Global Change Biology

Global Change Biology (2009), doi: 10.1111/j.1365-2486.2009.02043.x

Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold

JESSICA E. CARILLI*, RICHARD D. NORRIS*, BRYAN BLACK†, SHEILA M. WALSH* and MELANIE McFIELD‡

*Scripps Institution of Oceanography, University of California San Diego, 8675 Discovery Way, La Jolla, CA 92037, USA, †Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Dr., Newport, OR 97365, USA, ‡Smithsonian Institution, 1061 Queen Helmut St, Belize City, Belize, Central America

Abstract

Coral bleaching, during which corals lose their symbiotic dinoflagellates, appears to be increasing in frequency and geographic extent, and is typically associated with abnormally high water temperatures and solar irradiance. A key question in coral reef ecology is whether local stressors reduce the coral thermal tolerance threshold, leading to increased bleaching incidence. Using tree-ring techniques, we produced master chronologies of growth rates in the dominant reef builder, massive *Montastraea faveolata* corals, over the past 75–150 years from the Mesoamerican Reef. Our records indicate that the 1998 mass bleaching event was unprecedented in the past century, despite evidence that water temperatures and solar irradiance in the region were as high or higher mid-century than in more recent decades. We tested the influence on coral extension rate from the interactive effects of human populations and thermal stress, calculated here with degree-heating-months (DHM). We find that when the effects of chronic local stressors, represented by human population, are taken into account, recent reductions in extension rate are better explained than when DHM is used as the sole predictor. Therefore, the occurrence of mass bleaching on the Mesoamerican reef in 1998 appears to stem from reduced thermal tolerance due to the synergistic impacts of chronic local stressors.

Keywords: climate change, coral bleaching, Mesoamerican reef, *Montastraea faveolata*, resilience, sclerochronology

Received 7 April 2009; revised version received 22 July 2009 and accepted 24 July 2009

Introduction

Coral reefs are threatened by many human induced-impacts, including overgrowth by fleshy macroalgae, whether due to algal growth stimulation from nutrient pollution and/or a reduction in herbivory due to overfishing (Hughes, 1994; Lapointe, 1997; McCook, 1999; McCook *et al*., 2001; McClanahan *et al*., 2003; Smith *et al*., 2006); abrupt smothering or a slow reduction in fitness due to sedimentation (Dodge & Vaisnys, 1977; Rogers, 1990; Riegl & Branch, 1995; Fabricius & Wolanski, 2000); or direct damage due to destructive fishing practices (McManus *et al*., 1997), irresponsible tourism (Barker & Roberts, 2004), and boat damage (Saphier & Hoffmann, 2005). Coral diseases and bleaching (the phenomenon in which corals lose pigmentation associated with their symbiotic dinoflagellates, typically due to thermal stress) both appear to have increased in recent decades (Harvell *et al*., 1999; Hoegh-Guldberg, 1999) while live coral cover has declined (Gardner *et al*., 2003). Although reef degradation can be gradual, abrupt and severe episodes such as mass bleaching events can also lead to the sudden loss of corals (McField, 1999). An outstanding question is whether the amount of thermal stress a coral can tolerate before bleaching (Fitt *et al*., 2001) is affected by other local stressors (Knowlton & Jackson, 2008; Sandin *et al*., 2008). Indeed, a recent study investigating coral bleaching on the Great Barrier Reef found that thermal tolerance decreased with increased dissolved inorganic nitrogen sourced from land (Wooldridge, 2009). Here, we consider the effect of increasing general human impacts on the thermal tolerance threshold in *Montastraea faveolata*, using nearby human population over the past century as a proxy.

Scleractinian corals contain annual growth bands in their skeleton, which are revealed by X-rays (Knutson *et al*., 1972), and these preserved records of growth can

Correspondence: Jessica Carilli, tel. +1 858 822 2355, fax +1 858 822 3310, e-mail: jcarilli@ucsd.edu

be used to investigate how environmental change has affected coral health. Several studies have found that bleaching reduces skeletal growth in corals, leaving a record in the skeleton, often recognized by a high-density 'stress band' (Leder *et al*., 1991; Mendes & Woodley, 2002; Hendy *et al*., 2003b; Suzuki *et al*., 2003; Rodrigues & Grottoli, 2006). Coral bleaching appears to be increasing in frequency worldwide (Hoegh-Guldberg, 1999; Hughes *et al*., 2003). Despite a record of ecological surveys dating back to the 1950s, in Jamaica the first large-scale coral bleaching events were not observed until the 1980s (Goreau, 1992). Likewise, in coral skeletal records from Florida, Halley & Hudson (2007) found no record of bleaching before the mid-1980s, after which time multiple bleaching events were identified. On the Mesoamerican Reef, the first mass bleaching event wasn't recorded by observers using SCUBA until 1995 (McField, 1999) followed by a more severe event in 1998 (McField, 2000; Aronson *et al*., 2002b).

We investigated the history of bleaching on the Mesoamerican reef by applying tree-ring techniques to construct annually resolved, multidecadal records of growth from skeletal cores of massive *M. faveolata* corals. Growth chronologies and bleaching incidence were then compared with records of thermal stress and solar irradiance, as well as human impacts, using the population of Honduras as a proxy (population in 2006 $\sim$7.4 million). The population of Honduras is a good indicator of local human impacts because over 80% of land-based runoff in the region originates from Honduras, and this has increased over time along with population (Burke & Sugg, 2006). Indeed, Burke & Sugg (2006) modelled sediment and nutrient runoff in watersheds surrounding the Mesoamerican Reef for the current land use scenario and that for the hypothetical natural cover. They found that sedimentation increased over 20-fold, discharge doubled, nitrogen increased threefold and phosphorus increased sevenfold. Meanwhile, the human population has more than tripled in Honduras and Guatemala since the 1950s (United Nations Statistics Division, 2008). We investigated whether the history of coral bleaching on the Mesoamerican Reef could be explained by thermal stress alone, or whether bleaching was better explained by the combination of recent local human impacts and thermal stress.

Materials and methods

Coral collection and preparation

Ninety-two coral cores from *M. faveolata*, the dominant reef-builder on the fore-reef (Mcfield, 2000) were collected at four sites on the Mesoamerican reef: Turneffe Atoll and the Sapodilla Cayes in Belize; and Utila and Cayos Cochinos in Honduras (Fig. 1, Table 1). Cores were collected between 2.5 and 13 m depth in spur and groove habitat using a hand-held reversible air drill driven by a gasoline-powered air compressor. A custom-built stainless-steel core barrel 6 cm in diameter and 50 cm long fitted with a brass drill head containing carbide teeth was fashioned after the design developed by the Australian Institute for Marine Science. After core removal, precast concrete plugs were inserted to prevent colonization of the inside of the coral by boring organisms and allow coral regrowth. At each site, we collected cores from the largest heads within a 30-m radius from the anchor/buoy site. Cores were drilled vertically to obtain the clearest banding pattern along the maximum growth axis. Several cores were collected from dead coral heads to avoid biasing the record by analyzing growth rates only from survivors. After collection, tissue was removed using a waterpik and the cores were rinsed in fresh water and air-dried. A slab of 0.86 cm thickness was cut from the middle of each core using a water-lubricated double-bladed diamond table saw. Finally, core slabs were cleaned in deionized water and air-dried.

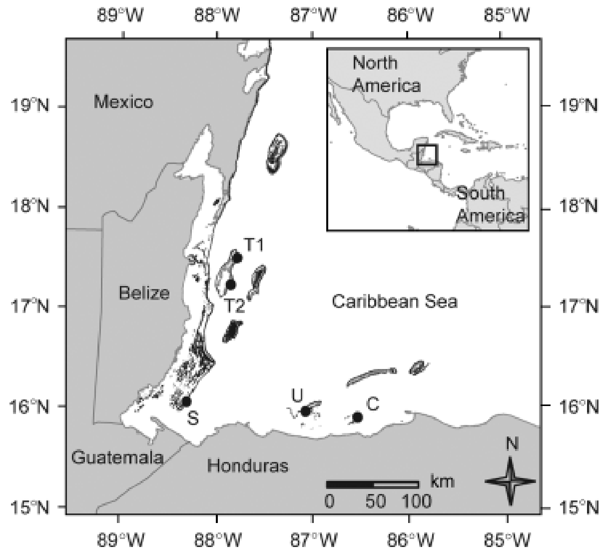

Fig. 1 Map of the Mesoamerican Reef showing locations of coral collection (black circles). Dark gray denotes coral, light gray denotes land areas. T1, T2, Turneffe Atoll (four cores from T1, 13 from T2), S, Sapodilla Cayes; U, Utila; C, Cayos Cochinos.

Core slabs were X-rayed at UCSD Thornton Hospital using a Siemens Polyphos 50 with a source-to-object distance of 40 in and a setting of 63 kV at 5 mA/s. Along with each core, 4 cm wide aluminum bars of the same thickness as the coral slabs (0.86 cm) were irradiated (Fig. S1). An aragonite wedge cut from a *Tridacna maxima* clam shell and three aluminum wedges, including one of the same dimensions as the shell, were also

Table 1 Coral core collection site locations, with dive site name or nearby caye, coordinates, number of cores from each site, along with growth anomalies in 1998

Site	Dive site name	Coordinates	Cores in master chronology	Total cores	1998 stress band
Turneffe 1	Dog Flea Caye	17°29′59″N, 87°45′30″W	9	17	12 (71%)
Turneffe 2	Harry Jones	17°18′25″N, 87°48′04″W			
Sapodilla	Frank's Caye, NE buoy	16°07′45″N, 88°14′59″W	21	44	44 (100%)
Utila	Diamond Caye	16°03′52″N, 86°57′30″W	9	17	17 (100%)
Cayos Cochinos	Pelican Point, Peli 2	15°58′41″N, 86°29′06″W	7	14	14 (100%)
		Total	46	92	87 (95%)

Table lists the total number of cores which were drilled and slabbed along the growth axis, the number of these included in each master chronology, and the percentage and number of the cores collected that have dense stress bands associated with the 1998 event.

irradiated to calibrate skeletal density based on X-ray brightness (Fig. S1). Digital X-ray cassettes were processed using an AGFA Musica ADC Compact Plus, and images saved in DICOM format, as well as hard copy films.

DICOM images were converted to BMP format using IMAGEJ (Rasband, 2007). We analyzed coral X-rays for annual linear extension, density, and calcification (the product of extension and density) using CoralXDS and the second derivative zero band delimiting function therein to objectively identify the beginning and end of each band (Helmle *et al*., 2002). The 'heel effect,' caused by differing intensity of the X-ray field along the anode–cathode axis (Carlton & McKenna-Adler, 1912), could influence density measurements and estimates of calcification. Using the same principle as a Carricart-Ganivet & Barnes (2007), the aluminum slabs irradiated in each coral X-ray were used to construct a background image with the same dimensions as the full X-radiograph. Each background image was then subtracted in CoralXDS to remove the heel effect. Note that for the two longest cores from Utila, the heel effect could not be sufficiently removed, so only extension rates are shown. For each coral core, three transects at various locations on the core were analyzed and averaged to account for slight variations in within-band extension and density. Transects were measured alongside of the axis of maximum growth. The vertical coral growth axis was avoided because growth band curvature within the maximum growth axis can artificially affect the measured parameters.

Chronology development

In the first step of chronology development, we ensured that all growth increments were assigned the correct calendar year through the tree-ring technique of crossdating (Fritts, 1976). Crossdating relies on the principle that individuals from a given site share growth patterns if the same limiting environmental factors control growth. The technique consists of matching synchronous growth patterns among multiple samples, beginning at the most recently formed increment and working back in time. If an increment is accidentally missed, the growth pattern in that individual will be offset by a year relative to the others in the sample set, indicating an error. Crossdating ensures the annual resolution of the final chronologies. Some corals contain distinct patterns in luminescent banding which can assist with chronology development (*Montastraea* corals from Florida, Hudson *et al*., 1994; *Porites* corals from Australia, Hendy *et al*., 2003a). However, no distinctive luminescent banding was evident in the *M. faveolata* from Mesoamerica. Instead, crossdating these corals relied on patterns in growth-increment width.

We used the program COFECHA to statistically validate crossdating (Grissino-Mayer, 2001). This program detrends each measurement time series with a cubic spline set to a 50% frequency response of 32 years and then removes any remaining autocorrelation so that the final time series meet the assumption of serial independence and have a mean of one. Next, COFECHA correlates each standardized time series with the average of all other standardized time series. A low correlation indicates a potential error and that the sample should be visually reinspected for false or missing bands. COFECHA was also used to verify the dating of cores collected from dead corals, based upon correlation with the live-collected cores. COFECHA also calculates series intercorrelation, the mean correlation between each standardized time series and the average of all others in the sample set. The high-frequency, between-year growth variability is described using the mean sensitivity, which for any pair of adjacent years ranges from zero (each year is the same width) to two (when a nonzero value is adjacent to a zero value; i.e. a missing increment) (Fritts, 1976) (Table 2). All samples with nonsignificant series intercorrelation values were visually checked and no errors were found. In addition,

Table 2 Series intercorrelation and average mean sensitivity of extension rates from corals at each site as calculated using COFECHA

Site	Series inter-correlation	Average mean sensitivity	Flagged, total segments
Turneffe Atoll	0.646	0.217	0, 13
Utila	0.575	0.177	3, 19
Cayos Cochinos	0.531	0.175	3, 22
Sapodilla Cayes	0.611	0.195	5, 42

The number of total correlated segments and the number of flagged segments (segments with $P > 0.01$) are also reported.

no series intercorrelation values were extremely low (lowest $r = 0.18$).

Extension rates had higher series intercorrelations compared with density and calcification (Table S1), and were therefore used for statistical trend analyses. Although calcification rate accounts for both skeletal extension and density, here we find that density does not vary widely and is not well correlated between heads, as exemplified by the lower series intercorrelation values. Instead, calcification in our corals appears to be mostly driven by fluctuations in extension (average R^2 between extension and calcification master chronologies = 0.76, and between density and calcification = −0.24), as was also found in a study by Lough & Barnes (2000). In addition, during and after the 1998 bleaching event, we find suppressed extension rates and increased density, especially at Sapodilla and Utila, though calcification remains almost constant. This indicates that analyses of calcification rates would ignore a potentially important biological signal, perhaps due to trade-offs between extension and density that do not affect overall calcification (Carricart-Ganivet & Merino, 2001; Carricart-Ganivet, 2004).

A total of 46 cross-dated cores were used to construct long-term master chronologies of coral growth; this subset had been accurately drilled and cut along the axis of maximum growth and therefore had clear X-rays (Table 1). First, each coral measurement time series was standardized by dividing by the mean growth-increment width. Standardized time series, each with a mean of one, were then averaged to produce the master chronology at each site (Fritts, 1976). Extension rate master chronologies are plotted in Fig. 2, while all three measures are plotted in Fig. S2. Because corals are not known to have any size or age-related growth trends, the records were not detrended with negative exponential functions or cubic splines as with tree-ring records (Fritts, 1976). Note that we do not evaluate differences in absolute growth rate, which do not necessarily reflect reef health (Edinger et al., 2000). Instead, we investigated long-term trends in relative growth rates to more accurately evaluate the impacts of coral bleaching within and among sites. Differences in both absolute extension rates among and within sites are discussed in Carilli et al. (2009).

Calculating thermal stress

Century-scale records of sea surface temperature (SST) are available on a monthly averaged basis. Given this temporal resolution, we calculated long-term records of thermal stress in terms of degree-heating-months (DHM) (Lough, 2000) using a methodology similar to that for degree-heating-weeks, which is a common way of quantifying coral thermal stress (Strong et al., 1997) (Fig. 3). Briefly, this method calculates DHM as the annual sum of the difference between average monthly SSTs that exceeded the long-term maximum monthly mean. We obtained long-term records of SST from two different globally gridded datasets; HadISST and ERSSTV2. Because of the grid sizes in each dataset, individual grid boxes for each site were not available; instead we chose two grid boxes from each dataset to represent the region. From the HadISST dataset (Rayner et al., 2003), we chose the $1 \times 1^\circ$ boxes centered on 17.5°N, 87.5°W to represent Turneffe and 16.5°N, 87.5°W to represent the southern sites. From the ERSSTV2 dataset (Smith & Reynolds, 2004), we chose the $2 \times 2^\circ$ boxes centered on 18°N, 88°W to represent Turneffe and Sapodilla and 18°N, 86°W to represent Cayos Cochinos and Utila. Heat stress in Jamaica (Fig. S3) was quantified using the ERSSTV2 dataset box centered on 18°N, 78°W representing Discovery Bay.

Total annual thermal stress was calculated for each 'coral-year', starting in October of 1 year and ending September of the next year (Fig. 3). To determine whether the long-term SST datasets accurately represented the temperatures experienced by the corals in Mesoamerica, we obtained 2 years (April 2000–May 2002) of *in situ* temperature measurements (0.0001 degree resolution) taken every ten minutes at Cayos Cochinos (at 5 m depth and the same site as our samples were collected) from the United States Geological Survey. In addition, we compared the *in situ* and long-term datasets to shorter, higher resolution time series from satellite measurements (Fig. S4): AVHRR from Glover's Reef, Belize (NOAA Coral Reef Watch) and the Integrated Global Ocean Services System (IGOSS) centered on 15.5°N, 86.5°W (Reynolds et al., 2002). While the long-term records, due to their coarser temporal resolution, do not capture the full range of short-term variability, the DHM measure has been shown to accurately predict bleaching in the western Indian Ocean (McClanahan et al., 2007). We also obtained data from the

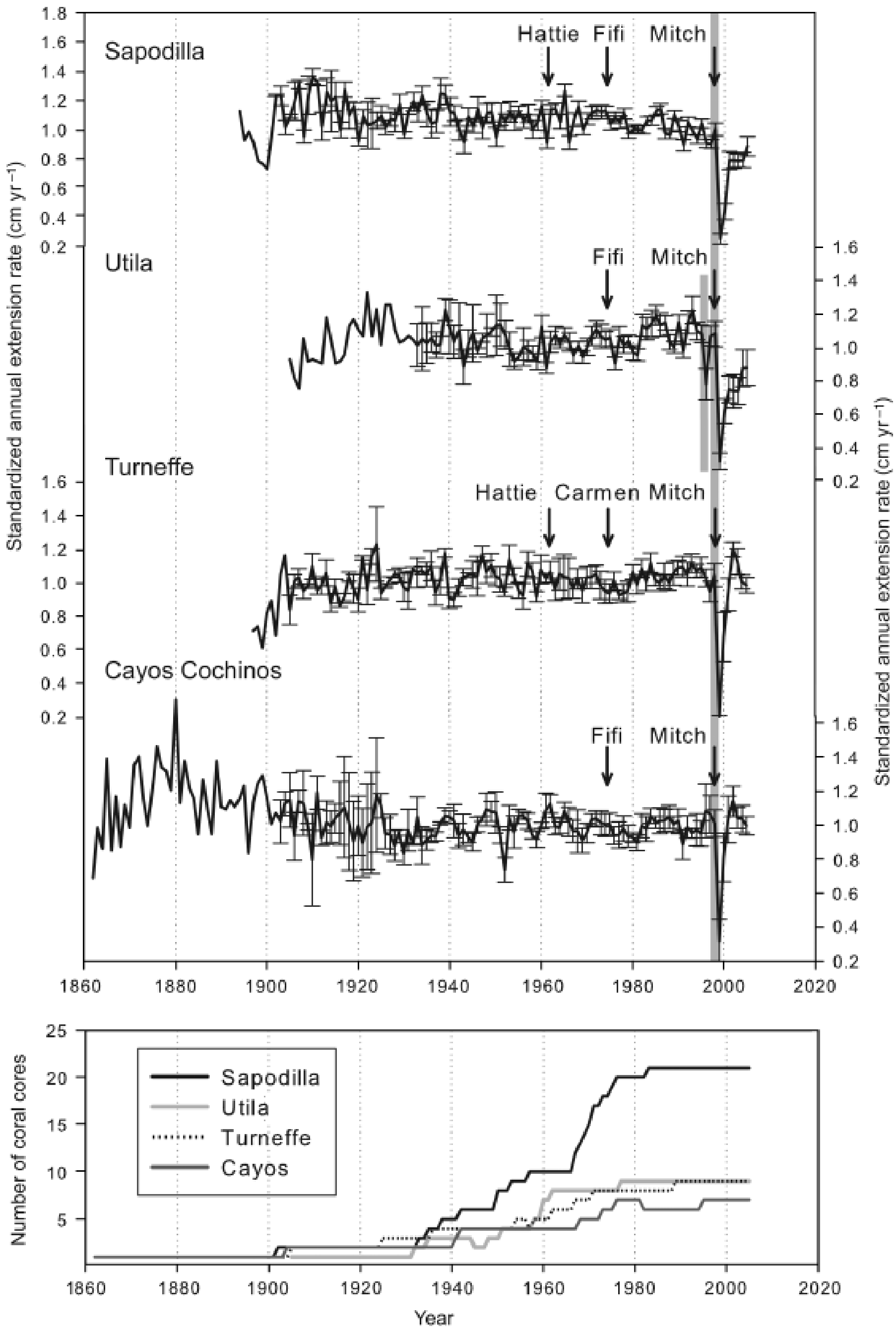

Fig. 2 Master chronologies of extension rates for each site (top), and the number of cores contributing to each chronology (bottom). See supplement for density and calcification records. Confidence intervals are the standard error for each year. Major hurricanes that passed close to each site are shown as arrows and are named, and the bleaching events of 1995 and 1998 are shown as vertical orange lines. Note that Sapodilla and Utila both show slight decreases in extension rates before 1998 (GLM: Sapodilla, $F_{(2,45)} = 7.41$, $P < 0.01$, $R^2 = 0.25$; Utila, $F_{(4,43)} = 3.66$, $P < 0.05$, $R^2 = 0.25$).

Comprehensive Ocean-Atmosphere Data Set on the density of shiptracks that supply most of the early SST data to verify that data are reliable (Woodruff *et al*., 1987). Those data after 1950 are based on a greater number of observations and are therefore more reliable.

Solar irradiance

In order to compare levels of solar irradiance in 1998 to those during warm periods in the middle of the 20th century (Fig. 3), we plotted the average monthly

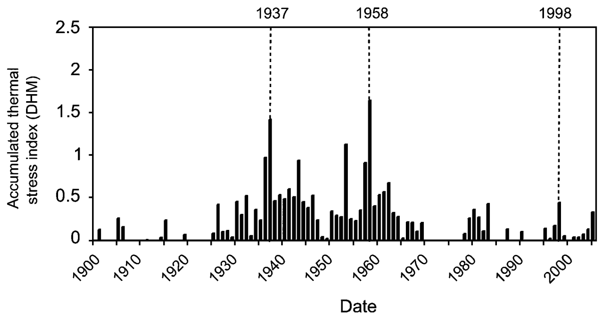

Fig. 3 Annual accumulated thermal stress index, or degree-heating-months (DHM). Thermal stress was calculated by summing the monthly temperature anomalies that exceed the long-term average maximum monthly temperature. Here, we show the average of the two grid cells used from two different long-term datasets: HadISST (Rayner *et al*., 2003) and ERSSTV2 (Smith & Reynolds, 2004). The individual records are available as a supplemental figure (Fig. S6).

cloudiness for a grid cell centered on 17°N, 87°W from COADS (Woodruff *et al*., 1987) (Fig. S5). Cloudiness is expressed in oktas: the number of eighths of the sky covered by clouds on a scale from 0 (no clouds) to 8 (completely covered).

Data analysis

The number of cores that comprise each master chronology decreases with age (Fig. 2), and the variance increases accordingly. Master chronologies must be interpreted with caution before approximately 1950 where the number of contributing colonies becomes quite low, often less than five. As noted above, in comparison with density and calcification, coral extension rates had the strongest common signal as gauged by the tree-ring statistic of series intercorrelation (Table 2), and were therefore the only measure of coral growth retained for further analysis.

We tested for trends using the master chronology extension rates from 1950 to 2007 to avoid bias associated with the decrease in chronology power with age. The timing of changes in extension rates from 1950 to 1997 was estimated by fitting a generalized linear model

$$(\text{extension} = \beta_0\text{year} + \beta_1\text{year} \times \text{post1955} + \ldots + \beta_9\text{year} \times \text{post1995})$$

(Table 3). Categorical variables representing time periods starting every five years after 1950 were included in the model. The categorical variable, post19XX, was assigned a value of one for years 19XX–1997 and zero otherwise. Variables were eliminated using a stepwise backward regression method with a tolerance of $P = 0.2$.

We used stress bands to investigate the history of coral bleaching. Stress bands were assumed to represent bleaching events and were identified as bands in which density exceeded the series average by at least 1.5 SDs. However, a potential complication to this reconstruction is that the surface of a coral head may not completely bleach (Rowan *et al*., 1997). Thus, a single core may not record a bleaching event if it passes through a region of the coral head that was not fully impacted. To address this issue, Hendy *et al*. (2003b) calculated the likelihood of sampling previous bleaching events based on the number of cores collected and the proportion of coral surface area that was bleached. We also calculated the likelihood that a prior mass bleaching event occurred, but was not recorded in our cores, using the incidence of stress banding in our cores and the equation:

$$\text{Probability} = \left[\frac{n!}{r!(n-r)!}\right] p^r (1-p)^{n-r},$$

modified from Hendy *et al*. (2003b), where n is the number of cores collected, r is the number of the collected cores with a stress band, and p is an estimate of the proportion of each colony that bleached. Although the scale of the 1998 bleaching event was extensive, and therefore the proportion of a colony's surface that was bleached may have been higher, we used $P = 0.3$ as a conservative proportion as in Hendy *et al*. (2003b).

To test for interactive effects on coral extension rate between DHM and human impacts, we fit a generalized linear model using extension rates, DHM of the previous year and the population of Honduras (United Nations Statistics Division, 2008) of any given year as a proxy for human impacts. We used DHM for the previous year because reduced coral growth due to bleaching typically occurs at the tail end of each 'coral-year,' (late summer and early fall) and therefore the following year records a smaller amount of skeletal growth. We fit the model

$$(\mathit{extension}_t = \beta_0 + \beta_1 \times \mathit{DHM}_{t-1} + \beta_2 \times \mathit{popXXpercentile}_t + \beta_3 \times \mathit{DHM}_{t-1} \times \mathit{popXXpercentile}_t),$$

where popXXpercentile was a categorical variable representing whether the human population in a given year was greater than or less than the 75th, 80th, 85th, 90th, and 95th percentile of population, taking value one if it was greater than or equal to the value of the specified percentile and zero if it was less. The DHM used here was the average from both grid-cells and datasets (Fig. 3), and we pooled extension rates from all four sites. The best model for each percentile was chosen by stepwise backward regression with tolerance $P = 0.2$. Model fits between percentiles were then compared using the

Table 3 Results of generalized linear model estimates for trends in extension over 1950 to 1997

	High Local Stress		Low Local Stress	
Predictor	Sapodilla Cayes	Utila	Turneffe Atoll	Cayos Cochinos
Year	–	–	−0.005**	−0.009**
Post 1955 × year	–	< −0.0005	–	< 0.0005
Post 1960 × year	–	< 0.0005	0.066	< 0.0005*
Post 1965 × year	–	–	–	–
Post 1970 × year	–	–	–	< 0.0005
Post 1975 × year	< −0.0005	–	–	–
Post 1980 × year	–	–	0.120**	< 0.0005
Post 1985 × year	–	< 0.0005*	–	< 0.0005*
Post 1990 × year	< −0.0005*	–	0.072*	–
Post 1995 × year	–	< −0.0005*	–	< 0.0005
Constant	1.078***	1.045***	11.672**	19.544**
N	48	48	48	48
F	7.41	3.66	4.91	2.24
P	0.002	0.012	0.002	0.050
R^2	0.25	0.25	0.31	0.22

A dash indicates that the variable was excluded from the model using stepwise backward regression with a tolerance of $P<0.2$. Significance levels are
* < 0.05,
** < 0.01,
*** < 0.001.

Akaike Information Criterion, and the 90th percentile (∼ 5.8 million people) had the best fit.

Results

At Turneffe and Cayos Cochinos, there are small but significant increases in extension rate during several time periods after 1950 (Table 3). Sapodilla Cayes has a slight decline in extension rates after 1975 ($P<0.2$) and a significant, steeper decline after 1990 (GLM: $F_{(2,45)}=7.41$, $P<0.01$, $R^2=0.25$, Table 3) while Utila has a significant decline after 1995 (GLM: $F_{(4,43)}=3.66$, $P<0.05$, $R^2=0.25$, Table 3).

We collected a total of 92 coral cores of which 87 (95%) have a stress band associated with the 1998 bleaching event (Table 1). There are only three individual years in different cores that contain a high-density stress band (defined here as density over 1.5 SDs higher than the mean) before 1998. One of the prior stress bands occurs in a core from Utila during 1995. The likelihood of missing an event on the scale of the 1998 bleaching event in our cores is vanishingly small ($P<<0.0001$) because of our large sample size. Therefore, bleaching on the scale of 1998 is unprecedented, at least in the past century.

Unlike evidence of mass bleaching, 1998 was not unique in terms of heat stress or irradiance on the Mesoamerican Reef. Our long-term DHM records show that on the Mesoamerican reef, heat stress was even higher in earlier years such as 1937 and 1958 than 1998 (Fig. 3), which agrees with the findings of Lough (2000) for the entire Caribbean region. Mid-century warmth is also supported by air temperature data from the Goldson International Airport (near Belize City). The cloudiness data demonstrate that solar irradiance was not exceptionally high in 1998 (Fig. S5). In Jamaica, the first bleaching events occurred in the 1980s (Goreau, 1992), but heat stress during those years was lower than during mid-century as well (Fig. S3).

The results of the generalized linear model showed that the best model was one where extension rates were affected by DHM_{t-1} as well as the interactive effect of high population and DHM_{t-1}, which changed the slope of the relationship (Fig. 4) ($F_{(3,409)}=26.92$, $P<0.0001$, $R^2=0.32$).

Discussion

We generated new time series of coral growth over the last century from four sites on the Mesoamerican Reef, utilizing the tree-ring technique of crossdating. These chronologies provide valuable information regarding long-term trends in relative growth rates, the history of coral bleaching, and how both thermal stress and local stressors affect coral growth. In particular, the four chronologies underscore an observed increase in bleaching frequency over recent years as well as the

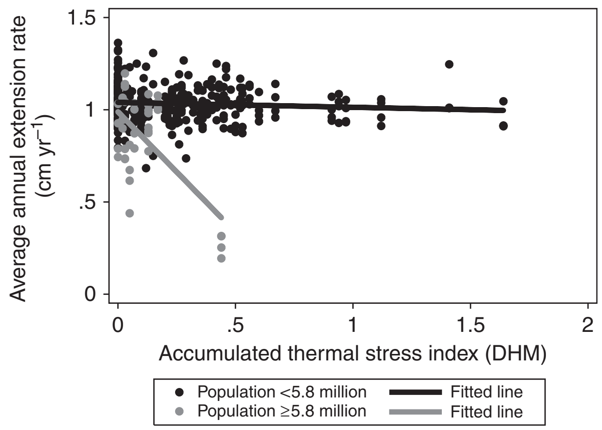

Fig. 4 Annual extension for all sites vs. DHM from the previous coral-year along with a linear regression on the extension rates that occurred when the human population of Honduras was <5.8 million (black) and those that occurred when population exceeded 5.8 million (gray) ($F_{(3,409)} = 26.92$, $P < 0.0001$, $R^2 = 0.32$). DHM_{t-1} alone is not a significant predictor of extension rates, but the relationship is improved when the effects of population are added.

severity of the 1998 bleaching event. Ecological surveys dating back to the 1970s confirm that the Mesoamerican Reef experienced its first documented bleaching event in 1995 (Glynn, 1993; McField, 1999), and a much more severe and widespread bleaching event in 1998 (Kramer & Kramer, 2000; McField, 2000; Aronson *et al*., 2002b). Indeed, the 1998 bleaching event was severe and widespread with reports of bleaching around the globe (Spencer *et al*., 2000; Wilkinson, 2000; Bruno *et al*., 2001; McGrath & Smith, 2003; Smith *et al*., 2008). On the Mesoamerican reef, the 1998 bleaching event was almost certainly unprecedented over the last century as evidenced by a lack of prior stress banding in our cores. Indeed, the 1998 bleaching event may be unprecedented over the last 3,000 years, as shown by exceptional species turnover in coral rubble cores from the Belize lagoon (Aronson *et al*., 2002a).

Coral bleaching is generally associated with high temperatures and solar irradiation, and indeed thermal stress was exceptional for many locations worldwide where bleaching occurred during 1998 (Lough, 2000). However, our calculated DHM, air temperature, and cloudiness records indicate that these variables do not explain the occurrence of mass bleaching on the Mesoamerican Reef in 1998. Warmer temperatures accompanied by higher levels of solar irradiance occurred mid-century, yet no evidence of bleaching could be identified in our samples. Using long-term SST reconstructions, Lough (2000) and Barton & Casey (2005) also found evidence for previous thermal stress comparable to recent levels on the Mesoamerican Reef and in the wider Caribbean. While some SST reconstructions may be affected by data gaps or incorrect spatial interpolation (Barton & Casey, 2005), our sites are relatively well-sampled over time (Woodruff *et al*., 1987). In addition, mid-century warmth is corroborated by high (warm) values of the Atlantic Multidecadal Oscillation, an indicator of climate variability based on Atlantic SST (Kerr, 2000), and proxy records of Caribbean SSTs. Coral stable oxygen isotope reconstructions (Gischler & Oschmann, 2005; Hetzinger *et al*., 2008), growth rates from the coral *Siderastrea siderea* from the Bahamas and Belize (Saenger *et al*., 2009), and coral and sclerosponge Sr/Ca records from Florida and Jamaica, respectively (Haase-Schramm *et al*., 2003; Maupin *et al*., 2008) all support mid-century warmth that was not accompanied by coral bleaching. Our finding that corals on the Mesoamerican Reef did not bleach mid-century despite high thermal stress is consistent with patterns of thermal stress and bleaching in Jamaica. There, underwater ecological observations date to the 1950s, with no reports of mass bleaching until 1987 (Goreau, 1992) despite thermal stress in 1957 and 1958 that was comparable to that during the first documented bleaching events in Jamaica (Fig. S3). While heat and solar irradiance stress in 1998 were not exceptional within the past century on the Mesoamerican Reef, local anthropogenic stress has increased in recent decades. Beyond a human population of ~ 6 million in Honduras, we found that DHM-related declines in extension became greater. Thus, the widespread and severe bleaching event on the Mesoamerican reef during 1998 appears to have resulted from increased local stresses, which lowered coral thermal tolerance and led to bleaching in response to only moderate warming.

Although the relationship between coral extension and local stressors is likely far more complex, the concept that local stress interacts with thermal stress is also consistent with differences in the resistance and resilience of corals among the four sites. At the Sapodilla Cayes and Utila, long-term decreases in extension rates may be the expression of long-term sublethal stress as these sites. Indeed, Sapodilla and Utila experience higher levels of chronic anthropogenic stress than Cayos Cochinos and Turneffe Atoll (Halpern *et al*., 2008; Carilli *et al*., 2009). Also, Utila, which experiences high relative chronic stress (Halpern *et al*., 2008; Carilli *et al*., 2009), is the only site where corals exhibit a significant depression in growth rates and a stress band associated with the 1995 bleaching event. Similar long-term reductions in coral growth rates are not exclusive to the Mesoamerican Reef and have also recently been reported on the Great Barrier Reef (De'ath *et al*., 2009), in Thailand (Tanzil *et al*., 2009), and near the Panama Canal (Guzman *et al*., 2008).

Repetitive bleaching or preexposure to high or more variable water temperatures or light may increase a coral's thermal tolerance threshold via acclimatization (Brown *et al*., 2002; Castillo & Helmuth, 2005), offering some potential protection from rising global temperatures. However, the continued acceleration of local stressors such as increased sedimentation through land clearing, marine dredging, and coastal development may depress a coral's energy reserves (Rogers, 1990), making it less likely to either resist bleaching or to survive and recover from a bleaching event (Rodrigues & Grottoli, 2006). Further observational studies, for instance with extensive *in situ* instrumentation in place before and during a bleaching event, are needed to identify how specific stressors interact to change the bleaching threshold. Experimental studies might also be useful to calculate the effects of different stressors, such as nutrients or sedimentation, on thermal tolerance thresholds.

Our data suggest that chronic local stressors depress the thermal tolerance threshold, increasing the likelihood of coral bleaching under only moderate thermal stress. Although our study addresses *M. faveolata*, the dominant reef framework builder in most of the Mesoamerican reef region, this finding may be common to other coral species and regions (Wooldridge, 2009). Therefore, local management strategies that reduce local stressors, such as creating effective marine reserves to protect from overfishing, or reducing runoff impact by watershed management and protecting or replanting coastal mangroves, may increase coral thermal tolerance and thus the associated likelihood of surviving future warming.

Acknowledgements

We thank M. Roldan for X-raying the cores repeatedly, and M. Carilli, B. Erisman, K. Hughen, E. Kisfaludy, N. Prouty, J. Shrives, A. Stumpf, and A. Young for help in the field. We thank R. Halley and C. Reich of USGS for providing *in situ* water temperature data. We thank the Belizean and Honduran governments for supplying permits and World Wildlife Fund Belize, The University of Belize, Reef Conservation International, The Honduran Coral Reef Foundation, and Operation Wallacea for logistical support. This research was supported by the PADI Foundation, B. Katz, and two anonymous donors.

References

Aronson R, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM (2002a) The expanding scale of species turnover events on coral reefs in Belize. *Ecological Monographs*, **72**, 233–249.

Aronson R, Precht WF, Toscano MA, Koltes KH (2002b) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology*, **141**, 435–447.

Barker NHL, Roberts CM (2004) Scuba diver behaviour and the management of diving impacts on coral reefs. *Biological Conservation*, **120**, 481–489.

Barton A, Casey KS (2005) Climatological context for large-scale coral bleaching. *Coral Reefs*, **24**, 536–554.

Brown N, Dunne R, Goodson M, Douglas A (2002) Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs*, **21**, 119–126.

Bruno J, Siddon CE, Witman JD, Colin PL, Toscano MA (2001) El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs*, **20**, 127–136.

Burke L, Sugg Z (2006) *Hydrologic Modeling of Watersheds Discharging Adjacent to the Mesoamerican Reef*. World Resources Institute, Washington DC.

Carilli JE, Norris RD, Black B, Walsh SW, McField M (2009) Local stressors reduce coral resilience to bleaching. *PLoS ONE*, **4**, e6324.

Carlton RR, McKenna-Adler A (1912) Principles of radiographic imaging. *Pathology*, **10**, 14–15.

Carricart-Ganivet J (2004) Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*. *Journal of Experimental Marine Biology and Ecology*, **302**, 249–260.

Carricart-Ganivet J, Barnes DJ (2007) Densitometry from digitized images of X-radiographs: methodology for measurement of coral skeletal density. *Journal of Experimental Marine Biology and Ecology*, **344**, 67–72.

Carricart-Ganivet JP, Merino M (2001) Growth responses of the reef-building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico. *Bulletin of Marine Science*, **68**, 133–146.

Castillo K, Helmuth BST (2005) Influence of thermal history on the response of *Montastraea annularis* to short-term temperature exposure. *Marine Biology*, **148**, 261–270.

De'ath G, Lough JM, Fabricius KF (2009) Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–120.

Dodge R, Vaisnys JR (1977) Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research*, **35**, 715–730.

Edinger E, Limmon GV, Jompa J, Widjatmoko W, Heikoop JM, Risk MJ (2000) Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health? *Marine Pollution Bulletin*, **40**, 404–425.

Fabricius KE, Wolanski E (2000) Rapid smothering of coral reef organisms by muddy marine snow. *Estuarine, Coastal and Shelf Science*, **50**, 115–120.

Fitt W, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal threshold in tropical corals. *Coral Reefs*, **20**, 51–65.

Fritts HC (1976) *Tree Rings and Climate*. Academic Press, New York.

Gardner T, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.

Gischler E, Oschmann W (2005) Historical climate variation in Belize (Central America) as recorded in scleractinian coral skeletons. *Palaios*, **20**, 159–174.

Glynn P (1993) Coral reef bleaching: ecological perspectives. *Coral Reefs*, **12**, 1–17.

Goreau TJ (1992) Bleaching and reef community change in Jamaica: 1951–1991. *American Zoologist*, **32**, 683–695.

Grissino-Mayer H (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, **57**, 205–221.

Guzman H, Cipriani R, Jackson JBC (2008) Historical decline in coral reef growth after the Panama Canal. *Ambio*, **37**, 342–346.

Haase-Schramm A, Böhm F, Eisenhauer A, Dullo WC, Joachimski MM, Hansen B, Reitner J (2003) Sr/Ca ratios and oxygen isotopes from sclerosponges: temperature history of the Caribbean mixed layer and thermocline during the Little Ice Age. *Paleoceanography*, **18**, 1073.

Halley RB, Hudson JH (2007) Fidelity of annual growth in *Montastraea faveolata* and the recentness of coral bleaching in Florida. In: *Geological Approaches to Coral Reef Ecology* (ed Aronson RB), pp. 166–177. Springer, New York.

Halpern BS, Walbridge S, Selkoe KA *et al*. (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.

Harvell CD, Kim KK, Burkholder JM *et al*. (1999) Emerging marine diseases–climate links and anthropogenic factors. *Science*, **285**, 1505–1510.

Helmle KP, Kohler KE, Dodge RE (2002) The Coral X-radiograph Densitometry System: CoralXDS. Nova Southeastern University. Available at http://www.nova.edu/ocean/coralxds/index.html (accessed 18 April 2006).

Hendy E, Gagan MK, Lough JM (2003a) Chronological control of coral records using luminescent lines and evidence for non-stationary ENSO teleconnections in northeast Australia. *The Holocene*, **13**, 187–199.

Hendy E, Lough JM, Gagan MK (2003b) Historical mortality in massive *Porites* from the central Great Barrier Reef, Australia: evidence for past environmental stress? *Coral Reefs*, **22**, 207–215.

Hetzinger S, Pfeiffer M, Dullo W-C, Keenlyside N, Latif M, Zinke J (2008) Caribbean coral tracks Atlantic multidecadal oscillation and past hurricane activity. *Geology*, **36**, 11–14.

Hoegh-Guldberg O (1999) Climate change, coral bleaching, and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hudson J, Hanson KJ, Halley RB, Kindinger JL (1994) Environmental implications of growth rate changes in *Montastraea annularis*: Biscayne National Park. *Florida Bulletin of Marine Science*, **54**, 647–669.

Hughes T, Baird AH, Bellwood DR *et al*. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**, 1547–1551.

Kerr RA (2000) A North Atlantic climate pacemaker for the centuries. *Science*, **288**, 1984.

Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLOS Biology*, **6**, 215–220.

Knutson D, Buddemeier RW, Smith SV (1972) Coral chronometers: seasonal growth bands in reef corals. *Science*, **177**, 270–272.

Kramer PA, Kramer PR (2000) Transient and lethal effects of the 1998 coral bleaching event on the Mesoamerican reef system. *Proceedings of the 9th International Coral Reef Symposium*, **2**, 1175–1180.

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography*, **42**, 1119–1131.

Leder J, Szmant AM, Swart PK (1991) The effect of prolonged "bleaching" on skeletal banding and stable isotopic composition in *Montastraea annularis*. *Coral Reefs*, **10**, 19–27.

Lough J (2000) 1997–98: Unprecendented thermal stress to coral reefs? *Geophysical Research Letters*, **27**, 3901–3904.

Lough J, Barnes D (2000) Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology*, **245**, 225–243.

Maupin CR, Quinn TM, Halley RB (2008) Extracting a climate signal from the skeletal geochemistry of the Caribbean coral *Siderastrea siderea*. *Geochemistry Geophysics Geosystems*, **9**, Q12012.

McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007) Effects of climate and seawater temperature variation on coral bleaching and mortality. *Ecological Monographs*, **77**, 503–525.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones SH IV (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Marine Ecology Progress Series*, **261**, 135–147.

McCook L (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences on the Great Barrier Reef. *Coral Reefs*, **18**, 357–367.

McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, **19**, 400–417.

McField MD (1999) Coral response during and after mass bleaching in Belize. *Bulletin of Marine Science*, **64**, 155–172.

McField MD (2000) Influence of disturbance on coral reef community structure in Belize. *Proceedings of the 9th International Coral Reef Symposium*, **1**, 62–68.

McGrath T, Smith GW (2003) Comparisons of the 1995 and 1998 coral bleaching events on the patch reefs of San Salvador Island, Bahamas. *Revista de Biología Tropical*, **51**, 67–75.

McManus JW, Reyes RB Jr, Nanola CL Jr (1997) Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environmental Management*, **21**, 69–78.

Mendes J, Woodley JD (2002) Effect of the 1995–1996 bleaching event on polyp tissue depth, growth, reproduction and skeletal band formation in *Montastraea annularis*. *Marine Ecology Progress Series*, **235**, 93–102.

Rasband WS (2007). U. S. National Institutes of Health, Bethesda, Maryland: Image J. Available at http://rsb.info.nih.gov/ij/ (accessed 1 August 2007).

Rayner N, Parker DE, Horton EB *et al*. (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research*, **108**, 4407.

Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An improved in situ and satellite SST analysis for climate. *Journal of Climate*, **15**, 1609–1625.

Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology*, **186**, 259–275.

Rodrigues L, Grottoli AG (2006) Calcification rate and the stable carbon, oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached and recovering Hawaiian corals. *Geochimica et Cosmochimica Acta*, **70**, 2781–2789.

Rogers C (1990) Responses to coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, **62**, 185–202.

Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature*, **388**, 265–269.

Saenger C, Cohen AL, Oppo DW, Halley RB, Carilli JE (2009) Low-latitude north Atlantic sea surface temperature trends and variability since 1552. *Nature Geoscience*, **2**, 492–495.

Sandin SA, Smith JE, DeMartini EE *et al*. (2008) Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE*, **3**, e1548.

Saphier AD, Hoffmann TC (2005) Forecasting models to quantify three anthropogenic stresses on coral reefs from marine recreation: anchor damage, diver contact and copper emission from antifouling paint. *Marine Pollution Bulletin*, **51**, 590–598.

Smith JE, Shaw M, Edwards RA *et al*. (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. *Ecology Letters*, **9**, 835–845.

Smith L, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs*, **27**, 197–205.

Smith TM, Reynolds RW (2004) Extended reconstruction of global sea surface temperatures based on COADS data (1854–1997). *Journal of Climate*, **17**, 2466–2477.

Spencer T, Teleki TK, Bradshaw C, Spalding MD (2000) Coral bleaching in the southern Seychelles during the 1997–1998 Indian Ocean warm event. *Marine Pollution Bulletin*, **40**, 569–586.

Strong A, Barrientos CS, Duda C, Sapper J (1997) Improved satellite techniques for monitoring coral reef bleaching. *Proceedings of the 8th International Coral Reef Symposium*, **2**, 1495–1498.

Suzuki A, Gagan MK, Fabricius K, Isdale PJ, Yukino I, Kawahata H (2003) Skeletal isotope microprofiles of growth perturbations in *Porites* corals during the 1997–1998 mass bleaching event. *Coral Reefs*, **22**, 357–369.

Tanzil JTI, Brown BE, Tudhope AW, Dunne RP (2009) Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs*, **28**, 519–528.

United Nations Statistics Division (2008). Estimates of mid-year population. Available at http://unstats.un.org/unsd/demographic/sconcerns/popsize/size2.htm (accessed 15 March 2009).

Wilkinson C), ed. (2000) *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Townsville.

Woodruff SD, Slutz RJ, Jenne RL, Steurer PM (1987) A comprehensive ocean-atmosphere data set. *Bulletin of the American Meteorological Society*, **68**, 1239–1250.

Wooldridge S (2009) Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **58**, 745–751.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. X-radiograph of 3 short cores from the Sapodilla Cayes. Core name labels and core tops are at left. Aluminum bars are on the top and bottom of the x-ray. Note the compressed growth in 1998 revealed as a bright, dense band and denoted by an arrow on the bottom core. Aragonite wedge is labeled, other wedges are aluminum.

Fig. S2. Master chronologies of extension (cm), density (g/cm3) and calcification (g/cm2) for each site (top) and the number of cores in each chronology (bottom). Major hurricanes that passed close to each site are shown as arrows and are named, and the bleaching events of 1995 and 1998 are shown as vertical orange lines.

Fig. S3. Accumulated thermal stress for Discovery Bay, Jamaica. Temperature stress was calculated by summing the monthly temperature anomalies that exceed the long term average of the maximum monthly temperatures. Data from the ERSSTV2 dataset (Smith and Reynolds 2004), centered on 18°N, 78°W was used. Stars indicate recorded mass bleaching in 1987, 1989, 1990, 1991, 1998, and 2005.

Fig. S4. Cayos Cochinos water temperature data from several sources. Water temperature data from in situ measurements at Pelican Point, Cayos Cochinos (measurements every 10 minutes, black) is compared with monthly long-term data from the HadISST (green) (Rayner *et al*. 2003) and ERSSTV2 (yellow) (Smith and Reynolds 2004) datasets, along with more recent satellite measurements from AVHRR (blue) (NOAA Coral Reef Watch) and IGOSS (pink) (Reynolds *et al*. 2002) datasets.

Fig. S5. (Top) Air temperature record from the Goldson International Airport, 1941–2004. Warm air temperatures in the late 1950's support our confidence in long sea surface temperature records. Dashed line delineates 30 °C air temperature. (Bottom) Monthly cloudiness record (black circles) from the grid cell centered on 17°N, 87°W, expressed in oktas, the number of eighths of the sky covered by clouds. A linear trend line is plotted in gray and the months June-September in 1958 and 1998 are shown for comparison (red boxes).

Fig. S6. Accumulated annual temperature stress. Temperature stress was calculated by summing the monthly temperature anomalies that exceed the long term average of the maximum monthly temperatures. Records from 2 grid cells (denoted by the latitude and longitude of the center of each cell) from each of 2 long-term temperature records: HadISST (Rayner *et al*. 2003) and ERSSTV2 (Smith and Reynolds 2004) are used, and the average of these four records is also shown (A). (B) and (D) represent Turneffe, (C) and (D) represent Sapodilla, and (C) and (E) represent Cayos Cochinos and Utila. Years with the highest heat stress in the average of all four temperature records are denoted by a dashed line.

Table S1. Interseries correlation values for the three growth measurements for each site.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

