of colonies in both the quadrat and close-up photographs, for aiding in species identification. Within the CPCe software, abundance data of the benthos was obtained by randomly laying down 50 points inside each quadrat, and classifying each according to the organism or substrate type beneath them. Maintaining equal point density for all quadrats is critical for assuring random unbiased sampling (Morrison et al., 2012; Pante & Dustan, 2012), so when two photoquadrats overlapped, the points within the overlapping area were considered only for one of the images, and classified as "invalid" for the other one. For each transect, all points were summed for each category and then divided by the total number of points (excluding those classified as "invalid"). The result obtained were thus percentage cover values per transect for every category observed.

For the categorization of the points, two classifications were simultaneously used: a general classification which includes all major groups and substrate types, and a more specific categorization which focuses on hard and soft coral taxa, and also including the zoanthid *Palythoa tuberculosa*. Thus, percentage cover values were obtained separately

for each classification system. For the more broad, general categorization, all points were classified into one of the following major groups: Hard corals (Hermatypic and ahermatypic scleractinians, as well as hermatypic hydrozoans), soft corals (alcyonaceans and gorgonians), zoanthids, sponges, other sessile fauna (includes all other sessile fauna observed such as tridacnid clams), red coralline algae, non-coralline algae (mainly consisting of turf), bare substrate (silt, sand, ruble, and exposed rock), bleached coral, dead coral (recently diseased colonies which were attached and whole, or dead parts of living colonies), and unknown (substrate of unknown identity). Furthermore, when the identification of the benthos was impaired by shadows, sediment, blurriness, etc., it was classified as "invalid" and was not taken into account when obtaining the cover estimates. Additionally, hard and soft corals were identified to the lowest possible taxonomic level. In most cases this was done to species level, but some hard corals and most soft corals were kept at the genus level. Members of Acroporidae and Poritidae in particular include genera whose visual identification can prove difficult, and species delimitation is often uncertain (Terraneo, 2019; Terraneo, Fusi, et al., 2019; Veron, 2000). Therefore, most instances of these families were categorized according to morphological characteristics such as the growth form and consistent surface characters, although in some cases species identification was possible and thus preferred. The vast majority of large poritids fell into two categories: 1) Massive or submissive colonies of *Porites* spp., hereafter shortened to "massive *Porites* spp.", whose general morphology was akin to that of *P. lutea*, *P. lobata* and *P. solida*. 2) Massive *Porites* spp. colonies which resembled both *P. rus* and *P. monticulosa*, and so were named "*P. rus*/*monticulosa*". Other less abundant poritids possessed columnar and encrusting growth forms, and thus were classified as "Columnar *Porites* spp." and "Encrusting *Porites* spp.", respectively. For the particularly diverse genus *Acropora*, colonies were classified into the following categories: staghorn-like (Stag), arborescent (Arb), stout corymbose clumps (CorC), sparse corymbose bushes with rounded corallites (CorBRC), corymbose plates (CorP), digitate (Dig), and horizontally branching tables (HBT). These categories were broadly based on morphological classification utilized by Veron (2000).

2.4 Statistical analysis

Average covers of live hard and soft corals, bleached coral, recently dead corals, and algae, were calculated for each study site in order to evaluate the current status of the reefs. Furthermore, species accumulation curves (SAC) were constructed for the study

sites and for each surveyed transect. The former allows to determine if the total site richness of hard corals was sampled, while the latter can elucidate if a 20 m transect is sufficient to capture the small-scale spatial heterogeneity of the hard coral community composition. Both were computed as the expected mean accumulated richness after performing 100 random permutations of the order in which new species were encountered. The transect accumulation curves were constructed utilizing the accumulated transect length rather than the number of photoquadrats analyzed, in order to account for the varying number of quadrats analyzed per transect (Table 1) despite all being of similar length.

To analyze the composition of the benthic reef communities, the square root-transformed percentage cover data for hard corals, soft corals and the zoanthid *P. tuberculosa* was utilized. Differences between sites were evaluated through Analysis of Similarity (ANOSIM), using the Morisita-Horn dissimilarity index (*MH*). These differences were subsequently visualized through non-metric multidimensional scaling. The Morisita-Horn distance was chosen as it is relatively robust against uneven sample sizes, and it is biased towards the most abundant taxa (Chao et al., 2006; Wolda, 1981). The latter characteristic proves useful when the sample size is low and the communities of interest were not fully sampled, resulting in multiple singletons and unseen rare species (Chao et al., 2006; Wolda, 1981). To evaluate if transects formed clusters according to the composition of hard and soft corals, the same dissimilarity matrix used for the ANOSIM was utilized to perform hierarchical cluster analysis (HCA). Ward's minimum variance criterion (Ward, 1963) was implanted to compute the HCA, which was then visualized through a dendrogram. Delimitation of clusters was performed utilizing a threshold height of 0.8. These clusters were then utilized to classify the transects into distinct communities. Significant differences in the composition of hard and soft corals between communities were then evaluated through an ANOSIM.

The average cover for all major categories (Hard corals, soft corals, etc.) was obtained for each habitat, and differences between habitats were evaluated using Analysis of Variance (ANOVA), or Kruskal – Wallis non-parametric tests whenever assumptions for parametric testing were not met. Post-hoc Tukey HDS tests, or non-parametric Conover-Iman tests (Conover & Iman, 1979) utilizing Holm's family-wise error rate correction method (Holm, 1979) were performed when appropriate to determine between which communities were there significant differences. The diversity of hard corals was

evaluated by obtaining for each community the richness, Shannon's index (*H'*), and Pielou's evenness index (*J'*). Differences between communities for all diversity information statistics were evaluated utilizing ANOVAs and post-hoc Tukey HDS comparisons were performed when appropriate. Additionally, depth profiles of the average hard and soft coral cover and of all diversity indices were constructed for each site. Finally, indicator species analysis (IndVal) was implemented to evaluate for significant associations between taxa and one or more communities. This procedure computes an index which measures the strength of the association between each individual taxon and a certain group or combinations of groups (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). The index used in this study was the group-equalized point-biserial correlation coefficient (r_{pb}^{g}) (De Cáceres & Legendre, 2009). To test whether the association between a taxon and community is significant, permutation tests (n = 9999) were implemented. A significant association indicates that the average abundance of a particular taxon is significantly higher for one community when compared to the remaining ones (De Cáceres & Legendre, 2009). Indicator species analysis also permits testing for significant associations of a species with multiple groups (De Cáceres et al., 2010). In ecological terms, this allows to identify the habitat preferences of specialists, which may occur in only one particular community, and generalists, that due to wider niche-breadths might potentially be common in multiple communities.

All statistical analyses were performed with the statistical software package R 4.1.0 (R Core team, 2021) through the interface RStudio 1.4.1103 (RStudio, 2021). The biodiversity information statistics, the species accumulation curves, as well as the multivariate analyses were constructed using the package vegan 2.5-7 (Oksanen et al., 2020). The Conover-Iman tests were carried out using the package conover.test 1.1.5 (Dinno, 2017). The Indicator species analysis was performed using the package indicspecies 1.7.9 (De Cáceres & Legendre, 2009). All figures were constructed with the aid of the package Tidyverse 1.3.1 (Wickham et al., 2019).

3. RESULTS

3.1 – General results

A total of 124 hard coral taxa were observed from both study sites. Of these, 119 are scleractinians, while the remaining four belong to Hydrozoa: three species in the genus *Millepora*, and the Blue Lace coral *Distichopora violacea*. Out of all scleractinian taxa, 91 were identified to species and 29 were kept at either the genus or morphological level. Additionally, 14 soft coral taxa were recorded, of which three were identified to species, 8 to genus, three to family level, and one remaining instance of a gorgonian could not be identified. See Annex 2 for the full list of recorded hard and soft corals. Notable findings include the hard coral *Favites micropentagona*, which in the scientific literature was previously unreported for the central Red Sea, and an unknown species of scleractinian, whose general morphology places it in the genus *Stylophora* but does not match any known species. In total, 104 hard coral taxa were observed in Merlot, compared with 89 at Sha'ab Rumi (Fig. 2). The species accumulation curves for hard coral taxa indicate that despite the difference in total richness observed, the accumulated richness with each additional transect rises in a similar manner at both sites (Fig. 2a). Furthermore, although neither the site or transect SACs seem to reach an asymptote, the latter ones approach a plateau (Fig. 2). Overall, both sites appear to present similar average covers of hard (~ 33 – 38%) and soft (~ 15%) corals, bleached corals (< 1%), recently dead corals (~ 5%) and algae (~ 4 – 6 %) (Table 2).

The composition of hard and soft corals differed between sites (R = 3.502, p = 0.005). These differences can be observed in the NMDS plot, as the Sha'ab Rumi transects cluster on the bottom-right corner of the biplot, while those from Merlot are found in the top portion and the bottom-left corner of the figure (Fig. 3). Interestingly, there are instances where the distance between Merlot transects appears larger than the distance between these and the Sha'ab Rumi transects (Fig. 3), which indicates there are cases where within-site dissimilarities that may prove more important than between-sites differences. This hypothesis is supported by the hierarchical cluster analysis, as the first branching of the resulting dendrogram (height = 1.47) does not separate the transects according to each site (Fig. 4). Instead, one cluster is composed of the shallowest Merlot transects (Depth range: 0 – 5 m), while the other is a combination of all the Sha'ab Rumi transects and the remaining ones from Merlot (Fig. 4). At a cut-off height of 0.8, four clusters were obtained (Fig. 4). Significant differences were found between clusters for

the community composition of hard and soft corals (R = 0.899, p = 0.001). Due to the high dissimilarity observed (Fig. 4) and notable differences in community composition, each cluster is assumed to represent a distinct reef community whose corresponding local habitat experiences a specific set of environmental conditions. Thus, the proposed communities were named according to the reef habitat in which they were located: reef edge, vertical wall, Merlot reef slope and Sha'ab Rumi reef slope (Fig. 4).

Significant differences in the average cover of hard corals were found between habitats (F = 4.34, d.f. = 3/18, p = 0.018), being higher at the reef edge than at the other three (Fig. 5). The soft coral cover also differed between habitats (H (3) = 11.78, p = 0.008), being significantly lower at the reef edge than at the two slope habitats (Fig 5). Although soft coral cover was similarly low at the vertical wall habitat (Fig 5), it only differed significantly from the Merlot reef slope. Differences between habitats were also found for the cover of bare substrate (H (3) = 10.33, p = 0.016), being highest at the slope habitats, followed by the vertical wall, and lowest at the reef edge (Fig. 5). Red coralline algae cover differed between habitats as well (H (3) = 12.67, p = 0.005), being higher at the reef edge and vertical wall than at the Merlot and Sha'ab Rumi reef slopes (Fig. 5). Similarly, the cover of non-coralline algae differed between habitats (F =12.78, d.f. = 3/18, p < 0.001) and was found to be higher at the vertical wall than at the three other habitats, and lower at the Merlot reef slope than at the Sha'ab Rumi reef slope (Fig. 6). Differences between habitats were also observed for the cover of sponges (H (3) = 8.40, p = 0.038), which was higher at the slope habitats than at the reef edge and vertical wall. The average cover of recently dead was found to differ between habitats, being higher at the reef edge than at the rest (F = 5.11, d.f. = 3/18, p = 0.009). Finally, no differences were found between habitats for the cover of bleached coral (H (3) = 3.79, p = 0.285). The statistical results for all post-hoc comparisons can be found in annex 1.

The richness of hard coral taxa differed between communities (F = 5.03, d.f. = 3/18, p = 0.011), being higher at the Merlot and Sha'ab Rumi reef slopes than at the reef edge (Fig. 7). Differences between communities were also found for Shannon's index (H (3) = 8.09, p = 0.044), which was higher at the Sha'ab Rumi reef slope than at the other communities (Fig. 7). Finally, Pielou's evenness differed between sites as well (H (3) = 9.74, p = 0.021), being higher at the Sha'ab Rumi reef slope than at the reef edge and the Merlot reef slope (Fig. 7). See annex 1 for details regarding the results of all post hoc-comparisons.

3.2 – Description of reef communities

The reef edge – Merlot: This community is located in very shallow waters (1 – 2 m), on the outer border of the reef flat where the descent towards the reef slope begins. It encompasses the Merlot transects PT45, PT46 and PT49 (Fig. 4, cluster 1). A similar habitat likely exists at Sha'ab Rumi, but was not sampled. It was characterized by the highest average hard coral cover (Figs. 5 & 9; $\bar{x}$ = 53.5 %) but an almost complete lack of soft corals (Figs. 5 & 9). It also possessed a higher cover of dead coral (Figs. 6 & 9; $\bar{x}$ = 10.0%) than the other habitats. Notably, water clarity was high and soft sediment bottoms were observed to be absent. Red coralline algae were fairly abundant in the reef edge (Fig. 5; $\bar{x}$ = 17.4%), being found in crevices among live coral colonies, or covering exposed substrate and dead coral colonies (Fig. 9). Due to the high coral and coralline algae cover, the reef edge presented the lowest average cover of bare substrate (Fig 5; $\bar{x}$ = 9.2%). Finally, non-coralline algae ($\bar{x}$ = 4.9%) were rare at this habitat, and sponges were not observed (Fig. 6). The diversity of hard corals was low when compared to the other habitats. It held the lowest average transect richness of hard coral taxa (Figs. 7 & 9; $\bar{x}$ = 21.7), and it possessed low Shannon ($\bar{x}$ = 2.08) and evenness ($\bar{x}$ = 0.681) values (Figs. 7 & 9). Multi-level pattern analysis revealed eleven taxa associated to the reef edge: massive/submassive *Porites* spp., *Leptoria phrygia*, *Stylophora wellsi*, *Pocillopora eydouxi*, *Goniastrea stelligera*, *Echinopora hirsutissima*, *Pocillopora verrucosa*, *Acropora* spp. (Digitate), and *Goniastrea edwardsii* / *retiformis*, the zoanthid *P. tuberculosa* and the hydrozoid *Distichopora violacea*; the latter was often observed among crevices and in between coral colonies (Table 3 & Fig. 10). The reef framework was observed to mainly consist of massive/submassive *Porites* spp., with large *E. hirsutissima* and *G. stelligera* also being highly abundant (Figs. 8 & 10). Branching *Pocillopora* spp. and *S. wellsi*, along with digitate *Acropora* spp. colonies were also common and usually observed scattered and growing over exposed substrate such as *Porites* colonies (Fig. 10). *P. tuberculosa* was at times very abundant, forming monospecific mats of moderate size (Fig. 10)

The vertical wall – Merlot: Found immediately bellow the reef edge, at 3 – 5 m depth, it comprised the Merlot Transects PT41, PT43 and PT48 (Fig. 4 & Table 1). The surrounding habitat was comprised of a sharp descent from the reef edge onto the reef slope. This incline was overall very steep but not consistently so, instead, the reef wall consisted of a mixture of overhangs, vertical inclines, small caves and protruding rocky

platforms, experiencing varying levels of light exposure. The most shaded parts lacked in hermatypic and most soft corals (Fig. 11), but coral development was high in areas hit by direct sunlight (Fig. 11). Notably, large amounts of sediment were observed raining down from over the reef edge (Fig. 11). The average hard coral cover was 34.0 %, similar to slope habitats (Figs. 5 & 9). Soft corals were present although fairly rare (Figs. 5 & 9; $\bar{x}$ = 5.5 %). The average cover of dead coral was low (3.87%) and comparable to the slope habitats (Fig. 6). Similar to the reef edge, red coralline algae were common here ($\bar{x}$ = 22.19 %), and more abundant than at the Sha'ab Rumi and Merlot reef slopes (Fig. 5). The cover of bare substrate ($\bar{x}$ = 20.94%) was lower than at the slope habitats but higher than at the reef edge (Figs. 5 & 10). Non-coralline algae were at their most abundant here, with their cover ($\bar{x}$ = 8.5 %) being higher than at all other habitats (Fig. 6). Although not significantly different from the other habitats, the transect average hard coral richness ($\bar{x}$ = 28.3) seems to be in between that of the reef edge and the slopes (Figs. 7 & 9). Similarly, the Shannon index values are moderate (Figs. 7 & 9; $\bar{x}$ = 2.39). Pielou's evenness ($\bar{x}$ = 0.717) was comparable to Sha'ab Rumi reef slope, and slightly higher than the other two habitats, though not significantly so (Figs. 7 & 9). Multi-level pattern analysis revealed seven taxa associated to this habitat: the ahermatypic scleractineans *Tubastrea coccinea* and *T. micrantha*, the soft corals Anthipathidae indet., and Neptheidae indet., the hermatypic coral *Pavona maldivensis*, and the hydrozoid *D. violacea* (Table 3 & Fig. 11), although most of these were not abundant. *T. coccinea* was the dominant coral, mostly being found in shaded areas such as under overhangs (Figs. 8 & 11). Although not associated to this habitat, hermatypic corals such as massive/submassive *Porites* spp. and *P. verrucosa* were some of the most common benthic organisms, despite being restricted to well-lit areas (Figs. 8 & 11).

The reef slopes – Merlot and Sha'ab Rumi: The only comparable habitats at both sites. The Merlot reef slope starts at the base of the vertical wall habitat somewhere between 5 and 9 m depth, where the incline of the reef structure becomes gentler. At merlot it is comprised of the remaining transects (PT36, PT37, PT38, PT39, PT40, PT42, PT44 and PT47) (Fig. 4), and covers a depth range of 9 to 20 m (Table 1). Meanwhile, the Sha'ab Rumi reef slope encompasses of all of the transects sampled at this site (Fig. 4; PT28 to PT35) and has a wider depth range (3 – 20 m) than at Merlot. The morphology of the surrounding habitat was similar at both sites, mainly consisting of a gradual incline. The slope angles were not constant however, as steeper sections resulted in small caves and

crevices, while in flat areas rubble, sand and other loose substrate tended to accumulate (Figs. 12 & 13). Although the average hard coral cover was similar between slopes, 34.0% at Merlot and 32.2% at Sha'ab Rumi (Fig. 5), its variation at Sha'ab Rumi was much greater, ranging from 22.5% at 8 – 10 m depth up to 51.6% at 20 m (Fig. 9). Soft corals were at their most abundant at these communities, with an average cover of 24.0% at Merlot and 15.0% at Sha'ab Rumi (Fig. 5). While the abundance of soft corals increased wit depth at Merlot (Fig. 9), at Sha'ab Rumi it remained relatively low (5.1 – 10.9 %), except for a a peak at 8 – 10 m depth ($\bar{x}$ = 31.5%) due to extensive *Paralemnalia* mats (Figs. 9 & 13). Areas of bare substrate were common at the reef slopes (Fig. 5; Merlot $\bar{x}$ = 26.6; Sha'ab Rumi $\bar{x}$ = 27.8%), mainly consisting of a mixture of exposed rock, and rubble and sand patches (Figs. 12 & 13). The cover of dead coral was low at both the Merlot ($\bar{x}$ = 3.85%) and Sha'ab Rumi ($\bar{x}$ = 4.53%) reef slopes (Fig. 6). Similarly, both red coralline algae (Merlot: $\bar{x}$ = 2.63%; Sha'ab Rumi: $\bar{x}$ = 6.23%), and non-coralline algae (Merlot: $\bar{x}$ = 2.64%; Sha'ab Rumi: $\bar{x}$ = 5.66%) were rare at these habitats (Fig. 6). In contrast, sponges were at their most abundant here (Fig. 6; Merlot $\bar{x}$ = 5.98; Sha'ab Rumi $\bar{x}$ = 5.56%). The slope habitats, particularly Sha'ab Rumi, held some of the highest hard coral diversity observed by this study. Both habitats were similarly rich in hard coral taxa, (Figs. 7 & 9; Merlot $\bar{x}$ = 36.1; Sha'ab Rumi $\bar{x}$ = 34.9). However, Shannon values were on average higher at the Sha'ab Rumi reef slope (Fig. 7; $\bar{x}$ = 2.77), remaining more or less constant with depth (Fig. 9). In contrast, Shannon values at the Merlot reef slope varied much more; these were on average slightly lower than at Sha'ab Rumi (Fig. 7; $\bar{x}$ = 2.39) but showed a strong increase with depth (Fig. 9). Similarly, Pielou's evenness at Sha'ab Rumi was also high ($\bar{x}$ = 0.784), while being low at Merlot ($\bar{x}$ = 0.668) (Fig. 7). Evenness values also appear to vary with depth, increasing at Merlot but decreasing at Sha'ab Rumi (Fig. 9).

Possessing a high richness of hard corals, the slope habitats held a wide variety of massive, branching, and encrusting corals, as well as multiple genera of soft corals (Figs 12 & 13). Many of these taxa were shared among the reef slopes, as few taxa were found to be associated to only one slope (see Table 3). Associated to the Merlot reef slope were the reef-building scleractineans *Stylophora pistillata*, *Stylocoeniella* spp. and massive/submassive *Porites* spp., as well was the soft corals *Melithaea rubrinodis*, *Anthelia* spp., and Xeniidae indet. (Table 3). The hermatypic corals *Seriatopora hystrix*, *Porites* spp. (encrusting) and Fungiidae indet, as well as the soft coral *Paralemnalia* spp.,

were found to be associated to the Sha'ab Rumi reef slope. In contrast, multiple taxa were found associated to both reef slopes: the hard corals *Porites rus*/*monticulosa*, *Acropora* spp. (Staghorn), *Montipora* spp. 2 (massive), *Echinopora forskaliana*, and *Acropora* spp. (Corymbose plates), as well as the soft corals *Litophyton* spp., *Sarcophyton* spp., *Sinularia* spp., and *Rhytisma fulvum* (Table 3). At Merlot, the reef slop was mainly dominated by large massive/submassive *Porites* spp. colonies (Fig. 12), while at Sha'ab Rumi, besides from the aforementioned *Paralemnalia* spp. mats (Fig 13), the most abundant coral was *P. rus/monticulosa*, followed closely by massive *Porites* spp. (Fig. 13)

4. DISCUSSION

4.1 Current status and diversity of hard corals at the study sites

The coral reefs at both sites (and in Sudan in general) were reported to be in moderate to good health by surveys performed in the early 2000's (Klaus, 2015; Kotb et al., 2004, 2008), despite a high thermal event in 1998 which resulted in mass bleaching across most of the Sudanese coast and that is thought to have resulted in high coral die-off at many sites including Sha'ab Rumi (Klaus, 2015; Nasr, 2015). Two subsequent bleaching events due to high thermal anomalies in 2010 and 2015 were observed to impact the central Saudi Arabian Red Sea (Furby et al., 2013; Monroe et al., 2018). The former was assumed to be localized to certain areas of the Saudi Arabian coast, based on *in situ* observations by Furby et al. (2013), but the latter seem to have been more widespread and similar to the 1998 event (Monroe et al., 2018). Despite this, field surveys carried out in 2017 seem to indicate little to no bleaching took place in the Sudanese coast after the 2015 high thermal anomaly (DeCarlo et al., 2020). The results obtained by this study seem to indicate both study sites continue to be in good condition. Bleached corals were seldom observed, and the average cover of non-coralline algae and dead coral remained low at both sites (Fig. 2), although the latter (Fig. 6; ~ 5 – 10 %) was higher when compared to previous observations of Sudanese reefs (0.1 – 2.5 %; DeCarlo et al., 2020; Nasr, 2015), and may be an indication the Merlot and Sha'ab Rumi reefs are currently under stress, or have recently experienced a somewhat severe disturbance event. The average hard coral cover observed at the Merlot and Sha'ab Rumi study sites (Table 2; 38.2% & 32.8 % respectively) falls within the range reported in earlier surveys (15% to 65%, average of 35%) (Klaus et al., 2008b; Klaus et al., 2008a as cited in Klaus, 2015). The site-average cover of soft corals (Table 2; ~15%) appears to be somewhat lower to previous observations (25 – 28.5%; Klaus et al., 2008a as cited in Klaus, 2015). Although these differences could be attributed to the higher dynamism of soft coral communities when compared as opposed to hard coral assemblages (Riegl & Velimirov, 1994; Schuhmacher et al., 1995), they could also be the result of methodological differences between this study and the aforementioned surveys. Unfortunately, no information is available on what techniques were used to sample the reefs, which depths ranges were considered or how many transects were performed at each reef. As a result, direct comparisons between the results of this study and the available data should be considered with care. Nevertheless, these results indicate that the bleaching events of 2010 and 2015

do not seem to have significantly impacted the coral communities of the Merlot and Sha'ab Rumi reefs. This falls in line with reports from the Arabian coast, which observed that offshore reefs were the least affected by these phenomena (Furby et al., 2013; Monroe et al., 2018).

Although more taxa were found at Merlot than at Sha'ab Rumi (104 vs 89 respectively), this is likely due to fewer transects being surveyed at the later study site, as the taxa accumulation curves rise similarly at both sites (Fig. 2). The transect SACs for the shallower transects appear to approach a plateau (Fig. 2); in these cases, most of the variation in the small-scale spatial heterogeneity of the hard coral assemblage is captured within a single 20 m transect. However, when the curves are steeper, such as in some of the deeper Merlot and Sha'ab Rum transects (Fig. 2), the full scale of the spatial heterogeneity may not have been fully captured. Such constraints can be remedied by utilizing longer transects, or by increasing the number of surveyed transects. The site SACs indicate that the hard coral communities were not fully sampled at either site, and there likely remain multiple unseen rare species at both localities, but specially at Sha'ab Rumi (Fig. 2). Furthermore, there is a considerable number of corals which were not identified to species level (further details in section 4.4). Of particular note are the poritids and acroporids, which are some of the most diverse families in the Red Sea (Berumen et al., 2019; Terraneo, Benzoni, et al., 2019; Terraneo, Fusi, et al., 2019). As a consequence, the real diversity of hard corals at both localities has been underestimated by this study. Despite this, these estimates still remain comparatively high. Hard coral richness at individual sites along the north and central Red Sea usually ranges from 20 to 98 species (DeVantier et al., 2000; Riegl et al., 2012; Riegl & Velimirov, 1994), although on occasion higher species numbers have been reported. Such was the case at the South Sinai Marine Protected Area, where the site-specific hard coral richness ranged from 90 to 131 species (Alter, 2004). Off-shore Sudanese reefs in particular appear to host a high diversity of hard corals for the north-central Red Sea. For example, detailed surveys of Sanganeb atoll, (closely located to Sha'ab Rumi) found a total of 89 species (Reinicke et al., 2003; Schuhmacher et al., 1995), and a 2007 survey of the Sudanese coast found 136 hard coral species on the reefs surrounding Seil Ada Kebir, the highest yet observed by the authors (Klaus et al., 2008a as cited in Klaus, 2015). As the hard coral communities at the study sites remain under sampled and many species likely remained unseen by this

study, it appears that the Merlot and Sha'ab Rumi hard coral communities maintain the trend of high diversity at Sudanese reefs.

4.2 The coral communities at Merlot and Sha'ab Rumi: comparisons with previous studies

Although not the only important factor, differences between the study sites play an important role in determining the taxa composition and diversity of the habitat types. Due to its location on the southern face of the reef platform (Fig. 1a), the Merlot study site is mostly sheltered from surface water currents, which flow on an N – S direction (Klaus, 2015). Furthermore, it appears that currents which do manage to penetrate into the inner parts of the reef result in suspension of fine sediment from the soft bottoms found in this area (Fig. 1c). These currents then carry the sediment over the southern reef edge where it deposits over the outer reef face, resulting in the high sedimentation and turbidity observed at this site (Fig. 10). In contrast, the study site at Sha'ab Rumi is more exposed to water movement, as it is located on the western side of the reef structure so the predominant surface water currents flow parallel to it (Fig. 1b). This results in higher water movement and clearer waters when compared to Merlot. One consequence of this is the clear dominance of the massive *Porites* spp. at all three of the Merlot habitats (Figs. 8, 9, 10 & 11). Likely, these corals mostly consist of *P. lutea* and *P. lobata*, which are hardy species that often dominate turbid and highly sedimented environments (DeVantier et al., 2000; Riegl & Piller, 1997; Riegl & Velimirov, 1994; Sheppard & Sheppard, 1991). In contrast, species less tolerant to sedimentation, such as *P. rus* / *monticulosa* (Sheppard & Sheppard, 1991) would be able to better thrive at Sha'ab Rumi (Figs. 8 & 13). Differences in the morphology of the reef structure at the study sites also result in varying community types at the same depth range. Such was the case for the vertical wall community, which was found at Merlot between 3 – 5 m depth, while part of the slope community could be found at the same depth range at Sha'ab Rumi.

The communities found in this study are for the most part similar to community types described previously for the north-central Red Sea, although some major differences were present. Firstly, no community type described by these works matches the characteristics of the vertical wall community. This community is lacking of most zooxanthellate hard and soft corals, instead being characterized mostly by ahermatypic anthozoans and other groups (Table 3 & Figs. 8 & 11). Furthermore, as it is restricted to parts of the reef dominated by low-light conditions, its extent within the reef structure is

likely very limited. Thus, it has either been overlooked or included within the more conspicuous surrounding communities. The latter possibility is likely, as on parts of the vertical wall habitat where good light availability allows for coral development (Fig. 11), the species composition seems to mostly hold elements from other habitats. For example, massive *Porites* spp., *P. verrucosa* and *E. hirsutissima*, while associated to the reef edge (Table 3), were all abundant at the vertical wall (Fig. 8).

In contrast, the reef edge coral community generally resembles exposed community types, such as communities 2 and 9 of Sheppard & Sheppard (1991), the leeward offshore reef described by Riegl & Velimirov (1994) and community B of DeVantier et al. (2000). Despite being sheltered from surface currents, the reef edge community does appear to experience high levels of water movement, likely from wave-action due to its shallow location. The absence of soft corals at the reef edge appears to be a consequence of this, as they very sensitive to mechanical stress (Fabricius, 1997), and are generally rare at the shallowest parts of the reef structure (Riegl & Velimirov, 1994). Furthermore, there was an abundance of hard corals with a preference to exposed environments such as *P. verrucosa*, *S. wellsi*, digitate *Acropora* spp. (Alter, 2004; Riegl & Velimirov, 1994; Sheppard & Sheppard, 1991) and the zoanthid *P. tuberculosa* (Irei et al., 2011) (Figs. 8 & 10). Increased water movement is likely also responsible for the lack of soft bottoms when compared to deeper parts of the Merlot study site, as any deposited sediment would be quickly resuspended. This is expected to result in reduced sedimentation, as evidenced by the abundance of *P. verrucosa* (Sheppard & Sheppard, 1991), *G. stelligera* (Veron, 2000) and *P. tuberculosa* (Irei et al., 2011), which are all sensitive to high levels of sediment deposition. However, the abundance of all these components typical of exposed reef environments was far lesser than expected. For example, Red Sea shallow exposed reef communities are generally described to be dominated by *Acropora* species (DeVantier et al., 2000), which was not the case at the reef edge. Furthermore, the dominance of massive *Porites* spp. at the reef edge (Fig. 10) is more akin of sheltered reef environments with low exposure to water movement (Riegl & Velimirov, 1994; Sheppard & Sheppard, 1991). The reef edge thus holds similarities with both shallow exposed and sheltered community types.

While possessing similar morphology, the slope habitats differ mainly in their exposure to water movement. On one hand, the coral community at the Merlot reef slope Merlot strongly resembles sheltered types such as community 4 of Sheppard & Sheppard

(1991) and community C of DeVantier et al. (2000), as well as the off-shore sheltered reefs of Riegl & Velimirov (1994). All these are characterized by high water turbidity, strong sedimentation, and dominance of *P. lutea* and *P. lobata*. In contrast, the Sha'ab Rumi reef slope community possesses elements of semi-exposed community types where generalist species that favor good water movement but no direct wave action tend to be abundant, such as communities 5, 6 and 10 of Sheppard & Sheppard (1991) and community A of DeVantier et al (2000). However, discrepancies between the reef slopes and the aforementioned community types start to arise when comparing the specific compositions of the hard coral assemblages. Firstly, of the indicator species mentioned in DeVantier et al. (2000) for communities A and C, none match the respective reef slope communities from this study, and many were not observed at all. In fact, some indicator species match instead taxa found associated to both reef slopes rather than to just one of them, such as various *Montipora* spp. (Table 3). A further peculiarity at the Sha'ab Rumi reef slope is the dominance of *Paralemnalia* spp. (Figs. 8 & 13). Monospecific stands of soft corals are a common occurrence in Red Sea reefs which, if given the right conditions, can quickly grow through asexual reproduction and come to dominate the benthos (DeVantier et al., 2000; Riegl & Piller, 1997, 1999; Schuhmacher et al., 1995; Sheppard & Sheppard, 1991). However, these are often formed by more ubiquitous groups such as xeniids, *Sinularia* spp., *Sarcophyton* spp. and *Litophyton* spp. (Benayahu et al., 2002; Benayahu & Loya, 1981; Dar et al., 2012; Mohamad et al., 2010; Mohammed, 2012; Perkol-Finkel & Benayahu, 2004). In fact, no record in the literature could be found for an instance of *Paralemnalia* as the dominant benthic organism in Red Sea reefs, or attaining such high cover values as observed in this study. Furthermore, the absence of xeniids at Sha'ab Rumi, a largely ubiquitous soft coral in Red Sea reefs (Benayahu & Loya, 1987; Perkol-Finkel & Benayahu, 2004; Reinicke et al., 2003; Riegl & Piller, 1997; Schuhmacher et al., 1995), is intriguing, as it is an ever-present component of both sheltered and exposed slope habitats (DeVantier et al., 2000; Sheppard & Sheppard, 1991).

As has been explained, the general characteristics of the communities found by this study mostly match those described in previous studies (except for the vertical wall community), but there are major discrepancies regarding the characteristic species used to define these community types or even among the expected dominant taxa. Here two possible explanations are proposed for these differences: methodological differences and

temporal changes in community composition. To start with, is likely that more species than just the ones determined in these works can potentially be used to define a community type. High diversity coral provinces, such as the Red Sea, contain a variety of different species groups that share similar traits, and so major ecosystem functional roles can potentially be filled by multiple species (McWilliam et al., 2018). As a result, random community assembly processes could result in two communities with differing hard coral assemblages, despite both possessing very a similar environmental setting and being overall functionally very similar. This is especially relevant for the works of Riegl & Velimirov (1994) and DeVantier et al. (2000), which notably did not study Sudanese reefs. It is then probable that not all possible characteristic species for each community type were determined. A second factor is differing utilization of soft coral community data by this study and previous works. Neither Sheppard & Sheppard (1991) nor Riegl & Velimirov (1994) utilized quantitative data on soft coral abundance to define reef community types; and although these were utilized in their multivariate analysis by DeVantier et al., (2000), they were not taken into utilized as part of their Indicator Species Analysis. Furthermore, for the determination of indicator species DeVantier et al. (2000) applied an indicator value index, while this study utilized a correlation index. The former, as the name implies, is generally used to determine indicator species which may help in defining a habitat, and it is commonly utilized for conservation and monitoring purposes (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). The latter is normally used to determine the ecological preferences of a set of species among a group of site or combinations of sites (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). Although these definitions can be argued to be very similar, and often these indices yield quantitatively similar results, differing results may be obtained depending on which is used (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). A final point of comparison with DeVantier et al. (2000) is the lack of site combinations when performing their indicator species analysis. The lack of this feature prevents DeVantier et al. (2000) from identifying coral species which may serve as indicator species for multiple community types.

A final consideration is how hard coral assemblages in the Red Sea have changed in recent years due to severe disturbance events such as mass bleaching of corals. The fieldwork from Sheppard & Sheppard (1991), Riegl & Velimirov (1994) and DeVantier et al. (2000) was carried out prior to the increase in the frequency of high thermal events

starting in 1998. Although there is evidence for previous coral bleaching in the central Red Sea, the extent and severity of these events is much reduced when compared to the past two decades (DeCarlo, 2020). Indeed, the current impact of bleaching events on Red Sea coral reefs is unprecedented (DeCarlo, 2020). Furthermore, other anthropogenic pressures such as marine pollution, coastal development and illegal fishing activities have all recently increased in intensity along the coast of Sudan (Klaus, 2015; Nasr, 2015; PERSGA, 2003, 2010). It is then likely that the communities sampled by Sheppard & Sheppard (1991) and DeVantier et al. (2000) were in better health than most current Red Sea reefs, and may have even possessed significantly different coral assemblages. Higher frequencies of severe disturbance events and increasing anthropogenic pressures in recent decades might have resulted in a community shift towards more stress-tolerant species, such as the widely distributed *P. lutea* and *P. lobata*, which generally are considered to be more resilient than other common reef-building groups such as pocilloporids and acroporids (Monroe et al., 2018). For example, the 2010 bleaching event resulted in high mortality of fast-growing branching corals (specially acroporids) in several Saudi Arabian reefs, and coral assemblages previously dominated by these groups were reported to shift to a poritid dominated community (Furby et al., 2013). Such a community shift could explain why the reef edge community appears to possess a lower proportion of exposed-reef components (e.g.: acroporids, pocilloporids) than would be expected. It should be then be considered that these past studies may not fully portray the status, diversity and distribution patterns of present-day Red Sea coral assemblages.

4.3 Diversity patterns across community types and depth zones

A general pattern of increasing hard coral diversity with increasing depth, down to 20 – 30 m, is often observed in reefs from all tropical regions of the world (Huston, 1985). This pattern appears to be largely ubiquitous as it takes form even when using different diversity measurements (e.g.: richness, evenness, dominance) (Huston, 1985). In general, such phenomenon can be observed at Merlot, but the pattern is much less clear at Sha'ab Rumi (discussed later in this section). The increase in coral diversity with depth is hypothesized to arise from the interaction of the depth-related light gradient and environmental disturbances (Huston, 1985), and the effects these have on coral growth rate, mortality, and competitive exclusion. In general, shallow habitats allow for better light availability and thus faster coral growth, which leads to a high coral cover but strong interspecific competition, particularly for space (Huston, 1985). This often results in the

exclusion of less competitive species from these environments, leading to low diversity levels (Huston, 1985). Constant levels of disturbance, such as from photoinhibition (Hoogenboom et al., 2006), wave action (Dollar, 1982) and tidal exposure (Loya, 1972), are theorized to prevent the system from reaching equilibrium and being dominated by monospecific coral communities (Huston, 1985). The reef edge is a good example of such a system, as it possesses the highest hard coral cover, but some of the lowest richness, Shannon and evenness values (Figs. 7 & 9). This community is clearly dominated by the competitive and stress-tolerant massive *Porites* spp. (Monroe et al., 2018; Sheppard & Sheppard, 1991), but wave action and some level of sedimentation likely serve to maintain moderate levels of hard coral diversity. The higher proportion of dead coral at this habitat (~ 10%) when compared to the other communities could be evidence of the higher biotic and abiotic stress (Fig. 9). In contrast, light attenuation in deeper habitats results in slower coral growth, but reduced interspecific competition (Huston, 1985). As a result, even low levels of disturbance are enough to maintain the community in a constant state of non-equilibrium, resulting in moderate coral cover but high diversity levels (Huston, 1985). The lower parts of the Merlot reef slope (13 – 20 m) fit this description well, being some of the most diverse transects observed in this study and possessing overall moderate covers of live hard corals (Figs. 5, 7 & 9). Furthermore, although also dominated by massive *Porites* spp., many of the species associated to this community and to the slopes in general (see table 3), are generalists, which are often common in a wide variety of reef ecosystems but do not tend to be dominant (e.g.: *P. varians, Montipora* spp., *Stylocoeniella* spp., *S. hystrix*, *E. forskaliana*) (Sheppard & Sheppard, 1991; Veron, 2000); their association to the slope communities indicates that the strength of competitive exclusion at this community is much reduced, as strongly competitive species have not managed to drive them out.

It is clear however, that increasing coral diversity with depth was not always the case at Merlot. Although the hard coral taxa richness does increase in a fairly constant manner with depth, major deviations can be observed for Shannon and Evenness values, such as comparable Shannon and evenness between the 3 – 5 m and 13 – 15 m depth ranges, and very low values of both indices at 8 – 10 m depth (Fig. 9). Firstly, as the 3 – 5 m depth range corresponds to the vertical wall habitat, the availability of light is generally lower than expected at these depths. As a consequence, coral growth and interspecific competition levels likely resemble more those from deeper areas of the reef,

thus resulting in high evenness and Shannon values than would otherwise be expected (Huston, 1985). Hard coral richness remains low however, likely because most corals inhabiting the vertical wall are competitive shallow water species from the reef edge community, plus a few low-light tolerant species found in very shadowed areas, such as *P. maldivensis* (Longenecker et al., 2019). On the other hand, the low diversity levels encountered at 8 – 10 m depth are likely the result of high sedimentation. Sediment deposition also impacts hard diversity coral depth diversity patterns, but unlike light availably or water movement, its effects are often very localized and can depend on micro-site differences, thus they may follow no clear pattern (Huston, 1985). As already mentioned, the Merlot study site appears to experience high levels of sediment deposition (Fig. 11), which likely originates from soft bottom areas in the center of the reef platform and it is carried southwards by shallow water movement. It is possible that when the sediment particles reach over the reef edge and fall into deeper waters, reduced water movement impedes their resuspension and thus they start depositing over the reef structure. Deposition at the reef wall was observed to be low, likely due to the high steepness of this habitat, and so most of the sediment load sinks past it and deposits directly onto the adjacent portion of the reef slope at 8 – 10 m depth. High sedimentation can often reduce coral diversity as only few species can tolerate it. Although poritids are generally poor at sediment removal (Duckworth et al., 2017; Stafford-Smith, 1993), their ability to episodically produce and shed mucus sheets in order to clean their surfaces allows them to tolerate high sediment loads and survive in turbid environments (Jones et al., 2019). This would explain the high dominance of massive *Porites* spp. and the reduced Shannon and evenness values at 8 – 10 m depth. As the horizontal distance from the vertical wall increases with slope depth, deeper portions of the slope likely receive smaller sediment loads and so the impact of sedimentation is reduced, allowing for a higher diversity of hard corals (Fig. 9).

The situation at the Sha'ab Rumi appears to be less clear. Overall, it appears to be a more diverse community than that of the Merlot reef slope, although the deeper portions of both slopes seem fairly comparable in all diversity indices (Figs. 7 & 9). It is in the shallower parts where strong differences seem to arise (3 – 10 m depth), as it is clear these are more diverse than at Merlot. Furthermore, although hard coral richness does generally increase with depth, no such pattern can be observed for the Shannon or evenness values; the latter even seems to decrease slightly with depth, contrary to what is expected. The

increase in hard coral cover with depth also seems to contradicts the expectations from the decrease in light availability with increasing depth, although the overwhelmingly dominant *Paralemnalia* mats at 8 – 10 m depth are likely responsible for the low hard coral cover at this part of the slope ($\bar{x}$ = 22.5%). The reasons behind the lack of the expected depth pattern are not clear, though multiple factors could be involved. High diversity at the shallow areas (8 – 10 m) could be due to lower sedimentation when compared to Merlot, as the location of the Sha'ab Rumi study site results in higher exposure. Strong water movement could also result in higher levels of disturbance, which could in theory help sustain higher hard coral diversity even in shallow waters where interspecific competition tends to be stronger (Huston, 1985). The lack of an increase in diversity towards the deeper areas could be due to the higher water clarity, which could result in higher photosynthetic activity at these depths and in turn result higher coral cover, faster coral growth rates and strong competition (Huston, 1985). In summary, it is hypothesized that higher vertical homogeneity in environmental disturbances and light availability at Sha'ab Rumi when compared to merlot, results in weaker hard coral diversity depth gradients. Lastly, methodological limitations should also be considered. As only one transect is available for the 13 – 15 m and 20 – 21 m depth ranges, it should be considered that the obtained diversity values are outliers and do not reflect how hard coral diversity changes with depth at Sha'ab Rumi.

4.4 Taxonomic and methodological considerations

One of the key features of point-based photoquadrat analysis is the number of random points laid out per unit of area (point density) (Jokiel et al., 2015; Kohler & Gill, 2006; Pante & Dustan, 2012). Higher point density results in more accurate cover estimates of the benthos, but also increases the time necessary to analyze the photoquadrats (Jokiel et al., 2015; Kohler & Gill, 2006). Ideally, an optimal point density (OPD) which yields sufficiently accurate cover estimates but minimizes analysis time, should be used. Many factors can influence the OPD required to meet these criteria, such as quadrat size, transect length, transect number, etc., but one of the main biological variables is the real cover of benthic organisms, as decreasing abundances necessitate increasing OPD to consistently obtain reliable cover estimates (Pante & Dustan, 2012). As a consequence, the point density of any given study should be established based on educated assumptions of the expected cover of the benthic groups of interest (Morrison et al., 2012; Pante & Dustan, 2012). Based on the simulations performed by Pante &

Dustan (2012), the point density utilized in this study (50 randomly laid points for a quadrat area of 0.25 m^2) should in theory be sufficient to accurately estimate the mean cover of the most abundant groups, such as hard and soft corals, coralline algae, and bare substrate. But the estimates for the average cover of less abundant categories such as dead and bleached coral, sponges, and algae, may be less reliable under the utilized methodology (Pante & Dustan, 2012). It is unfortunately not possible to assess whether the cover of these groups has been under- or overestimated. Simply increasing the point density is not an efficient solution however, as many of the very rare groups would require unreasonably high OPDs in order to attain reliable cover estimates. however, it should be taken into account that the uncertainty surrounding the cover estimates of less abundant groups is larger than for estimated cover of the dominant benthic groups.

A lack of taxonomic resolution was a significant limitation of this study, as of the 123 hard coral taxa encountered, the species identity could not be reliably determined for 29 of them. This pitfall is the result of two main factors: constraints related to the use of still photoquadrats images, and uncertain taxonomic relationships within some groups of Red Sea hard corals. First, the technical limitations of photoquadrat analysis will be addressed. When using photographs for coral identification, image resolution plays a key role in allowing for accurate assessment of the morphological details of coral colonies (Jokiel et al., 2015; Morrison et al., 2012). In many cases, fine skeletal features, such as septa and costae structure, number of septal cycles, structure of the columellae, etc., are not appreciable unless close-up photographs are taken, and even then, may not be visible in live coral specimens. In many diverse groups, these fine structures may be the only characters which can reliably be used to separate species (Veron, 2000). Thus, the use of photoquadrat analysis results in bias against species with small corallites and whose identification requires the study of small morphological features. In this study, such was the case for *Acropora* spp. (Veron, 2000), *Cyphastrea* spp. (Arrigoni et al., 2017), *Goniopora* spp. (Veron, 2000), *Leptastrea* spp. (Arrigoni et al., 2020), the agariciids *Pachyseris inattesa* and *Leptoseris foliosa* (Terraneo et al., 2014, 2017), *Montipora* spp. (Veron, 2000) and *Porites* spp. (Terraneo, 2019; Terraneo, Benzoni, et al., 2019; Terraneo, Fusi, et al., 2019). Such limitation can be remedied by the use of close-up images, which would allow to look at coral specimens in detail. An effective use of this technique would be for a second diver equipped with a high-resolution camera, to work along-side the main diver photographing quadrats and take close-up images of hard

corals. With prior knowledge of which coral taxa require close examination, the effort of attaining close-up images can be optimized, as they would only be needed in certain cases. Although this method doubles the number of individuals required to survey a single transect, sampling time should not significantly increase, and it would allow for most coral taxa to be reliably identified. As an example, the identification of *F. micropentagona* in this study would not have been possible without access of close-up images. Though fossil specimens of this species are common in Pleistocene reefs from Egypt and Saudi Arabia (Casazza, 2012, 2017; Khalil et al., 2021), it is currently unreported in the scientific literature on extant Red Sea reefs. The current closest locality where its recorded to occur is the Socotra Archipelago in the Gulf of Aden (DeVantier et al., 2004). Had it not been for close-up images allowing for detailed examination off the corallite size, specimens of *F. micropentagona* would have likely been misidentified as the closely related *F. pentagona*, which is reported to be common in the Red Sea (Sheppard & Sheppard, 1991). Due to the close resemblance of these species, such misidentifications have likely resulted in *F. micropentagona* having been unnoticed for many years as part of the north-central Red Sea coral community.

Reliable species identification is also impeded by unresolved species boundaries for some Red Sea genera, as is the case for *Porites* spp. (Terraneo, 2019; Terraneo, Fusi, et al., 2019) and *Stylophora* spp. (Arrigoni, Benzoni, Terraneo, et al., 2016). The taxonomy of *Porites* is particularly cumbersome, as it is a very diverse genus, traditional species identification can only be performed through detailed examination of fine corallite structures, and phylogenetic analysis has failed to resolve many of the already established species (Arrigoni, Benzoni, Terraneo, et al., 2016; Terraneo, 2019). For example, *P. rus* has been recognized as a common and conspicuous component of Red Sea coral communities (DeVantier et al., 2000; Sheppard & Sheppard, 1991). However, a species with a very similar morphology, *P. monticulosa*, which was previously thought to only occur in the southern Red Sea (Berumen et al., 2019), was found in the central Red Sea coast of Saudi Arabia in sympatry with *P. rus* (Terraneo, 2019). Furthermore, phylogenetic analyses were unable to distinguish between the two species, finding instead that specimens of both formed a single well-defined clade (Terraneo, 2019). To further complicate the issue, the massive growth form commonly attributed to Red Sea *P. rus* colonies (Sheppard & Sheppard, 1991) best match *P. monticulosa* as described by Veron (2000). Another example of this is the genus *Stylophora*, of which many species are

endemic to the Red Sea. Although *Stylophora* species seem to be morphologically well defined, there have been many reports of colonies whose characteristics seem to fit multiple species or none at all (Arrigoni, Benzoni, Terraneo, et al., 2016), an instance of which was encountered during this study (Fig. 11). Although the morphology of this colony clearly places it in *Stylophora*, it does not match the description of any known species. Many of these anomalous have been found to be the result of hybridization between sympatric *Stylophora* species (Arrigoni, Benzoni, Terraneo, et al., 2016). It has been proposed such phenomenon is the consequence of permeable species boundaries due to the recent diversification and origin of Red Sea *Stylophora* species (Arrigoni, Benzoni, Terraneo, et al., 2016). It is possible that the anomalous specimen encountered at Merlot corresponds to one such hybrid, although it could alternatively be an unusual ecomorph of an established species. Unfortunately, its possible reliable species identification of these particular groups cannot be achieved by using non-invasive techniques such as photoquadrats or *in situ* identification, and may not be possible at all even with detailed information of the morphological characteristics of collected specimens. More comprehensive studies are needed to resolve the species relationships within these groups and help determine the validity of the currently used taxonomy.

5. CONCLUSIONS

The results of this study indicate the Merlot and Sha'ab Rumi reefs are currently in moderate to good health, as live hard coral and soft coral cover values remain within the range of previous observations, while algae, bleached corals and dead colonies were seldom observed. This is in line with the available information from previous reports, which maintain that a despite concern due to growing anthropogenic pressures, central Red Sea reefs appear to remain in good condition. Although a higher average dead coral cover than expected could indicate the reefs are experiencing some level of stress. However, direct comparisons between the results of this study and the aforementioned reports should be considered with care, as little information is available on methodological differences which may result in either hidden or false differences. The Merlot and Sha'ab Rum reefs appear to be particularly diverse, as most previous studies from the north and central Red Sea report lower site-specific hard coral richness when compared to this study. These observations fall in line with previous affirmations that the central Red Sea may be the most diverse part of the ecoregion, and highlight the necessity of future studies. The differences in dominant taxa and indicator species observed between the communities found by this study and those described by previous studies could be an indication of a community shift. However, insufficient study of Sudanese reefs and methodological differences, may also be responsible for these discrepancies.

Through the implementation of photo-transects, 123 hard coral taxa were recorded. However, the species identity for 29 of them could not be determined. This speaks not only to the uncertain taxonomy on certain Red Sea groups, but also to the biases of coral species identification through the use of still photoquadrats. It is therefore recommended for future studies that additional close-up images directed specifically towards certain groups (e.g.: *Acropora, Montipora, Porites, Leptastrea, Cyphastrea*), be implemented alongside the use of photoquadrats, in order to increase the achievable taxonomical resolution. As an example of the usefulness of close-up images is the identification of *F. micropentagona*, which would otherwise like have been misidentified. In summary, the use of photo-transects proved to be an efficient and cost-effective technique to study the diversity of central Red Sea coral reefs, and its proper implementation in future studies could significantly aid in advancing our knowledge of coral reef diversity and ecology.

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7. TABLES

Table 1

Approximate depth and number of photoquadrats for each of the transects laid out at the Merlot and Sha'ab Rumi reefs

Merlot			Sha'ab Rumi		
Transect ID	Depth (m)	*n*	Transect ID	Depth (m)	*n*
PT45	1 – 2 *	45	PT28	3	54
PT46	1 – 2 *	45	PT29	4	49
PT49	1 – 2 *	57	PT30	4	41
PT48	3	40	PT31	9	49
PT41	4	58	PT32	9	48
PT43	4	53	PT33	10	54
PT36	9	52	PT34	13	53
PT37	9	40	PT35	21	49
PT39	9	59			
PT40	14	60			
PT42	15	57			
PT44	15	57			
PT38	20	67			
PT47	20	51			

* Depth range estimated based on in-situ observations.

n = Number of photoquadrats analyzed for each transect.

TABLE 2

Average percentage cover of hard and soft corals, as well as bleached and recently dead coral, for each study site.

Group	Merlot (%)	Sha'ab Rumi (%)
Live hard coral	38.2 ± 2.9	32.8 ± 3.8
Live soft coral	14.9 ± 3.2	15.9 ± 4.9
Bleached coral	0.11 ± 0.03	0.11 ± 0.06
Recently dead coral	5.2 ± 0.9	4.5 ± 1.0
Algae	4.4 ± 0.7	5.7 ± 0.7

Uncertainty values are presented as the standard error.

TABLE 3

Hard and soft coral taxa associated to each of the groups obtained from the dendrogram of the hierarchical cluster analysis, and their respective group-equalized point-biserial correlation coefficient (r_{pb}^{g}) and associated p-value.

Group and associated taxa	r_{pb}^{g}	p-value
Reef edge – Merlot (Cluster 1)		
Leptoria phrygia	0.991	0.001
Stylophora wellsi	0.959	0.001
Pocillopora eydouxi	0.944	0.001
Goniastrea stelligera	0.927	0.001
Echinopora hirsutissima	0.922	0.001
Pocillopora verrucosa	0.913	< 0.001
Palythoa tuberculosa	0.842	0.002
Acropora spp. (Digitate)	0.841	0.002
Goniastrea edwardsi/*retiformis*	0.647	0.036
Vertical wall – Merlot (Cluster 2)		
Tubastraea coccinea	0.970	0.001
Tubastraea micrantha	0.787	0.001
Antipathidae indet.	0.763	0.004
Pavona maldivensis	0.655	0.025
Neptheiidae indet.	0.606	0.045
Reef slope – Merlot (Cluster 3)		
Melithaea rubrinodis	0.865	< 0.001
Xeniidae indet.	0.805	< 0.001
Anthelia spp.	0.776	0.007
Stylophora pistillata	0.736	0.010
Stylocoeniella spp.	0.662	0.022

TABLE 3 (continued)

Group and associated taxa	r_{pb}^{g}	p-value
Reef slope – Sha'ab Rumi (Cluster 4)		
Seriatopora hystrix	0.797	< 0.001
Porites spp. (encrusting)	0.783	< 0.001
Goniastrea pectinata	0.754	0.004
Paralemnalia spp.	0.740	0.007
Fungiidae indet.	0.691	0.024
Reef slopes – Merlot & Sha'ab Rumi (Clusters 3 & 4)		
Porites rus/*monticulosa*	0.809	< 0.001
Acropora spp. (Staghorn)	0.767	0.001
Montipora morphospecies 2	0.728	0.005
Litophyton spp.	0.728	0.007
Sarcophyton spp.	0.707	0.008
Sinularia spp.	0.697	0.007
Echinopora forskaliana	0.680	0.020
Acropora spp. (Corymbose plates)	0.672	0.016
Rhytisma spp.	0.653	0.032
Pavona varians	0.580	0.048
Reef edge & Vertical wall – Merlot (Clusters 1 & 2)		
Distichopora violácea	0.739	0.008
Reef edge & Reef slope – Merlot (Clusters 1 & 3)		
Porites spp. (massive/submassive)	0.658	0.015

8. FIGURES

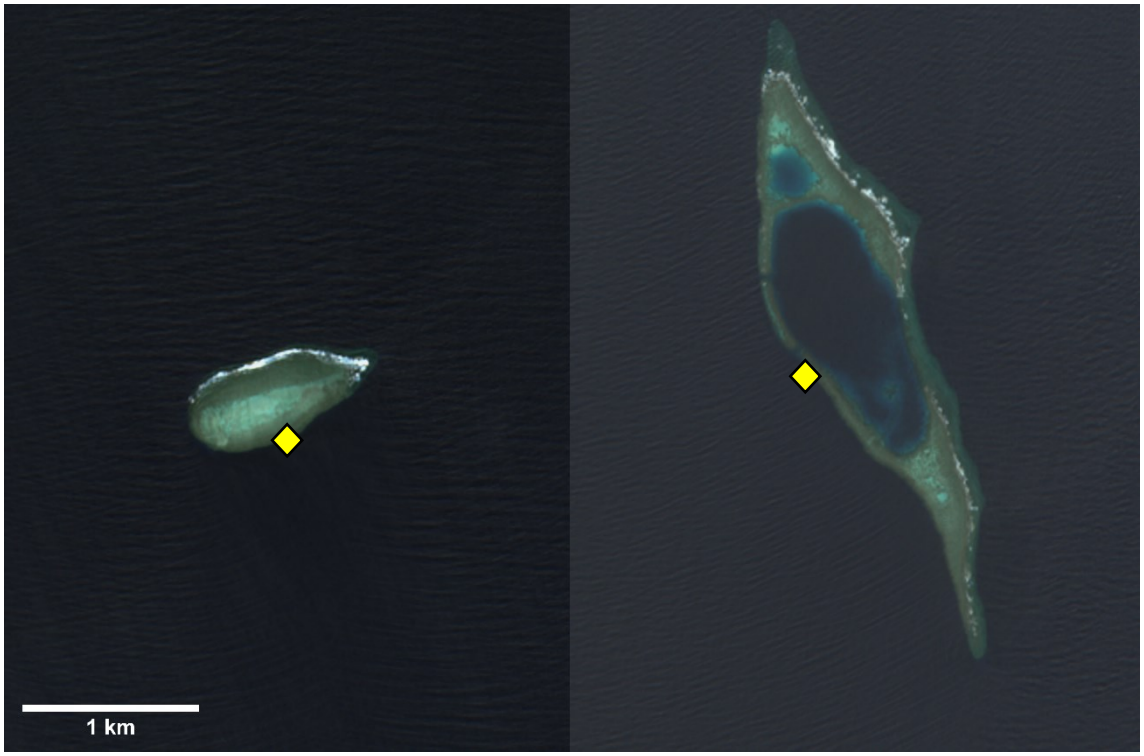

Figure 1: High resolution satellite imagery for the Merlot (A, taken on 01/10/2021) and Sha'ab Rumi (B, 26/09/2021) reefs, with the approximate location of the study sites marked. Note the soft bottoms on the southern part of the Merlot reef platform, visible due to the lighter color of the sediment. Images contain modified Copernicus Sentinel Data (2021), processed through the Sentinel Hub EO Browser (https://apps.sentinel-hub.com/eo-browser/, Sinergise Ltd.)

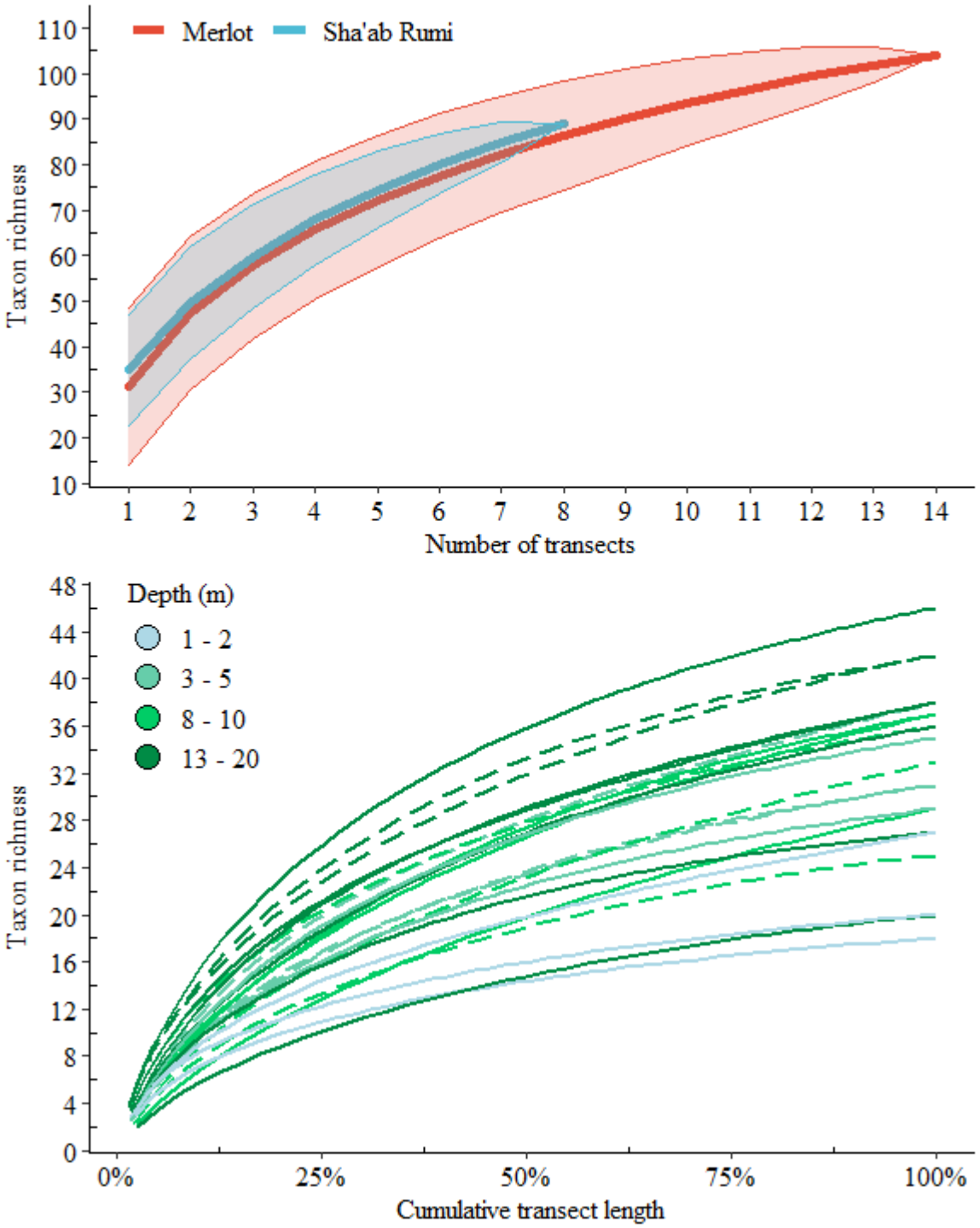

Figure 2: Species accumulation curves (SACs) of hard coral taxa according to site (top) and transect (bottom). The colored area around the site SACs represents the 95% confidence interval. Confidence intervals were removed from the transect SACs to facilitate visualization of the curves. Dashed line = Sha'ab Rumi; Solid line = Merlot.

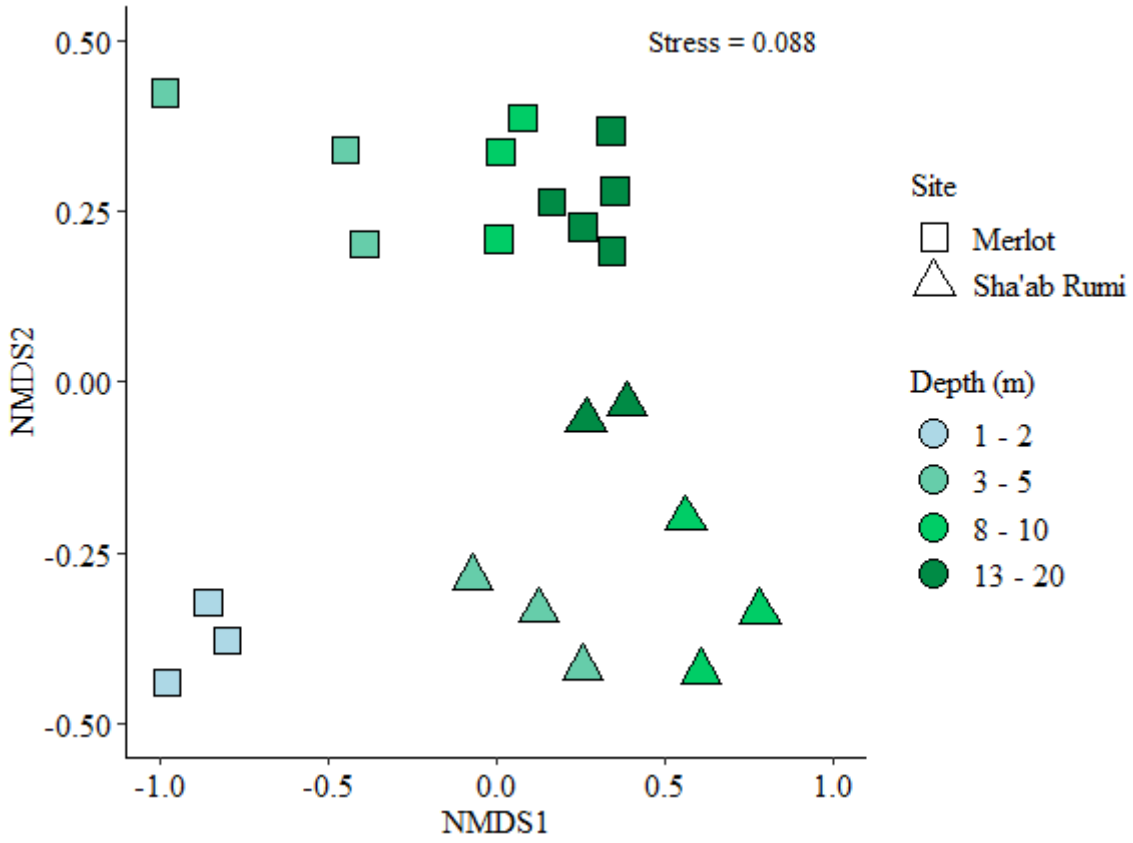

Figure 3: Nonmetric multi-dimensional scaling based on the composition of soft and hard coral taxa at the Merlot and Sha'ab Rumi reefs, utilizing the Morisita-Horn dissimilarity index.

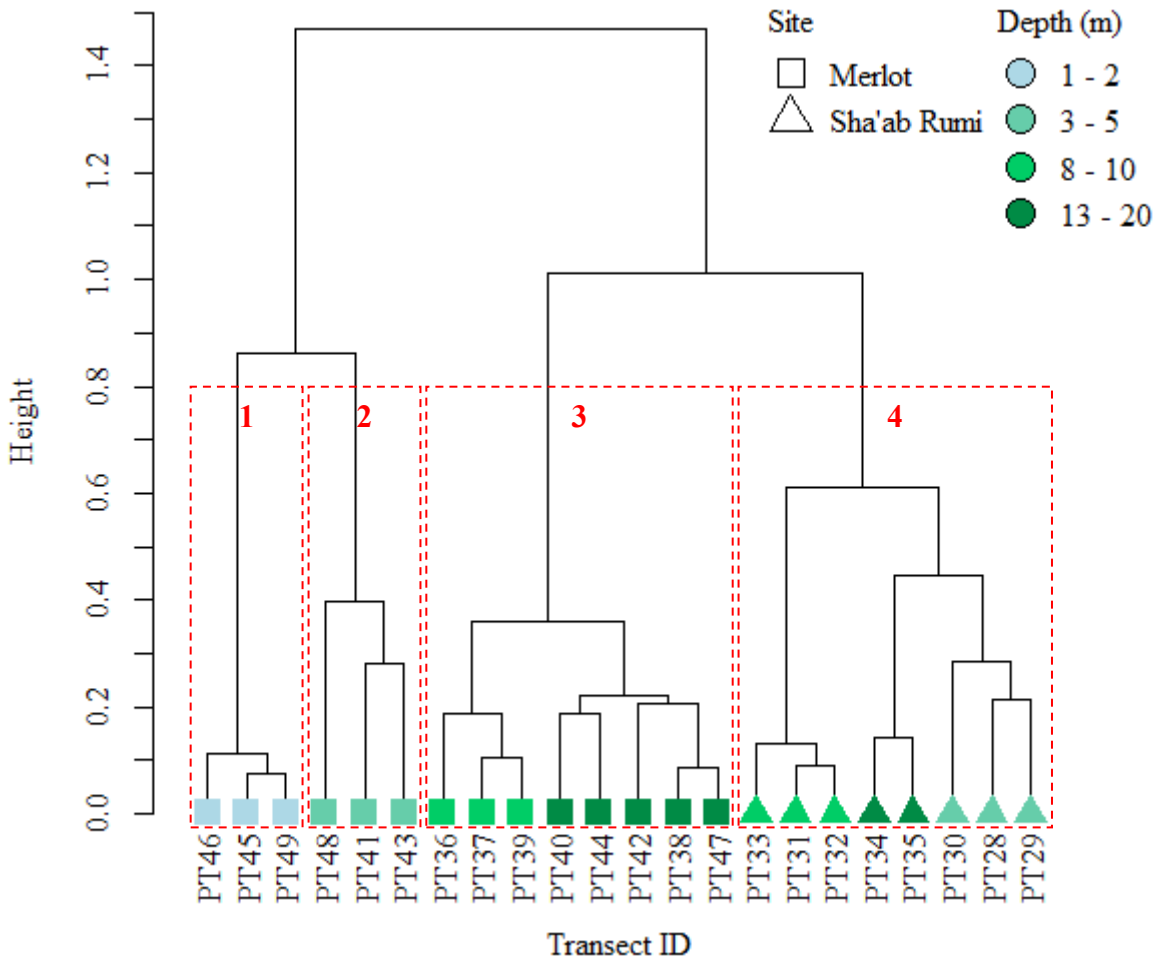

Figure 4: Dendrogram of the hierarchical cluster analysis for the composition of hard and soft corals at the Merlot and Sha'ab Rumi reefs. The highlighted clusters were obtained at a cut-off height of 0.8. Cluster 1 = Reef edge; cluster 2 = Vertical wall; cluster 3 = Merlot reef slope; cluster 4 = Sha'ab Rumi reef slope

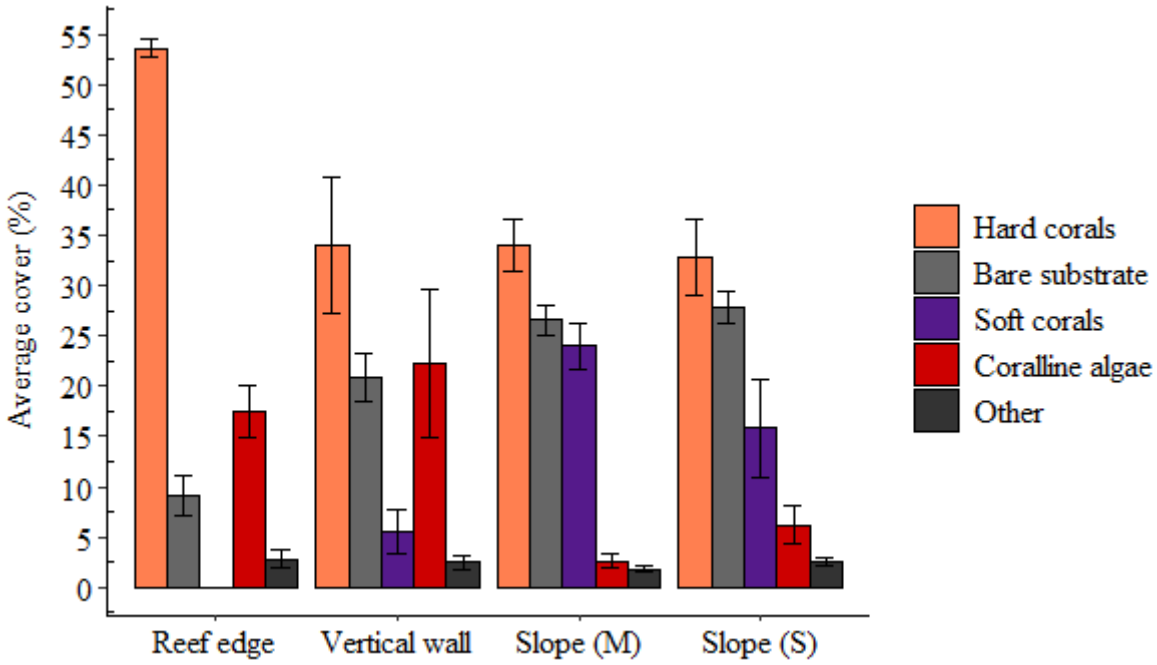

Figure 5: Average cover per transect of major groups, for each study site. "Other" refers to the combined mean cover of minor groups. Whiskers represent the standard error. Abbreviations: Slope (M) = Merlot reef slope; Slope (S) = Sha'ab Rumi reef slope.

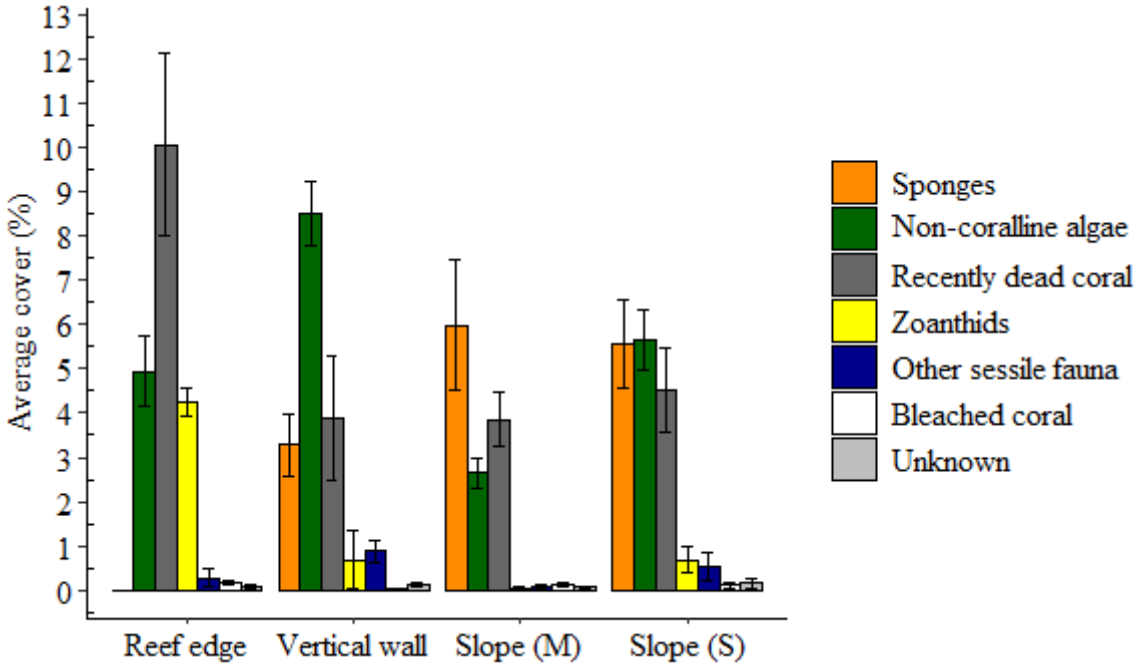

Figure 6: Average cover per transect of the remaining major groups not shown in Fig. 5 (classified as "Other"), for each habitat. Whiskers represent the standard error. Abbreviations: Slope (M) = Merlot reef slope; Slope (S) = Sha'ab Rumi reef slope.

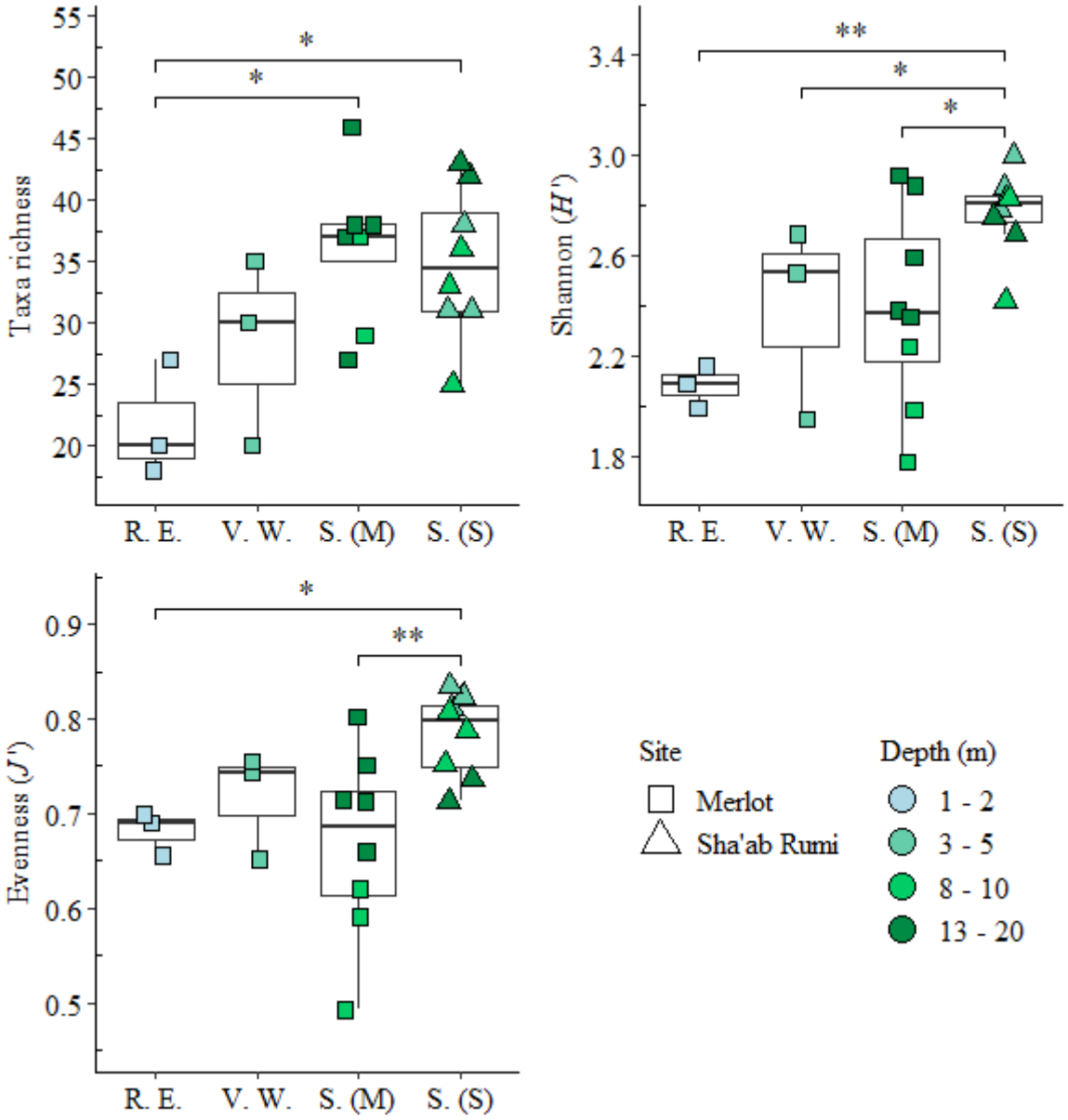

Figure 7: Taxon richness, diversity, dominance and evenness per transect, grouped according to habitat. A small amount of random noise (15%) in the horizontal axis has been added to each observation to aid in the visualization of overlapping points. Abbreviations: R.E = reef edge; V. W. = vertical wall; S. (M) = Merlot reef slope; S. (S) = Sha'ab Rumi reef slope.

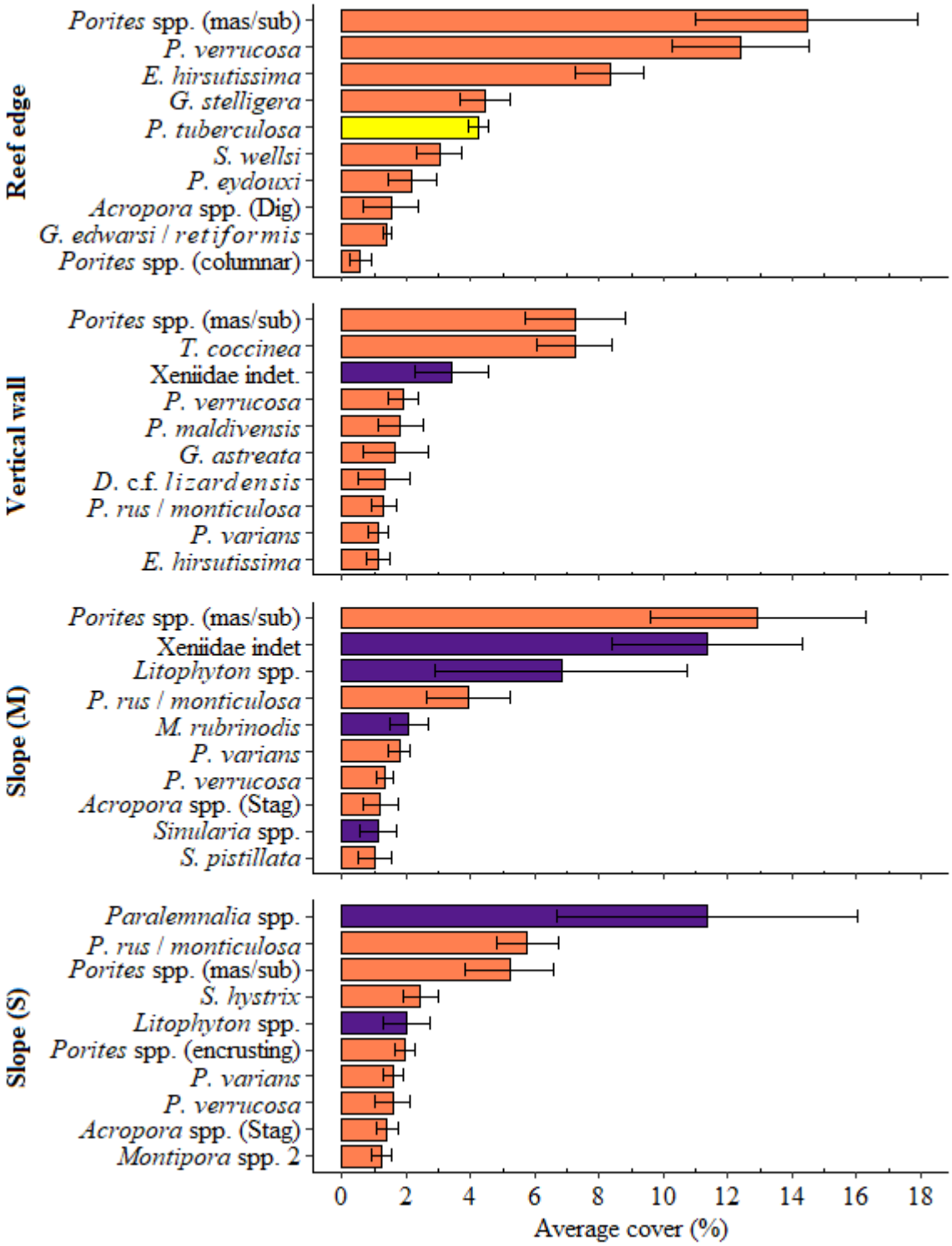

Figure 8: Average cover of the most abundant taxa for each of the proposed habitats. Whiskers represent the standard error. Coloration signifies taxon classification according to Figs. 1 & 2. Abbreviations: Slope (M) = Merlot reef slope; Slope (S) = Sha'ab Rumi reef slope; mas/sub = massive/submassive; Dig = Digitate; Stag = Staghorn.

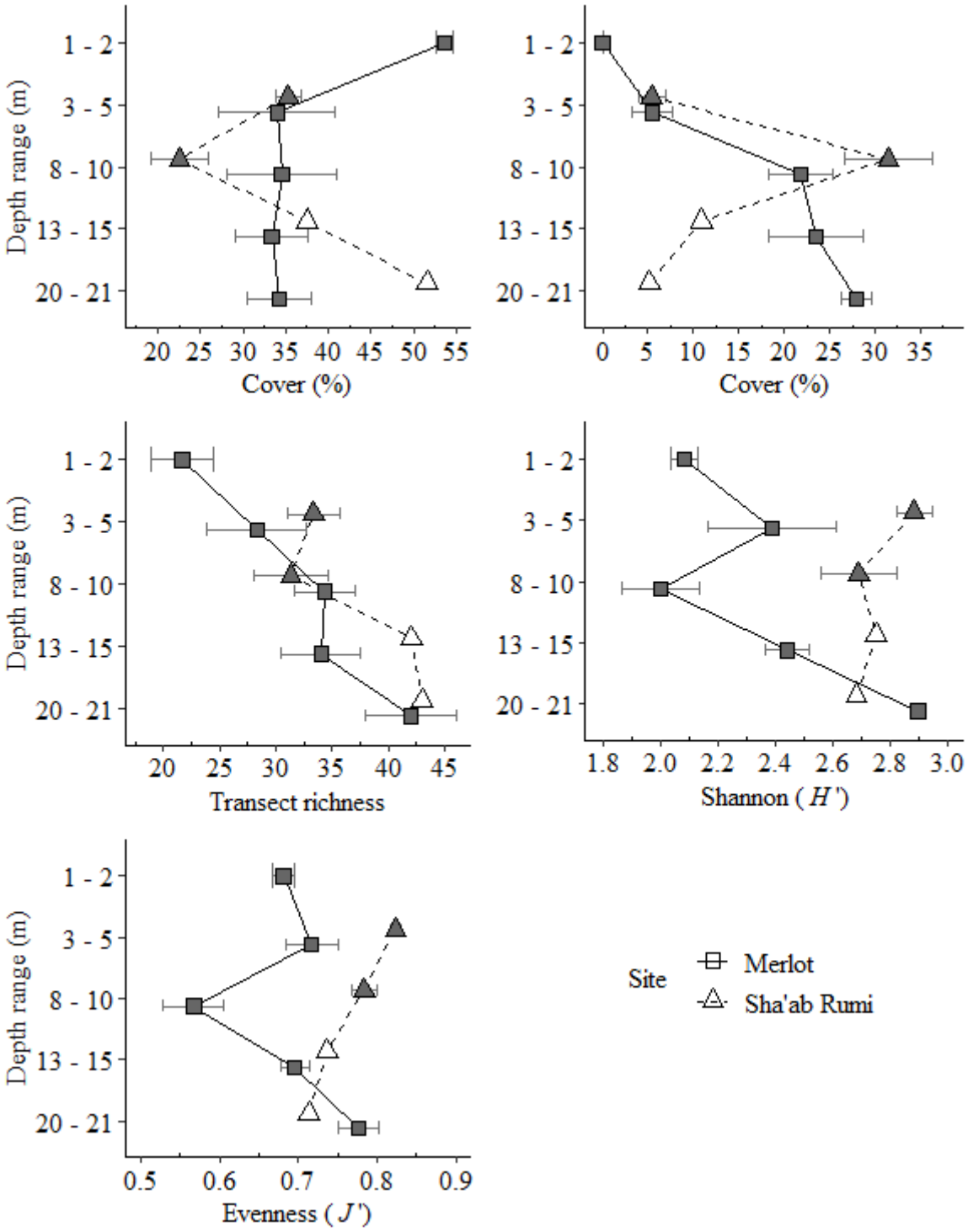

Figure 9: Hard and soft coral cover, and average hard coral taxon richness, Shannon's index (*H'*) and Pielou's Evenness (*J'*) at each sampled depth range for the two study sites. Grey symbols indicate average values, while white symbols correspond to single observations.

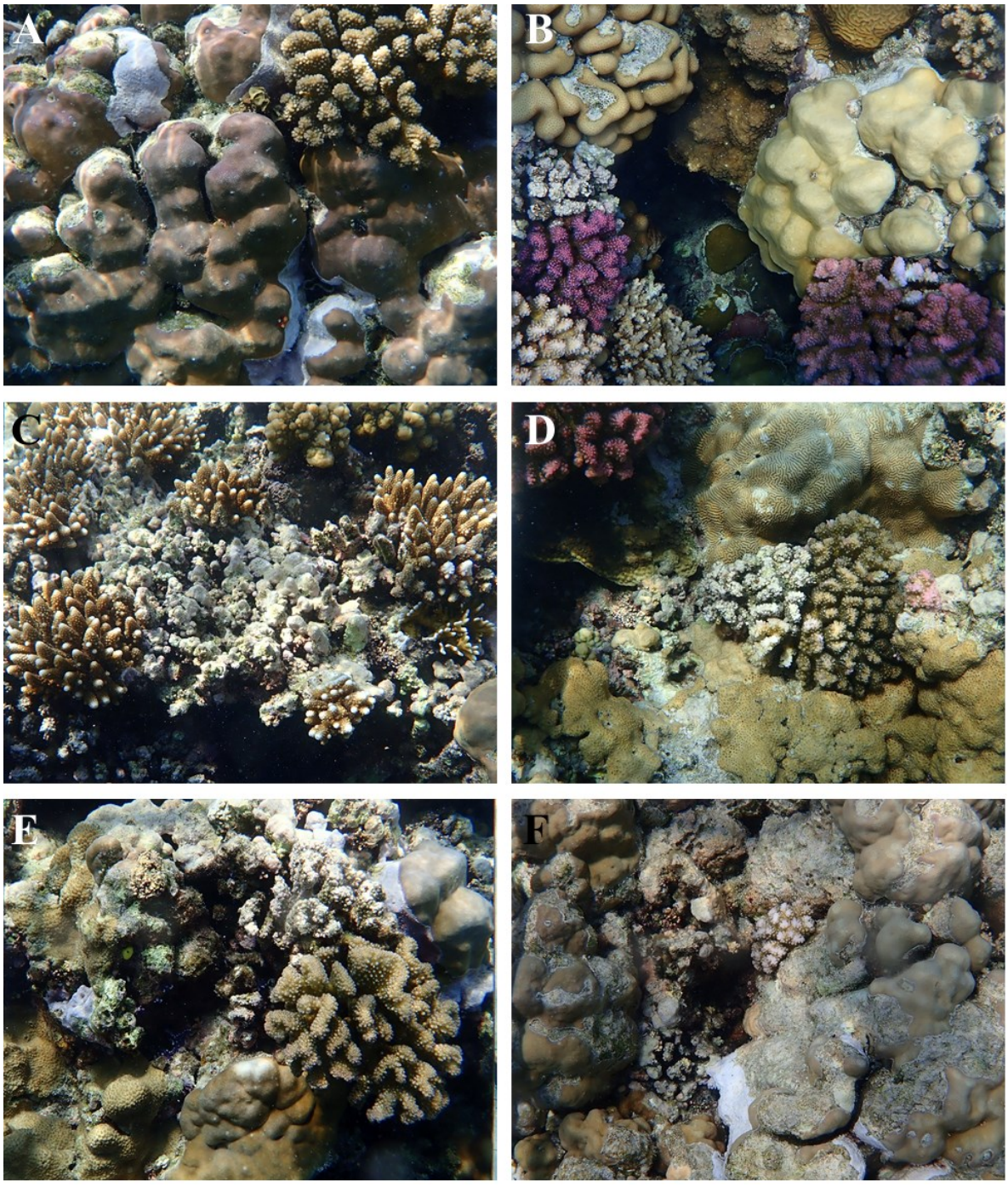

Figure 10: Photographs showcasing the reef edge community. A) The reef framework was composed of massive *Porites* colonies; note the coralline red algae among the coral. B) Examples of common coral taxa: *G. stelligera*, *P. verrucosa*, *E. hirsutissima* and massive *Porites* spp. C) Small colonies of digitate *Acropora* spp. and *S. wellsi*. D) Mat of *P. tuberculosa*, next to *L. phrygia*, *P. verrucosa* and *E. hirsutissima*. E) A *P. eydouxi* colony among massive *Porites* spp. F) *Porites* spp. colonies with a high incidence of dead coral.

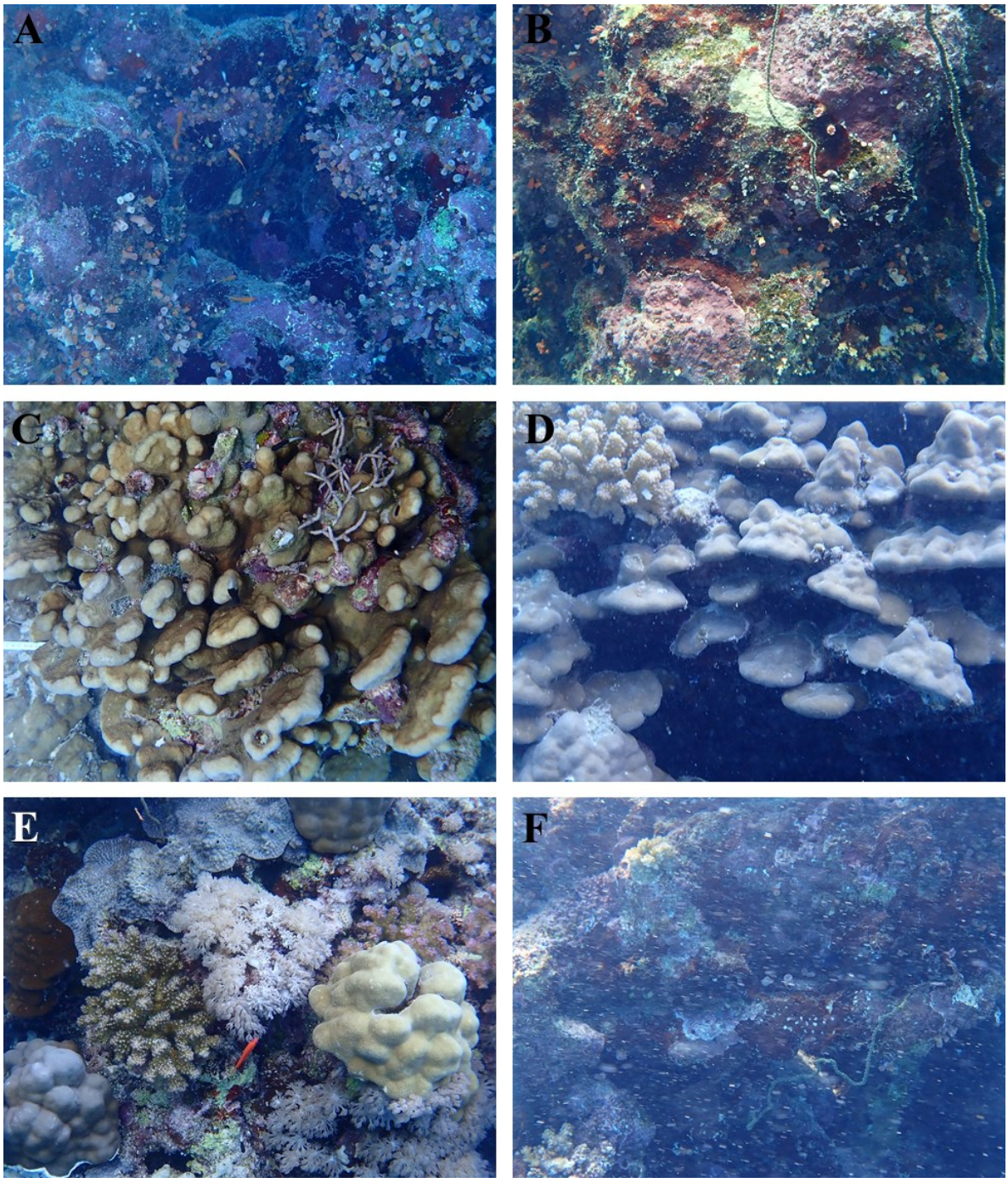

Figure 11: Photographs showcasing the vertical wall community. A) Low light environments were generally dominated by *T. coccinea*. B) Portion of the vertical wall with characteristic ahermatypic taxa such as Neptheidae, Antipathidae and *T. coccinea*; note the abundance of coralline red algae. C) A large colony of *P. maldivensis*. D) massive *Porites* spp. colonies creating overhangs. E) A well-lit area, dominated by zooxanthellate hard and soft corals. F) The high sedimentation at Merlot was appreciable in this habitat.

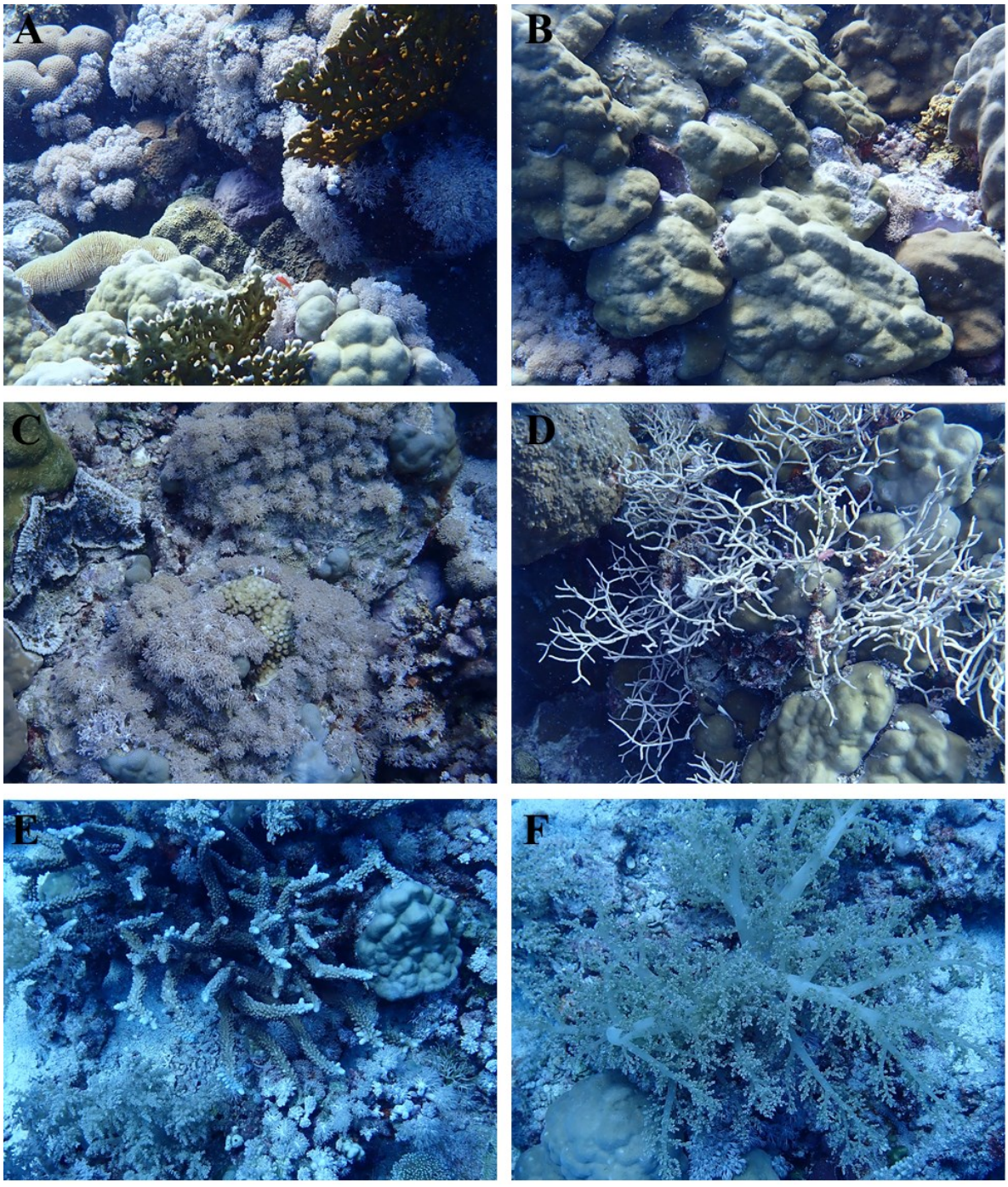

Figure 12: Photographs showcasing the Merlot reef slope community. A) Portion of the reef slope with multiple hermatypic corals such as Poritids, Merulinids, Milleporids and Fungiids. B) Dominance of massive *Porites* spp. colonies at 8 – 10 m depth. C) Xeniids colonies surrounding a small *E. forskaliana* coral. D) A large *M. rubrinodis* colony next to *Porites* spp. E) Staghorn-like *Acropora* spp. were a common occurrence at this community. F) Large *Litophyton* spp. colonies were especially abundant at 15-20 m depth.

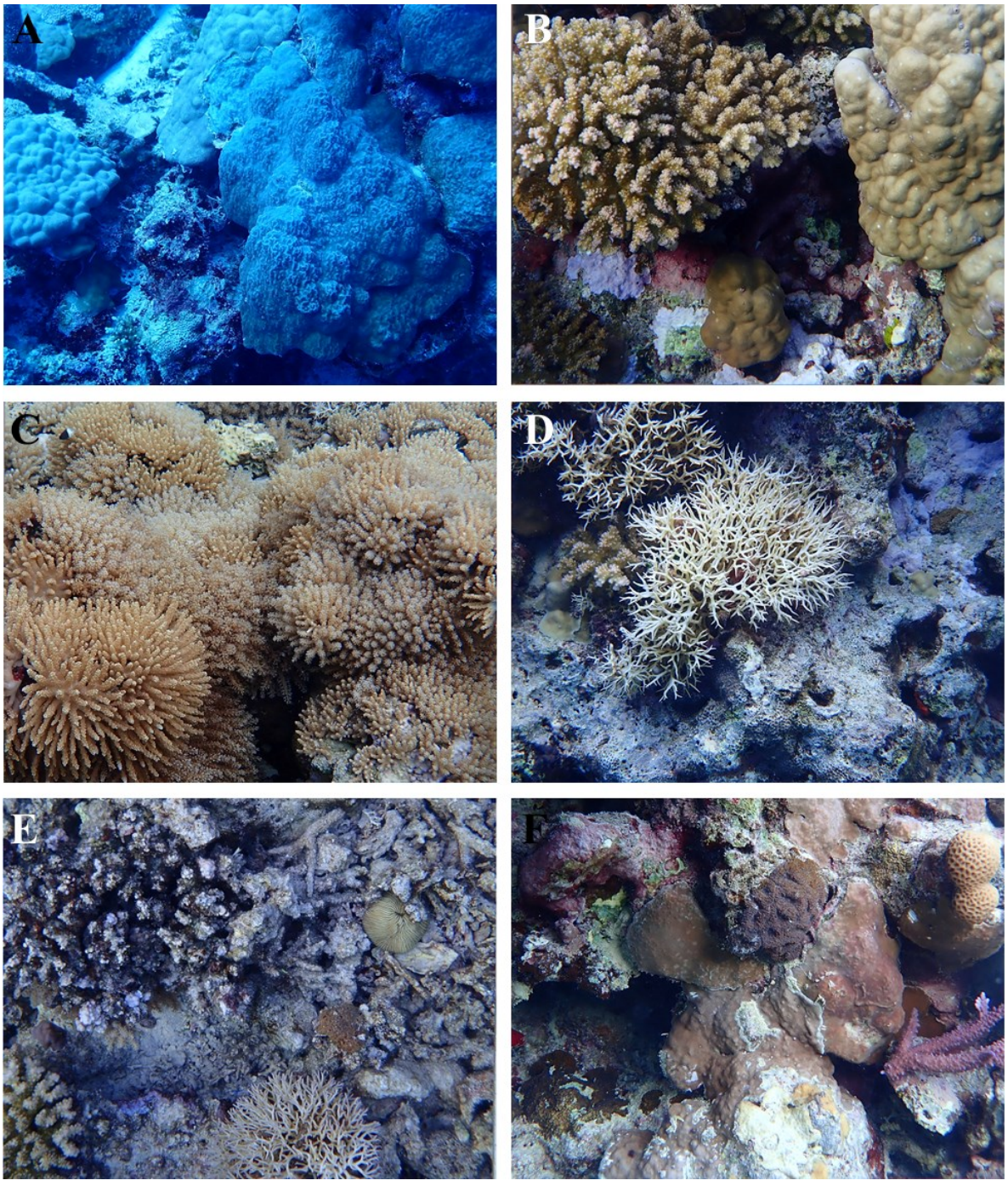

Figure 13: Photographs showcasing the Sha'ab Rimi reef slope community. A) *P. rus* / *monticulosa* was the most abundant hard coral. B) Other common corals: massive *Porites* spp., *P. verrucosa* (upper-left) and *P. damicornis* (lower-left corner). C) Extensive *Paralemnalia* spp. mats at 8 – 10 m depth. D) *S. hystrix*, a common coral at this site. E) Portion of the reef consisting mostly of lose substrate; a fungiid can be observed among the ruble. F) Encrusting colonies of *Porites* spp. were abundant at this site (lower-center).

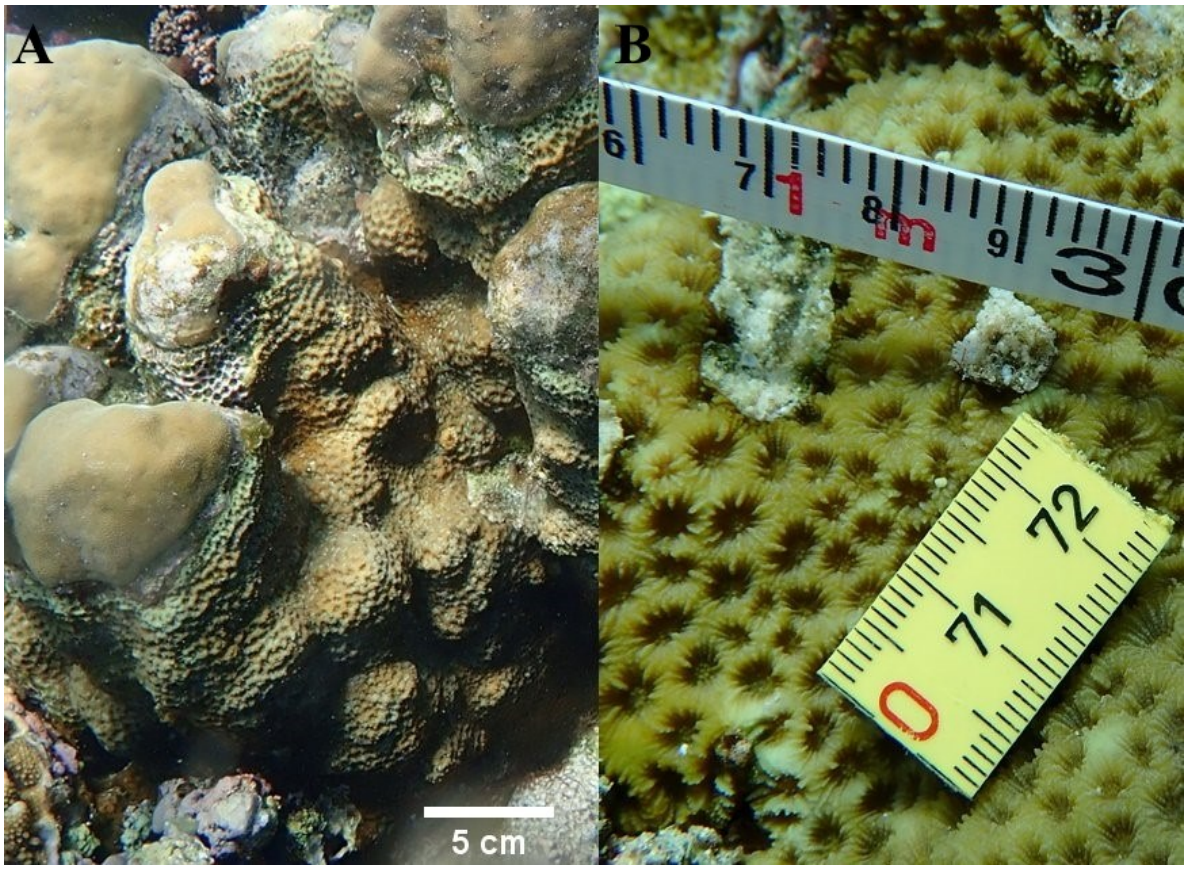

Figure 14: A) Photograph of an encrusting colony of *F. micropentagona*, found at the reef edge community in Merlot. B) Close-up photograph showing the corallite details of a *F. micropentagona* colony observed at the vertical wall community.

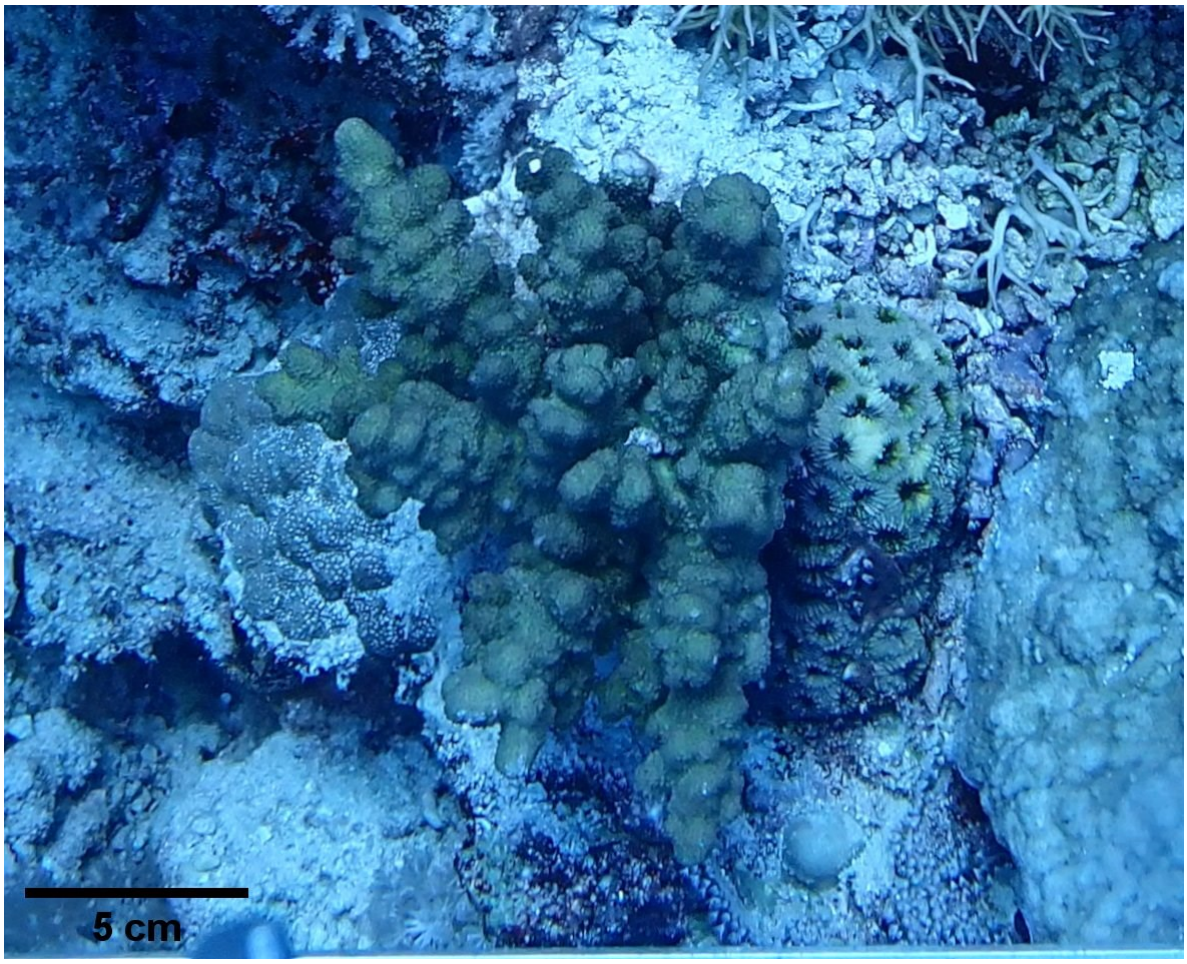

Figure 15: Photograph of an unknown scleractinian (branching colony in the center of the image), tentatively classified as *Stylophora* sp. Found in Merlot at a depth of 20 m.

ANNEX 1

Table 1

P-values of the post-hoc Tukey multiple comparisons test of differences between communities for the average cover of hard corals

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	**0.047**	**0.022**	**0.015**
Vertical wall		-	1.000	0.998
Reef slope (M)			-	0.994
Reef slope (S)				-

Table 2

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for the cover of soft corals

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.088	**0.013**	**<0.001**
Vertical wall		-	**0.024**	0.155
Reef slope (M)			-	0.136
Reef slope (S)				-

Table 3

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for the cover of bare substrate

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.104	**0.002**	**0.001**
Vertical wall		-	**0.046**	**0.021**
Reef slope (M)			-	0.295
Reef slope (S)				-

Table 4

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for the cover of red coralline algae

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.464	**0.002**	**0.015**
Vertical wall		-	**0.002**	**0.016**
Reef slope (M)			-	0.131
Reef slope (S)				-

Table 5

P-values of the Tukey multiple comparisons test of differences between communities for the average cover of non-coralline algae

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.040	0.139	0.887
Vertical wall		-	**<0.001**	**0.004**
Reef slope (M)			-	**0.049**
Reef slope (S)				-

Table 6

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for the cover of sponges

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.201	**0.015**	**0.015**
Vertical wall		-	0.311	0.422
Reef slope (M)			-	0.464
Reef slope (S)				-

Table 7

P-values of the Tukey multiple comparisons test of differences between communities for the average cover of dead coral

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	**0.030**	**0.007**	**0.018**
Vertical wall		-	0.999	0.979
Reef slope (M)			-	0.944
Reef slope (S)				-

Table 8

P-values of the Tukey multiple comparisons test of differences between communities for the average transect richness of hard coral taxa

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.585	**0.012**	**0.022**
Vertical wall		-	0.241	0.362
Reef slope (M)			-	0.982
Reef slope (S)				-

Table 9

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for transect Shannon (*H'*) index

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.192	0.093	**0.004**
Vertical wall		-	0.383	**0.034**
Reef slope (M)			-	**0.020**
Reef slope (S)				-

Table 10

P-values of the post-hoc Conover-Iman rank of sums test of differences between communities for transect Pielou's evenness (*J'*) index

	Reef edge	Vertical wall	Reef slope (M)	Reef slope (S)
Reef edge	-	0.473	0.353	**0.020**
Vertical wall		-	0.400	0.203
Reef slope (M)			-	**0.008**
Reef slope (S)				-

ANNEX 2

List of all hard and soft coral taxa observed at the study sites

	Merlot	Sha'ab Rumi
Anthozoa		
Scleractinea		
Acroporidae		
Acropora spp. (Arb)	X	X
Acropora spp. (CorC)	X	X
Acropora spp. (CorP)	X	X
Acropora spp. (Dig)	X	X
Acropora spp. (Stag)	X	X
Acropora spp. (CorBRC)	X	X
Acropora spp. (HBT)	X	X
Astreopora cucullata	X	
Astreopora gracilis	X	X
Astreopora suggesta		X
Montipora cryptus	X	X
Montipora danae	X	
Montipora efflorescens	X	X
Montipora maeandrina	X	X
Montipora stilosa / *tuberculosa*	X	X
Montipora venosa	X	
Montipora verrucosa		X
Montipora spp. morph. 1	X	X
Montipora spp. morph. 2	X	X
Montipora spp. morph. 3	X	X
Astrocoeniidae		
Stylocoeniella spp.	X	X
Pocilloporidae		
Pocillopora damicornis	X	X
Pocillopora eydouxi	X	X
Pocillopora verrucosa	X	X
Seriatopora hystrix	X	X
Stylophora danae	X	X
Stylophora mamillata		X
Stylophora pistillata	X	X
Stylophora subseriata/kuehlmanni	X	X
Stylophora wellsi	X	
Stylophora sp. 1	X	
Euphylliidae		
Galaxea astreata	X	X
Galaxea fascicularis	X	X
Gyrosmilia interrupta		X

ANNEX 2 (continuation)

List of all hard and soft coral taxa observed at the study sites

	Merlot	Sha'ab Rumi
Psammocoridae		
Psammocora nierstraszi	X	
Psammocora profundacella	X	X
Coscinaraeidae		
Coscinaraea monile	X	X
Agariciidae		
Gardineroseris planulata	X	X
Leptoseris explanata	X	
Leptoseris foliosa / *Pachyseris inattesa*	X	
Leptoseris incrustans	X	X
Leptoseris mycetoseroides	X	X
Leptoseris scabra / *hawaiiensis*	X	
Leptoseris sp. 1	X	
Pachyseris speciosa	X	
Pavona cactus		X
Pavona danai	X	
Pavona explanulata	X	X
Pavona frondifera		X
Pavona maldivensis	X	X
Pavona varians	X	X
Fungiidae		
Ctenactis spp.	X	X
Herpolitha spp.		X
Pleuractis spp.		
Fungiidae indet.	X	X
Lobophylliidae		
Acanthastrea brevis	X	
Acanthastrea faviaformis		X
Acanthastrea ishigakiensis		X
Acanthastrea c.f. *echinata*	X	X
Echinophyllia echinata		X
Echinophyllia orpheensis	X	
Lobophyllia erythraea	X	
Lobophyllia hataii	X	
Lobophyllia hemprichii		X
Lobophyllia robusta	X	X
Oxypora glabra		X
Oxypora lacera	X	X
Merulinidae		
Caulastrea tumida		X

ANNEX 2 (continuation)

List of all hard and soft coral taxa observed at the study sites

	Merlot	Sha'ab Rumi
Cyphastrea spp. 1	X	X
Cyphastrea spp. 2	X	
Dipsastraea danai	X	X
Dipsastraea favus	X	X
Dipsastraea lacuna		X
Dipsastraea laxa	X	X
Dipsastraea c.f. *lizardensis*	X	
Dipsastraea matthaii	X	X
Dipsastraea pallida	X	X
Dipsastraea rotumana	X	
Dipsastraea c.f. *speciosa*		X
Echinopora forskaliana	X	X
Echinopora fruticulosa	X	
Echinopora hirsutissima	X	X
Echinopora lamellosa		X
Favites abdita	X	
Favites halicora	X	X
Favites micropentagona	X	X
Favites pentagona	X	
Favites spinosa	X	
Goniastrea c.f. *australensis*	X	
Goniastrea edwardsi / *retiformis*	X	X
Goniastrea pectinata	X	X
Goniastrea stelligera	X	X
Hydnophora exesa	X	
Hydnophora microconos	X	
Leptoria phrygia	X	
Merulina ampliata	X	
Merulina scheeri		X
Mycedium elephantotus	X	X
Paramontastraea peresi	X	X
Platygyra crosslandi	X	X
Platygyra daedalea	X	X
Platygyra lamellina	X	
Platygyra pini	X	X
Poritidae		
Goniopora sp. 1	X	X
Goniopora sp. 2		X
Porites spp. (columnar)	X	X
Porites spp. (encrusting)	X	X

ANNEX 2 (continuation)

List of all hard and soft coral taxa observed at the study sites

	Merlot	Sha'ab Rumi
Porites spp. (massive / submassive)	X	X
Porites rus / *monticulosa*	X	X
Stylaraea punctata	X	
Dendrophylliidae		
Tubastraea coccinea	X	X
Tubastraea micrantha	X	
Turbinaria irregularis	X	
Turbinaria stellulata	X	X
Alcyonacea		
Alcyoniidae		
Rhytisma fulvum	X	X
Sarcophyton spp.	X	X
Sinularia spp.	X	X
Melithaeidae		
Melithaea rubrinodis	X	X
Neptheidae		
Litophyton spp.	X	X
Paralemnalia spp.	X	X
Stereonephthya spp.	X	
Neptheidae indet.	X	X
Tubiporidae		
Tubipora musica	X	X
Xeniidae		
Anthelia spp.	X	
Sympodium spp.	X	
Xeniidae indet.	X	X
Zoantharia		
Sphenopidae		
Palythoa tuberculosa	X	X
Hydrozoa		
Anthoathecata		
Milleporidae		
Millepora dichotoma	X	X
Millepora exaesa	X	X
Millepora platyphylla	X	X
Stylasteridae		
Distichopora violacea	X	X

APPENDIX

Zusammenfassung: Das Rote Meer besitzt die größte Vielfalt an Steinkorallen im Indischen Ozean, aber das zentrale und südliche Rote Meer ist wenig untersucht. Ziel dieser Studie war es daher, die Gemeinschaftszusammensetzung und Zonierung von Stein- und Weichkorallen an zwei küstenfernen sudanesischen Riffen, Merlot und Sha'ab Rumi, mit 22 Fototransekten, in Tiefen von 0-21 m, zu untersuchen. Drei unterschiedliche Lebensräume wurden beprobt: Riffkante, vertikale Wand und Riffhang. Nur letzterer trat an beiden Lokalitäten auf. Es wurden jeweils 104 und 89 Steinkorallentaxa gezählt. Dieser Artenreichtum ist höher als in den meisten früheren Berichten aus dem nördlichen und zentralen Roten Meer, was darauf hinweist, dass diese Riffe besonders vielfältig sind. Vergleiche mit früheren Studien zeigen, dass beide Riffe in gutem Zustand sind. Vier Korallengemeinschaften charakterisieren die Riffkante, die vertikale Wand und die zwei Riffhänge. Diese, weisen Ähnlichkeiten mit beschriebenen Gemeinschaftstypen auf, aber es gibt wichtige Unterschiede in den dominante Gruppen und Indikatorarten. Diese könnten auf methodische Unterschiede, unzureichende Kenntnis der sudanesischen Riffe oder auf eine durch Korallenbleiche verursachte Verschiebung der Artengemeinschaft zurückzuführen sein. Nur die Riffhanggemeinschaften waren zwischen den Standorten vergleichbar, wobei die bei Sha'ab Rumi war diverser war. Im Allgemeinen nahm die Steinkorallenvielfalt mit der Tiefe zu, was vermutlich auf die Wechselwirkung zwischen der Intensität von Umweltstörungen und der variablen Lichtverfügbarkeit zurückzuführen ist. Fototransekten erwiesen sich als effektiv, um mehrere Aspekte der benthischen Ökologie von Korallenriffen zu untersuchen. Die Verwendung zusätzlicher Nahaufnahmen zur genaueren Bestimmung einiger Taxa würde helfen, die taxonomische Auflösung zu erhöhen.