

Threshold Decline in Mesoamerican Coral Growth and Resiliency

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Caribbean coral reefs have been massively altered in recent decades due to human impacts, resulting in a dramatic reduction of live coral cover but quantitative data before the 1970's have not been available to assess how these changes came about^{1,2,3}. We produced master chronologies of growth rates in massive *Montastrea faveolata* corals from the Mesoamerican reef tract that provide a method for extending records of coral health further back into the past. Our records reveal a unique reduction in growth rate associated with the 1998 coral bleaching event that has no parallel in the past 75 to 150 years. Of 92 cores collected from live coral heads in 2006-2007, 94% have severely reduced growth rates and 14% exhibit partial mortality scars in 1998-1999 whereas only 3 stress bands are found in single cores prior to 1998, and none of these cores exhibited earlier partial mortality. Some corals returned to pre-1998 extension rates by 2001, although corals in areas affected by sediment-laden runoff or high human population density still had not fully recovered by the time of sample collection eight years later. Previous episodic stresses like hurricane strikes and a warming event in 1983 more severe than 1998 had little to no effect on *M. faveolata* growth rates. The 1998 event apparently surpassed a threshold in coral tolerance precipitating a catastrophic shutdown in growth that had lasting effects throughout the Mesoamerican reef system but was particularly prolonged in areas exposed to other stressors. These findings suggest that projected increases in global

temperatures over the next century are likely to result in drastic reductions in growth rather than a gradual decline in coral health, but that corals with fewer local stresses will be better able to survive bleaching events, underscoring the need for local conservation measures.

Semi-quantitative measures of reef condition have documented a worldwide decline in reef quality over the past several centuries^{1,4}. Unfortunately, the details of how this reduction in reef health occurred are poorly known in part because extensive ecological surveys typically began only a few decades ago². An outstanding issue is the extent to which stressors result in gradual changes in reef quality or whether there are tipping points in the ecology of reef species or communities that, when passed, result in abrupt major decline in reef condition. Also in question is whether the combination of multiple stressors reduces coral resistance to episodic events such as bleaching. Ecological studies have demonstrated that reefs are exposed to a slate of stressors ranging from coral diseases⁵, removal of grazing and predatory fish^{6,7}, and coastal development⁸ that are associated with the gradual loss of coral cover or overgrowth by fleshy algae. However, cases like the almost complete disappearance of the dominant *Agaricia* corals in the Belize lagoon in 1998 suggest there may also be threshold effects associated with episodic events that are still poorly understood⁹.

To test whether coral health declined gradually or abruptly, we collected drill cores from four fore-reef sites along a gradient of runoff exposure on the Mesoamerican Reef (Fig. 1). Our study utilizes 92 cores collected in 2006-2007, with the longest cores extending back to the 1860's, while the majority of the cores span the last 50-70 years. Coral growth rates, representing coral health, were measured based on annual density bands in the skeleton¹⁰ using the program CoralXDS¹¹. The growth record from each

core was standardized by dividing each year's growth by the long-term mean, and then all records were averaged from a site to construct a master chronology¹². Master chronologies capture the common environmentally driven coral growth signal and filter out micro-site differences (Fig. 2).

Annual growth rate data for all four sites are relatively invariant over the initial ~100 years of the record but nearly all corals display a prominent stress band in 1998, recognized by an increase in skeletal density, and 94% of corals show a marked reduction in extension rates that persists for two years or more (Fig. 3). Other than the 1998 event, stress bands are seen in three corals from different sites in 1950, 1965, and 1995 but no other corals from these sites displayed significant changes in growth during these years. Our longest core extends to 1861 (from Cayos Cochinos) and also shows no stress bands or growth interruptions prior to 1998. We conclude that the 1998 event is unique on the Mesoamerican reef for at least the last 50-75 years and very likely for the past 150 years.

We attribute the reductions in coral growth in 1998 largely to coral bleaching, in which scleractinian corals expel or kill their symbiotic dinoflagellate zooxanthellae when water temperatures become too high¹³. In 1998 massive bleaching events were reported worldwide, including on the Mesoamerican Reef^{9,14,15,16,17}. This year was the warmest on record on a globally averaged scale¹⁸ until it was surpassed by warming during 2005¹⁹. On the Mesoamerican Reef, *Montastrea faveolata* had the highest level of remnant bleaching compared to other species up to 10 months after the event started in August of 1998, and very high levels of mortality²⁰.

It may not have been just the extent of warming during 1998 that was particularly damaging to corals but also that the reef had passed a threshold in reef degradation that made bleaching much more severe than in earlier years. Heat stress was greater in 1983 than 1998 based upon a calculation of the degree-month heating index²¹ from the HadISST 1.1 1900-2005 data set²² (Fig. 4), yet no large-scale bleaching events were reported from the Mesoamerican Reef, and no stress bands or significant decrease in extension rates occurs at any site in 1983 or 1984. Another very warm event occurred in 1941, again with no evidence of extreme impacts on coral growth. We suggest that the 1998 event, with somewhat less extreme temperature stress than 1983, produced severe changes in coral growth as a result of more recent confounding factors such as stress from higher mainland-based runoff and impacts associated with high local human populations such as overfishing or sewage pollution.

The Mesoamerican Reef experienced its first documented bleaching event in 1995, but very few corals contain any signature of this in their growth patterns, probably because heating and bleaching was significantly less severe than in 1998²³. Still, bleaching developed in 1995 even though the 1995 event did not even register as a particularly warm year based on calculated accumulated heat-stress (Fig. 4). Moderate bleaching on the Mesoamerican reef also developed during 2005, but although the Caribbean as a whole experienced more intense warming in 2005 than 1998, this was centered near the Lesser Antilles, approximately 2000 km to the east. Ecological surveys confirm that bleaching is a relatively new phenomenon in the Mesoamerican Reef²³ and has developed in the past decade even during heating events that were not as severe as those observed in the past.

It is possible that hurricane Mitch (October 21-29, 1998, Category 5) played a role in coral mortality and reduced growth rates during 1998, but we find little evidence to support this hypothesis. Although hurricanes can be extremely destructive to branching and platy corals through mechanical damage, massive corals typically survive, so the loss of *Montastrea sp.* after 1998 and the reductions in growth rates reported here are likely due mainly to the bleaching event¹⁴. The associated runoff from hurricane Mitch extended over most of the southern portion of the Mesoamerican Reef and reduced water clarity for several weeks²⁴. However, we have found no geochemical signature associated with excessive runoff from Mitch, even in cores analyzed at extremely high resolution using laser ablation²⁵. The lack of signal indicates that the corals stopped calcifying due to the bleaching event (August 1998) prior to the hurricane. We have also detected little evidence of reduced growth from earlier hurricane strikes (Fig. 2). For instance, hurricane Hattie (Category 5) destroyed Belize City in 1961, and passed directly over Turneffe Atoll, while Fifi (Category 3) passed over the three southern sites in 1974. However, the only significant reduction in growth rates potentially associated with a hurricane is in 1961 at the Sapodilla Cayes (Fig. 2).

Supporting evidence for our suggestion that the Mesoamerican reef passed a tipping point in 1998 comes from a comparison of the recoveries of the different reef sites from the bleaching event. Our study sites span a range of exposure to runoff from the highest sedimentation at the Sapodilla Cayes to the lowest at Turneffe Atoll²⁶. Notably, extension rates from the Sapodilla Cayes still have not recovered completely in more than eight years while corals from Turneffe Atoll recovered in about three years (Fig. 2). These patterns correlate with post-bleaching survey data, which found that although the corals along the whole reef appeared to bleach uniformly in 1998, the southern reefs of Belize and Utila exhibited higher coral mortality than the rest of the Mesoamerican Reef²⁰. Levels of partial mortality also support a geographic difference

in overall mortality. For example, at Turneffe Atoll 6% of corals exhibit partial mortality and about 29% lack the 1998 stress band, while Sapodilla corals display 16% partial mortality and 100% have stress bands (Table 1). Much the same pattern is seen in our Honduras sites where corals at Utila still have not recovered to pre-1998 growth rates, perhaps due to high local stresses related to sewage effluent and overfishing associated with the large local human population. Utila is also the only site where corals have any significant change in growth rates and a stress band associated with the 1995 bleaching event. We suggest that corals growing in areas exposed to high chronic stresses such as sedimentation and large human populations were both less resistant and resilient to bleaching than corals from areas with lower chronic stress.

Widespread coral bleaching is usually associated with increased water temperatures, and bleaching appears to be increasing in frequency as the climate warms²⁷. Confounding stresses may increase coral susceptibility to bleaching or subsequent mortality. The Mesoamerican Reef, and Belize in particular, was considered relatively pristine until quite recently¹, with the first reef-wide bleaching event reported in 1995²³. The lack of previous stress bands or partial mortality events, compared with the immense reductions in growth rates and increased mortality in 1998 indicates that the 1998 event was unprecedented on the fore-reef in Mesoamerica. We propose that the 1998 event caused such widespread bleaching and mortality not seen during previous high temperature stress in 1983 and 1941 due to recent additional stress factors, including increased runoff. Our results suggest that corals in the Mesoamerican reef system have been able to maintain relatively stable growth rates even in the face of increasing pressures from runoff and reef habitat degradation over the past 50-150 years. However, the increase in the frequency of bleaching events in the past decade and the nearly complete cessation of growth associated with the 1998 event suggests that the reef system is becoming less resistant to episodic stressors, even in response to events

that do have historical parallels in the past century. Furthermore, the prolonged period required for coral extension rates to recover to pre-1998 levels, particularly in the more impacted reef systems, suggests that the predicted increase in heat stress events is likely to have catastrophic consequences for the Mesoamerican reef tract. However, the resistance and resilience of corals at Turneffe Atoll and Cayos Cochinos indicate that conservation measures that decrease localized stresses such as runoff may boost the ability of corals to survive future climate change.

Figure 1 | Map of the Mesoamerican Reef showing locations of coral collections as black circles. Dark grey denotes coral, light grey denotes land areas. T1, T2 = Turneffe Atoll (4 cores from T1, 13 from T2), S = Sapodilla Cayes, U = Utila, C = Cayos Cochinos.

Table 1 | Number of cores from each site, along with growth anomalies in 1998 and earlier

Site Name	Number of Cores	1998 stress band	Partial mortality in 1998	Previous stress bands
Sapodilla	44	100% (44)	16% (7)	0
Turneffe	17	71% (12)	6% (1)	2
Utila	17	100% (17)	12% (2)	1
Cayos Cochinos	14	100% (14)	21% (3)	0
TOTAL	92	95% (87)	14% (13)	3

Table lists the total number of cores which were drilled and slabbed along the growth axis, the percentage and number of these that have dense stress bands associated with the 1998 event, the percentage and number with partial mortality scars, and any previous individual stress bands.

Figure 2| Master chronologies for each site. Confidence intervals are the standard error for each year, and are only shown for the extension rates. Confidence intervals on density and calcification measurements are smaller. Major hurricanes that passed close to each site are shown as stars and are named, and the bleaching events of 1995 and 1998 are shown as grey bars.

Figure 3| X-radiographs showing the tops of 3 cores from each site. Arrows show compressed growth in 1998/1999. Circles delineate scars from partial mortality coincident with depressed growth.

Figure 4| 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, averaged between all 4 sites. Years with the highest heat stress are denoted.

1. Jackson, J.B.C., et al. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629-636 (2001).
2. Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. Long-term region-wide declines in Caribbean corals. *Science* **301**, 958-960 (2003).
3. Wilkinson, C. (ed) *Status of coral reefs of the world: 2004*. Australian Institute of Marine Science, Cape Ferguson and Dampier (2004).

4. Pandolfi, J.M., et al. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955-958 (2003).
5. Harvell, C. D., et al. Emerging marine diseases—Climate links and anthropogenic factors. *Science* **285**, 1505-1510 (1999).
6. Hughes, T.P. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–1551(1994).
7. McCook, L.J. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* **18**, 357-367 (1999).
8. Maragos, J.E. Impact of coastal construction on coral reefs in the US-affiliated Pacific islands. *Coastal Management* **21**, 235-269 (1993).
9. Aronson, R.B., Precht, W.F., Toscano, M.A. & Koltes, K.H. The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* **141**, 435-447 (2002).
10. Knutson, R.A., Buddemeier, R.W. & Smith, S.V. Coral chronometers: seasonal growth bands in reef corals. *Science* **177**, 270-212 (1972).

11. Helmle, K.P., Kohler, K.E. & Dodge, R.E. Relative Optical Densitometry and The Coral X-radiograph Densitometry System: CoralXDS. Presented Poster (omitted from abstract book, but included in program), Int. Soc. Reef Studies 2002 European Meeting. Cambridge, England. Sept. 4-7.

12. Fritts, H.C. *Tree rings and climate*. Academic Press, London (1976).

13. Glynn, P.W. Coral reef bleaching: facts, hypotheses and implications.

Glob. Chang. Biol. **2**, 495–509 (1996).

14. McField, M.D. Influence of disturbance on coral reef community structure in Belize.

Proc. 9th Int. Coral Reef Symp. **1**, 62-68 (2000).

15. Goreau, T., McClanahan, T., Hayes, R. & Strong, A. Conservation of coral reefs after the 1998 global bleaching event. *Conserv. Biol.* **14**, 5-15 (2000).

16. Bruno, J.F., Siddon, C.E., Witman, J.D., Colin, P.L. & Toscano, M.A. El Nino related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* **20**, 127-136 (2001).

17. McGrath, T.A. & Smith, G.W. Comparisons of the 1995 and 1998 coral bleaching events on the patch reefs of San Salvador Island, Bahamas. *Rev. Biol. Trop.* **51**, 67-75 (2003).

18. Hansen, J., Ruedy, R., Glascoe, J. & Sato, M. GISS analysis of surface temperature change. *J. of Geophys. Res.* **104**, 30,997-31,022 (1999).

19. Wilkinson, C. & Souter, D. *Status of Caribbean coral reefs after bleaching and hurricanes in 2005*. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Center, Townsville (2008).

20. Kramer, P.A. & Kramer, P.R. Transient and lethal effects of the 1998 coral bleaching event on the Mesoamerican reef system. *Proc. 9th Int. Coral Reef Symp.* **2**, 1175-1180 (2000).

21. Lough, J.M. 1997-98: Unprecedented thermal stress to coral reefs? *Geophys. Res. Lett.* **27**, 3901-3904 (2000).

22. Rayner, N. A., et al. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* **108**, 4407 (2003).

23. McField, M.D. Coral response during and after mass bleaching in Belize. *Bull. Mar. Sci.* **64**, 155-172 (1999).

24. Andréfouët, S., Mumby, P.J., McField, M., Hu, C. & Muller-Karger, F.E. Revisiting coral reef connectivity. *Coral Reefs* **21**, 43-48 (2002).

25. Koenig, A., Carilli, J. & Buster, N. A comparison of chemical records in *Montastraea faveolata* and *Siderastrea siderea* as examined by laser ablation ICP-MS: A look at methodology for Caribbean coral for seasonal and storm events. Poster 4.70 presented at 11th International Coral Reef Symposium, Fort Lauderdale, July 7-11, 2008.

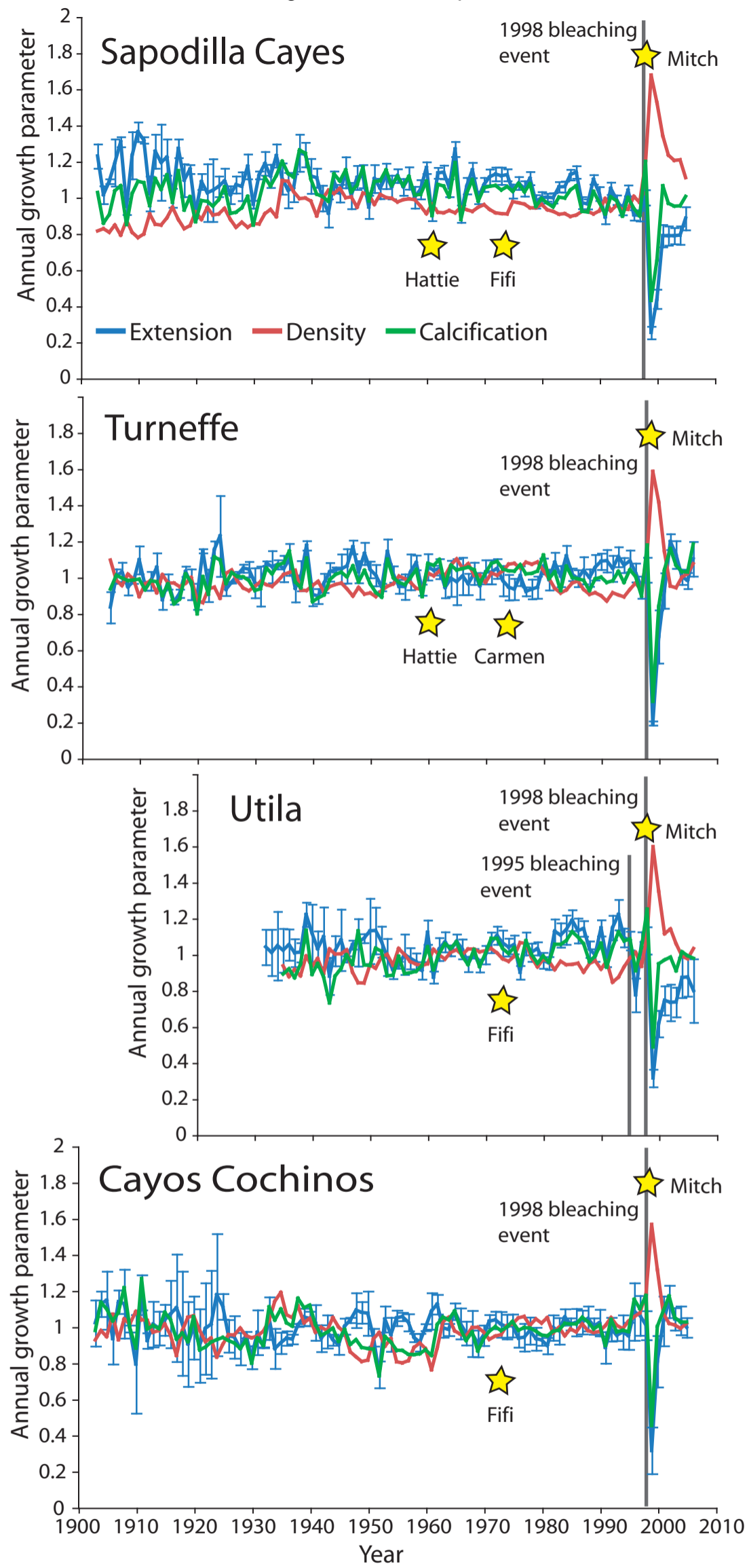
26. Prouty, N.G., Hughen, K.H. & Carilli, J.E. Geochemical Signature of Land-based Activities in Caribbean Coral Surface Samples. *Coral Reefs* in press (2008).

27. Hoegh-Guldberg, O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **50**, 839–866 (1999).

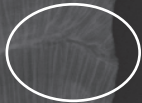
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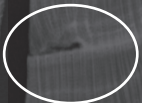
Cayos



Sapodilla



Turneffe



Utila



