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Selective deep water coral bleaching occurs through depth isolation

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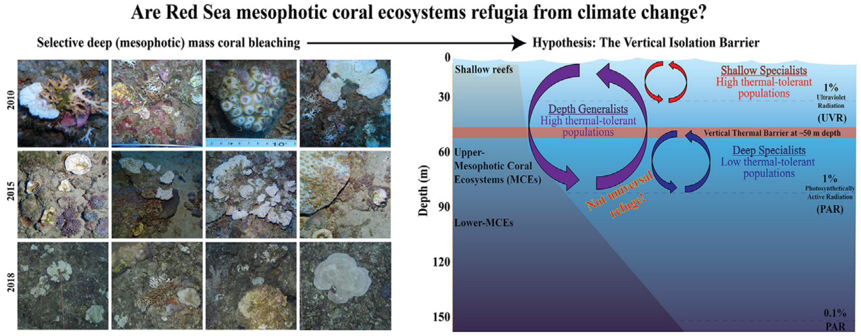
HIGHLIGHTS

- Mesophotic communities are not immune from coral bleaching, are in danger, and are degrading in the Red Sea.
- Heat accumulation at mesophotic depths is almost twofold higher than on adjacent shallow reefs.
- Bleaching events affect the deep-specialist coral populations, with ~50% coral community mortality at 60 m depth.
- The deeper benthic community lost framework builders, may result in lower complexity, fewer niches, and loss of biodiversity.
- Experimental evidence suggests that deep-specialist corals are less tolerant of heat stress and bleach more readily.

GRAPHICAL ABSTRACT

Mesophotic communities in the Red Sea are not immune from mass coral bleaching, are in danger, and are degrading over the last decade with 3 major bleaching events. Vertical isolation between shallow-specialist and deep-specialist corals structure three observed depth-based communities along a depth gradient, with different thermal-tolerance capabilities. Depths shallower than ~50 m act as a vertical high-temperature barrierwhich restricts deep-specialist taxa to the deeper zone only.



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ABSTRACT

Climate change is degrading coral reefs around the world. Mass coral bleaching events have become more frequent in recent decades, leading to dramatic declines in coral cover. Mesophotic coral ecosystems (30–150 m depth) comprise an estimated 50–80 % of global coral reef area. The potential for these to act as refuges from climate change is unresolved. Here, we report three mesophotic-specific coral bleaching events in the northern Red Sea over the course of eight years. Over the last decade, faster temperature increases at mesophotic depths resulted in ~50 % decline in coral populations, while the adjacent shallow coral reefs remained intact. Further, community structure shifted from hard coral dominated to turf algae dominated throughout these recurrent bleaching events. Our results do not falsify the notion of the northern Red Sea as a thermal refuge for shallow coral reefs, but question the capacity of mesophotic ecosystems to act as a universal tropical refuge.

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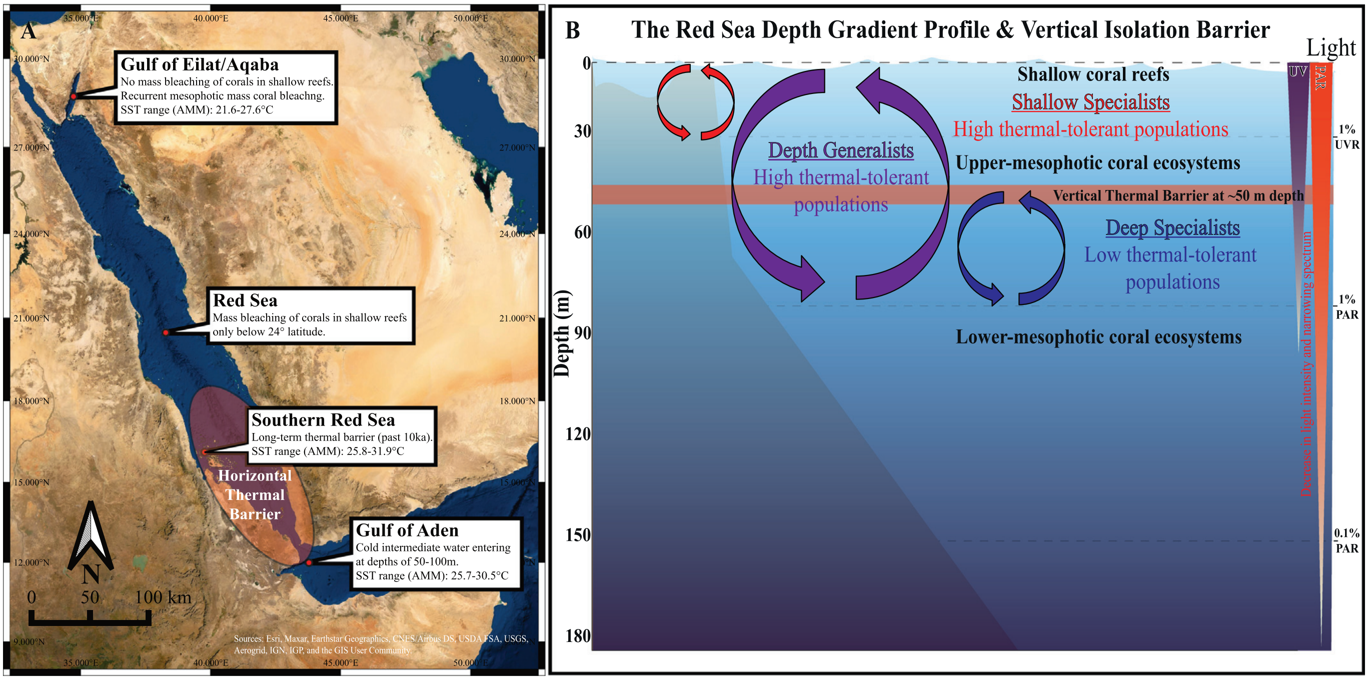
1. Introduction

Coral bleaching is one of the greatest contributors to global coral reef decline (Hughes et al., 2018). Reefs worldwide are experiencing severe degradation, most recently due to anthropogenic-induced thermal stress. However, shallow coral reefs (i.e., 0–30 m depth) in the high-latitude northern sections of the Red Sea are posited to be a refuge from ocean warming (Osman et al., 2018). Hermatypic (reef-building) corals in the northern Red Sea are recorded along a wide depth gradient down to 145 m (Fricke and Schuhmacher, 1983). Coral reefs flourish at shallow and mesophotic depths (i.e., 30–150 m depth) due to the clarity of the oligotrophic water in the region (Eyal et al., 2019). Globally, deeper light-dependent coral ecosystems are suggested to be less susceptible to coral bleaching due to the lower temperatures, reduced irradiance, and atmospheric effects with increasing depth (Glynn, 1996, Lesser et al., 2009). The lack of knowledge about mesophotic ecosystems signifies a large gap in our understanding of coral reefs globally, including the northern Red Sea coral reefs (Loya et al., 2016).

The Red Sea basin is around 2000 km long and 230 km wide (Fig. 1A). It diverges into the Gulf of Suez and the Gulf of Eilat/Aqaba in the north and is connected to the Gulf of Aden via the Bab el Mandeb straits in the south. The Bab el Mandeb straits are relatively shallow (~137 m deep) and are divided by Perim Island into a smaller and larger channel. Most of the water circulation is facilitated by the larger channel and the flow pattern is controlled by a sill situated at the northernmost part of the straits. The basic circulation pattern involves an inflow of water adjacent to the surface from the Gulf of Aden through the Bab el Mandeb straits and outflow through the bottom of the sill (Siedler, 1969; Siddall et al., 2004). New Gulf of Aden Surface Water (GASW; water from the surface of the Indian Ocean) enters the southern Red Sea via the straits, flows northward, and undergoes large rates of evaporation to form Red Sea Water (RSW) in the northernmost section. This results in hot and saline Red Sea Deep Water (RSDW; ~21.5 °C and 41 ‰, respectively) along the entire basin, as it is isolated from the oceanic global water circulation. This in turn creates uniquely appropriate environmental conditions for the development of productive coral reefs at a latitude of ~30° north, despite vertical deep-mixing events in the area (Genin et al., 1995). RSW flows south as a salty, high-density layer of cold water, yet below this layer, a relatively stationary layer of denser RSDW remains. Depending on the season, the mode of Red Sea water exchange with the Indian Ocean differs. During the winter, GASW enters above the layer of RSW forming a dominant 2-layer system and the RSDW exits the Red Sea at a slower rate than normal. During the summer, at the same time of the year in which most corals reproduce in the Red Sea (Shlesinger and Loya, 1985), the level of Gulf of Aden Intermediate Water (GAIW) increases and penetrates the southern part of the Red Sea as an intermediate layer. This layer persists for a few months before merging with the upper layer of RSW (Siddall et al., 2004). The cold (16–19 °C) GAIW enters the Red Sea at depths of 50–100 m in the straits of Perim-Bab el Mandeb (Maillard and Soliman, 1986; Sofianos et al., 2002).

During the Last Glacial Maximum (LGM) event that ended ~10 thousand years ago, global sea level fell by at least 120 m. The water depth in Bab el Mandeb sill dropped to <15 m, thereby restricting the volume of GASW entering the Red Sea from the Indian Ocean (Siddall et al., 2003). Subsequent evaporation increased salinity to levels likely inhospitable to corals (Sirocko, 2003, Biton et al., 2008). During this period of hyper salinity, there was an accumulation of organic-rich sediments and a humid climate persisted (Arz et al., 2003). Over the past 6–8 thousand years, after sea-level rose to present-day levels, corals started to recolonise the basin. Since then the climate has been predominantly dry, with super oligotrophic water. These conditions allowed the proliferation and growth of coral reefs across the Red Sea coastal waters (Thunell et al., 1988; Arz et al., 2003). A horizontal thermal barrier at the southern section of the Red Sea (Fig. 1A) is hypothesized to have created positive selection pressure for taxa resistant to high temperatures when colonizing the northern reefs after the sealevel rose (Fine et al., 2013). This horizontal thermal barrier in the shallow waters (< 50 m depth) of the southern Red Sea likely still exists because of the unique climatological conditions and oceanography of the region. The barrier may continue to shape a unique, thermally-tolerant coral



Sources: Esri, Maxar, Earthstar Geographics, CNES/Airbus DS, USDA FSA, USGS, Aerogrid, IGN, IGP, and the GIS User Community.

Fig. 1. Vertical isolation between shallow-specialist and deep-specialist corals in the Red Sea. (A) Map of the Red Sea indicating the cooler high-latitude Gulf of Eilat/Aqaba; the eight-thousand-year-old horizontal thermal barrier in the southern Red Sea; and the connection to the Indian Ocean through the Gulf of Aden's narrow and shallow sill of Bab al-Mandab's straits. Average monthly mean (AMM) temperature ranges were collected from NOAA Coral Reef Watch database (NOAA Coral Reef Watch, 2021). Map template (World Imagery base map) used in QGIS (QGIS.org, 2021). (B) Schematic illustration of the three observed depth-based communities along a depth gradient with hypothesized thermal-tolerance capabilities. Depths shallower than 50 m act as a vertical high-temperature barrier which restricts deep-specialist taxa to the deeper zone. Zonation by light boundaries calculated after Laverick et al. (2020).

community in shallow waters (Fine et al., 2013; Osman et al., 2018). Accordingly, a mass coral bleaching event has never been reported from reefs of the northern Red Sea, despite severe recurring bleaching on many reefs worldwide, including the warmer shallow water of the southern Red Sea (Furby et al., 2013; Osman et al., 2018).

Below this horizontal thermal barrier at the southern Red Sea, Mesophotic Coral Ecosystems (MCEs) exist (Fig. 1B). MCEs located between depths of 30–150 m, are generally considered less likely to suffer coral bleaching than their shallow water counterparts. The deep-reef-refugia hypothesis (DRRH) has proposed MCEs may serve as possible refugia for shallow water taxa, as deeper waters are thought to be protected from stressors and disturbance (Bongaerts et al., 2010). Studies investigating the DRRH suggest it only applies in specific cases (Bongaerts et al., 2017; Frade et al., 2018), and MCEs are in fact threatened by various anthropogenic, climatic, and natural disturbances similarly to shallow reefs (Smith et al., 2016; Rocha et al., 2018; Pinheiro et al., 2019, de Oliveira Soares et al., 2020). The frequency and intensity of such disturbances, however, decrease with depth in the northern Red Sea (Eyal et al., 2019).

The geological history, and the resultant environmental conditions of the Red Sea, provide the conditions for possible vertical isolation along the depth gradient and a hypothetical mechanism for the stratified patterns we observe in coral bleaching (Fig. 1B). We report on long-term field observations and in situ monitoring that captures deep water mass coral bleaching and the impact it has on the mesophotic coral ecosystem in the northern Red Sea. We used a multidisciplinary approach of: repetitive benthic surveys, long-term environmental monitoring, in situ analyses of coral physiological performance, and manipulative heat stress experiments to understand how selective coral bleaching occured in the deep environment.

2. Methods

2.1. Long-term environmental conditions

For almost two decades the Israeli National Monitoring Program (NMP) of the Gulf of Eilat has monitored the meteorological conditions, oceanographical regimes, and ecological status of coral reefs in the northern Red Sea (Shaked and Genin, 2020). Shallow water (~2 m depth) in situ temperature measurements were recorded at 10 min intervals. Monthly conductivity, temperature, and depth (CTD) profiler casts were performed along the entire depth gradient down to ~700 m, approximately 4 km from the reef (Fig. S1). For this research, we deployed additional in situ temperature loggers at 3 m, 5–10 m and 45–50 m for the entire period of July 21st 2011 to September 1st 2017 and at 60 m for the summer period of 2018, from July 11th to September 5th, on the reef in front of the Interuniversity Institute for Marine Sciences (IUI) (Fig. S1). Temperature was further analyzed for thermal dynamics from both NMP data and our loggers.

In addition to in situ measurements, we also retrieved daily remote-sensing sea-surface temperature (SST) data for the last 35 years at the Gulf of Eilat/Aqaba. We used the 5 km Regional Bleaching Heat Stress Time Series data product (Version 3.1) (NOAA Coral Reef Watch, 2021) to calculate regional SST thermal dynamics and compared them to the local in situ measurements to quantify measurement error and cross-correlation coefficients.

To determine the long-term Maximum Monthly Mean (MMM) for our open ocean CTD measurments, we took the hottest temperature in August during 2003–2019 and averaged those temperatures by depth bin to get the MMM per depth bin. We used the MMM determined over this period for the in situ data as well, for example, the MMM determined for the depth bin 49-62 m from the CTD was applied to the 45-50 m in situ logged data.

2.2. Bleaching observations and quantification

Mesophotic benthic observations at 50–65 m depth were conducted annually from June 2010 to December 2020. When coral mass bleaching became apparent at the end of 2010, 2015 and 2018, we conducted photographic surveys of 30–32 quadrat plots of 0.35 m^2 in front of the Interuniversity Institute for Marine Sciences in Eilat (IUI). All surveys were done by SCUBA using closed circuit rebreathers (CCRs) or open-circuit apparatuses. Survey photos were annotated in CoralNet (Beijbom et al., 2012), with 100 sampling points per photo in two stages, first to quantify benthic community structure using percent cover of major benthic groups, and second to quantify the percentage cover of bleached, partially bleached, and non-bleached coral colonies. Anecdotal bleaching observations were recorded for 2019 (N. Kramer, personal observation) and 2020 (Y. Lindemann, personal observation), but these were not quantitative surveys.

2.3. Temporal changes in benthic community composition and coral morphotype cover

Shifts in benthic communities were visualized using non-parametric multidimensional scaling (nMDS) using a Bray-Curtis dissimilarity matrix of square-root transformed cover data. Seven ecologically important benthic groups were included in the analysis: hard corals, soft corals, sponges, macroalgae, turf algae, crustose coralline algae (CCA), and black corals. We performed a multiple permutational analysis of variance (PERMANOVA) to determine significant differences in benthic composition among years. Pairwise PERMANOVA was used to identify significant differences among years.

Stacked bar charts were used to illustrate relative changes in the percent cover for each of the mass bleaching years (2010, 2015 and 2018) for the morphological groups (branching, encrusting, massive, and plate-like) according to their health status (bleached, partially bleached, and non-bleached). Due to violations of parametric test assumptions (e.g., normality and homogeneity of variances), we used a permutational ANOVA approach to assess differences in percent cover among years, morphotypes, and health status. When significant differences were found, permutational *t*-tests (999 permutations) were applied. All the analyses were performed in the R programming environment (Team, 2013), using the *vegan* (Oksanen et al., 2013), *RVAideMemoire* (Hervé and Hervé, 2020), and *lme4* (Bates et al., 2007) packages.

2.4. Physiological capacity of depth-generalists and deep-specialists corals to thermal stress

To assess the photosynthetic performance of mesophotic corals during the mass bleaching event of 2018, we used an underwater pulse amplitude modulated fluorometer (Diving-PAM; Walz GmbH, Germany) to conduct in situ rapid light-curve measurements at 60 m. During early morning, with ambient light of 30 μmol photons m^{-2} s^{-1}, the Diving-PAM was used to measure and calculate the effective quantum yield of photosystem- II (Y[II]), non-photochemical quenching (NPQ), and the approximate relative electron transport rate (rETR). Four bleached colonies of *Leptoseris glabra* (deep-specialist species) and four non-bleached colonies of *Porites lutea* (depth-generalist) corals were assessed. Non-bleached colonies of *Leptoseris glabra* could not be found. Chlorophyll *a* fluorescence was measured following a light saturation pulse (>4000 μmol photons m^{-2} s^{-1}, white light, 500 ms) after 2.5 min incubation at increasing actinic light intensities (30, 250, 340, 480, 640, 930, 1310, 1890 and 2950 μmol photons m^{-2} s^{-1}). Although corals at 60 m will never experience such high intensities, we found it important to measure the depth-generalist corals under these levels. We were not sure how sensitive depth-generalists are to light intensity and were concerned they may harbor shallow water symbionts. To get fair and comparable curves between taxa we used the same induction light levels on all corals, regardless of the risk of photoinhibition with high intensities. The main purpose of the light-curves was to compare between the two groups (bleached and non-bleached corals) at a constant mesophotic depth. The Diving-PAM setup parameters (gain and measuring intensity) were adjusted according to the F_0 of each colony, followed by an auto zero and stabilasing of the F_0 before light curve started. In paled and bleached colonies, we occasionally used the highest sensitivity of the device (levels 12) to get a proper signal of F_0 (always above 130 and preferably between 300 and 700).

In 2016, when deep water bleaching did not occur, we conducted aquaria-based thermal experiments on deep-specialist and depth-generalists corals. Six colonies of *L. glabra* (deep-specialist) were sampled (permit no. 2016/41525) at 50 m depth, and seven colonies each of *P. lutea* and *Montipora danae* (depth-generalists; permit no. 2016/41528) were collected at 10 m depth at the reef in front of the IUI. All colonies were broken into 4 × 4 cm fragments, resulting in n = 44, 32, and 29 fragments of L. *glabra*, *P. lutea*, and *M. danae*, respectively. Each fragment was glued to a 5 × 5 cm unglazed terracotta tile using underwater non-toxic epoxy glue. Corals were kept in the running sea water system at the IUI. L. *glabra* fragments were kept under a light barrier filter ("Lagoon blue", LeeFilters, UK) to mimic the mesophotic light environment at 50 m depth. Corals were randomly placed under ambient light in one of two treatments for 14 days: ambient sea temperature (AT; 25 °C equivalent to the MMM at 50 m), and high temperature (HT; +4 °C above ambient sea temperature, equivalent tothe MMM + 4 °C at 50 m). Water in the HT treatment was heated by 1 °C per day, reaching 29 °C, using three submersible aquarium heaters (250 W, Aqua One, China). Temperature and light intensity were recorded during the experiment using HOBO pendant temperature and light data loggers (Onset, USA) at 5 min intervals. Corals were imaged from a top view at days 1 (T_0), 5 (T_1), 10 (T_2), and 13 (T_3) next to the "Coral Health Chart" (CoralWatch, Australia) for colour indication (Siebeck et al., 2006). Maximal photosynthetic yield (F_v/F_m) was measured (n = 3 measurements for each fragment at each sampling point) using the Diving-PAM on the same days (i.e., T_0-T_3) an hour after sunset to assure all photosystem-II reaction centres were vacant. In 2016, we conducted aquaria experiments only and not in situ PAM surveys. Instead, we used the Diving-PAM to verify the maximal quantum yield (Fv/Fm) of several species under temperature stress in aquaria, not in the field. In 2018 we were not able to get a permit for collecting colonies, so we used light-curves as a non-extractive method of assessment of the photobiology of these corals.

3. Results

Despite the hypothesized Red Sea refuge (Fine et al., 2013) and the DRRH (Bongaerts, Ridgway et al. 2010), we report observed repetitive, severe, mass coral bleaching events on the MCEs of the northern Red Sea. These events took place in three non-consecutive years in the last decade: 2010, 2015 and 2018 (Fig. 2A) and were also observed, but not quantified, in 2019 and 2020 (Extended Data Fig. S2). These mesophotic-specific coral bleaching events corresponded with sharp temperature increases at mesophotic depths (Table 1; Fig. 2) and resulted in a large decline in coral populations over the last decade (Fig. 3A,B). The events were species-specific and mostly affected the specialized deep hermatypic corals displaying plate-like (tabular/foliose/laminar) growth forms, but also impacted other coral morphotypes (Fig. 3B; Fig. S2). Further, community structure shifted to lower hard-coral and higher turf-algae cover throughout these recurrent bleaching events (Fig. 3A).

The exposure of the mesopotic corals to increased thermal stress has resulted in significant community-level changes (PERMANOVA, F = 63.056,

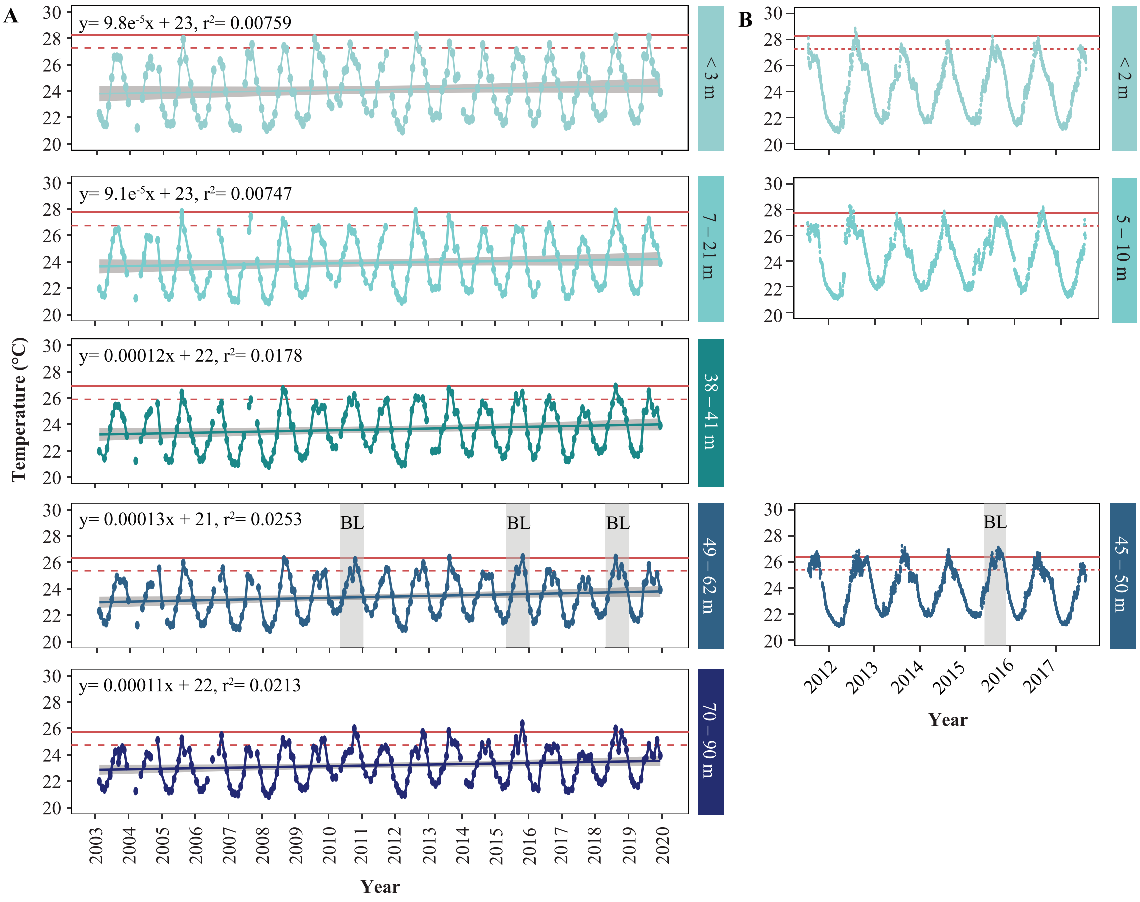


Fig. 2. Open ocean and in situ temperature monitoring adjacent to the bleached ecosystem. (A) Open ocean monthly temperature data from 2003 to 2019 collected by the Israeli National Monitoring Program of the Gulf of Eilat (NPM; Shaked and Genin, 2020). Trendlines show a consistent rise in temperature at all depth bins, with a steeper increase at depths below 38 m. (B) High-frequency (10-min interval) in situ temperature data over seven years at the study site. BL and grey transparent bars represent bleaching events in mesophotic depths; dashed red lines represent the averaged maximum monthly mean (MMM) and full red lines represent the bleaching threshold as MMM + 1 °C for each depth bin.

Table 1
In situ temperature data from the northern Red Sea. Data collected adjacent to the Interuniversity Institute of Eilat by HOBO temperature loggers during seven years and is presented annually.

Year	Depth (m)	Mean (°C)	SE	Minimum (°C)	Maximum (°C)	Mean daily amplitude (°C)	SE	Degree heating weeks	Degree heating days
2011[a]	2	25.061	0.139	21.713	28.112	0.605	0.033	0	0
	5–10	24.949	0.145	21.826	26.977	0.782	0.020	0	0
	45–50	24.871	0.120	21.991	26.731	0.543	0.034	3.24	15
2012	2	24.170	0.127	20.841	28.853	0.787	0.030	0	5
	5–10	23.988	0.119	21.063	28.284	0.839	0.021	2.32	10
	45–50	23.731	0.102	21.056	26.851	0.489	0.026	1.94	8
2013	2	24.154	0.093	21.554	27.637	0.753	0.027	0	0
	5–10	24.180	0.087	21.728	27.698	0.712	0.013	0	0
	45–50	23.985	0.079	21.822	27.215	0.414	0.020	**5.22**[c]	22
2014	2	24.008	0.095	21.601	27.916	0.771	0.028	0	0
	5–10	24.006	0.087	21.714	27.860	0.786	0.013	0.17	1
	45–50	23.799	0.074	21.819	26.910	0.364	0.015	2.41	12
2015	2	24.289	0.109	21.450	28.242	0.767	0.028	0	0
	5–10	25.080	0.084	21.762	27.462	1.903	0.065	0	0
	45–50	24.052	0.093	21.722	27.074	0.471	0.018	**8.75**[c]	49
2016	2	24.314	0.102	21.374	28.115	0.882	0.031	0	0
	5–10	24.452	0.096	21.502	28.186	1.286	0.036	0.35	7
	45–50	23.867	0.079	21.564	26.685	0.539	0.020	1.81	11
2017[b]	2	23.526	0.137	21.114	27.505	0.957	0.037	0	0
	5–10	23.673	0.140	21.209	27.436	1.266	0.025	0	0
	45–50	22.886	0.098	21.162	25.816	0.370	0.021	0	0

[a] Starting date of 21st July 2011.

[b] To end date of 1st September 2017.

[c] High thermal stress > 4 DHW.

$p < 0.001$). Specifically, a 46 % decline in hard coral cover between 2010 and 2018 was observed in response to the mass bleaching events (Fig. 3A). Consequently, these communities are no longer dominated by hard corals and have shifted toward turf algae throughout the decade. While there can be other causes of coral mortality within mesophotic ecosystems (Rocha et al., 2018), none have been observed to induce such a change in community structure. Substantial differences in coral cover were found between years and among hard coral morphological groups (permutational ANOVA, $F_{YEAR} = 9.429$, $F_{MORPH} = 30.528$, $p < 0.001$). Throughout the last decade, plate-like corals were the most affected by bleaching, as indicated by a decline in coral cover (Fig. 3B). In 2010, nearly three-quarters (73.8 %) of all coral colonies were either fully or partially bleached. Of the bleached colonies, plate-like corals were bleached at least three-fold more than any other morphological group (Fig. 3B). Despite the reduced abundance of these corals over time, plate-like corals continued to show a high bleaching proportion, compared to other morphological groups, in both 2015 and 2018 (Fig. 3B). These findings suggest that the ability of plate-like corals and possibly other deep-specialist corals to persist at mesophotic depths might be jeopardised by ongoing bleaching events.

Water temperatures have increased sharply over the last two decades in the northern Red Sea, in both bleaching-affected reefs as well as the adjacent non-affected shallow reefs (Table 1; Fig. 2). Monthly measurements taken by the Israel National Monitoring Program at the Gulf of Eilat (NMP) (Shaked and Genin, 2020) show that deeper water layers (below 38 m depth) are warming at a faster rate than shallower water layers (0–21 m). The highest increase per decade was observed within 49–62 m (+0.48 °C) compared to an increase of +0.31 °C between 7 and 21 m (Fig. 2A) and to global average increases of +0.18–0.19 °C per decade (Dunn et al., 2020). As a result, degree heating weeks (DHW) accumulated mostly in the deep-water environment, with temperatures passing the threshold for bleaching (Glynn and D'croz, 1990) in the summer for six of the seven years that we measured (Table 1; Fig. 2B). In the shallow depths, temperature records were generally below the bleaching threshold, or exceeded it for short periods (Table 1 - 'Degree heating days'; Fig. 2B). From our seven years of in situ high-resolution temperature measurements, DHW crossed the assumed coral mortality threshold (i.e., DHW > 8 °C week^{-1}) (Kayanne, 2017) only in 2015 at the 45–50 m depth. Currently, thermal stress on coral reefs is identified globally by remote sensing (e.g. (NOAA Coral Reef Watch, 2021), which does not detect temperatures below 10 m depth (Heron, Heron et al., 2013). We found discrepancies between our in situ shallow and deep temperature measurements and DHW calculated from remote sensing data (NOAA Coral Reef Watch, 2021), which highlights the inability to identify thermal stress in deeper environments without in situ temperature measurments (Tables 1, 2; Fig. 2; Figs. S3, S4, S5, S6).

In addition to trends in temperature, we found evidence that some deep-specialist corals are more vulnerable to changes in temperature and performed less efficiently physiologically during bleaching in both field and laboratory conditions (Figs. S7, S8). In situ photosynthetic performance measurements taken at 60 m depth during the 2018 bleaching event showed a 37.1 ± 9.8 % (mean ± SD) lower effective quantum yield of photosystem II (Y[II]), 46 ± 9.1 % higher non-photochemical quenching (NPQ), and 42 ± 9.2 % lower relative electron transport rates (rETR) for selected bleached deep-specialist corals compared to non-bleached depth-generalist corals (Fig. S7). Apparently, for both taxa assessed photoinhibition started around the same light intensity level (~1000 μmoles photons m^{-2} s^{-1}) regardless of the lower rETRmax of the deep-specialist corals. Furthermore, when experimentally testing the response of the deep-specialist coral *Leptoseris glabra* from 50 m to thermal stress compared to two depth-generalist coral species (*Porites lutea* and *Montipora danae*) from the shallow reef, we observed, in L. *glabra*, a significant decrease of 57 % in maximal quantum yield of photosystem II (F_v/F_m). This was accompanied by visually apparent bleaching after only nine days exposure to +4 °C above the averaged maximum monthly mean (MMM) at this depth (Fig. S8).

4. Discussion

Accurate data on the temporal patterns of coral bleaching are essential, both for understanding how coral ecosystems are being altered and predicting their future in an era of continuing climate change. The history of past coral bleaching events in most regions of the world is increasingly documented but is poorly studied in the northern Red Sea (Hughes et al., 2018, Monroe et al., 2018). This is especially true on MCEs (Eyal et al., 2019). We propose that bleaching in the mesophotic ecosystem of the northern Red Sea occurs because deep-specialist coral species in the region are less resistant to high temperatures than shallow taxa. As the larvae of deep-specialist corals originate at depths of approximately 50–100 m, they may pass under the thermal barrier in the southern Red Sea, along the subsurface intrusion of the Gulf of Aden Intermediate Water (GAIW)

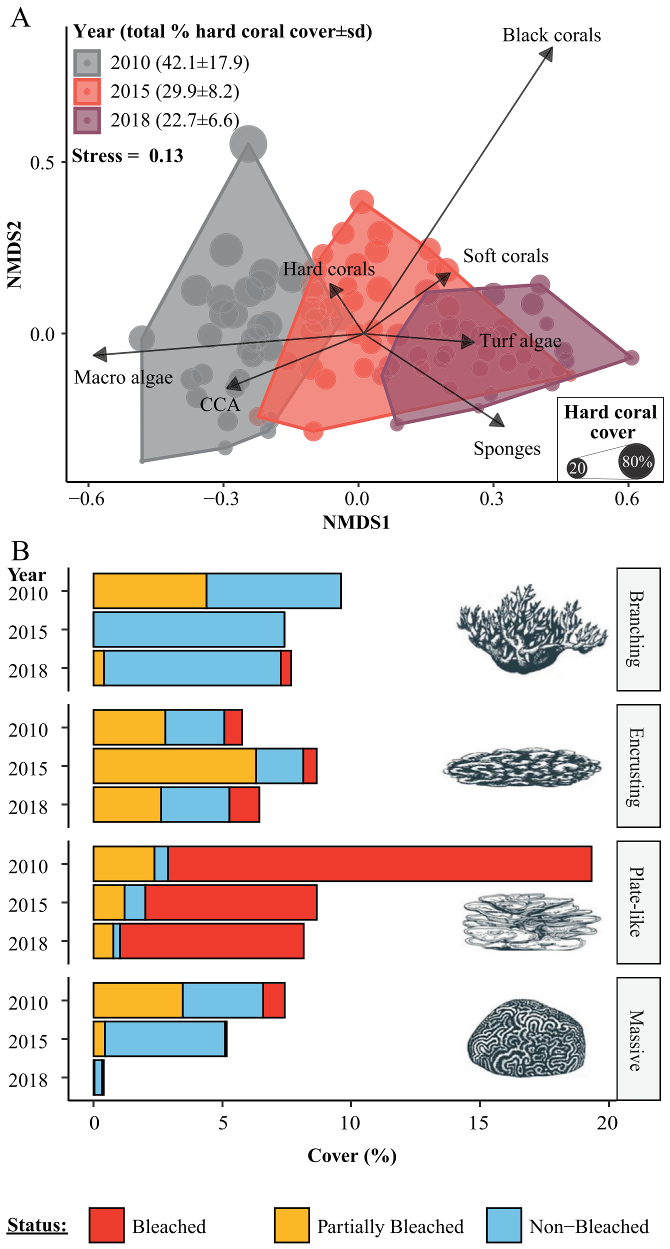


Fig. 3. Community dynamics across three mass bleaching events in the mesophotic ecosystem (55–65 m depth) of Eilat. (A) Non-metric multidimensional scaling (nMDS) ordination of the taxonomic composition of the benthic assemblages during the bleaching years. Vectors show the proportional influence of each benthic group on the ordination distribution. Circle sizes represent the hard coral cover (%) for each quadrat (n = 30–32 quadrats of 0.35m^2 per year). (B) Relative percentage contribution of each hard coral morphological group to the total coral cover in each year.

Table 2
Averaged Maximum Monthly Mean (MMM) of temperature from the northern Red Sea. Open ocean data collected in station A (Fig. S1) adjacent to Eilat by Seabird CTD every month from 2003 to 2019 by the Israeli National Monitoring Program of the Gulf of Eilat.

Depth (m)	Averaged MMM	SE
<3	27.272	0.174
7–21	26.739	0.180
38–41	25.900	0.156
49.9–62	25.369	0.156
70–90	24.730	0.149
99–161	23.993	0.161
175–760	21.925	0.080

(Maillard and Soliman, 1986, Sofianos et al., 2002, Dreano et al., 2016). These corals in the northern Red Sea, therefore, resemble the southern coral populations that experience the cooler GAIW temperatures (16–19 °C in summer months cf. 30 °C in the shallows of the northern Red Sea) (Maillard and Soliman, 1986, Sofianos et al., 2002, Wafar et al., 2016), possibly still maintaining horizontal connectivity with the Indian Ocean populations. This means the larvae avoid, or skip, the selective pressure for high thermal tolerance that renders shallow and depth-generalist corals resistant to bleaching (Fig. 1A). While it is possible that deep-specialist coral larvae disperse at shallow depths and are tolerant to high water temperatures, when they sink and settle in the deep, cooler environment, the adult colonies do not appear to be selectively resistant to high temperature stress and have limited plasticity in their thermal tolerance (Klepac and Barshis, 2020, Keshavmurthy et al., 2021).

Mass coral bleaching of shallow coral reefs in the Red Sea is rare, but has been documented in the central and southern parts (<24°N) in 2010 and 2015 (Furby et al., 2013, Monroe et al., 2018, Hammerman et al., 2022). However, in the northern part of the Red Sea, shallow reefs did not experience mass coral bleaching during any of the global coral bleaching events. The corals in this specific region are considered highly tolerant (Fine et al., 2013, Osman et al., 2018). The few MCE coral bleaching events reported from the region (Nir et al., 2014, Eyal et al., 2019, Eyal et al., 2021) are mostly episodic and limited to one or a few species. In other regions, MCEs are less affected by bleaching, mainly because of lower variability in temperature and light intensity. The unique case of thermally tolerant shallow communities that may not be genetically connected to the deeper communities, along with relatively elevated temperatures deeper in the water column, created the unfortunate situation that deeper communities suffered from mass coral bleaching at least three times over the last decade. It is possible that the mass bleaching in MCEs of the northern Red Sea are due to their longer exposure to thermal stress (Table 1) or faster increases in temperature at depth (Fig. 2). However, our aquaria experiments and other studies have revealed multiple shallow specialist coral species with exceptional thermal tolerance under experimental conditions (Fine et al., 2013, Bellworthy and Fine, 2017, Krueger et al., 2017).

Our physiological assessments of depth-generalist and deep-specialist corals suggest that deep-specialist corals suffer from bleaching events due to rising temperatures that induced damage in their photosynthetic capacity. PAM fluorometry revealed damaged photosynthetic performances with lower electron transport rates (rETRs) and higher non-photochemical quenchings (NPQs) of the bleached deep-specialist corals in 2018. Our heat-stress experiment in 2016 further indicated low resilience of the deep-specialist L. *glabra* to rising temperatures.

It is estimated that the top 100 m of the oceans have warmed by +0.33 °C since 1969 (Levitus et al., 2017). Most of the global warming occurred in the past 40 years, with the most recent decade being the warmest. The warming of the mesophotic water (49–62 m) in Eilat, at +0.48 °C per decade, was much higher than the global ocean average, indicating this region of Israel is a hot spot of global warming (Hochman et al., 2021). The Israel Meteorological Service (IMS) predicts an average increase in the mean annual temperature anomaly by ca. 4 °C by the end of the century (2100), under the 'business-as-usual' scenario RCP8.5 (Pörtner et al., 2019, Yosef et al., 2020). A trend of continous rising SST in Eilat has been evident since 1988 (Shaked and Genin, 2020). Of the continuous meteorological measurements conducted by the NMP over the past 15 years, the peak 2020 SST is noteworthy. The annual average temperature measured in 2020 was among the highest in the past thirty years. A short and very steep peak of SST was recorded in June, and then, during most of the summer, SST was higher than the yearly average and the 90th percentile for the season (Shaked and Genin, 2020). Minimal SST values were similar to those measured in recent years, but the maximal 2020 SST value measured (30.9 °C) is the highest measured by the NMP and nearly a full degree higher than the 2019 maximum value (Shaked and Genin, 2020).

In this long-term study, we found recurrent mass coral bleaching events in the mesophotic ecosystem of the northern Red Sea, previously assumed to be a geographic and depth refuge from thermal stress. These events transformed the benthic community, causing large decreases in coral cover over the last decade and disproportionately impacting specialized, thermally sensitive, taxa that inhabit deeper coral ecosystems. We identified faster increases in temperature at mesophotic compared to shallow depths and with the predictions of temperature increases in the region, we expect faster heat accumulation in deeper water. We therefore propose that a vertical thermal barrier segregates shallow (high thermal-tolerance) and mesophotic/deep (low thermal-tolerance) coral populations. The deep-specialized corals are more susceptible to bleaching, perhaps as these populations were not subjected to millennia of selection and thermal adaptation in the southern Red Sea, as they are still horizontally exposed to cooler Indian Ocean deep waters. Our results present an urgent need for the protection of these unique mesophotic ecosystems, which cannot be automatically considered as a refuge for shallow reefs in Eilat or globally.

Data and materials availability

All data are available in the main text or the supplementary materials. Datasets and codes available at https://github.com/gal4596/MCEs_Bleaching.

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CRediT authorship contribution statement

Conceptualization: GE, JMP.
Methodology: GE, JHL, OBZ, KTB, NK.
Investigation: GE, OBZ, NK, RT, YL.
Visualization: GE, JHL, KTB, NK.
Funding acquisition: GE, OBZ.
Supervision: OL, JMP.
Writing – original draft: GE.
Writing – review & editing: all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157180.

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