

Skeletal density and growth form of corals

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ABSTRACT: This paper explores inter-specific variation in the density of coral skeletons. I present new data on the porosity of 7 species of reef-building scleractinians, and briefly review 20 previous studies on approximately 23 additional corals. Although the total number of species examined so far is still small, the review reveals a consistent pattern of skeletal density among different morphological groups of corals. The most porous corals are massive or bushy. Delicate foliaceous corals are the most dense. Tall branching corals exhibit a marked axial gradient in density, i.e. growing tips are very porous while basal regions are extremely dense. These results are consistent with differences in the mechanical requirements of various colony shapes.

INTRODUCTION

Scleractinian corals have complex porous skeletons. The question of why the skeletons of some corals are naturally more porous (i.e. less dense) than others has puzzled reef workers for some time. Earlier studies postulated a negative relation between coral density and growth rate (e.g. Vaughan 1915) and susceptibility to boring (Connell 1973), but recently these hypotheses have been rigorously tested for the first time, and refuted (Highsmith 1981). The mechanical consequences of the presence of pores in an otherwise solid structure include a sharp decline in compressive and tensile strength, and in stiffness (e.g. Wainright et al. 1976, Chamberlain 1978, Tunnicliffe 1979, Schuhmacher & Plewka 1981). These properties may also limit the size or growth form of a coral colony. Therefore, I propose to test here the hypothesis that variation in skeletal density may be related in part to inter-specific differences in colony shape.

The most common growth forms exhibited by corals are branching, massive and foliaceous (e.g. Jackson & Hughes 1985). Branching corals, especially taller species, grow rapidly at their branch tips (e.g. Oliver et al. 1983, Tunnicliffe 1983), but are often easily broken during storms (Woodley et al. 1981). In some species, branch fragments may survive and propagate to form large clones (Highsmith 1982). In contrast, massive corals usually grow rather slowly (Connell 1973), and relatively uniformly (Land et al. 1975), over their hemispherically shaped surfaces. Because of their large basal area, massive colonies survive extreme

wave action which can destroy other growth forms (Woodley et al. 1981). Foliaceous corals form horizontally flattened, unifacial plates or lobes that are attached to the reef substrate from the basal (ventral) surface. Their flattened shape results from a strong tendency for radial (i.e. edge) rather than vertical extension (Dustan 1975, Hughes & Jackson 1985). Foliaceous corals are often thin and delicate, and many are found only in relatively calm, deep water (Goreau & Wells 1967).

In this paper, I first examine gross morphological differences among 7 species of foliaceous corals (*Agaricia agaricites*, *A. fragilis*, *A. lamarcki*, *A. undata*, *Leptoseris cucullata*, *Porites astreoides*, and *Montastrea annularis*), and then review measurements on approximately 20 other coral species with a wide variety of colony forms. My purpose is 2-fold: first, to quantify the extent of inter-specific variation in the skeletal density of corals, and second, to search for patterns which might indicate why such variation has evolved.

The density of a coral skeleton is a conservative variable, because it is constrained by a strictly defined upper limit of 2.94 g cm^{-3} , corresponding to the density of solid aragonitic CaCO_3 . Pores in the skeleton will effect a reduction from that maximum value, but there presumably must also be a minimum density caused by mechanical or other constraints. Therefore, interspecific differences in density might be expected to be small. Nevertheless, the data show that there are striking differences in skeletal density (more than 3-fold) between coral species, and indicate that much of

this variation is correlated with differences in growth form.

METHODS

Colonies of the 7 species of foliaceous corals were collected from depths of 5, 10, 20, 30 and 40 m at Rio Bueno, on the north coast of Jamaica. Although the primary purpose of the collections was to search for differences in morphology between species, intra-specific variation was also examined over the depth range of each species. Three of the species, *Agaricia agaricites*, *Montastrea annularis* and *Porites astreoides* are highly polymorphic, typically exhibiting a gradual change from massive or knobby colonies to foliaceous forms with increasing depth. Only foliaceous colonies were collected in the present study since the skeletal density of massive colonies of these 3 taxa is already well known (Baker & Weber 1975, Dustan 1975, Stearn et al. 1977, Chamberlain 1978, Highsmith et al. 1983, Tunnicliffe 1983, Dodge & Brass 1984).

Colonies with a maximum diameter smaller than 10 cm were avoided to control for changes in the ratio of surface area to volume associated with ontogeny. (The ratio of the surface area of the base of an inverted cone divided by its volume changes little above a radius of 5 cm [e.g. Fig. 3 in Porter (1976)], especially where the maximum height of the cone is less than about one fourth of the diameter.) One-way ANOVA's of the collections confirm no significant differences in colony diameter among depths or species.

Only corals with a complete covering of tissue (which in these foliaceous species is primarily limited to their upper surfaces), were collected to reduce variation caused by bioerosion. Colonies were dried in the

sun, and their undersurfaces cleaned of epibionts. Corals with excavations resulting from bioerosion were discarded. Because each species was rare at either shallow or deep sites, the number of sampled depths varied from 1 to 4 per species. Therefore, empty cells (not just missing values) preclude the use of a 2-way ANOVA, so the effects of species and depth were examined separately. The number of colonies analyzed per species per depth ranged from 5 to 17, giving a total of 207.

Two quantitative traits of coral morphology were measured: skeletal density, and the ratio of surface area of tissue to skeletal mass. Both relate to the way a coral uses calcium carbonate to manufacture its skeleton. The latter is a measure of the amount of skeletal material required by a coral to occupy a given amount of space, and has obvious ecological as well as morphological importance. Each coral was photographed on land with a scale, and the photographs were digitized to obtain the area of the upper surface. Skeletal density of whole colonies was measured using Archimedes' Principle by weighing them first in air and then suspended briefly from an analytic balance into freshwater (Graus & MacIntyre 1982). Skeletal volume was estimated as air weight divided by density.

RESULTS

In general, differences between the 7 foliaceous species in skeletal density were far greater than intra-specific variation within and between depths (Table 1). *Porites astreoides* was the most porous throughout its depth range from 5 to 30 m, while *Montastrea annularis* consistently ranked second. Colonies of

Table 1. Mean skeletal density \pm SE (g cm^{-3}) of foliaceous corals from Rio Bueno, Jamaica. Numbers in parentheses indicate number of colonies in each sample (total 207). Depth and species differences indicated by Kruskal-Wallis test. Blanks indicate approximate depth distribution of these species at Rio Bueno

Species	5m	10m	20m	30m	40m
<i>Porites astreoides</i> (ns)	1.69 \pm 0.02 (10)	1.62 \pm 0.03 (10)	1.68 \pm 0.04 (12)	1.67 \pm 0.03 (10)	—
<i>Agaricia agaricites</i> (p < 0.001)	1.91 \pm 0.04 (8)	1.99 \pm 0.02 (14)	2.08 \pm 0.06 (10)	2.14 \pm 0.03 (7)	—
<i>Montastrea annularis</i> (p < 0.01)	—	1.78 \pm 0.04 (10)	1.95 \pm 0.03 (10)	2.05 \pm 0.04 (9)	—
<i>Leptoseris cucullata</i> (ns)	—	2.15 \pm 0.06 (9)	2.26 \pm 0.04 (10)	2.29 \pm 0.05 (10)	2.25 \pm 0.05 (5)
<i>Agaricia lamarcki</i> (ns)	—	—	2.30 \pm 0.03 (10)	2.25 \pm 0.04 (17)	2.31 \pm 0.03 (12)
<i>Agaricia undata</i> (ns)	—	—	—	2.46 \pm 0.03 (7)	2.44 \pm 0.06 (6)
<i>Agaricia fragilis</i>	—	—	—	—	2.31 \pm 0.05 (11)
	p < 0.001	p < 0.001	p < 0.001	p < 0.001	(ns)

Agaricia spp. and *Leptoseris cucullata* were much more dense, especially in deep water. At 30 m, where collections of 6 species were taken, densities of *A. undata*, *L. cucullata*, *A. lamarcki*, *A. agaricites* and *M. annularis* were on average 47, 37, 35, 28 and 23 % greater, respectively, than *P. astreoides* (Kruskall-Wallis test, $p < 0.001$, Table 1).

Skeletal density of foliaceous *Agaricia agaricites* and *Montastrea annularis* increased significantly with depth (Table 1). The change was modest, amounting to an average increase of 12 % from 5 to 30 m in *A. agaricites*, and of 15 % from 10 to 30 m in foliaceous *M. annularis* (Kruskall-Wallis test, $p < 0.001$ and $p < 0.01$ respectively). In contrast, the remaining species showed no significant change in density over their depth range.

The foliaceous species also differed greatly in the area of substrate covered per unit weight of skeleton (Table 2). The characteristically thick plates of *Montastrea annularis* had by far the lowest value of all wherever it was collected, while the more delicate *Leptoseris cucullata* had the highest ratio throughout its depth range. Where they were both collected, from 10 to 30 m, *L. cucullata* covered the same amount of substrate with 4 to 5 times less skeletal mass than *M. annularis*, despite the considerably higher density of *L. cucullata*. Thus, the range between foliaceous species in surface area per unit weight of skeleton (from 0.39 to 2.14 cm² g⁻¹) was approximately 10 times greater than the more modest differences in density (ranging from 1.62 to 2.46 g cm⁻³).

There was a significant increase of surface area to weight ratios with depth among 2 species, *Agaricia agaricites* and *A. lamarcki* (Table 2). *A. agaricites* at 30 m covers the same area with an average of almost half the weight of skeleton than at 5 m. Similarly, *A. lamarcki* at 40 m occupies the same amount of space

with one third less skeletal mass than at 20 m. *Leptoseris cucullata* and *A. undata* showed similar trends, but they were not statistically significant. These changes were not due to a decline in skeletal density at greater depths, since density of each species either stayed the same or increased in deeper water (Table 1). Rather, the surface areas per mass of skeleton increased because deeper foliaceous corals were substantially thinner. This pattern of increasing flattening of corals also occurred inter-specifically (Table 2), as relatively robust species predominating in shallow water (e.g. *Porites astreoides*, *A. agaricites* and *Montastrea annularis*) were replaced by thinner, more delicate ones at greater depths (e.g. by *A. undata* and *A. fragilis*).

DISCUSSION AND REVIEW

Previous estimates of skeletal density are summarized in Table 3. (Several studies that were based on only a single colony or an unknown number of specimens were omitted.) I have divided the corals into 3 major categories, namely, branching, massive and foliaceous growth forms. Before describing the patterns, I should caution that some of the variation in the reported densities of corals may be due to differences in sampling and measurement techniques. For example, the size and position of each sample is important. Larger specimens will give smaller measurement errors of weight or displacement, but they are also more likely to be excavated by borers. In addition, colony extremities such as branch tips are often extremely porous compared to basal parts of branching colonies. At a smaller scale, cores or slabs of a few grams may differ in density because of their location in relation to individual calices or seasonal banding

Table 2. Area/weight ratio (cm² g⁻¹) ± SE of foliaceous corals from Rio Bueno, Jamaica. See Table 1 for explanation

Species	5m	10m	20m	30m	40m
<i>Porites astreoides</i> (ns)	0.78 ± 0.06 (10)	0.78 ± 0.05 (10)	0.78 ± 0.08 (12)	0.75 ± 0.07 (10)	—
<i>Agaricia agaricites</i> (p < 0.001)	0.53 ± 0.04 (8)	0.78 ± 0.09 (14)	0.88 ± 0.05 (10)	1.06 ± 0.07 (7)	—
<i>Montastrea annularis</i> (ns)	—	0.41 ± 0.02 (10)	0.39 ± 0.03 (10)	0.47 ± 0.04 (10)	—
<i>Leptoseris cucullata</i> (ns)	—	1.50 ± 0.19 (13)	2.05 ± 0.18 (12)	1.97 ± 0.18 (10)	2.14 ± 0.29 (5)
<i>Agaricia lamarcki</i> (p < 0.05)	—	—	0.98 ± 0.07 (10)	1.16 ± 0.07 (17)	1.33 ± 0.06 (12)
<i>Agaricia undata</i> (ns)	—	—	—	1.57 ± 0.12 (7)	1.74 ± 0.09 (6)
<i>Agaricia fragilis</i>	—	—	—	—	1.28 ± 0.16 (11)
	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001

Table 3. Summary of coral densities

Species	Morphology	Density (g cm ⁻³)	Depth (m)	Site	Remarks	Source
Ramose corals						
<i>Acropora cervicornis</i>	Erect	0.15–2.80	8	St. Croix	Axial gradient	Gladfelter 1982
<i>Acropora cervicornis</i>	Erect	1.20–2.48	5.5–27	Jamaica	Axial gradient	Tunncliffe 1983
<i>Acropora cervicornis</i>	Erect	1.79–2.18	?	Jamaica	Axial gradient	Schuhmacher & Plewka 1981
<i>Acropora formosa</i>	Erect	0.5–2.6	5–15	Davies Reef, GBR	Axial gradient	Oliver et al. 1983
<i>Acropora palmata</i>	Erect	1.47–2.23	?	Jamaica	Axial gradient	Schuhmacher & Plewka 1981
<i>Acropora palmata</i>	Erect	0.82–2.41	<10	Caribbean	Axial gradient	Shapiro 1980
<i>Acropora palmata</i>	Erect	2.02	<10	Caribbean		Chamberlain 1978
<i>Eusmilia fastigiata</i>	Short branches	1.30	7–12	Caribbean		Tunncliffe unpubl.
<i>Madracis mirabilis</i>	Short branches	1.68	7–15	Caribbean		Tunncliffe unpubl.
<i>Porites furcata</i>	Short branches	1.05	<3	St. Croix	30 % seasonal change	Meyer & Schultz 1985
<i>Porites porites</i>	Short branches	1.18	0–5	Barbados		Stearn et al. 1977
<i>Tubastrea aurea</i>	Plocoid	1.07	?	Pacific		Schuhmacher 1984
<i>Tubastrea micranthus</i>	Erect	1.91–2.47	?	Philippines	Axial gradient	Schuhmacher 1984
Massive (hemispherical or columnar) corals						
<i>Agaricia agaricites</i>		1.87	0–5	Barbados		Stearn et al. 1977
<i>Colpophyllia natans</i>	Meandroid	0.65	?	Jamaica		Tunncliffe 1983
<i>Colpophyllia natans</i>	Meandroid	0.84	?	Caribbean		Highsmith 1981
<i>Diploria labyrinthiformis</i>	Meandroid	1.57	1	Bermuda		Dodge & Thomson 1974
<i>Favia pallida</i>		1.43	2–29	Enewetak		Highsmith 1979
<i>Goniastrea retiformis</i>		1.70	6–17	Enewetak		Highsmith 1979
<i>Montastrea annularis</i>		1.28	2–8	St. Croix	<10 % seasonal change	Dodge & Brass 1984
<i>Montastrea annularis</i>		1.41	0–5	Barbados		Stearn et al. 1980
<i>Montastrea annularis</i>		1.47	?	Caribbean		Chamberlain 1978
<i>Montastrea annularis</i>		1.58	0–4.5	St. Croix		Baker & Weber 1975
<i>Montastrea annularis</i>		1.79	9–13.5	St. Croix	Depth gradient	Baker & Weber 1975
<i>Montastrea annularis</i>		1.71	8–24	Jamaica		Dustan 1975
<i>Montastrea annularis</i>		1.81	1–30	Belize	Depth gradient	Graus & McIntyre 1982
<i>Montastrea cavernosa</i>		1.60	5–26	Belize		Highsmith et al. 1983
<i>Montipora berryi</i>		1.58	?	Enewetak		Highsmith 1981
<i>Oulophyllia crispa</i>	Meandroid	0.98	?	Enewetak		Highsmith 1981
<i>Pavona clavus</i>		1.86	5–7	Gulf of Chiriqui	13 % seasonal change	Wellington & Glynn 1983
<i>Pavona clavus</i>		1.44	5–7	Gulf of Panama	35 % seasonal change	Wellington & Glynn 1983
<i>Pavona gigantea</i>		1.75	5–7	Gulf of Panama	20 % seasonal change	Wellington & Glynn 1983
<i>Porites astreoides</i>		1.48	1–15	Belize		Highsmith et al. 1983
<i>Porites astreoides</i>		1.40	0–5	Barbados		Stearn et al. 1977
<i>Porites astreoides</i>		1.26	<10	Jamaica		Tunncliffe 1983
<i>Porites lutea</i>		1.41	0–29	Enewetak		Highsmith 1979
<i>Porites</i> spp. (mostly)		1.30–1.65	2–30	Enewetak	10–30 % seasonal change	Buddemeir et al. 1974
<i>Porites</i> spp.		1.20	5–10	Dahu		Schneider & Smith 1982
<i>Porites</i> spp.		1.60	5–10	Midway	10–20 % seasonal change	Schneider & Smith 1982
<i>Porites</i> spp.		1.70	?	Abrolhos Is.		Schneider & Smith 1982
<i>Siderastrea radians</i>		1.82	?	Caribbean		Chamberlain 1978
<i>Siderastrea siderea</i>		1.61	0–5	Barbados		Stearn et al. 1977
Foliaceous (or flattened) corals						
<i>Agaricia agaricites</i>	Foliaceous	2.02	5–30	Jamaica	Depth gradient	Table 1
<i>Agaricia fragilis</i>	Foliaceous	2.31	40	Jamaica		Table 1
<i>Agaricia lamarcki</i>	Foliaceous	2.28	20–40	Jamaica		Table 1
<i>Agaricia undata</i>	Foliaceous	2.45	30–40	Jamaica		Table 1
<i>Dichocoenia</i> sp.	Flattened	2.30	?	Jamaica		Tunncliffe 1983
<i>Dichocoenia stokesi</i>	Flattened	2.04	?	Caribbean		Highsmith 1981
<i>Leptoseris cucullata</i>	Foliaceous	2.24	10–40	Jamaica		Table 1
<i>Montastrea annularis</i>	Foliaceous	1.96	18–27	St. Croix	Depth gradient	Baker & Weber 1975
<i>Montastrea annularis</i>	Foliaceous	1.76	10–50	Jamaica		Dustan 1975
<i>Montastrea annularis</i>	Foliaceous	1.92	10–30	Jamaica	Depth gradient	Table 1
<i>Porites astreoides</i>	Foliaceous	1.67	5–30	Jamaica		Table 1

patterns. High and low density portions of annual bands typically vary in porosity by 10 to 35 % (Buddemeier et al. 1974, Schneider & Smith 1982, Wellington & Glynn 1983, Meyer & Schultz 1985).

Skeletal density may also depend on the depth of collection. For example, the densities of *Montastrea annularis* and *Agaricia agaricites* increased in deeper water (Table 1). This relation has been shown before for *M. annularis* by Baker & Weber (1975), and by Graus & MacIntyre (1982), although Dustan (1975) found no consistent trend. However, as noted here for foliaceous corals (Table 1), intraspecific variations in density associated with change in depth are usually small compared with inter-specific differences. Only 2 of the species examined here showed a detectable change in density over their depth range, while inter-specific differences were highly significant at each sampled depth from 5 to 30 m.

Various related mechanisms may combine to cause a depth gradient in skeletal densities. For example, an increase in spacing of polyps (fewer polyps per unit area) with increasing depth has been described in *Dichocoenia stokesi* (Wells 1973), *Oculina varicosa* (Reed 1983), *Montastrea cavernosa* (Lasker 1981) and *Montastrea annularis* (Weber et al. 1976, Dustan 1979). As noted by Highsmith (1981), the density of a coral is influenced by the spacing and size of corallites, i.e. by the ratio of wall thickness to corallite diameter. Therefore, more widely spaced polyps should result in higher skeletal density, all else being equal. In addition, the proportion of each annual band pair that is composed of high density skeleton has been shown to be greater in deeper water in *Porites lutea* (Highsmith 1979), and *M. annularis* (Baker & Weber 1975). On a smaller scale, changes in density with depth may reflect variation in the micro-structure of skeletal elements (e.g. Foster 1979, 1980).

In spite of potential sources of variation, such as sampling technique or depth of collections, measurements of density made independently for the same species by different authors are usually fairly similar (Table 3). For example, Stearn et al. (1977) report a mean density of 1.87 g cm^{-3} for *Agaricia agaricites* at 0 to 5 m, which agrees well with values of 1.91 g cm^{-3} at 5 m reported here (Table 1). The biggest intra-specific range is shown by 7 studies on the density of *Montastrea annularis*, that give mean values from 1.28 to 1.96 g cm^{-3} (Dustan 1975, Baker & Weber 1975, Stearn et al. 1977, Chamberlain 1978, Graus & MacIntyre 1982, Dodge & Brass 1984; Table 1). However, even this considerable spread in values is small compared to inter-specific differences that span a 3-fold range (Table 3). Note, furthermore, that the lowest reported densities of *M. annularis* come from studies conducted at shallow sites: 1.28 g cm^{-3} at depths of 2 to 8 m

reported by Dodge & Brass (1984), 1.41 g cm^{-3} at 0 to 5 m by Stearn et al. (1977), and 1.58 g cm^{-3} at 0 to 4.5 m by Baker & Weber (1975). Baker & Weber (1975) also reported densities of 1.79 g cm^{-3} at 9 to 13.5 m and of 1.96 g cm^{-3} at 18 to 27 m, which closely match values for *M. annularis* of 1.78 g cm^{-3} at 10 m and 1.95 g cm^{-3} at 20 m reported in Table 1. This concurrence occurs even though Baker & Weber's measurements were made from calibrated X-ray exposures (photodensitometry), while mine were obtained more crudely by wet and dry weighings.

Branching corals

The most consistent characteristic of the density of tall, loosely-branched corals (Table 3) is a marked axial gradient due to secondary infilling of skeletal pores in older portions of the colony (Gladfelter 1982, Oliver et al. 1983, Tunnicliffe 1983, Schuhmacher 1984, Wellington & Trench 1985). Presumably, this is an adaptation that first allows rapid distal growth of branches (e.g. Tunnicliffe 1983, Oliver et al. 1983), which are later strengthened towards the base to avoid excessive breakage. Loosely branched corals are often broken up and passively dispersed during storms (Highsmith 1982). In moderate amounts, this process of asexual reproduction may be adaptive, but fragments that are too small are easily abraded and killed (Highsmith 1982, Hughes 1986).

Densities at the base of the staghorn corals *Acropora cervicornis* and *A. formosa* are the highest recorded for any scleractinian. However, the range of skeletal densities along a single branch of either of these species (Gladfelter 1982, Oliver et al. 1983, Tunnicliffe 1983), and in the closely related elkhorn coral *A. palmata* (Schuhmacher & Plewka 1981) is enormous (Table 3). (The rather high density of 2.02 g cm^{-3} reported by Chamberlain [1978] for cylindrical cores of branching *A. palmata* is probably due to their proximal position within the colony.) The same axial pattern is found in *Tubastraea micranthus*, a tall, branching dendrophyliid which lacks zooxanthellae (Schuhmacher 1984, Wellington & Trench 1985), indicating that this pattern of growth has evolved independently in morphologically similar, but distantly related, taxa. Because of these extreme intra-colony gradients, it is impossible to say whether the average densities of tall branching corals are significantly different from other morphologies. Clearly, the most striking trait of the group is the unique distribution pattern of skeletal material.

All of the erect species in Table 3 have extensive gastrovascular systems that ramify deeply into the skeleton (e.g. Fig. 2 in Gladfelter 1982, Fig. 2 in

Wellington & Trench 1985). Gladfelter (1982) proposed that this may be the means for inward transportation of ions required for mineralization, since non-perforate corals such as massive *Montastrea* spp. (which lack such an internal canal system) apparently do not exhibit comparable gradients in skeletal density (that is, on a spatial scale greater than a few millimeters, e.g. Schneider & Smith 1982). Infilling in branching corals results in a uniformly high density in older (proximal) skeleton, and may obscure changes in density associated with season (i.e. banding) or depth (Tunncliffe 1983, Gladfelter 1982, 1984). This is part of the reason why almost all banding studies have been conducted with massive corals.

There are apparently no corals with entirely porous skeletons that form tall branching colonies, and very few non-perforate ones. An example of the latter is the Caribbean pillar coral *Dendrogyra cylindrus*. As the name implies, this species forms extremely stout and vertical branches, which are up to an order of magnitude thicker than those of staghorn corals. *D. cylindrus* presumably has a uniformly high skeletal density to further reduce the likelihood of breakage, and grows much slower than branching acroporids (mean linear growth of 0.8 cm yr^{-1} in Curaçao at 7 m depth: R.P.M. Bak pers. comm.).

Other ramose corals in Table 3, *Eusmilia fastigiata*, *Madracis mirabilis*, *Porites furcata*, *P. porites* and *Tubastraea aurea*, have much shorter branches than the taller species discussed above, and are generally much more porous. Up to $\frac{2}{3}$ of their skeleton is composed of cavities, and they have not yet been reported to show axial gradients in density. Because of their more bushy morphology, they are not subjected to the same degree of mechanical stress from wave action, since the force acting on the base of a branch depends on its length (Wainwright et al. 1976, p. 248). In addition, shorter branches positioned closer to the substrate may encounter reduced amounts of water movement because of the shelter afforded by taller neighbours.

Massive corals

Whole skeletons of massive corals were often the least dense of the 3 major morphological groups (branching, massive, and foliaceous) in Table 3. Two species, *Colpophyllia natans* and *Oulophyllia crispa*, have densities of less than 1 g cm^{-3} . Both of these are brain corals, whose corallites are joined by common walls to form elongated valleys 10 to 15 mm across (Smith 1971, p. 83; Backhuys 1980, p. 68). A third brain coral, *Diploria labyrinthiformis*, has narrow valleys which are on average only 5 mm across (Smith 1971, p. 81), and has a higher density of 1.56 g cm^{-3} (Dodge

& Thompson 1974). Twelve other species of massive corals with distinct polyps (i.e. cerioid rather than meandroid coralla) have densities ranging from 1.20 to 1.87 g cm^{-3} , with an average of 1.61 g cm^{-3} . This range of values contrasts with 2.0 g cm^{-3} or more for most foliaceous corals (Mann-Whitney test, $p < 0.001$), and is also exceeded by the bases (but not the tips) of all tall branching corals. As a group, only bushy corals were less dense than massive colonies. (The mean for 5 bushy species was 1.26 g cm^{-3} versus 1.57 g cm^{-3} for all 16 massive species, Mann-Whitney test, $p < 0.05$). Although massive colonies are relatively porous (Table 3), their hemispherical shape and wide basal area of attachment makes them highly resistant to damage from storms and hurricanes (e.g. review by Jackson & Hughes 1985).

Foliaceous corals

Foliaceous corals as a group have the most dense skeletons yet reported for whole corals (Table 3). One obvious exception is the plate-like form of *Porites astreoides*, which like branching and massive poritids, is relatively porous even in deep water. Flattened plates of *P. astreoides*, and *Montastrea annularis* are thicker than deep-water species of *Agaricia* and *Leptoseris* (Table 2), and are commonly attached to the reef by a substantially greater part of their undersurface. The low density of *P. astreoides* and *M. annularis* compared to that of the thin, but very dense, plates of *Leptoseris* and *Agaricia* species indicates there is an inverse relation between density and plate thickness, analogous to the increase in density among foliaceous versus massive corals (Table 3). Indeed, a hypothetical foliaceous coral as thin as *L. cucullata* but with the density of *P. astreoides* would probably fall apart as it grew under its own weight. Foliaceous corals in shallow water are easily damaged by storms (Hughes 1984), and the most common of these species on exposed reefs are those which grow fast and have high rates of recruitment, such as *A. agaricites*, *P. astreoides* and *L. cucullata* (Hughes & Jackson 1985). Other species of *Agaricia*, *Dichocoenia*, and the plate-like morphology of *M. annularis* are most commonly found at depths greater than 15 to 20 m (Goreau & Wells 1967, Jackson & Hughes 1985).

There is no clear-cut relation between skeletal density and growth rates of the foliaceous species examined here. Growth rates of these and other species decline in deeper water (e.g. Baker & Weber 1975, Dustan 1975, Hughes & Jackson 1985, and many more), yet the density of *Agaricia lamarcki*, *A. undata*, *Leptoseris cucullata*, and *Porites astreoides* did not change significantly at greater depths (Table 1). The expected increase in density did occur among deep-

water colonies of *A. agaricites* and *Montastrea annularis*, but the lack of a similar relation for the majority of the species indicates the correlation between growth and density is merely fortuitous. Furthermore, growth rates of *L. cucullata* and *P. astreoides* are very similar (Fig. 9 & 10 in Hughes & Jackson 1985) although these species differ greatly in density (Table 1). In addition, foliaceous *M. annularis* grows much slower than any species of *Agaricia* or *L. cucullata* (*ibid*), even though the former is more porous (Table 1). These results support Highsmith's (1981) conclusion that extension rates and skeletal density of corals are only very weakly correlated.

CONCLUSIONS

High density reduces the likelihood of breakage (e.g. Wainright et al. 1976, Chamberlain 1978, Schuhmacher 1984), and has evolved to the greatest degree in species with otherwise delicate morphologies, i.e. among tall branching and thin foliaceous corals (Table 3). Why are not all corals, including massive and bushy ones, equally dense? Presumably, there are trade-offs between skeletal density and other factors. For example, a higher density would be likely if there was a reduction in the size of a colony's corallites (or an increase in corallite spacing), so that the ratio of wall thickness to corallite diameter increased (Highsmith 1981). But such a remodeling might also affect the coral's ability to feed, compete for space, clean itself of sediment, or alter the size of its gonads. Since some of these changes may not be adaptive, the benefits of enhanced density may be outweighed by such potential 'costs'.

The density patterns shown here have probably persisted throughout the evolution of corals. Thus, as far as I am aware, meandroid and cerioid colonies with large polyps have always been encrusting or massive, never tree-like. Similarly, there are no extant or fossil examples of erect, loosely branching *Porites* spp. analogous to thickets of acroporid staghorn corals, nor are there any massive *Acropora* spp. that resemble poritid mounds. It seems likely that these evolutionary patterns are due in part to mechanical or developmental constraints reflected in the density trends described here.

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