Coral bleaching responses in Sodwana Bay, South Africa

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Abstract

This study assessed the bleaching response (BR) of coral colonies within the central reef complex in Sodwana Bay, South Africa. Bleach surveys were conducted at 16 sites on 8 reefs over the period of 2007 to 2013. A total of 12 858 coral colonies from 30 taxa were randomly sampled and colonies were placed into 7 categories of bleaching response. This allowed for the calculation of taxon-specific BR as a weighted percentage of coral cover bleached. Continuous temperature records from a permanent temperature gauge on Two Mile Reef were used to assess thermal stress over this period. The percentage of coral colonies that bleached in 2007, 2008, 2011, 2012 and 2013 were 37.4%, 17.4%, 23.8%, 33.6% and 38.8% respectively. A binomial GLM model framework was used to separate the effects of year, reef and taxon on the bleaching response. Due to inconsistent sampling of sites over time, only data from the seven sites on Two Mile Reef (TMR) and the two sites on Nine Mile Reef (NMR) were included in the model. A total of 6758 coral colonies from the nine most abundantly sampled taxa were used in the assessment of bleaching response for TMR and NMR over the sample period. Taxon was shown to explain most of the variability in the bleaching response of TMR and NMR over time (40.9%). The standardized reef bleaching response of TMR and NMR indicated the same temporal trends with a range of 5% to 28% of live coral surface bleached. Standardized reef-specific BR showed periods of high (2007, 2012 and 2013) and low (2008 and 2011) bleaching response. Low BR in 2008 and 2011 did not correspond to thermal stress (≥27.5°C) suggesting that local upwelling buffered the effects of thermal stress experienced. Standardized taxon-specific bleaching response for TMR and NMR displayed large variability over time and ranged from 2.5% to 45% of live coral surface bleached, with *Montipora* being the most susceptible and *Galaxea* and *Playgyra* being the least. Mean site-specific BR averaged over all years, including all sites, found that *Coscinaraea, Montipora, Astreopora and Anomastrea* were the most susceptible taxa. This study and other recent studies draw attention to a trend of either episodic or an increasing frequency and intensity of bleaching in southern African reefs.

Introduction

Coral reefs are some of the most biologically diverse and economically significant ecosystems on Earth (Hoegh-Guldberg et al. 2007). They provide a vast array of ecosystem services and are fundamental to society and industry through fisheries, coastal protection, building materials, new biochemical compounds and tourism (Moberg and Folke 1999). The inaugural International Year of the Reef in 1997 signalled the world's attention to take action against reef deterioration (IYOR 2008). However reef deterioration has continued on a global scale from both direct and indirect human influence (Hughes et al. 2003; Bruno and Selig 2007).

Rapid increases in atmospheric carbon dioxide concentration ($[CO_2]_{atm}$) present the largest threat to coral reefs by driving global warming and ocean acidification (Kleypas and Langdon 2006; Hoegh-Guldberg 2007). The rise in $[CO_2]_{atm}$ during the 20th century has driven an average increase in global ocean temperature of 0.74°C and has depleted seawater carbonate concentrations by ~30 µmol kg^{-1} seawater and acidity by 0.1pH (IPCC 2007). The current rate of change exceeds even that of the ice age transitions and may surpass the capacity of most organisms to adapt (Hoegh-Guldberg 2007). Therefore understanding how corals and their endosymbiotic algae will respond to climate change impacts is imperative to managing marine ecosystems and will improve global climate change predictions for coral reefs (Glynn 1996, Brown 1997; Hoegh-Guldberg 1999).

Coral bleaching, the disintegration and ejection of the symbionts, is induced by a variety of stresses, but thermal stress has been causally linked to most of the large-scale bleaching events (Fitt and Warner 1995; Glynn 1996; Brown1997). The thermal sensitivity of corals and their associated endosymbiotic dinoflagellates (*Symbiodinium* spp.) has been well documented (Hoegh-Guldberg 1999; Hoegh-Guldberg 2003; Sebastian et al. 2009). *Symbiodinium* photosynthesize and provide more than 95% of the metabolic requirements of the coral host and subsequently maintain high calcification rates. Coral bleaching generally occurs when temperatures exceed summer maxima by 1° to 2°C for 3 to 4 weeks (Hoegh-Guldberg 1999). Bleaching mortality progressively worsens as the thermal anomalies lengthen and intensify resulting in mass bleaching. Coral bleaching has increased in both intensity and frequency in recent decades (Hoegh-Guldberg 1999; Doney et al. 2003; Donner et al. 2005; Hoegh-Guldberg 2005), disrupting coral-algae symbiosis (Donner et al. 2007; Kleypas et al. 2008; Jones et al. 2008). This has lead to large-scale mortality (Bruno and

Selig 2007; McClanahan et al. 2007a) with reported consequences for coral populations (Edmunds and Elahi 2007; McClanahan et al. 2008), ecology and biodiversity (Aronson et al. 2002; McClanahan 2008).

The largest mass coral bleaching event in the western Indian Ocean occurred in 1998, with reefs in the northern regions (especially Kenya, Maldives, and Seychelles) having experienced extensive loss of coral cover (McClanahan et al. 2007a; Sebastian et al. 2009). The impact of this mass bleaching event decreased in a southerly direction and bleaching was minimal on the high latitude reefs of South Africa (Goreau and McClanahan 2000; Wilkinson 2002; McClanahan et al. 2007b). Riegl and Piller (2003) therefore suggested that South African reefs can be considered as potential refugia from climate change. However in 2005, a warm-water anomalous event resulted in moderately high bleaching on South African reefs (McClanahan et al. 2007a, c). Differences in bleaching response (BR) observed during this event, on East African reefs, were linked to past bleaching, coral community structure and thermal stress (McClanahan et al. 2007c). Subsequently, the significant roles of acclimatisation, community change and adaptation has been increasingly recognised when assessing the response of coral reefs to environmental stress (Rowan et al. 1997; Brown et al. 2002; Baker et al. 2004; Ulstrup et al. 2006; Berkelmans and van Oppen 2006; McClanahan et al. 2007b, c; Maynard et al. 2008).

Considering that bleaching events have only recently increased on the high-latitude reefs of southern Africa, there is limited knowledge on how environmental stress induces bleaching on these reefs and their potential resistance, adaptation and community change (McClanahan et al. 2007a; Celliers and Schleyer 2008; Sebastian et al. 2009). With an expected increase in warm-water anomalies (Hoegh-Guldberg 1999), it is pertinent that the interaction between environmental stress and ecological response be understood in order to inform management decisions. Furthermore, the potential of southern and high-latitude reefs as refugia from climate change (Precht and Aronson 2004; Greenstein and Pandolfi 2008; Maina et al. 2008) needs to be investigated (Sebastian et al. 2009).

The high-latitude reefs of South Africa constitute the southern limit of the geographic range of western Indian coral reefs (Sebastian et al. 2009). These reefs are located within the iSimangoliso Wetland Park (iSWP), a world heritage site that incorporates the St. Lucia and Maputoland Marine Protected Areas (MPA; Celliers and Schleyer 2008). South African reefs are not formed from typical biogenic accretion but rather form a thin veneer on Pleistocene sandstone (Celliers and Schleyer 2002). Although not accretive, the coral communities of South African reefs are rich in biodiversity for a high latitude reef (Riegl 1996; Schleyer 2000; Schleyer and Celliers 2005). South African coral communities are grouped into the northern, southern and central reef complexes. Given that the southern complex has sanctuary status (no usage) and the northern complex is isolated from tourist activities, the central complex reefs constitute the recreational diving hub of South Africa (Schleyer and Tomlin 2000).

Celliers and Schleyer (2008) therefore highlighted that the central reef complex at Sodwana Bay presents the highest risk of direct anthropogenic degradation and requires consistent and long-term management intervention and strategy. Although the reefs were not severely damaged by the 1998 mass bleaching event (Schleyer et al. 1999; Schleyer and Celliers 2000; McClanahan et al. 2007a), there is evidence that the frequency and intensity of bleaching events increased in the proceeding decade (Celliers and Schleyer 2002; Floros et al. 2004; McClanahan et al. 2007b). Therefore there is a need to understand both the natural and anthropogenic risks that the central reef complex faces.

In this study, the bleaching responses of corals in Sodwana Bay, South Africa, will be assessed for the period 2007 to 2013. The aim of this study is to determine the variability in taxon-specific bleaching response over time and between the two reefs, Two Mile reef and Nine Mile reef (hereafter referred to as TMR and NMR respectively). TMR is the focus of SCUBA diving activity in Sodwana Bay (86% of diving launched in 1996; Schleyer and Tomlin 2000) and Celliers and Schleyer (2008) suggest that management intervention is essential. In contrast, the distance of NMR from Jesser Point, the boat launch site, has acted as an unintentional management measure and has limited diving pressure. However both these reefs are susceptible to coral bleaching due to their shallow depth and community structure (Celliers and Schleyer 2008). Therefore a differential bleaching response between the reefs may indicate potential causes.

Methods and Materials

Study sites

The major reefs at Sodwana Bay are known as Two-Mile, Five-Mile, Seven-Mile and Nine-Mile Reef (TMR, FMR, SMR and NMR respectively) and are located along a distance of approximately 16.7km (Celliers and Schleyer 2008), between 27°23' S and 27°32'S. Reef names refer to their respective distances, in nautical miles, from Jesser Point, the boat launch site for dive-charters and recreational fishing vessels (Fig. 1; Celliers and Schleyer 2008). The reefs are approximately equidistant from the shore (700-900m). TMR (1.9km^2) is the largest reef in central complex with a range in depth of 6-10m on its shallowest pinnacles, 14-19m on deep subtidal reef flats and 24-27m at the edge of the fore-reef. NMR (0.6km^2) consists of shallow platforms 6-18m deep and steep drop-offs from 12 to 22m (Ramsay 1996; Riegl et al. 1995; Schleyer 2000). Sea-surface temperature ranges from 22° in winter to 26°C in Summer with a range in salinity of 35.0% to 35.5% (Schleyer and Celliers 2000).

Schleyer (2000) described the community structure of the Maputoland reefs, noting 93 species of Scleractinia, 39 Alcyonacea, 30 Ascidiacea and over 20 Porifera. The corals are predominantly Indo-Pacific, however some are endemic species to the Maputoland reef complex (Schleyer 2000). Sodwana Bay reefs conform to the topography of the base substratum and lack well defined zonation of true coral reefs. Community structure can be separated into reef tops, dominated by soft corals, and gully communities dominated by hard corals (Schleyer and Celliers 2000).

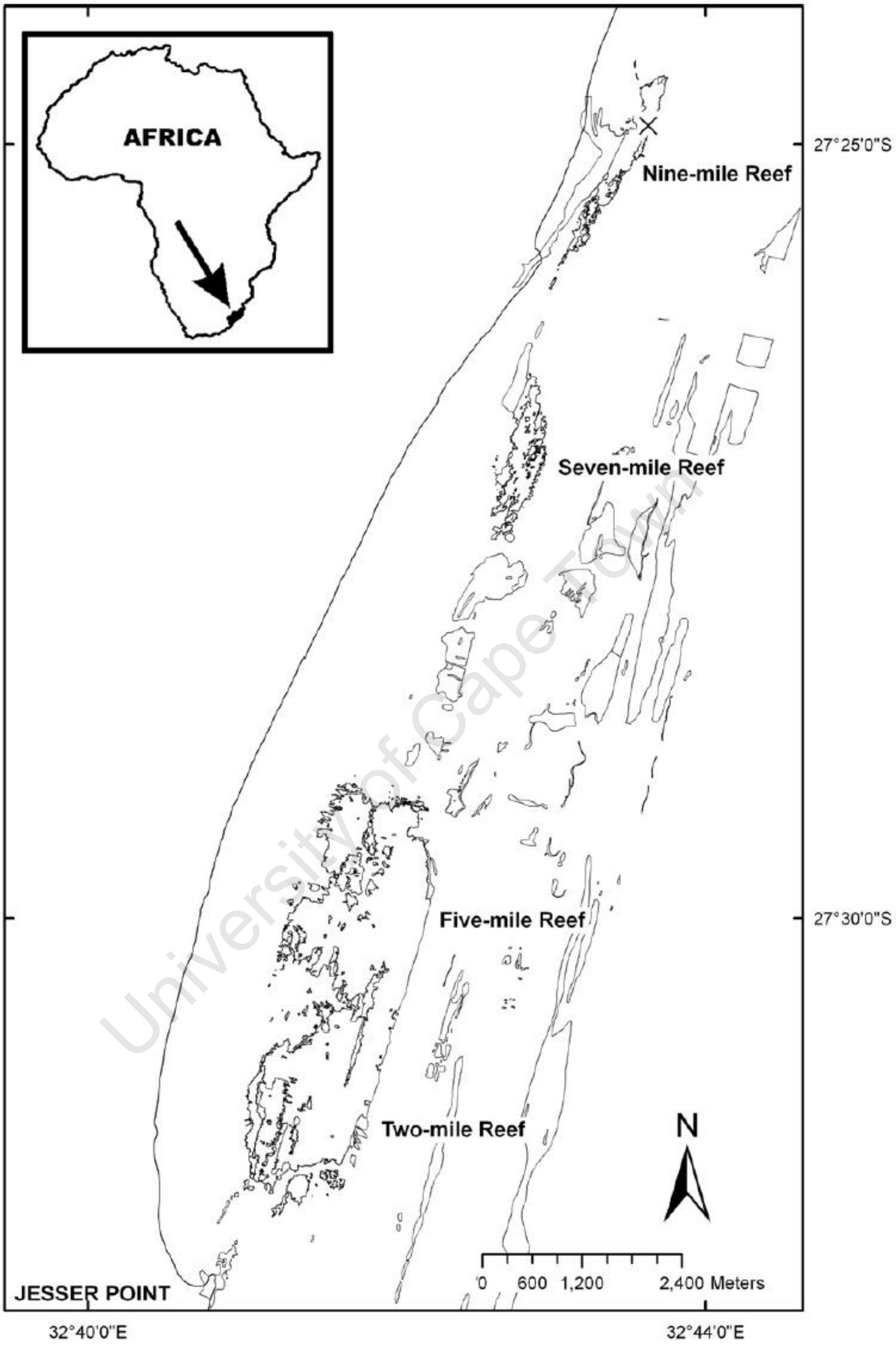


Figure 1. Map of the major reefs in the central complex at Sodwana Bay, South Africa (Celliers and Schleyer 2008)

Temperature data

On site seawater temperature values (°C) were continuously recorded from September 2005 to November 2012, at half hour intervals, by the Two Mile Reef temperature gauge (Star Oddi Starmon-mini). The gauge was located at a permanent site, 4 Bouy on TMR, at a depth of 12m. The bleaching threshold for coral colonies in Sodwana Bay has been estimated at 27.5 to 28.4 °C (Celliers and Schleyer 2002). The frequency of days between January and May in which mean daily temperature exceeded the minimum bleaching threshold (≥27°C) were plotted for 2005 to 2012. In addition, the frequency of days with a mean temperature ≥27.0°C (≥ 1°C above average summer maximum temperature; Schleyer and Celliers 2000) was plotted for the same period. This provided a snapshot of the thermal stress experienced in the months prior to and during bleaching surveys.

Data collection and calculation of bleaching response

Bleaching surveys were conducted at 16 sites in the central complex at Sodwana Bay, of which 7 sites were at TMR and 2 sites at NMR. These surveys were conducted during April and May for 2007 to 2013 (excluding 2009 and 2010). Sampling followed the peak temperature season in Sodwana Bay (January to March; Celliers and Schleyer 2002) when bleaching response is reportedly highest (Celliers and Schleyer 2002; McClanahan et al. 2007a; Sebastian et al. 2009). Observations in the field were conducted by SCUBA diving and the intensity of bleaching for coral colonies were recorded using the 7 category scale described in McClanahan et al. (2007a). This method involves randomly selecting coral colonies on the reef and categorizing them into 7 categories of coral bleaching, which allows for the scaling of bleaching by taxon and site (Gleason 1993, Edmunds et al. 2003, McClanahan 2004, Siebeck et al. 2006). Gleason (1993) originally proposed this method which was then modified by McClanahan et al. (2001) and tested between regions (McClanahan et al. 2004, McClanahan et al. 2009) and for differences between observers (Siebeck et al. 2006). In this study, all data were collected by a single observer (K. Sink).

The observer swam in randomly chosen directions and distances and periodically or randomly selected areas on the reef for sampling. All coral colonies in an approximately 2m radius were identified to the genus level and were assigned to one of 7 categories C_i of bleaching intensity: C_1 = normal (unbleached), C_2 = pale (lighter colour than usual), C_3 = 0-20% of live coral surface bleached, C_4 = 20-50%, C_5 = 50-80%, C_6 = 80-100% and C_7 =

recently dead. This random sampling was repeated at each site for approximately 40 minutes. The percentage of individual colonies per taxon in each category was calculated and the bleaching response (BR) for the site was calculated as a weighted average, and normalized with the formula:

$$\text{Bleaching response (BR)} = (0\%f_{C1} + 1\%f_{C2} + 2\%f_{C3} + 3\%f_{C4} + 4\%f_{C5} + 5\%f_{C6} + 6\%f_{C7}) / 6 \quad \text{(Eq.1)}$$

where c_i is a category of bleaching; f_{Ci} is the frequency of colonies in category C_i and $\%f_{Ci}$ is the relative percentage of coral colonies in category C_i. Taxon-specific BR was calculating as weighted averages using the percentage of colonies in each category C_i of bleaching intensity (Eq. 1). BR therefore represents the proportion, as a percentage, of the live coral surface bleached and is comparable between taxa, sites, reefs and over time. Each site sampled resulted in taxon-specific BR for the respective taxa sampled. Although sampling effort was similar among sites, the number of coral colonies per taxon and per site varied. This was attributed to differences in the benthic communities among sites (Sebastian et al. 2009).

Data analyses

To investigate taxon-specific susceptibility to bleaching, mean taxon-specific bleaching responses were averaged using data from all sites, across all sampled years. Taxa were disqualified if less than 60 colonies were recorded over the sample period (McClanahan et al. 2007a). Taxon-specific BR did not follow a normal distribution. Therefore differences in taxon-specific BR were tested for significance based on a non-parametric Kruskal Wallis ANOVA model and Tukey test for honest significant differences (HSD) with unequal sample size. All statistical analyses were performed using *Statistica 11.0*. Taxon-specific relative abundances for the most susceptible taxa were calculated as the relative percentage of colobies sampled at a site. Differences in the relative abundances per taxon over time were tested for significance with a Kruskal Wallis ANOVA model and Tukey HSD test. The percentage of colonies bleached for the most susceptible taxa, calculated as the percentage of colonies per taxon that displayed bleaching ($C_3 – C_7$; Eq. 1) at a site, was averaged per year and tested for significant differences over time with a Kruskal Wallis ANOVA model and Tukey HSD test. Investigating differences in site-specific bleaching responses over time was not in the scope of this study.

To separate the effects of year, reef and taxon on bleaching response generalised linear models (GLMs) of the form:

$$BR = \beta_0 + \beta_1(\text{Year}) + \beta_2(\text{Reef}) + \beta_3(\text{Taxon}) + \beta_4(\text{Year:Reef}) + \beta_5(\text{Year:Taxon}) + \beta_6(\text{Reef:Taxon}) + \varepsilon'$$

were applied using R 3.0.1 (R Development Core Team, 2013). Only data from TMR and NMR were included in the GLM framework as these were the most frequently sampled reefs across all years. Site effect for TMR and NMR were not considered in the model framework as not all sites were sampled across all years. Only the nine most abundantly sampled taxa for TMR and NMR were used in the model framework. The sampling method resulted in a variable number of colonies sampled per taxon. Therefore the bleaching response per taxon was weighted by the number of coral colonies sampled per taxon, in each field observation.

Bleaching response (Eq.1) was converted to a proportion from 0 to 1 through a division of 100. The distribution of bleaching response, as a proportion, was assumed to be binomial and the logit function (McCullagh and Nelder 1995) was used. Explanatory variables and interaction terms were first evaluated based on minimizations of model deviance and Akaike's Information Criterion (AIC; Akaike, 1973) using a forward stepwise selection procedure (Swartzman et al., 1992; Ortiz and Arocha, 2004). An analysis of variance was applied to the GLMs and the 'F' statistic and its p-value were used to test significance of the variation explained compared to the preceding GLM model. Residual plots and a quantile-quantile plot were plotted for the final GLM to test for violation of the assumed binomial distribution.

A reference set was created to standardize the reef-specific BR of TMR and NMR, by fixing taxa to *Acanthastrea* (Year * Reef * *Acanthastrea*), and plotted over time. This allowed for the interpretation of reef BR trends overtime with the effect of taxon-specific BR removed. Similarly, a reference set was created per taxon to standardize taxon-specific BR, by fixing reef to TMR (e.g. Year * TMR * Taxon) , and plotted over time.

Results

Underwater temperature recordings

The frequency of days exceeding the minimum bleaching threshold (Celliers and Schleyer 2002) in 2006 were similar to 2007 and 2008 (Fig. 2), with a highest frequency of days exceeding 27.5°C and 27.0°C (≥ 1°C above mean summer maximum temperature) in 2005. The years 2009 to 2011 displayed an increasing trend in both days exceeding the bleaching minimum threshold and 27°C. No days exceeded the minimum bleaching threshold in 2012, however there were 13 days that exceeded a mean daily temperature of 27°C. In all years, mean daily temperatures exceeding both 27.5°C and 27.0°C only occurred during January to March, implying that no thermal anomalies occurred during the sampling months of April and May.

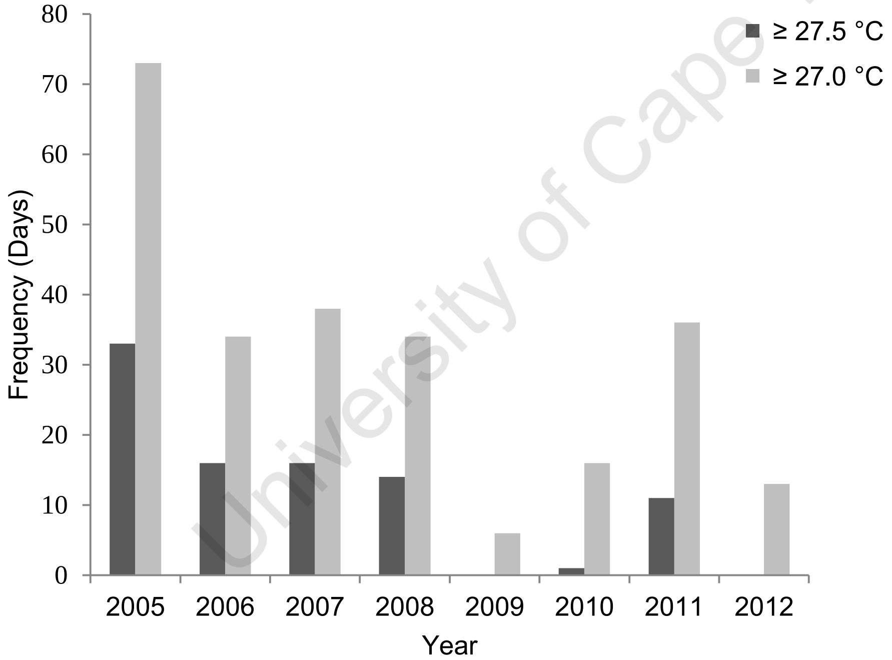


Figure 2. Frequency of days in January to May over 2005 to 2012, in which the daily mean temperature at TMR (4 Bouy site) exceeded the minimum bleaching threshold of 27.5 °C. The frequency of days exceeding a mean temperature of 27°C is also indicated.

Taxon-specific bleaching response

A total of 12 858 coral colonies were sampled over 2007 to 2013 (excluding 2009 and 2010) from 16 sites on 8 reefs in the central complex at Sodwana Bay (Table 1). Not all sites were sampled in all years and the number of colonies sampled per year for a site ranged from 125 to 691 colonies, with a mean sample size of 292 ± 101 (SD) colonies per site. The mean number of total colonies sampled per site in all years was 804 ± 409 (SD) colonies. A total of 30 taxa were sampled during the bleach surveys with a variable sample size per year (Table 2). Taxa with less than 60 colonies sampled across the sample period were disqualified, resulting in only 20 taxa being considered for taxon-specific BR analyses. The ten most abundantly sampled taxa over the study period were *Acropora* (N = 3211), *Pocillopora* (N = 1569), *Favites* (N = 1123), *Favia* (N = 1093), *Montipora* (N = 750), *Platygyra* (N = 726), *Acanthastrea* (N = 602), *Galaxea* (N = 563), *Echinopora* (N =424), *Porites* (N = 314). The percentage of colonies bleached in 2007, 2008, 2011, 2012 and 2013 were 37.4%, 17.4%, 23.8%, 33.6%, 38.8% respectively.

Table 1. Summary of the number of coral colonies sampled per year during bleach surveys at 16 sites in Sodwana Bay.

Reef	**Site**	**2007**	**2008**	**2011**	**2012**	**2013**	**Total**
Two Mile	4 Bouy	152	219	312		254	937
	Anton's	163	235	485		263	1146
	Chain	313		208	252	356	1129
	Coral Gardens	410	283	265	256	260	1474
	Wayne's World North	223	217	300		256	996
	Wayne's World South	210		230			440
	Stringer	125					125
Four Mile	Four Mile Reef			393			393
Five Mile	Five Mile				245		245
Seven Mile	Seven Mile			346	329	314	989
Eight Mile	Ramsey's	325		302			627
Nine Mile	Nine Mile Shallow	388	202	369		236	1195
	Nine Mile Deep	205			691	259	1155
Rabbit	Rabbit				256	256	512
Saxon Complex	Saxon North					375	375
	Tridacna			511	337	272	1120
Total per year		**2514**	**1156**	**3721**	**2366**	**3101**	**12858**

Table 2. Summary of colonies sampled per taxon during bleach surveys at 16 sites in Sodwana Bay over 2007 to 2013. NS = Total number of contributing sites over sample period. Disqualified taxa are in bold.

Taxon	NS	2007	2008	2011	2012	2013	Total (N= 12 858)
Acropora	47	475	197	898	643	998	3211
Pocillopora	47	242	172	443	236	476	1569
Favites	47	223	66	228	280	326	1123
Favia	47	242	76	211	256	308	1093
Montipora	47	222	78	190	95	165	750
Platygyra	47	147	86	200	163	130	726
Acanthastrea	46	183	56	130	123	110	602
Galaxea	45	113	106	123	108	113	563
Echinopora	43	91	48	111	91	83	424
Porites	42	76	43	81	35	79	314
Anomastrea	43	98	46	74	54	41	313
Coscinaraea	40	101	19	62	60	59	301
Astreopora	37	56	39	64	30	65	254
Echinophyllia	28	18	17	39	63	18	155
Oulophyllia	39	31	22	31	30	32	146
Hydnophora	30	14	23	37	28	18	120
Goniopora	31	42	11	27	4	4	88
Turbinaria	26	14	10	13	19	16	72
Alveopora	26	23	5	19	8	9	64
Gyrosmilia	27	34	10	11	7	2	64
Gardineroseris	**22**	**12**	**9**	**11**	**5**	**14**	**51**
Goniastrea	**25**	**5**	**3**	**18**	**8**	**14**	**48**
Symphyllia	**19**	**20**	**6**	**8**	**6**	**7**	**47**
Fungia	**14**	**13**	**0**	**4**	**11**	**8**	**36**
Seriatopora	**8**	**9**	**4**		**1**	**5**	**19**
Pavona	**8**	**1**	**0**	**8**	**1**	**1**	**11**
Coeloseris	**3**	**6**	**3**				**9**
Psammocora	**3**	**3**	**1**				**4**
Cyphastrea	**2**			**1**	**1**		**2**
Stylophora	**1**			**1**			**1**

A Kruskal-Wallis ANOVA showed significant variation among mean taxon-specific BR averaged across all years (H=313.13, N=785, p <0.001). The most susceptible taxa were *Coscinaraea*, *Montipora*, *Anomastrea* and *Astreopora* (in decreasing order of susceptibility, Fig. 3). These taxa had a significantly higher BR than other taxa sampled in this study (p < 0.05). The respective mean relative abundances (%) of the most susceptible taxa identified above were not significantly different overtime (Fig. 4). There was significant variation in the percentage of colonies bleached among years for *Coscinaraea* (H = 16.84, d.f.= 4, N = 40, p = 0.002), *Anomastrea* (H = 15.33, d.f.= 4, N = 43, p = 0.004) and *Astreopora* (H = 10.15, d.f. = 4, N = 37, p = 0.038) (Fig. 5). The percentage of colonies bleached for *Montipora* ranged between 50 to 78% bleached, but was not significantly different over time (H = 8.92, d.f. = 4, N = 47, p = 0.063). Between 60 and 80% of *Coscinaraea*, *Anomastrea* and *Astreopora* colonies bleached in 2007, with a lower percentage of colonies bleaching in 2008 (Fig. 5). Thereafter it appears that there is an increasing trend in the percentage of colonies bleaching for these taxa. However a post hoc Tukey test showed that no individual years were significantly different.

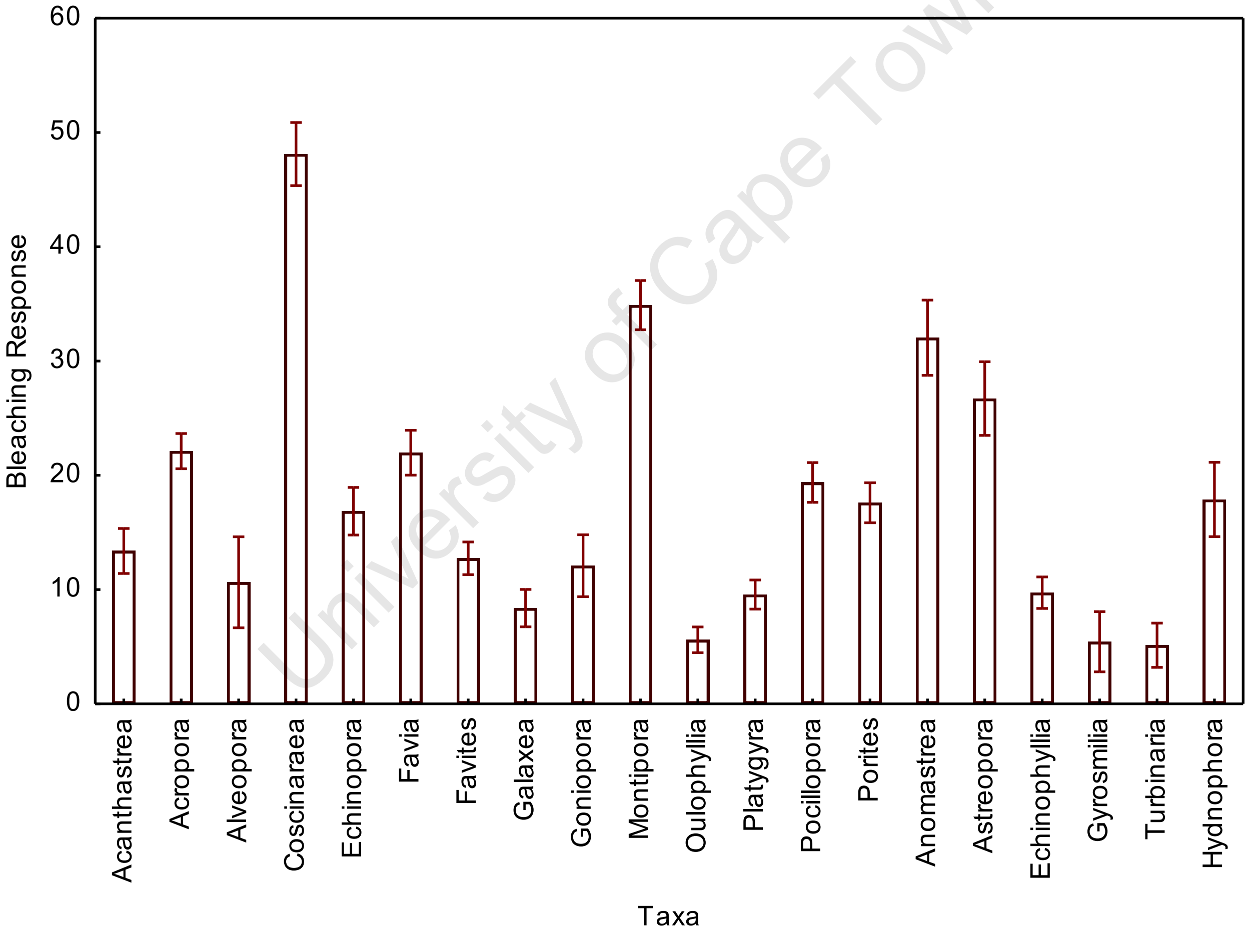


Figure 3. Mean taxon-specific bleaching response (±se) for Sodwana Bay averaged over the sampled period for all sites

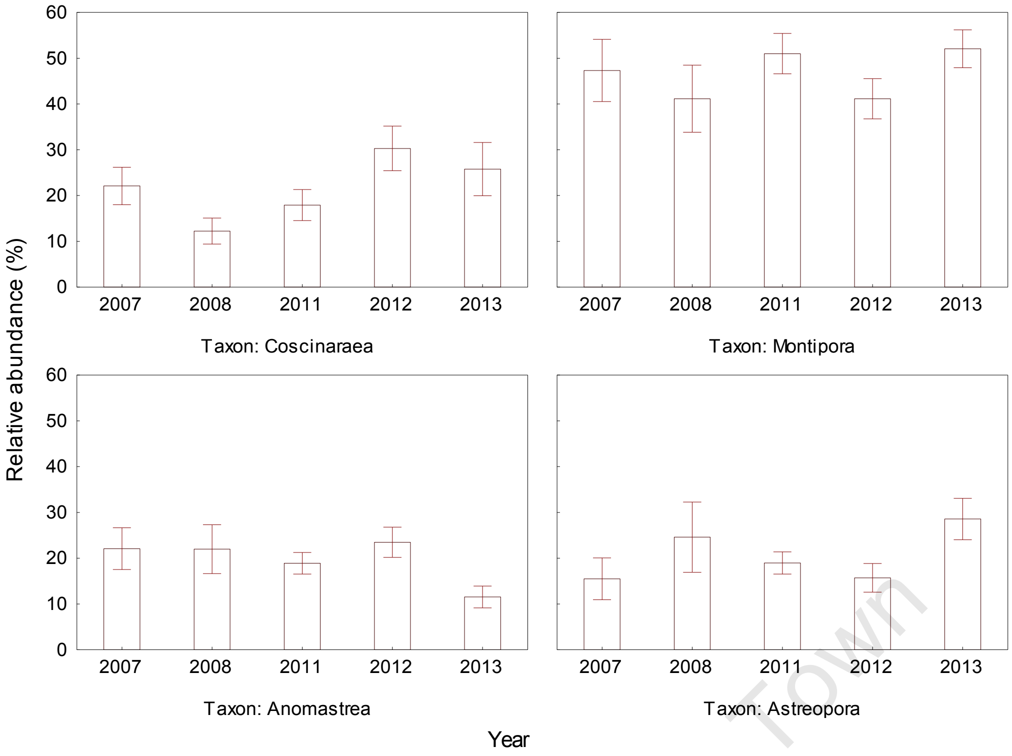


Figure 4. Mean relative abundance (%; ±se) for the most susceptible taxa (*Coscinaraea* , *Montipora, Anomastrea, Astreopora*) in Sodwana Bay over 2007 to 2013.

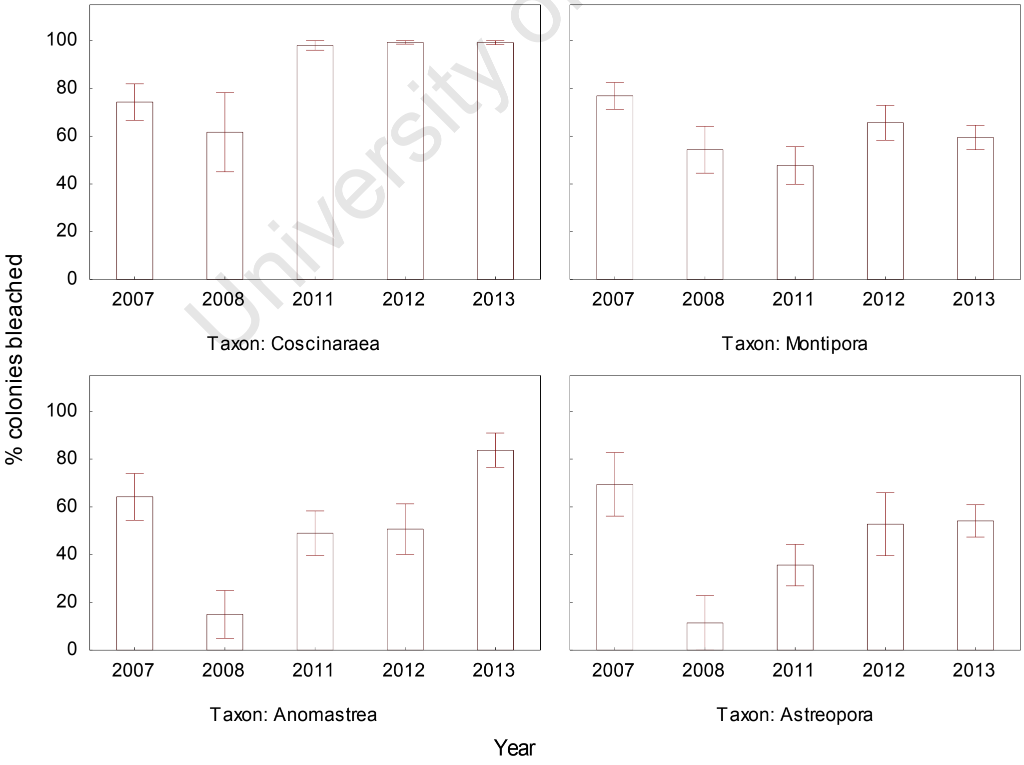


Figure 5. Mean percentage of colonies bleached (±se) per year for the most susceptible taxa sampled in Sodwana Bay.

The GLM framework incorporated a total of 6758 coral colonies from the nine most abundantly sampled taxa sampled from 7 sites on TMR and 2 sites on NMR sampled over 2007 to 2013 (excluding 2009 and 2010, Table 3, Table 1). The forward stepwise selection procedure found that all explanatory variables and interaction terms, except reef and reef:taxa, explained a significant amount of variation in the data (taxa > year:taxa > year > year:reef) and resulted in reductions of AIC. (Table 2). The final GLM explained a substantial amount of variation in the data ($R^2 = 0.64$) and had the form:

$$BR = \beta_0 + \beta_1(\text{Year}) + \beta_2(\text{Reef}) + \beta_3(\text{Taxon}) + \beta_4(\text{Year:Reef}) + \beta_5(\text{Year:Taxa})$$

Residual plots and the quantile-quantile plot indicated no violation of the assumed binomial error model (Fig. 6).

Table 3. Summary of the most abundantly sampled coral colonies at TMR and NMR incorporated in the GLM framework (N = 6758).

	2007	2008	2011	2012	2013	Total
Nine Mile Reef	496	172	259	594	459	1980
Acanthastrea	54	22	18	43	24	161
Acropora	156	37	77	176	217	663
Echinopora	11	5	19	34	16	85
Favia	82	18	12	68	47	227
Favites	80	26	18	101	32	257
Galaxea	9	8	13	21	19	70
Montipora	30	5	5	18	12	70
Platygyra	36	17	22	40	13	128
Pocillopora	38	34	75	93	79	319
Two Mile Reef	1181	713	1271	413	1200	4778
Acanthastrea	101	34	56	14	28	233
Acropora	244	160	380	104	424	1312
Echinopora	58	43	35	16	38	190
Favia	132	58	99	50	103	442
Favites	116	40	106	29	81	372
Galaxea	88	98	69	37	76	368
Montipora	160	73	123	33	89	478
Platygyra	98	69	108	42	61	378
Pocillopora	184	138	295	88	300	1005
Total	1677	885	1530	1007	1659	6758

Table 4. Summary statistics of binomial GLMs (link = logit) fitted to the bleaching response of coral colonies sampled on TMR and NMR in Sodwana Bay. Δ AIC is the difference in the AIC compared to the preceding model. Δ Deviance is the difference in deviance explained compared to the preceding model.

Model structure	Residual d.f.	Residual Deviance	Δ Deviance	% deviance explained	Cumulative % dev. Explained	R^2	F	P value	AIC	Δ AIC
Null	294	654.1							1353.76	
+Year	290	576.4	77.6	11.9	11.9	0.12	19.41	<0.001	1284.12	-69.641
+Reef	289	576.4	0.1	0	11.9	0.12	0.05	0.82	1286.07	1.948
+Taxa	281	340.9	235.5	40.9	52.8	0.48	29.44	<0.001	1066.58	-219.5
+Year:Reef	277	313.3	27.5	8.1	60.9	0.52	6.88	<0.001	1047.05	-19.53
+Year:Taxa	245	237.8	75.5	24.1	85	0.64	2.36	<0.001	1035.51	-11.531
+Reef:Taxa	237	225.1	12.7	5.3	90.3	0.66	1.59	0.12	1038.8	3.285

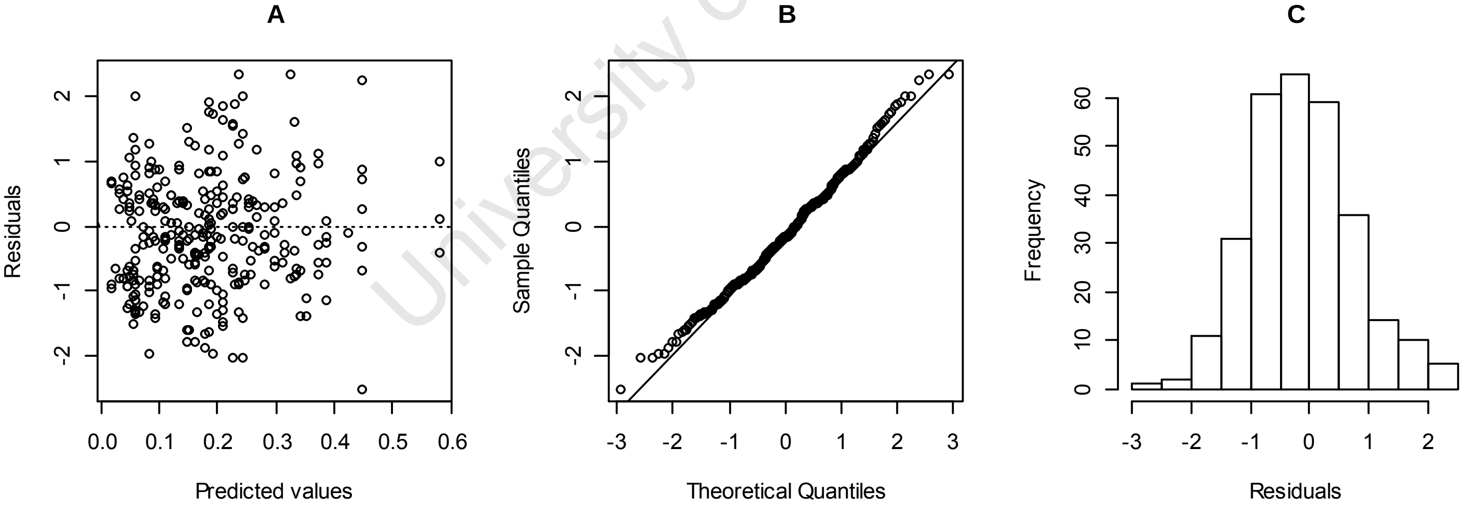


Figure 6. Residual scatterplot (A), quantile-quantile plot (B) and frequency distribution of residuals (C) of final GLM fitted to bleaching response of coral colonies in Sodwana Bay.

Standardized bleaching response for TMR and NMR followed the same trends over time (Fig. 7) with bleaching response ranging between 4.6 % and 28%. BR was highest in 2007 followed by a low BR in 2008. BR in 2011 was similar to that of 2008 and increased in 2012, followed by a decrease in 2013. Standard error bars are large for all years indicating that interpretations of bleaching response over time should be approached with caution.

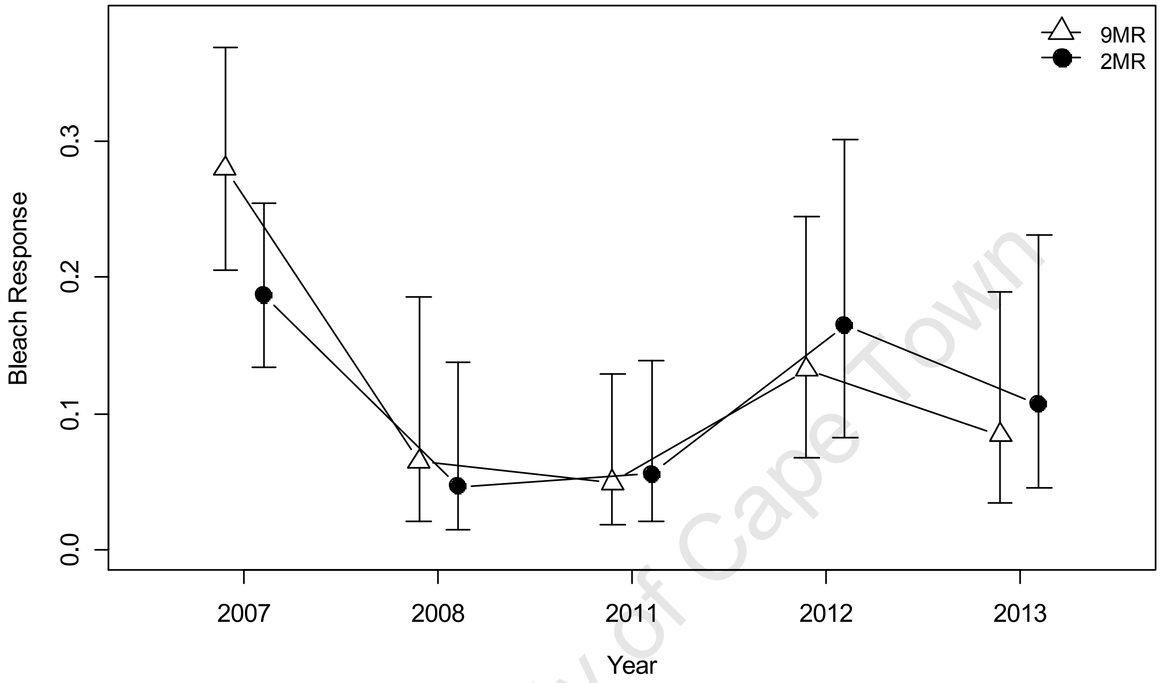
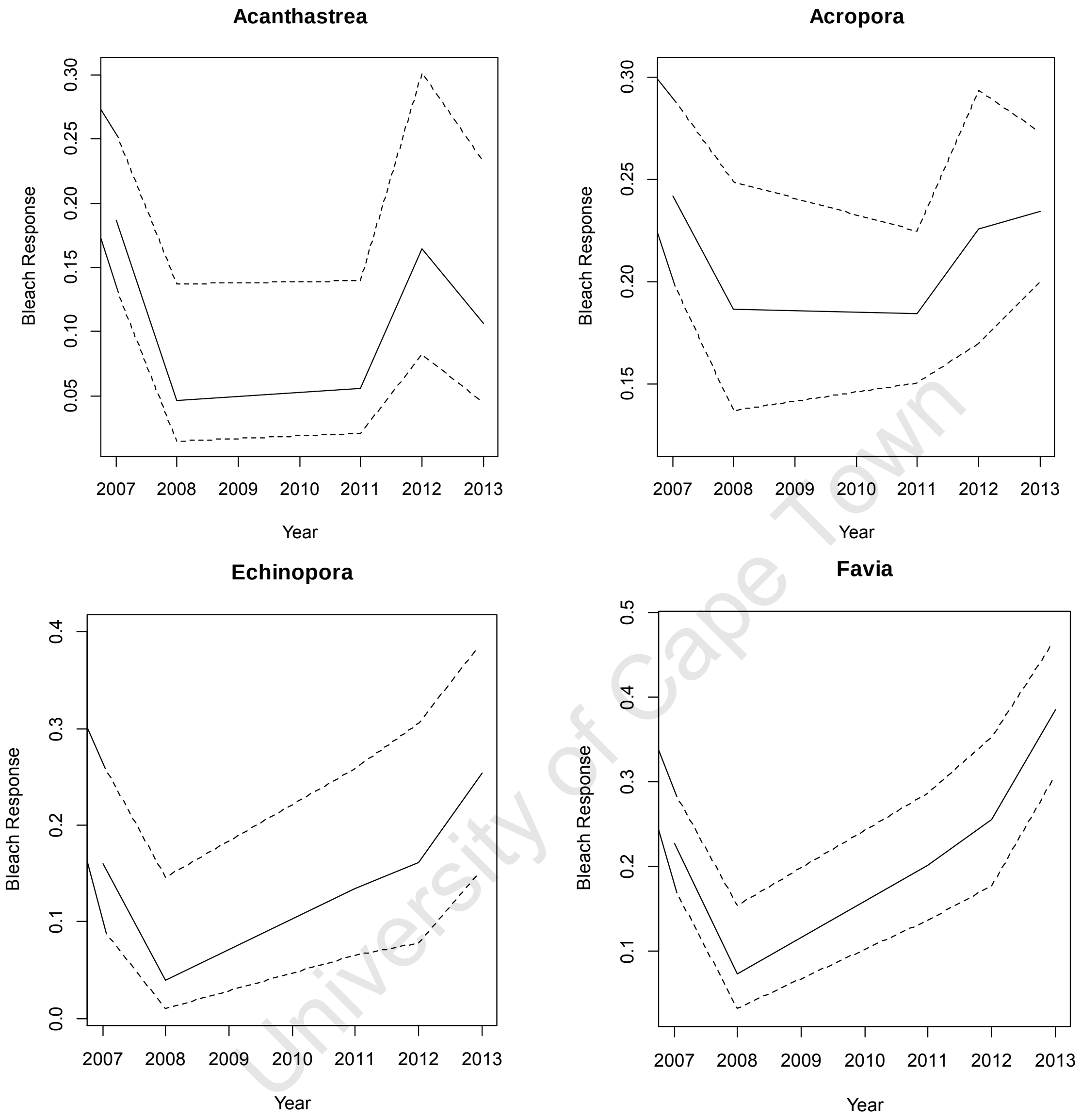


Figure 7. Mean reef-specific bleaching response (±se) for TMR and NMR standardized for taxon-specific effects and plotted over time.

Standardized taxon specific bleaching responses indicated variability in bleaching susceptability over time and between taxa (Fig. 8). Taxon specific bleaching responses ranged between 2.5 and 45% of live coral surface bleached. All taxa exhibited a higher bleaching response in 2007 (*Montipora* > *Acropora* > *Favia* > *Acanthastria* > *Favites* > *Echinopora* > *Pocillopora* > *Platygyra* > *Galaxea*) with a decrease in bleaching response in 2008, except for *Pocillopora* which showed an increase in 2008. Data were unavailable for 2009 and 2010 and therefore inferences about the bleaching response in these years cannot be made. All taxa exhibited an increase in bleaching response from 2011 to 2012, except for *Pocillopora* which showed the same bleaching response in both 2011 and 2012. *Acanthastrea* and *Favites* showed a decrease in bleaching response from 2012 to 2013, with the bleaching response of *Galaxea* remaining relatively the same. *Montipora*, *Acropora*, *Favia*, *Echinopora*, *Platygyra* and *Pocillopora* displayed an increasing trend in bleach response from 2012 to 2013 (*Favia* > *Montipora* > *Pocillopora* > *Acropora* > *Echinopora* > *Platygyra*).



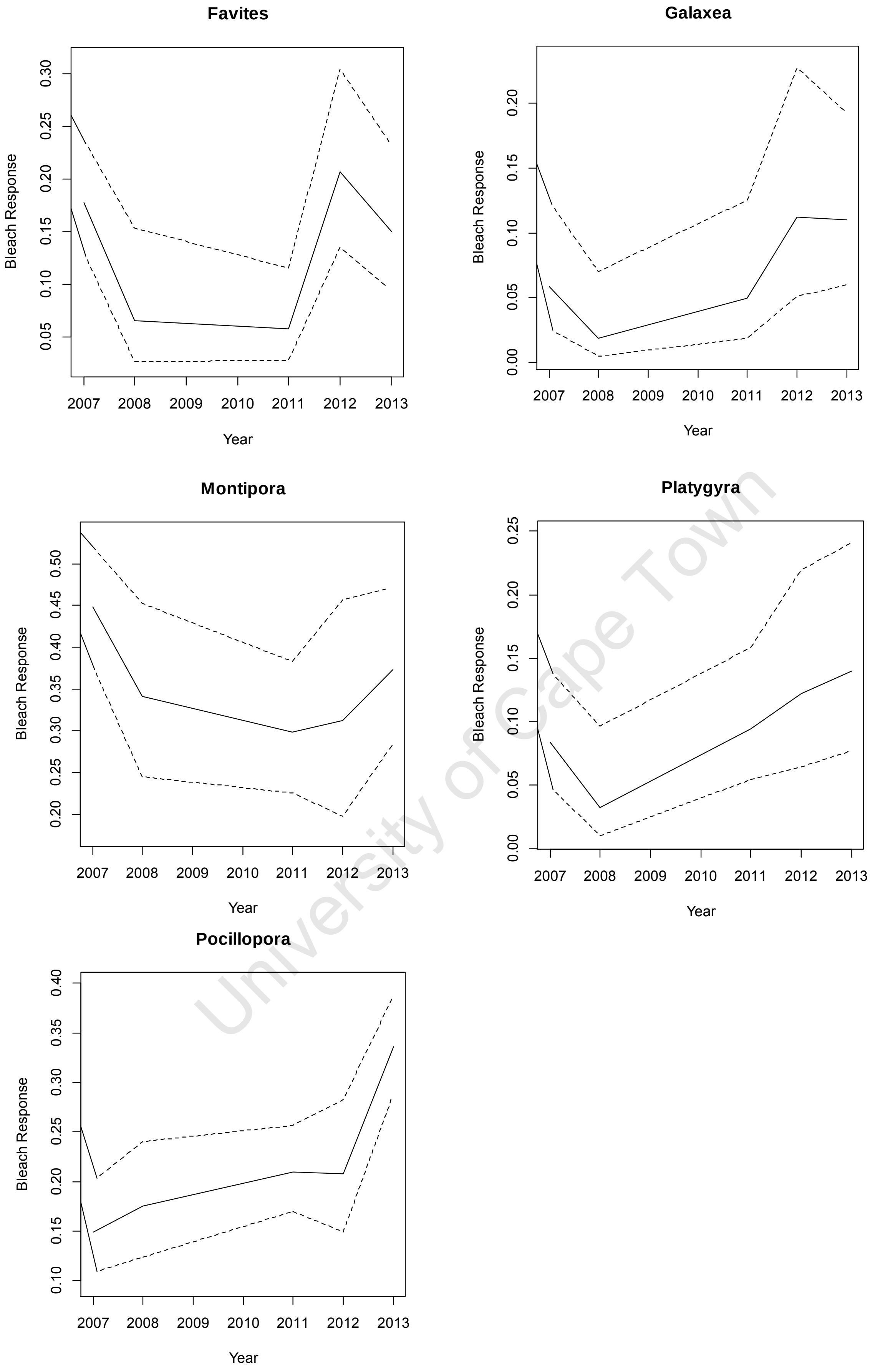


Figure 8. Taxon specific bleach response (±se), standardized for reef, and plotted over time for the nine most abundantly sampled taxa at TMR and NMR.

Discussion

This study provided a temporal analysis of the bleaching responses (BR) of coral communities in Sodwana Bay over the period of 2007 to 2013. Previous studies identified relatively minor bleaching responses in southern African reefs in 1998, 2000 and 2002 (Celliers 2000; Celliers and Schleyer 2002; Floros et al. 2004). However the warm water anomaly of 2005 resulted in unprecedented bleaching in Sodwana Bay (approximately 39% of coral cover bleached; Sebastian et al. 2009). The percentage of coral cover affected by bleaching over 2007 to 2013 was similar to the high bleaching in 2005 (38.8 % of coral cover bleached). Therefore the high BR in 2007 and the overall trend in BR from 2011 to 2013 further support evidence from previous studies that bleaching in South African reefs is increasing in frequency and intensity (Celliers and Schleyer 2002; Floros et al. 2004; McClanahan et al. 2007b).

Spatial variation in coral assemblage BR has been linked to taxonomic composition of reef sites and their bleaching history (Marshall and Baird 2000). However it was not in the scope of this study to assess site-specific differences in BR over time but rather focus on the most abundantly sampled reefs, TMR and NMR. Through a GLM model framework, this study was able to separate the effects of year, reef and taxa on the variability observed in bleaching response over the sample period. This allowed for the standardization of reef-specific and taxon-specific temporal trends in BR. Sebastian et al. (2009) noted that differences in taxon-specific BR would likely affect trends in reef-specific BR when coral communities differ between reefs. By only including the most abundantly sampled taxa for both reefs and weighting taxon-specific BR by the number of colonies sampled in each field observation, the potential bias of taxon-specific BR and unequal sample size were overcome.

The GLM model framework showed that variation in bleaching response over time in Sodwana Bay is predominantly explained by taxon-specific responses and annual effects. Previous studies that have quantified bleaching response with the same method (McClanahan et al. 2007a) have reported similar results (Marshall and Baird 2000; McClanahan et al. 2007a; Sebastian et al. 2009). In addition, reef effect was not significant which suggests that diving pressure, and associated diving-related coral damage (Schleyer and Tomlin 2000), has not resulted in an increased bleaching response of TMR.

This is of particular interest as diving pressure has been identified as a major local threat to reefs in the central complex at Sodwana Bay (Celliers and Schleyer 2002; 2008). Celliers and Schleyer (2008) reported similar coral communities on NMR and TMR. This implies that the model did not remove reef-specific taxa that might otherwise result in differences in reef-specific BR.

Warm water anomalies (particularly those exceeding the summer maximum by 1°C) are considered the primary cause for coral bleaching, although bleaching is also linked to solar radiation and coral-algal symbionts (Hoegh-Guldberg 1999; Fitt et al. 2001; Celliers and Schleyer 2002). Standardized trends in reef BR over time, through fixing taxon-specific BR, indicated periods of high and low BR. The large number of days in 2007 that exceeded the minimum bleaching threshold for Sodwana Bay reefs explains the high BR in this year. However 2008 experienced similar temperature anomalies but was characterized by a substantially lower bleaching response. Similarly 2011 experienced a high frequency of days exceeding the minimum bleaching threshold but was characterized by a low bleaching response.

Riegl (2003) proposed that local, small-scale upwelling events during the summer months act as a possible mechanism for reducing bleaching in Sodwana Bay. Reduced risk of bleaching is suggested to occur in one of two ways: the mixing of deep cooler waters with warm surface waters reduces the magnitude and duration of thermal stress on corals; or indirectly through thermal fluctuations that result in corals developing thermal tolerance over time (Salm et al. 2001; McClanahan et al. 2007b). In contrast, it has been hypothesized that acclimatization to upwelling has lowered thermal thresholds, making corals more susceptible to bleaching during anomalous warm water events ((D’Croz et al. 2001; D’Croz and Maté 2004; Sebastian et al. 2009). Therefore small scale upwelling events may have buffered the thermal stress observed in 2008 and 2011, resulted in the lower BR in these years.

Although no days in 2012 exceeded the bleaching threshold in Sodwana Bay, this year experienced higher bleaching than the previous year. A similar trend in Sodwana Bay was observed in 2000 (Celliers and Schleyer 2002), in which non-symptomatic bleaching was suggested to have occurred during 1999, resulting in more severe bleaching in 2000 despite lower thermal stress. Therefore non-symptomatic loss of algal symbionts in 2011 may have rendered corals more susceptible to lower levels of thermal stress (≥ 27.0°C) in 2012, resulting in a higher bleaching response. Bleaching responses on Kenyan reefs were best explained when past bleaching, community structure and thermal stress were considered (McClanahan et al. 2007c). The model framework standardized for community structure and therefore this study suggests past bleaching and thermal stress provide the best explanation for the trends in BR in Sodwana Bay.

Taxon-specific bleaching response

Differences in taxon specific bleaching response have been reported in previous studies and have been linked to growth form and algal symbionts (Hoegh-Guldberg and Salvat 1995; Marshall and Baird 2000; McClanahan et al. 2004; Sebastian et al. 2009). However taxon-specific differences in bleaching responses of Sodwana Bay corals are unrelated to different clades of algal symbionts (Sebastian et al. 2009). There is a predominance of putatively thermal-sensitive *Symbiodinium,* clade C, in southern Africa (Sebastian et al. 2009). This may reflect the limited bleaching experienced in these reefs and suggests that these reefs are vulnerable to mild thermal stress. Therefore Sebastian et al. (2009) concluded that diverse thermal tolerance, thermal acclimatization and the morphology of the host colony influence bleaching response of coral colonies in Sodwana Bay. Coral morphology is generally described as branching, encrusting, massive or submassive (McClanahan 2004). Fast growing branching and encrusting corals have been noted as the most susceptible growth forms to bleaching (Baker 2004, Marshall and Baird 2000), although this study identified variability in bleaching susceptibility both among and within growth forms.

Fast-growing, short-lived plate and branching *Montipora* spp. have been reported as highly susceptible (Marshall and Baird 2000, Celliers and Schleyer 2002), which corresponds to both the mean taxon-specific BR for *Montipora* and GLM standardized BR for this taxon. *Coscinaraea, Anomastrea and Astreopora* have not previously been identified as highly susceptible to bleaching, although *Astreopora* has been noted as having reduced potential mortality from loss of symbionts (McClanahan 2004). The significant increase in the percentage of colonies bleached for *Coscinaraea, Anomastrea and Astreopora* suggests an increasing susceptibility to bleaching over 2007 to 2013, explaining why previous studies did not report them as highly susceptible. Although the relative abundances of these taxa did not show any significant trends over time, this can be attributed to differences in the coral assemblages at the sampled sites.

Standardized taxon-specific BR of branching *Acropora* and *Pocillopora* observed in this study correspond to high levels of bleaching previously reported for these taxa (McClanahan et al. 2007a; Sebastian et al. 2009). Encrusting *Acanthastrea* did not experience severe bleaching over time, however encrusting *Echinopora* and *Montipora* were highly susceptible. Similar differences occurred within the massive and submassive growth forms as *Galaxea* and *Platygyra* were the least susceptible to bleaching and contrasted *Favia*, a submassive taxon that experienced the highest standardized taxon-specific BR in 2013. This study however did not record the exact growth form of individual colonies sampled and growth form inferences should be made with caution.

Future monitoring

McClanahan et al (2007a) noted that taxa with high bleaching responses and low abundances are those with the highest chance of regional extirpation. Under-sampling of rare taxa was unavoidable with the bleaching response method used in this study which and is likely a result of site-specific variables (McClanahan et al. 2007a). In addition, the method used was based on a few assumptions: bleaching is proportional to mortality and that the genus response reflects species response. These assumptions are challenged by previous studies (Vermeij 1993; Baker et al. 2004; McClanahan 2004). Although analyses of common genera has shown that bleaching often leads to mortality as a result of warm water anomalies, *Astreopora, Favia and Favites* are taxa shown to bleach but not die. In addition, taxa such as *Cyphastrea* have been shown to minimally bleach but die in response to warm water events (McClanahan 2004).

Therefore future monitoring should involve sufficient sampling of rare taxa to establish their long term susceptibility to bleaching. Assessing site-specific bleaching responses at Sodwana Bay was not in the scope of this paper as not all sites were sampled across all years. Future management efforts need to prioritize consistent sampling at all sites, across all years to establish site-specific time series of bleaching response. This will assist in identifying the most susceptible sites to environmental stress and inform management. Current reports assessing coral assemblages have identified stable and diverse reefs, such as Five Mile, Four Mile, Nine Mile and Two Mile Reef as susceptible to degradation and bleaching (Celliers and Schleyer 2008). Therefore sites on these reefs should be prioritized first if resources restrict consistent bleach surveys.

Bleaching has been significantly correlated with depth and algal symbionts in coral reefs in the Caribbean (Baker 1999), although depth was not found to be significant in the case of Sodwana Bay corals (Sebastian et al. 2009). Depth was not included in this study as only site estimates of depth were available and did not reflect the actual depth of sampling. Future monitoring should record the specific depth at which each colony is sampled in order to investigate depth more accurately. This is easily achieved through the use of dive computers worn by most SCUBA divers.

Colonies categorized as recently dead may not reflect true mortality as dead corals become smothered with algae within 2 weeks of dying, and are therefore overlooked by the current method (McClanahan et al. 2007a). "Silent" effects of thermal stress in Sodwana Bay have only recently been assessed using fixed transects on NMR (Schleyer and Celliers 2008). These include the remarkable diminishment of recruitment up to 2004, which has since improved, and the increase in hard coral cover following the reduction in soft coral cover. This emphasizes the need for fixed transects at TMR, as well as other sites in Sodwana Bay, to assess changes in community structure, species diversity and recruitment.

Although diving pressure at TMR appears to have not increased coral bleaching it may have resulted in degradation of reef health in other ways such as organic pollution. Fixed transects will allow for the investigation of coral-algal competition and alterations to reef composition over time. No major rivers lead into Sodwana Bay (Celliers and Schleyer 2008) and therefore levels of pollution have been largely overlooked. Therefore baseline studies into pollution levels need to be established to assess potential future impacts of pollution.

This study only assessed the bleaching response of scleractinian coral colonies and therefore conclusions about overall reef health should be made with caution, as Sodwana Bay is soft coral dominated (Schleyer et al. 2002). Personal field observations (K. Sink) noted bleaching and deterioration of soft coral colonies on TMR and NMR, although the method of quantifying bleaching (McClanahan et al. 2007a) does not extend to the assessment of soft corals. Therefore future bleaching surveys conducted on Sodwana Bay reefs should include the assessment of soft corals, with an appropriate method for quantifying soft coral bleaching response. Personal observations (K. Sink) also noted visible reductions in the abundance of photosynthesizing *Tridacna* clams on Tridacna reef over time, a northern reef in Sodwana aptly named for its abundance of *Tridacna* clams. Therefore future monitoring needs to investigate the apparent loss of these clams on the northern reefs in the central complex.

Celliers and Schleyer (2002) noted that the prevalence of coral disease on bleached colonies was higher than unbleached colonies in Sodwana Bay, although disease was not considered the putative cause of bleaching. Coral disease needs to be measured in conjunction with bleaching response to better represent coral colony health. Although declining aragonite saturation, through ocean acidification, has been identified as a major threat to coral reefs globally (Kleypas and Langdon 2006; Hoegh-Guldberg 2007; Knoll et al. 2008), pH has not been recorded and reported on for Sodwana Bay in previous literature. Future monitoring efforts need to prioritize the recording and evaluation of pH in Sodwana Bay. Hoegh-Guldberg (2007) highlighted that the synergistic impacts of temperature increases and declining pH on reefs will impact reef rugosity, species diversity, community structure and coral cover. Future monitoring should record and evaluate pH in Sodwana Bay in conjunction with temperature to establish synergistic impacts in Sodwana Bay over time.

Although small-scale upwelling events during the warmest months contribute to reducing thermal stress, exposure to cold water during intense upwelling and rapid rises after the upwelling subsides may play a significant role in the accumulation of environmental stress. Fine scale temperature data is therefore necessary to evaluate cold stress, caused by upwelling; heat shock, from rapid increases in temperature; and heat stress caused by persistent above-average temperatures (Sebastian et al. 2009).

Long term predictions of TMR and NMR response to climate change presents a challenge as the region experiences episodic fluctuations in water temperature (Sebastian et al. 2009) as well as the potential effects of upwelling, differential taxon-specific bleaching response and differences in symbiont communities. Although these reefs did not experience major bleaching responses in the past, this study and other recent studies draw attention to a trend of either episodic or an increasing frequency and intensity of bleaching. The refugia potentially created by upwelling (Riegl and Piller 2003) could also be reduced if the intensity of upwelling increases through climate change and results in lower temperatures or changes that are faster than tolerable by corals.

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