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EFFECTS OF CLIMATE AND SEAWATER TEMPERATURE VARIATION ON CORAL BLEACHING AND MORTALITY

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Abstract. Coral bleaching due to thermal and environmental stress threatens coral reefs and possibly people who rely on their resources. Here we explore patterns of coral bleaching and mortality in East Africa in 1998 and 2005 in a region where the equatorial current and the island effect of Madagascar interact to create different thermal and physicochemical environments. A variety of temperature statistics were calculated, and their relationships with the degree-heating months (DHM), a good predictor of coral bleaching, determined. Changes in coral cover were analyzed from 29 sites that span >1000 km of coastline from Kenya to the Comoros Islands. Temperature patterns are influenced by the island effect, and there are three main temperature environments based on the rise in temperature over 52 years, measures of temperature variation, and DHM. Offshore sites north of Madagascar that included the Comoros had low temperature rises, low DHM, high standard deviations (SD), and the lowest relative coral mortality. Coastal sites in Kenya had moderate temperature rises, the lowest temperature SD, high DHM, and the highest relative coral mortality. Coastal sites in the south had the highest temperature rises, moderate SD and DHM, and low relative coral mortality. Consequently, the rate of temperature rise was less important than background variation, as reflected by SD and kurtosis measures of sea surface water temperature (SST), in predicting coral survival across 1998. Coral bleaching responses to a warm-water anomaly in 2005 were also negatively related to temperature variation, but positively correlated with the speed of water flow. Separating these effects is difficult; however, both factors will be associated with current environments on the opposite sides of reefs and islands. Reefs in current shadows may represent refugia where corals acclimate and adapt to environmental variation, which better prepares them for rising temperature and anomalies, even though these sites are likely to experience the fastest rates of temperature rise. We suggest that these sites are a conservation priority and should be targeted for management and further ecological research in order to understand acclimation, adaptation, and resilience to climate change.

Key words: acclimation/adaptation; climate change; coral bleaching; coral cover; degree-heating weeks/months (DHW/DHM); East Africa; Indian Ocean; island effects; sea surface water temperature (SST); temperature history; temperature variation; water flow.

Introduction

Coral reefs are increasingly threatened by a variety of factors, including high and destructive fishing, sedimentation, pollution, and climate change (McClanahan 2002, Hughes et al. 2003). Climate change presents a unique challenge as the effects are broad scale and not easily alleviated by local action or management (Hughes et al. 2005). Therefore, a key concern of modern marine ecology and associated management is to identify sites or regions that are likely to persist as the climate changes and to develop management that will improve the chances for persistence. There is growing awareness of this need and to increase associated research and management activities (West and Salm 2003, Wooldridge and Done 2004, Wooldridge et al. 2005). Implementation requires an evaluation of large-scale patterns of environmental variation, changes over time, projections into the future, and consequences of environmental change for the acclimation/adaptation and persistence of the studied organisms and ecosystems. Additionally, to be confident about predictions, an improved understanding of the causation and the time scale of environmental variation, acclimation/adaptation, and persistence are needed. The patterns of causation are complex and interactive, sometimes counterintuitive, and an area for growth in scientific understanding (McClanahan et al. 2005*a*).

Coral reefs are among the ecosystems most threatened by climate change as corals live near their upper thermal limits and are sensitive to modest increases in background seasonal seawater temperatures (Kleypas et al.

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2001, Coles and Brown 2003, Guinotte et al. 2003, Berkelmans et al. 2004, Jokiel 2004). Seawater temperatures are predicted to rise further and cause coral mortality in the next few decades (Hoegh-Guldberg 1999, Hughes et al. 2003, Sheppard 2003). Elevated temperature interacting with other physicochemical, biological, and anthropogenic factors is generally considered to be the primary stress causing coral bleaching (Coles and Brown 2003). The understanding of water temperature regimes and organism survival is based on descriptive and often site-specific field studies (McField 1999, Loya et al. 2001, McClanahan et al. 2001, Mumby et al. 2001*a*, Aronson et al. 2002, Berkelmans 2002, Berkelmans et al. 2004) and laboratory experiments, usually with limited species, factors, acclimation and evolutionary histories, and time (Jokiel and Coles 1977, Berkelmans and Willis 1999, D'Croz et al. 2001, Jones and Hoegh-Guldberg 2001, Nakamura and van Woesik 2001, Nakamura et al. 2003, Warner et al. 2002, Lesser and Farrell 2005). In addition, comparing coral bleaching and mortality in sites with different environmental backgrounds has been insightful as they indicate the importance of the interaction between the environment and corals on a scale large enough to be relevant for field predictions and management priorities (Sheppard 1999, Glynn et al. 2001, Podesta and Glynn 2001, Berkelmans 2002, McClanahan and Maina 2003, Riegl 2003, Riegl and Piller 2003, McClanahan et al. 2005*b*, 2007*a, b*). These larger and synthetic studies lend insight into the species, sites, and factors that are expected to lead to persistence of corals and the coral reef ecosystem (Glynn 2000, McClanahan 2002).

The scientific and management challenge is to scale the above studies and important findings up to larger regions (Sheppard 2003, Wooldridge and Done 2004, Sheppard and Rioja-Nieto 2005), to test regional environmental models with field data, and to improve the understanding of causation between environmental histories, acclimation/adaptation, and survival in order to evaluate and predict the future of climate on corals (Wooldridge et al. 2005). Currently, we know that high SSTs above some site-specific threshold will lead to coral bleaching and mortality but that this threshold is sensitive to the taxa, regions, and associated environmental backgrounds (Coles et al. 1976, Coles and Brown 2003, Jokiel 2004, McClanahan 2004, McClanahan et al. 2004). There is considerable progress, but it is still less clear how the background temperature and environmental history influences acclimation, adaptation, and persistence within regions and different physicochemical environments (Riegl and Piller 2003). Past bleaching (Baker et al. 2004, Berkelmans and van Oppen 2006), water flow (Nakamura and van Woesik 2001, McClanahan et al. 2005*b*), temperature variation (Podesta and Glynn 2002, McClanahan and Maina 2003), persistence of cool water (Glynn et al. 2001, Riegl and Piller 2003), light (Iglesias-Prieto et al. 1992, Mumby et al. 2001*b*, Lesser and Farrell 2004, Gill et al. 2006), and inorganic nutrients (McClanahan et al. 2003) are all known to mediate the bleaching effect and influence the elasticity of the threshold. Therefore, environments with attenuating properties are likely to improve the chances for persistence of corals (Glynn 2000, Riegl and Piller 2003, West and Salm 2003, Barton and Casey 2005). Better understanding of these factors will improve predictions, and conservation and management priorities can be established, but only once the effects of these environmental factors have been tested with field studies at an appropriate scale (McClanahan et al. 2005*a*).

This paper advances the understanding by examining the spatial patterns of temperature variation and the recent temperature rise in the East African Coastal Current System from 1951 to 2002 and its possible relationship with the observed spatial variation in coral mortality that followed the 1998 El Niño Southern Oscillation (ENSO) event. The primary focus was to examine the interaction between the equatorial and coastal current system and the island of Madagascar and how their interaction influences the oceanographic and thermal environments and the potential for these environments to create acclimation/adaptation or refuge from climate change. Because this island–current interaction is widespread, our findings should have equally widespread application. Additionally, we examined the influence of a variety of environmental factors on a milder bleaching event in 2005 in an effort to distinguish the dominant attributes of temperature and other environmental variations on the intensity of bleaching. The combination of these studies increases the chances for determining causation and also factors that are good proxies for this causation. The ultimate purpose is to identify the spatial and temporal structure of the temperature rise and coral mortality to assist in making predictions concerning the expected temperature increase on reef organisms and to set associated regional priorities for research and conservation. The other principal objective of this study is to determine if useful indicator variables can be distinguished and also to identify areas that will either not experience high environmental stress or that have high resistance to stress and quick recovery, both of which are paramount to our understanding of coral reef resilience in the face of global climate change. Because SST is believed to be the dominant factor causing coral bleaching and mortality and because there are data sets of moderate spatial and temporal resolution, we explore variation in SST and coral mortality due to bleaching in East Africa on the scale of ~1000 km and ~50 years. We also combine these studies with more environmental variables to improve the chances for understanding the difference between causations and proxies of causation.

Methods

Study area and background

East Africa is well known for its dynamic oceanographic setting, covering several latitudes and different

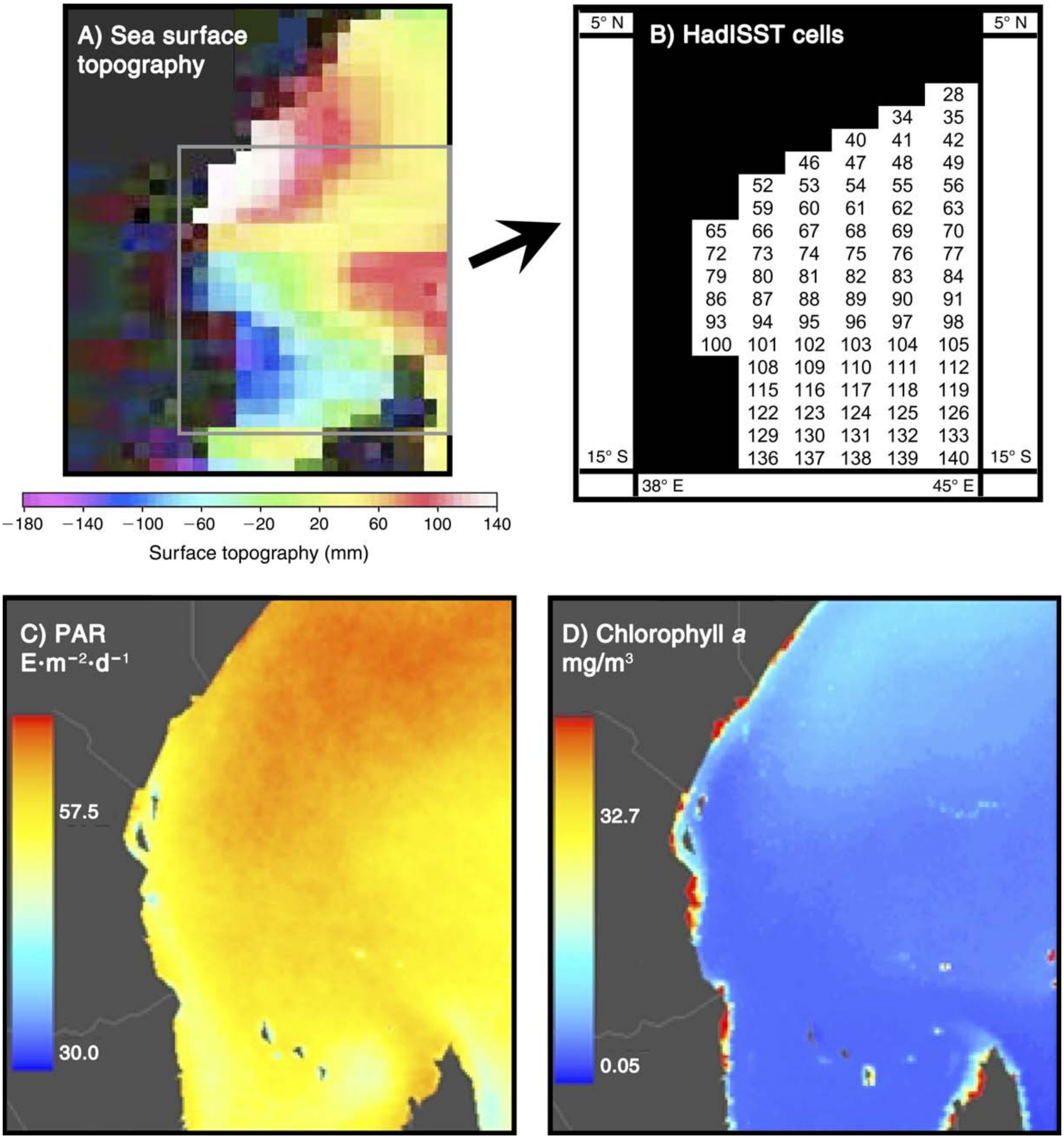

FIG. 1. Maps of (A) sea surface topography, (B) distribution of the cells used in the HadISST analysis, (C) photosynthetically active radiation (PAR), and (D) chlorophyll *a* in East Africa. Patterns roughly represent the hydrodynamics in the East African Coastal Current System and are more or less consistent among years and seasons. Sea surface topography data for 20 April 2005 are available at ⟨http//sealevel.jpl.nasa.gov/science/data.html⟩. Data for chl *a* and PAR are available at ⟨http://oceancolor.gsfc.nasa.gov/cgi/level3.pl?DAY=&PER=&TYP=swchl&RRW=16⟩.

marine habitats influenced by the Indian Ocean monsoon seasonality, tropical currents, and different topographies (Benny 2002; Fig. 1). The Equatorial Current in East Africa is displaced south of the equator such that it passes over northern Madagascar and swings north along the East African coastline where it is known as the East African Coastal Current (Benny 2002). There is a temporary reversal of the surface current during the northeast monsoon from November to March, but this only affects the most northern part of the study site. Wind, wave height, and current data suggest that the highest physical energy is found at the northern tip of Madagascar and then in the northern part of this region. Madagascar and to some extent the islands of Tanzania (Songo Songo, Mafia, Zanzibar, and Pemba) act as barriers to the larger Indian Ocean physical energy and

TABLE 1. Geographic positions, country names, and study sites in East Africa; coral cover before and after the 1998 bleaching event; and changes in cover relative to cover before the 1998 bleaching.

Country and location	Reef/site	Latiude	Longitude	Cover before 1998 (%)	Cover after 1998 (%)	Absolute change (%)
Comoros						
Comoros (CM)	Mitsamuli	−12.21	43.52	55	40	15
Comoros (CM)	Itsamia	−12.21	43.52	54	36	18
Kenya						
Kenya (KN)	Diani	−4.2117	39.3469	21.21	8.34	12.87
Kenya (KN)	Ras Iwatine	−4.0117	39.4357	17.78	5.26	12.52
Kenya (KN)	Mombasa	−3.593	39.4502	41.98	18.75	23.23
Kenya (KN)	Kanamai	−3.5524	39.4721	22.03	21.51	0.52
Kenya (KN)	Vipingo	−3.4796	39.5017	19.81	7.86	11.95
Kenya (KN)	Watamu	−3.2259	39.5933	37.67	8.99	28.68
Kenya (KN)	Malindi	−3.1534	40.0844	44.22	11.09	33.13
Kenya (KN)	Kisite	−4.709	39.3703	22.23	9.98	12.25
Tanzania						
Mafia (MA)	Tutia	−8.06552	39.38546	80	13	67
Mafia (MA)	Mange	−8.03063	39.35301	70	12	58
Mafia (MA)	Juani	−7.58518	39.48518	70	11	59
Mnazi Bay (MB)	Chumbo	−10.19162	40.21349	60	20	40
Mnazi Bay (MB)	Cha Kati	−10.18537	40.2208	60	20	40
Pemba (PM)	Misali3	−5.15127	39.35066	30	5	25
Pemba (PM)	Misali1	−5.14137	39.35396	74	17	57
Pemba (PM)	Misali2	−5.14012	39.35453	57	7	50
Songo songo (SS)	Amana	−8.42187	39.2622	35	30	5
Songo songo (SS)	Jewe	−8.38059	39.26151	30	30	0
Tanga (TN)	Upangu	−5.1857	39.04444	50	42	8
Tanga (TN)	Chanjale	−5.18308	39.03529	45	30	15
Tanga (TN)	Taa	−5.17357	39.05461	67	16	51
Tanga (TN)	Kitanga	−5.1713	39.04304	50	45	5
Unguja (ZN)	Kwale	−6.22519	39.16569	30	15	15
Unguja (ZN)	Chumbe	−6.16291	39.1025	52	42	10
Unguja (ZN)	Bawe	−6.08326	39.08051	53	45	8
Unguja (ZN)	Chapwani	−6.07174	39.11351	44	25	19
Unguja (ZN)	Changuu	−6.06522	39.10053	50	33	17

Notes: Absolute change is the difference between cover before 1998 and after the 1998 bleaching mortality. Relative change is the absolute cover over cover before 1998. Abbreviations are country and region names: KN is Kenya; MA is Mafia, southern-central Tanzania; MB is Mnazi Bay, southern Tanzania; PM is Pemba, northern Tanzania; SS is Songo Songo, southern-central Tanzania; TN is Tanga, northern Tanzania; ZN is Zanzibar, northern Tanzania; CM is Comoros.

create a low-energy shadow that extends from Mozambique to northern Tanzania (Fig. 1). This region is influenced by the El Niño Southern Oscillation (ENSO; Cole et al. 2000), and the Indian Ocean also contains its own endogenous cycle known as the Indian Ocean Dipole (IOD), which is a pressure gradient between Sumatra and the Arabian Peninsula and has greatest impacts in the eastern and western margins of the Indian Ocean (Saji et al. 1999, Webster et al. 1999, Kayanne et al. 2006). The natural variability of the western Indian Ocean SST dipole and ENSO has been detected from coral skeleton isotope records of the past 300 years (Charles et al. 1997, Cole et al. 2000, Zinke et al. 2004, 2005, Damassa et al. 2006, Kayanne et al. 2006).

DATA SOURCE AND ANALYSES

Temperature data

Four sources of temperature data were used in determining spatial variability in East Africa: direct readings from NOAA satellite images and calculated from the HadISST and JCOMMSST (satellite images *available online*).[6] The HadISST is a set of quality-controlled global long-term in situ SST data collected from ships and buoys (Rayner et al. 2003) and provided as monthly means for 1 × 1 degree longitude–latitude squares (data *available online*).[7] JCOMM is a shorter time series that includes SST data from satellites that are corrected using those recorded from in situ measurements and are presented as weekly and monthly means in 1 × 1 degree latitude–longitude squares (Reynolds et al. 2005; data *available online*).[8] We undertook analysis of the HadISST data from the East African coast from 16° S to 5° N and from 38° E to 45° E from 1951 to 2002. In situ temperatures were recorded using Hobo temperature loggers (Onset Corporation, Pocasset, Massachusetts, USA). Loggers were placed at eight Kenyan reef locations that covered ~200 km in a north–south direction along the coastline. Except the southern-most

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[6] ⟨http://www.osdpd.noaa.gov/PSB/EPS/SST⟩

[7] ⟨http://www.cru.uea.ac.uk⟩

[8] ⟨http://iri.Columbia.edu/climate/monitoring/ipb⟩

TABLE 1. Extended.

Relative change	Reference
0.27	Quod and Bigot (2000)
0.33	Quod and Bigot (2000)
0.61	McClanahan et al. (2001)
0.70	McClanahan et al. (2001)
0.55	McClanahan et al. (2001)
0.02	McClanahan et al. (2001)
0.60	McClanahan et al. (2001)
0.76	McClanahan et al. (2001)
0.75	McClanahan et al. (2001)
0.55	T. R. McClanahan, *unpublished data*
0.84	Muhando and Mohammed (2002)
0.83	Muhando and Mohammed (2002)
0.84	Muhando and Mohammed (2002)
0.67	Muhando and Mohammed (2002)
0.67	Muhando and Mohammed (2002)
0.83	Muhando and Mohammed (2002)
0.77	Muhando and Mohammed (2002)
0.88	Muhando and Mohammed (2002)
0.14	Muhando and Mohammed (2002)
0.00	Muhando and Mohammed (2002)
0.16	Muhando and Mohammed (2002)
0.33	Muhando and Mohammed (2002)
0.76	Muhando and Mohammed (2002)
0.10	Muhando and Mohammed (2002)
0.50	Muhando and Mohammed (2002)
0.19	Muhando and Mohammed (2002)
0.15	Muhando and Mohammed (2002)
0.43	Muhando and Mohammed (2002)
0.34	Muhando and Mohammed (2002)

site of Kisite, the reefs are lagoonal and isolated from the open ocean during low tide (tidal range of 4 m at spring low tide) and were not expected to differ significantly in their physicochemical properties. This isolation causes the temperature in the lagoons to rise above that of the open water during the warm season. The reefs differ in their distance from shore (0.1–1.0 km), the height of the reef above the datum, their proximity to channels or reef depressions that connect to open sea (McClanahan and Maina 2003). The physical differences, particularly the height and isolation of the reef from the open ocean, were expected to result in different SST environments, especially during the warm season (from February to April; McClanahan et al. 2001, McClanahan and Maina 2003). In situ temperature data are presented for the 2003–2005 time period when data were available for all sites. Means of the in situ data recordings from Mombasa, one of the sites most exposed to the open ocean, are highly correlated to those from NOAA SST ($R^2 = 0.86$; McClanahan et al. 2001).

Coral cover before and after the 1998 bleaching episode

Coral cover data before and after the bleaching event in 1998 was obtained from the literature and field survey data. We present data from reef areas that were surveyed or studied before the 1998 bleaching event (McClanahan et al. 1999, McClanahan et al. 2001, Muhando and Mohammed 2002; Table 1). A mixture of haphazard and permanent transects were used at each site. Permanent transects were recorded using 10–20 m Line Intercept Transects (LIT). Haphazard transects were sampled using the Line Point Intercept (LPI) method by dividing a 50-m transect into 200 points at intervals of 25 cm. Most sites were surveyed using 2–3 transects with the exception of the sites on Mafia Island (9–10 transects). Published and unpublished data collected by McClanahan and colleagues (1997 and 1999; McClanahan et al. 2001, McClanahan and Maina 2003) were used for most Kenyan sites. For Kisite Island, there were no 1997 and 1999 benthic cover data, but data from 1996 and 2001 were available and used. Coral cover in Kenya was surveyed using 10-m LIT (n = 9–12 transects at each site/reef). Information from Quod and Bigot (2000) was used for the two Comoros sites where cover data were gathered according to the Global Coral Reef Monitoring Network (GCRMN) rapid LIT assessment. Nineteen of the Kenyan and Tanzanian sites had data on community structure and analysis of taxa-specific bleaching mortality was possible.

Bleaching response in 2005

Following the appearance of a hot spot in the southern Indian Ocean in January 2005, we surveyed coral bleaching in eight reefs along the Kenyan coast in April 2005, a few weeks after peak water temperatures. Bleaching was defined as a loss of color and estimated by evaluating the color intensity of haphazardly selected corals within a radius of ~2 m (McClanahan et al. 2001, McClanahan 2004). This process was repeated several times, and between 486 and 992 coral colonies were sampled at each site and assigned to one of six categories: (1) unbleached (normal coloration), (2) pale (lighter color than usual for the time of the year), (3) 0–20% of the surface bleached (white coral skeletal coloration), (4) 20–50% bleached, (5) 50–80% bleached, and (6) 80–100% bleached. The assessment of bleaching from coloration, especially in colonies of the same species and the presence of genetically different symbionts with different environmental tolerances and light absorption capacities, poses a number of difficulties (Knowlton et al. 1992, Jones 1997, Enriquez et al. 2005). The field method was originally developed by Gleason (1993), modified by McClanahan et al. (2001), and tested between regions and observers (McClanahan et al. 2004); two related field and laboratory studies that found good correlations between color ranks and pigment concentrations and cell densities (Edmunds et al. 2003, Siebeck et al. 2006). Enriques et al. (2005) suggest that light absorption did not increase greatly for pigment concentrations above 20 mg chl a/m^2 in *Porites banneri* and light-absorption-based estimates of bleaching will not be accurate above this pigment concentration. Their data (Enriques et al. 2005: Fig. 3A) does, however, suggest a nearly linear relationship for absorption and pigment concentrations for samples below 50 mg/m^2 of chl *a* and very low samples sizes above this concentration. Other tests of color rank and pigment concentrations below this level have found good and nearly linear relationships between color ranks and light-absorption measures (Edmunds et al. 2003, Siebeck et al. 2006), and taking the three studies together would suggest a strong relationship with the range of pigment concentrations that are commonly found in field situations during warm seasons and bleaching events. This method has been shown to produce comparable results that will allow for scaling bleaching intensity and make comparisons between site, times, and regional and global comparison (McClanahan et al. 2004, 2007*a*). Bleaching response was calculated as a scaled percentage from the observations in each color category and a Bleaching Index (BI) generated as follows: BI (%) = $(0_{c1} + 1_{c2} + 2_{c3} + 3_{c4} + 4_{c5} + 5_{c6})/5$, where *c* is the percentage of observations in each of the six bleaching categories (McClanahan et al. 2005*b*). Most studies of pigment and cell density concentrations during bleaching events have found at least an order of magnitude reduction (Edmunds et al. 2003, Enriquez et al. 2005, Siebeck et al. 2006). Therefore, the spread in the BI response implied by this equation may be somewhat lower than found for pigment and cell concentrations.

In order to test for a relationship between water flow and bleaching, we estimated water flow speed using the dissolution of plaster of Paris (calcium sulfate) clod cards (Doty 1971) as described in McClanahan et al. (2005*b*). Water flow was sampled at each site, multiple times, between 2003 and 2005, and each sample was based on the deployment of 4–6 clods that were fastened to the reef surface such that the total sample number per reef was between nine and 27. Tests of the clod dissolution method to predict water-flow speed in experimental flumes have found strong relationships ($R^2 > 0.96$; Jokiel and Morrissey 1993, Anzai 2001).

Data analysis

Temperature data.—To determine temporal trends in East Africa, we undertook regression analysis of the monthly means of the averages, minima, and maxima of the HadISST data with time and also by separating out ENSO (El Niño–Southern Oscillation) and IOD (Indian Ocean Dipole) years. We used the ENSO and IOD years provided by Saji et al. (1999), which do not include weak events (ENSO years were 1957–1958, 1965–1966, 1972–1973, 1982–1983, 1987–1988, 1991–1992, and 1997–1998; IOD years were 1961, 1963, 1967, 1972, 1977, 1982, 1991, 1994, and 1997; ENSO–IOD years where both events coincide were 1972, 1982, and 1997). Within each geographic cell in the HadISST database, a variety of statistics of the SST data were calculated for the whole time series, and relationships among the different temperature statistics were investigated with Spearman's correlation analysis. Single model regression analysis was used to predict the influence of the mean, SD, minimum, maximum, median, kurtosis, and skewness of SST on the 1998 degree-heating months (DHM98). We present the best-fit model for either the linear or second degree polynomial selecting the model with the largest R^2. The properties of the distribution of the temperature data are expected to have a significant effect on short-term acclimation and longer term adaptation, and therefore, characterization of the data included skewness and kurtosis. These two measures have been widely used by physical scientists in describing distributions where skewness measures the distance of outliers and kurtosis the flatness or peakiness of the data distribution. The most important SST variables were identified with a stepwise multiple regression models—the SD was excluded due to the high correlation they have with the other SST statistics, and SD is a component of skewness and kurtosis.

Degree heating refers to the time that a temperature is above the mean maximum temperature for a specific site and is used to describe and predict the heating stress and bleaching in corals (Liu et al. 2005, McClanahan et al. 2007*a*). Often it is presented at NOAA web sites in weeks (degree-heating weeks, DHW; data *available online*).[9] For the HadISST data set it is, however, calculated in months (degree-heating months, DHM), as the data are compiled and presented as monthly means. Currently NOAA's DHW is calculated as the cumulative positive anomaly from the mean SST climatology of the climatologically warmest month at a location (Liu et al. 2005). It is presented as the accumulation of anomalies (also called hot spots) at a grid of 50 × 50 km over a rolling 12-week time period, and only anomalies of 1° and above are considered. Values <1°C are disregarded as insufficient to cause visible stress in corals (Liu et al. 2005). Degree-heating weeks or months for the HadISST and JCOMMSST data were calculated for each grid as the cumulative positive anomalies above the long-term mean summer maximum for the three warmest months: February, March, and April (Barton and Casey 2005). Anomalies were calculated from the long-term baseline: 1950–1997 for the HadISST data, 1981–1997 for the JCOMMSST data, and direct readings from satellite images for the NOAA data (1998) from February to April 1998. DHW were not calculated for the in situ seawater temperature data from Kenya, as the measurement time is not long enough to provide a reliable climatology for all the sites.

Change in coral cover.—Change in absolute coral cover was determined by calculating the difference between the pre- and post-1998 bleaching coral cover for each site or reef area. The relative cover was obtained as a percentage proportion of the absolute cover over the prebleaching cover. A single model regression analysis was conducted on the absolute cover

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[9] ⟨http://www.osdpd.noaa.gov/IPD/IPD.html⟩

as a function of the cover before 1998. In addition, the relationship between change in cover and cover of *Acropora* and non-*Acropora* before 1998 was analyzed in order to determine whether the change in cover was due to a higher differential mortality of *Acropora*, one of the most dominant taxa in the Indo–Pacific and highly susceptible to bleaching (see Plate 1). Temperature variations from in situ recordings in Kenya, expressed in coefficients of variation (CV) and standard deviations (SD), were used to describe between-site and reef variation. The effect of coral cover before 1998 on the absolute change in coral cover was compared between Kenya and Tanzania with a factorial ANOVA by taking country as a fixed variable and cover before 1998 as a continuous one. The effect of temperature variation (SD and CV) from in situ recordings on the absolute and relative change in coral cover was tested using a single regression model for Kenyan sites.

Bleaching response in 2005.—The site specific Bleaching Index (%BI) was calculated by pooling the BI of all taxa in each site in Kenya where in situ temperature data were available. The relationship between temperature variation (SD) and water flow was determined with single and multiple regression analysis. A stepwise multiple regression model with BI as a response and temperature SD and flow speed and their interaction as predictor variables was used. All statistical analyses were performed using JMP 5.1 for Mac (SAS Institute, Cary, North Carolina, USA) and SPSS 10.0 for Windows (SPSS, Chicago, Illinois, USA), and spatial analysis and mapping using ArcView GIS 3.2 (ESRI, Redlands, California, USA).

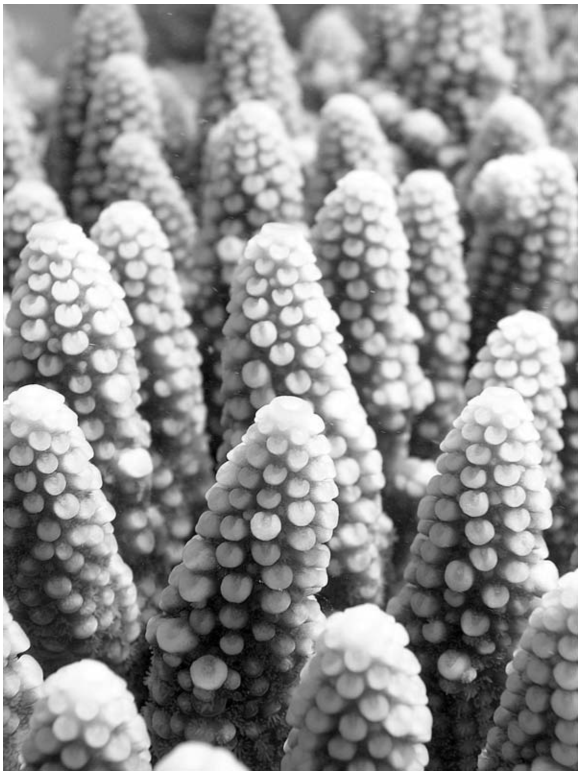

PLATE 1. Branching corals such as this species of *Acropora* are a complex but regular structure created by the coral animal, the algal symbiont, and the calcium carbonate skeleton. Photo credit: T. R. McClanahan.

RESULTS

Temporal variation in SST

The mean and maximum SSTs in East African coastal waters increased at a rate of 0.01°C/yr over the last ~50 years (Fig. 2; $R^2 = 0.37$; $P < 0.05$). The minimum increased at a rate of 0.007°C/yr. This amounts to a total rise of 0.5°C of the mean and maxima and 0.35°C of the minima in the last half a century. Analysis of individual confidence interval (95%) identified that mean SSTs of 1983, 1987, and 1998 were higher from the trend of SST increase over time ($P < 0.05$). Similarly, maxima of 1983 and 1998 and minima of 1972 and 1983 were notably higher. Minima of 1964 and 1996 were unusually lower ($P < 0.05$). Mean (27.88°C) and maximum (30.00°C) of 1998 were the highest and minimum of 1964 (24.44°C) the lowest. Generally second degree polynomials had good fit for all three SST parameters, but differences from the linear fit were small, respectively 0.7%, 4.2%, and 1.6% for the mean, maximum, and minimum. Analysis of the individual spatial cells indicated considerable spatial variation ranging from nonsignificant changes, to linear, to weak but also included decreasing second degree polynomials and weak exponential rises.

Non-ENSO, ENSO, IOD, and combination of IOD and ENSO (IOD-ENSO) years were analyzed separately due to the different patterns of these years. The mean SSTs increased significantly during both non-ENSO and ENSO years, respectively 0.0075°C/yr and 0.015°C/yr ($P < 0.05$), and the increases were higher during ENSO than non-ENSO years (Factorial ANOVA: non-ENSO/ENSO as fixed and year as continuous variable; $P = 0.038$). The increases in maximum SSTs were also higher during ENSO (0.021°C/yr) than non-ENSO years (0.0065°C/yr; $P = 0.006$). Increase in the minimum SST was significant only during non-ENSO years (0.006°C/yr; $P = 0.04$). The y-intercept was highest during IOD/ENSO years for mean and minima; ENSO years had higher values than non-ENSO years. IOD years had highest y-intercept for maxima; ENSO-IOD years were higher than ENSO and non-ENSO years.

The three ENSO events of 1982–1983, 1987–1988, and 1997–1998 had the highest recorded mean SSTs in East Africa (Figs. 2 and 3). Comparisons of the three indicate that both mean and maximum of 1997–1998 were the highest. Minimum temperatures were highest in 1987–1988; all three statistics were lower in 1982–1983 than in 1987–1988 and 1997–1998. The 1982–1983 ENSO did not warm as early or as quickly as in 1987 or 1997 and the 1997–1998 event persisted longer than the other two events. The 1982–1983 SSTs were higher only in the end of the warm season in June and July. The 1987–1988

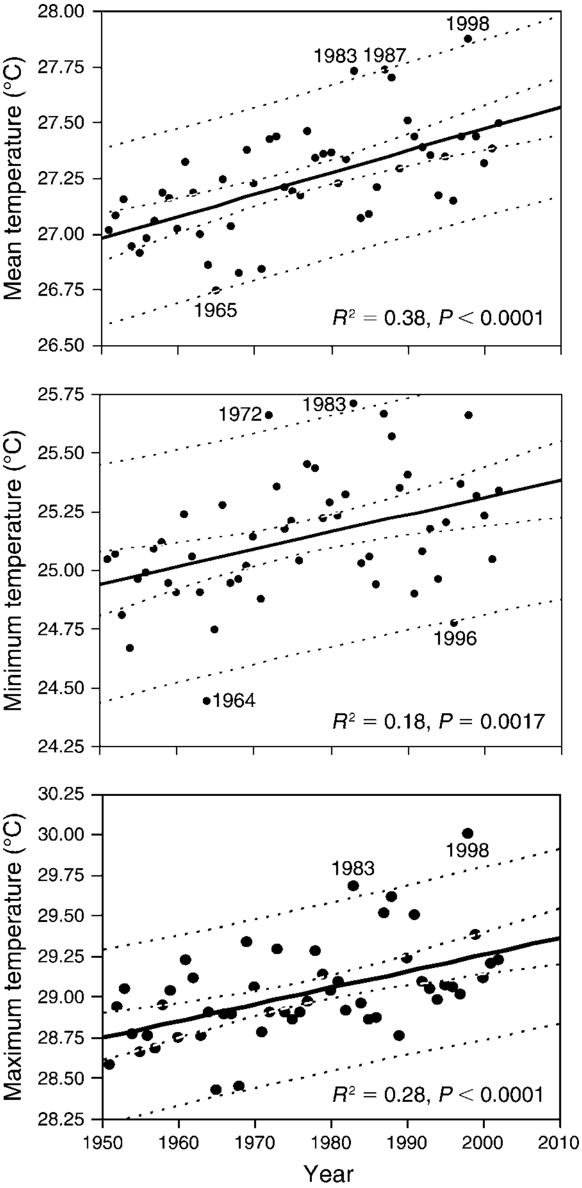

FIG. 2. Time series of annual mean, maximum, and minimum HadISST increases in East Africa. Inner dotted lines indicate 95% CI of the regression line, and outer lines indicate 95% CI of the individual points. Outliers are indicated. Data are pooled means of all cells.

ENSO event had an earlier and stronger build up in the cold season. During the hot season, January to April, the 1997–1998 event was the strongest followed by the 1987–1988 for the mean, maximum, and minimum SSTs.

Spatial variations in SST

The overall statistical properties and spatial distributions of the temperature data in the East African region show both latitudinal and longitudinal variation (Figs. 4–7). The mean, SD, and median SSTs showed similar trends (Figs. 4A–D and 5A) with values increasing to the south from southern Somalia to the Comoros. Values also decreased from the east off Madagascar to the west toward Tanzania and Mozambique, but this decrease was of a lower magnitude compared to the latitudinal trend. Modal SSTs generally had a weak but decreasing trend in a north–south direction (Fig. 5B). The few squares that had lower values were scattered mainly in offshore locations without a clear gradient in distribution.

The properties of the distribution of the temperature data were tested and, according to a test of significance for kurtosis and skewness (Tabachnick and Fidell 1996), all 81 cells in East Africa had significant negative kurtosis or a flat distribution; 45 had negative skewness and five had positive skewness. The remaining 31 cells

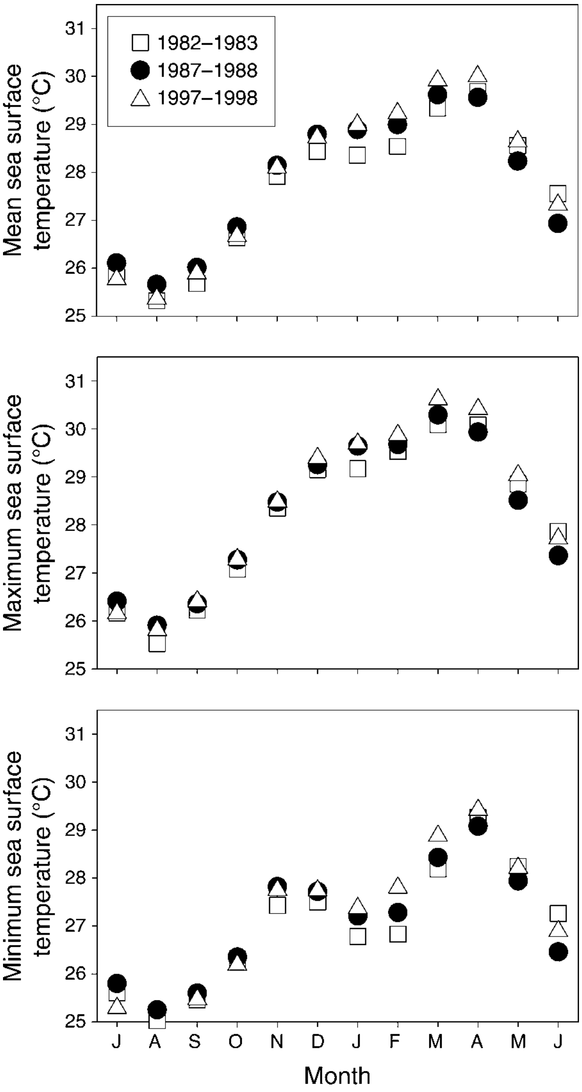

FIG. 3. Monthly mean, maximum, and minimum HadISST sea surface temperatures in East Africa during the 1982–1983, 1987–1988, and 1997–1998 ENSO events. Data are pooled means of all cells.

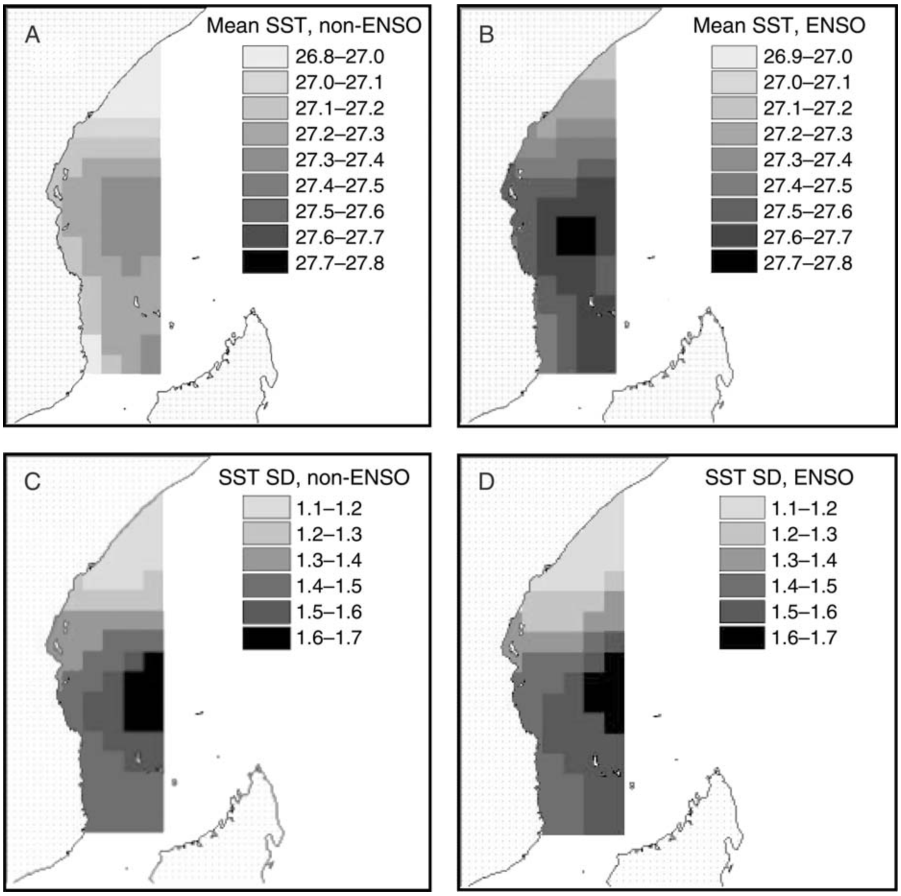

FIG. 4. Spatial distributions in (A, B) mean and (C, D) standard deviation of HadISST sea surface temperatures in East Africa for the 1951–2002 period. Non-ENSO and ENSO years are compared. See *Methods* section for classification of ENSO and non-ENSO years.

did not have significant skewness in SST distributions. Both SST skewness and kurtosis increased in a northerly direction (Fig. 5C, D). Patterns in maximum SSTs generally increased from inshore to offshore locations but had high variations (Fig. 6A).

Minimum SSTs increased in a south–north direction (Fig. 6B). Highest minima occurred in inshore and offshore Kenya and Somalia, and lowest values in inshore locations of Tanzania and Mozambique. Offshore sites had higher minimum SSTs than inshore locations in the southern sector. Mean SST values were higher in ENSO than during normal non-ENSO years for all sites (Fig. 4A, B), although the patterns in spatial distribution were similar between the two periods. Differences in temperature variations (SD) among the different sites between non-ENSO and ENSO years (Fig. 4C, D) were not as marked as the mean values. Many of the SST variables had significant correlations with each other (Table 2). The kurtosis and skewness were strongly correlated with the mean, median, and SD. The last three had significant positive correlations with each other.

Temperature rises and degree-heating months

The rates of temperature rise during ENSO years were higher than non-ENSO years for most of the squares (Fig. 7A, B). Nearshore and southern sites had the fastest rises, and the slowest rises were north of Madagascar and included the Comoros. Between-site variability was higher during non-ENSO years. Difference in mean annual temperatures between ENSO and non-ENSO years increased southward and reached highest in southern Tanzania–northern Mozambique while offshore sites of Kenya had the lowest values (Fig. 7C). Degree-heating months (DHM) in 1998 increased in a northerly direction with southern Somalia–northern Kenya having the highest values (Fig. 7D). Lowest values were distributed mainly offshore including the Comoros. Southern Tanzanian sites near Mafia, northern Mozambique, and south off the Comoros also experienced low DHM.

The relationship between the DHM and the different temperature statistics are worth noting as the degree-heating weeks (DHW) is often used for predicting coral

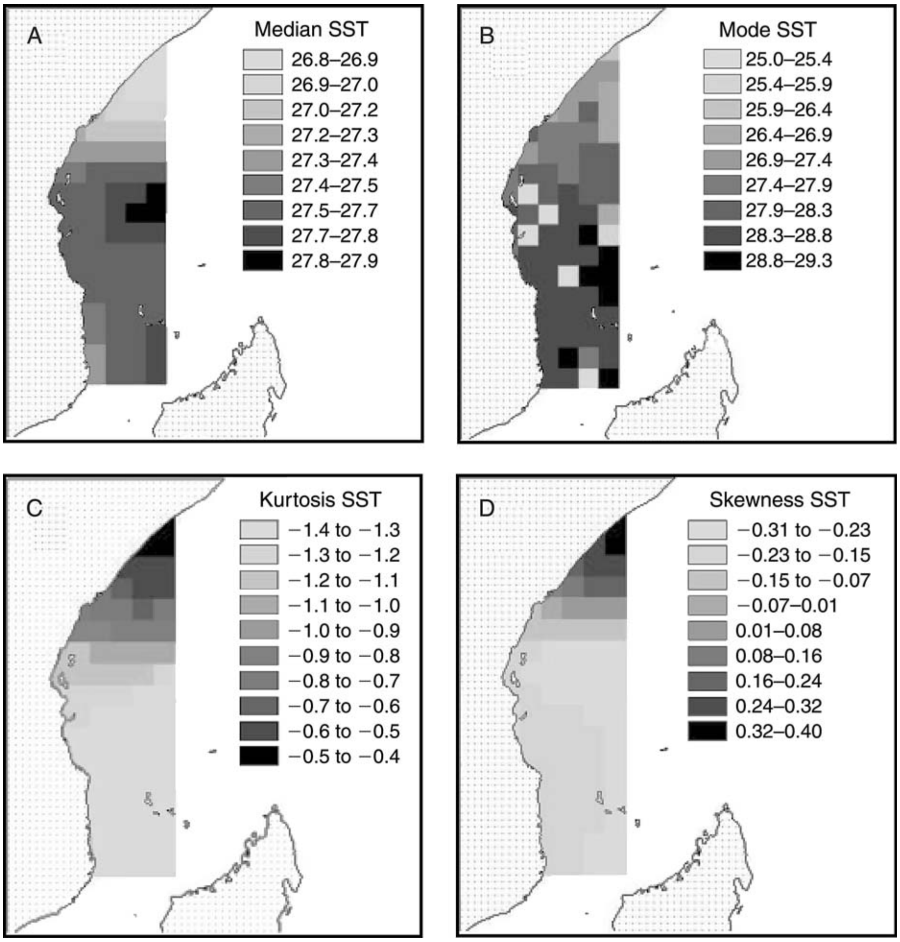

FIG. 5. Spatial distributions in (A) median, (B) mode, (C) kurtosis, and (D) skewness of HadISST sea surface temperatures in the grids for the 1951–2002 period in East Africa.

bleaching (data *available online*).[10] From simple regression models, mean ($R^2 = 0.84$), standard deviation ($R^2 = 0.80$) and kurtosis ($R^2 = 0.86$) gave very high fit with heating (Table 3). From stepwise multiple regressions, the mean, median, kurtosis, and maximum SST explained most of the variation in DHM ($R^2 = 0.89$; $F_{79,1} = 167.3$; $P < 0.0001$). Mean SST had a negative relationship with DHM, while the remaining variables all had positive relationships. DHM was mostly influenced by the variability in kurtosis SST (81.9%; Table 4). The remaining ~18% was explained by the median (8.9%), mean (6.3%), and maximum (2.9%). DHM98 linearly decreased with increase in SST SD (Fig. 8). It showed a very high latitudinal gradient in its distribution, the largest gradient occurs north of 10° S between Tanzania and Kenya (Fig. 9A). Related to the strong negative relationship between DHMs and SD, the latter has a very strong increase trend toward the south ($R^2 = 0.82$; $P < 0.0001$; Fig. 9B). There was no clear gradient in the relationship between longitude and DHM or longitude and SD ($P > 0.05$).

Change in coral cover following the 1998 bleaching event

Coral cover in East Africa appears to be affected by latitude and, in Kenya, management of fishing. All sites in Mafia, one site on Pemba, and two sites in Comoros had the highest coral cover. Unfished Kenyan reefs except Kisite had higher cover than fished Kenyan reefs. Most reefs in Tanga, on Zanzibar and Pemba had intermediate but higher cover than unfished Kenyan reefs. Except one site in Tanzania (Songo Songo), all reefs surveyed were affected by the bleaching as indicated by the significant decreases in cover (Fig. 10). All sites in Songo Songo, Chumbe and Bawe in Zanzibar, Upangu and Kitanga in Tanga, and the two sites in Comoros (Itsamia, Mitsamuli) had maintained relatively higher coral cover (30–45%) after bleaching in 1998. Tutia (Mafia Island) suffered the highest loss (67%), and only 13% remained in 1999. Other sites that suffered high losses of >50% were Mange (Mafia),

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[10] ⟨http://www.osdpd.noaa.gov/PSB/EPS/SST⟩

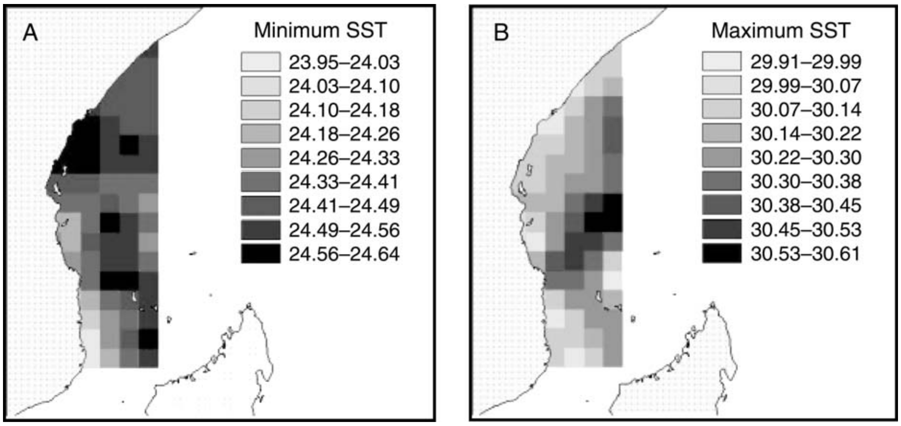

FIG. 6. Spatial distributions in (A) maximum and (B) minimum HadISST sea surface temperatures in the grids for the 1951–2002 period in East Africa.

Misali (Pemba), and Taa (Tanga). Kanamai was the least affected reef from Kenyan sites (0.53%), and the northern parks at Malindi (33%) and Watamu (29%) suffered most. Generally, reefs that were heavily fished were least affected in both Kenya and Tanzania (relative change in cover: fished reefs 0.43 ± 0.29; reefs closed to fishing 0.66 ± 0.23; $F_{76,4} = 4.87$; $P = 0.037$; absolute change in cover: fished reefs 0.18 ± 0.16; reefs closed to fishing 0.38 ± 0.21; $F_{76,4} = 8.43$; $P = 0.008$). However, the Kisite Park on the Kenyan–Tanzanian boundary had lower coral cover before 1998 (22.3%) and was less affected than the northern parks (12.3% loss), despite a comparable level of management protection to that of Malindi and Watamu parks.

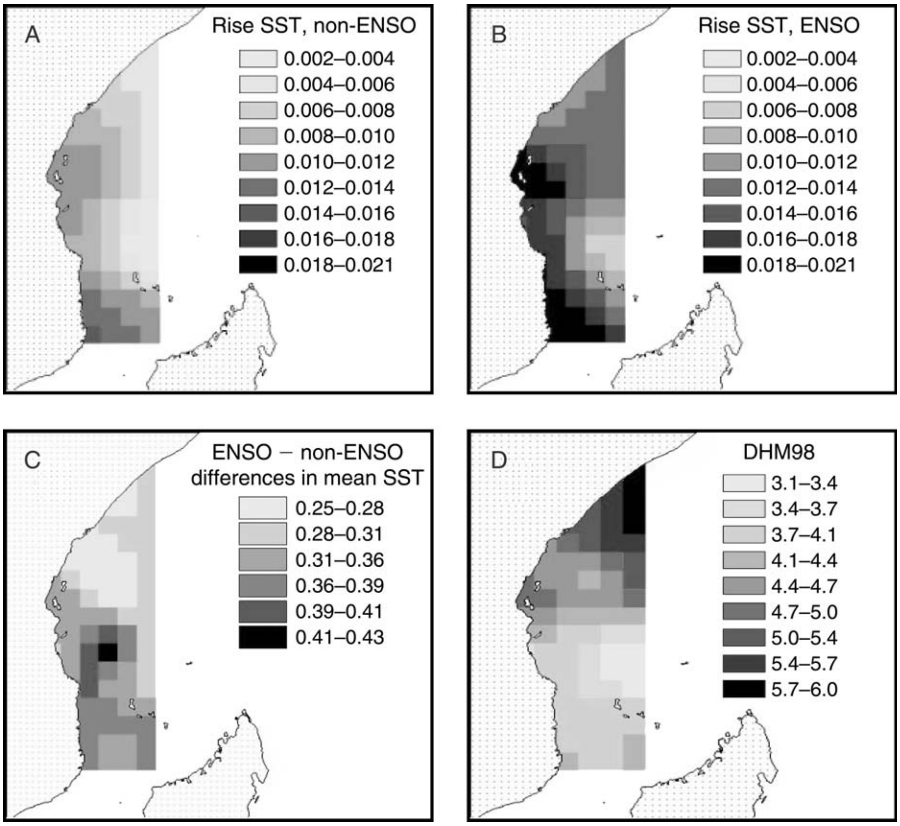

FIG. 7. Spatial distributions in mean sea surface temperature (SST) rises during (A) ENSO and (B) non-ENSO years, (C) mean differences between ENSO and non-ENSO events, and (D) degree-heating months in 1998 (DHM98) in the grids for the 1951–2002 period in East Africa. See the *Methods* section for classification of ENSO and non-ENSO years.

TABLE 2. Spearman's correlations among the different SST statistics.

	Mean	Median	SD of SST	CV of SST	Skewness	Kurtosis	Minimum
Median	0.97 (<0.0001)						
SD	0.87 (<0.0001)	0.85 (<0.0001)					
CV	0.87 (<0.0001)	0.84 (<0.0001)	1.0 (<0.0001)				
Skewness	−0.73 (<0.0001)	−0.82 (<0.0001)	−0.58 (<0.0001)	−0.58 (<0.0001)			
Kurtosis	−0.75 (<0.0001)	−0.73 (<0.0001)	−0.96 (<0.0001)	−0.95 (<0.0001)	0.58 (<0.0001)		
Minimum	0.090 (0.40)	−0.25 (0.06)	−0.26 (0.05)	−0.48 (0.0001)	0.50 (<0.0001)	−0.33 (0.01)	
Maximum	0.60 (<0.0001)	0.48 (0.0001)	0.48 (0.0001)	0.26 (0.05)	−0.38 (0.003)	0.23 (0.08)	0.03 (0.85)

Note: P values are in parentheses.

Coral mortality following the 1998 bleaching event showed a strong exponential relationship with coral cover (Fig. 10), with reefs that had high initial coral cover suffering the most. Change in cover was also significantly related to cover of *Acropora* ($R^2 = 0.40$; $P = 0.006$) and non-*Acropora* ($R^2 = 0.28$; $P = 0.025$). The change across 1998 could not be largely attributable to *Acropora* dominance at sites before 1998 as the change was nearly as strongly predicted by non-*Acropora* ($R^2 = 0.62$; $P < 0.0001$) as *Acropora* cover ($R^2 = 0.76$; $P < 0.0001$). Sites that had high initial coral cover of ~60% and were mostly from Tanzania. Below this level of cover, the mortality–cover relationship was highly variable. Generally, Kenyan reefs had higher change in cover or mortality than Tanzanian and Comorian reefs ($F_{\text{cntry}} = 9.4$; $P = 0.005$). The effects of cover before 1998 did not differ between Tanzania and Kenya. Tanzanian reefs of Songo Songo, Tanga, and Zanzibar, the shallow fished reef at Kanamai, Kenya, and the two reefs from Comoros suffered the least ($P < 0.05$). The unfished reefs of Kenya and Tanzanian reefs at Misali had higher relative coral mortality ($P < 0.05$). Unfished Kenyan sites suffered higher mortalities than their Zanzibar counterparts despite the lower cover they had before the bleaching episode.

Both absolute and relative changes in coral cover showed negative relationship with temperature variation (SD and CV) obtained from in situ measurements on Kenyan reefs ($P < 0.01$; Fig. 11). Results of mixed model regression analysis on absolute change showed significant effects of cover before 1998 and in situ temperature variation ($R^2 = 0.97$; $F = 37.9$; $P < 0.0001$) with no significant interaction ($P > 0.05$). The different SST statistics and DHM from the NOAA and HadISST data set did not give significant correlations with coral cover, mainly due to the low spatial resolution of the temperature data.

Bleaching response in 2005

The bleaching response in 2005 was highest in Malindi 2 (17.74%), Watamu (18.12%), Mombasa (Coral Garden, 13.59%), and lowest in Kanamai (0.85%; Fig. 12). Mean temperature did not show a significant effect on bleaching in 2005 ($P > 0.05$), but the relationship between bleaching and temperature variation (SD; Fig. 12A) was negative, while the relationship with water flow was positive (Fig. 12B). Temperature variation and water flow were strongly correlated ($r = -0.85$; $P = 0.008$). Stepwise multiple regression analysis showed significant effects only for water flow; temperature variation, mean temperature, and their interactions with water flow were removed from the model.

DISCUSSION

Temperature rise and ENSO events in East Africa

The level of rise in sea surface temperature in East Africa (Fig. 2) is in general agreement with other findings but indicates considerable spatial variation in

TABLE 3. Summary of simple regression analysis on the effects of the different SST statistics on degree-heating months (DHM98).

Predictor	R^2	$F_{79,1}$	P(F)	Term	t	Prob > |t|	Equation
Average	0.47	70.21	<0.0001	intercept	8.76	<0.0001	$y = 101.50 - 3.56x$
				x	−8.38	<0.0001	
SD	0.80	322.74	<0.0001	intercept	30.82	<0.0001	$y = 10.47 - 4.44x$
				x	−8.38	<0.0001	
Minimum	0.07	5.94	0.02	intercept	−2.08	0.04	$y = -25.89 + 1.24x$
				x	2.44	0.02	
Maximum	0.08	4.38	0.016	intercept	−0.07	0.94	$y = -1.18 - 0.19x - 7.39x^2$
				x	−0.35	0.73	
				x^2	−2.82	0.006	
Median	0.56	99.78	<0.0001	intercept	10.80	<0.0001	$y = 12.89 - 0.30x$
				x	−9.99	<0.0001	
Kurtosis	0.86	488.04	<0.0001	intercept	60.08	<0.0001	$y = 6.82 + 2.18x$
				x	22.09	<0.0001	
Skewness	0.60	117.51	<0.0001	intercept	72.68	<0.0001	$y = 4.88 + 3.31x$
				x	10.84	<0.0001	

Notes: The best-fit model between a linear and second-degree polynomial is presented for each variable. Direction of the relationship is indicated by the t ratio.

TABLE 4. Summary results of mixed model stepwise regression analysis on degree-heating months in 1998 (DHM98).

Predictor	Estimate	t	$F_{76,4}$	P
Intercept	24.44	2.31		
Mean SST	−4.01	−4.09	16.76	<0.0001
Median SST	2.58	4.87	23.68	<0.0001
Kurtosis SST	2.83	14.79	218.83	<0.0001
Maximum SST	0.70	2.80	7.82	<0.007

Notes: Only significant values are presented. Direction of the relationship is indicated by the t ratio. $R^2 = 0.89$; $F = 167.25$, df = 76, 4; $P < 0.0001$.

the responses. Global mean SSTs have increased by 0.4–0.8°C over the last ~100 years (Pittock 1999, McCarthy et al. 2001). Long-term temperature records for the Indian Ocean from coral cores taken in the Seychelles, Kenya, Madagascar, and Western Australia indicate a 0.8–1.4°C rise over the past ~200 years, with much of that rise reported since the mid 1970s (Charles et al. 1997, Kuhnert et al. 1999, Cole et al. 2000, Zinke et al. 2004, 2005). The Seychelles, Kenyan, and Tanzanian coral core records indicate cycles that average ~5.5 years but vary from 2–8 years and are contained in a longer cycle of about 8–14 years (Charles et al. 1997, Cole et al. 2000, Damassa et al. 2006).

Most of the outliers in the SST rise belong to ENSO, IOD, and ENSO-IOD events (Fig. 2). Some ENSO events, such as the ones in 1957–1958 and 1991–1992 (Goreau and Hayes 1994, Hoegh-Guldberg 1999, Saji et al. 1999, Edwards et al. 2001), were weak and not distinguished from background variability by our linear regression analysis. The 1996 minimum outlier from these data was not recorded as an ENSO, IOD, or ENSO–IOD event. SST rises in East Africa are higher during ENSO than non-ENSO years, and ENSO years have higher baselines (y-intercepts) indicating a higher SST buildup during those events.

The three ENSO events of 1982–1983, 1987–1988, and 1997–1998 have the highest recorded mean SSTs in East Africa (Figs. 2 and 3). Based on the response of the atmospheric climate, it has been suggested that the magnitude of the 1982–1983 event was higher than or equal to the 1997–1998 event (Wolter and Timlin 1998). The fact that South African locations suffered less severe drought and that the failure of the Asian Monsoon was less drastic in 1997–1998 than 1983–1984 was used as a correlate in comparing the two events. Our results do not support the contention that the 1982–1983 event was comparable in its strength to 1997–1998. Mean and maxima SSTs were higher in 1997–1998. The 1997–1998 event persisted longer; the 1982–1983 event was higher only in the end of the warm season of 1983 when SSTs had already started dropping below the mean annual maximum (Fig. 3; Spencer et al. 2000). During the bleaching season, 1997–1998 was highest followed by the 1987–1988 mean SSTs.

Differences in the intensity of coral bleaching, such as higher bleaching responses in 1982–1983 in some regions (Enfield 2001, Glynn et al. 2001), can not be used as evidence for a higher SST because corals undergo some acclimatization and adaptation to bleaching (Coles and Brown 2003, Baker et al. 2004, Berkelmans and van Oppen 2006, McClanahan et al. 2007*a*). In some studied Eastern Pacific reefs, coral bleaching was higher in 1982–1983 even though SST anomalies were lower or the same as in 1997–1998 (Glynn et al. 2001). Evidence for significant bleaching and mortality in the western Indian Ocean in 1982–1983 is scarce but may be due to a lack of investigation. The 1997–1998 event had both ENSO and IOD components (Saji et al. 1999), and from this and other analyses (Sheppard 2003), was the most geographically widespread and most severe anomaly in the Indian Ocean in recorded history.

Change in coral cover

The effect of the 1998 bleaching event is significantly related to coral cover, sites of high coral cover suffering the most. These are sites that mostly had high cover of branching and encrusting forms, which have thin tissue, high growths rates, and are highly susceptible to bleaching (Gates and Edmunds 1999, Marshall and Baird 2000, Loya et al. 2001, McClanahan 2004, McClanahan et al. 2007*b*). In many places during warm years, seasonally high water temperatures cause bleaching of the susceptible taxa, but recovery follows in a few months. In 1997–1998, even the more resistant forms were bleached, but mortality was higher in the fast-growing forms (McClanahan 2004). For example, Kenyan reefs in parks had the highest coral cover, the most susceptible branching and encrusting taxa, and the highest mortality. Coral cover on Kenyan reefs was reduced to 10–15% cover of mainly bleaching-resistant massive/sub-massive growth forms in both protected fishery closures and unprotected reefs (McClanahan et al. 2001). A direct physiological trade-off has been suggested between fast growth and resistance to

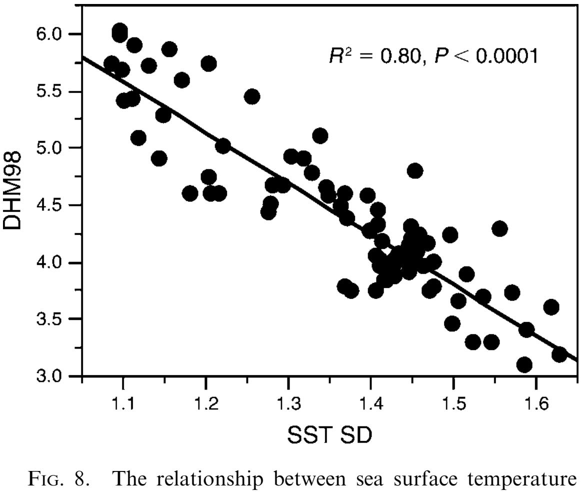

FIG. 8. The relationship between sea surface temperature standard deviation (SST SD) and degree-heating months in 1998 (DHM98) in East Africa.

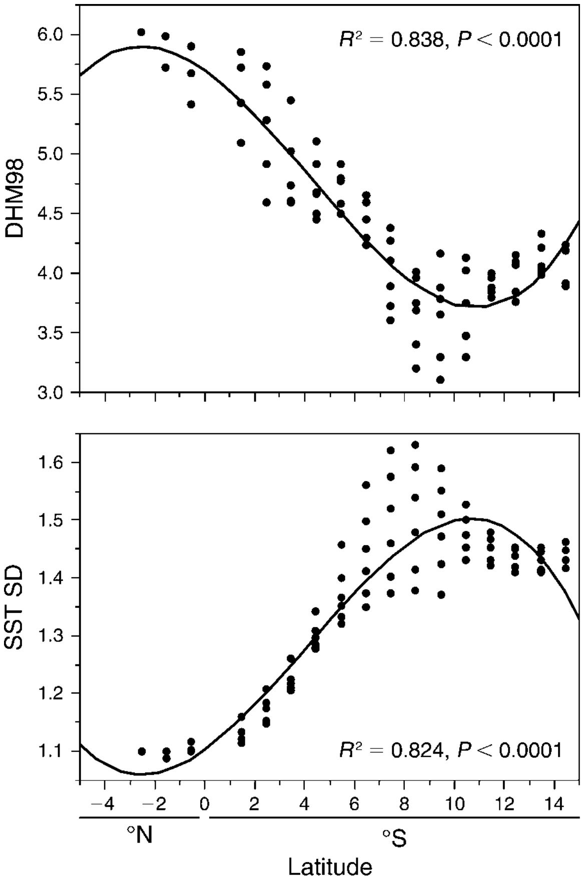

FIG. 9. Latitudinal variation in HadISST standard deviation (SST SD) and degree-heating months in 1998 (DHM98) in East Africa.

bleaching-induced mortality (Berkelmans and Wills 1999, Gates and Edmunds 1999, Loya et al. 2001). The change in coral cover in East Africa was significantly correlated with the cover of both *Acropora* and non-*Acropora,* indicating that variables other than the dominant taxa played a significant role either directly or by influencing community structure. On many Tanzanian reefs, where the overall change in coral cover was lower, mortality of *Acropora* was low and the genus is a main component of the community structure, especially on reefs protected from fishing (McClanahan et al. 2007*b*).

Despite the moderate fit, the relationship between absolute change in cover and temperature variation from in situ measurements (SD and CV) was not significant for Kenyan reefs, while the relative cover showed that mortality was higher in reefs with low temperature variance (Fig. 11). There are not a large number of reefs with long-term in situ data, so these relationships need confirmation from more study sites, but both plots indicate that reduced mortality did not occur until the SD was above 1.8 or a CV of >7%. The study underlines the importance of the initial level of coral cover and dominant taxa in determining absolute change across bleaching events. It is necessary to remove cover effects before examining for the effects of other environmental variables in analyses that involve spatial variations and between-site comparisons in change in cover (Côté et al. 2005).

Temperature variations, degree-heating months, and coral mortality

More relevant to the scope of this paper is the considerable spatial variation seen in the distribution of the different SST statistics in East Africa and how it may influence ecological communities. The strong negative relationship between SD and DHM may seem counterintuitive, but high SST SDs make it less likely that anomalies are rare events, and herein may lie the mechanism that creates the potential for acclimation/adaptation and persistence of corals through rare events. Northern sites, which have high DHM and coral mortality, have slightly lower mean and high skewness and kurtosis in SSTs. Relative differences in mean temperatures are considerably smaller compared to those of SDs and kurtosis (Fig. 4). The stronger effects of SD and kurtosis on DHM tend to override other temperature indices and are probably the key measures for associating with coral communities and the potential for acclimation/adaptation or susceptibility to bleaching and mortality (Table 4). Although all East African sites have negative kurtosis, low DHM sites have generally lower kurtosis or have platykurtic SST distributions that also tend to be concave and bimodal (Fig. 5D). High DHM sites have their temperatures more narrowly distributed around the mean, a tendency toward peakiness, and no evidence for bimodality.

Despite the strong relationship between change in hard coral cover or mortality and original cover, Kenyan reefs suffered higher mortality than Tanzanian or Comoros reefs relative to the initial coral cover. Tanzanian and Comoros sites had higher long-term SD and lower skewness and kurtosis in SSTs than Kenyan sites, whereas the differences in mean SSTs were not strong (respectively 27.43 and 27.53 for Kenya and Tanzania for the warmest month, April 1998). Stronger evidence for the influence of temperature variation comes from the in situ temperature data on Kenyan reefs, where the scale of sampling is more accurate and appropriate than the large-scale 36 × 36 km NOAA or 1 × 1° Hadley cells. The relationship between bleaching and mortality with temperature variation (CV and SD) becomes more robust and significant after controlling for cover before 1998. Kanamai, the shallow-most site with the highest temperature variation, experienced the least bleaching in 2005 and reduction in coral cover in 1998. Kanamai was an outlier when using large-scale data because of the shallowness and height of the reef and this produced higher temperature variation and low water flow and is a good example of how local- can

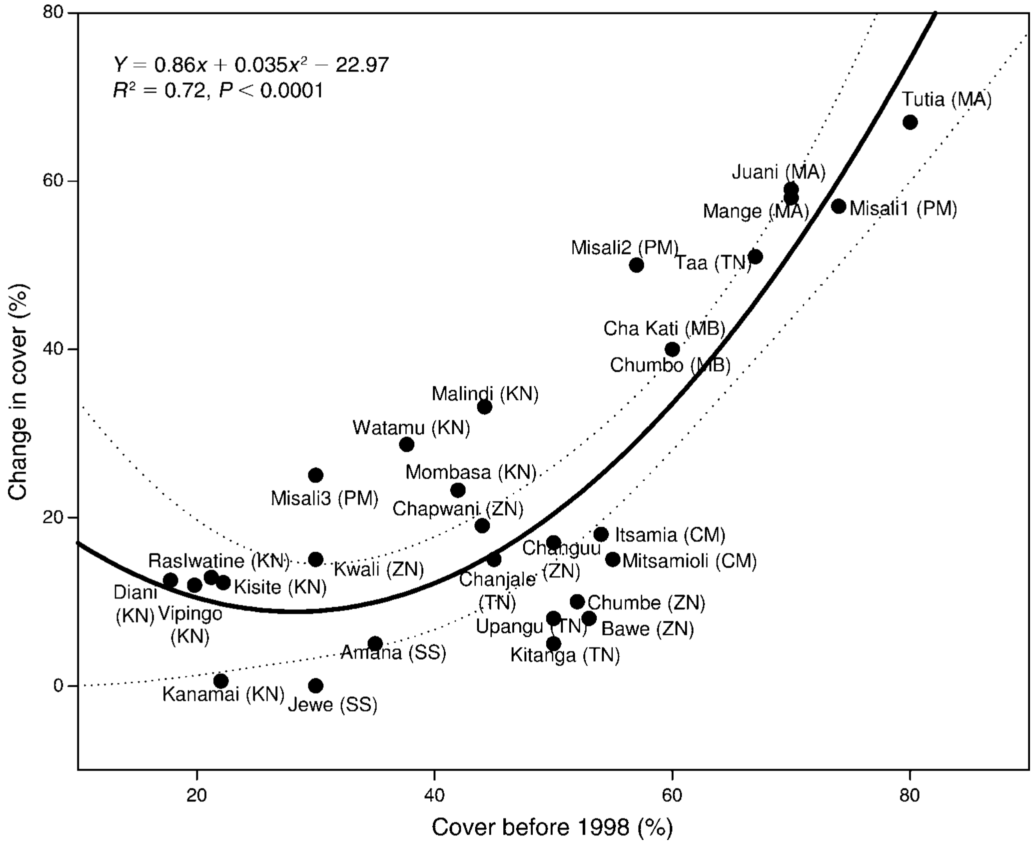

FIG. 10. The relationship between absolute change in coral cover and cover before 1998. Dashed lines indicate 95% CI of the regression equation. Absolute change is the difference between cover before 1998 and after the 1998 bleaching mortality. Relative change is the absolute cover divided by cover before 1998. Note that Cha Kati and Chumbo (MB) are represented by the same point. The location name is followed by a code that indicates country and region names: KN, Kenya; MA, Mafia, southern-central Tanzania; MB, Mnazi Bay, southern Tanzania; PM, Pemba, northern Tanzania; SS, Songo Songo, southern-central Tanzania; TN, Tanga, northern Tanzania; ZN, Zanzibar, northern Tanzania; CM, Comoros.

sometimes override large-scale factors (McClanahan and Maina 2003).

Spatial resolution and variability

Temperature data based on larger areas, such as the HadISST and JCOMMSST data sets, and to some extent the NOAA data, are useful for determining global or regional trends but in many cases are too crude in their spatial resolution to correctly predict coral bleaching at individual reefs as indicated by the low-fit and nonsignificant relationship between change in cover and the HadISST data. NOAA satellite data have a spatial resolution that is considerably finer than the HadISST data but are still not sufficiently resolved to be useful for some shallow nearshore and lagoonal reefs (Wellington et al. 2001). Temperature anomalies (Wooldridge and Done 2004) and bleaching (Andrefouet et al. 2002, McClanahan and Maina 2003, McClanahan et al. 2005*b*) are highly variable at small spatial scales. A large-scale study in the Indian Ocean indicated that as much as half of the response to bleaching may be due to the taxonomic composition of the corals at a site (McClanahan et al. 2007*a*).

Despite the devastating effects of the 1998 bleaching, the patterns in bleaching and mortality within the Indian Ocean were variable and contained many exceptions (Goreau et al. 2000, McClanahan et al. 2007*b*). Exploring these exceptions through analyzing the site-specific temperature history and its interactions with other local environmental parameters and the susceptibility of the coral community aids understanding on how corals cope with rare events (McClanahan et al. 2005*a, b*). Analysis of the Western Indian Ocean JCOMM–SST data indicates that DHM is significantly predicted by SD/kurtosis, maximum, median, minimum, and skewness (M. Ateweberhan and T. R. McClanahan, *unpublished data*). For example, in spite of their higher mean SST of 28.93°C, Maldivian reefs experienced the highest bleaching mortalities in 1998, with reefs having coral cover of <5% soon after 1998 (McClanahan 2000, Edwards et al. 2001). In contrast, mean JCOMMSST for Tanzania is 27.54°C. The oceanic Maldives has more

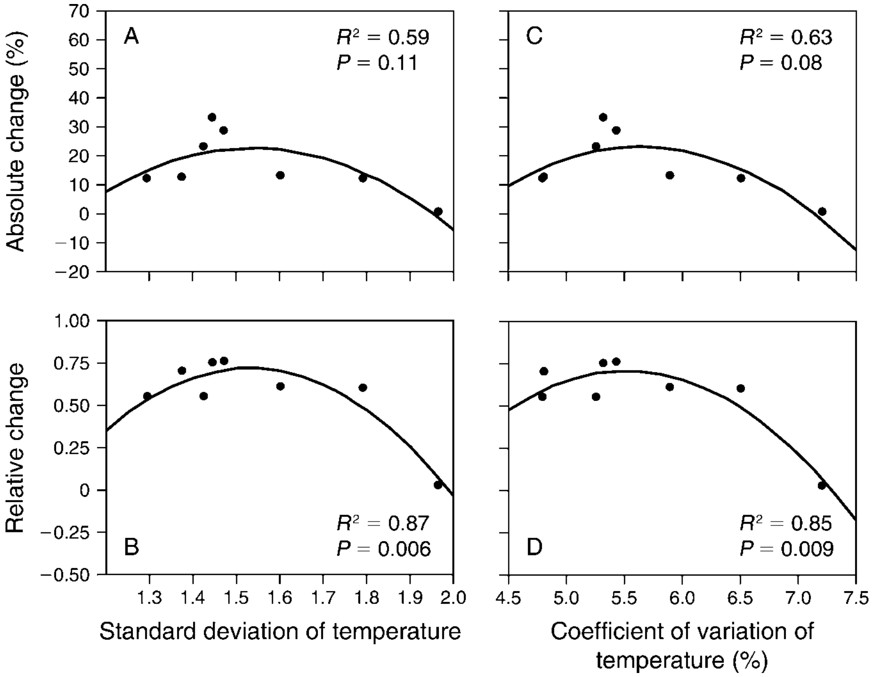

FIG. 11. Relationships between (A, C) absolute and (B, D) relative change in coral cover and in situ temperature variations (SD, CV) on Kenyan reefs. Absolute change is the difference between cover before 1998 and after the 1998 bleaching mortality; relative change is the absolute change divided by cover before 1998.

uniform and more rare warm temperatures (SD SST = 0.60, skewness = 0.50, kurtosis = −0.17) than Tanzania (SD = 1.41, skewness = −0.19, kurtosis = −0.17). The SD in East Africa is, in fact, 49–123% higher than the highest variation present in the entire Maldives (HadISST data). The more positive skewness of Maldivian temperatures reflects the occasional high DHM. In comparison, only a few squares (n = 9 squares; 17%) had significant positive skewness in East Africa and all of the East African cells with positive skewness had the highest DHM (5.4–6.0).

In contrast, reefs of Mauritius have some of the highest SD SSTs in the southern tropical Indian Ocean (1.70–1.82) and were among reefs least affected by the 1998 bleaching (McClanahan et al. 2005*b*). The temperature history of the sites has been overlooked and hardly reported, and the low bleaching in 1998 has been attributed to the cooling effect of Cyclone Anecelle, high cloud cover, and rainfall (Turner et al. 2000, Obura 2005). Windward and offshore sites are influenced most by oceanic effects, but they were reported as the most bleached (Turner et al. 2000). A study of the 2004 bleaching event in Mauritius indicated site-specific difference in bleaching that correlated well with temperature variation and water flow (McClanahan et al. 2005*b*). Bleaching correlated negatively with temperature variation (SD) but positively with water flow, and increased from the leeward to the windward side of the island as might be expected from temperature and water flow histories around islands. Similar to that in Mauritius, sites on Mafia and Misali at Pemba that receive direct oceanic waters suffered among the highest mortalities (Fig. 10; Mohammed et al. 2000). Glynn et al. (2001) also reported the highest mortality of corals across 1998 in the offshore islands of the eastern Pacific.

Lower DHWs/DHMs in Tanzania have been explained in terms of cooling effects of oceanic waters, high cloud cover and rainfall, and turbidity from river runoff (Muhando and Mohammed 2002, Obura 2005). Although other factors may have interacted with temperature, we hypothesize that the low DHM/DHW in Mauritius and East Africa resulted mainly from the effect of the high temperature variation. It is possible that some features, related to local hydrography and monsoon-related seasonality, localized upwelling, and protection could have interacted with temperature (Glynn 2000, Riegl and Piller 2003, Manzello et al. 2007). Nonetheless, because temperature is the principal factor affecting coral bleaching and mortality (Berkelmans and Willis 1999), anecdotal explanations of other effects and interactions should be considered carefully or investigated after controlling for the effects of temperature. Furthermore, prioritizing and planning for management requires permanent features such as island effects as opposed to what may largely be stochastic factors such as spatial and temporal changes in weather or light (Gill et al. 2006).

Given the small spatial scales at which temperature anomalies and bleaching operate, measurements of other environmental data that are expected to alleviate anomalous temperatures effects are best matched by similar spatial details as opposed to meteorological recordings in one or few stations or that average conditions over large areas. Similarly, there needs to be a matching of the temporal scale of environmental variables with the temporal scale of bleaching. The 1998 ENSO has been well identified for its steady warming over many months and bleaching is often a result of persistent warm water where DHW usually exceeds four weeks (Liu et al. 2005). It is less likely that short-term climatic events that pass in a few hours or days will have a significant effect on warming and bleaching. Cloud cover, although with exceptions such as the permanence of monsoons or other persistent weather events, is usually an impermanent and less reliable factor of attenuation. Similarly, aerosols have been shown to reduce bleaching effects but are often controlled by volcanic eruptions or other stochastic weather patterns (Gill et al. 2006). Shading by permanent objects, such as high islands, emergent rocks, and coral heads (West and Salm 2003), position on a reef in relation to depth (Riegl and Piller 2003), and coral orientation (Dunne and Brown 2001) are recognized as permanent and reliable attenuation factors from high radiation. Additionally, our study identifies the area from northern Madagascar to Comoros is an area of localized and weak upwelling, associated with the departure of the equatorial current from the island of Madagascar, that has both a low temperature rise and degree-heating profile that is likely to survive relatively well with a warming climate. This area is one of a number of similar small-scale upwelling areas reported to have low bleaching mortality and expected persistence (Glynn et al. 2001, Riegl and Piller 2003).

Water flow and coral bleaching

The effects of water flow and temperature variation on bleaching appear essentially the same but differ in their direction (McClanahan et al. 2005*b*) and are difficult to separate (van Woesik et al. 2005). This and a study in Mauritius indicate that water flow may be the dominant influence, but because both studies are based on correlations, this conclusion provokes the need for experimental studies that can tease apart these factors in the context of historical and genetic influences of the experimental taxa. A number of studies have shown that water flow has a positive effect on coral survival and recovery during warm water events in laboratory experimental studies (Nakamura and van Woesik 2001, Nakamura et al. 2003, Nakamura and Yamasaki 2005), but discrepancies with field observation indicate a need to reevaluate the mechanisms of bleaching and survival (McClanahan et al. 2005*a*). Warm water anomalies are often associated with reduced water flow and it may be that corals that originate from high water flow environments are less acclimated/adapted to the loss of flow that can occur during warm-water anomalies, and therefore more susceptible to bleaching and mortality (Sheppard 1999, McClanahan and Maina 2003). Consequently, using coral taxa that originate in different flow–temperature environments and including the loss of flow in temperature anomaly experiments are needed.

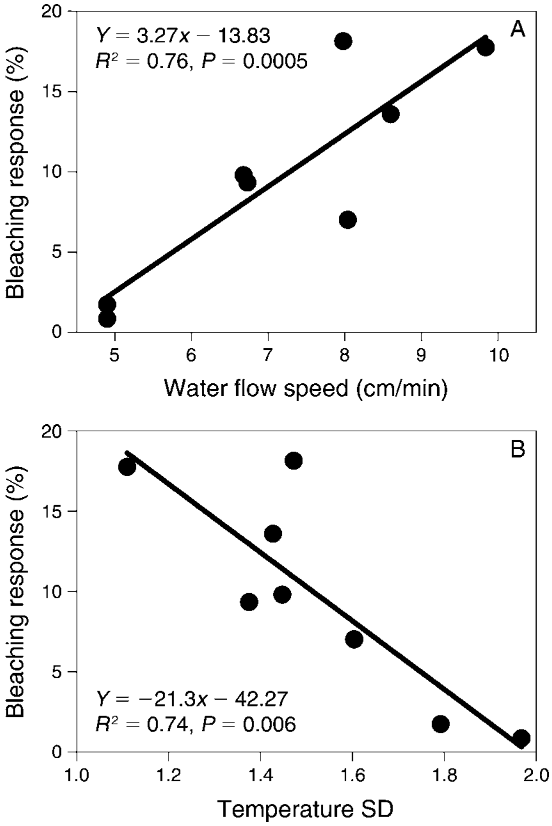

FIG. 12. Relationships between bleaching index and (A) water flow speed and (B) variation (SD) of in situ seawater temperature in 2005 on Kenyan reefs.

Bleaching predictions and models

Predictions for the future of coral reefs under climate change scenarios are based on the current and predicted rate of SST, thresholds for bleaching, and acclimation rates (Hoegh-Guldberg 1999, Hughes et al. 2003, Sheppard 2003). Projections in the Indian Ocean, based on pooling temperature data into large regions such as East Africa and the IPCC model of temperature projections, indicate that reefs will become susceptible to 1998-like conditions every five years by ~2030 and sooner in many latitudes (Sheppard 2003). Most models of temperature rise and bleaching predict a linear or even accelerating rise of 2–4°C in temperature to the year 2100 (ECHAM4/OPYC3 [Hoegh-Guldberg 1999]; IPCC models [McCarthy et al. 2001]; HADCM3 and IS92a [Sheppard 2003]). Saturation of temperatures is not predicted for most models until after 2100, where this decelerating rise is expected from an oceanic thermostat feedback mechanism, such as increased ocean mixing, clouds, or evaporative cooling (Li et al. 2000, Loschnigg and Webster 2000). If we use the data presented here and assume a linear increase for East Africa, at the current rise of mean SST in the warmest month (April; rise of 0.01°C/yr), the 1998 mean temperature of 30°C would be reached near 2077. This study suggests, however, that there is significant spatial heterogeneity and nonlinearity in temperature rise, thresholds, acclimation, and adaptation, and that pooling data and predictions for large areas will miss much of the spatial dynamics that may result in considerable deviation from predictions based on pooling.

Global patterns in warming are heterogeneous in space and time (Casey and Cornillon 2001, McCarthy et al. 2001, Barton and Casey 2005). Detailed analysis of each Hadley Cell in East Africa reveals significant between-site variations that roughly fall into three categories (Fig. 13). First, sites of highest DHM are well explained by a decreasing second-order polynomial function for SST with time (Fig. 13, cluster 1). For the span of the HadISST data set used, the highest rise in SST took place between the 1950s and mid 1970s, stability or decline started in the early 1980s, rose again from 1993–2003, and there was a notably large decline between 2003 and 2005 (Lyman et al. 2006). The small, improved difference in fit between the linear and second degree polynomial fit is mainly caused by the earlier marked rise relative to the later decrease. Similarly, recent analyses of satellite SST and in situ seawater temperatures indicate that the overall trend in SSTs in many tropical areas has been stable or has fallen during the last two decades (Barton and Casey 2005). Second, sites of lowest DHM do not show a strong rise in SST (Fig. 13, cluster 2). Third, as SST rise increases above 0.01°C/year in the southern part of this region, the relationship with DHM becomes flat (Fig. 13, cluster 3). Sites in the northern region, which have moderate temperature rise and high but variable DHM, are those sites most likely to experience the dual effect of the predicted temperature rise and anomalous temperatures, which is predicted to lead to mortality and possibly extinction of corals. Pooling data into regions and assuming mortality is proportional to the rise or when a threshold is reached will fail to detect the uniqueness of the categories displayed here, and this is also expected for larger scale global analyses.

Temperature patterns in East Africa are highly variable, depending on the location and temperature history of the sites, and predictions generally do not concur and may even contradict current models. The relationship between ocean warming and DHM appears to be strongly spatially dependent and therefore nonlinear such that baseline temperatures and rises cannot be directly translated into thresholds and DHM, the most likely cause of coral mortality. Assumptions of linear or exponential SST increases and coral mortality are likely to produce poor predictions, as our data suggest that the areas with the highest rise also have the highest SST SD and low relative mortality, which we expect is due to a combination of acclimation and local community or genetic adaptation. Understanding the importance of each of these factors will require further study. Temperature rise and variation are likely to increase together in coastal and leeward island sites, as the retention of water on coasts and behind islands is the likely cause of this positive covariance. Models that assume higher baselines and rises will certainly increase the predicted probability of recurrences of the anomalous events, but mortality will depend on the acclimation and adaptation rates relative to rates of rise (Hughes et al. 2003). Acclimation rates are likely to be slowest in low SST SD areas (Sheppard 1999, McClanahan and Maina 2003), and these are areas with the lowest temperature rise, probably associated with equatorial current downwelling on continental margins, but the highest mortality.

An alternative model is that coral acclimation only occurs on short time scales of less than a month (Coles and Brown 2003), upper thresholds to coral bleaching and mortality have little elasticity between sites and habitats (Berkelmans and Willis 1999, D'Croz et al. 2001), and this leads to little acclimation/adaptations or tolerance to environmental variation at the scale of months to years. If this second model were true, one would expect persistence of corals only in areas that maintain temperatures below these rigid mortality thresholds, such as 31°C (Coles and Brown 2003). Determining the correct model of coral acclimation/adaptation is critical to predictions and establishing management policies that prioritize areas based on a triage approach. Both models do, however, predict that areas that maintain stable cool water without rare anomalies will survive climate change and are a conservation priority (Glynn 2000, Riegl and Piller 2003, West and Salm 2003).

From this spatial analysis, we demonstrated that temperature variation (SD and kurtosis) is the best predictor of warming and the associated bleaching related mortality in East Africa. Water temperature history of a reef and the time corals spend at these temperatures determine their threshold for bleaching and survival (Coles and Brown 2003, McClanahan and Maina 2003, West and Salm 2003). The effect of temperature variability on the rise of DHW/DHM, and thus bleaching, is insufficiently addressed in coral research. Most studies focus on the effects of the mean and maximum threshold temperatures, and the variance is too often ignored. This has significant implications to our capacity to correctly predict responses of biological communities. The mean and maximum temperatures may be important in larger spatial comparisons but have low or no significant predictive power at site-specific or local scales (Table 4).

Diversity and acclimation/adaptation to bleaching

With the increasing threat to coral reefs from rising temperatures and other interacting factors, there has

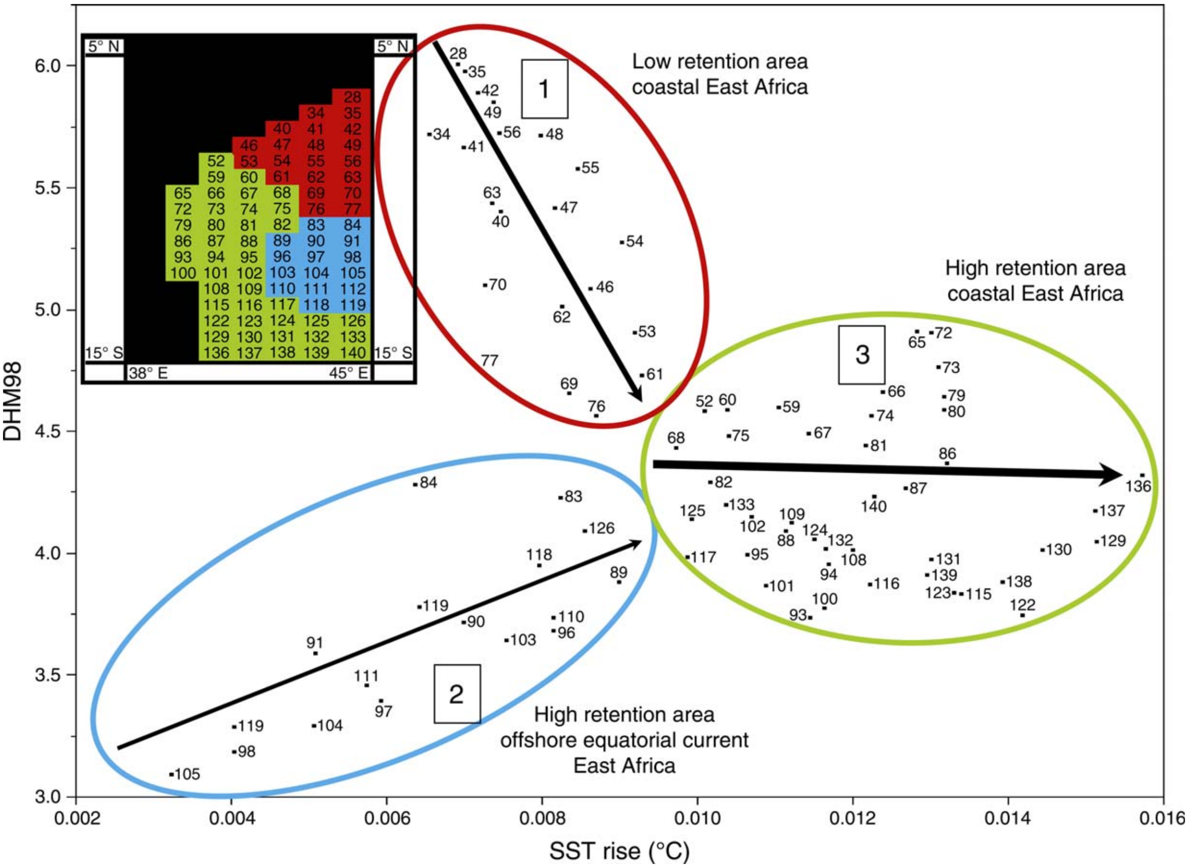

FIG. 13. Summary of the relationship between sea surface temperature (SST) rise and degree-heating months (DHM) in East Africa. Three main clusters are indicated; colors match those in the map (inset). Line widths and arrow directions represent relative strengths in model fit.

been a growing interest in identifying reefs that maintain high coral cover, biodiversity, and ecological functioning. This concept of resilience, addressing the capacity of ecosystems to recover and regenerate following major ecological disturbances, is increasingly becoming a main focus in ecological and resource management research (Hooper et al. 2005, Hughes et al. 2005). Although sources of resilience are expected to be complex and operate at multiple scales, biomass/cover and local and regional diversity have widely been recognized as the two main measurable components of resilience in coral reef ecology (McClanahan et al. 2002, Salm and West 2003, Bellwood et al. 2004, Hughes et al. 2005, Obura 2005).

This regional study and the bleaching survey in 2005 indicate that many Tanzanian reefs show high resistance to bleaching, fast recovery after bleaching, and maintain high coral cover and diversity. The bleaching study in 2005 also allowed analysis of community structure, and Tanzanian reefs were found to be some of the most diverse in the Indian Ocean, with a comparable generic diversity to that of the Maldives (McClanahan et al. 2007*b*). This observation is also in agreement with species diversity patterns for East Africa (McClanahan 1990). The hard coral species record from three publications is now 226 species, and Tanzanian reefs have relatively higher cover and species diversity (211 species) than their Kenyan counterparts (163 species; Hamilton and Brakel 1984, Lemmens 1993, Johnstone et al. 1998). Tanzanian sites, especially those in Songo Songo near the southern end of the geographic range of this study, have escaped the main effect of the 1998 bleaching and still maintain substantial cover of *Acropora* and other branching and encrusting taxa that are thought to be less tolerant of warm water and have become rare in Indian Ocean reefs affected by bleaching (Obura 2005; McClanahan et al. 2007*b*).

The environmental gradient and the resulting differential bleaching in East Africa is most likely created by the local hydrography linked to the position of the Island of Madagascar and, to a lesser extent, the other smaller islands along the Tanzanian coast, most notably Songo Songo, Mafia, Zanzibar, and Pemba. These islands reduce the influence of the Equatorial and East African Currents and result in higher water retention time and high temperature variation (Figs. 1 and 7). Coral and other taxa could be influenced in two interacting ways. First, the low to intermediate DHW reduce severe impacts of extreme conditions that might otherwise far exceed normal variation. Secondly, higher warming resulting from semi-isolation could create a selective pressure for taxa tolerant of warm water. Community change and genetically based adaptations might evolve as spatial variations in abiotic conditions impose divergent selective mechanisms and promote genetically based differentiation of zooxanthellae, host corals, or their symbiosis (Baker et al. 2004, Buddemeier et al. 2004, Berkelmans and van Oppen 2006). A thermal adaptation that operates at a regional scale of hundreds of kilometers as indicated for the Great Barrier Reef (Berkelmans 2002) could be inferred from the patterns observed in East Africa. The east African region, therefore, provides a unique environmental gradient to examine the relationships between environmental variation, climate change, and adaptation, and its consequences for biodiversity and ecological functions.

CONCLUSIONS

This investigation of the East Africa coastline reveals distinct regional variation in SST rise, variation and DHM, and response to the 1997–1998 bleaching event. This regional variation largely falls into three major categories which are expected to respond differentially to climate change and provide a basis for more comprehensive analyses of climate change predictions in other regions and on a global basis. Our data underline the need to evaluate the appropriate scale at which temperature operates in creating different acclimation/adaptation environments. Temperature baselines, rises, and thresholds are unlikely to predict the future of coral reefs unless they are based on more information about the temperature histories and acclimation/adaptation potential of corals within various thermal environments. The response of marine organisms to temperature variation can be complex and greatly depend on their history of exposure and ability to acclimate and adapt to changes (Berkelmans 2002, Coles and Brown 2003, Baker et al. 2004, Buddemeier et al. 2004). A view of coral reef ecosystems that emphasizes regional and historical variability and acclimation/adaptation to various environments (Lough 1994, Brown 1997) is likely to be more accurate than one that sees them as characterized by stable and benign temperature regimes close to their upper thresholds. This change in focus is likely to hold the key to viewing the persistence of reefs under future climate change predictions and increase the optimism needed to value further research and management efforts on coral reefs.

Corals acclimatized and adapted to thermal stress show more tolerance to elevated temperatures and radiation and bleach less (Goreau et al. 1992, Brown et al. 2000, 2002, West and Salm 2003) but often at the expense of losing taxa with low tolerance to environmental fluctuations (McClanahan and Maina 2003). With the need to understand coral reef resilience, recent research has focused on these stressed or marginal reefs (Perry and Larcombe 2003). Stressed locations where reefs are not at their most productive or diverse can provide important information on coral reef resistance, but more important to management of coral reef diversity is how resilience evolves in reefs that maintain high coral cover, high diversity, and ecological functioning. Tanzanian and Comorian (and probably northern Madagascar) reefs appear to provide these conditions as they have maintained high cover and species diversity over a period of extreme disturbance, and are, therefore, a high priority for future research and management.

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