

Light environment drives the shallow-to-mesophotic coral community transition

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Abstract. Light quality is a crucial physical factor driving coral distribution along depth gradients. Currently, a 30 m depth limit, based on SCUBA regulations, separates shallow and deep mesophotic coral ecosystems (MCEs). This definition, however, fails to explicitly accommodate environmental variation. Here, we posit a novel definition for a regional or reef-to-reef outlook of MCEs based on the light vs. coral community–structure relationship. A combination of physical and ecological methods enabled us to clarify the ambiguity in relation to the mesophotic definition. To characterize coral community structure with respect to the light environment, we conducted wide-scale spatial studies at five sites along shallow and MCEs of the Gulf of Eilat/Aqaba (0–100 m depth). Surveys were conducted by technical-diving and drop-cameras, in addition to one year of light spectral measurements. We quantify two distinct coral assemblages: shallow (<40 m) and MCEs (40–100 m), exhibiting markedly different relationships with light. The depth ranges and morphology of 47 coral genera were better explained by light than depth, mainly, due to photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) (1% at 76 and 36 m, respectively). Branching coral species were found mainly at shallower depths, that is, down to 36 m. Among the abundant upper-mesophotic specialist corals, *Leptoseris glabra*, *Euphyllia paradivisa*, and *Alveopora* spp. were found strictly between 40 and 80 m depth. The only lower-mesophotic specialist, *Leptoseris fragilis*, was found deeper than 80 m. We suggest that shallow coral genera are light-limited below a level of 1.25% surface PAR and that the optimal PAR for mesophotic communities is at 7.5%. This study contributes to moving MCE ecology from a descriptive phase into identifying key ecological and physiological processes structuring MCE coral communities. Moreover, it may serve as a model enabling the description of a coral zonation worldwide on the basis of light quality data.

Key words: coral community structure; corals; deep coral reefs; Gulf of Eilat/Aqaba; light; mesophotic coral ecosystems; photosynthetically active radiation; Red Sea; specialist vs. generalist species; twilight zone; zonation.

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INTRODUCTION

Coral reefs constitute spectacular and diverse marine ecosystems. As reef-building corals maintain a mutualistic symbiosis with photosynthetic

dinoflagellates (Trench 1993), light intensity and spectral quality play an important role in successful coral colonization (Frade et al. 2008). The light spectrum affects the initial stages of coral settlement, with planulae exhibiting

species-specific responses (Mundy and Babcock 1998). Additionally, the light regime is a key factor for various stony corals at advanced life stages, in determining their survival and growth (Mass et al. 2007, Lesser et al. 2009). Consequently, light can have a substantial effect on coral (Vermeij and Bak 2002, Hennige et al. 2010).

Light conditions, in both the ultraviolet radiation (UVR, 280–400 nm) and photosynthetically active radiation (PAR, 400–700 nm) spectra, undergo change with increasing depth. These changes are largely a function of the optical properties of the water itself (Kirk 2011). The absolute amount of downwelling irradiance (E_d) decreases with depth. The spectral composition also becomes increasingly dominated by the ultraviolet/blue part of the spectrum (Kirk 2011). This environmental gradient is an important factor in controlling the productivity, physiology, and ecology of corals (Gattuso et al. 2006, Frade et al. 2008, Cooper et al. 2010, Kahng et al. 2010, Ben-Zvi et al. 2015) with different species necessarily occupying different depth ranges or niches (Kahng and Kelley 2007, Bridge et al. 2012, Eyal et al. 2016). Light and physiological profiles may only loosely correlate with depth (Laverick et al. 2019), and even slight, temporary, changes in water transparency can exert a crucial effect on mesophotic reefs operating near the limits of photosynthesis (Kahng et al. 2010). Therefore, varying light conditions may affect how coral communities are structured in space (Kahng et al. 2010, Bauman et al. 2013).

The euphotic zone ends at the depth where 1% of surface PAR remains ($Z_{1\%}$; Kirk 2011). Given the relationship of stony corals with their photosynthetic endosymbionts, $Z_{1\%}$ is expected to have a notable influence on the depth distribution of various species, despite some exceptional corals capable of flourishing deeper than $Z_{1\%}$ (Fricke and Meischner 1985, Schlichter et al. 1994, Lesser et al. 2009, Pochon et al. 2015). The attenuation coefficient of downwelling PAR ($K_{d(\text{PAR})}$) describes the optical nature of water and relates directly to the euphotic zone according to the Lambert-Beer law ($I_z = I_0 e^{-K_d z}$; Kirk 2011). Light penetration into a water body linearly correlates with optical water quality (Gattuso et al. 2006, Kirk 2011). Therefore, even when light at the surface is equal for two

locations, its quality (i.e., intensity and spectrum) may differ at the same depths at those locations due to changes in $K_{d(\text{PAR})}$. Kahng et al. (2010) demonstrated the potential of $K_{d(\text{PAR})}$ to explain variation in the depth limits of zooxanthellate corals among locations worldwide. Moreover, the influence of light attenuation on the distribution of other light-dependent marine organisms has also been documented at local scales, albeit on much smaller scales (Manuel et al. 2013).

Though PAR enhances coral growth at certain depths, light (both PAR and/or UVR) can also have negative impacts (e.g., bleaching, reactive oxygen species [ROS], and photoinhibition; Dunne and Brown 1996, Tchernov et al. 2011, Ben-Zvi et al. 2019). Under high light levels, there is the potential for damage to the holobiont (bleaching; Dunne and Brown 1996). The biologically damaging effects of UVR are well known and include the direct effects of ultraviolet B radiation (UVB, 280–315 nm; Holm-Hansen et al. 1993), and possible effects mediated through ROS (Mallick and Mohn 2000, Tchernov et al. 2011, Ben-Zvi et al. 2019). Dunne and Brown (1996) tested the penetration of solar UVB radiation in shallow tropical waters and reported DNA damage. Their function returned a threshold for DNA damage at 1% surface UVB. Therefore, the 1% limit of both PAR and UVR is expected to have a crucial effect on coral distribution patterns.

Mesophotic coral ecosystems (MCEs) flourish under limited light and at greater depths than shallow reefs (Lesser et al. 2009). Despite the relatively large area occupied by MCEs (Lesser et al. 2018, Eyal et al. 2019), and a recent surge in research attention (Menza et al. 2007, Laverick et al. 2018), biogeographical and ecological data are sparse. Strong gradients exist in downwelling solar irradiance on mesophotic reefs (Lesser et al. 2009, Eyal et al. 2016), and a broader understanding of the abiotic factors (Lesser et al. 2018) may help to explain and predict patterns in coral reef communities along spatial and vertical scales.

Despite their close proximity to well-studied shallow reefs, and their inferred importance (Rocha et al. 2018), MCEs have remained poorly studied due to the technical limitations of diving (Pyle 2019). Basic data on the taxonomic composition, depth ranges, habitat preferences, abundance, and distribution of MCE taxa are scarce.

Moreover, the processes that structure these communities are virtually unknown (Hinderstein et al. 2010). One of the main outstanding issues is that of how species-specific responses to differing light conditions influence the transition from shallow-to-mesophotic communities. Edmunds et al. (2018) noted that “given the importance of light in the ecology of coral reefs, it may be timely to reconsider the value of high-resolution in situ sampling for this parameter for time-series analyses of coral reefs.” Moreover, Lesser et al. (2018) concluded that “to improve the current definition of MCEs, which may result in regional or reef-to-reef definitions, we need more studies that include community characterization throughout the entire depth range of 30–150 m, that are combined with studies on the optics of the water column.”

In this study, we sought to address this knowledge gap. We provide ecological data pertaining to stony corals across depth and space in the Gulf of Eilat/Aqaba (GoE/A), together with light quality data. The present work emphasizes the crucial importance of light regimes to the structure of coral communities in both vertical and horizontal space, while offering a novel model for coral reef zonation that combines physical and ecological methods.

MATERIALS AND METHODS

Data collection

Spatial benthic surveys were conducted over 10 km of reef at five sites along shallow reefs to MCEs (0–100 m depth). Belt transects, 50 m in length, were recorded at stratified depths between 5 and 100 m (5, 10, 20, 30, 40, 50, 60, 70–80, 90–100 m) parallel to the shoreline along the isobaths at each site. The transects were conducted using technical-diving and a drop-camera system tethered to the boat with a coax cable providing live plan view video, and a custom-made lighting system. Both were mounted on a tripod positioned over a photo-quadrant frame with a connected dive computer to confirm depth. 2320 photo-plots (70 × 50 cm) from all transects were analyzed for live coral cover and bathymetric substrate type (e.g., rock, gravel, and dead corals) and non-available settlement area (sand). We used the multiple points method in the CoralNet web interface ([\[sd.edu/\]\(http://sd.edu/\)\) to estimate percentage cover in the photo-plots. Out of 70 photo-plots at each site and depth \(50-m transect\), 30 photo-plots were randomly selected to record the abundance of coral genera, for community structure analysis. Genera/species distributions were determined based on the authors’ experience and knowledge assistance by the literature. In case of uncertainty at the species level, identification was left at the level of the genus.](http://coralnet.uc</p>
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Light and water temperatures were recorded monthly from August 2014 to July 2015, using a profiling reflectance radiometer (PRR800; Biospherical Instruments, San Diego, California, USA), which measures 19 channels (at 300–900 nm) and the integrated PAR. The instrument was deployed at midday (11:00–13:00), with clear skies, using the free-fall technique (Waters et al. 1990) to maintain a vertical position and avoid shading and reflectance from the boat. The measurement data were analyzed using the program PROFILER (Biospherical Instruments). An average depth for 1% irradiance of surface UVR and PAR, and 0.1% PAR (from eight locations, minimum depth 200 m), and PAR attenuation coefficients ($K_{d(\text{PAR})}$ from 19 different locations) were calculated as described by Kirk (2011). To describe the concentration of chlorophyll *a* in the GoE/A, and its potential influence on light and the shallow-to-deep transition, 14 yr of daily chlorophyll *a* concentration data were provided by the national monitoring program (NMP) in Eilat from 01 January 2004 to 31 December 2017 http://www.meteo-tech.co.il/EilatYam_data/ey_observatory_pier_download_data.asp.

Statistical analyses

The corals identified from 40 independent transects were treated as samples. Sample matrices were $\log(1 + x)$ -transformed to Bray–Curtis dissimilarity matrices. Analysis of similarity (ANOSIM; 999 permutations) was used to test for differences in a multivariate coral community matrix using pairwise dissimilarities. Similarity Percentages (SIMPER) analysis was used to determine which coral genera contributed to the differences observed between depths (Clarke 1993). Analyses were performed at the genus level using PRIMER-7 software. To visualize dissimilarities, a non-metric multidimensional scaling (nMDS) plot was created in R (R Core Team

2017) using the vegan package (Oksanen et al. 2011). Additionally, species richness and Hill number of Shannon diversity index (Shannon 1948) were calculated per depth.

We identified co-occurring assemblages of coral genera using a recently published approach derived from a mesophotic system in the Caribbean (Laverick et al. 2017). We performed a principal coordinate analysis (PCoA) on Hellinger-transformed data to enable a method based in Euclidean space. Data for each species in a photo-plot were standardized by total abundance across all photo-plots (Legendre and Gallagher 2001). The Euclidean distances between taxa in community space can be considered as measures of dissimilarity. We used *K*-means clustering (Hartigan and Wong 1979) to determine the optimal number of communities to fit to the PCoA. We trialed clustering solutions fitting 2–10 assemblages and selected the number of assemblages that maximized the Calinski criterion (Calinski and Harabasz 1974). The returned assemblages were tested statistically with a multi-response permutation procedure (MRRP) running 9999 iterations (Biondini et al. 1988). We performed a Dufrene-Legendre indicator species analysis (DF, 10,000 iterations; Dufrene and Legendre 1997) in the R package labdsv (Roberts 2016) on the photo-plot data. Our DF analysis returned how strongly each photo-plot resembled any assemblage identified by the PCoA with *K*-means clustering. Maximum indicator values occur when all Scleractinia observed in a photo-plot are from a single assemblage. The depth ranges of taxa forming each assemblage were compared in a *t* test to determine whether this depth range structured the reef community. Depth ranges were limited to the 10th–90th percentile of a taxon to remove the influence of extreme observations.

To assess the influence of light on community structure, DF indicator values for each assemblage at each photo-plot were plotted against % PAR and %UVR, pooled across sites. These variables were selected based on the assumption that the distribution of light-dependent corals would be affected primarily by the amount and quality of light penetrating the water column. Photosynthetically active radiation begins to limit photosynthesis between 1% and 0.1% surface irradiance (Gattuso et al. 2006, Kirk 2011).

Similarly, shorter wavelengths (UVR) may lead to damage at levels as low as 1% of the surface (UVB; Dunne and Brown 1996). Previous studies of light quality and light-dependent organisms commonly scale light levels to those at the surface, rather than using absolute intensity (Gattuso et al. 2006). Light levels relative to the surface, and light attenuation coefficients (K_d), can be easily calculated without measuring the light intensity at depth simply by using a Secchi disk (See Appendix S1 for other a discussion of available methods). Such calculations can be useful and used in comparing different sites.

Non-linear least-squares models were fitted to the data. Visual inspection of the community structure ~ light data relationships revealed differently shaped distributions for each cluster. The shallow community was modeled with a Michaelis–Menten equation to capture light limitation. The mesophotic community was modeled by a Weibull distribution, a flexible curve able to capture the bulk of observations at low light levels and outliers under high-light environments. A measure of model parsimony (Akaike information criterion, AIC) was used to determine the best model for explaining the ecological data based on depth, %UVR or %PAR, and monthly light data. To contextualize the light data, a time-series decomposition was performed using the package tseries (Trapletti et al. 2015) on 14 yr of chlorophyll *a* data. The seasonal effects were extracted to characterize the expectation for the annual spring phytoplankton bloom in the GoE/A.

RESULTS

Patterns in depth distributions for different genera and species were found to be correlated with light metrics, that is, UVR and PAR (1% at 36 and 76 m, respectively; Fig. 1). Similar to previous works (Laverick et al. 2017), we found on more than one occasion that communities identified as either shallow or mesophotic could be vertically separated by only 10 m of water, demonstrating remarkable changes in community structure as a result of minor changes in depth. Overall, there were significant differences in community structure between depths (ANOSIM, $R^2 = 0.76$, $P < 0.05$), but not among all five sites (ANOSIM, $R^2 = 0.061$, $P = 0.618$).

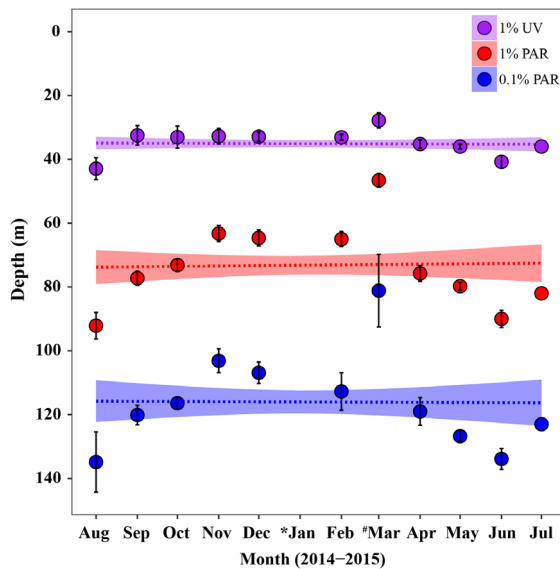


Fig. 1. Annual light penetration through depth, averaged over eight different sites (bottom depth deeper than 200 m) offshore Eilat. Dots represent the mean depth of 1% irradiance of surface ultraviolet radiation (purple—36 m), 1% PAR (red—76 m), and 0.1% PAR (blue—119 m) for each month with 95% confidence interval bars; horizontal lines denote the annual average value, with 95% confidence interval area (transparency). *(January) indicates no data, and # (March) indicates the range of measurements from March 2015 (affected by an algal bloom event). July was measured once. PAR, photosynthetically active radiation.

Patterns in coral zonation are correlated with coral morphology, that is, branching species dominate shallow depths (<40 m; Fig. 2) and foliaceous species dominate 40–80 m depth (Fig. 2), with a massive coral threshold at 70 m depth (Fig. 2). The spatial ordination of coral community structure revealed that the largest changes occurred at depths of 40 and 70 m (Fig. 2; Appendix S1: Table S1). Branching coral species are shallow-specialists, found mainly above 40 m (Figs. 2, 3). *Acropora* spp. and *Stylophora pistillata*, the most common branching corals at the GoE/A (Fig. 3), were found in limited abundance deeper than this line, with a reduction of 67% (*Acropora* spp.) and 96% (*S. pistillata*) in the number of colonies between 40 and 50 m. None of those genera were found deeper than 60 m. The maximum depth observed for the

third most common branching coral, *Seriatopora hystrix*, was 40 m.

Overall, we found a clear change in community structure at 40 m depth. Abundant corals, such as *Porites* spp., *Montipora* spp., *Favites* spp., and *Dipsastraea* spp., were found to flourish down to the maximum 1% PAR limit. Among the abundant upper-mesophotic specialist corals, *Leptoseris glabra*, *Euphyllia paradivisa*, and *Alveopora* spp. were found mostly between 40 and 80 m depth (Fig. 2). *Leptoseris glabra* was highly abundant at 60 m (1160 colonies, 386.6 ± 109 mean [\pm standard error, SE] per 10 m^2). Only a few colonies (27 colonies, 6.75 ± 2.5 mean [\pm SE] per 10 m^2) of this species were found at 30 m depth, the minimum depth of this species, and no colonies were observed below 70 m depth.

The strongest indication of a light-limited depth range can be seen in the distribution of *E. paradivisa*, which was observed strictly between the 1% UV and 1% PAR depths. *Euphyllia paradivisa* is restricted to 40–80 m (Eyal et al. 2016). In addition, clear changes in coral abundance along the depth gradient were found (Fig. 3a). The transition from shallow 0 to 40 m, which is dominated by branching and encrusting genera to deep-upper mesophotic 50–70 m, dominated by foliaceous genera, mostly *Leptoseris* spp. and “other” genera such as *Alveopora* spp. (Figs. 2, 3). The lower mesophotic below 70 m was dominated by *Leptoseris* spp. and azooxanthellate corals such as *Rhizopsammia* and *Dendrophyllia* spp. (Fig. 3a). Supporting these patterns, our SIMPER analysis returned a clear signal in community structure across the different depth zones (SIMPER and ANOSIM pairwise tests, global $R^2 = 0.833$, $P < 0.001$, stress = 0.07), shallow-mesophotic (≤ 40 m), upper-mesophotic (50–70 m), and lower-mesophotic (≥ 70 m) reefs (Appendix S1: Table S1). Further variability is noted between each 10 m depth interval (i.e., 10–20, 30–40, 40–50 m, etc.), implying further gradual change (Appendix S1: Table S2).

Overall, sharp changes in stony coral species diversity from the shallow to the upper-mesophotic reef (Appendix S1: Fig. S1), in tandem with changes in light, may indicate changes in physical properties of the water body. Corals found between 20 and 40 m were thriving reef communities, displaying the greatest richness and species diversity (Appendix S1: Fig. S1).

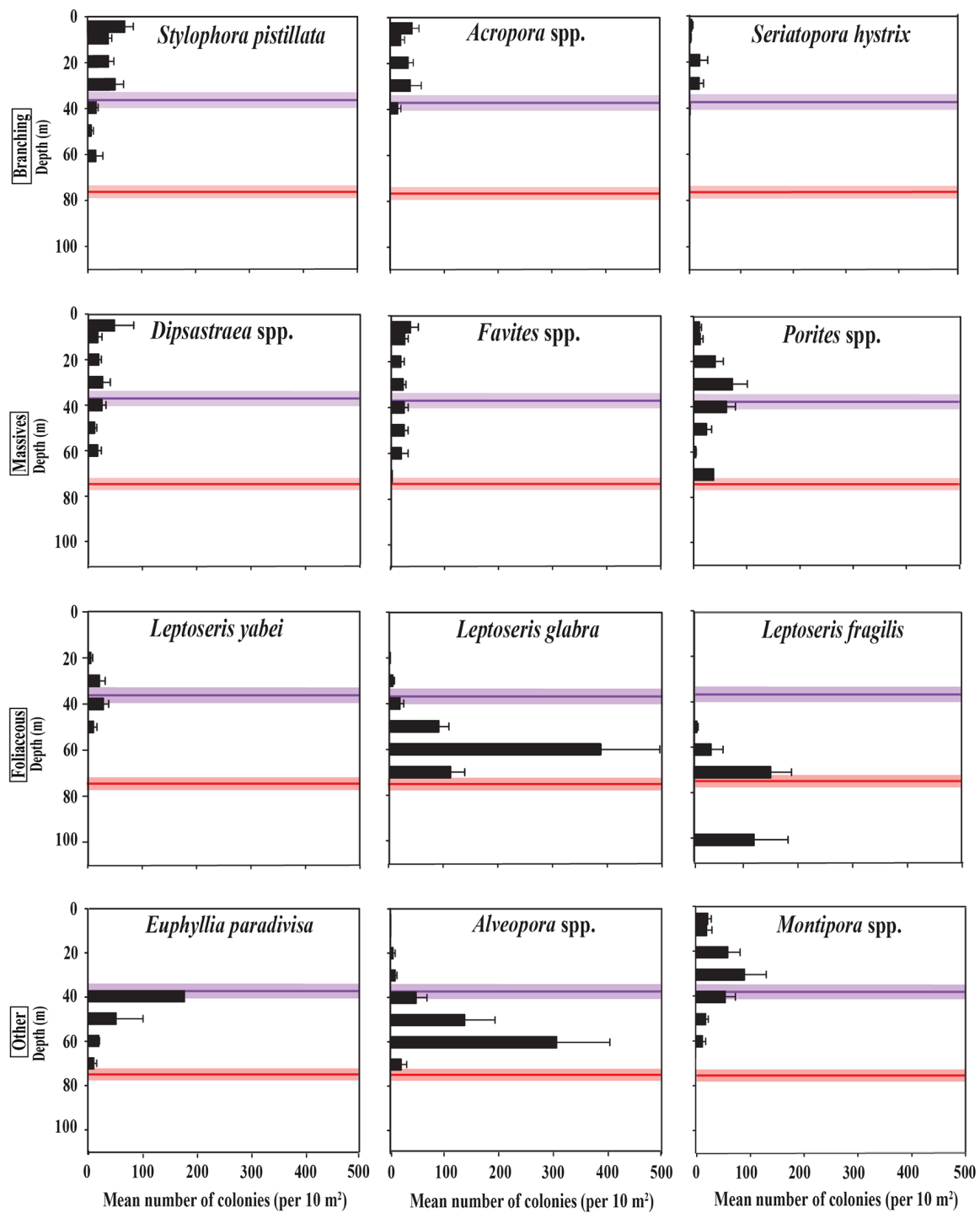


Fig. 2. The mean (\pm standard error) number of different species/genera of scleractinian coral colonies along a depth gradient of five survey sites. The purple line represents the annual average of 1% ultraviolet radiation (36 m depth) with 95% confidence interval (purple area). The red line represents the annual average of 1% photosynthetically active radiation (76 m depth) with 95% confidence interval (red area).

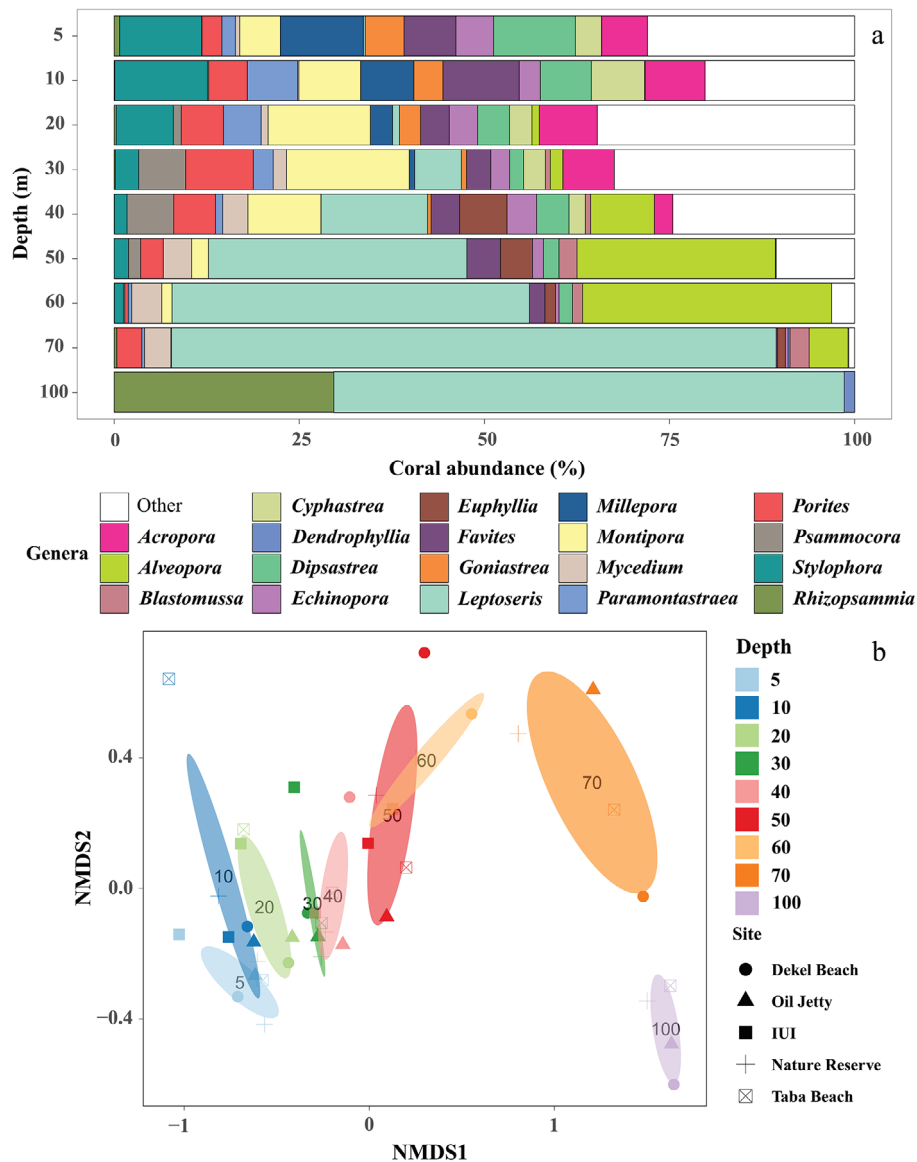


Fig. 3. (a) Total cumulative percentage of the relative abundance of the 19 most common scleractinian coral genera along a depth gradient at the five survey sites. (b) Non-metric multidimensional scaling ordination using scleractinian coral community composition from a depth gradient ranging from 5 to 100 m depth. Each color represents a particular depth and each dot the community composition at this depth for a given site, based on Bray–Curtis dissimilarity matrices (2D, stress = 0.07). Polygons are standard error of depth groups.

Our analysis further links variability with depth in the light environment to coral assemblages in the GoE/A. Two assemblages of coral genera returned an optimal fit to our data, following PCoA with clustering and a test of the difference between both assemblages (MRRP, $P = 0.004$; Fig. 4). The mean depth ranges of each

assemblage were not significantly different, with the mean range for clusters 1 and 2 as 30.5 and 35 m, respectively ($t = -1.04$, $P = 0.3$). Cluster 1 (red) comprises mainly shallow genera, with the average cluster 1 photo-plot capturing 8.8 genera (standard deviation [SD] = 4.7). Cluster 2 (blue) is more varied, but mainly contains deep genera,

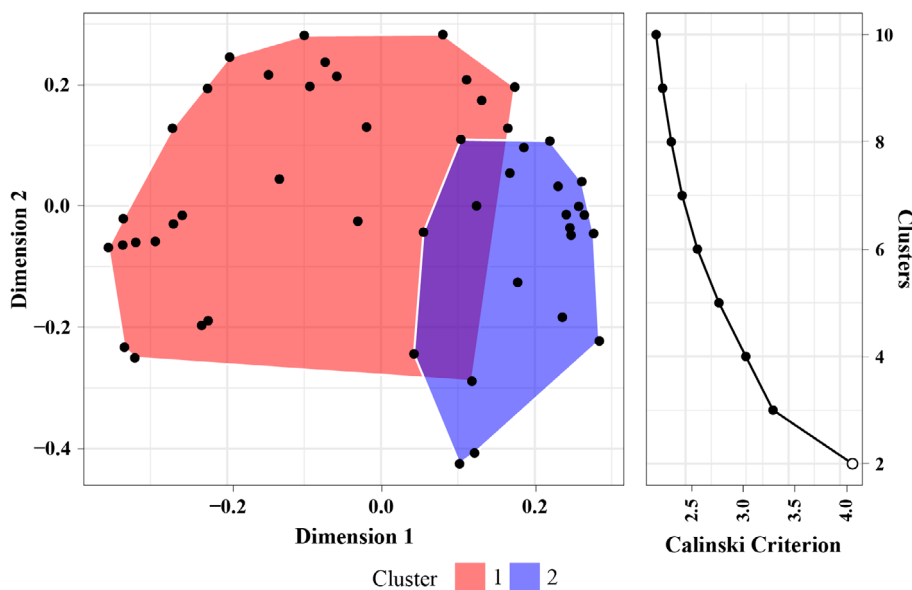


Fig. 4. Principal coordinate analysis of quadrat data was used to identify assemblages of co-occurring Scleractinia genera with K -means clustering (left). Polygons show the degree of overlap between clusters in taxon space. The Calinski criterion of proposed number of clusters to fit to the data is shown to the right. The optimal number of clusters was considered to be the number that maximized the Calinski criterion, marked as a hollow point.

with the average photo-plot capturing 3.3 genera ($SD = 2.8$). Plotting photo-plots spatially, colored according to the assemblage they most closely match (Fig. 5), further supports one of the assemblages as shallow and the other as mesophotic.

After plotting the DF indicator values for shallow genera (Cluster 1), we opted to fit a Michaelis–Menten equation (Eq. 1, Fig. 6):

$$DF \sim Vm * \frac{\text{Light}}{K + \text{Light}} \quad (1)$$

May returned the lowest AIC of any month when fitting %UVR to data, and March when fitting %PAR (Appendix S1: Table S3). We therefore use these months when evaluating models of DF indicator values against depth, %UVR, and %PAR. %UVR was a better predictor of Cluster 1 DF values than %PAR, although both light metrics were superior to depth (AIC = -1099, -1034, -666, residual SE = 0.12, 0.12, 0.15, respectively). Light metrics were able to explain more of the variation in community structure across our data than depth for shallow genera. V_{\max} (The asymptotic DF value) was estimated as 0.3 ± 0.01 ($t = 43.39$, $P < 0.001$) for %UVR

and 0.3 ± 0.01 ($t = 38.35$, $P < 0.001$) for %PAR. K (light required to reach halfway to asymptote) was estimated as $0.29\% \pm 0.04$ ($t = 7.43$, $P < 0.001$) for %UVR and $1.25\% \pm 0.15$ ($t = 8.16$, $P < 0.001$) for %PAR.

For mesophotic genera (Cluster 2), we opted to fit a Weibull model (Eq. 2; Fig. 6):

$$DF \sim \left(\frac{a}{b}\right) * \left(\frac{\text{Light}}{b}\right)^{a-1} * e^{-\left(\frac{\text{Light}}{b}\right)^a} \quad (2)$$

August returned the lowest AIC of any month when fitting %UVR to data, and June when fitting %PAR for cluster 2 (Appendix S1: Table S3). %PAR was a better predictor of Cluster 2 DF values than %UVR, returning a lower AIC and presenting a relationship with a mechanistic explanation. Both light metrics returned a lower AIC than depth (AIC = -3249, -2845, -2267, residual SE = 0.03, 0.03, 0.05, respectively). For %PAR, b (shape parameter) was estimated as 9.14 ± 0.16 ($t = 57.32$, $P < 0.001$), while for %UVR $b = 20.00 \pm 1.23$ ($t = 16.26$, $P < 0.001$). a (scalar term) was estimated as 1.89 ± 0.05 ($t = 40.34$, $P < 0.001$) for %PAR and 0.98 ± 0.01 ($t = 79.64$, $P < 0.001$) for %UVR. The median PAR value returned by the model is 7.5%, or

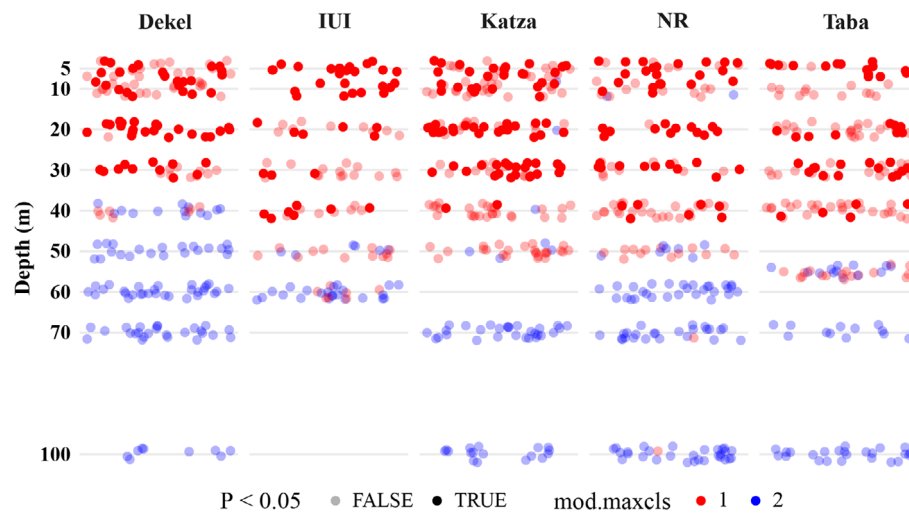


Fig. 5. Photo-plots are plotted as points in relation to their depth and site. Points are colored based on the coral assemblage the plot most closely matches, revealing spatial patterns in assemblages. How closely an observed quadrat aligns with the coral assemblage identified by PCoA was determined by the Dufrene-Legendre indicator analysis. Photo-plots are opaque if the P -value returned by indicator analysis is <0.05 ; otherwise the point is transparent.

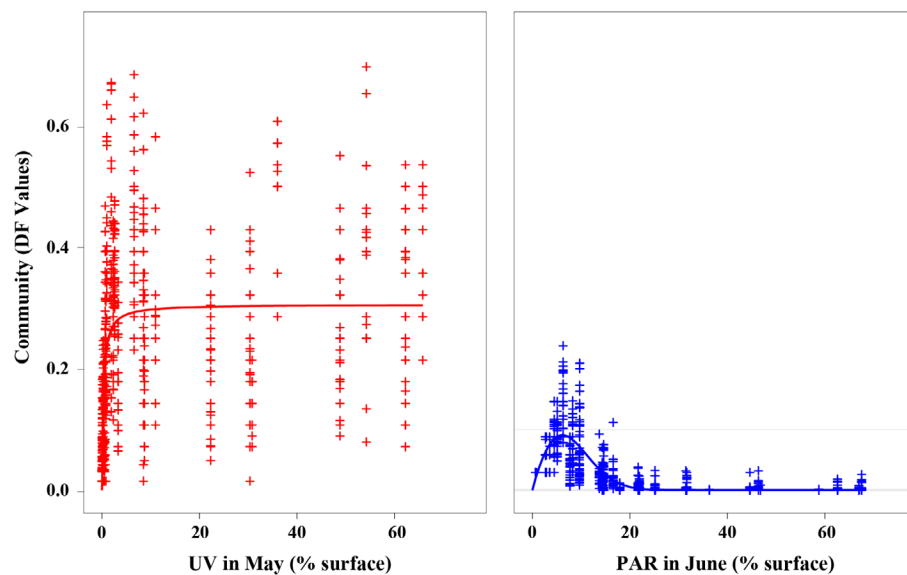


Fig. 6. The DF indicator values for cluster 1 (red, shallow) and cluster 2 (blue, mesophotic) are plotted for each photo-plot. The fitted lines show non-linear least-squares models after model selection, as described in the results.

13.8% UVR, indicating the preferred light environment of the observed mesophotic community.

The light environment of the GoE/A is modulated by an annual phytoplankton bloom. Time-series decomposition of chlorophyll a data reveals that the bloom peaks typically in March

(Fig. 7). Note that the seasonality displayed (Fig. 7) is only plotted for three years to improve legibility, but is estimated from all 14 yr of monitoring data. The height of the algal bloom in March increases the chlorophyll a content of the water by more than threefold in comparison with

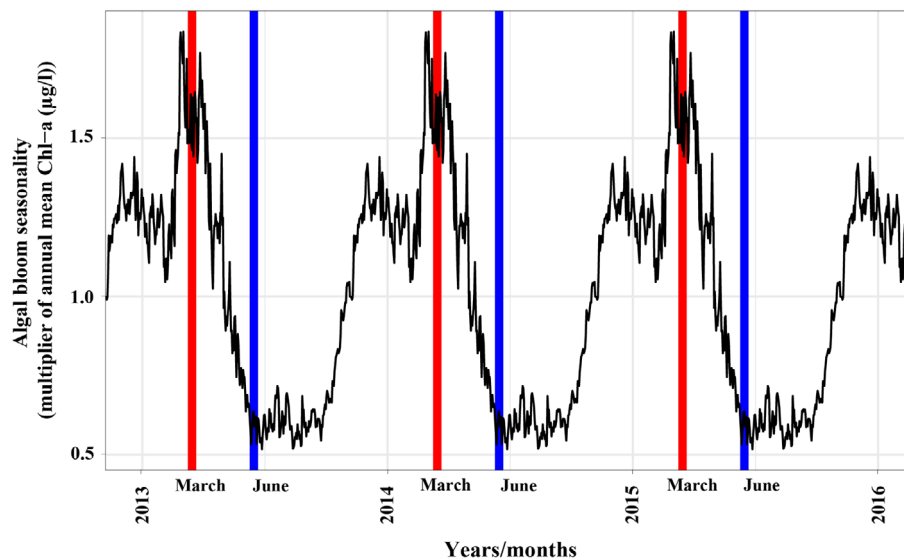


Fig. 7. The seasonal variation in ocean Chl-*a* concentration, calculated from 14 yr of monitoring data (black). A value of 1 on the *y*-axis is the annual average. The plotted values are the effect of a given month in the year; a month with a value of 0.5 expects a Chl-*a* concentration of half the annual average. The month of photosynthetically active radiation values that best explain shallow (red) and mesophotic (blue) genera distributions coincides with the peak and end of seasonal algal blooms in the northern Gulf of Eilat/Aqaba. The values displayed across years are identical and are repeated to illustrate the cyclical nature of the estimated seasonality of the algal bloom.

June through August and increases the attenuation of light with depth. Key features in this seasonal cycle coincide with the months independently identified as the best light readings to explain coral assemblage distributions.

Light attenuation coefficient ($K_{d(\text{PAR})}$) effect

The varied water characteristics across the GoE/A result in different light attenuation coefficients ($K_{d(\text{PAR})}$) across sites (Fig. 8a). In parallel to changes in the light attenuation coefficient ($K_{d(\text{PAR})}$), there is a dissimilarity in coral abundance at the different sites along the GoE/A (Fig. 8b). Overall, the limits of genera and species depth distribution are correlated with $K_{d(\text{PAR})}$ values. *Stylophora pistillata* is a depth-generalist coral with a depth range of 5–60 m at all the sites, except Dekel Beach, the most light-attenuated site ($K_{d(\text{PAR})}$ 0.076–0.078 annual average and summer average 0.068–0.07). At this site, *S. pistillata* reached a maximum depth of 40 m. *Montipora* spp. flourished at all depths down to 50–60 m at sites with lower $K_{d(\text{PAR})}$ values, whereas at Dekel Beach, this species was found

at a maximum depth of 40 m and with only five colonies (per 10 m²), constituting a reduction of 83% from 30 to 40 m. We found the same pattern for *Favites* spp., with a maximum depth of 40 m at Dekel Beach and 60 m at the other sites. The mesophotic species, *E. paradivisa* and *Alveopora* spp., were the dominant corals of the upper-mesophotic zone (40–70 m) except for one site—Katza. *Euphyllia paradivisa* at this site dominates between 40 and 60 m, while at the clearer water site, it flourishes at 60 m and mostly at 70 m. *Leptoseris fragilis* was the most abundant zooxanthellate coral below 70 m depth (Fig. 3), with no colonies being found shallower than 60 m.

DISCUSSION

The survival and growth of coral depend on variable environmental conditions such as light, seawater temperature, nutrient concentration, and salinity among others (Schlichter et al. 1994, Kleypas et al. 1999, Goodbody-Gringley et al. 2015). Still, even though light quality is a crucial physical factor in coral reef ecosystems, little

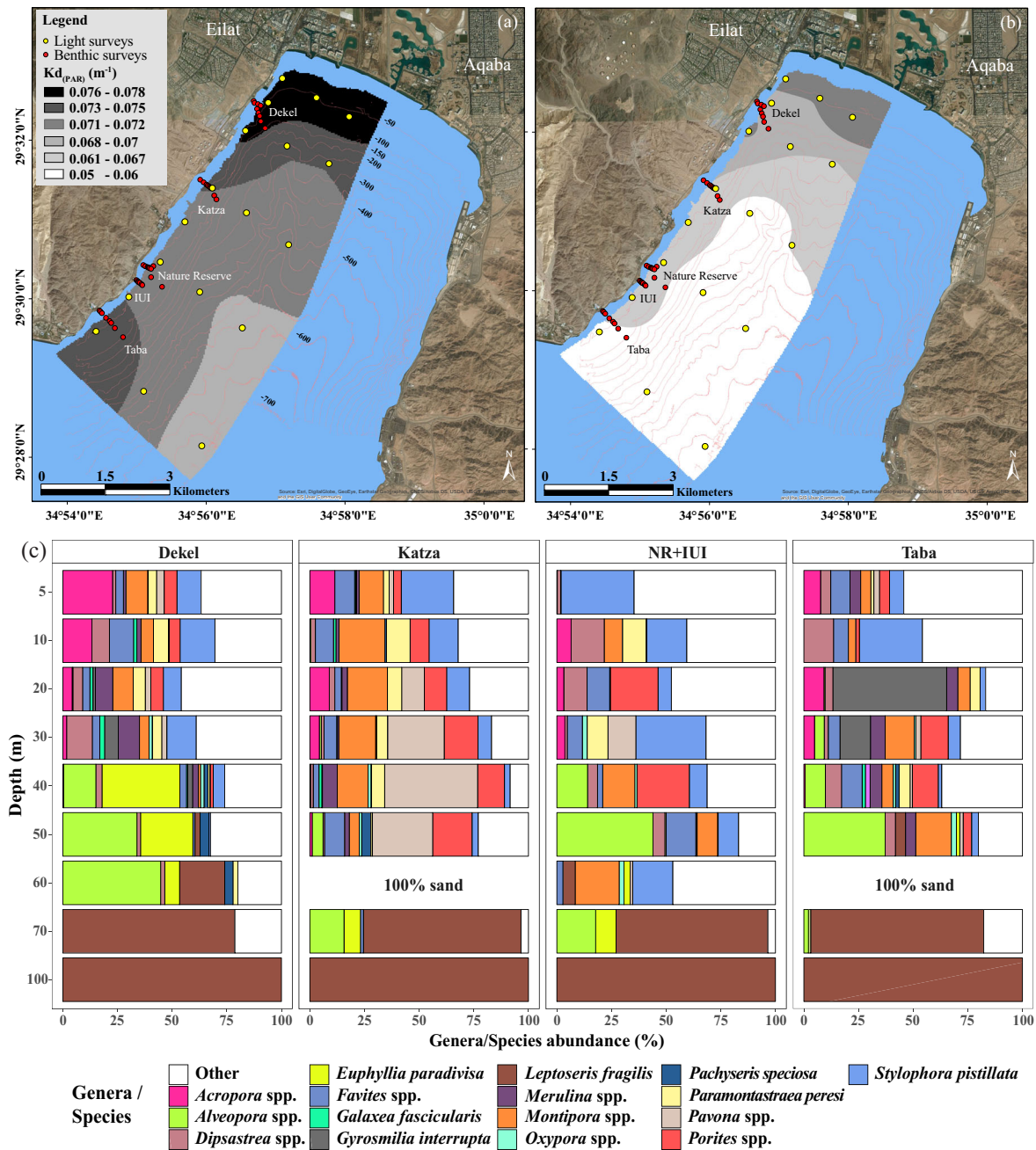


Fig. 8. The change in coral community structure as a function of light attenuation among the study sites (a) Annual 2014–2015 average $K_{d(PAR)}$ values range between 0.076–0.078 (black) and 0.068–0.07 (bright gray) and (b) summer (June–August) average range between 0.068–0.07 (dark gray) and 0.05–0.06 (white) at 30 m depth. Shapefile conducted between the Israeli territorial waters and the 30 m bathymetric depth contour. Yellow dots represent the spectral measurements location. Red points represent transects of all benthic survey site locations. Pink lines represent the bathymetric contours in 50-m intervals. (a–b) Maps were created using ArcGIS version 10.2.1 (ESRI) platform. (c) Cumulative percentage of the 17 zooxanthellate corals contributed (threshold, cum. <50%) to the dissimilarity among the various sites along a depth gradient at the five surveyed sites. IUI + NR sites represent a combination of the two sites. As a result of 100% sand cover at the Taba and Katza sites at 60 m, no data available.

attention has been given to light as a driving force of coral distributions (Edmunds et al. 2018, Lesser et al. 2018). Our results illustrate the importance of understanding light regimes when explaining the distribution and structure of zooxanthellate coral communities, across both depths and spatial gradients. Currently, the distinction between shallow and mesophotic reefs arbitrarily follows SCUBA limitations (Lesser et al. 2018, Eyal et al. 2019, Pyle 2019), or ecological patterns for the lower limit (Semmler et al. 2016, Laverick et al. 2017). We should question, however, whether these approaches can adequately assess between-site variation in rates of community transition with depth (Laverick et al. 2018). We suggest that the light conditions at a given site can be used to explain changes in community structure, when recognized.

Modern-day measurements are consistent with historical studies

Previous studies have documented the photo-adaptive mechanisms of corals, from morphological plasticity to *symbiodinium* density (Hoegh-Guldberg et al. 2007) and pigmentation concentration (Ben-Zvi et al. 2015, Muir et al. 2015), as well as light-enhanced calcification (Goreau 1959, Chalker and Taylor 1975). These mechanisms allow many coral species to maintain their metabolic functions over broad light ranges. Despite such adaptability, coral reefs in general do have minimum light requirements (Kirk 2011). Limiting-light depths will vary across locations and manifest as a crucial physical variable which may control the “ecological depth” of different species (Muir and Wallace 2016). It is therefore increasingly common to control for light in quantitative analyses (Kleypas et al. 1999). Similar to our findings, Fricke and Meischner (1985) reported 1% PAR at 90–100 m depth in Bermuda, comparable to Okinawa (Yamazato 1972), and measurements from the northern Red Sea (Eyal et al. 2016). These publications, however, contain limited replication in space and time. We argue that in considering the role of light quantity and quality in structuring coral communities along large depth gradients, extensive measurements and replications are necessary to uncover the variability in water quality (e.g., resulting from desert flash floods, algal blooms; Kirk 2011).

Light limitation and solar stress may control the shallow-to-mesophotic transition

Similar to previous studies (Semmler et al. 2016, Laverick et al. 2017), our ecological analysis revealed two coral assemblages (clusters) between the surface and 100 m depth. The switch from shallow genera to mesophotic genera occurs around 40–50 m (Appendix S1: Table S2). Dekel is a particularly unusual site, with a shift in coral community structure between 30 and 40 m (Fig. 5). Cluster 1 comprised mainly shallow genera. Depth ranges for cluster 2 were deep but more varied than cluster 1 (Fig. 9). Although our statistical analysis does not allow a clear statement with respect to coral assemblages differing as depth-specialist or depth-generalist taxa, the taxa in each cluster do segregate loosely by depth (Fig. 9).

The two assemblages exhibit different relationships with light (Fig. 9). The quadrats most closely mirror the shallow assemblage above 0.29% surface UVR. Below this, the shallow corals appear light-limited and their DF values rapidly decline. The quadrats match the mesophotic assemblage most strongly at 7.5% surface PAR, with a decline above and below this number. This suggests that mesophotic taxa may grow optimally within a narrow band of light values. This observation, that %UVR best predicts the occurrence of shallow coral communities, while the %PAR is more appropriate for mesophotic communities, may have several potential explanations. Mesophotic species may be light-limited, but, moreover, have a lower resilience to UVR and its potential damages (Ben-Zvi et al. 2019). Our results indicate below 7.5% PAR mesophotic taxa may be light-limited, while above this value solar stress may limit the distribution of genera. The model displays a tail toward high light levels containing a few non-zero DF values. As light readings were taken by casts in open water, they may not accurately reflect the light environment of a topographically complex reef. These non-zero DF values could have resulted from shaded photo-plots in shallow water. We are thus unable to disprove competing explanations for the loss of mesophotic taxa under higher light values. It may also be possible that competitive interactions with shallow taxa, which are better able to tolerate brighter conditions, restrict mesophotic taxa to darker reef niches. Both clusters are

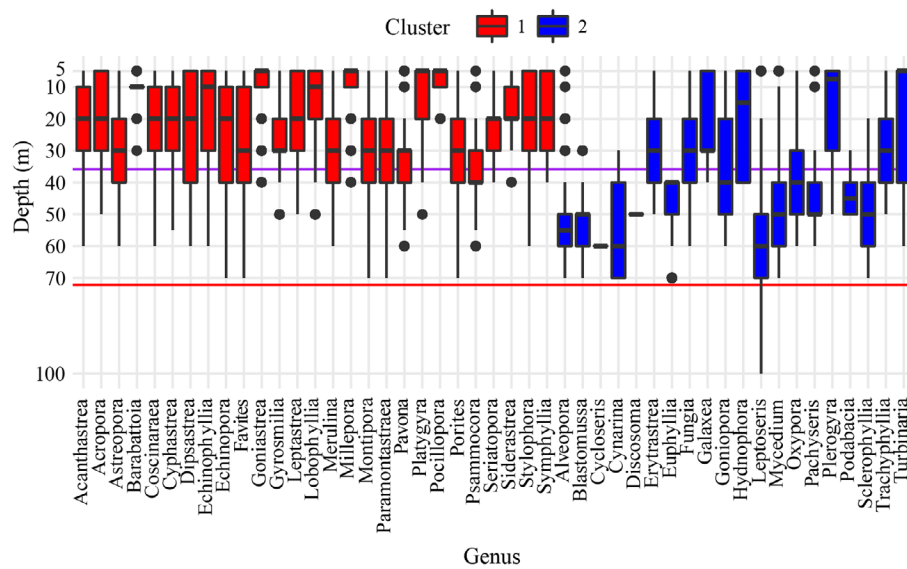


Fig. 9. Boxplots show the depth ranges of 47 genera generated from pooled data of all sites. Boxes are colored according to assemblage identified during PCoA. Cluster 1 (red) and genera from cluster 2 (blue). Whiskers of the boxplot extend 1.5 times the interquartile range, or to the most extreme observation, whichever is smaller. Points are outliers beyond 1.5 times the interquartile range from the median. The density curve on the right of the plot shows the distribution of all observed coral colonies with increasing depth. Horizontal black lines are the mean 1% UV (purple), and mean 1% photosynthetically active radiation (red) limits across all sites.

characterized by different morphological forms, which may reflect adaptations to physical conditions (Kahng et al. 2019).

It is worth noting that the asymptotic DF value for shallow assemblages in the quadrats is 0.3, twice the maximum value returned by the model for the mesophotic photo-plots. This can be explained by the average number of genera from each assemblage captured by the photo-plots. Plots assigned to cluster 1 on average captured 8.8 genera. Plots identified as cluster 2 captured 3.3 genera, despite both clusters containing similar numbers of genera. This suggests that mesophotic genera are spread more patchily through space, requiring larger or more sampling units to effectively capture mesophotic diversity and avoid methodological artifacts. These models indicate a physiological explanation for the community transitions found on coral reefs. In addition to solar radiation, temperature regimes too can influence corals (Cantin et al. 2010, Downs et al. 2013, Muir et al. 2015). In general, we found minimal changes in water temperatures across depth gradients and among sites throughout the year (Appendix S1: Fig. S2).

Seasonal algal blooms in the GoE/A modulate the light environment experienced by reefs, explaining the shallow-mesophotic reef transition

Tight relationships between physical and ecological patterns have been reported in previous studies (Labiosa et al. 2003, Boss and Behrenfeld 2010, Dishon et al. 2012). Similarly, we found that annual algal blooms in the GoE/A may limit the depth of shallow taxa. This ecological mechanism increases light attenuation, mainly in oligotrophic waters (Bricaud et al. 1998, Kirk 2011), and could also dictate the depths of mesophotic reefs (Fig. 8). The generalist coral *S. pistillata* was found to be a net producer of O₂ only during the summer in the GoE/A (Nir et al. 2014). This coincides with the lowest Chl-*a* concentrations in the water column. At the height of the algal bloom, *S. pistillata* must rely on heterotrophy to satisfy its energy demand. Similar to other locations, the spring bloom in GoE/A occurs as a result of the mixed-layer depth (MLD; Zarubin et al. 2017). Usually, the MLD maximum is reached in February–March, with substantial inter-annual variability in the maximum MLD between years (Zarubin et al. 2017). The cycles shown at Fig. 7

represent the relative difference in chlorophyll *a* concentration expected in the water column over the course of a year. This seasonality was calculated from 14 yr of monitoring data prior to the current study. Despite annual fluctuations, we can expect the benthic communities to respond to these long-term averaged signals. This can explain why March and June were selected by AIC as the best explanation of shallow and mesophotic community distributions, respectively, when considering PAR (Appendix S1: Table S3). Modern tools, such as remote sensing, may provide information on water quality and light conditions in space and time. Phytoplankton, which play an important role in locally modulating the bleaching response (e.g., during episodes of heat stress), may be an influential factor in a mitigating way by reducing harmful light stress (Maina et al. 2008). Thus, it may not only influence bleaching response but also recruitment success at depth ranges. We encourage other researchers to consider the importance of seasonal events that potentially modify the light field as explanations for the patterns found in deep-reef communities elsewhere.

Why should we adopt an environmental definition of MCEs?

Our data have revealed variation in coral community structure in tandem with light conditions, across different sites (Fig. 8). Therefore, any definition of a mesophotic reef should have a flexible depth limit to account for the environmental conditions at a particular site. The correlation between the physiology and ecology data could be explained by light penetrating less deeply at specific sites (i.e., Dekel; Figs. 6, 8). Although there were no statistically significant differences in community structure across sites, there are specific coral depth distributions which are affected by changes in light, mainly variation in $K_d(\text{PAR})$.

We should expect to find mesophotic species at shallow depths under certain light conditions (Kahng et al. 2010, Muir and Wallace 2016); that is, *Alveopora* spp. flourish at 70 m at the clearest water sites (Katz and IUI), while no colonies were found at this depth at Dekel. In general, this genus, as well as *E. paradivisa*, is distributed at deeper depths at sites with low $K_d(\text{PAR})$ values (Fig. 8b). Thus, by providing a clearer definition to light-limited coral communities inhabiting

MCEs, as the relative values we used (%PAR, % UVR, and $K_d(\text{PAR})$), we may be able to better predict the implications of these effects on the recruitment, and post-settlement survivorship of specific coral species. Those predictions can be achieved by further models, based on the above light quality variables combined with ecological data, and work which will provide the basis for such models through crucial spectral measurements. After this, we will be able to define mesophotic regions by light. This would assist us in predicting the distribution and community structure of deep and shallow reefs as well as the impact of environmental stress events which affect the quality of light in the water (e.g., eutrophication and algal blooms).

How variability in the light field affects coral species must be considered when projecting different futures for MCEs

Mesophotic coral ecosystems are likely sensitive to fluctuations in the light field, induced by local disturbance (e.g., eutrophication, algae blooms). To support the persistence of mesophotic populations, we need to predict future population changes under different environmental scenarios. Doing this accurately will require an understanding of the differing responses of coral groups (e.g., depth specialists or generalists, autotrophs, or mixotrophs) to a variety of pressures, including the competitive influences between them (Laverick et al. 2017). The ability to cope with changes in light quality, in combination with other stressors (e.g., thermal stress, acidification, and pollution), is expected to vary among species (Bauman et al. 2013).

Photosynthetic taxa in the lower mesophotic may be the most affected by changes in light (Bongaerts et al. 2015; Fig. 2; *E. paradivisa*, *Alveopora* spp., *L. fragilis*). This can be seen in the tight connection between different stony corals and the 1% PAR and UVR limits (Fig. 2). The changing depth distributions for these species among sites appear connected to light (Fig. 8). These relationships may influence competition and the available settlement area on MCEs, under environmental change, and subsequently impair coral resilience to other stressors.

By combining ecological and physical (light) data, it is possible to more accurately define a mesophotic and a shallow reef community. This

approach respects that an ecological pattern is dependent in part on physiological limitations. Further, it allows us to consider how reefs may respond to changing environmental conditions globally. Rapid changes in water quality may have a crucial effect, felt most keenly by depth-specialist taxa. These organisms may find themselves unable to keep pace with changes in the light regime, and so end up outside their preferred abiotic envelopes. Continuous ecological and physical monitoring is therefore needed to assess the health of sensitive mesophotic ecosystems. Consequently, when investigating the responses of corals on an ecological scale (e.g., changes in distribution and community structure), we suggest that experiments are needed to determine the environmental–physiological interactions that drive these patterns. By combining field and laboratory studies with light data, we can quantify the influence of light on the spatial distribution of stony corals.

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DATA AVAILABILITY

National monitoring program data available from http://www.meteotech.co.il/EilatYam_data/ey_observatory_pier_download_data.asp

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2839/full>