Seasonal variation in skeletal extension rate and stable isotopic (^{13}C/^{12}C and ^{18}O/^{16}O) composition in response to several environmental variables in the Caribbean reef coral *Siderastrea siderea*

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ABSTRACT: The potential of the massive reef building coral *Siderastrea siderea* to be a reliable archive of past environmental variations was investigated by means of a field experiment conducted on a fringing reef in Panama. Over a 14 mo experimental period, 5 closely spaced and shallow subtidal coral colonies were cored at 1 mo intervals. These cores were subsequently analysed to determine linear extension (growth) and the δ^{13}C and δ^{18}O of each monthly growth increment. Environmental conditions were recorded continuously by instruments deployed within a distance of 10 to 110 m from the corals. The environmental variables sea surface temperature (SST), salinity, wind, sun and rainfall were all well correlated with one another, reflecting the dominant seasonal cycle in the region. Of the 3 skeletal attributes considered in this study, skeletal δ^{18}O showed the strongest correlation with this seasonal cycle. The seasonal variations in skeletal δ^{18}O are attributed to changes in SST (accounting for ca 60% of the δ^{18}O signal) and inferred changes in water isotopic composition due to rainfall and runoff (ca 40% of the δ^{18}O signal). Although these results indicate that this coral is capable of yielding high-resolution paleoenvironmental records from retrospective analysis of the skeleton, there were significant and unexplained between-colony differences in mean δ^{18}O. Therefore, for this species of coral in this setting, great care must be taken before interpreting the regional environmental significance of either gradual changes in mean δ^{18}O through the length of a single long coral core, or differences between modern and ancient (fossil) colonies. Although skeletal δ^{13}C and growth rate did show some relatively weak but significant correlations with some of the environmental variables, especially when the records from all colonies were combined, it was concluded that these attributes have relatively low potential for regional paleoenvironmental reconstruction.

KEY WORDS: Coral skeleton · Stable isotopes · Panama · Reefs

INTRODUCTION

Skeletons of reef-building corals have been widely used as indicators of environmental and climate changes (reviews in Buddemeier & Kinzie 1976, Dodge & Vaišnys 1980, Dunbar & Cole 1993). The rationale behind these studies is that corals record information relating to the surrounding environment in their skeletal structure and chemistry. Since many massive corals have annual banding within their skeletons, retrospective analysis of cores from long-lived colonies can pro-

vide paleoenvironmental records of monthly to century time-scale variability (Knutson et al. 1972, Buddemeier & Kinzie 1976, Dodge & Vaišnys 1980, Barnes & Devereux 1988, Barnes & Lough 1990). However, the accuracy of the records so obtained depends upon endogenous factors which can also influence skeletal chemistry and structure, thereby partially or totally obscuring the exogenous (environmental) signal.

Water temperature, light intensity, upwelling/nutrients, cloud cover, habitat, and timing of reproduction have been highlighted as the most important variables controlling annual density variation and linear extension rates in coral skeletons (Buddemeier & Kinzie 1975, Dustan 1975, Weber et al. 1975, Foster 1977,

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Dodge & Vaišnys 1980, Dodge & Lang 1983, Wellington & Glynn 1983, Guzmán & Cortés 1989, Lough & Barnes 1990a, Klein & Loya 1991). The seasonal onset of density band formation varies widely among geographical areas and different coral species (Buddemeier & Kinzie 1976, Dodge & Vaišnys 1980, Lough & Barnes 1990b, Dunbar & Cole 1993); therefore, as would be expected, changes in coral density and linear extension rates cannot be explained or controlled globally by a single environmental factor (Dodge & Thomson 1974, Wellington & Glynn 1983).

Skeletal stable isotopic composition has been successfully used for reconstruction of climate variations on time scales of seasons to a few centuries (Dunbar & Wellington 1981, Pätzold 1984, Klein & Loya 1991, Klein et al. 1992, 1993, Cole et al. 1993, Carriquiry et al. 1994, Dunbar et al. 1994, Linsley et al. 1994, Tudhope et al. 1995). Oxygen isotope ($\delta^{18}O$) composition of the skeleton has received more attention than any other tracer, and would appear to be the most straightforward to interpret in climatic terms. Although out of isotopic equilibrium with the seawater from which it precipitates, coralline aragonite displays a temperature dependence such that for every 1°C increase in seawater temperature, the skeleton precipitated becomes about 0.2‰ depleted in $\delta^{18}O$ (Epstein et al. 1953, Weber & Woodhead 1970, Swart & Coleman 1980, Weil et al. 1981, Swart 1983, McConnaughey 1989a, Gagan et al. 1994). Skeletal $\delta^{18}O$ is also influenced by variations in seawater isotopic composition caused, for example, by rainfall or evaporation. Therefore, depending upon the climate and oceanography of the region, coralline $\delta^{18}O$ has been used either as a paleothermometer (e.g. Druffel 1985, Shen et al. 1992, Dunbar et al. 1994) or to reveal past variations in rainfall (e.g. Cole et al. 1993, Tudhope et al. 1995). ^{13}C contents are believed to be either depleted (Erez 1978) or enriched (Weber & Woodhead 1970, McConnaughey 1989a, Porter et al. 1989, Klein et al. 1992) due to increased photosynthetic activity in response to changes in the respiratory rates by the zooxanthellae, probably linked to changes in water temperature, light intensity, cloudiness, water column transparency, coral physiological stress, or annual coral spawning (McConnaughey 1989a, Porter et al. 1989, Klein et al. 1992, Carriquiry et al. 1994, Gagan et al. 1994, Wellington & Dunbar 1995).

The nature and magnitude of biologically induced skeletal variations depend upon, amongst other things, the species of coral. In this study we investigate the potential of the massive coral *Siderastrea siderea* (Ellis & Solander) for paleoenvironmental analysis. This coral has not been used hitherto for this purpose, yet it possesses several attributes which indicate that it may be an extremely valuable resource for information on

pollution and climatic change. These attributes include: (1) outstanding temperature and salinity tolerance (Macintyre & Pilkey 1969, Antonius 1980, Muthiga & Szmant 1987); (2) low growth rates (5 to 8 mm yr⁻¹) and considerable longevity (>100 yr), which means that long chronologies may be obtained from relatively short cores (Stearn et al. 1977, Guzmán et al. 1991); and (3) apparent resistance to oil, chemical and suspended-sediment pollution (Lewis 1976, Antonius 1980, Acevedo et al. 1989, Guzmán et al. 1994), which means that the coral may survive to record the nature and timing of pollution events which kill most other corals at a site (Guzmán & Jarvis 1996).

The specific objectives of this study were: (1) to quantify the between-colony and within-colony reproducibility of monthly growth rate (linear extension) and skeletal chemistry (stable oxygen and carbon isotopic composition) records in *Siderastrea siderea*; and (2) to assess the nature and significance of correlations between skeletal growth rate, skeletal chemistry and a wide range of environmental variables, and hence to identify which of the skeletal feature(s) may be reliably used to hindcast environmental conditions.

MATERIALS AND METHODS

Study area. The study was conducted at the Smithsonian Tropical Research Institute's Galeta Marine Laboratory (9° 24′ 18″ N, 79° 51′ 48.5″ W) located on the west side of Bahía Las Minas (Fig. 1). This site probably possesses the largest area of mangroves, seagrass meadows, and fringing reefs on the central Caribbean coast of Panama. The reef is a shallow windward fringing reef consisting of a large intertidal reef flat presently dominated by crustose coralline red algae, calcareous green algae, fleshy algae and seagrasses (Cubit 1985) as well as a subtidal reef that extends down to 12 m depth, with most of the reef growth occurring in the upper slope above 6 m (Macintyre & Glynn 1976, Guzmán et al. 1991). Coring has demonstrated that the Galeta Reef is at least 14 m thick and was originally built by *Acropora palmata* which became established about 7000 yr BP (before present), shortly after the end of the main post-glacial transgression. Subsequently, vertical and horizontal growth was restricted by changes in sea level and by unconsolidated sediments, respectively (Macintyre & Glynn 1976). The Galeta Reef has been protected from direct human disturbance during at least the last 30 yr; however, since the 1960s it has deteriorated due to indirect coastal impacts (e.g. dredging, oil spills, mangrove deforestation) occurring in the central area of Bahía Las Minas less than 2 km away (Guzmán et al. 1991). A major oil spill in 1986 reduced subtidal reef coral cover

(to less than 6%) and species diversity at Galeta (Guzmán et al. 1991, 1994). Subsequently, common Caribbean coral species (e.g. *A. palmata*, *Siderastrea siderea*, *Diploria strigosa*, *Montastraea annularis*, *M. faveolata*, *M. cavernosa*) declined in abundance or disappeared from the reef. However, *S. siderea* appears to have been one of the most durable species (Guzmán et al. 1991, 1994).

Sampling procedures. Five large (~1.5 to 2 m in diameter), healthy colonies of *Siderastrea siderea* were haphazardly selected and tagged along the eastern fore-reef upper slope at shallow depths (Fig. 1). All 5 colonies were sampled during the first week of each month from April 1991 to May 1992. Small cores (2 cm diameter × 4 cm length) were collected only from the rapidly-growing top/flat area of each colony (to minimize the influence on our data observations of varia-

tions in growth rates across the surface of the colony), as parallel as possible to the main axis of growth, using a hand pneumatic drill. A rubber plug was used to fill the holes to promote the fast regeneration rate known for this species (Guzmán et al. 1994). Samples within a colony were taken at least 12 cm apart to minimize possible interference of tissue regeneration with normal coral growth processes. One additional healthy colony (see asterisk in Fig. 1) was drilled in April 1992 to estimate the isotopic and growth variation within a colony; 5 replicate cores were taken from the center (top/flat area) of the colony and around a 15 to 20 cm radius (spacing between cores).

Coral samples were bleached with 2% sodium hypochlorite for 24 h to remove coral tissue and organic material in fresh water and then rinsed. Cores were sectioned longitudinally into two 4 to 5 mm thick slabs using a rock saw.

Growth rates and stable isotopes measurements. The first slab was X-rayed using a Universal 'Little Giant 30' machine with an exposure of 30 mA, 75 kVp for 15 s, source-to-film distance of 70 cm, and Kodak Industrex AA film. Contact prints were made on high contrast photographic paper. Monthly linear extension rates were estimated by measuring the distance from the living coral surface to a high-density 'marker' (the previous high-density band, which was clearly identifiable in all radiographs), then subtracting from this value the distance measured in the same way in the same colony the previous month. Previously, the annual growth pattern for *Siderastrea siderea* has been established by comparison of corals collected during different times of the year and by staining of corals with Alizarin Red (Guzmán et al. 1991, 1994). In general, the beginning of low density band formation coincides with the onset of the dry season in mid/late December (Cubit et al. 1989) and each pair of low and high density bands approximately corresponds with the calendar year (Guzmán et al. 1993, 1994).

The second slab was used for monthly measurement of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ stable isotope ratios. The outer 0.5 mm of the slab (the actual distance being adjusted to the measured linear extension for the previous month) was dissected off using a scalpel under a stereo-microscope (including the 5 additional cores used to estimate the isotopic variation within a colony). Samples were lightly crushed in an agate mortar and pestle and subsampled (1 ± 0.30 mg) just prior to analysis. Previous tests by us have indicated that this form of sample pretreatment does not lead to any isotopic fractionation. Samples were reacted at 90%C with 100% orthophosphoric acid and analyzed using a VG Isogas Prism mass spectrometer with automatic carbonate preparation system. The instrument was continuosly calibrated using a calcite standard reference material
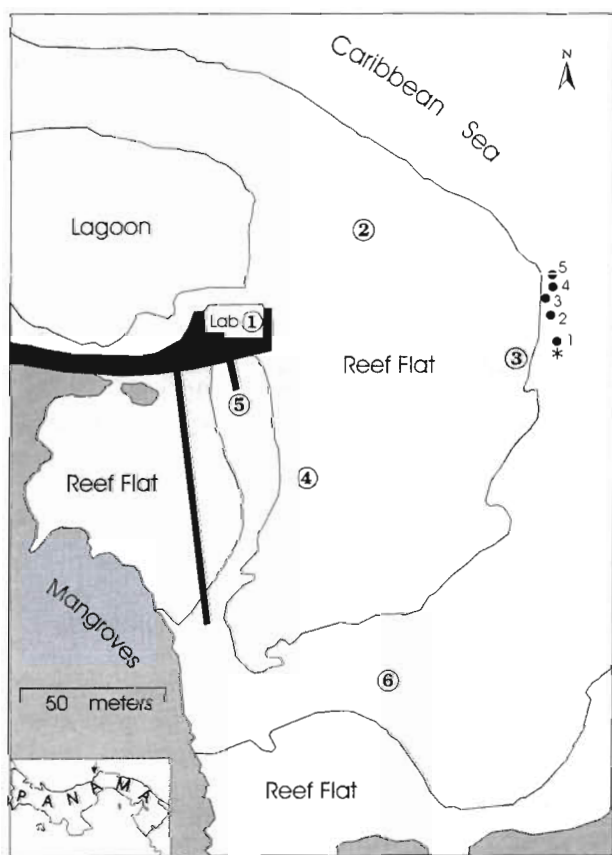

Fig. 1. Outline map of Galeta Reef, Panama, showing the location of the 5 colonies of *Siderastrea siderea* in the upper eastern slope (•), the additional healthy colony used for isotopic variation (∗), and the location of the instruments for the environmental monitoring (open circles with numbers): (1) solar radiation and rainfall; (2) water level; (3) wind speed; (4) reef-flat water temperature and solar radiation; (5) salinity; and (6) subtidal water temperature. See also Cubit et al. (1988, 1989) for a more detailed description of site and instruments

(NBS-19) and resulting values were converted into the conventional delta (δ) notation relative to PDB (Pee Dee Belemnite). Precision (1 σ) was 0.09‰ for $\delta^{18}O$ and 0.05‰ for $\delta^{13}C$ based on 17 analyses of an internal laboratory aragonite standard (COR1B).

Environmental monitoring. The meteorological and hydrographic conditions during the period of the experiment were continuously recorded by instruments deployed around the Galeta Marine Laboratory (part of the Smithsonian Institution Environmental Science Program) within a distance of 10 to 110 m from the colonies of *Siderastrea siderea* (Fig. 1). The following data were recorded: rainfall (cm), salinity (‰), solar radiation (W h m^{-2}), wind speed (km h^{-1}), water level (cm), subtidal water temperature at 3 m (°C), and suspended sediments (mg l^{-1}). Complete details about the type of instruments and calibration procedures are given in Cubit et al. (1988, 1989). All parameters with the exception of suspended solids were recorded hourly. Suspended sediment measurements are based on an average of data collected for 2 d per month from Bahía Las Minas from 1987 to 1991 (Guzmán et al. 1993), which provides an indication of turbidity in the area but which should not be viewed as a complete monthly estimation. Methods for measuring suspended sediments are described in detail in Cortés & Risk (1985) and Guzmán et al. (1993, 1994). Emersion time was estimated based on number of hours per month when the water level was below 25 cm (see Cubit et al. 1989). This is the period when the entire reef flat is exposed, and subtidal corals are closer to the sea surface.

RESULTS

Growth extension rates

Within-colony variation in growth rate was tested using each of 5 cores collected from the same colony of *Siderastrea siderea* in April 1992 (asterisk in Fig. 1). The average distance from the coral surface to the density marker in the skeleton was 4.7 ± 0.1 mm (SE), indicating relatively uniform linear extension across the top surface of the colony when averaged over an approximately 6 to 8 mo growth increment. This provides general support for the methodology used in the study to examine growth rates.

The mean annual linear extension for the 5 *Siderastrea siderea* during the period April 1991 to March 1992 was 7.6 ± 0.7 mm, about 2.4 mm higher than the previously reported decadal average of 5.2 mm (range 4.2 to 6.3 mm; 1976 to 1986) for Galeta Reef (Guzmán et al. 1991). Estimated monthly skeletal extension rates for individual colonies varied considerably during the experimental period. Due to this inter-month variability, there were no significant differences between the mean monthly growth rate values of each colony during the study period (Table 1). Although not statistically significant, it may be noted that the lowest skeletal extension was observed in the colony at the shallowest water depth (1.1 m), and maximum growth was recorded in the only male colony (Table 1). Combination of the monthly records from all colonies revealed no significant seasonal trends ($F = 1.04$, df = 12, p = 0.43; 1-way repeated measures ANOVA). With the data available, it is not possible for us to say whether the apparent lack of correlation between the colonies was due to real between-colony variations in growth rate or to an inability of our technique to accurately measure whole-colony linear extension rate at monthly resolution. The latter scenario could arise if linear extension rate varied across the top of the colony when considered at monthly periods, despite the demonstrated reproducibility when considered over a 6 to 8 mo increment. Although not statistically significant, the lowest monthly growth average was observed during September (bottom of Fig. 2), coinciding with the reproductive peak for the species in the area (Guzmán & Holst 1993). Interestingly, the only male

Table 1. Summary of monthly mean growth, and carbon ($^{13}C/^{12}C$) and oxygen ($^{18}O/^{16}O$) isotopes, of each individual tagged colony of *Siderastrea siderea* studied at Galeta Reef, Panama, from April 1991 to May 1992

Colony	Depth (m)	Sex	Growth rate[a] (mm mo^{-1})	Carbon[b] (‰ PDB)	Oxygen[b] (‰ PDB)
1	3.2	F	0.568	−2.397	−3.915
2	2.8	M	0.762	−2.581	−3.727
3	2.2	F	0.695	−2.138	−3.784
4	2.1	F	0.596	−2.392	−4.008
5	1.1	F	0.502	−2.681	−3.928

[a]Growth rate was not significantly different between colonies (Friedman Repeated Measures ANOVA; $F = 0.32$, p = 0.86, df = 4)
[b]Carbon and oxygen isotopes were significantly different between colonies (Friedman Repeated Measures ANOVA; $F = 12.7$ and $F = 12.3$, respectively, p < 0.001, df = 4)
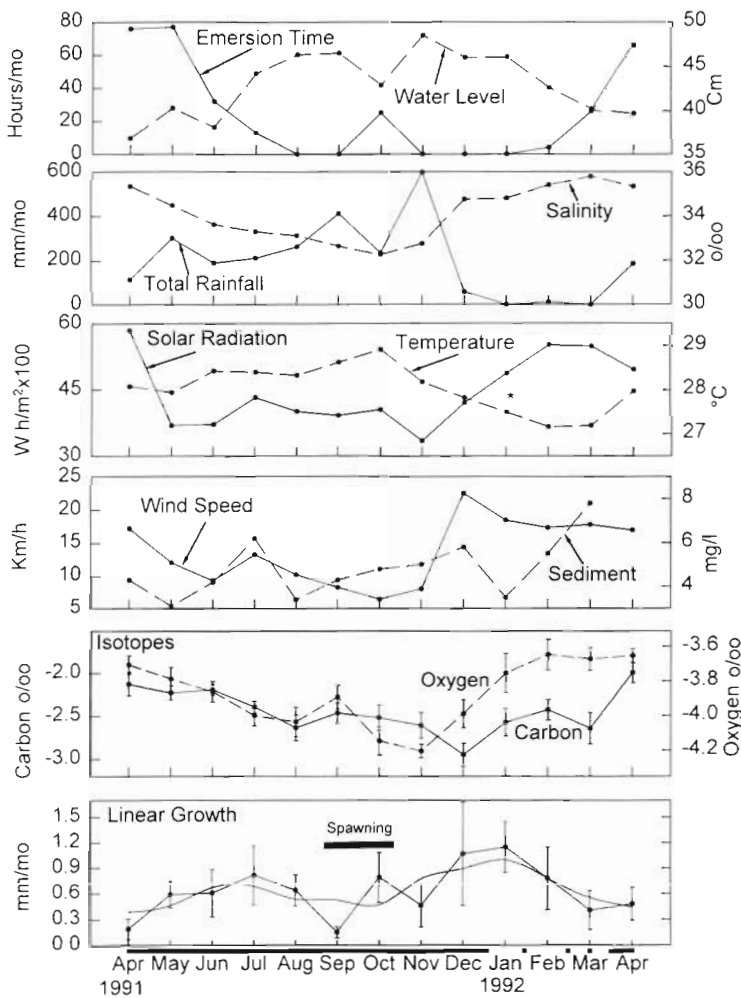
Fig. 2. Averaged monthly values for all measured environmental variables, carbon and oxygen isotope composition ($\delta^{13}C$ and $\delta^{18}O$), and linear growth rates (mm) for *Siderastrea siderea* at Galeta Reef, Panama. Variables to the left shown as solid lines, variables to the right shown as dashed lines. Seasonal changes in coral density are indicated at the bottom of the figure: high density (solid line), transition density (dashed line), and low density (dotted line). A 3-points growth moving average is shown as a thick solid line. Bars mark 1 standard error

colony (Table 1) showed the highest growth rates between December and February, a few months after spawning and the onset of the formation of new gametes (Guzmán & Holst 1993).

Dense band deposition started in early or mid April and continued until mid December (Fig. 2, bottom panel). Density banding formation was not clearly related to reproductive activity, although maximum growth and the formation of the low density band occurred during the months of lowest female and male gamete development (Guzmán & Holst 1993).

With the exception of a weak negative correlation with reef-flat emersion times and water level, seasonal skeletal extension rates did not correlate with any of the measured environmental variables (Table 2). There was no consistent relationship between inter-month variations in extension rates and skeletal $\delta^{18}O$.

Stable isotopic composition

Plots of $\delta^{13}C$ and $\delta^{18}O$ for each of the 5 colonies and for the combined records are presented in Fig. 3. In order to assess the true reproducibility of stable isotope determinations (taking into account within-colony variability, sub-sampling strategy and instrumental precision), the outer 0.5 mm of each of 5 cores collected from the same colony of *Siderastrea siderea* in April 1992 (asterisk in Fig. 1) were analyzed. The averages (SE) for carbon and oxygen were −2.60‰ (0.03) and −4.03‰ (0.03), respectively.

There were significant between-colony differences in values of $\delta^{13}C$ and $\delta^{18}O$ over the 13 mo study period (Table 1). Variation through time (13 mo; 5 colonies) was significant, with differences recorded for both isotopes ($F = 7.49$, df = 12, $p < 0.001$ for carbon and $F = 12.89$, df = 12, $p < 0.001$ for oxygen; 1-way repeated measures ANOVA). The depth range (1.1 to 3.2 m) was too small to test for an effect on isotope composition.

In general, all colonies (with the exception of Colony 4) displayed similar seasonal trends in $\delta^{13}C$, with the lowest value occurring around December during the progression from high to low skeletal density (Fig. 3). The colony from the shallowest water depth (Colony 5) had the lightest carbon isotopic composition. In all colonies, $\delta^{18}O$ was depleted toward the months of October to November, a period close to the formation of the low density band. Spawning seemed to have no clear effect on monthly-averaged carbon composition; however, the oxygen signal was depleted immediately after the spawning period (Fig. 3).

Table 2 and Fig. 2 present the results for coral growth and isotopic data averaged for all 5 colonies, compared against the environmental variables. For these averaged data, skeletal extension and skeletal $\delta^{13}C$ are both strongly correlated with water level and with emersion time. In addition, there was a significant inverse correlation between skeletal extension and $\delta^{13}C$, whereas no relationship was found between these 2 parameters and skeletal $\delta^{18}O$. Oxygen composition showed correlations with all the environmental

Table 2. Pearson product moment correlation coefficients (r) for monthly measured variables from April 1991 to April 1992 at Galeta Reef, Panama. Coral growth and isotope composition values are the average for all *Siderastrea siderea* colonies (n = 5). Temp.: subtidal temperature; Salin.: salinity; Emer.: emersion time; Sedim.: suspended sediments

	$\delta^{13}C$	$\delta^{18}O$	Growth	Rain	Solar	Temp.	Wind	Salin.	Level	Emer.	Sedim.
$\delta^{13}C$		0.48^{ns}	-0.58^{*}	0.06^{ns}	0.21^{ns}	0.12^{ns}	-0.16^{ns}	0.19^{ns}	-0.72^{*}	0.77^{*}	-0.37^{ns}
$\delta^{18}O$			-0.13^{ns}	-0.65^{*}	0.75^{*}	-0.66^{*}	0.60^{*}	0.86^{**}	-0.63^{*}	0.47^{ns}	0.09^{ns}
Growth				-0.24^{ns}	-0.09^{ns}	-0.28^{ns}	0.37^{ns}	0.07^{ns}	0.56^{*}	-0.69^{*}	0.12^{ns}
Rain					-0.75^{*}	0.58^{*}	-0.77^{*}	-0.74^{*}	0.41^{ns}	-0.07^{ns}	-0.31^{ns}
Solar						-0.62^{*}	0.68^{*}	0.79^{**}	-0.48^{ns}	0.26^{ns}	0.38^{ns}
Temp.							-0.74^{*}	-0.85^{**}	0.22^{ns}	-0.06^{ns}	-0.51^{ns}
Wind								0.86^{**}	-0.18^{ns}	0.08^{ns}	0.57^{ns}
Salin.									-0.52^{ns}	0.40^{ns}	0.30^{ns}
Level										-0.83^{**}	-0.05^{ns}
Emer.											-0.23^{ns}
Sedim.											

ns: not significant; $^{*}p < 0.05$, $^{**}p < 0.001$

variables with the exception of emersion time and suspended sediments. The strongest correlation coefficient was with salinity, followed by solar radiation (Table 2). However, a stepwise regression analysis run for $\delta^{18}O$, without forcing any of the 6 significant variables into the model, predicted a better linear combination with the independent variables wind speed (r = 0.90, p < 0.001) and salinity (r = 0.86, p < 0.001); the remaining variables (temperature, solar radiation, rainfall, sea level) did not significantly add to the ability of the equation to predict oxygen composition. Locally, all the environmental variables are closely related to each other (Fig. 2, Cubit et al. 1989), with salinity showing a strong correlation with wind speed, temperature and solar radiation, and a weaker correlation with rainfall. Interestingly, when only the total daily radiation during flat emersion times was considered, skeletal $\delta^{13}C$ was significantly correlated with solar radiation (r = 0.71, p = 0.006). This 'emersion time insolation' was, as expected, correlated to monthly emersion time and sea level (r = 0.71, p = 0.007 and r = −0.70, p = 0.009, respectively). However, no relationship between 'emersion time isolation' and growth rate was observed (r = −0.46, p = 0.12).

DISCUSSION

The environmental variables sea surface temperature, salinity, wind, sun and rainfall are all well correlated with one another. This simply reflects the dominant seasonal cycle in the region, i.e. relatively warm, wet, cloudy and calm summers (northern hemisphere) compared to relatively cool, dry, sunny and windy winters. Salinity changes are most probably a reflection of local and possibly regional rainfall and run-off. Of the 3 main skeletal attributes considered in this study (lin-

ear extension rate, skeletal $\delta^{18}O$ and skeletal $\delta^{13}C$), $\delta^{18}O$ shows by far the best correlation with this seasonal cycle, being significantly correlated with each of the 5 variables. This result suggests that intra-annual variations in skeletal $\delta^{18}O$ are predominantly affected by external environmental factors, and, therefore, that this may be a useful tracer of past environmental conditions.

From previous studies of $\delta^{18}O$ in skeletal carbonates, including corals, we anticipated that the seasonal $\delta^{18}O$ variations would reflect some combination of variations in water temperature and variations in water isotopic composition (due to influx of isotopically light water from rainfall and run-off), with or without some additional variations due to kinetic growth-rate effects. Using the standard paleotemperature equation (ca 0.21‰ decrease in $\delta^{18}O$ per °C rise in temperature) (Epstein et al. 1953), the measured range in monthly mean SST over the study period (ca 1.8°C) could account for about 60% of the total coral skeletal $\delta^{18}O$ range (ca 0.6‰). Assuming that the coral samples capture the full monthly-mean seasonal range, and assuming little influence from possible changes in kinetic fractionation effects, these data would imply that changes in water composition may account for about 0.22‰ (or 40%) of the coral $\delta^{18}O$ range. The accompanying seasonal salinity range is about 3‰. If an approximately linear relationship between salinity and local seawater $\delta^{18}O$ is assumed, these data in turn suggest that freshwater (from rainfall and runoff) is approximately 2.5‰ $\delta^{18}O$ isotopically lighter than mean seawater. We have no data on either the isotopic composition of seawater or freshwater input to the area over the experimental period; however, the derived estimate of freshwater being ca 2.5‰ lighter than normal seawater seems reasonable when compared to the −2 to −4‰ SMOW (Standard Mean Ocean Water) aver-
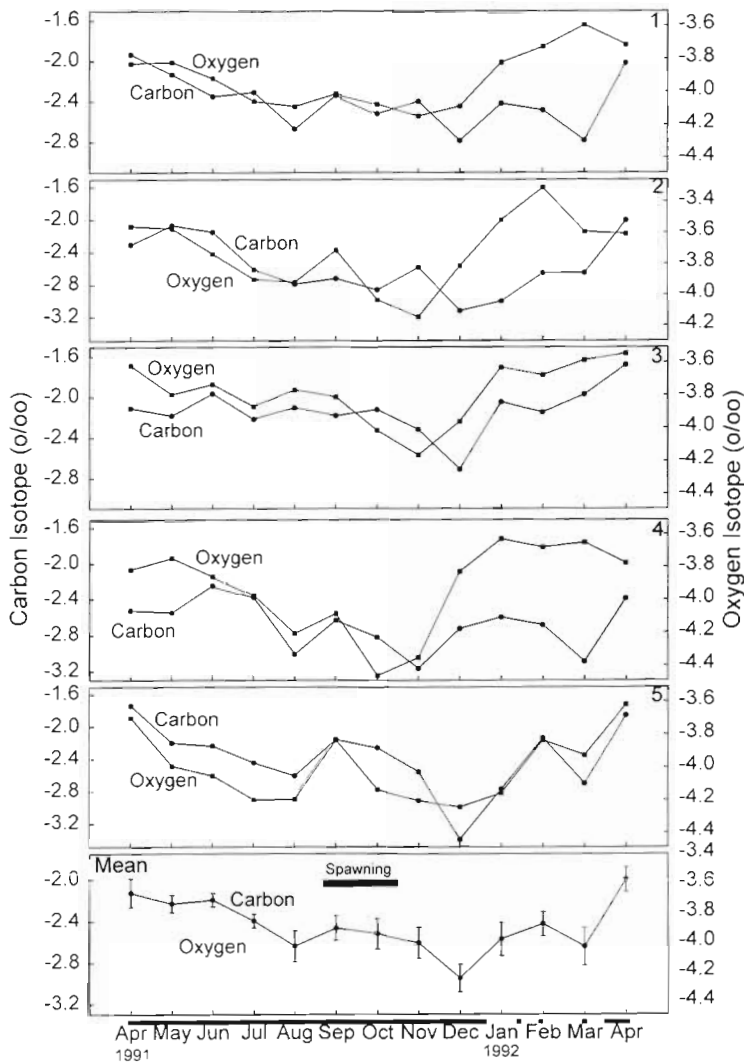
Fig. 3. Monthly variation in carbon and oxygen isotope composition ($\delta^{13}C$ and $\delta^{18}O$) for each colony of *Siderastrea siderea* (numbers 1 to 5 indicate the individual colonies), and the average signal (bottom) at Galeta Reef, Panama. Seasonal changes in coral density are indicated at the bottom of the figure: high density (solid line), transition density (dashed line), and low density (dotted line). Bars mark 1 SE

age for rainfall measured at the nearest International Atomic Energy Agency stations in the Central American region (Yurtsever & Gat 1981).

Stepwise linear regression indicated that, after salinity, the next most important environmental factor influencing $\delta^{18}O$ was wind speed. Since salinity and temperature are themselves so well correlated over the seasonal cycle, it is perhaps not surprising that temperature does not add to the ability of the equation to predict skeletal $\delta^{18}O$. A possible reason why wind speed may be an important secondary control on skeletal $\delta^{18}O$ is as follows. Most of the corals sampled were slightly shallower than the 3 m water depth of the temperature and salinity logging site. It could be that wind

exerts a significant control on the temperature structure in the upper 3 m of the water column and, therefore, wind could effect some small variations in temperature between the coral sites and the temperature logger site. For example, less wind could result in more thermal stratification in the upper few meters on a diurnal heating timescale. Possible support for this suggestion comes from the fact that skeletal $\delta^{18}O$ of the shallowest coral (Coral 5 at 1.1 m depth) shows the poorest correlation with temperature measured at 3 m, while the 2 deepest corals (Corals 1 and 2 at 3.2 and 2.8 m respectively) show the best correlation with temperature at 3 m.

Despite the fact that inter-annual variations in skeletal $\delta^{18}O$ are similar in all 5 colonies, there are significant differences in the mean compositions of the different colonies. We have no good explanation for these differences; they do not obviously relate to water depth, or to any other simple difference in coral location. They could relate either to differences in kinetic fractionation or to subtle differences between the local environments of each coral which we have not measured (e.g. degree of shading; influence of local reef morphology on wave energy and thermal stratification). This unexplained discrepancy between the corals indicates that great care must be taken before drawing inferences about the environment from small changes in mean skeletal $\delta^{18}O$ along the length of a long coral record, or from differences between the mean composition of different colonies (e.g. modern vs fossil).

Monthly skeletal $\delta^{13}C$ was not as well correlated between colonies as was $\delta^{18}O$, suggesting that endogenous or very local environmental factors play a more significant role. Several previous studies of skeletal $\delta^{13}C$ in zooxanthellate corals have indicated that sunlight exerts an important control on the seasonal cycle through its effect on photosynthesis by the algal symbionts; however, in this study, no significant relationship between sunlight and skeletal $\delta^{13}C$ was evident in the averaged monthly values for all the colonies combined. In contrast, there was a significant correlation between average monthly skeletal $\delta^{13}C$ and both water level and emersion time. There was a tendency for isotopically heavy skeleton to be deposited during periods of low water level and long emersion time, suggesting coral stress (see Carriquiry et al. 1994). A possible explanation for this is

that there may be greater photosynthesis by the algal symbionts during lower sea level (resulting in ^{12}C being selectively removed from the pool from which carbon is extracted for calcification); however, against this is the observation that this time is also one of relatively slow skeletal extension rate. Finally, there are significant differences in the mean isotopic composition of the different colonies which cannot be explained on the basis of the environmental parameters we measured. Taken together, the data for skeletal $\delta^{13}C$ indicates only a relatively low potential for seasonal-resolution environmental reconstruction from the corals and sites studied.

There was a very high degree of between-colony and between-month variability in our measurements of skeletal linear extension rate. These variations either could reflect genuine colony-wide variations or may represent, at least in part, intra-colony (spatial) variations in monthly extension (although over a 6 to 8 mo period, such intra-colony variability was not a major factor). A net result of the very high degree of between-month and between-colony variability in extension rate was that there was not a good correlation between the annual cycles of growth rate between the different colonies. When the monthly growth rate records from all colonies were averaged, there were relatively weak, but significant, correlations with water level and emersion time and with $\delta^{13}C$. Slow growth was correlated with low sea level and isotopically heavy skeleton. Although it is possible that the slow growth rate reflected an adverse response to extremely shallow water conditions, as noted above, the correlation with carbon isotopic composition is not so easily explained.

In our study, we sampled only the most recently accreted 1 mo of skeletal growth at the end of each month. Barnes et al. (1995) have suggested that not all calcification in all massive corals occurs at the outside margin of the coral. They argue that a certain percentage of the calcification occurs throughout the depth of the tissue layer, and that this must cause a degree of 'smoothing' of geochemical records derived from retrospective analysis of coral cores. *Siderastrea siderea* has a tissue layer thickness similar to the total annual linear extension (3.5 to 8 mm). Therefore, if Barnes' hypothesis applies to this coral, then we would anticipate that geochemical analysis of samples taken sequentially down through cores of this coral would yield a lower amplitude of seasonal variation than was seen in our study. Although this possibility should be borne in mind, even if some smoothing does occur, it will have little net effect on the inter-annual-centennial timescale variations which are the target of most coral-based paleoenvironmental studies.

CONCLUSIONS

The results of this study suggest the following:

(1) There appear to be large intra-annual variations in skeletal extension rate. Although we cannot absolutely exclude the possibility that these variations are the consequence of intra-colony (spatial) variations in monthly skeletal extension rates, these results indicate that caution is required in any attempt to infer a detailed chronology from coral records through simple linear interpolation between year boundaries. In addition, it suggests that care must be exercised in the environmental interpretation of seasonal trends in parameters which are known or thought to be affected by skeletal growth rates (e.g. $\delta^{13}C$, $\delta^{18}O$, Sr/Ca).

(2) There are significant between-colony variations in mean stable oxygen and carbon isotopic composition which presumably relate to different kinetic fractionation effects (sensu McConnaughey 1989a, b) and/or to the rather subtle variations in environmental conditions prevailing at each of the coral colonies. This suggests that accurate reconstruction of past environments from these corals would require analysis of several colonies in order to increase the signal/noise ratio. Trends in stable carbon isotopic composition do not always correlate significantly between colonies, indicating that this parameter is unlikely to be a useful indicator of past regional environmental conditions. There is no correlation between solar radiation and $\delta^{13}C$, but instead there are some correlations between $\delta^{13}C$ and growth rates, water level and emersion time. It is not clear if they are casual correlations. Further research needs to include the analysis of $\delta^{13}C$ in seawater for a better interpretation of any climatic signal (sensu Carriquiry et al. 1994).

(3) Intra-annual trends in stable oxygen isotope composition correlate well between colonies and, of the skeletal parameters measured, are best correlated with the dominant seasonal cycles in temperature, salinity, rainfall, sunlight and wind speed. The annual cycle in coral $\delta^{18}O$ is most probably a result of the combined effects of variations in SST (about 60% of the signal) and rainfall (about 40% of the signal), with warm and rainy summers (local wet season) giving rise to isotopically light skeleton. An apparent additional influence of wind speed on coral skeletal $\delta^{18}O$ (revealed by stepwise linear regression) could be the result of an effect of wind on the thermal stratification in the upper 3 m of the water column, i.e. it may well be an indirect influence.

(4) The strong and reproducible correlation between seasonal variation in skeletal $\delta^{18}O$ in *Siderastrea siderea* and environmental factors indicates a high potential for paleoenvironmental reconstruction, at least on seasonal and interannual timescales. How-

ever, the significant differences in mean isotopic composition between closely spaced colonies indicate that great care must be taken before interpreting the regional environmental significance of gradual (>decadal) changes in mean composition through the length of a single long coral record, or of differences between the mean composition of different colonies.

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