

Patterns of coral community structure of subtropical reefs in the Solitary Islands Marine Reserve, Eastern Australia

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ABSTRACT: Although the Solitary Islands Marine Reserve lies at latitude 30° S on the east coast of Australia, over 700 km south of the Great Barrier Reef, it contains benthic communities dominated by extensive areas of scleractinian corals. A qualitative survey published in 1974 reported a total of 34 coral species in the region, and more recent records include a total of 55 coral species. Here, we present the results of the first quantitative benthic surveys for 7 sites in the Solitary Islands Marine Reserve. As a result of these surveys, an additional 35 species of scleractinian coral have been recorded from the region, bringing the total to 90 coral species, in 28 genera from 11 families. However, 21 of the 55 coral species previously recorded were not found during this study. These results indicate that a dynamic temporal pattern of species recruitment and replacement is occurring within these subtropical coral communities. Scleractinian coral cover ranged from a low of 8.5% at Muttonbird Island, the reef closest to the coastline, to 50.9% at SW Solitary Island. These values are within the range of coral cover reported for tropical fringing reefs. Multidimensional scaling (MDS) analysis indicated 4 major site groupings: the 2 sites closest to shore; the most northern offshore site, which was different from all other sites; South Solitary Island; and the other 3 island sites which showed some similarity to one another. The major differences among sites were higher coral species richness and the relative importance of *Acropora* species on the more northern and offshore reefs, and higher abundance of large macroalgae close to the coastline. The Solitary Islands coral communities contain a unique association of tropical species near their southern latitudinal range, and subtropical scleractinian species which are rare or absent from the Great Barrier Reef region. Although coral cover is high at the Solitary Islands, these high-latitude sites are less diverse than tropical fringing reefs, with respect to both total number of coral species and the number of species per sampling unit. Furthermore, the primary substratum is formed by rock rather than limestone, so the extensive coral communities fail to form coral reefs at this latitude.

KEY WORDS: Subtropical reefs · Coral community structure

INTRODUCTION

Coral reefs are typically associated with warm shallow seas, and the geographic limits of coral reef formation generally fall within the band delineated by the northern and southern tropics (Stoddart 1969, Rosen 1988). However, in some regions, extensive coral communities may occur at higher latitudes (Veron 1974, Veron et al. 1974, Veron & Done 1979). These high-latitude coral communities have been little studied, compared with their tropical counterparts. A feature of high-latitude coral communities is that, despite high coral cover, they fail to form significant limestone

reef structures (Veron & Done 1979). Therefore, studies of these communities are important because they provide insights into factors controlling coral reef formation.

Before the 1970s, very few coral species had been recorded on the East Australian coastline south of Moreton Bay, Queensland (Fig. 1). Dakin (1952) reported only 1 coral species along the coast of New South Wales (NSW), and Wells (1955) reported 8 coral genera from the same region. Wells (1955) predicted that the number of coral genera should decline from 25 on the southern Great Barrier Reef to 12 in Moreton Bay and to 2 by the latitude of Sydney.

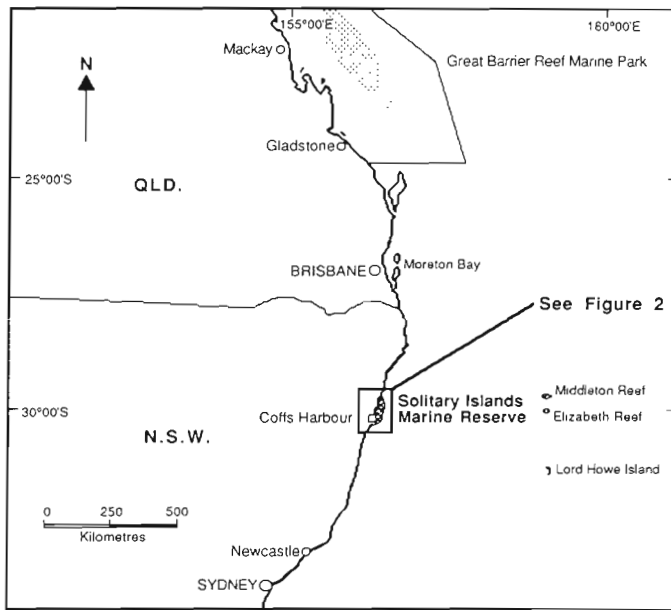


Fig. 1. Eastern Australia showing the location of the Solitary Islands Marine Reserve

There were no additional records of corals until a pioneering study of the coral communities of the Solitary Islands in northern NSW by Veron et al. (1974; Fig. 1). They recorded 34 scleractinian species in 18 genera, compared with the predicted number of fewer than 10 genera, and 100% coral cover in some localised areas. They concluded that the coral communities were similar on 4 of the 5 islands in the group, with the exception of North Solitary Island, which is further offshore and had species which were not present at the other more inshore islands. Recently Smith & Simpson (1991) have updated the records for corals from the major headlands and associated reefs within the Solitary Islands Marine Reserve, taking the nearshore species count to 15. However, there have been no additional published studies of coral communities in the main island group.

A reinvestigation of the coral communities of the Solitary Islands is timely for a number of reasons. Firstly, the Veron et al. (1974) surveys were not quantitative, and included coral cover estimates for only 1 island. Secondly, it is appropriate to examine whether there have been major changes in the coral community after an interval of almost 20 yr since the original surveys. Finally, advances in Australian coral taxonomy in the past 20 yr have resulted in changes to many of the species records in Veron et al. (1974), and some additional species have subsequently been collected from the Solitary Islands (Veron 1993). An updated coral species list for this region, and quantitative information on the structure of the benthic communities, are neces-

sary to form the basis for further ecological work and management of the Solitary Islands Marine Reserve.

METHODS

Benthic community structure was examined at 7 sites within the Solitary Islands Marine Reserve, at varying distances from the mainland, and covering a latitudinal distance of approximately 45 km (Fig. 2). The sites at Muttonbird Island and Woolgoolga Reef both lie in semi-protected areas on the northern side of headlands, and less than a few hundred metres from the shoreline. The other islands lie between 2 and 11 km offshore (Fig. 2).

As limited field time was available for the study, and the primary aim was to examine patterns in coral species richness and cover, a stratified sampling design was used. Preliminary snorkel and scuba surveys were used to establish the areas at each site with the best-developed coral communities, and the quantitative studies were done in

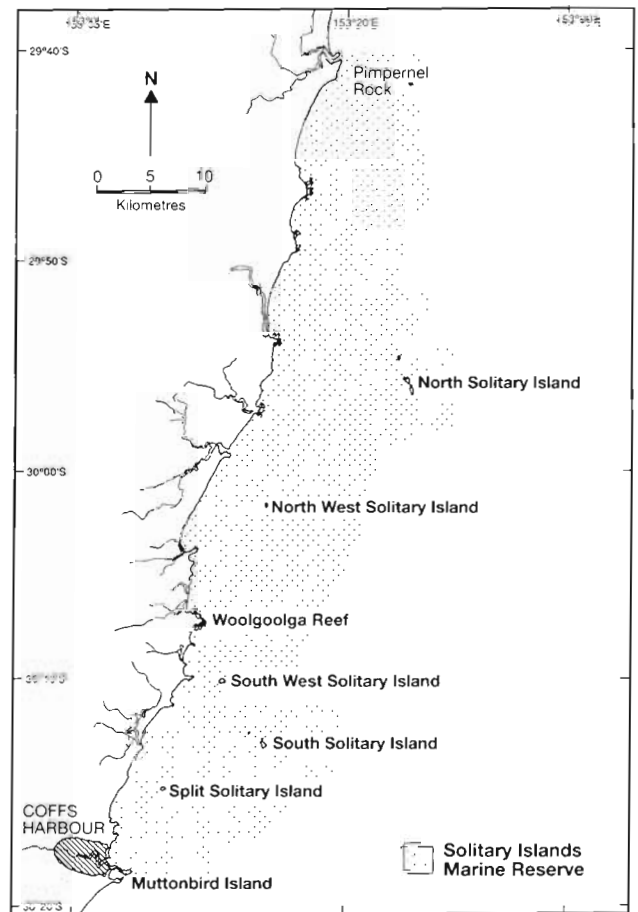


Fig. 2. Study locations within the Solitary Islands Marine Reserve

these areas. For this reason, the results presented here are for areas likely to have maximum coral cover at each site. The depth of the zone of maximum coral cover varied at each site, but all surveys were done at depths between 5 and 9 m. For each of the island sites, the zone of highest coral cover was on the northern or northwestern side of the island, possibly because of the protection afforded from the prevailing southerly or southeasterly wind and wave patterns.

Benthic community cover was quantified using line transects, with 4 transects of 20 m per site. Once the general area was selected, the 4 transects were established haphazardly within the area, and surveyed using a fibreglass tape measure. Cover was recorded by noting the length of the transect interval under the tape for each coral colony, other taxonomic groups, or substratum type. The results for each transect were collated as number of colonies, mean interval under the tape and cover for each taxonomic group or substratum type. At each site, the number of coral species recorded became asymptotic after 2 to 4 transects, indicating that the selected sampling unit of four 20 m line transects was appropriate for these sites. The sites at Woolgoolga Reef, SW Solitary, NW Solitary and North Solitary islands were surveyed during February 1992, while sites at Muttonbird, Split Solitary and South Solitary Islands were surveyed in November 1992.

At the 2 nearshore sites (Woolgoolga Reef and Muttonbird Island), sublittoral rocky outcrops are dominated by a mixed biotic community (Smith 1988, Smith & Simpson 1991), each component of which is frequently numerous and small (e.g. patches of calcareous and turfing algae, ascidians and anemones). The evaluation of each of these units separately would have resulted in a considerable increase in sampling effort, so they were pooled under the classification of 'mixed algal/invertebrate community'.

At the same time as the line transects were done, 2 divers scanned the surrounding area and compiled a list of scleractinian coral species present. Species which were not common in the area, or which were difficult to identify in the field, were photographed and a small sample removed with a hammer and chisel for taxonomic identification. These coral samples were returned to the laboratory where they were bleached in a concentrated chlorine solution and then identified using the taxonomic descriptions in Veron & Pichon (1976, 1980, 1982), Veron et al. (1977), Veron & Wallace (1984) and Veron (1986). Specimens of *Acropora* were sent to the Museum of Tropical Queensland, Townsville, Australia, where they were identified by Carden Wallace and Jacqueline Wolstenholme. Representative specimens of the *Acropora* colonies have been retained in the reference collection of the

museum. Additional coral species records from Smith & Simpson (1991) and subsequent surveys at the study sites during 1992 and 1993 have also been included in the species lists for each site (Table 1).

Patterns of benthic cover in the line transects were examined for differences among sites using nonmetric multidimensional scaling (MDS) ordination (Field et al. 1982). Essentially, this method uses measures of similarity or dissimilarity between pairs of samples as a starting point to graphically portray the relationships in a 2-dimensional plot. Replicates with similar biological composition tend to group together and are spatially removed from dissimilar groups.

As some species/habitat classifications differed between the nearshore sites and the islands, selected habitat types were pooled to make the data equivalent. Values for barnacles, ascidians and different types of algae (turfing, macro- and calcareous) were aggregated into 1 habitat group (equivalent to the nearshore mixed algal/invertebrate community).

Raw cover data were double square-root transformed and similarities between each pair of samples were calculated using the Bray-Curtis measure (Bray & Curtis 1957). MDS was performed on the resulting matrix to provide a 2-dimensional solution. Differences among sites were further evaluated using the nonparametric randomisation procedure ANOSIM (Clarke & Green 1988, Clark 1993). The procedure constructs a test statistic (R) based on similarities of replicates within and between sites. This value is then tested for significance against a null distribution constructed from random sampling of all possible permutations of the sample labels (Clarke 1993).

RESULTS

Coral species richness patterns

We recorded a total of 69 scleractinian coral species (26 *Acropora* species, 4 *Montipora* species and 39 species from other taxa) in surveys of the 7 sites (Table 1). In this study, 35 coral species were collected which had not previously been recorded from the Solitary Islands region (19 *Acropora* species, 2 *Montipora* species and 14 others). When these results are combined with the 55 species recorded prior to this study by Veron (1993), a total of 90 coral species in 28 genera from 11 families have now been recorded from the Solitary Islands region (Table 1). Twenty-one (38%) of the 55 species previously recorded from the Solitary Islands by Veron (1993) were not found during this study. The most speciose genus was *Acropora*, with 30 species, but these species are largely restricted to the 2 most northern islands (Table 1).

Table 1. Coral species recorded at the Solitary Islands during this study, and by Veron (1993). P: species present

| Family Species | Mutt. Is. | Wool. Reef | Split Sol. | SW Sol. | South Sol. | NW Sol. | North Sol. | Veron (1993) |
|--------------------------------|--------------|---------------|---------------|------------|---------------|------------|---------------|-----------------|
| Pocilloporidae | | | | | | | | |
| <i>Pocillopora damicornis</i> | P | P | P | P | P | P | P | P |
| <i>Stylophora pistillata</i> | | | P | | P | P | P | P |
| Acroporidae | | | | | | | | |
| <i>Acropora palmerae</i> | | | | | | P | P | |
| <i>A. danai</i> | | | | | | | P | P |
| <i>A. formosa</i> | | | | P | | | | |
| <i>A. robusta</i> | | | | | | P | P | |
| <i>A. millepora</i> | | | | | | P | P | P |
| <i>A. humilis</i> | | | | | | P | P | |
| <i>A. glauca</i> | | | | P | | P | P | P |
| <i>A. clathrata</i> | | | | | | P | P | |
| <i>A. polystoma</i> | | | | | | P | P | |
| <i>A. cytherea</i> | | | P | P | | P | P | P |
| <i>A. hyacinthus</i> | | | | | | P | P | P |
| <i>A. digitifera</i> | | | | P | | | | |
| <i>A. listeri</i> | | | | | | P | P | |
| <i>A. dendrum</i> | | | | | | P | P | |
| <i>A. solitariaensis</i> | P | P | P | P | P | P | P | P |
| <i>A. lutkeni</i> | | | | | | | P | |
| <i>A. valida</i> | | | P | P | P | P | P | P |
| <i>A. nasuta</i> | | | | P | | P | P | |
| <i>A. latistella</i> | | | | | | | | P |
| <i>A. pulchra</i> | | | | | | | P | |
| <i>A. chesterfieldensis</i> | | | | | | | P | |
| <i>A. cerealis</i> | | | | | | P | P | |
| <i>A. florida</i> | | | | P | | P | P | |
| <i>A. loripes</i> | | | | | | P | P | |
| <i>A. sarmentosa</i> | | | | | | P | | |
| <i>A. anthocercis</i> | | | | | P | | | |
| <i>A. granulosa</i> | | | | | | P | | |
| <i>A. verweyi</i> | | | | | | | | P |
| <i>A. willisae</i> | | | | | | | | P |
| <i>A. yongei</i> | | | | | | | | P |
| <i>Montipora venosa</i> | | | | | | P | P | |
| <i>M. spongodes</i> | | | | | | | P | P |
| <i>M. turtlensis</i> | | | | | | | P | |
| <i>M. efflorescens</i> | | | | | | | | P |
| <i>M. angulata</i> | | | P | | | P | P | P |
| <i>M. danae</i> | | | | | | | | P |
| <i>M. mollis</i> | | | | | | | | P |
| Poritidae | | | | | | | | |
| <i>Porites heronensis</i> | | | P | P | P | P | P | P |
| <i>Goniopora lobata</i> | | | P | | | P | | P |
| <i>G. djiboutiensis</i> | | | | | | P | | P |
| <i>G. stokesi</i> | | | | | | | P | |
| <i>G. norfolkensis</i> | | | | | P | | | |
| Siderastreidae | | | | | | | | |
| <i>Psammocora haimeana</i> | | | P | | | | | P |
| <i>P. superficialis</i> | P | P | P | P | P | P | P | P |
| <i>Coscinaraea mcneilli</i> | P | P | P | | | | P | |
| <i>C. columna</i> | | | | | | | | P |
| Agariciidae | | | | | | | | |
| <i>Pavona minuta</i> | | | | | | | | P |
| <i>P. varians</i> | | | | | | | | P |
| <i>P. explanulata</i> | | | | | | | | P |
| <i>P. venosa</i> | | | | | | | | P |
| <i>Leptoseris hawaiiensis</i> | | | | | | | | P |
| Fungiidae | | | | | | | | |
| <i>Cycloseris curvata</i> | | | | | | | | P |
| Pectiniidae | | | | | | | | |
| <i>Echinophyllia aspera</i> | | | | | | | | P |
| <i>Mycodium elephantotus</i> | | | | | | | | P |
| Mussidae | | | | | | | | |
| <i>Acanthastrea hillae</i> | | | | | | | | P |
| <i>A. bowerbanki</i> | | P | P | P | P | | | |
| <i>A. echinata</i> | | | | P | P | P | P | |
| <i>A. lordhowensis</i> | P | P | P | P | P | P | | |
| <i>Blastomussa merleti</i> | | | | | | | | P |
| <i>Scolymia australis</i> | | | | | | | | P |
| <i>Symphyllia radians</i> | | | | | | | | P |
| Merulinidae | | | | | | | | |
| <i>Hydnophora exesa</i> | | | | | | | | P |
| <i>H. microconus</i> | | | | | | | | P |
| <i>H. pilosa</i> | | | | | | | | P |
| Faviidae | | | | | | | | |
| <i>Plesiastrea versipora</i> | P | P | P | | | | | P |
| <i>Cyphastrea seraiilea</i> | | P | P | | P | P | | P |
| <i>C. chalcidicum</i> | | | | | | P | | |
| <i>Goniastrea australensis</i> | P | P | P | | P | P | P | P |
| <i>G. favulus</i> | | | | | | P | | |
| <i>G. pectinata</i> | | | | | | | | P |
| <i>Platygyra daedalea</i> | | | | | | | | P |
| <i>P. lamellina</i> | | | | | | | | P |
| <i>Leptastrea transversa</i> | | | | | | | | P |
| <i>Montastrea curta</i> | | | | | P | P | | P |
| <i>M. magnistellata</i> | | | | | P | | | P |
| <i>M. cf. valenciennesi</i> | | | | | | | | P |
| <i>Favites halicora</i> | | | | | | | | P |
| <i>F. flexuosa</i> | P | | | | | | | P |
| <i>F. abdita</i> | P | P | | | | | | P |
| <i>F. russelli</i> | | | | | | | | P |
| <i>Favia stelligera</i> | | | | | | | | P |
| <i>F. favus</i> | | | | | | | | P |
| Dendrophylliidae | | | | | | | | |
| <i>Turbinaria radicalis</i> | P | P | P | P | P | P | P | P |
| <i>T. mesenterina</i> | P | P | | P | P | P | | P |
| <i>T. frondens</i> | P | P | P | P | P | P | | P |
| <i>T. patula</i> | | | | | | | | P |
| <i>T. peltata</i> | P | | | | | | | P |
| <i>Heteropsammia cochlea</i> | | | | | | | | P |
| Species total: 90 | 13 | 14 | 23 | 21 | 19 | 38 | 49 | 55 |

Table 2. Summary of cover of dominant benthic organisms and substratum types in the Solitary Islands group as a mean of four 20 m line transects, and summary of coral species diversity for specimens collected during these surveys

| | Muttonbird Island | Woolgoolga Reef | Split Solitary | SW Solitary | South Solitary | NW Solitary | North Solitary |
|--|----------------------|--------------------|-------------------|----------------|-------------------|----------------|-------------------|
| Hard coral | 8.5 | 14.5 | 34.5 | 50.9 | 14.6 | 26.2 | 32.4 |
| Soft coral | 2.4 | 10.2 | 7.1 | 1.6 | 0.3 | 7.2 | 0.9 |
| Invertebrates ^a | 1.6 | 3.4 | 5.2 | 5.6 | 7.9 | 9.3 | 2.5 |
| Macroalgae dominated ^b | 55.5 | 70.4 | 0 | 0 | 0 | 0.9 | 0 |
| Mixed algae and invertebrates ^c | 17.8 | 0 | 44.0 | 4.1 | 44.3 | 27.1 | 5.2 |
| Dead coral | 0 | 0 | 0.8 | 0.4 | 1.6 | 4.7 | 5.9 |
| Rock | 0 | 0 | 0.4 | 29.4 | 17.9 | 13.4 | 52.0 |
| Sand and rock | 11.7 | 1.6 | 8.2 | 6.2 | 13.2 | 7.0 | 1.5 |
| No. coral species in line transects | 6 | 7 | 10 | 11 | 11 | 13 | 15 |
| Coral species in initial surveys: | | | | | | | |
| Total | 11 | 11 | 13 | 19 | 17 | 31 | 43 |
| Acroporidae | 1 | 1 | 2 | 6 | 2 | 13 | 18 |
| Non-Acroporidae | 10 | 10 | 11 | 13 | 15 | 18 | 25 |
| ^a Invertebrates, such as barnacles, solitary ascidians, zooanthids, echinoids and sponges, not generally found in a mixed algal community | | | | | | | |
| ^b Either entirely kelp dominated, or mixed closely with a mixed invertebrate community | | | | | | | |
| ^c Mixed turf algae, red algae and calcareous algae in small patches, and mixed with encrusting invertebrates | | | | | | | |

Coral species richness in the surveys ranged from 13 species at Muttonbird Island and at Woolgoolga Reef to 49 species at North Solitary Island (Tables 1 & 2). Fourteen (28%) of the 49 coral species recorded from North Solitary Island were found only at that site (Table 1). NW Solitary Island had the second-highest coral species richness, with 38 species. Split Solitary, SW Solitary and South Solitary Islands had an intermediate number of coral species present (23, 21 and 19 species respectively). Similar trends in species richness are evident from the numbers of coral species recorded in line transects at the 7 survey sites (Table 2). The Family Acroporidae shows the most significant variation in species richness between sites, ranging from 1 species at the onshore sites (<8% of coral species) to 21 species at NW Solitary and 24 species at North Solitary Islands (55 and 49% of coral species, respectively). Species from the other scleractinian families range from a minimum of 12 species at Muttonbird Island and at Woolgoolga Reef to a maximum of 25 species at North Solitary Island (Table 2).

Benthic community structure

The results of the line transect surveys show clear differences between the inshore sites, which are dominated by macroalgae and have relatively low hard coral cover (<15%), and the 5 island sites which generally have much higher coral cover and species rich-

ness, and lower algal cover (Table 2). Coral cover was highest at SW Solitary Island, with a mean of 50.9% cover in the area surveyed, and with cover approaching 100% in patches. South Solitary has the lowest coral cover of the offshore islands, with a similar coral cover (14.6%) to the inshore sites (Table 2). A summary of the dominant coral taxa at each site is given in Table 3. *Turbinaria* species tend to dominate onshore reefs, *Acropora* species dominate North Solitary Island, while the other islands are dominated by a range of *Acropora*, faviid and *Turbinaria* species, *Pocillopora damicornis* and *Porites heronensis*.

The results of the nonmetric MDS are shown in Fig. 3. Replicates from most sites group together, but there is some overlap between samples from NW, Split and SW Solitary Islands in the central part of the plot. Samples are grouped within the plot in an approximate gradient of distance offshore, along the principal (x) axis. Thus samples from the nearshore sites (WR and MI) and the site furthest offshore (N) group to the left and right respectively (Fig. 3).

Tests for differences among the sampling sites using ANOSIM (Clarke & Green 1988, Clarke 1993) indicated that with the exception of South Solitary Island versus NW Solitary Island ($p = 0.086$) all pairs of sites were significantly different from each other.

In order to determine which species/habitat types were primarily responsible for differences among the sites, SIMPER (similarity percentage) breakdowns were performed (Clarke 1993). This procedure deter-

Table 3. Summary of the scleractinian coral cover of the dominant species (>1% cover) from line transects at each site. Results show mean (SD) of percentage cover in four 20 m line transects

| | Muttonbird Island | Woolgoolga Reef | Split Solitary | SW Solitary | South Solitary | NW Solitary | North Solitary |
|---------------------------------|-------------------|-----------------|----------------|-------------|----------------|-------------|----------------|
| <i>Pocillopora damicornis</i> | 1.2 (2.4) | 1.9 (0.69) | 2.7 (1.23) | 5.3 (1.18) | 3.4 (1.50) | 4.1 (3.22) | 9.8 (4.88) |
| <i>Porites heronensis</i> | | | | 5.8 (4.06) | 1.0 (0.57) | 2.0 (1.90) | 1.0 (0.93) |
| <i>Acropora solitarilyensis</i> | | | 6.6 (4.23) | 9.6 (7.21) | 2.6 (2.73) | 7.7 (2.92) | |
| <i>A. nasuta</i> | | | | | | | 4.2 (3.98) |
| <i>A. hyacinthus</i> | | | | | | 1.2 (2.40) | |
| <i>A. robusta</i> | | | | | | | 8.2 (4.57) |
| <i>A. cerealis</i> | | | | | | | 2.1 (2.67) |
| <i>Turbinaria frondens</i> | | | 15.5 (6.17) | 13.3 (4.49) | | 7.7 (2.92) | |
| <i>T. mesenterina</i> | 3.1 (2.5) | 5.9 (2.74) | 1.1 (2.27) | | | | |
| <i>T. radicalis</i> | 2.3 (2.4) | | | 2.6 (3.07) | 2.1 (2.51) | | |
| <i>Goniastrea australensis</i> | 1.2 (1.0) | 1.5 (3.00) | 6.1 (3.31) | 9.3 (5.16) | 1.3 (2.60) | 4.9 (1.42) | |
| <i>Cyphastrea serailea</i> | | 1.5 (3.00) | | 1.9 (2.23) | 1.9 (2.59) | | |
| <i>Psammacora superficialis</i> | | 1.2 (1.70) | | | | | |

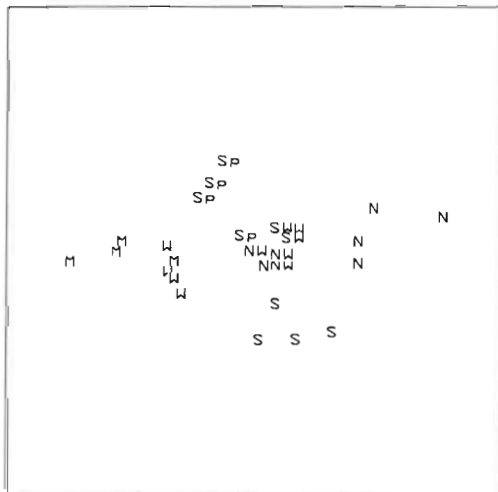


Fig. 3. MDS plot for data from benthic line transects at 7 sites within the Solitary Islands (Kruskal's stress = 0.136). M = Muttonbird Island, W = Woolgoolga Reef, Sp = Split Solitary Island, SW = South West Solitary Island, S = South Solitary Island, NW = North West Solitary Island, N = North Solitary Island

| | WR | Split | South | SW | NW | North |
|-------|----|-------|-------|----|----|-------|
| MBI | 33 | 34 | 34 | 34 | 34 | 34 |
| | 12 | 4 | 31 | 31 | 31 | 31 |
| | 13 | 12 | 33 | 16 | 16 | 12 |
| | 19 | 28 | 12 | 12 | 33 | 9 |
| WR | 30 | 14 | 32 | 4 | 12 | 6 |
| | 33 | 34 | 34 | 31 | 34 | 31 |
| | 4 | 28 | 27 | 16 | 16 | 28 |
| | 19 | 13 | 32 | 4 | 26 | 9 |
| Split | 32 | 30 | 30 | 32 | 32 | 6 |
| | 13 | 31 | 31 | 31 | 31 | 31 |
| | 33 | 28 | 33 | 32 | 28 | 9 |
| | 27 | 16 | 32 | 32 | 33 | 6 |
| South | 28 | 28 | 21 | 13 | 13 | 13 |
| | 13 | 17 | 17 | 27 | 27 | 9 |
| | 32 | 32 | 32 | 17 | 17 | 6 |
| | 28 | 16 | 26 | 13 | 32 | 26 |
| SW | 16 | 26 | 26 | 26 | 26 | 26 |
| | 18 | 28 | 28 | 28 | 28 | 6 |
| | 1 | 1 | 1 | 1 | 1 | 9 |
| | 21 | 21 | 21 | 21 | 21 | 26 |
| NW | 28 | 28 | 28 | 28 | 28 | 28 |
| | 27 | 27 | 27 | 27 | 27 | 9 |
| | 17 | 17 | 17 | 17 | 17 | 6 |
| | 17 | 17 | 17 | 17 | 17 | 6 |

Fig. 4. Results of SIMPER breakdowns to determine which species/habitat types contribute most to the average dissimilarity between sites (the 5 highest-ranked groups are shown). Species/habitats (coded) are presented in rank order for each comparison. The highest-ranked group (i.e. contributing the highest individual percentage to the average dissimilarity) appears first within each cell. Species/habitat codes are aligned to show at which site they had the higher cover.

- | | | |
|---|------------------------------------|---|
| 1: <i>Acanthastrea lordhowensis</i> | 16: <i>Porites heronensis</i> | 28: mixed algae and small sessile invertebrates |
| 4: <i>Acropora solitarilyensis</i> | 17: <i>Goniastrea australensis</i> | 30: sponge |
| 6: <i>A. nasuta</i> | 18: <i>Goniastrea favulus</i> | 31: bare rock/boulders |
| 9: <i>A. robusta</i> | 19: <i>Montastrea curta</i> | 32: sand/small boulders |
| 12: <i>Pocillopora damicornis</i> | 26: dead coral | 33: sand |
| 13/14: <i>Turbinaria (mesenterina and frondens)</i> | 27: soft coral | 34: kelp (<i>Ecklonia radiata</i>) |

mines which of the measured variables contributes the most, both to the average similarity within each site and also to the average dissimilarity between each pair of sites. In this case, the results of the latter procedure are of the most interest and are summarised in Table 4. The SIMPER procedure lists all species/habitat groups in rank order of their contribution to the average dissimilarity. For convenience, only the 5 highest ranked groups are displayed for each of the pairwise comparisons (Fig. 4).

Features of the nearshore sites which distinguish them from the island sites are the high cover of kelp, low cover of coral (in particular *Pocillopora damicornis*) and the low percentage of bare rock (Fig. 4). At the nearshore sites, bare rock is rare as mixed algal/sessile invertebrate communities cover most available substrata that are not occupied by larger biota (Smith 1988, Smith & Simpson 1991). Similarly, recurrent differences between North Solitary and the other islands are primarily due to the presence of *Acropora robusta* and *A. nasuta*, which were recorded in transects only at North Solitary Island.

Split Solitary Island differs from the other sites in the central cluster (SW and NW Solitary Islands) as a result of a higher percentage cover of sand, and also a lower percentage of bare substrata (Fig. 4). The factors which contribute most to the difference between SW and NW Solitary Islands are the greater cover of dead coral, soft coral, *Acanthastrea lordhowensis* and *Montastrea curta* at NW, and a higher cover of *Goniastrea favulus* at SW Solitary Island. South Solitary features a higher cover of the sand/small boulder habitat and a lower percentage cover of *Turbinaria* spp. when compared with most of the other island sites (Fig. 4).

DISCUSSION

Comparisons with tropical fringing reefs

Coral cover for the fringing coral communities of the Solitary Islands falls within the range recorded for inner reefs in the northern and central Great Barrier Reef in several studies (Table 4). Soft corals are less abundant at the Solitary Islands than on the Great Barrier Reef, but barnacles and ascidians make a major contribution to benthic cover on the subtropical reefs, while they were rarely abundant at more northern sites (Pichon & Morrissey 1981, Bull 1982, A.I.M.S. 1987). It is possible that the cover of soft corals at the Solitary Island sites may be low because the sites are periodically exposed to heavy wave action.

While the total of 90 coral species recorded at the Solitary Islands is considerably less than the approximately 356 species recorded for the Great Barrier Reef

(J. Veron pers. comm.), it is more meaningful to compare the number of species found per unit of sampling area for similar types of habitat (McGuinness 1990). There are 2 comparable studies of tropical fringing reefs using line transects, one at Lizard Island in the northern Great Barrier Reef (Pichon & Morrissey 1981) and one at Magnetic Island in the central Great Barrier Reef (Bull 1982). Percentage coral cover is similar or slightly higher in the high coral cover areas surveyed at the Solitary Islands, but species richness per line is less than half the values for the Great Barrier Reef sites (Table 4).

Spatial patterns

Two general patterns have been reported for cross-shelf changes in community structure on the Great Barrier Reef which are relevant to the Solitary Islands coral communities. Firstly, Pichon & Morrissey (1981) and Done (1982) reported that tall fleshy macroalgae declined in significance with distance offshore on the Great Barrier Reef. A similar pattern was evident in the present study. Secondly, coral species richness and, in particular, *Acropora* species richness, increases offshore on the Great Barrier Reef (Pichon & Morrissey 1981, Done 1982). With the exception of South Solitary Island, a similar pattern was found at the Solitary Islands.

While South Solitary Island lies at a similar distance offshore from the mainland to that of North Solitary Island, it has reduced coral cover and coral species

Table 4. Comparison of coral cover data from Solitary Islands and from shallow tropical inshore coral reefs at depths of 5 to 10 m with data collected using line transects

| | <i>Acropora</i> cover (%) ^a | Total coral cover (%) | Coral species per transect (mean) |
|------------------------------------|--|-----------------------------|---|
| Split Solitary Island ^a | 7 | 34 | 6.2 |
| SW Solitary Island ^a | 10 | 51 | 8.3 |
| South Solitary Island ^a | 3 | 15 | 5.8 |
| NW Solitary Island ^a | 5 | 26 | 8.3 |
| North Solitary Island ^a | 18 | 32 | 9.3 |
| Northern GBR ^b | 14 | 42 | |
| Lizard Island ^c | | 24 | 36.5 |
| Magnetic Island ^d | | 27 | 23.3 |

^aPresent study: four 20 m line transects per site (11 to 15 species per site)
^bA.I.M.S. surveys: 13 inshore reefs; mean of twenty-two 100 m lines
^cPichon & Morrissey (1981): three 30 m line transects (87 species)
^dBull (1982): four 30 m lines (69 species; 23 species per 30 m line)

richness, and a greater area of bare rock surface. Several hypotheses can be proposed to account for the differences between South Solitary and the other island sites. South Solitary Island lies more than 20 km to the south of the other 2 most offshore sites (North and NW Solitary Islands), and it is possible that the currents in the region may not be conducive to moving or returning coral larvae to this island. Alternatively, because the island is surrounded by only a small area of shallow rocky platform, compared with the more extensive shallow bays on the other islands, it may therefore support fewer coral species. Thirdly, the coral communities at South Solitary Island appear to have been subjected to strong wave action. The relatively unprotected nature of the shoreline may mean that coral colonies are damaged or removed by adverse hydrodynamic conditions more frequently at South Solitary Island compared with the other island sites.

Veron et al. (1974) concluded from their general surveys that coral communities on all the islands were similar with the exception of North Solitary Island. The quantitative data reported here largely support these conclusions, but also discriminate NW Solitary Island on the basis of a higher coral species richness and higher acroporid abundance, and South Solitary Island because of its low coral cover and only moderate species richness relative to the other more offshore islands.

Bare rock was a major component of the substratum at most of the island sites, while dead coral surfaces were generally not abundant. This reflects the fact that these communities, while having significant cover of coral, are not forming limestone reefs, and instead form a veneer of coral growing on rocky substrata. A small increase in the presence of dead coral surfaces was found for the most offshore reefs, and may indicate that these reefs lie along a spectrum with respect to reef formation. For some reason, the apparently healthy, high cover coral communities at the Solitary Islands fail to accrete at a rate which compensates for loss of the coral substratum over geological time scales. The reasons for this failure are presently unclear, but may include very slow growth rates of the corals (Johannes et al. 1983), periodic high mortality through sudden changes in minimum water temperature (Veron & Done 1979), failure of coral reproduction or recruitment (Yonge 1940, Wells 1957), or removal of the corals from the reef surfaces through periodic severe storms.

In the subtropical reefs of Western Australia, competition with macroalgae has been hypothesised as the most significant factor limiting coral reef formation (Johannes et al. 1983). At the Solitary Islands, fleshy macroalgae were relatively uncommon on the offshore islands and there was no evidence that competition

with macroalgae inhibits coral growth, although it is possible that competition with algae may operate at the recruitment stage. Long-term studies of these coral communities are required to test these hypotheses.

Coral biogeographic patterns

One of the most interesting aspects of the coral communities at the Solitary Islands concerns their diverse biogeographic origins. Unlike coral communities from the Great Barrier Reef region, which are totally dominated by tropical scleractinian species, the coral communities at the Solitary Islands contain a unique association of tropical species, some subtropical species, and a temperate water species. Of the 90 scleractinian species recorded from the Solitary Islands to date, 77 (85%) are essentially tropical species found throughout the Great Barrier Reef region, and which are at, or near, their southern distribution limit at the Solitary Islands (Table 1; Veron 1986, 1993). A further 11 species (12%) are generally rare or absent from tropical reefs, and are more common on subtropical and high-latitude reefs. The primarily subtropical suite of species comprises: *Acropora glauca* and *A. solitaryensis*, *Porites heronensis*, *Acanthastrea bowerbanki*, *A. hillae* and *A. lordhowensis*, *Scolymia australis*, *Hydnophora pilosa*, *Goniastrea australensis*, *Turbinaria patula* and *T. radicalis*. In contrast, *Plesiastrea versipora* is found throughout tropical and high-latitude reefs around Australia, while *Coscinaraea mcneilli* is a temperate water species restricted to southern Australia (Veron 1993).

Thus, the unexpectedly high number of coral species present at the Solitary Islands is partly attributable to the biogeographic overlap of different coral faunas. A similar biogeographic mixing of tropical, subtropical and temperate marine species has been reported in surveys of the fish fauna (Pollard 1982) and algae (Chidgey 1987, Millar 1990) in the Solitary Islands region. Together these data indicate that the Solitary Islands marine communities are important not only for their species diversity, but also for their unique biogeographic composition. Although the subtropical species account for only 12% of the total number of coral species recorded, many of them are locally abundant and make major contributions to coral cover. Among the subtropical species, *Acropora solitaryensis*, *A. glauca*, *Porites heronensis*, *Goniastrea australensis* and *Turbinaria radicalis* were dominant in line transects at some of the survey sites (Table 3).

Ten of the 35 species recorded for the first time in this study have not previously been recorded south of the Great Barrier Reef region along the east coast of Australia (Veron 1993). These include: *Acropora poly-*

stoma, *A. chesterfieldensis*, *A. formosa*, *A. dendrum*, *A. cerealis*, *A. loripes*, *A. granulosa*, *Goniopora stokesi*, *G. norfolkensis* and *Cyphastrea chalcidicum*. However, some of these species have recently been recorded in unpublished surveys of subtropical reefs at Moreton Bay, Brisbane (P. Harrison & N. Holmes unpubl.), and at Lord Howe Island (V. Harriott, P. Harrison & S. Banks unpubl.; Fig. 1). Most of the other species recorded for the first time at the Solitary Islands have previously been recorded at other subtropical reef sites along the east coast (Veron 1993). However, *Hydnophora pilosa* has not previously been recorded at a nearshore location along the east coast of Australia, and has only previously been recorded from the Elizabeth and Middleton reefs (Veron 1993; Fig. 1), and recently at Lord Howe Island (V. Harriott, P. Harrison & S. Banks unpubl.). In contrast, the most northern record for *Coscinaraea mcneilli* was previously the south coast of NSW (Veron 1993), hence the Solitary Islands represent a new northern distribution record for this species along the east coast.

Community changes over time

There are no obvious changes to the general condition and structure of the coral communities at SW Solitary Island approximately 20 yr after the surveys by Veron et al. (1974). The coral communities are dominated by the same species (taking into consideration likely name changes), and, where the quantitative surveys were done, areas of close to 100% coral cover are still present, as described by Veron et al. (1974). If major changes have occurred in the intervening period, then the communities have since recovered to be similar to those present in the earlier survey.

Patterns of coral community structure at the other island sites also appear to be similar to those described from qualitative surveys by Veron et al. (1974). However, the species composition appears to have changed over the intervening period. Twenty-one (38%) of the 55 species recorded previously by Veron (1993) were not found during this study. It is possible that some of these species may still be present at the Solitary Islands, but were not observed during this study. The fact that 35 previously unrecorded coral species (50% of the 69 species) were found in the coral surveys reported here, probably reflects at least some real changes in the coral community structure at these sites since the time of the original surveys. It is likely that future surveys over a greater area of reef will further increase the number of coral species recorded at the Solitary Islands.

With the exception of *Acanthastrea lordhowensis*, most of the new species recorded were relatively rare

at the study sites, and most were found at North Solitary Island. These corals may represent new arrivals since the time of the previous surveys. The results indicate that a dynamic temporal pattern of species recruitment, survival and subsequent local extinction is occurring within these subtropical coral communities. The dominant coral species appear to be relatively stable, whereas some of the rarer species seem to appear and then disappear over time. A similar increase in the number of relatively rare coral species has also been found in recent surveys of other subtropical coral communities at Moreton Bay, Brisbane (Lovell 1989, P. Harrison & N. Holmes unpubl.), and at Lord Howe Island off the NSW coast (Veron & Done 1979, DeVantier & Deacon 1990, V. Harriott, P. Harrison & S. Banks unpubl.).

It is possible that some coral species can temporarily recruit to, and subsequently survive at, these southern sites, but fail to establish self-maintaining populations because of the very small number of colonies in the population, and the likelihood of larval dispersal away from these small isolated reefs (reviewed by Harrison & Wallace 1990). The population of the species may then disappear from the community until new recruits arrive from northern tropical or subtropical reefs via larval dispersal in the East Australia current. The consequence of this may be that over a very long time span, a large proportion of the tropical species pool might be recorded from these southern reefs, but only a subset will be present at any one time. If so, the total list of recorded species would increase slowly over time, while species richness in surveys might be expected to remain relatively static.

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