

# Latitudinal variation in patterns of colonisation of cryptic calcareous marine organisms

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**ABSTRACT:** Few studies of fouling communities have directly compared colonisation patterns over wide geographical scales in similar community types. In this study, the recruitment and early growth of calcareous cryptic fouling organisms were examined on settlement panels at 2 tropical and 2 subtropical locations at varying distances from the mainland in eastern Australia. Species diversity and cover on the settlement panels after 6 mo were higher at the subtropical inshore site than at any of the offshore or tropical sites. Classification of the sites by multivariate cluster analysis and ordination showed clear distinctions between inshore and offshore sites, while sites separated by approximately 14° of latitude were less clearly distinguished. Inshore/offshore variation in the physical environment, especially turbidity and eutrophication, and the effects of longshore currents in the regions are possible explanations for these patterns. There was a significantly higher weight of calcified material at the subtropical inshore site than at the other 3 sites, attributable to higher cover of both bryozoans and barnacles; these taxa are likely to make a significant contribution to community calcification rates in subtropical coral communities. Competition for space with encrusting species is proposed as a potential mechanism limiting coral recruitment in coastal subtropical eastern Australia.

**KEY WORDS:** Settlement · Epibiota · Calcification · Fouling communities

## INTRODUCTION

Comparisons of species diversity and community ecology along latitudinal gradients have suffered from a lack of consistency in sampling methodology, and a paucity of studies comparing more than one site at each latitude (Schoener et al. 1978, Black & Prince 1983, Crossland 1988, Keough 1988, McGuinness 1990, Clarke 1992). Most studies employing settlement panels to examine patterns of recruitment and succession in cryptic fouling communities have been restricted to a single geographical location (reviewed in Schoener 1982). Since a variety of panel sizes, panel deployment patterns and analytical techniques have been used by various workers, evaluation of regional variation in these communities may be confounded by methodological variation (Jackson 1977a, Schoener et al. 1978, Harris & Irons 1982, Schoener 1982).

Habitat space for settlement of propagules is widely regarded as a limiting resource in many marine envi-

ronments (Dayton 1971, Jackson 1977a, Russ 1982, Connell & Keough 1985, Keough 1988) and the patterns of space occupation in the early successional stages may play a major role in determining community structure (Sutherland 1974). Discussions of what has recently been termed 'supply side ecology' (e.g. Underwood & Fairweather 1989) have re-emphasised the role of larval supply as a major factor in the development and maintenance of benthic communities (Keough 1988, Rodriguez et al. 1993). Studies of recruitment of propagules on fresh artificial settlement surfaces can show the range of sessile organisms that are available to settle, recruit and occupy space in the habitat (Schoener 1982). While artificial panels are unable to replicate the 3-dimensional structure of natural cryptic habitats (Ginsburg 1983, Gischler & Ginsburg 1996), they appear to be an effective way of examining small-scale, short-term processes of recruitment, with the term 'recruitment' used here to include the processes leading to settlement and metamorphosis of larvae and their survival until observation (Keough & Downes 1982, Rodriguez et al. 1993).

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Propagule availability at panel surfaces will be a function of several factors (Rodríguez et al. 1993), such as the location of breeding populations, the length of propagule life (Bingham 1992, Carlon & Olson 1993), the period of settlement competence and the hydrodynamic processes supplying propagules to a habitat, including recirculation (Black 1988, Sammarco & Andrews 1989, Sammarco et al. 1991). Biological influences such as predation of larvae may also operate in some circumstances (Young 1988) and the nature of the pre-existing biota (Benayahu & Loya 1984, Patzkowsky 1988) is frequently significant. Allelopathic interactions between space-occupying biota such as crustose coralline algae, soft corals and ascidians may accelerate (Sebens 1983, Standing et al. 1984) or inhibit (Breitburg 1984, Standing et al. 1984) recruitment or growth of cryptic organisms.

Recent studies on coral reefs have examined the timing and extent of early recruitment of coral spat, using natural substrata (Rylaarsdam 1983, Wallace 1985, Carleton & Sammarco 1987) and artificial settlement surfaces (van Moorsel 1988, Fisk & Harriott 1990, Smith 1992) at a variety of locations across the continental shelf (Sammarco 1983, Fisk & Harriott 1990) and at different latitudes (Harriott 1992, Harriott & Banks 1995). During investigations of coral recruitment at several tropical and subtropical sites (Fisk & Harriott 1990, Harriott 1992, Harriott & Banks 1995) it was observed that there were large differences in the abundance of cryptic encrusting calcareous organisms between sites, giving the opportunity of defining, on a broad scale, the general latitudinal and inshore/offshore variation in the recruitment of encrusting species in these regions. Because of the influence of larval availability, settlement and survival, panel assemblages at particular sites are likely to reflect those of nearby cryptic habitats, which may vary latitudinally or along an onshore-offshore gradient.

There are only a few similar studies of spatial variation in recruitment and abundance of other fouling taxa using consistent sampling techniques comparing latitudes (Schoener et al. 1978), or distance from the shore (Long & Rucker 1970, Hughes & Jackson 1992), but never both. The aims of this study are therefore to examine patterns in recruitment, species diversity, cover and calcification rates of cryptic calcareous taxa and to determine whether these vary spatially with latitude and distance from shore, and temporally with season.

## METHODS

Ceramic tiles, approximately 15 × 15 cm, were used as settlement panels and were submerged as described in Fisk & Harriott (1990) in about 6 to 9 m water depth and about 15 to 20 cm above the substratum. Panels were attached horizontally in pairs to steel racks with the unglazed tile surface downwards, for periods of 4 to 8 mo during winter (March to October approx.) and summer (October to March approx.). The sites (Fig. 1) and seasons of submergence were: Cape Tribulation (16°05'S), winter 1987 and summer 1987-88; Green Island (16°50'S), winter 1988 and summers of 1986-87 and 1987-88; Solitary Islands (30°S), winter 1991 and summers of 1990-91 and 1991-92; and Lord Howe Island (31°33'S), winter 1991 and summers of 1990-91 and 1991-92. The panels used in this study were a subset (7 to 10 panels per site per time, comprising panels not damaged in storage) of those used at each locality by Fisk & Harriott (1990), Harriott (1992) and Harriott & Banks (1995) for studies on coral recruitment.

On the mainland fringing reefs at Cape Tribulation, the coral communities extend from the outer reef flat to

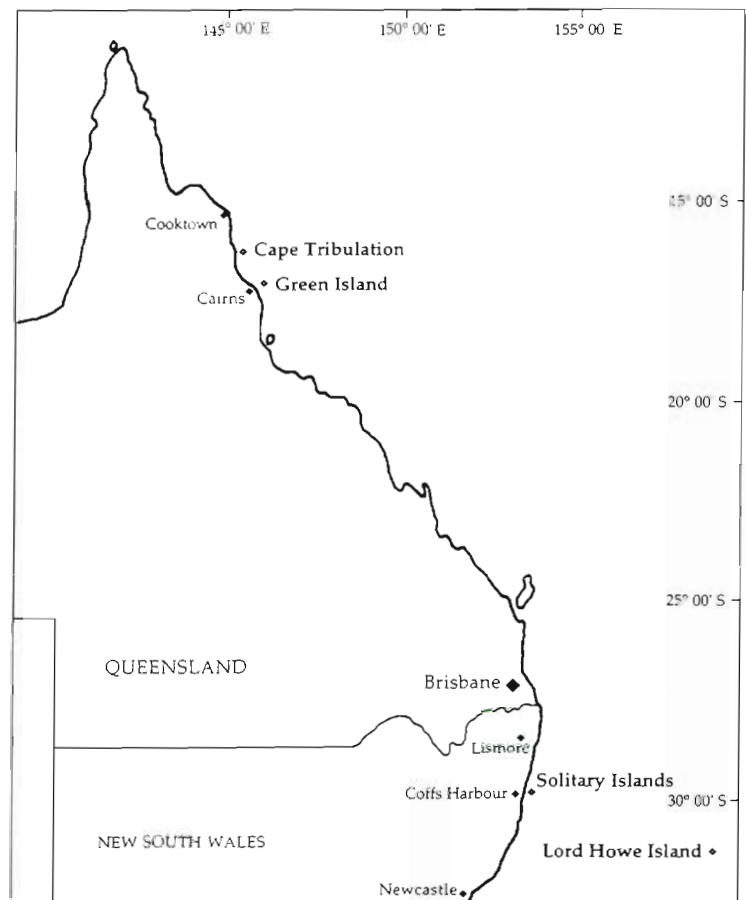


Fig. 1 Location of study sites on the east coast of Australia

a depth of about 5 m. They experience high turbidity and sedimentation rates, but have high coral cover of 33 to 63% (Ayling & Ayling 1987). Settlement panels were located on the seaward slope of 6 fringing reefs. The reefs at Green Island, 13 km northeast of Cape Grafton, surround a vegetated sand cay and were greatly affected by *Acanthaster planci* during the outbreaks of the late 1960s and early 1980s (Fisk et al. 1989). Racks were located on the forereef and backreef slopes and panels from both locations were analysed in this study.

At the Solitary Islands, racks were located about 10 to 20 m north and south of SW Solitary Island, in about 9 m water depth. The island is about 4 km from the mainland, and coral cover near the location of the northern panels was over 50% (Harriott et al. 1994). Approximately 90 coral species have been recorded from the Solitary Islands region, and their coral communities have a high cover of macroalgae and organisms more typical of temperate rocky reefs (Harriott et al. 1994). Lord Howe Island, about 600 km off the eastern Australian coast, is the southernmost true coral reef in the Pacific. About 80 coral species have been recorded from Lord Howe Island, and the community structure of reefs there has been described by Veron & Done (1979) and Harriott et al. (1995). Racks were located on the western edge of the lagoon, in approximately 5 to 8 m water depth (Harriott 1992).

On retrieval, panels were bleached to remove non-calcareous biota. The lower (unglazed) surface was examined under a stereo microscope for the presence of coral recruits and various calcareous space-occupying taxa, including Bryozoa, Mollusca (vermetid gastropods and oysters), serpulid and spirorbid Polychaeta and barnacles. The bleaching process removed non-calcareous algae and soft-bodied organisms such as ascidians, sponges and hydroids. These taxa were not a significant component of cover on the lower surfaces of settlement panels at any site apart from the Solitary Islands, where further long-term studies including all taxa in the fouling community are in progress.

For species abundance and taxonomic diversity data, all calcareous fauna were counted on each panel, using a dissecting microscope. Colonies of Bryozoa were separated at species level in most cases. The non-bryozoan animals such as corals and serpulids were generally identified at family level or higher. These taxa mostly consisted of 1 or a very few species each, however, so the loss of taxonomic resolution was not great. The Shannon-Wiener species-diversity index was calculated for each panel.

For the analysis of cover, each panel was photographed and the colour transparency examined under a 100-point random grid (Bohnsack 1979) to determine percentage cover of each calcareous taxon. The

images of organisms on panels were grouped into 9 categories: Bryozoa, calcareous algae, spirorbid and serpulid Polychaeta, corals, barnacles, dead barnacle bases, oysters and bare panel surface. The taxonomic resolution for panel-cover estimation was thus coarser than for the microscopic examination of panel biota.

Community structure was examined by multivariate cluster analyses and ordination of species abundance and cover data. For abundance data, all species with a mean of less than 1 specimen per panel in any site/season combination were excluded. The multivariate cluster analyses were based on Bray-Curtis similarities (Clarke & Green 1988, Clarke 1993) and used fourth-root data transformations to control the level of influence of rare species (Clarke 1993). These analyses were followed by non-metric multidimensional scaling ordination (MDS; Kruskal & Wish 1978, Clarke & Green 1988) to provide additional information on the nature of site/time groupings. Contributions of separate taxa to the dissimilarity patterns of species abundances and panel cover between sites were examined using the similarity percentage analysis (SIMPER) procedure of Clarke (1993). Multivariate analyses and associated test procedures were carried out using the PRIMER software package (Plymouth Marine Laboratories, UK).

Weight of calcified material on each panel was determined by hydrochloric acid treatment of dried and preweighed panels, followed by rinsing in distilled water, drying to constant weight and final weighing. Blank control panels were similarly treated to determine correction factors for loss of weight from the acid-treated ceramic material. Corrected weight losses of experimental panels were standardised to provide calcification values per month over the periods of exposure at each site and season.

Results for calcification rate of panels were analysed using 2-factor (site and season) ANOVA. Data for calcification rates were fourth-root transformed to normalise the data and homogenise variances across site/times (confirmed by the use of Bartlett's test; Snedecor & Cochran 1967). *A posteriori* pairwise comparisons of means were carried out using the Tukey HSD procedure (Winer 1971), selected following the critique of Day & Quinn (1989).

## RESULTS

### Species richness and diversity

A total of 81 bryozoan species and 13 other taxa was found over the entire study. Of the 81 bryozoan species, 45 were relatively rare, appearing on 3 or fewer of the 103 panels surveyed, while 3 bryozoan species

Table 1. Species richness and Shannon  $H'$  diversity of bryozoa and other taxa with site and season

Site	All samples		Winter			Summer		
	Species richness	Other taxa	Species richness	Other taxa	Shannon $H'$	Species richness	Other taxa	Shannon $H'$
	Bryozoa		Bryozoa		All taxa	Bryozoa		All taxa
Solitary Islands	46	11	24	7	0.93	43	11	1.71
Cape Tribulation	39	10	17	9	1.36	35	9	1.17
Green Island	21	10	3	8	1.21	20	10	1.43
Lord Howe Island	8	12	7	11	1.33	3	10	1.14

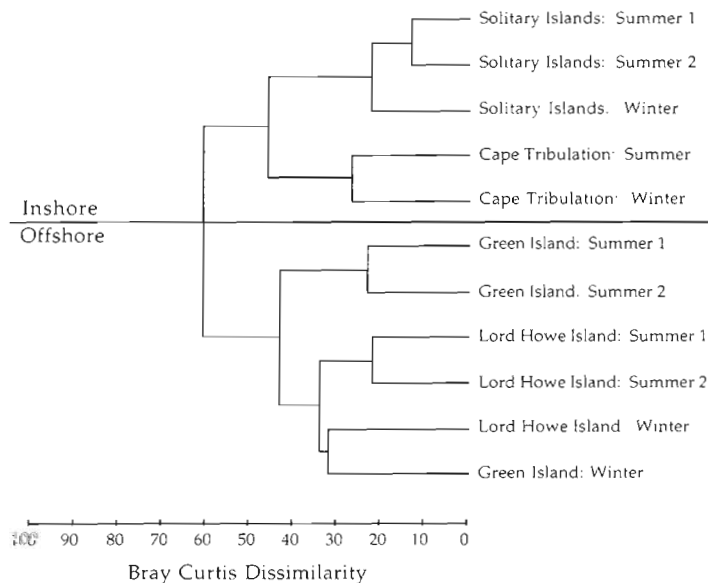


Fig. 2. Cluster analysis of sites/times in terms of species abundances on tiles. Note the marked inshore/offshore split

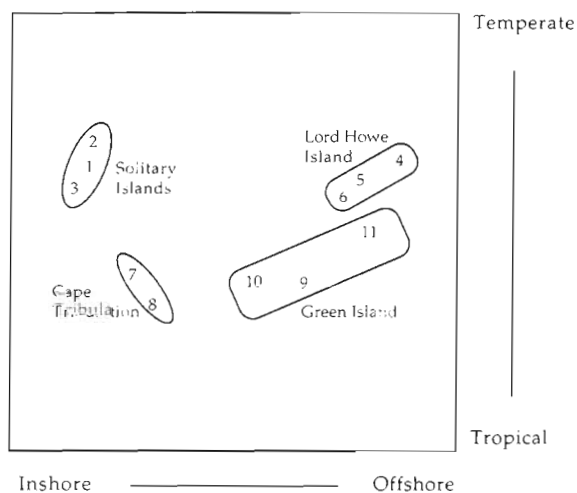


Fig. 3. MDS plot of sites/times in terms of species abundances on tiles.

- 1, 2, Solitary Islands summers  
3, Solitary Islands winter  
4, 5, Lord Howe Island summers  
6, Lord Howe Island winter  
7, Cape Tribulation summer  
8, Cape Tribulation winter  
9, 10, Green Island summers  
11, Green Island winter

(*Parasmittina* cf. *delicatula*, *Lichenopora* sp. and *Tubulipora* sp.) were common to all 4 locations. Non-bryozoan animal groups included juvenile vermetid molluscs, oysters, 2 species of serpulids, spirorbids, 5 taxa of coral juveniles and barnacles. Calcareous (encrusting coralline) algae were present at all sites.

The greatest species richness (57 species from 26 panels) was recorded from the subtropical inshore site (Solitary Islands), followed by the tropical inshore site (Cape Tribulation; 49 species, 19 panels), tropical offshore (Green Island; 31 species, 30 panels), and the subtropical offshore site (Lord Howe Island; 20 species, 27 panels) (Table 1). At the Solitary Islands, mean species diversity ( $H'$ ) in winter was about half the summer mean value (representing the lowest and highest values respectively), while at the other 3 sites, diversity varied little between sites or between the 2 seasons (Table 1).

### Community analyses

For the abundance data, cluster analysis showed a clear separation between inshore and offshore sites (Fig. 2). The 2 inshore sites (Cape Tribulation and Solitary Islands) were also well separated from each other, but the offshore sites (Green Island and Lord Howe Island) were less clearly distinguished. Multidimensional scaling of the data from these classifications (Fig. 3) showed a clear separation between the 4 sites, except for the Green Island winter sample which was not clearly separated from the Lord Howe Island group.

The SIMPER (similarity percentage; Clarke 1993) analyses, which indicate the taxa contributing most to the inter-group differences in the cluster analyses (Table 2), showed that differences between the Solitary Islands fauna and the other sites were attributable to good representation of barnacles and 2 bryozoan species (*Lichenopora* sp. and *Bryozoa* sp. 15) at the former site. Lord Howe Island was separated from other sites mainly because of poor representa-



Solitary Islands		Lord Howe Island	
Lord Howe Island	Barnacles Serpulids <i>Lichenopora</i> sp. <i>Celleporaria</i> sp. <i>Micropora</i> sp. Bryozoan sp. 15 <i>Parasmittina</i> sp. <i>Tubulipora</i> sp. Bryozoan sp. 4	Table 2. SIMPER results for species abundance at study sites, showing the species contributing the first 50% of cumulative abundance. Species in the left side of each cell were characteristic of sites named on the left of each row; species in the right side of each cell were characteristic of sites named at the head of each column	
	Lord Howe Island		
Cape Tribulation	Spirorbids Bryozoan sp. 74	Barnacles <i>Celleporaria</i> sp. <i>Micropora</i> sp. <i>Lichenopora</i> sp. Bryozoan sp. 15 Bryozoan sp. 4	Serpulids Spirorbids <i>Parasmittina</i> sp. Oysters
	Cape Tribulation		
Green Island	<i>Acropora</i> sp. <i>Pomatoceros</i> sp. 1 <i>Pocillopora</i> sp.	Barnacles <i>Lichenopora</i> sp. <i>Celleporaria</i> sp. <i>Micropora</i> sp. <i>Parasmittina</i> sp. Bryozoan sp. 15	Spirorbids <i>Acropora</i> sp. <i>Pomatoceros</i> sp. 1 Other serpulids Oysters
	Cape Tribulation		<i>Pocillopora</i> sp. <i>Acropora</i> sp. <i>Parasmittina</i> sp. Spirorbids Serpulids <i>Tubulipora</i> sp. Bryozoan sp. 74 Bryozoan sp. 70

tion of all counted groups, reflecting the relatively low species richness at this site. Cape Tribulation had a relatively good representation of spirorbid and serpulid polychaetes, which separated it from the Solitary Islands. Green Island was separated from the Solitary Islands because of the presence of corals and a species of the polychaete *Pomatoceros*. Green Island was distinguished from Lord Howe Island by its representation of polychaetes, acroporid corals and oysters, and from Cape Tribulation by the greater abundance of pocilloporid corals at Green Island and of

polychaetes, *Tubulipora* sp. and *Parasmittina* cf. *delicatula* at Cape Tribulation.

In the results for panel cover (Table 3), cover for calcareous fauna was highest at the 2 inshore sites (44.2 to 71.5% at the Solitary Islands and 27.8 to 44.9% at Cape Tribulation), while cover of calcareous algae was highest at the 2 offshore sites (31.5 to 86.3% at Lord Howe Island and 31.3 to 67.0% at Green Island). At the Solitary Islands, bryozoans were the dominant cover, followed by barnacles and calcareous algae. At Cape Tribulation, bryozoa were dominant, followed by cal-

Table 3. Mean percentage cover on panels for 9 image categories at study sites

	Calcareous algae	Bryozoa	Spirorbid	Serpulids	Corals	Barnacles	Barnacle bases	Oyster	Total fauna
Solitary Islands									
Summer 1990-91	9.9	58.2	0.2	1.4	0.1	11.1	0.3	0.4	71.5
Summer 1991-92	12.8	21.9	2.2	3.2	0.1	15.5	0.9	0.4	44.2
Winter 1991	19.5	30.1	0.2	4.4	0	22.1	0.6	0.1	57.5
Cape Tribulation									
Summer 1987-88	13.5	25.5	6.2	12.4	0.2	0	0	0.6	44.9
Winter 1987	14.2	24.8	1.4	1.2	0	0	0	0.4	27.8
Green Island									
Summer 1986-87	46.4	0.3	0.9	8.6	0.3	0	0	4.5	14.6
Summer 1987-88	31.3	4.5	1.3	6.3	0.6	0	0	2.5	15.2
Winter 1988	67.0	1.0	0.4	0.9	0.1	0	0	0.6	3.0
Lord Howe Island									
Summer 1990-91	55.9	0.4	0	0.14	0.7	0	0	0.1	1.34
Summer 1991-92	31.5	0.3	0.3	0.13	1.1	0	0.1	0.2	2.13
Winter 1991	86.3	2.7	0.3	1.0	0.1	0	0	0.3	4.4

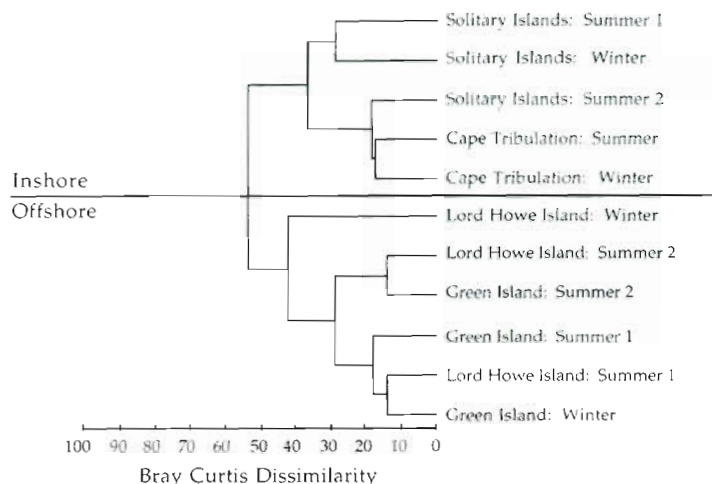


Fig. 4. Cluster analysis of sites/times in terms of tile cover of 9 image categories. Note inshore/offshore split

careous algae and serpulids. At Green Island and Lord Howe Island, calcareous algae formed the dominant category, with serpulids at Green Island the only other category contributing more than 5% cover (Table 3).

Multivariate cluster analyses of panel-cover data showed a clear distinction between inshore and offshore site/season groups (Fig. 4), similar to the results for taxonomic abundance. However, the classification did not clearly distinguish between sites within the offshore and inshore groups (Fig. 4), indicating that the broader level of taxonomic resolution for the cover analysis less clearly distinguishes sites from each other.

#### Calcification rates

The results of 2-way ANOVA of calcification by site and season showed significant effects of site and season on calcification rate of panels (site:  $F = 67.5$ ,  $df = 3$ ,

$p = 0.0001$ ; season:  $F = 8.74$ ,  $df = 1$ ,  $p = 0.004$ ), with no significant interaction between factors ( $F = 0.87$ ,  $df = 3$ ,  $p = 0.46$ ). A *posteriori* comparisons of the means (Tukey HSD) showed that the Solitary Islands mean calcification weights were significantly higher than those at the other 3 sites, which formed a coherent group (Table 4). On the basis of taxa contributing to panel cover (Table 3) the major contributors to calcification rates appear to be Bryozoa, barnacles and calcareous algae at the Solitary Islands, Bryozoa and calcareous algae at Cape Tribulation and calcareous algae at Green and Lord Howe Islands.

#### DISCUSSION

##### Species richness

The abundant taxa in this study are typical of those reported in other studies of fouling communities in eastern Australia. Bryozoans made the greatest contribution to species richness at the Solitary Islands, Green Island and Cape Tribulation, representing 68 to 81% of taxa recorded at these sites. At Lord Howe Island, overall species richness was lower and bryozoans represented 44% of species. In other studies of fouling communities in eastern Australia, Allen & Ferguson Wood (1950) recorded a total of 30 bryozoan species, which formed a large proportion of the growth on most panels at several sites on the Australian east coast. Wisely (1959) reported that the dominant organisms in Sydney Harbour ( $33^{\circ}50'S$ ) comprised barnacles, tube-worms, bryozoans and bivalve molluscs. Moran & Grant (1989) found that fouling communities at Wollongong ( $34^{\circ}27'S$ ) included 21 bryozoan species, and 15 other calcareous species, including bivalves, barnacles and polychaetes. Holmes (1982) found 33 species of Bryozoa on panels of 6 to 48 wk exposure in Port Phillip Bay, Victoria ( $37^{\circ}51'S$ ), but the dominant calcareous forms on 6 wk spring and summer panels were barnacles and serpulid worms.

The species richness of bryozoans recorded in this study was generally higher than the total of 12 species reported by Schoener & Schoener (1981) from Puget Sound (USA) and the 15 species recorded by Winston & Jackson (1984) on panels submerged for up to 3 yr in Jamaica. Schoener et al. (1978) reported up to 12 species of calcareous forms and algae, hydroids and ascidians on 6 mo panels in subtropical and tropical sites. They also noted that in both Thailand and Hawaii calcareous organisms predominated on their panels.

The high abundances of calcareous forms and the importance of bryozoans found in the present study thus reflect the findings from panel studies elsewhere.

Table 4. Results of Tukey HSD *a posteriori* comparisons of calcification rates (mean seasonal calcification, untransformed data,  $g\ tile^{-1}\ mo^{-1}$ ) at site/season combinations. Significance groupings of site/season combinations are separated

Site/season	No. of panels	Calcification
Solitary Islands, winter	8	1.155
Solitary Islands, summers	18	1.149
Green Island, winter	10	0.819
Green Island, summers	20	0.708
Lord Howe Island, winter	11	0.690
Cape Tribulation, winter	9	0.666
Lord Howe Island, summers	8	0.564
Cape Tribulation, summer	11	0.547

It appears, however, that the species richness of Bryozoa found on our panels, especially at the inshore sites, far exceeds that reported by other workers. Ryland (1974) noted that the Indo-Pacific region appeared to support more bryozoan species than the Caribbean. However, Kobluk et al. (1988) reported 75 species of bryozoans from cryptic reef habitats in the Caribbean, indicating that the Bryozoa are a diverse component of reef faunas. Choi & Ginsburg (1981, 1983) found marked zonation of cryptic faunas (including 29 species of Bryozoa) on a scale of about 10 km across the Florida Reef Tract in Biscayne Bay (USA).

### Inshore versus offshore sites

Spatial variations in community structure may result from interactions among (1) geographical distributions of breeding stocks of various taxa and the timing of breeding, (2) larval transport mechanisms, e.g. ocean and coastal currents (Roughgarden et al. 1987), (3) variations in water quality factors, e.g. turbidity and nutrients, and their effect on larval settlement (Schmidt 1982) and survival. All of these factors may vary along both latitudinal and inshore/offshore gradients and, in addition, small-scale factors (e.g. of habitat distribution in an area, see Choi & Ginsburg 1983) may distort or locally reverse a larger-scale trend.

In the present study the differences in panel biota between inshore and offshore sites were much greater than differences over a much larger latitudinal distance, e.g. fouling communities at Green Island were inseparable in some analyses from those at Lord Howe Island over 1600 km to the south and well off the edge of the continental shelf, but were clearly distinct from those at Cape Tribulation less than 100 km away. Inshore panels were more species-rich than offshore panels at a similar latitude, with the highest richness found at the subtropical inshore site. This pattern may reflect species representation in nearby cryptic habitats as well as larger-scale gradients in the distributions of communities.

On the Great Barrier Reef several studies have examined cross-shelf differences in coral reef communities (e.g. Done 1982, Williams et al. 1984). The gradient from more turbid, physically variable and nutrient-rich inshore waters to clear oligotrophic offshore water was reflected in significant variation in community structure for most taxa (Wilkinson & Cheshire 1989). Dinesen (1983) found that soft coral diversity increased with distance offshore in the central Great Barrier Reef and Sammarco (1983) found a broadly similar pattern for coral recruits. It has been suggested (e.g. Williams et al. 1984) that strong connections by long-shore currents due to the dominance of the East Australian Cur-

rent may inhibit cross-shelf transport, which would lead to cross-shelf variation in the suites of species available to settle. Farrell et al. (1991) showed that recruitment of coastal barnacles in California (USA) was affected by cross-shelf currents altered by changes in wind patterns, indicating that mesoscale water movements may exert a significant influence on larval supply.

Hughes & Jackson (1992) examined spatial patterns in the distribution of cryptic cheilostome bryozoans on the undersurfaces of coral colonies at 8 sites in and near the Caribbean coast of Panama. They reported higher cover of bryozoans at offshore sites than at mainland sites (the reverse of our findings), but no consistent pattern of species diversity. They concluded that exposure to mainland run-off was not a major determinant of bryozoan community structure in that area and that the effects of local topography on environmental heterogeneity (and, by implication, the distribution of cryptic habitats) may be more important.

Long & Rucker (1970), however, reported fewer bryozoan species on offshore settlement panels in Florida. They concluded that rate of colonisation was limited by the dispersal distance of larvae rather than the presence of unsuitable environmental conditions. These findings, also, suggest that local cryptic habitat distribution and its effects on larval supply may have important influences on panel biotas.

Calcareous algae were the dominant space-occupiers at the offshore sites at Green Island and Lord Howe Island, with propagules presumably derived from nearby habitats. The relatively low cover of calcareous algae at the inshore sites (Cape Tribulation and the Solitary Islands) might be attributable to low light levels in the more turbid coastal waters, to space pre-emption by other species or to lack of nearby breeding populations able to supply propagules to the panel sites, but there are insufficient data to evaluate these conjectures.

### Latitudinal differences

In the present study, latitudinal variation in species richness and community structure was less significant than cross-shelf differences. There was no consistent trend with latitude for species richness or diversity, with both the highest and lowest species richness and diversity found at the high latitude sites.

Latitudinal variations in marine species diversity and community structure have recently been discussed by Schoener et al. (1978), Black & Prince (1983), Crossland (1988), Keough (1988), McGuinness (1990), Clarke (1992) and other authors. Tropical habitats are commonly assumed to have a higher species richness

than similar habitats in higher latitudes but Clarke (1992) notes that some groups, including bryozoans and polychaetes, are species-rich in high southern latitudes.

Consistent with the result of the present study, McGuinness (1990) compared diversity in high and low latitude marine environments and concluded that temperate communities were not always less diverse than those in the tropics, at least at small spatial scales. Black & Prince (1983) examined patterns in species diversity in the fauna associated with heads of the coral *Pocillopora damicornis* at a number of sites at different latitudes and found a reduction in regional species richness in the high-latitude coral communities, but no clear pattern in the species diversity per unit sampled.

Schoener et al. (1978) concluded that initial colonisation rates on settlement panels were higher at tropical than at temperate sites, but that between 6 mo and 1 yr (when their study finished) the species richness of panels did not vary greatly with latitude. However, the overall species richness at each site was 2 to 3 times higher at their tropical and subtropical sites than at their temperate sites. They concluded that the greater species richness associated with tropical marine environments may be due to a greater variety of habitats present, rather than greater within-habitat diversity in the tropics.

In another comparison, Schoener & Schoener (1981) and Greene et al. (1983) concluded that space was occupied much more slowly on fouling panels at Jackson's (1977b) tropical site than in their studies in Puget Sound. Schoener & Schoener (1981) suggested that the contrast may reflect local habitat differences, a possibility supported by the lack of barnacles at Jackson's tropical site. However, comparison of the sites is complicated by the fact that Jackson's tropical study site was at 40 m depth, while the Schoeners' cool-temperate site was at about 1 m below water level in a site about 4 m deep, close to the shore.

In a separate study, Winston & Jackson (1984) also reported that recruitment and growth of tropical bryozoans (at a shallower site, 12 to 13 m, than that of Jackson 1977b) in Jamaica was lower than at temperate sites. In plates submerged for 7 mo, cover of cheilostome bryozoans ranged from 0.8 to 2.1%, and cover of calcareous algae ranged from zero to 0.4%. The cover of bryozoans was comparable with those reported here for our 2 offshore sites at Green Island and Lord Howe Island (means of 1.9% and 1.1% respectively; Table 3), but was significantly lower than mean bryozoan cover at the 2 inshore sites (the Solitary Islands 36.7% and Cape Tribulation 25.1%). At all our sites, mean cover of calcareous algae was much higher after 4 to 8 mo (9.9 to 86.3%; Table 3) than in Winston & Jackson's (1984) study after the first 7 mo, though

cover of calcareous algae on their 15 mo old panels was 52.5 and 33.8% at depths of 10 and 22 m respectively (Jackson & Winston 1982).

The higher species richness on subtropical than tropical panels at inshore sites found in our study thus appears to be broadly consistent with the findings of other studies. Bryozoans formed the major component of the Solitary Islands fauna and, since Ryland (1976) has noted that bryozoan larvae are usually brooded and have limited dispersal abilities, the high species richness at this site may reflect the presence of small-scale larval transport mechanisms bringing larvae from local subtidal habitats. In addition, the subtropical east coast of Australia contains a range of intertidal and subtidal rocky habitats, which may provide a high diversity of propagules on a subregional or smaller scale.

### Competition for settlement space

In a study of coral recruitment in areas of upwelling in the Eastern Pacific, Birkeland (1977) concluded that successful coral recruitment was a rare event in upwelling areas because of competition for settlement space with other organisms such as barnacles, bryozoans, tunicates and algae which quickly monopolised space on artificial settlement surfaces. Johannes et al. (1983), in an evaluation of the factors limiting the distribution of coral reefs at high latitudes, hypothesised that the poleward distribution of corals might be limited by the inability of corals to compete successfully, both as larvae and as adults, with temperate biota.

In the present study, the Solitary Islands panels had the highest cover of bryozoans, barnacles and other fauna, limiting the amount of free space on settlement panels submerged for approximately 4 mo. At the Solitary Islands, coral recruitment rates were lower than at the other 3 sites reported here (Harriott & Banks 1995). The high rate of colonisation of non-coral calcareous organisms at the Solitary Islands relative to other sites indicates that competition for space with calcareous fouling organisms may be a major factor that might limit coral recruitment in coastal subtropical eastern Australia. Where cover is very high, allelopathic interactions are likely to play a highly significant role in structuring these cryptic communities (Dyrynda 1983, Rodriguez et al. 1993, Maida et al. 1995a, b).

### Calcification rates

The calcification rate of the fouling communities at the Solitary Islands was significantly higher than at the other 3 sites (Table 4), reflecting the findings for abun-



dance and cover of calcareous organisms. Calcareous algae were important occupiers of panel space at all sites, but the Solitary Islands panels also supported a significant cover of bryozoans and barnacles, and the latter, especially, may have been important contributors to calcification at that site. Bryozoans have been found also to contribute significantly to calcification in warm temperate New Zealand (Smith & Nelson 1994).

Johannes et al. (1983) report that total community calcification at a subtropical coral community in Western Australia was not depressed relative to tropical reefs, despite a reduction in coral growth rate at the same site. They suggested that other (non-coral) calcifying biota might contribute more to community calcification at the high latitude reef than at tropical reefs. The present data suggest that barnacles, Bryozoa and calcareous algae are capable of significant contributions to community calcification on subtropical reefs.

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