



# Changes in coral sensitivity to thermal anomalies

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**ABSTRACT:** The 1998 and 2016 thermal anomalies were among the 2 most severe global-scale anomalies in recent history, with broad-scale impacts on reef condition. In 2 Kenyan fully protected national park reef lagoons, the water flow, light, and temperature exposure severity of these 2 events was grossly similar at  $7.3 \text{ cm s}^{-1}$ ,  $\sim 50 \text{ Einsteins m}^{-2} \text{ d}^{-1}$  and  $\sim 85$  degree-days above summer baseline. Yet, despite similarities in the coral communities' metrics over this time, the bleaching responses were diminished considerably across this 17 yr period. For example, the numbers of pale and bleached colonies declined from 73 to 27% and from 96 to 60% in the low and high thermal exposure reefs, respectively. A metric that weights bleaching by the intensity of the response and the number of individuals of each taxon also found a decline from 35 to 10% and from 65 to 33%. Of the 21 most common coral taxa, 11, including major contributors to coral cover such as *Porites* and *Acropora*, showed declines in their sensitivity. Ten taxa, including *Montipora* and *Pocillopora*, showed either little or weak evidence for change in sensitivity, and 1 taxon, *Acanthastrea*, was more sensitive to the exposure in 2016 than in 1998. Sampling limitations and qualitative differences in the pre-peak temperature conditions did not allow separating the influences of genetic adaptation, acclimatization, and community change.

**KEY WORDS:** Africa · Climate change · El Niño Southern Oscillation · ENSO · Indian Ocean · Stress · Time series · Vulnerability

## INTRODUCTION

Climate change and the associated warmer and more extreme sea surface temperatures (SSTs) are threatening the future of coral reefs (Hoegh-Guldberg et al. 2007, Hughes et al. 2017). Many reef corals reduce their symbiotic algae as a response to abnormally warm temperatures. This 'bleaching' phenomenon has been described as a stress response that precedes death but may also be an adaptation that reduces light absorption, host heat stress, and death (Buddemeier et al. 2004). Both resistance and death responses have been observed, but, regardless of the outcomes, the bleaching response reflects the intensity of environmental radiation exposure and remains a key metric for evaluating coral sensitivity (Brown et al. 2002, McClanahan 2004, Pratchett et al. 2013). How corals are changing and potentially

adapting to high thermal exposure events is key for predicting the future of corals and identifying their management needs (Edmunds & Gates 2008, Veron et al. 2009, Edmunds et al. 2014).

Future coral reef projection models with temperature rise and anomalies find that reef functions of coral growth and recruitment rates will decline as mortality increases (Hoegh-Guldberg 1999, Sheppard 2003, Donner et al. 2005, van Hooidonk & Huber 2012, Frieler et al. 2013, Logan et al. 2014). While environmental exposure influences and their rates of change are frequently measured, the rates at which corals respond are less well known (Brown et al. 2002, Baker et al. 2004, McClanahan et al. 2005, Middlebrook et al. 2008, Bellantuono et al. 2012, Grottoli et al. 2014, Palumbi et al. 2014, Putnam & Gates 2015, Cunning et al. 2016, Hughes et al. 2017). In order to predict the effects of longer-term climate change

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exposure, the multiple influences of genetic adaptation, acclimatization, and community change must be understood and quantified. Genetic adaptation is the population-level genetic change, acclimatization is the phenotypic change or response to environmental variation, and community change is the shift in the taxonomic composition of coral communities. Because these metrics of change are difficult to separate, I use adaptation in the generic sense of the capacity of a system (reef corals) to adapt to a changing environment. This is also the sense in which adaptation is used for calibrating models that attempt to predict the future of coral states, such as coral cover, or reef functions, such as calcification (Donner et al. 2005, Baskett et al. 2009, 2010, Frieler et al. 2013, Logan et al. 2014).

Genetic adaptation rates are considered by some to be too slow to be relevant to the current rapid rate of climate change (Hoegh-Guldberg et al. 2007, Császár et al. 2010). Regardless, depending on the response rates and interactions of each of these adaptation processes, some coral reef ecosystem states and services could be maintained over the coming decades (Edmunds & Gates 2008, Weis 2010, Pandolfi et al. 2011). Many studies have evaluated the acclimatization responses of coral species to different thermal environments (e.g. Jokiel & Coles 1977, Brown et al. 2002, Berkelmans & van Oppen 2006, Schoepf et al. 2015a, Louis et al. 2016) and some have evaluated adaptation to thermal exposure over meaningful ecological time (McClanahan & Maina 2003, Guest et al. 2012, 2016, Baker et al. 2013, Pratchett et al. 2013, McClanahan & Muthiga 2014). Studies of changing sensitivity over time are critical to resolving this issue and, to date, suggest that some generic adaptation is occurring (but see Hughes et al. 2017).

Finding evidence for or estimating rates of adaptation has the common field study problems of relying on proxies, estimates or incomplete knowledge, and on historical exposures that are difficult to compare. For example, many current predictions rely on static coral life history characteristics and their ability to act as indicators of disturbance histories (Darling et al. 2012, 2013, McClanahan et al. 2015a,b). Yet, to further complicate predictions, many corals' responses are contextual and result from recent acute and chronic interactions with their environment. Qualitative metrics at different time scales, such as the timing, fluctuations, and intensity of disturbances, will influence responses (McClanahan & Maina 2003, Ainsworth et al. 2016). For acute stress, depending on length, bimodal qualities of the pre-stress disturbances, and whether or not corals have saved or

depleted their energy reserves, coral taxa can be either more or less resistant to within-season thermal anomalies (Grottoli et al. 2014, Schoepf et al. 2015b).

To better understand bleaching responses and the above influences over time, I repeated surveys of bleaching sensitivity at 5 sites in 2 fully protected marine protected areas of Kenya where bleaching response data were collected during the 1997/98 and 2015/16 warm seasons. Despite some qualitative differences, both years experienced strong and similar temperature anomalies that provided a basis for evaluating adaptation/acclimatization over ecologically relevant time. Consequently, I tested the hypothesis that corals are adapting to warm climate disturbances and therefore that bleaching responses in 2016 should be less severe than those reported in 1998. Some combination of genetic adaptation/acclimatization/community change would promote this change, and quantification of the rates would provide population and community level estimates of changing exposure sensitivity.

## MATERIALS AND METHODS

### Study sites

Reef corals studied here were located in back reef lagoon environments in 2 marine protected areas where all forms of extractive resource use are prohibited (McClanahan 2014). Sites are carbonate reef bottoms often surrounded by sand and seagrass colonized by hard corals, of which the dominant coral is often the massive *Porites lutea*. Twenty-one common coral taxa (mostly genera) were present and abundant enough to achieve sufficient replication for bleaching evaluations. Three sites were studied in the Mombasa Marine National Park (MNP), of which 1 is a long-term monitoring site where benthic and coral cover are regularly measured. The other 2 sites were located along a ~1 km stretch of back reef and separated by seagrass and sand. The Watamu MNP was composed of 2 sites known as the Coral Gardens located along a coral outcrop area within the lagoon and surrounded by seagrass and sand. The northern and southern portions of these coral outcrops were selected as 2 separate sites, and regular benthic cover measurements have been made at the southern site. The Mombasa and Watamu sites were located within 1 km from shore along Kenya's fringing reef and separated from each other by ~80 km.

### Environmental metrics

Previous bleaching research has indicated that light and water temperature are major influences on bleaching in this region but there are other forces, such as water flow, that could ameliorate responses (Maina et al. 2008, McClanahan et al. 2005). Consequently, environmental metrics of SST, light, water flow, and Indian Ocean basin-scale temperature variation were either measured *in situ* or accessed from open data sources. *In situ* temperature gauges were located among 2 of the coral reefs (Hobo Water Temp Pro v2 Gauges type u22-001 [Onset] report a 0.35°C accuracy at 25°C). Temperature was continuously monitored at 3 h intervals at the 2 reef monitoring sites. The gauges were deployed and water temperatures measured from August 1996 in Mombasa and from August 2002 in Watamu. Both gauges were located at ~1 m depth at low tide but experienced a 4 m tidal range over the full tidal cycle. Gauges were contained within a PVC pipe with a screw cap, and this pipe was embedded in masonry cement in a crevice beneath a massive coral to avoid being tampered with and to be hidden from direct sunlight.

Water flow rates were estimated in these reefs using clod-cards (calcium sulfate) where the dissolution rates were converted to water flow estimates using equations developed from plume experiments (Anzai 2001). Three to 6 clod cards were periodically deployed next to corals for 24 h in the reef lagoons during spring tides between 2003 and 2013, and weight differences were used to estimate water flow. Sampling was done during the warm season and replicated 19 times in Mombasa and 9 times in Watamu. Means were compared between the 2 reefs for samples pooled within time periods.

Open data sources include the CoRTAD environmental database ([www.nodc.noaa.gov/sog/cortad/](http://www.nodc.noaa.gov/sog/cortad/)) that contains SST collected weekly at 4 km resolution offshore from the reef sites. The photosynthetically active radiation (PAR) data were monthly values at a 4 km resolution acquired from the GlobColour project ([hermes.acri.fr](http://hermes.acri.fr)). These data were a merged product obtained by averaging valid pixels from different sensors (SeaWiFS, VIIRS, and MODIS-Aqua). The PAR, hotspot days, and degree heating week (DHW) anomalies in the summer months of 1998 and 2016 are presented for 84 d before 4 April (Liu et al. 2014). The data come from offshore measurements nearest to the Mombasa and Watamu MNP study sites where land features do not influence satellite readings. Studies using these data sources frequently report bleaching when temperatures exceed +1°C above

the mean summer temperature, and bleaching alerts are reported after 4 wk of these conditions (Eakin et al. 2009).

The Indian Ocean Dipole (IOD) metric is the temperature difference between the eastern and western equatorial SST data, where positive values indicate warmer conditions in Kenya compared to Indonesia. The Dipole Moment Index (DMI) dataset was acquired from the JAMSTEC website ([www.jamstec.go.jp/frsgc/research/d1/iod/iod/dipole\\_mode\\_index.html](http://www.jamstec.go.jp/frsgc/research/d1/iod/iod/dipole_mode_index.html)). Weekly DMI data were derived from NOAA OISST Ver.2, and the monthly data were derived from the HadISST dataset. Here, I plotted the annual monthly summer period (September to March) dipole from 1997 to 2016 and compared the weekly metric for 1997/98 and 2015/16.

### Field methods

A 7-category bleaching scale was used to estimate the bleaching response or sensitivity of individual colonies to the environmental exposure at the above sites (McClanahan et al. 2007a,b). Observation in the field scaled individual coral colonies from normal coloration, to pale, to different percentages of surface area of the colony bleached to recently dead. During 2016, the cover of hard and soft coral and erect algae were visually estimated in each quadrat, and means were calculated per study site. Field observations were made while snorkeling during low tide and haphazardly identifying and classifying all coral colonies within a 2 m diameter circle. The haphazard process of selecting quadrats is repeated for ~40 min or until ~15 quadrats have been sampled, which typically results in classifying ~200 to 300 colonies per sample. This method was used in both 1998 and 2016 at the same sites and repeated within 50 d of the peak water temperatures. The peak temperatures were recorded in March, and sampling followed during comparable times in 1998 and 2016 in both parks (Table 1). This resulted in large and temporally replicated sampling for most coral taxa and the ability to compare taxa responses between years, such that the sample sizes and timing of the observations did not greatly influence calculated responses.

### Data and statistical analyses

The taxa-specific bleaching responses were calculated by increasing the weight given to each of the 7 bleaching categories (McClanahan et al. 2007a). The

Table 1. Summary of study site (Mombasa: 3.99°S, 39.75°E; Watamu: 3.38°S, 39.99°E) key descriptors and sampling dates, temperature statistics, and coral and benthic community variables (mean ± SEM). ND: no data available, SST: sea surface temperature

Metrics	Mombasa		Watamu	
	1998	2016	1998	2016
Sampling sites (n)	3	3	2	2
Sampling dates	27 March, 9 May	5 April, 12 May	14 April	13 April, 20 May
<b><i>In situ</i> temperature data</b>				
Mean summer temperature (°C)		28.07		28.14
Days above mean summer temp.	75	65	ND	59
Cumulative degrees above mean summer temp, degree-days (°C)	85.12	84.32	ND	95.95
Peak temperature (°C)	30.9	30.9	ND	31.5
Day of peak temperature	31 March	20 March	ND	19 March
28 <sup>th</sup> day bleaching alert +1°C above mean summer	2 April	27 March	ND	25 March
Maximum of the monthly mean SST climatology (°C)		28.77		28.75
Hotspot days >1°C	22	25	ND	38
Degree heating weeks (°C-weeks)	5.4	5.5	ND	12.5
<b>Satellite data</b>				
Hotspot days >1°C	26	14	31	12
Degree heating weeks (°C-weeks)	5.7	2.7	7.2	2.4
<b>Bleaching and benthic data</b>				
Bleached colonies (%)	73.18 ± 7.55	27.46 ± 6.32	95.88 ± 0.83	60.46 ± 6.87
Bleaching response index (%)	34.68 ± 9.56	10.31 ± 2.59	65.55 ± 1.4	33.15 ± 5.3
Site susceptibility (%)	19.06 ± 0.28	17.99 ± 0.29	17.96 ± 0.89	19.18 ± 0.6
Number of genera	18.5 ± 0.43	19.83 ± 1.56	17.5 ± 2.5	17.5 ± 2.5
Number of colonies	331 ± 30.72	201.83 ± 26.16	288 ± 15	193.5 ± 43.5
Coral diversity ( <i>D</i> )	0.88 ± 0.01	0.89 ± 0.01	0.87 ± 0.02	0.88 ± 0.02
Hard coral (%)	ND	19.86 ± 2.69	ND	24.96 ± 1.71
Erect macroalgae (%)	ND	9.35 ± 8.4	ND	22.73 ± 22.73
Soft coral (%)	ND	21.95 ± 4.56	ND	19.08 ± 18.58

bleaching site response was then calculated by multiplying the taxon bleaching response by the number of individuals sampled in that taxon and summed across all taxa. This produces a numbers-weighted bleaching response with values that potentially range from 0 (no bleaching observed) to 100 (all colonies recently died). The original field method was developed by Gleason (1993) and modified by McClanahan et al. (2001) and has been used broadly by other observers (McClanahan et al. 2007a,b, Guest et al. 2012, 2016).

A site susceptibility index was calculated by multiplying the number of colonies of each taxon by their mean bleaching response. The mean specific taxon response is based on a large sample of bleaching response observations taken from the western Indian Ocean (WIO) observation when >10% of the total colonies at a site were bleached (McClanahan et al. 2007a). High site susceptibility values indicate a community composed of bleaching-sensitive taxa.

The mean summer trends for Watamu and Mombasa MNPs were calculated using *in situ* daily temperature means for the local warm period, from 1 August to 31 March. This corresponds with the last coldest days to a few weeks after the warmest days of the year. *In situ* temperature data for the periods 1999 to 2015 and 2002 to 2015 were used to calculate the baseline for Mombasa and Watamu, respectively. From this mean baseline, the number of degree heating-days was calculated for 100 of the hottest summer days before 4 April. The warmest period started on either 25 or 26 December. Degree-heating day calculation subtracts the temperature on a given day from the summer mean and sums this difference for all warm period days. A 'bleaching alert' date for each *in situ* record was calculated as the day when the temperature was +1°C above the summer mean for 28 d (Eakin et al. 2009). The number of days that the temperature was above the summer mean was also calculated (Table 1).

Bleaching response values for taxa and sites were tested for differences between 1998 and 2016 using a *t*-test. Watamu sites were on a continuous and homogenous reef while Mombasa sites were more isolated; consequently, an unequal variance *t*-test was used in Mombasa and equal variance in Watamu. For some analyses, the taxa and sites were pooled and differences in responses over the 17 yr period were calculated and tested for associations with their change in bleaching. For the better represented taxa (>10 sampled colonies per location), these categories were as follows: no change, statistically significant reduction in sensitivity, increased sensitivity to exposure, and indeterminate change.

The change in percentage pale and bleached corals between these 2 years, comparison with past responses (a WIO bleaching database compilation), and coral mortality at these sites were presented as scatterplots. Coral mortalities at the taxon level and for the 2 monitoring sites were calculated as the differences in the number of colonies per meter of line transect before and after the 1998 thermal anomaly (McClanahan et al. 2001). Here, I pooled transect data collected in 1996 and 1997 and 1998 and 1999 for the before and after periods to reduce the variance and increase the sampling accuracy of all taxa, particularly the uncommon ones. Percent mortality was therefore the change across the mortality event divided by the pre-mortality cover. The coral taxon *Coscinaraea* was not encountered beneath transect lines before the 1998 bleaching and was therefore not included in this analysis.

## RESULTS

### Environmental factors

No significant differences were detected in PAR levels (in Einsteins  $\text{m}^{-2} \text{d}^{-1}$ ) for the 1997/98 and 2015/16 periods in Mombasa (1997/98 =  $49.49 \pm 1.98$  ( $\pm$ SE), 2015/16 =  $52.86 \pm 0.89$ ,  $t = 1.55$ ,  $df = 8, 31$ ) and Watamu (1997/98 =  $47.83 \pm 2.12$ , 2015/16 =  $52.44 \pm 0.95$ ,  $t = 1.98$ ,  $df = 8, 31$ ). Similarly, there were no significant differences in water flow (in  $\text{cm s}^{-1}$ ) estimates for data collected over the period 2003 to 2013 (Mombasa =  $7.55 \pm 0.60$ , Watamu =  $7.31 \pm 0.82$ ,  $t = -0.23$ ,  $df = 16, 67$ ).

Warm season temperature anomalies were observed in these reefs in 1998, 2010, 2013, and 2016, but with some differences in peak values between satellite and *in situ* metrics and threshold-based bleaching predictions (Fig. 1a). The *in situ* gauge

data from Mombasa indicated that 2010 and 2016 were the warmest warm seasons, followed by 1998 and 2013, whereas satellite data identified 1998 to be the warmest year, followed by 2016 and 2010, while 2013 was the coolest of the anomalously warm years. In 1998 and 2016, temperature stress anomalies were clearly observable as deviations from the mean summer temperatures of around  $28.1^\circ\text{C}$  (Fig. 1b). 2016 differed from 1998 in having a larger pre-maximum temperature rise in November and December that briefly exceeded the  $+1^\circ\text{C}$  bleaching threshold before declining until rising again from mid-February to the end of March.

There was a rising trend in the summer IOD over the period 1997 to 2016, with 1998 being the strongest positive anomaly followed by 2007 and 2016. The 1998 dipole was 82% higher than 2016 ( $t = -4.61$ ,  $p = 0.0001$ ; Fig. 2a). Across the September to April summer period, the 1998 dipole was higher and persisted longer than in 2016. The dipole stayed positive in 1998 until April, but in 2016 it became negative after December (Fig. 2b).

Despite the 80 km distance between sites, the *in situ* temperatures in Watamu and Mombasa tracked each other closely in 2016. Both reefs experienced peak temperatures in mid-March, with Mombasa experiencing  $30.9^\circ\text{C}$  on 20 March and Watamu  $31.5^\circ\text{C}$  on 19 March. During 1998, Mombasa experienced  $30.9^\circ\text{C}$  on 31 March. In 2016, cumulative degree heating days were slightly higher in Watamu than Mombasa, at 96 and 82 degree-days, respectively. However, the number of days above mean temperature was higher in Mombasa than Watamu with 65 and 59 d, respectively (Table 1). Cumulative temperatures in Mombasa in 1998 were nearly the same as in 2016 at  $\sim 85$  degree-days. No *in situ* temperature data were collected in Watamu in 1998.

Comparing reef water temperatures in 2016 by satellite indicated strong relationships for the full year evaluations ( $r^2 = 0.97$ ) that were somewhat weaker when evaluating the warm season ( $r^2 = 0.93$ ; Table 2). *In situ* gauge comparison of warm seasons was also weaker ( $r^2 = 0.78$ ) than the full-year comparisons ( $r^2 = 0.91$ ). Even weaker were the comparisons of satellite and *in situ* data during the warm season (Watamu  $r^2 = 0.75$  and Mombasa  $r^2 = 0.67$ ). The satellite and *in situ* temperature data were also inconsistent in terms of the hot spot and DHW metrics, which differed between years and sites based on the source of the data. Satellite data exhibited more hotspot days and DHW in 1998 than 2016, with higher values in Mombasa than Watamu (Table 1). Consequently, it appears that the 2 locations follow similar patterns,

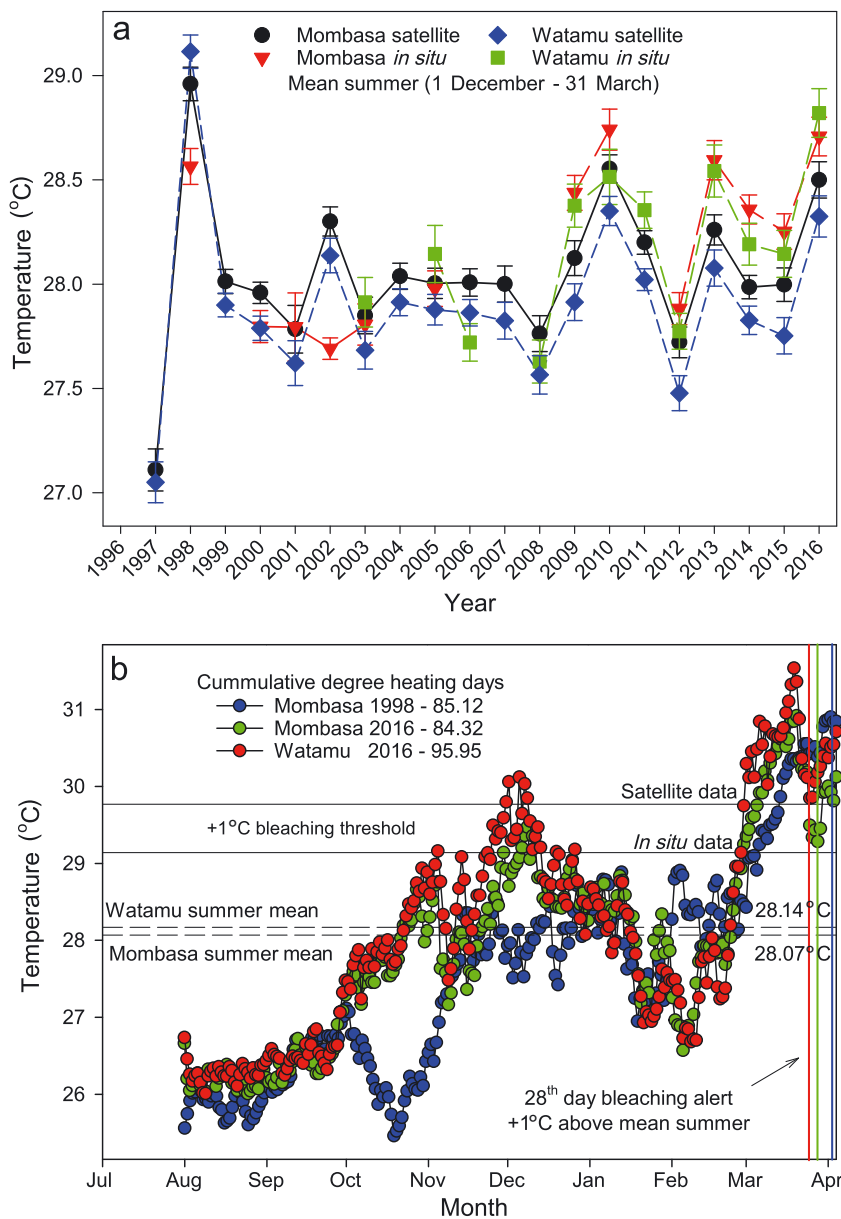


Fig. 1. Time series of the (a) mean ( $\pm$  SEM) warm season temperature for satellite and *in situ* measurements between 1997/98 and 2015/16 and (b) daily mean *in situ* temperature in the Mombasa and Watamu Marine National Parks during the 1998 and 2016 temperature anomalies (no gauges were employed in Watamu in 1998). Presented are the mean summer trends for Watamu and Mombasa, the number of degree-days above this mean value, the +1°C threshold for bleaching, and the 28 d bleaching warming period. Some years are missing for Mombasa and Watamu in the calculation of summer means due to times of deployment and lost temperature gauges

but there were warm-season differences, and satellite data were not accurate during the warm period or between the 2 studied years. Nevertheless, while they differed in distinguishing peak years, the general temporal trends in the *in situ* and satellite data were similar (Fig. 1b). Based on the more accurate *in*

*situ* data from Mombasa, which had the same maximum temperatures and degree-heating days during the 2 years, differences in the overall thermal stress between 1998 and 2016 were probably small. Nevertheless, there were qualitative differences associated with more pre-peak temperature variation or bimodality in 2016 than during 1998.

## Ecological and bleaching responses

### Benthic cover

Hard coral and erect algal cover changed in the Mombasa and Watamu MNPs over the study period (Fig. 3). Hard coral declined in both parks from ~42 to ~12% after 1998. This was followed by rapid recovery to ~38% in Mombasa by 2005 but a very minor increase (~3%) in Watamu until 2011, after which time cover exceeded 20%. Coral recovery in Mombasa reversed early in 2007 and declined to ~19% by 2013. Erect algae cover was variable in Mombasa, increasing rapidly after 1998 but declining again in 2002 before increasing again, with a large increase to ~33% after 2006. Cover of erect fleshy algae was less variable in Watamu but declined from ~10 to 1.4% between 1999 and 2004 and rose to ~10% by 2010 and 20% by 2016.

### Bleaching responses

Marked differences in the bleaching responses were evident between sites and years as measured by the percentage of colonies bleaching and the weighted bleaching response (Table 1). More intense bleaching was observed in Watamu than Mombasa in both years and by both metrics. Between 1998 and 2016, the number of pale and bleached colonies declined from 96 to 60% in Watamu and from 73 to 27% in Mombasa. The

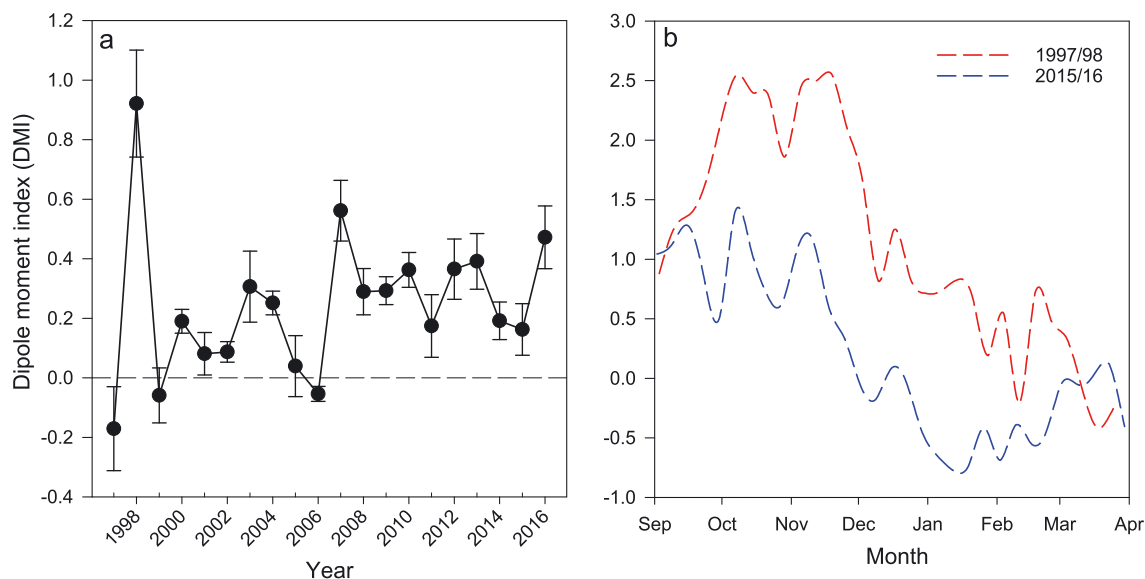


Fig. 2. Time series of the Indian Ocean Dipole moment index presented for (a) summer, annually from 1997 to 2016 and (b) weekly for 1997/98 and 2015/2016. The annual values are means ( $\pm$ SE) based on monthly estimates from September to March of each year, and the weekly values show trends for September to April

weighted bleaching response showed larger relative declines, with a 65 to 33% decline in Watamu and a 35 to 10% decline in Mombasa. This is despite small differences in the sites' bleaching susceptibility index, numbers of genera, and diversity between years.

Taxa-specific responses reflect an overall reduced sensitivity but indicate clear differences between taxa and reefs (Fig. 4). For example, 8 and 9 taxa showed a statistically lower sensitivity or response to the thermal exposure in Mombasa and Watamu between the 2 events, respectively. The responses of 12 and 5 of

Table 2. Relationship between satellite and *in situ* recorded temperatures for the period 1996–2016 in Mombasa and Watamu. Relationships are presented for the full year and the warm season period (1 December to 31 March)

Site	Period	Parameter	Estimate ( $\pm$ SE)	<i>t</i> ratio	$r^2$	<i>p</i>	Number of days
<b>Satellite vs. satellite</b>							
Mombasa satellite vs. Watamu satellite	Full period	Intercept	0.17 $\pm$ 0.05	3.3	0.97	<0.0001	7524
		Slope	0.10 $\pm$ 0.002	507.1			
	Warm season	Intercept	2.51 $\pm$ 0.14	17.8	0.93	<0.0001	2516
		Slope	0.92 $\pm$ 0.01	181.6			
<b><i>In situ</i> vs. <i>in situ</i></b>							
Mombasa <i>in situ</i> vs. Watamu <i>in situ</i>	Full period	Intercept	2.67 $\pm$ 0.13	20.7	0.91	<0.0001	3566
		Slope	0.90 $\pm$ 0.004	190.8			
	Warm season	Intercept	6.33 $\pm$ 0.33	18.9	0.78	<0.0001	1180
		Slope	0.77 $\pm$ 0.01	65.4			
<b>Satellite vs. <i>in situ</i></b>							
Watamu satellite vs. <i>in situ</i>	Full period	Intercept	3.69 $\pm$ 0.15	25.2	0.85	<0.0001	4611
		Slope	0.85 $\pm$ 0.01	160.8			
	Warm season	Intercept	9.21 $\pm$ 0.28	32.4	0.75	<0.0001	1426
		Slope	0.66 $\pm$ 0.01	65.7			
Mombasa satellite vs. <i>in situ</i>	Full period	Intercept	1.63 $\pm$ 0.15	10.5	0.85	<0.0001	4901
		Slope	0.94 $\pm$ 0.01	165.6			
	Warm season	Intercept	8.09 $\pm$ 0.34	23.9	0.67	<0.0001	1743
		Slope	0.71 $\pm$ 0.01	59.2			

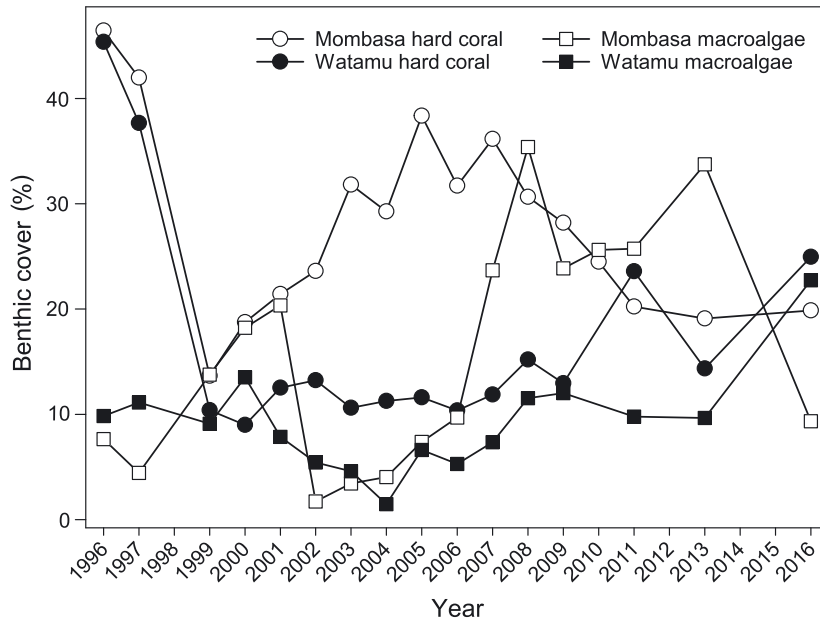


Fig. 3. Changes in hard coral and erect algal cover in the Mombasa and Watamu Marine National Parks monitoring sites between 1996 and 2016

the taxa did not change significantly across time in Mombasa and Watamu, respectively, for the sampling and variance characteristics at the sites. The dominant cover taxa *Porites*, *Acropora*, *Galaxea fascicularis*, and *Favia* showed consistently less bleaching in 2016 than 1998 in both reefs. Some taxa, such as *Echinopora*, *Favites*, *Millepora*, *Platygyra*, and *Pocillopora* had statistically significant responses in one but not the other reef. Some taxa, such as *Acanthastrea*,

*Coscinaraea*, *Cyphastrea*, *Gonipora*, *Goniastrea*, *Leptoria*, *Pavona*, and *Synarea* (= *Porites rus*), were not found in sufficient numbers or present over time to make comparisons.

Pooling taxa for both reefs and evaluating change in bleaching for the full sample size indicated a good positive relationship between the bleaching response and the percentage of pale and bleached colonies within taxa ( $r^2 = 0.58$ ; Fig. 5a). There was, however, no relationship between the mean 2016 bleaching response and the larger pre-2016 WIO bleaching compilation (Fig. 5b). Among the 21 most abundant taxa, 11 showed less response to the thermal exposure in 2016 than in 1998, 6 taxa showed no change (*Favites*, *Goniastrea*, *Hydnophora*, *Montipora*, *Platygyra*, and *Pocillopora*), 3 taxa

were inconclusive due to insufficient samples or high between-reef variation (*Favia*, *Coscinaraea*, and *Synarea*), and 1 taxon, *Acanthastrea*, was more sensitive to exposure in the Watamu reef. The difference or reduction in bleaching sensitivity in the 11 less sensitive taxa was  $83.3 \pm 4.1\%$  ( $\pm 95\%$  CI; Table 3). Taxa changes in sensitivity were not related to their mortality rates across the 1998 event (Fig. 5c). The mean mortality rate for corals showing significant

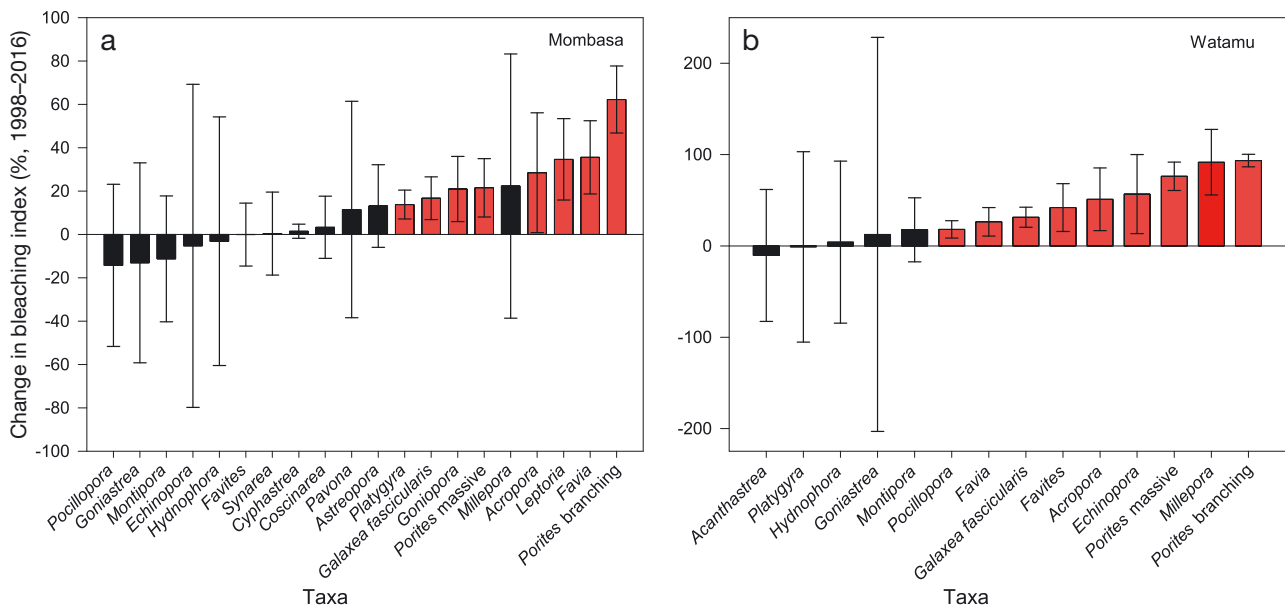


Fig. 4. Change in the bleaching response of the dominant corals (mean  $\pm$  95% CI) between 1998 and 2016 for (a) Mombasa and (b) Watamu Marine National Park sites. Positive values (red) indicate a reduced bleaching response over time



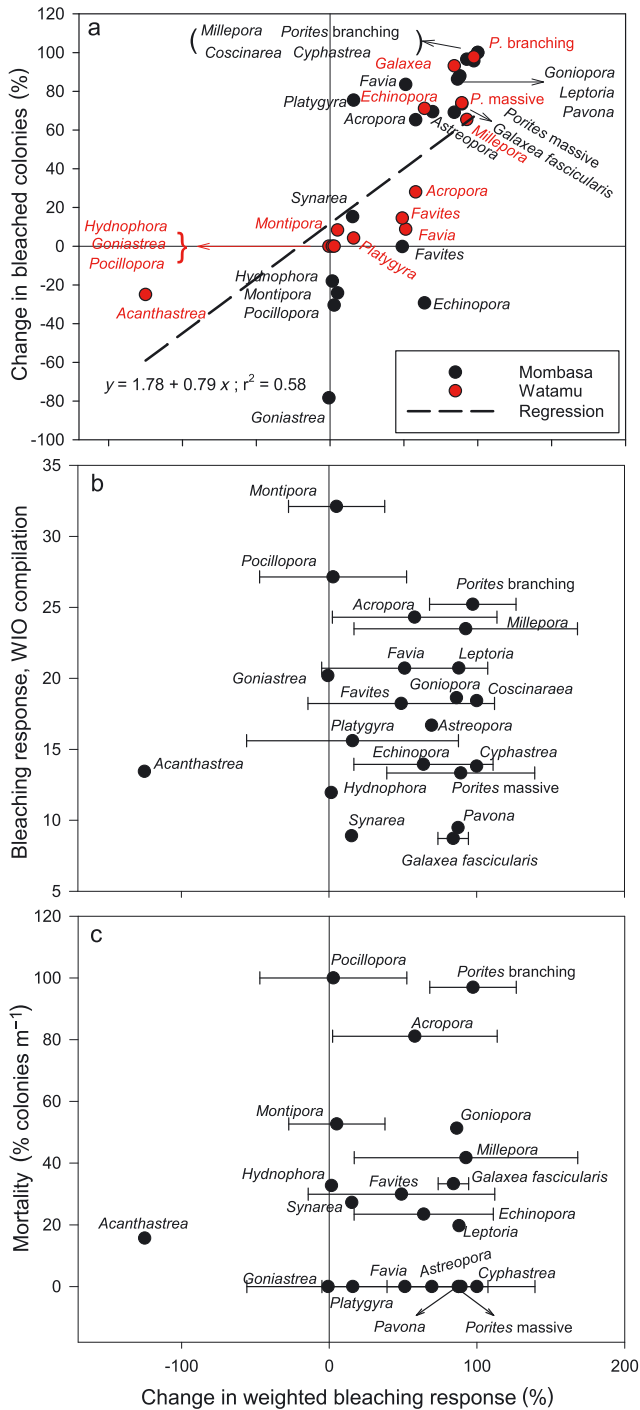


Fig. 5. Relationships between the change in the weighted bleaching response in Mombasa and Watamu Marine National Parks over the 17 yr period for the dominant coral taxa and (a) the % pale and bleached colonies (*P.* = *Porites*), (b) the mean historical bleaching response of these taxa in the Western Indian Ocean, and (c) mortality rates across the 1998 thermal anomaly based on coral monitoring data in the 2 park locations. Taxa without error bars represent 1 reef location because the taxa had <10 colonies at 1 of the 2 locations (e.g. *Synarea* was only found in Mombasa). Positive values indicate a reduced bleaching response over time

declines in bleaching was  $31.6 \pm 10.2\%$  and was not different for those showing no or indeterminate change at  $35.0 \pm 15.3\%$ . Some taxa however, such as *Pavona* and possibly *Leptoria* and *Goniastrea*, did not clearly experience significant mortality in 1998 and showed lower sensitivity to the thermal exposures in 2016 than in 1998.

### DISCUSSION

The 2 study locations experienced unusually high summer thermal stresses in 1998 and 2016. There were differences in the satellite and gauge ranking of warm season thermal stress, but the more accurate *in situ* data indicated that these 2 years and 2010 represent the largest thermal anomalies during the past 2 decades. These events were associated with positive El Niño Southern Oscillation (ENSO) or IOD states. Yet, the relative influences of these oceanographic forces differentially affected the timing and intensity of the high temperatures and coral stress. In Kenya, the IOD force is likely to be a stronger inter-annual force than ENSO, but their contributions to warm water differ between years (Nakamura et al. 2011). For example, given the very similar excess temperature in 1998 and 2016, it is likely that heating due to IOD and ENSO were stronger in 1998 and 2016, respectively. Possibly the early pre-peak temperature rise in 2016 were driven by ENSO forces, while the later and prolonged warm temperatures in 1998 were influenced by a strong and persistent IOD. Moreover, the complex interactions between these and other oceanographic oscillations, such as the Pacific Decadal Oscillation, are likely to result in complex East African temperature anomalies (Cole et al. 2000, Zinke et al. 2009). Despite the strong similarity in gross thermal exposures between 1998 and 2016, differences in pre-bleaching temperature fluctuations probably influenced bleaching responses. Consequently, despite a coincidental correspondence of cumulative temperature stress, the same field methods and observers, and the lack of differences in light and water flow between reefs, these qualitative differences could challenge efforts to directly compare and quantify coral adaptation needed to make future predictions.

Watamu was more severely influenced by temperature anomalies than Mombasa, as reflected in the higher degree-heating days and weeks in 2016 and the higher levels of observed bleaching in both years. Watamu also had slower recovery of corals than Mombasa after the 1998 event. The exposure levels

Table 3. Change (mean  $\pm$  SEM) in bleaching response and mortality rates of sensitive, less sensitive, and the non-changing or indeterminate coral taxa between 1998 and 2016. Mortality rates are from benthic line transects completed before and after the 1998 thermal anomaly in the 2 reef locations

Bleaching change category	Coral taxa (number of taxa)	Change in bleaching response (%)	Mortality rates, % colonies m <sup>-1</sup>
More sensitive	<i>Acanthastrea</i> (1)	-125	15.7
No change	<i>Favites</i> , <i>Goniastrea</i> <sup>a</sup> , <i>Hydnophora</i> , <i>Montipora</i> , <i>Platygyra</i> <sup>a</sup> , <i>Pocillopora</i> (6)	20.3 $\pm$ 9.7	35.9 $\pm$ 15.3
Less sensitive	<i>Acropora</i> , <i>Astreopora</i> <sup>a</sup> , <i>Cyphastrea</i> <sup>a</sup> , <i>Echinopora</i> , <i>Galaxea fascicularis</i> , <i>Goniopora</i> , <i>Leptoria</i> , <i>Millepora</i> , <i>Pavona</i> <sup>a</sup> , branching <i>Porites</i> , massive <i>Porites</i> <sup>a</sup> (11)	83.3 $\pm$ 4.1	31.6 $\pm$ 10.2
Indeterminate	<i>Favia</i> <sup>a</sup> , <i>Coscinaraea</i> <sup>b</sup> , <i>Synarea</i> (3)	39.3 $\pm$ 37.4	13.6 $\pm$ 13.6

<sup>a</sup>Corals with negative mortality values were set to 0  
<sup>b</sup>*Coscinaraea* was excluded from mortality calculations, as it was not encountered during the 1998 benthic surveys

in 1998 and 2016 were, however, grossly similar as indicated by the Mombasa gauge and the strong coincidence in degree-heating days between years. The poorer correspondence between *in situ* and satellite data suggests limits to the accuracy of satellite predictions for shallow reefs, particularly during the warm season. Poor correspondence between satellite and gauges may include poor regional satellite coverage and local nearshore heating and cooling. These problems have been noted in previous satellite data-bleaching survey studies in East Africa, and blending satellite with *in situ* data may increase accuracy (McClanahan et al. 2007b).

There was reduced exposure sensitivity at the whole community level and for a number of taxa between the 2 anomalous times. Adaptations were likely caused by a combination of genetic adaptation, acclimatization, and community change. Community sensitivity was reduced more than the individual taxa because abundant taxa, such as *Acropora* and branching *Porites*, had among the most reduced sensitivities. Taxa evaluations indicated 3 gross responses to between-year exposure, namely reduced sensitivity (11 taxa), no or indeterminate change in sensitivity (9 taxa), and increased sensitivity for 1 taxon at 1 site (Fig. 6). Each form of adaptation has separate causes, mechanisms, and temporal and spatial scales of response. For example, genetic adaptation is caused by changes in gene frequency due to differential birth and death processes. Additionally, epigenetic changes due to externally modified up-regulated genes result in greater tolerance of corals to heat stress (Dixon et al. 2015) and represent a form of acclimatization that may also result in reduced sensitivity of coral offspring (van Oppen et al. 2015).

Reports and evidence for acclimatization of corals to background temperature variation is common. Consequently, it is expected that acclimatization and epigenetic changes contributed to the reduced bleaching response in 2016 compared to 1998. Acclimatization, however, is likely to depend on the coral holobiont and the strength of the chronic and acute pre-stress exposures and the time between stresses (Grottoli et al. 2014). Some pre-bleaching acute fluctuations will promote acclimatization while others increase sensitization (Edmunds & Gates 2008, Ainsworth et al. 2016). Consequently, even though these 2 study years had very similar gross anomalies, the pre-stress temperature fluctuations were differ-

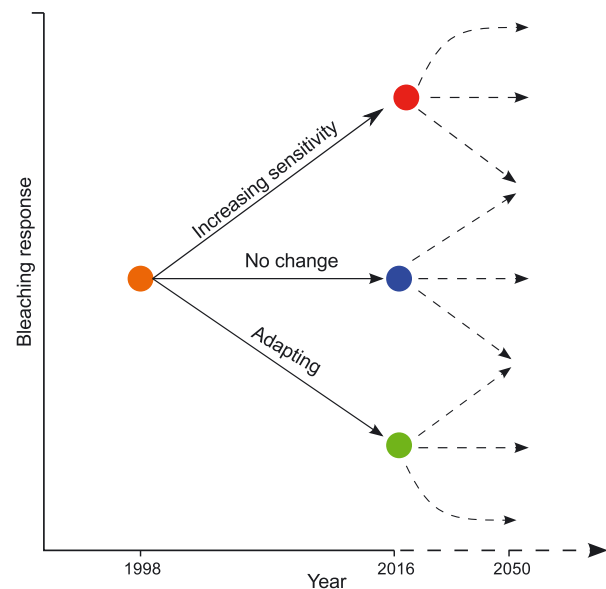


Fig. 6. Possible adaptation scenarios for the 3 response groups (increasing sensitivity, no change, and adapting) found in this study

ent enough to produce different responses. While not enough research has been undertaken to evaluate pre-stress influences on many taxa, greater bimodality has been shown to increase rather than decrease bleaching in the well-studied *Acropora aspera* (Ainsworth et al. 2016). Pre-peak temperatures in 2016 exhibited greater bimodality than in 1998, which indicates that the reduced temperature stress sensitivity of corals in 2016 occurred even in the presence of higher bimodality. Clearly, the scale, directions, rates, and potential for reversal need further study, but temperature acclimatization experiments have found that genetic and epigenetic changes can explain a good portion of the response of heat-exposed corals (Palumbi et al. 2014, Dixon et al. 2015).

Community change can occur due to changes in the composition of coral taxa and the endosymbionts and other species associated with the coral holobiont (McClanahan & Maina 2003, Bourne et al. 2008, Jones et al. 2008, Mills et al. 2013). For example, a relaxation or decline in the density of symbionts that confer heat resistance in corals took ~5 yr in Kenya after the 1998 thermal anomaly (Baker et al. 2013). Symbiont change may be even more dynamic than found in Kenya because the coral holobiont is composed of many difficult to detect taxa, including genetically variable and promiscuous symbiont algae (Mieog et al. 2007, Silverstein et al. 2011, Ladner et al. 2012, Cunning et al. 2015a,b). Symbiont type did not, however, clearly result in higher survival and recovery rates of common Kenyan corals over a 20 yr study period (McClanahan et al. 2015a). Therefore, other factors associated with the host or the holobiont are likely to be important for survival (Smith-Keune & van Oppen 2006, Ulstrup et al. 2006, Cunning et al. 2016). Genotype studies suggest that host genetic expression differs between contrasting thermal environments and changes further when exposed to novel thermal stresses (Barshis et al. 2010, Császár et al. 2010, Howells et al. 2013).

Species or subspecies level changes in the studied coral communities over time were likely responsible for some of the measured change in bleaching, particularly in the more diverse genera, such as *Acropora* and *Pavona* (McClanahan 2014). Species-level change is less of a methodological or species-identification concern for other taxa such as massive and branching *Porites*, which are nearly all *P. lutea* and *P. palmata* (described by Moothien-Pillay et al. 2002) but sometimes referred to as *P. nigrescens*. Similarly, based on many years of observations in these 2 reefs, *Synarea* is composed of only *Porites rus* and *Leptoria* contains only *L. phrygia*. Moreover,

some genera have dominant species where >90% of the individuals were from 1 species; for example, *Montipora* is mostly *M. aequituberculata* with some *M. foliosa* and a few other rare taxa. Similarly, *Pocillopora* is dominated by *P. verrucosa*, *Hydnophora* is largely *H. exesa* with fewer *H. microconos*, *Platygyra* is *P. lamellina* and some *P. daedalea*, *Goniastrea* is *G. retiformis* and some *G. edwardsi*, and *Acanthastrea* is largely *A. brevis* with some *A. echinata* (Lemmens 1993). Therefore, most of the change in sensitivity to exposure found here is likely to be intra-species change. *Acropora* and *Pavona*, in contrast, had too many species to determine whether changing sensitivity was due to intra- or interspecies influences.

Genetic adaptation should be the slowest process and driven by death and birth processes that drive evolutionary selection. Given the high mortality observed after the 1998 event, the most exposure-sensitive genotypes should have been greatly reduced. Prior to 1998, there was probably high but unrecorded mortality in 1988 and 1983 when bleaching was first recorded in the region (Faure et al. 1984, my pers. obs.). Consequently, the history of these reefs is one of repeated selective pressure created by a series of high mortality temperature anomalies prior to 1998 and changes in taxonomic composition and ecological dominance (McClanahan 2014). Nevertheless, the poor relationship between coral sensitivity, coral mortality, and the mean WIO bleaching response indicates the complexity of the forces influencing corals (McClanahan 2004). Some sensitive taxa displayed strong reductions in sensitivity while others, such as *Montipora* and *P. verrucosa*, exhibited little difference in bleaching between 1998 and 2016. Moreover, some taxa like *Acanthastrea*, *Goniastrea*, and *Hydnophora* had both low and between-year changes in sensitivity. This supports the argument that bleaching is just one of a number of possible responses to climate stress exposure, is not always associated with mortality, and can vary over time and space (Buddemeier et al. 2004, McClanahan 2004).

While there is evidence for phenotypic differences in bleaching responses among a number of the studied taxa over 17 yr, differences over time can be caused by many forces and are not easily distinguished from within-year forces. Additionally, establishing evidence for genetic adaptation to climate based on phenotypic change is challenging (Merilä & Hendry 2014). For example, other forcing factors or disturbances, including fishing impacts and diseases, are known to influence changes and could be responsible for genetic adaptation (Darling et al. 2012,

2013, Smith et al. 2013). Plots of the change in bleaching response versus mortality suggest no clear mortality-driven relationships. Rather, responses to mortality are taxa-specific. *P. palmata*, for example, had high mortality and reduced sensitivity, whereas *Acanthastrea* had moderate mortality and increased sensitivity. Additionally, some of the massive taxa, like massive *Porites*, had low mortality and a large reduction in sensitivity, whereas *Pavona* had low mortality and little change. A low mortality–large sensitivity reduction response might appear to be an optimal life history strategy in high-exposure environments, but it is probably obtained at the cost of low growth and competitive ability (Darling et al. 2012). Branching taxa are more likely to have a fast-growing competitive life history niche but frequently pay a high mortality price when acutely stressed (Darling et al. 2013).

Overall patterns are suggestive of considerable potential of decreased sensitivity among key coral cover contributors, but not all coral taxa, although these findings are based on a limited number of locations and observations. Some bleaching responses appear to have strong associations at the genus level across broad scales (McClanahan et al. 2004). Yet, these relationships change over time (Guest et al. 2012, 2016, Pratchett et al. 2013) and may differ with low and naïve versus high and experienced exposure locations and corals (McClanahan & Muthiga 2014). For example, studies of consecutive bleaching events in Moorea, French Polynesia, found reduced bleaching responses in a number of taxa over a 16 yr period, most clearly in *Acropora*, but also among *Pocillopora* and *Montipora* (Pratchett et al. 2013), 2 taxa that had low rates of change in this Kenya study. These regional comparisons warn against generalizations about adaptation based on taxa. Most experimental studies show strong biological–environmental interactions within taxa and environments that can complicate location, taxa, and temporal change patterns (Bourne et al. 2008, Barshis et al. 2010, Palumbi et al. 2014). For example, reports of the lack of reduced bleaching response to corals on the Great Barrier Reef over the 1998 to 2016 period may be due to a continuous increase in temperature stress over time that did not create conditions for acclimatization/community change/population adaptation between subsequent events (Hughes et al. 2017). There could also be some threshold response where anomalous heating may need to exceed some level before the various forces of changes are initiated. Consequently, unraveling these environmental–life history complexities, thresholds, and trade offs will require

examination over more sites, taxa, and scales of biological and ecological organization.

Another caveat is that environmental factors other than temperature can influence bleaching responses (Jokiel & Coles 1990, Brown et al. 2002). Consequently, while I found strong correspondence in the temperature exposure between the 2 years, other factors such as radiation and water flow and quality could have influenced bleaching responses (McClanahan et al. 2005, Maina et al. 2008). Because I sampled the same locations and found no differences in light and water flow between them, I suspect that these 2 factors could have but did not influence responses. Similar to other studies that have not accounted for the many potential influences and interactive responses, omissions of measurements could challenge estimating rates of change to exposure. A large survey of Indian Ocean reefs found that predicting the impacts of thermal anomalies on corals required more than temperature stress histories but also required other and weighted environmental variables to explain patterns (McClanahan et al. 2015b). However, Hughes et al. (2017) did not find water quality to be an influence in the Great Barrier Reef of Australia when examined as a single variable. Most future projections treat corals as a single adaptive group responding primarily to thermal stress and less to other sources of environmental exposure, let alone the diversity of taxa and communities. Field studies, such as mine, suggest that various taxonomic, site, and other environmental factors have the potential to moderate future predictions (Pandolfi et al. 2011, Palumbi et al. 2014).

Do the lower sensitivity and high rates of change found here predict a more adaptive and persistent scenario for coral reefs than previous predictions? The answer may depend on the extent to which the reported decline in exposure sensitivity will or will not track rates of climate change (Hughes et al. 2003, 2017) (Fig. 6). The changes observed here, where anomalies in 3 years since 1997 were similar, indicate rapid change for many key taxa. Consequently, if impacts are similar in the future and not rising strongly, there is potential for adaptation. Yet, many acclimatization/adaptation responses are not linear but saturating and can even be reversed when stress frequencies and intervals exceed physiological acclimatization, epigenetic, and genetic limits. If early-rapid responses are evaluated rather than late-slow responses, rates could overestimate the potential for long-term change. Kenyan corals were probably exposed to strong thermal anomalies in 1983 and 1988, which makes this early-response argument less

likely. The adaptive potential could be further overestimated if living becomes more costly and depletion of coral reserves more frequent in the future (Grottoli et al. 2014, Ainsworth et al. 2016, Albright et al. 2016). Moreover, bleaching is only one of many possible responses and strategies that can result in adaptation to thermal stress (Buddemeier et al. 2004, McClanahan 2004). For example, some corals may have fugitive life history strategies of dying and rapid colonization (e.g. *Pocillopora*), and there are other host-associated responses to heat exposure (Bellantuono et al. 2012, McClanahan 2014, Palumbi et al. 2014). Despite the many caveats and interpretations of these results, this study provides one of the first response rate estimates for many common corals at the population level. It therefore provides a basis for future studies and improving model predictions and the types of evaluations needed to address the future health of coral reefs.

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