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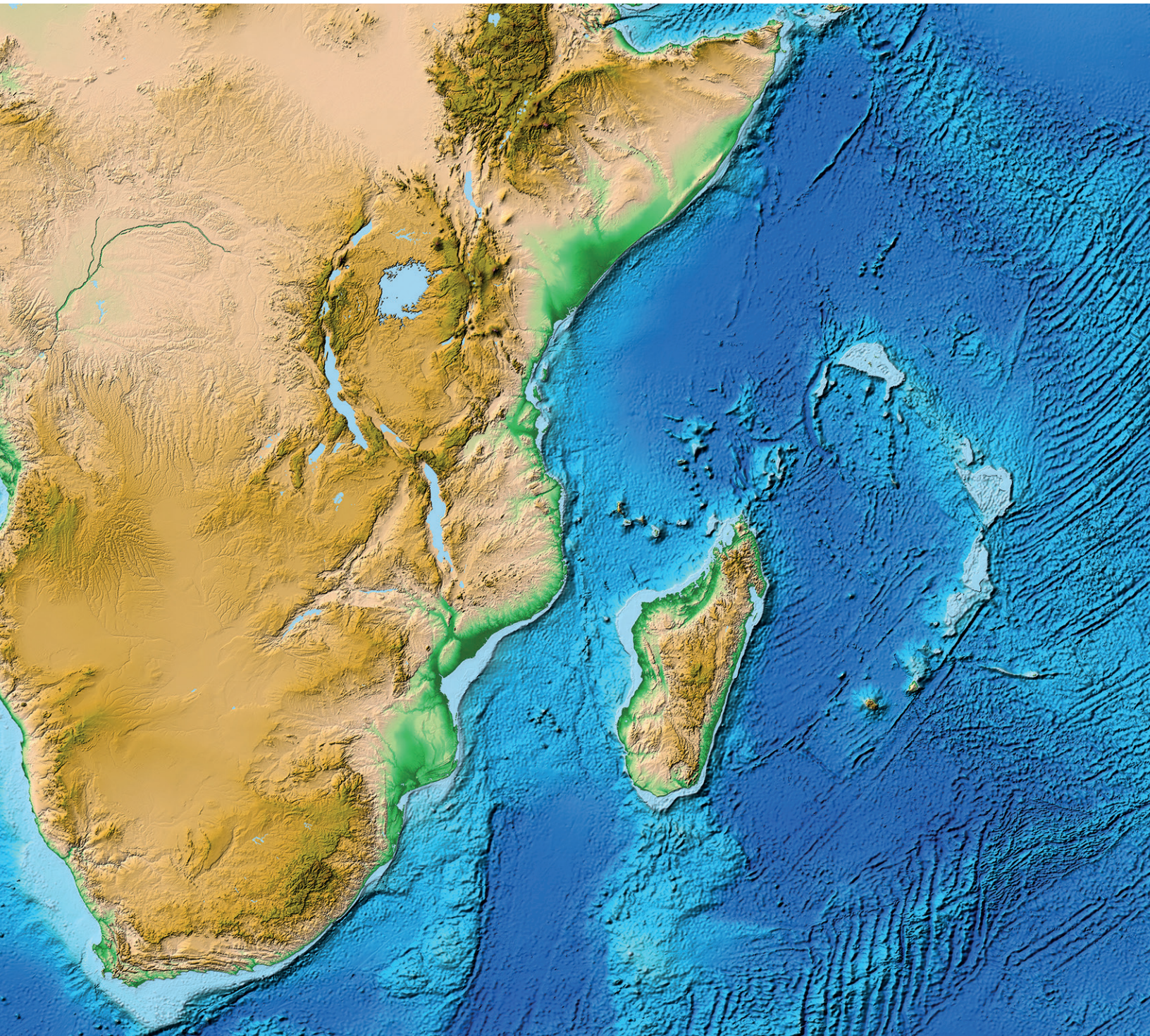

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Cover image: Relief model of the WIO surface that integrates land topography and ocean bathymetry. Amante and Eakins / National Geophysical Data Center, NOAA (2009)

Seasonal fluctuations in photochemical efficiency of *Symbiodinium* harbored by three reef-building corals that differ in bleaching susceptibility

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Abstract

Coral reefs are amongst the most vulnerable ecosystems to climate change. This study was conducted to evaluate the fluxes in the adaptations of reef-building corals to climate change. In order to explore this, chlorophyll *a* fluorescence, *Symbiodinium* abundance and types were monitored in nursery-reared corals for two years in three species that differ in bleaching susceptibility. The species were *Pocillopora verrucosa*, *Porites cylindrica* and *Acropora formosa*. Internal transcribed spacer two (ITS-2) region of nuclear ribosomal DNA genes (rDNA) was used in monitoring the *Symbiodinium* types associated with the studied coral species. Pulse Amplitude Modulated (PAM) fluorometry was used to determine seasonal changes in chlorophyll *a* fluorescence. In this study, it was found that *A. formosa*, *P. verrucosa* and *P. cylindrica* maintained their *Symbiodinium* types; C3u, C1h, and C15 respectively throughout the seasons. *A. formosa* and *P. verrucosa* responded significantly to seasonal fluctuation in both solar radiation and sea surface temperature by regulating their *Symbiodinium* cell density and photochemical efficiency whereas *P. cylindrica* did not. However, such seasonal fluctuations in these environmental parameters are not accompanied by acquisition of foreign *Symbiodinium* types from the environmental pool. It is concluded that seasonal fluctuations in both solar radiations and sea surface temperatures are not intense enough to effect acquisition of foreign *Symbiodinium* types by reef building corals in Zanzibar waters.

Keywords: Coral Reefs, Chlorophyll *a* fluorescence, *Symbiodinium*, PAM fluorometry, Photosynthesis, Resilience

Introduction

Coral reefs, often referred to as 'the rain forests of the ocean' (Reaka-Kudla, 1995), play a key role in the functioning of tropical coastal ecosystems by sheltering a huge diversity of sessile and free-living organisms. They are also economically important because of their ability to provide critically important goods and services to over 500 million people worldwide through fisheries and tourism industries (Moberg and Folke, 1999). The ecological success of the coral reef ecosystem is primarily driven by a mutualistic endosymbiosis between corals and photosynthetic dinoflagellates in the genus *Symbiodinium* (Muscatine, 1990). Unfortunately, the past few decades have witnessed an increase in coral bleaching events (Hoegh-Guldberg, 1999; Baker *et al*., 2004). Bleaching in this study is defined as the whitening, or paling of corals and other invertebrate taxa, resulting from the loss of symbiotic zooxantheallae and/or a reduction in photosynthetic pigment concentrations in zooxanthellae residing within scleractinian corals.

Coral bleaching has become one of the greatest threats to the survival of coral reef ecosystems (Hughes *et al*., 2003; Wilkinson, 2002; Hoegh-Guldberg, 2004). Many of the reef systems in the Western Indian Ocean region have remained severely damaged following the 1997/1998 El-Niño that caused massive coral mortality (Obura, 2005; McClanahan *et al.,* 2007; Mbije *et al.,* 2010). In most cases, coral bleaching events result from a sustained increase in SST (Fitt and Warner, 1995; Berkelmans and Willis, 1999; Winters *et al*., 2003;

Jokiel and Brown, 2004). Seasonal fluctuations in sea surface temperatures may result in localized seasonal bleaching events (Chen *et al*., 2005). Such bleaching events have been accompanied with seasonal fluctuations in *Symbiodinium* cell abundance in some coral species (Fitt *et al*., 2000, Mwaura *et al*., 2009), photosynthetic capacities (Warner *et al*., 2002), and change in *Symbiodinium* types (Chen *et al*., 2005). Moreover, fluctuation in photochemical efficiency of *Symbiodinium* was found in corals that occur in higher latitudes where seasonal fluctuations in both solar radiation and SST are very high (Fitt *et al.,* 2000, Warner *et al.*, 2002). Very little is known about seasonal fluctuations in photochemical efficiency of *Symbiodinium* cells in corals in lower latitude areas closer to the equator, where seasonal fluctuation in both SST and solar radiation is low. A study by Mwaura *et al*. (2009) showed significant seasonal fluctuations in *Symbiodinium* density in most corals species growing in low latitudes environments. However, few coral species maintained their *Symbiodinium density* throughout the year (Mwaura *et al*., 2009), although it is not known whether seasonal fluctuation in cell *density* correlates to its changes in type and photochemical efficiencies.

Coral reef monitoring programmes in Tanzania showed seasonal bleaching events to occur from February to May (Mohammed *et al*., 2000; 2002). Based on these observations, this study aimed at establishing the relationship between the seasonal fluctuations in photosynthetic efficiency and *Symbiodinium* types hosted by young nursery-farmed coral species. To accomplish this, monitoring of *Symbiodinium* density and types, photosynthetic pigment concentration and maximum quantum yield (F_v/F_m) was monitored monthly in a mid-water coral nursery (Mbije *et al*., 2010). *Pocillopora verrucosa*, *Porites cylindrica* and *Acropora formosa* were studied at Chumbe Island in Zanzibar, from September 2008 to August 2010.

Materials and Methods

Sampling site and experimental design

The study was conducted in Chumbe Island Marine Park (39010'32.20"E, 6016'39.67"S) (Figure 1), which was chosen as it is a no-take marine protected area thus offering a protected experimental setting. Chumbe is located about 12 km from the main Zanzibar urban area, and the coral reef sanctuary receives little land based pollution as compared to other reefs close to the city centre. Information related to solar radiation was gathered from the Zanzibar Meteorological Agency whereas SST data were obtained by converting data from temperature data loggers located below the established hanging coral nurseries. These temperature loggers were set to record at 15 minute intervals. From the 15 minute interval data, the mean daily temperature was calculated.

A. formosa, *P. verrucosa* and *P. cylindrica* were selected for this study because of their differences in bleaching susceptibilities and *Symbiodinium* types they host (Marshall and Baird, 2000). While the 1997/98 warming in East Africa resulted into massive mortality of many coral reef species, the most severely affected were the Acroporids (Wilkinson *et al*., 1999; Lindahl *et al*., 2001). Subsequently, many reefs have remained barren without Acroporids signifying that they are very susceptible to environmental perturbations (Garpe and Öhman, 2003). On the other hand, *Porites* has been found to be bleaching-tolerant compared to other species (Marshall and Baird, 2000; Sampayo *et al*., 2008). The selection of the three species considered these differences and the data were collected from the established coral nursery located at Chumbe coral sanctuary. The coral nursery was established as per Shafir and Rinkevich (2010). Basically, the nurseries were situated in mid-water, above the substrate to

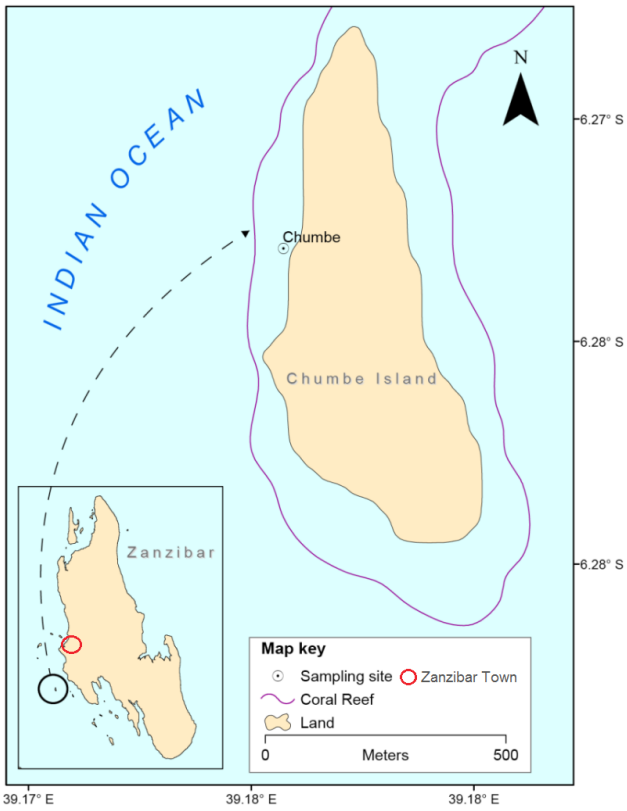

Figure 1. Map of Zanzibar (Unguja Island) showing the location of Chumbe Island Coral Park where *in-situ* experiments to investigate seasonal fluctuations in photochemical efficiency of coral species that differ in bleaching susceptibilities was conducted. [IMS base Maps]

avoid sedimentation; far from the reef to avoid corallivorous species; in an area sheltered from storms and wave action but sufficiently shallow (5 m below sea level during low tide) to provide good light conditions for fast growth and easy maintenance. The nurseries remained in place for two years from August 2008 to July 2010 with monthly monitoring surveys during the second week of each month. To make sure that all coral branches received similar solar radiation, the nursery was established at 5m depth during the lowest tide. Each coral species was represented by 200 branches.

Fluorescence measurements

In situ measurements of maximum quantum yields (F_v/F_m) were calculated for the transplants of *A. formosa*, *P. verrucosa* and *P. cylindrica* by using a diving Pulse Amplitude Modulated Fluorometer (Diving PAM, Walz, Germany) (Hoegh-Guldberg and Jones, 1999; Winters *et al*., 2003). *In situ* chlorophyll fluorescence signatures provide insight into the daily homeostasis and stress response of the symbiotic algae (Winters *et al*., 2003). PAM fluorometry induced chlorophyll fluorescences were measured *in vivo* in order to estimate the potential quantum yield of photosystem II during photosynthesis, a parameter that correlates with more traditional measures of photosynthetic rate such as CO_2 uptake and O_2 evolution (Beer *et al*., 1998). During the use of the fluorometer, an opaque plastic fiber-optics holder was used to maintain equal distances between the fiber-optics tip and the coral surface (10 mm) in each sampling. In order to allow dark adaptation of coral fragments all sampling was done in the evening, about 15 minutes after sunset. According to Winters *et al*. (2003), this period is sufficient to maximize the frequency of open-reaction centres in PSII so as to record maximum quantum yield of photosystem II (F_v/F_m), where F_v = variable fluorescence and F_m = maximum fluorescence for the dark-adapted sample.

Monitoring *Symbiodinium* abundance and Chlorophyll *a* concentration

During each sampling session, small (2-3 cm) coral branches (n=5 for each species) were randomly taken for both analysis of *Symbiodinium* cell abundance and chlorophyll *a* concentration. Upon detachment, the branches were immediately put in plastic bags that were kept in a cool box at a temperature of 4-5°C ready for transportation to the Institute of Marine Science, where analysis of *Symbiodinium* abundance and chlorophyll *a* concentration was done. By using filtered seawater (0.45 µm mesh) through a water pick, coral tissues was extracted. To ensure the majority of algae and tissue were extracted, the coral fragment samples were washed until the coral skeletons were completely white. Each tissue sample was then homogenized for 30 seconds in 10 ml of filtered seawater in a blender. To separate *Symbiodinium* cells from the host tissues, the resulting slurry from homogenized tissue was centrifuged for 5 min at 6000 rpm at 4°C. After centrifugation, an aliquot containing *Symbiodinium* and another containing host tissue were obtained.

To determine the *Symbiodinium* cell density, 1 ml of *Symbiodinium*-containing aliquots were preserved with 10% formalin. Such aliquots were later loaded into a haemocytometer. *Symbiodinium* cells in 10 random quadrants in the haemocytometer were counted from each replicate (n = 5) using a light microscope at 400 X magnification. The surface area of the coral skeleton was determined by using the aluminum foil method (Naumann *et al*., 2009). In this technique, aluminum foil was wrapped over and fitted to the surface of each coral fragment; the foil was then removed, and its area determined. Thus, *Symbiodinium* density was expressed in terms of number of cells divided by the surface area of the coral tissue estimated by using the aluminum foil method.

To determine the chlorophyll *a* concentration, 2 ml of the *Symbiodinium* -containing aliquots was re-suspended in 8 ml of 100% acetone and incubated at 2°C for 24 h for extraction of photosynthetic pigments. On the following day, the sample was centrifuged again for 10 minutes at 2000 rpm. The supernatant was transferred to a quartz cuvette and its absorbance was determined at 750, 663, 630, 480 and 510 nm using a Genesys 5 spectrophotometer™ (Spectronic Instruments, Rochester, NY, USA). The coral surface area, obtained as explained above, together with the estimated coral mass were used to determine the concentration of chlorophyll *a*. The concentration of Chl *a* (µgcm^{-2}) was calculated using equation presented by Jeffrey and Humphrey (1975):

$$[\text{Cl-}a\ (\text{mg Ml}^{-1})] = 11.43 * (E664 - E750) - 0.64 * (E630 - E750)$$

Where; 11.43 and 0.64 are constants, while E630, E663, and E750 are spectrophotometric readings at 630, 663 and 750, respectively.

Determination of seasonal change in *Symbiodinium* type

In order to determine whether seasonal fluctuation in photochemical efficiency can cause changes in *Symbiodinium* type as an adaptation strategy, coral fragment samples were collected and analysed during the

months that differ in terms of temperature and solar radiation. The months included January 2008, April 2008, August 2008, June 2009, October 2009 and December 2009 (Table 2). Both SST and solar radiation data in Zanzibar showed the mentioned months to differ. In order to analyse the *Symbiodinium* types in the coral tissue, total DNA was extracted from the collected coral fragments using a protocol adopted from LaJeunesse *et al*. (2003). Amplification of the extracted DNA was done by targeting the ITS-2 region of ribosomal DNA (rDNA) genes as these genes have been successfully used in the analysis of *Symbiodinium* types. PCR was performed by using forward primer ITSintfor2, 5'GAATTGCAGA ACTCCGTG 3' with a GC clamp and the reverse ITSintrev2, 5' GGGATCCAT ATGCTTAAGTT CAGCGGGT 3' designed by LaJeunesse and Trench (2000). The PCR cycling conditions were as follows: denaturing step of 4 minutes at 94°C, 30 cycles at 60 seconds at 94°C, 60 seconds at 57°C, and 60 seconds at 72°C, with extension of 5 minutes at 72°C. The PCR products were checked on 1.5% agarose gels stained with ethidium bromide.

Successful PCR products were subjected to DGGE as described in Chauka (2012). All dominant bands in DGGE gel profiles were carefully cut and diluted overnight in 500 µl dH2O and re-amplified on the following day using ITS-2 with no GC clamp. The products of the re-amplified excised bands were purified using the UltraClean PCR purification Kit (Molecular Biology Laboratories, USA). Purified PCR products were sent for sequencing using the forward (ITSintfor2) or reverse (ITS2reverse) primers in separate runs at the Pennsylvania State University Science Facility. The obtained sequences were identified from the Genbank by using the Basic Local Alignment Search Tool (BLAST).

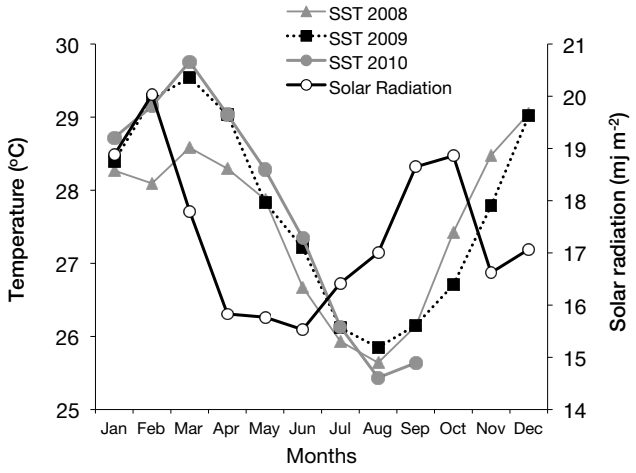

Figure 2. Mean measured sea surface temperature and solar radiation in Chumbe Island Coral Park where in-situ experiments to investigate seasonal fluctuations in photochemical efficiency of coral species that differ in bleaching susceptibilities was conducted.

Data analysis

The R – Statistic package was employed in analysis where Two-way Analysis of Variance (ANOVA) was used to examine the influence of sampling date and coral species on photosynthetic efficiencies of photosystem II of *Symbiodinium* cells. In these analyses, *Symbiodinium* density, maximum quantum yields and chlorophyll *a* concentrations were independently analysed. In addition, the Tukey HSD test was used to find specific difference among the months and species. Before analysis, the normality of data was tested.

Results

Monthly fluctuation in temperature and solar radiation

SST data presented were collected for two years (between August 2008 and September 2010). The data show monthly SST in Chumbe Island Marine Park ranged from 25.8°C in July to 30.0°C in March. Highest SST occurs during the Northeast monsoon season while the lowest occurs during the southeast monsoon season (Figure 2). The difference in SST between the two seasons is about 4°C. In addition to the measured SST, data obtained from the Tanzania Meteorological Agency shows solar radiation in Zanzibar to range from 15.5 (mj m^{-2}) in June to 20.03 (mj m^{-2}) in February (Figure 2).

Seasonal fluctuation in *Symbiodinium* density, types and photosynthetic pigments

Except in *P. cylindrica,* paling in most colonies of *P. verrucosa* and *A. formosa* were observed in March and April; probably due to decreased *Symbiodinium* densities and/or photosynthetic pigments as shown in Figure 3. In those corals colonies that exhibited signs of bleaching, paling was homogeneous, especially on the sides that were directly exposed to solar radiations. *Symbiodinium* densities ranged from 1.84 ± 0.015 million cells cm^{-2} sampled in *P. verrucosa* in April to 3.188 ± 0.021 million cells cm^{-2} sampled in *A. formosa* sampled in July (Figure 3). Chlorophyll *a* concentration ranged from 1.958 recorded in *P. verrucosa* in February to 3.313 ± 0.065422 in *A. formosa* recorded in July (Figure 3). After subjecting the data to a one-way ANOVA test, it was revealed that both chlorophyll *a* concentrations and *Symbiodinium* densities significantly fluctuated over time in all species (Table 1). However, *P. cylindrica* was less affected by seasonal fluctuation in both SST and solar radiation when compared with other species (Figure 3). A seasonal fluctuation in *Symbiodinium* types was also investigated and

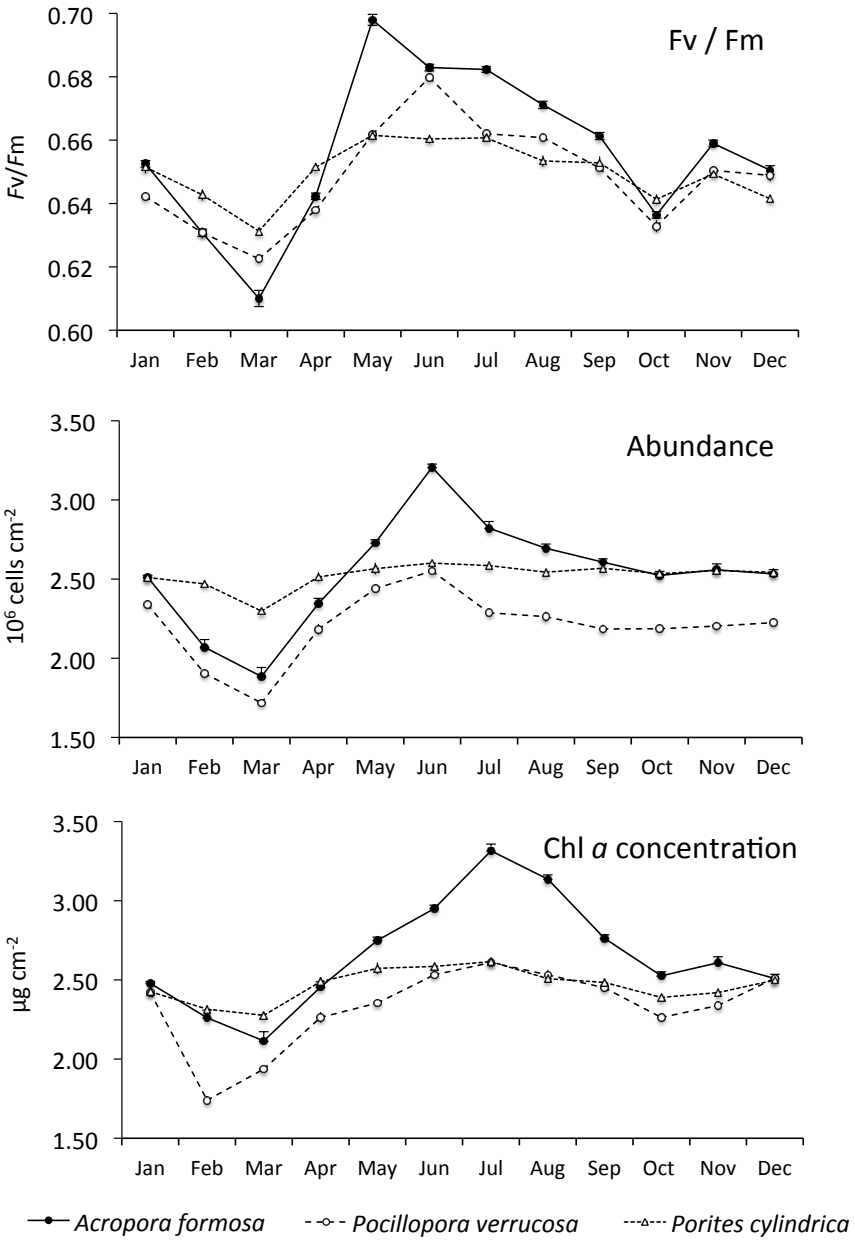

Figure 3. Seasonal variation in maximum quantum yield (F_v/F_m), zooxanthellae abundance and chlorophyll *a* concentrations in corals *Pocillopora verrucosa* (PV), *Porites cylindrica* (PC) and *Acropora formosa* (AF) found in Zanzibar reefs as recorded from September 2008 to August 2010 in coral nursery established in Chumbe Island Coral Park (±SE).

it was found that coral-*Symbiodinium* symbioses were stable throughout the year in all species (Table 2).

Seasonal fluctuation in F_v/F_m of studied coral species

Generally, maximum quantum yield as expressed in F_v/F_m fluctuated seasonally in all species (Figure 3). A mean F_v/F_m of 0.6966 ± 0.008649 was the highest recorded, in *A. formosa* in July, the coldest month when solar radiation was also relatively low compared with other months (Figure 3). Moreover, the lowest mean F_v/F_m value (0. 0.6176 ± 0.0273) was recorded in *A. formosa* in April, which was amongst the hotter months indicating the influence of temperature on photosynthetic efficiency of *Symbiodinium* harbored by corals. This has also been noted in other studies (Winters *et al*., 2003). When the data were subjected to two-way ANOVA, sampling date was found to have significant effects on F_v/F_m values (Table 1). After subjecting the data to the Tukey HSD test for specific differences, it was found that only F_v/F_m values of *A. formosa* and *P. verrucos*a were significantly affected by sampling date ($p < 0.05$). By using the same test, it was found that *P. cylindrica* was not significantly affected by sampling date ($p = 0.096375$).

Table 1. Two-way ANOVAs of photosynthetic parameters of transplants of **corals** *P. verrucosa, P. cylindrica* **and** *A. formosa* after 24 months kept in Chumbe Island Coral Park, Zanzibar.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Fv/Fm					
Month	11	0.05238	0.004762	307.8	<2e-16 ***
Species	2	0.00265	0.001323	85.5	<2e-16 ***
Month x Species	22	0.01113	0.000506	32.7	<2e-16 ***
Residuals	180	0.00278	0.000015		
Zoozanthellae abundance					
Month	11	8.522	0.7747	189.63	<2e-16 ***
Species	2	5.078	2.5391	621.5	<2e-16 ***
Month x Species	22	2.743	0.1247	30.52	<2e-16 ***
Residuals	180	0.735	0.0041		
Chlorophyll *a* concentration					
Month	11	9.841	0.8946	387.57	<2e-16 ***
Species	2	3.863	1.9315	836.79	<2e-16 ***
Month x Species	22	3.263	0.1483	64.25	<2e-16 ***
Residuals	180	0.415	0.0023		

Table 2. Influence of seasonality on the diversity and distribution of *Symbiodinium.* The clade type is denoted by letters in uppercase; the ITS-2 DGGE fingerprint type is shown by a number followed by letters in lower case. The number of samples analysed and found to have a particular *Symbiodinium* type is shown in parenthesis.

Species / Sampling	Jan-08	Apr-08	Jun-09	Aug-08	Oct-09	Dec-09
Pocillopora verrucosa	C1h (4)	C1h (4)	C1h (4)	C1h (4)	C1h (4)	C1h (4)
Porites cylindrica	C15 (4)	C15 (4)	C15 (4)	C15 (4)	C15 (4)	C15 (4)
Acropora formosa	C3u (4)	C3u (4)	C3u (4)	C3u (4)	C3u (4)	C3u (4)

Discussion

The current observations on seasonal fluctuation in both chlorophyll *a* concentration and *Symbiodinium* densities concur with previous studies (Fitt *et al*., 2000; Warner *et al*., 2002; Mwaura *et al.,* 2009) in the sense that photochemical efficiencies of corals responded to seasonal change in both SST and solar radiation. However, our data deviate from the data presented by Mwaura *et al*. (2009) in that statistically significant low values of *Symbiodinium* density were recorded during the hotter months with higher solar radiation. This might be attributed to the slight differences in temperature and solar radiation patterns between Mwaura's study in Mombasa, and Zanzibar (see Mwaura *et al*., 2009 figures compare with Figure 2). Significantly low *Symbiodinium* density and chlorophyll *a* concentrations in the hotter months with higher solar radiation in all species studied indicate that they have similar bleaching strategies (Douglas, 2003). Thus, *A. formosa*, *P. verrucosa* and *P. cylindrica*

bleach by losing both *Symbiodinium* cells and/or the degradation of photosynthetic pigments. Some coral species (e.g., *Montipora capitata*) do not exhibit these characteristics as they bleach by losing only photosynthetic pigments. Such species might be resilient to bleaching inducers as they maintain their algal cells during the episodes of high temperatures. However, the data from the current study excludes *P. verrucosa*, *A. formosa* and *P. cylindrica* from the category of species that bleach by losing only photosynthetic pigments.

Seasonal change in coral colouration and its relation to photochemical efficiency of coral transplants

Paling of transplants of studied coral species that was observed in the months of March and April reflect the seasonal variations in sea surface temperature (Figure 1). These signs of bleaching are suggested to be attributed to photoinhibition as they were accompanied by reduction in F_v/F_m (Winters *et al*., 2003). Although signs of bleaching were observed in March and April, the *Symbiodinium* abundances in bleached colonies were above the suggested level of 0.5×10^6 cells cm^{-2} (Fitt *et al*., 2000). It is possible that visual signs of bleaching are subjective and can vary from one species to another. In this study, a 40% and 25% decrease in *Symbiodinium* density was enough to cause the appearance of signs of bleaching in *A. formosa* and *P. verucosa* respectively.

An interesting trend was found in *P. cylidrica* where sampling date was found to significantly affect *Symbiodinium* density and chlorophyll *a* concentration, but not the maximum quantum yield of *Symbiodinium* cells harbored by *P. cylindrica* (Table 1). The results of this study therefore support the findings of Fitt *et al.* (2009) who suggest a special mechanism is employed by *P. cylindrica* to maximize photosynthetic efficiency during high temperatures and solar radiation. In their study, Fitt *et al.* (2009) observed low light-induced excitation pressure on the C15 *Symbiodinium* hosted by *P. cylindrica* and therefore relatively high quantum yield of PSII fluorescence at noon ($\Delta F/F$m′) was maintained. It is possible therefore that the ability of *P. cylindrica* to maintain high F_v/F_m throughout the year regardless of temperature and solar radiation change is attributed to its ability to synthesize high concentrations of heat-stress protein (HSP) 70 and superoxide dismutase (SOD) as reported by Fitt *et al.* (2009). This ability, which is influenced by both the host (*P. cylindrica*) and the symbiont (*Symbiodinium* C15), is responsible for bleaching resistance of *P. cylindrica.*

Seasonal change in *Symbiodinium* types in coral tissue

Reef building corals can acquire foreign *Symbiodinium* types when the populations of the resident *Symbiodinium* types are very low (Brown *et al.,* 1995; Hoegh-Guldberg and Smith, 1989; Fautin and Buddemeier, 2004; Baker *et al*., 2004). However, significant reduction in populations of dominant resident *Symbiodinium* types is required to either induce proliferation of background resident populations or for secondary acquisition from the environmental pool (Fautin and Buddemeier, 2004; Baker *et al*., 2004). This is probably why Chen *et al.* (2005) were able to detect clade D *Symbiodinium* type in *Acropora palifera* during the hotter months while *Symbiodinium* clade C type dominated colonies of the same species during the colder seasons. Existence of a similar pattern of seasonal distribution was not found in Zanzibar, even in coral species which harbour more than one *Symbiodinium* type, as these coral species maintained their *Symbiodinium* types as previously found by LaJeunesse *et al.* (2010) and Chauka (2012).

Secondary acquisition of *Symbiodinium* types is complex. When secondary acquisition occurs following a bleaching event, the foreign *Symbiodinium* types exist for shorter periods of time (usually 1-3 years after the bleaching event) (Thornhill *et al*., 2006; LaJeunesse *et al*., 2009). Since the well-known and documented bleaching event took place ten years prior to the present study, and while reef building corals need only about two years to return to their original symbionts (Thornhill *et al*., 2006), it is possible that coral species in Zanzibar have reverted to their original *Symbiodinium* type and established stable symbioses. Thus, seasonal bleaching events that have occurred are likely to not have been intense enough to cause secondary acquisition of *Symbiodinium* type.

In conclusion, this is the first study to use the PAM fluorometry method in determining coral health in Zanzibar waters. This study shows that Zanzibar corals respond to seasonal fluctuation in both solar radiation and sea surface temperature by regulating their *Symbiodinium* density and chlorophyll *a* concentrations. However, such seasonal fluctuations in these environmental parameters are not accompanied by acquisition of foreign *Symbiodinium* types from the environmental pool. Therefore, it is concluded that seasonal fluctuations in both solar radiation and sea surface temperature are not intense enough to effect acquisition of foreign *Symbiodinium* types by reef building corals in Zanzibar waters.

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