Spatial variability of scleractinian coral bleaching susceptibility in 2010 El Niño–Southern Oscillation between northern and southern reefs, Kenya

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Abstract — Coral bleaching events are occurring more frequently worldwide and vary in severity. This study examined the spatial extent and taxonomic nature of coral bleaching and associated mortality at reefs in two widely geographically separated regions in Kenya during a bleaching event in 2010, and determined whether there were any spatial differences among habitats (wave-exposed versus wave-sheltered) and/or biogeographic regions (northern upwelling versus southern non-upwelling). Northern reefs had a higher abundance of intermediate and resistant corals to bleaching (e.g., *Goniastrea* and massive *Porites*), while southern reefs had more of susceptible corals (e.g., *Acropora* and *Pocillopora*). Coral bleaching susceptibility was significantly lower in the northern region than in the southern region, as a result of coral community composition and oceanographic conditions that reduced thermal stress anomalies. Reduced bleaching and mortality response of the similar coral species in wave-sheltered southern reefs seemed to be explained by their increased tolerance to thermal stress in relatively warm, stagnant conditions. This study suggest, therefore, that much of the spatial variation in bleaching susceptibility of corals was related to assemblage composition (taxa susceptibilities), thermal acclimation and upwelling conditions, which underscores the importance of reef assessment on different locations and in different zones/habitats during large-scale bleaching episodes.

Keywords: Coral bleaching, coral reefs, upwelling, climate change, Kenya

Introduction

Scleractinian corals are important ecosystem engineers and form the foundation of one of the most productive and diverse marine ecosystems (Wilkinson 2008). Coral reefs provide myriad ecological goods and services, such as fisheries and tourism, particularly to the millions of coastal people that live in tropical developing nations (Moberg and Folke 1999, Guest et al. 2012). However, coral reefs are increasingly threatened by a variety of factors, including heavy and destructive fishing, sedimentation, pollution and climate change (McClanahan 2002, Hughes et al. 2003, McClanahan et al. 2007). Increased sea surface temperatures exert tremendous stress on corals reefs, and scleractinian corals are especially sensitive to such impacts. Coral bleaching events associated with climate change are becoming more frequent and now represent a significant threat to many coral reef regions, together with the many local threats affecting coral reefs (McClanahan 2000, Obura 2005).

Studies of the mass bleaching response of corals due to an anomalous ocean warming event in 1997–98 demonstrated that there can be substantial variability in bleaching extent both regionally (Obura 1999, McClanahan et al. 2001) and globally (Wilkinson et al. 1999, Goreau et al. 2000, Obura 2001). In Kenya, the extent of bleaching following this event varied regionally, as corals in southern Kenyan reefs bleached at higher levels (50–60%) (McClanahan et al. 2001), while northern reefs impacted negligibly (5–10%) (Church and Obura 2005). This difference highlights the importance of understanding the drivers of spatial variability in reef coral bleaching susceptibility during warm water anomalies. Such information is necessary for improved conservation of coral reefs, especially given that most recent projections predict increases in the incidence and severity of temperature-induced coral bleaching and mortality events (Hoegh-Guldberg 1999, Obura 2005). Spatial variability in coral bleaching susceptibility at reef scale may be due in part to differences in coral community composition (intrinsic factor), as coral species differ in their susceptibility to bleaching (Loya et al. 2001, McClanahan et al. 2002, McClanahan et al. 2004). However, among locations with similar species compositions, the variability may also be due to local ocean-

ographic conditions (Glynn 1996, West and Salm 2003, Obura 2005). Furthermore, apart from the spatial heterogeneity of ocean temperatures, local habitat characteristics may also influence the response of corals to thermal stress (McClanahan and Maina 2003, Grimsditch et al. 2010). Although many studies document coral bleaching and mortality patterns, there are few studies that have examined the spatial variability of bleaching response at the level of the coral assemblage during large-scale warm water anomalies (McClanahan et al. 2007, Wagner et al. 2010).

A monsoonal climate dominates the entire Kenyan coast, blowing from the northeast (October–March) and southeast (April–September) (McClanahan 1988). The reefs on the southern coast of Kenya are influenced by the northward-flowing waters of the East Africa coastal current (EACC) throughout the year. By contrast, during the northeast monsoon (NEM), the reefs on the northern coast of Kenya are subjected to cool upwelling waters when the EACC converges with the southward Somali Current (SC) (Figs. 1b and c) (Schott and McCreary 2001). Coastal upwelling results from the action of increased winds parallel to the coastline that generate an Ekman drift off the coast, lead-

ing to an upwelling of cool sub-surface waters in the northern coastal zones of Kenya during the NEM season (Varela et al. 2015). These oceanographic dynamics differences between the regions could cause in part differences in species recruitment within scleractinian coral communities (Visram et al 2007), and could also influence spatial patterns of bleaching during elevated temperature anomalies, known to occur during the dry NEM season, a period when solar irradiance and water temperatures reach annual peaks (McClanahan 1988, McClanahan et al. 2001, Mwaura et al. 2009). In addition, reefs along Kenyan coast support abundant coral populations that inhabit wave-sheltered lagoons and outer wave-exposed habitats, which often experience different water temperature (Grimsditch et al. 2010). In this respect, Kenyan coast could provide good study sites to examine spatial variation in bleaching response of the coral assemblages during large-scale thermal anomalies.

In this study, our main objectives were to: (1) conduct underwater surveys in order to describe coral community assemblages and the variations in bleaching intensity of common scleractinian corals during the 2010 El Niño–Southern Oscillation event in the northern and southern reefs of
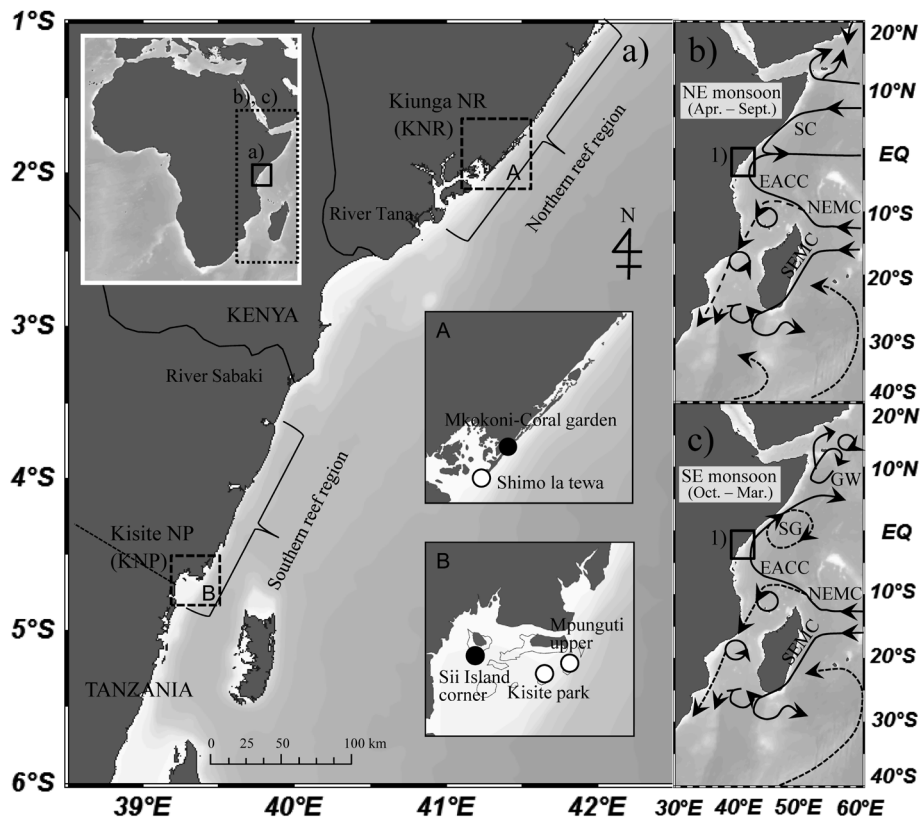

Fig. 1. (a) Map of Kenya showing the two regional reef areas: (A) Northern Kiunga National Reserve (NR) and (B) Southern Kisite National Park (NP), as well as the reef sites surveyed during March 2010 (black circle: wave-sheltered; white circle: wave-exposed). Currents during the (b) Northeast Monsoon and (c) Southeast Monsoon (Schott and McCreary 2001). Major ocean currents in the Indian Ocean are also shown schematically. SEC, the South Equatorial Current; SECC, South Equatorial Counter Current, EACC: the northward-flowing East African Coastal Current; SCC, the southward-flowing Somali Counter Current; NEMC and SEMC, Northeast and Southeast Madagascar Current; SG, Southern Gyre; and GW, Great Whirl.

Kenya, at different reef habitats (wave-exposed and wave-sheltered) in each region (northern upwelling versus southern non-upwelling), and (2) shed light on the principal factors influencing the spatial differences in bleaching susceptibilities of corals.

Materials and methods

Survey locations and environmental background

The coral reefs of Kenya are located in two distinct marine regions; the southern region is characterised by an almost continuous fringing reef, while northern reefs are discontinuous and patchy. These two complex reef regions are separated by a coral-free gap approximately 100–150 km long due to the historical discharge of freshwater and sediments from the two main rivers, the Sabaki and the Tana (Obura 2001, Visram et al. 2007) (Fig. 1a). This study was conducted in the Kiunga National Reserve (KNR) (2°00′S, 41°30′E), located on the northern coast of Kenya, and in Kisite National Park (KNP) (4°42′S, 39°22′E), located on the southern coast of Kenya (Fig. 1a). Reef corals in Kenya are typically distributed in back-reef lagoons, characterized by high temperature fluctuations and stagnant waters (i.e., wave-sheltered), and outer-reef areas, which display lower temperature variations and influenced by high sea currents and oceanic waves (i.e., wave-exposed) (Grimsditch et al. 2010). Therefore, we randomly surveyed sites with high coral cover and similar depth (3–5 m at low tide) at wave exposed (Shimo La Tewa) and at wave-sheltered (Mkokoni Coral Garden) located in the northern region, while in the southern region, 2 sites in wave-exposed (Mpunguti Upper and Kisite Park) and wave-sheltered (Sii Island Corner) were surveyed (Fig. 1a). Two sites were surveyed only at the wave-exposed habitats in the south, because it was not possible to get additional sites with similar high coral cover and depth (3–5 m) for the other habitats.

Benthic surveys

Field surveys were conducted in the two study regions from 22 to 30 March, 2010, one week after the onset of the bleaching event, which corresponded to the period of warmest sea water temperatures. Quantitative benthic surveys were conducted at each of the wave-exposed and wave-sheltered sites by laying out three randomly placed 25×1-m belt line intercept transects on the benthos, arranged in a non-overlapping manner parallel to the coastline (English et al. 1997). Within each transect, the observer (J. Mwaura) counted all visible coral colonies >10 cm (max. diameter). Only the colonies whose center lies within 0.5 m of either side of the transect line were identified to the genus level as described in Obura and Grimsditch (2009), and their growth forms were recorded following the work of Veron (2000).

Table 1. Scleractinian coral genera classified by susceptibility to bleaching [adapted from Marshal and Baird (2000) and Obura and Grimsditch (2009)].

Susceptible	Intermediate	Resistant
Acropora	*Alveopora*	*Coscinarea*
Montipora	*Echinopora*	*Pavona*
Pocillopora	*Favia*	*Porites (massives)*
Seriatopora	*Favites*	
Stylophora	*Fungia*	
	Galaxea	
	Goniastrea	
	Goniopora	
	Hydnophora	
	Leptoria	
	Lobophyllia	
	Platygyra	
	Porites (branching)	

The surveyed coral genera were later ranked into three groups (Table 1) according to their reported bleaching susceptibility (Marshal and Baird 2000, Obura and Grimsditch 2009).

Coral bleaching and mortality response

During the surveys of the bleaching and mortality responses, we classified each of the identified coral genera into one of five states of coral conditions, which were estimated visually as the proportion of colony surface tissue affected by thermal stress, according to McClanahan et al. (2001, 2004). The five states are as follows: 1) "Normal": coral colonies with 100% normal colouration, 2) "Low-bleached": colonies with less than 40% of the surface area bleached, 3) "Moderately bleached": colonies with 40–70% loss of colouration, 4) "Highly bleached": colonies with more than 70% loss of colouration and 5) "Recently dead": coral colonies with no tissue and/or bare skeleton overgrown by fine brown filamentous algae.

A bleaching and mortality index (BMI) of coral responses or susceptibility to the bleaching event was calculated for each taxon and location based on the five coral condition categories described above, using a formula modified from McClanahan (2004):

$$\text{BMI} = (0C_1 + 1C_2 + 2C_3 + 3C_4 + 4C_5)/4$$

where C_1 to C_5 are the five coral condition categories (% occurrence) described above (i.e., C_1=normal, C_2=low-beached, etc.). In this formula, coral condition of each category (C_1–C_5) was multiplied by a score (0–4) to weigh the different categories according to their bleaching response (normal=0, low-bleached=1, etc.) following McClanahan et al. (2004). The resulting sum of the five categories was divided by 4 to produce a BMI (%) on a 0–100 scale (McClanahan et al. 2004).

Sea surface temperature

Sea surface temperature (SST) data were obtained from the second version of the Coral Reef Temperature Anomaly Database (CoRTAD). This database contains global SSTs and related thermal stress metrics from measurements taken by the advanced very high resolution radiometer (AVHRR) on-board National Oceanic and Atmospheric Administration (NOAA) orbiting satellites. The use of these data for global coastal applications has been evaluated and found adequate, even though remotely sensed SST measurements do not capture subsurface waters (Maina et al. 2011). The satellite-derived SSTs were acquired on a weekly basis and mean composite SSTs were calculated as a representative of long-term mean SST for each location (KNR and KNP) for the last week of every month. Thermal Stress Anomalies (TSA), defined as temperature excesses $\geq 1°C$ above the climatologically (long-term average) warmest week of the year (i.e., the warmest of 52 weeks averaged over 27 years) (Selig et al. 2010, Maina et al. 2011), were also extracted from the CoRTAD V4 database Please remove the URL (https:/~), because it is not accessible now. Instead, please add the following citations, which well described the CoRTAD database. (Selig et al. 2010, Maina et al. 2011). SSTs above the locally calculated temperature threshold were considered as thermal stresses (Tosic and Navas-Camacho 2012, Bayraktarov et al. 2013).

Data analysis

To examine the drivers of differential bleaching responses, three factors (coral genera, habitat and region) were tested using the nine coral genera with the greatest numbers of bleached colonies [*Pocillopora*, *Acropora*, *Goniastrea*, *Porites* (massive), *Echinopora*, *Favites*, *Favia*, *Hydnophora*, and *Platygyra*] and for all genera combined (data pooled). Prior to analysis of variance (ANOVA), BMI data were tested for normality and heterogeneity of variance using Levene's test and, where necessary, arcsine-transformed. We used one-way ANOVA to evaluate habitat-specific differences within regions and three-way ANOVA to test the influence of region and habitat on bleaching intensity for all pooled genera. Statistical analyses were performed using STATISTICA ver.7.0 (Statsoft 2004) and Microsoft Excel.

Results

Sea surface water temperature

Based on MODIS-derived data, the highest SSTs were recorded on 27 March, 2010, during our field surveys, with KNR in the north peaking at 30°C and KNP in the south peaking at 32°C (Fig. 2a). Although the long-term average SSTs in the northern and southern regions had only slight differences throughout the year (e.g., 28.0°C and 28.6°C in
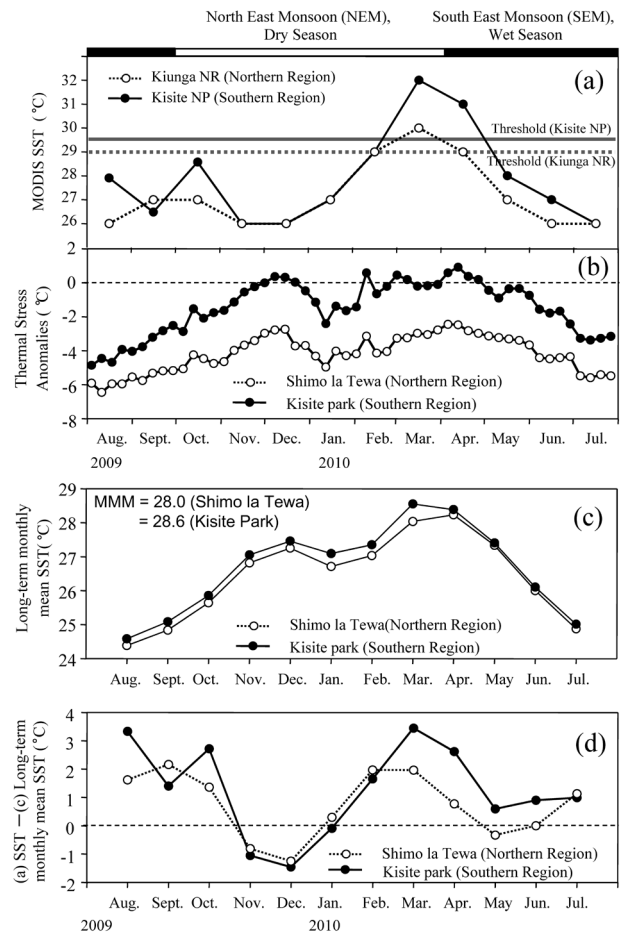

Fig. 2. Time-series average of sea surface temperature (SST) and temperature-related indices at Kisite National Park (NP) in southern Kenya and Kiunga National Reserve (NR) in northern Kenya.

(a) Average daily satellite SST and (b) thermal stress anomalies extracted from the CoRTAD V4 database from August 2009 to July 2010. Horizontal grey solid and dotted lines in (a) indicate theoretical thermal thresholds for scleractinian corals at Kisite NP and Kiunga NR, respectively, calculated following the work of McClanahan et al. (2004). (c) The long-term average SSTs, which were only available at the wave-exposed sites in both regions, were calculated using data from 1982 to 2010. (d) The deviation of average daily SST from the long-term average was calculated based on Figs. 2a and c.

the north and south, respectively, during March; Fig. 2c), the deviations in the March 2010 SSTs from the long-term averages were clearly different between the two regions (2.0°C in the north and up to 3.4°C in the south; Fig. 2d). Therefore, corals in the southern region experienced greater thermal stress than those in the northern region during March 2010. The MODIS-derived data confirmed that the bleaching threshold, defined as 1°C above the maximum long-term monthly mean (McClanahan et al. 2004), was exceeded by 1°C and 2.4°C in the northern and southern regions, respectively (Fig. 2a).

Coral community composition

A total of 31 coral genera were recorded over the entire course of the bleaching surveys, with southern reefs having higher diversity (28 taxa, n=242 at sheltered reef, n=770 at 2 exposed reefs) than northern reefs (22 taxa, n=116 at sheltered reef, n=286 at exposed reef). 19 taxa were found common in both regions and the most abundant 15 taxa were selected in each region. Among the selected 15 common genera, there were fine-scale differences in coral assemblages and their susceptibility to bleaching (Fig. 3, Table 1). Corals susceptible to bleaching (e.g., *Acropora* and *Pocillopora*) dominated the coral community in southern reefs, while intermediate (i.e., *Goniastrea* and *Favites*) and resistant corals (e.g., massive *Porites*) were more abundant in northern reefs (Fig. 3). The proportion of susceptible branching genera was slightly higher in wave-sheltered (59.5%) than in wave-exposed reefs (44.9%) in the south, while the proportions of the corals in intermediary and resistant submassive and massive genera were similar between wave-sheltered and wave-exposed reefs in both regions (65–68% in the north, and 38–40% in the south; Fig. 4). Overall, the proportion of branch-
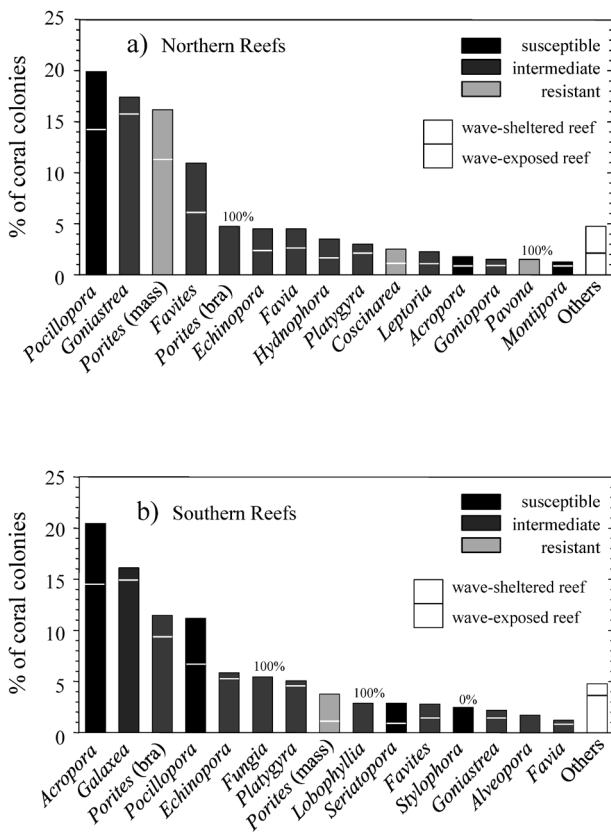
ing species was higher in the south (45–60%) than in the north (22–28%) (Fig. 4).

Coral bleaching and susceptibility

A total of 1,414 colonies were observed during bleaching episodes; normal and low-bleached corals accounted for 49.1% and 26.6%, while 14.5% and 5.5% were moderately or highly bleached, respectively, and only 4% had recently died (Fig. 5). Among pooled coral genera, the proportion of bleached colonies (low-, moderately and highly bleached and recently dead) was higher in the south (59.0%) than in the north (30.6%) (Fig. 5). In addition, corals in wave-exposed sites suffered most extensive bleaching and mortality (63.2%) than at sheltered-wave sites (45.5%) in the southern region (ANOVA, P<0.05) (Fig. 5). However, there were no significant differences in the ratio of bleached corals among

Fig. 3. Percentage of the coral community made up of the most abundant 15 coral genera recorded in both study regions. The crossbar in the bar graph separates the contribution of the colony numbers from wave-sheltered (upper) and wave-exposed (lower) to the total numbers, respectively. 100% and 0% mean the contribution of the colony numbers from wave-exposed reef to the total.
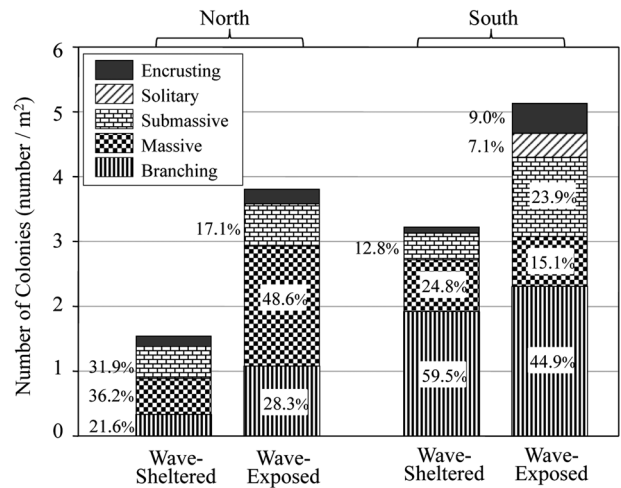

Fig. 4. Mean colony densities (number/m²) for each of the different growth forms of corals surveyed at each habitat type. The number of the colonies in each category at each transect (i.e., totally 6 transects at wave-exposed habitats in the south, and 3 transects at the other habitats) were compiled respectively and standardized per the surveyed area.
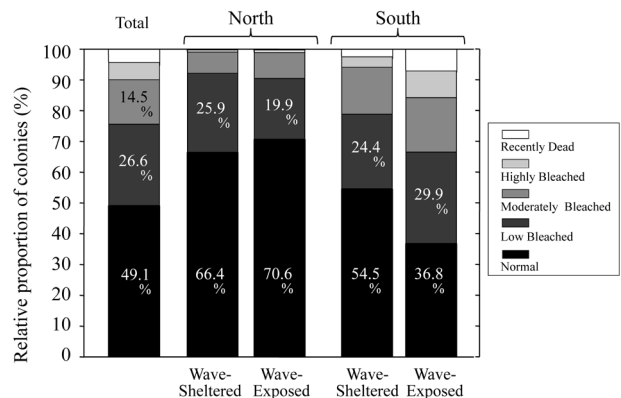

Fig. 5. Relative percentage of total scleractinian colonies impacted at different levels by thermal stress at each region and habitat type.
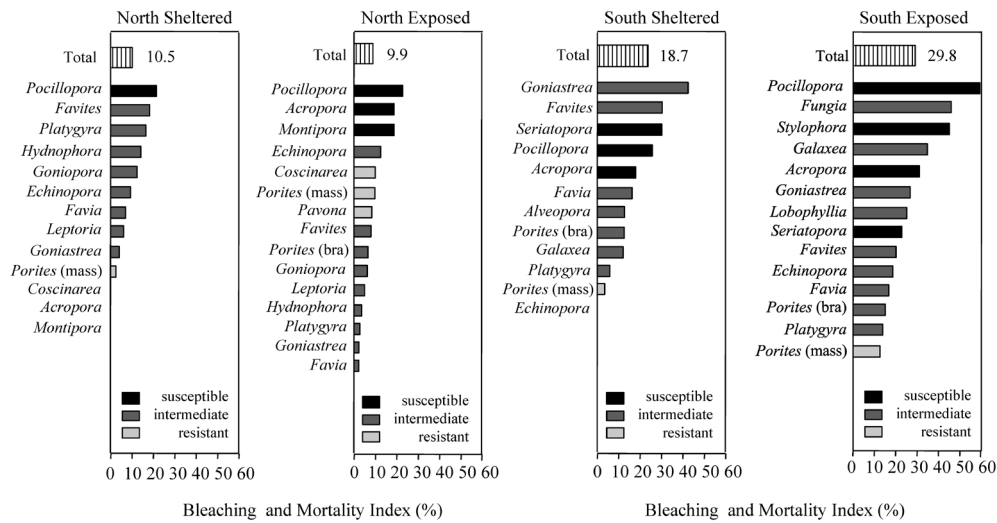
Fig. 6. Bleaching and Mortality Index (BMI) for each of the top 15 abundant coral taxa at each habitat in both regions, sorted from the most impacted to the least. BMI in total at each location is average values of all genera including minor species.

habitats in the northern region (p=0.28) (Fig. 5). The BMIs were minimal in the northern region for the sheltered (10.5%) and exposed sites (9.9%), whereas in the southern region they were much higher at sheltered (18.7%) and exposed sites (29.8%) (Fig. 6). In the southern region, where bleaching susceptibility indices were high, susceptible corals (*Pocillopora*, *Acropora and Stylopora*) suffered the most extensive bleaching (35–60%) at the wave-exposed sites, whereas intermediate corals (*Goniastrea*, *Fungia and Galaxea*) also had relatively higher bleaching incidences (30–42%) (Fig. 6). By contrast, bleaching and mortality at both habitats did not differ significantly in the northern region, albeit more of intermediate corals (*Favites*, *Platygyra*, *Goniopora* and *Hydnophora*) and a few of susceptible corals (*Pocillopora*) were recorded at low to moderately bleached categories (Fig. 7). Although most common coral genera exhibited variations in bleaching, only *Pocillopora* showed significant variations between regions and among habitats, while *Goniastrea* exhibited significant variations only among habitats (p<0.05, Table 2). Significant variations and interactions of factors driving bleaching responses were shown by the three-way ANOVA (all genera, habitats and regions) (p<0.05, Table 2).

Discussion

SSTs reaching 30.0–32.0°C during the late NEM season of 2010 were the second highest recorded after those from the March–April 1997/1998 bleaching event (McClanahan et al. 2001), and seem to have triggered a mass bleaching event across the study regions and habitats in Kenya. However, the results had a wide spread and varied among habitats and between the two regions. Although the seawater anomaly was a strong driver of bleaching, several factors may explain the variation in bleaching susceptibility of corals at the spatial scales examined in our study. Marshal and Baird (2000) indicated that environmental factors (e.g., the increase of temperature and light intensity) may explain large-scale patterns of bleaching, while small-scale patterns are determined by biological factors such as acclimatization of coral communities to environmental stresses (e.g., increased temperature) or ecological factors such as the assemblage compositions and their susceptibility to bleaching.

The coral colonies we surveyed varied considerably in compositions (taxa susceptibility) and may have influenced spatial bleaching differences observed between the two regions. In particular, the lower incidences of bleaching and no recently dead corals observed at either wave-exposed or wave-sheltered reefs in the northern reefs (Fig. 5) were likely a consequence of community composition, as the north had significantly lower abundances of susceptible species (Fig. 3). Although the branching and highly susceptible *Pocillopora* was dominant in the northern region, common and more abundant taxa belonged to sub-massive "intermediate" (e.g., *Gonistrea* and *Favites*) and massive "resistant" (e.g., *Porites* (mass)) groups (Figs. 3, 4). This trend may be typical after previous bleaching events (e.g., in 1997–98), where thermal stress may have reduced populations of susceptible species and/or limited their recovery, thereby facilitating the propagation of more intermediate and resistant coral groups (Visram et al. 2007, Thomson and van Woesik 2009). A comparative study of coral recruitment concluded that recruitment limitations in the northern reefs of Kiunga NR contributed to the collapse of bleaching susceptible corals *Pocillopora* and *Acropora* after the 1997/98 bleaching event (Visram et al. 2007), and this hypothesis was further confirmed by this study. By contrast, the coral bleaching response was
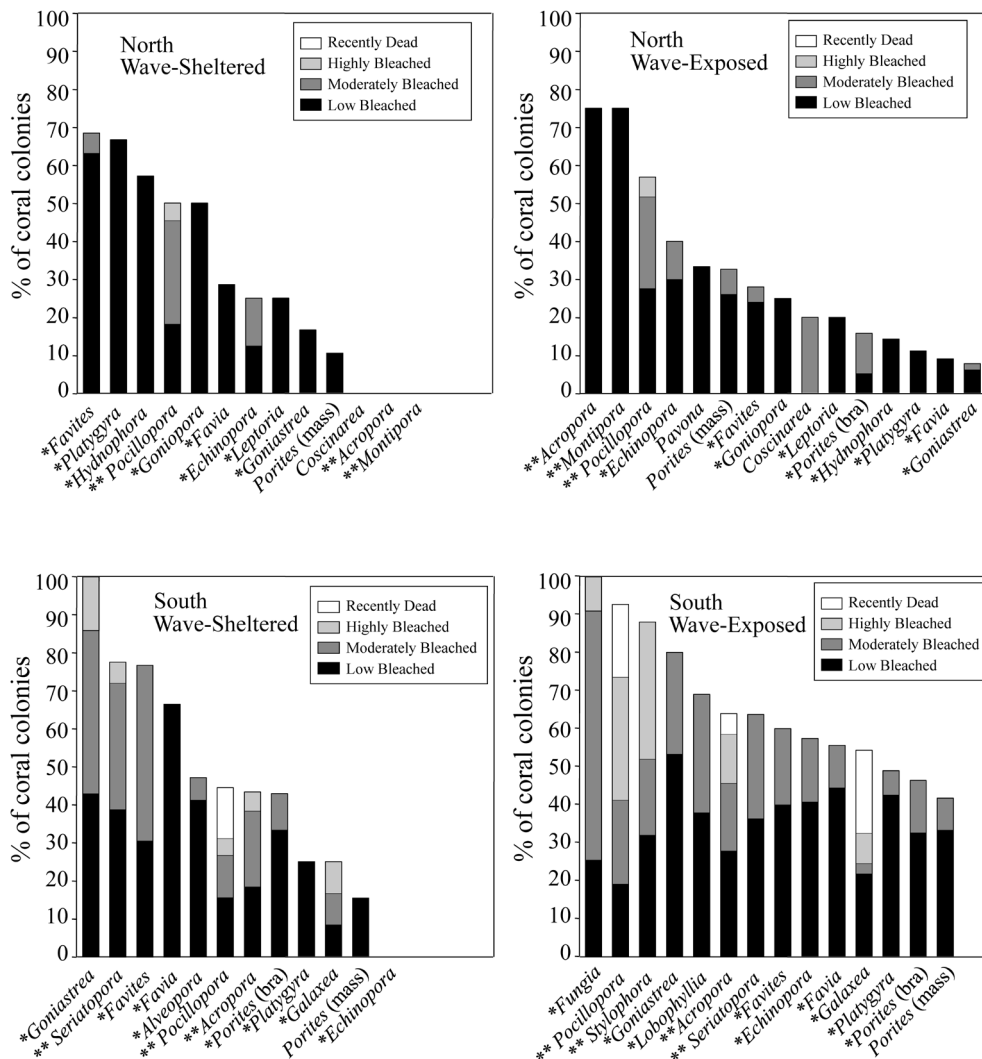
Fig. 7. Relative percentages of colonies of each coral genus at each level of bleaching. Only the 15 most abundant genera are presented at each region and habitat. The number of asterisks attached to species names indicates susceptibility to bleaching (**:susceptible, *:intermediate, no asterisk: resistant).

particularly high in the southern region, which also exhibited recently dead corals on wave-exposed reefs (Fig. 5), probably because the southern reefs supported more of the susceptible corals (*Pocillopora*, *Acropora* and *Stylophora*) showing the most extensive bleaching and mortality incidences (Figs. 3, 6). Therefore, the spatial difference of bleaching response of corals observed between the regions (north *vs.* south) primarily seemed to be consequences of coral species assemblages (i.e., susceptibility to bleaching).

On the other hand, the bleaching response of the susceptible corals in the southern region showed lower BMI in wave-sheltered reefs than those in wave-exposed reefs even among same genera (i.e., 26.1 *vs.* 59.2 for *Pocillopora*, 18.3 *vs.* 31.0 for *Acropora* and 30.6 *vs.* 45.0 for *Stylophora*; Fig. 6), indicating another factors affecting bleaching susceptibility in coral communities. Unfortunately the seawater temperature data was not available at the exact locations both at wave -sheltered and -exposed reefs in our study. In general,

however, the coral assemblages inhabiting the wave-sheltered stagnant reefs are exposed to constantly high temperatures or live in more fluctuating thermal and light environments than wave-exposed ones, and even the susceptible corals are acclimated to the daily fluctuating environmental conditions, which may lead to greater tolerance during episodes of thermal stress (Craig et al. 2001, McClanahan and Maina 2003, Wagner et al. 2010). This high level of stressful environmental conditions (i.e., substantial fluctuations in the temperature and irradiance levels) daily and throughout the year may generate pressures to develop resilience mechanisms for the coral holobiont (coral host, algal symbionts, microbial associates) and support more numerous resistant genotypes (adaptation) and/or phenotypes (acclimation), enabling them to adjust to unexpected bleaching event (Brown et al 2002a, Brown et al 2002b; Baker et al 2008; Oxenford and Vallés 2016). In contrast, corals inhabiting wave-exposed environment experience less variable and milder conditions of sea

Table 2. Results of ANOVA on the effects of geographic region and habitat upon coral colonies for all genera, as well as for the nine major genera (*Pocillopora*, *Acropora*, *Goniastrea*, *Porites* massive, *Echinopora*, *Favites*, *Favia*, *Hydnophora* and *Platygyra*). df, degrees of freedom; MS, mean square. The number of asterisks attached to species names indicates susceptibility to bleaching (see Fig. 3).

	Effect	SS	df	MS	F	*p*
All genera pooled	Region	3.18E+04	1	3.18E+04	17.62	**0.000***
	Habitat	7071	1	7071	3.910	**0.048***
	Region × Habitat × Genera	1488	9	12.52	2.83	**0.003***
*Pocillopora***	Region	1481	1	1481	4.881	**0.033***
	Habitat	2478	1	2478	8.164	**0.007***
	Region × Habitat	1461	1	1461	4.815	**0.034***
*Acropora***	Region	400	1	400	0.205	0.651
	Habitat	4797	1	4797	2.464	0.119
	Region × Habitat	1285	1	1285	0.660	0.418
*Goniastrea**	Region	1.99E+04	1	1.99E+04	51.09	**0.000***
	Habitat	182	1	182	0.470	0.504
	Region × Habitat	101	1	101	0.260	0.618
Porites massive	Region	15	1	15	0.013	0.912
	Habitat	1369	1	1369	1.164	0.290
	Region × Habitat	1	1	1	0.001	0.979
*Echinopora**	Region	71	1	71	0.055	0.816
	Habitat	2450	1	2450	1.901	0.176
	Region × Habitat	876	1	876	0.679	0.415
*Favites**	Region	2327	1	2327	0.990	0.331
	Habitat	964	1	964	0.410	0.529
	Region × Habitat	31	1	31	0.013	0.909
*Favia**	Region	4527	1	4527	2.058	0.179
	Habitat	503	1	503	0.229	0.642
	Region × Habitat	27	1	27	0.012	0.914
*Hydnophora**	Region	1807	1	1807	1.297	0.288
	Habitat	498	1	498	0.357	0.567
	Region × Habitat	2105	1	2105	1.511	0.254
*Platygyra**	Region	56	1	56	0.026	0.874
	Habitat	179	1	179	0.082	0.776
	Region × Habitat	2023	1	2023	0.928	0.341

water temperature and light regime. Therefore, hard corals within wave-sheltered habitats may be intrinsically more resistant that help to prevent thermal stress severity and damage (i.e., lower BMI) than hard corals inhabiting wave-exposed habitats in the southern region (Fig. 6) during the regional temperature anomaly in 2010.

A third plausible explanation for spatial variation of bleaching response is exposure to upwelling conditions that cause a localised thermal stress decrease during unusual elevated sweater temperature (West and Salm 2003; Wang et al 2007). While we observed dramatic coral bleaching from south to north during the warm water anomaly in March 2010, the bleaching response (i.e., BMI) of some susceptible branching corals in northern reefs were surprisingly low (i.e., 0–18%, and 22–23% for *Acropora* and *Pocillopora*, respectively) with no proportions of recently dead corals even at wave-exposed reefs, compared to southern reefs (i.e., 18–31% and 26–59%, respectively) (Figs. 6, 7). This suggests that regional bleaching differences may have been also medi-ated by another localised factor, in addition to the difference in the coral species assemblages (see above). One important parameter that may partially explain the observed regional differences in response among the same coral species and habitats is the magnitude of thermal stress (Marshal and Baird 2000, McClanahan et al. 2007, Klyepas et al. 2008, Oxenford and Valles 2016). Bleaching severity has been shown to vary substantially as a consequence of the severity of thermal stress (Kleypas et al 2008, Guest et al 2012). In our study regions, the surface water temperatures exceeded the coral bleaching threshold by 2.4°C at KNP in the south and 1.0°C at KNR in the north (Fig. 2a). The calculated thermal stress anomaly values were positive at KNP and negative at KNR (Fig. 2b). The lower thermal stress and negative anomalies in the north, coupled with reduced coral bleaching, particularly among susceptible species, may potentially indicate the presence of hydrodynamic phenomena that caused a localised temperature decrease in the northern region during this warm water anomaly (Obura 2001, Riegl

and Piller 2003, Pineda et al. 2013). Several studies have discussed the mitigating effect of decreased water temperatures induced by upwelling on coral bleaching during warm water anomalies (Glynn 1996, Riegl and Piller 2003, Glynn and Leyte-Morales 1997, Bayraktarov et al. 2013). Jimenez et al. (2001) provided further evidence for this, such as seasonal upwelling in Costa Rica, which experienced reduced warming and consequently less coral bleaching than at locations with no upwelling. Glynn (1996) hypothesised that upwelling locations may serve as refuge areas for corals by counteracting seawater temperature increases that provoke coral bleaching; this has subsequently been supported by more recent studies which suggested that seasonal upwelling coinciding with severe warming events could reduce bleaching severity of corals due to upwelling-induced seawater temperature decrease (West and Salm 2003, Riegl and Piller 2003, Chollett et al. 2010). In this study, seasonally cool waters of upwelling in the northern reefs may have contributed to lowering SSTs during the dry NEM season of 2010 than in the southern reefs subject to more thermally stable waters throughout year (Fig. 2d, see study site descriptions in the Introduction). Additional studies have provided evidence for reduced thermal stress and bleaching incidence in other regions with seasonal upwelling, including the western coast of Mexico (Glynn and Leyte-Morales 1997, Reyes-Bonilla 2001, Reyes-Bonilla et al. 2002), the Gulf of Panama (Glynn et al. 2001, Podesta and Glynn 1997), the Gulf of Papagayo/ Costa Rica (Jimenez et al. 2001), the Bahamas (Riegl and Piller 2003), South Africa (Riegl 2003), northern Madagascar (McClanahan et al. 2007) and the Colombian Caribbean (Rodriguez-Ramirez et al. 2008, Bayraktarov et al. 2013). The reduced coral bleaching in the northern region, especially among highly susceptible corals (*Pocillopora* and *Acropora*), indicates that the future impacts of bleaching will not be as uniform as anticipated (Pandolfi et al. 2011) and that even highly susceptible taxa are likely to persist in some regions despite increases in the frequency of thermal stress events. If our findings apply more generally, then the northern reefs in Kenya may be designated as a conservation priority.

The combined interactions among the three studied factors (all genera, habitats and regions) contributed significantly to bleaching variation (Table 2). It is thus clear that the myriad factors driving coral bleaching responses cannot be adequately addressed independently, which highlights the importance of assemblage composition (taxa susceptibilities) and thermal stress history (acclimatization) as well as exposure to oceanographic conditions (seasonal upwelling) in understanding the underlying factors driving spatial variability in bleaching responses of corals between widely separated regions and among habitats during warm water anomalies.

In conclusion, our study supports the notion that coral bleaching and mortality responses to warm water anomalies along the Kenyan coast can be highly variable across regions and habitats. In this instance, the spatial variability in bleaching response of reef corals could be attributed, in part, to coral-community assemblages (differential susceptibility to bleaching), and thermal stress history of the habitat (thermal acclimation) and hydrodynamic conditions that reduce thermal stress (seasonal upwelling), which has been suggested by other field studies (McClanahan and Maina 2003, McClanahan et al. 2004, Riegl and Piller 2003, Van Woesik et al. 2012). However, other factors such as the water quality and light regimes could also be investigated as potential causes of the observed spatial patterns of bleaching. While there were resource constraints (e.g. some factors receiving no attention or difficult to quantify during limited field observation), our results emphasize the need of considering regional and habitat-specific assessments during large-scale warm water anomalies to describe and understand the factors driving variability in coral bleaching severity. The knowledge of this spatial variability may be fundamental in promoting coral resistance and resiliency of coral reefs, in the face of rapid anthropogenically-induced changes (West and Salm 2003; Obura 2005; Alemu and Clement 2014). For example, the ability of reef building corals in wave-sheltered sites to adapt/acclimatize stronger and more frequent bleaching events, should be adequately coupled with the reef management to protect this reefs from local stressors (e.g., water quality and destructive fishing) for conservation of Kenya's coral reefs. Therefore, we suggest that conservation policy and management that optimize the strategies against climate change-induced disturbances should include prioritisation of the sites and coral taxa that confer potential thermal tolerance as they may fare better to future global climate change.

Acknowledgements

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