A statistical analysis of coral community responses to the 1982–83 El Niño in the Thousand Islands, Indonesia

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Abstract. Changes in species composition of coral communities at South Pari and South Tikus Islands, Indonesia, were examined through six sampling occasions over the period 1981 to 1988. In addition to computation of standard univariate measures of species diversity, techniques developed for use with soft-sediment community data were applied. These included graphical descriptors (k-dominance curves) and multivariate ordinations (multidimensional scaling), together with associated nonparametric multivariate significance tests which allowed hypotheses about community change to be examined. Both univariate and graphical methods illustrated clearly the major community changes following the 1982–83 El Niño, though the multivariate techniques were more sensitive in monitoring the recovery stages in later years.

Introduction

Long term changes in the structure of coral communities as a result of both natural and anthropogenic disturbances have principally been studied by analyses of changes in univariate measures such as total percentage coral cover and various diversity and evenness indices (Tables 1 and 2 in Brown and Howard 1985). Multivariate statistical methods have been used in few cases (e.g. Tomascik and Sander 1987). By contrast, studies of perturbations of soft-bottom (sand and mud) communities have involved a broader range of analytical techniques, perhaps because of the possibility of more strictly quantitative sampling. In addition to the "traditional" univariate measures such as species diversity, graphical depiction of relative species abundances is frequently employed, for example the rarefaction curves of Sanders (1968), the k-dominance curves of Lambshead et al. (1983) or simple rank species abundance curves. Also a wide variety of multivariate classification and ordination methods is used (Clarke and Green 1988). With adequate sample replication, the statistical significance of changes in the univariate indices can be assessed using standard tests, but methodologies for testing differences between graphical distribution plots and multivariate structures have only recently been developed (Clarke 1988, in press), employing permutation/simulation tests. Also fairly recently, the level of taxonomic discrimination required to detect community level changes has been investigated, and in many cases the response has been clearly demonstrated using data on higher taxa (genera, families and even phyla), with little loss of information compared with the species level analyses (Warwick 1988 a, b; Heip et al. 1988). Low levels of perturbation in communities may be detected with greater sensitivity using multivariate rather than univariate analyses (Warwick et al., in press). All these recent developments have greatly improved the utility, sensitivity and cost-effectiveness of the community approach to biological effects monitoring. Here, we take the opportunity of testing some of these techniques on coral community data concerning the damage and recovery of two reefs in the Thousand Islands complex, Indonesia, resulting from the 1982–83 El Niño.

Methods

Sampling design

The previous paper (Brown and Suharsono, 1990) gives details of the background, sampling sites and sampling methods for coral data from the islands of South Pari and South Tikus, Indonesia, for the years 1981, 1983, 1984, 1985, 1987 and 1988. Ten 30 m line transects, taken perpendicularly to one main transect at each site, were sampled in each year. The transects at a site are treated in this paper as independent replicates for each year; they were all at approximately the same depth and no consistent changes in community structure across them are apparent in the multivariate ordinations described later. It is not clear how one could carry out a formal test for this absence of a "block effect" (in what is a multivariate equivalent of a two-way layout with one replicate per cell) but the analogy with the univariate case shows that the treatment of transects as ("non-blocked") replicates is a conservative procedure. That is, the multivariate tests for comparison of years, described later, will underestimate the true statistical significance of any differences in community structure.

Univariate indices

Following Tomascik and Sander (1987) we calculated total coral cover and, based on the total coverage of each individual species on each transect, the species richness (Margalef's d), Shannon diversity (H') and evenness (Pielou's J), using logarithms to the base e in the calculations throughout. The significance of year to year changes in these measures was determined by oneway ANOVA. The same analyses were repeated with the species data aggregated to genus level (there were 75 species in 24 genera).

Graphical descriptors

k-dominance curves (Lambshead et al. 1983), in which the species are ranked in order of dominance on the x-axis (logarithmic scale) with percentage dominance on the y-axis (cumulative scale), have been constructed for the totals of the ten replicate transects in each year, and for the individual replicates separately to visualise variability within years. The significance of differences between years has been tested by comparison with similarity of replicate samples within years. For any pair of replicate samples j and k, a difference measure is computed as:

$$D = \Sigma_i |y_{j(i)} - y_{k(i)}|,$$

where, for example, $y_{j(i)}$ is the cumulative percentage dominance for the ith most dominant species in replicate j. When computed for all replicate pairs, either between or within years, the D values can be ranked and the ranks displayed in a lower triangular dissimilarity matrix. A test of the hypothesis that differences in dominance curves are no greater between than within years can then be performed, exactly as described for the dissimilarities between all sample pairs that arise from a multivariate analysis; see the description of Analysis of Similarities (ANOSIM) in the next section.

Multivariate methods

Multi-Dimensional Scaling ordination (MDS, Kruskal and Wish 1978), a nonparametric method which uses the rank order of similarities between samples rather than their absolute values, was chosen because it has several conceptual advantages over other methods (Clarke and Green 1988) and has been shown empirically to be very robust for analysing benthic data. The ordination procedure results in a scatter plot in which each replicate sample is represented by a point, the distances between points following (ideally) the same rank order as the pairwise dissimilarities in species composition between samples. The extent to which this ideal is realised, in a two-dimensional plot say, is indicated by a "stress" coefficient.

The Bray-Curtis measure of dissimilarity δ (Bray and Curtis 1957) was used on the square-root transformed species coverage data, and also with the species aggregated into genera. δ takes values in the range (0,100), where $\delta = 0$ only if two samples have identical patterns of species (genera) cover, and $\delta = 100$ corresponds to a situation in which the two samples have no species (genera) in common.

The ANOSIM test (Clarke 1988) was used to assess the significance of differences between years. This program ranks the elements of the Bray-Curtis dissimilarity matrix computed between all samples, and calculates the statistic:

$$R = (\bar{r}_B - \bar{r}_W)/[N(N-1)/4],$$

were N is the total number of replicates across all years, $\bar{r}_B$ is the average ranked dissimilarity *between* every pair of replicates from different years and $\bar{r}_W$ is the average ranked dissimilarity for every pair of replicates *within* the same year. Clearly, R = 0 corresponds to the situation where there are no year to year differences, so that all samples look like replicates from a single population. The denominator of R is chosen so that R can only take values in the range

$-1 < R < 1$, with R = 1 corresponding to the case where all replicates within a year are more similar to each other than to any replicates in another year. (Significant negative values of R occur only if replicates within a year are more similar to those in other years than to each other, an unlikely event in practice.)

Some care has to be taken in constructing a test for significant year-to-year differences (R > 0) because the rank dissimilarities making up the mean ranks $\bar{r}_B$, $\bar{r}_W$ are far from being statistically independent variables. However, such problems can be avoided altogether by a randomisation procedure, in which the observed value of R is compared with simulated values under the "null" hypothesis of no year to year differences. The simulated values are obtained by repeatedly assigning the full set of replicates arbitrarily to the different years (with the same number of replicates assigned to each year as for the real data), and recomputing R. If the observed value of R is greater than 95% of the simulated values, the null hypothesis is rejected at the 5% significance level. Follow-up tests on individual year pairs can be carried out in the same way, though note that these are not true multiple comparison tests because they do not allow for the multiplication of "Type I" errors arising from repeated significance tests.

The species responsible for the discrimination observed between years in the multivariate analysis can be ascertained by dissection of the Bray-Curtis dissimilarity matrix. For each pair of years, and separately for each species (i), an average is computed of contributions ($\bar{\delta}_i$) to the dissimilarities between all possible cross-year pairs of replicates. These averages can then be ranked across species, to give an ordering from most to least important species in the determination of that year to year difference. Summed over all species, this gives the average dissimilarity ($\bar{\delta}$) between the two years, and the percentage contribution of each species to that overall dissimilarity can be determined and cumulated across species (as in Tables 3 and 4).

Results

Univariate indices

In most cases there were significant differences in univariate measures between years ($P < 5\%$), using global F-tests, except for d at the generic level at South Pari ($P = 9\%$), and J at the species level at South Tikus ($P = 33\%$).

At South Pari (Fig. 1) there was an immediate drop in coral cover after the El Niño (between 1981 and 1983), followed by a gradual recovery, although even by 1988 total cover was lower than in 1981. The number of species, species richness (d) and species diversity (H') also dropped significantly after the El Niño, but by 1985 had recovered to the pre-El Niño (1981) level, after which (in 1987 and 1988) there was a further reduction. Evenness (J) did not follow this pattern: it was not significantly reduced immediately after the El Niño, but was significantly reduced by 1984, after which it followed a similar pattern to d, H' and J. The same trends were also apparent at the generic level for all indices except Evenness, although they were less clear-cut (i.e. greater overlap of confidence intervals and fewer significant differences in multiple comparisons of means). Evenness increased significantly after the El Niño, gradually declining to a level similar to that of 1981 by the end of the sampling period (1987 and 1988).

At South Tikus (Fig. 2), there was a sharp post-El Niño decline in total cover, number of species, species richness and Shannon diversity, followed by an apparent gradual recovery until 1985, but not achieving 1981
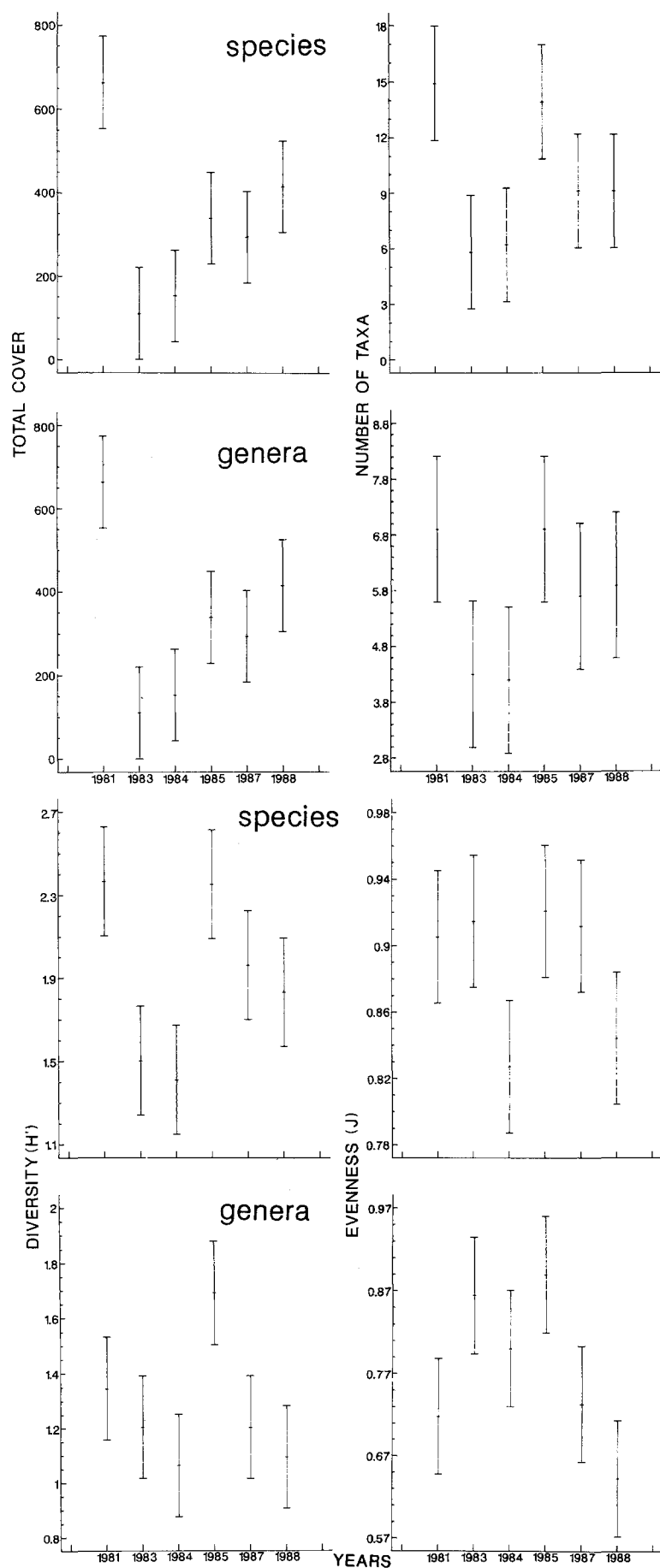
Fig. 1. South Pari. Yearly changes in univariate indices: total cover (cm/30 m), number of taxa, Shannon Diversity and Evenness. Mean and 95% confidence intervals are displayed, for species (first and third row) and genera (second and fourth row). The pattern for Species Richness was virtually identical to that for the number of taxa, and is therefore not shown
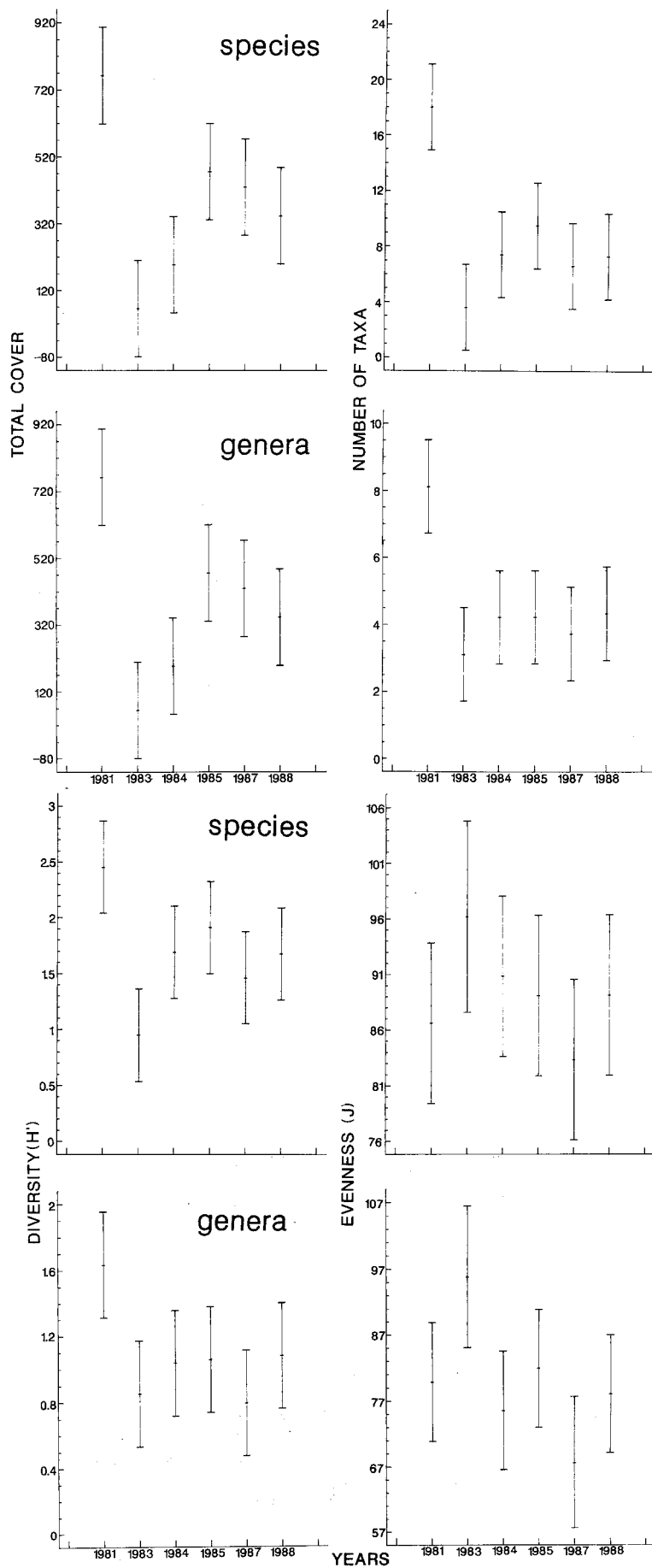
Fig. 2. South Tikus. Yearly changes in univariate indices, as for Fig. 1
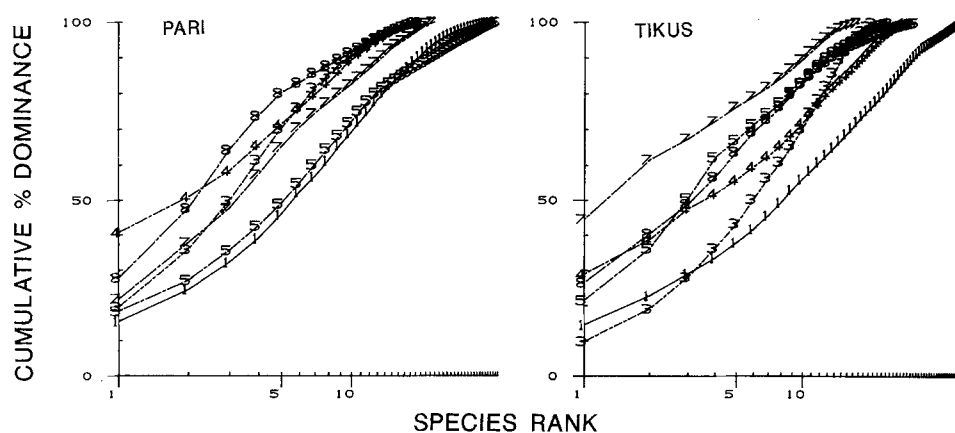
Fig. 3. k-dominance curves for totals of all 10 replicates in each year for Pari and Tikus. 1=1981, 3=1983 etc.
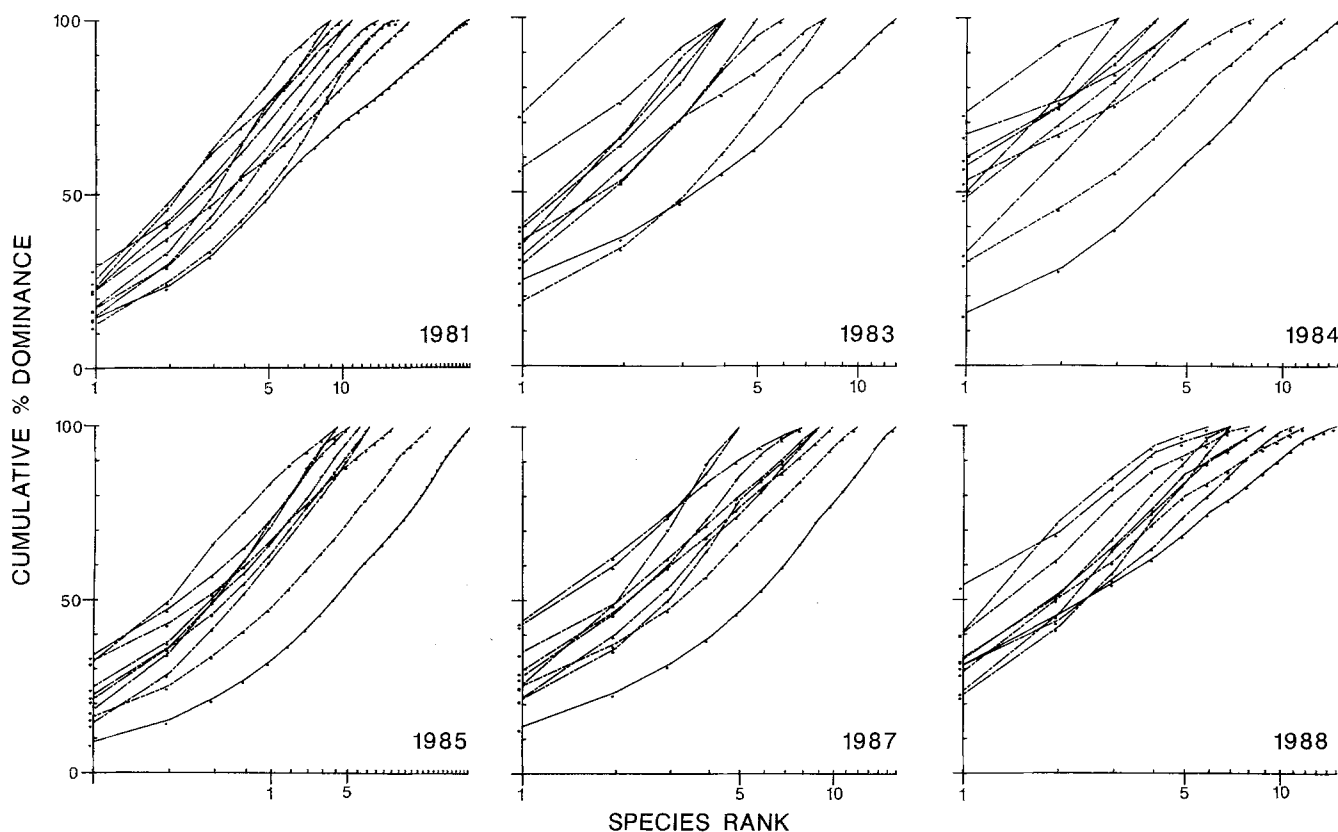

Fig. 4. Individual k-dominance curves for each replicate in each year at South Pari. Note the increased variability after 1981 and the decrease by 1988

levels, remaining stable thereafter. The changes in evenness were not statistically significant. As at Pari, similar trends were evident at the generic level, but in this case they were almost as equally clear-cut as for the species level analyses.

Graphical distributions

There is an immediate post-El Niño reduction in diversity, as indicated by k-dominance species curves for the replicate totals in each year (Fig. 3) for South Pari (curves for 1983 and 1984 are entirely above that of 1981). In 1985 there is a return to the pre-El Niño condition, the curves for 1985 and 1981 being closely coincident. There is a subsequent reduction in diversity, with the curves for 1987 and 1988 being close to those of 1983 and 1984. At South Tikus, though the 1981 and 1983 curves start from similar points, the 1983 curve is much steeper, reflecting the large reduction in numbers of species. From 1984 onwards the curves lie entirely above that of 1981, indicating a reduced diversity profile with no apparent recovery.

These conclusions can be examined more formally by ANOSIM tests, which compare the variability in k-dominance curves between replicates with that between years. Variability in replicate curves for South Pari increases considerably between 1981 and 1983, with a gradual re-

Table 1. Results of the ANOSIM test for differences between cumulative species dominance curves in pairwise comparisons between years

Years compared	Pari		Tikus	
	Statistic value (R)	% Sig level	Statistic value (R)	% Sig level
(1983, 1981)	0.39	0.1	0.59	0.1
(1984, 1981)	0.45	0.3	0.20	2.4
(1984, 1983)	−0.01	52.2	0.08	11.8
(1985, 1981)	−0.05	92.6	0.19	2.8
(1985, 1983)	0.34	0.3	0.18	2.3
(1985, 1984)	0.40	0.1	−0.03	58.5
(1987, 1981)	0.08	8.7	0.32	0.6
(1987, 1983)	0.11	7.0	0.03	22.6
(1987, 1984)	0.25	1.4	−0.04	63.6
(1987, 1985)	0.08	8.8	0.03	24.2
(1988, 1981)	0.25	0.3	0.27	0.8
(1988, 1983)	0.07	13.1	0.10	6.7
(1988, 1984)	0.20	1.4	−0.04	68.2
(1988, 1985)	0.22	0.5	0.00	35.0
(1988, 1987)	−0.05	80.2	−0.03	54.4

covery to closer similarity between replicates by 1988 (Fig. 4). The ANOSIM test (Table 1) confirms the perceived difference (in Fig. 3) of the 1981 and 1985 curves from those for other years, and (less clearly) distinguishes as two separate groups (1983, 1984) and (1987, 1988). At South Tikus (figure not shown) there is again close similarity between replicates in 1981 with an immediate increase in variability in 1983. However, by 1988 the replicate curves were still highly variable. This results in fewer significant differences being detectable between the later years (Table 1), though their departure from the 1981 pattern is markedly significant in all cases. It is notable that the results of Table 1, for both Pari and Tikus, follow quite closely the patterns apparent for Shannon diversity (Figs. 1 and 2).

Multivariate analyses

The two-dimensional MDS configuration for the replicate totals for each year, with both sites in the same analysis (Fig. 5), shows that the pattern of change in species composition at the two sites is rather similar. At both Pari and Tikus, 1983 is the most dissimilar from 1981, and in 1984 and 1985 there is a gradual return towards the 1981 position. At Pari the species composition becomes slightly less similar to that of 1981 again in 1987 and 1988, while at Tikus the 1988 species composition is the most similar to that of 1981, although there is a departure from this gradual return to the 1981 composition in 1987.

The two-dimensional MDS configuration for the individual replicate species data for South Pari (Fig. 6A) shows a clear location shift to the right between 1981 and 1983. In subsequent years there is a gradual return towards the 1981 position in a horse-shoe shaped curve, but recovery to the 1981 condition is not complete. The ANOSIM test indicates that there are significant differ-

ences in species composition between all years (Table 2). The highest values for the R statistic (>0.9) are between 1981 and 1983/4, and the lowest value (0.45) is between 1987 and 1988. The pattern is very similar at the generic level (Fig. 6 B), with significant changes in species composition between all years (Table 2). Although the MDS configuration suggests less coherence of replicates and less clear differences between years, the R statistics and significance levels are very comparable.

At South Tikus (Fig. 6C) there is no obvious location shift between 1981 and 1983. Rather, there is a broad scattering of 1983 replicates around the more tightly clustered 1981 replicates, indicating the much greater variability in 1983. In subsequent years the replicates begin to converge again, but to a point located above the 1981 replicates. The ANOSIM test (Table 2) shows that the R statistics are not as high as those for South Pari, and neither are the differences between years so highly significant, but all satisfy the $P < 5\%$ criterion. The MDS configuration, R statistics and significance levels for differences between years are very similar at the generic level compared with the species level (Fig. 6C, 6D and Table 2).

For South Pari, the species principally responsible for the year to year changes in community structure (as measured by the Bray-Curtis dissimilarity) are given in Table 3, where we have only presented the data for successive years rather than all 15 possible pairwise year combinations. The initial change between 1981 and 1983 results for the most part from the almost total loss of many species, most importantly several *Acropora* species, together with *Montipora digitata, Porites nigrescens* and *P. cylindrica*. Changes between 1983 and 1984 result in part from increases in certain species, notably *Heliopora coerulea* and *Porites cylindrica* but also by losses of more species such as *Favites abdita*. Changes between 1984 and 1985 result for the most part from increases in several species, most importantly *Favia speciosa, F. pallida, Leptastrea purpurea, Goniastrea retiformis, Porites nigrescens* and *Coeloseris mayeri*. Changes between 1985 and 1987 are again dominated by losses of certain species, particularly *Heliopora coerulea, Favia pallida, Favia speciosa, Goniastrea retiformis* and *Leptastrea purpurea*, but there are also further increases in species such as *Porites nigrescens, P. lobata* and *P. lutea*. In 1988 the changes on balance result from recoveries in abundance, particularly of *Heliopora coerulea, Porites lichen, P. nigrescens* and *P. cylindrica*, but there are also a few losses such as *Porites lobata* and *Montipora digitata*.

At South Tikus (Table 4) the initial change from 1981 to 1983 again results almost entirely from losses of species, but *Acropora* species are not predominant in this respect, the most important species being *Montipora digitata, Favites abdita, Platygyra daedalea, Montipora foliosa, Pocillopora damicornis, Favites chinensis* and *Heliopora coerulea*. Changes in 1984 are dominated by increases, notably in three *Montipora* species, *M. digitata, M. foliosa* and *M. monasteriata*. Changes are dominated by further species increases in 1985, with *Porites nigrescens, P. cylindrica, P. stephensoni, Montipora digitata, M. foliosa* and *M. tuberculosa* being the most impor-
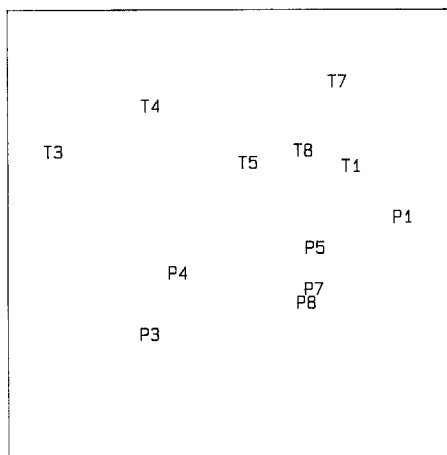
Fig. 5. Two-dimensional MDS configuration for root-transformed year totals of species cover data, showing a similar pattern for the two sites of a marked change in community composition between 1981 and 1983, followed by a gradual recovery. P = Pari, T = Tikus; 1 = 1981, 3 = 1983 etc. (stress = 0.11)

Table 2. Results of the ANOSIM test from the multivariate analyses: values of the R statistic in pairwise comparisons between years for the South Pari and South Tikus species and genera data. In all cases year differences were significant at $P < 1\%$, except those marked †, for which $P < 5\%$

Years compared	Pari species	Pari genera	Tikus species	Tikus genera
(1983, 1981)	0.91	0.83	0.43	0.55
(1984, 1981)	0.94	0.92	0.72	0.87
(1984, 1983)	0.39	0.34	0.24 †	0.33
(1985, 1981)	0.92	0.84	0.64	0.78
(1985, 1983)	0.86	0.85	0.34	0.52
(1985, 1984)	0.61	0.86	0.29	0.46
(1987, 1981)	0.84	0.69	0.50	0.50
(1987, 1983)	0.80	0.69	0.38	0.50
(1987, 1984)	0.62	0.67	0.26 †	0.46
(1987, 1985)	0.68	0.61	0.33	0.42
(1988, 1981)	0.88	0.86	0.62	0.59
(1988, 1983)	0.82	0.78	0.31	0.27
(1988, 1984)	0.63	0.76	0.50	0.50
(1988, 1985)	0.76	0.71	0.29	0.35
(1988, 1987)	0.45	0.25	0.26 †	0.24 †

tant species involved. Between 1985 and 1987 there are some reductions and some increases: those declining include *Porites nigrescens, P. cylindrica, P. stephensoni* and *Montipora tuberculosa,* and those increasing include *Montipora digitata, M. foliosa* and *Acropora hyacinthus. Montipora digitata* and *M. foliosa* both decrease again in 1988, but there are increases in *Porites nigrescens* and *P. cylindrica.*

Discussion

The immediate post El Niño effect on the coral community was dramatic and obvious. At both sites, substantial reduction in coral cover was accompanied by significant reductions in the number of species, species richness and
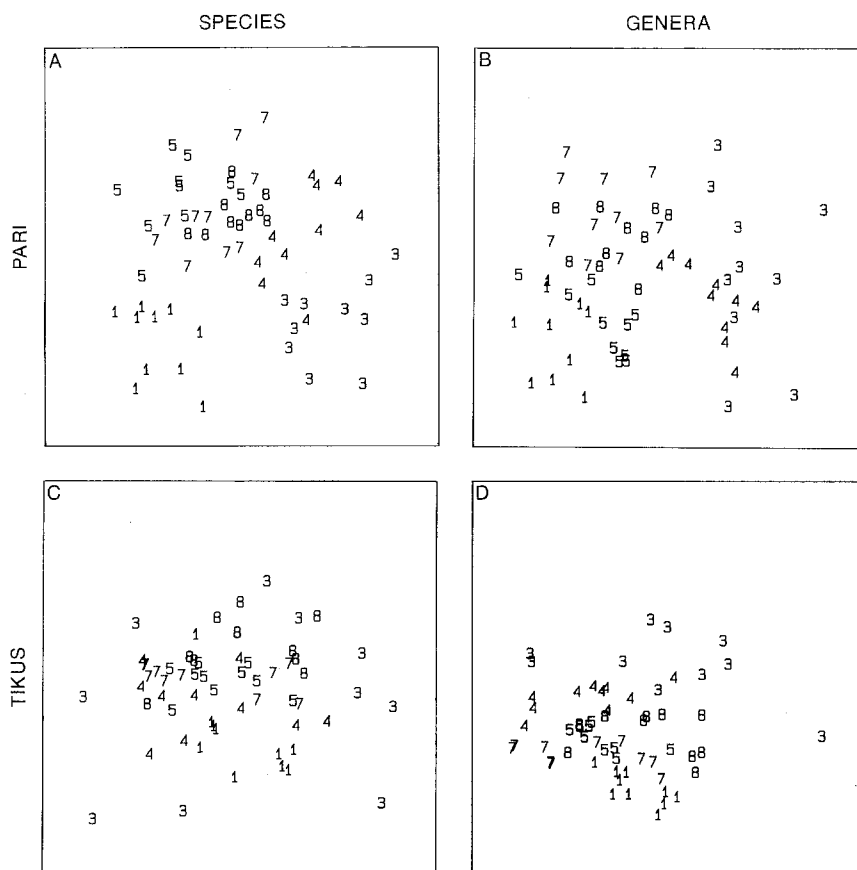

Fig. 6 A–D. Two-dimensional MDS configurations for individual replicates of root transformed species and genus cover data for Pari and Tikus (see text for interpretation). 1 = 1981, 3 = 1983 etc. (stress values: A = 0.25, B = 0.23, C = 0.19, D = 0.17)

Table 3. South Pari. Comparison between successive years in species cover (cm/30 m transect), averaged over the 10 replicates for each year. $\bar{\delta}_i$ is the contribution of the ith species to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the two years, also expressed as a cumulative percentage ($\Sigma\bar{\delta}_i\%$). Species are listed in decreasing order of importance in contributions to $\bar{\delta}$, with a cut-off at 50% of $\bar{\delta}$

Average dissimilarity between 1981 and 1983, $\bar{\delta}=81.1$

Species	1983	1981	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Acropora hyacinthus	0.0	102.3	8.1	10.1
Acropora formosa	0.0	60.9	5.8	17.2
Acropora bruegemanni	0.0	45.6	4.3	22.6
Montipora digitata	0.0	42.6	4.0	27.6
Porites nigrescens	9.6	45.0	3.9	32.4
Acropora intermedia	0.0	28.5	3.8	37.2
Porites cylindrica	2.1	30.0	3.2	41.2
Acropora grandis	0.0	18.9	3.0	44.9
Acropora palifera	0.0	21.6	2.8	48.4
Porites lichen	15.3	11.7	2.7	51.8

Average dissimilarity between 1983 and 1984, $\bar{\delta}=67.4$

Species	1984	1983	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Heliopora coerulea	62.4	21.6	7.5	11.1
Porites cylindrica	15.6	2.1	6.5	20.8
Favites abdita	0.0	12.9	6.1	29.9
Pavona varians	11.4	18.0	5.9	38.7
Porites lichen	8.7	15.3	5.2	46.5
Porites nigrescens	11.1	9.6	4.8	53.7

Average dissimilarity between 1984 and 1985, $\bar{\delta}=66.2$

Species	1985	1984	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Favia speciosa	30.0	0.6	6.0	9.1
Favia pallida	24.0	0.9	4.9	16.6
Leptastrea purpurea	20.1	0.0	3.9	22.5
Goniastrea retiformis	21.3	5.1	3.9	28.5
Porites nigrescens	18.0	11.1	3.2	33.4
Coeloseris mayeri	12.0	0.0	3.2	38.3
Heliopora coerulea	62.4	62.4	3.0	43.0
Porites lichen	15.1	8.7	3.0	47.6
Acropora formosa	11.1	0.0	2.9	51.9

Average dissimilarity between 1985 and 1987, $\bar{\delta}=65.5$

Species	1987	1985	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Heliopora coerulea	28.8	62.4	4.9	7.5
Favia pallida	0.0	24.0	4.1	13.9
Favia speciosa	5.7	30.0	4.1	20.1
Porites nigrescens	64.2	18.0	3.7	25.8
Goniastrea retiformis	0.0	21.3	3.5	31.3
Porites lobata	28.5	12.9	3.3	36.3
Leptastrea purpurea	1.2	20.1	3.0	41.1
Porites lutea	22.5	7.2	2.9	45.6
Coeloseris mayeri	9.0	12.0	2.6	49.6
Montipora digitata	16.2	2.8	2.6	53.6

Average dissimilarity between 1987 and 1988, $\bar{\delta}=54.7$

Species	1988	1987	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Heliopora coerulea	68.7	28.8	5.4	10.0
Porites lichen	39.6	0.0	5.3	19.8
Porites lobata	0.0	28.5	4.2	27.5
Porites nigrescens	115.5	64.2	3.9	34.7
Montipora digitata	5.4	16.2	2.6	39.5
Porites cylindrica	82.5	47.2	2.6	44.4
Porites lutea	26.4	22.5	2.5	49.0
Acropora hyacinthus	11.4	6.9	2.4	53.5

Table 4. South Tikus. Pairwise comparisons between years (as Table 3)

Average dissimilarity between 1981 and 1983, $\bar{\delta}=93.9$

Species	1983	1981	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Montipora digitata	3.0	63.6	6.7	7.2
Favites abdita	0.0	48.0	6.3	13.9
Platygyra daedalea	0.0	33.0	3.9	18.2
Montipora foliosa	2.4	28.8	3.9	22.4
Pocillopora damicornis	0.0	30.0	3.8	26.4
Favites chinensis	6.4	34.2	3.7	30.5
Heliopora coerulea	0.0	110.7	3.7	34.5
Acropora aspera	0.0	13.9	3.3	38.0
Pocillopora verrucosa	0.0	19.2	2.9	41.1
Porites nigrescens	4.0	12.6	2.8	44.1
Acropora pulchra	0.0	18.6	2.7	47.1
Acropora diversa	0.0	13.5	2.7	50.0

Average dissimilarity between 1983 and 1984, $\bar{\delta}=88.6$

Species	1984	1983	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Montipora digitata	57.0	3.0	14.0	15.8
Montipora foliosa	19.5	2.4	7.9	24.8
Montipora monasteriata	17.4	0.0	6.7	32.3
Porites stephensoni	6.0	4.5	4.3	37.2
Cyphastrea serailia	7.6	5.4	4.1	41.9
Montipora hispida	7.5	1.5	4.0	46.5
Porites cylindrica	8.4	3.0	3.7	50.7

Average dissimilarity between 1984 and 1985, $\bar{\delta}=71.0$

Species	1985	1984	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Porites nigrescens	68.7	2.7	7.9	11.1
Porites cylindrica	70.2	8.4	6.6	20.4
Montipora digitata	102.3	57.0	5.8	28.6
Montipora foliosa	55.5	19.5	5.6	36.5
Porites stephensoni	21.3	6.0	3.7	41.7
Montipora tuberculosa	22.5	2.4	3.5	46.7
Montipora monasteriata	14.1	17.4	3.2	51.2

Average dissimilarity between 1985 and 1987, $\bar{\delta}=70.6$

Species	1987	1985	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Montipora digitata	191.1	102.3	7.6	10.8
Porites nigrescens	12.5	68.7	6.7	20.3
Porites cylindrica	21.0	70.2	5.6	28.3
Montipora foliosa	73.5	55.5	5.5	36.2
Montipora tuberculosa	0.0	22.5	3.2	40.8
Porites stephensoni	0.0	21.3	3.1	45.3
Acropora hyacinthus	25.5	2.1	2.9	49.5
Montipora monasteriata	9.9	14.1	2.5	53.0

Average dissimilarity between 1987 and 1988, $\bar{\delta}=74.8$

Species	1988	1987	$\bar{\delta}_i$	$\Sigma\bar{\delta}_i\%$
Montipora digitata	91.0	191.1	12.4	16.6
Montipora foliosa	26.7	73.5	8.1	27.5
Porites nigrescens	48.0	12.5	6.5	36.2
Porites cylindrica	29.4	21.0	4.5	42.3
Acropora hyacinthus	23.7	25.5	4.3	48.1
Acropora bruegemanni	19.5	17.1	3.6	53.0

diversity, and significant differences in k-dominance curves. Evenness, however, was not significantly affected, so that decreases in Shannon diversity were largely due to reductions in species richness rather than the evenness component. At both sites there was a marked increase in

variability between replicate k-dominance profiles. The multivariate response was also clear-cut, and at both sites the greatest differences between years were between 1981 and 1983, which showed the highest average Bray Curtis dissimilarities (Tables 3 and 4). However, this multivariate response was different in certain respects between the two sites. At Pari, the changed species composition resulted in a marked location shift of replicates between 1981 and 1983 (Fig. 6), but the variability between replicates in these two years was roughly comparable. At Tikus there was a marked increase in variability between replicates but no clear location shift. The ANOSIM test showed significant differences between these two years at both sites, indicating a useful feature of the ANOSIM test. Though it is primarily designed to detect a location shift in a multivariate ordination, it also has some power to discriminate variability changes, i.e. dissimilarities which are consistently lower within one (or more) years than in other years. This contrasts with the analogous univariate ANOVA test, which is only sensitive to location shifts and, in fact, assumes constant variance within years.

There is general agreement between all the analyses that recovery towards the pre-El Niño condition progressed between 1983 and 1985, but that between 1985 and 1987 there was an interruption to this recovery, manifested by:

1. reductions in some of the univariate measures, and a raising of the k-dominance curve, at Pari;
2. an increase in variability between replicate k-dominance curves at Tikus;
3. a departure in the multivariate analyses from the gradual recovery towards the 1981 condition (Fig. 6), resulting largely from losses of species at both sites (Tables 3 and 4).

It is hypothesised that this interruption to the coral community recovery, which had not previously been recognised, resulted from some unidentified stress over this period.

In monitoring the subsequent recovery from the El Niño event, multivariate analyses proved in some respects to be more sensitive than the univariate measures or graphical descriptors. At Pari, by 1985 the number of species, species richness, diversity, evenness and k-dominance curves were statistically indistinguishable from those of 1981. However, the MDS (Fig. 6 A) shows that the species composition was still clearly different, and these differences were statistically significant (Table 2), comparison of 1981 and 1985 producing a very high R-statistic value (0.92). At Tikus, numbers of species, species richness and diversity had not recovered to the 1981 level by 1985, suggesting a more severe impact of the El Niño at this site, and the indications of recovery in the univariate measures between 1983 and 1988 were not marked. Also, the k-dominance curves over this period (Fig. 3) were generally overlapping and were (in all but one case) not significantly different from each other (Table 1). Multivariate analyses, however, showed clear signs of the evolution of the community towards the pre-El Niño condition, and statistically significant differences

in community composition between years. At neither site was recovery from the El Niño complete by 1988.

In both the univariate indices and multivariate analyses, response patterns were very similar when the species were aggregated into genera, with little loss of information. It is possible for data at the generic level to be collected by non-experts in coral taxonomy, and this would be much less time-consuming than the very painstaking species analysis undertaken in this study. Coupled with the use of recently developed statistical methodologies, which provide a powerful suite of techniques for assessing the extent and significance of changes in community structure, this augurs well for the utility, sensitivity and cost-effectiveness of the community approach to biological effects monitoring on coral reefs.

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