Dynamics of shelf edge coral reef-associated macroalgae at La Parguera, Puerto Rico

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Abstract.—Percentage cover of coral reef associated algae increased significantly from 2003 to 2007 at two shelf edge sites in southwest Puerto Rico (42.8 % to 75.3% at Weinberg Reef and 67.4% to 81.8% at El Hoyo). While the increase was driven largely by increase in cover of *Lobophora variegata,* percent cover of the individual spatially dominant algal species was highly variable temporally. The variability was apparent even at the subquadrat level (0.0625m^2) for which adjacent subquadrats demonstrated little concordance in species cover over subsequent sampling periods.

Introduction

Algae are well known to be important components of coral reef communities. They provide (i) structural framework (Adey 1976, 1978; Wray 1977), (ii) physical consolidation (Borowitzka *et al*. 1974), (iii) food (Borowitzka 1981; Carpenter 1981; Hay 1984); (iv) contribution to reef sediment (Wray 1977; Bach 1979); (v) primary productivity (Vooren 1981; Hawkins and Lewis 1982; Morrissey (1985); (vi) nitrogen-fixation (Wiebe (975; Mague and Holm-Hansen 1975); and (vii) high species diversity (Van Den Hoek *et al*. 1975; Wanders 1976; Connor and Adey 1977; Littler and Littler 1994). Despite their recognized roles in the natural function of coral reefs, algal cover on reefs is commonly and increasingly related to coral reef decline. There is substantial evidence that removal of top down control through herbivore removal and augmentation of bottom up control through anthropogenic nutrient increase has resulted in increased algal growth on coral reefs on a world-wide basis (Littler and Littler, 1984; Hughes et al., 1999; LaPointe, 1999). Algal-coral interactions are typically detrimental to the coral and such algal effects have been reviewed by Mumby et al. (2005). In extreme situations, perturbation may result in phase shifts from coral dominated communities to those dominated by fleshy algae (Hughes, 1994).

Despite the recognized decline of corals worldwide, there is a relative stasis in major benthic components of the community in the short-term. That is over short periods of time, cover and species present within defined areas, vary little for scleractinian and alcyonarian corals and sponges. On superficial examination, the same may be assumed for algae. However, in a limited number of cases it has been demonstrated that coral reef-associated algae may show rapid turn-over (Ruyter van Steveninck and Breeman, 1987, 1988; Stiger and Payri, 1999; Mumby et al., 2005). The latter authors were perhaps the first to recognize that actual dynamics (as opposed to overall cover) of macroalgae on coral reefs had specific implications for algal-coral interactions, i.e. the ecological functions of a persistent patch as opposed to dynamic systems. Nevertheless, these studies focused on only a single or two species. In this contribution, we address algal dynamics across a suite of algal species at two shelf break coral reef habitats in southwest Puerto Rico, Caribbean Sea.

Materials and methods

The study was undertaken at two sites at the insular shelf break off La Parguera, Puerto Rico. Weinberg Reef (17°53.429′ N; 66°59.320′ W) is a well developed bank reef system with spur and groove formations characterized by high density and live cover of coral species and coralline algae ranging from 18 to 30 meters deep, located 10.2 km from shore. El Hoyo Reef (17°52.559′ N;

67°02.619′ W), is dominated by a coral-octo-coral-sponge community on a low vertical relief hard bottom. Depths vary between 20-25 m and the site is located 10.3 km from shore.

The percentage cover of macroalgae species was quantified within permanent quadrats established in 2003 and photographically sampled biannually through 2007. Nine 0.25 m² (0.61 m x 0.42 m) quadrats were each divided into four 1/16 (.0625) m² subquadrats (N=36 subquadrats) at each of two depth intervals (20m and 25m) at each reef (N=72 total subquadrats per reef). Each subquadrat was labeled with an identification number for reference. At each sampling period, photographs of each subquadrat were taken with a digital camera (Cannon Rebel 300D) in an underwater housing (Sea & Sea DX-300D) fitted with a strobe. For each digital photograph, percent cover of the recognizable algal elements was calculated by overlaying with 100 (randomly stratified points) using Coral Point Count with an Excel extension (CPCe) (Kohler & Gill, 2006).

Mean differences in total cover were compared using a 1-way ANOVA without replication following arcsine-transformation to meet the assumptions of normality and homogeneity of variance. Kendall's coefficient of concordance *(W)*, a nonparametric multi-sample rank correlation statistic, was used to test for similarities in algae abundances within quadrats and across sampling periods (Sokal and Rohlf 1995). All analyses were performed with Statistica software version 7.1.

Results

At the outset of the study there was a bloom of the cyanobacteria *Schizothrix* sp., the first observance of such a cyanobacterial bloom at these offshore coral reef areas (based on observations for over 25 years) (Fig. 1). While not reflected in the cover data, however, based on visual observation *Schizothrix* recurred at varying degrees during subsequent yearly warmest months. At the subquadrat level, *Schizothrix* occupied up to 88% substratum cover. When present, *Schizothrix* typically persisted from two

to three months. Other than *Schizothrix*, the most abundant algal species encountered in quadrats at both reef sites were *Neogoniolithon accretum, Lobophora variegata, Dictyota humifusa* plus a mixed species algal turf, each present in the subquadrats during every sampling with a frequency greater than 50% (Table 1). Nevertheless, most of the algal species richness occurred in the algal turf element which was comprised of numerous species. The total algal percent cover over the period of study increased at both Weinberg (42.8 % to 75.3%) and El Hoyo (67.4% to 81.8%) (Fig. 1). The cover increase was statistically significant at both reefs (Weinberg Reef: $p< 0.01$; $r^2=0.90$ and El Hoyo $p< 0.01$; $r^2=0.70$). Much of the overall increase in cover appears to be driven by *Lobophora variegata* at both sites. Despite the gradual increase in cover at Weinberg and El Hoyo Reefs, when the average cover of individual species is plotted, a high degree of variation is apparent (Figs. 2, 3). This is dramatically illustrated by the case of *L. variegata* in which changes in cover in individual subquadrats (0.165 m²), were calculated to be up to 900% between subsequent samplings. When change in percent cover between all subsequent sampling periods was calculated for all subquadrats, percentage change in cover for *L. variegata* averaged 158% at Weinberg and 179% at El Hoyo. Average change per subquadrat for *Dictyota humifusa* was 279% and 247%; *Neogoniolithon* 166% and 218%; *Schizothrix* sp. 199% and 542% at Weinberg and El Hoyo reefs respectively (Table 2).

These substantial temporal changes were largely independent of change in neighboring quadrats. That is, changes in algal cover for one subquadrat was largely independent of change in the adjacent subquadrats. This is illustrated for *Lobophora variegata* in the subquadrats comprising a single 0.25 m² quadrat (Fig. 4). To examine the independence of cover change in adjacent subquadrats, Kendall's coefficient of concordance, *W*, was calculated for cover change in all quadrats for each sampling interval. Tables 3 and 4 show these values for Weinberg and El Hoyo Reefs. Kendall's *W* coefficient ranges from 0 (when there is no association) to 1 (when there is complete agreement
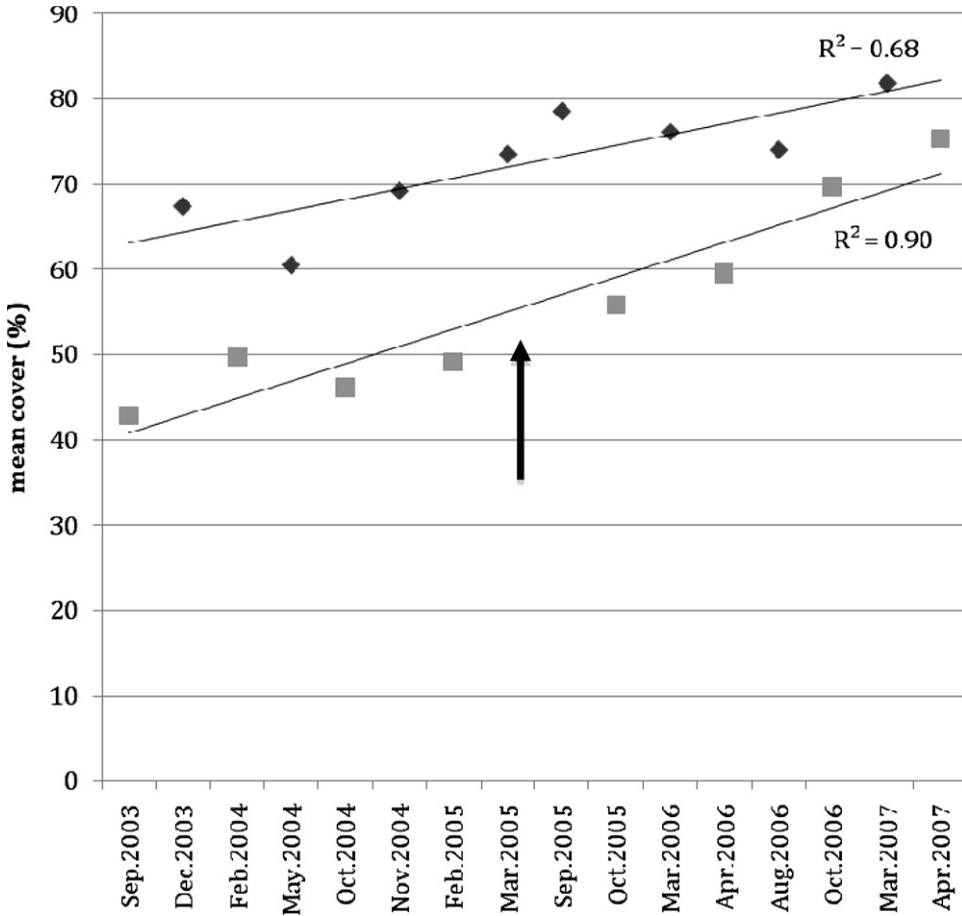
Fig. 1. Temporal changes (mean cover) in the abundances of macroalgae between 2003 and 2007 at Weinberg Reef and Hoyo Reef. Arrow in the graph indicates timing of coral bleaching event.

among the ranking of all groups). On rare occasions (indicated by asterisks), there was a significant degree of concordance; however, in most quadrats concordance was low ($W < 0.25$ for over 2/3 of quadrats) for each of the major substratum occupying species (i.e. *Lobophora variegata*, *Dictyota humifusa*, *Neogoniolithon accretum*, *Schizothrix* sp. and turf).

Aside from the substantial changes in cover for the principal space occupying species, variability is also indicated by small scale (seen at the level of the subquadrats) recruitment and extinction events. For example between the February and October 2005 sampling periods, *Dictyota humifusa* recruited into 21 and disappeared from 12 of the 72 subquadrats. Recruitment and extinction events occurred for both more common as well as the less common species. The more ephemeral species included *Halimeda goreauii*, *Caulerpa serrulata*, *C. racemosa* and *Amphiroa* spp.

DISCUSSION

Offshore reefs in southwest Puerto Rico had been previously considered to be relatively undisturbed prior to the onset of this study. As such, the original *Schizothrix* blooms, which recurred at varying intensities during subsequent yearly warmest months, undoubtedly represented an early signal of perturbation that was subsequently reflected by the increase in total algal cover during the duration of the study. Marine

Table 1. Total mean cover and frequency of macroalgal species identifiable from digital photographs at Weinberg Reef. (R) = Rhodophyta; (P) = Phaeophyceae; (C) = Chlorophyta; (Cyan) = cyanobacteria.

Algal species/Group	Mean Cover (%)	Frequency
Neogoniolithon accretum (Foslie & M.Howe) W.H.Adey (R)	13.34	94.79
Lobophora variegata (J.V.Lamour.) Womersley (P)	15.80	86.97
Dictyota humifusa Hörnig, Schnetter & Bula-Meyer (P)	8.51	80.20
Turf	5.66	71.18
Schizothrix sp. (Cyan)	4.94	53.99
Dictyota spp. (P)	1.82	28.12
Peyssonnelia sp. . (R)	1.19	23.95
Wrangelia sp. . (R)	1.21	10.76
Peyssonnelia flavescens D.L.Ballant & Ruiz . (R)	0.13	5.55
Peyssonnelia sp. . (R)	0.18	5.20
Peyssonnelia boergesenii Weber Bosse . (R)	0.06	2.10
Amphiroa spp. (R)	0.02	0.69
Caulerpa racemosa (Forssk.) J.Agardh (C)	0.02	0.53
Halimeda goreauii W.R.Taylor (C)	0.01	0.52
Caulerpa serrulata (Forssk.) J.Agardh (C)	0.01	0.18
Martensia fragilis Harv. (R)	0.01	0.17

cyanobacterial blooms have been attributed to increased nutrient levels (Glibert et al. 2004; Elmetri and Bell 2004); however, Todd et al. (2009) suggested that anthropogenic nutrients do not reach the La Parguera shelf edge. Paerl and Huisman (2008) and Jöhnk et al. (2008), however, have provided evidence that increased water temperature may be the most important element in triggering cyanobacterial blooms. The cyanobacterial blooms had very high cover over the bottom substratum, and also was observed to overgrow living coral tissue. The precise physiological effects of cyanobacteria on corals are not known; however, Kuffner et al. (2006) indicated that cyanobacteria blooms possessed the capacity to reduce survival and recruitment of corals and octocorals. Furthermore, the cyanobacterial blooms were coincident with the annual spawning season of corals. Thus cyanobacterial cover during these periods possibly pre-empted available substratum that coral recruits required for settlement.

None of the more common species of algae quantified (Table 1) exhibited clear seasonal fluctuations in abundances, despite the visual recognition of *Schizothrix* principally in summer months. These species were persistent year-round at both the Weinberg and El Hoyo reefs. The 43% increase in algal cover at Weinberg roughly parallels a 52% decline in living coral tis-

sue that was measured over the same time period in the vicinity of our quadrats (Weil, unpublished data). Thus increase in algal cover over the duration of this study suggest that the algal cover increase is at the expense of living coral cover and perhaps reflects a developmental stage in a phase shift from coral-dominated reef to algal reef. A substantial bleaching event occurred in October 2005 (Weil, unpublished data) and subsequent increase in coral disease has undoubtedly contributed to the increase in hard substratum becoming available for algal colonization.

The substantial variability both in terms of relative change in composition and cover, demonstrated herein probably represents an underestimate. Mumby et al. (2005) estimated that colonization rates of coral reef algae would be underestimated by 9% if sampled at 3 month intervals; however, measurement of extinction rates are not similarly influenced. They (op. cit.) concluded, nevertheless, that quarterly to annual sampling intervals are appropriate for quantifying the dynamics of *L. variegata* and *Dictyota pulchella* Hörnig *et* Schnetter. Ruyter van Steveninck and Breeman (1987) indicated that individual fronds of *Lobophora variegata* had a half life of only 15 to 39 days and the half-life was temporally variable. This reflects that life history characteristics of benthic algae in general
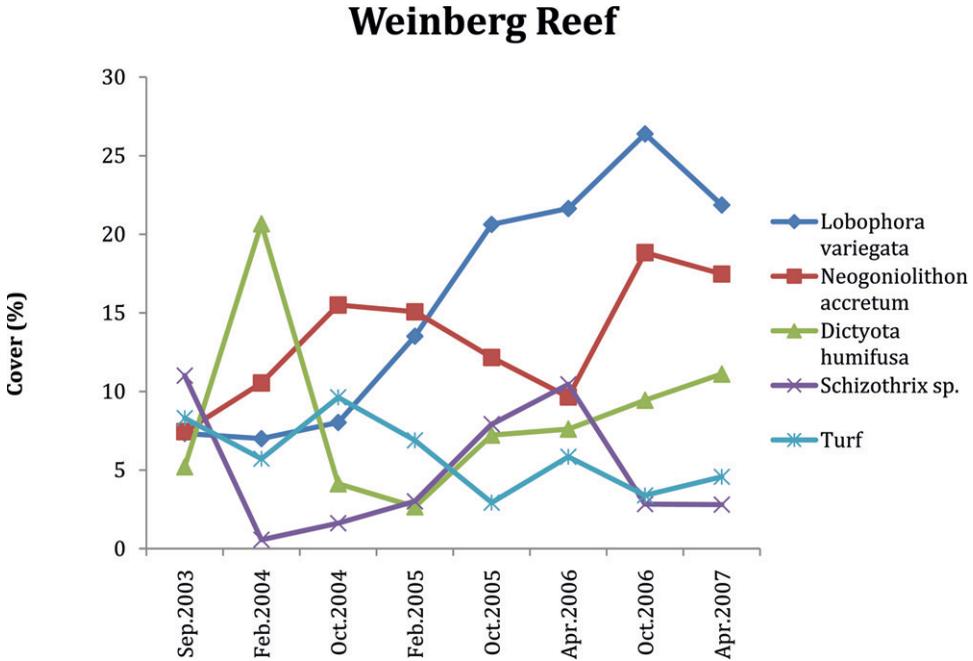
Weinberg Reef

Fig. 2. Variations in benthic cover of macroalgal species at Weinberg Reef monitored between September 2003 to April 2007.
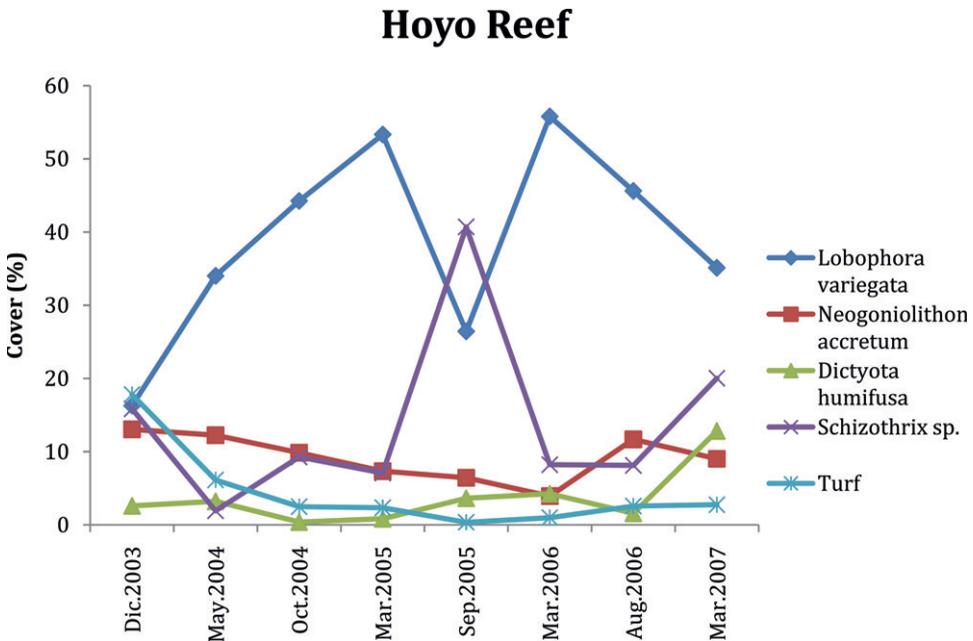
Hoyo Reef

Fig. 3. Variations in benthic cover of macroalgal species at Hoyo Reef monitored between December 2003 to March 2007.

differ from the other longer-lived coral reef inhabitants. The short life periods of individual fronds is basic to the high demographic variability. Thus the relatively high degree of both recruitment and extinction events is undoubtedly a result of short life histories and short individual frond half-life.

The cover data for *Neogoniolithon* and possibly for *Peyssonnelia* species are at times quantified as being lower than they are. These species may become overgrown and hence not seen in the quantification analyses. Nevertheless, some coralline algal species are capable of living for decades (B. Steneck, pers. comm.) and certainly persist despite overgrowth by other species, even for years (Airoldi 200, Underwood 2006). Declines and increases in cover for *Neogoniolithon accretum* is thus due to increases and declines in cover by overgrowing algae such as *Lobophora* and

Dictyota. Other *Neogoniolithon* decline was due to a crustose coralline algal disease condition (Ballantine et al. 2005).

The fact that individual subquadrats behaved independently, is somewhat surprising. If the entire shelf edge algal community, was reacting to the same controlling factors (such as similar conditions of nutrients, light irradiance and herbivory), one would expect that at the 0.25 m^2 spatial scale, the algae would respond similarly. However, even among adjacent 0.25 m^2 quadrats, algae displayed different patterns of cover. This fact is further supported by a general lack of concordance among the subquadrats within the 0.25 m^2 quadrats. This would suggest that other factors may drive community dynamics. While speculative, brief frond half-lives, differences in microhabitat, stochastic recruitment, and extinction events, spatial competition and perhaps small scale differences in herbivory, may explain these differences. Obviously during the sampling interval employed here, a number of complete algal turnovers may occur.

TABLE 2. Average percent change in macroalgal species cover, calculated for sequential sampling periods for all subquadrats at Weinberg and El Hoyo Reefs between 2003 and 2007.

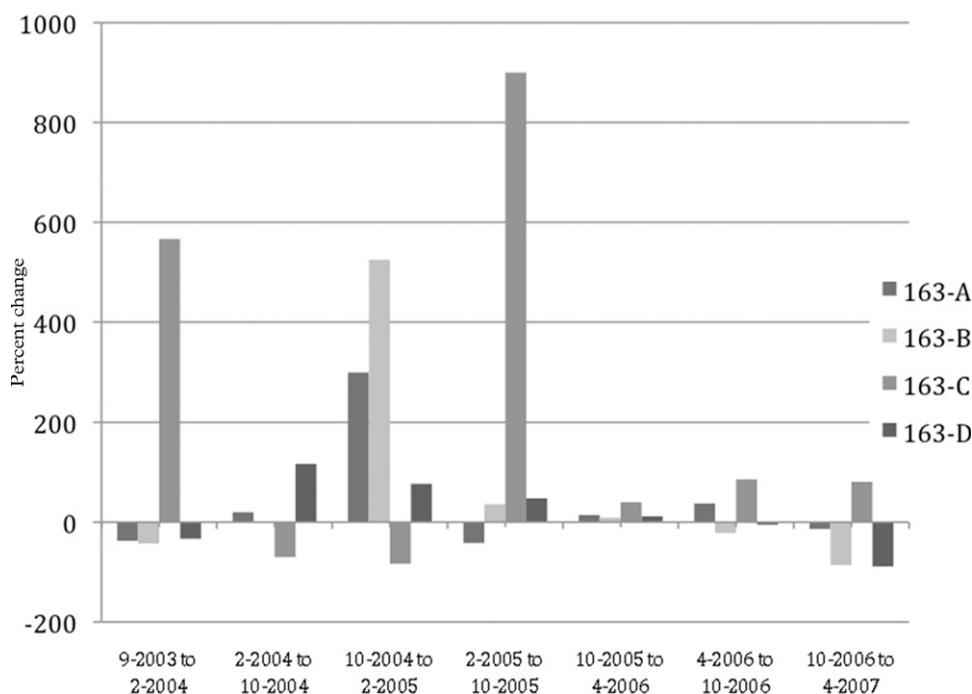| Major Species	Weinberg	Hoyo
Lobophora variegata	158%	179%
Dictyota humifusa	279%	247%
Neogoniolithon accretum	166%	218%
Schizothrix sp.	199%	542%
Turf	165%	120%

FIG. 4. *Lobophora variegata* cover in four adjacent subquadrats within quadrat 163 at Weinberg Reef between Sep.2003 and Apr.2007.

TABLE 3. Concordance (*W*) vslues for macroalgal cover change among 4 subquadrats during the period September 2003 to April 2007 for different species of macroalgae at Weinberg Reef (* indicates statistical significance (p <0.01).

Coefficient of concordance (*W*)					
Quadrat	*Lobophora variegata*	*Dictyota humifusa*	*Neogoniolithon accretum*	*Schizothrix* sp.	Turf
163	0.17	0.22	0.37	0.08	0.56*
164	0.06	0.33	0.28	0.26	0.09
165	0.31	0.07	0.48*	0.38	0.48*
166	0.66*	0.23	0.39	0.05	0.22
167	0.13	0.41	0.16	0.13	0.30
168	0.71*	0.22	0.77*	0.07	0.18
169	0.13	0.40	0.05	0.44	0.01
170	0.42	0.41	0.61*	0.03	0.51*
171	0.35	0.29	0.61*	0.09	0.46
175	0.17	0.11	0.30	0.24	0.09
176	0.26	0.23	0.25	0.16	0.16
177	0.08	0.21	0.32	0.33	0.28
178	0.30	0.14	0.13	0.21	0.07
179	0.24	0.12	0.22	0.10	0.19
181	0.09	0.37	0.50*	0.31	0.27
182	0.43	0.47*	0.30	0.09	0.06
183	0.10	0.21	0.08	0.29	0.14
192	0.36	0.29	0.40	0.06	0.18

TABLE 4. Concordance (*W*) vslues for macroalgal cover change among 4 subquadrats during the period September 2003 to April 2007 for different species of macroalgae at El Hoyo Reef (* indicates statistical significance (p <0.01).

Coefficient of concordance (*W*)					
Quadrat	*Lobophora variegata*	*Dictyota humifusa*	*Neogoniolithon accretum*	*Schizothrix* sp.	Turf
12	0.62*	0.18	0.42	0.11	0.46*
13	0.16	0.02	0.48*	0.17	0.32
14	0.27	0.26	0.51*	0.16	0.07
47	0.22	0.07	0.16	0.13	0.17
124	0.19	0.06	0.17	0.06	0.07
135	0.08	0.27	0.14	0.40	0.11
136	0.14	0.19	0.03	0.04	0.15
137	0.27	0.33	0.19	0.08	0.14
193	0.02	0.06	0.14	0.17	0.40
15	0.54*	0.09	0.17	0.26	0.24
17	0.09	0.05	0.06	0.67*	0.20
19	0.18	0.06	0.23	0.23	0.01
38	0.41	0.04	0.28	0.05	0.18
39	0.19	0.55	0.40	0.19	0.30
40	0.44	0.10	0.23	0.29	0.01
41	0.08	0.02	0.26	0.16	0.25
42	0.08	0.19	0.42	0.04	0.29
194	0.19	0.25	0.30	0.02	0.17

In conclusion, shelf edge benthic algae in southwest Puerto Rico have demonstrated a significant increase in cover. This study also provides evidence for the highly dynamic aspect of the different elements comprising the algal community. Further research applied to a number of species, could include study of individual thallus longevity and spreading rates, algal-algal interactions, recruitment dynamics on settling plates, and

a monthly or biweekly sampling interval which would contribute to a higher resolution level of understanding of the complexity of short term algal population dynamics.

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