

Thermal spatial heterogeneity and coral bleaching: implications for habitat refuges

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Abstract. Mass coral bleaching/mortality, due to elevated seawater temperature (ST) anomalies, is increasing in intensity and frequency worldwide. However, coral bleaching/mortality at a finer scale, for example within a reef, have yet to be thoroughly examined. This study compares coral bleaching and underwater temperature/light from November 2010 till March 2011 using data loggers deployed at three stations: near the coast (S1); in the middle of the lagoon (S2); and on the reef flat (S3), at Flic-en-Flac (FEF) and Belle Mare (BM), Mauritius. At FEF STs were above 31°C for S1 beginning late December 2010, and for S2 and S3 beginning late January 2011, while at BM such STs for S1 occurred since mid January 2011, and for S2 and S3 in late February 2011. Moreover, the number of observations of maximum STs of 32°C or above was 4 at S1 in late February 2011 and none at S2 and S3 for BM, while at FEF, number of observations of STs of 32°C or above was 5 at S1 and 1 at S2 in late February 2011 and none at S3. However, at the end of March 2011, bleaching of *Acropora muricata* was observed only at S2 and S3, and no bleaching was observed at S1 at both FEF and BM. These results indicate that though *A. muricata* were exposed to higher maximum STs near the coast, it did not experience bleaching compared to the lagoonal and reef flat sites and thus suggest potential occurrence of thermal ‘habitat’ refuges within coral reefs.

Key words: *A. muricata*, Coral bleaching, Differential susceptibility, Thermal variability.

Introduction

Coral bleaching, loss of their endosymbiotic dinoflagellates (commonly known as zooxanthellae) (Hoegh-Guldberg & Smith 1989, Glynn & D' Croz 1990) and/or their photosynthetic pigments (Kleppel et al. 1989), has been reported to increase in frequency. Mass bleaching has been mainly linked to high temperature anomalies (Glynn 1993, Brown 1997, Lesser 2004) related to global warming due to climate change and high solar irradiance (Hoegh-Guldberg 1999).

The year 1998 witnessed widespread heavy coral bleaching/mortality occurrences due to the 1997-1998 El Niño event. This event resulted in loss of an almost one-sixth of world's coral reefs. Some reefs in the Indian Ocean suffered up to 90% mortality of shallow-water corals. Surface seawater temperature (SST) based prediction models at larger scales suggested that some reefs of the Indian Ocean may go “extinct” between the years 2010-2090 (Sheppard 2003). Bhagooli & Sheppard (2012) have suggested ‘extinction dates’ of years 2025-2070 depending on the bleaching/mortality thermal thresholds. It is noteworthy that these dates could be prolonged for a century or so if reef-building corals are able to

acclimate by as little as 2°C (above previously lethal SSTs) over this timeframe.

Mauritius escaped the 1998 massive bleaching/mortality event most probably due to coinciding cyclonic events. The Mauritian reefs suffered a mild bleaching (< 10%) event in 1998 and coincided with a tropical cyclone, Anacelle, which brought in high cloud cover and enhanced mixing of the water thus preventing the occurrence of an elevated temperature anomaly event (Turner et al. 2000). In 2004, a more intense bleaching (about 24%) event took place in Mauritius (McClanahan et al. 2005). In 2009, there was a severe bleaching/mortality occurrence due to a thermal anomaly event and intra-specific and inter-specific differential bleaching/mortality were exhibited by reef-building corals (Bhagooli & Sheppard 2012). Variable bleaching/mortality have been quite well-documented both through field-based observations (Marshall & Baird 2000, Spencer et al. 2000, Loya et al. 2001) and laboratory-based experiments (Warner et al 1996, Bhagooli & Yakovleva 2004). Differential vulnerability of corals to thermal bleaching have been documented on the Great Barrier Reef, Australia (Marshall and Baird 2000), in the Indian Ocean

(Spencer et al. 2000) and in Okinawa, Japan (Loya et al. 2001). Previous studies on mass coral bleaching have reported differences in bleaching susceptibility between corals of different growth rates, with faster growing corals (e.g. acroporids and pocilloporids) being more severely affected by bleaching than slower growing species (e.g. poritids and faviids) in the Indo-Pacific region (Brown and Suharsono 1990). Another hypothesis suggests that bleaching susceptibility depends on the genetic constitution of the symbiotic algae (Rowan et al. 1997). In an attempt to explain why massive and encrusting coral species were less susceptible than the branched ones during the 1998 bleaching event in Okinawa, Loya et al. (2001) advanced two hypotheses: preferential survival of thick-tissued species (massive corals) and shape-dependent differences in colony mass-transfer efficiency (favoring encrusting species). Warner et al. (1996) claimed that differences in heat dissipation capacities in PSII of zooxanthellae residing in different coral species determine bleaching susceptibility. These differential responses might be explained by differences in tolerance among the hosts (Brown et al. 2002, Bhagooli & Hidaka 2003) and/or zooxanthellae clades/ITS types (Rowan 2004, Sampayo et al. 2008, Bhagooli 2009, 2010). Another plausible explanation could be variability in thermal (Nadaoka et al. 2001a) and hydrodynamic/water flow (Nadaoka et al. 2001b, Nakamura 2003) variability in the surrounding environment.

To date spatial variation in seawater temperature within reefs at a finer scale and bleaching occurrences, including intra-specific differential bleaching vulnerabilities, remain uncharted in the Mauritian waters. This study aims at quantifying and comparing seawater temperature variations within and across two coral reefs sites and bleaching occurrences in the most abundant branching coral, *Acropora muricata*, at two sites around Mauritius Island.

Material and Methods

The spatial thermal and bleaching occurrence variability were investigated in two lagoons of Mauritius, namely, Flic-en-Flac (FEF) and Belle Mare (BM), which are located in the western and eastern part of the island, respectively (Fig. 1A). Underwater temperature and light data loggers (Hobo data loggers) were deployed for monitoring of seawater temperature and light variations within and across FEF and BM for the period November 2010 to March 2011 (Fig. 1). The data loggers were deployed along transects extending from the coastline to the reef (Fig. 1B, 1C). Data loggers were replaced with clean ones almost every three weeks during the study period to avoid inappropriate light data collection resulting

from bio-fouling and/or deposition of particulate matter.

The study sites were divided into three parts, namely the water adjacent to the coast (referred to as 'coast'), the lagoon and the reef. FEF is a one of the highly utilized public beaches with a lot of coastal activities and modification of the coastline due to ongoing development. The less developed BM does experience some level of coastal macroalgal blooms possibly due to run-off from nearby agricultural fields or sewage discharge. Methoo (2010) documented a higher building density, including hotels, near the coast at FEF than BM. These two sites were selected because of their differing topography, environmental pressures and percentage coral cover. The reefs at BM and FEF are about 850 m and 500 m from the coast, respectively (MoE 2004), implying a greater lagoonal area and thus possibly implying higher thermal variation at BM than at FEF. A higher percentage and more evenly distributed live coral cover are found at BM than at FEF (MoE 2004). BM has a slightly higher percentage of macroalgae (8%) compared to FEF (6%). The bottom type at BM and FEF consists of sand, rock and boulders, live and dead coral patches, macroalgal patches, coral rubble patches.

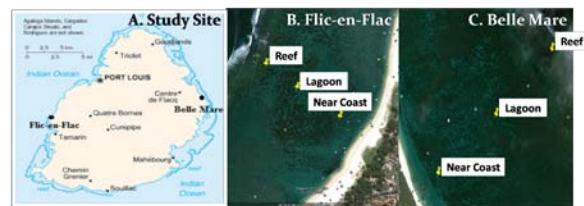


Figure 1: Map of Mauritius (Source: Exotic Mauritius, 2005 - 2012) indicating study sites, Flic-en-Flac (FEF) and Belle Mare (BM) (A), the representative transects and stations (Source: Google Earth) at FEF (B) and BM (C). Station 1 (S1) = Near coast; Station 2 (S2) = Lagoon; and Station 3 (S3) = Reef.

Coral bleaching surveys consisted of swimming and observing bleaching occurrence in the coral *Acropora muricata*. The bleaching survey included at least 30 colonies per station within the vicinity of the deployed data loggers along the indicated transects (Fig. 1B, C) and along two more parallel transects some 80 m and 500 m apart at FEF and BM, respectively, with similar stations. 3-way ANOVA was used to analyse the effects of sites, stations and time of survey on percentage of bleached coral colonies observed. Tukey posthoc comparison of means was used to test significant differences between sites, stations and time of survey.

Results

Seawater temperatures recorded varied at both studied sites. At FEF, temperatures above 31°C were recorded for station 1 (S1, coast) beginning at the end of December 2010, and for station 2 (S2, lagoon) and

station 3 (S3, reef) beginning at the end of January 2011. The number of observations of maximum seawater temperatures exceeding 31°C, a temperature at which many corals usually bleach, was 36, 16, & 3 for S1, S2 & S3, respectively (Fig. 2A-C). The number of observations of seawater temperatures of 32°C or above was 5 at S1 & 1 at S2 at the end of February 2011 & none at S3. As for the BM site, temperatures above 31°C were recorded for S1 beginning in the second week of January 2011 & for S2 and S3 beginning in the last week of February 2011. The number of observations of maximum seawater temperatures exceeding 31°C was 25, 5, and 4 for S1, S2 & S3, respectively. Number of observations of maximum seawater temperatures of 32°C or above was 4 at S1 at the end of February 2011 & none at S2 & S3 for BM (Fig. 3A-C).

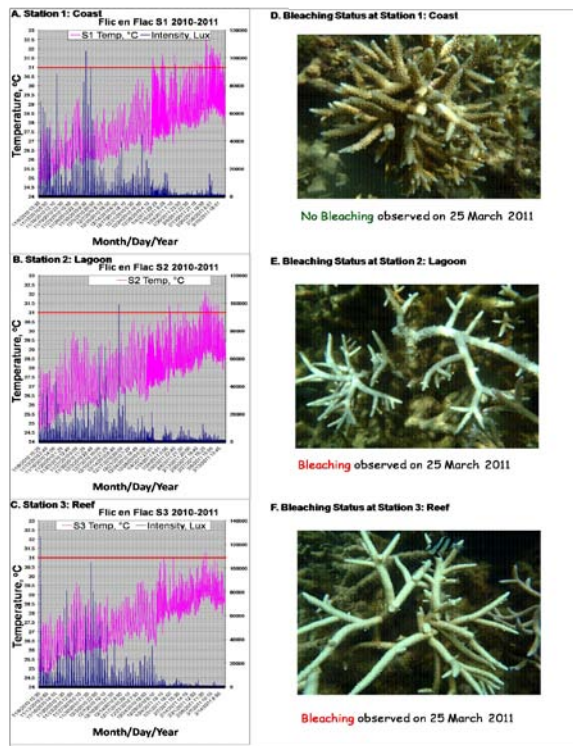


Figure 2: Seawater temperature (pink) and light intensity (lux) from November 2010 to March 2011 (A-C) and bleaching in *Acropora muricata* in March 2011 (D-F) near the coast (A,D), in the lagoon (B,E) and on the reef flat (C,F) at Flic-en-Flac (FEF), Mauritius. The red solid line at 31°C is used as a reference line.

A detailed analysis of the distribution of the different temperatures at the two sites revealed considerable shifts in dominance of particular temperatures with time at the three stations studied.

At both sites occurrence of temperatures below 27.99°C tended to fade out while temperatures above 28°C increased with time (Figs. 4 and 5). At FEF, lowest temperature recorded was 24°C and increased by almost 1°C for each of the following months

studied. The dominant temperatures at FEF were 25.00 to 26.99, 26.00 to 27.99, 27.00 to 27.99, 28.00 to 28.99 and 28.00 to 29.99°C over time.

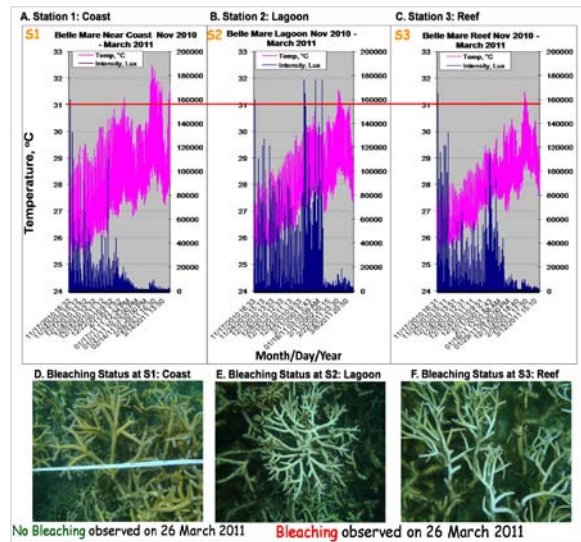


Figure 3: Seawater temperature (pink) and light intensity (lux) from November 2010 to March 2011 (A-C) and bleaching in *Acropora muricata* in March 2011 (D-F) near the coast (A,D), in the lagoon (B,E) and on the reef flat (C,F) at Belle Mare (BM), Mauritius. The red solid line at 31°C is used as a reference line.

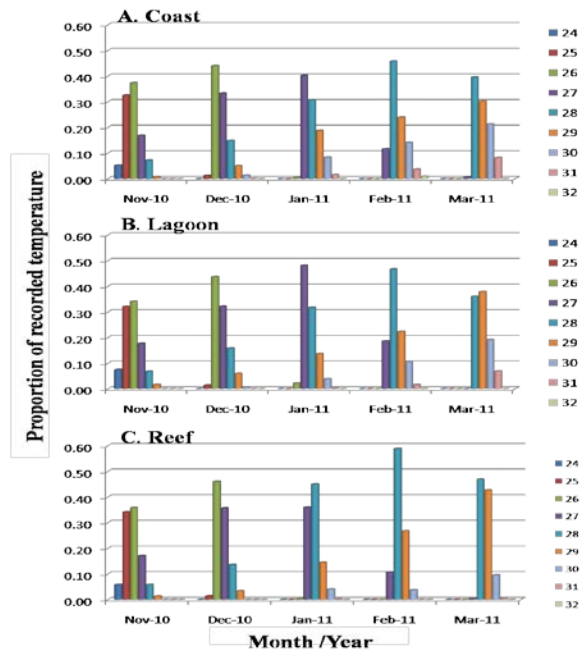


Figure 4: Proportion of different temperature recorded for each month November 2010 to March 2011 at three stations, Coast (A), Lagoon (B) and Reef (C) at FEF. Temperature legends are 24=24.00-24.99; 25=25.00-25.99; 26=26.00-26.99; 27=27.00-27.99; 28=28.00-28.99; 29=29.00-29.99; 30=30.00-30.99; 31=31.00-31.99; and 32=32.00-32.99°C.

Temperatures of 30°C emerged in December 2010 for the coast and in January 2011 for both the lagoon and reef. The temperature 31°C appeared in January 2011 and February 2011 for the coast and the lagoon,

respectively, while the reef did not experience it at all (Fig. 4).

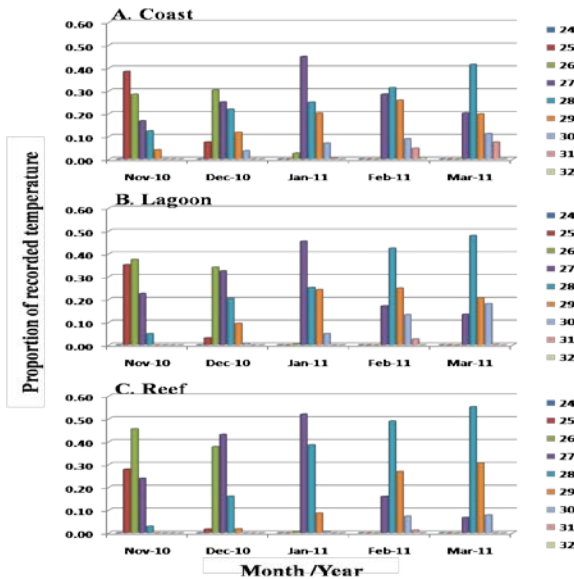


Figure 5: Proportion of different temperatures recorded for each month November 2010 to March 2011 at three stations, Coast (A), Lagoon (B) and Reef (C) at BM. Temperature legends are 24=24.00-24.99; 25=25.00-25.99; 26=26.00-26.99; 27=27.00-27.99; 28=28.00-28.99; 29=29.00-29.99; 30=30.00-30.99; 31=31.00-31.99; and 32=32.00-32.99.

For BM, the lowest recorded seawater temperature in this study was 25°C, which decreased considerably during the following month and disappeared for the rest of the study period. The temperature 31°C was recorded from January and February for the coast and the lagoon/reef, respectively. The coast area experienced higher occurrences of 31°C with some instances of 32°C, while both the lagoon and reef areas had very few occurrences of 31°C.

Table 1: Multiple comparison of mean ranks for all stations following Kruskal-Wallis ANOVA test by ranks analyses of temperature and light at two sites (BM and FEF) with three stations (coast-S1, lagoon-S2, reef-S3) at each site and time of the year (Nov and Dec 2010, and Jan, Feb and March 2011). Asterisks represent significant difference **P < 0.01 and ***P < 0.001.

		Temp			Light		
Flic-en-Flac	Station	S1	S2	S3	S1	S2	S3
	S1	-	***	**	-	**	NS
	S2	***	-	NS	**	-	NS
	S3	**	NS	-	NS	NS	-
Belle Mare	S1	-	***	***	-	***	***
	S2	***	-	***	***	-	***
	S3	***	***	-	***	***	-

Temperature varied significantly among studied stations (Figs. 4 & 5, Table 1) [Kruskal-Wallis test: H (2, N=70295) = 19.77, P < 0.001 at FEF; H (2, N = 65535) = 1107.97, P < 0.001 at BM] and months [Kruskal-Wallis test: H (4, N = 70295) = 33836.67, P < 0.001 at FEF; H (4, N = 65535) = 28265.05, P <

0.001]. Irradiance also varied among stations (Figs 2 & 3, Table 1) [Kruskal-Wallis test: H (2, N = 70295) = 10.09, P < 0.01 at FEF; H (2, N = 65535) = 426.40, P < 0.001 at BM] and months [Kruskal-Wallis test: H (4, N = 70295) = 2544.00, P < 0.001 at FEF; H (4, N = 65535) = 2720.75, P < 0.001] of the study. At FEF, stations did not differ in irradiance except for S1 and S2 (P < 0.01), while all the studied months differed significantly (P < 0.001) among each other. At BM all the three stations differed significantly (P < 0.001) in irradiance intensity over the studied period, Both at FEF and BM, irradiance differed significantly among the studied months, except for months February and March.

The bleaching surveys revealed that during the study period bleaching of *A. mucricata* was observed only at S2 and S3, and no bleaching was observed at S1 (Fig. 6) at both FEF (Fig. 2D-F) and BM (Fig. 3D-F). A 3-way ANOVA test showed that site, station and time had significant influence and their interactions were also significant in bleaching occurrences quantified (Table 2, Fig. 6). Tukey post-hoc tests indicated that the proportion of bleached colonies were significant different between the coast and either the lagoon and the reef at both studied sites. The proportion of bleached colonies differed significantly between the lagoon and reef areas only in March 2011 (P < 0.001) (Fig. 6). It was also found that in March 2011, the reef at BM exhibited significantly higher proportion of bleached colonies that at FEF (P < 0.001).

Discussion

Variability in seawater temperatures have been so far reported on reefs worldwide at different latitudes, within tidal pools, in the back reef of Moorea (Putnam & Edmunds 2011) and American Samoa (Craig et al. 2001), and inshore versus offshore (Naodaka et al. 2001b). The present study explores differences in variations in seawater temperatures by analyzing the coast, lagoon and reef area waters at two reefs of Mauritius and documents higher temperatures and their high frequency of occurrences in the coastal areas than the lagoon and reef areas.

Table 2: 3-Way ANOVA analyses of percentage of bleached colonies at two sites (BM and FEF) with three stations (coast-S1, lagoon-S2, reef flat-S3) at each site and time of the year (Nov and Dec 2010 and Jan, Feb and March 2011). Asterisks represent significant difference **P < 0.01 and ***P < 0.001.

Source of Variation	SS	df	MS	F	P
Site	0.05	1	0.05	24.44	***
Station	4.14	2	0.07	1062.91	***
Time	3.01	4	0.75	386.78	***
Site*Station	0.03	2	0.01	6.46	**
Site*Time	0.06	4	0.02	8.25	***
Station*Time	1.69	8	0.21	108.19	***
Site*Station*Time	0.05	8	0.01	3.34	**

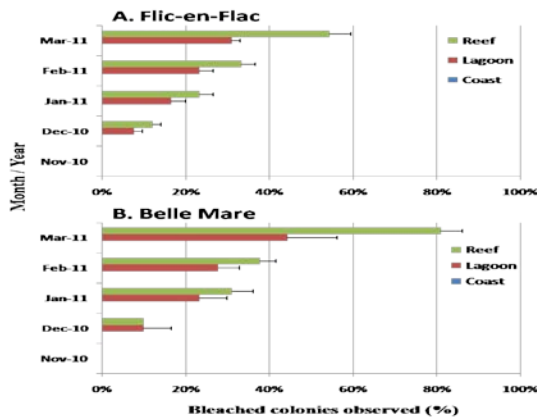


Figure 6: Bleaching (percentage colonies bleached out of 30 observed ones) in *A. muricata* from November 2010 till March 2011 at three stations (coast-S1, lagoon-S2, reef flat-S3) at FEF (A) and BM (B).

Bleaching of *A. muricata* colonies were more evident in the lagoon and reef areas than the coast area. It was recorded during late December 2010 at both sites during this study. The dominant seawater temperatures at these two areas were between 26.00 and 27.99°C. The coast area where no bleaching of *A. muricata* colonies was recorded had similar dominant temperatures during Dec 2010 but later had higher temperature maxima. These findings suggest that within a coastal area, there are several thermal bleaching thresholds. This might have implications for large scale bleaching/mortality predictions using one general threshold for a given large area.

Some studies (Berkelmans 2002, Manzello et al. 2007) have reported differential bleaching thresholds only among several reefs around the world. Differential responses of reef building corals have been attributed to several factors such as thermally robust coral hosts (Bhagooli & Hidaka 2003), thermally robust zooxanthellae (Warner et al. 1996, Bhagooli and Yakovleva 2004, Rowan 2004, Bhagooli 2010), and water flow (Nakamura 2003) among others. In this study it plausible that the *A. muricata* colonies in the coast area have better acclimatization and/or adaptation advantages to be capable of not exhibiting bleaching responses even upon exposure to higher temperatures than other studied stations, though other factors warrants further investigations to be able thoroughly understand the involved mechanism.

Irradiance can also determine the pattern of bleaching due to topography variation within a coral colony (Rowan et al. 1997) or due to depth variation. In this study, irradiance differed significantly among the stations with lagoon>reef flat>coast at BM and coast>lagoon at FEF. The low irradiance recorded at BM could possibly be explained by turbidity levels, which was not quantified in this study. There was no

consistent pattern in order of high to low irradiance intensities among the stations at both studied sites. High irradiance occurrence did not seem to be clearly linked to high bleaching incidences at all the stations in this study.

These results indicate that though the coral *Acropora muricata* were exposed to higher maximum seawater temperatures near the coast, it did not experience bleaching compared to the lagoon and reef area stations. This is suggestive of the near coast stations harbouring thermally more robust *A. muricata* and/or acting as ‘habitat’ refuges within a coral reef site and thus having restoration, conservation and management implications especially in the wake of global warming.

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