Introduction.

During the last three decades, coral reef assessments in Puerto Rico have shown sings of moderate to severe degradation (Mckenzie and Benton, 1972; Goenaga and Cintrón, 1979; Goenaga, 1988; Goenaga and Boulon, 1992; Hernández-Delgado, 1992, 2000, 2001, in press; Hernández-Delgado and Sabat, 2000; Weil et al., 2002; García et al., in press). The most significant threatening anthropogenic factors affecting coral reefs in Puerto Rico include water quality degradation, sedimentation, eutrophication, overfishing, loss of essential fish habitats, collection of reef fishes and invertebrates for the aquarium trade, historical coral collection, uncontrolled recreational activities and military activities (Goenaga, 1986, 1991; Hernández-Delgado, in press). Most coral reefs are characterized by showing a shift towards dominance by filamentous algae and macroalgae, with a simultaneously high partial coral tissue mortality and bioerosion rates (Hernández-Delgado, 2000). Although there is a major concern that coral reefs are also rapidly declining within most of the Natural Reserve systems in Puerto Rico, there is a general lack of quantitative information.

Severe degradation has been extensive on most inshore coral reefs, while those coral reefs located far offshore showed a less degraded environmental condition (Hernández-Delgado, 2000). Quantitative assessments have also shown that remote coral reef epibenthic and fish communities are generally in better ecological condition than those inshore (Hernández-Delgado, 2000; Hernández-Delgado and Sabat, 2000). However, some remote and apparently healthy coral reefs, such as those within the Luis

Peña Channel Marine Fishery Reserve (LPCMFR), Culebra Island, are already showing significant sings of degradation possibly as an indirect result of overfishing (Hernández-Delgado, 2000; Hernández-Delgado et al., 2000), in combination with acute White Plague Type II outbreaks (Hernández-Delgado, 2001; in review) and potential water quality degradation (Hernández-Delgado, 2001). Thus, one of the major concerns for the Puerto Rico Department of Natural and Environmental Resources (PRDNER) to designate the LPCMFR in year 1999, besides the protection and restoration of reef fishery resources, was to eliminate major stressing factors causing coral reef declines within the Reserve. Therefore, it was expected that, recovery of reef fish resources within the LPCMFR following its designation (see Hernández-Delgado and Sabat, 2002) should have been of major benefits for the coral reef epibenthic community. But that has not been the case. Hernández-Delgado (2001) reported a continuous major decline of coral reef epibenthic communities, even following the LPCMFR's designation. Major causes pointed out were coral disease outbreaks (mostly White Plague Type II) and preemptive competition and overgrowth by macroalgae. It was suggested that overfishing was not anymore one of the major causes of coral decline, as suggested previously by Hernández-Delgado (2000). Instead, water quality degradation (i.e., chronic low, but steady eutrophication) was suspected as a major cause of concern. These findings are in contrast with the paradigm that predicts that restoration of overfished reef fish communities will contribute to prevent or stop declines of coral reef epibenthic communities.

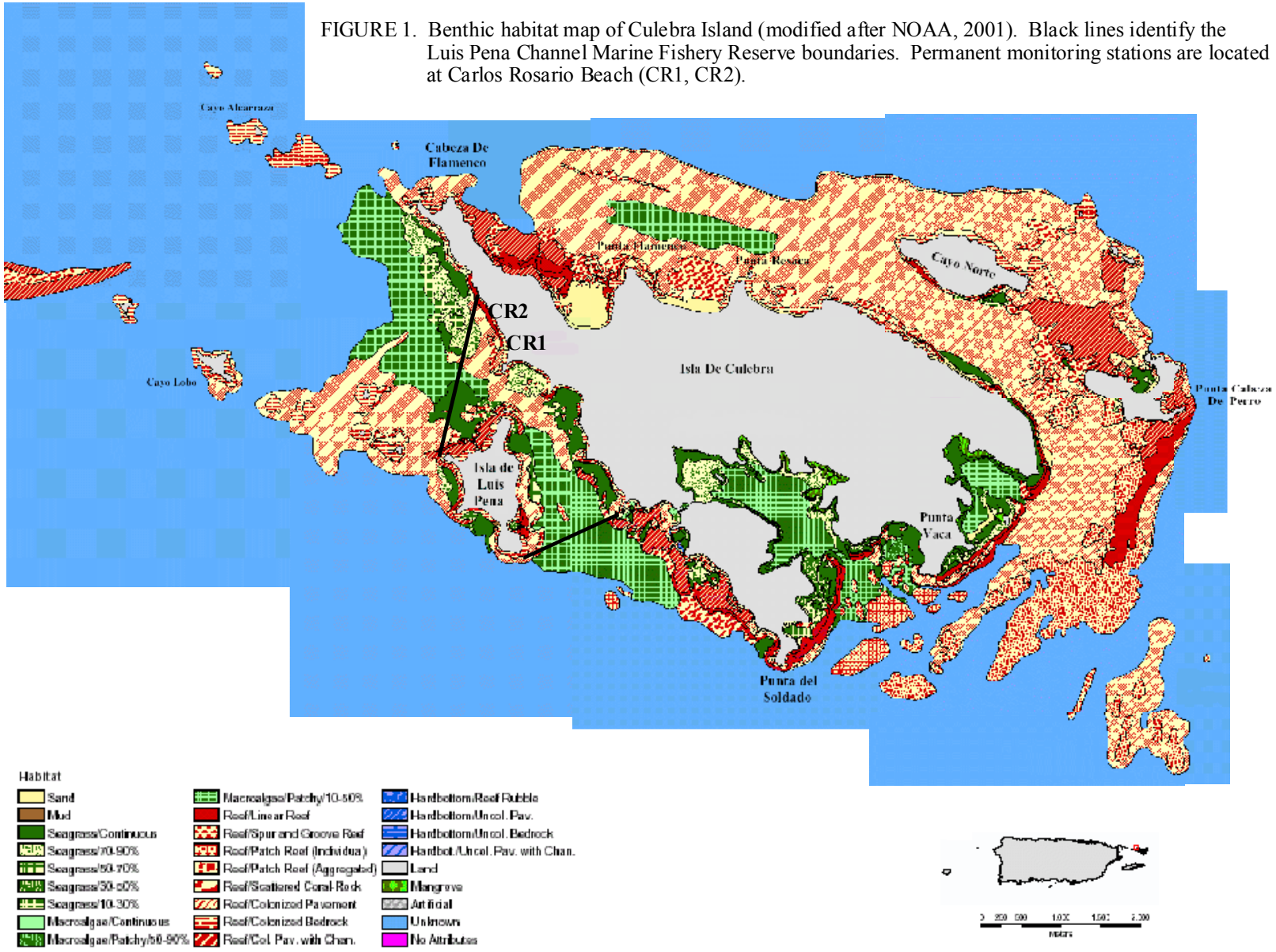
The main objective of this study was to expand the existing baseline data bank regarding the ecological status of the coral reef epibenthic communities within the LPCMFR by evaluating long-term ecological change at two study sites located within the Reserve between the years of 1997 and 2002. Our second objective was to evaluate the effectiveness of the LPCMFR in enhancing the overall coral reef essential fish habitat (EFH) quality by maintaining a high percentage of living coral cover and a highly diverse coral community in a good ecological condition. By "good ecological condition" we mean a coral reef community that is not showing a statistically significant decline or a shift towards algal dominance. Finally, multivariate analysis techniques were tested for their ability to discriminate patterns of temporal variation in the structure of coral reef epibenthic communities at each site.

Methods.

Study sites.

The quantitative long-term monitoring of coral reef epibenthic communities was carried out in the coral reefs off Carlos Rosario Beach, Culebra, Puerto Rico (Figure 1). The two sampling stations are located at: CR1 (18°19.570' E; 65°19.911' W) and at CR2 (18°19.746' E; 65°19.959' W). Major descriptions of habitat types within the MFR, coral, fish, macroinvertebrates and algal species checklists can be found at Pagán-Villegas et al. (1999), Hernández-Delgado (2000, 2001, in press a,b), Hernández-Delgado and Sabat (2000), Hernández-Delgado et al. (2000, 2002), and at Hernández-Delgado and Rosado-

FIGURE 1. Benthic habitat map of Culebra Island (modified after NOAA, 2001). Black lines identify the Luis Pena Channel Marine Fishery Reserve boundaries. Permanent monitoring stations are located at Carlos Rosario Beach (CR1, CR2).



Matías (in preparation). Data was collected in years 1997, 1998, 1999, 2001, and 2002 at CR1, and in years 1997, 1998, 2001, and 2002 at CR2.

Long-tem monitoring of coral reef epibenthic communities.

Each long-term monitoring station was permanently marked in 1997 with masonry nails driven to the reef bottom. Colored tags were used to facilitate their relocation. Ten replicate 10-m long transects were placed parallel to the shoreline following three different depth zones: I (<4 m); II (4-8 m); and III (>8 m). A total of 2 replicate transects were established at depth zone I, and 4 at each one of zones II and III. But in year 2001, transect replicates were increased to 4 at zone I to increase statistical power of the data at this zone (Hernández-Delgado, 2001). Depths at CR1 ranged from 4 to 8 m, while depths at CR2 ranged from 3 to 11 m.

In order to answer the first question, if there were any significant short-term changes in coral reef epibenthic communities, the line-intercept transect (LIT) method (Loya and Slobodkin, 1971) was used, in combination with videotaping (video-LIT method). Data was collected using a DCR-PC-110 digital video camera recorder (Sony Corp.), provided with a Baja UW Housing (Gates Underwater Products), color correcting filter, and DVM80EX2 cassettes (Sony Corp.). Distance between the camera and the transect line was kept constant at approximately 75 cm. Any coral colony or other epibenthic component was identified under the transect line, counted and their projected length under the transect line was measured to the nearest cm. According to Loya (1978), an individual colony is defined as "any colony growing independently of its

neighbors (i.e., whenever an empty space is recorded between two adjacent colonies)". In cases where an individual colony under the transect line was partially separated into two or more portions by tissue mortality, but there was still physiological connection between the partially separated tissues outside of the transect line, it was considered as one individual. But, in cases where an individual colony under the transect line was completely separated into two or more portions by tissue mortality (physiological fragmentation), each individual fragment was considered as a separate individual. This aspect is very important given the fact that partial colony mortality can produce physiological splitting of corals (Bythell et al., 1993; Hernández-Delgado 2000; 2001). In the case of two or more colonies growing one above the other and underlying the transect line, the projected length of the largest colony was recorded for living coverage analysis (Loya, 1978).

The video-LIT method allowed us to determine the coral species richness, colony abundance, percentage cover of all major epibenthic components (i.e., corals, algal functional groups, sponges, other macroinvertebrates), and to document the coral species diversity index, H'n and H'c (Shannon and Weaver, 1948) and evenness, J'n and J'c (Pielou, 1966a,b). H'n was calculated according to the following formula:

$$\mathbf{H'n = -\ p_i\ (\ln p_i),}$$

where p_i is the proportion of the number of colonies of the *i*th species from the total number of coral colonies of all species, and ln is the natural logarithm of p_i. J'n was calculated according to the following formula:

J'n= H'n observed/H'n max,

where H'n max= lnS, and S is the coral species richness of the sample. A similar approach was followed to calculate H'c and J'c, but all coral species proportions data was substituted by the relative percentage of coral cover for each species.

No significant difference was observed between the standard LIT method and the modified video-LIT method for coral/algal cover and species diversity (Hernández-Delgado, unpublished data; as cited by Hernández-Delgado, 2001). Data on counts (i.e., species richness, colony abundance) was square root-transformed (X'= √X; or X'= √(X+0.5) if there were zeros), while data on proportions was transformed to arcsine (√X), as described by Zar (1984). Data was analyzed between years and transects by means of a non-parametric Friedman two-way ANOVA (Hernández-Delgado, 2000).

The statistical power of sampling effort was calculated for each depth zone per year using the following formula: 1-(Standard error/Mean). Data was summarized in Tables A1 and A2 in the Appendix and shows that statistical power is generally strong for the most significant indicator parameters, particularly with increasing time. Also,

increasing the number of replicate transects in the shallowest depth zone in 2001 has increased the statistical power of the data.

Multivariate analysis of coral reef communities.

Multivariate analysis techniques were tested for their ability to discriminate patterns of temporal variation in the structure of coral reef epibenthic communities at each site. The coral reef community data set, based on the proportional cover of each major benthic component category, was compiled into a matrix and imported into PRIMER ecological statistics software package (Clarke, 1993; Clarke and Warwick, 1994, 2001) for multivariate analysis. Raw proportional cover values were square-root transformed in order to appropriately weight the less abundant benthic categories (Clarke and Warwick, 2001; McField et al, 2001). Data from each year was first classified with hierarchical clustering (CLUSTER) using the Bray-Curtis group average linkage method (Bray and Curtis, 1957; Simboura et al., 1995) and then ordinated using a non-metric multidimensional scaling (MDS) plot (Kenny and Rees, 1994; Clarke and Warwick, 2001). Depth zones were used as replicates (n=3) per year (n=5 at CR1; n=4 at CR2). Sample labels corresponded to replicate transects per year. Variable labels corresponded to the epibenthic components categories (i.e., coral species, algal functional groups, cyanobacteria, sponges).

Significant differences between groups of years were tested using PRIMER's multivariate equivalent of an ANOVA called ANOSIM, which means "analysis of similarities" (Clarke and Green, 1988; Clarke, 1993; Clarke and Warwick, 2001). Both,

global and pairwise tests were carried out by means of ANOSIM. The global ANOSIM test was used to test the hypotheses that there were no significant differences in the structure of coral reef epibenthic communities between years, and between depth zones. A 2-way crossed ANOSIM test was used to test the hypothesis that there were no interaction effects between years and depth zones. A pairwise ANOSIM was used to test the hypothesis that there was no difference in the structure of coral reef epibenthic communities between different pairs of years, and between different pairs of depth zones. All of these tests were based on 5000 permutations and had no built in assumptions about the data distribution (Mcfield et al., 2001). They key taxa responsible for the differences between groups of sites were determined using PRIMER's SIMPER routine (Clarke, 1993; Clarke and Warwick, 2001).

Indicators of disturbance effects.

Several univariate measurements of diversity were used to document the effects of disturbance at the community level. The Caswell (1976) neutral model was used to compare the observed coral species diversity with an ecologically "neutral" community constructed by the model using the same number of species and individuals as the observed community. The neutral model assumes random birth (recruitment) and death, random immigrations and emigrations, and no interaction between species. The equitability component of the coral species diversity at each study site was compared with a theoretical expectation for diversity by calculating the Caswell's *V* statistic using the PRIMER ecological statistics software package (Clarke and Warwick, 2001) for univariate analysis. *V* statistic values >+2 or <-2 indicate significant departures from

neutrality. A value of zero for the *V* statistic indicate neutrality, positive values indicate greater diversity than predicted and negative values lower diversity (Clarke and Warwick, 2001). This test was used to test the hypothesis that there were no significant departures from neutrality in the observed coral species diversity between depth zones per year, and between years. Any significant departure would be considered an indicator of disturbance.

Additional measurements of coral species diversity were used to document the dynamics of the coral community and determine if there were any relationships between changing diversity and disturbance. These measurements included species richness (*S*) and colony abundance (*N*). The Margalef's species richness index (*d*) was used as a measure of the number of species present for a given number of individuals [$d = (S-1)/\log(N)$]. Also, we calculated the Pielou (1966a,b) coral species evenness (J'n), the Brillouin's diversity index [$H = N^{-1}\log_e\{N!/(N_1!N_2!\ldots N_s!)\}$] (Clarke and Warwick, 2001), the Fisher's α index (Fisher et al., 1943), the Shannon and Weaver (1948) species diversity index (H'n) calculated using the $\log_e$, and the Simpson (1949) evenness [$1-\lambda' = 1-\{\Sigma_i N_i(N_i-1)\}/\{N(N-1)\}$]. Draftman plots were produced for each year of sampling to correlate all different coral diversity measurements at CR1 and at CR2 using the PRIMER ecological statistics software package (Clarke and Warwick, 2001) and were included in the Appendix section. A correlation analysis was performed to each data set per year at each site to determine if there was any pattern of variation in diversity associated to disturbance.

Finally, a *K*-dominance curve (Lambshead et al., 1983) was constructed based on the % of cumulative dominance (abundance) of corals and species ranks to determine if there was any significant disturbance effect on the coral community. Any shift in the position of the *K*-dominance curve could be an indicator of stressful conditions (Warwick, 1986).

Results.

Ecological change at CR1.

Epibenthic community data summaries from years 1997 to 2002 have been summarized in Tables 1 to 4. There was a significant 32 to 40% decline in the mean coral species richness between years 1997 and 2002 at all depth zones (Figure 2), with a peak decline of 40% for the depth zone II. Annual species richness decline averaged 8% at this zone. The cumulative coral species richness also showed a major decline through time (Figure 3, Table 5). There was also a significant 32 to 58% decline in the mean abundance of coral colonies per transect (Figure 4). The sharpest decline in colony abundance was observed at depth zone I, with 58%, which averaged nearly a 12% annual decline. The cumulative abundance of corals also declined with the simultaneous decline in the cumulative species richness (Figure 5, Table 6). Differences observed in the above parameters were significant for both, the *year* and *depth* factors (Table 3). There has been a continuous trend of declining colony abundance of the dominant species, *Montastrea annularis*, as a result of partial colony mortality, followed by physiological fragmentation of parental colonies, and subsequent mortality of the surviving fragments (Figure 6). In addition, there has been a substantial loss of many rare and low-abundant coral species.

There were significant changes in the percentage cover of the major coral reef epibenthtic components at CR1 during the same period of time. Living coral cover declined significantly by a factor of 33 to 50% (Figure 6), an average annual decline of 7

TABLE 1. Summary of the coral community data at CR1 (1997-2002)*.

Parameters	97-I	97-II	97-III	98-I	98-II	98-III	99-I	99-II	99-III	01-I	01-II	01-III	02-I	02-II	02-III
Species richness	7.0 ±0.0	8.8 ±0.9	10.8 ±0.5	7.5 ±1.5	8.8 ±1.0	10.8 ±0.8	7.0 ±0.0	9.3 ±0.9	12.0 ±0.4	5.3 ±0.8	6.0 ±1.0	5.8 ±0.6	4.5 ±0.3	5.3 ±1.1	7.3 ±0.8
Colony abundance	38.0 ±8.0	27.5 ±3.2	39.0 ±2.5	42.0 ±10.0	34.8 ±2.7	42.8 ±5.3	41.0 ±10.0	32.8 ±1.0	44.8 ±1.5	22.8 ±1.5	19.3 ±2.2	29.5 ±1.7	16.0 ±1.3	18.8 ±2.9	26.0 ±2.9
% coral cover	49.8 ±17.5	75.5 ±7.4	59.7 ±3.7	51.2 ±17.4	64.7 ±5.9	57.7 ±7.5	43.9 ±14.1	53.1 ±3.6	49.9 ±4.1	37.9 ±4.3	42.4 ±2.2	38.1 ±2.1	33.3 ±4.4	37.9 ±2.6	35.2 ±5.5
% total algae	50.0 ±17.9	27.9 ±6.6	37.2 ±5.4	49.7 ±14.8	35.8 ±6.0	37.1 ±3.8	55.7 ±12.4	47.0 ±4.0	48.6 ±4.1	59.1 ±3.9	55.9 ±1.7	56.7 ±2.2	60.3 ±6.5	48.3 ±3.2	54.0 ±4.3
% macroalgae	5.5 ±1.9	2.2 ±1.7	7.8 ±1.4	4.5 ±2.2	7.9 ±1.3	14.3 ±4.3	5.4 ±2.8	5.9 ±2.5	20.0 ±2.1	15.6 ±2.6	18.9 ±1.6	20.3 ±5.0	24.5 ±6.0	14.4 ±3.3	31.8 ±7.7
% filamentous algae	37.4 ±23.4	24.0 ±7.2	27.7 ±4.1	40.4 ±19.9	23.8 ±3.0	22.2 ±4.9	41.6 ±18.7	34.1 ±6.3	26.7 ±4.7	38.8 ±6.2	26.2 ±2.2	34.1 ±3.8	29.3 ±2.4	27.5 ±2.4	17.1 ±4.8
% calcareous algae	N.D.	N.D.	N.D.	0.15 ±0.05	0.13 ±0.08	0.5 ±0.3	0.9 ±0.5	1.7 ±0.4	2.0 ±0.2	0.0 ±0.0	0.08 ±0.08	0.8 ±0.5	0.0 ±0.0	0.4 ±0.3	0.3 ±0.3
% *Halimeda*	3.7 ±2.1	0.5 ±0.3	1.5 ±1.0	2.9 ±1.7	0.3 ±0.1	0.6 ±0.6	5.0 ±1.4	3.2 ±1.1	0.4 ±0.4	0.5 ±0.3	1.7 ±0.5	1.8 ±0.1	0.3 ±0.2	0.4 ±0.2	0.2 ±0.2
% encrusting algae	5.5 ±1.8	4.4 ±3.7	1.2 ±0.7	2.4 ±0.3	6.4 ±3.2	1.9 ±0.9	4.9 ±1.3	4.4 ±1.2	4.3 ±0.8	4.2 ±2.0	9.6 ±2.4	1.3 ±0.2	6.3 ±1.9	5.7 ±2.1	3.2 ±2.1
% cyanobacteria	4.3 ±2.3	1.4 ±1.2	2.4 ±1.2	2.3 ±1.2	2.2 ±1.1	1.9 ±0.8	2.0 ±0.7	2.8 ±0.7	3.8 ±1.0	2.8 ±1.3	1.6 ±0.7	2.1 ±1.5	4.2 ±2.7	13.3 ±1.7	9.4 ±3.7
% sponges	0.2 ±0.2	0.4 ±0.3	0.9 ±0.3	0.5 ±0.5	0.8 ±0.4	2.2 ±0.5	0.7 ±0.5	1.3 ±0.5	1.5 ±0.6	0.4 ±0.2	0.6 ±0.2	3.6 ±0.8	0.4 ±0.2	0.8 ±0.4	0.8 ±0.2
H'n	1.4113 ±0.0852	1.6593 ±0.1130	1.7272 ±0.1139	1.3158 ±0.3203	1.6031 ±0.1491	1.6575 ±0.0690	1.2507 ±0.1614	1.5021 ±0.1040	1.8303 ±0.0646	1.0614 ±0.1611	1.2089 ±0.2502	1.0956 ±0.0902	1.0822 ±0.0548	1.0339 ±0.2017	1.3853 0.1105
J'n	0.7253 ±0.0438	0.7720 ±0.0251	0.7263 ±0.0349	0.6501 ±0.0945	0.7425 ±0.0360	0.6996 ±0.0167	0.6427 ±0.0829	0.6775 ±0.0177	0.7366 ±0.0192	0.6452 ±0.0425	0.6672 ±0.0832	0.6385 ±0.0098	0.7221 ±0.0131	0.6372 ±0.0627	0.7218 ±0.0336
H'c	0.6726 ±0.1526	0.7557 ±0.1094	1.0783 ±0.1887	0.6413 ±0.2536	0.8290 ±0.1976	1.1086 ±0.0528	0.7425 ±0.0797	0.8925 ±0.1685	1.3171 ±0.1395	0.4635 ±0.0801	0.5358 ±0.1463	0.7616 ±0.1588	0.4402 ±0.0765	0.4994 ±0.1492	0.7937 ±0.1220
J'c	0.1068 ±0.0179	0.1135 ±0.0173	0.1677 ±0.0294	0.1003 ±0.0342	0.1271 ±0.0305	0.1713 ±0.0087	0.1209 ±0.0064	0.1399 ±0.0269	0.2072 ±0.0234	0.0779 ±0.0128	0.0889 ±0.0245	0.1290 ±0.0276	0.0771 ±0.0141	0.0850 ±0.0257	0.1378 ±0.0221

*Mean±one standard error; N.D.= Not determined.

TABLE 2. Summary of the % of relative coral cover at CR1 (1997-2002).

Species	97-I	97-II	97-III	98-I	98-II	98-III	99-I	99-II	99-III	01-I	01-II	01-III	02-I	02-II	02-III
M.ann.	82.19	81.04	72.93	84.80	79.0.9	71.69	81.65	77.76	63.36	89.49	87.34	81.39	89.28	87.30	78.23
M.cav.	0	3.46	5.11	0	2.18	2.19	0	2.55	5.02	0	0.21	0	0	1.84	5.53
C.nat.	0	2.23	0.45	0	3.97	1.88	0	2.79	2.78	0	3.08	0	0	1.17	0
D.stri.	0	0	0	0	0.40	0.57	0	0.73	0	0	0	0	0	0.13	0
D.cli.	0	0.35	0.95	0	0.08	1.05	0	1.15	0.49	0	0.47	0	0	0.82	0
D.lab.	0	1.97	1.35	1.42	0	0.70	1.07	0	1.57	0.64	0.64	1.54	0.94	0.97	1.08
S.sid.	0	0.55	1.11	0	0.81	2.51	0	2.21	1.91	0	0.53	0.90	0	0	1.54
M.dec.	0	0	0	0	0	1.23	0	0	0	0	0	0	0	0	0
M.mea.	0	0	1.56	0	0	0	0	0	0	0	0	0	0	0	0
A.cer.	0	0	0.89	0	0	0	0	0	0	0.29	0	0	0.66	0	0.07
P.por.	0.93	0.54	2.14	2.96	1.99	1.65	2.88	2.90	3.05	3.53	0.33	4.24	3.39	0.18	1.17
P.ast.	9.80	4.18	2.16	5.91	4.15	4.41	7.03	3.79	4.10	2.95	4.46	1.03	2.67	5.74	5.26
A.aga.	3.47	1.77	2.11	2.71	1.75	1.44	3.91	0.54	5.07	1.50	0.89	2.93	1.71	0.96	2.03
A.hum.	0.14	0.22	1.43	1.93	0.64	0.27	0	0.22	0.32	0	0	0	0	0	0
A.frag.	0	0.12	0	0	0	0.26	0	0	0	0.61	0.11	0.34	0	0	0.77
A.lam.	0	0	1.44	0	0	0	0	0	0	0	0	0	0	0	0
L.cuc.	0	0.06	0.04	0.32	0	0.85	0	0	0.86	0	0	0	0	0	0
M.fer.	0	0.21	0	0	0.24	1.38	0	0.48	0.45	0	0.43	0.39	0	0	0.21
M.lam.	0	0	0	0	0	0.31	0	0	0	0	0	0	0	0	0
Myc. sp.	0	0	0	0	0.04	0	0	0	0	0	0	0	0	0	0
M.ali.	0.13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F.frag.	0.29	0	0	0.28	0	0.03	0	0	0.08	0	0	0	0	0	0
I.sin.	0	0.11	0	0	0	0	0	0.24	0.26	0	0	0	0	0	0
E.fas.	0	0	0.19	0	0	0.46	0	0.58	0.46	0	0	0	0	0	0
S.lac.	0	0.08	0	0.13	0	0	0.08	0.16	0.04	0	0	0	0	0	0
T.aur.	0	0	0.08	0	0	0	0	0	0	0	0	0	0	0	0
M.alc.	1.36	0.35	1.44	1.07	0.70	0.90	1.62	0.25	0.29	0.65	0.17	0.24	1.13	0	0.70
M.com.	0	0.17	0	0	0	0	0	0.12	0.62	0	0.33	0	0	0.29	0
M.squ.	0	0	0.10	0	0	0.15	0	0	0.11	0	0	0	0	0	0.21
E.car.	1.68	2.60	4.91	1.48	3.97	6.29	1.80	3.52	9.19	0.35	1.03	7.00	0.22	0.60	2.07

TABLE 3. Friedman 2-way ANOVA for the coral reef community data at CR1.

Parameter	Factor	D.F.*	Friedman Statistic	*P* value**
Species richness***	Year	4	10.18	0.0376 (S) *3,2,1,4,5*
	Depth	2	8.40	0.0150 (S) *3,2,1*
Colony abundance	Year	4	11.47	0.0218 (S) *2,3,1,4,5*
	Depth	2	8.40	0.0150 (S) *3,1,2*
% Coral cover	Year	4	11.47	0.0218 (S) *1,2,3,4,5*
	Depth	2	10.00	0.0067 (S) *1,3,2*
% Total algal cover	Year	4	10.93	0.0273 (S) *4,5,3,1,2*
	Depth	2	10.00	0.0067 (S) *1,3,2*
% Macroalgal cover	Year	4	9.33	0.0533 *5,4,3,2,1*
	Depth	2	7.60	0.0224 (S) *3,2,1*
% Filamentous algal cover	Year	4	4.53	0.3386 *3,4,1,2,5*
	Depth	2	7.60	0.0224 (S) *1,2,3*
% Erect calcareous algal cover	Year	3	5.90	0.1168 *3,2,4,5*
	Depth	2	4.50	0.1054 *3,2,1*
% Halimeda spp. cover	Year	4	6.58	0.1600 *3,1,2,4,5*
	Depth	2	3.60	0.1653 *1,2,3*
% Encrusting algal cover	Year	4	2.24	0.6922 *5,4,3,2,1*
	Depth	2	7.60	0.0224 (S) *1,2,3*
% Cyanobacterial cover	Year	4	5.07	0.2805 *5,1,3,4,2*
	Depth	2	0.40	0.8187 *1,3,2*
% Sponge cover	Year	4	6.71	0.1519 *3,2,4,5,1*
	Depth	2	8.40	0.0150 (S) *3,2,1*
Coral H'n	Year	4	9.87	0.0427 (S) *1,2,3,5,4*
	Depth	2	6.40	0.0408 (S) *3,2,1*
Coral J'n	Year	4	5.60	0.2311 *1,2,3,5,4*
	Depth	2	1.60	0.4993 *2,3,1*
Coral H'c	Year	4	10.93	0.0273 (S) *3,2,1,4,5*
	Depth	2	10.00	0.0067 (S) *3,2,1*
Coral J'c	Year	4	10.93	0.0273 (S) *3,2,1,4,5*
	Depth	2	10.00	0.0067 (S) *3,2,1*

*D.F.= Degrees of freedom.

**(S)= Significantly different. Numbers in *italics* at the factor *Year* represent mean ranks per year (1=1997; 2=1998; 3=1999; 4=2001; 5=2002) and at the factor *Depth* represent mean ranks per depth zone (1= < 4 m; 2= 4-8 m; 3= >8 m).

***Species richness and colony abundance were √x-transformed. Coral, total algal, macroalgal and filamentous algal, *Halimeda* spp., encrusting algal, cyanobacterial and sponge cover were Arcsin (√x)-transformed. Calcareous algal cover was Arcsin (√x+0.00075).

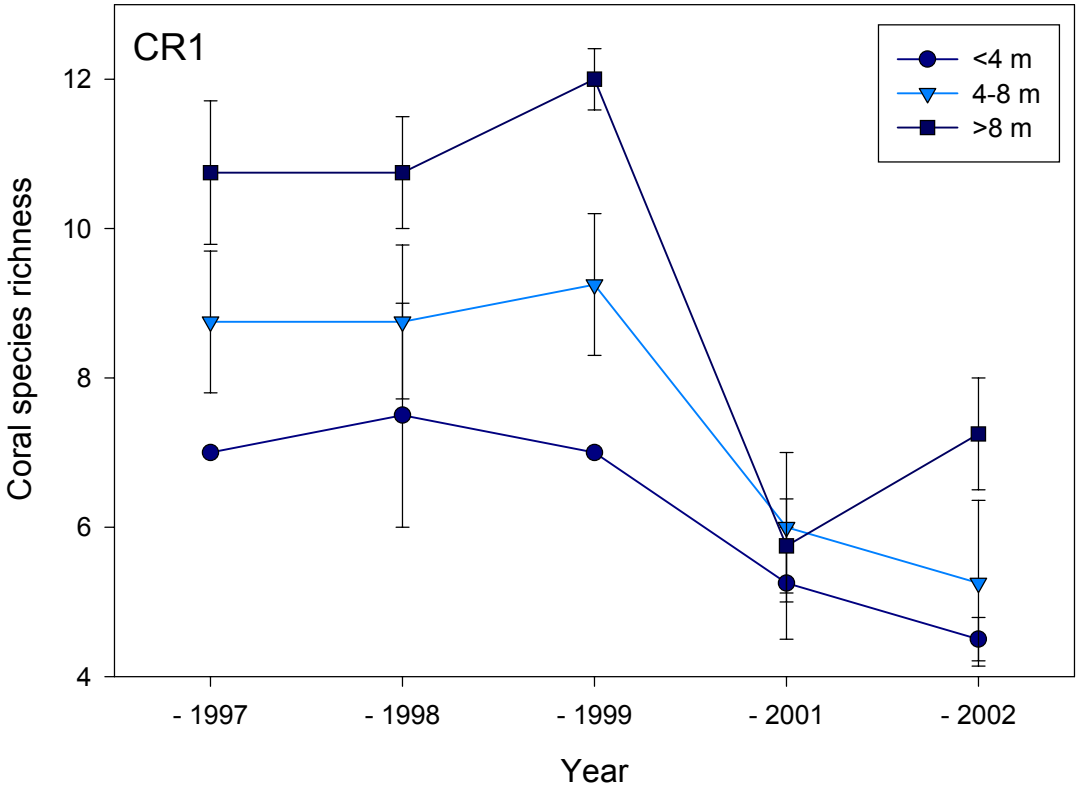
TABLE 4. Friedman 2-way ANOVA for the % of relative coral cover data at CR1.

Parameter	Factor	D.F.*	Friedman Statistic	*P* value**
Montastrea annularis	Year	4	11.47	0.0218 (S) *4,5,1,2,3*
	Depth	2	10.00	0.0067 (S) *1,3,2*
Montastrea cavernosa	Year	4	5.60	0.2311 *1,3,5,2,4*
	Depth	2	7.05	0.0743 *3,2,1*
Colpophyllia natans	Year	4	5.45	0.2454 *2,3,4,1,5*
	Depth	2	9.33	0.0094 (S) *2,3,1*
Diploria strigosa	Year	4	5.38	0.2505 *2,3,5,1,4*
	Depth	2	3.20	0.2019 *2,3,1*
Diploria clivosa	Year	4	1.33	0.8557 *3,1,2,5,4*
	Depth	2	5.78	0.0566 *2,3,1*
Diploria labyrinthiformis	Year	4	0.61	0.9619 *3,1,4,5,2*
	Depth	2	2.87	0.2415 *3,1,2*
Siderastrea siderea	Year	4	6.40	0.1712 *2,3,1,5,4*
	Depth	2	7.68	0.0214 (S) *3,2,1*
Madracis decactis	Year	4	4.00	0.4060 *2,1,3,4,5*
	Depth	2	2.00	0.3679 *3,1,2*
Meandrina meandrites	Year	4	4.00	0.4060 *1,2,3,4,5*
	Depth	2	2.00	0.3679 *3,1,2*
Acropora cervicornis	Year	4	4.50	0.3425 *5,1,4,2,3*
	Depth	2	2.60	0.2725 *1,3,2*
Porites porites	Year	4	3.47	0.4830 *4,3,2,1,5*
	Depth	2	2.80	0.2466 *3,2,1*
Porites astreoides	Year	4	1.33	0.8557 *5,1,2,3,4*
	Depth	2	1.60	0.4493 *1,2,3*
Agaricia agaricites	Year	4	2.93	0.5690 *1,3,2,4,5*
	Depth	2	4.80	0.0907 *1,3,2*
Agaricia humilis	Year	4	8.59	0.0721 *2,1,3,4,5*
	Depth	2	0.67	0.7165 *3,2,1*
Agaricia fragilis	Year	4	4.89	0.2989 *4,5,1,2,3*
	Depth	2	1.08	0.5836 *3,1,2*
Agaricia lamarcki	Year	4	4.00	0.4060 *1,2,3,4,5*
	Depth	2	2.00	0.3679 *3,1,2*
Leptoseris cucullata	Year	4	4.51	0.3410 *2,1,3,4,5*
	Depth	2	2.36	0.3067 *3,2,1*
***Mycetophyllia* sp.**	Year	4	4.00	0.4060 *2,1,3,4,5*
	Depth	2	2.00	0.3679 *2,1,3*

Mycetophyllia ferox	Year Depth	4 2	6.40 5.44	0.1712 0.0657	*3,2,4,1,5* *2,3,1*
Mycetophyllia lamarckiana	Year Depth	4 2	4.00 2.00	0.4060 0.3679	*2,1,3,4,5* *3,1,2*
Mycetophyllia aliciae	Year Depth	4 2	4.00 2.00	0.4060 0.3679	*1,2,3,4,5* *1,2,3*
Favia fragum	Year Depth	4 2	3.50 2.60	0.4779 0.2725	*2,1,3, 4,5* *1,3,2*
Isophyllia sinuosa	Year Depth	4 2	7.08 2.00	0.1319 0.3679	*3,1,2,4,5* *2,3,1*
Eusmilia fastigiata	Year Depth	4 2	6.76 8.40	0.1492 0.2019	*2,3,1,4,5* *3,2,1*
Scolymia lacera	Year Depth	4 2	7.24 2.60	0.1238 0.2725	*3,2,1,4,5* *2,1,3*
Tubastrea aurea	Year Depth	4 2	4.00 2.00	0.4060 0.3679	*1,2,3,4,5* *3,1,2*
Millepora alcicornis	Year Depth	4 2	6.67 8.40	0.1546 0.0150 (S)	*1,2,3,5,4* *1,3,2*
Millepora complanata	Year Depth	4 2	2.67 4.77	0.6151 0.0921	*4,3,5,1,2* *2,3,1*
Millepora squarrosa	Year Depth	4 2	4.00 8.00	0.4060 0.0183 (S)	*5,2,3,1,4* *3,1,2*
Erythropodium caribaeorum	Year Depth	4 2	8.80 10.00	0.0663 0.0067 (S)	*3,2,1,4,5* *3,2,1*

*D.F.= Degrees of freedom.

**(S)= Significantly different. Numbers in *italics* at the factor *Year* represent mean ranks per year (1=1997; 2=1998; 3=1999; 4=2001) and at the factor *Depth* represent mean ranks per depth zone (1= < 4 m; 2= 4-8 m; 3= >8 m). All proportions were Arcsin(√x)-transformed. If there were 0 values in the data matrix, then proportions were Arcsin(√x + *the lowest value of non-zero proportions*)-transformed.



Friedman 2-Way ANOVA
Year: d.f.= 4; Friedman statistic= 10.175; *p*=0.0376
Depth: d.f.= 2; Friedman statistic = 0.0150; *p*=0.0150

FIGURE 2. Change in coral species richness (mean±one standard error).

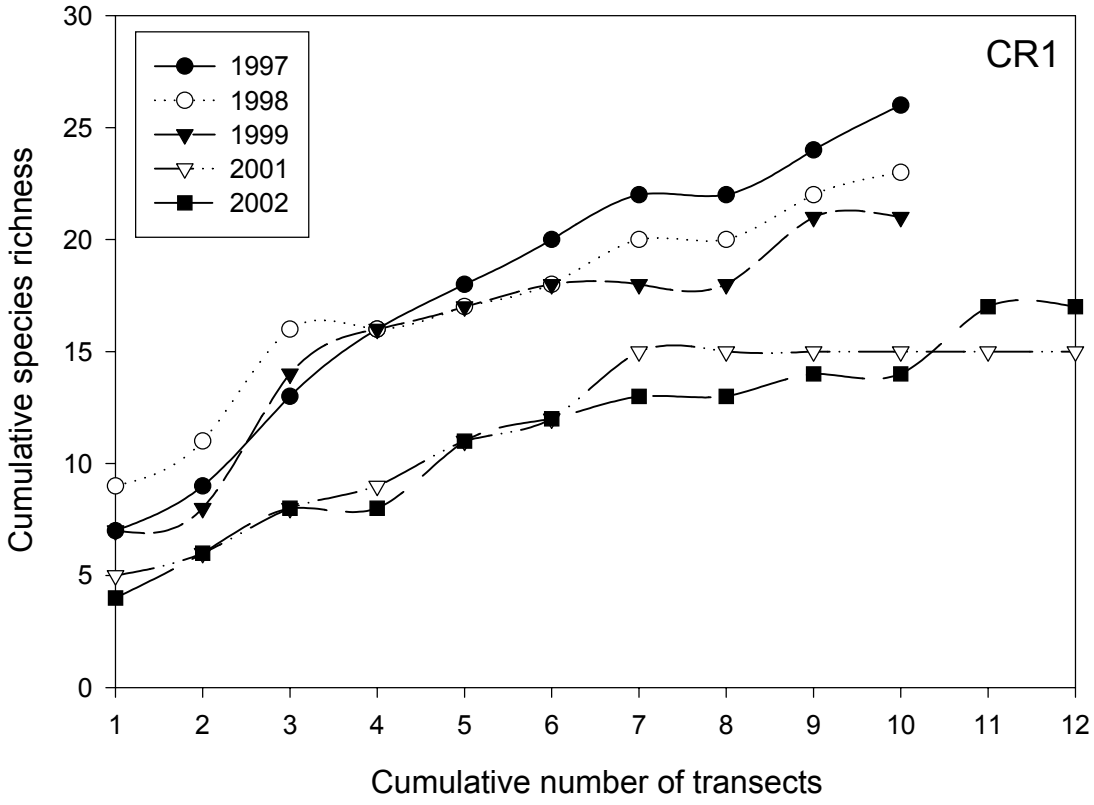
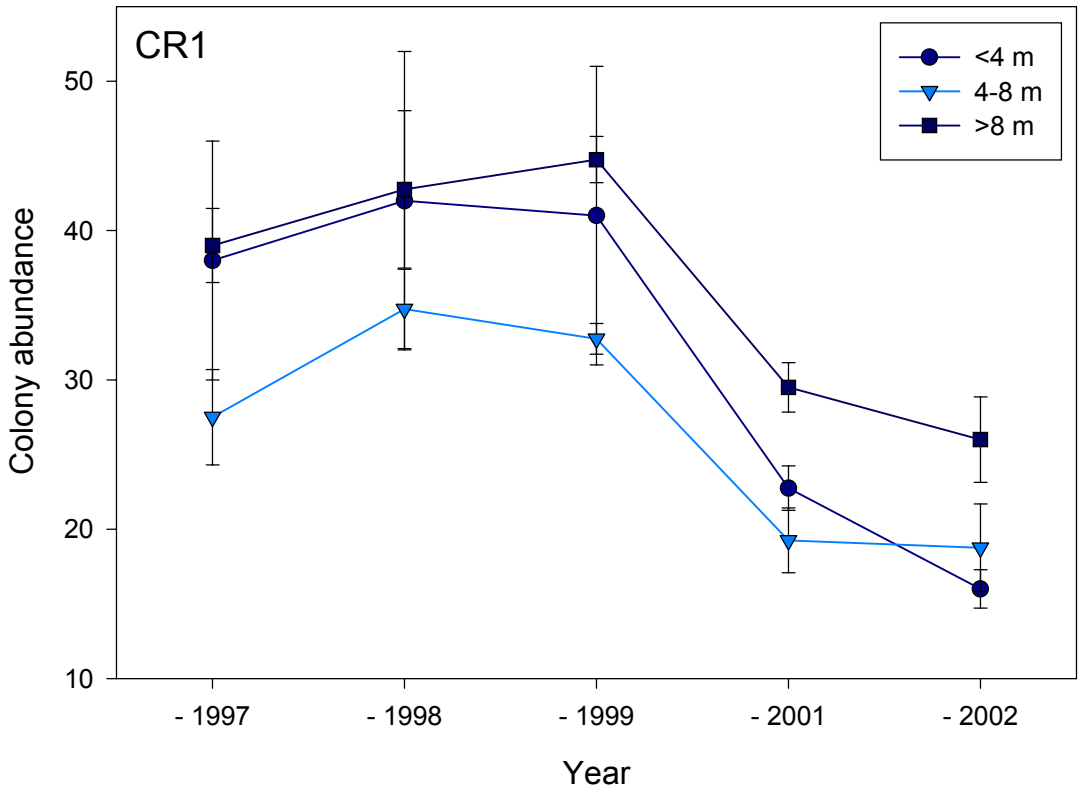


FIGURE 3. Change in coral cumulative species richness at CR1.

TABLE 5. Exponential regression analysis between the cumulative coral species richness and the cumulative number of replicate transects at CR1.

Year	Regression formula	r^2 value
1997	$y= 28.98(1-e^{-0.0199x})$	0.9844
1998	$y= 21.82(1-e^{-0.0371x})$	0.9104
1999	$y= 21.19(1-e^{-0.0318x})$	0.9453
2001	$y= 16.70(1-e^{-0.0232x})$	0.9489
2002	$y= 18.74(1-e^{-0.1675x})$	0.9568



Friedman 2-Way ANOVA
Year: d.f.= 4; Friedman Statistic= 11.467; *p*=0.0218
Depth: d.f.= 2; Friedman Statistic= 8.40; *p*=0.0150

FIGURE 4. Change in coral colony abundance at CR1 (mean±one standard error).

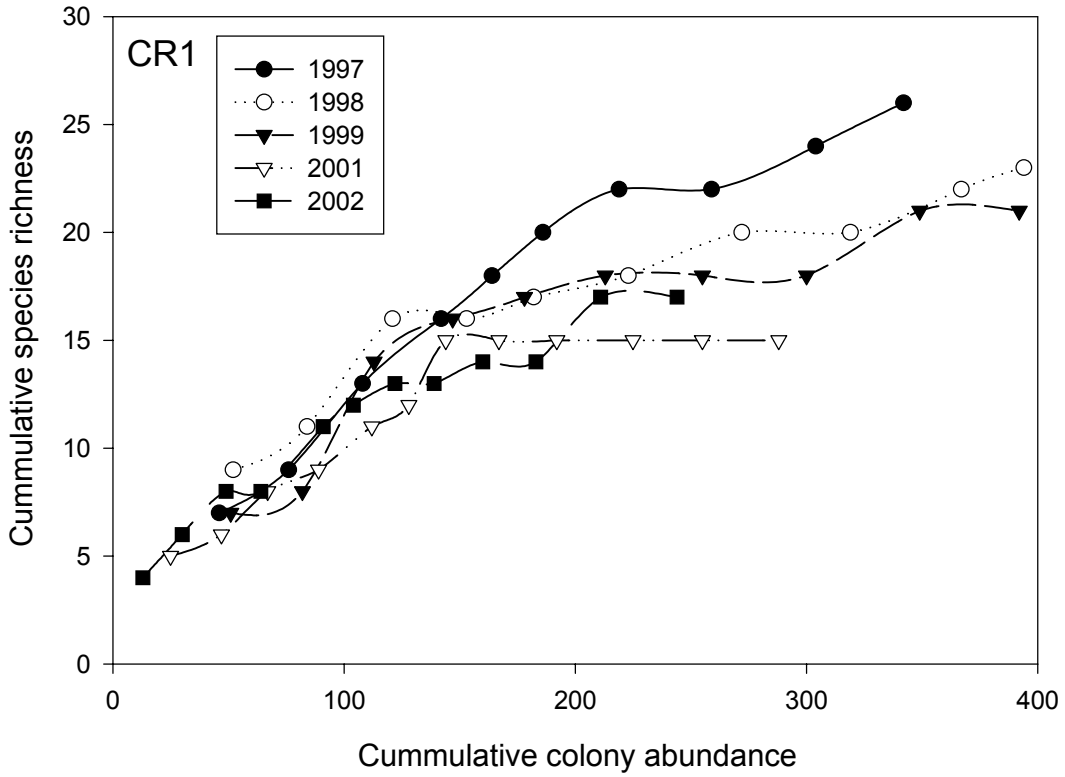


FIGURE 5. Relationship among the cumulative coral colony abundance and species richness

TABLE 6. Exponential regression analysis between the cumulative coral species richness and the cumulative colony abundance at CR1.

Year	Regression formula	r^2 value
1997	$y= 30.99(1-e^{-0.0052x})$	0.9881
1998	$y= 22.45(1-e^{-0.0085x})$	0.9536
1999	$y= 21.69(1-e^{-0.0079x})$	0.9404
2001	$y= 16.57(1-e^{-0.0108x})$	0.9381
2002	$y= 17.43(1-e^{-0.0112x})$	0.9512

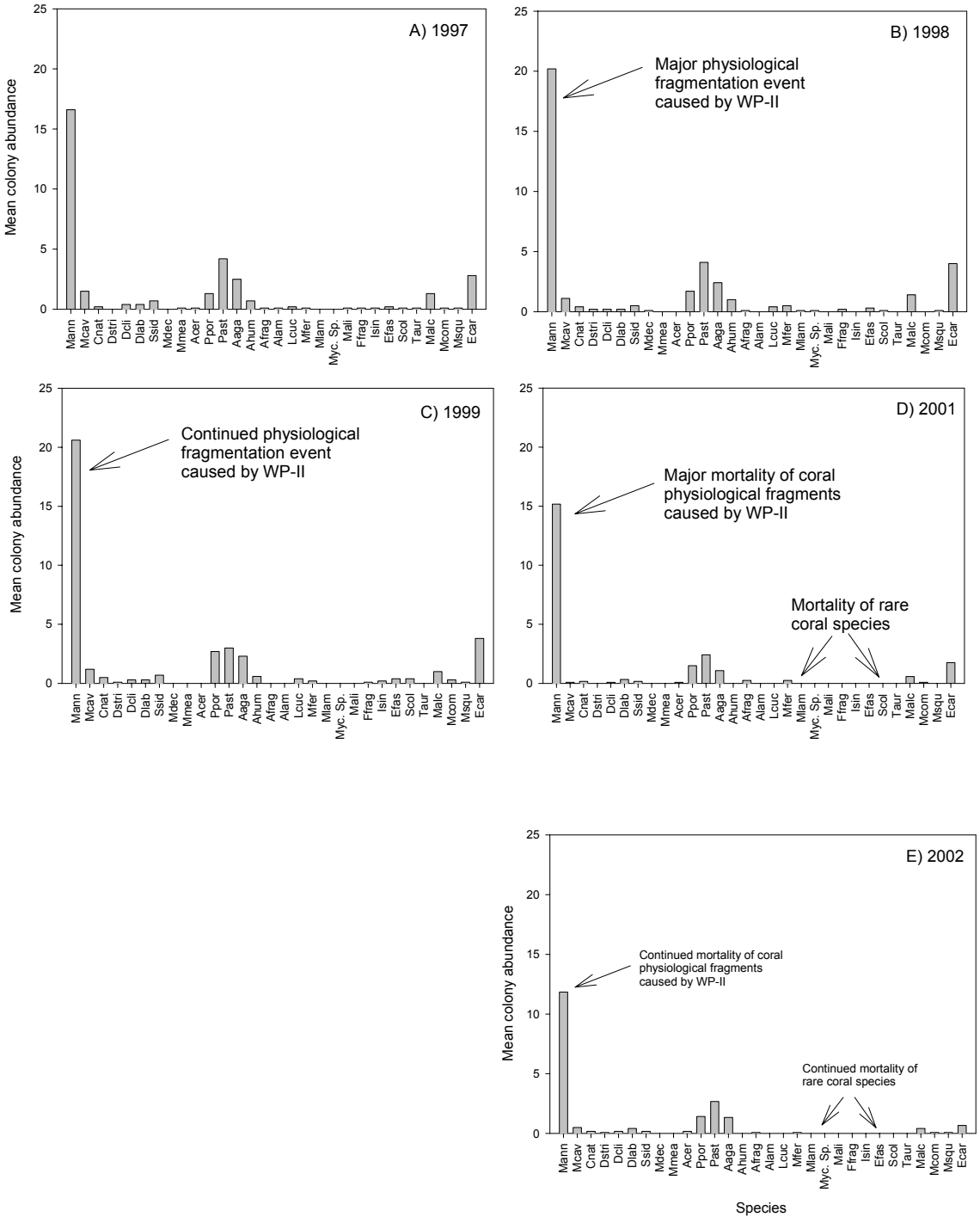


FIGURE 6. Dynamics of the mean colony abundance at CR1 (1997-2002).

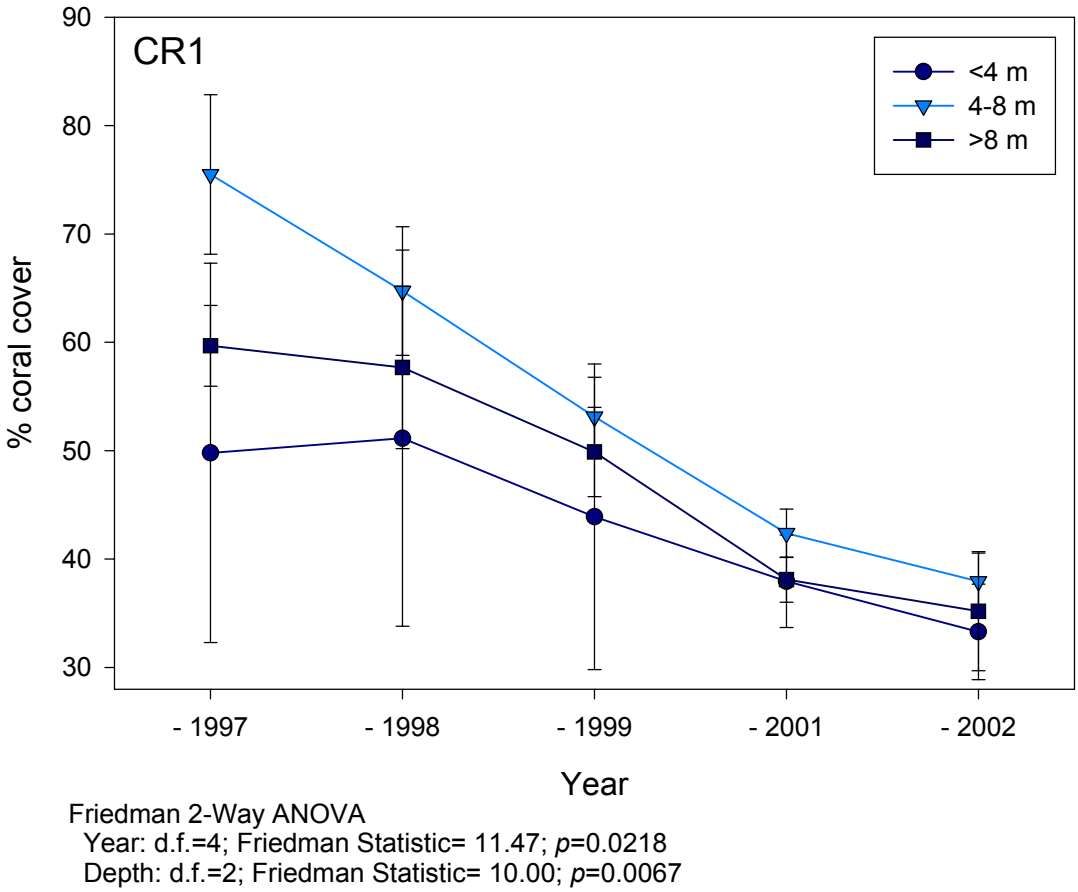


FIGURE 7. Change in the % of living coral cover at CR1 (mean±one standard error).

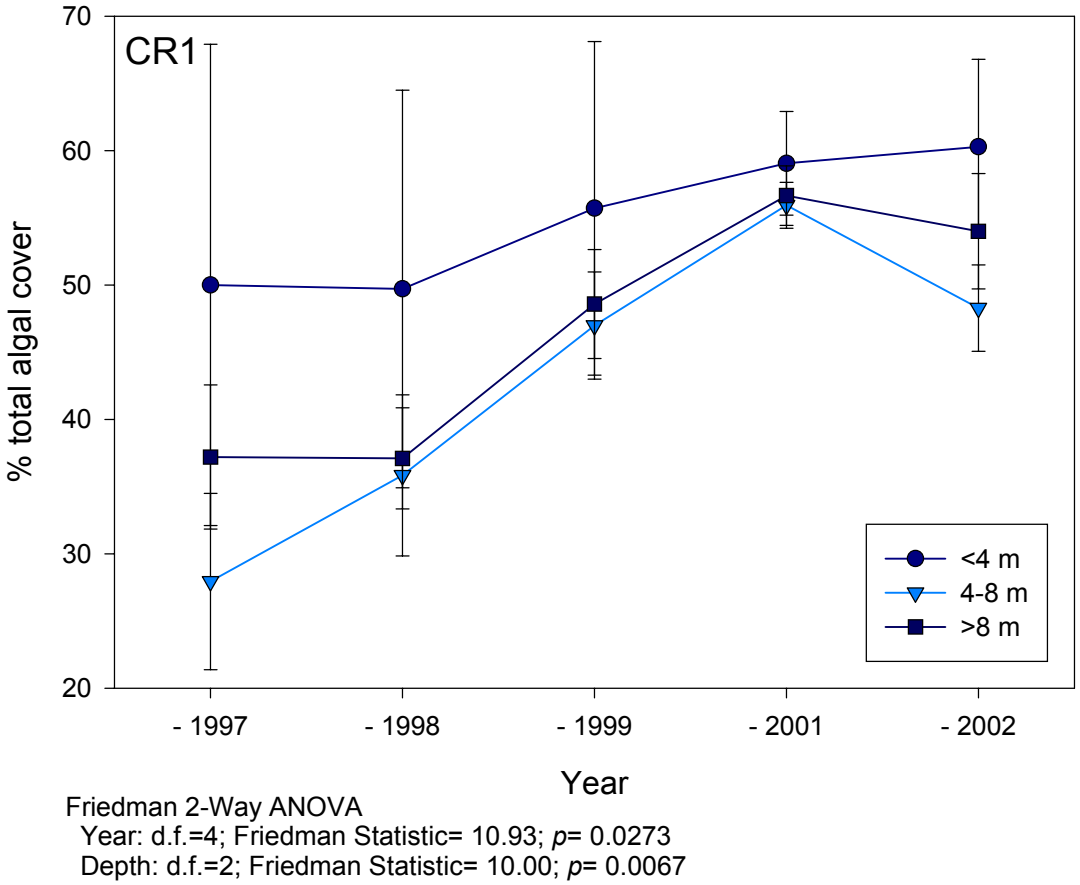


FIGURE 8. Change in the % of total algal cover at CR1 (mean±one standard error).

to 10%. Differences were significant at both, the *year* and *depth* factors (Table 3). But in contrast, total algal cover showed a highly significant 21 to 73% increase (Figure 8), with the highest increase documented at the depth zone II. Annual mean increase fluctuated between 4 and 15%. Among the different algal functional groups, macroalgae showed the highest increase in cover, with 308 to 555%, with a mean annual increase of 62 to 111% (Figure 9). Macroalgal cover was significantly higher on deeper habitats (Tables 1 and 3). However, filamentous algal cover was significantly higher in shallower habitats (Figure 10), but fluctuations were no different in time (Table 3). Cover values of other minor algal groups, such as erect calcareous algae, *Halimeda* spp., and encrusting algae (Tables 1 and 3) showed non-significant fluctuations in time and depth, with the exception of the encrusting algal cover that was significantly higher at shallower depths.

Cyanobacterial cover showed a minor fluctuation during the initial four years of the long-term study (Figure 11). However, although there was no difference in the shallower depth zone, there was a major increase in the % of cyanobacterial cover, which reached a 292% increase in depth zone III, and rocketed also by a factor of 850% at depth zone III. Large variation due to the patchy nature of cyanobacterial distribution, however, caused this increase to be statistically non-significant (Table 3). Although sponge cover increased by a factor of 100% at both, depth zone I and II, this fluctuation was not significant in time. However, sponge cover was significantly higher at deeper zones (Tables 1 and 3).

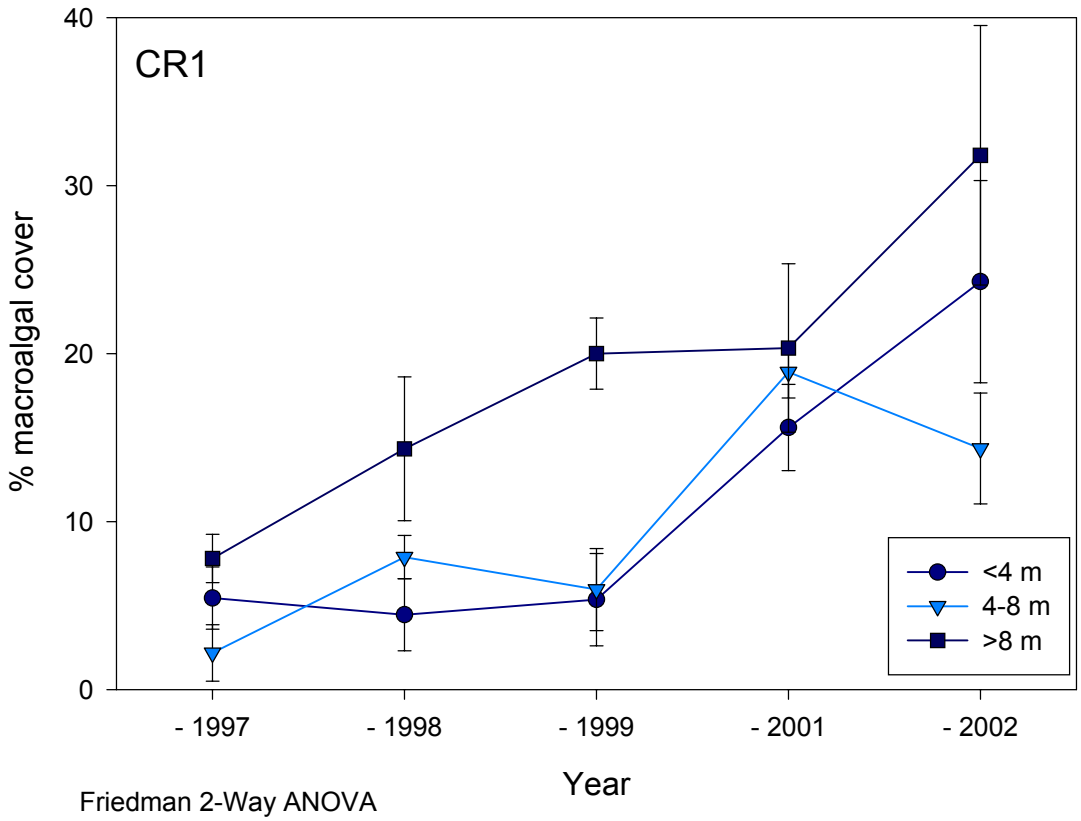


FIGURE 9. Change in the % of macroalgal cover at CR1 (mean±one standard error).

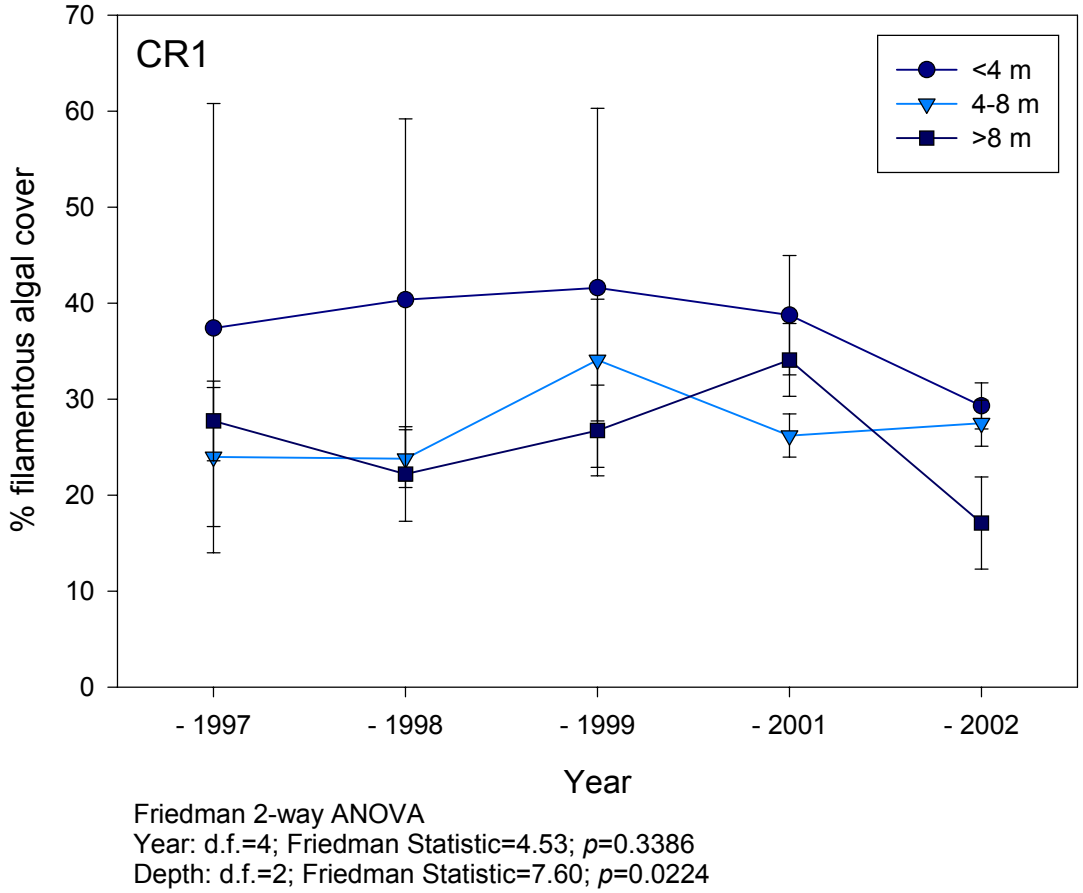


FIGURE 10. Change in the % of filamentous algal cover at CR1 (mean±one standard error).

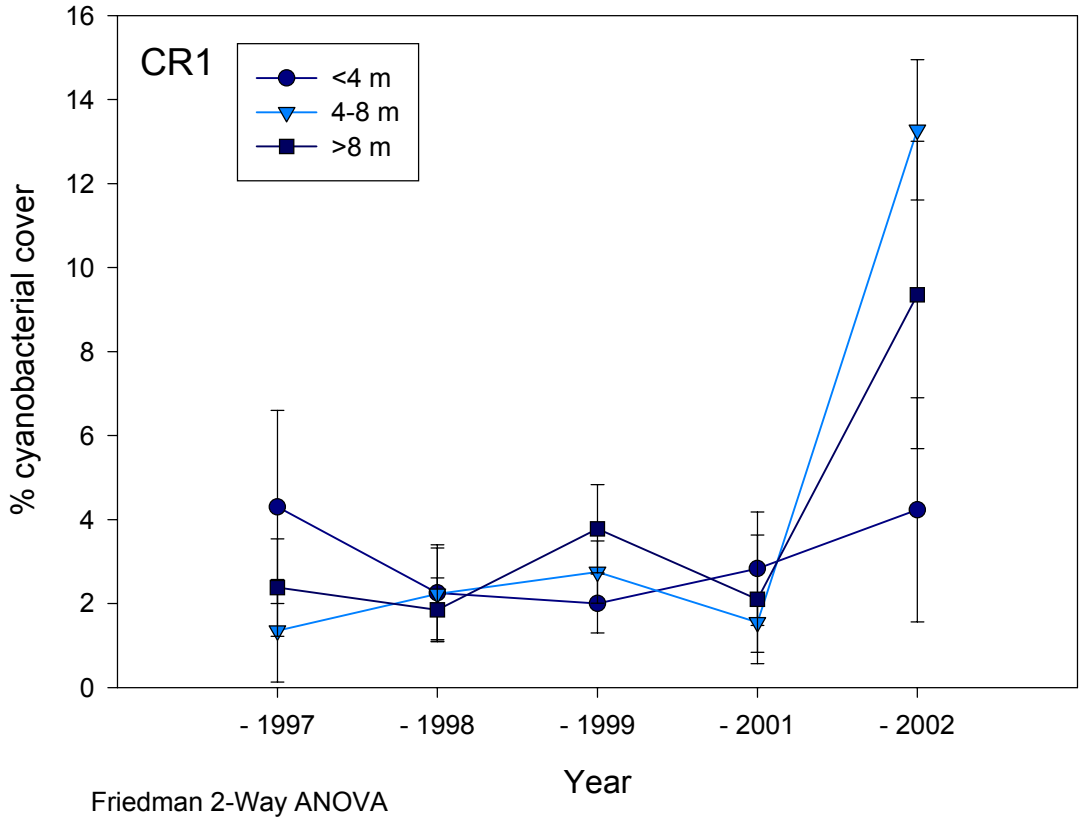


FIGURE 11. Change in the % of cyanobacterial cover at CR1 (mean±one standard error).

A total of 30 coral species have been identified from the permanent transects through the study (Table 2). *Montastrea annularis* was the dominant reef-building coral species at CR1 through the study. It showed a consistently significant increase in the mean relative cover (Table 4). Although many rare coral species have disappeared during the study (Figure 6), these differences were not significant (Table 4), mostly as a result of the large variation in the data, which is normal for rare species. During 1997, the top three dominant species per depth zone were: I= *M. annularis* (82%), *Porites astreoides* (10%), and *Agaricia agaricites* (3%); II= *M. annularis* (81%), *P. astreoides* (4%), and *M. cavernosa* (3%); and III= *M. annularis* (73%), *M. cavernosa* and *Erythropodium caribbaeorum* (5%). During 1998, the top three dominant species per depth zone were: I= *M. annularis* (85%), *P. astreoides* (6%), and *P. porites* (3%); II= *M. annularis* (79%), *P. astreoides*, *Colpophyllia natans* and *E. caribbaeorum* (4%); and III= *M. annularis* (72%), *E. caribbaeorum* (6%), and *P. astreoides* (4%). At 1999, dominant species were: I= *M. annularis* (82%), followed by *P. astreoides* (7%), and *A. agaricites* 4%); II= *M. annularis* (78%), *P. astreoides* (4%), and *E. caribbaeorum* (3%); and III= *M. annularis* (63%), followed by *E. caribbaeorum* (9%), and . *A. agaricites* and *M. cavernosa* (5%). During year 2001, the dominant coral species were: I= *M. annularis* (89%), followed by *P. porites* (4%), and *P. astreoides* (3%); II= *M. annularis* (87%), *P. astreoides* (4%), and *C. natans* (3%); and III= *M. annularis* (81%), *E. caribbaeorum* (7%), and *P. porites* (4%). Finally, during year 2002, dominant species included: I. *M. annularis* (89%), *P. porites* (3%), and *P. astreoides* (2%); II= *M. annularis* (87%), *P.*

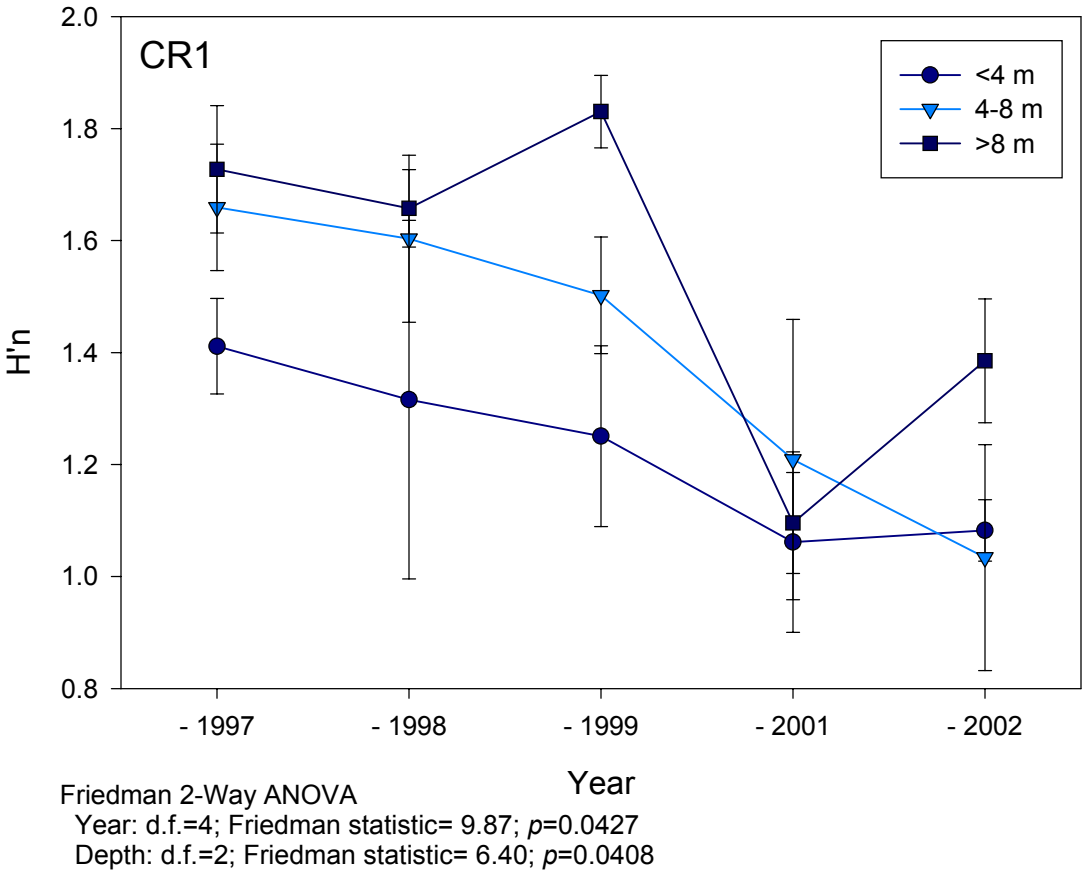


FIGURE 12. Change in the coral species diversity index at CR1 (mean±one standard error).

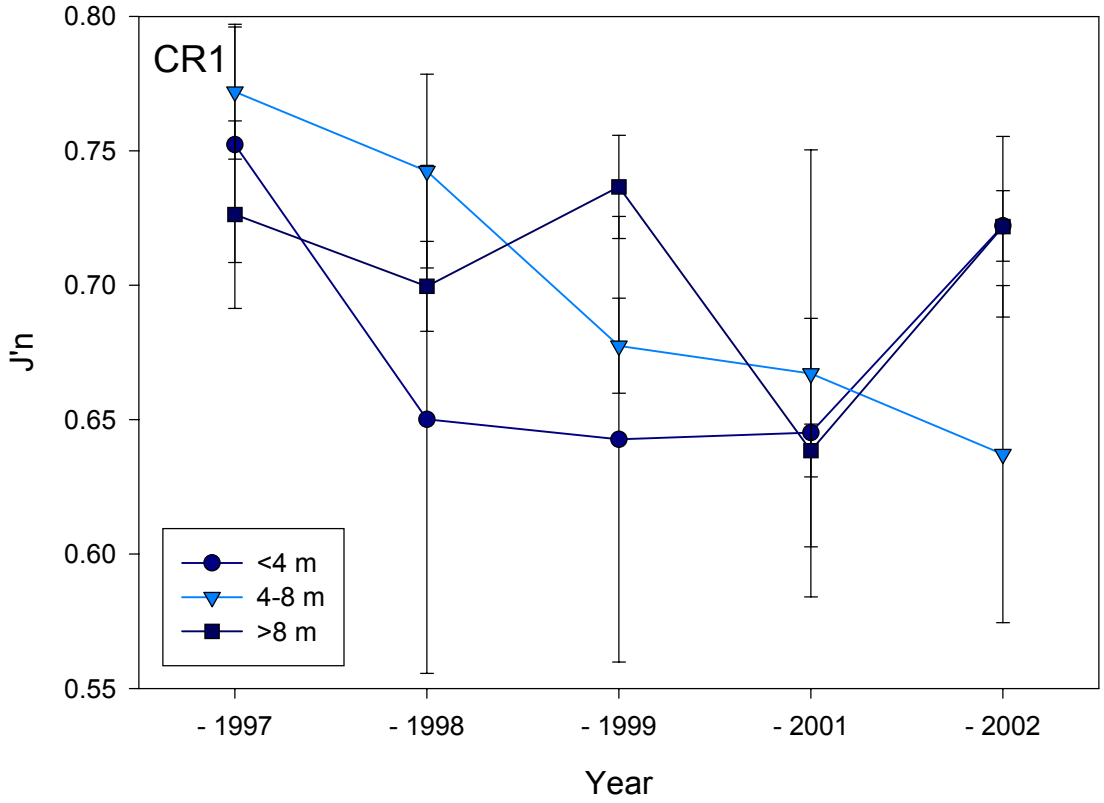


FIGURE 13. Change in the coral species evenness at CR1 (mean±one standard error).

astreoides (6%), and *Montastrea cavernosa* (2%); and III= *M. annularis* (78%), followed by *M. cavernosa* (6%), and *Porites astreoides* (5%).

The coral species diversity index (H'n) showed a significant decline (Figure 12), which had a magnitude of 20 to 38% of the original value at the beginning of the study (Table 1). However, coral species evenness (J'n) showed minor non-significant fluctuations (Figure 13). But, both, H'c and J'c showed significant fluctuations during the study (Tables 1 and 3).

A quadratic regression analysis was carried out at each depth zone between the % of total algal cover and three coral parameters, including species richness, colony abundance, % of coral cover and H'n (Table 7). In general, there was a moderate to strong negative relationship between the % of total algal cover and species richness, with r^2 values ranging from 0.4573 to 0.9748. There was a similarly moderate to strong negative relationship between the % of total algal cover and coral colony abundance, with r^2 values fluctuating between 0.5434 and 0.9728. Algal cover also showed a consistently strong negative relationship with the % of coral cover, with r^2 values of 0.8849 to 0.9728. Also, it showed a moderate to strong negative relationship with coral H'n, with r^2 values ranging from 0.6187 to 0.9931. These results suggest that algal growth during the last five years could explain most of the coral declines observed so far at CR1. This was more evident at depth zones I and III, but not at II.

TABLE 7. Summary of the quadratic regression analysis results between the % of total algal cover and several coral parameters.

Parameters	Depth zone	Equation	r^2
% Algal cover vs Species richness	I	$y= -118.8+4.841x+(-463.9)x^2$	0.9748
	II	$y= 5.027+0.2588x+(-0.0004)x^2$	0.4573
	III	$y= -71.43+3.848x+(-0.044)x^2$	0.9674
% Algal cover vs Colony abundance	I	$y= -1408+55.06x+(-0.5216)x^2$	0.9728
	II	$y= -22.85+2.976x+(-0.0403)x^2$	0.5434
	III	$y= -145.9+8.849x+(-0.1027)x^2$	0.7323
% Algal cover vs % Coral cover	I	$y= -210.8+10.89x+(-0.1134)x^2$	0.9919
	II	$y= -153.8-3.498x+(0.0264)x^2$	0.8849
	III	$y= 44.99+1.404x+(-0.0278)x^2$	0.9275
% Algal cover vs Coral H'n	I	$y= -2.640+0.1715x+(-0.0018)x^2$	0.9090
	II	$y= 2.277-0.0218x+(0.00003)x^2$	0.6187
	III	$y= -8.235+0.4629x+(-0.0053)x^2$	0.9931

Multivariate analysis of coral reef communities at CR1.

A hierarchical cluster analysis was carried out based on a Bray-Curtis dissimilarity matrix on the proportion of major epibenthic components to characterize the structure of the coral reef communities through time (Figure 14). In addition to the relative proportion of coral species, we included the relative proportion of algal functional groups, cyanobacteria and sponges. This approach is more representative of the coral reef community (Mcfield et al., 2001). Dissimilarity through the study averaged 27%. However, this classification of sites based on broad categorical data did not clearly differentiate sites by time, particularly during the first three years of the study. Temporal-based clusters were more clearly distinguished in the MDS ordination (Figure 15). The global 2-way crossed ANOSIM test (Table 8) revealed a highly significant difference (0.6%) of the coral reef community structure between years, but no difference between depth zones (28.2%). However, the interaction of years x depth was highly significant (0.5%). The pairwise ANOSIM test (Table 9) revealed highly significant differences in the coral reef community structure at CR1 between years 1997 and 2001 (0.4%), 2001 and 2002 (0.2%), 1999 and 2001 (1.4%), and between 1999 and 2002 (0.3%). Difference between years 1998 and 2001, and between 2001 and 2002 was marginally significant (5.5%, respectively). A pairwaise ANOSIM test between depth zones (Table 10) revealed no significant differences. The results of the SIMPER analysis comparing change from year 1997 to the subsequent years until 2002 (Table 11) revealed that change in the proportion of macroalgae was the most significant factor influencing the observed differences in the structure of coral reef epibenthic communities at CR1.

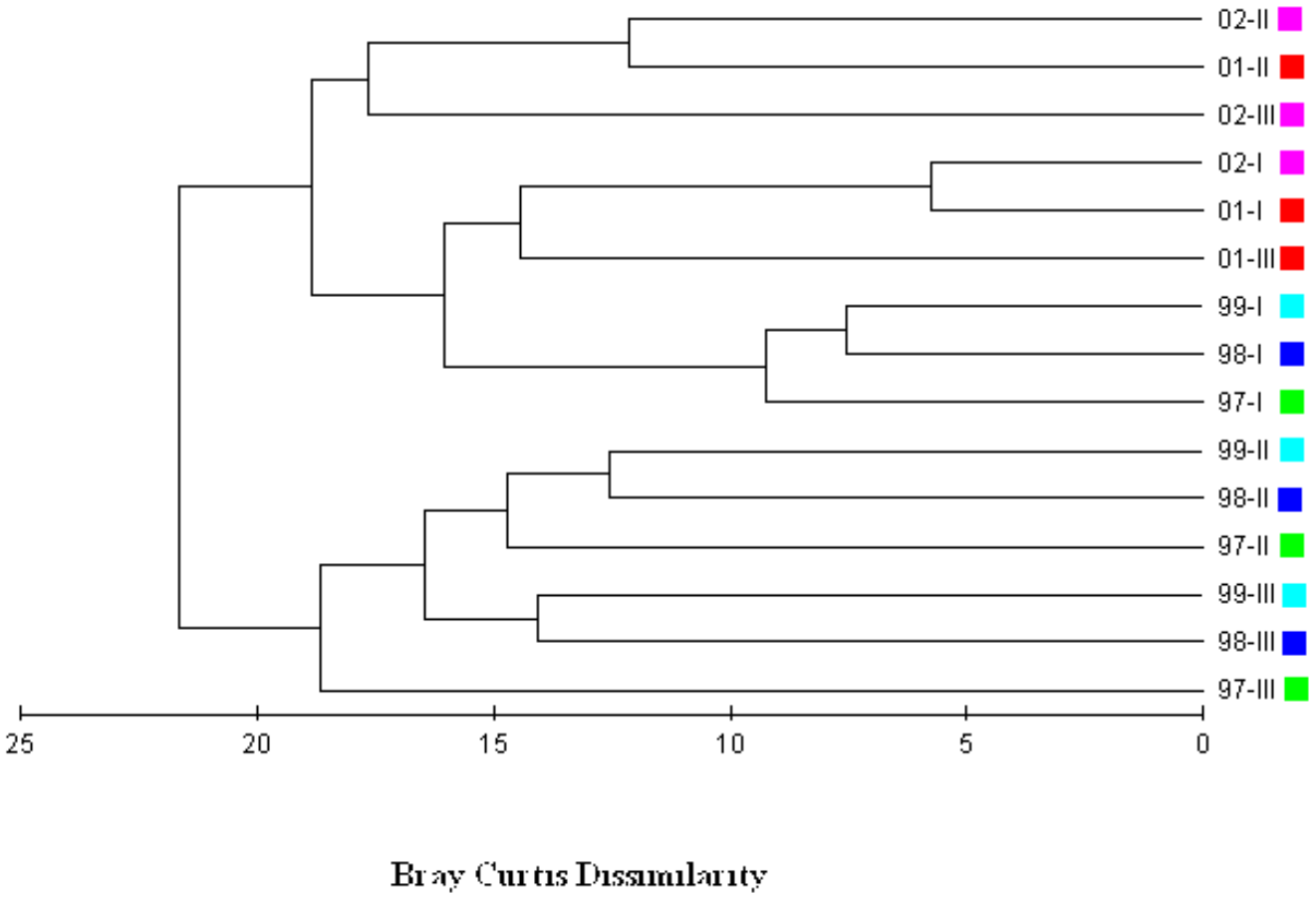


FIGURE 14. Bray-Curtis dissimilarity classification of years (with depth zones as replicates) based on the proportion of coral reef epibenthic categories at CR1.

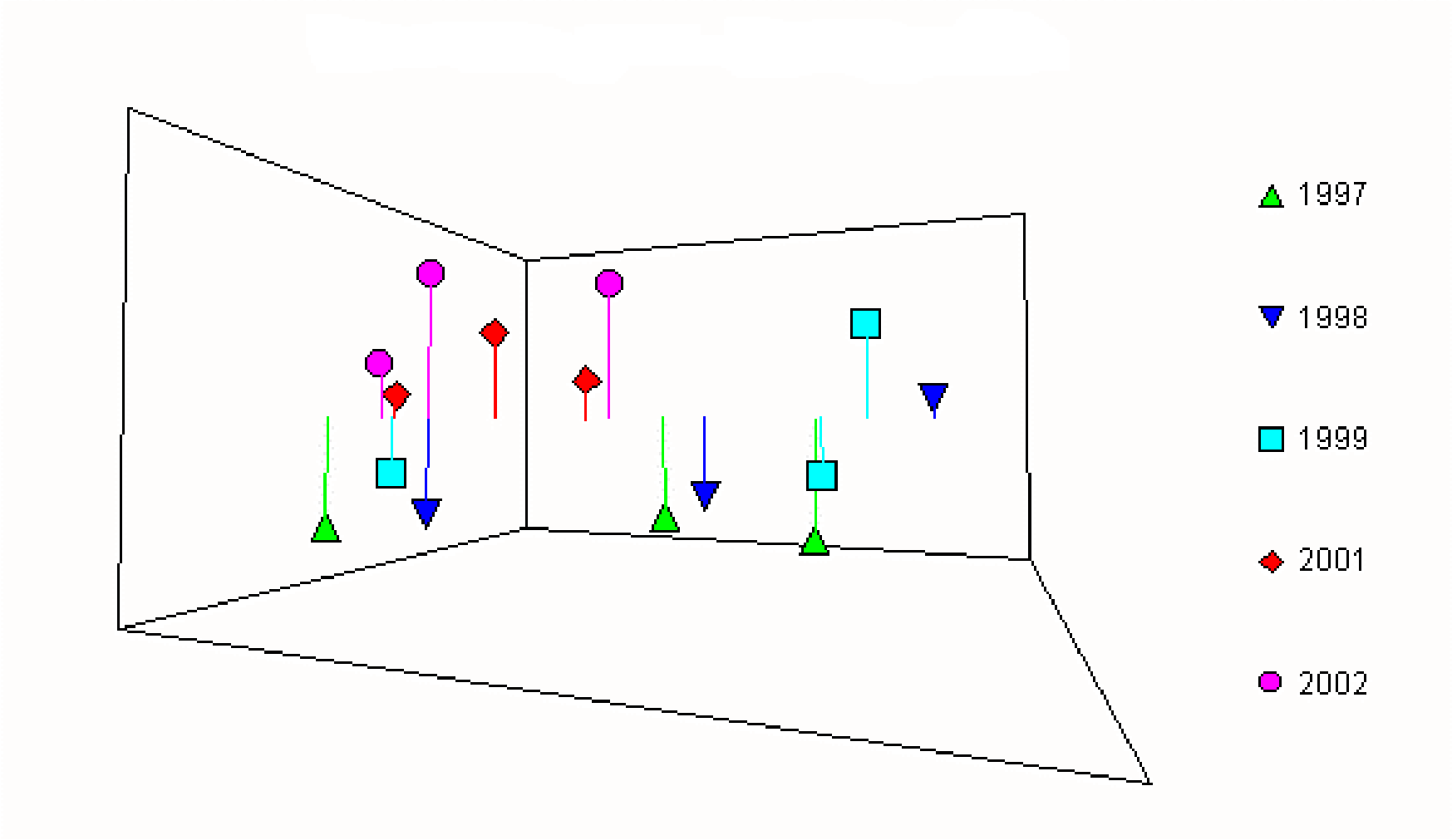


FIGURE 15. MDS-ordination plot of years (with depth zones as replicates) based on the proportion of coral reef epibenthic categories at CR1. Stress level = 0.08.

TABLE 8. Results of the 2-way crossed ANOSIM test* for significant differences of the structure of coral reef epibenthic communities at CR1.

Compared factors	Global R value	Significance level
Year	0.158	**0.6%**
Depth	0.040	28.2%
Year x Depth	0.289	**0.5%**

*Square-root transformed data. Based on 5,000 permutations.

TABLE 9. Results of the pairwise ANOSIM significance test* between years at CR1.

Years compared	Global R value	Significance level
1997 vs 1998	-0.910	77.7%
1997 vs 1999	0.148	13.7%
1997 vs 2001	0.343	**0.4%**
1997 vs 2002	0.347	**0.2%**
1998 vs 1999	-0.180	54.1%
1998 vs 2001	0.193	**5.5%**
1998 vs 2002	0.206	**5.5%**
1999 vs 2001	0.306	**1.4%**
1999 vs 2002	0.363	**0.3%**
2001 vs 2002	-0.104	84.2%

*Square-root transformed data. Based on 5,000 permutations.

TABLE 10. Results of the pairwise ANOSIM significance test* between depth zones at CR1.

Depth zones compared**	Global R value	Significance level
I vs II	-0.027	56.6%
I vs III	0.057	29.0%
II vs III	0.096	14.3%

*Square-root transformed data. Based on 5,000 permutations.
**I= <4 m; II= 4-8 m; III= >8 m.

Filamentous algae, total algae and cyanobacteria were also important factors. A similar analysis carried out to data from years 1998 and 1999 (Table 12a) showed that filamentous algae were the most significant epibenthic component affecting the coral reef community variation between both years. But, the encrusting gorgonian, *Erythropodium caribbaeorum* (Table 12b) caused the most significant variation in the coral reef community between years 1998 and 2001. Finally, for the period of 1998 to 2002, macroalgae cause the most significant variation in the coral reef community structure (Table 12c). *Erythropodium caribbaeorum* caused the most significant variation in community structure for the periods of 1999 to 2001 (Table 13a) and 1999 to 2002 (Table 13b). Cyanobacteria caused the most significant variation for the period of 2001 to 2002 (Table 14). This analysis showed that coral reef communities are highly dynamic and change in community structure can result from shifts in the dynamics of different coral reef epibenthic components.

TABLE 11a. Results of the SIMPER analysis of years 1997 vs 1998 at CR1.

Group	Species/category	Percentage	Abundance	Abundance
1997 vs 1998	Macroalgae	6.56	0.05	0.10
(28.41%)	Filamentous algae	6.53	0.28	0.26
	Encrusting algae	6.08	0.03	0.04
	Montastrea cavernosa	5.87	0.03	0.02
	Total algae	5.76	0.36	0.39

TABLE 11b. Results of the SIMPER analysis of years 1997 vs 1999 at CR1.

Group (% dissimilarity)		Percentage contribution	1997	1999
1997 vs 1999	Macroalgae	7.22	0.05	0.11
(28.63%)	Filamentous algae	6.45	0.28	0.33
	Total algae	6.35	0.36	0.49
	Montastrea cavernosa	5.95	0.03	0.03
	Encrusting algae	5.53	0.03	0.04

TABLE 11c. Results of the SIMPER analysis of years 1997 vs 2001 at CR1.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1997	Abundance 2001
1997 vs 2001	Macroalgae	10.49	0.05	0.18
(28.98%)	Total algae	8.50	0.36	0.57
	Encrusting algae	6.60	0.03	0.05
	Erythropodium caribbaeorum	6.50	0.03	0.03
	Filamentous algae	6.43	0.28	0.33

TABLE 11d. Results of the SIMPER analysis of years 1997 vs 2002 at CR1.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1997	Abundance 2002
1997 vs 2002	Macroalgae	12.16	0.05	0.24
(30.03%)	Cyanobacteria	8.05	0.02	0.09
	Total algae	7.54	0.36	0.54
	Encrusting algae	6.28	0.03	0.05
	Montastrea cavernosa	6.22	0.03	0.02

TABLE 12a. Results of the SIMPER analysis of years 1998 vs 1999 at CR1.

Group (% dissimilarity)	**Species/category**	**Percentage contribution**	**Abundance 1998**	**Abundance 1999**
1998 vs 1999	Filamentous algae	6.30	0.26	0.33
(25.88%)	Macroalgae	5.98	0.10	0.11
	Montastrea cavernosa	5.54	0.02	0.03
	Colpophyllia natans	5.48	0.02	0.02
	Erythropodium caribbaeorum	5.47	0.04	0.05

TABLE 12b. Results of the SIMPER analysis of years 1998 vs 2001 at CR1.

Group (	**Species/category**	**contribution**	**Abundance**	**Abundance**
1998 vs 2001	*Erythropodium caribbaeorum*	7.60	0.04	0.03
(26.67%)	Total algae	7.08	0.39	0.57
	Macroalgae	7.04	0.10	0.18
	Porites astreoides	6.18	0.05	0.03
	Filamentous algae	6.08	0.26	0.33

TABLE 12c. Results of the SIMPER analysis of years 1998 vs 2002 at CR1.

Group (%)	**Species/category**	**Percentage contribution**	**Abundance**	**Abundance**
1998 vs 2002	Macroalgae	8.83	0.10	0.24
(28.02%)	Cyanobacteria	7.32	0.02	0.09
	Erythropodium caribbaeorum	6.77	0.04	0.01
	Total algae	6.10	0.39	0.54
	Porites astreoides	5.97	0.05	0.05

TABLE 13a. Results of the SIMPER analysis of years 1999 vs 2001 at CR1.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1999	Abundance 2001
1999 vs 2001	*Erythropodium caribbaeorum*	8.23	0.05	0.03
(24.94%)	Macroalgae	7.02	0.11	0.18
	Filamentous algae	5.55	0.33	0.33
	Porites astreoides	5.30	0.05	0.03
	Agaricia agaricites	5.12	0.03	0.02

TABLE 13b. Results of the SIMPER analysis of years 1999 vs 2002 at CR1.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1999	Abundance 2002
1999 vs 2002	Macroalgae	8.56	0.11	0.24
(26.64%)	*Erythropodium caribbaeorum*	7.30	0.05	0.01
	Cyanobacteria	6.19	0.03	0.09
	Montastrea cavernosa	5.98	0.03	0.02
	Filamentous algae	5.71	0.33	0.25

TABLE 14. Results of the SIMPER analysis of years 2001 vs 2002 at CR1.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 2001	Abundance 2002
2001 vs 2002	Cyanobacteria	10.53	0.02	0.09
(21.69%)	Macroalgae	7.38	0.18	0.24
	Porites astreoides	7.32	0.03	0.05
	Filamentous algae	6.62	0.33	0.25
	Porites porites	6.61	0.03	0.02

Indicators of disturbance effects at CR1.

The equitability component of the coral species diversity at CR1 was compared with a theoretical expectation for diversity by calculating the Caswell's *V* statistic for each depth zone and each year (Table 15). *V* statistic values were consistently negative and significantly distant from neutrality at all depth zones and all years, with the exception of depth zone I during 1997 and 2002. These observations suggest that CR1 showed a coral diversity below the neutral model predictions and that some kind of stressful disturbance has caused a significant decline in diversity at all depth zones and at all years during the 5-year long study. These results are consistent with the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979).

The Pearson correlation matrix for CR1 is summarized at Table 16. The correlation between species richness (*S*) and abundance (*N*) was fairly poor for years 1997 to 2001, but increased to 0.938 in year 2002. Initially, there were a few species with a high number of colonies and many colonies with a low abundance, a condition which caused a lack of correlation between both parameters. However, there was a significant decline in the abundance of colonies of dominant coral species, mostly, *Montastrea annularis* (Figure 6), as a result of recurrent White Plague outbreaks and algal overgrowth. Also, there was a simultaneous disappearance of rare coral species. This shift in the community structure of coral reefs at CR1 caused an increase in the correlation pattern between *S* and *N*.

TABLE 15. Summary of the Caswell's neutral model *V* statistics for CR1.

Year	Depth zone I	Depth zone II	Depth zone III	Mean
1997	-0.9993*	-5.2823	-12.2823	**-6.1880**
1998	-2.1551	-3.3620	-8.1620	**-4.5597**
1999	-2.5605	-9.174	-6.5805	**-6.1050**
2001	-4.9121	-6.0230	-4.2388	**-5.0580**
2002	-1.7424*	-8.2584	-4.2930	**-4.7646**
Mean	***-2.8739***	***-6.4199***	***-7.1113***	***-5.3351***

*Non-significant departures from neutrality. Values >+2 or <-2 indicate significant departures from neutrality.

TABLE 16. Summary of Pearson correlation matrix for different coral species diversity indices at CR1 through time.

Variable 1*	Variable 2*	Correlation 1997	1998	1999	2001	2002
	N	0.390	0.519	0.279	0.261	0.938
S	*d*	0.958	0.967	0.980	0.969	0.991
S	J"n	0.129	0.485	0.709	0.840	0.285
S	Brillouin	0.793	0.843	0.897	0.960	0.878
S	Fisher	0.865	0.890	0.930	0.875	0.981
S		0.827	0.858	0.947	0.964	0.979
S	1-λ	0.440	0.757	0.846	0.940	0.647
	d	0.120	0.293	0.090	0.024	0.886
N	J'n	-0.009	0.185	0.682	0.135	0.239
	Brillouin	0.475	0.534	0.612	0.312	0.829
N	Fisher	-0.077	0.095	-0.030	-0.190	0.855
	H'n (log *e*)	0.284	0.411	0.478	0.185	0.805
N	1-λ	0.142	0.383	0.608	0.241	0.583
d	J'n	0.162	0.502	0.618	0.851	0.313
	Brillouin	0.721	0.795	0.813	0.921	0.879
d	Fisher	0.971	0.976	0.981	0.965	0.997
	H'n (log *e*)	0.818	0.849	0.893	0.959	0.889
d	1-λ	0.447	0.745	0.766	0.924	0.667
	Brillouin	0.662	0.855	0.936	0.943	0.696
J'n	Fisher	0.219	0.459	0.556	0.820	0.282
J'n	H'n (log *e*)	0.660	0.862	0.897	0.951	0.698
	1-λ	0.931	0.920	0.968	0.966	0.911
Brillouin	Fisher	0.647	0.697	0.733	0.828	0.853
	H'n (log *e*)	0.973	0.987	0.986	0.990	0.997
Brillouin	1-λ	0.851	0.967	0.984	0.993	0.923
	H'n (log *e*)	0.784	0.782	0.831	0.896	0.867
	1-λ	0.462	0.672	0.698	0.856	0.638
H'n (log *e*)	1-λ	0.851	0.970	0.967	0.993	0.925

**S*= Species richness; *N*= Abundance; *d*= Margalef's species richness [*d*= (*S*-1)/Log(*N*)]; J'n= Evenness; Brillouin [$H = N^{-1}\log_e\{N!/(N_1!\ N_2!\ldots\ N_s!)\}$; Fisher= Fisher's α; 1-λ'= Simpson evenness [$1\text{-}\lambda' = 1\text{-}\{\Sigma_i\ N_i(N_i\text{-}1)\}/\{N(N\text{-}1)\}$].

There was a very strong correlation between *S* and the Margalef's species richness (*d*) at all years, which can be explained by the fact that *d* changes with any change in *S* and in the log *N*. *S* and J'n showed a highly variable correlation pattern, with a weak correlation at the beginning (1997, 1998) and at the end of the study (2002), but with stronger correlations during years 1999 and 2001. This pattern could be explained by the fact that during 1997 and 1998 the coral community was dominated by a few species with a high abundance. There were also several species with very low abundances. This caused the J'n to be relatively high, but variable, causing a lack of correlation with *S* that is a fixed value. This was followed in years 1999 to 2001 by a major physiological fragmentation process of the colonies of dominant corals, such as *Montastrea annularis* (Figure 6), as a result of recurrent White Plague Type II outbreaks and subsequent algal overgrowth. This caused an effect of increasing the abundance of *M. annularis* colonies. During that time many rare species also disappeared from CR1, causing a consistent decline in J'n. Given the lower variation in J'n, there was a stronger correlation. At 2002, J'n showed a mean increase, but also with an increase in its variation that caused another decline in the correlation pattern. A similar pattern was also observed between *S* and 1-λ'.

S and Brillouin showed also a high correlation, since values of the Brillouin index vary with the variation in *S* and *N* (Table 16). A similar pattern was observed between *S* and Fisher's α, and between *S* and H'n. Finally, a *K*-dominance curve (Lambshead et al., 1983) was constructed based on the % of cumulative dominance (abundance) of corals and species ranks to determine if there was any significant disturbance effect on the coral

community (Figure 16). There was a major shift in the position of the *K*-dominance curve per year that could indicte stressful conditions at CR2 (Warwick, 1986).

Ecological change at CR2.

Epibenthic community data summaries from years 1997 to 2002 have been summarized in Tables 17 to 20. There was a 23% decline in the mean coral species richness between years 1997 and 2002 at depth zones II and III, but a 5% increase at depth zone I (Figure 17). There were significant differences only between depth zones, but not between years (Table 18). The cumulative coral species richness also showed a major decline through time (Figure 18, Table 21). There was also a 27 to 36% decline in the mean abundance of coral colonies per transect (Figure 19), with an estimated annual rate of decline of 5 to 7%. But, coral abundance at depth zone I increased by nearly 8% as a result of coral physiological fragmentation. There were significant differences only between depth zones, but not between years (Table 18). The cumulative abundance of corals also declined with the simultaneous decline in the cumulative species richness (Figure 20, Table 22). In most cases, there has been a continuous trend of declining colony abundance of the dominant species, *Montastrea annularis*, as a result of partial colony mortality, followed up by physiological fragmentation of parental colonies, and subsequent mortality of the surviving fragments. In addition, there has been a substantial loss of many rare and low-abundant coral species (Figure 21).

There were significant changes in the percentage cover of the major coral reef epibenthtic components at CR2 during the period of 1997 to 2002 (Figure 22). Living coral cover declined by factors of 37 to 54%, which means that there were annual decline rates of 7 to 11% in coral cover, which is also considered dangerously high. Differences were significant at both, the *year* and *depth* factors (Table 18). But in contrast, total algal cover showed a 12 to 107% increase (Figure 23), with the highest increase documented at the depth zone I. Annual mean increase fluctuated between 2 and 21%. Total algal cover was significantly higher on deeper habitats (Tables 7 and 19). Among the different algal functional groups, macroalgae showed a 25 to 231% increase in cover at depth zones II and III, respectively, with a mean annual increase of 5 to 46% (Figure 24). However, filamentous algal cover showed a 3,895% increase in shallower habitats (Figure 25), but 64 to 66% in deeper zones. Differences were not significant due to the large variances.

Cover values of other minor algal groups, such as erect calcareous algae, *Halimeda* spp., and encrusting algae (Tables 17 and 19) showed non-significant fluctuations in time and depth.

Cyanobacterial cover was low during 1997 and 2001, but high during 1998 (ENSO year) and even higher during year 2002 (Figure 26). The magnitude of increase was from 301 to 3,200%, an annual mean of 60 to 640%. There were significant differences in time, but not in depth, suggesting that this phenomenon was widespread through the entire coral reef. Sponge cover increased by a factor of 78 to 500% at depth

zone II and III, this fluctuation was only significant through depth zones (Tables 17 and 19).

A total of 30 coral species have been identified from the permanent transects through the study (Table 18). *Montastrea annularis* was the dominant reef-building coral species at CR2 through the study. It showed a consistently high mean relative cover, being significantly higher at shallower reef zones (Table 20). Although many rare coral species have disappeared during the study (Figure 21), these differences were not significant (Table 20), mostly as a result of the large variation in the data, which is normal for rare species. During 1997, the top three dominant species per depth zone were: I= *M. annularis* (83%), *Porites astreoides* (7%), and *Agaricia agaricites* (4%); II= *M. annularis* (78%), *P. astreoides* (10%), and *A. agaricites* (3%); and III= *M. annularis* (57%), *Siderastrea siderea* and *Erythropodium caribbaeorum* (8%).

During 1998, the top three dominant species per depth zone were: I= *M. annularis* (80%), *P. astreoides* (7%), and *A. agaricites* (4%); II= *M. annularis* (72%), *P. astreoides* (11%), and *E. caribbaeorum* (5%); and III= *M. annularis* (42%), *E. caribbaeorum* (17%), and *P. astreoides* (9%). During 2001, dominant species were: I= *M. annularis* (76%), followed up by *P. porites* (13%), and *A. agaricites* (5%); II= *M. annularis* (84%), *P. porites* and *P. astreoides* (3%); and III= *M. annularis* (61%), followed by *Colpophyllia natans* (11%), and *P. porites* (7%).

TABLE 17. Summary of the coral community data at CR2 (1997-2002)*.

Paramet	97-I	I	97-III	8-I	98-II	98-I	01-I	01-II	II	02	02-II	02
Species richness		7.5±1.7	8.8±1.1		7.5±1.0	11.8±	4.3±0.5	5.5±0.3		4.8±0.9		6.8
Colony abundance	19.0±2.0		38.0±8.7	31.5±1.5		55.0±	21.3±1.9	26.0±2.5	29.3±5.0	20.5±1.2	25.5±2.0	24.5±2.4
% coral cover	82.4±5.2		44.2±3.7	65.9±10.7	44.1±5.2	42.2±2.4		32.6±6.4	25.5±3.0	37.9±5.1	32.3±5.6	23.0±2.3
% total algae	19.8±10.1	45.9±3.7	53.0±6.2	31.5±1.5		50.6±2.7		63.7±6.8	66.7±2.8	40.8±5.4	51.5±5.9	61.6±6.1
% macroalgae	19.6±10.1	29.8±8.1	14.2±8.3		19.6±3.3	32.4±2.7		43.5±4.2	38.4±2.7	15.2±1.3	37.3±5.4	47.0±3.4
% filamentous algae	0.5±0.3	27.7±8.9	40.6±13.3	11.4±4.8		18.8±0.2		17.4±2.3	23.3±5.1	20.0±4.5	10.0±2.4	13.7±3.5
% calcareous algae	N.D.	N.	N.D.	2.1±0.2		0.0±0.0		0.0±0.0		0.5±0.2		0.3
% *Halimeda*	0.0±0.0	1.7±1.2	0.9±0.6	9.5±8.2		1.8±1.8		1.9±1.6		0.3±0.2		0.0
% encrusting algae	0.0±0.0	1.7±1.7	0.3±0.3	5.3±4.7		0.8±0.4		1.0±0.5		5.6±1.5		0.7
% cyanobacteria	0.0±0.0	3.9±3.4	0.4±0.2	6.8±6.1		9.5±2.1		0.5±0.3		19.3±4.0	15.6±2.7	11.6±2.8
% sponges	0.0±0.0	0.1±0.1	1.3±0.7	0.4±0.1		5.0±1.0		3.2±1.1		1.3±0.4		2.2
H'n	±0.0419	1.3095 ±0.1465	1.5671 ±0.0688	1.3287 ±0.0795	1.3615 ±0.1328	1.8717 ±0.0662	±0.2202	1.0262 ±0.1152	±0.1081	1.0694	1.1318 ±0.1566	1.3 ±0.1160
J'n	±0.0300	0.6777 ±0.0433	0.7310 ±0.0116	0.7139 ±0.0720	0.6808 ±0.0388	0.7612 ±0.0223	±0.1103	0.6034 ±0.0664	±0.0774	0.6753	0.6528 ±0.0492	0.7 ±0.0454
H'c	±0.1422	0.8135 ±0.1174	1.3632 ±0.1587	0.7680 ± 0.216	0.9966 ±0.1278	1.7362 ±0.0955	±0.2024	0.6343 ±0.1272	±0.1051	0.6176	0.6547 ±0.1398	1.2 ±0.1412
J'c	±0.0113	0.1268 ±0.0166	0.2213 ±0.0155	0.1173 ± 0.036	0.1555 ±0.0194	0.2738 ±0.0169	±0.0361	0.1118 ±0.0230	±0.0198	0.1064	0.1160 ±0.0262	0.2 ±0.0279

*Mean±one standard error; N.D.= Not determined.

TABLE 18. Summary of the % of relative coral cover at CR2 (1997-2002).

Species	97-I	97-II	97	98-I	98	98-III	0	01-II	01	02-I	02	02-III
M.ann.	83.20	9	56.	79.73	71.60	5	75.	83.84	61.38	9	83.67	8
M.cav.	2.35		3.8	1.12	1.74		0		5.62		1.83	
C.nat.	0		5.6	0	0.63		0		10.95		0.78	4
D.stri.	0		1.4	0	0		0.4	0	0	0	0	0
D.cli.	0		0		0		0		0	0.56	0	0
D.lab.	0.61		1.1	0	0		0		0	0	0	0
S.sid.	0		7.9	0	0.25		0		1.94		0	2.41
S.rad	0		0.0	0	0		0		0	0	0	0
S.mich.	0		0		0		0		0	0	0	0
M.mea	0		3.4	0	0		0		1.71		0	1.81
M.mir	0		0.5	0	0		0		0	0	0	0
M.dec	0	0	1.1	0	0.06		0		0.30		0	0.45
A.cer.	0	0.21	0		0		0		0	0	0	0
P.por.	1.85	0.62	2.2	3.29	1.94		13.	3.22	7.40	3	3.23	
P.ast.	7.47	10.17	4.8	6.95	11.16		2.8	3.48	2.83		4.32	
A.aga.	4.05	2.64	0		4.11		4.7	1.57	2.58		3.42	
A.hum.	0.48	0.98	0.3	0.360	0.54		0		0	0	2.94	
L.cuc.	0	0.92	0.1	0	0.19		0		0	0	0	0
M.ali	0	0	0.5	0	0		0		0	0	0	0
M.lam.	0	0.21	0		0		0		0	0	0	0
M.dan	0	0	0		0		0		0	0	0	0
Myc. sp.	0	0	0		0		0		0	0	0.31	
I.sin.	0	0	0		0		0		0	0	0.24	
E.fas.	0	0	0		0		0		0	0	0	0
S.lac.	0	0	0		0		0		0.46		0	0
T.aur.	0	0.30	0.1	0	0.85		0		0	0	0	0
M.alc.	0	1.39	1.4	0	1.85		0.32		5.24		1.60	
M.com.	0	0.64	0		0		0		0	0	0.23	
E.car	0	1.06	7.9	3.97	5.09	7	2.68		7.04		0.08	
C.ris	0	0	0.3	0	0		0		0	0	0	0

TABLE 19. Friedman 2-way ANOVA for the coral reef community data at CR2.

Parameter	Factor	D.F.*	Friedman Statistic	*P* value**
Species richness***	Year	3	7.29	0.0633 *2,1,4,3*
	Depth	2	8.00	0.0183 (S) *3,2,1*
Colon n c	Year	3	6.60	0.0858 *2,1,3,4*
	Depth	2	6.50	0.0388 (S) *3,2,1*
% Coral cov	Year	3	9.00	0.0293 (S) *1,2,3,4*
	Depth	2	8.00	0.0183 (S) *1,2,3*
% To a v	Year	3	7.00	0.0719 *3,4,2,1*
	Depth	2	6.50	0.0388 (S) *3,2,1*
% Ma g o	Year	3	5.80	0.1218 *3,4,1,2*
	Depth	2	3.50	0.1738 *2,3,1*
% Filamentous algal cover	Year	3	2.20	0.5319 *1,3,2,4*
	Depth	2	1.50	0.4724 *3,1,2*
% Erect calcareous algal cover	Year	2	2.67	0.2636 *4,2,3*
	Depth	2	0.55	0.7613 *1,2,3*
% Ha a .	Year	3	5.40	0.1447 *2,3,1,4*
	Depth	2	3.50	0.1738 *1,2,3*
% Encrusting algal cover	Year	3	4.20	0.2407 *4,2,3,1*
	Depth	2	0.50	0.7788 *2,1,3*
y c ia	Year	3	8.20	0.0421 (S) *4,2,3,1*
	Depth	2	2.00	0.3679 *2,1,3*
p o	Year	3	5.80	0.1218 *3,4,2,1*
	Depth	2	6.50	0.0388 (S) *3,2,1*
al H'n	Year	3	6.60	0.0858 *2,1,3,4*
	Depth	2	8.00	0.0183 (S) *3,2,1*
a	Year	3	3.40	0.3340 *2,1,34*
	Depth	2	6.50	0.0388 *3,1,2*
a	Year	3	6.60	0.0858 *2,1,3,4*
	Depth	2	6.50	0.0388 (S) *3,2,1*
al J	Year	3	5.80	0.1218 *2,3,4,1*
	Depth	2	8.00	0.0183 (S) *3,2,1*

*D.F.= Degrees of freedom.

**(S)= Significantly different. Numbers in *italics* at the factor *Year* represent mean ranks per year (1=1997; 2=1998; 3=2001; 4=2002) and at the factor *Depth* represent mean ranks per depth zone (1= < 4 m; 2= 4-8 m; 3= >8 m).

***Species richness and colony abundance were √x-transformed. Coral, total algal, macroalgal and filamentous algal cover were Arcsin (√x)-transformed. The remaining parameters were transformed as follows: Calcareous algae and *Halimeda* spp. cover: Arcsin (√x+0.002); Incrustring and Cyanobacterial cover: Arcsin (√x+0.003); and Sponge cover: Arcsin (√x+0.001).

TABLE 20. Friedman 2-way ANOVA for the % of relative coral cover data at CR1.

Parameter	Factor	D.F.*	Friedman Statistic	*P* value**
Montastrea annularis	Year	3	1.80	0.6149 *3,1,4,2*
	Depth	2	6.00	0.0498 (S) *1,2,3*
Montastrea cavernosa	Year	3	1.55	0.6704 *4,2,3,1*
	Depth	2	7.05	0.0388 (S) *3,2,1*
Colpophyllia natans	Year	3	5.40	0.1447 *3,4,2,1*
	Depth	2	7.60	0.0224 (S) *3,2,1*
Diploria	Year	3	2.00	0.5724 *1,3,2,4*
	Depth	2	1.00	0.6065 *1,3,2*
Diploria	Year	3	3.00	0.3916 *4, 1,2,3*
	Depth	2	2.00	0.3679 *1,2,3*
Diploria labyrinthiformis	Year	3	3.80	0.2839 *1,2,3,4*
	Depth	2	3.71	0.1561 *3,1,2*
Siderastre	Year	3	3.72	0.2933 *1,2,3,4*
	Depth	2	6.53	0.0381 (S) *3,2,1*
Siderastrea radians	Year	3	3.00	0.3916 *1,2,3,4*
	Depth	2	2.00	0.3679 *3,1,2*
Stephanocoenia michelini	Year	3	3.00	0.3916 *2,1,3,4*
	Depth	2	2.00	0.3679 *3,1,2*
andrin	Year	3	3.00	0.3916 *1,4,3,2*
	Depth	2	8.00	0.0183 (S) *3,1,2*
drac bil	Year	3	3.00	0.3916 *1,2,3,4*
	Depth	2	2.00	0.3679 *3,1,2*
drac cactis	Year	3	5.25	0.1544 *2,1,4,3*
	Depth	2	7.54	0.0231 (S) *3,2,1*
opora	Year	3	3.00	0.3916 *1,2,3,4*
	Depth	2	2.00	0.3679 *2,1,3*
ites	Year	3	8.20	0.0421 (S) *3,4,2,1*
	Depth	2	6.00	0.0498 (S) *1,3,2*
ites astreoides	Year	3	8.20	0.0421 (S) *2,1,4,3*
	Depth	2	6.00	0.0498 (S) *2,1,3*
ricia agaricites	Year	3	3.40	0.3340 *2,3,4,1*
	Depth	2	4.50	0.1054 *1,2,3*
ricia	Year	3	8.79	0.0323 (S) *1,2,4,3*
	Depth	2	7.43	0.0244 (S) *2,1,3*
tose ullata	Year	3	5.33	0.1490 *1,2,3,4*
	Depth	2	3.00	0.2231 *2,3,1*
cetophyllia aliciae	Year	3	3.00	0.3916 *1,2,3,4*
	Depth	2	2.00	0.3679 *3,1,2*

Mycetophyllia lamarckiana	Year	3	3.00	0.3916	*1,2,3,4*
	Depth	2	2.00	0.3679	*2,1,3*
Mycetophyllia danaana	Year	3	3.00	0.3976	*2,1,3,4*
	Depth	2	2.00	0.3679	*3,1,2*
	Year	3	2.00	0.5724	*2,4,1,3*
	Depth	2	1.00	0.6065	*1,2,3*
Isophyllia sinuosa	Year	3	3.00	0.3916	*3,4,1,2*
	Depth	2	4.00	0.1365	*2,1,3*
	Year	3	3.00	0.3916	*2,1,3,4*
	Depth	2	2.00	0.3679	*3,1,2*
	Year	3	3.00	0.3916	*3,1,2,4*
	Depth	2	2.00	0.3679	*3,1,2*
	Year	3	6.00	0.1116	*1,2,3,4*
	Depth	2	4.00	0.1353	*2,3,1*
Millepora alcicornis	Year	3	3.21	0.3608	*4,3,2,1*
	Depth	2	8.00	0.0183 (S)	*3,2,1*
Millepora complanata	Year	3	3.00	0.3916	*1,4,2,3*
	Depth	2	4.00	0.1353	*2,1,3*
	Year	3	5.80	0.1218	*2,3,1,4*
	Depth	2	3.50	0.1738	*3,2,1*
Carijoa riseii	Year	3	3.00	0.3916	*1,2,3,4*
	Depth	2	2.00	0.2976	*3,1,2*

*D.F.= Degrees of freedom.

**(S)= Significantly different. Numbers in *italics* at the factor *Year* represent mean ranks per year (1=1997; 2=1998; 3=2001; 4=2002) and at the factor *Depth* represent mean ranks per depth zone (1= < 4 m; 2= 4-8 m; 3= >8 m). All proportions were Arcsin(√x)-transformed. If there were 0 values in the data matrix, then proportions were Arcsin(√x + *the lowest value of non-zero proportions*)-transformed.

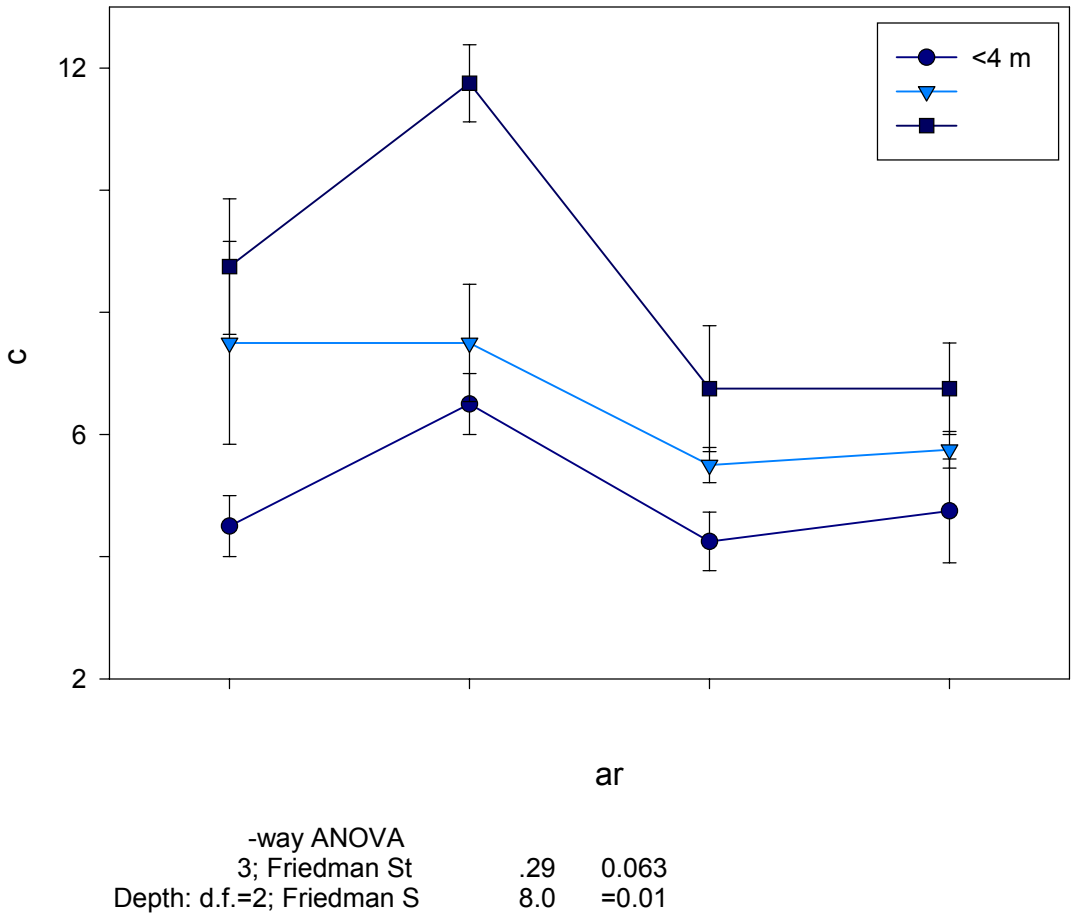


FIGURE 17. Change in coral species richness (mean±one standard error).

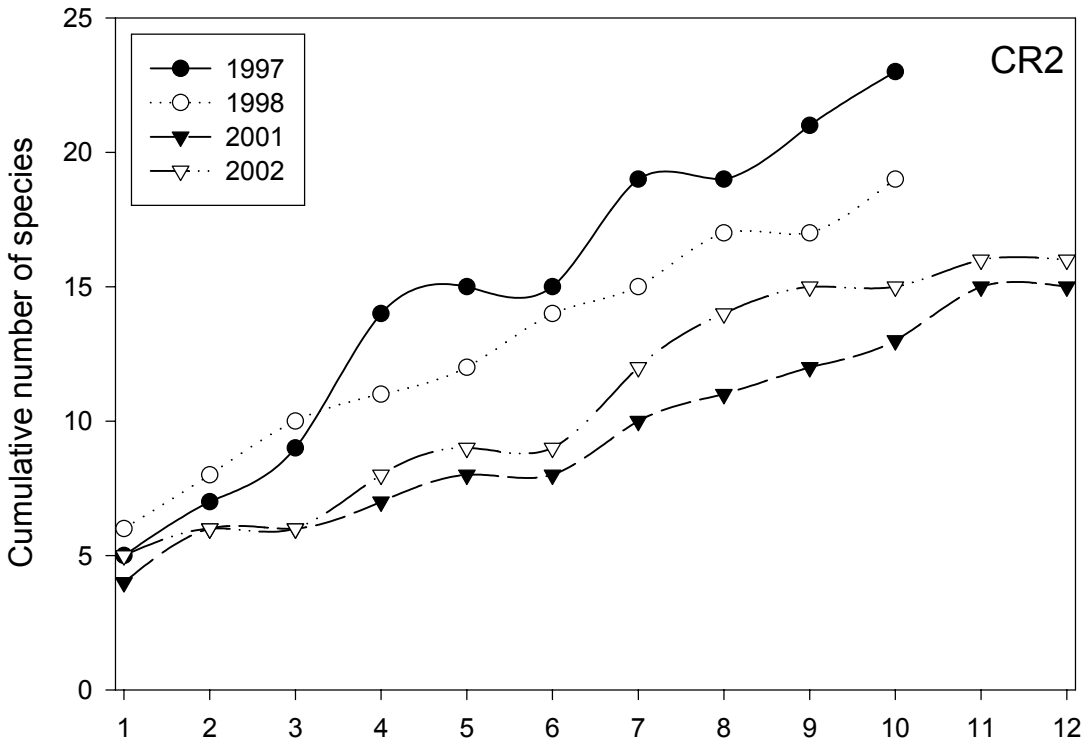


FIGURE 18. Change in coral cumulative species richness at CR2.

TABLE 21. Exponential regression analysis between the cumulative coral species richness and the cumulative number of replicate transects at CR2.

Year	Regression formula	r^2 value
1997	$y=30.08(1-e^{-13.44x})$	0.9724
1998	$y= 20.09(1-e^{-21.65x})$	0.9376
2001	$y= 20.04(1-e^{-0.1074x})$	0.9092
2002	$y= 21.43(1-e^{-0.1199x})$	0.9233

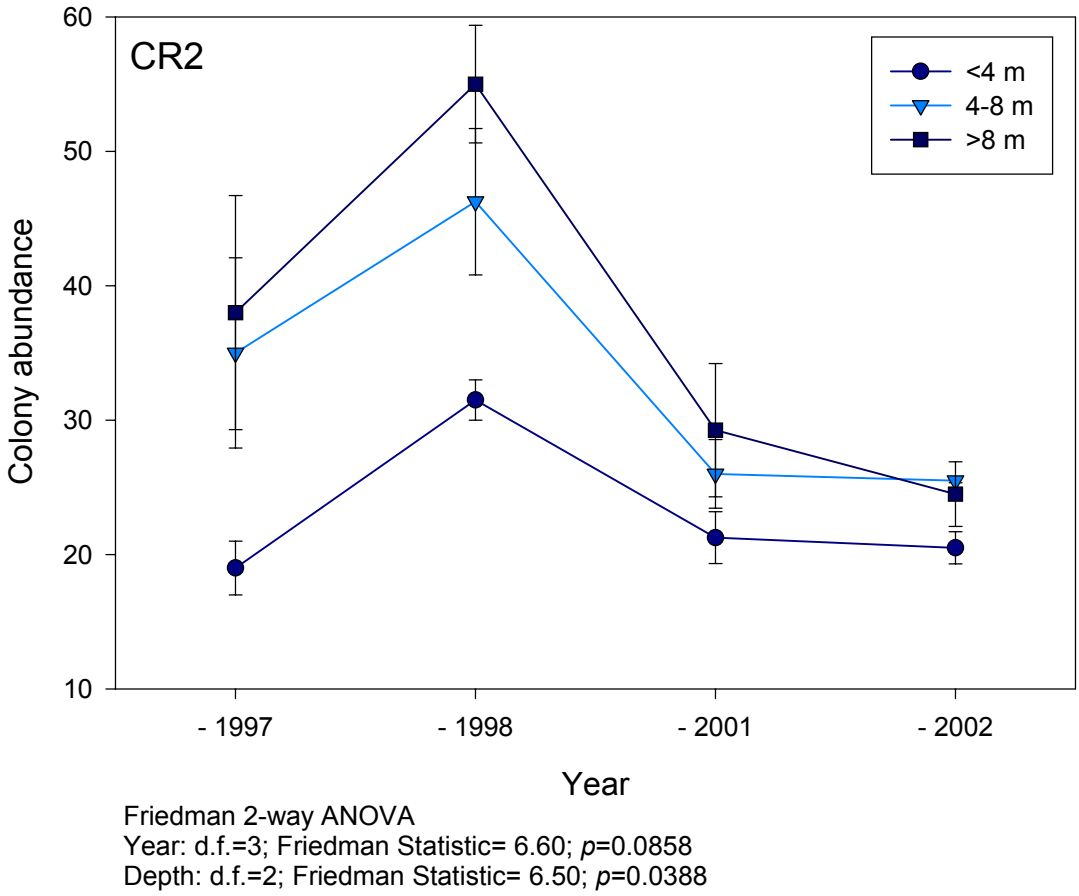


FIGURE 19. Change in coral colony abundance at CR2 (mean±one standard error).

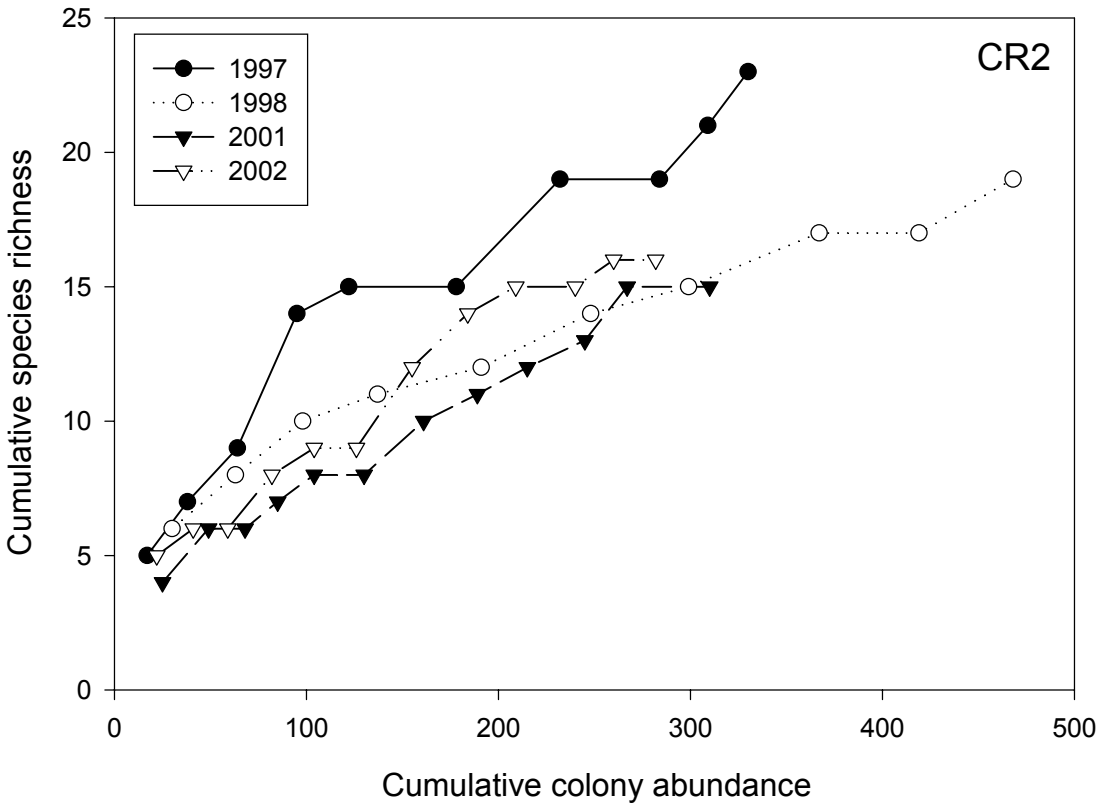


FIGURE 20. Relationship among the cumulative coral colony abundance and species richness.

TABLE 22. Exponential regression analysis between the cumulative coral species richness and the cumulative colony abundance at CR2.

Year		r^2 value
1997	$y= 21.96(1-e^{-0.0091x})$	0.9420
1998	$y= 17.73(1-e^{-0.0076x})$	0.9030
2001	$y= 17.45(1-e^{-0.0059x})$	0.9322
2002	$y= 18.90(1-e^{-0.0068x})$	0.9360

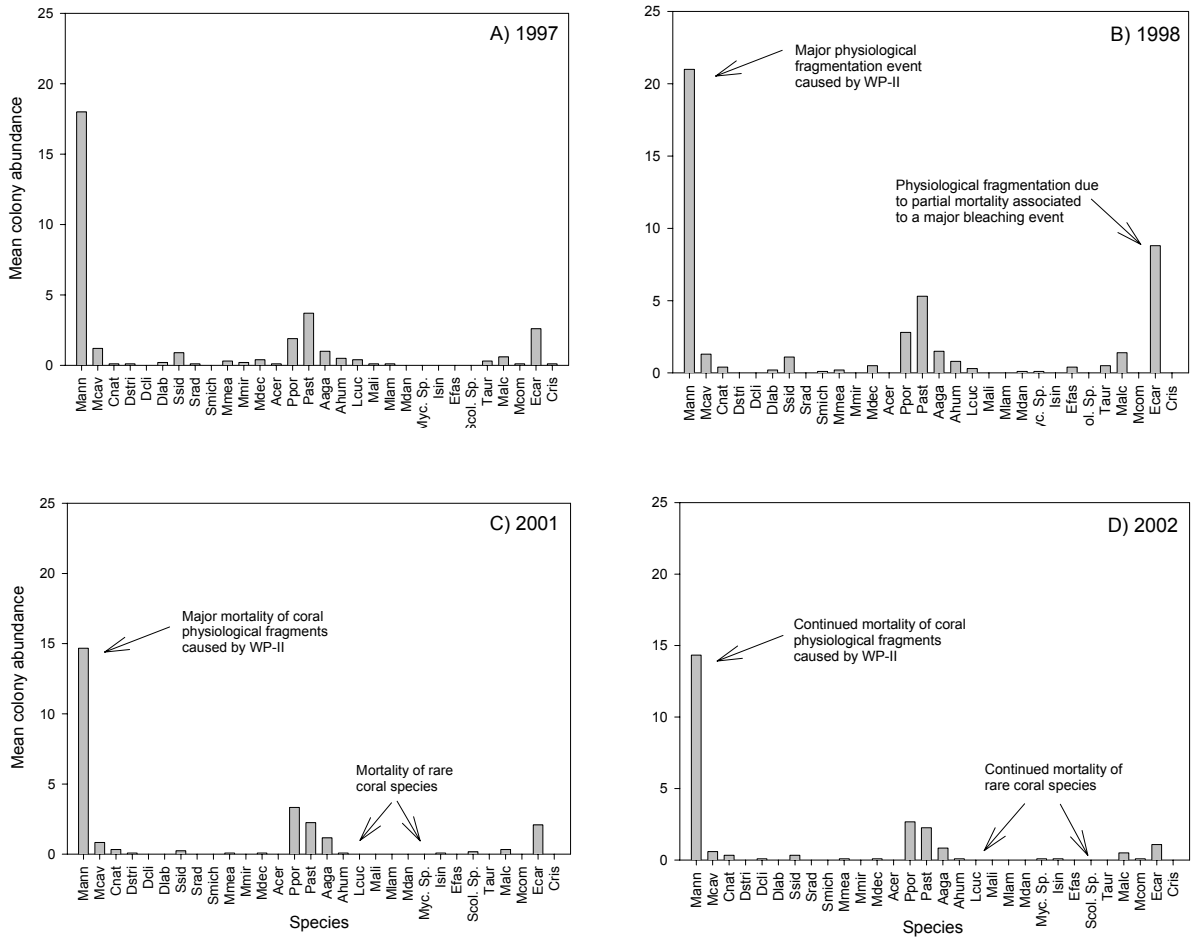


FIGURE 21. Dynamics of the mean colony abundance at CR2 (1997-2002).

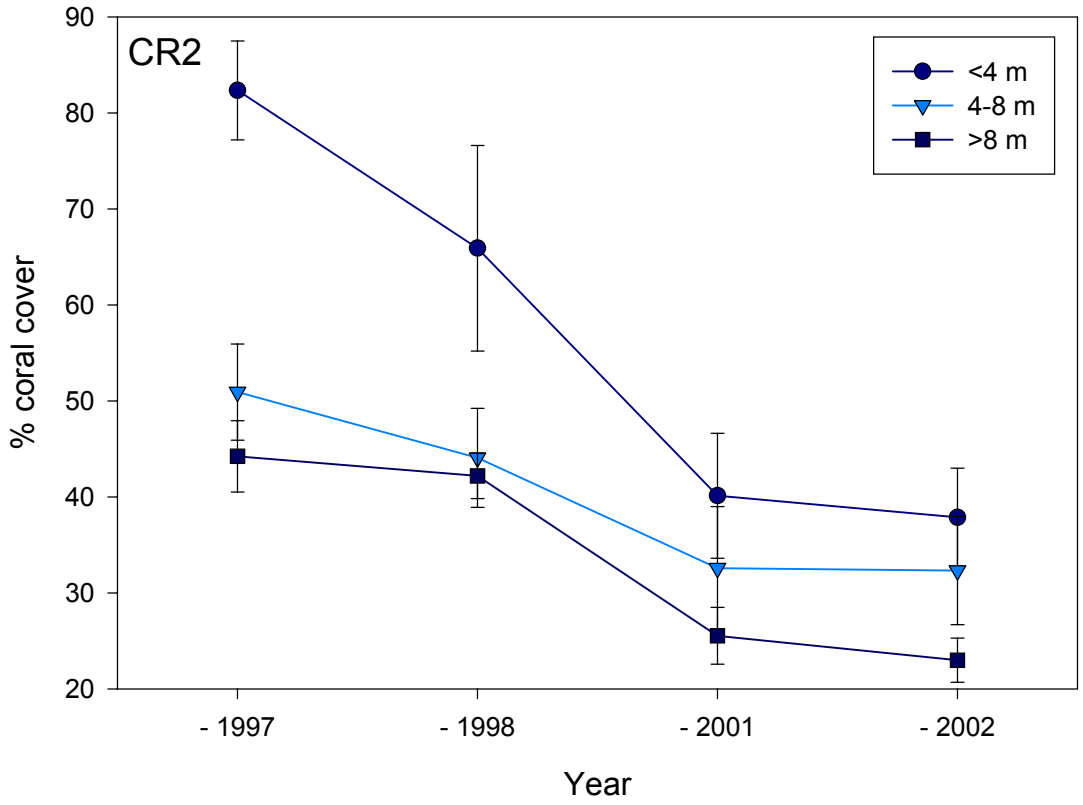


FIGURE 22. Change in the % of living coral cover at CR2 (mean±one standard error).

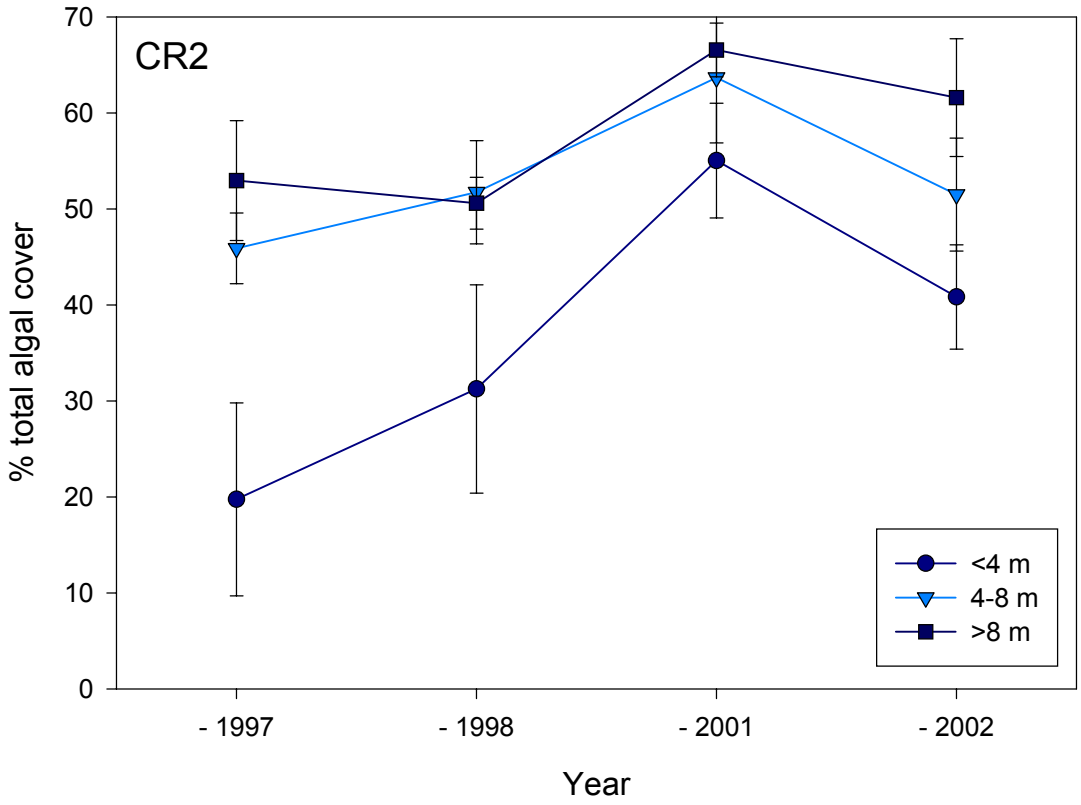
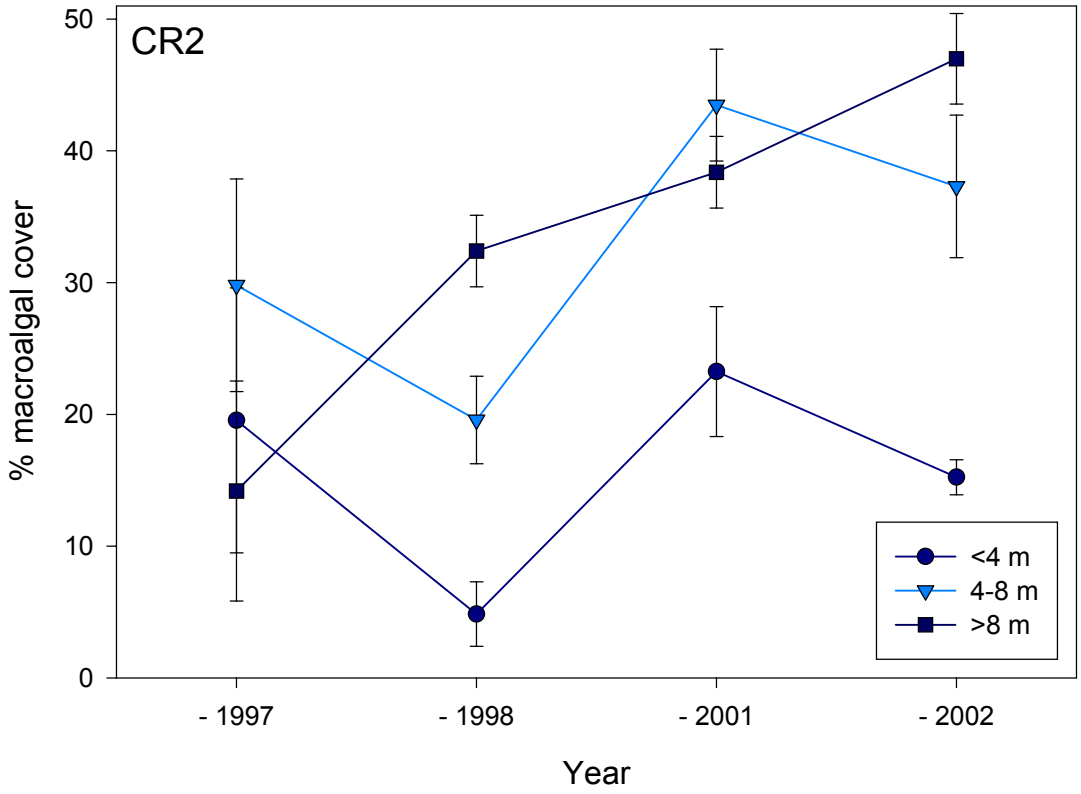


FIGURE 23. Change in the % of total algal cover at CR2 (mean±one standard error).



Friedman 2-way ANOVA
Year: d.f.=3; Friedman Statistic= 5.80; *p*=0.1218
Depth: d.f.=2; Friedman Statistic= 3.50; *p*=0.1738

FIGURE 24. Change in the % of macroalgal cover at CR2 (mean±one standard error).

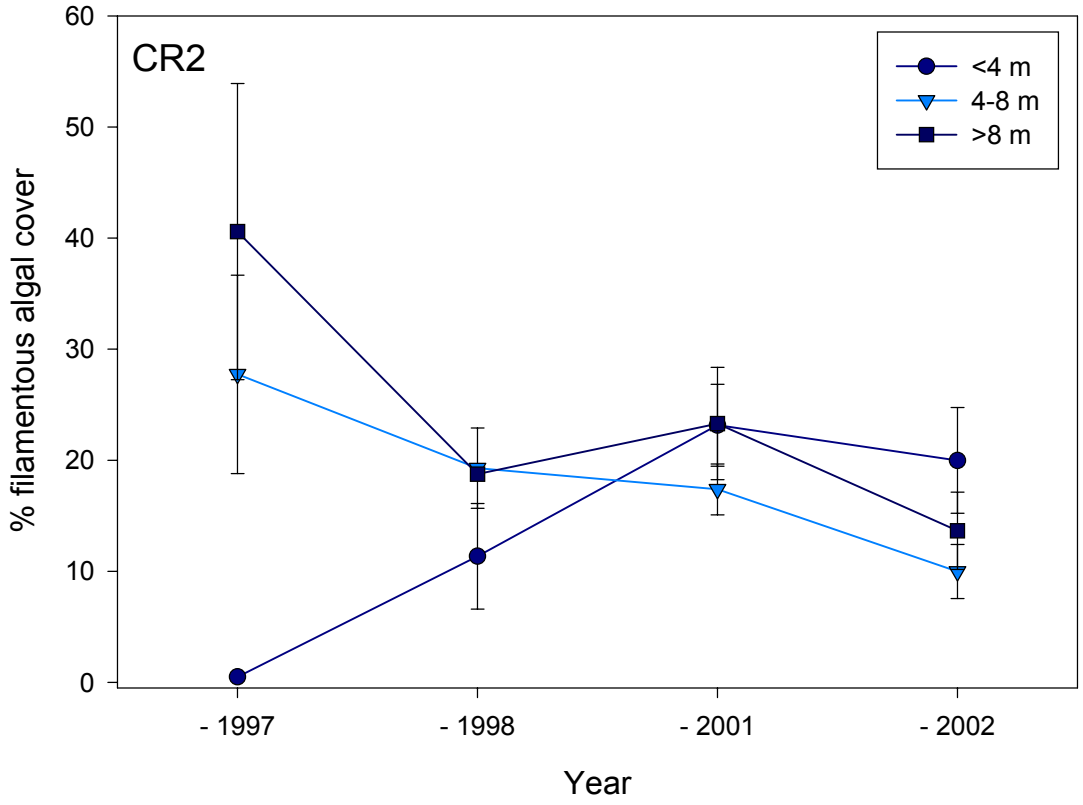


FIGURE 25. Change in the % of filamentous algal cover at CR2 (mean±one standard error).

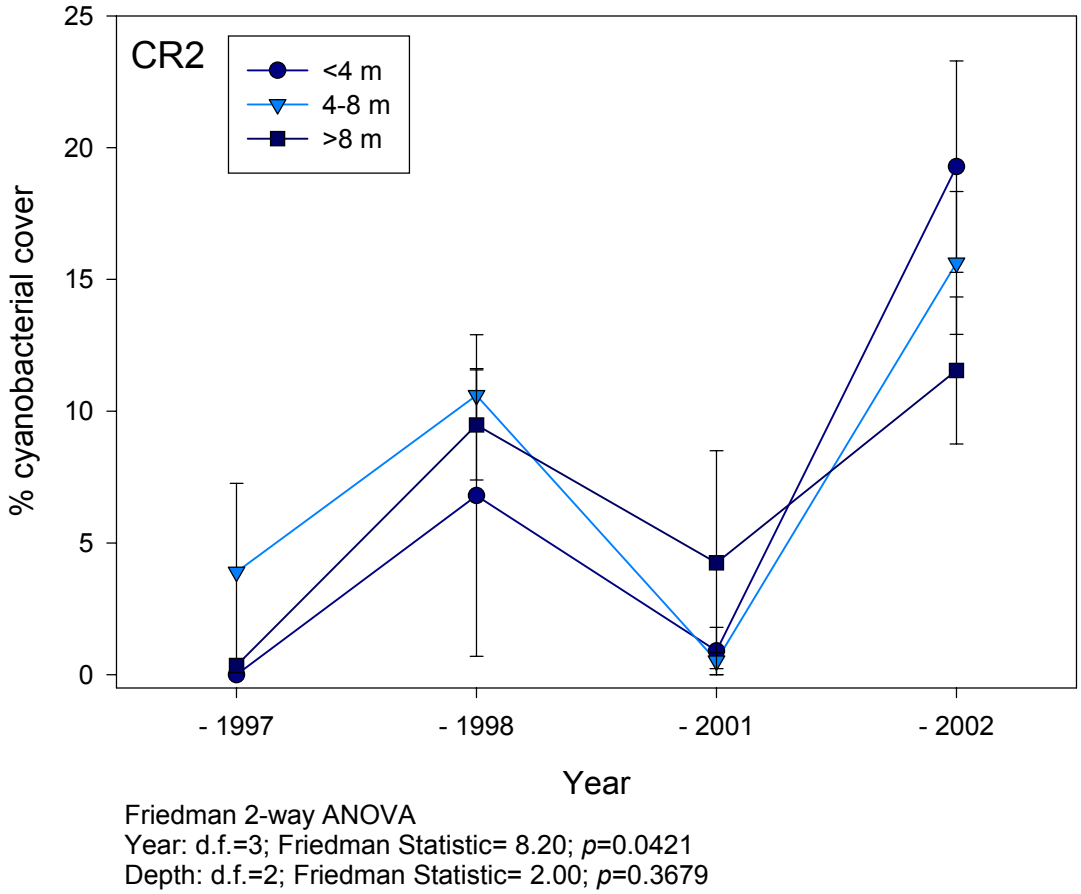
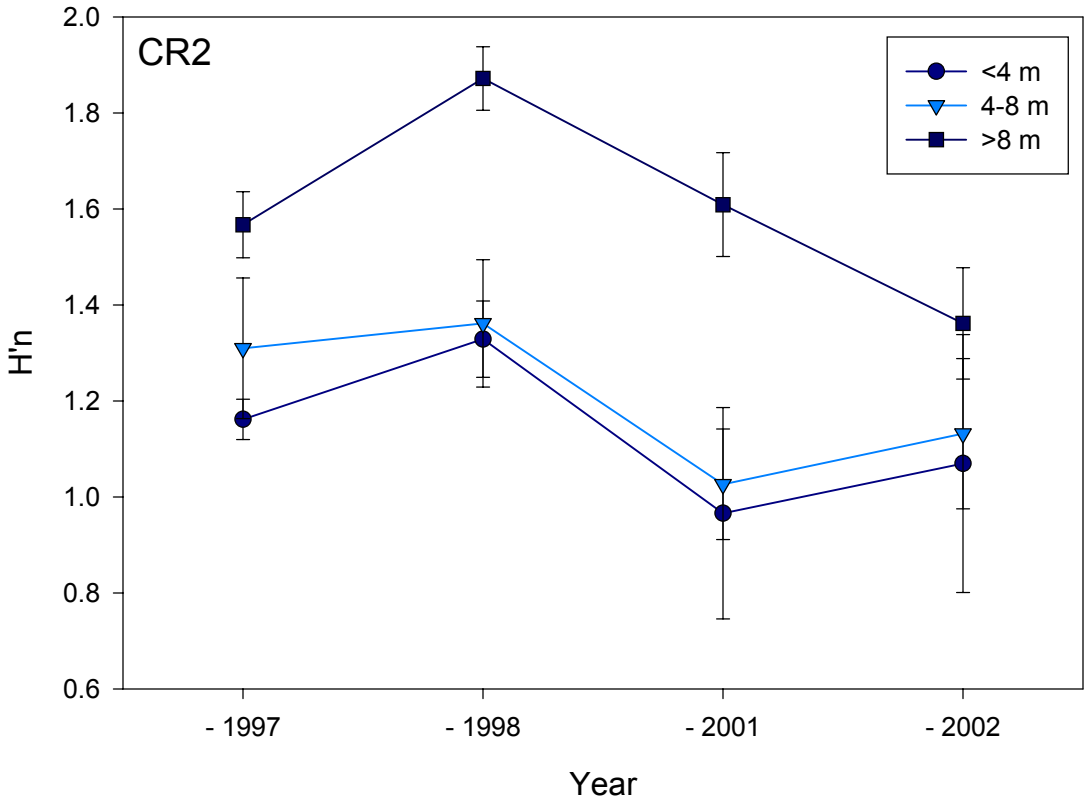


FIGURE 26. Change in the % of cyanobacterial cover at CR2 (mean±one standard error).

Finally, during year 2002, dominant species included: I. *Montastrea annularis* (78%), *Porites astreoides* (4%), and *Agaricia agaricites* (3%); II= *M. annularis* (84%), *P. astreoides* (4%), and *A. agaricites* (3%); and III= *M. annularis* (57%), followed up by *Colpophyllia natans* (12%), and *M. cavernosa* (7%).

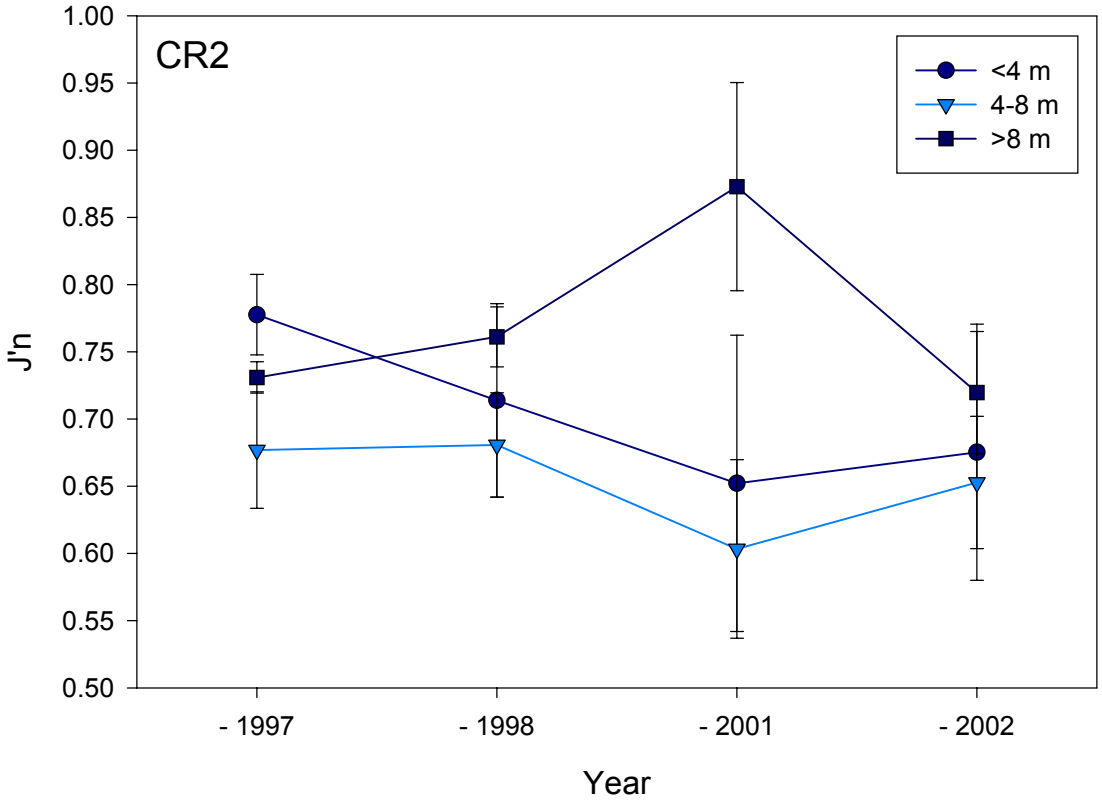
The coral species diversity index (H'n) showed a 8 to 14% decline (Figure 27) when compared to the original value at the beginning of the study (Table 17). H'n was significantly different among depths with higher values at deeper zones. No temporal effects were detected. Coral species evenness (J'n) showed a 2 to 13% decline (Figure 28) and mean values were significantly higher in deeper reef zones. H'c showed a 2 to 20% decline, while J'c showed significant fluctuations during the study with a 8% decline at depth zone II, a 3% increase at depth zone III, but a 16% increase at depth zone I. These differences between depth zones were significant, but no temporal effects were observed.

A peak log-normal regression analysis carried out at depth zone I between the % of total algal cover and coral species richness (Table 23) showed a moderately strong negative relationship (r^2=0.7290). Exponential decay regression analysis at depth zone II showed a moderately negative relationship (r^2=0.5523), but a very strong one at depth zone III (r^2=0.9980). The negative relationship between algal cover and colony abundance was weak at depth zone II, and moderately weak at depth zone I, but strong at depth zone III (r^2=0.9674). However, there were moderately strong to strong negative



Friedman 2-way ANOVA
Year: d.f.=3; Friedman Statistic= 6.60; *p*=0.0858
Depth: d.f.=2; Friedman Statistic= 8.00; *p*=0.0183

FIGURE 27. Change in the coral species diversity index at CR2 (mean±one standard error).



Friedman 2-way ANOVA
Year: d.f.=3; Friedman Statistic= 3.40; *p*=0.3340
Depth: d.f.=2; Friedman Statistic=6.50; *p*=0.0388

FIGURE 28. Change in the coral species evenness at CR2 (mean±one standard error).

TABLE 23. Summary of regression analysis results between the % of total algal cover and several coral parameters.

Parameters	Depth zone	Equation	r^2
% Algal cover vs Species richness	I*	$y= 5.985e^{[-0.5(\ln(x/30.95)/0.6284)^2]}$	0.7290
	II**	$y= 3.271e^{(25.27/(x-15.02))}$	0.5523
	III**	$y= 5.954e^{(2.045/(x-47.59))}$	0.9980
% Algal cover vs Colony abundance	I*	$y= 27.56e^{[-0.5(\ln(x/32.24)/0.6168)^2]}$	0.5025
	II***	$y= -114.7 + 5.951x - 0.0588x^2$	0.2415
	III***	$y= 1019-32.53x+0.2655x^2$	0.9674
% Algal cover vs % Coral cover	I***	$y= 155.2-4.382x+0.0411x^2$	0.9182
	II***	$y= 380.1-11.61x+0.0966x^2$	0.7058
	III***	$y= 422.4-12.10x+0.0920x^2$	0.8803
% Algal cover vs Coral H'n	I***	$y= 0.8918+0.0233x-0.0004x^2$	0.6909
	II***	$y= 0.6976+0.0342x-0.0005x^2$	0.6277
	III***	$y= 24.24-0.7684x+0.0064x^2$	0.9783

*Peak log-normal regression (3 parameters).
**Exponential decay regression (Modified single, 3 parameters).
***Quadratic regression.

relationships between the algal cover and coral cover (r^2=0.7058 to 0.9182). Finally, there was a moderate to strong negative relationship between algal cover and H'n (r^2=0.6277 to 0.9783). These results suggest that algal growth during the last five years could explain most of the coral declines observed so far at CR2. This was more evident at depth zone III, but in a lesser degree at depth zones I and II.

Multivariate analysis of coral reef communities at CR2.

A hierarchical cluster analysis was carried out based on a Bray-Curtis dissimilarity matrix on the proportion of major epibenthic components as discussed above to characterize the structure of the coral reef communities through time (Figure 29). Dissimilarity through the study averaged 32% at CR2. However, this classification of sites based on broad categorical data did not clearly differentiate sites by time. Temporal-based clusters were more clearly distinguished in the MDS ordination (Figure 30). The global 2-way crossed ANOSIM test (Table 24) showed a highly significant difference (0.0%) of the coral reef community structure between years and between depth zones. The interaction of years x depth was also highly significant (2.8%). The pairwise ANOSIM test (Table 25) showed highly significant differences in the coral reef community structure at CR2 between all pairs of years (0.0 to 5.0%). A pairwaise ANOSIM test between depth zones (Table 26) also revealed highly significant differences between all pairs of depth zones (0.0 to 3.9%). The results of the SIMPER analysis comparing change from year 1997 to the subsequent years until 2002 (Tables 27-29) revealed that change in the proportion of cyanobacteria was the most significant

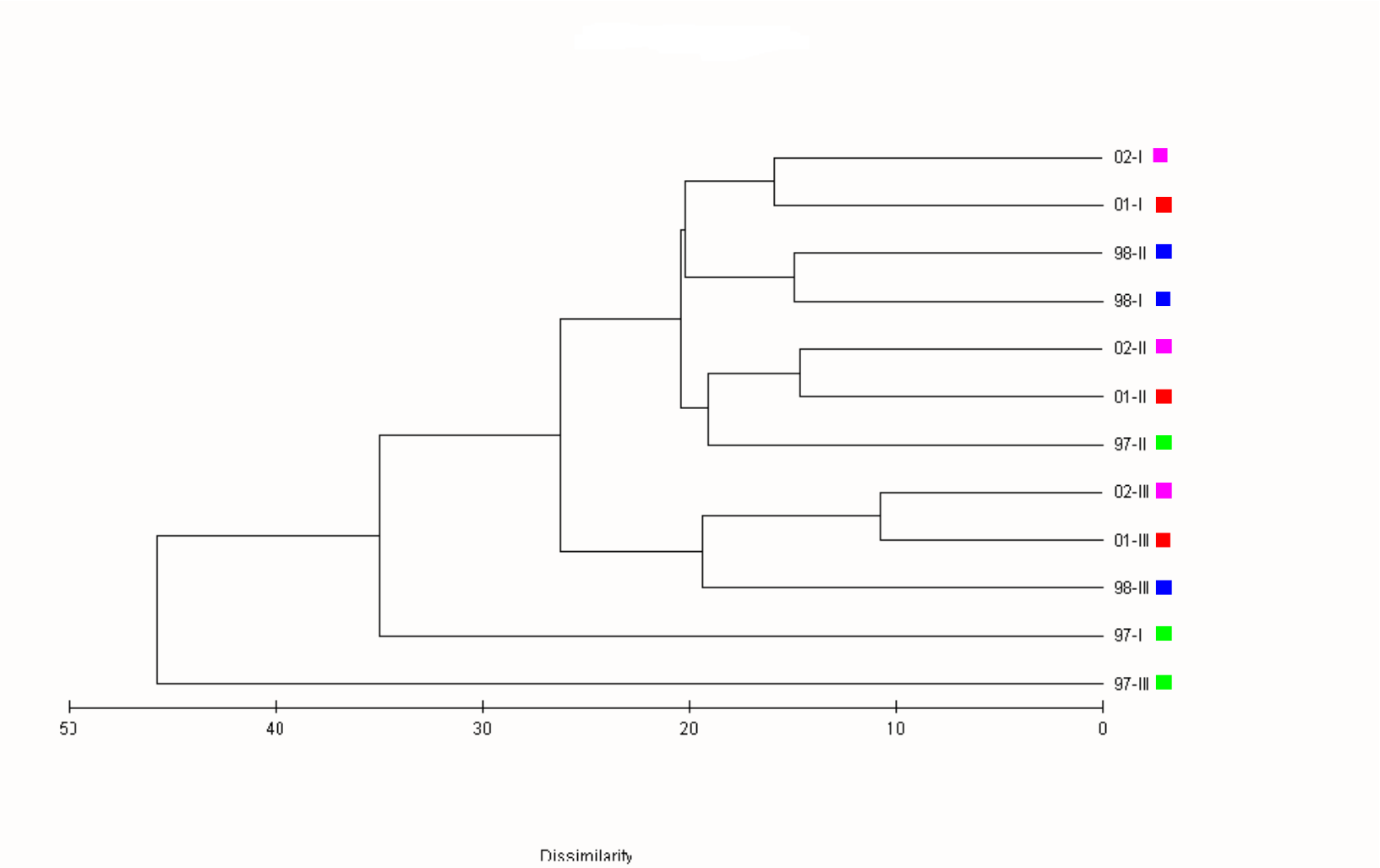


FIGURE 29. Bray-Curtis dissimilarity classification of years (with depth zones as replicates) based on the proportion of coral reef epibenthic categories at CR2.

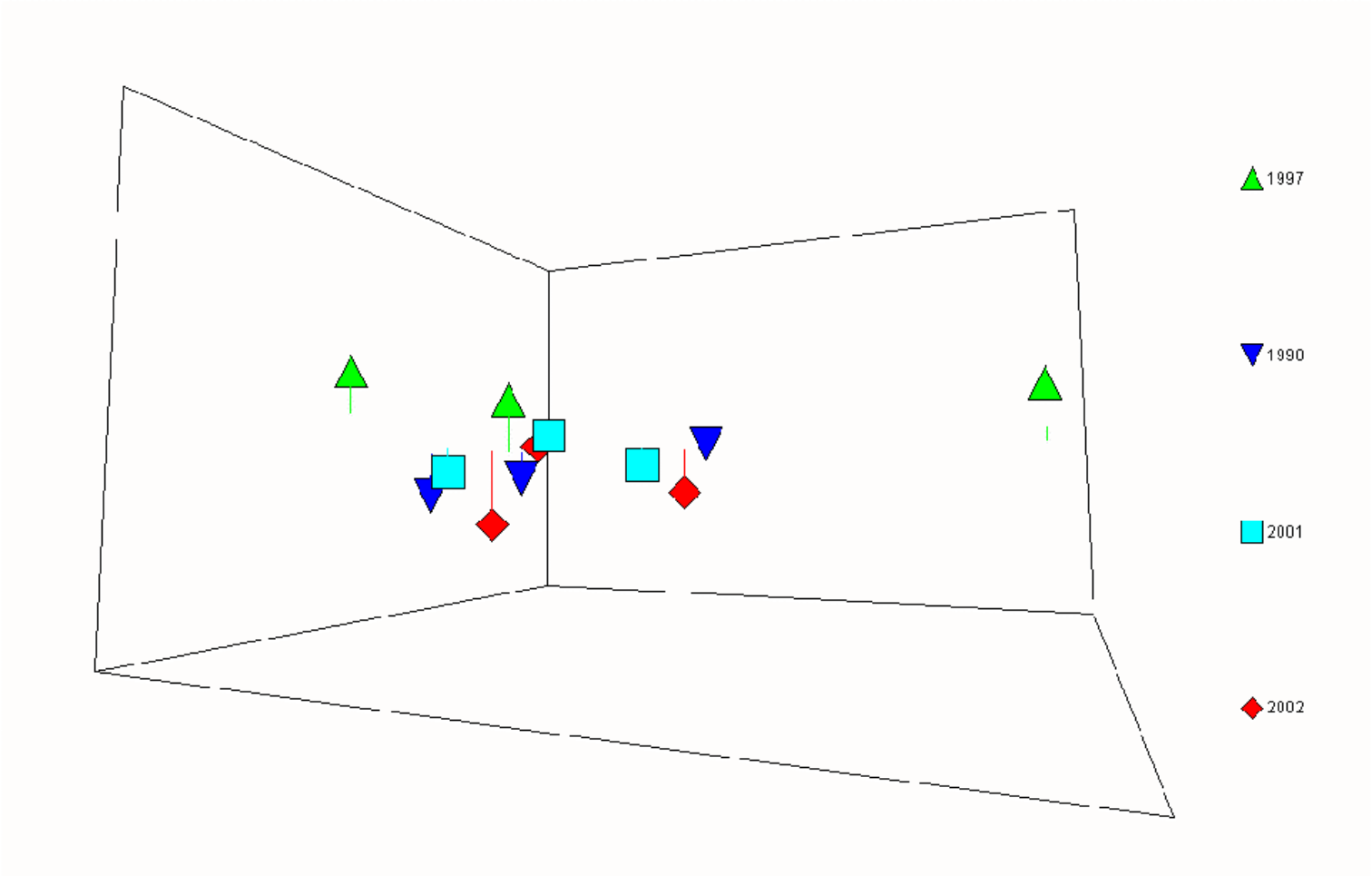


FIGURE 30. MDS-ordination plot of years (with depth zones as replicates) based on the proportion of coral reef epibenthic categories at CR2. Stress level = 0.04.

TABLE 24. Results of the 2-way crossed ANOSIM test* for significant differences of the structure of coral reef epibenthic communities at CR2.

Compared factors	Global R value	Significance level
Year	0.400	**0.0%**
Depth	0.380	**0.0%**
Year x Depth	0.256	**2.8%**

*Square-root transformed data. Based on 5,000 permutations.

TABLE 25. Results of the pairwise ANOSIM significance test* between years at CR2.

Years compared	Global R value	Significance level
1997 vs 1998	0.225	**5.0%**
1997 vs 2001	0.300	**1.0%**
1997 vs 2002	0.450	**0.2%**
1998 vs 2001	0.677	**0.1%**
1998 vs 2002	0.520	**0.0%**
2001 vs 2002	0.281	**0.8%**

*Square-root transformed data. Based on 5,000 permutations.

TABLE 26. Results of the pairwise ANOSIM significance test* between depth zones at CR2.

Depth zones compared**	Global R value	Significance level
I vs II	0.191	**3.9%**
I vs III	0.613	**0.0%**
II vs III	0.378	**0.0%**

*Square-root transformed data. Based on 5,000 permutations.
**I= <4 m; II= 4-8 m; III= >8 m.

TABLE 27a. Results of the SIMPER analysis of years 1997 vs 1998 at CR2.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1997	Abundance 1998
1997 vs 1998	Cyanobacteria	8.25	0.02	0.09
(35.74%)	Filamentous algae	7.81	0.27	0.17
	Erythropodium caribbaeorum	7.76	0.04	0.10
	Macroalgae	7.28	0.22	0.22
	Halimeda spp.	5.44	0.01	0.05

TABLE 27b. Results of the SIMPER analysis of years 1997 vs 2001 at CR2.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1997	Abundance 20
1997 vs 2001	Filamentous algae	10.04	0.27	0.37
(33.47%)	Macroalgae	7.74	0.22	0.23
	Porites porites	6.72	0.02	0.08
	Total algae	6.57	0.43	0.63
	Erythropodium caribbaeorum	6.29	0.04	0.04

TABLE 27c. Results of the SIMPER analysis of years 1997 vs 2002 at CR2.

Group (% dissimilarity)	Species/category	Percentage contribution	Abundance 1997	Abundance 20
1997 vs 2002	Cyanobacteria	11.73	0.02	0.15
(35.70%)	Filamentous algae	9.16	0.27	0.33
	Macroalgae	7.64	0.22	0.15
	Porites porites	5.92	0.02	0.07
	Encrusting algae	5.05	0.01	0.03

TABLE 28a. Results of the SIMPER analysis of years 1998 vs 2001 at CR2.

Group (% dissimilarity)	Species/category	Percentage ution	Abundance	Abundance
1998 vs 2001	Cyanobacteria	9.24	0.09	0.01
(31.12%)	Filamentous algae	7.22	0.17	0.37
	Erythropodium caribbaeorum	6.15	0.10	0.04
	Porites astreoides	5.96	0.09	0.03
	Porites porites	5.81	0.04	0.08

TABLE 28b. Results of the SIMPER analysis of years 1998 vs 2002 at CR2.

Group (% diss	Species/category	Percentage contribution	Ab 1998	nce 2002
1998 vs 2002	*Erythropodium caribbaeorum*	8.38	0.10	0.02
(29.64%)	Filamentous algae	6.74	0.17	0.33
	Halimeda spp.	6.36	0.05	0.00
	Macroalgae	6.21	0.22	0.15
	Porites porites	5.93	0.04	0.07

TABLE 29. Results of the SIMPER analysis of years 2001 vs 2002 at CR2.

Group (% dissimilarity	Species/category	Percentage contribution	2001	e 2002
2001 vs 2002	Cyanobacteria	14.54	0.01	0.15
(28.45%)	*Porites porites*	7.35	0.08	0.07
	Colpophyllia natans	6.47	0.04	0.04
	Erythropodium caribbaeorum	6.33	0.04	0.02
	Filamentous algae	6.22	0.37	0.33

factor influencing the observed differences in the structure of coral reef epibenthic communities at CR2. Filamentous algae, the encrusting gorgonian, *Erythropodium caribbaeorum*, and macroalgae were also important factors influencing community change between years 1997 and subsequent years (Table 27). A similar analysis carried out to data from years 1998 and subsequent years (Table 28) showed that cyanobacteria, *E. caribbaeorum*, filamentous algae and *Porites porites* were the most significant epibenthic components affecting the coral reef community variation. Finally, for the period of year 2001 to 2002, cyanobacteria causd the most significant variation in the coral reef community structure (Table 29). This analysis showed that coral reef communities are highly dynamic and change in community structure can result from shifts in the dynamics of different coral reef epibenthic components within relatively short time spans.

Indicators of disturbance effects at CR2.

The equitability component of the coral species diversity at CR2 was compared with a theoretical expectation for diversity by calculating the Caswell's *V* statistic for each depth zone and each year (Table 30). *V* statistic values were consistently negative and significantly distant from neutrality at depth zones II and III and all years, with the exception of depth zone III during 2001. V value at depth zone I was significantly distant from neutrality only in year 2002. Mean values through time were significantly distant from neutrality at depth zones II and III. But, yearly mean values were consistently distant from neutrality. These observations suggest that CR2 showed a coral diversity below the neutral model predictions and that some kind of stressful disturbance has

TABLE 30. Summary of the Caswell's neutral model *V* statistics for CR2.

Year	D	Depth zone II	Depth zone III	Mean
1997	-0.1242*	-6.0812	-10.8311	**-5.6788**
1998	-1.2956*	-2.6715	-3.0122	**-2.3264**
2001	-1.9351*	-6.0715	-0.6977*	**-2.9014**
2002	-3.8291	-4.5971	-5.3966	**-4.6076**
Mean	***-1.796****	***-4.8553***	***-4.9844***	***-3.8786***

*Non-significant departures from neutrality. Values >+2 or <-2 indicate significant departures from neutrality.

TABLE 31. Summary of Pearson correlation matrix for different coral species diversity indices at CR2 through time.

Variable 1*	Variable 2*	Correlation	Correla 1998	2001	Correlation 2002
S	*N*	0.572	0.669	0.151	0.287
S		0.962	0.990		0.990
S		-0.371	0.448		0.589
S	Brillo	0.889	0.910		0.836
S	Fishe	0.881	0.970		0.960
S	H'n (l	0.890	0.917		0.864
S	1-λ	0.432	0.777	0.615	0.757
N	*d*	0.335	0.561	-0.032	0.157
	J'n	-0.638	0.200	0.276	-0.008
N	B	0.520	0.660	0.359	0.199
N	Fisher	0.137	0.469	-0.126	0.050
N	H'n (log *e*)	0.323	0.600		0.146
N	1-λ	-0.066	0.48	0.238	0.125
d	J'n	-0.246	0.465		0.611
d	Brillouin	0.845	0.893		0.835
d		0.973	0.994		0.986
d	H'n (l	0.915	0.913		0.872
d	1-λ		0.778		0.766
J'n	Brillo	-0.016	0.755	0.921	0.929
J'n	Fishe	-0.138	0.461		0.546
J'n	H'n (l	0.048	0.759		0.914
J'n	1-λ	0.638	0.897	0.956	0.970
rillouin	Fisher	0.753	0.863	0.644	0.767
Brillouin	H'n (log *e*)	0.966	0.996	0.991	0.996
Brillouin	1-λ	0.746	0.951	0.979	0.987
Fisher	H'n (log *e*)	0.871	0.891	0.726	0.815
Fisher	1-λ	0.496	0.764	0.588	0.699
H'n (log *e*)	1-λ	0.778	0.952	0.976	0.979

**S*= Species richness; *N*= Abundance; *d*= Margalef's species richness [*d*= (*S*-1)/Log(*N*)]; J'n= Evenness; Brillouin [H= $N^{-1}\log_e\{N!/(N_1!\ N_2!\ldots\ N_s!)\}$; Fisher= Fisher's α; 1-λ'= Simpson evenness [1-λ'= 1-{$\Sigma_i\ N_i(N_i-1)\}/\{N(N-1)\}$].

caused a significant decline in diversity at all depth zones and at all years during the 5-year long study. These results are consistent with the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979).

The Pearson correlation matrix for CR2 is summarized at Table 31. The correlation between species richness (*S*) and abundance (*N*) was moderate for years 1997 and 1998, but fairly poor in the remaining years. There were a few species with a high number of colonies and many colonies with a low abundance, a condition that caused a lack of a significant correlation between both parameters. There was a very strong correlation between *S* and the Margalef's species richness (*d*) at all years, which can be explained by the fact that *d* changes with any change in *S* and in the log *N*. *S* and J'n showed a highly variable correlation pattern, with a weak negative correlation at the beginning (1997, 1998) and a moderately positive at the end of the study (2002). A similar pattern was observed between d and J'n. This pattern could be explained by the fact that during 1997 and 1998 the coral community was dominated by a few species with a high abundance. There were also several species with very low abundances. This caused the J'n to be relatively high, but variable, causing a lack of correlation with *S* that is a fixed value. This was followed in years 1999 to 2001 by a major physiological fragmentation process of the colonies of dominant corals, such as *Montastrea annularis* (Figure 21), as a result of recurrent White Plague Type II outbreaks and subsequent algal overgrowth. This caused an effect of increasing the abundance of *M. annularis* colonies. During that time many rare species also disappeared from CR1, causing a consistent

decline in J'n. Given the lower variation in J'n, there was a stronger correlation. A relatively similar pattern was also observed between *S* and 1-λ'.

S and Brillouin showed also a high correlation, since values of the Brillouin index vary with the variation in *S* and *N* (Table 16). A similar pattern was observed between *S* and Fisher's α, and between *S* and H'n. Also, between *d* and Brillouin, Fisher and H'n, between Brillouin and H'n, and between Brillouin and 1-λ'. Fisher and H'n, and H'n and 1-λ' showed also significant correlations.

Finally, a *K*-dominance curve (Lambshead et al., 1983) was constructed based on the % of cumulative dominance (abundance) of corals and species ranks to determine if there was any significant disturbance effect on the coral community (Figure 31). There were shifts in the position of the *K*-dominance curve for each year that could indicate stressful conditions at CR2.

Discussion.

Shifts in the structure of coral reef communities.

Comparison of annual coral decline rates with the wider Caribbean region.

There have been major shifts in the structure of coral reef epibenthic communities within the LPCMFR between years 1997 and 2002 (Tables A3 and A4). The % of living coral cover has plummeted a magnitude of 41 to 55% at CR1 and from 37 to 54% at CR2. Assuming a linear decline through time, annual coral decline rates at CR1 have fluctuated between 8.21 and 11.04%, and between 7.31 and 10.80% at CR2. Mean values were 9.74% at CR1 and 9.23% at CR2. These rates are considered dangerously high and only a total of 14 out of 71 surveyed coral reefs (19.7%) not deeper than 12 m, with long-term monitoring programs with more than 5 years of data, and with an initial % of coral cover of at least 20%, have shown annual coral decline rates of 7.31% (lower value documented in this study) or higher (Table A5, modified after Gardner, 2002). The northern Caribbean sub-region (Florida, Bermuda) had a mean coral annual decline of 1.61%, with 2 out of 14 surveyed reefs (14.3%) showing annual coral decline rates higher than 7.31%. Those included Jaap Reef (8.27%) and Western Sambo Reef (12.77%). The central Caribbean sub-region (Jamaica) showed the highest mean annual coral decline rate of the wider Caribbean with 6.58%. A total of 4 out of 20 surveyed reefs (20%) showed annual coral decline rates higher than 7.31%. These included the *Acropora palmata* zone (7.65%) and other reef zone close to the Discovery Bay Marine Laboratory

(9.87%). Also, the Pear Tree Bottom Reef (12.29%) and Montego Bay (14.18%), which was the highest mean value of the entire Caribbean region.

Mean annual coral decline in the northeastern Caribbean sub-region (Puerto Rico, U.S. Virgin Islands) averaged 3.56%, ranking third among all biogeographic regions of the Caribbean. A total of 6 out of 21 surveyed reefs (28.6%) showed mean annual coral declines equal or higher than 7.31%. All of these were documented in this study at LPCMFR. Therefore, it is alarming that coral reefs within the LPCMFR are showing the highest annual coral decline rates ever documented for this region of the Caribbean. The Meso-Caribbean sub-region (México, Belize, Costa Rica, Panamá) showed the second highest annual coral decline rate (6.00%), with 2 out of 10 surveyed reefs (20%) showing mean values larger than 7.31%. These included Porvenir Reef and Wichubhuala Reef, Panamá, with 8.75 and 8.80%, respectively. Finally, none of the 6 surveyed reefs from the southern Caribbean sub-region reached annual coral decline rates of 7.31% or higher.

A total of 13 out of the 71 surveyed reefs (18.3%) showed an increase in coral cover through the wider Caribbean region (Table A5). But, only 5 out the 71 reefs (7%) showed an annual coral decline rate exceeding 10%, and 2 of these are located at the depth zone I of CR1 (11.04%) and CR2 (10.80%), respectively. An alarming total of 6 out of the 14 surveyed reefs (43%) through the wider Caribbean region showing an annual coral decline of 7.31% or higher are located within the LPCMFR. Thus, this suggests that coral decline rates documented in this study in Culebra Island are not normal and can be comparable to coral reefs which have collapsed due to a combination

of natural and anthropogenic factors which include hurricanes, the Long-Spined Sea Urchin, *Diadema antillarum*, die-off, coral disease outbreaks, herbivore overfishing and water quality degradation (Knowlton et al., 1990; Hughes, 1993, 1994; Steneck, 1993; Shulman and Robertson, 1996; Hernández-Delgado, 2000, 2001; Keller, 2001; Wheaton et al., 2001; Porter et al., 2002).

The role of algae and cyanobacteria on the coral reef phase shifts.

Besides the coral cover decline, there were also major declines in coral species richness of 33 to 40% at CR1, and about 23% at the two deepest depth zones at CR2, between years 1997 and 2002. Also, colony abundance declined by a factor of 32 to 58% at CR1, and 27 to 36% at the two deepest depth zones at CR2, while coral species diversity (H'n; H'c), and evenness (J'n; J'c) showed also a decline during the same period of time. But, there were significant increases in the % of total algal cover of magnitudes that ranged from 21 to 73% at CR1, and from 12 to 107% at CR2. Similarly, macroalgal cover showed a dramatic increase of 308 to 560% at CR1, and from 25 to 231% at the two deepest depth zones at CR2. There was also a 3,895% increase in the % of filamentous algal cover at depth zone I of CR2. These results account for a major phase shift in the dominance of corals to a dominance by algae.

Coral:algal ratios at depth zone I in CR1 showed a decline from the original value of 0.996:1 in 1997, to 0.369:1 in 2002 (Table A6). At depth zone II, there was also a major decline in the coral:algal ratio, from 2.706:1 in 1997 to 0.785:1 in 2002. A similar trend was documented at depth zone III, with a decline from 1.605:1 in 1997 to 0.652 in

2002. Coral:algal ratios showed a similar trend at CR2 during the same period of time (Table A7). At depth zone I it declined from 4.162:1 to 0.382:1, while at depth zone II, there was a drop in the coral:algal ratio from 1.109:1 to 0.627:1. There was a similar trend at depth zone III, with a drop from 0.834:1 to 0.373:1. These observations suggest that coral mortality has been widespread through the different depth zones of the reef community. The observed increase in algal cover in Culebra, coupled with the decline in coral cover and the physiological fragmentation of large coral colonies between 1997 and 1998, followed by a major mortality of many of the surviving physiological fragments and the small-sized, rare species, between 1998 and 2002, might be an unequivocal first sign of a catastrophic coral reef decline associated to a possible combination of long-term effects of coral disease outbreaks, still low sea urchin densities, chronic water quality degradation, remote sedimented runoff and indirect fishing effects, as suggested previously by Hernández-Delgado (2000, 2001).

Several studies have documented significant increases in algal cover in Caribbean coral reefs associated to simultaneous catastrophic declines in living coral cover. Liddell and Ohlhorst (1993) observed an increase in macroalgal cover in Jamaica with a magnitude of 1,535%, and a 117% increase in filamentous algal cover within a period of 9 years, an annual increase rate of 171% and 13%, respectively. Hughes (1994) documented a 2,200% increase in algal cover in Jamaica within a period of 17 years, an annual increasing rate of 138%. Shulman and Robertson (1996) observed an annual increase in macroalgal cover of 186% and in filamentous algal cover of 29% in Panamá. In addition, Ogden and Ogden (1993) reported that coral reefs in Panamá were 50-100%

overgrown by algae within a period of two decades. Steneck and Dethier (1994) also documented that following the mass mortalities of *Diadema antillarum* in Jamaica, there was a 14% increase in macroalgal biomass in a 1 m deep backreef community within a period of 9 years (1.5% annual increase rate). But, filamentous algal turf biomass increased by a factor of 162% (18% annual increase rate), a fact that suggests that territorial damselfishes could have successfully taken over the reef in the absence of competition by *D. antillarum*. At the shallow forereef, macroalgae, which were totally absent from their study area, successfully invaded the reef and became the dominant algal functional group in terms of biomass. Algal turf biomass also increased by a factor of 28% (3% annual increase rate). However, at the deep forereef, algal turf biomass declined by a factor of 77% within a period of 5 years (15% annual decline rate), but macroalgal biomass increased by a dramatic magnitude of 22,156% (4,431% annual increase rate). These data further suggest that, following a major decline in herbivory, coral reef epibenthic communities can rapidly shift from a coral-dominated state to an algal-dominated one, and that this could be irreversible even within nearly a human generation time scale. It also suggests that in coral reefs subjected to intense overfishing, such as Jamaica (Munro, 1983; Koslow et al, 1988; Hughes, 1994), annual algal cover increases can be more dramatic. But, when herbivory decline occurs with a simultaneous increase in nutrient concentrations, sedimentation, etc. (discussed below), these phase shifts could be more pronounced.

Other epibenthic components showed minor to wide fluctuations at the LPCMFR during this study, but the % of cyanobacterial cover rocketed by a factor of 294 to 883%

at depth zones II and III of CR1, respectively, when compared to 1997 levels. At CR2, cyanobacterial cover increased by a factor of 183 to 3,200%. As a matter of fact, most of the shifts observed in the algal community between years 2001 and 2002 were associated to the cyanobacterial bloom. In addition, the % of sponge cover increased at CR1 by 94 to 113% at depth zones II and I, respectively, and from 78 to 560% at CR2 during the same period of time. These results are in agreement with previous observations made by Hernández-Delgado (2000, 2001) and by Hernández-Delgado et al. (2000). Previous investigations of phase shifts in coral reef communities have often overlooked benthic, filamentous cyanobacteria, which generally have been grouped with turf algae (i.e, Steneck and Dethier, 1994). Benthic cyanobacteria could play an important role in the coral reef phase shifts, as they can be early colonizers of recently dead coral surfaces and disturbed substrates (Tsuda and Kami, 1973; Borowitzka et al., 1978; Larkum, 1988; Thacker et al., 2001). Large cyanobacterial mats have been similarly observed in freshwater benthic communities following disturbance. But its role has been mostly overlooked most probably because traditional monitoring methods have not been adequate in discriminating cyanobacteria in the field and traditional statistical analyses have failed to weight and discriminate their effects on producing phase shifts in the coral reef community structure. This is one of the most powerful reasons to support the use of multivariate analysis to characterize these phase shifts throughout long-term monitoring.

Cyanobacteria can rapidly overgrow exposed coral skeletons following disturbance associated to disease outbreaks (i.e., White Plague, any of the band diseases), predation, tissue abrasion or other epizootics, by preemptive outcompetition of other

coral reef taxa. Such rapid colonization can result in highly localized increased nitrogen fixation rates (Larkum, 1988), which could produce a localized "micro-eutrophication" effect by refueling unpalatable macroalgal overgrowth such as the one observed in this study with the brown algae *Dyctiota* spp. Thus, the possible combination of this natural increase in nitrogen fixation by cyanobacteria in small spatial scales with the low but chronic suspected eutrophication in the coastal waters within the LPCMFR could be further indirectly triggering additional coral mortality beyond the direct mortality associated to the recurrent disease outbreaks observed within the period of 1998 to 2002. Eutrophication itself can trigger cyanobacterial mat blooms (Fong et al., 1993), and the combination of eutrophication and reduced herbivory levels can also promote an outburst of cyanobacterial growth (Miller et al., 1999). However, there have been studies showing a lack of correlations with either nitrogen or phosphorous concentrations (Colwell and Botts, 1994; Thacker and Paul, 2001).

Filamentous cyanobacteria are known to produce a wide variety of secondary metabolites, many of which are toxic or pharmacologically active (Nagle and Paul, 1998). Many of these compounds can deter feeding by several species of herbivorous fishes, sea urchins and decapod crustaceans (Pennings et al., 1996, 1997; Nagle and Paul, 1998, 1999; Paul, 2001). Therefore, it is suggested that blooming filamentous cyanobacterial mats can potentially escape herbivory due to the presence of toxic or unpalatable secondary metabolites. But also, the usually intermingled presence of cyanobacterial mats and unpalatable macroalgae, such as *Dyctiota* spp. can be the result of selective preference of palatable species by herbivores. Selective browsing by

herbivorous fishes on relatively palatable macroalgae might remove these competitors and allow establishment of relatively unpalatable macroalgae and cyanobacteria (Tsuda and Kami, 1973). Experimental evidence by Thacker et al. (2001) supports this idea.

The observed phase shifts in the structure of coral reef communities suggest that, besides the no-take zone designation back in 1999, epibenthic coral reef communities within the LPCMFR have kept declining at an alarming rate during the last five years and that there has been a major shift from coral-dominated- towards algal-dominated communities. Furthermore, data suggest that different epibenthic components could be significantly influencing the observed phase shifts and only multivariate statistical techniques can discriminate among these.

Detection of shifts in community structure by multivariate analyses.

Multivariate statistical techniques have been used very rarely on coral reef ecosystems. This includes the studies of Márquez et al. (1997), and Murdoch and Aronson (1999). But their approaches were focused on octocorals and scleractinian corals, respectively. Only McField et al. (2001) focused on the whole reef community level, therefore, including coral, different algal functional groups and Porifera. In this study, we used a similar approach. The combined use of multivariate and univariate analysis of digital video-based abundance (proportional cover) community data was able to discriminate significant differences in the structure of coral reef epibenthic communities at CR1 and at CR2 across a 5-year temporal scale. The method used in this study requires less time in the field than traditional quantitative methods and provides a

permanent qualitative and quantitative data archive capable of multiple analyses for various purposes. Another benefit of digital video-based sampling is that larger spatial units can be sampled with less effort (i.e., bottom time), thus reducing the typical small spatial scale heterogeneity (Carleton and Done, 1995). Digital video images are high quality and can allow us to identify reef epibnethic components to the lowest taxon possible, thus producing data with a significantly high taxonomical resolution. Classification and ordination analysis performed to categorical data with high resolution was more powerful than traditional methods in demonstrating that a major shift in the structure of coral reefs epibenthic communities have occurred at Culebra Island within the period of 1997 to 2002, despite the overall high similarity among sites and among successive years.

MDS ordination is considered the preferred alternative to represent the relationships among sites (Clarke, 1993). In this study, we used MDS ordination to represent relationships across a 5-year temporal scale with a relatively low stress (<0.08) that indicates a good tridimentional representation of a multidimensional coral reef community data set. Overall, the postulated differences between years at CR1 and CR2 appear to be valid and constitute unequivocal evidence that a major coral decline has produced a significant change in the structure of coral reef communities. Also, the SIMPER analysis technique was able to identify total algae, macroalgae and cyanobacteria as the most important indicator species, which accounted for the differences between years. Thus, this type of analysis could allow us to design specific studies and experiments to determine what environmental factors and mechanisms could

explain the observed changes. If such indicator species can be linked to specific environmental stressors (e.g., nutrients, sedimentation, turbidity), then the presence/absence or low abundance of these specific organisms would be useful in rapid ecological assessments (McField et al., 2001).

Causes of coral decline.

Caribbean-wide mechanisms or local causes?

The health of coral reefs at a global scale is of great concern. Through an elegant meta-analysis of a region-wide synthesis of temporal coral cover data, Gardner (2002) was able to demonstrate that a massive coral reef decline has occurred at all sub-regions through the wider Caribbean since the 1970s. The temporal variation in coral decline was highly significant both for the annual rate of change and for the absolute change of the % of coral cover. This suggests Caribbean-wide mechanisms rather than local causes. All time periods, except that of 1990-95, exhibited mean annual rates of declines that were negative and significantly different from zero. Also, only the time intervals of 1980-1985 and 1985-1990 showed significant negative changes in the absolute coral cover. During the last two decades, annual trends of coral decline at a Caribbean-wide basis showed negative peak levels in 1980, 1986, 1989, and 1998 (Gardner, 2002). This pattern coincided with the impacts of hurricanes during 1979 and 1980 (1980), and with a major increase in the % of macroalgal cover following the 1983-84 massive die-off of *Diadema antillarum* (1986). Also, it coincided with the coral mortality associated to the 1987-88 global coral bleaching event (1989) and with the 1998 El Niño-related regional

coral bleaching event (1998). The northeastern Caribbean sub-region showed the second highest mean annual rate of coral decline with nearly 7% (Gardner, 2002). However, according to his data, this sub-region ranked 5th among the 6 sub-regions in terms of the absolute change in the % of coral cover, with a mean decline of 6%. The highest mean absolute coral decline was observed in Jamaica (32%). Garnder (2002) data also suggest that there was a substantially high annual rate of coral decline (10%) during the 1980s in the northeastern Caribbean, but during the 1990s, annual decline rate dropped to about 1%.

The significance of our findings in Culebra Island is that the observed absolute coral decline of 37 to 55% within a period of only 5 years (1997-2002) has been about 517 to 817% higher than the absolute change in the mean % of coral cover for the northeastern Caribbean sub-region documented by Gardner (2002) and Gardner et al. (in review). Moreover, annual rates of decline in Culebra Island has been about 731 and 1,104% higher than those documented for the 1990s in the northeastern Caribbean sub-region. These levels resemble a lot to the massive coral decline that occurred throughout the entire Caribbean during the 1980s, particularly in this sub-region. Also, this decline rate can be compared to recent accounts of coral decline of approximately 54% (13% annual decline rate) during the mid 1990s at San Salvador Island, Bahamas (Ostrander et al., 2000). The lack of correspondence of the data from the LPCMFR with that of the northeastern Caribbean sub-region suggests that, although there could still be several Caribbean-wide phenomena occasionally affecting Culebra Island (e.g., storms, temperature stress, predation, disease), it appears that local anthropogenic factors (e.g.,

water quality degradation, eutrophication, sedimentation, overfishing) could be having a more significant impact on the observed coral reef decline rates. It also suggests that observed coral decline rates in Culebra are unprecedented for this sub-region of the Caribbean.

Local factors and their synergism with regional factors.

A combination of several regional natural and local anthropogenic factors have been pointed out as the major causes of the coral decline in Culebra Island. These include a possible synergistic combination of long-term effects of coral disease outbreaks, still low sea urchin densities, chronic water quality degradation, remote sedimented runoff and indirect fishing effects.

White Plague Type II.

Disease and epizootic outbreaks have become one of the most significant causes of mass mortalities of reef fauna through the wider Caribbean region during the last two decades (Lessios, 1988; Gladfelter, 1982; Rützler et al., 1983; Hughes, 1994; Clarke, 1996; Aronson and Precht, 1997, 2001; Bruckner and Bruckner, 1997; Santavy and Peters, 1997; Antonius and Ballesteros, 1998; Goreau et al., 1998; Richardson, 1998; Harvell et al., 1999, 2001; Alker et al., 2001; Cervino et al., 2001; Garzón-Ferreira et al., 2001). But one of the most dramatic coral decline effects caused by disease outbreaks during the 1990s has been that of the White Plague Type II (Richardson et al., 1998). There have been significant recurrent White Plague Type II outbreaks in Culebra Island between late 1997 and mid 2002 that have caused major localized coral mortality, mostly

affecting the *Montastrea annularis* species complex. This has been the major cause of coral decline due to its rapid propagation, at rates ranging between 1 and 3 cm/d (Hernández-Delgado, in review). Also, this has been the major cause of the coral species loss within the permanent monitoring transects, particularly of rare species with originally low abundances. No net tissue regeneration has ever been documented in White Plague-infected colonies of *M. annularis* (Hernández-Delgado, in review; unpublished data). In a minor degree, sporadic white band disease infections during the study, followed by a major outbreak during the summer of 2001, which affected 51% of the *Acropora cervicornis* colonies surveyed at the study site (Hernández-Delgado, unpublished data) was another cause of mortality. The 1998 El Niño event caused a major world-wide coral bleaching event (Wilkinson, 1998) which affected about 80% of the coral colonies at the study site (Hernández-Delgado, in preparation). However, there was no significant coral mortality in Culebra associated to this event.

Low herbivory or selective herbivory: The top-down model.

The fact that total algal cover has increased and that macroalgae have rocketed from the 1997 levels within the LPCMFR are in complete agreement with other studies which have documented coral mortality within other no take reserves. MacClahan et al. (2001b) found at a MFR in Kenya that, following the major coral mortality after the 1998 El Niño-related coral bleaching event, there was a 88% and 115% increase in turf and macroalgal cover, respectively, within a year within the MFR boundaries, and a 220% increase in macroalgal cover, with no significant change in filamentous turfs in those coral reefs under fishing pressure. These results suggested that low herbivory activities

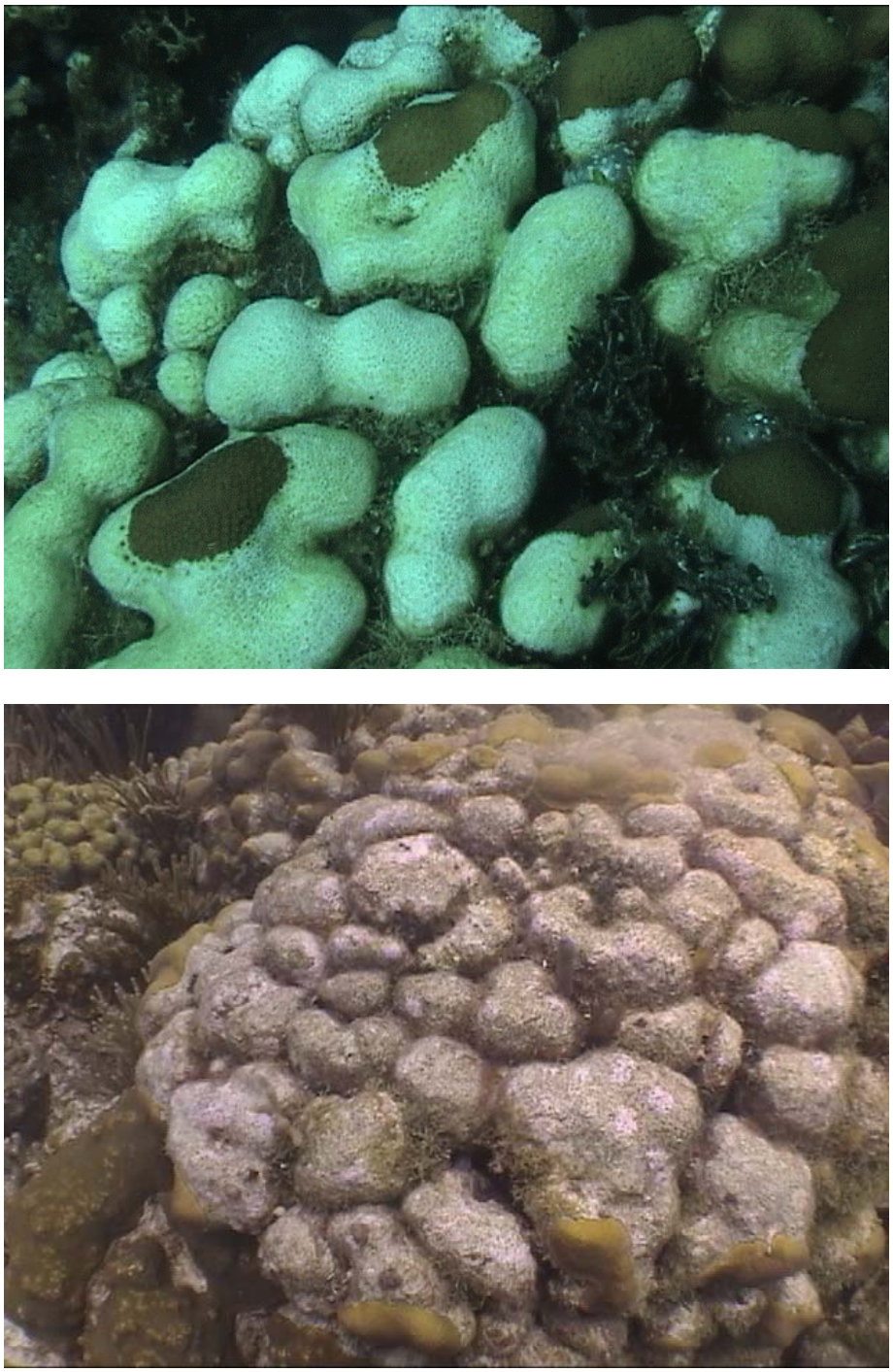


FIGURE 32. White Plague Type II mortality in *Montastrea annularis* (Ellis & Solander): A) Recent mortality (< 1 week); B) Old mortality (> 1 year).

upon macroalgal groups in overfished coral reefs, including no take reserves, rocketed algal cover atop of recently dead coral colonies. Thus, it is suggested that one of the alternative explanations to the observed algal increase could be that herbivory levels within the 3-year old LPCMFR are still low enough to allow a rapid increase in macroalgal cover following coral mortality, in this case, caused by lethal disease outbreaks.

But a major question arises. Is there lack of herbivory or actually selective herbivory upon palatable algal species, leaving behind the unpalatable ones? The observed condition of coral reefs in Culebra Island in this study resembles to what might be considered to be the early signs of a catastrophic chronic degradation rate similar to that observed in Jamaican coral reefs. There is evidence that algal cover dramatically increased in Jamaica following the mass mortality of *Diadema antillarum* (Liddell and Ohlhorst, 1986, 1987; Hughes, 1994). Coral reef fish stocks have also been severely overfished in Jamaica, including piscivore predators and large herbivores, such as scarids and acanthurids (Munro, 1983; Koslow et al., 1988). In addition, there is circumstantial evidence suggesting that territorial damselfishes (Pomacentridae) are the dominant fish group in many Jamaican coral reefs (Smith et al., 1993), thus further suggesting the onset of a cascade top-down driven effect caused by fishing activities, and providing a possible explanation to the increasing biomass of filamentous algal turfs in shallow coral reef zones.

Coral mortality triggered by diseases during this study was immediately followed by a rapid colonization by filamentous algae (Hernández-Delgado, 2000, 2001). Filamentous algae and macroalgae play a dominant role in the trophodynamics of coral reefs (Hatcher, 1997). Turf algae take advantage on the complex coral reef topography and are grazed by a diversity of species (Carpenter, 1997; Hixon, 1997, Penning, 1997) and are kept at exponential growth rate by continuous grazing (Carpenter, 1986). Filamentous algal cover at LPCMFR has kept consistently high due to the high densities of territorial damselfishes (Pomacentridae) (Hernández-Delgado, 2000). Hatcher and Larkum (1983) observed that turf algal stands showed little fluctuations under intensive grazing over time. Hernández-Delgado (2000) also documented experimental evidence that damselfish territorial behavior caused a significant decline in the tissue regeneration abilities of *Montastrea annularis*, due to preemptive competition by filamentous algae that rapidly colonized bare coral skeletons. Coral ability to regenerate tissue lesions is known to decline with lesion size (Bak and Van Es, 1980). Thus, large-sized lesions caused by coral disease outbreaks, bleaching-related mortality, and by parrotfish and damselfish bites are unlikely to recover due to the preemptive competition exerted by algae as suggested by other experimental studies (Lirman, 2001; McCook, 2001; McCook et al., 2001).

Filamentous algal turfs are the dominant stage in coral reefs under eutrophic conditions but with moderate herbivory (Hernández-Delgado, 2000; Fabricius and De'ath, 2001), suggesting that down-top regulatory processes (i.e., increasing dissolved nutrient concentrations) can also have a chronic mid- to long-term effect in shifting the

structure of coral-dominated to algal-dominated reef habitats (Knowlton, 1992). However, there are no evident direct signs of eutrophication at the study site (e.g., sewage outfalls, major sedimented run-off plumes). Hernández-Delgado (2000) demonstrated that damselfish densities showed a consistent significant increase at the study site, in combination with declining piscivore fish populations due to recreational spearfishing, suggesting that overfishing-related top-down regulation, in combination with coral lethal disease outbreaks, had become important indirect factors causing phase-shifts in the structure of coral reef epibenthic communities. Damselfish densities are still considerably high at the LPCMFR. However, predator fish populations are showing a significant recovery at the study site (Hernández-Delgado and Sabat, in preparation). Therefore, we can most probably discard the overfishing-related top-down short-term effect on coral decline at this stage. However, there is still selective illegal fishing pressure upon piscivore and large herbivore species within the LPCMFR. Thus, it is suggested, that we might be facing a shift in the structure of the coral reef epibenthic communities as a long-term indirect result of ecosystem overfishing. Also, it suggests that, even under recovering populations of fishery target species within the LPCMFR, coral reef epibenthic communities are not showing signs of recovery. This is in agreement with McClanahan et al. (2001a), which found that there were no significant effects of management within the Glover Reef Atoll no take zone, at Belize, and macroalgae were the dominant component of coral reef epibenthic communities regardless of fishing pressure. Thus, lack of management in the LPCMFR might be negatively affecting its coral reef epibenthic communities.

Another major concern is that most of the observed macroalgal cover increases were produced by the brown algae *Lobophora variegata* and *Dictyota* spp. Both species are known to produce secondary metabolites that make them unpalatable to most herbivore fish species. *Diadema antillarum* was a major herbivore upon both species (Szmant, 2001). This species suffered a massive die-off throughout the wider Caribbean (Lessios, 1988) and its recovery has been extremely slow (Moses and Bonem, 2001). Lack of sea urchin herbivory results in a major increase of macroalgae (Sammarco et al., 1974). Thus, it is suggested that moderate fish herbivory levels can remove most of the palatable algal cover, but lack of sea urchin herbivory, can allow brown algae to thrive. This dominance can become more strong due to the recent association between brown macroalgae and filamentous cyanobacterial mats. The latter also is known to produce toxic secondary metabolites that can deter grazers. But the panorama can be completely different if algal growth is fueled by an unsuspected factor: dissolved nutrients.

Interaction among degrading factors: The down-top model.

The observed increase in the % of macroalgal cover brings into light some other possible causes of coral decline that have not been completely understood at the LPCMFR: dissolved nutrients. According to Carpenter (1997), under elevated nutrient concentrations and reduced grazing pressure, macroalgal biomass and cover can show a significant increase. There is a direct interaction among nutrient concentrations and herbivore activity in determining the dominant benthos in the coral reef (Littler and Littler, 1984). Under low nutrient concentrations, abundant herbivory can shift the epibenthic community structure from one dominated by filamentous algae to one

dominated by corals. This is due to the opening of reef substrate to coral recruits (Sammarco, 1980) and the exploitative competition between herbivore fishes and *Diadema antillarum* (Hixon, 1997). But, under high nutrient concentrations, abundant herbivory could shift the community structure from filamentous-dominated to coralline algae-dominated (Smith et al. 2001). However, under low herbivory levels, as a result of the mass mortality of *D. antillarum* (Liddell and Ohlhorst, 1986) and/or as a result of serial or ecosystem overfishing (Williams and Polunin, 2001), coral reef communities could shift from coral-dominated to filamentous algae-dominated. Similar observations were already suggested within the LPCMFR (Hernández-Delgado, 2000, 2001). However, under low herbivory levels, and under moderate to high nutrient levels, the coral reef community structure could shift from coral-dominated, or filamentous algae-dominated, to macroalgae-dominated (Smith et al., 2001; Stimson et al., 2001). Therefore, even a slight increase on dissolved nutrient concentrations (i.e., as a result of remote untreated sewage outfalls, infiltration of septic tanks, and/or increasing volumes of sedimented run-off), could trigger a major mid- to long-term increase in macroalgal cover. Culebra Island suffer from these three anthropogenic threats to coastal water quality, but there is no recent quantitative monitoring data to support this hypothesis.

The eutrophication hypothesis suggests that increasing nutrient levels, coupled with still low fish herbivory levels, should have produced an increase in the palatable macroalgal cover. However, this study showed that actually unpalatable brown algal corticated macrophytes *Lobophora variegata* and *Dyctiota* spp. are the dominant components of the algal community, thus suggesting that the low densities or nearly

absence of *Diadema antillarum* appears to be more significant than the moderately low densities of large herbivore fishes such as parrotfishes (Scaridae). McClanahan et al. (2001a) found also that brown fleshy algae were the dominant algal group within a no take fishery reserve in Belize. Recent studies regarding the ecological aspects of algal community dynamics have failed to find effects of nutrient enrichment on individual taxonomic algal groups (Thacker et al. 2001). However, Steneck and Dethier (1994) suggested that algal functional groups, instead of taxonomic groups, show a more predictable response to disturbance in a long-term basis. The observations made within the LPCMFR are in complete agreement with the model of Steneck and Dethier (1994) for a Caribbean coral reef algal community, which predicts that under low to moderate physical disturbance, and a high productivity potential, there will be a high biomass production by corticated macrophyte functional groups. Also, the relatively unchanged abundance of cyanobacterial mats during early years of this study, with the exception of years 2001 and 2002, was in agreement with the finding of Thacker et al. (2001), which found no response in this group to nutrient enrichment, even under low herbivory levels. This was also in agreement with the model of Steneck and Dethier (1994) for Caribbean coral reefs, which predicted no major changes with disturbance for this functional group. But then, it could be possible that the 2-year long cyanobacterial bloom could be a consequence of the increasing cover by brown macroalgal groups by taking advantage of the "natural refuge" created by the lack of herbivory upon the unpalatable algae. This is something that requires further studies.

Most of the macroalgal cover documented in this study (>90%) was actually the brown algae *Lobophora variegata* and *Dictyota* spp., which are known to produce secondary metabolites which provide them with a sort of unpalatable chemical compounds (Hay and Fenical, 1988). Similar observations were made by Goreau (1991) in Negril, Jamaica. Most herbivore fishes do not graze upon these algae. But, *Diadema antillarum*, has shown preference for these algal groups (Szmant, 2001). This can suggest that: 1) although densities of large individuals of herbivore parrotfishes are still low to moderate within the LPCMFR, fish herbivory activities within the LPCMFR could still be enough to exclude most of the other foliose palatable macroalgae; and 2) the low densities or nearly absence of *D. antillarum* has allowed both brown algal groups to dominate over filamentous and palatable foliose algae. Thus, it is hypothesized that actual shifting trends at the LPCMFR could be the result of the long-term top-down effects of natural mass mortalities of *D. antillarum* (Liddell and Ohlhorst, 1986; Hughes et al., 1987), the indirect long-term top-down effects of serial and ecosystem overfishing (Roberts, 1995), a combination of both (Hughes, 1994), and the possible down-top effect of slowly, but steadily increasing nutrient concentrations (Lapointe, 1997), which benefit nutrient-limited algal groups over nutrient-sufficient groups (Delgado and Lapointe, 1994; Schaffelke, 1999, 2001). Finally, the low, but steady increase in the abundance of incrusting red algae during our study, could point out an unsuspected sedimentation problem (Steneck and Dethier, 1994; Fabricius and De'ath, 2001), which has not been quantitatively assessed yet at the study site. There are no river plumes in the area, but major deforestation on a steep dirt road is frequent and runoff due to rain downpours could be an occasional source of sediment-laden run-off. In addition, frequent

recreational boat traffic close to CR1 when approaching Carlos Rosario Beach entrance can resuspend fine sediments (Hernández-Delgado, personal observations). There are no boat speed limit regulations within the LPCMFR. But, it is suggested that boat speeding could be causing sediment resuspension and a chronic long-term localized sedimentation effect on corals. This requires further investigation.

Increasing nutrient concentration and sedimentation rates are the final suspected cause of concern that could explain the observed changes in the structure of the LPCMFR coral reefs epibenthic communities. Hernández-Delgado (2000; in press) reviewed the existing literature regarding sedimentation effects in Puerto Rican coral reef communities and concluded that the majority of coral reefs have been subjected to heavy chronic sedimentation rates that have caused considerable long-term degradation. In the particular case of Culebra Island, there is an increasing concern that the rapidly increasing land clearing activities and development will adversely affect the coral reef and fish communities, which are the most significant tourist attraction of the Island. Hernández-Delgado et al. (2002) already observed highly significant differences in the structure of seagrass bed communities in Culebra Island when comparing the LPCMFR and other control stations outside the reserve that have been severely degraded due to upland activities such as land clearing causing highly sedimented run-off. The other major potential source of nutrients in Culebra is raw sewage. There is no sewage treatment plant, thus sewage can access the ocean via illegal discharges or through groundwater infiltration of septic tanks. Another potential source of nutrients and sediments is the Culebra Island municipal landfill which is adjacent and part of the

eastern boundary of the LPCMFR, and is a major source of runoff (Hernández-Delgado, 1994; personal observations). Hernández-Delgado et al. (2002) informed a high frequency of cyanobacterial mats in the seagrass habitats located close to the landfill, which might suggest potential groundwater infiltration. But this is something that require investigation.

A proposed mechanism of coral reef decline.

Rapid coral decline, in combination with macroalgal increases in Culebra Island, coral reefs suggest that eutrophication, sedimentation or a combination of both, could be one of the major causes of concern for the observed declines. The most feasible hypothetical explanation could be that the most significant cause of coral mortality has been the recurrent White Plague Type II disease outbreaks (Figure 33). Fueled by low, but increasing nutrient levels (e.g., from remote sources of raw sewage and sedimented run-off), macroalgae have successfully occupied recently opened coral skeleton surfaces by pre-emptive outcompetition of coral tissue. McCook (2001) found experimental evidence that, even under eutrophic conditions, algal turfs did not outcompeted *Porites lobata* in the Great Barrier Reef, Australia. In contrast, coral tissue was able to regrow and outcompete algal turfs under eutrophic conditions. Hernández-Delgado (2000) observed that tissue regeneration in *Montastrea annularis* was more vigorous under eutrophic conditions in Fajardo, P.R., when compared to coral colonies from Culebra Island, under more oligotrophic conditions. But, Hernández-Delgado (unpublished data) has never observed tissue regeneration on White Plague Type II-infected colonies of *M. annularis* in Culebra Island. Thus, it is suggested that some factor directly or indirectly

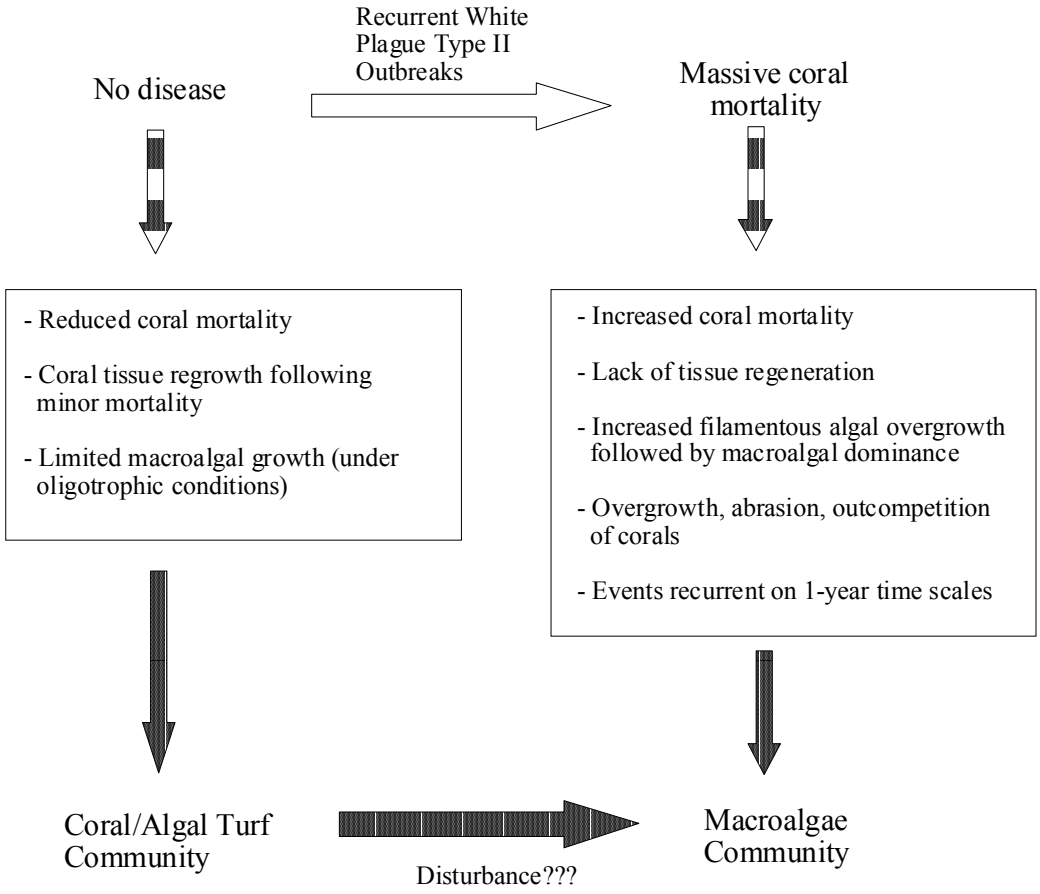


FIGURE 33. Top-down regulation model of a White Plague Type II disease outbreak. Each outbreak could cause major coral tissue mortality. Corals can not regenerate lost tissue and can become rapidly overgrown by algae. Damselfish territorial activities, low herbivory by *D. antillarum* and increasing nutrient concentrations could accelerate the onset of an algal-dominated stable state.

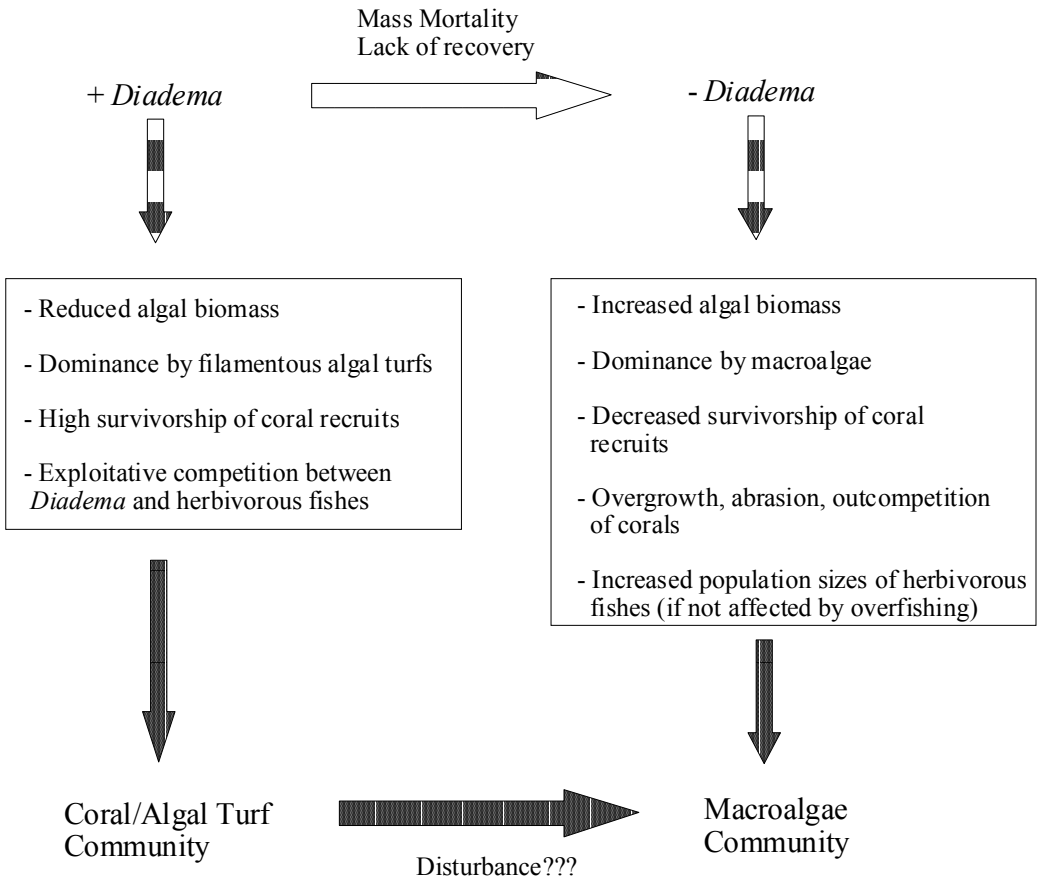


FIGURE 34. Top-down regulation model of herbivory by the Long-Spined Sea Urchin, *Diadema antillarum*. Low densities of *D. antillarum* can result in increased biomass of unpalatable brown algae (e.g. *Dictyota* spp., *Lobophora variegata*) which can occupy recently exposed coral skeletons following major disturbance (e.g., coral disease outbreaks). Increasing nutrient levels could accelerate the onset of an algal-dominated stable state. Modified after Carpenter (1997).

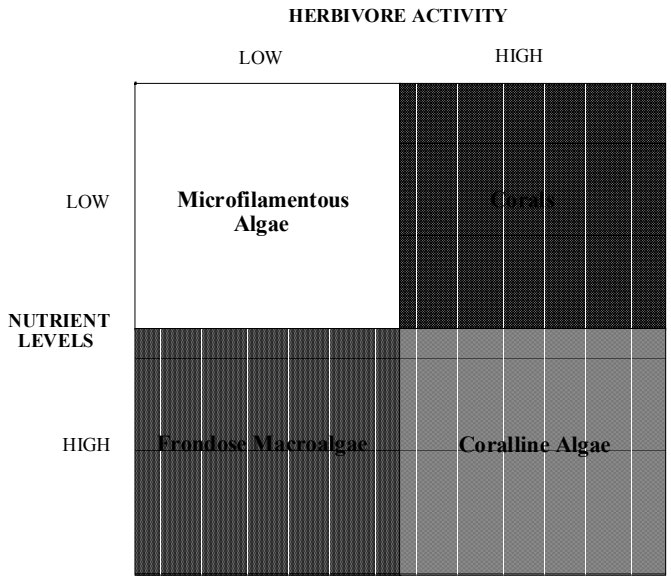


FIGURE 35. Theoretical predicted interactions among herbivory and long-term euttophication effects in determining the dominant epibenthic components on shallow coral reef systems (from Littler and Littler, 1984). Data from this study suggests that herbivore activity within the LPCMFR is still moderate to low and the observed shift from coral-dominated communities to macroalgal-dominated communities suggests that nutrient concentrations could be increasing. However, a comprehensive water quality monitoring program is required to assess such a major concern.

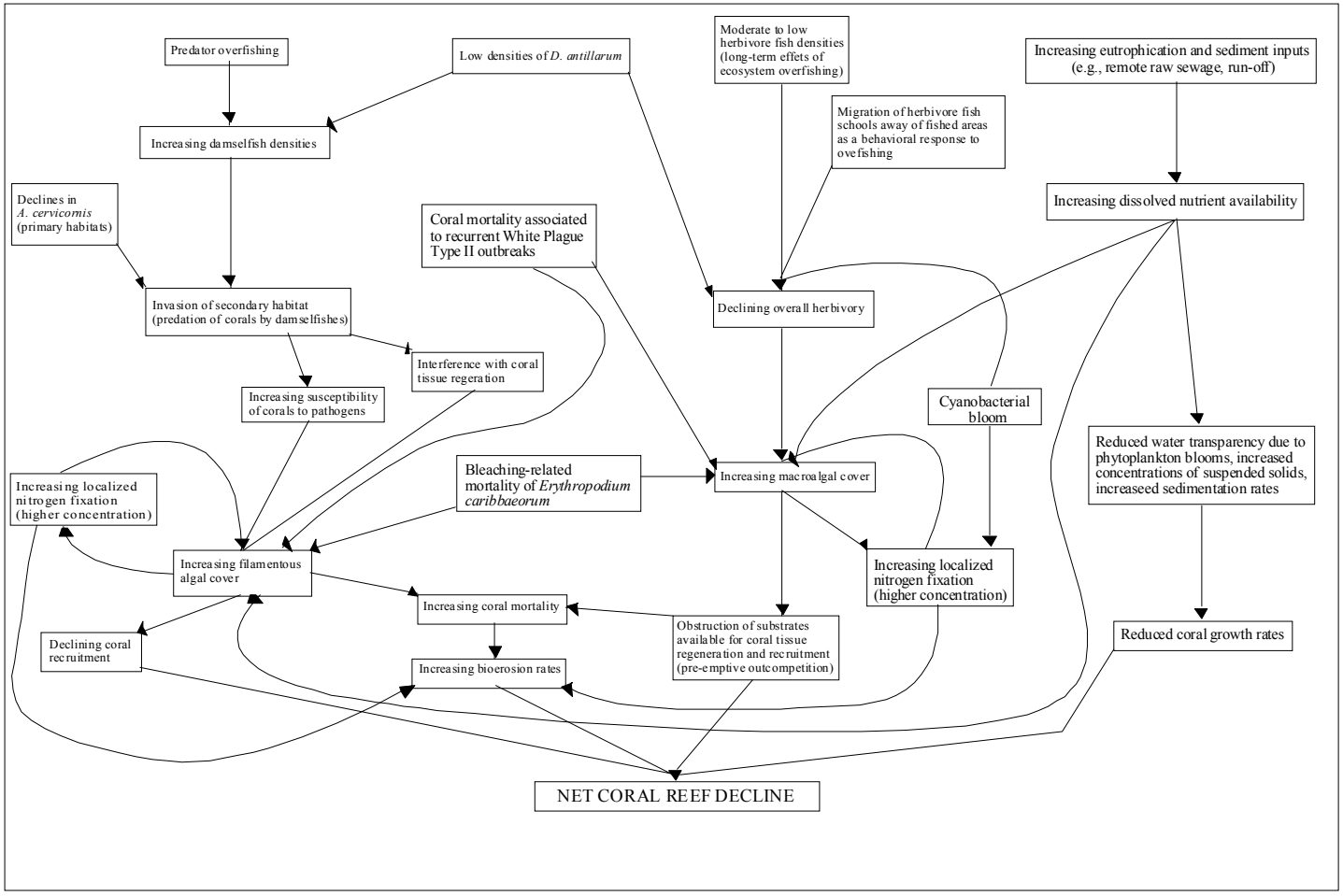


FIGURE 36. Combined top-down and bottom-up theoretical mechanisms involved in the recent coral reef decline documented in the LPCMFR. A combination of Caribbean-wide and local factors are being pointed out as major causes of decline (modified after Hernandez-Delgado, 2000, 2001).

associated to the disease itself could prevent tissue regeneration to occur. Therefore, algal turfs and/or macroalgae can become dominant by means of pre-emptive outcompetition of corals. Damselfish territorial behavior could also be influencing coral mortality rates (Kaufman, 1977; Lobel, 1980; Hernández-Delgado, 2000) and opening new reef surface to algal colonization. In addition, low herbivory associated to the still low densities of *Diadema antillarum* and still moderately low densities of Scarid herbivore fishes allow for a still high algal biomass (lack of top-down regulation of algal communities) (Figure 34). Finally, the cyanobacterial bloom could also influence to deter herbivores due to their intermingled growth with macroalgae and their production of toxic secondary metabolites. An integration of the herbivory and nutrient concentration interactions and the overall mechanisms have been outlined in Figures 35 and 36, respectively.

However, no attempts have been made yet to systematically measure sedimentation rates and/or sedimentation potential of cleared steep slopes and dirt roads in Culebra as done in other studies in the U.S. Virgin Islands (MacDonald et al., 1997; Anderson and MacDonald, 1998; MacDonald et al., 2001). Nutrients from sedimented run-off are known to promote heavy algal growth (Costa et al., 2000; in press). This has been already suggested for seagrass habitats in Culebra Island (Hernández-Delgado et al., 2002). A high density of unpaved roads in St. John (USVI) was associated to high sedimentation potential, high sedimentation rates, declining coral cover, poorer coral health and dominance by sediment-tolerant coral species (Nemeth et al., 2001). Thus,

sedimentation potential and sedimentation rates must be incorporated to any future long-term monitoring activities within the LPCMFR.

Effects on species diversity: Regional vs. local factors, threshold effects, multiple stable states, and Allee effects.

The use of univariate methods (e.g. Caswell test) showed that there was a significant decline in coral species diversity at both sampling stations within the LPCMFR. This brings into discussion if such a condition can cause a shift towards an alternate stable state (Knowlton, 1992) in the structure of coral community or in the overall coral reef community. The maintenance of a high coral species richness, as well as many other vital coral reef processes, can be influenced by a combination of regional and local factors, which can affect recruitment and post-recruitment processes (Cornell and Karlson, 1996). Regional factors include coral species pool, and larval transport, effects of lethal disease outbreaks, coral bleaching, sea surface current patterns, and the frequency and severity of hurricanes. Local factors include environmental conditions of the coral reef (e.g., water quality, sedimentation rates), local oceanography, local coral species pool, success of larval recruitment and post-recruitment processes, and a sort of anthropogenic factors, which include land clearing, sewage pollution and overfishing, among many others. Hernández-Delgado (2000) predicted that the onset of severe local chronic anthropogenic disturbances could significantly modify the environmental conditions of coral reefs by significantly influencing coral reefs over regional factors. For example, in the case of coral reefs in northeastern Puerto Rico, sedimentation and eutrophication is having the long-term effect of restricting the availability of local

habitats suitable for recruitment to the regional pool of potential colonists. A similar effect can have the rapid algal overgrowth within the LPCMFR. It is being proposed that local factors might have become more important in determining coral species richness in coral reefs under chronic anthropogenic degradation by eliminating rare and sensitive coral species. This may help to explain the dominance of disturbance-tolerant species and the absence of rare and low-recruiting coral species in anthropogenically-disturbed coral reefs. In addition, disturbance-tolerant species are typically brooding species characterized by having a highly aggregated distribution, a short larval stage, and high recruitment rates (Harrison and Wallace, 1990). Thus, coral reefs under degraded conditions do not depend much on the regional species pool to maintain richness, since disturbance-tolerant species are already dominant in a local scale.

Another important aspect regarding the influences of local vs. regional factors is that it is predicted that an increasing severity of local chronic anthropogenic disturbances can significantly enhance the adverse effects of any regional-scale disturbance (e.g., hurricanes, disease outbreaks, bleaching events) by producing a synergistic effect. Natural recovery of coral reefs from chronic disturbance is significantly slower than recovery from acute disturbance (Connell et al. 1997). Under this prediction, it is proposed that local anthropogenic stressors such as chronic slowly, but steady increases in nutrient concentrations and sedimentation rates, could trigger a severe negative effect of regional factors, thus most probably accelerating coral mortality rates and by significantly reducing coral tissue regeneration abilities. This could produce a cascade phase shift in a coral-dominated stage to an algal-dominated one (Knowlton, 1992). Such

type of potential sudden changes can be referred to as threshold effects (Knowlton, 2001).

Threshold effects can be described as non-linear responses of biological systems, including coral reefs, to any individual or group of environmental factors, where a variable (e.g., coral calcification) may remain constant over a range of saturation states, but then drop abruptly below some threshold value. Threshold effects are still unknown for many of the coral parameters (e.g., growth rates, calcification rates, reproduction, survival rates). Thus it is not surprising that massive coral declines are not linear events through time and future trends can not be accurately predicted unless we find a way to understand threshold effects. Allee effects (Knowlton, 1992, 2001) are classic threshold phenomena. For example, one immediate consequence of declining coral densities for a given species (e.g., *Acropora palmata, Acropora cervicornis*) will be a decline in gamete densities at a reef-wide scale caused by low population densities. This could result in gamete wasting, asynchronous reproduction, or low reproductive output per individual that can lead to recurrent reproductive failure. In the long-term, a sustained coral decline rate as the one documented in this study could produce a significant Allee effect for many rare coral species that could impair reproduction and might result in a long-term decline in coral species diversity. The observed decline in coral species diversity in our permanent transects could be reflecting the first stages of such process.

These conditions have been already documented within the LPCMFR coral reef systems (Hernández-Delgado, 2000; in review *a*).

Modeling alternate states of coral reefs in the LPCMFR.

Thus far, 5-year long-term data from the LPCMFR has shown a rapid coral reef decline, which was associated to a possible synergistic effect of regional factors and local chronic anthropogenic factors. If the actual decline trend sustains during the next few years, we might expect a catastrophic decline in living coral cover and a major phase shift in the structure of epibenthic communities within the next decade or two, probably beyond a point which could exceed the natural ability of recovery for coral reefs.

A model describing the different alternate states of coral reefs and the processes describing their dynamics was developed by Hernández_Delgado (2000), and applied to the LPCMFR coral reef systems (Figure 37). The model predicts that local anthropogenic stresses can rapidly drive a stable coral reef in a natural dynamic equilibrium to a threatened alternate state by means of a threshold effect. Depending on the frequency and severity of the causal factors, this process could occur in a temporal scale of months to a few years, similar to the one documented during this study in Culebra Island. According to the model, stable coral reefs, which are coral-dominated and characterized by having a high coral species richness, high percentage of living coral cover, high frequency of large colonies, high recruitment rates and low coral tissue mortality, would shift to a gradual decline to an alternate threatened state. In this alternate state, there would be a decline in coral species richness and non-reef-building species may become dominant. Also, there would be a decline in the percentage of living coral cover and in recruitment rates, particularly in massive, low-recruiting species (e.g.,

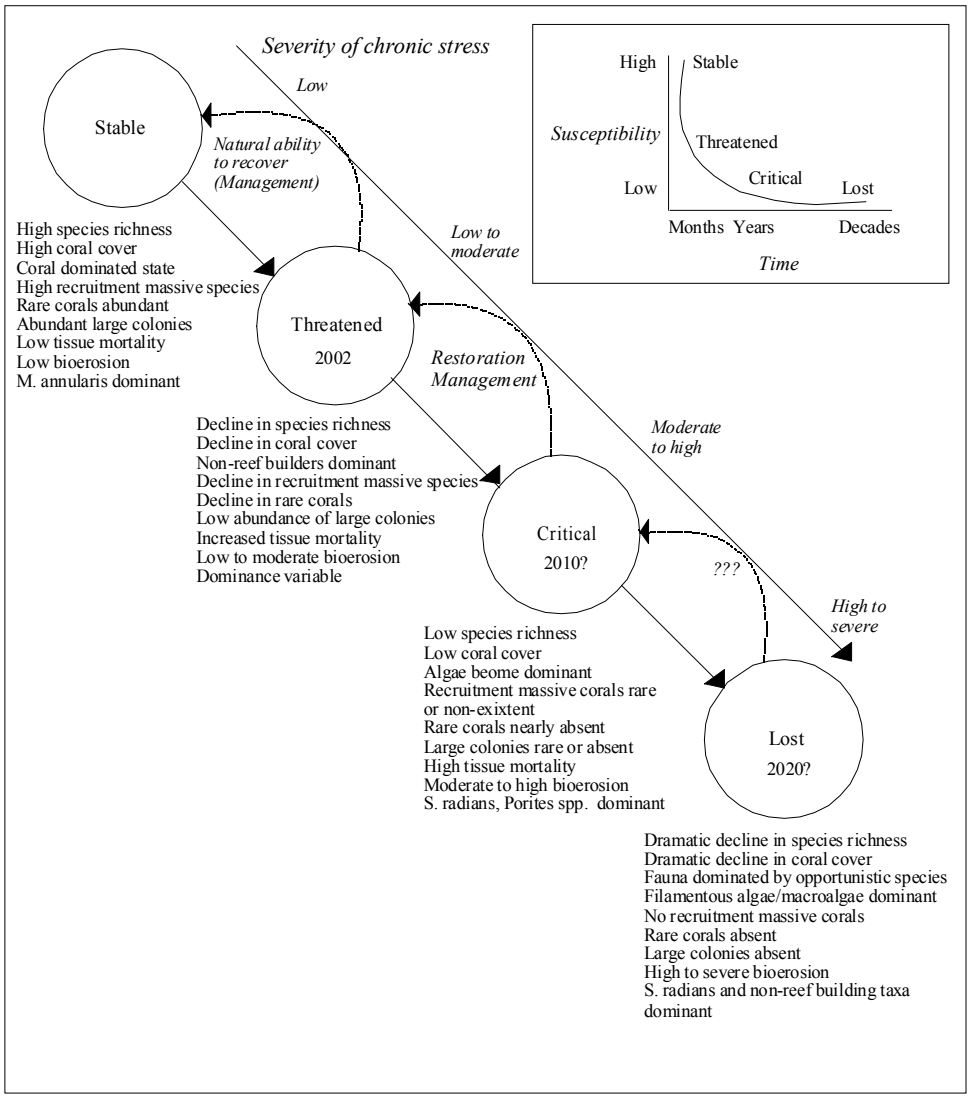


FIGURE 37. Theoretical predictions of alternate stable states of the LPCMFR coral reefs (based on Hernández-Delgado, 2000). The model predicts that the actual condition of the LPCMFR is a threatened one. But given the actual trends, and if there is no change in terms of the rapid coral reef declining rate, it is predicted that within the next decade or so, the LPCMFR may shift from a threatened condition to a critical condition within the next 5-8 years or so, and to a lost condition within the next 10-20 years or so.

Montastrea annularis) within the next 5 to 10 years. In addition, there would be a decline in the abundance of large coral colonies, an increase in partial tissue mortality, and bioerosion rates would be low to moderate. It is predicted that threatened coral reefs could still naturally revert to previous stable conditions if stressful conditions disappear or are eliminated though adequate management. This is where the LPCMFR coral reefs are standing now. Thus, it is imminent that further decline should continue unless immediate adequate management measures are implemented and enforced regarding the fishing prohibition and regarding controlling water quality, sedimentation rates, the operation of the Culebra Municipal Landfill, and the development activities in the steep slopes that characterize the western coast of the Island. This points out at the imperative need of a Culebra Island-wide management plan and land use plan, instead of only a LPCMFR-based management plan.

The model predicts that a further increase in the severity of chronic anthropogenic stressing conditions within the LPCMFR would drive threatened coral reefs within a decade or two to a decade into a critical condition (Figure 37). In this case, the alternate critical state would be characterized by having a lower coral species richness, a higher algal dominance and a significant decline in coral cover. Recruitment of massive coral species would be almost non-existent and recruitment would be dominated by opportunistic species. Rare coral species would be largely absent. Coral colonies would also suffer high partial tissue mortality and moderate to high bioerosion rates. Critical coral reefs may not have the ability to naturally recover from this state and may require a major time-consuming and costly restoration and management effort.

An additional increase in the severity of chronic anthropogenic stress will drive critical coral reefs into a lost state within a decade or two, which will be irreversible in terms of a human generation time scale (Figure 37). Severe degradation would include a dramatic decline in species richness and normally abundant coral species would become rare. Also, coral reef fauna would be dominated by opportunistic and non-reef-building species. Filamentous algae and macroalge would become the dominant epibenthic component, a trend which has already been documented within the LPCMFR coral reefs. Also, there will be a dramatic decline in coral cover, usually to values below 5%, as elsewhere in the main island of Puerto Rico (Hernández-Delgado, 2000; in press). Recruitment of massive coral species would be basically non-existent and rare coral species would be extremely rare or absent. Coral mortality would become a major cause of reef decline. Finally, these coral reefs would be subjected to severe bioerosion rates.

Conclusions.

Coral reef communities within the LPCMFR in Culebra Island are showing unequivocal signs of a severe rapid decline from a coral-dominated stage to an algal-dominated stage. Such coral reef decline rate is among the highest ever documented through the entire Caribbean region and is the highest ever documented in the northeastern Caribbean sub-region. Multivariate analysis showed that the major cause of changes in the structure of coral reef communities have been total algae, macroalgae, and cyanobacteria. This study suggests that we are starting to face the early results of a

combination of adverse effects associated to Caribbean-wide natural acute factors, such as recurrent White Plague Type II disease outbreaks, and the long-term local chronic anthropogenic effects of ecosystem overfishing, and sediment- and pollution-related increasing nutrient concentrations, which could accelerate this phase shift through different simultaneous top-down and down-top cascade pathways which require major studies.

These observations bring us back several facts. First, the LPCMFR is still lacking continuous vigilance. Therefore, illegal fishing activities are still occurring within the MFR boundaries without any regular enforcement by the PRDNER personnel. It is of paramount importance that fishing prohibition regulations are strictly enforced in a daily basis. This is difficult to accomplish when there is a lack of trained personnel and when the DNER assigns many other tasks to the management officer and patrolling personnel that are unrelated to the LPCMFR. There is a need to assign a higher budget and more management and patrolling personnel to the LPCMFR.

In addition, land-clearing and construction activities in Culebra Island have increased significantly in recent years due to the fast tracking procedures in the government permitting processes, which have resulted in an accelerated rate of project development and land-clearing activities. There has to be a serious commitment by the State Government of Puerto Rico and the Municipal Government of Culebra Island to cease approving and endorsing development projects through a fast tracking procedure for the ecologically-sensitive Culebra Island without the proper environmental

conservation measures. Third, there is an almost total lack of enforcement of environmental laws and regulations in Culebra Island. Therefore, land-clearing activities are undergoing unmonitored and unregulated in a daily basis. Thus, sedimented run-off has become one of the most severe anthropogenic threats to the coastal habitats of the Island, including seagrass beds and coral reefs. There is a need to establish Culebra Island-wide measures to prevent sedimented run-off to access sensitive coastal communities.

Moreover, it is still alarming that, without a few exceptions, *Diadema antillarum* is nearly absent from the whole LPCMFR. Thus, it is suggested that, together with a more serious enforcement of the fishing prohibition regulations within the LPCMFR, an experimental re-introduction of *D. antillarum* should be implemented to test if they can control the increasing brown macroalgal densities. In addition, there is a need to carry out a major characterization of water quality parameters within and around the LPCMFR, including sedimentation rates. The long-term effects of increasing small amounts of sedimented run-off and nutrients derived from storm waters, sedimented run-off and untreated wastewaters (due to the lack of a sewage treatment plant in Culebra Island) could be starting to have negative chronic effects in the structure of coral reef epibenthic communities within the LPCMFR. Data from coral reefs elsewhere in Culebra Island is already suggesting that (Hernández-Delgado, in preparation). Therefore, a permanent water quality monitoring program should be incorporated immediately to any long-term monitoring protocol for the LPCMFR.

A final recommendation to the DNER is that they should review their top priorities of the long-term coral reef conservation strategy and put more attention into studying the causes of coral reef decline in the LPCMFR, as well as in other Natural Reserves. This might require major funding for experimental studies. Another priority must be coral reef restoration, particularly within Natural Reserves. Population levels of candidate endangered species *Acropora cervicornis* and *A. palmata* have drop significantly during the last decade or so, that there might be an Allee effect strong enough that natural recovery is mostly impossible and will require a major restoration effect by means of coral farming methods. This will require major funding as well. All of these research efforts should provide the DNER with the basic tools to prepare a sound coral reef conservation and management plan for the LPCMFR. This should be a top one priority at this moment. Such efforts must provide a major participation to local base and fishermen communities and should seriously consider the possibility of developing a Culebra Island-wide management plan that can address the major land use problems as well. Too much funding and research efforts are being put into isolated merely scientific-based research projects, and more attention should be given in the future to management-oriented research.

It has been already shown that a marine protected area designation has not been enough to prevent further loss of coral species and living coral cover. This major decline requires management action well beyond the limits of the LPCMFR. The development model of Culebra Island requires a major review and reconceptualization from the actual one to an ecologically sustainable one. Otherwise, we will face a total coral reef collapse

within the next decade or two. A co-management model is the only alternative to establish and enforce conservation-oriented regulations within and outside the LPCMFR.

Acknowledgments.

This study was funded through the U.S. Coral Reef Initiative under contract #2002-000430. Also, previous parts of this study (1997-2002) were made possible by funding provided by the U.S. Coral Reef Initiative, the University of Puerto Rico-Sea Grant College Program (Omnibus Proposals Program), University of Puerto Rico-Dean of Graduate Studies and Research, the Caribbean Marine Research Center (National Undersea Research Program), and by PADI Foundation. Special thanks to the unconditional collaboration of many voluntary field assistants during long and tedious field surveys, specially to Jovino Márquez, Edgardo Acosta, and Mary Ann Lucking.

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