



The effect of colony topography on climate signals in coral skeleton

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Abstract—The stable oxygen isotope composition of the aragonitic skeleton of hermatypic corals is a potential archive of paleotemperature and rainfall data. Biological processes also influence coral $\delta^{18}\text{O}$ although it has been difficult to determine which processes are involved and whether or not they dominate the stable isotope signal. We show here that colony topography, or surface bumpiness, is associated with significant differences in $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and the timing of high-density band formation between same-age corallites in the central and fastest-growing region of a coral colony. These differences reflect changes experienced by individual corallites as they grow from the summit of a bump toward the bottom of a valley. Corallites on the bump record isotopic temperatures more than 1°C higher and accrete high-density skeleton about 2 months earlier than their valley counterparts just 20 mm away. We propose that these changes are not caused by corallite “aging” but rather by changes in the overall rate and timing of light-enhanced calcification, which is lower and occurs later in shaded valleys than it does on exposed bumps. Although we conclude that sea temperature is the dominant influence on $\delta^{18}\text{O}$ values in our coral, our results show that significant isotopic variations may be expected over a small surface area in a single colony. The production of accurate and reproducible coral-based climate records thus requires an understanding of the complexities of coral growth processes and incorporation of this knowledge into sampling strategies and interpretation of data. Copyright © 1997 Elsevier Science Ltd

1. INTRODUCTION

There has been considerable recent interest in describing climate variations on decadal and longer timescales, motivated in part by a need to distinguish natural modes in the ocean-atmosphere system from those caused by anthropogenic impacts on global climate. Records obtained from instrumental and satellite data are spatially incomplete and generally too short to extract the full range of variability likely to be present in the climate system. As a result, much of our knowledge of past climate and climate changes on long timescales is based on proxy-data, including records of temperature and precipitation derived from analysis of tree-rings, sediments, corals, and ice-cores. Recently, massive hermatypic corals have received increased attention in this regard. Individual colonies of some species can live for several hundred years and accrete as many as several centimeters of new skeleton each year in paired high- and low-density bands. These attributes make corals uniquely suited to the construction of continuous, multi-century long records of tropical and subtropical climate at resolutions of weeks to years (Druffel and Griffin, 1993; Cole and Fairbanks, 1990; Quinn et al., 1993; Dunbar et al., 1994; Linsley et al., 1994; Wellington and Dunbar, 1995).

Although a variety of geochemical tracers have been developed in reef corals, the oxygen isotope ratio of skeletal aragonite remains the most widely used and easily measured as a tracer of ocean temperature, especially in the eastern equatorial Pacific as an indicator of past ENSO occurrences (Dunbar et al., 1994; Wellington and Dunbar, 1995). In some locations, where temperature-dependent changes in skeletal $\delta^{18}\text{O}$ are small and salinity-related changes in $\delta^{18}\text{O}$ of seawater are large, $\delta^{18}\text{O}$ has been used as a tracer of

rainfall or river discharge (Cole and Fairbanks, 1990; Cole et al., 1993).

Coral $\delta^{18}\text{O}$ is several permil more depleted than is expected from skeleton accreted in isotopic equilibrium with seawater (McConnaughey, 1989a). The usefulness of corals as recorders of temperature and precipitation depends on the assumption that this departure from equilibrium remains constant and that downcore $\delta^{18}\text{O}$ variations are driven by equilibrium processes. The results of several studies, however, question this assumption, indicating instead that the rate of skeletal accretion is an important influence on coral $\delta^{18}\text{O}$, causing significant ^{18}O depletion when accretion rates are high (Land et al., 1975; McConnaughey, 1989a; de Villiers et al., 1995; Allison et al., 1996). Skeletal growth involves two variables: calcification and extension. The relationship between them varies and determines both the average skeletal density and the seasonal, within-colony density changes which produce annual density bands (Fig. 1a). Linear extension can be estimated directly from x-radiographs by measuring the width of each annual density couplet. Consequently, this aspect of skeletal growth is the most commonly reported (Lough and Barnes, 1997), and growth-rate related isotopic variations in coral skeleton are most often linked to variations in linear extension rather than calcification (Land et al., 1975; Aharon, 1991; de Villiers et al., 1995; Allison et al., 1996). Long-core $\delta^{18}\text{O}$ records are sometimes crosschecked against average annual extension rate to rule out kinetic effects as a significant contributor to the stable isotope signal (Dunbar et al., 1994; Tudhope et al., 1995).

Skeletal architecture and growth mechanisms are also potential sources of signal variability within and between colonies. Skeletal thickening involves deposition of new CaCO_3 below the colony surface onto pre-existing skeletal elements.

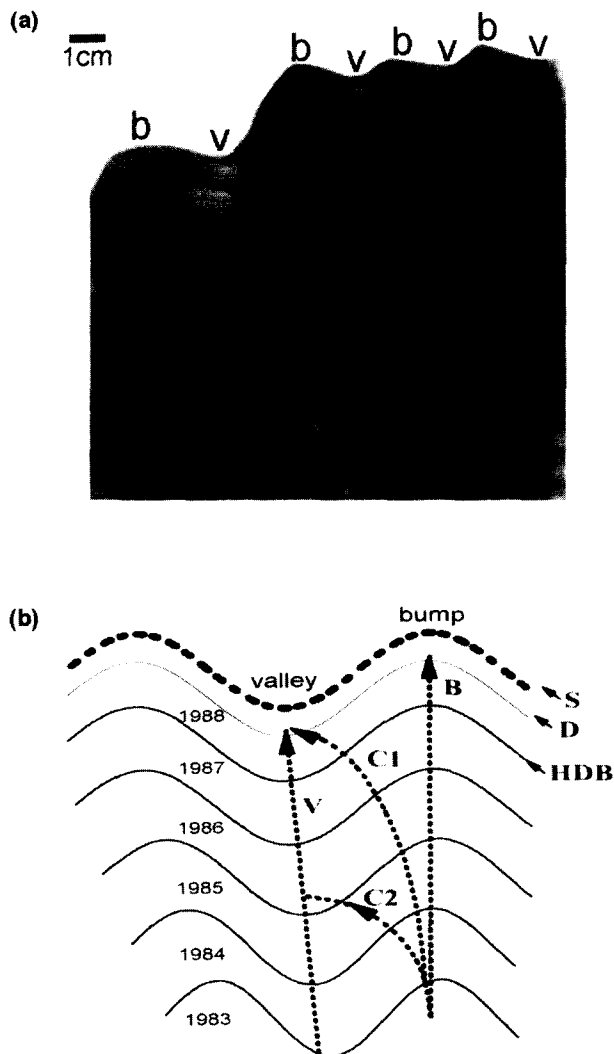


Fig. 1. X-radiographic positive of a comparable *Porites* slab cut along the vertical growth axis of a colony illustrating the main topographical and density features referred to in the text (a) and a schematic representation (not to scale) of the sampling area on colony 141-B05-S3 (b). In (a), *b* = bumps, *v* = valleys. Dark areas represent areas of high skeletal density, light areas are low skeletal density. Corallites are fine lines perpendicular to the growth surface, which diverge from the centre of bumps and converge in the valleys. In (b), sampling tracks (dark dotted lines) down the bump (*B*), valley (*V*), and two discrete corallites (*C1*, *C2*) are indicated. *S* = colony surface, *HDB* = high-density bands. Direction of growth along each axis is indicated by the arrows. The first sample along each of tracks *B*, *V* and *C1* was drilled at the base of the youngest dissepiment (*D*), 4 mm below the colony surface.

By combining new and old skeletal material, the coral itself is effectively averaging new and old environmental information. While it is generally accepted that some degree of skeletal thickening does occur in *Porites* species, there is a considerable range of estimates of what percentage of new skeleton is deposited below the surface (Barnes and Lough, 1989; Tudhope et al., 1996). Furthermore, thickening can only occur through the depth of skeleton occupied by living tissue. Because tissue thickness varies both within and be-

tween colonies of the same species, the extent of signal averaging may also vary (Barnes and Lough, 1993; Barnes et al., 1995; Taylor et al., 1995; Lough and Barnes, 1997). There is a growing awareness of the complexities involved in reading coral data as climate data. Nevertheless, it has proven quite difficult to pinpoint with any degree of confidence, the extent to which either chemical disequilibria or mechanisms of skeletal accretion confuse the environmental signal.

Previous explorations of within-colony isotope variability compared growth axes or regions with significantly different rates of linear extension (Land et al., 1975; McConnaughey, 1989a; de Villiers et al., 1995; Allison et al., 1996). Consequent upon the conclusions of earlier authors (McConnaughey, 1989a; de Villiers et al., 1995), the faster-growing centres (axes of maximum growth), rather than the slower-growing sides of domed colonies, are targeted for climate reconstructions. In this study, we focus on variations in the inclusive signal about the axis of maximum growth where significant changes occur in the growth geometry and position of individual corallites as they grow. Massive, bumpy *Porites* colonies, which are used in many coral-based climate reconstructions, usually have multiple growth axes, each of which terminates in a discrete bump at the colony surface (Fig. 1a,b). New polyps are inserted only at the summits of bumps, from where corallite growth proceeds upwards and outwards in a three-dimensional fan until corallites from adjacent bumps occlude each other and growth is terminated in a valley (Barnes, 1973; Darke and Barnes, 1993; see Fig. 1a,b). Thus, each "growth axis" comprises three separate but contemporary regions where active skeletal growth is in progress: the bump summit where new corallites are added, the trajectories of individual corallites, and the valley bottom, where the older polyps die and, as a consequence, corallite growth is terminated. Although skeletal extension rate is not significantly different between bumps and adjacent valleys, polyps are exposed to quite different conditions between birth at the top of a bump and extinction at the bottom of a valley. At the bump summit, space for growth is optimal and polyps are not shaded by their neighbors (Barnes, 1973). However, as each polyp ages and enters a valley, it encounters restricted space, occlusion by incoming corallites, and shading by adjacent, elevated bumps. Calices (i.e., that part of the corallite tube occupied by tissue) in the valleys tend to be misshapen, smaller in diameter, thinner-walled, and less dense than those on the summits of bumps (Darke and Barnes, 1993; see Fig. 1a). In this paper, we report on the effects of surface bumpiness, or colony topography, and changes in the position of individual calices from the top of a bump to the bottom of a valley on the stable isotope signal in the skeleton of a *Porites solida* colony collected on the Great Barrier Reef.

2. SAMPLING AND ANALYTICAL TECHNIQUES

Colony 141-B05 was collected in June 1989, at 151°E, 21°S by Dr. David Barnes of the Australian Institute for Marine Science (AIMS), cut into 7 mm-thick slabs, and x-rayed at AIMS. Our analyses were conducted on slab 3. Isotope profiles were constructed along the central axis of the highest bump in the colony (*B*), the

central axis of an adjacent valley (V), and two discrete corallite trajectories (C1,C2) which began on the bump and ended in the valley (Fig. 1b). The top of the bump was 20 mm higher than the bottom of the valley and separated by a horizontal distance of 20 mm at the surface. Sample powder was removed at successive 0.5 mm intervals along continuous grooves cut by a tapered, diamond-tipped drillbit in a hand-held dremmel-tool. Each groove was ~1 mm wide and 1 mm deep, equivalent to the space occupied by a single corallite. The bump, valley, and younger corallite (C1 in Fig. 1b) tracks were drilled downward from the base of the last, youngest dissepiment. Dissepiments are thin aragonitic sheets thought to be accreted simultaneously throughout the colony over a two-day period at monthly intervals (Barnes and Lough, 1993). We have used the last, youngest dissepiment, which is easily identified at the base of the tissue layer, as a time-line from which to compare isotope data obtained from "same-age" samples. Samples weighing between 50 μg and 100 μg were measured for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ on an automated VG-PRISM micromass spectrometer outfitted with a 40-sample carousel. Measurement precision for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of NBS-19 standards are 0.07‰ and 0.04‰, respectively.

Average annual extension rate of the coral was estimated by measuring, directly from the x-radiograph, the distance between the first (1987/88) and fifth (1983/84) high-density bands along both axes: 10 mm/y along the bump and 9.2 mm/y along the valley. We used X-rays in combination with optical density traces (courtesy of Monty Devereux, AIMS) made along the B1 and V1 tracks to fix the absolute distance of each high-density band from the colony surface and their positions relative to each other. Tissue depth, measured from the tops of calices at the surface of the colony down to the youngest dissepiment, was 4 mm and did not vary significantly along the surface of the colony between the bump summit and the valley bottom.

3. RESULTS AND DISCUSSION

3.1. $\delta^{18}\text{O}$ Profiles on a Bump and Adjacent Valley

$\delta^{18}\text{O}$ profiles along the bump and valley tracks are shown in Fig. 2a,b. In Fig. 2a, $\delta^{18}\text{O}$ values are plotted against depth from the first dissepiment. The distance of each high-density band from the colony surface is also indicated. The most important observations are as follows:

1) Each $\delta^{18}\text{O}$ profile shows strong seasonal variations with similar amplitudes. These are, on average, $0.94 \pm 0.12\text{‰}$ on the bump and $1.00 \pm 0.08\text{‰}$ in the valley, equivalent to a temperature range of about 5.5°C (using $\Delta\delta^{18}\text{O} = 0.18\text{‰}/^\circ\text{C}$; Gagan et al., 1994). This agrees well with the average annual recorded temperature range at this site (COADS Climate Data for the GBR supplied by Janice Lough, AIMS).

2) ^{18}O maxima and minima in the bump profile are depleted (lower) relative to the valley profile by an average of 0.19‰ , which is equivalent to a 1.06°C higher SST. At the youngest dissepiment, the difference between bump and valley values is 0.26‰ ($\sim 1.44^\circ\text{C}$).

3) The isotope cycles appear out-of-phase between the valley and bump profiles. Valley cycles lag those on the bump, suggesting that either valley $\delta^{18}\text{O}$ or bump $\delta^{18}\text{O}$ or both are out-of-phase with the environmental forcing.

4) The position of each annual high-density band relative to the seasonal $\delta^{18}\text{O}$ cycle is fairly consistent from year to year on the bump and from year to year in the valley. However, high-density band formation on the bump appears to lag that in the valley by several months each year.

Good agreement between the measured amplitude of the

seasonal $\delta^{18}\text{O}$ cycle and that expected from recorded SSTs at this site suggests that intra-annual $\delta^{18}\text{O}$ variability along both the bump and valley tracks is strongly temperature-dependent. On the contrary, the significant difference in absolute measured $\delta^{18}\text{O}$ between skeleton accreted just 20 mm apart at the top of a coral dome indicates that superimposed upon the environmental forcing signal is one which is biological in origin. Similar isotope discrepancies have been reported between growth axes with different extension rates (Land et al., 1975; McConnaughey, 1989a; de Villiers et al., 1995; Allison et al., 1996). However, the difference in rate of linear extension between bump and valley axes is probably not large enough to produce the significant $\delta^{18}\text{O}$ offset we observe between them. Indeed, extrapolation of the equation derived by Allison et al. (1996) for *Porites* from Thailand predicts an 0.05‰ difference in $\delta^{18}\text{O}$ between axes with extension rates of 10 mm/y and 9.2 mm/y. We measured a $\delta^{18}\text{O}$ difference four times greater than this.

Mismatches between the environmental forcing and the phasing and/or magnitude of the inclusive signal in coral skeleton have been reported in other studies (Emiliani et al., 1978; Leder et al., 1991; Allison et al., 1996). Two independent models, one related to skeletal growth processes (Barnes et al., 1995; Taylor et al., 1995) and the other to sampling frequency (Leder et al., 1996) predict that such phase offsets are an inherent problem in the generation of coral-based time-series. The first assumes that corals thicken their skeletons by accreting a significant amount of new skeletal material below the colony surface. Thus "new" environmental information will be mixed with "old" information through a depth equivalent to that occupied by tissue, as much as 10 mm or 10 months in some colonies (Barnes and Lough, 1993). Phase offsets are accompanied by significant dampening of the amplitude of the annual $\delta^{18}\text{O}$ cycle. The second model predictions are similar but are induced by low or inadequate sampling frequency (Leder et al., 1996). We argue that, at least in this case, the apparent $\delta^{18}\text{O}$ phase offset is not real for two reasons: first, mathematical models indicate the magnitude of difference in extension rate between two growth axes needed to produce the magnitude of the observable phase offsets is 3 to 6 times greater than we actually measured between the bump and valley axes (Barnes et al., 1995). Second, average annual extension along the valley was slightly lower than that along the bump over the time period analyzed. If either skeletal thickening or inadequate sampling resolution were responsible for the phase offset, the amplitude of the annual $\delta^{18}\text{O}$ signal would be dampened along one or both tracks. On the contrary, we note that the amplitude of the annual cycles along both tracks are equivalent and in good agreement with the instrumental SST range and that no signal attenuation is apparent.

In Fig. 2b, we have made a correction for the slightly lower extension rate along the valley track. The correction is simple because it does not take into account possible intra-annual changes in extension rate. Nevertheless, two important observations can be made:

1) The bump and valley $\delta^{18}\text{O}$ cycles are approximately coincident and in-phase, suggesting that both are driven by a common forcing.

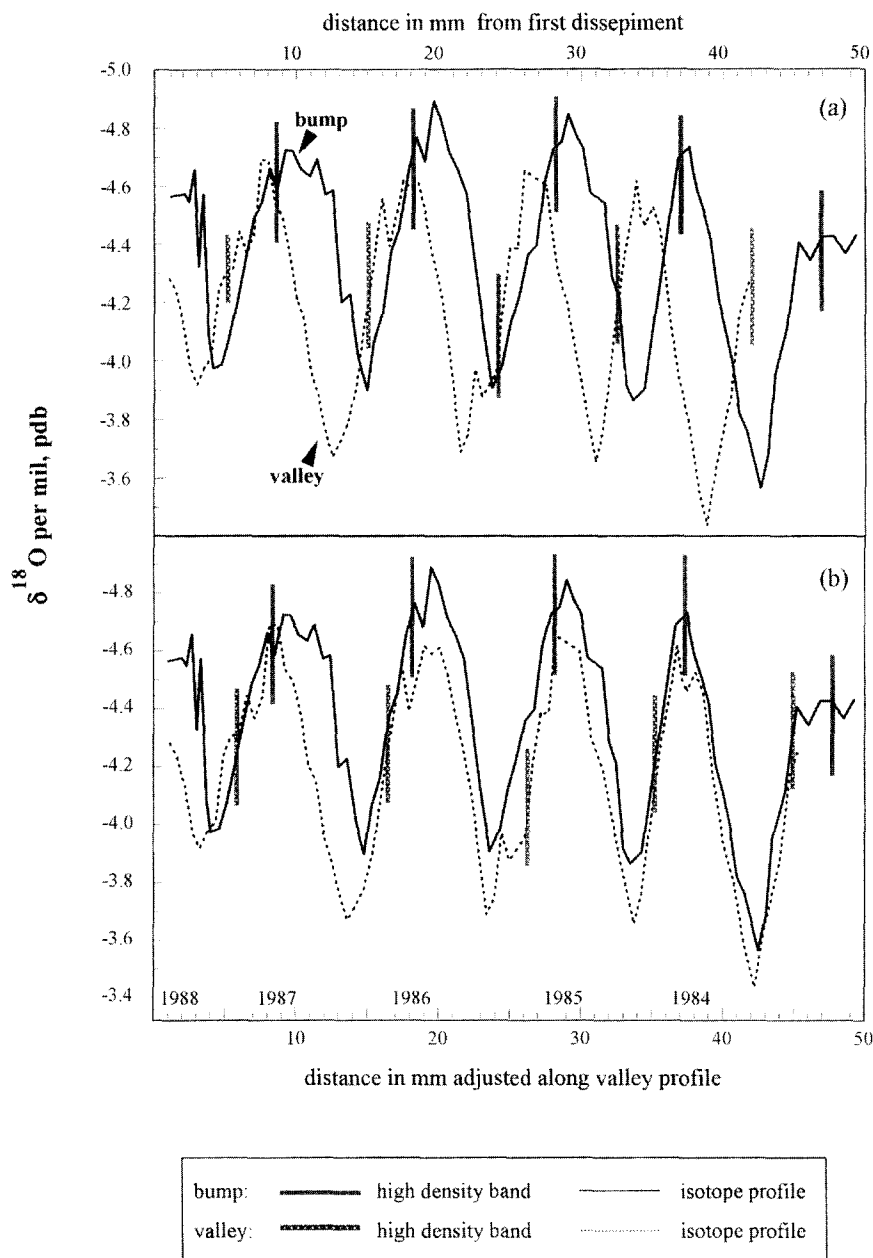


Fig. 2. $\delta^{18}\text{O}$ profiles from samples drilled along the central bump axis (solid line) and adjacent valley (dotted line). The position of each high-density band is indicated by vertical bars. In (a), isotope values in each profile are plotted against sample spacing down from the base of the dissepiment; (b) is as in (a) except that sample spacing along the valley track is increased by a factor of 1.087 to correct for different extension rates of the bump and valley axes.

2) High-density bands along the bump track remain offset from those along the valley track by an average of 1.75 mm each year.

Alignment of the $\delta^{18}\text{O}$ profiles in Fig. 2b supports our conclusion that the phase offset in Fig. 2a is not real nor is it the product of skeletal thickening or inadequate sampling frequency. In contrast, we argue that the density band offset is real and indicates a difference in the timing of high-density band formation between the bump and the valley. High-density bands on the bump coincide with the isotopically

lighter part of each annual cycle, indicating summertime accretion of high-density skeleton. This observation agrees well with results of independent studies of the timing of density-band formation in the majority of *Porites* colonies on the GBR (Isdale, 1984; Lough and Barnes, 1990). However, high-density bands in the valley of the same colony coincide most often with declining (fall) temperatures in the annual cycle, lagging those on the bump by an equivalent of 2.6 months. The implication that high-density band formation is not necessarily simultaneous within a single coral colony is

significant because density bands provide the basic chronology in most coral-based time series. Although no independent evidence yet exists to support our assertion, some authors have reported differences in the timing of density-band formation between closely-situated colonies of the same species on the same reef (Brown et al., 1986; Lough and Barnes, 1990).

3.2 $\delta^{18}\text{O}$ Profiles and Skeletal Density along Discrete Corallites

Figure 3 shows $\delta^{18}\text{O}$ profiles constructed along the growth trajectories of two individual corallites. The position of each annual high-density band relative to the isotope cycle is also indicated. These "life-history" profiles demonstrate clearly the evolution of the isotope signals and density-band trends seen only as endmembers along our bump and valley tracks (Fig. 3). The younger corallite (C1) emerged from the bump summit at the 1983/84 high-density band and disappeared into the valley at the youngest dissepiment at the base of the tissue layer. The older corallite (C2) emerged from the bump just prior to the 1982/83 high-density band, disappearing into the adjacent valley three years later. As each corallite emerges and diverges from the centre of the bump, its $\delta^{18}\text{O}$ values approximate those measured along the bump track during comparable years. However, upon entering the valley, $\delta^{18}\text{O}$ values increase relative to those on the bump and approximate more closely those measured in the valley during comparable years. This change in $\delta^{18}\text{O}$ associated with changing position of the corallite is clearly demonstrated by comparing $\delta^{18}\text{O}$ values of C1 and C2 skeleton accreted during 1984/85 (see Fig. 1b), when C1 had emerged from the bump summit and C2 was approaching the bottom of the

valley. ^{18}O maxima and minima of the C1 track are depleted by an average of 0.25‰ relative to those measured along track C2. This difference is equivalent to that observed between bump and valley $\delta^{18}\text{O}$ values at the base of the first dissepiment (Fig. 2).

Changes in the relative position of high-density bands are also observed as the corallites shift between the bump summit and valley bottom (Fig 3). The high-density bands for corallites at or recently emerged from the bump coincide with $\delta^{18}\text{O}$ minima, as they do along the bump axis. As each corallite enters the valley, the bands become progressively displaced toward the cooler part of the isotope year. These data further support our assertion that the discrepancies we observe are not related to skeletal extension rate. During 1984, the valley axis (V in Fig. 1b) extended by 8.5 mm, but the older corallite, which was approaching the valley bottom, extended only 6.5 mm. Nevertheless, $\delta^{18}\text{O}$ maxima and minima along each growth axis were almost identical, as are the positions of the high-density bands which coincide with declining temperatures in the isotope year along both tracks.

3.3. $\delta^{13}\text{C}$ Profiles on a Bump and Adjacent Valley

The carbon isotope profiles along the bump and valley tracks are shown in Fig. 4a,b (with the $\delta^{18}\text{O}$ data). All profiles are plotted against depth from the first dissepiment. The distance of each high-density band from the colony surface is also shown. The most important observations are as follows:

1) Mean ^{13}C values along the bump track are depleted relative to those along the valley track by an average of 0.50‰.

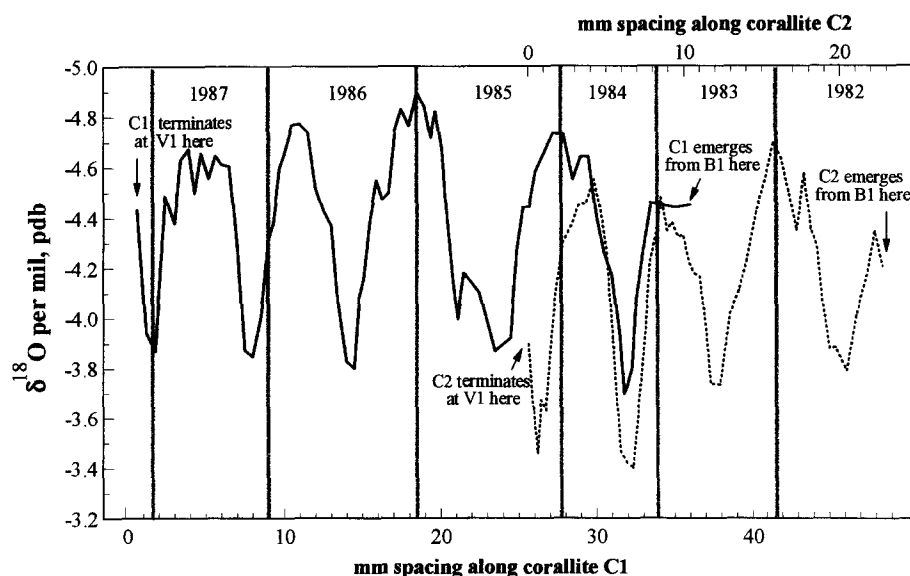


Fig. 3. $\delta^{18}\text{O}$ profiles along two discrete corallites (C1 solid line, C2 dotted line), tracking each from their emergence at the bump summit to their extinction at the valley bottom. Sample spacing and depth from the base of the youngest dissepiment is read along the lower x-axis for C1. Sample spacing for C2 and distance from the point where this corallite meets the valley are read along the upper x-axis. The position of the high-density bands is indicated by vertical bars.

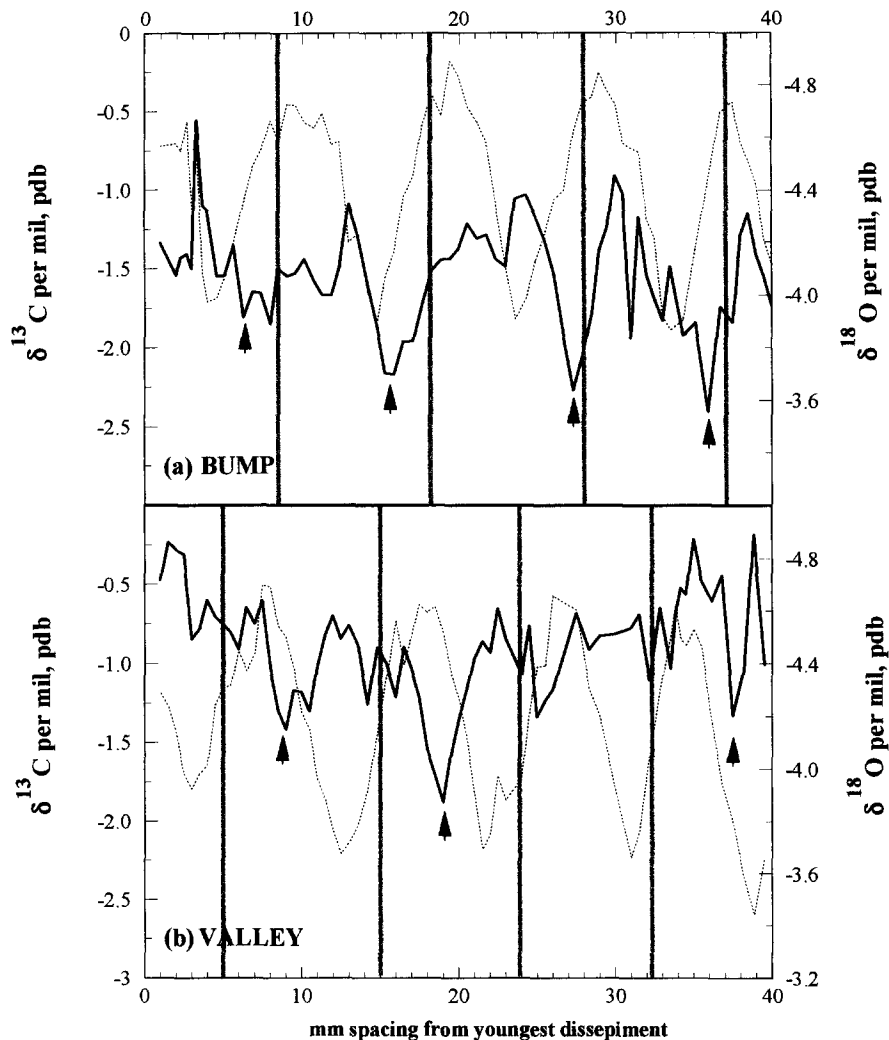


Fig. 4. $\delta^{13}\text{C}$ profiles (solid lines) plotted against $\delta^{18}\text{O}$ cycles (dotted lines) from samples drilled along the bump (a) and valley (b) axes. Sample spacing along the valley x-axis is uncorrected. The position of annual high-density bands are indicated by the vertical bars. Most depleted $\delta^{13}\text{C}$ values in each annual cycle, which we interpret as coincident with maximum photosynthetic activity, are indicated by the arrows.

2) $\delta^{13}\text{C}$ profiles along both the bump and the valley, although expectedly noisy, exhibit seasonal cycles.

3) Seasonal $\delta^{13}\text{C}$ cycles along the bump and valley tracks are out-of-phase with each other and the $\delta^{18}\text{O}$ cycles. $\delta^{13}\text{C}$ minima in the valley obtain prior to annual $\delta^{18}\text{O}$ minima (i.e., late spring to early summer), whereas $\delta^{13}\text{C}$ minima on the bump obtain later in the isotope temperature cycle, in what appears to be late summer or fall.

4) The position of the high-density bands along both the bump and the valley tracks is, in general, coincident with "heavier" $\delta^{13}\text{C}$ values in each annual cycle.

Simultaneous depletion of both ^{13}C and ^{18}O is characteristic of kinetic fractionation associated with rapid calcification (McConnaughey, 1989a). Adopting this model, we propose that the observed shift in carbon and oxygen isotope values between bump and valley skeleton is driven by higher year-round calcification rates on the bump summit relative to the

valley bottom. Although we have not quantified calcification rates along either track, our proposition is supported by independent evidence for significantly higher skeletal densities along central bump axes than along adjacent valleys (Darke and Barnes, 1993; Lough and Barnes, 1997; M. Devereux, pers. commun., 1996) and which is easily noted in the x-radiograph (Fig. 1a) where all valleys are lighter (less dense) than all adjacent bumps. Since extension rates along the bump axis of our coral colony are slightly higher than those along the valley, the calcification rate of new skeleton must be higher on the bump to account for higher skeletal density observed here.

Seasonal cycles of $\delta^{13}\text{C}$ in coral skeleton probably reflect the level of photosynthetic activity of symbiotic zooxanthellae in coral tissue, either directly or indirectly through the relationship between photosynthesis and calcification (Fairbanks and Dodge, 1979; Patzold, 1984; Goreau, 1977a,b;

Swart, 1983; Erez, 1978; McConnaughey, 1989a; Swart et al., 1996). The relationship could be direct and negative via incorporation of isotopically light CO_2 into the skeleton (Erez, 1978; McConnaughey, 1989), direct and positive if photosynthesis causes enrichment of the ^{13}C pool from which skeletal carbon is drawn (Patzold, 1984), or indirect and negative, if photosynthesis increases calcification rate (Barnes and Chalker, 1990) and hence kinetic fractionation of the stable isotope signal. A recent calibration study concludes that $\delta^{13}\text{C}$ and photosynthesis are inversely correlated (Swart et al., 1996). Applying this model to our data would imply two things: first, that photosynthetic activity on the bump and in the valley varies seasonally and second, that cycles of photosynthesis are out-of-phase between polyps on the bump and those in the adjacent valley. At this latitude on the GBR, irradiance levels are lowest and cloud cover is highest during early summer (COADS Climate Data for the GBR). We propose that highest annual rates of photosynthesis ($\delta^{13}\text{C}$ minima) obtain after midsummer (i.e., lag annual $\delta^{18}\text{O}$ minima) on the bump summit but before midsummer at the valley bottom, a phase difference caused by their relative exposure to light and irradiation at different times of the year.

No independent evidence yet exists for the differential distribution of annual cycles of photosynthetic activity along the top of a *Porites* colony, so we have borrowed ideas from a similar hypothesis relating to the generation of wave-like growth patterns in tabletop *Acropora* (Stimson, 1996). On the top of a *Porites* dome, polyps at the tops of bumps are, by virtue of their elevated position and alignment of calices, more directly exposed to radiation than those entering the bottoms of valleys. Increasing and high light levels during the spring and summertime might actually inhibit photosynthesis on the tops of bumps but be optimal for polyps already shaded-out at the bottom of valleys. Hence, an annual high in photosynthesis occurs in the valley at this time. The situation reverses when radiation levels begin decreasing in the fall and light levels are optimal for photosynthesis on the tops of bumps but suboptimal at the bottom of valleys; an annual high in photosynthesis occurs at the bump summit at this time. At no time, however, does either photosynthesis or calcification rate at the bottom of the valley match that occurring at the top of the bump.

Our use of the "Swart" model implies that the high-density portion of each annual high-and low-density couplet is formed when photosynthetic rates are relatively low (i.e., when $\delta^{13}\text{C}$ values are high). It would also imply that high-density skeleton is accreted when calcification rates are relatively low. This is in contradiction to our explanation for the generally depleted ^{13}C values of higher-density bump skeleton compared with those from the valley. However, high-density skeleton can be produced either by decreasing extension rate or by increasing calcification rate. Therefore, it is probable that the process responsible for the overall density difference between bump and valley skeleton (i.e., the difference in year-round calcification rate) is different from that which determines intra-annual changes in skeletal density along a single growth axis. We suggest that intra-annual changes in extension rate (lower extension rates dur-

ing midsummer on the bump summit, during late fall at the valley bottom) may be responsible for the formation of annual high-and low density couplets on the bump and valley axes.

4. CONCLUSIONS

The isotope and phase offsets reported here are surprisingly large considering the proximity of the sample tracks and the location of the bump and valley axes in the central and fastest-growing region of the coral colony. This region is usually targeted for geochemical analyses and assumed "safe" from growth-related variations in the inclusive signal. On the contrary, our data show that significant $\delta^{18}\text{O}$ differences may be measured along sample tracks only 2 cm apart, and it is clear that small deviations from a sampling track otherwise exactly perpendicular to the colony surface may produce large variations in the inclusive signal which are biological rather than environmental in origin. This is important in long-core reconstructions where it is often necessary to sample along several different growth axes to produce a continuous dataset. We propose that the isotope and density-band offsets we observe in this coral would be magnified in colonies with even bumpier surfaces, but might be lower or insignificant in colonies with smooth surfaces.

Our results indicate that isotope differences between bump and valley skeleton are not caused by differences in extension rate but most likely by the rate at which new skeleton is made, i.e., calcification rate, as described by McConnaughey (1989b). Thus, extension rate alone is not a good measure of potential biological effects on the stable isotope signal. Nevertheless, good agreement between the amplitude of the annual $\delta^{18}\text{O}$ cycles on both the bump and valley tracks and actual measured SSTs in this region lead us to conclude that the $\delta^{18}\text{O}$ cycles in this coral are driven largely by sea temperature. Calcification-rate driven kinetic fractionation of both isotopes causes isotope variations which are potentially significant when interpreting paleoclimatic data. However, the biological forcing is not large enough to override the temperature-dependent signal. Our conclusion contradicts that reached by Aharon (1991) and Allison et al. (1996), who determined that growth rate effects, specifically extension rate, dominate coral $\delta^{18}\text{O}$.

We interpret the phase difference in seasonal $\delta^{13}\text{C}$ cycles and differences in the relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles from the bump and the valley as a reflection of differences in the timing of the annual photosynthetic cycle. Furthermore, and as a result of this phase offset in photosynthesis, we observe differences in the timing of high-density band formation between the bump and the valley.

Coral $\delta^{18}\text{O}$ has been shown to be a valuable tool in paleoclimate reconstructions and our data confirm this. Nevertheless, the results of this study clearly demonstrate that complexities relating to coral growth and the position and arrangement of skeletal structures can induce mismatches in the inclusive signal over a relatively small sampling area, even in the region of maximum growth. We argue that the usefulness and accuracy of coral-based climate records will be enhanced by adopting sampling strategies which recognize and accommodate these complexities.

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