

Surface Growth Rings of *Porites lutea* Microatolls Accurately Track Their Annual Growth

Abstract

Microatolls are disk-shaped coral colonies, having perimeters of live coral surrounding dead centers, that are limited in their upward growth by exposure at extreme low tide. We looked at surface annuli of microatolls of *Porites lutea* on the open ocean reef flat of Abaiang Atoll, in the Republic of Kiribati, as potential external indicators of microatoll yearly growth pattern. We measured surface annuli width and disk diameters of 10 microatolls, from March 1998 to October 2000, and found a mean growth rate of 2.2 cm/yr. X-radiography was used to establish a direct connection between surface annuli and internal growth bands. Comparison of the growth pattern of surface annuli to observed monthly mean lower low waters showed that these corals closely track fluctuations in local mean sea level. This suggests that there is a potential for using the surface annuli of *Porites lutea* microatolls on well drained, open ocean reef flats as an ongoing, low cost, non-destructive method of assessing trends in local mean sea level.

Introduction

Microatolls are disk-shaped shallow water corals that are limited vertically by prolonged sub-aerial exposure around mean lower low water (MLLW), and constrained to grow only laterally at their circumferences, leaving flat or concave,

dead upper surfaces that become covered by sediments, algae, and sessile animals (Figure 1). Water temperature and the duration and intensity of sunlight are important factors limiting photosynthetic activity of zooxanthellae in corals, and thus coral growth, but seasonal fluctuations in water temperature and sunlight on atolls near the equator are not large. On the reef flat, on the other hand, corals experience greater variation in both regimes as a direct consequence of the frequency and level

¹Author to whom correspondence should be addressed.
E-mail: scubajer@aol.com

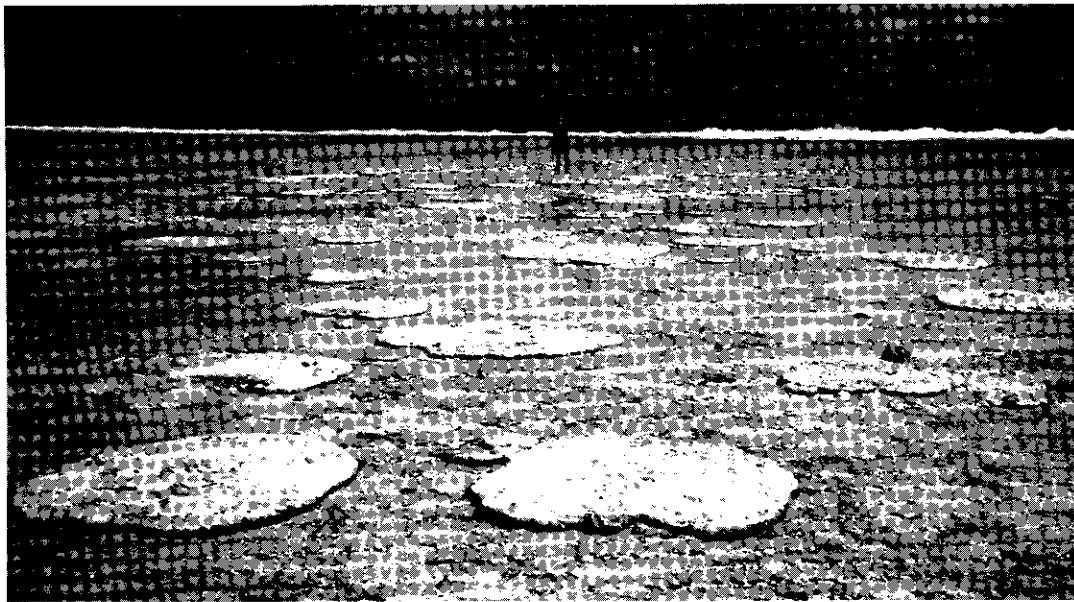


Figure 1. View looking toward reef crest across length of microatoll patch on ocean reef flat, Tabwiroa, Abaiang Atoll, Republic of Kiribati, showing microatolls exposed at low tide.

of extreme low tides. Temperatures in the shallow waters of the reef flat at low tide increase as the substrate warms, and the filtering effect of seawater against harsh sunlight is lost. Thus, frequency and level of extreme low tides can have important consequences for microatoll growth beyond direct desiccation due to exposure.

Although the formation of microatolls has been discussed in the literature by a number of authors (summarized by Stoddart and Scoffin 1979), little attention had been paid to surface features of microatolls until Woodroffe and McLean (1990) related surface features of microatolls of *Porites* sp. in Kiribati and the Cocos (Keeling) Islands to sea level changes, and (in Kiribati) to the 1982-83 El Niño-Southern Oscillation (ENSO). Spencer et al. (1997) used surface features of *Porites lutea* microatolls on Tongareva Atoll, Northern Cook Islands, to reconstruct sea levels for the previous 57 yr. Smithers and Woodroffe (2000) found that elevation among *Porites* microatolls they surveyed in the Cocos Islands varied more than 40 cm across a range of intertidal environments. Microatolls in open reef flat habitats had the narrowest and most consistent elevation range. They went on to establish chronologies for variations in *Porites* microatoll surface morphology and to correlate these in microatolls from separate reef flat sites in the Cocos Islands (Smithers and Woodroffe 2001).

Of all the different corals that form microatolls, *Porites lutea* is especially interesting to us because it is the only one we have seen that develops distinct and regular concentric rings on the upper surface. We hypothesized that these surface rings (annuli) reflect the annual growth of these microatolls, and proposed a possible link between annulus width on microatolls of *P. lutea* on the island of Mauke, Cook Islands to ENSO frequency (Flora et al. 1996). At that time, however, we did not have the means to test this link adequately.

In 1998, we measured surface annulus widths and corallum diameters of microatolls of *Porites lutea* in the ocean reef flat environment of Abaiang Atoll to determine their rate of growth, and used X-radiography to evaluate the potential connection between surface annuli, internal density bands, and local mean sea level (MSL).

Porites lutea has been widely reported to have a high linear annual growth rate, especially in

shallow water. Knutson et al. (1972) used auto- and X-radiography to quantify growth rate and density variation in seven species of reef corals on Enewetak Atoll and reported a linear growth rate for *P. lutea* of 1.35 cm/yr. Buddemeier et al. (1974), continuing this line of inquiry, looked at 15 species of corals collected from various depths at Enewetak Atoll and found that growth rate was a function of both species and depth. Their reported annual growth rate for *P. lutea* ranged from 4-5 mm at a depth of 30 m, to 13.5 mm at depths of 3-4 m. Highsmith (1979) studied growth rates in three massive corals, *Favia pallida*, *Goniastrea retiformis*, and *Porites lutea*, also at Enewetak Atoll. Mean linear growth rate for *P. lutea* was only 7.6 mm, but was the highest of the three species. Growth rates for all three declined with depth, being greatest in <5 m of water. Scoffin et al. (1992) studied growth rates in *P. lutea* at sites in South Thailand with different exposures to wave energy, and reported that linear growth rates decreased with increased hydraulic energy. They found that growth rates for *P. lutea* in protected shallows were as high as 2.5 cm/yr.

X-radiography of density bands within the coral skeleton has been widely used for the past 30 yr to assess coral growth rates and environmental factors affecting growth (Knutson et al. 1972, Buddemeier et al. 1974, Weber and White 1977, Highsmith 1979, Barnes and Devereux 1988). It has also been important in evaluating the potential of microatolls to record historical sea levels (Woodroffe and McLean 1990, Spencer et al. 1997, Smithers and Woodroffe 2001). This and other methods, such as auto-radiography and Alizarin staining, are destructive to the reef because they require the collection of all or part of the coral for the analysis. They are also expensive because of the equipment required, and sampling in remote locations like the mid-ocean atolls of Kiribati involves greater logistical problems. We reasoned that if our hypothesis was correct, the widths of surface annuli of *P. lutea* microatolls could be used for ongoing, low-cost, non-intrusive assessment of the coral's growth response to environmental changes on the reef flat, especially to changes in local MSL.

Methods

The study site is a large oval patch 30 m wide by 100 m long, perpendicular to reef crest and shore.

of ~630 microatolls of *Porites lutea* (Figure 1), located on the windward, open ocean reef flat of Abaiang Atoll, in the Republic of Kiribati. It is ~850 m northwest of the large fish trap outside of St. Joseph's College, in the village of Tabwiroa, and ~125 m out toward the reef crest from the

beach (Figure 2). Tides in Kiribati are semidiurnal, with a range of ~2 m and a frequent diurnal inequality of several centimeters. The patch is well drained, and the upper surfaces of microatolls often stand several centimeters above extreme low water (Figure 1).

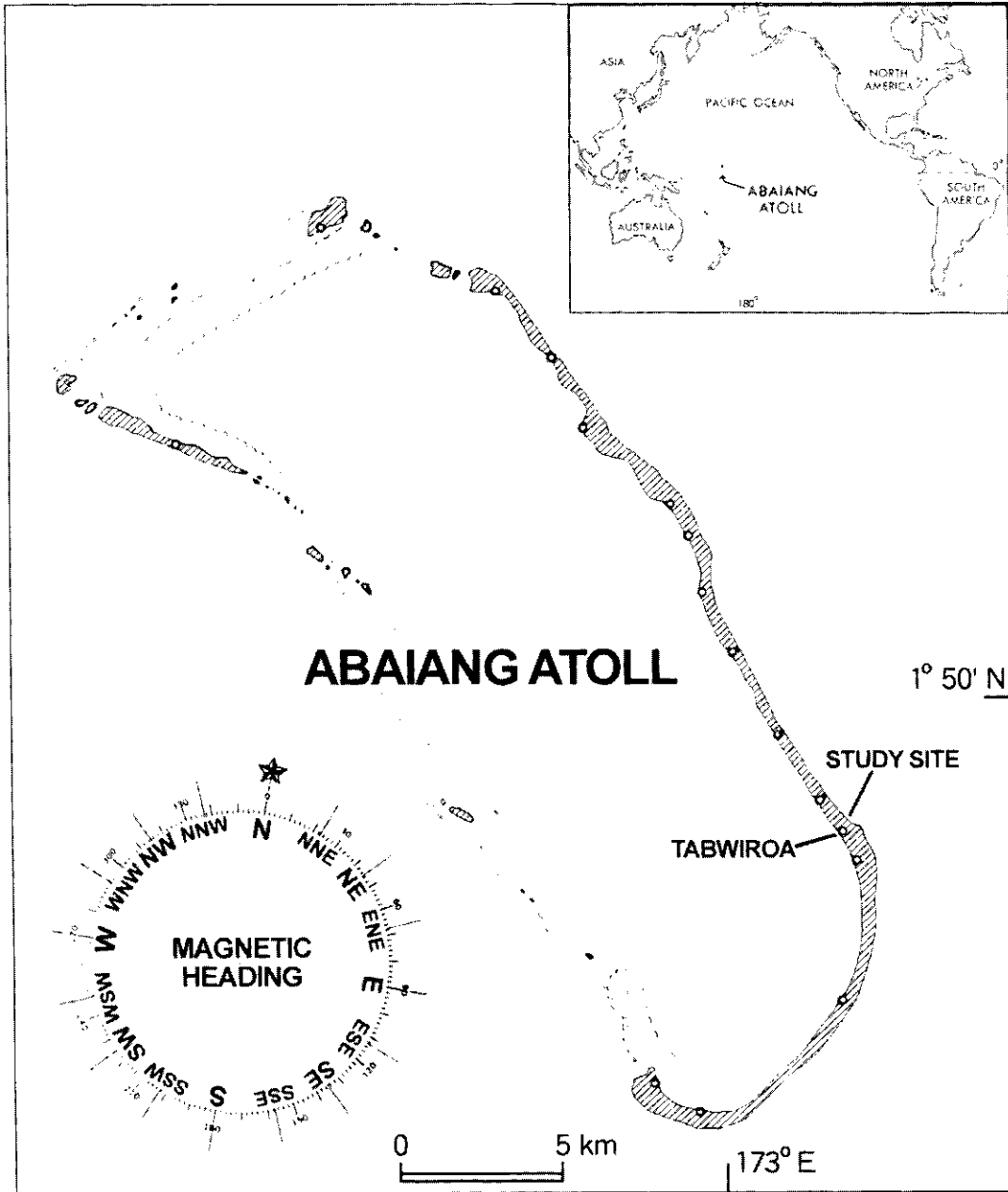


Figure 2. Abaiang Atoll, Republic of Kiribati.

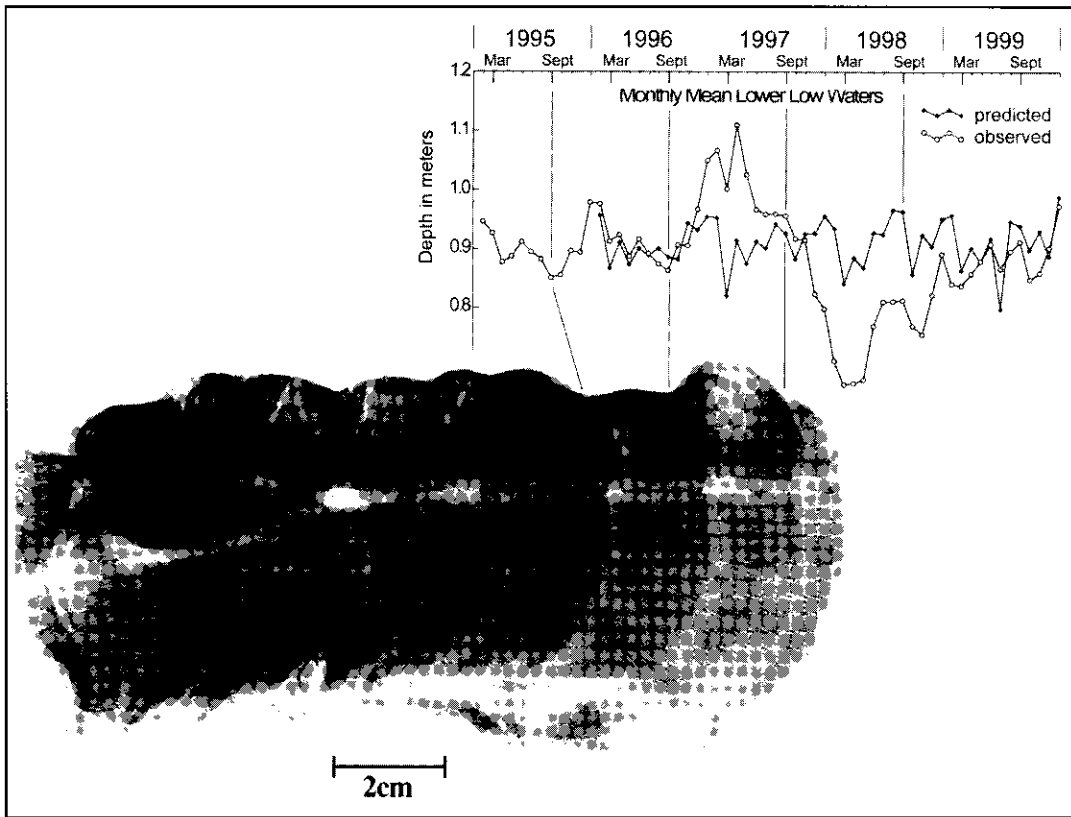


Figure 3. X-radiograph of microatoll #1 vertical cross section, showing internal annual density bands connecting directly with grooves between surface annuli. The outside edge of the microatoll is on the right. Graph compares surface annuli with observed and predicted MLLW for the period 1996-1999.

We identified this coral to species through microscopic examination of calicular features given by Veron (1986), and comparison with other known species of *Porites*. Most important characters were a fused triplet, five palli, and five radii.

Two methods were used to assess growth rate of *Porites lutea* microatolls. The first method measured surface annuli. The boundaries between surface annuli in *P. lutea* microatolls are represented by grooves in the microatoll surface corresponding to periods of retarded or arrested growth of the coral skeleton (Figures 3, 4). However, build-up of coralline algae, and the effects of mechanical and bio-erosion can obscure grooves between annuli, especially toward the microatoll center. Thus, the newest annuli, at the perimeter, are most distinct, while those toward the center become less distinct. Most microatolls in this study contained 9-10 annuli clear enough to be reliable.

Mean annual growth rate was calculated on the measurement of these clear annuli.

In March and April, 1998, 10 microatolls in the patch, 40–100 cm in diameter, were chosen for the clarity of their surface annuli (i.e., a minimum of breakage, erosion, or excessive overgrowth by coralline algae). The upper surfaces of the microatolls were cleaned of sediment and fleshy algae to reveal their annulations more clearly. Of the 10 microatolls, 9 were sketched, and all 10 were photographed, at the time of measurement. Their locations were recorded, based on their distance and magnetic compass bearing from each other and from the beach. Three transects, separated by as much as 45°, were measured across the top of each microatoll. The direction of each transect was recorded as the compass bearing the investigator faced, (90° to the line of the transect itself) while recording transect measurements. A

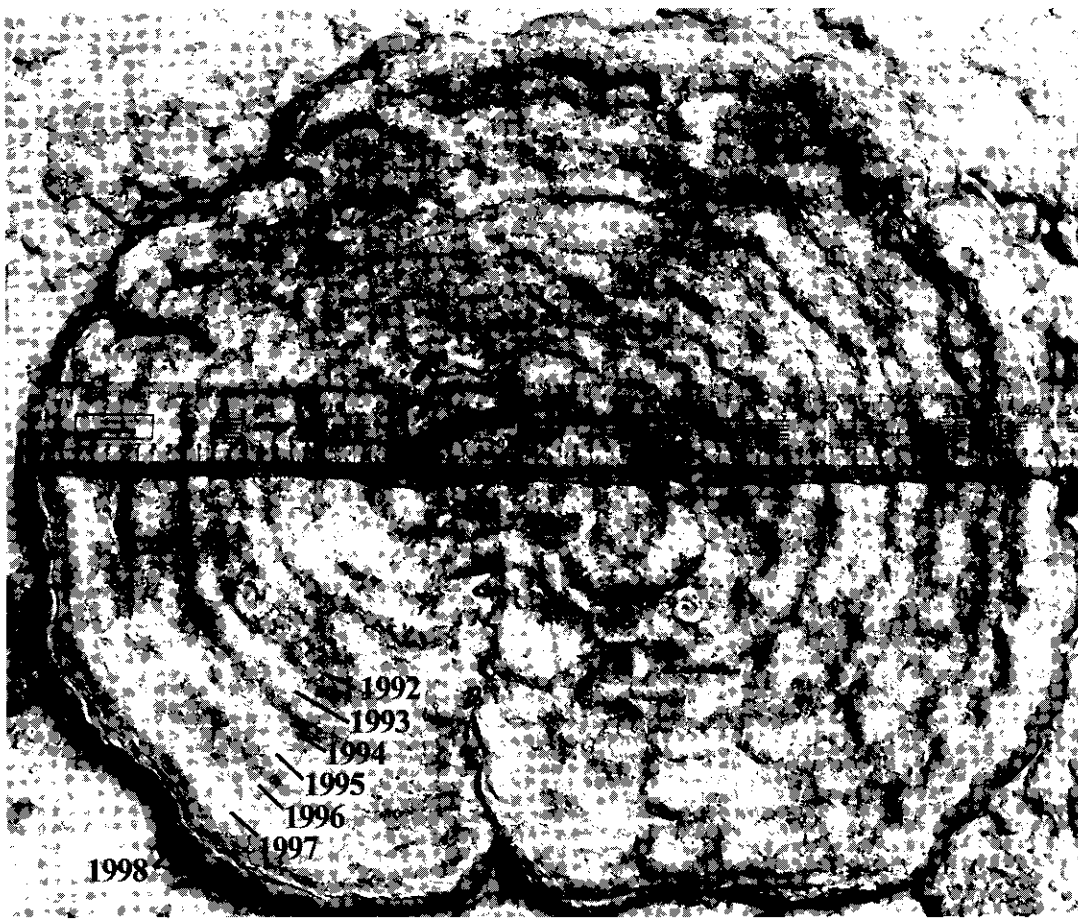


Figure 4. Transect measurement of a cleaned microatoll (Microatoll #3).

meter stick was laid across the full diameter of the microatoll, excluding live coral tissues at the perimeter, and passing as closely as possible through its estimated center (Figure 4). The maximum diameter was read as the distance from the interface between live coral tissues and dead coral skeleton on one side, to the same interface on the opposite side. The width of each growth band, or annulus, was measured from groove to groove, starting from the outside edge at either end of each transect, and working toward the center insofar as the annuli remained distinct enough to

read with reasonable certainty. Thus each transect gave two radii, recorded as left and right for each transect number, for a total of six radii per microatoll.

The growth pattern of a single microatoll can vary from one spot to another only centimeters apart, making evaluations based upon only a few measurements unreliable. We averaged all measurements, across all transects, from 10 microatolls to arrive at the mean values for each individual annulus reported in Table 1. This allowed us to project an archetypal or representative microatoll.

TABLE 1. Mean annulus widths (cm) of *Porites lutea* microatolls by deposition year. Means with the same superscripted letters are not significantly different.

Deposition year	1997	1990	1989	1991	1995	1992	1988	1993	1994	1996
Mean annulus width	2.75	2.37 ^a	2.32 ^{ab}	2.21 ^{ab}	2.17 ^{ab}	2.02 ^{ab}	2.0 ^{abc}	1.97 ^{bc}	1.70 ^{cd}	1.64 ^{cd}

TABLE 2. Annual growth rate of *Porites lutea* microatolls by measurement of increase in diameter over 30 mo from March, 1998 to October, 2000.

Microatoll number	Mean radius increase (cm)	Mean radius increase (cm) per day	Mean radius increase (cm) per year
2	4.90	0.0052	1.90
3	5.30	0.0058	2.12
4	5.80	0.0065	2.39
5	5.55	0.0061	2.23
6	6.35	0.0070	2.54
7	4.65	0.0051	1.88
8	6.10	0.0068	2.48
9	5.85	0.0065	2.38
10	5.30	0.0059	2.16

By this method, we evaluated both intra-annual and inter-annual growth patterns with greater confidence.

The second method assessed growth rate of *Porites lutea* microatolls by measuring the increase in outside diameter of microatolls over time. In September and October, 2000, these same transects, except those of #1, were measured again to determine the increase in diameters of the nine microatolls over the intervening 30 mo. The number of days between measurements in 1998 and 2000 varied among microatolls and were used accordingly to calculate mean radius increase in cm/yr for each microatoll (Table 2). These values were then used to arrive at an overall mean annual growth rate for *P. lutea*. The distinctly wider and more vertically prominent 1997 annulus was used as a marker for visually assessing the increase in the number of annuli during this time period (Figure 5).

The possible correlation between surface annuli and internal growth bands within the coral skeleton was assessed on microatoll #1. A vertical slab of the coral, 1.3 cm wide, was cut parallel to the growth axis, from circumference to center, and an X-ray exposure was made using a Bennett 100/300 radiographic unit on 800 speed ImageTek-B film at 50 kv for 4/10 of a second.

We compared the pattern of annulus growth in the photographs taken in 2000 and the X-ray image of microatoll #1 to plots of predicted monthly MLLW for 1996–1999 and observed monthly MLLW for 1995–1999 (Figure 3). These predicted and observed levels of monthly MLLW were derived from hourly MSL data provided by the

National Tidal Facility (NTF) at Flinders University of South Australia from their KIR1 tide gauge at Betio, Tarawa. The NTF was not producing official tidal predictions for Kiribati prior to 1997, but kindly generated residuals (observations minus predictions) for us using their 2003 basis for predictions.

Results

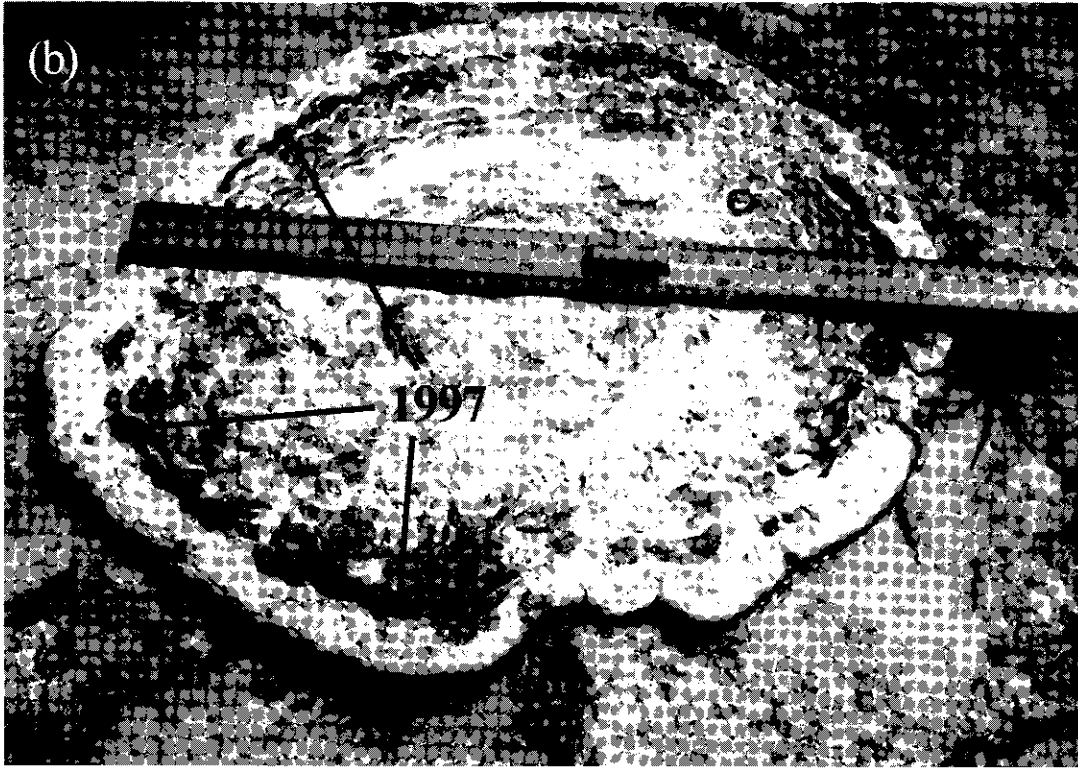
Overall mean growth rate estimated by measuring annulus width was 2.12 ± 0.10 cm/yr, compared to 2.23 ± 0.08 cm/yr for diameter increase. Both methods produced similar results, with a difference of merely 0.11 cm.

The 1997 annuli were significantly wider ($P=0.05$) than any other year, based on ANOVA and multiple range tests (Table 1). These annuli were the widest and most vertically prominent of the 10 annuli measured (Figure 5). At the low end of the scale, the differences among 1988, 1993, 1994, and 1996 were not significant. However, 1993 and 1988 were part of a continuum of non-significant differences that extended through the remaining years (Table 1), which confuses the overall relationships. Generally, these other years varied slightly around the overall mean (2.04), whereas the ENSO year (1997) was clearly wider.

Annual growth data measured over 30 mo on 9 microatolls were remarkably similar. Mean radius increase during the study ranged from 4.9 to 6.4 cm, and mean daily radius increase ranged from 0.0051 to 0.0070 cm/day (Table 2).

X-radiography of the cross section of microatoll #1 confirmed a direct relation between surface annuli and internal growth bands in the skeletal matrix (Figure 3). The curve of the convex upper surface of each annulus continues into the matrix of the coral skeleton as a distinctly denser band in the growth pattern. The arrested growth represented by this high density portion of the skeleton seems to occur around September each year during our sample period. We based this assumption

Figure 5. (Opposite) Microatoll growth over 30 mo. (a) photograph of Microatoll #7 taken in April 1998. The 1997 annulus is the first annulus inside live growth at the perimeter. (b) photograph of Microatoll #7 taken in October 2000. The 1997 annulus is well inside (>5 cm) live growth at the perimeter representing the year 2000, with two new annuli (1998 and 1999) between.



on the relative distance between the growing edge (collected in March) and the first high density band, compared to that between the first and second high density bands bracketing the 1997 annulus.

There was a marked difference between predicted and observed tidal levels for 1997 and 1998 acquired from NTF data (Figure 3). Observed MLLW values for 1997 were approximately 15 cm higher than predicted values, while observed values for 1998 were roughly the same magnitude below predicted values. This discrepancy was reflected in the growth patterns observed in *Porites lutea* microatoll annuli for the same period.

Discussion

Our reported growth rate of 2.2 cm/yr for *Porites lutea* at <2 m depth is consistent with growth rates, ranging up to 2.5cm/yr, arrived at by earlier investigators for this species in shallow water. The increase over time that we measured in microatoll diameter and concomitant increase in number (2) of surface annuli (Figure 5), together with the direct connection we found between surface annuli and internal growth bands through X-radiography (Figure 3), confirmed our hypothesis that surface annuli accurately reflect annual growth in this coral.

The height of the 1998 annulus was sub-normal, while the 1999 annulus was approximately the same level as those previous to 1997 (Figure 5). This constraint of the 1998 growth is similar to that reported by Woodroffe and McLean (1990), who associated a 1983 hiatus in the growth pattern of *Porites* microatolls on Abemama with the 1982-83 ENSO. However, they reported no increase in *Porites* growth in 1982, while the increase we observed in 1997 was marked. They reported only a slight increase in local MSL in 1982, followed by a drop of about 15 cm in 1983. The increase we observed in *P. lutea* microatoll growth in 1997 and subsequent hiatus in 1998 is comparable to the rise and fall in observed monthly MLLW for Kiribati during that same period (Figure 3).

Normal annual tidal fluctuations can be seen in the regular growth pattern of surface annuli in reef flat *Porites lutea* microatolls. However, normal tidal levels on the reef flat may be augmented during the early part of a strong ENSO event when surface waters, normally stacked up in the equa-

torial western Pacific by strong trade winds, flow eastward when the trade winds are disrupted under ENSO conditions. Abaiang Atoll experienced strong westerly winds during the 1997 ENSO, and some villages sustained flood damage due to higher than normal waves coming across the lagoon from the west. These unusual effects on the tide are reflected in Figure 3 in the comparison between predicted MLLW for 1996-1999 and observed MLLW for the same period. The anomalous tidal levels during the 1997-98 ENSO were not forecast in the normal tidal predictions because they were caused by different phenomena, but they show up clearly in the observed MLLW, which are based on hourly sea level measurements.

Our findings corroborate those of Woodroffe and McLean (1990) and Spencer et al. (1997), and demonstrate that the growth patterns in the upper surface of the *Porites lutea* microatolls we studied on Abaiang Atoll closely reflect variations in local MSL. Furthermore, while previous research has required X-radiography and other destructive means to elucidate historical data, we have shown that surface annuli of *P. lutea* microatolls can be used to track ongoing variations visually, without damage to the corals, and with a minimum of equipment. Thus, with sufficient replication to ensure a statistically meaningful sample size, the surface annuli of *P. lutea* microatolls in the open ocean reef flat of mid-Pacific atolls could be measured annually for an ongoing, low-cost, non-intrusive assessment of the coral's response to fluctuations in local MSL. As inner annuli become less distinct and drop out of the record, the newest outer annuli are added, maintaining a consistent, but dynamic data base of about 10 annuli each year. Cumulatively, these data would represent an important adjunct to tide gauge records and, where tide gauges are not available, a significant record in their own right.

Acknowledgements

We would like to thank Fred Hunziker, D.C., of Bellingham, Washington, for all X-radiography of coral samples, and Mike Davis of the National Tidal Facility in Flinders, Australia, for tidal information. We would also like to thank Rosemary Flora, Tina Kum Kee, Moatau Tekabwere, Cleo Vilett, and Kacy Lafferty for their assistance in the field.

Literature Cited

- Barnes, D. J., and M. J. Devereux. 1988. Variations in skeletal architecture associated with density banding in the hard coral *Porites*. *Journal of Experimental Marine Biology and Ecology* 121:37-54.
- Buddemeier, R. W., J. E. Maragos, and D. W. Knutson. 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology* 14:179-200.
- Flora, C. J., R. Flora, P. Ely, and E. C. Parish. 1996. Ringed coral disks on Mauke in the Cook Islands and El Niño frequency. Page 63 *In* H. A. Lessios (editor), 8th International Coral Reef Symposium Abstracts, Panama City, Panama.
- Highsmith, R. C. 1979. Coral growth rates and environmental control of density banding. *Journal of Experimental Marine Biology and Ecology* 37:105-125.
- Knutson, D. W., R. W. Buddemeier, and S. V. Smith. 1972. Coral chronometers: seasonal growth bands in reef corals. *Science* 177:270-272.
- Scoffin, T. P., A. W. Tudhope, B. E. Brown, H. Chansang, and R. F. Cheeney. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs* 11:1-11.
- Smithers, S. G., and C. D. Woodroffe. 2000. Microatolls as sea-level indicators on a mid-ocean atoll. *Marine Geology* 168:61-78.
- Smithers, S. G., and C. D. Woodroffe. 2001. Coral microatolls and 20th century sea level in the eastern Indian Ocean. *Earth and Planetary Science Letters* 191:173-184.
- Spencer, T., A. W. Tudhope, J. R. French, T. P. Scoffin, A. Utanga. 1997. Reconstructing sea level change from coral microatolls, Tongareva (Penrhyn) Atoll, Northern Cook Islands. 8th International Coral Reef Symposium, Panama 1:489-494.
- Stoddart, D. R., and T. P. Scoffin. 1979. Microatolls: review of form, origin, and terminology. *Atoll Research Bulletin* 224:1-17.
- Veron, J. E. N. 1986. *Corals of Australia and the Indo-Pacific*. University of Hawaii Press, Honolulu, Hawaii.
- Weber, J. N., and E. W. White. 1977. Caribbean reef corals *Montastrea annularis* and *Montastrea cavernosa*: long-term growth data as determined by skeletal X-radiography. *Reefs and related carbonates - ecology and sedimentology*. American Association of Petroleum Geologists, Tulsa, Oklahoma.
- Woodroffe, C., and R. McLean. 1990. Microatolls and recent sea level change on coral atolls. *Nature* 344:531-534.

Received 15 May 2002

Accepted for publication 30 April 2003