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Influence of local environmental conditions and bleaching histories on the diversity and distribution of *Symbiodinium* in reef-building corals in Tanzania

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Pollution, turbidity and coral bleaching history, as well as coral diversity, vary along the Tanzanian coastline. Prior to this study, it was not known whether exposure to such environmental variation might have influenced the diversity and distribution of *Symbiodinium* along this coastline. Such information can provide insight into whether Tanzanian reef-building corals develop adaptation to current trends of climate change. Here, 10 reef-building coral samples were collected from different reefs along the Tanzanian coast with different micro-environments and bleaching histories. The ITS-2 region of ribosomal DNA was employed in the characterisation of *Symbiodinium* harboured by reef-building corals. DGGE fingerprints and DNA sequences showed that most coral species host a single *Symbiodinium* type, which is maintained throughout the coast regardless of local environmental differences. We present polymorphic symbioses in *Acropora* spp., *Millepora* sp. and *Galaxea fascicularis* in mainly turbid and warm environments as a sign of adaptation to harsh conditions. However, such adaptation may not provide marked resistance to bleaching because *Acropora* is a bleaching-susceptible genus.

Keywords: climate change, coral bleaching, ITS-2, turbidity

Online supplementary material: All sequences with their respective accession numbers can be found online in Supplementary Table S1 at http://dx.doi.org/10.2989/1814232X.2015.1123771.

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Introduction

Most cnidarians, including reef-building scleractinians (stony corals), have established symbioses with photosynthetic dinoflagellates that belong almost exclusively to the genus *Symbiodinium*. Coral–*Symbiodinium* mutualisms are believed to underpin the success of hermatypic (reef-building) corals in nutrient-poor tropical environments (Howells et al. 2011). In mutualisms, *Symbiodinium* cells translocate most of their photosynthetic products to coral tissues to fuel metabolic demand of the host, including calcification. In return, *Symbiodinium* cells are provided with protection, organic raw materials and an enhanced micro-environment for photosynthesis. In the past few decades there has been a global increase in the frequency of coral bleaching events (Hoegh-Guldberg 1999; Baker 2003). Coral bleaching is the breakdown of symbiosis between coral and symbiotic algal cells and/or degradation of the photosynthetic pigments of the algal cells, resulting in white host tissue and calcium skeletons (Douglas 2003). Bleaching is believed to be a symptom of stress largely induced by high temperature and insolation (Brown 1997; Douglas 2003; Winters et al. 2003). However, other factors such as low temperature (Hoegh-Guldberg et al. 2005), bacterial infection (Rosenberg and Falkovitz 2004), lowered salinity and pollution (Glynn 1993) have been found to cause minor local bleaching events.

Previous studies (e.g. Toller et al. 2001; Fabricius et al. 2004; Rowan 2004; Chen et al. 2005) have shown various *Symbiodinium* types to differ in terms of environmental tolerance. Among the *Symbiodinium* types, clade D has been found to be the most tolerant of environmental variability (Stat et al. 2006, 2009; Stat and Gates 2011). Differing environmental tolerance is believed to be among the major factors that influence *Symbiodinium* partitioning along environmental gradients (Frade et al. 2008; Howells et al. 2008; Sampayo et al. 2008). Factors that can influence the distribution of *Symbiodinium* include thermal tolerance (Baker et al. 2004), photo-protection (Iglesias-Prieto et al. 2004; Frade et al. 2008; Hennige et al. 2010) and photosynthetic rate (Cantin et al. 2009).

Knowledge of factors that contribute to patterns in coral–*Symbiodinium* symbioses and the physiological range of host–*Symbiodinium* combinations is useful in understanding adaptive capacities of coral reefs, especially in the context of current trends of climate change (Sampayo et al. 2008; LaJeunesse et al. 2010a, 2010b). Although it is well known that coral–*Symbiodinium* associations show high degrees

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of specificity (LaJeunesse et al. 2003, 2004; Stat et al. 2006), sampling different symbionts in colonies within the same localities and intracolony variation of *Symbiodinium* types facilitates further investigation of the influence of local environmental differences on the diversity and distribution of *Symbiodinium* (Ulstrup and Van Oppen 2003).

Tanzanian coral reefs are exposed to different environments in terms of pollution, turbidity and water temperature (Wagner 2004). Some reefs, such as Mbudya in Dar es Salaam and Changuu in Zanzibar, are located close to terrestrial influences, whereas others are not (Figure 1). Tanga Mjini is close to the equator whereas Mikindani is in the south of the country (Figure 1). It is probable that such differences are responsible for differences in reef types and coral diversity along the Tanzanian coast (Wagner 2004; Obura 2012). The severity of the 1998 worldwide bleaching event differed in magnitude on the reefs across Tanzania (Mohammed et al. 2000). Kitutia Reef was among the most affected with coral mortality of 80%, whereas Changuu and Mbudya reefs were less affected with mortality of about 11%. Other reefs such as Chumbe and Mikindani experienced coral mortalities ranging from 30% to 50% (Muhando and Mohammed 2002). Recovery also differed along the Tanzanian coast (Muhando and Francis 2000). Based on knowledge of the contribution of *Symbiodinium* to bleaching resistance (Toller et al. 2001; Fabricius et al 2004; Sampayo et al. 2008; Stat and Gates 2011), differences in *Symbiodinium* diversity might have influenced such variations in the severity of coral bleaching and on resilience among reefs along the coast. It has been suggested that coral–*Symbiodinium* symbioses vary latitudinally (Macdonald et al. 2008), along turbidity gradients (LaJeunesse et al. 2010a) and with bleaching histories (Chen et al. 2005). The aim of this study was to investigate the influence of local environmental differences on *Symbiodinium* genetic diversity and distribution in different reef-building coral species on the Tanzanian coast. Such information could provide insight into how these corals might adapt to current trends of climate change in Tanzanian waters.

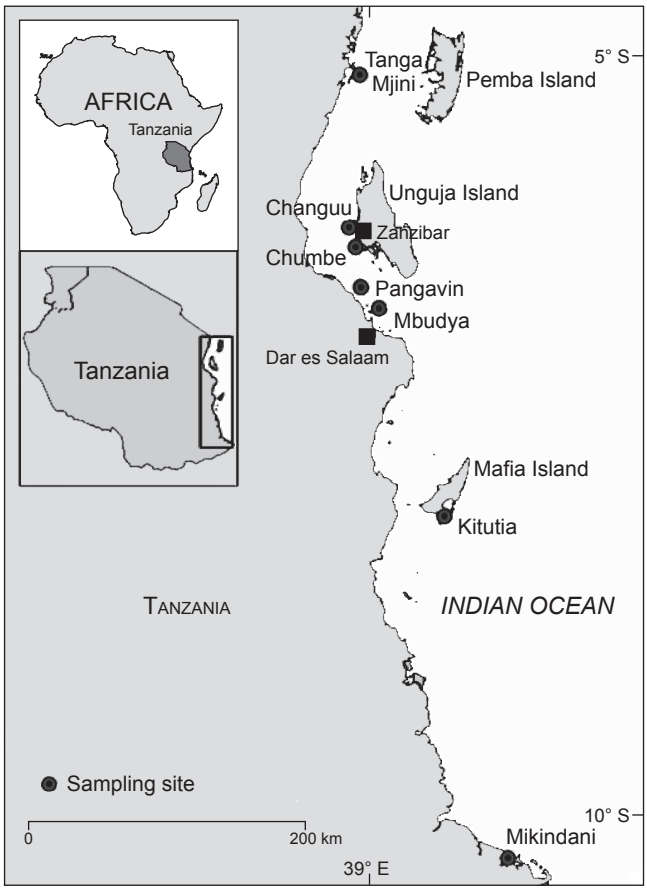


Figure 1: Map of the Tanzanian coast showing locations of sampling sites. A summary description of each site is provided in Table 1

Material and methods

Coral fragment sampling and processing

In August 2009 coral fragments were collected from seven reefs along the Tanzanian coast: Changuu and Chumbe (Zanzibar), Tanga Mjini (Tanga), Mbudya and Pangavin (Dar es Salaam), Kitutia (Mafia) and Mikindani (Mtwara) (Figure 1, Table 1). The seven reefs were selected because of differences in their exposure to anthropogenic disturbances (Table 1), coral species diversity, distance from mainland influence, latitude, and occurrence of the coral species under study. To investigate the influence of local environmental differences on the distribution of *Symbiodinium*, coral fragment sampling at both Dar es Salaam and Zanzibar was conducted on two reefs which differed in turbidity and exposure to anthropogenic disturbance. Turbidity is high in Mbudya and Changuu, whereas Chumbe and Pangavin reefs are characterised by low turbidity (Table 1). In order to test for statistical differences in turbidity among the sites under study, turbidity estimates were based on light attenuation with depth. Percentages of light attenuated were calculated from the differences in photosynthetically active radiation (PAR) measured simultaneously at the surface and at 7 m depth over a period of five months, using a light sensor incorporated in a diving pulse-amplitude-modulated (PAM) fluorometer (Diving PAM, Walz, Germany).

At each site (visited by snorkel and/or SCUBA), small (1–3 cm) healthy coral fragments were broken off from the parent colonies at about 4–7 m depth. Preliminary surveys had shown that the majority of the studied coral species were not found at depths below 7 m. For each species, eight samples were collected at each study site. The samples were taken about 10 m apart from each other. The coral species sampled were *Seriatopora hystrix*, *Porites rus*, *Porites cylindrica*, *Millepora* sp., *Echinopora lamellosa*, *Pocillopora verrucosa* and *Pocillopora damicornis*, all of which acquire symbionts through a vertical transmission strategy (Stat et al. 2006; LaJeunesse et al. 2010a). Three other coral species, *Galaxea fascicularis*, *Acropora formosa* and *Acropora hemprichii*, were also sampled because they acquire symbionts through a horizontal transmission strategy. During each sampling session, each species was photographed using a waterproof digital Sony camera, prior to breaking off a sample. Photographs were then compared

Table 1: Description of sampling sites on the Tanzanian coast with a qualitative summary of abiotic factors experienced by reef-building corals

Site	Location	Bleaching history	Anthropogenic disturbances	Environmental factor	Coordinates
Changuu	Zanzibar	Low	High	High turbidity	39°08′09.64″ E, 06°09′09.44″ S
Chumbe	Zanzibar	Medium	Very low	Low turbidity	39°10′32.20″ E, 06°16′39.67″ S
Tanga Mjini	Tanga	Medium	High	Low turbidity	39°06′53.84″ E, 05°09′13.74″ S
Mbudya	Dar es Salaam	Low	High	High turbidity	39°14′52.45″ E, 06°39′33.76″ S
Pangavin	Dar es Salaam	Low	Medium	Low turbidity	39°14′17.77″ E, 06°40′27.37″ S
Kitutia	Mafia	High	Low	Low turbidity	39°45′06.16″ E, 08°01′01.87″ S
Mikindani	Mtwara	Low	Low	Low turbidity	40°09′45.35″ E, 10°13′38.06″ S

with those documented by Veron (2000) for correct identification. The coral fragment samples were preserved in a preservation buffer comprising 20% DMSO, 0.25 M EDTA and NaCl-saturated water. The samples were then shipped to Pennsylvania State University for molecular analysis.

DNA extraction, polymerase chain reaction (PCR) and denaturing gradient gel electrophoresis (DGGE)

DNA extraction from the fragments was done following a non-toxic protocol developed by LaJeunesse et al. (2003). Amplification of *Symbiodinium* DNA was performed using the nuclear ribosomal internal-transcribed-spacer-2 (ITS-2) region. The ITS region of nuclear ribosomal DNA has been used successfully in determining *Symbiodinium* diversity and distribution (LaJeunesse 2001; LaJeunesse et al. 2003; Sampayo et al. 2009) due to its unconserved nature (Stat et al. 2006; Sampayo et al. 2009). The set of primers used included the forward primer ITSintfor2, 5′ GAATTGCAGA ACTCCGTG 3′ with GC clamp, and the reverse ITSintrev2, 5′ GGGATCCAT ATGCTTAAGTT CAGCGGGT 3′ (LaJeunesse 2001). Cycling conditions were as follows: a denaturing step of 4 min at 94 °C, 30 cycles at 94 °C for 60 s, 57 °C for 60 s and 72 °C for 60 s, with an extension step of 5 min at 72 °C. The PCR products were then subjected to electrophoresis using 45–80% denaturing gradient gels for 18 h on a CBS Scientific system (Del Mar, California, USA). Gels were stained with 16SYBR Green (Amresco, diluted 10 times from stock) for 20 min, and visualised using a UV-Doc digital camera gel imaging system. About five representative bands that were found to be in the same level, and which had more PCR products than others at the same level in the DGGE gel profiles, were carefully cut out and diluted overnight in 500 µl dH_2O and then reamplified the following day using ITS-2 primers without GC clamp.

Sequencing and sequence analyses

Products of reamplified excised bands were purified using an UltraClean PCR purification kit (Molecular Biology Laboratories, USA) and then sequenced using forward (ITSintfor2) and reverse (ITSintrev2) primers in separate runs. The obtained DNA sequences were inspected and assembled by using BioEdit Sequence Alignment Editor 7.0.9 (Hall 1999), an open-source program, and then identified by using the nucleotide basic local alignment search tool (BLASTN) in GenBank with a minimum *E*-value requirement of 1E−5. The sequences were also assigned names according to their similarity to those found in the GenBank.

Data analysis

Percentage data pertaining to light attenuation were not normally distributed and hence were subjected to the Kruskal–Wallis test in R (R Core Team 2015) to determine whether there were differences between the seven reefs under study.

Determination of *Symbiodinium* diversity at each site was expressed in terms of the Shannon–Wiener diversity index (H'):

$$H' = -\Sigma p_i \ln p_i$$

where p_i is the number of individuals of species i divided by the total number of individuals.

Determination of *Symbiodinium* diversity in relation to environmental factors (location [latitude], bleaching history, anthropogenic disturbance and turbidity) was performed using permutational multivariate ANOVA (PERMANOVA) in R with the vegan package (Oksanen et al. 2015). In this analysis, *Symbiodinium* types were treated as present/absent, together with their respective abundances.

Results and discussion

Light attenuation with depth, as a proxy for turbidity, differed among the seven reefs. Chumbe, Pangavin, Tanga Mjini, Kitutia and Mikindani reefs had low turbidity, whereas Mbudya and Changuu had higher turbidity (Figure 2). The difference was significant ($H = 178.77$, df = 6, $p = 6.19 \times 10^{-16}$).

Generally, DGGE profiles and sequences of *Symbiodinium* types generated from this study did not differ from those observed by LaJeunesse et al. (2010a) and Chauka (2013) (Supplementary Table S1). Therefore, this study does not report novel sequences different from those reported earlier from the Tanzanian coast.

Variation in coral–*Symbiodinium *symbioses along the Tanzanian coast

Most of the coral species under study hosted a single *Symbiodinium* type, which was maintained along the coast regardless of latitude (Table 2). Some samples from *A. formosa* and *A. hemprichii* collected from Mbudya, Kitutia and Changuu hosted more than one *Symbiodinium* type. In addition, only two samples of *G. fascicularis*, collected from Tanga Mjini and Changuu, hosted more than one *Symbiodinium* type, namely, *Symbiodinium* D1 and C3u types (Table 2). Latitudinal differences do not appear to

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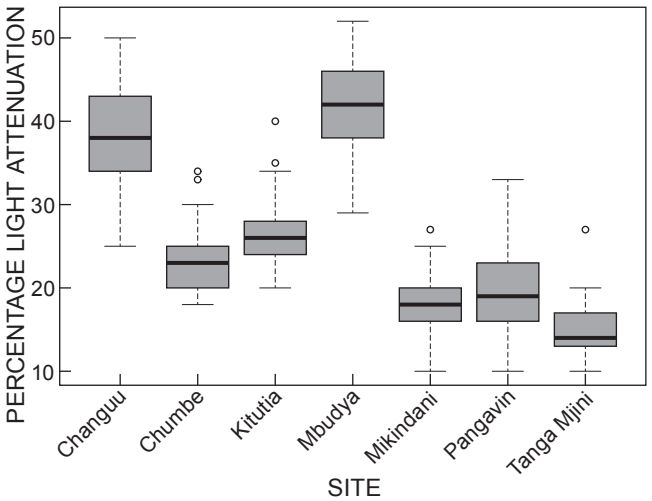


Figure 2: Box-and-whisker plot of mean estimations of percentage light attenuation at 7 m depth at different reefs along the Tanzanian coast. The box indicates the interquartile range and the whiskers 95% confidence intervals, with the circles representing outliers

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influence symbiotic differences, because most samples collected from widely separated reefs, such as Tanga Mjini in the north and Mikindani in the south, hosted similar *Symbiodinium* types. Our data did not show whether strategies used by different coral species to acquire *Symbiodinium* cells have influenced coral–*Symbiodinium* symbioses on the Tanzanian coast. This is because observed polymorphic symbiosis was both in corals that employ horizontal strategies (e.g. *Acropora* and *Galaxea*) and in corals that employ vertical strategies (such as *Millepora*).

Unlike in other regions, therefore, most surveyed coral species exhibited an inability to associate with multiple *Symbiodinium* types even when exposed to different environmental conditions. For example, elsewhere in the Indian Ocean, *P. verrucosa* and *P. damicornis* were found to associate with multiple *Symbiodinium* types (LaJeunesse et al. 2010a; Yang et al. 2012). Likewise, *Porites* has been found to associate with multiple *Symbiodinium* types in some parts of the world, especially those with high seasonal variation in temperature and solar radiation (Mostafavi et al. 2007). However, our study showed that these species hosted only a single *Symbiodinium* type along the Tanzanian coast. This reduced polymorphic symbiosis might be a reflection of limited environmental variation along the Tanzanian coast.

Influence of turbidity on Symbiodinium *diversity and distribution*

The PERMANOVA analysis showed that none of the factors/predictors considered affected the *Symbiodinium* diversity when *Symbiodinium* types were treated in terms of a presence/absence index (Table 3). However, when *Symbiodinium* types were treated with their respective abundances at each site, the analysis showed turbidity to influence the diversity of *Symbiodinium* ($p = 0.048$). The sites with high turbidity (Changuu and Mbudya) were characterised by anthropogenic disturbances, including fishing and activities related to tourism.

Exposure to different environments, especially light conditions, have been found to influence partitioning in *Symbiodinium* communities (Iglesias-Prieto et al. 2004; Frade et al. 2008; LaJeunesse et al. 2010a). According to Putnam et al. (2012), susceptible genera such as *Pocillopora*, *Seriatopora* and *Acropora* are expected to have endosymbiotic flexibility. Some of these genera occur on the Tanzanian coast, where they have been reported to be susceptible to bleaching (Lindahl et al. 2001; Garpe and Öhman 2003). However, among the most bleaching-susceptible genera in our study, only *Acropora* conformed to the prediction of Putnam et al. (2012) by showing flexibility in symbiosis with members of *Symbiodinium.* It is likely that, in order to exhibit flexibility in symbioses, other bleaching-susceptible genera such as *Pocillopora* and *Seriatopora* require larger environmental perturbations than occur on the Tanzanian coast. Also, it is possible that coral genera that have successfully established symbiosis with *Symbiodinium* types with broad environmental tolerance (Sampayo et al. 2008) may not need polymorphic symbiosis that allows flexibility, polymorphism being a strategy that is thought to confer environmental adaptation on the coral (Baker 2003; Rowan 2004). Thus, the stable association of *Porites* and *Seriatopora* with *Symbiodinium* C15 and D1 types, respectively, along the Tanzanian coast might be attributed to environmental tolerance of these *Symbiodinium* types (Sampayo et al. 2008; Stat and Gates 2011). Potentially, minor environmental differences that might trigger secondary acquisition of *Symbiodinium* types in other corals such as *Acropora*, *Millepora* and *Galaxea* to enhance survival might not have the same effect in *Porites* and *Seriatopora.*

The highest diversity of *Symbiodinium* was found in Changuu (Zanzibar) followed by Mbudya (Dar es Salaam) and Kitutia (Mafia), as indicated by the Shannon–Wiener diversity indices (Table 2), and the Zanzibar reefs, collectively, had the highest *Symbiodinium* species richness (Figure 3). A number of host genera were associated with single *Symbiodinium* types throughout the Tanzanian coast, including *Porites*, *Echinopora*, *Pocillopora* and *Seriatopora* (Table 2). By contrast, *Acropora* was associated with eight different *Symbiodinium* types. In Changuu, *Acropora* established symbiosis with C109a, C109a-c, C109a-b, C109b, C115a, C3z, C3u and D1a (Table 2). In the same reef, *Millepora* sp. was associated with the A15, A16 and C57 *Symbiodinium* types, whereas this species at other sites maintained symbiosis with A15 only. *Galaxea fascicularis* was associated with both C3u and D1 in Changuu and at Tanga Mjini. The fact that *Acropora*, *Millepora* sp. and *G. fascicularis* were associated with more than one *Symbiodinium* type at some reefs but not at others suggests the presence of particular environmental factors at those reefs that might induce acquisition or proliferation of background *Symbiodinium* types. In particular, a number of *Symbiodinium* types were found at Changuu reef only, and it is possible that this reflects the influence of factors such as turbidity and pollution.

Symbiodinium clade D has been classified as environmentally tolerant because its distribution is associated with elevated temperature (Chen et al. 2005) and disturbances (Stat et al. 2006). In their review, Stat and Gates (2011) associated clade D with stressful environmental conditions

Table 2: Distribution of ITS-2 *Symbiodinium* types in reef-building coral species collected at seven different sampling sites in Tanzania. Clade type is denoted by a letter in upper case and the ITS-2 DGGE fingerprint type is shown by a number followed by letters in lower case. *Symbiodinium* types marked with an asterisk were always found in association with other types within samples. Numbers at each site indicate number of samples in which a given symbiont type was detected. Numbers in brackets indicate samples with more than one symbiont type at a given site. *H′* = Shannon–Wiener diversity index

Species	Symbiont type	Sampling site						
		Tanga Mjini	Mbudya	Pangavin	Kitutia	Mikindani	Changuu	Chumbe
Pocillopora verrucosa	C1h	8	8	8	8	8	8	8
Pocillopora damicornis	C1h	8	8	8	8	8	8	8
Porites rus	C15	8	8	8	8	8	8	8
Porites cylindrica	C15	8	8	8	8	8	8	8
Seriatopora hystrix	D1	8	8	8	8	8	8	8
Acropora formosa	C3u	8	8	4	8	8	8(2)	8
	C3z*	0	0	0	0	2	2	0
	C109a*	0	0	0	0	0	1	0
	D1a*	0	3	0	2	0	(2)	0
	C109a-b*	0	0	0	0	0	2	0
	C109a-c*	0	0	0	0	0	4	0
Acropora hemprichii	C3u	8	8(2)	8	8	8	8(2)	8
	C3z*	0	0	0	0	0	(2)	0
	C115a*	0	0	0	0	0	(2)	0
	C109b*	0	0	0	0	0	(1)	0
	D1a*	0	(2)	0	(2)	0	(1)	0
Galaxea fascicularis	C3u	8	8	8	8	8	6	4
	D1	(1)	0	0	0	0	(1)	0
Millepora sp.	A15	8	8	8	8	8	8(2)	4
	A16	0	0	0	0	0	(2)	0
	C57	0	0	0	0	0	4(2)	0
Echinopora lamellosa	C3u	6	8	8	8	8	8	4
H′		1.3077	1.3799	1.2981	1.3799	1.2981	2.1057	1.2981

Table 3: Summarised results of a PERMANOVA analysis of the influence of environmental parameters on the diversity of *Symbiodinium* along the Tanzanian coast. Among the four environmental parameters tested, only turbidity was found to have a significant influence on diversity (significant result shown in bold)

Dissimilarity index	Model	*F*-ratio	r^2	*p*-value
Relative abundance (Bray–Curtis)	Latitudinal location of the reef	0.28419	0.36240	0.9271
	Bleaching history	0.60494	0.23223	0.5345
	Anthropogenic disturbances	0.63261	0.24030	0.5445
	Turbidity	4.87960	0.49391	**0.04895**
Presence/absence (Jaccard)	Latitudinal location of the reef	0.35274	0.41365	0.7582
	Bleaching history	0.49997	0.19999	0.6234
	Anthropogenic disturbances	0.49409	0.19811	0.8671
	Turbidity	3.83160	0.43385	0.1389

resulting from either elevated sea surface temperatures or sedimentation. Similarly, LaJeunesse et al. (2010a) found significantly elevated frequencies of clade D in corals collected from warm and turbid sites of the north-eastern Indian Ocean. Changuu and Mbudya reefs are close to sources of terrestrial pollution leading to high sedimentation that elevates turbidity (see Figure 2). Mbudya, for example, unlike Pangavin reef which is also in Dar es Salaam, is located close to streams that discharge terrestrial sediments that limit the amount of solar radiation reaching the surfaces of coral colonies. Therefore, the presence of *Symbiodinium* D1a in some colonies of *Acropora* spp. and D1 in *G. fascicularis* collected from Mbudya and Changuu reefs might be attributed to high turbidity (Figure 2), and/or possibly industrial pollution and lowered salinity.

Regarding patterns of the 1998 bleaching severity and recovery, Changuu and Mbudya reefs were less impacted compared with other reefs (Muhando and Muhammed 2002). Although there are no data on *Symbiodinium* diversity before the 1998 bleaching event, such bleaching trends might have been attributable to the presence of *Symbiodinium* D1a in these reefs. It is also possible that the lower levels of bleaching were attributed to the higher turbidity in these locations, which might have provided protection to the corals from photodamage.

Influence of bleaching history on Symbiodinium *distribution*

The PERMANOVA analysis showed that coral bleaching history has no significant influence on the diversity and

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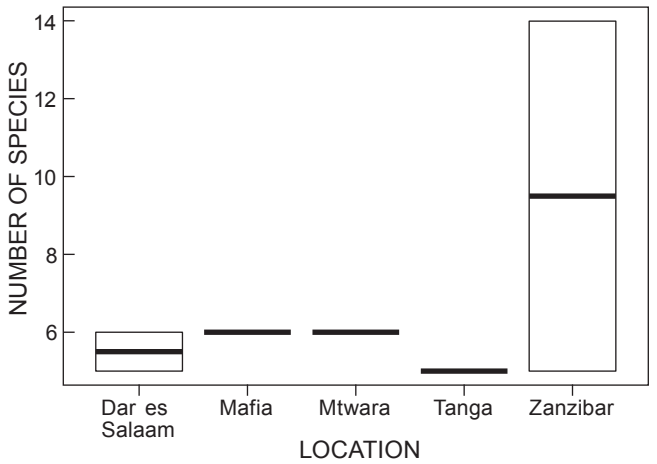


Figure 3: *Symbiodinium* species richness along the Tanzanian coast. In this box plot, two reefs at Zanzibar (Chumbe and Changuu) and two at Dar es Salaam (Mbudya and Pangavin), respectively, were pooled

distribution of *Symbiodinium* along the Tanzanian coast (Table 3). However, there may be a link between bleaching history and the distribution of the D1a symbiont in *Acropora*, which was recorded at Changuu, Mbudya and Kitutia (Table 2). Although turbidity might explain the presence of the D1 symbiont at Changuu and Mbudya, Kitutia and Tanga Mjini reefs do not have high turbidity (Figure 2). One possible explanation for this could be the history of bleaching. The global coral bleaching event in 1998 led to different magnitudes of coral mortality in Tanzania (Muhando and Mohammed 2002). Kitutia was one of the most affected, with about 80% of the corals suffering mortality, but Chumbe, Tanga Mjini and Mikindani experienced mortalities ranging between 30% and 50%, and Changuu and Mbudya were among the least affected with mortalities of about 11%. These reefs showed different rates of recovery, with those at Mtwara (Mikindani) recovering faster than other reefs (Muhando and Mohammed 2002), due to lower anthropogenic stress at that location. Although the type of *Symbiodinium* associations with *Acropora* spp. that existed before the 1998 bleaching event is unknown, the prevalence of *Acropora*–C3u associations in other reefs across the country (Chauka 2013) suggests that a similar association existed before the event. This is because the secondary acquisition of foreign *Symbiodinium* types that occurs during recovery from a bleaching event is not permanent (Toller et al. 2001; Fabricius et al. 2004; Chen et al. 2005). Studies that have monitored *Symbiodinium* diversity over 30 years show endosymbiont populations to revert to their original dominant *Symbiodinium* type at some point during recovery, usually 1–3 years after a bleaching event (Thornhill et al. 2006). Since the 1998 bleaching event that caused 80% mortality took place >10 years ago, it is possible that *Acropora* has reverted to its original *Symbiodinium* type. However, the reefs at Mafia Island are frequently affected by mild seasonal bleaching events (Mbije et al. 2013). This is because the reefs are subjected to a higher seasonal variation in temperature caused by the South Equatorial Current, which elevates temperatures during the South-East Monsoon in Mafia (Pickard and Emery 1995). Hence this frequent seasonal bleaching might have induced *Acropora* to establish a symbiosis with the D1a *Symbiodinium* type, i.e. its presence may be due to long-term ecological and evolutionary mechanisms (LaJeunesse et al. 2010b).

Conclusions

We show a potential effect of local environmental differences and bleaching histories on *Symbiodinium* diversity and distribution in only a few species of reef-building coral, namely *A. formosa*, *A. hemprichii*, *Millepora* sp. and *G. fascicularis*. Most Tanzanian coral species have single *Symbiodinium* types along the coast, probably because environmental variation is small. The presence of the *Symbiodinium* D1a type, a thermal symbiont type in two *Acropora* spp. sampled in an area that is prone to bleaching events, suggests that its presence may have been associated with bleaching resistance. However, turbidity appeared to be associated with higher *Symbiodinium* diversity, including the presence of D1a, than bleaching history. Given that *Acropora* is among the most bleaching-susceptible coral genera, its symbiosis with D1a may not contribute extensively to resistance to bleaching. Thus, we conclude that Tanzanian reef-building corals do not appear to be well-adapted to current trends of climate change. Most bleaching-susceptible genera such as *Pocillopora* and *Seriatopora* have failed to establish symbioses with multiple symbiont types, which hypothetically would confer increased bleaching resistance on the holobionts. In addition, only a few species were found to host thermal-tolerant *Symbiodinium* types.

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