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SCLERACTINEAN CORALS FROM CANE BAY AND
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ABSTRACT

Growth rates were determined for 95 specimens of *Montastrea annularis* and 25 samples of 6 other scleractinean species. Samples were collected along five transects at Cane Bay and Salt River submarine canyon on St. Croix, USVI. *Montastrea annularis* was the fastest-growing species in shallow water (0.4–1.2 cm/yr). Others ranged from 0.15–0.45 cm/yr (maximum). While a general trend of decreasing growth rate with depth (3–40 m) was observed for all corals, rates for *Montastrea annularis* clustered into two groups: 0.7–0.9 cm/yr in water depths less than 12 m, and 0.20 cm/yr below 18–20 m. The dramatic decrease in growth rate between these depths may reflect a "light compensation depth," below which photosynthetically driven calcification rapidly declines. Analyses suggest water depth, light level, turbidity and sedimentation rate as major controls of coral-growth rate. Slope of the substrate exhibits a secondary but inconsistent control.

A coral reef is the result of the complex interaction of constructive processes that build solid framework, and destructive processes that alter and remove that material. Of primary importance in understanding the overall forces that shape the reef, is a quantification of the individual contributions made by the carbonate-producing organisms that live in and on it. Primary among these in present-day reefs are the scleractinean corals.

Certain hermatypic corals exhibit density-banding patterns in their skeletons that can be discerned by X-radiography (Knutson et al., 1972). An annual growth increment is represented by a thin band of high-density skeletal material coupled with a band of lower-density material (Weber et al., 1975; Hudson et al., 1976). A yearly rate of extension can be determined by measuring the interval between successive density couplets. Linear extension rates of local *Montastrea annularis* colonies at depths of 2 and 10 m, based on Alizarin staining (Gladfelter et al., 1978), compare favorably with rates at the same depths, using X-radiographs, thus supporting the annularity of the bands in St. Croix corals. For purposes of general discussion, linear extension and coral growth are used synonymously in this manuscript.

Density band analyses have been used for a variety of tasks. Hudson et al. (1976) used the technique to investigate the near-death of a small reef system in the Florida Keys. They observed periodic occurrences of wide, high-density stress bands within the normal lower-density bands. Based on historical meteorological records, they concluded that these were related to drastic reductions in ambient water temperature. The degradation of the reef was likely related to natural phenomena.

In another study, Dodge and Vaisnys (1977) linked dredging effects to a decline in coral-growth rate in Castle Harbor, Bermuda. It was suggested that the absence of living corals older than 45 yr was related to intensive dredging in the harbor between 1941 and 1943. In other studies, coral-growth bands have been used to investigate effects of military weaponry practice on a Caribbean reef (Dodge, 1981), to study earthquake displacement of modern coral reefs (F. Taylor, cited

in Shinn, 1981), and to determine coral-growth rates in ancient reefs (Runcorn, 1967; Hubbard et al., in prep.¹).

The present investigation of coral-growth rates was part of a larger study to determine the magnitude of carbonate production, destruction and transportation on the St. Croix insular shelf (Hubbard et al., 1981). While the primary goal of this larger study was not an exhaustive treatment of coral calcification, the large volume of coral-growth data that were generated significantly expands existing information on the subject. This paper does not discuss short-term variations in growth rate, but rather concentrates on the more general roles played by light, water depth, sedimentation and shelf slope in determining long-term coral-growth rates.

The dominant controls of coral-growth rate have been discussed by numerous investigators (summarized in Buddemeier and Kinzie, 1976; Highsmith, 1979). Dustan (1975), using Alizarin staining of *Montastrea annularis*, postulated that the dominant axis of corallite growth changed from vertical to horizontal with depth, thus controlling the growth rate of that species. Grauss and Macintyre (1976; 1982) postulated a direct relationship between coral calcification and light intensity, which decreases exponentially with depth. While the precise relationship between photosynthesis by zooxanthellae and carbonate calcification has not yet been determined, light is acknowledged as a major factor controlling the rate at which a coral will add skeletal material.

Other studies have reported the growth rates of individual corals within limited depth ranges (Bak, 1974; Gladfelter et al., 1978; Ghiold and Enos, 1982, among others). The main body of data presented in this paper are based on *Montastrea annularis* specimens collected in water depths varying from 3–40 m. This coral was used because it dominated most of the shelf being investigated, and also lent itself to X-radiography. Fewer data were collected on *M. cavernosa*, *Siderastrea siderea*, *Diploria clivosa*, *Agaricia agaricites*, *Porites astreoides* and *Stephanocoenia michelini* occurring in water depths of 6–40 m.

METHODS

Between June 1981 and April 1982, a total of 198 coral specimens belonging to 6 genera and 7 species were collected along four transects at Cane Bay, and one transect at Salt River submarine canyon (Fig. 1). Coral morphology ranged from primarily hemispherical to flattened. Bottom slopes along three of the transects at Cane Bay (CB-01, 02 and 03) varied substantially along the profiles (0–49°; Fig. 2). Transect CB-04 had a uniform slope, and was chosen to eliminate the effect of slope on measured coral-growth rates. Collections were made using SCUBA at 10-ft (ca. 3-m) depth intervals between 3 and 40 m.

Entire colonies ranging from 1.2–23.4 cm in height, and in age from 10–30 yr, were collected with a hammer and chisel. Two to five heads of *Montastrea annularis* were collected at each site for replicate measurements. Generally, only one sample of the other species was collected. Of the 198 specimens collected, 34 (primarily *Agaricia* and *Diploria*) did not show density banding that could be detected. An additional 44 samples exhibited banding patterns that were sufficiently obscure or complex to make the measurements suspect. Of the remaining 120 corals that were measured, 95 were *Montastrea annularis*.

Corals were soaked overnight in a mild sodium hypochlorite (Clorox) solution and sprayed with a high-pressure hose to remove dead tissue. Each coral skeleton was cut with a rock saw along a plane intersecting the axis of maximum corallite growth. Slabs 0.4–2.0 cm thick were sectioned and X-radiographed with a Faxitron model 806 industrial radiographic inspection unit on Dupont "Cronex Lo Dose" mammography film. Exposure settings ranged from 59–61 KVP for 2 min. An intensifying screen was used to enhance the image.

¹ Hubbard, D. K., R. P. Burke and I. P. Gill. Patterns of reef development on the walls of Salt River submarine canyon, St. Croix, USVI; submitted to *Journal of Sedimentary Petrology*.

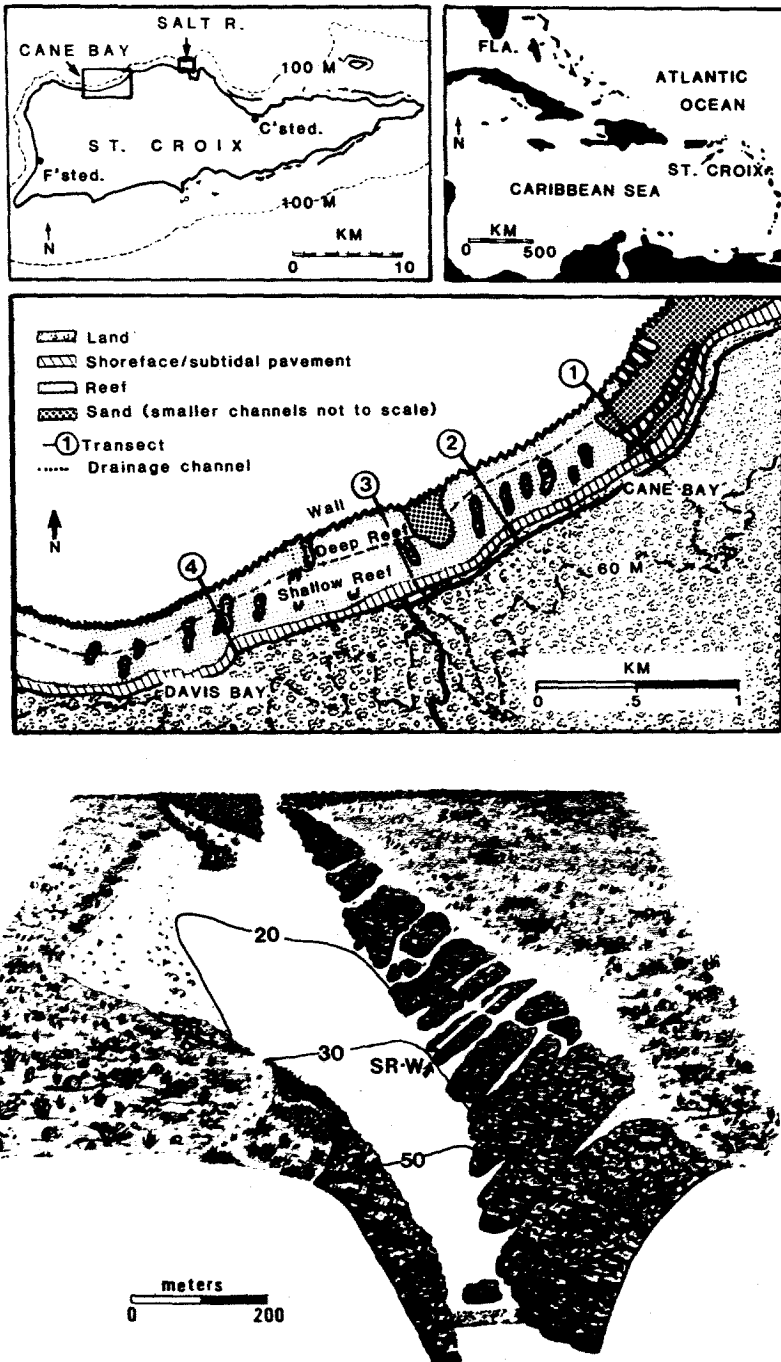


Figure 1. Maps showing the locations of the areas discussed in the text. The map of Cane Bay (middle) and the three-dimensional sketch of Salt River submarine canyon (lower) show the locations of the transects sampled in this study.

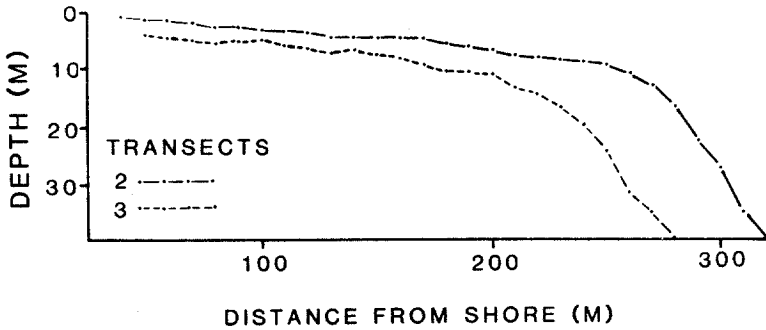


Figure 2. Bottom profiles along transects CB-02 and CB-03 (see Fig. 1 for locations). Note the change in bottom slope around 12–15 m.

Growth-banding and corallite patterns were traced off the X-ray negative. X-ray positives were not used as the stress bands that can be mistaken for annual bands are virtually absent in coral samples from Cane Bay and Salt River. The narrow shelf and stable tropical water-temperature patterns on St. Croix result in a distinct seasonality free from cold-water incursions as documented by Hudson et al. (1976) and Walker et al. (1982) in the Florida Keys.

As a double check of this method, one sample was taken from each of the four Cane Bay transects at depths of 9.2 and 30.5 m. Extension rates measured on the positives by a separate individual were not significantly different from those on the X-rays (Student's *t*-test). As a further precaution, 44 specimens which were originally used, but did not exhibit distinct and uniform banding patterns were removed from the sample pool, and all statistical tests were rerun. The removal of these samples did not change any of the original statistical results.

The interval between each visible pair of high-density bands was measured for all years along at least five corallite axes (perpendicular to the bands) using a Houston Instruments HIPAD electronic-field digitizer. Lines of measurement were placed evenly between (and including) the maximum and minimum growth axes of each sample. In a few samples, X-ray quality prevented the measurement along five axes. These samples are marked on Table 1.

All individual measurements from each specimen were averaged to yield a rate for that sample. At each sample site, all rates for individual samples were averaged to determine extension rate at that depth along that transect. Rates from individual corals, and averages for each site, are given in Table 1. The data do not specifically address temporal variations in extension rate, except as reflected in the standard deviation values provided.

Average bottom slope was also determined along two transects (CB-02 and CB-03, Fig. 1B). Water depth at each sample site was measured with a calibrated depth gauge, and the horizontal distance between sample sites was measured with a fiberglass tape measure; slope was trigonometrically calculated. Profiles CB-02 and CB-03 are shown in Figure 2. While the actual slope under each specimen was not measured by this method, it was thought that a general slope measurement would eliminate any sampling bias that might have been introduced by our admittedly subjective method of choosing specific specimens (basically, ease of sampling).

RESULTS

Variations in water depth, bottom slope and growth rate of several Caribbean scleractinian corals along five transects are summarized in Tables 1–3 and Figures 3–5. Colony morphology for each specimen is also shown. The distinction between columnar (C), hemispherical (H) and platy (P) is based on surficial morphology and internal banding character. The divisions are admittedly subjective, but provide the reader with a general idea of the nature of the corals sampled.

Average growth rates of *Montastrea annularis* varied from a minimum of 0.06 cm/yr at a depth of 36.6 m to a maximum of 1.23 cm/yr at 3.1 m. Rates tended to cluster around two values, one at 0.7–0.9 cm/yr in water depths less than 12 m (range = 0.43–1.23 cm/yr), and the other around 0.2 cm/yr below 18–20 m

Table 1. Coral-growth data for Cane Bay and Salt River submarine canyon

Depth (m)	Coral type	Morph	Sample No.	$\bar{x} \pm SD$	n	Average	N
Transect CB-01							
3.05	<i>M. annularis</i>	H	1B	1.23 ± 0.42	24	1.07 ± 0.35	44
	<i>M. annularis</i>	H	2B	0.87 ± 0.27	20		
6.10	<i>M. annularis</i>	H	3A	0.98 ± 0.22	80	0.83 ± 0.17	240
	<i>M. annularis</i>	H	4B	0.86 ± 0.14	60		
	<i>M. annularis</i>	H	5A	0.69 ± 0.16	100		
9.10	<i>M. annularis</i>	H	1B	0.80 ± 0.21	90	0.78 ± 0.24	350
	<i>M. annularis</i>	H/C	2B	0.86 ± 0.26	90		
	<i>M. annularis</i>	C	3A	0.70 ± 0.24	60		
	<i>M. annularis</i>	H/C	4B	0.75 ± 0.24	110		
12.2	<i>M. annularis</i>	H	1A	0.74 ± 0.22	80	0.83 ± 0.20	282
	<i>M. annularis</i>	H/C	2A	0.94 ± 0.14	42		
	<i>M. annularis</i>	H	3A	0.88 ± 0.20	100		
	<i>M. annularis</i>	H	4B	0.76 ± 0.20	60		
15.2	<i>M. annularis</i>	H/C	1	0.74 ± 0.21	60	0.74 ± 0.21	60
18.3	<i>M. annularis</i>	H	3B	0.43 ± 0.14	60	0.42 ± 0.26	134
	<i>M. annularis</i>	H	4A	0.21 ± 0.47	50		
	<i>M. annularis</i>	H	5A	0.83 ± 0.14	24		
21.3	<i>M. annularis</i>	P	1A	0.25 ± 0.07	30	0.25 ± 0.07	30
24.4	<i>M. annularis</i>	P	4A	0.15 ± 0.03	42	0.15 ± 0.03	42
30.5	<i>M. annularis</i>	P	1A	0.15 ± 0.06	24	0.15 ± 0.05	69
	<i>M. annularis</i>	P	2A	0.15 ± 0.03	22		
	<i>M. annularis</i>	P	3A*	0.16 ± 0.07	23		
36.6	<i>M. annularis</i>	P	1B	0.18 ± 0.03	50	0.15 ± 0.03	75
	<i>M. annularis</i>	P	2A	0.10 ± 0.03	25		
Transect CB-02							
3.05	<i>M. annularis</i>	C	1A*	1.19 ± 0.39	27	0.96 ± 0.33	47
	<i>M. annularis</i>	H	1D	0.65 ± 0.24	20		
6.10	<i>M. annularis</i>	C	2A	0.54 ± 0.20	120	0.58 ± 0.22	220
	<i>M. annularis</i>	H	1B	0.63 ± 0.24	50		
	<i>M. annularis</i>	C	1C	0.65 ± 0.23	50		
9.10	<i>M. annularis</i>	C	2A	0.51 ± 0.13	45	0.68 ± 0.15	95
	<i>M. annularis</i>	C	1C	0.83 ± 0.16	50		
12.2	<i>M. annularis</i>	C	1A	0.72 ± 0.25	50	0.67 ± 0.20	166
	<i>M. annularis</i>	H	1B*	0.43 ± 0.14	60		
	<i>M. annularis</i>	C	1D	0.88 ± 0.21	56		
15.2	<i>M. annularis</i>	H	1A	0.25 ± 0.07	55	0.34 ± 0.10	105
	<i>M. annularis</i>	H	2B	0.36 ± 0.11	60		
18.3	<i>M. annularis</i>	P	1A	0.26 ± 0.05	50	0.24 ± 0.05	150
	<i>M. annularis</i>	P	2B*	0.22 ± 0.06	60		
	<i>M. annularis</i>	P	1D*	0.24 ± 0.03	40		
21.3	<i>M. annularis</i>	P	2D	0.18 ± 0.03	45	0.18 ± 0.03	45
30.5	<i>M. annularis</i>	P	4	0.17 ± 0.03	25	0.16 ± 0.03	70
	<i>M. annularis</i>	P	8	0.16 ± 0.03	25		
	<i>M. annularis</i>	P	10	0.16 ± 0.04	20		
36.6	<i>M. annularis</i>	P*	2	0.24 ± 0.04	40	0.22 ± 0.04	107
	<i>M. annularis</i>	P	3	0.38 ± 0.08	27		
	<i>M. annularis</i>	P	6	0.10 ± 0.02	40		
12.2	<i>A. agaricites</i>	P	A	0.16 ± 0.02	25	0.16 ± 0.02	25
18.3	<i>A. agaricites</i>	P	A	0.16 ± 0.02	25	0.16 ± 0.02	25
6.10	<i>D. labyrinth.</i>	H	A	0.34 ± 0.05	30	0.34 ± 0.05	30

Table 1. Continued

Depth (m)	Coral type	Morph	Sample No.	$\bar{x} \pm SD$	n	Average	N
18.3	<i>D. labyrinth.</i>	P	A2	0.29 ± 0.04	30	0.33 ± 0.06	84
	<i>D. labyrinth.</i>	P	B*	0.36 ± 0.07	39		
30.5	<i>D. labyrinth.</i>	P	A	0.46 ± 0.09	39	0.46 ± 0.09	39
12.2	<i>C. natens</i>	H	A*	0.41 ± 0.06	9	0.41 ± 0.06	9
12.2	<i>M. cavernosa</i>	H	A	0.45 ± 0.08	20	0.45 ± 0.08	20
17.0	<i>M. cavernosa</i>	H	A	0.32 ± 0.08	37	0.32 ± 0.08	37
18.3	<i>M. cavernosa</i>	H	A1	0.37 ± 0.07	25	0.34 ± 0.06	39
	<i>M. cavernosa</i>	H	B*	0.31 ± 0.04	24		
24.4	<i>M. cavernosa</i>	P	B*	0.29 ± 0.04	40	0.29 ± 0.04	40
12.2	<i>P. astreoides</i>	H	A	0.31 ± 0.05	30	0.31 ± 0.05	30
18.3	<i>P. astreoides</i>	H	A	0.29 ± 0.05	20	0.25 ± 0.05	50
	<i>P. astreoides</i>	H	B	0.23 ± 0.03	30		
24.4	<i>P. astreoides</i>	H	A	0.19 ± 0.04	25	0.19 ± 0.04	25
6.10	<i>S. siderea</i>	H	A	0.30 ± 0.03	35	0.31 ± 0.04	70
	<i>S. siderea</i>	H	B	0.31 ± 0.05	35		
12.2	<i>S. siderea</i>	H	A	0.26 ± 0.03	30	0.26 ± 0.03	30
18.3	<i>S. siderea</i>	P	A	0.25 ± 0.05	35	0.25 ± 0.05	35
24.4	<i>S. siderea</i>	H	A*	0.23 ± 0.04	21	0.23 ± 0.04	21
39.7	<i>S. siderea</i>	P	A	0.16 ± 0.03	45	0.15 ± 0.03	80
	<i>S. siderea</i>	P	B	0.14 ± 0.02	35		
30.5	<i>Stephanocoenia</i>	P	A	0.18 ± 0.03	21	0.18 ± 0.03	21
3.05	<i>M. annularis</i>	H	A	0.61 ± 0.19	50	0.61 ± 0.19	50
6.10	<i>M. annularis</i>	H	A	0.86 ± 0.21	35	0.76 ± 0.24	90
	<i>M. annularis</i>	H	B	0.78 ± 0.24	30		
	<i>M. annularis</i>	H	C	0.61 ± 0.29	25		
9.10	<i>M. annularis</i>	H	A	0.98 ± 0.23	25	0.92 ± 0.19	125
	<i>M. annularis</i>	H/C	B	0.91 ± 0.18	100		
12.2	<i>M. annularis</i>	C/H	A	0.96 ± 0.32	31	1.02 ± 0.25	110
	<i>M. annularis</i>	C/H	B	1.06 ± 0.28	39		
	<i>M. annularis</i>	C	C	1.04 ± 0.16	40		
15.2	<i>M. annularis</i>	H	A	0.61 ± 0.24	60	0.74 ± 0.24	201
	<i>M. annularis</i>	H	B	0.79 ± 0.28	110		
	<i>M. annularis</i>	H	C	0.82 ± 0.11	31		
18.3	<i>M. annularis</i>	P/H	A	0.27 ± 0.09	30	0.28 ± 0.07	70
	<i>M. annularis</i>	P/H	C	0.29 ± 0.05	40		
21.3	<i>M. annularis</i>	P	A2	0.25 ± 0.04	20	0.24 ± 0.04	120
	<i>M. annularis</i>	P	B	0.29 ± 0.05	55		
	<i>M. annularis</i>	P	C	0.17 ± 0.04	45		
24.4	<i>M. annularis</i>	P	A	0.24 ± 0.04	60	0.23 ± 0.04	85
	<i>M. annularis</i>	P	C	0.19 ± 0.04	25		
30.5	<i>M. annularis</i>	P	C	0.18 ± 0.04	80	0.18 ± 0.04	80
36.6	<i>M. annularis</i>	P	B	0.06 ± 0.01	12	0.07 ± 0.01	16
	<i>M. annularis</i>	P	C*	0.09 ± 0.02	4		
Transect CB-04							
3.05	<i>M. annularis</i>	H	A	0.71 ± 0.17	45	0.75 ± 0.27	84
	<i>M. annularis</i>	H	B*	1.03 ± 0.26	16		
	<i>M. annularis</i>	H	C*	0.63 ± 0.24	23		
6.10	<i>M. annularis</i>	H	A	0.89 ± 0.26	25	0.89 ± 0.26	25
9.10	<i>M. annularis</i>	H	A	0.84 ± 0.31	38	0.93 ± 0.28	64
	<i>M. annularis</i>	H	B*	1.07 ± 0.23	26		
12.2	<i>M. annularis</i>	P	A	0.54 ± 0.13	33	0.54 ± 0.13	33

Table 1. Continued

Depth (m)	Coral type	Morph	Sample No.	$\bar{x} \pm SD$	n	Average	N
15.2	<i>M. annularis</i>	C	A	0.44 ± 0.29	60	0.46 ± 0.25	120
	<i>M. annularis</i>	H	B	0.49 ± 0.20	60		
18.3	<i>M. annularis</i>	P	C*	0.34 ± 0.08	23	0.34 ± 0.08	23
21.3	<i>M. annularis</i>	P	C	0.18 ± 0.05	75	0.18 ± 0.05	75
24.4	<i>M. annularis</i>	P	B	0.23 ± 0.03	35	0.22 ± 0.04	75
	<i>M. annularis</i>	P	C	0.21 ± 0.04	40		
30.5	<i>M. annularis</i>	P	A	0.17 ± 0.04	35	0.17 ± 0.03	90
	<i>M. annularis</i>	P	B	0.17 ± 0.03	55		
Transect SR-W							
9.10	<i>M. annularis</i>	C	B1	0.52 ± 0.15	4	0.53 ± 0.13	24
	<i>M. annularis</i>	H	B2	0.53 ± 0.13	20		
12.2	<i>M. annularis</i>	C	A	0.39 ± 0.17	45	0.29 ± 0.13	140
	<i>M. annularis</i>	P	B1	0.25 ± 0.05	45		
	<i>M. annularis</i>	H	C1	0.22 ± 0.04	50		
15.2	<i>M. annularis</i>	C	B	0.83 ± 0.28	18	0.83 ± 0.28	18
18.3	<i>M. annularis</i>	P	A	0.18 ± 0.04	30	0.20 ± 0.04	70
	<i>M. annularis</i>	P	B	0.21 ± 0.04	40		
21.3	<i>M. annularis</i>	P	C1	0.15 ± 0.04	35	0.15 ± 0.04	35
24.4	<i>M. annularis</i>	P	B	0.14 ± 0.02	25	0.14 ± 0.02	25
30.5	<i>M. annularis</i>	P	A	0.11 ± 0.02	26	0.13 ± 0.02	51
	<i>M. annularis</i>	P	B	0.16 ± 0.02	25		

* Marks samples in which less than five axes could be clearly identified.

(range = 0.06–0.29 cm/yr; Fig. 3). Based on a 1-sided *t*-test, the shallower corals (less than 15 m) had extension rates higher than those in deeper water (greater than 18 m) at a significance level of 0.005 ($t = 48.03$; $N = 83$).

On transects CB-01, 02 and 03, the transition between the two groups corresponded to a significant increase in bottom slope. Along transect CB-04, however, a similar decrease in extension rate occurred despite the lack of any slope variation.

Growth rates for other species (except *Stephanocoenia michelini*—only one specimen) varied between 0.12 and 0.45 cm/yr (Fig. 3C). Because of the narrow depth ranges of the data on these "other" corals (Fig. 4), and the necessary assumption that the density bands they exhibit are annual (verified only for *Montastrea annularis*), these rates are tentatively offered, but will not be discussed in detail below.

Cane Bay growth rates were consistently higher than those from similar depths at Salt River (Tables 1 and 3). Mean extension rate at each depth at both locales was computed by averaging rates from all specimens (Table 3). A paired *t*-test of the Cane Bay and Salt River data indicated that the difference in extension rates between the two areas was statistically significant at a level of 0.005 when comparing *Montastrea annularis* growing in water depths between 9.15 and 30.48 m (i.e., the range sampled at Salt River).

Growth data are summarized in Tables 1–3. In general, coral-growth rate decreased with increasing water depth (Table 1) and bottom slope (Table 2). Along transects CB-02 and CB-03, coral-growth rate correlated highly with both shelf slope and water depth ($\alpha = 0.005$; $N = 45$; $r = -0.8167$ and -0.7477 , respectively). Along transects CB-01, CB-04 and SR-W, where only depth and growth data are available, these two variables were again highly correlated ($\alpha = 0.005$; $r = -0.85$). A multiple linear regression of slope and depth on growth rate im-

Table 2. Bottom slope vs. extension rate (transects CB-02 and CB-03)

CB-02			CB-03		
Depth (m)	Extension (cm/yr)	Slope (°)	Depth (m)	Extension (cm/yr)	Slope (°)
3.05	1.19	0.9	3.05	0.61	0.0
	0.65	0.9	6.10	0.86	1.8
6.10	0.54	3.2		0.78	1.8
	0.63	3.2		0.61	1.8
	0.65	3.2	9.10	0.98	7.0
9.10	0.51	5.3		0.91	7.0
	0.83	5.3	12.2	0.96	14.1
12.2	0.72	12.3		1.06	14.1
	0.43	12.3		1.04	14.1
	0.88	12.3	15.2	0.61	14.1
15.2	0.25	21.5		0.79	14.1
	0.36	21.5		0.82	14.1
18.3	0.26	37.6	18.3	0.27	17.8
	0.22	37.6		0.29	17.8
	0.24	37.6	21.3	0.25	27.2
21.3	0.18	37.6		0.29	27.2
30.5	0.17	49.5		0.17	27.2
	0.16	49.5	24.2	0.24	31.4
	0.16	49.5		0.19	31.4
36.6	0.24	27.2	30.5	0.18	29.1
	0.38	27.2	36.6	0.06	27.2
	0.10	27.2		0.09	27.2

Note: see Table 1 for standard deviations.

proved the correlation only slightly (r^2 for growth vs. slope = 0.6563; r^2 for growth vs. depth = 0.6529; R^2 for growth vs. slope and depth = 0.7200). Partial correlations of either depth or slope on extension rate, holding the other variable constant, resulted in similar coefficients (0.34 and 0.35), and a significance level of 0.01 for both.

These results, combined with the high correlation between bottom slope and water depth ($r = 0.8162$; $N = 20$; $\alpha = 0.005$) make it difficult to objectively separate the effects of water depth and bottom slope on coral growth. This is discussed below.

DISCUSSION

Methods of Measurement.—Many studies to date have measured one growth axis (usually the maximum), and related it to whatever factor was being considered. Data for this study were initially collected to determine rates of carbonate production in various areas of the reef (Hubbard et al., 1981), and average growth rates were therefore required. These rates, based on average colony accretion, can vary noticeably from those based on measurements of only one or two axes (especially the maximum).

To quantify the differences likely to occur between methods, multiple-axis (usually 5) growth data from this study were compared with measurements of one, two and three axes of growth on the same samples (Fig. 5). The curves based solely on vertical growth increment were consistently above those produced from the same samples using the multi-axis method. Measurements based on horizontal and vertical axes deviated less (Fig. 5), and the curve based on the maximum,

Table 3. Coral-growth rate vs. depth at Cane Bay vs. Salt River

Depth	Growth rate	
	Cane Bay	Salt River
9.10	0.83 ± 0.15 (10)	0.53 ± 0.01 (02)
12.2	0.81 ± 0.20 (11)	0.29 ± 0.09 (03)
15.2	0.56 ± 0.21 (08)	0.83 (01)
18.3	0.34 ± 0.19 (09)	0.20 ± 0.02 (02)
21.3	0.22 ± 0.05 (06)	0.15 (01)
24.4	0.20 ± 0.04 (05)	0.14 (01)
30.5	0.17 ± 0.03 (09)	0.14 ± 0.04 (02)

Note: values in parentheses are the numbers of corals used to compute the means. Standard deviations are based on the rates for whole samples at each depth (i.e., not individual growth bands as in Table 1).

minimum and intermediate growth axes showed generally good agreement (Fig. 5C).

The degree to which the number of axes measured affects the resulting growth rates is largely a function of the depth in which the corals are growing. In shallow water, the maximum growth orientation is in the vertical plane (Grauss and Macintyre, 1982), and a measurement based on this axis only will be higher than an average for the entire colony. In deeper water, growth is reasonably evenly distributed across the platy surface, and single-axis vs. multiple-axis measurements show less variation from one another.

The curves based on one and two axes of measurement bias the data away from an average (Fig. 5). The implication here clearly is not that measurement of only the maximum growth axis is necessarily wrong. In fact, in some cases, a measurement of maximum growth might be more revealing. If, however, a quantitative picture of the overall response of a coral colony to decreasing light (or whatever factor) is desired, then measurement of a single axis of upward growth would seem less appropriate than multiple measurements along several axes. While single-axis measurements may still often reveal the general nature of such a relationship, the differences shown in Figure 5 are obvious, and should be kept in mind.

A reasonable alternative to the multi-axis method is to X-radiographically determine the age of individual corals in core, and then geometrically calculate an average rate of growth for the entire colony (Ghiold and Enos, 1982). This method will have some inaccuracies due to necessary simplifications of colony morphology (especially in non-hemispherical forms), and provides little or no information about short-term variability in three-dimensional growth patterns. It does, however, provide a reasonably non-destructive means of measuring coral-growth in colonies of any size.

Controls of Growth Rate. — SLOPE AND DEPTH. Both water depth and bottom slope correlated highly with coral-growth rate. Because depth and slope also correlated highly with one another, however, the two become difficult to separate as potential controls. Attempts to statistically separate the two met with little success. A closer examination of the data themselves, however, can shed some light on this problem.

Growth rates for *M. annularis* at Cane Bay fell into two groups with a dramatic transition in between (Fig. 3). Along transects CB-01, 02 and 03, this transition corresponded to a change from low to high bottom slopes. It was initially suspected that this sudden drop in growth rate was affected by a change in substrate orientation, and thus growth form of the corals. The segregation of coral-growth

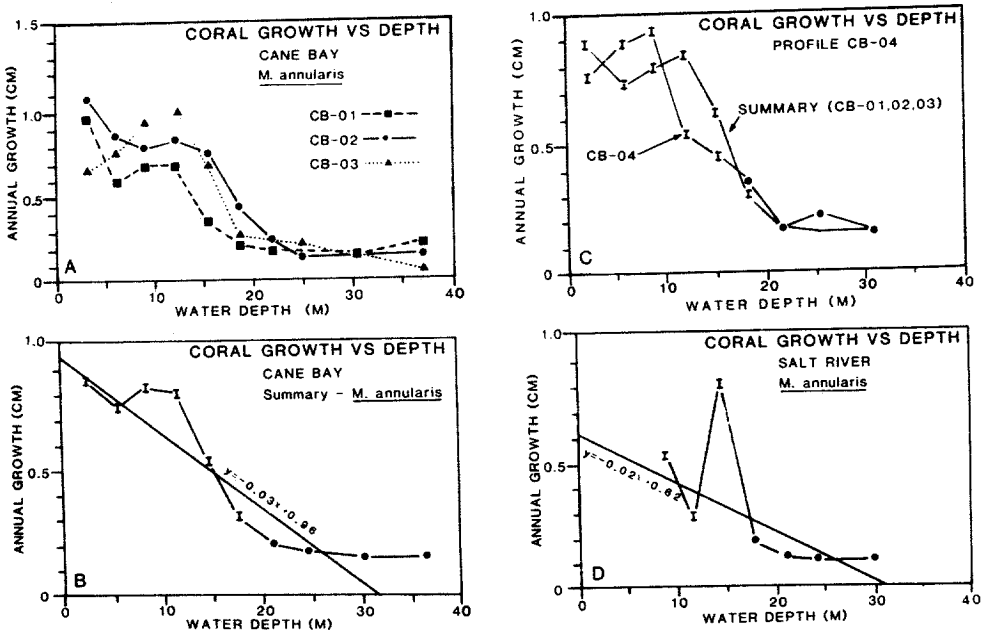


Figure 3. Coral-growth rate vs. water depth along four transects at Cane Bay and Salt River (see Fig. 1 for locations). Error bars signify one standard deviation unit. Deviations less than 0.10 cm are too small to plot, and are indicated with a dot. A. Individual curves for *Montastrea annularis* along transects CB-01, 02 and 03. See individual curves in Figure 5 for error bars. B. Summary curve for the four transects at Cane Bay. A statistically determined best fit line is also shown. C. Comparison of coral-growth trends in areas of widely varying bottom slope (SUMMARY) vs. uniform slope (CB-04). D. Growth rates of *Montastrea annularis* along the west wall of Salt River submarine canyon. A best fit line is also shown. Note that growth rates are lower than those from similar depths at Cane Bay (2B).

rates into two distinguishable groups (statistically significant at $\alpha = 0.005$; $t = 15.03$; $N = 15$) still occurred along profile 4 (Fig. 3C), however, despite no noticeable slope change as seen on the other three transects. A paired t -test could not distinguish the growth curve for line CB-04 from the cumulative curve for the other three transects ($t = -1.5901$; $N = 9$; $\alpha = 0.20$). This drop in growth rate at between 15 and 18 m seems to occur equally well with or without a corresponding change in bottom slope. Therefore, while the authors do not propose that substrate angle bears no effect on coral-growth rate, we do feel that it is at best secondary to light effects more directly related to water depth.

In the zone shallower than 15 m, all four profiles have similar and slight slopes, but growth rates are highly divergent. The relationship between growth rate and substrate inclination is highly variable, and seems to be positive, contrary to the overall trend for the lines as a whole (i.e., the faster growing corals were occurring on higher, not lower, slopes within shallow water). This may reflect locally enhanced growth where gravity can help corals remove sediment in this nearshore area of locally high sedimentation.

SEDIMENTATION AND TURBIDITY. Along the west wall of Salt River submarine canyon, growth rates for *Montastrea annularis* were significantly ($t = 3.64$; $N = 64$; $\alpha = 0.005$) lower than at similar depths in Cane Bay. Salt River is consistently

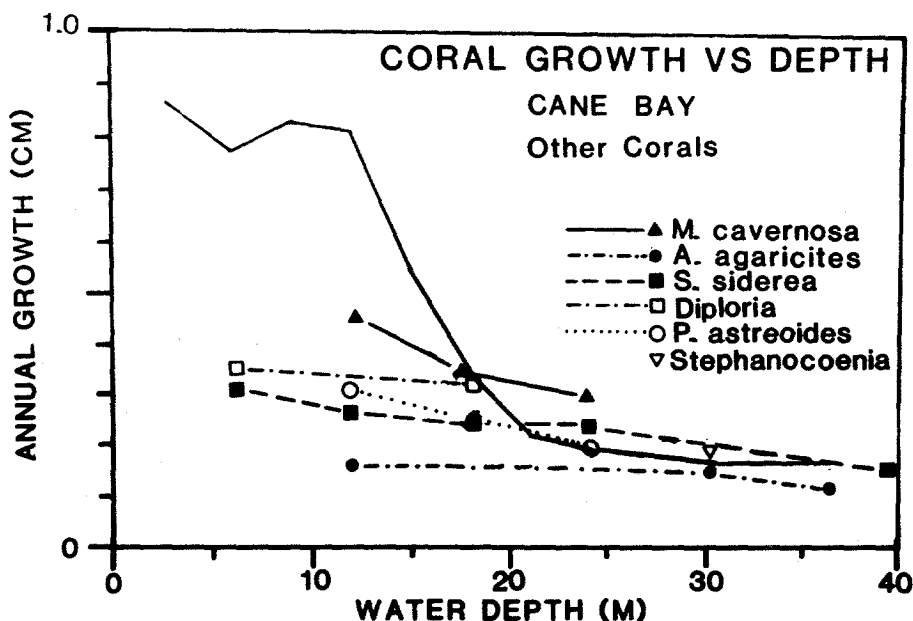


Figure 4. Growth data for six other species of corals along transect CB-02. The summary curve for *M. annularis* is given for reference.

more turbid than Cane Bay, and the differences in growth rates are undoubtedly due to the attenuation of light by the higher suspended load at Salt River.

In the nearshore zone at Cane Bay, depth effects appear to be somewhat modified by bedload sedimentation and turbidity within the water column. Along lines CB-03 and CB-04, extension rates actually increased with depth between 3 and 9–12 m (Fig. 3). This may be a response to increased bedload transport of sand along the inner sections of these transects.

Transects CB-02 and CB-04 were noted to be more turbid along their inner margins than the other two Cane Bay profiles, and have correspondingly lower rates of growth at 3.1 m. On transect CB-02, however, growth rates based on the maximum growth axis only are noticeably higher than the averages based on multi-axis measurements (Fig. 4A). Most of this difference is due to the columnar forms occurring along the inner portion of the more turbid transect (note the higher abundance of columnar forms on line CB-02; Table 1). The differences in the curves may in part reflect a response whereby the colony maximizes upward growth to elevate the colony to a position of either more light, less abrasion by moving sand, or both.

LIGHT. Not surprisingly, this study has done nothing to contradict light as the major factor controlling coral-growth rates and patterns. Although light intensity was not measured in the field, the same light data (Jerlov, 1970) used by Dustan (1975) for his studies led to similar results. Light and growth rate correlated at $a = 0.005$.

Most interesting, however, is the curious drop in growth rates between 12 and 18 m of water depth. Despite the high statistical significance ($r = 0.8053$; $N = 83$; $a = 0.005$) of the correlation between water depth and growth rate, the as-

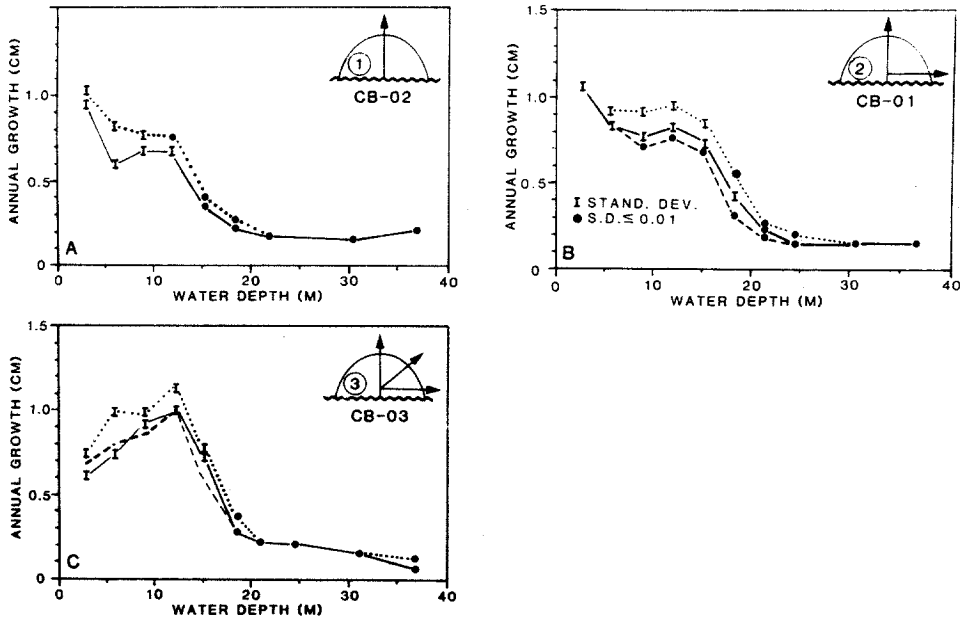


Figure 5. Comparison of growth rates based on our multi-axis measurements (solid lines) and values from the maximum growth axis (dotted lines) only. Curves based on two (B) and three (C) axes are also shown (dashed lines). Data for the one-, two- and three-axis curves were drawn from the multi-axis set. Note the gradual increase in agreement as axes of measurement are added. To simplify the diagrams, standard deviation bars are given only for maximum and multi-axis curves. Deviations less than 0.10 cm are too small to plot, and are indicated with a dot.

sociated regression line is not a particularly good predictor of growth rate at any one depth (Fig. 3B). There is a reasonable possibility that the relationship is non-linear, however, no statistical test could be found to fit a curve with two inflections. Nevertheless, data from this study, as well as others (Highsmith, 1979) strongly hint at a non-linear relationship.

This value of 12–18 m is curiously popular in the literature (Adey (1978) cites 15 m as a controlling depth for reef initiation after Holocene sea-level rise slowed; it is also the cutoff between shallow and deep reef species on many Caribbean reefs). Rapidly changing bottom slope at this depth at Cane Bay seems an unlikely cause for the sharp decline in coral-growth rates. Therefore, one is faced with either explaining the pattern, or else dismissing it as an artifact of the data.

The data may reflect the position of a light threshold below which calcification is dramatically reduced. This light-compensation depth has been suggested by others (Kornwisher and Wainwright, 1967; Chalker, 1975),² and should represent a fruitful avenue of future research. The model for coral growth proposed by Grauss and Macintyre (1982) shows a dramatic decrease in calcification rate below approximately 200 footcandles of light. While their computed curves show this value at depths below 12–18 m, the concept of a dramatic decrease in calcification at some threshold is still suggested. Carefully designed field studies should be able to determine whether the growth-rate pattern observed in this study is related to

² Chalker, B. E. 1975. Calcification metabolism and growth by the staghorn coral, *Acropora cervicornis*. Ph.D. Dissertation, Univ. of Miami. Unpublished.

such a factor, or is simply a linear response to exponentially decreasing light levels. This relationship may have been somewhat obscured in the past by the use of maximum growth-rate data rather than averages for entire colonies.

CONCLUSIONS

Based on the above data, we offer the following conclusions: (1) Water depth plays the major role in controlling *Montastrea annularis*-growth rate at Cane Bay and Salt River. Most likely, this reflects a response to changing light levels. (2) Growth rates for *Montastrea annularis* tend to cluster at two levels: 0.7–0.9 cm/yr in water depths less than 12 m, and 0.2 cm/yr below 18–20 m. This sudden drop through intermediate depths is not slope dependent, and may be a response to reaching a light threshold below which photosynthesis and calcification are dramatically inhibited. (3) Growth habit and rate are strongly affected by sedimentation and turbidity levels, both locally between transects at Cane Bay, and on a larger scale between Cane Bay and Salt River submarine canyon. (4) Multi-axis (at least three) measurements are preferable if one's purpose is to characterize the overall growth rate of an individual colony. Single-axis measurements produced different growth rates which are highly dependent on growth habit.

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