

**CORAL ASSEMBLAGES ON
CONTINENTAL ISLANDS IN THE
SOUTHERN
GREAT BARRIER REEF,
AUSTRALIA.**

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EXECUTIVE SUMMARY

This report is a summary of the first 5 chapters of my PhD, with additional discussions on management implications. The entire thesis is available at the Great Barrier Reef Marine Park Authority, it is entitled "Ecology of coral assemblages on continental islands in the southern section of the Great Barrier Reef, Australia". The report is divided into two sections. The first describes the coral assemblages on continental islands between 20°S and 23°S and assesses why there is a lack of fringing reef development in the vicinity of 21°S. Differences in coral abundance, morphology and size are examined north and south of 21°S. The second section examines environmental gradients in order to quantitatively assess which gradients reflect biological composition.

Fifteen coral assemblages are described which account for 79% of the variation in the data. Major framework builders, massive and branching corals (acroporids, faviids, poritids and pocilloporids), dominated reefs north of 21°S but significantly declined at 21°S where fast-growing, plate-like and encrusting corals (*Montipora* and *Turbinaria*) were most common. Results suggest that coral growth rates and reef accretion are not directly related and harsh regional conditions have influenced coral composition and coral morphology to such a degree that poor reef development has occurred at 21°S through the Holocene period.

Direct gradient analysis of scleractinian (hard) corals and alcyonacean (soft) corals and eight environmental gradients indicated that variation in coral composition was significantly correlated with depth, exposure, tidal amplitude and distance from the mainland. Tidal fluctuations in Broad Sound (10m) induce high turbidity and reduce the euphotic zone which has suppressed reef development in this region through the Holocene period.

MANAGEMENT IMPLICATIONS

The inshore region of the southern Great Barrier Reef is arguably one of the fastest-growing tourist and commercial centres within the Great Barrier Reef province. A focus on fringing reefs is becoming increasingly necessary in order to understand the inshore reef ecosystem most likely to be influenced by terrestrial factors and contemporary man, particularly reefs in close proximity to areas of urbanization and agriculture. Baseline information collected during this study provides a catalogue of benthic assemblages to aid zoning and management of the coastline. Reef composition on nearshore islands was virtually unknown before this study.

The last 6,000 years have been central to fringing reef development on the Great Barrier Reef. The amount of carbonate accumulation around islands can be used as an indicator of naturally favourable conditions for coral growth. It is assumed that areas with minimal reef development have been unfavourable for coral growth. An examination of the regional variation in coral distribution and abundance in the vicinity of a naturally stressed area (21°S) provides a quantitative inventory on which to examine possible causative gradients for the poor antecedent foundations. The large tides at 21°S induce consistently high turbidity which has led to a considerable reduction in the vertical extent of the biotic zone and minimal reef accretion.

This study also revealed morphological and compositional changes to the coral communities at 21°S and identified indicator species most resilient to the extreme conditions. These species are central to coral ecology because they are the last species to survive before a reef collapses and is overtaken by non-coral organisms. In contrast, Van Woessik 1992 studied mild disturbances and identified coral species most vulnerable to stress, thereby identifying two extremes along a stress response continuum.

Although the composition of the coral communities in this naturally stressed location is of prime interest to managers, consequences of a narrow euphotic zone is also critical. It appears that deep sites are first to be effected by environmental degradation and reefs start to decline from the "bottom up". Another example is the reduction of the euphotic zone in Jakarta Bay, Indonesia, due to anthropogenic input (T. Tomascik pers. comm.). Under low light conditions corals may not settle on deep slopes merely through their inability to compensate their photosynthetic rates. Reef flats are also prone to anthropogenic impact, which may lead to a "squeeze" (from the top and bottom) on the communities effected by increases in pollution, sedimentation and low light. Contemporary environmental impact studies concentrate on mid-slopes which may be the last area to be effected by anthropogenic impact.

Spatial studies, such as this, are still necessary on the Great Barrier Reef, in a time where emphasis tends toward manipulative experiments, as still little is known about what grows where. Coral reef systems may be operating in considerably different ways to temperate and terrestrial systems upon which current ecological theory is based (Steele 1985). The framework in which we define our conservation units, for example on an island by island basis, or bay by bay in some instances, maybe disjunct from the manner in which reef systems function. Regional management and zoning on a island group basis may be more appropriate. The transfer of ecological theory to management has at times lead to the collapse of the industry it set out to manage by using management strategies based on concepts of optimization and ecological models (May *et al* 1979). Considering the immaturity of ecology, especially coral reef ecology, a sound understanding of the distribution and abundance of coral reef organisms is necessary, on both a spatial and temporal scale. It seems most logical to implement a conservative strategy, to reduce anthropogenic interference, pending a more thorough understanding of the ecosystem. The spatial data collected here are relevant towards addressing such questions as what units, and at what scale, should we be managing the reefs. However temporal data is vital, although scarce, to our understanding of coral communities.

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SECTION 1.

INTRODUCTION

Rationale and objectives

Hopley (1982) stated that fringing reefs on the Great Barrier Reef were poorly developed south of 21°S (Figure 1). However, further investigations indicated that extensive fringing reefs do in fact occur at the Keppel Islands at 23°S (Van Woesik 1989). Clearly, latitudinal effects *per se* do not directly suppress reef development. In order to elucidate why Holocene fringing reef growth has been limited at 21°S two objectives were defined;

- 1 Examine the biological composition of coral assemblages in the vicinity of 21°S;
- 2 Assess the relationships between benthic composition and environmental gradients.

A focus on fringing reefs is becoming increasingly necessary in order to understand the inshore reef ecosystem most likely to be influenced by terrestrial factors and contemporary man, particularly reefs in close proximity to areas of urbanization and agriculture. In contrast to mid and outer shelf coral reef assemblages, fringing reefs were originally described as simplistic (Steers and Stoddart 1977). However, more recently certain fringing reefs have been recognised for their diversity (Veron 1986), high coral cover (pers. obs.), high rates of coral growth and geomorphological accretion (Isdale 1981; Hopley 1982).

This report describes the nearshore coral assemblages in the southern Great Barrier Reef on the basis of coral composition, abundance, colony morphology and size. Comparative analyses were undertaken to determine whether the regions in the vicinity of 21°S differed in total coral abundance and/or coral morphology. Massive and branching colonies are the main frame-work builders of the Great Barrier Reef (Davies 1983), any regional variation in their abundance may influence the capacity of a reef to fully develop. Whether distribution patterns reflect environmental gradients is examined in section 2 of this report.

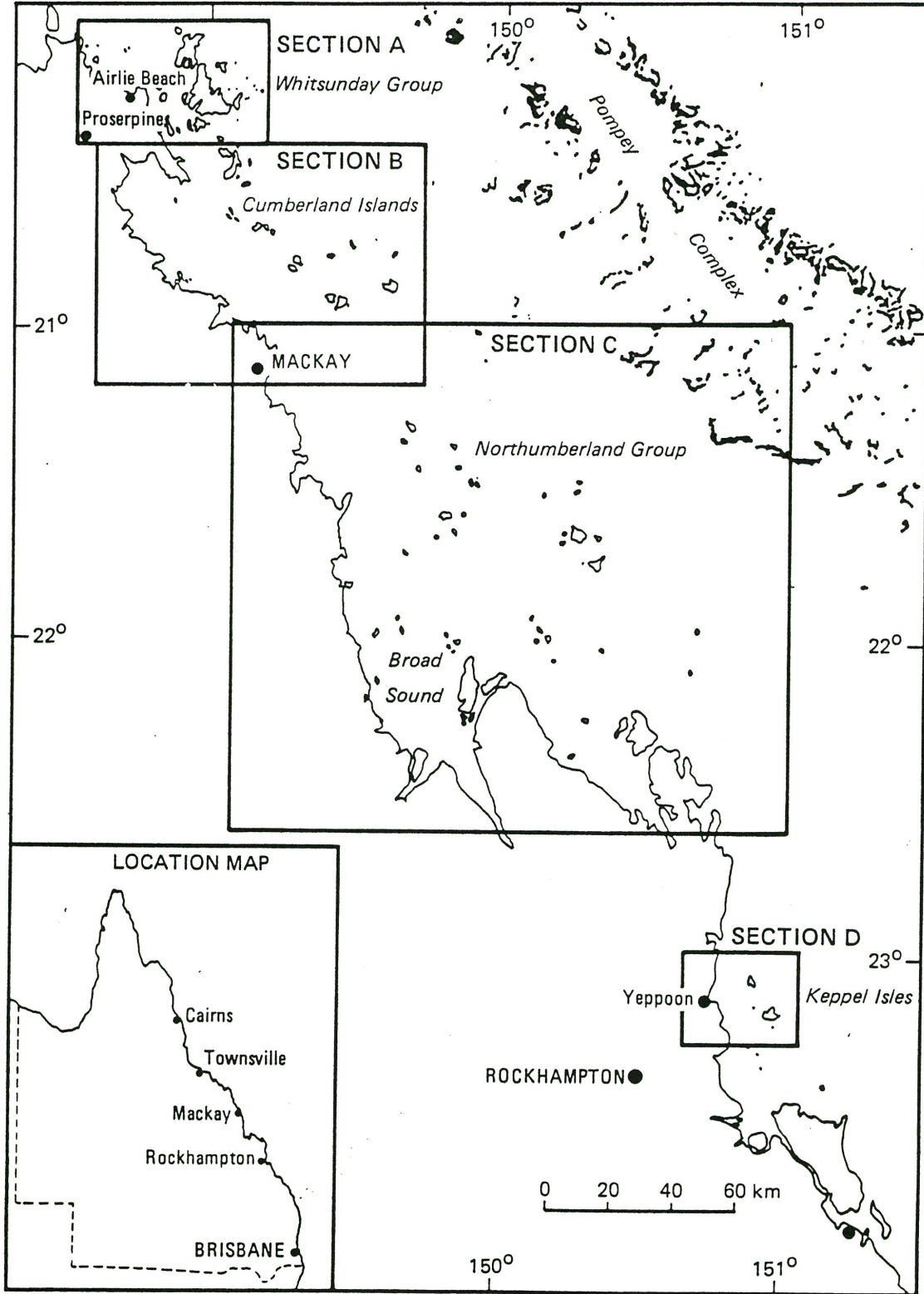
Study location

The study area was situated off the central coast of Queensland, Australia, along the southern section of the Great Barrier Reef (Figure 1). Thirty-four continental islands were examined from 20°05'S to 23°10'S. The area was divided into four major sections; the Whitsunday, Cumberland, Northumberland and Keppel Islands. The total area was approximately 6000 km².

Reef geomorphology

A drilling programme on six reefs in the Cumberland and Northumberland Islands indicated that Holocene reef initiation took place within a narrow time period some 7200-8000 years before present (Kleypas 1992). It appears that reefs throughout this study region have been close to modern sea-level for approximately 6000 years and growth has been mainly through lateral extension. However, reefs on Middle Percy Island (in the Northumberland region, 21°S) appear to date back only to 3720 years before present (Kleypas 1992). This delayed "turn-on" (Buddemeier and Hopley 1988) may be a consequence of harsh regional conditions for reef initiation.

Figure 1. The study area; A Whitsunday Islands, B Cumberland Islands, C Northumberland Islands, D Keppel Islands.



Only on Hayman and Cockermouth Islands are reefs developed on old carbonate foundations whereby an initial framework was isolated offshore and filled in by terrigenous and biogenic carbonate deposits. On most windward edges reefs formed on the foundation of rocky shores during the Holocene transgression (Figure 2). Reef flat development is limited as most transgressional growth has been to low water mark from deep rocky foundation (after Hopley and Partain 1986). On the lee of most of islands reefs developed on pre-existing sedimentary structures. The inner Cumberland (Table 1) and Northumberland Islands (Table 1) have minimal reef flat development. Van Woesik (1992) found a significant difference ($p = 0.023$) in reef development between the Whitsunday and Northumberland Islands. In fact 73% of incipient reefs found on the Great Barrier Reef were located between 21°S and 23°S (Hopley *et al* 1989).

METHODS

Field methods

One hundred and twenty-five study sites were examined on thirty four continental islands. The position of each site was fixed using compass bearings on headlands and other landmarks (Van Woesik 1992). Each site measured 20m by 10m and was divided into 5m by 5m subsections to enhance recording accuracy. Sites were primarily located on shallow reef slopes with the longitudinal axis oriented along the depth contour. Surveys were conducted on SCUBA.

The size and identity of all the scleractinian corals (Veron and Pichon 1976; 1980; 1982; Veron and Wallace 1984; Veron 1986) and alcyonacean corals (Bayer *et al* 1983) were recorded. Colonies were recorded to species except for the genera *Acropora* and *Montipora* and the families Poritidae and Fungiidae. Alcyonacean corals were recorded to genus throughout. Each coral colony was allocated to one of four size classes based on maximum diameter: A 1-50cm; B 51-100cm; C 101-300cm; D > 301cm.

Statistical analyses

Species abundance data were analysed via a Canonical Correspondence Analysis (CCA). It produces a configuration of points, representing sites, where their distance apart reflects similarity based on species composition. T-tests were used to examine the null hypothesis that the two regions, the Whitsunday and Northumberland Islands, supported a similar number of coral colonies. In order to balance the design, ten sites were selected randomly from the Whitsunday region as only 10 sites were surveyed in the Northumberland group. Analyses were undertaken for total scleractinian corals, 'fast growing', 'massive', and 'arborescent' scleractinian corals and alcyonacean corals (Table 2). Variation in size structure was examined graphically.

Normality of data was examined via a Wilk-Shapiro statistical test (Shapiro and Francia 1972). Problems of unequal variances was overcome with a test adopted from Snedecor and Cochran (1980) that does not require variances to be equal. Degrees of freedom are expressed to one decimal point, which was calculated using the Satterthwaite's approximation (Snedecor and Cochran 1980).



a.

Figure 2 Varying degrees of fringing reef development .

a Poor reef development, South Percy Island, Northumberland islands.

b Intermediate development, Prudhoe Island, Northumberland islands.

c Extensive development, Cockermouth Island, Cumberland islands.



b.



c.

Table 1. Degree of reef development for island groups; 1 (poor development), 2 (intermediate development) and 3 (extensive development). Reef development based on Great Barrier Reef Gazetteer, Hopley (1982), Hopley *et al* (1989).

Region	Latitude	Island group	Reef type	Sites (n)
1	20°05'S	Hayman Is.	3	3
2	20°06'S	Langford region	3	3
3	20°10'S	Hook Island inlet	2	2
4	20°18'S	Molle Islands	2	5
5	20°20'S	Shute Harbour	3	4
6	20°22'S	Long Is.	1	3
7	20°18'S	Whitsunday Is.	2	4
8	20°21'S	Hamilton Is.	2	5
9	20°33'S	Thomas Is.	1	2
10	20°40'S	Goldsmith Is.	1	20
11	20°48'S	Carlisle/Brampton Islands	2	16
12	20°46'S	Cockermouth Is.	3	6
13	20°52'S	Scawfell Is.	3	12
14	21°01'S	Penrith Is.	3	9
15	21°20'S	Prudhoe Is.	2	2
16	21°36'S	Curlew Is.	1	3
17	21°30'S	Digby Is.	1	5
18	21°40'S	Percy Islands	2	10
19	23°10'S	Keppel Islands	3	8

Table 2. Morphological groups used in comparative analyses, exclusions within each family are listed separately in tables to follow, references provide a basis for morphological categorisation.

	MASSIVE CORALS	ARBORESCENT CORALS	FAST GROWING CORALS
SPECIES	Faviidae, Poritidae, Agariciidae, <i>Galaxea</i> spp., Mussidae, <i>Pectinia</i> spp., Siderastreidae, Caryophylliidae.	<i>Acropora</i> spp., <i>Porites cylindrica</i> , <i>Porites nigrescens</i> , Pocilloporidae, <i>Millepora tenella</i> .	<i>Acropora</i> spp., <i>Montipora</i> spp., Pocilloporidae, <i>Millepora tenella</i> , <i>Turbinaria</i> spp.
REFERENCES	Isdale 1981, Done 1982, pers. obs.	Pers. obs.	Oliver <i>et al</i> 1983, Simpson 1988, pers. obs.

RESULTS

Regional variation

A total of 90 taxa from scleractinian corals, alcyonacean corals and the hydrozoan *Millepora* spp. were used to describe the variation in composition between the four regions; Whitsunday, Cumberland, Northumberland and Keppel Islands. The outer Whitsunday and Cumberland Island reefs were most diverse. The number of taxa declined south of 21°S. (Table 3).

Table 3. Regional variation in taxa.

Island Group	Number of taxa	Latitude
Whitsunday Islands (north)	77	20°05'S
Whitsunday Islands (central)	79	20°18'S
Whitsunday Islands (south)	73	20°22'S
Cumberland Islands (inner)	73	20°40'S
Cumberland Islands (outer)	78	20°52'S
Northumberland Islands	65	21°30'S
Percy Islands	58	21°40'S
Keppel Islands	38	23°10'S

Family

Faviidae was the most widespread family, occurring at 97% of the sites (Table 4). Acroporidae had the highest overall mean. Poritids, mussids and fungiids were also common throughout, although most prolific on Whitsunday reefs. Pocilloporids were widespread although rarely dominant at any site, they were most common on Whitsunday and Keppel reefs. Dendrophylliidae dominated Northumberland reefs. Other scleractinian families were less prolific

Species-genus

Overall, the most widespread scleractinian genera were *Favia*, *Goniastrea*, *Favites*, *Platygyra*, *Acropora*, *Porites*, *Goniopora* and *Pocillopora* respectively. Highest mean number of colonies per site was recorded for the genera *Montipora*, *Goniastrea*, *Favites*, *Porites* 'massive', *Favia* and *Goniopora*, respectively. Ninety six percent of the sites supported soft corals with a mean abundance of 0.6 colonies per square meter. Most common and abundant soft corals were from the genera *Sarcophyton*, *Xenia*, *Alcyonium*, *Simularia* and *Lobophytum*.

Table 4. Relative abundance of scleractinian corals, where frequency of occurrence is expressed as FREQ., MEAN is the overall mean abundance calculated over sites. Mean values are presented for each region separately. (Penrith Island data are not included because of the island's mid-shelf location and the lack of slope data).

TAXA	FREQ.	MEAN	Whit. Is.	Cumb. Is.	North. Is.	Keppel Is.
Acroporidae	96.5	60.4	67.1	47.3	76.9	85.0
Faviidae	97.4	41.5	85.6	20.4	39.6	22.4
Poritidae	93.0	30.5	65.9	13.4	34.2	3.8
Pocilloporidae	90.4	18.5	31.0	14.3	6.8	28.7
Dendrophylliidae	63.5	7.6	6.7	2.7	23.7	5.5
Mussidae	79.1	6.8	13.3	5.3	3.9	0.5
Agariciidae	66.1	6.8	7.2	6.1	10.3	1.4
Fungiidae	59.1	5.0	12.5	2.9	0.7	0.6
Pectiniidae	57.4	3.8	6.7	3.1	2.6	-
Merulinidae	67.8	3.3	4.8	3.3	1.9	1.1
Oculinidae	50.4	2.8	4.2	3.2	0.4	-
Caryophylliidae	37.4	1.1	2.3	0.8	0.6	-
Siderastreidae	13.0	0.4	0.4	0.3	0.7	-

Regional variation in benthic assemblages

The Whitsunday and Cumberland regions were dominated by acroporids, faviids, poritids and pocilloporids. In the Northumberland region however, Acroporidae and Dendrophylliidae became dominant; specifically the genera *Montipora* and *Turbinaria*. Acroporidae (mainly *Acropora* spp.) was most common in the Keppel Islands.

Whitsunday Islands

On a site by site basis, massive *Porites* spp. were the most abundant and frequently occurring corals in the Whitsunday Islands (90% of sites). Massive faviids were also widespread and abundant, especially *Favia* spp. (mean colony number per square meter = 0.12), *Favites* spp. (n = 0.11) and *Goniastrea* spp. (n = 0.10) species. *Montipora* spp. was the 5th most abundant taxa, followed by *Goniopora* spp., (hydrocoral) *Millepora tenella*, *Seriatopora hystrix*, *Stylophora pistillata*, *Lobophyllia hemprichii* and *Porites cylindrica*. The soft corals *Sarcophyton* spp. were ubiquitous (in 80% of sites examined) although *Alcyonium* spp. and *Xenia* spp. had the highest mean abundance per site (n = 0.50 and 0.25 m²).

Cumberland Islands

Macroalgae cover was exceptionally high on inner islands but decreased offshore. Coral cover and diversity increased in accordance with lack of macrophytes. Although the faviids, *Favia* spp. and *Favites* spp. and *Goniopora* spp., occurred at most sites. Fast growing caespitose *Acropora* spp., encrusting *Montipora* spp., *Pocillopora damicornis* and *Seriatopora hystrix* were also common throughout the region. *Sarcophyton* spp. were found at 62% of the sites and had the highest mean abundance ($n = 0.08 \text{ m}^{-2}$). *Xenia* spp., *Lobophytum* spp. and *Briareum* spp. were also common.

Northumberland Islands

Penrith Island was an anomaly due to its distance offshore (74km). It was more akin to a mid-shelf reef in terms of composition and geomorphology. Massive faviids dominated the shallow crest and arborescent *Acropora* spp. the slopes. In contrast, the inner islands supported minimal arborescent or massive colonies. *Montipora* spp. and *Turbinaria* spp. corals were dominant (mean colony number per site, $n = 0.18 \text{ m}^{-2}$ and 0.10 m^{-2} respectively), followed by *Goniopora* spp. and encrusting *Porites* spp. *Pocillopora damicornis* and *Goniastrea* spp. were well dispersed throughout the region although their abundance was low. Most common alcyonacean corals were *Capnella* spp., *Briareum* sp. and *Lobophytum* spp.

In comparison to reefs further north, the Northumberland Islands did not appear to support any particular species not found elsewhere, except for *Duccanopsammia axifuga*. However many species found north of 21°S were not found in the Northumberland Islands. These include: *Diploastrea heliopora*, *Astreopora* spp., *Leptoseris* spp., *Catalaphyllia jardinei*, *Plerogyra sinuosa*, *Physogyra lichtensteini*, some fungiids (*Heliofungia actiniformis*, *Herpolitha* sp., *Polyphyllia talpina*), *Pavona cactus*, *Millepora tenella*. Notably only 2 colonies of *Porites cylindrica* were recorded in the Northumberland Islands.

Keppel Islands

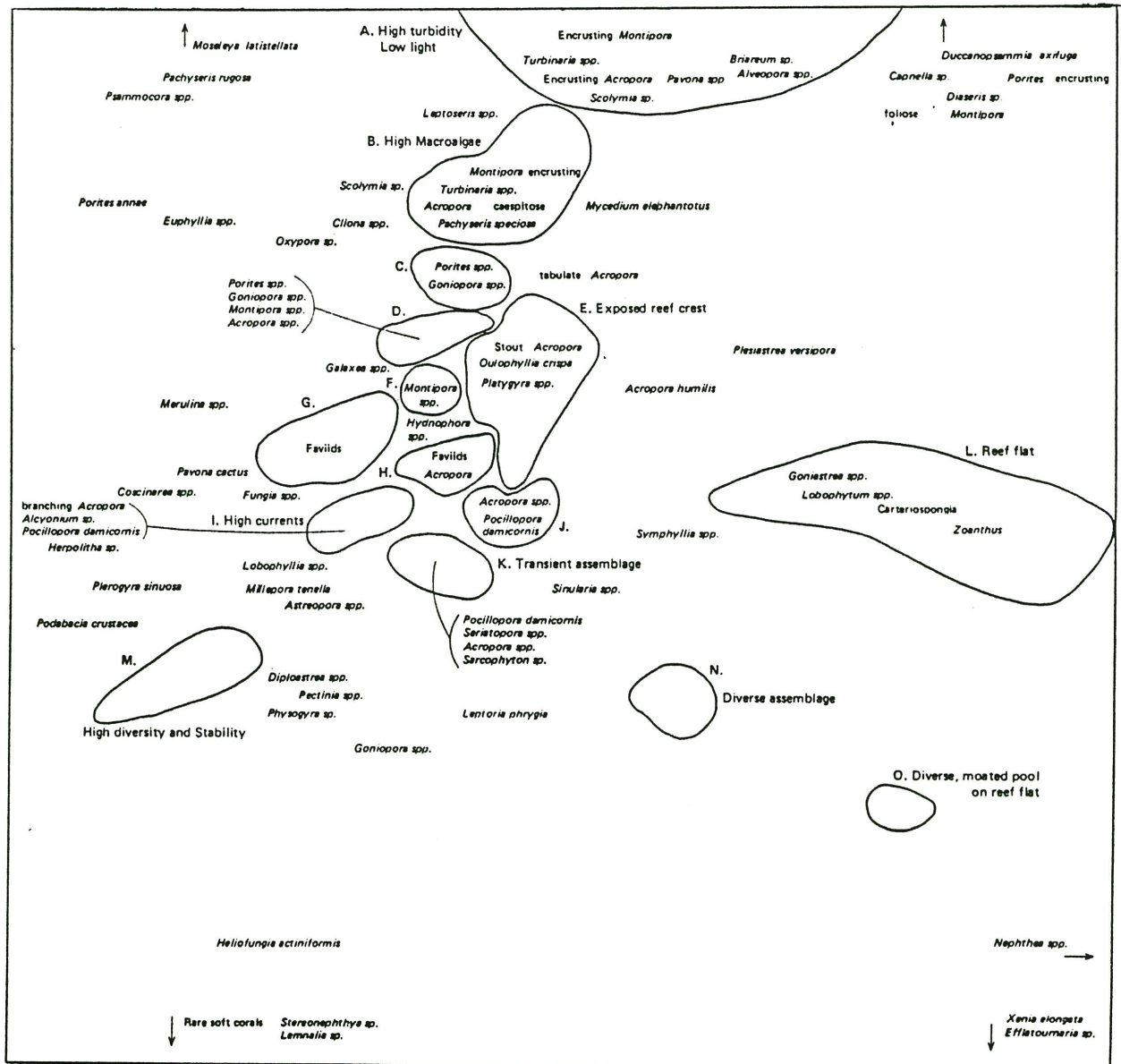
The Keppel Islands were dominated by *Acropora* spp.: *A. formosa*, *A. microphthalma* and *A. millepora*. Leeward reefs were shallow, supporting large monospecific stands of *Acropora* spp. and small colonies of *Pocillopora damicornis* and *Sarcophyton* spp. Windward slopes (east) lacked reef flats although coral diversity was high compared to leeward. Faviids, and the soft corals *Xenia* spp. and *Simularia* spp. were more common on windward slopes.

Recurrent coral assemblages

Quantitative analysis

In order to assess the spatial relation of sites with similar (species-genus) composition an analysis was sought which explained a considerable proportion of the overall variance. The first (constrained) and fourth (unconstrained) eigenvalues were simultaneously plotted explaining 79% of the overall variance (axis 1 and 4, $0.28 + 0.51 = 79\%$). The sites fall into groups which have been enclosed by subjective boundaries based on proximity. They have been labelled A to O (Figure 3). Rarely did all the sites of any particular island group together, except those on Penrith and Hayman Island (group L and M). The position of each taxon illustrates its relative position in terms of frequency of occurrence and abundance.

Figure 3. Schematic representation of results from Canonical Correspondence Analysis, accounting for 79% of the variation in the data. Coral species are grouped into 15 clusters labelled A to O. Corals outside enclosed lines are more loosely associated with the groups.



Group A sites were assemblages dominated by macroalgae (Table 5; Figure 4a,b,c), *Montipora* spp., *Turbinaria* spp., encrusting *Porites* spp. and (less common) encrusting *Acropora* spp., *Alveopora* spp. and the soft coral *Briareum* sp.. These assemblages were located on the inner islands of the Northumberland group, and less frequently on upper slopes of the Whitsunday and Cumberland Islands (Figure 5).

Group B was similar to A although not dominated as much by macrophytes. Caespitose *Acropora* spp. colonies and agariciids were common (Figure 4d). These assemblages were widespread throughout the study area. Group C were assemblages composed of massive *Porites* spp. and *Goniopora* spp. (Figure 4e). These corals dominated the Whitsunday Islands and were found on upper and lower slopes of the Cumberland and Northumberland Islands respectively (Figure 5). Group D was similar to C, although arborescent corals were found in association with poritids (Figure 4f). These assemblages were exclusive to the Whitsunday and Cumberland Islands.

The degree of regional exposure decreases from right to left in Figure 3. The most exposed assemblages were found on Penrith Island reef flat, assemblage L. Assemblage E and J were crest and upper slope assemblages dominated by *Acropora* spp. and *Pocillopora damicornis* (Figure 4g, Figure 6c). Assemblages F and G were generally depauperate in composition, they were common on inner Cumberland Islands (Goldsmith and Carlisle, Figure 4h and 6a). The reefs supporting these assemblages were poorly developed (incipient). Faviid and *Acropora* spp. corals dominated assemblage H. This is a very common assemblage found on slopes of the Keppel, Cumberland and Whitsunday Islands (Figure 5).

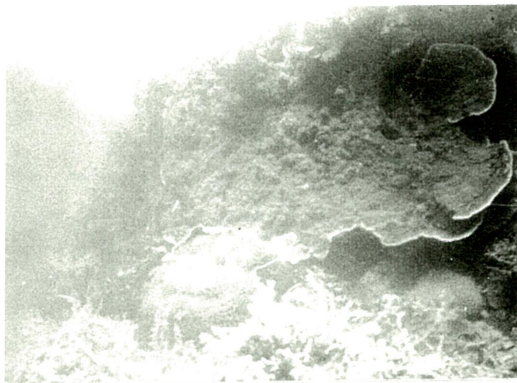
Transient or interchangeable assemblages are evident near the centre of Figure 3, groups G,H,I,J and K, and stable or predictable assemblages are most evident near the periphery. Diversity tends to be high in groups M, N and O, and low in groups A,B and C, indicating that diversity increases from top to bottom in Figure 3. Notably surveys were restricted to < 10m, due to extensive bottom time (SCUBA) required to collect data. However, deep habitats were consistently observed to support foliose and encrusting pectiniids and agariciids (assemblage P). In overview, these findings indicate that distinct or extreme environments (habitat or region) may promote the existence of characteristic species groups, and away from extremes species distribution patterns become unpredictable.

Coral abundance and morphology

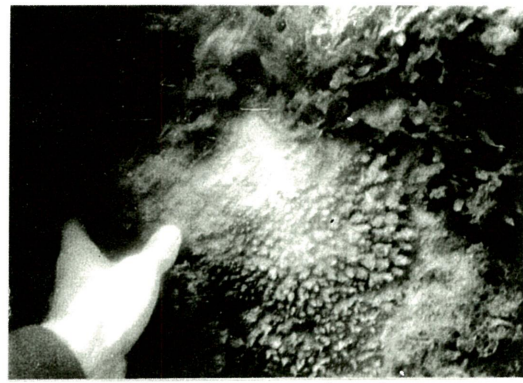
There was no significant difference in overall coral abundance between the two regions ($p = 0.94$) (Figure 7a). However, a comparison of means (*a posteriori* Tukeys test) indicated that the Whitsunday reefs supported more corals than the Northumberland reefs (Whitsundays mean = 480.0, SE 95.64, and Northumberland mean = 288.0, SE 47.65). Small corals (between 1-10cm) were considerably more abundant on Whitsunday reefs. The abundance of fast-growing corals (*Acropora* spp., *Montipora* spp., Pocilloporidae, *Millepora* spp., *Turbinaria* spp.) did not differ significantly between regions ($p = 0.071$), although the Northumberland reefs did support, on average (Tukey test), more fast growing corals (Northumberland mean = 193.5, SE 41.86 and the Whitsundays mean = 98.60, SE 24.99). Coral colonies between 11-50 cm in size were most abundant, and considerably more common on Northumberland reefs (Figure 7b).

Table 5. Assemblage groups defined by canonical correspondence analysis (see Figures 4 and 6 for photos).

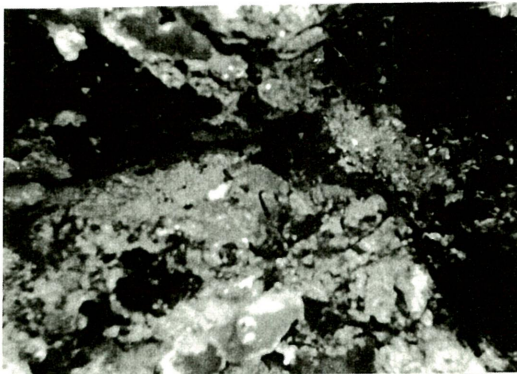
	Species composition	Description and general location
A	<i>Montipora</i> spp., <i>Turbinaria</i> spp., <i>Briareum</i> sp., <i>Pavona venosa</i> , encrusting <i>Acropora</i> spp. and <i>Porites</i> spp. (<i>Sargassum</i> spp., <i>Padina</i> spp.).	Incipient reef slopes, Northumberland Islands
B	<i>Montipora</i> spp., <i>Turbinaria</i> spp., encrusting <i>Porites</i> spp., caespitose <i>Acropora</i> spp., <i>Pachyseris speciosa</i> .	Upper slope assemblage - Whitsunday and inner Cumberland Islands
C	Massive <i>Porites</i> spp., (<i>P. lutea</i> , <i>P. mayeri</i> , <i>P. lobata</i>) and <i>Goniopora</i> spp. (<i>Sinularia</i> spp.).	Poritidae: Widespread, leeward and windward
D	<i>Porites</i> spp., <i>Goniopora</i> spp., <i>Montipora</i> spp., <i>Acropora</i> spp.	Poritidae and Acroporidae: Leeward assemblage
E	<i>Acropora</i> spp. (<i>A. palifera</i> , <i>A. humilis</i> , <i>A. millepora</i> , <i>A. secale</i>), <i>Oulophyllia crispa</i> , <i>Platygyra</i> spp.	Exposed reef crest
F	Foliose <i>Montipora</i> spp., <i>Acropora</i> spp.	Acroporidae: NW slope, Cumberland Islands
G	<i>Favia</i> spp., <i>Favites</i> spp., <i>Cyphastrea</i> spp., <i>Leptastrea</i> spp., <i>Echinopora</i> spp., <i>Galaxea astreata</i> , <i>Galaxea fascicularis</i> , <i>Fungia</i> spp., <i>Merulina ampliata</i> .	Faviidae, Oculinidae and Fungiidae: Depauperate assemblage, leeward Whitsunday and Cumberland Islands
H	Faviids and <i>Acropora</i> spp.	Faviidae and Acroporidae, Widespread
I	<i>Millepora tenella</i> , <i>Alcyonium</i> spp., <i>Pocillopora damicornis</i> , <i>Stylophora pistillata</i> .	Pocilloporidae, Alcyonacean and Hydrocorals: High current area (pers. obs.)
J	Pocilloporidae, <i>Acropora</i> spp.	Fast growing corals, widespread
K	<i>Pocillopora damicornis</i> , <i>Seriatopora hystrix</i> , <i>Acropora valida</i> , <i>Sarcophyton</i> sp., <i>Sinularia</i> spp.	Fast growing, transient, early successional corals (pers. obs.)
L	<i>Goniastrea</i> spp., <i>Lobophytum</i> spp., <i>Carteriospongia</i> , <i>Zoanthus</i> sp., <i>Acropora aspera</i> .	Reef flat - Penrith Island, Percy Island
M	<i>Porites annae</i> , <i>Porites lutea</i> , <i>Porites mayeri</i>	Hayman Island - Poritidae
N	<i>Acropora</i> spp.	Scawfell Island- Acroporidae
O	Outlier: Diverse assemblage	Penrith Island, moated pool.
P	Pectiniid and Agariciid corals.	Deep slopes below 10m LWD.



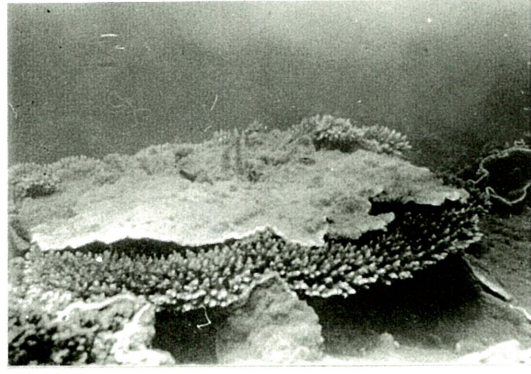
a. Assemblage A.



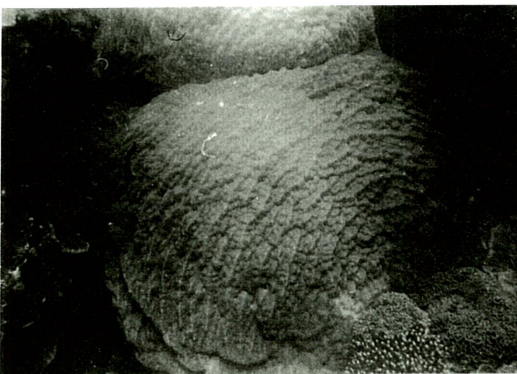
b. Assemblage A, encrusting *Acropora*.



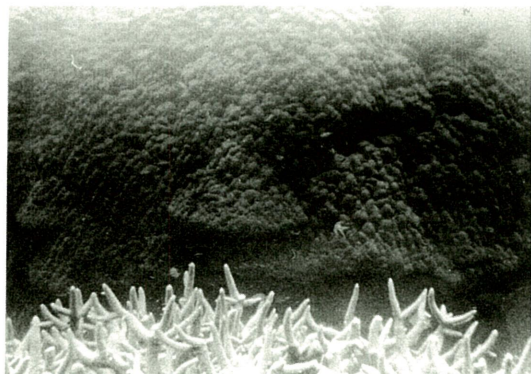
c. Assemblage A, encrusting *Porites*.



d. Assemblage B, *Montipora* and *Acropora*.



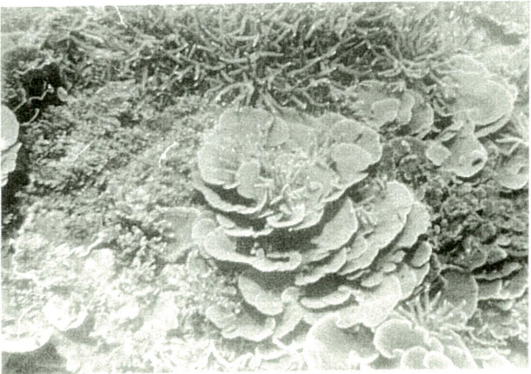
e. Assemblage C, massive *Porites*.



f. Assemblage D, *Porites* and *Acropora*.



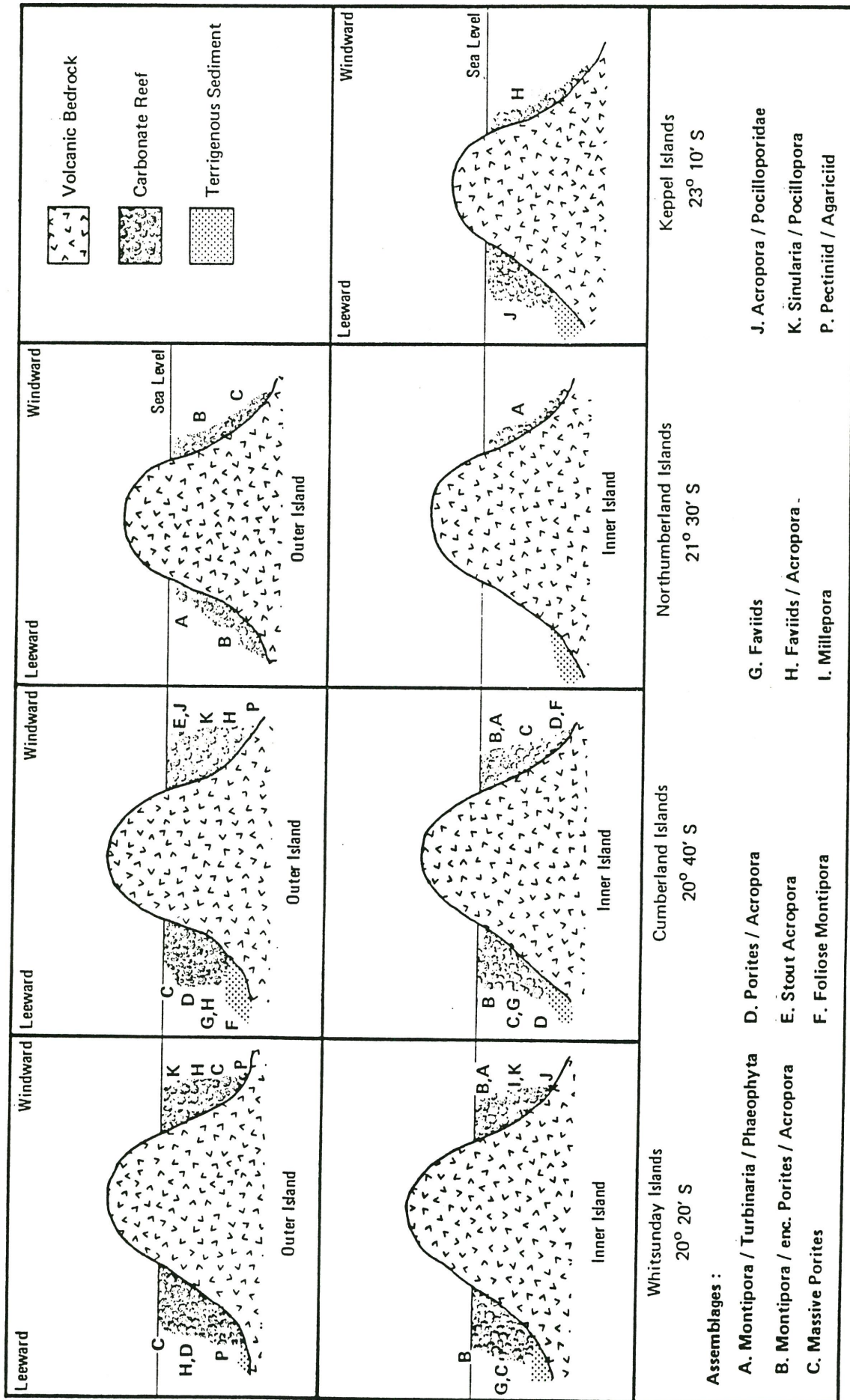
g. Assemblage E, outer island reef crest.

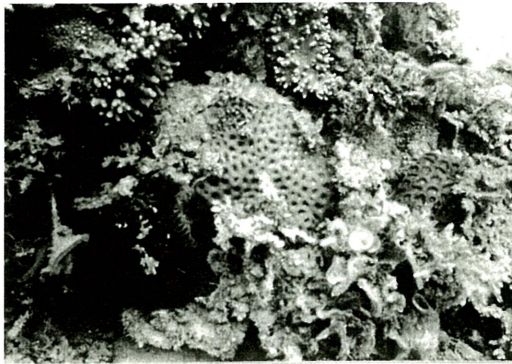


h. Assemblage F, *Montipora* and *Acropora*.

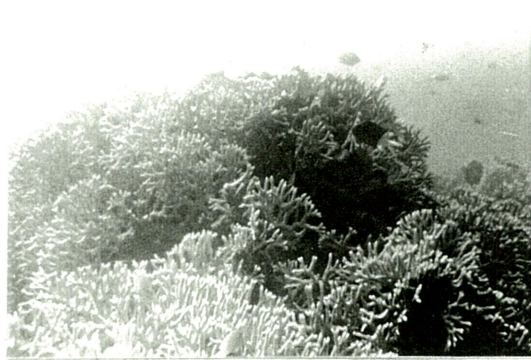
Figure 4 Assemblage groups defined in Table 5.

Figure 5. Spatial distribution of major coral assemblages in the Whitsunday, Cumberland, Northumberland and Keppel Islands.

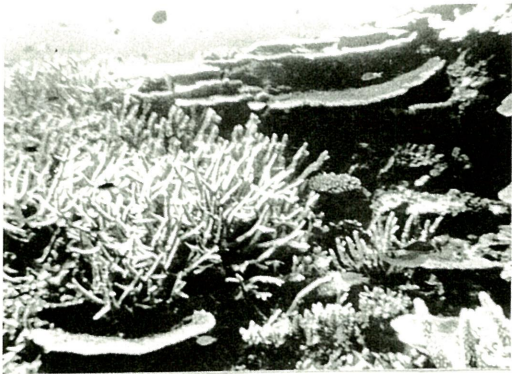




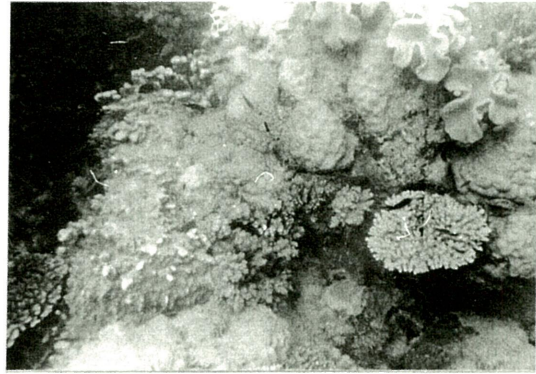
a. Assemblage G.



b. Assemblage I, *Millepora* colonies.



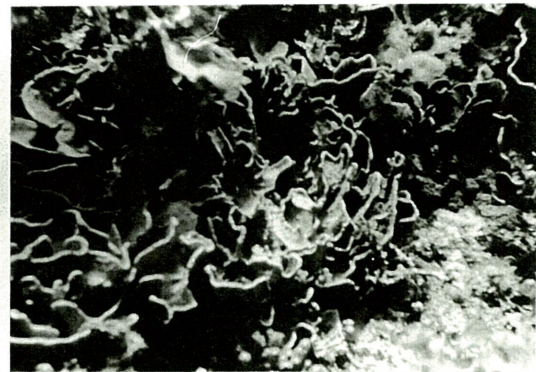
c. Assemblage J, fast growing corals.



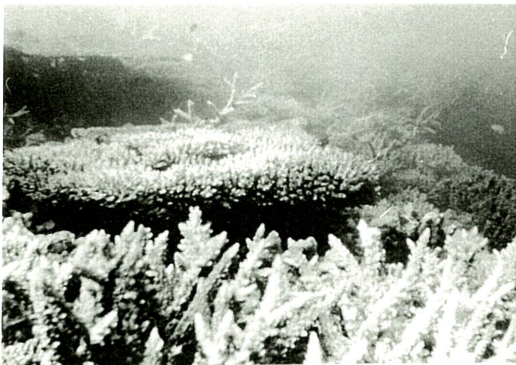
d. Assemblage K, transient assemblage.



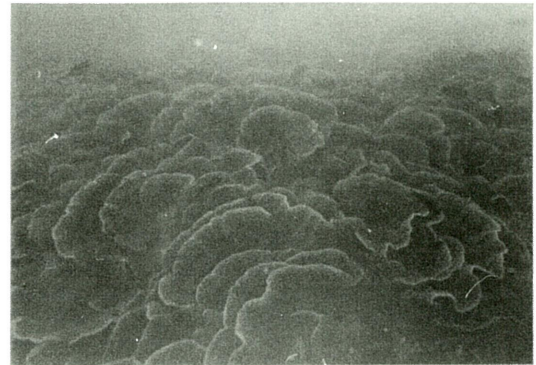
e. Assemblage L, reef flat *Goniastrea*.



f. Assemblage L, *Carteriospongia*.



g. Assemblage N, Scawfell Island *Acropora*.



h. Assemblage P, deep water *Agariciids*.

Figure 6 Assemblage groups defined in Table 5.

In contrast, the Whitsunday reefs supported significantly ($p = 0.016$) more massive colonies than the Northumberland reefs (Faviidae, Poritidae, Agariciidae, *Galaxea* spp., Mussidae, *Pectinia* spp., Siderastreidae, Caryophylliidae [excluding *Echinopora lamellosa*, *Porites cylindrica*, *Porites nigrescens*, *Pavona cactus*, *Hydnophora rigida*, *Echinophyllia* spp. and *Oxypora* spp.]). The abundance of small colonies (1-10cm and 11-50cm) was considerably greater on Whitsunday reefs (Figure 7c). The Whitsunday reefs also supported significantly ($p = 0.026$) more arborescent corals than the Northumberland reefs (*Acropora* spp., *Porites cylindrica*, *Porites nigrescens*, *Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*, *Palauastrea ramosa*, *Millepora tenella*). Colony abundance was greater for all size classes, especially colonies between 11-50cm (Figure 7d). The abundance of alcyonacean corals did not significantly differ between the two regions ($p = 0.218$), although colony size varied between regions. The abundance of small corals (1-10 cm) was considerably greater on Whitsunday reefs.

DISCUSSION

Regional variation

This study suggests that the composition and dominance of benthic assemblages on fringing reefs varies considerably between regions. Reefs in the Whitsunday Islands were large and diverse, both inshore and offshore. *Porites* spp. and faviids were the dominant corals, colonies were often larger than 2m diameter. Inshore reefs in the Cumberland Islands were narrow, with low coral diversity and abundant macrophytes. Offshore islands supported large reefs with complex coral assemblages. Acroporidae and Pocilloporidae were most prolific. Northumberland reefs were small and restricted to windward slopes. *Montipora*, *Turbinaria* species and macrophyte (Phaeophyta) assemblages were most common. Few coral species occupied the macroalgae understorey (faviids, small *Porites* spp., *Montipora* spp. and occasionally *Acropora* spp.), presumably due to consistently low light levels and abrasion. Further south, around the Keppel Islands, extensive reef flats were evident, and *Acropora* spp. dominated. These contemporary findings are consistent with results from the geological drilling programme, which show considerable geographic variation in reef composition (Kleypas 1992).

Community theory

Coral distribution patterns are consistent with theoretical concepts described by MacArthur and Wilson (1967) and Gauch and Whittaker (1972), where abundance is a construct of major and minor genera (and families) varying as a consequence of regional circumstances. Major scleractinian groups are *Acropora* spp., *Montipora* spp., poritids, faviids, pocilloporids, dendrophylliids and agariciids. Minor groups include merulinids, oculinids, pectiniids, mussids, fungiids, and caryophylliids.

Distribution patterns have also been defined across the central Great Barrier Reef (GBR) for scleractinian corals (Done 1982) and alcyonacean corals (Dinesen 1983). Done described four assemblage types from two inshore reefs. Many assemblages described on mid-shelf reefs in the central GBR were similar to those described here (assemblage D, E, H, J, K). Done's study, which incidentally covered the same geographic area as the present study, 6000km², suggested that as most corals broadcast their gametes, potentially they allow their distribution range to be extended, cross shelf isolation and larval availability was the process driving cross-shelf variability. This may be correct for patterns across the Great Barrier Reef, however, along the Great Barrier Reef favourable

Figure 7. Comparison between the Whitsunday and Northumberland reefs. A. Total coral abundance and size structure (Error bars are 1 standard deviation). B. Abundance and size of fast-growing corals. C. Abundance and size of massive corals.

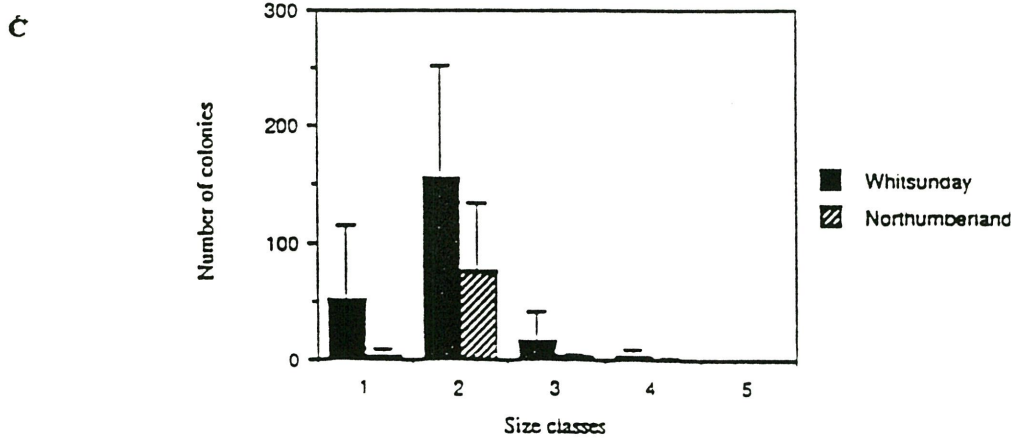
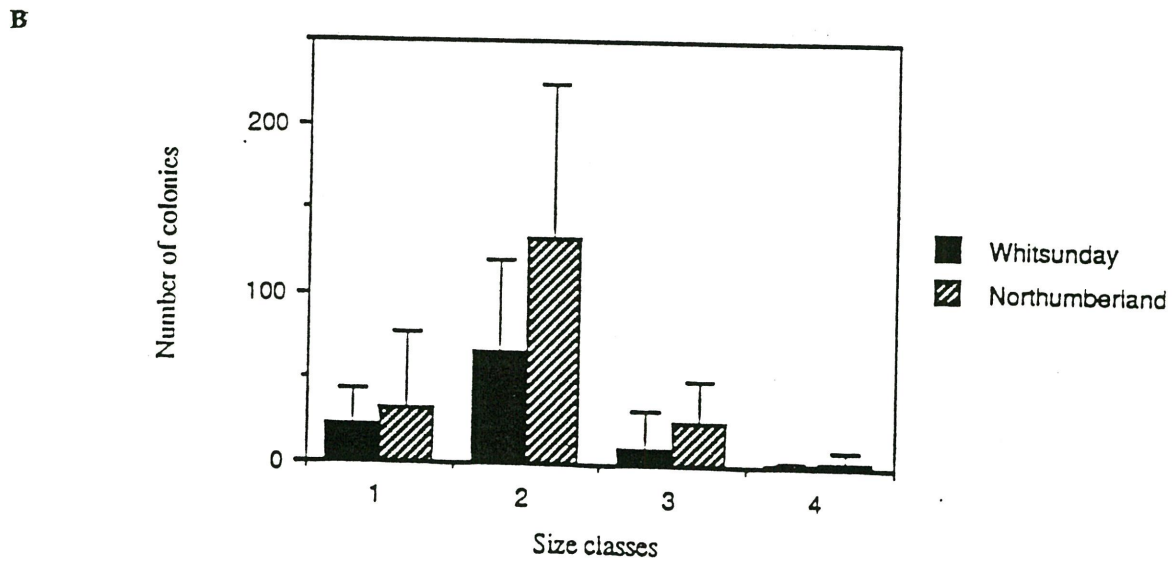
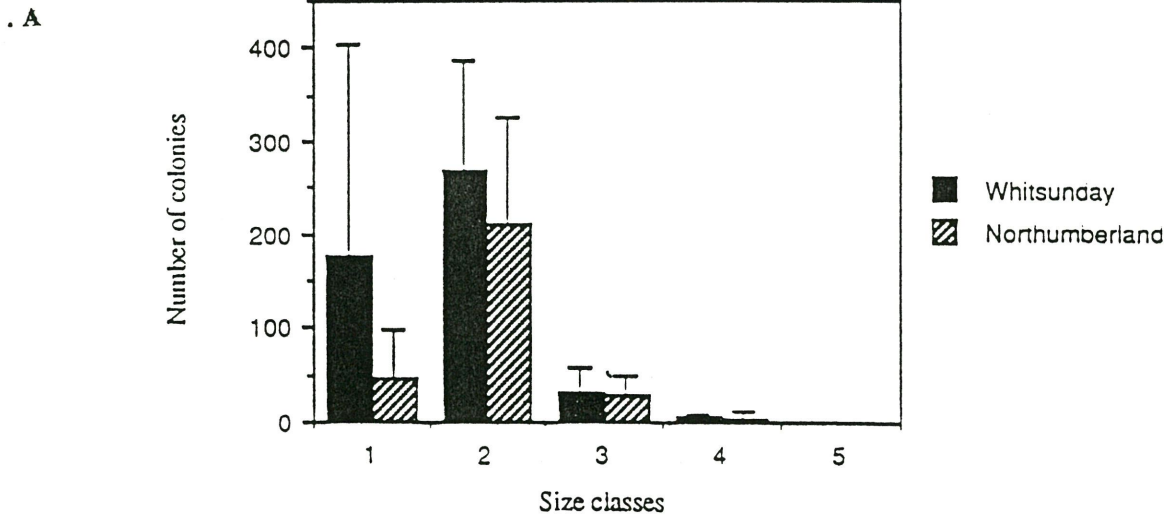
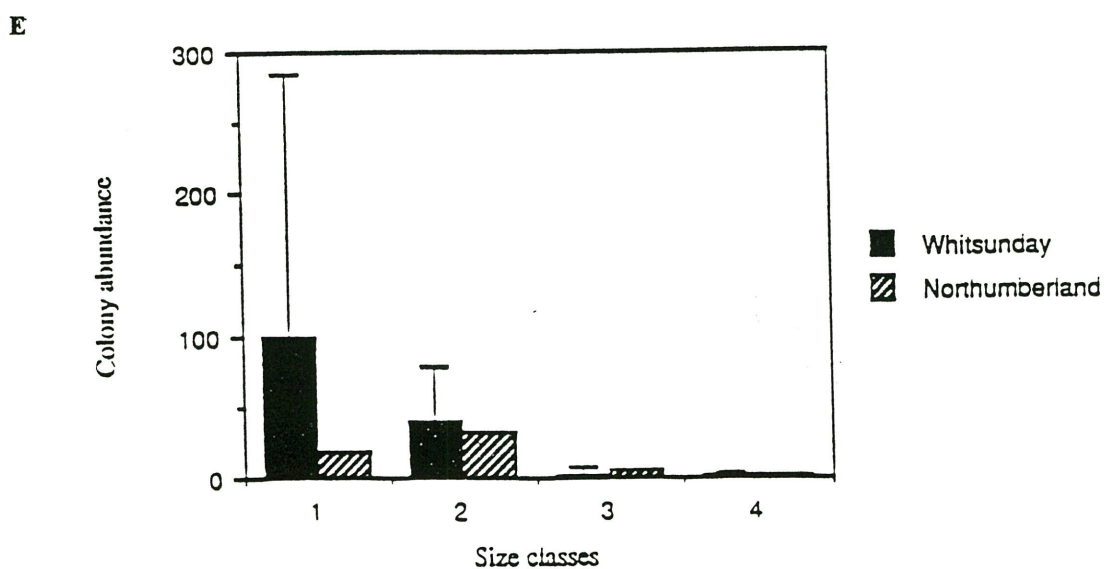
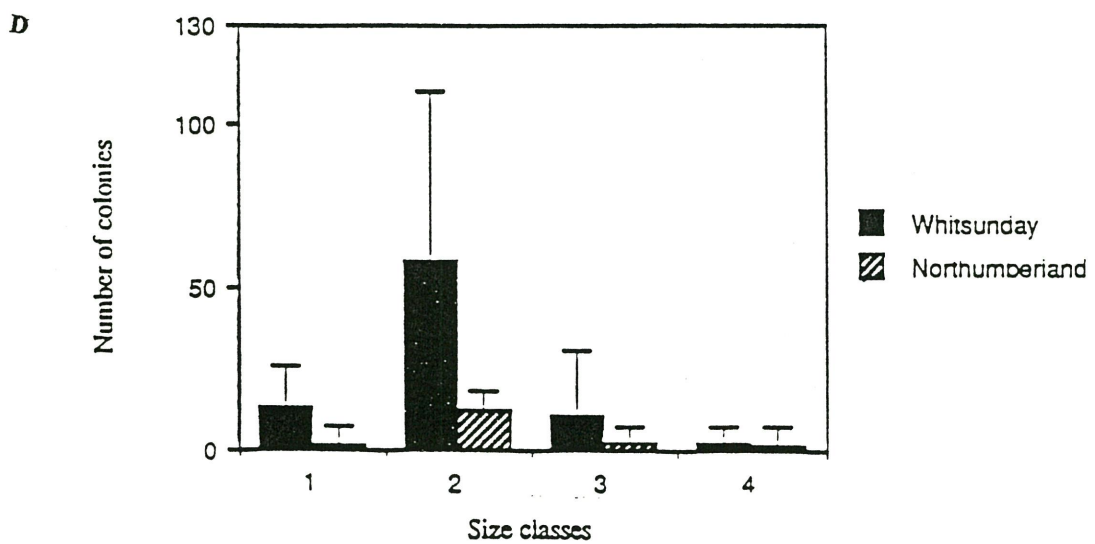


Figure 7. continued. Comparison between Whitsunday and Northumberland reefs. D. Abundance and size of arboresecent corals. E. Abundance and size of soft corals.



connectivity has been reported (Bode and Stark 1983; Dight *et al* 1988). Since distribution patterns vary considerably along the inshore region, a scenario which Done refuted may be more appropriate in explaining the distribution patterns observed along fringing reefs in the southern GBR "The larval pool is thoroughly mixed and recruits to a given reef include many species not represented as adults. Differences between reefs are determined by a differential post-settlement survival in favour of species already present" (Done 1982). Whether the patterns are determined by pre or post-settlement selection is unclear.

Colony abundance and morphology

A comparison of coral abundance, coral morphology and size on reefs in the Whitsunday and Northumberland Islands showed that although overall abundance did not significantly vary, significant morphological differences were evident. Major framework builders, massive and branching corals, dominated reefs between 20°S and 21°S. They significantly declined at 21°S (especially massive *Porites* spp., *Acropora formosa*, *Acropora nobilis*, *Porites cylindrica* and *Millepora tenella*). Their decline is not constrained by latitude as these corals were observed on the Keppel Island reefs and the Capricorn Bunker reefs (further offshore 23°S). Fast growing, encrusting and plate-like corals were dominant in the Northumberland Islands. Even the normally massive *Porites* spp. were encrusting. Many other caespitose colonies had tightly packed branches. Regional changes in morphology are likely to be a response towards maximising available light.

Thickets of *Millepora tenella* and *Porites cylindrica* were rarely recorded on the slopes of Northumberland reefs. Large monospecific stands of *Acropora* spp. (*A. formosa*, *A. nobilis*, *A. grandis*) were also relatively scarce, except on Prudhoe Island which is located in the northern extreme of the island group. However, *Acropora* spp. dominated the Keppel Island reefs and *Porites cylindrica* and *Millepora tenella* have been observed further south in the Capricorn Bunker group of reefs (23°35'S) (pers. obs.). Their decline, therefore, is not a direct restriction of latitude.

These findings do not suggest that *Acropora* spp. are absent on Northumberland reefs, as many caespitose and tabular acroporids (*A. valida*, *A. divaricata*, *A. cerealis*, *A. carduus*, *A. latistella*, *A. cytherea* and *A. clathrata*) were found on Curlew and Digby Island. It suggests a definite lack of massive *Porites* spp. and large monospecific stands of *Acropora* spp., the major framework builders of the Great Barrier Reef. Total reef accretion may be markedly reduced through the absence of these corals.

The two regions supported coral colonies of considerably different size structure. Colonies were generally between 11-50cm in the Northumberland Islands, however size was more variable in the Whitsunday Islands. An absence of small and large colonies may signify low recruitment rates, high post-settlement mortality and/or restricted growth (or a combination of these). Such a phenomena may be a consequence of environmental conditioning where the Northumberland reefs are under more stress. Indeed, suppressed coral recruitment has previously been recorded on inshore reefs when compared with mid-shelf reefs (Sammarco 1992).

Reef growth

Fast growing, opportunistic corals were significantly more abundant on Northumberland reefs. Assemblages were dominated by *Montipora* spp., *Turbinaria* spp., pocilloporids, *Sinularia* spp., *Briareum* spp., *Lobophytum* spp. and caespitose *Acropora* spp. Opportunism often leads to ephemeral assemblages. Transient assemblages and high colony turnover may extend to transient reefs, as suggested by the dead Holocene reef on Marble Island (22°S) (Kleypas pers. comm.). Slopes may have supported major framework builders through the Holocene however their vulnerability to episodic disturbance (Van Woesik 1992) in combination with stressful regional conditions allowed only temporary reef colonization. Geological evidence further indicates that a 4,000 year delay in reef initiation was evident at Middle Percy Island (21°40'S) (Kleypas 1992). The adverse conditions in the Northumberland Islands may have caused a time-delay in reef initiation. The region still appears to be a stressful environment for coral growth judging by the transient nature of the contemporary assemblages and growth forms adapted to low light conditions.

High concentrations of suspended sediment (up-to 89mg/l⁻¹) were consistently detected 75-100km from Broad Sound which impinged on the Northumberland Islands, bi-monthly during spring tides. These observations were made by Kleypas (1992) via NOAA AVHRR satellite imagery. Channel 1 reflectance values correlated strongly with suspended sediment concentrations. High turbidity has been shown to restrict coral growth because of sub-optimal light conditions and as a partial function of calcification efficiency (Cortes and Risk 1985; Barnes and Taylor 1973). Consistently high turbidity may induce changes in coral morphology. Many corals which are normally open caespitose and plate-like, such as *Pocillopora damicornis* and *Turbinaria reniformis*, had tightly packed branches and were columnar (respectively) on Northumberland reefs. The areal exposure of the zooxanthellate polyp is increased by adopting such growth forms. Hubbard and Scaturo (1985), reported a similar phenomena in highly turbid environments, and also indicated that such adaptations maximise light and minimise sediment build-up.

This project examined why fringing reef development was poor around 21°S. The Northumberland reefs supported few framework builders. Encrusting and plate-like corals were more adapted to the regional conditions. However encrusting growth forms do not contribute overly to reef development. Restricted coral growth and reef initiation appears to have limited carbonate accretion in the Northumberland Islands through the Holocene period.

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SECTION 2.

Environmental Gradients

INTRODUCTION

Some environmental factors, for example salinity, temperature and nutrient loading cause a measurable physiological response in a coral colony and can influence its spatial distribution (Yonge and Nicholls 1930). Others, such as water depth, have no direct effect on corals. Rather the consequences of depth (attenuation of ambient light and wave exposure) substantially influence the vertical distribution of coral types (Bradbury and Young 1981; Dustan 1982). The primary objective of this section was to compare sites with similar composition and abundance and assess whether distribution patterns are reflected in the environmental gradients. The gradients assessed were depth, exposure, (local and regional) location, tidal amplitude, distance from mainland, distance from the nearest river and shelf depth.

It is evident that the study region has some anomalous characteristics and supports coral assemblages along several macroscale gradients (see section 1). The geological foundation of reefs in the Northumberland region is considerably different from all other areas drilled on the Great Barrier Reef, because their initiation was delayed some 4000 years (Kleypas 1992). Tidal amplitudes (10m) are higher than anywhere else on the Great Barrier Reef and a considerable variation in the distribution of continental islands along other environmental gradients (proximity to three river systems, distance of sites from the mainland and shelf depth) provides an ideal study area for comparative analyses on reef assemblages. Whether benthic assemblages reflect environmental gradients is investigated using direct gradient analysis techniques.

METHODS

Field methods

One hundred and twenty-five study sites were examined on thirty four continental islands (as in section 1). Sites measured 20m by 10m. Surveys were conducted on SCUBA. The size and identity of all the scleractinian and alcyonacean corals were recorded. Each coral colony was allocated to one of four size classes based on maximum diameter: A 1-50cm; B 51-100cm; C 101-300cm; D > 301cm.

Environmental variables

In order to determine whether coral distribution patterns are reflected along macroscale gradients (10's of kms), the following information was recorded for each site: distance to mainland; distance to nearest river; annual mean tidal range; shelf depth; depth (relative to Low Water Datum, LWD); region of study. Each island was also allocated a number for comparative analyses and each site was categorised as either 0 or 1, based on whether the site was sheltered by a bayhead or not. This was termed an exposure index.

Analytical techniques

Analytical approach

Both ordination (Whittaker 1967) and clustering techniques (Clifford and Stevenson 1975) have been used extensively to describe distribution patterns in nature. They distinguish differences between sites and assist in narrowing down the number of variables that might be determining distribution patterns. However, the influence of specific environmental parameters is difficult to test directly. Problems can be envisaged using these techniques in isolation, since a lack of understanding or stratification of the environment under investigation may lead to the masking of any patterns that may exist and erroneous environmental gradients may be identified if indirect gradient analyses are used in isolation (Austin 1985).

Canonical Correspondence Analysis (Ter Braak (1986), is a direct gradient analysis procedure. It is a combination of an ordination and a multiple regression. It extracts the dominant pattern of variation in community composition from the species data. It then attempts to relate the first few ordination axes with the environmental variables. As a result the ordination axes appear in order of explained variance by linear combinations of environmental variables. The resultant species response curves are unimodal with centroids identifying the optimum of the curve. These are displayed in relation to the ordination axes (eigenvalues).

The significance of eigenvalues can be tested via Monte Carlo permutation tests. If only one environmental gradient is tested at any one time, via a partial Canonical Correspondence Analysis (defining other gradients as covariables), then a significance test on the eigenvalue will be similar to a significance test on the correlation between the environmental gradient and species distribution and abundance patterns (centroids).

The Monte Carlo test is based on the principles of permutation and randomisation (Hope 1968). It uses the similarity matrix to test the significance of the canonical axes (eigenvalues). This test gives rise to a random data set within the confines of the estimated correlation matrix. It randomly permutes a link between the species data and the environmental data. For each random dataset an eigenvalue is calculated. The number of random permutations was restricted to 99 for all these analyses.

There is no reason why species response curves cannot take another form to that of a unimodal curve. Indeed, Greig-Smith (1983) discussed the concept that species response curves may not necessarily be symmetrical and Austin and Smith (1989) and Minchin (1989) recently argued that these (unimodal) types of models lack a sound biological basis and are not representative of physiological response patterns. They add that realistically most response patterns are skewed for populations measured.

Logarithmic transformations and standardising may remove that skewness (Okland 1986). However, one will be testing the median values as opposed to the mean values of the population (LaBarbera 1986). If there is a response of a population along an environmental gradient the response of the population mean is most valuable, not the median value. For this reason species abundances were not transformed and a unimodal response model is assumed around the mean. Notably, such an argument would be invalid for parametric analyses.

The usefulness of any model, in practice, relies on the robustness against violations of the model conditions. The robustness of correspondence analysis has been tried and tested extensively and found to be considerably robust (Hill and Gauch 1980; Ter Braak 1985). The analyses can test variables directly and falsify any inappropriate or non-correlating parameters thereby allowing a more definitive exploration of nature.

Data analysis

Species data were directly compared with environmental variables using the multivariate packages ECOPAK (Minchin 1986) and CANOCO (Ter Braak 1987). Environmental variables were standardised by dividing by the standard deviation. Standardisation was considered essential since the environmental variables were measured at a number of scales (eg. tide 1-5, depth 1-3, Table 2.1)). These manipulations gave the variables equal weight in the analyses. Analyses were undertaken on matrices containing both hard and soft corals, and on independent matrices for hard and soft corals.

In order to objectively test environmental variables which have a significant correlation with the biological assemblages a series of partial Canonical Correspondence Analyses (Ter Braak 1988) were undertaken. Testing was performed in an iterative manner. Firstly, one variable was tested, for example depth, against the species dataset. The first canonical axis derived from this analysis was then tested for variation from random via a Monte Carlo permutation test. If found significant it was defined as a covariable, to regress out its effect, and used in combination with the following variables to test their significance. This process was repeated for all eight variables. All significant variables were then utilised within a full Canonical Correspondence Analysis.

Analyses produced canonical coefficients which express the degree of change in community composition per unit change in an environmental variable (or a suite of environmental variables simultaneously). These correlations are linear combinations of environmental variables where all variables are held constant. However the analyses also produced intraset coefficients, which are correlation coefficients between environmental parameters and the ordination axis produced when the environmental variables are assumed to covary. Canonical coefficients and intraset coefficients give the same information only in the special case when environmental variables are mutually uncorrelated. The later coefficients however do not suffer from multi-colinearity problems when variables are related (Ter Braak 1986), therefore interpretation focused on these coefficients.

Table 2.1. Regional location of islands surveyed and three environmental variables; extent of tidal fluctuation, distance from mainland (km) and distance from nearest river (km). Each island was allocated a number between 1 and 5, in accordance with mean tidal amplitude, where - 1 is 3-4m, 2 is 4-5m, 3 is 5-6m, 4 is 6-7m and 5 is 7-8m (data derived from Queensland Official Tide Tables, 1990, Department of Harbours and Marine).

ISLAND	REGION	TIDE	DIST.MAIN	DIST.RIVER
Hayman	Northern Whitsunday	1	24km	80km
Langford	Northern Whitsunday	2	22km	76km
Hook	Northern Whitsunday	2	15km	71km
Molle	Inner Whitsunday	2	3km	55km
Daydream	Inner Whitsunday	2	3km	57km
Shute	Inner Whitsunday	2	0.5km	53km
Long	Inner Whitsunday	4	1km	45km
Pine	Inner Whitsunday	4	5km	43km
Whitsunday	Central Whitsunday	2	15km	55km
Hamilton	Central Whitsunday	2	12km	50km
Thomas	Cumberland	3	18km	40km
Goldsmith	Cumberland	3	35km	49km
Carlisle	Cumberland	3	28km	40km
Brampton	Cumberland	3	25km	36km
Cockermouth	Cumberland	3	40km	46km
Scawfell	Cumberland	3	45km	52km
Penrith	Outer Northumberland	3	74km	80km
Prudhoe	Northumberland	4	42km	56km
Curlew	Northumberland	5	40km	80km
Digby	Northumberland	5	48km	90km
N.Percy	Northumberland	4	64km	88km
S.Percy	Northumberland	4	48km	74km
Keppel	Keppel	2	14km	30km

Table 2.4. Results of Monte Carlo test on the eigenvalues derived from a series of partial Canonical Correspondence Analyses using the species-genus data (for both scleractinia and alcyonaria) and eight environmental variables.

Depth	Unique	Region	Tide	D.main	D.river	Sh.dep.	Expo
0.03	0.26	0.29	0.09	0.02	0.42	0.18	0.04
*	ns	ns	ns	*	ns	ns	*

Table 2.5. Results of Monte Carlo eigenvalue tests from a series of partial Canonical Correspondence Analyses using the species-genus data (for both scleractinia and alcyonaria corals), colony size and eight environmental variables.

Depth	Unique	Region	Tide	D.main	D.river	Sh.dep	Expo
0.05	0.05	0.24	0.03	0.02	0.31	0.10	0.03
*	*	ns	*	*	ns	ns	*

Table 2.6. Canonical Correspondence Analysis using the species-genus dataset, for both scleractinian and alcyonacean corals. Size classes were amalgamated.

Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.280	0.110	0.051
Correlation Coefficient	0.856	0.624	0.656
			0.000

Variable	Canonical Coefficient		Intraset Correlation Coefficient	
	Axis 1	Axis 2	Axis 1	Axis 2
Depth	-0.276	0.088	-0.759*	-0.153
Mainland	0.432	0.077	0.722*	0.157
Exposure	0.191	-0.332	0.322	-0.576*

Vertical distribution

Throughout the study area most scleractinian corals were found in distinct habitats, ie. had a negative correlation with depth (Table 2.6 and 2.7). Recurring species were observed in four general zones: 1 the shallow macroalgae zone on inshore islands and the faviid, *Acropora* spp. zone on outer islands; 2 the reef crest zone which is composed of large monospecific colonies; 3 the diverse upper slope classified as the *Acropora* spp./mussid zone.; 4 the pectiniid/agariciid zone on the lower slopes. However, reef crests were absent on Northumberland Island reefs (Curlew and Digby Islands).

Table 2.7 Canonical Correspondence Analysis on species-genus data and environmental variables, for scleractinian (hard) corals only.

	Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.207	0.08	0.062	0.457
Correlation Coefficient	0.764	0.608	0.521	0.000
Variable	Canonical Coefficient		Intraset Correlation Coefficient	
	Axis 1	Axis 2	Axis 1	Axis 2
Depth	-0.277	0.255	-0.685*	0.704
Mainland	0.360	0.190	-0.890*	0.526
Exposure	-0.127	-0.065	-0.320	-0.184

Table 2.8. Canonical Correspondence Analysis of species-genus data and environmental variables, for alcyonacean (soft) corals only.

	Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.374	0.065	0.029	0.488
Correlation Coefficient	0.786	0.427	0.336	0.000
Variable	Canonical Coefficient		Intraset Correlation Coefficient	
	Axis 1	Axis 2	Axis 1	Axis 2
Depth	-0.310	-0.118	-0.482	-0.200
Mainland	0.403	0.084	0.629*	0.143
Exposure	0.397	-0.230	0.677*	-0.428

Macroalgae was a major influence on the reef flat and crest communities on inshore islands, restricting coral growth. Reef flat assemblages were generally composed of *Montipora* spp., *Turbinaria* spp., *Porites* spp., *Pavona varians*, and several *Acropora millepora* and *Acropora valida*. Reef crests were often supported only a small number of species which formed large monospecific stands, especially massive *Porites* spp., *Acropora* spp. and *Sinularia* spp.. This zone extends to some 3m (LWD). The upper slope generally supported the highest diversity of corals. Below 6-10m, light levels are highly attenuated and slopes support mainly cryptic pectiniid, agariciid and caryophylliid corals.

Soft corals were evenly dispersed with depth (Table 2.8) although Nephthiid type corals (*Nephthea* spp., *Dendronephthaea* spp. and *Stereonephthaea* spp.) were mainly found on deep slopes. *Anthelia* spp. and *Efflatourmaria* spp. were generally found at mid depth (0-3m). *Alcyonium* spp. were also most common on mid-slopes, on sandy substrate, adjacent to large *Porites* spp. colonies. *Sinularia* spp. and *Lobophytum* spp. were most common on shallow slopes and crests.

Table 2.9. Vertical distribution of scleractinian species.

<p>SHALLOW HABITAT > 0m LWD. <i>Goniastrea</i> spp., <i>Leptastrea</i> spp. <i>Porites</i> 'encrusting', <i>Acropora millepora</i>, <i>Acropora aspera</i>, <i>Astreopora</i> spp., <i>Coscinaraea</i> spp., <i>Pavona varians</i>.</p>
<p>0 - 3m LWD. <i>Platygyra</i> spp., <i>Plesiastrea versipora</i>, <i>Lobophyllia</i> spp., <i>Porites cylindrica</i>, <i>Porites</i> 'massive', <i>Porites annae</i>, <i>Alveopora</i> spp., <i>Goniopora</i> spp., <i>Acropora</i> 'tabulate', <i>Acropora formosa</i>, <i>Pocillopora damicornis</i>, <i>Seriatopora</i> spp., <i>Stylophora pistillata</i>, <i>Herpetoglossa simplex</i>, <i>Fungia</i> spp., <i>Polyphyllia talpina</i>, <i>Herpolitha limax</i>, <i>Plerogyra sinuosa</i>, <i>Cynarina lacrymalis</i>, <i>Pachyseris rugosa</i>, <i>Palauastrea ramosa</i>, <i>Duccanopsammia axifuga</i>, <i>Catalaphyllia jardinei</i>, <i>Clavarina triangularis</i>, (hydrocoral) <i>Millepora tenella</i>.</p>
<p>> 3m LWD. <i>Echinopora</i> spp., <i>Caulastrea</i> spp., <i>Diploastrea heliopora</i>, <i>Leptoria phrygia</i>, <i>Moseleya latistellata</i>, <i>Oxypora</i> spp., <i>Pachyseris speciosa</i>, <i>Pavona cactus</i>, <i>Leptoseris</i> spp., , <i>Echinophyllia</i> spp., <i>Euphyllia</i> spp., <i>Pectinia</i> spp., <i>Podabacia crustacea</i>, <i>Merulina ampliata</i>, <i>Acanthastrea</i> spp., <i>Archelia horrescens</i>, <i>Sandalolitha robusta</i>, <i>Physogyra lichtensteini</i>, <i>Scolymia</i> spp., <i>Pseudosiderastrea tayamai</i>.</p>
<p>ALL DEPTHS. <i>Favites</i> spp., <i>Favia</i> spp., <i>Oulophyllia crispa</i>, <i>Cyphastrea</i> spp., <i>Acropora palifera</i>, <i>Acropora valida</i>, <i>Symphyllia</i> spp., <i>Galaxea</i> spp., <i>Mycedium elephantotus</i>, <i>Hydnophora</i> spp., <i>Montipora</i> spp., <i>Turbinaria</i> spp., <i>Heliofungia actiniformis</i>.</p>

Distance from the mainland

Distance from mainland was highly correlated with coral distribution patterns (Table 2.4, 2.5 and 2.6). Few scleractinian species were restricted to offshore locations, although abundance of *Acropora* spp. increased considerably. Some species were more prolific nearshore: *Goniastrea* spp., *Cyphastrea* spp., *Leptastrea* spp., *Diploastrea heliopora*, *Moseleya latistellata*, *Pseudosiderastrea tayamai*, *Astreopora* spp., *Herpolitha limax*, *Polyphyllia talpina*, *Alveopora* spp., *Goniopora* spp., *Podabacia crustacea*, *Porites cylindrica*, *Catalaphyllia jardinei*, *Palauastrea ramosa*, *Seriatopora hystrix*, *Clavarina triangularis* (rare), *Turbinaria* spp., *Plerogyra sinuosa*. Alcyonacean corals were more irregularly distributed although *Alcyonium* spp., was most common nearshore and *Efflatournaria* sp. were restricted to offshore locations.

Exposure

Degree of exposure was consistently correlated with benthic composition although more strongly weighted toward soft than hard corals (cf. Table 2.7 and 2.8). At exposed sites predominant species were fast growing corals with opportunistic life-history strategies (after Jackson and Hughes 1985): *Acropora humilis*, *Porites cylindrica*, *Porites annae*, *Stylophora pistillata*, *Pocillopora damicornis*, *Seriatopora hystrix*, (hydrocoral) *Millepora tenella*, *Acropora* 'tabulate', and the soft corals *Simularia* spp., *Efflatournaria* sp., *Alcyonium* spp.

Colony size and environmental gradients

Based on species components, similar sites were grouped independent of location *per se.*, and distribution patterns correlated with depth, exposure and distance from mainland. However, once colony size was included, there were some contrasting features:

1. tidal range became an important variate in addition to distance from the mainland, depth and exposure;
2. adjacent sites tend to be more closely clumped together (within the 2-Dimensional configuration), indicating similarities in not only faunistic composition but also in size structure of the coral colonies.

Ordinations based solely on faunistic composition reflect only major environmental gradients. However, analyses incorporating size have a strong location effect whereby neighbouring sites group together (Figure 2.1). Notably, intraset correlations were low when hard and soft corals were combined (Table 2.10), however the 'tide' and 'unique' variables (distinguishing tidal amplitude and location effect, respectively) were high for analysis on hard corals alone (Table 2.11).

The Northumberland Islands (groups A, B, E, Figure 2.1) and Pine Island (group C) were closely associated. Pine Island lies in the direct vicinity of the Proserpine/O'Connell river discharge, and had similar assemblages as Percy and Curlew Island. The slopes supported numerous small *Montipora* spp. and *Turbinaria* spp. colonies. This result suggests that extreme tidal conditions and river discharge have a similar influence on the settlement, survival and/or growth potential of coral species.

Colony size tended to increase north of the Northumberland Islands. In fact sites at the top of Figure 2.1 supported mainly small colonies, with abundance of large colonies increasing towards the bottom of the figure. The inner Cumberland Islands (group F,G,H and K) supported larger colonies, especially *Montipora* spp.. Groups M and N were located on the reef flat of Penrith and south Percy Island respectively. Growth is normally suppressed in these habitats, supporting only small faviids, encrusting *Porites* spp. and some Carteriosponges. Scawfell Island (group I), Keppel Islands (group J), and the southern slopes of Hamilton Island (group L) supported large monospecific stands of arborescent *Acropora* spp., whereas large *Porites* spp. dominated the northern Whitsunday Islands (group O and P).

Table 2.10. Full Canonical Correspondence Analysis on species-genus data and colony size, for both scleractinian (hard) and alcyonacean (soft) corals.

	Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.320	0.311	0.148	0.100
Correlation Coefficient	0.899	0.862	0.729	0.681

Variable	Canonical Coefficient		Intraset Correlation Coefficient	
	Axis 1	Axis 2	Axis 1	Axis 2
Depth	-0.158	0.141	-0.041	-0.031
Unique	0.296	0.008	0.075	0.002
Tide	-0.479	0.510	-0.130	0.116
Mainland	0.458	0.087	0.121	0.019
Exposure	0.054	0.183	0.017	0.049

Figure 2.1. Schematic representation of all 125 sites positioned in terms of similarity in composition and abundance of hard and soft corals. Environmental variables are displayed as vectors. The angle of each vector was the greatest variance explained by the environmental variable juxtaposed on species responses to that variable. Vectors with long axes were most correlated with biological composition.

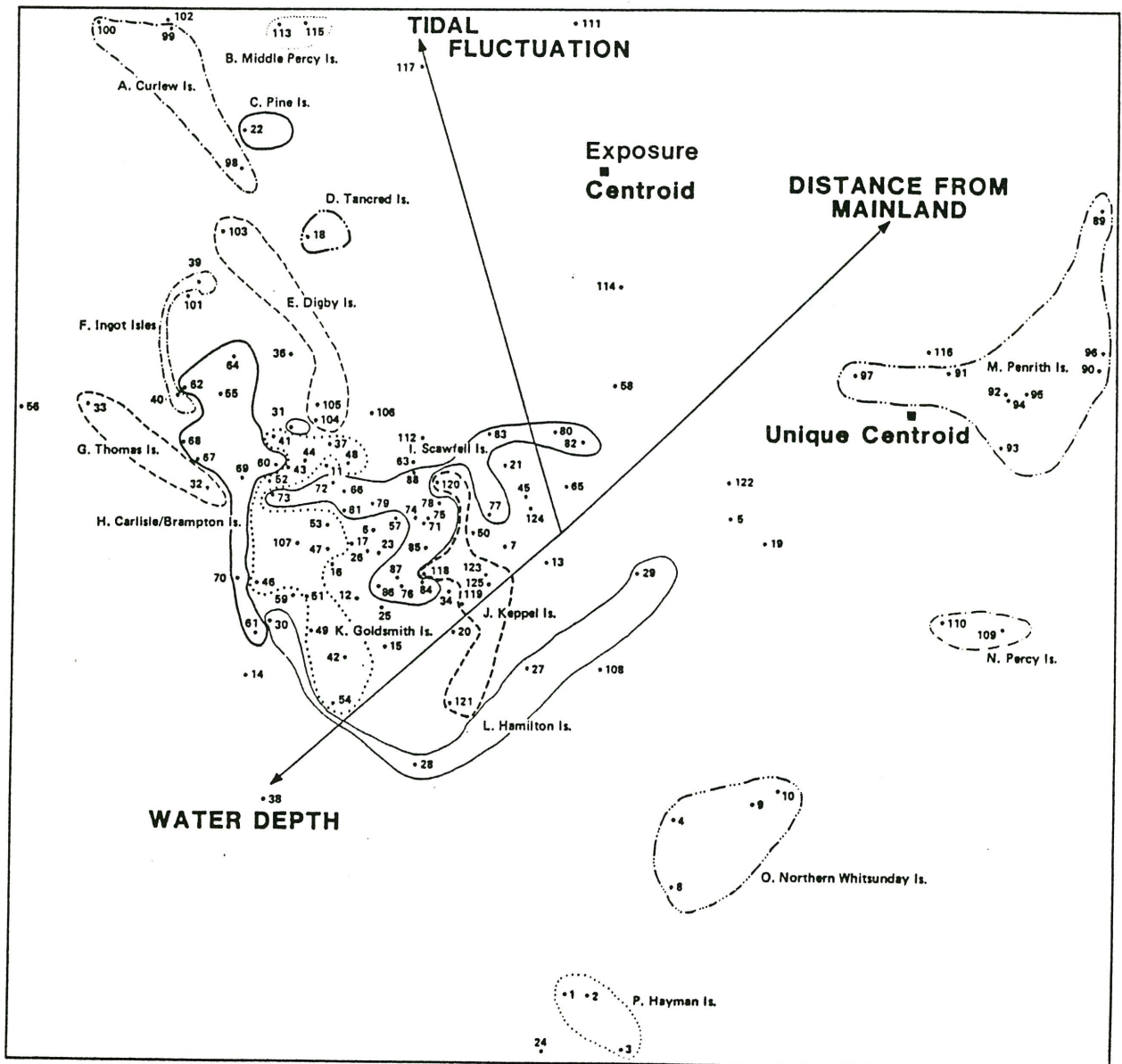


Table 2.11. Canonical Correspondence Analysis undertaken on species-genus data and colony size for scleractinian (hard) corals only.

		Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.259	0.221	0.126	0.088	
Correlation Coefficient	0.849	0.758	0.739	0.730	
Variable		Canonical Coefficient		Intraset Correlation Coefficient	
		Axis 1	Axis 2	Axis 1	Axis 2
Depth		-0.233	-0.082	-0.582	-0.163
Unique		-0.250	-0.005	0.631*	-0.011
Tide		-0.359	0.459	-0.877*	0.930*
Mainland		0.376	0.091	0.932*	0.181
Exposure		-0.110	0.016	-0.317	-0.037

Table 2.12. Canonical Correspondence Analysis undertaken on species-genus data and colony size for alcyonacean (soft) corals only.

		Axis 1	Axis 2	Axis 3	Axis 4
CCA Eigenvalue	0.460	0.300	0.156	0.088	
Correlation Coefficient	0.861	0.796	0.708	0.559	
Variable		Canonical Coefficient		Intraset Correlation Coefficient	
		Axis 1	Axis 2	Axis 1	Axis 2
Depth		0.231	0.147	-0.427	0.452
Unique		-0.049	-0.304	0.298	-0.629*
Tide		0.643	0.503	-0.775*	0.214
Mainland		0.066	-0.364	0.479	-0.392
Exposure		0.349	-0.120	0.517	-0.108

DISCUSSION

The distribution and abundance of corals were significantly correlated with depth. Descriptions on zonation are prevalent in the literature (Wells 1954; Geister 1977; Chappell 1980). Done (1983), described zonation as "not due to environmental variability *per se* but to its stratification on the reef's surface (ie. environmental zonation)". Similarly, Chappell (1980) defined zonation as a response to numerous stress gradients attenuating down the reef slope (wave action, subaerial exposure, and illumination). In this study vertical distribution patterns appeared to be largely a function of tolerance to aerial exposure and local light conditions.

Corals can tolerate aerial exposure for some time, although prolonged and frequent exposure is harmful. Coral settlement and growth may also be restricted by harmful ultra-violet light (Jokiel 1980). Faviids and *Porites* spp. appear most resilient to such conditions as they were most common on shallow slopes. Acroporids and mussids dominated mid slopes and agariciids and pectiniids the lower slopes.

Vertical distribution patterns may stem from responses very early in a corals life-history and may not be merely a consequence of post-settlement selection. Indeed, coral species appear phototactic at the pre-settlement stage (R. Babcock pers. comm.), and settle on environmental cues (Morse *et al* 1988). These adaptations ensure that optimal conditions are met very early in the life of a coral colony.

Exposure was also significantly correlated with species assemblages. The amount of water movement has often been regarded as a major determinant structuring coral assemblages (Bradbury and Young 1981; Done 1982, Sheppard 1982). In previous work, exposure was described as a wave-attenuating factor, and corals were distributed in accordance (Roberts *et al* 1974; Rosen 1975; Geister 1977; Dana 1979). However, in this study the protective influence of bayheads were significantly correlated with the distribution of coral assemblages. The incidence of fast growing opportunistic corals in exposed sites, especially alcyonacean corals appears to be a consequence of intermittent disturbance through lack of shelter by a headland.

Tidal amplitude also was highly correlated with coral composition and colony size. Semi-diurnal tidal fluctuations have a distinct latitudinal component along the Great Barrier Reef. To the south of Mackay the tides are the highest on the east coast of Australia, ranging to 10 meters in Broad Sound (22°S). Because of the dense nature and broad expanse of the outer reefs very little tidal movement is directed across the reefs (Flinders 1814). Most of the input of tidal energy is propagated through the Capricorn Channel to the south, and Hydrographers Passage to the north. Maximum tides in Broad Sound are a consequence of local resonance amplifying tidal range within these narrow passages (Middleton *et al* 1983).

Extreme tidal fluctuations enhance aerial exposure on low tide and reduce light conditions on high tide. More precisely, an increase in tidal range effectively raises the Mean High Water Spring (MHWS), and lowers the Mean Low Water Spring (MLWS) levels which normally regulate or restrict the vertical growth capacity of a reef. It is not the high tidal fluctuations alone which influence the corals, rather the consequences of the large fluctuations (10m) in the nearshore environment which cause high turbidity (Kleypas 1991).

Light decreases most rapidly in the first 3m of water (Dustan 1982), however an input of suspended sediments along shallow inshore environments exacerbates this limiting effect and appears to compress the euphotic zone. In the Northumberland Islands, reef crest assemblages were completely absent and corals found at depth (8-10m) on Whitsunday and Cumberland reefs were found at 3-4m on Northumberland reefs. This finding suggests a reduction in light transmission and a narrowing of the photic zone.

Reduction of the euphotic zone and the communities in these naturally stressed locations is of prime interest to managers. Deep sites are first to be effected by environmental degradation (T. Tomascik pers. comm.), and reefs start to decline from the "bottom up". Low light conditions, a consequence of high turbidity, can considerably suppress growth forms (section 1) and cause stress which may lead to mortality (Rogers 1979). Corals may not settle on deep slopes merely through their inability to compensate their photosynthetic rates (McCloskey *et al* 1978). The Northumberland reefs may support significantly less carbonate than other fringing reefs because of the high tidal fluctuations projecting a hemi-sphere of influence from Broad Sound, inducing high turbidity which indirectly affects coral growth.

The inshore area between 23°S and the 20°30'S has been reported as devoid of fine muds (< 1%) (Maxwell 1968). Shallow bathymetry and constant exposure to predominant winds prevents fine sediment from settling. As a consequence, fine muds remain in suspension producing consistently high turbidity (Kleypas 1991). The Whitsunday Islands act as a barrier. The migration of fine mud ceases in leeward embayments of the Whitsunday Islands. Any residual drift of fine sediments north of here is minimal (Maxwell 1968).

In conclusion, coral distribution and abundance patterns were reflected along several environmental gradients; tidal fluctuations, depth, exposure, and distance from the mainland. Similar sites were grouped independent of location, except in extreme habitats. However, once size was considered there was a strong location effect, that is neighbouring sites and sites on adjacent islands grouped. These findings suggest that regional conditions have a strong influence on species composition and growth form in this study region. A corollary of this is that coral/coral interactions may have minimal influence on macroscale distribution and abundance patterns, defining only small scale patterns and local variability.

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