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Research Article

Spatial variation of hermatypic coral assemblages in Cayos Cochinos Archipelago, Honduras

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ABSTRACT. Spatial variations of hermatypic coral assemblages were evaluated at five sites in Cayos Cochinos Archipelago, Honduras, in February 2008. Richness and coverage of corals and other benthic morpho-functional groups were estimated using 56 videotransects. Topographic complexity and depth were also measured by transect. Twenty-two coral taxa were recorded for Cayos Cochinos. Total species richness was similar (16 and 17 taxa) at all sites, whereas species richness by transect was different among sites (6-12 taxa). Shannon diversity showed weak differences among sites (1.46-2.13), whereas Pielou evenness was not different among sites. Simpson dominance was low with weak differences among sites (0.15-0.27). The total cover of hermatypic coral was 16.5% at Roatan Bank, 10.5% at Salamandinga, 9.7% at Punta Pelicanos, 7.6% at La Grupera, and 6.9% at Mariposales. The ANOSIM revealed assemblages of different corals between sites, except between La Grupera, Punta Pelicanos, and Salamandinga. The NMDS associated La Grupera, Punta Pelicanos, and Salamandinga given the greater contribution of *Porites astreoides*, *Agaricia agaricites*, and *Montastraea annularis*; whereas the NMDS differentiated Mariposales and Roatan Bank, which had more dissimilar assemblages with a greater predominance of *Montastraea cavernosa*, *Agaricia agaricites*, and *Diploria labyrinthiformis*. According to the BIO-ENV method, coral composition and abundance were correlated with the cover of articulated calcareous algae, sandy substrate, total hermatypic corals, rocky-calcareous substrate, fleshy macroalgae, and hydrocorals. In general, the differences found in the coral assemblages of Cayos Cochinos could be due to geomorphological characteristics as well as the effects of human activities in the study area.

Keywords: hermatypic coral assemblages, spatial variation, community ecology, Cayos Cochinos, Honduras.

Variación espacial de los ensamblajes de corales hermatípicos en el archipiélago Cayos Cochinos, Honduras

RESUMEN. La variación espacial del ensamblaje de corales hermatípicos se evaluó en cinco sitios del archipiélago Cayo Cochinos, Honduras, durante febrero 2008. La riqueza y cobertura de corales y otros grupos morfo-funcionales bentónicos se estimaron con 56 videotransectos. La complejidad topográfica y profundidad fueron medidas por transecto. Se registraron 22 taxa de coral para Cayos Cochinos. La riqueza total fue similar para todos los sitios entre sí (16-17 taxa), pero la riqueza por transecto fue diferente (6-12 taxa). La diversidad de Shannon presentó diferencias significativas entre sitios (1,46-2,13), mientras que la equidad de Pielou no mostró diferencias. La dominancia de Simpson fue baja con diferencias entre sitios (0,15-0,27). La cobertura total de coral hermatípico fue de 16,5% en Roatan Bank, 10,5% en Salamandinga, 9,7% en Punta Pelicanos, 7,6% en La Grupera y 6,9% en Mariposales. El ANOSIM evidenció ensamblajes de coral diferentes entre sitios, excepto entre La Grupera, Punta Pelicanos y Salamandinga. El MDS asoció La Grupera, Punta Pelicanos y Salamandinga por la mayor contribución de *Porites astreoides*, *Agaricia agaricites* y *Montastraea annularis*, en tanto diferenció a Mariposales y Roatan Bank con ensamblajes más disímiles con una mayor dominancia de *Montastraea cavernosa*, *Agaricia agaricites* y *Diploria labyrinthiformis*. El método BIO-ENV mostró que la composición y abundancia de corales se correlacionaron con la cobertura total de algas calcáreas articuladas, arena, coral hermatípico, sustrato calcáreo e hidrocorales. En general, la variación de los ensamblajes de coral podría deberse a las características geomorfológicas y a los efectos de actividades humanas presentes en el área de estudio.

Palabras clave: Ensamblajes de corales hermatípicos, variación espacial, ecología de comunidades, archipiélago Cayos Cochinos, Honduras.

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INTRODUCTION

Cayos Cochinos Archipelago, located in the southern zone of the Mesoamerican Barrier Reef System (MBRS), is a protected marine area declared to be a National Marine Monument by the Honduran Government (Andraka *et al*., 2004). The coral reefs of Cayos Cochinos are important (both economically and ecologically), and they make up part of an inter-connected system of coastal habitats and marine currents that extend beyond the basin of the Caribbean Sea (Paris & Cherubin, 2008). These reefs are thought to make an important contribution to the biodiversity of the MBRS.

Several studies have analyzed the structure of hermatypic coral assemblages (Karlson & Cornell, 2002; Ruiz-Zárate *et al*., 2003; Ruiz-Zárate 2005) or the condition of the reefs (Kramer, 2003; Arias-González *et al*., 2008; Carpenter *et al*., 2008; Alvarez-Filip *et al*., 2011a, 2011b; Arias-González *et al*., 2011) in the Caribbean Sea. At present, the reefs of this reef province have different degrees of health, with species of *Montastraea* having the greatest coverage (Kramer, 2003). Geomorphological features and "reefscape" attributes such as live coral cover, reef area, and habitat complexity are good proxies that explain the coral species composition and coral richness on multiple spatial scales (Arias-González *et al*., 2008, 2011). However, mean local richness shows a general pattern of consistent variation across habitats. This pattern is widely recognized on coral reefs (Karlson & Cornell, 2002), and some evidence even points to a relationship between coral species richness and latitude (see Willing *et al*., 2003).

The few reef studies carried out in Cayos Cochinos, Honduras, have focused on taxonomic and systemic studies of marine species from the region (Bermingham *et al*., 1998; Guzmán, 1998; Jacome, 1998; Ogden & Ogden, 1998). Bermingham *et al*. (1998) published taxonomic lists of the terrestrial species and marine birds of Cayos Cochinos; Guzmán (1998) compiled a taxonomic list of hermatypic corals of the cays; and Medina-Hernández (2005) evaluated the structure of the fish assemblages of the reef and their relationship with the benthic habitat in this protected area. Other studies mention only the geological characteristics (Ogden & Ogden, 1998), decapod species (Jacome, 1998), or echinoids (Lessios, 1998) of the area. None of the aforementioned works broach the topics of the composition and heterogeneity of the hermatypic coral species of Cayos Cochinos. Given the relevance of these organisms, the purpose of this study is to describe the structure of the hermatypic coral assemblage and its relationship with the benthic habitat. Thus, this work describes the richness, evenness, and abundance of the hermatypic coral and its relationship with other structural elements of the habitat. This information may support the policies and strategies that favor the management and conservation of biodiversity in Cayos Cochinos.

MATERIALS AND METHODS

Cayos Cochinos is located in the Bay Islands Department (Fig. 1), Honduras, and has a surface of 485.3 km^2 (Andraka *et al*., 2004). The two larger islands, Cochino Mayor and Cochino Menor, are made up of metamorphic schist and batholiths, whereas the lesser cays have coral origins (Coates, 2003). The shallow areas around the islands and cays contain gardens of octocorals and seagrass beds, whereas the deeper zones consist of sandy habitats with small coral patches, except to the west (Andraka *et al*., 2004).

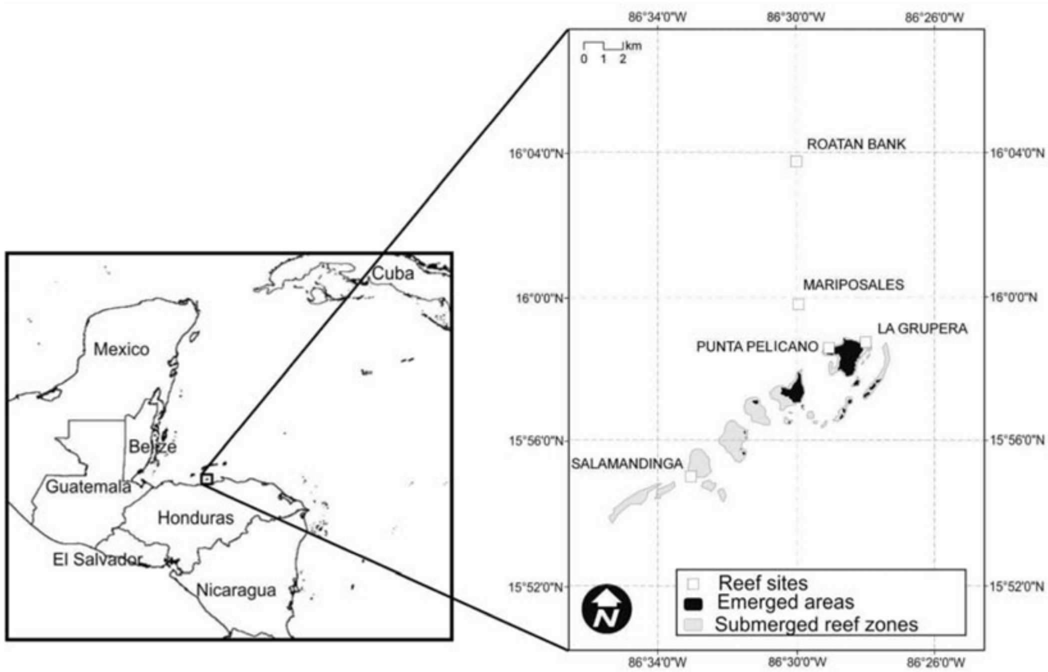

Figure 1. Study area and location of the sampling sites in Cayos Cochinos Archipelago, Honduras.
Figura 1. Área de estudio y ubicación de los sitios de muestreo en el archipiélago Cayo Cochinos, Honduras.

North of Cayos Cochinos, deep zones (30-100 m) predominate, with few shallow areas. The area south of the cays is dominated by depressions of 5 to 30 m depth, with trenches of up to 40 m. The depth around the islands and cays reaches 30 m (Bermingham *et al*., 1998). The average annual temperature oscillates between 25 and 29°C, and annual precipitation exceeds 2,000 mm (Brenes *et al*., 1998). Despite intense precipitation, annual variations in temperature and salinity are limited by the influence of the westward-flowing Caribbean currents (Coates, 2003).

Field data were collected in February 2008, from five sampling sites: Punta Pelicanos, La Grupera, Mariposales, Salamandinga, and Roatan Bank (Fig. 1). Sampling was done using a nested, unbalanced, hierarchical design, and the total effort consisted of 56 videotransects (50 x ~0.4 m, filmed at 0.4 m from the bottom). From each video, 40 frames were sub-sampled, and 13 fixed points from each frame were used to estimate the richness and cover of hermatypic coral, other benthic morpho-functional groups (hydro-corals, octocorals, fleshy macroalgae, sponges, seagrass, crustose calcareous algae, articulated calcareous algae), and substrate type (sandy, rubble, rocky-calcareous) based on the criteria of Arias-González *et al*. (2008). The topographic complexity of each transect was measured with a 10-m-long measuring tape following Aronson *et al*. (1994). The depth (m) by transect was measured using a scuba dive computer at the beginning of each transect.

The sampling effort for the study area was evaluated with species accumulation curves (*S*), Bootstrap procedures, the reciprocal of Simpson's dominance index (*1/D*), and the Shannon diversity index (*H'*, estimated by natural logarithm). The curves were constructed with 10,000 random combinations without replacement in EstimateS V8 (Colwell, 2009). Species diversity was analyzed with three indexes: Shannon diversity (*H'*), Pielou evenness (*J'*), and Simpson dominance (*D*). Because all the variables did not fit a normal curve and did not have equal variances, we use a non-parametric Kruskal-Wallis (H) test to compare the number of coral taxa per transect, Shannon diversity (*H'*), Pielou evenness (*J'*), Simpson dominance (*D*), and the total cover of hermatypic coral, benthic morpho-functional groups, and different types of substrate among the studied sites. Dunn's method was used as a non-parametric multiple comparison test to find statistical differences among sites, using a $P = 0.05$.

The similarity between coral assemblages was determined using a one-way analysis of similarity (ANOSIM), testing the statistical significance with 10,000 permutations and a $P = 0.05$. A non-metric multidimensional scaling (NMDS) analysis was also carried out. Both types of analysis were based on

Bray-Curtis similarity matrixes using data that had been previously transformed with square roots. This kind of transformation was used because the most and least abundant coral species differed by several orders of magnitude. The contribution of the coral species per site was estimated with a similarity percentage (SIMPER) analysis. Multidimensional analyses were done in Primer V6 (Clarke, 1993; Clarke & Warwick, 2001).

We applied the BIO-ENV method to relate the coral assemblages to the structure of the benthic habitat. The biological matrix was the same as that used in the NMDS. The environmental matrix was constructed using the averages for the total cover of hermatypic coral and the benthic morpho-functional groups, as well as the measurements of topographic complexity and depth. The Euclidean distance was used to build a resemblance matrix of environmental variables. The BIO-ENV procedure was applied to estimate the highest Spearman correlation (ρ) between biological and environmental variables. The statistical significance was tested with 10,000 permutations in Primer V6 (Clarke, 1993; Clarke & Warwick, 2001).

RESULTS

The evaluation of the sampling effort showed that it was representative of the richness, composition, and abundance of the coral species, since the accumulation curves of species observed and estimated with Bootstrap did not differ significantly and the accumulated curves of the reciprocal of Simpson's dominance (*1/D*) and Shannon diversity (*H'*) indexes showed an asymptote (Fig. 2). Twenty-two taxa of hermatypic coral were recorded, corresponding to 13 genera and 10 families (Table 1). The total species richness was similar at the studied sites, but species composition was different. Punta Pelicanos, La Grupera, and Salaman-dinga presented 17 taxa each, whereas Mariposales and Roatan Bank had 16 taxa apiece. Species richness by transect was significantly different among sites ($P = 0.004$); the main differences were found between Roatan Bank (12 taxa) and La Grupera (~6 taxa). Shannon diversity (*H'*) showed significant differences among sites ($P = 0.012$): diversity was highest at Roatan Bank and lowest at La Grupera. Pielou evenness (*J'*) was not significantly different among sites. Values of *J'* ranged between 0.84 and 0.89, revealing high evenness of species among sites. Simpson dominance (*D*) was lower, with significant differences among sites ($P = 0.028$). The highest species dominance was found at La Grupera, whereas the lowest was estimated at Roatan Bank (Fig. 3). The similarity of the coral assemblages was significantly different among sites (ANOSIM, $R = 0.172$, $P = 0.0001$), except between Punta Pelicanos and La Grupera, Punta Pelicanos and Salamandinga, and La Grupera and Salamandinga (Table 2). Species composition and abundance differed most between the sites Roatan Bank and Mariposales. Table 3 shows the species contributing the most to the average similarity (95%) per site. According to the NMDS, La Grupera, Punta Pelicanos, and Salamandinga constitute a group

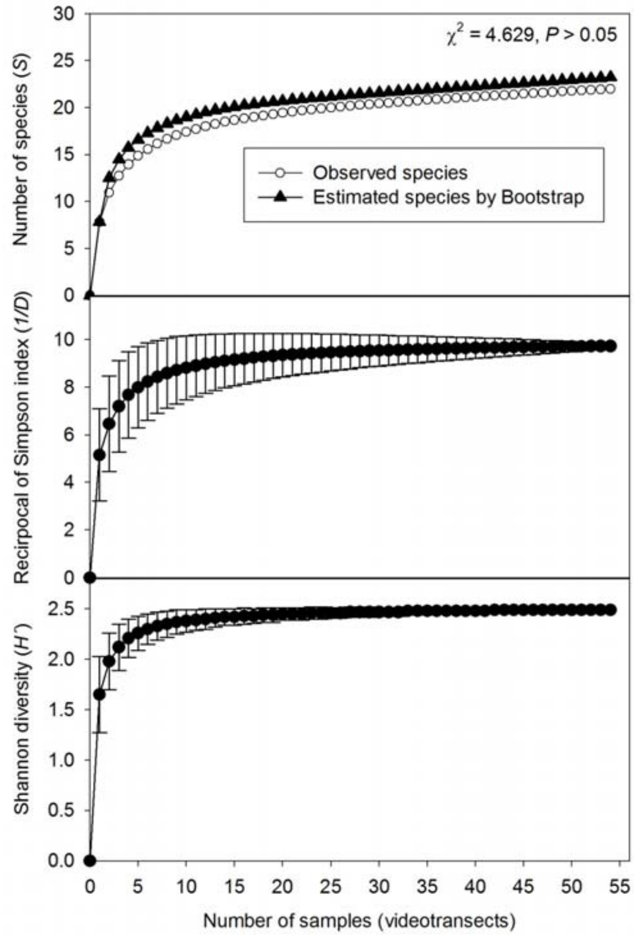

Figure 2. Evaluation of the sampling effort with accumulation curves of observed species and species estimated with Bootstrap, reciprocal of Simpson dominance index (*1/D*), and the Shannon diversity index (*H'*). A Chi-square goodness-of-fit test (χ^2) was used to compare the observed richness against estimated richness by Bootstrap.

Figura 2. Evaluación del esfuerzo de muestreo con curvas de acumulación de especies observadas y especies estimadas con Bootstrap, reciproco del índice de Simpson (*1/D*), e índice de diversidad de Shannon (*H'*). Se usó una prueba de bondad de ajuste chi-cuadrado (χ^2) para comparar la riqueza observada contra la riqueza estimada por Bootstrap.

Table 1. Taxonomic list and record of thermatypic coral species, by sampling site, in Cayos Cochinos Archipelago, Honduras. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Tabla 1. Listado taxonómico y registro de las especies de corales hermatípicos por sitio de muestreo en el archipiélago Cayo Cochinos, Honduras. PP: Punta Pelicano, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Family	Species	PP	GP	MP	SM	RB
Acroporidae	*Acropora cervicornis*	x				
	Acropora palmata		x			
Agaricidae	*Agaricia agaricites*	x	x	x	x	x
	Agaricia carinata			x		
	Agaricia tenuifolia	x	x	x	x	x
Astrocoeniidae	*Stephanocoenia intersepta*	x	x			
Caryophillidae	*Eusmilia fastigiata*	x	x	x	x	x
Faviidae	*Colpophylia natans*	x	x	x	x	
	Diploria clivosa				x	x
	Diploria labyrinthiformis	x	x	x	x	x
	Diploria strigosa	x	x	x	x	x
	Montastraea annularis	x	x	x	x	x
	Montastraea cavernosa	x	x	x	x	x
	Montastraea faveolata	x	x		x	x
	Montastraea franksi		x	x	x	x
Meandrinidae	*Dichocoenia stokesii*			x	x	
	Meandrina meandrites	x	x	x	x	x
Mussidae	*Mycetophylia* spp.	x			x	x
Pocilloporidae	*Madracis* spp.	x	x	x		x
Poritidae	*Porites astreoides*	x	x	x	x	x
	Porites porites	x	x	x	x	x
Siderastreidae	*Siderastrea* spp.	x	x	x	x	x
	TOTAL	17	17	16	17	16

with a similar assemblage of coral species (group 1), whereas the assemblages at Mariposales (isolated entity 2) and Roatan Bank (isolated entity 3) are made up of dissimilar species, differing both between these two sites and with group 1 (Fig. 4).

With respect to the elements of the benthic habitat, the total cover of hermatypic coral differed significantly among sites (P = 0.003). The greatest coral cover was estimated to be at Roatan Bank (16.5%) and Salamandinga (10.5%) (Fig. 4), whereas the lowest values were estimated for Punta Pelicanos (9.8%), La Grupera (7.6%), and Mariposales (6.9%) (Fig. 5). Likewise, statistical differences were found between sites in terms of the cover of sandy substrate, octocorals, and rubble, as well as the depth (Fig. 5). In contrast, no significant differences were observed in the cover of hydrocorals, sponges, fleshy macroalgae, crustose calcareous algae, articulated calcareous algae, other organisms, rocky-calcareous substrate, or topographic complexity (Fig. 5). The BIO-ENV method showed that the composition and abundance of coral species were more significantly correlated ($0.90 < \rho < 0.94$, $0.007 < P < 0.05$) with the cover of articulated calcareous algae, sandy substrate, hermatypic coral, rocky-calcareous substrate, fleshy macroalgae, and hydrocorals (Table 3).

DISCUSSION

The richness of scleractinian coral species recorded in this study constituted 33% (22 taxa) of the 66 species reported by Guzmán (1998) and Andraka *et al*. (2004)

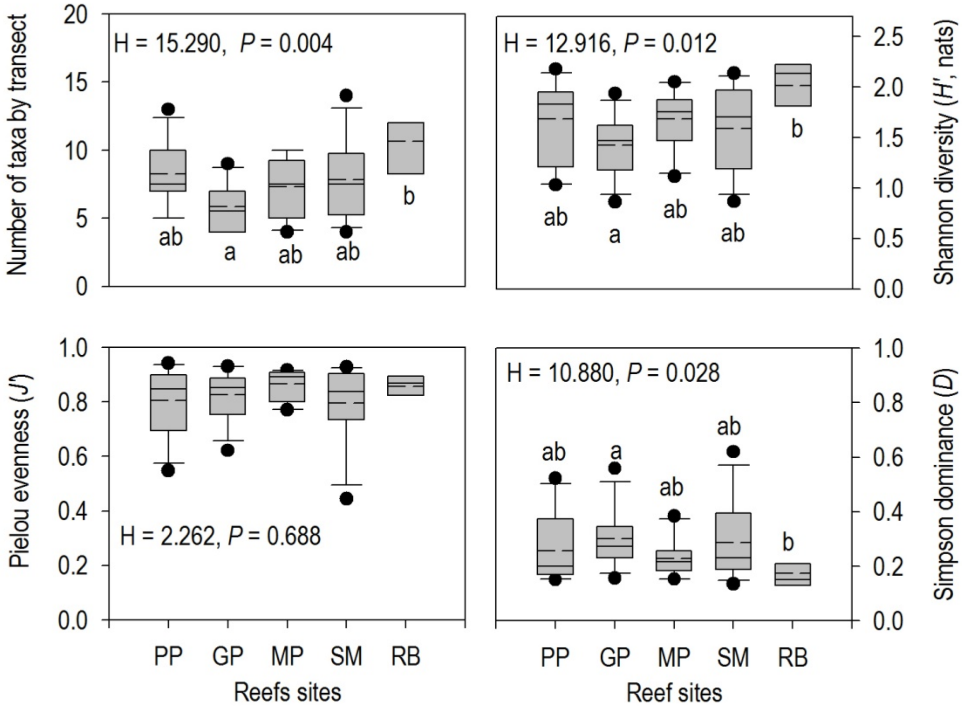

Figure 3. Box plots of the number of coral taxa by transect, and Shannon diversity (*H'*), Pielou evenness (*J'*), and Simpson dominance (*D*) indexes. The solid line is the median; the dashed line is the mean; the boxes show the 25 and 75% percentiles; the error bars are the 5 and 95% percentiles; the dots correspond to outliers. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank. A Kruskal-Wallis test (H) was used to compare each variable among reef sites considering $P \leq 0.05$. Reef sites with the same letters do not differ significantly ($P > 0.05$) based on the results of the Dunn method.

Figura 3. Gráficos de barras y bigotes del número de taxa de coral por transecto a índices de diversidad de Shannon (*H'*), equidad de Pielou y Dominancia de Simpson (*D*). La línea continua es la mediana; la línea segmentada es el promedio; las cajas representan los percentiles del 25 al 75%; las barras de error son los percentiles del 5 y 95%; los puntos corresponden a los datos extremos. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank. La prueba de Kruskal-Wallis (H) fue usada para contrastar cada variable entre los sitios arrecifales con base en una $P \leq 0{,}05$. Los sitios arrecifales con letras similares no tienen diferencias significativas entre sí ($P > 0{,}05$) con base en los resultados del método de Dunn.

This low representativeness may be due to the bias of the method used to register the species of this study, as it did not take into account the cryptic habitats. Moreover, this study excluded deep or extremely shallow sites, and the area of the filmed videotransects was small (~1,120 m^2). In contrast, the study by Guzmán (1998) lasted longer (20 months *versus* 1 month) and included deeper areas (shallow to >35 m).

The dominance of the coral assemblages of the Caribbean Sea is generally high, due mainly to the species of the complex *Montastraea* (Kramer, 2003; Rodríguez-Zaragoza, 2007). In the Mexican Caribbean, the relative covers of *M. faveolata* and *M. annularis* exceed 60% of the total live coral cover (Rodríguez-Zaragoza, 2007). In Cayos Cochinos, however, species of *Montastraea* constitute 14 to 35% of the total live cover, with *M. faveolata* and *M. annularis* only making up between 7 and 28% of the total cover, respectively. These results agree with Colombian Caribbean reefs from the oceanic region where species of *Montastraea* are dominant; *M. annularis* is only present in this kind of reef (in contrast with continental reefs), where its mean cover ranges from >10% to ~30 at 44% of the sites on these reefs. *Montastraea. faveolata* is present in both oceanic and continental reefs but with low mean cover (0-16% at all sites) (Díaz-Pulido *et al*., 2004).

Nevertheless, the most abundant coral species in Cayos Cochinos are *P. astreoides*, *A. tenuifolia*, *A. agaricites*, and *Siderastrea* spp., which have combined relative covers of 42 to 67% (see Table 3). This indicates that the composition and abundance of coral

Table 2. One-way similarity analysis (ANOSIM), results from comparing the structure of the hermatypic coral assemblages at five sampling sites in Cayos Cochinos Archipelago, Honduras. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Tabla 2. Resultados del análisis de similitudes (ANOSIM) de una vía para comparar la estructura del ensamblaje de corales hermatípicos en cinco de muestreo en el archipiélago Cayo Cochinos, Honduras. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Test	R statistic	Significance level
Global	0.172	0.0001
Pairwise		
PP, GP	0.055	0.164
PP, MP	0.162	0.020
PP, SM	0.045	0.188
PP, RB	0.273	0.004
GP, MP	0.206	0.006
GP, SM	0.052	0.164
GP, RB	0.324	0.003
MP, SM	0.196	0.008
MP, RB	0.315	0.002
SM, RB	0.275	0.006

species in the reefs of Cayos Cochinos are different from those of other Caribbean reefs. This difference could be due to a succession of species triggered by some change in the dominant environmental conditions since at least one of the studied sites (Punta Pelicanos) was once dominated by *D. strigosa* and *S. siderea* (Andraka *et al*., 2004) but is now dominated by *P. astreoides* (see Table 3).

The results of the BIO-ENV method suggest that the sites with greater species richness and evenness are those correlated with the highest cover by calcareous substrate and the lowest cover of sandy substrate and fleshy macroalgae. This may be due to the fact that the calcareous substrate favors the growth and recruitment of coral, whereas sandy substrate reduces its development (Sorokin, 1995). Moreover, fleshy macroalgae rapidly colonize the substrate and may lead to competitive inhibition of coral growth and recruitment, since their greater growth rate allows them to cover a large part of the reef in little time and because, given their large size, fleshy macroalgae can generate a shadow effect over the coral and cause abrasions on their tissues (Hughes, 1994; McCook *et al*., 2001). Díaz-Pulido & McCook (2004) showed that healthy corals are able to prevent the attachment or survival of recruits of these macroalgae; this is a significant point, since it suggests that the replacement of corals by algae often requires prior stress or death in the coral tissue. The changes of phase that have occurred in some areas of the Caribbean Sea since the 1980s have affected the coral reefs, decreasing the coral cover therein (Hughes, 1994). In Cayos Cochinos, the fleshy macroalgae cover is considerably high (on average, >50% at all studied sites; Fig. 4). Therefore, coral richness and diversity may be influenced by the availability of a substrate that is adequate for coral recruitment in conjunction with the cover of fleshy macroalgae.

At present, the structure of the coral assemblages in the Caribbean Sea is known to be influenced by the geomorphology of the reef and the structural elements of the habitat (Arias-González *et al*., 2008, 2011). The results of the BIO-ENV method obtained in this study show that, at the analyzed sites, the total cover of articulated calcareous algae, sandy substrate, hermatypic coral, rocky-calcareous substrate, fleshy macroalgae, and hydrocorals are correlated with the composition and abundance of the coral species of Cayos Cochinos. Punta Pelicanos, La Grupera, and Salamandinga have the most similar coral assemblages and also share certain geomorphological characteristics and similar structural elements. At all these sites, reefs grow in the shallow zones (<12 m depth) around the islands and cays where the cover of hydrocorals, articulated calcareous algae, and sandy substrate is high and that of hermatypic coral and

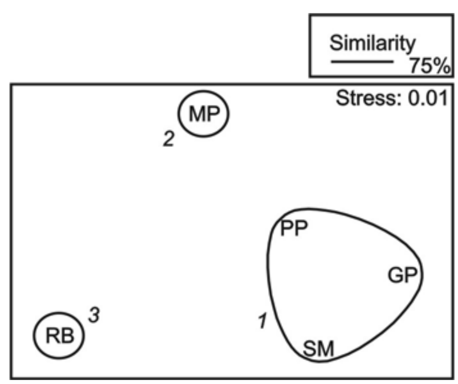

Figure 4. Species similarity among sites, analyzed using a NMDS ordering. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Figura 4. Similitud de especies entre los sitios, usando una MDS. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank.

Table 3. Results of the similarity percentage (SIMPER) analysis and percentages of absolute and relative coral cover per species. For SIMPER, only those species contributing 95% of the average similarity within each sampling site in the Cayos Cochinos Archipelago, Honduras, are presented. %AC: percentage of absolute cover per site, %RC: percentage of relative cover per site, %C: percentage of contribution to the average similarity per site, Cum%: percentage of accumulated contribution to the average similarity per site.

Tabla 3. Resultados del análisis de similitud en porcentaje (SIMPER) y de los porcentajes de cobertura absoluta y relativa para cada especie de coral. Para el SIMPER se presentan sólo las especies que contribuyeron a un 95% de la similitud promedio dentro de cada sitio de muestreo en el archipiélago Cayo Cochinos, Honduras. %AC: porcentaje de cobertura absoluta por sitio, %RC: porcentaje de cobertura relativa por sitio, %C: porcentaje de contribución a la similitud promedio por sitio, Cum%: porcentaje de contribución acumulada a la similitud promedio por sitio.

Species	%AC	%RC	%C	Cum%	Species	%Cov	%RC	%C	Cum%
Punta Pelicanos					La Grupera				
P. astreoides	1.73	17.68	24.37	24.37	*P. astreoides*	1.66	21.80	31.33	31.33
A. agaricites	0.92	9.49	15.19	39.56	*Siderastrea* spp.	0.83	10.90	28.43	59.75
M. annularis	1.4	14.40	13.6	53.15	*A. agaricites*	0.75	9.85	16.29	76.05
Siderastrea spp.	0.7	7.20	13.19	66.35	*A. tenuifolia*	0.67	8.81	6.33	82.38
M. cavernosa	0.68	7.04	11.03	77.38	*M. annularis*	0.72	9.43	5.09	87.46
D. strigosa	0.84	8.67	9.78	87.15	*D. strigosa*	0.6	7.97	4.8	92.27
A. tenuifolia	1.4	14.40	2.55	89.7	*M. cavernosa*	0.28	3.77	3.61	95.87
Mycetophylia spp.	0.2	2.13	2.29	91.99					
P. porites	0.36	3.76	2.22	94.22					
M. faveolata	0.28	2.95	2.11	96.33					
Mariposales					Salamandinga				
M. cavernosa	0.78	11.33	21.74	21.74	*P. astreoides*	1.23	11.74	21.1	21.1
A. agaricites	0.86	12.43	19.89	41.63	*A. tenuifolia*	3.8	36.43	19.61	40.72
D. labyrinthiformis	0.61	8.84	16.19	57.82	*A. agaricites*	1.15	10.98	17.18	57.9
P. astreoides	1.6	23.20	11.88	69.7	*M. annularis*	0.65	6.25	10.5	68.4
Siderastrea spp.	0.5	7.18	9.56	79.26	*D. strigosa*	0.8	7.62	9.98	78.38
M. annularis	0.8	11.60	8.02	87.28	*Siderastrea* spp.	0.78	7.47	9.67	88.05
A. tenuifolia	0.96	13.81	5.35	92.63	*M. cavernosa*	0.64	6.10	7.01	95.06
M. meandrites	15	2.21	4.36	96.98					
Roatan Bank					Roatan Bank				
A. agaricites	3.29	19.86	19.32	19.32	*A. tenuifolia*	1.4	8.55	5.77	74.7
M. cavernosa	1.99	12.03	14.57	33.88	*M. annularis*	0.96	5.80	4.97	79.67
P. astreoides	1.65	10.00	11.55	45.44	*Siderastrea* spp.	0.55	3.33	4.8	84.47
M. faveolata	1.89	11.45	8.3	53.74	*P. porites*	0.76	4.64	4.64	89.11
D. labyrinthiformis	0.88	5.36	8.19	61.93	*M. meandrites*	0.62	3.77	4.11	93.22
M. franksi	0.96	5.80	7	68.93	*D. strigosa*	0.76	4.64	3.71	96.93

rocky-calcareous substrate is moderate. These characteristics are correlated with greater contributions of the species *P. astreoides*, *A. agaricites*, *Siderastrea* spp., and *A. tenuifolia*. The species of *Porites* are characterized as opportunistic in shallow habitats, where they generate coral patches (Sorokin, 1995). *Agaricia* spp. lives in zones with high topographic complexity, and some species (*e.g.*, *A. tenuifolia*) have an encrusting-foliose form that allows them to reduce the stress generated by waves in

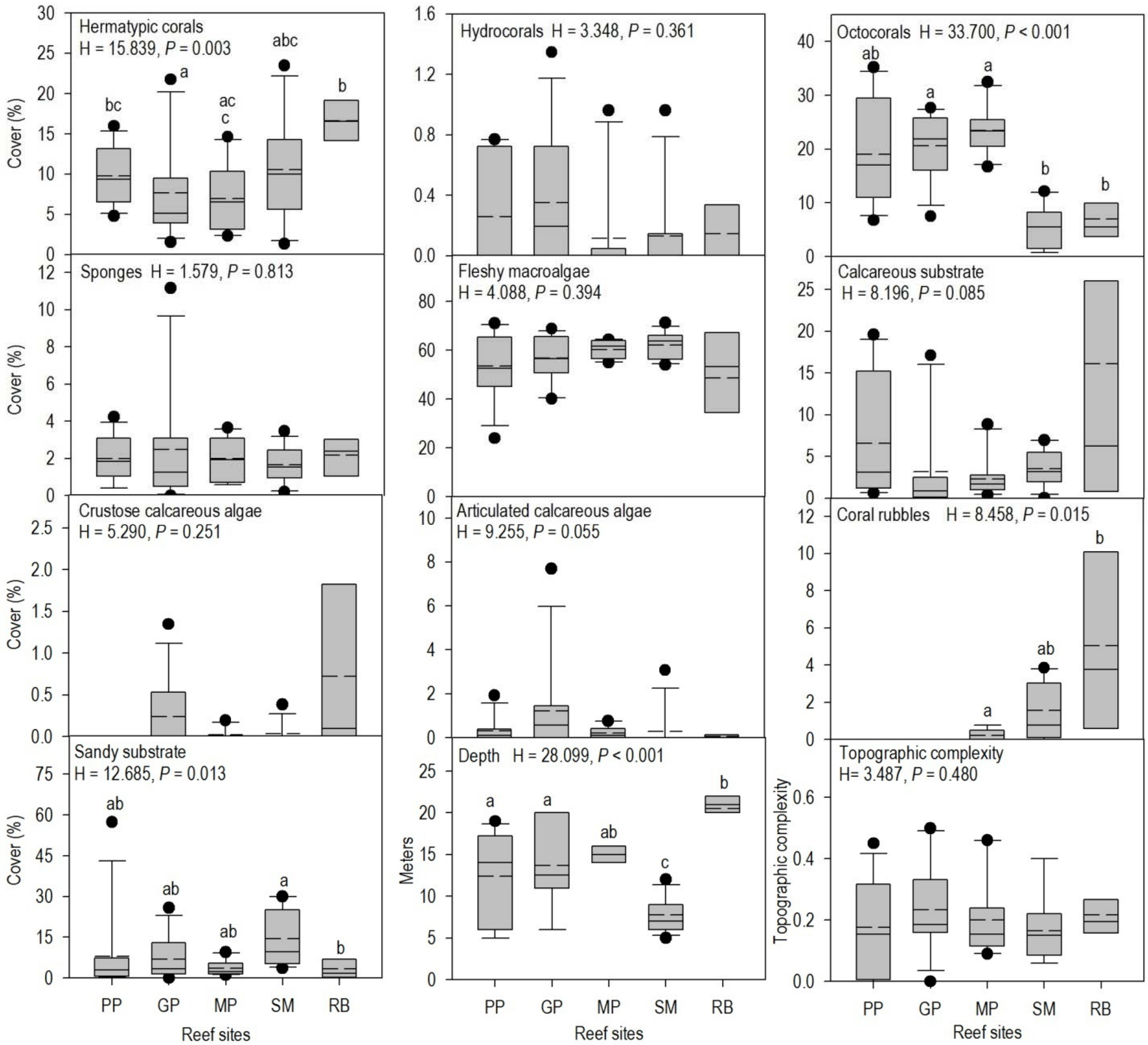

Figure 5. Box plots of the representative variables of the geomorphology and the benthic habitat. The solid line is the median; the dashed line is the mean; the boxes show the 25 and 75% percentiles; the error bars are the 5 and 95% percentiles; the dots correspond to outliers. H: Kruskal-Wallis statistic, PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank. A Kruskal-Wallis test (H) was used to compare each variable among the reef sites considering $P \leq 0.05$. Reefs sites with the same letters do not differ significantly ($P > 0.05$) based on the results of the Dunn method.

Figura 5. Gráficos de barras y bigotes de las variables representativas de la geomorfología y del hábitat bentónico. La línea continua es la mediana; la línea segmentada es el promedio; las cajas representan los percentiles del 25 al 75%; las barras de error son los percentiles del 5 y 95%; los puntos corresponden a los datos extremos. PP: Punta Pelicanos, GP: La Grupera, MP: Mariposales, SM: Salamandinga, RB: Roatan Bank. La prueba de Kruskal-Wallis (H) fue usada para contrastar cada variable entre los sitios arrecifales con base en una $P \leq 0,05$. Los sitios arrecifales con letras similares no tienen diferencias significativas entre sí ($P > 0,05$) con base en los resultados del método de Dunn.

shallow reefs (Rodríguez-Zaragoza, 2007). The genus *Siderastrea* is considered to be important in the reef crests since it presents an adequate resistance to the waves (Sorokin, 1995). *Porites astreoides*, *A. agaricites*, *Siderastrea* spp., and *A. tenuifolia* are found in more adverse environments but generate poor reef development in terms of hermatypic coral cover, topographic complexity, and richness of organisms.

In contrast, the coral reefs at Mariposales and Roatan Bank have a different geomorphology and

Table 4. Results of the BIO-ENV method used to relate the coral assemblages with the representative variables of the structure of the benthic habitat. The ten best results are shown with their Spearman correlation (ρ) and statistical significance. LCC: total live hermatypic coral cover, HC: hydrocoral cover, FMA: fleshy macro algae cover, CCA: crustose calcareous algae cover, ACA: articulated calcareous algae cover, RU: coral rubble cover, SS: sandy substrate cover, CS: rocky-calcareous substrate cover.

Tabla 4. Resultados del método BIO-ENV usado para relacionar los ensamblajes de coral con las variables representativas de la estructura del hábitat. Se presentan los diez mejores resultados con su correlación de Spearman (ρ) y significancia estadística. LCC: cobertura total de coral hermatípico, HC: cobertura de hidrocorales, FMA: cobertura de macroalgas carnosas, CCA: cobertura de algas calcáreas costrosas, ACA: cobertura de algas calcáreas articuladas, RU: cobertura de escombro de coral, SS: cobertura de sustrato arenoso, CS: cobertura de sustrato rocoso-calcáreo.

Number of selected variables	ρ	Significance level	Selections
6	0.939	0.018	LCC, HC, FMA, ACA, SS, CS
5	0.927	0.026	LCC, HC, ACA, SS, CS
7	0.927	0.023	LCC, HC, FMA, CCA, ACA, SS, CS
7	0.927	0.023	LCC, HC, FMA, ACA, SS, RU, CS
3	0.915	0.031	LCC, FMA, ACA
4	0.915	0.025	FMA, ACA, SS, CS
5	0.915	0.016	LCC, ACA, SS, RU, CS
3	0.903	0.036	LCC, ACA, SS
4	0.903	0.032	LCC, FMA, ACA, SS
5	0.903	0.008	HC, FMA, ACA, SS, CS

habitat structure because they are located on deeper shelves. Thus, these coral assemblages are the most dissimilar of the study area. The coral assemblages at Mariposales and Roatan Bank have a greater dissimilarity with the other sites studied due to a greater contribution by the species of *Montastraea* (>30% contribution). The colonies of *Montastraea* are characterized by massive forms inhabiting deeper, darker waters (Sorokin, 1995). Moreover, these species have more efficient sediment removal rates (Huston, 1985). Because these species are also more aggressive and competitive in terms of the substrate (Lang & Chornesky, 1990), they colonize this more efficiently. Finally, these corals are k-strategy species; they are slow to develop and mature; they are found in places with less adverse conditions, reach more stable populations, and present larger colonies and, in turn, higher percentages of coverage (Sorokin, 1995).

The differences between the coral assemblages at Mariposales and Roatan Bank can be summarized as follows: (1) at Mariposales, live coral cover and rocky-calcareous substrate are low (as is topographic complexity), which may affect the structure of the coral assemblage since coral recruitment depends on high live coral cover and a large availability of hard substrate; (2) Roatan Bank has the highest hermatypic coral cover and rocky-calcareous substrate, favoring the development of hermatypic corals. Moreover, Roatan Bank is a deeper reef and is located farther from the cays, characteristics that should diminish the human impact at this site. This isolation and poor accessibility may have generated a better condition of the reef at Roatan Bank, giving rise to more dissimilar coral assemblages with the greatest species diversity and evenness. These results agree with those of Clifton & Clifton (1998), who report that this site is characterized by a better reef condition and distinct characteristics given its degree of isolation.

The condition of the coral reefs of Cayos Cochinos is inadequate due to the low hermatypic coral cover and the high fleshy macroalgae cover. Nonetheless, this condition is similar to that of most reefs in the Caribbean (Hughes, 1994; Jackson *et al*., 2001; Kramer, 2003). The total hermatypic coral cover has been used as an indicator of reef health since coral and many associated species depend on this variable to be able to recruit in the reefs (Knowlton & Jackson, 2001; Ruíz-Zarate *et al*., 2003; Arias-González *et al*., 2008, 2011; Rodríguez-Zaragoza *et al*., 2011). The present condition of the reefs of Cayos Cochinos Archipelago may reflect impacts generated by the fisheries carried out by the local populations, tourism, and the sedimentation and eutrophication that come from the continent. Fisheries began on this archipelago in the 1980s (Clifton & Clifton, 1998), and fishing has affected the reef conditions of the Caribbean Sea through the changes of phase it has provoked therein (Jackson *et al*., 2001). Fishing is one of the few economic and subsistence activities available in Cayos Cochinos, and it is often done by local artisanal fishermen.

On the other hand, eutrophication has increased the biomass of fleshy macroalgae. Prouty *et al*. (2008) used Ba and Mn concentrations as geochemical indicators of land-based activities, demonstrating the strong impact of terrestrial runoff and anthropogenic activities on coastal water quality of the Bay Islands in Honduras. Additionally, the coral reefs of the Bay Islands have been affected by considerably high sedimentation rates (Mehrtens *et al*., 2001). Because Cayos Cochinos is located near the mouths of several rivers and receives nutrient contributions from human populations and agricultural activities, this archipelago may be affected by important eutrophication and sedimentation. The resulting nutrient concentrations may favor the growth of fleshy macroalgae and, in turn, decrease the richness, diversity, and abundance of hermatypic coral in the area.

In general, the coral reefs of Cayos Cochinos can be considered to be in a state of deterioration, making it necessary to establish strategies that would augment the dominance of hermatypic coral, thereby maintaining the global biodiversity of this marine protected area so that it can continue to provide ecosystem services.

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