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Skeletal Extension Rates of Cenozoic Caribbean Reef Corals

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There has been significant biological and environmental change in Caribbean coral reefs during the past 30 million years, including two periods of accelerated turnover of species in the zooxanthellate coral biota that may have been correlated with changes in regional sea-surface productivity during the Early Miocene and the Early Pleistocene. Skeletal extension rates measured on x-radiographs of 11 massive genera of fossil corals collected from Late Oligocene to Pleistocene units from across the Caribbean were analyzed to determine whether average coral growth responded to these regional environmental changes. The observed patterns were evaluated by comparisons with records of Recent coral growth rates taken from published literature. These analyses suggest that there is significant variation in average growth rate among corals living in the Recent Indo-west Pacific, eastern Pacific, and Caribbean, even when broad ranges of taxa and habitats are intermingled. When applied to fossils, a similar analysis suggests that rates of growth do not change overall through time. One exception is during the Late Miocene, when rates of growth were significantly lower than from other fossil units or for Recent colonies from the Caribbean. However, the Late Miocene colonies sampled for this study lived in relatively deep, turbid habitats, so the observed reduced growth rates may have resulted from local low availability of light. Similar facies were not sampled in other stratigraphic intervals, so there is no strong evidence for reduced regional average growth rates for Caribbean corals during the past 30 million years.

INTRODUCTION

During the past 30 million years, there were two major ecological transitions in the zooxanthellate coral fauna of the Caribbean—one associated with the Oligocene/Miocene boundary, and the other approximately coinciding with the Pliocene/Pleistocene boundary. Both transitions resulted in taxonomic turnover in the Caribbean coral fauna (Frost, 1977; Budd et al., 1994, 1996; Budd, 2000), and strongly altered the ecological context of the regional reef-coral fauna. The Oligocene reef biota constructed the most extensive set of reef complexes ever developed in the region (Frost, 1977), but Miocene and Pliocene reef tracts were likely to be smaller, and zooxanthellate coral communities more often lived on carbonate platforms or siliciclastic-dominated settings with poorly defined zonation (Vaughan, 1919; Budd et al., 1989; Johnson et al., 1995; Johnson, 2001; Klaus and Budd, 2003; Johnson and Kirby, 2006). Reef building recovered during the Pleistocene, as seen by the extensive development of late Pleistocene and Holocene reef tracts in the modern Caribbean (Spalding et al., 2001).

Both the Oligocene/Miocene and the Pliocene/Pleistocene transitions are associated with regional changes in ocean-surface productivity (Edinger and Risk, 1995; Jackson and Johnson, 2000; Allmon, 2001). Abundant evidence suggests that regional planktonic productivity increased from Late Oligocene to Middle Miocene time (Edinger and Risk, 1994, 1995; Curry et al., 1995; Mutti, 1999), and that productivity later declined during the Pliocene/Pleistocene (Vermeij and Petuch, 1986; Allmon et al., 1996; Collins, 1996; Todd et al., 2002).

Regional differences between Miocene and Quaternary environments in the Caribbean might be similar to modern differences between the Caribbean and eastern Pacific regions. Much of the coastal eastern Pacific is characterized by seasonal upwelling of cold, nutrient-rich water, which has obvious consequences for the coral fauna of the region (Glynn, 1976). Can the modern eastern Pacific be used as a model for the Caribbean in the Miocene? This question is especially relevant in that many of the genera that dominate modern reefs in the eastern Pacific became extinct in the Caribbean during the late Neogene (Budd et al., 1994).

The observed temporal pattern of reef-building likely is correlated with variation in planktonic productivity in the Caribbean region. Coral reefs are dynamic systems defined by the in-place accumulation of wave-resistant carbonates produced by biological processes (Hubbard, 1997). The persistence of reef structure depends on the relative rate of carbonate-sediment production and the removal of carbonate from the system through physical and biological processes. The relative abundance of reef constructors and reef eroders tends to be controlled by similar environmental factors, but, in general, conditions that are favorable for reef constructors are detrimental to bioeroders (Glynn, 1997). On most tropical reefs, the primary producers of calcium carbonate are autotrophic or mixotrophic, but most bioeroders are heterotrophic. Therefore, environmental conditions that are favorable for heterotrophy, such as increased planktonic productivity, will promote erosion relative to construction (Hallock and Schlager, 1986). If the scarcity of major reef buildups during the Miocene and Pliocene was caused by increased regional surface productivity, evidence for increased bioerosion and reduced coral growth might be expected (Edinger and Risk, 1994; Edinger et al., 2000). The purpose of this work is to determine whether average regional coral growth was reduced during the Miocene and Pliocene by studying

TABLE 1—Number of colonies processed and number of density-band couplets measured from each stratigraphic unit. Collections from the Pleistocene terraces of Curacao and the southern Dominican Republic are grouped in this table. Geographic regions also are shown in Fig. 1; codes for the regions are A = Antigua, C = Curacao, CR = Costa Rica, DR = Dominican Republic, J = Jamaica, P = Panama, and PR = Puerto Rico. Brief summaries of the dominant lithologies and depositional environments for each unit are given in Appendix 1, reposited online at <http://www.sepm.org/archive/index.html>.

Stratigraphic unit	Age	Region	Number of colonies processed	Colonies with preserved couplets	Number of couplets measured
Pleistocene Terrace	Pleistocene	DR	2	1	8
Falmouth Formation	Pleistocene	J	4	0	0
Middle Terrace	Pleistocene	C	3	1	3
Seroe Domi Formation	Pliocene	C	18	2	11
Mao Formation	Pliocene	DR	4	3	15
Moin Formation	Pliocene	CR	12	2	10
Cercado Formation	Late Miocene	DR	11	9	73
Gurabo Formation	Late Miocene	DR	10	2	10
Valiente Formation	Middle Miocene	P	2	0	0
Baitoa Formation	Early/Middle Miocene	DR	2	2	7
Culebra Formation	Early Miocene	P	6	0	0
Antigua Formation	Late Oligocene	A	41	5	16
Moneague Formation	Late Oligocene	J	4	1	12
Montebello Member	Late Oligocene	PR	10	1	3
Newport Formation	Late Oligocene	J	3	0	0
Juana Diaz Formation	Late Oligocene	PR	14	1	2
Lares Formation	Late Oligocene	PR	39	3	8
Total			185	33	178

average rates of growth on ancient Caribbean corals through examination of skeletal density on x-radiographs.

METHODS

Rates of skeletal extension in zooxanthellate corals are controlled by a combination of environmental and biological factors. External environmental factors are not independent of one another, and include light availability, temperature, and water quality (Lough and Barnes, 2000). Relatively small changes in these parameters can have large effects on coral extension rates, which, by extrapolation to a larger scale, should have an effect on overall reef size and development. Therefore, a broad-scale approach involving 11 genera of massive reef corals from a range of reef environments has been adopted to study regional controls on average coral growth. Colonies from a wide range of habitats from multiple stratigraphic units have been analyzed to explore the changing regional pattern of coral growth during the past 30 million years. Obviously, this approach has limited power to resolve small differences caused by minor local variations in water depth or turbidity that cannot be detected in the fossil record. In addition, a similar broad-scale analysis was performed on a literature-based dataset to examine regional variation in skeletal extension rates on Recent reefs to determine the sensitivity of the broad approach applied to the fossils.

FIGURE 1—Sketch map of the Caribbean Region showing the geographic distribution of stratigraphic units from which fossil coral skeletons were collected.

To study colony growth rates on ancient reefs, 185 colonies were selected from 18 stratigraphic units located in Antigua, Costa Rica, Curacao, the Dominican Republic, Jamaica, Panama, and Puerto Rico (Table 1; Fig. 1). Brief summaries of the general lithology and depositional environments for each unit are provided in Appendix 1, and a complete list of samples and measurements is included as part of the online SEPM data archive, located at <http://www.sepm.org/archive/index.html>. Collections were obtained from the Department of Invertebrate Paleontology at the Natural History Museum of Los Angeles County (LACMIP), the Paleontological Repository of the University of Iowa (SUI), and the Natural History Museum-Basel (NMB). More information is available on the LACMIP database (Johnson et al., 2005), the NMITA website (Budd et al., 2004), and the database of the Panama Paleontology Project (Collins and Coates, 1999).

Age determinations for each of these units were not well resolved, so collections were grouped into five large-scale time intervals for comparison using the timescale of Berggren et al. (1995). These include Late Oligocene, Early–Middle Miocene, Late Miocene, Pliocene, and Quaternary. Each specimen was identified to species using the taxo-

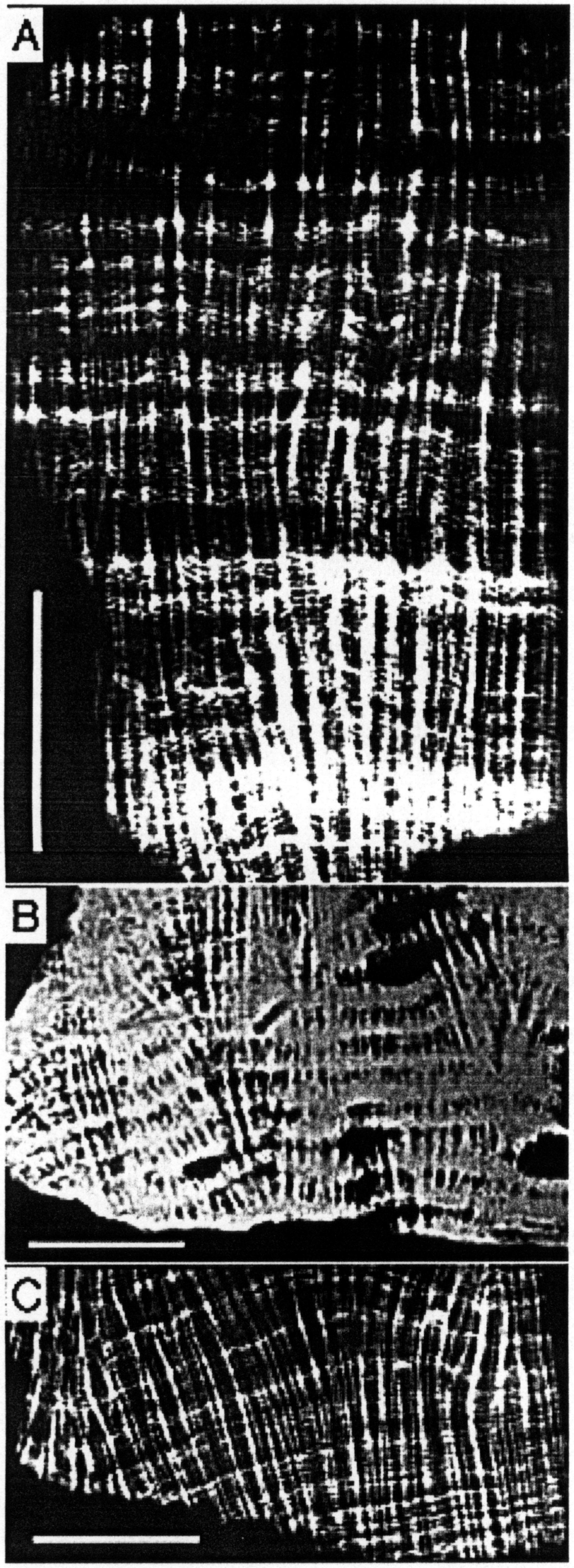

FIGURE 2—X-radiographs of fossil corals illustrating skeletal-density banding; scale=2 cm. Repository abbreviations: NMB=Naturhistorisches Museum Basel; LACMIP=Department of Invertebrate Paleontology, Natural History Museum of Los Angeles County; SUI=Paleontological Repository of the University of Iowa. (A) *Montastraea limbata* (Duncan, 1863), specimen NMB D5593, locality NMB 15822, Mao Formation, Lower Pliocene, Dominican Republic. (B) *Porites* sp. Link, 1807, specimen LACMIP TYPE 8218, locality LACMIP 17693, Moneague Formation, Upper Oligocene, Brown's Town Jamaica. (C) *Montastraea limbata*, specimen SUI 102507, locality Bel-1 of Klaus and Budd (2003), Upper Miocene Cercado Formation, Dominican Republic.

study of skeletal-density banding on x-radiographs. For this meta-analysis, median growth rate was recorded for coral genera living at one site or reef. The geographic locality, habitat, and water depth also were recorded, if such information was available. Although species identifications were usually available, information was compiled for genera to avoid taxonomic discrepancies and to facilitate inter-regional comparisons. If multiple measurements were provided for a particular genus at one locality, medians were calculated as an average value of coral growth for that locality. The compilation is available for download from the SEPM data archive, http://www.sepm.org/archive/index.html.

RESULTS

Density-band couplets (n=178) were measured on 33 of the 185 studied colonies, with an average yield of 18% (Table 1). Average yield for Upper Miocene and Pliocene collections was relatively high, so that 18 of the 55 processed colonies (33%) produced usable data. Yield for Lower to Middle Miocene collections was lower, and density-band couplets were measured on only two colonies from the Lower to Middle Miocene units (20%). Upper Oligocene material was, in general, not well preserved. Only 11 of 111 (10%) colonies tested were used in the analysis. The best material was obtained through exceptional preservation of colonies in the Upper Miocene Gurabo Formation in Arroyo Bellaco (Klaus and Budd, 2003). Density banding is well preserved on many colonies (Fig. 2), although the variation in skeletal structure responsible for density variation is not always evident (Barnes et al., 1989; Le Tissier et al., 1994). For these *Montastraea* species, variation in skeletal density appears to be related to differences in the spacing of dissepiments and, perhaps, to slight thickening of the wall and other vertical elements.

For the fossil data, there is significant difference in growth rate among colonies collected from differing stratigraphic intervals (Kruskal-Wallis chi-square=88.3, 4 df, $p<0.001$). Multiple comparison tests suggest that growth rates were lower in the Late Miocene than in the other intervals (Table 3). Median growth rate for Late Oligocene is 6.6 mm/year, but declines to 3.8 mm/year in the Late Miocene. In addition, average growth rates were higher during the Pleistocene than growth rates estimated from Oligocene to Pliocene samples. Mean extension rate of 9.1 mm/year was calculated for the Pleistocene colonies. Three outliers observed from the Pliocene interval correspond to a columnar colony of *Montastraea limbata* (Duncan, 1863) collected from the Mao Formation in the Early Pliocene of the Dominican Republic (locality NMB 16884). Columnar growth results from rapid linear extension along the main axis of coral colonies. Removing this fast-growing colony from the analysis did not alter the result

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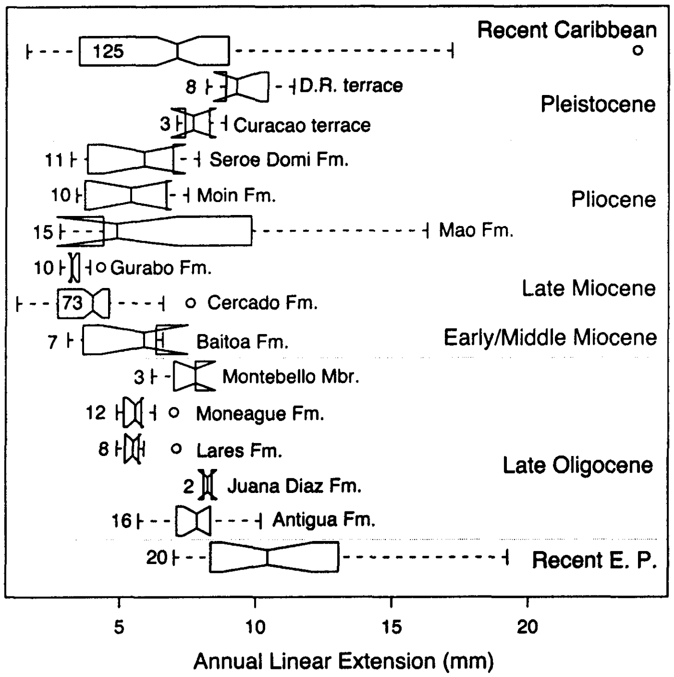

FIGURE 4—The distribution of linear skeletal extension rates of modern and ancient corals grouped by age and stratigraphic unit. As in Figure 3, the combined distribution of growth rates on Recent Caribbean reefs is shown near the top of the figure, and the distribution of growth rates of colonies from Recent eastern Pacific sites is shown near the base of the figure. Sample sizes are indicated for each box.

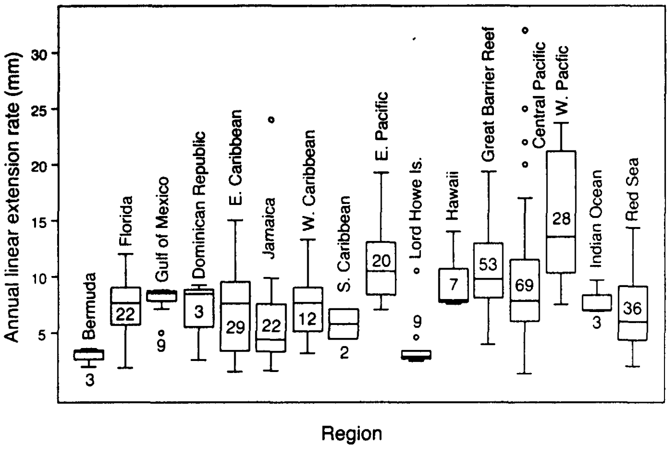

FIGURE 5—Box-and-whisker plots showing the distribution of average linear extension rates of massive corals on Recent reefs. The distributions were drawn from a compilation of growth rates from the published literature, including 68 reef sites from all reef-growing regions of the world. Reef sites were grouped into 16 regions to explore broad-scale patterns in average regional coral growth rate. For each box-and-whisker plot, the box is drawn from the approximate first and third quartile of the distribution; the median also is shown; whiskers extend out from the box to the most extreme data point that is no more than 1.5 times the length of the box away from the box. Circles beyond the whiskers indicate extreme values. The number of colonies summarized by each box is shown.

tic and Pacific, so that average rates measured for corals in the high-latitude reefs of Bermuda and Lord Howe Island (Logan and Tomascik, 1991; Harriott, 1999) can be an order of magnitude lower than rates reported from the tropical Caribbean or Indo-Pacific. Excluding these reefs, corals growing on reefs in the Pacific Ocean have higher extension rates than corals living in the Atlantic (Kruskal-Wallis chi-square=33.5, 1 df, $p<0.001$). The highest average extension rates occur in the western Pacific coral triangle (Roberts et al., 2002), including data compiled here from studies in Thailand, the Philippines, Indonesia, and Melanesia. This region is characterized by the global center of diversity of zooxanthellate corals and other reef organisms, with extensive reef development (Spalding et al., 2001). The surface of the ocean in this region also is characterized by being the warmest on Earth, with temperatures consistently above 28°C (Yan et al., 1992).

Comparison of growth rates from the fossil collection with growth rates compiled from the literature on Recent corals shows some interesting patterns (Fig. 3). There is significant variation among growth rates for fossils, Recent Caribbean, and Recent eastern Pacific corals (Kruskal-Wallis chi-square=50.2, 2 df, $p<0.001$). Estimates of median growth are significantly higher on reefs in the eastern Pacific (10.45 mm/year) than on Recent Caribbean reefs (7.5 mm/year; Table 3). Median extension rates on Recent eastern Pacific reefs also are higher than rates estimated from all pre-Pleistocene intervals. In contrast, growth rates on Recent Caribbean reefs are significantly lower than rates estimated from Pleistocene samples and significantly greater than estimates from Late Miocene samples (Table 3).

In summary, there is significant variation among genera and formations. Overall, regional average growth rates were significantly lower in the Late Miocene than rates estimated from the other time intervals or compiled from the literature concerning Recent reefs in the Caribbean. Growth rates were higher in the Pleistocene than other stratigraphic intervals, and growth rates in the Recent eastern Pacific are higher than ancient or modern rates of growth in the Caribbean.

DISCUSSION

Although the analyses presented here are necessarily coarse scaled, the analysis of regional variation in growth rate among Recent corals suggests that the approach is valid. On the other hand, there are potential sources for error that could not be considered in this study of fossil coral skeletons. For example, density-band couplets might not always represent a true annual signal, both because of the likely presence of sub-annual bands or due to lacunae caused by lack of growth over a long period (Buddemeier and Kinzie, 1975). For living corals, study of seasonal variation in stable isotopic composition can be used to confirm that well-defined density-band couplets approximate an annual signal (e.g., Dunbar et al., 1994), but a similar geochemical study usually is not possible for pre-Quaternary fossils because the aragonitic skeletons of scleractinians inevitably are altered during diagenesis.

On living reefs, there is significant variation in linear extension rate among coral taxa. However, besides limiting the samples to taxa characterized by massive colony form, it was not possible to control for taxonomic variation in growth rates adequately. The reef-coral fauna of the Caribbean has been influenced strongly by at least two episodes of rapid taxonomic turnover (Budd, 2000; Jackson

However, this study only concerns coral taxa with massive colony forms, and more intensive sampling with more precise environmental control is required to fully document the relationship between atmospheric carbon dioxide and calcification. Additional studies of Paleogene reef coral and coral-reef facies might be a fruitful approach.

CONCLUSIONS

(1) Linear skeletal extension rates can be obtained from fossil corals using standard sclero-chronological methods. Analysis of similar data from Recent corals suggests that this approach provides useful proxy data to assess past near-shore oceanographic conditions from the Cenozoic of the Caribbean.

(2) Analysis of fossils suggests that average growth rates of zooxanthellate corals were lower in the Late Miocene than in the Late Oligocene, Pliocene, or Quaternary, but this pattern is most likely a result of unbalanced sampling of slow-growing colonies from siliciclastic facies deposited in deep water as represented by the Cercado and Gurabo formations of the Dominican Republic.

(3) Recent eastern Pacific corals grow more quickly than either living Caribbean or ancient Caribbean corals, suggesting that paleoenvironments of the Caribbean were never similar to the Recent eastern Pacific.

(4) Although sea-surface productivity may have increased during the Miocene, levels did not reach concentrations sufficient to inhibit coral growth. Similarly, as levels of atmospheric carbon dioxide decreased through the Neogene, there was no significant reduction of average regional skeletal extension rate.

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