

# Seasonality in Algal Assemblages on Upwelling-influenced Coral Reefs in the Colombian Caribbean<sup>1</sup>

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Seasonal changes of benthic algal assemblages have been studied mainly in temperate and sub-tropical areas. It is not clear how natural processes contribute to the seasonal dynamics of algal assemblages on coral reefs, particularly in areas influenced by relatively cold upwelling waters. To investigate the seasonality in algal assemblages we monitored the percent cover of species and algal groups over one year (1994–1995) at two rocky-coral reefs at depths of 9–12 m on the Colombian Caribbean coast (Bahía Chengue, Tayrona National Natural Park, TNNP). The presence of relatively cold waters with temperatures of 25 °C and salinities of 36 ppt is indicative of upwelling events, while warm waters of 28–29 °C and salinities of 33 ppt indicate the rainy seasons in the area. The algal assemblage changed in composition and abundance throughout the year with a bimodal cover pattern observed for macroalgae and turf algae. During the rainy seasons (May to June and October to December) the assemblage was dominated by algal turfs (up to 43 % cover) and showed low macroalgal cover (< 20 %). In contrast, during the two upwelling periods (February and July to August) it was dominated by macroalgae (up to 44 % cover). Cover of brown macroalgae *Dictyota* spp. (mainly *D. bartayresiana*) declined from ≈ 34 % during the upwelling to only 5 % in the non-upwelling rainy seasons. Environmental data revealed a significant inverse correlation between water temperature and macroalgal cover, suggesting that increases in macroalgae are favoured by the presence of cold, upwelling events. It is likely that upwelling events bring nutrient rich waters that stimulate macroalgal growth, however, the role of nutrients regulating the abundance of macroalgae in the TNNP is yet to be investigated. The results of this study support the argument that benthic algal assemblages of coral reefs are a highly dynamic component of these ecosystems.

## Introduction

Marine benthic algae (algal turfs, crustose algae and macroalgae) play important roles in coral reef ecosystems. Algal turfs contribute significantly to primary production and have a key role in reef trophodynamics. Calcareous algae consolidate the reef material and contribute to reef construction (Littler and Littler 1984, Adey 1998). Macroalgae, on the other hand, potentially play a significant role in coral reef degradation, especially during phase shifts from corals to algal dominated reefs (Littler and Littler 1984, Hughes 1994). Despite their importance, very little is known about the seasonal changes of algal assemblages in reef ecosystems. Knowledge of algal seasonality is important when establishing monitoring programs in coral reef ecosystems, and the lack of information of these dynamics may lead to inaccurate conclusions about the patterns of algal abundance and their role in reef degradation.

Temporal changes in the structure, composition and distribution of benthic algal assemblages have been widely studied in temperate and subtropical areas (Gunnarsson and Ingolfsson 1995, Kim *et al.* 1998, Nuñez-Lopez and Valdez 1998). These studies indicate that the species composition and abundance of algal assemblages change over time, and that the changes are generally related to fluctuations of environmental variables (e.g. temperature, salinity, light, and nutrients). Endogenous, circannual clocks, which may be triggered by or synchronised to environmental factors, may also regulate macroalgae seasonality (Lüning 1993, Makarov *et al.* 1999). Coral reef macroalgae also exhibit seasonal changes (Tsuda 1982, Carpenter 1986, Liddell and Ohlhorst 1986, Steneck and Dethier 1994, Vuki and Price 1994, McCook *et al.* 1997, Rogers 1997, Schaffelke and Klumpp 1997, Lirman and Biber 2000), however, it is not clear how natural processes contribute to this seasonality.

It has been shown that upwelling events affect algal populations from subtropical and temperate areas (de Guimaraens and Coutinho 1996, Kiirikki and Blomster 1996). On the other hand, few studies have

<sup>1</sup> This contribution is dedicated to the memory of the late Dr Germán Bula-Meyer (1948–2002), prominent phycologist and Professor of the Universidad del Magdalena, Colombia.

investigated the relationship between upwelling and the structure of algal assemblages in tropical areas (Ormond and Banaimoon 1994), particularly in subtidal coral reefs. Seasonal upwelling events that occur in the area of the Tayrona National Natural Park (TNNP) in the southern Caribbean, apparently affect the composition and abundance of algal assemblages in sand plains adjacent to rocky-coral reefs (Bula-Meyer 1990) and seem to reduce coral reef development (Garzón-Ferreira 1998). In this study we investigated how the algal composition and abundance change over time in coral reefs of the TNNP, in relation to changes in environmental variables.

## Material and Methods

### Study area

The study was carried out in Chengue Bay ( $11^{\circ} 20'N$  and  $74^{\circ} 08'W$ ), located in the TNNP on the Caribbean coast of Colombia (Fig. 1). The regional climate and oceanography are strongly determined by high coastal topography and trade wind incidence (Garzón-Ferreira 1998). There are two main seasons in the year: 1) a dry season (from December–January to April), when strong NE trade winds (mean  $3.5 \text{ m s}^{-1}$ )

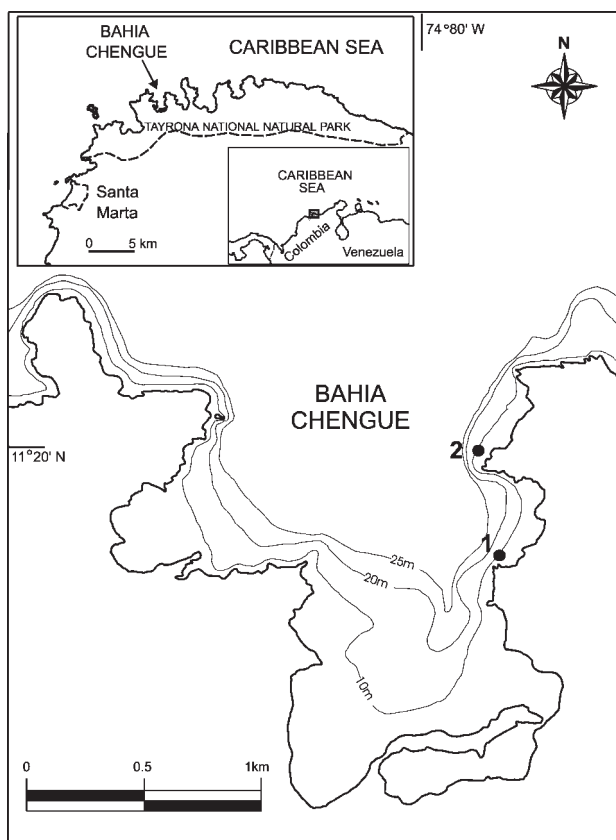


Fig. 1. Study area, Bahía Chengue, Tayrona National Natural Park, Colombia, Southern Caribbean and sampled sites.

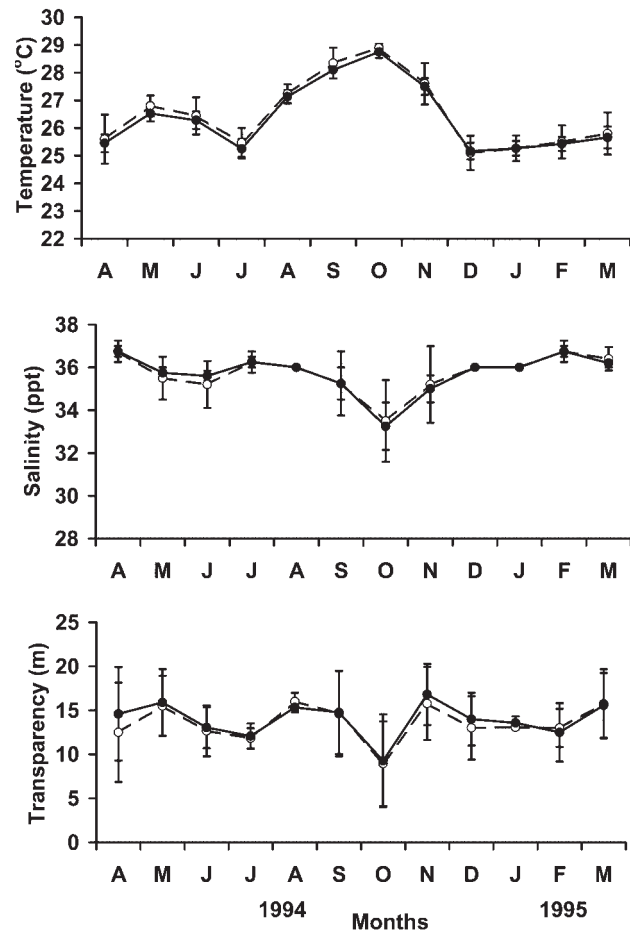


Fig. 2. Surface water temperature ( $^{\circ}C$ ), salinity (ppt) and transparency of the water column (m) over time at Site 1 ( $\circ$ ) and 2 ( $\bullet$ ) in Bahía Chengue. Data are monthly means ( $\pm$  SD).

$s^{-1}$ ) reduce precipitation and generate an upwelling that transports water of low temperatures (mean  $25.5^{\circ}C$ , but as low as  $21^{\circ}C$ ) from depths of 100–200 m to the surface. A short period of upwelling also occurs in July–August (Fig. 2); 2) a rainy season (from September–October to November–December), with low trade wind incidence (mean  $1.5 \text{ m s}^{-1}$ ), reduced upwelling occurrence, and higher seawater temperature at the surface (mean  $28.0^{\circ}C$ ). A brief period of rainfall also occurs between May and June. More than 80% of the total annual rainfall occurs during the rainy periods. Currents of reduced salinity and high turbidity commonly enter the Bay during the rainy seasons. Coral reef communities in the study sites are narrow fringes growing over a shore belt of metamorphic rocks, which extends as a reef slope down to a depth of 15–20 m. Massive and encrusting corals of *Diploria* spp., *Montastraea* spp., *Colpophyllia natans* (Houttuyn) and *Porites astreoides* Lamarck dominate these fringing reefs (Garzón-Ferreira 1998). Live coral cover in the study area at a depth of 9–12 m is  $\approx 35\%$  and has not changed over the last 7

years (1993–1999), while algae have been the predominant reef component (40–53 %) over the same period (Garzón-Ferreira *et al.* 2000).

### Field methods

To investigate the variability in algal assemblages on rocky-coral reefs over time we monitored the percentage cover and composition of benthic algae every two months for one year (1994–1995). This allowed us to compare the assemblages between upwelling and non-upwelling periods. To explore the between site variability we selected two sites 500 m apart, at the protected NE side of Bahía Chengue. One of the sites (Site 2) was slightly more exposed to wave action than Site 1 (Fig. 1). At each site, five permanent 50 × 50 cm quadrats were haphazardly placed over the reef substratum between depths of 9 and 12 m. The percentage cover of algal species and algal groups (turf algae, macroalgae and crustose algae) were recorded *in situ* employing a grid of 25 squares. Representative specimens were collected for further taxonomic determinations and were preserved in 4 % Formalin in seawater and on herbarium sheets (collection of the first author). Species were identified based on literature described in Wynne (1998). To examine the relationship between algal structure and environmental variables, data of surface water temperature and salinity, and transparency (vertical visibility of a 30-cm Secchi disc without visor) were collected weekly.

### Data analysis

In order to infer spatial and temporal patterns of the structure of the coral reef algal assemblage, the percentage cover of species was averaged by site and sampling date and classified to discriminate samples with similar composition. We employed a cluster analysis (based on the Bray-Curtis dissimilarity index, unweighted pair-groups method using arithmetic averages [UPGMA], and arcsine transformation) and a non-metrical multidimensional scaling (MDS) to explore the temporal and spatial patterns as described by Field *et al.* (1982). To identify the characteristic species of the algal assemblages, we used the inverse analysis proposed by Kaandorp (1986). Spearman correlations were used to determine the relationship between the algal abundance and the environmental data.

## Results

### Spatial variability

The algal assemblage was segregated into two main groups of samples, reflecting Sites 1 and 2 (Fig. 3). Both sites were dominated by species of the brown macroalga *Dictyota*, algal turfs (mainly *Gelidium*

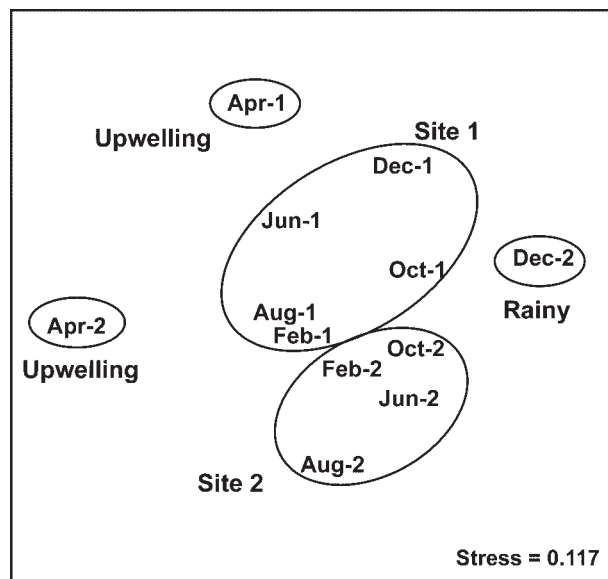


Fig. 3. Results of classification and ordination (MDS) analyses showing segregation of the algal assemblage. The numbers following the month abbreviation correspond to the site. Clusters are segregated at a similarity of 70 %.

spp., *Jania adhaerens*, *Cladophora* sp., Oscillatoriaceae spp. and *Polysiphonia* spp.), and by the crustose alga *Lithophyllum congestum* (Table 1). The differences in species composition and algal groups between sites were very subtle, with a similarity of 70 % between the two sites (Fig. 3). However, both sites exhibited characteristic species that did not occur in the other. For example, four unidentified crustose coralline algae occurred exclusively at Site 2, while *Amphiroa tribulus*, a branched articulated macroalga, was present at Site 1 but absent from the more exposed site (Fig. 4).

### Seasonal changes

The species composition and abundance of algal species and functional groups changed over time (Table 1, Fig. 5). Algal turfs and macroalgae showed a bimodal seasonal pattern through the year (Fig. 5). During the rainy seasons (April to June and October to December) algal turfs dominated the assemblage (up to 43 % cover) and macroalgal cover was low (< 20 %). In contrast, during the two upwelling periods (August and February), macroalgae predominated with up to 44 % cover (Fig. 5). A negative correlation was observed between algal turfs and macroalgal cover (Spearman,  $r = -0.886$ ,  $p < 0.05$ ). Crustose algae cover (Corallines and *Peyssonnelia* spp.) changed over the course of the year at both stations without a clear pattern.

The differences between these seasons are also demonstrated by a decrease in cover of the dominant brown upright macroalgae *Dictyota* spp. (mainly *D. bartayresiana* and *D. pinnatifida*), decreasing

Table 1. Mean absolute cover (%; n = 5) of algal taxa over time and seasons at two sites (1 and 2) in Bahía Chengue, Colombian Caribbean, during 1994–95.

Taxa	Cover (%)											
	April Upwelling		June Rainy		August Upwelling		October Rainy		December Rainy		February Upwelling	
Months Seasons	1	2	1	2	1	2	1	2	1	2	1	2
<b>Blue-green algae</b>												
<i>Oscillatoriaceae</i> spp.	12.0	0.9	1.3	0.4	0.1	0.1	0.2	0.7	2.9	0.7	0.7	0.8
<i>Microcoleus lyngbyaceus</i> (Kützing) Crouan	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
<i>Porphyrosiphon notarsii</i> (Meneghini) Kützing												
<i>Schizothrix calcicola</i> (C. Agardh) Gomont			0.1	0.1								
<i>Schizothrix tenerima</i> (Gomont) Drouet							0.1	0.1				
<i>Spirulina subsalsa</i> Oersted							0.1	0.1				0.1
<i>Oscillatoria lutea</i> C. Agardh (cotton-like tufts)			0.2		0.1		0.4	0.1	0.1			0.1
<b>Red algae</b>												
<i>Hydroolithon boergesii</i> (Foslie) Foslie	1.6	12.0	5.6	0.2	5.8	1.0	2.4	1.9	12.1	2.0	10.2	4.2
<i>Neogoniolithon</i> sp.								0.1				
<i>Lithophyllum congestum</i> (Foslie) Foslie	0.4		1.8	2.4	4.2	12.6	10.8	4.4	4.0	0.2	1.6	7.2
<i>Lithophyllum prototypum</i> (Foslie) Foslie			0.2		0.2	0.3	0.2	0.4	0.1	0.1		
<i>Corallinaceae</i> sp. 1				0.4	0.2	0.4	0.0	0.1	0.2			0.1
<i>Corallinaceae</i> sp. 2				0.6								
<i>Corallinaceae</i> sp. 3				0.8								
<i>Corallinaceae</i> sp. 4				0.8								
<i>Jania adhaerens</i> Lamouroux			2.8			0.1	0.1	0.1	0.2			
<i>Amphiroa fragilissima</i> (Linnaeus) Lamouroux			0.1		0.9		0.2					
<i>Amphiroa tribulus</i> (Ellis et Solander) Lamouroux	0.4		1.7		0.5		2.3		1.8		2.1	
<i>Amphiroa</i> sp.								0.6				
<i>Gelidium</i> spp.												
<i>Galaxaura marginata</i> (Ellis et Solander) Lamouroux	2.6	6.8	1.5	3.2	3.7	3.7	0.9	6.4	3.0	5.4	1.0	2.4
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman et Townsend	1.0	1.0	0.1	0.2	0.2	0.2	0.2		0.1	0.1	0.1	0.1
<i>Hypnea musciformis</i> (Wulfen in Jacquin) Lamouroux	1.6	0.6	0.1		0.2						0.2	0.2
<i>Hypnea spinella</i> (C. Agardh) Kützing							0.1					
<i>Kallymenia westii</i> Ganesan		1.7			0.4	1.2						
<i>Predaea weldii</i> Kraft et Abbott			0.1									
<i>Peyssonnelia</i> sp. 1	0.1	0.6	0.3	0.4	0.5	1.2	1.9	0.9	0.2	1.2	0.1	0.1
<i>Peyssonnelia</i> sp. 2		2.4	0.1	2.4	0.1	3.8	0.2	3.6	0.3	0.6	0.2	1.5
<i>Peyssonnelia</i> sp. 3				1.2	0.6	1.2	0.4	1.0	0.3	0.3	0.1	1.8
<i>Peyssonnelia</i> sp. 4		2.8	3.5	0.2	3.5	1.0	4.0	1.1	3.7	0.5	1.8	1.0
<i>Peyssonnelia</i> sp. 5		0.3		0.2					1.1	0.6	0.6	0.2
<i>Peyssonnelia</i> sp. 6	0.3				0.5	0.1						
<i>Anotrichium tenue</i> (C. Agardh) Nägeli								0.1				
<i>Ceramium</i> spp.	0.1	0.1		0.1		0.1	0.1		0.1	0.1	0.1	
<i>Wranglia argus</i> (Montagne) Montagne	5.8	0.6	3.9	0.2	1.8	0.2	0.2		3.8	0.8	0.5	
<i>Ceramium</i> sp.				0.2	0.1		0.1		0.2	1.5	0.1	0.3
<i>Dasya antillarum</i> (Howe) Millar			0.1		0.1						0.1	
<i>Hypoglossum sub simplex</i> Wynne												
<i>Martensia fragilis</i> Harvey	4.0	5.3	2.5	1.3	5.8	7.6	0.4	2.0	2.0	0.1	3.8	3.4

Table I. Continued.

Taxa	Cover (%)											
	April Upwelling		June Rainy		August Upwelling		October Rainy		December Rainy		February Upwelling	
Months Seasons	1	2	1	2	1	2	1	2	1	2	1	2
<b>Brown algae</b>												
<i>Dictyota bartayresiana</i> Lamouroux	6.3	6.4	14.6	18.2	23.6	29.2	5.1	7.7	0.5	0.4	30.0	27.2
<i>Dictyota hamifera</i> Setchell			0.1	0.2			0.2	0.2	0.3	0.3	0.4	0.4
<i>Dictyota pfaffii</i> Schmetter	3.2	0.1	0.2	1.8	0.5	3.4	2.4	3.4	3.7	7.2	1.9	3.6
<i>Dictyota pinnatifida</i> Kützting					1.2	1.4	0.2	0.8	0.6	0.3	2.3	3.2
<i>Dictyota pulchella</i> Hörnig et Schmetter							0.1					
<b>Green algae</b>												
<i>Anadyomene saldanhae</i> Joly et Oliveira												0.1
<i>Cladophora</i> sp.	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
<i>Ventricaria ventricosa</i> (J. Agardh) Olsen et J. West	0.1		0.1		0.2							
<i>Ernodesmis verticillata</i> (Kützting) Børgesen						0.1				0.1		
<i>Bryopsis pennata</i> Lamouroux												
<i>Bryopsis plumosa</i> (Hudson) C. Agardh												
<i>Codium intertextum</i> Collins et Hervey	0.1	0.1			0.4	0.7	0.2	0.2	0.1		0.2	
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh		0.1										

from approximately 35% during the upwelling seasons (February and August) to only 5% in the rainy seasons (Fig. 6). Parallel cover measurements, achieved by means of chain transects at weekly intervals, showed that *Dictyota* spp. cover can be reduced by 50% within two weeks following the highest peaks of abundance reached during the upwelling periods (Garzón-Ferreira unpubl.). Not all species of *Dictyota* exhibited the same trend in abundance in the same season. For example, a creeping *Dictyota*, *D. pfaffii*, was more abundant during the rainy seasons and scarce during upwelling periods (Fig. 6).

Classification and ordination analyses also revealed temporal patterns in the abundance and compositions of algal species. Samples collected at the end of the main upwelling season (April) from both sites were segregated from the other groups of samples in the ordination MDS plot (Fig. 3). These changes in species composition were, however, very subtle and restricted to a few taxa. For example, the red macroalgae *Martensia pavonia*, *Predaea weldii* and *Hypnea spinella* showed seasonal patterns, with peaks of cover at the end of the upwelling season in April and declines during the warm rainy seasons, when they were scarce or absent (Table I, Fig. 4). Despite the fact that these species were characteristic of the upwelling, they exhibited a low percentage cover (< 4%). Blue-green algae were also seasonal exhibiting a peak in abundance during April at the most exposed location (Fig. 4).

#### Relationship with environmental variables

Water temperature, salinity and transparency showed seasonal changes throughout the year. Water temperature was low (25 °C) in July and between December and April (25 °C), but high in October (29 °C). Salinity exhibited the opposite pattern: low values in October (33 ppt) and high in December to April (36 ppt) (Fig. 2). Transparency exhibited the lowest value during the rainy season in October (8 m Secchi disk). The presence of cold waters and high salinities indicated the upwelling periods, which coincided with the dry seasons in the TNNP. Warm and low salinity waters were indicative of the rainy seasons. Monthly means of water temperature and macroalgal cover were inversely correlated (Spearman,  $r = -0.89$ ,  $p < 0.05$ ). However, the two peaks of macroalgal abundance did not necessarily coincide with the lowest temperature data at the same time, probably due to a delayed response of the algal community, which apparently takes 7 to 30 days. The other environmental variables (salinity and transparency) were not significantly correlated with algal abundance. Although a positive trend between visibility and percentage cover of algal turfs was observed, the correlation was not significant (Spearman,  $r = 0.83$ ,  $p < 0.1$ ).

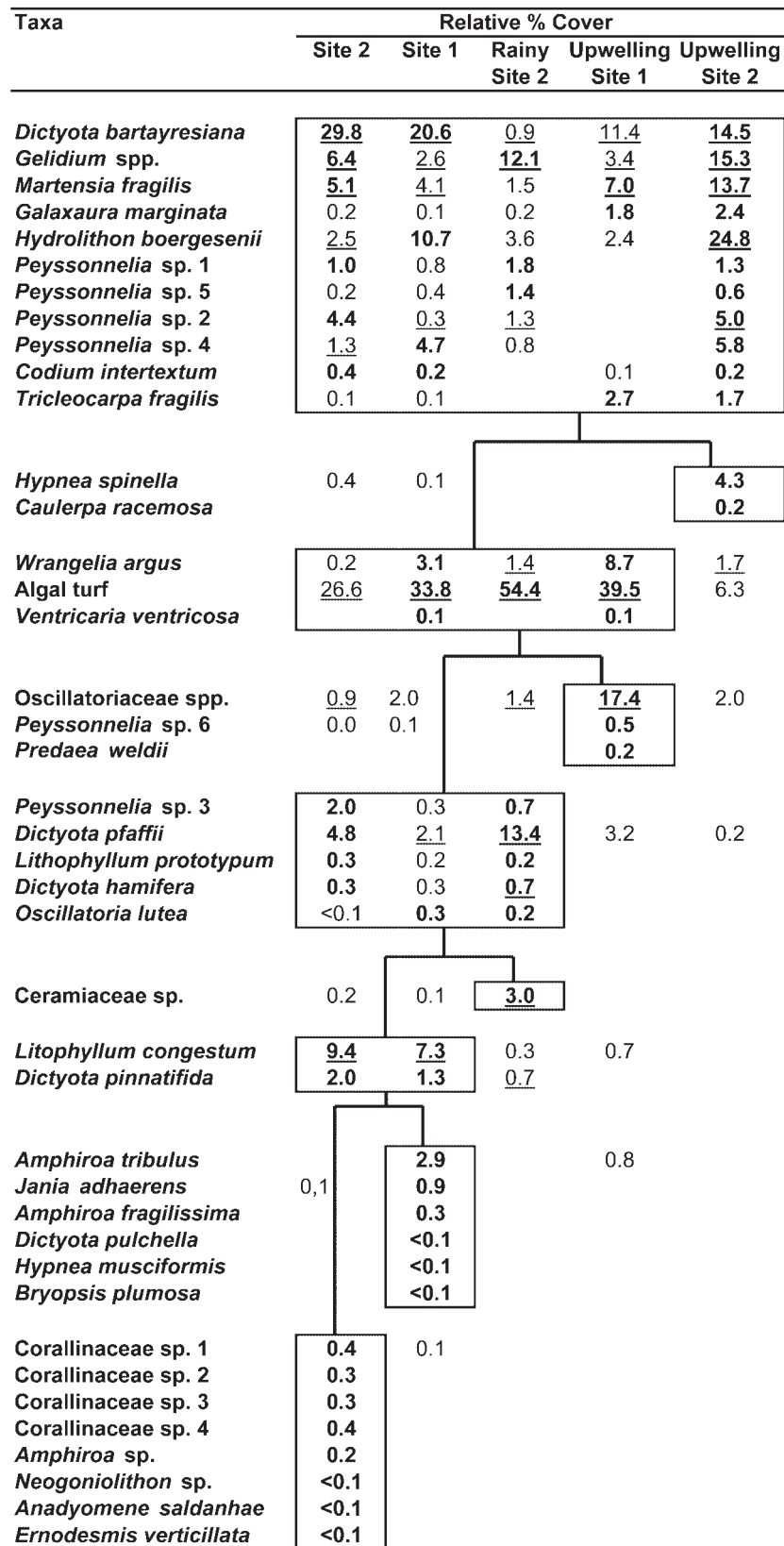


Fig. 4. Inverse dendrogram of Kaandorp showing the relative percent cover of algal taxa in the assemblages as identified by cluster analysis of Fig. 3. The analysis indicates the characteristic algal species (in boxes) of each cluster or group of clusters. For the bold values the cover in the assemblages is within the accumulated 70 % of its total. Underlined values indicate species with a frequency  $\geq 70\%$ .

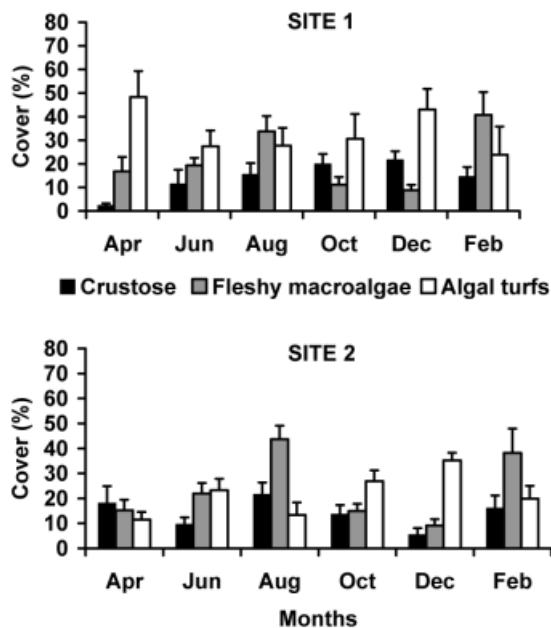


Fig. 5. Mean percent cover of crustose algae, fleshy macroalgae and algal turfs over time at two sites (mean  $\pm$  SE,  $n = 5$ ).

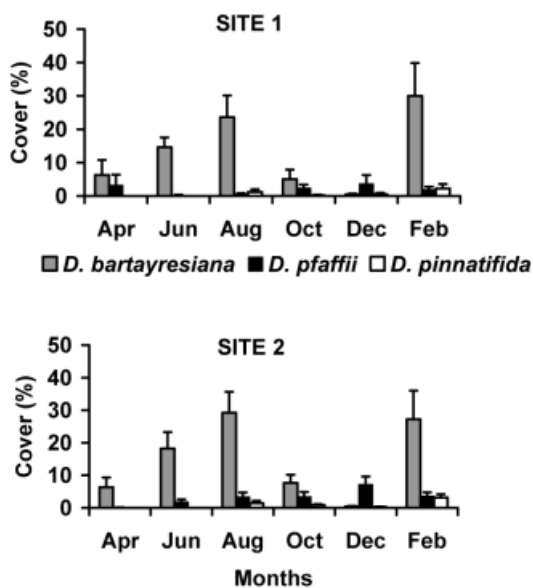


Fig. 6. Mean percent cover of *Dictyota* spp. over time at two sites (mean  $\pm$  SE,  $n = 5$ ).

## Discussion

The benthic algal assemblage of the rocky-coral reefs studied exhibited a bimodal seasonal pattern of abundance throughout the year. High abundance of macroalgae was associated with relatively cold periods of upwelling (Fig. 5). The increases in the abundance of macroalgae during the cold upwelling months and the thalli senescence during warmer rainy months seem to be related to water temperature variability rather than to changes in salinity or

turbidity. Temperature has been considered an important factor determining seasonal changes in subtropical and temperate areas (Kaldy *et al.* 1995, Kim *et al.* 1998). In the tropics, despite temperature changes not being as large as in temperate or subtropical areas, many macroalgae are highly seasonal and this seasonality is likely to be related to changes in water temperature (Benayahu and Loya 1977, Tsuda 1982, Klumpp and McKinnon 1989, Bula-Meyer 1990, Martin-Smith 1993, Naim 1993, Vuki and Price 1994, Stimson *et al.* 1996, McCook *et al.* 1997).

Nevertheless, a seasonal influence of factors, such as nutrients or their interaction with temperature, cannot be ruled out. It is likely that nutrient pulses brought up by the seasonal upwelling affect the tropical algal assemblages. It has been suggested that upwelling events may enhance nutrient concentrations of surface water and, as a consequence, algae may exhibit higher growth rates (Ormond and Banaimoon 1994, Kiirikki and Blomster 1996, Szmant 1997). Despite the upwelling of the TNNP being oligotrophic, some nutrients can show slight increases in concentration in coastal waters during this season but also during the rainy months (Garzón-Ferreira unpubl. data). However, the roles of nutrients in the dynamics of algal assemblages of the TNNP are yet to be investigated.

*Dictyota* spp. were the dominant macroalgae at the study sites and contributed significantly to the seasonal changes of the algal assemblage. *Dictyota* species are also very common and abundant and can be the predominant algal component of shallow and deep coral reefs throughout the Caribbean, such as in Panama (Shulman and Robertson 1996), Belize (McClanahan *et al.* 1999), and Jamaica (Lapointe *et al.* 1997). De Ruyter van Steveninck and Bak (1986) observed an increase in cover of *Dictyota* spp. from 4% to 17% after the mortality of the black sea urchin *Diadema antillarum* Philippi in Curacao, but at the end of their study (November) the abundance of *Dictyota* spp. was at the original low level. This reduction was apparently of a seasonal nature. In contrast to our data, coral reefs from the Virgin Islands in the Caribbean exhibited high abundance of macroalgae (> 30%; mainly *Dictyota*) during October–November and low during March–August (Rogers *et al.* 1997). Rogers *et al.* (1997) suggested that these changes might be related to changes of grazing pressure. A temperate member of the order Dictyotales, *Glossophora kunthii* (C. Agardh) J. Agardh, exhibited seasonal changes: erect fronds grow during winter and in some locations fronds disappear in summer (Malbran and Hoffmann 1990). Our data support the observations of de Ruyter van Steveninck and Bak (1986), Rogers *et al.* (1997) and Lirman and Biber (2000) showing that *Dictyota* spp. form a dynamic component of coral reef communities.

The benthic algal flora of the rocky reefs investigated was similar to other reef algal floras in the

Caribbean (Littler and Littler 1997). Thirty-five out of the 41 taxa found in our study were widely distributed in the Caribbean. During the surveys in the upwelling periods we did not record species with temperate or subtropical affinities, which may suggest that the upwelling from the TNNP area is not strong enough or does not occur for long enough periods of time to bring elements from temperate origins. Márquez and Guillot (1983) found only one species of macroalga (*Porphyra*) with sub-tropical affinities during surveys in the TNNP. An important difference between the coral reef algal assemblages described here and others from the Caribbean is the absence of the brown macroalga *Lobophora variegata* (Lamouroux) Womersley ex Oliveira and the green *Halimeda*. These algae are very common and abundant in the Caribbean (Diaz-Pulido and Diaz 1997) and Great Barrier Reef areas (McCook *et al.* 1997, pers. obs). However, in the TNNP, only a few specimens of *Lobophora variegata* have been observed in very shallow areas and in sand plains at depths > 18 m. *Halimeda* occurs in the TNNP but mainly in seagrass beds. The reasons for these differences are still unknown.

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- In conclusion, the algal assemblage of rocky reefs in the TNNP exhibited seasonal changes in abundance and composition of species and algal groups, and the changes seemed to be related mainly to changes in water temperature during the alternated upwelling and rainy periods. The same seasonal pattern has been observed in the years following this study. Therefore, seasonality of benthic algae should be taken into account when addressing issues of coral reef status based on algal abundance.

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