

DEPTH-RELATED MORPHOLOGY OF SCLERACTINIAN CORALS ON SINGAPORE REEFS

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ABSTRACT

Three surveys were carried out at 12 coral reef sites in Singapore using depth-specific line transects with a total length of 100m. The foliose growth form was the dominant morphological type on Singapore reefs, occupying at least two times the amount of colonisable space on any reef compared with other growth forms. These corals dominated transects at the reef crest, 3m and 6m below the crest. Composition at the 10m transect was more even, with no marked dominance by any particular growth form. Patterns of distribution of other coral ecomorphs are largely a function of their competitive relationships with the foliose corals, with photosynthetic efficiency, sediment tolerance/removal ability, wave action and ultra-violet inhibition postulated to play a part.

INTRODUCTION

Species distribution of hard corals at different zones of a reef is strongly associated with the ecological, biological and environmental conditions present (Barnes, 1987; Clareboudt & Bouillon, 1987; Fishelson, 1973). At the same time, environment-related, within-species variation in morphology is also known (Foster, 1979; Fricke & Meischner, 1985; Stephenson, 1933). Helmuth & Sebens (1993) attributed morphological variations in *Agaricia agaricites* to selective pressures, including particle-feeding, light capture, sediment removal, gas and nutrient exchange and spatial competition. Graus & Macintyre (1976) demonstrated the control of coral morphology by light (the quality and quantity of which is directly related to its attenuation by water depth) using computer simulation models.

Lane (1991) provided indirect evidence that corals of different growth forms responded unequally to changes in an environmental parameter. He found that corals of different growth forms in Singapore are affected to differing degrees by high sedimentation. A generally lower growth rate for branching corals, but a comparable rate for massive corals when compared with similar growth studies on reefs in clearer waters was reported. Respiration in reef corals was studied in relation to growth form by Davies (1980). He found that at any particular depth, growth forms with higher surface area-volume ratios had higher rates of respiration. Because the photosynthetic zooxanthellae are found in the endodermal layer of corals, the surface area-volume ratio also affects the conversion of light energy in the same way as it does for respiration. Colony morphology was found to influence feeding in a hydroid (Hunter, 1989) but a recent study on the scleractinian *Agaricia agaricites* (Helmuth & Sebens, 1993) suggested that colony morphology does not represent an adaptation to prey capture. In terms of skeletal density, a consistent pattern related to coral growth forms was reported by Hughes (1987). He also found that foliose corals possessed the most dense skeleton. Hughes & Jackson (1985) studied foliaceous corals on Jamaican reefs and reported that this growth form predominated at most of their study sites. Within these corals, those that occurred in shallow waters had higher growth rates but were less robust than the deeper water colonies. Fricke & Meischner (1985) studied 17 species of hermatypic corals in Bermuda and found a general trend towards flatter shapes with depth.

Corals of the foliose growth form have also been reported to predominate reef sites in Singapore (Chua & Chou, 1991). Beyond this observation, the pattern of distribution of hard coral morphological types on Singapore reefs is not known. This paper addresses this question in relation to water depth and relates the patterns to the environmental conditions at each depth.

MATERIALS AND METHODS

Three surveys (29 April 1986 - 11 April 1989; 7 April 1990 - 7 May 1992; 8 June 1993 - 2 Nov 1993) using the depth-specific Line Intercept Transect method (Dartnall & Jones, 1986) were conducted on 12 reef sites (see Fig. 1, Low & Chou, this volume) as part of the ASEAN-Australia Marine Science Project: Living Coastal Resources. At each site, transects were placed on the reef crest (0m), and 3m, 6m and 10m below the crest. The first two surveys used lines that were 100m long; in the third survey, five 20m replicate transect lengths were employed. The reefs and sites surveyed were: Cyrene Reef (C1 and C2), Hantu West Reef (HW1 and HW2), Pulau Hantu (H1 and H2), Pulau Semakau (S1 and S2), Raffles Lighthouse (R1 and R2) and Lazarus Island (L2 and L4).

The following abbreviations are used to denote the various coral growth forms: CF=foliose; CM=massive; CE=encrusting; CMR=mushroom; CS=submassive/digitate; CB=branching; CT=tabulate; CME=*Millepora* spp.; CHL=*Heliopora* spp. (the last two categories are included together with the other scleractinians because they also deposit calcium carbonate skeletons that contribute to the framework of a reef). Percentage cover of only the more common scleractinian growth forms encountered in the transects are presented. Rarely encountered coral growth form categories (CT, CME and CHL), non-scleractinians and abiota are not considered in this analysis. Percentage cover is expressed in terms of total (live and dead) coral cover to reflect the competitive ability of each coral growth form within the colonisable space on each reef.

RESULTS

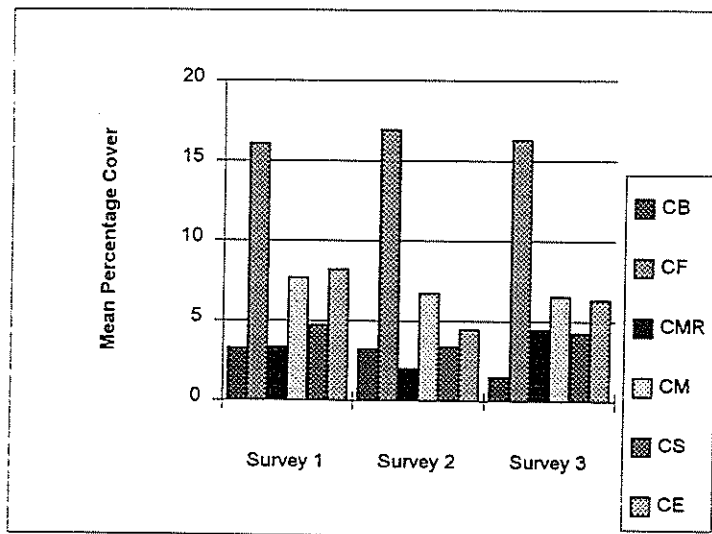


Fig. 1 Mean percentage cover (average of means from the 12 sites and 4 depths) of selected growth forms for surveys 1,2 and 3.

Among the different coral growth forms, the foliose corals occurred most frequently in all the surveys (Fig. 1). Massive and encrusting corals formed the next dominant ecomorphs on Singapore reefs. Branching corals had the lowest mean percentage cover for surveys 1 and 3. In terms of depth distribution, foliose corals had maximum cover at the 3m transect, but this decreased both up and down the reef slope (Fig. 2). The cover of branching, massive and submassive corals decreased with depth from 0m to 6m (lowest cover), then increased again at the 10m transect. There was an increase in the percentage cover of mushroom corals with depth, with a pronounced jump from 6m to 10m for surveys 1 and 3.

Foliose corals were most abundant (lowest mean ranking score) at the 0m, 3m, and 6m transects for all three surveys (Fig. 3). At the 0m and 3m transects (also in all three surveys), massive corals had the second lowest scores, while the encrusting growth form was the third-most abundant. At 6m below the reef crest, encrusting corals were ranked below the foliose corals and above the massive growth form in surveys 1 and 3 but this growth form was third in the hierarchy for survey 2 after the foliose and massive corals. Branching and mushroom corals were the least commonly found growth forms at the reef crest and 3m below the crest for all

three surveys. The branching morphology was also the least abundant growth form at the 6m transect. At the 10m transect, no clear pattern of growth form dominance could be discerned.

Statistical analysis (General Linear Models procedure, Duncan test) using the software package SAS (Statistical Analysis System) differentiated transect depths in the groups shown in Table 1a (considering all growth forms simultaneously). The rankings for the 0m, 3m and 6m transects were grouped together for surveys 2 and 3. When different growth forms were considered individually (Table 1b), seven of the fourteen cases where groupings occurred had the same result. In addition, three other groupings isolated the 10m transect from the other transects. A distinction between the 3m and 6m depths was found in three cases. This distinction was also evident from survey 1 in the overall analysis (Table 1a).

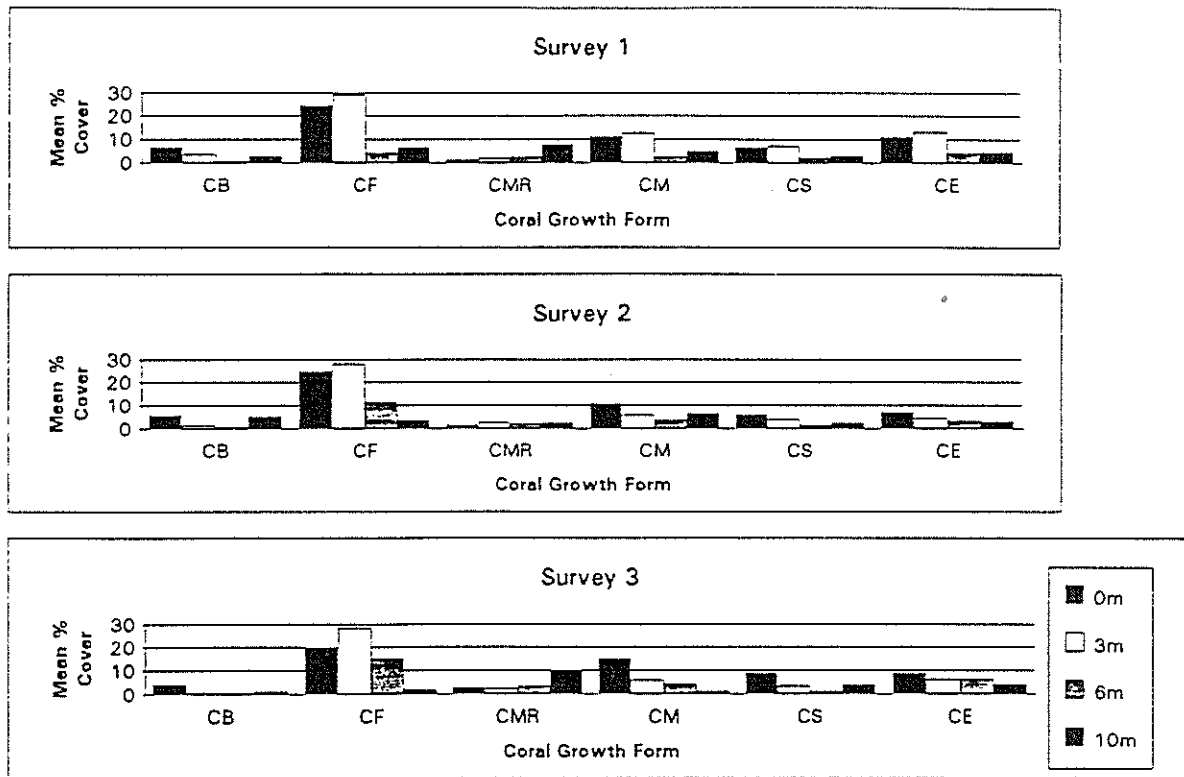


Fig. 2 Mean percentage cover of selected coral growth forms at 4 transect depths.

Table 1. Duncan groupings based on ranking scores from 12 survey sites (transects within separate parentheses are significantly different at the 95% confidence level).

a. Overall (all growth forms taken into account) groupings.

SURVEY		
1	2	3
(0m, 3m) (6m, 10m)	(0m, 3m, 6m) (10m)	(0m, 3m, 6m) (10m)

b. Individual growth form groupings.

SURVEY	CORAL GROWTH FORM					
	CB	CF	CMR	CM	CS	CE
1	(0m, 3m, 10m) (6m)	(0m, 3m) (6m, 10m)		(0m, 3m) (6m, 10m)	(0m, 3m, 6m) (10m)	
2	(0m) (6m, 10m)	(0m, 3m, 6m) (10m)		(0m, 3m, 6m) (10m)	(0m) (10m)	(0m, 3m, 6m) (10m)
3	(0m, 3m) (6m, 10m)	(0m, 3m, 6m) (10m)	(6m) (10m)	(0m) (6m) (10m)		(0m, 3m, 6m) (10m)

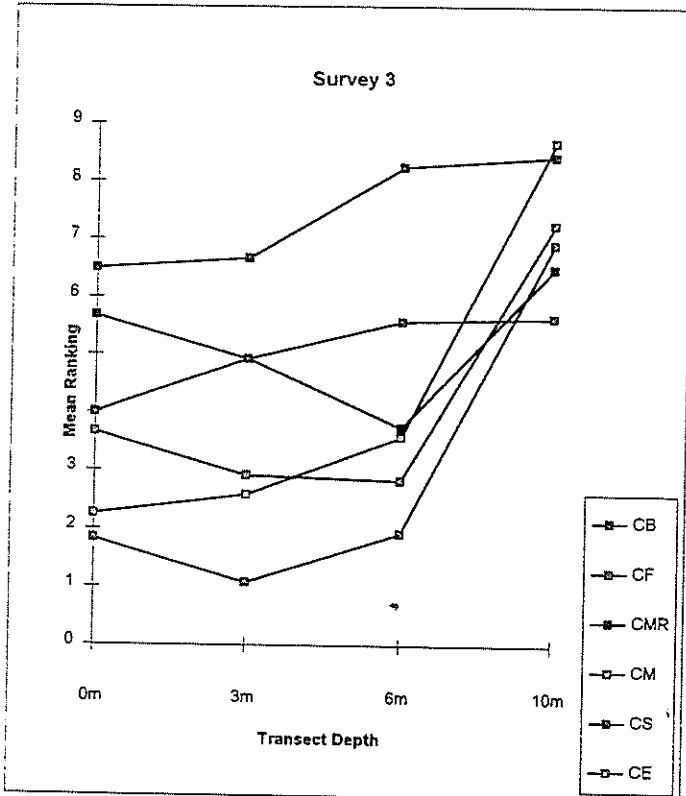
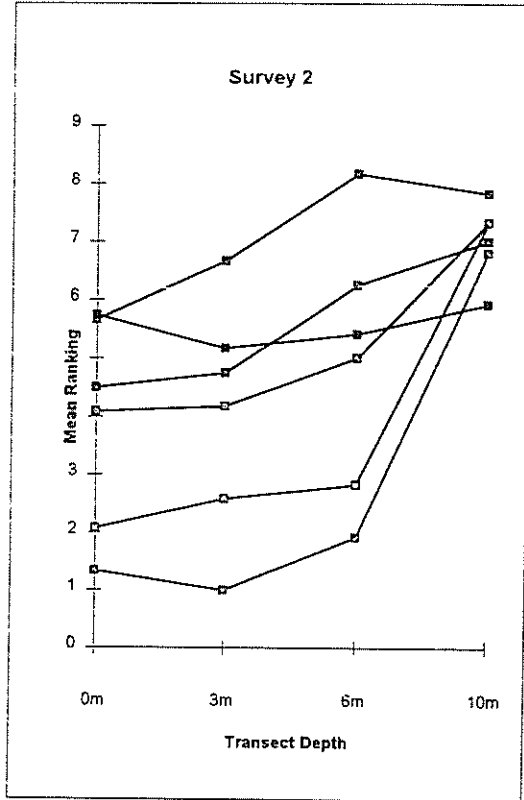
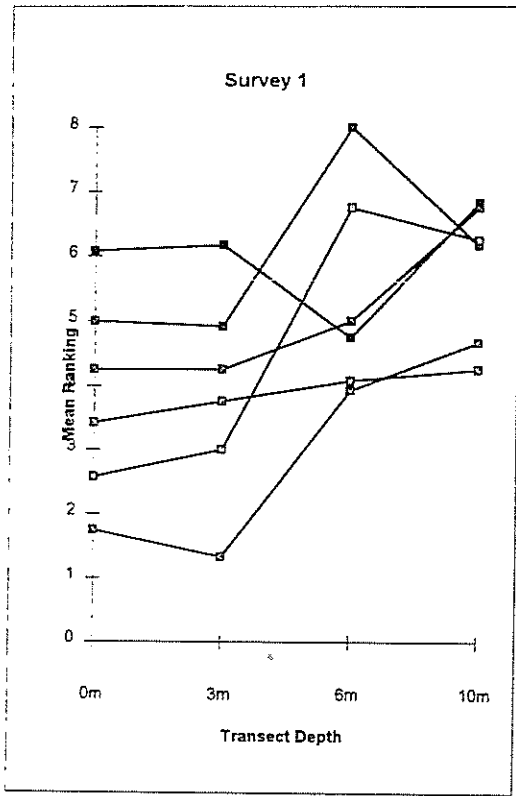


Fig. 3. Mean ranking of coral growth forms for the four transect depths, based on mean percentage cover (rankings in ascending order; lowest score = most abundant).

DISCUSSION

The relative abundance of a coral at a particular depth is linked to its competitive ability against other corals and to its biological/physical/mechanical adaptations to conditions present where it grows. Two important parameters that are known to vary with depth are light intensity/quality and water movement. Areas that experience strong wave action show a marked decrease in water movement at deeper sites on the reef (Sebens & Johnson, 1991). Decreased water movement reduces the rate of diffusion of gases across the coral body, limiting respiration and more importantly, the utilisation of carbon dioxide from the water for the photosynthetic process (Dennison & Barnes, 1988). As for the reefs at Eilat (Bouchon, 1980), this is probably not the case in Singapore as wave action is generally weak and the difference in depth is relatively small (10 m). Light intensity would therefore be the major depth-dependant factor operating in the sheltered and turbid waters of Singapore.

In all three surveys, foliose corals exhibited at least a two-fold advantage in mean percentage cover (taking the mean of all four depths) over other growth forms (Fig. 1). Foliose corals generally have a larger surface area-volume ratio compared to other coral growth forms. This characteristic gives them two related advantages: increased ability to trap light energy for photosynthesis because of the larger surface area exposed, and relatively faster linear extension rates resulting from a flattened morphology. This enables foliose corals to overtop competitors which are not able to grow as quickly. However, their dominance only extends from 0m to 6m (Fig. 3). At 10m, factors other than light capturing capacity must come into play since this factor is independent of ambient light conditions and hence, depth. One factor that could explain this phenomenon is that the efficiency in utilisation of light (not to be confused with capacity for light capture) of foliose corals is not linearly related to the decrease in light intensity. A 'photocline' may exist for the photosynthetic machinery of foliose corals between the 6m and 10m transects which causes a disproportionate and sudden decrease in productivity. Wells (1954) described the bathymetric distribution of corals in terms of 'surface' or 'nonsurface' genera. A similar categorisation of coral growth forms may be possible although at the present time, this has to remain an idea. Support for this theory comes from the work of Wethey & Porter (1976) who found differences in the productivity of corals exposed to different light intensities, and of Done (1983), who reported photosynthetic inefficiency of corals at reduced irradiance levels.

Distribution of foliose corals on the lower slope (10m) may also be constrained by higher rates of sediment settlement and (within species) variation in growth rate with depth. Porter (1976) found a growth-inhibitory effect of sediment accumulation on fast-growing species with large horizontal surfaces (like the foliose corals). The success of coral growth forms at this depth may then be understood in terms of sediment-removing ability (Dodge et al., 1974; Bak, 1978) rather than direct competitive prowess. Hughes & Jackson (1985) reported a greater degree of calcification and slower growth rates in foliose corals at deeper compared to shallower sites, providing an alternative explanation for the loss of dominance at the 10m transect. This loss of dominance of the foliose corals at the 10m transect suggests that other coral morphotypes may have either: 1. higher photosynthetic efficiency, 2. lower energy requirements, 3. greater ability in heterotrophic feeding than foliose corals, characteristics which enable them to compete with the (assumed) faster growing foliose corals when the latter are limited by environmental conditions.

Titlyanov & Latypov (1991) reported that coral colonies tended to flatten with depth in turbid waters of the Gulf of Siam, but no corroborative evidence is apparent from the ecomorph distributional patterns in Singapore. The 'pattern' actually tends towards randomness with depth, especially at the 10m transect.

At the reef crest (0m), intolerance of ultra-violet radiation (Jokiel, 1980) and mechanical stress and breakage caused by wave action during storms may curb the competitive advantages of the foliose morphology (Fig. 3). Following this trend of thought, the dominance of the foliose ecomorph at 3m suggests that at this depth, the level of photosynthetically useful light is optimal and ultra-violet radiation, wave action and sediment settlement are at acceptable levels.

From the shape of the graphs in Fig. 3, branching, massive and encrusting corals appear to be affected by environmental factors in a manner similar to the foliose corals. These factors that affect the foliose corals would also constrain these coral morphotypes. At the shallower depths (0m, 3m, 6m) the ranking of these coral growth forms appears to be mainly a function of their competitive interactions with the foliose corals. When the competitive pressure of the foliose corals is removed at the 10m transect, these corals can rank above the foliose growth form, suggesting that the depth-related environmental factors that affect the foliose corals affect

them to a lesser degree. Mushroom corals have the ability to expand their tissues with water to dislodge sediment. Faster growing or more aggressive coral species may prevent their proliferation at the shallower depths, but they increase in mean percentage cover (Fig. 2) and rankings (Fig. 3) when competition is removed or weakened by inhibitory light or sedimentation levels, especially at the 10m transect.

Taking all coral growth forms into account (Table 1a), there was a distinction in the distribution (ranking) of coral morphotypes between the shallower (0m and 3m) and the deeper (6m and 10m) transects in survey 1. In the second and third surveys, the 10m transect was separated from the other transects, which were grouped together. Analyses within each coral growth form (Table 1b) showed similar distinctions. Branching (survey 3), foliose and massive (survey 1) corals were also separated at the 3m-6m interphase, while distinct groupings at the 6m-10m interphase was shown in all the coral growth forms: branching (survey 1), foliose (surveys 2 and 3), mushroom (survey 3), massive (surveys 2 and 3), submassive (surveys 1 and 2) and encrusting (surveys 2 and 3) corals. The existence of differences in ecologically important parameters between the 3m and 6m transect and between the 6m and 10m transect are implied in these observations. The nature of these parameters is not known at the moment but is likely to be depth-dependant.

It is suggested that competition between coral ecomorphs is an important factor in their relative distribution on Singapore reefs. The foliose growth form is the most efficient/aggressive in competition for space, occupying at least twice the amount of colonisable space on a reef compared to any other growth form. The depth-related patterns of distribution for the other coral ecomorphs is a function of competition with the foliose corals, mediated by other factors, including photosynthetic efficiency, sediment-removal ability, wave action during storms and ultra-violet tolerance. Foliose corals appear to be more sensitive to changes in these parameters between the 6m and the 10m transects. This 6m-10m interphase is also a significant dividing line in all the other coral morphotypes examined. Investigations into the effects of these parameters on coral growth form distribution should provide a more complete understanding of the ecology of coral morphological types.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Australian International Development Assistance Bureau under the ASEAN-Australia Economic Co-operative Programme for the ASEAN-Australia Marine Science Project: Living Coastal Resources. Field surveys were undertaken by the Reef Ecology Study Team, Department of Zoology, National University of Singapore. We are also grateful to Maylene Loo for help in data retrieval and analysis.

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