ABSTRACT

Southwestern Caribbean oceanic atolls are characterized by open lagoons occupied in considerable proportion by reefs with exuberant algal communities. In order to determine patterns of algal distribution among lagoonal reefs of four such atolls (Albuquerque Cays, Courtown Cays, Serrana Bank and Roncador Bank), relative cover, water depth, and wave exposure, as well as samples were collected at a total of 41 stations, which encompassed representative examples of the different Caribbean reef types defined by Geister (1977) that were found within the lagoonal basin of each atoll. Cover of algal species was estimated at each station by randomizing five (0.25 m²) square frames over homogeneous algal-covered reef bottoms (Connor and Adey 1977; Diaz-Pulido 1995), therefore this estimation represents values that are relative to algal cover. Additionally, algal cover relative to hard bottom and substrate rugosity (linear length/chain length) were estimated by L.S. Mejía and Gerzón-Ferreira in press., employing a modified stationary visual census method, as a measure of grazing pressure (MacIntyre et al. 1987; Reinthal and MacIntyre 1994). Classification and ordination techniques (Clarke and Warwick 1994) were employed on the algal species cover by station matrix to discriminate groups of stations with similar composition (i.e. assemblages) and infer spatial patterns of community structure. Cover values of all species within stations clusters were averaged to determine their characteristic and exclusive species (Raandorp’s inverse analysis; see Díaz et al. 1995). Analysis of similarity (ANOSIM, Clarke and Warwick 1994) tests were carried out to compare algal communities among different reef types. Kruskal-Wallis tests were performed to compare various attributes between cluster station groups.

RESULTS

Variations of algal community structure (Fig. 1a), reveal a zonation pattern related mainly to depth (Fig. 2a), wave exposure (Fig. 2b) and density of herbivorous fishes, Acanthurus spp. (Fig. 2d). Two major groups of stations representing respectively shallow (-0.4 to -3.5 m) and deep (-4 to -12 m), calm environments were segregated at 61% of dissimilarity (Fig. 1a and 2a). At a scale of 408, six minor groups of stations were identified and named as assemblages according to characteristic species and/or the dominant algal group of each cluster.

Among those assemblages which developed in shallow areas, the first type (Tithonetera-Porolithon. cluster A) occurred in all four lagoons associated with dead Acropora palmata-reefs (0.4-3.5 m depth), enduring high wave exposure. Some shallow Montastreales reefs (< 2 m depth) are also suitable locations for this assemblage (Fig. 1b). Crustose corallines (mainly P. pachydermum and T. bermudensis) and turfs are dominant categories yielding about 75% of relative cover in this assemblage (Table 1). Some almost emergent, wave-exposed peripheral reefs (occurring only at Courtown Cays, but not quantified due to strong surf), are dominated by Porolithon, resembling coralline algal ridges. The herbivorous chiton, Chomeplax lata, was observed in high numbers upon the Porolithon surface. Very shallow depth (mean 0.9 m), these reefs may be exposed to desiccation at mean low tide. Milliman (1969) pointed out that if macroalgae are exposed to the air for relatively long periods, they are able to survive by means of intermittent surf splash. The second type of shallow algal assemblage (Cluster B, Turbinaria spp.) occurs only at Serrana Bank in some relatively highly wave-exposed reefs composed of dead A. palmata. Prudens brown macroalgae of the genera Turbinaria and Sargassum

MATERIALS AND METHODS

The atolls studied are part of the Colombian archipelago of San Andrés and Old Providence, which lies adjacent to the Central American continental shelf. Complete descriptions of the regional geology, geomorphology, oceanography and marine habitats of these reef-complexes can be found elsewhere (cf. Milliman 1969; Geister 1992; Diaz et al. 1995). Both geomorphological features and ecological zonation patterns are quite similar among these reef-complexes (Milliman 1969; Geister and Díaz in press).
grow over the A. palmata framework forming dense canopies 0.5 m in height. Algal turfs and F. pachycladum are also common. All elements of this assemblage (Table 1). The third type of shallow-water assemblage (cluster C) also only occurs at Serrana Bank, primarily in calm waters on reefs composed of A. cervicornis and Montastraea spp. (Fig. 1b). The ruffled form of Lobophora variegata is the dominant alga in this assemblage, taking up to 70% of the algal cover (Table 1). This particular form of Lobophora also covers extensive areas of the sandy lagoon floor in Serrana Bank at depths ranging from 4 and 5 m, but is scarce at the other sites.

Four station groups, segregated among cem and deep Montastraea spp. reefs at a dissimilarity level of 46% (Fig. 1a), were broadly dominated by frondose macroalgae and to a lesser proportion by turfs. Limits between showed no significant differences among station clusters (p = 0.05, Kruskal-Wallis test). Acanthura densities were greater (p = 0.05, Mann-Whitney U test) in the low exposed Titanoderma-Porolithon community (21.6 ind/150 m², sd = 20.9, n = 8) than in the mixed Lobophora (2.9 ind./150 m², sd = 2.2, n = 6) and L. variegata shelf form communities (8.4 ind./150 m², sd = 12.7, n = 20) (Fig. 2d). Neither total herbivorous fish densities nor individual densities of Scarida genera showed a clear relation to algal structure.

On the whole, the majority of lagoon reefs exhibited medium to high spatial complexity. The index of substrate rugosity did not differ significantly between algal assemblages (p = 0.2, Kruskal-Wallis test), evidencing no clear relation to biotic ordination (Fig. 2c).

### Table 1: Relative percent algal cover (± standard deviation) in different algal assemblages of lagoon patch reefs as identified by cluster analysis. A: Titanoderma-Porolithon. B: Turbinaria spp. C: Lobophora (ruffled form). D: Mixed Lobophora forms. E: Lobophora (shelf form). F1 and F2: Dicoryta spp. Results of the inverse analysis are also shown, indicating the characteristic algal item (in boxes) of each cluster or group of clusters. For the underlined values the cover in the assemblages is within the accumulated 70% of its total.

<table>
<thead>
<tr>
<th>Algal taxa, form</th>
<th>SHALLOW</th>
<th>DEEP</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>0.9 ± 1</td>
<td>1.0 ± 0</td>
<td>2.7 ± 1.2</td>
</tr>
<tr>
<td>Sampled stations</td>
<td>n = 9</td>
<td>n = 2</td>
<td>n = 6</td>
</tr>
</tbody>
</table>

### Table 2: Mean densities of key taxa in each cluster (± standard deviation).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Cluster A</th>
<th>Cluster B</th>
<th>Cluster C</th>
<th>Cluster D</th>
<th>Cluster E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthura</td>
<td>26.9 ± 6</td>
<td>15.3 ± 8</td>
<td>3.8 ± 1.2</td>
<td>1.2 ± 0.3</td>
<td>0.7 ± 0.2</td>
</tr>
<tr>
<td>Dicoryta</td>
<td>3.4 ± 0.8</td>
<td>2.1 ± 0.1</td>
<td>5.1 ± 3.2</td>
<td>2.3 ± 1.5</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td>Porolithon</td>
<td>27.4 ± 12</td>
<td>15.3 ± 8</td>
<td>4.1 ± 2.3</td>
<td>1.2 ± 0.3</td>
<td>0.7 ± 0.2</td>
</tr>
<tr>
<td>Titanoderma</td>
<td>6.8 ± 0.5</td>
<td>3.2 ± 0.4</td>
<td>0.5 ± 0.7</td>
<td>0.2 ± 0.5</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td>Laurencia</td>
<td>6.8 ± 0.5</td>
<td>3.2 ± 0.4</td>
<td>0.5 ± 0.7</td>
<td>0.2 ± 0.5</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td>Turbinaria</td>
<td>0.7 ± 0.2</td>
<td>21.3 ± 0.8</td>
<td>1.4 ± 1.5</td>
<td>0.3 ± 0.6</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td>L. variegata</td>
<td>3.4 ± 0.8</td>
<td>2.1 ± 0.1</td>
<td>5.1 ± 3.2</td>
<td>2.3 ± 1.5</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td>Total turfs</td>
<td>36.7 ± 11</td>
<td>22.8 ± 4</td>
<td>7.5 ± 0.2</td>
<td>3.9 ± 1.6</td>
<td>2.7 ± 1.4</td>
</tr>
<tr>
<td>Total macroalgae</td>
<td>24.8 ± 11.5</td>
<td>46.3 ± 13.5</td>
<td>60.4 ± 14.8</td>
<td>67.7 ± 19.5</td>
<td>60.3 ± 17.1</td>
</tr>
<tr>
<td>Total crustose algae</td>
<td>38.9 ± 14.5</td>
<td>25.6 ± 14.2</td>
<td>12.3 ± 14.5</td>
<td>1.8 ± 1.1</td>
<td>8.4 ± 0.9</td>
</tr>
<tr>
<td>Absolute algal cover/Chain method</td>
<td>36.7 ± 11</td>
<td>22.8 ± 4</td>
<td>7.5 ± 0.2</td>
<td>3.9 ± 1.6</td>
<td>2.7 ± 1.4</td>
</tr>
</tbody>
</table>

### Discussion

Clusters D, E and F1 are not sharply defined, perhaps reflecting the homogeneity of environmental features such as depth (Fig. 2a), spatial complexity (Fig. 2c) and Acanthura spp.-density (Fig. 2d). Cluster D, which corresponds mainly to assemblages occurring at Serrana Bank, is a mixed community of Lobophora forms (Table 1), including components of both the C and E assemblages. Cluster E occurs in the lagoons of all four atolls, being dominated by the shelf form of L. variegata (Table 1). The remaining two clusters (F1 and F2) correspond to the last community type (F), dominated by Dicoryta spp. (relative cover >50%, Table 1), especially D. cervicornis, and occurs in two isolated reefs in Courtenay Cays and Roncoron Bank at depths between 5 and 6 m (Fig. 1a, stations 4 and 29).

A total of 73 species of algae (considered algal turfs as one entity) were found within the 205 quadrats sampled. All six assemblages showed similar mean values of Shannon’s diversity index and of total number of species (not significant, p > 0.01, Kruskal-Wallis test). Mean species number among assemblages ranged from 17.5 (sd 2.1) to 22 (sd 4.3).

Density of herbivorous fishes other than Acanthura spp.
Algal Assemblages in Lagoonal Reefs

Fig. 1: MDS ordination (stress, 0.176) and cluster analysis results: a) MDS of sampling stations, indicating algal assemblages (clusters of stations A to F) named after the dominant and/or the characteristic algal categories. Bold lines represent group clustering at 68% dissimilarity and non-bold lines at 46%. Stations: 1-5 (Courtown Caye); 6-11 (Alubquerque Cayes); 12-26 (Serrana Bank); 27-41 (Roncador Bank). b) The same MDS with superimposed letters representing reef types.

ALGAL ASSEMBLAGES

A. Titanoderma- Porolithon
B. Turbinaria spp.
C. Lobophora (ruffled form)
D. Mixed Lobophora forms
E. Lobophora (shelf form)
F. Dictyota spp.

REEF TYPE

M= Montastrea spp.  C= A. cervicornis
MC= M. spp. - A. cervicornis
SM= Siderastrea spp. - M. spp.
PD= Acropora palmata (dead) - Diploria
PC= A. palmata - A. cervicornis

extremely shallow, medium-low wave-exposed Montastrea spp.-reefs are colonized by the algal assemblage characteristic of wave-exposed A. palmata-reefs, suggesting a partial control of wave exposure on the structure of algal communities.

DISCUSSION

The spatial distribution of the algal communities on lagoonal patch reefs is controlled by a combination of abiotic and biotic factors. Variables best explaining the observed algal structures are (in order of relevance, as shown by the MDS ordination): depth, wave exposure and grazing pressure (density of Acanthurus spp.). These parameters are inversely related, i.e. an increase in depth leads to a decrease in both wave exposure and grazing pressure. Geiser's (1977) model of reef coral zonation controlled by depth and wave exposure agrees relatively well with the coral zonation observed at these atolls. To some extent, algal zonation patterns were also related to the coral zonation patterns. Van den Heuvel et al. (1978) and Littler et al. (1987) also observed some correspondence between algal and coral zonations in other Caribbean locations. However, in some cases (extremely shallow Montastrea spp.-reefs), it seems likely that additional physical factors such as desiccation play an important role in the manifestation of the community.

High surf turbulence, coupled with grazing pressure by surgeonfishes and Chonephila late in shallow areas help to maintain the algal community of the studied atolls in a crustose-corralline-turf stage by the removal of frondose macroalgae; these algae (crustose and turf) can withstand extreme conditions (Steneck 1988; Hackney et al. 1989). Such algal assemblages have been reported from many reef areas (Ady 1978; Hackney et al. 1989).

High primary production of algal turfs in shallow zones is stimulated by high irradiance and herbivorous activity, maintaining an elevated trophic carrying capacity for grazing fishes (Steneck 1988). This may be the main reason for the observed high densities of Acanthurus spp. therein. On the other hand, the particular association between Porolithon pachydermum and the chiton C. lateus has been explained as a process increasing the survival rate of the former by the removal of competitively superior frondose and turf algae (Littler et al. 1995a).

Below the surf zone, Turbinaria spp. and many species constituting the algal turfs are also good settlers in wave-exposed environments. Several frondose macroalgae e.g. Laurencia spp., Halimeda spp. also reached high relative cover in some of these shallow zones. These algae may withstand strong turbulence because of their elasticity and their thallus counteracting drag with deflection (Vogel 1981). On the other hand, due to the presence of secondary metabolites in L. obtusa and H. opuntia (Norris and Penical 1987; Hahl and Van Dijk 1992) and to the possible combined effect of CuCo in the latter (see Hay et al. 1994), these macroalgae are avoided by most generalist herbivores. Therefore, they persist in shallow areas of high grazing pressure. Large, erect macroalgae like Turbinaria may also provide refuge for smaller algae by presenting a physical barrier to the grazing fishes. The occurrence of spatial refuges against grazers has been documented for algae on tropical reefs (see Littler et al. 1986).

In the atolls studied, Turbinaria seems to be little grazed by herbivores as shown by the exuberant populations observed. This contrast with the results of Lewis (1986) at Belize, who observed that this species was actively consumed by grazing fishes. Perhaps Turbinaria at the Colombian atolls have higher concentrations of polyphenols (Hay 1984) than those studied by Lewis, as an adaptive response to a more intense herbivory, as suggested by Hay and Penical (1998) for other reef algae.

The transition to a stage dominated by frondose macroalgae in deeper reefs seems likely to be due to decreasing grazing pressure with depth, confining many macroalgae species to deeper zones. Similar observations upon the distribution of herbivorous fishes and their impact on the dominance of functional groups of macroalgae have been made in other tropical reefs (Hay 1981; Lewis 1986; Littler et al. 1987; Steneck 1988; Hackney et al. 1989; Bula-Meyer 1992; Klumpp and McKinney 1992; Steneck and Dethier 1994). This reduction in herbivory has been documented as a result of both diminishing trophic carrying capacity (Hay and Goertemiller 1993) and increasing risk of predation (Littler et al. 1987);
Fig. 2: Relation of station groups to environmental factors. HAB ordination with clusters delineated as in Fig. 1. a) Relation of station groups to depth. b) Relation of station groups to wave exposure. c) Relation of station groups to rugosity index: high values of rugosity indicate great spatial complexity and vice versa. 7 outside pentagons: no data, 7 inside pentagons: visually estimated rugosity. d) Relation of station groups to density of Acanthurus spp.

Reinthal and MacIntyre (1994). The former cause may well apply to the reefs investigated here as the argument concerning risk of predation cannot be supported because the availability of refuge sites for macrograzing fishes in these patch reefs does not seem to be a limiting factor due to the observed medium to high bottom complexity (Fig. 2c). The algal cover found in the four lagoons are well over the normal values expected for oceanic Caribbean reefs, although they do not reach the extremely high cover values (more than 90%) reported from Jamaican reefs in both shallow and deep settings, which have also been attributed to low grazing pressure (Hughes et al. 1987; Hughes, 1995). Although algal turfs are also quite common in deeper reefs (Table 1), they are exploited mainly by territorial fishes (i.e. Scorpaenas spp., Pomacentridae, pers. obs.). Territorial competitors have also been suggested to affect the distribution of reef fishes (see Lewis and Wainwright, 1985). Since light intensity also decreases with depth, it has been suggested also as a prime factor influencing bathymetric distribution of lagoonal algae (Gilmartin 1960).

Herbivorous fishes graze as well on the psammophytic algal meadows around deep patch reefs, being responsible for the formation of the so-called halos or bare zones that surround lagoonal reefs and are easily recognizable on aerial photographs. Ogden et al. (1973) stated that the absence of seagrasses in the halos is mainly a result of the grazing activity of the urchin Diadema antillarum. Because this species is currently very scarce in the reefs visited, we conclude that this urchin presently exerts little control on epilithic and psammophytic algal communities. Our observations suggest that besides some gastropods (e.g. Strombus pugilus, S. gigas), herbivorous fishes rather than urchins are responsible for halo formation. It is also possible that the grazing pressure over the local epilithic algae is directed towards the psammophytic algae. In spite of the presence of diverse secondary compounds and CaCO3 in psammophytic algae (May et al. 1994), these sand-plain plants (i.e. Udotea spp., Rhipecephalus phœnix) are grazed by several herbivorous fishes (Barile 1972). Mixed schools of reef fishes including both carnivorous (Nemulon spp.) and herbivorous species (Acanthurus spp., Sparisoma spp. and Scarus spp.) were occasionally observed on sandy plains surrounding the patch reefs (L.S. Mejía, pers. com.).

In general terms, a great proportion of hard bottom within the four lagoons is currently dominated by benthic algae. These bottoms recently underwent a phase shift from a coral-dominated to an algal-dominated system, as
part of a widespread process of coral decline around the world (Ginsburg 1994; Hughes 1994; Banks and Harriott 1995). In the atolls studied; the shelf form of L. variegata has been recognized as one of the most abundant algal species covering surfaces which were earlier apparently occupied by living corals in the lagoons of Caribbean and west Pacific atolls and other reef complexes, especially in the deepest zones (Tsuda 1981; Jordan and Martin 1987; de Ruyter van Steveninck and Breeeman 1987; Banks and Harriott 1995). The ruffled form of this species (see Littler et al. 1989) prefers shallower zones than the shelf form, and, according to Littler et al. (1989, 1995b), it is a characteristic form in habitats of low grazing pressure. According to our results, fish densities were not significantly different between sites with ruffled Lobophora and other algal assemblages, it seems possible that ruffled and shelf Lobophora might have proliferated in response to the lowering of grazing pressure since the die-off of D. antillarum, an active Lobophora consumer (de Ruyter van Steveninck and Breeeman 1987; Morrison 1988). In his comprehensive description of the marine habitats of Serrana Bank, Milliman (1969) made no statement about the vast meadows of ruffled Lobophora that we found covering wide portions of the lagoon floor. Although it would sound plausible that these meadows could have developed more recently, seasonal fluctuations in populations of this species cannot be discounted. Such a case has been recently described by Banks and Harriott (1995) at some Australian reefs. Overexploitation of queen conch populations, Strombus gigas, in the studied atolls is remarkable (Diaz et al. 1996). and this may constitute a further factor permitting the proliferation of macroalgae.

ACKNOWLEDGMENTS

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