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Variability of stable isotopes and maximum linear extension in reef-coral skeletons at Kaneohe Bay, Hawaii

Received: 6 October 1998 / Accepted: 8 July 1999

Abstract Stable-isotope and growth records of coral skeletons are often used to reconstruct tropical paleoclimate, yet few surveys have systematically examined the natural variability in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal extension (MLSE) across depth. Here, interspecific, intraspecific, and geographical variations in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE were examined in the corals *Porites compressa*, *P. lobata*, and *Montipora verrucosa* grown at 1.7, 5.0, and 8.3 m depth from August 1996 to March 1997 at The Point Reef and Patch Reef #41 field sites in Kaneohe Bay, Hawaii. Coral skeletal $\delta^{13}\text{C}$ values significantly decreased with depth and differed between species, but did not vary between field sites. $\delta^{18}\text{O}$ values were not significantly different across depth within a species, but did differ among species and field sites. High-resolution analysis of the intra-annual variation in skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in *P. compressa* at 2.0 m depth confirms that these isotopes reflect changes in solar irradiance and temperature, respectively. Changes in MLSE across depth were consistent within, but highly variable among, species. Peak MLSE occurred at 1.7, 5.0, and 8.3 m for *P. lobata*, *P. compressa*, and *M. verrucosa*, respectively. Such interspecific variation in MLSE patterns may be attributable to one or more of the following: increases in zooplankton in the diet, changes in metabolic processes, or changes in growth form with depth. Overall, these results imply that natural inter- and intraspecific vari-

ability in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE should be considered when interpreting and comparing coral-based tropical paleoclimate data from various coral species, depths, and field sites.

Introduction

Recent studies indicate that the stable isotope and growth records in scleractinian coral skeletons can be used to reconstruct high-resolution paleoclimatic records from tropical latitudes (Dunbar and Cole 1993; Druffel 1997; Fairbanks et al. 1997). Coral skeletal-growth records are essential for establishing accurate chronologies (e.g. Hudson et al. 1976; Dunbar et al. 1994, 1996; Wellington and Dunbar 1995; Alibert and McCulloch 1997) and for reconstructing environmental parameters such as light levels, temperature seasonality, and environmental stress (Table 1). The most commonly used isotope tracer, $\delta^{18}\text{O}$ [$^{18}\text{O}:^{16}\text{O}$ with respect to the Peedee Belemnite limestone-1 standard (PDB-1)], has proven to be a reliable recorder of sea-surface temperatures and salinities (Table 1).

$\delta^{13}\text{C}$ (the ratio of the stable carbon isotopes $^{13}\text{C}:^{12}\text{C}$ with respect to PDB-1 standard) in symbiotic reef-coral skeletons is believed to be predominantly influenced by metabolic fractionation (Swart 1983; McConnaughey 1989a, b; Muscatine et al. 1989; Allison et al. 1996; McConnaughey et al. 1997; Grottoli-Everett 1998; Grottoli and Wellington 1999). Therefore, environmental variables influencing coral metabolism such as light (which drives photosynthesis) and zooplankton abundance (upon which heterotrophy is dependent) should also affect skeletal $\delta^{13}\text{C}$ levels. Recent experimental work on Hawaiian and Panamanian corals has shown that variation in coral skeletal $\delta^{13}\text{C}$ values reflects changes in both solar irradiance and zooplankton abundance (Grottoli-Everett 1998; Grottoli and Wellington 1999). $\delta^{13}\text{C}$, however, does not respond to changes in light and zooplankton to the same degree in

Communicated by M.H. Horn, Fullerton

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Table 1 Environmental variable(s) that can be reconstructed from coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal extension (MLSE) records

Environmental variable	Literature source
$\delta^{13}\text{C}$	
Light (across depth)	Land et al. (1975), Weber et al. (1976), Fairbanks and Dodge (1979), McConnaughey (1989a), Muscatine et al. (1989), Aharon (1991), Leder et al. (1991), Bosscher (1992), Carriquiry et al. (1994), Juliet-Leclerc et al. (1997), Grottoli and Wellington (1999)
Light (cloud cover)	Fairbanks and Dodge (1979), Pätzold (1984), Quinn et al. (1993), Tudhope et al. (1995), Grottoli-Everett (1998)
Light (seasonality)	Emiliani et al. (1978), Fairbanks and Dodge (1979), Weil et al. (1981), McConnaughey (1986, 1989a), Cole and Fairbanks (1990), Klein et al. (1992, 1993), Shen et al. (1992), Carriquiry et al. (1994), Gagan et al. (1994), Wellington and Dunbar (1995), Swart et al. (1996b), Grottoli and Wellington (1999)
Nutrient/zooplankton levels	Felis et al. (1998), Grottoli-Everett (1998), Grottoli and Wellington (1999)
$\delta^{18}\text{O}$	
Sea-surface temperature	Weber and Woodhead (1972), Emiliani et al. (1978), Fairbanks and Dodge (1979), Dunbar and Wellington (1981), Weil et al. (1981), Druffel (1985), McConnaughey (1986), Carriquiry et al. (1988), Klein et al. (1992), Shen et al. (1992), Quinn et al. (1993, 1996), Dunbar et al. (1994, 1996), Gagan et al. (1994, 1998), Wellington and Dunbar (1995), Leder et al. (1996), Tudhope et al. (1996), Wellington et al. (1996), Charles et al. (1997), Fairbanks et al. (1997), Guzmán and Tudhope (1998)
Sea-surface salinity	Cole and Fairbanks (1990), Cole et al. (1993), Linsley et al. (1994), McCulloch et al. (1994), Tudhope et al. (1995, 1996), Wellington and Dunbar (1995), Swart et al. (1996a), Fairbanks et al. (1997)
MLSE	
Light	e.g. Dodge and Vaisnys (1975), Wellington (1982), Gladfelter (1984), Hubbard and Scaturro (1985), Huston (1985), Guzmán and Cortés (1989), Logan and Tomascik (1991), Bosscher (1992), Suresh and Mathew (1993), Meesters et al. (1994), Insalaco (1996), Custodio and Yap (1997)
Stress, water motion or sedimentation	e.g. Dodge et al. (1974), Hudson (1981), Scott (1990), Scoffin et al. (1992), Miller and Cruise (1995), Suresh and Mathew (1995), Heiss (1996)
Seasonality	e.g. Knutson et al. (1972), Dodge and Vaisnys (1975), Weber et al. (1975a, b), Hudson et al. (1976), Guzmán and Cortés (1989), Lough and Barnes (1990), Klein and Loya (1991), Wellington et al. (1996), Alibert and McCulloch (1997), Vago et al. (1997)

all coral species at all depths. Only a few surveys have examined skeletal $\delta^{13}\text{C}$ variation within and among species across depth. Some of these earlier studies have shown that $\delta^{13}\text{C}$ gradually decreases with depth (Table 1), whereas others have reported maximum $\delta^{13}\text{C}$ at intermediate depths (Land et al. 1975; Erez 1978; Guzmán and Tudhope 1998). In addition, the relationship between the variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal extension (MLSE) across depth, within and among species and field sites, has not been studied. MLSE is known to vary with seasonal and depth-related changes in light levels, temperature, and other environmental parameters (Table 1). Patterns in skeletal $\delta^{13}\text{C}$ across depth and among species may be linked to patterns in MLSE. The work reported here adds to previous studies by increasing sample size and statistically evaluating the data. I expected that: (1) skeletal $\delta^{13}\text{C}$ and MLSE would vary across depth and among species, whereas (2) $\delta^{18}\text{O}$ would be consistent within a species across depth and vary inter-specifically, reflecting species-specific offsets in skeletal $\delta^{18}\text{O}$.

Inter- and intraspecific variations in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE were examined in the reef corals *Porites compressa*, *P. lobata*, and *Montipora verrucosa* at The Point Reef, Kaneohe Bay, Hawaii, at 1.7, 5.0 and 8.3 m. In addition, variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE among field sites was assessed in *P. compressa* at The

Point Reef and Patch Reef #41 field sites, Kaneohe Bay. Finally, intra-annual variation in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was measured in *P. compressa* to evaluate seasonal changes in both isotopes. This systematic assessment of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE enhances our understanding of the natural variation in isotopic signatures and growth patterns in corals used for coral-based, tropical paleoclimate reconstruction.

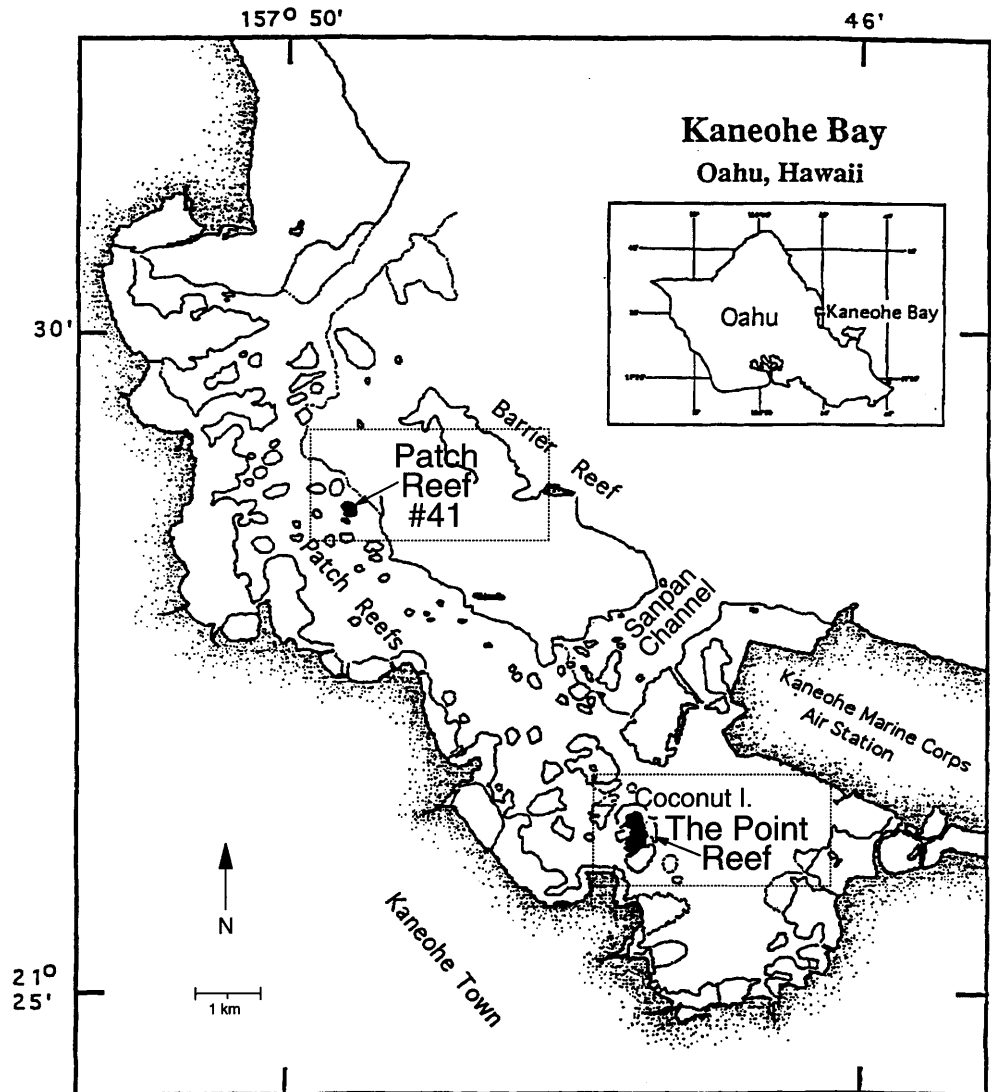
Materials and methods

Field sites

Kaneohe Bay is on the windward side of the island of Oahu, Hawaii. It is a eutrophic bay, 12.7 km long \times 4.3 km wide, with diurnal tidal fluctuations ranging from 0.5 to 2 m (Bathen 1968). The rainy season extends from mid-November to mid-April, followed by a dry season from April to November. Corals were surveyed on The Point Reef (Coconut Island), Kaneohe Bay, Hawaii (21°26.18'N; 157°47.56'W) and Patch Reef #41, Kaneohe Bay, Hawaii, USA (21°28.64'N; 157°49.57'W) (Fig. 1). These two field sites were \approx 6 km apart. Coral cover on the reef slope at both field sites approached 100%, and consisted primarily of *Porites compressa* (Dana) and *Montipora verrucosa* (Lamarck), with some *Pocillopora damicornis* in the shallower regions. *Porites lobata* (Dana), *P. lutea*, and *Pocillopora meandrina*, three other coral species common to Kaneohe Bay, were predominantly found in the deeper, faster current regions of the Sanpan Channel and Barrier Reef (Fig. 1).

The three coral species examined here were *Porites compressa*, *P. lobata*, and *Montipora verrucosa*. *P. compressa* is a finger-like

Fig. 1 Map of study field-sites in Kaneohe Bay, Hawaii: The Point Reef, Coconut Island and Patch Reef #41 (dotted-line boxes)



coral, ranging in color from yellow-brown, to dark brown with small calices (1.5 to 2 mm diam) that lie flush with the surface. *P. lobata* is a massive coral, whose tissue color varies from green to brown; it has small, sharp calices (1.5 to 2 mm diam) with elevated walls. *M. verrucosa* is a dark to light brown coral with beige to white-colored tips. Its form ranges from plating (predominantly at deeper field sites) to branching (predominantly in shallower regions), and more than one form is often expressed within a single colony. The upper surfaces are covered with small papillae adjacent to small calices (1 mm diam).

Sea-surface temperatures (SST) at 2.0 m depth were automatically measured six times each hour by two onset temperature loggers at The Point Reef. The calibrated, pooled data were averaged hourly and plotted (Fig. 2). Hourly SST between 29 August and 21 November 1996 averaged $27.5^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$ (1SE) ($n = 1997$) and ranged from 23.0 to 30.3°C . During the experimental period, there were two intervals [29 August to 7 September (10 d) and 3 to 11 October (8 d)] in which daily maximum SST exceeded 29°C . No temperature measurements were taken at Patch Reef #41. Ambient sunlight levels were continuously monitored at 2.0 m depth on The Point Reef by an onset Hobo light logger. Measurements taken every 24 to 36 min revealed a consistent diurnal fluctuation in light levels and a gradual decrease in daylight intensity with the onset of the rainy season (Fig. 3).

Field manipulations

The Point Reef coral survey: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE across depth and between species

The natural variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE across depth and between species was assessed in *Porites compressa*, *P. lobata*, and *Montipora verrucosa* coral fragments at The Point Reef. On 25 August 1996, a single coral fragment was collected from each of five colonies of *P. compressa* and *M. verrucosa* at 1.7 m depth. They were stained with Alizarin Red for 3 h and cemented directly to the reef at 1.7 m depth using Splash Zone[®] compound. This procedure was repeated at 5.0 m with corals from 5.0 m and again at 8.3 m with coral fragments collected at that depth.

Porites lobata is found on The Point Reef, but is not abundant. Therefore, on 25 August 1996, three coral fragments of *P. lobata* were collected from each of five colonies at a depth of 15 m in the Sanpan Channel, stained with Alizarin Red and transported to The Point Reef. One fragment from each colony was cemented to the reef beside the *P. compressa* and *Montipora verrucosa* coral fragments at 1.7, 5.0 and 8.3 m depth. All coral fragments (Fig. 4) were restrained on 21 November 1996 and collected on 1 March 1997. One *P. lobata* fragment at 1.7 m depth died before the end of

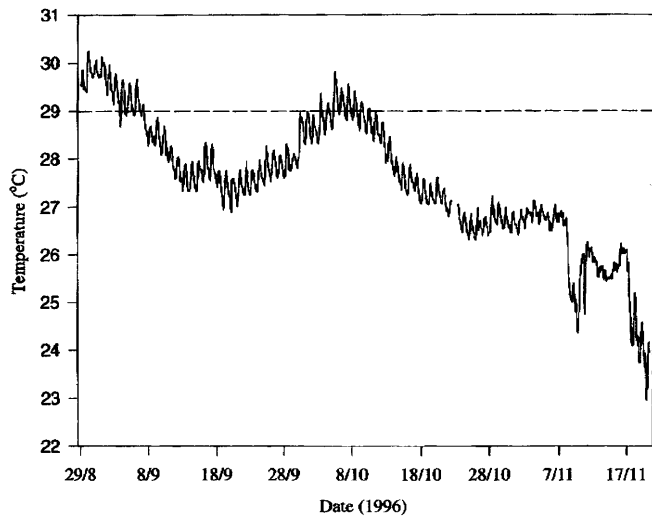


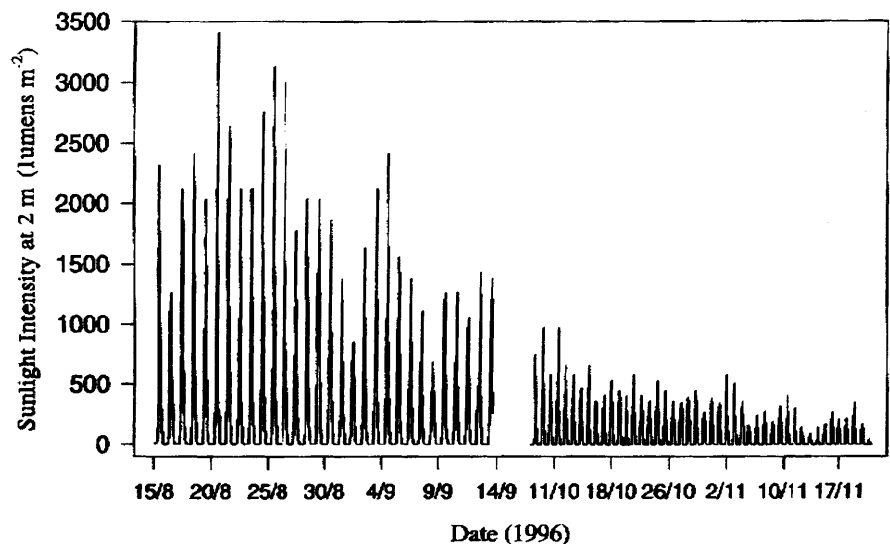
Fig. 2 Mean hourly seawater temperatures at 2.0 m depth measured by two onset temperature loggers between 29 August and 21 November 1996 on The Point Reef. Six temperature measurements were made each hour per logger; calibrated, pooled data were averaged hourly and plotted (total hours = 1997). Standard error of each hourly mean ranged from 0 to 0.14 °C and averaged 0.02 °C (standard errors are not plotted, since they were barely distinguishable from mean). Data were not collected between 22 October (16:00 hrs) and 23 October (14:00 hrs) 1996, during which time data from loggers were downloaded (Dashed line 29 °C)

the experiment. Overall, there were 44 coral fragments (5 fragments \times 3 depths \times 3 species – 1 dead fragment = 44 fragments).

Porites compressa on The Point Reef and Patch Reef #41: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE between field sites

Variation in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE among field sites was assessed by comparing *Porites compressa* coral fragments surveyed across depth at The Point Reef and Patch Reef #41. The initial collection on 26 August 1996, manipulation and staining of *P. compressa* at Patch Reef #41 were identical to that for its conspecifics at The Point Reef. *P. compressa* fragments at Patch Reef #41 (Fig. 5) were not restrained after 26 August 1996, and were collected on 1 March 1997. One *P. compressa* fragment at 5.0 m

Fig. 3 Ambient sunlight intensity (lumens m^{-2}) measured at 2.0 m on The Point Reef every 24 to 26 min by a Hobo Light Logger from 15 August to 21 November 1996. Data were not collected between 9 September and 8 October 1996



depth at Patch Reef #41 died before the end of the experiment. Overall, there were 29 coral fragments (5 fragments \times 3 depths \times 2 field sites – 1 dead fragment = 29 total fragments).

Intra-annual variation in Porites compressa skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Intra-annual variation in skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was measured in two additional *Porites compressa* colonies identified on The Point Reef at a depth of 2.0 m, and was compared to the intra-annual variation in solar irradiance and temperature measurements, respectively. On 2 August 1996 two fragments (\approx 6 cm tall) were collected from each coral head (2 fragments \times 2 coral colonies = 4 fragments), stained with Alizarin Red, and cemented back onto the reef at 2.0 m depth. Fragments were restrained on 17 October and 22 November 1996 to mark temporal references in the skeleton and collected on 2 March 1997. Fig. 6 shows one such fragment.

Isotopic and statistical analyses

All coral fragments were cleaned of tissue with high-pressure tap water, and were allowed to dry at room temperature for at least 5 d. Fragments were cut in half along the major axis of growth with a circular, diamond-tipped 3 mm-thick masonry blade. The cut was made slightly off-center to compensate for the thickness of the blade. This technique produced (1) one fragment-half with a face directly along the major axis of growth, which was used for sample extraction and isotope analysis; and (2) a smaller fragment-half which was discarded. The cut fragments were rinsed with high-pressure tap water followed by 3 min of sonication in distilled water to clean the coral surface of dust. The fragments were then dried in an oven at 64 °C for 48 h. This low temperature does not affect the isotopic composition of the skeletal material (D. Mucciaroni personal communication). At this point, stain lines were still not completely visible because of coral tissue deep within the skeleton. Therefore, fragments were soaked in distilled water for 4 d and recleaned with high-pressure tap water to remove any remaining tissue. Following 3 h drying at 64 °C, fragments were allowed to dry at room temperature for at least 2 d.

Variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE across depth, between species and field sites

A 1 mm-deep, homogenized bulk sample was extracted from the first stain line to the tip of all coral fragments from The Point Reef ($n = 44$) and Patch Reef #41 ($n = 29$) (representing growth from

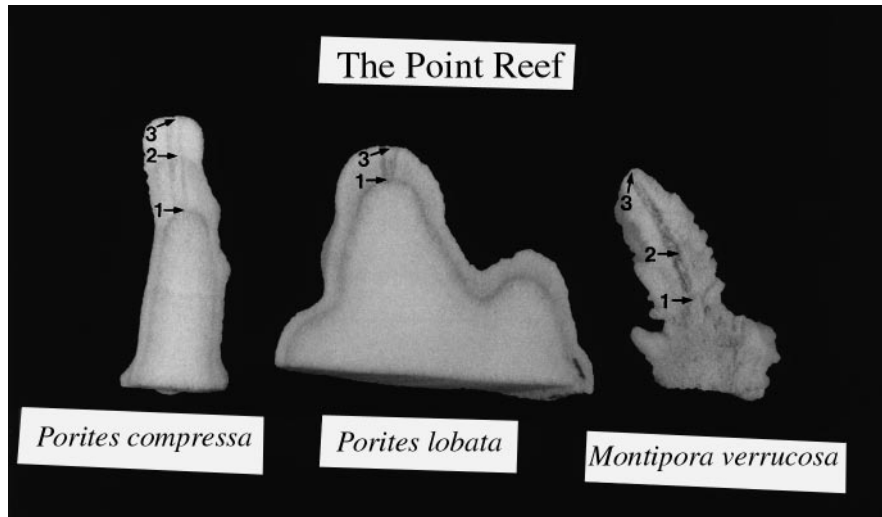


Fig. 4 *Porites compressa*, *P. lobata*, and *Montipora verrucosa*. Cross-section of one fragment of each coral taken at 1.7 m depth from The Point Reef. Stain Line 1 (1) corresponds to 25 August 1996; *P. compressa* and *M. verrucosa* have a second stain line (2) corresponding to 21 November 1996. All corals were collected on 1 March 1997 (3). Bulk skeletal sample was extracted along major axis of growth between first stain line (1) and tip of each coral fragment (3), as indicated by resulting shallow furrow. Arrows 1 and 3 also mark base and tip of drilled furrow, respectively. Distance from Stain Line 1 to tip (3) of *P. compressa*, *P. lobata*, and *M. verrucosa* fragments are 1.4, 0.5, and 2.2 cm, respectively

August 1996 to March 1997) using a low-speed 1 mm dental drill with diamond-tipped dental bits. When *Porites compressa* or *Montipora verrucosa* coral fragments consisted of several branches, the branch with the greatest vertical growth along its central axis was selected. For all three coral species, bulk skeletal samples were consistently extracted, and MLSE measurements made, in the center of the fragment along the major axis of growth (Figs. 4, 5). The MLSE of each fragment was measured once (in millimeters to two decimal places) from the first stain line to the tip of the fragment with calipers, under a dissecting microscope. Entire bulk skeletal samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ with an automated carbonate device by completely dissolving samples individually in 100% H_3PO_4 (common acid bath at 90 °C), and then analyzing the resulting CO_2 gas with a Finnigan-MAT 251 gas-ratio mass spectrometer. The external precision was calculated from replicate analyses of the internal laboratory calcite standard (0.02‰ for $\delta^{13}\text{C}$ and 0.03‰ for $\delta^{18}\text{O}$). Data were corrected for the usual isobaric interferences using the equations of Craig (1957) modified for a triple-collector mass-spectrometer, and are reported relative to PDB-1 standard.

The data were analyzed statistically in two ways. First, the effects of depth and species on skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and MLSE at one field site were evaluated using The Point Reef coral-survey data. Data were tested for normality using a Shapiro–Wilk test. Depth and species effects were statistically evaluated by two-way analysis of variance (ANOVA). A posteriori Tukey tests were used to determine which depths and species differed from each other. Second, the effects of depth and field sites within a species was determined from the survey data of *Porites compressa* at The Point Reef and Patch Reef #41. Data were tested for normality using a Shapiro–Wilk test. The effects of depth and field site on normally and non-normally distributed data were statistically evaluated using a two-way analysis of variance (ANOVA) and a two-way Kruskal–Wallis test, respectively. The Kruskal–Wallis test was calculated by hand according to Zar (1984). All other computations were done using Statistical Analysis Systems programs (SAS Institute Inc 1989). Null hypotheses were rejected at a probability level of ≤ 0.05 .

Intra-annual variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

A series of 1 mm-deep \times 2 mm-long homogenized samples were taken consecutively along the major axis of growth from 2 August 1996 to 1 March 1997 from four *Porites compressa* fragments (example in Fig. 6). Skeletal samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ with an automated carbonate device according to the procedure outlined above. MLSE among fragments ranged from 14.82 to 16.65 mm. Therefore, 7 or 8 skeletal samples were extracted for isotope analysis from each fragment, depending on MLSE. In addition, growth rate varies over time. To obtain a mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ time-series of the four fragments and to compensate for

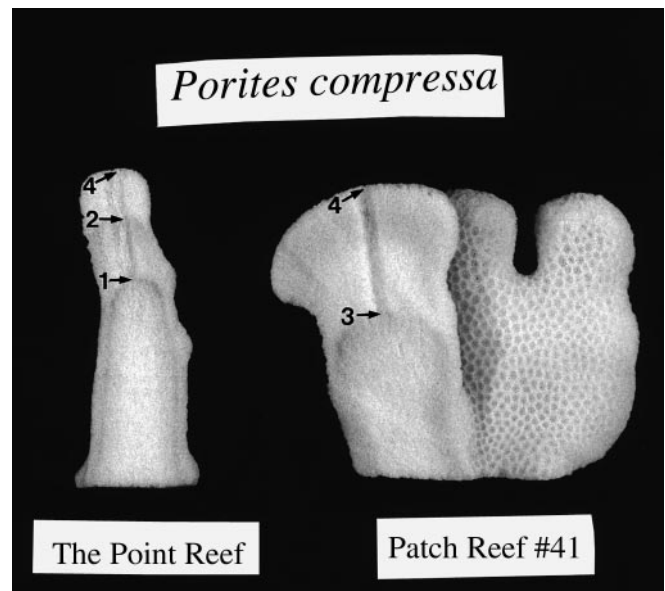


Fig. 5 *Porites compressa*. Cross-section of one fragment from The Point Reef and one from the Patch Reef #41 taken at 1.7 m depth. Stain lines on The Point Reef fragment correspond to 25 August (1) and 21 November (2) 1996; Stain Line 3 on Patch Reef #41 fragment corresponds to 6 August 1996. All corals were collected on 1 March 1997 (4) bulk skeletal sample was extracted along major axis of growth between first stain line (1 in The Point Reef corals and 3 in Patch Reef #41 corals) and tip of each coral fragment (4), as indicated by resulting shallow furrow. Arrows 1 and 3 also mark base of the furrow, and Arrow 4 the tip. Distance from Stain Line 1 to tip (4) of The Point Reef fragment is 1.4 cm; distance from Stain Line 3 to tip (4) of Patch Reef #41 fragment is 1.5 cm

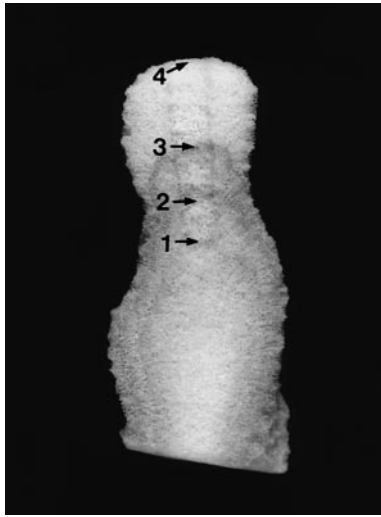


Fig. 6 *Porites compressa*. Intra-annual variation in stable isotopes. Cross-section of fragment from The Point Reef taken at 2 m depth. Stain lines correspond to 2 August (1), 17 October (2), and 22 November (3) 1996. Coral fragment was collected on 2 March 1997 (4). Sequential 2 mm skeletal samples were extracted along major axis of growth between first stain line (1) and tip of coral fragment (4), as indicated by resulting shallow furrow. Arrows 1 and 4 also mark base and tip of furrow, respectively. Distance from Stain Line 1 to tip of fragment is 1.5 cm

greater sample representation during periods of higher growth, the program “Timer” (Arand Software, courtesy of P. Howell) was used. This program adjusts for differential growth rates between fragments by using the stain lines as common time-frame references among all fragments, and interpolation. Here, the time frame was established using the three stain lines and the tip of the fragment as reference frames (Fig. 6). Each series was adjusted through interpolation to contain nine evenly spaced data points equivalent to 26 d of growth. A mean (\pm 1 SE) time-series was constructed using the adjusted time-series of all four fragments. Averaging the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ time-series of four fragments decreases variation due to genetic differences among coral fragments and increases the signal-to-noise ratio (Juillet-Leclerc et al. 1997; Guzmán and Tudhope 1998).

Results

The Point Reef coral survey: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE across depth and between species

Forty-four fragments from The Point Reef (*Porites compressa* $n = 15$, *P. lobata* $n = 14$, *Montipora verrucosa* $n = 15$) were analyzed. Skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and MLSE data were normally distributed (Table 2). In general, coral skeletal $\delta^{13}\text{C}$ values significantly decreased with depth and differed between species (Table 3, Fig. 7A, B). Results from a posteriori Tukey tests indicated that: (1) skeletal $\delta^{13}\text{C}$ in corals was significantly higher at 1.7 and 5.0 m than at 8.3 m (Fig. 7A) and (2) skeletal $\delta^{13}\text{C}$ of each species differed significantly from one another, with lowest to highest $\delta^{13}\text{C}$ values recorded in *P. compressa*, *P. lobata* and *M. verrucosa*, respectively (Table 4, Fig. 7B). Patterns in skeletal $\delta^{13}\text{C}$ values across depth were consistent among species, but signif-

Table 2 *Porites compressa*, *P. lobata*, and *Montipora verrucosa*. Shapiro–Wilk test for normality of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal extension (MLSE) residuals [$W:N$ ratio of Wilk’s statistic to normal, ranges from 0 (non-normal distribution) to 1 (normal distribution); $p < W$ of ≥ 0.05 indicates data are normally distributed]. Variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and MLSE across depth and between species were evaluated using The Point Reef data set (*P. compressa* $n = 15$, *P. lobata* $n = 14$ and *M. verrucosa* $n = 15$). Variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE between field sites were assessed in *P. compressa* (The Point Reef $n = 15$, Patch Reef #41 $n = 14$)

	The Point Reef ($n = 44$)			<i>P. compressa</i> ($n = 29$)		
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	MLSE	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	MLSE
W:N	0.981	0.987	0.955	0.987	0.940	0.874
$p < W$	0.782 ^a	0.945 ^a	0.131 ^a	0.974 ^a	0.113 ^a	0.002

^a Data are normally distributed

icantly offset from one another (Fig. 7B; Table 3 shows no significant interaction effect). When each species was examined individually, $\delta^{13}\text{C}$ decreased significantly with depth for both *P. compressa* and *P. lobata* (Table 5, Fig. 7B). No significant change in $\delta^{13}\text{C}$ was detected in *M. verrucosa* across depth (Table 5, Fig. 7B).

MLSE generally increased with depth (Table 3, Fig. 7C), and differed significantly between species (Table 3, Fig. 7D). An a posteriori Tukey test revealed that MLSE differed between each species, with lowest to highest overall mean MLSE recorded in *Porites lobata*, *P. compressa* and *Montipora verrucosa*, respectively (Table 4, Fig. 7D). When each species was examined individually, the pattern of MLSE across depth differed (Fig. 7D), as indicated by a significant interaction term (Table 3). Peak MLSE occurred at 1.7, 5.0 and 8.3 m depths for *P. lobata*, *P. compressa* and *M. verrucosa*, respectively (Fig. 7D). However, peak MLSE was significantly higher in *M. verrucosa* alone (Table 5). Changes in MLSE across depth in *P. compressa* and *P. lobata* were not statistically significant (Table 5).

Skeletal $\delta^{18}\text{O}$ values did not differ significantly with depth (Table 3). There was, however, a significant species effect (Table 3). Skeletal $\delta^{18}\text{O}$ values in *Porites compressa* and *P. lobata* were both significantly lower than in *Montipora verrucosa* (Table 4).

Porites compressa on The Point Reef and Patch Reef #41: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE between field sites

Skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data for 29 fragments of *Porites compressa* (The Point Reef $n = 15$, Patch Reef #41 $n = 14$) were normally distributed while MLSE was not (Table 2). In general, coral skeletal $\delta^{13}\text{C}$ values decreased significantly with depth, but did not differ between field sites (Table 6, Fig. 8A, B). An a posteriori Tukey test showed that the mean skeletal $\delta^{13}\text{C}$ value at 1.7 m was significantly greater than at 5.0 and 8.3 m (Fig. 8A). *P. compressa* at both The Point Reef and

Fig. 7 *Porites compressa* (*Pc*), *P. lobata* (*Pl*), and *Montipora verrucosa* (*Mv*). Mean skeletal $\delta^{13}\text{C}$ values and maximum linear skeletal extension (*MLSE*) across depth at The Point Reef. **A** Mean $\delta^{13}\text{C}$ across depth for all species combined; **B** mean $\delta^{13}\text{C}$ across depth for individual species; **C** mean *MLSE* across depth for all species combined; **D** mean *MLSE* across depth for individual species (* in **A**, **B**, **D** and † in **B** indicate means that differ significantly from means without such symbols). In **A** and **C**, sample sizes are indicated above each mean, and statistics are given in Table 3; for **B** and **D**, $n = 5$ in all cases (except for *P. lobata* at 1.7 m, where $n = 4$), and statistics are given in Tables 3, 4 and 5

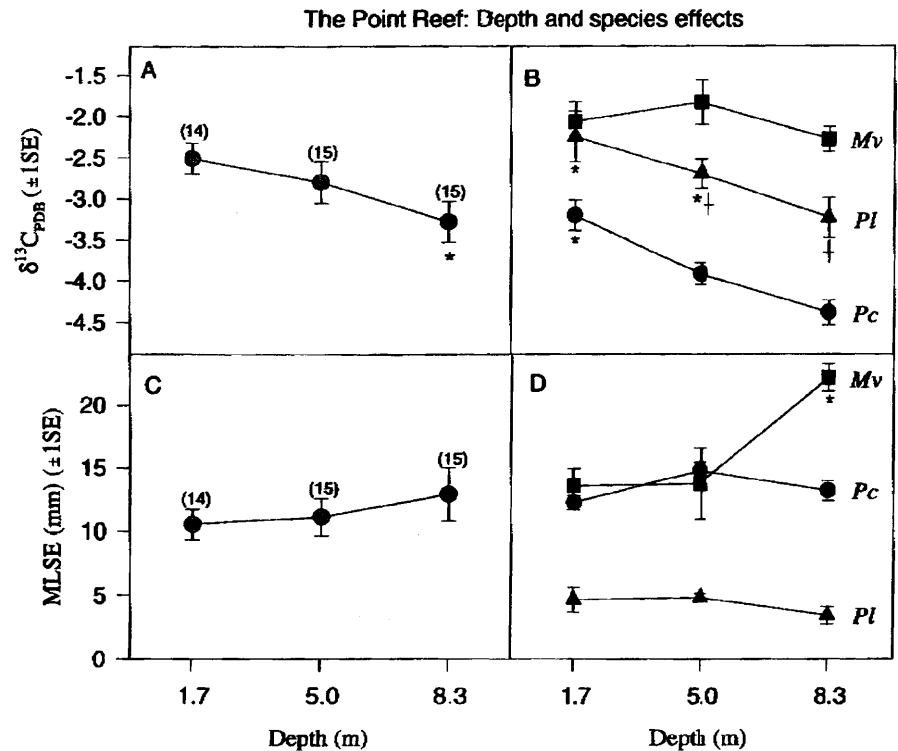


Table 3 *Porites compressa*, *P. lobata*, and *Montipora verrucosa*. Two-way Model III ANOVA of depth (1.7, 5.0 and 8.3 m) and species effects on skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal

extension (*MLSE*) at The Point Reef. Overall $\delta^{13}\text{C}$ model $r^2 = 0.80$, $n = 44$; $\delta^{18}\text{O}$ $r^2 = 0.57$, $n = 44$; *MLSE* $r^2 = 0.84$, $n = 44$ (*SS* sum of squares; * $p < 0.05$; *** $p < 0.0005$)

Source	(df)	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$			<i>MLSE</i>		
		SS	<i>F</i> ratio	Prob > <i>F</i>	SS	<i>F</i> ratio	Prob > <i>F</i>	SS	<i>F</i> ratio	Prob > <i>F</i>
Model	(8)	29.906	17.65	0.0001***	1.933	5.73	0.0001***	1419.527	22.87	0.0001***
Depth	(2)	4.585	10.83	0.0002***	0.035	0.42	0.6627	57.334	3.70	0.0275*
Species	(2)	23.876	56.37	0.0001***	1.385	16.42	0.0001***	1143.450	73.69	0.0001***
Depth × species	(4)	1.644	1.94	0.1254	0.504	2.99	0.0318*	200.885	6.47	0.0005***

Patch Reef #41 field sites exhibited the same pattern (Fig. 8B; Table 6 shows no significant interaction effect). When each field site was examined individually, $\delta^{13}\text{C}$ values decreased significantly with depth in *P. compressa* at The Point Reef and non-significantly at Patch Reef #41 (Table 7, Fig. 8B).

Overall, *MLSE* did not significantly differ with depth, but was significantly higher at Patch Reef #41 than at

The Point Reef (Table 6, Fig. 8D). *MLSE* exhibited a non-linear response with depth (Fig. 8C, D), with maximum growth occurring at mid-depth at both field sites (Fig. 8D). Mean skeletal $\delta^{18}\text{O}$ did not significantly differ across depth, but was significantly lower at Patch Reef #41 by $\sim 0.23\text{‰}$ [(mean $\delta^{18}\text{O}_{\text{PDB}}$ at The Point Reef = -4.16‰ ($n = 15$), Patch Reef #41 = -4.39‰ ($n = 14$)] (Table 6).

Table 4 *Porites compressa*, *P. lobata*, *Montipora verrucosa*. Mean (\pm 1SE) skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and maximum linear skeletal extension (*MLSE*) for each species at The Point Reef [* means that do not significantly differ for a given variable (a posteriori Tukey test)]

Variable	<i>P. compressa</i> ($n = 15$)	<i>P. lobata</i> ($n = 14$)	<i>M. verrucosa</i> ($n = 15$)
$\delta^{13}\text{C}$ (‰PDB)	-3.81 (0.15)	-2.74 (0.17)	-2.04 (0.13)
$\delta^{18}\text{O}$ (‰PDB)	-4.16 (0.02)*	-3.98 (0.08)*	-3.73 (0.06)
<i>MLSE</i> (mm)	13.38 (0.46)	4.27 (0.40)	16.48 (1.48)

Table 5 *Porites compressa*, *P. lobata*, *Montipora verrucosa*. Effect of depth on skeletal $\delta^{13}\text{C}$ and maximum linear skeletal extension (*MLSE*) for each coral species at The Point Reef (one-way ANOVAs; * $p < 0.05$; ** $p < 0.005$)

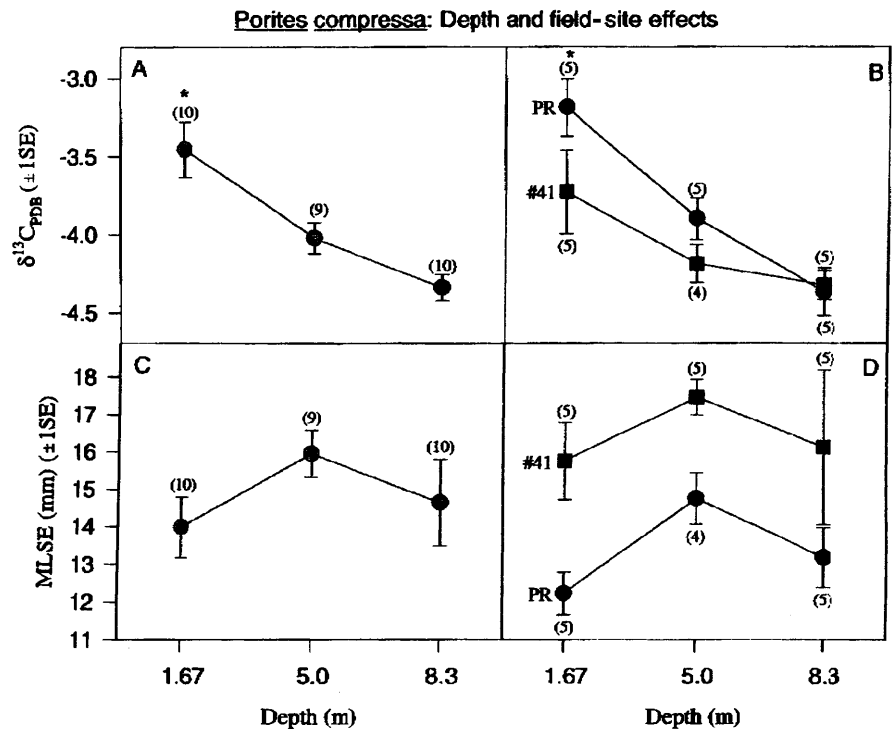
Species	(df)	$\delta^{13}\text{C}$		<i>MLSE</i>	
		<i>F</i>	<i>p</i> <	<i>F</i>	<i>p</i> <
<i>P. compressa</i>	(14)	14.17	0.0007**	3.41	0.067
<i>P. lobata</i>	(13)	4.11	0.047*	1.40	0.288
<i>M. verrucosa</i>	(14)	0.97	0.405	6.56	0.012*

Table 6 *Porites compressa*. Two-way Model III ANOVA of depth (1.7, 5.0 and 8.3 m) and field site (The Point Reef and Patch Reef #41) effects on skeletal $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, and two-way Kruskal–Wallis rank test of depth and field-site effects on maximum linear skeletal extension (MLSE). For each source, a Kruskal–Wallis H ratio was computed using MLSE ranks (H

ratio = source SS \div total mean square), and significance was determined by χ^2 approximation with df appropriate for each source (Zar 1984). Overall $\delta^{13}\text{C}$ model $r^2 = 0.60$, $n = 29$; $\delta^{18}\text{O}$ $r^2 = 0.53$, $n = 29$ (SS sum of squares; * $p < 0.05$; ** $p < 0.005$; *** $p < 0.0005$)

Source	(df)	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$			MLSE		
		SS	F ratio	Prob > F	SS	F ratio	Prob > F	SS	H ratio	Prob > χ^2
Model	(5)	4.928	6.95	0.0004***	0.418	5.19	0.0025**	1163.50	15.01	0.025*
Depth	(2)	4.040	14.25	0.0001***	0.038	1.19	0.3338	250.40	3.23	0.10
Field site	(1)	0.490	3.46	0.0758	0.352	21.86	0.0001***	907.50	11.71	0.001**
Depth \times field site	(2)	0.425	1.50	0.2446	0.012	0.38	0.6858	5.60	0.07	0.95

Fig. 8 *Porites compressa*. Mean skeletal $\delta^{13}\text{C}$ values and maximum linear skeletal extension (MLSE) across depth at two field sites, The Point Reef (PR) and Patch Reef #41 (#41). **A** Mean $\delta^{13}\text{C}$ across depth for both sites combined; **B** mean $\delta^{13}\text{C}$ across depth for individual sites; **C** mean MLSE across depth for both sites combined; **D** mean MLSE across depth for individual sites. Sample sizes are indicated above or below each data point (* in **A**, **B** indicates mean differs significantly), and statistics are given in Tables 6 and 7



Intra-annual variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Examination of intra-annual skeletal isotope values in *Porites compressa* revealed that $\delta^{18}\text{O}$ varied with temperature, reflecting warmer conditions from August to October and cooler winter temperatures from November to February (Figs. 2, 9). Estimates indicated that an

Table 7 *Porites compressa*. Effect of depth on $\delta^{13}\text{C}$ and maximum linear skeletal extension (MLSE) in coral at The Point Reef and Patch Reef #41 (one-way ANOVAs) (** $p < 0.005$)

Area	(df)	$\delta^{13}\text{C}$		MLSE	
		F	p <	F	p <
The Point Reef	(14)	14.17	0.0007**	3.41	0.067
Patch Reef #41	(13)	2.96	0.093	0.35	0.711

increase of 0.1‰ $\delta^{18}\text{O}$ corresponded to an approximate decrease in temperature of 1.0 C° [Approximately monthly (~ 26 d) mean $\delta^{18}\text{O}$ values from 28 August to 13 November 1996 were correlated with mean temperature measurements for the same intervals. Temperature ($^\circ\text{C}$) = $-10.12 \times \delta^{18}\text{O}_{\text{PDB}} - 13.82$, $r^2 = 0.64$, $n = 4$, $p < 0.20$, Pearson correlation coefficient = -0.80 .] Skeletal $\delta^{13}\text{C}$ reflected decreases in solar irradiance with the onset of the rainy season in mid-October (Figs. 3, 9). Estimates indicated that a decrease of 0.1‰ $\delta^{13}\text{C}$ corresponded to an approximate decrease in solar irradiance of 18 lumens m^{-2} . [Approximately monthly (~ 26 d) $\delta^{13}\text{C}$ means from 2 August to 13 November 1996 were correlated with mean solar irradiance measurement for the same time intervals. Light (lumens m^{-2}) = $176.1 \times \delta^{13}\text{C}_{\text{PDB}} + 674.2$, $r^2 = 0.79$, $n = 5$, $p < 0.04$, Pearson correlation coefficient = 0.89 .]

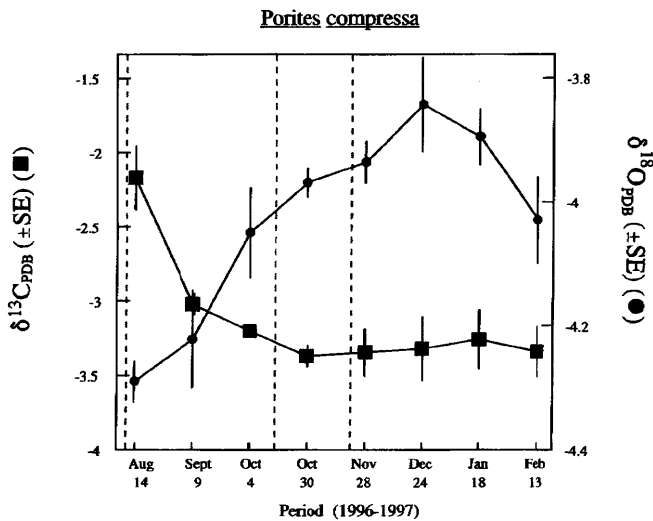


Fig. 9 *Porites compressa*. Time-series of skeletal $\delta^{13}\text{C}$ (\pm 1SE) and $\delta^{18}\text{O}$ values (\pm 1SE) in coral monitored on The Point Reef at 2.0 m depth. Time frame was established using the three stain lines and tips of the fragments as reference frames. Adjustments for differential growth rates between fragments were performed using program "Timer" ($n = 4$ for each mean) (Dashed vertical lines: first, second and third stain lines, corresponding to 2 August, 17 October and 22 November 1996, respectively)

Discussion

The Point Reef coral survey: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE across depth and between species

Overall, skeletal $\delta^{13}\text{C}$ decreased with depth at The Point Reef (Fig. 7A) and varied between species. Although $\delta^{13}\text{C}$ values in both *Porites compressa* and *P. lobata* decreased at the same rate with depth (Fig. 7B), they were offset by $\approx 1.0\text{‰}$. Decreases in $\delta^{13}\text{C}$ with depth have also been recorded for *P. lobata* (Carriquiry et al. 1994), *Acropora formosa* (Juillet-Leclerc et al. 1997), *Montastrea annularis* [Land et al. 1975 (columnar form); Weber et al. 1976; Bosscher 1992], and *Acropora cervicornis* (Land et al. 1975). *Montipora verrucosa* had the highest skeletal $\delta^{13}\text{C}$ values at all depths, varied the least across depth, and had maximum $\delta^{13}\text{C}$ at mid-depth (Fig. 7B). These findings are inconsistent with results of Weil et al. (1981), who showed that $\delta^{13}\text{C}$ in *M. verrucosa* in Hawaii decreased continuously with decreasing light under tank-cultured conditions. These results suggest that coral metabolic behavior and carbon isotopic fractionation may differ under field versus tank conditions. Other studies, on *Acropora variabilis* (Erez 1978), *Agaricia undata* (Land et al. 1975), *Siderastrea siderea* (Guzmán and Tudhope 1998), and *Montastrea annularis* (flat morphology) (Land et al. 1975), also showed maximum $\delta^{13}\text{C}$ values at mid-depth. Erez proposed that photoinhibition may reduce photosynthesis in shallow-water corals, leading to a decrease in $\delta^{13}\text{C}$ at shallower depths and maximum $\delta^{13}\text{C}$ levels at mid-depth. Experimental manipulation of light levels in tank-reared *P. compressa* corals supports this photoinhibition hypothesis (Grottoli-Everett 1998).

MLSE was significantly greatest at 8.3 m in *Montipora verrucosa* (Fig. 7D) and heavily influenced the overall increase in MLSE across depth (Fig. 7C). Most studies report a decrease in MLSE with depth for most corals at most field sites (Buddemeier et al. 1974; Dustan 1975; Highsmith 1979; Hudson 1981; Wellington 1982; Highsmith et al. 1983; Hubbard and Scaturro 1985; Huston 1985; Guzmán and Cortés 1989; Logan and Tomascik 1991; Bosscher 1992; Klein et al. 1993; Custodio and Yap 1997). A few studies have reported peak MLSE at intermediate and maximum depths for some corals (Buddemeier et al. 1974; Baker and Weber 1975; Oliver et al. 1983; Hubbard and Scaturro 1985; Huston 1985; Guzmán and Tudhope 1998; Harriott 1998). The data presented here further indicate that MLSE varies interspecifically across depth. This may reflect interspecific differences in physiological processes such as photosynthesis and heterotrophy, and should be considered when interpreting coral growth patterns for paleoclimate reconstruction.

Variation in MLSE with depth did not correspond in any predictable manner with variation in $\delta^{13}\text{C}$ levels. Decreases in skeletal $\delta^{13}\text{C}$ values strongly support the idea that the rate of photosynthesis decreases with depth in *Porites compressa* and *P. lobata* (Fig. 7B). The observed slight increases in MLSE in *P. compressa* between 1.7 and 5.0 m and the dramatic increase in MLSE in *Montipora verrucosa* between 5.0 and 8.3 m may be a result of increases in heterotrophically acquired carbon (zooplankton) in the coral's diet. Increases in zooplankton abundance resulted in skeletal $\delta^{13}\text{C}$ decreases and increased MLSE in the Panamanian corals *Pavona clavus* and *P. gigantea* (Grottoli and Wellington 1999). Furthermore, the effect of zooplankton on the skeletal $\delta^{13}\text{C}$ values in both *P. clavus* and *P. gigantea* was greater in deeper corals (Grottoli and Wellington 1999). Therefore, increases in heterotrophy coupled with decreases in photosynthesis could explain the increases in MLSE with decreases in $\delta^{13}\text{C}$ levels across depth for *Porites compressa* and *M. verrucosa*. In the case of *M. verrucosa*, an alternative explanation for the significant increase in MLSE may be attributable to a change in morphology from a predominantly finger-like form at 1.7 m to a plate-like form at 8.3 m. To assess changes in growth, calcification rates may be a better factor to measure in corals with varying morphology.

$\delta^{18}\text{O}$ did not differ across depth within a species but did differ among species. Consistency in $\delta^{18}\text{O}$ across depth has also been reported in *Montastrea annularis* (Bosscher 1992), and is presumed to reflect constant temperature. Species-specific offsets in $\delta^{18}\text{O}$ have also been reported by Weil et al. (1981) and Wellington et al. (1996).

Porites compressa on The Point Reef and Patch Reef #41: variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE between field sites

Skeletal $\delta^{13}\text{C}$ decreased with depth at both field sites (Fig. 8B), and converged to approximately -4.3‰ at

8.3 m. This common lower limit in $\delta^{13}\text{C}$ at both field sites suggests a threshold for metabolic carbon fractionation in Hawaiian *Porites compressa*. The only other species for which $\delta^{13}\text{C}$ has been measured across depth at more than one field site is the Caribbean coral *Montastrea annularis*. The results indicate a consistent decrease in $\delta^{13}\text{C}$ within a morphological form (Land et al. 1975; Weber et al. 1976; Bosscher 1992). Further investigation is needed to confirm the suggestion that variation in $\delta^{13}\text{C}$ across depth is consistent within a coral species.

MLSE was highest at mid-depth (Fig. 8C, D), and significantly higher at Patch Reef #41 than at The Point Reef (Table 6). In other coral species, maximum MLSE has been shown to vary between field sites (Baker and Weber 1975; Hudson 1981; Highsmith et al. 1983; Hubbard and Scaturro 1985; Huston 1985; Logan and Tomascik 1991; Harriott 1998). However, field sites often differ drastically (i.e. different oceans or coastal regimes), and many factors may be influencing MLSE. Harriott suggests that calcification rate is the same in *Acropora formosa* from different field sites even though MLSE significantly differs. The results presented here emphasize that the response in $\delta^{13}\text{C}$ and MLSE within *Porites compressa* is generally consistent but that results can be offset between field sites. Such differences are most probably attributable to variation in the immediate environment (Wellington et al. 1996; Guzmán and Tudhope 1998). Skeletal $\delta^{18}\text{O}$ at Patch Reef #41 was significantly lower by 0.23‰ than that at The Point Reef (Table 6), indicating a slightly warmer or less saline environment (Wellington et al. 1996). Given that MLSE was greater at Patch Reef #41 than at The Point Reef and that Hawaiian corals tend to display increased growth rate with moderate increases in temperature (Jokiel and Coles 1977, 1990), the offset in $\delta^{18}\text{O}$ between the two field sites probably reflects slight temperature differences.

Intra-annual variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Skeletal $\delta^{13}\text{C}$ values decreased as solar irradiance levels decreased over time in *Porites compressa* reared at 2.0 m depth (Figs. 3, 9). This result is consistent with decreases in $\delta^{13}\text{C}$ observed (1) in *P. compressa* and *P. lobata* with decreasing light across depth (Figs. 7, 8), (2) in tank-reared *P. compressa* with decreases in light from ambient (Grottoli-Everett 1998), and (3) in field-reared *Pavona clavus* and *P. gigantea* with experimentally reduced light (Grottoli and Wellington 1999). Together, these findings strongly support the potential application of skeletal $\delta^{13}\text{C}$ of *Porites* and *Pavona* corals for paleoreconstruction of solar irradiance.

Skeletal $\delta^{18}\text{O}$ in *Porites compressa* at 2.0 m depth increased with the general decreases in temperature over time (Figs. 2, 9). The warm SST anomalies recorded from 29 August to 7 September and 3 to 11 October, however, were not detected. Samples were extracted

every 2 mm along the major axis of growth, representing ≈ 26 d of growth. Since each warm event was shorter in duration than that represented by each skeletal sample, their effect was averaged over the entire 26 d period. One would expect to detect the warm events with samples taken every 0.5 mm (representing ≈ 7 d). Alternatively, the warm events may not have been detectable in the skeletal $\delta^{18}\text{O}$ record as a result of heat-induced stress slowing or shutting down calcification. Estimates of the correlation between $\delta^{18}\text{O}$ and SST revealed a decrease of ~ 1.0 C° per 0.1‰ increase in skeletal $\delta^{18}\text{O}$. Most studies report an average decrease of ~ 1.0 C° for each 0.20‰ increase in skeletal $\delta^{18}\text{O}$ (e.g. Wellington and Dunbar 1995; Wellington et al. 1996). The difference between the current and previously reported correlation between SST and $\delta^{18}\text{O}$ may be attributable to species-specific effects, low sampling resolution, or both. No other study has measured $\delta^{18}\text{O}$ in Hawaiian corals. Further study of skeletal $\delta^{18}\text{O}$ in Hawaiian corals is needed to confirm the observed correlation between SST and skeletal $\delta^{18}\text{O}$ in *P. compressa* in Kaneohe Bay.

Summary and implications for paleoclimate reconstruction

Natural variation in skeletal $\delta^{13}\text{C}$ values and MLSE across depth are consistent within but not among the species studied here. Depth and species-specific variations in $\delta^{13}\text{C}$ levels at a single field site have also been observed by Land et al. (1975) and Erez (1978). Inter- and intraspecific variations in the contribution of photosynthesis and heterotrophy to skeletal $\delta^{13}\text{C}$ (Grottoli and Wellington 1999) may account for the observed species-specific offsets and variability in $\delta^{13}\text{C}$ patterns across depth and among species. Experimental reduction of light from ambient levels and natural decreases in solar irradiance over time have yielded consistent decreases in $\delta^{13}\text{C}$ values for *Montipora verrucosa* (Weil et al. 1981), *Pavona clavus* and *P. gigantea* (Grottoli and Wellington 1999), and *Porites compressa* (Grottoli-Everett 1998; present study). These results support the hypothesis that for a given species, the contribution of photosynthesis and heterotrophy is consistent within a given depth. Finally, differences in MLSE and skeletal $\delta^{18}\text{O}$ levels between two field sites occurred on a very small geographical scale (i.e. field sites were only separated by ~ 6 nautical kilometers). Overall, these results emphasize that species-specific, depth-related, and field-site-specific variation in coral skeletal $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and MLSE should be considered when interpreting and comparing coral-based tropical paleoclimate data from various species, depths and field sites.

Acknowledgements Special thanks to G. Wellington, E. Druffel, R. Dunbar, P. Jokiel, C. Masiello, M. Horn, and two anonymous reviewers for valuable discussion or comments on various aspects of this manuscript. Many thanks to my field assistants C. Grottoli and S. Lamont; my dive buddies I. Kuffner, R. Sahaghian, K. Longenecker, K. Sherwood, J. Collier and J. Fender; P. Jokiel

and all the faculty, students and staff at the Hawaii Institute of Marine Biology; P. Swart for his generosity with the isotope analysis, A. Saied and all the members of the Swart laboratory. I thank W. Everett and my parents A. B. Grottoli and L. Grottoli for their support and encouragement. This work complies with the current laws of the country in which it was performed, and it was supported by the Environmental Protection Agency STAR Graduate Fellowship (U-914955-01-0), Sigma Xi Student Research Grant (1996), Seaspace Student Fellowship (1996), and the Environmental Institute of Houston (1996).

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