Skeletal Structural Basis of Density Banding in the Reef Coral *Montastrea Annularis*

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Abstract. Density banding in coral skeletons can provide for reconstruction of the coral's growth environment over long periods. The physical differences between low and high density portions of a skeletal band are not well understood. The skeletal architecture of *M. annularis* from Southeast Florida, the Florida Keys, St. Croix, the Bahamas, and Mexico was compared in X-ray revealed high density (HD), low density (LD), and stress HD bands. Density changes arose from differences in the size, but not spacing, of exothecal structural elements (horizontal dissepiments and vertical costae). Endothecal architecture size (e.g., columella, dissepiments, septa) was relatively constant between density band types. Results have implications for studies of coral growth, sclerochronology, and isotopic/trace element composition.

Introduction

The calcium carbonate skeletons of many reef-building corals contain growth increments, composed of alternating cycles of high and low bulk density. These density bands are visible through X-radiography of medial skeletal slabs and form annually (Knutson et al., 1972; Dodge and Thompson, 1974; Hudson et al., 1976; Wellington and Glynn, 1983). The coral skeleton, therefore, contains a chronology of annual growth variations during an often long life span. In addition, density bands provide a framework within which to mea-

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sure various types of chemical information locked within the coral skeleton, including trace and minor elements, organic material, and stable isotopes of oxygen and carbon. Quantitation of skeletal growth changes or chemical signals can provide important environmental information on past climate or ecological events or processes which have influenced the health of the coral animal.

A variety of studies have utilized coral growth banding per se for evaluating climate and environmental relationships or perturbations. Dodge et al. (1974) found growth rates of *Montastrea annularis* in Discovery Bay, Jamaica were decreased in specimens from regions of high resuspension of bottom sediment. This has been supported by other research in Puerto Rico (Loya 1976), Bermuda (Dodge and Vaisnys 1977), the Florida Keys (Hudson 1981), St. Croix (Dodge and Brass 1984), Barbados (Tomascik and Sander 1985), and Costa Rica (Cortes and Risk 1985). Dodge and Lang (1983), Dodge and Vaisnys (1975), Hudson et al. 1989, and Lough and Barnes (1990) have explored coral climate relations. The oxygen and carbon isotope composition of the coral skeleton can provide important environmental information (e.g., Fairbanks and Dodge 1974; Swart 1983; McConnaughey 1989; Leder et al. 1991). Skeletal extension, density, and calcification are all parameters which can provide information on environmental effects (Buddemeier 1974; Dodge and Thompson 1974; Dodge and Brass 1984).

Coral sclerochronology has been heralded implicitly and explicitly as the marine counter-part to terrestrial dendrochronology and dendroclimatology. Work with tree rings has been productive in relating growth to climate (Fritts 1976; Hughes et al. 1982). This success has been enjoyed in part because of the understanding of the growth re-

sponse of trees to their environment which has developed over many years of research. Similar understanding in terms of coral skeleton organization and coral growth response is less well developed for sclerochronology (Lough and Barnes 1990).

Previous work relating banding to skeletal structure

It is notable that there has been relatively little work describing the physical differences in structure between coral skeleton containing the high and low density bands. Such work is important because it is basic to the understanding of the coral annual band and to the productive use of bands for reconstruction of environmental information.

One group of investigators has felt that thickness of skeletal architecture is most important for determining type of band expressed in the X-radiograph. Macintyre and Smith (1974) reported for *Pavona gigantea* from Panama that dissepiment spacings did not vary within dense and less dense bands (within and throughout the annual cycle). In Atlantic *Solenastrea hyades* the dense band portions were reported by Macintyre and Smith (1974) to be related to a thickening or coalescing of exothecal dissepiments. Buddemeier and Kinzie (1975) indicated for *Porites lobata* from Hawaii that density variations are associated with systematic variations in the thickness and possibly alignment of the trabeculae. Emiliani et al. (1978) considered that the high density layer of *Montastrea annularis* "appears to be produced by a temporary thickening of dissepiment structures and closer bundling of sclerodermites".

An alternative hypothesis of the physical cause of density banding has been presented by Buddemeier et al. (1974). From microscopic and SEM examinations of *Favia* and *Astreopora*, they reported the impression that size variations in skeletal elements were inadequate to account for bulk density variations and proposed that the density changes result from long-term variations in the orderliness of packing of the aragonite needles. This is based largely on Barnes' (1970) observations that lowered calcification at night results in ordered, closely packed aragonite needles while more rapid daytime calcification produces more random and less dense packing (see also Gladfelter, 1982, 1983, 1984).

Buddemeier et al. (1974) report that variability in either the organic content or the trace element composition of coral skeletons is insufficient to account for observed density changes which manifest themselves in the X-ray revealed banding. They discussed two possible sources for the X-ray banding: changes in bulk density due to aragonite needle packing within skeletal structures and organization of the skeletal structures themselves. Barnes and Devereux (1988) have termed crystal packing as skeletal micro-architecture. They term skeletal meso-architecture as "the way in which the skeletal elements" (septa, thecae, and dissepiments) "are arranged to form the fundamental unit of a coral colony, the corallite; and where appropriate, the arrangement of skeletal elements linking adjacent corallites." Macro-architecture is described as the arrangement of corallites within a colony. For *Porites* Barnes and Devereux (1988) conclude that X-ray density of *Porites* can be essentially entirely explained by variation in meso-architecture. Barnes and Lough (1989) declared that "the annual banding pattern in *Porites*, and in many, if not all, massive corals, appears to be composed of" groupings of fine dense bands, arising from alignment of thickened skeletal spines.

Purpose of this paper

In this paper we report on measurements and observations of skeletal structures within high density (HD) and low density (LD) band portions of *Montastrea annularis*. We adopt the term meso-architecture of Barnes and Devereux (1988) to describe arrangement and size of the familiar skeletal structural building blocks (septa, dissepiments, costae, columella, etc.). We accept the premise of Barnes and Devereux (1988) that micro-architecture is not a primary cause of density banding.

The coral species currently known as *M. annularis* has been one of the most abundant, widely distributed, and widely studied in the Caribbean and tropical Atlantic (Knowlton et al. 1992, Buddemeier and Kinzie 1975). It is often the coral of choice for studies involving banding and environmental relationships (e.g., Fairbanks and Dodge 1979; Hudson 1981; Dodge and Lang 1983; Leder et al. 1991). Nevertheless, there has never been a systematic study of the architectural nature of banding in this general species (or in its three sibling species) other than Emiliani et al.'s (1978) observations.

Methods

Work described here was conducted with specimens of the reef building coral *Montastrea annularis* collected from five different locations and encompassing the three morphotypes of Knowlton et al. 1992. The samples are described in more detail

below. Figure 1 shows X-radiograph positives of four specimens. The fifth specimen is shown in Figure 8.

• Southeast Florida, specimen numbers BR-8 and BR-2, were collected March, 1984 from 6 m depth on the Second Reef off Ft. Lauderdale, Florida. The growth forms of each were approximately hemispherical and were morphotype 2. BR-8 was used for the LD-HD dissepiment thickness-spacing measurements. BR-2 was used for costae and septa thickness measurements. X-radiography revealed a time span of 1984–1914 for BR-2 and for 1984–1950 for BR-8.

• Florida Keys, specimen number MR-2, was cored (5 cm diameter) Aug., 1986 by Harold Hudson in 5 m depth from an approximately hemispherical, morphotype 2 colony on Molasses Reef, Key Largo National Marine Sanctuary. X-radiography revealed a time span of 1986–1933. A portion of the coral containing normal banding as well as the 1970 stress band (as described by Hudson et al. 1976) was used.

• Bahamas, specimen number C3X-C, was cored (3 cm diameter) July, 1990 (Szmant et al. 1991) in 5 m depth from a hemispherical, morphotype 2 colony on Jolters Key, Bahamas. X-radiography revealed a time span of 1990–1984.

• Mexico, specimen number MX-2, was collected by John Tunnell in Jan., 1986 from shallow depth from Alacran Reef off the Yucatan, Mexico. This morphotype 3 colony was approximately 60 cm in diameter. X-radiography revealed a time span of approximately 1985–1966.

• St. Croix, specimen number C-91 was collected from the back reef at Tague Bay, St. Croix, USVI in 6 m depth in Dec., 1980. Growth form was columnar, morphotype 1. X-radiography revealed a total year span of 1980–1956 (Dodge and Brass 1984).

Sectioning, X-radiography, and macrophotography

For initial X-radiography, coral specimens were cut with masonry saws into parallel sided slabs, normal to growth band boundaries. Separate slabs ranged in thickness from approximately 5 mm to 2 mm. Slabs were X-radiographed onto paper covered Kodak AA Industrex X-ray film using a source to subject distance of 1 m and exposure of 50 KVP, 10 ma, and from 5 to 20 seconds. X-ray negatives were

SE Florida

St. Croix
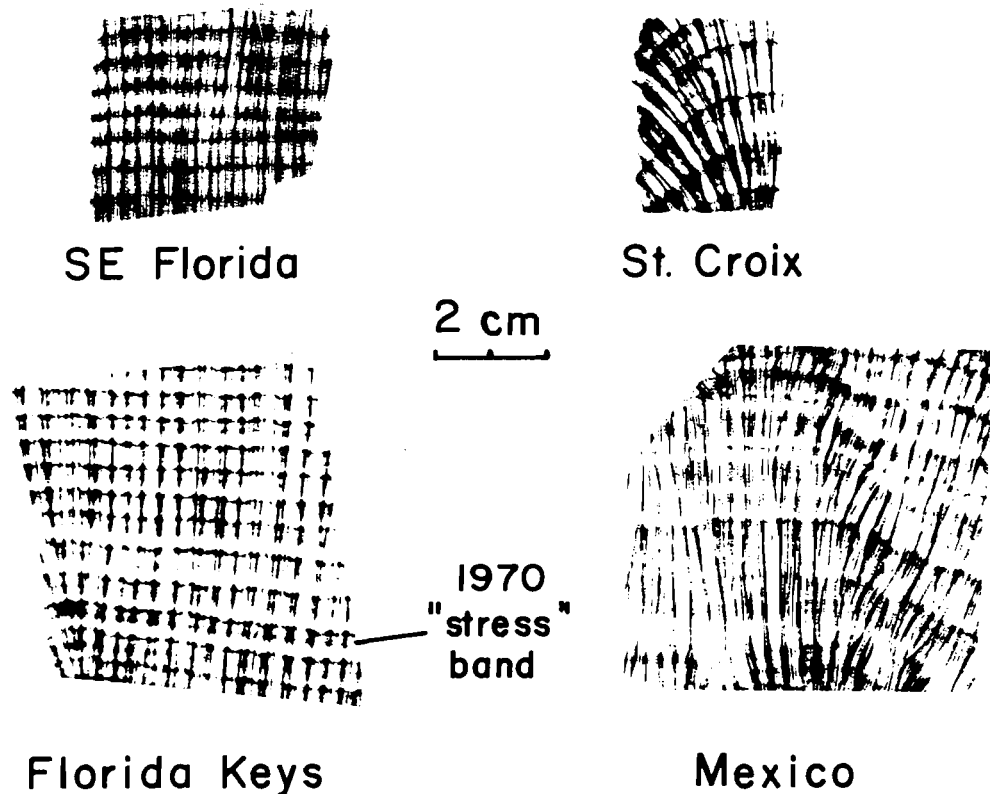
2 cm

1970
"stress"
band

Florida Keys

Mexico

Fig. 1. X-radiograph positive prints of portions of skeletal slabs from *M. annularis* specimens collected from Southeast Florida (BR-8), St. Croix, the Florida Keys, and Mexico. Details of specimens are given in text. Measurements were taken on skeleton comprising selected contiguous HD and LD band portions. For the Florida Keys coral, measurements were also taken from the indicated 1970 HD, stress, and LD band.

developed and printed onto to produce X-ray positives.

For samples from Southeast Florida (BR-8) and St. Croix, smaller pieces (approximately 2.5 cm by 2.5 cm) of the original slab, encompassing these areas, were cut and used for more detailed procedures. In order to provide a stable platform (for later grinding), the coral pieces were attached using Epoxy to glass slides. Reference holes were placed into the slabs with a fine dentist drill. These specimens were sequentially ground away in 0.1 mm intervals using a geologist's thin section maker. After each grinding, specimens were dried briefly and macrophotographed using a 35 mm TTL camera with 35 mm lens and 28 mm extension tube. Exposure was set according to the light meter of the camera; however, a +1 lens aperture opening was found to provide the best exposure. A bullseye level was used to maintain the camera film parallel to the subject. X-radiographs of each slab were taken at 1 mm intervals. Thus approximately 50 photographs and 5 X-radiographs were available for each slab. These provided a suite of internal views of the coral macro- and meso-architecture as well as X-radiography of the same slab at varying thicknesses. X-radiograph negatives were subsequently printed on paper to make positives. To facilitate comparisons, X-radiograph negatives and positives were macrophotographed at the same scale as the slab macrophotographs.

Similar procedures of initial X-radiography, isolation of areas of interest, and macrophotography (both photographic and video) were followed for specimens from the Florida Keys, the Bahamas, and Mexico but sequential grinding was not conducted on these specimens. For the Bahamas specimen several sections at varying thicknesses were produced to determine whether slab thickness influenced the measurement of bulk density. Each of these slabs was X-radiographed and assessed for use in dissepiment measurements. For the Florida Keys coral, a separate additional area of interest encompassing the 1970 "stress" band was macrophotographed.

In order to observe horizontal cross sections of skeletal structure within various band densities, cubes of skeleton from a Southeast Florida (BR-2) and the St. Croix coral were cut from portions of each colony where the growth surface was nearly flat. A thin slab was taken from one side of each cube (perpendicular to the growth surface) and X-radiographed. Revealed density bands were used to locate band positions in the cubes. The cubes were ground parallel to the growth surface to levels coincident with the high and low density bands. Ma-

crophotographs were taken of the surface of the cube at each interval to provide a plan section view of the polyp architecture corresponding to high density and low density band portions.

Measurements

Measurements were made of meso-architecture structures within high and low density band portions for each of the corals. The general measurement tool was the JAVA image analysis system (Jandel Scientific). Macrophotographs (or in some cases the coral slabs) were imaged using a high resolution (greater than 500 scanning lines) RCA video tube or CIDTEC CCD television camera. Images were next digitized using a Data-Translation frame capture board at resolution of 512 × 512 pixels. Java software allows the user to select points of interest and obtain distance measurements between them. Areas of interest were chosen subjectively as those locations which showed good examples of well formed density banding. Areas of poor banding were avoided for detailed analysis.

Exothecal dissepiment thickness and spacing (vertical sections)

Measurements were taken along transects established parallel to the growth direction and placed on selected exothecal areas which spanned density band couplets (Fig. 2). (Endothecal areas did not show clear visual architectural differences and were not measured in vertical sections). Typically one to three bands of each type were selected and from four to five vertical transects were placed through the bands. Thicknesses of horizontal exotheca dissepiments were measured along each transect. The spacing was measured from dissepiment midpoint to dissepiment midpoint along the transect. The measurements were categorized as within the high or low density band portions. The categories of high and low density were assigned by comparison of the macrophotograph of the X-radiograph to the slab macrophotograph. Drill hole landmarks on the coral slab were often used for aligning X-radiography and macrophotography and for scaling. Two separate sections were observed for the Southeast Florida (BR-8), the Florida Keys regular and stress band samples, and the Bahamas corals. For the St. Croix and Mexico corals, 4 sections were observed.

Exothecal and endothecal thickness of costa and septa (horizontal sections)

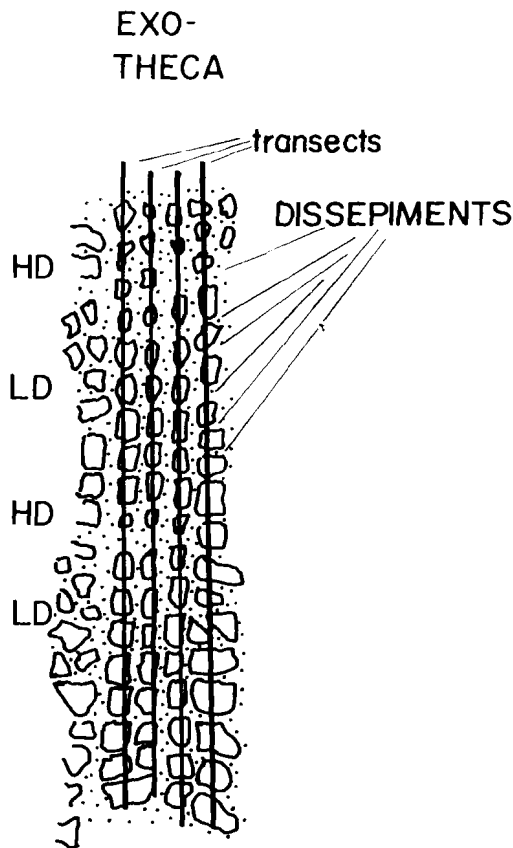Plan view macrophotographs of horizontal sections through high density and low density skeleton were

Fig. 2. Sketch of vertical section of exothecal area of a coral skeleton. Stippled areas represent skeleton, blank areas represent void space. Black vertical lines depict transect positions along which dissepiment thickness and spacing were measured. The approximate position of HD and LD bands are shown as derived from X-radiography of the section.
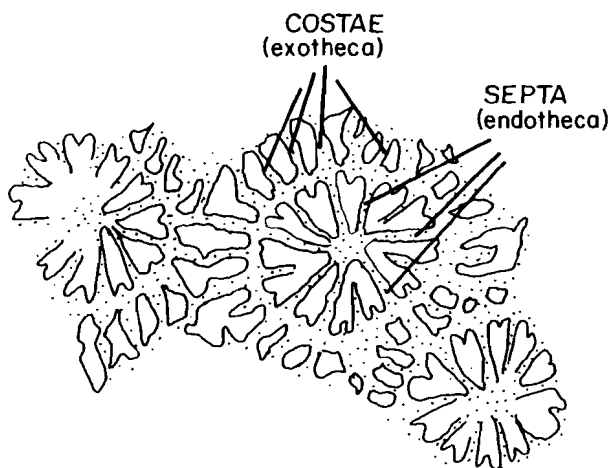
video imaged and digitized as described above. Measurements were made in corresponding regions of the high and low density band sections surrounding and within 5 corallites (polyps). Thickness of costae was measured in exothecal areas. Thickness of primary septa was measured in endothecal areas. For Southeast Florida coral (BR-2) costa thicknesses were measured on two HD and two LD bands. For both the Southeast Florida coral (BR-2) and the St. Croix coral (C-91), exotheca costa thicknesses and endotheca septum thickness were measured on one HD and one LD band. Fig. 3 illustrates a sketch plan view of costae and septa.

Results

Exothecal dissepiment thickness and spacing (vertical sections)

Figures 4 & 5 show mean LD and HD exotheca dissepiment thickness and spacing measurements for each coral. Mean thickness and spacing for each density type were compared by one-way ANOVA. Low density band dissepiment thickness is significantly lower ($p < 0.05$) than thickness of the corresponding high density band in every comparison (Fig. 4). There is no significant difference in each comparison between dissepiment spacing within the low density and high density bands for each coral (Fig. 5).

Exotheca Dissepiment Thickness

Fig. 3. Sketch illustrating a plan view section of skeleton of *M. annularis*. Stippled area represents skeleton; blank area represents void space. Thicknesses of primary septa and of costae were measured for and surrounding five corallites (polyps).
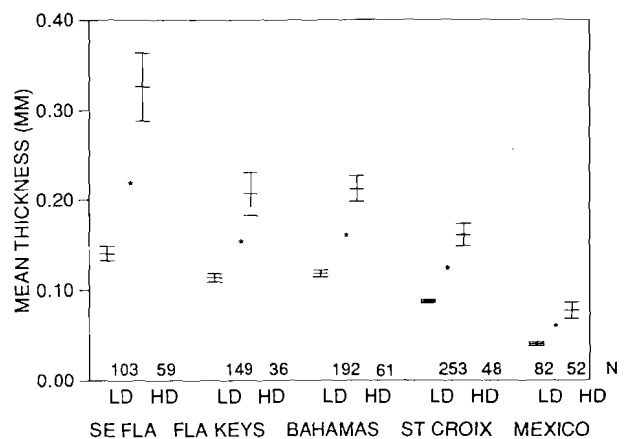
Fig. 4. Mean exothecal dissepiment thickness (mm) for LD and HD bands in *M. annularis corals* from Southeast Florida, Florida Keys, Bahamas, St. Croix, and Mexico. Error bars represent ±1 standard error. An asterisk, when present, between indicated LD-HD pairs indicates significant difference by t test among those means at least at the $p < 0.05$ level. Numbers indicate sample size (N) of means.
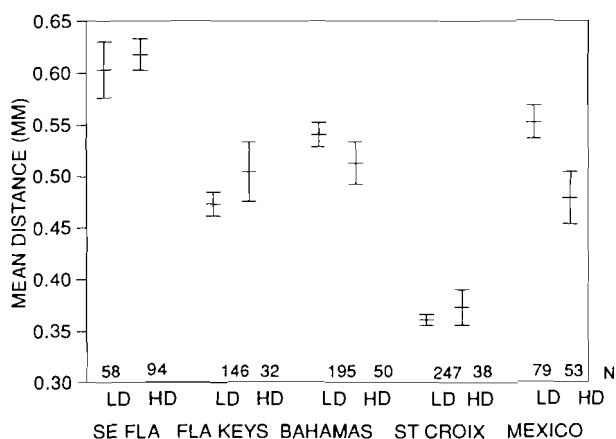
Exotheca Dissepiment Spacing

Fig. 5. Mean exothecal dissepiment spacing (mm) for LD and HD bands in *M. annularis* corals from Southeast Florida, Florida Keys, Bahamas, St. Croix, and Mexico. Error bars represent ±1 standard error. An asterisk, when present, between indicated LD-HD pairs indicates significant difference among those means by t test at least at the p < 0.05 level. Numbers indicate sample size (N) of means.

Exotheca Dissepiment
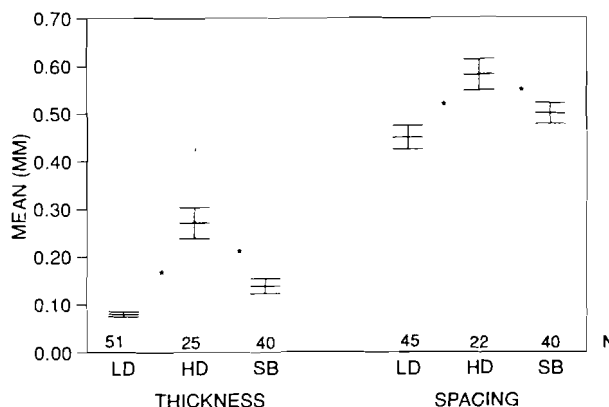### Regular (HD & LD) & Stress Bands

Fig. 6. Mean exothecal dissepiment thickness and spacing (mm) for LD, HD, and SB (stress bands) bands in a colony of *M. annularis* from the Florida Keys. Error bars represent ±1 standard error. An asterisk, when present, between indicated LD-HD pairs indicates significant difference among those means by t test at least at the p < 0.05 level. Numbers indicate sample size (N) of means.

Figure 6 shows means of exotheca dissepiment thickness and spacing measurements from sections of the Florida Keys coral which included the 1970 stress band (as described by Hudson et al. 1976). Dissepiment thickness is significantly different among band types and is greater in the HD band portion, intermediate in the stress band portion, and lowest in the LD band portion. Mean spacing shows similar, but less pronounced differences.

Exothecal and endothecal thickness of costa and septa (horizontal sections)

Figure 7 shows mean exotheca costa and endotheca septum thickness measurements from horizontal sections of LD and HD bands of the Southeast Florida (BR-2) and the St. Croix specimens. Exothecal costae thicknesses are significantly greater in HD band portions for both specimens. However, endothecal septum thicknesses are not significantly different between HD and LD bands.

Density band location in skeletal architecture

Observation of the continuity and position of HD and LD bands within the coral skeleton was facilitated by sequential grinding of coral sections coupled with X-radiography at intervals as well as X-radiography of multiple slabs of various thickness from the same coral. When slab thickness was substantially greater than 1 corallite in thickness (ap-

Element Thickness
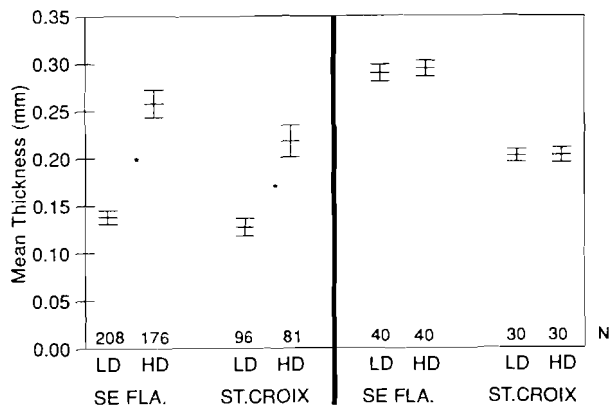### COSTAE   SEPTA

Fig. 7. Mean exothecal costae thickness and endothecal septa thickness (mm) for LD and HD (stress bands) bands in horizontal sections of *M. annularis* from the Southeast Florida and St. Croix. Error bars represent ±1 standard error. An asterisk, when present, between indicated LD-HD pairs indicates significant difference among those means by t test at least at the p < 0.05 level. Numbers indicate sample size (N) of means.

proximately 2 mm), high density bands appeared generally continuous and parallel to the growth surface. As the slab became thinner and when corallites were centered within the slab, HD bands became discontinuous and isolated within exothecal skeleton areas. Fig. 8a shows an X-radiograph of a 1.7
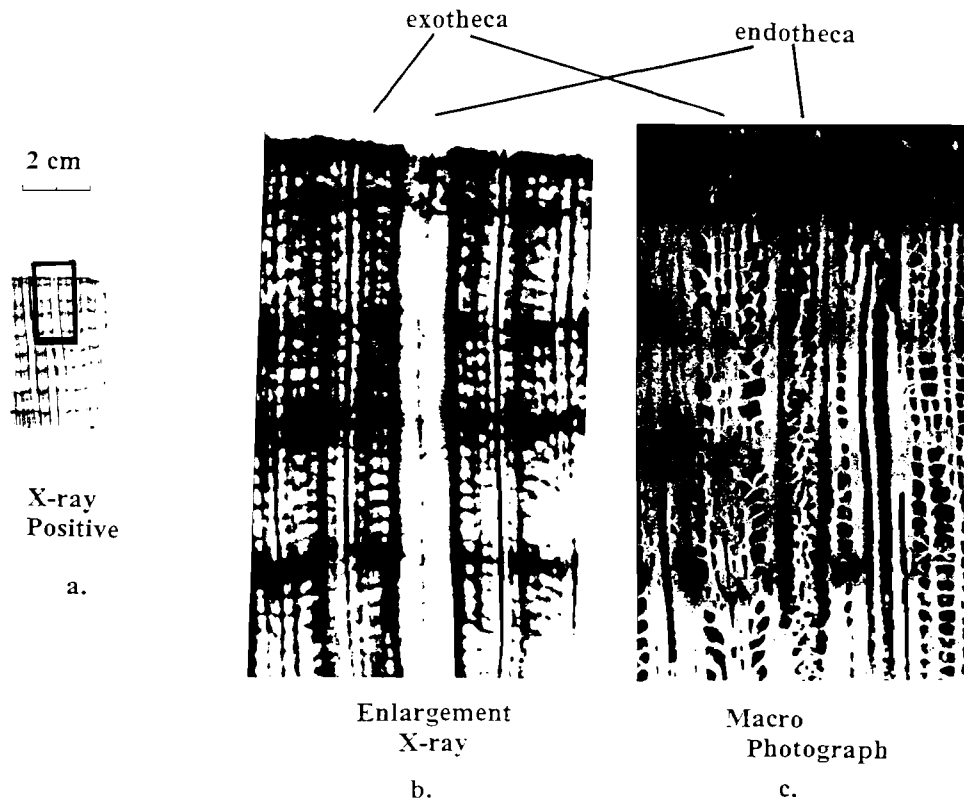
Fig. 8. a) X-radiograph positive print of 1.7 mm thick slab of Bahamas *M. annularis*. Black outlined area shows b) enlargement of X-radiograph with exothecal and endothecal areas included. c) macrophotograph enlarged to same scale as enlarged X-ray. HD bands appear restricted to exothecal area.

mm slab of the Bahamas coral. Fig. 8b (enlargement of 8a) shows an area of good bisection of a corallite. HD density bands do not traverse the endothecal area. Fig. 8c is a macrophotograph of one side of the X-rayed slab enlarged to the same scale as the X-ray positive, showing that the thickening and thinning of skeletal meso-architecture appears more dominant in the exotheca.

Discussion

Review of skeletal meso-architecture

Veron (1986) succinctly describes architectural arrangements within a coral skeleton. The skeleton of a polyp (termed corallite) is a tube containing vertical plates radiating from the tubes center. The tube is the corallite wall. The vertical plates are septa when they are within the tube (endotheca) and costa when they are not (exotheca). Tubes are connected together by horizontal structures. Wells (1956) indicates that costae can also be confluent between corallites. Dissepiments are more or less horizontal partitions cutting off coral tissue from lower parts. Dissepiments between septa within the corallite are endothecal. Dissepiments outside the

corallite between costae are exothecal. These may be vesicular (blister like) nearer the corallite walls or generally tabular (flat).

Banding and meso-architecture

We have investigated changes in thickness and spacing of skeletal meso-architectural elements in high and low density band portions of various specimens of the coral *Montastrea annularis*. Our general results indicate the following. High density banding is primarily a consequence of exothecal horizontal dissepiments and vertical costae which are thicker, but not differently spaced than in low density band portions. The endothecal areas of the skeleton appear relatively free of density band and meso-architectural changes. Figure 9 is a sketch of our interpretation.

Apparently, there is a dichotomy in density banding between thecal and non-thecal areas of the skeleton. Reasons for such differences are not known. It appears that differential calcium carbonate deposition may take place on skeletal architectural elements in exothecal areas outside the polyp living space. We have not yet conducted detailed measurements of polyp living area over time. Fos-
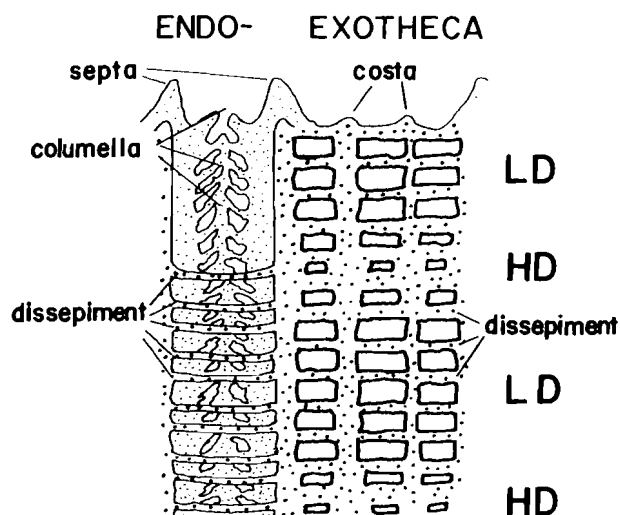
Fig. 9. Sketch of vertical section through *M. annularis* skeleton showing endothecal (corallite) and exothecal area. Stippled area indicates skeleton. Blank area indicates void space. High density (HD) and low density (LD) skeletal portions are indicated. HD banding results primarily from thickening of exothecal dissepiments and costa.

ter (1980) compared corallite dimensions of colonies of *M. annularis* from different collection sites. She attributed between-site differences to adjustment of polyp living space requirements by *M. annularis*. Polyp living space may adjust over the annual cycle in some kind of synchrony with exothecal density banding.

Stress banding, at least in the Florida Keys specimen analyzed, appears to be a transitional form between HD and LD bands. Exotheca dissepiment thickness and spacing of stress bands was less than HD but more than LD bands.

Figures 4 and 5 show a large difference between the mean thickness and spacing of exothecal dissepiments in HD and LD bands of corals collected at widely separated collection locations. In our study we have used generally one specimen from each locality (2 from Southeast Florida). In addition, our specimens include all three reported morphotypes of Knowlton et al. (1992). While we feel confident in the generality of our explanation of the structural difference between density band types, we can not confirm the existence of latitudinal gradients in skeletal architecture without more measurements on samples of each morphotype. Foster (1979) reported that *M. annularis* specimens show significant differences in coenosteum (exothecal dissepiments and costae) among environmentally distinct locations on the same reef. Although her results do not appear to take seasonal changes (ie., density bands) within colonies into account, it is nevertheless clear that within-reef variability must

be addressed in any study comparing widely separated reefs.

Implications for seasonal isotopic sampling and interpretation

The above results indicate there is differential skeleton deposition between exothecal and endothecal areas. Exothecal regions are actively growing at the outermost edge of the coral skeleton (vertical costae and horizontal dissepiments). Endothecal areas, on the other hand, comprise actively growing skeleton at various levels: the outer edge (septal tops), intermediate depths (columella and septa edges), and lower within the skeleton at the polyp base (endothecal dissepiment). Consequently, time lines of skeletal deposition comprise a much greater vertical dimension than from a corresponding exothecal area. This implies that skeletal samples for isotopic analysis should provide a more faithful chronology when restricted to exothecal regions. It may well be that much of the variability in isotopic determinations designed to show seasonal or even monthly changes is a result of cross sampling between endothecal and exothecal areas which were deposited during different times.

Fine banding

Buddemeier (1974) and Buddemeier and Kinzie (1975) have described finer density banding structures within seasonal density banding of Porites. Such fine bands were more readily observed in X-rays of thinner slabs and have been equated with lunar periodicity. Barnes and Lough (1989) performed extensive observations on Porites and concluded from observations of smooth surfaced, fast growing specimens that the annual banding pattern "in many, if not all, massive corals, appears to be composed of such fine bands". They were unable to relate periodic groupings in dissepiment sheets with groupings of the fine bands. Instead, they invoked fine banding to be the result of thickening of the tips of thecal wall spines which terminate at a "consistent level". Fine banding was not always detectable, which they attributed to orientation of the skeletal elements with regard to the X-ray beam.

We did not investigate fine banding *per se* but did look for it in our preparations of *M. annularis*. Barnes and Lough (1989) reported seeing fine-banding in published X-radiographs of this species (in Druffel and Linick 1978 and Hudson 1977) but do not provide a precise definition or other photographs to document their interpretation. Subannual

banding within *M. annularis* has been reported previously (Hudson et al. 1976) and is sometimes referred to as stress banding. This type of banding is defined as "wide" and as forming in response to winter cold water stress. It is our experience that bands intermediate in position (and size) between the normal HD-LD cycles are relatively common. They may be wide or thin, but are not as distinct as the annual cycle and do not seem to qualify as the "fine" banding of Barnes and Lough (1989). In fact, fine banding on the order of 12 per year has not been reported for *M. annularis* nor does fine banding appear to occur in this species as described by Barnes and Lough (1989) for Porites. Skeletal meso-architecture is quite different between *Montastrea* and *Porites*. Close examination under magnification of our X-radiographs reveal what might be called fine banding, but which are, in fact, individual dissepiments that can be resolved by examination of very thin slabs. This indicates, as Barnes and Devereau (1988) have suggested, the importance of section thickness to the interpretation of coral skeletal X-radiographs. In thicker slabs complicated patterns may result from slightly offset lattice works of dissepiments (of varying thicknesses). In thicker slabs, X-rays can "average" away these effects and provide a gradational view of changes in skeletal bulk density.

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