Limnol. Oceanogr., 51(2), 2006, 1142–1148

Heterogeneity of coral skeletons isotopic compositions during the 1998 bleaching event

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Abstract

The vulnerability of coral reefs to climate change, such as regional warming, became fully evident during the strong 1997–1998 El Niño event. This El Niño episode was associated with elevated sea-surface temperatures and caused mass mortality throughout many of the world's coral reefs. We analyzed the isotopic manifestation of this event in six *Porites* sp. coral skeletons from different localities in a small atoll (Alphonse) at the Seychelles Island. The aim was to validate the use of coral stable isotope compositions as recorders of such events in the past. The coupling between local-scale environment and global warming was weaker then expected, with regional warming being evident only when data from five colonies were averaged. Local conditions had a large effect on the isotopic compositions of coral skeletons. We conclude that future paleoclimate reconstructions, especially those attempts to identify past El Niño events, must be based on more than a single coral record. Moreover, the strong effect of local habitat on the isotopic composition of *Porites* sp. has to be considered when interpreting $\delta^{13}C$ and $\delta^{18}O$ records.

Coral reefs are among the most diverse ecosystems of the world and maintain one of the largest remaining reservoirs of biodiversity on Earth's surface. Coral skeletons contain a rich archive of past variation in seawater temperature and chemistry. They are often used to reconstruct tropical paleoclimate and past occurrence of El Niño Southern Oscillation (ENSO) events (Barnes and Lough 1996; Charles et al. 1997; Cole et al. 2000; Gagan et al. 2000; Cobb et al. 2003). There is strong evidence that coral-reef ecosystems around the world are deteriorating due to a complex suite of reasons, including climate change, human activity, and diseases (Harvell et al. 1999; Roberts et al. 2002). The 1997–1998 El Niño event affected large parts of the tropical oceans and caused mass coral bleaching and mortality in the Indo-Pacific and the Caribbean (Berkelmans and Oliver 1999; Aronson et al. 2002; Coles and Brown 2003), with sea surface temperature (SST) anomalies of +1–3°C sustained over two years (Wilkinson et al. 1999; McClanahan 2000). Temperature records show that the 1982–1983 and 1997–1998 El Niño were the strongest since 1877 (Spencer et al. 2000), and that the 1997–1998 event was probably the strongest of the millennium (Mann et al. 1998, 1999; Salingo 1998). The 1997–1998 El Niño event exhibited the most rapid initial warming ever documented and showed an extended period of high temperature with maxima during both July 1997–August 1997 and March 1998–April 1998 (McPhaden 1999).

Mass coral bleaching events are linked to elevated SST, generally considered to be the primary cause of coral stress worldwide. In the central and western Indian Ocean, approximately 59% of the reefs were damaged during 1998 (Wilkinson et al. 1999; Abram et al. 2003; Hughes et al. 2003), while recovery was observed only during 2002. The effect of these unusually warm ocean temperatures on the long-term health of coral reefs is of concern; the frequency of such events is likely to increase with global warming.

The main objective of this study is to characterize the isotopic signature of a severe bleaching event in the coral skeleton. Understanding the signature of such events is critical for identification of such events in the past and to establish the frequency with which it occurred under undisturbed, natural conditions.

In January 2002, massive *Porites* corals were sampled from a pristine area located in Alphonse atoll, a Southern Seychelles Island in the Indian Ocean that was affected by the 1998 El Niño event.

Continuous coral isotope records from 1982 and 2001 depict the isotopic manifestation of the 1998 bleaching episode. Measurements of $\delta^{18}O$ and $\delta^{13}C$ within the annual density bands also provided information about the development of stress signals in corals and their subsequent recovery. In addition, isotope data from several coral cores sampled from different local habitats at the same atoll shed light on coral metabolism, the bleaching phenomenon, calcification, and survival in different marine environments that are in close proximity. Such comparisons establish the natural variability of $\delta^{18}O$ and $\delta^{13}C$ of corals at a local scale and allow comparison with large-scale events that are globally significant.

Materials and methods

Alphonse Atoll (7°0′S, 52°45′E) is a small (6 × 4 km) sea-level atoll, 415 km south of Mahé, the largest Island in the Seychelles Bank (Spencer et al. 2000). It represents an open-ocean region with minimal direct human interference on its coral reef system (Fig. 1A). Hence, climate variability should be the dominant impact on its coral survival. Six *Porites* corals were cored from several peripheral reefs surrounding the atoll and from the inside lagoon that reaches a depth of ~10 m at its center. During March 1998–April 1998, sea-surface temperatures increased to almost 2°C above normal in the region of the Seychelles Islands (Fig. 1B) and 74% of the normal coral cover on the outer reef slopes in Alphonse was recorded as bleached or recently dead (Spencer et al. 2000). The sampled corals live in dif-

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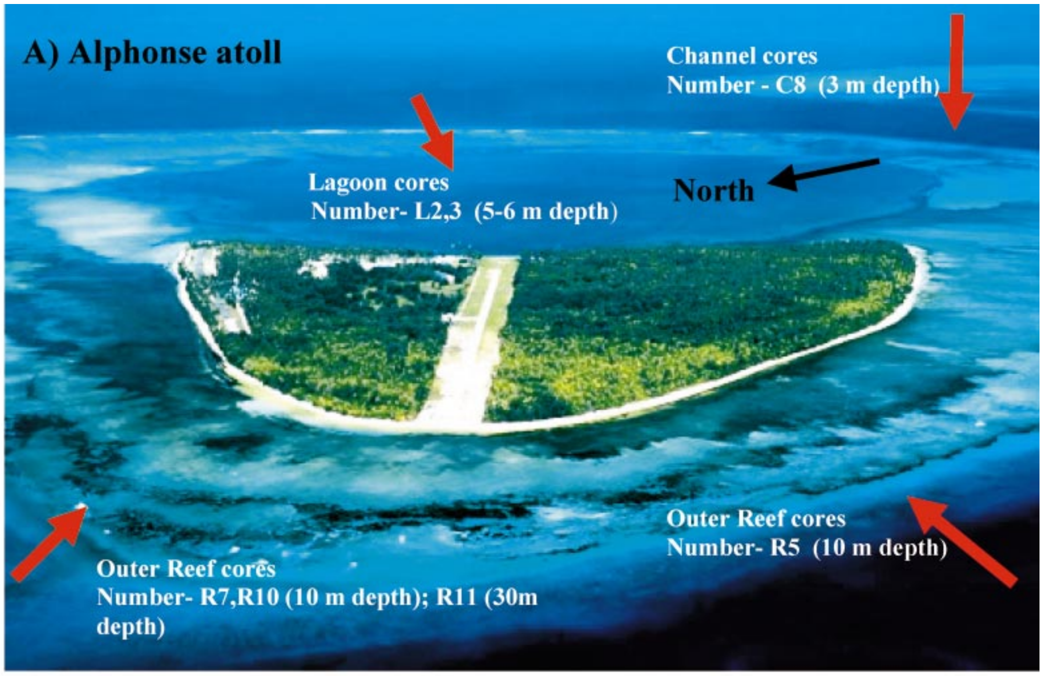
Acknowledgments

We thank D. Barnes for his help with density measurements undertaken at AIMS, Australia. We thank Yosef Ashkenazy and D. Barnes for their constructive suggestions and comments on the manuscript.



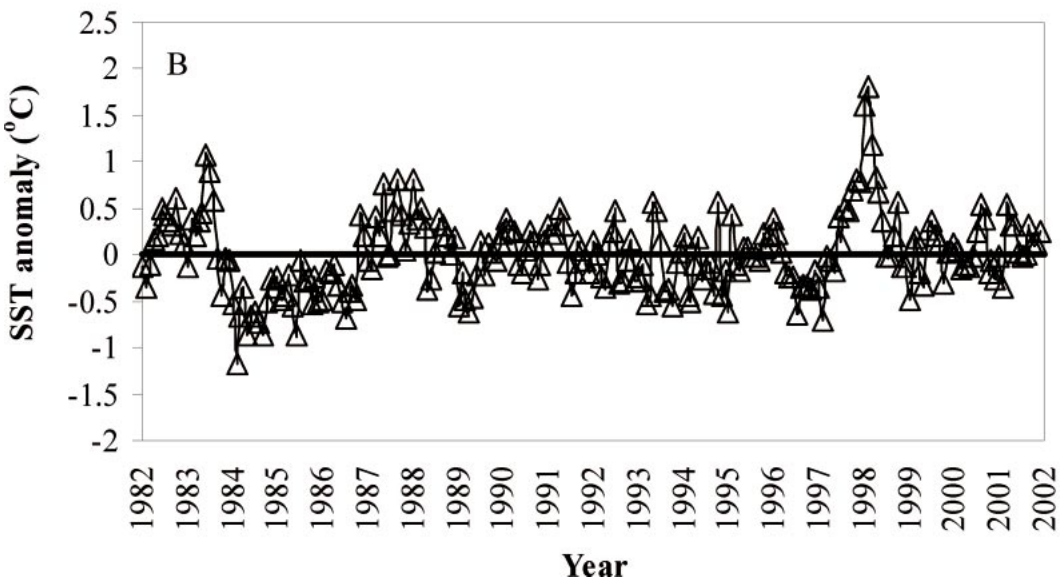


Fig. 1. (A) Alphonse atoll, Seychelles (7°0′S, 52°45′E) and location of the sampling sites. (B) Monthly sea surface temperature anomalies for the region (SST 4° × 4° grid box; 4–8°S, 52–56°E; SST. http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.SST/).

ferent environments. The reefs inside the lagoon are subject to high freshwater flux drained from the island and carry large amounts of dissolved organic matter from the densely forested island. However, all water samples analyzed during a 1998 cruise in this Island had almost the same water $\delta^{18}O$ (range of 0.15‰ for more than 15 samples within the Island vicinity; Shemesh, unpublished data), which indicates a very short residence time of the water within the lagoon. The outer reefs are better developed and are subject to clear, open surface waters of the Indian Ocean. One core was recovered from the channel connecting the lagoon with the open sea (Fig. 1A).

Corals cores of *Porites* sp. were drilled using SCUBA diving and a pneumatic drill to obtain 30–50-cm-long cores along the major growing axis. The cores were washed, dried, and sectioned into 7-mm-thick slabs. X-ray-positive prints of the slabs revealed the annual density banding patterns characteristic of massive corals as *Porites* and were used as a guide for microdrilling along the major axis of growth (Linsley et al. 1999). Samples of 100–150 μg $CaCO_3$ pow-

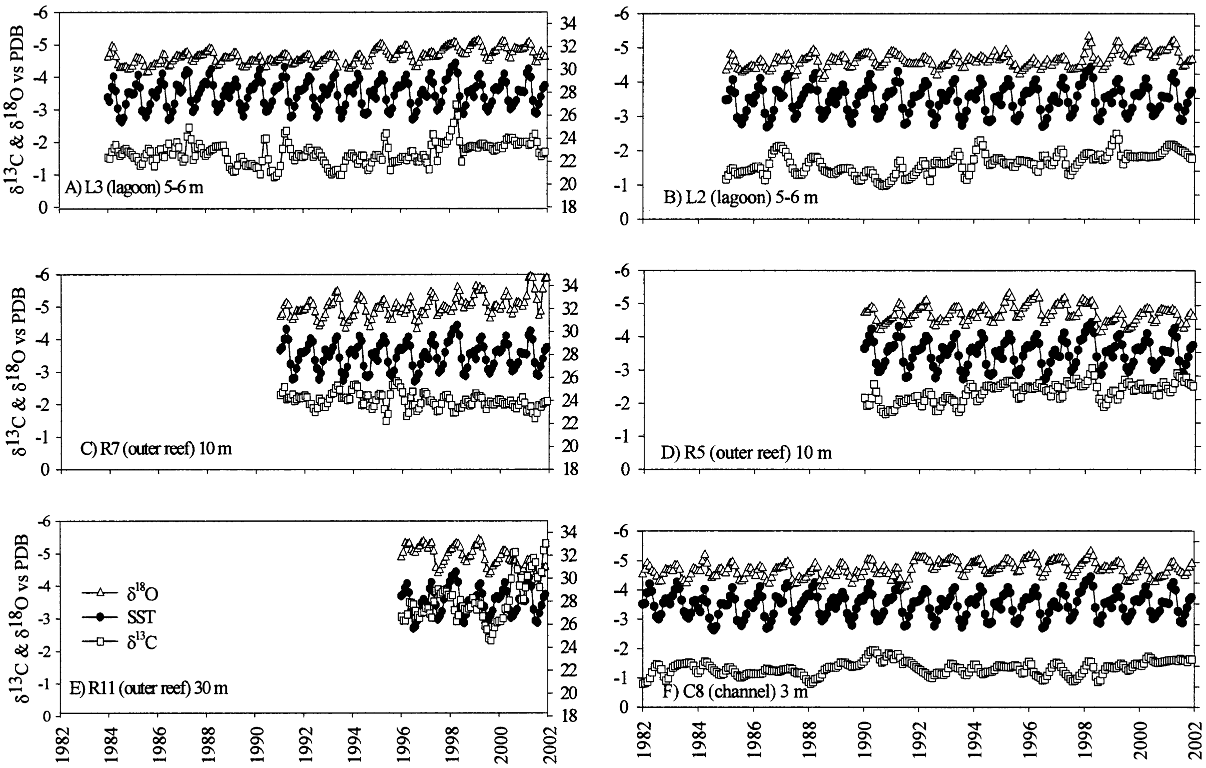


Fig. 2. Monthly variability in skeletal $\delta^{18}O$ and $\delta^{13}C$ for six *Porites* sp. coral cores (A–F) retrieved from different habitats in Alphonse atoll compared with monthly SSTs (black line). Depletion in $\delta^{18}O$ during 1998 was observed only in cores L2 from the lagoon and C8 from the channel.

der were collected every 0.7 mm using a dental drill. This drilling spacing yields 10–15 samples per annual density band. Because corals grow 8–15 mm per year, this sampling method provides bimonthly–monthly resolution. $CaCO_3$ samples for $\delta^{18}O$ and $\delta^{13}C$ analyses were reacted with 100% orthophosphoric acid and the CO_2 was measured using online GasBench II connected to MAT 252 mass spectrometer. Calibration was maintained by routine analyses of internal and international standards. The long-term precision of our internal laboratory standard is 0.06‰ and 0.10‰ for carbon and oxygen, respectively.

Even-spaced time series (monthly) were obtained by interpolating the raw data using Analyseries program (Paillard et al. 1996) from isotopic minima and maxima. Results are reported in per-mill units relative to the international Vienna-Peedee Belemnite Limestone Standard (V-PDB). Density measurements of the cores were obtained by gamma densitometer parallel to the drilling profile track. The coral slice was moved in steps of 0.254 mm by linear pass beneath the gamma source with resolution of 0.254 mm per step (Chalker and Barnes 1990; Barnes et al. 2003). Calcification rate was calculated by multiplying the density value of each annual band by its corresponding skeletal extension.

Results

Generally, $\delta^{18}O$ minima in *Porites* correspond to periods of high water temperature during the summer (Weber and Woodhead 1970; Juillet-Leclerc and Schmidt 2001). Our measurements show that $\delta^{18}O$ varied inversely with temperature in all six corals (Fig. 2A–F). However, there was no systematic depletion in $\delta^{18}O$ during 1998. We also did not trace any growth hiatus in the X-ray prints during the period of 1997–1998. Only one core from the lagoon and one from the channel (L2 and C8, respectively) recorded extreme depletion in $\delta^{18}O$ values during the 1998 warming (Fig. 2B–F). Correlations between monthly SST and $\delta^{18}O$ of $r = -0.61$ and -0.63, with a slope of -0.118‰/°C were found in cores from the lagoon (L2 and L3, respectively). The channel coral's (C8) correlation was $r = -0.66$, with slope of -0.147‰/°C; and for the outer reef corals, the correlations were -0.74, -0.62, and -0.49 (R5, R7, and R11, respectively) with slopes between 0.14 and 0.176‰/°C (All correlations were significant; see Table 1). In contrast with the monthly annual temperature–$\delta^{18}O$ correlations, the monthly anomalies (calculated as deviation from the series mean) were not significantly correlated (Table 1). Linear extension rates (Land et al. 1975), calculated from the annual $\delta^{18}O$ profiles, were significantly different among the corals from the three habitats; lagoon, channel, and outer reef (one-way analysis of variance [ANOVA] followed by the least significant difference post hoc test, $p < 0.05$, $n = 78$). Maximum growth was found in the channel coral C8, with average extension rate of 14.81 ± 3.42 mm yr^{-1}. Minimum growth was calculated for the lagoon corals (L2, L3), with average extension of 8.48 ± 1.89 mm yr^{-1}; and intermediate values of 10.64–13.51 mm yr^{-1} were calculated for the outer reef corals R11, R7, and R5.

Table 1. Correlations between monthly $\delta^{18}O$ anomaly and temperature for the six coral cores, Alphonse atoll region. All correlations were significant ($p < 0.05$).

Coral name	Monthly correlations between temperature and $\delta^{18}O$ (r)	Slope (‰/°C)	Anomaly between temperature and $\delta^{18}O$ (r)	Number of samples (n)
L2	−0.61	−0.119	−0.2	204
L3	−0.63	−0.117	−0.33	213
C8	−0.66	−0.147	−0.08	240
R5	−0.74	−0.163	−0.216	144
R7	−0.72	−0.176	−0.14	132
R11	−0.49	−0.14		72

Calcification rates show a similar pattern to that of the extension rates, with higher rates in the channel corals and low rates in the lagoon area (Fig. 3A). The lowest skeletal density was found in the lagoon corals, while the highest was observed in the channel coral.

The skeletal $\delta^{18}O$ and $\delta^{13}C$ also provide information on the ecological plasticity (adaptation) and photoacclimation of a coral to its local surrounding. The aragonite deposited by scleractinian corals is usually depleted in $\delta^{13}C$ relative to equilibrium deposit in ambient seawater as a result of kinetic and metabolic fractionation (McConnaughey 1989). Additional metabolic fractionation is caused by changes in photosynthesis and respiration (Swart 1983), while skeletal $\delta^{18}O$ remains unchanged by these metabolic effects. Therefore, the relationship between $\delta^{18}O$ to $\delta^{13}C$ is used to distinguish between kinetic and metabolic effects. Strong metabolic effects are identified as offset from the kinetic line in $\delta^{13}C$ versus $\delta^{18}O$ plots (Maier et al. 2003). Strong metabolic effect is observed in the lagoon coral C8 and in coral R5 from the outer reef. The relation between annual averaged $\delta^{18}O$ and $\delta^{13}C$ for each coral reveals positive correlation for the lagoon corals ($r = 0.55$ and 0.77 for L2 and L3, respectively) and strong negative correlation for the outer reef corals R7 and R11 ($r = -0.66$ and -0.81, respectively). The channel coral C8 and the outer reef coral R5 show weak correlations ($r = -0.17$ and 0.23, respectively).

Four clusters emerge when $\delta^{13}C$ is averaged for each coral (Fig. 3B). The first cluster, with maximum $\delta^{13}C$, corresponds to the coral from the channel (C8) at 3 m depth. The second, with minimum values, corresponds to the 30-m-deep coral from the outer reef (R11). Corals from the lagoon region, representing the third cluster (L2, L3), had similar values and were not significantly different from each other. We also found no significant changes between corals R5 and R7 of the fourth group from the outer reef, 10 m depth, but both corals were clearly depleted relative to the channel and the lagoon clusters (Fig. 3B; one-way ANOVA followed by the least significant difference post hoc test, $p < 0.05$). The high correlation between $\delta^{13}C$ and depth (Fig. 3C) reflects the relation of carbon isotopes fractionation to light intensity as a function of depth (Goreau 1977; Grottoli 1999; Reynaud-Vaganay et al. 2001). Hence, the differences between the carbon values are not restricted to the different habitats of the corals, but also to the depth habitat of the corals (Grottoli and Wellington 1999). Correlations between cloud cover; and $\delta^{13}C$ were not significant ($p>0.05$) in all sampled corals.

The $\delta^{13}C$ and $\delta^{18}O$ from five corals was averaged since 1991 (the minimum period common for five corals). The averaged $\delta^{18}O$ from five corals emphasizes the clear depletion in oxygen isotope during the 1998 bleaching event ($\delta^{18}O = -5.23$‰; Fig. 4A,C). The mean $\delta^{13}C$ of the five corals during the peak of 1998 was significant ($\delta^{13}C = -2.31$‰; Fig. 4B,C), while the mean $\delta^{13}C$ during 1991–1997 was -1.79 ± 0.1‰ and the postbleaching value for 1999–2002 was -1.97 ± 0.05‰ (t-test, $p < 0.001$).

Discussion

Our observations indicate that the isotopic compositions of *Porites* sp. corals are determined by local habitats, such as the lagoon, the channel, and the outer reef, even in a small atoll like Alphonse. The variability in both extension and calcification rates among the corals reflect the impact of the local habitat on the skeleton's growth (Fig. 3A). The heterogeneity of the different environments is also evident in the isotopic signals. The fact that lighter values of $\delta^{13}C$ occur during the warm season and coincide with minimum values of $\delta^{18}O$ in the lagoon corals suggests that photosynthesis was photo-inhibited during the warm season (McConnaughey 1989; Grottoli 2002). The lack of correlation between cloud cover and $\delta^{13}C$ suggests that seasonality governs the coral's photosynthesis. The opposite trend, where heavier carbon isotopes values coincide with low $\delta^{18}O$ values, was observed in two corals from the outer reef region (R7 and R11, same location), indicating intense photosynthesis during the warm season in these colonies. Fade seasonal variation was observed in corals C8 and R5, with low $\delta^{18}O$ to $\delta^{13}C$ correlations, pointing to constant rates of photosynthesis all year long, with much less seasonal dependence.

The averaged monthly $\delta^{18}O$ and $\delta^{13}C$ measurements of five corals from 1991 were done to reduce the variability associated with local habitat effect and to explore the relationship to the global event. The averaged $\delta^{18}O$ from five corals emphasizes the clear depletion in oxygen isotope during the 1998 bleaching event (Fig. 4A,C), while mean $\delta^{13}C$ values of the five corals during the peak of 1998 bleaching also brings into focus a significant depletion ($\delta^{13}C = -2.31$‰; Fig. 4B,C). This indicates a decrease in the photosynthetic activity of the symbiotic algae (Leder et al. 1989; Grottoli et al. 2004) and reveals a slow recovery during the 3 yr that followed the warming. The monthly correlation between av-

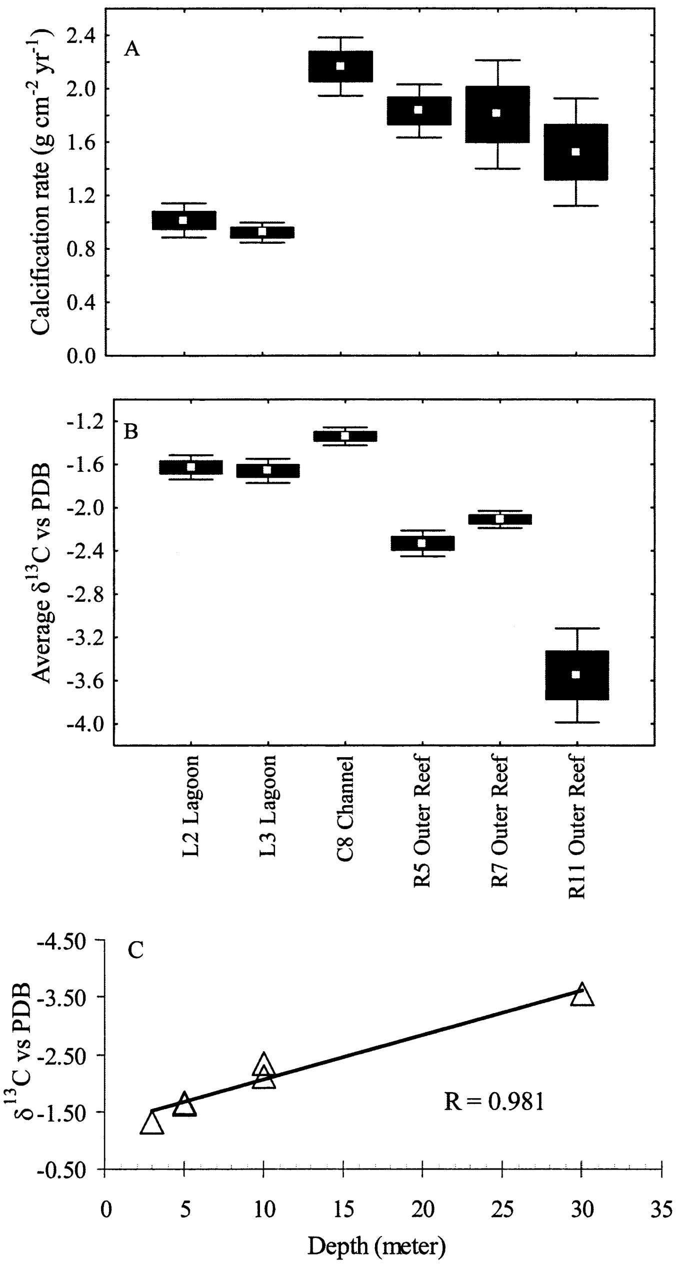


Fig. 3. (A) Calcification rate of *Porites* sp. in three different environments at Alphonse atoll. Calcification rate was significantly different among the lagoon, channel, and the outer reef (one-way ANOVA followed by least significant difference test $p < 0.05$; values are mean ± SE). (B) Average $\delta^{13}C$ in individual *Porites* coral skeleton showing four significant clusters (one-way ANOVA followed by least significant difference test, $p < 0.05$; values are mean ± SE). (C) The dependency of average $\delta^{13}C$ value with depth in six *Porites* coral skeletons.

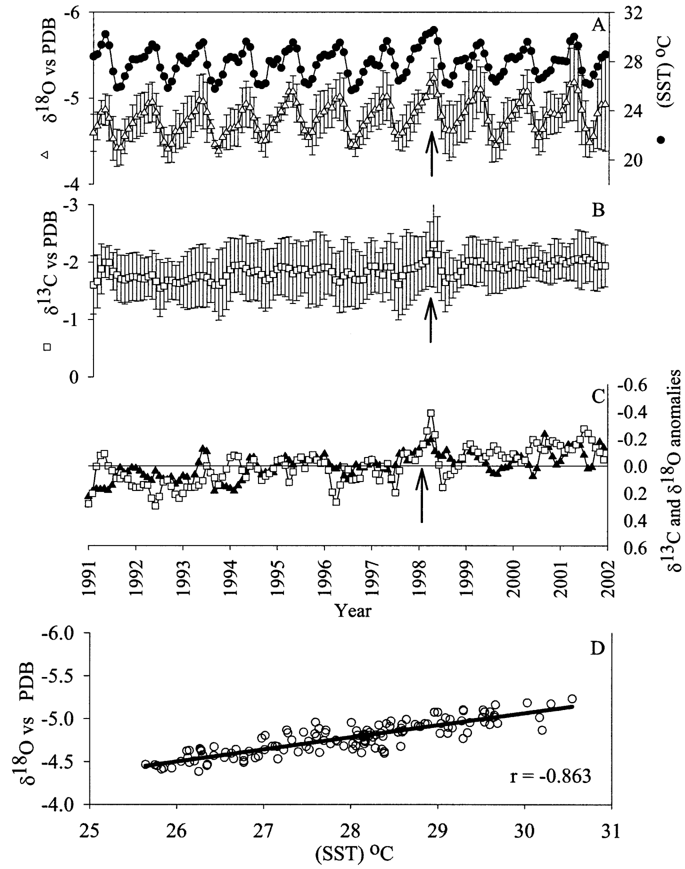


Fig. 4. (A) Mean (±SD) of five corals average skeletal $\delta^{18}O$ since 1991 showing the $\delta^{18}O$ depletion associated with the 1998 El Niño (black arrow). (B) Mean (±SD) of five corals average skeletal $\delta^{13}C$ since 1991 showing the $\delta^{13}C$ depletion during 1998 (black arrow). (C) The monthly average anomalies for carbon and oxygen isotopes since 1991 of the five cores. The data clearly show the depletion in both $\delta^{18}O$ and $\delta^{13}C$ during the 1998 bleaching event (black arrow). (D). The correlation ($r = -0.863$) between SST and $\delta^{18}O$ after averaging five corals since 1991. The slope is −0.140‰/°C.

erage $\delta^{18}O$ of the five corals and SST ($r = -0.863$, $p < 0.001$, $n = 132$; Fig. 4D) is the highest, compared with non-averaged individual corals ($r = -0.49$ to -0.74).

The Alphonse results suggest that the $\delta^{18}O$ and $\delta^{13}C$ of individual corals are mainly controlled by the local environment during growth and that this can mask global-change signals, such as strong El Niño events (Suzuki et al. 2003). Thus, past climate reconstructions based on a single coral isotope record may underestimate the occurrence and the magnitude of global events. We propose that average isotopic compositions of several corals retrieved from different habitats in the same region should be used to characterize large-scale marine phenomenon, such as ENSO events. The exact number of corals needed to capture a global signal was tested by incremental averaging of different numbers of coral $\delta^{18}O$ versus SST combinations since 1991. We found that the correlation of both annual cycles and anomalies increased when combining the mean of five corals (Fig. 5). The increase in relative correlation coefficient with the sampling number enables us to distinguish between local and global effects on the isotopic composition of *Porites* corals. However, in the dendroclimatology research area averaging several records to enhance the common regional-scale signal and minimize the non-climatic noise has been common practice for many years (e.g., Fritt, 1976). Unfortunately, this important procedure has not been routinely applied to coral

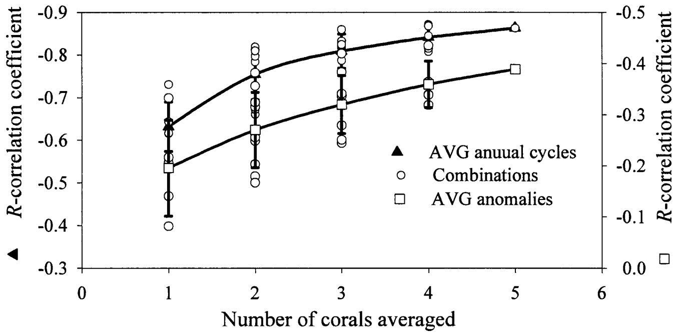


Fig. 5. The number of corals needed to be averaged since 1991 to increase the relative correlation coefficient. Both annual cycles and anomalies are tested for different numbers of coral combinations. Highest correlations were achieved after averaging five corals and the differences between local and global effects are evident (maximum r reaches steady value of -0.863 for the annual cycles and $r = -0.39$ for the anomalies).

records with the exception of two recent articles: the first by Hendy et al. (2002), who averaged several coral records, although at 5-yearly resolution; and Lough (2004), who considers some of the problems associated with relying on a single coral record.

Natural variation in skeletal δ^{18}O and δ^{13}C implies that corals are mostly affected by their microenvironment and may respond differentially to temperature elevation and bleaching events. We found significant variability in the isotopic signatures among *Porites* sp. corals sampled from the lagoon, the channel and the outer reef of a small atoll. Only one core from the lagoon and one core from the channel recorded extreme depletion in δ^{18}O during the 1998 bleaching event. This has implications for future environmental reconstruction research using individual coral cores. However, the global ENSO signal was captured when these isotope values of five corals were averaged. This result implies that future paleoclimate reconstructions, especially those that attempt to identify past ENSO events, should rely on larger sampling size and larger diversity of the oceanographic setting from which the corals are selected. The strong impact of local habitats on the isotopic composition of *Porites* ssp. has to be considered when interpreting δ^{13}C and δ^{18}O records.

References

ABRAM, N. J., M. K. GAGAN, M. T. MCCULLOCH, J. CHAPPELL, AND W. S. HANTORO. 2003. Coral reef death during the 1997 Indian Ocean dipole linked to Indonesian wildfires. Science **301:** 952–955.

ARONSON, R. B., W. F. PRECHT, M. A. TOSCANO, AND K. H. KOLTES. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. Mar. Biol. **141:** 435–447.

BARNES, D. J., AND J. M. LOUGH. 1996. Skeletons: Storage and recovery of environmental information. Global Change Biol. **2:** 569–582.

———, R. B. TAYLOR, AND J. M. LOUGH. 2003. Measurement of luminescence in coral skeletons. J. Exp. Mar. Biol. Ecol. **295:** 91–106.

BERKELMANS, R., AND J. K. OLIVER. 1999. Large scale bleaching on the Great Barrier Reef. Coral Reefs **18:** 55–60.

CHALKER, B. E., AND D. J. BARNES. 1990. Gamma densitometry for the measurement of coral skeletal density. Coral Reefs **4:** 95–100.

CHARLES, C. D., D. E. HUNTER, AND R. G. FAIRBANKS. 1997. Interaction between the ENSO and the Asian monsoon in a coral record of tropical climate. Science **277:** 925–928.

COBB, K. M., C. D. CHARLES, H. CHENG, AND R. L. EDWARDS. 2003. El Niño/Southern Oscillation and tropical Pacific climate during the last millennium. Nature **424:** 271–276.

COLE, J. E., R. B. DUNBAR, T. R. MCCLANAHAN, AND N. A. MUTHIGA. 2000. Tropical Pacific forcing of decadal SST variability in the Western Indian Ocean over the past two centuries. Science **287:** 617–619.

COLES, S. L., AND B. E. BROWN. 2003. Coral bleaching—capacity for acclimatization and adaptation. Adv. Mar. Biol. **46:** 183–223.

FRITTS, H. C. 1976. Tree rings and climate. Academic Press, New York. [Reprinted 2001. Blackburn Press, Caldwell, New Jersey.]

GAGAN, M. K., L. K. AYLIFFE, J. W. BECK, J. E. COLE, E. R. M. DRUFFEL, R. B. DUNBAR, AND D. P. SCHRAG. 2000. New views of tropical paleoclimates from corals. Quat. Sci. Rev. **19:** 45–64.

GOREAU, T. J. 1977. Carbon metabolism in calcifying and photosynthetic organisms: Theoretical models based on stable isotope data, p. 395–401. *In* Proc 3rd Int Coral Reef Symp, Miami, Florida.

GROTTOLI, A. G. 1999. Variability in stable isotopes and maximum linear skeletal extension in reef corals in Kaneohe Bay, Hawaii. Mar. Biol. **135:** 437–449.

———. 2002. Effect of light and brine shrimp levels on the skeletal δ^{13}C values of the Hawaiian coral *Porites compressa*: A tank experiment. Geochim. Cosmochim. Acta **66:** 1955–1967.

———, L. J. RODRIGUES, AND C. JUAREZ. 2004. Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressae* and *Montipora verrucosa* following a bleaching event. Mar. Biol. **145:** 621–631.

———, AND G. M. WELLINGTON. 1999. Effects of light and zooplankton on skeletal δ^{13}C values in the Eastern Pacific corals *Pavona clavus* and *P. gigantea.* Coral Reefs **18:** 29–41.

HARVELL, C. D., AND OTHERS. 1999. Emerging marine diseases climate links and anthropogenic factors. Science **285:** 1505–1510.

HENDY, E. J., M. K. GAGAN, C. A. ALIBERT, M. T. MCCULLOCH, J. M. LOUGH, AND P. J. ISDALE. 2002. Abrupt decrease in tropical Pacific sea surface salinity marks end of Little Ice Age. Science **295:** 1511–1514.

HUGHES, T. P., AND OTHERS. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301:** 929–933.

JUILLET-LECLERC, A., AND G. SCHMIDT. 2001. A calibration of the oxygen isotope paleothermometer of coral aragonite from Porites. *Geophys. Res. Lett.* **28:** 4135–4138.

LAND, L. S., J. C. LANG, AND D. J. BARNES. 1975. Extension rate: A primary control on the isotopic composition of West Indian (Jamaican) scleractinian coral skeletons. Mar. Biol. **33:** 221–233.

LEDER, J. J., A. M. SZMANT, AND P. K. SWART. 1989. The effect of prolonged ‘bleaching’ on skeletal banding and stable isotopic composition in *Montastraea annualaris.* Coral Reef **10:** 19–27.

LINSLEY, B. K., R. G. MESSIER, AND R. B. DUNBAR. 1999. Assessing between colony oxygen isotope variability in the coral *Porites lobata* at Clipperton Atoll. Coral Reefs **18:** 13–27.

LOUGH, J. M. 2004. A strategy to improve the contribution of coral data to high-resolution paleoclimatology. Palaeogeogr. Palaeoclimatol. Palaeoecol. **204:** 115–143.

MAIER, C., J. PATZOLD, AND R. P. M. BAK. 2003. The skeletal isotopic composition as an indicator of ecological and physiological plasticity in the coral genus *Madracis.* Coral Reefs **22:** 370–380.

MANN, M. E., R. S BRADLEY, AND M. K. HUGHES. 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature **392:** 779–787.

———, ———, AND ———. 1999. Northern Hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. Geophys. Res. Lett. **26:** 759–762.

MCCLANAHAN, T. R. 2000. Bleaching damage and recovery potential of Maldivian coral reefs. Mar. Pollut. Bull. **40:** 587–597.

MCCONNAUGHEY, T. A. 1989. C13 and O18 isotopic disequilibrium in biological carbonates: I. Patterns. Geochim. Cosmochim. Acta **53:** 151–162.

MCPHADEN, M. J. 1999. Genesis and evolution of the 1997–98 El Niño. Science **283:** 950–954.

PAILLARD, D., L. LABEYRIE, AND P. YIOU. 1996. Macintosh Program performs time-series analysis. Eos Trans. Am. Geophys. Union **77:** 379.

REYNAUD-VAGANAY, S., A. JUILLET-LECHERC, J. JAUBERT, AND J.-P. GATTUSO. 2001. Effect of light on skeletal $\delta^{13}C$ and $\delta^{18}O$, and interaction with photosynthesis, respiration and calcification in two zooxanthellate scleractinian corals. Paleoclim. Paleoecol. **175:** 393–404.

ROBERTS, C. M., AND OTHERS. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science **295:** 1280–1284.

SALINGO, J. 1998. The 1997/1998 El Niño. Weather **53:** 274–281.

SPENCER, T., K. A. TELEKI, C. BRADSHAW, AND M. D. SPALDING. 2000. Coral bleaching in southern Seychelles during the 1997–1998 Indian ocean warm event. Mar. Pollut. Bull. **40:** 569–586.

SUZUKI, A., M. K. GAGAN, K. FABRICIUS, P. J ISDALE, I. YUKINO, AND H. KAWAHATA. 2003. Skeletal isotope microprofiles of growth perturbations in *Porites* corals during 1997–98 mass bleaching event. Coral Reefs **22:** 357–369.

SWART, P. K. 1983. Carbon and oxygen isotope fractionation in scleractinian corals. Earth. Sci. Rev. **19:** 51–80.

WEBER, J. N., AND P. M. J. WOODHEAD. 1970. Carbon and oxygen isotope fractionation in the skeletal carbonate of reef-building corals. Chem. Geol. **6:** 93–117.

WILKINSON, C., O. LINDEN, H. CESAR, G. HODGSON, J. RUBENS, AND A. E. STRONG. 1999. Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change? Ambio **28:** 188–196.

Received: 7 March 2005
Accepted: 10 August 2005
Amended: 22 September 2005