Ecological condition of coral reef assemblages in the Cuban Archipelago

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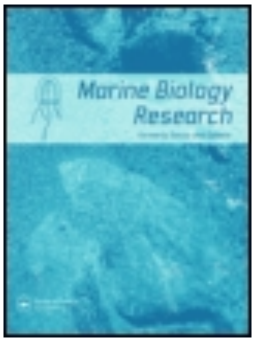

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ORIGINAL ARTICLE

Ecological condition of coral reef assemblages in the Cuban Archipelago

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ABSTRACT
The condition of coral reefs in the Cuban Archipelago is poorly known. We aimed to analyse coral assemblages across 199 reef sites belonging to 12 localities. Crest and fore reefs were assessed using six metrics: species richness, density, coral cover, mortality, coral size and reef complexity. The condition of reefs varied across the archipelago from healthy to depleted reefs. The localities with best scores were Cienfuegos, Bahía de Cochinos and Cazones. These reefs have values of living coral cover (>20%) and complexity (>50 cm) similar to the best preserved Caribbean reefs. However, the majority of crest biotopes suffered important deterioration with old mortality of *Acropora palmata* populations and moderate coral cover (15%); although crest reefs still maintained their structural complexity. Despite moderate levels of coral cover in fore reefs (18%), their condition was alarming because 25% of the sites had cover below the recovery threshold of 10%, accumulated mortality and structural flattening. Compared with the 1980s, the species richness was roughly the same (42) for crest and fore reefs, although dominance has changed to widespread tolerant species. Coral reef assemblages varied at local and regional scales in similar magnitude, suggesting the combined effects of natural and anthropogenic drivers.

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Introduction

Coral reefs are unique ecosystems that harbour biodiversity hotspots, support high biological productivity and provide goods and services to society. Caribbean coral reefs account for only 7% of the worldwide extent but play a vital role in the economy of the region due to tourism and fisheries (Jackson et al. 2014; Mumby et al. 2014). However, Caribbean coral reefs are threatened by a combination of natural and anthropogenic pressures such as hurricanes, diseases, ocean warming, pollution and overfishing (Harborne et al. 2017). Coral assemblages respond to these pressures through three processes (Obura and Grimsdith 2008; Alvarez-Filip et al. 2009, 2013; Perry et al. 2013): (i) persistence, the ability to resist the stressors without appreciable change; (ii) resilience, the ability to survive stress and subsequent recovery; and (iii) phase shift, when the habitat complexity and diversity of coral assemblage are reduced.

Surveys about the ecological conditions of coral reefs in the Caribbean Sea have reported a steady decline in the last five decades (Gardner et al. 2003; Côté et al. 2005; Wilkinson and Souter 2008; Schutte et al. 2010; Jackson et al. 2014). Indeed, many reefs face a phase shift with the substitution of corals by macroalgae (Kramer 2003; Burke and Maidens 2004). In addition, many Caribbean reefs show a decrease of coral reproduction and recruitment survival rates (Quinn and Kojis 2005). The main anthropogenic stressors causing this regional coral reefs decline are overpopulation, coastal pollution and overfishing (Jackson et al. 2014); further global stressors such as ocean warming and acidification also play a role (Noonan and Fabricius 2016; Smith et al. 2016).

The Cuban Archipelago contains the largest island in the Caribbean Sea and myriads of small keys bordered by extensive tracts of coral reefs. It is reasonable to consider that the status of Cuban coral reefs may contribute significantly to the regional condition due to: (i)

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their spatial extent and benthic habitat heterogeneity (Ruiz-Abierno and Armenteros 2017; Armenteros et al. 2018); (ii) the moderate physical and genetic connectivity among coral populations (Galindo et al. 2006); and (iii) the similarity in coral species composition (Miloslavich et al. 2010). However, there is a paucity in the published scientific literature about the condition of the coral reefs of the Cuban Archipelago, its geographic variability and ecological drivers of spatial changes. Some surveys in Cuban coral reefs pointed to a general decline in condition (e.g. González-Ferrer et al. 2007; Alcolado et al. 2010; González-Díaz et al. 2013), but others have shown reefs with high coral diversity and living coral cover suggesting high resilience (e.g. Caballero et al. 2004, 2007; Alcolado et al. 2013). Recently, González-Díaz et al. (2018) confirmed the existence across seven reef localities of an overarching trend from healthy to degraded coral reef status. However, there remain knowledge gaps, namely: (i) many unexplored reefs without any assessment of condition; and (ii) the magnitude of associated changes at different spatial scales from 10^0 (within reefs) to 10^3 km (between localities).

This contribution was the largest characterization of structure and condition of coral assemblages ever done in the Cuban Archipelago. The survey spanned 199 reef sites grouped in 12 localities, including the four main reef systems of the archipelago (i.e. Canarreos, Colorados, Jardines de La Reina and Sabana-Camaguey). The assessment was based on the Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology providing a snapshot of the current structure, condition and architectural complexity of coral reefs in this area (Kramer 2003). The AGRRA methodology focuses on those scleractinean and hydrozoan species that contribute the most to the construction and maintenance of the three-dimensional framework of the reef ecosystems. The assessment includes the spatial variation of six metrics of coral assemblages: species richness, density, living coral cover, coral size, colony mortality and complexity.

Based on previous knowledge, we proposed two working hypotheses: (1) coral reefs in the Cuban Archipelago largely vary geographically from healthy to degraded reef condition; and (2) most (>50%) of the variation in coral assemblage structure occurs on a locality scale (10^2–10^3 km) as compared to a site scale (10^0 km). Therefore, the aims of this study were to evaluate the condition of coral reefs around the Cuban Archipelago, and to describe the coral assemblage structure at two nested spatial scales (locality and reef site). The obtained results constitute an updated baseline for Cuban coral reefs and would be the basis for further hypotheses about tendencies of decline/recovery in a regional context.

Materials and methods

Studied reefs

The study covers 12 coral reef localities across the Cuban Archipelago (Figure 1). We selected *a priori* groups of reefs geographically near each other and subjected to broadly similar environmental settings (including anthropogenic pressures) for defining the grouping factor 'locality'. Distance between localities varied according to the geography of the archipelago but in general ranged from 10^2 to 10^3 km. Sites were selected within each locality taking into account the reef biotope: crest and/or fore reefs. Crests were mostly constituted by Elkhorn coral *Acropora palmata* (Lamarck, 1816) and fire coral *Millepora complanata* (Lamarck, 1816) and depth varied from 1 to 3 m. Fore reefs were more heterogeneous in depth (between 10 and 20 m)

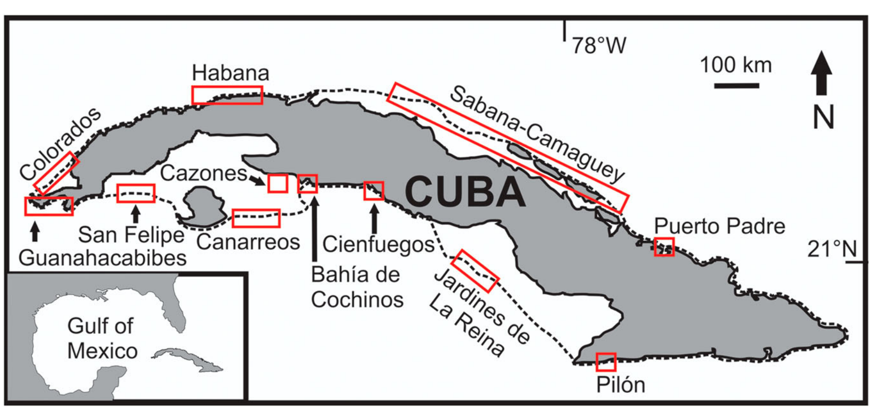

Figure 1. Map of the localities studied in the Cuban Archipelago. Dashed line indicates the approximate border of the shelf (~200 m).

Table I. List of studied localities and the number of sites per locality for the two biotopes. Total of localities, sites and transects per biotope are also given.

Locality	Acronym	Biotopes Crest	Fore reef
Colorados	COL	3	19
Habana	HAB	4	13
Sabana-Camaguey	SC	15	27
Canarreos	CAN	3	7
Cazones	CAZ	4	14
Cienfuegos	CIE	2	12
Pilón	PIL	5	4
Guanahacabibes	GUA	–	32
Bahía de Cochinos	BP	–	11
Jardines de La Reina	GQ	–	13
San Felipe	SF	–	6
Puerto Padre	PP	–	5
Total of localities		7	12
Total of sites		36	163
Total of 10-m transects		503	2468
Reef structure		*Acropora palmata* and *Millepora complanata*	Shallow terrace / shallow scarp / spur and grooves / reef wall

and physiography, with different subzones such as shallow terrace, shallow scarp, spurs and grooves, and reef wall. The number of studied sites per locality and the number of transects per site varied according to reef occurrence, sampling restrictions and extent of the system. In total, we counted 25,288 coral colonies from 2971 transects in 199 reef sites (Table I). Details of the sites (e.g. names and geographic coordinates) per locality are given independently for crest and fore reefs in the Supplemental Material (Supplemental Appendix 1). In a broad sense, 'site' has the same meaning as 'reef'.

Sampling methodology

Coral reefs were sampled between 2010 and 2013 using the AGRRA protocol (Kramer and Lang 2003). The sampling unit was a 10-m long linear transect and was used as a replicate within sites. A site was defined as a continuous reef with an extent of at least 200 m along correspondent isobaths. The distance between two adjacent sites was at least 100 m but in most of the cases was near to 10^0 km. At each site, we made between 10 and 22 transects. In each transect, we quantified six condition metrics of the coral assemblages:

(a) Species richness (SR). Number of species with living colonies > 10 cm diameter.
(b) Density (colonies 10 m^{-1}). The number of living colonies (> 10 cm diameter) per species within a 10-m transect.
(c) Living coral cover (%): Average of living coral tissue percentage that intercepted each transect.
(d) Coral size (cm): Maximum linear distance measured from top view and including dead parts of the colonies; it is equivalent to the maximum diameter of the colony.
(e) Mortality (%): Average of dead coral tissue percentage that intercepted each transect. Totally dead colonies, very eroded and/or covered by other organisms were not included.
(f) Reef complexity (cm): The averaged vertical distance between highest and lowest points in the bottom relief (including the corals) in an area of one metre radius. Five measures were made along each transect each 2 m (i.e. 0, 2, 4, 6, 8 m from the starting point).

Coral assemblages were defined by those containing species of the orders Scleractinia (stony corals) and Milleporina (fire corals). Coral species were identified according to Budd et al. (2012).

Data analysis

The six metrics were represented per locality and using scatterplot graphs with the median as measure of central tendency in an Excel macro (Weissgerber et al. 2015). All the other analyses were made using the software PRIMER 6.1.15 (Clarke and Gorley 2006) and a permutational analysis of variance (PERMANOVA + 1.0.5) (Anderson et al. 2008). Curves of accumulation of species versus number of transects were made to ensure that the sample size was large enough to accurately represent the SR within a site.

Differences of reef metrics were tested using a PERMANOVA. PERMANOVA analyses may be carried out using a similarity matrix based on Euclidean distances. A two-way unbalanced nested design was applied with locality (fixed effect), site (random effect) nested within locality, and transect as replicates within site. This design allowed the test for nested spatial scales. The magnitude of the effects per source of variation (i.e. locality, site, residual) were assessed by the estimates of components of variation (ECV). Analyses were carried out separately for crest and fore reefs.

Principal component analyses (PCA) were made separately for crests and fore reefs looking for patterns across localities based on the six condition metrics. The values used in the PCA were the median of the reefs per locality and data were normalized due to different units. Variables (i.e. metrics) were scaled and represented as eigenvectors in the plot for indicating the correlation among variables. The direction and slopes of the six eigenvectors defined regions in the plots with better/worse condition where most of the variables indicated good/bad values respectively. That is, reefs in better condition would tend to located near the positive values of the eigenvectors such as living coral cover and at the same time close to negative values of mortality. The opposite would apply for those reefs in worse condition. The interpretation of reef condition must be necessarily qualitative since no straightforward translation can be done from PCA scores to biologically meaningful scores of condition.

Non-metric multidimensional scaling ordination (NMMDS) was made separately for crests and fore reefs looking for similarity patterns in coral assemblage structure based on species density across localities. The matrix of species density × site was characterized by high dominance of a few species and many rare species. Therefore, the matrix was shortened by selecting only the species that individually contribute at least to 5% of the total density. The similarities among sites were calculated using the Bray–Curtis similarity index. These settings were also used for the above-mentioned PERMANOVA on species composition. Subsequently, a similarity percentage analysis (SIMPER) was performed to identify the coral species that most contribute to the similarity within each locality.

Results

Metrics of coral reef condition

The species richness (SR) was accurately estimated, for both crests and fore reefs, as indicated by the asymptotic shape of most of the cumulative curves (ESM Appendix 2). The total number of species per locality is given in the ESM Appendix 3. The median SR across the localities was 13 species (range: 2–28 species). In crests, SR did not significantly vary among localities, neither among sites nested within localities (Figure 2(a), Table II). In fore reefs, SR significantly varied across localities and across sites nested within localities. The estimates of components of variation (ECV) were similar in magnitude for locality and site nested within locality (Table III). Cienfuegos had the more diverse assemblages, followed by San Felipe, Bahía de Cochinos and Cazones. The less diverse localities were Puerto Padre, Pilón and Canarreos (Figure 2(b)).

The median coral density across all the localities was 9 colonies 10 m^{-1} (range: 2–17 col. 10 m^{-1}). In crests, density significantly varied among localities and among sites nested within localities. The ECV for locality and site within locality had similar magnitude (Table II). Pilón had the highest density and Cienfuegos the lowest, while Sabana-Camaguey was intermediate but

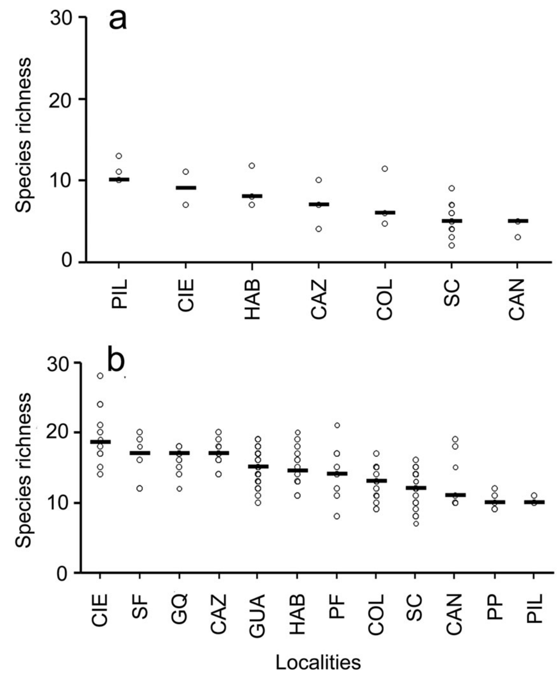

Figure 2. Species richness (medians and observed values) of coral assemblages in the Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. The sampled size is standardized to 10 transects. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

with large variability (Figure 3(a)). In fore reefs, density significantly varied among localities and among sites nested within localities. The ECV associated to locality

Table II. Results of a nested permutational analysis of variance (PERMANOVA) for six metrics of condition and coral assemblage composition (multivariate) for crest biotope. Significant differences at $P < 0.05$ in bold type. ECV = Estimates of Components of Variation, perms = permutations, Lo = Locality, Si = Site, Res = Residual.

Metric	Source of variation	*P*-value	ECV %	Unique perms
Species richness	Lo	0.34	6	6085
	Si (Lo)	0.54	6	9892
	Res		88	
Density	Lo	**0.04**	18	9964
	Si (Lo)	**0.0001**	25	9918
	Res		56	
Living coral cover	Lo	0.12	18	9940
	Si (Lo)	**0.0001**	39	9898
	Res		43	
Coral size	Lo	**0.0008**	22	9956
	Si (lo)	**0.0001**	19	9898
	Res		59	
Mortality	Lo	0.22	7	9995
	Si (Lo)	**0.001**	20	9953
	Res		73	
Reef complexity	Lo	**0.005**	24	9956
	Si (Lo)	**0.0001**	28	9877
	Res		47	
Assemblage composition	Lo	**0.001**	21	9913
	Si (Lo)	**0.0001**	32	9795
	Res		47	

Table III. Results of a nested permutational analysis of variance (PERMANOVA) for six metrics of condition and coral assemblage composition (multivariate) for fore reef biotope. Significant differences at $P < 0.05$ in bold type. ECV = Estimates of Components of Variation, perms = permutations, Lo = Locality, Si = Site, Res = Residual.

Metric	Source of variation	P-value	ECV %	Unique perms
Species richness	Lo	**0.0001**	30	993
	Si (Lo)	**0.0001**	28	996
	Res		42	
Density	Lo	**0.0001**	37	935
	Si (Lo)	**0.0001**	27	780
	Res		36	
Living coral cover	Lo	**0.0001**	36	932
	Si (Lo)	**0.0001**	29	972
	Res		35	
Size	Lo	0.93	10	999
	Si (lo)	**0.001**	24	999
	Res		67	
Mortality	Lo	0.5	2	999
	Si (Lo)	**0.001**	21	997
	Res		77	
Reef complexity	Lo	**0.001**	30	999
	Si (Lo)	**0.001**	35	999
	Res		35	
Assemblage composition	Lo	**0.0001**	17	999
	Si (Lo)	**0.0001**	30	997
	Res		54	

was larger than the one associated to site (Table III). Sabana-Camaguey, Puerto Padre and Colorados had the lowest values of density (Figure 3(b)).

The median living coral cover across all the localities was 15% (range: 3–63%). In crests, coral cover did not significantly vary among localities but significantly varied among sites nested within localities with larger ECV in the latter (Figure 4(a), Table II). In fore reefs, coral cover significantly varied among localities and among sites nested within localities. The ECV had similar magnitude in locality and site within locality (Table III). Bahía de Cochinos, Cazones, Cienfuegos and Jardines de la Reina had the highest values of coral cover; meanwhile Puerto Padre, Colorados and Sabana-Camaguey had the lowest (Figure 4(b)).

The median coral size across all localities was 28 cm (range: 13–122 cm). In crests, coral size significantly varied among localities and among sites nested within localities. The ECV had similar magnitude for locality and site (Table II). Pilón had the lowest median coral size (Figure 5(a)). In fore reefs, coral size only significantly varied among sites with relatively low ECV when compared with residual (Figure 5(b), Table III).

The median coral mortality was 8% across all the localities (range: 0–45%). In crests, mortality did not show significant differences across localities but among sites within localities (e.g. Cienfuegos, Canarreos, Cazones and Sabana-Camaguey) (Figure 6(a), Table II). In fore reefs, mortality showed the same trend with significant differences only among sites nested within localities

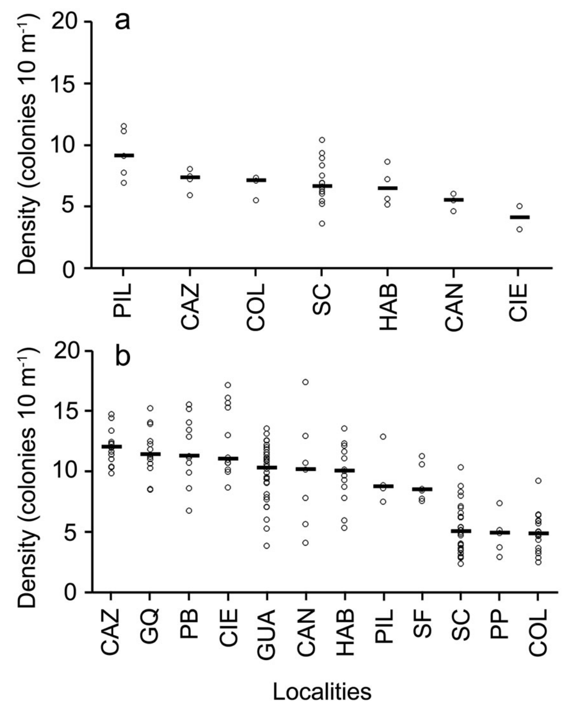

Figure 3. Density (medians and observed values) of corals in the Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

(Table III). The lowest values of mortality occurred in Cienfuegos and Jardines de La Reina (Figure 6(b)).

The median reef complexity across localities was 51 cm (range: 12–143 cm). In crests, reef complexity significantly varied among localities and among sites. The ECV was similar for both locality and site within locality (Table II). Canarreos, Cazones and Cienfuegos had highest complexity while lowest and more variable complexity occurred in Sabana-Camaguey (Figure 7(a)). In fore reefs, complexity significantly varied among localities and among sites. The EVC had similar magnitude for both locality and site (Table III). Highest complexity occurred in Bahia de Cochinos and Cienfuegos. Canarreos, Cazones and Guanahacabibes had the largest variability. Lowest complexity occurred in Sabana-Camaguey and Puerto Padre (Figure 7(b)).

The six condition metrics in crests were weakly correlated as indicated by the vector slopes in PCA ordination. However, richness, density and living coral cover were more correlated each other. Similarly, mortality and size were more correlated to each other when compared with the rest of the metrics (Figure 8(a)). The general picture in the ordination was a broad dispersion of points (i.e. sites) instead of clear clusters, although some trends emerged. Pilón had the best scores of species richness, living cover and density of colonies.

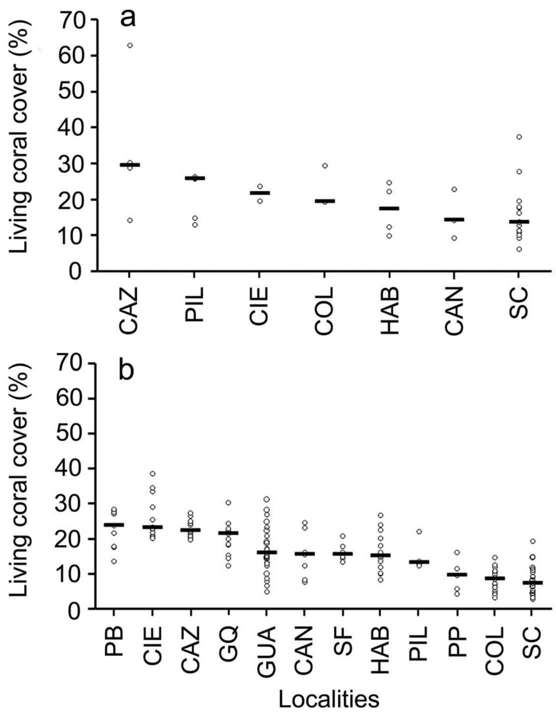

Figure 4. Living coral cover (medians and observed values) in the Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

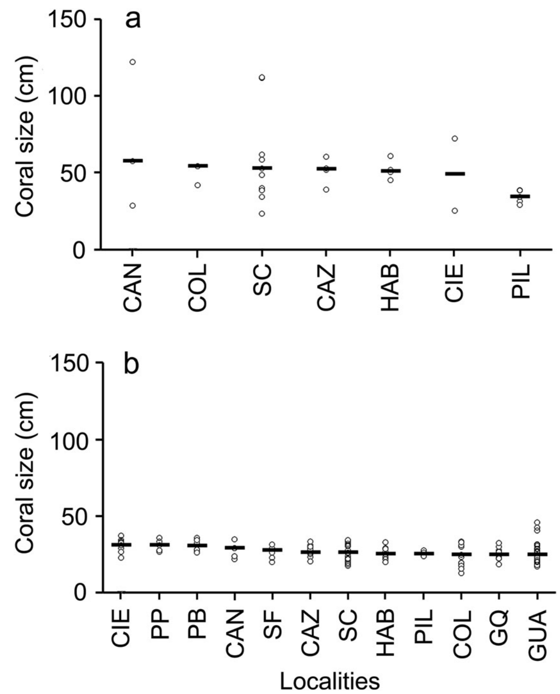

Figure 5. Colony coral size (medians and observed values) in Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

Colorados and Habana had similar intermediate positions in the ordination. Sabana-Camaguey had the worst conditions with high mortality, lowest complexity and low living coral cover (Figure 8(a)).

The six condition metrics in fore reefs were weakly correlated as indicated by the vector slopes in PCA. Four metrics were largely correlated to each other: SR, density, living coral cover and complexity (Figure 8(b)). No separated groups were clearly evident in the ordination instead a continuum of points. However, the ordination consistently clustered fore reefs of the same localities along the PC1 indicating that Bahía de Cochinos, Cienfuegos and Cazones had the best scores of reef condition. Sabana-Camaguey, Colorados and Puerto Padre had the worst scores. The PC2 mostly varied according to recent mortality, suggesting that lowest mortality occurred in Jardines de La Reina, Cienfuegos and some sites in Habana; Canarreos and Pilón had the highest mortality (Figure 8(b)).

Coral assemblage composition

The crests harboured coral assemblages constituted by 21 species (ESM Appendix 3). There was high dominance with 77% of the total density constituted by only three species: *M. complanata*, *A. palmata* and *Porites astreoides* (Lamarck, 1816). There were 15 rare species, each contributing less than 1% of total density. Species composition varied significantly among localities and among sites within localities. The magnitude of ECV was larger for site than for locality (Table II). The MDS ordination did not suggest any clustering according to the localities (Figure 9(a)).

The fore reefs had coral assemblages constituted by 39 species (ESM Appendix 3). There was high dominance with the same set of species constituting around 75% of the total density: *Siderastrea siderea* Ellis & Solander, 1786, *Agaricia agaricites* (Linnaeus, 1758), *Orbicella faveolata* Ellis & Solander, 1786, *P. astreoides*, *Montastraea cavernosa* Linnaeus, 1767, *Porites porites* (Pallas, 1766) and *Stephanocoenia intersepta* (Lamarck, 1816). There were around 15 rare species, each contributing less than 1% of total density. Species composition varied significantly among localities and among sites within localities. The ECV was larger for site than for locality (Table III). The MDS ordinations did not suggest any clustering according to the localities (Figure 9(b)). The results of SIMPER analyses for crests and fore reefs are reported in the ESM Appendix 4.

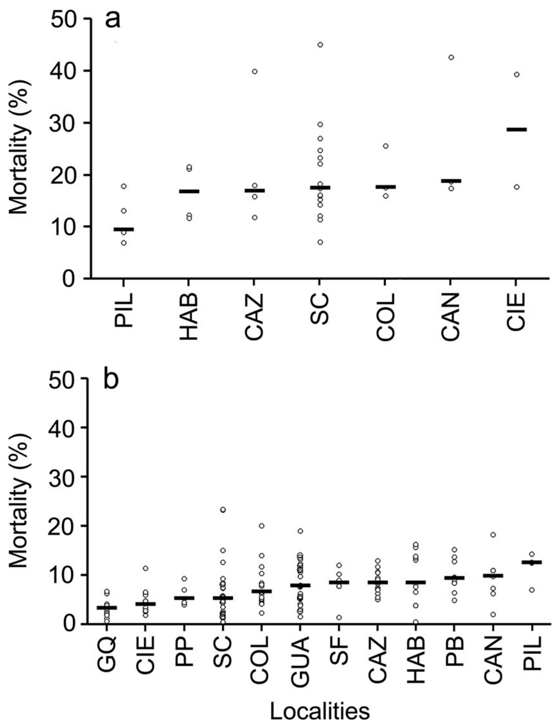

Figure 6. Mortality (medians and observed values) of corals in the Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

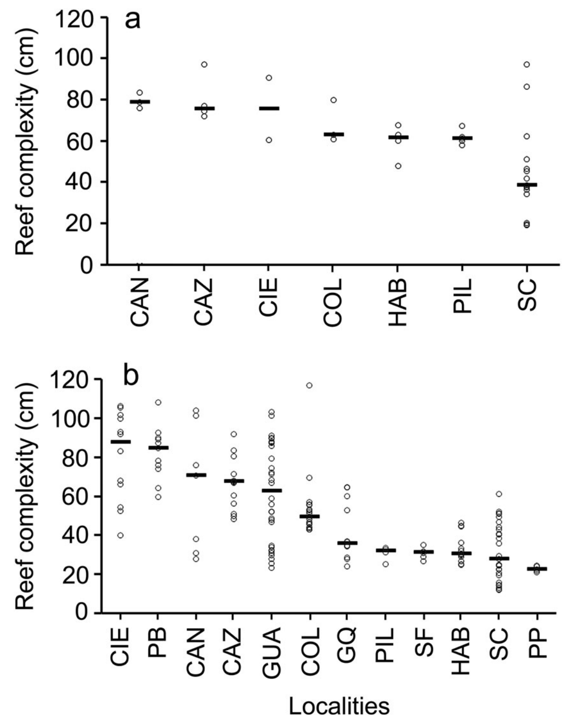

Figure 7. Reef complexity (medians and observed values) of corals in the Cuban Archipelago in two biotopes: (a) crests and (b) fore reefs. Abbreviations of localities: BP: Bahía de Cochinos, CAN: Canarreos, CAZ: Cazones, CIE: Cienfuegos, COL: Colorados, GQ: Jardines de La Reina, GUA: Guanahacabibes, HAB: Habana, PIL: Pilón, SC: Sabana-Camagüey, SF: San Felipe.

Discussion

The first hypothesis was supported by our results since we found a large variation in the reef condition across the 12 localities from healthy to degraded reefs. The second hypothesis could be rejected due to evidence of considerable variation in coral assemblage at site scale (10^0 km) when compared with locality scale (10^2–10^3 km). We further discussed the possible processes explaining these patterns.

A geographically broad spectrum of reef condition

The species richness in our study represented an important fraction of the 60 reef-builder coral species reported for the Cuban Archipelago (González-Ferrer et al. 2004). This finding highlighted the completeness of the sampling scheme despite the limitations of AGRRA methodology that does not quantify small-sized species (< 10 cm) or habitats such as seagrass beds or mesophotic reefs. This high diversity of Cuban coral reefs contrasted with other Caribbean reefs where coral diversity has depleted in the last 20 years due to high mortality (Cramer et al. 2012; Jackson et al. 2014). Caribbean reefs also showed the prevalence of opportunist coral species with short life-spans and fast growth (Côté and Darling 2010).

The living coral cover of Cuban coral reefs resembled other estimates published for the region (Table IV). We reported slightly higher coral cover when compared with the median for the tropical western Atlantic of 14.5% (range: 3–53%) (Jackson et al. 2014). The historical trend in the Caribbean Sea since the 1960s is the depletion of coral assemblages in crests mainly due to the decline of *A. palmata* populations (Aronson and Precht 2001; Schutte et al. 2010). Our study has updated previous assessments of coral cover in Cuba by reporting consistently lower values than those found by Jackson et al. (2014) from three reef systems.

At present, some reefs of the Caribbean have living coral cover values around 30%, such as 'Dairy Bull Reef' in Jamaica (Idjadi et al. 2010), Exuma Keys in Bahamas (Mumby and Harborne 2010) and the smallest Antilles Islands (Williams et al. 2017). In our study, only 36% of the sites (58 out of 163 fore reefs) had living coral cover equal or above 20% and only 4% equal or above 30% (six out of 163 fore reefs). A striking case of unusually healthy crest reef is Faro de Cazones with coral living

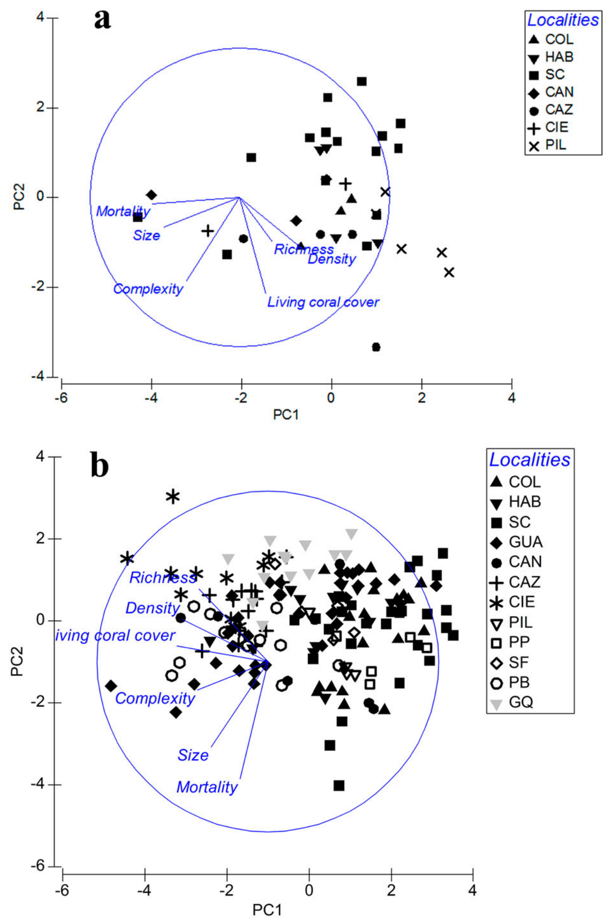

Figure 8. Principal component analyses of coral assemblages based on the six condition metrics. (a) Crest reefs. Explained variance (EV) by the two first axes: 78%. The eigenvectors: PC1 = -0.6M-0.5CS + 0.5D-0.4C + 0.2LC + 0.2SR; PC2 = -0.6LC-0.6C-0.4D-0.2SR-0.2CS + 0.0M. (b) Fore reefs. The eigenvectors: C1 = -0.5LC-0.5D-0.4C-0.4SR-0.3CS-0.2M. PC2 = -0.7M-0.5CS + 0.4SR-0.2C + 0.1D + 0.1LC. (EV) by the two first axes: 70%. D: density, CS: coral size, M: mortality, SR: species richness, LC: living cover, C: complexity.

cover of 62%. The most plausible explanation is a large coral resiliency due to the combination of the remote location of this reef, which prevents overfishing and pollution, and a favourable hydrodynamic regime enhancing the coral heterotrophy (Alcolado et al. 2010, 2013; Caballero et al. 2016).

However, many coral reefs in the region have been reported with living coral cover below 10%, which is a critical threshold for long-term survival by accretion (Perry et al. 2013). Cuban reefs have 8% of crest reefs below this 10% threshold (three out of 36 crests). In the case of fore reefs the proportion of depleted reefs in terms of coral living cover was 25% (40 out of 163), which is alarming. Most of these depleted reefs were in Sabana-Camaguey and Colorados, which should be targeted as priorities for the management and conservation of coral reef ecosystems. Both localities had an adverse physical environment that constrained the development of coral assemblages. Sabana-Camaguey was exposed to a strong and chronic wave regime while Colorados has suffered a high hurricane incidence (Chollet et al. 2012). Besides, both localities were also affected by widespread stressors causing the regional mortality of coral reefs (i.e. diseases, overfishing and ocean warming).

The large geographic variability in complexity indicates that Cuban coral reefs have very diverse architecture complexity at the present time. The comparison with data from Caribbean sites suggested that Cuban crest reefs have similar complexity because the colonies remaining are still standing and maintain their physical structure despite the high mortality in some reefs. Our data also suggested that many Cuban fore reefs have suffered the flattening that has been observed across the Caribbean Sea (Alvarez-Filip et al. 2009) as evidenced by low complexity values and high mortality.

In the Cuban coral reefs, the mortality of the colonies was mostly old whereas evidence of recent mortality was scant. This highlights the role of chronic disturbance (e.g. eutrophication, bioerosion) that started many decades ago on the reefs as well as intermittent disturbances (e.g. hurricanes, diseases and bleaching) (Meester et al. 1996a, 1996b). The mortality

Table IV. Summary of the coral assemblage metrics (medians or means, range in parentheses) for the Cuban Archipelago in this study and reference values from other studies in the Caribbean. FR = fore reef.

	Present study	Deleveaux et al. (2013)	Bruckner et al. (2014)	Jackson et al. (2014)	Williams et al. (2015)	Williams et al. (2017)	de la Cruz-Francisco and Bandala-Pérez (2016)
No. sites	199	23	18	88	92	30	12
Area	Cuba	Bahamas	Jamaica	Western Atlantic	Caribbean	East Caribbean	Veracruz
Species richness	Crest: 21 FR: 39	38	33	–	–	29	29
Living coral cover (%)	Crest: 15 FR: 18	12 (5–38)	9	15 (3–53)	*Orbicella* reef: 24 Gorgonian reef: 10	*Orbicella* reef: (22–30)	FR: 10
Mortality (%)	8 (0–45)	19 (11–29)	10	–	–	–	–
Coral size (cm)	28 (13–122)	22	20	–	–	–	–
Complexity (cm)	Crest: 61 FR: 48	73	–	–	–	–	–

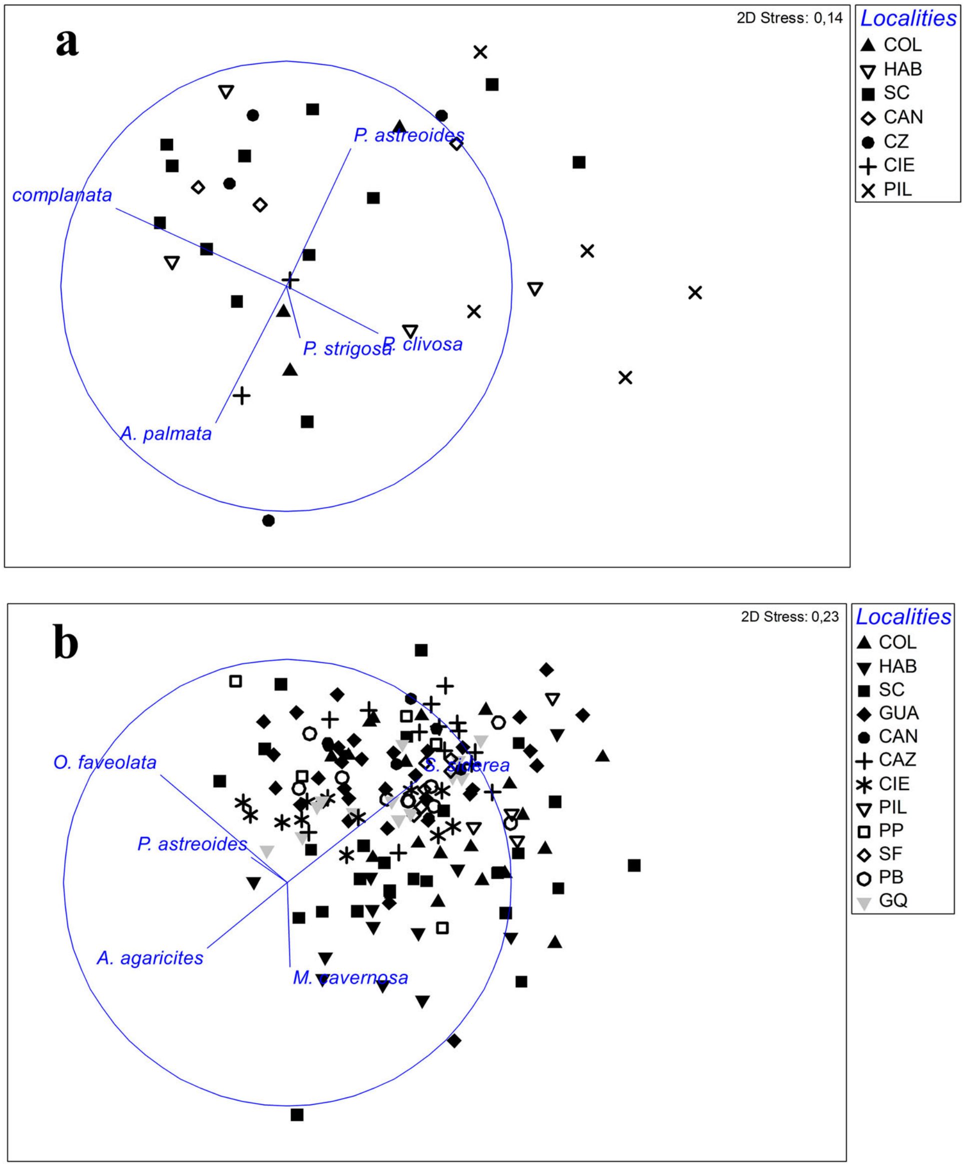

Figure 9. Multidimensional scaling ordination of sites in two biotopes coded by localities based on coral species composition and density. (a) Crest reefs. (b) Fore reefs.

reported in our study could be interpreted as relatively low; for instance, it was rarely larger than 13% in a single reef. The large spatial variability of coral mortality could be explained by the bioerosion and physical forces influencing the process of coral degradation from recent mortality to coral debris/rubber (Kramer 2003). However, many of the observed coral colonies were not quantified because they were completely dead, very eroded and/or covered by other organisms (e.g. algae, sponges, tunicates). This constituted a bias and our estimates of mortality should be considered as the lowest limit in the studied reefs.

Single metrics (e.g. species richness, living coral cover) cannot encompass the whole condition of coral reefs due to the multidimensional nature of this concept. For instance, in reef crest from Cienfuegos the complexity was high despite large coral mortality. Therefore, we believe that reef condition could be better described using the multivariate PCA based on the six metrics. In addition, the continuum of reef condition from healthy to degraded status was evident in the scatterplot of points (i.e. sites) in the ordination both for crest and fore reefs. We noted that our assessment focused on coral assemblages (e.g. diversity, abundance, mortality), which may indirectly indicate the environmental quality of the reef, but it did not directly measure any impact variable (e.g. nutrient load, fishing pressure).

The coral reefs in better condition in Cuba according to their metric-based scores were Cienfuegos, Bahía de Cochinos and Cazones. These localities shared three features that may enhance the coral reef resilience: located geographically close each other, low wave exposure and important inputs of organic matter by runoff from adjacent swamps or mountains. However, studies on genetic connectivity and nutrient cycling are needed to disentangle the ecological drivers explaining the good condition of these coral reefs.

Coral assemblage composition and spatial scale

Cuban coral reefs maintained roughly similar species composition compared with a 1980s report (Martínez-Estalella 1986). The crest reefs, compared with fore reefs, presented a lower number of coral species due to wider environmental fluctuations of temperature, light and waves typical of shallow waters. The species *A. palmata*, *M. complanata* and *P. astreoides* dominated in the more exposed and shallow reefs, whereas *Pseudodiploria* spp. also occurred in shallow reefs with higher turbidity (*Acropora* Biological Review Team 2005; Alcolado et al. 2010). *A. palmata* was numerically dominant only in five out of 36 crest reefs indicating an important decrease in the dominance of this species when compared with historical data from the region (Jackson et al. 2014). We observed a great number of standing, but dead, colonies of *A. palmata* in many of the studied crest reefs supporting the past dominance of the species. The depletion of *A. palmata* populations has been associated to massive mortality events due to diseases (e.g. white band), bleaching and hurricanes (Aronson and Precht 2001; Wilkinson and Souter 2008).

Coral species composition in Cuban fore reefs features the dominance of a few species, namely *S. siderea*, *A. agaricites*, *Orbicella* spp., *P. astreoides* and *M. cavernosa*; in deep sites (~20 m), *A. lamarcki* was also dominant. *S. siderea* was the most abundant species in Cuban reefs in agreement with Martínez-Estalella (1986). The species occurs in a broad range of depths due to its tolerance to physical disturbance and sedimentation (Meesters et al. 1992; Torres and Morelock 2002) and their first-stage recruits are resistant to stress (Bak et al. 1977; Bak and Steward 1980). Recent studies have shown a great recovery of *S. siderea* after bleaching and disease events in some Cuban reefs (Caballero and Perera 2014). *A. agaricites* was second in dominance rank, which can be attributed to its broad tolerance to environmental changes (Green et al. 2008; Alvarez-Filip et al. 2011, 2013). Our data supported the progressive substitution of *O. annularis* complex by the opportunistic species *A. agaricites* (Aronson et al. 2014). *Orbicella* spp. dominated only in the deepest fore reefs (20 m) as the species is considered to be typical of low-exposure reefs (Chollet and Mumby 2012; Williams et al. 2015). The decline of species of the genus *Orbicella* has also been reported in the western Atlantic due to mortality events between 1998 and 2000 (Roff et al. 2015a, 2015b).

In contrast to crest reefs, fore reefs showed larger variability in terms of identity of dominant coral species. As suggested by Jackson et al. (2014) for the wider Caribbean, the large geographic variation found in reef structure and condition across the Cuban Archipelago pointed to unique trajectories of events affecting individual reefs (e.g. overfishing, pollution, hurricanes) rather than some pervasive force throughout the entire region. The decrease of the distribution of historically dominant species (e.g. *A. palmata* and *O. annularis*) and the increase of opportunistic species also pointed to larger influence of ecological drift promoting stochastic distribution.

In our study, local ecological drivers at site scale (10^0 km) broadly had the same importance of regional drivers at locality scale (10^2–10^3 km) for explaining the variation in coral assemblage composition (also for the six condition metrics). Therefore, our hypothesis of greater importance of regional (i.e. locality) versus local (i.e. site) scales must be rejected. Local ecological drivers of coral assemblages probably include reef topography and biological interactions, although anthropogenic stressors (e.g. fishing and eutrophication) may play an important role (Duran et al. 2018). Meanwhile, broad-scale drivers of coral assemblages probably include the oceanographic regime (e.g. wave patterns and hurricanes) and anthropogenic disturbances (e.g. water warming). The combined effect of ecological drivers acting at several spatial scales resulted in large variability of coral reef assemblages around the Cuban Archipelago.

In summary, the condition of Cuban coral reefs showed large spatial variability at local and regional scales. Most of the crest reefs suffered important deterioration although they still maintained their structural complexity. The condition of fore reefs was also alarming with resilience in many sites (mostly in Colorados and Sabana-Camaguey) compromised due to low coral living cover and relief flattening. However, the Cuban reefs in better condition (Cienfuegos, Bahía de Cochinos and Cazones) had values of coral cover and complexity similar to other healthy Caribbean reefs. Compared to the 1980s, the coral species richness was roughly the same, although the dominance has changed from key (e.g. *A. palmata* and *O. annularis*) to opportunistic species (e.g. *S. siderea* and *A. agaricites*). Coral reef assemblages varied at local (10^0 km) and regional (10^2–10^3 km) scales with similar magnitude suggesting the combined effects of natural and anthropogenic drivers acting at several scales.

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