Latitudinal variation in patterns of colonisation of cryptic calcareous marine organisms

N. J. Holmes*, V. J. Harriott, S. A. Banks

School of Resource Science and Management, Southern Cross University, PO Box 157, Lismore, New South Wales 2480, Australia

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 environments (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).
Propagule availability at panel surfaces will be a function of several factors (Rodriguez 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 1993). 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 x 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...
Holmes et al. - 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 bryozoans and other taxa with site and season

<table>
<thead>
<tr>
<th>Site</th>
<th>All samples</th>
<th>Winter</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Species richness</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bryozoa Other taxa</td>
<td>Bryozoa Other taxa</td>
<td>All taxa</td>
</tr>
<tr>
<td>Solitary Islands</td>
<td>46 11</td>
<td>24 7</td>
<td>43 11</td>
</tr>
<tr>
<td>Cape Tribulation</td>
<td>39 10</td>
<td>17 9</td>
<td>35 9</td>
</tr>
<tr>
<td>Green Island</td>
<td>21 10</td>
<td>3 8</td>
<td>20 10</td>
</tr>
<tr>
<td>Lord Howe Island</td>
<td>8 12</td>
<td>7 11</td>
<td>3 10</td>
</tr>
</tbody>
</table>

Non-bryozoan animal groups included juvenile vermetid molluscs, oysters, 2 species of serpulids, spirobids, 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-
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, bryozoans were dominant, followed by cal-
Careful 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 ($F = 67.5, \text{df} = 3, p = 0.0001$; season: $F = 8.74, \text{df} = 1, p = 0.004$), with no significant interaction between factors ($F = 0.87, \text{df} = 3, p = 0.46$). 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.

**Species richness**

The abundant taxa in this study are typical of those reported in other studies of fouling communities in eastern Australia. Bryozoa 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°50'S) comprised barnacles, tube-worms, bryozoans and bivalve molluscs. Moran & Grant (1989) found that fouling communities at Wollongong (34°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°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**

<table>
<thead>
<tr>
<th>Site/season</th>
<th>No. of panels</th>
<th>Calcification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solitary Islands, winter</td>
<td>8</td>
<td>1.155</td>
</tr>
<tr>
<td>Solitary Islands, summers</td>
<td>18</td>
<td>1.149</td>
</tr>
<tr>
<td>Green Island, winter</td>
<td>10</td>
<td>0.819</td>
</tr>
<tr>
<td>Green Island, summers</td>
<td>20</td>
<td>0.708</td>
</tr>
<tr>
<td>Lord Howe Island, winter</td>
<td>11</td>
<td>0.690</td>
</tr>
<tr>
<td>Cape Tribulation, winter</td>
<td>9</td>
<td>0.666</td>
</tr>
<tr>
<td>Lord Howe Island, summers</td>
<td>8</td>
<td>0.564</td>
</tr>
<tr>
<td>Cape Tribulation, summer</td>
<td>11</td>
<td>0.547</td>
</tr>
</tbody>
</table>
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 & 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
other 3 sites (Table 4), reflecting the findings for abun-
dant zoological communities (Jackson 1984) after the first 7 mo, though
the Solitary Islands was significantly higher than at the
other sites, mean cover of calcareous algae was much higher
inshore sites (the Solitary Islands 36.7% and Cape Tribulation 25.1%
respectively; Table 3), but was significantly lower than
and Lord Howe Island (means of 1.9% and 1.1%
% respectively; Table 3), suggesting 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 a greater depth (4 m), while the Schoener’s 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 bry-
ozoans (at a shallower site, 12 to 13 m, than that of Jackson 1977) in Jamaica was lower than at temper-
ate 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 6 mo (9.9 to 86.3%, Table 3) than in Winston
& Jackson’s (1984) study after the first 7 mo, though

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 Schoener’s 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 bry-
ozoans (at a shallower site, 12 to 13 m, than that of Jackson 1977) in Jamaica was lower than at temper-
ate 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 6 mo (9.9 to 86.3%, Table 3) than in Winston & Jackson’s (1984) study after the first 7 mo, though

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 higher 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.

**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 occupants 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.

Acknowledgements. Thanks are due to Dr S. D. A. Smith for comments on an earlier draft of this paper, to Dr Phil Bock for assistance with identifying bryozoans, and to 2 anonymous reviewers for suggesting significant improvements to the manuscript. This project was funded by an Internal Research Grant from Southern Cross University.

LITERATURE CITED


Wilkinson CR, Cheshire AC (1989) Cross-shelf variations of...

This article was submitted to the editor

Manuscript received: April 16, 1997
Revised version accepted: June 18, 1997