



## Status of Cuban coral reefs

<sup>1</sup> Centro de Investigaciones Marinas, Universidad de La Habana, Calle 16 No. 114, Miramar, Playa, Havana 11300, Cuba.

<sup>2</sup> Departamento de Estudios para el Desarrollo Sustentable de la Zona Costera, Universidad de Guadalajara, Gómez Farías 82, San Patricio-Melaque, Cihuatlán, Jalisco, CP 48980, Mexico.

<sup>3</sup> Canadian Rivers Institute, 100 Tucker Park Rd, Saint John, NB E2L 4A6, Canada.

\* Corresponding author email: <patricia@cim.uh.cu>.

**Patricia González-Díaz** <sup>1</sup> \*  
**Gaspar González-Sansón** <sup>2, 3</sup>  
**Consuelo Aguilar Betancourt** <sup>2, 3</sup>  
**Sergio Álvarez Fernández** <sup>1</sup>  
**Orlando Perera Pérez** <sup>1</sup>  
**Leslie Hernández Fernández** <sup>1</sup>  
**Víctor Manuel Ferrer Rodríguez** <sup>1</sup>  
**Yenisey Cabrales Caballero** <sup>1</sup>  
**Maickel Armenteros** <sup>1</sup>  
**Elena de la Guardia Llanos** <sup>1</sup>

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**ABSTRACT.**—Cuban coral reefs have been called the “crown jewels of the Caribbean Sea,” but there are few comparative data to validate this claim. Here, we provide an overview of Cuban coral reefs based on surveys carried out between 2010 and 2016 on seven of the main Cuban coral reef systems: Havana, Artemisa, Los Colorados, Punta Francés, Los Canarreos Archipelago, Península Ancón, and Jardines de la Reina. Ecological indicators were evaluated for each of these areas at the community level. Results suggest differences among benthic communities (corals, sponges, and gorgonians) that are most evident for reefs that develop near highly urbanized areas, such as Havana, than for those far from the coast and less accessible. Offshore reefs along the south-central coast at Jardines de la Reina and Península Ancón exhibited high coral density and diversity. *Acropora cervicornis* (Lamarck, 1816) and the *Orbicella* complex corals were uncommon, possibly indicating losses prior to our study due to coral diseases or competition with macroalgae. *Siderastrea siderea* (Ellis and Solander, 1786) was the most consistently-abundant species at all reef sites. The ecological condition at Jardines de la Reina and Península Ancón is comparatively healthy. Our study supports claims that some Cuban coral reef systems are probably among the best preserved in the Caribbean basin, but other highly impacted areas exhibit many of the degradation patterns that are common to the rest of the Caribbean region. Strong conservation strategies are required with regard to subsistence fisheries and pollution at highly-impacted reefs to stop further degradation, and reefs that appear healthy need protection to avoid degradation and maintain resilience.

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Marine Ecology and Conservation  
in Cuba

**Guest Editors:**  
**Joe Roman, Patricia González-Díaz**  
**Guest Section Editor:**  
**Joe Roman**

Date Submitted: 6 April, 2017.  
Date Accepted: 12 March, 2018.  
Available Online: 29 March, 2018.

Coral reefs have suffered significant declines caused by anthropogenic stressors and climate change in the last few decades (Mumby et al. 2014, Graham et al. 2015). Anthropogenic stressors, such as overfishing, land-based pollution resulting in decreased water quality, and tourism, have negatively affected the status of Caribbean coral reefs (Jackson et al. 2014, Risk 2014). Macroalgae are abundant, in part due to the mass mortality of the black-spined urchin, *Diadema antillarum* (Philipi, 1845), in 1983 (Hughes 1994). Caribbean reefs have also experienced numerous strong hurricanes (categories 4 and 5) in 2005 and 2008. Synergistic effects of stressors on Caribbean coral reefs caused a phase shift from a reef system dominated by corals to one dominated by macroalgae (Harborne et al. 2017). The different responses to these stressors are probably related to differences in reef resilience (Mumby et al. 2014) and to the effect of interactions among functional groups (Harborne et al. 2017). The characterization of the ecological status of coral reef communities and of the main processes and functions that have been disrupted by human activities is crucial to improve coral reef conservation and management strategies (González-Díaz et al. 2010, Micheli et al. 2014, De Bakker et al. 2016).

Cuba is the largest Caribbean archipelago (approximately 110,000 km<sup>2</sup>) with about 3966 km of coral reef tracts along 98% of the long shelf edge (Wilkinson 2008). All of these coral reefs have strong ecological connectivity with mangrove and seagrass ecosystems (González 2000). Long stretches of the Cuban coast remain undeveloped, with relatively high levels of fish biomass and marine biodiversity (Whittle and Rey Santos 2006, Newman et al. 2006, Pina-Amargós et al. 2012). At the same time, Cuba has transformed its agricultural production; since the 1990s, when support from Russia ended along with the dissolution of the Soviet Union, it turned to low-input production methods, such as organic farming and agriculture.

Reef structure varies greatly around Cuba. Reefs on the north coast are fringing reefs that occur no farther than 200–300 m from the coast. Southern reefs lie well offshore with more than half separated from the main island by keys and broad shallow lagoons with many patch reefs. Their greater distance has provided protection from human pressures, except for commercial fishing and some dive tourism. The main coral reef systems south of Cuba, including Los Canarreos and Jardines de la Reina, have been described as among the least damaged reefs in the Caribbean Sea (Newman et al. 2006, Wilkinson and Souter 2008, Figueredo-Martín et al. 2010, Pina-Amargós et al. 2014; Fig. 1).

Data about Cuban coral reefs are sparse and published mostly in Spanish, thus resulting in a low dissemination to the international scientific community. For example, Jackson et al. (2014) published an overview on main trends in Caribbean coral reefs from 1970 to 2012, but few Cuban reefs were included because the data were not available for analysis. It has been suggested that Cuban coral reefs are the “ecological crown jewel” of the Caribbean Sea (e.g., Whittle and Rey Santos 2006, Figueredo-Martín et al. 2010, Ferrer et al. 2016), a statement that attracts international tourism and supports one of the most valuable sectors of Cuba’s economy. Mangrove forests are largely intact and function as nursery areas for top predators that are abundant as adults in Jardines de la Reina (Newman et al. 2006, Figueredo-Martín et al. 2010, Pina-Amargós et al. 2012, 2014). The present study is aimed at assessing the ecological status of coral reef communities along the Cuban shelf and placing them in the broader context of Caribbean-wide reefs. We hypothesized that observed variation in the composition of main benthic communities among coral reef systems are the

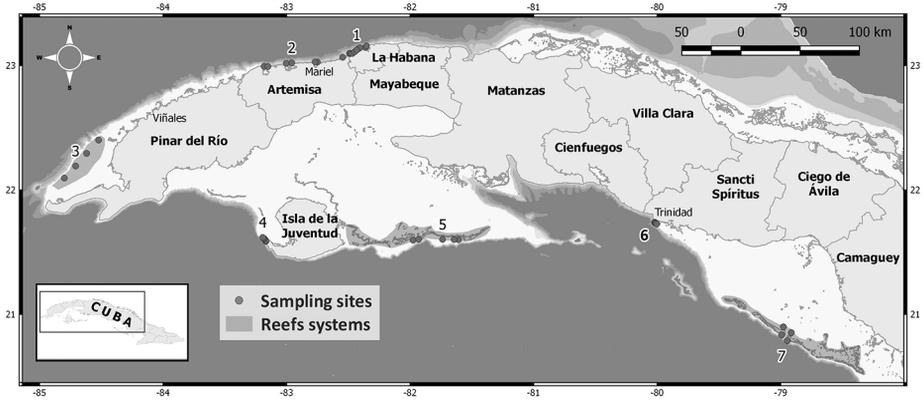


Figure 1. Distribution of coral reefs systems and the provinces of Cuba. White color indicates shallow shelf regions, and gray areas within the shelf are reef systems; darker gray areas are offshore deeper waters. The seven sampling sites are: 1 = Havana, 2 = Artemisa, 3 = Los Colorados, 4 = Punta Francés, 5 = Los Canarreos, 6 = Península Ancón, 7 = Jardines de la Reina.

consequence of differences in natural conditions and anthropogenic stressors prevailing in each region.

## MATERIALS AND METHODS

**CLIMATIC AND OCEANOGRAPHIC CONDITIONS.**—Cuba has a tropical climate, with an average annual precipitation of 1375 mm, and a daily tidal range of around 20 cm. However, conditions vary markedly along the 5700-km coast. The main two seasons that produce climatic differences are (1) the dry season from November to April, and (2) the rainy season from May to October (Cuban Office of Statistics 2016). Changes in patterns of rainfall over the past 5 yrs have caused considerable drought that has severely affected mangroves and dried up many estuaries.

Cuba also has been in the path of many major hurricanes; hurricane season runs from June 1 to November 30 each year. However, in the last 6 yrs (2010–2016), no significant hurricane has passed through the western Cuban provinces, and only one large hurricane (Sandy) has affected the eastern Cuban provinces (Hurricane Irma made landfall in northern Cuba in 2017). Hurricanes can provoke deep-water mixing, cloudy and rainy days, and strong waves. All of these factors can result in lower sea-surface temperatures (Heron et al. 2008); and the reduced hurricane activity has resulted in increased temperatures in coastal waters off Cuba.

The Caribbean Current and the Loop Current are the main oceanic currents affecting Cuba (Arriaza et al. 2012). Offshore, oceanic currents flow to the east in the northwest part of the country, and to the west in the south and northeast. Along the shelf of northwestern Cuba, countercurrents move from east to west. Local currents also play a role, for example, with self-recruitment. In some cases, these local currents evoke upwelling and increase nutrient concentrations in Cuba's typically oligotrophic waters (González 2000).

**STUDY AREA.**—Surveys were conducted between 2010 and 2016 in seven coral reef systems: (1) Havana, (2) Artemisa, (3) Los Colorados, (4) Punta Francés, (5) Los Canarreos, (6) Península Ancón, and (7) Jardines de la Reina (Table 1, Fig. 1). The main difference among these are related to: (1) kind of reefs (fringing in the north,

Table 1. Main characteristics of the coral reef systems studied, including region and code (see Fig. 1), estimated length of the reefs (where available), the distance from the shore to each reef, how the reef can be accessed, whether the region is a marine protected area (MPA), whether the region is a recreational dive site, and descriptions of the nearby coastal ecosystems and sources of anthropogenic stressors.

Code	Region	Reef system	Reef length	Distance from the shore	Access to reef	MPA	Dive site	Nearby coastal ecosystems	Main sources of anthropogenic stressors
1	Northwest coast	Havana	200 km	200–300 m	Directly swimming from the coast	No	No	Rocky shore, estuaries (bays and mouth of rivers)	Havana Bay, Almendares River, Qubú River, illegal fishing
2	Northwest coast	Artemisa		200–300 m	By private or tourist boat and also directly swimming from the coast	No	No	Mangroves, seagrass, estuaries (bays)	Maríel Bay, Cabañas Bay, Honda Bay
3	Northwest coast	Los Colorados	43 km	20–40 km	By private or tourist boat	No	No	Mangroves, seagrass, estuaries (coastal lagoons)	
4	Southwest	Punta Francés	5.7 km	1 km	By private or tourist boat	National Park, 3,036 ha	Yes	Mangroves, seagrass, sand beaches	Tourist facilities
5	Los Cánarros	Cayo Largo, Cayo Estopa, Cayo Rosario, Cayo Cantiles	38.2 km	67 km	By private or tourist boat	Faunal Refuge, 89,130 ha	Yes	Mangroves, seagrass, sand beaches	Tourist facilities
6	Península Ancón	Ancón	3.5 km	0.1–1 km	By private or tourist boat and also directly swimming from the coast	No	Yes	Mangroves, seagrass, estuaries (coastal lagoons), sand beaches	Tourist facilities, illegal fishing
7	Southcentral	Jardines de la Reina		91 km	By private or tourist boat	National Park, 200,957 ha	Yes	Mangroves, seagrass, sand beaches	Tourist facilities

offshore in the south); (2) distance from shore (typically close in the north, except at Los Colorados reef, vs 10–80 km from shore in the south); (3) presence of many cays or broad shallow lagoons in the south, with many patch reefs; (4) great reef development in the south; and (5) greater abundance of mangroves and seagrasses in the south.

The northwest coast has been divided into three reef regions to reflect strong differences in the area—the city of Havana, northwestern central (Artemisa), and northwestern Los Colorados Archipelago—based on natural geomorphological characteristics of the coastal zone, and following other studies of benthic and fish assemblages carried out in the same region (Aguilar et al. 2004, González-Sansón et al. 2009a, González 2010). The northwestern region includes the capital of the country (Havana, with almost 2 million people), and four bays with different geomorphological characteristics, sources of impacts, and human population densities. Havana Bay, Almendares River, and Quibu River (region 1 in Fig. 1) are the three main land-based pollution sources among all studied reefs systems. In addition, in this narrow shelf of Havana, subsistence fishing is stronger than in other regions because: (1) higher accessibility to the reefs (no boats are necessary); (2) the reef is in front of the coast without other ecosystems, such as seagrasses or mangroves; and (3) this is the highest urban population center of the country.

We sampled 37 sites interspersed among the seven coral reef systems. We selected terrace edge for comparison among sites because this biotope is present in all sites and reef systems. The terrace edge consists of a rocky bottom dominated by corals and gorgonians, with high structural heterogeneity and depth ranging from 9 to 15 m. An inventory of human settlements and associated anthropogenic activities in the proximity to each reef system indicated that land-based pollution and subsistence fishing could be important stressors.

**SAMPLING PROCEDURE.**—First, we conducted a pilot study in each reef system. To determine the number of sampling units (each sampling unit defined by a 1-m<sup>2</sup> frame) needed to determine reliable estimates of abundance and density of targeted groups (corals, gorgonians, and sponges) and coral species, we examined the curves of the cumulative number of species vs cumulative number of sampling units for each reef. The number of sampling units defining an asymptotic curve was considered as the appropriate sample size. We established the highest sample size found in pilot studies (30) as the common sample size in the study for all seven regions. These 30 sampling units, or SUs, were haphazardly placed parallel to the coastline on the terrace-edge substrate (Weinberg 1981, Dodge et al. 1982). To collect samples from the entire biotope in each site, we established 10 SUs on the high part of the terrace edge (9–10 m), 10 SUs in the middle (12–13 m), and 10 SUs on the bottom (14–15 m). A square sampling frame was made of PVC tubes approximately 2.5 cm wide. All coral colonies that were present in the square frame were recorded regardless of size. A coral was considered an individual colony when the tissue was distinctly separated in space from the tissue of any neighboring corals. Colonies were identified to species level, following the criteria of Zlatarski and Martínez-Estalella (1980) and González (2004) for in situ coral identification and used the term corals *sensu lato* scleractinian, soft corals, and hydrozoans (e.g., *Millepora*). In cases of uncertain in situ identification of a species, a photo was taken for later identification in the laboratory. The total number of gorgonian colonies and sponges was also recorded at each SU.

**DATA ANALYSES.**—Nonparametric multidimensional scaling (MDS) was performed using the Bray-Curtis index as similarity measure on fourth-root transformed abundances. One-factor permutational multivariate variance analysis (PERMANOVA) was applied on the same similarity matrix used for MDS analyses. Homogeneity of dispersions was tested using PERMDISP procedure. Analyses were performed using PRIMER 6.0 (Clarke and Gorley 2006) with PERMANOVA+ (Anderson et al. 2008).

Generalized linear models (GLM) were applied to abundance data by species groups (corals, sponges, and gorgonians) and for the coral species that had  $>0.2$  colonies  $m^{-2}$  to test differences among regions. Poisson distribution with log link was used for the response variable and a nominal predictive variable, corresponding to reef codes, was included in the model's independent variables. Significance of the model was tested with a deviance analysis, using the likelihood ratio test with an approximated  $\chi^2$  probability distribution. If the model terms emerged significant ( $P < 0.05$ ), a post hoc pairwise Tukey's test was performed. The above analyses were performed in the R statistical environment (R Core Team 2016).

## RESULTS

MDS based on relative abundance of corals, sponges, and gorgonians yielded an ordination of samples according to reef system with Havana sites well separated from most other sites, which generally clustered together (Fig. 2). Permanova results supported MDS ordination with significant differences among the studied reef systems (Pseudo- $F_{(6,30)} = 10.912$ ,  $P = 0.0001$ ).

The density of corals and gorgonians were positively associated, whereas sponges were negatively associated with these two groups (Fig. 3). Coral density differed significantly among reef systems ( $\chi^2_{(1)} = 2284.9$ ,  $P < 0.001$ ). A pairwise post hoc test indicated that the highest mean values were in Jardines de la Reina [21.2 (SE 1.1) colonies  $m^{-2}$ ] and Península Ancón [19.3 (SE 1.8) colonies  $m^{-2}$ ], followed by Punta Francés [15.6 (SE 2.4) colonies  $m^{-2}$ ] and Artemisa [13.8 (SE 1.3) colonies  $m^{-2}$ ]. There were significant differences between Punta Francés and Artemisa (Fig. 3). The other three systems—Los Canarreos, Los Colorados, and Havana—were not grouped with any other reefs and were significantly different from each other (Fig. 3). The lowest density was found in Havana [3.4 (SE 1.1) colonies  $m^{-2}$ ] (Fig. 3).

Significant differences among reefs were also found for sponge density ( $\chi^2_{(1)} = 567.9$ ,  $P < 0.001$ ). After the pairwise comparisons, they were distributed in several groups: highest density at Havana [9.7 (SE 3.2) colonies  $m^{-2}$ ], followed by Artemisa [7.2 (SE 0.7) colonies  $m^{-2}$ ]; an intermediate group formed by Península Ancón reef [5.9 (SE 0.8) colonies  $m^{-2}$ ], Punta Francés [5.4 (SE 0.8) colonies  $m^{-2}$ ], and Los Canarreos [5.0 (SE 0.3) colonies  $m^{-2}$ ]; and a low density group formed by Jardines de la Reina [4.0 (SE 1.2) colonies  $m^{-2}$ ] and Los Colorados [3.2 (SE 1.2) colonies  $m^{-2}$ ] (Fig. 3).

Gorgonian density (Fig. 3) also varied among regions ( $\chi^2_{(1)} = 1768.9$ ,  $P < 0.001$ ). Three groups emerged: Jardines de la Reina with highest densities [12.4 (SE 4.5) colonies  $m^{-2}$ ] and Havana with lowest densities [0.1 (SE 0.1) colonies  $m^{-2}$ ]. An intermediate group included all other regions with density values between 7.9 (SE 0.6) (Punta Francés) and 6.1 (SE 0.9) colonies  $m^{-2}$  (Artemisa) (Fig. 3).

Complementary analyses based on quantitative composition of coral assemblages for different reef systems using MDS (Fig. 4) indicated samples from Havana

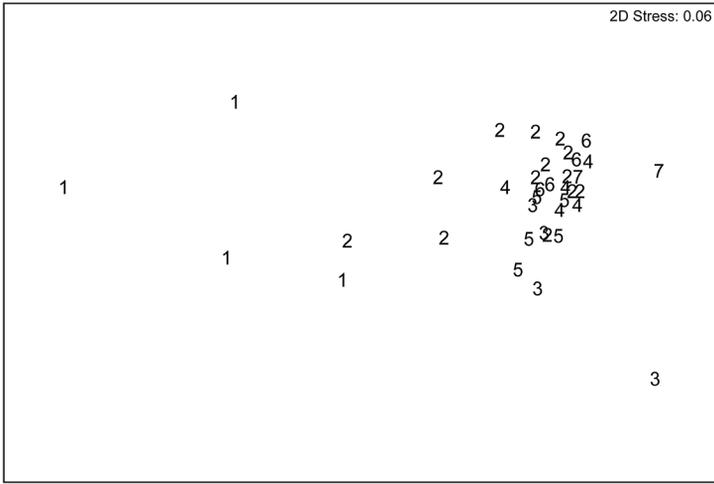


Figure 2. Multidimensional scaling ordination of samples based on coral, gorgonian and sponge abundance. 1 = Havana, 2 = Artemisa, 3 = Los Colorados, 4 = Punta Francés, 5 = Los Canarreos, 6 = Península Ancón, 7 = Jardines de la Reina.

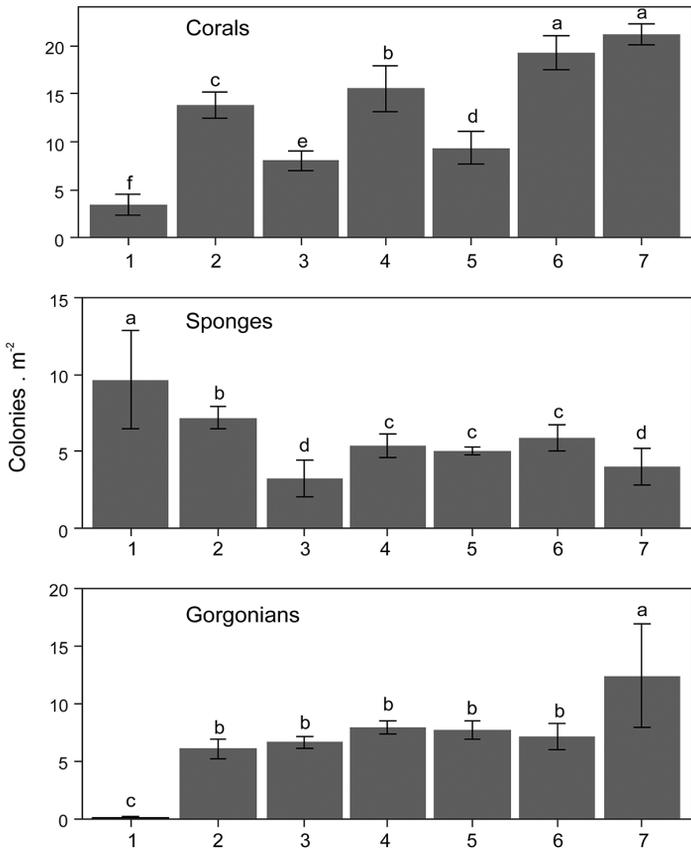


Figure 3. Mean density values (with standard error) by reef system for corals, sponges, and gorgonians. Letters over bars indicate differences in mean pairs. 1 = Havana, 2 = Artemisa, 3 = Los Colorados, 4 = Punta Francés, 5 = Los Canarreos, 6 = Península Ancón, 7 = Jardines de la Reina.



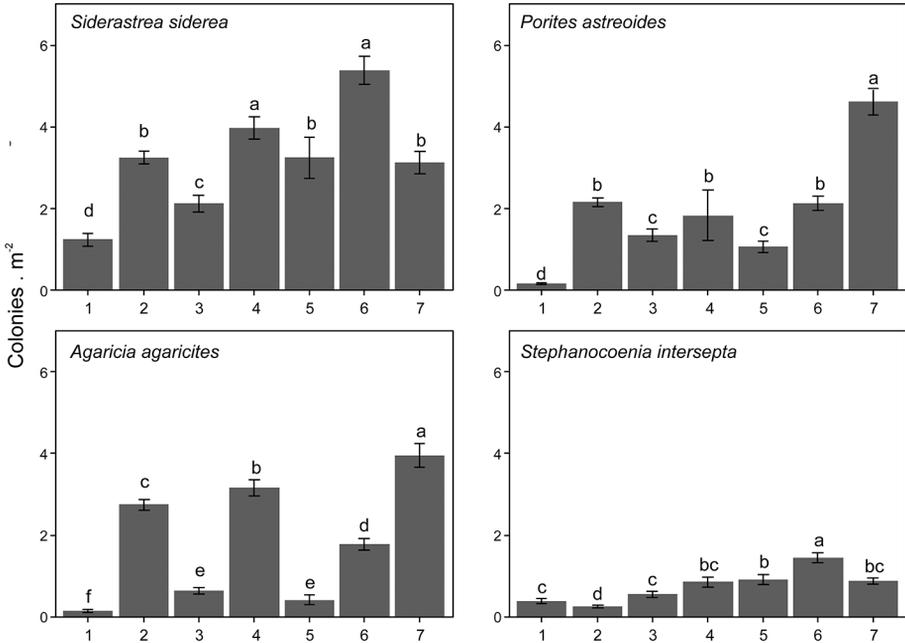


Figure 5. Mean abundances (with standard error) of four most abundant coral species in each reef system. Equal letters indicate non-significant differences after Tukey's test. 1 = Havana, 2 = Artemisa, 3 = Los Colorados, 4 = Punta Francés, 5 = Los Canarreos, 6 = Península Ancón, 7 = Jardines de la Reina.

*Porites astreoides* (Lamarck, 1816) had a similar general pattern (Fig. 5). Results suggested that the seven reefs systems were divided in four groups with highly significant differences among them ( $\chi^2_{(1)} = 474.7$ ,  $P < 0.01$ ). The four groups could be distinguished: (1) Jardines de la Reina with the highest densities [4.59 (SE 0.26) colonies  $m^{-2}$ ]; (2) Península Ancón [2.13 (SE 0.15) colonies  $m^{-2}$ ], Artemisa [1.34 (SE 0.12) colonies  $m^{-2}$ ], and Punta Francés [1.83 (SE 0.17) colonies  $m^{-2}$ ]; (3) Los Colorados [1.34 (SE 0.12) colonies  $m^{-2}$ ] and Los Canarreos [1.06 (SE 0.14) colonies  $m^{-2}$ ], and (4) Havana [0.1 (SE 0.01) colonies  $m^{-2}$ ] (Fig. 5).

*Stephanocoenia intersepta* (Lamarck, 1816) did not follow the same pattern as the above species (Fig. 5). Although differing significantly among reef systems were found ( $\chi^2_{(1)} = 446.9$ ,  $P < 0.01$ ), a pairwise test failed to separate Havana [0.37 (SE 0.06) colonies  $m^{-2}$ ] from the other regions (Fig. 5). Jardines de la Reina [0.85 (SE 0.10) colonies  $m^{-2}$ ] had the highest mean value, with the lowest density in Artemisa [0.24 (SE 0.03) colonies  $m^{-2}$ ] (Fig. 5).

## DISCUSSION

The seven coral reef systems around Cuba exhibited a wide range of ecological conditions. The virtual absence of *A. cervicornis* and uncommon-to-rare occurrence of *Orbicella* species that formerly dominated the entire Caribbean region suggest considerable degradation in several Cuban locations. However, *Orbicella* spp. are moderately common at Península Ancón and Jardines de la Reina, and diversity and abundance are high, making them comparable to some of the healthier reefs

described by Jackson et al. (2014). As expected, reefs near Havana were the most degraded in all aspects.

We found differences in species abundance among Cuban coral reef systems. The observed variation can be explained by the combined effects of: (1) geomorphological characteristics of Cuban shelf (reefs at different distances from the coast, proximity of rivers and bays, presence or absence of adjacent mangroves and seagrasses); (2) anthropogenic impacts; and (3) implementation of the management of marine protected areas (MPAs). The main anthropogenic impacts identified were land-based pollution from coastal settlements, with a direct consequence on water quality, and subsistence overfishing by local inhabitants. The distance of coral reefs from the main island reduces access by fishers, and consequently, limits their impact. An additional natural factor that may affect some reef systems is the natural nutrient delivery from rivers and streams. The implementation of MPAs affects the current status of coral reefs, with evidence of change in fish biomass, apex predators, and coral cover (Newman et al. 2006, Pina-Amargós et al. 2014). Wilkinson and Souter (2008) recognized that >50% of Cuban reefs are separated from the main island by keys or broad shallow lagoons with many patch reefs. This separation has provided protection for the outer reefs from human pressures, except for commercial and private fishing and some tourist diving.

**STATUS OF CUBAN REEFS.**—In general terms, overfishing is the major concern for Cuban coral reefs, as in the rest of the Caribbean Sea. Artisanal coral reef fisheries have traditionally been among the most important sources of protein and livelihood throughout Caribbean coastal communities (Jackson et al. 2014, Mumby et al. 2014). However, as human populations have grown, overfishing has resulted in the widespread collapse of reef fish stocks with direct consequences not only for people's livelihoods and nutrition, but also for the ecological condition of coral reefs (Hughes 1994, Hawkins and Roberts 2004). For Cuba, Baisre (2018) found that 74% of fisheries are overexploited and 5% have collapsed. Overfishing is strongly correlated with the ecological collapse of reef ecosystems as defined by absence of apex predators, decrease in coral cover and recruitment, and increase in macroalgal abundance, cyanobacterial mats, sponges, and coral diseases (Hughes 1994, Sandin et al. 2008, De Bakker et al. 2016, Harborne et al. 2017). González-Sansón et al. (2009b) studied the influence of habitat and fishing on reef fish assemblages in Cuba. The authors concluded that one factor influencing the spatial variation appeared to be overfishing on an east-west gradient, with lower abundances of commercially targeted species near the city of Havana in the east (area under direct influence of Havana Harbor and Almendares River). Many studies (Hughes et al. 2007, Mumby et al. 2014, Perera Valderrama et al. 2018, among others) have shown that the removal of grazers can result in an explosive increase in macroalgal abundance. The most relevant exception to these patterns in Cuba is the reef system at Jardines de la Reina, where enforcement of the protected area is visible, strong, and well organized (Pina-Amargós et al. 2014).

Severely impacted reefs have low coral and gorgonian density. Havana Harbor and Almendares River are well documented as two of the most-impacted coastal zones in the country (Alvarez 2016). Duran et al. (2018) found that coral reefs near Havana are in poor condition and nitrogen content in algal tissue increased with proximity to the city. They suggested both an increase in N availability and increasing contribution of

anthropogenic N sources to reefs. Many ecological assessments have focused on the effect of these pollution sources on different marine communities at diverse organizational levels. Caballero and de la Guardia (2003) found that a reef close to Havana, affected by river discharges rich in organic compounds and close to a tourist center, had a coral density of 2.6 corals  $\text{m}^{-2}$ . In contrast, coral density was high (7–9 corals  $\text{m}^{-2}$ ) in the relatively remote and protected Jardines de la Reina (Pina et al. 2008), as we found in our study. We also found a high density of corals along Ancón Península, in central Cuba, although an increase in tourism and development in the area could threaten the future status of this system. Establishing MPA status for this region should be a high priority.

Density of corals, gorgonians, and sponges and coral species composition differed markedly among reef systems. The lowest densities of corals and gorgonians were found off Havana, which is consistent with the findings in our study that the most impacted areas were located around Havana City, namely Havana Harbor, and Almendares and Quibu rivers (González-Díaz et al. 2003, González 2010). Rey-Villiers (2014) concluded that urban pollution caused by Havana Harbor had a negative effect on morphometric indicators in the two species of gorgonians—*Eunicea flexuosa* (Lamouroux, 1821) and *Plexaura kukenthalii* Moser, 1921. Risk et al. (2014) studied the ratios of stable isotopes of nitrogen ( $^{15}\text{N}$ ) and carbon in the species *Plexaura homomalla* (Esper, 1794) in Guantánamo Bay. Their results indicate a strong negative correlation of reef health with proximity to the river plume. Other studies based on the assessment of fish assemblages using stable isotopes (Aguilar et al. 2008, Cabrera Páez et al. 2012), morphological characteristics related to reproductive status (Aguilar et al. 2007), and influence of habitat and fishing (González-Sanson et al. 2009b) concluded that proximity to Havana Harbor and Almendares River is one of the most important factors. In contrast, among the reef systems studied, coral and gorgonian densities at Jardines de La Reina and Ancón Peninsula had the best ecological status (higher densities and species richness values).

In general, corals and gorgonians had lower abundance in areas where sponge abundance was high, such as the reefs near Havana Harbor and Almendares and Quibu river, as nutrients and sediments have different effects on corals and sponges. Organic pollution in moderate quantities can benefit sponges by providing nutrients for heterotrophic bacteria, which are a food source for sponges (Rützler 2004, Ward-Paige et al. 2005, Costa et al. 2008, McMurray et al. 2017). Coral biomass decreases on reefs stressed by pollution and siltation (Aerts and van Soest 1997, Nugues and Roberts 2003, Harborne et al. 2017). Guardia and González-Sanson (2000b) sampled terrace-edge coral communities in a highly polluted reef adjacent to the Havana Bay entrance, finding levels of coral (3.3 colonies  $\text{m}^{-2}$ ) and gorgonian (0.7 colonies  $\text{m}^{-2}$ ) densities that were lower than in our studied reef systems. Their sponge density (10.4 colonies  $\text{m}^{-2}$ ) values were similar to ours in Havana, possibly reflecting high organic pollution around Havana Harbor. González-Ferrer (2000) investigated terrace-edge biotopes in two healthy reefs near Havana, and found coral and sponge density values similar to our sites in Punta Francés and Cayo Largo (Los Canarreos). Our findings match well with those of one study in the Florida Keys, which found sponge cover negatively correlated with hard coral cover (Maliao et al. 2008). De Bakker et al. (2016) analyzed the change in benthic communities in the last 40 yrs in Curaçao and Bonaire. These authors found a significant increase in sponge cover (0.5% to 2.3%)

coinciding with a decreased cover of calcifying organisms like corals (32.6% in 1973 to 9.2% in 2013) and crustose coralline algae (6.4% to 1%).

**DOMINANT CORAL SPECIES.**—Many studies conducted in different islands of the Wider Caribbean region—Florida Keys (Brandt 2009), St. Croix (Clark et al. 2009), St. Lucia (Nugues and Roberts 2003), Turks and Caicos (Dikou et al. 2009)—exhibited similar coral community composition to that found in ours. *Siderastrea siderea*, a spawning and gonochoristic species, is a relatively widespread and disease tolerant species (Fisher et al. 2008). Banks and Foster (2017) noted that *S. siderea* may be among the coral species that will succeed following elevated temperature anomalies, which are predicted to occur with increasing frequency and severity as a result of climate change. In Cuban coral reef systems, it is also one of the most abundant species, though it is susceptible to bleaching and dark spot disease (Guardia et al. 2004a, Caballero et al. 2007, Hernández et al. 2011, González-Díaz et al. 2010, Busutil et al. 2011). After *S. siderea*, the most abundant coral species found in Cuba are *P. astreoides*, *A. agaricites*, and *S. intersepta*. For reefs with different levels of disturbances in Florida, Lirman and Fong (2007) found the following abundance order: *S. siderea* (33%), *P. astreoides* (32%), *S. radians* (16%), *M. faveolata* (7%), and *M. cavernosa* (5%). Jackson et al. (2014) found that *P. astreoides* and Agaricids were common species in Barbados and Belize, though their cover decreased from the 1970s to 2010. This suite of species, along with *S. radians* and *M. cavernosa*, are considered to be among the most resistant to environmental stress (Guardia and González-Sansón 2000b, Guardia et al. 2001, González-Díaz et al. 2003). All of these species (except *A. agaricites*) have been identified as having a colony structure with the capacity to resist high turbulence and sedimentation (Herrera and Martínez-Estalella 1987, Meesters et al. 1992).

Several of the most abundant corals in reefs near Havana are brooding species, such as *A. agaricites* and *P. astreoides*. Duran et al. (2018) also observed them as being predominant on these reefs. They noted that these species usually have larvae with short planktonic durations and low dispersal distances, which promote larval retention. Brooding species are often associated with unstable or degraded habitats (Duran et al. 2018).

González-Díaz et al. (2010) have discussed the unexpected abundance of *S. intersepta* found in Los Colorados reefs of northwest Cuba. These are the only known reefs in Cuba where this coral species is the most abundant. Steiner (1999) measured relative abundance values for this species between 5.5% and 11.4% in South Caicos, in the southeastern Bahamian archipelago. Schmahl et al. (2004) reported deep coral assemblages at McGrail Bank in the northwestern Gulf of Mexico (39–44 meters deep). In these assemblages, *S. intersepta* was the most abundant species with a percent cover of approximately 30%. In the Florida Keys, Brand (2009) found that colonies of *S. intersepta* were the least susceptible to bleaching. The abundance of this species in our study could be an indication of recent changes in coral community composition. Usually, coral reefs are formed by engineering species (*S. siderea*, *Orbicella* species complex, *M. cavernosa*). They are recognized as such for providing three-dimensional structure to the reefs, when dominant (higher abundances). The presence of *S. intersepta* instead of the above-mentioned species needs to be addressed carefully in future studies. Jackson et al. (2014) and De Bakker et al. (2016) also found a decline in coral cover of engineering species [*Orbicella*

*annularis* (Ellis and Solander, 1786), *M. cavernosa*, and other massive species] for Belize, Bonaire, Curaçao, and Dry Tortugas (Florida, USA). Their data indicated a shift from communities dominated by framework building species (e.g., *Orbicella* species) to communities consisting of small opportunistic, phenotypically plastic species, including few remaining structural colonies as *Madracis myriaster* (Milne-Edwards and Haime, 1850), *P. astreoides*, *P. strigosa*, and *Agaricia lamarcki* Milne-Edwards and Haime, 1851.

Our finding of high *A. agaricites* abundance is consistent with findings by Guardia et al. (2006), Caballero et al. (2007) and Perera-Valderrama et al. (2016). Similar results were also obtained by González-Díaz et al. (2003) and Caballero and de la Guardia (2003) in reefs exposed to low human impact near Havana, which are considered as reference sites on a local scale. Sullivan (2004) and Beltran-Torres et al. (2003) found that *A. agaricites* was vulnerable to sedimentation and occurred in high densities in healthy reefs. Vega Thurber et al. (2013) found that elevated nutrient loading increased coral bleaching for *S. siderea* and *Agaricia* spp., and after nutrient enrichment had been terminated for 10 mo, there were no differences in coral disease or coral bleaching prevalence between the previously-enriched and control treatments. This finding demonstrates that some regulations at the local level can be very effective for the conservation of coral reef ecosystems.

Unexpectedly, *Meandrina meandrites* (Linnaeus, 1758) and *M. decactis* were the most abundant species in highly-impacted reefs. Other studies reported that both species occurred in reefs that are in relatively good condition (Caballero et al. 2007, Pina et al. 2008, Busutil et al. 2011, Perera-Valderrama et al. 2016). It is possible that these species are resistant to land-based anthropogenic impacts, with inherent resilience mechanisms. For future ecological assessments, we recommend careful tracking of the abundance and diversity of both species.

This is the same situation that took place in many Caribbean reefs where engineering species have been substituted by others (Done 1992, Hughes 1994, Pandolfi et al. 2005, Hubbard 2015). The *A. cervicornis* and most *Orbicella* spp. complex are uncommon or rare. However, they were abundant in late Pleistocene reefs all around Cuba (Zlatarski and Martínez-Estalella 1980). Jardines de la Reina and Península Ancón seem to be in pretty good condition. However, more studies are necessary to address the scientific questions regarding with resilience patterns that take place in those reefs.

## CONCLUSIONS

That Cuban coral reefs are considered to be an “ecological crown jewel” of the Caribbean Sea is a clear example of shifting baseline syndrome. In our study, the reefs examined had uncommon or rare species—*A. cervicornis* and the *Orbicella* spp. complex—reflecting ecological degradation similar to reefs through the Caribbean region. However, *S. siderea* remains as a more abundant coral. The abundances of *M. meandrites*, *M. decactis* and *S. intersepta* in our study suggest that more research is necessary to determine whether the coral community compositions found reflect a substitution of engineering species.

Additional negative impacts are evident in some reef systems, probably more related to land-based pollution and subsistence overfishing. The other reefs subjected to less human impact appear to be more resilient. Coral reef systems that exist far

from the coast and urban centers are undoubtedly among the best preserved in the Caribbean basin due to the minimal coastal development and the fact that many reefs are offshore and outside the impact range of land-based pollution sources (Wilkinson and Souter 2008).

We would like to emphasize concerns regarding illegal fishing on Cuban reefs, similar to that of other Caribbean areas (Jackson et al. 2014, Baisre 2018, Puga et al. 2018). Fishing pressure and the state of reef fish populations varied greatly among Caribbean reef locations in the 1970s due to a complex mix of fishing practices, economics, and cultural traditions that are beyond the scope of the present study (Newman et al. 2006, Jackson et al. 2014). Nevertheless, certain patterns are clear. Densely populated areas, with a long history of sugar economies based on slavery, developed labor-intensive artisanal fisheries that resulted in overfishing by the early 21<sup>st</sup> century. In contrast, reefs along less densely populated coasts of Florida, Mexico, the Mesoamerican Barrier Reef, and northern South America were less heavily fished until 1970s–1990s (Jackson 1997).

Our results indicate the need of mitigation strategies for the reduction of land-based impact sources that cause severe degradation in coral reefs. The reefs that are not exposed to land-based pollution are under other increasing threats, such as tourism-related fishing and diving, which demand a more efficient use of MPAs. Better coordination among stakeholders is needed, along with better enforcement of MPAs, including the improvement of regulation and infrastructure, and additional personnel (Perera Valderrama et al. 2018). Equally important are global changes like severe warming events and ocean acidification, which are likely to compromise the ability of corals and other calcareous reef species to form skeletons.

Although some Cuban reefs appear to be in decline, those that are in good ecological condition can help us improve our studies on the effects of human activities, both on land and at sea, on reef processes. The well-preserved reefs, such as Jardines de la Reina and Ancón Peninsula, highlight the necessity to increase the study of these systems. Coral reef ecological processes are complex; there are likely synergistic effects of natural stressors and anthropogenic impacts. Thus, we need to consider the connectivity and dynamic nature of these systems, including mangrove swamps, seagrass beds, and reef seascapes; also taking into account oceanographic conditions and population genetics (Harborne et al. 2017, García-Machado et al. 2018). Important next steps are to examine patterns of population connectivity, including the larval behavior of species and the microbiology of coral diseases and bleaching. Protecting these reefs will require enforcement of current laws, engagement of local communities, and restoring those areas in decline through integration of science, management, and conservation policies.

#### ACKNOWLEDGMENTS

We are very grateful for the field assistance provided by the divers from the Center for Marine Research of the University of Havana: I Rodríguez Mauri, E Alonso, and R Volta (technician). Also, we want to thank A Martínez, geographer from the Center for Marine Research, who helped us in draw the map (Figure 1). We deeply appreciate the initiative and support of J Roman and D Whittle who encouraged us to write this paper. Discussions and opinions of JB Jackson were useful in writing it. Grammar and style were improved thanks to the help of D Greger (University of Florida) and MM Rivero Fernández (Instituto de Ciencias del Mar). We also want to express our sincere gratitude to both reviewer who helped to improve the quality of this article.

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