

# Patterns of Coral Distribution and Benthic Space Partitioning on the Fringing Reefs of Southern Taiwan

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With 13 figures

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**Abstract.** The distribution pattern of corals and benthic space partitioning patterns on the fringing reefs of southern Taiwan were studied by the line-transect method. The bathymetric distribution of corals in the study area was basically homogeneous except on the protected reef slopes and the exposed reef fronts and terraces. Corals on protected reef slopes are mainly foliaceous, including *Montipora foliosa*, *Merulina ampliata*, *Mycedium elephantotus*, and *Pachyseris speciosa*, but the dominant species on a reef slope vary from site to site. The formation of the foliaceous coral community is possibly related to a complex of environmental factors, chance, and biological interactions. The reef fronts and submarine terraces of exposed areas are dominated by alcyonacean corals. The most abundant species are *Sarcophyton trocheliophorum*, *S. crassocaule*, and *Lobophytum sarcophytoides*; their distributions are relatively homogeneous. The formation of alcyonacean-dominated assemblages can be related to the special adaptive strategies of these corals. In regard to space partitioning patterns, the major space occupiers on those reefs exposed to storm disturbances are alcyonacean soft corals, scleractinian corals, and algae; on reefs protected from storms, scleractinian corals and algae dominate. Two conspicuous features of the study area are the high proportion of space occupied by algae and the abundant unoccupied space. The dense algal cover is possibly caused by sewage pollution and overfishing of the reef area. The unoccupied space is most likely related to the high frequency of typhoon disturbances.

## Problem

The description of zonation patterns on coral reefs is long-standing (*e. g.*, MARSHALL, 1931; WELLS, 1954; GOREAU, 1959). Reef zonations have been determined on the basis of (1) the predominance of one or several species (LOYA & SLOBODKIN, 1971; ROSEN, 1971; SHEPPARD, 1980), (2) the topographic regions (GOREAU, 1959; BAK, 1977; BOUCHON, 1981), (3) the predominance of specific growth forms (PICHON, 1978), and (4) the overall faunal affinity by using multivariate techniques (LOYA, 1972; VAN DEN HOEK *et al.*, 1978; MOLL, 1986; TOMASCIK & SANDER, 1987). It is generally accepted that biotic zonations are less obvious in the Indo-Pacific than in the Atlantic Ocean (SHEPPARD, 1982; DONE,

1983), partly because of the many more species on Indo-Pacific reefs. Quantitative descriptions of biotic zonation patterns of Atlantic reefs have been reported by many authors (*e. g.*, VAN DEN HOEK *et al.*, 1978; LIDDELL & OHLHORST, 1987) but relatively few such attempts have been conducted in the vast Indo-Pacific coral reef areas (SHEPPARD, 1980; DONE, 1983). Some recent studies have shown that similar zonation patterns based on coral morphology may exist between Indo-Pacific and Atlantic reefs (SHEPPARD, 1980; DONE, 1983; DAI, 1988a). Quantitative descriptions of coral distribution patterns on different Indo-Pacific reefs are thus necessary.

Hermatypic hard corals, alcyonacean soft corals, and algae are the major space occupiers on many Indo-Pacific coral reefs (*e. g.*, LOYA, 1972; BENAYAHU & LOYA, 1977a; SHEPPARD, 1982). However, most of the coral community studies to date deal only with hermatypic hard corals. Only recently have ecological studies focused on chemical ecology (LA BARRE, 1983), distribution (TURSCH & TURSCH, 1982; DINESEN, 1983), and competitive strategies (*e. g.*, BENAYAHU & LOYA, 1977a, b; SAMMARCO *et al.*, 1983; LA BARRE *et al.*, 1986; DAI, 1990) of coexisting scleractinian and alcyonacean corals. The relative abundance and distribution patterns of these two groups on reefs remain poorly understood.

It is often assumed that space on a coral reef is limited, and that corals compete for it (LANG, 1973; CONNELL, 1976; SHEPPARD, 1979, 1982). In the few cases where unoccupied reef substrate has been measured, however, up to 20 or 35 % is devoid of macrofauna and flora even on crowded reefs (BAK & LUCKHURST, 1980; SHEPPARD, 1980, 1985; BENAYAHU & LOYA, 1977a). The occurrence of unoccupied space on coral reefs has rarely been studied, and even the quantity of such space appears to have been overlooked in many studies.

Studies of coral communities on the fringing reefs of southern Taiwan were initiated by JONES *et al.* (1972). They provided qualitative descriptions of the reef morphology and biotic communities. Subsequent studies by YANG & DAI (1980) and YANG (1985) quantitatively described the coral communities in Nanwan Bay. DAI (1988a) extended the study to include the west coast of Hengchun Peninsula, where faunal compositions and community structures were described. In this paper, I describe the distribution patterns of both scleractinian and alcyonacean corals on the fringing reefs of southern Taiwan based on quantitative data. Space partitioning patterns among hard corals, soft corals, and algae as well as the distribution of unoccupied reef space are also discussed.

## Material and Methods

### 1. Study site

The study area, Hengchun Peninsula, is located at the southern tip of Taiwan (Fig. 1; 21° 55'–22° 00'N, 120° 40'–120° 52'E). The peninsula is surrounded by well-developed fringing reefs inhabited by a very rich coral fauna (DAI, 1991a).

Six sites on the coast of Hengchun Peninsula, two on the west coast (A, B) and four in Nanwan Bay (C, D, E, F), were selected for this study (Fig. 1). Sites C and D are exposed to strong currents and storm disturbances, Sites B, E, and F are protected from such disturbances, and Site A is

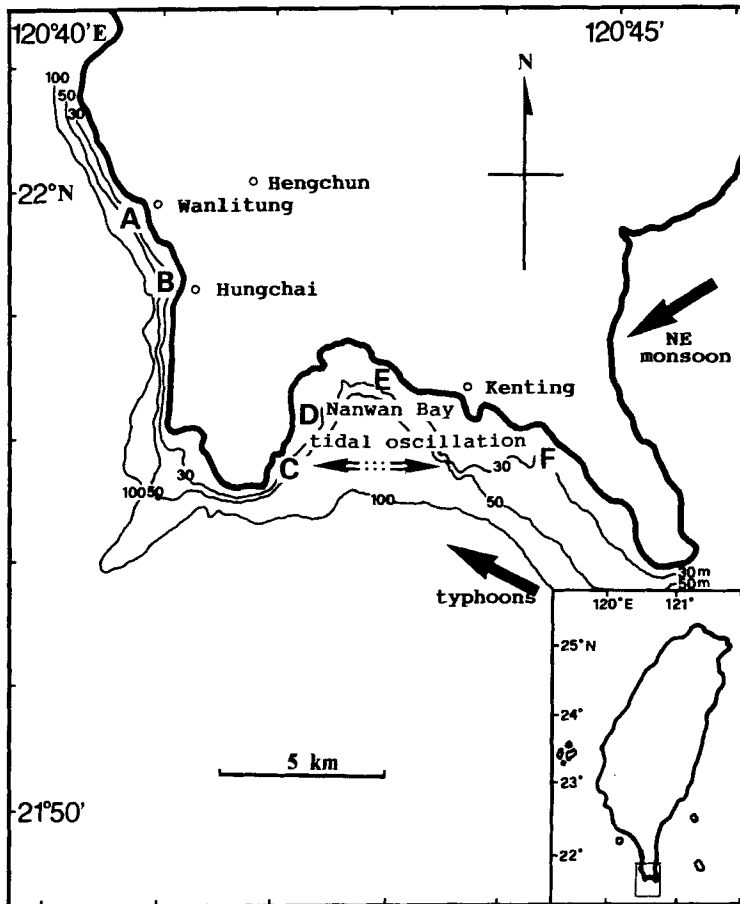


Fig. 1. Southern Taiwan with the study sites (A-F).

exposed to strong tidal currents but protected from storm disturbances (DAI, 1991a). Coral communities at Sites A, B, E, and F are dominated by scleractinian corals, those at Sites C and D by alcyonacean corals (DAI, 1988a).

## 2. Sampling method

At each site, a transect was established perpendicular to the coast and extending seaward to the reef edge (ca. 25 m in depth). A 10 m chain line with links 1.5 cm in length was laid parallel to the depth contour at intervals and with its center lying on the transect. The 10 m chain line has been widely adopted in the study of coral communities (*e. g.*, LOYA, 1972; PORTER, 1972; TOMASCIK & SANDER, 1987; GUZMÁN & CORTES, 1989) and has been proved to be suitable for sampling in southern Taiwan (YANG & DAI, 1980). The transect was sampled at 15 m distance intervals parallel to depth contours along the transect; an exception was the submarine terrace of site D, where the reef was flat and a 25 m interval was applied. A total of 25–30 lines was sampled at each site. All benthic organisms under the line were recorded and the length of each organism that intercepted the line was measured to the nearest 0.5 cm and recorded. All scleractinian, alcyonacean, and hydrozoan corals were

identified to species. Whenever confronted with an unknown coral colony, a color photograph was taken with a Nikonos V camera and a small sample was taken for further identification in the laboratory. No effort was made to identify the species of algae, sponges, and other benthic organisms; these organisms were recorded as easily recognizable classes or phyla. A coral colony was defined as any continuous tissue growing independently of its neighbors. In cases with two or more overlapping colonies, the intersected length was divided evenly between the top and the underlying colonies. Unoccupied space was measured and classified into sand and bare rocks. Thus, the benthic space occupiers were classified into six groups, *i. e.*, hard corals (including scleractinians, *Millepora* spp., and *Heliopora coerulea* [PALLAS]), soft corals, algae, others (bryozoans, sponges, etc.), sand and bare rocks; finally, the space partitioning patterns along the bathymetric depths of the six sites were analyzed.

## Results

### 1. Reef topography

Reef profiles of the six sites are shown in Figs. 2–7. The terminology used by JONES *et al.* (1972) such as reef flat, reef margin, reef front, and submarine terrace was adopted here. Most of the living reefs in the study area are relatively narrow, extending to approximately 200–300 m from shore and terminating on sandy bottom at a depth of 15 to 30 m. The only exception is the reef at Site D; it extends over 1000 m from shore and is the widest living reef of the study area. In general, the reefs are cut by surge channels in littoral zones and by submarine grooves in sublittoral zones due to the abrasion and erosion by currents and swells. These channels and grooves are contiguous and perpendicular to the seashore. Adjacent channels and grooves are interconnected and give rise to spurs and buttresses of various shapes and sizes. In exposed areas (Sites A, C, D), the reefs are tooth-shaped on their frontal edge, possibly due to erosion by strong currents. Huge blocks with a width and height of 10 m are common at depths below 15 m. In protected areas (Sites B, E, F), the reef topography is relatively smooth. Here, the surface is interwoven by surge channels in shallow waters (<5 m) and extends to a small terrace and a smooth slope at the reef front.

### 2. Coral distribution patterns

A total of 214 species representing 62 genera of corals was recorded during the sampling survey at the six sites (DAI, 1988b). Of this total, 170 species in 50 genera of scleractinians, 39 species in 11 genera of alcyonaceans, and 4 species of *Millepora* were recorded. Among them, only 45 species were recorded at all sites and 135 species were recorded at 3 to 6 sites. The presence of more than 100 coral species at each site and their sporadic distribution makes it superfluous to illustrate the distributions of all species: only the ten most abundant species at each site were selected (Figs. 2–7). The relative abundance of each species is represented by percent cover as calculated from the results of chain-line sampling. Subdivision of zones along each transect was determined by considering both topographic features and the results of multivariate analysis. These data have been reported elsewhere (DAI, 1988b).

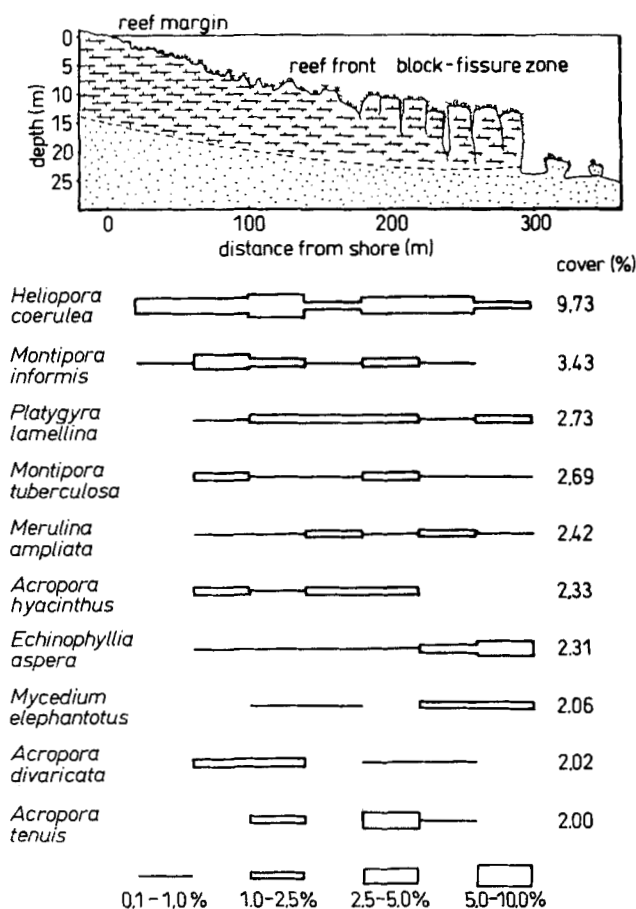


Fig. 2. Reef profile and bathymetric distribution of the ten most abundant species of Site A. Relative abundance of coral species is shown as percent cover. In Figs. 2-13: hatched: limestone platform; stippled: non-limestone basement rock.

Two of the most abundant coral species at Sites A and B on the west coast of Hengchun Peninsula are the blue coral, *Heliopora coerulea* (PALLAS), and *Montipora informis* BERNARD; both have a wide bathymetric distribution (Figs. 2, 3). Distributions of other species at Site A are relatively homogeneous except that the foliaceous *Echinophyllia aspera* (ELLIS & SOLANDER) mainly occurs in deeper waters and the branching *Acropora tenuis* (DANA) in intermediate depths (Fig. 2). At Site B, the foliaceous corals *Montipora foliosa* (PALLAS) and *Mycedium elephantotus* (PALLAS) are more abundant below 15m; the encrusting *Montipora spumosa* (LAMARCK) and branching *Seriatopora hystrix* DANA are more abundant in shallow waters; and the branching *Acropora formosa* (DANA) and *Stylophora pistillata* (ESPER) are more abundant in intermediate depths (Fig. 3).

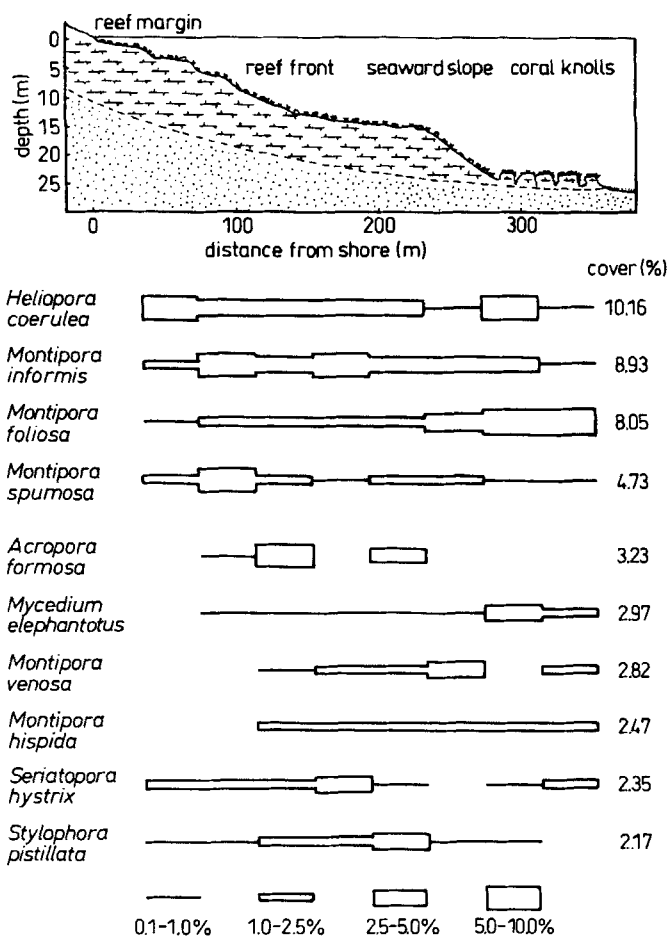


Fig. 3. Reef profile and bathymetric distribution of the ten most abundant species of Site B. Relative abundance of coral species is shown as percent cover.

Coral communities at Sites C and D are dominated by alcyonacean corals (more than 70% of the total coral cover). Eight of the ten most abundant species are alcyonacean soft corals. The three most abundant species at the two sites, *Sarcophyton trocheliophorum* VON MARENZELLER, *Lobophytum sarcophytoides* MOSER, and *S. crassocaule* MOSER, are widely distributed throughout the reefs (Figs. 4, 5). They are mushroom- or cup-shaped. Other alcyonaceans have a relatively narrow range of distribution. For example, the encrusting *Sinularia exilis* TIXIER-DURIVAUT, *S. facile* TIXIER-DURIVAUT, and *Lobophytum solidum* TIXIER-DURIVAUT mainly occur in shallow water, while the branching *Nephthea erecta* KÜKENTHAL of Site C and *Sinularia granosa* TIXIER-DURIVAUT of Site D are more abundant in intermediate depths.

The most abundant species of Site E, such as *Merulina ampliata* (ELLIS &

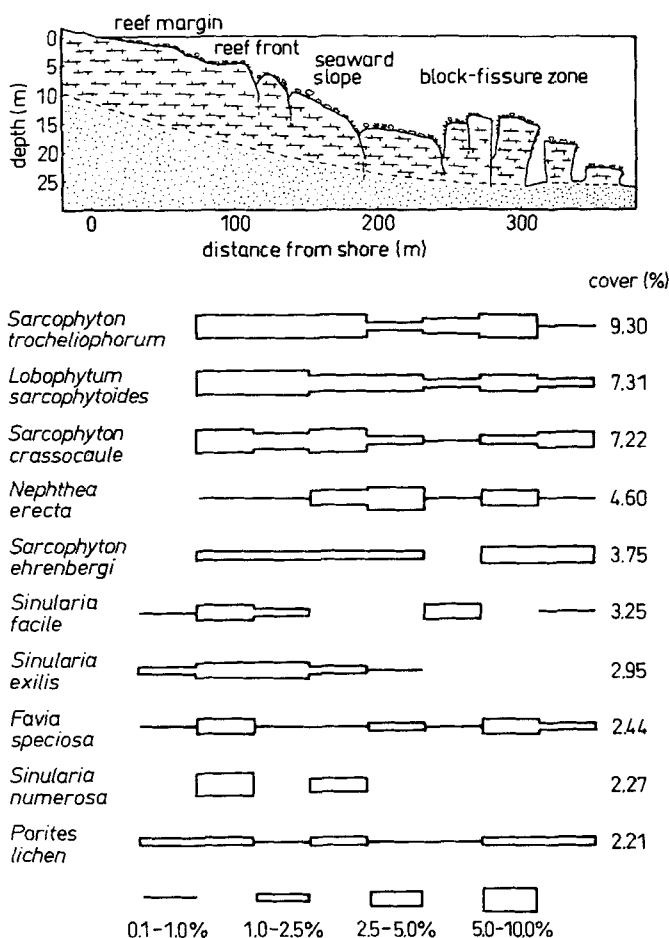


Fig. 4. Reef profile and bathymetric distribution of the ten most abundant species of Site C. Relative abundance of coral species is shown as percent cover.

SOLANDER), *Mycedium elephantotus*, and *Montipora foliosa*, are foliaceous; they are dominant in deep waters (Fig. 6). The alcyonacean on the list of Site E, *L. sarcophytoides*, has a narrow range of distribution in shallow waters. Other species listed here are low in cover (<2.2%) and basically homogeneous in distribution. At site F (Fig. 7), *Montipora informis* is more abundant in shallow water, *M. foliosa* and *Pachyseris speciosa* (DANA) in deep waters. Foliaceous *Merulina ampliata* and *Montipora verrucosa* (LAMARCK) are also more abundant in deep waters. Other species have a homogeneous distribution.

In general, coral distribution patterns in the areas exposed to strong currents (Sites A, C, D) are relatively homogeneous, while in protected areas (Sites B, E, F), foliaceous corals dominate the reef slopes (below 15 m). Species occurring in shallow water areas display massive and encrusting forms such as

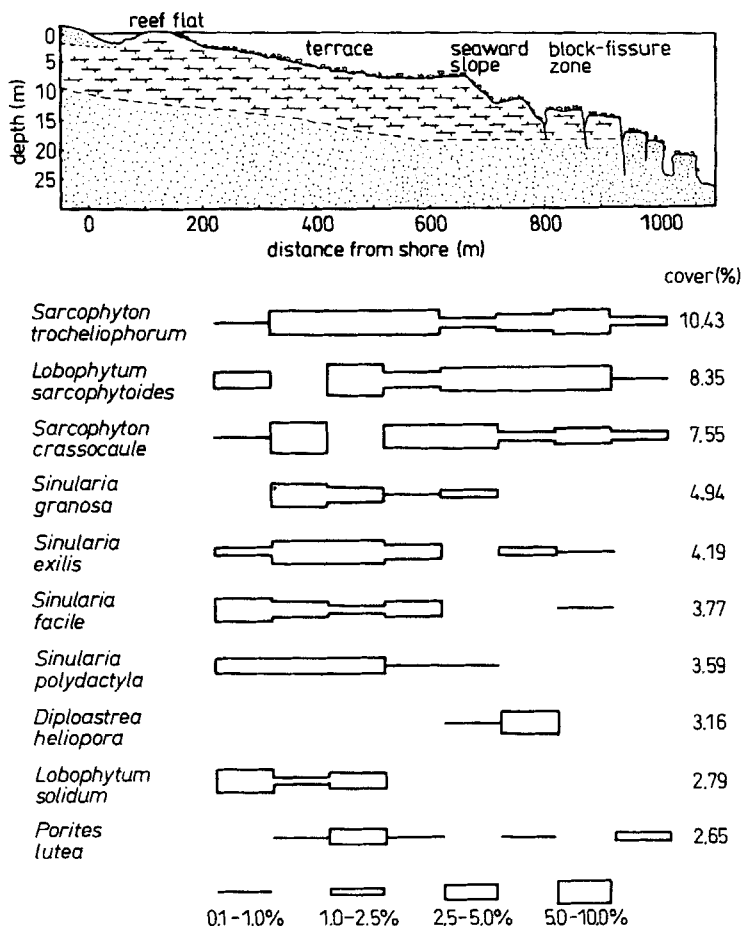


Fig. 5. Reef profile and bathymetric distribution of the ten most abundant species of Site D. Relative abundance of coral species is shown as percent cover.

*Montipora spumosa*, *Pocillopora verrucosa* ELLIS & SOLANDER, *Porites australiensis* VAUGHAN, *Porites (Synaraea) rus* (FORSKAL), *Montastrea valenciennesi* (ELLIS & SOLANDER), *Leptoria phrygia* (ELLIS & SOLANDER), *Favites pentagona* (ESPER), *Cyphastrea microphthalma* (LAMARCK), *Goniastrea australiensis* (EDWARDS & HAIME), and *Millepora platyphylla* HEMPRICH & EHRENBERG. The foliaceous corals typical of deep waters include *Montipora foliosa*, *Merulina ampliata*, *Mycedium elephantotus*, *Oxypora lacera* (VERRILL), *Pachyseris speciosa*, *Echinophyllia aspera*, and *Echinopora lamellosa* (ESPER). Most of the deep-water species are rarely present in shallow waters (0-5 m), although shallow-water species sometimes occur in deep waters.



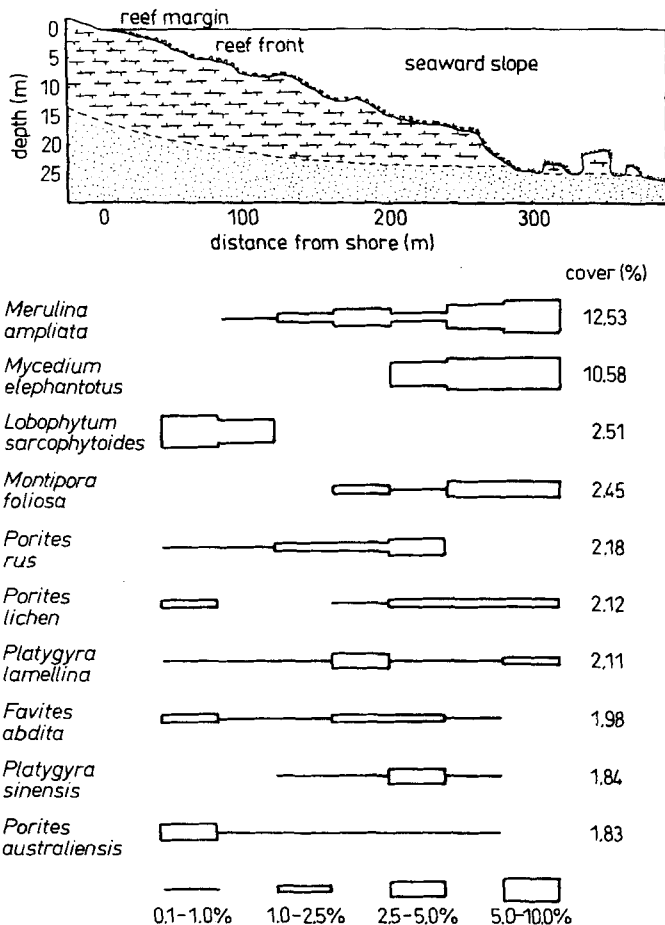


Fig. 6. Reef profile and bathymetric distribution of the ten most abundant species of Site E. Relative abundance of coral species is shown as percent cover.

### 3. Space partitioning patterns

The percent of substrate occupied by the six groups along the bathymetric zones at the six study sites is shown in Figs. 8-13.

The major space occupiers in protected areas (Sites A, B, E, and F) are hard corals and algae. Soft corals usually comprise less than 5% of the total cover except in shallow waters of Site E (Fig. 12). Algae occupy more than 40% of the substrate in most parts of Site A except at the block-fissure zone, where the unoccupied space is above 30% (Fig. 8). Hard corals, including scleractinians and the blue coral *Heliopora coerulea*, occupy about 25 to 40% of the substrate. Soft corals are present throughout Site A, but their cover is low. Unoccupied space ranges from 11 to 32% here; bare rocks are the main component.

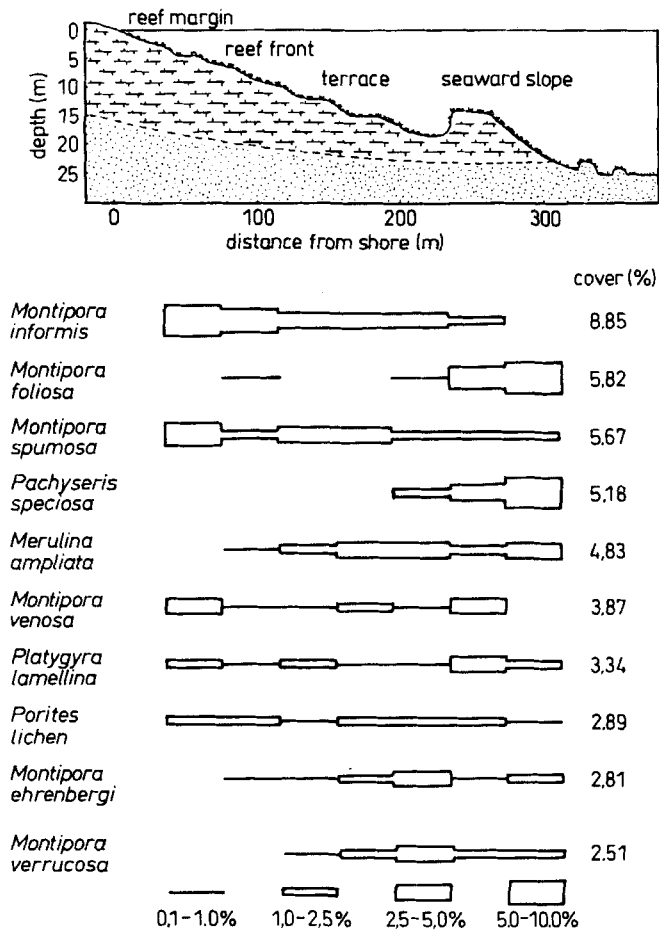


Fig. 7. Reef profile and bathymetric distribution of the ten most abundant species of Site F. Relative abundance of coral species is shown as percent cover.

Hard corals and algae are the major space occupiers at Site B (Fig. 9), with more than 40% and between 27 and 45% coverage, respectively. Unoccupied space at Site B ranges from 13 to 34%, with similar amounts of sand and bare rocks. The benthic space partitioning pattern at Site E differs from Sites A, B, and F. The space occupied by hard corals increases in deeper waters, where they cover more than 50% of the substrate on reef slope. Soft corals occupy about 20% of the surface on the shallow water reef margin (3–6 m depth), but decrease abruptly in deep waters. Algae are less abundant at Site E (< 20% cover). The high percentage of unoccupied space at Site E (22–43%) primarily consists of bare rocks in shallow waters (3–10 m) and sand in deeper waters (11–23 m). Hard corals and algae are the major space occupiers at Site F (Fig. 13). They display an opposite trend of distribution along the reef zones: hard corals are more abundant in shallow and deep waters, algae in intermediate depths.

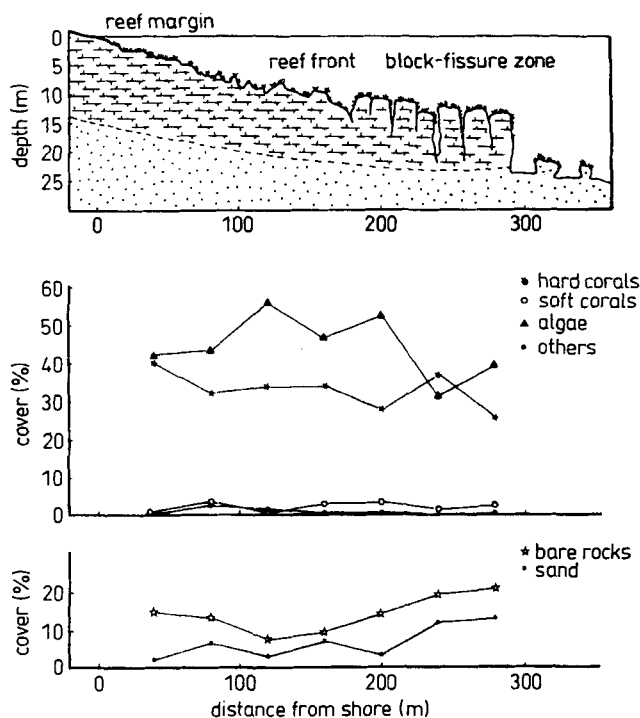


Fig. 8. Percent cover of the six groups of space occupiers along the bathymetric zones of site A.

Soft corals, hard corals, and algae are the major space occupiers of Sites C and D (Figs. 10 and 11). Soft corals dominate at the reef front and seaward slope (6–17 m) of Site C and at the submarine terrace and seaward slope (5–12 m) of Site D. At the reef margins and block-fissure zones of both sites, however, hard corals are more abundant. Algae tend to increase toward deep waters at the two sites. Unoccupied substrate here is mainly composed of bare rocks; it ranges from 20 to 54%. The high proportions of bare rocks at the reef margins and block-fissure zones of Sites C and D suggest a high water energy here.

## Discussion

### 1. Coral distribution patterns

This study reveals that the bathymetric distribution of corals on the fringing reefs of southern Taiwan is basically homogeneous. This may be due to the high species diversity of corals and the narrow reef areas (DAI, 1988 b). Most of the recorded species are either sporadically distributed or widely scattered throughout the reefs. The high degree of species overlap between topographic zones makes zonal delineation on the basis of species composition difficult. Coral zonation is noticeable only on protected reef slopes, exposed reef fronts,

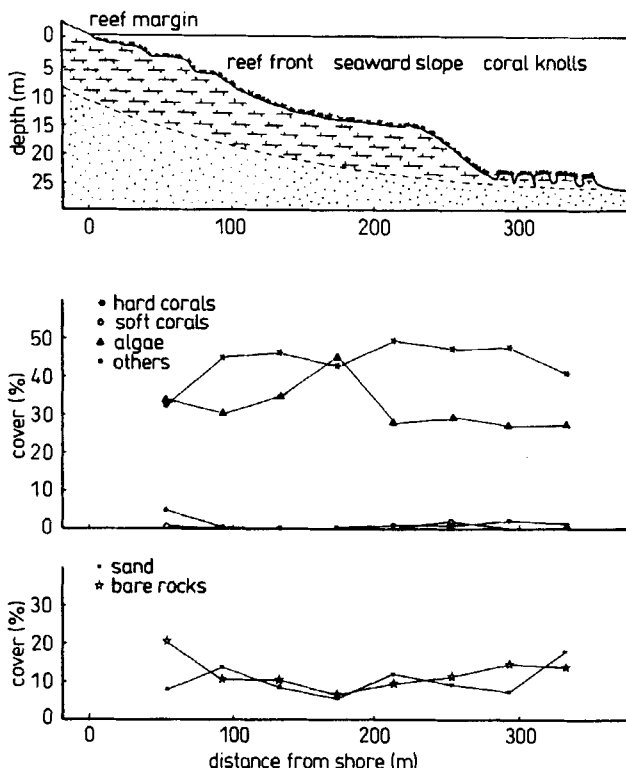


Fig. 9. Percent cover of the six groups of space occupiers along the bathymetric zones of site B.

submarine terraces, and seaward slopes. Foliose corals are common on protected reef slopes in southern Taiwan and include *Montipora foliosa*, *Merulina ampliata*, *Mycidium elephantotus*, *Echinophyllia aspera*, *Pachyseris speciosa*, and *Echinopora lamellosa*. Alcyonaceans dominate coral communities on reef fronts, submarine terraces, and seaward slopes of reefs exposed to both strong currents and storm disturbances.

A foliose coral community of deep-water reef slopes has been reported on most Indo-Pacific and Atlantic reefs (*e.g.*, WELLS, 1954; STODDART, 1969; DINESEN, 1977; SHEPPARD, 1980, 1982; DONE, 1983; KÜHLMANN, 1983). WELLS (1954) reported two zones dominated by foliose corals on the reef slope of Bikini: (1) the *Echinophyllia* zone, from 18 to 91 m depth, and (2) the *Leptoseris* zone, from 91 to 146 m. YAMAZATO (1969) recognized similar zones in the deep-sea corals of the Ryukyu Islands. In the Indian Ocean, PICHON (1978) recognized the *Agariciidae* and *Pectiniidae* zone below 15 m on the reef slope of Tulear, Madagascar. SHEPPARD (1980) identified a *Pachyseris* zone (25–45 m) and an *Agariciella* zone (below 50 m) on the reef slope of the Chagos Atoll. An equivalent type of reef slope community in Caribbean reefs was described by GOREAU & HARTMAN (1963) as the *Agaricia* community (deeper outer slope, 40–70 m). LIDDELL & OHLHORST (1987) recognized a similar community as the

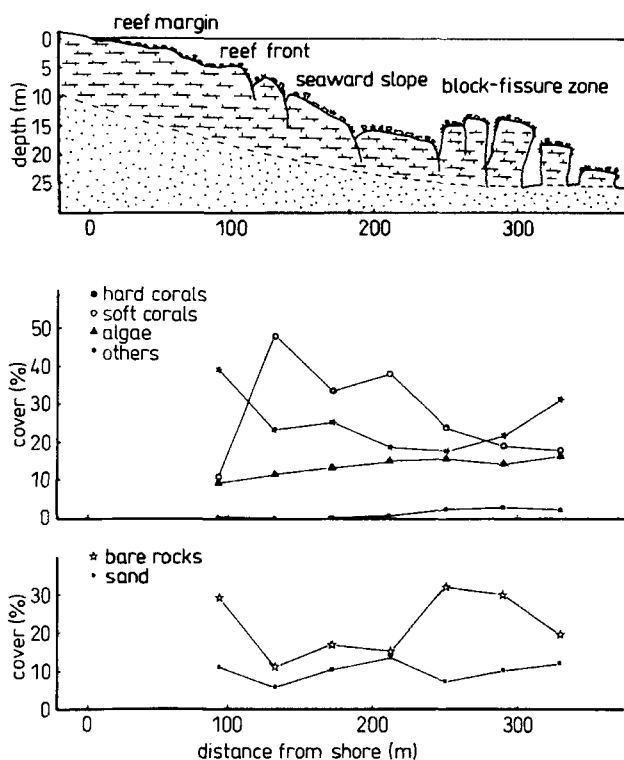


Fig. 10. Percent cover of the six groups of space occupiers along the bathymetric zones of site C.

'fore reef slope' community from 30 to 60 m depth on a North Jamaican reef. KÜHLMANN (1983) reported 'deep-water coral associations' on several reefs in the Red Sea, Pacific Ocean, and western Atlantic Ocean. This type of coral community is clearly widely distributed on deep-water reef slopes throughout the world and is characterized by foliaceous corals. Based on the dominant corals, I suggest naming this community 'the foliaceous coral community'.

The present study in southern Taiwan recorded the foliaceous coral community at a depth of 15 to 25 m on protected seaward slopes. This is shallower than in most previous studies. KÜHLMANN (1983), for example, reported this type of coral below 12 m deep at Matanzas, Cuba. He suggested that such a deep-water community would occur in shallower water on protected reefs: the environmental conditions such as hydrodynamics and sedimentation on shallow protected reef slopes are comparable to those on the deep reef slopes of exposed reefs (KÜHLMANN, 1980).

Although the members of foliaceous coral communities are similar in morphology, the dominant species often vary from area to area. Only few of the many species reported in this community dominate a reef slope. Even on neighboring reefs of southern Taiwan, the dominant species on different reef slopes differ; for example, *M. foliosa* at Site B, *M. ampliata* and *M. elephantotus*

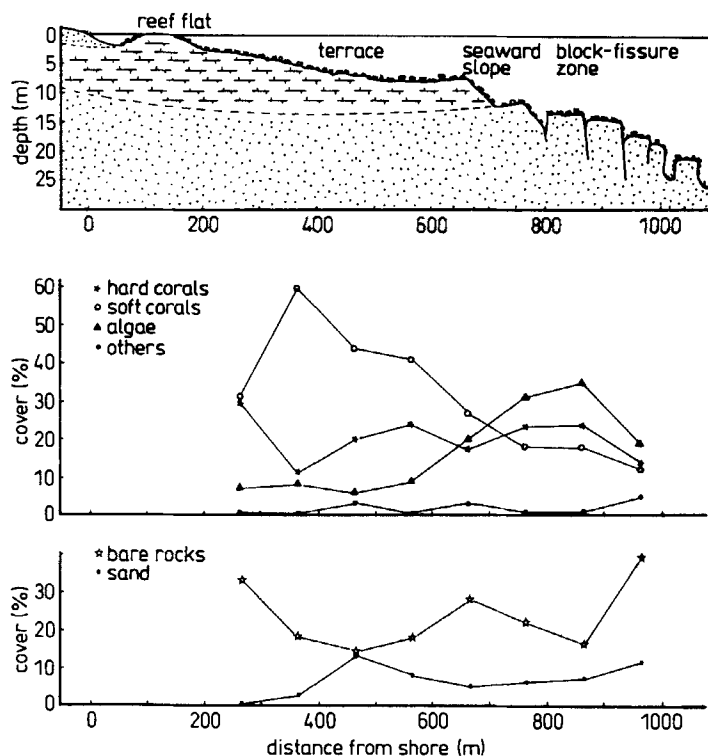


Fig. 11. Percent cover of the six groups of space occupiers along the bathymetric zones of site D.

at Site E, and *M. foliosa* and *P. speciosa* at Site F. This phenomenon suggests that chance might be one of the factors determining the species composition of this community.

Several factors have been suggested as governing the formation of the foliaceous coral community, including a complex of mechanical factors (KÜHLMANN, 1983) and the trophic features of corals (HUGHES & JACKSON, 1985). Chance and interspecific competition may also play a role. Since the environment of the deep reef slope is relatively stable and the dominant corals are good competitors (SHEPPARD, 1979; DAI, 1990), community formation may be partly attributed to the competitive dominance of foliaceous corals. Physical factors such as hydrodynamic conditions, substrate conditions, and sedimentation are considered to determine which species inhabit the reef slope. Which species will reach a particular reef slope, however, is dependent on chance and life history characteristics. Then, biological processes such as competition and predation will structure the community.

The alcyonacean-dominated community exists in areas exposed to both strong tidal currents and typhoon disturbances (DAI, 1991a). Community formation can be related to the special adaptive strategies of alcyonacean corals (DAI, 1991b). They can resist mechanical stress by significantly altering their

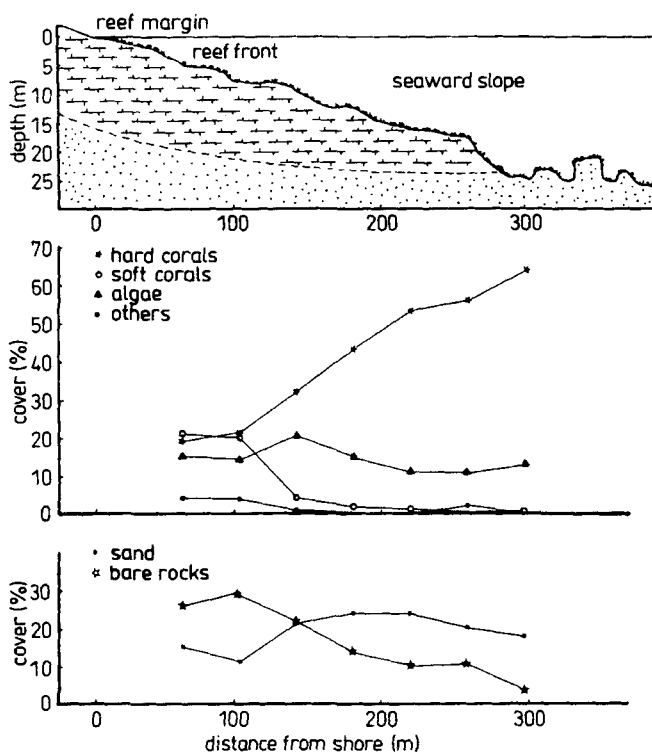


Fig. 12. Percent cover of the six groups of space occupiers along the bathymetric zones of site E.

morphology and body volume (KOEHL, 1982). In addition, vegetative growth enables rapid recovery after partial mortality due to severe storms (DAI, 1991 b). Studies on the effect of water movement on scleractinian corals suggest that high water energy excludes corals with fragile skeletal morphologies and favors growth of species with high skeletal plasticity or compact growth forms (GRAUS *et al.*, 1977; CHAPPELL, 1980). Most scleractinian corals inhabiting alcyonacean-dominated communities are massive or encrusting (DAI, 1988 b). This phenomenon is a further indication of high water energy here.

## 2. Space partitioning patterns

Soft corals, hard corals, and algae are the major benthic space occupiers on reefs exposed to storm disturbances, while hard corals and algae are the major space occupiers on protected reefs of southern Taiwan. The other benthic organisms found here such as bryozoans, sponges, sea anemones, and hydrozoans are mainly cryptic; their utilization of open space on these reefs is negligible. Two noticeable features of the study area are the high proportions of space occupied by algae and of unoccupied space.

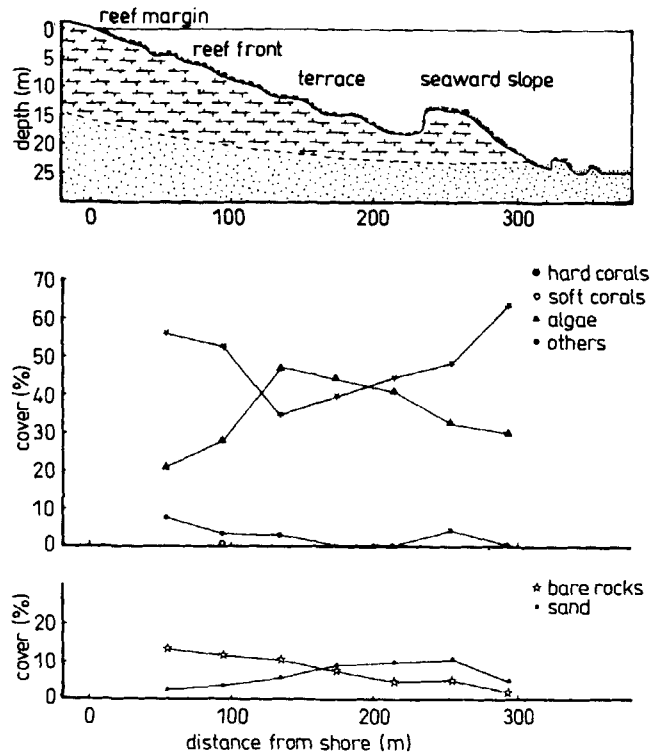


Fig. 13. Percent cover of the six groups of space occupiers along the bathymetric zones of site F.

The high algal cover on coral reefs is probably a result of biological and ecological attributes such as short generation times, rapid growth rates, opportunistic life histories, and wider tolerance ranges (MORRISSEY, 1980). FISHELSON (1973) pointed out that dense covers of marine algae on coral reefs are a symptom of eutrophication. The main components in southern Taiwan are filamentous and fleshy algae. Such a dense cover is possibly related both to the influx of excessive nutrients and the low population density of herbivorous animals in the study area (HUNG *et al.*, 1988). HATCHER & LARKUM (1983) showed that the inorganic nitrogen supply is the main factor limiting the growth of the epilithic algal community on coral reefs. The unusually high concentration of total dissolved nitrogen in the study area – possibly caused by domestic sewage discharges – may have altered the former reef system, allowing the algae to dominate all year long (HUNG *et al.*, 1988; DAI, 1991 a). Grazing activities by herbivorous fishes and sea urchins have been shown to suppress algal monopolization of space (OGDEN & LOBEL, 1978; VAN DEN HOEK *et al.*, 1978; SAMMARCO, 1980; LEWIS, 1986). WANDERS (1976) has shown that 'undergrazing' by herbivores is the main cause for excessive growth of fleshy and filamentous algae. Overfishing (mainly by dynamite fishing and spearfishing) in the coastal waters of southern Taiwan may also have reduced the population density of herbivorous fishes and led to the excessive algal growth.



The unoccupied space on the reefs of southern Taiwan is higher than that found on reefs elsewhere (*e. g.*, BAK & LUCKHURST, 1980; SHEPPARD, 1980, 1985; BENAYAHU & LOYA, 1977 a). The high proportion of bare rocks appears to be related to the hydrodynamic energy of the environment: in shallow water (3–5 m) mainly due to wave force and in deep-water block-fissure zones possibly due to strong currents. The formation and maintenance of unoccupied substrate on coral reefs may be attributed to the combined effects of biological and physical factors. SAMMARCO (1980) noted that grazers such as sea urchins create bare space on coral reefs. BAK & LUCKHORST (1980) attributed unoccupied substrate partly to shifting sand, while DOLLAR (1982) demonstrated that storms are the major force. Allelochemicals from other benthic invertebrates may also play a role (BAKUS *et al.*, 1986). SHEPPARD (1985) reported that corals maintain unoccupied substrate around themselves and suggested that the interactive mechanisms of corals are important in maintaining the unoccupied space on reefs.

A comparison with the survey data of coral reefs elsewhere allows the unoccupied space on the southern Taiwan reefs to be classified into two categories, *i. e.*, lower than 30 % (as normally recorded by other studies) and higher than 30 % (which is unusual). The unusually high proportions of unoccupied space were recorded from the wave-exposed reef margins and the block-fissure zones exposed to strong currents. It is likely that this unoccupied space was created by the frequent typhoon storms (DAI, 1991 a) and, afterwards, the constant high water energy retarded the recovery and new settlement of benthic organisms. On the other hand, the relatively low proportion of unoccupied space (< 30 %) on the submarine terraces and reef slopes may be attributed to shifting sand as caused by terrestrial runoff and to biological interactions.

## Summary

1) The bathymetric distribution of corals on the fringing reefs of southern Taiwan is basically homogeneous. Most of the species recorded are either sporadically distributed or widely scattered throughout the reefs.

2) Two types of coral communities are distinguishable on the basis of species composition, *i. e.*, the foliaceous coral community on protected reef slopes from 15 to 25 m depth and the alcyonacean-dominated community on exposed reef fronts, submarine terraces, and seaward slopes from 6 to 15 m.

3) Foliaceous corals are common on protected reef slopes in southern Taiwan. They include *Montipora foliosa*, *Merulina ampliata*, *Mycedium elephantotus*, *Echinophyllia aspera*, *Pachyseris speciosa*, and *Echinopora lamellosa*.

4) Coral communities on reef fronts, submarine terraces, and seaward slopes of reefs exposed to both strong currents and storm disturbances are dominated by alcyonacean corals. The most abundant species are *Sarcophyton trocheliophorum*, *Lobophytum sarcophytoides*, and *S. crassocaule*.

5) Soft corals, hard corals, and algae are the major benthic space occupiers on reefs exposed to storm disturbances, while hard corals and algae are the major space occupiers on protected reefs.

6) The high proportions of space occupied by algae (10–55%) and of unoccupied space (11–50%) are the two conspicuous features of southern Taiwan reefs.

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