

## **GLOBAL CORAL REEF BLEACHING AND SEA SURFACE TEMPERATURE TRENDS FROM SATELLITE-DERIVED HOTSPOT ANALYSIS**

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### **ABSTRACT**

Coral reefs are among the first ecosystems threatened by global climate change: since 1982, repeated episodes of high sea temperature and large-scale bleaching stress have imposed accelerating and unprecedented morbidity and mortality in coral reefs, affecting even the most remote areas unstressed by direct human impacts. Analyses of global satellite-derived sea surface temperature anomalies and coral reef bleaching reports since 1982 show that both are rapidly increasing. During 1998 record numbers of reef-building corals died following exposure to abnormally warm waters in the Indian Ocean, Western Pacific Ocean, and Caribbean. Although temperatures were higher in the Eastern Pacific Ocean in 1998 than in 1983, mortality was lower, perhaps because only high temperature tolerant corals had survived. Sea surface temperature trends for 207 coral reef sites since 1984 show average increases of 0.32° C / decade, more than twice average global warming rates, and show strong regional and latitudinal patterns. These tendencies indicate that tropical waters are warming faster than temperate and boreal zones, in contrast to most climate model simulations, and imply that large-scale regional changes in ocean circulation may be taking place. Bleaching has occurred in locations both positively and negatively correlated with the concurrent El Niño Southern Oscillation Index (ENSO). Sub-threshold bleaching events, due to other than high temperature causes, are infrequent and appear to be declining slightly. Near threshold bleaching events linked to near critical, but non-fatal, temperature anomalies have until recently dominated the record, but appear to be increasing slightly with time. Supra-threshold bleaching events with temperatures above critical levels, followed by catastrophic mortality have recently been increasing significantly with time, and now dominate our records. ENSO-like periodicity in bleaching reports may result from global warming driving El Niño events above regional temperature thresholds in those areas with strong positive ENSO correlations, however bleaching events will soon approach

annual recurrence if warming continues, placing many reef tracts at high risk of catastrophic mass mortality from bleaching. These changes are concurrent with declining live coral cover, ecosystem function, and economic values of coral reefs from both emerging diseases and other anthropogenic and natural stresses, but have greatly exceeded their cumulative impact in 1998. Over 100 countries face potentially crippling losses from coral reef deterioration if increasing temperatures continue throughout the tropics, with the greatest risks to the atoll island nations of the Pacific and Indian Oceans.

### **INTRODUCTION: CORAL BLEACHING AND OCEAN HOTSPOTS**

Large-scale coral reef bleaching has appeared repeatedly since the 1980s (Williams & Bunkley-Williams, 1990; Jokiel et al., 1990; Glynn, 1991; Goreau et al., 1993; Goreau and Hayes, 1994; Goreau and Hayes, 1995; Goreau et al., 2000). All known bleaching events prior to this period were of local extent and due to small-scale local stresses (Mayor, 1918; Yonge & Nicholls, 1931; Goreau, 1964; Jaap, 1979; Goenaga & Canals, 1979).

Coral reef bleaching results from expulsion of coral's symbiotic unicellular dinoflagellate algae (zooxanthellae). Bleaching is a generalized sub-lethal stress response. Bleached corals lose their natural pigmentation, become pale or transparent, and usually appear white, as the underlying calcium carbonate skeleton becomes visible. Physiological and metabolic consequences of uncoupling of symbiosis are reduction in organic and gaseous nutriment for the coral (Yonge & Nicholls, 1931; Goreau et al., 1971), cessation of tissue growth and reproduction (Glynn, 1993; Szmant & Gassman, 1990), and halting growth of limestone skeleton (Goreau & McFarlane, 1990). The impacts are primarily due to thermal damage to the algae followed by expulsion (Iglesias-Prieto et al., 1993; Iglesias-Prieto & Trench, 1997; Iglesias-Prieto 1997; Warner et al., 1996, 1999; Hoegh-Guldberg & Jones, 1999)

The sensitivity of reef corals to abnormal elevations in water temperature has been known for many years (Mayor, 1918; Yonge & Nicholls, 1931; Jokiel & Coles, 1977). Tropical coral reefs are living just below their maximum temperature limits and only slight increases above historic values cause bleaching.

Experimental and field evidence shows no sign of physiological capability to adapt to higher temperatures. The most sensitive corals may die but the survivors repeatedly bleach at the same temperatures (Goreau et al., 1993; Goreau & Hayes, 1994; Goreau, 1999). Large-scale bleaching episodes indicate that coral reefs are likely to be one of the first ecosystems damaged or destroyed by global climate change (Hayes & Goreau, 1991). Sessile tropical coral reefs are uniquely

threatened by global warming, because they cannot relocate to more favorable conditions and be replaced by immigrant organisms from regions adapted to higher temperatures, because such habitats do not exist (Goreau & Hayes, 1994).

Bleaching recurs at a threshold water temperature (Glynn, 1991, 1993; Goreau, 1990). Analysis of satellite and *in-situ* temperature data showed that threshold monthly average temperature values preceding bleaching were near or above 1 degree above climatological averages in the warmest months in the Caribbean (Goreau et al., 1993) and in the Indo-Pacific (Goreau & Hayes, 1994). Surface water that equals or exceeds the widespread bleaching threshold of + 1.0° C above long-term averages for the warmest month in coral reef regions is defined as a "HotSpot" (Goreau & Hayes, 1994). These anomalous seawater conditions are sufficient to cause most corals to bleach under experimental laboratory conditions as well as in the field (Hoegh-Guldberg & Smith, 1989; Glynn et al., 1992), although natural, much milder, reductions in zooxanthellae density may occur at lower temperatures or seasonally (Fagoonee et al., 1999).

Recovery from bleaching can occur after SST drops below threshold levels. After a lag that depends on the species and the intensity and duration of the stress, re-population of corals by zooxanthellae restores algal densities characteristic of the symbiotic relationship before bleaching (Hayes & Bush, 1990). But this is possible only if high temperature stress is sufficiently moderate and brief, and if no other excessive stresses prevail during this critical time. If sea surface temperatures exceed the long term average by 2.0° C or more during the warmest month, or remain at or above 1.0° C for several months, then partial or total colonial mortality results. Of course these are round numbers that approximate continuous thermal response that vary between species. Since 1991 the location and timing of all major thermal bleaching events have been successfully predicted in real time by using NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite temperature data alone to identify HotSpots (Goreau et al., 1993; Goreau & Hayes, 1994; Strong et al. 1997; Strong, 1998, Strong et al., 1998, Strong et al. 2000, Goreau and Hayes, 2004a) and all major events since 1982 have been successfully hindcast. HotSpot maps are available at <http://www.osdpd.noaa.gov/PSB/EPS/SST/climo&hot.html>

## **METHODS**

We have analyzed all satellite SST records since 1982 at 207 reef locations worldwide. These sites cover every major reef area in the world (Table 1 gives the names, latitudes, and longitudes of each site, along with the mean rate of warming calculated two different ways. The sites are shown on a color map at

[www.globalcoral.org](http://www.globalcoral.org) ). Since HotSpot boundaries are not sharp and fluctuate with local weather patterns, reef organisms near the margin of HotSpots are also exposed to physiologically significant temperature stress. During 1998, the HotSpot areas of the tropical ocean (35°N to 35° S latitude), in which water temperatures exceeded coral bleaching thresholds, surpassed those of any previous year measured by NOAA satellite data (color maps of HotSpots from 1982 through 1998 are shown [www.globalcoral.org](http://www.globalcoral.org) with bleaching locations). Over half of these 207 sites reported coral reef bleaching in 1998 (although reports of confirmation were not received from many sites), making it the worst year ever observed for coral bleaching. Bleaching actually began in the Eastern Pacific in late 1997, following very high seawater temperatures attributable to the El Niño

**Table 1** Locations

NAME	LONGITUDE	LATITUDE	EDITED	RAW
Abrolhos-Au	113	-28.6	2.5946	1.3
Abrolhos-Br	-39	-18	-1.6817	2
Addu	73	-1	2.5807	3
Aitutaki	-160	-18.5	3.1237	1.9
Alacran	-89.5	22.5	5.6507	4.5
Aldabra	46	-9	-0.95902	0.5
Alor	125	-8	-1.0399	2
Ambon	127.8	-4	-1.091	3.4
Amirantes	53	-7	0.95518	1.8
Andaman	93	11	0.78598	2.8
Anguilla	-63.1	18.3	3.4501	5.5
Antigua	-62	17	3.6651	4.9
Arraial do Cabo	-41.5	-23	2.1839	1.9
Aruba	-70	12.3	1.3312	5.7
Bahrein	50.6	26.3	10.86	7.5
Balicasag	124	9	2.2712	3.9
Banda Aceh	95	5	2.8589	3.1
Bandanaira	130	-4.5	-1.3597	3.4
Barbados	-59.7	13.2	4.7638	4.5
Barbuda	-62	17.7	3.3742	5.1
Batangas	120.7	13.5	5.2264	4.9
Belize - Glovers	-88	17.4	4.4854	5.7
Belize - North	-87.9	17.8	4.2671	5.4
Belize - South	-88.3	16.1	4.8565	5.9
Bermuda	-62.8	32.4	4.7403	5.3
Beverley	150	-21.5	-3.4839	0.5

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Biak	135	-0.6	4.062	4.3
Bikini	165.5	11.9	2.3837	3.3
Bocas del Toro	-82	9.5	5.5169	6.8
Bolinao	120.2	16.5	6.3625	7.2
Bonaire	-68.4	12.1	3.5582	4.8
Boracay	122.2	12	2.0267	4.5
Canton	-172	-2.5	4.374	1.3
Cape Bougainville	126	-13.5	0.17587	2.2
Cartagena	-75.5	11	6.6128	7.6
Cayman	-81.2	19.4	4.8993	5.7
Cayo Largo	-81.5	21.5	4.5613	5.1
Chagos	72	-6	1.5888	2.9
Cheju	126	33	15.786	8.3
Chinchorro	-87.5	18.5	4.2957	5.3
Christmas A	105.6	-10.4	0.62324	2.2
Clipperton	-109	10	3.3924	2.5
Coco	-87	6	10.704	6.8
Cocos Keeling	96.9	-12	1.3467	2.8
Coiba	-82	7	19.504	10.9
Cozumel	-85.7	20.6	4.8655	4.3
Curacao	-68.9	12.1	3.3871	5.2
Dahlak	39.6	16	9.6068	10.5
Darwin	130.2	-12.5	0.62718	1.3
Djibouti	43.5	11.7	5.232	9.9
Dubai	55.4	25.4	11.21	7.9
Easter	-109.2	-27	-5.7532	-0.4
Elat	34.75	29.25	3.3613	3.1
Enewetak	162	11	2.3388	3.5
Farasan	42	16.4	10.104	12.1
Fernando de Noronha	-33	-3.6	-1.2447	2.4
Flinders	148.3	-17.7	-2.2373	1.4
Florida Keys	-81.5	24.5	6.3989	5
Flower Gardens	-94	29	-2.2946	-0.4
Funafuti	179	-8.5	5.452	2.8
Galapagos	-90.5	-1	-4.8033	-0.7
Galle	80	6	0.62868	2.7
Gorgona	-78.5	3	22.675	11.8
Grand Turk	-72	22	4.3679	8.6
Grenada	-62	12	4.9624	4.2
Guam	144.8	13.4	0.63236	3.9
Hainan	109.5	18	3.958	3.8

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Haiti	-73	20	7.6468	8.8
Heron	152.2	-23.5	-2.3668	1.5
Hinchinbrook	146.5	-18.5	-3.4747	-0.1
Honiara	160	-10.2	1.5575	4.8
Hurghada	34	27	3.2504	0.4
Inhaca	33	-25.8	-1.4252	2.4
Ishigaki	124	24.1	5.0772	11.1
Jakarta	107	-5.5	5.3617	4.4
Jamaica - North	-77.5	18.5	4.8213	6.3
Jamaica-West	-78.5	18.3	5.2145	6.3
Jidda	39	21.5	8.2747	9.4
Johnson	-169.5	16.8	1.959	1.7
Kaohsiung	120	22.2	9.1987	10.5
Kapingamarangi	155	2	3.9715	3.6
Kavaratti	72.5	11	0.83116	2.6
Kepulauan	124	-6	-1.1081	3.1
Kinabalu	116.2	6.2	4.5355	5.5
Kiritimati	-157.5	1.8	1.971	0.9
Kosrae	163	5.4	3.3527	3
Kutch	68.5	23	7.1915	4.5
Kuwait	48.4	29.3	2.476	4.6
Kwajalein	167.9	9	3.1958	2.7
Lau	-179	-18	1.5029	3.1
Lihou	152	-17.5	-2.6105	2.5
Lizard	145.5	-13.5	-2.4172	0.7
Lord Howe	159.1	-31.7	1.1519	1.6
Los Roques	-67	12	3.5069	3.6
Low Isles	145.7	-16	-3.2808	0.6
Madang	146	-5	3.3518	4.2
Mafia	40	-8	-0.68922	0.7
Magnetic Pass	147.5	-18.3	-1.539	0.9
Mahe	55.5	-5	2.1575	2.9
Majuro	171	7	4.56	2.5
Male	73	4	0.36773	3.6
Malindi	40.5	-3	0.37115	1.7
Malpelo	-81	4	19.376	11.1
Manado	125	2	4.4819	4.6
Mandapam	79	9	2.0963	3.9
Mangareva	-135	-23.2	-5.3915	0.1
Manihiki	-162	-11	2.5149	1.7
Manila	120	14	5.4186	5.1

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Margarita	-65	11	3.798	2.3
Mau	-156	21	0.59401	4.5
Mauritius	57.7	-19.8	-4.0335	-0.7
Mayotte	45	-12.5	-1.0429	0.1
Mentawai	98	0	3.9017	3.4
Mer	144	-10	-3.0073	2.2
Midway	-177.4	28.3	-1.151	8.2
Milne Bay	151	-11	-3.6363	3.3
Miskito	-83	14.5	4.4158	5.6
Moresby	147	-9.7	-1.9385	2.5
Mururoa	-139	-22	-2.1389	1.3
Muscat	58	24	9.5259	7.3
Nandi	177	-18	1.4057	3.4
Nassau	-77.4	24.8	6.3202	6
Nauru	166.9	-0.3	4.7869	2.4
Netanya	34.5	32.5	9.2021	9.7
New Britain	151	-5	5.2564	4.2
New Caledonia-Northeast	165	-20	-2.2098	1.1
New Caledonia-Southwest	166	-23	-2.1626	2.7
Nicobar	94	8	0.54776	2.7
Ningaloo	114	-21.5	-0.52168	0.4
Niue	-170	-19	2.4859	2.8
Nosy Be	48	-13.2	-0.20952	-1.1
Nuku Hiva	-140.2	-8.9	0.1788	0.2
Nusa Penida	115	-9	-1.0116	3.5
Okinawa	128	26	3.5217	9.2
Oshima	139.5	35	-1.0599	2.7
Palau	134.5	7	1.3552	3.6
Palawan	119	11	4.6453	4.5
Palmyra	-162	6	5.7754	1.6
Pandora Pass	144	-12	-3.7745	2.2
Parguera	-67	17.9	4.3136	6.6
Pemuteran	115	-8	1.1776	1.8
Perlas	-79	8	2.7268	14.9
Phuket	97.8	8	1.8122	3.2
Pitcairn	-130	-25	-4.4218	0.7
Pohnpei	158.3	7	2.8012	3.5
Port Vila	168	-18	-0.60515	3.3
Portobelo	-80	9.5	5.4989	6.4
Praia	-23.4	15.1	6.6751	5.4
Providencia	-81.5	13.4	4.1971	6

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Puerto Plata	-71	20	4.9431	8.5
Rangiroa	-148	-15	0.16749	0.8
Rapa	-145	-27.5	-0.23726	1.3
Rarotonga	-160	-21	2.4856	1.6
Ras Muhammad	34.2	27.5	3.2642	2.9
Recife	-34.3	-8.5	-1.5749	1.5
Reina	-79	20.5	4.5959	5.6
Reunion	55.5	-21.5	-3.2572	0.2
Roatan	-86.5	16.5	4.4258	5.9
Rodriguez	63.5	-20	6.2623	-3.4
Roti	122.7	-11	0.031898	2.2
Rotuma	175	-12	4.7037	3.5
Rowley	119	-17.5	-0.73797	1.1
Rurutu	-151	-22	0.98174	1.2
Saipan	145.9	15	0.76368	3.9
Salvador	-38	-13	-2.1993	0.8
San Blas	-78	9.5	6.942	7.6
San Juan	-66.5	18.6	3.1517	7.3
San Lucas	-110	22.5	10.362	2.8
San Salvador	-74.5	24.4	5.9383	6.6
Sangalaki	119	4	4.1	4.3
Santa Clara	-80	23	7.2813	7.3
Santiago	-76	19.5	5.3663	6.3
Sao Sebastiao	-46	-24.1	-0.4806	3
Sao Tome	6.7	0.2	0.15405	5.4
Saya de Malha	60	-10	0.28121	1.6
Singapore	105	0.2	6.961	5.9
Socotra	54	12	2.7305	4.4
Sondwana	33	-28	-2.0115	0.03
South Maldives	72	1.5	1.3003	3.2
Spratly	112	8	4.3058	4.8
St. John	-64.7	18.2	4.0304	5.7
St. Kitts	-62.9	17.4	4.0918	5
St. Lucia	-60.9	13.7	4.6134	4.5
Suakin	37.7	19	7.6262	9.1
Swain	152.5	-22	-0.48034	2.1
Tahiti	-149	-17	0.57715	1.7
Taka bone rate	121	-7	-0.8638	2.2
Tampico	-97.5	22	2.724	3.9
Tarawa	172	1.5	5.7935	2.8
Tobago	-61	11	4.8351	4.2



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Toggian	122	0	2.7521	5.3
Tokelau	-172	-9	3.6918	2.1
Tingareva	-158	-9	1.7377	0.9
Tongatapu	-175	-21	-0.46503	2.2
Trincomalee	81.5	8.5	3.6321	3.5
Truk	151.7	7.5	2.7533	3.7
Tubbataha	120	9	3.1065	4.3
Tubuai	-149	-23	1.3001	1.4
Tulear	43.6	-23.3	-1.085	1.8
Tutuila	-170.7	-14.1	4.6044	3.1
Ujung Pandang	119	-5.6	-1.0784	3.4
Uvea	-176.5	-13.5	4.4087	3
Vavau	-174	-19	1.7046	2.9
Whitsunday	150	-20	-4.0732	0.07
Yap	138.2	9.5	0.76768	3.8
Zamboanga	121.5	7	3.6833	4
Zanzibar	39	-6	-0.35589	0.7

event. In early 1998, researchers in the Southern Indian Ocean, Australia, and Brazil were alerted that bleaching conditions appeared imminent. As a result of these early warnings, based upon satellite HotSpot information, many research teams were able to get into the field to record the onset of bleaching (Goreau et al., 2000).

#### **DATA SOURCES**

The databases used here include two sets of the satellite AVHRR data, a raw form and an edited form. The data for the period from 1982 -1997 were provided by Al Strong. These were then "edited" by removal of El Niño Years, and of the period of one year following the large volcanic eruptions of 1982 and 1991 to provide the edited data set. In 1982 and 1991 volcanic aerosols gave incorrectly lowered values by large amounts in those areas most affected by the plumes. Areas that are strongly warmed in El Niño years are not included in the edited data set, so for such places the edited data set underestimates the rates of warming. For the period from 1998 - 2003 the data were taken from the NOAA Climate Diagnostics Bulletin, very similar to the database used by Strong, although at a lower spatial resolution (Goreau & Hayes, 2004a). These were added to the previous data set to give the complete raw data version, a complete time series, including the years that had been edited out. For reasons of space only a few of these time series can be shown here, but all of these time series graphs

for all locations can be found on the web at the Global Coral Reef Alliance Web Site, [[www.globalcoral.org](http://www.globalcoral.org)].

Table 1 shows the names, altitudes, longitudes, mean slope of the edited data, and mean slope of the raw data. The raw data tends to overestimate the edited values at lower rates of warming, but underestimates it at the high warming rates. The raw data overestimates at low rates of warming largely because of the bias caused by El Chichon in 1982. The underestimation at high rates of warming suggests that removing El Niño years makes warming even greater at the fastest warming sites, indicating that their temperature is negatively correlated to El Niño, since a positive correlation would weaken the warming in the edited data set. This strongly suggests that global warming, not El Niño, is the dominant factor in bleaching at most sites.

### **SYSTEMATIC ERRORS**

These data were taken from pixels located in offshore water nearby. They represent offshore, open water conditions, not those in more protected coastal habitats, which can be quite different. Calibration of satellite against in situ data showed that the satellite reading was generally within 0.2° C of the real value, but tended to underestimate it at the highest rates of warming, apparently due to bias caused by interference with the thermal image from increased small sub-pixel size clouds in the hottest images. The calibration data were originally reported by Goreau & Hayes (1994), but are documented in this volume (Goreau and Hayes, 2004).

The 1982-1997 data were read from digital files and estimated to the nearest 0.2°C. The 1998-2003 data were generally interpolated to the nearest 0.1°C. This was generally possible with fairly high confidence except in certain cases. These less precise data are mainly from locations where there are very sharp local regional gradients in temperature, such as at capes with upwelling on one side. Examples of this include Cabo San Lucas in Mexico, Milne Bay in Papua New Guinea, Cabo Frio in Brazil, and Socotra in Yemen. The temperature isotherms can be so densely bunched around these sites they are very hard to read precisely. Similar examples also take place near the extreme example around Japan, Korea, China, and Taiwan. A special problem was found in the Red Sea, Persian Gulf, and Mediterranean, where the contours were often poorly marked and hard to read. 3 sites were dropped after 1997 because they were too hard to read reliably from the charts. The data before 1997 have higher spatial resolution, so the later data will tend to underestimate maximum values at sites with strong locally generated cloud cover or offshore thermal gradients (Goreau & Hayes, 2004a).

## **DATA INTERPRETATION**

These data should be useful for all looking to correlate coral bleaching, diseases, fisheries data, or other phenomena affected by local sea surface temperatures such as coastal rainfall. In virtually every known case the location, timing, and severity of major coral bleaching events are clearly indicated from the temperature records. Also seen are temperature extremes where bleaching is thought to have taken place, but was not reported. Caution should be exercised in use of this data: It must be emphasized that near shore reefs, especially in protected areas, may vary much more than these offshore values, and that they are based on monthly average night time values, not short term extremes. In some sites the readings in the raw data are biased downwards in areas affected by the plumes of El Chichon in 1982 and Mount Pinatubo in 1991, especially in the Caribbean. These years should be edited out in estimating long term trends, with or without El Niño years. All data shown in graphs here are based on the edited dataset, except where noted. By not including El Niño years, this removes the hottest years from trends in those areas where there is a strong positive link to El Niño, and so underestimates overall trends where temperatures are positively correlated with El Niño.

## **RESULTS**

### **CORAL BLEACHING AND TEMPERATURE ANOMALIES**

The impacts of 1998 bleaching were worst in the Indian Ocean, where virtually every reef tract was affected. Some reefs remained above local threshold temperatures for over five months. In addition to bleaching, coral mortality there exceeded 90% in many reefs (Goreau et al., 2000). As temperatures reached their maxima in the Northern Hemisphere, severe bleaching set in across the Northern Indian Ocean, Western Pacific and Caribbean. The majority of all reefs in the world had already been severely impacted by the end of 1998. 83 of the 207 monitored sites (40.1%) were directly in the path of the HotSpots during 1998. Twenty-eight of these sites are in the Western Hemisphere and fifty-five are in the Eastern Hemisphere. The reef sites in the Western Hemisphere exposed to HotSpots represent 32.2% of the total sites in that hemisphere (N = 87). In the Eastern Hemisphere, 45.8% of the total sites monitored in that hemisphere (N = 120) are included within HotSpots. However, an additional 71 (34.3%) of the 207 sites were within 0.2° C of HotSpot boundaries. Only 25.6% of the reef sites were not affected by anomalies adequate to produce notable bleaching in 1998. Most of these sites were in the Central Pacific and the northern Red Sea.

The magnitude and duration of extreme high temperature events is an

important factor determining rates of recovery from bleaching and the incidence of mortality after bleaching. While it might be thought that additional stresses from other factors would make bleaching worse, in fact turbid areas show much lower rates of bleaching, though the affected corals recover more slowly (Goreau, 1992; Goreau et al., 2000). Our analysis of trends for the 207 sites of reported bleaching events, categorized by the maximum temperature anomalies achieved, shows that bleaching events reported for temperature anomalies less than 0.7° C above normal maximum temperatures are infrequent and decreasing slightly with time ( $P=0.483$ , trend not significant). Bleaching reports for anomalies between 0.7 and 0.9° C anomalies (typical of mild bleaching with nearly complete zooxanthellae recovery) have dominated the record events before 1998, and are increasing slightly with time ( $P=0.9258$ , trend not significant). Bleaching events linked to thermal anomalies exceeding 0.9° C above average (characteristic of high coral mortality) are markedly increasing with time ( $P=0.0187$ , significant trend, see Figure 1). The global trend for coral bleaching events is therefore towards thermal anomalies which are hotter, more frequent, and more prolonged, as is predicted in most climate change models (Hansen et al., 1988, Hoegh-Guldberg, 1999). However the data implies that these limits are much more imminent than the models suggest.

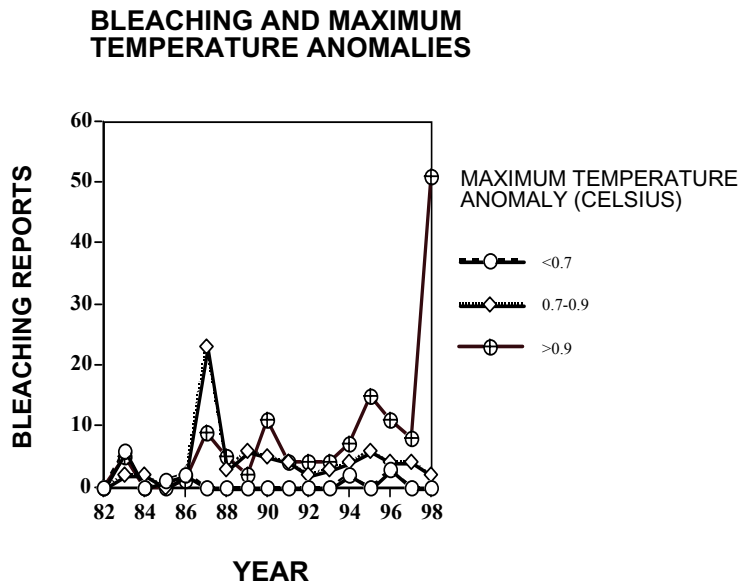
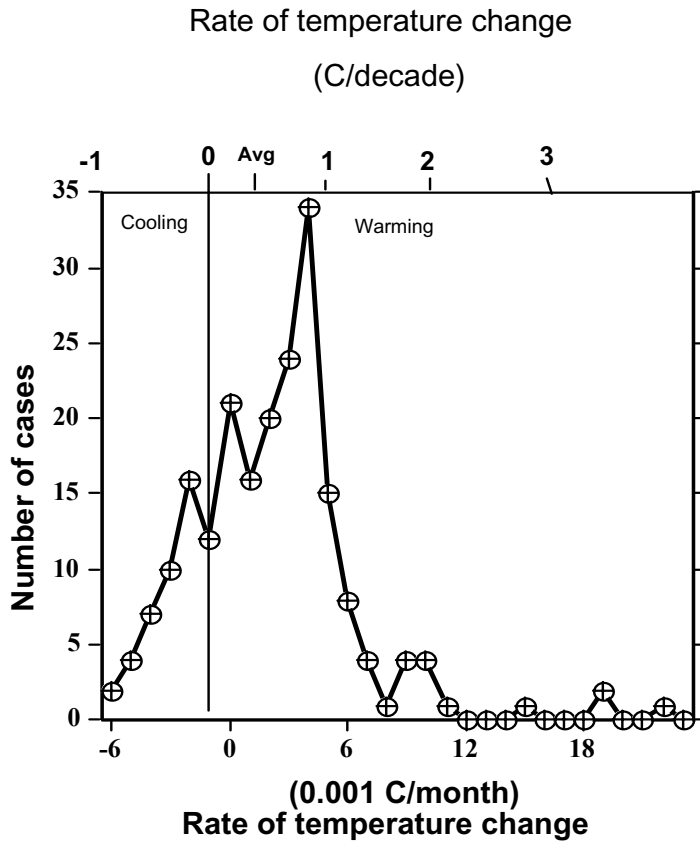


Figure 2 Bleaching trends as a function of thermal anomaly magnitude

**LONG TERM RATES OF TEMPERATURE CHANGE**

Detailed analysis of the 1982-1998 temperature trends from 207 coral reef sites (Figure 2) shows that coral reef areas are warming at an average rate of 0.32°C/decade, more than the reported global warming average of 0.14°C/decade (Angell, 1999). In comparison, night time satellite-derived trends for the entire global oceans (60°N to 60°S latitude, are upward at +0.05° C/decade. In the Northern Hemisphere oceans, this trend is greater and is statistically significant as 0.20° C/decade (Strong, et al., 2000). This indicates that coral reef regions are warming faster than the oceans as a whole. Yet, there are also strongly significant latitudinal differences in warming rates, frequency of bleaching, and potential



**Figure 3** Histogram of rate of temperature change for all sites

ecosystem impacts (Figure 3, also see color global map of smoothed trends at [www.globalcoral.org](http://www.globalcoral.org) ). Reefs in the Caribbean, Red Sea, and Persian Gulf (i.e., Northern Hemisphere) have warmed most rapidly in the past 17 years, while some South Pacific reefs actually show a cooling trend. Changes in ocean

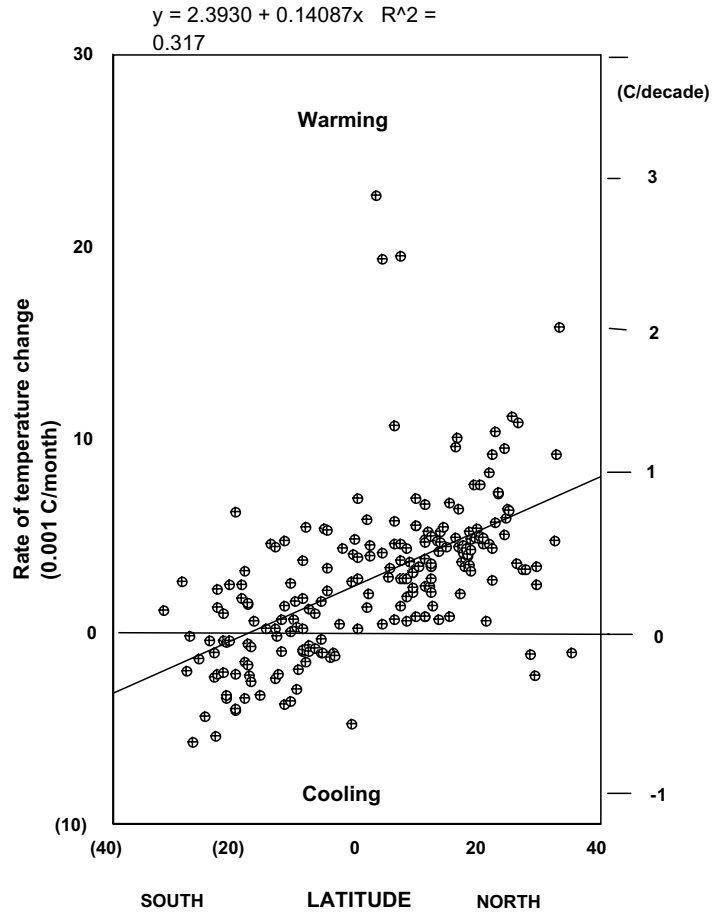


Figure 4 Temperature change as a function of latitude

temperatures and circulation have widespread climatic impacts (McPhaden, 1998; Takayabu et al., 1999). Regional cooling can occur during global warming

where increased wind velocities (Flohn & Kapala, 1989; Takayabu et al., 1999), resulting from changes in horizontal atmospheric temperature and pressure gradients, drive increased vertical upwelling caused by changes in surface wind stress and divergence (Flohn & Kapala, 1989; Chu & Wang, 1997; Chavez et al., 1999; Curran et al., 1999).

### **BLEACHING AND EL NIÑO**

While the pattern of bleaching reports shows an apparent El Niño periodicity (Goreau & Hayes, 1994; Wilkinson, 1998; Wilkinson et al., 1999); this is because regions strongly positively linked to ENSO are pushed above the threshold in these years. We regard this as a transient threshold phenomenon at sites with strong positive links to the ENSO index that will disappear as global warming increases and excessive temperatures become annual. Bleaching is seen to take place in areas both positively and negatively correlated with ENSO, and during both El Niño and non-El Niño years. In La Niña years, coral bleaching appears in reefs well removed from the Equator (e.g., Red Sea, Persian Gulf, Bahamas, and Bermuda). During 1998 severe bleaching took place in areas such as Australia, Indonesia, and the Philippines, which cool down in El Niño years. In 2002, which was not an El Niño year, there was record bleaching and coral mortality in the South Pacific all the way from the Great Barrier Reef to South America. The spatiotemporal pattern of bleaching fits a global warming pattern much better than an El Niño pattern.

While El Niño is a proximate cause of bleaching in areas with strong positive ENSO correlations that normally warm sharply during El Niño events, the ultimate cause is believed to be the rising baseline caused by global warming, which causes each major El Niño to be hotter than its predecessor, on the average (Williams & Bunkley-Williams, 1990; Huppert & Stone, 1998; Trenberth, 1989; Timmerman et al., 1999), unless the unusually rapid switch-over to La Niña conditions in mid-1998 contributed to the late-year bleaching in Indonesia and the Philippines.

The fact that corals up to a thousand years old, that had undergone hundreds of previous El Niño events, died in 1998 indicates that none of these previous events were as severe (Goreau, 1998a,b,c). The rate of temperature increase at most locations is such that the normal maximum seasonal temperatures will become above bleaching thresholds every year within years to decades if present trends continue. Bleaching would become annual at these locations, if corals were able to survive. Figure 4 shows the trends of maximum and minimum

1982-1998 Maximum and Minimum temperatures: Male and Addu, Maldives

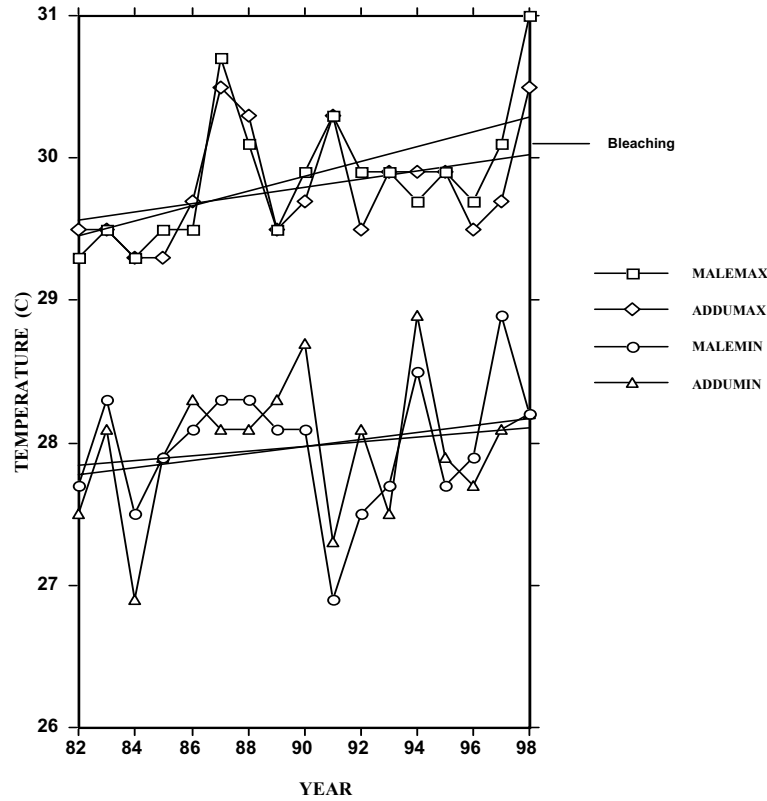


Figure 5 Maximum and minimum temperatures in the Maldives

seasonal temperatures in the central and southern Maldives. Continuing these present trends, the average maximum temperatures will exceed the bleaching threshold around the year 2000, and every subsequent "normal" year would at that time become warm enough to cause bleaching, if the corals survive. This is not exceptional, as the rate of increase of temperature in the Maldives is close to the global reef average.



## **CHANGES IN EXTREME EVENTS AND SEASONALITY**

The data presented here includes change in the mean SST at each site, and also in the maximum monthly (HotSpot) temperature. Other characteristics are also important, including trends in the minimum monthly temperatures and the seasonal range. In the dataset (see GCRA website) there are many examples where the maximum and minimum temperatures are both increasing, but some where they are both decreasing, where the maximum increases while the minimum decreases, and vice versa. Many of the sites especially those near the Equator, show what appear to be longer term cycles, often at around 20 years, which may be related to long term ocean dipole oscillations, such as the El Nino Southern Oscillation, the North Pacific Oscillation, the North Atlantic Oscillation, or the Indian Ocean Oscillation. As a result some of these places have suppressed seasonal amplitudes, others larger ones, and in some the recovery period between bleaching events is decreasing because minima are rising. Examples of all of these patterns can be seen in the selected examples below, which include both typical and extreme examples.

### **Specific Examples**

Note: in the examples below the raw data is shown, not the edited data. The graphs for these and all sites, and color maps of thermal anomalies can be found at <http://www.globalcoral.org>

#### **High Increases:**

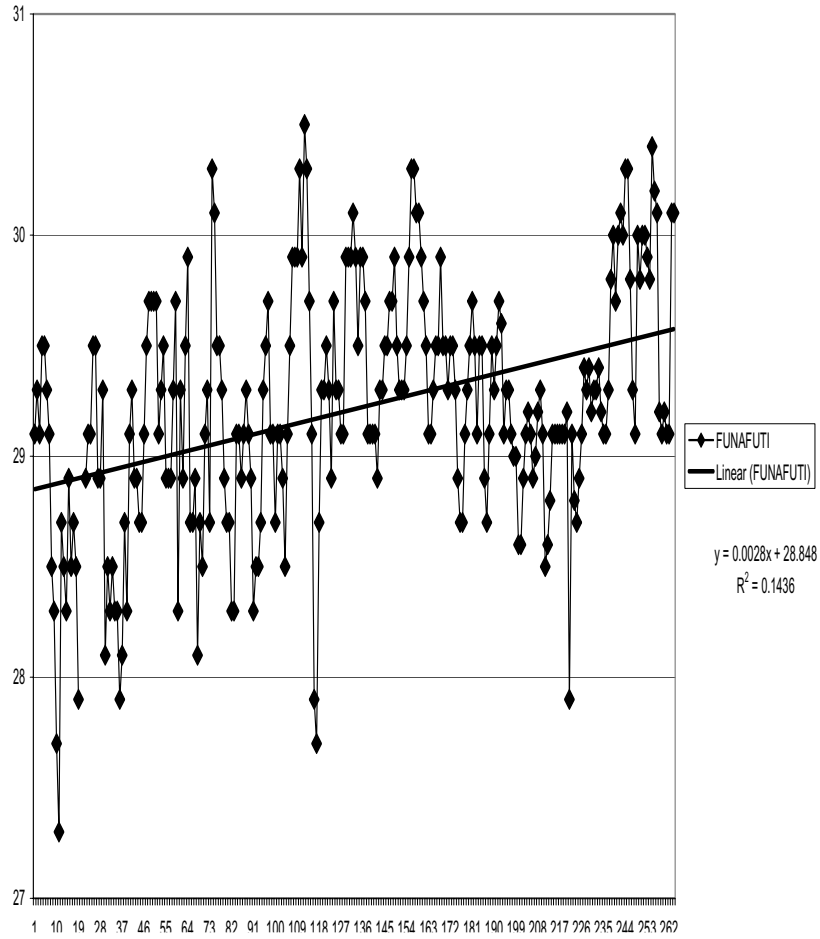
Farasan, Saudi Arabia (Figure 5). There has been very strong increase in temperature in the southern Red Sea, but not in the Northern Red Sea. Farasan represents the hot area.

Dubai, United Arab Emirates (Figure 6). The hottest year here was in 1996, but the trends are up. Bleaching mortality there attributed to the 1998 bleaching event was probably the result of that two years earlier. Kuna Yala (San Blas) Panama (Figure 7), in the Southwest corner of the Caribbean, with 2003 the warmest year. This site, like all the Caribbean, was strongly affected by El Chichon in 1982.

#### **Medium Increases:**

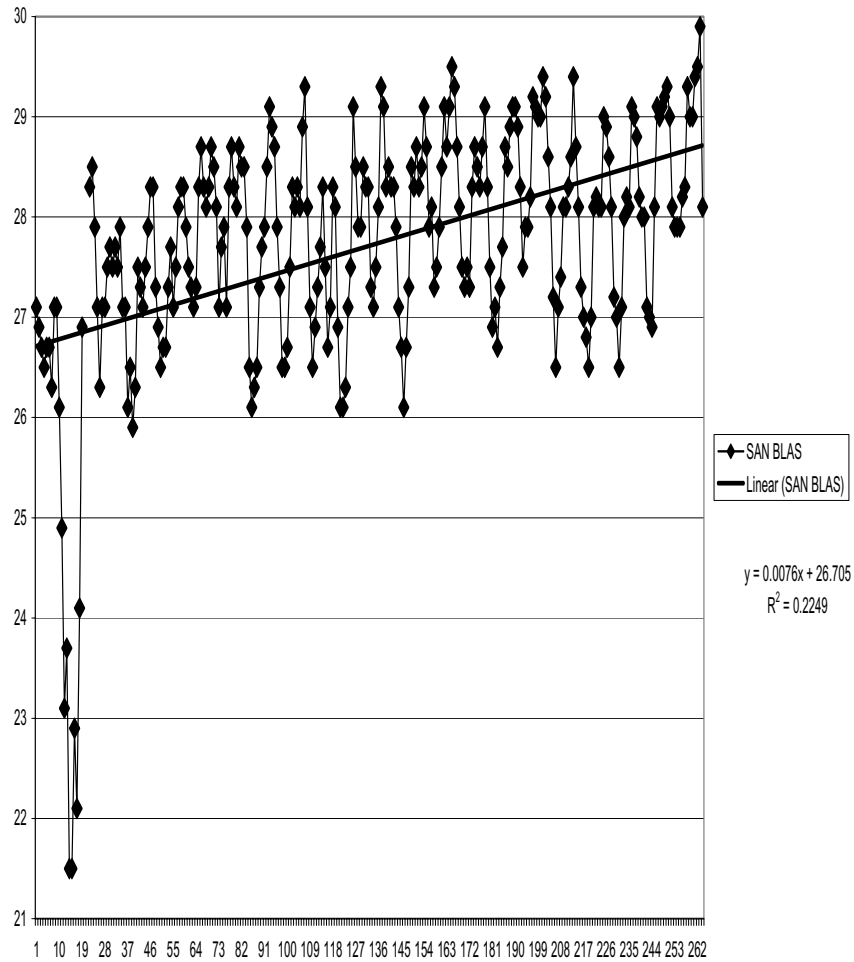
Male, the Maldives (Figure 8): an equatorial site and the lowest country in the world, with a steady increase in both maxima and minima. The mean maximum will soon pass the bleaching threshold, after which

FUNAFUTI, TUVALU



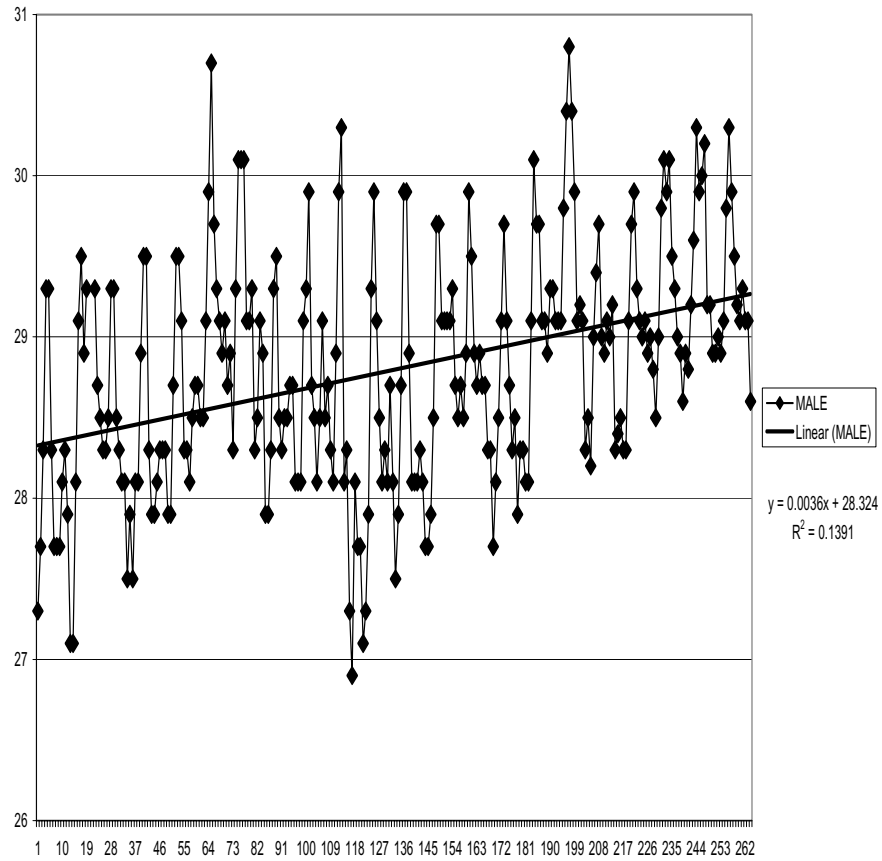
**Figure 7** Dubai, United Arab Emirates, Persian Gulf - There is around a 2 degree rise in mean temperature in the southern Persian Gulf, with the hottest year in 1996.

KUNA YALA, PANAMA



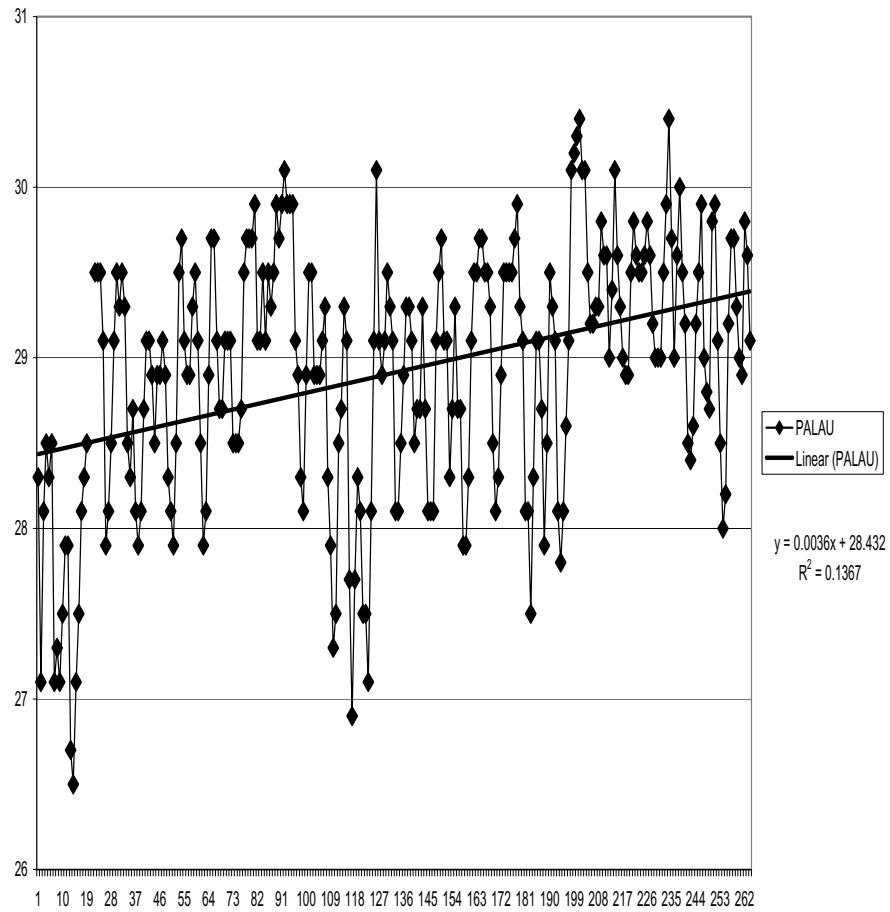
**Figure 8** Kuna Yala, San Blas, Panama, Southwestern Caribbean - The whole Caribbean shows a strong cooling in 1982 due to El Chichon volcano, but even without it there is a strong increase at all sites. 2003 was the warmest year in the record.

MALE, MALDIVES

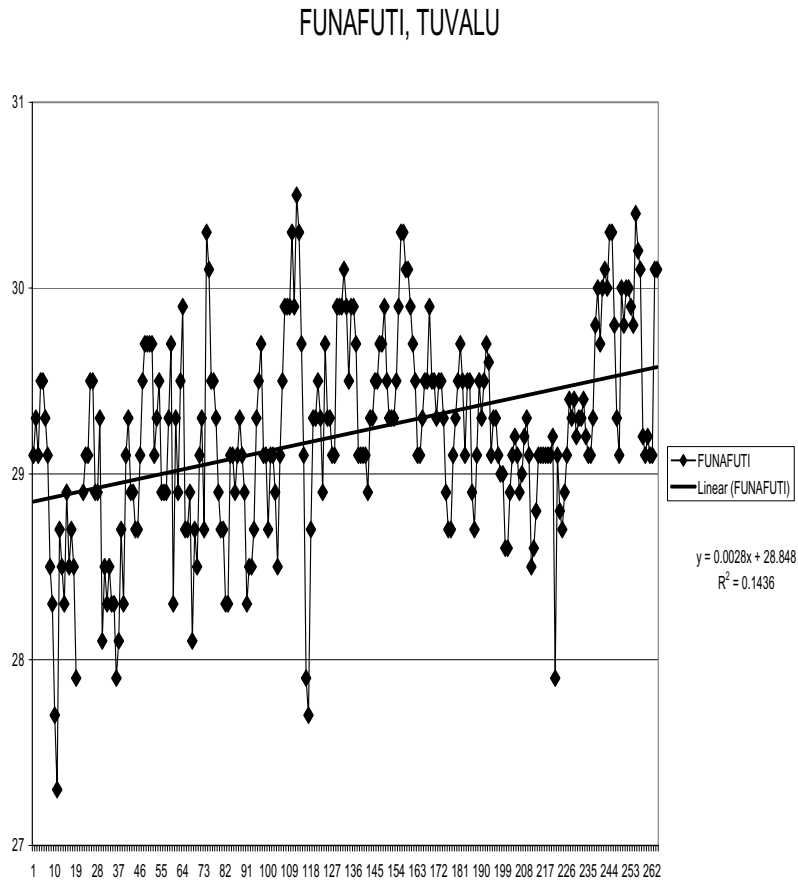


**Figure 9** Male, Maldives, Central Indian Ocean - There has been a 1 degree C rise in Make, with 1998 the hottest year, followed by 1987. The Maldives is the lowest country in the world, and healthy reefs are essential to the preservation of the islands.

KOROR, PALAU



**Figure 10** Koror, Palau, Western Pacific - There has been a 1 degree C rise in mean temperature, with 1998 the hottest.



**Figure 11** Funafuti, Tubvalu, Central Pacific - Tuvalu, near the equator, shows a rise about 0.7 C, and longer term cyclic oscillations that are greater than seasonal variations. Tuvalu is one of the lowest lying countries in the world.

bleaching conditions could happen almost every year.

Koror, Palau (Figure 9) where the major bleaching mortality also happened in 1998.

**Equatorial Cycles:**

Funafuti in Tuvalu (Figure 10) shows an equatorial site with small seasonal amplitude in which the minima are rising faster than the maxima, and long term cycles are apparent. Many other sites in the central Pacific, Sao Tome in West Africa, Fernando de Noronha in Brazil, Indonesia, the Philippines, and other equatorial locations show long term cycles clearly too. These long-term cycles may reflect ocean dipole oscillations such as the El Niño Southern Oscillation, the North Atlantic Oscillation, the North Pacific Oscillation, and the Indian Ocean Oscillation. Longer time series are clearly needed to delineate the longer term cycles, but even so some sites show clear cycles approaching the data length.

**Decreasing Temperatures:**

The sharpest decreases in the raw data are 7 sites with decreasing mean temperature. Most of these sites are affected by open ocean upwelling, but two are subjected to strong continental influences.

Rodrigues (Figure 11) has the sharpest decrease, and this appears to be due to decreasing minimum temperatures, apparently due to more upwelling in the southeast Indian Ocean. Nosy Be (Figure 12) in Madagascar and Mauritius also show decreases to less robust degrees.

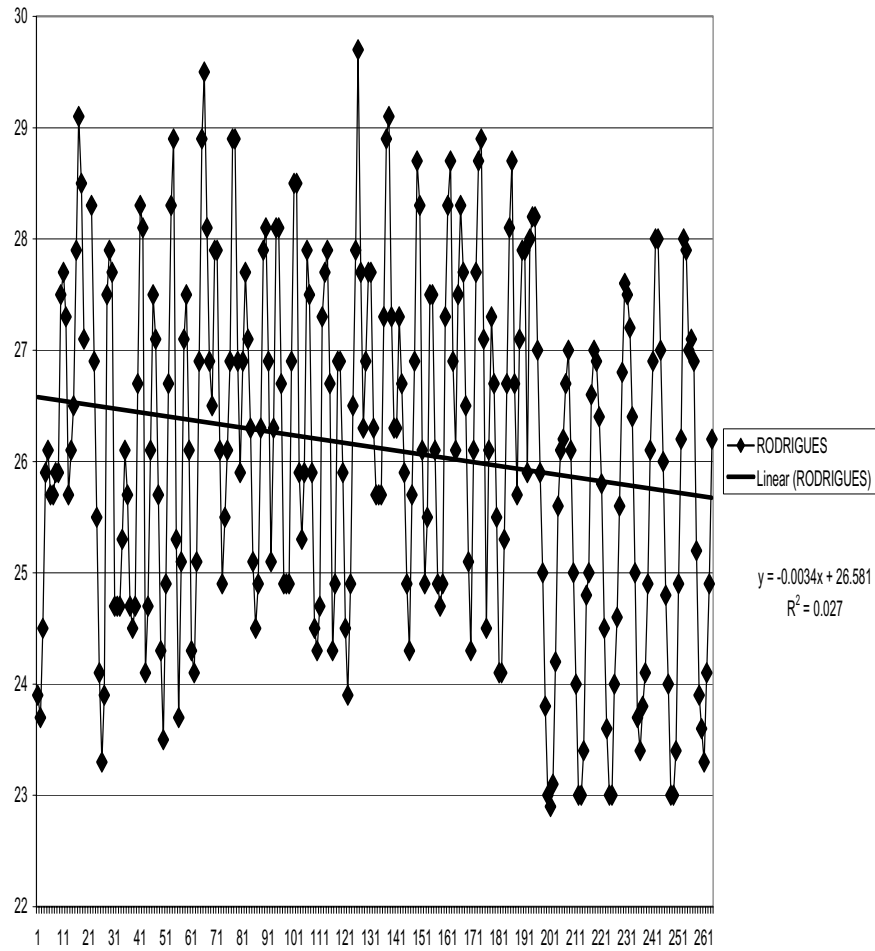
Easter Island (Figure 13) shows a decrease that may be accounted for by increased upwelling in the south east Pacific Ocean.

Galapaogos (Figure 14), in the core of the El Niño area, shows a decreasing temperature. One site in the Great Barrier Reef, Hinchinbrook Island, shows a small decrease, but all the other sites in Australia are increasing. Another odd isolated case is the Flower Gardens Bank, off Texas. The reason why appears to be that the winter minima are decreasing, apparently due to extreme cold winter events in North America. All other sites in the Caribbean region show strong increases.

**Upwelling Areas:**

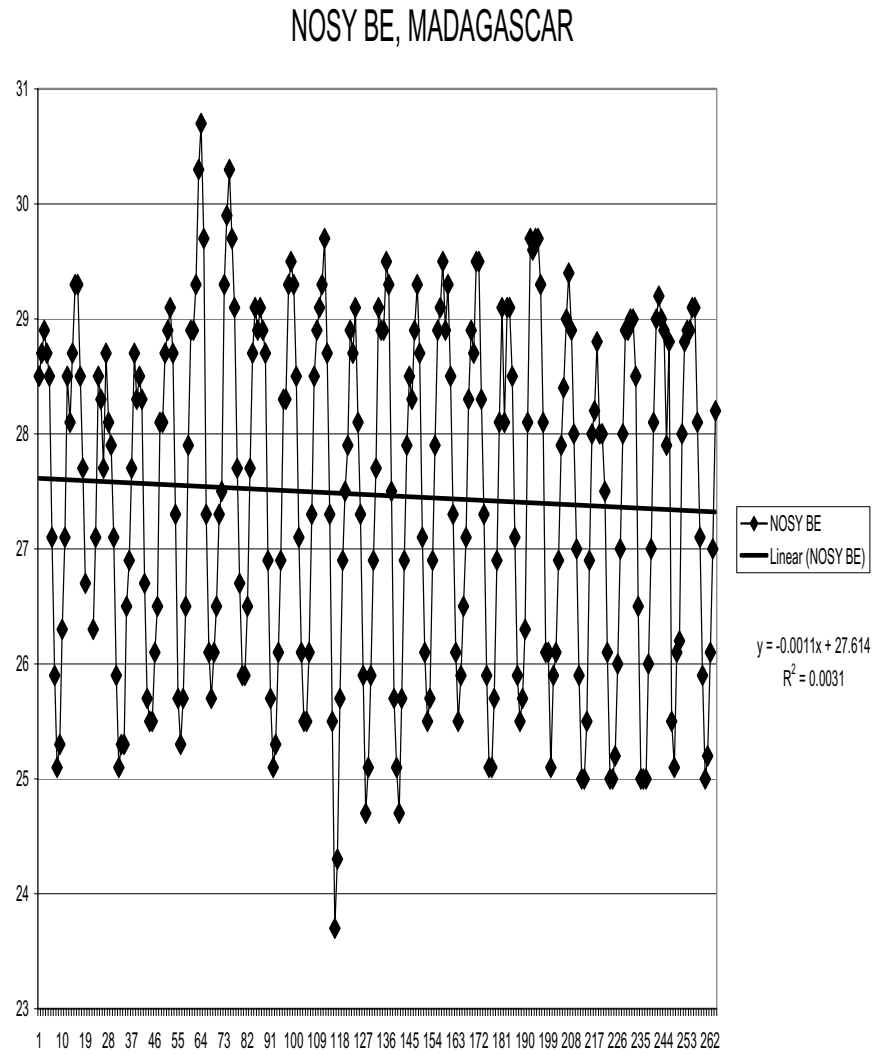
Virtually all the coastal upwelling areas show strong increases in the minimum temperatures, which seems to suggest reduced upwelling intensity. These include sites all across Indonesia and the Philippines, the Indian Ocean, New Guinea, across the Pacific, and the Gulf of Guinea. It is strongest in the East Pacific, where upwelling seems to have nearly stopped.

### RODRIGUES

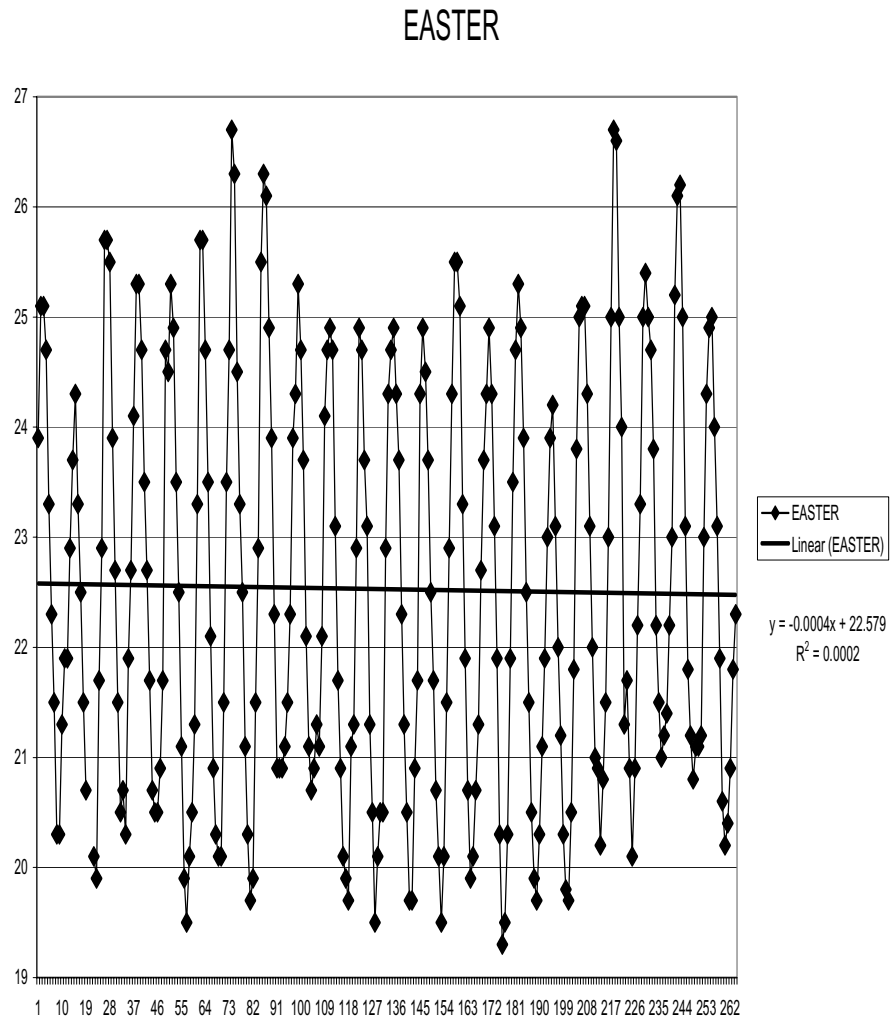


**Figure 12** Rodrigues, Mauritius, South Indian Ocean - Rodrigues has the fastest decline in mean temperature of all sites, 1 degree C. Minimum temperatures have dropped sharply, and the bimodal annual cycle has become unimodal.



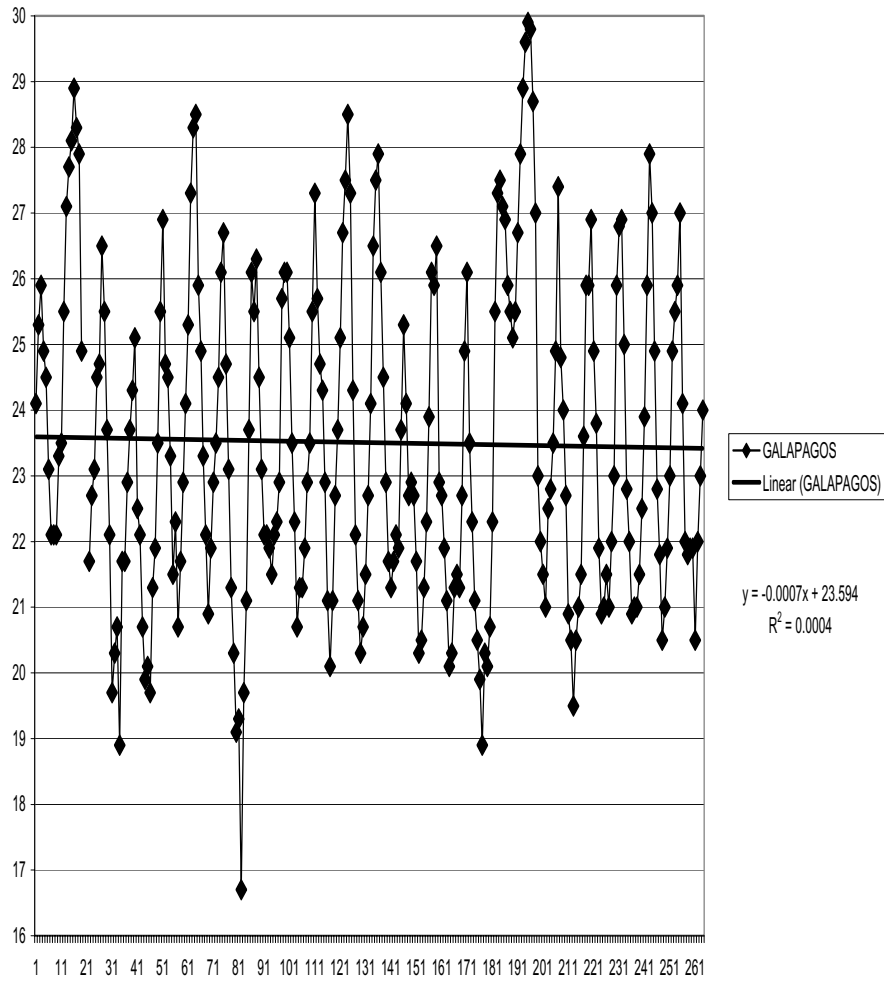


**Figure 13** Nosy Be, Madagascar, West Indian Ocean - Bony Be has the second fastest decline in mean temperature of all sites, about 0.3 C. The hottest year was in 1987.



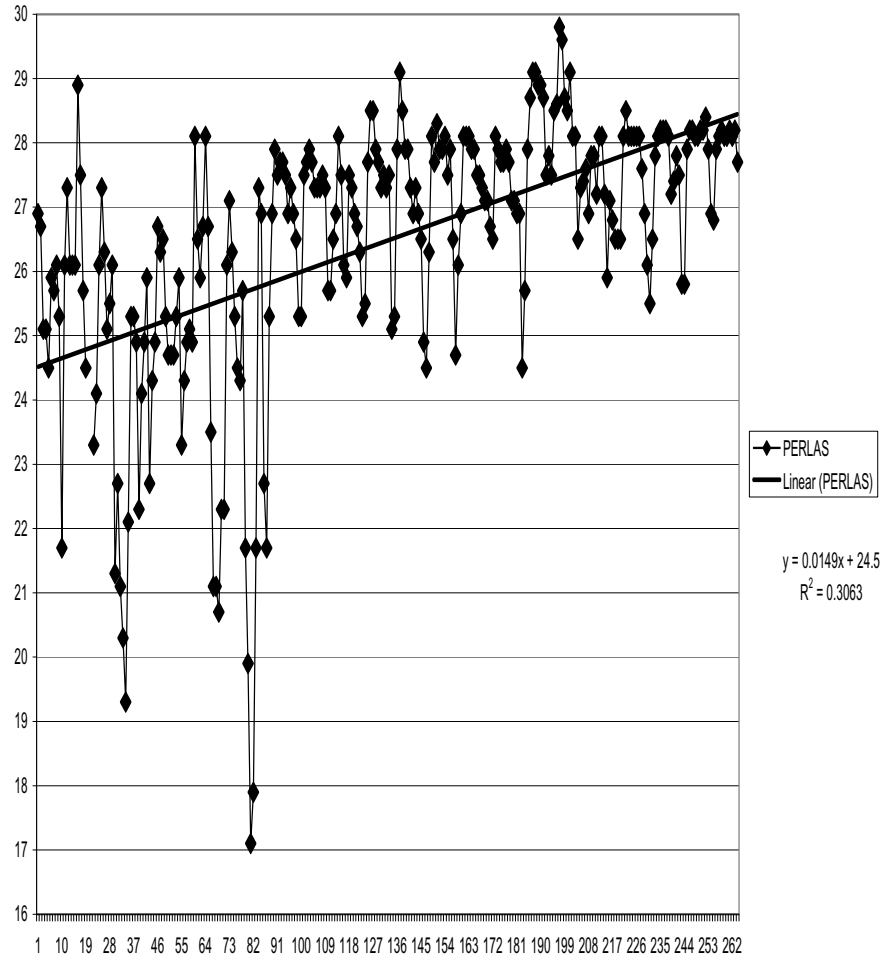
**Figure 14** Easter Island, Chile, Southeast Pacific - Easter Island has a slow decline in mean temperatures, largely due to declining maximums. 200 and 1988 were the hottest.

### GALAPAGOS, ECUADOR



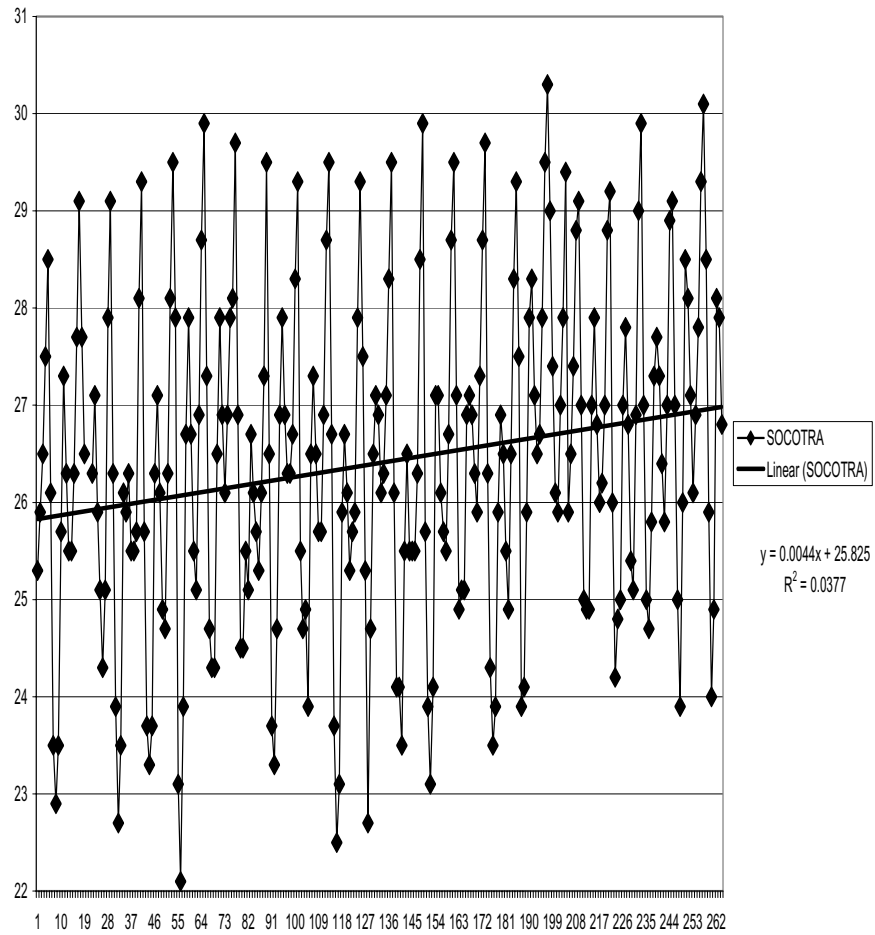
**Figure 15** Galapagos, Ecuador, East Pacific - Galapagos, in the core of the El Nino area, shows a slow decline in mid temperatures. Note the 1987 - 1988 and 1982 - 1983 maxima superimposed over a mean decline.

LAS PERLAS, PANAMA



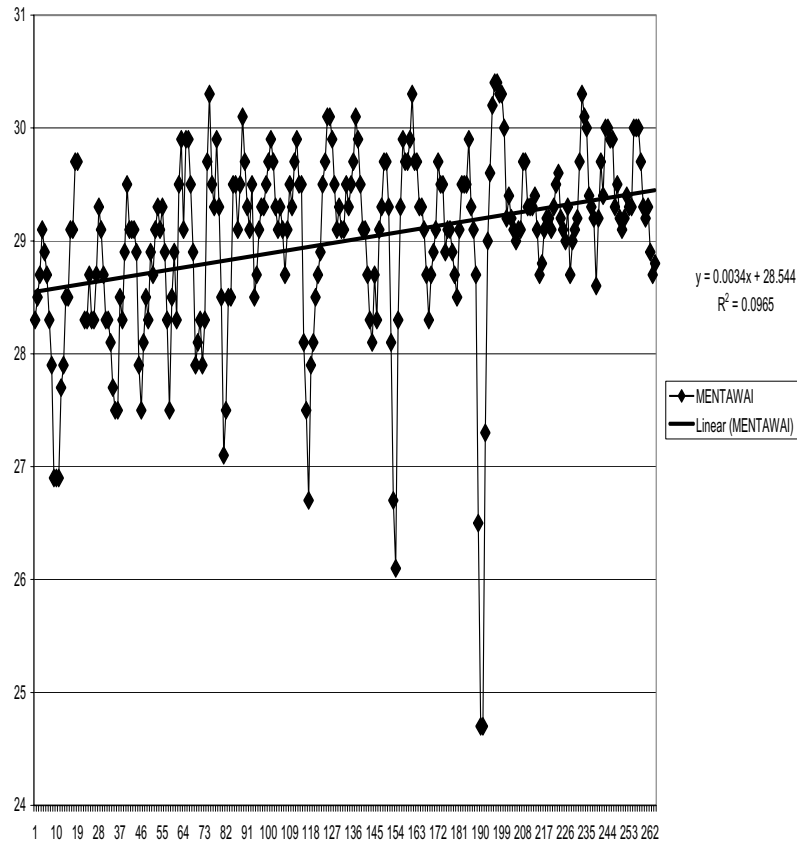
**Figure 16** Las Perlas, Panama, East Pacific - This site has the largest rise in mean temperature of all sites, about 4 degrees C. Major upwelling events have ceased since 1989 in this and about half a dozen other North east Pacific sites, while maxima are rising.

SOCOTRA, YEMEN



**Figure 17** Socotra, Yemem, Northwest Indian Ocean - Socotra, near the core of the Somalia Upwelling system, shows a strong increase in minimum temperatures as upwelling appears to be slowing down.

MENTAWAI, INDONESIA



**Figure 18** Mentawai, Indonesia, East Indian Ocean - Intense upwelling events every third year have stopped after 1998.

Las Perlas (Figure 15), in the Gulf of Panama, has seen cold upwelling virtually cease. The same is seen in all other east Pacific sites, including Coiba, Coco, Gorgona, and Malpelo.

Socotra, Yemen, (Figure 16) is in the Somalia upwelling system, and shows complex long-term cycles with a decrease in upwelling minimum temperatures.

Mentawai, Indonesia, (Figure 17) is an especially interesting example. The first half of the record shows intense and increasing upwelling every third year, but this suddenly shuts off later. Interestingly, the coldest temperatures take place in 1997, and are immediately followed by the hottest in 1998. A recent paper suggests that the large mortality of corals in that area in that period was due to ash from forest fires during the cold period (Abram et al., 2003). Those authors suggested that the corals were overgrown by algae fertilized by forest fire ash and dust nutrients, especially iron. The muddy waters around reefs of west Sumatra are not likely to be iron-limited, and it seems more likely that these corals died of high temperature bleaching in 1998 as did most other corals in the Indian Ocean in areas not affected by the forest fire ash.

## **DISCUSSION**

Live coral cover has been observed to be steadily declining for several decades in almost all long-studied coral reefs (Porter & Meier, 1992; Jaap et al., 1999, Hodgson, 1999), but nearly half of all the world's coral reefs were severely damaged by bleaching in 1998 alone (Goreau et al., 2000). Bleaching and diseases have caused more coral mortality in the last two years than all previous human damage to reefs. Recovery of coral reefs from morbidity caused by severe bleaching and diseases is likely to be very prolonged, if it happens at all. Coral reefs damaged by severe episodic local stresses such as ship groundings, storms, or predatory outbreaks can recover in a few decades as long as surrounding reefs are healthy and water quality is satisfactory, but bleaching and disease stresses are far more widespread and progressively increasing.

Because near total mortality of the most abundant and rapidly growing branching and plate corals took place in the Indian Ocean and large parts of the Pacific Ocean in 1998 (Goreau et al., 2000), there may be fewer corals of these species reproducing in coming years, and hence less recruitment of new coral larvae. Recovery is unlikely near populated shores, even if there were an adequate supply of coral larvae, unless pollution from sewage, soil erosion, fertilizers, and physical damage are halted. Recovery will be impossible even in areas which are totally unaffected by human activities if extreme high temperature stress continues.

During the 1982-83 coral bleaching event in the eastern Pacific, there were 2-3 episodes of bleaching. These events were followed within 2-4 weeks by death of the bleached coral colonies. In Costa Rica, Panama and Colombia, 70-90% mortality was reported; in the Galapagos Islands (Ecuador), mortality exceeded 95% (Glynn, 1990). This bleaching event was the first to occur in the

region throughout the last 200 years, based on the fact that large old corals died. It was attributed to the ENSO event, and was considered far more devastating to the reefs than periodically intense upwellings in the area (Glynn, 1990).

In 1997-1998, another wave of coral reef bleaching struck the eastern Pacific. Panama; the Galapagos islands and coastal Ecuador were affected. In 1987-88, there were two events, one in October, 1987, and the other in March, 1988. However, temperatures were 1 degree hotter, and lasted longer in 1998 (figure 13), Coral mortalities, depending upon the region surveyed, were 0-26.2 % in 1997-98, a significantly lower impact than the 52-97% mortalities observed in 1982-83 (Glynn et al., 2001). It was suggested that the spatial/temporal variability as well as the long term history of stresses endured by the eastern Pacific reef communities be considered in analyses of responses of reefs to coral bleaching.

Although adaptation is a possible explanation for this difference in survival, lower mortality during the second hotter event could be due to the fact that only high temperature tolerant corals survived the first event. This would not be evidence of adaptation but of selective elimination of sensitive populations. In addition the residual population could have been made up primarily of young corals, which may be more tolerant of high temperatures. Areas with severe coral mortality in the Seychelles, Maldives, and Palau were observed to be transformed from *Acropora* dominated reefs to *Porites* dominated reefs, because virtually all *Acropora* died while most *Porites* survived due to higher tolerance (Goreau 1998, a, b, c). In addition the only survivors of the temperature sensitive species were very young corals, often in cryptic habitats. Since many corals reproduce in the warm season, and allocate large fractions of their energy reserves to gonad production, pre-reproductive corals may have more energy for resisting environmental stress.

Large increases in algae, and declines in fish and invertebrate populations are also observed to follow catastrophic bleaching (Goreau 1998a, b, c). Rapid loss of biodiversity in reefs will cause a transition to species-poor communities dominated by a few "weedy" species, with seriously altered ecosystem functioning. Such ecosystems are coral communities dominated by algae or filter feeding soft corals, sponges, and tunicates. Their reef structures are degrading, eroded by wave forces and bio-erosion, rather than functioning coral reefs with growing frameworks that provide habitat to all other reef organisms and protect coastlines from erosion (Williams et al., 1999).

The importance of coral reef ecosystems for providing most of the marine biodiversity, fisheries, tourism, white sand supply, and shore protection for over 100 countries is difficult to estimate with precision. Because reefs provide cost-free ecosystem services, their real functional value is typically



underestimated by standard economic analyses. Nevertheless, coral reefs clearly represent the most economically valuable coastal ecosystem in the tropics. When fish must be imported to feed local populations, when sand must be dredged to replace eroded beaches, when tourists stop returning, when jobs evaporate, and when seawalls must be built along tens of thousands of kilometers of coastline formerly protected by reefs, their true economic value will become clear. The cost of replacing their lost services will reach as high as tens of millions of dollars per kilometer of coastline of reef (Chan, 1992). Most coral reef countries are unable to bear these costs without significantly increased financial resources, especially in the low-lying atoll nations of the Indo-Pacific, which are also threatened by global sea level rise.

Coral reefs are not just essential to the people of insular and coastal countries. Their protection is the truest test of commitment to sustainable development because they appear to be already right at the limit of what they can take and are very likely close to total collapse. Unless destructive practices in reefs are dramatically slowed, unless sewage treatment is upgraded to tertiary levels, unless degraded watersheds are reforested, unless agricultural practices that conserve soil and soil fertility are mandated, and unless excessive CO<sub>2</sub> release from fossil fuels into our atmosphere is addressed, these problems within the coral reef ecosystem will only worsen. All these corrective measures must be accomplished simultaneously for the coral reefs of the world to be preserved for the future.

#### **FIGURE CAPTIONS**

Figure 1. Year by year trends of bleaching reports as a function of maximum monthly average temperature anomalies (MMA). Class #1 consists of reports from locations where MMA less than 0.7° C above average. It consists of all records of bleaching due to other than high temperature causes, including low temperature, fresh water, mud, high light, and erroneous confusion with *Acanthaster planci* damage, diseases, or physical damage, as well as unknown causes. Class #1 also includes bleaching reported due to highly localized high temperatures resulting from poor water circulation during low tides in lagoons below the spatial resolution of satellite imagery. Class #2 consists of reports of bleaching in locations where MMA was between 0.7 and 0.9° C above warmest averages. Class #2 includes almost entirely events in which bleaching affected some, but not all, corals, and in which almost all bleached corals survived and recovered zooxanthellae with minor mortality. Class #3 consists of bleaching reports from sites where MMA was more than 0.9° C above average. Class #3 reports showed near complete bleaching of all coral colonies with mortality

ranging up to over 99%. The number of reports in Class #1 or “sub-threshold bleaching” is low, averaging around 1 per year, and shows a non-significant decreasing trend with time ( $P=0.4830$ ). The number of reports in Class #2, categorized as “threshold bleaching”, averages around four reports per year, with a sharp peak in 1987, and shows a non-significant increasing trend with time ( $P=0.9258$ ). Reports in Class #3, or “supra-threshold bleaching”, dominate reports in 1998 and show a sharply increasing and significant increase in time ( $P=0.0187$ ). The size, frequency, intensity, and duration of the most extreme hot spots, which are capable of causing severe coral mortality, are increasing sharply.

Figure 2. Histogram of mean rate of temperature change for coral reef sites monitored worldwide with coordinates as shown in Figure 1. The mean rate of temperature change is  $0.0027 \pm 0.0041^{\circ}\text{C} / \text{month}$ , or  $0.32 \pm 0.49^{\circ}\text{C} / \text{decade}$ . The P value that the mean is equal to zero is  $<0.0001$ ; therefore, the mean temperature increase is highly significantly different than zero.

Figure 3. Mean rate of temperature change for monitored coral reef localities plotted against latitude. There is a highly significant increase in mean warming rate with latitude ( $P < 0.0001$ ). The greatest warming is occurring in the north, and sites with long term cooling are confined to the Southern Hemisphere.

Figure 4. Extreme Temperature Event Indexes for the Maldives: Temperature trends of maximum and minimum monthly average temperatures for Male and for Addu, in the central and southern Maldives respectively. Bleaching years are marked, as are the bleaching threshold temperatures. The average maximum temperatures are rising faster than the minimum temperatures, and will intersect the bleaching threshold temperature around 2000. This suggests that every “normal” year in the future will be a bleaching year as long as there are corals left. The slopes of the extreme temperature event indices in Figure 7 include all the warmest month averages experienced since 1982. These slopes are higher than those used in the calculation of the long term slopes used in previous figures, because the previous long term slopes were conservatively calculated, including all monthly averages year-round (not just the extremes) and excluded values from all El Niño years, including 1997 and 1998. Those values are for Addu:  $.00258^{\circ}\text{C} / \text{month}$  ( $0.31^{\circ}\text{C} / \text{decade}$ , equal to the global average); and for Male  $.0038^{\circ}\text{C} / \text{month}$  ( $.044^{\circ}\text{C} / \text{decade}$ ). Even at the most conservative rate all normal years will surpass bleaching thresholds within a few years. The slope of all the extreme events shown are more relevant to coral bleaching than the average of all months except El Niño years used in the previous figures, because bleaching is intrinsically a response to extreme supra-threshold warm events, not long term rates of change. Slopes used in the previous figures therefore provide conservative underestimates of the rate of change with regard to the likelihood of bleaching from supra-threshold temperatures at locations where extreme El Niño events are

correlated with bleaching, if extreme temperatures are affected by changes in El Niño intensity, duration, or frequency. This illustrates some of the statistical complexity of developing biologically relevant climate change indices.

Figures 5-17. Complete Raw data time series for 12 locations showing some of the distinct regional patterns found. (NB Captions for Figures 5-17) are in the attached file with the graphs

**SUPPLEMENTARY COLOR FIGURES ON THE WEB AT**  
[www.globalcoral.org](http://www.globalcoral.org)

Figure A. Global map showing latitude and longitude of 207 coral reef sites whose detailed SST records were analyzed in this study.

Figure B (a-p) HotSpots and bleaching year by year from 1982 through 1997. Purple areas reached a maximum monthly average temperature of 0.3 - 0.7° C above, blue areas reached 0.7 - 0.9° C above, yellow areas reached 0.9 - 1.3° C above, and orange areas reached more than 1.3° C above the average monthly maxima for the hottest month (NOAA satellite data compiled by A. E. Strong). Red dots mark locations where bleaching reports have been recorded in the Global Coral Reef Alliance database. In many cases multiple bleaching reports from nearby sites have been clustered to avoid overlapping symbols. A few minor local bleaching reports in the database have been deleted from the maps on grounds of insignificance (e.g. from use of the fish poison, rotenone, in a tide pool or from corals exposed to air at unusual low tides, etc.). In several cases bleaching events have taken place in very small yellow HotSpot areas that are hidden by the red bleaching symbols.

Figure C. Map of HotSpots and bleaching reports in 1998. The total area of tropical ocean water temperatures more than 1.0° C above average was the most extensive on record in 1998, as was the number of bleaching events reported.

Figure D. Contour plot of long term rates of change of coral reef site SST as a function of latitude and longitude, smoothed using the distance weighted least squares method. There is no significant trend with longitude. The maximum rate of increase is found in the Persian Gulf and the minimum in the Southeast Pacific (compare to Figure 1 for locations of 207 data points, and the locations of ocean boundaries). Note that the coral reef locations are not evenly distributed across the entire tropical ocean because they reflect sites from which frequent diving takes place, and these are relatively concentrated in the northern hemisphere, especially the Caribbean, because large areas of the southern ocean are lack shallow water coral habitat, and because coral reefs are rarely found in cooler upwelling areas, that are predominantly located in the southern hemisphere

cooling regions. Therefore the slopes in this figure derived from the population of 207 coral reef sites shown in Figure 1 may be expected to be slightly higher than the average based on rates of change of the entire ocean basin, as derived by Strong, which includes values from the surface of the deep cold ocean sites where corals can not grow. Nevertheless the plot above from the population of coral sites gives regional temperature change patterns that are strikingly similar to that of the tropical ocean as a whole.

*ACKNOWLEDGMENT:* We gratefully thank Al Strong for providing temperature data, HotSpot maps, and helpful discussions. We thank the reviewers for helpful comments clarifying several issues.

## REFERENCES

- Abram, N.J., M.K. Gagan, M.T. McCulloch, J. Chappell and W.S. Hamtoro, Coral reef death during the 1997 Indian Ocean dipole linked to Indonesian wildfires, *Science*, **301**, 952-955 (2003).
- Allison, W.R., Changes in the Maldivian reef system, *Coastal Management in Tropical Asia*, **4**, 6-8 (1998).
- Angell, J.K., Comparison of surface and tropospheric temperature trends estimated from a 63-station radiosonde network, 1958-1998, *Geophys. Res. Lett.*, **26**, 2761-2764 (1999).
- Cane, M.A., A.C. Clement, A. Kaplan, Y. Kushnir, D. Pozdnyakov, R. Seager, S. Zebiak and R. Murtugudde, Twentieth century sea surface temperature trends, *Science*, **275**, 957-960 (1997).
- Chan, F., Coral Reefs: Ecology and Economics of Ecosystem Conservation, *B.A. Thesis*, Hampshire College, Amherst, MA (1992).
- Chavez, E.P., P.G. Strutton, G.E. Friedrich, R.A. Feely, G.C. Feldman, D.G. Foley and M.J. McPhaden, Biological and chemical response of the Equatorial Pacific Ocean to the 1997-98 El Niño, *Science*, **286**, 2126-2131 (1999).
- Chu, P.S. and J.B. Wang, Recent climate change in the tropical Western Pacific and Indian Ocean regions as detected by outgoing longwave radiation records, *J. Climate*, **10**, 636-646 (1997).
- Curran, L. M., I. Caniago, G.D. Paoli, D. Astianti, M. Kusnati, M. Leighton, C.E. Niranta and H. Haeruman, Impact of El Niño and logging on canopy tree recruitment in Borneo, *Science*, **286**, 2184-2188 (1999).
- Fagoonee, I., H.B. Wilson, M.P. Hassell and J.R. Turner, The dynamics of zooxanthellae populations: a long-term study in the field, *Science*, **283**, 843-845 (1999).
- Flohn, H., and A. Kapala, Changes in tropical sea-air interaction processes over a 30-year period, *Nature*, **338**, 244-246 (1989).
- Glynn, P., *Coral mortality and disturbances to coral reefs in the tropical eastern Pacific*, In *Global Ecological Consequences of the 1982-83 El Niño-Southern Oscillation*, Elsevier Oceanographic Series, P.W. Glynn (ed.), Elsevier, Amsterdam (1990).
- Glynn, P.W., Coral bleaching in the 1980s and possible connections with global warming,

- Trends Ecol. Evol.*, **6**, 175-179 (1991).
- Glynn, P.W., Coral reef bleaching: ecological perspectives, *Coral Reefs*, **12**, 1-17 (1993).
- Glynn, P., J. Mate, A.C. Baker and M. Calderon, Coral bleaching and mortality in Panama and Ecuador during the 1987-88 El Nino-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-83 event., *Bull. Mar. Sci.*, **69**, 79-109 (2001).
- Glynn, P.W., R. Imai, K. Sakai, Y. Nakano and K. Yamazoto, Experimental response of Okinawan (Ryukyu Islands, Japan) reef corals to high sea temperature and UV radiation, *Proc. 7th Int. Coral Reef Symp.* (1992).
- Goenaga, C. and M. Canals, Relacion de mortandad masiva de *Millepora complanata* (Cnidaria, Anthozoa) con alta pluviosidad y escorrentia del Rio Fajardo en Cayo Abogado., *Symp. Nat. Res. San Juan Puerto Rico*, **6**, 84-95 (1979).
- Goreau, T.F., Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora, *Science*, **145**, 383-386 (1964).
- Goreau, T.F., N.I. Goreau and C.M. Yonge, Reef corals: autotrophs or heterotrophs, *Biol. Bull.*, **141**, 247-260 (1971).
- Goreau, T.J., Coral bleaching in Jamaica, *Nature*, **343**, 417 (1990).
- Goreau, T.J., Coral reef protection and coastal development in western Jamaica, pp. 39-65 in *Protecting Jamaica's Coral Reefs: Water Quality Issues*, K. Thacker (ed.), Negril Coral Reef Preservation Society (1992).
- Goreau, T.J., Coral Bleaching in the Seychelles: Impacts and recommendations, *Report to the Seychelles Marine Park Authority* (1998a).
- Goreau, T.J., Coral recovery from bleaching in Alphonse and Bijoutier, Seychelles, December 1998, *Report to the Seychelles Marine Park Authority* (1998b).
- Goreau, T.J., Coral recovery from bleaching in Seychelles, December, 1998, *Report to the Seychelles Marine Park Authority* (1998c).
- Goreau, T.J., Weighing up the threat to the world's corals, *Nature*, **402**, 457 (1999).
- Goreau, T.J. and A.H. Macfarlane, Reduced growth rate of *Montastrea annularis* following the 1987-1988 bleaching event, *Coral Reefs*, **8**, 211-216 (1990).
- Goreau, T.J., R.L. Hayes, J.W. Clark, D.J. Basta and C.N. Robertson, Elevated sea surface temperatures correlate with Caribbean coral reef bleaching, pp. 225-255 in R.A. Geyer (ed.), *A Global Warming Forum: Scientific, Economic, and Legal Overview*, CRC Press, Boca Raton, Florida (1993).
- Goreau, T.J. and R.L. Hayes, Coral bleaching and ocean Hot Spots, *Ambio*, **23**, 176-180 (1994).
- Goreau, T.J. and R.L. Hayes, Monitoring and calibrating sea surface temperature anomalies using satellite and in-situ data to study the effects of weather extremes and climate changes on coral reefs, *Proceedings Conference on Remote Sensing for Environmental Monitoring and the Sustainable Development of the Americas, San Juan, Puerto Rico* (1995a).
- Goreau, T.J. and R.L. Hayes, *Coral reef bleaching in the South Central Pacific during 1994*, p. 201, Global Coral Reef Alliance, New York (1995b).
- Goreau, T.J., R.L. Hayes and A.E. Strong, Tracking South Pacific coral reef bleaching by satellite and field observations, *Proc. 8th Int. Coral Reef Symp.*, **2**, 1491-1494 (1997).

- Goreau, T.J., T. McClanahan, R. Hayes and A. E. Strong, Conservation of coral reefs after the 1998 global bleaching event, *Conservation Biology*, **14**, 5-15 (2000).
- Goreau, T.J. and R.L. Hayes, Monitoring and calibrating sea surface temperature anomalies with satellite and in-situ data to study the effects of weather extremes and climate changes on coral reefs, *World Res. Review* (this volume) (2005).
- Hansen, J., I. Fung, A. Lacis, D. Rind, S. Lebedeff, R. Ruedy and G. Russell, Global climate changes as forecast by Goddard Institute of Space Studies three dimensional model, *J. Geophys. Res.*, **93**, 9341-9346 (1988).
- Hayes, R.L. and T.J. Goreau, The tropical coral reef ecosystem as a harbinger of global warming, *World Res. Rev.*, **3**(3), 306-322 (1991).
- Hayes, R.L. and P. Bush, Microscopic observations of recovery in the reef building scleractinian coral, *Montastrea annularis*, after bleaching on a Cayman reef., *Coral Reefs*, **5**, 201-204 (1990).
- Hodgson, G., *A global assessment of human effects on coral reefs*, Mar. Poll. Bull. 38: 345-355 (1999).
- Hoegh-Guldberg, O., Coral bleaching, climate change and the future of the world's coral reefs, *Mar. Fresh. Res.*, **50**, 839-866 (1999).
- Hoegh-Guldberg, O and R. Jones, Diurnal patterns of photo-inhibition and photoprotection in reef-building corals, *Mar. Ecol. Prog. Ser.*, **183**, 73-86 (1999).
- Hoegh-Guldberg, O. and G.J. Smith, Light, salinity, and temperature and the population density, metabolism, and export of zooxanthellae from *Stylophora pistillata* and *Seriatopora hystrix*, *J. Exp. Mar. Biol. Ecol.*, **129**, 279-303 (1989).
- Huppert, A., and L. Stone, Chaos in the Pacific's coral bleaching cycle, *Am. Nat.*, **152**, 447-459 (1998).
- Iglesias-Prieto, R., Temperature-dependent inactivation of photosystem II in symbiotic dinoflagellates, *Proc. 8th Int. Coral Reef Symp.*, **2**, 1313-1318 (1997).
- Iglesias-Prieto, R. and R.K. Trench, Photoadaptation, photoacclimation and niche diversification in invertebrate-dinoflagellate symbiosis, *Proc. 8th Int. Coral Reef Symp.*, **2**, 1319-1324 (1997).
- Iglesias-Prieto, R., J. Matta, W. Robins and R.K. Trench, The photosynthetic response to elevated temperature I: the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture, *Proc. Nat. Acad. Sci. USA* **89**, 10302-10305 (1993).
- Jaap, W., Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys, *Bull. Mar. Sci.*, **29**, 414-422 (1979).
- Jaap, W., P. Dustan, J. W. Porter and J.L. Wheaton, Florida Keys National Marine Sanctuary water quality protection plan: Coral reef and hard bottom monitoring project annual report, p. 9, *US EPA*, Atlanta, GA. (1999).
- Jokiel, P. and S. Coles, Effect of temperature on the mortality and growth of Hawaiian reef corals., *Mar. Biol.*, **43**, 201-208 (1977).
- Jokiel, P. and S. L. Coles Response of Hawaiian and other Indo-Pacific corals to elevated temperatures, *Coral Reefs*, **8**, 155-162 (1990).
- Jones, R., O. Hoegh-Guldberg, A.W.L. Larkum and U. Schreiber, Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae, *Plant Cell*

- Envir.*, **21**, 1219-1230 (1998).
- Mayor, A.C., Toxic effects due to high temperature, Carnegie Institute of Washington Papers in *Marine Biology*, **12**, 175-178 (1918).
- McPhaden, M.J., Genesis and evolution of the 1997-1998 El Nino, *Science*, **283**, 950-954 (1998).
- Porter, J.W. and O. Meier, Quantification of loss and change in Floridian reef coral populations. *Amer. Zool.*, **23**, 625-640 (1992).
- Reynolds, R.W. and T.M. Smith, Improved global sea surface temperature analysis using optimum interpolation, *J. Climate*, **7**, 929-948 (1994).
- Saji, N.H., B.N. Goswami, P.N. Vinayachandran and T. Yamagata, A dipole mode in the tropical Indian Ocean, *Nature*, **401**, 360-363 (1999).
- Strong, A.E., C.B. Barrientos, C. Duda and J. Sapper, Improved satellite techniques for monitoring coral reef bleaching, *Proc. 8th Int. Coral Reef Symp.*, **2**, 1495-1498. (1998).
- Strong, A.E., First year's report on NOAA's new interactive "HotSpot" WebSite for coral reef bleaching, *In Proceedings ERIM 5th International Conference on Remote Sensing for Marine and Coastal Environments, October 5-7, 1998*, San Diego, CA (1998).
- Strong, A.E., E.J. Kearns and K. Gjovig, Sea surface temperature signals from satellites, an update, *Geophys. Res. Lett.*, **27**, 1667-1670 (2000).
- Strong, A.E., T.J. Goreau and R.L. Hayes, Ocean HotSpots and coral reef bleaching, January-July, 1998, *Reef Encounters*, **24**, 20-22 (1998).
- Szmant, A.M. and N.J. Gassman, The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*, *Coral Reefs*, **8**, 217-224 (1990).
- Takayabu, Y.N., T. Iguchi, M. Kachi, A. Shibata and H. Kanzawa, Abrupt termination of the 1997-98 El Niño in response to a Madden-Julian oscillation, *Nature*, **402**, 279-282 (1999).
- Timmerman, A., J. Oberhuber, A. Bachner, M. Esch, M. Latif and E. Roeckner, Increased El Niño frequency in a climate model forced by future greenhouse warming, *Nature*, **398**, 694-696 (1999).
- Trenberth, K., TOGA and atmospheric processes, pp.117-125, *in Understanding Climate Change*, A. Berger, R.E. Dickinson and J.W. Kidson (eds.), *Amer. Geophys. Union*, Washington DC (1989).
- Warner, M.E., W.K. Fitt and G.W. Schmidt, The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral, *Plant Cell Envir.*, **19**, 291-299 (1996).
- Warner, M.E., W.K. Fitt and G.W. Schmidt, Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching, *Proc. Nat. Acad. Sci., USA* **96**, 8007-8012 (1999).
- Webster, P.J., A.M. Moore, J.P. Loschnigg and R.R. Leben Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997-1998, *Nature*, **401**, 356-360 (1999).
- Wilkinson, C., O. Linden, H. Cesar, G. Hodgson, J. Rubens and A. Strong, Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change?, *AMBIO* **28**, 188-196 (1999).

Wilkinson, C.O., *The status of the coral reefs of the world: 1998*, Australian Institute of Marine Sciences: Global Coral Reef Monitoring Network, Townsville, Australia (1998).

Williams, E.H. and L. Bunkley-Williams, The worldwide coral bleaching cycle and related sources of coral mortality, *Atoll Res. Bull.*, **335**, 1-71 (1990).

Williams, E.H., P.J. Bartels and L. Bunkley-Williams, Predicted disappearance of coral reef ramparts: a direct result of major ecological disturbances, *Global Change Biology*, **5**, 839-845 (1999).

Yonge, C.M. and A.G Nicholls, Studies on the physiology of corals, *Great Barrier Reef Expedition Scientific Papers*, 135-211 (1931).

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