SKELETAL EXTENSION, DENSITY AND CALCIFICATION RATE OF THE REEF BUILDING CORAL *MONTASTRAEA ANNULARIS* (ELLIS AND SOLANDER) IN THE MEXICAN CARIBBEAN

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ABSTRACT

Growth parameters (skeletal extension, density, and calcification rate) were determined using annual growth bands along 12 slabs of skeletons of the reef building coral *Montastraea annularis*, collected at 1.5 m depth in Puerto Morelos and at 10 m depth in Xahuayxol, in the Mexican Caribbean. X-radiography contact prints revealed that the high-density annual growth band is formed during summer, possibly between July and September, when the sea water temperatures are highest in the Mexican Caribbean. Skeletal extension, density and calcification rates obtained were within the range of values presented by other authors for *M. annularis* in different reefs distributed throughout the Atlantic Ocean. Only slight trends could be identified for the time span represented by the slabs (1980–1995) for the three parameters, suggesting that the environmental conditions have been quite similar for the past 1.5 decades. Using the available environmental data, it seems that, at least, water temperatures have been similar for the period of time studied in the two reef zones. In addition, the observed relationships among the growth parameters were similar to those previously described by other authors. An alternative to the more expensive density measurement procedures is described and discussed.

Since the discovery of the annual density banding of massive coral skeletons by Knutson et al. (1972), the bands have proved to hold useful information about coral growth and coral growth histories (Hudson, 1981; Dodge and Brass, 1984; Guzmán and Cortés, 1989; Carricart-Ganivet et al., 1994), and also about the environmental conditions under which the growth took place (Dodge and Vaisnys, 1975; Flor and Moore, 1977; Dodge et al., 1984; Tomascik and Sander, 1985). At the annual scale, coral skeletal growth can be described by three different variables: extension, density, and calcification of the deposited skeleton. Previous work (Dodge and Brass, 1984) has shown that these variables are not redundant and contain complementary information. Statistical relationships between them have also been found and discussed (Dodge and Brass, 1984; Scoffin et al., 1992).

Along the east coast of the Yucatán Peninsula, in the Mexican Caribbean, there is an extensive reef formation. Jordán (1979) and Jordán et al. (1981) have described these inshore reefs, but there has been no research on coral growth for this zone of the Caribbean. The aim of this paper is to add information regarding skeletal extension, density and calcification rate to the data bank on coral growth of the dominant Caribbean reef building coral *Montastraea annularis* (Ellis and Solander, 1786) sensu Weil and Knowlton (1994), in two zones of the Mexican Caribbean, to widen our range of observations of this kind and to increase our understanding of coral growth.

Material and Methods

Several specimens, each at least 10 cm high, of the hermatypic coral *M. annularis* were collected in two reef zones of the Mexican Caribbean (Fig. 1). The specimens from Puerto Morelos were

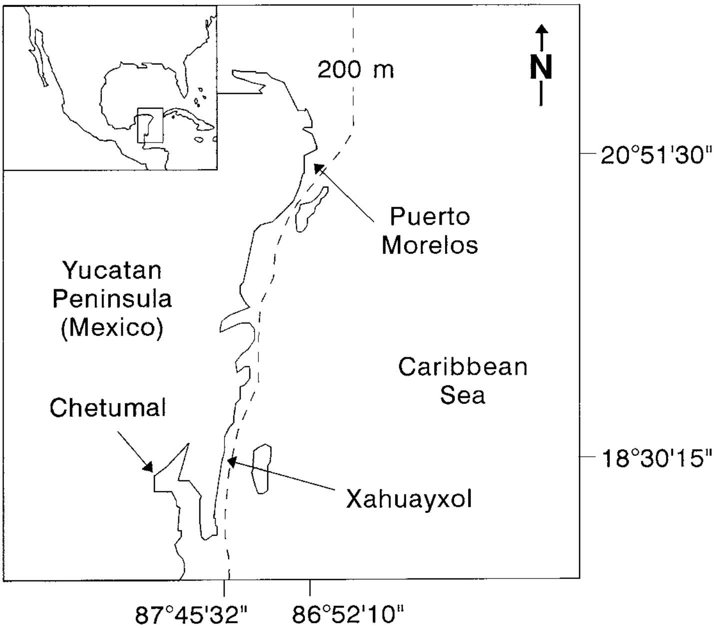

Figure 1. Location of the sampled reef sites in the Mexican Caribbean.

collected on May 1995, in the reef lagoon at 1.5 m depth, and those from Xahuayxol were collected on October 1996, from the fore-reef at 10 m depth.

Skeletal extension (cm) was measured by conventional X-radiograph technique (Knutson et al., 1972; Baker and Weber, 1975; Hudson, 1981). Following the main growth axis, slabs were cut to a width of 0.5 ± 0.1 cm with a rock saw (4 mm kerf). Slabs were then exposed to X-rays from CGR equipment (Trendix 525) with the following conditions of exposure: 43 kv, 5 MAS, 50 MA, 0.10 s, and 100 cm of focal distance; in all cases a Cassette Kodak 14 × 17 in, Lanex Fast X-Omatic was used. As suggested by Guillaume (1994), X-radiographs were selected that showed the highest contrast and the most exact reproduction of internal variations in density. Annual bands were identified from mid-summer to next mid-summer (Hudson et al., 1976), and measurements were made along the main axis of skeleton growth with a caliper and a stereoscopic microscope (0.1 mm precision) using the b/w contact prints of the X-radiographs (Carricart-Ganivet et al., 1994).

To measure density (g cm^{-3}), each annual growth band (0.44–1.54 cm wide) was cut off from the slab along the mid-summer edge of the high-density annual growth band (Hudson et al., 1976). To ensure exact cutting of the annual band, the mid-summer line was traced from the b/w contact prints of the X-radiograph onto the slab using translucent drawing paper. To cut the band, we used a low-speed motor and a disk saw with a kerf of only 0.6 mm (Dentorium Item # 223) to minimize material loss. Density was measured on growth-band fragments of variable width (0.3–0.7 cm) and weight (0.2–0.5 g). To make triplicate determinations of density, three of these fragments were taken from the same section of each band where skeletal extension was measured. Each fragment was submerged in distilled water for 24 h, to ensure complete water infiltration of all skeletal interstices, then frozen while still submerged. Excess exterior ice was removed with a scalpel, with excision of part of the skeleton fragment when needed to ensure complete removal of exterior ice. Before it thawed, each fragment was weighed on a 0.001 g precision balance (Mettler, AE163). Each fragment was then dried for 48 h in an oven at 80°C before being weighed again. Density of each annual growth band was calculated using the following formula:

$$d_b = W_d / ((W_d / d_{ar}) + ((W_f - W_d) / d_{ice}))$$

where d_b is the density of the annual growth band (g cm^{-3}); W_d is the dry weight of fragment (g); d_{ar} is the density of aragonite, 2.93 g cm^{-3} (Liley and Gambill, 1986); W_f is the frozen weight of fragment (g) and d_{ice} is the density of ice, 0.915 g cm^{-3} (Liley and Gambill, 1986).

To verify the precision of this method, ten replicate measurements of density were made on 20 coral fragments of different densities (1.17–2.17 g cm^{-3}). The variation coefficient for each set of measurements ranged between 0.18 and 0.56%, and averaged 0.3%.

The annual calcification rates (gcm^{-2} yr^{-1}) were calculated by multiplying the density value of each annual growth band by its corresponding skeletal extension. For each reef, and for the two reefs together, temporal variations in the three growth parameters were analyzed by one-way ANOVA with Tukey's HSD (Zar, 1984). Relationships among the three variables were assessed by correlation analysis, and index values and index master chronologies were computed (Tomascik, 1990) for the three variables.

Results and Discussion

Contact prints with clear, unambiguous banding, of 12 specimens were obtained: five from Puerto Morelos, and seven from Xahuayxol. The contact prints of the specimens collected in Puerto Morelos (May) showed their low-density annual growth band in their apex (Fig. 2A), while those collected in Xahuayxol (October) showed their high-density annual growth band in their apex (Fig. 2B). From this observation, we conclude that *M. annularis* develops its high-density annual growth band some time between May and October in the Mexican Caribbean.

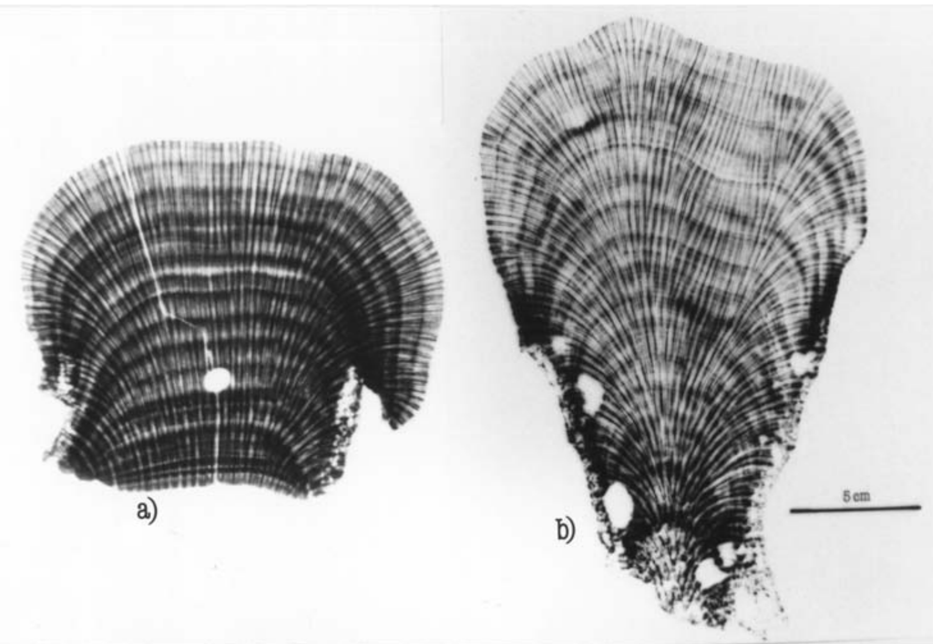

Figure 2. X-radiograph positives of *Montastraea annularis* from a) Puerto Morelos and b) Xahuayxol.

Table 1. Skeletal extension (cm) of *Montastraea annularis* in the Mexican Caribbean.

Reef	Years															
	95	94	93	92	91	90	89	88	87	86	85	84	83	82	81	80
PM		0.91	0.84	0.75	0.84	0.70	0.62	0.98	0.78	0.98	0.94	**0.55**	0.64	0.62	0.58	0.73
PM		0.99	0.86	0.77	0.75	0.75	0.87	0.71	0.81	0.86	0.67	0.82	0.75	0.81	1.00	0.90
PM		0.80	0.93	0.71	1.02	0.48	0.85	0.67	0.88	0.75						
PM		0.90	1.01	0.97	0.82	0.71	0.73	0.76	0.83							
PM		0.91	**1.20**	0.92	0.99	1.01	0.68	0.77	0.85							
Mean		0.90	**0.97**	0.82	0.88	0.73	0.75	0.78	0.83	0.86	0.81	**0.69**	0.70	0.72	0.79	0.82
Mean skeletal extension in Puerto Morelos = **0.82**																
XH	0.92	1.09	**1.54**	1.07	0.96	1.25	1.07	1.11	0.99	1.33	0.99	1.19	1.00	0.91	0.90	
XH	0.95	0.87	0.93	0.97	1.06	0.75	1.05	1.08	0.84	1.00	0.89	0.84				
XH	0.70	0.88	1.02	0.85	0.85	0.75	0.87	0.73	0.83	0.70						
XH	0.99	0.76	0.82	0.87	0.72	0.82	0.65	0.60	0.66	0.70						
XH	1.05	1.14	0.84	0.92	0.90	0.80	0.73	0.83	1.00	0.84						
XH	0.89	0.89	1.04	0.95	0.94	0.73	1.01	1.08								
XH	0.80	0.95	0.73	0.70	0.75											
Mean	0.90	0.94	0.99	0.90	0.88	**0.85**	0.90	0.91	0.86	0.91	0.94	**1.02**				
Mean skeletal extension in Xahuayxol = **0.91**																
Mean skeletal extension per year for the two reefs																
	0.90	0.92	**0.98**	0.87	0.88	0.80	0.83	0.85	0.85	0.90	0.87	0.85	0.80	**0.78**	0.83	0.82
Mean skeletal extension for the two reefs = **0.87**																

PM = Puerto Morelos; XH = Xahuayxol; minimal and maximal values in bold

Hudson et al. (1976) reported that *M. annularis* forms its high-density annual growth band between July and September in Florida correlated with higher temperatures. Carricart-Ganivet et al. (1994) found that this species also forms this sub-annual band between these months in reefs of the southern Gulf of Mexico, when the sea water temperatures are higher (Hernández-Téllez et al., 1993; Sánchez-Juárez and Aldeco, 1995). Seawater temperatures at the reef lagoon of Puerto Morelos also are higher between July and September (unpubl. data: from 1982 to 1983, M.M; from 1992 to 1997, F.G. Ruiz-Rentería). So, it is possible that the “coral-year” of *M. annularis* also begins in July in the Mexican Caribbean, in agreement with Hudson et al.’s (1976) report.

The intra-annual regulation for the formation of the sub-annuals bands is not clear at this moment. Suggested factors are: sea water temperature (Highsmith, 1979; Hudson et al., 1976), available sunlight level (sunshine or cloud cover) (Buddemeier, 1974), a combination of both water temperature and light level (Schneider and Smith, 1982; Heiss et al., 1993), rainfall (Buddemeier, 1974; Buddemeier et al., 1974), suspended particulate matter (Dodge et al., 1974; Cortés and Risk, 1985; Tomascik and Sanders, 1985), sedimentation rate (Brown et al., 1986), and a combination of salinity (precipitation), available light (cloud cover, turbidity) and time of reproduction (Guzmán and Cortés, 1989).

Values of skeletal extension, density and calcification rate were obtained from 125 annual growth bands (Tables 1,2,3, respectively). The number of annual growth bands averaged 10.4 per specimen, and ranged from 5 to 15 yrs in the 12 specimens. In Puerto Morelos the average was 11 annual growth bands per specimen, ranging from 8 to 15 yrs, and in Xahuayxol it was 10 annual growth bands per specimen, ranging from 5 to 15 yrs.

Table 2. Density (gcm^{-3}) of *Montastraea annularis* in the Mexican Caribbean.

Reef	Years															
	95	94	93	92	91	90	89	88	87	86	85	84	83	82	81	80
PM		1.72	1.87	2.07	2.03	1.94	1.47	1.66	1.59	1.36	**1.32**	**2.10**	1.84	2.03	1.92	1.76
PM		1.55	1.77	1.57	1.66	1.47	1.67	1.72	1.63	1.71	1.56	1.59	1.72	1.67	1.83	2.01
PM		1.84	2.00	2.04	2.06	1.99	2.00	2.03	2.07	1.79						
PM		1.85	1.89	1.72	1.59	2.00	2.05	1.82	1.89							
PM		1.66	1.95	1.92	1.59	1.70	1.89	1.47	1.82							
Mean		1.72	**1.90**	1.86	1.79	1.82	1.82	1.74	1.80	1.62	**1.44**	1.85	1.78	1.85	1.88	1.89
Mean density in Puerto Morelos = **1.79**																
XH	1.56	1.58	1.82	1.58	1.88	1.68	1.60	1.72	1.44	1.55	1.58	1.54	1.52	1.56	1.77	
XH	1.48	1.41	1.59	1.56	1.53	1.40	1.60	1.44	1.46	1.53	1.58	1.50				
XH	1.80	1.57	1.78	1.84	2.00	1.95	1.57	1.81	1.86	**2.08**						
XH	2.05	1.75	1.97	2.04	1.96	1.93	1.94	1.95	1.79	1.71						
XH	1.78	1.75	1.76	1.85	1.67	1.86	1.79	1.86	1.87	1.84						
XH	1.66	1.59	1.34	1.69	1.65	1.55	1.38	**1.30**								
XH	1.87	1.64	1.74	1.73	1.57											
Mean	1.74	1.61	1.71	**1.76**	1.75	1.73	1.65	1.68	1.68	1.74	1.58	**1.52**				
Mean density in Xahuayxol = **1.69**																
Mean density per year for the two reefs																
	1.74	1.66	1.79	1.80	1.77	1.77	1.72	1.71	1.74	1.70	**1.51**	1.68	1.69	1.75	1.84	**1.89**
Mean density for the two reefs = **1.74**																

PM = Puerto Morelos; XH = Xahuayxol; minimal and maximal values in bold

Table 3. Calcification rate (gcm^{-2}/yr) of *Montastraea annularis* in the Mexican Caribbean. PM = Puerto Morelos; XH = Xahuayxol; minimal and maximal values in bold.

Reef	Years															
	95	94	93	92	91	90	89	88	87	86	85	84	83	82	81	80
PM		1.56	1.57	1.56	1.71	1.36	0.91	1.62	1.24	1.32	1.24	1.15	1.18	1.26	1.11	1.28
PM		1.54	1.52	1.21	1.25	1.10	1.45	1.22	1.32	1.47	1.05	1.30	1.29	1.35	1.83	1.81
PM		1.47	1.86	1.45	2.10	0.95	1.70	1.36	1.82	1.35						
PM		1.66	1.91	1.67	1.31	1.42	1.50	1.38	1.57							
PM		1.51	**2.34**	1.77	1.57	1.72	1.28	1.13	1.54							
Mean		1.55	**1.84**	1.53	1.59	1.31	1.37	1.34	1.50	1.38	**1.15**	1.23	1.24	1.31	1.47	1.55
Mean calcification rate in Puerto Morelos = **1.46**																
XH	1.43	1.72	**2.80**	1.69	1.81	2.10	1.71	1.91	1.43	2.07	1.56	1.83	1.52	1.42	1.59	
XH	1.40	1.22	1.48	1.51	1.62	**1.05**	1.68	1.56	1.23	1.53	1.41	1.26				
XH	1.26	1.38	1.81	1.56	1.70	1.46	1.36	1.32	1.54	1.45						
XH	2.03	1.33	1.62	1.77	1.41	1.58	1.26	1.17	1.18	1.20						
XH	1.87	1.99	1.47	1.70	1.51	1.49	1.31	1.55	1.87	1.54						
XH	1.47	1.41	1.40	1.60	1.55	1.13	1.40	1.41								
XH	1.49	1.56	1.27	1.21	1.18											
Mean	1.56	1.52	**1.69**	1.58	1.54	1.47	**1.45**	1.49	**1.45**	1.56	1.49	1.55				
Mean calcification rate in Xahuayxol = **1.53**																
Mean density per year for the two reefs																
	1.56	1.53	**1.75**	1.56	1.56	1.40	1.41	1.42	1.47	1.49	**1.32**	1.39	1.33	1.34	1.51	1.55
Mean calcification rate for the two reefs = **1.50**																

PM = Puerto Morelos; XH = Xahuayxol; minimal and maximal values in bold

Table 4. Skeletal extension (cm), density (gcm^{-3}) and calcification rate (gcm^{-2}/yr) of *Montastraea annularis* in several localities of the Atlantic. Minimum and maximum values for the variables are included in parenthesis. * = calculated values with skeletal extension and density means.

Author	Location	Depth (m)	n	Extension	Density	Calcification rate
Baker & Weber, 1975	St. Croix, Virgin Islands	4.5–18	60	0.91 (0.65–1.04)	1.73 (1.60–1.82)	1.57 (1.18–1.76)
Dustan, 1975	Discovery Bay, Jamaica	8–24	–	0.38 (0.17–0.67)	1.71 (1.39–1.94)	0.65*
Graus & Macintyre, 1982	Carrie Bow Cay, Belize	1–25	–	0.76 (0.63–0.93)	1.80 (1.55–1.99)	1.35*
Dodge & Brass, 1984	Buck Island, St. Croix, Virgin Islands	3–8	607	0.98 (0.61–1.44)	1.28 (0.78–1.63)	1.23 (0.77–1.58)
Here in	Mexican Caribbean	1.5–10	125	0.87 (0.55–1.54)	1.74 (1.30–2.10)	1.50 (0.91–2.80)

The values of skeletal extension, density and calcification rate reported here are within the range of values presented by other authors for *M. annularis* in reefs distributed throughout the Atlantic Ocean (Table 4). The range of values observed could be explained mostly in terms of the different environmental conditions involved, which represent most of the tolerance range of the species. Earlier reports on coral growth of *M. annularis* did not consider that this species has more recently been determined to be a complex of sibling species

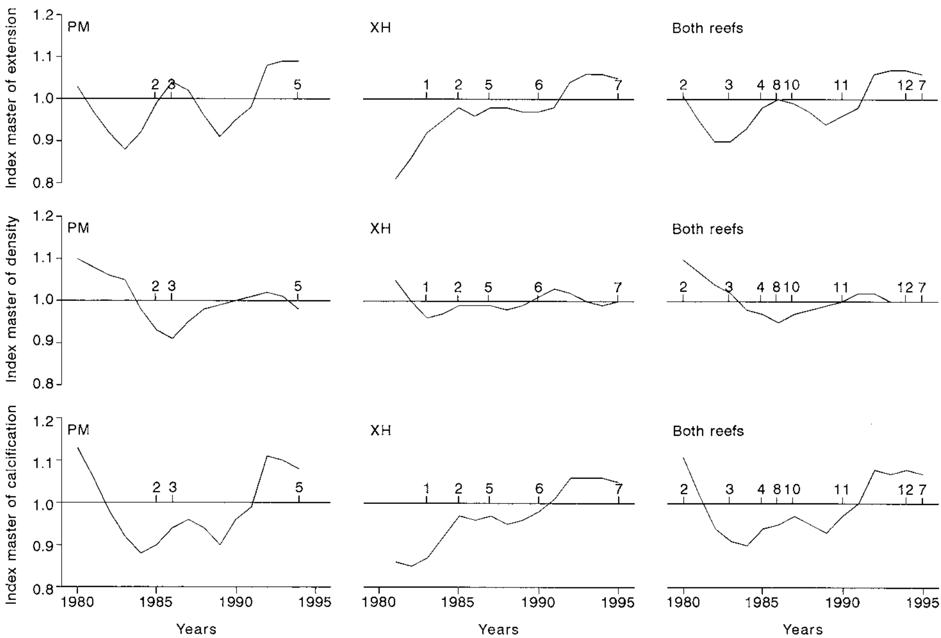

Figure 3. Three-year moving average of index master chronologies of extension, density and calcification rate of *Montastraea annularis* at each study site and at both reefs together. PM = Puerto Morelos, XH = Xahuayxol. The numbers along the horizontal axis indicate the number of corals used in the chronology in the specified year.

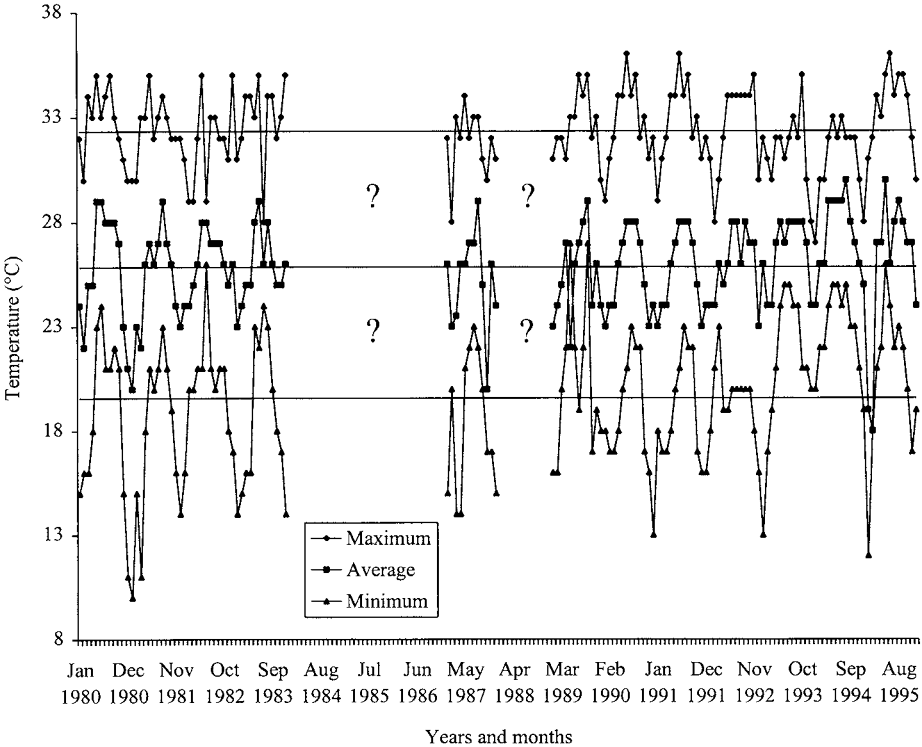

Figure 4. Maximum, average and minimum air temperatures from January 1980 to December 1995 from Chetumal. ? = Not available data.

(Knowlton et al., 1992; Weil and Knowlton, 1994). Since it is not clear which of the currently recognized species pertains to each earlier report attributed to *M. annularis*, only reports on “columnar” and “hemispheroidal” growth forms are considered in this table.

The one-way ANOVA’s showed that extension, density and calcification rate did not differ significantly over time at Puerto Morelos (P = 0.20, P = 0.60 and P = 0.09, respectively), at Xahuayxol (P = 1.00, P = 0.89 and P = 1.00, respectively) and for the data of the two reefs together (P = 0.62, P = 0.62 and P = 0.19, respectively). Nevertheless, slight trends were observed for some growth parameters at the two reefs zones and for the two reefs together (Fig. 3). The fact that no significant differences and only slight trends were observed for the three growth parameters for the period of time represented by the slabs (1980–1995) suggests that environmental conditions have been quite similar for the past one and a half decades. The only available environmental data for the two study sites are those of water temperature from Puerto Morelos. On the other hand, air temperature data are available for Chetumal, located 300 km south-southwest far from Puerto Morelos (Fig. 1). These data have similar trends and do not show any overall tendency for the period of time represented by the slabs (Fig. 4). A correlation analysis between the water temperature data from Puerto Morelos with their corresponding year and month air temperature data from Chetumal was significant (r = 0.93, P < 0.0001). Thus, it can be inferred that, at least, water temperatures have been similar for the period of time studied at the two reef zones.

Table 5. Coefficients of correlation (r) between the three growth parameters for each of the reefs. The asterisks indicate significant correlations ($P<0.05$, NS= no significative). PM = Puerto Morelos; XH = Xahuayxol.

Reef	Density vs Extension	Density vs Calcification	Extension vs Calcification
All data (n = 125)	–0.33*	0.28*	0.81*
PM (n = 55)	–0.18NS	0.43*	0.81*
XH (n = 70)	–0.35*	0.25*	0.82*

Table 5 shows the coefficients of correlation and their significances between the three growth parameters for the whole data set and for each reef sampled. Correlations of skeletal extension vs calcification rate are highly significant, with a high percentage of the variability explained, for all data (66%), as well as for the data from each reef sampled (66% in Puerto Morelos and 67% in Xahuayxol). The relationships among the growth parameters are similar to those described by other authors, particularly by Dodge and Brass (1984) in their detailed analysis.

Driven by resource limitations, we have developed the simple and inexpensive new method for the determination of density in coral skeletons as described above. Measurement repetition showed that better than 1% precision can be obtained using this method. Therefore, our freezing method can be used as a valid alternative when other techniques for measuring coral skeleton density are not available or when cost is a limiting factor. As demonstrated by the lack of observed differences between our results and those of previous authors, the new freezing method described herein can be used with confidence when more sophisticated and costly techniques are not necessary to measure density of coral skeletons.

Acknowledgments

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