Benthic macroalgal distribution in coastal and offshore reefs at Porto Seguro Bay, Brazilian Discovery Coast.

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Abstract Macroalgae are major components of Atlantic shallow coral reef communities and potentially a major competitor with corals. This study investigates the spatial and seasonal distribution of macroalgal species, which includes fleshy algae, turf algae and some geniculate and non-geniculate corallines, on two coastal and one offshore reef from Porto Seguro Bay, Brazil. Data were collected during the dry season (July/August 1999) and the rainy season (February/March 2000), with samples being taken from the reef wall (at 1, 3 and 5 m depth) and from the reef flat. Macroalgal cover ranged from 33% (reef wall) to 60% (reef flat) on the coastal reefs, and from 36% (reef wall) to 50% (reef flat) on the offshore reef. The most diverse group was the Phaeophyta (19 taxa), followed by Rhodophyta (17 taxa) and then Chlorophyta (15 taxa). The largest number of infrageneric taxa was recorded during the rainy season (February/March 2000), the most abundant genera being *Sargassum*, *Padina*, *Dictyota*, *Dictyosphaeria*, *Caulerpa* and *Amphiroa*. Two species were recorded for the first time in the region: *Tricleocarpa cylindrica* (Rhodophyta, Galaxauraceae) and *Avrainvillea longicaulis* (Chlorophyta, Udoteaceae). Algal turf dominated the community structure at all reef sites and habitats. Fleshy algae are the second most conspicuous group on the reef flat in both coastal and offshore reefs. In terms of dominance, on the reef wall, corals and zoanthids are second to turf algae in the offshore reef and coastal reefs respectively. This paper is the first of a series describing the distribution of benthic components within coral reef communities of the Brazilian Discovery coast.

Key words: macroalgae, coral reef, benthic community distribution, tropical seaweed, Brazil

Introduction

The last decades have seen increasing concern about the effect of human disturbance on coral reef communities. Recently, some studies have focused on coral reef algal community dynamics (Aronson & Precht 2000; Hay 1997; Larned 1998; Lundberg & Popper 1999; McCook 1999; McCook et al. 2001; Miller et al. 1999; Smith et al. 2001), paying attention to their roles in both reef construction (Adey 1998) and destruction (Hughes 1994). Some authors (Womersley & Bailey 1969; Round 1981) state that since algae and not corals are dominant in most of reef formations, especially in the surf zone, the misleading name coral reef should be abandoned, suggesting that the term "biotic reef" would be a better representation. This debate has continued, especially with the recent discussions about coral-algal phase shifts, in which the macroalgal growth outcompetes corals after changes driven by physical and anthropogenic disturbances (Hughes et al. 1999; Lapointe 1999; McManus et al. 2000; Stiger & Payri 1999).

In Brazilian reefs, however, the scarcity of baseline information makes it difficult to establish any trends. The state of Bahia has the most extensive coastline (830-km), as well as the largest and richest coral reefs of Brazil, but their macroalgal flora remains amongst the least studied in the country. The first published work on Bahian seaweed dates from more than a century ago (Dickie 1874), but only recently have efforts been made to catalogue Bahian macroalgae (Martins et al. 1991; Nunes 1998). Prior to this current study, 253 taxa had been identified from Bahian coastal waters (139 Rhodophyta, 49 Phaeophyta, and 66 Chlorophyta).

The purpose of the present study is to describe the distribution of the benthic macroalgae communities, as well as the abundance of each component (namely fleshy algae, turf algae and corallines), on the coastal and offshore reefs of Porto Seguro bay within the Brazilian Discovery Coast, southern Bahia. Also included is the distribution of other major groups (corals, hydrocorals, sponges, zoanthids and soft corals), as this study constitutes the first description of the benthic community in this region.

Materials and Methods

Study sites

The Discovery Coast is a small section (~100-km) of the east Brazilian coast, located between 16°00'S and 17°30'S (Fig. 1). Despite being the birthplace of modern Brazil, the region remains comparatively unknown, containing the least studied coral reefs on the entire Bahian coast.

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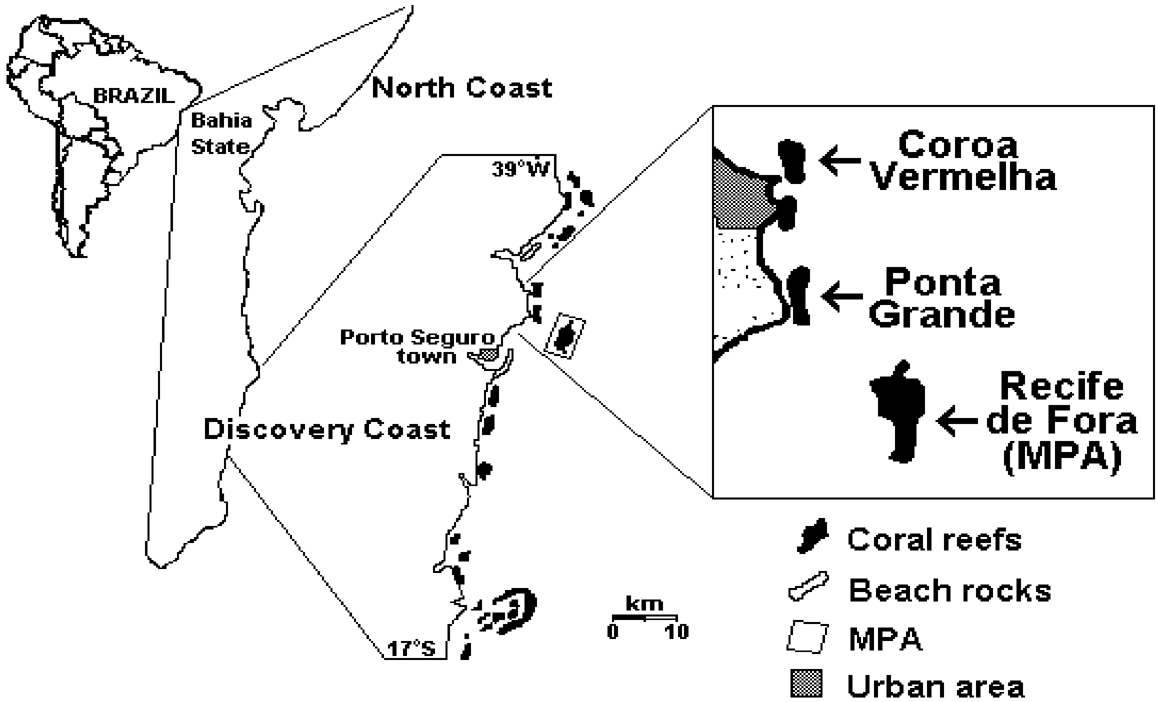

Fig. 1 Map of the Brazilian Discovery Coast, Southern Bahia, Brazil, and location of the studied reefs at Porto Seguro Bay.

The coastal reefs (Coroa Vermelha reef and Ponta Grande reef) occur adjacent to the beach, thus forming discontinuous structures parallel to the coastline. Although these reefs are close to each other (~ 6km distance), they were both surveyed because Coroa Vermelha, unlike Ponta Grande, is under the influence of a small village, where the lack of a sewerage treatment plant and widespread use of septic tanks are likely to be contaminating the groundwater (see Costa et al. 2000). Water depth around the reefs varies from 6 to 9 m and the bottom sediment is extensively covered by a siliciclastic mud up to 30 cm thick. The reef flat is emersed during low tides (6-9 hours per day) and dense algal mats cover the area. They share the intertidal zone with extensive aggregations of the genera *Palythoa* and *Zoanthus* (Anthozoa: Hexacorallia: Zoanthidea) which grow above dead coral. Another common feature of these coastal reefs is the occurrence of dense colonies of the hydrocoral *Millepora* in the reef crest (at about 1m depth below the mean tide level - MTL).

The offshore reef (Recife de Fora) is located 5 km from the coast. The area of the periodically emerse reef flat is about 2.5 km² and it is part of a Marine Protected Area (MPA) of 17.5 km², created in December 1997. This reef was chosen to provide a comparison between offshore and nearshore communities. Water depth around the reef varies from 8 m (landward) to 15 m (seaward).

Field sampling

Data were collected during the dry season (July/August 1999) and the rainy season (February/March 2000). In the coastal reefs, the survey was performed on the reef flat and on the seaward reef wall (at 1m and 3 m depth below the MTL). In the offshore reef, samples were collected from both seaward and landward reef walls (at 1, 3 and 5 m depth below the MTL), as well as on the reef flat. The 1m-depth contour was chosen because it includes the reef crest and is exposed to air during the lowest spring tides. The 3m-depth contour, which always remains underwater, constitutes one of the areas with maximum reef development. Finally, the 5m-depth contour (only surveyed at the offshore reef) was chosen to give an indication of how the community structure changes as the light incidence is reduced.

The methodology used was essentially as described in the algal survey of the AGRRA Rapid Assessment Protocol (Ginsburg et al. 1998). The repeated sampling unit consisted of algal counts undertaken using a 25x25cm quadrat placed above a 10 m transect. A total of 350 quadrats were quantified, 150 on the offshore reef and 100 on each of the coastal reefs. The survey encompassed approximately 250m on each side of the reef and on the reef flat. Algal samples were collected for subsequent identification and are deposited in the Herbarium of the Institute of Biology, State University of Rio de Janeiro, Brazil.

The non-geniculate corallines are still under identification and therefore do not appear on the species list (Table 1). Their contribution to the reef cover, however, is included in both the figures and discussion. Of the geniculate corallines, only the genera *Amphiroa* and *Haliptilon* were recorded out of the six that occur in Brazil (which also includes *Arthrocardia*, *Cheilosporum*, *Corallina* and *Jania*).

Data analysis

Univariate indices, such as Shannon-Wiener diversity (H') and Pielou's evenness (J'), along with total number of species, were used to measure some attributes of community structure within and between reef habitats, sites and seasons. Diversity profiles are also presented using *k*-dominance curves (Lambshead et al. 1983). The purpose of this distributional representation is to extract information on patterns of relative species abundance and dominance. This technique can be considered as intermediate between *univariate* summaries and

Table 1 Distribution (presence/absence) of algal taxa on the reef flat and reef wall (1m, 3m, 5m) of the coastal and offshore reefs. d = dry season; r = rainy season. Names of authors of plant taxa are as in Wynne (1998).

	Coastal reefs			Offshore reef						
				Landward				Seaward		
Taxa	**Flat**	**1m**	**3m**	**1m**	**3m**	**5m**	**Flat**	**1m**	**3m**	**5m**
Phaeophyta										
Colpomenia sinuosa (Roth) Derbès & Solier	d/r								d/r	
Dictyopteris delicatula J.V.Lamour.				r						
Dictyopteris justii J.V.Lamour.								r		
Dictyopteris plagiogramma (Mont.) Vickers			r	d/r			d/r	d/r	d/r	r
Dictyota cervicornis Kütz.		d/r	d/r				d/r	d/r	d/r	d/r
Dictyota ciliolata Sond. ex Kütz.									r	
Dictyota jamaicensis W.R. Taylor						r				r
Dictyota mertensii (Mart.) Kütz.		d/r	d/r	d/r		d/r	d/r	d/r	d/r	d/r
Dictyota pulchella Hörnig & Schnetter									r	
Hydroclathrus clathratus (C. Agardh) M. Howe								d/r		
Lobophora variegata (J.V.Lamour.) Womersley		d/r	d/r		d/r	d/r		d/r	d/r	d/r
Padina sp						d/r				
Padina gymnospora (Kütz.) Sond.				d/r			d/r	d/r	d/r	
Sargassum spp	d/r	d/r	d/r				d/r	d/r	d/r	
Sargassum vulgare C. Agardh				r						
Sargassum cymosum C. Agardh				r					r	
Spatoglossum schroederi (C. Agardh) Kütz.						r		r	r	
Stypopodium zonale (Lamour.) Papenf.			d/r	d/r				d/r		r
Zonaria tournefortii (J.V.Lamour.) Mont.					d/r	r		d/r		
Rhodophyta										
Acanthophora spicifera (Vahl) Børgesen						r		r		
Amphiroa spp	d/r		d/r	d/r			d/r			
Botryocladia occidentalis (Børgesen) Kylin				d/r						d/r
Digenia simplex (Wulfen) C. Agardh									r	
Galaxaura marginata (J.Ellis & Sol.) J.V.Lamour.						r				
Galaxaura obtusata (J.Ellis & Sol.) J.V.Lamour.						r				
Gelidiella acerosa (Forssk.) Feldmann & Hamel	d	d	d		d		d	d		
Gracilaria cervicornis (Turner) J. Agardh						r		r	r	r
Haliptilon subulatum (J.Ellis & Sol.) H.W. Johans.				r						
Hypnea musciformis (Wulfen in Jacqu.) J.V.Lamour.		d/r						r	r	
Hypnea spinella (C. Agardh) Kützing									r	
Laurencia spp		d/r				d/r			d/r	
Laurencia papillosa (C. Agardh) Grev.	r								d/r	
Liagora sp									r	
Ochtodes secundiramea (Mont.) M. Howe		r				r	d/r			
Tricleocarpa cylindrica (J.Ellis & Sol.)Huisman & Borow.		r								
Tricleocarpa fragilis (L.) Huisman & R.A. Towns.						r	r			
Chlorophyta										
Avrainvillea sp						r				
Avrainvillea longicaulis (Kütz.) G. Murray & Boodle					r					
Caulerpa cupressoides (H. West in Vahl) C. Agardh	d/r	d/r	d/r				d/r	d/r	d/r	r
Caulerpa prolifera (Forssk.) J.V.Lamour.									r	
Caulerpa racemosa (Forssk.) J. Agardh	d/r	d/r	d/r	d/r						
Caulerpa serrulata (Forssk.) J. Agardh							d/r			
Caulerpa verticillata J. Agardh						d/r				r
Cladophora sp									r	
Codium isthmocladum Vickers		d/r	d/r							
Dictyosphaeria versluysii Weber Bosse	d/r	d/r		d/r					d/r	
Halimeda discoidea Decne.		d/r	d/r	d/r	d/r			d/r	d/r	r
Halimeda tuna (J.Ellis & Sol.) J.V.Lamour.						r	r			
Neomeris annulata Dickie			d/r				d/r	d/r		
Udotea flabellum (J.Ellis & Sol.) J.V.Lamour.			d/r				d/r			r
Ulva lactuca L.	d/r	d/r		d/r		r	d/r	d/r	d/r	

full *multivariate* analyses (Clarke 1990). The curves presented are cumulative ranked abundance plotted against species rank (logged axis). Shallow curves tend to correspond to communities with high levels of dominance, whereas steep curves reflect a more balanced, diverse community. *Multivariate methods* used included hierarchical agglomerative clustering, based on Bray-Curtis similarity matrices (Bray & Curtis 1957), in order to delineate groups of habitats with distinct community structures. Multidimensional scaling (MDS) was the chosen method of ordination (Clarke & Green 1988), also based on Bray-Curtis similarity matrices. Formal significance tests for differences between reef sites and habitats were performed using the ANOSIM randomisation test (Clarke & Green 1988).

Results

Species composition

A total of 51 taxa were identified during the study, comprising 19 Phaeophyta, 17 Rhodophyta and 15 Chlorophyta (Table 1). Two species were recorded for the first time in Bahia: *Tricleocarpa cylindrica* (Rhodophyta, Galaxauraceae) and *Avrainvillea longicaulis* (Chlorophyta, Udoteaceae). *Tricleocarpa cylindrica* and *Codium ishtmocladum* were found only in the coastal reefs (Table 1). *Caulerpa* and *Dictyota* were the genera with the highest number of taxa (five each), with *Dictyota mertensii* demonstrating the widest distribution, being able to colonize all reef habitats. Moreover, *D. mertensii* occurred over a broad range of vertical distribution, whilst the similar species *D. jamaicensis* appeared restricted to deeper areas (5-9m).

Total number of species (*S*) for each reef habitat is presented in Figs. 2a and 2b. The most diverse reef habitat was the Recife de Fora reef wall at 3m, in which 24 taxa were found in the rainy season (Table 1). However, the reef wall communities within samples (quadrats) were highly variable, as can be seen in Fig. 2. Patterns of diversity (*H'e*) are shown in Figs. 2c and 2d, fluctuations in *H'* being more pronounced seasonally than spatially. The diversity on the reef wall, especially during the rainy season, was generally higher than on the reef flat (Figs. 2c and 2d). Moreover, the Ponta Grande reef wall, in addition to being one of the habitats with high number of species (Fig. 2b), presented the highest diversity of the study during the rainy season (Fig. 2d). The level of equability (*J'*), which expresses how evenly the individuals are distributed among different species (often termed evenness), is displayed in Figs. 2e and 2f. Low evenness (i.e. high dominance) can be seen in Ponta Grande reef wall, especially during the dry season (Fig. 2f), whilst in the reef flat an opposite pattern occurred and Ponta Grande presented one of the highest evenness values (Fig. 2e).

Dominance curves

Seven taxa were dominant over the study area. These taxa are *Dictyota mertensii, Padina gymnospora* and *Sargassum* spp. (Phaeophyta), *Amphiroa* spp. (Rhodophyta), *Caulerpa cupressoides*, *C. racemosa,* and *Dictyosphaeria versluysii* (Chlorophyta). This shared dominance between the most abundant macroalgal taxa is reflected by *k*-dominance curves (Fig. 3), which also shows that diversity is generally higher on reef wall habitats (positioned below reef flat curves), especially at Recife de Fora sites (Fig. 3c and 3f). The only exception is the Coroa Vermelha site during the dry season, where the reef flat presented a slightly higher diversity than the reef wall (Fig. 3a). The *k*-dominance curves presented in Fig. 3 also emphasize the higher number of species on the reef wall (more squares than triangles) in all studied reefs and seasons. At the same time, the shape of the reef flat curves (triangles at Fig. 3) suggests high dominance by the 5 most common taxa. Together these taxa comprise more than 80% of the total fleshy algal cover.

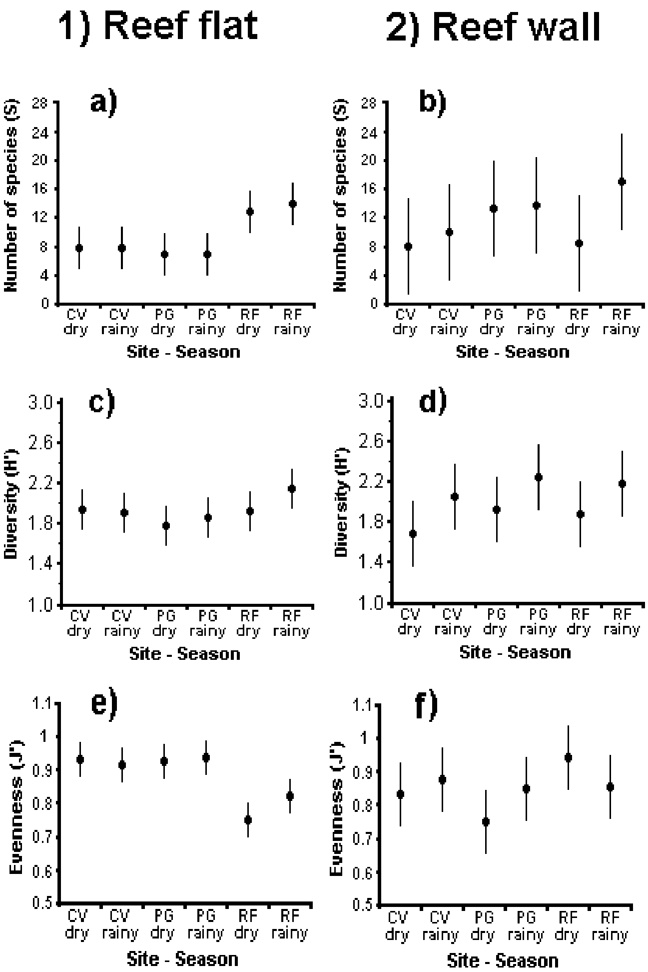

Fig. 2 Total number of species (S), diversity (H'e) and evenness (J') based on data for macroalgal cover (95% confidence intervals) along transects on the reef flat (column 1) and reef wall (column 2). Sites: CV = Coroa Vermelha; PG = Ponta Grande; RF = Recife de Fora.

Seasonal variation

The rainy season (end of the austral summer) presented a higher number of species, as well as diversity, the reef wall being the habitat where this seasonal variation was more accented (Figs. 2b and 2d).

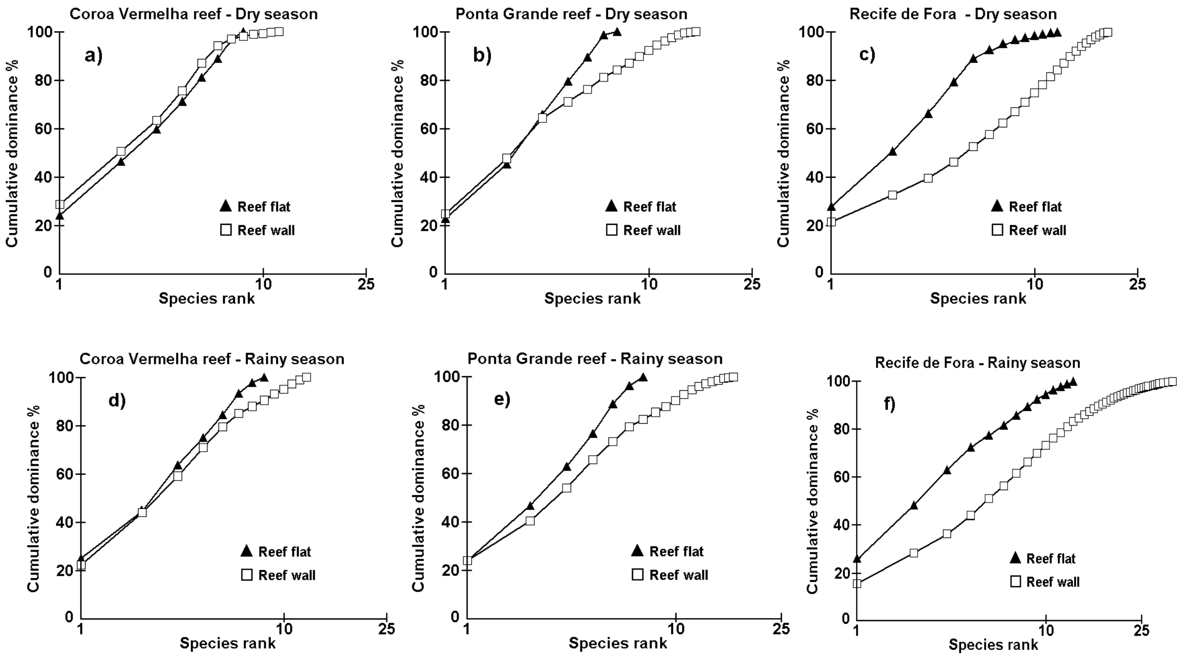

Fig. 3 *k*-dominance curves (x-axis logged) for macroalgal species abundance for all sampling sites and seasons.

Most of the reef habitats also presented a more even distribution during the rainy season, the only exceptions being the reef flat at Coroa Vermelha and the reef wall at Recife de Fora (Figs. 2e and 2f). Most of the taxa identified in the dry season were present during the rainy season, apart from *Gelidiella acerosa*, which was not found in either coastal or offshore reefs at this time. During the dry season, *Gelidiella acerosa* was among the most common taxa with a wide distribution throughout both coastal and offshore reefs (Table 1). In the rainy season, the Phaeophyta genera *Dictyota* and *Padina* dominated the algal community, occupying large patches on both reef flat and reef wall. There were 23 taxa identified during the rainy season that did not occur on the dry season (Table 1).

When comparing the three algal functional groups, algal turf appears as the dominant feature in all sites and habitats, the highest percentage cover occurring at the rainy season (Fig. 4). Fleshy algae also presented higher abundance during the rainy season at most reef sites and habitats, the only exception being the Coroa Vermelha reef wall (Fig. 4b). When comparing all the benthic groups, the overall percentage cover of macroalgae (i.e., fleshy algae + turf algae + corallines) was also higher during the rainy season in all sites and reef habitats (Fig. 5).

Spatial variation

There was a marked variation in the spatial distribution of species, both between coastal and offshore reefs and within specific habitats (reef flat and reef wall). In the coastal reefs (Coroa Vermelha and Ponta Grande), high macroalgal abundance was recorded from the reef flat (always above 50% - Fig. 5a), from which ~35%

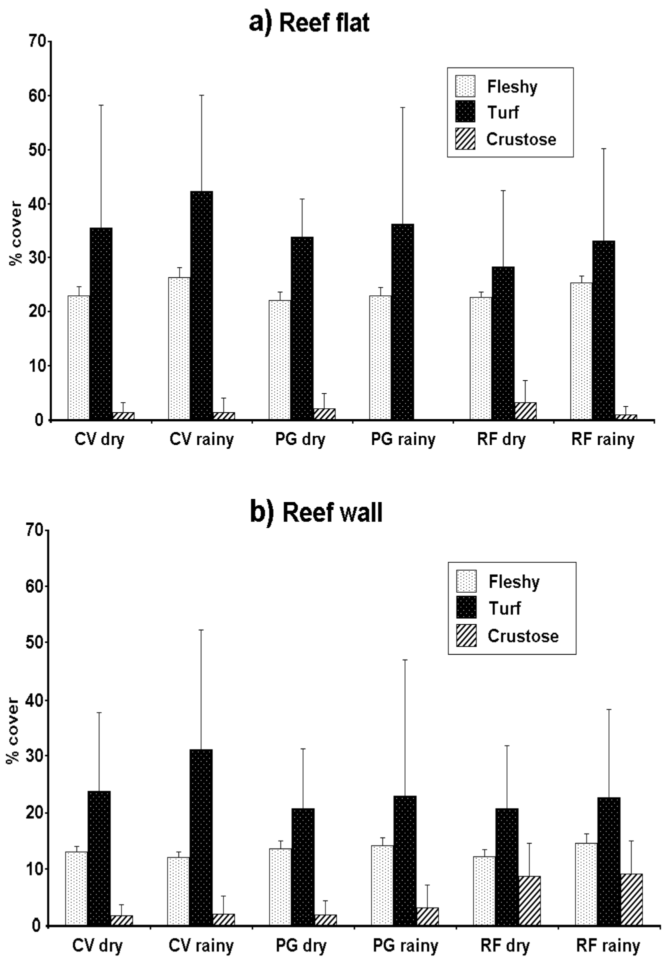

Fig. 4 Distribution of the macroalgal functional groups (mean ± 1 SD) on the reef flat (a) and the reef wall (b) for all sites and seasons. CV = Coroa Vermelha; PG = Ponta Grande; RF = Recife de Fora.

was due to algal turf (Fig. 4a). Fleshy algae also presented higher values at the reef flat but only 9 species were found (Table 1). This dense macroalgal cover is dominated primarily by *Caulerpa* (7.58% ±0.67%), *Sargassum* (5.58% ±0.72%) and *Dictyosphaeria* (3.79% ±1.43%).

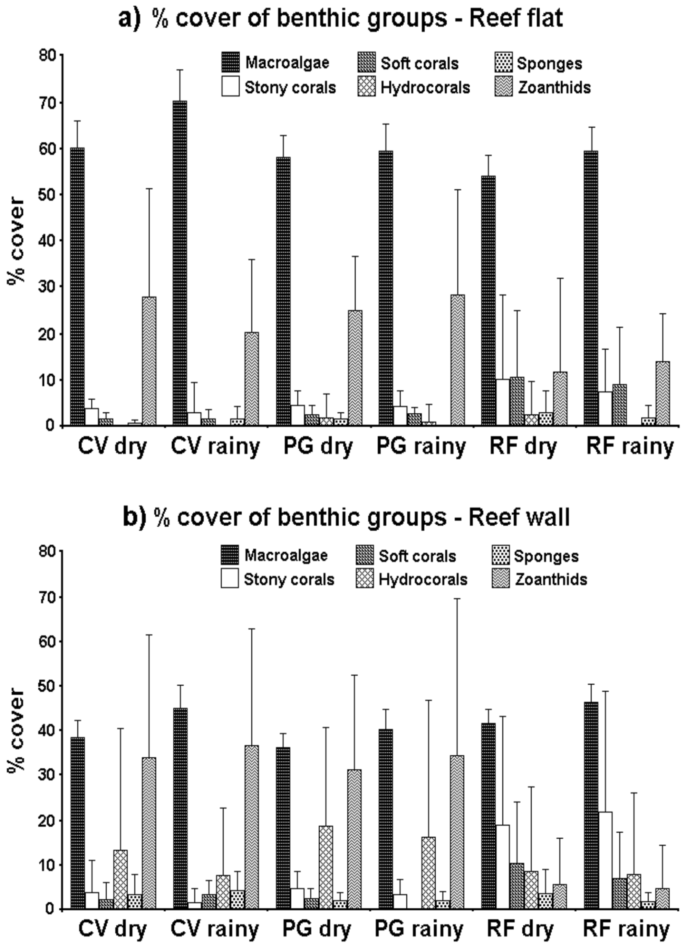

Fig. 5 Percentage cover (mean ± 1 SD) of the major groups of benthic organisms on (a) the reef flat and (b) the reef wall, in all sites and seasons. Macroalgae includes turf, fleshy and crustose coralline. CV = Coroa Vermelha; PG = Ponta Grande; RF = Recife de Fora.

The distribution of fleshy algae on the reef flat followed a zonation pattern. Close to the beach, large patches of fine sediment hamper the development of any species. Any hard substrate that emerges from the sediment is commonly colonized by mats of *Ulva lactuca* and *Dictiosphaeria versluysii*. *Gelidiella acerosa* and *Laurencia* spp. also appear in great numbers, especially in the inner zone. In tide pools, *Sargassum* is the most common genus, sharing the borders with zoanthids and crustose corallines; it is also conspicuous on the outer reef flat, along with *Ulva* and *Amphiroa*. The siphonous green algae (Caulerpales), which have extensive systems of rhizoids, colonize the sandy bottoms. Zoanthids are also common on the reef flat, with abundance varying between 20% and 28% (Fig. 5a).

At the 1m-depth zone, which includes the reef crest, the most common feature was the occurrence of extensive beds of zoanthids (above 40% cover - Fig. 6a), along with large patches of the hydrocoral *Millepora alcicornis* (Hydrozoa: Milleporidae), especially at Ponta Grande reef (Fig. 5b). The combined cover of fleshy, turf and coralline algae, however, did not exceed 33% (Fig. 6a). Despite the lower algal cover, at this depth zone the number of species was higher than on the reef flat, with 15 out of the 22 taxa being recorded (Table 1).

At the 3m-depth zone, the reduction in the abundance of zoanthids (21%) and hydrocorals (9.2%) was proportional to the increase in the macroalgal cover, which rose to about 40% (Fig. 6a). Also noticeable was the increase in sand patches and bare substrate (16.4% at 3m, compared with 0.9% at 1m and 8.5% in the flat). In that reef zone, 14 out of 22 algal taxa were recorded (Table 1). Live coral cover, however, was always below 6.5%, with the highest value being reached at the 3m-depth zone (Fig. 6a).

On the offshore reef (Recife de Fora), the number of species was much higher. A total of 49 infrageneric taxa was recorded (Table 1), compared with only 22 from the coastal reefs. Between the algal groups, a slight reduction in the turf abundance was accompanied by an increase in crustose corallines, especially on the reef wall (Fig. 4b).

Between all benthic groups, the most conspicuous changes from coastal to offshore reef was observed in the cover of stony corals (a threefold increase in the reef flat and sevenfold in the reef wall) and soft corals (a fivefold increase in both reef flat and wall) as can be seen in Fig. 5. Also significant was the reduction of zoanthids (Fig. 5).

At the whole reef level, three major habitats were apparent (Figs. 6b and 6c). The reef flat was the area with highest macroalgal abundance - 53.7% - and lowest live coral cover - 9.9% (Fig. 6b). The maximum period of reef flat air exposure during low tides was 6 hours/day, and 15 of the total 49 infrageneric fleshy alga taxa were found to occur on the flat (Table 1).

The landward reef wall consists of a sheltered area in which 31infrageneric taxa were identified, 16 in the dry season and 30 in the rainy season (Table 1). It also held the highest live coral cover of all sites, 22.7% at the 3m-depth zone (Fig. 6b). The overall macroalgal cover was higher at 1m depth (47.7%) with turf algae (21.6%) being the dominant feature (Fig. 6b), frequently covering dead coral heads of *Mussismilia brasiliensis* and *Siderastrea stellata*, two endemic species.

The third major reef habitat was the seaward reef wall (Fig. 6c), which consisted of areas with high energy and sediments of high grain size. Live coral cover was lower than the landward reef wall, whilst the cover of hydrocorals (*Millepora* spp.) was higher, especially at 1m depth (Fig. 6c). The percentage cover of crustose coralline species was also higher than the sheltered reef wall with values up to 12.7% (at 1m depth), 9.4% (at 3m) and 8% (at 5m) - see Fig. 6c. Although the overall macroalgal percentage cover at this habitat was lower than both the landward reef wall (Fig. 6b) and coastal reefs (Fig. 6a), it presented the highest number of species of the whole studied area, with 35 out of 49 taxa identified, being 19 in the dry season and 34 in the rainy season (Table 1).

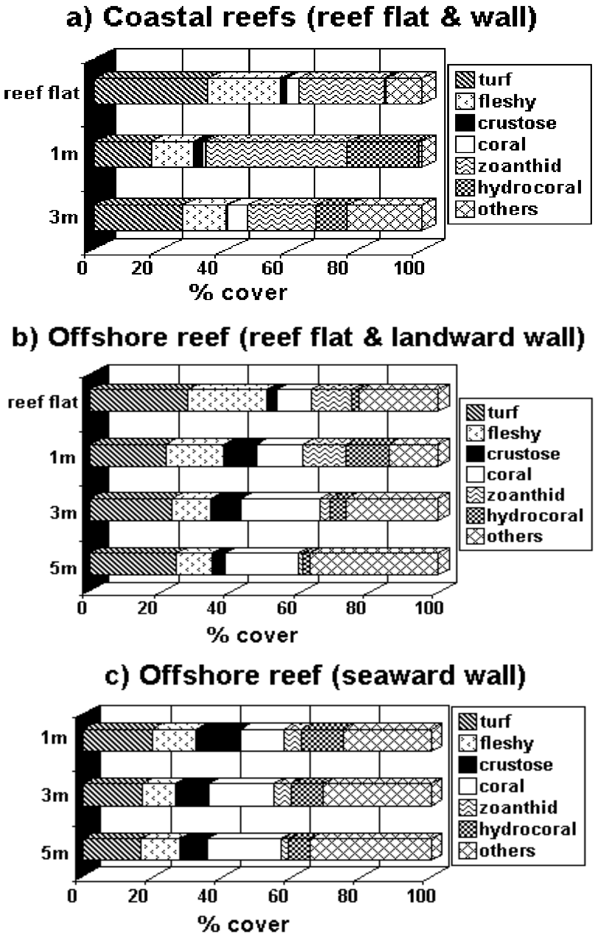

Fig. 6 Vertical distribution of the major groups of benthic organisms on (a) coastal reefs, (b) offshore reef - landward and (c) offshore reef - seaward. Macroalgae are grouped as turf, fleshy or crustose, and "others" includes soft corals, sponges, sand and bare areas.

Multivariate analysis of all reef habitats is presented in Fig. 7. There appears to be differences in community patterns within reef habitats, generating six meaningful clusters of habitats at a similarity of 45% (Fig. 7a). This is supported by ANOSIM tests for differences between sites and habitats (global R = 0.43, $p < 1.4\%$). MDS ordination was also performed in conjunction with the cluster analysis, the clusters originating from the 45% similarity threshold annotated onto the resulting plot (Fig. 7b). Four of the six clusters comprise sites from the offshore reef, namely: (1) the landward reef wall at 3m depth; (2) the 5m-depth zone at dry season; (3) the 5m-depth zone at rainy season; and (4) the landward reef wall at 1m depth. The last two clusters included habitats from both offshore and coastal reefs. They are: (5) the reef flat; and (6) the seaward reef wall at 1m and 3m-depth zones.

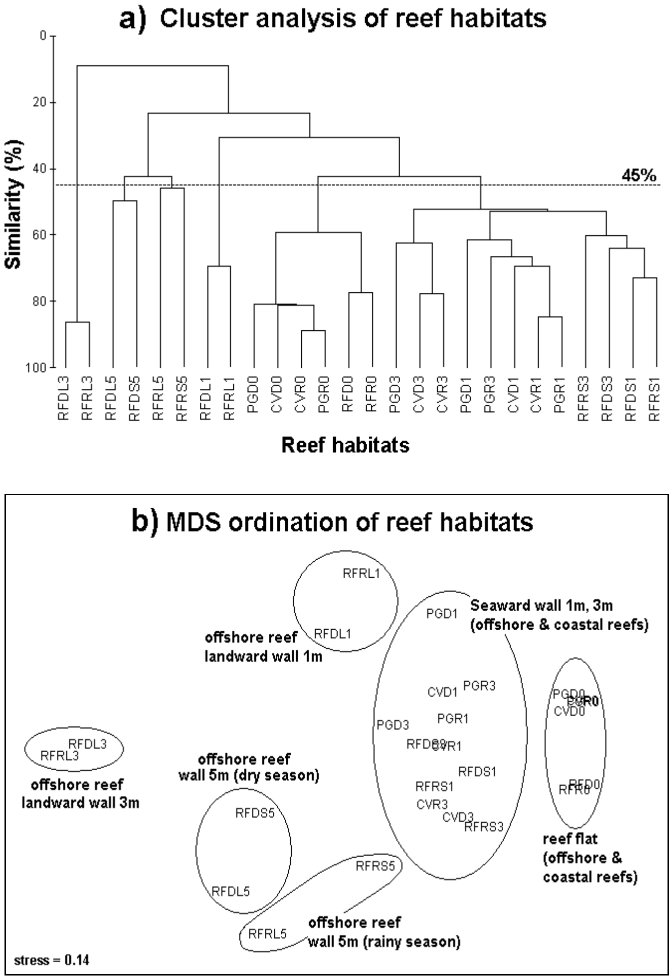

Fig. 7 Dendrogram for hierarchical clustering of algal communities (similarity threshold at 45%) based on Bray-Curtis similarities (a) and MDS ordination with clusters from Fig. 7a superimposed (b). Sites: CV = Coroa Vermelha, PG = Ponta Grande, RF = Recife de Fora; Seasons: D = dry season, R = rainy season; Habitats: 0 = reef flat; L1, L3, L5 = landward wall at 1, 3 and 5m; S1, S3, S5 = seaward reef wall at 1, 3 and 5m.

Discussion

The contribution of algae and other benthic organisms varied considerably not only between offshore and coastal reefs, but also between windward and leeward sides of the offshore reef, thus providing various reef habitats. This within-reef variation is consistent with the literature, which since the thirties have shown that corals are more developed in the calmer waters landward of the algal ridge and on deeper areas of the seaward reef wall (Round 1981).

Community structure

The pattern of community structure on the studied reefs suggests similarities with the Caribbean model (Adey 1998). Algal turf is the dominant component in all reef sites and habitats, reaching highest development in the partially exposed areas of the reef flat, growing above dead coral skeletons. On the reef wall, they also occur in patches between live coral colonies and as epiphytes on large frondose algae like *Lobophora*, *Sargassum*, *Stypopodium* and *Zonaria*.

On the coastal reefs, fleshy algae are the second most common group on the reef flat, whilst zoanthids follows turf algal dominance in the reef wall. The reef flat also presented a species zonation between the shore and the first slopes of the reef wall. A similar zonation pattern has been recorded on the literature (Round 1981) and was found to be a result of differential effects of environmental factors (i.e. variations in wave energy, substrate type, light intensity, salinity and temperature). At the reef border, the density of zoanthids increases rapidly, especially the genus *Palythoa*. In areas of high abundance, colonies cover most of the available substrate, forming mats that extend for up to 30 square meters.

Since the effects of density in marine hard substrate communities are mediated by competition for space (Tanner 1997), the high cover of zoanthids in the coastal reefs may suggest a competitive edge over the fleshy algae, especially at the 1m-depth zone. Although there is no previous work describing the community structure of the study area, there are some reports in the literature showing that zoanthids are conspicuous inhabitants of tropical, turbulent waters on reef crests of some Australian reefs (Burnett et al. 1994; Tanner 1997). Additionally, their growth is not restricted to a predefined shape and so they can probably take advantage of any free space in its vicinity. This assumption is supported by the fact that available space is lowest at the 1m-depth zone (0.9% in Coroa Vermelha and 0% in Ponta Grande).

On the offshore reef, turf algae was, again, the most abundant group, followed by fleshy algae on the reef flat and stony corals on the reef wall. Although the number of fleshy species was double that of the coastal reefs, the overall percentage cover was comparable to that on both the reef flat and wall of the coastal reefs. Visible changes from coastal to offshore reefs occurred in the abundance of turf (6% lower) and crustose coralline algae, with the latter demonstrating a threefold increase. Also noticeable was the drastic reduction of zoanthids, especially on the reef wall, suggesting that the same conditions that allowed great development of zoanthids in the coastal reefs are not apparent on the offshore reef.

Factors controlling algal distribution

On coastal reefs, algal abundance was inversely related to zoanthid abundance and directly related to the amount of available space for settlement. On the offshore reef, however, the inverse was observed and algal cover increased with both zoanthids and available space being reduced. This pattern suggests that available hard substrate may be the primary limiting factor for algal settlement and growth in the coastal reefs, especially if the potentially low herbivory pressure due to overfishing is considered (N.B. although there is no study regarding herbivory in the area, this assumption is based on field observations and on recent changes in fishery practices, e.g., previously unfished groups of species are now targeted due to the lack of commercial groups).

Differential herbivory between offshore and coastal reefs may also be inferred from the comparison of abundance between the algal functional groups. Turf algae, which along with fleshy algae is the main group targeted by herbivorous fish (Hackney et al. 1989), are more abundant in the coastal reefs, whereas crustose coralline algae, a group that take advantage of herbivory/grazing activity (Hackney et al. 1989), reaches maximum development on the offshore reef.

Additionally, the nutrient availability is higher in the coastal reefs (Costa et al. in prep), a combination of factors that could lead to a much higher algal abundance (Aronson & Precht 2000; Lapointe 1997; Lapointe 1999; Miller et al. 1999; Smith et al. 2001). However, at 1m and 3m depths, the algal abundance is lower than on the offshore reefs, where herbivory is supposedly higher (i.e. low fishing pressure due to the MPA), and the nutrient availability is reduced (Costa et al. in prep).

In the offshore reef, zoanthids occur predominantly in reef flat pools and the whole flat remains underwater most of the time. This combination of factors provides the necessary balance of light and settlement space that allow better development of fleshy and turf algae, which cover, respectively, 22.4% and 28.2% of the flat. In this reef, the status of MPA and less disturbed conditions has supposedly preserved the fish stock, and herbivory is likely to be the dominant force driving the distribution and abundance of reef macroalgae. In addition, the data suggest that highly variable physical disturbance (like wave energy and low tidal exposure) between seaward and landward reef sides can result in a distinctive algal distribution pattern, intimately related to gradients in exposure and wave energy. This may explain the differences in macroalgal abundance between the low tide emersed reef flat, the high-energy reef wall (seaward) and the sheltered area (landward). Therefore, Connell et al.'s (1997) prediction for corals appears to be similarly valid for algae, i.e. the spatial and temporal scales of declines and recoveries in macroalgal abundance are much smaller on the wave-exposed side of the reef than on the protected side. This can generate patchy distributions of macroalgae over the reefs.

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