Coral Reefs (1996) 15:43–57

Coral Reefs
© Springer-Verlag 1996

Factors influencing the stable carbon and oxygen isotopic composition of *Porites lutea* coral skeletons from Phuket, South Thailand

N. Allison[1,*], A. W. Tudhope[1], A. E. Fallick[2]

[1] Department of Geology and Geophysics, Grant Institute, West Mains Road, Edinburgh EH9 3JW, UK
[2] Isotope Geosciences Unit, Scottish Universities Research Reactor Centre, East Kilbride, Glasgow G75 OQU, UK

Accepted: 12 May 1995

Abstract. We determined the $\delta^{18}O$ and $\delta^{13}C$ composition of the same fixed growth increment in several *Porites lutea* coral skeletons from Phuket, South Thailand. Skeletal growth rate and $\delta^{18}O$ are inversely related. We explain this in terms of McConnaughey's kinetic isotopic disequilibria model. Annual trends in $\delta^{18}O$ cannot be solely explained by observed variations in seawater temperature or salinity and may also reflect seasonal variations in calcification rate. Coral tissue chlorophyll *a* content and $\delta^{13}C$ of the underlying 1 mm of skeleton are positively related, suggesting that algal modification of the dissolved inorganic carbonate pool is the main control on skeletal $\delta^{13}C$. However, in corals that bleached during a period of exceptionally high seawater temperatures in the summer of 1991, $\delta^{13}C$ of the outer 1 mm of skeleton and skeletal growth rate (over 9 months up to and including the bleaching event) are inversely related. Seasonal variations in $\delta^{13}C$ may reflect variations in calcification rate, zooxanthellae photosynthesis or in seawater $\delta^{13}C$ composition. Bleached corals had reduced calcification over the 9-month period up to and including the bleaching event and over the event they deposited carbonate enriched in ^{13}C and ^{18}O compared with unaffected corals. However, calcification during the event was limited and insufficient material was deposited to influence significantly the isotopic signature of the larger seasonal profile samples. In profile, overall decreases in $\delta^{18}O$ and $\delta^{13}C$ were observed, supporting evidence that positive temperature anomalies caused the bleaching event and reflecting the loss of zooxanthellae photosynthesis.

Introduction

The aragonite deposited by scleractinian corals is usually depleted in ^{13}C and ^{18}O, relative to equilibrium with ambient seawater. McConnaughey (1989a) attributes these isotopic disequilibria to kinetic and metabolic effects. The former, resulting from kinetic isotope fractionation during CO_2 hydration and hydroxylation, cause simul-taneous depletion of ^{18}O and ^{13}C. Deviations from the skeletal $\delta^{13}C$ expected from kinetic fractionation are attri-buted to metabolic isotopic effects caused by modification of $\delta^{13}C$ of the internal dissolved inorganic carbon (DIC) pool by zooxanthellae photosynthesis and by algal and coral respiration. In addition, a depletion in carbonate $\delta^{18}O$ occurs as temperature increases in inorganic (O'Neil et al. 1969) and biogenic carbonates. Several palaeo-thermometer equations describing this effect have been proposed for *Porites* corals, including:

$\delta c - \delta w = 0.577 - 0.203T$ (McConnaughey 1989a, coral from Galápagos, wrt PDB)

$\delta c - \delta w = 0.641 - 0.214T$ (Chakraborty and Ramesh 1993, coral from the Arabian Sea)

where $\delta c = \delta^{18}O$ of CO_2 released by reaction of $CaCO_3$ with H_3PO_4 at 25 °C (wrt PBD), $\delta w = \delta^{18}O$ of CO_2 equilibrated with supernatant seawater at 25 °C, T = temperature (°C).

These two equations are in good agreement and correspond to a decrease in skeletal $\delta^{18}O$ of approximately 0.21% per 1 °C seawater temperature increase. However, not all authors have observed the skeletal $\delta^{18}O$ variations expected from consideration of temperature dependent fractionation effects (Emiliani et al. 1978; Goreau 1977), and the reasons for this are unclear. The sampling frequencies (4–6 samples per annual growth band) used by the authors may have been insufficient to accurately trace skeletal $\delta^{18}O$ variations. Alternatively, temperature effects may have been obscured by changes in seawater $\delta^{18}O$ composition or by some physiological effect produced by the organism. There are several reports of a relationship between skeletal growth rate and isotopic values. Land et al. (1975) observed greater depletion in skeletal ^{13}C and ^{18}O in the faster growing areas of single coral colonies and also in the faster growing skeletal elements from the same calice. McConnaughey (1989a) reported an inverse

* *Present address:* Department of Environmental Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

relationship between linear extension and $\delta^{13}C$ and $\delta^{18}O$ in the outermost carbonate of *Pavona clavus* heads from Galápagos but only for those parts of the coral growing at less than 5 mm year^{-1}. For more rapidly growing parts of the coral, calcification rate did not appear to have a significant effect.

The present study investigates the various controls on the $\delta^{13}C$ and $\delta^{18}O$ composition of *Porites lutea* coral skeletons from the Phuket area of South Thailand. Seasonal variations in $\delta^{18}O$ and $\delta^{13}C$ are considered in relation to seawater temperature and salinity data and the relationship between the chlorophyll *a* concentration of the overlying coral tissue and the isotopic composition of the skeleton is investigated. Around Phuket large variations in the skeletal growth rates of colonies from the same site, water depth and reef-front location occur (Scoffin et al. 1992), and the effect of this on skeletal isotopic composition is explored. We also examine the effect of a local coral bleaching event on skeletal isotopic composition.

Materials and methods

Description of study area

Ko Phuket is an island on the SW coast of Thailand in the Andaman Sea at latitude 8 °00′N and longitude 98 °20′E (Fig. 1). The area has a monsoonal climate, with a dry north-east monsoon from November to March and a wet south-west monsoon from April to October. Cloud cover is lowest and sunshine highest between November and May. Rainfall measured at the Phuket Town weather station from January 1982 to June 1992 ranged from 0 to 881 mm month^{-1} (Fig. 2). Seawater salinity data were collected weekly or biweekly from the pier station at Phuket Marine Biological Station between March 1982 and November 1986 and between September 1990 and June 1991 (Vudichai Janekarn, personal communication, 1992; Fig. 2). Illustrated data are the monthly means of the 2 and 4 m water depth measurements, corresponding to the depth range of the corals sampled. Salinity usually varied by 0.1–0.3‰ over the whole depth range measured from the water surface to the bottom of the reef front (at about 7 m depth). The annual salinity range is 1–2.0‰ but seasonal trends are not consistent. In some years (1983 and 1985) highest and lowest salinities were recorded between April and June and between November and January, respectively. However, in other years no seasonal trend is apparent (1984) or the trend appears to be reversed (1986). The few data available for the period of this study (November 1988 to June 1992) illustrate an increase in salinity from September 1990 to January 1991 followed by a decrease up to April 1991. This is largely expected from the rainfall data which is lowest between November and February. However, it is unclear why the strongly seasonal rainfall is not always reflected by seawater salinity variations. It is possible that in some years a time lag occurs between rainfall and freshwater discharge into the sea. Alternatively, the salinity trend expected from rainfall may be swamped by the influx of another water body of higher or lower salinity. Hydrodynamics in the area are principally determined by the two monsoon seasons. During the south-west monsoon, airflow results in the movement of surface waters north. On the east side of Ko Phuket these surface waters move up into Phangnga Bay and the bottom currents in the Bay move south. This situation is reversed during the north-east monsoon (Carr 1992).

Monthly mean surface seawater temperatures for the 5° latitude by longitude area, including the sea around Phuket, ranged from 27.9 °C in January to 29.4 °C in May (from 1951 to 1980, Overseas Development Administration environmental data, Fig. 3). These tem-peratures are in reasonable agreement with data collected from the pier station at the Phuket Marine Biological Centre. Between March 1981 to December 1986 and July 1990 to June 1992 temperatures ranged from approximately 26 °C in December and January to 30 °C in May and June (Vudichai Janekarn, personal communication, 1992). Temperatures varied by ±0.1–0.2 °C over the depth range measured, from the water surface to the bottom of the reef front (at about 7 m depth).

Extensive coral bleaching was observed in the Phuket area from early June 1991 onwards and affected many branching and massive corals on the fringing reefs around the Phuket Marine Biological Centre. There were marked differences in the degree of bleaching in adjacent *Porites* colonies of apparently the same species. Visibly unaffected corals retained their usual dark brown pigmentation, while bleached corals became very pale or even white. Partial recovery of pigmentation was observed in several *Porites* colonies towards the end of July, and over the following weeks many of the

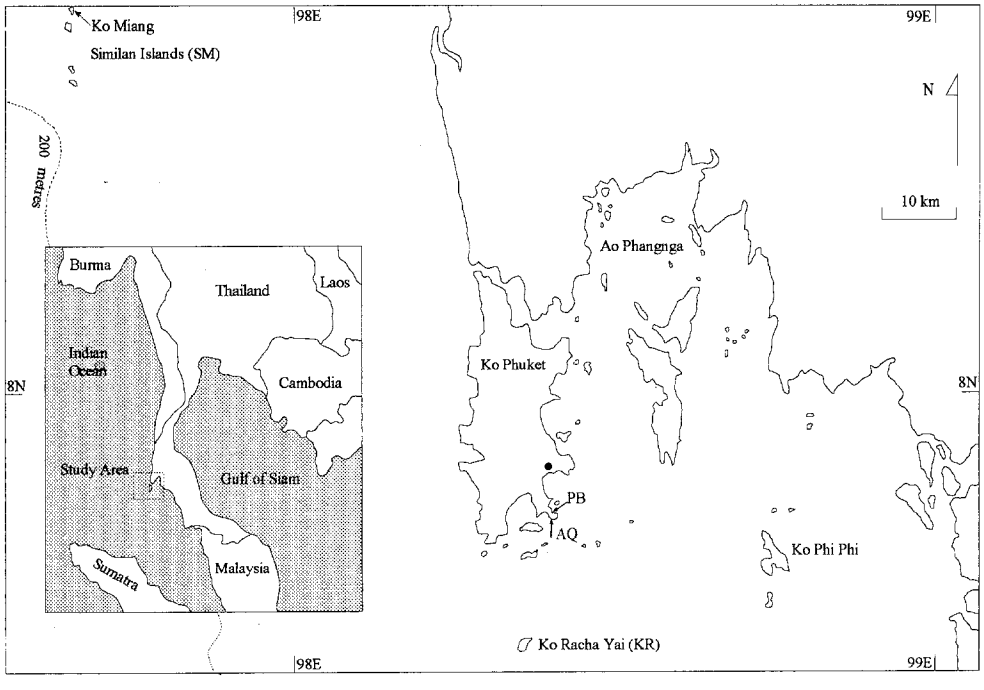

Fig. 1. Map of the study area in Phuket, South Thailand, showing the reef sampling sites Porites Bay (*PB*) and Aquarium reef (*AQ*) and the position of Phuket Town (●). The 200 m depth contour is shown

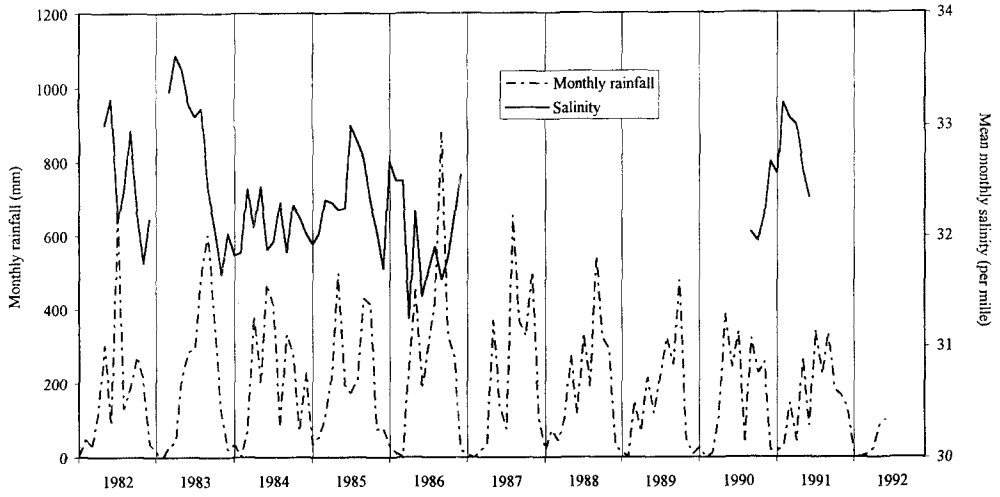

Fig. 2. Monthly rainfall (from the Phuket Town weather station) and mean monthly salinity data (from the pier station, Phuket Marine Biological Centre)

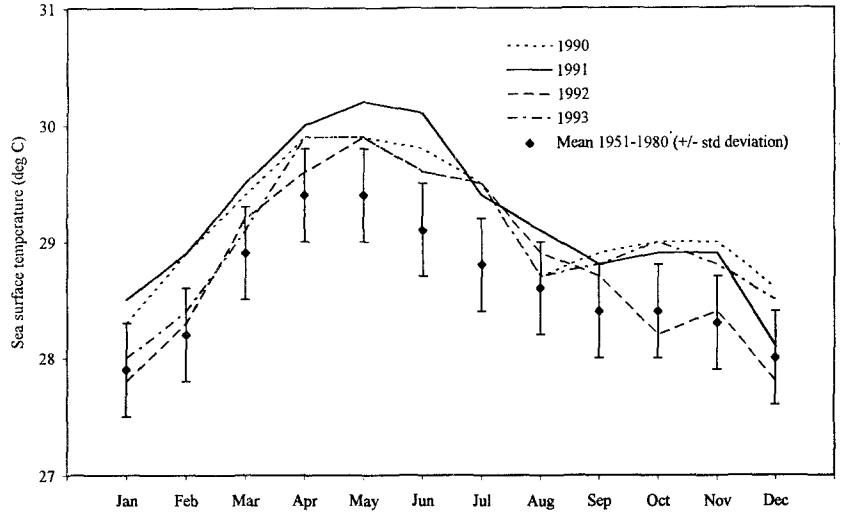

Fig. 3. Average monthly seawater temperature data from the 5 degree longitude/latitude square containing Phuket Island

affected corals recovered to normal pigmentation (Niphon Phongsuwan, personal communication, 1991). Surface seawater temperatures had been up to 1 °C above normal since December 1990, and the bleaching event approximately coincided with the annual maximum of 30.2 °C (Fig. 2). In common with many other bleaching reports, there is good circumstantial evidence that this event was primarily temperature induced.

Coral specimens were collected from the Porites Bay reef on the SE coast of Phuket Island. This is an inshore fringing reef, typical for the muddy waters of Phuket's SE coast (Brown et al. 1986; Scoffin et al. 1992). The reef consists of an inter-tidal reef flat 100–150 m wide and a near vertical reef slope leading down to muddy (terrigenous clay-rich) fore-reef sediments at 4–6 m water depth. The turbidity of local waters is largely due to resuspension of this fore-reef mud by tidal and wind-driven currents. The reef front is dominated by large colonies of *Porites*, up to 4 m in diameter. The upper surfaces of *Porites* colonies in this area are hummocky, with prominent knobs or heads having up to 30 cm relief. Colonies were sampled by removal of these heads, in whole or in part, underwater using a hammer and chisel. All samples were collected from Porites Bay between 1 and 3 m below mean low water levels, within a 15-day period during July 1991. Corals were collected within 30 m of each other. In addition one specimen was collected from the Aquarium Reef in July 1992. Similar to Porites Bay in morphology, this reef occurs on the opposite (south) side of the headland, approximately 0.5 km from Porites Bay.

Biogenic carbonate samples are commonly treated before geochemical analysis to remove organic contamination. However McConnaughey (1989a) found that neither vacuum roasting coral samples at 250–300 °C or treating with hydrogen peroxide improved sample reproducibility. Gaffey and Bronnimann (1993) concluded that sodium hypochlorite was the most effective solution at removing organic material from biogenic carbonates and we used this to remove organics from the samples analysed during the present study. Coral heads were soaked in a diluted solution of sodium hypochlorite (ca. 3–4%) for 48 h after collection and briefly rinsed in tap water. On arrival in Britain, prepared samples were soaked in a similar solution for 2–3 days and rinsed for 48 h. This treatment did not appear to significantly affect stable isotope ratios for alternate sodium hypochlorite-treated and -untreated samples along a growth band ($\delta^{18}O = -5.66‰ \pm 0.05$ and $-5.68‰ \pm 0.04$; $\delta^{13}C = -2.84‰ \pm 0.12$ and $-2.75‰ \pm 0.16$ respectively [all standard deviations are 1σ]). Although this pretreatment did not improve sample reproducibility it was necessary to remove tissue and other organic contamination, particularly in the outermost samples.

Corallite skeletal structure was examined by binocular and scanning electron microscopy. Only corals exhibiting morphological char-acteristics of *Porites lutea* (using the keys of Veron 1986) were used in this study.

To investigate the controls of $\delta^{13}C$ and $\delta^{18}O$ in the corals of this area we adopted several strategies:

1. Growth increment experiment. We analysed the isotopic compositions of the same growth increment from different coral colonies and from replicate samples within the same colony. Isotopic composition was related to skeletal growth measured as linear extension, skeletal bulk density and calcification.

2. Isotopic profile experiment. We constructed profiles of seasonal variations in $\delta^{13}C$ and $\delta^{18}O$ across the three most recent years of growth in several coral colonies. Seasonal variations in $\delta^{18}O$ and $\delta^{13}C$ were considered with reference to seawater temperature and salinity data, while profile differences between corals were related to variations in linear extension. In addition, data produced from profiles spanning the bleaching episode were used to establish the effects of this event.

3. Analysis of the outer 1 mm of skeleton. We analysed the isotopic composition of the outermost 1 mm of several coral skeletons collected during the bleaching event. Bleached and unbleached samples were compared to assess the effect of the bleaching event. The isotopic composition was also related to the chlorophyll *a* concentration of the overlying coral tissue.

Growth increment experiment

Analyses were made on samples from nine colonies collected from Porites Bay in July 1991. All colonies appeared unaffected by the bleaching event in progress at the time. Colonies were sectioned along the axis of maximum growth into slices of 10–16 mm thickness, which were photographed under ultraviolet radiation to record fluorescent banding patterns. Bright-dull fluorescent couplets represent approxi-mately annual growth in corals in this area, with bright band accretion beginning in approximately November (Scoffin et al. 1992). In this area, bright fluorescent banding does not correlate directly with local rainfall (November is the start of the dry season) which differs from previous reports from other areas (Isdale 1984; Boto and Isdale 1985). However, alizarin red S ground-truthing and extensive observations of the fluorescent banding in coral from the Phuket area, leaves no doubt that bright band deposition commences at about November. Skeletal density banding was not used to produce chronologies as it has proved to be ambiguous in the corals of this area with some corals producing two pairs of dense/less dense bands per year (Brown et al. 1986). Linear growth, skeletal bulk density and calcification were calculated for each sample for the growth increment from the start of the last bright fluorescent band (approximately November 1990) to the outermost part of the coral skeleton (July 1991). Although this growth increment may not exactly correspond to the 9-month period described, we can be sure that the same time interval was sampled from each coral, allowing intercolony comparisons. Between one and seven samples were prepared from the top of each coral head.

Linear extension was measured along the axis of maximum growth, and the skeletal bulk density of the growth increment was determined by cutting out a rectangular block of coral (approximately 10 mm × 5 mm × linear extension) and measuring its weight and volume (dimensions measured using callipers). Calcification for the time interval was calculated as a product of linear extension and skeletal bulk density. Repeat measurements on same samples indi-cated that errors in measurement were less than 5%.

Sample blocks were analysed for $\delta^{13}C$ and $\delta^{18}O$. Each block was ground to a fine powder immediately before analysis and a subsample of 0.09–0.14 mg weighed. Samples were reacted at 90 °C with 100% orthophosphoric acid (s.g. 1.9) and the resulting CO_2 was analysed using a VG Isogas Prism mass spectrometer. The machine was calibrated using a standard marble reference (SM1) and values were converted to a PDB standard. The standard deviation (1σ) for 100 analyses of the standard carbonate (SM1), carried out over several months, was ±0.068‰ for $\delta^{18}O$ and ±0.054‰ for $\delta^{13}C$. Duplicate analyses of coral samples gave replication (1σ) of better than ±0.05‰ for oxygen and ±0.1‰ for carbon. Duplicate analyses on the outer-most parts of the coral skeleton showed the highest $\delta^{13}C$ variability, probably due to the presence of increased concentrations of organic material not removed by the sodium hypochlorite pretreatment. Reproducibility of other carbon analyses was frequently better than ±0.05‰. An anonymous reviewer of this manuscript reports obtaining anomalous isotope values for samples from the outermost parts of the skeleton which are occupied by the tissue layer. In our studies of isotope profiles, including material taken from the tissue layer (notably from corals sampled in 1990, before the bleaching event occurred), we have found no evidence that material from the tissue layer produces anomalous values once treated to remove organic material.

Isotopic profile experiment

Five isotopic profiles were established from four corals collected from Porites Bay in July 1991. Coral PB9 appeared unaffected by the bleaching event while corals PB4, PB7 and PB8 all appeared bleached. Coral heads were sectioned along the axis of maximum growth and photographed under ultraviolet radiation to record fluorescent banding patterns as before. Detailed isotopic profiles (8–10 samples per annual growth band) were constructed across the three most recent years of growth, up to and including the bleaching event. For each profile, a thin strip of skeletal material, approximately 3 mm × 3 mm, was cut along the maximum growth axis of each coral from the start of the bright band deposited in approximately November 1988 to the outermost part of the skeleton (July 1991). Each strip was ultrasonically cleaned, dried at 50 °C and divided, using a fine scalpel blade, into samples of measured length. Samples were treated, powdered, weighed and analysed as before. A second series of samples were prepared from coral PB9, called PB9b. These samples were prepared from a growth axis close to the base of the coral which had a linear extension of about half of that observed along the maximum growth axis. An additional profile was also prepared from colony AQNEW, a coral collected from the Aquarium Reef in July 1992, which had apparently been unaffected by the bleaching event 1 year previously. In this case the profile spanned the time period approximately November 1989 to July 1992.

Analysis of the outer 1 mm of skeleton

Samples were prepared from nine colonies collected from Porites Bay in July 1991. Five appeared unaffected by the bleaching event in progress at the time, while four were extensively bleached (all virtually white). Five sample pairs were prepared from the top of each colony. One half of each pair, approximately 100 mm^2, was analysed for chlorophylls within 1 h of collection of the coral (see below) and the other half, approximately 10 × 5 × 20 mm (deep), was returned to Britain for stable isotope analysis. It was not possible to measure the rate at which the outermost 1 mm of skeleton was deposited. However heads on eight of the coral colonies (four bleached, four unbleached) were treated with alizarin red S stain, which colours skeleton deposited during stain exposure and acts as a time reference plane. In situ corals were enclosed in plastic bags containing the stain for 6–7 h; the bags were then removed and the corals were collected after another 3 weeks. Isotope samples were also examined under ultraviolet radiation and the widths of the outer most growth increments (approximately November 1990 to July 1991) were recorded. Since this growth increment contains approximately 1 month of the bleaching event, any major changes in growth rate over the bleaching event would manifest themselves as small variations in net accretion over this nine month growth increment.

Immediately prior to isotopic analysis, the outermost 1 mm of the skeleton was scraped away using a fine scalpel blade. Samples were powdered, weighed and analysed as before. It is not possible to be certain that the same growth increment was sampled in each coral. However, corals were collected 4–6 weeks after the bleaching began, so this increment should consist predominantly of material deposited during the bleaching event (assuming some skeletogenesis).

Each sample for chlorophyll analysis consisted of an area of approximately 100 mm^2 coral tissue and its underlying skeletal material to a depth of about 5 mm. Samples were analysed according to the methodology of Jokiel and Coles (1974). In summary, the area of each sample was measured using calipers and the sample was

then finely ground in 10 ml 90% acetone using a mortar and pestle. Samples, including all the associated material, were decanted into glass test-tubes, wrapped in silver foil and stored in a refrigerator for 24 h. At the end of this period the samples were reshaken, centrifuged and the supernatant liquid decanted. The volume of the supernatant liquid was measured, it was diluted if necessary, and the light extinction, in 10 mm cells, was measured in a Toshiba spectrophotometer at 750, 665, 645 and 630 nm. Concentrations of chlorophylls *a*, *b* and *c* were determined using the formulae of Strickland and Parsons (1968). Repeat analyses of replicates indicated that standard deviations of measurement were ±2% for chlorophyll *a* and ±5% (1σ) for chlorophyll *b*. Coral zooxanthellae contain no chlorophyll *b*, so its presence was assumed to originate from contamination of the sample by filamentous algae, which infest the coral skeleton below the layer of living tissue (Jokiel and Coles 1974). Analyses performed on skeletal material containing only filamentous algae and no coral tissue showed that the chlorophyll *a*: chlorophyll *b* ratio of these algae was constant (chl *a*/chl *b* = 1.32 ± 0.09, 1σ). Consequently the chlorophyll *b* concentration of the coral samples could be used to determine the relative concentrations of chlorophyll *a* due to filamentous algae and to symbiotic zooxanthellae. The chlorophyll *a*: chlorophyll *c* ratio in the filamentous algae was not constant, so we were unable to calculate coral chlorophyll *c* concentrations. In general the chlorophyll *a* concentrations attributed to the filamentous algae were about a tenth to a twentieth of those attributed to the zooxanthellae. The chlorophyll *a* concentration attributed to the zooxanthellae was corrected for differences in measured tissue surface area and supernatant volume to give a chlorophyll *a* concentration in mg cm^{-2} coral tissue. This method makes no correction for variations in the depth of the tissue layer between samples.

Results

Growth increment experiment

Skeletal growth and isotopic measurements for the outermost growth increment are shown in Appendix 1. $\delta^{18}O$ values varied from −5.18 to −6.16‰ and $\delta^{13}C$ values from −2.47 to −4.51‰. Regressions were calculated (method as in Wetherill 1982) between $\delta^{13}C$ and $\delta^{18}O$ values and all the growth measurements (Figs. 4, 5). Regression equations, Pearson's correlation coefficients (*r*) and levels of significance are superimposed onto each graph. There are good correlations between all growth measurements (linear extension, skeletal density and calcification) and $\delta^{18}O$ (all significant at the 0.001 level). Multiple isotopic measurements were made on four of the coral heads (PB3, PB5, PB6 and PB9, see Fig. 6). Only the samples from colony PB6 exhibit a similar linear extension versus $\delta^{18}O$ relationship, within colony. The lack of a clear intracolony relationship in the other corals is discussed later. Correlations between $\delta^{13}C$ and all the growth measurements are poor.

Isotopic profiles experiment

Fluorescent banding patterns for the corals studied are shown in Fig. 7. There is little variation in the linear extension between corals PB7, PB8 and PB9a over the time period analysed (45, 43 and 45 mm respectively), but substantial differences occur in corals PB9b and PB4. Bright fluorescent bands from PB9b and PB4 have similar widths to those of PB9a at the beginning of the record in November 1988 (approximately 5 mm), but extension rates subsequently diverge and by the outermost growth increment band widths in PB9b and PB4 are less than half the width of PB9a (3.5, 4.5 and 10 mm respectively). Coral AQNEW extends by 54 mm over the time period studied.

Seasonal $\delta^{13}C$ and $\delta^{18}O$ trends are shown in Figs. 8 (corals PB9a, PB9b and PB4) and 9 (corals PB7, PB8 and AQNEW). All isotopic determinations are detailed in Appendix 2. The relative position of each sample in the annual band has been calculated by dividing the distance of the middle of each sample along the annual band by the width of the annual band. This allows all the corals to be shown on the same chronological axis, despite variations in linear extension between corals. Representing the data

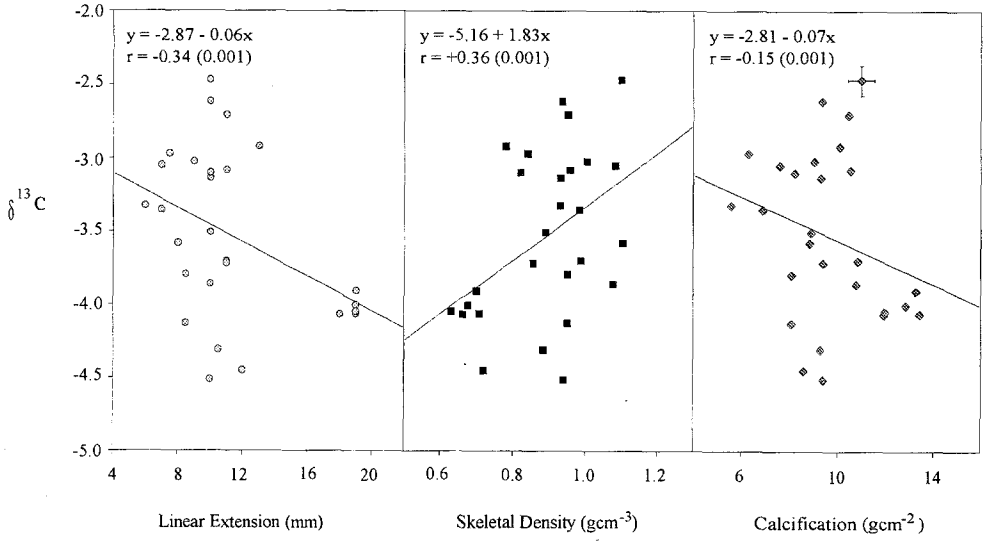

Fig. 4. Regressions of $\delta^{13}C$ of the outer skeletal growth interval (approximately November 1990 to July 1991) versus linear extension, skeletal bulk density and calcification. Standard deviations for isotopic and growth measurements are shown for one point in the graph at the far right. Regression equations, Pearson's correlation coefficients (*r*) and levels of significance (in parentheses) are superimposed onto each graph

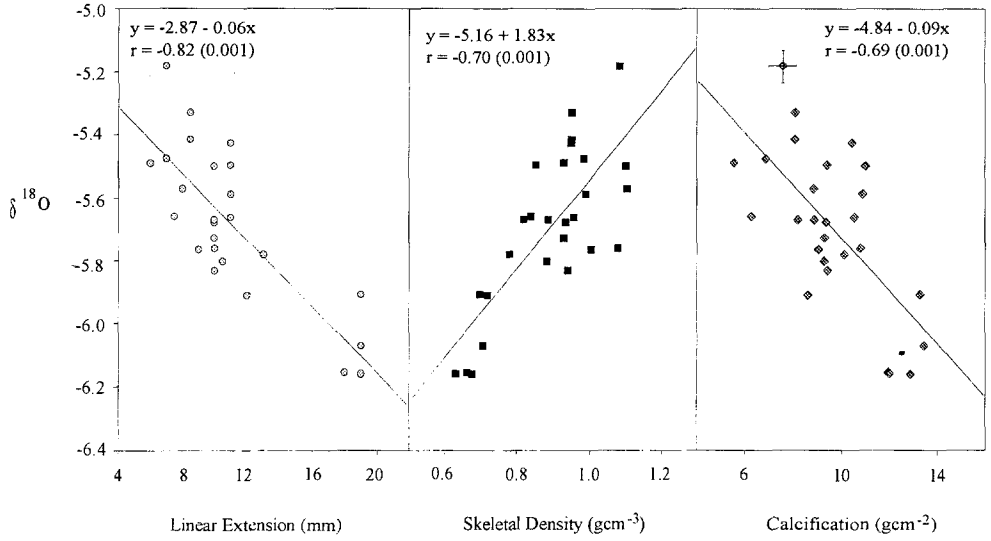

Fig. 5. Regressions of $\delta^{18}O$ of the outer skeletal growth interval (approximately November 1990 to July 1991) versus linear extension, skeletal bulk density and calcification. Standard deviations for isotopic and growth measurements are shown for one point in the graph at the far right. Regression equations, Pearson's correlation coefficients (r) and levels of significance (in parentheses) are superimposed onto each graph

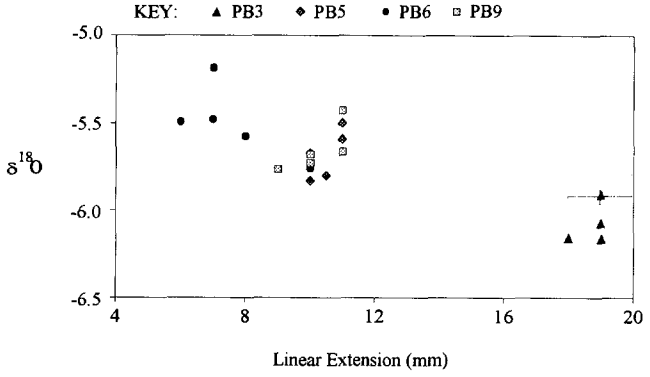

Fig. 6. Plot of $\delta^{18}O$ versus linear extension for multiple samples (over the growth interval approximately November 1990 to July 1991) from four coral colonies. Standard deviations (1σ) of measurements are shown on one point

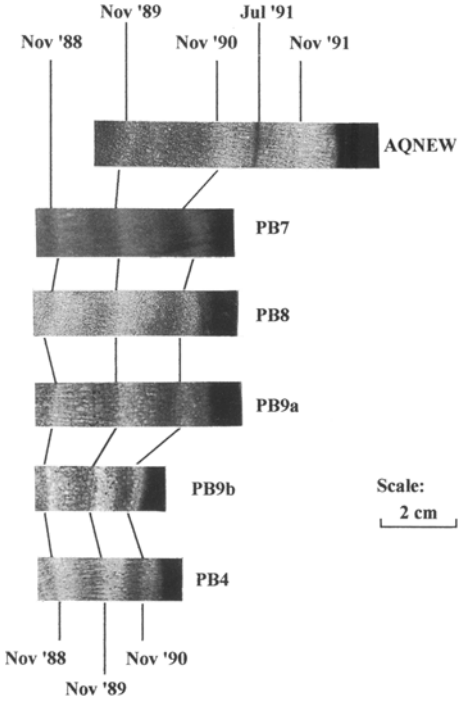

Fig. 7. Fluorescent banding patterns in this corals examined in the present study. Approximate deposition dates are shown (bright band deposition begins in approximately November). All corals were collected in July 1991 with the exception of coral AQNEW (collected in July 1992)

in this manner makes no allowance for seasonal variations in linear extension rate. However, we assume that these seasonal variations would be similar between colonies.

The corals in both Fig. 8 and Fig. 9 show similar trends in $\delta^{18}O$, with the isotopically lightest oxygen deposited around the beginning of the bright fluorescent bands (approximately November) and the heaviest deposited between bright bands (approximately April to June). Corals PB7, PB8, PB9a and AQNEW exhibit annual $\delta^{18}O$ ranges of 0.4–0.6‰. Corals PB8, PB9a and AQNEW deposited similar values of $\delta^{18}O$, but coral PB7 generally deposited higher $\delta^{18}O$ values (by about 0.3‰). Corals PB4 and PB9b deposited similar $\delta^{18}O$ values to those of PB9a at the start of the record (November 1988), but they show a greater enrichment in ^{18}O as the record proceeds. By July 1991 these corals deposited $\delta^{18}O$ 0.5 to 0.8‰ higher than the faster growing material in coral PB9a.

All corals show similar $\delta^{13}C$ annual trends, but records from different corals or even from different axes of the same coral show widely varying values. Each coral exhibits an annual $\delta^{13}C$ range of 1.2–2.0‰, with the isotopically lightest carbon deposited around the beginning of the bright fluorescent bands (approximately November) and the heaviest deposited between bright bands (approximately April to June). Corals PB9 and PB7 deposited

similar values of $\delta^{13}C$, but corals PB8 and AQNEW deposited carbonate relatively enriched in ^{13}C (by about 1.0–1.5‰). Carbonate $\delta^{13}C$ from coral PB9b is usually lower than that at the top of the coral (PB9a) by −1.0 to −1.5‰. $\delta^{13}C$ in coral PB4 is enriched by 1.0–1.5‰ compared with the material deposited by coral PB9a.

The carbonate deposited in the fluorescent couplet containing the bleaching event shows a slightly different $\delta^{18}O$ and $\delta^{13}C$ trend from that observed in the previous and following years. In a 'normal' fluorescent couplet a peak of relatively high $\delta^{18}O$ is deposited midway between the start of bright bands, in approximately April to June. This peak is either absent (AQNEW) or is substantially reduced (PB7, PB8 and PB9) during the year containing the bleaching event. The carbon isotopic record follows a similar seasonal trend to that of oxygen during fluorescent couplets deposited under 'normal' conditions. Coral PB9 follows this trend during the bleaching event with highest $\delta^{13}C$ values deposited in approximately April to June. Coral PB8 produced a small peak of high $\delta^{13}C$ values in approximately February to April, but then values decrease. Coral AQNEW produced two peaks of high $\delta^{13}C$ values during the fluorescent couplet containing the bleaching event.

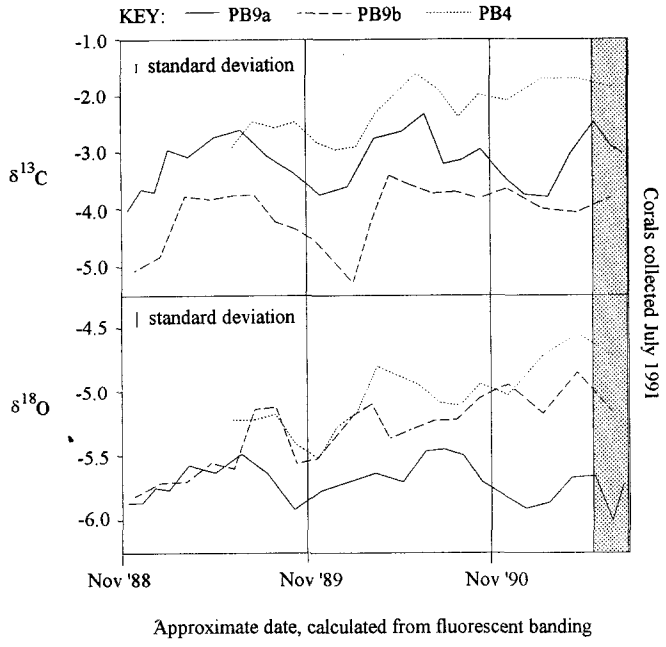

Fig. 8. Seasonal variations in the $\delta^{13}C$ and $\delta^{18}O$ compositions of two corals exhibiting widely different growth rates. Standard deviations (1σ) of analysis are shown. The approximate period of the bleaching event is shaded

Analysis of the outer 1 mm of coral skeletons

All the corals treated with alizarin red S incorporated some of the stain into the skeleton, indicating that despite the high degree of bleaching in some corals all were still depositing calcium carbonate. However, extensively bleached colonies incorporated only small amounts of the stain, indicating extremely limited calcification in comparison with the apparently unaffected colonies that deposited distinct stain lines. In addition, the unbleached colonies obviously deposited up to 1 mm of fresh carbonate over the stain line in the period between staining and sample collection (3 weeks). The unbleached corals appeared pale pink from the outside at the time of sample collection suggesting calcification over this 3 week period was insufficient to cover the original uptake of stain. In summary, the unaffected colonies appearing to be calcifying more quickly than those which were extensively bleached.

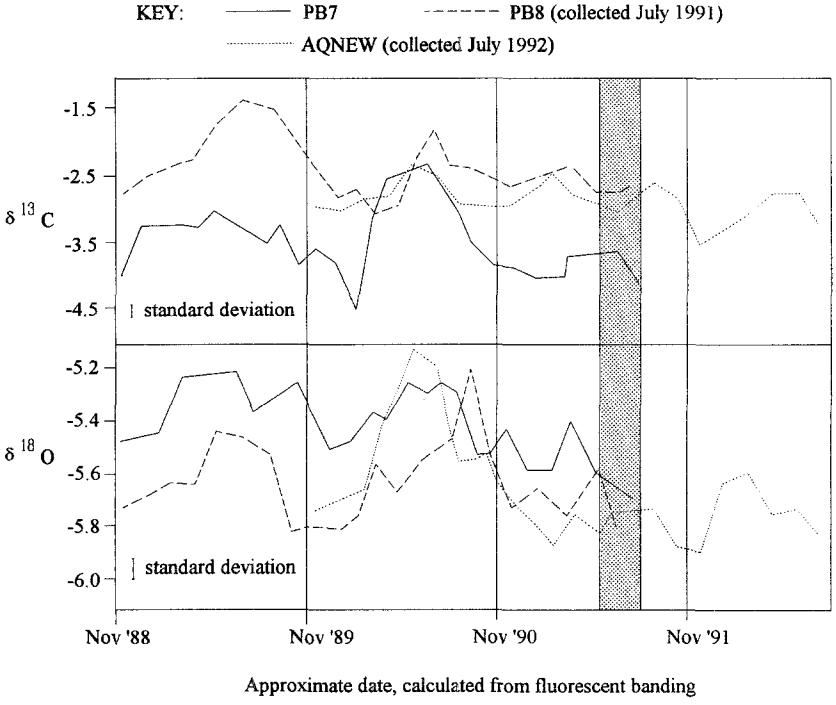

Fig. 9. Seasonal variations in the $\delta^{13}C$ and $\delta^{18}O$ compositions of corals PB7, PB8 and AQNEW. Standard deviations (1σ) of analysis are shown. The approximate period of the bleaching event is shaded

Linear extension, chlorophyll *a* concentrations and $\delta^{13}C$ and $\delta^{18}O$ measurements are shown in Appendix 3. No chlorophyll *a* detected in the material collected from the four bleached corals from Porites Bay was attributed to zooxanthellae. Zooxanthellae chlorophyll *a* concentrations in the unbleached corals varied from 5.7 to 22.2 mg cm^{-2}. $\delta^{13}C$ and $\delta^{18}O$ in these samples varied from −2.70 to −5.50‰ and from −5.28 to −6.94‰ respectively. Regressions of $\delta^{13}C$ and $\delta^{18}O$ versus chlorophyll *a* concentration are shown in Fig. 10. The equation, correlation coefficient and level of significance for each regression are superimposed onto each graph. Chlorophyll *a* concentration and $\delta^{13}C$ showed a broad positive correlation in the unbleached corals ($r = +0.64$, significant at the 0.001 level). There is no significant relationship between $\delta^{18}O$ and chlorophyll *a*.

$\delta^{13}C$ and $\delta^{18}O$ in the bleached coral samples varied from −1.47 to −4.68‰ and from −3.71 to −5.20‰ respectively. The Mann-Whitney U test (a non-parametric test sensitive to differences between medians) was employed to test the significance of differences in stable isotopic composition between the outer 1 mm of skeleton in bleached and unbleached corals. Mann-Whitney U values and levels of significance are shown in Table 1. This test was also used to test the significance of differences in the linear extension between bleached and unbleached corals over the outermost growth increment (approximately November 1990 to July 1991). $\delta^{13}C$ and $\delta^{18}O$ were significantly higher in the bleached corals (both at 0.01 levels of significance). However, bleached corals also had significantly lower rates of linear extension (0.01 significance level), so lower $\delta^{18}O$ values should be expected in these samples. To separate growth rate effects from those of the bleaching event, regressions between linear extension and skeletal $\delta^{13}C$ and $\delta^{18}O$ are compared in bleached and unbleached corals (Fig. 11). Regression equations, coefficients and levels of significance are superimposed onto each graph. A good correlation is observed between $\delta^{18}O$ and linear extension in the unbleached corals ($r = -0.81$). However, the correlation between $\delta^{18}O$ and linear extension in the bleached corals is poor ($r = -0.42$). The two regression equations were compared using the formulae of Wetherill (1982) but were not significantly different ($t = 0.134$, $d.f. = 38$, level of significance = 0.90). No correlation is observed between linear extension and $\delta^{13}C$ in the unbleached corals ($r = -0.10$) although there is some evidence of a positive relationship in the bleached coral specimens ($r = -0.54$). Although these regression equations appear quite separate, the spread of the data is such that they are not

Table 1. Mann-Whitney U-values and levels of significance between linear extension (of the outer growth increment) and $\delta^{13}C$ and $\delta^{18}O$ of the outer 1 mm of skeleton from bleached and unbleached corals from Porites Bay. Numbers of bleached (BL) and unbleached (UN) corals in each group are shown

Characteristic	Mann-Whitney value	Significance
Linear extension (Nov 1990–July 1991)	106.5	< 0.01
$\delta^{13}C$ (BL = 20, UN = 22)	94.0	< 0.01
$\delta^{18}O$ (BL = 20, UN = 22)	0	< 0.01

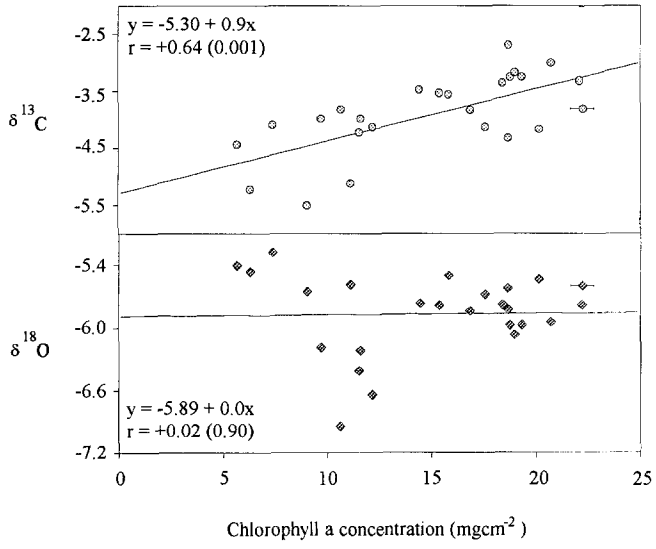

Fig. 10. Regressions between chlorophyll *a* concentration of coral tissue and stable isotopic composition of the underlying 1 mm of skeleton in samples from five coral colonies. Standard deviations (1σ) of chlorophyll analysis are shown on each graph. Deviations of isotopic measurements are about the same size as the symbols. Regression equations, Pearson's correlation coefficients (*r*) and levels of significance (in parentheses) are superimposed onto each graph

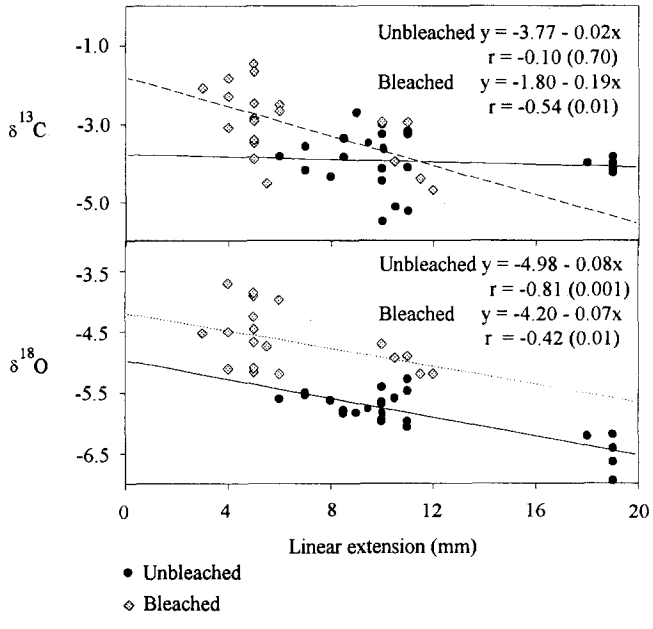

Fig. 11. Regressions between linear extension of the outer growth increment (approximately November 1990–July 1991) and $\delta^{13}C$ and $\delta^{18}O$ of the outer 1 mm of skeleton in bleached (pale diamonds and dotted lines) and unbleached (dark circles and solid lines) coral specimens. Standard deviations of isotopic analysis are about the same size as the symbols. Regression equations, Pearson's correlation coefficients (*r*) and levels of significance (in parentheses) are superimposed onto each graph

significantly different (t = 2.39, $d.f.$ = 38, level of significance = 0.90).

Discussion

Linear extension and $\delta^{18}O$

Calcification and linear extension both show a strong inverse relationship with $\delta^{18}O$ in the data for the outer growth increments (approximately November 1990 to July 1991). This supports the model proposed by McConnaughey (1989b) to explain isotopic disequilibria. He suggested that oxygen isotopic disequilibria occur due to discrimination against the heavier isotopes during CO_2 hydration and hydroxylation in the extracytoplasmic calcifying fluid (ECF) immediately before calcification. For these disequilibria to be maintained in the carbonate, calcification rate must be sufficiently high for the CO_3^{2-} units in the crystal to be buried before they can isotopically equilibrate with the H_2O present in the ECF, which is isotopically indistinct from seawater. During slow calcification, substantial equilibration may occur and the carbonate isotopic composition may approach equilibrium values. Our $\delta^{18}O$ data from the outer growth increments support this, with the slowest extending corals depositing carbonate closest to equilibrium values. We observe a better relationship between skeletal growth rate and $\delta^{18}O$ with the linear extension data than with the rates of calcification. We would expect that a coral skeleton produced by quick linear extension with a relatively low density will be depleted in ^{18}O compared with a skeleton extended less quickly but of a higher density, which may have a similar calcification rate to the first coral.

Differences between the oxygen isotopic profiles of corals PB9a, PB9b and PB4 support this skeletal growth rate/$\delta^{18}O$ relationship. The decrease in linear extension (and calcification) in the slow growing corals (PB4 and PB9b) may be responsible for the relative enrichment of ^{18}O in the skeleton. Linear extension rates in PB4 and PB9b for the fluorescent couplet November 1988–November 1989 are 14 and 10 mm respectively. In the approximate 9-month interval from November 1990, linear extension rates are 4.5 and 3.5 mm, and it seems likely that linear extension for the annual band, November 1990 to November 1991, would have been approximately half of that from November 1988 to November 1989. A decrease in annual linear extension of approximately 5–8 mm corresponds with a relative ^{18}O enrichment of 0.3–0.5‰ in the skeleton (calculated from the regression equation determined in Fig. 3a). This is reasonable agreement with the observed shift of 0.5–0.8‰.

However, this growth rate/$\delta^{18}O$ relationship is rarely apparent between multiple samples from the same colony, and the reason for this is unclear. The range of linear extension rates observed in each coral is small (1, 1, 2 and 4 mm), and it is only over the widest range (in coral PB6) that the growth rate/$\delta^{18}O$ relationship is observed. We suggest that in the other corals this growth range is too small and the scattering of points may reflect an inherent variability in the degree of isotopic equilibriation reached in each sample. In addition, boundaries between bright and dull fluorescent bands are not sharp, and it is possible that not all samples covered exactly the same time interval. It is also possible that very local differences in growth rate occur across the colony throughout the year and this may account for some of the observed scatter.

Variations between the profiles of corals cannot always be explained simply as a function of growth rate. Coral PB7 extends at a similar rate to corals PB8 and PB9a but generally deposits carbonate enriched in ^{18}O by about 0.3‰. Coral AQNEW deposits $\delta^{18}O$ values similar to corals PB8 and PB9, although AQNEW has a substantially higher rate of linear extension. These offsets between colonies may reflect some genetic differences between the corals which alter the extent of isotopic disequilibria. Despite these deviations the differences between the isotopic profiles of the fast- and slow-growing axes of coral PB9 convince us that calcification rate has an important influence on $\delta^{18}O$. Interestingly, McConnaughey (1989a) only observed the growth rate/$\delta^{18}O$ relationship in parts of the corals extending at less than 5 mm year^{-1}, while we have observed it at all linear extension rates. His work was on a coral of a different genera (*Pavona clavus*), but we currently have no explanation for this discrepancy.

Seasonal variation in $\delta^{18}O$

Seasonal variations in oxygen isotopic composition are typically related to changes in seawater temperature and/or seawater composition. The annual seawater temperature range in this area is 2–4 °C, with lowest and highest seawater temperatures occurring in January and May respectively. The observed range of skeletal $\delta^{18}O$ (0.5–0.6‰) correlates well with the range predicted from seasonal variations in seawater temperature (2–4 °C = 0.4–0.8‰, using McConnaughey's equation 1989a). However if the observed seasonal variation in $\delta^{18}O$ were a function of seawater temperature then the lowest $\delta^{18}O$ carbonate would be deposited in May to June, approximately halfway between the start of each bright fluorescent band, not in about November as observed. Given that we are confident in dating the fluorescent banding chronology, i.e. bright band accretion begins in approximately November, we conclude that some other factor is influencing skeletal $\delta^{18}O$ and effectively masking any trend attributable to seawater temperature.

Rainfall, seawater evaporation, freshwater runoff and/or ocean circulation may all alter significantly the oxygen isotopic composition of local seawater and the subsequently precipitated carbonate. These changes are usually accompanied by changes in salinity (Lowenstam and Epstein 1957; Swart and Coleman 1980). It is difficult to assess the influence of salinity variations in this study as no consistent seasonal trends in seawater salinity were found in the area and few data are available for the period covered by the study. Between September 1990 and January 1991 salinity increased from 32‰ to 33‰ and then decreased to 32.4‰ in April 1991. This trend in salinity correlates well with the observed skeletal $\delta^{18}O$ pattern with lowest $\delta^{18}O$ values deposited during the

period of lowest salinity. However it is unlikely that this salinity change (1‰) is sufficient to be entirely responsible for the observed $\delta^{18}O$ skeletal signal (0.4–0.6‰). Annual mean measurements of $\delta^{18}O$ of atmospheric waters from Bangkok and Singapore yield values of −5‰ and −7‰ respectively (Yurtsever and Gat 1981). Assuming that rainfall at Phuket is −6‰, then to produce a change in seawater $\delta^{18}O$ composition of 0.6‰ (the maximum annual $\delta^{18}O$ range observed in the corals) would require a 1 in 10 dilution of this rainwater which would be accompanied by a salinity change of about 3‰. In reality this is an underestimate of the change required as seawater composition must alter sufficiently to cause the annual $\delta^{18}O$ skeletal trends and to swamp the 0.4–0.8‰ annual signal expected from temperature variations. In the limited data collected over the study period the salinity range is about 1‰, and in other years the annual range does not exceed 2‰. We conclude that it is very unlikely that the seasonal variations in skeletal $\delta^{18}O$ are caused solely by changes in seawater composition, and we suggest that another possible influence exists.

We have observed an inverse relationship between $\delta^{18}O$ and skeletal growth rate in the outer growth increments of corals from this area and we suggest that the annual skeletal $\delta^{18}O$ trend may at least in part reflect seasonal variations in skeletal growth rate. There is evidence that seasonal variations in skeletal growth rate occur in corals around Phuket. Chansang et al. (1992) observed an approximate doubling in the extension rates of massive *Porites* corals during the dry monsoon (November to March) when they examined corals repeatedly stained with alizarin red S in situ from reefs to the north west of Phuket island. Charuchinda and Hylleberg (1984) examined monthly variations in linear extension rate in branching *Acropora* from the Aquarium Reef site. Extension rate was highest and lowest in December to February and June to August respectively. It is difficult to infer seasonal variations in growth from the corals in our study, as the bleaching event in progress at the time of their collection may have affected skeletal growth rate even in apparently unbleached specimens. However, the observed enrichment in skeletal ^{18}O values around the wet season in our study may reflect a higher degree of equilibration between the carbonate and the extracytoplasmic calcifying fluid due to a decrease in skeletal growth rate. The observed skeletal $\delta^{18}O$ pattern and the possible influences on it, i.e. seawater temperature, salinity and skeletal growth rate, are summarised in Fig. 12. An approximate doubling of skeletal linear extension between wet and dry seasons from 5 to 10 mm (causing an annual band width of 15 mm) would correspond to a depletion in skeletal ^{18}O of 0.4–0.5‰ (using the regression equation in Fig. 5). This acts in positive combination with the skeletal variations (0.2–0.4‰) expected from salinity variations (1–2‰) and in negative combination with skeletal variations (0.4–0.6‰) expected from seawater temperature (2–3 °C) to yield an expected skeletal $\delta^{18}O$ range of 0–0.6‰. This is in reasonable agreement with the observed range of 0.4–0.6‰.

There are no previous reports of seasonal growth rate variations affecting skeletal $\delta^{18}O$ although such a relationship may explain why a seawater temperature/skeletal $\delta^{18}O$ correlation has not been found in some palaeoceanographic studies. Of course, several studies have reported excellent seawater temperature/skeletal $\delta^{18}O$ relationships, and we can only conclude that seasonal variations in skeletal growth rate either do not occur at these sites or that they are small or are overshadowed by other influences. Much more work on the seasonality of growth rate in corals and its effect on skeletal isotopic composition remains to be done.

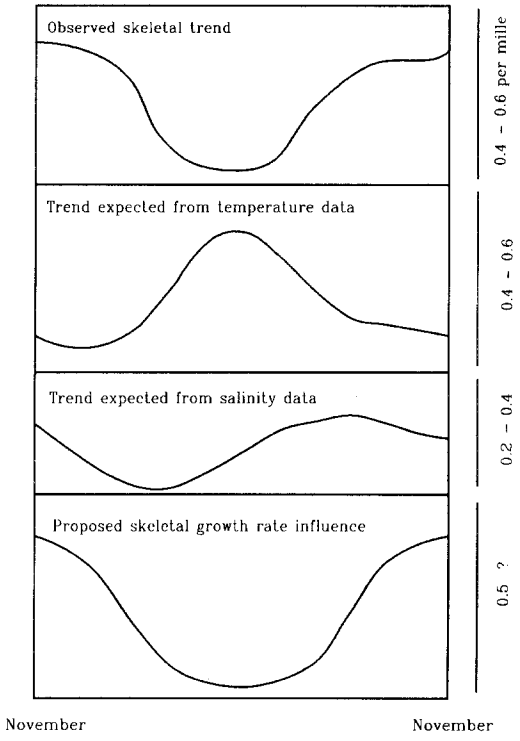

Fig. 12. A simplified representation of the observed annual $\delta^{18}O$ skeletal trend and the expected inputs of seasonal variations in seawater temperature, salinity and skeletal growth rate

Factors influencing $\delta^{13}C$

No significant relationship is observed between $\delta^{13}C$ and any of the growth measurements in the outer growth increment samples prepared from the unbleached corals ($r = -0.34$). Similarly, corals with similar rates of linear extension (PB7, PB8 and PB9a) deposited widely varying $\delta^{13}C$ values. Departures from skeletal $\delta^{13}C$ values expected from kinetic behaviour are called metabolic effects (McConnaughey 1989a).

We observed a positive relationship between the $\delta^{13}C$ of the outer 1 mm of the coral skeletons and the chlorophyll *a* concentration of the overlying tissue in the unbleached coral samples ($r = +0.64$). ^{12}C is preferentially fixed in photosynthesis by the enzyme ribulose biphosphate carboxylase leaving the DIC pool, and subsequently the deposited carbonate, relatively enriched in ^{13}C (reviewed in Swart 1983). From our data it appears that fixation of ^{12}C and modification of the DIC pool is highest in the corals containing high concentrations of chlorophyll *a*. This is in

agreement with the negative relationship between skeletal $\delta^{13}C$ and chlorophyll *a*/chlorophyll *c* ratio (which increases as available light decreases) observed by Weil et al. (1981). We suggest that metabolic effects modify the DIC pool to such an extent in these corals that the growth rate/$\delta^{13}C$ relationship is effectively masked.

No relationship was observed between skeletal $\delta^{18}O$ and chlorophyll *a* concentration of the overlying coral tissue, although respired CO_2, produced by both the coral and the zooxanthellae, is depleted in ^{13}C and ^{18}O relative to the DIC pool. The enzyme carbonic anhydrase accelerates ^{18}O exchange between this respired CO_2 and H_2O in the coral tissue which is in equilibrium with seawater (McConnaughey 1989b). This oxygen exchange will remove any relative enrichment of ^{16}O in the DIC pool.

A weak inverse relationship is observed between $\delta^{13}C$ of the outermost 1 mm of skeleton and linear extension (of the outer growth increment) in the bleached coral specimens. We suggest that the loss of the symbiotic algae and/or their pigments in these bleached corals has removed the metabolic influences which typically modify the DIC pool. In this case the DIC pool is modified by kinetic effects only and both $\delta^{13}C$ and $\delta^{18}O$ are inversely related with linear extension. The regression coefficients between linear extension and both $\delta^{13}C$ ($r=-0.54$) and $\delta^{18}O$ ($r=-0.42$) are considerably less than that observed between $\delta^{18}O$ and linear extension in the outer growth increment experiment. However, it was impossible to en-sure that the same growth increment was sampled in each coral in the outer 1 mm experiment, and we suggest that the sampling of slightly different growth increments, both between and within corals, has increased the degree of scatter observed in the plots.

Seasonal variation in $\delta^{13}C$

Seasonal trends in $\delta^{13}C$ are similar to those of $\delta^{18}O$ with highest and lowest values deposited in approximately April to June and November respectively. Although no significant relationship is observed between skeletal $\delta^{13}C$ and growth rate in the outer growth increment experiment, it is still possible that annual $\delta^{13}C$ trends reflect seasonal variations in growth rate. It seems likely that the $\delta^{13}C$/growth rate relationship in the outer growth increment experiment was masked by varying degrees of modification of the dissolved inorganic carbon (DIC) pool by the different corals and their algae, i.e. metabolic effects. However, if these metabolic effects were relatively con-stant for each coral throughout the year, then seasonal trends in $\delta^{13}C$ would reflect variations in the kinetic effect, i.e. skeletal growth rate. There is evidence that skeletal growth varies seasonally. In addition, the similarity be-tween the $\delta^{13}C$ and $\delta^{18}O$ profiles supports the theory that seasonal trends reflect kinetic effects. Carbon and oxygen disequilibria will be similarly affected by kinetic effects while metabolic effects will influence $\delta^{13}C$ only.

However, annual trends in $\delta^{13}C$ may also reflect some seasonal variations in metabolic effects, i.e. photosynthetic and respiratory modification of the DIC pool. Higher concentrations of chlorophyll *a* have been detected in reef flat corals in the Phuket area in the wet season (April to October) than in the dry season (Barbara Brown, personal communication, 1993). If similar seasonal variations in chlorophyll concentration occur in corals along the reef front, then increased algal fixation of the isotopically lighter carbon during periods of high chlorophyll content (April to October) could account for the relative enrichment of ^{13}C in the coral skeleton (approximately June to July).

Finally, the DIC pool and subsequently skeletal $\delta^{13}C$ will be influenced by variations in seawater $\delta^{13}C$ composition. Seawater $\delta^{13}C$ may be affected by freshwater runoff or by algal blooms which preferentially fix ^{12}C during photosynthesis. At present few data are available on seawater productivity for the Phuket area so we are unable to speculate on the possible influence of such variations.

The effect of the 1991 bleaching event on $\delta^{13}C$ and $\delta^{18}O$

Visibly bleached corals had significantly reduced growth characteristics compared with unbleached corals during the 9-month period up to and including the bleaching event. There were no significant differences between the growth characteristics of the same corals for the fluorescent couplet deposited before the bleaching event, i.e. approximately November 1989 to November 1990 (Tudhope et al. 1992) so it seems that the reduction in calcification in the bleached corals is an effect of the bleaching event and the conditions leading up to it and is not a characteristic of corals that are more susceptible to bleaching. Bleached corals were significantly enriched in ^{18}O and ^{13}C in the outer 1 mm of skeleton compared with unbleached specimens. However, as growth rate appears to inversely affect skeletal $\delta^{18}O$, an enrichment in ^{18}O is expected in these slower growing corals. In an attempt to separate the effects of skeletal growth rate and bleaching, we compared regressions between linear extension and $\delta^{18}O$ in samples from the outermost 1 mm of the skeletons from bleached and unbleached corals. Although not significantly different from that for the unbleached corals, the regression equation for the bleached corals is offset towards more positive $\delta^{18}O$ values, suggesting that the bleached corals are depositing carbonate even more enriched in ^{18}O in the outer 1 mm of skeleton than expected from considerations of skeletal growth rate. This may reflect a more pronounced decrease in the growth rate of these corals over the actual bleaching event.

However this enrichment in ^{18}O is not observed in the isotopic profiles of the bleached corals (PB7 and PB8) up to and including the bleaching event. We suggest that calcification in the affected corals over the bleaching event was very limited and insufficient ^{18}O enriched material was deposited to impact on the profile samples. In fact all the corals, bleached and unbleached, show a reduced ^{18}O enrichment for that time of year. By the time of the bleaching event, seawater temperatures were about 1 °C above normal, which would correspond to a depletion in $\delta^{18}O$ of 0.21‰ relative to the values normally observed (McConnaughey 1989a). This depletion in $\delta^{18}O$ disguised the usual seasonal trends.

The bleached coral skeletons deposited significantly higher $\delta^{13}C$ values in the outer 1 mm of skeleton than apparently unaffected corals. Although the removal of the zooxanthellae, which preferentially fix ^{12}C, will increase the proportion of ^{12}C in the DIC pool, it appears that calcification, at this point, was reduced to such an extent that newly deposited carbonate was able to come closer to isotopic equilibrium with the carbon in the extracytoplasmic fluid. This is supported by the observation of a inverse relationship between $\delta^{13}C$ of the outer 1 mm of the bleached coral skeletons and linear extension (of the outer growth increment). This relationship is not observed in unbleached corals. In summary, in the outer 1 mm of the coral skeleton, algal modification of the DIC pool is the main control on skeletal $\delta^{13}C$ in the unbleached corals while skeletal growth rate is the primary influence in the bleached specimens.

There is no evidence that the bleaching event affected the seasonal $\delta^{13}C$ trend in coral PB9 (unbleached). This coral produced a typical peak of ^{13}C, between the beginning of bright fluorescent bands, in approximately April to June. This trend was not observed in corals PB8 (bleached) and AQNEW (unbleached). Both produced a relatively small $\delta^{13}C$ peak early on in the fluorescent couplet. Coral AQNEW also produced a second peak later in the couplet. These variations probably reflect the state of the zooxanthellae in the coral tissue over the bleaching event. Both corals began to produce the usual ^{13}C peak in approximately February to April but then deposited lighter carbon than expected. If zooxanthellae numbers or chlorophyll content are reduced then the amount of ^{12}C fixed by photosynthesis will also decrease. The DIC pool becomes relatively enriched in ^{12}C and the skeleton deposited from it contains relatively low $\delta^{13}C$ values. Although coral AQNEW did not appear visibly affected by the bleaching event, zooxanthellae numbers or chlorophyll content may have been reduced from earlier in the year. A recovery in zooxanthellae numbers or chlorophyll content towards the end of the bleaching event would account for the second $\delta^{13}C$ peak observed towards the end of the fluorescent couplet.

Conclusions

1. Skeletal growth rate has a powerful influence on skeletal $\delta^{18}O$ in *Porites lutea* corals from Phuket, South Thailand. We suggest that the observed $\delta^{18}O$ annual trend reflects a combination of seawater temperature, salinity and skeletal growth rate variations. Seasonal and longer term variations in skeletal growth rate must be considered when interpreting palaeoenvironmental records from stable oxygen isotopic chemistry of coral skeletons.

2. A similar relationship is observed between $\delta^{13}C$ and growth rate in the outermost skeletal material of bleached coral specimens. However, in the unbleached corals metabolic modifications of the dissolved inorganic carbonate pool (DIC) mask any such relationship. In these corals $\delta^{13}C$ and coral tissue chlorophyll *a* content are positively related, suggesting that algal modification of the DIC pool is the main control on skeletal $\delta^{13}C$. Seasonal variations in $\delta^{13}C$ may reflect variations skeletal growth rate, changes in the photosynthetic activity of the zooxanthellae or variations in the $\delta^{13}C$ composition of seawater.

3. Corals that bleached during the period of elevated seawater temperatures at Phuket in the summer of 1991 had significantly reduced skeletal growth rates and deposited skeletons significantly enriched in ^{13}C and ^{18}O compared with corals that appeared unaffected. This enrichment coincides with a reduction in skeletal growth rate.

4. The ^{13}C and ^{18}O enrichment observed in the surface material deposited during the bleaching event was not observed when isotopic profiles were prepared from either the bleached or the unbleached corals at a frequency of 8–10 samples per annual growth band. Calcification at this time was probably so limited that insufficient material was deposited to impact on the profile samples. An enrichment in these isotopes may have been observed if a higher sampling frequency had been employed. Instead skeletal material deposited in the months before and during the bleaching event was relatively depleted in ^{18}O, supporting the theory that positive temperature anomalies occurred during the beaching event and may have been its cause. Whole or partial expulsion of zooxanthellae (or loss of their pigments) was manifest as a relative depletion in ^{13}C, reflecting the impact of the algae on skeletal $\delta^{13}C$.

Acknowledgements. We wish to thank Terry Donnelly for technical assistance with the mass spectrometer at SURRC. We are grateful to the Director and staff of the Phuket Marine Biological Centre for their continued support. In particular we thank Vudichai Janekarn for his generosity in supplying the seawater temperature and salinity data collected from the centre. Other seawater temperature data were obtained as part of a project funded by the Overseas Development Administration, Natural Resources and Environmental Department and were compiled by Richard Dunne. Rainfall data were supplied by the Phuket Town weather station. This manuscript has been improved by the comments of several anonymous reviewers. This work has been supported financially by the UK Natural Environment Research Council (research studentship no. GT4/90/G3/47 to NA; and grant no. GR3/5857 to AWT). The Isotope Geosciences Unit at SURRC is supported by NERC and the Scottish Universities.

References

Boto K, Isdale P (1985) Fluorescent bands in massive corals result from terrestrial fulvic acid inputs to nearshore zone. Nature 315: 396–37

Brown BE, Le Tissier MDA, Howard LS, Charuchinda M, Jackson JA (1986) Asynchronous deposition of dense skeletal bands in *Porites lutea* (Edwards and Haime). Mar Biol 93:83–89

Carr DJ (1992) Quaternary sediments of a tropical estuary and bay: Phangnga Bay, South Thailand. Unpublished PhD thesis, University of Edinburgh

Chakraborty S, Ramesh R (1993) Monsoon-induced sea surface temperature changes recorded in Indian corals. Terra Nova 5:545–551

Chansang H, Phongsuwan N, Boonyanate P (1992) Growth of corals under effect of sedimentation along the northwest coast of Phuket Island, Thailand. Proc 7th Int Coral Reef Symp 1:241–248

Charuchinda M, Hylleberg J (1984) Skeletal extension of *Acropora formosa* at a fringing reef in the Andaman Sea. Coral Reefs 3:215–219

Emiliani C, Hudson JH, Shinn EA, George RY (1978) Oxygen and carbon isotopic growth record in a reef coral from the Florida Keys and a deep sea coral from Blake Plateau. Science 202: 627–629

Gaffey SJ, Bronnimann CE (1993) Effects of bleaching on organic and mineral phases in biogenic carbonates. J Sediment Petrol 63: 752–754

Goreau TJ (1977) Coral skeletal chemistry: physiological and environmental regulation of stable isotopes and trace metals in *Montastrea annularis*. Proc R Soc Lond B 196:291–315

Isdale P (1984) Fluorescent bands in massive corals record centuries of coastal rainfall. Nature 310:578–579

Jokiel PL, Coles SL (1974) Effects of heated effluent on hermatypic corals of Kahe Point, Oahu. Pac Sci 28:1–18

Land LS, Lang JC, Barnes DJ (1975) Extension rate: a primary control on the isotopic composition of West Indian (Jamican) scleractinian reef coral skeletons. Mar Biol 33:221–233

Lowenstam HA, Epstein S (1957) On the origin of sedimentary aragonitic needles of the Great Bahama Bank. J Geol 65:364–375

McConnaughey T (1989a) ^{13}C and ^{18}O isotopic equilibrium in biological carbonates. I. Patterns. Geochim Cosmochim Acta 53: 151–162

McConnaughey T (1989b) ^{13}C and ^{18}O isotopic equilibrium in biological carbonates. II. In vitro simulation of kinetic isotope effects. Geochim Cosmochim Acta 53: 163–171

O'Neil JR, Clayton RN, Mayeda TK (1969) Oxygen isotope fractionation in divalent metal carbonates. J Chem Phys 51:5547–5558

Scoffin TP, Tudhope AW, Brown BE, Chansang H, Cheeney RF (1992) Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. Coral Reefs 11: 1–13

Strickland JDH, Parsons TR (1968) A manual of seawater analysis. Bull Fish Res Bd Can 167–211

Swart PK (1983) Carbon and oxygen isotope fractionation in sclerac-tinian corals: a review. Earth Sci Rev 19:51–80

Swart PK, Coleman ML (1980) Isotopic data for scleractinian corals explain their palaeotemperature uncertainties. Nature 283:557–559

Tudhope AW, Allison N, Le Tissier MDA, Scoffin TP (1992) Growth characteristics and susceptibility to bleaching in massive *Porites* corals, South Thailand. Proc 7th Int Coral Reef Symp 1: 64–69

Veron JEN (1986) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu, p 224

Weil SM, Buddemeir RW, Smith SV, Kroopnick PM (1981) The stable isotopic composition of coral skeltons: control by environmental variables. Geochim Cosmochim Acta 45:1147–1153

Wetherill GB (1982) Elementary statistical methods. Chapman and Hall, London

Yurtsever Y, Gat JR (1981) Atmospheric waters. In: Gat JR, Gonfiantini R (eds) Stable isotope hydrology: deuterium and O-18 in the water cycle. (IAEAA technical report series no. 210) pp 103–142

Appendix 1

Growth rate measurements and the stable isotopic composition of samples from the outer growth increment (approximately November 1990 to July 1991) of six *Porites lutea* colonies from Porites Bay

Coral sample	Linear extension (mm)	Skeletal density (g cm^{-3})	Calcification (g cm^{-2})	$\delta^{13}C$ (wrt PDB)	$\delta^{18}O$
PB1-1	8.5	0.95	8.1	−4.13	−5.42
PB1-2	8.5	0.95	8.1	−3.80	−5.33
PB2-1	13.0	0.78	10.1	−2.92	−5.78
PB3-1	18.0	0.66	11.9	−4.07	−6.16
PB3-2	19.0	0.68	12.9	−4.01	−6.16
PB3-3	19.0	0.71	13.4	−4.07	−6.07
PB3-4	19.0	0.63	12.0	−4.05	−6.16
PB3-5	19.0	0.70	13.3	−3.91	−5.91
PB5-1	11.0	0.99	10.9	−3.70	−5.59
PB5-2	10.0	0.89	8.9	−3.51	−5.67
PB5-3	11.0	0.86	9.4	−3.72	−5.50
PB5-4	10.5	0.88	9.3	−4.31	−5.80
PB5-5	10.0	0.94	9.4	−4.51	−5.83
PB6-1	6.0	0.93	5.6	−3.32	−5.49
PB6-2	7.0	0.98	6.9	−3.36	−5.48
PB6-3	7.0	1.08	7.6	−3.05	−5.18
PB6-4	8.0	1.10	8.8	−3.58	−5.57
PB6-5	10.0	1.08	10.8	−3.86	−5.76
PB9-1	9.0	1.00	9.0	−3.02	−5.76
PB9-2	10.0	0.94	9.4	−2.62	−5.68
PB9-3	11.0	0.95	10.5	−2.71	−5.43
PB9-4	11.0	0.96	10.5	−3.08	−5.66
PB9-5	10.0	0.93	9.3	−3.14	−5.73
PB13-1	12.0	0.72	8.6	−4.45	−5.91
PB14-1	7.5	0.84	6.3	−2.97	−5.66
PB15-1	10.0	1.10	11.0	−2.47	−5.50
PB15-2	10.0	0.82	8.2	−3.10	−5.67

Appendix 2

$\delta^{13}C$ and $\delta^{18}O$ of profile samples from corals PB4, PB7, PB8, PB9a, PB9b and AQNEW. The relative position of each sample in the annual band was calculated by dividing the distance of the middle of each sample along the band by the width of the band. Samples prefixed by 10 were deposited in the couplet approximately Nov 1990 to Nov 1991; by 9 in the couplet Nov 1989 to Nov 1990 etc.

Sample	$\delta^{13}C$	$\delta^{18}O$	Relative position	$\delta^{13}C$	$\delta^{18}O$	Relative position	$\delta^{13}C$	$\delta^{18}O$	Relative position
	PB4			PB9a			PB9b		
1	−1.84	−4.72	10.66	−3.02	−5.73	10.72	−3.80	−5.16	10.66
2	−1.69	−4.55	10.47	−2.90	−6.00	10.66	−4.06	−4.85	10.47
3	−1.70	−4.72	10.28	−2.47	−5.66	10.56	−3.99	−5.17	10.28
4	−2.08	−5.03	10.09	−3.03	−5.67	10.44	−3.64	−4.94	10.09
5	−1.98	−4.94	9.94	−3.79	−5.87	10.31	−3.82	−5.05	9.94
6	−2.37	−5.11	9.83	−3.75	−5.91	10.19	−3.70	−5.22	9.81
7	−1.88	−5.09	9.72	−3.40	−5.80	10.06	−3.73	−5.23	9.69
8	−1.60	−4.94	9.60	−2.94	−5.71	9.95	−3.57	−5.30	9.56
9	Sample	Lost		−3.14	−5.50	9.85	−3.40	−5.37	9.45
10	−2.14	−4.80	9.38	−3.20	−5.45	9.75	−4.23	−5.10	9.35
11	−2.30	−5.16	9.27	−2.31	−5.46	9.65	−5.29	−5.19	9.25
12	−2.90	−5.28	9.16	−2.63	−5.71	9.52	−4.57	−5.53	9.05
13	−2.95	−5.52	9.06	−2.76	−5.64	9.37	−4.35	−5.56	8.94
14	−2.83	−5.41	8.94	−3.61	−5.70	9.22	−4.22	−5.12	8.83
15	−2.46	−5.18	8.83	−3.75	−5.77	9.07	−3.75	−5.14	8.72
16	−2.56	−5.22	8.71	−3.35	−5.92	8.93	−3.76	−5.60	8.61
17	−2.45	−5.22	8.60	−3.06	−5.64	8.79	−3.83	−5.56	8.48
18	−2.92	−5.36	8.49	−2.60	−5.49	8.65	−3.77	−5.70	8.34
19	Sample	Lost		−2.74	−5.63	8.50	−4.83	−5.71	8.21
20	Sample	Lost		−3.08	−5.57	8.36	−5.07	−5.82	8.07
21	Sample	Lost		−2.95	−5.77	8.25			
22	Sample	Lost		−3.71	−5.75	8.18			
23				−3.65	−5.87	8.11			
24				−4.02	−5.87	8.04			
	PB7			PB8			AQNEW		
1	−4.09	−5.70	10.70	−2.66	−5.74	10.72	−3.26	−5.83	11.69
2	−3.47	−5.60	10.61	−2.74	−5.81	10.64	−2.67	−5.74	11.56
3	−3.52	−5.55	10.56	−2.76	−5.57	10.53	−2.77	−5.76	11.44
4	−3.58	−5.32	10.44	−2.32	−5.76	10.38	−3.08	−5.59	11.31
5	−4.02	−5.56	10.31	−2.52	−5.66	10.23	−3.30	−5.65	11.19
6	−4.06	−5.55	10.19	−2.63	−5.73	10.08	−3.54	−5.89	11.06
7	−3.77	−5.40	10.06	−2.53	−5.49	9.95	−2.82	−5.88	10.94
8	−3.79	−5.53	9.96	−2.36	−5.20	9.86	−2.54	−5.74	10.82
9	−3.52	−5.52	9.87	−2.35	−5.46	9.77	−2.72	−5.86	10.71
10	−2.94	−5.23	9.79	−1.80	−5.53	9.67	−3.04	−5.74	10.62
11	−2.69	−5.24	9.71	−2.19	−5.56	9.58	−2.88	−5.82	10.53
12	−2.32	−5.29	9.62	−2.93	−5.68	9.48	−2.81	−5.75	10.41
13	−2.35	−5.24	9.53	−3.12	−5.56	9.37	−2.45	−5.88	10.29
14	−2.52	−5.42	9.43	−2.63	−5.70	9.27	−2.74	−5.76	10.18
15	−3.22	−5.38	9.34	−3.13	−5.85	9.16	−2.94	−5.68	10.06
16	−4.37	−5.49	9.24	−2.51	−5.81	9.05	−2.96	−5.52	9.94
17	−3.82	−5.53	9.15	−1.64	−5.64	8.93	−2.91	−5.56	9.81
18	−3.50	−5.42	9.05	−1.46	−5.52	8.80	−2.47	−5.19	9.69
19	−3.84	−5.22	8.95	−1.33	−5.46	8.67	−2.31	−5.13	9.56
20	−3.16	−5.30	8.85	−1.73	−5.44	8.54	−2.80	−5.37	9.44
21	−3.58	−5.38	8.75	−2.25	−5.64	8.41	−2.81	−5.66	9.31
22	−3.27	−5.14	8.65	−2.33	−5.63	8.29	−3.02	−5.71	9.19
23	−3.02	−4.97	8.55	−2.52	−5.69	8.18	−2.93	−5.74	9.06
24	−3.31	−5.22	8.45	−2.77	−5.73	8.06			
25	−3.21	−5.25	8.35						
26	−3.21	−5.42	8.25						
27	−3.23	−5.48	8.15						
28	−3.98	−5.52	8.05						

Appendix 3

Linear extension, coral tissue chlorophyll *a* and stable isotopic measurements of bleached and unbleached corals from Porites Bay. Linear extension measurements were performed on the outer growth increments (approximately November 1990–July 1991), stable isotopic analysis on the outermost 1 mm of the skeleton and chlorophyll *a* measurements on the overlying coral tissues

Coral sample	Linear Growth mm	Chl *a* mgcm^{-2}	$\delta^{13}C$ (wrt PDB)	$\delta^{18}O$	Coral sample	Linear Growth mm	Chl *a* mgcm^{-2}	$\delta^{13}C$ (wrt PDB)	$\delta^{18}O$
Unbleached corals					Bleached corals				
PB1-1	8.5	18.4	3.36	−5.78	PB4-1	5.0	0.0	−1.47	−4.26
PB1-2	8.5	16.9	−3.83	−5.84	PB4-2	4.0	0.0	−1.83	−3.71
PB1-3	10.0	21.6	−3.56	−5.85	PB4-3	5.0	0.0	−3.47	−3.91
PB1-4	10.0	14.0	−3.62	−5.85	PB4-4	6.0	0.0	−2.51	−3.98
PB1-5	9.0	15.4	−3.58	−5.88	PB4-5	5.0	0.0	−1.66	−3.86
PB3-1	18.0	11.6	−3.98	−6.22	PB7-1	5.5	0.0	−4.51	−4.74
PB3-2	19.0	10.6	−3.83	−6.94	PB7-2	5.0	0.0	−3.89	−4.67
PB3-3	19.0	11.5	−4.23	−6.41	PB7-3	5.0	0.0	−3.40	−4.46
PB3-4	19.0	9.7	−3.98	−6.19	PB7-4	4.0	0.0	−3.09	−4.51
PB3-5	19.0	12.2	−4.13	−6.64	PB7-5	3.0	0.0	−2.08	−4.53
PB5-1	11.0	7.4	−4.10	−5.28	PB8-1	4.0	0.0	−2.28	−5.11
PB5-2	10.0	5.7	−4.44	−5.41	PB8-2	5.0	0.0	−2.47	−5.17
PB5-3	11.0	6.3	−5.22	−5.47	PB8-3	6.0	0.0	−2.67	−5.20
PB5-4	10.5	11.1	−5.12	−5.59	PB8-4	5.0	0.0	−2.85	−5.11
PB5-5	10.0	9.0	−5.50	−5.65	PB8-5	5.0	0.0	−2.92	−5.11
PB6-1	6.0	22.2	−3.92	−5.60	PB12-1	10.0	0.0	−2.95	−4.71
PB6-2	7.0	15.8	−3.56	−5.50	PB12-2	11.0	0.0	−2.95	−4.91
PB6-3	7.0	20.2	−4.17	−5.54	PB12-3	12.0	0.0	−4.68	−5.20
PB6-4	8.0	18.7	−4.33	−5.62	PB12-4	11.5	0.0	−4.39	−5.20
PB6-5	10.0	17.6	−4.13	−5.68	PB12-5	10.5	0.0	−3.95	−4.94
PB9-1	9.0	18.7	−2.70	−5.83					
PB9-2	10.0	18.8	−3.26	−5.98					
PB9-3	11.0	19.0	−3.17	−6.07					
PB9-4	11.0	19.3	−3.25	−5.97					
PB9-5	10.0	20.7	−3.00	−5.95					