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Simulation and observations of annual density banding in skeletons of *Montastraea* (Cnidaria: Scleractinia) growing under thermal stress associated with ocean warming

Abstract—We present a model of annual density banding in skeletons of *Montastraea* coral species growing under thermal stress associated with an ocean-warming scenario. The model predicts that at sea-surface temperatures (SSTs) <29°C, high-density bands (HDBs) are formed during the warmest months of the year. As temperature rises and oscillates around the optimal calcification temperature, an annual doublet in the HDB (dHDB) occurs that consists of two narrow HDBs. The presence of such dHDBs in skeletons of *Montastraea* species is a clear indication of thermal stress. When all monthly SSTs exceed the optimal calcification temperature, HDBs form during the coldest, not the warmest, months of the year. In addition, a decline in mean-annual calcification rate also occurs during this period of elevated SST. A comparison of our model results with annual density patterns observed in skeletons of *M. faveolata* and *M. franksi*, collected from several localities in the Mexican Caribbean, indicates that elevated SSTs are already resulting in the presence of dHDBs as a first sign of thermal stress, which occurs even without coral bleaching.

Knutson et al. (1972) discovered that massive coral skeletons show annual variations in density as paired, subannual bands of high and low density in X-radiographs of skeletal slices taken along the growth axis. This banding pattern allows dating and quantification of average-annual growth characteristics for massive coral colonies. Annual growth characteristics that can be recovered from such bands include skeletal density (bulk density), extension rate, and calcification rate. Annual calcification rate is calculated by multiplying the annual-average skeletal density by its corresponding annual extension rate ($\mathrm{g\ cm^{-3}} \times \mathrm{cm\ yr^{-1}} = \mathrm{g\ cm^{-2}\ yr^{-1}}$) (Dodge and Brass 1984).

Since their discovery, annual density bands have been shown to provide useful information not only about coral growth rates but also about the environmental conditions that accompany coral growth (e.g., Barnes and Lough 1996). To derive environmental information from measurements of coral growth and density, we need to better understand how biological and environmental factors influence coral growth (Lough and Barnes 1990).

For example, annual density bands provide records of the response of massive corals over space (environment) and time. These records have allowed the identification of major environmental controls on coral growth (e.g., Grigg 1997; Lough and Barnes 2000; Carricart-Ganivet 2004) and projection of possible effects on coral-reef ecosystems resulting from increased sea-surface temperatures (SSTs), which have been proven to accompany the enhanced accumulation of greenhouse gases (e.g., IPCC 2001).

Calcification is one of the most important processes occurring in coral reef systems. Reef-building corals produce large amounts of calcium carbonate substratum, which counters physical erosion of the reef structure. Short- and long-term experiments have shown that, as temperature increases, coral calcification rates increase until they reach a maximum; thereafter, calcification rates decline (e.g., Marshall and Clode 2004).

The thermal sensitivity of reef-building corals has been pointed out as their Achilles' heel. Coral reefs are among the first ecosystems to exhibit the impacts of climate warming, e.g., coral bleaching and mortality (Hoegh-Guldberg 1999). One subject that is often left out of the discussion of the impacts of climate change on the health of coral reefs is the sublethal and/or chronic effects of thermal stress that bring about changes in growth rate, calcification, and age structure, which, in turn, fundamentally affect reef function, resilience, and survival. In general, reef-building corals that experience thermal stress exhibit reduced growth and calcification rates and are more susceptible to other stresses (Goreau and MacFarlane 1990; Meesters and Bak 1993).

Montastraea species are the major reef-building massive corals in the West Atlantic Ocean, and they also are the most commonly used in sclerochronological studies in that region (Knowlton et al. 1992). Their skeletons have been used to provide records of local and global environmental change (e.g., Druffel 1982; Dodge and Lang 1983). In *Montastraea*, high-density band (HDB) formation has been thought to be related to seasonal increases in SSTs, whereas low-density bands (LDB) occur during seasonal low SSTs (Hudson 1981; Carricart-Ganivet et al. 1994, 2000).

Dodge and Brass (1984) found that the calcification rate of *Montastraea* was higher during HDB formation than during LDB formation. Cruz-Piñón et al. (2003) found that the intra-annual extension rate of *M. annularis* and *M. faveolata* did not vary significantly over the annual cycle, and Carricart-Ganivet (2004) observed that *Montastraea* invests calcification resources into skeletal density. Consequently, annual density banding in *Montastraea* species

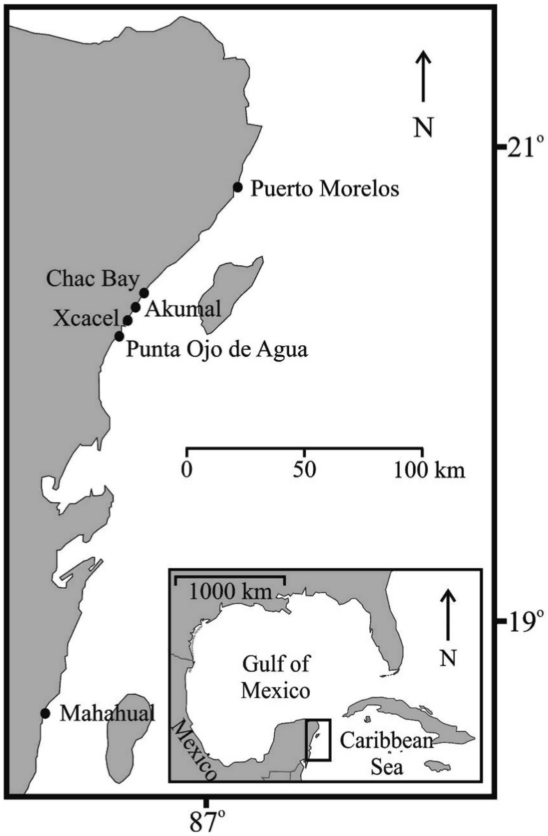

Fig. 1. Location of sampling sites.

arises from differences in calcification rate, and, therefore, it can be considered a good estimator of calcification rate in these species.

We present a simple model of annual density banding in skeletons of *Montastraea* species growing under the thermal stress associated with an ocean-warming scenario. We validate the model by showing that the annual density banding pattern generated by it, using SST data from the Mexican Caribbean from 1985 to 2004, is in accord with observed annual density banding patterns found in samples of *M. faveolata* and *M. franksi* collected from a number of sites in the Mexican Caribbean.

Materials and methods

We collected 17 cores from healthy specimens of *M. faveolata* and *M. franksi* growing in shallow water (0.5–2 m). The corals were obtained from several localities within the Mexican Caribbean (Fig. 1; Table 1). All core samples were collected along the main growth axis of the coral by a scuba diver using a rotary pneumatic hand drill fitted with a 3-cm-diameter, 38-cm-long diamond-bit core barrel. A polystyrene ball was inserted into the core hole to prevent bioerosion by rock-boring organisms. The ball also provided a hard substrate over which coral growth could spread, in time completely covering the polystyrene ball.

From each core, a 7-mm-thick slice was obtained using a rock saw equipped with a diamond-tipped blade. The slices were then X-rayed using a conventional CGR X-ray source under the following conditions: 44 kV, 50 mA, 3.75 mAs at 1.8 m of focal distance. A 14-in × 17-in Kodak® T–Mat G/RA film in a Kodak® Lumex Fast Screens X-OMAT cassette was used.

Developed X-ray films were digitized with a ScanMaker 9800XL using a transparent media adapter (TMA) 1600 lid for transparent films (MICROTEK; http://www.microtek.com) at 300 dpi (dots per inch) resolution. Digitized images were inverted to provide X-ray positives using Adobe Photoshop (Adobe Systems). Annual bands identified from mid-summer to mid-summer were dated retrospectively (Carricart-Ganivet et al. 2000).

Two SST data sets for the period 1985 to 2004, one associated with northern coral sampling localities (Puerto Morelos, Chac Bay, Akumal Bay, Xcacel, and Punta Ojo de Agua), and the other one with the Mahahual locality (Table 1), were obtained from the Hadley Centre Sea Ice and SST (HadISST) data set produced by the United Kingdom Meteorological Office. These data are monthly averages of SST measurements taken from the Met Office Marine Data Bank (MDB), which also includes data received through the Global Telecommunications System (GTS) from 1982 onward. Where there are no MDB data, the HadISST data set uses monthly median SSTs for 1871 to 1995 from the Comprehensive Ocean-Atmosphere Data Set (COADS) in order to enhance data coverage (*see* Rayner et al. 2003).

Table 1. Mexican Caribbean sampling sites and collection dates of the collected cores of *Montastraea faveolata* and *M. franksi*.

Sampling site	Species	Collection date	Collected cores
Puerto Morelos	*M. faveolata*	Jun 2006	3
Chac Bay	*M. franksi*	Jul 2005	2
Akumal Bay	*M. faveolata*	Jun 2006	1
	M. franksi	Jul 2005	1
	M. franksi	Jun 2006	2
Xcacel	*M. franksi*	Jun 2006	1
Punta Ojo de Agua	*M. franksi*	Jun 2006	1
Mahahual	*M. faveolata*	Apr 2006	3
	M. franksi	Apr 2006	3

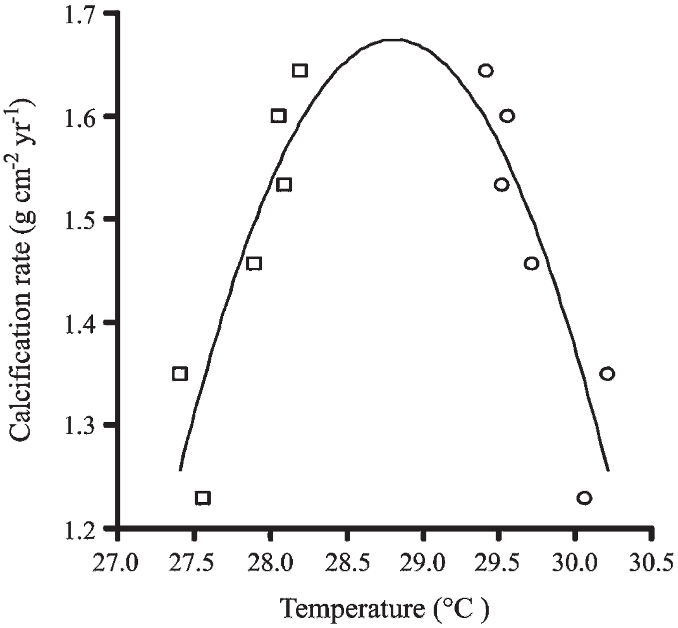

Fig. 2. Theoretical Gaussian-like distribution curve of calcification rate as a function of temperature for *Montastraea* species growing in the Mexican Caribbean. Open squares are Carricart-Ganivet's (2004) calcification rate data of *M. annularis* and *M. faveolata* growing in a SST spatial gradient in the Caribbean, and open circles are the corresponding symmetrical values of them (i.e., mirror image), assuming that maximum calcification rate occurs at 28.8°C (see text for details). The equation for the calcification curve is: Calcification rate = $-0.21T^2 + 12.26T - 174.86$, where temperature (T) is in degrees Celsius.

Results and discussion

Calcification rates—To the best of our knowledge, published experiments that indicate the response of coral calcification rates to temperatures above the optimal temperature maximum do not exist for any *Montastraea* species. To obtain such a relation, we used Carricart-Ganivet's (2004) calcification rate data for *M. annularis* and *M. faveolata*, across a SST spatial gradient, to obtain a fit to a binomial equation (Gaussian distribution) (Fig. 2). Maximum (optimal) calcification rate was assumed to occur in Mexican Caribbean *Montastraea* species at 28.8°C. This value is the mean SST value at the coral sampling areas during the warmest months (June to November) between 1985 and 2004.

Gaussian distributions of calcification rates with respect to temperature also have been observed by other authors for several coral species (e.g., Marshall and Clode 2004). Our assumption that the mean SST value of the warmest months from 1985 to 2004 is equivalent to the optimal temperature at which maximum calcification of *Montastraea* species occurs is supported by the study of Marshall and Clode (2004). These authors found that *Galaxea fascicularis* and *Dendrophyllia* sp. have their maximum calcification rate at 25°C, a value nearly the same as the mean SST value of the warmest months where these authors collected their corals (Heron Island; *see* fig. 3 in Marshall and Clode 2004).

The density banding model—To determine how an increase in SST might affect annual density banding, we invoked a simple SST increase where the mean-annual ocean temperature linearly increased by 2.5°C over 20 yr. At the beginning of the period, the SST oscillation remains under 28.8°C (the maximum-calcification-rate temperature). At the end of the 20-yr period, the SST oscillation occurs above the maximum-calcification-rate temperature (Fig. 3). The rate of change of the mean-annual SST is arbitrary and does not necessarily correspond to any model of ocean warming. However, the simulated period serves to illustrate the change in density structure and calcification rate due to a 2.5°C increase in the mean-annual SST, a value toward the upper range predicted for tropical oceans by the end of this century (IPCC 2001). To facilitate visual identification of emerging density patterns from the model, a modeled X-ray pattern was generated by transforming values of the modeled calcification rate to values of optical density (the gray-scale value of pixels; 0–255).

When the SST oscillation does not exceed 28.8°C, HDBs form during the warmest months of the year (Fig. 3). This is consistent with a variety of observations of *Montastraea* species from the West Atlantic Ocean (Hudson 1981; Carricart-Ganivet et al. 1994, 2000). When the SST oscillation exceeds 28.8°C, the model predicts that HDBs will be formed during the coldest months of the year. This is because the optimal temperature for calcification occurs during the coldest months under these conditions. Between these two extremes in temperature, an annual "HDB doublet" (dHDB) occurs in which two relatively narrow HDBs are formed. This is due to the SST oscillation crossing the maximum-calcification-rate temperature twice a year and suppression of calcification during the intervening period. The presence of these dHDBs can be considered to be a symptom of thermal stress suffered by the coral. Under the increasing SST scenario, calcification rates are more variable but smaller on average during the coolest and warmest intervals. The finding that mean-annual calcification rate will decrease with increasing temperature contradicts the results of McNeil et al. (2004), who suggested that rising SSTs would have a uniformly positive effect on coral calcification over the coming century. Kleypas et al. (2005) argued that many of the critical assumptions of McNeil et al. (2004) were not supported by existing information on the limits of coral growth and calcification, by present-day coral reef distributions, and by the responses of coral growth to temperature. We must note that our model ignores the negative effects on coral calcification rate caused by the decrease in the seawater aragonite saturation state and changes in ocean acidity due to atmospheric $p\mathrm{CO}_2$ increase (Kleypas et al. 1999).

Model-data comparison—When using the two SST data sets obtained here, our model shows the formation of dHDBs in the annual density banding model (Fig. 4). Although we found a clear visual match between the formation of dHDB predicted by the model in the modeled X-ray pattern and those observed in the X-ray contact prints (e.g., Fig. 4), this match was not always very clear in all X-ray contact prints. In order to test the statistical significance of the overall match between the modeled X-ray pattern and the observed pattern

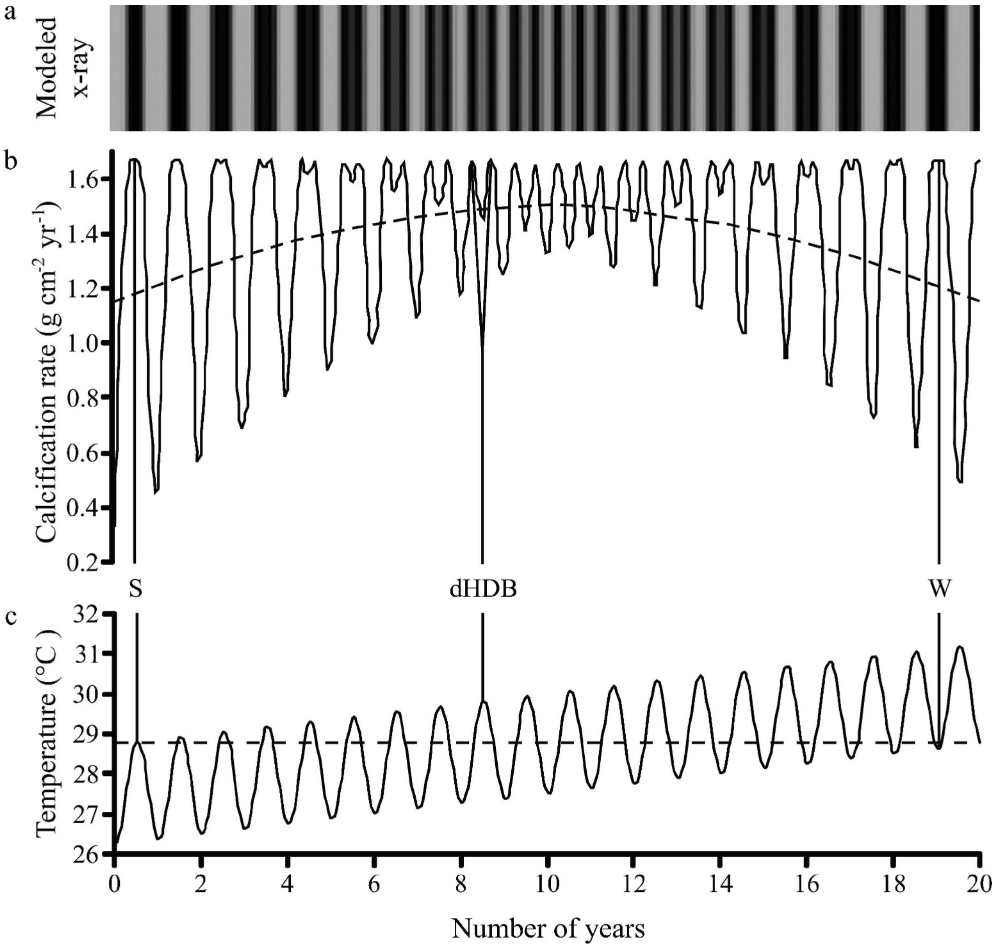

Fig. 3. Modeled density banding pattern in *Montastraea* species for a theoretical SST increase of 2.5°C in 20 yr. (a) Modeled X-ray of density banding pattern generated by transforming the predicted calcification rate values to gray-scale value of pixels. S = formation of the HDB during the warmest months of the year, and W = formation of the HDB during the coldest months of the year. The dHDBs appear when the temperature oscillates around 28.8°C (see text for details). (b) Predicted calcification rate in 20 yr calculated using equation from Fig. 2 for the theoretical SST increase. The dashed line is the predicted mean calcification rate. (c) Theoretical SST increase of 2.5°C in 20 yr. The horizontal dashed line marks the assumed optimal temperature for calcification rate in *Montastraea* species growing in the Mexican Caribbean.

in all X-ray contact prints, we used a generalized linear model of the binomial family that was fitted using the "glm" package in R (R Development Core Team 2006). We used the default "logit link" function. Model prediction of presence or absence of a clearly identifiable dHDB was the binary response variable.

In order to provide a detailed test, we included sampling sites, species, and model prediction as explanatory variables. Sampling sites and species were included as a fixed rather than a random factor in the statistical model in order to look for explainable causes of discrepancies between the model and observations. Because there were separate observations for each of the 20 yr (1985–2004) analyzed, we were able to include an interaction term in the model. This allowed us to test whether the match between model prediction and observation was significantly better or worse in certain sampling sites or with certain species.

The modeled presence of dHDBs was a highly significant ($p < 0.01$) predictor of the observed presence of dHDBs in all coral X-ray contact prints. Sampling sites and species were not found to have an overall significant influence when modeled as a fixed effect ($p = 0.93$ and $p = 0.2$, respectively), suggesting that either variability between cores was idiosyncratic rather than systematic or that we had insufficient replication to allow a clear, statistically significant sampling-site or species-specific pattern to be detected. Interactive effects between species or sampling sites and model predictions were not significant ($p = 0.45$ and $p = 0.55$, respectively).

The presence of dHDBs is not reported in older *Montastraea* density banding published reports, neither for the study sites (e.g., Carricart-Ganivet et al. 2000), nor for other reef locations in the Atlantic Ocean (e.g., Hudson 1981; Dodge and Brass 1984). Thus, the occurrence of dHDBs signals the

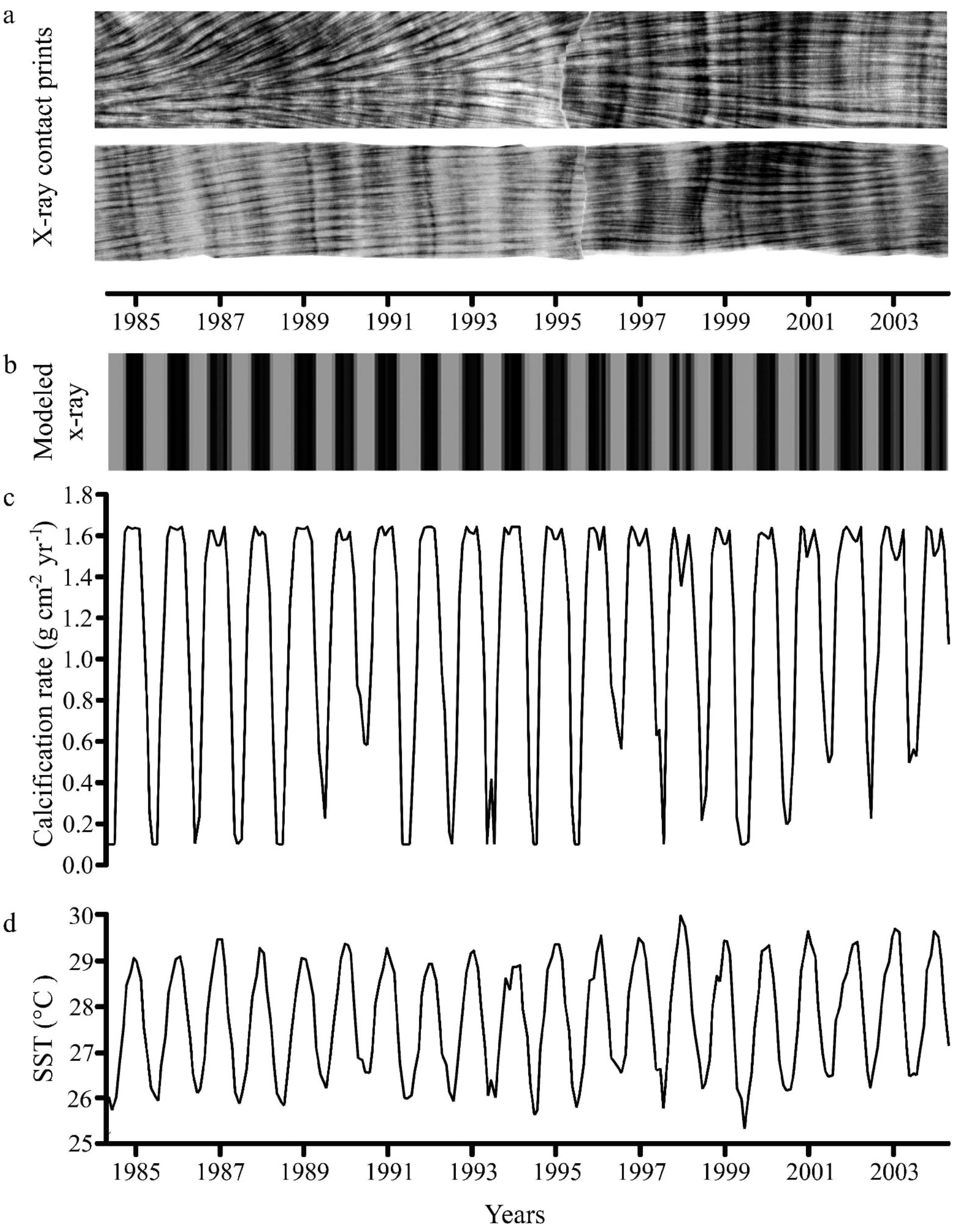

Fig. 4. Visual comparison of the density banding pattern from 1985 to 2004 observed in the X-ray contact prints of two slices of two specimens of *M. franksi* collected in Mahahual with the "modeled X-ray" density banding pattern for the same period of time in *Montastraea* species growing in the Mexican Caribbean. (a) X-ray contact prints of two slices of two specimens of *M. franksi* collected in Mahahual showing the density banding pattern. The upper contact print is the worst visual match between the formation of dHDB predicted by the model in the modeled X-ray pattern and those observed in the X-ray contact prints found in the *Montastraea* specimens collected in Mahahual, and the lower one is the best visual match found in the specimens collected in the same locality. (b) Modeled X-ray of density banding pattern generated by transforming the predicted calcification rate values to gray-scale value of pixels. (c) Predicted calcification rate using equation from Fig. 2 with monthly mean SST from 1985 to 2004 in Mahahual. (d) Monthly mean SST from 1985 to 2004 in Mahahual.

presence of thermal stress suffered by the coral caused by higher SSTs than the optimal temperature of the maximum calcification rate of *Montastraea* species, in some years from 1985 to 2004, and it may therefore be taken as a first sign that coral species are not adapting to rapidly increasing SST as suggested by some authors (e.g., Edmunds 2005). Moreover, thermal stress that causes dHDB formation does not necessarily cause coral bleaching; bleaching events are expected to occur when the current SST reaches 1°C over the maximum monthly mean SST (http://www.osdpd.noaa.gov/PSB/EPS/CB_indices/coral_bleaching_indices.html). Between 1985 and 2004, bleaching events occurred three times (1995, 1997, and 1998) in Puerto Morelos (R. Iglesias-Prieto pers. comm.). Finally, the presence of dHDBs in the density banding pattern of *Montastraea* species can be used as a simple tool for monitoring their health as well as the health of the entire coral-reef ecosystem in the future. It is worth mentioning that a similar characteristic signal of thermal stress would not be expected in the density banding pattern of massive *Porites* species, the most commonly used corals in the Indian and Pacific Oceans, since these species invest calcification resources in extension rate (Lough and Barnes 2000; Carricart-Ganivet 2004), and density banding arises from thickening of the skeleton through the depth of the tissue layer (Barnes and Lough 1993).

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References

Barnes, D. J., and J. M. Lough. 1993. On the nature and causes of density banding in massive coral skeletons. J. Exp. Mar. Biol. Ecol. **167:** 91–108.

———, and ———. 1996. Coral skeletons: Storage and recovery of environmental information Global Change Biol. **2:** 569–582.

Carricart-Ganivet, J. P. 2004. Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*. J. Exp. Mar. Biol. Ecol. **302:** 249–260.

———, A. U. Beltrán-Torres, M. Merino, and M. A. Ruiz-Zárate. 2000. Skeletal extension, density and calcification rate of the reef building coral *Montastraea annularis* (Ellis and Solander) in the Mexican Caribbean. Bull. Mar. Sci. **66:** 215–224.

———, G. Horta-Puga, M. A. Ruiz-Zárate, and E. Ruiz-Zárate. 1994. Tasas retrospectivas de crecimiento del coral hermatípico *Montastrea annularis* (Scleractinia: Faviidae) en arrecifes al sur del Golfo de México. Rev. Biol. Trop. **42:** 517–523.

Cruz-Piñón, G., J. P. Carricart-Ganivet, and J. Espinoza-Avalos. 2003. Monthly skeletal extension rates of the hermatypic corals *Montastraea annularis* and *Montastraea faveolata*: Biological and environmental controls. Mar. Biol. **143:** 491–500.

Dodge, R. E., and G. W. Brass. 1984. Skeletal extension, density and calcification of the reef coral, *Montastrea annularis*: St. Croix, U.S. Virgin Islands. Bull. Mar. Sci. **34:** 288–307.

———, and J. C. Lang. 1983. Environmental correlates of hermatypic coral (*Montastrea annularis*) growth on the East Flower Gardens Bank, northwest Gulf of Mexico. Limnol. Oceanogr. **28:** 228–240.

Druffel, E. M. 1982. Banded corals: Changes in oceanic carbon-14 during the Little Ice Age. Science **218:** 13–19.

Edmunds, P. J. 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Oecologia **146:** 350–364.

Goreau, T. J., and A. H. MacFarlane. 1990. Reduced growth rate of *Montastrea annularis* following the 1987–1988 coral-bleaching event. Coral Reefs **8:** 211–215.

Grigg, R. W. 1997. Paleoceanography of coral reefs in the Hawaiian-Emperor Chain—revisited. Coral Reefs **16:** S33–S38.

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

Hudson, J. H. 1981. Growth rates in *Montastrea annularis*: A record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. Bull. Mar. Sci. **31:** 444–459.

IPCC (Intergovernmental Panel on Climate Change). 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Kleypas, J. A., R. W. Buddemeier, D. Archer, J.-P. Gattuso, C. Langdon, and B. N. Opdyke. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science **284:** 118–120.

———, ———, C. M. Eakin, J.-P. Gattuso, J. Guinotte, O. Hoegh-Guldberg, R. Iglesias-Prieto, P. L. Jokiel, C. Langdon, W. Skirving, and A. E. Strong. 2005. Comment on "Coral reef calcification and climate change: The effect of ocean warming. Geophys. Res. Lett. **32**, L08601, doi:10.1029/2004GL022329.

Knowlton, N., E. Weil, L. A. Weigth, and H. M. Guzmán. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. Science **255:** 330–333.

Knutson, W., R. W. Buddemeier, and S. V. Smith. 1972. Coral chronometers: Seasonal growth bands in reef corals. Science **177:** 270–272.

Lough, J. M., and D. J. Barnes. 1990. Possible relationships between environmental variables and skeletal density in a coral colony from the Central Great Barrier Reef. J. Exp. Mar. Biol. Ecol. **134:** 221–241.

———, and ———. 2000. Environmental controls on growth of the massive coral *Porites*. J. Exp. Mar. Biol. Ecol. **245:** 225–243.

Marshall, A. T., and P. Clode. 2004. Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. Coral Reefs **23:** 218–224.

McNeil, B. I., R. J. Matear, and D. J. Barnes. 2004. Coral reef calcification and climate change: The effect of ocean warming. Geophys. Res. Lett. **31**, L22309, doi:10.1029/2004GL021541.

Meesters, E. H., and R. P. M. Bak. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. Mar. Ecol. Prog. Ser. **96:** 189–198.

R Development Core Team. 2006. R: A language and environment for statistical computing.R Foundation for Statistical Computing. Available from http://www.R-project.org. Vienna. Accessed 2007.

Rayner, N. A., D. E. Parker, E. B. Horton, C. K. Folland, L. V. Alexander, D. P. Rowell, E. C. Kent, and A. Kaplan. 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. J. Geophys. Res. **108**, 4407, doi:10.1029/2002JD002670.

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