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Thermal Resilience of Corals in the Southern Egyptian Red Sea Reefs

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ABSTRACT

The Red Sea, particularly its northern region, has long been regarded as a thermal refuge for coral reefs due to their remarkable resilience to elevated sea surface temperatures associated with climate change. However, this perception has been increasingly challenged by recent mass bleaching events recorded in 2012, 2020, 2023, and most recently in 2024. This study systematically evaluated coral resilience patterns following the September 2023 mass bleaching event along the southern Egyptian Red Sea coast. During the summer of 2023, prolonged marine heatwaves in the northwestern Red Sea (Egyptian coast) triggered a severe bleaching event, with sea surface temperatures (SST) exceeding the summer monthly maximum mean (MMM; ≥32°C), the established bleaching threshold, from July to October. Post-bleaching assessments revealed significant interspecific and colony-level variability in resilience. While some corals exhibited full recovery, others suffered high mortality, with site-specific recovery rates ranging from 34 to 56%. Massive corals, particularly *Porites*, demonstrated the highest resilience (82% recovery), whereas branching genera such as Acropora and Stylophora showed the lowest recovery rates (29-31%) and the highest mortality (52% for Acropora sp.). Surprisingly, depth (2–10m) and cross-shelf position (inshore vs. offshore) had minimal influence on recovery outcomes, suggesting that coral responses were primarily shaped by species-specific traits, microbiome composition, and local environmental conditions. Despite the Red Sea's reputation as a thermal refuge, the 2023 event underscores that even thermally tolerant reefs are highly vulnerable to prolonged heat stress. These findings highlight the urgent need for targeted conservation strategies, including microbiomeassisted resilience interventions, to safeguard these critical ecosystems in the face of intensifying climate-driven bleaching events.

INTRODUCTION

Over the past three decades—the warmest globally on record—rising sea surface temperatures (SST) have triggered four pan-tropical mass coral bleaching events, occurring in 1998, 2010, 2016, and 2020, all linked to anthropogenic climate change (Berkelmans *et al.*, 2004; Hughes *et al.*, 2017a). Among these, the 2016 event was exceptionally severe, affecting more than 60% of global coral reefs, a fourfold increase in







impact compared to the 1998 and 2010 events (**Hughes** *et al.*, **2017a**). Compounding this threat, coral recovery rates have drastically declined, dropping from an average of 27 years between bleaching events in the 1980s to just 5 years by 2016. This trend is strongly correlated with rising global temperatures (**Hughes** *et al.*, **2018**). The accelerated frequency and intensity of bleaching events underscore a critical threat to the long-term viability of coral reefs. Under current projections, bleaching events will worsen by 2050, further shortening recovery windows (**Van Hooidonk** *et al.*, **2016**). Even under the Paris Climate Agreement's 1.5°C warming target, 70–90% of global reefs face potential mortality (**Kleinhaus** *et al.*, **2020**). Despite these alarming trends, few studies have thoroughly examined coral adaptive capacity, leaving critical gaps in understanding how reefs might persist in a rapidly warming ocean (**Baskett** *et al.*, **2010**; **Bay** *et al.*, **2017**; **Matz** *et al.*, **2018**).

Coral recovery following bleaching events is influenced by a combination of ecological, environmental, and biological factors. Resilience—the capacity of corals to resist and recover from stress—depends on the coral holobiont's ability to regain symbiotic zooxanthellae (Symbiodiniaceae), maintain a stable microbiome, and repair tissue damage (Hughes et al., 2019). The loss of zooxanthellae during bleaching disrupts coral energetics, but some corals can either repopulate their symbionts from the environment or retain thermally tolerant clades, enhancing recovery (Torda et al., 2017). The prokaryotic microbiome associated with corals also plays a critical role in resilience by facilitating nutrient cycling, pathogen resistance, and stress adaptation (Peixoto et al., 2017). Post-bleaching shifts in microbial community composition may either enhance recovery and increase coral resilience (e.g., through proliferation of beneficial taxa) or accelerate deterioration (e.g., through pathogen dominance) (McDevitt-Irwin et al., 2017).

Environmental conditions such as water quality, temperature stability, and herbivory can further mediate recovery by reducing algal competition and facilitating coral recruitment (**Graham** *et al.*, 2015). However, repeated bleaching events, combined with pollution and ocean acidification, can disrupt both symbiont and eukaryotic microbiome stability, compromising resilience and triggering ecosystem shifts (**Peixoto** *et al.*, 2017; **Maher** *et al.*, 2019).

Nevertheless, corals in the Red Sea are known for their remarkably high resilience and their ability to thrive in extreme environmental conditions, including summer SSTs that can exceed 32°C (Eladawy et al., 2022). Despite this resilience, the specific adaptive strategies of the Red Sea corals to cope with extreme thermal conditions remain poorly understood. Hypotheses suggest that these corals may possess unique molecular and metabolic traits not found in other reef systems (Osman et al., 2018; Voolstra et al., 2021). Corals in this region are adapted to their unique geographical and physiological limits, making them exceptionally resilient (Fine et al., 2013). This resilience highlights

the Red Sea coral reefs as novel candidates for future studies of coral survival under climate change, thereby contributing to the development of effective global conservation and restoration strategies.

Egypt's coral reefs, which span approximately 400km along the western coast of the northern Red Sea, represent a critical portion of the region's biodiversity and are increasingly recognized as a potential thermal refuge under climate change (**Osman** *et al.*, 2018). Unlike other reefs, those in the northern Red Sea, particularly in Egypt, exhibit remarkable thermal resilience with bleaching thresholds up to 5–6°C above summer maxima, attributed to local adaptation and historical selection (**Fine** *et al.*, 2013; **Voolstra** *et al.*, 2021). However, bleaching events have impacted Egypt's reefs, though predominantly in the southern region, where temperatures exceed regional averages. This thermal gradient has created a distinct bleaching susceptibility threshold, with southern reefs experiencing two to three times greater bleaching prevalence than northern reefs during thermal stress events (**Hanafy & Dosoky**, 2023; **Hanafy & Salem**, 2024). For instance, the 2012 and 2020 bleaching events caused moderate bleaching in southern Egyptian reefs (**Dosoky** *et al.*, 2021).

The aim of this study was to assess the resilience of southern Egyptian coral reefs to the 2023 bleaching event, with a focus on understanding the recovery potential of various coral genera in response to thermal stress. By evaluating the effects of bleaching severity, depth, and reef location on coral recovery, this study seeked to identify patterns of resilience among different coral species and their associated habitats. Moreover, it aimed to fill the existing knowledge gap regarding genus-specific responses to bleaching, thereby providing critical insights for effective conservation and management strategies in the face of ongoing climate change.

MATERIALS AND METHODS

1. Study area and thermal conditions

In the summer of 2023, satellite-derived SST reached unusually high levels across the Red Sea (Fig. 1). Along the Egyptian coast, southern coral reefs from Marsa Alam to Shalateen experienced prolonged thermal stress, with temperatures exceeding 30°C for more than three months (July–October). This resulted in widespread bleaching across many southern reefs, whereas northern reefs remained relatively unaffected, with no significant heat-induced bleaching reported (Hanafy & Dosoky, 2023).

2. Site selection

Coral resilience was assessed in the southern region (between 24.23° N and 25.24° N), spanning from Marsa Alam to Lahami. Sites were chosen based on their minimal exposure to anthropogenic impacts and their location within the 2023 bleaching zone (Fig. 1). The selection also allowed for comparisons of coral resilience across shallow (2–5 m) and deeper waters (8–10 m), as well as between inshore and offshore reefs (Table 1). Additionally, these sites were characterized by high coral diversity, ensuring the representation of the genera included in this study.

Table 1. Number of tagged coral colonies in the study sites. A total of 288 colonies belonging to six coral genera were checked in September 2023 for their responses to bleaching event. Subsequently, the same colonies were re-checked in November 2023 to assess their response to recovery.

Site	Latitude	Longitude	Reef	De	Depth	
	(° N)	(° E)	system	2-5m	8-10m	
Marsa	25.24454	34.79679	Inshore	26	13	
Shagara						
Gottaa	25.07592	34.93673	Offshore	4	13	
Marsa Nakari	24.92665	34.96237	Inshore	25	22	
Gorgonia	24.70467	35.09097	Inshore	21	24	
Reef						
Keshta	24.67241	35.13323	Offshore	23	19	
Shelineat	24.66863	35.13111	Offshore	24	24	
Lahmi	24.23791	35.41597	Inshore	28	22	

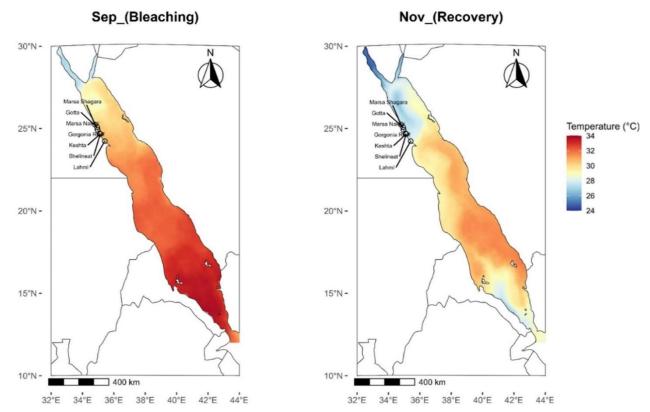


Fig. 1. Location of the study sites along the Egyptian coast of the Red Sea. The two maps depict the mean SST(°C) during September (bleaching event), and November 2023 (recovery).

3. Coral genera and tagging of colonies

In September 2023, a total of 288 bleached colonies representing six key coral genera were tagged at the study sites using uniquely numbered labels secured with rubber straps. Colonies were carefully selected to capture varying degrees of bleaching severity. The chosen genera were also selected based on their dominance and prevalence across the Egyptian Red Sea reefs, making them suitable indicators for assessing reef recovery potential in the southern region. These included *Montipora* (n = 52), *Acropora* (n = 48), *Pocillopora* (n = 55), *Stylophora* (n = 34), *Porites* (n = 49), and the non-scleractinian coral *Millepora* (n = 50). The same colonies were reassessed in November 2023 to evaluate post-bleaching recovery and resilience.

4. Assessing bleaching severity and recovery of corals

At the colony scale, bleaching severity was assessed visually using a 1–6 scoring system from the coral health chart (**Hoegh-Guldberg** *et al.*, **2006**). Each colony was evaluated *in situ* at five points across its entire surface. Based on the mean score, bleaching severity was categorized into four classes: Moderate (26–50%), High (51–75%), Severe (76–99%), and Complete (100%).

Coral recovery was assessed using a five-point scale (0–1), where 0 indicated 'dead' and 1 indicated 'live.' Colonies were then classified into three categories: Totally Recovered (all points scored 1), Partially Recovered (at least one point scored 0), and Totally Dead (all points scored 0).

5. Statistical analysis

To analyze coral recovery following the 2023 bleaching event, several statistical methods were applied. Shapiro–Wilk and Levene's tests were used to assess data normality and homogeneity, respectively. The one-way analysis of variance (ANOVA) tested the differences in the relative frequencies of fully recovered, partially recovered, and totally dead colonies among study sites, depth ranges (shallow vs. deep), and reef locations (inshore vs. offshore). Post hoc Dunn's test was used to identify specific differences in recovery rates across bleaching severity categories.

Bray–Curtis dissimilarity matrices were generated to evaluate similarities in coral recovery responses between study sites and among coral genera. A dendrogram based on these matrices was constructed to visualize clustering patterns of recovery. Principal coordinates analysis (PCoA) was performed to illustrate relationships among coral genera based on their recovery patterns, using the ggplot2 (Wickham, 2009) and vegan package (Oksanen, 2015) in R. In addition, permutational multivariate analysis of variance (PERMANOVA, 999 permutations) (Anderson, 2001) was conducted to test for significant differences in recovery potential among coral genera.

All statistical analyses were performed in R (v4.4.2), and statistical significance was determined at P < 0.05.

RESULTS

1. Resilience of southern Egyptian coral reefs to 2023 bleaching event

Assessment of 288 tagged coral colonies revealed clear variations in recovery responses to the 2023 bleaching event across the seven study sites. Overall, 50% of colonies (n = 145) demonstrated high resilience and fully recovered. The remaining colonies (n = 143) exhibited lower resilience, with incomplete or no recovery (Fig. 2). Of these, approximately 22% showed partial recovery, while 28% (n = 80) were severely impacted and failed to recover, resulting in total mortality (Table 2).

Bleaching severity strongly influenced recovery outcomes. Colonies that experienced complete bleaching had a much lower probability of recovery compared to those moderately bleached. Of the 208 colonies that underwent complete bleaching, only 91 (44%) fully recovered. In contrast, 28 of 38 colonies (74%) recovered completely

following moderate bleaching. Statistical analysis confirmed that bleaching severity had a significant effect on coral recovery, as more than half of the colonies subjected to complete bleaching failed to recover fully, compared to moderately and highly bleached colonies (Post hoc Dunn's test, P < 0.05; Table 3).

Table 2. Number of coral colonies that have been tagged during bleaching event (September-October 2023) and re-monitored during recovery period (November 2023) in the NRS. Four bleaching severity categories were used to examine the recovery potential of corals. Resilience was assessed based on the number of colonies in three recovery categories; totally recovered, partially recovered, and totally dead. The potential of corals for the full recovery was determined for each bleaching severity as the proportion of fully recovered colonies to the total number of colonies (N).

Bleaching severity (%)	N	Totally dead	Partially recovered	Totally recovered	Relative frequency of fully recovered colonies (%)
Moderate (26-50%)	38	5	5	28	73.7
High (51-75%)	26	2	8	16	61.5
Severe (76-99%)	16	3	3	10	62.5
Complete (100%)	208	70	47	91	43.8
Total number of colonies	288	80	63	145	50.3

Table 3. Pairwise comparisons (Post-hoc Dunn test) of the full recovery potential of coral colonies affected by different levels of bleaching severities (Moderate-Complete) across the study sites. There were significant differences between the number of the fully recovered colonies after being impacted by complete bleaching and those impacted by only moderate or high bleaching levels.

Comparison	Z	Padj
Complete (100%) - High (51-75%)	-2.03	0.04
Complete (100%) - Moderate (26-50%)	-2.35	0.02
Complete (100%) - Severe (76-99%)	-1.89	0.06
High (51-75%) - Moderate (26-50%)	-0.32	0.75
High (51-75%) - Severe (76-99%)	0.06	0.95
Moderate (26-50%) - Severe (76-99%)	0.37	0.71

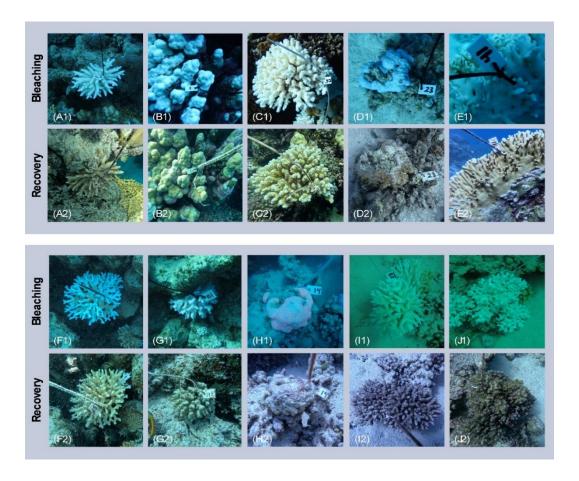


Fig. 2. Examples of tagged coral colonies examined at three sites during bleaching in September (A1-J1) and during recovery in November (A2-J2). Colonies were classified according to their response to recovery as Totally recovered (A2-E2), Partially recovered (F2), or Totally dead (G2-J2).

2. Limited variation between sites on coral resilience

On average, 51.3% of colonies per site fully recovered, while 26.0% per site experienced total mortality. The present study showed no significant differences among sites in coral recovery from the 2023 bleaching event. Tagged colonies exhibited similar resilience patterns and did not follow a distinct north—south gradient in recovery potential (Fig. 3). This was supported by statistical analysis, which revealed that geographic location (latitudinal variation) did not significantly influence the relative frequency of fully recovered (One-way ANOVA, P > 0.05), partially recovered (One-way ANOVA, P > 0.05), or totally dead colonies (One-way ANOVA, P > 0.05).

Nevertheless, variation in recovery outcomes was observed across sites. The proportion of fully recovered colonies ranged from 34% at Marsa Nakari to nearly 59% at Gottaa (Table 4). The lowest resilience and highest mortality were recorded at Lahmi in

the far south, where 42% of all tagged colonies died. In contrast, the lowest mortalities and highest recovery rates were recorded at Gottaa, Keshta, and Shelineat, which were located farther offshore.

Patterns of recovery similarity between sites were further assessed using a Bray–Curtis dissimilarity matrix (Fig. 4). The analysis showed that Shelineat and Lahmi clustered together, exhibiting relatively low similarity in recovery states. In contrast, the other five sites formed a separate cluster, characterized by high similarity in recovery responses.

Table 4. Resilience of corals across the study sites during 2023 recovery period in the NRS. The potential of corals for the full recovery was determined for each site as the proportion of fully recovered colonies to the total number of colonies (N)

Site	N	Totally dead	Partially recovered	Totally recovered	Relative frequency of fully recovered colonies (%)
Marsa	39	9	10	20	51.3
Shagara					
Gotta'a	17	2	5	10	58.8
Marsa Nakari	47	17	14	16	34.0
Gorgonia Reef	45	13	7	25	55.6
Keshta	42	9	10	23	54.8
Shelineat	48	9	12	27	56.3
Lahmi	50	21	5	24	48.0

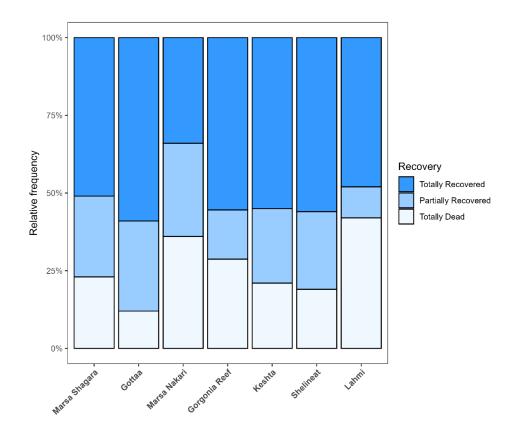


Fig. 3. Relative frequency of the three recovery states (i.e., totally recovered, partially recovered, and totally dead) of the tagged corals in the study sites

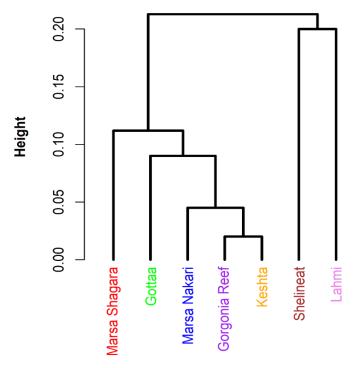


Fig. 4. The similarities between sites in the coral recovery responses (i.e., totally recovered, partially recovered, and totally dead) based on Bray-Curtis method

3. Effect of depth on coral recovery

Coral resilience to the 2023 bleaching event was also examined across two depth ranges: shallow (2–5 m; n = 151) and deep (8–10 m; n = 137). The results indicated that corals at both depth ranges exhibited comparable recovery rates (Fig. 5). Statistical analysis confirmed that there were no significant differences in the proportion of fully recovered (One-way ANOVA, F = 0.05, P > 0.05), partially recovered (One-way ANOVA, F = 0.52, P > 0.05) between shallow and deep sites. The detailed recovery status of tagged colonies across depth ranges is presented in Table (5).

Table 5. Resilience of corals across two depth ranges during 2023 recovery period in the NRS (Egyptian coast). The potential of corals for the full recovery was determined for each depth range as the proportion of fully recovered colonies to the total number of colonies (N)

Depth (m)	N	Totally dead	Partially recovered	Totally recovered	Relative frequency of fully recovered colonies (%)
2-5m	151	44	34	73	48.3
8-10m	137	36	29	72	52.6

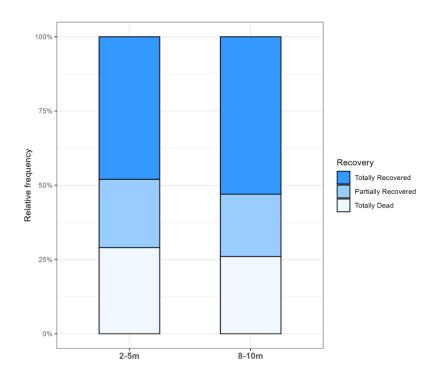


Fig. 5. Coral resilience following 2023 bleaching event across two depth ranges. Relative frequency of coral recovery was recorded in both surface (2-5m) and deep (8-10m) waters.

4. Coral resilience in inshore and offshore reefs

The influence of reef location relative to the shoreline on coral recovery was also assessed. Overall, the proportion of fully recovered colonies in offshore reefs was approximately 9% higher than in inshore reefs (Table 6). Likewise, colony mortality in offshore reefs was 15% lower compared to inshore reefs (Fig. 6). Despite these differences, statistical analysis revealed no significant variation in the relative frequencies of fully recovered (One-way ANOVA, F = 2.81, P > 0.05) or partially recovered colonies (One-way ANOVA, F = 1.26, P > 0.05) between inshore and offshore reefs. However, a marked difference was detected in the frequency of totally dead colonies, with significantly higher mortality observed in inshore reefs (One-way ANOVA, F = 7.78, P < 0.05).

Table 6. Number of re-surveyed coral colonies in inshore and offshore reefs during 2023 recovery period in the NRS. The potential of corals for the full recovery was determined for each reef system as the proportion of fully recovered colonies to the total number of colonies (N).

Reef System	N	Totally dead	Partially recovered	Totally recovered	Relative frequency of fully recovered colonies (%)
Inshore	181	60	36	85	47.0
Offshore	107	20	27	60	56.1

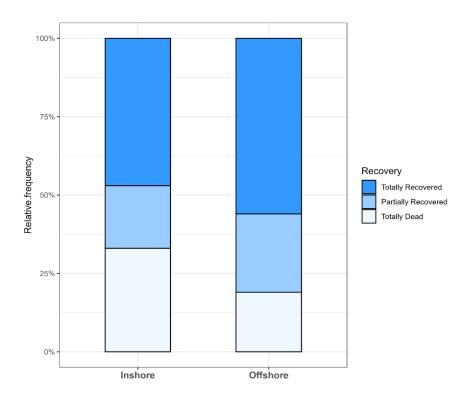


Fig. 6. Post-bleaching recovery of corals in relation to the distance from the shore at NRS

5. Inter-generic variation in coral recovery potential

Results indicated significant differences in recovery potential among the six coral genera (PERMANOVA, F = 3.11, $R^2 = 0.31$, P < 0.05). The PCoA based on the Bray–Curtis dissimilarity matrix revealed similarities in recovery responses among *Montipora*, *Pocillopora*, and *Millepora*, and to a lesser extent *Stylophora* (Fig. 7). These genera experienced moderate total mortality, ranging from 24 to 32%.

In contrast, *Porites* exhibited a distinct recovery response compared to all other genera, with approximately 82% of tagged colonies fully recovered (Table 7). Conversely, *Acropora* showed the lowest resilience, with the highest overall mortality at ~52% (Fig. 8), reflecting a limited capacity for recovery.

Table 7. Number of coral colonies in six genera tagged during 2023 bleaching event in the NRS. The potential of coral genera for the full recovery was determined as the proportion of fully recovered colonies to the total number of colonies (N)

Genus	N	Totally dead	Partially recovered	Totally recovered	Relative frequency of fully recovered
					colonies (%)
Acropora	48	25	8	15	31.3
Montipora	52	13	16	23	44.2
Pocillopora	55	14	12	29	52.7
Stylophora	34	11	13	10	29.4
Porites	49	5	4	40	82
Millepora	50	12	10	28	56.0

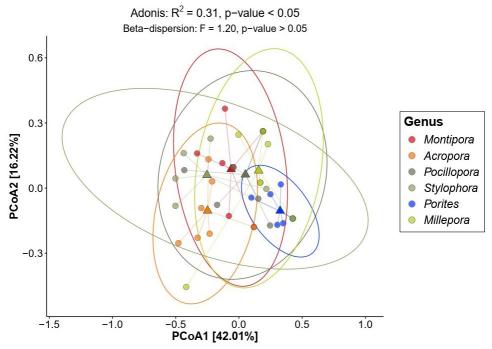


Fig. 7. PCoA of coral genera according to their recovery responses. Distances between points were calculated based on Bray-Curtis dissimilarity matrix in recovery patterns (i.e., totally recovered, partially recovered, and totally dead) among six coral genera.

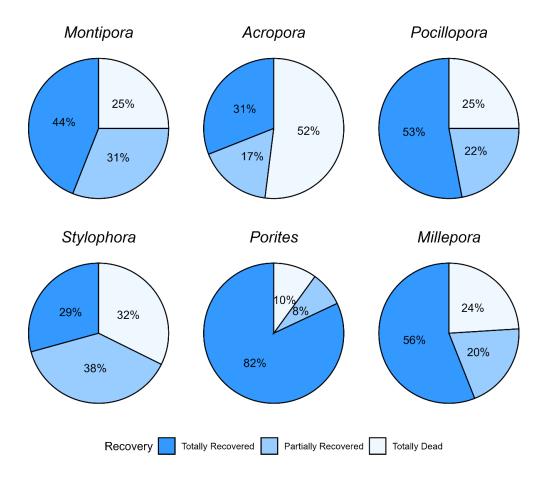


Fig. 8. Recovery responses of six coral genera after 2023 bleaching event in the NRS. Among all genera, *Porites* was the most resilient while *Acropora* was the most vulnerable

DISCUSSION

During the summer of 2023, sea surface temperatures (SST) along the Egyptian coast of the Red Sea reached the NOAA-defined bleaching threshold from late July to October. This aligns with previous studies indicating that Red Sea corals generally display high thermal tolerance, with bleaching thresholds of ~32°C or higher (Eladawy et al., 2022). In this study, we conducted a comprehensive assessment of coral resilience along the southern Egyptian Red Sea coast (northwestern Red Sea), focusing on recovery trajectories following the severe bleaching event of September 2023 (Hanafy & Dosoky, 2023). Given the scarcity of post-bleaching recovery data from this region, our findings provide critical baseline information on the status of dominant coral populations after the 2023 thermal stress event. While geographic factors may pre-adapt these populations to moderate heat stress, the 2023 event demonstrates that even thermally refugial ecosystems remain vulnerable to substantial mortality and long-term decline under intensifying bleaching events.

Coral bleaching typically occurs when SST exceeds the local maximum monthly mean (MMM) by >1°C for prolonged periods (Goreau & Hayes, 1994). In 2023, bleaching in the northwestern Red Sea was triggered by a prolonged marine heatwave (July–October), with SST peaking near 32°C in late July and remaining above 28°C for over 100 days (NOAA). Coral responses ranged from full recovery to total mortality, with site-specific recovery rates ranging from 34% at Marsa Nakari to 56% at Shelineat. This variation likely reflects localized differences in thermal responses. Notably, bleaching peaked in September, not July, underscoring the cumulative impact of prolonged exposure rather than short-lived temperature maxima in driving symbiont dysfunction (Hughes *et al.*, 2017b). As temperatures declined gradually from ~32°C in August to ~27°C in November, some colonies recovered while others succumbed, highlighting both the sensitivity and resilience of northwestern Red Sea corals.

The severity and duration of thermal stress critically shaped recovery outcomes. Moderately bleached colonies (26–50% affected) exhibited a 74% recovery rate, whereas fully bleached colonies (100%) showed only 44% recovery, with 22% total mortality. Intermediate bleaching severities produced variable recovery outcomes, reflecting a direct correlation between stress intensity and resilience. Interestingly, even conspecific colonies within the same site displayed divergent recovery trajectories, suggesting an important role for colony-specific physiology or microbiome-mediated resilience (Ziegler *et al.*, 2017a; Drury *et al.*, 2022; Voolstra *et al.*, 2023).

Spatial factors also influenced outcomes. Offshore colonies exhibited ~9% higher recovery and 15% lower mortality compared to inshore colonies, likely due to reduced exposure to runoff, sedimentation, and coastal development (**Portilho-Ramos** *et al.*, **2022**). However, total and partial recovery rates did not differ significantly between offshore and inshore reefs. Similarly, depth had no strong effect on recovery or mortality between 2–5m and 8–10m, contrasting with reports of depth-dependent reductions in mortality elsewhere (**Safaie** *et al.*, **2018**). Our data suggest that within this shallow depth range, coral populations share functional similarities, including physiological traits (**Ziegler** *et al.*, **2017a**), and experience overlapping environmental conditions (light, flow, temperature) insufficient to drive divergent recovery outcomes.

Taxonomic differences were a stronger determinant of recovery. *Porites* emerged as the most resilient genus, with 82% of colonies recovering and only ~10% mortality, consistent with their classification as "thermal winners" (**Loya** *et al.*, **2001**; **Guest** *et al.*, **2012**). Their resilience may derive from thicker tissues, slower growth rates, and robust skeletal structures. In addition, inter-colonial variation in endosymbiont composition may enhance thermal tolerance (**Osman** *et al.*, **2020**). In contrast, *Acropora* showed the highest mortality (~52%) and the lowest recovery (31%), consistent with its global vulnerability to bleaching (**Winslow** *et al.*, **2024**). Their thin tissues and branching morphology heighten thermal sensitivity (**Loya** *et al.*, **2001**). Nonetheless, localized recovery in some *Acropora* colonies suggests potential microhabitat refugia, reef

morphology effects (e.g., slope shading, altered flow), or genetic adaptation (**Fabricius** *et al.*, **2014**; **Osman** *et al.*, **2020**; **Gonzalez-Espinosa** *et al.*, **2021**). *Stylophora* also showed low recovery (29%), whereas *Pocillopora* exhibited >50% recovery, possibly linked to colony size; all tagged colonies were ≤28 cm, aligning with evidence that smaller colonies often recover faster due to lower energy demands (**Hall** *et al.*, **1996**; **Loya** *et al.*, **2001**; **Winslow** *et al.*, **2024**).

The resilience of *Porites* observed here contrasts with recent reports of shifting susceptibility (**Burn** *et al.*, **2023**), suggesting potential selection for stress-tolerant lineages or site-specific microbial partnerships in the Red Sea. Indeed, *Porites* in this region commonly host *Cladocopium* symbionts and are associated with flexible bacterial communities, enhancing local acclimatization (**Osman** *et al.*, **2020**). These taxon-specific differences underscore the importance of microbiome composition, thermal history, and host-specific traits in shaping coral survival (**Wagner** *et al.*, **2010**; **Osman** *et al.*, **2020**).

While some studies have framed the Red Sea as a potential "last refuge" for corals (Fine et al., 2013; Bellworthy et al., 2017; Fine et al., 2019), this assumption must be approached cautiously. Laboratory studies, though mechanistically informative, may not capture the ecological complexity of field conditions, where sudden environmental fluctuations and multiple stressors interact. This highlights the importance of complementary field-based and experimental approaches in evaluating reef refuge potential. Furthermore, recovery dynamics in other parts of the Red Sea (e.g., Gulf of Aqaba, Saudi Arabian reefs) remain poorly documented, with only limited baseline data published (Gonzalez et al., 2024).

Overall, our findings suggest that coral resilience in the northwestern Red Sea is driven more by interspecific differences and colony-level variability than by depth or cross-shelf gradients. Despite high bleaching severity and mortality, many colonies demonstrated strong recovery, supporting the relative resilience of this region compared to reefs such as the Great Barrier Reef. Nonetheless, resilience is not uniform, and vulnerable taxa like *Acropora* highlight ongoing risks. Effective conservation strategies in this region must therefore consider taxon-specific dynamics and integrate microbiomefocused approaches, which may unlock mechanisms underlying differential recovery and mortality (**Peixoto** *et al.*, 2022).

CONCLUSION

Despite its status as a potential climate refuge, the northern Red Sea exhibited pronounced genus-specific mortality during the prolonged 2023 thermal stress event, demonstrating that refuge potential is not universal. Our results reveal a clear resilience dichotomy: massive *Porites* showed exceptional recovery (82%), whereas branching *Acropora* suffered severe mortality (52%). The delayed bleaching peak and site-specific recovery variation (34–56%) indicate that local conditions modulate thermal-stress

responses. Nevertheless, prolonged exposure to elevated temperatures (>32°C for 100+ days) caused substantial coral loss, underscoring that no ecosystem is immune to escalating climate change.

These findings call for a dual strategy. Locally, conservation efforts should prioritize research into the mechanisms underlying taxon-specific resilience (e.g., *Porites* tolerance vs. *Acropora* vulnerability) and advance microbiome-assisted restoration tools. Globally, the long-term survival of this refuge—and coral reefs worldwide—remains irrevocably dependent on rapid reductions in greenhouse-gas emissions to curb further warming.

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REFERENCES

- Baskett, M. L.; Nisbet, R.M.; Kappel, C.V.; Mumby, P.J. and Gaines, S.D. (2010). Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. Global Change Biology, **16**(4): 1229-1246. doi: 10.1111/j.1365-2486.2009.02062.x
- Bay, R.A.; Rose, N.H.; Logan, C.A. and Palumbi, S.R. (2017). Genomic models predict successful coral adaptation if future ocean warming rates are reduced. Science Advances, 3(11): e1701413. doi: 10.1126/sciadv.17014
- **Bellworthy, J. and Fine, M.** (2017). Beyond peak summer temperatures, branching corals in the Gulf of Aqaba are resilient to thermal stress but sensitive to high light. Coral Reefs, **36**(4): 1071-1082. Do:10.1007/s00338-017-1598-1
- Berkelmans, R.; De'ath, G.; Kininmonth, S. and Skirving, W. J. (2004). A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral reefs, 23: 74-83. doi.org/10.1007/s00338-003-0353-y
- Burn, D.; Hoey, A.S.; Matthews, S.; Harrison, H.B. and Pratchett, M.S. (2023).

 Differential bleaching susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia's Great Barrier Reef and Coral Sea Marine Parks. Marine Pollution Bulletin, 191: 114907.

 doi:10.1016/j.marpolbul.2023.114907

- **Dosoky, M.Y.A; Ismail, M.A.; Madkour, F.F. and Hanafy, M.H.** (2021). Coral bleaching occurrence along the Egyptian coast of the Red Sea during the summer heat stress period, 2020. Egyptian Journal of Aquatic Biology and Fisheries, **25**(5): 17-37. doi: 10.21608/ejabf.2021.196904
- Eladawy, A.; Nakamura, T.; Shaltout, M.; Mohammed, A.; Nadaoka, K.; Fox M.D. and Osman, E.O. (2022). Appraisal of coral bleaching thresholds and thermal projections for the northern Red Sea refugia. Frontiers in Marine Science, 9: 938454. doi.org/10.3389/fmars.2022.938454
- **Fabricius, K. E.; Logan, M.; Weeks, S. and Brodie, J.** (2014). The effects of river runoff on water clarity across the central Great Barrier Reef. Marine pollution bulletin, **84**(1-2): 191-200. doi: 10.1016/j.marpolbul.2014.05.012
- 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. Regional Studies in Marine Science, 25: 100498. doi:10.1016/j.rsma.2018.100498
- **Fine, M.; Gildor, H. and Genin, A.** (2013). A coral reef refuge in the Red Sea. *Global change biology*, **19**(12): 3640-3647. doi: 10.1111/gcb.12356
- Gonzalez, K.; Daraghmeh, N.; Lozano-Cortés, D.; Benzoni, F.; Berumen, M.L. and Carvalho, S. (2024). Differential spatio-temporal responses of Red Sea coral reef benthic communities to a mass bleaching event. Scientific Reports, **14**(1): 24229. doi:10.1038/s41598-024-74956-7
- **Gonzalez-Espinosa, P.C. and Donner, S.D.** (2021). Cloudiness reduces the bleaching response of coral reefs exposed to heat stress. Global Change Biology, **27**(15): 3474-3486. doi:10.1111/gcb.15676
- **Goreau, T.J. and Hayes, R.L.** (1994). Coral bleaching and ocean hot spots. Ambio-Journal of Human Environment Research and Management, **23**(3): 176-180.
- Graham, N.A.J.; Jennings, S.; MacNeil, M.A.; Mouillot, D. and Wilson, S.K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature, 518(7537): 94-97. doi: 10.1038/nature14140
- Guest, J. R., Baird, A. H.; Maynard, J. A.; Muttaqin, E.; Edwards, A.J.; Campbell, S.J.; Yewdall, K.; Affendi, Y.A. and Chou, L.M. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PloS one, **7**(3): e33353. doi:10.1371/journal.pone.0033353
- **Hall, V.R. and Hughes, T.P.** (1996). Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology*, **77**(3): 950-963. doi:10.2307/2265514
- **Hanafy, M.H. and Dosoky, M.Y.A.** (2023). Bleach Watch Egypt: Coral Bleaching Event of 2023 on the Egyptian coast of the Red Sea: Distribution, species sensitivity, and recovery potential. Periodic Report on Coral Reefs Status by

- Hurghada Environmental Protection and Conservation Association (HEPCA), Egypt. https://hepca.org
- **Hanafy, M.H. and Salem, M.** (2024). Bleach Watch Egypt: Coral bleaching in the Egyptian Red Sea under climate change (September 2024 report). Periodic Report on Coral Reefs Status by Hurghada Environmental Protection and Conservation Association (HEPCA), Egypt. https://hepca.org.
- Hughes, T. P.; Barnes, M.L.; Bellwood, D.R.; Cinner, J.E.; Cumming, G.S.; Jackson, J.B.C.,;Kleypas, J.; van del Leemput, I.A.; Lough, J.M.; Morrison, a T.H; Palumbi, S.R; van Nes, E.H, and Scheffer, M. and Morrison, T.H. (2017a). Coral reefs in the Anthropocene. Nature, 546(7656): 82-90. doi:10.1038/nature22901
- Hughes, T.P.; Anderson, K.D.; Connolly, S.R.; Heron, S.F.; Kerry, J. T.; Lough, J. M.; Baird, A.H.; Baum, J.K.; Berumen, M.L.; Bridge, T.C. and Wilson, S.K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science, 359(6371): 80-83. doi: 10.1126/science.aan80
- Hughes, T.P.; Kerry, J.T.; Connolly, S.R.; Baird, A.H.; Eakin, C.M.; Heron, S.F.;
 Hoey, A.S.; Hoogenboom, M.O.; Jacobson, M.; Liu, G.; Pratchett, M.S.;
 Skirving, W. and Torda, G. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change, 9(1): 40-43. doi:10.1038/s41558-018-0351-2
- Hughes, T.P.; Kerry, J.T.; Álvarez-Noriega, M.; Álvarez-Romero, J.G.; Anderson, Baird, A.H.; Babcock, R.C.; Beger, M.; Bellwood, D.R.; **K.D.**; Bridge, T.C.; Butler, I.R.; Byrne, M.; Berkelmans, R.; Cantin, N.E.; Comeau, S.; Connolly, S.R.; Cumming, G.S.; Dalton, S.J.; Diaz-Pulido, G.; Eakin, C.M.; Figueira, W.F.; Gilmour, J.P.; Harrison, H.B.; Heron, S.F.; Hoey, A.S.; Hobbs, J.P.A.; Hoogenboom, M.O.; Kennedy, E.V.; Kuo, C.Y.; McCulloch, .T.; Malcolm, H.A.; Lough, J.M.; Lowe, R.J.; Liu, G.; McWilliam, M.J.; Pandolfi, M.J.; Pears, R.J.; Pratchett, M.S.; Schoepf, V.; Simpson, T.; Skirving, W.j.; Sommer, B.; Torda, G.; Wachenfeld, D.R.; Willis, B.L. and Wilson, S.K. (2017b). Global warming and recurrent mass bleaching of corals. Nature, **543**(7645): 373-377. Doi:10.1038/nature21707
- Kleinhaus, K.; Al-Sawalmih, A.; Barshis, D.J.; Genin, A.; Grace, L.N.; Hoegh-Guldberg, O.; Meibom, O.; Osman, E.O.; Ruch, J.D.; Shaked, Y.; Voolstra, C.R., Zvuloni, A. and Fine, M. (2020). Science, diplomacy, and the Red Sea's unique coral reef: It's time for action. Frontiers in Marine Science, 7: 90. doi:10.3389/fmars.2020.00090
- Loya, Y.; Sakai, K.; Yamazato, K.; Nakano, Y.; Sambali, H. and Van Woesik, R. (2001). Coral bleaching: the winners and the losers. Ecology letters, 4(2): 122-131. doi:10.1046/j.1461-0248.2001.00203.x

- Maher, R.L.; Rice, M.M.; McMinds, R.; Burkepile D.E. and Vega Thurber, R. (2019). Multiple stressors interact primarily through antagonism to drive changes in the coral microbiome. Scientific Reports, 9(1): 6834. doi.org/10.1038/s41598-019-43274-8
- Matz, M. V.; Treml, E.A.; Aglyamova, G.V. and Bay, L.K. (2018). Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. PLoS genetics, 14(4): e1007220. doi: 10.1371/journal.pgen.1007220
- McDevitt-Irwin, J.M.; Baum, J.K.; Garren, M. and Vega Thurber, R.L. (2017). Responses of coral-associated bacterial communities to local and global stressors. *Frontiers in Marine Science*, **4**: 262. doi: 10.3389/fmars.2017.00262
- Oksanen, J. (2015). Vegan: community ecology package. R package version 2: 3.
- Osman, E.O.; Smith, D.J.; Ziegler, M.; Kürten, B.; Conrad, C.; K.M. El-Haddad, Voolstra, C.R. and Suggett, D.J. (2018). Thermal refugia against coral bleaching throughout the northern Red Sea. Global change biology, **24**(2): e474-e484. doi: 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), 8. doi:10.1186/s40168-019-0776-5
- Peixoto, R.S.; Rosado, P.M.; Leite, D.C.A.; Rosado, A.S. and Bourne, D.G. (2017).

 Beneficial microorganisms for corals (BMC): proposed mechanisms for coral health and resilience. Frontiers in microbiology, 8: 341. doi: 10.3389/fmicb.2017.00341
- Peixoto, R.S.; Voolstra, C.R.; Sweet, M.; Duarte, C.M.; Carvalho, S.; Villela, H., Lunshof, J.E.; Gram, L.; Woodhams, D.C.; Walter, J.; Roik, A.; Hentschel, U.; Vega Thuber, R.; Daisley, B.; Ushijima, B.; Daffonchio, D.; Costa, R.; Keller-Costa, T.; Bowman, J.S.; Rosado, A.S.; Reid, G.; Mason, C.E.; Walker, J.B.; Thomas, T.; Berg. G. and Walter, J. (2022). Harnessing the microbiome to prevent global biodiversity loss. Nature Microbiology, 7(11): 1726-1735. Doi:10.1038/s41564-022-01173-1
- Torda, G., Donelson, J.M.; Aranda, M.; Barshis, D.J.; Bay, L.; Berumen, M.L.; Bourne, D.G.; Cantin, N.; Foret, S.; Matz, M.; Miller, D.J.; Moya, A.; Putnam, H.M.; Ravasi, T.; van Oppen, M.J.H.; Thurber, R.V.; Vidal-Dupiol, J.; Voolstra, C.R.; Watson, S.A.; Whitelaw, E.; Willis, B.L. and Munday, P.L. (2017). Rapid adaptive responses to climate change in corals. Nature Climate Change, 7(9): 627-636. doi: 10.1038/nclimate3374
- Van Hooidonk, R.; Maynard, J.; Tamelander, J.; Gove, J.; Ahmadia, 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. Scientific Reports, **6**(1): 39666. <u>doi: 10.1038/srep39666</u>
- Voolstra, C.R.; Valenzuela, J.J.; Turkarslan, S.; Cárdenas, A.; Hume, B.C.C.; Perna, G.; Buitrago-López, C.; Rowe, K.; Orellana, M.V.; Baliga, N.S.; Paranjape, S.; Banc-Prandi, G.; Bellworthy, J.; Fine, M.; Frias-Torres, S. and Barshis, D.J. (2021). Contrasting heat stress response patterns of coral holobionts across the Red Sea suggest distinct mechanisms of thermal tolerance. Molecular Ecology, 30(18): 4466-4480. doi: 10.1111/mec.16064
- Wagner, D. E.; Kramer, P. and Van Woesik, R. (2010). Species composition, habitat, and water quality influence coral bleaching in southern Florida. Marine Ecology Progress Series, 408: 65-78. doi:10.3354/meps08584
- **Wickham, H. and Sievert, C.** (2009). ggplot2: elegant graphics for data analysis, springer New York.
- Winslow, E.M.; Speare, K.E.; Adam, T.C.; Burkepile, D.E.; Hench, J.L. and Lenihan, H.S. (2024). Corals survive severe bleaching event in refuges related to taxa, colony size, and water depth. Scientific Reports, 14(1): 9006. doi:10.1038/s41598-024-58980-1
- Ziegler, M.; Arif, C.; Burt, J.A.; Dobretsov, S.; Roder, C.; LaJeunesse, T.C. and Voolstra, C.R. (2017b). Biogeography and molecular diversity of coral symbionts in the genus Symbiodinium around the Arabian Peninsula. Journal of Biogeography, 44(3): 674-686. doi: 10.1111/jbi.12913
- Ziegler, M.; Seneca, F.O.; Yum, L.K.; Palumbi, S.R. and Voolstra, C.R. (2017a). Bacterial community dynamics are linked to patterns of coral heat tolerance. Nature communications, 8(1): 14213. doi:10.1038/ncomms14213