

Impact of the 1998 bleaching event on $\delta^{18}\text{O}$ records of Okinawa corals

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ABSTRACT: Oxygen isotope compositions of *Porites* sp. were measured in order to examine the effect of the 1998 bleaching event on the skeletal record of 6 neighboring colonies from Sesoko Island, Okinawa, Japan. A $\delta^{18}\text{O}_c$ -SST dependency of 0.18‰/°C was calculated using a 10 yr record, well within accepted calibrations. The skeleton portion accreted during 1998 exhibited 0.3‰ enrichment in $\delta^{18}\text{O}$, which differs from the depleted values expected during abnormally high SST conditions. Growth rate changed significantly during the bleaching event, and its manifestation in skeletal $\delta^{18}\text{O}$ masked the temperature signal. The $\delta^{18}\text{O}$ variance among the 6 colonies was noticeably higher during 1998 in comparison with 1997 and 1999. A residual analysis revealed that 75% of the interannual variation of the $\delta^{18}\text{O}$ record is explained by variation in annual extension rate. The increase in $\delta^{18}\text{O}$ variance is proposed as a novel indicator for stressful environmental conditions.

KEY WORDS: Coral · Stable isotopes · Sea surface temperature · Bleaching

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INTRODUCTION

Bleaching, the color loss of reef-building corals, is the result of mass expulsion of the symbiotic algae (zooxanthellae) living within the coral tissue and/or the decrease of photosynthetic pigment content within an individual alga (Brown 1997). The dissociation of the symbiotic relationship between algae and coral impairs the host's energy budget and can lead in extreme cases to mortality of the entire colony, and subsequently to degradation of the entire reef ecosystem. The factors said to cause corals to bleach are numerous and generally include stress situations such as extremely high or low water temperatures (Hudson 1981), pollution (Jones & Hoegh-Guldberg 1999), unusually high or low light intensities (Lesser et al. 1990) and bacterial infection (Kushmaro et al. 1996). By far the most commonly reported trigger causing coral bleaching is an anomalously high sea surface temperature (SST).

Mass bleaching events have been documented since the late 1970s. Since then the frequency and intensity of these events appear to be on the rise (Goreau & Hayes 1994, Hoegh-Guldberg 1999). This raises the

question of whether bleaching events were a habitual phenomenon in the past, even before anthropogenic effects seemed to influence the reef ecosystems, or whether these events have become more frequent since the 1980s. To answer this question it is necessary to establish methods able to trace past bleaching events.

Massive hermatypic corals store within their layered skeleton geochemical signals that are used to reconstruct environmental conditions of their living habitats. The oxygen isotopic ratio of a coral skeleton ($\delta^{18}\text{O}_c$) tracks the variability of both SST and the surrounding seawater $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{sw}}$); the latter depends on the local balance of net evaporation, precipitation, and runoff or sea surface salinity (SSS). The carbon isotopic ratio of a coral skeleton ($\delta^{13}\text{C}_c$) is predominantly affected by metabolic fractionation. This proxy reflects several physiological and environmental factors, including respiration and photosynthesis by the coral and zooxanthellae (McConaughey 1989), light availability to the zooxanthellae (Weber & Woodhead 1970) and the reproductive cycle of the colony (Gagan et al. 1994).

Growth and calcification rates may also influence the isotopic composition of a coral skeleton (Land et al.

1975, McConaughey 1989, Rosenfeld et al. 2003). The 'vital effect' causes both $\delta^{18}\text{O}_c$ and $\delta^{13}\text{C}_c$ of aragonite formed during the dynamic process of skeletal accretion to be out of thermodynamic equilibrium. A relatively slow skeletal accretion rate will allow the isotopic composition of the skeleton to approach the thermodynamic equilibrium, and vice versa. Consequently, relatively slow-growing colonies or regions within a colony, or even slow-growing elements within a single calyx, are displaced toward the thermodynamic equilibrium (Land et al. 1975, McConaughey 1989). It is generally believed, however, that the kinetic effect has only a minor impact on the isotopic composition of the skeleton along the major growth axis within a single colony, where extension and calcification rates are maximal (McConaughey 1989). Nevertheless, seasonal variations in extension and/or calcification rate have been suggested as an additional possible source of isotope fractionation that could mask or mimic the effect of the environment (Allison et al. 1996).

The effects of coral bleaching on coral skeletal records have been the subject of numerous studies. These addressed reduced calcification and linear skeletal extension rate due to uncoupling of the coral algae symbiotic system (Jokiel & Coles 1977, Goreau & Macfarlane 1990) and $\delta^{18}\text{O}_c$ depletion due to abnormally high SST (Carriquiry et al. 1988, Porter et al. 1989, Leader et al. 1991, Suzuki et al. 2000).

The extensive bleaching episode that occurred during 1998 was linked to a severe El Niño-Southern Oscillation (ENSO) event (Lough 2000). It is considered to have been the worst ever recorded, both in magnitude and in spatial coverage (Wilkinson 2000). Unprecedented summer SSTs were recorded around Okinawa Island, Japan. Temperature reached a maximum of 31°C, ~3°C higher than the long-term average of maximal summer temperatures, and it was the first

bleaching event reported around the Ryukyu Islands (Suzuki et al. 2000).

In this study, we measured a 10 yr oxygen isotope record of an Okinawa coral, and compared its skeletal isotopic composition against local SST data. To focus our investigation on the 1998 bleaching event, additional isotopic profiles were obtained in 5 neighboring colonies for the years 1997 to 1999. Our data demonstrate that the 1998 bleaching event was manifested by increasing variations of isotopic composition among replicated coral records.

MATERIALS AND METHODS

Six *Porites* sp. colonies (S3, S4, S6, S7, S9, S10) were drilled in June 1999 from the reef in front of the Tropical Biosphere Research Center, Sesoko Island, Okinawa, Japan (26°38'N, 127°52'E). The colonies were located within 10 m of each other at a depth of 2 m below mean sea level. Upon collection, the corals were rinsed with fresh water, air-dried and then sectioned into 5 mm thick slabs using a diamond saw. The slabs were 40 mm in length, except for S4, which was 150 mm long. An X-radiograph of the slab cut along the major growth axis of S4 shows a clear density band pattern (Fig. 1). Cohen & Hart (1997) pointed out possible problems associated with choosing the position of the skeletal profile to be sampled and analyzed. To avoid problems of minor variations in isotopic composition due to different skeletal orientation and position, we systematically collected skeletal samples, weighing between 100 and 150 µg, along the maximal growth axis of each colony. Sampling was done using a low speed drill, 0.5 mm in diameter with 0.6 mm step size. This scheme provided 13 to 22 samples per year. Skeletal samples were reacted in 100% orthophosphoric acid to produce CO₂ for mass spectrometric analyses on a GasBench II connected in-line to a Finigan MAT 252. Results are reported in per mill units relative to the VPDB (Vienna PeeDee Belemnite) standard. Long-term precision of replicated analysis of our internal laboratory standards are 0.06 and 0.1‰ for carbon and oxygen, respectively. The distance between the samples with seasonal $\delta^{18}\text{O}_c$ maxima (i.e. winter values) was used to estimate annual extension rates (Fig. 1).

Monthly SST was compiled from daily temperature data, collected at the study site since 1989 by the Okinawa Prefectural Sea Farming Center. In order to develop an age model, we assigned the warmest and coldest SST in each year to the lightest and heaviest $\delta^{18}\text{O}_c$ values respectively. We then assigned an approximate

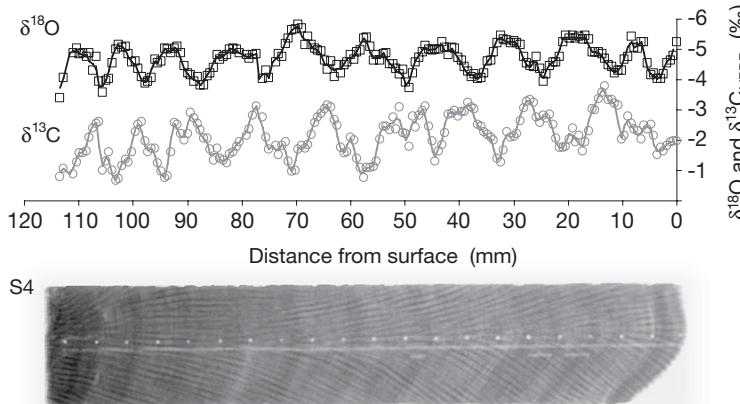


Fig. 1. *Porites* sp. X-Radiograph and skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ as a function of distance from the surface of coral core S4 growing on the reef in front of the Tropical Biosphere Research Center, Sesoko Island, Okinawa, Japan. VPDB: Vienna PeeDee Belemnite standard

date to each intermediate sample by assuming a constant intra-annual growth rate using the software package AnalySeries 1.1 (Paillard et al. 1996). Isotopic time series of the 6 records were re-sampled by means of linear interpolation to produce 12 equally spaced, isochronic values per year corresponding to the same underlying environmental regime. This enabled us to calculate average isotopic composition of the 6 records and its variance.

RESULTS

Among the 6 records obtained, 5 span almost 3 yr pre-collection, from January 1997 to June 1999 (S3, S6, S7, S9, S10), and one spans 10 yr pre-collection, from 1989 to 1999 (S4).

Mean ($\pm \text{SD}$) annual linear extension rate of colony S4 was $11.7 \pm 1.8 \text{ mm yr}^{-1}$. The highest linear extension rate of this coral was 13.8 mm during 1993 and the lowest was 7.8 mm in 1998 (Fig. 1). Monthly SST data measured close to the study site are illustrated in Fig. 2. Between 1989 and 2000, a maximal temperature of 27.7°C was recorded during July-August and a minimal temperature of 20.1°C was usually recorded during February-March. During 1998 however, when the bleaching episode occurred, both winter and summer SST deviated from the long-term monthly average by ca. 1°C and 3°C , respectively.

The monthly $\delta^{18}\text{O}_c$ record of the S4 coral is also shown in Fig. 2. Between 1989 and 2000, the average minimal value corresponding to summer was $-5.12\text{\textperthousand}$ and the maximal value corresponding to winter was $-3.96\text{\textperthousand}$. During 1998, maximal and minimal $\delta^{18}\text{O}_c$ values were -4.2 and $-5.2\text{\textperthousand}$ respectively. $\delta^{13}\text{C}_c$ also shows a distinct annual periodicity, with average annual amplitude of $1.73\text{\textperthousand}$ (Fig. 2). Along this record, $\delta^{13}\text{C}_c$ maxima usually lead $\delta^{18}\text{O}_c$ minima by 1 to 2 mo. However, for 1998, a $\delta^{13}\text{C}_c$ maximum is missing.

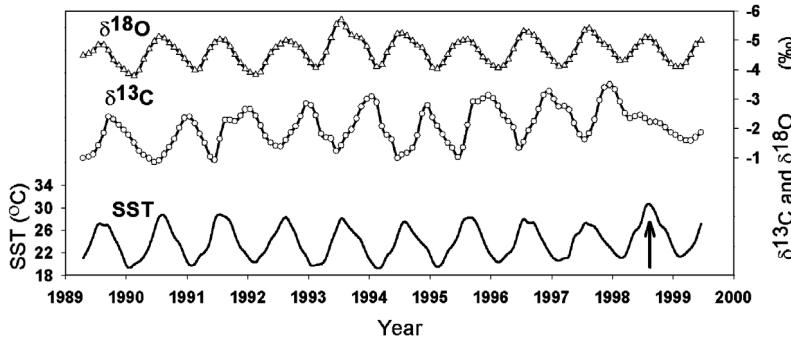


Fig. 2. Observed mean monthly SST at the study site along with *Porites* sp. skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ after developing an age model for the coral marked S4. Arrow points to the bleaching event of 1998

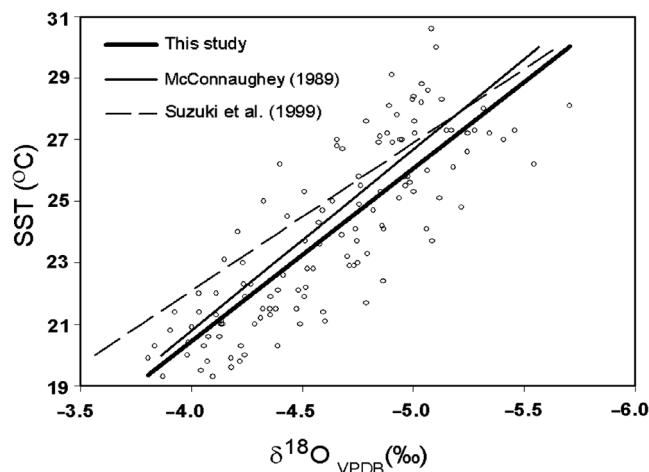


Fig. 3. *Porites* sp. Local calibration of SST against oxygen isotopic composition of the S4 colony skeleton. Other correlations are also shown for comparison (McConaughey 1989, Suzuki et al. 1999)

The average annual SST amplitude throughout the decade following 1989 was 7.6°C and that of $\delta^{18}\text{O}_c$ was $1.16\text{\textperthousand}$ (Fig. 2). The average annual temperature is poorly correlated with average annual $\delta^{18}\text{O}_c$ ($r = -0.37$, slope of $-0.15\text{\textperthousand}/^\circ\text{C}$) while correlation between the mean monthly values is significant (Fig. 3; $r = -0.83$; $p < 0.001$) with a higher slope of $-0.18\text{\textperthousand}/^\circ\text{C}$, relative to the annual calculation, probably due to the inclusion of the seasonal cycles. Two additional *Porites* spp. correlation lines, adopted from McConaughey (1989) and Suzuki et al. (1999), are also plotted in Fig. 3, showing comparable $\delta^{18}\text{O}_c$ -SST dependency.

To focus our investigation on the 1998 bleaching event, oxygen and carbon isotopic records of the 6 corals were plotted on a common scale along with the average of the 6 corals and its variance (Fig. 4). A depletion of $0.13\text{\textperthousand}$ can be observed in the average $\delta^{18}\text{O}_c$ composition between the summers of 1998 and 1997. A considerably high $\delta^{18}\text{O}_c$ variance among the 6 records was detected during 1998, and reached a peak 2 mo after the maximum SST. By contrast, the $\delta^{13}\text{C}_c$ values of the 6 corals are not harmonic. Nevertheless, the average $\delta^{13}\text{C}_c$ of the 6 corals does show a coherent annual cycle, with timing similar to the $\delta^{13}\text{C}_c$ record of the long S4 record (Fig. 2).

DISCUSSION

The main controlling factor of $\delta^{13}\text{C}_c$ is zooxanthellae photosynthetic activity within the coral tissue, which is sensitive to radiation. Accordingly, $\delta^{18}\text{O}_c$ minima

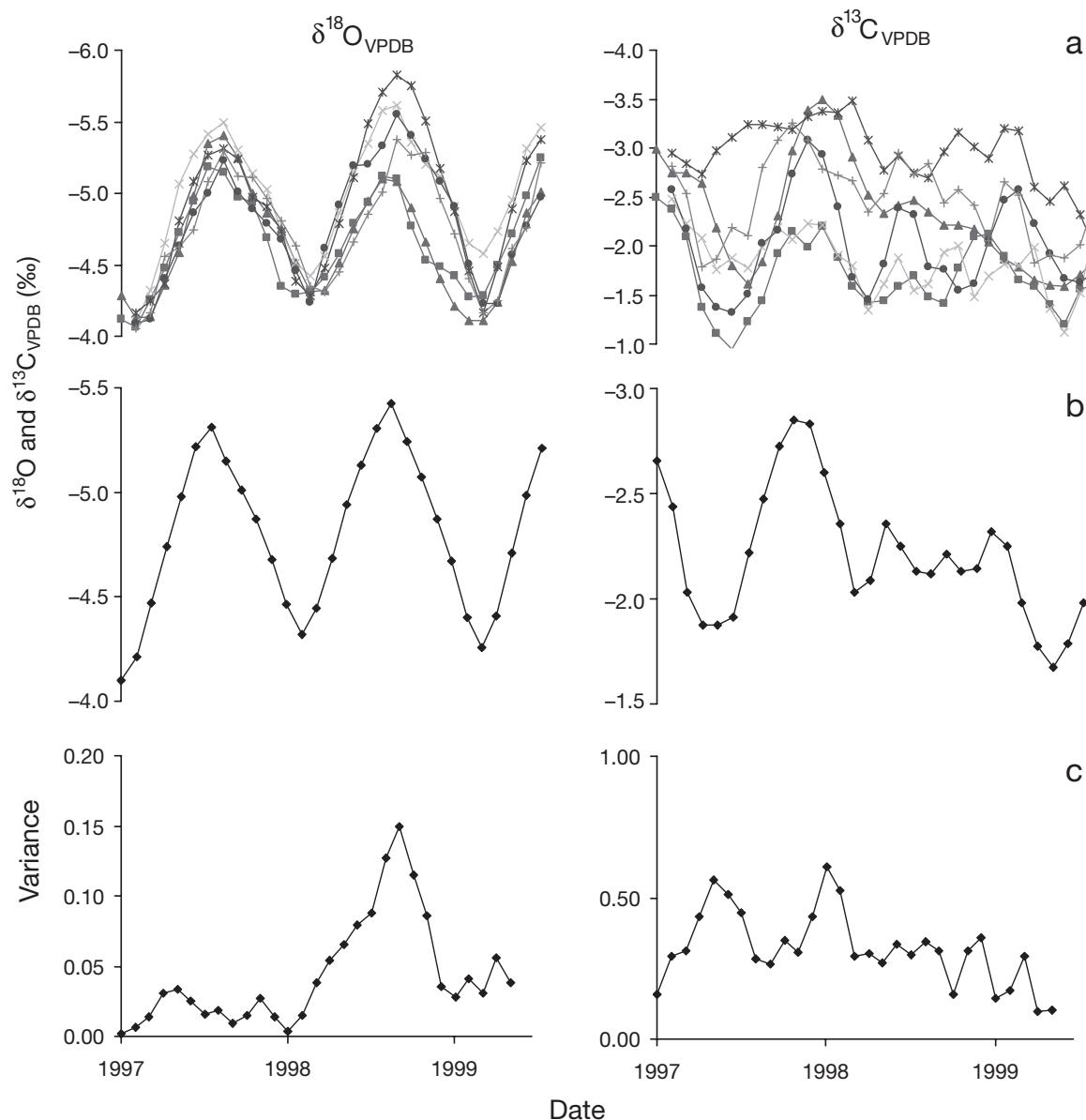


Fig. 4. *Porites* sp. (a) Skeletal oxygen and carbon isotopic composition of coral cores S3, S4, S6, S7, S9 and S10, plotted for the years 1997 to 1999. (b) Average skeletal oxygen and carbon isotopic composition of 6 corals. (c) Variance of the average isotopic compositions

lag $\delta^{13}\text{C}_c$ maxima by 1 to 2 mo along the long record (S4). This lag corresponds to a 2 mo shift between maximal values of SST and solar radiation, and is common in shallow skeletal records in northern subtropical latitudes (Suzuki et al. 2001, Rosenfeld et al. 2003). $\delta^{13}\text{C}_c$ records of the 6 corals are disharmonic and do not show a common trend (Fig. 4). Their average, on the other hand, does show a relation to solar radiation. Average $\delta^{13}\text{C}_c$ time-series timing (Fig. 4) is similar to the long record (S4) and to other $\delta^{13}\text{C}_c$ records from this area (Abe et al. 1998, Suzuki et al. 1999, 2003). During 1997, average $\delta^{13}\text{C}_c$ maximum, which is associated

with a peak in photosynthesis activity by the symbiotic algae during the warm season, led average $\delta^{18}\text{O}_c$ minima by 2 mo. For 1998, the average $\delta^{13}\text{C}_c$ maximum is absent, implying a reduction in photosynthetic activity (Leader et al. 1991, Grottoli et al. 2004).

The impact of evaporation, precipitation and runoff on isotopic variations is considered minimal at this site. Thus, $\delta^{18}\text{O}_c$ mainly reflects seasonal variations in SSTs rather than variations in SSS/ $\delta^{18}\text{O}_{\text{sw}}$ (Mitsuguchi et al. 1996, Suzuki et al. 1999). The temperature dependency of oxygen isotope fractionation found in coral S4 ($\delta^{18}\text{O}_c = 0.36 - 0.18 \text{ SST}$) is in good agreement with

other *Porites* spp. calibrations which had slopes varying between -0.18 and $-0.21\text{‰}/^{\circ}\text{C}$ (McConaughey 1989, Gagan et al. 1994). Calibration studies conducted at the relatively nearby site of Ishigaki Island, Japan, revealed a somewhat lower $\delta^{18}\text{O}_c$ -SST dependence that ranged from -0.13 to $-0.17\text{‰}/^{\circ}\text{C}$ (Abe et al. 1998, Suzuki et al. 1999, 2003). These calibrations were calculated using seasonal rather than monthly SSTs and $\delta^{18}\text{O}_c$ values. If seasonal averages are applied to our data, the calibration slope is $-0.17\text{‰}/^{\circ}\text{C}$, in agreement with the Ishigaki calibrations (Abe et al. 1998, Suzuki et al. 1999).

Models of $\delta^{18}\text{O}$ fractionation in corals predict that as SST rises, $\delta^{18}\text{O}_c$ will be depleted and the accreted skeleton will be isotopically lighter, and indeed, previous studies have reported depletion of $\delta^{18}\text{O}_c$ associated with extremely high SSTs that initiated bleaching events (Porter et al. 1989, Leader et al. 1991, Suzuki et al. 2000). Surprisingly, however, the $\delta^{18}\text{O}_c$ record of colony S4 reveals enrichment of 0.3‰ between the summers of 1997 and 1998 rather than the expected depletion. An average isotopic composition time series was obtained by stacking this record with 5 additional, conspecific colonies that were growing in close proximity to colony S4 (Fig. 3). This was done to reduce variability associated with individual colonies and local habitat effects and to explore the relationship with the bleaching event. Although colony S4 did not show the expected depletion associated with the increase in SST between the summers of 1997 and 1998, the average record did. It is represented as an average depletion of 0.13‰ from -5.30‰ in 1997 to -5.43‰ in 1998.

The variance in $\delta^{18}\text{O}_c$ composition of the 6 records is ca. 4 times higher for the anomalously warm 1998 in comparison to 1997 and 1999 during which SSTs were normal (0.15 and 0.03 , respectively) (Fig. 4). For comparison, a baseline variance of ca. 0.04‰ was reported in a study assessing the variability among 6 neighboring *Porites lobata* corals (Linsley et al. 1999, see their Fig. 7B). Furthermore, while Linsley et al.'s (1999) corals were collected at a distance of 2 km from each other and at a depth range of 6.1 to 13.1 m, our colonies were only 10 m apart, and grew at the same depth. Hence, one might expect that if Linsley et al.'s (1999) corals had been found closer to each other and at the same depth; their baseline variance would have been even lower.

Not all the colonies collected recorded the unusually warm SSTs throughout 1998. Two colonies (S3 and S4) did not show the expected $\delta^{18}\text{O}_c$ depletion, while 4 colonies (S6, S7, S9, S10) did record depleted values. Colonies S4 and S7 represent the 2 extreme situations in responding to the extraordinarily warm summer of 1998. The differences between the isotopic signals

recorded in colonies S4 and S7 in the summers of 1997 and 1998 are -0.30‰ and $+0.52\text{‰}$, respectively. The minimal $\delta^{18}\text{O}_c$ value corresponding to the summer of 1997 was -5.40‰ , while that of 1998 was -5.10‰ . The enrichment in colony S4 cannot be explained either by higher SST or by SSS variations during summer 1998. The depletion in colony S7 on the other hand, corresponds well to a warming of 2.5 to 3.3°C , according to calculations based on conventional $\delta^{18}\text{O}_c$ calibrations (McConaughey 1989, Suzuki et al. 1999, this study).

The most notable difference between colonies S7 and S4 is that of their annual extension rates during 1998. While colony S7 maintained an extension rate of 12 mm yr^{-1} in both 1997 and 1998, a 40% reduction in extension rate is observed in colony S4, dropping from 13.2 mm in 1997 to 7.8 mm in 1998 (Fig. 5). The variation found in extension rate appears to be associated with the ability to trace abnormally high SSTs. This observation calls for examination of the impact of extension rate variations on $\delta^{18}\text{O}_c$ composition along the maximal growth axis within a single colony.

A residual analysis was conducted on the 10 yr record of colony S4 to examine the effect of growth rate variations on its isotopic composition. The measured SSTs were converted to equivalent expected $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_e$) using the relationship between $\delta^{18}\text{O}$ and SST revealed in this study ($\delta^{18}\text{O}_c = 0.36 - 0.18 \text{ SST}$). The measured $\delta^{18}\text{O}_c$ values were subtracted from the expected values to remove the temperature effect from the record and to produce the $\delta^{18}\text{O}$ residual ($\Delta\delta^{18}\text{O}$). These values are presented as departure from the mean $\Delta\delta^{18}\text{O}$ as calculated for the entire record. An average annual $\Delta\delta^{18}\text{O}$ value was obtained by aggregating monthly $\Delta\delta^{18}\text{O}$ from winter to winter (Fig. 6a). The departure of the annual extension rate in each year from the entire record average annual extension rate is plotted in Fig. 6a. The correlation between $\Delta\delta^{18}\text{O}$ and the annual extension rate is highly significant (Fig. 6b). It appears that 75% of the residual interannual $\delta^{18}\text{O}$ variations in *Porites* sp. colony from Sesoko Island can be explained by the variability in the annual extension rate of the coral along the maximal growth axis of the colony. In the anomalously warm 1998, the reduction in annual extension rate corresponds well with enriched $\delta^{18}\text{O}_c$ values. Likewise, in 1993, a year when average annual extension rate in this record was relatively high, $\delta^{18}\text{O}_c$ values were depleted correspondingly.

It is well documented that $\delta^{18}\text{O}_c$ in slow-growing colonies, regions within a single colony and regions within a single calyx are enriched in ^{18}O relative to faster growing elements (Land et al. 1975, McConaughey 1989). Based on the 40% reduction in growth rate we hypothesize that colony S4 was bleached. The coral-algae symbiosis dissociation caused a slower

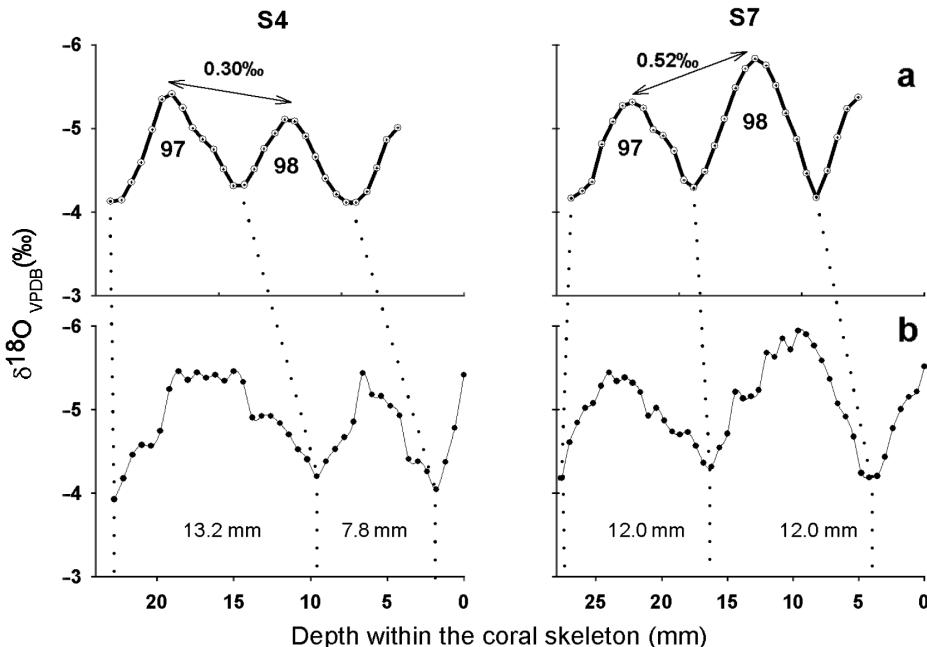
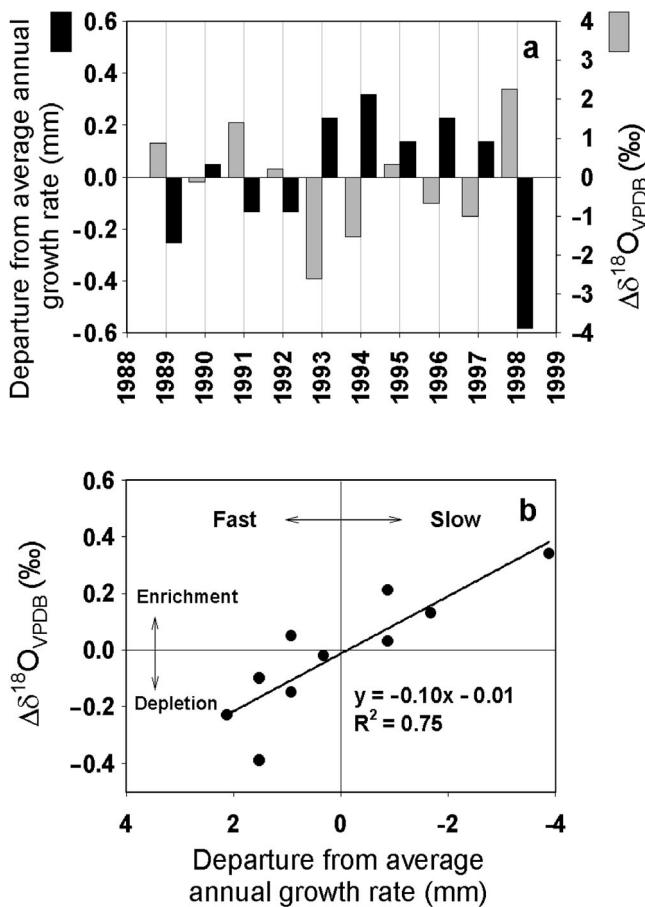


Fig. 5. Skeletal oxygen isotopic composition of S4 and S7 colonies, which represent 2 extreme situations in that the S4 record does not exhibit the anomalously warm SSTs measured during 1998, and S7 does. (b) The 2 records (S7 and S4) are plotted versus distance from the surface of the core, showing the different extension rates during 1997 and 1998 and (a) after developing an age model, against time



growth rate during 1998, which, in turn, resulted in $\delta^{18}\text{O}_c$ enrichment of the corresponding skeletal portion due to kinetic effects. S7, on the other hand, withstood the anomalous SST and did not bleach. Since extension rate in both 1997 and 1998 was maintained, kinetic effects did not affect $\delta^{18}\text{O}_c$ and, hence, S7 was able to record the anomalously warm SSTs. Interestingly, during 1993, although both SST and SSS were normal, for some reason, annual extension rate was relatively high.

The increase in $\delta^{18}\text{O}_c$ variance among the 6 colonies during 1998 in comparison to 1997 and 1999 might be the outcome of a differential response of each colony to the anomalously high SSTs. In typical years $\delta^{18}\text{O}_c$ values of all colonies are positioned around a certain mean with a certain degree of variation among them (1997 and 1999 in this study; Linsley et al. 1999). In an anomalously warm year such as 1998, bleaching, which is a stress response of corals subjected to warmer than normal SST, probably changes growth

Fig. 6. Residual analysis results examining the relation between deviations from average annual extension rate and deviations from expected skeletal oxygen isotopic composition. (a) Average annual $\Delta\delta^{18}\text{O}$ calculated by subtracting the observed from the expected skeletal oxygen isotopic composition and deviations of annual extension rate of each year from the entire record average annual extension rate. (b) Correlation between coral $\Delta\delta^{18}\text{O}$ and deviations from average annual extension rate

rates in certain colonies and to different extents, generating increasing $\delta^{18}\text{O}_c$ variance due to variations in the 'kinetic effects'. This has several implications on coral-based environmental reconstructions. It suggests that environmental conditions can be reconstructed with a relatively high degree of certainty during normal years, but the uncertainty of the reconstruction increases during anomalous years. It appears that coral $\delta^{18}\text{O}_c$ tends to undervalue anomalously warm years since the impact of SST and growth rate on skeletal $\delta^{18}\text{O}$ is opposite. In an extreme situation, the temperature effect is overcome by the reduction in growth rate. We propose therefore that the variance in $\delta^{18}\text{O}_c$ composition of several neighboring colonies might be used to trace stressful environmental conditions such as an unusually high SST.

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