

Bleaching and Recovery patterns of corals in Palk Bay, India: An indication of bleaching resilient reef

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Abstract

Frequency and severity of coral bleaching events increased in recent years affecting the recovery and resilience of corals. In this study, influence of bleaching and recovery patterns of corals on the resilience potential of Palk Bay reef was assessed over a period of two years 2013 and 2014. Individual coral colonies of five different genera were tagged and monitored for their bleaching and recovery pattern during 2013 and 2014. Variation in the bleaching and recovery response among different coral genera were quantified and compared. Also, sea surface temperature (SST) and photosynthetically active radiation (PAR) were monitored simultaneously and compared. Results showed an increase in the intensity of SST and PAR in 2014 compared to 2013. Correspondingly, the average percentage of severely bleached corals was also high in 2014. *Favites* and *Leptastrea* spp. were more sensitive, being the first to bleach. Whereas, *Porites* spp. exhibited a delayed response to bleaching as the SST rose above 30 °C. *Cyphastrea* spp. and some colonies of *Leptastrea* spp. were unresponsive to bleaching and remained healthy. The recovery process also varied, as the *Favia* and *Favites* spp. recovered under environmental conditions in which the *Porites* spp. still continued to bleach. Subsequent surveys revealed complete recovery of all coral colonies without any post-bleaching mortality. Results of this study indicated that an increase in the intensity of bleaching conditions did not have any significant impact on the survivability of corals on a reef which is dominated by stress-tolerant coral species. This may enhance the resilience potential of the Palk Bay reef by ensuring the presence of healthy live corals, which in turn contributes to the functional diversity of the reef and its resistance to the future disturbances.

Key words: Corals; Bleaching; Palk Bay; Resilience; Recovery; Resistance

1. Introduction

Coral reefs are under severe threat due to the changing climate and local stressors. Mass coral bleaching associated with increased sea surface temperature (SST), photosynthetically active radiation (PAR) drive the degradation of corals at a larger scale [1]. Globally, coral bleaching events were predicted to increase in their frequency and turn out to be an annual event with the present trend of changing climate and environmental scenarios [2]. As a consequence, the time available for the corals to recover from the bleached state becomes less and that could be a reason for their mortality and permanent loss. However, different species of corals respond differently to bleaching stress and the type of coral taxa present in a reef can influence the overall response of a reef towards bleaching [3]. Determining the bleaching and recovery response in corals to the changing environmental conditions, will help in identifying the most resilient reefs and also enable to predict the future responses of coral reef systems to the bleaching related disturbances.

Coral bleaching often results in mass mortality of corals and enable ecological phase shifts [4, 5]. However, numerous studies reported the recovery of corals following major bleaching events [6, 7]. Recovery of corals following a bleaching event depends on several factors such as food availability [8], replenishment of energy reserves and tissue biomass by the corals [6], availability of new coral recruits [9], reduced pressure from local and regional scale stressors [10], presence of healthy reef fish stock [11] and the effective management through marine protected areas [12]. Berkelmans (2002) [13] demonstrated the linkage between dissolved inorganic nitrogen loading in the reef environment and the upper thermal bleaching thresholds of corals on the inshore reefs. Improved coral reef management that minimizes terrestrial inputs will also help the corals to resist bleaching and its related effects [14].

History on the exposure of corals to various stress events is an important aspect in determining the fate of individuals especially to the thermal tolerance [15]. There were no reports on coral bleaching in India until the 1998 mass bleaching event that resulted in the significant loss of corals in all the major reefs of India [16, 17, 18]. A reduction in coral cover of over 80% was reported from Gulf of Mannar reef located in the southeast coast of India [16]. Post-bleaching recovery processes among corals were slow and the local processes strongly influenced the recovery process [19]. After 1998, two other bleaching events were reported in 2002 [20] and 2010 [21, 22] respectively that also contributed in the reduction of the live coral cover. Although coral bleaching was occasionally reported in the Indian reefs, local reef users suggest it to be an annual event affecting the corals (Personal communication).

In this study, five genera of the coral colonies including *Porites*, *Favia*, *Favites*, *Leptastrea* and *Cyphastrea* spp. that were abundant in Palk Bay were observed, at regular intervals of every 8 days

for 7 months (March – September) to compare the patterns of response to the annual bleaching events in 2013 and 2014. Recovery and mortality of corals after the bleaching event were documented as well the relationship between SST, PAR and severity of bleaching at the study sites were examined. While observing the coral colonies, SST and PAR were also recorded in 2013 and 2014 to relate their influence over the severity of bleaching. This study will help to determine the species specific response in corals to the environmental factors during bleaching events and their recovery to determine the overall resilience of the system to the changes in the environmental thresholds.

2. Materials and Methods

2.1. Study sites

The study was carried out at Palk Bay reef, located at the southeast coast of India. Palk Bay comprises a narrow reef, running parallel to the shore in the east-west direction between 9°55' - 10°45'N and 78°58' - 79°55'E. Coral reefs in Palk Bay are of fringing type, located 200 m - 500 m away from the shore and are discontinuous. The substratum is mostly composed of sand, mud and rubble with an average depth of 4 m. Palk Bay reef is separated by a narrow channel of 9 m deep that permits the passage of fishing vessels and large ships. The diversity of corals and other associated fauna and flora in Palk Bay are well documented [23, 24]. Palk Bay reef also serves as an important fishing ground for small scale fishermen. Two sites were identified for this study namely Vedhalai and Mandapam as a representative site of Palk Bay to study the overall bleaching response in corals (Fig. 1).

2.2. Survey method

Coral bleaching, recovery and post-bleaching mortality were observed underwater from March to July in 2013 and 2014 at weekly intervals following the permanent quadrat method [25] with slight modifications. An area of 100 m² was demarcated at vedhalai and mandapam reefs, using 5 mm thick poly propylene as described in [26] and fixed in permanence. All the coral colonies within the effective area of the quadrat were tagged for continuous monitoring during the study period. The corals were photographed using an Olympus µtough 8000 camera in underwater macro mode for identification. The corals were identified to the genus level using high resolution photographs using the standard identification keys [27, 28].

Coral colonies were categorized into four types, namely severely bleached (completely turned white); moderately bleached (became pale in color); unbleached (did not bleach and appears healthy) and recovering (bleached colonies becoming normal by gaining color). Measure of coral bleaching is reported as the average percentage of coral colonies that exist in each bleaching category relative to the total number of coral colonies that were tagged. Observations on the coral bleaching and their

recovery were extended till September with same time interval to account for potential post-bleaching mortality among tagged coral colonies. In situ observations were not possible from October to February due to poor visibility because of the onset of northeast monsoon, characterized by very high wave action and strong winds.

2.3. Environmental conditions during bleaching

SST and PAR are the two critical factors responsible for coral bleaching. SST over the Palk Bay region was monitored continuously during the study period between March and July 2013 and 2014. Data on SST were obtained from a daily 9 km optimum interpolated global SST (MODIS+TMI) dataset (www.misst.org). From these data, average SST for every eight days was calculated corresponding to our observation eight days interval *in-situ* observations and plotted.

PAR is defined as the integration of the solar flux reaching the ocean surface and denoted as Em^2d^{-1} . In this study, PAR data at the ocean surface was obtained from the moderate resolution imaging spectroradiometer (MODIS) satellite. Similar to SST, PAR values averaged for every eight days were obtained for the period from March to July in 2013 and 2014. The data was downloaded from <http://oceandata.sci.gsfc.nasa.gov>. The MODIS-Aqua satellite has ocean bands 8, 9, 10, 11, 12, 13, 14 in the visible range and PAR values were derived using these bands with specific algorithms [29]. Data was flagged off for few days within the study period due to its poor quality. The accuracy of PAR data from MODIS-Aqua has average errors on the order of 5-8%, with individual estimation errors as high as 21% [30]. High-resolution PAR measurements were not available in this region. Since the sampling depth is approximately 2 m in clear water, PAR levels at the depth may not be substantially different from surface values.

2.4. Analysis

Data on the bleaching and recovery patterns of corals were proportion of coral colonies in each bleaching category at the given time of field observation. Proportion of coral colonies were determined by summing up the number of coral colonies in each bleaching category relative to the total number of coral colonies tagged for continuous observation. Data from Vedhalai and Mandapam reefs were processed together, since there were no marked variations in the environmental conditions and reef characteristics between them (Unpublished data). The average proportion of coral colonies in each bleaching category attained from the quadrats were pooled together to get the overall average values representative of the entire Palk Bay. Variations in bleaching and recovery response among coral colonies between the years 2013 and 2014 were determined using analysis of variance after log transformation of the data with year as the fixed factor and the number of coral genera was nested

within the site. Multiple regression analysis was done to determine the combined effects of SST and PAR over the proportion of severely bleached coral colonies in the years 2013 and 2014 and the analysis was performed using SPSS statistical software version 22.0.

3. Results

A total of 256 coral colonies representing five genera were recorded from the permanent quadrats established Palk Bay reef. *Leptastrea* spp. was dominant (58.1%) followed by *Porites* spp. (18.1%), *Favia* spp. (12.7%), *Favites* spp. (6.3%) and *Cyphastrea* spp. (4.5%). The proportion of severely bleached colonies was high in 2014 compared to 2013, corresponding to the increase in the intensity of SST and PAR in 2014. Colonies from different genera differed in their sensitivity to bleaching and *Favites* spp. and *Leptastrea* spp. were more sensitive, being the first to bleach. *Cyphastrea* spp. and few colonies of *Leptastrea* spp. were unresponsive to bleaching.

3.1. Bleaching event 2013

There was a statistically significant variation in the temporal pattern of SST during the study period in 2013 ($p = 0.0001 < 0.05$). However, the PAR values did not differ significantly during the study period ($p = 0.11 > 0.05$). Mean SST and PAR was ≤ 30 °C (Mean \pm SE) and ≥ 50 $\text{Em}^{-2}\text{d}^{-1}$ respectively, during March 2013 (Fig. 2). Coral colonies appeared normal without any signs of bleaching during the first two weeks of March 2013. *Favites* and *Leptastrea* colonies were the first to bleach during the third week of March 2013. During this period, $2.7 \pm 17.1\%$ of the colonies belonging to *Favites* sp. and *Leptastrea* sp. were moderately bleached. The mean SST continued to increase above 30 °C and PAR values were stable ≥ 50 $\text{Em}^{-2}\text{d}^{-1}$. Correspondingly, the proportion of moderately bleached colonies increased to 10 % by the end of March 2013.

Mean SST and PAR values were ≥ 30 °C and 52 $\text{Em}^{-2}\text{d}^{-1}$ respectively in the first week of April, when 4.5 ± 0.9 % of the colonies of *Favites* spp. and *Leptastrea* spp. were severely bleached and $11.8 \pm 8\%$ of the colonies comprising *Favia* spp. and *Leptastrea* spp. were moderately bleached. Average SST and PAR values continued to increase ≥ 31 °C and 53 $\text{Em}^{-2}\text{d}^{-1}$ respectively by the third week of April 2013. Correspondingly, the proportion of severely bleached and moderately bleached colonies, including *Favites* spp, *Leptastrea* spp. and *Favia* spp also increased to $11.8 \pm 6.4\%$ and $17.3 \pm 2.5\%$, respectively. Though the average PAR values dropped below 50 $\text{Em}^{-2}\text{d}^{-1}$ by the last week of April 2013, the SST was well above 31 °C and increased the proportion of severely bleached colonies to $13.6 \pm 8.2\%$. Massive colonies of *Porites* spp. started

bleaching during this period and increased the percentage of moderately bleached colonies to $27.3 \pm 7.5\%$.

In May 2013, the average SST was above $30\text{ }^{\circ}\text{C}$ and PAR values varied between a maximum of $52.7 \pm 2.65\text{ Em}^{-2}\text{d}^{-1}$ to a minimum of $48.9 \pm 1.15\text{ Em}^{-2}\text{d}^{-1}$. Majority of the *Porites* spp. turned pale in color and increased the proportion of moderately bleached coral colonies to $43.6 \pm 23.8\%$ by the third week of May. Also, $13.6 \pm 8.2\%$ of the corals of *Favites* and *Leptastrea* spp. were severely bleached. However, $3.6 \pm 6.7\%$ of the corals of *Favites* spp., those were severely bleached showed signs of recovery during this period. The proportion of recovering coral colonies increased to $8.2 \pm 2.1\%$ as the average SST and PAR values dropped below $30\text{ }^{\circ}\text{C}$ and $50\text{ Em}^{-2}\text{d}^{-1}$ respectively by the end of May 2013.

Corals of *Favia*, *Favites* and *Leptastrea* spp. that were severely and moderately bleached regained their color and recovered to their normal state as the average SST and PAR values dropped below $30\text{ }^{\circ}\text{C}$ and $48\text{ Em}^{-2}\text{d}^{-1}$, respectively in the second week of June 2013. However, $2.7 \pm 2.7\%$ of the corals comprising *Porites* spp. remained severely bleached, $26.3 \pm 6.5\%$ comprising *Porites* and *Leptastrea* spp. were moderately bleached, $22.7 \pm 12.4\%$ of the *Leptastrea* spp. and *Favia* spp. were recovering and $48 \pm 16.5\%$ of the corals were healthy, including those corals that had recovered from bleaching by the end of June. *Porites* spp. were observed to be recovering by the second week of July 2013 as the average SST and PAR values decreased below $29\text{ }^{\circ}\text{C}$ and $48\text{ Em}^{-2}\text{d}^{-1}$. Majority of *Porites* spp. had recovered and $5.4 \pm 4.9\%$ of *Porites* spp. was still recovering by the end of July. The bleaching and recovery response of corals in 2013 is summarized in Fig. 3. In total, $33.6 \pm 30.9\%$ of the coral colonies comprising *Cyphastrea* spp. and a few *Leptastrea* spp. were unresponsive to bleaching and remained healthy during the entire bleaching episode. Subsequent observations in August and September 2013 revealed the recovery of all bleached coral colonies without any mortality. Multiple regression analysis revealed that the changes in the proportion of severely bleached coral colonies is highly correlated with the combined effect of SST and PAR ($r^2 = 0.794$). Variation in the SST and PAR, explains 63% of the variation in the proportion of severely bleached coral colonies ($r^2 = 0.63$) and it is statistically significant

($p\text{ value} = 0.0005 < 0.05$).

3.2. Bleaching event 2014

Overall bleaching and recovery responses of corals in Palk Bay differed significantly in 2014 compared to 2013 ($p = 0.009$). The coral colonies that were tagged in 2013 were observed continuously for bleaching and recovery response in 2014. Temporal patterns of SST and PAR in 2014 are presented

in Fig. 4. Unlike 2013, both SST ($p = 0.0001 < 0.05$) and PAR ($p = 0.03 < 0.05$) varied significantly in their temporal pattern during the study period in 2014. The bleaching and recovery patterns among corals in 2014 are summarized in Fig. 5.

In March 2014, mean SST was ≤ 30 °C and the PAR values were high at a range of $51.03 \pm 0.44 \text{ Em}^{-2}\text{d}^{-1}$ to $54.3 \pm 3.71 \text{ Em}^{-2}\text{d}^{-1}$. Initial signs of bleaching were witnessed during the second week of March, comparatively earlier than in 2013. In total, $19.1 \pm 11.03\%$ of corals, including *Leptastrea*, *Favia* and *Favites* spp were moderately bleached by the second week of March 2014. As the average PAR value increased $\geq 54 \text{ Em}^{-2}\text{d}^{-1}$ by the third and fourth week of March 2014, $1.8 \pm 14.5 \%$ of corals of *Favites* spp. were severely bleached and $30.9 \pm 0.77\%$ of corals of *Favites*, *Leptastrea* and *Porites* spp were moderately bleached. Like 2013, colonies of *Cyphastrea* spp. and few colonies of *Leptastrea* spp. showed no response to the increase in both SST and PAR.

The proportion of severely and moderately bleached coral colonies increased to $8.2 \pm 8.16 \%$ and $40 \pm 9.87 \%$, respectively, by the second week of April 2014. During this period, average SST fluctuated between 30 °C - 31.5 °C and average PAR values were $\geq 54 \text{ Em}^{-2}\text{d}^{-1}$. After that, average PAR values dropped below $52 \text{ Em}^{-2}\text{d}^{-1}$ by the third week of April 2014. However, average SST increased ≥ 31 °C and the proportion of severely and moderately bleached coral colonies rose to $15.5 \pm 0.86 \%$ and $56.4 \pm 26.27 \%$ respectively, by the last week of April 2014. In total, $3.6 \pm 11.9 \%$ of the *Porites* spp. was severely bleached, which increased the proportion of severely bleached colonies to $25.4 \pm 9.04 \%$ by the second week of May 2014. Besides, $62.7 \pm 32.57 \%$ of corals including *Porites*, *Leptastrea* and *Favia* spp were moderately bleached during this period.

The proportion of severely bleached coral colonies gradually increased to a maximum of $53.6 \pm 37.24 \%$ by the first week of June 2014 during which the average SST was ≥ 30 °C and PAR were $\leq 50 \text{ Em}^{-2}\text{d}^{-1}$. Recovery signs were observed among the coral colonies during the second week of June 2014 as the average SST and PAR values dropped below 30 °C and $50 \text{ Em}^{-2}\text{d}^{-1}$ respectively. In total, $8.2 \pm 6.89 \%$ of corals including *Leptastrea* spp and *Favites* spp showed signs of recovery during this period. Though the average PAR values fluctuated between a maximum of $51.5 \pm 0.91 \text{ Em}^{-2}\text{d}^{-1}$ to a minimum of $47.9 \pm 2.69 \text{ Em}^{-2}\text{d}^{-1}$, the average SST was consistent below 30 °C till the end of June 2014. Corresponding to this, the proportion of severely bleached coral colonies also reduced to $16.4 \pm 0.1\%$ with a simultaneous increase in the percentage of recovering coral colonies to $55.5 \pm 40.41\%$.

Subsequently, *Favia* spp and *Favites* spp recovered from bleaching. However, recovery was slow among *Porites* spp. and few *Leptastrea* spp. which together added $19 \pm 4.01 \%$ to the total percentage of recovering coral colonies by the end of July 2014. Further

observations in August and September revealed recovery of all the tagged coral colonies with zero percent mortality. Based on multiple regression analysis, 32% of the variation in the proportion of severely bleached coral colonies is explained by the variation in SST and PAR values in 2014 ($r^2 = 0.32$). The proportion of severely bleached coral colonies showed a strong positive correlation with the SST and PAR values ($r = 0.626$). Both, SST and PAR contributed statistical significance to the variation in the proportion of severely bleached coral colonies ($F_{2, 17} = 5.48$; p value = $0.015 < 0.05$).

4. Discussion

Results showed that the corals in Palk Bay recovered to their normal state without mortality despite the increase in average SST and PAR during the study period. Elevated SST is considered to be the most common factor causing bleaching in corals [31, 32]. However, continuous observations on the bleaching and recovery patterns of corals along with SST and PAR in Palk Bay suggested that PAR triggered the bleaching response among corals that is further exacerbated by SST. Production of reactive oxygen species (ROS) by the symbiotic zooxanthellae in response to an increase in PAR plays a critical role in triggering bleaching through photo-inhibition of photosynthesis in corals [33]. Comparison of the climatic conditions of the previous bleaching events in 1998 and 2002 with that of 2013 and 2014 showed an increase in the level of bleaching thresholds of corals in Palk Bay. An average PAR and SST of $47 \text{ Em}^{-2}\text{d}^{-1}$ and $30 \text{ }^\circ\text{C}$, respectively, resulted in severe bleaching among corals in the Gulf of Mannar and Lakshadweep reefs in 2002 [34]. In contrast, initial signs of bleaching were observed only after the average PAR and SST exceeded $50 \text{ Em}^{-2}\text{d}^{-1}$ and $30 \text{ }^\circ\text{C}$, respectively during the bleaching events in 2013 and 2014 in this study. Increase in the bleaching threshold among corals might result from adaptation and acclimatization in response to the previous bleaching events. The ability of corals to shuffle their symbionts towards thermal and photo-tolerant clades of zooxanthellae [35] is one possible mechanism of resistance to increasing SST and PAR.

The coral colonies recovered to their normal state without mortality despite an increase in the average SST and PAR in 2014 compared to 2013. The continued increase in the mean SST in 2014 also accompanied by an increase in the overall bleaching rate among the coral colonies compared to 2013. Though the average PAR intensity varied between their minimum and maximum values during the bleaching event, the SST was $\geq 30 \text{ }^\circ\text{C}$ for a maximum of 8 and 11 weeks, respectively in 2013 and 2014. Such prolonged temperature anomaly affected the stability of symbiosis between the coral and their zooxanthellae [36], resulting in the expulsion of zooxanthellae. Though the high SST did not affect the survivability of corals, other impacts associated with it need to be investigated. For example, bleaching has been shown to impair the reproductive potential of corals [37].

Favites and *Leptastrea* spp. were the most sensitive, being the first to bleach, although the average SST was <30 °C. Whereas, *Porites* spp. and *Favia* spp. bleached only when the average SST rose above 30 °C. *Cyphastrea* spp. and few colonies of *Leptastrea* sp was not affected by bleaching and remained normal during the entire bleaching episode in both 2013 and 2014. The unresponsive nature of *Cyphastrea* spp to bleaching has been previously reported from other reefs in the world [3]. Whereas for *Leptastrea* spp, their niche under the holes and crevices of the dead corals and rocks would have offered protection against radiation and contributed to their resistance to bleaching. Variation in the susceptibility to bleaching among different coral species is attributed to many factors, including the type of symbiont associated with corals [38, 39], tissue thickness, colony growth morphology [40] and the size structure of corals [41]. In addition, Ravindran et al. (2013) [42] reported the presence of UV-absorbing bacteria in the coral mucus which is suspected of producing UV absorbing compounds thereby ameliorating the effects of harmful UV radiation during bleaching events. Massive *Porites* spp. resists bleaching by withdrawing their polyps to a deeper shaded region [43]. However, elevated SST and PAR may have overwhelmed the resistance of the massive coral colonies in Palk Bay. Recovery was slow among the massive corals and recovery signs were observed only after the SST dropped below 29 °C.

There was no post bleaching mortality among the corals in Palk Bay unlike the previous bleaching events observed during 2002 and 1998 [16, 44]. Though this appears to be a positive sign of resilience, the zero mortality was largely due to the presence of thermotolerant coral species in abundance compared to the thermally sensitive ones. The total reef area of Palk Bay has been widely reduced since 1996 with a simultaneous increase in the area cover of seaweeds and sand [45]. In connection to this, the species diversity of corals also reduced to a greater extent, possibly due to natural selection of those species which could tolerate the stress conditions prevailing in Palk Bay. Earlier, 63 species of corals of 23 genera were recorded in Palk Bay reef [23] and at present only 34 species of 15 genera were recorded [46]. It took ten years after the 1998 bleaching event for the Sesoko reef to recover its coral species diversity [47]. However, there are no signs of recovery of coral species diversity in Palk Bay reef. Thermally tolerant *Porites*, *Favites* and *Favia* spp. [48] are relatively abundant and *Acropora* corals are scarce in Palk Bay reef. Though *Leptastrea* spp. was abundant concerning the number of colonies compared to other massive forms, they occurred as small encrusting colonies and contribute least to the live coral cover. The 1998 bleaching event and the subsequent coral recovery was not documented on Palk Bay reef, giving no clue about the factors responsible for an increase in the relative abundance of massive and encrusting coral species over other forms of corals.

Frequent bleaching events may minimize the time available for corals to recover and lead to their mortality. Whereas, Brown et al. (2002) [49] suggested that exposure of corals to frequent stressors can reduce their susceptibility to bleaching. Bleaching events and their frequency are not well documented on Indian reefs due to lack of intensive field research in the country. Three major bleaching events have been reported on Indian reefs since 1998 [16, 17, 20, 21]. However, coral bleaching occurs every year in Palk Bay and Gulf of Mannar reefs as reported by fishermen and local reef users and it remains undocumented by scientific communities. Frequent bleaching events and the presence of regular stress conditions render the coral host with the potential to resist bleaching related stress by shuffling their symbiotic algal partner [50] and acclimatizing to the environmental stress [51, 52]. The reef environment in Palk Bay is often stressful due to excessive sedimentation, increased anthropogenic activities [26] and high temperature during summer [21, 53]. Though the corals in Palk Bay were unable to resist bleaching despite frequent stress conditions, they were able to recover back to their normal state. Survival and recovery of corals during and after bleaching event is largely influenced by the prevalence of secondary stressors such as overgrowth of macroalgae, diseases and predator outbreaks [54, 55]. Overgrowth of macroalgae was reported to hinder the recovery of corals during the 2010 bleaching event in Palk Bay [21]. The absence of such macroalgae overgrowth aided the rapid recovery of corals following the bleaching event in 2013 and 2014.

In conclusion, our study showed that an increase in the intensity of bleaching conditions during 2013 and 2014 triggered and lengthened the bleaching response among corals without any mortality. Abundance of thermal tolerant coral colonies and absence of *Acropora* corals suggested that Palk Bay reef faced frequent bleaching events in the past that lead to a shift in the coral species composition towards the thermally tolerant ones. Though these thermal tolerant corals experience bleaching, they were able to recover back to their normal state without mortality. This may enhance the resilience potential of the reef by ensuring the presence of healthy live corals, which in turn contributes to the functional diversity of the reef and its resistance to the future disturbances.

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References

- [1] B. E. Brown, Coral bleaching: causes and consequences, *Coral reefs*. 16 (1997) s129-s138.
- [2] O. Hoegh-Guldberg, Climate change, coral bleaching and the future of the world's coral reefs, *Mar. Freshwater. Res.* 50 (1999) 839-866.
- [3] P.A. Marshall, A.H. Baird, Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa, *Coral reefs*. 19 (2000) 155-163.
- [4] G. Diaz-Pulido, L.J. McCook, The fate of bleached corals: patterns and dynamics of algal recruitment, *Mar. Ecol. Prog. Ser.* 232 (2002) 115-128.
- [5] J.F. Bruno, H. Sweatman, W.F. Precht, E.R. Selig, V.G. Schutte, Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*. 90 (2009) 1478-1484.
- [6] L.J. Rodrigues, A.G. Grottolo, Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnol. Oceanogr.* 52 (2007) 1874-1882.
- [7] J.P. Gilmour, L.D. Smith, A.J. Heyward, A.H. Baird, M.S. Pratchett, Recovery of an isolated coral reef system following severe disturbance, *Science*. 340 (2013) 69-71.
- [8] S.R. Connolly, M.A. Lopez-Yglesias, K.R.N. Anthony, Food availability promotes rapid recovery from thermal stress in a Scleractinian coral, *Coral reefs*. 31 (2012) 951-960.
- [9] T.P. Hughes, A.H. Baird, E.A. Dinsdale, N.A. Moltschaniwskyj, M.S. Pratchett, J.E. Tanner, B.L. Willis, Patterns of recruitment and abundance of corals along the Great Barrier Reef, *Nature*. 397 (1999) 59-63.
- [10] N.A.J. Graham, K.L. Nash, J.T. Kool, Coral reef recovery dynamics in a changing world, *Coral Reefs*. 30 (2011) 283-294.
- [11] P.J. Mumby, A. Hastings, H.J. Edwards, Thresholds and the resilience of Caribbean coral reefs, *Nature*. 450 (2007) 98-101.
- [12] P.J. Mumby, A.R. Harborne, Marine reserves enhance the recovery of corals on Caribbean reefs, *PLoS ONE*. 5 (2010) e8657.
- [13] R. Berkelmans, Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef, *Mar. Ecol. Prog. Ser.* 229 (2002) 73-82.
- [14] S.A. Wooldridge, Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar. Poll. Bull.* 58 (2009) 745-751.
- [15] T.P. Hughes, Community structure and diversity of coral reefs: the role of history, *Ecology*. 70 (1989) 275-279.
- [16] R. Arthur, Coral bleaching and mortality in three Indian reef regions during an El Niño southern oscillation event. *Curr. Sci.* 79 (2000) 1723-1729.
- [17] J. Ravindran, C. Raghukumar, S. Raghukumar, Disease and stress-induced mortality of corals in Indian reefs and observations on bleaching of corals in the Andamans, *Curr. Sci.* 76 (1999) 233-237.
- [18] L.I.D.A. Pet-Soede, M.V.M. Wafar, K. Venkataraman, P.T. Rajan, D. Wilhelmsson, The status of the coral reefs of India following the bleaching event of 1998, *CORDIO Status Report*. (2000).
- [19] R. Arthur, T.J. Done, H. Marsh, V. Harriot, Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands, *Coral Reefs*. 25 (2006) 427-440.

- [20] A.K. Kumaraguru, K. Jayakumar, C.M. Ramakritinan, Coral bleaching 2002 in the Palk Bay, southeast coast of India, *Curr. sci.* 85 (2003) 1787-1793.
- [21] J. Ravindran, E. Kannapiran, B. Manikandan, R. Mani Murali, A. Joseph, Bleaching and secondary threats on the corals of Palk Bay: A survey and Proactive conservation needs, *Ind. J. Geo-Mar. Sci.* 41 (2012) 19-26.
- [22] R. Vinoth, M. Gopi, T.T.A. Kumar, T. Thangaradjou, T. Balasubramanian, Coral reef bleaching at Agatti Island of Lakshadweep atolls, India. *J. Ocean Univ. China.* 11 (2012) 105-110.
- [23] C.G. Pillai, The distribution of corals on a reef at Mandapam (Palk Bay), S. India. *J. Mar. Biol. Ass. India.* 11 (1969) 62-72.
- [24] M.U. Rao, Coral reef flora of the Gulf of Mannar and Palk Bay. Proc. 1st Int. symp. corals and coral reefs, Marine Biological Association of India, Mandapam camp, India, 1972.
- [25] S. English, C. Wilkinson, V. Baker, Survey Manual for Tropical Marine Resources, second ed., Australian Institute of Marine Science, Townsville, Australia, 1997.
- [26] B. Manikandan, J.Ravindran, S. Shrinivaasu, N. Marimuthu, K. Paramasivam, Community structure and coral status across reef fishing intensity gradients in Palk Bay, Southeast coast of India, *Env. Monit. Ass.* 186 (2014) 5989-6002.
- [27] J.E.N. Veron, Corals of the world, Vol 1-3, Australian Institute of Marine Science, Townsville, Australia, 2000.
- [28] K. Venkataraman, Handbook on hard corals of India, Zoological Survey of India, Kolkatta, India, 2003
- [29] R. Frouin, S.F. Iacobellis, Influence of phytoplankton on the global radiation budget, *J. Geophys. Res: Atmospheres.* 107 (2002) D19.
- [30] P.E. Van Laake, G.A. Sanchez-Azofeifa, Mapping PAR using MODIS atmosphere products. *Remote. Sens. Environ.* 94 (2005) 554-563.
- [31] P.L. Jokiel, S.L. Coles, Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature, *Coral reefs.* 8 (1990) 155-162.
- [32] P. Krishnan, S. Dam Roy, G. George, R.C. Srivastava, A. Anand, S. Murugesan, M. Kaliyamoorthy, N. Vikas, R. Soundararajan, Elevated sea surface temperature during May 2010 induces mass bleaching of corals in the Andaman, *Curr. Sci.* 100 (2011) 111-117.
- [33] D.J. Smith, D.J. Suggett, N.R. Baker, Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals?, *Global. Change. Biol.* 11 (2005) 1-11.
- [34] P.N. Sridhar, M.M. Ali, M.V. Rao, P.V. Nagamani, Photosynthetically active radiation, a critical parameter for mass coral bleaching in the North Indian Ocean, *Curr. Sci.* 102 (2012), 114-118.
- [35] A.M. Jones, R. Berkelmans, M.J. van Oppen, J.C. Mieog, W. Sinclair, A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization, *Proc. Royal. Society B: Biol. Sci.* 275 (2008) 1359-1365.
- [36] P.W. Glynn, L. D'croz, Experimental evidence for high temperature stress as the cause of El Nino-coincident coral mortality, *Coral reefs.* 8 (1990) 181-191.
- [37] A. Szmant, N.J. Gassman, The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*, *Coral reefs.* 8 (1990) 217-224.
- [38] R. Rowan, N. Knowlton, A.C. Baker, J. Jara, Landscape ecology of algal symbiont communities explains variation in episodes of coral bleaching, *Nature.* 388 (1997) 265-269.

- [39] E.M. Sampayo, T. Ridgway, P. Bongaerts, O. Hoegh-Guldberg, Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type, *Proc. Natl. Acad. Sci.* 105 (2008) 10444-10449.
- [40] Y. Loya, K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, R. Van Woesik, Coral bleaching: the winners and the losers, *Ecol. Lett.* 4 (2001) 122-131.
- [41] V.J. Harriott, Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar. Ecol. Prog. Ser.* 21 (1985) 81-88.
- [42] J. Ravindran, E. Kannapiran, B. Manikandan, K. Francis, S. Arora, E. Karunya, A. Kumar, S.K. Singh, J. Jose, UV-absorbing bacteria in coral mucus and their response to simulated temperature elevations, *Coral reefs.* 32 (2013) 1043-1050.
- [43] R.J. Jones, S. Ward, A.Y. Amri, O. Hoegh-Guldberg, Changes in quantum efficiency of Photosystem II of symbiotic dinoflagellates of corals after heat stress, and of bleached corals sampled after the 1998 Great Barrier Reef mass bleaching event, *Mar. Freshwater. Res.* 51 (2000) 63-71.
- [44] A.K. Kumaraguru, K. Jayakumar, C.M. Ramakritinan, Coral bleaching 2002 in the Palk Bay, southeast coast of India, *Curr. Sci.* 85 (2003) 1787-1793.
- [45] R. Sridhar, T. Thangaradjou, L. Kannan, S. Astalakshmi, (2010). Assessment of coastal bio-resources of the Palk Bay, India, using IRS-LISS-III data, *J. Ind. Soc. Remote Sens.* 38 (2010) 565-575.
- [46] K. Venkataraman, R. Rajkumar, Status of coral reefs in Palk Bay, *Rec. Zool. Surv. India.* 113 (2013) 1-11.
- [47] R. Van Woesik, K. Sakai, A. Ganase, Y. Loya, Revisiting the winners and the losers a decade after coral bleaching, *Mar. Ecol. Prog. Ser.* 434 (2011) 67-76.
- [48] C.A. Baker, P.W. Glynn, B. Riegl, Climate change and coral reef bleaching: An ecological assessment of long term impacts, recovery trends and future outlook, *Est., Coast. Shelf. Sci.* 80 (2008) 435-471.
- [49] B. Brown, R. Dunne, M. Goodson, A. Douglas, Experience shapes the susceptibility of a reef coral to bleaching, *Coral Reefs.* 21 (2002) 119-126.
- [50] R.W. Buddemeier, A.C. Baker, D.G. Fautin, J.R. Jacobs, The adaptive hypothesis of bleaching, in: E. Rosenberg, Y. Loya (Eds.), *Coral health and disease*, Springer, Berlin, Heidelberg, 2004, pp. 427- 444.
- [51] T.A. Oliver, S.R. Palumbi, Many corals host thermally resistant symbionts in high-temperature habitat, *Coral Reefs.* 30 (2011) 241-250.
- [52] J.M. West, R.V. Salm, Resistance and resilience to coral bleaching: implications for coral reef conservation and management, *Conserv. Biol.* 17 (2003) 956-967.
- [53] J.J. Wilson, N. Marimuthu, A.K. Kumaraguru, Sedimentation of silt in the coral reef environment of Palk Bay, India. *J. Mar. Biol. Ass. India.* 47 (2005) 83-87.
- [54] J. Miller, R. Waara, E. Muller, C. Rogers, Coral bleaching and disease combine to cause extensive mortality on reefs in US Virgin Islands, *Coral Reefs.* 25 (2006) 418-418.
- [55] J.E. Carilli, R.D. Norris, B.A. Black, S.M. Walsh, M. McField, Local stressors reduce coral resilience to bleaching, *PLoS One.* 4 (2009) e6324.

Figures

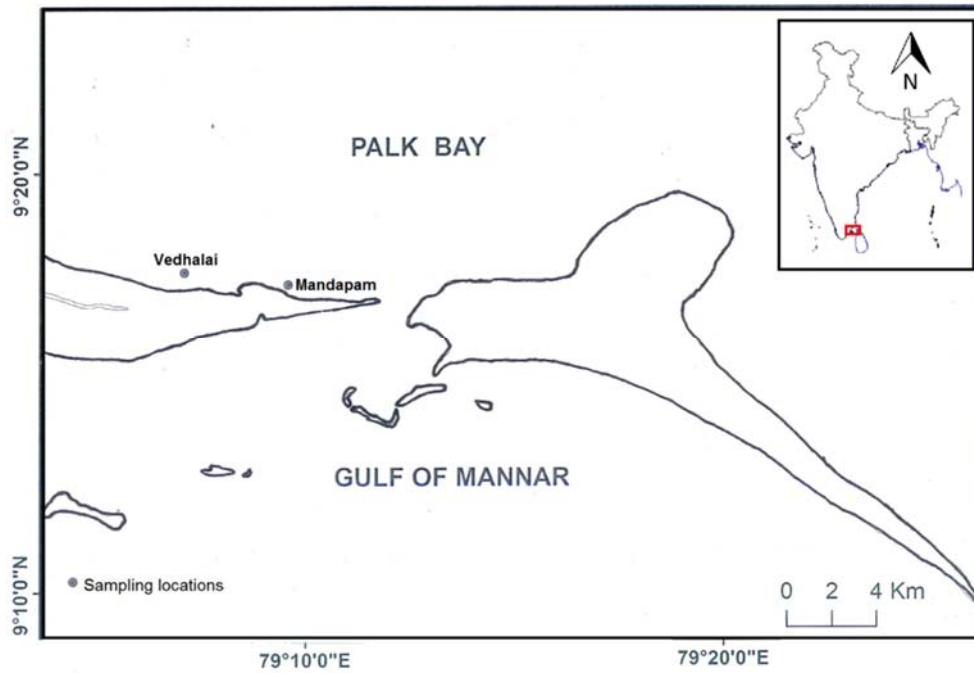


Figure 1: Map showing the locations of study sites at Vedhalai and Mandapam reef along Palk Bay where the permanent quadrats were setup for continuous observations.

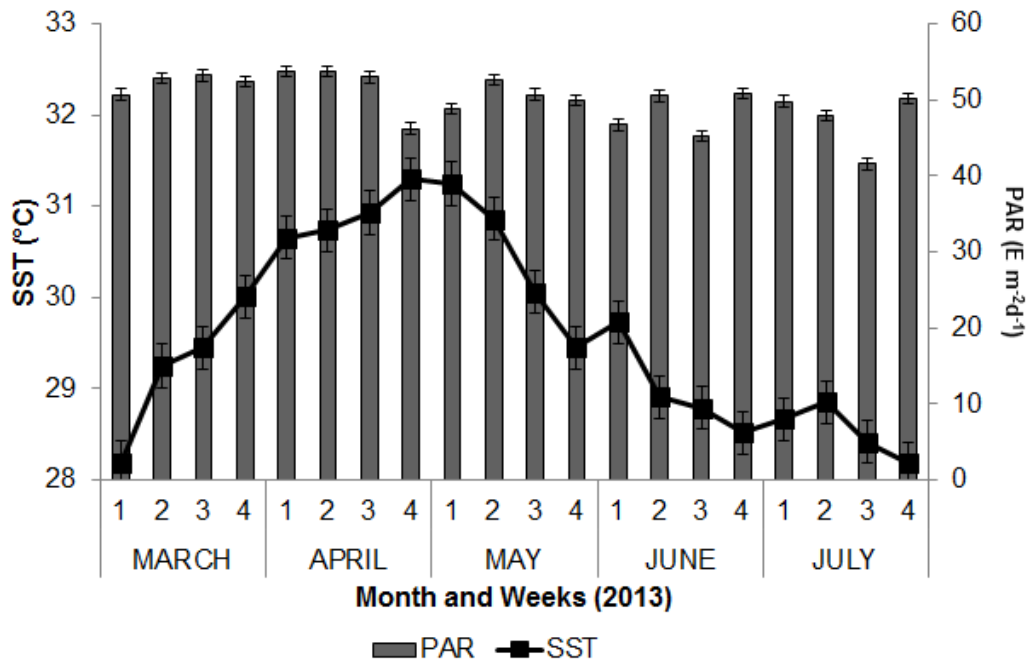


Figure 2: Temporal pattern of Sea Surface Temperature (SST) and Photosynthetically Active Radiation (PAR) during the bleaching event in 2013. Error bars indicate standard error.

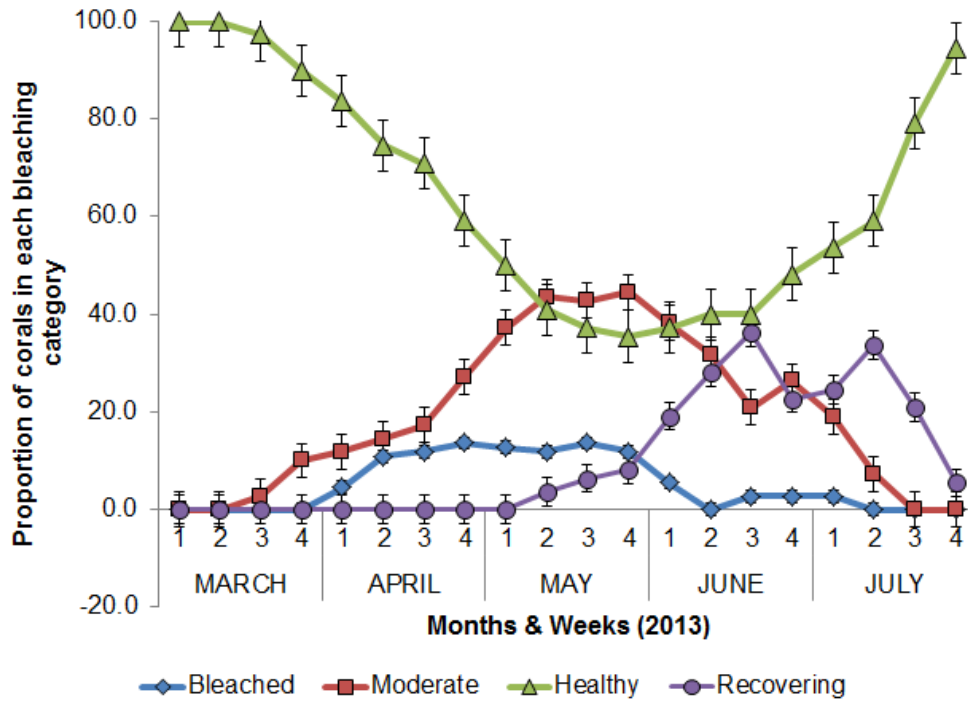


Figure 3: Bleaching and recovery response among coral colonies at Palk Bay reef during the bleaching event in 2013. Error bars indicate standard error.

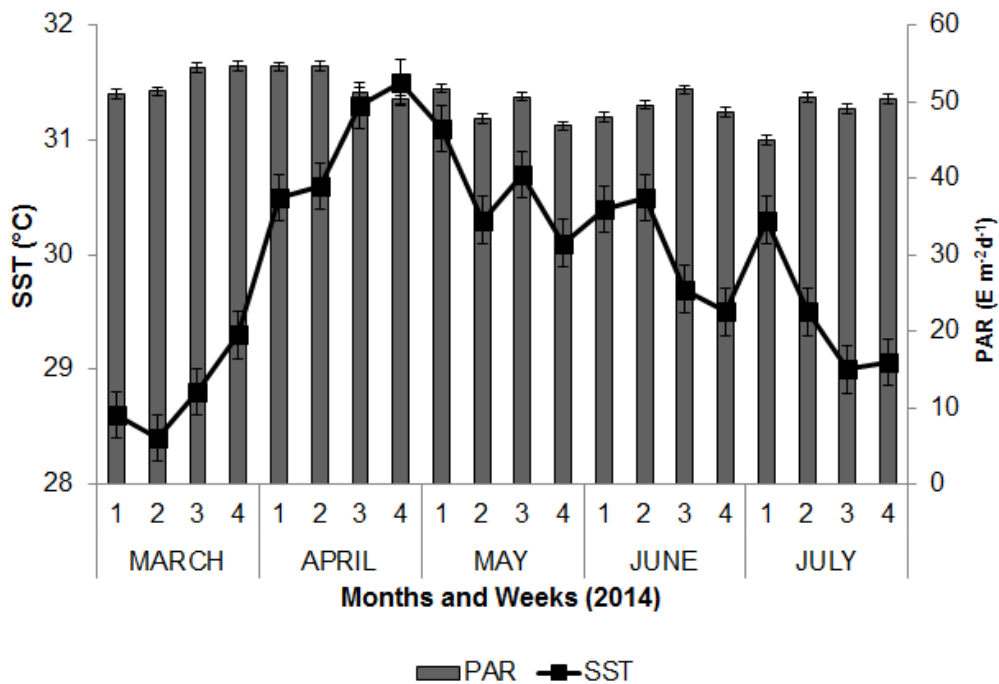


Figure 4: Temporal pattern of Sea Surface Temperature (SST) and Photosynthetically Active Radiation (PAR) during the bleaching event in 2014. Error bars indicate standard error.

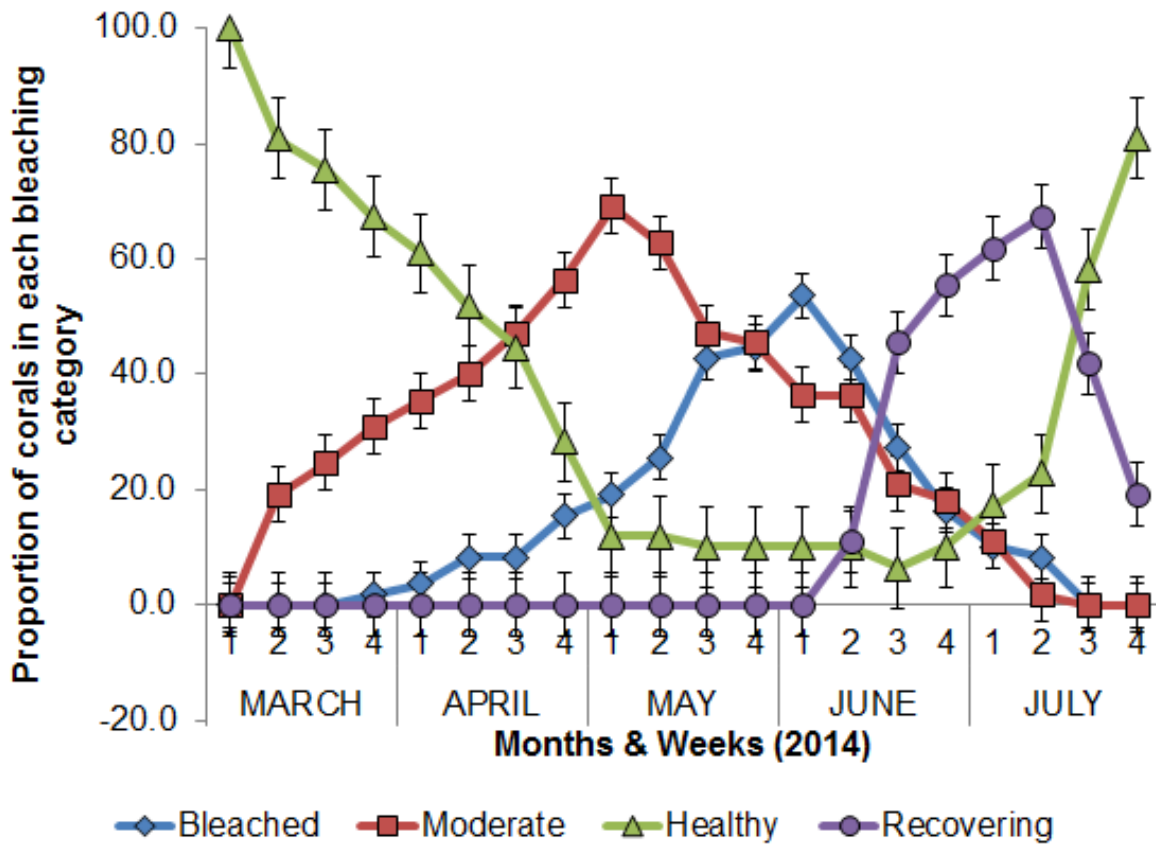


Figure 5: Bleaching and recovery response among coral colonies at Palk Bay reef during the bleaching event in 2014. Error bars indicate standard error.