

REPORT

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Composition and community structure of the coralline algal reefs from Atol das Rocas, South Atlantic, Brazil

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Abstract Coralline-algal frameworks from Atol das Rocas reefs were sampled along windward and leeward transects, and multivariate statistical analysis was used to investigate the composition and community structure of the encrusting community. The following components of the reefs were identified in slabbed and polished reef blocks sampled along each transect: encrusting coralline algae dominated by *Porolithon* cf. *pachydermum*, vermetid gastropods, *Homotrema rubrum*, acervulinid foraminiferans, molluscs, corals, polychaete tubes, clioid sponge borings, polychaete/sipunculid borings, cemented sediments, and growth cavities. Q-mode cluster analysis correctly classified 78% of all windward samples and 69% of all leeward samples, and R-mode separated reef components adapted to high wave energy environments from those adapted to low wave energy. Separate classification and ordination of samples from each transect indicate that seriation breakdown occurs in the windward reef between 25 and 45 m from the reef front. In the leeward reef between 75 and 90 m from the leeward reef front, seriation breakdown was not found to be significant. These results confirm that seriation (zonation) is best developed in the windward reef, as has been documented in coral-dominated reefs.

Introduction

Variations in the structure of frameworks from tropical intertidal coralline-algal buildups are strongly controlled by hydrodynamic energy. Massive coralline algal ridges

are well developed in windward settings of Indo-Pacific coral reefs (Ladd et al. 1950), and well-developed algal reefs are also found in the Caribbean (Adey and Burke 1976). Moderate wave energy favours rapid vertical growth characterised by branching, porous, and uncemented frameworks, while high wave energy favours slow but compact growth where thick coralline crusts form dense and less porous frameworks (Adey 1978; Bosence 1983; Adey 1986; Gherardi 1996; Gherardi and Bosence 1999). The hydrodynamic energy gradient on reefs in general is thought to produce compositional changes in the structure of reef-building communities such as clear-cut zonation patterns (Sheppard 1982; Wellington 1982; Grauss and Macintyre 1989). ‘Zonation’ describes the generation of discontinuous bands of different assemblages of reef-building organisms. However, in the example studied here (Atol das Rocas), this is not the case as there are continuous changes in community structure across the reef flat from windward to seaward sites. We therefore prefer to use the more general term ‘seriation’ to describe such changes and suggest that zonation should be considered a special case of seriation (cf. Clarke et al. 1993).

Atol das Rocas is a unique coralline-algal atoll located in the equatorial South Atlantic close to the northeast Brazilian continental shelf. This atoll is differentiated from Indo-Pacific and Caribbean reefs by the following:

1. A reef rim composed almost exclusively of coralline red alga, vermetid gastropods, and encrusting foraminiferans. This is supported by evidence shown in this study and from shallow drilling (Gherardi 1996).
2. A lagoon restricted to the northeast part of the atoll with a maximum depth of 5 m and the central part of the atoll are dominated by an intertidal hard ground over which most of the reef-derived coralline algal dominated detritus is transported.
3. No association between coralline-algae and coral frameworks is found in excavated blocks (this paper),

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and in the extensive shallow (≤ 1 m) drilling programme carried out on the atoll (Gherardi 1996).

Radiocarbon dating of drilled frameworks (Gherardi 1996) showed that the oldest top-core samples, collected from the reef-crest and reef-flat system, are SRR5528 – 1720 ± 45 conventional ^{14}C years and SRR5531 – 1500 ± 45 ^{14}C years, respectively (NERC Radiocarbon Laboratory, UK). These samples were collected from eroded surfaces, which can be easily differentiated from the surrounding modern reefs. Conventional radiocarbon dates from windward and leeward reef-crest top-core samples collected from modern reefs in the same localities of the surveyed transects gave the following ages: leeward (SRR5545) – 655 ± 45 ^{14}C years; windward (SRR 5542) – 490 ± 45 ^{14}C years. Reef samples used in the present study come from modern reefs (based on the above evidence) and all surfaces bearing any evidence of antiquity were avoided.

This paper uses numerical data derived from point counts of slabbed reef-surface samples collected from windward and leeward reef transects to characterise the reef framework composition and community structure. Multivariate statistical techniques were applied to these data to investigate the differences in community structure of Atol das Rocas reefs between and within transects, and to quantify the influence of decreasing hydrodynamic energy from the reef front/reef crest to the inner reef flat on the community seriation pattern.

Component classes identified from both windward and leeward reef sites are: coralline red algae, vermetid gastropods, encrusting foraminifera *Homotrema rubrum*, encrusting acervulinid foraminiferans, molluscs, corals, polychaete tubes, clionid sponge borings, polychaete/sipunculid borings, cemented sediments, and growth cavities. The main reef framework builder is the coral-line algal genus *Porolithon* cf. *pachydermum* which occurs associated with four other coralline algae: *Popolithon* sp.; *Lithophyllum* sp.; *Lithoporella* sp.; and *Sporolithon* sp. (Gherardi and Bosence 1999).

Our results indicate that the frameworks of these reefs are predominantly constructed of coralline algae, that high energy windward frameworks can be differentiated from more protected leeward frameworks, and that there is a gradual change in community structure across the reef flat rather than a well-established zonation.

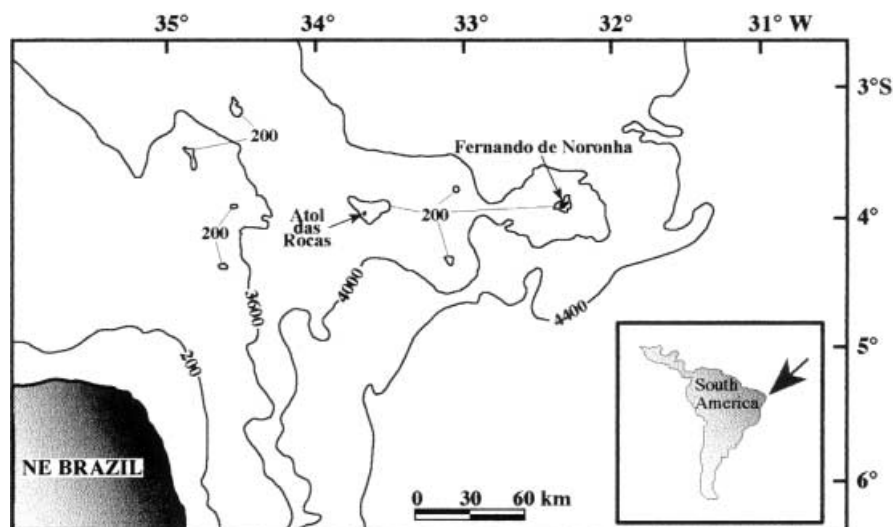
Materials and methods

Study area

The Atol das Rocas is situated in the Atlantic Ocean south of the equator at latitude $3^{\circ}51'S$, longitude $33^{\circ}49'W$, 266 km offshore and northeast of the city of Natal (Rio Grande do Norte State/northeast Brazil; Fig. 1). It is an oceanic atoll with a shallow (< 100 m) elliptical platform 28×8 km, and a more or less continuous raised reefal rim (the term reef rim is used here to designate the structure composed by the reef front, reef crest, and reef flat that encircles the sand-flat). The atoll has a slightly elliptical shape, measuring 3.5×2.5 km, interrupted by the northeast and the northwest reef passes (Fig. 2). Like the neighbouring Fernando de Noronha archipelago, it is thought to rest on a volcanic pedestal rising some 4000 m from the sea floor (Ottmann 1962; Gherardi 1995; Kikuchi and Leão 1997). The direction and speed of the trade winds in the Atol das Rocas area vary seasonally, with a frequency of 50% for SE winds and 35% for E winds during the austral summer. There is an intensification of SE winds during the winter to a frequency of 70%, with 25% for E winds, and a maximum wind speed of 11 m s^{-1} (Höfllich 1984). Waves are wind generated and are concentrated on the SE portion (windward) of the atoll, although wave refraction on the atoll shelf can also generate large breaking waves on the leeward side (SW and W parts of the atoll; Fig. 2). There are also historical accounts of storm waves hitting the atoll during the months of September and October (Rodriguez 1940). Mean wave heights measured on the nearby island of Fernando de Noronha, 110 km to the east, vary from 1.1 m in February and April to 1.6 m from July to September (Höfllich 1984). Periodicity of storm surges has not been determined, but they occurred twice during 1999 and 2000.

The tide regime in the atoll is semi-diurnal and mesotidal with an HHWS (highest high water springs) height of 3.8 m above zero datum. This large tidal range ensures that a large portion of the atoll profile is affected by breaking waves twice a day, that the whole atoll is subaerially exposed at low tide and that the atoll is

Fig. 1 Location and general bathymetry of the Atol das Rocas and Fernando de Noronha archipelago. Depth contours are in metres (after Zemruski and França 1976)



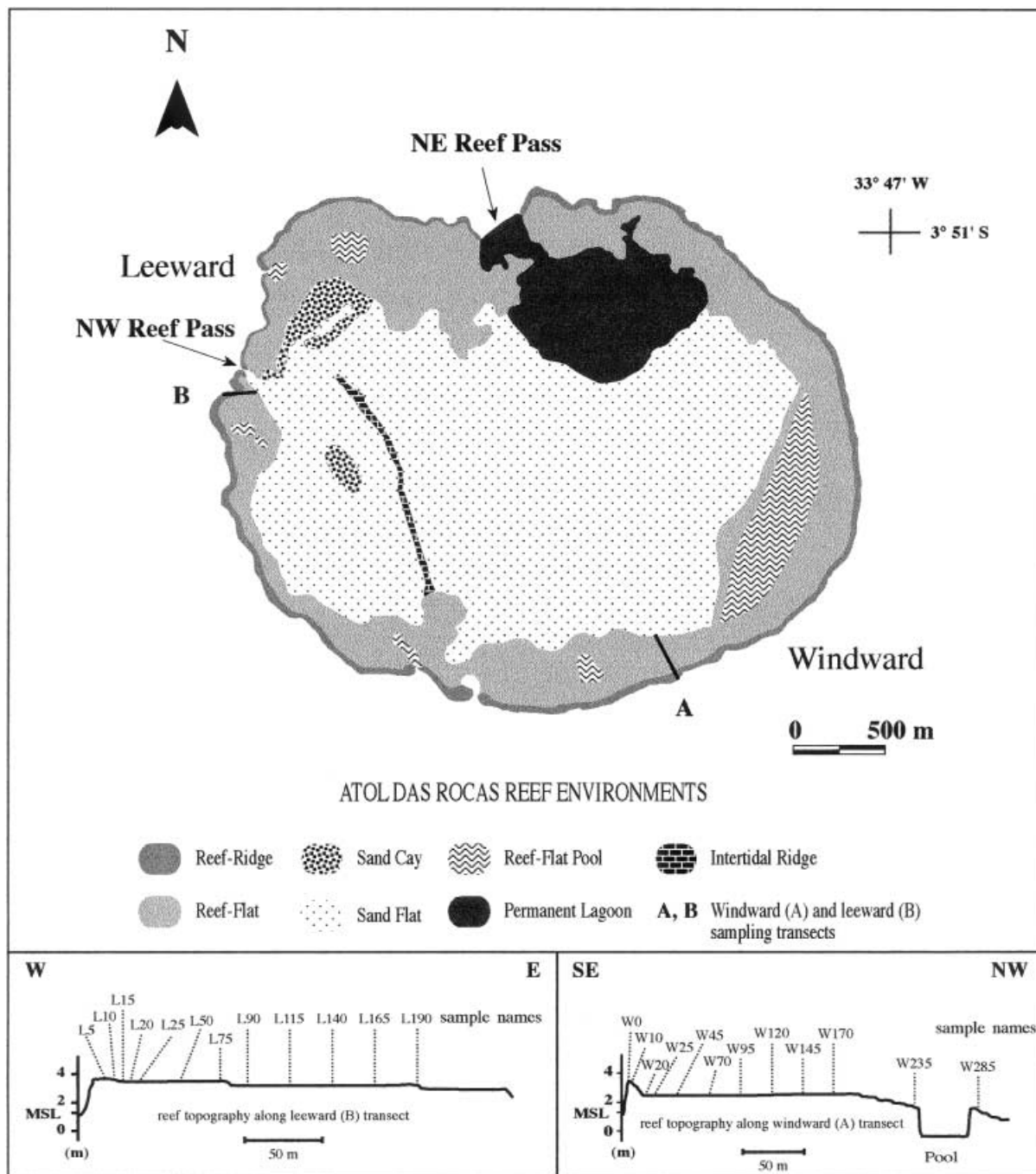


Fig. 2 Reef environments on Atol das Rocas and location of sampling transects

swept by strong tidal currents as the lagoon drains out on the falling tide. Atol das Rocas is dominated by the South Equatorial Current (SEC) which is essentially driven by atmospheric forcing (Peterson and Stramma 1991). Based on data collected by ship drifts, Richardson and Walsh (1986) found that the SEC along the 4° parallel (thus crossing Atol das Rocas) has a mean speed of 30 cm s^{-1} and the seasonal variation of velocity around this annual mean is 10 cm s^{-1} . Salinities of surface waters are around 36 and 37‰, and monthly mean sea surface temperature varies from 26 °C in September to 28.3 °C in April (Höflich 1984; Servain et al. 1987).

Field and laboratory techniques

The atoll environments (Fig. 2) were mapped using two TM-Landsat images (bands 1, 2 and 4) between 30 June 1991 and 7 November 1992. These were processed by the Instituto Nacional de Pesquisas Espaciais-SP (Brazil), nautical chart (No. 51) issued by the Serviço de Hidrografia e Navegação – Marinha do Brasil, and by extensive field surveying using GPS (global positioning system). Collection of large (20- to 30-cm-long and 10- to 18-cm-wide) surface reef samples was undertaken using a hammer and chisel along a transect perpendicular to the reef crest across the reef rim on the

windward and leeward sides of the atoll (Fig. 2). When single, large reef samples could not be collected, a sequence of smaller samples were collected from the same point. Samples were collected from 25 sites at 5- to 25-m intervals distributed as follows: 13 from the windward transect and 12 from the leeward transect. Two samples from the windward reef front (W0) were also used so that the whole reef-lip structure could be represented. A sampling procedure based on transect lines was deliberately chosen so that visual differences in reef structure (reef crest vs. reef flat) as seen in the field could be related to community gradients (internal or taxometric analysis sensu Gauch 1994, p 37).

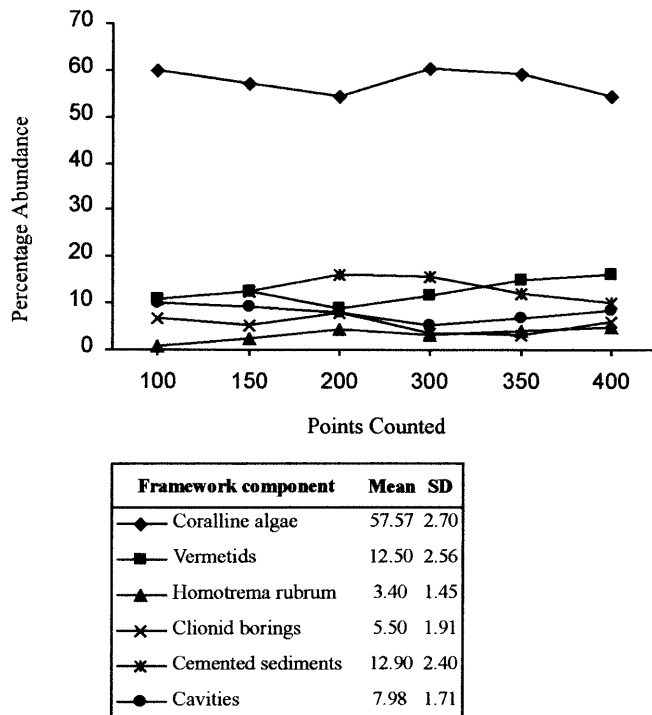


Fig. 3 Percentage abundance of each framework component of a windward reef-lip sample as a function of total number of points counted. Mean and one standard deviation show little variation of relative abundances despite the wide range (from 100 to 400 points) of total points counted. All framework components could be recorded within this range

Samples were vertically slabbed, polished, and one surface was point counted using a 8 × 8 mm grid printed on a plastic transparency sheet. The number of points counted varied from 167 to 639 (average 293) according to sample size. Results from rarefaction curves (Fig. 3) indicated that a minimum of 150 points should be counted in each sample to avoid loss of information. The reef component located under the centre point of each counted grid square was recorded to establish its occurrence and abundance (Tables 1 and 2). In the present study, the term abundance is used to indicate the percent cross-sectional area as a means to describe the relative contribution of each component to reef formation. Classification of the main components involved in coralline reef construction was based on Bosence (1984). Primary framework counts made no distinction between different coralline algae genera because this can only be achieved by inspection of thin sections. Infilling cemented sediments were counted, making no distinction between cavities generated by framework growth and bioerosion. Distinction between micritic rim cements and corallines were generally straightforward because there is a sharp colour contrast between the light-to-dark grey cements and the bright white appearance of coralline thalli.

Classification and ordination techniques

Classification (Q-mode and R-mode cluster analysis) and ordination are complementary techniques that have been adopted by a number of palaeontologists, sedimentologists and reef ecologists to represent data structure and to elucidate intrinsic patterns within data sets (e.g. Logan et al. 1984; Springer and Bambach 1985; Boss and Liddell 1987; Liddell and Ohlhorst 1987, 1988; Bak and Povel 1989; Zenetos 1991; Stemann and Johnson 1992; Clarke et al. 1993; Tanner et al. 1994; Pachut et al. 1995; Patzkowsky 1995). The multivariate techniques used here are based on the work of Clarke and Green (1988), Clarke (1993), Clarke and Ainsworth (1993), Clarke et al. (1993), and Warwick and Clarke (1993). The software package used to perform the multivariate analyses was the PRIMER v. 4.0 beta (Plymouth Routines in Multivariate Ecological Research).

To perform the Q-mode cluster analysis, initial transformation of the original abundance data is carried out using $\log(1 + x)$ to determine the relative weight given to rare and common species in assessing differences between samples. Conversely, row (species) standardisation is carried out prior to R-mode cluster analysis in place of transformation, to reduce disparities in counts between species. A similarity coefficient is applied to the transformed/standardised data producing a triangular matrix of similarities in species abundances between every pair of samples/species. This is used to discriminate sites/species from each other on the basis of their composition/abundances, to cluster sites into groups that have

Table 1 Percentage abundance of reef components in the windward (W) samples. Numbers following W are metres from the reef front

Reef components	Windward sample number												
	Reef front		Reef crest		Reef flat								
	W0	W0	W10	W20	W25	W45	W70	W95	W120	W145	W170	W235	W285
Coralline algae	67	72.3	70	48.1	37.3	44.2	48.4	36.3	37.4	54.8	48.6	38.2	59.9
Vermetids	7.3	6.5	10.2	7.7	20.3	2.7	5	3.3	2.8	0.8	4.1	2.6	3
<i>Homotrema rubrum</i>	0.6	0.7	3.4	2.2	6	5.4	10	11.1	7.5	2.5	0.5	3	3.6
Acervulinids	0	0	0	2.2	0	0	0.6	4.8	0	0.8	7.7	0	3.6
Molluscs	0	0	0	0	0	1.8	1.2	0	5.1	0	0	2.1	0
Coral	0	0	0	0	0	6.6	0	0	0	1.7	0	0	1
Polychaete tubes	0	0	0	0	4.1	0	0	0	0	0	5.9	0	0
Clionid borings	1	2	0	4.2	2.3	6.9	1.2	14	22.5	20.6	10.1	8.7	0.6
Polychaete/sipunculid borings	1.3	4.5	0	2.7	3.7	0	14.3	12.6	3.9	4.3	6.5	8.7	1.3
Cemented Sediments	21.3	11	12.5	27.2	1.3	20	13.1	5.3	3.1	7.7	3.5	7.8	19
Growth Cavities	1.5	3	3.9	5.7	25	12.4	6.2	12.6	17.7	6.8	13.1	28.9	8
Total points counted	460	400	175	400	216	200	200	266	335	200	167	228	300

Table 2 Percentage abundance of reef components in the leeward (L) samples. Numbers following L are metres from the reef front

Reef components	Leeward sample number											
	Reef crest			Reef flat								
	L5	L10	L15	L20	L25	L50	L75	L90	L115	L140	L165	L190
Coralline algae	22.4	13.2	50.7	34.2	31.4	44.4	21.1	40.1	29	37.8	36.4	22.8
Vermetids	14.8	16.3	8.1	15.9	6.6	2.9	0.9	4	3	0.8	5.8	3
<i>Homotrema rubrum</i>	9.2	5.6	3.6	3.5	4.7	1.7	2.5	4.3	7.4	8.8	7.5	6.7
Acervulinids	9.6	4	0.4	4.6	1.8	1.7	0.9	0	2.6	3.5	5.4	6.3
Molluscs	2.4	0	0.4	0.3	5.6	0	0.3	0	0.8	0.8	1.3	0.6
Coral	0	0	0	0	0	0	34.1	0	4.8	1.3	1.3	6.5
Polychaete tubes	0	0.3	0	0.3	0	0	0.4	4.3	0.8	0	1	1
Clionid borings	11.6	34.4	15	2.4	18.3	20	9.7	20	22.8	20.2	3.4	9.3
Polychaete/Sipunculid borings	18	13.7	8.5	5.6	19.6	16.4	23.4	3.6	6.6	6.6	12.3	9.3
Cemented Sediments	3.6	3.1	2	14.8	9.8	4.1	0.3	0	7.6	9.2	3	1.3
Growth Cavities	8.4	9.4	11.3	18.4	2.2	8.8	6.4	23.7	14.6	11	22.6	33.2
Total points counted	250	200	246	282	300	170	639	240	470	227	292	460

similar communities and to cluster species that tend to co-occur in similar ratios across the transects. The similarity coefficient used in the present paper is the 'Bray-Curtis' (B-C; Clarke and Green 1988; Clarke and Ainsworth 1993; see also Jackson et al. 1996) and is defined by the following equation:

$$S'_{jk} = 100 \left(1 - \left[\frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right] \right) \quad (1)$$

Here, y_{ij} represents the entry in the i th row and j th column of the data matrix, i.e. the abundance for the i th species in the j th sample ($i = 1, 2, \dots, p$; $j = 1, 2, \dots, n$). Similarly, y_{ik} is the count for the i th species in the k th sample.

With the original data matrix replaced by pairwise similarities, a hierarchical agglomerative cluster analysis (i.e. classification) is used to link samples/species that have mutually high levels of similarity. The linkage option is the group-averaging method that is more balanced and produces a moderate number of medium-sized clusters that are only grouped at a later stage (Johnson and Wichern 1992).

A non-metric multidimensional scaling (MDS) ordination is applied to the rank similarity matrix to define and visualise community patterns. This summarises the data through statements such as 'sample A is more similar to sample B than it is to sample C' (Clarke 1993; see also Pielou 1979). The graphic output of an MDS ordination is a 'map' or configuration of the samples in two (or three) dimensions, and a measure of goodness-of-fit of the ordination is given by a stress value. This stress value should be < 0.15 to minimise misinterpretation.

An index of multivariate seriation (IMS, see Clarke et al. 1993) is calculated to determine the extent to which the community changes in a smooth and regular fashion along each transect. The IMS is obtained as a Spearman rank correlation coefficient computed between the corresponding elements of two triangular matrices of rank dissimilarities. The first is that of B-C coefficients calculated for all pairs from the n reef transect samples and the second is from the inter-point distances of n points laid out, equally-spaced, along a line. If the community changes exactly match this linear line then the IMS takes the value 1. The percent significance levels calculated for each IMS are based on a Monte Carlo permutation test for absence of seriation (Clarke and Green 1988). Finally, the average dissimilarity between all pairs of inter-group samples (i.e. every sample from the windward transect paired with every sample from the leeward transect) is computed and then the separate contributions from each species to the average dissimilarity is broken down. To do so, first the B-C dissimilarity $\delta_{jk}(i)$ is calculated to give the contribution of the i th reef component to the dissimilarity between samples j and k using the following equation:

$$\delta_{jk}(i) = 100 \cdot |y_{ij} - y_{ik}| / \sum_{i=1}^p (y_{ij} + y_{ik}) \quad (2)$$

Then, $\delta_{jk}(i)$ is averaged over all pairs (j, k) to give the average contribution $\bar{\delta}_i$ from the i th reef component to the overall dissimilarity $\bar{\delta}$ between windward and leeward samples. So, the reef component with the largest $\bar{\delta}_i/SD(\bar{\delta}_i)$ ratio will be the one that will consistently contribute most to the dissimilarity between transects. This is useful in order to identify a species or a group of species and/or reef component that better discriminates the windward and leeward transects.

Results

Composition of the windward reef

The windward reef is constructed almost exclusively by the encrusting coralline red algae *Porolithon* cf. *pachydermum* (Gherardi and Bosence 1999). *Lithophyllum* is the second most important coralline algal genus present in the primary framework. *Sporolithon* and *Lithoporella* were also found but are rare in this reef section, and *Sporolithon* was not found in the reef front (Gherardi and Bosence 1999). Our point-counting indicates that up to 72.3% of the total reef framework (with an average of 70%) in the reef front is built by the primary framework builders. The relative abundance of primary framework observed in the reef crest varies from 48.1 to 70%, and attains an average of 60%. Along the reef flat, maximum abundance is 59.9% with a minimum of 36.3% and an average of 45% (Fig. 4). Coralline algal growth form varies from thick, densely overgrowing crusts in the reef front and reef crest to thinner crusts, protuberant and knobby forms in the reef-flat frameworks (for details see Gherardi and Bosence 1999).

A total of five different classes of organisms (see Fig. 4) were identified as secondary framework builders, as follows: vermetid gastropods (mainly *Dendropoma* sp.); *H. rubrum* (encrusting foraminiferan); acervulinids (encrusting foraminiferan); polychaete worm tubes; and small unidentified corals. Molluscs found in the surveyed frameworks (mainly *Hyponix antiquatus*) cannot be considered true secondary framework builders because they are not sessile organisms encrusting the primary framework, and should be simply considered as

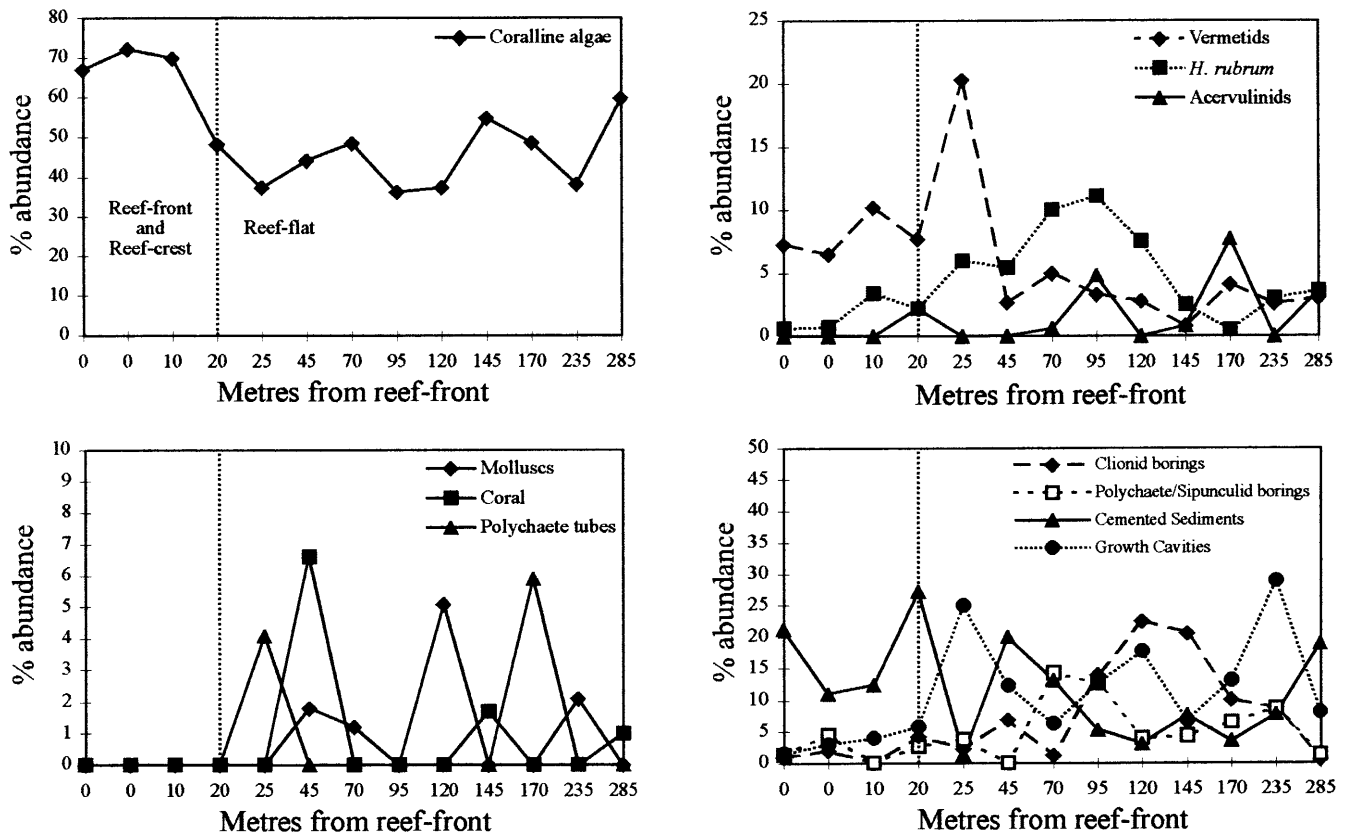


Fig. 4 Changes in percentage abundance of primary and secondary framework builders, bioeroders, cemented sediments and growth cavities along the windward reef transect

epibionts. The most abundant secondary framework builders were vermetid gastropods, with relative abundances ranging from 20.3% at the interface between the reef crest and the reef flat to 0.8% 145 m from the reef front, and an average abundance of 5.2% along the windward reef transect.

The encrusting foraminiferan *H. rubrum* is present as globose, arborescent and encrusting growth forms and may occur associated with acervulinid foraminiferans. Abundance of *H. rubrum* varies from 11.1% at 95 m from the reef front to 0.5% in the inner part of the reef flat (Fig. 4; average of 4.5% of the reef composition along the windward reef transect). Acervulinid foraminiferans have a patchy distribution occurring in only 23% of the surveyed windward reef samples (Fig. 4). Where present, they comprise 0.6 to 7.7% of the framework (average of 1.1%). Polychaete worm tubes are unimportant as a secondary framework, although they occur in almost all samples. Their presence reaches a maximum of 5.9% (sample W170) of the total reef framework and they may occur as closely packed tubes forming crusts up to 1 cm thick. They occur as isolated tubes encrusting cavity walls or in small groups of a few individuals. Molluscs are found preserved inside irregular cavities generated by the protuberant and knobby growth of the coralline framework. These cavities

are apparently used by the gastropods as grazing sites, and when they die their shells are incorporated and overgrown by encrusting coralline-algal framework. Eventually, the shells become filled with internal sediment which is later cemented. Abundances range from 1.2 to 5.1% and occur mainly in the middle segment of the reef flat. They occur, however, only in 31% of the surveyed windward reef samples.

Identified macroborings were those produced by clionid sponges and polychaete/sipunculid worms. Clionid sponge boring is the major bioerosional process observed in this windward transect. *Cliona* has been recognised by others as one of the most important marine borers due to its abundance and widespread distribution (cf. Warne 1975). *Cliona* sp. borings occupy up to 22% of windward reef samples and mostly occur in the reef crest and between 100 and 150 m from the reef front (averaging 8.9% along the windward reef transect; Fig. 4). Polychaete/sipunculid borings in the surveyed reef samples range from 1- to 5-mm in diameter, sometimes with smooth-walled borings and with rounded terminations (which are possibly produced by sipunculid worms). Some branching borings were also found. Most of the borings, however, are up to 4 cm long with cross sections varying from laterally elliptical to circular. Diameters range from 0.8 to 7 mm, and are comparable to borings produced by polychaetes (Bromley 1978). These borings comprise up to 14.3% of the total reef rock in the outer portion of the reef flat between 70 and 100 m from the reef front. They are less abundant

(0–4.5%) in the reef front and reef crest samples (average of 1.9%). In the windward reef flat the average abundance of polychaete/sipunculid boring is 6.4%, and the average along the windward reef transect is 4.9%.

Reef-front and reef-crest framework cavities display planar, lens or wedge shapes varying from 1 to 4 mm in length. These cavities average 3.5% of total windward reef framework, whereas in the reef flat this figure rises to 14.5% (average 11.1%; Fig. 4). Growth cavities show their greatest development in the reef flat, accounting for up to 28.9% of total reef rock. These cavities have different shapes in different environments, mainly due to changes in the growth form of the primary framework. In the windward reef-flat, framework cavities are rather irregular due to the protuberant and knobby growth form of the coralline algal framework, forming a network of irregular cavities with diameters ranging from 0.5 to 2 cm. Visual estimation showed that cemented sediments found in cavities (Table 3) are moderately well sorted skeletal wackestones to very poorly sorted, sand-sized packstones (Gherardi 1996). The abundance of cemented sediment in the reef rock (Fig. 4) is higher in the first 50 m of the transect (from reef front to outer reef flat) with a maximum of 27.2% (average 15.6%). The major change in the contribution of cemented sediment to the reef occurs between 95 and 240 m from the reef front with percentages as low as 3.1%, and an average of 5.5%. The overall transect average is 11.7%.

Composition of the leeward reef

Abundances of primary framework vary from 13.2 (sample L10) to 50.7% (sample L15; average 28.8%), whereas in the reef flat it varies from 21.1 to 44.4% (average 33%). The average abundance of primary framework along the leeward reef transect is 31.9%. *Porolithon* cf. *pachydermum* is again the main primary framework builder in the leeward reef crest, *Lithophyllum* sp., *Sporolithon* sp., *Lithoporella* sp., and thin *Porolithon* sp. crusts are also present (Gherardi and Bosence 1999). Primary frameworks in the reef crest vary from thick encrusting forms to knobby and irregular forms. Reef-flat samples show the same diversity of primary

framework growth forms as at the reef crest, and open branching frameworks are rare.

As with the windward reef, vermetid gastropods are the main encrusters of the leeward reef with high abundances (up to 16.3%) in the reef-crest samples (Fig. 5). The lowest abundance (0.8%) was found in the reef flat some 140 m from the reef front, and the average was 6.8% along the leeward reef transect. *Homotrema rubrum* is the second most abundant encruster (Fig. 5), and occurs mainly as globose and arborescent forms which are considered to be more adapted to sheltered microenvironments and cavities (cf. Rooney 1970). This encrusting foraminiferan mainly occurs at reef-crest sites (9.2%) and in inner parts of the reef flat 140 m from the reef front (8.8%). The average abundance along the leeward reef transect is 5.5%. Acervulinids (Fig. 5), the second most important encrusting foraminiferan, are also more abundant in the leeward reef crest (9.6%), but are absent some 90 m away from the reef front, and attain an average abundance along this transect of 3.4%. Corals are restricted to the inner part of the leeward reef flat, comprising 1.3 (sample L140 and L165) to 6.5% (sample L190) of the total framework. Only one sample of the leeward reef flat had 34.1% of the framework built by one single coral colony of *Siderastrea* sp. Mollusc shells are not present in significant amounts (0–5.6%). When reef samples are cut, their presence is readily noticed as loose shells inside cavities, but after cutting and polishing the samples it is clear that few are really incorporated into the framework.

The organisms responsible for leeward reef rock bioerosion are clionid sponges and polychaete and sipunculid worms (Fig. 5). Maximum clionid sponge boring activity occurs in the reef crest (34.4% of total reef framework) but it is also abundant throughout the leeward reef transect (average 15.6%). Polychaete/sipunculid borings are more abundant in middle sections of the leeward reef transect, with a maximum of 23.4%. The inner reef flat shows a maximum abundance of 12.3% with an overall average on this transect of 12%.

Irregular cavities (Fig. 5) are widespread, encompassing a variety of sizes, from 0.5 to 5.5 cm and comprise on average 14.2% of total reef rock. The abundance of cavities increases from the reef crest to the inner part of the reef flat, ranging from 8.4 to 33.2%

Table 3 Main internal sediment producers of the Atol das Rocas reefs

Nature of grain	Range of particle size (μm)	Breakdown and transport	Shape
Coralline algal crusts	60–1200	Mechanical breakage by waves of crust tips or bioeroded parts	Shapes vary from square, rectangular and triangular to irregular, circular or elongate
Codiacean algae	120–600	Decomposition of soft tissue after death with subsequent separation of segments	Tubular segments that in thin-section may appear as discoidal or U-shaped fragments
Benthic foraminifera	400–750	Brought to cavities by sea-water circulation	Whole tests circular to ellipsoidal and sometimes broken
Mollusc shells	100–1400	Broken or bored in situ	Generally rectangular, concave, or irregular due to bioerosion

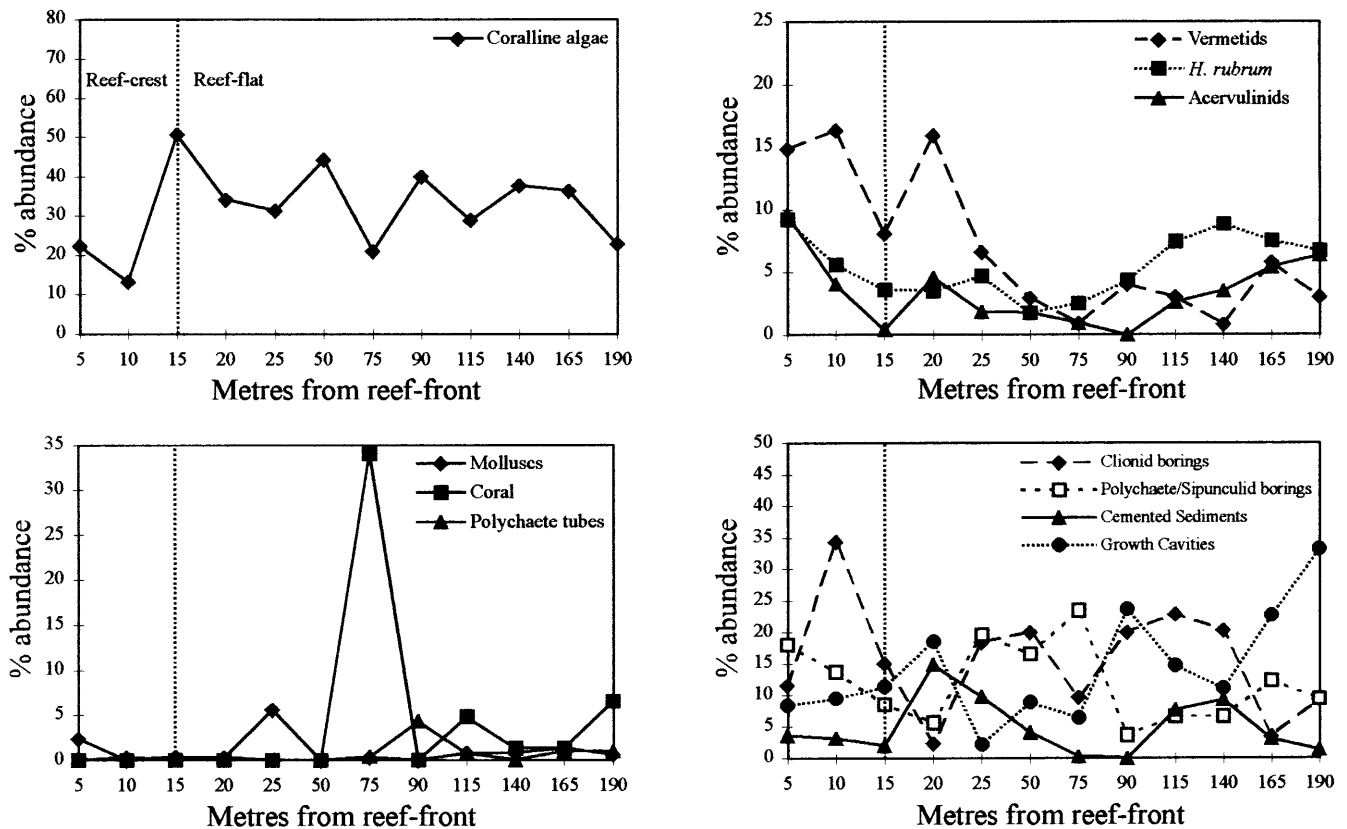


Fig. 5 Changes in percentage abundance of primary and secondary framework builders, bioeroders, cemented sediments and growth cavities along the leeward reef transect

(Fig. 5). The average abundance of cemented sediments (Fig. 5) along the leeward reef transect is 4.9% and the highest percentage (14.8%, sample L20) was found some 20 m from the reef front in the interface between the reef crest and reef flat. Cemented sediment texture and composition are comparable to windward reefs with wackestones being more abundant than packstones.

Multivariate analyses

The Q-mode cluster analysis (sampling sites dendrogram; Fig. 6) indicates that, overall, the reef samples are similar in composition, with B-C similarity indices of 80% or more. The B-C similarity index also gives reasonably discrete groups of samples according to their positions relative to the leeward (groups A1, A2, and A3, with 69% of all leeward samples) and windward transects (groups B1 and B2, with 78% of all windward samples). The classification of reef components (R-mode cluster analysis; Fig. 6) separates coralline algae, vermetid gastropods and cemented sediments in group I, reef borers in group II, and *H. rubrum* and growth cavities in group III. This discrete clustering illustrates the components that tend to co-occur and can be used to interpret how specific ecological requirements control their abundances in each reef environment.

The MDS configuration for both transects (not shown) displays all samples spread along the x axis, but the high stress value (0.17) indicates that the two-dimensional map is a poor representation of community structure. The average dissimilarity between windward and leeward transects is 26.38% and the main discriminating component classes are clionid sponge borings, cemented sediments, and polychaete and sipunculid borings, which together account for 36.85% of calculated dissimilarity (Table 4).

In order to refine the analysis, a separate classification (Figs. 7A, 8A) and ordination (Figs. 7B, 8B) of samples from each transect was carried out. This procedure allows the identification of specific patterns of change in community structure, such as seriation breakdown across the reefs. Note, however, that sample W285 (inner reef flat, 285 m from reef front) has not been included in the analysis of windward transect samples (Fig. 7A). The reason is that it groups with reef-front and reef-crest samples (group X), suggesting that communities from both extremes of the transect are similar. This is a very unlikely possibility for the following reasons:

1. Differences in composition and abundance are easily identified along both windward and leeward transects.
2. Field observations show that different hydrodynamic regimes dominate reef-front and inner reef-flat settings (Gherardi and Bosence 1999).
3. Results of extensive shallow drilling and radiocarbon dating carried out on the Atol das Rocas reefs (Gherardi 1996) indicate that fossil (mid-Holocene) coralline-algal

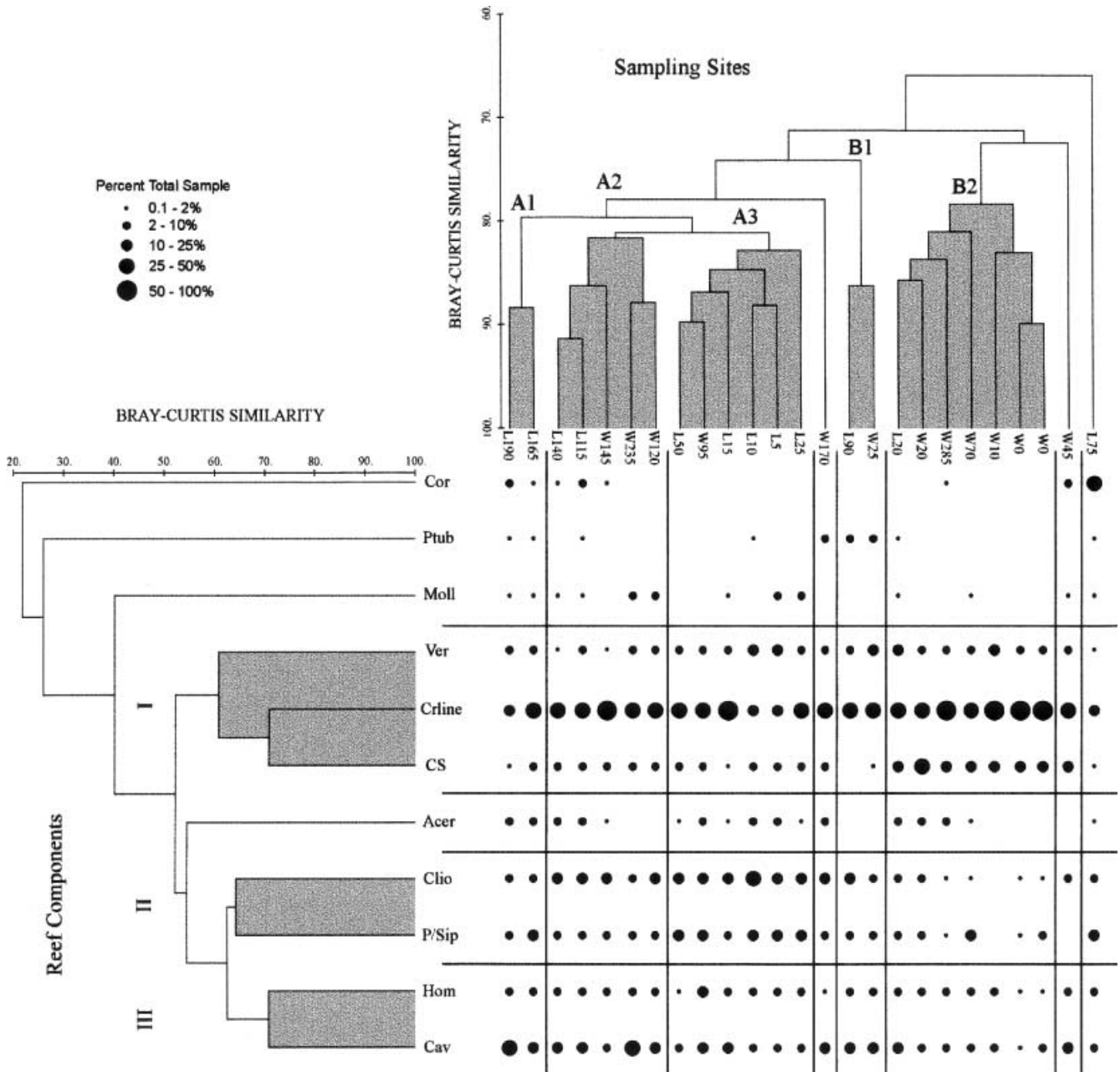


Fig. 6 Q-mode (sampling sites) and R-mode (reef components) cluster analysis of percentage abundance data from windward and leeward transects. Clusters are based on their descriptive utility rather than some arbitrary level of similarity. Sampling sites are labelled as follows: *W* windward transect, *L* leeward transect. Numbers following *W* and *L* are metres from the reef front. Percent relative abundance in the total sample of each reef component is given by the size of the dots. *Cor* Coral, *Ptub* polychaete tube, *Moll* mollusc, *Ver* vermetids, *Crline* coralline algae, *CS* cemented sediments, *Acer* acervulinids, *Clio* clionid sponge boring, *P/Sip* polychaete and sipunculid boring, *Hom* *Homotrema rubrum*, *Cav* cavity

reef. Furthermore, the exclusion of sample W285 does not change the MDS configuration of Fig. 7B.

Two distinct groups of samples can be established in each reef transect, corresponding to exposed (reef front and reef crest, group X) and protected sites (reef flat, group Y) sites. The MDS maps not only reproduce these groups but also show a spatial arrangement of samples indicating a clear change in community structure (breakdown of seriation) across the windward transect (Fig. 7B) and a less clear change in community structure across the leeward transect (Fig. 8B). Stress values for each MDS ordination are 0.12 and 0.14, respectively. Results of the Spearman rank correlation and the Monte Carlo permutation test applied to each transect produced an IMS of 0.43 (significance level of 0.3%) for

frameworks are present in the interface between the reef flat and the sand flat (inner reef flat). The composition of these frameworks is likely to bear no relation to the present-day environment and could mislead interpretation of possible controls on community change on the windward

Table 4 Contribution of each reef component to the average dissimilarity between the windward and leeward reef transects. Average dissimilarity between transects is 26.38%

Reef components	$\bar{\delta}_i$	$\bar{\delta}_i/SD(\bar{\delta}_i)$	Contribution to dissimilarity (%)	Cumulative %
Clionid sponge boring	3.46	1.27	13.10	13.10
Cemented sediments	3.15	1.30	11.96	25.06
Polychaete and sipunculid boring	3.11	1.25	11.79	36.85
Acervulinids	3.01	1.60	11.39	48.24
Corals	2.34	0.76	8.88	57.12
Cavities	2.33	1.32	8.84	65.96
Vermetids	2.22	1.37	8.42	74.39
<i>Homotrema rubrum</i>	2.03	1.38	7.69	82.08
Molluscs	1.74	1.17	6.61	88.68
Polychaete tubes	1.54	0.88	5.83	94.51

the windward transect and 0.13 (significance level of 16%) for the leeward transect.

Discussion

Between transect variation in community structure

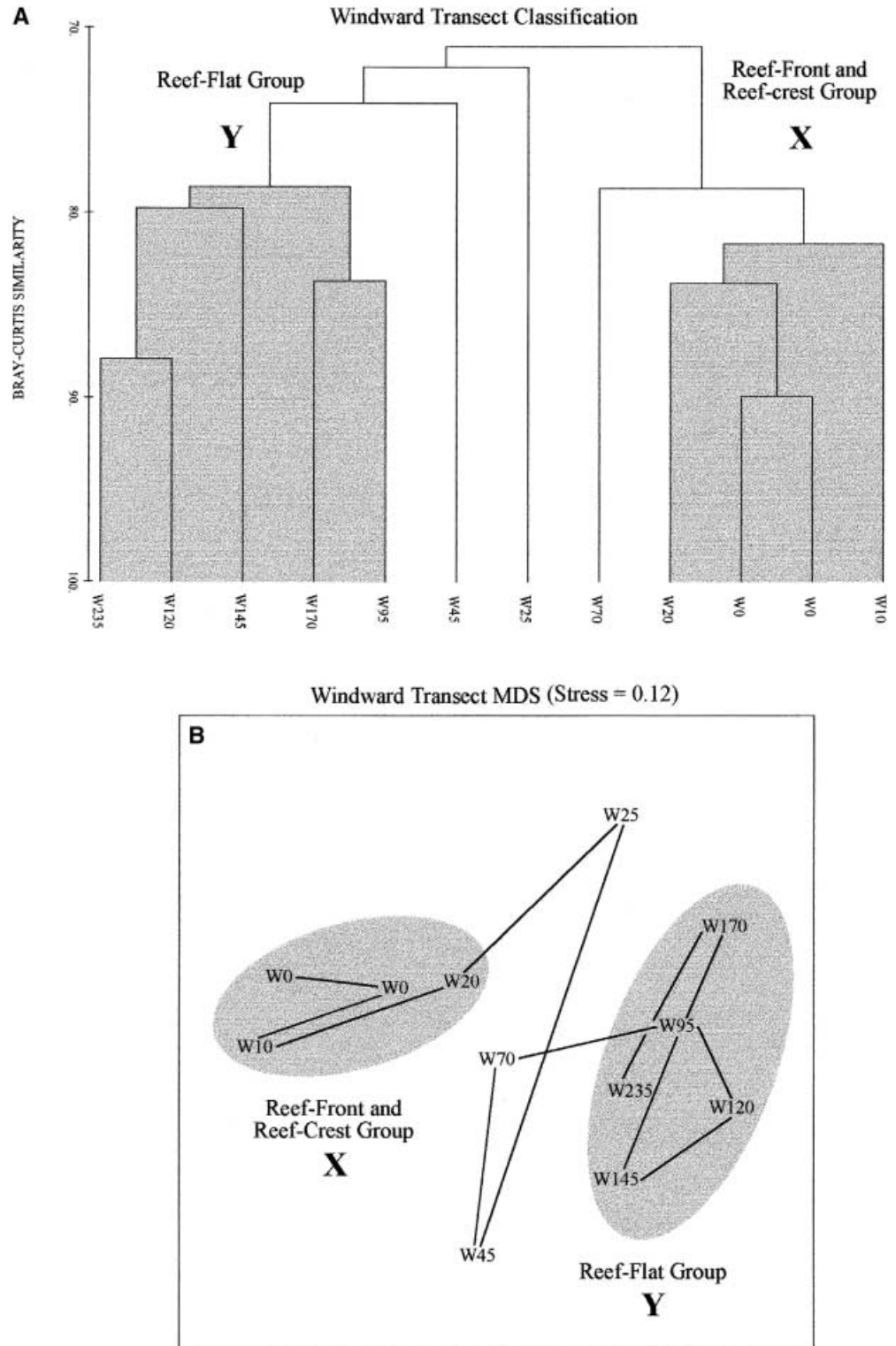
Results of the cluster analysis and MDS ordination (not shown) of the complete data set show that rather than clear-cut changes in community composition between the surveyed transects, there is a sequential pattern of community change. Evidence of this sequential pattern can be seen in the sampling sites dendrogram (e.g. Fig. 6, subgroup A2) where some windward reef-flat samples are grouped with leeward reef-flat samples because of a high similarity in composition. This similarity contributes to the lack of a complete separation between both transects since almost all samples share the same reef components and differences are mainly related to their abundances. This overall similarity is confirmed by the low (26.38%) dissimilarity between both transects. Nevertheless, there is fairly good separation between the surveyed transects, which may be related to specific patterns of community structure intrinsic to windward and leeward reef environments. These patterns can also be depicted from the R-mode dendrogram where wave-resistant organisms (Fig. 6, group I), such as coralline algae and vermetids, co-occur in the same ratio, with cemented sediments being more abundant in the windward than leeward reef. Higher cementation in the windward than leeward reef is likely to reflect increased seawater pumping inside reef pores and cavities. In contrast, the group composed of the reef bioeroders (polychaete/sipunculid and clionid borings; Fig. 6, group II) is consistently more abundant in leeward than windward samples. Bioeroders may take advantage of the fact that the leeward reef framework has more open cavities, relating to the less dense and irregular growth forms of the coralline algae (Gherardi and Bosence 1999). Further evidence of the relationship between the abundance of growth cavities and secondary framework organisms can be found in group III (Fig. 6), where *H. rubrum* groups with growth cavities. Groups II (bioeroders) and III could easily be clumped together in one larger group, with similarities over 60% (Fig. 6).

Within transect variation in community structure

The Q-mode cluster of windward reef samples clearly separates the reef-front and reef-crest samples (Fig. 7A, group X) from the reef flat (Fig. 7A, group Y). Note, however, that samples W25 (25 m from the reef front), sample W45 (45 m from reef front) and sample W70 (70 m from the reef front) are somewhat isolated in the middle of the dendrogram. This can also be seen in the MDS map (Fig. 7B) and may be interpreted as the result of a breakdown of community seriation from the wave exposed reef-front and reef-crest samples (group X) to the more protected reef-flat samples (group Y). This analysis also shows that there are two distinct end members in the community structure of the windward transect as a result of higher abundances of coralline algae, cemented sediments, and lower abundances of borings and cavities in the reef-front and reef-crest samples (Fig. 6). The stress value for this MDS is 0.12, which corresponds to a good ordination with little risk of drawing false inferences. The calculated IMS for this transect is 0.43 (significance level of 0.3%), suggesting a linear sequence of community change. Therefore, it is safe to infer some relationship between the community structure and distance from reef front.

Two groups of samples are also discernible in the leeward transect Q-mode cluster, separating reef-crest and outer reef-flat samples (Fig. 8A, group X) from the mid and inner reef flat (Fig. 8A, group Y). Again, two samples (L75, 75 m from the reef front; and L90, 90 m from the reef front) are isolated on the right of the dendrogram, corresponding on the MDS map (Fig. 8B) to a region where apparent breakdown of community seriation occurs. The leeward transect MDS does not show the same linearity in the distribution of samples as does the windward transect and this is confirmed by a low IMS value of 0.13. This suggests that the relationship between community structure and distance from the reef front is non-monotonic, with groups of samples located at opposite ends of the transect being more similar to each other than they are to the mid-transect samples (L75 and L90). Interpretations based on the leeward transect seriation breakdown should be made cautiously because the Monte Carlo test for seriation gives a significance level of 16%, which is not low enough to

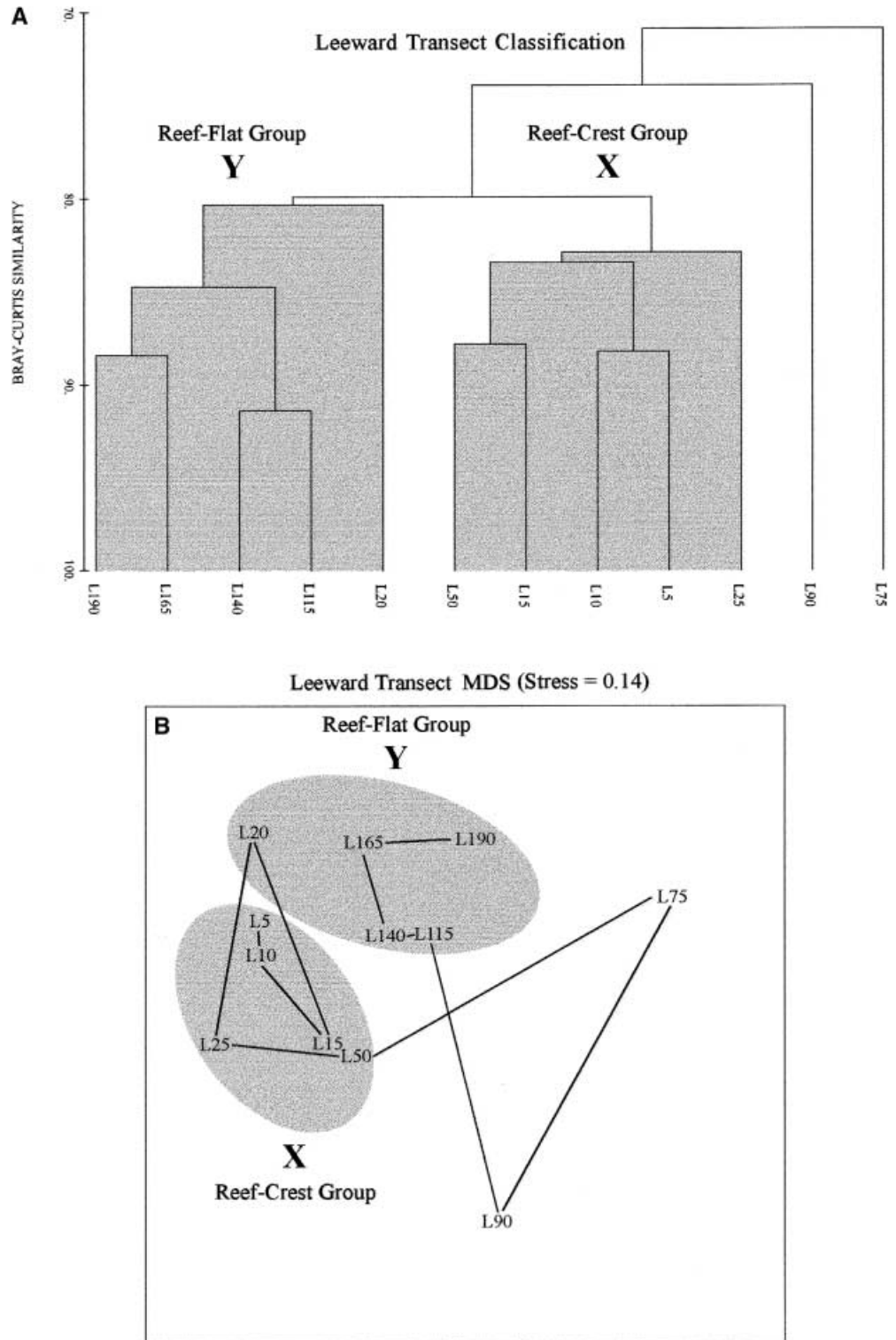
Fig. 7 Q-mode cluster analysis of the windward samples that discriminates samples according to their distances from reef front. *Cluster X* comprises samples 0 to 20 m from the reef front and *cluster Y* of samples from 95 m (mid section of the reef flat) to 235 m (inner reef flat) from the reef front. Seriation breakdown is indicated by the isolated samples W25, W45, and W70. **B** MDS ordination of windward samples showing group *X* and *Y*. Seriation breakdown occurs between 25 m and 70 m from the reef front (stress value is 0.12)



reject the null hypothesis. Changes in abundances of reef components like vermetids, *H. rubrum* and acervulinid foraminiferans are likely to be responsible for the isolation of samples L75 and L90 (see secondary framework builders in Fig. 5). The stress value for the leeward samples ordination is 0.14, which although not

ideal, still produces a usable representation. The above results point clearly towards a strong influence of hydrodynamic energy on community structure of the windward reefs and a rather weak influence on leeward reefs, where clear changes in the community structure could not be detected.

Fig. 8 Q-mode cluster analysis of the leeward samples that discriminates samples according to their distances from reef front. *Cluster X* comprises samples from 5 m to 50 m from the reef front and *cluster Y* is made of samples 115 m (mid section of the reef flat) to 190 m (inner reef flat) from the reef front. Seriation breakdown is indicated by the isolated samples L75 and L90. **B** MDS ordination of leeward samples showing group *X* and *Y*. Seriation breakdown occurs between 75 and 90 m from the reef front (stress value is 0.14)



Relationship between hydrodynamic energy and reef framework

Because the composition of the coralline-algal reef frameworks from Atol das Rocas varies mainly with regard to windward and leeward location, it is likely that the main control on the community structure is

hydrodynamic energy rather than subaerial exposure or insolation. The intertidal setting of the surveyed reefs, the presence of constant SW trade winds, and a semi-diurnal tidal range of 3.8 m, suggest that emergence and insolation may be secondary controls. Other possible controls, such as drainage and permeability are also likely to be downplayed by the high amplitude

semidiurnal tide regime. Intertidal organisms are well adapted to this predictable disturbance factor and frequent submergence helps reef organisms to cope with desiccation, temperature and salinity oscillations. The high wave energy and the semi-diurnal tide regime also reduces the impact of most predators and grazers (cf. Adey and Vassar 1975; Steneck and Adey 1976).

Within each transect the way breakdown in seriation occurs is similar, and can be seen in the MDS maps where reef-front and reef-crest communities differ from reef-flat communities. Whether location acts on growth and survivorship of competing individuals or whether it mediates the competitive outcome among encrusters (see Steneck et al. 1991) is difficult to ascertain. Considering that competitive dominance of coralline algae increases with increasing crust thickness (Steneck et al. 1991) and assuming (based on field evidence) that herbivore-induced disturbance either by fish or limpets is low, it is reasonable to suggest that the abundance of encrusters (secondary framework) will increase where coralline-algal crusts grow more slowly and/or irregularly (forming more cavities). The co-occurrence of *H. rubrum* and cavities shown by the R-mode cluster analysis (group III, Fig 6) supports this hypothesis. Similarly, where hydrodynamic control is inferred to be weaker (e.g. leeward reefs) bioerosion is likely to be proportionately more intense. This is demonstrated by the fact that clionid sponge and polychaete/sipunculid borings are more abundant in leeward than windward reefs (group II, Fig. 6). Increased clionid sponge boring in 'shallow-water quiet areas' has also been reported by Bromley (1978) for several reefs in Bermuda.

Another important ecological aspect to be considered is that any factor affecting abundant habitat-structuring organisms such as coralline algae will inevitable affect their associates (i.e., secondary framework builders) such as vermetid gastropods (group I, Fig. 6). The ability of *Porolithon* sp. to tolerate high wave energy, heating, desiccation, and direct sunlight leading to relatively higher growth rates on intertidal ridges (Doty 1974; Adey and Vassar 1975; Littler and Doty 1975; Bosence 1983, 1984; Littler and Littler 1984; Matsuda 1989) gives further indication that the hydrodynamic energy gradient is likely to be the main controlling factor on the Atol das Rocas reefs.

Most secondary framework builders and bioeroders have a common characteristic, i.e. both are suspension-feeders (Scoffin and Garrett 1974; Bromley 1978), and must maintain access to seawater whether they are living on the reef surface or in cavities. High sedimentation may bury them or reduce their ability to collect food. This may explain why vermetids are mostly concentrated on the reef crest and in the interface between the reef crest and reef flat, but are much less abundant on the reef front (Figs. 4 and 5). Lower abundance of vermetids on the reef front could also be explained by the fact that their main source of food is particles trapped on the mucous net secreted by their large pedal gland (Hughes 1979), and the direct impact of waves on the reef front would

possibly destroy this mucous net. The relative position of the seriation breakdown in the windward reef, located between 25 and 45 m from the reef front seems to corroborate this. *Homotrema rubrum* and acervulinid foraminiferans are not grouped in the R-mode cluster analysis (reef components, Fig. 6), suggesting that they have different strategies of occupation of free space and/or different ecological requirements. Elliot et al. (1996) found evidence in reefs from Bermuda that the distribution and abundance of *H. rubrum* in cryptic habitats is controlled by sedimentation, but they also suggested that it is better adapted to environments where sedimentation and competition are intense. In contrast, some acervulinids (such as *Acervulina inhaerens*) are free-living in their early growth stages, becoming attached to a substratum only after the construction of the third or fourth layer of lateral chambers (Perrin 1994).

Polychaete and sipunculid borings correlate inversely with the abundance of cemented sediments in frameworks from the leeward transect (Fig. 5). Also, they are much less abundant along the windward reef transect, which has a much higher percentage of cemented sediments within the framework. The constant flushing of seawater through reef cavities may be responsible for the abundance of cemented sediments in the windward reef. Such a mechanism has also been invoked to explain intensive submarine cementation in present-day (Marshall 1983) and fossil reefs (e.g., Devonian atoll, Gischler 1995). These results tie in very well with those produced by the R-mode cluster analysis of Fig. 6, where wave-tolerant organisms (coralline algae and vermetids) are grouped with cemented sediments (group I). The extent of the inverse relation between framework borers and cemented sediment is evident in the result of the similarity breakdown analysis which shows that they contribute up to 36.85% (Table 4) of the calculated dissimilarity between the windward and leeward transects.

Finally, it should be highlighted that data exploration techniques, such as the B-C similarity index and MDS ordination, can be extremely useful for the investigation of synecological patterns of modern and fossil reef biota in the absence of contemporaneous environmental data.

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