

Spatial and Seasonal Distribution of Seaweeds on Coral Reefs from Southern Bahia, Brazil

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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 inshore 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 slope (at 1, 3 and 5 m depth) and from the reef flat. Macroalgal cover ranged from 33 % (reef slope) to 60 % (reef flat) on the nearshore reefs, and from 36 % (reef slope) to 50 % (reef flat) on the offshore reef. 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 inshore and offshore reefs. On the reef slopes, corals and zoanthids are second to turf algae in the offshore reef and nearshore reefs respectively.

Introduction

The last decades have seen increasing concern about the effect of human disturbance on coral reef communities. Recently, some studies have focused on the macroalgae communities of coastal reefs (Larned 1998, Lundberg and Popper 1999, McCook 1999, Miller *et al.* 1999, Aronson and Precht 2000), paying attention to their roles in both reef construction (Adey 1998) and destruction (Hughes 1994). Some authors (Womersley and Bailey 1969, Round 1981) state that since algae and not corals are dominant in most 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 (Schaffelke 1999, Stiger and Payri 1999, McManus *et al.* 2000).

In Brazilian reefs, however, the scarcity of baseline information makes it difficult to establish any trends. The Bahia State 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 (Oliveira Filho 1977, Oliveira 1989). This situation is even more critical in the region called 'Discovery Coast', a section of about

150 km in the extreme south of the Bahia State in which the European settlers made the first contact with the native people in April 1500.

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 1997, 1998, Nunes and Paula 2000). Richard Rathbun also collected algae during his visit to the coral reefs of Bahia (Rathbun 1876, 1879a,b). This collection was studied by Oliveira (1989) who also revised the material collected by Dickie (Oliveira 1974). Most of these studies, however, have focused on locations either around Salvador (due to the proximity of the Federal University of Bahia) or in the Abrolhos Marine Park (the first Marine Protected Area in the country) with the Discovery Coast being largely overlooked. Prior to this current study, 253 taxa have been identified from Bahian coastal waters, comprising 139 Rhodophyta, 49 Phaeophyta, and 66 Chlorophyta (Nunes 1998).

The non-geniculate corallines are still under identification and therefore they do not appear in the species list (Table I). 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*).

Table I. Distribution (presence/absence) of algal taxa on the reef flat and slopes (1 m, 3 m and 5 m) of the nearshore and offshore reefs.

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

d = dry season and r = rainy season. Names of authors of plant taxa are as in Wynne (1998).

The purpose of the present study is to describe the distribution of the benthic macroalgal community, as well as identifying its components, on the nearshore and offshore reefs of Cabralia and Porto Seguro Bays on the Brazilian Discovery Coast, southern Bahia State. Additionally, the distribution of other major groups (stony corals, hydrocorals, zoanthids, gorgonians and sponges) is included, as this study constitutes the first description of the benthic community in that area.

Material and Methods

Study sites

The Discovery Coast is located on the east Brazilian coast between 16°00'S and 17°30'S (Fig. 1). Despite being the birthplace of Brazil, the region remains comparatively unknown, having the least studied coral reefs on the entire Bahian coast. In the study area, the nearshore 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 (~ 6 km distance), they were both surveyed as Coroa Vermelha, unlike Ponta Grande which 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 emerges 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 alcicornis* Linnaeus on the reef crest (at about 1 m depth below the mean tide level [MTL]).

The offshore reef (Recife de Fora) is located 8 km from the coast. The area of the intertidal 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). On the nearshore reefs, the survey was performed on the reef flat and on the seaward reef slope (at 1 m and 3 m depth below the MTL). On the offshore reef, samples were collected from both seaward and landward reef slopes (at 1, 3 and 5 m depth below the MTL), as well as on the reef flat. The 1 m-depth contour was chosen because it includes the reef crest and is exposed during the lowest spring tides. The 3 m-depth contour, which always remains underwater, constitutes one of the areas with maximum reef development. Finally, the 5 m-depth contour (only surveyed on the offshore reef) was chosen to give an indication of how the community structure changes as the light incidence is reduced.

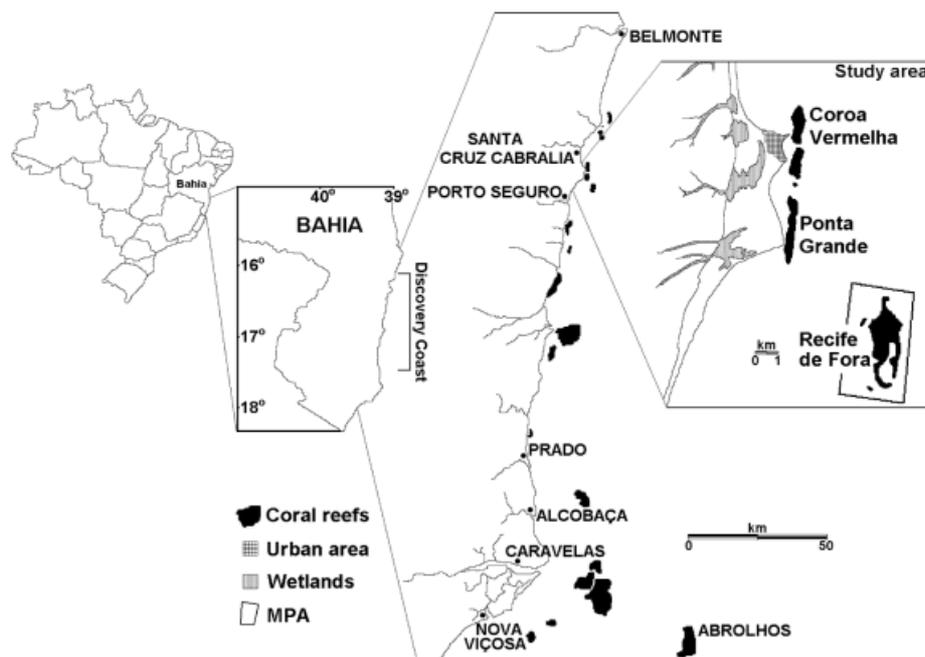


Fig. 1. Map of the Brazilian Discovery Coast, Southern Bahia, Brazil, and location of the reefs studied.

The methodology used was essentially as described in the algal survey of the Atlantic and Gulf Rapid Reef Assessment Protocol (AGRRA; Pattengill-Semmens 2000). The repeated sampling unit consisted of algal counts undertaken using a 25 x 25 cm quadrat placed above a 10-m transect. A total of 350 quadrats was quantified, 150 on the offshore reef and 100 on each of the coastal reefs. The survey encompassed approximately 250 m on each side of the reef and on the reef flat. Algal samples were collected for subsequent identification and are deposited in the Herbaria of the State University of Rio de Janeiro and the Federal University of Bahia, Brazil.

Data analysis

Univariate indices, such as Shannon-Wiener diversity (H') and Pielou's evenness (J'), along with total number of species (S), were used to measure some attributes of community structure within and between reef habitats, sites and seasons (Clarke and Warwick 1994).

Diversity profiles are also presented using k -dominance curves (Lambhead *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 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 and Curtis 1957), in order to delineate groups of habitats with distinct community structures. Multidimensional scaling (MDS) was the chosen method of ordination (Clarke and Green 1988), also based on Bray-Curtis similarity matrices. Formal significance tests for differences between reef sites and habitats were performed using the analysis of similarity (ANOSIM) randomisation test (Clarke and Green 1988).

Results

Species composition

A total of 51 taxa were identified during the study, comprising 19 Phaeophyta, 17 Rhodophyta and 15 Chlorophyta (Table I). The dominance of brown algae is an artefact of the sampling process. If turf and epiphytic algal species, as well as the non-geniculate corallines, were included, the Rhodophyta would certainly have outnumbered the Phaeophyta. Two species were recorded for the first time from Bahia state: *Tricleocarpa cylindrica* (Rhodophyta, Galaxau-

raceae) and *Avrainvillea longicaulis* (Chlorophyta, Udoteaceae). *Tricleocarpa cylindrica* and *Codium isthmocladum* were found only on the nearshore reefs (Table I). *Caulerpa* and *Dictyota* were the genera with the highest number of taxa (five each), with *Dictyota mertensii* demonstrating the widest distribution, being able to colonise 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 (5–9 m).

The most diverse reef habitat was the Recife de Fora reef slope at 3 m depth, on which 24 taxa were found during the rainy season (Table I). However, the reef slope communities within samples (quadrats) were highly variable (Fig. 2a,b). Fluctuations in diversity ($H'e$) were more pronounced seasonally than spatially (Fig. 2c,d). The diversity on the reef slope, especially during the rainy season, was generally higher than on the reef flat (Fig. 2c,d). Moreover, the Ponta Grande reef slope, in addition to being one of the habitats with a high number of species (Fig. 2b), presented the highest diversity of the study during the rainy season (Fig. 2d). Low evenness (i.e. high domi-

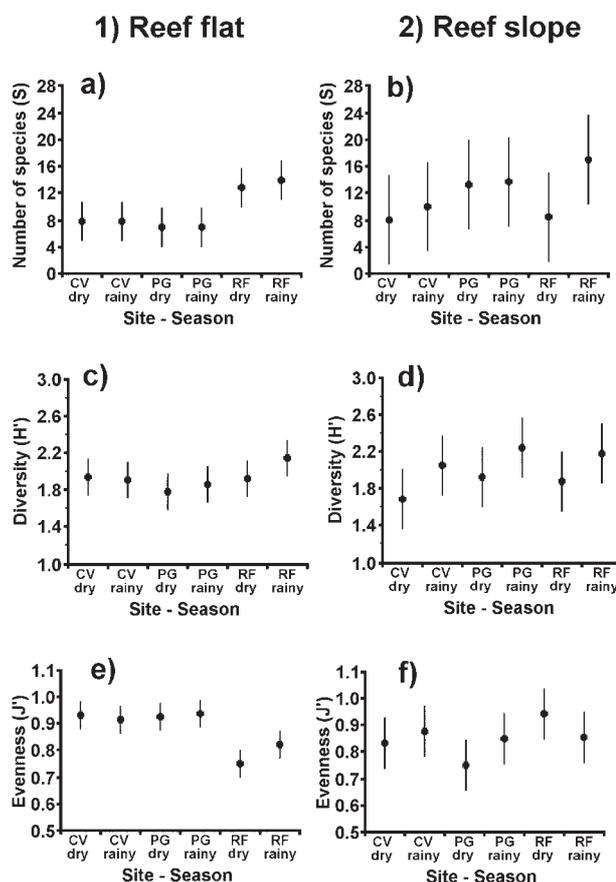


Fig. 2. Total number of species (S), diversity ($H'e$) and evenness (J') based on data for macroalgal cover (mean \pm 95% confidence intervals) along transects on the reef flats (column 1) and slopes (column 2) during dry and rainy seasons. CV = Coroa Vermelha, PG = Ponta Grande and RF = Recife de Fora.

nance) can be seen on Ponta Grande reef slope, especially during the dry season (Fig. 2f), whilst on 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 the reef slopes (positioned below reef flat curves), especially at Recife de Fora sites (Fig. 3c,f). 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 also emphasise the higher number of species on the reef slopes (more squares than triangles) in all reefs studied and at all seasons. At the same time, the shape of the reef flat curves suggests high dominance by the five most common taxa. Together these taxa comprise more than 80% of the total fleshy algal cover (Fig. 3).

Spatial variation

There was a marked variation in the spatial distribution of species, both between nearshore and offshore reefs and within specific habitats (reef flats and slopes). On the nearshore reefs (Coroa Vermelha and Ponta Grande), high macroalgal cover was recorded from the reef flat (always above 55% – Fig. 4a), from which ~35% was due to algal turf (Fig. 5a). Fleshy algae also presented higher values on the reef flat but only 9 species were found (Table I). This dense

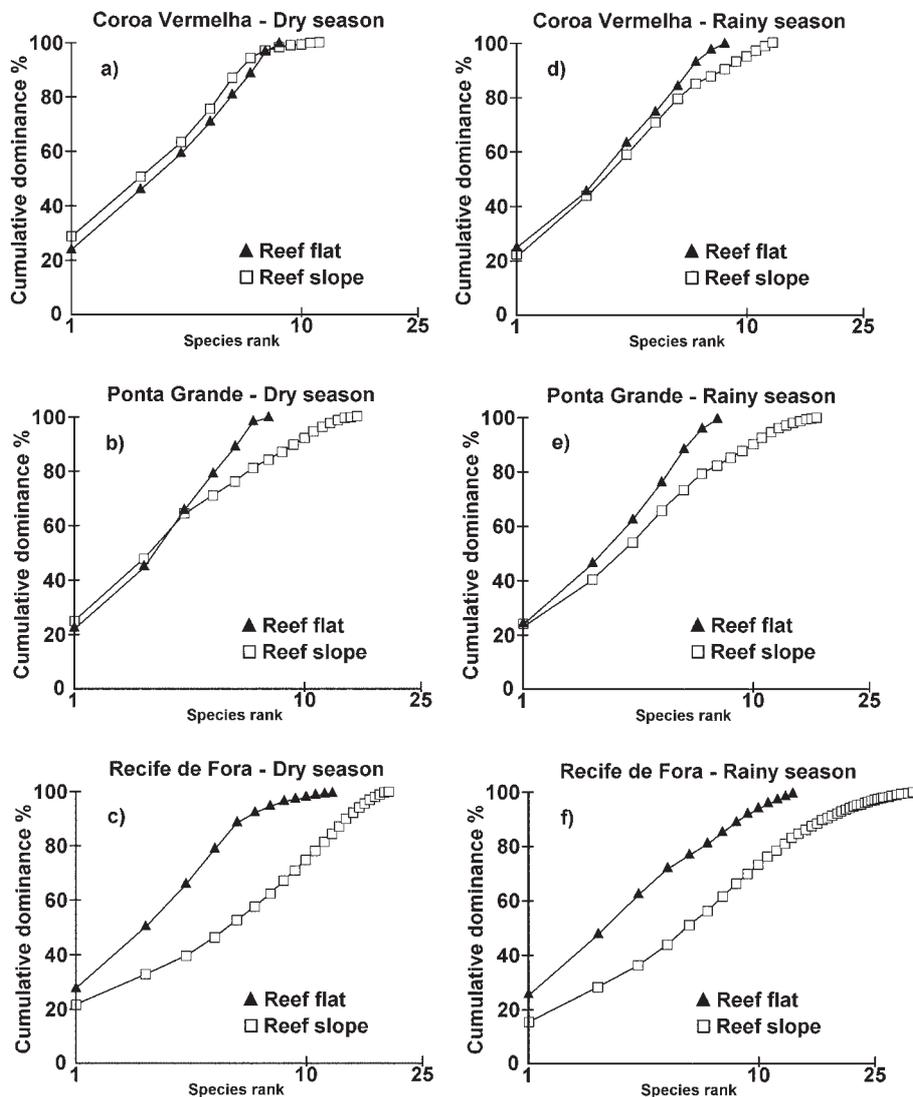


Fig. 3. *k*-dominance curves (x-axis logged) for macroalgal species abundance in all sampling sites and seasons.

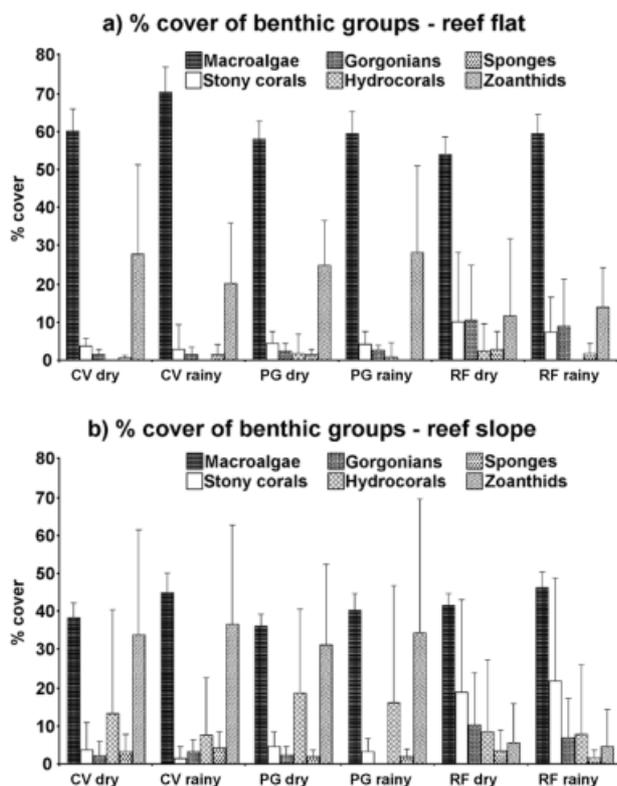


Fig. 4. Percentage cover (mean \pm 1 SD) of the major groups of benthic organisms on (a) the reef flats and (b) the reef slopes in all sites and seasons. Macroalgae include turf, fleshy and crustose coralline. CV = Coroa Vermelha, PG = Ponta Grande and RF = Recife de Fora.

macroalgal cover is dominated primarily by *Caulerpa* (7.58% \pm 0.67%), *Sargassum* (5.58% \pm 0.72%) and *Dictyosphaeria* (3.79% \pm 1.43%).

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. Mats of *Ulva lactuca* and *Dictyosphaeria versluysii* commonly colonize any hard substrate that emerges from the sediment. *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 an extensive system of rhizoids, colonise the sandy bottoms. Zoanthids are also common on the reef flat, with a percentage cover around 25% (Fig. 4a).

At the 1 m-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*, 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, the number

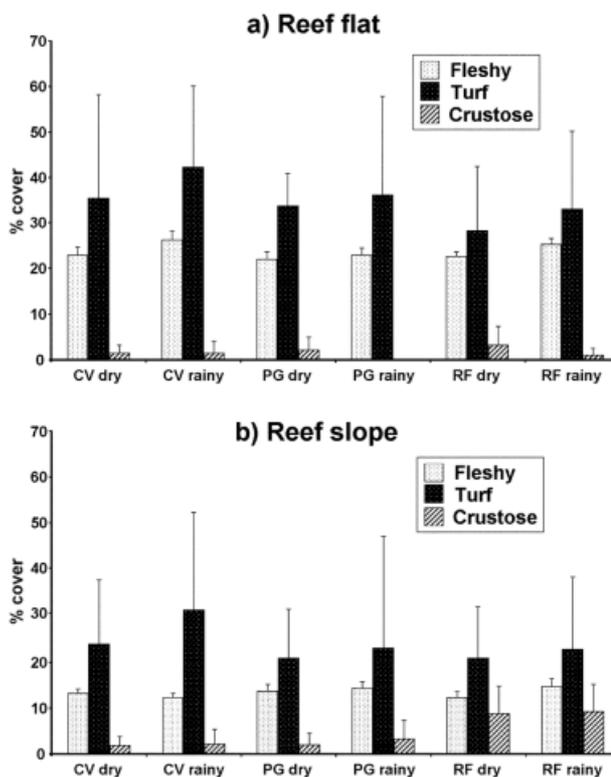


Fig. 5. Distribution of the macroalgal functional groups (mean \pm 1 SD) on (a) the reef flat and (b) the reef slopes for all sites and seasons. CV = Coroa Vermelha, PG = Ponta Grande and RF = Recife de Fora.

of species at this depth zone was higher than on the reef flat, with 15 out of the 22 taxa being recorded (Table I). At the 3 m-depth zone, the reduction in the abundance of zoanthids (21%) and hydrocorals (9%) was proportional to the increase in macroalgal cover, which rose to about 40% (Fig. 6a). Also noticeable was the increase in sand patches and bare substratum (16% at 3 m, compared with 1% at 1 m and 9% on the reef flat). At this depth, 14 out of 22 algal taxa were recorded (Table I). Live coral cover, however, was always below 7%, the highest value being reached at 3 m depth (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 I), compared with only 22 from the nearshore reefs. Between the algal groups, a slight reduction in the turf abundance was accompanied by an increase in crustose corallines, especially on the reef slopes (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 on the reef flat and sevenfold on the reef slope) and soft corals (a fivefold increase on both reef flat and slope). Also significant was the reduction of zoanthids (Fig. 5). The reef flat was the area with highest macroalgal abundance (54%) and lowest stony coral cover (10%, Fig. 6b). The maximum period of reef

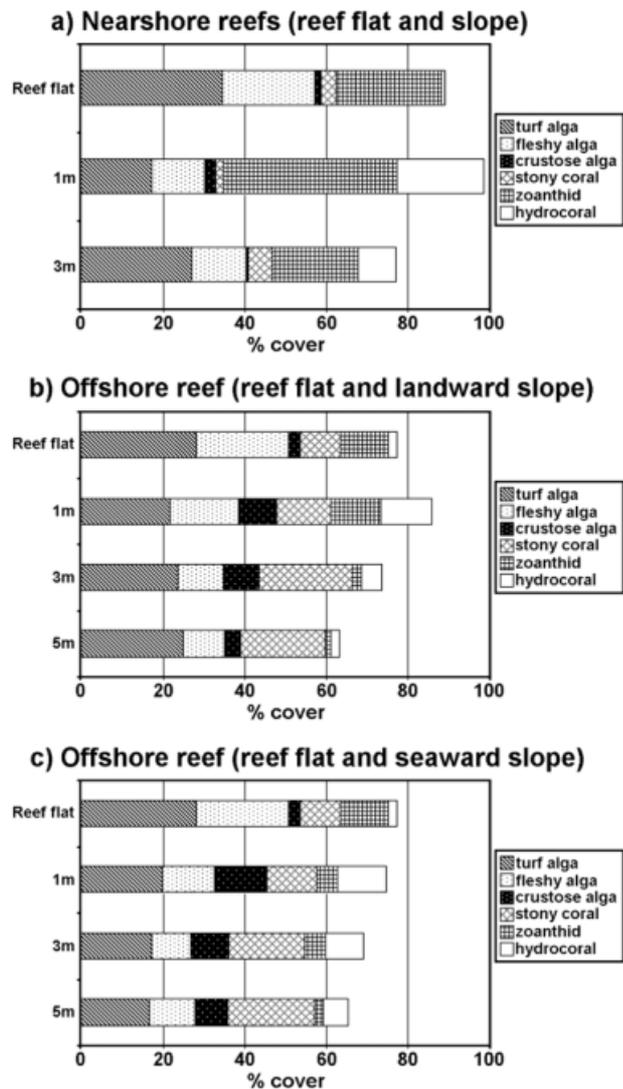


Fig. 6. Vertical distribution (depth zonation) of the major groups of benthic organisms within reef habitats on the nearshore (a) and offshore (b, c) reefs.

flat air exposure during low tides was 6 hours/day, and 15 of the total 49 infrageneric fleshy algal taxa were found to occur on the flat (Table I).

The landward reef slope consists of a sheltered area in which 31 infrageneric taxa were identified, 16 during the dry season and 30 during the rainy season (Table I). It also had the highest stony coral cover of all sites, 23% at the 3 m-depth zone (Fig. 6b). The overall macroalgal cover was higher at 1 m depth (48%) with turf algae (22%) being the dominant feature (Fig. 6b), frequently covering dead coral heads of the stony corals *Mussismilia brasiliensis* Verrill and *Siderastrea stellata* Verrill.

The third major reef habitat was the seaward reef slope (Fig. 6c), which consisted of areas with high energy and sediments of high grain size. Live coral cover was lower than the landward slope, whilst the cover of hydrocorals (*Millepora* spp.) was higher, especially at

1 m depth (Fig. 6c). The percentage cover of crustose coralline species was also higher than the sheltered reef slope with values up to 13% (at 1 m depth), 9% (at 3 m) and 8% (at 5 m). Although the overall macroalgal percentage cover at this habitat was lower than both the landward slope (Fig. 6b) and the nearshore reefs (Fig. 6a), it presented the highest number of species of the whole area studied, with 35 out of 49 taxa identified, being 19 during the dry season and 34 during the rainy season (Table I).

The differences in community patterns within reef habitats generated six meaningful clusters at a similarity of 45% (Fig. 7a). This is supported by the ANOSIM test for differences between sites and habitats (global R = 0.43, p < 1.4%). An 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 slope at 3 m depth; (2) the 5 m-depth zone at dry season; (3) the 5 m-depth zone at rainy season; and (4) the landward slope at 1 m depth. The last two clusters includ-

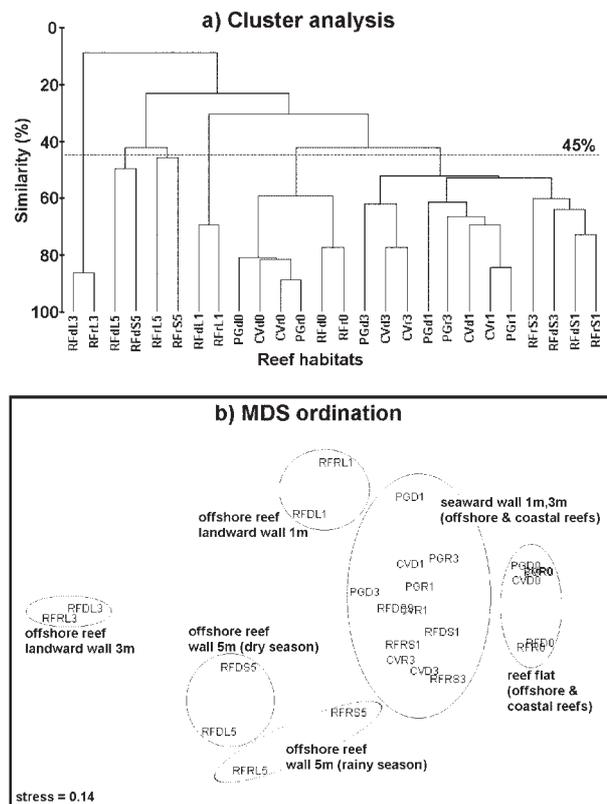


Fig. 7. Dendrogram for hierarchical clustering of algal communities (similarity threshold at 45%) based on Bray-Curtis similarities (a) and MDS ordination with clusters from Fig. 7a superimposed (b). CV = Coroa Vermelha, PG = Ponta Grande and RF = Recife de Fora; D = dry and R = rainy seasons; 0 = reef flat, L = landward slope and S = seaward slope; 1 = 1 m, 3 = 3 m and 5 = 5 m depth.

ed habitats from both offshore and nearshore reefs. They are: (5) the reef flats; and (6) the seaward slope at 1 m and 3 m-depth zones.

Seasonal variation

The rainy season (end of the austral summer) presented a higher number of species, as well as diversity, the reef slopes being the habitat where this seasonal variation was more accentuated (Fig. 2b,d). Most of the taxa identified in the dry season were present during the rainy season, the only exception being *Gelidiella acerosa*. This species, although being considered as perennial, was not found on either nearshore or offshore reefs during the second sampling (rainy season). During the dry season, *Gelidiella acerosa* was the most common taxon with a wide distribution throughout the study area (Table I). In the rainy season, the Phaeophyta genera *Dictyota* and *Padina* dominated the algal community, occupying large patches on both reef flat and slopes. A total of 23 taxa identified during the rainy season did not occur during the dry season (Table I).

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

Discussion

Community structure

The pattern of community structure on the reefs studied 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*, *Styopodium* and *Zonaria*.

On the nearshore reefs, fleshy algae are the second most common group on the reef flat, whilst zoanthids follow turf algal dominance on 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 in 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 *Pa-*

lythoa. In areas of higher abundance, colonies cover most of the available substrate, forming mats that extend for up to 30 m².

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 1 m-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 in Australia (Burnett *et al.* 1994, Tanner 1997) and the Caribbean region (Haywick and Mueller 1997). Additionally, their growth is not restricted to a predefined shape and so they can probably take advantage of any free space in their vicinity. This hypothesis is supported by the fact that available space is lowest at the 1 m-depth zone (1% in Coroa Vermelha and 0% in Ponta Grande).

On the offshore reef, turf algae was, again, the most conspicuous group, followed by fleshy algae on the reef flat and stony corals on the reef slopes. Although the number of fleshy species was double that of the nearshore reefs, the overall percentage cover was equivalent. Visible changes from coastal to offshore reefs occurred in the percentage cover 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 slopes, suggesting that the same conditions that allowed great development of zoanthids in the nearshore reefs are not apparent on the offshore reef.

Factors controlling algal distribution

On nearshore reefs, algal percentage cover 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 substratum may be the primary limiting factor for algal settlement and growth on the nearshore 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 nearshore reefs may also be inferred from the comparison of percentage cover from 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 2001), which, if combined with low herbivory, could lead to much higher algal abundance (Lapointe 1997, Miller *et al.* 1999, Aronson and Precht 2000, Smith *et al.* 2001). Notwithstanding, at 1 m and 3 m depths, the algal percent cover 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 2001).

On 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 allows better development of fleshy and turf algae, which cover, respectively, 22% and 28% of the flat. On 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 sug-

gest that highly variable physical disturbance (e.g. wave energy and tidal exposure) between seaward and landward slopes can result in a distinctive algal distribution pattern, intimately related to gradients of such disturbances. This may explain the differences in macroalgal percentage cover between the low tide emerged reef flat, the high-energy reef slope (seaward) and the sheltered area (landward). Therefore, the Connell *et al.* (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.

Acknowledgements

This research is supported by a CNPq (Brazilian Research Council) scholarship to O. Costa.

Accepted 16 March 2002.

References

- Adey, W. H. 1998. Coral reefs: algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J. Phycol.* 34: 393–406.
- Aronson, R. B. and W. F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnol. Oceanogr.* 45: 251–255.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27: 325–349.
- Burnett, W. J., J. A. H. Benzie, J. A. Beardmore and J. S. Ryland. 1994. High genetic variability and patchiness in a common Great Barrier Reef zoanthid (*Palythoa caesia*). *Mar. Biol.* 121: 153–160.
- Clarke, K. R. 1990. Comparisons of dominance curves. *J. Exp. Mar. Biol. Ecol.* 138: 143–157.
- Clarke, K. R. and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. *Mar. Ecol. Prog. Ser.* 46: 213–226.
- Clarke, K. R. and R. M. Warwick. 1994. *Change in Marine Communities. An Approach to Statistical Analysis and Interpretation*. Natural Environment Research Council, Bournemouth, U.K. 97 pp.
- Connell, J. H., T. P. Hughes and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.* 67: 461–488.
- Costa, O. S., Jr. 2001. Nutrifcation and its effects on coral reefs from Southern Bahia, Brazil. PhD Thesis, Department of Biological Sciences, University of Plymouth, Plymouth, U.K. 281 pp.
- Costa, O. S., Jr., Z. M. A. N. Leão, M. Nimmo and M. J. Attrill. 2000. Nutrifcation impacts on coral reefs from northern Bahia, Brazil. *Hydrobiologia* 440: 307–315.
- Dickie, G. 1874. Enumeration of algae collected from Bahia by H. N. Moseley, M. A., naturalist to H. M. S. "Challenger". *J. Linn. Soc. (Bot.)* 14: 1–377.
- Hackney, J. M., R. C. Carpenter and W. H. Adey. 1989. Characteristic adaptations to grazing among algal turfs on a Caribbean coral reef. *Phycologia* 28: 109–119.
- Haywick, D. W. and E. M. Mueller. 1997. Sediment retention in encrusting *Palythoa* spp. – a biological twist to a geological process. *Coral Reefs* 16: 39–46.
- Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. *Science* 265: 1547–1551.
- Lambhead, P. J. D., H. M. Platt and K. M. Shaw. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *J. Nat. Hist.* 17: 859–874.
- Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and Southeast Florida. *Limnol. Oceanogr.* 42: 1119–1131.
- Larned, S. T. 1998. Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Mar. Biol.* 132: 409–421.
- Lundberg, B. and N. Popper. 1999. Algal vegetation in the Eilat Coral Reef Reserve. *Israel J. Plant Sciences* 47: 111–121.
- Martins, D. V., M. Cordeiro-Marino, N. B. Boccanera and J. M. C. Nunes. 1991. Cloroficeas marinhas bentônicas do município de Salvador, Bahia, Brasil. *Hoehnea* 18: 115–133.
- McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357–367.

- McManus, J. W., L. A. B. Menez, K. N. Kesner-Reyes, S. G. Vergara and M. C. Ablan. 2000. Coral reef fishing and coral-algal phase shifts: implications for global reef status. *ICES J. Mar. Sci.* 57: 572–578.
- Miller, M. W., M. E. Hay, S. L. Miller, D. Malone, E. E. Sotka and A. M. Szmant. 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnol. Oceanog.* 44: 1847–1861.
- Nunes, J. M. C. 1997. Hypneaceae, Rhodomeniaceae, Ceramiaceae e Rhodomelaceae (Rhodophyta) das Praias de Placafor e Itapoã, município de Salvador, Bahia, Brasil. *Biotemas* 10: 61–75.
- Nunes, J. M. C. 1998. Catalogo de algas marinhas bentônicas do Estado da Bahia, Brasil. *Acta Bot. Malacitana* 23: 5–21.
- Nunes, J. M. C. and E. J. Paula. 2000. Estudos taxonômicos do gênero *Padina* Adanson (Dictyotaceae – Phaeophyta) no litoral do Estado da Bahia, Brasil. *Acta Bot. Malacitana* 25: 21–43.
- Oliveira, E. C. 1974. An annotated list of Brazilian seaweeds in Dickie's Herbarium. *J. Linn. Soc. (Bot.)* 69: 229–238.
- Oliveira, E. C. 1989. Uma antiga coleção de algas marinhas do litoral brasileiro. *Ci. Cult. J. Braz. Ass. Adv. Sci.* 41: 402–403.
- Oliveira Filho, E. C. 1977. Algas Marinhas Bentônicas do Brasil. DSc Thesis, Universidade de São Paulo, São Paulo, Brazil. 407 pp.
- Pattengill-Semmens, C., S. R. Gitting and T. Shyka. 2000. *Flower Garden Banks National Marine Sanctuary: a Rapid Assessment of Coral, Fish and Algae Using the AGRRA Protocol*. U.S. Department of Commerce, National Oceanic and Administration, Silver Spring, U. S. A. (Marine Sancturaries Conservation Series MSD-00-3). 15 pp.
- Rathbun, R. 1876. Extinct coral reef at Bahia, Brazil. *Amer. Nat.* 10: 439–440.
- Rathbun, R. 1879a. Prof. Hartt on the Brazilian sandstone reefs. *Amer. Nat.* 13: 347–358.
- Rathbun, R. 1879b. Brazilian corals and coral reefs. *Amer. Nat.* 13: 535–551.
- Round, F. E. 1981. *The Ecology of Algae*. Cambridge University Press, Cambridge, U.K. 653 pp.
- Schaffelke, B. 1999. Short-term nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. *Mar. Ecol. Prog. Ser.* 182: 305–310.
- Smith, J. E., C. M. Smith and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19: 332–342.
- Stiger, V. and C. E. Payri. 1999. Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. *Mar. Ecol. Prog. Ser.* 191: 91–100.
- Tanner, J. E. 1997. The effects of density on the zoanthid *Palmyra caesia*. *J. Anim. Ecol.* 66: 793–810.
- Womersley, H. B. S. and A. Bailey. 1969. The marine algae of Solomon Islands and their place in Biotic Reefs. *Phil. Trans. Roy. Soc. London* 255(B): 433–442.

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