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Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii

PAUL L. JOKIEL and ERIC K. BROWN
Hawaii Coral Reef Assessment and Monitoring Program (CRAMP), Hawaii Institute of Marine Biology, PO Box 1346, Kaneohe, HI 96744, USA

Abstract

Hawaiian waters show a trend of increasing temperature over the past several decades that are consistent with observations in other coral reef areas of the world. The first documented large-scale coral bleaching occurred in the Hawaii region during late summer of 1996, with a second in 2002. The bleaching events in Hawaii were triggered by a prolonged regional positive oceanic sea surface temperature (SST) anomaly greater than 1 °C that developed offshore during the time of annual summer temperature maximum. High solar energy input and low winds further elevated inshore water temperature by 1–2 °C in reef areas with restricted water circulation (bays, reef flats and lagoons) and in areas where mesoscale eddies often retain water masses close to shore for prolonged periods of time. Data and observations taken during these events illustrate problems in predicting the phenomena of large-scale bleaching. Forecasts and hind-casts of these events are based largely on offshore oceanic SST records, which are only a first approximation of inshore reef conditions. The observed oceanic warming trend is the ultimate cause of the increase in the frequency and severity of bleaching events. However, coral reefs occur in shallow inshore areas where conditions are influenced by winds, orographic cloud cover, complex bathymetry, waves and inshore currents. These factors alter local temperature, irradiance, water motion and other physical and biological variables known to influence bleaching.

Keywords: coral bleaching, global warming, Hawaii, sea surface temperature

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Introduction

Coral bleaching can occur when elevated temperature and high solar radiation cause the degeneration and expulsion of symbiotic algae known as zooxanthellae from the coral host. As a result, the white skeleton becomes visible through the transparent coral tissue giving the organism a 'bleached' white appearance. In severe cases, high mortality occurs among the bleached corals (e.g. Wilkinson *et al*., 1999). The zooxanthellae supply their coral hosts with photosynthetic products vital to meeting host energetic requirements (Falkowski *et al*., 1984). Bleached reef corals cannot survive very long unless conditions change and the symbiosis is reestablished. Since the 1980s, regional bleaching events have occurred on coral reef areas throughout the world with increasing frequency and increasing geographic extent. These large-scale bleaching events correlate with elevated sea surface temperatures (SSTs). The increase in SST is generally believed to be the result of climate change because of anthropomorphic release of carbon dioxide and other gasses (reviewed by Jokiel & Coles; 1990; Williams & Bunkley-Williams; 1990; Goreau, 1992; Glynn, 1993; Pittock, 1999; Fitt *et al*., 2001; Coles & Brown 2003; Jokiel 2004).

Coral bleaching is a highly subjective term used to describe a variety of conditions pertaining to low symbiont densities (reviewed by Fitt *et al*., 2001; Jokiel, 2004). Bleaching can be caused by changes in a wide range of environmental variables acting alone or in combination. These include increased SST (Jokiel & Coles, 1990), low temperature (Gates *et al*., 1992), increased irradiance (Lesser *et al*., 1990), decreased

Correspondence: Paul L. Jokiel, fax +808 236 7443,
e-mail: jokiel@hawaii.edu

irradiance (Franzisket, 1970), altered spectral quality in the visible range (Kinzie *et al*., 1984), altered spectral quality in the ultraviolet radiation (UVR) range (Gleason & Wellington, 1993), low salinity (Coles & Jokiel, 1978), sedimentation (Meehan & Ostrander, 1997; Philipp & Fabricius, 2003), infectious disease (Ben-Haim & Rosenberg, 2002), exposure at low tide (Vaughan, 1914), oil contamination (Guzman *et al*., 1991) and exposure to toxic materials (Jones, 1997). The current study is focused on the large-scale bleaching events associated with abnormally high-temperature and high irradiance regimes.

The first extensive work on thermal bleaching of corals was conducted in Hawaii (Jokiel & Coles, 1974, 1977; Coles *et al*., 1976). The global dimension did not emerge until the 1980s (Glynn, 1991) with increasing frequency and severity of large-scale bleaching events over the following decade (Hoegh-Guldberg, 1999; Wilkinson *et al*., 1999; Wilkinson, 2000).

High irradiance, as well as high temperature, is a major factor influencing bleaching (Jokiel & Coles, 1977; Coles & Jokiel, 1978; Hoegh-Guldberg & Smith, 1989; Goenaga & Canals, 1990; Fitt & Warner, 1995; Brown *et al*., 1996). High-temperature anomalies in the Society Islands during 1998 did not result in a bleaching episode, apparently because high cloud cover reduced solar radiation (Mumby *et al*., 2001).

Until recently, the isolated subtropical location of Hawaii has been perceived as a haven from conditions that have ravaged coral reef communities in other areas of the world. The first large-scale bleaching event in the Hawaii region occurred during the late summer of 1996 and was monitored closely in Kaneohe Bay throughout the period of onset, bleaching and recovery. A second major bleaching event occurred in the Northwest Hawaiian Islands (NWHI) during the summer of 2002 (Brainard, 2002; Aeby *et al*., 2003).

This paper focuses on the factors controlling recent bleaching events in Hawaii in relation to previous information on coral temperature tolerance, historical temperature data and other bleaching accounts. These data provide a useful description of local and regional patterns of warming and bleaching, with implications for the future of Hawaiian reefs.

Methods

SST records based on satellite and other data at weekly intervals on a 1° latitude–longitude grid were obtained from the Integrated Global Ocean Services System (IGOSS) at the International Research Institute for Climate and Prediction web site. These data are produced at the US National Meteorological Center (NMC) using optimum interpolation (OI) analysis of SST fields blended from ship, buoy and bias-corrected satellite data. Where satellite data are used, they are adjusted for biases using the method of Reynolds (1988) and Reynolds & Marsico (1993). A description of the OI analysis can be found in Reynolds & Smith (1994). Reynolds (1993) gives examples of the effect of recent corrections. Four IGOSS–NMC data sets were analyzed for the time period from November 1981 to 2002. The data set for 28–29°N, 177–178°W is termed 'offshore Midway Island'. The data set for 23–24°N, 166–167°W is termed 'offshore French Frigate Shoals (FFS)'. The data set for 21–22°N, 157–158°W covers all waters offshore off east Oahu including areas of specific interest that will be termed 'offshore Koko Head' and 'offshore Kaneohe Bay'. The data set for 16–17°N, 169–170°W is termed 'offshore Johnston Atoll'. Weekly IGOSS–NMC temperature plots and temperature anomaly plots for the Hawaiian region (16–33°N, 150–180°W) were also analyzed.

Historical data from Kaneohe Bay, Midway Island and Johnston Atoll (US Department of Commerce 1970) were compared for latitudinal and seasonal differences in annual temperature range. Summaries of temperatures taken manually from 1944 to 1969 at Midway Island, from 1957 to 1969 in Kaneohe Bay and from 1947 to 1969 at Johnston Atoll are reported. IGOSS–NMC data for the Oahu region, Johnston Island, Midway Island, FFS and various areas of interest in Hawaii were also evaluated from a spatial as well as temporal perspective. Temperature trends were analyzed using linear regression using Statistica® 6.0 software.

A 47-year time series of twice weekly SST taken at Koko Head on Oahu, Hawaii was developed by the National Marine Fisheries Service (NMFS) from 1955 to 1992. The sampling site was located along the steep cliffs that extend into deep water at 21°17′N; 157°41′W. SST at this location is representative of offshore central Pacific surface waters because of deep-water exposure and strong onshore currents (Seckel & Yong, 1977). The IGOSS–NMC and the NMFS time series overlap between 1 November 1981 and 19 March 1992. An analysis of temperature records from the two sources during the overlap period determined the legitimacy of combining the NMFS and IGOSS–NMC data into a single record. First, the NMFS data points during the overlap period were averaged for weekly time intervals to produce a NMFS time series comparable with the weekly IGOSS–NMC data series (Fig. 1). A correlation plot of the NMFS vs. IGOSS–NMC temperature yielded an r-value of 0.92. Mean temperature during the overlap period was 0.19 °C higher for the IGOSS–NMC series, so this value was subtracted for the period 1992–2002. The correction was applied to the IGOSS–NMC data because we assumed that the direct thermometer readings of the NMFS data set were more

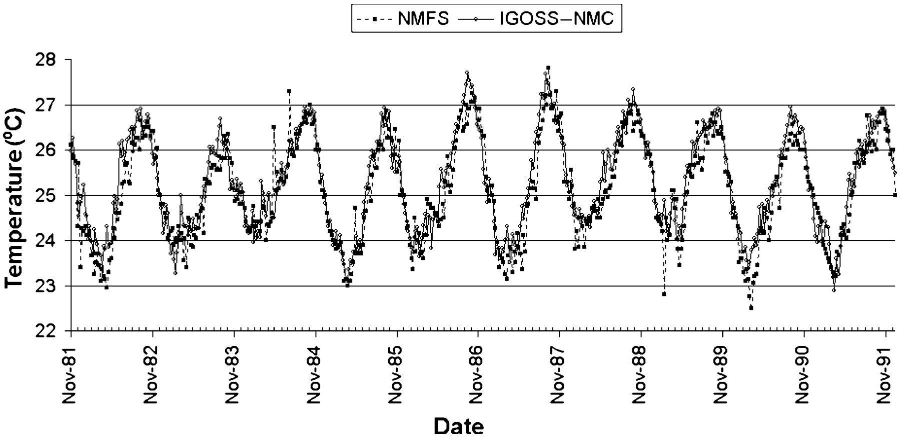

Fig. 1 Comparison of weekly averaged points for National Marine Fisheries Service (NMFS) temperature series taken at Koko Head, Oahu (21°17′N, 157°41′W) and weekly Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC) data series (21–22°N, 157–158°W) during the period of overlap.

accurate than the satellite data. The corrected IGOSS–NMC values from 1992 to 2002 were combined with the NMFS data series into a single time series.

Mean summer monthly temperature in the Hawaiian region is approximately 27 + 1 °C (Jokiel & Coles, 1977). A 30-day exposure to temperatures of only 29–30 °C (mean = 29.6 °C) will cause extensive bleaching in Hawaiian corals (Jokiel & Coles, 1990). Thus, for purposes of this study the mean of the warmest four consecutive weeks is an appropriate indicator of bleaching susceptibility. Mean temperature during the warmest four consecutive week period for offshore Midway Island (28–29°N 177–178°W), offshore Oahu (21–22°N, 157–158°W) and offshore Johnston Atoll (16–17°N, 169–170°W) were calculated for the years 1981–2002 using the IGOSS–NMC data sets.

Meteorological variables and ocean temperature were monitored throughout the bleaching event of 1996 with an automatic recording weather station located on Coconut Island reef at the Hawaii Institute of Marine Biology (HIMB) (Fig. 2). Data were taken continuously for wind speed, wind direction, rainfall, air temperature and SST. Solar input was monitored with an Eppley (295 nm to 385 nm) UV radiometer, a LiCor Brand 200SZ Pyranometer and a LiCor Brand Quantameter (both Li-Cor Inc., Lincoln, NE, USA), which measured photosynthetically active radiance (PAR) between 400 nm and 700 nm. SST was recorded using a thermister (Cole-Parmer Instrument Co., Vernon Hills, IL, USA) located at a depth of 1 m on the Coconut Island Reef slope in an area of high coral coverage. Relationships between these variables were tested by correlation analysis using Statistica® 6.0 software.

Broad scale surveys of corals throughout of Kaneohe Bay were made on a weekly basis. Quantitative coral

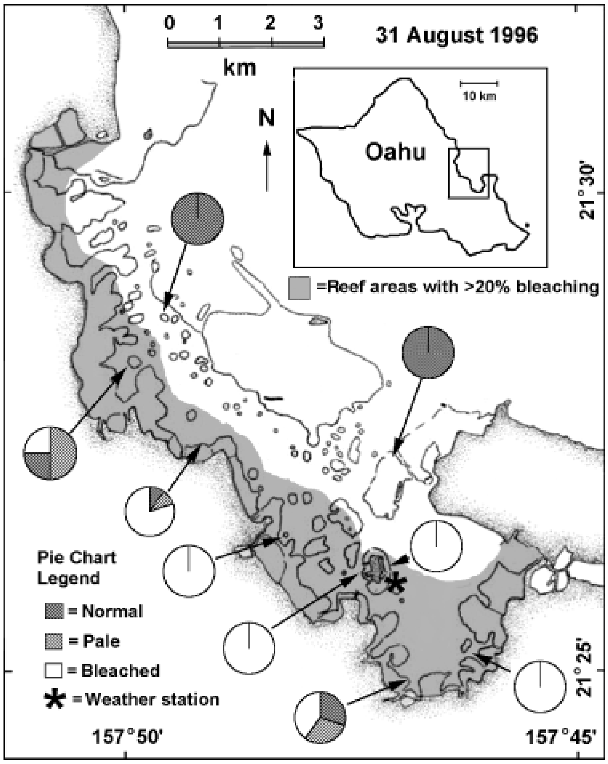

Fig. 2 Map of Kaneohe Bay and location of automatic weather station. Shaded area shows reef areas with a high proportion of bleached corals (>20%) on 31 August 1996. Pie charts show relative portions of bleached, pale and normal coral coverage on transects located throughout Kaneohe Bay at that time.

transects were made at various sites in the bay (Fig. 2) using a continuous belt transect method measuring 1 m wide by 25 m long. Percent coral coverage in each 1 m^2 quadrat was estimated visually along the 25 m length of the transect. Coral condition was classified visually as 'bleached' (pure white), 'pale' (obvious pigment loss but some color) and 'normal' using the same methodology and classification originally established by Jokiel & Coles (1974). Transects were located at a depth of 1 m along reef slopes with high (>90%) coral cover. Kaneohe Bay is dominated by the 'finger coral' *Porites compressa*, which accounts for over 90% of the coral coverage (Maragos, 1972). Bleaching observations were also compiled through personal communication with researchers working at other sites in Hawaii.

Forecasting and hind-casting

The Hadley Centre has compiled a global sea surface and sea ice record (HadISST) that reports mean monthly offshore SST within 1° latitude–longitude grid cells from 1870 to present (Rayner *et al*., 2003). SST bucket corrections have been applied from 1870 to 1941 (Rayner *et al*., 2003). Satellite observations as well as *in situ* temperature observations have been used to develop the SST data in recent decades. The usefulness of these data for the hind-casting of bleaching events was evaluated using the Hadley data for the Kaneohe Bay offshore area (21–22°N, 157–158°W). This grid cell encompasses eastern Oahu and the major sea-lanes of Hawaii and presumably contains adequate ship bucket temperature and buoy data for years preceding the availability of satellite data ca. 1981. The Hadley data were compared with the IGOSS–NMC data set from the same 1° grid cell, NMFS data from the Koko Head sampling location and biological/physical information on bleaching events in Kaneohe Bay.

Results

Decadal record of warming

The longest accurate temperature record available for Hawaiian waters is the NMFS–IGOSS–NMC Koko Head record shown in Fig. 3. The linear trend line fitted to these data (1956–1992) showed a significant positive slope ($F = 85.0$, df = 1,3176, $P < 0.001$). Likewise, the trend line for the combined series (1956–2002) indicated increasing mean temperature over time ($F = 85.6$, df = 1,3697, $P < 0.001$). Parameters for the trend lines are presented in Table 1.

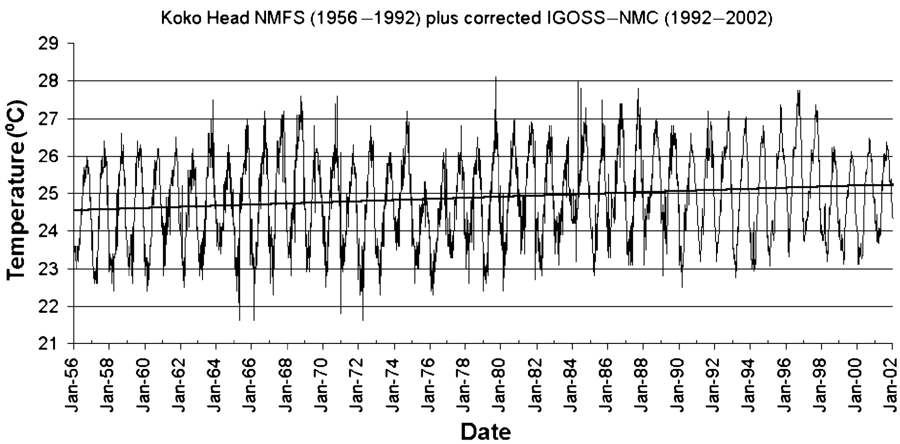

Fig. 3 Combined sea surface temperature (SST) record using National Marine Fisheries Service (NMFS) data for Koko Head, Oahu (1956–1992) and corrected Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC) temperature data (1992–2002). Parameters for the trend line are presented in Table 1.

Table 1 Parameters for linear trend lines shown in Figs 3 and 4

Location	Slope × 10^{-6}	Intercept	r^2	P	Yearly increase (°C)	Decadal increase (°C)
Offshore Midway 21 year record	166.25	17.6	0.0170	<0.00001	0.0607	0.607
Offshore FFS 21 year record	78.311	22.5	0.0138	<0.00010	0.0286	0.286
Koko Head Oahu 46 year record	40.659	23.7	0.0226	< 0.00000	0.0150	0.150
Offshore Oahu 21 year record	3.3411	25.1	0.0000	<0.82640	0.0012	0.012
Offshore Johnston 21-year record	0.4994	26.6	0.0000	<0.97050	0.0002	0.002

IGOSS–NMC temperature data for offshore Midway Island, offshore Oahu and offshore Johnston Atoll are shown in Fig. 4 for the time period 1981–2002. Parameters for the fitted trend lines for Midway, FFS, Kaneohe Bay and Johnston Atoll are presented in Table 1. The 1981–2002 record did not show increasing temperature at either offshore Oahu ($F = 0.05$, df = 1,1098, $P = 0.83$) or offshore Johnston Atoll ($F = 0.002$, df = 1,1098, $P = 0.97$). However, a significant increasing trend occurred at both offshore Midway ($F = 19.0$, df = 1,1098, $P < 0.001$) and offshore FFS ($F = 19.0$, df = 1,1098, $P < 0.001$) over the same time period. Adjusted r^2 values were small ($r_a^2 = 0.02$) for both Midway and FFS because of the seasonal fluctuations in temperature that were not explained by a simple linear relationship.

Comparison of 1944–1969 monthly mean SST, mean of maximum monthly SSTs for each year and their difference is shown in Table 2. These data are bucket temperatures from inshore reef areas and predate the period of major reported regional bleaching events, which began in the early 1980s. The mean annual temperature and winter temperature decreases substantially with increasing latitude, but the differences between mean monthly temperature and mean monthly maximum temperature (i.e. high-temperature variability) increase with latitude. Summer inshore temperature is similar over the full latitudinal range of reefs (16–28°N), even though there is a considerable difference in winter temperature.

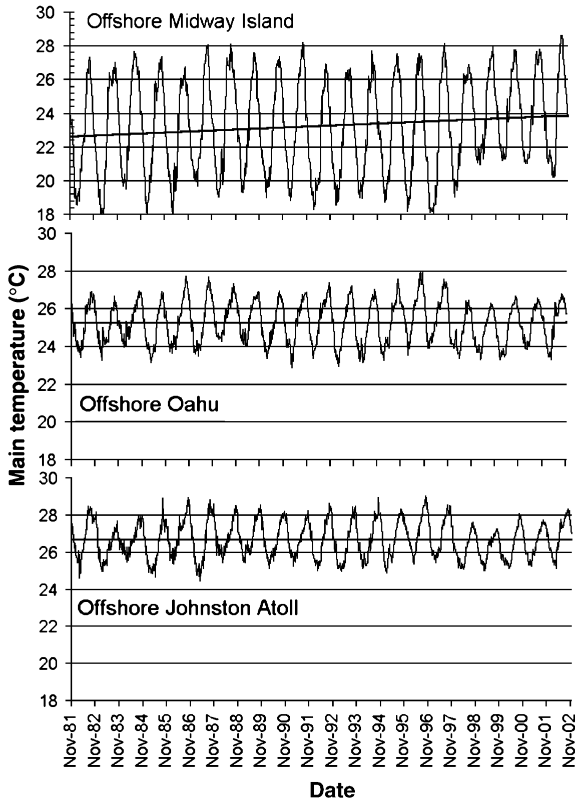

Fig. 4 Mean weekly ocean sea surface temperature (SST) (Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC data)) for offshore Midway Island (28–29°N 177–178°W), offshore Oahu (21–22°N, 157–158°W), offshore Johnston Atoll (16–17°N, 169–170°W). Data for offshore French Frigate Shoals (23–24°N, 166–167°W) is intermediate between Oahu and Midway temperatures and not shown to reduce complexity of the figure. Parameters for the trend lines are presented in Table 1.

IGOSS–NMC data were used to generate a plot of the warmest four consecutive weeks per year for each year from 1982 to 2002 for the offshore waters at each site (Fig. 5). This plot shows high variability of summer temperature at the high latitudes coupled with an increasing temperature trend. Temperatures at offshore Midway Island (28°N) routinely exceeded temperature at offshore Oahu (21°N) during this time interval and more recently exceeded the temperature at offshore Johnston Atoll (16°N). The result was the large-scale bleaching that occurred during 2002 in the NWHI (Brainard, 2002; Aeby *et al*., 2003).

Ocean temperature anomalies and bleaching events

The 1996 and the 2002 bleaching events in Hawaii were triggered by positive summer open ocean temperature anomalies exceeding 1 °C (Fig. 6). The 1996 event impacted the northern part of the Main Hawaiian Islands, while the majority of the NWHI showed no warming (top Fig. 6). In contrast, the 2002 showed positive anomalies in the northern part of the archipelago, with cool conditions in the Main Hawaiian Islands (bottom Fig. 6).

Chronology and extent of the 1996 bleaching event

Changes in the key environmental variables of temperature, solar energy, wind speed and bleaching response of corals at the Coconut Island (Oahu) monitoring site are shown in Fig. 7 for July–October 1996. Previous laboratory and field studies on Hawaii corals have shown that bleaching occurs with prolonged exposure to temperatures of 29–30 °C at high irradiance (summarized by Jokiel & Coles, 1990). Thus, prolonged temperatures exceeding 28 °C at high irradiance can be considered stressful with a bleaching threshold of 29–30 °C. Gradual warming occurred during July as solar input increased and wind speed diminished. By 21 August 1996 mean SST in Kaneohe Bay reached 28.5 °C and was increasing rapidly. Wind speed dropped to a low level. Solar irradiance was near

Table 2 Comparison of mean monthly temperature and mean monthly maximum temperature for Midway Island (28°13′N, 177°22′W), Kaneohe Bay (21°26′N, 157°48′W) and Johnston Atoll (16°45′N, 169°31′W)

	Midway Island			Kaneohe Bay			Johnston Atoll		
Month	Mean temperature (°C)	Mean maximum (°C)	Difference (°C)	Mean temperature (°C)	Mean maximum (°C)	Difference (°C)	Mean temperature (°C)	Mean maximum (°C)	Difference (°C)
Jan	19.7	21.2	1.5	22.8	23.7	0.9	25.2	26.1	0.9
Feb	19.6	20.8	1.2	22.8	24.2	1.4	24.8	25.7	0.9
Mar	20.2	21.9	1.7	23.3	24.7	1.4	24.8	25.6	0.8
Apr	20.9	22.9	2.0	24.0	25.4	1.4	25.3	26.2	0.9
May	22.6	24.5	1.9	25.2	26.4	1.2	25.9	26.9	1.0
Jun	25.1	26.7	1.6	26.4	27.3	0.9	26.7	27.4	0.7
Jul	26.4	27.4	1.0	26.4	27.3	0.9	27.2	28.1	0.9
Aug	26.9	28.1	1.2	26.8	27.7	0.9	27.5	28.3	0.8
Sep	26.9	28.3	1.4	26.7	27.7	1.0	27.6	28.4	0.8
Oct	25.2	26.8	1.6	26.3	27.3	1.0	27.4	28.3	0.9
Nov	23.2	24.8	1.6	24.9	26.3	1.4	26.8	27.7	0.9
Dec	21.3	23.1	1.8	23.2	24.4	1.2	25.9	26.7	0.8
Mean	23.2	24.7	1.5	24.9	26.0	1.1	26.3	27.1	0.9

Data from US Department of Commerce (1970).

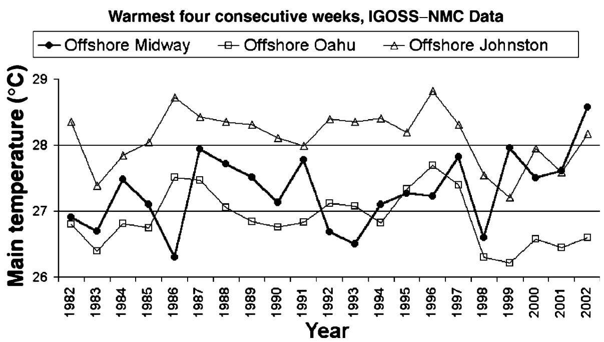

Fig. 5 Oceanic mean temperature for the warmest four consecutive week period (1982–2002) based on Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC) data for offshore Midway Island (28–29°N, 177–178°W), offshore Oahu (21–22°N, 157–158°W), offshore Johnston Atoll (16–17°N, 169–170°W).

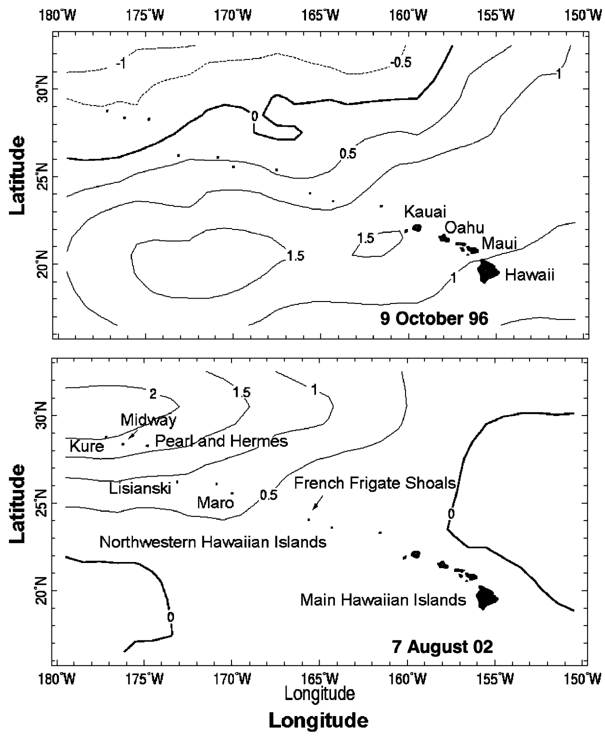

Fig. 6. Chart of the Hawaii region showing mean oceanic temperature anomalies (°C) for the week of 9 October 1996 (top) and 7 August 2002 (bottom).

its annual maximum with little cloud cover. Corals throughout the inner portion of Kaneohe Bay began to show signs of stress including contracted polyps, mucous secretion and some discoloration. Maximum mid-day temperature on the reef began to exceed 30 °C starting on 26 August 1996. By 31 August 1996 the daily mean SST exceeded 30 °C with mid-day maximum approaching 30.7 °C (not shown). By this time the bleaching process was conspicuously underway in corals throughout the inner portion of the bay (Fig. 2). Large tracts of corals throughout the inshore portion of Kaneohe Bay became highly bleached by 4 September. Areas with significant amounts of bleaching were confined to the inner portion of Kaneohe Bay (Fig. 2). The proportion of coral heads that bleached throughout the affected area varied from less than 5% in some areas

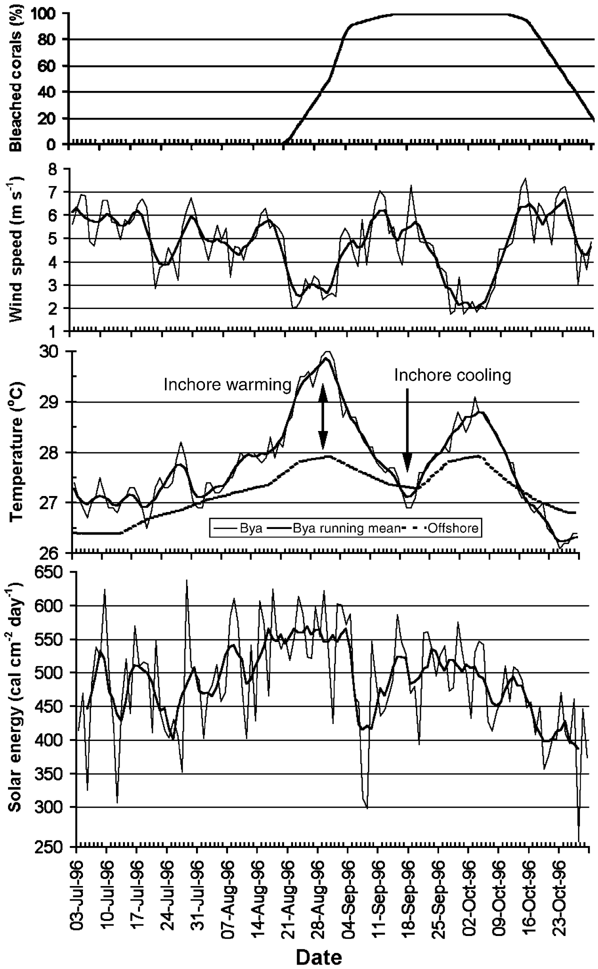

Fig. 7 Weekly mean oceanic sea surface temperature for Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC) data (21–22°N, 157–158°W), and daily mean Kaneohe Bay temperature, total solar radiation, and daily mean wind velocity measured at Coconut Island Reef (21°26′21″N, 157°47′21″W). The dark line is a 5-day running average centered on each value. Top panel shows percentage bleached corals on Coconut Island reef in area where water temperature was recorded.

to 100% over large sections of reef. The percent of bleached corals diminished near stream discharge points or other areas where turbidity was high. Bleaching decreased with depth, especially in localized areas of high turbidity. The period of highest thermal stress (inshore SST in excess of 28 °C) occurred between 14 August and 5 September (22 days). During this time period, the mean daily temperature remained in the 29–30 °C range. The corals became progressively more bleached throughout September even though temperature was declining, but remained above 28 °C. Maximum bleaching occurred from 2 to 4 weeks after the peak of highest temperature (or 3–5 weeks after SSTs rose above 28 °C). A second less severe warming episode developed in early October, but peak temperature remained below 29 °C (Fig. 7) and did not appear to further increase the extent of bleaching, but rather prolonged the event. By mid-October, temperatures diminished to within the normal range and recovery of bleached corals was underway. Corals that were only slightly bleached ('pale' condition defined by Jokiel & Coles (1974) were the first to regain pigmentation. The remaining zooxanthellae in the lower shaded portions of bleached colonies of bleached corals began to rapidly re-infect the upper surface bleached areas. This process of re-infection and spread of zooxanthellae in Hawaiian corals was previously described for Hawaiian *P. compressa* that had been bleached by being held in darkness (Franzisket, 1970). Most of the colonies throughout the bay had recovered by mid November. A few coral colonies persisted in a highly bleached state until late November, but regained full pigment by the end of December 1996. Different species of corals showed different sensitivity to bleaching with variation between individual colonies of the same species. Species showing highest resistance to bleaching included *P. evermanni*, *Cyphastrea ocellina*, *Fungia scutaria*, and *P. brighami*. Moderate resistance was observed in *P. compressa*, *P. lobata*, *Montipora patula* and *M. capitata*. Species with low resistance to bleaching included *M. flabellata*, *Pocillopora meandrina*, *Pocillopora damicornis* and *M. dilitata*.

Overall coral mortality during the event was less than 2%. Mortality was largely confined to the most sensitive species and to those colonies that became highly bleached early in the bleaching event. Rate of recovery was related to bleaching sensitivity. The first corals to bleach were the last to recover.

Bathen (1968) has described the heat budget of Kaneohe Bay relative to the open ocean. The total heat exchange at the surface of the Bay (Q_T) is equal to the total incoming radiation (Q_I) minus the energy loss because of back radiation (Q_B), evaporation (Q_E) and sensible heat transfer (Q_S). Q_I is highest during the summer months, during periods of low cloud cover, while Q_B, Q_E and Q_S are influenced mainly by wind velocity (see equations in Bathen, 1968). In other words, periods of clear sky and low wind velocity during the summer months led to rapidly increasing water temperature in the bay. During the summer months the bay and the surrounding ocean show a net gain of heat because of solar input, but the temperature of the bay rises more rapidly because of the shallowness (<10 m) of the water mass. Consequently, the temperature of Kaneohe Bay typically runs between 1 and 2 °C warmer than the adjacent open ocean during the summer months. High offshore temperature, high solar input and lack of wind resulted in abnormally high temperatures in Kaneohe Bay during the summer of 1996 (Fig. 7). Note also that the Kaneohe Bay temperature record during the bleaching event of 1996 (Fig. 7) is essentially a mirror image of the wind speed. Temperature rises as wind speed falls and temperature declines as wind speed increases because of evaporative cooling and sensible heat transfer.

Solar energy was highly correlated with PAR ($r = 0.97$) and UV ($r = 0.97$). PAR was highly correlated with UV ($r = 0.91$). Therefore, all three of these variables can be considered to be interchangeable in the analysis (Clarke & Gorley, 2001). Thermal properties of water result in temperature lags that follow solar input and wind speed (Fig. 7), while solar input and wind speed work against each other in producing temperature change. Other complex factors such as tide and currents modify local water temperature. Nevertheless, there is a significant negative correlation between wind and temperature and a significant positive relationship between solar energy and temperature (Table 3). Precipitation is related to cloud cover and showed a negative correlation with solar energy.

The island of Oahu showed the most severe impact with less bleaching reported on the islands of Maui and Hawaii. The lagoon of Johnston Atoll to the southwest of Hawaii was also severely impacted (Cohen *et al.*, 1997). On the island of Oahu, corals on reef flats of Kailua Bay suffered the same pattern of bleaching as observed in Kaneohe Bay, with substantially higher mortality (C. Hunter, personal communication). Bleaching of *Montipora* spp. was observed to depths of 5 m at Hanauma Bay, with little or no mortality (J. Kuwabara, personal communication). Corals at Kahe Point along the open coastline on the west shore of Oahu showed minor bleaching with no mortality (S. Coles, personal communication).

On the island of Maui, weekly temperatures on coral reefs at eight locations on the SW coastline of Maui showed a range of 28.0–28.5 °C in late August and early September (E. Brown, unpublished data). Peak temperatures of near 29 °C occurred at some inshore sites near the end of August. The corals *P. compressa* and *M. capitata* began to bleach at Olowalu, Maui in late August. Extent and severity of bleaching was minor, with less than 10% of the corals being affected. The IGOSS–NMC offshore mean temperature from mid-August to mid-September for this area was 27.6 °C, or approximately 1 °C less than inshore temperature. The additional degree of inshore warming observed along the leeward coast of Maui can be attributed to restricted circulation along the shoreline or to mesoscale eddies (Patzert, 1969) that retain and entrap water in the lee of the island as discussed by Jokiel & Coles (1990). Solar irradiance is very high under the clear skies in the lee of the larger main Hawaiian Islands that block the NE Trade Winds.

Fishing charter boats on the west side of Hawaii reported surface water temperature off west Hawaii that exceeded 29 °C during late August and early September (P. Hendricks, personal communication). Monthly water temperatures taken at four sites off Kawaihae in west Hawaii showed temperatures of approximately 27.5 °C in June and July increasing to 28.5–29 °C in mid-August 1996. By September the temperature reached 29.0–29.8 °C with little or no vertical stratification on the reefs (Dollar, 1996). *Pocillopora meandrina* and *Montipora* spp. occurring in shallow water became highly bleached in the Kawaihae area (P. L. Jokiel monthly observations). The IGOSS–NMC temperature from mid-August to mid-September in this region is 27.4 °C, which is 1–2 °C less than inshore temperature. As in the case of Maui, the higher values in the lee of the island can be attributed to retention of water in mesoscale eddies that retain water for prolonged periods under conditions of high irradiance and low wind.

Johnston Atoll lagoon experienced massive bleaching during 1996 (Cohen *et al.*, 1997). This atoll is the tropical end-member of the Hawaii faunal province with a coral species list is similar to that of Hawaii (Maragos & Jokiel, 1986; Jokiel & Tyler, 1992). Observers were not

Table 3 Correlation analysis displaying Pearson' product-moment correlation coefficients for each of the variables

	Temperature	Wind	Precipitation	Energy	PAR	UV
Temperature	1.00					
Wind	**−0.55**	1.00				
Precipitation	**0.22**	−0.10	1.00			
Energy	**0.41**	**−0.20**	**−0.20**	1.00		
PAR	**0.40**	**−0.25**	**−0.25**	**0.97**	1.00	
UV	**0.38**	−0.14	−0.18	**0.97**	**0.91**	1.00

r-Values in bold indicated a significant relationship.
PAR, photosynthetically active radiance; UV, ultraviolet.

present on Johnston Atoll during the onset of bleaching. The first observations were made on 10 September 1996 (Cohen *et al*., 1997). Recording thermographs showed a maximum temperature slightly exceeding 30 °C on 25 August 1996, which is approximately the same maximum observed in Kaneohe Bay. All *Montipora* spp. and *Pocillopora* spp. were affected. Bleaching was not observed in *Acropora cytheria*, the dominant coral species at Johnston Atoll. During the summer months, lagoon temperatures at Johnston Atoll are warmer than the open ocean by 0.5–1.0 °C (P. L. Jokiel, unpublished data). The IGOSS–NMC record showed prolonged oceanic SST of 28.5–29.0 °C from August to September of 1996. These oceanic temperatures translate into lagoon temperatures between 29 °C and 30 °C, or approximately the same temperature range that produced large-scale bleaching in Kaneohe Bay.

Chronology and extent of the 2002 bleaching event

The NWHI is a remote area. Observers were not present during the time when the corals bleached. During July 2002 AE Strong of the National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data and Information Service (NESDIS) issued a 'bleaching alert' for the northern portion of the Hawaiian Archipelago, which was showing a positive temperature anomaly exceeding 1 °C (Strong *et al*., 1997; Liu *et al*., 2003). By early August 2002, the positive temperature anomaly at the northwest portion of the archipelago exceeded 2 °C (Fig. 6, bottom), with offshore oceanic temperature exceeding 28 °C. Satellite data show that offshore temperature anomalies exceeding + 1 °C continued in the area until early September 2002. During September of 2002, a research team visited the NWHI on the NOAA vessel Townsend Cromwell (Brainard, 2002; Aeby *et al*., 2003). Substantial bleaching had occurred on reefs at the three northwestern-most atolls of the Hawaiian Archipelago: Kure, Midway and Pearl and Hermes. There was less bleaching on Lisianski and Maro. The extent of bleaching ranged from 20% to 100%. Buoys recorded *in situ* temperature offshore of Pearl and Hermes Atoll above 27 °C on 18 July 2002 and over 29 °C on 3 August. The buoy offshore of Midway recorded temperatures above 28 °C for the entire month of August, with occasional increases to 29.5 °C (Brainard, 2002). The shallow inshore areas of these atolls normally experience a temperature of approximately 1 °C higher than the open ocean (P. L. Jokiel, unpublished data), so the bleaching threshold (29.0–30.5 °C) in the NWHI is similar to the bleaching thresholds observed in Kaneohe Bay and Johnston Atoll. As in the case of the 1996 bleaching event in Kaneohe Bay, mortality was low and pigment had recovered in all but the most sensitive species by December 2002 (G. Aeby, personal communication). Wave energy is important in flushing of shallow areas in the NWHI. Significant wave height in the NWHI (WAVE model data as reported by the Naval Oceanographic Office) was very low during the bleaching event (significant wave height of 1–2 m from SE from July to late October). The pattern shifted to NW swell and increased in height to 3–4 m during November and December 2002 as the temperature decreased.

Hind-casting using the HadISST data set

Mean monthly offshore oceanic temperature at 21–22°N, 157–158°W for the years 1968–1999 were derived from Hadley Centre data set (HadISST) as shown in Fig. 8. These data are from the same 1° latitude–longitude grid cell as used for the IGOSS–NMC data for comparison with NMFS Koko Head temperatures and for the Kaneohe Bay offshore temperature comparison. The 1996 value (i.e. offshore maximum of 27.4 °C, with 1 month exceeding 27.0 °C) is known to have caused extensive bleaching and is logically considered to be the hind-cast threshold for bleaching conditions in Kaneohe Bay. Given these assumptions, the hind-cast data (Fig. 8) indicate that severe bleaching should have occurred during 1968 (maximum 28.0 °C, with 4 months exceeding 27.0 °C) and 1974 (27.8 °C, with 3 months exceeding 27.0 °C). However, we can state with confidence that large-scale bleaching absolutely did not occur during the years 1968 and 1974. Extensive

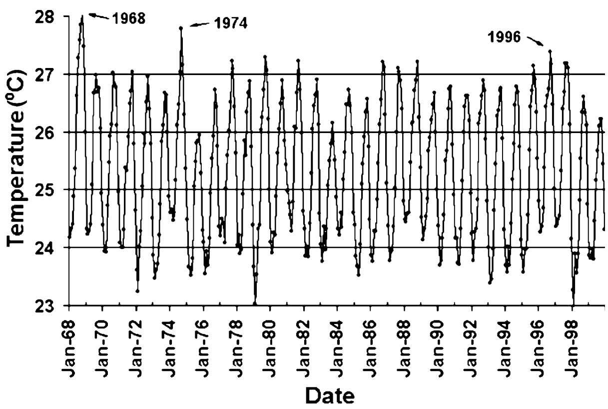

Fig. 8 Mean monthly offshore oceanic temperature at 21–22°N, 157–158°W (Oahu, same grid cell used for comparison of National Marine Fisheries Service (NMFS) Koko Head data and Integrated Global Ocean Services System–National Meteorological Center (IGOSS–NMC data) for years 1968–1999 derived from Hadley Center data set 'HadISST'. This data set is a hind-cast of open ocean SST off Kaneohe Bay, Oahu. Wide-scale bleaching occurred in Kaneohe Bay during 1996, but not in 1968 or 1974.

scientific observations were being made in Kaneohe Bay during that time by a number of scientists operating from HIMB at Coconut Island, which is located in Kaneohe Bay. Throughout 1968, Jim Maragos conducted surveys of the entire bay on a continuous basis as part of his PhD dissertation (Maragos, 1972). He emphatically states that no bleaching occurred (J. Maragos, personal communication 27 June 2003). Major studies involving ecological field surveys throughout the Bay also occurred during 1968 (Smith *et al*., 1973) with no reports of bleached corals. Likewise Franzisket (1970) conducted work in Kaneohe Bay during that time, holding corals in darkness to rid them of algae and studying their subsequent regeneration. He certainly would have noticed any corals in the field that had lost their pigmentation as part of his study. Johannes (1973) also was very active in the summer of 1998 and conducted field surveys in Kaneohe Bay during this time and would have noticed a bleaching event. Likewise, there were no other reports of coral bleaching from Oahu or any of the Hawaiian Islands.

Paul Jokiel has worked continuously as a coral reef researcher at HIMB in Kaneohe Bay since 1968. Starting in the1970s, a series of studies of coral bleaching in response to temperature and irradiance were conducted in an experimental facility at HIMB located on Coconut Island in Kaneohe Bay (Jokiel & Coles, 1974, 1977; Coles & Jokiel, 1977, 1978). The bleached corals produced in these experiments were the first ever seen by other experienced coral reef biologists who worked at HIMB over preceding decades (V. Brock, S. J. Townsley, A. H. Banner, L. Zukeran, personal communication, ca. 1970). Classic experiments on thermal tolerance in reef corals (Coles *et al*., 1976) were being conducted in Kaneohe Bay during 1974. These skilled observers conducted the original work on thermal bleaching and certainly would have noticed a large-scale bleaching event if it had occurred that year as predicted by hind-casting. Thus, such hind-casting results on coral bleaching events must be viewed with great caution.

Discussion

Coral reefs of the Hawaiian region will be increasingly vulnerable to large-scale bleaching events if the observed trend of increasing ocean temperatures continues. There is widespread agreement that global warming because of the production of anthropogenic gasses and the 'greenhouse effect' is responsible for large-scale bleaching throughout the world (e.g. Hoegh-Guldberg, 1999; Pittock, 1999). However, the Pacific Interdecadal Oscillation (PDO) also influences SST off Hawaii (Mantua *et al*., 1997; Minobe, 1997). Twentieth century PDO fluctuations have been observed at two general periodicities, one from 15 to 25 years, and the other from 50 to 70 years (Minobe, 1997). Cool PDO regimes occurred from 1890 to 1924 and again from 1947 to 1976, while warm PDO regimes dominated the North Pacific from 1925 to 1946 and from 1977 through the present. Causes of the PDO are not known, so the relative contribution of the PDO and the greenhouse effect on bleaching of corals in Hawaii cannot be established.

The first bleaching events in Hawaii occurred during periods of offshore positive temperature anomalies of 1–2 °C in the summer months. Sites that bleached were all shallow areas with restricted circulation that showed additional temperature increases of 1–2 °C above offshore conditions. If regional SST continues to increase, these areas will become more severely impacted with likely increasing mortality while open coastal situations adjacent to deep oceanic water are likely be the last to be effected. Mean offshore temperature in Hawaii must reach the bleaching temperature of approximately 29–30 °C (a 2 °C increase over present summer offshore temperature during summer) before corals along open coastlines adjacent to deep water will be impacted. By that time, most species of corals in areas of restricted circulation (bays, lagoons, etc.) will probably have been largely eliminated by known lethal temperatures of 32 °C.

Several major factors were involved in Hawaii bleaching events observed to date. First, a temperature anomaly (as reported by IGOSS–NMC) that exceeded + 1 °C occurred for offshore waters during the period of maximum seasonal water temperature. The + 1 °C temperature anomaly was exceeded at both offshore Johnston Atoll, offshore Kaneohe Bay, offshore west Maui and offshore west Hawaii during the 1996 bleaching event. Anomalies ranging from + 1.6 to + 2.0 °C were recorded for 4 consecutive weeks in August 2002 in the offshore Midway Island area during the recent large-scale bleaching in that region. To date, the offshore warming in Hawaii has been insufficient in itself to bring water temperatures into the range of 29–30 °C required for bleaching. The second factor was a period of prolonged low cloud cover and low winds that produced further heating of shallow inshore surface waters. The third bleaching factor in the Hawaii region to date has been restricted water circulation (bays, lagoons, reef flats, back-reefs), resulting in retention of water and localized heating above the offshore values. Mesoscale eddies in the lee of large islands (Patzert, 1969) can also retain water masses under high irradiance and low wind stress and thereby increase temperature to the bleaching threshold (Jokiel & Coles, 1990). The importance of solar input and low wind speed in producing the high temperature required for bleaching in a restricted area of circulation (Kaneohe Bay) is shown in Fig. 7.

High SST is associated with high levels of incident total solar energy simply because high solar input causes temperature to rise. High surface incidence of total solar energy, PAR and UVR occurred in Kaneohe Bay during the 1996 bleaching event (Fig. 7), with all three factors being highly correlated. PAR and UVB are simply portions of the solar spectrum that are dependent variables on total solar radiation. PAR and UVR reaching the corals was further elevated because water transparency increased during the warming period. Water transparency in Kaneohe Bay shows a negative correlation with wind speed (Smith *et al*., 1981), because wind-induced water motion resuspends bottom sediments that in turn reduce light penetration. Decreased wind speed during the bleaching event (Fig. 7) led to higher water transparency. PAR and UVR are frequently implicated as factors that increase bleaching. High PAR in conjunction with heat stress reduces photosynthetic rate of the zooxanthellae (Coles & Jokiel, 1977, 1978; Lesser *et al*., 1990; Jones *et al*., 1998). UVR may also be a detrimental factor that aggravates bleaching in corals (Jokiel, 1980; Lesser *et al*., 1990; Gleason & Wellington 1993). Observations during the 1996 bleaching event show the importance of irradiance in accelerating bleaching. Areas of Kaneohe Bay near stream mouths where turbidity is high suffered little or no bleaching even though the corals experienced the same temperature as their bleached counterparts in clear water. Phongsuwan (1998) made similar observations in the Andaman Sea. Individual corals usually show more pronounced bleaching and mortality on upper surfaces and of the colony exposed to higher irradiance. Turbidity reduces penetration of PAR and UVR. Corals at shallow depths are exposed to higher irradiance and bleached more readily than those at greater depths at the same temperature. Also, upper surfaces bleached while under surfaces and shaded areas of the same colonies did not bleach. Similar observations have been made by Fisk & Done (1985), Oliver (1985), Lang *et al*. (1988), Wilkinson *et al*. (1999) and Marshall & Baird (2000). Conditions of very low rainfall existed in the Kaneohe Bay region during the bleaching, so lower salinity did not play a role in the event.

Intraspecific and interspecific variation in thermal tolerance followed the same pattern as reported previously (Jokiel & Coles, 1974). Some colonies remain well pigmented while adjacent colonies of the same species underwent complete bleaching (Fig. 2), which demonstrates some genetic plasticity in response to high temperature. Further increases in temperature led to bleaching of the remaining colonies. The most sensitive species in Kaneohe Bay is the rare species *M. dilitata*, which was the first to bleach. Few of this species survived the bleaching event. In general, *Montipora* spp. and *Pocillopora* spp. were most sensitive as shown previously by many studies (e.g. Jokiel & Coles, 1974; Cohen *et al*., 1997; Marshall & Baird, 2000). As the stress subsided, corals regained their pigment at rates dependent on the intensity and duration of the bleaching stress as noted by Hoegh-Guldberg (1999). Most of the Kaneohe Bay corals recovered. However, anticipated future increases in the intensity or duration of such events probably will lead to increasing rates of mortality.

Regional patterns in bleaching and bleaching tolerance

Laboratory and field experiments indicate that the upper lethal temperature and the bleaching threshold temperature of Hawaiian corals is approximately 2 °C less than for congeners from the tropical Pacific (Coles *et al*., 1976). Thermal thresholds for bleaching appear to vary across the globe with some evidence for decreased bleaching tolerance at high latitudes in some regions (Hoegh-Guldberg, 1999). There does not appear to be substantial differences in thermal tolerance within the Hawaiian region over the entire latitudinal range from Johnston Atoll (16.5°N) to Midway Island (28.5°N). Cohen *et al*. (1997) suggested that corals at Johnston Atoll might have a higher bleaching threshold than corals in the main Hawaiian Islands. This observation is not supported by analysis of thermograph data in their report, which is nearly identical to the pattern in the Kaneohe Bay record (Fig. 7). The Johnston Atoll record shows two peaks, the first with a maximum temperature of approximately 30 °C on 25 August 1996 and the second with a maximum of 29.5 °C on 14 September 1996. Brainard (2002) reports that temperatures of 29–30 °C for the 2002 bleaching event at Pearl and Hermes Atoll, Midway and Kure Atoll. The lack of genetic adaptation to high temperature over 12° of latitude is not surprising because of the fact that the summer maximum temperature (Fig. 4, Table 2) across entire region is the same (approximately 28 °C). There has been no selective pressure to produce different populations with different bleaching thresholds.

Bleaching and global climate change

The increase of approximately 0.7 °C over the course of the 46-year record from Hawaii (Fig. 3) translates into a 0.15 °C increase per decade. This value falls within the 0.07–0.5 °C increase per decade range measured on various coral reefs throughout the world (summarized by Fitt *et al*., 2001). The 46-year record is the longest series of precise SST measurements available for Hawaii, but still falls short of being a true long-term record. The PDO has a periodicity of 20–30 years or more, so the 46-year record is insufficient to determine if PDO is exerting an influence on Hawaiian SST. The 21-year NOAA/NESDIS data set is not long enough by itself to detect the longer-term trend shown in the 46-year record. As can be seen in Fig. 4, the 21-year SST data series shows trends that are only significantly positive at Midway, whereas Oahu and Johnston Atoll are flat. Much longer-term data sets will be required to answer many of the questions raised by this analysis.

Pittock (1999) compared latitudinal variation in temperature for simulated global warming using 10 different global climate change models. All 10 models predict higher rates of warming with increasing latitude in the Northern Hemisphere. The observed higher rate of temperature increase at high latitudes in Hawaii (Fig. 5) is consistent with the model results.

Increased SST and large-scale bleaching events on regional and global scales have been linked to recent major El Niño events (Glynn, 1993; Wilkinson *et al.*, 1999; Wilkinson, 2000). El Niño has increased in frequency and intensity over the last two decades. Severe and extensive bleaching events throughout the tropics occurred in 1997–1998 (Wilkinson, 2000) during one of the most intense El Niño yet recorded in the modern record. Hawaii escaped the initial bleaching impact of this El Niño. In fact, summer temperature at Oahu and Johnston Atoll decreased during 1997–1998, but SST has been increasing since that time (Fig. 4). Winter temperature at Midway Island increased substantially during the 1997–1998 El Niño, but has been decreasing since then. Mean temperature for the warmest month at Midway has dramatically increased since 1998 (Fig. 4) and finally surpassed the warmest month temperature at Johnston Island in 2002 (Fig. 5). The 1997–1998 El Niño did not cause large-scale bleaching in Hawaii as it did throughout much of the world. However, major changes in SST patterns in the Hawaiian region did occur. Perhaps the changes that occurred during the 1997–1998 El Niño caused the bleaching in the NWHI during 2002. An alternate explanation is that the change noted at Midway is related to the POD and not to El Niño or global warming.

Forecasting and hind-casting of bleaching events

Coles *et al.* (1976) concluded that corals throughout the world are living within 1–2 °C of their upper limit during the summer months in both tropical and subtropical environments. This observation has proven to hold predictive value and subsequently has been substantiated by numerous other studies (Table 4). The 1–2 °C threshold has been observed universally at sites where adequate temperature records are available. The relationship holds, even though maximum seasonal temperature varies by 9 °C or more over the geographic

Table 4 Estimated bleaching thresholds in relation to mean summer maximum sea surface temperature (SST) at various geographic locations

Location	Mean summer maximum (°C)	Bleaching threshold (°C)	Increase above summer maximum (°C)	Reference
Easter Island	25.0	27.0	2.0	Wellington *et al.* (2001)
Sodwana Bay, South Africa	26.5–27.0	27.5–28.8	1.0–1.8	Celliers & Schleyer (2002)
Hawaii	27.0–28.0	29.0–30.0	1.0–2.0	Jokiel & Coles (1990)
Gulf of Panama	28.0	–	–	Glynn (1977)
Gulf of Panama	–	30.0	2.0	Glynn & D'Croz (1990)
Gulf of Chiriqui	28.0	–	–	Glynn (1977)
Gulf of Chiriqui	–	30.0	2.0	Glynn & D'Croz (1990)
Bermuda	28.0	30.0	2.0	Cook *et al.* (1990)
Tahiti	28.2	29.5	1.3	Brown (1997)
Johnston Atoll	28.4	–	–	US Dept Commerce (1970)
Johnston Atoll	–	30.0	1.6	Cohen *et al.* (1997)
Puerto Rico	29.0	30.0	1.0	Goenaga & Canals (1990)
Enewetak	29.0–30.0	31.0–32.0	1.0–2.0	Coles *et al.* (1976)
Lizard Island, Australia	29.0	30.0	1.0	Hoegh-Guldberg & Smith (1989)
Papua, New Guinea	29.0	30.3	1.3	Davies *et al.* (1997)
Phuket, Thailand	29.5	30.1	0.7	Brown *et al.* (1996)
Belize	29.5	30.0–30.5	1.0–1.5	Aronson *et al.* (2000)
Palau	29.7–30.0	31.0	1.0–1.3	Bruno *et al.* (2001)
Maldives	30.3	31.4	1.1	Edwards *et al.* (2001)
Arabian Gulf	34.0	–	–	Coles (1988)
Arabian Gulf	–	35.0–36.0	1.0–2.0	Wilkinson *et al.* (1999)

range of these corals. Goreau & Hayes (1994) determined that bleaching episodes between 1983 and 1991 were preceded by positive oceanic SST anomalies of $+1\,^{\circ}$C during the warm season and designated these as ocean 'hot spots'. Their analysis methodology involved hind-casting using satellite-derived SST and direct temperature measurements where available. Thus, 'Bleaching Hot Spot Alerts' (early warnings of reefs likely to suffer from large-scale bleaching) have been automated by NOAA/NESDIS. These alerts are now issued on their web site for areas showing positive oceanic SST anomalies that exceed mean maximum summer SST by $1\,^{\circ}$C (Strong *et al*., 1997; Liu *et al*., 2003).

The satellite-based records frequently are the only comprehensive SST data available and are therefore used in the retrospective analysis of cause (e.g. Goreau & Hayes, 1994; Strong *et al*., 1997). Inshore conditions of temperature on shallow coral reefs can depart substantially from offshore oceanic temperature. Bays, estuaries and lagoons show marked departures from ocean temperature. Inshore conditions can differ markedly from offshore conditions in many other respects that influence bleaching. Increased cloud cover and higher turbidity in proximity to landmasses can reduce irradiance. Landmass and inshore bathymetry influence wave action, inshore currents and wind conditions in the near-shore reef environments. Hind-casting using presatellite broad-scale data sets from offshore sources might be appropriate for establishing regional and global trends in wide-scale bleaching, but lacks the data density and fine-scale accuracy needed to detect the short-term warming events associated with bleaching events such as those observed in Hawaii (Fig. 8).

Observations of decadal-scale water temperature increase in Hawaiian waters led Jokiel & Coles (1990) to forecast that 'A continuation of the warming trend in Hawaii would lead to large-scale bleaching similar to those observed recently in other geographic locations.' The first large-scale bleaching event did in fact occur in 1996 in the main Hawaiian Islands and again in 2002 in the Northwestern Hawaiian Islands. The role of the PDO (Mantua *et al*., 1997; Minobe, 1997) to the observed warming in the Hawaiian region is not known, but could be a factor. Nevertheless, the global atmosphere and the oceans have warmed and will continue to warm over the next century (Levitus *et al*., 2000, 2001; Houghton *et al*., 2001) because of increased anthropogenic greenhouse gas production. The result is predictable; if the warming trend continues, bleaching events will continue to occur in the Hawaiian region with increasing frequency and severity. Initially, bleaching with increasingly high rates of mortality will occur in shallow areas with restricted water circulation. Eventually, bleaching will become more severe even along exposed coastlines. There is speculation that corals may somehow be able to adapt to rapid warming and other negative anthropogenic changes over the next century (Coles & Brown, 2003). However, there is no solid evidence to date that coral populations can adapt rapidly enough to meet anticipated temperature increases (Hoegh-Guldberg, 1999; Jokiel, 2004). Much remains to be learned about the future trend of global temperatures and the response of coral reef communities to altered environmental conditions.

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Errata:

The original of Figure 7 as supplied to GCB is shown below. Someone at the journal modified the figure in the final production stage and inserted two typographical errors. Inshore was modified to “Inchore” and Bay was modified to “Bya” in an a peculiar act of mischief or sabotage. The figures were supplied in TIF and PSD format and would have to be physically modified in a program such as photoshop before going to press– there is no other explanation The originals did not have these errors.