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Coral Reefs

Patterns in the Distribution of Soft Corals Across the Central Great Barrier Reef

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Abstract. Distribution patterns of soft coral genera were examined at 11 reefs situated in a broad transect from inshore to the Coral Sea in the central region of the Great Barrier Reef. Twenty-five genera representing the Orders Alcyonacea and Stolonifera were recorded, and the survey also included one genus of the Order Gorgonacea. Total living soft coral cover is greatest on outershelf reef slopes, and is often less than and inversely related to the cover by stony corals. Soft coral diversity is generally low on reef flats, where soft coral cover is low or nil except in protected, inshore areas. The most diverse assemblages occur on reef slopes in midshelf and outershelf areas, where *Efflatounaria* and nephtheid genera predominate, and widely distributed alcyoniid genera are common. These richer assemblages are less well represented in the Coral Sea, while innershelf reefs support a less diverse fauna of somewhat different generic composition. Distribution patterns of soft corals across the transect broadly match similar variations in the distributions of stony corals and fishes, inshore reefs being generally depauperate. Such variations across the continental shelf are closely associated with changes in prevailing environmental conditions, but further research will be required to elucidate the effects of environmental parameters on benthic community structure.

Introduction

Fleshy Alcyonaria or "soft" corals are widespread throughout the tropical Indo-Pacific region. Cary (1931) and Crossland (1938) drew attention to the abundance of soft corals on Indo-Pacific reefs, their ecological significance in reef communities and their important contribution to reef structure. Despite such observations made some five decades ago, very few studies have been carried out of the ecology of the Indo-Pacific Octocorallia.

General descriptions of Indo-Pacific coral reef biota have given only minor attention to the soft coral component (e.g,. Barnes et al. 1971; Faure 1974; Pichon 1978). Only in the Red Sea have there been any continuing attempts to investigate the role of soft corals in reef communities. Earlier work by Gohar on the biology of xeniids (e.g., Gohar 1940) has been followed by various ecological studies of soft corals (e.g., Fishelson 1970, 1973; Schuhmacher 1973, 1975; Mergner and Schuhmacher 1974, 1981; Benayahu and Loya 1977, 1981; Mergner and Svoboda 1977).

Most accounts of the Great Barrier Reef (G.B.R.) soft coral fauna have dealt with their systematics (Hickson 1931; Macfadyen 1936; d'Hondt 1977; Verseveldt 1977) or with alcyonarian chemistry (Coll et al. 1977, and subsequent publications). The only significant investigation of the biology and ecology of G.B.R. octocorals is contained in a preliminary report by Garrett (1975).

The aim of the present study is to describe the distribution of soft corals across the continental shelf and out into the Coral Sea in the central region of the Great Barrier Reef. The paper is complementary to companion studies of the distributions of fishes (Williams 1982) and stony corals (Done 1982). This survey includes the Alcyonacea[1], the most conspicuous order of the shallow water Indo-Pacific octocoral fauna (Bayer 1957), plus the closely related Stolonifera and Telestacea and one genus of scleraxonian gorgonian. Because of the difficulties associated with octocoral systematics at specific level, the survey is confined to soft coral genera.

Materials and Methods

Study Areas

Soft coral surveys were conducted by SCUBA diving between November 1980 and November 1981. The study reefs include innershelf, midshelf, outershelf and Coral Sea reefs (Fig. 1); reef morphology and environment of such reefs have been summarized in Fig. 2, and by Done (1982). With one exception, the reefs surveyed fall within a transect running from inshore to offshore in a SW-NE direction. Davies Reef was included as it has been the site of various detailed surveys by the Australian Institute of Marine Science. Localities include a range of windward and

1 Classification is that traditionally used for Octocorallia (see Bayer 1956), but Bayer (1982) has suggested a revised classification

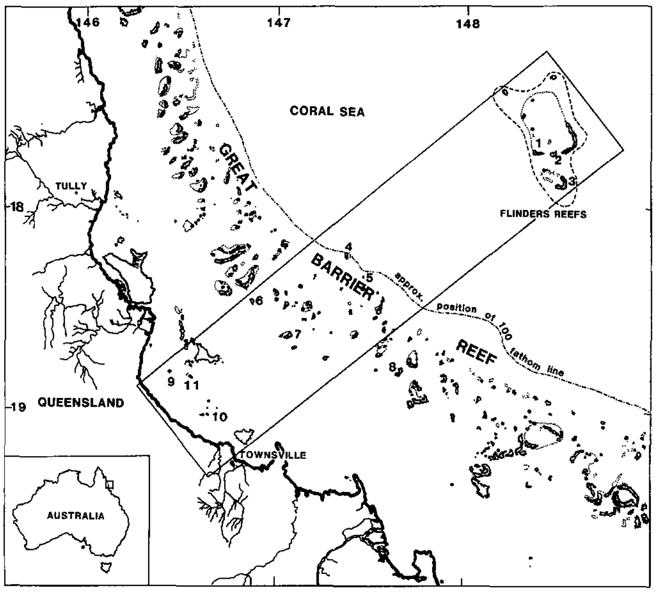

Fig. 1. Central region of the Great Barrier Reef, showing locations of study reefs. Reef numbers: *1*, Flinders "Southwest" (2); *2*, Flinders "Cay" (4); *3*, Flinders "South" (6) (Coral Sea, partially submerged atolls); *4*, Myrmidon (6); *5*, Dip (6) (outershelf, resorbed reefs, sensu Maxwell 1968); *6*, Rib (6); *7*, John Brewer (5); *8*, Davies (5) (midshelf, resorbed reefs); *9*, Pandora (5); *10*, Phillips (3) (innershelf, coral rubble covered reefs on granite outcrop); *11*, Havannah (2) (innershelf, fringing reef of high island). (Numbers in parentheses indicate number of localities surveyed at each reef)

more protected areas at each of these reefs, except at Flinders "Southwest" and Havannah Reefs where fewer localities were surveyed.

The innershelf platform reefs differ markedly from the reefs further offshore, not only in hydrological terms, but also regarding the reef size, morphology, and development of the reef flat. For comparison with inshore platform reefs, a nearshore fringing reef of a "continental" island (the predominant reef type in this inshore area) was also investigated.

Survey Methods

A semiquantitative survey method was used, based on visual estimates of percentage cover using a graded cover scale (see below). This method has been used successfully for surveys of stony corals (Veron and Done 1979; Done 1982). Done (1977) showed that semiquantitative, graded data provide classifications of coral communities very similar to those derived from quantitative, line transect data. Surveys using graded cover data have the advantage that more sites can be surveyed per unit of time spent in the field, hence classifications can be based on a larger data set.

The reef slope was surveyed in contiguous sections of approximately 5 m depth, e.g. crest–5 m, 5–10 m (approximately below low water datum). The sections, hereafter termed "sites", were about 25–40 m in length but they were not physically demarcated in any way. On inner- and midshelf reefs maximum survey depth was determined by the substratum type (where sand or silt largely replaced hard substrata, surveys were discontinued). Surveys at outershelf reefs were conducted to a maximum of 25 m and at Coral Sea reefs to 40 m, although hard substratum often persisted beyond these depths.

Brief visual surveys across a number of reef flat transects revealed that all but the most protected reef flats supported very low, sometimes nil, soft coral cover, hence no surveys of entire reef flats were carried out. Only the reef flat areas adjacent to the reef slope locations were surveyed. Reef flat sites were generally some 40 m in length (parallel to the reef edge) and 30–40 m wide. Since soft corals were sparse here, these sites were considerably larger than slope sites so that a representative generic list could be compiled.

A check list of soft coral genera present was compiled for each site. The total percentage cover of soft corals and the relative percentage cover (i.e. the percentage contribution to the total soft coral cover) of each genus were visually estimated using a 7-point graded cover scale. The scale, based on that of Kenchington (1978) and Dinesen (1980), was as follows: 0 = 0%; 1 = 1–5%; 2 = 6–15%; 3 = 16–30%; 4 = 31–50%; 5 = 51–75%; 6 = 76–100%. Some 400 specimens not identifiable to genus underwater were collected for laboratory identification.

At each site the following environmental data were also recorded: exposure to swell and wave action (exposed, semiexposed or protected); depth; angle of slope (on a 5-point scale, horizontal, gradual, intermediate ($\sim 45°$), steep or vertical); approximate percentages of hard and soft substrata; relative proportions of hard substrata (stag rubble, small or large coral blocks, solid platform) and soft substrata (mud, sand, gravel); approximate total percentage cover of hard corals.

Analytical Methods

For each depth zone at each reef, mean values were calculated for percentage living cover by soft and hard corals. These were plotted for each reef as shaded "kite" diagrams.

To obtain an overview of generic composition and diversity of soft corals at each reef, the percentage of the total number of sites in which each genus occurred was calculated for each reef. Reef slope and reef flat sites were treated separately.

Numerical classification was used to identify broad-scale patterns of distribution. Graded cover values were treated as numeric. An agglomerative classification of the sites was carried out using as fusion strategy the method variously known as error sum of squares (Ward 1963) or incremental sum of squares (Burr 1970). The dissimilarity index was that

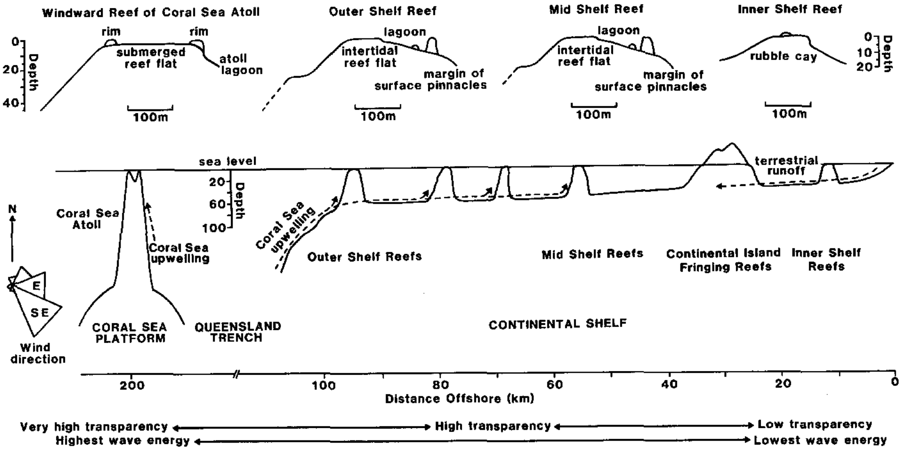

Fig. 2. Schematic profiles of the study reefs and summary of reef environments. (After Done 1982)

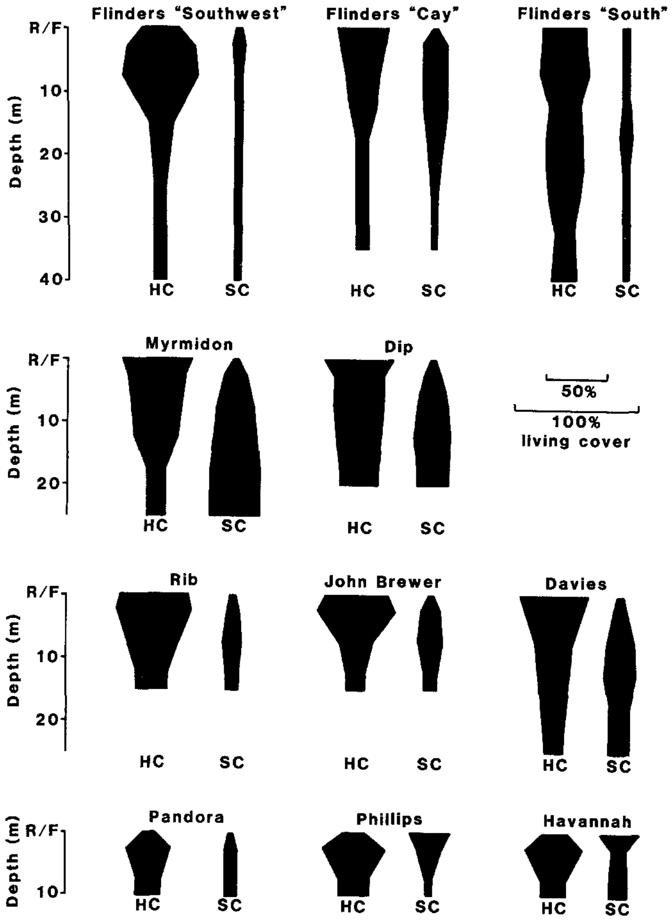

Fig. 3. Average percentage living cover by soft and hard corals on the study reefs. *HC*, hard coral cover; *SC*, soft coral cover; *R/F*, reef flat

of Bray and Curtis (1957) in its computationally more convenient form $\sum_j |X_{1j}-X_{2j}| / \sum_j (X_{1j}+X_{2j})$. This index does not pair zero-zero matches, hence absence of rarely recorded genera would not serve to link otherwise dissimilar sites. For comparison, a divisive classification was conducted using POLYDIV (Williams and Lance 1975) with Euclidean distance. Both classifications produced broadly similar dendrograms, and results are presented in detail only for the agglomerative classification. Cluster diagnostics used were the cluster mean values of the genera [i.e. the mean values of the graded cover scale; calculated using program GROUPER (Lance et al. 1968)]; and the percentage of the total number of sites in a cluster in which a genus was present. In presenting the results, genera are listed in descending order of cluster mean values, and only those genera occurring in 40% or more of sites in a cluster are included. In summarizing environmental data for exposure, slope and amounts of hard and soft substrata, descriptions refer to conditions at 75% or more of sites within a cluster. Predominant substratum type is shown only for hard substatum where this exceeded 75% cover at 75% or more of sites. Cluster compositions are indicated in terms of position on the cross-shelf transect, and site depths refer to at least 75% of sites at that transect position.

Results

Percentage Cover of Living Soft and Hard Corals

Percentage cover patterns have been summarized in Fig. 3 on a reef by reef basis.

At the Coral Sea reefs, soft coral cover is generally very low, soft corals being best represented on reef slopes at Flinders "Cay". Hard coral cover is greatest in the upper 15 m or so, though the cover at Flinders "South" is still substantial at 40 m.

Soft corals achieve greatest cover on the slopes of outershelf reefs. Below about 10 m, soft coral cover roughly equals that of stony corals, and at Myrmidon Reef soft coral cover exceeds hard coral cover below 15 m. A steady decrease in soft coral cover with decreasing depth is matched by an increase in the amount of hard coral, which is greatest on reef flats.

Cover patterns at midshelf reefs are broadly similar to those at outershelf reefs, but overall cover of soft corals is rather lower. Hard coral cover generally increases in shallower water, and on two of the three reefs is maximal on the shallow reef slope rather than on the reef flat.

On innershelf reefs, soft coral cover is moderate to low, except on the reef tops at Phillips and Havannah Reefs, where this exceeds hard coral cover. On all three reefs hard coral cover is greatest in the upper 5 m of the slope.

Although these coral cover patterns represent average data for each reef, some definite general patterns emerge. While soft coral cover is often lower than hard coral cover, soft corals nevertheless make a significant contribution to the cover by reef benthos. Except in more protected inshore areas, soft coral cover is very low on reef tops, increases with depth, and either declines slightly or remains constant at the lower limit of survey. In contrast, hard coral cover is greatest on reef flats or in the upper 10 m of the reef slope. There is frequently an inverse relationship between soft and hard coral cover. On all these reefs (except perhaps Pandora) the depth at which maximum soft coral cover is achieved does not coincide with that of greatest hard coral cover. In most cases, soft coral cover peaks at depths below the maximum hard coral cover.

Distribution of Soft Coral Genera on the Study Reefs

A total of 26 genera was recorded at the 201 sites surveyed. These represent the families Clavulariidae and Tubiporidae (Order Stolonifera), Alcyoniidae, Asterospiculariidae, Nephtheidae, Nidaliidae and Xeniidae (Order Alcyonacea), and Briareidae (Order Gorgonacea, suborder Scleraxonia). No representatives of the Order Telestacea were encountered during the surveys.

The distributions of these genera are summarized on a reef by reef basis in Fig. 4. The separate treatment of reef flat and reef slope sites clearly illustrates the absence of many genera from reef flats, and the low frequency of most of those which were found here. As the number of reef flat sites is less than the number of reef slope sites, incautious interpretation of this diagram may lead to an overestimate of the contribution by genera on the reef flat. For example, only two reef flat sites were surveyed at Phillips Reef and one at Havannah; the frequency of genera on these reef flats may therefore seem artificially high.

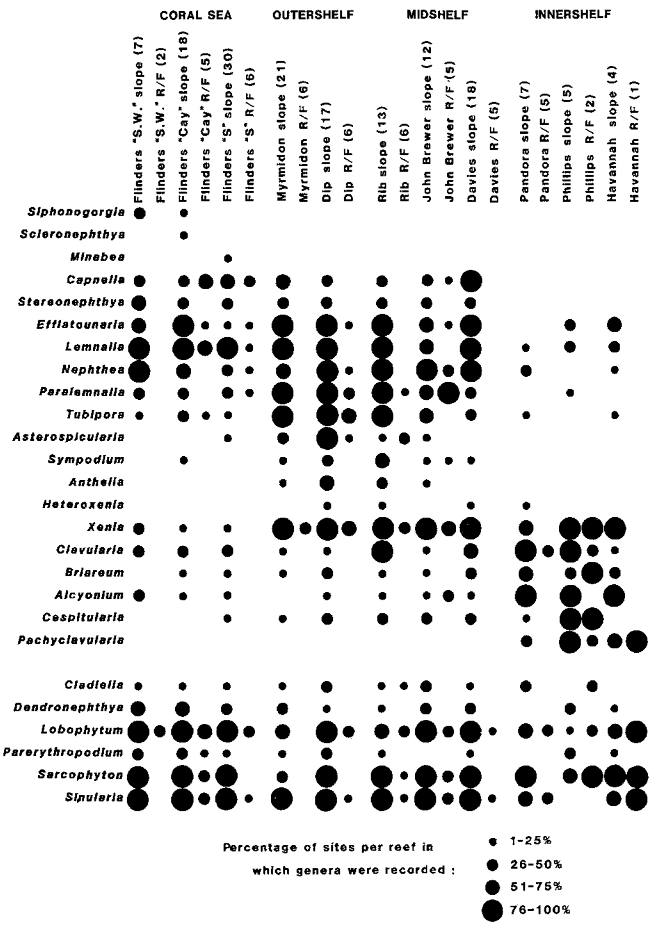

Fig. 4. Distribution of genera on reef slopes and reef flats on the study reefs. Numbers in parentheses show number of sites per reef. *R/F*, reef flat

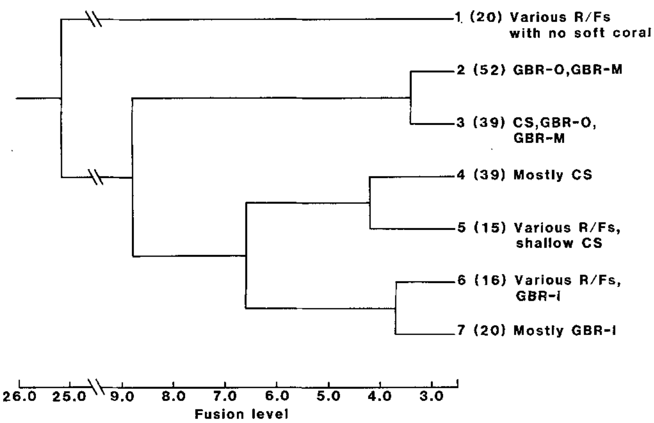

Fig. 5. Major clusters of dendrogram for numerical classification of soft coral data. Numbers in parentheses show number of sites per cluster. *CS*, Coral Sea; *GBR-O*, outershelf; *GBR-M*, midshelf; *GBR-I*, innershelf. Sites are principally from reef slopes unless reef flats (*R/Fs*) are specifically indicated. See Table 1 for summary of cluster compositions

Distribution patterns are discussed primarily with reference to reef slopes.

Several genera, notably alcyoniids, seem to occur with approximately equal frequency from inshore through to the Coral Sea (these are grouped in the lower part of Fig. 4). However, many genera occur more frequently in certain portions of the transect (upper part of Fig. 4). The greatest number of genera was recorded on outer- and midshelf reefs, which are all rather similar in generic composition. Several genera, *Asterospicularia* and the less common xeniids, were found most often or only on these reefs. These reefs are notable for the high frequency of the xeniids *Efflatounaria* and *Xenia*, nephtheids (especially *Nephthea*, *Lemnalia* and *Paralemnalia*), and *Tubipora*, in addition to the commonly occurring alcyoniids. The Coral Sea reefs are broadly similar to those of mid- and outershelf areas. However, on these oceanic reefs, the number of commonly occurring soft corals is somewhat smaller. Moreover, the xeniid/nephtheid components are generally less well represented in the Coral Sea, and many xeniid genera (except *Efflatounaria*) are scarce. Three genera were recorded only at Flinders Reefs, but two of these (*Siphonogorgia* and *Scleronephthya*) have been observed on mid- and outershelf reefs although not during the surveys.

The innershelf areas, both platform and fringing reefs, are very different from the others. A smaller range of soft coral genera was commonly encountered here, and the composition of the assemblages has a different emphasis. Alcyoniids such as *Sarcophyton* and *Lobophytum* are common, but the xeniid/nephtheid component is largely lacking. In these two families only *Xenia* and *Cespitularia* are well represented, the latter being most common in inshore areas (notably on the submerged reef flat at Phillips Reef). *Alcyonium* and *Clavularia* are conspicuous here, and *Pachyclavularia* was recorded only on these reefs.

Table 1. Cluster diagnostics and summary of environmental data for site groups from classification of soft coral data (see Fig. 5). CS = Coral Sea; GBR-O = outershelf; GBR-M = midshelf; GBR-I = innershelf; HS = hard substratum; PHST = predominant hard substratum type; SS = soft substratum; PSST = predominant soft substratum type; HC = hard coral cover; SC = soft coral cover. See Analytical Methods for explanation of cluster diagnostics and environmental data

Cluster 1	
Cluster composition	20 sites. CS: 6. GBR-O: 5. GBR-M: 6. GBR-I: 3. All R/F
Exposure	40% semiexposed; 35% exposed
Slope	100% horizontal
Substratum	HS: >75% at all sites. PHST: platform at 85% of sites
Living cover	HC: 31–50% at 40% of sites; 51–75% at 30% of sites; 6–15% at 10% of sites. SC: Nil at all sites
Cluster 2	
Cluster composition	52 sites. GBR-O: 31, mostly ~1–15 m. GBR-M: 21, mostly ~1–15 m
Exposure	58% semiexposed; 37% exposed
Slope	42% intermediate; 38% gradual
Substratum	HS: >75% at 67% of sites; 51–75% at 25% of sites. PHST: platform at 90% of sites
Living cover	HC: 31–50% at 40% of sites; 16–30% at 35% of sites. SC: 16–30% at 35% of sites; 31–50% at 33% of sites; 6–15% at 23% of sites

Table 1 (continued)

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Efflatounaria	3.54	98
Xenia	2.17	98
Lemnalia	1.46	87
Sinularia	1.29	81
Nephthea	1.19	87
Sarcophyton	1.15	73
Paralemnalia	1.04	81
Lobophytum	0.87	79
Tubipora	0.81	79
Capnella	0.67	56

Number of genera present: 23

Cluster 3

Cluster composition	39 sites. CS: 16, mostly ~1–15 m. GBR-O: 7 sites, mostly ~1–15 m. GBR-M: 16 sites, mostly ~1–10 m
Exposure	54% semiexposed; 33% exposed
Slope	41% steep; 28% intermediate; 21% gradual
Substratum	HS: >75% at 72% of sites; 51–75% at 23% of sites. PHST: platform at all sites
Living cover	HC: 31–50% at 44% of sites; 6–15% at 21% of sites; 51–75% at 15% of sites. SC: 6–15% at 38% of sites; 1–5% at 28% of sites; 16–30% at 23% of sites

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Efflatounaria	2.23	90
Sinularia	2.15	95
Nephthea	1.62	85
Lemnalia	1.31	87
Lobophytum	1.26	85
Sarcophyton	1.08	87
Capnella	1.03	72
Paralemnalia	0.77	62
Tubipora	0.72	59
Xenia	0.51	46
Stereonephthya	0.51	46

Number of genera present: 26

Cluster 4

Cluster composition	39 sites. CS: 36, ~1 through 40 m. GBR-M: 3, ~1–5 m and 15–20 m
Exposure	92% exposed
Slope	44% vertical; 36% steep; 15% intermediate
Substratum	HS: >75% at 95% of sites. PHST: platform at all sites
Living cover	HC: 6–15% at 39% of sites; 16–30% at 39% of sites. SC: 1–5% at 59% of sites; 6–15% at 33% of sites

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Lemnalia	1.72	90
Sinularia	1.46	90
Lobophytum	1.26	90
Sarcophyton	1.18	87
Dendronephthya	1.03	59
Capnella	0.90	51
Nephthea	0.59	46

Number of genera present: 22

Table 1 (continued)

Cluster 5

Cluster composition	15 sites. CS: 8, R/F and ~1–10 m. GBR-M: 5, mostly R/F. GBR-I: 2, R/F
Exposure	40% exposed; 33% semiexposed; 27% protected
Slope	66% horizontal; 13% gradual; 13% vertical
Substratum	HS: >75% at all sites. PHST: platform at 93% of sites
Living cover	HC: 16–30% at 27% of sites; 31–50% at 27% of sites; 51–75% at 27% of sites. SC: 1–5% at 73% of sites; 6–15% at 20% of sites

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Lobophytum	3.33	100
Sinularia	2.53	73
Sarcophyton	0.93	47

Number of genera present: 14

Cluster 6

Cluster composition	16 sites. GBR-O: 7, all R/F. GBR-M: 4, all R/F. GBR-I: 5, mostly ~1–10 m
Exposure	38% semiexposed; 38% protected
Slope	75% horizontal
Substratum	HS: >75% at 94% of sites. PHST: platform at 69% of sites; stag rubble at 31% of sites
Living cover	HC: 31–50% at 63% of sites; 51–75% at 25% of sites. SC: 1–5% at 81% of sites

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Xenia	3.38	88

Number of genera present: 19

Cluster 7

Cluster composition	20 sites. CS: 2, ~1–5 m and 35–40 m. GBR-M: 4, R/F and 5–10 m. GBR-I: 14, mostly ~1–10 m
Exposure	75% protected
Slope	60% gradual; 20% horizontal
Substratum	HS: 51–75% at 45% of sites; >75% at 45% of sites. PHST: stag rubble at 55% of sites; platform at 45% of sites. SS: 31–50% at 30% of sites; 16–30% at 25% of sites; nil at 20% of sites. PSST: mud at 50% of sites; sand at 35% of sites
Living cover	HC: 16–30% at 40% of sites; 51–75% at 25% of sites; 6–15% at 15% of sites. SC: 1–5% at 60% of sites; 6–15% at 25% of sites

	Cluster mean cover value	Percentage of sites in cluster in which genus occurred
Sarcophyton	1.75	95
Alcyonium	1.60	90
Clavularia	1.60	60
Sinularia	1.45	65
Xenia	1.15	75
Lobophytum	1.05	75
Nephthea	0.80	40
Efflatounaria	0.55	45
Lemnalia	0.55	40

Number of genera present: 21

Numerical Classification of Soft Coral Data

Classification of sites produced patterns largely in accordance with those suggested by examination of data on a reef by reef basis. The analysis (see Fig. 5, Table 1) produced three major site groups: sites with no soft corals (reef flats only); reef slope sites from outer- and midshelf reefs and some Coral Sea locations; and sites from reef flats at many locations, innershelf reef slopes, and the majority of those from Coral Sea reefs slopes.

From the classification, several assemblage types may be distinguished, and these are named after the dominant or characteristic genera.

Diverse Efflatounaria/Nephtheid Assemblages. Most of the sites from reef slopes at mid- and outershelf reefs, plus a number of reef slope sites from the Coral Sea (Clusters 2 and 3) are characterized by the dominant genus *Efflatounaria* and codominant nepththeids *Nephthea* and *Lemnalia*. Many genera were frequently recorded here, among which *Xenia* and the alcyoniids *Sinularia*, *Sarcophyton* and *Lobophytum* are conspicuous. Though present at most sites, *Sinularia* is most evident and often dominant in the shallowest reef slope sites. These exposed and semiexposed locations are faunistically similar, but xeniids are most notable on reef slopes with higher soft coral cover (Cluster 2). Alcyoniids are better represented on those slopes with slightly lower living cover (Cluster 3).

Other, Less Diverse Assemblages. The innershelf reef slope sites, reef flat sites (except "empty" sites), and most of the Coral Sea reef slope sites are grouped together (Clusters 4 to 7). In general, the soft coral assemblages here are rather less diverse than those of mid- and outershelf reef slope areas; the richer assemblages, dominated chiefly by *Efflatounaria*, nephtheids and sometimes by genera such as *Xenia* and *Sinularia*, are lacking here.

On reef flats only a few genera predominate, principally *Lobophytum*, *Sinularia* and *Sarcophyton*, and sometimes other genera such as *Xenia*. These widely distributed alcyoniid genera appear relatively more important in the less diverse Coral Sea and innershelf sites than on mid- and outershelf reef slopes. Hence these alcyoniids are another factor linking reef flats, innershelf reef slopes, and the majority of Coral Sea reef slope sites.

Lemnalia/Alcyoniid Assemblages. Although a fair range of genera is represented in many of the Coral Sea reef slope sites (Cluster 4), *Lemnalia* and alcyoniids are most conspicuous among the fauna.

Lobophytum/Sinularia Assemblages. These genera are characteristic of some of the shallowest Coral Sea slope sites, and of many reef flat sites from various locations (Cluster 5). Few other genera were encountered here.

Xenia Assemblages. Xenia is the single dominant soft coral in a number of reef flat sites and some innershelf slope sites (Cluster 6). There is a marked paucity of other soft coral genera. Note that the very high mean values of genera in these areas with low soft coral cover and diversity (Clusters 5 and 6) is due to the use of relative cover values: although scarce, these genera are dominant among the impoverished octocoral fauna here and hence receive a high relative rating.

Sarcophyton/Alcyonium Assemblages. At many of the protected, innershelf reef slope sites (Cluster 7), several genera were recorded fairly frequently. Dominant are alcyoniids, especially *Sarcophyton* and *Alcyonium*. Stoloniferan genera such as *Clavularia* are also conspicuous on these inshore reefs.

Site groups to some extent represent the position of slope sites on the cross-shelf transect (Coral Sea, outer- plus midshelf, innershelf). Accordingly, these groups reflect in some cases the degree of exposure of the locations, notably in Clusters 4 and 7 (see Table 1). Summaries of cluster compositions do not indicate individual reefs; but sites were not obviously subgrouped according to reef, but rather according to general position on the transect. For example, Clusters 2 and 3 each contain sites from all midshelf and outershelf reefs sampled, and all three reefs from the Coral Sea are represented in Cluster 4.

The analysis tends to segregate reef flat sites from the richer reef slope sites. However, the comparatively larger size of the reef flat sites is not considered to have contributed to this pattern. On the contrary, while a larger sampling area serves to increase the number of genera recorded here, these sites are still depauperate relative to many reef slope sites. Cluster groups do not otherwise seem to reflect sampling depth, as reef slope sites from a wide range of depths are grouped together, e.g. sites in Cluster 4 include all depths from shallow slope down to 40 m in the Coral Sea.

At most sites, the amount of hard substratum greatly exceeds the amount of soft substratum, and the predominant hard substratum type is solid platform (see Table 1). Only at sites in Cluster 7 (chiefly inshore sites) is stag rubble usually the predominant hard substratum type. There is also here a relatively higher proportion of soft substratum, and in contrast to other clusters, the predominant soft substratum type at these sites is mud rather than sand.

Soft coral cover is generally low at sites in all clusters except Clusters 2 and 3, which include most outer- and midshelf reef slope sites. Hard coral cover values are very variable both within and between clusters.

Discussion

In contrast to Schuhmacher's (1975) assertion that soft corals are "rare" on the G.B.R., this study indicates that soft corals are a major component of the sessile reef benthos of the central G.B.R.

On outer- and midshelf reef slopes, the high water clarity, good water circulation and associated conditions are apparently favourable to growth of a wide range of soft corals, notably *Efflatounaria* and nephtheids. Although assemblages in both areas are faunistically similar, the consistently greater cover by soft corals on outershelf reefs means that soft corals here make a much greater contribution to sessile benthic community structure. No obvious reasons can be suggested for differences in total soft coral cover between outer- and midshelf reefs.

Extreme wave action is a probable reason for the relatively depauperate nature of soft coral communities at the Coral Sea sites, and generally on reef flats. This could also account for the observed increase in soft coral cover with increasing depth at all but the most protected reefs. Fishelson (1970) and Schuhmacher (1975) have both suggested that the damaging effect of wave action is a major factor inhibiting the growth of soft corals. This view is substantiated by the predominance of low, encrusting forms on many reef flats and shallow, wave-exposed reef slopes (pers. obs.), as noted in the Red Sea by Fishelson (1970). Cary (1917) also remarked on the scarcity of soft corals on exposed reef flats at Tutuila (American Samoa). Benayahu and Loya (1977, 1981) found that average soft coral cover in the Eilat region was approximately the same on reef flats and upper fore-reef slopes, but these Red Sea reefs are more sheltered than most of the G.B.R. study reefs.

The Coral Sea reefs are separated from those of the G.B.R. by a considerable stretch of deep water, which might act as a barrier to recruitment by larvae from other areas. Hence the isolation of these reefs may in part account for the relatively lower diversity of the fauna, but verification of this hypothesis requires significant advances in knowledge of larval dispersal patterns and longevity.

Reasons for the comparatively depauperate nature of soft coral communities on inshore reefs are not clear, but it seems likely that only a limited number of taxa are adapted to such silty, turbid environments. Certain genera appear to flourish in inshore areas, for example on the submerged top of Phillips Reef, where patchy cover by *Xenia* and *Cespitularia* in some places reaches 100% over areas of tens of square metres. However, the results of this survey clearly do not support the assertion of Fishelson (1970) and Schuhmacher (1975), that soft corals as a group are more tolerant of stressful conditions such as high turbidity and sedimentation than the Scleractinia.

Patterns in the distribution of soft coral genera have some similarities to the cross-shelf distributions of stony corals (Done 1982) and fishes (Williams 1982). Generic diversity of soft corals and species diversity of both scleractinians and fish are low on inshore reefs. Diversity of both soft and hard corals (but not fish) is also low in the Coral Sea relative to midshelf and outershelf reefs. Furthermore, the composition of both soft and stony coral communities on innershelf reefs is basically different from that found elsewhere on the cross-shelf transect.

A species level study of soft corals would probably permit a greater differentiation of community types than could be established at generic level, and would probably provide sharper distinctions between site groups, for example among reef flat, inshore and Coral Sea areas. Certainly some genera, such as the alcyoniids *Lobophytum*, *Sarcophyton* and *Sinularia*, are known to contain a large number of species, and their rather even distribution across the entire transect might well prove discontinuous or only partially overlapping at species level. In other cases, however, generic distributions appear closely representative of species distributions. For example, *Efflatounaria*, a major component of outer- and midshelf communities, is represented by only a few species, the principal species being common on both outer- and midshelf reefs (Dinesen, in preparation). The lower diversity in inshore areas apparently holds true also at species level. Certainly the *Cespitularia*, *Xenia*, *Pachyclavularia*, *Clavularia* and *Briareum* conspicuous here seem to represent only a small number of species. In any case, the fact that these generic data produced patterns broadly similar to those for stony coral surveys conducted at species level suggests that a substantial degree of resolution is derived at generic level.

This survey allows further regional comparisons of octocoral fauna. Although alcyonaceans are generally sparse on the Coral Sea reefs, gorgonians are extremely abundant here, from shallow water (where isidids predominate) down to at least 40 m. The predominance of gorgonians among the octocoral fauna is a situation similar to that found on Atlantic reefs (Bayer 1957; Kinzie 1973).

While *Telesto* and *Carijoa* do occur in the central G.B.R. area (pers. obs.), the absence of Telestacea from the study areas demonstrates their insignificance in reef communities in this region.

Bayer (1957) reported that the shallow water Indo-Pacific octocoral fauna is dominated by three alcyonacean families, principally by the Alcyoniidae. The soft coral fauna of the central G.B.R. is frequently dominated by one or a few genera, among which xeniids are very conspicuous. Xeniids also predominate in some reef environments in the Red Sea (Fishelson 1970; Benayahu and Loya 1981; Mergner and Schuhmacher 1981). The importance of this alcyonacean family in reef environments has until recently been underestimated.

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References

Barnes J, Bellamy DJ, Jones DJ, Whitton BA, Drew EA, Kenyon L, Lythgoe JN, Rosen BR (1971) Morphology and ecology of the reef front of Aldabra. Symp Zool Soc London 28:87–114

Bayer FM (1956) Octocorallia. In: Moore RC (ed) Treatise on invertebrate paleontology, pt F: Coelenterata. Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp F166–F231

Bayer FM (1957) Recent octocorals. In: Hedgpeth JW (ed) Treatise on marine ecology and paleoecology, vol 1: Ecology. Geological Society of America, Memoir 67, Boulder, Colo, pp 1105–1108

Bayer FM (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. Proc Biol Soc Wash 94:902–947

Benayahu Y, Loya Y (1977) Space partitioning by stony corals, soft corals and benthic algae on the coral reefs of the northern Gulf of Eilat (Red Sea). Helgol Wiss Meeresunters 30:362–382

Benayahu Y, Loya Y (1981) Competition for space among coral-reef sessile organisms at Eilat, Red Sea. Bull Mar Sci 31:514–521

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Burr EJ (1970) Cluster sorting with mixed character types. II. Fusion strategies. Aust Comput J 2:98–103

Cary LR (1917) The part played by Alcyonaria in the formation of some Pacific coral reefs. Proc Natl Acad Sci 3:545–548

Cary LR (1931) Studies on the coral reefs of Tutuila, American Samoa with special reference to the Alcyonaria. Pap Dept Mar Biol Carnegie Inst Wash 27:53–98

Coll JC, Hawes GB, Liyanage N, Oberhansli W, Wells RJ (1977) Studies of Australian soft corals, pt I. Aust J Chem 30:1305–1309

Crossland C (1938) The coral reefs at Ghardaqa, Red Sea. Proc Zool Soc London Ser A 108:513–523

Dinesen ZD (1980) Some ecological aspects of coral assemblages of the Great Barrier Reef Province. PhD thesis, James Cook University of North Queensland

Dinesen ZD (in preparation) Three new and one old species of the xeniid soft coral genus *Efflatounaria* from the Great Barrier Reef

Done TJ (1977) A comparison of units of cover in ecological classifications of coral communities. Proc 3rd Int Coral Reef Symp 1: 9–14

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1:95–107

Faure G (1974) Morphology and bionomy of the coral reefs discontinuities in Rodriguez Island (Mascarene Archipelago, Indian Ocean). Proc 2nd Int Coral Reef Symp 2:161–172

Fishelson L (1970) Littoral fauna of the Red Sea: the population of non-scleractinian anthozoans of shallow waters of the Red Sea (Eilat). Mar Biol 6:106–116

Fishelson L (1973) Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). Mar Biol 19:183–196

Garrett RN (1975) A preliminary report of studies on Great Barrier Reef Octocorallia. In: Crown-of-thorns starfish. Seminar Proceedings, Brisbane, 6 September 1974. Australian Government Publishing Service, Canberra, pp 135–147

Gohar HAF (1940) Studies on the Xeniidae of the Red Sea. Publ Mar Biol Stn Ghardaqa Red Sea 2:25–118

Hickson SJ (1931) The alcyonarian family Xeniidae, with a revision of the genera and species. Sci Rep Gt Barrier Reef Exped 4(5):137–179

Hondt MJ d' (1977) Some Octocorallia (Coelenterata) from Australia. Aust J Mar Freshwater Res 28:241–259

Kenchington RA (1978) Visual surveys of large areas of coral reefs. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. UNESCO, Paris, pp 149–161

Kinzie RA (1973) The zonation of West Indian gorgonians. Bull Mar Sci 23:93–155

Lance GN, Milne PW, Williams WT (1968) Mixed-data classificatory programs. III. Diagnostic systems. Aust Comput J 1:178–181

Macfadyen LMI (1936) Alcyonaria (Stolonifera, Alcyonacea, Telestacea and Gorgonacea). Sci Rep Gt Barrier Reef Exped 5(2):19–71

Maxwell WGH (1968) Atlas of the Great Barrier Reef. Elsevier, Amsterdam

Mergner H, Schuhmacher H (1974) Morphologie, Ökologie und Zonierung von Korallenriffen bei Aqaba (Golf von Aqaba, Rotes Meer). Helgol Wiss Meeresunters 26:238–358

Mergner H, Schuhmacher H (1981) Quantitative Analyse der Korallenbesiedlung eines Vorriffareals bei Aqaba (Rotes Meer). Helgol Wiss Meeresunters 34:337–354

Mergner H, Svoboda A (1977) Productivity and seasonal changes in selected reef areas in the Gulf of Aqaba (Red Sea). Helgol Wiss Meeresunters 30:383–399

Pichon MM (1978) Recherches sur les peuplements à dominance d'anthozoaires dans les récifs coralliens de Tuléar (Madagascar). Atoll Res Bull 222:1–447

Schuhmacher H (1973) Die lichtabhängige Besiedlung von Hafenstützpfeilern durch sessile Tiere und Algen aus dem Korallenriff bei Eilat (Rotes Meer). Helgol Wiss Meeresunters 24:307–326

Schuhmacher H (1975) Die Rolle der Weichkorallen (Alcyonacea, Octocorallia) innerhalb der Riffbiozönosen des Roten Meeres und des australischen Großen Barriereriffs. Verh Dtsch Zool Ges 67:380–384

Veron JEN, Done TJ (1979) Corals and coral communities of Lord Howe Island. Aust J Mar Freshwater Res 30:203–236

Verseveldt J (1977) Australian Octocorallia (Coelenterata). Aust J Mar Freshwater Res 28:171–240

Ward JH (1963) Heirarchical grouping to optimize an objective function. J Am Stat Assoc 58:236–244

Williams DMcB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1:35–43

Wiliams WT, Lance GN (1975) POLYDIV: a divisive classificatory program for all-numeric data. Aust Comput J 7:144