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REPORT

Higher species richness of octocorals in the upper mesophotic zone in Eilat (Gulf of Aqaba) compared to shallower reef zones

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Abstract Mesophotic coral-reef ecosystems (MCEs), which comprise the light-dependent communities of corals and other organisms found at depths between 30 and ~ 150 m, have received very little study to date. However, current technological advances, such as remotely operated vehicles and closed-circuit rebreather diving, now enable their thorough investigation. Following the reef-building stony corals, octocorals are the second most common benthic component on many shallow reefs and a major component on deep reefs, the Red Sea included. This study is the first to examine octocoral community features on upper MCEs based on species-level identification and to compare them with the shallower reef zones. The study was carried out at Eilat (Gulf of Aqaba, northern Red Sea), comparing octocoral communities at two mesophotic reefs (30–45 m) and two shallow reef zones (reef flat and upper fore-reef) by belt transects. A total of 30 octocoral species were identified, with higher species richness on the upper MCEs compared to the shallower reefs. Although the MCEs were found to host a higher number of species than the shallower reefs, both featured a similar diversity. Each reef zone revealed a unique octocoral species composition and distinct community structure, with only 16% of the species shared by both the MCEs and the shallower reefs. This study has revealed an almost exclusive dominance of zooxanthellate species at the studied upper MCE reefs, thus indicating an adequate light regime for photosynthesis there. The findings should encourage similar studies on other reefs, aimed at understanding the spatiotemporal features and ecological role of octocorals in reef ecosystems down to the deepest limit of the MCEs.

Keywords Octocorallia · Soft corals · Deep reef · Mesophotic coral-reef ecosystem (MCE) · Biodiversity · Red Sea

Introduction

Mesophotic coral-reef ecosystems (MCEs) have been defined as comprising the light-dependent communities of corals and other organisms found at depths below 30 to >150 m in tropical and subtropical regions (Puglise et al. 2009). Due to technical difficulties, until the last decade most coral-reef studies were restricted to the upper ~30 m and, therefore, data on the MCEs have been sparse (Menza et al. 2008; Loya et al. 2016). Current technological advances, however, such as autonomous underwater vehicles, remotely operated vehicles, and closed-circuit rebreather diving, have now facilitated the investigation of MCEs, as reviewed by Kahng et al. (2010).

Octocorals are the second most common group of macrobenthic animals on many Indo-Pacific and Caribbean reefs after the reef-building stony corals (Fabricius and Alderslade 2001). Members of this group have been the subject of various studies, yet have always lagged behind their scleractinian counterparts in regard to our knowledge of species

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composition and distribution (Fabricius and De'Ath 2008). To date, there have been very few studies on octocoral assemblages that provide data at species resolution. This applies not only to reef systems at depths down to 30 m, but to an even greater extent to MCEs, thus further highlighting the significance of this study. Several studies have been conducted on mesophotic octocoral community composition, divided into upper MCEs (30–60 m) and lower MCEs (60–150 m) (e.g., 50–140 m: Kahng and Kelley 2007; 30–110 m: Bare et al. 2010; 30–150 m: Bongaerts et al. 2011; 47–163 m: Bridge et al. 2012; 72–111 m: Appeldoorn et al. 2016; 11–60 m: Etnoyer et al. 2016). However, most of these studies have been limited to photographic recognition of the resident taxa, mostly at the family level, and have thus often underestimated their actual species composition and abundance, or even lack any such information. For example, in American Samoa a towed camera system revealed a gradual increase in the percentage of octocoral cover down to 70 m and then a decrease down to 100 m (Bare et al. 2010), but listed only the octocoral genera *Sarcophyton* and *Lobophytum* and the rest under "other colonizers." These findings contrast to those for the stony corals there, which feature maximum cover at 30 m and then a decrease toward deeper water. A study conducted in Hawaii by Kahng and Kelley (2007) demonstrated increased cover of the stony coral *Leptoseris* spp. toward 90 m, with a similar increase in *Carijoa riisei*, an invasive octocoral there, which reached maximum cover at 100 m. The same study also demonstrated that the cover of other stony and soft corals decreased with depth, emphasizing the fitness of only those two taxa for the deeper reefs, as other taxa were sparse. A study conducted in the Coral Sea (Australia) revealed that depths of <30 m mostly featured juvenile stony corals over bare substrate, with low cover due to past cyclone damage and bleaching events (Bongaerts et al. 2011). These findings were in stark contrast to the steep reef walls at 40–100 m that were extensively covered by *Halimeda* algal curtains alongside a diverse stony coral community. Bongaerts et al. (2011) also recorded diverse azooxanthellate octocorals down to 150 m, but no taxonomic composition was presented. Bridge et al. (2012), who conducted the only study to date investigating MCE octocorals of the Great Barrier Reef (Australia), described diverse benthic communities there. That study recorded 27 octocoral genera at 47–159 m, eight of which were not recorded in the shallow waters, indicating that other taxa considered as rare in the shallow reefs might be widespread at the mesophotic depths. Etnoyer et al. (2016) dealt with the effect of the Macondo oil well spill (Gulf of Mexico) on gorgonian octocorals, providing data based on generic and species levels. In contrast, a study on MCEs under anthropogenic stress in Puerto Rico referred to that group as comprising gorgonians alone (Appeldoorn et al. 2016).

The northern Red Sea octocorals have been extensively studied, albeit mostly confined to the reefs above 30 m, including, among other aspects, community structure (Benayahu and Loya 1977, 1981), life history (e.g., Kahng et al. 2011 and references therein; Mandelberg-Aharon and Benayahu 2015), recruitment capabilities (e.g., Perkol-Finkel and Benayahu 2004, 2005), and taxonomy (e.g., Verseveldt and Benayahu 1983; Haverkort-Yeh et al. 2013; Van Ofwegen et al. 2013, 2016; Halàsz et al. 2014). Undoubtedly, these studies have revealed vast octocoral richness in the Red Sea, including new species; however, the octocorals of the MCEs in the Red Sea have remained little studied. Although Eilat has well-developed MCEs with high diversity of stony corals (Eyal 2014), there is an important gap in our knowledge regarding the mesophotic octocorals, despite evidence showing that they occur. Eyal (2014) recorded 8% octocoral coverage at 40 m, decreasing to 1% at 60 m, assigning the taxa to the families Alcyoniidae, Melithaeidae, and Xeniidae. Recently, Loya et al. (2016) presented an underwater photograph of the deeper Eilat MCE (80–146 m) with an abundant gorgonian population, but no quantitative data were provided. Regarding the environmental consequences posed by global change (e.g., Pandolfi et al. 2011; Spalding and Brown 2015), it has been widely suggested that MCEs might serve as refugia for depth-generalist species that are under threat in the degraded shallow reefs (e.g., Lesser et al. 2009; Bongaerts et al. 2010; Holstein et al. 2015; Loya et al. 2016). Moreover, the evidence suggests that deep reefs may provide a source of propagules, thus enabling replenishment of the degraded shallow-water reefs (Van Oppen et al. 2011), and that deeper populations are sometimes more fecund (Holstein et al. 2015). Although situated at the northernmost boundary of coral-reef distribution (ca. 30°N), the coral reefs of the northern Gulf of Aqaba (Fig. 1) exhibit among the highest within-habitat coral species diversity in the world (Rosenberg and Loya 2004). These reefs have been chronically perturbed by anthropogenic activities and have severely deteriorated over the last four decades (Rosenberg and Loya 2004). Consequently, studies on the MCEs are required to better evaluate the reef ecosystem along its entire depth range (see also Loya et al. 2016).

It is well accepted that coral growth is affected by light flux and wave action, leading to zonation of the different species, as each thrives in its own unique niche (Reece et al. 2013). In the Gulf of Aqaba, the reef down to 30 m features three distinct zones: the reef flat, the vertical upper fore-reef, and the gradually descending reef slope (Loya 1972). As each of these reef zones features a unique octocoral community (Benayahu and Loya 1977), the MCE is expected to similarly accommodate a distinct octocoral community.

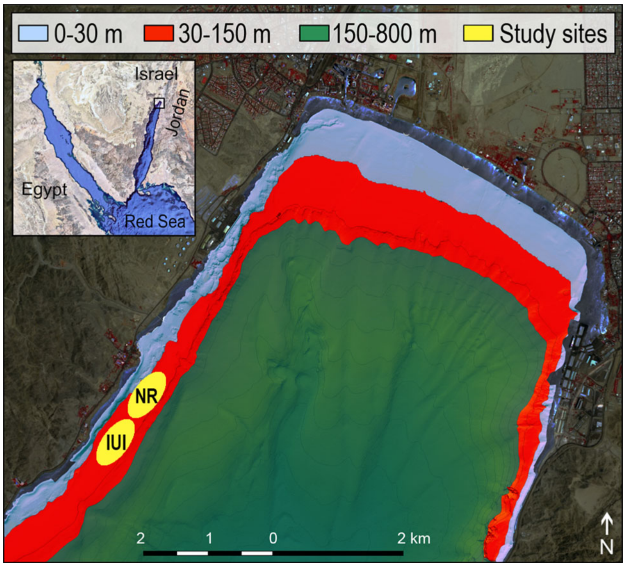

Fig. 1 Study sites at Eilat (*NR* Nature Reserve; *IUI* Interuniversity Institute for Marine Sciences), Gulf of Aqaba, northern Red Sea (*yellow ellipses*), and three bathymetric zones: shallow water (*blue*, 0–30 m), mesophotic zone (*red*, 30–150 m), and the deep waters (*green*, 150–800 m). Following Sade et al. (2008)

The scarce data available on MCE octocorals in general and in the Red Sea in particular motivated us to conduct this study testing the hypothesis that the upper MCE octocoral community structure at Eilat differs from that of the shallower one. Specifically, this study addressed the following questions: (1) What is the octocoral species composition in Eilat's upper MCEs compared to that of the reef flat and upper fore-reef, and (2) what are their community features in terms of richness, diversity, evenness, and spatial distribution of the different species?

Materials and methods

Study sites and field data collection

The mesophotic octocoral survey took place in Eilat, at a depth of 30–45 m and at two adjacent sites: the reef across from the Interuniversity Institute for Marine Sciences (IUI) and the "Coral Beach" Nature Reserve (NR) (Fig. 1). The IUI site features a moderate slope mostly covered with gravel and coral patches, while the NR site features a steep wall. The shallow site comprised the NR reef flat (~ 1 m) and its upper fore-reef (1–4 m).

A 10×1 m belt transect survey was used to obtain colony count data. A total of 80 transects were deployed parallel to the beach along depth contours, and the number of colonies of each taxon was recorded. At the MCE, a total of 45 transects were conducted in three depth zones: 30–35, 35–40, and 40–45 m, 15 transects in each (7 at the NR and 8 at the IUI). On the shallow reef, a total of 22 transects were run on the reef flat and 13 on the upper fore-reef (see also Benayahu and Loya 1981). Underwater studies were carried out using open-circuit technical SCUBA with N_2 and O_2 mixture (NITROX: 25% O_2 at 20–45 m and 50% O_2 at 0–20 m) on the MCE, SCUBA on the upper fore-reef, and snorkeling on the reef flat.

Coral sample collection and identification

The transects were videoed, and additional still photographs of individual soft coral colonies were taken using a Cannon G9 camera with an underwater casing and an Intovatec Galaxy video light. During the survey, samples were removed from octocoral colonies for taxonomic identification, using the reference collection of the Zoological Museum of Tel Aviv University and relevant publications. For this purpose, prior to collection each colony was photographed in situ with a numbered label next to it, and the sample was then transferred to a Ziploc bag with the corresponding number. In the IUI laboratory, a small subsample was removed and preserved in 100% ethanol for future molecular work, and the original sample was placed in 70% ethanol.

Statistical analysis

All statistical analyses were performed using R version 3.0.2 and RStudio version 0.98.976 with statistical significance set at $\alpha < 0.05$. A data table containing the species identity and abundance per transect was imported into R (R Core Team 2014). Following import, the relative abundance was calculated as percentage of colonies of each species of the total number of recorded colonies there. Mean values of abundance were obtained for each of the study sites and depth intervals. Tests for significant deviations from normality and homogeneity of variance in total octocoral abundance were conducted by shapiro.test and bartlett.test functions in R. Both tests revealed significant deviations from normality ($p < 0.05$) and, therefore, Kruskal–Wallis tests were used to compare abundance averages. Permutational multivariate analysis of variance (PERMANOVA), using the Adonis function in R, compared species composition among sites and depths. Significance tests were conducted using *F*-tests based on sequential sums of squares from permutations of the raw data and not permutations of residuals. Permutations of the raw data may provide better small sample characteristics than permutations of the residuals (McArdle and Anderson 2001). Non-metric multidimensional scaling (nMDS) was performed using the function "metaMDS" in the Vegan package (Oksanen et al. 2013), for visualization of the associations of octocorals within and among the different reef zones (reef flat, upper fore-reef, and MCE). The data were not transformed, and a two-dimensional Bray–Curtis ordination was plotted. Each point in the graph stands for an individual transect. Standard error is represented by the ellipses, created by the “ordiellipse” function.

Community indices

The following indices were calculated to examine octocoral community features: species richness (S), Shannon–Wiener index of diversity (H': Shannon and Weaver 1949), and evenness index (J': Pielou 1969). In order to compare diversity between communities, a Hill numbers plot (Chao et al. 2014) was generated using the Rényi function in the vegan package (Oksanen et al. 2013), by calculating the Rényi diversity (Rényi 1960) of order α as the following equation: $H\alpha = 1/(1-\alpha)\log\sum_{i=1}^{s} Pi^{a}$ where α is a scale parameter. Rényi diversity was then transformed to “Hill numbers” or “effective number of species” (Hill 1973), defined as $N\alpha = \exp(H\alpha)$. Some Hill numbers are known diversity indices, such as the number of species (richness) with $\alpha = 0$, or the exponent of Shannon diversity with $\alpha = 1$, and the inverse Simpson with $\alpha = 2$ and $1/\max(p)$ with $\alpha = \infty$.

Species accumulation curves (SAC) were used to compare diversity of community data sets, using different accumulator functions. The classic method is “random,” which finds the mean SAC and its standard deviation from random permutations of the data or subsampling without replacement (Gotelli and Colwell 2001).

Patchiness of octocoral colonies was tested using Lloyd’s index of patchiness (LIP; Lloyd 1967) calculated according to the following equation:

$$\mathrm{LIP} = \left(\frac{\mathrm{mean}+\mathrm{variance}}{\mathrm{mean}-1}\right)\Big/\mathrm{mean}$$

where LIP = 1 for a random distribution, >1 for aggregated distributions, and <1 for regular distributions.

Results

A total of 30 octocoral species of 16 genera and 7 families were recorded in all reef zones, with 21 species, 14 genera, and 7 families on both studied upper MCEs (Table 1). The reef flat and the upper fore-reef featured a smaller number of families (three and four, respectively), both with a similar number of genera and species (five in both these zones vs. 14 in the MCE and 13, 14, and 21 species on reef flat, upper fore-reef, and MCE, respectively). Most taxa in both MCE sites exhibited a wide depth distribution and were recorded at 30–45 m, except *Lobophytum depressum*, which was found at 35–45 m, *Sinularia licroclados* at 30–40 m, and *Junceella juncea* at 45 m. The following taxa were rare and found in only one transect of a particular reef: *J. juncea* on the IUI MCE; *S. levi* on both the NR reef flat and upper fore-reef; and *S. erecta S. polydactyla*, *S. portieri*, *S. querciformis,* and *Litophyton* sp. on the upper fore-reef. A significantly higher average number of octocoral colonies per belt transect were found on the IUI MCE than on the NR MCE (31.8 ± 6.7, 53.1 ± 6.1, respectively, Kruskal–Wallis, $p = 0.016$; Table 1), while no other significant differences in abundance were found among the different sites (MCEs and shallow reefs). Plotting the octocoral species accumulation curves (i.e., number of species against number of belt transects for the two MCE sites and combined data of both the NR reef flat and upper fore-reef) presented a plateau and thus confirmed a sufficient survey effort (Electronic Supplementary Material, ESM Fig. S1).

The nMDS based on the octocoral species composition identified three distinct groups: the reef flat and upper fore-reef presented isolated clusters, and both upper MCEs overlapped in multidimensional space (untransformed data, Bray–Curtis ordination, stress = 0.17; Fig. 2). Numbers, which represent species scores, show the correspondence of each species to the different reef zones.

There was significant difference in the octocoral species composition among the groups (pooled NR and IUI MCEs, the reef flat, and the upper fore-reef, PERMANOVA, $r^2 = 0.2$, $p = 0.001$). Furthermore, a significant difference in species composition was revealed between the two MCEs (NR and IUI, PERMANOVA, $r^2 = 0.05$, $p = 0.047$) and also between the two shallow reefs (reef flat and upper fore-reef, PERMANOVA, $r^2 = 0.15$, $p = 0.001$). Similarly, a significant difference in octocoral species composition was found between the combined shallow reef data (reef flat and upper fore-reef) and the pooled MCE data (PERMANOVA, $r^2 = 0.17$, $p = 0.001$).

Additional investigation of Eilat’s upper MCEs revealed that *Xenia* sp. and *Ovabunda* sp. featured the highest relative abundance (33.7–42 and 33.6–37.3%, respectively; Table 1), and *Rhytisma fulvum fulvum* and *Briareum hamrum* were significantly more abundant in the IUI MCE than the NR MCE (Kruskal–Wallis, $p < 0.01$; ESM Fig. S2). *Litophyton* sp. and *J. juncea* were recorded only at the IUI MCE and *S. licroclados* only at the NR MCE (Table 1; ESM Fig. S2).

The reef flat and the upper fore-reef featured greater dissimilarity among transects than did the upper MCEs (Table 1; ESM Fig. S3). For example, *S. polydactyla* was highly abundant in the former, yet very rare in the latter. *Cladiella pachyclados* and *S. recurvata* were similarly absent from the upper fore-reef, while *S. querciformis*,

Table 1 Octocoral species composition in the upper mesophotic coral ecosystems (MCEs) near the Interuniversity Institute for Marine Sciences in Eilat (IUI) and Nature Reserve (NR), NR reef flat, and upper fore-reef zone, with relative abundance (%) of colonies of the total number of colonies recorded in the respective reefs, and the respective mean colony count per transect (±SE)

#	Taxa	Relative abundance (%)				Mean abundance (colony count ±SE)			
		NR MCE (21)	IUI MCE (24)	Reef flat (22)	Upper fore-reef (13)	NR MCE (21)	IUI MCE (24)	Reef flat (22)	Upper fore-reef (13)
Family Alcyoniidae									
1	*Cladiella pachyclados* (Klunzinger, 1877)	0	0	0.76	0	0	0	0.4 ± 0.2	0
2	*Klyxum utimonii* (Verseveldt, 1971)	2.4	1.57	0	0	0.8 ± 0.4	0.8 ± 0.2	0	0
3	*Lobophytum depressum* Dixier-Durivault, 1966	0.15	1.02	0	0	0	0.5 ± 0.3	0	0
4	*Rhytisma f. fulvum* (Forskål, 1775)	1.65	7.61	4.46	9.32	0.5 ± 0.2	4 ± 0.8	2.1 ± 0.6	6.4 ± 2.2
5	*Sarcophyton auritum* Verseveldt & Benayahu, 1978	0	0	0.76	1.57	0	0	0.4 ± 0.3	1.1 ± 0.5
6	*Sarcophyton glaucum* (Quoy & Gaimard, 1833)	1.35	0.78	0	0	0.4 ± 0.2	0.4 ± 0.2	0	0
7	*Sinularia cruciata* Tixier-Durivault, 1970	0	0	1.61	1.91	0	0	0.8 ± 0.4	1.3 ± 0.9
8	*Sinularia erecta* Tixier-Durivault, 1945	0	0	8.63	0.11	0	0	4.1 ± 2	0.1 ± 0.1
9	*Sinularia hirta* (Pratt, 1903)	3.3	0.31	0	0	1 ± 0.7	0.2 ± 0.1	0	0
10	*Sinularia humesi* Verseveldt, 1971	0.3	0.55	0.57	8.31	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.2	5.7 ± 2.4
11	*Sinularia levi* Ofwegen, McFadden & Benayahu, 2015	0	0	0.47	0.9	0	0	0.2 ± 0.2	0.6 ± 0.6
12	*Sinularia leptoclados* (Ehrenberg, 1834)	0	0	3.42	36.7	0	0	1.6 ± 1.2	25.2 ± 13.3
13	*Sinularia licroclados* Verseveldt & Benayahu, 1983	1.05	0	0	0	0.3 ± 0.2	0	0	0
14	*Sinularia polydactyla* (Eherenberg, 1834)	0	0	48.2	6.62	0	0	23.1 ± 7.1	4.5 ± 3.9
15	*Sinularia portieri* Verseveldt, 1980	0	0	2.18	3.7	0	0	1 ± 1	2.5 ± 2.5
16	*Sinularia querciformis* (Pratt, 1903)	0	0	0	4.49	0	0	0	3.1 ± 3.1
17	*Sinularia recurvata* Verseveldt & Benayahu, 1983	0	0.31	1.71	0	0	0.2 ± 0.2	0.8 ± 0.6	0
18	*Sinularia terspilli* Verseveldt, 1971	0.6	0.39	0	11.9	0.2 ± 0.1	0.2 ± 0.1	0	8.2 ± 5
19	*Sinularia vrijmoethi* Verseveldt, 1971	4.95	1.88	0	11.78	1.6 ± 0.6	1 ± 0.3	0	8.1 ± 6.2
Family Briareidae									
20	*Briareum hamrum* (Gohar, 1948)	1.05	4.94	0	0	0.3 ± 0.3	2.6 ± 0.6	0	0
Family Ellisellidae									
21	*Junceella juncea* (Pallas, 1766)	0	2.12	0	0	0	1.1 ± 1.1	0	0
Family Nephtheidae									
22	*Litophyton* sp.	0	0.47	27.4	1.8	0	0.2 ± 0.1	13 ± 3.4	1.2 ± 0.4
23	*Paralemnalia thyrsoides* (Ehrenberg, 1834)	1.35	0.39	0	0	0.4 ± 0.3	0.2 ± 0.2	0	0
24	*Scleronephthya corymbosa* Verseveldt & Cohen, 1971	1.35	2.2	0	0	0.4 ± 0.3	1.2 ± 0.6	0	0
25	*Scleronephthya lewinsohni* Verseveldt & Benayahu, 1978	2.85	2.59	0	0	0.9 ± 0.3	1.4 ± 0.4	0	0
Family Nidaliidae									
26	*Siphonogorgia* sp.	0.3	0	0	0	0.1 ± 0.1	0	0	0

Table 1 continued

#	Taxa	Relative abundance (%)				Mean abundance (colony count ±SE)			
		NR MCE (21)	IUI MCE (24)	Reef flat (22)	Upper fore-reef (13)	NR MCE (21)	IUI MCE (24)	Reef flat (22)	Upper fore-reef (13)
Family Tubiporidae									
27	*Tubipora musica* Linnaeus, 1758	0.9	1.49	0.19	0.9	0.3 ± 0.1	0.8 ± 0.2	0.1 ± 0.1	0.6 ± 0.4
Family Xeniidae									
28	*Anthelia* sp.	0.75	0.31	0	0	0.2 ± 0.2	0.2 ± 0.2	0	0
29	*Ovabunda* sp.	33.6	37.3	0	0	10.7 ± 3.9	19.8 ± 6.4	0	0
30	*Xenia* sp.	42	33.7	0	0	13.3 ± 6.5	17.9 ± 4.9	0	0
Total						31.8 ± 6.7	53.1 ± 6.1	47.9 ± 10.5	68.5 ± 17.4
Families	7	6	7	3	4	Pooled MCEs		Combined reef flat and upper fore-reef	
Genera	16	12	14	5	5	43.1 ± 4.7		55.6 ± 9.3	
Species	30	19	20	13	14	($n = 45$)		($n = 35$)	

Total number of families, genera, and species for each reef zone, pooled MCEs, and combined reef flat and upper fore-reef are presented at bottom of table. Number of belt transects conducted at each reef is indicated in brackets

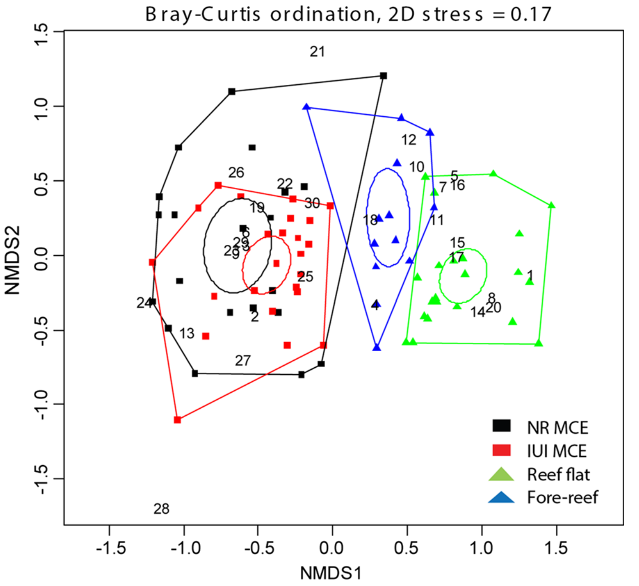

Fig. 2 Multidimensional scaling plot (Bray–Curtis ordination, 2D stress level = 0.17) based on octocoral species composition recorded for each transect at each of the different study sites: upper mesophotic coral ecosystem near the Interuniversity Institute for Marine Sciences in Eilat (IUI MCE, *red rectangles*) and the Eilat Nature Reserve (NR MCE, *black rectangles*), NR reef flat (*blue triangles*), and NR upper fore-reef (*green triangles*). *Ellipses* represent standard error at the different sites. *Numbers* represent species scores listed in Table 1

S. terspilli, and *S. vrijmoethi* were abundant in the upper fore-reef and absent from the reef flat. The most abundant taxa on the NR reef flat were *S. polydactyla* and *Litophyton* sp. (48.2 and 24%, respectively; Table 1), and the most abundant on the upper fore-reef were *S. leptoclados, S. terspilli*, and *S. vrijmoethi* (36.7, 11.9, and 11.8%, respectively; Table 1). *Sinularia leptoclados* and *S. humesi* were significantly more abundant on the upper fore-reef than on the reef flat (Kruskal–Wallis, $p < 0.01$; ESM Fig. S3). *Litophyton* sp. was more abundant in the reef flat than in the upper fore-reef (Kruskal–Wallis, $p < 0.01$; ESM Fig. S3). *Rhytisma fulvum fulvum* was the only octocoral displaying high relative abundance at all depth zones, comprising 5.6, 4.5, and 9.3% of the colonies in the MCEs, reef flat, and upper fore-reef, respectively.

A Hill diversity plot revealed only subtle differences in diversity features among the studied reefs (Fig. 3), indicating that the upper MCEs feature a higher richness but are dominated by fewer species. Notably, both MCE sites featured higher, though not significant, species richness (Scale = 0) than the shallow reefs. Correspondingly, this comparison also revealed a lower Shannon's diversity (Scale = 1), inverse Simpson index (Scale = 2), and dominance index (Scale = Inf). Overlapping of the lines in Fig. 3 indicates no difference in the diversity profiles between the different reef zones.

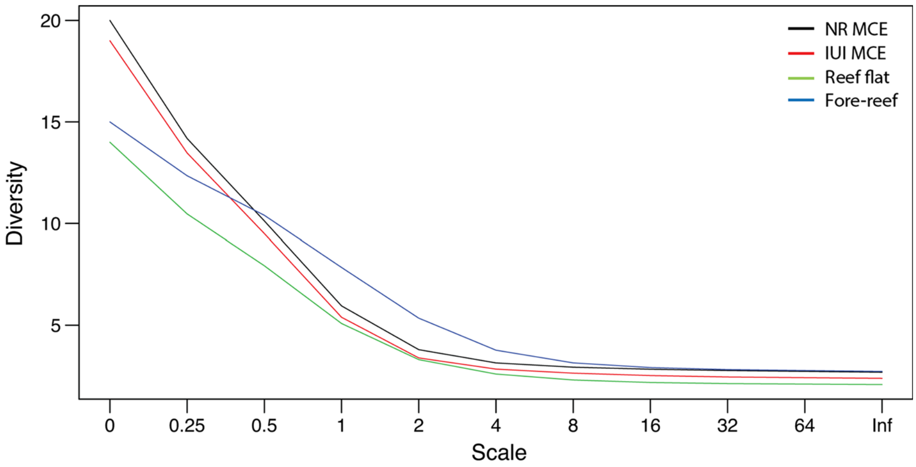

Fig. 3 Hill diversity profiles for upper mesophotic coral ecosystems near Interuniversity Institute for Marine Sciences in Eilat (IUI MCE, *red*), Eilat Nature Reserve (NR MCE, *black*), NR reef flat (*green*), and NR upper fore-reef (*blue*)

The results indicate a significantly higher mean octocoral richness per belt transect for the pooled upper MCEs data compared to that of the reef flat and the upper fore-reef (Kruskal–Wallis, $p < 0.03$; Fig. 4). Similarly, species richness was also higher than that of the combined data of the reef flat and upper fore-reef (Kruskal–Wallis, $p = 0.027$; Fig. 4). No significant differences were found when comparing the octocoral community mean diversity (Shannon's H': range 0.85–1.06; ESM Fig. S4a) and evenness (Pielou's J: range 0.58–0.75; ESM Fig. S4b), of the different reef zones (Kruskal–Wallis test, $p > 0.05$). LIP indicated that the vast majority of octocoral species in all the reef zones displayed a patchy distribution (LIP > 1; ESM Fig. S5), except for the rare species with a very low colony count per transect, such as *Siphonogorgia* sp. and *Sinularia recurvata* (Table 1).

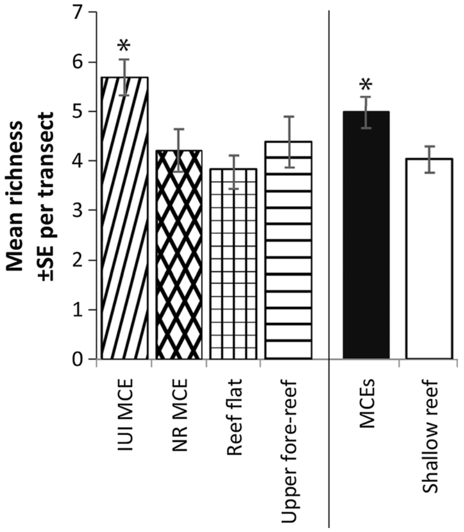

Fig. 4 Octocoral mean richness (± SE) per belt transect (1 × 10 m) on upper mesophotic coral ecosystems (MCEs) near the Interuniversity Institute for Marine Science in Eilat (IUI) and the Eilat Nature Reserve (NR), NR reef flat, NR upper fore-reef, pooled data of both MCEs (*black*), and combined data of the reef flat and the upper fore-reef (*white*)

Discussion

Our results confirm the hypothesis that the upper MCE octocoral community structure at Eilat differs from the community structure of the reef flat and the upper fore-reef. Each reef zone features a specific species composition and abundance, with higher species richness in the MCE (Table 1; Fig. 2). The study has yielded the first octocoral species list for Eilat's upper mesophotic reefs and an expanded one for its shallow reefs. A total of 30 species from 16 genera and seven families were recorded in the three studied reef zones where species accumulation curves indicated that most species were likely to be found (ESM Fig. S1). Consequently, this is the first reliable and updated quantitative inventory for shallow and mesophotic octocoral species in Eilat (Table 1), as no single, comprehensive species inventory of Red Sea octocorals has been published. All the noted species have been previously reported in taxonomic surveys from the Red Sea shallow reefs (<30 m) (e.g., Verseveldt 1980, 1983; Verseveldt and Benayahu 1978, 1983; Van Ofwegen 2002; McFadden et al. 2011; Haverkort-Yeh et al. 2013; Van Ofwegen et al. 2013, 2016), except *Scleronephthya lewinsohni,* which was reported at the mesophotic depth of 55–82 m (Verseveldt and Benayahu 1978). Our study has yielded a higher octocoral species richness for Eilat than previously reported: 30 in comparison to the 16 and 11 species found by Benayahu and Loya (1977, 1987), 19 found by Perkol-Finkel and Benayahu (2005), and the three octocoral genera listed for the MCE by Eyal (2014). Such differences in richness found between previous studies and the current one derive from the more thorough collections, also covering the upper MCE, as well as from advances in

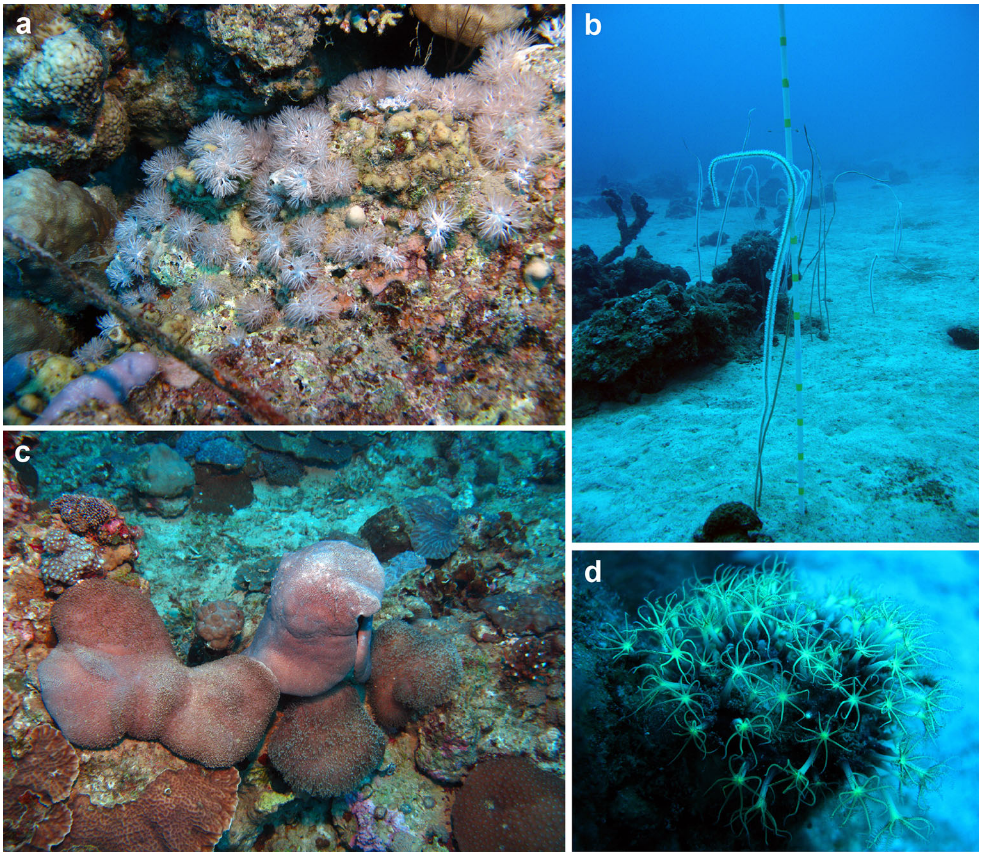

Fig. 5 Eilat's upper mesophotic octocorals. **a** Colonies of *Ovabunda* sp. dominating deep reefs. **b** Patch of depth-specialist *Junceella juncea*. **c** Patch of *Lobophytum depressum* colonies. **d** *Briareum hamrum*, an encrusting deep resident

taxonomic expertise, as also reflected in the extensive phylogenetic and taxonomic studies conducted in the region (references above). Future identification to species level of members of the families Nephtheidae and Xeniidae from the MCE, or any additional ones when encountered, is expected to further increase the number of species in the MCE. Moreover, surveys at a depth range of 4–30 m, and certainly below 45 m, will undoubtedly reveal increased octocoral richness for Eilat's reefs across a wider depth range. Previous studies have noted the remarkable species diversity of the genus *Sinularia* in the Red Sea, being the highest in its entire Indo-Pacific distributional range (Van Ofwegen 2002: 38 species) and similarly found in the current study to be the most speciose in Eilat, contributing 13 species in total (Table 1). Interestingly, soft coral surveys conducted in the west Indian Ocean yielded a considerable number of octocoral species (e.g., KwaZulu-Natal: 38 species, Tanzania: 46, Mozambique: 53; Benayahu et al. 2003; Chagos Archipelago: 62, Mayotte: 72; Schleyer and Benayahu in press). Those surveys aimed at providing a species inventory and were based on collections for taxonomic purposes in large reef areas, rather than seeking to quantify the community features at designated sites, as in this study. Undoubtedly, quantitative studies similar to ours are much needed to compare the soft coral richness in the Red Sea to that of the Indian Ocean at large.

The Eilat upper mesophotic octocoral community is numerically dominated by two zooxanthellate taxa, *Ovabunda* sp. and *Xenia* sp. (Fig. 5a), suggesting the existence of adequate light for these autotrophic taxa (e.g., Barneah et al. 2004) down to at least 45 m (Table 1). In contrast, these two genera were not recorded from the reef flat and upper fore-reef zone, most probably due to prevailing wave action there and occasional exposure during low tide (Rosenberg and Loya 2004). Interestingly, a single patch of the azooxanthellate *Junceella juncea* (Fig. 5b) was found at the IUI MCE, representing its uppermost depth distribution in the region. Together with *Scleronephthya corymbosa*, *S. lewinsohni,* and *Siphonogorgia* sp., these four constitute the only azooxanthellate species found in the upper MCEs at Eilat and are only a minor component of the soft coral community (Table 1: 4 species of 20). This finding in turn reflects the predominance of zooxanthellate taxa in the deep study site, thus further indicating that an adequate light regime for photosynthesis of the symbiotic algae exists in the Eilat upper MCEs (30–45 m).

Differences in species composition between the two upper mesophotic reefs were represented by two encrusting octocorals, *Briareum hamrum* and *Rhytisma fulvum fulvum,* as well as the depth-specialist *J. juncea*, all found in higher numbers at the IUI site. In addition, there was presented a higher mean number of colonies per belt transect at the IUI site than at NR (53 vs. 32; Table 1), along with a higher mean richness per transect (6 vs. 4; Fig. 4). These differences might have resulted from topographic differences between the two sites; the IUI site features a moderate slope with patches of gravel and sand, while the NR site features a steep, continuous, hard calcareous reef substrate. Such differences might lead to more diverse niches and facilitate a richer coral community at the IUI site (e.g., Pittman et al. 2007).

The higher total richness and mean richness per belt transect found in the upper MCEs than the NR reef flat and the NR upper fore-reef (Table 1; Fig. 4) concur with other studies that found high octocoral richness on some mesophotic reefs (American Samoa, 30–110 m; Bare et al. 2010; Puerto Rico, 30–50 m; Garcia-Sais 2010; and Australia, 47–163 m: Bridge et al. 2012). In this respect, therefore, the Eilat upper MCE resembles other MCEs, suggesting that upper mesophotic octocoral richness is high across circumtropical zoogeographical regions. Future studies of a larger variety of habitats and depth zones would help to clarify the extent of this pattern.

Although the three reef zones studied here demonstrate differences in species composition and richness, they all possess a similar mean colony count per transect, Shannon's diversity, and Pielou's evenness values (Table 1; Figs. 2, 4; ESM Fig. S5). The dominance of only a few species in each reef zone (Table 1; Fig. 2) suggests a strong effect of the rare species in the upper MCEs on the diversity and evenness values and indicates that the MCEs feature a higher richness but are dominated by fewer species. Consequently, if those rare species that were recorded in only a few transects were omitted, a higher evenness than that of the shallow reefs would be expected. This conclusion is further demonstrated by the Hill diversity (Fig. 3), which indicates an overlap in the functions found for the different reef zones, indicating a similar diversity in the reef flat and both MCEs (Chao et al. 2014). The current findings provide deeper insights into the diversity patterns, thus revealing a slightly more diverse community in the IUI MCE than in both the NR MCE and NR reef flat, as noted from the lack of overlap in diversity profiles along the entire scale (Fig. 3).

Past studies have commonly indicated an aggregated spatial distribution for octocorals, which may derive from both larval behavior and asexual reproduction (e.g., Carlon and Olson 1993; Dahan and Benayahu 1997). The current study yielded similar findings for both the shallow reefs and the upper MCEs (ESM Fig. S6), thus suggesting the prevalence of this feature across a wide depth range.

The question of whether mesophotic octocorals reproduce and can thus replenish the larval supply to shallow reefs is of particular interest (e.g., Bongaerts et al. 2010; Van Oppen et al. 2011; Slattery et al. 2011; Holstein et al. 2016). Previous studies have demonstrated that in the northern Gulf of Aqaba, octocorals sexually reproduce at 27–30 m (*Rhytisma fulvum fulvum*: Benayahu and Loya 1983; *Ovabunda macrospiculata*: Benayahu and Loya 1984a, b; and *Sarcophyton glaucum*: Benayahu and Loya 1986). This study demonstrates that 16% of the octocoral species occur in both the shallow and mesophotic reefs. Since some of which feature viable sexual reproduction adjacent to the upper mesophotic depths (references above), it is suggested that they also reproduce in the mesophotic depths. If this is indeed validated (study in progress), it is conceivable that the deep octocoral populations also contribute propagules to the shallow reefs. The relatively small overlap in species composition between depth zones may also increase when comparable data from 3 to 30 m become available, thus enabling analysis of the communities along the entire depth range. Since Xeniidae are abundant in Eilat's MCE (this study) and also at 4–30 m (Benayahu and Loya 1985), they probably feature a remarkable connectivity along a wider depth range than most other species (Table 1). In the current study, *Briareum hamrum* and *Lobophytum depressum* (Fig. 5c, d) were recorded only in the upper MCEs, in contrast to the findings of Benayahu and Loya (1977) and Benayahu (1989), who recorded the former on the NR reef flat only (*Clavularia hamra* = *Briareum hamrum*; see Alderslade 2000) and the latter exclusively in the upper fore-reefs (Y Benayahu, personal observations). If these two species do sexually reproduce in deeper waters, these populations might in the future replenish their extinct shallow reef populations in Eilat. Undoubtedly, the possible vertical connectivity between the shallow- and deep-reef octocoral populations still requires an in-depth study.

Recently, Loya et al. (2016) listed gaps, priorities, and recommendations for future studies on MCEs, all of which are relevant to octocorals, bearing in mind that the gaps in our knowledge concerning this group are substantially wider than those regarding stony corals. This study has revealed for the first time the octocoral community features of Eilat's upper MCEs, which differ from those of both the reef flat and the upper fore-reef zone. The MCEs were found to host a higher number of species than the shallower zones, although their species diversity was similar. Questions concerning the distributional range of octocorals with depth, down to the lower limits of the mesophotic zone, and the processes governing them, are still open.

Coral reefs are in decline worldwide, which threatens the food security of millions of people. Adopting an ecosystem-scale approach that protects both deep and shallow reefs would result not only in improving the state of coral reefs, but also in social and economic benefits (Bridge et al. 2013). In Eilat, which is extensively visited by recreational divers and tourists alike (Zakai and Chadwick-Furman 2002), the shallow reefs are much more susceptible to anthropogenic impact than the MCEs, which so far have not been affected by recreational activities. However, with the increased popularity of technical diving, it is recommended to include the MCEs in future management and conservation initiatives. This study is the first of its kind to be based on a thorough taxonomic knowledge, thus providing comparative quantitative data at a species-level resolution for octocoral communities from shallow reefs to the mesophotic depth, while also highlighting the almost exclusive dominance of zooxanthellate species on the MCEs (30–45 m). These findings should encourage similar studies in other regions, which will undoubtedly shed light on the octocoral community features, spatiotemporal nature, and dynamics and thereby contribute to their conservation.

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References

Alderslade P (2000) Four new genera of soft corals (Coelenterata: Octocorallia), with notes on the classification of some established taxa. Zoologische Mededelingen 74:237–249

Appeldoorn R, Ballantine D, Bejarano I, Carlo M, Nemeth M, Otero E, Pagan F, Ruiz H, Schizas N, Sherman C, Weil E (2016) Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico. Coral Reefs 35:63–75

Bare AY, Grimshaw KL, Rooney JJ, Sabater MG, Fenner D, Carroll B (2010) Mesophotic communities of the insular shelf at Tutuila, American Samoa. Coral Reefs 29:369–377

Barneah O, Weis VM, Perez S, Benayahu Y (2004) Diversity of dinoflagellate symbionts in Red Sea soft corals: mode of symbiont acquisition matters. Mar Ecol Prog Ser 275:89–95

Benayahu Y (1989) Reproductive cycle and developmental processes during embryogenesis of *Clavularia hamra* (Cnidaria: Octocorallia). Acta Zool 70:29–36

Benayahu Y, Loya Y (1977) Space partitioning by stony corals, soft corals and benthic algae on the coral reefs of the northern Gulf of Eilat (Red Sea). Helgol Wiss Meeresunters 30:362–382

Benayahu Y, Loya Y (1981) Competition for space among coral-reef organisms at Eilat, Red Sea. Bull Mar Sci 31:514–522

Benayahu Y, Loya Y (1983) Surface brooding in the Red Sea soft coral *Parerythropodium fulvum fulvum* (Forskål, 1775). Biol Bull 165:353–369

Benayahu Y, Loya Y (1984a) Life history studies on the Red Sea soft coral *Xenia macrospiculata* Gohar, 1940. I. Annual dynamics of gonadal development. Biol Bull 166:32–43

Benayahu Y, Loya Y (1984b) Substratum preferences and planulae settling of two red sea alcyonaceans: *Xenia macrospiculata* Gohar and *Parerythropodium fulvum fulvum* (Forskl). J Exp Mar Bio Ecol 83:249–260

Benayahu Y, Loya Y (1985) Settlement and recruitment of a soft coral: why is Xenia macrospiculata a successful colonizer? Bull Mar Sci 36:177–188

Benayahu Y, Loya Y (1986) Sexual reproduction of a soft coral: synchronous and brief annual spawning of *Sarcophyton glaucum* (Quoy & Gaimard, 1833). Biol Bull 170:32–42

Benayahu Y, Loya Y (1987) Long-term recruitment of soft corals (Octocorallia: Alcyonacea) on artificial substrata at Eilat (Red Sea). Mar Ecol Prog Ser 38:161–167

Benayahu Y, Shlagman A, Schleyer MH (2003) Corals of the south-west Indian Ocean: VI. The Alcyonacea (Octocorallia) of Mozambique, with a discussion on soft coral distribution on south equatorial East African reefs. Zoologische Verhandelingen 345:49–58

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327

Bongaerts P, Bridge TCL, Kline DI, Muir PR, Wallace CC, Beaman RJ, Hoegh-Guldberg O (2011) Mesophotic coral ecosystems on the walls of Coral Sea atolls. Coral Reefs 30:335

Bridge TC, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. Nat Clim Chang 3:528–530

Bridge TC, Fabricius KE, Bongaerts P, Wallace CC, Muir PR, Done TJ, Webster JM (2012) Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia. Coral Reefs 31:179–189

Carlon DB, Olson RR (1993) Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. J Exp Mar Bio Ecol 173:247–263

Chao A, Chiu CH, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu Rev Ecol Evol Syst 45:297–324

Dahan M, Benayahu Y (1997) Reproduction of *Dendronephthya hemprichi* (Cnidaria: Octocorallia): year-round spawning in an azooxanthellate soft coral. Mar Biol 129:573–579

Etnoyer PJ, Wickes LN, Silva M, Dubick JD, Balthis L, Salgado E, MacDonald IR (2016) Decline in condition of gorgonian octocorals on mesophotic reefs in the northern Gulf of Mexico: before and after the Deepwater Horizon oil spill. Coral Reefs 35:77–90

Eyal (2014) Ecology and taxonomy of mesophotic communities in Israel (Red Sea and Mediterranean). M.Sc. thesis, Tel-Aviv University, Tel Aviv, Israel

Fabricius KK, Alderslade PP (2001) Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville, Australia

Fabricius K, De'Ath G (2008) Photosynthetic symbionts and energy supply determine octocoral biodiversity in coral reefs. Ecology 89:3163–3173

Garcia-Sais JR (2010) Reef habitats and associated sessile-benthic and fish assemblages across a euphotic–mesophotic depth gradient in Isla Desecheo, Puerto Rico. Coral Reefs 29:277–288

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Halàsz A, Reynolds AM, McFadden CS, Toonen RJ, Benayahu Y (2014) Could polyp pulsation be the key to species boundaries in the genus *Ovabunda* (Octocorallia: Alcyonacea: Xeniidae)? Hydrobiologia 759:95–107

Haverkort-Yeh RD, McFadden CS, Benayahu Y, Berumen M, Halász A, Toonen RJ (2013) A taxonomic survey of Saudi Arabian Red Sea octocorals (Cnidaria: Alcyonacea). Mar Biodivers 43:279–291

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432

Holstein DM, Smith TB, Gyory J, Paris CB (2015) Fertile fathoms: deep reproductive refugia for threatened shallow corals. Sci Rep 5:12407

Holstein DM, Paris CB, Vaz AC, Smith TB (2016) Modeling vertical coral connectivity and mesophotic refugia. Coral Reefs 35:23–37

Kahng SE, Kelley CD (2007) Vertical zonation of megabenthic taxa on a deep photosynthetic reef (50–140 m) in the Au'au Channel, Hawaii. Coral Reefs 26:679–687

Kahng SE, Benayahu Y, Lasker HR (2011) Sexual reproduction in octocorals. Mar Ecol Prog Ser 443:265–283

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275

Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. J Exp Mar Bio Ecol 375:1–8

Lloyd M (1967) Mean crowding. J Anim Ecol 36:1–30

Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar Biol 13:100–123

Loya Y, Eyal G, Treibitz T, Lesser MP, Appeldoorn R (2016) Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9

Mandelberg-Aharon Y, Benayahu Y (2015) Reproductive features of the Red Sea octocoral *Sarcophyton auritum* are uniform within generic boundaries across wide biogeographical regions. Hydrobiologia 759:119–132

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

McFadden CS, Benayahu Y, Pante E, Thoma JN, Nevarez PA, France SC (2011) Limitations of mitochondrial gene barcoding in Octocorallia. Mol Ecol Resour 11:19–31

Menza C, Kendall M, Hile S (2008) The deeper we go the less we know. Rev Biol Trop 56:11–24

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MH, Wagner H (2013) Vegan: community ecology package. R package version 2.0-10

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422

Perkol-Finkel S, Benayahu Y (2004) Community structure of stony and soft corals on artificial and natural reefs in Eilat (Red Sea): comparative aspects and implications. Coral Reefs 23:195–205

Perkol-Finkel S, Benayahu Y (2005) Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Mar Environ Res 59:79–99

Pielou EC (1969) An introduction to mathematical ecology. Wiley Interscience, New York, p 286

Pittman SJ, Christensen JD, Caldow C, Menza C, Monaco ME (2007) Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecol Model 204:9–21

Puglise KA, Hinderstein LM, Marr JCA, Dowgiallo MJ, Martinez FA (2009) Mesophotic coral ecosystems research strategy: international workshop to prioritize research and management needs for mesophotic coral ecosystems, Jupiter, Florida, 12–15 July 2008. NOAA Technical Memorandum NOS NCCOS 98 and OAR OER 2. NOAA National Centers for Coastal Ocean Science, Silver Spring, MD, 24 pp

Reece JB, Urry LA, Cain ML, Wasserman SA, Minorsky PV, Jackson R, Campbell NA (2013) Campbell biology, 10th edn. Pearson, Boston

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rényi A (1960) On the central limit theorem for the sum of a random number of independent random variables. Acta Mathematica Hungarica 11:97–102

Rosenberg E, Loya Y (2004) The coral reefs of Eilat—past, present and future: three decades of coral community structure studies. Coral reef health and disease. Springer, Heidelberg, pp 1–34

Sade AR, Hall JK, Tibor G, Niemi TM, Ben-Avraham Z, Al-Zoubi AA, Hartman G, Akawwi E, Abueladas AR, Amitc G (2008) The Israel national bathymetric survey: Northern Gulf of Aqaba/Eilat Poster. Israel Journal of Earth Sciences 57:139–144

Schleyer MH, Benayahu Y (in press) A checklist of the soft corals (Octocorallia: Alcyonacea) of Mayotte. Mar Biodivers

Shannon CE, Weaver W (1949) The mathematical theory of information. University of Illinois Urbana, Champaign, IL

Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ (2011) Connectivity and stability of mesophotic coral reefs. J Exp Mar Bio Ecol 408:32–41

Spalding MD, Brown BE (2015) Warm-water coral reefs and climate change. Science 350:769–771

Van Ofwegen LP (2002) Status of knowledge of the Indo-Pacific soft coral genus Sinularia May, 1898 (Anthozoa: Octocorallia). Proc 9th Int Coral Reef Symp Vol 1

Van Ofwegen LP, Benayahu Y, McFadden CS (2013) *Sinularia leptoclados* (Ehrenberg, 1834) (Cnidaria, Octocorallia) re-examined. Zookeys 272:29

Van Ofwegen LP, McFadden CS, Benayahu Y (2016) *Sinularia polydactyla* (Ehrenberg, 1834) (Cnidaria, Octocorallia) re-examined. Zookeys 581:71

Van Oppen MJH, Bongaerts P, Underwood JN, Peplow LM, Cooper TF (2011) The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. Mol Ecol 20:1647–1660

Verseveldt J (1980) A revision of the genus *Sinularia* May (Octocorallia, Alcyonacea). Zoologische Verhandelingen 179:1–28

Verseveldt J (1983) A revision of the genus *Lobophytum* von Marenzeller (Octocorallia: Alcyonacea). Zoologische Verhandelingen 200:1–103

Verseveldt J, Benayahu Y (1978) Descriptions of one old and five new species of Alcyonacea (Coelenterata: Octocorallia) from the Red Sea. Zoologische Mededelingen 53:57–74

Verseveldt J, Benayahu Y (1983) On two old and fourteen new species of Alcyonacea (Coelenterata, Octocorallia) from the Red Sea. Zoologische Verhandelingen 208:1–33

Zakai D, Chadwick-Furman NE (2002) Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biol Conserv 105:179–187