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Status of Symbiodiniaceae abundance in hard corals during the 2020 bleaching event along the Egyptian Red Sea coast

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ABSTRACT

In the present study, the density of endosymbiotic dinoflagellates (Family: Symbiodiniaceae) has been used as a measure to investigate the effect of summer heat stress on the hard corals inhabiting the Egyptian coast of the Red Sea. Count data were collected between September and October 2020 throughout a microscopic examination of eight keystone coral genera (n= 301) sampled from three sectors (contain six sites), two reef localities (inshore and offshore), two depth ranges (0-5 m and 10-15 m), and four bleaching severity states (from 0% unbleached to 51-99% highly bleached colonies). The results indicated that coral samples collected from the southern sites (Sector_3) were associated with lower densities of Symbiodiniaceae compared to coral samples collected from the northern (Sector_1) or mid sites (Sector_2). Also, samples collected from the surface water had demonstrated lower Symbiodiniaceae density compared to those collected from the deep. Conversely, our results indicated that there was no effect for the distance from the shore on the Symbiodiniaceae density in the examined samples. Furthermore, our analysis revealed that *Millepora* was particularly associated with the lowest Symbiodiniaceae density among the other genera. On the other hand, the density of Symbiodiniaceae cells decreased – as expected – with increasing bleaching severity in the study samples (n= 131). However, this discrimination between bleached and unbleached colonies was largely restricted to acute bleaching severities. Taken together, these results suggest that while the corals at the northern Egyptian coast of the Red Sea look more tolerant, corals at the southern reefs may be threatened by the summer heat stress.

1. INTRODUCTION

While coral reefs represent one of the most important marine ecosystems, their construction and persistence are primarily dependent upon a consolidate setup between the coral host and a wide array of unicellular mutualistic dinoflagellates from the family Symbiodiniaceae (formerly genus *Symbiodinium*) **(LaJeunesse *et al.*, 2018)**. In general, these endosymbiotic algae live in association with the coral animal and many prokaryotes as a single unit known as a holobiont in which all partners are mutually linked by physiological pathways in an integrative framework **(Voolstra and Ziegler, 2020)**.

However, to maintain its integrity, corals endosymbiotic systems are considered dynamical systems in which the number of endosymbionts, and may be the composition, can be changed according to many physiological and environmental parameters **(Stimson, 1997; Fitt *et al.*, 2000; Sivaguru *et al.*, 2021)**. This fluctuation in endosymbionts abundance represents one of the regulatory means by which coral host adjusts its symbiotic machinery to reach the highest benefit and maximum performance **(Davy *et al.*, 2012; Cunning and Baker, 2014)**. Under normal conditions the typical coral's endodermal cell can harbor between 1-6 Symbiodiniaceae cells; depending on the host/symbiont cell size ratio **(Muscatine *et al.*, 1998)**. Consequently, millions of cells are usually distributed per cm^2 of the host area and interfere with the host's pigments to give the ultimate colony color.

Among many parameters, the density of *in hospite* Symbiodiniaceae cells can be influenced by multiple environmental perturbations **(Qin *et al.*, 2019)**. Nevertheless, thermal stresses resulting from climatic changes is one of the most important challenges facing coral reefs at the present time, as they negatively affect the abundance and genetic diversity of Symbiodiniaceae in coral colonies. When the period of heat stress prolonged, the thermosensitive corals show rapid response to the elevated sea surface temperature and exhibit noticeable fading in colony color that varies in degree according to the severity of the stress. The colony color reduction can be used as alarming sign for the loss of Symbiodiniaceae cells or their photosynthetic pigments and is considered the most known diagnostic feature for 'coral bleaching' **(Kleppel *et al.*, 1989; Grottoli *et al.*, 2021)**. However, recent studies indicated that the bleaching process proceeds according to complex and regulatory molecular mechanisms that often drive coral to eliminate harmful cellular products of Symbiodiniaceae cells during the period of heat stress **(Oakley and Davy, 2018)**. In this context, as the prevailing temperature exceeds the maximum monthly mean (MMM) temperature, endosymbionts algal cells begin to produce protein-damaging free oxygen radicals called reactive oxygen species (ROS). As the temperature above the MMM accumulates (degree heating weeks; DHWs≥4°C-weeks), host cell suffers overproduction of ROS to the extent that derives oxidative stress with which the host cell cannot maintain the algal symbiont **(Skirving *et al.*, 2020)**.

Thermal stress, therefore, is considered to be costly for corals, as the decrease in the number of Symbiodiniaceae cells can lead to a deficiency of up to 90% of the nutritional allocates transferred to the host, as well as a decrease in its growth performance and calcification rate **(Muscatine and Porter, 1977; Cantin *et al.*, 2010; Colombo-Pallotta *et al.*, 2010; Roth *et al.*, 2012)**. Despite that, the most insidious threat is that whenever the thermal stress reaches the bleaching threshold (MMM+1°C). At the bleaching thresholds and above, heat stress effects accumulate and unless the starved coral was not able to recover in the real-time, it dies. On this basis, frequent bleaching incidents can cause delay in the recovery of the endosymbiotic systems of corals and can

deteriorate coral growth and reef developments on the large-scale **(Grottoli *et al.*, 2014; Schoepf *et al.*, 2015; Neal *et al.*, 2017; Osborne *et al.*, 2017; Hughes *et al.*, 2018)**.

The aim of the present study was to investigate the potential effects of 2020 summer heat stress on Symbiodiniaceae abundance (hereafter Symbiodiniaceae density) in eight common reef-building coral genera along the Egyptian coast of the Red Sea. We further conjugate field data with microscopic examination in 131 coral samples (43.52% of the total study samples) to test the relationship between bleaching severity and Symbiodiniaceae density. Also, the difference between bleached and non-bleached colonies has been studied in each coral genus to test whether the density of Symbiodiniaceae was related to bleaching observations or not.

2. MATERIALS AND METHODS

2.1. Study sites and coral sampling

During the 2020 bleaching event, between September and October, coral fragments of eight genera (n= 301) had been collected from eight reefs located in six study sites along the Egyptian coast of the Red Sea (Fig. 1). These study sites are located within three sectors (each contains two sites). The first sector (Sector_1) is in the north and comprises reefs of Hurghada and Safaga. The second sector (Sector_2) is in the middle between Al-Quseir and Port Ghaleb. Samples from the southern sites (Sector_3), on the other hand, were collected from Marsa Alam and Wadi El-Gemal. Samples were randomly collected from the surface (0-5 m) and deep waters (10-15 m) of the inshore and offshore reefs as in Table "1". All samples were specifically collected from *Montipora*, *Acropora*, *Stylophora*, *Pocillopora*, *Porites*, *Echinopora*, *Goniastrea*, and *Millepora* colonies using hammer and chisel in prelabelled plastic bags by SCUBA diving. Later, coral tissue was air brushed and the resultant slurry was homogenized then centrifuged at 10,000 rpm for 10 min and finally resuspended in a known volume of filtered seawater. To avoid the underestimation of cell density, particularly in genus *Acropora*, fragments below 1-2 cm from the tip were used.

To assess the density of Symbiodiniaceae cells in the bleached and non-bleached corals and to determine the levels of cell loss in different coral genera during the heat stress period, the bleaching severity in 131 coral colonies had been recorded *in situ* before sampling. Accordingly, coral samples of the eight study genera (Table 2) had been collected from colonies that experienced 0%, 1-10%, 11-50%, and 51-99% bleaching symptoms [*sensu* **Baird and Marshall (2002)**].

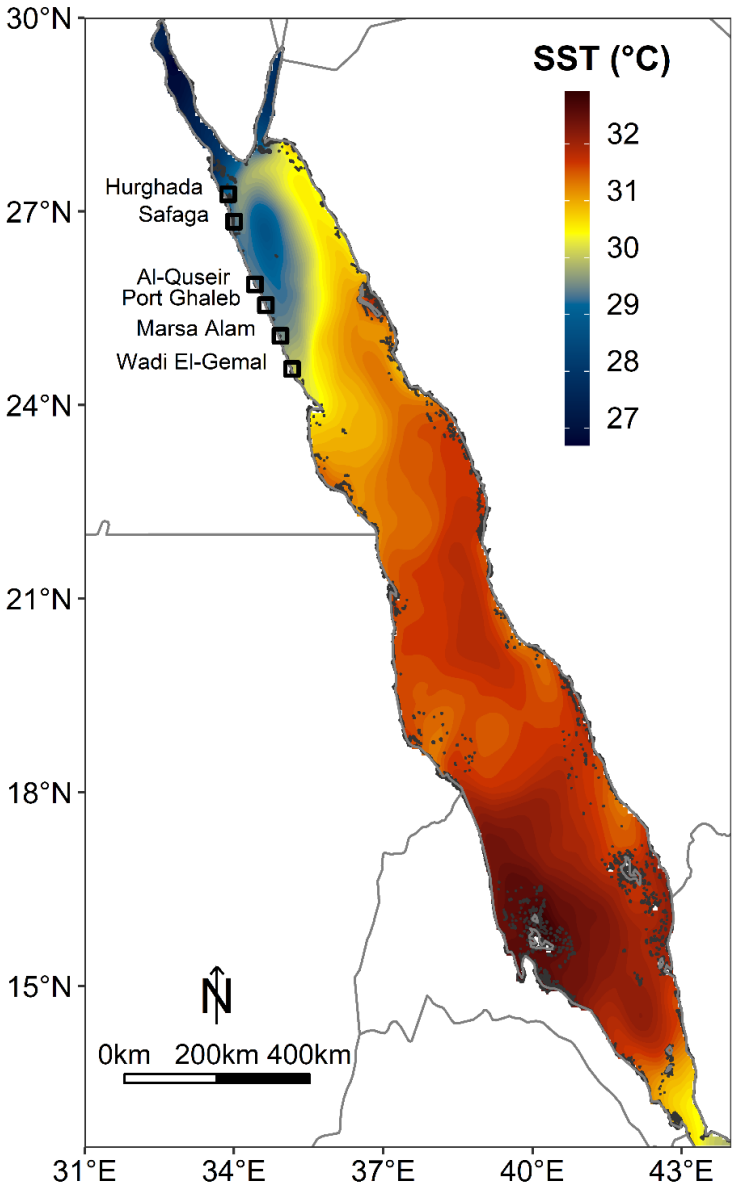

Fig. 1. Sampling sites at the Egyptian coast of the Red Sea (black rectangles). The map represents the mean SST pattern in the Red Sea during the period from 01 August to 31 October 2020.

2.2. Symbiodiniaceae cell count

Microscopic examination of three subsamples derived from each cell suspension was conducted using hemocytometer to estimate the average cell numbers in 1.0 mL. At this step, the cell density was calculated by multiplying the average cell number in 1.0 mL by the total volume of cell suspension. After that, to determine the Symbiodiniaceae cell density per cm^2 of the coral fragment, 3D surface area of each skeleton was determined using the paint coating method; an analogue to the wax weight method **(Stimson and Kinzie, 1991)**. Firstly, dry fragments of hard corals had been weighted using an

analytical balance. Then, the cutting area of the coral surface that was containing no tissue was sealed by hot glue to prevent covering of this area with paint. Each fragment was then dipped in a matt paint and vigorously shacked in the air five times and left to dry. This step was repeated twice to guarantee that all skeleton surfaces are fully covered with the paint. After drying, the glue was removed, and the coral fragment was re-weighted. To get the surface area of the fragments, a standard curve of known areas against the standard paint weight was constructed. The curve was used to generate the straight-line equation that was used to calculate the surface area of the fragments. The density of Symbiodiniaceae cells was finally normalized to 1.0 cm^2 of the total calculated area.

Table 1. Number of coral samples collected from each study site.

Sector	Site	Reef	Location		Reef distance	Depth		Total
			Lat. (°N)	Long. (°E)		Surface	Deep	
Sector_1	Hurghada	Magaweesh	27.14	33.87	Offshore	22	23	**45**
	Safaga	Soma Bay	26.84	34.00	Inshore	30	-	**30**
Sector_2	Al-Quseir	Mangrove Bay	25.87	34.42	Inshore	33	26	**59**
	Port Ghaleb	Port Ghaleb	25.55	34.64	Inshore	36	-	**36**
Sector_3	Marsa Alam	Marsa Asalaya	25.16	34.85	Inshore	24	-	**24**
	Marsa Alam	Shaab Marsa Alam	25.07	34.94	Offshore	26	13	**39**
	Marsa Alam	Marsa Samadai	25.01	34.93	Inshore	21	21	**42**
	Wadi El-Gemal	Ras-Hankourab	24.56	35.17	Inshore	26	-	**26**
Total						**218**	**83**	**301**

Table 2. Number of coral samples examined in each bleaching category. Because coral colonies showing incidence of 51-99% bleaching severity were not common in most genera, some samples in this category have not been collected and consequently given here as NA.

Genus	0%	1-10%	11-50%	51-99%	Total
Montipora	6	5	5	2	**18**
Acropora	10	2	5	1	**18**
Stylophora	9	4	1	NA	**14**
Pocillopora	9	10	2	2	**23**
Porites	4	8	2	NA	**14**
Echinopora	6	5	1	NA	**12**
Goniastrea	2	6	3	1	**12**
Millepora	5	6	8	1	**20**
Total	**51**	**46**	**27**	**7**	**131**

2.3. Statistical analysis

Data of Symbiodiniaceae density were tested for normality and homogeneity using Shapiro and Levene's tests, respectively. Subsequently, effects of the location, distance from the shore, depth, host identity, and bleaching severity level on the Symbiodiniaceae density were analyzed using One-Way ANOVA and Kruskal-Wallis test. Multiple comparisons using Tukey's and Dunn's *post hoc* tests were also applied to test the differences between sectors and between sites. To determine whether the paling of the colony color in the studied genera was attributed to cell loss or not, a receiver operating characteristic curve (ROC curve) was constructed and the area under the curve (AUC) was determined using ROCit package. This approach was used for different bleaching categories of corals suffering different degrees of color variability. ROC analysis was performed using density data collected from 131 coral samples against their bleaching status of binary levels (i.e., non-bleached colonies = 0 and bleached colonies = 1) for each bleaching severity category. All statistical analyses were conducted using R **(Team, 2020)**.

3. RESULTS

The overall density of symbiont cells in the studied samples (n = 301) ranged between 0 and 4.151877×10^6 cell/cm^2 with average $(0.705801 \pm 0.03426031) \times 10^6$ cell/cm^2 during the period of the study. However, the microscopic examination of coral samples collected from surface water of all study sites (n = 218) revealed that corals collected from Sector_3 have harbored the lowest mean Symbiodiniaceae cell density [$(0.3518495 \pm 0.03000495) \times 10^6$ cell/cm^2]. Compared to this, the mean Symbiodiniaceae cell number was 48.76% and 39.82% higher in corals of Sector_1 and Sector_2, respectively (One-Way ANOVA; df = 2, F = 50.23, $p<0.05$). In contrast, the mean Symbiodiniaceae density in corals of Sector_1 was only 11.10% higher than the mean density in corals of Sector_2, whereby there was no significant difference between them (Tukey's test; $p>0.05$). Regarding the sites, samples collected from Hurghada showed the highest mean Symbiodiniaceae density [$(1.2837652 \pm 0.19317672) \times 10^6$ cell/cm^2] followed by Port Ghaleb, Safaga, and Al-Quseir (Fig. 2a). Despite our analysis showed significant different between all sites (One-Way ANOVA; df = 5, F = 23.09, $p<0.05$), corals in these four sites had almost harbored similar densities of Symbiodiniaceae cells (Table 3). On the other hand, corals in Sector_3 had suffered high reduction in the mean Symbiodiniaceae content that did not exceed $(0.3645873 \pm 0.03459194) \times 10^6$ cell/cm^2 in Marsa Alam and $(0.3170652 \pm 0.06068173) \times 10^6$ cell/cm^2 in Wadi El-Gemal. The present results also indicated that although the Symbiodiniaceae density was not different in coral samples collected form these two sites, it was highly lower than the densities in the other sites.

The current study moreover showed that corals present at the surface water were associated with mean endosymbionts density of (0.6589247 ± 0.03773269) × 10^6 cell/cm^2, while those found deeper (i.e., beyond 10 m) were harboring (0.8289220 ± 0.07363400) × 10^6 cell/cm^2 (Fig. 2b). The results indicated that the depth from which coral samples were taken had influenced the density of Symbiodiniaceae where the surface water samples (n = 218) were associated with Symbiodiniaceae cell content 11.43% lower than those present in the deep (n = 83) (Kruskal-Wallis test; df = 1, χ^2= 4.15, p<0.05). On contrary, despite the samples collected from the inshore reefs (n = 170) had harbored Symbiodiniaceae density lower by 10.85% than those collected from offshore reefs (n = 48), there was no significant different in the Symbiodiniaceae content between them (Kruskal-Wallis test; df = 1, χ^2 = 0.27, p>0.05) (Fig. 2c).

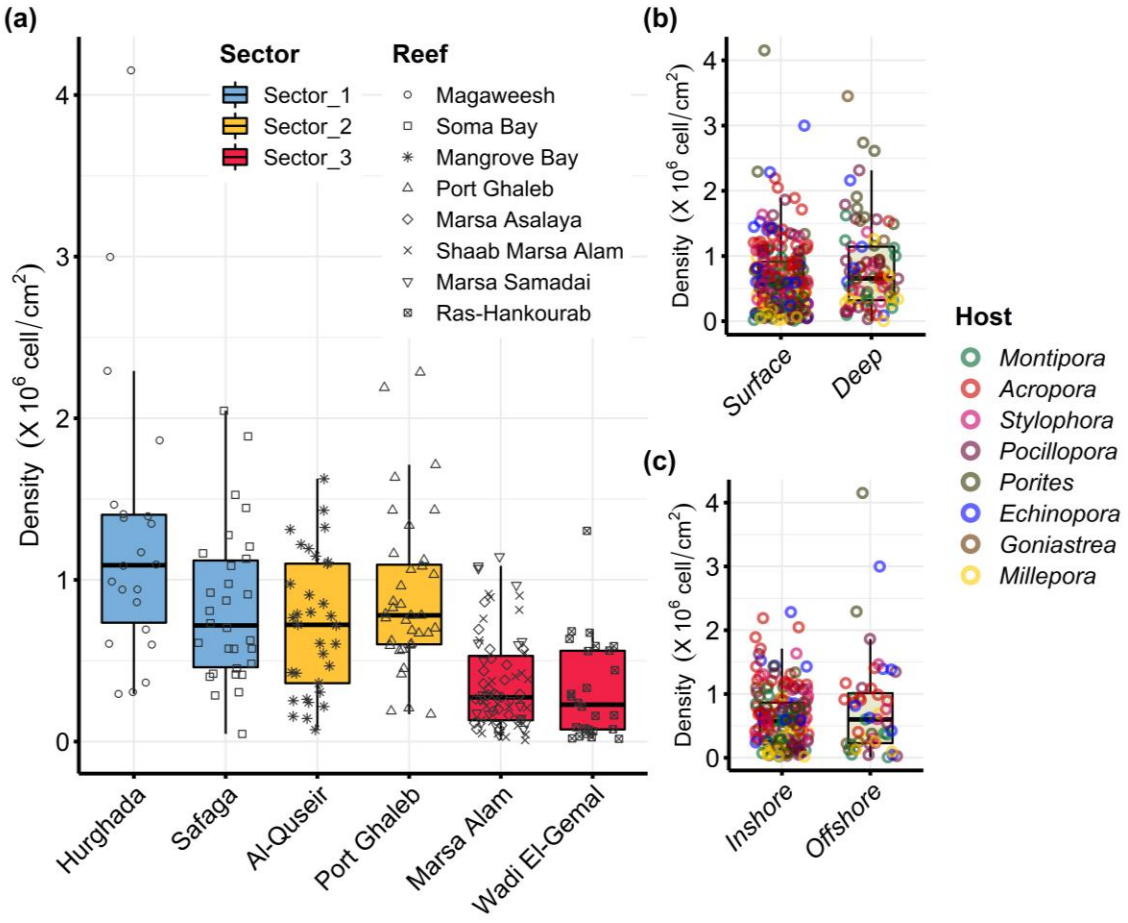

Fig. 2. Patterns of Symbiodiniaceae cell density during the heat stress period along the Egyptian coast of the Red Sea. (a) Density of Symbiodiniaceae in coral samples collected from eight reefs of six study sites and three sectors. (b) Density of Symbiodiniaceae associated with studied genera collected from surface and deep waters. (c) Symbiodiniaceae density within coral genera inhabiting inshore and offshore reefs.

Whether the examined samples were collected from north or south, surface or deep, or from inshore or offshore reefs, density of Symbiodiniaceae was also affected by the host identity (Kruskal-Wallis test; df = 7, χ^2 = 53.10, p<0.05). Among the eight

examined hosts, *Millepora* (n = 40) exhibited the lowest Symbiodiniaceae cell content of (0.3053746 ± 0.03998895) × 10^6 cell/cm^2. The pairwise Dunn's test on the other hand showed that all genera, except *Stylophora*, collected from Sector_3 had contained significantly low densities of Symbiodiniaceae compared to those collected from Sector_1 (p<0.05). In contrast, there was no difference in the Symbiodiniaceae density between Sector_1 and Sector_2 in all coral genera (Fig. 3). Furthermore, in *Acropora*, *Pocillopora*, *Echinopora*, and *Goniastrea*, the pattern of Symbiodiniaceae density was similar and the collected samples from Sector_3 showed significantly lower Symbiodiniaceae density than sample of Sector_2. A different pattern, however, had been reported in *Montipora*, *Porites*, and *Millepora* where Symbiodiniaceae density decreased gradually from north to south with no difference between each two adjacent sectors.

Table 3. Tukey's *post hoc* pairwise comparisons test of Symbiodiniaceae density between the study sites.

Site		difference	lower	upper	*p*
Safaga	**Hurghada**	-454644.09	-832322.77	-76965.41	0.076
Al-Quseir	**Hurghada**	-561131.04	-931475.45	-190786.63	**0.005**
Port Ghaleb	**Hurghada**	-379520.92	-743640.61	-15401.23	0.243
Marsa Alam	**Hurghada**	-919177.88	-1247495.14	-590860.61	**<0.0001**
Wadi El-Gemal	**Hurghada**	-966699.96	-1356476.20	-576923.71	**<0.0001**
Al-Quseir	**Safaga**	-106486.95	-445913.21	232939.31	0.934
Port Ghaleb	**Safaga**	75123.17	-257500.27	407746.61	0.984
Marsa Alam	**Safaga**	-464533.78	-757531.10	-171536.46	**<0.0001**
Wadi El-Gemal	**Safaga**	-512055.87	-872584.26	-151527.47	**<0.0001**
Port Ghaleb	**Al-Quseir**	181610.12	-142661.61	505881.85	0.542
Marsa Alam	**Al-Quseir**	-358046.84	-641527.40	-74566.27	**<0.001**
Wadi El-Gemal	**Al-Quseir**	-405568.92	-758406.73	-52731.10	**<0.001**
Marsa Alam	**Port Ghaleb**	-539656.96	-814955.70	-264358.21	**<0.0001**
Wadi El-Gemal	**Port Ghaleb**	-587179.04	-933477.59	-240880.48	**<0.0001**
Wadi El-Gemal	**Marsa Alam**	-47522.08	-355956.46	260912.30	0.924

As it was expected, density of Symbiodiniaceae decreased in the examined host samples (n = 131) with increasing bleaching severity. This was the case between the non-bleached and all bleaching severities and between the low (1-10%) and high (51-99%) bleaching severities (Fig. 4). In contrast, the examined coral samples collected from colonies experienced 11-50% bleaching severity showed non-significant difference in Symbiodiniaceae density when compared with 1-10% and 51-99% bleached colonies (Tukey's *post hoc* test, p>0.05). As indication for cell loss, ROC curve showed that the discrimination between the non-bleached corals and those partially bleached increases as the severity increases. Our analysis indicated that the low bleaching severity of 1-10% was not necessarily expresses a loss in endosymbionts cells (AUC = 0.67). However, the

chances to lose endosymbionts were high in coral colonies demonstrating mid and high bleaching severities (11-50% and 51-99%; respectively) (Fig. 5a).

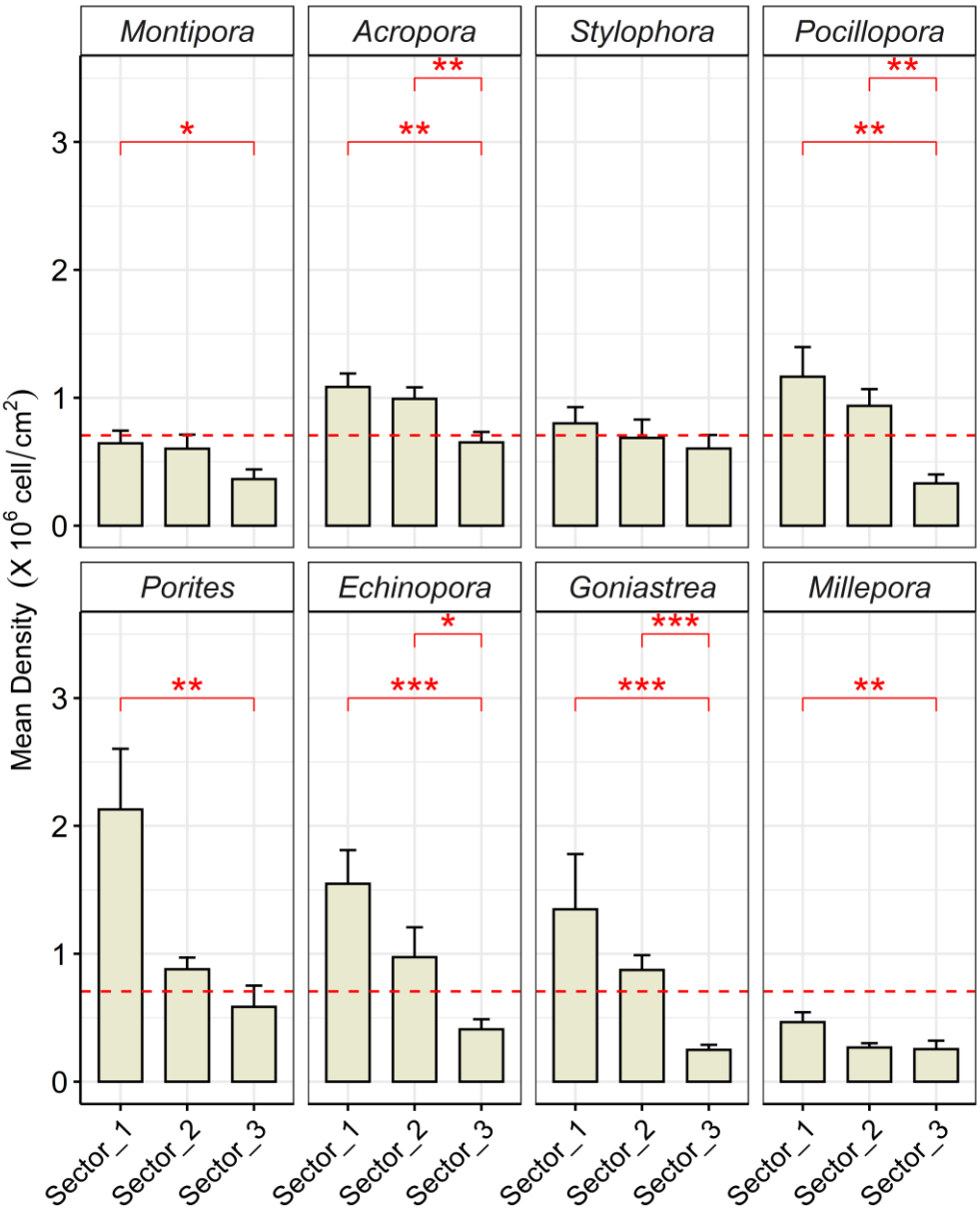

Fig. 3. Symbiodiniaceae density in coral genera within each sector. The Red dashed line represents the overall mean density of Symbiodiniaceae in all genera and sectors. The pairwise difference between each two sectors was tested using Dunn's test and only significant *p* values are denoted with the red top asterisks. The number of red asterisks indicates the level of significance; $p<0.05$ (*), $p<0.001$ (**), and $p<0.0001$ (***).

Results also showed that the field discrimination between bleached and non-bleached corals was consistent with count data of Symbiodiniaceae content in most hosts. This was apparent in coral hosts such as *Montipora*, *Pocillopora*, *Echinopora*, *Goniastrea*, and

Millepora where the AUC exceeded 0.7 (Fig. 5b). Unlikely, our field observations in the other host genera were less matched with microscopic examination. For example, and more interestingly, despite *Porites* colonies showed high levels of bleaching severity, they were associated with high Symbiodiniaceae cell content (Fig. 6). Similar pattern was also recorded in *Acropora* and *Stylophora* where both bleached and non-bleached corals exhibited similar Symbiodiniaceae cell content.

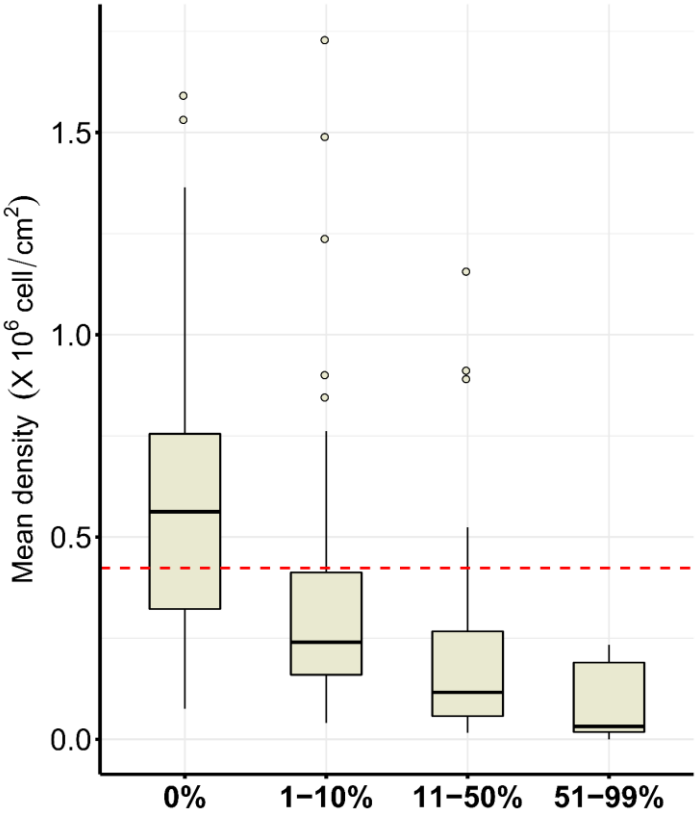

Fig. 4. Symbiodiniaceae density limits in coral samples experienced different bleaching severities. Horizontal (red) dashed line represents the overall mean density.

4. DISCUSSION

The current study points out the effect of 2020 summer heat stress on common reef-building corals inhabiting the Egyptian coast of the Red Sea by focusing on Symbiodiniaceae abundance in eight keystone coral genera collected from six sites (between Hurghada and wadi El-Gemal), two reef localities (inshore and offshore), two depth ranges (0-5 m and 10-15 m), and different bleaching severities (0% unbleached to 51-99% bleached colonies). Results indicated that corals inhabiting the northern Egyptian reefs were associated with high density of Symbiodiniaceae when compared with corals of the southern sites. This pattern was in compliance with the recorded bleaching pattern along the Egyptian coast of the Red Sea **(Hanafy *et al.*, 2012)**.

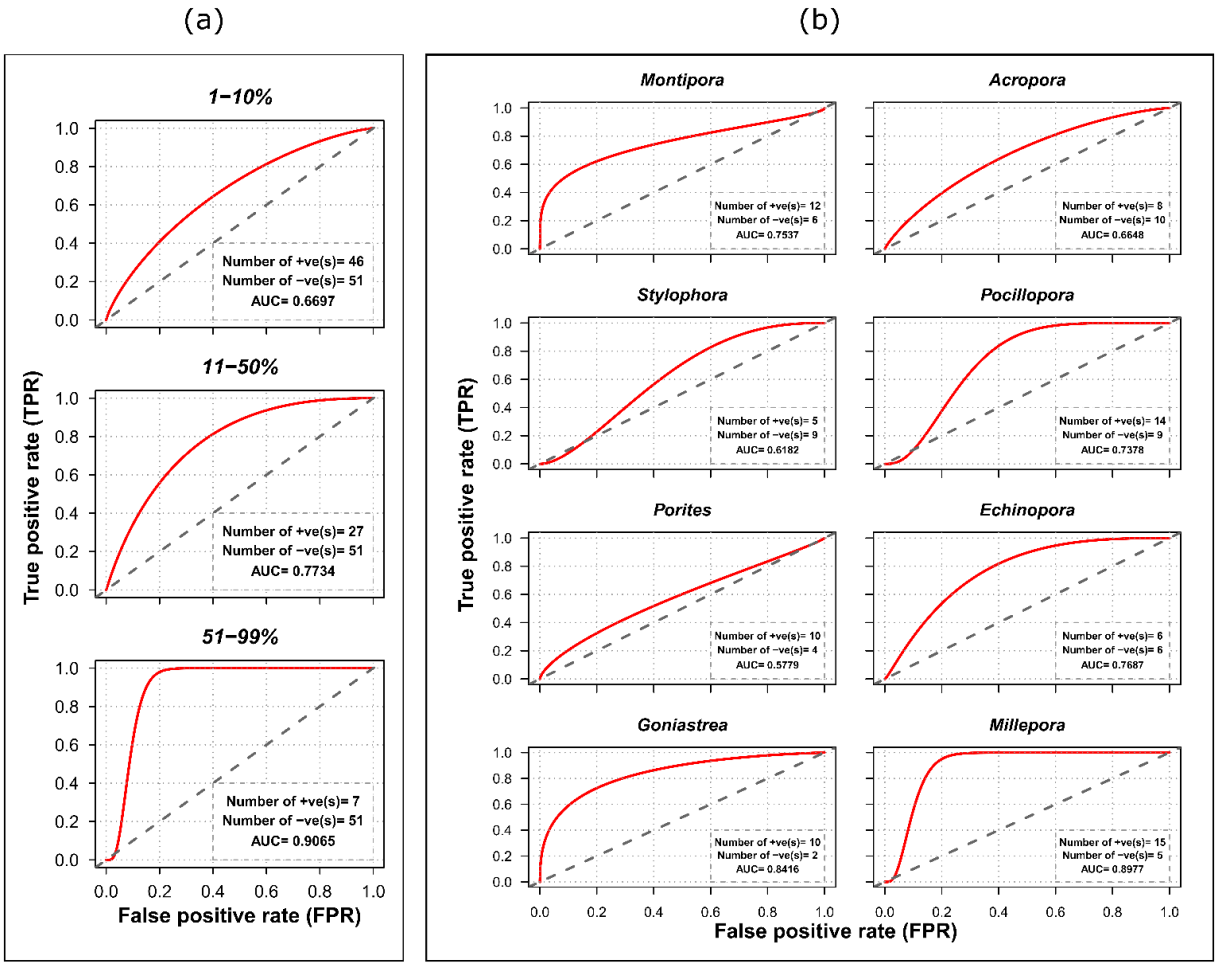

Fig. 5. Evaluation of bleaching severities based on Symbiodiniaceae cell density. (a) ROC discrimination curves of low (1-10%), mid (11-50%), and high (51-99%) bleaching severities. Note that the AUC increases as the severity increased. (b) Individual ROC discrimination curves for each coral genus. Notably, in *Porites*, bleached colonies were most likely unrelated to the loss of Symbiodiniaceae cells.

Despite we have not introduced any before-after comparative data, but we can derive speculation on the implications of the recorded Symbiodiniaceae density reduction from the north to the south. Our results imply that corals in the south may experience more reduction in the growth performance if the increased heat stress is sustained. This speculation can be evident by many studies that showed supportive evidence for the effects of Symbiodiniaceae density on the growth rate of the host [*see* **Grottoli *et al.* (2021)**]. For instance, **Cantin *et al.* (2010)** have shown that the consequences of the frequent heat stresses in the central Red Sea can extend to affect the growth rate of corals even if they have not notable bleaching susceptibility. Given that the concentration of the nutrients in the northern Red Sea is so limited **(Sawall *et al.*, 2015)**, the density of Symbiodiniaceae may be critical for coral growth. In this regard, **Rouzé *et al.* (2019)** have recently indicated that the growth of corals tends to be dependent and more likely controlled throughout quantitative and qualitative traits of Symbiodiniaceae assemblages. Therefore, our results propose that despite most corals at the Egyptian coast of the Red Sea exhibit relatively high thermal tolerance and demonstrating a low incidence of bleaching cover during the heat stress period **(Osman *et al.*, 2018; Genevier *et al.*, 2019)**, the low Symbiodiniaceae density may drive a reduction in the photosynthates consumed by the coral and can ultimately lead to decrease in coral growth and fitness.

Another aspect was that although offshore reefs usually demonstrate a little incidence of coral bleaching compared with inshore conspecifics **(Furby *et al.*, 2013; Monroe *et al.*, 2018)**, our results had indicated no contribution of the distance from the shore on Symbiodiniaceae density. In the present study, offshore reefs were not much far from the inshore reefs and the thermal stress is consequently more similar between the two reef systems. This is corroborated by results from **Hanafy *et al.* (2012)** who indicated that inshore and offshore reefs have the same response to coral bleaching and both may be susceptible to heat stress along the southern Egyptian coast. On contrary, the effect of the depth was more apparent where the surface water corals had been influenced by summer heat stress. The reduction in the Symbiodiniaceae density in corals inhabiting shallow depths may be attributed to the synergistic effect of heat stress and high irradiance during the summertime **(Sivaguru *et al.*, 2021)**.

In a more interesting insight of the present study, the reduction in Symbiodiniaceae density associated with coral genera like *Montipora* and *Millepora* suggests thermosensitive traits for these genera. By comparing such results with corals demonstrating high Symbiodiniaceae density (e.g., *Echinopora* and *Porites*), despite the presence of heat stress, a growing body of evidence can attribute this effect to the differences in the genetic composition of Symbiodiniaceae assemblages harbored by these genera. Here, we noted that the low Symbiodiniaceae density was mostly associated with corals harboring *Symbiodinium*, while corals that known to harbor *Durusdinium* and to a lesser extent *Cladocopium* were associated with high densities **(Ziegler *et al.*, 2017;**

Ziegler *et al.*, 2019; Hume *et al.*, 2020). Given that the *Symbiodinium* and *Cladocopium* are more dominant in corals of the northern Red Sea **(Ziegler *et al.*, 2019; Osman *et al.*, 2020)**, our results imply that the increasing effect of the heat stress may drive adverse consequences on reef corals at the Egyptian coast and may deteriorate community composition therein.

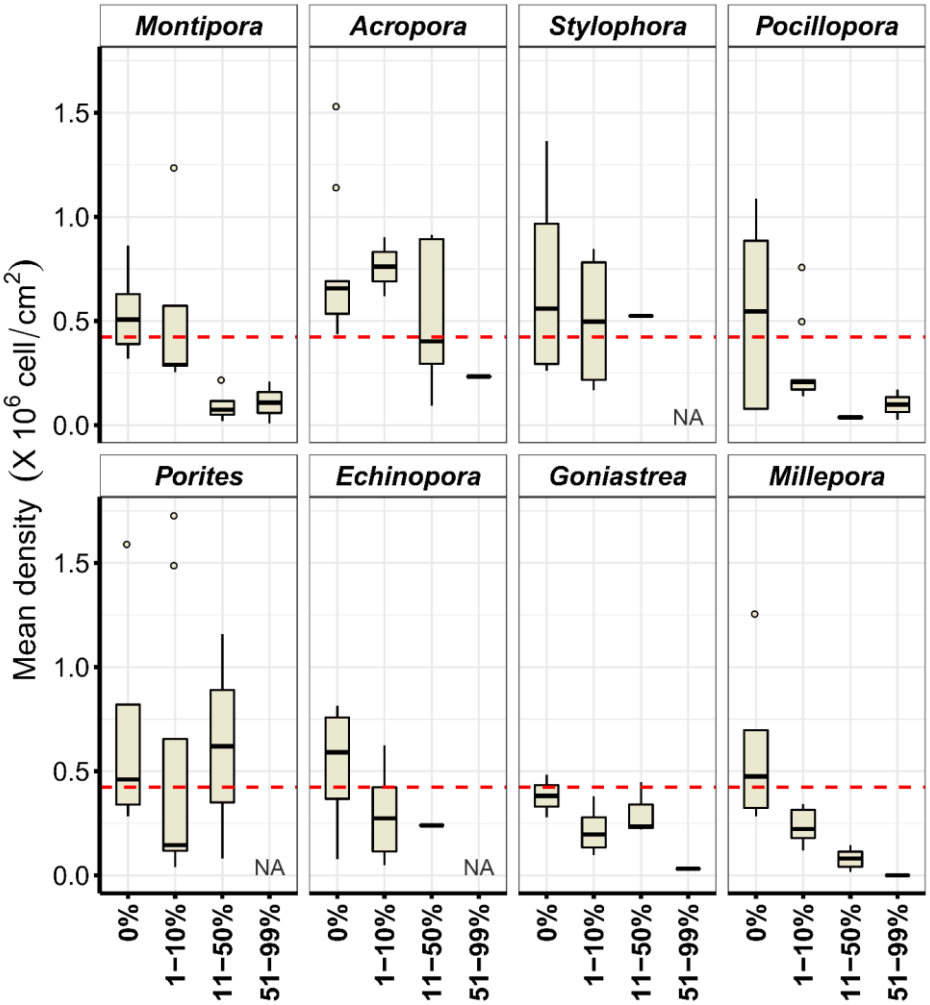

Fig. 6. Symbiodiniaceae density in different host genera experienced different levels of bleaching severities. Horizontal (red) dashed line represents the overall mean density.

The current study revealed that the increasing severity of bleaching was mostly associated with declining in Symbiodiniaceae cell density. Microscopic examination, however, had revealed that this pattern was not true for all bleaching severities and host genera. In this regard, our results suggested that corals manifested 1-10% bleaching severity would not necessarily suffer cell density loss. Accordingly, the recorded ambiguous patterns between bleached and non-bleached colonies of some hosts may indicate a reduction in the photosynthetic pigment content rather than partial or total loss of cell content. Similarly, corals such as *Porites*, although among the highly affected

genera by thermal stress at northern and central Red Sea **(Hanafy *et al.*, 2012; Monroe *et al.*, 2018)**, there is little evidence for Symbiodiniaceae cell loss. Recently, **Terraneo *et al.* (2019)** had shown that the endosymbiotic systems associated with *Porites* have relative abundance changes in the three Symbiodiniaceae genera (i.e., *Symbiodinium*, *Cladocopium*, and *Durusdinium*) along the thermal gradient environment of the Red Sea. In the light of the present data, we therefore suggest high resilience of this genus. This also can be supported by the flexibility of this genus to harbor multiple Symbiodiniaceae genera.

5. ACKNOWLEDGEMENTS

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