The Red Sea: Israel

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Abstract

The mesophotic coral ecosystems (MCEs) of Eilat, in the Northern Red Sea, are among the best-studied worldwide, as demonstrated by the high number of publications from the region. Nonetheless, Eilat's MCEs remain relatively unexplored compared to its shallow reefs. Its MCEs host diverse benthic communities that are potentially linked ecologically to shallow reefs. Here, we summarize the history of MCE research and compare the shallow and mesophotic reefs using long-term biotic and abiotic data. Eilat's MCEs exhibit lower fluctuations in temperature, light, sedimentation, and a decreased frequency of shore-related disturbances than adjacent shallow reefs, supporting the hypothesis that key environmental parameters become more stable with increasing depth. However, nutrient concentrations are more variable in MCEs than nearby shallow reefs. We provide a novel definition of the upper (30–80 m) and lower (80–160 m) mesophotic zone boundaries in Eilat, based on the degree of light penetration, as well as the relative abundance of major fauna and flora. Scleractinian coral diversity increases with depth, as well as the abundance of specialist taxa. Corals (93 spp.) comprise the major organisms contributing to living benthic cover. A mass coral-bleaching event took place in 2015 that exclusively affected MCEs, and we discuss the event's potential mechanisms and consequences for shallow vs. mesophotic coral assemblages. Protection and regulations of MCEs are needed to maintain and support these unique ecosystems.

Keywords

Mesophotic coral ecosystems · Gulf of Eilat/Aqaba · Biodiversity · Light · Deep-water bleaching

11.1 Introduction

The Red Sea, including its two northern extensions, the Gulf of Eilat/Aqaba (GoE/A) and Gulf of Suez, is a long (ca. 2000 km), narrow, deep sea extending from 12.5° to 29.5° N at the northwestern extremity of the Indian Ocean. The Red Sea was a blind-ended ocean in its early phase but is today connected to the Indian Ocean at the southern end by the Bab-el-Mandeb straits and the Gulf of Aden (Fig. 11.1). As a young ocean basin, only 10 Ma years ago, the whole water body was super saline (Bosworth et al. 2005). Today, only shallow oceanic waters from the Indian Ocean enter creating hot, deep water throughout the entire ocean basin. This deep water does not connect fully to global water circulation; thus unique oceanographic conditions persist enabling development of massive coral reef structures at very high latitudes (almost 30° N).

The fringing coral reefs situated on the upper part of the steeply sloping seafloor of the Red Sea reflect the region's young geological history. The environment here is conducive to the growth of hermatypic scleractinian corals to depths

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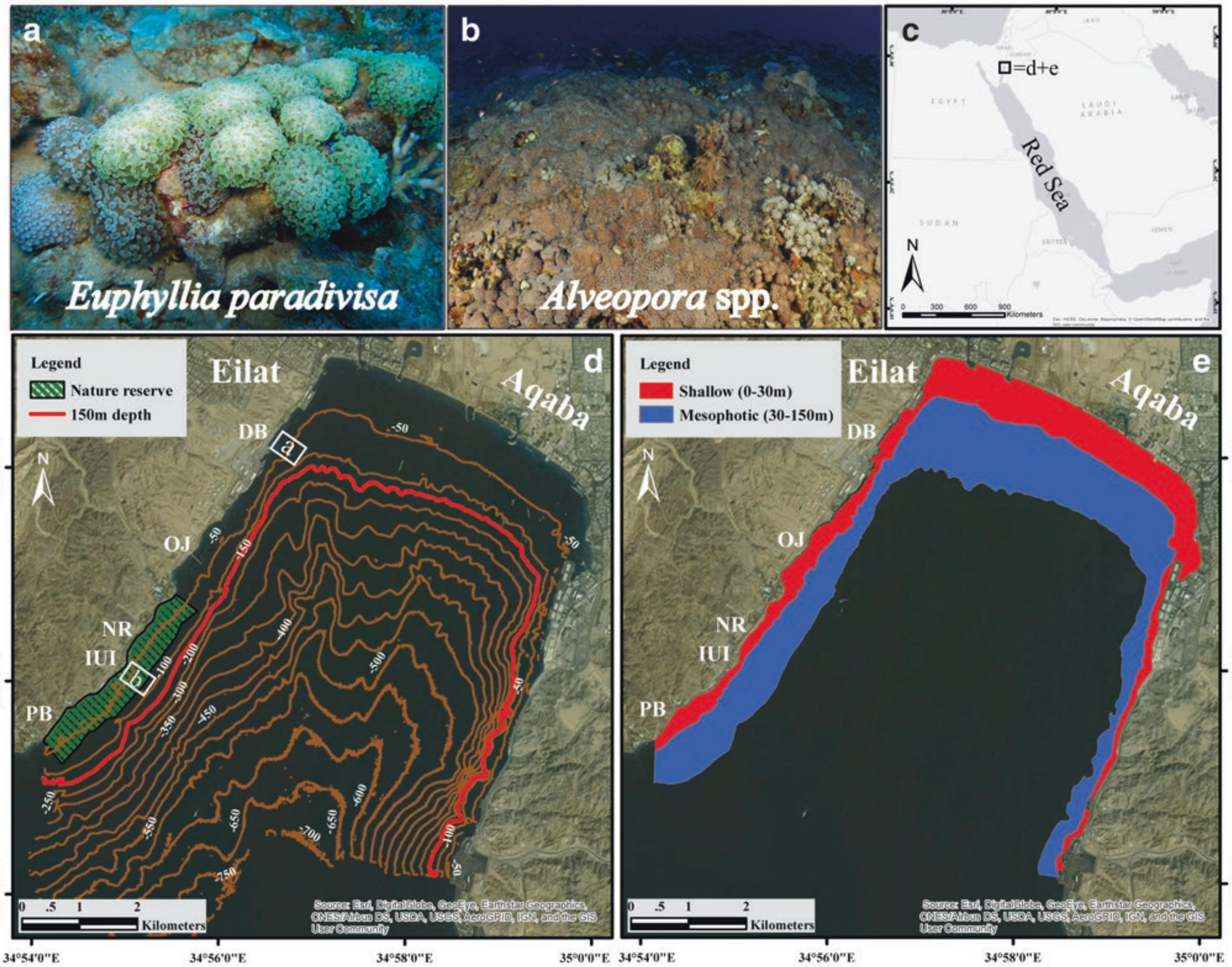

Fig. 11.1 Map of the study sites and habitats in the GoE/A. (**a**) *Euphyllia paradivisa*, the dominant species in the northern MCEs of Eilat, offshore of the Dekel Beach (DB) at depths of 36–72 m; (**b**) thriving community of *Alveopora* spp. offshore IUI at depths of 40–60 m; (**c**) wide view of the GoE/A and the Red Sea; (**d**) representation of the Nature Reserve area off Eilat with the main sites surveyed in the last decade, DB, Oil Jetty (OJ), Coral Beach Nature Reserve (NR), IUI, and Princess Beach (PB); contour intervals of 50 m with the 150 m depth highlighted in red; and (**e**) the mesophotic reef (blue) area is ca. double the shallow reef (red) area in the northern GoE/A. (Photo credits: (**a** and **b**) G. Eyal)

where light irradiance is less than 1% of surface levels (80–150 m depth) and barely sufficient for normal photosynthetic activity. Consequently, the Red Sea has had a long history of mesophotic coral ecosystem (MCE) research. Early MCE research was conducted primarily using submersibles (Fricke 1996), but more recently the development of technical diving and the availability of small but efficient remotely operated vehicles (ROVs) have accelerated investigation of the mesophotic flora and fauna in Eilat.

The GoE/A head is 8.5 km long and 5–8 km wide (~53 km^2), bounded in the north by the cities of Eilat (Israel) and Aqaba (Jordan) and open on the south to the main water body of the GoE/A, with the Egyptian coast of Sinai on the west and Saudi Arabia coast on the east (Fig. 11.1). The MCEs in this region are structured from ancient submerged reefs with recent coral coverage and gravel-like reef structures with corals and other reef-building organisms/materials cementing landslides mostly in intermediate depth of 30–65 m.

This review highlights the current state of knowledge on the MCEs of the Red Sea in general and Eilat in particular. It presents new biotic and abiotic characterizations of the shallow vs. MCE environments on temporal and spatial scales.

11.1.1 Research History

The Red Sea has a long history of scientific expeditions, research, and discoveries by European scientists. These began with the Danish "Arabia Felix" expedition, followed by the important studies by Forsskäl (1761–1762), Savigny (1779–1801), and Hemprich and Ehrenberg (1820–1826). Further contributions were made by Rüppell (1826–1828, 1835), Klunzinger (1870–1872), Hackel (1876), and Walther (1888). In the early twentieth century, Cyril Crossland became head of the Marine Laboratory at Al Ghardaqa, Egypt, and contributed considerably to knowledge of coral reefs in the region. The second half of the twentieth century witnessed a substantial increase in studies of littoral and deep-sea habitats in the Red Sea (Fishelson 1971; Loya and Slobodkin 1971; Fricke 1996). Around the same time, permanent study sites in Egypt, Israel, Sudan, Jordan, and Yemen were established, and intensive coral reef work was initiated but focused mostly on shallow benthic fauna (see Fishelson 1971, 2009).

The first official documentation of deep-water (>30 m) organisms in the Red Sea was provided by the German research vessel *Meteor*. Despite considerable interest in deep-sea exploration, MCEs remained relatively unexplored (Fricke 1996). Since the 1950s, the short coastline of Eilat, Israel, has been a hub of research in the GoE/A. Eilat has become a leading site for MCE research, contributing ca. 8.3% of all mesophotic publications, compared to 13.9% for Australian reefs (the Great Barrier Reef and others) and 13.1% for US Pacific reefs (Turner et al. 2017). Indeed, some of the earliest studies of MCEs globally were conducted in Eilat in the early 1980s and 1990s. With the aid of the research submersibles *Geo* and *Jago*, Hans Fricke and colleagues carried out MCE studies at various locations along the Red Sea coast off Djibouti, Sudan, Egypt, and Israel. The topics covered included biology, microbiology, physiology, geology, geophysics, and oceanography (reviewed by Fricke 1996). The geological setting of the Red Sea has important advantages for MCE research, due to the comparatively inexpensive and easy access from shore. Additionally, permanent and regular monitoring of the reefs and the open sea is performed in Eilat (NMP 2004–2016). Eilat's mesophotic reefs constitute highly productive study sites for long-term observational studies and short-term in situ experiments (Eyal et al. 2016). Following the first *International MCE Workshop* organized by the US National Oceanic and Atmospheric Administration and the US Geological Survey in 2008 (Puglise et al. 2009; Hinderstein et al. 2010), several groups have started to explore Eilat's MCEs using technical diving and closed-circuit rebreathers (CCR). A milestone in MCE research advances took place with the *Second International MCE Workshop* (MCE Israel) held at the Interuniversity Institute for Marine Sciences (IUI) in Eilat in 2014. This workshop had a substantial impact on the research community in Israel and on coral reef researchers worldwide, enhancing interest in the biology, ecology, and geology of Red Sea MCEs (Loya et al. 2016).

11.2 Environmental Setting

The unique geography of the Red Sea, including the narrow and shallow straits at its entrance, results in a strong latitudinal salinity gradient ranging from 36‰ near the Indian Ocean to over 41‰ in Eilat (NMP 2004–2016). The region is characterized by uniquely warm deep water (ca. 21 °C at 700 m depth) caused by winter flushing in the northern parts of the Gulf of Suez and the GoE/A (Manasrah et al. 2004). Regional water circulation is driven by a combination of wind, evaporation, heat fluxes, and tidal regimes. This creates a seasonal overturning circulation in the Red Sea (Yao et al. 2014) and the GoE/A (Biton and Gildor 2011).

In the summer, from April to October, an almost constant north-northwest wind blows across the Red Sea, with speeds frequently exceeding 50 km h^{-1}. In winter, the same northerly wind dominates the northern part of the basin to ~18° N, while a south-southeast wind, associated with the northeast monsoon in the Indian Ocean, prevails in more southerly latitudes (Langodan et al. 2014).

In Eilat, scleractinian coral species diversity and community structure show considerable spatial variability. In addition to depth zonation and changes in the abundance and the composition of different taxa along the depth gradient (Loya 1972), Eilat's MCEs also exhibit spatial differentiation between sites (Eyal 2012; Eyal and Loya 2016). Along the northern shore of the GoE/A, the "Ayla" is a submerged fossil reef ridge (60–63 m deep) that supports very low coral cover (Tibor et al. 2010). However, dense coral cover has been observed along the western shore of the GoE/A at 40–60 m depth, composed of large (monospecific) colonies of the strictly MCE coral *Euphyllia paradivisa* in the northwest (Eyal et al. 2016) and *Alveopora* spp. (Eyal-Shaham et al. 2016) in the southwest coast of Eilat (Fig. 11.1a, b).

Sea-surface temperatures (SSTs) at 1 m depth offshore of the IUI ranged from 20.7 to 30.1 °C between 2011 and 2016 (Fig. 11.2a; NMP 2004–2016). Multiyear monitoring at three different locations recorded in situ temperatures ranging from 20.7 to 30.3 °C at 10 m depth (Fig. 11.2b) and 20.9–27.8 °C at 50 m depth (Fig. 11.2c). The low variation between depths is also reflected in the similar yearly average temperatures of 24.2 °C of SST, 24.4 °C in shallow waters, and 24.1 °C at mesophotic depths.

Light quality (intensity and spectrally), one of the most important factors influencing the ecology of photosynthetic organisms, decreases exponentially with depth (Kirk 1994). Monthly measurements of light quality using a SeaWiFS-compliant, high-resolution, profiling reflectance radiometer (PRR-800; Biospherical Instruments, Inc., San Diego) were performed during 2014–2015 at eight different sites (bottom deeper than 200 m) offshore Eilat (Tamir 2015). Based on these measurements combined with concomitant changes in benthic composition, the MCEs of Eilat have been classified into two distinctive light habitats: the upper mesophotic zone (30–80 m), which is characterized by a high diversity of depth-generalist coral species, and the lower mesophotic zone (80–160 m) dominated by the depth-specialist coral *Leptoseris fragilis*. The upper depth limit for *L. fragilis* occurs at ~1% of surface irradiance (76 m depth), while the maxi-

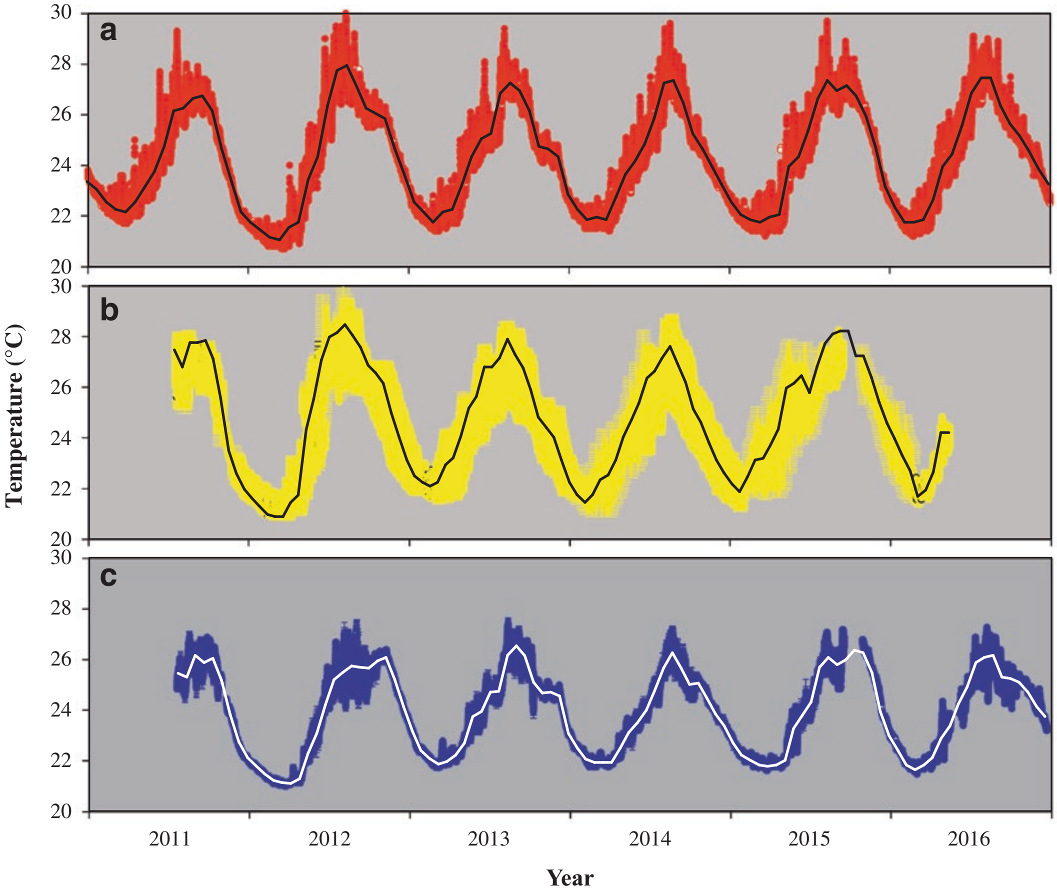

Fig. 11.2 Multiyear temperature oscillations offshore from Eilat. (**a**) Sea-surface temperatures at IUI: red dots represent 10-min interval measurements, and black line shows running median of the measurements. (**b**) In situ temperatures at 10 m depth at three sites (DB, OJ, and NR): yellow dots represent site averages of 10-min interval measurements with 95% confidence interval error bars, and black line shows running median of the measurements. (**c**) In situ temperatures at 50 m depth at three sites (DB, OJ, and NR): blue dots represent site averaged 10-min interval measurements with 95% confidence interval error bars, and white line shows running median of the measurements

mum depth of the species corresponds to the lower limit of the mesophotic zone at 156 m depth, where light irradiance is 0.1% surface light [Fig. 11.3; measured in situ or calculated after Sverdrup (1953), where 0.1% is deeper than the depth range of the radiometer (i.e., >130 m)]. The transition between upper and lower mesophotic zones differs among geographic regions and will be locally variable due to environmental factors such as terrestrial influences. Consequently, the definition of upper and lower mesophotic boundaries should take into account the range of light penetration, as well as the relative abundance of the major fauna and flora.

Overall, nutrient concentrations in the GoE/A are relatively low. Total organic nitrogen (TON) increases below 80 m depth and reaches a maximum at 400–500 m, where it stabilizes until the seafloor at 700 m. This is equivalent to deep-sea water in the open ocean. SiO_4, PO_4, and NO_3 increase between 100 and 200 m, reaching a maximum at 400 m, which is maintained down to the seafloor. NO_2 peaks at 80–300 m, with undetectable concentrations below 300 m (NMP 2004–2016). The deep chlorophyll maximum (DCM) ranges seasonally between a depth of 40–140 m, and the maximum concentration of chlorophyll *a* can be >0.75 μg L^{-1} at mesophotic depths (NMP 2004–2016).

Sedimentation rates offshore of Eilat are highly variable and depend on several sources including (1) desert dust that introduces fine material from the Sahara region, as well as locally eroded materials; (2) bioerosion and resuspension of reef fine materials; and (3) periodic flash floods and runoff from the nearby terrestrial environments (Goudie and Middleton 2001; Yahel et al. 2002; Katz et al. 2015; Andradi-Brown et al. 2016). Monthly trap collection rates from the shallow (10 m) and mesophotic (50 m) reefs off Eilat at three sites (Dekel Beach [DB], Oil Jetty [OJ], and Coral Beach Nature Reserve [NR]; Fig. 11.1d, e) demonstrate significantly higher sedimentation rates for both organic (Mann-Whitney test, U = 419.5, $p < 0.001$) and inorganic (Mann-Whitney test, U = 1174, $p < 0.001$) material on shallow compared to mesophotic reefs (Fig. 11.4).

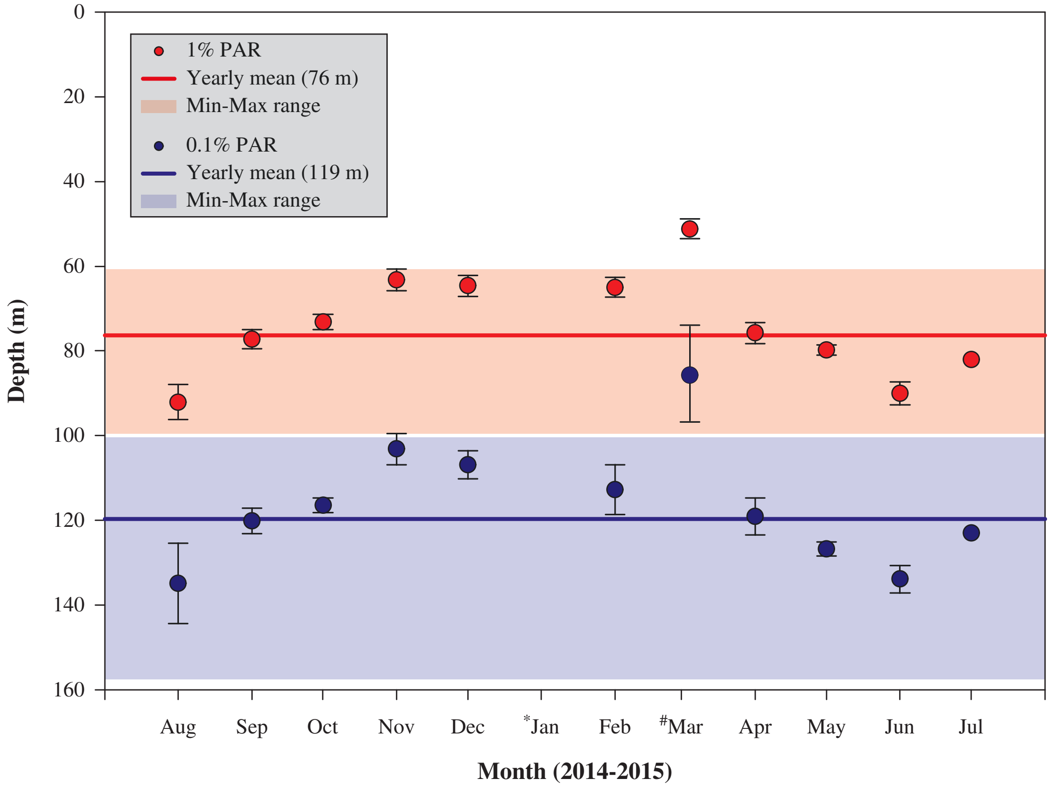

Fig. 11.3 Annual light depth penetration averaged over eight different sites (deeper than 200 m) offshore of Eilat. Red dots show mean depth of 1% irradiance of surface light with 95% confidence interval error bars; red line represents the annual averaged value (76 m depth) and minimum to maximum range. Blue dots show mean depth of 0.1% irradiance of surface light with 95% confidence interval error bars; blue line represents the annually averaged value (119 m depth) and minimum to maximum range. * indicates no data sampled in January 2015, and # indicates exclusion of range measurements from March 2015 (affected by algal bloom event)

11.3 Habitat Description

The northwestern GoE/A is characterized by scattered shallow reefs. In contrast, the MCEs in the same area are well developed, with several terraces along the shore occurring to at least 130 m depth (Table 11.1). The fauna comprises many specialist species found only at the mesophotic depths (Eyal 2012), such as the hermatypic corals *Alveopora allingi*, *A. ocellata*, *Euphyllia paradivisa*, *Leptoseris fragilis*, and *Stylophora kuehlmanni* and azooxanthellate corals such as *Balanophyllia* spp., *Dactylotrochus cervicornis*, *Madracis interjecta*, and *Polycyathus hodgsoni*. Many depth-specialist fishes also inhabit these reefs (Brokovich et al. 2008).

Many corals that exhibit complex three-dimensional branching structures in shallow waters become encrusting or platelike at mesophotic depths, thus maximizing light utilization (Fig. 11.5; Dubinsky et al. 1990; Mass et al. 2007). This pattern has been observed in many depth-generalist species in Eilat, including *Dipsastraea favus*, *Paramontastrea peresi*, *Porites lutea*, *Stylophora pistillata*, and *Turbinaria reniformis* (Fig. 11.5). This flattening creates a relatively low complexity and low rugosity of reef structure on MCEs (Kahng et al. 2010; Abbey et al. 2011), where coral growth rates are also comparatively low (Baker and Weber 1975; Fricke et al. 1987; Kahng et al. 2010). Therefore, MCEs exhibit lower niche diversification compared to shallower reefs and are expected to support lower species diversity (Fricke and Knauer 1986).

Worldwide, many extant MCEs occur on fossil fringing reefs that grew during lower sea levels during the Pleistocene and have subsequently drowned due to rapid sea level rise since the last glacial maximum (Abbey et al. 2013; Baker et al. 2016). Eilat features numerous late-Pleistocene/Holocene reefs in mesophotic depths, including at 60–70 m and at 90–130 m along the western coastline where shallow reefs are widespread (Shaked and Genin 2011), and the Ayla fossil reef ridge (60–63 m) along the northern shoreline where there are no modern shallow reefs (Tibor et al. 2010). These ancient reefs exhibit relatively high rugosity and therefore enable higher niche diversification than less rugose reefs elsewhere in the region. Other mesophotic reef structures have developed along gravel landslides with fragile attachment to the bottom or even laying over the sandy seabed in several locations down to 72 m (Table 11.1). In some cases, these former reef structures support lower coral biodiversity but a high abundance of only one or a few species (e.g., Eyal et al. 2016; Eyal-Shaham et al. 2016).

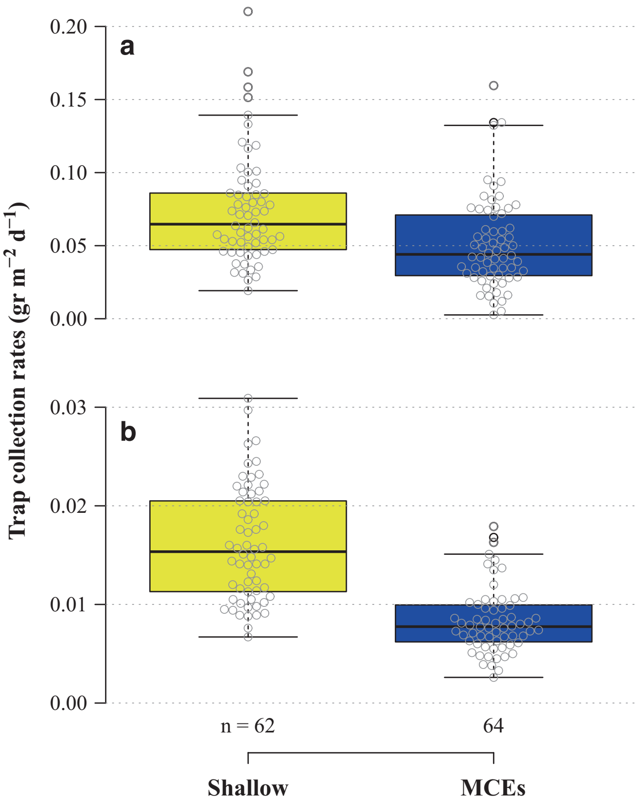

Fig. 11.4 Annual sedimentation rates on shallow and mesophotic reefs measured by sediment traps. (**a**) Lithogenic components and (**b**) organic matter collected monthly throughout 2012 at three sites (DB, OJ, and NR; two to three traps per site/depth). Boxplot centerlines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5-fold the interquartile range from the 25th and 75th percentiles; and data points and outliers are plotted as gray dots. Yellow boxes show shallow-water reef (10 m depth), and blue boxes show MCE (50 m depth) measurements. n = 62 or 64 samples as indicated under the box

11.4 Biodiversity

Benthic communities on natural reefs and artificial substrate were examined using photo surveys at numerous sites along the coastline of Eilat. The first survey examined shallow (10 m) and mesophotic (50 m) depths at three sites (Fig. 11.1; DB, OJ, and NR) from 2011 to 2017. Settlement tiles (n = 288) were deployed at 18 monitoring stations (Kramer et al. 2019). Each monitoring station comprised a triangular prism constructed from stainless steel bars, featuring 16 settlement tiles made of terracotta (20 × 20 × 1 cm). Each side of the station displayed eight tiles, oriented on a 45° angle. The second survey was performed at five sites (Fig. 11.1; DB, OJ, NR, IUI, and Princess Beach [PB]) from 2014 to 2017, along

Table 11.1 Differences between the shallow-water coral reefs and the MCEs in Eilat

	Shallow-water coral reef ecosystems	Mesophotic coral ecosystems (MCEs)
Depth range and bathymetry	0–30 m with gravel boundary layer at some sites	30–76 m continuation of the shallow reefs
	Mostly undeveloped fringing reefs and scattered knoll-like structures	65 m ancient fringing reef along the north shore
	Gaps in the reef around desert flash flood river inlets	75, 90, 110, and 130 m submerged ancient ridges
		Generally continuous reef
Dominant habitat-building taxa and families	**Scleractinian corals:** Acroporidae, Pocilloporidae, Merulinidae	**Scleractinian corals:** Agariciidae, Lobophylliidae, Euphylliidae, Poritidae
	Hydrozoa: Milleporidae	**Crustose coralline algae**
Habitat structure and coral growth forms	Complex and rugose	Flat and encrusting
	Hemispherical growth	Platelike growth
Light quality	High variability per depth	Low variability per depth
	200–2000 μmol photons m^{-2} s^{-1}	1–200 μmol photons m^{-2} s^{-1}
	Wide spectrum	Narrow spectrum
Thermal regime	High seasonal fluctuations per depth	Low seasonal fluctuations per depth
	20.7–30.3 °C	20.9–27.8 °C
	No coral bleaching with coral thermal-tolerance capabilities	Species-specific partial coral bleaching reported
Hydrodynamic and oceanographic regime	High-energy environments	Low-energy environments
	Anticlockwise circulation and dominant downwelling driven by northern winds	Crosscurrents driven by tidal regimes
	Thermocline in summer, deep-water mixing in winter, and algal blooms in spring	Deep chlorophyll maximum varies between 40 and 140 m
	Periodic flash floods and southern storm events affect nearshore dynamics	Flood hyperpycnal plume and biological sediment resuspension transport of fine materials and nutrients to deep water

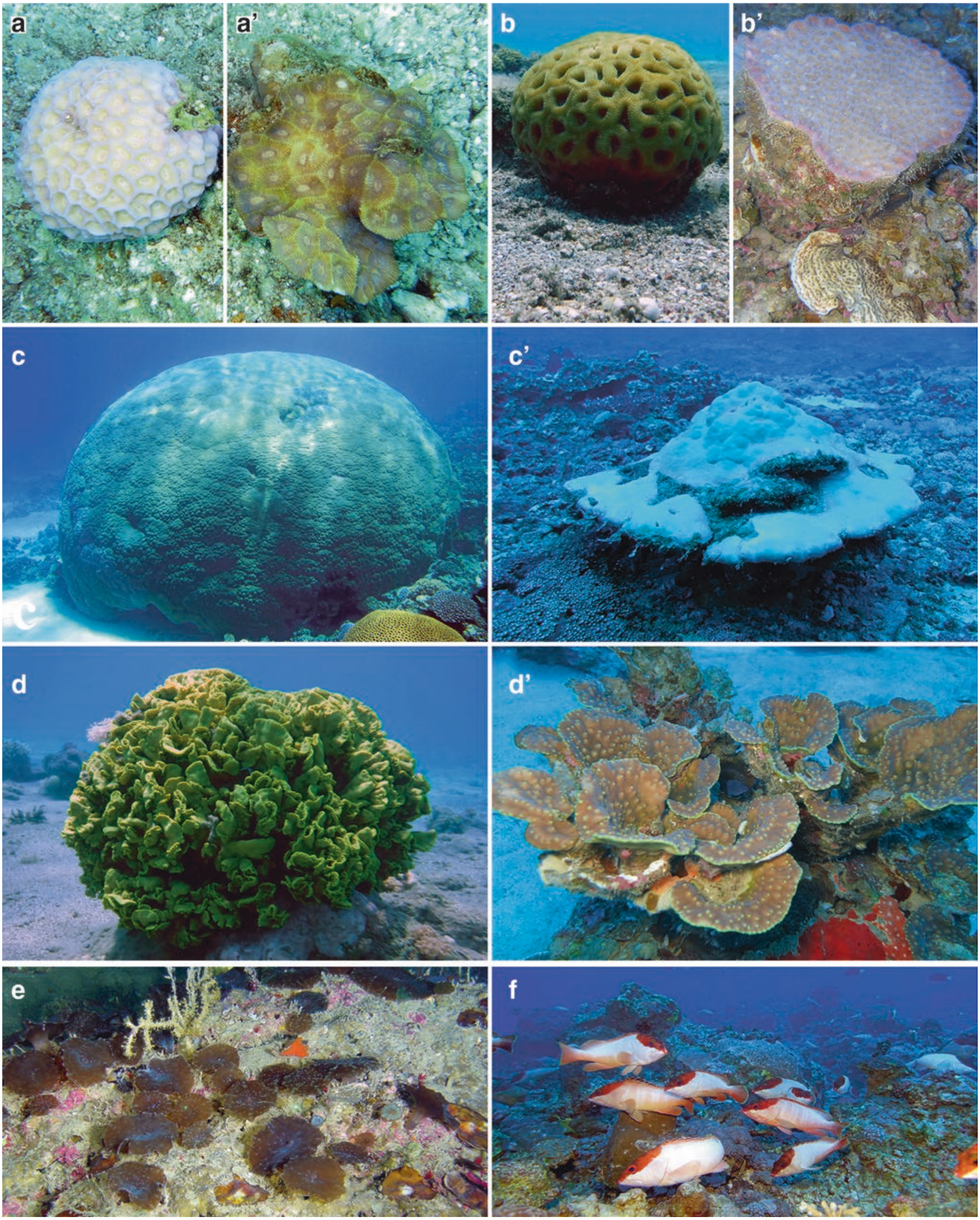

Fig. 11.5 Typical generalist and specialist scleractinian coral species in Eilat's shallow (**a**–**d**) and mesophotic (**a**′–**d**′) reefs, respectively; (**a**–**a**′) massive hemispherical and flat growth of the generalist coral *Paramontastraea peresi* at 5 and 60 m depth; (**b**–**b**′) massive hemispherical and cup-like growth of the generalist coral *Dipsastraea favus* at 5 and 60 m depth, respectively; (**c**–**c**′) massive hemispherical and cone-like growth of the generalist coral *Porites lutea* at 5 and 45 m depth, respectively; (**d**–**d**′) the foliose generalist coral *Turbinaria reniformis* in its shallow and mesophotic morphs at 5 and 55 m depth; the deeper morph exhibits fewer plates and polyps per unit area; (**e**) low profile reef structure at 80 m depth with dominance of Corallimorpharia, Octocorallia, and the specialist hermatypic coral *Leptoseris fragilis*; and (**f**) aggregations of the generalist grouper *Epinephelus fasciatus* aggregation at 50 m depth offshore of IUI. (Photo credits: G. Eyal)

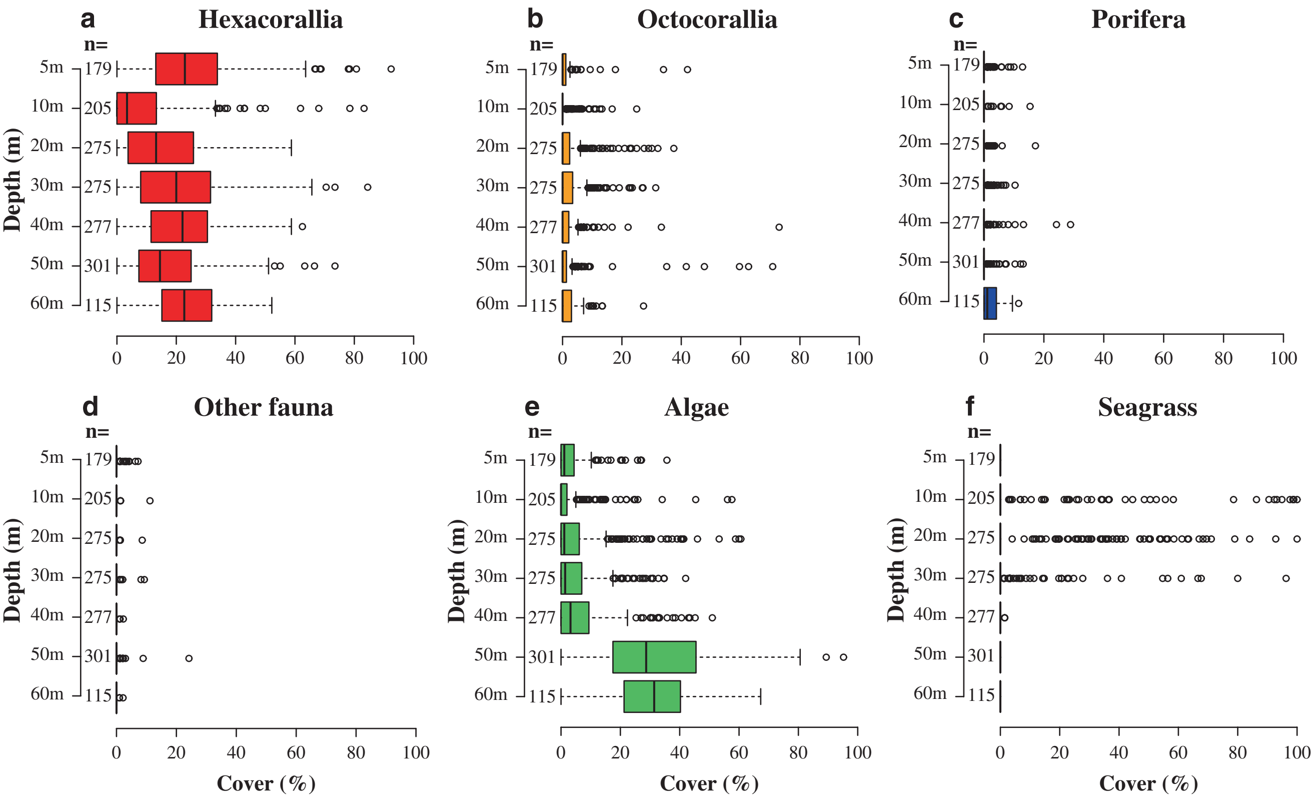

Fig. 11.6 Current benthic cover of the main taxa along the shallow to deep gradient at four different sites (DB, NR, IUI, and PB) in Eilat recorded during 2014–2017: (**a**–**c**) represent the main three fauna, stony reef-building corals (Hexacorallia), soft corals (Octocorallia), and sponges (Porifera); (**d**) other live organisms; and (**e**–**f**) represent the main flora (i.e., algae [including CCA] and seagrass). Boxplot centerlines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5-fold of the interquartile range from the 25th and 75th percentiles; outliers are represented by blank circles. Number of sampled quadrats of 0.35m^2 (n) indicated left of the box

a wide depth gradient from shallow (5 m) to mesophotic (60 m) depths. In total, 1627 plots of 0.35 m^2 were photographed. Analyses of benthic cover were conducted using the CoralNet web interface (https://coralnet.ucsd.edu/). In the following sections, we use existing knowledge combined with the findings from these new surveys to assess the biodiversity and ecological features of shallow reefs vs. MCEs in the GoE/A.

11.4.1 Macroalgae and Macrophytes

Fleshy algae flourish in the MCEs of Eilat and are sometimes present on top of reef structures and sandy bottoms at a higher coverage than in shallower environments (Fig. 11.6). Filamentous algal blooms occur down to 25 m depth in summers following very cold winters (Genin et al. 1995) but have never been observed in high abundance at mesophotic depths. Turf and other macroalgae were found to grow faster in shallow-water environments despite the grazing pressure by herbivorous fishes decreasing with depth (Brokovich et al. 2010b).

Another group of algae, crustose coralline algae (CCA), are among the most significant contributors to the reef structure, cementing together sediment and carbonate particles to form a stabilized complex habitat (Setchell 1930). CCA are very important to the resilience of reefs because coral larvae preferentially settle and develop on particular CCA species (Price 2010). CCA abundance on the natural mesophotic benthic habitat in Eilat is higher than on the shallow reefs (Figs. 11.6e and 11.7l).

Among the most dominant microalgae on coral reefs are the dinoflagellate symbiotic zooxanthellae. Several studies have verified the efficiency of the different clades of *Symbiodinium microadriaticum* along the depth gradient (e.g., Frade et al. 2008), especially under the very low-light conditions at mesophotic depths. Depth zonation among clades has been demonstrated in the GoE/A, with clade A being dominant in shallow corals and clade C in mesophotic corals (Daniel 2006). During reciprocal translocation experiments, no clade shifts were observed over a period of 3–5 years, with all corals retaining their original symbionts (Einbinder et al. 2016).

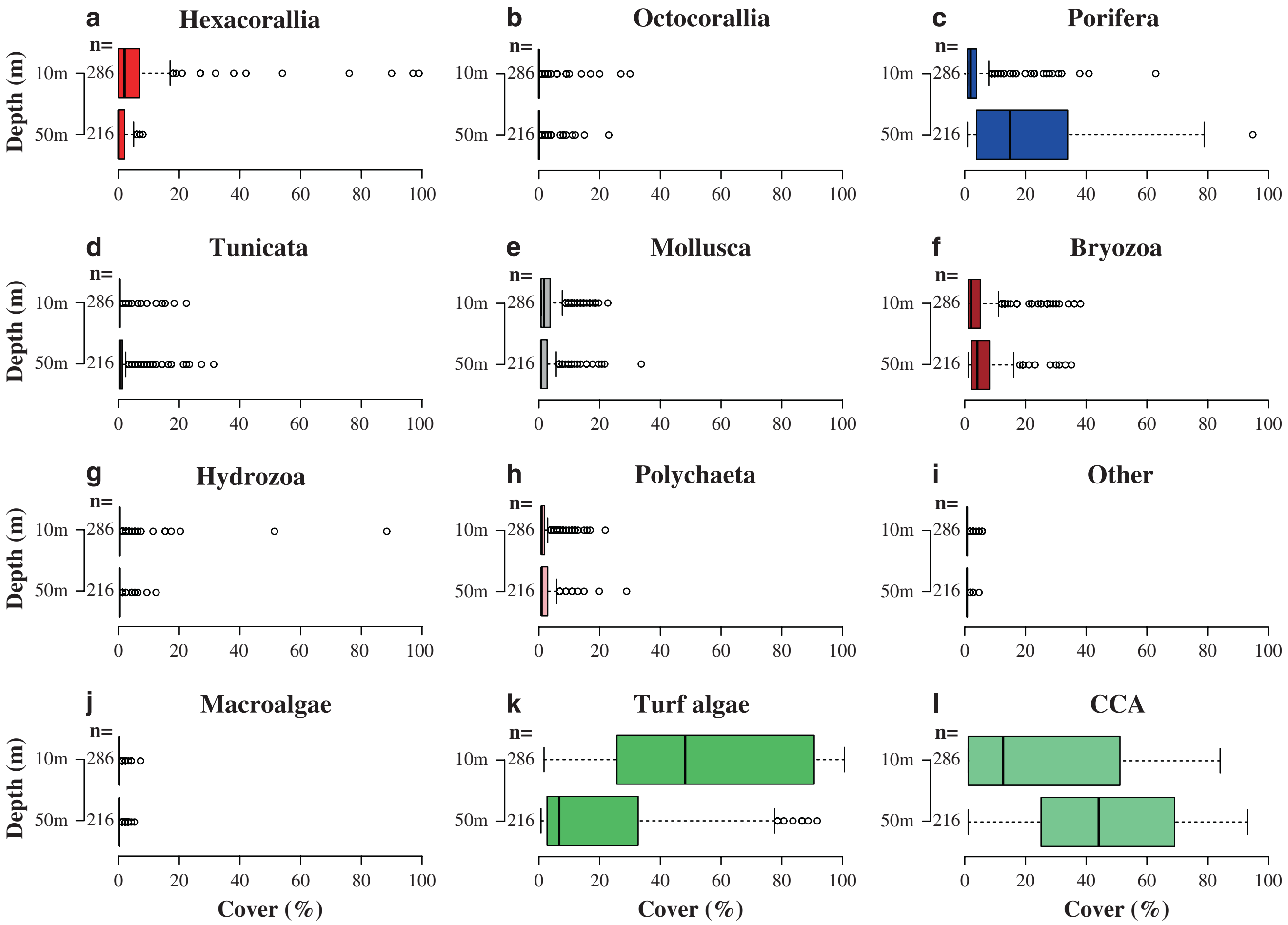

Fig. 11.7 Benthic cover of settled invertebrates on settlement tiles after 6 years (2011–2017) at shallow (10 m) and mesophotic (50 m) depths at three different sites (DB, OJ, and NR) in Eilat: (**a**) hard corals (Hexacorallia); (**b**) soft corals (Octocorallia); (**c**) sponges (Porifera), one of the dominant fauna; (**d**–**h**) other invertebrate groups, less noticeable and dominant; (**i**) other fauna; and (**j**–**l**) the main algal groups. Boxplot centerlines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5-fold of the interquartile range from the 25th and 75th percentiles; outliers are represented by blank circles. Number of sampled 20 x 20 terracotta tiles (n) indicated left of the box

Endolithic filamentous algae from the genus *Ostreobium* are found in the carbonate substrate and living skeletons of both the shallow and mesophotic corals down to 190 m depth (Fricke 1996). Genetic studies have reported depth zonation of specific clades of *O. quekettii* (Gutner-Hoch and Fine 2011). Another macrophyte found in MCEs is the seagrass *Halophila stipulacea*, which mainly occurs at depths of 10–30 m (Fig. 11.6f) but extends down to 50 m (Sharon et al. 2011; Winters et al. 2017). This exceptional depth range is possibly due to photosynthetic adaptation enabling *H. stipulacea* to alter its photosystem 1 (PSI) relative to its photosystem 2 (PSII) according to the irradiance level (Sharon et al. 2011). In addition, the algae *Colpomenia* sp., *Dictyota* sp., *Padina* sp., and *Turbinaria* sp. that dominate shallow reefs can be found in MCEs down to a depth of over 90 m.

11.4.2 Anthozoans

Scleractinian corals are the dominant habitat-forming taxon on MCEs in Eilat. Coral cover varied with depth from 5 to 60 m, and shallower depths exhibited a higher variability in coral cover between plots (Fig. 11.6a). A recent taxonomic assessment of mesophotic corals in the GoE/A revealed a relatively high diversity of 93 coral species (81 zooxanthellate and 12 azooxanthellate corals) belonging to 13 families (Eyal 2012), which is similar to the shallow reef area in Eilat (Loya and Slobodkin 1971). Preliminary findings indicate new species and new geographic records for the region (Eyal and Loya 2016). A combination of photo-acclimation and morphological adaptations facilitates the large bathymetric ranges of both depth-generalist corals, such as *D. favus* (Stambler et al. 2008; Alamaru et al. 2009), *Seriatopora hystrix* (Nir et al. 2011), and

S. pistillata (Alamaru et al. 2009; Einbinder et al. 2009, 2016; Mass et al. 2007, 2010), and depth-specialists such as *A. allingi* and *A. ocellata* (Eyal-Shaham et al. 2016), *E. paradivisa* (Eyal et al. 2016), *Leptoseris* spp. (Fricke et al. 1987; Ziegler et al. 2015), *Pachyseris* sp., and *Podabacia* sp. (Ziegler et al. 2015). A diverse range of fluorescent pigments also occur in mesophotic corals, which have been suggested to act as photo protectors in shallow environments and photosynthesis enhancers at mesophotic depths (Ben-Zvi et al. 2015; Eyal et al. 2015; Smith et al. 2017). MCEs also support azooxanthellate corals that demarcate the boundary between the euphotic and aphotic ocean (Fricke and Hottinger 1983; Fricke and Knauer 1986).

Soft corals (Octocorallia) are the second most abundant faunal group in the MCEs of Eilat. Octocorals have a moderate cover of 3–10% along the entire depth gradient but rarely cover more than 20% of the substrate (Fig. 11.6b). Shoham and Benayahu (2017) found a higher number of octocoral species in the upper mesophotic zone but similar diversity to shallow reef sites. They reported the occurrence of 21 octocoral species from MCEs, only 16% of which are shared by both shallower and mesophotic reefs (Shoham and Benayahu 2017). Additionally, new octocoral species and genera have been identified in the MCEs of the GoE/A (Benayahu et al. 2017a, b, 2019).

11.4.3 Sponges

The composition of benthic communities shifts from phototroph-dominated to primarily heterotrophic communities with increasing depth (Kahng et al. 2010), and sponges are considered among the dominant habitat-forming taxa in lower mesophotic communities (Baker et al. 2016; Turner et al. 2017). In contrast to stony corals, sponges in Eilat's MCEs flourish at depths of 60 m and probably even deeper. However, sponges do not exceed 30% cover in the upper mesophotic zone and in the majority of cases cover an area of less than 5% (Fig. 11.6c). Living sponge covers on settlement tiles examined after nearly 6 years of colonization in the upper mesophotic zone show similar patterns to the natural community. Sponge cover in MCEs exceeds that of shallow reefs by sixfold (Fig. 11.7c), accounting for 21% of the fauna at mesophotic depths. Quantitative data on species richness of sponges are sparse, but it appears that MCEs support a higher abundance and probably also a higher biodiversity (G. Eyal, pers. obs.). Most of the sponges on the settlement tiles are encrusting species (Fig. 11.8a, b), known for protecting the substrate from bioerosion.

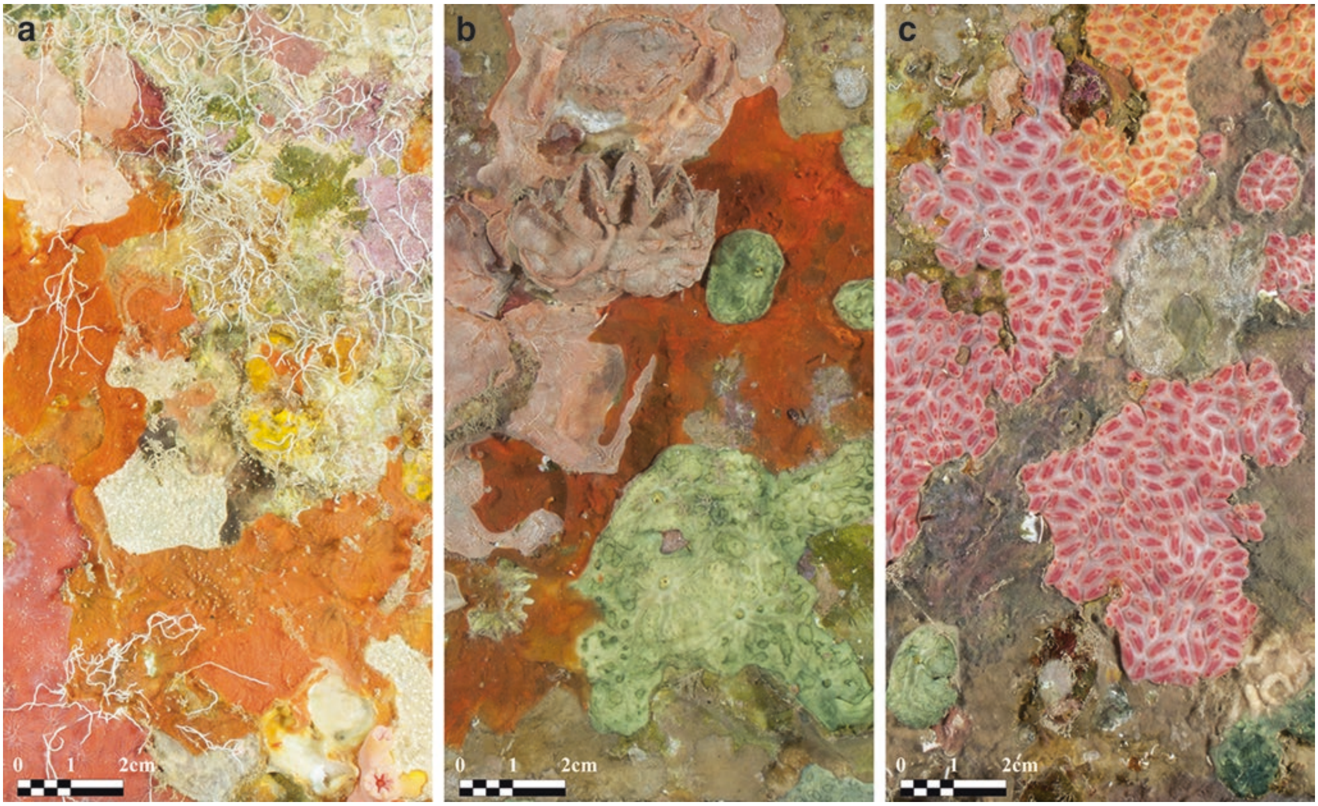

Fig. 11.8 Mosaic of Red Sea mesophotic benthic invertebrates on settlement tiles (depth 50 m). (**a**, **b**) High coverage and biodiversity of sponges and mollusks. (**c**) A generalist colonial ascidian, *Eusinstyela latericius.* (Photo credits: G. Eyal)

11.4.4 Fishes

Even though MCEs are adjacent to the shoreline, the reef fish assemblages reveal a change along the depth gradient of the Red Sea due to the steep bathymetry of the region. Changes in the benthic communities, and hence structural complexity, are likely to affect the distribution of fish species (Brokovich et al. 2008). Along the depth gradient from the shallow to mesophotic reefs, coral abundance may decrease, but sponges and other benthic organisms can provide a structurally complex habitat at mesophotic depths. This change in benthic assemblage composition was found to be correlated to a decrease in the abundance of branching corals with depth. Reef fish richness peaks at 30 m and in β-diversity between 30 and 50 to 65 m. The 30 m depth serves as a transitional zone, with representatives of both deep and shallow assemblages (Brokovich et al. 2008). MCEs also serve as a nursery for juveniles of some shallow-water species (e.g., *Genicanthus caudovittatus*), perhaps because this zone harbors fewer predators (Brokovich et al. 2007). Although fish feeding efficiency generally decreases in dim light, individuals of the zooplanktivorous damselfish (*Dascyllus marginatus*) originating from deeper habitats exhibited greater visual acuity than shallow conspecifics in an experimental low-light environment. Such adaptations could explain the ability of this and potentially other depth-generalist species to inhabit deeper reef zones (Brokovich et al. 2010a).

The abundance, biomass, and density of herbivorous fish from the families Acanthuridae and Siganidae decreased along the depth gradient in the GoE/A, potentially resulting in reduced grazing pressure on MCEs (Brokovich et al. 2010b). Herbivory plays an important role on coral reefs by mediating competition between the fast-growing algae and the relatively slower-growing stony corals. Lower grazing pressure likely explains the increased algae cover at mesophotic depths, with algae becoming the dominant benthic group at 50–60 m depth (Fig. 11.6e). Algae dominated all available substrate, probably due to the low light available for photosynthesis and the small amount of herbivory that still takes place at this depth. Although MCEs in Eilat are low in predatory fishes in general (Brokovich et al. 2008), some localities host permanent (year-round) aggregations of predators such as the blacktip grouper (*Epinephelus fasciatus*), with hundreds of individuals aggregating over a few dozen cubic meters (Fig. 11.5f).

11.4.5 Other Biotic Components

Other invertebrate groups are known to occur on MCEs in the GoE/A, although they constitute only minor benthic components (Fig. 11.6d). Organisms such as various worms (Wielgus et al. 2006), sea cucumbers (Cherbonnier 1980), sea urchins, and starfish (Dafni 2008) can be found across a wide depth range in the GoE/A, including on MCEs.

No quantitative data are available on the abundance of these groups in MCEs. However, the percentage cover of certain groups has been calculated on settlement tiles following nearly 6 years of deployment (Kramer et al. 2019). These groups mostly belong to the cryptofauna (species that inhabit the hidden sides of foliaceous corals or cave-like environments) and play an important ecological role as bioeroders (Glynn and Manzello 2015; Weinstein et al. 2019), consuming benthic biomass and constituting important prey for fish and upper trophic level organisms. The mesophotic tiles varied in their percent cover of fauna such as worms (1.7%), ascidians (2.1%), bryozoans (4.8%), and mollusks (2.4%), with similar trends between depths among these groups in percent cover of total fauna (Fig. 11.7). However, 79% of the total 2.1% ascidian cover (i.e., shallow and mesophotic) were recruited on the mesophotic tiles (i.e., 1.66% cover on the mesophotic tiles), which suggests that ascidians either have a higher abundance or faster growth rates in deeper waters than in the shallows (Kramer et al. 2019). Generalist invertebrates, including colonial ascidians such as *Eusinstyela latericius* (Fig. 11.8c), display a seasonal variability in abundance (Shenkar et al. 2008).

11.5 Ecology

The first ecological studies of MCEs in the region were conducted from submersibles and included descriptive and manipulative experiments (Fricke 1996). These studies provided some of the first observations in the world of mesophotic corals in the lower mesophotic zone and present ecological data on the depth limits of phototrophic Scleractinia (Fricke and Schuhmacher 1983), spatial patterns and diversity of mesophotic corals (Fricke and Knauer 1986), coral bioherms in the lower mesophotic zone and in the deep sea (Fricke and Hottinger 1983), photoecology and light harvesting of MCE corals (Schlichter et al. 1986; Fricke et al. 1987; Schlichter and Fricke 1990, 1991), and adaptation of zooxanthellae to mesophotic depths (Kaiser et al. 1993).

More recently, researchers began using technical open-circuit SCUBA, CCRs, and remotely operated vehicles (ROVs) to study MCEs. These technologies have expanded the potential scope of MCE research to include fish ecology and biodiversity (Brokovich et al. 2008, 2010a, b); coral morphology and diet (Alamaru et al. 2009; Einbinder et al. 2009; Nir et al. 2011); coral metabolism, photosynthesis, and calcification (Mass et al. 2007, 2010; Nir et al. 2014; Einbinder et al. 2016; Eyal et al. 2016); coral reproduction (Eyal-Shaham et al. 2016; Feldman et al. 2018; Shlesinger and Loya 2019; Shlesinger et al. 2018); coral competition and survival (Ben-Zvi et al. 2015; Eyal et al. 2016); and biodiversity of benthic organisms (Eyal 2012; Eyal et al. 2015; Eyal and Loya 2016; Benayahu et al. 2017a, b; Shoham and Benayahu 2017).

11.6 Threats and Conservation Issues

The towns of Eilat and Aqaba, located on the northernmost coast of the GoE/A, are both large population centers with significant infrastructure development. Extensive areas of reef have been destroyed as a result of multiple factors, including recreational diving (Wilhelmsson et al. 1998), sewage spills (Loya 2004), oil spills (Loya and Rinkevich 1980), port activities (Loya 1976), phosphorus and fine particle enrichment (Loya 2007), net-pen fish cages, garbage and urbanization (Loya 2004, 2007), and light pollution (Tamir et al. 2017), as well as natural disturbances such as algal blooms (Genin et al. 1995), extreme low tides (Loya 1976), flash floods (Katz et al. 2015; Andradi-Brown et al. 2016), and severe storms (Eyal et al. 2011).

The shallow corals of Eilat are considered heat tolerant and resilient to thermal stress (Fine et al. 2013; Krueger et al. 2017) and have been described as “super corals” that are resistant to natural bleaching (Grottoli et al. 2017). Nevertheless, *S. pistillata*, the most abundant generalist coral in the coral reefs of Eilat, suffers from periodic nonfatal bleaching in the summer months at 40–60 m depth (Nir et al. 2014). Recently, we observed, for the first time, mass coral bleaching in the MCEs of Eilat (G. Eyal, pers. obs.), which occurred toward the end of summer 2015 at 45–60 m depth. This event affected several depth-generalist coral species that have never been observed to bleach on shallow reefs but mostly affected MCE specialists (Fig. 11.9). Some of the affected corals fully recovered after a few months, but most of the severely (> 50%) bleached colonies eventually died (e.g., Fig. 11.9b–d). One possible explanation for this exclusively deep-water bleaching is inherent within the hypothesis of the Northern Red Sea being a bleaching refuge (Fine et al. 2013), which suggests that the shallow corals of Eilat are less susceptible to thermal stress bleaching due to a selective heat barrier at the southernmost end of the Red Sea over the last millennia. Hence, propagules of deeper taxa, crossing the Bab-el-Mandeb straits (depth of 137 m) at a deeper depth and settling in the MCEs, do not necessarily experience this thermal barrier found in shallower water and, consequently, are not genetically selected for elevated temperatures. These findings put into question the hypothetical connectivity between MCEs and their shallow-water coral counterparts in the Northern Red Sea (e.g., Bongaerts et al. 2010, 2017; Bongaerts and Smith 2019). Furthermore, it raises the possibility that mesophotic coral species are more susceptible to bleaching than their shallow counterparts in the northern GoE/A, although this could also be a combined effect of rising temperature and increasing light intensity.

Storms and waves generally do not directly affect MCEs in the GoE/A. However, periodic flash flood events can cover both the shallow and mesophotic reefs with fine, clastic, and organic-rich materials that impact the benthic biota directly by covering the substrate and indirectly by reducing light for photosynthetic organisms and loading the deeper water with terrestrial nutrients (Katz et al. 2015). The oligotrophic nature of the GoE/A enables coral reefs to flourish in this high latitudinal area. At the same time, the high nutrient levels in the deep sea in the region vertically mix almost every year and create massive phytoplankton blooms in the open sea, which in turn affects water and light quality (Genin et al. 1995; Zarubin et al. 2017).

In Eilat, only a small portion of MCEs are protected as a nature reserve (Fig. 11.1d). In 2009, an expansion of the nature reserve from the shore to 500 m offshore, which included part of the MCEs present, was authorized by the Israel Nature and Park Authority following a detailed scientific evaluation (Bridge et al. 2013). Today, the nature reserve covers approximately 1.3 km^2 of protected area down to a depth of only 80 m, which is ca. 12.7% of the Israeli Red Sea marine area from shore to 150 m depth (see Fig. 11.1d, e). Hence, a major part of the MCEs in Eilat (ca. 87%) are still unprotected and severely impacted by many stressors, such as garbage, fishing, fishing accessories, boat and anchoring aids, port activities, military activities, and more. Consequently, the implementation of protection plans for these important ecosystems is crucial to conserve the gene pool and biodiversity of all the coral reef ecosystems and specifically those of MCEs, for possible future reseeding of lost species from both the shallow and mesophotic depths.

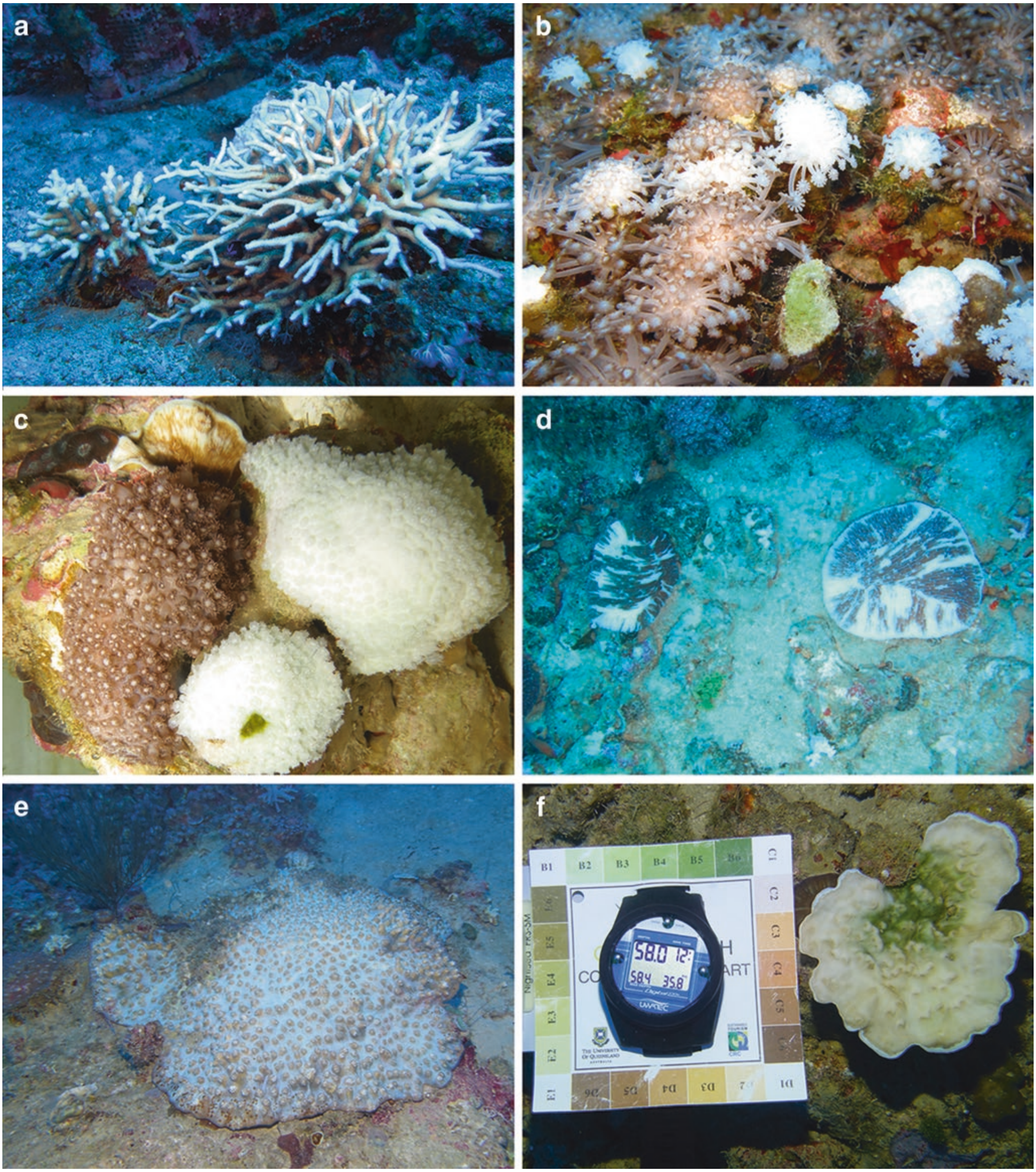

Fig. 11.9 Partially bleached generalist corals (found at 1–76 m depth) and specialist corals (found strictly in the deep reef) in the northern GoE/A: (**a**) specialist *Stylophora kuehlmanni* (right) and generalist *S. pistillata* side by side at a depth of 45 m; (**b**) specialist *Alveopora allingi* at 55 m depth; bleached and non-bleached colonies side by side; (**c**) specialist *Goniopora minor* at 60 m depth; bleached and non-bleached colonies side by side; (**d**) generalist *Herpolitha limax* at 50 m depth; (**e**) large colony (~1 m diameter) of the generalist *Echinopora* sp. at 60 m depth; and (**f**) specialist *Leptoseris glabra* with a notable appearance of endolithic algae in the middle of the colony at 58 m depth. (Photo credits: G. Eyal)

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