CORAL GROWTH RATES REVISITED AFTER 31 YEARS: WHAT IS CAUSING LOWER EXTENSION RATES IN *ACROPORA PALMATA?*

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ABSTRACT

Linear extension of branches in the same *Acropora palmata* (Lamarck, 1816) population in Curaçao was measured, employing exactly the same methods, in 1971–1973 and in 2002–2004, and the resulting coral growth rates are compared. Linear growth shows the same pattern over seasons in both periods with growth being significantly higher in summer than in winter. Growth in the 2002–2004 time interval was significantly slower than in 1971–1973. Mean monthly growth ranged from 0.69 cm (winter) to 0.81 cm (summer) in 1971–1973 and from 0.62 cm (winter) to 0.75 cm (summer) in 2002–2004. This means that linear growth rates in 2002–2004 were 7.2% lower in summer and 10.7% lower in winter compared with 1971–1973. Considering possible causative environmental factors relating to these decreases in growth rate, we cannot preclude the possibility that a change in ocean pH could be responsible for the drop in extension rate.

Growth of reefs was of great importance in Charles Darwin's reef studies (Darwin, 1851). Biologists and geologists after him realized that growth, and variation in growth, of the coral organism are basic to the growth of reef structures. Coral growth rates are of interest because they are species-specific and they have been used as measures of condition, metabolic performance, or as measures of environmental impact (e.g., Bak, 1976, 1978; Buddemeier and Kinzie, 1976; Cortes and Risk, 1985; Guzman et al., 1994; Lirman, 2000). Of course, interest in coral growth has widened enormously and now includes all aspects of calcification and skeletal construction, and understanding coral growth is crucial to using corals as fine temporal scale paleoclimatic indicators (e.g., Barnes and Lough, 1993; Cohen et al., 2004; Maier et al., 2004; Kaandorp et al., 2005).

Today, with the realization that the marine environment of the earth is undergoing great physical and chemical, as well as ecological changes (e.g., Jackson et al., 2001; McClanahan et al., 2002; Hughes et al., 2003; Pandolfi et al., 2003; Birkeland, 2004; Hoegh-Guldberg et al., 2007), the rates of coral growth measured in the early last century could be of major importance if these rates can be appropriately compared to rates measured today. Attempts have been made using coral skeletal records, such as variation in banding characteristics, to study change in coral growth over the last century (e.g., Lough and Barnes, 1997; Bessat and Buiges, 2001; Müller et al., 2004), but the results of the different studies are not unequivocal. Alterations in chemical composition of coral skeletons over time may limit the possible interpretation of changes in skeletal density (Müller et al., 2004).

In situ measured growth rates of fast growing corals such as *Acropora* spp. (± 10 cm yr^{-1}, Tunnicliffe, 1983; Gladfelter, 1984) would be more likely to show change over time if, indeed, there is any. However, it is impossible to compare present day growth rates of *Acropora* to these or prior studies, such as Vaughan (1915) because, even if the location of the experimental corals was precisely known, the corals and the coral populations measured have disappeared, are changed, or possibly live in a changed

environment in terms of habitat characteristics. Also it may be difficult to reproduce precisely the same methodology in repeating the measurements.

From reefs in Curacao, we have *in situ* records of rates of coral growth from three decades ago. We measured *Acropora palmata* (Lamarck, 1816) linear extension rates of branches from 1971 to 1973 and we exactly repeated these measurements during 2002–2004. If there were any change in growth rates between 1971 and today, it would be most easily seen in a species such as *A. palmata* because growth rates of this species that are among the highest in the Caribbean (± 9 cm yr^{-1} in Curaçao, Bak, 1976).

In 2002, the population of *A. palmata* that we measured in 1971–1973 existed in the same place and appeared to be in excellent condition. There were no apparent signs of change in the environmental conditions on the reef. There were no signs of abnormalities such as white band disease or neoplasia on the corals (Bak and Criens, 1982a; Gladfelter, 1982; Bak, 1983). In repeating our measurements of 1971 on those corals we sampled the same *A. palmata* population because sexual recruits are rare in this species (Dustan, 1977; Bak and Engel, 1979; Rylaarsdam, 1983; Baums et al., 2005) and recruitment to an adult population is largely through fragmentation of colonies and subsequent growth of ramets, including fusion of ramets from different parent colonies (Bak and Criens, 1982b; Highsmith, 1982; Lirman, 2000).

We posed two simple questions in this study: (1) Was linear growth in the *A. palmata* population at CARMABI Buoy One as fast in 2002–2004 as it was in 1971–1973? And, (2) if growth was different, can it be explained?

Materials and Methods

The methodology used in 2002–2004, including the labeling of coral branches, the measurements, and use of human resources, was an exact replication of the procedures employed in 1971–1973 (Bak, 1976). The same *A. palmata* population, situated at depths of 2–3 m at CARMABI Buoy One (Curaçao), was used to measure linear growth of branches in each period. The length of branches was measured at each data point using calipers and a transparent ruler. The only manipulation of the *A. palmata* colonies was that a plastic band was fastened around a branch of a colony at a distance of 15 cm from the tip of the branch. The band served as a point of reference for the measurements of branch linear growth. In order to minimize the possible effect of fixing the band, this was done months in advance of the start of the growth measurements. Linear extension of individual branches was measured each month from Oct 1971 to March 1973. The recent period of measurements was November 2002 to September 2004, when colonies were measured every 4 mo. Temperature was measured by SCUBA divers using thermometers (1971–1973), and dive computers and SEAMON Mini temperature-loggers (2002–2004). *Acropora palmata* linear growth declines when branch tips degenerate and change color; the normally white branch tips darken to attain the brown color displayed by the general surface of the colony (Bak, 1976; Oliver, 1984). Such branches were not included in the analyses.

In the statistical analysis we compared the linear growth measurements obtained in winter (December to March) and summer (April to November) for 1971–1973 (n = 21 branches) and 2002–2004 (n = 49 branches). We used a linear mixed effect model using restricted maximum log-likelihood (REML) fitting to account for the repeated measurements (Pinheiro and Bates, 2000). We also needed to use a different variance structure for data from the two periods because samples from the period 2002–2004 showed more variation than samples from the earlier period (P = 0.045 when comparing the final model with and without the variance structure). The average variance factor for 2002–2004 was 1.21 with a 95% confidence limit

of 1.01–1.45 (relative to 1971–1973 which was set to one). We also checked for autocorrelation by plotting a variogram for the within-group residuals and by trying different correlation structures, but models including the error term correlation structure were not significantly better than the model without the error term (Pinheiro and Bates, 2000). The semi-variogram for the within-group residuals from the mixed model fit did not show any effect of time on the correlation between errors. Therefore we did not include a correlation structure in the model. Diagnostic plots showed no violations of assumptions. We also tested for an interaction between period and season, but this was far from significant (P = 0.7). For the analyses we used the statistical package R Development Core Team (2006).

Results

There was a significant difference in *A. palmata* growth rates between 1971–1973 and 2002–2004. Linear extension of *A. palmata* branches was significantly more rapid in 1971–1973 than 2002–2004 (Table 1) at both times of year measured. The pattern of growth remained the same, i.e., summer growth was significantly greater than winter growth, during both 1971–1973 and 2002–2004 (Fig. 1; Table 1). Mean monthly growth ranged from 0.69 cm (winter) to 0.81 cm (summer) in 1971–73 and from 0.62 cm (winter) to 0.75 cm (summer) in 2002–2004.

Discussion

The mean monthly growth rates would translate to a yearly branch extension of between 8.3 and 9.7 cm for 1971–1973, and a growth of between 7.4 and 9.0 cm year^{-1} for 2002–2004. Such rates are within the normal range for *A. palmata*, also found at other sites in the Caribbean e.g., 6.9 cm in Florida (Lirman, 2000) and 4.7–9.9 cm in St. Croix (Gladfelter et al., 1978). Differences in growth rate among locations will be induced by the variance in latitude, which means differences in water temperature and pCO_2 (Gledhill et al., 2008) and by differences in colony position on the reef. Gladfelter et al. (1978) found growth rates to differ between lagoon, and deep and shallow forereef. These authors found summer vs winter growth differences to vary from 0.3 to 3.5 cm, depending on colony position on the reef.

The differences we found in *A. palmata* growth rate in Curaçao, when repeating our measurements after 30 yrs, are obviously not caused by differences in colony position as measurements were made in exactly the same locality. The question then is: what is the causative factor behind the change? An obvious factor known to influence coral growth rate is temperature. Water temperature during both periods showed the normal temperature pattern over the year, varying from winter to summer be-

Table 1. Linear Mixed Effect Model for differences in branch growth of *Acropora palmata* in season (winter and summer) and period (1971–1973 and 2001–2004) in Curaçao. Coral branches were modeled as a random factor (n = 70).

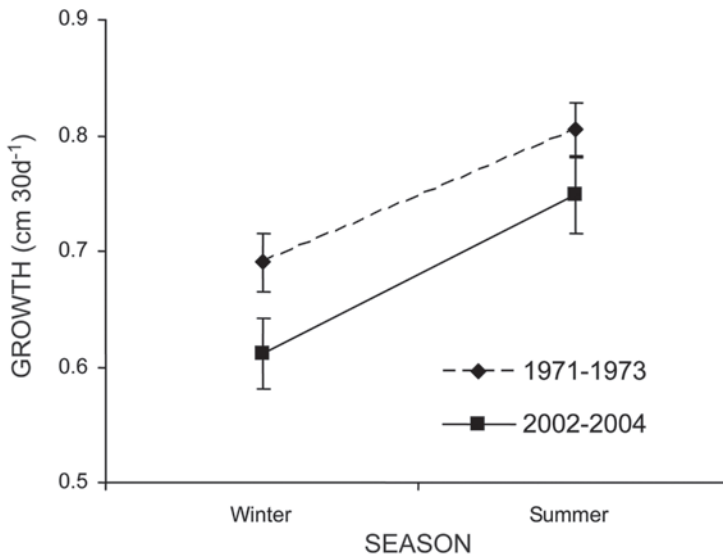| Fixed effects	Numerator df	Denominator df	F-value	P-value	
Period	2	68	335.451	< 0.0001	
Season	1	224	11.008	0.0011	
Coefficients	Value	Std Error	df	t-value	P-value
Years: 2002–2004	0.6475	0.03088	68	20.970	< 0.0001
Years: 1971–1973	0.7506	0.04296	68	17.473	< 0.0001
Season: winter	−0.0755	0.02277	224	−3.318	0.0011

Figure 1. *Acropora palmata*. Linear growth (mean ± SE) of branches in 1971–1973 and in 2002–2004 in Curaçao.

tween 25–29.5 °C. Offshore long-term sea surface temperature data (HadSST2 data, Rayner et al., 2006) indicate that the average temperature was 0.8 °C higher in 2002–2004 than in 1971–1973. Because the highest linear growth rates in 1971–1973 and 2002–2004 were measured during the season with the highest temperatures (summer) (Fig. 1), an increase in temperature cannot be responsible for the 2002–2004 reduction in linear growth. Higher growth rates of *A. palmata* in St. Croix were also associated with higher temperatures, up to 29.5 °C (Gladfelter et al., 1978).

Has there been a change in the physical environment? There has been no local coastal development at our study reef site. Up-current coastal development has been limited in the period between 1971 and 2004. The number of hotels has increased at a distance of ± 1.5 km from the reef, but nutrient levels (N, P) have not increased at our study reef compared with more remote, undisturbed reef environments in Curaçao (Gast et al., 1999; Scheffers et al., 2004). In June 1972, in the midst of the first years of our *A. palmata* growth measurements, the entrance to the up-current Piscadera Bay was dredged. This resulted in high turbidity over the reefs, which had a significant negative effect on coral calcification in coral species such as *Madracis mirabilis* Duchassaing and Michelotti, 1860 and *Agaricia agaricites* (Linnaeus, 1758) (Bak, 1978). This raises an interesting point: despite the indication of lowered calcification rates in some coral species for June/August 1972, *A. palmata* growth rate was high in the summer of 1972 compared to summer during 2002–2004. It is reasonable to assume that *A. palmata* may also have been negatively influenced by the high turbidity condition in 1972, and that, in absence of the dredging event, the difference in summer growth between 1971–1973 and 2002–2004 may have been even greater.

There are at least two possible explanations for the difference in growth rate between the 1971–1973 and 2002–2004 time intervals. The first is that this is simply normal variability in growth. It is unknown if such variation in growth rates occurs over years in *A. palmata*. We have no indication of variation in growth between consecutive years during each of our study periods. There was no significant dif-

ference in growth between the successive winters in each of the two time intervals (Two-Sample t-test: P = 0.12, P = 0.10, respectively) and within each period, there is a consistent difference between the winter and summer seasons.

There remains the possibility that a change in pCO_2 is responsible for the lower skeletal extension rates. Ocean acidification, the lowering of the pH of seawater (e.g., Kleypas et al., 1999; Bates et al., 2007), is expected to affect calcification in marine organisms, especially in organisms that construct aragonite skeletons such as corals (e.g., Marubini et al., 2001; Leclerq et al., 2002; Reynaud et al., 2003; Feely et al., 2004; Andersson et al., 2006; Schneider and Erez, 2006). Experimental studies demonstrate a decrease in coral calcification related to linear extension (Jokiel et al., 2008; Marubini et al., 2008). In a field study on the Great Barrier Reef, Cooper et al. (2008) studied calcification in massive *Porites* spp. They detected a reduction in linear extension rate of 1.02% yr^{-1}, resulting in a decrease in linear extension of 16% over the last 16 yrs. In our study, *A. palmata* growth rates in 2002–2004 were 7.2% lower in summer and 10.7% lower in winter compared to those in 1971–1973. Such a decrease would be considerable, even alarming, if related to ongoing ocean acidification. However, available data on lower aragonite saturation for the Greater Caribbean (Gledhill et al., 2008) do not include Curaçao.

Of course, our study has the strong and weak points of all field studies: the data are real world phenomena but explanations are necessarily based on correlative evidence. Nevertheless, field data are needed and we urge marine scientists to investigate if lower growth rates are found in molluscs, foraminifera, coralline algae, and other calcifying organisms.

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