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RECOVERY FROM THE 2004 CORAL BLEACHING EVENT IN THE GILBERT ISLANDS, KIRIBATI

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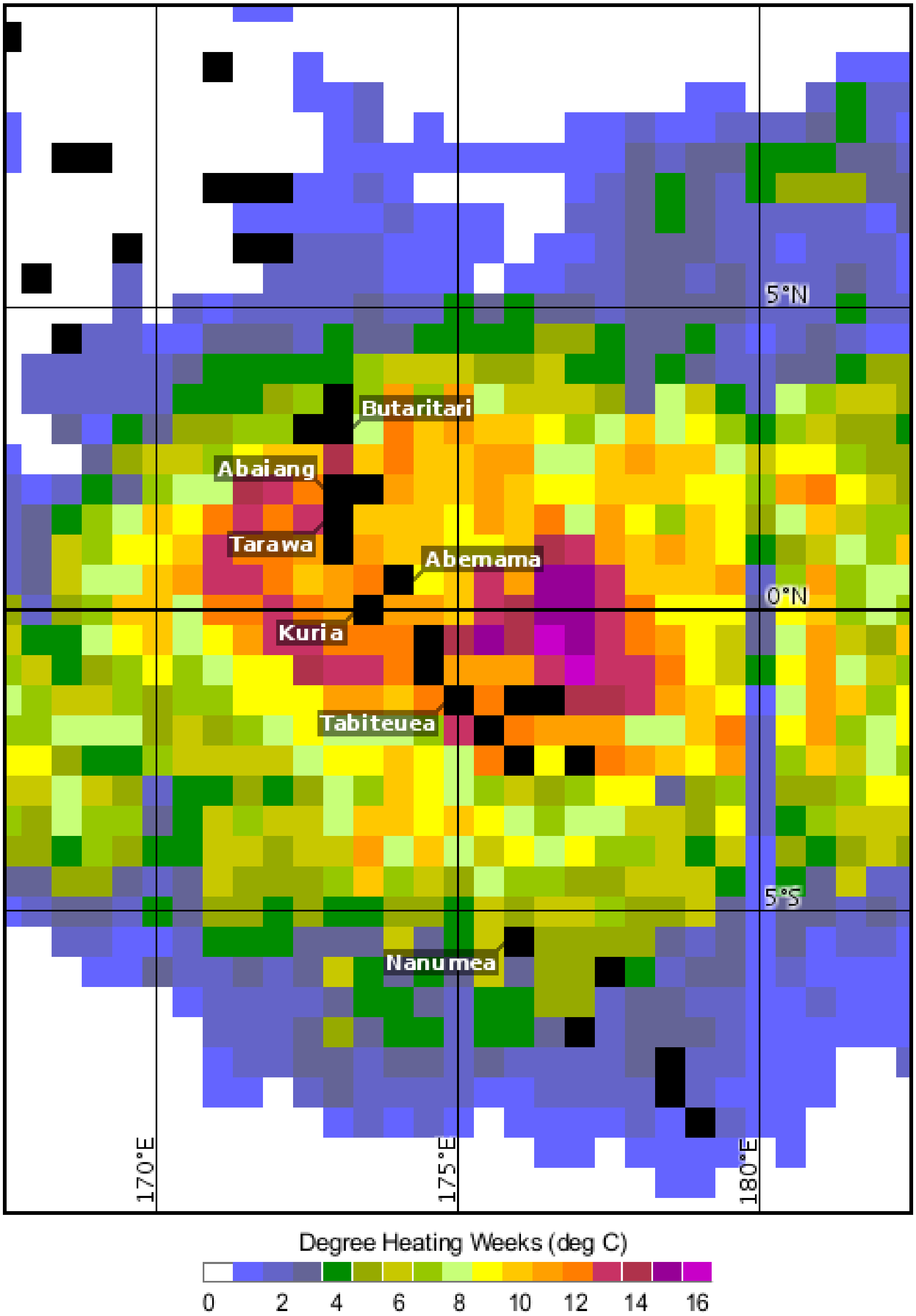

Figure 1. Map of degree-heating-weeks (DHW, inºC-week) of Kiribati's Gilbert Islands and the surrounding region (10ºN-10ºS, 167.5ºE-177.5ºW) for mid-November, 2004. The 0.5º x 0.5º data is derived from the Pathfinder retrospective SST dataset used by NOAA Coral Reef Watch. Nanumea is the northernmost atoll of Tuvalu.

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ABSTRACT

Over the past three decades, periods of anomalously warm ocean temperatures have been observed to cause mass coral bleaching, a paling of corals and other reef organisms due to the loss of dinoflagellate *Symbiodinium*. During late 2004, warming of the surface waters in the Central Equatorial Pacific occurred in association with a moderate El Nino event. The accumulation of degree-heating-weeks, a measure of thermal stress experienced by corals, reached the highest level on record in parts of the Gilbert Islands of Kiribati in November, 2004. The warm water anomaly led to the first ever reports of mass coral bleaching from the Gilbert Islands.

This study describes the development of the mass bleaching event, the extent and pattern of coral mortality, and the post-bleaching change in coral cover around little-studied Tarawa and Abaiang Atolls. Random surveys, conducted at shallow depths in 2004, 2005, and 2009 via free-diving due to limited local infrastructure, provide preliminary evidence that the outer reef coral communities have become increasingly dominated by more bleaching-resistant coral taxa since the 2004 bleaching event. There was a significant recovery in coral cover at the three Abaiang sites, which are less influenced by human disturbance and wave activity, from 2005 to 2009. This change included an increase in the area of the less bleaching-sensitive *Heliopora coerulea* and massive *Porites* and a widespread loss of the more bleaching-sensitive *Pocillopora* spp Recovery of coral cover was observed only at one Tarawa site, due to a significant increase of the resilient *Porites rus*.

Historical meteorological and SST data also indicate that the coral reefs of the Gilbert Islands may have been subject to other episodes of thermal stress sufficient to cause coral bleaching before 2004, due to the occurrence of "Central Pacific" El Nino events. Further monitoring of this relatively unstudied island chain is necessary to evaluate whether the frequent El Nino-driven thermal stress has affected coral community structure and resilience to future warm water events.

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INTRODUCTION

Warm water temperatures and high ultraviolet radiation can cause coral bleaching, the paling of coral is due to a breakdown of the symbiosis between the reef-building animal with the dinoflagellate "*Symbiodinium*" (Hoegh-Guldberg, 1999). Mass coral bleaching events and associated coral mortality in the past three decades have been linked to periods of anomalous surface ocean temperatures (Glynn, 1991; Hoegh-Guldberg, 1999, Wellington et al., 2001; Baker et al., 2008). Climate warming over the next half-century is expected to increase the frequency and intensity of mass coral bleaching events, possibly leading to long-term declines in coral cover and ecological phase shifts (Donner et al., 2005; Munday et al., 2008; Donner, 2009). Identifying the response of coral communities to mass bleaching events as well as the physical and biological factors which confer resilience are critical to understanding the future of coral reefs in a warmer future. For example, recent evidence suggests that coral communities exposed to higher background temperature variability may be more resistant to thermal stress (Thomson and van Woesik, 2009; Oliver and Palumbi, 2009).

The equatorial atoll nation of Kiribati has been subject to high year-to-year variability in ocean temperatures due to the El Nino / Southern Oscillation (ENSO), particularly over the past thirty years (Ashok et al., 2007; Kug et al., 2009). In late 2004, a warm water anomaly associated with a "El Nino" or positive ENSO event developed around Kiribati's Gilbert Islands and the northern islands of Tuvalu. Scientists from the Secretary of the Pacific Community conducting a fisheries assessment noted bleaching of 10-30% of live coral around Nukufetau Atoll, Tuvalu from Oct 26 – Nov 4 (Friedman, 2004). An assessment of Abaiang Atoll, Kiribati three weeks later (November 12–21) detected 40-80% coral mortality in shallow waters as well as bleaching and mortality down to 35 m depth (Friedman, 2004). Distribution of a "hot spot" alert by the NOAA Coral Reef Watch program brought further anecdotal reports of coral bleaching in Kiribati's Tarawa Atoll and Tabiteuea Atoll.

These were the first-ever international reports of mass coral bleaching from the Gilbert Islands of Kiribati (and Tuvalu). The coral reefs of the Gilbert Islands have been subject to little research in the past due to the relative isolation of the island chain and to the limited local medical and SCUBA facilities, particularly outside of the capital of Tarawa Atoll (Zann and Bolton, 1985; Lovell, 2000; Paulay and Kerr, 2001). The frequency of ENSO events suggests the Gilbert Islands have been subject to warm water anomalies sufficient to cause coral bleaching in the past. The lack of bleaching reports prior to November 2004 may be due to limited capacity for monitoring and communication of findings, rather than the lack of prior bleaching events. In hopes of establishing a locally appropriate benthic monitoring program, the Global Coral Reef Monitoring Network sponsored simple snorkel-based benthic surveys using small local boats were conducted at sites around Tarawa and two outer atolls in May of 2004, prior to the reports of bleaching (Vieux, 2004).

This study examines the effect of the 2004 mass coral bleaching event on benthic cover at sites around Kiribati's Tarawa and Abaiang Atolls. First, we examine the development of the late 2004 thermal anomaly in contrast to previous events using satellite-based reconstructions of sea surface temperatures and available local meteorological data. Second, we contrast benthic cover from the initial 2004 pre-bleaching surveys with follow-up surveys conducted in 2005 and 2009. Supplementary data from Tarawa, Abaiang and Butaritari Atolls was obtained from a 2007 training exercise conducted as part of the World Bank / GEF Kiribati Adaptation Project (Donner, 2007). The results provide evidence of a shift towards more bleaching-resilient coral taxa since the 2004 event at some sites, and also demonstrate the advantages and disadvantages of locally appropriate low technology surveys.

STUDY AREA

The atolls of Tarawa and Abaiang lie north of the equator in the Central Gilbert Islands and experience weather typical of the equatorial Pacific. Temperatures range from 25 ºC to 34 ºC throughout the year with average humidity of over 75%. Annual rainfall averages 2000 mm in Tarawa, most of which falls during a bimodal wet season between November and April. The islands are prone to droughts of up to a year in length, often related to the presence of negative ENSO or "La Nina" conditions.

Tarawa is a roughly triangular shaped coral atoll, enclosed almost entirely to the south and east and with a submerged western reef (Fig. 2a). It is home to over 45 000 people, most of whom live in crowded islets of Bairiki and Betio in the southern arm of the atoll. The high population, lack of sewage treatment and construction of causeways in South Tarawa is thought to cause high sediment, nutrient and bacteria levels in surrounding waters. The neighboring oval-shaped atoll of Abaiang to the north is home to 5000 people who are engaged largely in subsistence activities (Fig. 2b).

The full list of coral reef sites and surveys is provided in Table 1. In May, 2004, photo-quadrat surveys of outer reef coral cover at three sites around Tarawa (TRW01, TRW02, TRW03) and three sites around the atolls of Kuria and Abemama were conducted as parts of a Global Coral Reef Monitoring Network assessment by C. Vieux and T. Kirata (Vieux, 2004). In February and March, 2005, S. Donner and T. Kirata conducted photo-quadrat surveys at the three Tarawa sites and at the three Abaiang sites (ABG01, ABG02, ABG03) where bleaching was observed during the 2004 SPC Fisheries Assessment. Access to Kuria and Abemama at the time was limited due to weather and logistics. The Tarawa and Abaiang surveys were repeated in May, 2009 by S. Donner with the assistance of Ministry of Fisheries and Marine Resource Development (MFRMD) staff.

In addition, benthic data was obtained from the report of a 2007 benthic monitoring training program conducted through the GEF/World Bank Kiribati Adaptation Program (Donner, 2007). The data includes point-intercept and line-intercept training transects conducted at some of the Abaiang sites, additional sites around Tarawa (TRW04, TRW05), and the more northerly atoll of Butaritari.

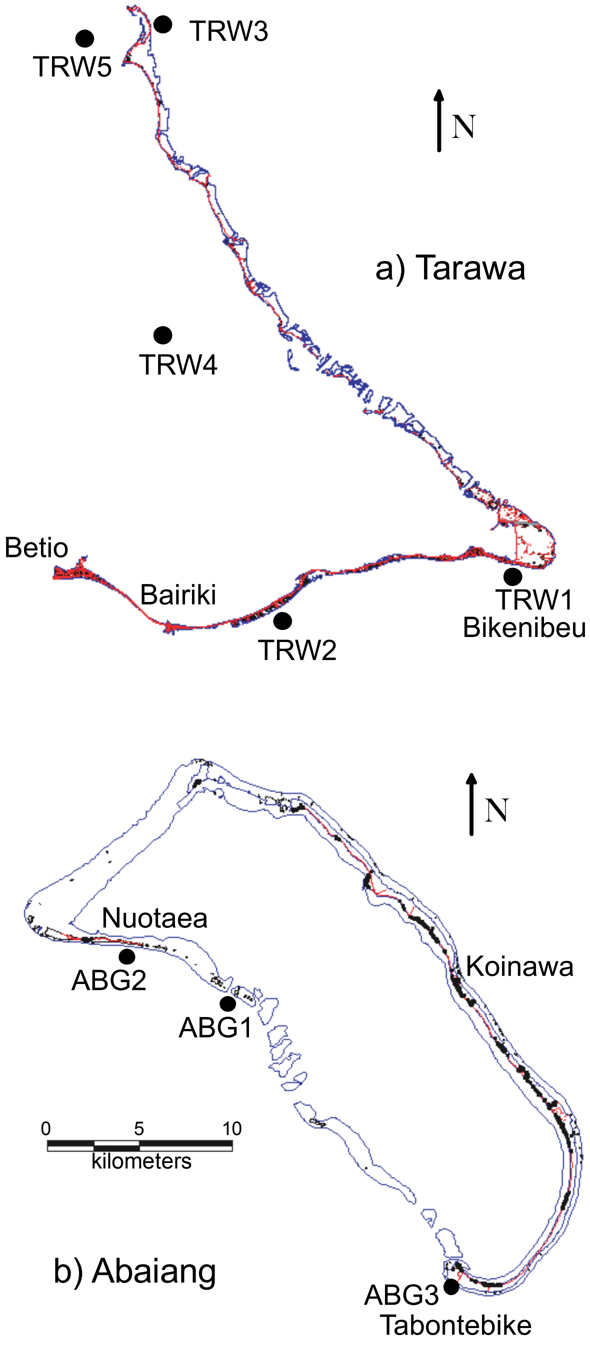

Figure 2. Map of a) Tarawa Atoll and b) Abaiang Atoll with survey sites marked. The blue lines represent the shallows difficult to navigate at low tide; red lines denote local paths and roads.

Table 1. List of sampling sites

ID	Site	Latitude	Longitude	Date	Lead observer	Method
TRW01	Bikenibeu	N 01°21.48	E173°08.75	May 2004 March 2005 May 2009	Vieux Donner Donner	Quadrats Quadrats Quadrats
TRW02	Teaoraereke	N 01°19.99	E173°01.30	May 2004 March 2005 Nov 2007 May 2009	Vieux Donner Donner[a] Donner	Quadrats Quadrats PIT[b] (10 m) Quadrats
TRW03	Na'a	N 01°37.95	E172°58.04	May 2004 Feb 2005 May 2009	Vieux Donner Donner	Quadrats Quadrats Quadrat
TRW04	Central Lagoon	N 01'25.86	E172°59.21	Nov 2007	Donner[a]	LIT[c] (3 m)
TRW05	NW Reef	N 01'37.07	E172°56.02	Nov 2007	Donner[a]	PIT (3m, 10m)
ABG01	Confusion Reef	N 01°51.46	E172°52.77	Feb 2005 Nov 2007 May 2009	Donner Donner Donner	Quadrat Quadrat Quadrat
ABG02	Nuotaea	N 01°52.92	E172°49.08	Feb 2005 Nov 2007 May 2009	Donner Donner[a] Donner	Quadrat PIT (3m, 10m) Quadrat
ABG03	Tabonetebike	N 01°42.86	E172°59.19	Feb 2005 Nov 2007 May 2009	Donner Donner[a] Donner	Quadrat PIT (3m, 10m) Quadrat

[a] data collected as part of training workshop (Donner, 2007)

[b] Point intercept transects (see text) [c] Line intercept transects (see text)

METHODS AND MATERIALS

Climate Analysis

Historical twice-weekly sea surface temperatures (SST) for the central Pacific at 0.5° x 0.5° lat-lon resolution were obtained from AVHRR Pathfinder retrospective dataset (1985-2007) made available by the NOAA Coral Reef Watch Program (http://coralreefwatch.noaa.gov). Several grid cells in the region of the Gilbert Islands appear as land in the retrospective dataset (Fig. 2). The data for the 0.5° x 0.5° grid cell that is closest to the sampling sites for both Tarawa and Abaiang was analyzed. An additional data point that corresponds with the Butaritari Atoll sampling sites visited during the 2007 KAP training program is also presented for comparison.

The historical temperature data was contrasted with four different El Nino / Southern Oscillation (ENSO) indices. Monthly values since 1985 for the NINO3 index, based on SST anomalies for the region (5°N-5°S, 150°W-90°W) where the largest SST variability occurs on ENSO time scales, and the NINO4 index (5°N-5°S, 160°E-150°W), which encompasses the Gilbert Islands, were obtained from the LDEO /IRI Data Library (http://iridl.ldeo.columbia.edu/index.html). Monthly values for the Southern Oscillation Index and the Multivariate El Nino Index were obtained from the NOAA Climate Prediction Centre (http://www.cpc.noaa.gov) and the NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/).

The thermal stress experienced by the coral reefs of the Gilbert Islands is represented by “degree heating weeks” (DHW), the metric used by the NOAA Coral Reef Watch Program to predict the likelihood of mass coral bleaching in real-time (Liu et al., 2003; Skirving et al., 2006; Eakin et al., 2008). The DHW value is the accumulation of weekly temperatures in excess of the maximum in a monthly climatology (maximum monthly mean, or MMM) over a rolling twelve week period. For example, if November is the warmest month in the SST climatology, one DHW (°C-week) is equal to one week of SST that is 1°C greater than the November SST in the monthly climatology. Only anomalies in excess of 1°C are included because smaller SST spikes are insufficient to cause thermal stress (i.e. a weekly anomaly of 1.2 °C increases the DHW value by 1.2 °C-week; an weekly anomaly of 0.8°C does not increase the DHW value). Independent coral bleaching reports have indicated that some coral bleaching will begin to occur when the DHW > 4, and more severe bleaching with some coral mortality will begin to occur when the DHW > 8 (Skirving et al., 2006).

For this study, a second version of the DHW time series was calculated using an alternate method for computing the maximum monthly mean (Donner, 2009). Unlike most regions of the tropics, the timing of the seasonal peak in SST varies from year to year in the Gilbert Islands because of the small seasonal variability but large ENSO-driven inter-annual variability. Therefore, the maximum SST from a monthly climatology (i.e. November from the SST climatology) is likely to be lower than the mean of the maximum monthly SST experienced each year (i.e. November some years, October other years). The alternative DHW time series for the Gilbert Island grid cells is computed using the mean of the maximum monthly SST of each year during the climatological period employed by NOAA Coral Reef Watch as the maximum monthly mean (MMM_{max}).

Historical meteorological data for the Gilbert Islands was also obtained from the Kiribati Meteorological Office. The colonial British Administration of the then Gilbert and Ellice Island Colony began collecting meteorological data in the Gilbert Islands in the 1930s, including stations in Tarawa Atoll (Betio), Beru to the south and Butaritari Atoll to the north. The early records are not continuous; most records were interrupted during World War II and also for short periods in recent decades due to equipment, weather and staffing issues. Available monthly mean data since 1947 on daily mean, maximum and minimum temperature, extreme maximum and minimum temperature; rainfall; number of rain days; and sunshine hours were obtained for the Betio, Tarawa station and the Butaritari station.

Benthic Cover Surveys

The photo quadrat surveys were conducted on the outer reef slopes at 5-7 m depth by two observers free diving from small local boats with a randomly placed 0.83 m^2 quadrat. Benthic cover was estimated using analysis of random points within each image, using the CPCe software package (citation). For each site, the benthic cover was analyzed at 320 randomly assigned points (16 images x 20 points per image); the number of images and the points per image were found to be sufficient to represent outer reef benthic cover in a statistical analysis done for the 2004 GCRMN survey (Vieux, 2004). This inexpensive and low technology survey technique is well suited to the Gilbert Islands where access to SCUBA gear, boats and emergency equipment as well as local experience identifying benthic taxa can be limited.

Benthic cover was divided into six main categories (hard coral, soft coral, algae, dead coral, sand, rubble and "other" live cover) with sub-categories for the live coral taxa (*Acropora*, *Heliopora*, *Pocillopora*, *Porites*, etc.), algae (macroalgae, *Halimeda*, encrusting coralline algae) and dead coral (pavement, recently dead, dead coral with algae, diseased, bleached). Coral rock covered with thin layers of algal turf was classified as dead coral with algae ("DCA"), rather than in the broader algae category. Soft corals were present at only one site, and in low abundance (<1%), so those data are not shown here.

The benthic cover at each survey site were compared to estimate the impact of the bleaching event on coral cover, where possible, and the change in benthic cover from 2005 to 2009. There were no major storms and no evidence for crown-of-thorns starfish outbreaks since the GCRMN survey, so any change in benthic composition is presumed to be a result of bleaching-related mortality. For consistency, the 2009 images and the earlier images discussed in previous reports (e.g., Vieux, 2004) were all re-analyzed by a single observer. The data for each site is presented here in terms of percent benthic cover and, for corals, as percent of coral cover. The difference in benthic cover between years at each site is evaluated using a Mann-Whitney U two-sample rank sum test contrasting the number of point observations in each set of quadrat images ($n_1=n_2=16$).

An additional analysis of the number of living and dead pocilloporid colonies was conducted. The family pocilloporid is selected because of the high pre-bleaching cover at several sites, the visibly high mortality during the bleaching event and the ability to identify dead colonies, predominately *Pocillopora eydouxi* and *Pocillopora verrucosa*, in the 2005 and 2009 post-bleaching images. The count of dead colonies includes recently dead corals, colonies covered in a thin layer of turf algae and those encrusted in coralline algae.

RESULTS AND INTERPRETATION

Development of the 2004-05 Mass Bleaching Event

The 2004 thermal anomaly around the Gilbert Islands and Tuvalu began developing during boreal summer (July and August). Periods of westerly winds between June to October pushed the West Pacific warm pool, the stretch of warm open ocean water normally centered east of Papua New Guinea, further eastward to the central Pacific (Lyon and Barnston, 2005; IRI, 2005). These westerly winds initiated eastward propagating Kelvin waves. During typical ENSO events, Kelvin waves travelling across the equatorial Pacific cause anomalously warm SSTs in the east-central and eastern equatorial Pacific (IRI, 2005). In 2004, strong eastern trade winds and related upwelling in the Eastern Pacific stopped the Kelvin waves from propagating far across the International Dateline (Lyon and Barnston, 2005; IRI, 2005). The warm waters were advected towards the Gilbert Islands and northern Tuvalu, but not further eastward.

The value of the ENSO indices suggests the development of a partial ENSO event, centered in the Central Pacific rather than the Eastern Pacific. The mean SOI (-0.68), mean MEI (0.64) and mean NINO3 (0.66 ºC) for September-December 2004 all indicate the presence of weakly positive ENSO (“El Nino”) conditions. According to these standard indices, more positive or stronger September-December ENSO conditions have occurred eight times since 1985, including 1986, 1987, 1991, 1992, 1994, 1997, 2002 and 2006. Alternatively, the mean September-December 2004 value of the NINO4 index (1.11 ºC) was the second highest since 1985. The NINO4 index is calculated from SST anomalies over a region including the Gilbert Islands (5°N-5°S, 160°E-150°W) which is to the west of the region which typically experiences anomalous warming during ENSO positive events. The NINO4 index has recently been used to characterize “Central Pacific” ENSO events like the 2004-5 event as distinct from typical “Eastern Pacific” ENSO events (Kug et al., 2009).

The SST in the Gilbert Islands remained more than 1.5 ºC greater than the monthly climatological values for September through December in 2004, according to the Pathfinder retrospective data. The thermal stress, measured in DHW, peaked at 10 – 15 °C-week in the waters around the central Gilbert Islands during mid-November (Fig. 1). In the 0.5 º x 0.5 º grid cell that encompasses the waters around Tarawa and southern Abaiang, the DHW value reached a maximum of 11.6ºC-week from November 12-15, the highest value in the satellite record (Fig. 3a). The magnitude of the hotspot declined northward from the equatorial central Gilberts, with max DHW of 7.6ºC-week in Butaritari also during mid-November (Fig. 3b). The thermal anomaly is notable for its duration as well as its magnitude. For example, for Tarawa and southern Abaiang, the bi-weekly SST was in excess of the maximum monthly mean (a “hotspot”) from May 31st through Dec 31st, including three weeks with hotspot values in excess of 1.5°C (Fig. 4). The only warm period of similar duration in the satellite record occurred in the previous year; the lower magnitude and discontinuous nature of the 2003 thermal anomaly limited the maximum DHW value to 6.4ºC-week (Fig. 3a; Fig. 4)

Trade wind reversals in association with ENSO events and anomalously warm SSTs typically also bring increased cloudiness and increased storm activity to the Gilbert Islands. Reduced incoming radiation due to cloudiness has been reported to prevent mass coral bleaching events (Mumby et al., 2001). Bleaching occurred on the SPC Fisheries Assessment in Tuvalu and Kiribati at or before the onset of a period of extended cloudiness. The South Pacific convergence zone, a regional spur of the Inter-Tropical Convergence Zone (Philander and Rasmusson, 1985) that often drives convective activity and cloudiness in the central Pacific, migrate northeast into the Gilbert Islands in mid-November 2004 (NIWA, 2005). The months of November, December and January experienced only 95 hours of sunshine, 83% below the 1978-2006 mean, according to data collected at Betio, Tarawa. It is possible that the extended cloudiness forestalled bleaching or bleaching-induced mortality in some locations.

The period of anomalously warm SST continued until late March, according to the Pathfinder retrospective data. The period from November 2004 through April 2005

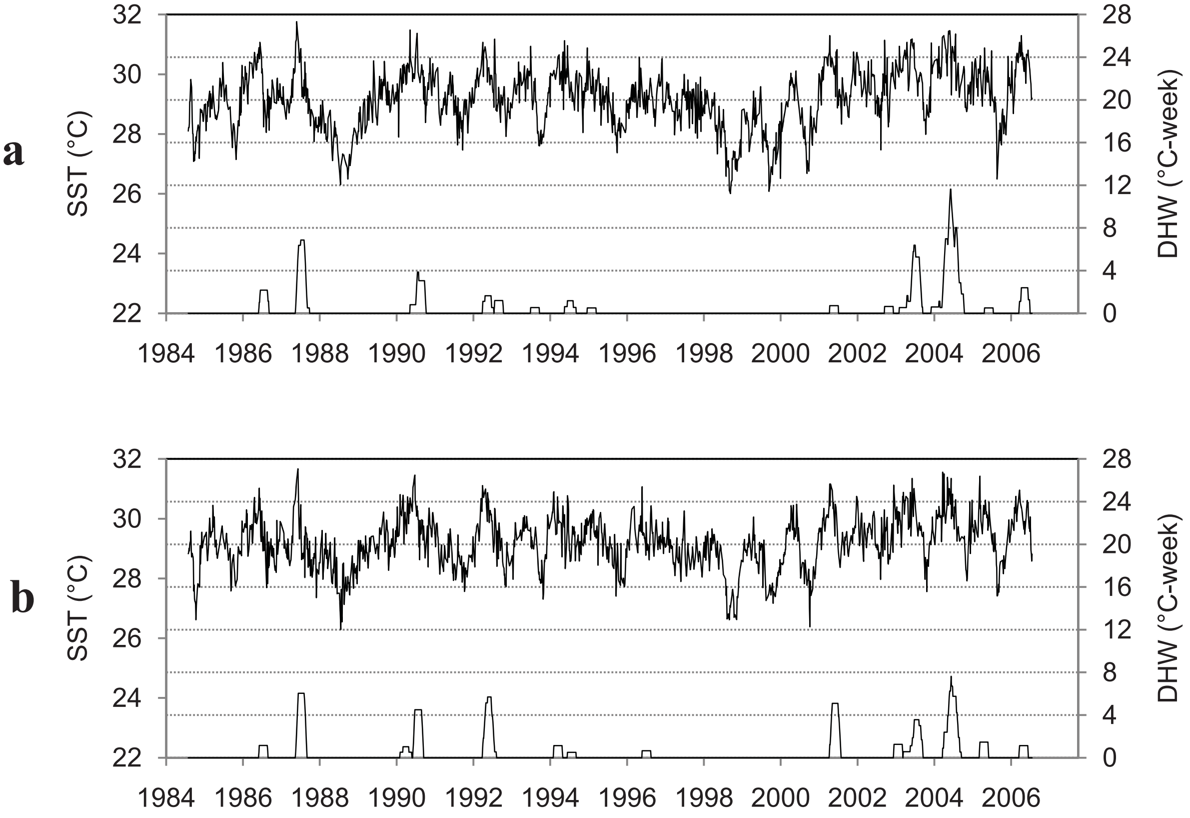

Figure 3. Sea surface temperature (SST) and Degree Heating Weeks (DHW) for a) Tarawa / Southern Abaiang, and b) Butaritari (west) from 1985 through 2007 in Pathfinder retrospective data.

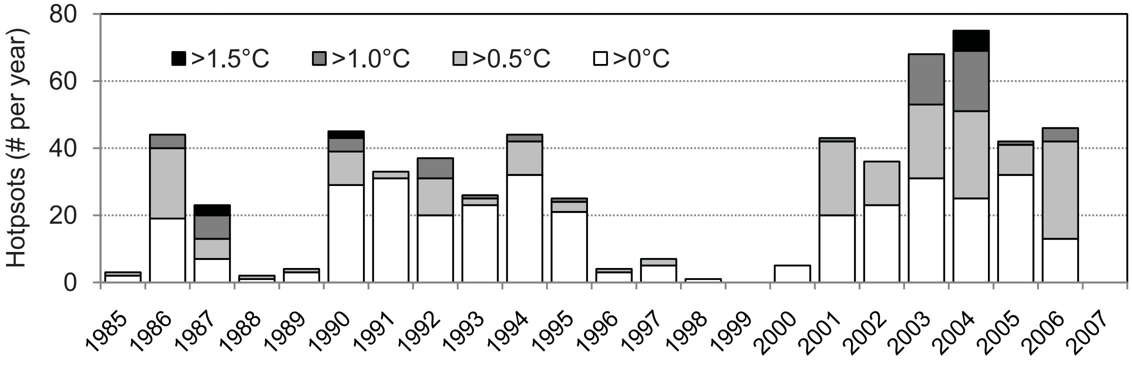

Figure 4. Number of "hotspots" (bi-weekly SST values in excess of the maximum monthly mean) per calendar year.

was the warmest such period since the modern meteorological station at Betio, Tarawa (1.35° N, 172.93°W) was established in 1947 (data available through 2008). The mean daily air temperature for the period was 1.3 °C above the long-term mean of 27.9 °C; the mean daily minimum and daily maximum air temperatures were also the highest reported. The meteorological data also confirms that the thermal anomaly decreased northwards from the equator. Mean air temperatures at the Kiribati Meteorological Weather station at Butaritari (3.07° N, 172.78°W), 190 km to the north, were only 0.2 °C above the long-term mean (1957-2008) from November, 2004 through April, 2005.

The magnitude of the 2004 thermal anomaly was lower when computed using MMM$_{max}$, the alternate formulation of the MMM designed to account for year-to-year variability in the timing of peak temperatures (Fig. 5). Using MMM$_{max}$, DHW peaked in 2004 at 6.2ºC-week in Tarawa / Southern Abaiang and 4.6ºC-week in Butaritari, rather than 11.6ºC-week and 7.6ºC-week respectively using the standard MMM formulation. Analysis of the retrospective data since 1985 indicates the frequency of thermal anomalies depends on the MMM formulation. The maximum annual DHW exceeded the lower bleaching threshold (DHW > 4°C- week) four times in Tarawa / Southern Abaiang (Fig 4) and five times in Butaritari from 1985-2005 (Fig 3b) in the Coral Reef Watch retrospective data. If the DHW values are computed with MMM$_{max}$, the maximum annual DHW only exceeded the lower bleaching threshold in 2004 in Tarawa/Southern Abaiang (Fig 4) and also Butaritari (not shown). With the alternative MMM formulation, there was no DHW accumulation during long periods of anomalous warm SSTs in 2003 and during the 1990-1994 period of moderate ENSO conditions.

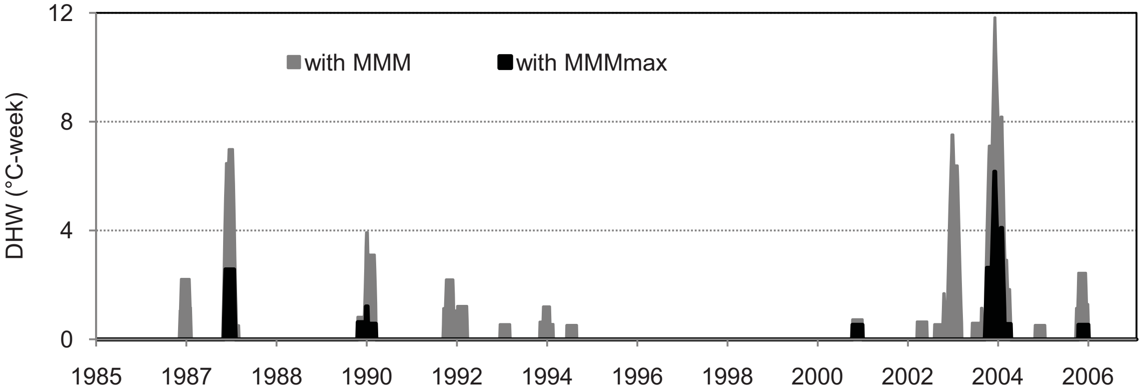

Figure 5. Degree Heating Week (DHW, in ºC-week) values for Tarawa / Southern Abaiang from the Pathfinder Retrospective data. The DHW values are computed using the standard MMM (SST of the maximum month in the NOAA Coral Reef Watch climatology) and the MMMmax (mean of the maximum monthly temperature in each year of the climatology). Dashed lines show the low and high bleaching thresholds (DHW = 4, 8 ºC-week).

Benthic Cover

Observations during the surveys and other studies indicate that the central Gilbert atolls including Tarawa and Abaiang feature similar patterns of reef morphology (Zann and Bolton, 1985; Lovell, 2000; Donner, 2007). The outer reefs feature spur and groove patterns from the reef crest seaward to approximately 10-15 m depth. The southeastern and eastern outer reefs that are more exposed to prevailing easterly winds and swells generally have narrower reef terraces than the more sheltered western outer reefs (submerged in Tarawa). Coral cover in the sandy lagoons is limited to small patch reefs (Paulay and Kerr, 2001; Donner, 2007). The results of the surveys for the individual sites are presented below and in Table 2 through Table 5.

Tarawa Atoll: TRW01 – Bikenibeu. The site offshore of the Tarawa hospital on the southeastern islet of Bikenibeu featured 23% hard coral cover in the 2004 pre-bleaching survey (Table 2). Coral cover was dominated by the encrusting *Porites rus*, with some *Pocillopora* and the octocoral *Heliopora coreulea* but little cover of *Acropora* (Table 3). The benthic cover is dominated by reef pavement (38%) on the reef spurs and sand/rubble (22%) in the grooves. Lovell (2000) found hard coral cover of 7% at 3 m depth and 28% at 10 m depth offshore of the hospital, also with low *Acropora* cover. The low pre-bleaching hard coral cover may be attributed to the high wave activity on the SE coast, and possibly also local sewage discharge.

Table 2. Benthic cover at the Tarawa Atoll sites

TRW 01	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2004	23 ± 15%	6 ± 5%	10 ± 8%	38 ± 13%	22 ± 16%	0%
2005	25 ± 13%	1 ± 1%	28 ± 13%	21 ± 12%	24 ± 15%	1%
2009	41 ± 24%	1 ± 2%	8 ± 5%	28 ± 20%	21 ± 13%	1%
TRW 02	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2004	23 ± 9%	4 ± 3%	35 ± 16%	23 ± 8%	15 ± 9%	0%
2005	14 ± 10%	7 ± 5%	46 ± 16%	26 ± 9%	5 ± 4%	3%
2007 (10m)	29 ± 22%	23 ± 15%	15 ± 17%	6 ± 10%	1 ± 3%	0%
2009	18 ± 6%	8 ± 4%	27 ±15%	24 ± 12%	24 ±10%	0 %
TRW 03	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2004	60 ± 8%	10 ± 6%	8 ± 5%	16 ± 8%	6 ± 4%	0%
2005	18 ± 8%	12 ± 11%	24 ± 8%	35 ±15%	10 ± 4%	1%
2009	21 ± 8%	12 ± 7%	24 ± 12%	36 ±13%	5 ± 5%	1%

Table 3. Coral cover by taxa for Tarawa Atoll sites (as a % of live coral)

TRW 01	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2004	5 ± 9%	0%	3 ± 4%	13 ± 22%	0%	20 ± 30%	49 ± 33%	9±16%
2005	0%	0%	0 ± 0%	13 ± 20%	1 ± 3%	29 ± 37%	54 ± 34%	4±13%
2009	1 ± 2%	0%	2 ± 8%	19 ± 22%	0%	8 ± 9%	67 ± 30%	3±9%
TRW 02	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2004	9 ± 18%	12 ± 16%	4 ± 6%	26 ± 25%	0%	27 ± 18%	4 ± 7%	18±14%
2005	0%	24 ± 35%	0%	11 ± 9%	11 ± 11%	26 ± 22%	22 ± 24%	7±18%
2007 (10m)	12 ± 17%	0%	0%	12 ± 21%	0%	8 ± 14%	37 ± 29%	32±37%
2009	13 ± 34%	0%	0%	52 ± 36%	0%	14 ± 23%	13 ± 19%	9±14%
TRW 03	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2004 *	2 ± 3%	6 ± 8%	0%	33±20%	17 ± 20%	6 ± 6%	8 ± 11%	28±14%
2005	0%	9 ± 10%	0%	0%	41 ± 33%	0%	41 ± 30%	9±11%
2009	3 ± 5%	25 ±15%	0%	0%	36 ± 26%	3 ± 7%	0%	33±10%

After the bleaching event, there was no significant change in hard coral cover or in the cover of the common taxa *Porites* and *Pocillopora*, or the locally common *Heliopora coreulea*. By 2009, there was a significant increase in coral cover increased to 41% (Mann-Whitney $U_{2005} = 1$, p=0.02). This change was driven by the expansion of *Porites rus* from 28% of benthic cover in 2005 to 67% of total coral cover (Fig. 6). This represents a significant increase in total cover of *Porites rus* from before the 2004 bleaching to 2009 is ($U_{2004} = 167.5$, p=0.04). Other species present in 2009 include *Heliopora coreulea* (19% of coral cover), *Pocillopora eydouxi* and *Pocillopora verrucosa* (8% of coral cover)*,* *Lobophyllia hemprichii* (categorized as "other") as well as low levels of fungiids and *Acropora* spp.

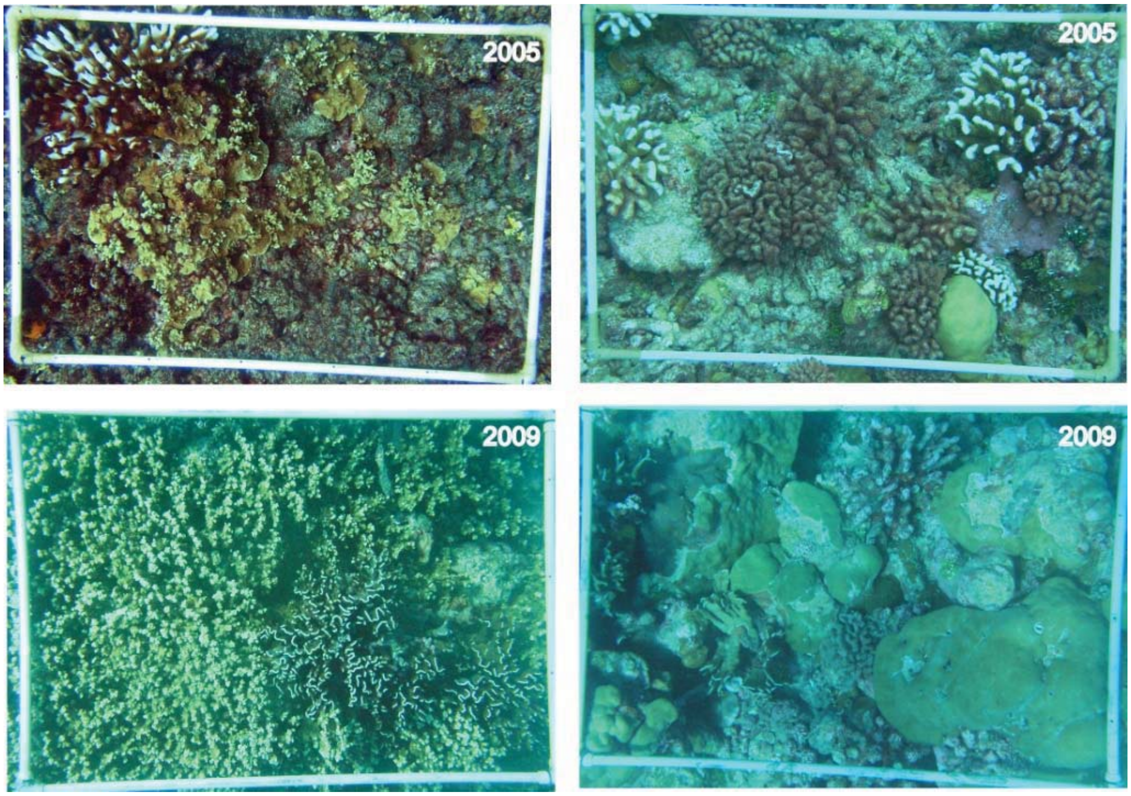

Figure 6. Sample quadrat photos from TRW01 (Bikenibeu, on left) and ABG01 (Confusion Reef) from 2005 (top row) and 2009 (bottom row). Individual images are from randomly placed quadrats and should not be directly compared.

TRW02 – Teaoraereke. The other South Tarawa outer reef site featured a similar level of pre-bleaching coral cover (23%), dominated by *Heliopora coreulea* (26% of coral cover) and *Pocillopora* spp. (27% of coral cover), and high cover of dead coral (35%), pavement and rubble (Table 2, Table 3). After the bleaching event, there was a significant decrease in coral cover to 14% ($U_{2005} = 82$, p=0.02). Dead coral cover, including recently dead coral and dead coral covered in thin algal turf, increased to 46% ($U_{2004} = 70.5$, p<0.01) . There was no significant change in coral taxa, although there was a rise in massive *Porites* and *Porites rus* as a fraction of live coral cover.

In the 2009 survey, coral cover increased slightly to 18%, but the change since 2005 was not significant. Over half of the live coral cover (52%) was *Heliopora coerulea*, representing a significant increase since 2005 ($U_{2005} = 175$, p<0.04). The remaining live coral taxa included *Pocillopora,* massive *Porites* and *Acropora*, as well as mussids and fungiids. Unlike the Bikenibeu site, there was little *Porites rus*. Zooanthids and a red turf algae streaked on dead colonies were also present.

It should be noted that other pre- and post-bleaching studies noted higher coral and algal cover at depth near Teaoraereke and the central southern coast of Tarawa. In the training program conducted three years post-bleaching Donner (2007) noted 39% live hard coral and 26% algae cover, including *Halimeda* and crustose coralline algae, at 10 m depth. The live coral also displayed more generic diversity, including *Symphyllia*, *Favites*, *Pachyseris*, *Favia* and *Montipora* in addition to the taxa observed in the 2009 photo-quadrat survey. Lovell (2000) also noted 33-44% coral cover at 3 m depth and 53-56% coral cover at 10 m depth at other south coast sites with similar morphology within 6 km of the Teaoraereke site.

TRW03 – Na'a. The site off the village of Na'a at the northern tip of Tarawa has high coral cover at 60%, composed of mostly *Heliopora coerulea* and *Montipora* spp. (Table 2, Table 3) Discrepancies over the site location preclude direct statistical comparison of the pre-bleaching and post-bleaching surveys. The strong wave action and the alongshore currents south of the northern tip of Tarawa can limit safe anchorage and free-diving and likely caused the observers in subsequent surveys to drift from the initial coordinates set in 2004. Rough seas have routinely spoiled attempts to access and stake the site (Donner, 2007). Although the reef slope is relatively homogenous, and interspersed with narrow, shallow (< 1m) grooves of sand and rubble, the marked differences in coral taxa between 2004 and the later surveys (notably the absence of *Heliopora coerulea* in 2005) suggest that the minor (<200 m) observer drift around the northern tip likely affected the benthic cover surveys.

The 2005 surveys found a largely abiotic reefscape with 18% hard coral cover and 59% either dead coral or reef pavement. Encrusting *Montipora* and massive *Porites* composed 90% of the living coral cover. The effects of the bleaching event were evident in the 16% cover of recently dead coral, largely composed of *Pocillopora* colonies, and the presence of fully- or partially-bleached *Pocillopora* and *Porites* colonies. There was no living *Acropora* cover in the quadrat images and little evidence of *Acropora* in the rubble or recently dead coral colonies.

The change in live hard coral cover, algae or abiotic cover from 2005 to 2009 was not significant ($U_{2005} = 101$, $p=0.15$ for hard coral cover). The live hard coral taxa included encrusting *Montipora*, *Favites*, *Platygyra* and *Lobophyllia*. *Acropora*, absent in the 2005 survey, were rare, at less than 1% of benthic l cover and 3% of the coral cover. Coral colonies were all smaller than 0.5 m in diameter. The visible dead coral cover included pocilloporids (*P. Eyxdouxi*, *P. Verrucosa*, *Stylophora pistillata*) and digitate *Acropora*. Informal surveys at 10 – 15 m depth indicated higher coral cover (estimated at 20-40%) including presence of *Heliopora coerulea, Porites rus*, massive *Porites* and *Turbinara.*

Abaiang Atoll: ABG01 – Confusion reef. The three Abaiang atoll sites are on the accessible western outer reefs that were visited during the 2004 SPC fish survey; no benthic cover data was collected during that 2004 survey. Each site features a spur-and-groove morphology along the reef terrace, and a steep reef slope beginning at 8-10 m depth. The only previous survey near the central western site ABG01 noted coral cover of 37% at 3m depth and 28% at 10 m depth, dominated by *Heliopora coerulea* and with little *Acropora* (Lovell, 2000).

In 2005, the live coral cover at the central western site ABG01 was 26% and composed of a mix of massive *Porites*, *Pocillopora*, *Montipora*, *Heliopora*, *Favia, Favites* and *Platygyra* (Table 4, Table 5). There was a high cover of dead coral and reef pavement (50%), and partial bleaching was evident in some massive *Porites* and *Pocillopora* colonies. Dead *Pocillopora* colonies dominated the recently dead coral (20%) and benthos covered in crustose coralline algae (6%).

Table 4. Benthic cover at the Abaiang Atoll sites

ABG 01	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2005	26 ± 9%	12 ± 6%	35 ± 11%	15 ± 6%	9 ± 7%	3 ± 3%
2007	32 ± 11%	28 ± 10%	18 ± 9%	8 ± 5%	13± 10%	1%
2009	47 ± 6%	16 ± 14%	24 ± 13%	8 ± 6%	4 ± 5%	0%
ABG 02	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2005	14 ± 9%	23 ± 7%	31± 10%	13 ± 9%	17 ± 10%	2%
2007 (3m)	16 ± 11%	36 ± 21%	22 ± 27%	12 ± 15%	10 ± 13%	4%
2007 (10m)	25 ± 14%	59 ± 20%	3 ± 8%	2 ± 5%	11 ± 13%	1%
2009	25 ± 11%	15 ± 13%	26 ± 14%	18 ± 10%	16 ± 5%	0%
ABG 03	**Hard Coral**	**Algae**	**Dead coral**	**Pavement**	**Sand/Rubble**	**Other**
2005	23 ± 11%	18 ± 11%	25 ± 9%	20 ± 9%	12 ± 7%	3 ± 3%
2007 (3 m)	36 ± 10%	34 ± 14%	16 ± 6%	9 ± 7%	4 ± 4%	1%
2007 (10 m)	35 ± 15%	43 ± 17%	8 ± 13%	11 ± 11%	2 ± 0%	1%
2009	41 ± 12%	30 ± 10%	21 ± 10%	6 ± 5%	2 ± 2%	0%

Table 5. Coral cover by taxa for Abaiang Atoll sites (as a % of live coral)

ABG 01	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2005	0%	7 ± 11%	0%	13 ± 25%	22 ± 26%	15 ± 13%	34 ± 31%	9±10%
2007	1 ± 4%	5 ± 6%	1 ± 2%	11 ± 22%	4 ± 9%	7 ± 11%	60 ± 20%	11±27%
2009	0%	9 ± 9%	3 ± 4%	7 ± 10%	2 ± 4%	7 ± 6%	62 ± 16%	11±6%
ABG 02	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2005	0%	4 ± 15%	0%	13 ± 23%	13 ± 24%	11 ± 15%	53 ± 35%	4±5%
2007 (3m)	0%	20 ± 21%	0%	28 ± 37%	18 ± 33%	0%	12 ± 24%	22±32%
2007 (10m)	3 ± 13%	34 ± 26%	14±24%	14 ± 21%	3 ± 12%	0%	27 ± 37%	5±13%
2009	1 ± 4%	8 ± 12%	3 ± 4%	21 ± 20%	3 ± 4%	10 ± 13%	28 ± 21%	28±29%
ABG 03	**Acropora**	**Faviid**	**Fungiid**	**Heliopora**	**Montipora**	**Pocillipora**	**Porites**	**Other**
2005	0%	14 ± 30%	0%	16 ± 14%	3 ± 9%	1 ± 2%	51 ± 27%	15±23%
2007 (3m)	0%	10 ± 9%	0%	12 ± 15%	6 ± 6%	0%	66 ± 17%	6±11%
2007 (10m)	1 ± 6%	26 ± 20%	1 ± 6%	18 ± 18%	7 ± 18%	5 ± 12%	2 ± 11%	39±30%
2009	0%	10 ± 14%	2 ± 5%	27 ± 16%	21 ± 9%	2 ± 3%	26 ± 23%	13±9%

By 2009, there was a significant increase in live hard coral cover to 47% ($U_{2005} = 47.5$, $p<0.01$). The increase in coral cover was dominated by an increase ($U_{2005} = 29$, $p<0.01$) in massive *Porites* (*P. lobata* and *P. lutea*) from 9% of total benthic cover in 2005 to 29% in 2009 (Fig. 6). The remaining live coral taxa included *Heliopora coerulea*, *Favia*, *Favites*, *Pocillopora,* as well as *Hydnophora*, *Lobophyllia* and *Turbinara* (each classified as 'other live coral'). *Acropora* was uncommon. *Halimeda* was common (11%) as at other Abaiang sites.

ABG02 – Nuotaea (NW reef). This site near the small village of Nuotaea is more directly exposed to wave activity and features a steeper reef slope than the more southerly Abaiang sites. Lovell (2000) noted 42% live coral and 36% coralline algae at 3 m depth, and noted 50% live coral and 16% *Halimeda* at 10 m depth at a site within 1 km.

In 2005, the live hard coral cover (14%) was the lowest of the three Abaiang sites (Table 4). The reefscape was dominated by dead coral and pavement (44%) and coralline algae (19%). Partially bleached *Pocillopora* sp. and massive *Porites* sp. (*P. lutea* and *P. lobata*) were present (2%) as at site ABG01. Live coral taxa was dominated by massive *Porties* along with *Pocillopora*, *Montipora*, *Heliopora coerulea, Favites* and *Platygyra* (Table 5)

Though not directly comparable, benthic cover data collected at 3 m and 10 m depth (2 x 50m PIT) as part of the 2007 training program suggests no statistically significant increase in coral cover (Donner, 2007). Hard coral cover was reported at 16% at 3 m depth and 25% at 10 m depth. *Halimeda* (29%) and encrusting coralline algae (29%) dominated the cover at 10 m depth.

By 2009, live coral cover in the photo-quadrat surveys increased to 25%, indicating a significant since 2005 ($U_{2005} = 67.5$, $p <0.01$). This may be driven by an increase in mean cover of *Heliopora coerulea* and "other" coral taxa *Hydnophora*; the change in mean cover from 2005 to 2009 was not statistically significant for any individual coral taxa. Small (<20 cm) *Favia*, *Favites* and *Acropora* recruits were evident in the surveys but composed a small fraction of global cover. The dead coral cover (26%) included was dominated by dead colonies of *Pocillopora*, indistinguishable massive colonies and some *Acropora*. There was also 10% cover of *Halimeda*. There apparent increase from 1% in 2005 to 10% in 2009 is not statistically significant; the site has large spatial variability in the *Halimeda* cover at the shallow depths surveyed.

ABG03 – Tabonetebike. The benthic cover offshore of Tabonetebike near the southwestern tip of Abaiang is similar to ABG01, but features a more heterogeneous reefscape, including several 2-3 m high spurs and deeper sandy grooves. Surveys by Lovell (2000) on a southwestern outer reef noted the highest coral and *Acropora* cover of any Abaiang sites. Coral cover was 52% at 3m depth and 66% (35% *Acropora*) at 10 m depth.

In 2005, the photo-quadrat surveys found live coral cover was 23% and dominated by massive *Porites* (51% of coral cover) and included *Favia*, *Heliopora coreulea* and mussids (Table 4). There was a high proportion of dead coral cover and reef pavement (45%) and bleaching was still evident among some coral colonies (2%). Algae cover totaled 18%, including *Halimeda* (10%) and coralline algae (8%).

Data collected at 10 m depth during the 2007 training program found 35% hard coral cover - composed primarily of *Heliopora coerulea* and the taxa *Porites, Favites*, *Favia*, *Platygyra* and *Lobophyllia* – and noted a large population of coral recruits. The deeper survey also noted abundant *Halimeda* (25%), coralline algae (18%) and dead coral and rubble dominated by *Pocillopora*.

The 2009 photo-quadrats surveys found significant increase in live coral cover to 41% since 2005 ($U_{2005} = 56.5$, $p<0.01$), including a significant increase in *Montipora* spp. ($U_{2005} = 54$, $p<0.01$) and a weakly significant increase in *Heliopora coerulea* ($U_{2005} = 105.5$, $p=0.08$). There was also a significant increase in the algae *Halimeda* from 2005 to 2009 ($U_{2005} = 100$, $p=0.04$). In addition to *Heliopora coerulea* and *Montipora*., the live coral taxa were dominated by massive *Porites*, *Favia* spp. and mussids (Table 5). A number of recruits (<20 cm) including small *Acropora* were noted by the observers. Dead *Pocillopora* colonies were common, often encrusted in coralline algae or a thin algae turf (classified as dead coral).

Changes in *Pocillopora* Cover

In order to better assess the anecdotal observations of high mortality and limited recovery of pocilloporids at most sites, the number of visible living and dead colonies, including pocilloporid colonies covered in turf or coralline algae, were counted in each of the photo quadrats. Two-tailed t-tests found a significant decrease in the number of living pocilloporid colonies at the two South Tarawa sites after the bleaching event (Table 6). The increase in the number of colonies from 2004 to 2005 at the TRW03 may be a result of the aforementioned observer drift at the exposed site. The high fraction of living colonies (84%) in the 2004 survey and lack of living colonies in the 2005 survey suggests high bleaching-induced mortality in the area.

Analysis of the 2005 and 2009 surveys indicates no significant recovery of pocilloporids at any of the Abaiang sites, and only weakly significant recovery (p=0.16) at one Tarawa site (Table 6). Notably, the total number of living and dead colonies decreased from 2005 to 2009 at each site, including decreases of over 50% at two Abaiang sites and one Tarawa site. Colonies killed during the bleaching event may have been converted to rubble or obscured by algae by 2009.

Table 6. Number of Pocilloporid colonies

	TRW01		**TRW02**		**TRW03**		**ABG01**		**ABG02**		**ABG03**	
Year	#	% live	#	% live	#	% live	#	% live	#	% live	#	% live
2004	49	78%	66	61%	19	84%	n/a					
2005	28	39%	62	11%	38	0%	91	13%	90	3%	64	3%
2009	22	41%	22	32%	23	9%	35	40%	35	20%	57	7%
p(04-05)[1]	<0.01		<0.01		n/a		n/a					
p(05-09)[1]	0.67		1.0		0.16		0.73		0.32		0.46	

The low post-bleaching cover of pocilloporids is supported by data from the 2007 training surveys from Tarawa, Abaiang and also the more northerly Butaritari Atoll. Live pocillioporids composed less than 4% of benthic cover at 10 m depth at ABG02, ABG03, TRW02 and a site on the submerged western reef of Tarawa (Donner, 2007). An initial site visit to Butaritari's western outer reef noted dead colonies covered in coralline algae were common at all four outer reef sites, and live colonies appeared at only one site (Donner, 2007).

DISCUSSION

The little-studied coral reefs of the Gilbert Islands may provide some insight into the response of Indo-Pacific coral communities to repeat thermal stress events. The 2004-5 thermal anomaly has recently been classified by several researchers as a distinct type of ENSO event known as a "Central Pacific" ENSO (Kao and Yu, 2009), or alternatively an "El Nino Modoki" (Ashok et al., 2007) or "Warm Pool" ENSO (Kug et al., 2009). The ratio of Central Pacific (CP) to the standard "Eastern Pacific" (EP) ENSO events may have increased in the past three decades (Kug et al., 2009; Yeh et al., 2009). Analysis of historical SST, wind, current and sea surface height data has identified only one CP ENSO before 1980, but at least five since (Ashok et al., 2007; Yeh et al., 2009). The CP events include a 1986-87 event and the mildly persistent ENSO conditions from 1990 through 1994, both of which are apparent in the thermal stress record for the Gilbert Islands (Fig 3a, 3b). There was also a 2002-3 CP ENSO event centered east of the International Dateline which caused mass coral bleaching in Kiribati's neighboring Phoenix Islands (Ailing et al., 2007).

Despite the evidence for multiple thermal anomalies in excess of the lower bleaching threshold in the Gilbert Islands prior to 2004-5, a thorough survey of the published literature, grey literature, the online dataset Reefbase and local experts found no reports of bleaching prior to 2004. It is plausible that episodes of bleaching may have gone unreported due to the relative isolation of Kiribati and the lack of regular benthic monitoring. Alternatively, the threshold for the onset of bleaching may be higher in the Gilbert Islands than in other regions due to acclimation or adaptation to the ENSO-driven thermal stress events in the recent or distant past. In that case, employing the $\mathrm{MMM}_{\mathrm{max}}$ or a similar metric that accounts for year-to-year variability in the timing of peak SSTs in the calculation of thermal stress may improve bleaching prediction in the region. Such a metric could capture temperature acclimation or adaptation by corals (and their symbionts) that may have arose due to past ENSO events.

Coral Cover and Response to Bleaching Event

The data presented here and past surveys from the 1980s (Zann and Bolton, 1985) and past decade (Lovell, 2000; Paulay and Kerr, 2001; Donner, 2007) indicate some general spatial patterns in coral cover in the central Gilbert atolls. These include i) pre-bleaching outer reef coral communities dominated by common Indo-Pacific taxa like

Pocillopora, Porites, Montipora, Favia, Favites and *Platygyra*, as well as the regionally uncommon taxa *Heliopora* (Zann and Bolton, 1985; Lovell, 2000; Donner, 2007); ii) similar coral cover and diversity in the protected northwestern reefs, like the Abaiang sites and northwest Tarawa (Lovell, 2000); iii) decrease in coral cover and diversity from North Tarawa, including the northern tip of the submerged western tip, towards Southern Tarawa (Lovell, 2000; Paulay and Kerr, 2001); iv) low macroalgae at most sites; and, v) limited coral cover in the Tarawa's central and southern lagoon outside of small *Acropora*-dominated patch reefs (Lovell, 2000; Paulay and Kerr, 2001; Donner, 2007). The notable difference between the 1980s surveys and more recent pre-2004 surveys is the extent of *Acropora* on the South Tarawa outer reef. Unlike Lovell (2000), Zann and Bolton (1985) noted *Acropora* among the dominant taxa, including *A. formosa*, a species not observed on the outer reef in any of the surveys presented here. Photo-quadrat surveys conducted at Kuria and Abemama Atolls in conjunction with the 2004 pre-bleaching surveys similarly found low cover of *Acropora* (Vieux, 2004).

The 2004 mass bleaching event appears to have caused coral mortality at several sites and precipitated changes in coral cover. The lack of pre-bleaching surveys outside the three Tarawa outer reef sites limits computation of bleaching-induced coral mortality. Evidence of morality includes the change in coral cover between 2004 and 2005 at two of three Tarawa sites and the appearance of recently dead coral and colonies covered in algal turf or coralline algae in the post-bleaching surveys (Fig. 7a). Coral cover in post-bleaching surveys is lower than that reported for the Tarawa and Abaiang outer reefs in earlier surveys. For the Abaiang and Tarawa outer reefs, Lovell (2000) reported 33-57% hard coral cover at 3 m depth and 28-72% at 10 m depth, with the exception of one site near the Tarawa hospital in Bikenibeu (discussed below). The Lovell (2000) coral cover observation for all Tarawa and Abaiang sites lie outside the range of 2005 post-bleaching cover observations (14-26%) reported here.

In addition, data collected in the Tarawa lagoon, Tarawa's submerged western reef and the northern atoll of Butaritari as part of the 2007 training program (Donner, 2007) provide further anecdotal evidence of a previous large disturbance event. First, line-intercept transects (4 x 25 m) conducted in November 2007 at an *Acropora*-dominated lagoon patch previously visited by Lovell (2000) found 36% live hard coral cover with 40% rubble suggesting recent mortality. Lovell (2000) reported 60% hard coral cover, dominated by branching *Acropora*. In 2007, the coral cover was still dominated by branching *Acropora*, notably *A. formosa* and *A. grandis*, but 69% of the colonies were less than 40 cm in length. Second, live hard coral cover at site on Tarawa's western submerged reef declined from 57% to 25% at 3 m depth, and 41% to 31% at 10 m depth, between the Lovell (2000) survey and the transects conducted in late 2007. Finally, shallow surveys and manta tows conducted in Butaritari in 2007 noted high cover of recently dead colonies, particularly pocilloporids. Dead coral and colonies covered in coralline algae represented 38-50% at two western outer reef sites.

Coral Recovery Since Bleaching Event

The change in coral cover from 2005 to 2009 (Fig. 7b) provides some anecdotal evidence for greater recovery in sites with lower direct human pressure. A closer examination suggests that the spatial pattern in recovery is likely due to a range of factors that includes local human disturbance, but also state of the pre-bleaching coral community and the local hydrodynamics. The increase in hard coral cover was significant at all the Abaiang sites, where land-based pollution is limited and fishing pressure is lower than in Tarawa. The pattern in recovery could, alternatively, be related to hydrodynamics and wave action. For example, there was no significant recovery at the North Tarawa site, which features similarly low human pressure to the Abaiang sites but is more exposed to ocean swells and higher wave energy. Bleaching intensity has been positively associated with water flow (McClanahan et al., 2005a), although there are contrary examples in the literature (Loya et al., 2001; Nakamura and van Woesik 2001).

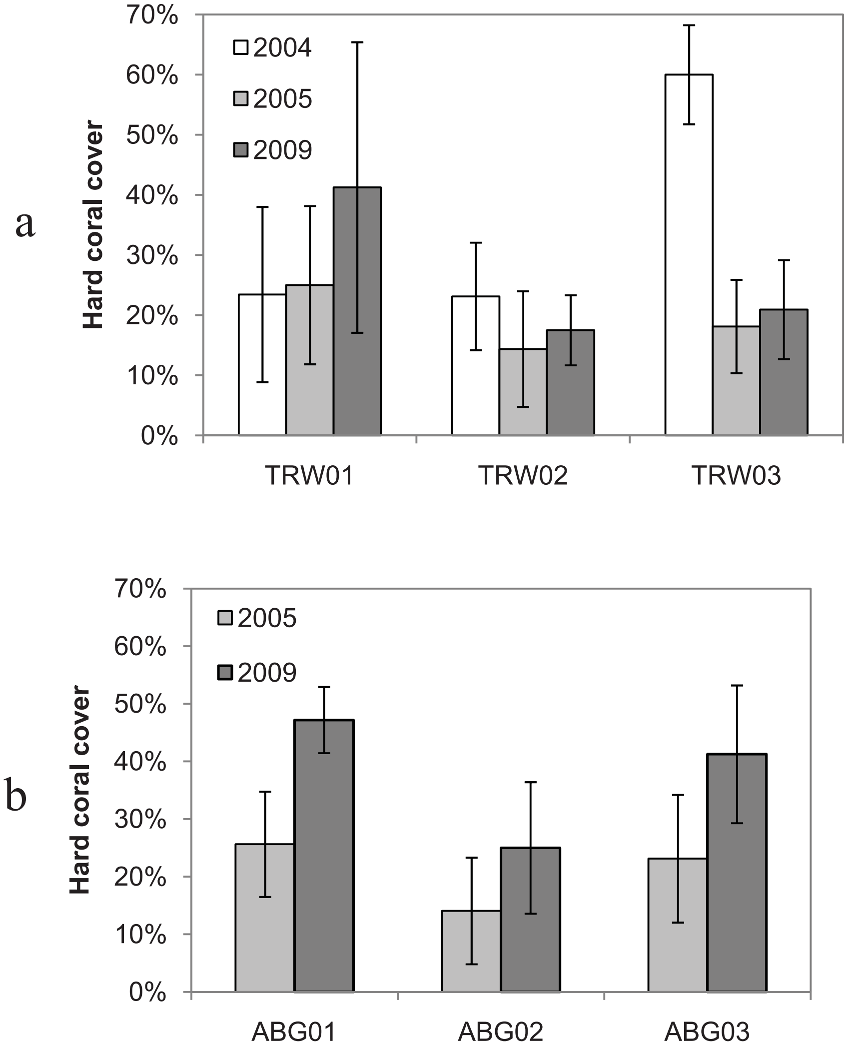

Figure 7. Live hard coral cover (in % cover) for the a) Tarawa Atoll sites, and b) Abaiang Atoll sites. Error bars are standard deviation as calculated in the text.

Contrary to expectation, the only Tarawa site that exhibited statistically significant recovery of coral cover since 2009 was the most disturbed site (TRW01, near the Tarawa Hospital in Bikenibeu). This increase in percentage of coral cover was due to the expansion of a single encrusting species, *Porites rus*, known to be more resistant to high temperatures and UV light, as well as crown-of-thorns starfish outbreaks and wave activity (Quinn and Kojis, 2003; Pinca et al., 2005; Lenihan et al., 2008). Lovell (2000) observed colonies of *Porites rus* along the southeast coast but not specifically near the Tarawa Hospital, where coral cover was reported as only 7% at 3m depth. The southeast coast of Tarawa may be an example of bleaching leading to the aggressive expansion of a single resilient species, even if only in the short-term. The rate of expansion at the hospital site may be enhanced by the sewage discharge; in an experimental setting, growth rates of *Porites rus* benefited from nutrient enrichment (Dizon and Yap, 2005).

The other less disturbed sites experienced increases in more resilient or opportunistic taxa, similar to that observed after mass bleaching events elsewhere in the Indo-Pacific (Loya et al., 2001; Baird and Marshall, 2002; Schuhmacher et al., 2005). This includes i) a widespread loss of *Pocillopora* spp.; ii) statistically significant increases in the blue coral *Heliopora coerulea* at three of six sites; and, iii) statistically significant increase in massive *Porites* (*P. lobata* and *P. lutea)* at two sites (Fig. 8a,b). First, mortality and slow recovery of *Pocillopora* relative to *Porites*, *Montipora* and other broadcast spawners has been noted after a number of mass bleaching events, including events in the Maldives (Schumaker et al., 2005) and Kiribati's Phoenix Islands (Ailing et al., 2007). Second, *Heliopora coerulea* is generally less susceptible to bleaching (Harii et al., 2002) and has thrived after mass bleaching events in locations where it is common (Kayanne et al., 2002; Schumaker et al., 2005). Third, massive *Porites* are generally more resistant to bleaching than other taxa due to several factors including thicker, deeper tissues (Loya et al., 2001). The observations of only partial post-bleaching mortality in massive *Porites* colonies at the Abaiang sites in 2005 likely enabled the post-bleaching recovery at those sites (Baird and Marshall, 2002; McClanahan, 2004; Baker et al., 2008).

The post-bleaching coral community also reflects the unusual absence of the normally common taxa *Acropora* from the outer reefs and the dominance of the usually rare *Heliopora coerulea* noted in the 2004 pre-bleaching surveys and previous studies. Available data for the Gilbert Islands indicates that as of 2004, *Acropora* was only common on some lagoonal patch reefs, some protected outer reefs in Butaritari and the tidally exposed reef flats of southern Tarawa. Zann and Bolton (1985) found *Helipora coerulea*, abundant at 6-10 m depth in 70% of sites in South Tarawa, tended to co-exist with *Porites* and *Montipora* but not *Acropora*. Since *Acropora* is bleaching sensitive and whole colony mortality is common, a loss of cover is typically observed in the short-term after bleaching (Baird and Marshall, 2002; Golbuu et al., 2007). It is possible that frequent thermal stress and high wave activity on the outer reefs has limited *Acropora* cover over time and favored the more resilient species like *Heliopora coerulea*, and in some locations, *Porties rus*. Surveys at more sites and variable depths are required to collect sufficient data to statistically test such anecdotal coral community patterns observed in this study.

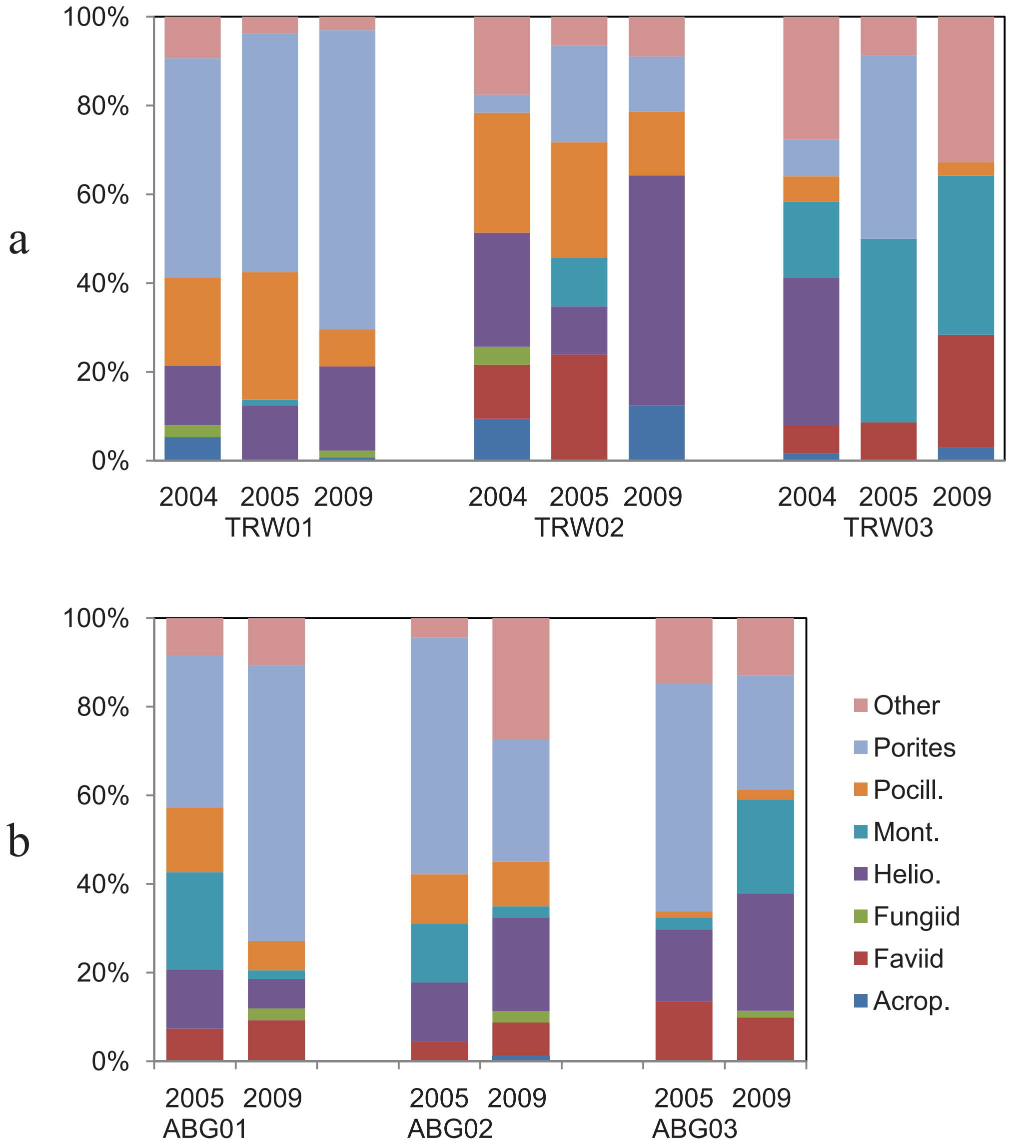

Figure 8. Fraction of live hard coral cover (% of live coral cover) by taxa for the a) Tarawa Atoll sites and b) Abaiang Atoll sites.

CONCLUSION

The coral reefs of the Gilbert Islands have been the subject of little research due to factors like remoteness and the limits of local expertise and infrastructure. This study intentionally employed inexpensive, low-technology, photography-based surveys in hopes of establishing a realistic precedent for independent future benthic monitoring around Tarawa and the less accessible outer atolls by the Kiribati government. The trade-off of this method is the data quality. Snorkel-based surveys via small boats limit access to greater depths and more distant or exposed sites, as well as collection of other ecological data (e.g. fish communities). Future work through the Kiribati Adaptation

Project and outside partnerships may increase the ability of the local government to work with outside scientists on more extensive, coordinated benthic monitoring with SCUBA gear (Donner, 2007).

The data from this study, while not sufficient to quantitatively test hypotheses about the effect of hydrodynamics, human disturbance and past temperature experience on bleaching resistance and resilience, does provide preliminary evidence that the outer reef coral communities of Tarawa and Abaiang have experienced an increase in the dominance of bleaching-resistant coral taxa since the 2004 event. Long-term surveys conducted after other Indo-Pacific bleaching events suggests such shifts in the coral community could be short-lived, as the more bleaching-sensitive taxa will expand over time absent further disturbances (e.g., Golbuu et al, 2007). It is possible, though untestable with existing data that past unreported disturbances in the Gilbert Islands before 2004 may have promoted the cover of more bleaching-resistant taxa. The predicted increase in the occurrence of CP El Nino events due to global climate change (Yeh et al., 2009) could cause long-term shifts to more resistant taxa and declines in live coral cover in the Gilbert Islands. Further monitoring and research will be critical to better quantifying the long-term response of the coral community, and other associated reef organisms, to past and future bleaching events.

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