

Deep water vegetations of *Lobophora variegata* (Phaeophyceae) in the coral reef of Curaçao: population dynamics in relation to mass mortality of the sea urchin *Diadema antillarum*

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ABSTRACT: Cover, blade size, growth rate, longevity and reproduction of the foliose brown macroalga *Lobophora variegata* (Lamouroux) Womersley were recorded in 2 deep-water populations (25 to 35 m) in the coral reef of Curaçao (Netherlands Antilles) for over a year. No seasonal effects were observed. Although mean cover was relatively constant, turnover rates were very high with half-life of blades being, on average, only ca 20 d. During this study the herbivorous sea urchin *Diadema antillarum* Philippi suffered mass mortality. The effect of the disappearance of this grazer was evident at one of the 2 locations, where *D. antillarum* densities had been highest, *L. variegata* cover lowest and blade sizes smallest. At this station, following *D. antillarum* mortality, cover and blade size increased significantly and reached a new equilibrium after ca 6 mo.

INTRODUCTION

Fleshy and filamentous algae are generally inconspicuous on coral reefs (reviews by Ogden & Lobel 1978, Borowitzka 1981, Gaines & Lubchenco 1982, Littler & Littler 1984), although dense macroalgal vegetation is often found in shallow intertidal reefs and wave-washed reef parts (e.g. Randall 1961, van den Hoek et al. 1975, 1978, Ogden 1976, Adey et al. 1977, Hatcher 1981, Hay 1981). Deep reef zones may also bear conspicuous algal vegetation (van den Hoek et al. 1978, Hay 1981, Littler & Littler 1984, Morrison 1984b). In these cases, reduced grazing seems to be the main factor allowing the development of macroalgae.

Lobophora variegata (Lamouroux) Womersley (syn. *Pocockiella variegata* [Lamouroux] Papenfuss), a brown, foliose macroalga with a worldwide distribution in tropical to warm temperate seas (cf. Earle 1969, Stephenson & Stephenson 1972), has been reported from many Caribbean and Indo-Pacific reefs. In Curaçao, Netherlands Antilles, van den Hoek et al. (1978) found this species forming distinct belts in the deep algal community (> 30 m depth) as well as in the eulittoral community, whereas it was absent in the intermediate reef zones. This discontinuous depth

range has been attributed to intensive grazing in the areas devoid of *L. variegata* (van den Hoek et al. 1978).

Studies on (sub)tropical, subtidal macroalgae have shown seasonal changes in growth, abundance and reproduction for several species (reviewed by Morrison 1984a), but so far, no extensive ecological study has been carried out on algal species occurring in the deeper zones of coral reefs. Yet, this kind of study is essential if spatial and temporal distribution patterns of algae in coral reefs are to be understood (Littler & Littler 1984).

In the present study 2 deep-water populations (> 25 m) of *Lobophora variegata*, from 2 locations at Curaçao differing in visual *L. variegata* cover and in densities of the herbivorous sea urchin *Diadema antillarum* Philippi, were monitored for over a year. Cover, blade size, growth rate, longevity and presence of sporangia were recorded. The results are interpreted in relation to the disappearance of the *D. antillarum* population, which suffered mass mortality in the course of this investigation (Bak et al. 1984, de Ruyter van Steveninck & Bak 1986). All through 1984 and 1985 *D. antillarum* remained virtually absent from the coral reef of Curaçao (Table 1).

MATERIAL AND METHODS

Location. This study was carried out in the coral reef off the leeward southwest coast of Curaçao (Netherlands Antilles) between February 1983 and February 1985 (Fig. 1). For a general description of the area see

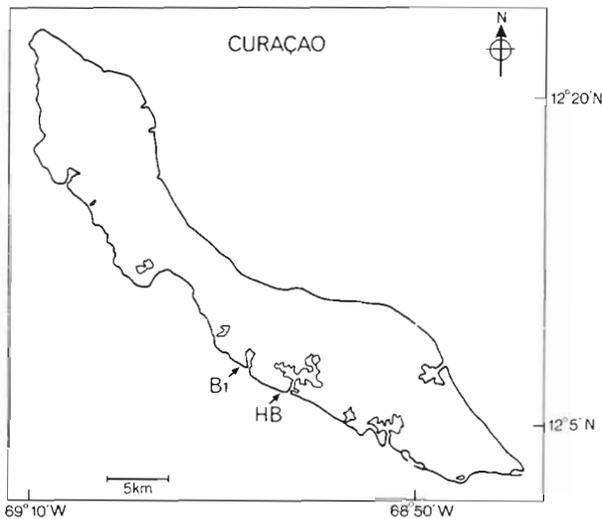


Fig. 1. Map of Curaçao (Netherlands Antilles) showing the 2 locations. HB: reef in front of the Holiday Beach Hotel; B1: CARMABI Buoy 1, in front of Klein Piscadera

van den Hoek et al. (1975). In the period of investigation mean monthly water temperatures at 30 m depth fluctuated between 25.9 and 28.1 °C (Fig. 2). Global radiation ranged from 358 to 572 cal cm⁻² d⁻¹ (Fig. 2). In February 1983, 2 locations (Fig. 1) were selected in the deep reef zone (ca 25 to 35 m) which strongly differed in visual *Lobophora variegata* cover and in the density of the herbivorous sea urchin *Diadema antillarum*: (1) the reef in front of the Holiday Beach Hotel (HB), with a dense *L. variegata* vegetation consisting of large frondose plants (Fig. 3) extending from 20 m downward and high *D. antillarum* densities occurring at shallow depths only (Table 1); and (2) the reef in

front of Klein Piscadera, CARMABI Buoy 1 (B1) with a sparse *L. variegata* vegetation consisting of small, more or less crustose plants extending no higher than 25 m and high *D. antillarum* densities down to 12 to 20 m depth (Table 1). This was before the occurrence of mass mortality in the *D. antillarum* population, which took place in October 1983 (Bak et al. 1984).

Quadrats. Cover, blade size, growth rate and persistence of *Lobophora variegata* blades were monitored at monthly intervals over various periods (Table 2). For this purpose, permanent quadrats (16 × 11.5 cm) were marked with steel nails in relatively dense *L. variegata* patches. Using a Nikonos underwater camera, equipped with a Nikon close-up lens in combination with a 28 mm lens and with flashlight, colour slides (Kodak Ektachrome 200 ASA) were made, which were projected with a darkroom enlarger with a 50 mm lens for further analysis. At first, the quadrats were photographed once every 4 wk. However, after some time it became clear that the *L. variegata* vegetation was very dynamic in character: most of the blades having disappeared within a single month. Therefore, new sets of quadrats were selected at both locations, which were photographed more frequently, in principle once every 2 wk. This enabled an estimation of blade persistence and growth rates over short periods.

Cover. *Lobophora variegata* cover was monitored in 4 to 9 permanent quadrats over various periods (Table 2). In order to estimate cover, the slides were projected on a grid with 100 points. Counts were made of points with and without plants present (Littler & Littler 1985). This gave the percentage *L. variegata* cover within each quadrat at the various dates. Since blades can overlap (Fig. 3), cover data actually represent the projected area covered by *L. variegata*.

Blade size and growth rate. In order to establish blade size and growth rates of the circular to kidney-shaped *Lobophora variegata* blades, the 'radius' of the blade was constructed following a standardised method (Fig. 4). This parameter was chosen because in many cases only part of the blade was visible, which

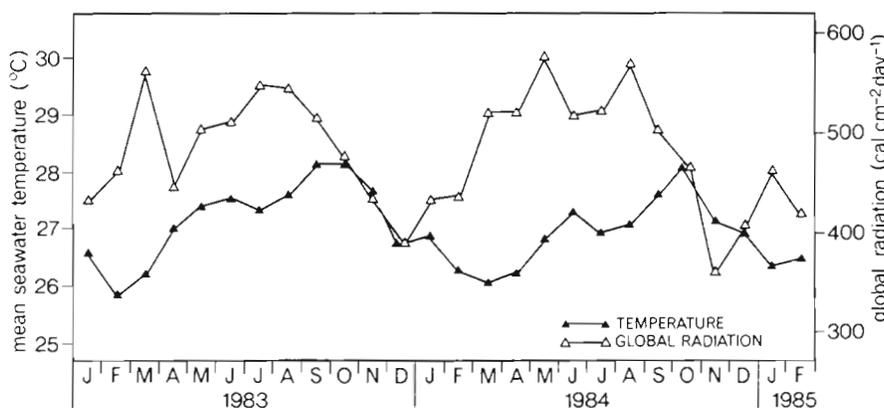


Fig. 2. Mean monthly water temperatures at 30 m depth (data from CARMABI) and monthly global radiation (Eppley Black & White Solarimeter, Meteorological Service Curaçao)



Fig. 3. *Lobophora variegata* at Holiday Beach, 27 m depth (Oct 1983), $\frac{2}{3} \times$ natural size

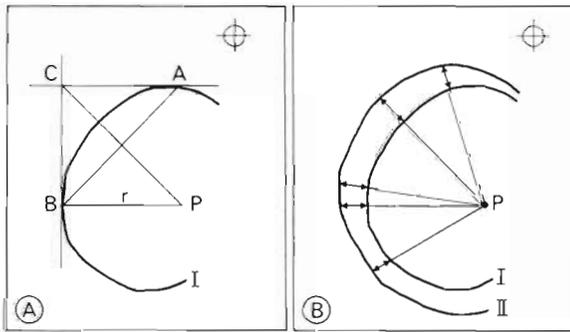


Fig. 4. *Lobophora variegata*. Parameters for measuring blade size and growth rates on the basis of an estimation of the 'radius' in the circular to kidney-shaped blades. (A) Determination of 'radius' as follows: choose tangent AC at random; construct tangent BC perpendicular to AC; construct CP = AB, where CP halves the angle ACB; find P as the 'circle's' central point; find 'radius' r. (B) Determination of growth rates: line I = blade margin at $t = 0$; P = 'circle's' central point at $t = 0$; line II = blade margin at $t = x$, 13 to 22 d after $t = 0$. (NB: PVC reference mark in quadrat ensures correct position.) Find 'radius' enlargement during $t = x - 0$ for 5 randomly chosen 'radii'

prohibited the measurement of e.g. surface areas. Blade size was estimated monthly in 15 to 30 randomly chosen plants at each location (Table 2). Growth rates were measured monthly over a 13 to 22 d period as the increase in blade 'radius' during this period. For this purpose, only blades with intact margins were considered (Table 2) as this will give an impression of the actual growth potential of the *L. variegata* blades at the 2 locations in different seasons. Increase in blade 'radius' was consistently logarithmic with time and independent of blade size. Growth was expressed as the Specific Growth Rate (percentage increase per day) defined as:

$$\text{S.G.R.} = \frac{\ln (r_x/r_0)}{t_x - t_0} \times 100 \% \quad (1)$$

where r_0 = 'radius' at a specific time t_0 ; r_x = 'radius' at a subsequent time t_x (Fig. 4).

Persistence of blades. Persistence of the blades was measured as half-lives. In each month, 13 to 30 individual blades were selected on each location and subsequently the presence of these blades was checked at intervals of 2 wk until all blades had disappeared. Depletion curves were constructed (Harper 1977), from which the number of days after which half of the blades had disappeared was calculated for each month.

Reproduction. In order to establish the occurrence of reproduction in the *Lobophora variegata* populations 14 to 28 plants were sampled once a month at both locations from outside the quadrats between September 1983 and November 1984. The number of reproductive plants was expressed as a percentage of the total number of blades collected on each sampling date.

Transects at Buoy 1. Changes in the depth distribution of *Lobophora variegata* during the 16 mo following *Diadema antillarum* mass mortality were studied in 4 permanent transects over the reef slope between 19 and 41 m depth at CARMABI Buoy 1. Surveys were

Table 1. *Diadema antillarum* (D.a.) and *Lobophora variegata* (L.v.). Occurrence at various depths at 2 locations before and after *D. antillarum* mass mortality in October 1983. +++: abundant; ++: patchy (L.v.); +: present; -: absent

Depth (m)	Before mortality				2 yr after mortality			
	Holiday Beach		CARMABI Buoy 1		Holiday Beach		CARMABI Buoy 1	
	D.a.	L.v.	D.a.	L.v.	D.a.	L.v.	D.a.	L.v.
5	+++	-	+++	-	-	-	-	-
12	+	-	+++	-	-	+	-	-
20	-	+++	+	-	-	+++	-	-
25	-	+++	+	+	-	+++	-	++
30	-	+++	+	+	-	+++	-	++
35	No data		-	++	No data		-	++

made in April and October 1984 and in February 1985. In each transect *L. variegata* cover was estimated using the Braun-Blanquet scale within a 1 m² frame. When 2 or more quadrats in a transect were situated at the same depth, the mean cover from these quadrats was taken for that particular depth.

Statistical analyses. One-way ANOVA was carried out on blade size and specific growth rate data to test for significant variation over time. Random sampling within the quadrats and high turnover rates of individual *Lobophora variegata* blades provided independence of data over time, thus meeting the requirements of ANOVA (Sokal & Rohlf 1981). As cover data are not independent over time, 2-way ANOVA without replication, with dates and quadrats as the 2 factors, was used in statistical analysis. If necessary (Tukey's Test for Nonadditivity: Sokal & Rohlf 1981) data were transformed with logarithmic transformation to meet the assumption of additivity. In cases where an ANOVA revealed significant variation over time the nature of this variation was further analysed in an 'a posteriori' test by the 'Sum of Squares Simultaneous Test Procedure' (SS-STP: Sokal & Rohlf 1981). In comparisons between 2 sample means 1-way ANOVA or t-tests were used. Percentages (cover, specific growth rates) were transformed with the angular transformation (Sokal & Rohlf 1981). When variances were non-homogeneous (Cochran's Test of the Equality of several variances: Sachs 1982; F-test: Sokal & Rohlf 1981) the data were properly transformed (see 'Results') before carrying out an ANOVA or t-test. Finally, Spearman's Rank Correlation was applied to analyse possible correlations between 2 variables. When attempting to correlate temperature and light conditions with cover or blade size, mean temperature and light values in the preceding month were used. All statistical tests were considered significant if $p < 0.05$.

RESULTS

Temporal variations in *Lobophora variegata* cover in the permanent quadrats at Holiday Beach (HB) and CARMABI Buoy1 (B1) were analysed (Fig. 5a; Table 2). Table 2 lists ANOVA results for the various quadrat sets monitored; Fig. 5a illustrates cover at HB and B1 during the periods when the maximum number of quadrats was monitored at each location (9 and 8, respectively).

Analyses of variance revealed no significant variation over time at HB (Table 2), indicating that *Lobophora variegata* cover did not change seasonally at this station. Variation between quadrats was high: highest cover in one quadrat coincided with low cover in another and vice versa. Also, cover within quadrats

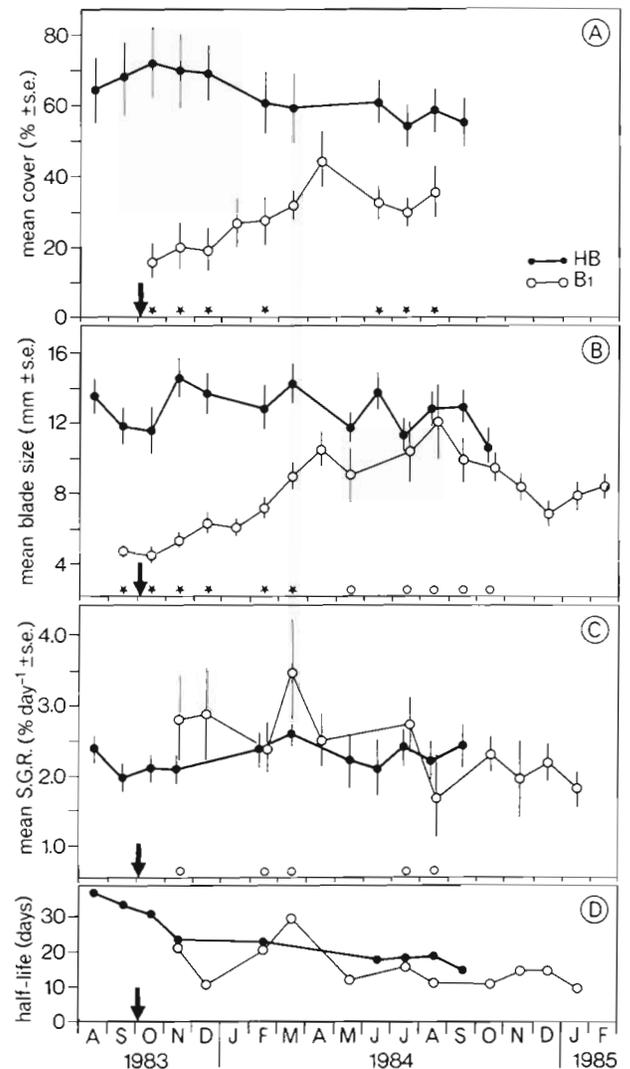


Fig. 5. *Lobophora variegata* at Holiday Beach (HB) and CARMABI Buoy 1 (B1). (a) Mean percentage cover based on $n = 9$ (HB) and $n = 8$ (B1) permanent quadrats respectively; (b) mean blade size (as 'radius') based on 15 to 30 plants; (c) mean specific growth rate (5 to 24 plants); (d) half-lives (13 to 30 plants). Results of statistical analysis between locations shown on abscissa (1-way ANOVA). * $p < 0.05$; (○) not significant ($p > 0.05$). Arrow indicates *Diadema antillarum* mass mortality

fluctuated strongly from less than 10% to more than 90% within a single year (Fig. 6).

At Buoy 1 cover was significantly lower than at Holiday Beach (Fig. 5a). Analyses of variance showed significant variation over time at B1 for all sets of quadrats (Table 2). Except for a significant negative correlation with seawater temperature in Quadrats 1 to 4 between February 1983 and August 1984, there were no significant correlations with seawater temperature at 30 m depth, nor with global radiation in the 3 sets of quadrats monitored (Spearman's Rank Correlation), making

Table 2. *Lobophora variegata*. Analysis of temporal variations in cover, blade size and specific growth rate (S.G.R.) at 2 locations. Cover: 2-way ANOVA; blade size and specific growth rate: 1-way ANOVA. * $p < 0.05$; ns: not significant ($p > 0.05$)

	Holiday Beach			CARMABI Buoy 1		
	Period	Quadrat number	F-value	Period	Quadrat number	F-value
Cover	Feb 83–Sep 84	1–4	$F_{(15,45)} = 0.17$ ns	Feb 83–Aug 84	1–4	$F_{(16,48)} = 4.72^*$
	Aug. 83–Sep 84 ¹	1–9	$F_{(10,60)} = 0.15$ ns	Oct 83–Feb 85 ¹	5–8	$F_{(8,5,45)} = 2.72^*$
				Oct 83–Aug 84	1–8	$F_{(9,63)} = 7.29^*$
		Number of blades			Number of blades	
Blade size	Aug 83–Oct 84	29–30	$F_{(12,375)} = 1.40$ ns	Sep 83–Feb 85 ²	15–20	$F_{(16,309)} = 5.75^*$
S.G.R.	Aug 83–Sep 84	24–30	$F_{(10,162)} = 0.80$ ns	Nov 83–Jan 85	5–12	$F_{(10,77)} = 1.24$ ns

¹ After log transformation
² After $1/\sqrt{x+1}$ transformation

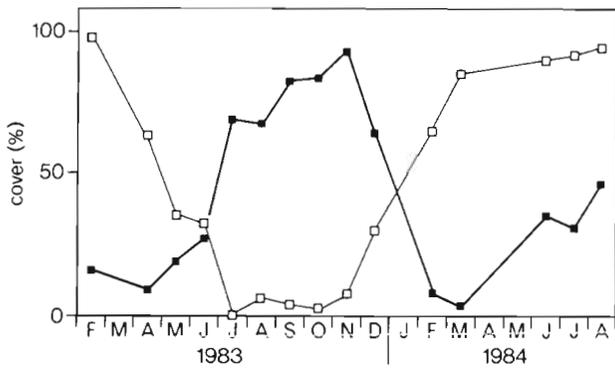


Fig. 6. *Lobophora variegata*. Cover at Holiday Beach in 2 individual quadrats between Feb 1983 and Aug 1984 to illustrate high variation between and within quadrats

seasonal control of *Lobophora variegata* cover at B1 very unlikely. Major changes in *L. variegata* cover occurred between October 1983, when mass mortality of *Diadema antillarum* occurred, and April 1984 (Fig. 5a). Prior to October 1983 no significant variation over time had been observed (Quadrats 1 to 4: Feb to Oct 1983, SS-STP) indicating that there had been an equilibrium in *L. variegata* cover. Between October 1983 and April 1984 cover increased significantly (Quadrats 1 to 8, SS-STP) to reach a new equilibrium level by April 1984, after which month cover no longer varied over time (Quadrats 1 to 8: to Aug 1984; Quadrats 5 to 8: to Feb 1985, SS-STP).

At HB mean blade size (as 'radius') of *Lobophora variegata* (Fig. 5b) ranged from $10.4 \text{ mm} \pm 5.5$ (SD) to $14.6 \text{ mm} \pm 6.1$, $n = 30$, and was fairly constant between August 1983 and October 1984 with no significant annual variations in blade size (Table 2).

At B1 an analysis of variance on blade size revealed significant variation over time (Table 2). This may be

attributed to a significant (SS-STP) increase between October 1983 ($4.4 \text{ mm} \pm 1.7$ [SD], $n = 15$) and April 1984 ($10.4 \text{ mm} \pm 3.9$, $n = 20$), the 6 mo immediately after *Diadema antillarum* mass mortality. No significant correlation with seawater temperature or global radiation was detected. Between April 1984 and February 1985, no significant variation over time was observed (SS-STP), indicating that a new equilibrium level had been established. This trend paralleled that observed in cover (Quadrats 1 to 8; Spearman's Rank Correlation). About 7 mo after *D. antillarum* mortality, the initial difference in mean blade size between Holiday Beach and Buoy 1 had disappeared (Fig. 5b).

Mean specific growth rates of *Lobophora variegata* blades ranged from $1.97 \% \text{ d}^{-1} \pm 1.02$ (SD), $n = 24$, to $2.59 \% \text{ d}^{-1} \pm 0.67$, $n = 15$, at HB and from $1.73 \% \text{ d}^{-1} \pm 1.37$, $n = 5$, to $3.46 \% \text{ d}^{-1} \pm 2.06$, $n = 9$, at B1. There was no significant difference between the 2 locations nor was there a significant variation over time at any of the 2 locations, precluding seasonal control of growth of *L. variegata* (Fig. 5c; Table 2). Evidently, the increase in cover and blade size at B1 between October 1983 and April 1984 cannot be attributed to increased growth rates.

Turnover rates of *Lobophora variegata* blades (Fig. 5d) were high at both locations. At HB half-lives ranged from 15 to 39 d and decreased significantly between August 1983 and 1984 (linear regression), and this was paralleled by a slight, although not significant, decrease in cover (Fig. 5a). During this period, increased sedimentation (de Ruyter van Steveninck pers. obs.) may have been responsible for the decrease in half-lives.

At B1, half of the blades had disappeared within 9 to 29 d. At this station half-lives were significantly higher ($20.3 \text{ d} \pm 7.4$ [SD], $n = 4$) between November 1983 and

March 1984, the 5 mo immediately after *Diadema antiillarum* mass mortality, than in the following 10 mo ($12.3d \pm 2.1$, $n = 7$) when cover and mean blade size had also levelled off (t-test on log-transformed data).

Reproductive plants were present during the entire period (Sep 1983 to Oct 1984) at HB (Fig. 7) but relative

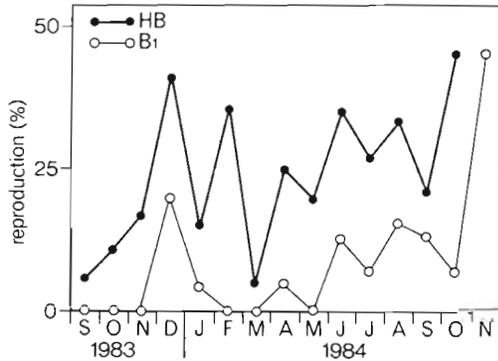


Fig. 7. *Lobophora variegata*. Percentage of reproductive plants at Holiday Beach (HB) and CARMABI Buoy 1 (B1). $N = 14$ to 28 blades, sampled at random from ca 30 m depth outside the permanent quadrats

numbers did not correlate with water temperature at 30 m nor with global radiation (Spearman's Rank Correlation). At B1, reproductive plants were absent during some months, and again, no correlation with temperature or light was found. However, there was a significant correlation between the fluctuations observed at HB and B1 (Spearman's Rank Correlation) suggesting some external regulating factor.

At B1, the vertical range of *Lobophora variegata*

increased after *Diadema antillarum* mass mortality. Between April 1984 and February 1985 (Fig. 8), mean vertical range of *L. variegata* over the reef slope expanded from 7.2 to 14.1 m, a 2-fold increment, and the mean number of quadrats in which it was present in the 4 transects increased significantly from 4.3 ± 1.3 to 11.0 ± 1.2 (t-test for paired comparisons). However, in quadrats with existing *L. variegata* patches cover did not increase (Fig. 8), which is in agreement with the newly established equilibrium levels in the permanent quadrats after April 1984 (Fig. 5a).

DISCUSSION

Seasonality in growth, abundance and reproduction in subtidal, (sub)tropical algae has been observed in green (Bach 1979, O'Neal & Prince 1982, Morrison 1984a), brown (Umamaheswara Rao 1969, Umamaheswara Rao & Kalimuthu 1972, Kaliaperumal & Kalimuthu 1976, Prince & O'Neal 1979, Prince 1980) and red algae (Rama Rao 1970, Dawes et al. 1974, Josselyn 1977, Hay & Norris 1984); all, however, inhabiting relatively shallow depths (14 m maximum).

The present study indicates that abundance, size, growth and reproduction of the brown, foliose macroalga *Lobophora variegata* in the deep coral reef of Curaçao is not significantly influenced by season. At Holiday Beach, a location with a well-developed *L. variegata* vegetation from ca 20 m downward, no variation over time was demonstrated for cover, blade size and growth rate. In addition, variation in cover be-

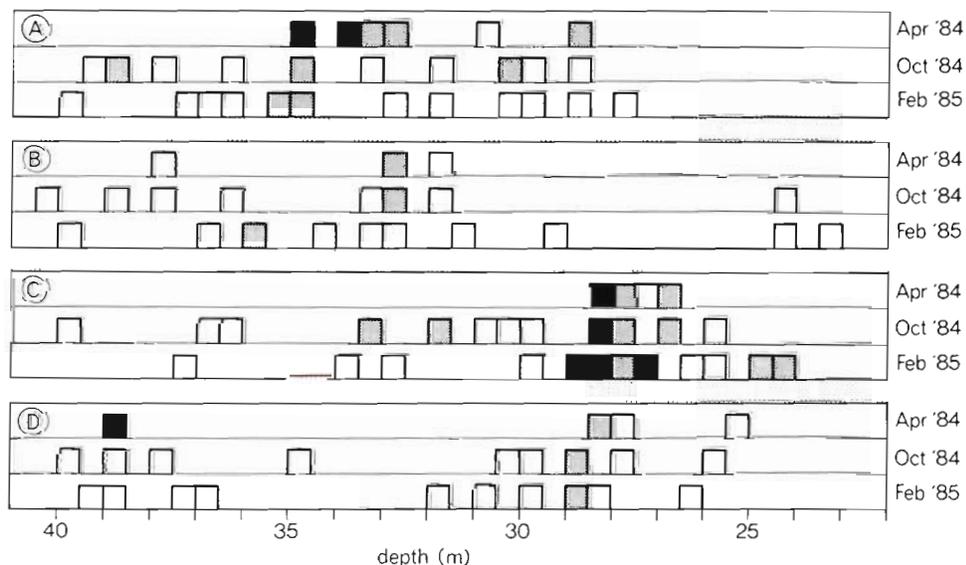


Fig. 8. *Lobophora variegata*. Changes in depth distribution at CARMABI Buoy 1 as observed in 4 transects between Apr 1984 and Feb 1985. Cover in 1 m^2 quadrats estimated using the Braun-Blanquet scale: white, up to 1%; stippled, 1 to 5%; black, 5 to 25 %

tween quadrats was large (Fig. 6) and peaks in abundance did not coincide for the various quadrats, making seasonal trends unlikely.

At Buoy 1, *Lobophora variegata* formed an indistinct component of the vegetation at 30 m depth at the start of this investigation, while it was more conspicuous deeper (ca 35 m). Mean cover in permanent quadrats between 30 and 35 m increased significantly in the course of this study. This increase was most prominent between October 1983 and April 1984 and paralleled the same trend in mean blade size. But, as fluctuations in mean growth rate were not significant, and as trends at B1 (with high pre-mortality *Diadema antillarum* densities) were not paralleled by similar trends at HB (with low premortality *D. antillarum* densities), we attribute this increase to an effect of *D. antillarum* mass mortality (Bak et al. 1984, de Ruyter van Steveninck & Bak 1986) rather than to seasonal effects.

Year-round presence of *Lobophora variegata* has also been reported in other studies (e.g. Bernatowicz 1952, Croley & Dawes 1970, Tsuda 1972, 1974, Peckol 1982, Peckol & Searles 1983, 1984), one of which (Tsuda 1972) included a deep coral reef population. In the (sub)tropics, seasonal changes in abundance were observed by Bernatowicz (1952) and Tsuda (1972, 1974), while in collections by Dawes & Van Breedveld (1969), Tsuda & Kami (1973) and Mathieson & Dawes (1975) *L. variegata* was not represented during part of the year. On the North Carolina continental shelf, where *L. variegata* reaches its northern distribution limit, *L. variegata* showed large seasonal and year-to-year fluctuations in abundance (Peckol & Searles 1984). The characterization of *L. variegata* as a perennial alga in Florida (Croley & Dawes 1970) and in North Carolina (Peckol 1982, Peckol & Searles 1984) is supported by its year-round occurrence at Curaçao. In view of its morphology, however, it is difficult to distinguish individual *L. variegata* plants. The single blades considered in the present study are not perennial, as these had half-life spans of less than a month. But encrusting remnants, which cannot be separated as individuals, probably produce new blades constantly and thus are perennial. The problem of characterizing red and brown crusts with regard to their annual or perennial nature has previously been raised by Sears & Wilce (1975).

In contrast to North Carolina, where reproductive *Lobophora variegata* is limited to late spring (Peckol 1982), reproductive *L. variegata* was present the whole year round at Curaçao. The absence of reproductive plants during some months at B1, while they were present at HB, may be a consequence of life spans, which on average were shorter at B1 than at HB, preventing plants from becoming fertile.

Comparison of the developments in the *Lobophora*

variegata populations after *Diadema antillarum* mass mortality (Bak et al. 1984) at the 2 studied locations (Holiday Beach and Buoy 1) may explain the differences in *L. variegata* cover that existed between both locations originally. Growth rates at HB are comparable with those at B1 (Fig. 5c), demonstrating that growth itself did not limit *L. variegata* distribution and cover at B1. At first, blades were smaller here, but by May 1984, this difference had disappeared (Fig. 5b). Cover in the quadrats changed similarly, although differences between both locations remained significant (Fig. 5a). Thus, disappearance of *D. antillarum* led to an initial increase of *L. variegata* cover and blade size at B1, which levelled off about 6 mo later to reach new equilibrium levels.

Half-lives of the *Lobophora variegata* blades concurred with the observed shifts in cover and blade size. Before April 1984 half-lives were significantly higher than thereafter and allowed *L. variegata* to grow longer and thus to reach higher cover and blade size. Higher disappearance rates between May 1984 and January 1985, probably as a consequence of increased grazing by herbivorous fishes (Ogden et al. 1973, Hay & Taylor 1985), limited further expansion of the *L. variegata* vegetation and a new equilibrium was reached between *L. variegata* cover and grazing. It is interesting that de Ruyter van Steveninck & Bak (1986) observed the same shift in the abundance of algal turfs: 7 mo after *Diadema antillarum* mass mortality cover of turf algae at 27 m depth, at location B1, had reached a new equilibrium level, ca 20% higher than that in October 1983.

These results and evidence that *Lobophora variegata* is indeed consumed in considerable quantities by herbivores (Lewis 1985, de Ruyter van Steveninck & Breeman unpubl.) confirms the hypothesis raised by van den Hoek et al. (1978), that grazing can restrict *L. variegata* distribution. At location HB, with low pre-mortality *Diadema antillarum* densities in the deep reef (0.4 and 0.1 m⁻² at depths of 12 and 25 m, respectively; Bak et al. 1984, de Ruyter van Steveninck pers. obs.) and relatively high *L. variegata* cover, no effect of the disappearance of *D. antillarum* was observed on cover and blade size of *L. variegata*. At B1, pre-mortality densities of *D. antillarum* were relatively high in the deep reef (2.5 and 0.4 m⁻² at depths of 12 and 25 m, respectively; Bak et al. 1984, de Ruyter van Steveninck pers. obs.) while cover of *L. variegata* was low. After mortality in October 1983 both cover and blade size increased significantly, while the depth range and frequency of *L. variegata* in the monitored reef transects also increased (Fig. 8). The fact that cover of existing *L. variegata* patches in these transects did not increase is in agreement with the observation that cover within *L. variegata* vegetations had reached a

new equilibrium level after April 1984 (Fig. 5a). Evidently, this does not mean that *L. variegata* cannot extend its distribution by colonizing newly available substratum. According to Carpenter (1981), *D. antillarum* can control macroalgal abundance by ingesting germlings and sporelings, thus preventing successional dominance of macroalgae. Possibly spores and torn-off pieces of blades (de Ruyter van Steveninck pers. obs.) have a better chance of becoming established in a situation without grazing by *D. antillarum*. Extension of *L. variegata* at B1, after *D. antillarum* mass mortality, was also reported by de Ruyter van Steveninck & Bak (1986) and in Jamaica by Morrison (1984b) and Liddel & Ohlhorst (1986).

The high turnover rates of *Lobophora variegata* blades (half-lives of 9 to 39 d) and the results of grazing experiments (de Ruyter van Steveninck & Breeman unpubl.) are evidence of heavy grazing pressure on *L. variegata* even after *Diadema antillarum* mass mortality. Contradictory observations on the susceptibility of *L. variegata* to various grazers (Earle 1972, Brawley & Adey 1977, Hay 1981, 1984, Norris & Fenical 1982, Hay & Goertemiller 1983, Morrison 1984b, Lewis 1985, Paul & Hay 1986, de Ruyter van Steveninck & Breeman unpubl.) probably are the results of geographical, habitat or individual variation in plant defenses and/or of differences in herbivore guild composition (Lewis 1985) as well as the availability of other, more palatable algal species.

Lobophora variegata does not fit into the functional-form groups as proposed by Littler et al. (1983a, b), who placed this species in the thick-leathery group on the basis of its morphology and productivity studies. Species belonging to this group should show low productivity combined with low losses to grazing. However, Littler et al. (1983a, b) did not test the susceptibility of *L. variegata* to grazing. In their productivity studies these authors found low productivity values for a shallow-water form, which probably differs in morphology from the deep-water form in the present study (cf. Norris & Bucher 1982). Smith (1981), however, also found low productivity values in a deep water form of *L. variegata* in North Carolina.

Thus, at Curaçao, *Lobophora variegata*, a foliose macroalga, which can be distinct in the deep coral reef, has an opportunistic strategy of reducing grazing losses, namely by maintaining growth rates high enough to compensate for these losses (Littler & Littler 1980, Littler et al. 1983b). The apparently rather constant cover of *L. variegata* (e.g. at HB, Fig. 5a) is, in fact, the result of a very dynamic balance between growth and (grazing) losses with turnover rates being very high.

Only detailed analyses of growth rates and longevity of individual plants can elucidate these kinds of pro-

cesses, knowledge of which is indispensable in understanding community organization.

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LITERATURE CITED

- Adey, W. H., Adey, P. J., Burke, R., Kaufman, L. (1977). The Holocene reef systems of Eastern Martinique. *Atoll Res. Bull.* 218: 1–40
- Bach, S. D. (1979). Standing crop, growth, and production of calcareous siphonales (Chlorophyta) in a south Florida lagoon. *Bull. mar. Sci.* 29: 191–201
- Bak, R. P. M., Carpay, M. J. E., Ruyter van Steveninck, E. D. de (1984). Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Mar. Ecol. Prog. Ser.* 17: 105–108
- Bernatowicz, A. J. (1952). Seasonal aspects of the Bermuda algal flora. *Pap. Mich. Acad. Sci.* 36: 3–8
- Borowitzka, M. A. (1981). Algae and grazing in coral reef ecosystems. *Endeavour, N. S.* 5: 99–106
- Brawley, S. H., Adey, W. H. (1977). Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environ. Biol. Fish.* 2: 45–51
- Carpenter, R. C. (1981). Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community (1981). *J. mar. Res.* 39: 749–765
- Croley, F. C., Dawes, C. J. (1970). Ecology of the algae of a Florida Key. I. A preliminary checklist, zonation, and seasonality. *Bull. mar. Sci.* 20: 165–185
- Dawes, C. J., Mathieson, A. C., Cheney, D. P. (1974). Ecological studies of floridian Eucheuma (Rhodophyta, Gigartinales). I. Seasonal growth and reproduction. *Bull. mar. Sci.* 24: 235–273
- Dawes, C. J., Van Breedveld, J. F. (1969). *Memoirs of the Hourglass Cruises. Vol. I, Part II: Benthic marine algae.* *Mar. Res. Lab. St. Petersburg, Florida*, p. 1–47
- Earle, S. A. (1969). Phaeophyta of the Eastern Gulf of Mexico. *Phycologia* 7: 71–254
- Earle, S. A. (1972). The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. In: Colette, B. B., Earle, S. A. (ed.) *Results of the Tektite program: ecology of coral reef fishes.* Natural History Museum, Los Angeles County, *Sci. Bull.* 14: 17–44
- Gaines, S. D., Lubchenco, J. (1982). A unified approach to marine plant-herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.* 13: 111–138
- Harper, J. L. (1977). *Population biology of plants.* Academic Press, London
- Hatcher, B. G. (1981). The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. *Proc. 4th Int. Coral Reef Symp., Manila, Vol. 2:* 515–524

- Hay, M. E. (1981). Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat. Bot.* 11: 97–109
- Hay, M. E. (1984). Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia (Berl.)* 64: 396–407
- Hay, M. E., Goertemiller, T. (1983). Between-habitat differences in herbivore impact on Caribbean coral reefs. In: Reake, M. L. (ed.) *The ecology of deep and shallow coral reefs*. Symposia Series for Undersea Research, Vol. 1. NOAA, Rockville, Maryland, p. 97–102
- Hay, M. E., Norris, J. N. (1984). Seasonal reproduction and abundance of six sympatric species of *Gracilaria* (Gracilariaceae: Rhodophyta). *Hydrobiologia* 116/117: 63–72
- Hay, M. E., Taylor, R. (1985). Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia (Berl.)* 65: 591–598
- Hoek, C. van den, Breeman, A. M., Bak, R. P. M., Buurt, G. van (1978). The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. *Aquat. Bot.* 5: 1–46
- Hoek, C. van den, Cortel-Breeman, A. M., Wanders, J. B. W. (1975). Algal zonation in the fringing coral reef of Curaçao, Netherlands Antilles, in relation to zonation of corals and gorgonians. *Aquat. Bot.* 1: 269–308
- Josselyn, M. N. (1977). Seasonal changes in the distribution and growth of *Laurencia poitei* (Rhodophyceae, Ceramiales) in a subtropical lagoon. *Aquat. Bot.* 3: 217–229
- Kaliaperumal, N., Kalimuthu, S. (1976). Changes in growth, reproduction, alginic acid and mannitol contents of *Turbinaria decurrens* Bory. *Botanica mar.* 19: 161–178
- Lewis, S. M. (1985). Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia (Berl.)* 65: 370–375
- Liddel, W. D., Ohlhorst, S. L. (1986). Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *J. exp. mar. Biol. Ecol.* 95: 271–278
- Littler, M. M., Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116: 25–44
- Littler, M. M., Littler, D. S. (1984). Models of tropical reef biogenesis: the contribution of algae. In: Round, F. E., Chapman, D. J. (ed.) *Progress in phycological research*, Vol. 3. Biopress Ltd., Bristol, p. 323–364
- Littler, M. M., Littler, D. S. (1985). Nondestructive sampling. In: Littler, M. M., Littler, D. S. (ed.) *Handbook of phycological methods. Ecological field methods: Macroalgae*. Cambridge University Press, Cambridge, p. 161–175
- Littler, M. M., Littler, D. S., Taylor, P. R. (1983a). Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol.* 19: 229–237
- Littler, M. M., Taylor, P. R., Littler, D. S. (1983b). Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2: 111–118
- Mathieson, A. C., Dawes, C. J. (1975). Seasonal studies of Florida sublittoral marine algae. *Bull. mar. Sci.* 25: 46–65
- Morrison, D. (1984a). Seasonality of *Batophora oerstedii* (Chlorophyta), a tropical macroalga. *Mar. Ecol. Prog. Ser.* 14: 235–244
- Morrison, D. (1984b). Mass mortality of *Diadema antillarum* on a Jamaican coral reef: effect on the algal community. *Advances in Reef Science, RSMAS, Miami*, p. 85–86
- Norris, J. N., Bucher, K. E. (1982). Marine algae and seagrasses from Carrie Bow Cay, Belize. In: Rützler, K., Macintyre, I. G. (ed.) *The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize*. *Smithson. Contr. mar. Sci.* 12: 167–238
- Norris, J. N., Fenical, W. (1982). Chemical defense in tropical marine algae. In: Rützler, K., Macintyre, I. G. (ed.) *The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize*. *Smithson. Contr. mar. Sci.* 12: 417–431
- Ogden, J. C. (1976). Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquat. Bot.* 2: 103–116
- Ogden, J. C., Brown, R. A., Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian Patch reefs. *Science* 182: 715–717
- Ogden, J. C., Lobel, P. S. (1978). The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.* 3: 49–63
- O'Neal, S. W., Prince, J. S. (1982). Relationship between seasonal growth, photosynthetic production and apex mortality of *Caulerpa paspaloides* (Chlorophyceae). *Mar. Biol.* 72: 61–67
- Paul, V. J., Hay, M. E. (1986). Seaweed susceptibility to herbivory: chemical and morphological correlates. *Mar. Ecol. Prog. Ser.* 33: 255–264
- Peckol, P. (1982). Seasonal occurrence and reproduction of some marine algae of the continental shelf, North Carolina. *Botanica mar.* 25: 185–190
- Peckol, P., Searles, R. B. (1983). Effects of seasonality and disturbance on population development in a Carolina continental shelf community. *Bull. mar. Sci.* 33: 67–86
- Peckol, P., Searles, R. B. (1984). Temporal and spatial patterns of growth and survival of invertebrate and algal populations of a North Carolina continental shelf community. *Estuar. coast. Shelf Sci.* 18: 133–143
- Prince, J. S. (1980). The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida. II. Seasonal photosynthesis and respiration of *S. pteropleuron* and comparison of its phenology with that of *S. polyceratium* Montagne. *Phycologia* 19: 190–193
- Prince, J. S., O'Neal, S. W. (1979). The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida. I. Growth, reproduction and population structure. *Phycologia* 18: 109–114
- Rama Rao, K. (1970). Studies on growth cycle and phycocolloid content in *Hypnea musciformis* (Wulf) Lamour. *Botanica mar.* 13: 163–165
- Randall, J. E. (1961). Overgrazing of algae by herbivorous marine fishes. *Ecology* 42: 812
- Ruyter van Steveninck, E. D. de, Bak, R. P. M. (1986). Changes in abundance of coral reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar. Ecol. Prog. Ser.* 34: 87–94
- Sachs, L. (1982). *Applied statistics. A handbook of techniques*. Springer Verlag, New York
- Sears, J. R., Wilce, R. T. (1975). Sublittoral, benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity and floristic composition. *Ecol. Monogr.* 45: 337–365
- Smith, W. O., Jr. (1981). Photosynthesis and productivity of benthic macroalgae on the North Carolina continental shelf. *Botanica mar.* 24: 279–284
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry*, 2nd edn. W. H. Freeman and Co., San Francisco
- Stephenson, T. A., Stephenson, A. (1972). *Life between tidemarks on rocky shores*. W. H. Freeman Co., San Francisco
- Tsuda, R. T. (1972). Marine benthic algae of Guam. I. Phaeophyta. *Micronesica* 8: 87–115
- Tsuda, R. T. (1974). Seasonal aspects of the Guam Phaeophyta

-
- (brown algae). Proc. 2nd Int. Coral Reef Symp. 1. Great Barrier Reef Committee, Brisbane, p. 43-47
- Tsuda, R. T., Kami, H. T. (1973). Algal succession on artificial reefs in a marine lagoon environment in Guam. *J. Phycol.* 9: 260-264
- Umamaheswara Rao, M. (1969). Seasonal variations in growth, alginic acid and mannitol contents of *Sargassum wightii* and *Turbinaria conoides* from the Gulf of Mannar, India. Proc. 6th Int. Seaweed Symp.: 579-584
- Umamaheswara Rao, M., Kalimuthu, S. (1972). Changes in mannitol and alginic acid contents of *Turbinaria ornata* (Turner) J. Agardh in relation to growth and fruiting. *Botanica mar.* 15: 57-59

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