Spatiotemporal variations of live coral cover in the northern Mesoamerican Reef System, Yucatan Peninsula, Mexico

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Summary: Evaluating the response of coral assemblages to different disturbances is important because variations in species composition may have consequences for ecosystem functioning due to their different functional roles in coral reefs. This study evaluates changes in diversity, structure and composition of coral assemblages of the coral reefs of two national parks in the northern sector of the Mesoamerican Barrier Reef System spanning the period from 2006 to 2012, just after the impact of two hurricanes in the area. Coral assemblages in the Cancún National Park included fewer species and lower live coral coverage (<15%) than those recorded in Cozumel. In the Cancún National Park, the species with the highest coral cover was *Porites astreoides* (more than 40% relative cover), and no significant temporal changes were observed in live coral cover and species composition. On the other hand, in the Cozumel National Park the dominant species were *Agaricia agaricites*, *Siderastrea siderea* and *Porites astreoides*, and the coral reefs showed an increase in live coral cover from 16% in 2006 to 29% in 2012. The dynamics of coral assemblages differed between the two parks: while there is an apparent stability in the current composition of the Cancún reefs, the Cozumel reefs show an increase in the abundance of the aforementioned dominant species. However, it is possible that the population characteristics of the species that dominate the coral assemblages in both national parks, such as those of fast population growth and of small colony size, do not entirely fulfill the main function of accretion and habitat heterogeneity, and more research is therefore needed to test this hypothesis.

Keywords: coral assemblages; resilience; ecosystem functioning; coral reefs; Caribbean; Mexico.

Variación espacio-temporal de la cobertura de coral del norte del Sistema Arrecifal Mesoamericano, Península de Yucatán, México

Resumen: Evaluar la respuesta de las comunidades de coral a diferentes perturbaciones es importante ya que las variaciones en la composición de las especies pueden tener consecuencias en el funcionamiento del ecosistema, debido a los diferentes roles funcionales que cada especie tiene dentro de él. En este estudio se evaluaron los cambios en la diversidad, estructura y composición de las comunidades en los arrecifes de dos Parques Nacionales ubicados en el sector norte del Sistema Arrecifal Mesoamericano, durante el periodo 2006-2012, justo después del impacto de dos huracanes en la zona. En el Parque Nacional Cancún se registraron pocas especies de coral y una cobertura de coral vivo baja (<15%) sin cambios temporales significativos; la especie más dominante en este parque fue *Porites astreoides* con más del 40% de cobertura relativa. Por otro lado, los arrecifes de coral del Parque Nacional de Cozumel mostraron un incremento en la cobertura de coral del 16% en 2006 a 29% en 2012; las especies dominantes, y que incrementaron su cobertura en este periodo, fueron *Agaricia agaricites, Siderastrea siderea* y *P. astreoides*. Aunque la dinámica de las comunidades de coral fue diferente en ambos parques, es posible que las características poblacionales de las especies que dominan las comunidades de coral en todos los arrecifes no cumplan por completo con las funciones principales de acreción y heterogeneidad de hábitat; sin embargo se necesita más investigación para poder evaluar esta hipótesis.

Palabras clave: comunidades de coral; resiliencia; funcionamiento del ecosistema; arrecifes de coral; Caribe; México.

INTRODUCTION

The increasing degradation of coral reefs is a global concern (Gardner et al. 2003). These ecosystems have been severely impacted by natural and anthropogenic disturbances causing the loss of live coral cover (LCC) (Hughes et al. 2003, Bellwood et al. 2004). Particularly in the Caribbean, LCC has decreased by 80% since the 1980s (Gardner et al. 2003), resulting in phase changes and/or stable alternative states represented by an increase in coverage of other benthic components, such as fleshy algae and sponges (Norström et al. 2009). Usually, the condition of reef health is evaluated by monitoring these changes at community level of the benthos, but the change in abundance is only one aspect of coral assemblages. These assemblages also change in their structure, composition and species richness (Aronson et al. 2002).

Variations at assemblage level are important because the species have different ecological roles in the ecosystem. For example, species with branching (e.g. *Acropora palmata*) or massive growth (*Orbicella* spp.) support the functions of structural complexity and accretion, which in turn promote the stability and diversity of other species in these ecosystems (Aronson and Precht 2001, Rodríguez-Zaragoza and Arias-González 2015). It is possible that changes in the abundance of some key species have consequences in the architectural complexity of coral reefs and thus in the ecosystem functioning, even if the overall coral cover remains stable (Green et al. 2008, Álvarez-Filip et al. 2011). Therefore, a long-term evaluation is essential in order to better understand the natural population dynamics (West and Salm 2003), how species respond to natural and anthropogenic stresses (Hughes et al. 2003) and, indirectly, the resistance and resilience of coral reef ecosystems through the evaluation of their functional groups (Bellwood et al. 2004, Petchey and Gaston 2006). Long-term studies of these variations help us to evaluate and develop conservation and management strategies aimed at protecting key species (Rodríguez-Zaragoza and Arias-González 2015).

Most studies focusing on the community structure and assemblage composition of corals in the Mesoamerican Reef System (MRS) have been short in space and/or time (e.g. Álvarez-Filip et al. 2009, Carriquiry et al. 2013, Rodríguez-Zaragoza and Arias-González 2015). In this study, we evaluate the changes in diversity, structure and composition of coral assemblages during the period from 2006 to 2012, shortly after two Category 5 hurricanes (Emily and Wilma) hit the area in 2005. We therefore had an opportunity to assess the response of coral assemblages to two large physical disturbances. Additionally, in this study we monitored eleven reefs distributed in two Natural Protected Areas (NPAs) in the northern sector of the MRS, namely the "Parque Nacional de la Costa Occidental de Isla Mujeres, Punta Cancún y Punta Nizuc (PNIMCN)" (hereinafter Cancún National Park or simply Cancún) and the "Parque Nacional Arrecifes de Cozumel (PNAC)" (hereinafter Cozumel National Park or simply Cozumel). Different recreational activities are allowed in these parks to promote economic development in the area (Reyes-Bonilla et al. 2012). Both Cancún and Cozumel are the top tourist destination areas of the Mexican Caribbean, representing a significant economic benefit for Mexico (Ardisson et al. 2011). Thus, management and conservation of the coral reefs of these two national parks is of great ecological and economic importance.

MATERIALS AND METHODS

Study area

Five coral reef sites distributed within three polygons that encompass the Cancún National Park and six others spread over the Cozumel National Park were evaluated (Fig. 1). There are clear differences in the geomorphology of these reefs. The coral reefs of Cozumel are structurally complex, reach greater depths, have higher coral species richness and LCC, and have greater diversity of habitats (Jordán-Dahlgren and Rodríguez-Martínez 2003, Ardisson et al. 2011). In contrast, the coral reefs of Cancún are shallow and discontinuous formations (Núñez-Lara et al. 2005) with fewer coral species (Carriquiry et al. 2013).

In general, the area is influenced by the Yucatan Current, which flows from the south and passes through the Yucatan Channel. The annual average sea surface temperature is 27.9°C, ranging from 29.0°C in summer to 26.0°C in winter (Carricart-Ganivet 2004). The average weather conditions are characterized by three periods: i) a dry season from February to May, ii) a rainy season from June to September, when tropical storms and hurricanes develop, and iii) a period of winter rain called "Nortes" from October to February (Díaz-Ruiz et al. 1998).

Live coral cover database

LCC was recorded at each site with five linear transects in Cancún and six in Cozumel (30 m long) parallel to the coast and placed randomly on the area of the crest and front reef. We used the Intercept Point Method to obtain the LCC and the rest of the benthic components. Using this method, we recorded the species of hermatypic coral to the lowest possible taxon every 25 cm along the transect (i.e. 120 dots per transect) (Almada-Villela et al. 2003). The surveys were made between July and September, from 2006 to 2012 (except 2008 in the Cancún), totalling 150 transects in Cancún and 252 transects in Cozumel.
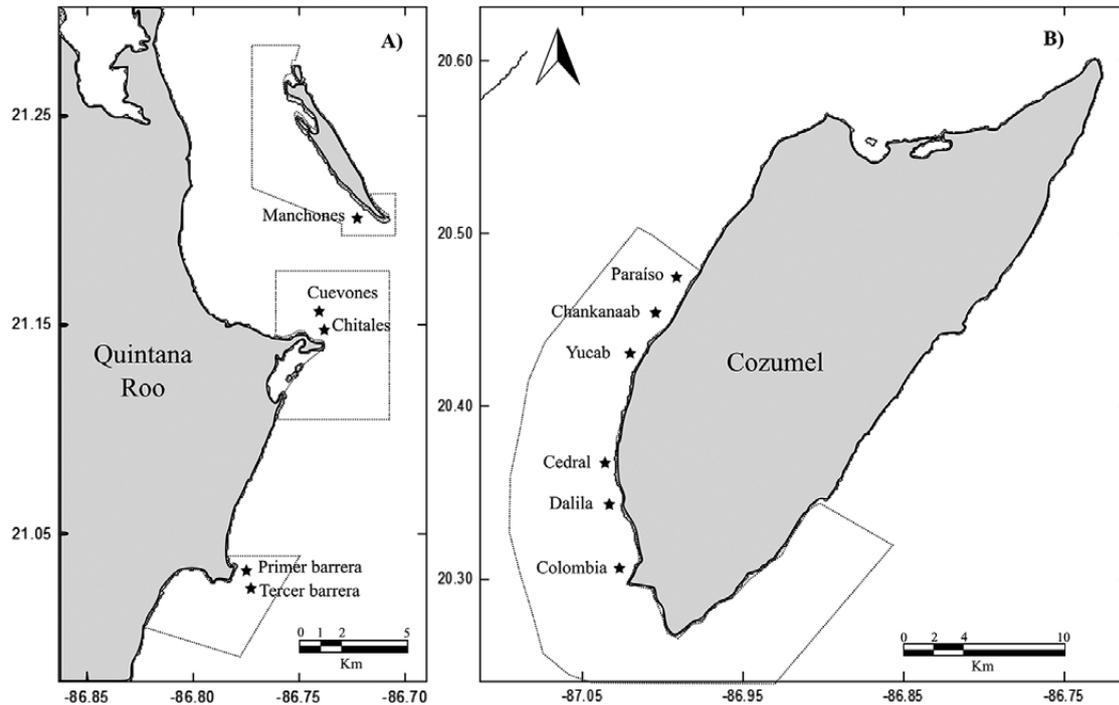
Fig. 1. – Study area. A, Yucatan Peninsula; B, Cozumel Island. The continuous line delimits the polygons of Cancún National Park and Cozumel National Park. The dots represent the sampled sites.

Data analysis

In order to check whether the sampling effort was representative in each NPA and year, species accumulation curves and non-parametric procedures such as Chao 2, Jackknife 1 and Jackknife 2 were performed as estimators of expected richness (Gotelli and Colwell 2011) from 10000 random combinations without replacement (Estimates V.9.1, Colwell 2013).

Analyses of non-metric multidimensional scaling (NMDS) were used to determine the similarity of coral assemblages among sampling sites and years for each NPA (Clarke and Warwick 2001). Prior to analysis, the data were square-root transformed to reduce the bias by the most abundant species so that the similarities depended not only on these but also on the less common species. Similarity matrices were constructed using the Bray-Curtis coefficient (Clarke and Warwick 2001). Two-way non-parametric permutational multivariate analyses of variance (PERMANOVA), using crossed factors and fixed effects, were performed to test the spatial and temporal changes in the composition and coverage of coral assemblages. The general linear model constructed was

$$Y = \mu + site_i + year_j + site_i \times year_j + \varepsilon_{ij} \qquad (1)$$

where Y is the variability across the set of observations; μ is the average value of the observations; $site_i$ is the fixed factor that represents the five sites at Cancún National Park or the six sites at the Cozumel National Park; $year_j$ is the fixed factor corresponding to the seven years of sampling (except 2008 in Cancún); $site_i \times year_j$ is the interaction term that exists between the two fac-

tors; and ε_{ij} is the accumulated error of model. All the PERMANOVAS were calculated with a type III sum of square (Anderson et al. 2008). Statistical significance was tested with 10000 permutations under a reduced model. The contribution of the species per site and year were estimated with a similarity percentage analysis (SIMPER) (Clarke and Warwick 2001). Both methods were run in the PRIMER v6.1 and PERMANOVA+ program (Plymouth Marine Lab. UK).

Coral diversity was estimated from the average species richness (S), LCC (%), the Shannon diversity (H', nits), Pielou evenness (J') and Simpson dominance (λ) (Clarke and Warwick 2001). Analyses of variance (ANOVA) based on permutations were used to test spatial and temporal variation of these indices following the experimental design of Equation 1, because parametric assumptions were not met. These ANOVA designs were performed with Euclidian distance matrices following the criteria of Anderson et al. (2008). Finally, the percentage of change from 2006 to 2012 was calculated as the difference in the average LCC.

RESULTS

A total of 38 species of hermatypic corals belonging to 20 genera and 11 families were recorded altogether in the two NPAs. Of these, 22 species were in Cancún and 36 in Cozumel (Tables S1 and S2 in supplementary material). Only two species, *Acropora palmata* (Lamarck 1816) and *A. prolifera* (Lamarck 1816), were not recorded in Cozumel. Based on the cumulative curves, we were able to find 77% of the species richness expected for Cancún and 85% for Cozumel. The maximum ex-

Table 1. – Summary of two-way crossed factors and fixed effects ANOVAs and PERMANOVA of the coral assemblages and diversity index of Cancún National Park and Cozumel National Park. Statistical significant results (p<0.05) are indicated in bold.

Analysis	Factors	Cancún		Cozumel	
		Pseudo-F	P(perm)	Pseudo-F	P(perm)
Permutational based ANOVA	Site	12.11	**0.0001**	10.07	**0.0001**
	Year	1.85	**0.0031**	9.90	**0.0001**
	Site×Year	1.16	0.1180	1.48	**0.0001**
Number of species (S)	Site	1.99	0.0723	17.29	**0.0001**
	Year	1.56	0.1454	32.72	**0.0001**
	Site×Year	1.24	0.2027	1.32	0.0858
Shannon diversity (H')	Site	0.91	0.4818	8.29	**0.0001**
	Year	1.10	0.3585	17.21	**0.0001**
	Site×Year	1.12	0.3074	1.08	0.3123
Pielou evenness (J')	Site	0.69	0.6373	6.74	**0.0001**
	Year	1.56	0.1560	1.32	0.1313
	Site×Year	0.66	0.9128	0.76	0.9862
Simpson dominance (λ)	Site	1.10	0.3434	4.61	**0.0001**
	Year	1.37	0.2270	17.08	**0.0001**
	Site×Year	0.98	0.4998	0.91	0.6343
Live coral cover (%)	Site	8.72	**0.0001**	33.21	**0.0001**
	Year	0.57	0.8383	44.56	**0.0001**
	Site×Year	0.60	0.9801	2.28	**0.0001**

pected richness was 31 species for Cancún and 46 for Cozumel (Jackknife 2). Inventories higher than 70% were achieved in most years, except for 2007 (64.29%) and 2009 (63.34%) at Cozumel, with an observed richness of 27 (2007) and 26 (2009) species. The maximum expected richnesses for these years were 42 (Chao 2) and 41 (Jackknife 2) species, respectively.

Cancún National Coral Reef Park (PNIMCN)

Reefs in the Cancún National Park had low total LCC that varied significantly between sites but not between years or in the interaction between the two factors (Table 1, Fig. 2). Spatial differences mainly originated from the first barrier (with the lowest coverage: 4.72%±2.52) and the third barrier (with the highest coverage: 13.68%±6.54) of Punta Nizuc; they were significantly different from other reefs and from each other (Fig. 2A). Though differences between years were not statistically significant, a decrease in coral cover was observed in Chitales (–0.52%±4.83) and the third barrier (–4.78%±7.79) from 2006 to 2012 (Fig. 3A). It is important to mention that the change in the third barrier was caused by a 7.85% decrease in the cover of *Acropora palmata*. PERMANOVA results showed that coral assemblages varied significantly between sites and years, but the interaction between the two factors was not significant (Table 1, Fig. 4A).

The pair-wise comparisons at site level showed significant differences between the five reefs studied; Cuevones and the first and third barrier of Punta Nizuc were the most dissimilar (>60%). Based on the SIMPER analysis, *Porites astreoides* (Lamarck, 1816) contributed over 40% to the structure of assemblages at the Manchones, Cuevones and Chitales reefs. At the first and third barrier of Punta Nizuc, species that contributed the highest percentage to the assemblage structure were *Orbicella annularis* (Ellis, 1786) (37%) and *A. palmata* (42.4%) respectively, with *P. astreoides* as the second most abundant species in these reefs. Moreover, the temporal variability of coral assemblages was
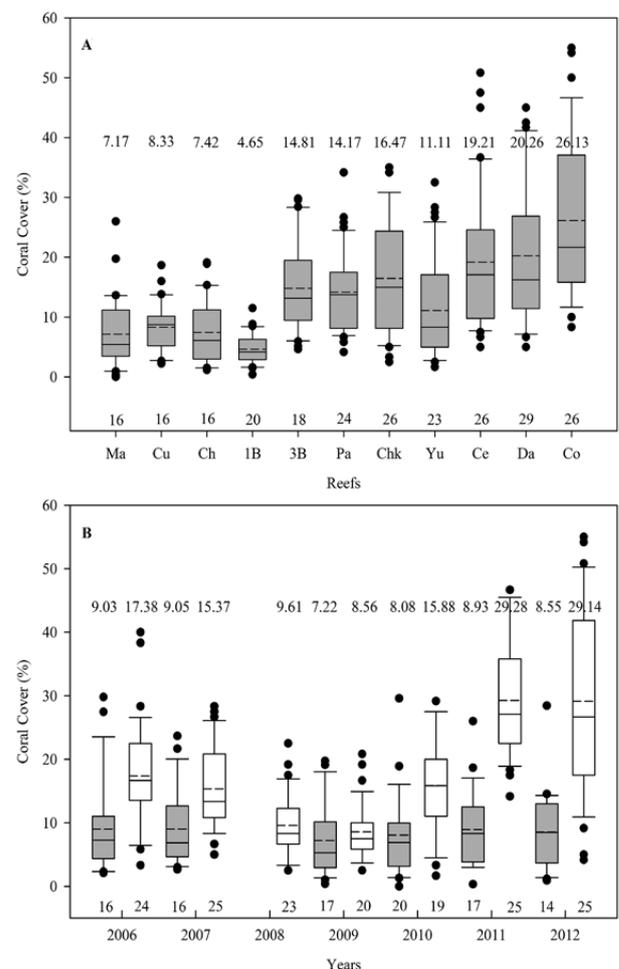
Fig. 2. – Box plot of live coral cover by reef site (A) and year (B) for Cancún and Cozumel. The solid line in the box represents the median; the dotted line represents the average. The bottom and top bars in the boxes represent the 25th and 75th percentiles; whiskers above and below the box are the 10th and 90th percentiles, respectively. The dots represent the outliers. The numbers above the boxes are the values of the average coral cover and the base the total number of species.
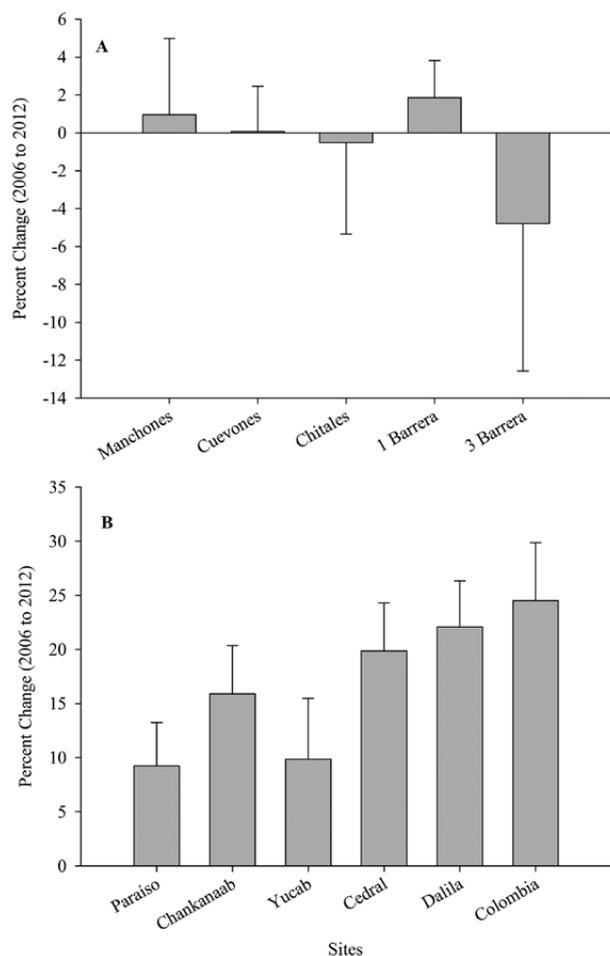
Fig. 3. – Coral cover percentage change from 2006 to 2012 (±SE) of the studied reefs at Cancún (A) and Cozumel (B).

Fig. 4. – NMDS results displaying the similarity of coral assemblages at Cancún (A) and Cozumel (B) during the period 2006-2012. Ma, Manchones; Cu, Cuevones; Ch, Chitales; 1B, primer barrera; 3B, tercer barrera; Pa, Paraíso; Chk, Chankanaab; Yu, Yucab; Ce, Cedral; Da, Dalila and Co, Colombia.

significantly different between the pairs of years 2006 vs 2007, 2007 vs 2009 and 2011 vs 2012. Based on the SIMPER analysis, changes from 2006 to 2009 were characterized by an increase in the abundance of *P. astreoides* and *P. porites* (Pallas, 1766), whereas change from 2011 to 2012 were characterized by a decrease in the abundance of *A. palmata*, *P. astreoides*, *P. porites* and *Siderastrea siderea* (Ellis, 1786).

As for the analysis of diversity, no significant differences between sites, years or the interaction of the two factors were detected in any of the estimated indexes: average number of species (S), Shannon diversity (H'), evenness (J') and dominance (λ) (Table 1). The average number of species was between four and five per transect in these reefs. The diversity estimated was between H'=0.99 (±0.34) and H'=1.22 (±0.50). The evenness index value was from J'=0.69 (±0.18) to J'=0.76 (±0.15), suggesting a tendency to become more dominated by one coral species. Finally, the dominance value was between λ=0.48 (±0.18) and λ=0.40 (±0.21) (Supplementary Material Table S3).

Cozumel National Coral Reef Park (PNAC)

For the Cozumel National Park, the LCC changed significantly between sites, years and the interaction of the two factors (Table 1, Fig. 2B). At a spatial scale, the same trend was observed in all sampling years: reefs located north of Cozumel (i.e. Paraíso, Chankanaab and Yucab) had a lower LCC than the southern reefs (i.e. Cedral, Dalila and Colombia) (Table S3, Fig. 2A). At a temporal scale, two types of trends occurred in all reefs: LCC decreased from 2006 to 2009, being significant only between 2007 and 2008; and also, starting from 2009 LCC increased to 29.14% (±12.73) in 2012, with significant differences between years, except for 2011 vs 2012 (Fig. 2B). The change in LCC from 2006 to 2012 was characterized by an increasing gradient from north to south, with a higher recovery in Cedral, Dalila and Colombia (Fig. 3B). This increase was determined by the species of the genera *Agaricia* spp., *Porites* spp. and *Siderastrea* spp.

The structure of coral assemblages was significantly different between sites, years and the interaction of the two factors (Table 1); this is shown in the NMDS in which major changes were observed between the sites over the years (Fig. 4B). In the pair-wise test of the term site*year interaction, temporal changes of coral assemblages in each reef were significant from 2009 in Paraíso, Chankanaab and Colombia and from 2010 in Yucab, Cedral and Dalila. These changes were mainly characterized by the increase in the abundance of the species *Agaricia agaricites* (Linnaeus, 1758), *Porites astreoides*, *P. porites* and *Siderastrea siderea*. Particularly in the Colombia reef, changes in the cover

of *Orbicella annularis*, *O. faveolata* (Ellis, 1786) and *Agaricia tenuifolia* (Dana, 1848) determined the observed dissimilarities. With regard to spatial changes, significant differences were detected in 2006 between the reefs located north of the island (i.e. Paraíso, Chankanaab and Yucab) and those to the south (i.e. Cedral, Dalila and Colombia); in the remaining years, the differences between the reefs to the north and south were not evident. At all sites during the seven years of sampling, the species *Agaricia agaricites* showed the highest LCC (Table S2). This species, together with *Siderastrea siderea*, *P. astreoides* and *P. porites* contributed more than 50% of the coral cover assemblages. At a spatial level, the greatest dissimilarities between sites (>60%) started in 2008, particularly within the Yucab reef, which showed the lowest values of LCC (11.11±8.81%).

Finally, the analyses of diversity structure showed significant differences between sites and years, but not in the interaction between the two factors. The observed differences were in the number of species, Shannon diversity and Simpson dominance. Significant differences in the evenness index were detected only at site level (Table 1). Spatially, the number of species and Shannon diversity showed a similar trend: lower values on the reefs to the north of the island (i.e. Paraíso, Chankanaab and Yucab) than on those to the south (i.e. Cedral, Dalila and Colombia). The lowest values for both indices were recorded in the Yucab reef while the highest were recorded in the Colombia reef (Table S3). The evenness index showed an inverse trend: relatively higher values at the north of the island decreasing towards the south; however these values were between J'=0.91 (±0.06) in Paraíso and J'=0.85 (±0.09) in Dalila, reflecting a high evenness in the structure of assemblages in the Cozumel National Park. This finding is reinforced by the relatively low values in the dominance index, which were between 0.22 (±0.06) in Colombia and 0.28 (±0.12) in Yucab (Table S3). Two types of temporal trends were observed in both the number of species and Shannon diversity: a decreasing trend between from 2006 to 2009 and an increasing trend from 2009 to 2012 (Table S3). The lowest values were observed in 2009, with 5.35 (±1.85) species per transect and H'=1.45 (±0.34), while the highest were observed in 2012, with 11.04 (±4.43) species and H'=2.04 (±0.34). Evenness values ranged from 0.87 (±0.09) to 0.90 (±0.08), but no clear temporal trend was observed. The dominance index values observed were between 0.17 (±0.06) in 2012 and 0.29 (±0.13) in 2010, with an inverse trend in the number of species and the Shannon index (Table S3). The pair-wise comparisons for all indexes showed no significant difference in the early years until 2010 (except 2007 vs 2008), while from 2010 to 2012 changes were statistically significant.

DISCUSSION

The coral species richness recorded in our study (a total of 38 species) represents 74% of total species reported for reefs in Cozumel (51 species) (Fenner 1999).

This apparently low representation can be explained by the sampling strategies employed. While sampling in this study was restricted to the crest and front reef area (usually 1-10 m deep), the species richness reported by Fenner (1999) is a taxonomic list comprising several sampling areas at different depths (up to 30 m) during more than a decade of studies; no single study has been able to record all those species in their surveys. In other studies where only the reef crest was sampled, only 21 (Fenner 1988) to 23 species (Álvarez-Filip et al. 2009) were reported; therefore, both sampling effort and the number of species recorded in this study were representative of the area.

In Cancún National Park LCC was low (<15%) and no significant changes were observed during the sampling period. At the assemblage level, *P. astreoides* contributed more than 40% of the relative cover and was the most dominant species except in the reefs of Punta Nizuc, where *O. annularis* (in the first barrier) and *A. palmata* (in the third barrier) contributed ~40% (Table S1). However, in the late 1980s, *A. palmata* was the most important species in this area. On the Chitales reef, located at Punta Cancún, monospecific patches and large colonies (1.5 m high) have been reported (Jordán-Dahlgren and Rodríguez-Martínez 1998). For 1999-2000, after the 1998 global beaching event, Rodríguez-Zaragoza and Arias-González (2015) reported that coral assemblages at Punta Nizuc were dominated by *A. palmata*, *Siderastrea* spp. and *Pseudodiploria strigosa* (Dana, 1848), but there are no published data for other reefs in this park. Finally, the most recent surveys carried out between 2006 and 2012 (this study) indicate that fast-growing species that form small colonies (e.g. *P. astreoides*) dominate the assemblages, coinciding with similar reports elsewhere in the Caribbean (Green et al. 2008, Álvarez-Filip et al. 2013). Additionally, the high dominance of only two species is reflected in the evenness and dominance index, without showing significant spatial or temporal changes.

The presence of the genus *Acropora* spp. in Cancún National Park is of particular importance. The species *A. palamata* is a key structural component that contributes significantly to the reef accretion and development of the structural framework in these reefs (Rodríguez-Zaragoza and Arias-González 2015) and also provides habitats for a wide variety of species (Precht et al. 2002). Given their importance and apparent vulnerability to perturbations, both *A. palmata* and *A. cervicornis* are subject to special protection under national regulations (NOM-059-SEMARNAT-2010). However, their decline of up to 50% in relative cover from 2006 to 2012 in the third barrier at Punta Nizuc (from 15.5% to 7.65%, Table S1) requires special attention from the park authorities. The populations of these species are susceptible to fragmentation by physical impacts caused by the inappropriate use of anchors from tourist boats, by diving activities (Reyes-Bonilla et al. 2012) and by the effect of storms and hurricanes (Hughes and Connell 1999). In national parks, the regulations prohibit the use of anchors within the protected area, but recreational activities such as snorkelling and scuba diving are widespread and very difficult

to control (Tratalos and Austin 2001). Although the fragmentation of colonies can promote asexual reproduction, especially in the species of branched forms (Aronson and Precht 2001), recent studies suggest that fragmentation may also facilitate the outbreak of diseases (Lamb et al. 2014). Finally, an additional cause of the decline in cover of *Acropora s*pp. is the erosion of beach areas, previously restored through a governmental programme, which were lost to the passing of hurricane "Wilma" in 2005 (McField et al. 2008). The third barrier of Punta Nizuc seems to have the best conditions of the Cancún National Park, based on higher LCC, species richness and cover of *A. palmata*. Thus, implementing strategies of protection and recovery of all reefs within the park should be a priority.

The coral reefs of Cozumel showed a period of apparent recovery in LCC. In 2012, on average, LCC (29.14±14.15%) was 25% greater than the cover that had been reported in 2005, before the passage of hurricanes Emily and Wilma (Álvarez-Filip et al. 2009). The initial decreasing trend in LCC from 2006 to 2009 may have been due to the cumulative effect of the impact of two hurricanes (Álvarez-Filip et al. 2009), which left exposed a large area of abiotic components such as sand, rubble and bare rock (Álvarez del Castillo-Cárdenas et al. 2008, Carriquiry et al. 2013). The increase in LCC from 2009 to 2012 may have resulted in part from the survival and growth of the coral fragments broken during the storms (Gardner et al. 2005), especially since there was newly available substrate for the establishment and settlement of other species (Lugo et al. 2000), and particularly for the branched, foliose or finger forms that are more susceptible to physical shock, whose subsequent fragmentation becomes an important form of asexual reproduction (Aronson and Precht 2001). An increase in the relative cover of the more abundant species was observed in the reefs of Cozumel, especially Colombia reef. The species with the greatest increase from 2006 to 2012 were *A. tenuifolia* (foliose growth) and *P. porites* (digitiform growth) (Table S2).

The dominant species were *A. agaricites*, *S. siderea* and *P. astreoides*. These species have already been reported as the most abundant before the hurricanes of 2005 (Álvarez-Filip et al. 2009). In the reefs of Cozumel, species richness and the contribution of more than two species to 50% of the assemblage is reflected in the diversity index, with higher values than those reported for reefs at Cancún. However, it is important to note that the most abundant species are characterized by a high population change and small colonies (Darling et al. 2012). In terms of ecological roles, these species could not fulfil the functions of accretion and heterogeneity of habitat that are provided by massive or branched colonies (e.g. *Orbicella* spp., *Acropora palmata*). Therefore, the direction of change in the structure of species assemblages towards smaller colonies and reduced structural complexity could affect the ecosystem functioning (Álvarez-Filip et al. 2011, Álvarez-Filip et al. 2013, Perry et al. 2014).

Although the reefs appear to show the same general pattern of change in the coral assemblages, multivariate analyses reveal that the assemblages on each reef exhibit different patterns of temporal variation in terms of their composition and structure. This can be evaluated by other factors acting at the regional level (i.e. evolutionary and geological history, ocean transport and larval connectivity, and reef landscape configuration) or the local level (e.g. intensity and frequency of storms, environmental gradients, habitat specialization and intra-, inter-specific interactions) (Somerfield et al. 2008).

In summary, although seven years is a relatively short period of time, two different dynamics in the structure and composition of coral assemblages were observed after the strong impact of the physical disturbance caused by two hurricanes. In Cancún (PN-IMCN), coral reefs maintained a low LCC and low richness, diversity and evenness during the study period, with a significative change only in the abundance of *Acropora* spp. in the third barrier of Punta Nizuc. In Cozumel (PNAC), the coral reefs were characterized by an increase in LCC and high richness, diversity and evenness, with *Porites* spp. and *Agaricia* spp. showing the most significant increases. However, the question remains whether dominant species, such as those forming small colonies, carry out functions of accretion and provide heterogeneity of habitats of these ecosystems, and thus potentially limiting the performance of these ecosystems in terms of resistance and resilience to future disturbances.

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SUPPLEMENTARY MATERIAL

The following material is available through the online version of this article and at the following link:
http://www.icm.csic.es/scimar/supplm/sm04294esm.pdf

Table S1. – Mean coral cover (± 1SD) of the species recorded in the Cancún National Park.

Table S2. – Mean coral cover (± 1SD) of the species recorded in the Cozumel National Park.

Table S3. – Ecological indexes of coral assemblages in Cancún National Park and Cozumel National Park as a function of locality and year. Codes: S is the average species richness; H' is Shannon diversity; J' is Pielou evenness; λ is Simpson dominance; LCC is live coral cover.

Spatiotemporal variations of live coral cover in the northern Mesoamerican Reef System, Yucatan Peninsula, Mexico

Linda M. Barranco, José D. Carriquiry, Fabián A. Rodríguez-Zaragoza, Amílcar L. Cupul-Magaña, Julio A. Villaescusa, Luis E. Calderón-Aguilera

Supplementary material

Table S1. – Mean coral cover (±1SD) of the species recorded in the Cancún National Park.

	2006	2007	2009	2010	2011	2012
Acropora cervicornis	0.23 (±0.52)	0.15 (±0.46)	0.35 (±0.91)	0.14 (±0.52)	0.23 (±0.66)	0.04 (±0.18)
Acropora palmata	4.10 (±7.52)	2.26 (±4.23)	2.20 (±4.24)	2.72 (±6.46)	1.91 (±3.19)	2.91 (±6.18)
Acropora prolifera	0.06 (±0.29)			0.09 (±0.35)	0.05 (±0.18)	0.15 (±0.50)
Agaricia agaricites	0.29 (±0.62)	0.02 (±0.06)	0.54 (±1.41)	0.20 (±0.32)	0.32 (±0.48)	0.17 (±0.45)
Agaricia fragilis	0.03 (±0.17)					
Agaricia tenuifolia		0.75 (±3.27)	0.10 (±0.42)	0.09 (±0.34)	0.21 (±0.73)	0.28 (±1.03)
Colpophyllia natans		0.06 (±0.30)	0.10 (±0.35)	0.35 (±1.32)	0.16 (±0.80)	0.62 (±1.82)
Dichocoenia stokesii				0.02 (±0.09)		
Diploria labyrinthiformis				0.04 (±0.19)		
Favia fragum			0.01 (±0.03)			
Isophyllastrea rigida				0.01 (±0.05)	0.03 (±0.09)	
Meandrina meandrites						0.01 (±0.04)
Montastrea cavernosa	0.06 (±0.13)	0.29 (±0.69)	0.05 (±0.12)	0.19 (±0.58)	0.05 (±0.21)	0.08 (±0.21)
Orbicella annularis	0.41 (±0.93)	0.62 (±1.43)	0.63 (±1.41)	0.56 (±0.97)	0.67 (±1.45)	0.87 (±1.66)
Orbicella faveolata	0.12 (±0.35)		0.17 (±0.48)	0.39 (±1.22)		
Porites astreoides	2.33 (±2.26)	2.33 (±2.62)	1.70 (±2.46)	1.82 (±1.92)	2.93 (±4.09)	2.16 (±2.57)
Porites porites	0.84 (±1.91)	0.91 (±1.71)	0.71 (±0.68)	0.39 (±0.46)	0.76 (±1.11)	0.50 (±0.99)
Pseudodiploria clivosa	0.02 (±0.08)	0.13 (±0.34)			0.05 (±0.21)	
Pseudodiploria strigosa	0.09 (±0.32)	0.26 (±0.65)	0.01 (±0.07)	0.22 (±0.67)	0.27 (±0.79)	0.48 (±1.69)
Siderastrea radians	0.04 (±0.10)	0.24 (±0.40)	0.03 (±0.08)	0.01 (±0.04)	0.03 (±0.09)	
Siderastrea siderea	0.23 (±0.47)	0.71 (±1.91)	0.46 (±0.95)	0.38 (±0.66)	0.56 (±0.77)	0.25 (±0.79)
Stephanocoenia intersepta		0.01 (±0.07)	0.01 (±0.06)	0.01 (±0.04)		0.03 (±0.11)

Table S2. – Mean coral cover (±1SD) of the species recorded in the Cozumel National Park.

	2006	2007	2008	2009	2010	2011	2012
Acropora cervicornis		0.01 (±0.10)	0.01 (±0.10)			0.01 (±0.10)	0.01 (±0.10)
Agaricia agaricites	5.16 (±3.19)	4.91 (±3.22)	3.72 (±2.61)	3.06 (±2.36)	3.82 (±2.97)	4.97 (±2.92)	6.82 (±4.25)
Agaricia fragilis					0.01 (±0.10)		0.46 (±0.85)
Agaricia grahamae							0.02 (±0.14)
Agaricia humilis	0.10 (±0.39)		0.02 (±0.14)	0.01 (±0.10)	0.08 (±0.37)	0.19 (±0.53)	0.05 (±0.24)
Agaricia lamarcki	0.09 (±0.36)	0.03 (±0.17)	0.03 (±0.22)	0.01 (±0.10)	0.12 (±0.47)	0.09 (±0.30)	0.24 (±0.58)
Agaricia tenuifolia	0.32 (±0.68)	0.30 (±0.69)	0.35 (±0.70)	0.53 (±0.93)	0.29 (±0.69)	1.08 (±2.20)	1.90 (±3.41)
Colpophyllia natans	0.17 (±0.54)	0.02 (±0.20)	0.13 (±0.48)	0.01 (±0.10)	0.06 (±0.21)	0.08 (±0.35)	0.15 (±0.49)
Dichocoenia stokesii	0.05 (±0.24)	0.07 (±0.23)	0.01 (±0.10)			0.17 (±0.42)	0.15 (±0.32)
Diploria labyrinthiformis	0.15 (±0.38)	0.17 (±0.46)	0.08 (±0.32)	0.08 (±0.29)	0.12 (±0.29)	0.17 (±0.50)	0.22 (±0.50)
Eusmilia fastigiata	0.36 (±0.57)	0.46 (±0.76)	0.17 (±0.39)	0.17 (±0.39)	0.24 (±0.43)	0.81 (±0.90)	1.18 (±1.18)
Favia fragum			0.01 (±0.10)	0.03 (±0.22)			0.17 (±0.39)
Isophyllastrea rigida	0.08 (±0.29)	0.16 (±0.39)	0.05 (±0.24)	0.08 (±0.29)	0.13 (±0.36)	0.02 (±0.14)	0.02 (±0.14)
Isophyllia sinuosa		0.01 (±0.10)					
Leptoseris cucullata	0.01 (±0.10)	0.01 (±0.10)	0.01 (±0.10)	0.01 (±0.10)			0.01 (±0.10)
Madracis decactis	0.23 (±0.53)	0.08 (±0.25)	0.12 (±0.29)	0.06 (±0.21)	0.07 (±0.27)	0.24 (±0.45)	0.43 (±0.63)
Madracis mirabilis			0.01 (±0.10)				
Manicina areolata			0.02 (±0.20)			0.09 (±0.30)	
Meandrina meandrites	0.28 (±0.52)	0.56 (±0.84)	0.37 (±0.81)	0.17 (±0.42)	0.31 (±0.69)	0.59 (±0.88)	0.78 (±0.99)
Montastrea cavernosa	1.32 (±1.30)	1.72 (±1.64)	0.69 (±0.79)	0.98 (±1.04)	1.45 (±1.44)	1.62 (±1.59)	1.79 (±1.34)
Mussa angulosa						0.01 (±0.10)	0.16 (±0.57)
Mycetophyllia lamarckiana	0.07 (±0.27)	0.1 (±0.31)	0.02 (±0.20)	0.01 (±0.10)	0.01 (±0.10)	0.13 (±0.39)	0.22 (±0.40)
Orbicella annularis	1.02 (±1.85)	1.3 (±2.30)	0.27 (±0.84)	0.14 (±0.59)	0.23 (±0.64)	1.62 (±2.64)	1.72 (±2.56)
Orbicella faveolata	0.64 (±1.24)	0.79 (±2.02)	0.86 (±1.19)	0.61 (±1.03)	1.28 (±2.41)	0.41 (±0.86)	1.49 (±2.22)
Orbicella franski	0.02 (±0.14)	0.09 (±0.09)	0.02 (±0.14)				
Porites astreoides	1.94 (±1.56)	1.60 (±1.26)	1.31 (±1.38)	1.06 (±1.11)	1.11 (±1.36)	1.76 (±1.94)	3.55 (±2.14)
Porites colonensis				0.01 (±0.10)			
Porites porites	0.57 (±0.93)	0.51 (±0.92)	0.59 (±0.91)	0.76 (±1.30)	1.24 (±1.99)	2.82 (±3.28)	4.38 (±4.89)
Pseudodiploria clivosa	0.02 (±0.14)	0.01 (±0.10)				0.03 (±0.17)	0.07 (±0.27)
Pseudodiploria strigosa	0.06 (±0.26)	0.14 (±0.42)	0.12 (±0.29)	0.14 (±0.44)	0.09 (±0.30)	0.28 (±0.67)	0.37 (±0.75)
Scolymia cubensis				0.02 (±0.10)			
Scolymia lacera							0.01 (±0.10)
Siderastrea radians	0.10 (±0.31)	0.01 (±0.10)	0.02 (±0.14)	0.05 (±0.19)		0.25 (±0.55)	0.36 (±0.59)
Siderastrea siderea	1.76 (±1.42)	2.20 (±1.58)	1.62 (±1.20)	1.08 (±1.07)	1.27 (±1.14)	2.56 (±1.99)	4.00 (±2.14)
Solenastrea bournoni						0.02 (±0.14)	
Stephanocoenia intersepta	0.13 (±0.30)	0.17 (±0.44)	0.05 (±0.24)	0.09 (±0.30)	0.02 (±0.14)	0.34 (±0.60)	0.47 (±0.67)

Table S3. – Ecological indexes of coral assemblages in Cancún National Park and Cozumel National Park as a function of locality and year. Codes: S is the average species richness; H' is Shannon diversity; J' is Pielou evenness; λ is Simpson dominance; LCC is live coral cover.

		S (per transect)	H' (loge)	J'	λ	LCC (%)
Cancún	Manchones	4.22 (±1.31)	0.99 (±0.34)	0.69 (±0.18)	0.48 (±0.18)	7.17 (±5.76)
	Cuevones	4.80 (±1.54)	1.11 (±0.35)	0.74 (±0.16)	0.43 (±0.16)	8.33 (±3.98)
	Chitales	4.43 (±1.30)	1.06 (±0.30)	0.74 (±0.16)	0.44 (±0.15)	7.42 (±5.27)
	1 barrier	4.21 (±1.70)	1.05 (±0.36)	0.76 (±0.15)	0.44 (±0.16)	4.65 (±2.52)
	3 barrier	5.63 (±2.11)	1.22 (±0.50)	0.71 (±0.20)	0.40 (±0.21)	14.81 (±6.54)
Cozumel	Paraíso	6.90 (±2.59)	1.68 (±0.37)	0.91 (±0.06)	0.23 (±0.09)	14.17 (±7.09)
	Chankanaab	6.55 (±2.96)	1.57 (±0.38)	0.88 (±0.06)	0.26 (±0.09)	16.47 (±9.43)
	Yucab	5.64 (±3.07)	1.47 (±0.46)	0.92 (±0.06)	0.28 (±0.12)	11.11 (±8.81)
	Cedral	7.96 (±3.22)	1.73 (±0.39)	0.86 (±0.07)	0.24 (±0.10)	19.21 (±10.60)
	Dalia	7.92 (±3.75)	1.67 (±0.44)	0.85 (±0.09)	0.26 (±0.12)	20.26 (±11.38)
	Colombia	8.29 (±2.64)	1.77 (±0.28)	0.86 (±0.06)	0.22 (±0.06)	26.13 (±12.74)
Cancún	2006	5.13 (±1.36)	1.07 (±0.29)	0.67 (±0.15)	0.46 (±0.14)	9.03 (±6.07)
	2007	4.30 (±1.26)	1.10 (±0.34)	0.78 (±0.17)	0.41 (±0.16)	9.05 (±5.90)
	2009	4.28 (±1.77)	1.07 (±0.37)	0.78 (±0.16)	0.43 (±0.16)	7.22 (±5.63)
	2010	5.00 (±2.21)	1.13 (±0.47)	0.72 (±0.18)	0.43 (±0.15)	8.08 (±6.28)
	2011	4.96 (±1.49)	1.19 (±0.36)	0.76 (±0.15)	0.40 (±0.15)	8.93 (±5.86)
	2012	4.22 (±1.68)	0.94 (±0.41)	0.67 (±0.19)	0.51 (±0.20)	8.55 (±4.57)
Cozumel	2006	7.07 (±2.69)	1.64 (±0.37)	0.87 (±0.08)	0.25 (±0.10)	17.38 (±7.34)
	2007	7.06 (±2.09)	1.67 (±0.30)	0.87 (±0.06)	0.24 (±0.08)	15.37 (±7.05)
	2008	5.72 (±1.76)	1.50 (±0.29)	0.89 (±0.08)	0.27 (±0.08)	9.61 (±5.19)
	2009	5.35 (±1.85)	1.45 (±0.34)	0.90 (±0.08)	0.28 (±0.10)	8.56 (±5.12)
	2010	5.81 (±2.05)	1.47 (±0.38)	0.87 (±0.09)	0.29 (±0.13)	15.88 (±7.05)
	2011	8.44 (±3.70)	1.78 (±0.44)	0.88 (±0.06)	0.22 (±0.10)	29.28 (±11.38)
	2012	11.04 (±3.43)	2.04 (±0.34)	0.87 (±0.05)	0.17 (±0.06)	29.14 (±12.73)