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SKELETAL EXTENSION, DENSITY AND CALCIFICATION OF THE REEF CORAL, *MONTASTREA ANNULARIS*: ST. CROIX, U.S. VIRGIN ISLANDS

Richard E. Dodge and Garrett W. Brass

ABSTRACT

Parameters of the annual and subannual skeletal growth of 61 *Montastrea annularis* corals, collected at a variety of shallow depth sites on reefs of St. Croix, U.S. Virgin Islands, are determined by X-radiography and scanning densitometry for each year in the 10-year period, 1970–1979. Extension (linear growth) of the coral skeleton is correlated negatively with bulk density (mass per unit volume) and positively with calcification (mass addition). Density and mass are slightly positively correlated. No one parameter, however, is a perfect predictor of another. At least two parameters, from which the third can be calculated, are required for complete description of coral growth. The variations of parameters of subannual density bands in this study do not convey information additional to those of annual bands.

When compared to a pristine site in St. Croix, coral from Round Reef within Christiansted Harbor (a location of past dredging and sewage pollution) have equivalent (and high) extension but significantly lower density and calcification. On the south coast, corals from a location of major dredging activity in the past have relatively low extension and calcification. These growth anomalies are probably pollution related. Collections of corals from one south coast site may have been biased by hurricane effects to nonrepresentative samples.

The island of St. Croix, U.S. Virgin Islands, is located in the northeastern Caribbean sea at 17°45′N and 64°52′W. Surrounding the island on most sides are coral reefs, some of which have been described (Ogden, 1972; Adey, 1975; Adey et al., 1977). This study evaluates annual and subannual skeletal growth of a major coral species, *Montastrea annularis,* from various reef areas. Relationships of the parameters—extension, density, and calcification—are investigated. Growth is typically considered an index of viability of an organism and for corals can be an important indicator of their state of health. St. Croix is not highly developed, but sources of pollution do exist. We have found that coral growth in certain areas appears to reflect the presence of environmental degradation.

A number of methods are available to measure skeletal growth of scleractinian corals and a variety of studies have been done (Buddemeier and Kinzie, 1976). We wished to evaluate natural in situ growth over a decade and used the X-radiography method (Buddemeier, 1978; Dodge and Vaisnys, 1980) to reveal annual and subannual skeletal density variations or bands (Knutson et al., 1972; Dodge et al., 1974; Macintyre and Smith, 1974; Hudson et al., 1976). Width of growth increments measures extension of the coral skeleton. Bulk density measures the distribution of $CaCO_3$ within the skeleton. The mass of $CaCO_3$ deposited (over time) is the calcification (rate) of the coral. If any two of the parameters are known, the third can be calculated. A variety of studies have been done on the individual variability of at least two of these parameters (e.g., for extension: Weber and White, 1977; Weber et al. 1975; Glynn and Stewart, 1973; Isdale, 1977; Dodge et al., 1974; Hudson, 1981; and for calcification: Goreau and Goreau, 1959; Jokiel and Coles, 1977; Coles and Jokiel, 1978; Bak, 1974; 1978). The inter-relationships and simultaneous variability of each of the parameters are only beginning to be understood (Dodge and Thomson, 1974; Buddemeier et al., 1974). Barnes and Taylor (1973), Dustan (1975), and Baker and Weber (1975) have

investigated parameter changes over depth with sometimes conflicting results. We have compared skeletal extension, density, and calcification for many individual colonies of the same species over the same time periods between locations (2–8 m depth range) within a reef system. This has proved valuable to assess the information content of each parameter as well as for adequate characterization of the growth of corals.

METHODS AND MATERIALS

Species of Interest.—*Montastrea annularis* was chosen as the species of investigation because of its abundance on St. Croix reefs and its general ecological importance on reefs of the Atlantic and Caribbean (Goreau, 1959). *M. annularis* contains well-defined annual density bands (Dodge et al., 1974; Macintyre and Smith, 1974; Hudson et al., 1976). The high density portion of the annual cycle forms some time in the late summer and fall (Hudson et al., 1976; Fairbanks and Dodge, 1979; Stearn et al., 1977). Extension growth of this species has been studied in St. Croix (Baker and Weber, 1975; Gladfelter et al., 1978) and elsewhere in the Atlantic and Caribbean (Aller and Dodge, 1974; Dodge, 1978; Dustan, 1975; Hudson, 1981).

Collection.—Specimens of *M. annularis* were obtained in early Dec. 1980 by snorkel divers using hammer and chisel to break corals from the substrate or parent colony. Corals were collected at a variety of sites (Fig. 1, Table 1) over a total depth range of 2–8 m.

M. annularis can occur as three gradational morphological types: hemispherical (colony very rounded, tissue covers most of visible skeleton), columnar (colony with rounded tissue-covered top but often with long sides which are sometimes devoid of tissue), and platy (colony flattened and may occur as shingle-like plates overlapping each other, or as part of the basal or side portions of more massive colonies). The platy form is generally most common in depths below the range of this study. Lewis (1960) has discussed the origin of columnar colonies on the shallow seaward slope of Barbados reefs (5–6 m depths) and indicates that as hemispherical colonies grow closer together over time, individual colonies become elongated so that each hemisphere forms a cap of living tissue on top of a long column of dead skeleton. In this explanation, space limitation at the sides of colonies produces the eventual shape. Graus and Macintyre (1976) suggest that light level is responsible for colony shape producing a gradation of hemispherical, columnar, to platy forms with increasing depth and decreasing light. At most of our sites we observed hemispherical, columnar, and forms transitional between these two. We restricted collection to primarily the columnar, but transitional varieties were sometimes obtained. Table 1 provides information on the type of colony growth forms collected at each site.

Sites were chosen as representative of general reef areas and some were in proximity to known or suspected pollution influences (Fig. 1). Table 1 provides information on site abbreviations, locations, depths of sampling, and numbers of specimens collected. Sites are further described below.

North
CHF (Christiansted Harbor Fore-Reef)

Long Reef protects Christiansted Harbor. The fore-reef zone (Fig. 1, upper inset) is populated primarily by *Acropora palmata* from 0 to 5 m. A head coral zone occurs below. Specimens were collected in 5–8 m depth, seaward of the reef crest and approximately 0.5 km east of a municipal raw sewage outfall which exits in 7 m depth on the fore-reef zone on Long Reef. Prevailing wind and currents distribute sewage solids along the reef itself but dissolved material is carried over the reef-crest and back into the harbor (Adams, 1974; Dong et al., 1972). The collection site was probably sufficiently removed from the outfall to be outside the influence of its pollution.

CHB-RR (Christiansted Harbor Back-Reef)

The major back-reef area of Christiansted Harbor (Fig. 1, upper inset) runs along the western portion of Long Reef and is composed of shallow sand and hard ground with low living coral coverage. In several hours of reconnaissance only one suitable *M. annularis* (#C-97) was found (Fig. 1). The bulk of sampling was conducted in 2–3 m water depths at Round Reef (Fig. 1, upper inset), a patch reef on the eastern margin of Christiansted Harbor. At collection time this site was turbid from resuspended sediment.

Christiansted Harbor has often been disturbed by the activities of man. Dredging for sand mining between 1962 and 1968 removed over 2 million cubic yards of sand (Adams, 1974) primarily for cement production. In addition, dredging has continued for construction and maintenance of several
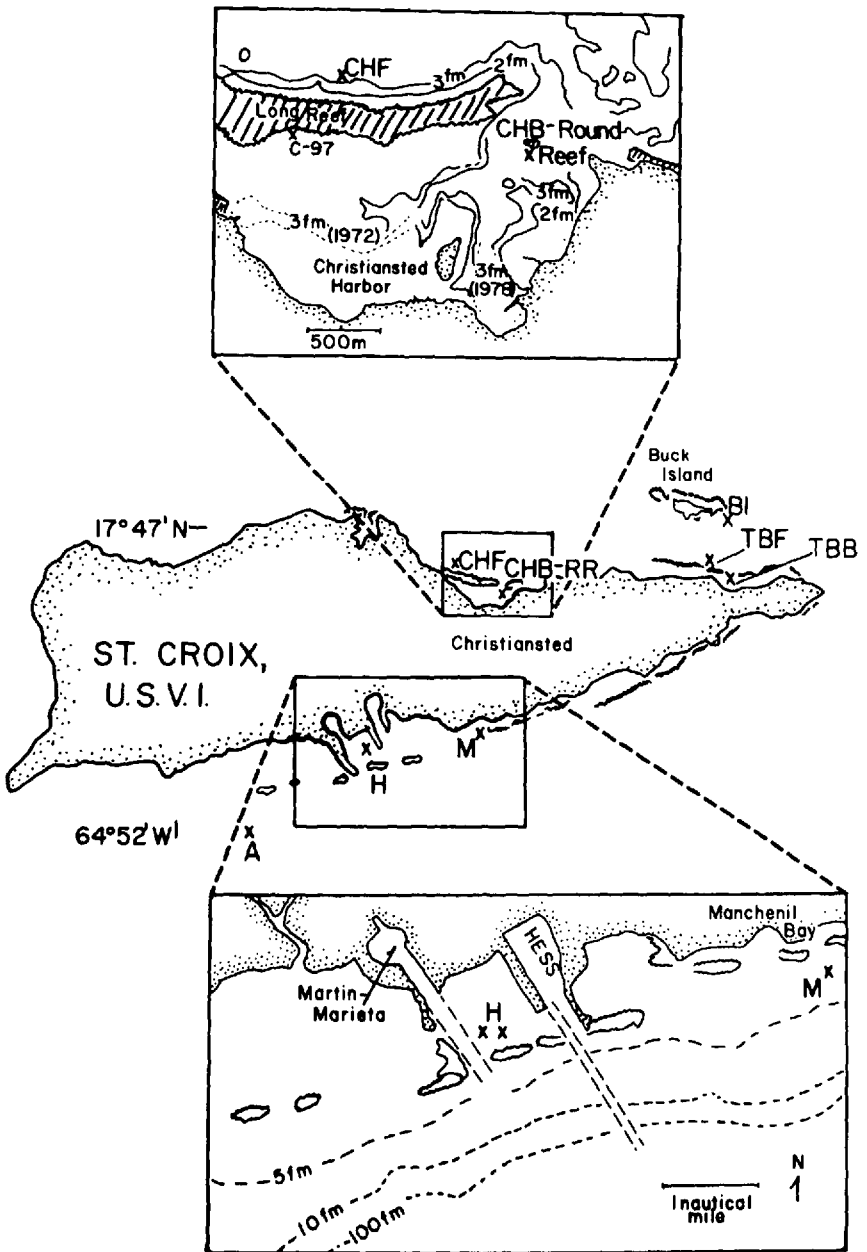
Figure 1. (Center) Sketch map of St. Croix, U.S. Virgin Islands. Collection sites are designated by X. Station initials are described in the text. (Top) Expansion of Christiansted Harbor area. 0 indicates the position of the sewer outfall on the fore-reef of Long Reef. (Bottom) Expansion of the Hess-Manchenil Bay area.

channels within the Harbor, apparently during the 1970's. Several studies (Dong et al., 1972; Nichols et al., 1972) have documented detrimental effects from dredging within the harbor. Sewage pollution also exists from the community of Christiansted. Until 5 years ago, a major portion of its raw sewage was piped across the harbor to an outfall on the seaward side of Long Reef. Today the pipe carries

Table 1.

Site	Location	Depth (m)	Colony Form	# Specimens Collected	No. Discarded				No. Analyzed
					Unclear Bands	Poor Section	Rolled	Too Small	
		North Coast Sites							
CHF	Christiansted Harbor Fore-Reef	5–8	columnar	13	4	1	1		7
CHB-RR	Christiansted Harbor Back-Reef-Round Reef	2–3	columnar & transitional	10	1				9
TBF	Tague Bay Fore-Reef	6	columnar & transitional	10	1		2	1	6
TBB	Tague Bay Back-Reef	2–3	columnar & transitional	10	2		1		7
BI	Buck Island	8	columnar	11	2				9
		South Coast Sites							
A	Airport Back-Reef	5–7	columnar	10	2				8
H	Hess (Krause Lagoon)	3	columnar	16 (8 + 8)	8 (7 + 1)				8
M	Manchenil Bay	3–5	columnar & transitional	9	2				7

city storm drainage as well as sewage overload. Dissolved material, being typically less dense than seawater, rises and is carried back into the harbor (Dong et al., 1972). Additional sources of sewage exist along the water front area of Christiansted (Nichols et al., 1972).

A current analysis (Dong et al., 1972) indicates that a counter-clockwise pattern results from the northeast trades pushing water over the western and major portion of Long Reef. This water exits primarily to the east through the ship channel and also over Round Reef (CHB-RR). Sewage discharge and/or dredging-induced sedimentation and turbidity might be expected to contact Round Reef in this way.

TBF (Tague Bay Fore-Reef)

The reef at Tague Bay (Fig. 1, center) is a well-developed Caribbean bank-barrier structure dominated at the crest by *Acropora palmata*, and grading with depth into a *Montastrea annularis* zone (Ogden, 1972). This site was not expected to be influenced by man-induced pollution. Specimens were collected in approximately 6 m depth.

TBB (Tague Bay Back-Reef)

A back-reef portion of the Tague Bay reef (Fig. 1, center) (leeward of the crest and terminating at the lagoon margin) was sampled in approximately 2–3 m depth. This site is not expected to be affected by pollution; however, it is subject to higher degrees of natural resuspended sediment than the fore-reef.

BI (Buck Island)

The fore-reef zone (Fig. 1, center) of the reef surrounding the eastern margin of Buck Island was sampled at approximately 8 m depth. *M. annularis* was abundant, growing in large columnar clusters. Our sampling site was outside the boundary of the Buck Island National Monument and seaward of the well-defined *A. palmata* zone. The site is expected to be the most pristine, being located at the extreme eastern and windward portion of St. Croix. The site has been described in detail by Adey et al. (1977).

South

The reefs of St. Croix were exposed to the force of Hurricanes David and Frederic in 1979 (Rogers et al., 1982). The storms caused considerable damage and the common reef crest zone of *A. palmata* is frequently missing, having been destroyed and reduced to rubble in many locations. Other species were probably killed and damaged in the high wave energy of the storms. South coast reefs were more greatly affected by the hurricanes. South collection sites were chosen at what were judged to be back-reef areas and in those locations where living corals were still relatively abundant.

A (Back-Reef Area, Seaward of Airport)

M. annularis were collected in 5–7 m depth. Site A (Fig. 1, center) is well offshore and far down current from the effluent or dredging effects from the land-based Hess refinery and the Martin Marietta Alumina plant (Fig. 1). This site was observed to have had only relatively minor hurricane damage.

H (Hess Reef)

In this area was formerly located Krause Lagoon (Fig. 1, lower inset) which was dredged and filled for the construction of the Hess oil refinery. Another industry, the Martin Marietta Alumina plant, is located nearby to the east in Limetree Bay. Major dredging of the lagoon and shelf for harbor construction was conducted in the area from 1963–1964 for Martin Marietta and from 1965 to 1967 for the Hess turning basin and a channel 22 m deep. Dredging for channel maintenance and deepening is still occurring (1970–1971 for Hess deepening), although settling ponds have been introduced to reduce turbidity (Adams, 1974).

A reef-crest is located approximately midway between the dredge cut channels for the Hess refinery on the east and Martin Marietta on the west (Fig. 1). The fore-reef and crest were devoid of living corals, probably due to past dredging effects complemented by hurricane influence. Reconnaissance of the extensive back-reef lagoon revealed two large columnar clusters of *M. annularis* (approximately 10–15 m in diameter by 5 m in height) from each of which eight colonies (16 total) were sampled at
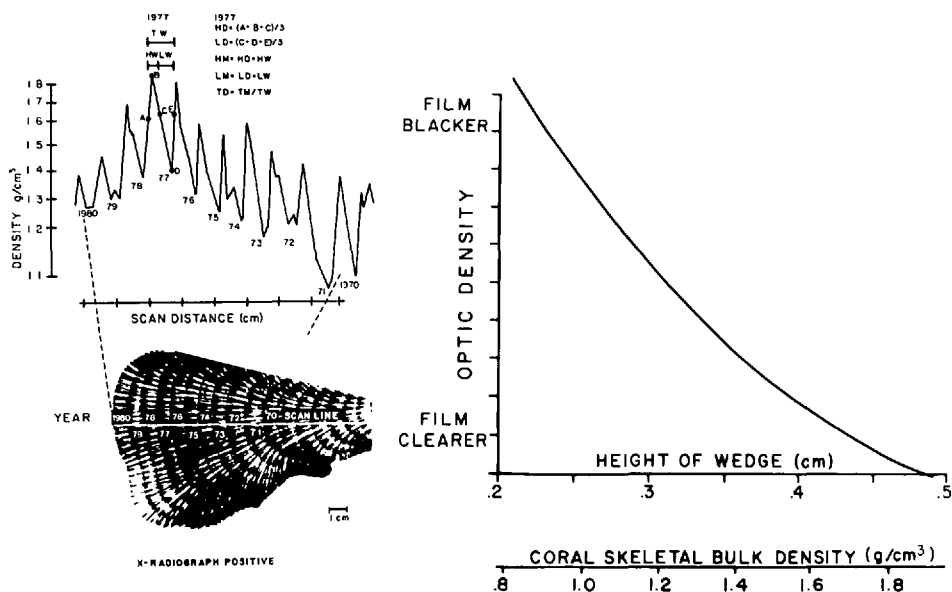
Figure 2.   (Left) Typical densitometer output from a scan of an X-radiograph negative. The location of the scan transect is depicted on the lower X-radiograph (positive) for illustration. Skeletal density bands have been dated from the known date of collection. The vertical scale is coral skeletal density (g/cm^3), obtained from calibration of film optic density (Fig. 3). Measurement and calculation procedure for annual and subannual extension, density, and mass for the year 1977 is shown and further described in the text.

Figure 3.   (Right) Densitometer scan of X-radiograph of calcium carbonate wedge. The vertical axis is optic density. The horizontal axis is distance along the scan transect of the wedge from thin end to thick. The upper horizontal scaling is given as the height of the wedge in cm. The lower horizontal scaling is a conversion to skeletal bulk density (g/cm^3) using a slab thickness of 0.64 cm, values of mass absorption coefficients at 30 Kev for the standard ($CaCO_3$ wedge) of 1.80 and for the coral ($CaCO_3$ + 2% CH_2O + 0.8% Sr) of 1.95 as provided by Buddemeier (1974), and a density of the wedge of 2.71 g/cm^3. The optic density values can be converted to bulk density values through use of the curve. This has been done in Figure 2.

3 m depth (Table 1). We were unable to locate a living reef immediately to the west of the Martin Marietta plant.

M (Manchenil Bay)

The eastern-most south coast site sampled was Manchenil Bay (Fig. 1, lower inset). Reefs here were heavily affected by hurricane action. *A. palmata* was rare and only in scattered and relatively protected areas were remnants of the former lush stands. Site M was chosen for availability of *M. annularis* corals, but was near or in a former *A. palmata* zone. Specimens were collected in 3–5 m depth. The site has no obvious influences from pollution.

Sample Preparation and Measurements. —After collection and labeling, specimens were cut with a large masonry saw to obtain at least one 0.5 to 0.7 cm thick parallel sided slab which included (as far as possible) the plane intersecting the colonies' origin and points of highest relief on the growth surface. Each slab was X-radiographed on Kodak AA-2 Industrex X-ray film using a non-collimated dental unit X-ray source (70 KVP, 15 ma, 127 cm source to subject distance, typical exposure time 10–20 seconds). A wedge of $CaCO_3$ (calcite) of known dimensions was included on each X-radiograph for later calibration of film optic density to skeletal density (Buddemeier, 1974; Dodge, 1980).

X-ray negatives were contact printed on photographic paper and positives were inspected for quality of density banding. Some specimens were discarded from further analysis (Table 1) because of errors in cutting (poor section), obvious changes in orientation resulting from prior breakage (rolled), poor

Table 2.

Growth Parameter	Time Span	Abbreviation	Explanation
Extension	subannual	HW	width (cm) of the high density band portion (high width)
	subannual	LW	width (cm) of the low density band portion (low width)
	annual	TW	width (cm) of the entire annual band (total width)
Density	subannual	HD	average density (g/cm³) of the high density band portion (high density)
	subannual	LD	average density (g/cm³) of the low density band portion (low density)
	annual	TD	average density (g/cm³) of the entire annual band (total density)
Mass	subannual	HM	calculated mass (g/cm²) of the high density band portion (high mass)
	subannual	LM	calculated mass (g/cm²) of the low density band portion (low mass)
	annual	TM	calculated mass (g/cm²) of the entire band (total mass)

banding or banding obscured from boring organisms (unclear bands), or too few annual growth bands recorded (too small). Of the 91 *M. annularis* corals collected, 61 were retained for further analysis. On the X-radiographs of these retained specimens, annual growth bands, each composed of a high and low (H and L) density portion, were assigned appropriate years of formation from the known date of collection.

A scanning densitometer was used to obtain quantitative information on annual and subannual extension, density, and mass (Dodge and Thomson, 1974; Buddemeier, 1974; Buddemeier et al., 1974; Dodge, 1978). Each coral X-radiograph negative was scanned along a straight line coincident with the axis of maximum growth and normal growth band boundaries. This provided a curve of variations in X-ray film optic density along the scan transect (Fig. 2). The $CaCO_3$ (calcite) wedge included in each X-radiograph was also scanned to calibrate the film optic density to coral skeletal density or bulk density (Fig. 3). Scan distance along the wedge was scaled as wedge height. This was converted to coral bulk density (g/cm³) using the formula and mass absorption coefficients of Buddemeier (1974) at 30 KeV for the calcite wedge ($CaCO_3$) and for the coral ($CaCO_3$ + 2% organics + 0.8% Sr), and the appropriate coral slab thickness. Given uncertainties in the actual wedge and coral composition, we estimate a possible systematic error of estimate to be ±5%. The procedure provides a calibration curve of optic density versus skeletal density for each coral. Figure 3 illustrates a typical calibration for a coral slab of 0.64 cm thickness.

Figure 2 shows a typical densitometer output with a coral X-radiograph positive attached to illustrate the orientation of the skeletal scan transect. The vertical axis is optic density calibrated to skeletal density according to the relationships of Figure 3. Each peak of the scan trace corresponds to an H band portion and each valley represents an L band. Years of formation were assigned to H-L couplets by comparison to the coral X-radiograph positive and are indicated on the curve. Data were extracted for the 10-year inclusive period 1970–1979 (1980 was omitted because surface relief on some specimens did not allow a complete and accurate scan of that year). Subannual and annual parameters of growth measured for each year were: extension (HW, LW, TW), density (HD, LD, TD) and mass (HM, LM, TM). Table 2 lists these parameters, their abbreviations, and an explanation for convenience.

The average skeletal density for each subannual and annual band (HD, LD, TD) was determined from the densitometer scan of each coral X-radiograph, as shown for example in Figure 2. The calibrated densitometer output was a chart recorder trace of continuous density variations (g/cm³) along the scan transect. To find the average density of a portion of the skeleton, it was necessary to integrate over that portion of the curve corresponding to the skeletal area of interest along the scan transect. We used a simplified method as illustrated for year 1977 in Figure 2. The peak identified as point B is equivalent to the maximum density of the high density (HD) band for 1977. Similarly the

valley at point D is the minimum density of the 1977 low density (LD) band. The average density for the 1977 HD band was calculated as the average of the values of three points: A, B, and C. Point A is the density midway between 1978 minimum density and 1977 maximum density. Point C is the density midway between 1977 maximum density and 1977 minimum density. An analagous procedure was performed to determine average low density (LD). The valley about point D is the curve portion of interest. The three values averaged for 1977 LD density were the points C, D, and E. Point C is the density midway between 1977 maximum density and 1977 minimum density. Point D is the minimum density of the 1977 LD band. Point E is the density midway between 1977 minimum density and 1976 maximum density. Accuracy of this three point averaging method was confirmed by comparing results on selected corals calculated in the above way to a more detailed graphical integration at ½ mm intervals (Dodge, 1978).

Extension of band portions (HW and LW) was measured by the horizontal linear distance (appropriately scaled to cm) between youngest and oldest values of a peak (for 1977: distance between A to C) or valley (for 1977: C to E) of the scan for a particular year. Annual extension (TW) was the sum of the HW and LW for that year.

The mass of $CaCO_3$ accumulated for subannual bands (HM and LM) was calculated by the product of band portion density and band portion extension to provide a value in g/cm^2 (i.e., $HM = HW \cdot HD$; $LM = LW \cdot LD$). Annual mass (TM) was the sum of HM and LM for a given year. Finally, annual density (TD) for each year was calculated by dividing TM (g/cm^2) by TW (cm).

Only extension and mass for annual bands can be considered as rates. For subannual portions a precise time interval of formation is not yet known. It is still valid to compare characteristics of the H and L bands, but their actual rates could be quite different. For annual bands, rates are valid because their characteristics are representative for their time of formation: 1 year.

RESULTS

Table 3 presents for each of the 61 corals: averages of growth parameters for the subannual and annual bands over the 10-year period 1970–1979. Averages by site over all measurements within the site for each parameter are also presented in Table 3.

To assess relationships, correlation coefficients (r) were calculated and are presented in Table 4. Within each parameter grouping, subannual bands are positively related to their annual counterparts. For density, correlations are very high, indicating that annual and subannual bands have nearly identical variations. For extension and mass, the L bands are more strongly related to the annual values than are the H bands, and the H and L bands are not highly correlated.

Comparisons between parameter groupings indicate that extension is correlated negatively to density and, in general, positively to mass. This means that wide annual (or subannual) bands, although typically less dense, still have greater mass than thin ones. For example, TW is negatively correlated to TD and positively correlated with TM. Figure 4 presents scatter plots of the relationships between the annual parameters (a) TW:TD, (b) TM:TW and (c) TM:TD. The straight line drawn in each is the functional or geometric mean (G.M.) regression (Ricker, 1973). Each G.M. regression is significant ($P < 0.05$) based on the appropriate r value (Table 4) and calculations of the two linear regressions for each paired data set. Although the regressions are significant, their predictive ability is not high. The correlation coefficient squared (r^2) indicates the percent of variance that one variable can explain of another. For TW:TD and TM:TW this is 31% and 36% respectively. For TM:TD, the value is 8%. It should be noted that if there is a linear relationship between two of the three variables, the relationship between any one of these two and the third will *not* be linear because of the product equation defining calcification or mass (i.e., $TM = TW \cdot TD$). The curved lines in Figure 4b and c are the calculated functional relationships of one variable on another using the linear relation of annual extension and density (Fig. 4a). These curves are obtained using one of the equations for extension and density and

TABLE 3. AVERAGE AND STANDARD DEVIATION OF EACH GROWTH PARAMETER FOR EACH CORAL (OVER THE 10-YEAR PERIOD 1970-1979) AND FOR EACH SITE (AVERAGE OF ALL MEASUREMENTS)

SITE	CORAL #	EXTENSION (cm)						DENSITY (g/cm^3)						MASS (g/cm^2)					
		HW	s.d.	LW	s.d.	TW	s.d.	HD	s.d.	LD	s.d.	TD	s.d.	HM	s.d.	LM	s.d.	TM	s.d.
TBF	1	.46	.14	.46	.14	.95	.23	1.19	.11	1.11	.07	1.14	.08	.54	.16	.53	.19	1.08	.25
	2	.41	.21	.50	.16	.94	.10	1.61	.12	1.53	.10	1.58	.15	.69	.38	.80	.21	1.49	.21
	5	.47	.34	.62	.25	1.08	.33	1.41	.13	1.26	.11	1.34	.09	.66	.48	.78	.34	1.44	.45
	6	.23	.06	.38	.10	.61	.13	1.35	.12	1.23	.08	1.28	.09	.32	.10	.47	.13	.78	.19
	7	.35	.21	.49	.20	.84	.23	1.44	.11	1.34	.07	1.37	.07	.50	.28	.66	.31	1.16	.35
	9	.31	.15	.65	.27	.96	.20	1.38	.13	1.31	.10	1.33	.11	.43	.22	.85	.35	1.28	.29
n = 60		.37	.21	.51	.21	.90	.26	1.40	.17	1.30	.15	1.34	.16	.52	.31	.68	.29	1.21	.38
CHF	17A	.31	.15	.63	.12	.94	.21	1.54	.11	1.43	.08	1.46	.09	.48	.27	.90	.16	1.38	.36
	17B	.29	.04	.70	.17	1.00	.16	1.45	.09	1.36	.06	1.41	.08	.43	.08	.96	.23	1.40	.21
	19	.48	.29	.55	.26	1.03	.23	1.47	.12	1.39	.11	1.44	.11	.70	.41	.76	.35	1.47	.26
	20	.44	.21	.46	.23	.90	.39	1.68	.12	1.59	.12	1.63	.12	.74	.37	.73	.36	1.47	.65
	21	.26	.15	.81	.15	1.07	.12	1.47	.12	1.35	.08	1.39	.09	.38	.22	1.09	.19	1.47	.14
	24	.24	.09	.42	.18	.66	.25	1.66	.11	1.55	.09	1.59	.09	.40	.15	.64	.25	1.03	.35
	26	.33	.19	.75	.25	1.09	.22	1.12	.09	1.05	.07	1.08	.06	.37	.20	.80	.27	1.17	.23
n = 70		.34	.19	.62	.23	.95	.26	1.48	.20	1.39	.19	1.43	.19	.50	.29	.84	.29	1.34	.37
TBB	31	.69	.33	.71	.14	1.39	.23	1.05	.08	.97	.06	1.01	.06	.70	.29	.69	.16	1.39	.20
	34	.31	.11	.51	.09	.82	.08	1.45	.05	1.36	.06	1.39	.05	.44	.16	.69	.13	1.13	.13
	35	.50	.18	.46	.14	.96	.28	1.41	.08	1.34	.07	1.38	.06	.71	.27	.61	.17	1.32	.37
	89	.24	.10	.55	.19	.79	.18	1.24	.09	1.21	.10	1.30	.10	.31	.12	.67	.26	.97	.29
	90	.32	.10	.47	.20	.80	.27	1.52	.07	1.49	.08	1.57	.10	.51	.15	.71	.29	1.21	.42
	91	.29	.10	.50	.09	.79	.11	1.33	.11	1.22	.09	1.26	.09	.38	.13	.62	.11	.99	.13
	93	.47	.15	.43	.15	.90	.21	1.60	.11	1.53	.09	1.57	.08	.75	.20	.66	.23	1.41	.29
n = 70		.40	.22	.52	.17	.92	.28	1.37	.19	1.30	.19	1.35	.20	.54	.24	.66	.20	1.20	.30
BI	38	.63	.25	.57	.27	1.26	.10	1.26	.05	1.16	.05	1.21	.03	.79	.30	.67	.33	1.46	.13
	39	.64	.25	.67	.31	1.31	.23	1.17	.08	1.08	.09	1.12	.08	.74	.27	.73	.35	1.46	.22
	40A	.54	.24	.67	.22	1.21	.21	1.22	.07	1.18	.06	1.23	.07	.69	.29	.79	.27	1.48	.26
	40B	.42	.26	.78	.34	1.19	.24	1.31	.14	1.23	.10	1.26	.10	.54	.31	.96	.41	1.50	.29
	42	.33	.09	.81	.17	1.14	.15	1.34	.09	1.25	.05	1.28	.05	.44	.12	1.02	.20	1.46	.16
	43	.36	.16	.61	.12	.98	.16	1.41	.09	1.30	.08	1.35	.08	.51	.23	.80	.17	1.32	.22
	44	.30	.24	1.02	.27	1.31	.22	1.25	.07	1.16	.08	1.18	.06	.36	.30	1.18	.34	1.55	.26
	46	.30	.12	.80	.19	1.10	.16	1.42	.06	1.33	.05	1.35	.04	.42	.17	1.05	.25	1.48	.23
	47	.49	.13	.50	.21	1.00	.20	1.38	.08	1.30	.09	1.32	.12	.65	.18	.65	.26	1.30	.22
n = 90		.45	.24	.72	.27	1.16	.21	1.31	.12	1.22	.11	1.26	.10	.57	.28	.87	.33	1.44	.23
H	54	.37	.20	.60	.17	1.01	.28	1.43	.10	1.36	.07	1.33	.18	.52	.28	.81	.24	1.33	.30
	56	.39	.22	.56	.28	.95	.24	1.28	.11	1.18	.05	1.23	.08	.50	.28	.66	.33	1.17	.32
	58	.48	.23	.61	.36	1.00	.31	1.26	.08	1.19	.07	1.22	.07	.61	.28	.61	.43	1.22	.37
	59	.34	.25	.50	.13	.84	.21	1.32	.12	1.28	.16	1.30	.14	.44	.31	.64	.20	1.09	.28
	60	.33	.18	.48	.21	.81	.15	1.28	.10	1.23	.08	1.26	.09	.43	.26	.59	.26	1.02	.21
	61	.35	.08	.47	.17	.81	.17	1.52	.08	1.46	.06	1.49	.07	.53	.14	.68	.24	1.20	.24
	62	.25	.20	.48	.16	.72	.15	1.32	.10	1.26	.09	1.28	.10	.32	.27	.60	.23	.92	.20
	63	.28	.17	.47	.16	.75	.15	1.36	.14	1.28	.12	1.32	.12	.38	.22	.60	.19	.98	.17
n = 80		.35	.20	.52	.21	.86	.23	1.35	.13	1.28	.12	1.30	.13	.47	.26	.65	.27	1.12	.29

substituting the known relationship that calcification equals density times extension. For example, one of the G.M. regression equations in Figure 4a is $TW = -1.06 \, TD + 2.33$. We have defined $TM = TW \cdot TD$ or $TW = TM/TD$. Substituting the latter form, we arrive at $TM/TD = -1.06TD + 2.33$ or $TM = 2.33TD - 1.06TD^2$ as the equation of the curve in Figure 4c.

Magnitude characteristics of the subannual growth increments can be summarized from the averages over all corals and sites at the end of Table 3. HW is less than LW, HD is greater than LD (also by definition), and HM is less than LM. In other words, a typical H band portion has less extension and mass than an L band.

For comparison of growth characteristics among and within sites, a one-way nested analysis of variance (Sokal and Rohlf, 1969) was performed on the data sets of each growth parameter. We used a mixed model, assuming fixed effects among sites and random effects for corals within sites and for measurements within corals. For each parameter the analyses provide evidence for a significant variance component among sites and if there are significant added variance components among corals within the sites. Prior to analysis of variance, an F max

TABLE 3. (Continued)

SITE	CORAL #	EXTENSION (cm) HW	s.d.	LW	s.d.	TW	s.d.	DENSITY (g/cm) HD	s.d.	LD	s.d.	TD	s.d.	MASS (g/cm) HM	s.d.	LM	s.d.	TM	s.d.
M	67	.27	.08	.45	.18	.72	.21	1.37	.07	1.32	.09	1.34	.08	.37	.11	.59	.22	.96	.27
	68	.35	.16	.39	.14	.75	.17	1.33	.06	1.27	.06	1.29	.06	.47	.20	.49	.16	.96	.21
	69	.41	.18	.42	.19	.84	.14	1.44	.09	1.40	.08	1.42	.08	.59	.24	.59	.27	1.19	.21
	70	.53	.24	.40	.19	.94	.33	1.19	.05	1.14	.06	1.17	.06	.64	.30	.46	.22	1.10	.41
	72	.39	.18	.47	.15	.85	.13	1.37	.07	1.32	.06	1.36	.08	.53	.25	.62	.20	1.15	.15
	73	.27	.14	.54	.15	.81	.27	1.50	.10	1.43	.08	1.46	.08	.42	.23	.77	.20	1.18	.40
	74	.28	.07	.34	.09	.61	.11	1.33	.08	1.22	.07	1.27	.08	.36	.09	.40	.09	.77	.12
n = 70		.36	.18	.43	.16	.79	.22	1.36	.12	1.30	.12	1.33	.12	.48	.23	.56	.22	1.04	.30
A	77	.26	.13	.68	.12	.95	.12	1.51	.05	1.42	.06	1.45	.05	.39	.18	.97	.18	1.37	.18
	78	.45	.29	.60	.16	1.04	.29	1.41	.07	1.32	.08	1.36	.08	.63	.41	.79	.23	1.42	.40
	79	.49	.33	.64	.36	1.13	.08	1.24	.06	1.17	.04	1.21	.05	.61	.41	.75	.41	1.36	.06
	81	.26	.13	.51	.19	.78	.17	1.14	.08	1.05	.09	1.09	.08	.31	.16	.53	.16	.83	.15
	82	.43	.26	.52	.20	.95	.17	1.41	.14	1.33	.12	1.36	.15	.62	.43	.70	.28	1.32	.36
	84	.49	.23	.47	.24	.95	.30	1.25	.10	1.16	.10	1.19	.09	.60	.27	.54	.29	1.14	.38
	85	.37	.37	.71	.29	1.08	.22	1.31	.09	1.20	.07	1.24	.07	.48	.46	.86	.36	1.33	.27
	86	.42	.28	.73	.31	1.15	.10	1.44	.07	1.35	.06	1.38	.07	.60	.40	.98	.41	1.58	.11
n = 80		.40	.27	.61	.29	1.00	.22	1.34	.14	1.25	.14	1.28	.14	.53	.36	.76	.33	1.29	.33
CHB-RR	97	.55	.31	.72	.44	1.77	.34	1.11	.08	1.07	.08	1.09	.06	.60	.39	.78	.48	1.38	.34
	100	.48	.11	.66	.24	1.14	.22	.91	.06	.81	.05	.85	.05	.43	.09	.53	.19	.96	.16
	101	.39	.17	.58	.15	.96	.26	1.33	.06	1.27	.04	1.29	.05	.51	.23	.73	.19	1.24	.34
	102	.34	.06	.54	.20	.88	.23	1.42	.12	1.34	.13	1.38	.12	.48	.11	.71	.22	1.19	.25
	103	.59	.20	.71	.17	1.30	.29	.81	.06	.77	.05	.78	.05	.47	.15	.54	.13	1.01	.21
	104	.46	.14	.75	.21	1.21	.24	.87	.06	.78	.07	.81	.06	.39	.11	.58	.15	.97	.16
	105	.49	.18	.57	.24	1.06	.15	1.07	.06	1.02	.04	1.04	.05	.52	.19	.58	.23	1.10	.13
	106	.45	.16	.74	.17	1.19	.20	1.00	.05	.93	.06	.96	.05	.46	.18	.68	.15	1.14	.20
	107	.66**	.21	.83*	.22	1.44*	.18	.99**	.06	.92*	.06	.99*	.15	.66**	.22	.76*	.19	1.36*	.19
n =		.48 88	.20	.68 87	.25	1.15 87	.28	1.06 88	.21	.99 87	.21	1.02 87	.21	.50 88	.21	.65 87	.24	1.14 87	.27
GRAND MEAN n =		.39 608	.22	.58 607	.24	.98 607	.28	1.32 608	.20	1.24 607	.19	1.28 607	.20	.51 608	.28	.71 607	.30	1.23 607	.33

1979-1973*
1979-1972**

Table 4.   Correlation coefficient matrix (Each parameter contains 61 values, i.e., the mean values of each coral) (N = 61, d.f. = 59, if $r \geq +0.25$ or ≤ -0.25, P is at least ≤ 0.05)

		Extension HW	LW	TW	Density HD	LD	TD	Mass HM	LM	TM
Extension	HW									
	LW	0.17								
	TW	0.69	0.82							
Density	HD	−0.47	−0.38	−0.54						
	LD	−0.46	−0.41	−0.57	0.99					
	TD	−0.44	−0.41	−0.56	0.99	0.99				
Mass	HM	0.78	−0.02	0.45	0.08	0.09	0.11			
	LM	−0.15	0.76	0.47	0.30	0.26	0.26	0.05		
	TM	0.35	0.56	0.62	0.30	0.28	0.29	0.61	0.80	

test (Sokol and Rohlf, 1969) was performed to verify that each group (site) contained either homogeneity of variance or only moderate heterogeneity. The nested ANOVA is insensitive to moderate heterogeneity when sample size is large and nearly the same among groups, as in the case for our data.

Table 5 presents results. Parameter abbreviations are listed at the top and sources of variation determined by the nested ANOVA's are listed at the side. An asterisk (*) indicates significance at least at the $P < 0.01$ level. The numbers
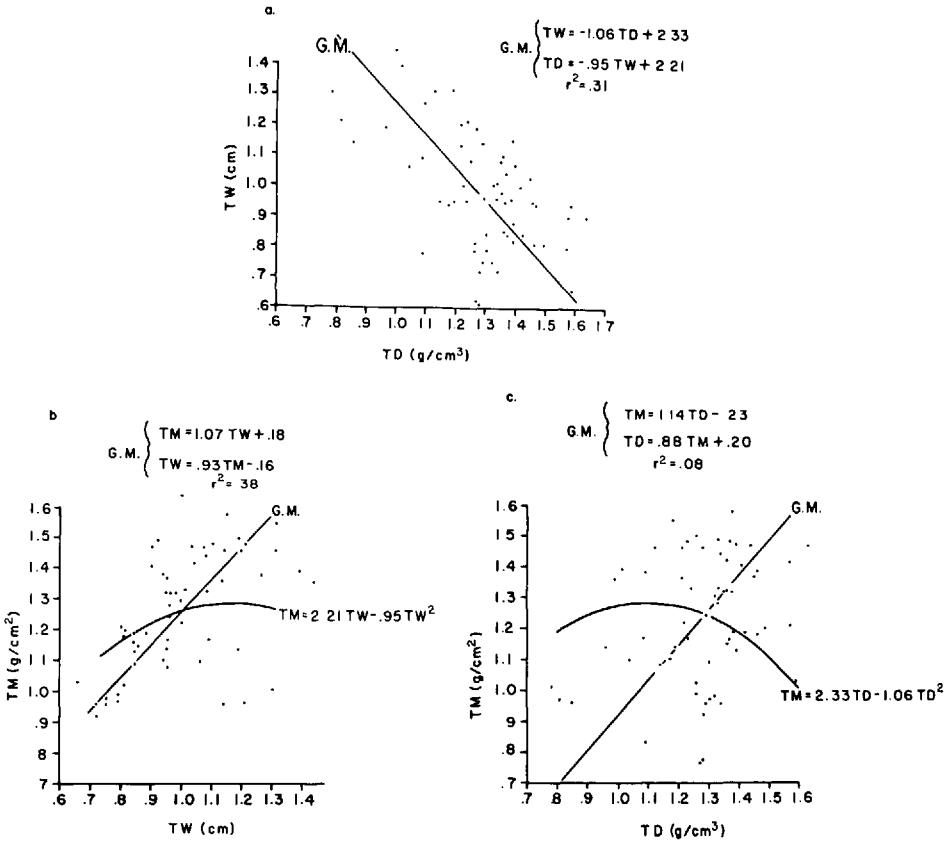
Figure 4. Scatter plot of: a, annual extension (TW) versus annual density (TD); b, annual calcification (TM) versus annual extension (TW); c, annual calcification (TM) versus annual density (TD). In each the straight line designated at G.M. is the geometric mean regression of the indicated variables. Both equations for this line are provided as well as the correlation coefficient squared (r^2) value. The curved line in Figure 4b and in 4c is the calculated relationship between the indicated parameters derived from the equation of Figure 4a and the TM = TW·TD relation, as described in the text. The equation of each curved line is presented in the figure.

are the percentage of total variance that may be ascribed to individual components. The results indicate that within each site and for each parameter, there is significant variability among corals. For parameters other than HW and HM, significant differences among sites are also indicated.

To evaluate specific site differences for those parameters which were indicated as portraying site differences by the ANOVA, we employed the SNK test (Zar, 1974; Sokal and Rohlf, 1969). This test uses the error variance of each one way ANOVA and assigns a significance to differences between site means. Site means are calculated as the average of all measurements for a parameter at a site (Table 3); however, the ANOVA error variance has been adjusted for variability associated with differences among corals within the site. Table 6 lists results at least at the $P < 0.01$ level for each parameter. These are described in more detail below.

Table 5.   One-way nested ANOVA (Mixed model: fixed effects for sites, random effects for subgroups) (Sokal and Rohlf, 1969)

Source of Variation	Parameters								
	HW	LW	TW	HD	LD	TD	HM	LM	TM
Among Sites	NS 1	* 11	* 18	* 29	* 27	* 28	NS 0	* 9	* 11
Among Corals, within Sites	* 16	* 12	* 22	* 50	* 55	* 53	* 11	* 13	* 20
Within Corals (error)	83	77	60	21	18	20	89	77	68
Total %	100	100	100	100	100	100	100	100	100

* Significant at least at the $P < 0.01$ level; NS = not significant; numbers are the percentage each variance component contributes to the total.

Extension

The sites of highest annual extension rate (TW) are BI (Buck Island) and CHB-RR (Round Reef in Christiansted Harbor) at 1.16 cm/yr and 1.15 cm/yr. Both are statistically indistinguishable and significantly greater than other sites. There are differences among other sites. Site A (airport) is greater than site H and M (Manchenil Bay). Site H (Hess) located near the Hess Oil Refinery and Martin Marietta Alumina plant is relatively low in extension rate and is significantly different from site M which has the lowest extension rate of all sites.

Relationships of LW between sites are similar to those for TW. There are no differences among sites for HW.

Density

For density parameters, the ordering of sites from highest to lowest changes dramatically in comparison to that for extension. This is reasonable given the negative correlation of density and extension in Table 4. Site ordering is similar for each density parameter, which is expected because of the high positive correlation of HD, LD, and TD.

Sites CHF, TBB, and TBF have highest density while sites A, BI and CHB-RR have lowest. Site CHF is significantly greater than all other sites. CHB-RR (e.g., TD = 1.02 g/cm³) has a significantly lower density than all others including the next to lowest, site BI (e.g., the range in TD is 1.43 g/cm³ for CHF to 1.26 g/cm³ for BI). Differences among sites for the parameters of HD and LD are very similar to those for TD.

Mass (Calcification)

Ordering of sites from highest to lowest annual calcification rate (TM) is similar to that for extension (TW) with an important exception. Whereas CHB-RR has the second highest extension, its TM is among the lowest sites. These lowest sites (CHB-RR, H, M, respectively) are significantly less than the highest TM sites (BI, CHF, and A).

Site ordering and significant differences for LM are similar to those for TM with somewhat fewer differences noted. There are no significant differences between sites for HM.

DISCUSSION

Relationships of Subannual and Annual Bands

The density characteristics of subannual and annual bands are highly correlated. For extension and mass parameters, characteristics of low density (L) and annual

Table 6.   SNK test results for differences between site means (for annual growth parameters, sites are arranged from highest to lowest mean; left to right and top to bottom)

EXTENSION

	BI	CHB-RR	A	CHF	TBB	TBF	H	M
BI	----	--------	-----	-----	-----	-----	-----	----
CHB-RR		-------	-----	-----	-----	-----	-----	----
A	*†	*	----	-----	-----	-----	-----	----
CHF	*	*		----	-----	-----	-----	----
TBB	*†	*†			----	-----	-----	----
TBF	*†	*†				----	-----	----
H	*†	*†	*†				----	----
M	*†	*†	*†	*†	*			--

DENSITY

	CHF	TBB	TBF	M	H	A	BI	CHB-RR
CHF	-----	------	------	------	------	------	------	-------
TBB	*0†	-----	------	------	------	------	------	-------
TBF	*0†		-----	------	------	------	------	-------
M	*0†			-----	------	------	------	-------
H	*0†	*			-----	------	------	-------
A	*0†	*†	*0†	*†		-----	------	-------
BI	*0†	*0†	*0†	*0†	*†		-----	-------
CHB-RR	*0†	*0†	*0†	*0†	*0†	*0†	*0†	---

MASS

	BI	CHB	A	TBF	TBB	CHB-RR	H	M
BI	----	-----	-----	-----	-----	--------	-----	----
CHF		----	-----	-----	-----	--------	-----	----
A	*		----	-----	-----	--------	-----	----
TBF	* †	†		----	-----	--------	-----	----
TBB	* †	†			----	--------	-----	----
CHB-RR	* †	* †	*			-------	-----	----
H	* †	* †	*				----	----
M	* †	* †	* †	*	*			--

* For TW, TD, TM; † for LW, LD, LM; and ° for HW, HD, HM indicate difference between indicated stations at least at the $P < 0.01$ level.

(T) bands are also highly correlated (those of high density (H) bands are more independent but, as indicated in the between site comparisons, are relatively constant between sites). These results suggest that subannual band characteristics over the 10-year (1970–1979) period evaluated in St. Croix do not supplement information from annual bands.

In other studies Hudson et al. (1976) and Hudson (1981) have discussed stress bands as subannual band anomalies of often high density occurring within the normal low density band formation, where for Florida this condition is most likely caused by thermal environmental stress. In such a context subannual bands would indeed supplement and extend information from annual bands. In our case we examined normal subannual bands and found variability in characteristics to be approximately the same or slightly less than for annual bands. It is possible at certain, as yet unexamined, sites, or over longer or different time spans than the 1970–1979 (10-year) period we examined, that subannual band characteristics might assume more importance and provide information additional to that from annual bands.

As previously discussed, our parameterization of subannual extension and calcification (mass) are not rates because the exact time duration over which they formed is not known. Relationships between true rates of subannual extension and calcification may be different than for characteristics given above. For example, the results indicate H bands have less extension and mass, but greater density than L bands. If, as indicated by some studies (Hudson et al., 1976; Stearn et al., 1977) H bands form over a very short period, their extension and calcification *rates* may be significantly higher than those of L bands.

Relationships of Growth Parameters

In general, extension is correlated negatively to density and positively to mass. For annual parameters, the correlations are significant but not high, indicating that any single parameter is not an especially good predictor of another. This is graphically shown in Figure 4 where the scatter of data points about the G.M. regression lines is high and the r^2 values are low. If a linear relation with high predictive ability (e.g., $r^2 > 0.90$) had been found between two of the three parameters, then any one of these two and the third parameter would be related but not linearly because of the equality of mass as the product of extension and density. We used the G.M. regression of TW:TD (Fig. 4a—because each was a measured parameter) and then substituted the appropriate form of TM = TW·TD to arrive at the equations of the curves in Figure 4b and 4c. As is evident the curves do not fit the data appreciably better than the G.M. regression lines calculated for the indicated paired data sets. The results suggest that knowledge of one parameter alone is not sufficient for a complete description of coral growth. One variable would be enough only if that variable was highly correlated with another (and the predictive relationship known). We have found parameters to be correlated, but not highly. In addition, we have found that all three parameters vary and are not constant.

A negative relationship between extension and density has been found in other corals. Buddemeier et al. (1974), suggested for Eniwetok corals that because parameters of extension and density varied by roughly equal amounts, their product (mass) would be the least variable of the three. Dodge and Thomson (1974) suggested for Bermuda corals that because extension was found to be more variable than density, the product of the two (mass) would be correlated with extension variations. Given the M = W·D relation, if any two parameters are highly cor-

related and linearly related, the third parameter will vary with the square of any of the other two. The exact variability will depend both upon the slope and constant of the linear relationshps between the original two parameters. The curves of Figure 4b and 4c indicate the relationship between TM and TW, and TM and TD respectively, assuming the G.M. line of Figure 4a described TW and TD completely. In both cases the curves show less range with respect to the TM axis than do the appropriate G.M. lines. Our actual data (Table 3) show, however, that the mass is as variable as extension, and that both mass and extension are more variable than density. Part of this variability is accounted for by measurement error, although the contribution is assumed to be small. (Our estimation procedure for density determination of subannual and annual bands might be improved by image analysis techniques where graphical integration would be facilitated.) Some of the variability arises from the curvilinear relationships but much probably results from environmental factors to be discussed.

Coral Growth in St. Croix

Previous Work.—Gladfelter et al. (1978) determined extension rate on 30 *M. annularis* corals from the reef off the east of Buck Island to be 0.76 cm/yr. Their site was similar in depth and location to site BI of this study, however, our results of 1.16 cm/yr are different. Gladfelter et al. (1978) used a staining methodology to extrapolate each coral's annual growth from only a 3 to 5 month interval during one calendar year. The values obtained in the present study measured extension rate over 10 years on each coral and differences between studies may be explained in this way.

Baker and Weber (1975) reported extension, density, and calcification results determined on St. Croix *M. annularis* corals from an unspecified location and at various depths of collection. Within 0–9 m depths their annual extension values fall within the range of our results. Their average densities are greater than for any of our sites and consequently their average calcification values are also greater. The lack of information on collection location, coupled with their use of a slightly different measurement method for density and mass, precludes a complete understanding of reasons for the differences.

This Study.—Corals from Buck Island (BI), one of the most pristine fore-reef environments of St. Croix had as high an extension rate as those corals primarily from Round Reef within Christiansted Harbor (CHB-RR), a back-reef area under at least some influence of pollution (dredging-induced turbidity and sedimentation, sewage). However, corals at CHB-RR were significantly less dense giving rise to a calcification rate among the lowest of all sites. In comparison, the calcification rate of corals from BI was the highest of any site. It is clear that coral growth at different areas may be similar in certain parameters (in this case extension) but significantly different in others (density and mass) and that measurement of only one parameter does not provide complete information. This result is particularly important but has received only limited attention (Dustan, 1975; Buddemeier et al., 1974). Barnes and Crossland (1980) have shown that subdaily extension rate in the branching coral *Acropora acuminata* does not vary in phase with calcification rate. Gladfelter et al. (1978), demonstrated differential rates of calcification and extension in St. Croix *A. palmata.* Few field or laboratory coral studies, however, determine more than one parameter of skeletal growth sometimes under the implied assumption that extension and calcification rates are equivalent (apparently relying on density as a constant conversion factor). Density is neither constant over time, between corals, nor between sites. Had

extension rate alone been considered in this study, no significant differences between two of the most dissimilar St. Croix sites (CHB-RR and BI) would have been detected.

It should be noted that the results do not indicate and we are not suggesting a rejection of the use of extension rate to characterize coral growth. The significant point to be drawn is that other parameters (density and mass) are available and, at least for this study, provide additional information on growth. Evaluation of a single growth parameter therefore should not be taken as equivalent to analysis of all parameters.

For complete clarification of issues it should also be noted that this study has evaluated growth within individual corals over the same 10-year growth period. Size and age relationships, from which size-frequency distributions and survivorship/mortality curves might be derived, are not considered here. Thus, the cautions about colony partial mortality, fission, and fusion expressed by Hughes and Jackson (1980) do not apply. Rather than size, we have assessed a most direct means of coral growth, internal time-dependent skeletal banding which can record the growth processes of the coral over many years in the past.

Reasons for variability between growth parameters and between sites are not completely understood. Water temperature is considered a major control on coral growth (Weber and White, 1977); however, we lack a detailed temperature history of each site over time. The general Caribbean setting and relatively rapid rates of water mixing around St. Croix would, however, seem to argue against any substantial average temperature difference between sites. Light level, necessary for coral zooxanthellae photosynthetic activity, is well known to control coral calcification to some extent (Goreau and Goreau, 1959). A comparison of growth parameters with collection depth of a site reveals no obvious depth relationship. This is not unreasonable given that Baker and Weber (1975) found fairly homogenous growth characteristics (extension, density, and calcification) within sites 9 m or less in depth, but more pronounced changes over greater depth ranges. Finally, we are aware of no quantitative comparison of growth rate differences between hemispherical and columnar growth forms of *M. annularis* sampled at similar locations. In this study we restricted attention to columnar forms and those forms transitional between hemispherical and columnar (Table 1). There was no obvious relationship between site growth parameters and general colony growth form; however, slightly differing growth forms may introduce extra variability into the results.

For the case of CHB-RR, with low density and calcification, it is possible that the environment is a major influence promoting growth anomalies. Massive dredging within the Harbor has occurred many times for sand mining and channel construction and maintenance. A sewage outfall is present seaward of Long Reef and raw sewage also enters the Harbor directly along the city waterfront. Wind-forced circulation results in sewage and natural and/or dredge-related sedimentation and turbidity exiting the Harbor through the western ship channel and over Round Reef (Dong et al., 1972), the site of our collection for CHB-RR. Bak (1978) has shown that dredging-induced turbidity can depress coral calcification. Phosphate is also considered a detriment to calcification in reef corals (Simkiss, 1964) and elevated levels are present in the Harbor from sewage. It is unclear why extension rate at CHB-RR is high. Turbidity and sedimentation can depress coral extension under some conditions (Dodge et al., 1974; Dodge and Vaisnys, 1977; Loya, 1976); however, this effect is not observed in the CHB St. Croix corals.

Harbor conditions may have been only sufficiently adverse to have depressed calcification while extension was unaffected (or possibly promoted). In other words,

corals could have maintained extension rates but were unable to calcify normally because of dredging and/or sewage pollution. This does not satisfactorily explain why CHB extension rates should be among the highest of any group of corals examined in St. Croix. Several alternatives are possible. The high extension of CHB corals could be a response to moderately adverse Harbor conditions where the corals are maximizing extension in an attempt to gain elevation (and distance away from irritants—either or both sedimentation and sewage) as rapidly as possible. Barnes and Crossland (1980) have indicated extension is dependent upon the form of the architectural elements of the skeleton while calcification is more controlled by their bulk or size. Certain stress situations may promote scaffold building (extension), even while bricks and mortar (calcification) are relatively unavailable to shore up the structural framework. Another possibility is that the high extension rate is a response to increased nutrient loading from sewage, even in the face of lowered calcification rates. Several other studies (Dodge and Vaisnys, 1975; Glynn, 1977) have shown that coral extension appears positively correlated to nutrient supply. Perhaps for site CHB-RR, increased phosphate levels are inhibiting calcification while general increased nutrients are at the same time promoting extension. Continued analysis will be necessary to more precisely identify causation of the observed growth anomalies.

Limitations on coral growth between sites along the south coast of St. Croix are more complex. The force of Hurricanes David and Frederic in 1979 was concentrated on the south coast and caused widespread, but patchy, damage and mortality (Rogers et al., 1982; personal observation). Woodley et al. (1981) has described the effects of a similar storm (Hurricane Allen in 1980) on Jamaican reefs as impressive for their speed, magnitude and patchiness. Our collection locations of M and A were originally chosen as possible controls for site H. Site M was, however, the most clearly affected by storm damage, while site A was the least. Hurricane effects have allowed collection of only those corals which survived the storms. The growth of these corals probably does not represent prior average reef conditions, but rather is related to factors promoting survival. Such factors could have included a habitat overshadowed by former lush *A. palmata* stands which, however, was not conducive to optimum growth for protected understory head corals. If site M is omitted from comparisons, site H (near the location of massive prior dredging, possible oil spills, and industrial effluent) has the lowest extension and calcification of any site.

Depressed growth at site H may be the result of pollution effects. Our collection area in the back-reef lagoon did not include a former *A. palmata* community and storm-induced coral breakage and mortality was not obvious. Corals collected at site H also had the highest rejection rate from analysis (Table 1). At one of the columnar clumps that we sampled, 7 of the 8 collected corals were acceptable. At the other clump, 7 of the 8 collected specimens were discarded because of unclear banding. We are unable to provide a satisfactory explanation for this because the collections were in the same general environment and water depth. In addition to the low calcification and extension of corals measured at site H, we have identified elevated levels of trace metals within the skeletons of selected specimens. The chemical pollution indicators appear related to dredging events (Brass and Dodge, in preparation).

Further growth studies would be helpful to assess relationships of pollution and corals. Given the variability within sites found in this study, it would be prudent to include both an increased number of sites, depth intervals, and specimens per site and perhaps a comparison between growth forms. It should be noted that the results presented here are only valid for the 10-year period, 1970–1979. For

Christiansted Harbor large-scale environmental degradation began in the mid-1960's with sand mining; however, dredging and sewage pollution have also been a feature of the 1970's. The corals are recording both 1970's activities and cumulative effects from earlier times including disruption of natural bottom, characteristics which have created greater mobilization of sediment and turbidity. Similarly for the Hess lagoon site, maintenance dredging in the 1970's as well as cumulative effects from the large-scale disturbance in the 1960's are probably influencing the coral growth record. For more confidence in assessing coral/environmental relations, a longer span of growth data is desirable.

Further growth studies would also be helpful for understanding the linkages between extension, density, and calcification of the coral skeleton. This study has shown there are relationships between the three parameters but that no one parameter alone is a perfect predictor of another. Genetic and/or environmental factors are the ultimate controls on each aspect of coral growth and continued investigation is necessary for complete understanding.

CONCLUSIONS

The low density portion of the annual band cycle in *Montastrea annularis* has greater extension, lower density, and greater mass than the corresponding high density portion. Variability is concentrated in annual and low density bands, characteristics of which are highly correlated. The high density band portion is relatively less variable (for extension and mass) and its characteristics are not well correlated to the other bands. The characteristics of the parameters of annual bands contain as much or more information than those of the subannual bands.

Skeletal extension, density, and mass of *M. annularis* corals are correlated. No parameter alone, however, is a perfect predictor of another. At least two, from which the third can be calculated, are required for a complete description of coral growth.

Coral growth at separate sites can have similar magnitudes in one parameter but can be different in other parameters. While the extension rates of sites BI and CHB are similar, site CHB has significantly reduced density and calcification rate.

Depressed calcification and density at CHB is probably related to environmental pollution (dredging and sewage) within Christiansted Harbor. Dredging and/or other pollution effects near site H are possibly reflected in the relatively low extension and calcification of its corals. Hurricane effects may have biased some south collections, thus complicating the interpretation of the south coast data.

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LITERATURE CITED

Adams, J. B. 1974. Environmental geology of St. Croix: the impact of man on the natural resources of an island. Pages 145–154 *in* H. G. Multer and L. C. Gerhard, eds. Guidebook to the geology and ecology of some marine and terrestrial environments, St. Croix, U.S. Virgin Islands. Spec. Pub. 5. West Indies Lab, Fairleigh Dickinson Univ.

Adey, W. 1975. The algal ridges and reefs of St. Croix: their structure and Holocene development. Atoll Res. Bull. No. 187. 66 pp.

———, W. Gladfelter, J. Ogden and R. Dill. 1977. Field guidebook to the reefs and reef communities of St. Croix, Virgin Islands. 3rd Symp. on Coral Reefs, Univ. of Miami, Miami, Florida. 52 pp.

Aller, R. C. and R. E. Dodge. 1974. Animal-sediment relations in a tropical lagoon—Discovery Bay, Jamaica. J. Mar. Res. 32: 209–232.

Bak, R. P. M. 1974. Available light and other factors influencing growth of stony corals through the year in Curacao. Proc. 2nd Int. Coral Reef Symp. 2: 229–233.

———. 1978. Lethal and sublethal effects of dredging on reef corals. Mar. Poll. Bull. 9: 14–16.

Barnes, D. J. and C. J. Crossland. 1980. Diurnal and seasonal variations in the growth of a staghorn coral measured by time-lapse photography. Limnol. Oceanogr. 25: 1113–1117.

——— and D. L. Taylor. 1973. *In situ* studies of calcification and photosynthetic carbon fixation in the coral *Montastrea annularis*. Helgol. Wiss. Meers. 24: 284–291.

Buddemeier, R. W. 1974. Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. Proc. 2nd Int. Coral Reef Symp. 2: 259–267.

———. 1978. Coral growth: retrospective analysis. Pages 551–571 *in* D. R. Stoddart and R. E. Johannes, eds. Coral reefs: research methods. UNESCO, Paris.

——— and R. A. Kinzie. 1976. Coral growth. Oceanog. Mar. Biol. Ann. Rev. 14: 183–225.

———, J. E. Maragos and D. W. Knutson. 1974. Radiographic studies of reef coral exoskeleton: rates and patterns of coral growth. J. Exp. Mar. Biol. Ecol. 14: 179–200.

Coles, S. L. and P. L. Jokiel. 1978. Synergistic effects of temperature, salinity, and light on the hermatypic coral *Montipora verrucosa*. Mar. Biol. 49: 188–195.

Dodge, R. E. 1978. The natural growth records of reef building corals. Ph.D. Thesis, Yale Univ., New Haven. 237 pp.

———. 1980. Preparation of coral skeletons for growth studies. Pages 615–618 *in* D. C. Rhodes and R. A. Lutz, eds. Skeletal growth of aquatic organisms. Vol. 1. Topics in geobiology. Plenum, New York.

——— and J. Thomson. 1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. Earth Planet Sci. Lett. 23: 313–322.

——— and J. R. Vaisnys. 1975. Hermatypic coral growth banding as environmental recorder. Nature. 258: 706–708.

——— and ———. 1977. Coral populations and growth patterns: response to turbidity and sedimentation associated with dredging. J. Mar. Res. 35: 715–730.

——— and ———. 1980. Skeletal growth chronologies of recent and fossil corals. Pages 493–517 *in* D. C. Rhodes and R. A. Lutz, eds. Skeletal growth chronologies of aquatic organisms. Vol. 1. Topics in geobiology. Plenum, New York.

———, R. A. Aller and J. Thomson. 1974. Coral growth related to resuspension of bottom sediments. Nature 247: 574–577.

Dong, M., J. Rosenfeld, G. Redmann, M. Elliott, J. Balazy, B. Poole, K. Ronnholm, D. Kenigsberg, P. Novak, C. Cunningham and C. Karnov. 1972. The role of man-induced stresses in the ecology of Long Reef and Christiansted Harbor, St. Croix, U.S. Virgin Islands. West Indies Lab Rept. Fairleigh Dickinson Univ., St. Croix. 190 pp.

Dustan, P. 1975. Growth and form in the reef-building coral *M. annularis*. Mar. Biol. 33: 101–107.

Fairbanks, R. G. and R. E. Dodge. 1979. Annual periodicity of the $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios in the coral *Montastrea annularis*. Geochim. Cosmochim. Acta 43: 1009–1020.

Gladfelter, E. H., R. K. Monahan and W. B. Gladfelter. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. Bull. Mar. Sci. 28: 728–734.

Glynn, P. W. 1977. Coral growth in upwelling and non-upwelling areas off the Pacific coast of Panama. J. Mar. Res. 35: 567–585.

——— and R. H. Stewart. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol. Oceanogr. 18: 367–379.

Goreau, T. F. 1959. The ecology of Jamaican coral reefs. 1. Species composition and zonation. Ecology 40: 67–90.

——— and N. I. Goreau. 1959. The physiology of skeletal formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. Biol. Bull. 117: 239–247.

Graus, R. R. and I. G. Macintyre. 1976. Light control of growth forms in colonial reef corals: computer simulation. Science 193: 895–897.

Hudson, J. H. 1981. Growth rates in *Montastrea annularis*: a record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. Bull. Mar. Sci. 31: 444–459.

———, E. A. Shinn, R. B. Halley and B. Lidz. 1976. Sclerochronology: a tool for interpreting past environments. Geology 4: 361–364.

Hughes, T. P. and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. Science 209: 713–715.

Isdale, P. 1977. Variations in growth rate of hermatypic corals in a uniform environment. Proc. 3rd Int. Coral Reef Symp. 2: 403–408.

Jokiel, P. L. and S. L. Coles. 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. Mar. Biol. 43: 201–208.

Knutson, D. W., R. W. Buddemeier and S. V. Smith. 1972. Coral chronometers: seasonal growth bands in reef corals. Science 177: 270–272.

Lewis, J. B. 1960. The coral reefs and coral communities of Barbados, W.I. Canadian Jour. Zoology 36: 1133–1145.

Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. Bull. Mar. Sci. 26: 450–466.

Macintyre, I. G. and S. V. Smith. 1974. X-radiograph studies of skeletal development in coral colonies. Proc. 2nd Int. Coral Reef Symp. 2: 277–287.

Nichols, M., D. Grigg, A. Sallenger, R. van Eepoel, R. Brody, J. Olman and R. Crean. 1972. Environment, water, and sediments of Christiansted Harbor. St. Croix–Caribbean Research Institute. 125 pp.

Ogden J. C., ed. 1972. An ecological study of Tague Bay reef, St. Croix, U.S. Virgin Islands. West Indies Laboratory Spec. Publ. 1. 51 pp.

Ricker, W. E. 1973. Linear regression in fisheries research. Jour. Fish. Res. Board Canada 30: 409–434.

Rogers, C. S., T. H. Suchanek and F. A. Pecora. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. Bull. Mar. Sci. 32: 532–548.

Simkiss, K. 1964. Phosphates as crystal poisons of calcification. Biol. Rev. 39: 487–505.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco. 776 pp.

Stearn, C. W., T. P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I. Zonation and productivity. Bull. Mar. Sci. 27: 479–510.

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. Pages 171–179 *in* S. H. Frost, M. P. Weiss and J. B. Saunder, eds. Reefs and related carbonates—ecology and sedimentology. A.A.P.G. Studies in Geology No. 4.

————, ————— and P. H. Weber. 1975. Correlation of density banding in reef coral skeletons with environmental parameters: the basis for interpretation of chronological records preserved in the coralla of corals. Paleobiology 1: 137–149.

Woodley, J. D., P. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdam, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Nigel and E. M. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214: 749–755.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 620 pp.