

The Effects of Habitat on Coral Resistance and Resilience to Bleaching

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ABSTRACT

This study examines the bleaching responses of scleractinian corals at four sites in Kenya (Kanamai, Vipingo, Mombasa Marine Park and Nyali) representing two distinct lagoon habitats (relatively shallow and relatively deep). Bleaching responses were monitored for the general coral community and zooxanthella densities and chlorophyll levels were monitored for target species (*Pocillopora damicornis*, *Porites lutea* and *Porites cylindrica*) during a non-bleaching year (2006) and a year of mild bleaching (2007). The objective of this study is to determine whether corals in different habitats display varying resistance and resilience to bleaching stress and to indicate which environmental characteristics are responsible for the variation in response. Considerable differences in bleaching responses between shallower and deeper lagoon sites were observed, with shallower sites Kanamai and Vipingo exhibiting much lower bleaching and paling incidence than deeper sites Nyali and Mombasa Marine Park. These shallower lagoons display much more fluctuating thermal and light environments than the deeper sites, with higher

maximums, lower minimums, higher standard deviations and higher diel variation. These results suggest that corals in the shallower lagoons have acclimatized and/or adapted to the fluctuating environmental conditions they endure on a daily basis and have become more resistant to bleaching stress. Furthermore, in deeper sites that did exhibit significant bleaching (Mombasa Marine Park and Nyali), it was found that coral recovery occurred more quickly in the protected area compared to the non-protected area.

INTRODUCTION

Climatic changes are causing increased frequency of coral bleaching events worldwide. Coral bleaching events are usually associated with above-average water temperatures and high irradiance levels that cause the disruption of the obligate symbiosis between corals and micro-algal zooxanthellae. The zooxanthellae are expelled and the coral is left in a weakened state that can eventually lead to mortality of colonies and even a phase shift from a coral-dominated to an algal-dominated reef and a subsequent loss of biodiversity.

Obura, D.O., Tamelander, J., & Linden, O. (Eds) (2008). *Ten years after bleaching - facing the consequences of climate change in the Indian Ocean. CORDIO Status Report 2008. Coastal Oceans Research and Development in the Indian Ocean/Sida-SAREC. Mombasa.* <http://www.cordioea.org>

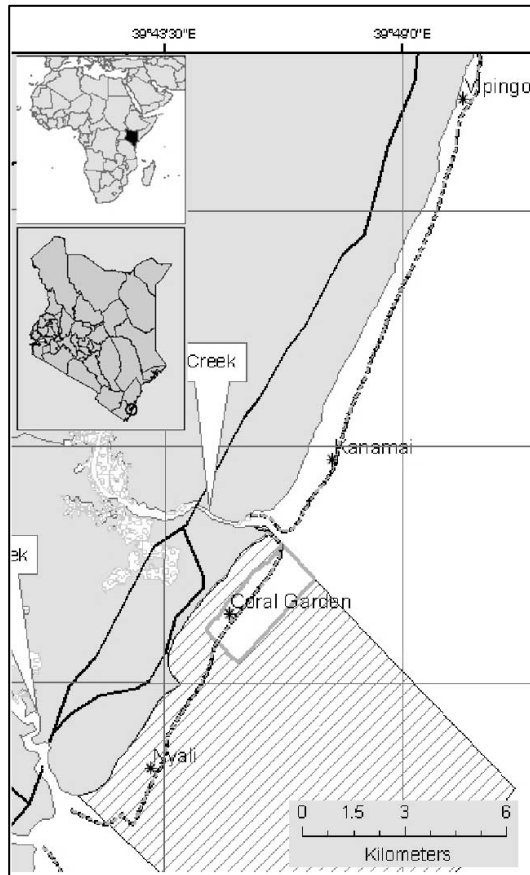


Figure 1. Map of study sites.

However, it is possible for corals to either resist conditions that cause coral bleaching or to recover from bleaching events (resilience). Resistance can be defined as the ability of an ecosystem or individual to withstand disturbance without undergoing a phase shift or losing neither structure nor function (Odum, 1989). Resilience can be defined as the ability of a system or an individual to absorb or recover from disturbance and change, while maintaining its functions (Carpenter et al, 2001). Several ecological and environmental factors can affect a coral reef's resistance and resilience to bleaching events. These include the coral reef's community species composition, herbivory levels, zooxanthellae population, temperature and irradiance history,

connectivity to other reefs, water movement, and shading or screening properties (Grimsditch and Salm, 2006; Hoegh-Guldberg, 1999; West and Salm, 2003).

Furthermore, it has been shown that it is possible for colonies to acclimatize to increased temperatures and high irradiance levels so that they are able to resist bleaching events when they occur. Acclimatization can be defined as the ability of an organism to undergo phenotypic changes in response to stress in the natural environment that result in the readjustment of the organism's tolerance levels to that stress (Coles and Brown, 2003). Threshold temperatures that induce coral bleaching-related mortality vary worldwide (from 27°C in Easter Island; Wellington et al, 2001, to 36°C in the Arabian Gulf; Riegl, 1999) according to the maximum water temperatures that are normal in the area, implying a capacity of corals and/or zooxanthellae to survive higher temperatures for a certain period of time. Furthermore, corals that are regularly exposed to stressful environmental conditions have been shown to acclimatize and exhibit physiological tolerance to elevated temperatures and UV-radiation that exceed normal thresholds (Brown et al, 2000; Brown et al, 2002a; Brown et al, 2002b, Coles and Brown, 2003).

In order to combat the worst effects of climate change and to conserve this valuable ecosystem, it is important to determine which factors affect coral reef bleaching resistance and resilience and to apply this knowledge in management plans. Although bleaching events cannot be prevented by managers, by implementing appropriate management responses it is possible to help a coral reef recover from bleaching and to mitigate the worst effects.

This study examines the bleaching responses of corals at four sites (Nyali, Mombasa Marine Park, Kanamai and Vipingo, Fig. 1) representing two distinct lagoonal habitats on the Kenyan coast (deeper and shallow lagoons). The sites were characterized using environmental parameters such as depth, water flow, light and temperature. Bleaching responses were monitored for the general coral community and zooxanthellae densities and chlorophyll levels were

monitored for target species (*Pocillopora damicornis*, *Porites lutea* and *Porites cylindrica*) during a non-bleaching year (2006) and a mild bleaching year (2007). The objective of this study is thus to determine whether corals in different habitats display different bleaching responses (i.e. resistance and resilience) and to suggest which environmental characteristics are responsible for the variation in response.

MATERIALS AND METHODS

Five large and healthy coral colonies for each target species (*Pocillopora damicornis*, *Porites cylindrica* and *Porites lutea*) were mapped at two shallow lagoons (Kanamai and Vipingo, 0.4m depth and 0.6m at low tide respectively) and two deeper lagoons (Mombasa Marine Park and Nyali, 1.4m and 1.8m depth at low tide respectively) along the Kenyan coast (Fig. 1). Target species were chosen according to general abundance and bleaching susceptibility, with one highly susceptible (*Pocillopora damicornis*), one moderate (*Porites cylindrica*) and one tolerant (*Porites lutea*) target species. Coral size class and line intercept transect data were also collected for two fixed 25x2m transects at each site.

The bleaching season in Kenya occurs during the late northeast monsoon from mid March when doldrum conditions become most intense to late April when the first storms of the southeast monsoon induce cooling of surface waters. In the two years of the study, sampling began before bleaching during the northeast monsoon (February and early March), continued during bleaching season of the northeast monsoon (late March and April) and finished during the recovery period of the southeast monsoon (May, June and July).

Coral fragments were collected from the mapped colonies using a chisel. The fragments were transported to the laboratory submerged in seawater in small plastic bottles and were held in an aerated seawater tank. Coral tissue was removed from the

skeleton using a water jet. Seawater was then added to the tissue to make up a practical volume, usually 500 ml. The tissue slurry was homogenised and 1.0 ml of homogenate was loaded into a Sedgwick-Rafter chamber. Using a compound binocular microscope and a magnification of x400, the number of zooxanthellae in 10 random quadrats was recorded. The counting chamber was then reloaded and another 10 random quadrats were counted. The area of the coral skeleton was measured using the foil method; the area/weight ratio of aluminium foil was determined and coral skeletons were then wrapped in this foil. The foil was then trimmed to fit the skeleton area and weighed. Using the weight of the trimmed foil and the area/weight ratio for the foil, the skeleton area could be determined.

To measure chlorophyll *a* levels, a known volume of the sample was filtered through a GF/F filter paper and the filtrate was dissolved in 10ml of 90% acetone. It was then centrifuged for 10 minutes at 2000rpm and the chlorophyll absorbance was read using a spectrophotometer.

If it was observed, bleaching incidence was recorded in the water using a random swim method. This consists of noting the size class, genus and bleached/pale/dead percentages of each bleached colony in 20 haphazard 2m² areas at each site.

Water temperature was monitored using underwater temperature loggers that were left at each site during the entire duration of the study. Light was monitored using a light meter for only 24-hour periods on the same day at each site to avoid theft and overgrowth of the light meter. Water flow was measured using a clod card method (McClanahan et al, 2005). Plaster-of-Paris clod cards were made in an ice-cube tray, dried and weighed before being deployed in the field in small net bags that were tied to the substrate. They were collected 24 hours later, dried and weighed again in order to determine how much had dissolved.

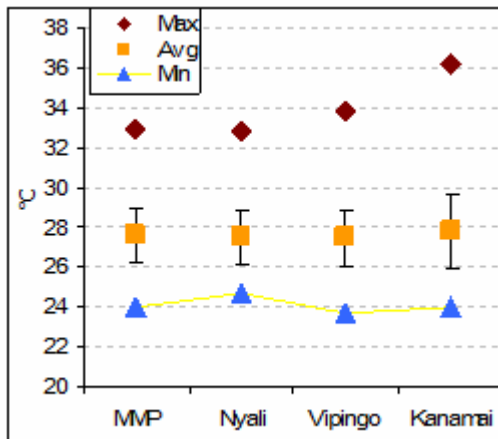


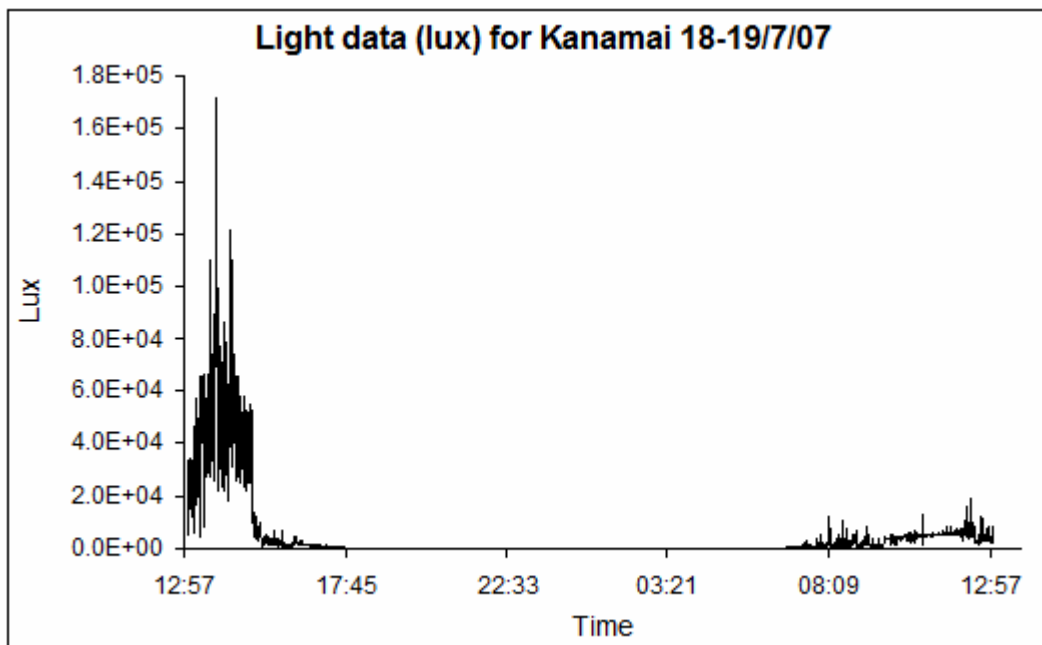
Figure 2. Average (\pm standard deviation), maximum and minimum water temperatures during study period.

RESULTS

Temperature

The shallow lagoons Kanamai and Vipingo displayed the most extreme temperature conditions, with higher standard deviations ($\pm 1.9^{\circ}\text{C}$ and $\pm 1.5^{\circ}\text{C}$ respectively), higher maximum temperatures (36.2°C and 33.8°C respectively), lower minimum temperatures (24.0°C and 23.7°C respectively) and bigger differences between diurnal and nocturnal temperatures ($+0.9^{\circ}\text{C}$ and $+0.4^{\circ}\text{C}$ respectively) than the deeper lagoons. Between the two, Kanamai displayed the more extreme fluctuations, as well as the highest average temperature overall (27.8°C) (Fig. 2).

The deeper lagoons of MMP and Nyali displayed less pronounced temperature variations with lower standard deviations (both $\pm 1.4^{\circ}\text{C}$) as well as smaller



Site	Average	Standard deviation	Max
Kanamai	4,913	14,315	170,846
Vipingo	4,758	10,489	110,223
MMP	518	879	5,167
Nyali	n/a	n/a	n/a

Figure 3. Light levels during a 24-hour period (18-19 July 2007) at Kanamai. Light data for each site during the same period is summarized and tabulated below the graph. All data is in Lux.

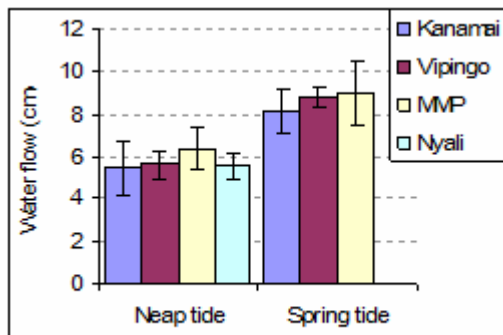


Figure 4. Average water flow (cm/s) at sites for neap and spring tides over a 24-hour period. Unfortunately, data for Nyali spring tide is unavailable due to technical difficulties.

maximum-minimum (+8.9°C and +8.1°C respectively) and diurnal-nocturnal (both +0.2°C) differences than the shallower lagoons. However, the deeper lagoons displayed bigger temperature increases from the 2006 to 2007 northeast monsoon bleaching seasons, with a +0.9°C increase in Nyali and a +0.8°C increase in MMP compared to a +0.7°C increase in both Kanamai and Vipingo.

Light

As expected, the shallow lagoons Kanamai and Vipingo also displayed more extreme light regimes than the deeper lagoon MMP. Unfortunately, light data for Nyali was not available due to technical problems. Kanamai (4913±14,315 lux) and Vipingo (4758±10,489 lux) both displayed much higher average light levels, higher standard deviations and higher maxima (70,846 lux and 110,223 lux respectively) than MMP (average of 518±879 lux, maximum of 5167 lux) (Fig. 3). Although light data is unavailable for Nyali, it can be assumed that the light regime is similar (with perhaps even lower averages) to MMP due to the depth and sediment levels of the site.

Water Flow

There was no clear trend between water flow at deeper and shallower lagoons. MMP consistently displayed the highest average water flow during both neap (6.4

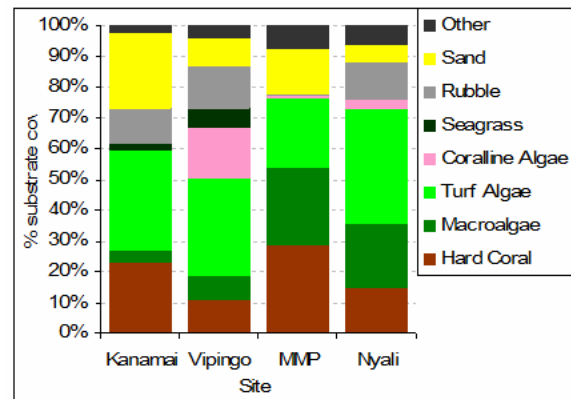


Figure 5. Substrate cover (%) at study sites.

cm/s) and spring tide cycles (9.0 cm/s). Kanamai (5.4 cm/s) displayed similar water flow to Nyali (5.5 cm/s) and Vipingo (5.6 cm/s) during neap tide and, although unfortunately data for spring tide at Nyali is unavailable, it appears that MMP stands out as the site displaying highest water flow. Overall, Kanamai displayed the lowest water flow during both neap and spring tides (8.1 cm/s) (Fig. 4).

Substrate Cover

MMP and Kanamai displayed higher hard coral cover (28.4% and 23.0% respectively) while Nyali and Vipingo displayed lower hard coral cover (14.7% and 10.6% respectively), showing no trend with depth. Macroalgal cover was higher in deeper sites MMP (25.5%) and Nyali (21.0%) than in shallower sites Vipingo (8.3%) and Kanamai (3.7%) (Fig. 5).

Coral Cover

All sites are dominated by massive and branching *Porites* colonies. 90.5% of MMP, 80.3% of Kanamai, 59.9% of Nyali and 42.2% of Vipingo coral cover was massive and branching *Porites*. Vipingo (10.2%) and Nyali (8.3%) displayed the highest relative coral cover of the more bleaching-susceptible genera *Acropora* and *Pocillopora*. *Acropora* and *Pocillopora* only accounted for 3.7% of Kanamai's coral cover and 0.7% of MMP's coral cover (Fig. 6).

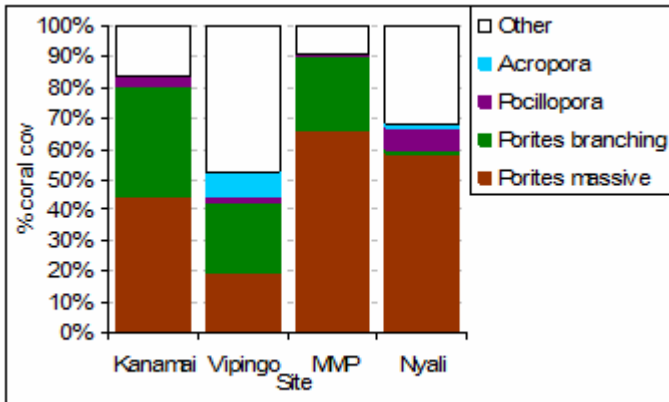


Figure 6. Percentage of coral area covered by each genus.

Bleaching and Mortality Incidence

Bleaching was first observed during late April of 2007. The shallow lagoons Kanamai and Vipingo exhibited lower levels of combined paling, bleaching and mortality (4.4% and 6.3% of total coral area respectively) than the deeper lagoons Nyali and MMP

(35.1% and 26.9% of total coral area respectively). During the recovery period, MMP still exhibited relatively high bleaching incidence (9.8%) but low mortality (0.9%). Nyali exhibited the highest mortality (11.7%) and also relatively high bleaching (4.5%). In July, mortality increased to 13.1% in Nyali and 2% in MMP, but bleaching incidence in MMP decreased to 6.0%, indicating recovery (Fig. 7). Overall, *Pocillopora* and *Porites* accounted for the highest proportion of bleached colonies, but differed greatly in their mortality rates. In MMP, Nyali and Vipingo, *Pocillopora* accounted for 37%, 47.1% and 33.3% of bleached colonies respectively. In Kanamai, MMP and Nyali, *Porites* accounted for 47.2%, 28.3% and 13.8% of bleached colonies respectively (Fig. 8). However, during the recovery period of June and July, *Porites* experienced low bleaching-related mortality while *Pocillopora* experienced high mortality. *Porites* colonies only experienced mortality in Vipingo, where they accounted for 12.5% of total bleaching-related

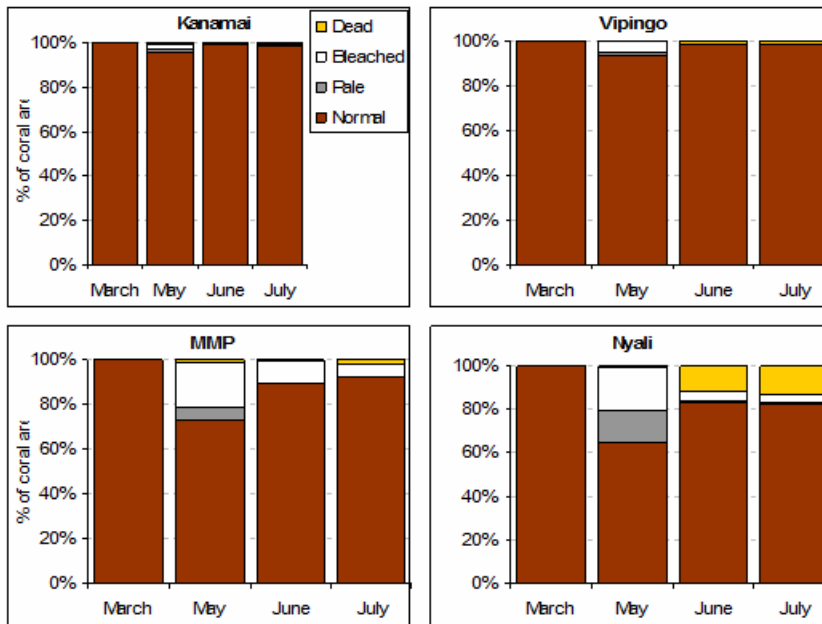


Figure 7. Bleaching, paling and mortality incidence during 2007.

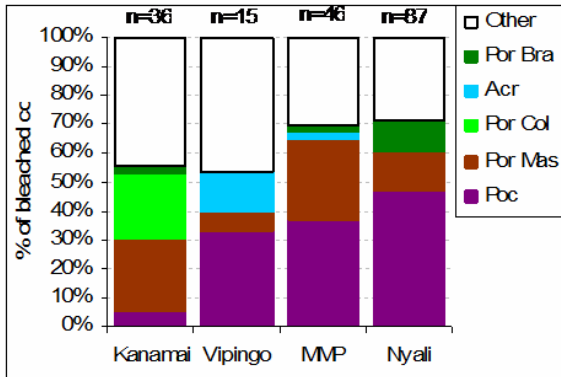


Figure 8. Proportion of bleached corals by genera.

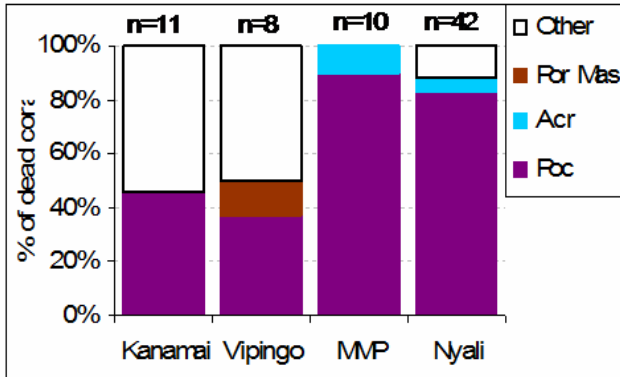


Figure 9. Proportion of corals exhibiting bleaching-related mortality by genera.

mortality, whereas *Pocillopora* accounted for the highest proportion of bleaching-related mortality in all sites (from 37.5% in Vipingo to 90% in MMP; Fig. 9). Furthermore, of the three species only *Pocillopora damicornis* suffered significant mortality in both 2006 (50% overall mortality) and 2007 (47% overall mortality) with colonies in Kanamai experiencing the lowest mortality rate in both years.

Zooxanthellae Densities

Average zooxanthellae densities for marked colonies (*Pocillopora damicornis*, *Porites lutea* and *Porites cylindrica*) were higher for all species at all sites in

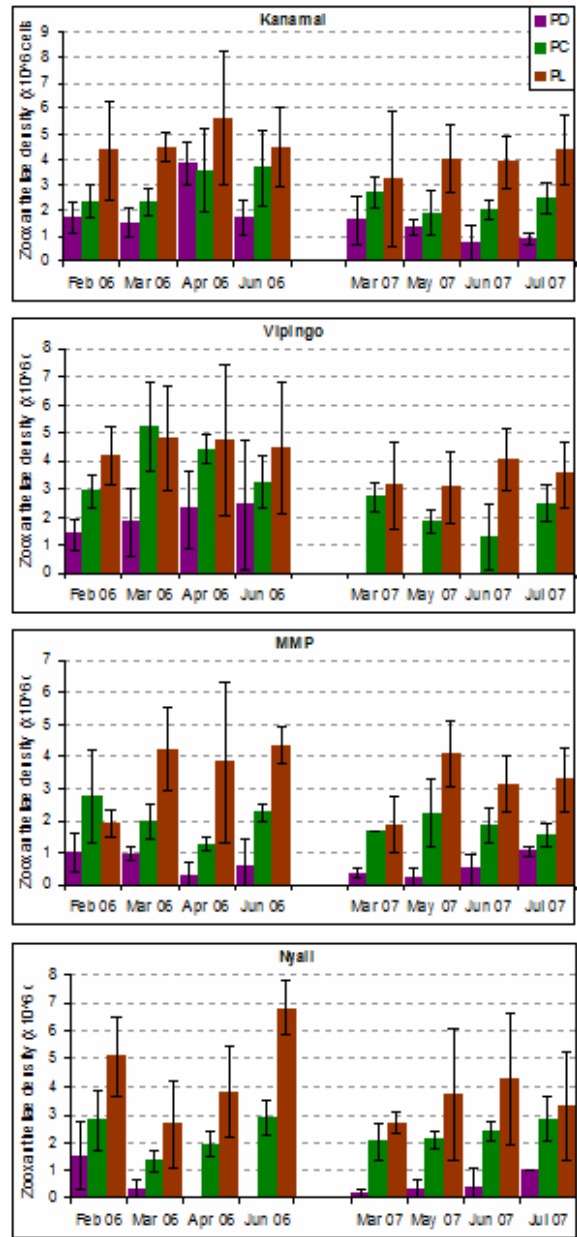


Figure 10. Average zooxanthellae densities for mapped corals (*Pocillopora damicornis*, *Porites cylindrica* and *Porites lutea*) during 2006 and 2007.

2006 than in 2007. Average zooxanthellae densities were also higher in shallower sites Kanamai and

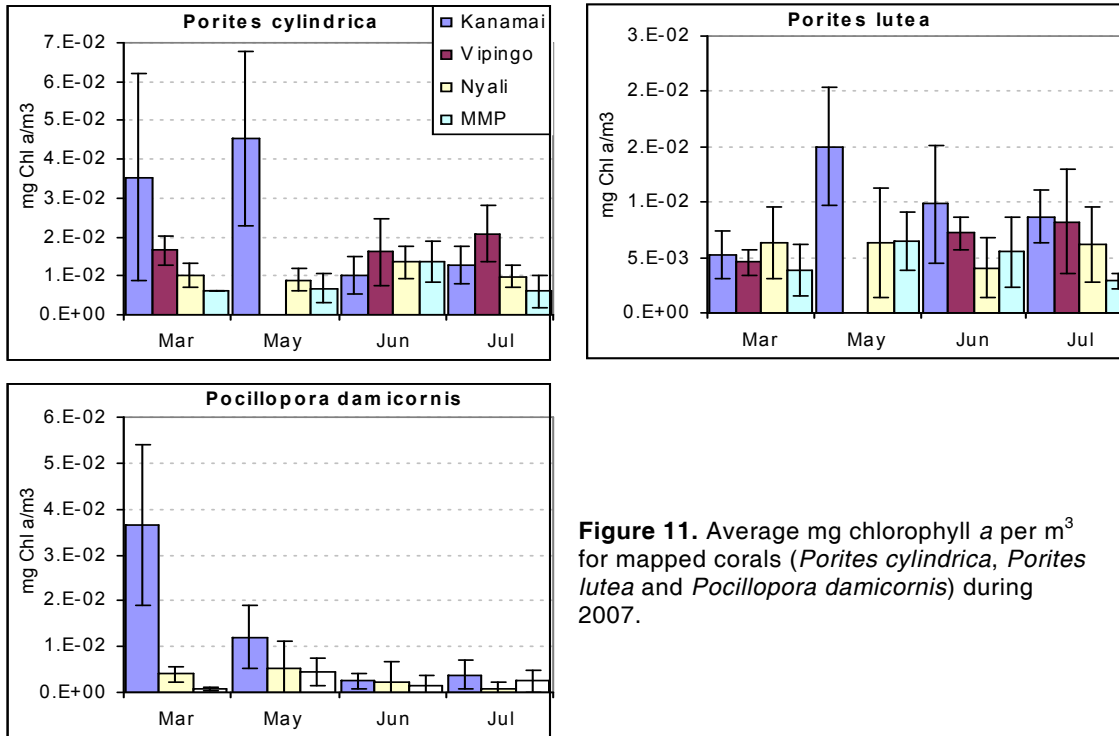


Figure 11. Average mg chlorophyll a per m³ for mapped corals (*Porites cylindrica*, *Porites lutea* and *Pocillopora damicornis*) during 2007.

Vipingo that in deeper sites MMP and Nyali for all species. In general, Kanamai exhibited the highest average zooxanthellae densities while MMP displayed the lowest. *Porites lutea* colonies exhibited the highest zooxanthellae densities while *Pocillopora damicornis* displayed the lowest densities, with *Porites cylindrica* in between the two (Fig. 10).

In 2006, colonies in MMP, Nyali and Kanamai displayed similar zooxanthellae density trends in most species with decreases in the warm months of February and March, and recovery in the following months as temperature decreased. Colonies in Vipingo, on the other hand, exhibited increasing densities for all species during February and March followed by decreases from April to June. In 2007, average zooxanthellae densities in *Pocillopora damicornis* remained very low ($<1 \times 10^6$ cells cm⁻²) in all sites with recovering densities in July. *Porites lutea* and *Porites cylindrica* colonies showed a general increasing trend

in average zooxanthellae densities from March to July (Fig. 10).

Chlorophyll a Levels

Chlorophyll a concentrations were generally higher at shallower sites Kanamai and Vipingo than at deeper sites Nyali and MMP, and Kanamai exhibited by far the highest chlorophyll a concentrations while MMP exhibited the lowest. *Porites cylindrica* consistently exhibited the highest chlorophyll a concentrations at all sites, while *Pocillopora damicornis* consistently displayed the lowest concentrations, with *Porites lutea* in between the two (Fig. 11).

Chlorophyll a concentrations in *Pocillopora damicornis* colonies generally decreased progressively at all sites from March to July as colonies bleached and failed to recover. *Porites lutea* and *Porites cylindrica* colonies in the shallow site Kanamai displayed peaks during March and then decreasing

concentrations to July. In MMP and Nyali, the concentration peaks for these two species were not as pronounced and generally occurred in May or June (Fig. 11).

DISCUSSION AND CONCLUSION

Considerable differences in bleaching responses during 2007 between shallow and deeper lagoonal sites were observed, with shallower sites Kanamai and Vipingo exhibiting much lower bleaching and paling incidence than deeper sites Nyali and MMP in both haphazard sampling and marked *Pocillopora damicornis* colonies. These results suggest that corals in the shallower lagoons have acclimatized to the more extreme environmental conditions they endure on a daily basis and have become more resistant to thermal stress than corals in the deeper lagoons.

Shallow sites Kanamai and Vipingo displayed more extreme temperature and light regimes than deeper sites Nyali and MMP with higher maxima, lower minima, larger standard deviations and larger diel variations. The smaller volumes of water in the shallower lagoons probably explain the difference in temperature and light regimes; shallower lagoons absorb but also lose heat more quickly and attenuate less light than in the deeper lagoons.

Moreover, differences in temperature and light regimes could explain differences in bleaching responses between similar-depth sites. Kanamai is a shallower site than Vipingo, displaying higher average temperatures, standard deviation in temperatures, difference between maximum and minimum temperature, diel temperature variation, maximum light level and standard deviation in light levels. This may explain why Kanamai also displayed lower bleaching incidence and bleaching-related mortality than Vipingo. Similarly, MMP is a shallower site than Nyali, displaying higher average temperatures and difference between maximum and minimum temperature. Nyali experienced increased warming during the 2007 northeast monsoon bleaching period (+0.9°C to 2006) compared to MMP (+0.8°C to 2006). These factors could explain why Nyali

exhibited higher bleaching incidence than MMP.

On the other hand, water flow did not correlate well with depth and bleaching incidence, and although corals in Nyali suffered much higher bleaching incidence than Kanamai and Vipingo, all these sites displayed very similar water flow velocities. It therefore appears that light and temperature histories were more influential than water flow in determining the bleaching responses of corals.

Moreover, average zooxanthellae densities and chlorophyll *a* concentrations are higher in Kanamai and Vipingo than in Nyali and MMP, with highest densities in Kanamai. Studies in the region have shown that corals with higher zooxanthellae densities are more resistant to bleaching (Grimsditch et al, 2007), a hypothesis that is further confirmed by these results. In addition, *Porites lutea* displayed the highest densities and was the most tolerant to bleaching, while *Pocillopora damicornis* exhibited the lowest densities and was the most susceptible to bleaching. Zooxanthellae population dynamics could thus also partly explain bleaching responses at different sites.

Interestingly, species that suffered less bleaching (*Porites lutea* and *Porites cylindrica*) did not exhibit decreases in chlorophyll *a* concentrations through time, and actually exhibited increases in chlorophyll *a* during bleaching and recovery months in some cases. However, *Pocillopora damicornis*, which was more susceptible to bleaching, displayed decreasing chlorophyll *a* concentrations with time, indicating that bleaching events cause disruptions in pigments as well as symbionts.

The genus most affected by bleaching at Nyali, MMP and Vipingo was *Pocillopora*, and it accounted for most of the bleaching-related mortality in all sites. *Porites* also made up significant proportions of bleached corals in MMP, Nyali and Kanamai. However, *Porites* colonies hardly exhibited any bleaching-related mortality, showing that although this genus does bleach and pale it is tolerant to bleaching. Despite their susceptibility to bleaching, *Acropora* corals form a very small proportion of bleached corals in most sites because they are scarce, except for in Vipingo where they form a larger

proportion of the total coral are and subsequently also a larger proportion of bleached corals.

All sites were dominated by massive and branching *Porites* corals, discounting the possibility that large variations in coral community compositions determined bleaching responses. Bleaching-susceptible genera such as *Pocillopora* and *Acropora* did not necessarily form a larger proportion of the coral population in sites most affected by bleaching. The highest area percentage covered by these genera occurs in Vipingo, which is a shallow site exhibiting low bleaching incidence. However, differences in community composition could partially explain varying bleaching responses between similar-depth sites. Nyali exhibited higher bleaching incidence than MMP and also a higher proportion of area covered by bleaching-susceptible genera. The same applies to Vipingo compared to Kanamai.

During the recovery period, colonies in Nyali displayed higher mortality than those in MMP, while a higher proportion of corals in MMP remained bleached but did not die. It thus seems that colonies in Nyali were being overgrown by algae more quickly than those in MMP, which remained in a bleached state longer. This could be due to the protected status of MMP and the possibility that herbivory levels are higher than in Nyali. In fact, populations of important herbivores such as parrotfish and surgeonfish have been shown to be significantly higher in protected areas than in non-protected areas along the East African coast (McClanahan and Arthur, 2001).

In conclusion, the data from this study show that during the 2007 bleaching season, corals in the shallow lagoons of Kanamai and Vipingo were more resistant to bleaching stress than corals in the deeper lagoons of MMP and Nyali, probably due to a history of higher light and temperature extremes and variation at the shallower sites. Interesting differences were also found between the deeper lagoons at Nyali and MMP – on the one hand MMP reefs experience slightly larger diel variation in temperature, and on the other they experienced less warming in 2007. Whether this acclimatization is due to short-term phenotypic

changes or due to a longer-term process of adaptation through natural selection is a question that could be further researched. *Pocillopora* was the genus most susceptible to bleaching-related mortality, especially at Nyali, and *Porites* branching, massive and columnar all displayed high tolerance to bleaching. Among all these patterns of bleaching susceptibility, it is not clear whether the acclimatization is host-based or symbiont-based, and monitoring of the zooxanthellae clades in corals at these sites could help in answering this question. Finally, bleached corals in MMP suffered lower levels of mortality than in Nyali, possibly associated with higher rates of herbivory due to MMP's protected status. While herbivory is often related to resilience of reefs and the influence of herbivores assisting recovery by coral recruits, this result suggests herbivory may also mediate interactions between algae and bleached corals, and assist in the survival of bleached corals.

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