# Spatial patterns in coral reef benthos: multiscale analysis of sites from three oceans

R. E. Reichelt and R. H. Bradbury

Australian Institute of Marine Science, P. M. B. No. 3, Townsville MS Queensland, Australia 4810

ABSTRACT: The spatial patterns of coral reef benthos from the Great Barrier Reef (Heron reef, 45 spp. scleractinian corals only), the Red Sea (Eilat, 88 spp. scleractinian corals only) and the Caribbean (Florida to Haiti, 126 spp. scleractinian corals, alcyonarians and sponges) were analysed at the local scale of neighborhood patterns and larger scales of cross reef and regional zonation patterns. Relations between local and larger scale patterns were explored statistically to test for coupling between the scales. Small-scale analysis showed that there were relatively few non-random neighbor patterns. The number of types (i.e. different species pairs) of non-random adjacencies was 6 at Eilat, 5 at Heron, and 3 in Caribbean. The distribution of all non-random adjacencies was not coupled with large-scale structure. Some individual species were significantly more abundant in transects where that species was involved in significant non-random adjacencies. Because the 3 data sets were collected each in a different manner, a cautious interpretation of results is warranted. With that proviso, we conclude that coupling between small- and large-scale spatial patterns through processes influencing individual neighbors is very weak at the community level but strong for a few individual species (e.g. *Pocillopora damicornis*).

## INTRODUCTION

Theories that encompass the behaviour of biological communities (Ulanowicz, 1979a; Botkin, 1982) must accommodate both the complexity and the multilevel organization of the system. Following Levins and Lewontin (1980), the present study tests for the relations between ecological entities representing two separate levels of organization in coral reef benthic communities.

The 2 ecological entities considered here are the local scale distribution of corals, that is neighborhood patterns, and the large-scale patterns of coral distribution across reefs, that is reef zones (e.g. Wells, 1957; Glynn, 1973), and between reefs. Our aim is to test whether the patterns observed at each of these 2 levels can be interpreted as a propagation of effect from the small scale to the large scale. Our null hypothesis, in the sense of Strong (1982), is that, at the local scale, the neighbors are random, i.e. no overriding physical or biological factor is imposing observable structure on the neighborhood patterns. We will invoke departure from randomness as evidence for structuring processes at the local scale and then investigate the propagation of such effects to the larger scale.

In coral reef communities, of the processes influencing the distribution of organisms, most attention has been given to grazing and predation (Day, 1977; Neudecker, 1979; Sammarco, 1980; Wellington, 1982), physical factors (Geister, 1977; Bradbury and Young, 1981; Highsmith, 1982), interspecific aggression between corals (Lang, 1971, 1973; Richardson et al., 1979; Wellington, 1980; Sheppard, 1982a, b) and physical disturbance (Connell, 1978; Bak and Luckhurst, 1980; Porter et al., 1981). We do not seek, in this study, to establish which of these physical or biological processes is causing non-random patterns at the local scale. Rather we will attempt to establish if the observed local scale patterns could be reasonably considered to be the result of any such processes. If such local patterns can be detected we then ask whether the local patterns correspond with large scale patterns in a way that represents correlative evidence of cross-scale effects on coral communities.

## SITES AND SAMPLING METHODS

The 3 independent data sets have been described previously (Table 1) and the important differences

Table 1. Data sets

|  | Eilat | Heron | Caribbean |
|---|---|---|---|
| Authors (collectors) | Loya (1972) | Bradbury & Young (1981) | Bunt et al. (1982) |
| Collection sites | Eilat nature reserve, ca. 1 km, Red Sea, reef flat and slope | Heron Reef, 2.2 km, West Pacific, reef flat and lagoon | 15 Caribbean islands Florida to Haiti, ca. 800 km approx, Caribbean, deep reef terraces |
| Sampling depths | 0–30 m | 0–1 m | 14–38 m |
| Transects | 84 × 10 m transects | 45 × 30 m transects | 46 × 10 m transects |
| Methods | Line transects, continuous recording, gap size > 20 cm | Line transects, sample points every 20 cm | Line transects, continuous recording |
| Benthos recorded | Hard corals | Hard corals | Hard corals, sponges, gorgonians |

among the 3 sets all relate to the spatial distribution of samples. Firstly, the data sets come from different oceans. Secondly, the Eilat and Heron transects cover small geographic areas and the Caribbean set covers a large geographic area. Thirdly, the 3 sets of data come from a variety of reef habitat types, including sheltered back-reef and lagoon regions, reef slopes and deep reef terraces (see the original authors for more detail).

For Eilat and Heron, where hard corals dominate, only the hard corals were recorded. In the Caribbean samples, where hard corals are less dominant, the data include hard corals, sponges, algae and gorgonians.

The 3 sets are similar in that they were all collected using line transect methods, thereby preserving the sequence of benthic species along each transect.

At Eilat, Loya (1972) did not record a space between coral colonies unless the gap between them was greater than 20 cm. Thus we considered coral colonies to be adjacent at Eilat if no such gap was recorded. In the Heron data, each point along the transect was recorded, either as a coral species or a space (no corals). Thus we considered coral colonies to be adjacent at Heron if the adjacent points were both corals. The Caribbean data accurately represent the real distance between colonies, so the gaps between corals, gorgonians and sponges were variable in length. When a gap between 2 colonies is greater than a certain distance, those 2 colonies can no longer be considered to be adjacent. In the Caribbean data, we considered a gap to exist and hence adjacency not to exist if the space between 2 colonies was greater than 5 cm. This value was chosen following Sheppard (1982b) where the aggressive reach of corals is described as 5 cm or less. As a test of the sensitivity of this value we repeated some analyses with it set at a more conservative 10 cm.

Table 2. Analysis of local scale patterns. Fisher's and binomial tests

|  |  | Eilat | Heron[*] | Caribbean-5[**] | Caribbean-10[***] |
|---|---|---|---|---|---|
| (a) | Number of species recorded | 88 | 45 | 126 | 126 |
| (b) | Number of types of adjacency events that occurred | 2503 | 545 | 859 | 1111 |
| (c) | Number of types of adjacency events that showed cases departing from random, $p < 0.05$ | 98 | 24 | 8 | 15 |
| (d) | Number of cases (Fisher's tests) that included the event types in (c) | 2336 | 239 | 116 | 188 |
| (e) | Number of event types that were significant under the binomial test, $p < 0.05$ | 6 | 5 | 3 | 5 |
| (f) | Number of cases (Fisher's tests) that included the event types in (e) | 33 | 22 | 12 | 16 |

[*] Results summarized from Bradbury and Young (1983); species i/species i cases excluded
[**] Gap length 5 cm between colonies; see text
[***] Gap length 10 cm between colonies; see text

## NUMERICAL METHODS

### Large-scale structure

Each of the data sets had been reduced, by multivariate classificatory methods, to groups of transects according to similarities and differences in the species composition of each transect (see the original papers cited in Table 1). The results of these analyses are adopted here as the best available description of the large-scale structure within each set. At Eilat and Heron, this structure is represented as zonation across each reef. In the Caribbean, the structure is on a larger geographic scale with the data being reduced by Bunt et al. (1982) to groups of islands. In the original analyses of the Heron and Caribbean data, the classifications were augmented by ordination and nearest neighbor network approaches, respectively.

### Small-scale structure

As in Bradbury and Young (1983), the component of small-scale structure used here is the spatial pattern of

Table 3. Distribution of significant event types with the groups (reef zones or islands) defined as large-scale structures within each data set

**Eilat**

| | Zone | No. of corals | No. of events Obs. | No. of events Exp. |
|---|---|---|---|---|
| I | Rear reef, reef flat | 1119 | 11 | 8.39 |
| II | Millepora | 600 | 2 | 4.50 |
| III | Echinopora (3–7) | 944 | 8 | 7.08 |
| IV | Echinopora (8–12) | 698 | 3 | 5.23 |
| V | Acropora | 259 | 3 } 9 | 1.94 } 7.81 |
| VI | Porites | 783 | 6 | 5.87 |

$\chi^2 = 3.45$, df $= 4$, p $> 0.05$ n.s.

**Heron**

| | Zone | No. of corals | No. of events Obs. | No. of events Exp. |
|---|---|---|---|---|
| I | South reef crest, South reef flat | 685 | 5 | 6.9 |
| II | Lagoon, Pocillopora | 553 | 8 | 5.6 |
| III | North reef flat, North reef crest | 945 | 9 | 9.5 |

$\chi^2 = 1.58$, df $= 2$, p $> 0.05$ n.s.

**Caribbean-10**

| | Group | No. individuals* | No. of events Obs. | No. of events Exp. |
|---|---|---|---|---|
| I | Long Reef | 244 | 1 | 3.32 |
| II | Grand Bahama | 547 | 7 | 7.44 |
| III | Outer Islands | 187 | 3 } 8 | 2.54 } 5.25 |
| IV | Inner Islands | 199 | 5 | 2.71 |

$\chi^2 = 1.96$, df $= 2$, p $> 0.05$ n.s.

**Caribbean-5**

| | Group | No. individuals* | No. of events Obs. | No. of events Exp. |
|---|---|---|---|---|
| I | Long Reef | 244 | 1 | 2.49 |
| II | Grand Bahama | 547 | 6 | 5.58 |
| III | Outer Islands | 187 | 2 } 5 | 1.91 } 3.94 |
| IV | Inner Islands | 199 | 3 | 2.03 |

$\chi^2 = 0.475$, df $= 2$, p $> 0.05$ n.s.

* Includes sponges and gorgonians as well as hard corals

each species within a transect, as estimated by the frequency with which a species occurs adjacent to all of the other species in the transect. Given the observed abundances of species i and j within one transect, the exact probability of the observed number of cases of species i occurring next to species j is calculated using a Fisher exact probability test (Kendall and Stuart, 1979). This is done under the null hypothesis that the patterns of adjacencies within the transect are random. A significant probability indicates that some process (or set of processes) has caused the species pair concerned to have occurred adjacent to each other more or less often than would be expected by chance.

The $2 \times 2$ contingency table of the frequency of occurrence of particular species pairs and the Fisher's test were fully described in Bradbury and Young (1983) and are similar to Turkington and Harper's (1979) neighbor analysis. We have not analysed the pattern of individuals occurring next to conspecific individuals in the Heron data set because the point sampling method used there would not distinguish a single large colony from several colonies next to each other. The single species cases were included in the Eilat and Caribbean analyses.

We tested whether some of the significant Fisher's test results (p < 0.05) could have occurred by chance. Since a large number of tests was involved, the binomial test indicates which of the event types (species i occurring next to species j) tested contained enough significant Fisher's test cases for the overall result to be considered significant.

## Coupling between scales

Two approaches were taken in the search for links between the 2 levels of organization, the local scale spatial patterns and the large scale distributions of the community. Firstly, we sought a link between the total abundance of all benthic species in different zones or regions and the distribution of significant (after the binomial test) local scale adjacency events. Using $\chi^2$, we tested the independence of the frequency of significant adjacency events and the large-scale spatial patterns, the zones or groups of transects.

Secondly, we tested for a relationship between the abundances of individual species involved in significant events and the distribution of those events on a large scale. A Mann-Whitney U test (Kendall and Stuart, 1979) was used to determine if the abundance of a species in those transects where significant adjacency events occurred was different from the abundance of that species in the sites where significant adjacency events did not occur.

Table 4. Comparisons of abundance of species from significant event types between significant and nonsignificant

| Species x | Species y | Type of association** | Number of sites | | Mann-Wh. test*** | |
|---|---|---|---|---|---|---|
| | | | Sign. | Nonsig. | sp. x | sp. y |
| Eilat | | | | | | |
| Stylophora pistillata | Stylophora pistillata | + | 14 | 47 | **(+) | No test |
| Acropora hemprichii | Acropora hemprichii | + | 7 | 35 | **(+) | No test |
| Echinopora gemmacea | Echinopora gemmacea | + | 6 | 40 | **(+) | No test |
| Montipora lobulata | Porites lutea | +/− | 3 | 21 | n.s. | n.s. |
| Favia stelligera | Millepora dichotoma | − | 1 | 0 | No test | No test |
| Leptoseris tubulifera | Favia speciosa | − | 1 | 0 | No test | No test |
| Heron | | | | | | |
| Acropora cuneata | Pocillopora damicornis | − | 8 | 21 | n.s. | **(+) |
| Acropora cuneata | Symphyllia radians | − | 1 | 0 | No test | No test |
| Pocillopora damicornis | Porites lichen | − | 10 | 11 | **(+) | **(+) |
| Acropora aspera | Acropora millepora | − | 2 | 3 | n.s. | n.s. |
| Acropora millepora | Porites lutea | − | 1 | 0 | No test | No test |
| Caribbean* | | | | | | |
| Montastrea annularis | Montastrea annularis | − | 6 | 15 | **(+) | No test |
| Siderastrea siderea | Siderastrea siderea | − | 6 | 22 | **(+) | No test |
| Meandrina meandrites | Diploria labyrinthiformis | + | 1 | 0 | No test | No test |

\* Caribbean-10 results; Caribbean-5 was similar but with fewer significant species pairs
\*\* Indicates whether species were more, or less often neighbors than expected by chance
\*\*\* **, p 0.01; n.s., not significant; (+) species significantly more abundant in sites with significant species pairs

## RESULTS

### Small-scale spatial pattern

The results of tests for significant adjacency patterns are presented in Table 2. Although a large number of Fisher's tests showed significant results, particularly in Eilat, the number of different species involved in these Fisher's tests was relatively small compared with the number of species pairs possible. The number of species pairs that were significant after the binomial tests was very small (Table 2, row e).

Not surprisingly, the analysis of the Caribbean data set, with a space between colonies being defined as gaps greater than 10 cm rather than 5 cm, produced both higher frequencies of adjacencies and a larger number of species pairs that showed significant Fisher's tests. However, the number of pairs significant after the binomial tests increased only from 3 to 5 when using the more conservative 10 cm gap criterion.

A limitation of the Heron and Eilat data is that corals up to 20 cm apart could have been represented as adjacent. The results, therefore, are potentially biased in favour of showing some species as clumping together when actually they are random or overdispersed with respect to each other.

Attention should be drawn to the problems inherent in applying Fisher's exact test to the frequency of adjacency events in line transects. In a sequence of 3 adjacent organisms, there are 2 adjacency events. However the middle organism of the 3 is 'used' twice in recording the adjacencies. This has the effect of reducing the underlying error term, because errors are partially correlated, and the result of this is to boost the significance level of the test. In other words, the Fisher's tests will produce more significant departures from random than actually exist. In our study, more corals will appear to have neighbors in a non-random manner than is really the case. Table 4 may show more species associations to be significant than it should.

### Coupling between scales

The frequency analyses testing the independence of significant adjacency events and the large-scale spatial pattern are shown in Table 3. All $\chi^2$ results were nonsignificant suggesting that the frequency of significant adjacency events does not vary between reef zones, after the abundance of the benthic species has been taken into account.

The Mann-Whitney results, given in Table 4, are a test of whether individual species effects can be observed on a large scale. Do species involved in significant local scale events show a large-scale varia-

tion in abundance related to the large-scale distribution of those significant local scale events?

At Eilat, *Stylophora pistillata*, *Acropora hemprichii* and *Echinopora gemmacea* were significantly more abundant in transects where they were positively associated with themselves (i.e. clustered) on a local scale. *Montipora lobulata* and *Porites lutea* were involved with each other in significant local scale events with a sometimes negative, sometimes positive association. However, their abundance in transects where the association was non-random was not significantly different from their abundance in transects where the association was random.

At Heron reef, 2 species were more abundant in transects where they were involved in non-random association patterns. These were *Pocillopora damicornis* and *Porites lichen*. Note that intraspecific effects were not studied at Heron because of the point sampling method employed there.

In the Caribbean, *Montastrea annularis* and *Siderastrea siderea* were more abundant in transects where their respective distributions were overdispersed. No interspecific cases of large-scale differences in abundance were found in the Caribbean.

## DISCUSSION

The results indicate that, at the local scale, the neighbors of corals are mostly random and that our null hypothesis is largely supported. There were however some non-random neighborhood patterns observed. Viewed in isolation, these non-random cases are of autecological significance for the species concerned. However, from the viewpoint of community ecology, we need to assess whether the processes leading to the few significant results described in Table 4 are a dominant influence on community structure. On a local, within-transect scale the small number of interspecific cases of non-random neighbor events at all three sites indicates that such patterns are important only when the species pairs involved represent the bulk of the assemblage.

On the larger, between-transect scale the results can be viewed in the same two ways described above for the small scale patterns. Firstly, dealing with all species at once, the 'community ecology' approach, we can ask whether the processes causing specific individuals to have other species as neighbors with unequal probability have an observable large scale effect. To this end, we tested whether the variation in frequency of significant neighborhood events among the groups of transects (the large-scale structure discussed earlier) was independent of those groups. Since none of the tests was significant (Table 3) we conclude

that these processes alone do not have an overriding influence on the pattern seen on the large spatial scale. This was true for both the geographic scale groups (Caribbean) and the reef zone scale groups (Heron and Eilat).

Having found that the significant neighborhood events taken collectively show no relationship with the large-scale structure in any of the data sets, we now adopt the second approach and deal with individual species. Retreating from the community level to that of single species, a different kind of structure was imposed on each set of data. We tested whether the between-transect distribution pattern of significant neighborhood events involving a particular species mapped onto the distribution of that species. These were the Mann-Whitney tests of Table 4.

The general result of these tests is that at Heron there were 2 species that were more abundant in those transects where they were involved in non-random neighbor events with other species. Similar interspecific effects were not found at either of the other 2 sites. Three species at Eilat were significantly more abundant in transects where they occurred next to a conspecific individual more often than expected by chance. In the Caribbean, 2 species were more abundant in transects where they occurred next to a conspecific individual less often than expected by chance.

The results obtained here indicate that the distributions of these species (Table 4) are likely to be influenced by local scale adjacency phenomena. Note that *Pocillopora damicornis* was found with fewer *Acropora cuneata* and *Porites lichen* neighbors than expected in some of the transects at Heron and was also found to be significantly more abundant in those transects. This same species, *P. damicornis*, is cited by Sheppard (1982a) as one of the main framework builders in Indo-Pacific reefs and among the most highly aggressive species.

In ecosystem theory we have, as yet, no parallel to the multiscale approaches that are developing in other fields (e.g. fractal theory – Mandelbrot, 1977; renormalization group – Wilson, 1979). However, the search for macroscopic ecological theories is long-standing, as indicated by the popularity of stability and diversity concepts. Ulanowicz (1979a, b) proposed a 'self-organizing' cabability as yet another macroscopic property of ecosystems, and observed that 'radical progress in the understanding of ecosystems will ensue only by expanding the scales of observation'. While this is probably true, at present it is unclear which ecosystem properties are best observed and at what scales.

The question of how best to analyse complex ecological systems is an equivocal, divisive issue among ecologists (e.g. Levins and Lewontin, 1980; Simberloff,

1982). Many community ecologists have a scale-oriented, often hierarchical, concept of ecosystems (assemblages, communities), so why is it not clear how best to tackle the analyses of these hierarchies? Although the idea of a multi-dimensional niche is generally accepted as a good way to describe the relationship between species and their environment there is no such well-ordered concept for entities at the community level. Classifications of species tend to have large spans with few levels because the classifications are based on relatively few biological aspects of the assemblages. A good example is the trophic-level concept where the criterion for allocating a species to a particular trophic level is very simple and ignores the many other interactions an organism has with its environment. Parenthetically, May (1983) reported the interesting finding of Briand that food webs in 2-dimensional environments (benthic) tended to be wider and shorter – more species per trophic level and fewer trophic levels – than food webs in 3-dimensional environments.

In the light of these prevailing conceptions of ecosystems, our results highlight the difficulties involved in the analysis of community-wide patterns and point to the problem inherent in extrapolating analyses of single processes to the community level. In an assemblage of more than a few species it may be that analyses of one or a few processes will not suffice to dissect, or explain, hierarchies with each level containing a very diverse array of entities. For the same reasons, single-factor explanations are a malediction for sociologists (Bennett and Dando, 1983) dealing with similarly complex systems.

## CONCLUSIONS

Coupling between small and large scale patterns through processes influencing individual (colony) neighbors is very weak at the multi-species community level but strong for a few individual species, and these cases should be investigated. This supports and extends the similar conclusions drawn by Bradbury and Young (1983) for the Heron data set and those of Bak et al. (1982) in the Caribbean. In addition to incorporating data from a variety of coral-reef habitats, both shallow and deep, the present analysis has covered a greater variety of spatial scales.

The 'null hypothesis = random distribution' approach taken here has highlighted the important correlation between local neighborhood patterns and large-scale distribution for a few coral species. Possible causal mechanisms for this correlation include processes like interspecific aggression, partial mortality of colonies and reproduction by fragmentation. The

problem remains that for many species the null hypothesis was accepted and this can shed no light on the complex of factors influencing these species' distributions. In spite of this, our results indicate that links between levels of organization in ecological communities can be examined by avoiding the 2 extremes of single-factor explanation and superorganism approach, both of which are inappropriate for community ecology (Levins and Lewontin, 1980).

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