

NOTE

Cross-shelf trends in skeletal density of the massive coral *Porites lobata* from the Great Barrier Reef

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ABSTRACT: Colonies of the massive coral *Porites lobata* collected from the Great Barrier Reef show a highly significant increase in skeletal density across the continental shelf. Near-shore colonies have skeletal density values of ca 1.1 g cm⁻³, while offshore values are ca 1.4. This trend could be caused by increased nutrients inshore acting as calcification inhibitors, or by increased light penetrating offshore, inducing a cross-shelf heterotrophy-autotrophy gradient.

Density banding in coral colonies has been the focus of a great deal of recent research, because of the environmentally important information contained therein. It is now known that many corals contain annual density bands (Buddemeier & Kinzie 1975), and that study of these bands, combined with other types of chemical and biological analyses, can shed light on the effects of siltation (Dodge et al. 1974, Cortes & Risk 1985), water temperature (Schneider & Smith 1982, Carriquiry et al. 1988), general climatic and oceanographic conditions (Highsmith 1979, Druffel 1982), and freshwater river runoff (Isdale 1984, Boto & Isdale 1985), to name just a few.

There is a huge body of research based on the preserved density bands in coral skeletons, but only limited work has been done on changes in bulk density of scleractinian corals due to environmental changes. Yamazato (1970) suggested that coral calcification may be suppressed by large amounts of phosphate in the surrounding waters. Kinsey & Davies (1979) showed that calcification and skeletal density of corals were reduced upon addition of commercial fertilizers, Schneider & Smith (1982) presented correlations between skeletal density and both light and temperature (also see Wellington & Glynn 1983), and Rasmussen (1988) showed that the skeletons of *Acropora formosa*, in controlled laboratory experiments, became less dense under elevated nutrient loading.

The possibility therefore exists that the average

density of reef corals may be a reliable indicator of nutrient levels via an onshore-offshore density gradient. Such a relationship could be of value in environmental studies on coral reefs, as a synoptic indicator of nutrient stress. In coral calcification work, it may have use as a possible measure of the trophic status of a given coral species, and, in paleoceanography, as a potential indicator of paleoshorelines.

Here we report the results of a cross-continental shelf survey of skeletal density in the massive coral *Porites lobata* from the central region of the Great Barrier Reef. In this region, the shelf is ca 120 km wide, bordered by land on one side and the Coral Sea on the other. The Burdekin River also flows into the Great Barrier Reef lagoon in this region, and its peak flow during the monsoon season has been measured to be up to ca 10 000 Ml d⁻¹ (see Sammarco & Crenshaw 1984). This river drains 130 000 km² of central and western Queensland.

Samples were taken during July 1988 as part of a larger, ongoing study of cross-continental shelf trends in bioerosion and nutrient supply (Risk et al. 1988, Sammarco & Risk 1990). *Porites lobata* was chosen because this species is well represented throughout the Indo-Pacific, the massive colonies may live to be several centuries old, and the mechanical properties of the skeleton are well-known (see Scott & Risk 1988). *P. lobata* has one of the most porous skeletons of any scleractinian coral. Corals were collected from 9 reefs, shown in Fig. 1: Middle Reef, Alma Bay (Magnetic Island), Orpheus Island (lee side), Pandora Reef, Great Palm Island (lee), Morinda Shoals, Little Broadhurst Reef, Bowden Reef, and Grub Reef. Several colonies 30 to 50 cm in diameter were collected from depths of 3 to 5 m from each reef. Corals were frozen immediately on shipboard, then freeze-dried and shipped to Canada for further analysis.

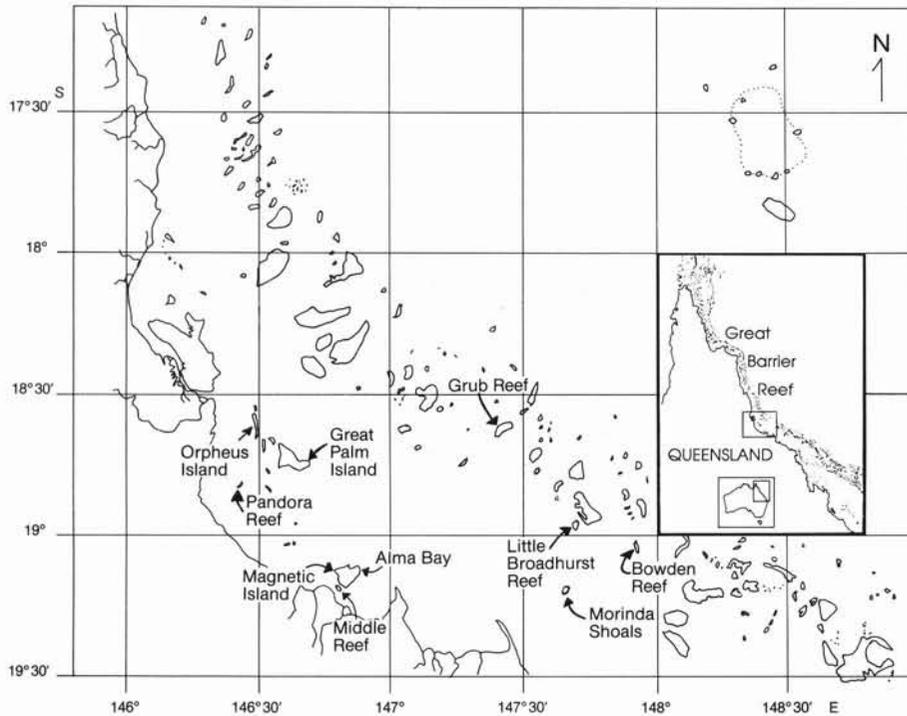


Fig. 1. Central region of the Great Barrier Reef, depicting the 9 reefs sampled in this study

Coral heads were slabbed (1 cm thick) and x-radiographs taken to determine growth rates. Subsamples for density analysis (ranging from 4 to 12 g, averaging about 10 g) were cut from the slabs with a diamond bandsaw, below the tissue layer. Any areas showing signs of internal bioerosion were avoided. The same number of annual bands were included in each density sample, to avoid confounding density values with annual variations in growth rate. Samples were immersed in hydrogen peroxide to remove organic matter, passed through an ultrasonic bath to remove adhering sawdust and loose chips, dried at 90°C for 48 h, and weighed. Each sample was then briefly dipped in melted histological paraffin, excess paraffin shaken off, and the submerged weights determined for specific gravity calculations.

All laboratory processing was performed by a single individual working 'blind', i.e. who had no knowledge of the origin of the samples with respect to distance from shore. A large number of density determinations were obtained from one coral colony, collected at Grub Reef, to gain a high-resolution estimate of intracolony sample variance. Subsamples of the corals used in this study are archived in the Department of Geology, McMaster University.

The results from the single colony show a high degree of replicability in the density determinations: average density 1.46 g cm^{-3} , $n = 27$, $SD = 0.0027$, range = 1.34 to 1.55 (Table 1).

Our data clearly demonstrate that skeletal density increased significantly with distance from shore

Table 1. *Porites lobata*. High resolution estimate of intracolony variance in density. Data from 27 samples taken from a single head. Nominal variance shown

Sample	Coral mass (g)	Weight in H ₂ O (g)	Density (g cm ⁻³)
1	6.987	2.366	1.512
2	5.416	1.746	1.476
3	12.365	4.020	1.482
4	5.028	1.392	1.383
5	4.007	1.307	1.484
6	4.363	1.106	1.340
7	5.474	1.656	1.434
8	4.113	1.366	1.497
9	11.345	3.657	1.476
10	8.222	2.680	1.484
11	7.497	2.476	1.493
12	5.363	1.539	1.402
13	4.658	1.374	1.418
14	9.526	3.207	1.508
15	8.997	2.375	1.359
16	5.510	1.713	1.451
17	7.325	2.410	1.490
18	8.899	2.960	1.498
19	5.929	2.006	1.511
20	6.440	1.954	1.436
21	5.067	1.620	1.470
22	8.697	2.605	1.428
23	7.913	2.829	1.556
24	7.766	2.275	1.414
25	9.330	3.061	1.488
26	9.677	3.205	1.496
27	7.034	2.483	1.546

$\bar{x} = 1.464 \text{ g cm}^{-3}$
 $s^2 = 2.662 \times 10^{-3}$

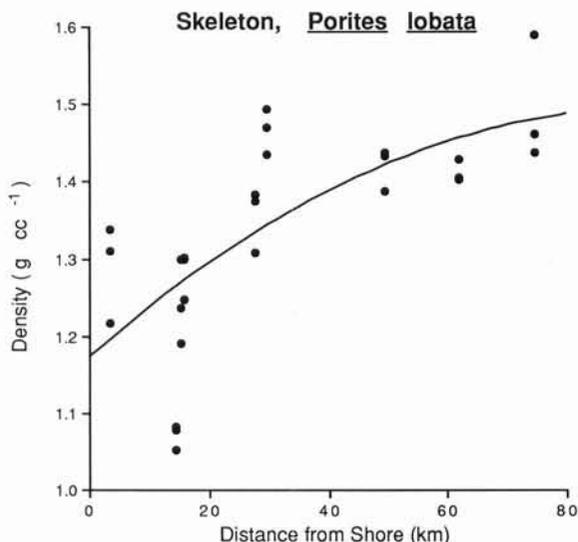


Fig. 2. *Porites lobata*. Relationship between density of skeleton in g cm^{-3} , as a function of distance from shore in km. Highly significant difference between sites ($p < 0.001$, 2-level nested ANOVA). A highly significant curvilinear relationship exists ($p < 0.001$), described by the following second degree polynomial regression: $y = 3.58 \times 10^{-5} x^2 + 6.79 \times 10^{-3} x + 1.172$ ($R^2 = 0.50$)

(Fig. 2). Skeletal specific gravity ranged from as low as 1.053 at nearshore sites to 1.589 at our offshore location (Fig. 1, Table 2). The fitted second degree polynomial is highly significant ($p < 0.001$). Nested analysis of variance revealed that 89.1% of the total variance observed was accounted for by between-reef differences, and that only 10.9% of the total variance was attributable to within-reefs differences. This relationship is even more striking when one considers that the seemingly anomalous low values detected 25 km from shore (see Fig. 2) are actually from Orpheus Island, a 'high continental island' (Birkeland 1987) which most likely has runoff characteristics similar to that of the mainland.

Examination of the skeletons under scanning electron microscopy revealed that density changes are produced by changes in thickness of individual skeletal elements, and not by changes in the number of spacing of septa and dissepiments (Fig. 3). This agrees with Barnes & Devereux (1988), who found that the density changes associated with annual banding in corals were caused by changes in the 'meso-architecture' of the skeleton: the arrangement of skeletal elements within and between corallites.

Although the relationship is clear, reasons for its existence are less so. Two of the physical characteristics of the Great Barrier Reef waters which are markedly influenced by distance from shore are nutrient levels and water clarity. Inshore areas in our study are characterized by low wave energy, salinities and tem-

perature more variable than those offshore, as well as higher zooplankton, chlorophyll *a* and nutrient levels (Ikeda et al. 1980, Andrews 1983, Sammarco & Crenshaw 1984). We speculate that the skeletal changes described herein are produced by changes in light levels and/or nutrient concentrations.

The effect of turbidity per se on corals may be divided into reduction in light penetration and effects of direct sediment loading, resulting in a metabolic drain on the corals. These 2 effects may be difficult to separate, and in fact may act synergistically (Cortes & Risk 1985). As distance from shore increases, the corals in our sample area would experience a graded reduction in nutrient levels, increase in light availability, and a reduction in sediment loading. Average water temperatures are not significantly different between our inshore and offshore sites (Sammarco & Crenshaw 1984, Pickard et al. 1977, in press).

The density gradient we have observed may also be a product of nutrients, especially phosphate, acting as inhibitors of calcification in nearshore waters. Simkiss (1964) has demonstrated that phosphates are crystal poisons of calcification, and Kinsey & Davies (1979) showed reduced skeletal density and calcification rates in corals treated with elevated phosphate and nitrate concentrations. If this factor has played a major role in influencing the observed gradient, then density determinations such as this may well be used as synoptic and retrospective indicators of nutrient levels (see Dodge et al. 1984, Rasmussen 1988).

It is well known that one of the primary controls on coral calcification and skeletal density is the symbiotic coral-zooxanthellar association (Goreau & Goreau 1959). Cowen (1983) suggested that presence of similar symbiotic associations may be recognized in fossil organisms by skeletal massiveness. The metabolism of most reef corals is probably a combination of autotrophy (symbiosis with zooxanthellae), heterotrophy (feeding on zooplankton), and direct uptake of dissolved organic matter from seawater. Uptake of terrestrial organic matter by *Porites* growing in nearshore environments has already been demonstrated using stable carbon isotope ratios (Risk et al. 1988) from which one would predict a gradient of increasing offshore autotrophy, driven by enhanced light levels. If this is the origin of the density trend we have reported here, then skeletal density in *Porites lobata* would be a indicator of the degree of autotrophy of an individual coral, and perhaps even an indirect indicator of water clarity. Schneider & Smith (1982) suggested that the annual abrupt increase in skeletal density exhibited by Hawaiian *Porites* spp. signals a change from optimal to suboptimal growing conditions.

It is possible that sediment particles may cause decreased skeletal density by acting as crystallization

Table 2. *Porites lobata*. Density determinations of skeletons derived from each of 3 heads sampled from 9 reefs, spanning most of the continental shelf in the central region of the Great Barrier Reef

Reef	Distance from shore (km)	Sample	Mass (g)	Wt in H ₂ O (g)	Density (g cm ⁻³)
Middle Reef	3.5	1	10.850	2.736	1.337
		2	5.419	0.962	1.216
		3	3.523	2.010	1.309
					$\bar{x} = 1.287$ $s^2 = 4.103 \times 10^{-3}$
Alma Bay Magnetic Is.	14.3	1	7.441	0.377	1.053
		2	7.39	0.561	1.082
		3	5.535	0.405	1.079
					$\bar{x} = 1.017$ $s^2 = 0.255 \times 10^{-3}$
Orpheus Is.	15.4	1	5.002	0.955	1.236
		2	6.983	1.114	1.190
		3	8.941	2.060	1.299
					$\bar{x} = 1.242$ $s^2 = 2.995 \times 10^{-3}$
Pandora Reef	15.9	1	6.355	1.255	1.246
		2	10.279	2.359	1.298
		3	8.498	1.967	1.301
					$\bar{x} = 1.282$ $s^2 = 0.957 \times 10^{-3}$
Great Palm Is.	27.8	1	7.890	2.150	1.375
		2	11.169	3.100	1.384
		3	7.654	1.791	1.307
					$\bar{x} = 1.355$ $s^2 = 1.773 \times 10^{-3}$
Morinda Shoals	29.6	1	8.263	2.509	1.436
		2	9.014	2.975	1.493
		3	10.214	3.263	1.469
					$\bar{x} = 1.466$ $s^2 = 0.819 \times 10^{-3}$
Little Broadhurst	49.5	1	6.899	1.924	1.387
		2	11.242	3.418	1.437
		3	8.498	2.569	1.433
					$\bar{x} = 1.419$ $s^2 = 0.772 \times 10^{-3}$
Bowden Reef	67.9	1	9.870	2.850	1.406
		2	11.679	3.346	1.402
		3	14.015	4.198	1.428
					$\bar{x} = 1.412$ $s^2 = 0.178 \times 10^{-3}$
Grub Reef	74.5	1	10.197	3.103	1.437
		2	11.817	4.380	1.589
		3	9.658	3.046	1.461
					$\bar{x} = 1.496$ $s^2 = 6.678 \times 10^{-3}$

inhibitors. Constanz (1988) has described termination of growth of aragonite skeletal elements by deposition of micrite granules. This mechanism seems unlikely, however, given the relatively low amounts of siliclastic sediment trapped within the skeletons of these corals (Fingland 1987) and the pervasive skeletal changes shown in Fig. 3. Whether the observed density differences are ecophenotypic responses to environmental gradients, or due to a much longer-term response of evolution of genetically different strains of *Porites lobata*, remains to be demonstrated.

The significance of these findings to modern reef ecology and ancient reef studies will be determined only through further work with this and other species. For now, however, a small forest of overall changes in skeletal density has been discerned behind the trees of annual density banding.

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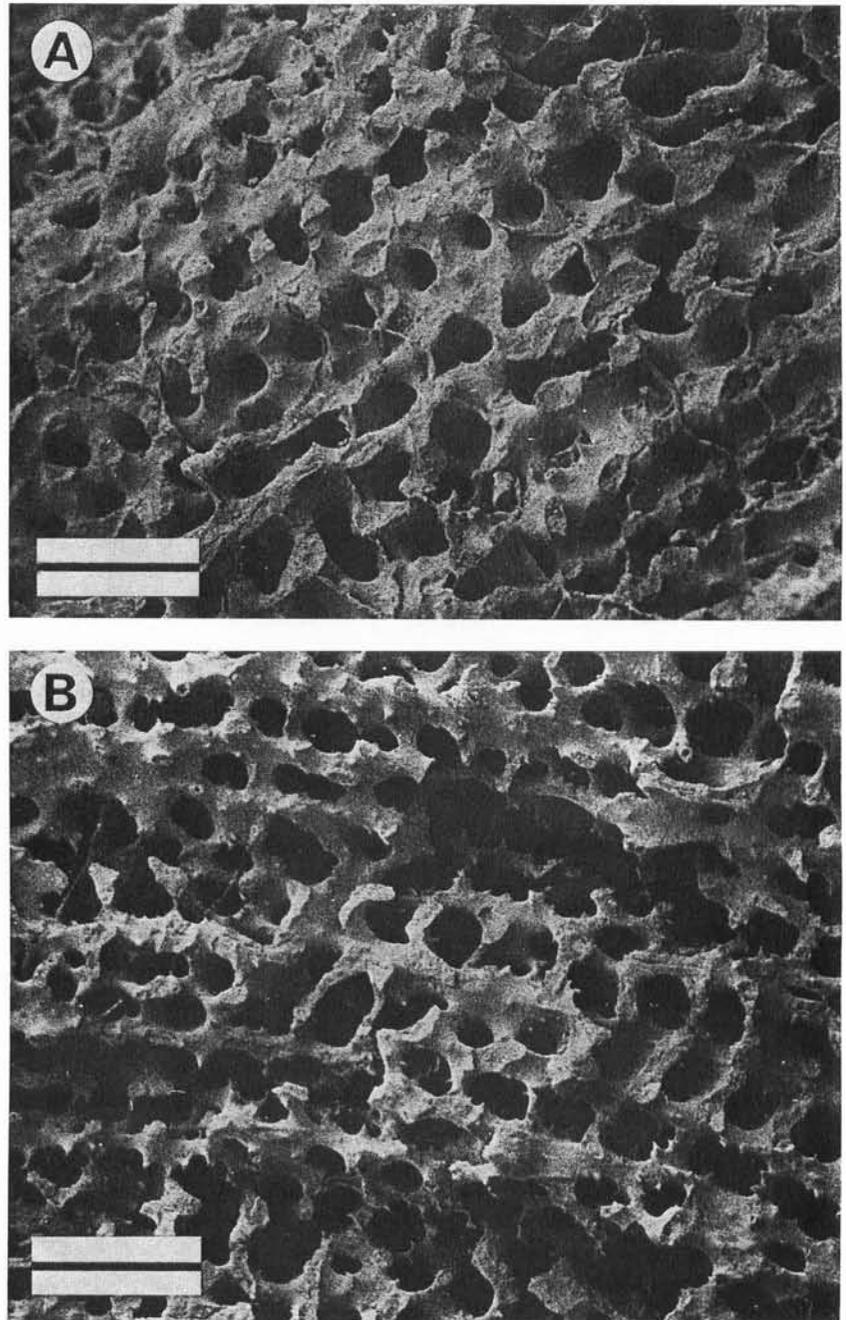


Fig. 3. *Porites lobata*. Scanning electron micrographs of skeletal architecture. (A) From Grub Reef; (B) from Alma Bay, Magnetic Island. Scale bars = 0.5 mm

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