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POST-HURRICANE INITIAL RECOVERY OF *ACROPORA PALMATA* IN TWO REEFS OF THE YUCATÁN PENINSULA, MEXICO

Eric Jordán-Dahlgren and Rosa E. Rodríguez-Martínez

ABSTRACT

The initial recovery process of *Acropora palmata* in two distant reefs, impacted in 1988 by a hurricane (class V) and a tropical storm, was analyzed for a five year period. The reefs are located in different environmental settings and subject to moderate local human influence. Recovery estimations were based on censuses of live cover, size and number of colonies on the reef crest of both reefs, comprising different spatial scales and reef morphologies. It was observed that after a variable lag period the recovery process was well underway in both reefs. The main trend observed in the recovery patterns between and within the reefs is a high variability at different spatial scales, related to both the past spatial structure of *A. palmata*, and also to the new conditions resulting from the storm's impact. The implications of this variability in terms of assessing recovery at local (reef) scales are discussed.

The reef environment has been subject to relatively frequent storm-induced perturbations, both in past (Ball et al., 1967; Shinn, 1976; 1980), and present times (Stoddart, 1974; Woodley et al., 1981; Done, 1992). Scleractinian corals are affected in different degrees by storm waves, depending on colony form, condition and size (Glynn et al., 1964; Woodley et al., 1981; Massel and Done, 1993). Colonies of *A. palmata* are prone to storm damage because the species colonize the shallow areas of the reef, and its colonies show a relatively fragile branching growth-form (Glynn et al., 1964; Highsmith et al., 1980; Rogers et al., 1982). Such a situation is of interest because *A. palmata* has been a dominant species in most shallow water Caribbean reefs (Lightly et al., 1982; Lewis, 1984; Shinn, 1963), thus implying that the species should be able to rapidly recover from these natural catastrophes.

However, in reefs impacted by catastrophic storms, *A. palmata* surviving fragments and/or early settlers tend to suffer a high mortality on a local scale (Rogers et al., 1982; Rosesmyth, 1984). Historical evidence also indicates a decrease in the spatial extension of *A. palmata* on several reefs, both during recent (Jaap et al., 1989; Davies, 1982; Jordán-Dahlgren, 1992) and remote times (Shinn, 1963; Shinn et al., 1981). From these observations arises a concern that in present times success of recovery of *A. palmata* may be somehow inhibited, more so if the basic structure of the community is shifted by additional forcing factors (Hughes, 1994).

Are these observations temporal and spatially limited or are significant trends at a regional scale? *A. palmata* abundance changes on relatively short time frames (tens of years) may reflect a natural phenomenon typical of non-equilibrium communities (Connell, 1978; Knowlton, 1992; Rogers, 1993), driven by physical events and/or biological interactions (Antonius, 1981; Bak and Criens, 1981; Gladfelter, 1982). On the other hand, these changes may also reflect or be enhanced by anthropogenic effects at local, regional or global scales (Smith and Buddemeier, 1992).

Here, we report our findings on the recovery of *A. palmata* on reefs catastrophically impacted by a hurricane (Class V) and a tropical storm during the same year; severely affecting former healthy and abundant *A. palmata* stands. Recovery is understood in this

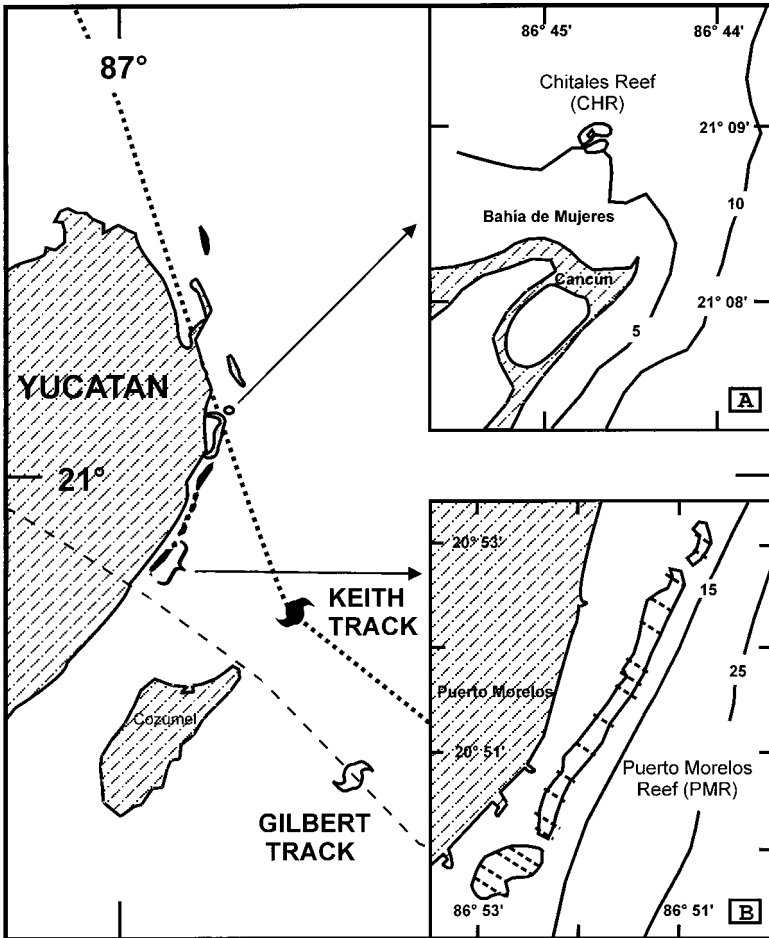


Figure 1. Study sites location and 1988 storm tracks. A. Chitalas Reef (CHR), square indicates sampled area. B. Puerto Morelos Reef (PMR), black dashed lines indicate the approximate location of transects. (Depth in meters).

paper as the capacity of the species to repopulate a reef zone to a similar dominance ranking as before the storms impact. Our observations are limited to the initial stages of the recovery process (up to 5 yrs after the storms) in different spatial scales and in different reef settings. This report does not evaluate the mechanisms (re-growth of survivors or sexual recruits) that allow for the recovery, but concentrates on analyzing the variability of the recovery process in a relatively large area.

STUDY AREA

This study was carried out on the reef crest of two reefs: Chitalas Reef (CHR) and Puerto Morelos Reef (PMR), in slightly different environmental settings, on the northeast coast of the Yucatán peninsula of Mexico (Fig. 1). CHR reef is a 200-m long bank reef (crest average depth of 1.5 m), located on the exposed eastern entrance of a shallow (-8 m), wide channel separating Isla Mujeres from the mainland. PMR is a 7-km long barrier

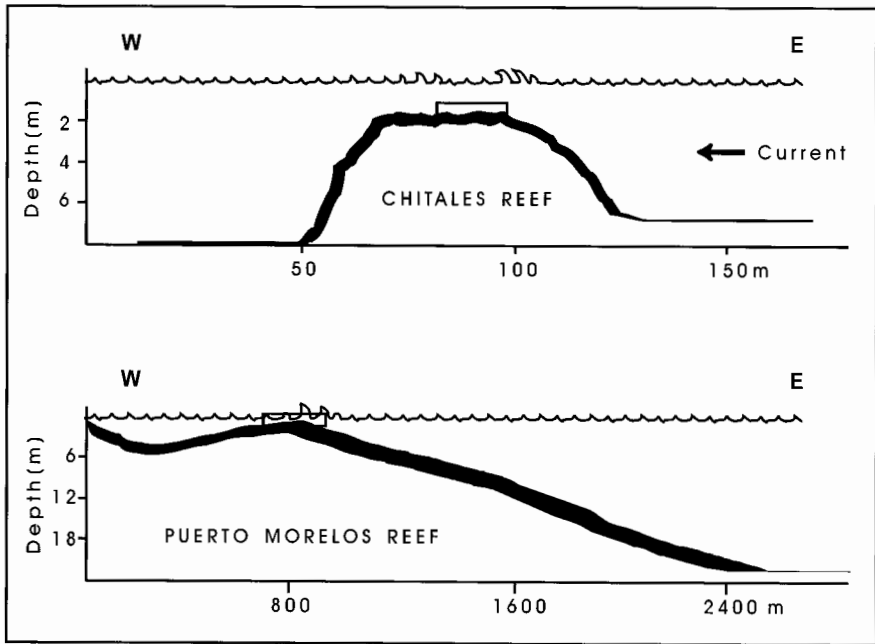


Figure 2. Reef profiles and location of sampled areas.

reef of low relief (Fig. 2), running parallel to the eastern mainland of the Yucatán (Jordán et al., 1981; Jordán, 1989a; Rodríguez, 1993), some 40 km south of CHR.

Both reefs face the Caribbean Sea and are exposed to waves induced by trade winds, as well as from storms approaching from the east and south quadrants. CHR setting is relatively more protected from large storm waves than PMR, by an extensive shallow platform (Figs. 1,2). These reefs are also exposed to winter north winds, more so CHR than PMR, although fetch is limited in Bahía de Mujeres (Fig. 1). The hydrodynamic setting of both reefs differs: In CHR a branch of the Yucatán current permanently flows through Bahía de Mujeres (0.5 to 2.0 kn; Pilot Charts). PMR is not directly influenced by this current, although at times oceanic water intrusion from the Yucatán current has been detected over the reefs (Merino and Otero, 1991). Land influence upon the reefs is negligible because water drainage is basically underground due to the karstic nature of the continental landmass and scarcity of soils (Ward, 1985). To the best of our knowledge there were no severe biological (white band disease, bleaching) or human disturbances affecting the *A. palmata* stands of these reefs prior to the 1988 storms. In PMR human influence is mostly related to fishing activities and recreational uses. Human influence in CHR is mainly related with recreational uses, although partially protected, boating, fish feeding and sporadic fishing still take place.

STORM HISTORY.—Eight storms passed within 80 km of PMR and CHR from 1915 to 1993 (Neuman et al., 1978; Monthly Weather Reviews). One was in 1916 and the other seven between 1961 and 1988. Four of these storms passed over the study area reefs, two of them in 1988 (Table 1). The return period of storms in the last decades has been in the order of 7–9 yrs, but intense storms appear not to be so common within this 80 km radius

Table 1. Storms that passed within an 80 km radius of Puerto Morelos and Chitales Reefs in the last 80 yrs. (* Storm paths that passed directly over, or very close to the reefs)

Year	Name	Direction	Maximum sustained wind speed (km/h)	Minimum central pressure (mb)
1916	No.1	N	171	—
1961	Carla	N	180	968
1967	Beulah*	WNW	180	964
1970	Ella*	NW	54	—
1972	Agnes	NNE	90	998
1975	Eloise*	NW	90	1,000
1988	Gilbert*	WNW	288	888
1988	Keith*	NNW	108	985

(Table 1). Large, far-off storms may have had a minor influence on the local *A. palmata* stands. As an example, hurricane Allen (Class V, 1980) track passed over 150 km off PMR reef (Jordán, 1989b), and the waves generated were able to break branching scleractinians and dislodge gorgonians on the fore reef and reef crest.

In September 1988, hurricane Gilbert, the largest storm registered in the Caribbean region (Monthly Weather Review), reached its lowest central pressure of 888 mb just before crossing over PMR on a WNW track. Two months later, tropical storm Keith, in the verge of reaching the hurricane category (central pressure 985 Mb), passed over PMR and CHR on a northward track (Monthly Weather Review), adding a new impact vector on the already severely affected coral communities.

METHODS

The purpose of this study was to evaluate the spatial variability in the recovery of *A. palmata* after being struck by the 1988 storms, in PMR and CHR. Therefore, our design places more importance on having numerous sampling areas, rather than a few detailed ones (Kinzie and Snider, 1978; Green, 1979). The core data for this study derives from video recordings taken on both CHR and PMR in 1993. However, as PMR has been under scientific observation since 1979, and CHR since 1990, we used these historical data for a better understanding of the 1993 patterns. These data were originally obtained to analyze coral community structure, by means of line intercept method in PMR and by photo-quadrats in CHR. All sampling was carried out during calms and flat seas at the end of summer.

VIDEO-TRANSECTS.—Video-transects (Carleton and Done, 1992; Uychiaoco et al., 1992) were recorded along previously fixed transects with a Hi-8 mm camcorder, using a high resolution tape (metal-E) in a Sony Handycam underwater housing (MPK-TRS), with a wide angle lens. Camera to surface distance was controlled by means of a projecting 40 cm long aluminum rod, ending in a horizontal scale. The scale was kept as close as possible to the surface ($\pm 2-3$ cm) while recording from a vertical view. The recorded images averaged 0.5 m wide and had a resolution of less than 0.5 cm. The guiding transect was established by means of 50-m long measuring tapes, providing spatial control for the recordings.

In PMR, pre-sampling indicated that the mean size of *A. palmata* colonies was in the order of 80 cm². The average size of a still video-screen in our recordings is 1976 cm² (± 145 cm²), roughly 20 times larger than the mean colony size, and thus it was select as sample unit size (Green, 1979). Pre-sampling also indicated a strong patchiness in the abundance of *A. palmata* colonies, resulting in a non-normal, highly aggregated distribution with no discernible spatial pattern (Morisita Index = 2.10). A minimum sample size of 60 sampling units (Fig. 3) was estimated determining, by eye, the

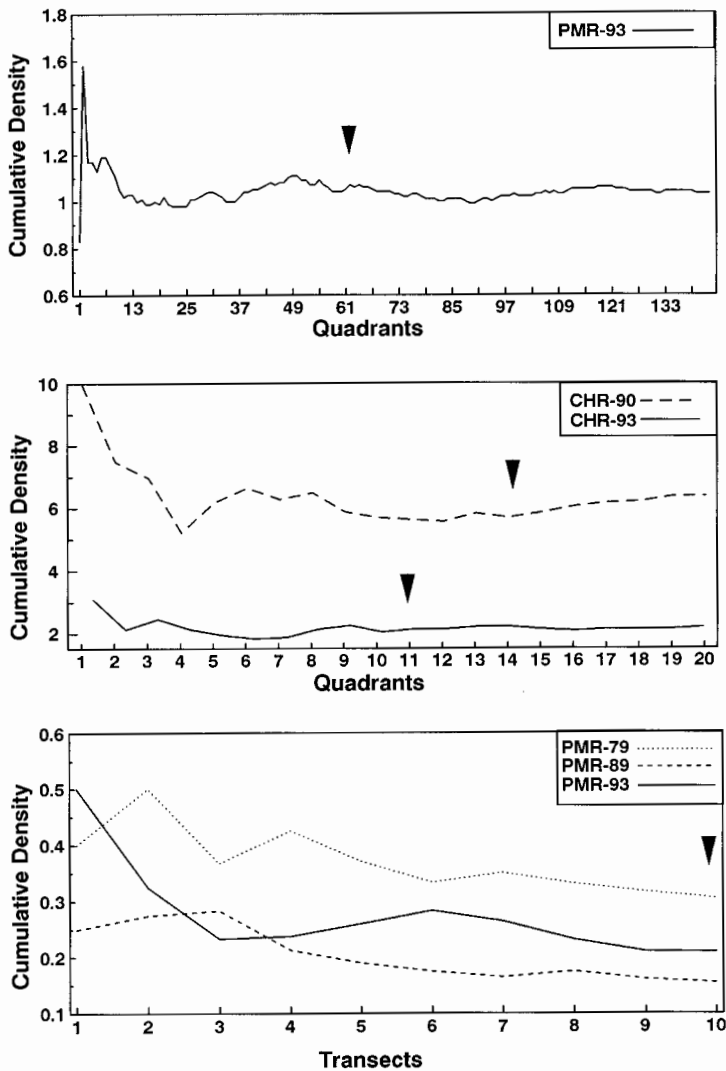


Figure 3. Randomized cumulative density curves used to determine sampling size. Arrows indicate the point chosen as an adequate sampling size. Each curve was constructed by averaging five randomly ordered curves.

point where fluctuations of a randomized cumulative curve of the mean number of colonies per sampling unit tended to be stabilized (Kershaw, 1978). However, as *A. palmata* colonies clumping across the reef crest was high and variable, the final criteria was to sample transects all across the crest (transect length varied from 40 to 540 sampling units). Eighteen such transects were randomly placed across the reef crest, along 7 km of reef tract. Distance between adjacent transects varied between 92 and 919 m (Fig. 1). Total sampled area was 440 m².

In CHR-93 22, 10-m long, video-transects were recorded over the same area previously sampled in 1990 (see below), in a systematic order. Distance between two adjacent transects was in the order of 0.5 m. Minimum sample size was estimated in 14 quadrats (40×50 cm) following a similar procedure as above, for PMR (Fig. 3). Total sampled area was 84.3 m².

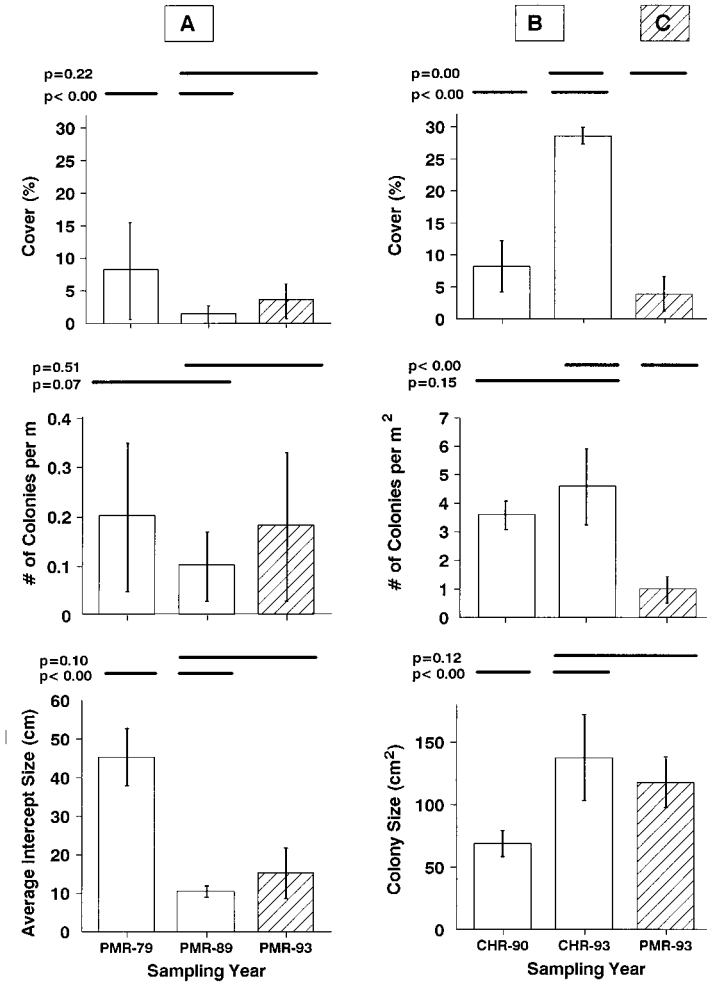


Figure 4. Median values of cover, density and colony size of live *Acropora palmata*. A. Puerto Morelos Reef (PMR-79/89/93). Lineal data for PMR-93 obtained from video-tapes. B. Chitales Reef (CHR- 90/93). C. Puerto Morelos Reef (PMR-93). Vertical lines in bars show 95% confidence interval of the median. Horizontal lines on top of graphs indicate significant differences and its probability among consecutive pairs of medians (Mann-Whitney).

PHOTO TRANSECTS.- In CHR-90, 17 10.0×1.2 m adjacent transects were sampled to collect data for a community structure analysis. Each transect was composed of 20 0.66 m² (±0.06 m²) quadrats. Quadrats were recorded in color photographs, taken with Nikonos cameras mounted on a PVC frame with linear levels on the two horizontal axis to guarantee vertical exposures. Photographs allowed for an overlap of 20 to 30% to diminish edge effects. Each quadrat had a scale and identification tag, obtaining a resolution in the order of 7 mm. Minimum transect length was estimated by plotting cumulative number of species as a function of distance along a transect, following the concept of Gleason (1922). The number of transects was determined in order to cover a fixed area in the reef as required for an EIA (unpublished results). In order to assess if these data were adequate to estimate mean abundance and cover values of *A. palmata*, a posteriori analysis was carried out by plotting a randomize cumulative mean curve of number of *A. palmata* colonies per

quadrat. The curve fluctuations tend to stabilize at 11 quadrats, thus a transect (± 20 quadrats) was considered as an adequate sample size (Fig. 3).

IMAGE ANALYSIS.—Number of *A. palmata* colonies m^{-2} , colony size (horizontal projected living area along the substratum) and percent cover, were estimated from still-video and photographic images. Both video and photographic images were fully analyzed, no sub-sampling was carried out. Small *A. palmata* colonies are easily identified in the images because their whitish-yellowish coloration makes a sharp contrast with the surrounding darker substrate. However, as the line of sight of cameras is vertical (view angle $<45\%$), cryptic young colonies or spat could not be detected by these methods.

Colony area was measured overlaying square grid (1.5 cm^2) acetates upon the images. To correct for quadrat side-effects in colony size analysis, data from complete colonies were treated separately from incomplete ones. Crustose and branching growth-form colonies were also recorded at this stage. While *A. palmata* colonies growth-form is still crustose, colony surface area is efficiently estimated from photo and video images. Once colonies have well developed branches this technique is less reliable to estimate differences in size, as the ratio of colony surface to projected area is no longer predominantly lineal.

LINE-INTERCEPT METHOD.—In 1979 and 1989, 10 20-m long chain-transects were randomly laid at PMR's crest, to collect data for a scleractinian community structure analysis. The number of chain-links laid over every scleractinian and milleporid colony under the transect were recorded on an underwater slate (Loya, 1972; Porter, 1972). Relative species coverage and number of colonies were obtained from these data. Transect length was determined by plotting cumulative number of species as a function of distance along pre-sampled transects, following the concept of Gleason (1922). The larger value obtained (that of the rear reef zone) was taken as standard sample size for all other reef zones (Jordan et al., 1981; Rodríguez, 1993). The number of transects was also determined by means of randomized cumulative species as a function of transects. An a posteriori analysis of cumulative curves of mean number of *A. palmata* colonies per transect, indicate that the 10 transects were an adequate sample size for an overall estimator of lineal density (Fig. 3).

To be able to compare PMR-93 data with that of PMR-79 and PMR-89, a comparison of *A. palmata* live cover estimation by both methods was performed by simulating chain-transect sampling on the 1993 PMR video recordings. Ten 20-m line-transects were randomly "laid on" the tapes, and the length of all intercepted *A. palmata* colonies were measured. After testing for equality of variances ($P > 0.05$), percentage of living *A. palmata* cover estimated by the line-intercept method ($3.4\% \pm 3.6\%$) was arcsine transformed, and compared to cover estimated from colony projected area measurements on the same section of the video-transects ($4.1\% \pm 4.0\%$). The difference was not significant ($P = 0.80$).

Statistical procedures were carried out following: Sokal and Rohlf (1981); Siegel and Castellan (1988), Davis (1986) and Salgado-Ugarte (1992).

RESULTS

PUERTO MORELOS REEF (PMR), 1979-1993.—In 1979, *A. palmata* was relatively abundant and co-dominant with *Millepora complanata* on the reef's crest. Although the largest stands were found on the rear reef zone. *A. palmata* on the shallow crest showed a variable lineal live coverage ranging from 3.4 to 34.3% (Jordan et al., 1981). Variability in number of colonies among chain-transects was also high with values ranging from 0.10 to 0.61 colonies m^{-1} (Fig. 4A). From 1979 until mid 1988, *A. palmata* showed no evident decrease in its relative abundance or distribution patterns as no physical or biological disturbances of importance occurred (Jordan, pers. observ.).

By 1989, one year after the Gilbert and Keith's impacts, overall median lineal cover of *A. palmata* in PMR was reduced to 18% of 1979 values (Fig. 4A). Overall median num-

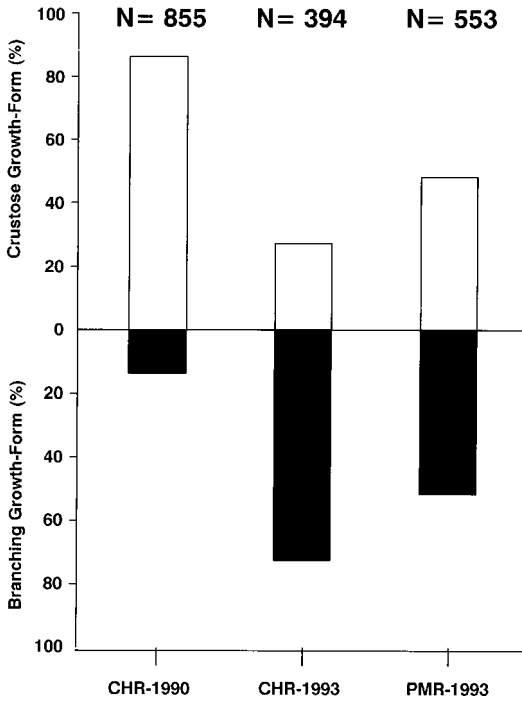


Figure 5. Percent number of *Acropora palmata* colonies as a function of growth-form stage. CHR = Chitales Reef; PMR = Puerto Morelos Reef; N = number of colonies.

ber of colonies was reduced in 50% and median intercept size to less than 25% of 1979 values (Rodríguez, 1993). These changes are significant in terms of percent cover and colony (intercept) size, but not in number of colonies (Fig. 4A). The relatively high colony density in 1989 resulted from a set of standing colony remains with partial tissue mortality, surviving fragments, and perhaps some recruits as well.

By 1993, almost 60 mo after Gilbert's and Keith's impact, there was an apparent increment in the overall values of *A. palmata* (Fig. 4A). However, in spite of the presence of larger and more abundant colonies, these differences were not significant. As discussed below, these non-significant differences in overall values result mostly from a high spatial variability in the recovery process.

Table 2. Media value (\pm 95% confidence interval) of *Acropora palmata*'s colony density (col m^{-2}) in Chitales Reef in 1990 and 1993 in four contiguous groups of transects regrouped for comparison of equivalent areas in both periods. (p = probability of Mann-Whitney test)

Group	1990		1993		p
	N	Median density col m^{-2} (\pm 95% C.I.)	N	Median density col m^{-2} (\pm 95% C.I.)	
I	3	3.15 (0.68)	4	4.44 (4.28)	1.00
II	4	2.06 (2.12)	5	4.47 (1.00)	0.14
III	5	3.20 (0.93)	6	5.98 (2.10)	0.01
IV	5	5.20 (2.69)	7	3.63 (3.37)	0.22

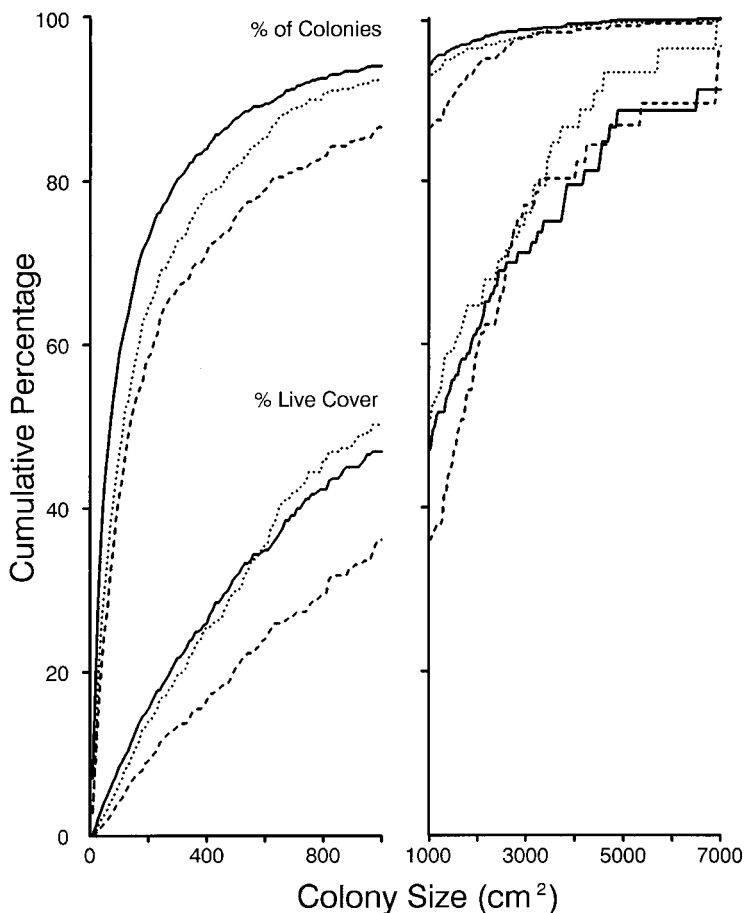


Figure 6. Cumulative percentage of number of colonies and live cover of *Acropora palmata* plotted against colony size, for Chitales Reef (CHR-90 —; CHR-93 - - -), and Puerto Morelos Reef (PMR-93 ···). Sample sizes as in figure 3.

CHITALES REEF (CHR), 1990-1993.—No sampling was carried out on CHR before it was struck by Gilbert and Keith in 1988. However, CHR has been commonly visited and there are many personal observations and underwater pictures of the site prior to 1988. These pictures show a very dense and almost monospecific *A. palmata* coverage, with large colonies rising to the water's surface (± 1.5 m high). We consider that live cover of *A. palmata*, before the 1988 storms, was higher in the crest of CHR than that at PMR crest.

In May 1990, 20 mo after the storms, only a few dislodged branches of the former large *A. palmata* colonies survived. Live cover (median = 8.2%) was probably rather low than before the storms. Overall density of colonies was apparently high (median = 3.6 col m²), and as observed in PMR, these were mostly of small size (median = 68.6 cm²) (Fig. 4B). Most live colonies (84.5%) were small and flattish, forming crusts upon the substrate, suggesting an early growth stage. The high proportion of crustose *A. palmata* colonies is similar in 16 out of 17 transects (Contingency Table: $P = 0.26$; Fig. 5).

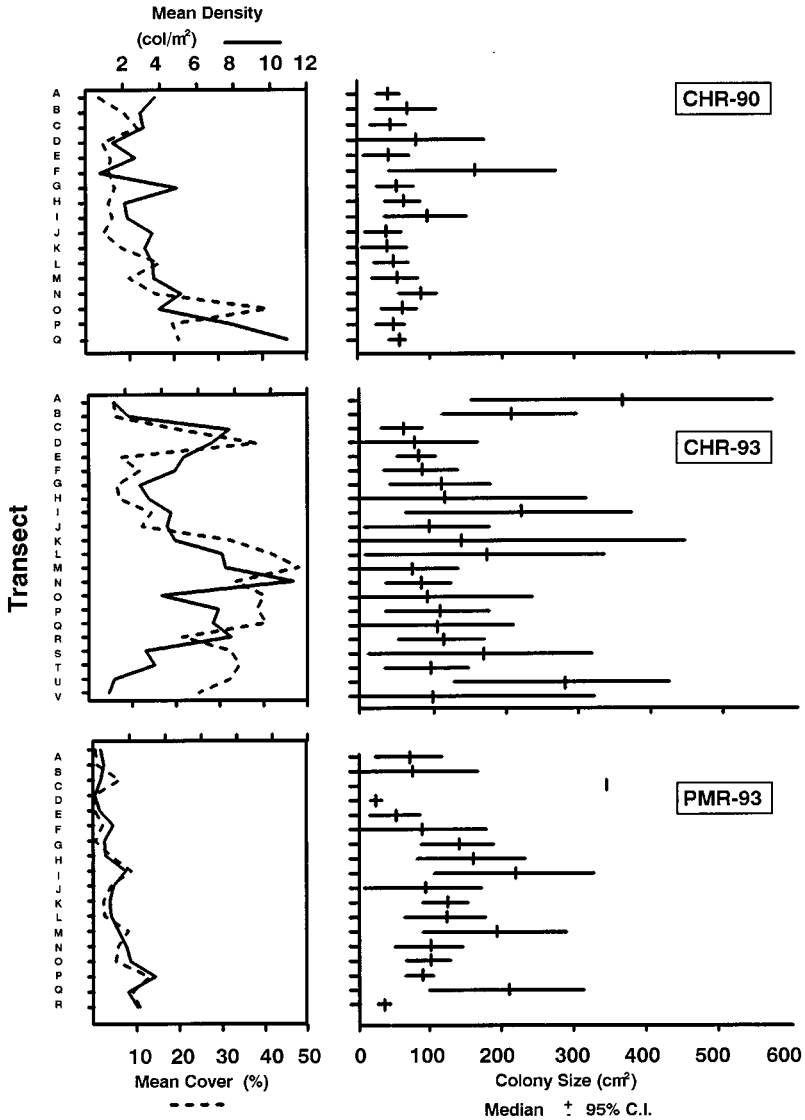


Figure 7. Transect values of *Acropora palmata* at Chitales Reef (CHR-90/93), and at Puerto Morelos Reef (PMR-93). A. Mean density (col m²) and cover (%). B. Median colony size (cm²) (\pm 95% confidence interval). Large outliers have been removed.

By September 1993, 60 mo after the storms, a significant increase in *A. palmata* cover (Fig. 4B), over the 1990 values, was evident. An increase in colony size seems the more likely cause, since only an intermediate group of transects show a significant increase in colony density (Table 2). In accord with the colony size increase in 1993, branching colonies now outnumbered crustose ones in all transects (Contingency Table; $P = 0.17$; Fig. 5).

COMPARISONS AMONG REEFS.—As indicated above the pre-storms population structure of *A. palmata* in PMR and CHR was different, perhaps indicating a differential historical

Table 3. Percent cover of *Acropora palmata* in 10-m long sections for the 18 transects sampled on Puerto Morelos Reef. (Distance among transects starting from number one)

#	Transects		10-m Sections								
	Distance (m)		1	2	3	4	5	6	7	8	9
A	0						0.2				
B	92					0.8	0.0	0.0	2.3		
C	200						5.9				
D	362	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	
E	686			3.5	0.0	1.2	2.8	0.0	2.1		
F	956			1.9	0.1	1.5	5.4	0.8			
G	1,443				0.1	0.2	0.7				
H	1,821	3.5	7.1	2.4	0.0	0.9	6.9	5.0	7.4	0.2	
I	2,253					13.4	9.9	2.6			
J	3,172			0.9	0.8	4.0	1.2	12.5			
K	3,659		0.9	0.1	0.1	1.1	5.0	5.1	2.3		
L	3,875		2.6	1.6	0.4	0.3	2.6	6.5			
M	3,983			16.4	4.9	1.6	8.7				
N	4,848	4.9	0.0	3.6	6.4	0.2	3.1	6.7	7.2	8.4	
O	5,443			5.7	11.9	2.1	1.7	3.9			
P	6,092		22.1	38.2	27.1	1.2	1.0	6.4	5.5	2.5	
Q	6,741				2.3	15.5					
R	6,903				0.5	6.9	24.0				

impact level and/or suitability conditions for *A. palmata* recovery and growth, as CHR is relatively more protected from large storm waves.

Strongly skewed colony size distributions in CHR-90/93, and PMR-93 (Fig. 6), indicate a strong predominance of colonies of small size ($g_1 = 9.69; 4.25; 4.93$ respectively; $P < 0.05$ for the three cases). This structure is in strong contrast to the former predominantly large colonies, indicating a severe storm impact and an initial recovery phase. Although it has been documented that size-age relationships in corals are rather complex resulting in colony sizes that may be age-independent (Hughes, 1984; Hughes and Jackson, 1985; Hughes and Connell, 1987; Babcock, 1991); it has also been recognized that in terms of the whole size structure there is a positive, although indeterminate, relationship between size and age in corals (Hughes and Connell, 1987; Babcock, 1991). This positive relationship is more evident during the first years (Hughes and Connell, 1987), and perhaps more so in fast growing branching corals (Gladfelter et al., 1978), in the absence of additional catastrophic events, as our data suggests.

Outliers, detected by exploratory analysis (values which are larger or smaller than 1.5 times the value of the interquartile range), corresponded exclusively to large size colonies in these data sets. Large outliers were found in almost all transects in both reefs, although their relative abundance varied considerably. Less than 10% of the number of colonies comprised more than 50% of the total cover, and a few of those surviving colonies were holding up to 11% of the total cover (Fig. 6). The similarity of the size distributions, together with the subtle shift toward larger colonies in CHR from 1990 to 1993, suggest common and relatively recent re-growth and/or recolonization processes.

Overall mean live cover and density values per transect at PMR-93 were significantly lower than those found at CHR-90/93 (Fig. 7). A difference that probably also existed

before the storms. However, median colony size, in PMR-93, was not significantly different from that of CHR-93 (Fig. 4). Colony size comparison of transects, with outliers removed, by means of Kruskal-Wallis test, showed no significant differences in CHR-90/93 ($P = 0.42$; 0.14 , respectively), while it was significant at PMR-93 ($P < 0.00$; Fig. 7). Colony growth-form (crustose vs branching) proportionality among transects in PMR was not homogeneous ($P < 0.00$), emphasizing the greater variability at PMR. The proportions of colony growth-forms in PMR-93 (Fig. 5), were significantly different ($P < 0.05$), and intermediate between those of CHR-90 and CHR-93.

By 1993, high spatial variability in the abundance of *A. palmata* was evident at quite different spatial scales, involving up to three orders of magnitude: at tens of square meters (between contiguous transects in CHR or within transects in PMR); at 100s to 1000s of meters (between PMR transects), and at tens of kilometers (between CHR and PMR). As reef size and the sampled area at PMR is much larger than that at CHR, the above differences may be enhanced by the more heterogeneous environment at PMR. Comparisons of live *A. palmata* cover between CHR-93 transects and 10-m long sections of the PMR-93 transects (equivalent size areas of 10×0.5 m), showed that only two 10-m sections of PMR (both on transect P) out of 89, had a cover value greater than the average value at CHR ($24.99 \pm 14.05\%$; Table 3). Also, only one third of those sections, had a cover value greater than the minimum cover value (5.72%) found in any transect in CHR-93 (Fig. 7). Although CHR sampling was concentrated in a small area with limited spatial variability, maximum values in any similar size area in PMR were rarely as high as those at CHR. As expected average values in both reefs are also quite different.

The observed variability at PMR can not be explained solely on the pre-storm variability in the *A. palmata* structure. While in some reef sections initial recovery is quite evident, in others where very large and lush stands of *A. palmata* dominated before 1988 (as in the area of transects A to C in PMR), no initial recovery is evident at present. The possibility of faster recovery due to a better environmental setting was further tested in PMR, where there was an apparent increase in percentage cover following a south-north tendency (Fig. 7; Table 3). The significance of this pattern was tested by means of a trend surface analysis (Davis, 1986), showing a poor goodness-of-fit ($r^2 = 59.34\%$), due to a high variability and a correspondingly low multiple correlation coefficient ($r = 0.77$). Variability in recovery is also evident between reef zones. On the shallow fore reef of PMR, were formerly *A. palmata* was restricted to a relatively few large and sturdy colonies, now (1995) show a much higher colony abundance. Similar observations had been made on other reefs impacted by storms (Done et. al., 1991; Rogers, 1993).

Overall recovery at the CHR and PMR reefs seems to be well in progress as indicated by our measurements up to 60 mo after the 1988 storm impacts. Although no quantitative studies were made after 1993, continuous observations to 1995, allow us to state that an evident change in the appearance of the reef crest (as compared to 1989 and 1993 observations) is taking place at an accelerated rate in both reefs, as *A. palmata* stands rapidly expand.

DISCUSSION

Our observations coincide with reports that suggest fast recovery rates for Acroporids in longer term observations, such as that of Shinn (1976) for *A. cervicornis*, and the inferred growth rates of *A. palmata* stands in Jamaica (1 m in 12 yrs), proposed by Woodley

(1992) for inter-storm periods. But also, in PMR the recovery process was not evident during the first years after the storms. Therefore our observations also coincide, for a period, with those of Bak and Engel (1979), Hughes (1984), Knowlton et al., (1981), Rogers et al., (1982) and Rosesmyth (1984), regarding delayed mortality of survivors and poor success of new recruits.

The other evident trend observed in these reefs is a considerable spatial variability in the recovery process. Particularly at PMR where a distinct pre-storm variability was detected, but it was also observed that post-storm spatial variability was not necessarily related to the former spatial structure of *A. palmata*. Differential and complex storm impacts at local scales, may result from even minor variations of reef profile and morphology in relation to the changing approaching wave pattern as the storm moves (Kjerfve et al., 1986). Greater changes may occur if a subsequent storm strikes the same area in a short period, further diminishing the relative importance of pre-storm conditions and perhaps enhancing the vulnerability of colonies and stands, which is strongly determined by their previous storm-history (Done, 1992; Massel and Done, 1993). Thus, quite variable conditions may exist after the storms impact inducing a patchiness which may be further enhanced by temporal replacement by other species, mostly algae (Glynn et al., 1964; Woodley et al., 1981). On the short term, substrate overgrowth by filamentous and fleshy algae, at least for a couple of years after the impacts, may have "delayed" the initial recovery process on the PMR (pers. observ.).

Local recovery in the strict sense of returning to pre-catastrophe conditions (Pearson, 1981; Rogers, 1993), may take a long time or never be achieved, or may even surpass the originally reported condition. For example, the initiation of recovery can be relatively short as discussed above, or relatively long as it has been documented for Belizean (Stoddart, 1974) and Gulf of Mexico reefs (Jordán-Dahlgren, 1992). It seems unlikely that a set of similar impacts, and similarly "initial" and "recovery" conditions will occur locally within a short time frame. Also, survivorship, recruitment, colony fission and colony growth, as well as colonial and partial mortality, may be highly variable (Highsmith, 1982; Hughes, 1984; Hughes and Connell, 1987; Babcock, 1991; Rogers, 1993); moreover if anthropogenic influences are present. As corals are long-lived species, local changes driven by natural causes and observed during a few years, may not necessarily imply a definitive trend on a longer time frame.

Physiographical differences in the reef's setting and subsequent differential relative development of local *A. palmata* populations, both before and after the storms, clearly results in "different recovery rates". However, the spatial variability of the process was only evident when larger reef areas were studied.

As recovery at al local scale is influenced by the former population structure, the past history of the stand, the relative magnitude of the storm's impact and the suitability of the average environmental regime in the reef, it seems evident that assessments based on small area sampling can lead to biased conclusions, if extended to a reef system. Therefore, proper evaluation of recovery in a reef following an acute natural disturbance require, in addition to long-term observations (Dollar and Tribble, 1993; Rogers, 1993), widely spaced sampling as large local variations are to be expected. Also, while assessing recovery in short time frames, the observed rates are perhaps better understood in a flexible, time dependent context.

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