



Coral bleaching occurrence along the Egyptian coast of the Red Sea during the summer heat stress period, 2020

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ABSTRACT

The Red Sea is considered one of the few environments that accommodate a wide diversity of thermotolerant corals. However, the recent bleaching events had revealed that some Red Sea coral species may be under threat and may face a more dramatic future. Here, we investigate the pattern of bleaching in hard corals inhabiting the Egyptian coast of the Red Sea (from Hurghada, at the north, to Wadi El-Gemal, at the south) during the 2020 summer heat stress period. Field data on the cover, number of colonies, and severity of the bleaching were collected using the line-intercept transect method from three geographical sectors (each contains two study sites), two depth ranges (0-5m and 10-15m), and two reef systems (inshore and offshore reefs) during the period from September to October 2020. The results indicated that the bleaching symptoms of different severities had appeared on 32.74% (460/1405) of the total examined colonies (36.66% of the total coral cover). Our survey, however, revealed that corals in the southern reefs (Sector_3) were more susceptible to bleaching than those present in the north (Sector_1). We also noted that the bleaching intensity was more concentrated between 0-5m, while colonies beyond 10m were more sheltered. In contrast, the results revealed that both inshore and offshore reefs were vulnerable to bleaching with no effect for the distance from the shore on coral resistance. Furthermore, the results indicated that coral genera like *Millepora*, *Montipora*, *Pocillopora*, *Acropora*, and *Porites* showed high bleaching cover and severity whereby they may be more threatened by the thermal stress than the others. In the light of these results, the current study provides field evidence on the potential role of the northern reefs as a refugium for the Red Sea corals and suggests that the high latitudinal reefs may be the last to decline due to climate change. On the other hand, the recorded bleaching pattern at the southern coasts, albeit less acute, may raise the concern on the vulnerability of these reefs to the heat stress than was expected.

1. INTRODUCTION

Coral reefs are one of the most prominent marine ecosystems that have been affected by the brunt of the climate change. This is because these changes are usually accompanied by thermal stresses that directly affect the reef-building corals. The ecological vulnerability,

however, increases whenever the thermal stress drives the bleaching events – the most dramatic challenge for the existence of coral reefs on the earth – to spread over. The consequences of these events can extend on reef, local, and regional scales, and have resulted in a significant global decrease in the total live cover of most reefs (**Hughes *et al.*, 2018**). Due to the increasing frequency of the heat stress, such reduction in the benthic cover of corals had resulted in an overall reduction in the fecundity and size of reef corals (**Baird and Marshall, 2002; Riegl *et al.*, 2018; Johnston *et al.*, 2020**). Recently, it had been shown that the dynamics of heat stress can also affect synchronization of coral spawning where seawater temperature is considered one of the main cues for timing mass spawning of reef corals (**Shlesinger and Loya, 2019**). The implications of bleaching episodes can moreover extend to include alteration in the benthic structure and can cause a considerable decline in the services of reefs (**van Woesik *et al.*, 2011; McClanahan *et al.*, 2014; Hughes *et al.*, 2017; Riegl *et al.*, 2018**). As such, by the end of the present century and under the sustained industrialization pace, the severity rate of the heat stress may exceed 2°C above the current levels and if corals would not have to adopt a scenario of 0.2°C/decade, it is expected that >80% of the worldwide coral cover will be deteriorated (**Kubicek *et al.*, 2019**).

Many field studies had shown that the heat stress can lead to different bleaching patterns between regions, reefs, depths, or coral species (**Muir *et al.*, 2017; Monroe *et al.*, 2018; McClanahan *et al.*, 2020**). This difference is mostly related to factors such as coral genetics, morphology, or endosymbiont genotype (**McClanahan, 2004; Sampayo *et al.*, 2008; Thomas *et al.*, 2018; Manzello *et al.*, 2019; Qin *et al.*, 2019; Mies *et al.*, 2020**). This may explain why some reefs have thermal tolerance despite receiving heat stress above the bleaching thresholds of others. At the Red Sea, however, corals are thriving in extreme summer conditions of high temperature, nutrients deficiency, and high salinity while they maintain thermal tolerance and growth performance at optimum levels that make them extraordinarily ‘super-corals’ (**Krueger *et al.*, 2017; Ellis *et al.*, 2019**). Yet, it has been noted that the warming rate of seawater increases beyond the global thresholds from the south to the north by 0.3 °C/decade (**Chaidez *et al.*, 2017; Geneviev *et al.*, 2019**). As such, Red Sea corals may encounter challenging conditions of +3 °C above the contemporary thermal limits by 2100 (IPCC-RCP8.5 scenario) (**Geneviev *et al.*, 2019**). Given that they can thrive under temperature exceeds the global limits, it had been proposed that northern Red Sea (NRS) coral reefs are the last to decline and are on the head candidates for worldwide reef restoration (**Fine *et al.*, 2019; Kleinhaus *et al.*, 2020**).

The Egyptian coast of the Red Sea extends northwestward for about 1,800 km (between 22° N and 30° N) and occupies the major proportion of the NRS at the western side. Coral reefs at this upper geographic range cover approximately 3,800 km² (1.34% of the total coral cover on the earth) by which they are ranked fifteenth among 80 top countries that have considerable reefs (**Spalding *et al.*, 2001**). In terms of ecological and

economic values, the Egyptian coral reefs accommodate more than 200 reef-building coral species (**Wilkinson, 1998**) and each square kilometer is estimated to have a value of more than 908,000 US\$ (**Fine *et al.*, 2019**). Moreover, corals in the surface water of the Egyptian Red Sea coast are particularly thriving at an annual SST of 26.06 ± 2.42 °C and seasonal thermal variability of approximately 3-8 °C (**Osman *et al.*, 2018**; **Shaltout, 2019**). This wide thermal seasonality that may occasionally reach 11 °C in the Egyptian Red Sea proper and Gulf of Aqaba or 13 °C in the Gulf of Suez had conferred thermotolerant traits to the NRS corals and gave them the potency to adapt with a wide range of thermal dynamics (**Osman *et al.*, 2018**).

A recent study by **Genevier *et al.* (2019)** showed that most of the recorded bleaching events over 31 years (between 1985 and 2015) were concentrated on the eastern coast of the Red Sea whereas the western reefs, particularly at the NRS, experienced little incidence of these events [in total three events had been reviewed by **Osman *et al.* (2018)**]. However, most studies may have given somewhat speculative assessments on the thermal tolerance of corals at the Egyptian coast rather than supported by adequate evidence. For instance, the projection of **Genevier *et al.* (2019)** lacked concomitant field evidence to figure out the effects of the recorded stress on coral reefs. In contrast, the field survey conducted by **Osman *et al.* (2018)** during the 2015 El Niño event was restricted to sites in the Gulf of Aqaba and did not introduce any field data about the effects of the heat stress on corals in the Red Sea proper; despite the heat stress outside the gulf is more intensive compared to inside (maximum DHWs ranged from 15.1 to 18.9°C-weeks at Hurghada and Wadi El-Gemal, respectively). Furthermore, experimental work carried by the later study tends to be specific to the study species and probably to the study site (i.e., four coral species collected from Hurghada) but not necessarily reflect the effects of the heat stress on the whole Egyptian coast that comprises a wide diversity of coral species.

As the data available on the number, frequency, pattern, and intensity of the bleaching events are very limited, little is known on the vulnerability of corals to the heat stress at the Egyptian coast of the Red Sea. Most of the data represent either unpublished periodic reports that are almost unavailable for the scientific community or whenever available are more general with no details on the threatened coral taxa. Also, most of the data available lack detailed information on the severity of the bleaching events along this part of the Red Sea. Here, we assess the susceptibility of these corals to the thermal stress throughout a short-term field survey conducted during the bleaching event of 2020. At the same time, we address the potential effects of such stress on corals inhabiting the inshore and offshore reefs and between the surface and deep waters. In addition, the present study aims to broadly examine the thermal tolerance of different coral genera inhabiting the Egyptian coast of the Red Sea.

2. MATERIALS AND METHODS

2.1. Study sites

The status of reef-building corals was monitored in three geographical sectors along the Egyptian coast of the Red Sea between 27.50°N and 24.50°N (and within no more than 20km from the shore) during the period from 24 September to 11 October 2020 (Fig. 1). The first sector (Sector_1) is located in the north and comprises sites of Hurghada and Safaga. The second sector (Sector_2), in the middle between the north and the south, comprises reefs of Al-Quseir and Port Ghaleb. At the south (Sector_3), coral bleaching data were collected from four reefs in Marsa Alam and Wadi El-Gemal. Generally, data were collected by SCUBA diving from surface (0-5m) and deep waters (10-15m) and from inshore and offshore reefs as in table 1.

2.2. Field survey

At each reef, the number and cover of the bleached colonies were recorded using 10m line-intercept transect method. Because the mass bleaching events of complete colony whitening is rare at the Egyptian coast, we used a broad bleaching severity ranking following **Baird and Marshall (2002)** to visually assess the bleaching symptoms at the colony level. Briefly, coral colonies that showed no signs of bleaching and maintained their bright color were recorded as 'non-bleached' and were classified within the 0% bleaching category. In contrast, coral colonies suffering partial bleaching of mild, white-free, color paling took a rank of 1-10%. The partial bleaching symptoms of severe paling with white spots in some parts of the colony or those showed high incidence of white color that dominates the whole surface of the colony were either grouped in 11-50% or 51-99% bleaching categories, respectively. On the other hand, coral colonies were recorded under 100% bleaching severity category whenever they showed pure white color of the whole colony. Finally, coral colonies that displayed complete white skeleton with initial growth of filamentous algae as a result of heat stress (no signs of diseases or herbivory) were diagnosed as 'recently dead' (**Obura, 2001**). Along each surveyed transect, the growth form and macromorphological features of the colony were used to identify corals at the genus level.

2.3. Statistical analysis

All data were primarily tested for normality and homogeneity using Shapiro and Levene's tests, respectively. Data that did not meet the parametric assumptions were transformed then ANOVA was conducted. When the parametric assumptions were violated even after transformation, the Kruskal-Wallis test was applied. Following this, multiple pairwise comparisons were conducted to test the difference between the levels of studied variables. Regarding this, we first compared the difference in the benthic and bleaching covers of hard corals between sectors, sites, depths, and reefs.

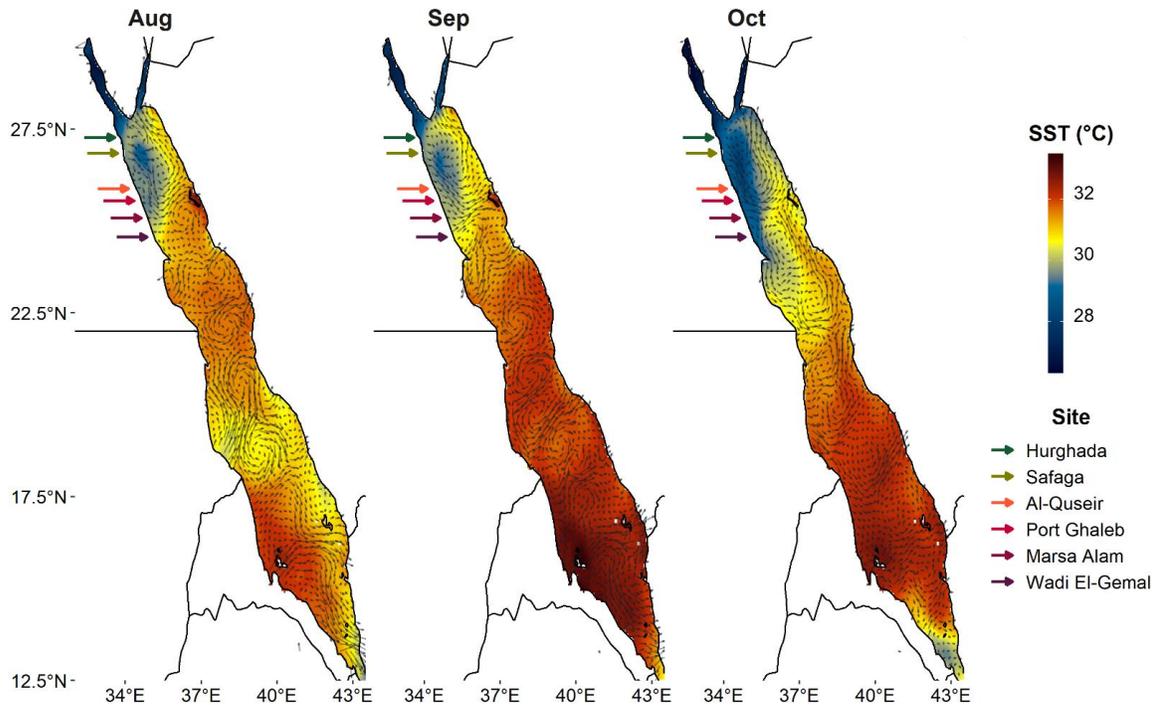


Fig. 1. The study area at the Egyptian coast of the Red Sea. The area had been divided into three sectors and each sector comprises two study sites. In the north (Sector_1), a total of four reefs were surveyed in Hurghada and Safaga. In the middle, coral bleaching at Al-Quseir and Port Ghaleb (Sector_2) was recorded in only two reefs. To the south, in addition, our study extended to include four reefs in Marsa Alam and Wadi El-Gemal (Sector_3). The pattern of the SST and the flow of the water currents between 01 August and 31 October 2020 illustrate the extent of the summer heat stress received by the study sites at the NRS. Data of SST (Dataset ID: NOAA_DHW) and geostrophic currents (Dataset ID: miamicurrents) had been downloaded from ERDDAP server (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>), while data of coral bleaching were collected by a filed survey conducted between September and October.

Dunn’s *post hoc* non-parametric test was subsequently used to assess the differences in the cover of each bleaching severity category between the three sectors. Moreover, the Two-Way ANOVA was used to test the effect of the depth and distance from the shore on the cover of bleaching severity categories and in order to determine the susceptibility of corals within different reef systems. Finally, the sensitivity of the most affected coral genera to the heat stress conditions was assessed between sectors using Kruskal-Wallis test. Also, our analysis included the investigation of the responsiveness of the highly affected genera to the thermal stress between sectors using Two-Way ANOVA. In all cases, to ensure the representativeness of the effects of each factor and to avoid the possible bias due to the differences in sampling strategy at each site (Table 1), only data collected from the same conditions were compared. For example, it was not possible to survey reefs at the deep water in all sites. Therefore, to eliminate the effect of the depth, we tested the differences in the total coral cover and bleaching pattern between the studied sites at the surface water only. Also, to study the effect of the distance from the shore on the coral cover and

bleaching pattern, we used surface water data only. All statistical analyses and data visualizations were executed using R (Team, 2020).

Table 1. Number of line-transects surveyed at each study site.

Site/Sector	Reef	Location		Reef distance	Depth		Total
		Lat. (°N)	Long. (°E)		Surface	Deep	
Hurghada	El-Fanadeer	27.30	33.83	Offshore	6	NA	6
	Fanous Reef	27.27	33.88	Offshore	5	NA	5
	Magaweesh	27.14	33.87	Offshore	3	3	6
Safaga	Soma Bay	26.84	34.00	Inshore	5	NA	5
Sector_1					19	3	22
Al-Quseir	Mangrove Bay	25.87	34.42	Inshore	3	3	6
Port Ghaleb	Port Ghaleb	25.55	34.64	Inshore	4	NA	4
Sector_2					7	3	10
Marsa Alam	Marsa Asalaya	25.16	34.85	Inshore	4	NA	4
	Shaab Marsa Alam	25.07	34.94	Offshore	5	3	8
	Marsa Samadai	25.01	34.93	Inshore	2	3	5
Wadi El-Gemal	Ras-Hankourab	24.56	35.17	Inshore	6	NA	6
Sector_3					17	6	23
Total					43	12	55

3. RESULTS

3.1. Bleaching severity

In total, 32.74% (460/1405) of the total number of surveyed coral colonies (36.66% of the total hard coral cover) showed different degrees of bleaching (Fig. 2). Regardless of the site, distance from the shore, depth, and identity factors, bleaching had averaged $36.62 \pm 4.27\%$ of the total coral cover surveyed along 10m line transect (n= 55) in the study area. Our diagnosis for the bleaching symptoms, however, revealed a presence of six severity levels. Among all, corals with no signs of bleaching (i.e., 0% category) were generally the most dominant and had represented $66.71 \pm 4.13\%$ of the total hard coral cover. On the other hand, corals that demonstrated bleaching symptoms were mostly restricted to 1-10% and 11-50% bleaching categories. Both two low-severity categories had formed $21.40 \pm 2.39\%$ and $17.99 \pm 2.78\%$ of the total hard coral cover and had affected 19.00% (267/1405) and 10.20% (143/1405) of the total number of examined colonies, respectively. Conversely, corals that showed 51-99% and 100% bleaching severity symptoms were uncommon and the susceptibility to severe bleaching was limited in the study area. Overall, only 2.99% (42/1405) of coral colonies had been affected by 51-99% bleaching severity level (averaged $8.90 \pm 1.91\%$ of the total coral cover). Similarly, the

totally bleached colonies were rare and had only been detected in 0.50% (7/1405) of the total number of surveyed colonies ($3.06 \pm 1.76\%$ of the total coral cover). Our survey had additionally revealed that the mortality due to 2020 thermal stress was not completely absent but rather was rare and had been observed in only one coral colony (0.07% of the total number of coral colonies).

3.2. Spatial pattern of bleaching

Data on the benthic cover of hard corals in the six study sites were collected from 43 line transects laid out in the surface water of each site. On average, zooxanthellate corals have covered $55.90 \pm 2.26\%$ per 10m transect in the surveyed reefs. The results have also revealed that the cover of the hard corals was different between the study sites (Kruskal-Wallis test; $df= 5$, $\chi^2= 14.278$, $p<0.05$); where the highest coral cover was recorded in Al-Quseir and Port Ghaleb (Sector_2), while the lowest cover was recorded in Hurghada (Table 2). The results pertaining to the bleaching pattern, on the other hand, showed that the cover of the bleached corals in Sector_1 was much limited compared to the cover of the non-bleached corals (One-Way ANOVA; $df= 1$, $F= 85.37$, $p<0.05$). Our results showed that the number of the affected colonies in that sector was lower than the number of the healthy ones by 69.44%. The bleaching cover, however, increased in Sector_2 to the extent with which there was no significant difference between the cover of the bleached and non-bleached colonies (One-Way ANOVA; $df= 1$, $F= 2.93$, $p>0.05$). Differently, we recorded an increase in the bleaching cover in Sector_3 (One-Way ANOVA; $df= 1$, $F= 11.76$, $p<0.05$) and there were about 60.12% (297/494) of the examined colonies had suffered different levels of bleaching symptoms. As such, our survey revealed that the cover of the bleaching had increased southward from Sector_1 to Sector_3 (One-Way ANOVA; $df= 2$, $F= 21.72$, $p<0.05$). Regarding their intermediate position, reefs of Sector_2 were susceptible to intermediate bleaching levels between Sector_1 and Sector_3 (Table 2). The Dunn's pairwise test had moreover indicated that the response of corals to severe bleaching in Sector_3 was higher than that in Sector_1, but it was not different from Sector_2 (Fig. 3).

3.3. Effect of the depth and distance from the shore

We additionally studied the effect of the 2020 heat stress on corals inhabiting different reef systems along the Egyptian coast to determine the extent of bleaching incidence in these systems. Generally, the cover of hard corals was higher at the depth range of 0-5m than at 10-15m (One-Way ANOVA; $df= 1$, $F= 20.29$, $p<0.05$). However, the cover of the different bleaching categories was related to the depth (Two-Way ANOVA; $df= 2$, $F= 5.02$, $p<0.05$), and corals of surface water were more susceptible to different degrees of bleaching than those beyond 10m (Table 3). Our results accordingly showed that the number of susceptible colonies was higher by 29.14% in surface water than in deep ones. In surface water, the present study on

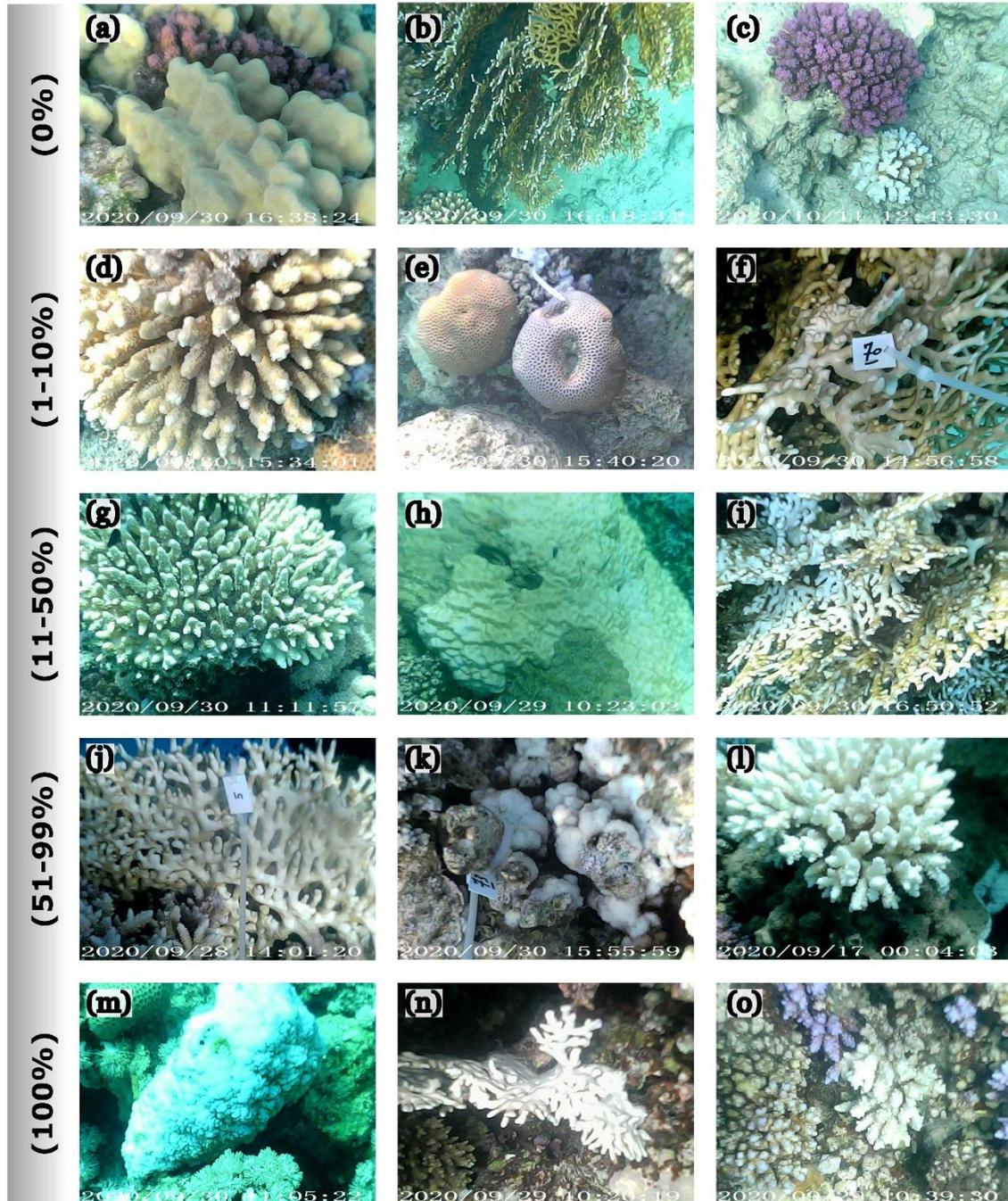


Fig. 2. The different severities of bleaching symptoms experienced by corals in the study area during the 2020 bleaching event. Bleaching symptoms included: (a-c) no signs of bleaching (0% category); (d-f) a mild color paling (1-10% category); (g-i) Loss of up to 50% of the original colony color (11-50% category); (j-l) a barely observable color with exposed white skeleton almost in the entire of the colony (51-99% category); and (m-o) complete bleaching by which the white skeleton of the colony is fully bare and fluorescent (100% category).

Table 2. The mean percentage cover ($\% \pm SE$) and the number of the examined colonies (n) of hard corals in the surface water of each site. The benthic cover represents the overall mean percentage cover of all hard corals in each site. The bleaching cover for each category was calculated relative to the total coral cover. All cover measurements were averaged per 10m transect, while the number of colonies was summarized as totals.

Site/Sector	Benthic cover		Categories of the bleaching severity					Bleaching cover	
		Number of colonies (n)	0%	1-10%	11-50%	51-99%	100%	Recently Dead	Total number of bleached colonies
Hurghada	%	45.44±4.41	83.33±4.12	14.04±3.79	6.33±1.53	5.52±2.55	0.00	0.00	17.96±4.23
	n	307	255	31	16	5	-	-	52
Safaga	%	60.94±4.58	87.65±5.23	13.49±4.45	6.54	1.28	0.00	0.00	15.44±5.44
	n	125	111	11	2	1	-	-	14
Al-Quseir	%	74.77±0.86	39.14±13.87	32.37±1.46	17.58±12.75	10.38±2.75	1.6	0.00	60.86±13.87
	n	94	36	34	17	6	1	-	58
Port Ghaleb	%	65.00±4.75	85.29±5.84	16.12±6.94	3.49±1.55	0.00	0.00	0.00	14.71±5.84
	n	142	124	14	4	-	-	-	18
Marsa Alam	%	56.73±2.37	37.10±7.49	37.11±3.64	20.82±4.36	13.51±4.52	1.66	0.00	62.90±7.49
	n	321	133	122	48	17	1	-	188
Wadi El-Gemal	%	59.07±6.39	33.45±8.89	21.53±7.21	37.84±7.61	5.77±2.18	4.01±3.03	2.25	66.55±8.89
	n	173	64	43	47	13	5	1	109
Overall cover	%	55.90±2.26	62.14±4.64	23.45±2.53	17.46±3.05	8.90±1.91	3.06±1.76	2.25	39.70±4.67
Total number of colonies	n	1162	723	255	134	42	7	1	439

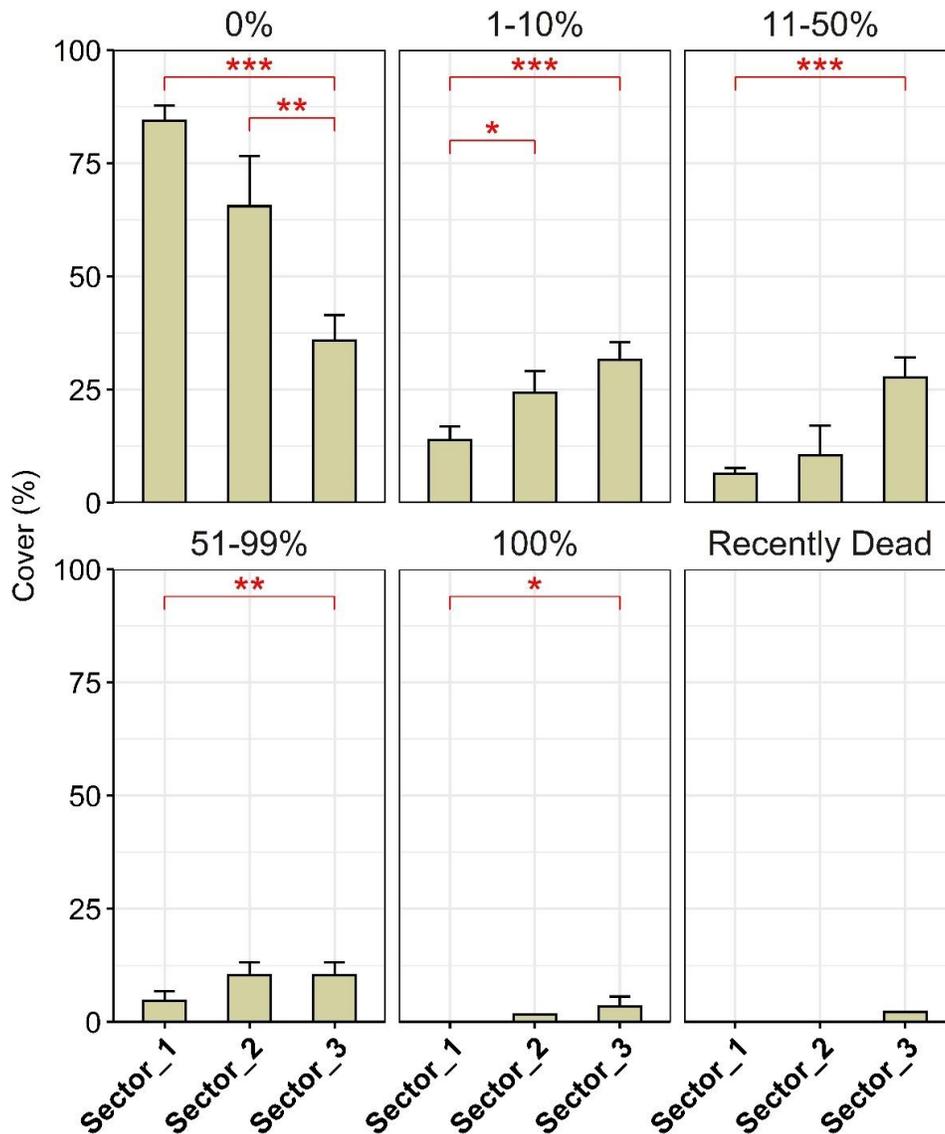


Fig. 3. Percentage cover of the bleaching categories relative to the total coral cover within each sector. As Dunn's test indicated, for the low and high severity levels, the cover of the bleaching was particularly significant between Sector_1 and Sector_3 (the top red asterisks). The cover of bleaching in Sector_2 was intermediate, and in most cases, it was nonsignificant compared to Sector_1 and Sector_3.

the other hand showed that the coral cover in the inshore reefs was higher than the coral cover in the offshore reefs (One-Way ANOVA; $df = 1$, $F = 8.439$, $p < 0.05$). Nonetheless, at each reef system, the number of the affected colonies was nearly 38.00% of the total number of surveyed colonies (Table 3) and both inshore and offshore corals were alike vulnerable to low and high bleaching severities (Two-Way ANOVA; $df = 3$, $F = 0.78$, $p > 0.05$).

Table 3. The mean percentage cover (%) per 10m transect and the total number of examined colonies (n) of each bleaching severity category according to the distance from the shore and depth. For the distance from the shore, only the percentage cover and number of colonies in the surface water were compared.

Bleaching severity	Depth		Distance from shore		
	Surface	Deep	Inshore	Offshore	
0%	%	58.37±4.60	29.13±7.19	59.71±5.67	65.22±7.80
	n	723	222	448	275
1-10%	%	21.64±2.35	1.77±0.39	23.68±2.89	23.14±4.62
	n	255	12	159	96
11-50%	%	16.46±2.95	3.38±0.95	20.90±4.62	13.28±3.64
	n	134	9	82	52
51-99%	%	8.07±1.81	-	6.66±1.48	11.63±3.77
	n	42	-	22	20
100%	%	2.95±1.78	-	3.06±1.76	-
	n	7	-	7	-
Recently Dead	%	2.25	-	2.25	-
	n	1	-	1	-
Overall bleaching	%	36.85±4.38	3.27±0.85	42.04±5.63	36.72±7.99
	n	439	21	271	168
Total number of examined colonies	n	1162	243	719	443

3.4. Sensitivity of coral genera

A total of 1405 colonies that had been examined in all surveyed reefs (n= 10), in surface and deep waters along 55 transects, indicated that the effect of the bleaching had extended to 17 genera of hard corals. In terms of their cover, the colonies of *Millepora*, *Montipora*, *Pocillopora*, *Acropora*, and *Porites* were the most susceptible to severe bleaching levels than the others (Fig. 4). Both *Millepora* and *Montipora* were particularly the most thermally susceptible genera where they had been affected by a bleaching incidence of >50% relative to their total cover in all sites, including the northern sites of Sector_1 (Fig. 5). We additionally documented about 61.94% (83/134) of *Millepora* and 42.55% (40/94) of *Montipora* colonies that had shown high levels of severe bleaching symptoms. The results as well indicated that the total cover and the number of bleached colonies of the most susceptible genera, except *Pocillopora*, were not different between sectors (Kruskal-Wallis test; df= 2, $p>0.05$). More interestingly, the bleaching severity of *Millepora*, *Montipora*, and *Porites*, was also independent on the location (Table 4), and whether their conspecifics were present in the north or in the south were susceptible to severe bleaching conditions.

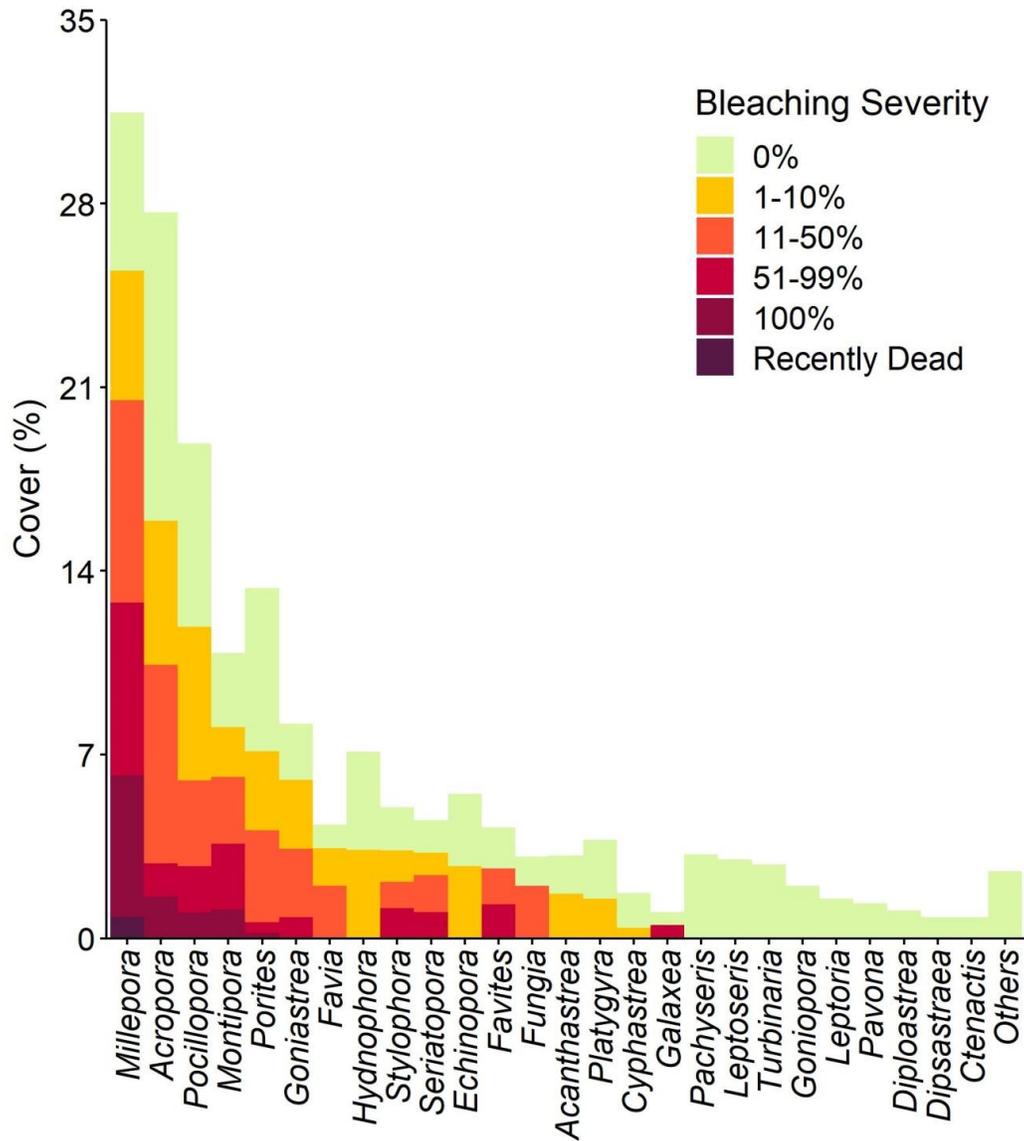


Fig. 4. The overall mean bleaching cover (%) in different coral genera per 10m transect.

4. DISCUSSION

At the time that most reefs on the earth are suffering periodic bleaching episodes, Egyptian reefs remain among a few that experienced low records of mass bleaching events. To the best of our knowledge, the last and perhaps the only detailed report on coral bleaching was introduced by **Hanafy *et al.* (2012)**, and since that time there is a gap in reporting coral status at the Egyptian coast in spite of the increasing alerts of the heat stress. Therefore, the present study introduces a more recent assessment on the status of corals inhabiting this part of the Red Sea during the summer heat stress period and reports the incidence of bleaching in the NRS reefs in 2020.

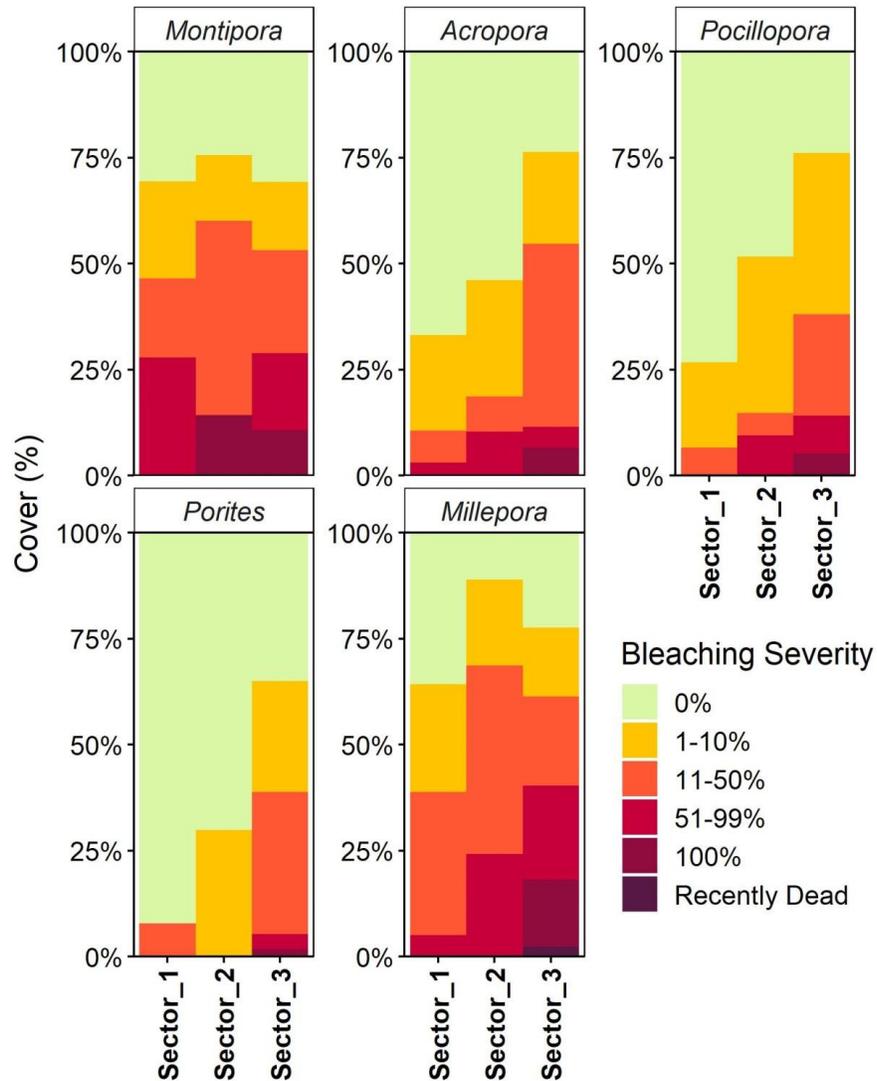


Fig. 5. Bleaching susceptibility of the five most affected coral genera at each sector. The percentage cover of bleaching severity categories was calculated for each genus relative to the total cover of that genus within the sector.

Here, we documented that the heat stress had led to the emergence of bleaching symptoms that varied in severity according to location, depth, and coral genera. Yet, the bleaching severity was mostly restricted to 1-10% and 11-50% categories while complete colony bleaching or mortality due to the thermal stress were rare at the Egyptian coast. Our findings as such were largely in agreement with the findings of **Hanafy *et al.* (2012)** in terms of the geographical range, depth, and coral identity effects on the bleaching pattern. Given that the bleaching severity increases substantially from north to south, the southern reefs may particularly be more susceptible to the heat stress and more vulnerable to the bleaching events. In contrast, the recorded bleaching pattern provides filed evidence on the buffering properties of the northern region to the heat stress and

underpins the potential role of this region as a natural coral refuge (Osman *et al.*, 2018). In the light of the knowledge that the severity of bleaching can affect the structure of the reef and delay its recovery rate (Berumen *et al.*, 2019; Koester *et al.*, 2020), our study underlines that the frequency of the heat stress episodes may threaten corals over the time and can drive acute effects on the Egyptian reefs, especially at the southern coast.

Table 4. Effect of the geographical range on the degree of bleaching in the most susceptible genera. The Two-Way ANOVA included the individual effects of location (Sector) and bleaching categories (Severity) as well as the interaction between them (Sector:Severity).

Genus		df	Sum Square	Mean Square	F value	p	Sig.
<i>Montipora</i>	Sector	2	2298	1148.800	0.817	0.448	
	Severity	4	9179	2294.700	1.632	0.183	
	Sector:Severity	6	2694	448.900	0.319	0.923	
	Residuals	44	61859	1405.900			
<i>Acropora</i>	Sector	2	4.100	2.052	3.246	0.046	*
	Severity	4	21.000	5.249	8.301	<0.0001	***
	Sector:Severity	6	12.000	1.999	3.162	0.009	**
	Residuals	61	38.570	0.632			
<i>Pocillopora</i>	Sector	2	69.800	34.910	9.663	<0.001	***
	Severity	4	114.400	28.590	7.914	<0.0001	***
	Sector:Severity	5	165.800	33.160	9.179	<0.0001	***
	Residuals	94	339.600	3.610			
<i>Porites</i>	Sector	2	1208711	604355	16.794	<0.0001	***
	Severity	4	279459	69865	1.941	0.115	
	Sector:Severity	2	65456	32728	0.909	0.408	
	Residuals	60	2159160	35986			
<i>Millepora</i>	Sector	2	41.370	20.686	3.890	0.027	*
	Severity	5	28.700	5.739	1.079	0.383	
	Sector:Severity	6	18.180	3.031	0.570	0.752	
	Residuals	53	281.840	5.318			

Despite the recorded spatial pattern of bleaching can be attributed to the genetic traits and the local adaptation of corals between the north and the south, some previous studies had indicated that corals have a little or no genetic differentiation and experience low adaptation schemes along the Red Sea (Robitzch *et al.*, 2015; Sawall *et al.*, 2015). In a more recent study, Osman *et al.* (2020) had also shown that there was no difference in the genetic diversity of Symbiodiniaceae in four scleractinian coral species along the Egyptian coast of the Red Sea. The same study had also revealed no difference in the

genetic structure of corals endosymbiotic systems between surface and deep water. Therefore, it is more unlikely that the differences in coral response to the heat stress between the northern and southern reefs of the Egyptian coast are related to the genetic differentiation of coral host or its endosymbionts. We instead attribute this pattern more likely to the pattern of water currents that may control the direct of marine heatwaves in the NRS. On this basis, we acknowledge the low occurrence of coral bleaching in the northernmost parts of the Red Sea proper at the Egyptian coast (i.e., Sector_1) to the geographic position away from the path of the heatwaves coming from the eastern coast (Fig. 1). However, at the south (Sector_3), coral reefs are more adjacent to the heat stress hotspot in the NRS.

Another factor that may explain the spatial pattern of the bleaching along the Egyptian coast is the difference in the intensity of UV irradiance between the north and south. Generally, the exposure of corals to incident UV increases from the north to the south along the Red Sea (**Overmans and Agustí, 2020**). Despite the local data is critically required in this context, **Overmans and Agustí (2020)** had indicated that coral reefs in the central Saudi Arabian coast of the Red Sea are receiving 24% higher maximum daily UV irradiance during summer compared to those located at the north in the Gulf of Aqaba. Our findings consequently propose that Red Sea corals can potentially tolerate thermal stress unless the UV irradiance was not stressful. This assumption can also interpret the differences in the bleaching cover and severity, even in the same site, between the surface and deep corals where the latter are usually sheltered from the effects of high light and temperature (**Overmans and Agustí, 2020**). Contrary to the findings of **Monroe *et al.* (2018)** at the central Red Sea, we had reported no effect for the distance from the shore on the bleaching cover. Because the surveyed reefs are located in no more than 20km from the shore, one possible explanation for this pattern is that the offshore reefs were not far enough away from the coastal southward heatwaves and both reef systems may be vulnerable to the same heat stress conditions.

According to **van Hooidonk *et al.* (2016)**, it is expected that the bleaching episodes will affect most of the coral reefs, including reefs of the Red Sea at the Egyptian coast. Indeed, bleaching episodes or at least their consequences had already reached the Egyptian coast during 1998 (**Hassan *et al.*, 2002**), 2007 (**Kotb *et al.*, 2008**), 2012 (**Hanafy *et al.*, 2012**), and more recently in 2020 (the present study). Together with the other records in the Red Sea, previous bleaching events had indicated that the impact of the heat stress was more influential on some specific coral species (**Furby *et al.*, 2013**; **Monroe *et al.*, 2018**). In 2012, for example, the bleaching pattern that extended along the southern Egyptian coast of the Red Sea (up to Al-Quseir) and reached up to 10m depth, had particularly affected *Montipora*, *Porites*, *Stylophora*, *Pocillopora*, and *Millepora* (**Hanafy *et al.*, 2012**). In the current study, the same genera had demonstrated similar susceptibility during 2020 heat stress period. The detailed diagnostic results introduced here offer a solid evidence that some keystone genera are highly thermosensitive even at

the northern reefs (e.g., *Millepora* and *Montipora*), while others can be more thermotolerant even at the southern reefs (e.g., *Echinopora*). Our study, thus, emphasizes that the recent thermal stress conditions can drive dramatic effects on some keystone corals especially at the southern Egyptian coast. This pattern of bleaching severities between coral genera is most likely related to the differences in the composition of Symbiodiniaceae assemblages that directly outline the thermal tolerance of the host (Ziegler *et al.*, 2019). In this sense, the most susceptible genera to the 2020 heat stress event are those known to harbour *Symbiodinium* while corals experienced low bleaching severities are most known to associate with thermotolerant Symbiodiniaceae genotypes (i.e., those belonging to *Cladocopium* and *Durusdinium*) (Ziegler *et al.*, 2019). On the other hand, the bleaching severity may secondarily relate to the growth form of the coral colony (Hoogenboom *et al.*, 2017). In the present study, most of the threatened coral genera are those having branched growth form and those demonstrated high thermal tolerance are mostly massive with thick tissue layer (Loya *et al.*, 2001).

5. CONCLUSION

Despite our study does not provide any follow up data on coral recovery, however, it addresses the vulnerability of the NRS corals to the periodic summer heat stresses. Also, despite the recorded bleaching pattern was less acute at the Egyptian coast, current results suggest that the accumulated annual loss of coral cover can be magnified on the time-scale and may result in reef degradation particularly with increasing pace of recent thermal stress. In parallel, climate changes may derive dramatic changes in community structure of hard corals at the southern Egyptian reefs due to susceptibility of some keystone reef building corals to heat stress. Furthermore, the lack of periodic monitoring programs and the scarce of the published data on the previously recorded bleaching patterns at the Egyptian coast may incorrectly underrepresent the southern coasts on the regional map of coral bleaching hotspots in the Red Sea. On the other hand, the present study underlines the potential role of the northern reefs as a refugium for corals and hypothesizes that the high latitudinal reefs of the Red Sea may be the last to decline due to thermal stress. Finally, as a general trait for Red Sea corals, the present results highlight the thermal tolerance of some coral genera that may guide for reef conservation and restoration strategies for the worldwide community.

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7. REFERENCES

- Baird, A. and Marshall, P.** (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 237: 133-141. <https://doi.org/10.3354/meps237133>
- Berumen, M.L.; Arrigoni, R.; Bouwmeester, J.; Terraneo, T.I. and Benzoni, F.** (2019). Corals of the Red Sea. In: "Coral Reefs of the Red Sea." Voolstra, C.R. & Berumen, M.L. (Eds.). Cham, Switzerland: Springer, pp. 123-155. https://doi.org/10.1007/978-3-030-05802-9_7
- Chaidez, V.; Dreano, D.; Agusti, S.; Duarte, C.M. and Hoteit, I.** (2017). Decadal trends in Red Sea maximum surface temperature. *Sci. Rep.*, 7(1): 1-8. <https://doi.org/10.1038/s41598-017-08146-z>
- Ellis, J.I.; Jamil, T.; Anlauf, H.; Coker, D.J.; Curdia, J.; Hewitt, J.; Jones, B.H.; Krokos, G.; Kürten, B.; Hariprasad, D.; Roth, F.; Carvalho, S. and Hoteit, I.** (2019). Multiple stressor effects on coral reef ecosystems. *Glob. Chang. Biol.*, 25(12): 4131-4146. <https://doi.org/10.1111/gcb.14819>
- Fine, M.; Cinar, M.; Voolstra, C.R.; Safa, A.; Rinkevich, B.; Laffoley, D.; Hilmi, N. and Allemand, D.** (2019). Coral reefs of the Red Sea—Challenges and potential solutions. *Reg. Stud. Mar. Sci.*, 25: 1-13. <https://doi.org/10.1016/j.risma.2018.100498>
- Furby, K.A.; Bouwmeester, J. and Berumen, M.L.** (2013). Susceptibility of central Red Sea corals during a major bleaching event. *Coral Reefs*, 32(2): 505-513. <https://doi.org/10.1007/s00338-012-0998-5>
- Genevier, L.G.C.; Jamil, T.; Raitzos, D.E.; Krokos, G. and Hoteit, I.** (2019). Marine heatwaves reveal coral reef zones susceptible to bleaching in the Red Sea. *Glob. Chang. Biol.*: 2338–2351. <https://doi.org/10.1111/gcb.14652>
- Hanafy, M.H.; Ismail, M.; Abu El-Regal, M.A.; Agnese, M.; Maaty, M.; Dosoky, M.Y.; Nagm, M. and EL-Sadek, I.** (2012). *Climate change and its effect on the Egyptian coast of the Red Sea: The first recorded coral mass bleaching event.* Hurghada Environmental Protection and Conservation Association (HEPCA), Egypt.
- Hassan, M.; Kotb, M. and Al-Sofyani, A.** (2002). Status of Coral Reefs in the Red Sea-Gulf of Aden. In: "Status of coral reefs of the world, 2002 " Wilkinson, C. (Eds.). Townsville, Queensland, Australia: Australian Institute of Marine Science, pp. 45-53
- Hoogenboom, M.O.; Frank, G.E.; Chase, T.J.; Jurriaans, S.; Álvarez-Noriega, M.; Peterson, K.; Critchell, K.; Berry, K.L.E.; Nicolet, K.J.; Ramsby, B. and Paley, A.S.** (2017). Environmental Drivers of Variation in Bleaching Severity of

- Acropora* Species during an Extreme Thermal Anomaly. *Front. Mar. Sci.*, 4(376): 1-16. <https://doi.org/10.3389/fmars.2017.00376>
- Hughes, T.P.; Barnes, M.L.; Bellwood, D.R.; Cinner, J.E.; Cumming, G.S.; Jackson, J.B.C.; Kleypas, J.; van de Leemput, I.A.; Lough, J.M.; Morrison, T.H.; Palumbi, S.R.; van Nes, E.H. and Scheffer, M.** (2017). Coral reefs in the Anthropocene. *Nature*, 546(7656): 82-90. <https://doi.org/10.1038/nature22901>
- Hughes, T.P.; Kerry, J.T.; Baird, A.H.; Connolly, S.R.; Dietzel, A.; Eakin, C.M.; Heron, S.F.; Hoey, A.S.; Hoogenboom, M.O.; Liu, G.; McWilliam, M.J.; Pears, R.J.; Pratchett, M.S.; Skirving, W.J.; Stella, J.S. and Torda, G.** (2018). Global warming transforms coral reef assemblages. *Nature*, 556(7702): 492-496. <https://doi.org/10.1038/s41586-018-0041-2>
- Johnston, E.C.; Counsell, C.W.W.; Sale, T.L.; Burgess, S.C. and Toonen, R.J.** (2020). The legacy of stress: Coral bleaching impacts reproduction years later. *Funct. Ecol.*, 34(11): 2315-2325. <https://doi.org/10.1111/1365-2435.13653>
- Kleinhaus, K.; Al-Sawalmih, A.; Barshis, D.J.; Genin, A.; Grace, L.N.; Hoegh-Guldberg, O.; Loya, Y.; Meibom, A.; Osman, E.O.; Ruch, J.-D.; Shaked, Y.; Woolstra, C.R.; Zvuloni, A. and Fine, M.** (2020). Science, Diplomacy, and the Red Sea's Unique Coral Reef: It's Time for Action. *Front. Mar. Sci.*, 7(90): 1-9. <https://doi.org/10.3389/fmars.2020.00090>
- Koester, A.; Migani, V.; Bunbury, N.; Ford, A.; Sanchez, C. and Wild, C.** (2020). Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles. *Sci. Rep.*, 10(1): 1-14. <https://doi.org/10.1038/s41598-020-74077-x>
- Kotb, M.; Hanafy, M.; H, R.; S, M.; Al-Sofyani, A.; G, A.; G, B. and Al-Horani, F.** (2008). Status of Coral Reefs in the Red Sea and Gulf of Aden in 2008. In: "Status of coral reefs of the world, 2008." Wilkinson, C. (Eds.). Townsville, Queensland, Australia: Australian Institute of Marine Science, pp. 67-78
- Krueger, T.; Horwitz, N.; Bodin, J.; Giovani, M.-E.; Escrig, S.; Meibom, A. and Fine, M.** (2017). Common reef-building coral in the Northern Red Sea resistant to elevated temperature and acidification. *R. Soc. Open Sci.*, 4(5): 1-13. <https://doi.org/10.1098/rsos.170038>
- Kubicek, A.; Breckling, B.; Hoegh-Guldberg, O. and Reuter, H.** (2019). Climate change drives trait-shifts in coral reef communities. *Sci. Rep.*, 9(1): 1-10. <https://doi.org/10.1038/s41598-019-38962-4>
- Loya, Y.; Sakai, K.; Yamazato, K.; Nakano, Y.; Sambali, H. and van Woesik, R.** (2001). Coral bleaching: the winners and the losers. *Ecol. Lett.*, 4(2): 122-131. <https://doi.org/10.1046/j.1461-0248.2001.00203.x>

- Manzello, D.P.; Matz, M.V.; Enochs, I.C.; Valentino, L.; Carlton, R.D.; Kolodziej, G.; Serrano, X.; Towle, E.K. and Jankulak, M.** (2019). Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Glob. Chang. Biol.*, 25(3): 1016-1031. <https://doi.org/10.1111/gcb.14545>
- McClanahan, T.** (2004). The relationship between bleaching and mortality of common corals. *Mar. Biol.*, 144: 1239-1245. <https://doi.org/10.1007/s00227-003-1271-9>
- McClanahan, T.R.; Ateweberhan, M.; Darling, E.S.; Graham, N.A.J. and Muthiga, N.A.** (2014). Biogeography and Change among Regional Coral Communities across the Western Indian Ocean. *PLoS One*, 9(4): 1-9. <https://doi.org/10.1371/journal.pone.0093385>
- McClanahan, T.R.; Darling, E.S.; Maina, J.M.; Muthiga, N.A.; D'agata, S.; Leblond, J.; Arthur, R.; Jupiter, S.D.; Wilson, S.K.; Mangubhai, S.; Ussi, A.M.; Guillaume, M.M.M.; Humphries, A.T.; Patankar, V.; Shedrawi, G.; Pagu, J. and Grimsditch, G.** (2020). Highly variable taxa-specific coral bleaching responses to thermal stresses. *Mar. Ecol. Prog. Ser.*, 648: 135-151. <https://doi.org/10.3354/meps13402>
- Mies, M.; Francini-Filho, R.B.; Zilberberg, C.; Garrido, A.G.; Longo, G.O.; Laurentino, E.; Güth, A.Z.; Sumida, P.Y.G. and Banha, T.N.S.** (2020). South Atlantic Coral Reefs Are Major Global Warming Refugia and Less Susceptible to Bleaching. *Front. Mar. Sci.*, 7(514): 1-13. <https://doi.org/10.3389/fmars.2020.00514>
- Monroe, A.A.; Ziegler, M.; Roik, A.; Röthig, T.; Hardenstine, R.S.; Emms, M.A.; Jensen, T.; Woolstra, C.R. and Berumen, M.L.** (2018). In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. *PLoS One*, 13(4): 1-13. <https://doi.org/10.1371/journal.pone.0195814>
- Muir, P.R.; Marshall, P.A.; Abdulla, A. and Aguirre, J.D.** (2017). Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? *Proc. Royal Soc. B* . 284(1864): 1-7. <https://doi.org/10.1098/rspb.2017.1551>
- Obura, D.** (2001). Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress. *Bull. Mar. Sci.*, 69: 421-442.
- Osman, E.O.; Smith, D.J.; Ziegler, M.; Kürten, B.; Conrad, C.; El-Haddad, K.M.; Woolstra, C.R. and Suggett, D.J.** (2018). Thermal refugia against coral bleaching throughout the northern Red Sea. *Glob. Chang. Biol.*, 24(2): e474-e484. <https://doi.org/10.1111/gcb.13895>

- Osman, E.O.; Suggett, D.J.; Voolstra, C.R.; Pettay, D.T.; Clark, D.R.; Pogoreutz, C.; Sampayo, E.M.; Warner, M.E. and Smith, D.J.** (2020). Coral microbiome composition along the northern Red Sea suggests high plasticity of bacterial and specificity of endosymbiotic dinoflagellate communities. *Microbiome*, 8(1): 1-16. <https://doi.org/10.1186/s40168-019-0776-5>
- Overmans, S. and Agustí, S.** (2020). Unraveling the Seasonality of UV Exposure in Reef Waters of a Rapidly Warming (Sub-)tropical Sea. *Front. Mar. Sci.*, 7(111): 1-19. <https://doi.org/10.3389/fmars.2020.00111>
- Qin, Z.; Yu, K.; Chen, B.; Wang, Y.; Liang, J.; Luo, W.; Xu, L. and Huang, X.** (2019). Diversity of Symbiodiniaceae in 15 Coral Species From the Southern South China Sea: Potential Relationship With Coral Thermal Adaptability. *Front. Microbiol.*, 10(2343): 1-12. <https://doi.org/10.3389/fmicb.2019.02343>
- Riegl, B.; Johnston, M.; Purkis, S.; Howells, E.; Burt, J.; Steiner, S.C.C.; Sheppard, C.R.C. and Bauman, A.** (2018). Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Glob. Chang. Biol.*, 24(6): 2447-2462. <https://doi.org/10.1111/gcb.14114>
- Robitzch, V.; Banguera-Hinestroza, E.; Sawall, Y.; Al-Sofyani, A. and Voolstra, C.R.** (2015). Absence of genetic differentiation in the coral *Pocillopora verrucosa* along environmental gradients of the Saudi Arabian Red Sea. *Front. Mar. Sci.*, 2(5): 1-10. <https://doi.org/10.3389/fmars.2015.00005>
- Sampayo, E.M.; Ridgway, T.; Bongaerts, P. and Hoegh-Guldberg, O.** (2008). Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. *PNAS*, 105(30): 10444-10449. <https://doi.org/10.1073/pnas.0708049105>
- Sawall, Y.; Al-Sofyani, A.; Hohn, S.; Banguera-Hinestroza, E.; Voolstra, C.R. and Wahl, M.** (2015). Extensive phenotypic plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential to warming. *Sci. Rep.*, 5(1): 1-9. <https://doi.org/10.1038/srep08940>
- Shaltout, M.** (2019). Recent sea surface temperature trends and future scenarios for the Red Sea. *Oceanologia*, 61(4): 484-504. <https://doi.org/10.1016/j.oceano.2019.05.002>
- Shlesinger, T. and Loya, Y.** (2019). Breakdown in spawning synchrony: A silent threat to coral persistence. *Science*, 365(6457): 1002-1007. <https://doi.org/10.1126/science.aax0110>
- Spalding, M.D.; Ravilious, C. and Green, E.P.** (2001). *World atlas of coral reefs*. Berkeley, USA: University of California Press, 424pp.

-
- Team, R.C.** (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Thomas, L.; Rose, N.H.; Bay, R.A.; López, E.H.; Morikawa, M.K.; Ruiz-Jones, L. and Palumbi, S.R.** (2018). Mechanisms of Thermal Tolerance in Reef-Building Corals across a Fine-Grained Environmental Mosaic: Lessons from Ofu, American Samoa. *Front. Mar. Sci.*, 4(434): 1-14. <https://doi.org/10.3389/fmars.2017.00434>
- van Hooidek, R.; Maynard, J.; Tamelander, J.; Gove, J.; Ahmadi, G.; Raymundo, L.; Williams, G.; Heron, S.F. and Planes, S.** (2016). Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci. Rep.*, 6(1): 1-8. <https://doi.org/10.1038/srep39666>
- van Woesik, R.; Sakai, K.; Ganase, A. and Loya, Y.** (2011). Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.*, 434: 67-76. <https://doi.org/10.3354/meps09203>
- Wilkinson, C.** (1998). Status of coral reefs of the world: 1998. Townsville, Australia: Australian Institute of Marine Science, 184pp.
- Ziegler, M.; Arif, C. and Voolstra, C.R.** (2019). Symbiodiniaceae Diversity in Red Sea Coral Reefs & Coral Bleaching. In: "Coral Reefs of the Red Sea." Voolstra, C.R. & Berumen, M.L. (Eds.). Cham, Switzerland: Springer, pp. 69-89. https://doi.org/10.1007/978-3-030-05802-9_5