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REPORT

Coral mortality associated with thermal fluctuations in the Phoenix Islands, 2002–2005

D. Obura · S. Mangubhai

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Abstract The Phoenix Islands (Republic of Kiribati, 172–170°W and 2.5–5°S) experience intra- and inter-annual sea surface temperature variability of ≈2°C and have few local anthropogenic impacts. From July 2002, a thermal stress event occurred, which peaked at 21 Degree Heating Weeks (DHW) in January 2003 and persisted for 4 years. Such thermal stress was greater than any thermal event reported in the coral reef literature. Reef surveys were conducted in July 2000, June 2002, and May 2005, for six of the eight islands. Sampling was stratified by exposure (windward, leeward, and lagoon) and depth (5, 10, 15, and 25 m). The thermal stress event caused mass coral mortality, and coral cover declined by approximately 60% between 2002 and 2005. However, mortality varied among sites (12–100%) and among islands (42–79%) and varied in accordance with the presence of a lagoon, island size, and windward vs. leeward exposure. Leeward reefs experienced the highest and most consistent decline in coral cover. Island size and the presence of a lagoon showed positive correlations with coral mortality, most likely because of the longer water residence time enhancing heating. Windward reefs showed cooler conditions than leeward reefs. Recently dead corals were observed at depths >35 m on windward and >45 m on leeward reefs. Between-island variation in temperature had no effect on between-island variation in coral mortality. Mortality levels reported here were comparable to those reported for the most extreme thermal stress events of 9–10 DHW in other regions. These results highlight the high degree of acclimation and/or adaptation of the corals in the Phoenix Islands to their local temperature regime, and their consequent vulnerability to anomalous events. Moreover, the results suggest the need to adjust thermal stress calculations to reflect local temperature variation.

Keywords Coral bleaching · Thermal stress · Sea surface temperature · Central Pacific · Degree heating weeks · Inter-annual variability

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D. Obura (✉)
CORDIO East Africa, PO Box 10135,
80101 Bamburi, Mombasa, Kenya
e-mail: dobura@cordioea.org

D. Obura
New England Aquarium, Central Wharf, Boston,
MA 02110, USA

S. Mangubhai
The Nature Conservancy, Indonesia Marine Program,
Jalan Pengembak 2, Sanur, Bali 80228, Indonesia

Introduction

The coral reefs of the Phoenix Islands in the Republic of Kiribati, in the central Pacific Ocean, are among the most remote in the world (Fig. 1). Relatively untouched by man, these reefs support some of the most pristine coral and fish communities that have been documented (Obura and Stone 2003; Obura et al. in press). The reefs contain over 120 scleractinian coral species with coral cover ranging from 40 to near 100% in 2000 and 2002. The coral community of *Acropora* tables in the Kanton lagoon remained relatively unchanged since the 1970s (Jokiel and Maragos 1978; Maragos and Jokiel 1978). Allen and Bailey (in press) compiled a list of 518 species of reef fish, documented large aggregations of schooling fish, and high densities of long-lived apex predators.

Separated by more than 1,000 km from populated island groups to the east and west, and by 500 km from Tokelau

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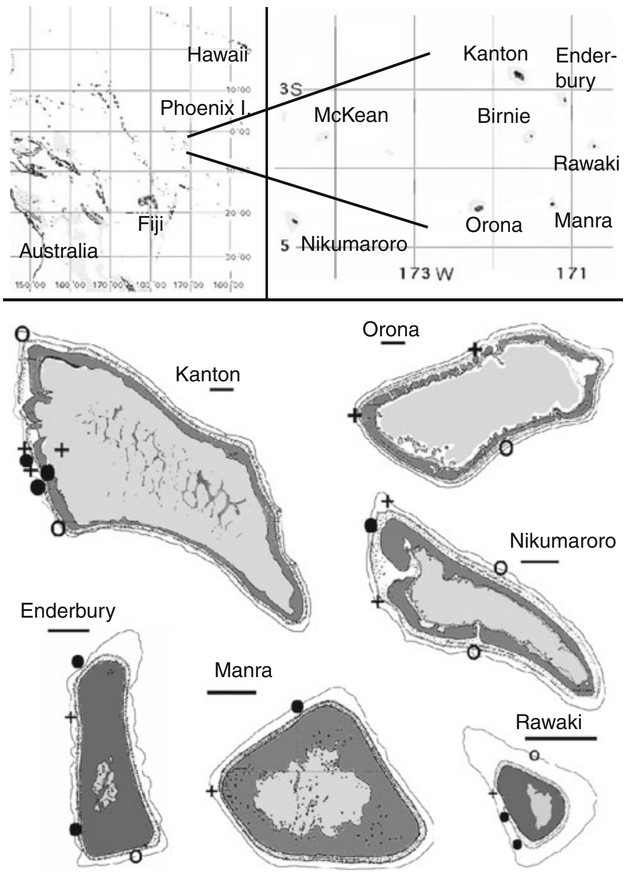

Fig. 1 The Phoenix Islands Protected Area in the central Pacific, and location of each island (*above*). The six islands for which repeat surveys in 2000 or 2002 (before bleaching) and in 2005 (after bleaching) were conducted are shown (*below*). *Darkest shading* represents land, with *light gray* showing lagoons in the atolls and central ponds on the islands. The outermost *solid line* represents the reef edge at approximately 15–20 m depth. Symbols: *plus* sites with both photograph quadrat and visual estimation of benthic cover; *open ciecle* windward sites with visual estimation only, *black dot* leeward sites with visual estimation only (see "Methods"). *Scale bars* under each island name represent 1 km

to the south, the reefs of the Phoenix Islands have not been subject to commercial fishing, and human settlement has been extremely limited. In the last 30 years, a small administrative population of ca. 30 people has resided on the largest island, Kanton, and a resettlement village of some 170 people was attempted on the second largest island Orona, but only lasted 2 years, from 2001 to 2003. Both of these settlements practice subsistence fishing, which appears to have minimal impact on the coral reef communities (Obura and Stone 2003; Obura et al. in press).

The central Pacific region has a low annual range in sea surface temperatures (SST), on the order of 2–4°C (Brainard et al. 2005), combined with a high degree of inter-annual variability due to multi-year and decadal cycles (McPhaden 2004). As a result, thermal stress patterns in the region differ from other coral reef regions globally. Based on climate change projections, the central Pacific Ocean may be subjected to greater thermal stress and the earlier occurrence of critical temperatures than other localities (Donner 2009).

From June 24, 2002, early stages of coral bleaching were noted in Kanton and Orona lagoons and on some reef slopes, at the onset of a SST hotspot that remained stationary over that part of the central Pacific (http://coralreefwatch.noaa.gov/) during a strong El Niño event (McPhaden 2004). A bleaching event in the Phoenix Islands was predicted (Obura and Stone 2003), but confirmation of its occurrence was only obtained in December 2004, when near-100% mortality of corals was documented in Kanton lagoon and 62% mortality on leeward reefs (Alling et al. 2007).

The vulnerability of corals and coral reefs to thermal stress that causes bleaching and mortality is hypothesized to relate to a broad suite of site and organismal characteristics (West and Salm 2003; Obura 2005). These have been investigated in multiple reef systems, but often with unclear or conflicting results. Distinguishing the contribution among multiple and complex factors is difficult, particularly where anthropogenic factors interact with the multiple natural factors that may cause bleaching (Brown 1997). With negligible human population, the Phoenix Islands offer an opportunity to study the impact of thermal stress and bleaching without confounding by local anthropogenic factors. This paper investigates the spatial differences in coral mortality in the Phoenix Islands during the El Niño-related thermal stress event from 2002 to 2003.

Materials and methods

Site description

The Phoenix Islands are the central island group of the Republic of Kiribati, located between longitudes 174.8° to 170.1°W and latitudes 2.5° to 5°S (Fig. 1). The group comprises three atolls, five islands, and two submerged reef systems belonging to Kiribati, with two outlying islands north of the equator, Baker and Howland, in the United States (Brainard et al. 2005). The Phoenix Islands Protected Area (PIPA) was designated in 2006 and extended in 2008 to cover 408,250 km^2, at the time the largest Marine Protected Area globally. The islands have historically been protected by their isolation, but now in the PIPA a 12 nautical mile limit around each island protects all coral reefs as strict no-take zones, with the exception of Kanton, where subsistence fishing for the $\approx$30 island residents is permitted. Surveys of the coral reefs of the Phoenix Islands were conducted in July 2000, June 2002, and May 2005 over 11, 21 and 11 days, respectively. McKean and Birnie islands were only visited once each in 2000 and 2002, respectively, and therefore are not included in this analysis.

The typical reef structure for the Phoenix Islands comprised four zones on the outer reefs (Obura in press). The three largest islands, Nikumaroro, Orona, and Kanton, also have lagoon and channel habitats. The outer reef zones included, from deep to shallow: (a) the reef slope, steeply sloping (>45°) from depths >100 m to about 20 m at its shallowest; (b) the reef edge, at a variable depth between 12 and 20 m, forming the transition between the reef slope and platform; (c) the reef platform, gently sloping (<30°) from the reef edge to the shallow surge zone at approximately 6–8 m depth; and (d) the surge zone from the shallow edge of the platform to the surface, which can be flat or carved into intricate buttresses and surge channels with up to 3-m vertical relief. Sampling at these depth zones occurred at approximately 5, 10, 15, and 25 m.

Atoll outer reef communities in the central/south Pacific (Brainard et al. 2005), and of the Phoenix Islands (Obura et al. in press; Obura in press), are highly uniform in community structure and composition, being strongly driven by exposure, and have uniform geomorphology and a restricted species pool. Study sites were located on leeward, windward, and lagoon reefs (Fig. 1b), though surveys of windward sites were highly constrained by wind and swell conditions and diver safety, particularly for repeat sampling in more than 1 year. Lagoon sites were few because of the patchy distribution of the hard substrate. Within each zone, site selection was done by observation of reef structure and topography, selecting locations typical to each island. In the 3 years of sampling, a total of 70 different sites have been surveyed on scuba and snorkeling. The sites, sampled before and after the thermal stress event from 2002 to 2003, were observed to be representative of reef communities throughout the island group.

Sea surface temperatures

Seven in situ SST loggers (HOBO Tidbit) were deployed in June 2002, of which five were retrieved with useful data in May 2005. Of the retrieved loggers, three were placed at 15 m depth on the leeward reefs at the north, east, and south of the island group (Kanton, Rawaki, and Nikumaroro, respectively). One logger was placed at 37 m depth directly below the 15-m logger at Kanton, and one was placed in Kanton lagoon at 5 m depth. One logger was placed on a windward reef at 15 m (Nikumaroro), but was lost. The interval selected for temperature readings (1 h 36 min) was set to maximize data collection over the life of the batteries and to obtain sufficient resolution to record diel variation. HOBO Tidbit temperature loggers have a factory-tested accuracy of ±0.2°C at 20°C. Field calibration of the loggers was done pre- and post-deployment. Prior to deployment, a mean difference of 0.15 ± 0.19°C (mean ± SD, 60 readings) was found between the coldest and hottest loggers. Post-deployment, the two loggers still running were calibrated against a new logger of the same make and exhibited a drift of −1.74 ± 0.15 and −0.38 ± 0.17°C (15 readings). The smoothness of the curves suggests there were no sudden changes that contributed to this drift, so the data were corrected by a linear conversion for these amounts over the 3 years. Because drift for the other three loggers could not be determined, and inspection by eye did not reveal any clear drift over time, their data are presented uncorrected.

SST anomalies from the National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch program (http://coralreefwatch.noaa.gov/) were downloaded for the period 1997–2007 at approximately 2-week intervals. The value of the temperature anomaly was read off the color-coded maps to give two datasets: (a) for the entire period available (1997–2007) for a region of 4–5 pixels in the center of the Phoenix Islands (within this sample area, the minimum anomaly was recorded) and (b) for individual pixels located as closely as possible to each island. Each pixel has sides of 0.5° or approximately 50 km. Because of the proximity of Enderbury and Rawaki (Fig. 1), a single pixel was read for both. Heat accumulation was calculated in Degree Heating Weeks (DHW, in °C weeks) following the methods of Liu et al. (2005) by multiplying the anomalies recorded above by the time interval (ca. 2 weeks) and accumulated over a 12-week window. From empirical findings, Liu et al. (2005) state the following thresholds of bleaching and mortality with respect to DHW: at DHW ≥4, bleaching of corals is expected; at DHW ≥8, widespread bleaching of corals is expected, accompanied by mortality, and at DHW approaching 12 and greater, high levels of coral mortality are expected. Thermal stress parameters used in the analysis included climatological maximum monthly mean (MMM), maximum temperature anomaly experienced, and maximum DHW.

Benthic cover

The reef platform of the Phoenix Islands is typically <100 m wide (Obura in press) and within a similar distance from the shoreline. Consequently, relocation of sites by GPS position and visual recognition of coastal and underwater features are highly accurate to within 10 s of meters. Sites for data collection were located in areas of uniform coral communities, representative of the different exposures of the islands (see "Site description"). Underwater, sampling units were placed haphazardly while swimming above the substrate.

Benthic cover was sampled using two methods: photograph quadrats, which give high-resolution data but were limited to a few sites and a single depth by logistics, and visual estimates, which give less accurate data but were collected at many sites and across the full range of depths. Eighteen sites were sampled using photograph quadrats before and after the bleaching (Fig. 1). Of these, one was a lagoon site (on Kanton), five were windward sites (Orona, Manra, Nikumaroro, and Enderbury), and the remaining 12 were leeward sites on all six islands. Photograph quadrats were collected at a single depth (10–12 m on the fore reefs, 5 m in Kanton lagoon). Visual estimates of bottom cover were conducted in 2002 and 2005 at the same sites as photograph quadrats and at an additional five sites (totaling 2 lagoon, 9 windward, and 12 leeward sites), covering four depth zones at outer reef sites where possible (5, 10, 15, and 25 m), with the 10 m depth corresponding to photograph quadrat samples on the reef platform.

For photograph quadrats, digital images were used (video in 2000, stills in 2002 and 2005), with the camera held approximately 60 cm above the substratum and the image plane parallel to the surface. Within the sites, image frames were taken haphazardly. Analysis of the images was done within 1 week of field collection. For the lower-resolution video images (640 × 480 pixels per frame), five points were recorded per frame (four corners and center of a rectangle), the video being freeze-framed at approximately 2–3 s intervals, or longer to ensure no overlap of frames. Twenty frames were aggregated (100 points) as a sample. For the higher-resolution still images (5–8 Mega pixels per image), 25 points were recorded, laid out in an even 5 × 5 grid. Four images were aggregated (100 points) as a sample. Where possible, between four and 10 samples were scored per site for analysis, but this varied in the different years and sites due to field logistics and the time and objectives for the expeditions each year. Benthic cover categories identified were hard coral, soft coral, other sessile invertebrates, algal turf (including ‘bare rock’), coralline algae, fleshy algae, *Halimeda* algae, rubble, sand, and ‘unknown’.

Visual estimation of bottom cover was conducted in haphazardly selected approximately 10 m^2 circles (radius *ca*. 1.8 m), selecting areas representing the principal coral habitat and assemblage for each location (see “Site description”). Estimates were made by a single observer in all years (DO) and calibrated against photograph quadrat estimates where they were collected together. Visual estimation can approach the accuracy of quantitative sampling such as with line transects, particularly with experienced observers, and reducing errors associated with multiple observers (Wilson et al. 2007). Cover was estimated for the 4–6 dominant cover types using the same categories as photograph quadrats. As far as possible, three samples were recorded at each depth zone, with the average of these samples reported here. Results are presented here only for the four dominant cover types: hard coral, coralline algae, turf algae, and rubble, because the proportionate error in estimating lower-density categories was high.

Statistical analysis

Statistical tests were used to investigate changes in temperature and benthic cover between 2002 and 2005. A Wilcoxon rank sums nonparametric test was run to compare in situ daily mean temperature between two periods in the dataset. Differences in each benthic cover category were analyzed using one-way ANOVA after arcsin transformation of the mean cover for each site at each time. ANOVA, linear regression, and Student’s *t*-test were used to investigate the relationship between changes in coral cover with different factors describing island and reef structure and thermal stress. For continuous factors, linear fits were conducted with associated ANOVA results. For nominal factors, ANOVA was conducted where the number of factor levels was >2, and a Student’s *t*-test for factors with 2 levels. Transformations were conducted on the two continuous variables (mortality, by arcsin; coral cover in 2002, by arcsin of the square root) that did not satisfy the normal distribution requirements. Statistics were conducted using JMP statistical software (v 6.0.0).

Results

In situ SST recorded in the Phoenix Islands ranged between 27.9 and 31.1°C from June 2002 to May 2005 (Table 1). All five sites showed a highly consistent increase in temperatures from June to November 2002, with stable temperatures above 30°C from August/September 2002 to February 2003, with maxima in November/December 2002 (Table 2). After February 2003, temperatures were significantly cooler and showed considerable spatial variation. By inspection, February to March 2003 represents a transition from one temperature regime to another. A Wilcoxon rank sums nonparametric test comparing in situ daily mean temperature for June 2002–February 2003 against March 2003–May 2005 showed significant differences for all sites ($P < 0.001$). During both of these periods, the hottest sites were on Kanton (leeward reef at 15 m and in the lagoon), while leeward reefs at 15 m on Nikumaroro and Rawaki were cool and broadly similar. In March 2003–May 2005, the logger at 37 m on Kanton showed the lowest temperatures, and this site and Nikumaroro showed the lowest levels of variation (in both range and variance). Variability in daily mean temperatures at individual sites was very low, varying from 1.60 to 2.12°C over the 27 mo from March 2003 to May 2005 (Table 1), slightly higher than the diel variation measured of 0.6–1.5°C.

The remote sensing dataset showed extensive high-temperature events in the Phoenix Islands (Fig. 2) starting with a hotspot that reached 9–11 DHW in May 1997 and stayed at this level for almost 1 years until March 1998. Subsequently, a multi-peaked hotspot developed and extended for 4 years from July 2001 to July 2005, nearly dissipating in June 2002 and May 2004. Over this period, the highest peak occurred at the end of 2002, at 21 DHW, with secondary peaks in September 2004 (12 DHW), January 2004, and July 2005 (7 DHW). The main peak at the end of 2002 corresponded to the high-temperature event recorded in situ (Table 1).

Table 1 In situ seawater temperatures recorded in the Phoenix Islands, June 2002–May 2005 (mean, minimum, maximum, standard deviation and range [maximum–minimum])

Site	Nikumaroro 15 m lee	Rawaki 15 m lee	Kanton 15 m lee	8 m lagoon	37 m lee
June 2002–February 2003					
m	30.0	30.0	30.3	30.2	30.0
Min	29.4	29.3	29.5	29.3	29.1
Max	30.9	30.7	31.1	31.1	30.8
SD	0.37	0.38	0.40	0.45	0.38
Range	1.6	1.4	1.6	1.8	1.7
March 2003–May 2005					
m	29.2	29.1	29.5	29.3	28.8
Min	28.4	27.9	28.2	28.3	28.0
Max	30.0	30.0	30.4	30.2	29.6
SD	0.32	0.38	0.38	0.36	0.29
Range	1.6	2.1	2.1	1.9	1.6
Mean difference (2002–2003/2005)					
m	0.84	0.86	0.81	0.90	1.28
Max	0.93	0.72	0.72	0.88	1.16

See text for rationale for splitting June 2002–February 2003 samples ($n = 250$) from March 2003–May 2005 samples ($n = 808$). Sites are ordered by decreasing mean temperature in June 2002–February 2003

The SST climate among the individual islands differed, with an increase in temperature of 0.3°C with latitude, shown by an increase in MMM, from the northern islands at 2°45′S (Kanton, Rawaki and Enderbury, 28.8–28.9°C) to the southern islands at about 4°40′S (Nikumaroro, Manra and Orona, 29.1°C; Table 2). DHW calculated for individual islands indicate differential thermal exposure among the islands (Table 2); heating at Kanton, Enderbury, and Rawaki increased the fastest to a peak of 18–21 DHW, Birnie and McKean showed intermediate peaks at ≈16 DHW and Manra, Orona and Nikumaroro showed slower rates of increase and low peaks at ≤14 DHW. Thermal stress, measured by DHW, was thus inversely related to MMM (Pearson correlation coefficient, $r = -0.734$).

The remote sensing and in situ temperature datasets showed similar patterns, although the remote sensing data were approximately 0.6–0.8°C cooler. The contribution of the island mass to the remotely sensed temperature is likely to be negligible: Kanton atoll, the largest of the islands, is triangular in shape at approximately 14 × 5 km, covering only 2.8% of the pixel area. The datasets were consistent for thermal stress, both with a high peak in late 2002/early 2003, a cooler period through to the middle of 2004 and warmer conditions in late 2004 into 2005. DHW calculated for the in situ data were consistent, with a peak hotspot of 21 DHW from 2002 to 2003 and lesser hotspots up to 12 DHW from 2004 to 2005. In both datasets, Kanton showed highest levels of thermal stress compared with the other islands.

Benthic cover in both 2000/2002 and 2005 was measured at 18 sites (Table 3). Coral cover in 2000/2002 averaged 45.4% (±5.4 SE), and in 2005 was 13.7 ± 3.2%, a decrease of 72%. A complementary change in cover of algal turf occurred from 12.6 ± 4.2 to 42.8 ± 6.0%. The overall cover of coralline algae decreased marginally from 2000/2002 to 2005, while rubble increased. Fleshy algal cover was low both before and after bleaching at 0.2 and 2%, respectively. The one-way ANOVA on

Table 2 Thermal climate for the Phoenix Islands, including the climatological maximum monthly mean (MMM) and the dates and maxima of SST anomaly and DHW during the thermal stress event of 2002–2003 (source: http://coralreefwatch.noaa.gov/)

	Kanton	Enderbury/Rawaki	Birnie	McKean	Nikumaroro	Orona/Manra
Latitude (°S)	2.78	3.12/3.72	3.59	3.4	4.68	4.52/4.46
MMM (C)	28.9	28.8/9	29	29	29.1	29.1
Thermal event, 2002–2003						
Anomaly (C)						
Max	2.5	2.25	2	1.75	1.75	1.25
Date	16-Nov-02	1-Nov-02	1-Nov-02	16-Nov-02	16-Dec-02	1 Nov to 16 Dec-2002
DHW						
Max	21.4	19.0	16.9	15.5	14.3	13.8
Date	16-Dec-02	13-Jan-03	13-Jan-03	13-Jan-03	13-Jan-03	13-Jan-03

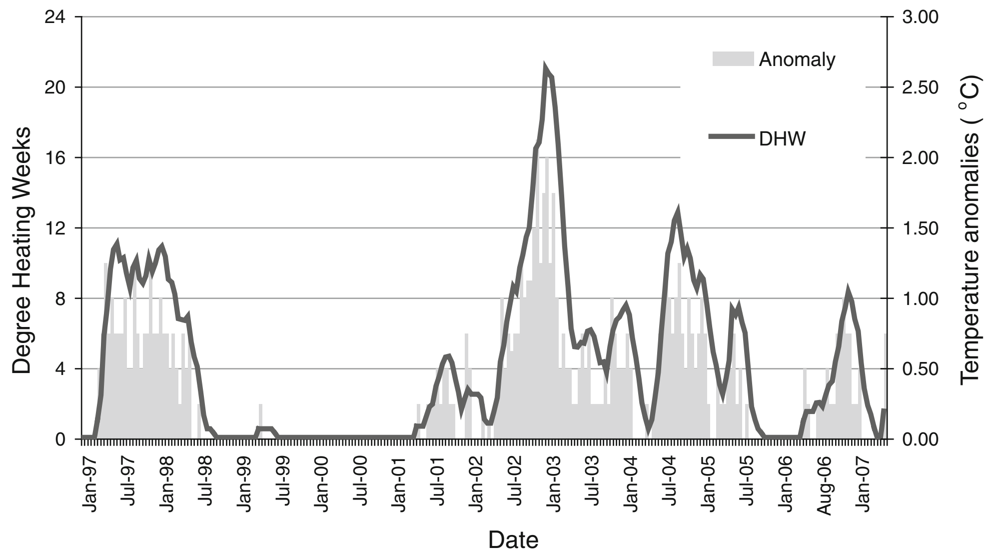

Fig. 2 Temperature anomalies above MMM + 1°C (*gray columns*, *right* *y*-axis) and Degree Heating Weeks (*continuous line*, *left* *y*-axis) for the Phoenix Islands from 1997 to 2007 (*source*: http://coralreefwatch.noaa.gov/)

arcsin-transformed site means showed that there were significant differences in hard coral cover and algal turfs between 2000/2002 and 2005 (Fig. 3a, $P < 0.001$). The most dramatic change in coral cover was for the lagoon site in Kanton, which had the highest coral cover of any site in 2002 at 79 and 0% in 2005 (Table 3). Two sites recorded an increase in coral cover, of which one (Southern Ocean, Enderbury) had a high variance in 2005. At this site, both the high variance and the increase were likely due its highly structured topography with more vertical than horizontal surfaces, resulting in a high degree of sampling error. This site was, therefore, excluded from the analysis below.

The coral decline from 2002 to 2005 varied by island and by degree of exposure, but sampling with photograph quadrats was not sufficient to statistically test island/exposure combinations. Overall, leeward reefs experienced the highest and most consistent decline in coral cover of 71 ± 7.1% (mean ± SE) while windward reefs experienced a lower but more variable average decline of 55 ± 22.6% with one site recording an increase in cover of 9%. Coral decline was highest at Kanton (87 ± 6.4%) and Nikumaroro (84 ± 6.7%), intermediate at Manra (70 ± 5.9%) and Orona (50 ± 30.5%) and lowest at Enderbury (44%, $n = 1$ site) and Rawaki (31 ± 13.1%). In 2005 mean coral cover was lowest at sites on the larger islands Kanton, Orona and Nikumaroro, approximately a third to half that on the smaller islands, Enderbury and Rawaki.

Visual estimates of bottom cover were made at all island/exposure combinations and across a full depth range (5, 10, 15, and 25 m) on outer reefs. The two methods gave consistent coral cover estimates before bleaching, though with less consistency after bleaching (Table 4, $r^2 = 0.836$ and 0.501, respectively). There was a consistent tendency for visual estimates to record a lower coral cover than photograph quadrats (slope < 1). The calculated decline in coral cover from 2002 to 2005 from photograph quadrat and visual assessment data were virtually identical (slope = 1.027, $r^2 = 0.789$, Table 4).

By visual estimation, the loss of coral cover from 2002 to 2005 was 57% (from 37 ± 1.5 to 16 ± 1.2%, Fig. 4a), slightly lower than that estimated by photograph quadrats (Fig. 3). Visual estimates of coralline algae, algal turf, and rubble all increased from 2002 to 2005 (Fig. 4a). The differences between windward, leeward, and lagoon reefs, of coral cover before and after bleaching, and amount of coral decline, were also consistent between visual estimates and photograph quadrats (Fig. 4b, compared to Fig. 3b). Visual estimates of decline in coral cover were highest for leeward reefs (63%) and lower for windward and lagoon reefs (45 and 49%, respectively).

Coral decline also varied strongly with depth (Fig. 5). In 2002, coral cover was highest on the reef platform at 10 m on leeward reefs (52%), and in Kanton lagoon (58%), and on the reef edge between 10 and 15 m on windward reefs (40%). In 2005, maximum coral cover decreased on leeward reefs to 15 m (18%) and on windward reefs coral cover was uniformly distributed across all depths from 5–25 m at approximately 20%. For leeward reefs, coral decline was highest in the shallows and decreased with depth (Fig. 5b), but for windward reefs, coral decline peaked at 57% at 10 m, was equivalent to leeward decline at 15 m and then decreased strongly at 25 m to 20%. Coral decline was noted at depths exceeding 30–35 m on both leeward and windward reefs, though was less on windward reefs. A depth below which coral decline was clearly zero was not apparent in the data or in field observations.

To identify the main factors influencing differential decline of corals among sites on the islands studied, three sets of factors were investigated: geophysical aspects of

Table 3 Cover of hard coral, coralline algae, algal turf, and rubble from photograph quadrats before (2000 or 2002) and after (2005) bleaching in the Phoenix Islands (m ± sd)

Island/Site/Exposure		*n*		Hard coral					Coralline algae				Algal turf				Rubble			
		2000/ 2002002	2005	Before		After			Before		After		Before		After		Before		After	
				m	s	m	s	%	m	s	m	s	m	s	m	s	m	s	m	s
Enderbury																				
Lone Palm	Lee	5	10	77.0	10.0	42.8	19.8	−44.4	10.2	5.0	7.3	4.6	2.6	2.2	26.7	15.7	5.4	3.4	20.0	23.6
Southern Ocean	Wind	5	4	20.7	6.7	35.8	23.8	72.8	15.7	3.1	7.3	4.6	3.1	2.7	34.5	21.6	37.3	15.0	14.5	13.7
Kanton																				
Coral castles	Lag	5	10	**79.4**	12.5	**0.0**	0.0	**−100.0**	0.2	0.4	7.2	13.3	4.8	5.4	64.4	24.3	5.0	3.5	10.5	14.9
Satellite beach	Lee	5	10	**71.4**	19.8	**9.1**	5.9	**−87.3**	12.8	9.7	13.8	8.0	8.6	5.9	40.1	22.2	6.0	5.7	32.4	27.3
Six sticks	Lee	5	4	41.6	13.9	15.0	9.9	−64.0	6.6	6.8	10.8	6.7	19.0	12.8	23.5	7.4	20.9	17.5	50.8	16.9
Weird Eddie	Lee	5	10	**83.0**	6.7	**2.5**	3.4	**−97.0**	11.8	4.2	3.5	2.7	**1.8**	1.8	**67.7**	22.4	2.4	2.5	25.6	23.8
BritGas/ PresTayl	Lee	5	4	28.6	13.3	2.5	3.3	−91.3	0.6	0.9	0.0	0.0	**25.2**	15.3	**86.0**	10.9	20.2	5.8	3.0	3.8
Manra																				
Harpoon corner	Lee	5	10	**55.6**	14.9	**13.2**	9.2	**−76.3**	33.0	13.3	12.8	8.2	**5.6**	3.5	**60.2**	11.0	0.2	0.4	7.0	5.4
NorthExp/ Lee	Wind	4	4	26.0	8.1	9.3	9.6	−64.4	30.4	10.5	24.3	6.1	11.5	12.7	58.3	27.7	26.7	21.4	0.0	0.0
Nikumaroro																				
Amelia's lost causeway	Lee	5	10	**38.2**	3.2	**7.8**	8.7	**−79.6**	48.6	8.5	28.9	8.8	12.4	9.0	42.1	12.7	0.8	1.8	19.3	14.5
Nai'a point	Lee	5	4	**25.7**	8.3	**1.8**	2.4	**−93.2**	18.1	7.2	23.0	15.4	20.2	8.1	42.5	15.9	30.7	13.7	31.8	26.1
Windward wing	Wind	5	10	58.6	23.5	1.9	2.4	−96.8	13.2	5.4	32.3	15.0	1.4	0.9	8.1	9.8	6.4	6.5	43.7	21.3
SWCrnr/ Elektra	Wind	5	4	41.0	18.8	13.3	12.0	−67.7	24.2	4.5	38.5	12.1	0.6	0.9	11.3	8.1	5.5	4.0	7.8	11.8
Orona																				
Algae corner	Lee	5	10	10.0	2.8	3.2	5.5	−68.0	2.0	3.9	2.1	2.6	78.6	8.9	92.6	6.4	6.2	7.1	1.9	3.9
Dolphin ledge	Lee	5	10	**40.6**	3.6	**3.3**	4.0	**−91.9**	43.6	10.7	14.5	10.5	2.6	1.8	17.8	15.0	9.0	9.6	45.1	27.8
Aerials/ backdoor	Wind	3	4	19.7	10.7	21.5	4.7	9.3	**57.7**	8.4	**11.5**	6.0	**13.3**	8.7	**57.8**	6.2	6.3	3.8	5.3	5.0
Rawaki																				
Clearwater	Lee	5	4	32.7	14.5	26.8	21.2	−18.2	14.6	10.3	41.5	17.1	6.5	5.3	19.0	6.8	35.1	16.0	6.5	5.1
Deepwater	Lee	5	10	67.6	14.2	37.6	17.4	−44.4	10.2	3.8	29.2	10.8	9.6	4.0	18.7	6.5	2.6	2.9	8.0	8.7

Differences between before/after cover for each site and category were tested with a Student's t-test calculated using the difference of means, pooled variance and appropriate degrees of freedom from before and after samples (see "Methods"). Comparisons for which $P \leq 0.01$ are shown in bold

reef structure (island size, presence of lagoon, depth zone), pre-bleaching coral community (coral cover), and aspects of thermal stress (MMM, maximum anomaly, and maximum DHW). This analysis (Table 5) showed that island structure (presence/absence of a lagoon, island size, and exposure) most significantly affected the degree of coral decline; the presence of a lagoon, large island size, and leeward exposure were associated with the highest declines in coral cover. By contrast, pre-bleaching coral cover and depth were not significantly correlated with coral decline, and neither was any indicator of differential thermal stress among the sites.

The Phoenix Islands have an estimated reef area of 3,394 ha split into various categories by island, exposure, habitat, and depth zone (Obura in press). Using these estimates of reef area and estimates of coral decline by reef exposure and depth zone, total loss of coral between 2002 and 2005 was calculated. Windward reefs comprised

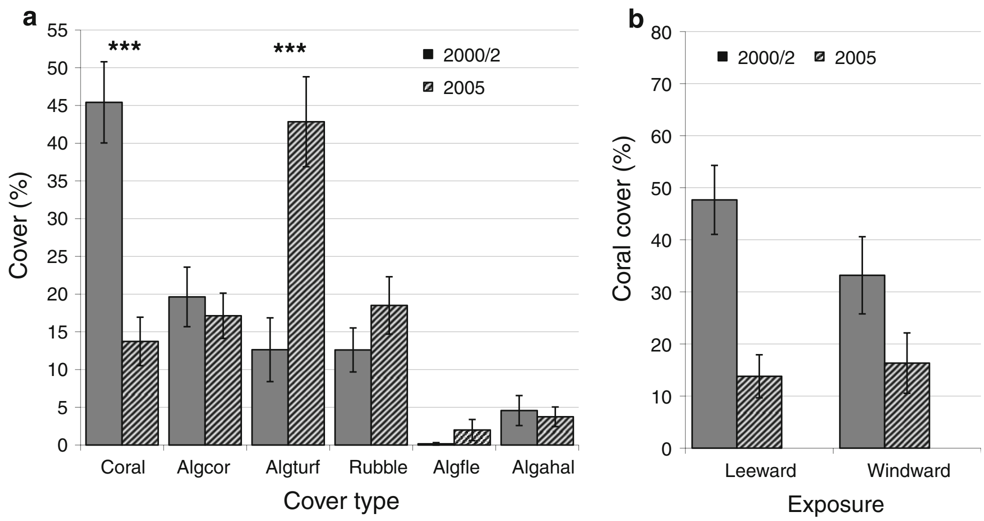

Fig. 3 **a** Benthic cover (mean ± SE) from photograph quadrats in 2000/2002 and 2005 at 18 sites in the Phoenix Islands. Coral and algal turf showed significant differences between the times in a one-way ANOVA on arcsin-transformed site averages (shown by asterisks ***$P < 0.001$; r^2 for hard coral = 0.41, for algal turf = 0.30, JMP 6.0.0). **b** Coral cover in 2000/2002 and 2005 (mean ± SE) for windward and leeward reefs (only one lagoon reef was sampled, in Kanton). Algcor: coralline algae, Algturf: turf algae, Algfle: fleshy algae, AlgHal: *Halimeda* algae

Table 4 Linear regressions among photograph quadrat and visual estimate results of coral cover and mortality for leeward reefs at 15 m

Comparison	Slope	Intercept	r^2
Coral cover			
Before (2000/2002)	0.874	9.036	0.836
After (2005)	0.809	5.615	0.501
Mortality	1.027	−6.625	0.789

Photograph quadrat data were used as the independent variable and visual estimates as the dependent variable

approximately 75% of total reef area in the Phoenix Islands and suffered slightly lower decline than leeward reefs (59% vs. 64%, respectively). Total coral decline in the lagoons was estimated at 61%. The shallow platform from approximately 8–15 m depth on outer reefs comprised the largest area of reef (56%) and suffered 64% decline. Among the islands, Nikumaroro suffered the highest loss of corals (79%) followed by Kanton (66%). The majority of other islands experienced 54–58% decline, with the least change on Enderbury (42%). By depth, loss in coral cover was least at 25 m (37%) and greatest at 5 m (69%). In total, the decline in coral cover in the Phoenix Islands over the study period is estimated at 60%.

Discussion

The Phoenix Islands experience a temperature regime with an unusually low range of variability, between daily minimum and maximum temperatures at any given site (0.6–1.5°C), annual minimum and maximum (1.7–3.3°C), and daily mean temperature (1.60–2.12°C in 'normal' years, Table 1). Inter-annual variability in temperatures is similar to intra-annual variability, with annual mean temperatures calculated from NOAA Pathfinder AVHRR data varying by <2°C. The temperature climate in the islands, as shown by the MMM from remote sensing data is similarly narrow though highly consistent, warming by 0.3°C from the northern to the southern islands. This warming is associated with equatorial divergence and appears as a tongue of cooler water extending west from the eastern

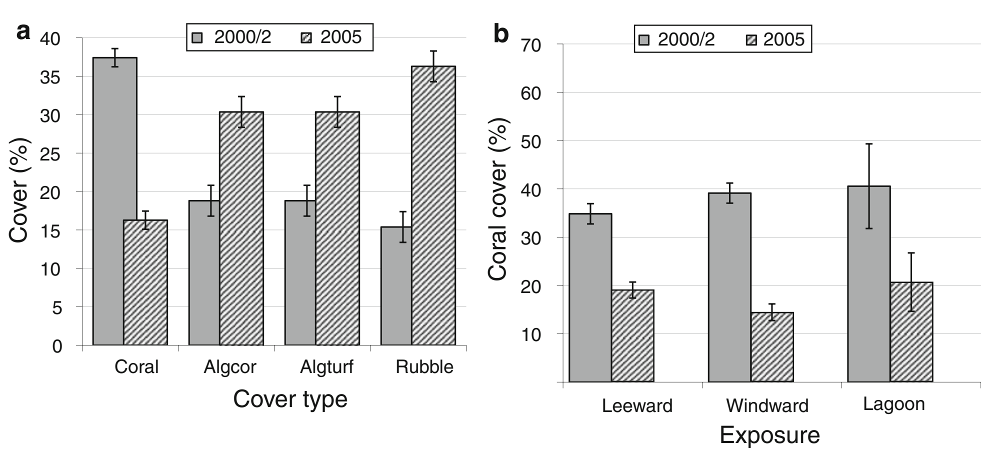

Fig. 4 **a** Benthic cover (mean ± SE) from visual estimates in 2000/2002 and 2005 at 23 sites in the Phoenix Islands for four dominant cover types. **b** Coral cover in 2000/2002 and 2005 (mean ± SE) for windward, leeward and lagoon reefs

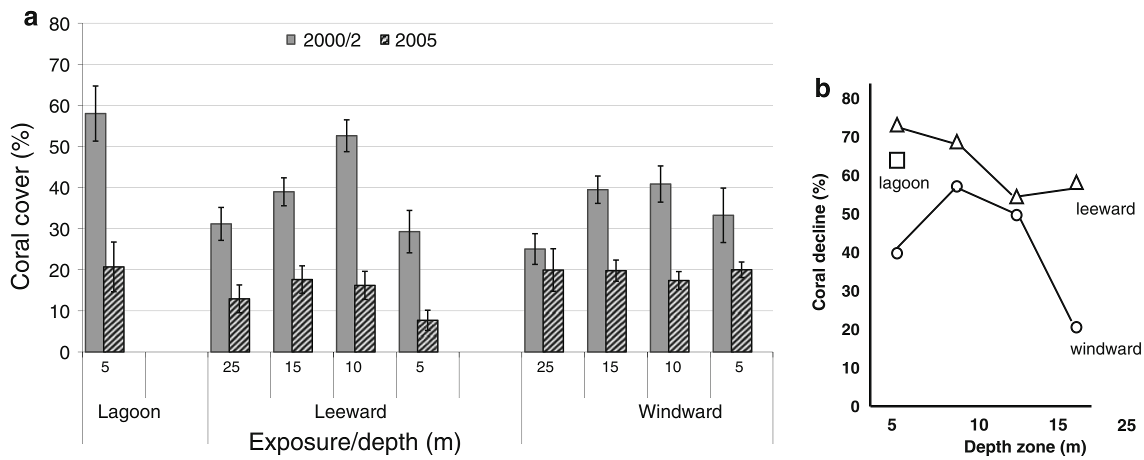

Fig. 5 **a** Visual estimates of hard coral cover in 2000/2002 and 2005 (mean ± SE) and **b** percent decline, by depth zone for lagoon, leeward and windward habitats, Phoenix Islands

Table 5 Significant statistical tests of variation in coral mortality between 2000/2002 and 2005, on variables of island and reef structure, coral community and thermal stress

Variable	Type	Levels	Test	r^2	*df*	*F/t*	*P*	Additional
Presence of lagoon	N	Present/absent	T test	0.161	54	3.218	0.001	Equal variance, 1 tail
Island size	C	Reef area, range 0.74–10.4 km^2	Linear fit	0.147	1/54/55	9.319	0.004	$a = 32.15$, $b = 3.394$
Exposure	N	Lagoon, lee, wind	ANOVA, Tukey HSD	0.141	2/53/55	4.368	0.018	Lee > wind

Variables with nonsignificant *P* values included coral cover in 2002, MMM, DHW and maximum anomaly (using linear fits), and reef zone (using ANOVA)

Type: *N* nominal, *C* continuous, *df* degrees of freedom are given for each test, overall for *t*tests, and factor/error/overall for linear regressions and ANOVA. *F*/*t* − *F* ratio is shown for ANOVA and linear fit, *t* value for *t* tests

Pacific (Brainard et al. 2005). The range of temperatures in the Phoenix Islands is very low compared with other coral reef regions where daily and annual ranges of >10°C can occur (e.g., Red Sea, Sheppard et al. 1992) and with proportionately lower inter-annual variability.

In 1997–1998, 2001–2005, and 2006–2007, the region experienced persistent high temperatures, or thermal events, as compared with the baseline period of 1985–1996 and the period from 1998 to 2001 (Fig. 2). Both remotely sensed and in situ measurements of SST show that June 2002 to February 2003 was unusually hot and consistent among the islands, with monthly maximum in situ temperatures of 30.6–31.0°C, compared with 29.4–30.3°C from March 2003 to June 2005. This warm period coincided with a positive phase of the Multivariate ENSO index (i.e., in an El Niño phase) that was moderate in magnitude (Wolter 2009) but took an uncharacteristically long time to dissipate (McPhaden 2004), lasting until mid-2004 (Fig. 2).

The 60% decline in coral cover recorded in the Phoenix Islands from 2002 to 2005 is dramatic. However, since direct observations of the decline were not made, it must be determined whether this change was real and if so what was its likely cause. Was it a result of sampling error and/or methodological artifacts? Considering sampling errors and artifacts first, the haphazard nonpermanent sampling method used here is the least sensitive of standard monitoring methods (see English et al. 1996) as it may sample spatial variability within a site. This error can be minimized by selection of representative and uniform sites. The study sites selected were typical of the reef habitats of the islands and were selected due to their uniform coral community over a larger area than the sampling stations. In 2000 and 2002, the coral communities in all habitats consisted of consistent cover of acroporids, and on the fore reefs of pocilloporids and faviids, among others (Fig. 6, left panel). The appearance of the study sites in 2005 was completely different (Fig. 6, right panel); in many cases, individual coral heads and reef fronts known to be alive in 2000 and 2002 were dominated by dead coral, recognizable to the genus level, but with thick encrusting of coralline algae and in some places algal turf (Fig. 6, inset), consistent with mortality at least 2 years previously (D. Obura pers. obs.). The difference in coral cover over time could not be attributed to random placement of sample units. Given the high cover and large size of corals in 2002, this decline can only be a result of mortality of corals of all

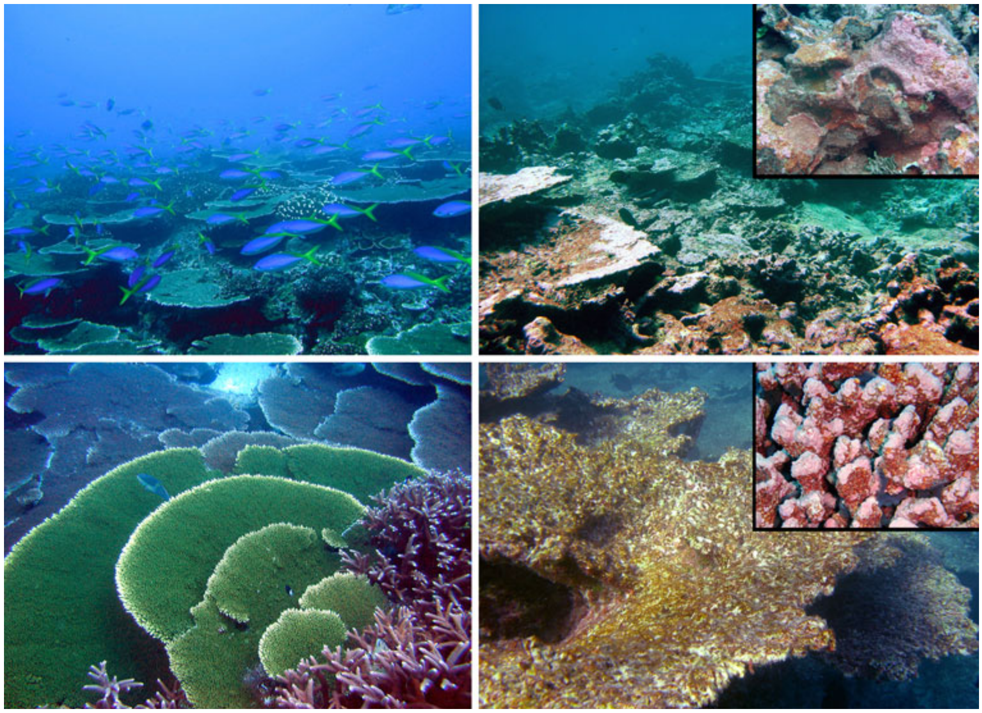

Fig. 6 Benthic views in 2002 (*left*) and 2005 (*right*) from the leeward outer reef at 15 m (*top*) and climax *Acropora* community in the lagoon (*below*) at Kanton. The mass mortality of individual coral heads is clearly visible in the 2005 photographs, particularly their homogeneous appearance and consistent algal community (coralline algae and grazed turfs). *Insets* right (*upper* and *lower*), encrusting coralline and turf algae on recently dead corals

sizes, and not of any natural attrition or mortality of old corals over time. Further, in spite of the low power of this technique to record change, the decrease in coral cover and increase in algal turf cover were highly significant statistically ($P < 0.001$, Fig. 3a).

The decline in coral cover could potentially be attributed to progressive or sudden changes, or to multiple causative factors. Elsewhere, widespread coral mortality and reef degradation have been reported from reef sites as a result of sedimentation (Rogers 1990), reduced salinity from rivers (Goreau 1964), *Acanthaster planci* and other predator outbreaks (Moran 1986), upwelling cold waters (Glynn 1977), high-temperature events (Glynn 1993a), pollutants (Walker and Ormond 1982), coral diseases (Harvell et al. 2004), and human interference such as by fishing (Jennings and Polunin 1996) and land-based development (Lundin and Linden 1993). In 2000 and 2002, the reefs of the Phoenix Islands were reported to be among the most pristine in the world (Obura and Stone 2003; Obura et al. in press) and in four expeditions (2000, 2002, 2005, and 2009) with 55 days of diving, and over 2,200 dives, the following observations have been made. The islands are flat coralline islands with negligible human habitation and visitation. This rules out the possibility of sedimentation, salinity, pollution, fishing, and construction as potential causes of the coral mortality. We have also observed fewer than ten *Acanthaster planci,* low levels of *Drupella* and other predators, very low levels of evidence of predation (such as isolated dead corals or dead corals with characteristic predation scars or mortality patterns), and the near absence of coral disease. Cold water upwelling resulting in coral mortality is a possibility, though this has been reported only in regions where temperatures go below 18–20°C in areas with strong upwelling features (e.g., Panama, Glynn and Steward 1973; Oman and the Gulf of Aden, Glynn 1993b), and such events have not been reported from the Phoenix Islands nor from similar island groups in the central, south, west, or north Pacific.

The only agent known to cause a massive decline in the cover of corals in a short space of time, and has been documented in the Phoenix Islands, is high-temperature stress. ENSO-related warming conditions are highly correlated with coral bleaching events (Hoegh-Guldberg 1999; Liu et al. 2005; Hoegh-Guldberg et al. 2008). The observation of bleaching in July 2002 along with paling of corals in situ prompted a warning of potential bleaching of corals (Obura and Stone 2003). The significant decline in coral cover was first confirmed in December 2004 (Alling et al. 2007). The degree of thermal stress recorded in the Phoenix Islands was calculated at 21–22 DHW, which is far above the 'normal' maxima associated with catastrophic mortality (Liu et al. 2005). Indian Ocean bleaching-related coral mortality in 1998 was the highest in that year and has been extensively reported with peak mortalities of 75–90% at the scale of individual reef sites and of 40–75% for broader areas and regions (Goreau et al. 2000; Linden et al. 2002; Wilkinson 2000), at maximum DHW of 9–10 (McClanahan et al. 2007). The Caribbean suffered its most severe bleaching and mortality event in 2005 (Wilkinson and Souter 2008), with mortality levels up to 50% at maximum reported DHW of 10–13. We therefore strongly infer that the decline in coral cover in the Phoenix Islands from 2002 to 2005 was a consequence of thermal stress and subsequent coral bleaching and mass coral mortality.

Just as notable is the high variability of mortality among study sites, from a minimum of 12% to a maximum of near 100%. Alling et al. (2007) surveyed the worst impacted sites, reporting 100% mortality in the lagoon of Kanton and 62% mortality on leeward reefs. These results are comparable with those reported here for the same habitats, which comprise approximately 335 ha (Obura in press) or about 10% of the total reef area in the Phoenix Islands. High variability in bleaching and mortality has become increasingly recognized to be the norm, with many factors affecting the degree to which individual corals and sites experience thermal stress (West and Salm 2003; Obura 2005). In this study, the most important factors contributing to variability in coral mortality were the presence of a lagoon and island size. Following these, and particularly comparing sites on a single island, the degree of exposure also influenced coral mortality. While clear patterns in differential coral mortality were documented with depth, this was masked by the island and exposure effects. None of the variables quantifying differential thermal stress among the islands (MMM, maximum anomaly, and maximum DHW) was significant in explaining differential coral mortality at individual sites.

Island size may affect coral mortality as water heats up in contact with the benthos, an effect that is enhanced by prolonged residence time of water on large islands compared with small islands. The presence of a lagoon may affect these results because lagoons are found only on the largest three islands (Fig. 1). Lagoons also have a real effect on water temperatures, as greater residence time of lagoon waters results in enhanced heating, and this may affect corals on outer reef slopes through tidal exchange. Exposure may influence coral mortality by the effects of water flow and wind and wave exposure. Cooler waters may be upwelled by current forcing on the island slopes, and heavy wave action also results in mixing of deeper cool water. Heating of water in contact with island slopes results in warming from upstream (windward) to downstream (leeward) sides of the islands. Furthermore, the flow of currents around an island can result in trapping of water on the leeward sides, particularly if these are fully sheltered and concave or straight, as in the case of Nikumaroro and Kanton (Fig. 1). Finally, because the lagoons all empty on the leeward western sides of the atolls, repeated cycles of warming between lee and lagoon waters, exchanged through tidal action, may occur. Such an exchange would enhance the warming effect on leeward sides. The main current affecting the islands is the westward flowing South Equatorial Current, and all winds and wave exposures are from the southeast, so the net effect of these factors in the Phoenix Islands is for warmer conditions on the western leeward reefs, particularly on large islands with lagoons. We observed that the thermocline was noticeably shallower on the windward (eastern) sides of the islands, and coral mortality was consistently less at all depths on windward reefs (Fig. 5) particularly around the depth of the thermocline. The largest difference in coral mortality between windward and leeward occurred at 25 m, at 20% on windward reefs and 60% on leeward reefs. We were not able to observe a depth below which no mortality occurred, but estimate that this may have been >35 m on windward reefs and >45 m on leeward reefs, exceeding levels reported for oceanic islands and atolls in the Indian Ocean (Sheppard et al. 2002; Sheppard and Obura 2004).

Similar effects of island size and lagoon/exposure patterns occur in other locations. In the northern Line Islands (central Pacific), while the principal factor explaining reef condition was human use and degradation (Sandin et al. 2008), a parallel trend to that reported here occurred. We consistently noted poor reef condition on leeward shores exposed to lagoon outflow on the largest islands (Kiritimati and Tabuaeran atolls) and good reef condition on the smaller islands with better flow and more open lagoons (Palmyra and Kingman reefs). Similarly, in the Indian Ocean, coral mortality from thermal stress in 1998 was greatest on the granitic islands on the extensive Mascarene plateau where heating was greatest, and mortality was less on outer isolated islands of the Seychelles (Spencer et al. 2000), and greater on the extensive Chagos Bank than on smaller atolls surrounding it (Sheppard et al. 2002). On Aldabra and St. Pierre islands in the Seychelles, coral mortality was greater on leeward than windward reefs (Spencer et al. 2000). Farquhar atoll in the Seychelles is on a large shallow platform and suffered very high mortality levels in 1998 (D. Obura, pers. obs.).

Degree Heating Weeks for the Phoenix Islands calculated using the NOAA dataset and standard procedures (Liu et al. 2005) were higher and longer than any reported in the literature. In 1997 to 1998, a hotspot of similar magnitude to those reported elsewhere associated with high coral mortality occurred (10–12 DHW), but persisted for 12 months over the usual 2–4 months. However, in 2000, no signs of recent mass coral mortality were recorded as cover on many reefs was over 60%, dominated by bleaching-susceptible corals (Obura et al. in press). From 2002 to 2005, the hotspot in the Phoenix Islands was of a greater magnitude and duration than reported elsewhere: It reached a maximum of 21 DHW in January 2003, and showed secondary peaks of >12 in September 2004 and >7 in January 2004 and July 2005, and did not dissipate fully for 4 years. The level of coral mortality associated with this event was on a similar scale to the most extreme heating events reported in the literature. However, sites with similar mortality only registered 9–10 DHW, in the case of many parts of the Indian Ocean in 1998 (McClanahan et al. 2007) and the Caribbean in 2005 (Wilkinson and Souter 2008). This raises two main issues. First is whether the region around the Phoenix Islands is so frequently exposed to severe thermal stress that local corals may have developed a high degree of resistance, through acclimatization or adaptation, raising their bleaching and mortality threshold (Craig et al. 2001; McClanahan and Maina 2003). Second is that the approach for calculating heat stress (i.e., DHW) may not be appropriate for this particular region.

The Phoenix Islands are located where the central Pacific warm pool intensifies during El Niño events, which is distinct from the better-known eastern Pacific warming associated with ENSO events (Kim et al. 2009; Yeh et al. 2009). Yeh et al. (2009) found that the frequency of warm central Pacific events has increased dramatically since 1990 compared to the previous 100 years. However, Kim et al. (2009) indicated that the central Pacific warm pool is more predictable than the eastern Pacific warming, at least in terms of climate prediction for Atlantic cyclones. The coral community of the Phoenix Islands in 2000 and 2002 was not characteristic of a high thermal stress regime and was typical of pristine central Pacific remote reefs (Obura et al. in press; Brainard et al. 2005; Sandin et al. 2008). The community response documented here, between 2002 and 2005, is typical of reef systems exposed to severe and unusual thermal stress (Goreau et al. 2000; Wilkinson and Souter 2008).

Current practice for calculation of DHW uses a baseline period from 1985 to 1997 to calculate a maximum monthly mean (MMM), adding a constant of +1°C above the MMM to identify a threshold above which thermal stress occurs (Liu et al. 2005). Above the threshold, heat stress is accumulated as a function of magnitude and time. The threshold of MMM +1°C may be appropriate for reef areas with annual variation of several degrees, e.g., from 5 to 10°C annually, and where this is greater than inter-annual variation. But the Phoenix Islands experience annual variation of only 1.5°C, i.e., an amplitude of 0.75°C above or below the mean, and a standard deviation of mean monthly temperatures of 0.2°C (Table 1). A threshold of 1°C above MMM far exceeds these narrow temperature ranges. Trial calculations using in situ temperatures (2003–2005) to calculate MMM, and a threshold of one standard deviation above MMM for accumulating heat stress, produced DHW values between 6 and 12, with highest heat accumulation at Kanton. This is more consistent with both the highest levels of mortality reported at Kanton (60 to near 100% for maximum DHW of 10–12) and high levels of variability in mortality and DHW among islands (<50% mortality for maximum DHW <9). These calculations suggest a threshold based on variability of local temperatures, which may be more appropriate than a global constant for heat stress calculations. A more locally sensitive application of heat stress calculations to this region may provide a more accurate indication of the actual degree of thermal stress experienced.

The contribution of intra-annual versus inter-annual modes of temperature variability and how they superimpose on long-term trends in influencing thermal stress is currently poorly understood. In the central Pacific, inter-annual SST variability is on a similar magnitude to intra-annual, or seasonal, variability. For the AVHRR record of 1985–2007 for the central Pacific, mean annual temperatures varied by 1.92°C, comparable with annual variability of 1.5°C. This contributes to the region being expected to suffer critical warming as a result of climate change earlier than other coral reef regions (Donner 2009). Corals found in reef regions with historically high-temperature variability have clearly acclimatized and adapted to these conditions (Coles 1997; Coles and Brown 2003) and a common question is whether exposure to highly variable temperatures historically may confer the ability to adapt to long-term climate change (see West and Salm 2003; Obura 2005). These findings from the Phoenix Islands do not support this hypothesis as high variability and high mortality were found, but confounding this interpretation is the very narrow temperature range both on annual and inter-annual levels. With no local anthropogenic stressors masking the response signal to thermal stress, coral recovery and future responses to thermal stress in the Phoenix Islands will provide a valuable reference for understanding coral and reef responses to climate change.

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