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Distribution, abundance, and health indicators of the critically endangered coral species *Acropora cervicornis* in Los Roques National Park, 2014

Stephanie J. Martinez[1,2], Francoise Cavada-Blanco[1,3,4], José Cappelletto[5,6], Esteban Agudo-Adriani[1,7], Aldo Cróquer[1,8]

[1]Experimental Ecology Laboratory, Department of Environmental Studies, University Simón Bolívar, Caracas, Venezuela; [2]Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands; [3]Institute of Marine Science, School of Biological Sciences, University of Portsmouth, UK; [4]EDGE of Existence Programme, Conservation and Policy, Zoological Society of London, UK; [5]I+D Group in Mechatronics, University Simón Bolívar, Caracas, Venezuela; [6]Maritime Robotics Laboratory, Southampton Marine and Maritime Institute, University of Southampton, UK; [7]Department of Biology, The University of North Carolina, Chapel Hill, USA; [8]Marine Innovation Center, The Nature Conservancy, Punta Cana, República Dominicana.

ABSTRACT

Acropora cervicornis is one of the most important coral species in shallow reefs of the Caribbean as it provides habitat and structural complexity to several species of invertebrates and fish. However, the distribution range of *A. cervicornis* has shrunk and collapsed considerably in the last five decades, due to a combination of factors including the increase of disease prevalence, storm frequency, and anthropogenic threats. Despite being classed as "Critically Endangered" in the IUCN Red List, information regarding its population status and condition across large Caribbean coralline areas is limited. Herein we conducted the first Marine Protected Area (MPA) scale survey for this species at the Los Roques archipelago, which included visual census across 127 sites to determine the abundance, spatial distribution, habitat type, and patch morphology of *A. cervicornis*. We selected 11 sites, where this species was predicted and reported to be ubiquitous, to determine live *A. cervicornis* cover, its recent and old mortality cover, and white band disease prevalence as proxies for coral health. We found *Acropora cervicornis* in only 29% of the surveyed sites, with dispersed and scattered patches prevailing upon continuous patches. Moreover, the latter were located near the largest human population settlements, and inside the low protection zones of the MPA where fishing and touristic activities are permitted. The photomosaic survey showed that more than 75% *A. cervicornis* patches showed an average live cover above 27%, low prevalence of white band disease (<7%), and low macroalgal abundance (<10%); suggesting that Los Roques still holds healthy populations. Our results indicate that the persistence of this species urgently requires re-evaluating current MPA zoning, especially following recent evidence of overfishing and inadequate law enforcement. This study provides a baseline of *A. cervicornis* populations in Los Roques and Southern Caribbean that can be later used for local population management and conservation.

INTRODUCTION

Coral reefs cover only a small portion of the tropical ocean's surface (0.1-0.5%), yet they provide habitat for thousands of marine species, making these ecosystems one of the most diverse on Earth (Moberg and Folke 1999; Roberts *et al*. 2002; Mora *et al*. 2011; Fisher *et al*. 2015). Scleractinian corals, especially members of the Acroporidae family, are foundational species in modern tropical reefs since they are the major providers of structural complexity (Bellwood *et al*. 2004; Idjadi and Edmunds 2006; Wallace 2012; Raza *et al*. 2015). Their ability to adopt different growth morphologies through environmental gradients adds spatial heterogeneity to the reef substrate, allowing many species to coexist (Pratchett *et al*. 2015). Before the onset of their population's collapse during the late '70s in the Caribbean, *Acropora palmata* (elkhorn coral) and *Acropora cervicornis* (staghorn coral) formed dense, monospecific and structurally complex patches that contributed significantly to calcium carbonate accretion along the fore reef of many Caribbean coral reefs (Aronson and Precht 2001; Precht and Aronson 2004; Wapnick *et al*. 2004). These species also played a vital role in the maintenance of healthy and productive reefs by providing critical habitat and reef complexity for a large diversity of fish and other organisms (Rogers *et al*. 1982; Gates and Ainsworth 2011). Moreover, compiling evidence shows that Caribbean acroporids played these roles for thousands of years until their populations were reduced during the last five decades (Aronson and Precht 2001; Jackson 2001; Pandolfi and Jackson 2006; Pandolfi and Jackson 2007).

Different studies have shown that the distribution range of this species has shrunk considerably, with some cases reporting more than 90% of area loss *(*Aronson and Precht *2001;* Jackson *et al*. 2014; García Urueña *et al*. 2020), and a lack of recovery since its regional decline (Vargas-Angel *et al*. 2003; Keck *et al*. 2005; Busch *et al*. 2016). The underlying causes of the regional collapse of *A. palmata* and *A. cervicornis* populations have been firmly established, and includes a combination of diseases, particularly white band disease (WBD; Aronson and Precht 2001; Acropora Biological Review Team 2005; Miller *et al*. 2014), increased storm frequency (Woodley *et al*. 1981; Lirman and Fong 1997), and the increase of anthropogenic threats such as sediment load and overfishing (Bruckner 2002; Precht *et al*. 2002; Greer *et al*. 2009).

Reduction in the populations of these two species led to significant and unprecedented changes in the structure and function of Caribbean coral reef ecosystems (Pandolfi and Jackson 2006; Pandolfi and Jackson 2007). Increasing erosion and bioerosion rates (Edinger *et al*. 2000), species replacement (Aronson *et al*. 1998), and loss of spatial heterogeneity and biodiversity are amongst the most dramatic effects reported in the literature (Bruckner 2002; Acropora Biological Review Team 2005; Alvarez-Filip *et al*. 2011). Because of the sudden decline of *Acropora palmata* and *A. cervicornis*, combined with their current critical status, both species were listed as threatened under the United States Endangered Species Act, and classed as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Aronson *et al*. 2008).

Acropora palmata and *Acropora cervicornis* are broadcasting species, and both are known to be highly vulnerable to natural and anthropogenic disturbances (Vargas-Ángel *et al*. 2006; Schopmeyer *et al*. 2011; Miller *et al*. 2014; Mercado-Molina *et al*. 2015). However, *A. cervicornis* is capable of fast growth through asexual reproduction via fragmented branches, and thus it has the potential of quick recovery by forming monotypic patches/thickets within just a few years (Bruckner 2002; Acropora Biological Review Team 2005; Lucas and Weil 2016). Similar to *Acropora palmata,* There are examples in a few locations where *A. cervicornis* has indeed managed to persist after its regional collapse (Vargas-Angel *et al*. 2003; Acropora Biological Review Team 2005; Walker *et al*. 2012). However, the increased frequency and intensity of natural and human disturbances have decreased the survival rates and reduced the probability of broken fragments attaching to suitable and stable substrates, jeopardizing a good prognosis of recovery (Lirman and Fong 1997; Goergen *et al*. 2019). Thus, developing standard restoration methods to help this species come back has become a priority for conservation and local legislations in the region (Schopmeyer *et al*. 2017).

To success in an effective population restoration, the paucity of geographically extended demographic and ecological data of *Acropora cervicornis* needs to be addressed since it limits the planning for proper and coordinated conservation actions (Bruckner 2002; Precht *et al*. 2002; Mercado-Molina *et al*. 2015). Therefore, the identification of locations where *A. cervicornis* populations of this species still exist as shallow reef-builders, the characterization of these habitats, and the proper evaluation of potential local threats are all critical to improve the impact of local and regional conservation efforts (Bruckner *et al*. 2002; Aronson *et al*. 2008).

Within the Southern Caribbean, Archipelago Los Roques National Park ("Los Roques") has been highlighted as one of the healthiest reef ecosystems due to its coral cover remaining above the regional average (Villamizar *et al.* 2003; Jackson *et al*. 2014; Debrot *et al*. 2019; Miyazawa *et al*. 2020). Furthermore, different studies have identified this location as a potential stronghold for *Acropora palmata* (Zubillaga *et al*. 2008; Croquer *et al*. 2016). However, the available reports on *Acropora cervicornis* for the MPA are scarce and outdated, mostly collected during the mid-'80s (Sandía and Medina 1987) and originated from studies focused on characterizing benthic communities across the archipelago rather than specifically assessing this species (Villamizar *et al*. 2003; Weil 2003). This study aimed to conduct the first systematic assessment on the status of *A. cervicornis* at Los Roques, and to produce a baseline on the species' local distribution, abundance, and health. Even though the data presented here does not represent the current status of the species, it enhances local and regional knowledge while filling gaps about the spatial distribution of this critically endangered coral species.

METHODS

Study area

Archipelago Los Roques National Park is an oceanic coral reef system located 170 km north of the Venezuelan coast (REGVEN/UTM 19N 721011-7671071324721-1297746; Figure 1). The reef system includes more than 50 coralline cays with fringing reefs, patch reefs, over 200 sandbanks, and extensive mangrove forests and seagrass beds (Weil 2003; Croquer *et al.* 2016). The MPA zoning encompasses nine different use zones, including four coastal-marine habitats, making Los Roques a multi-use MPA (Croquer *et al*. 2016). The MPA zones range from high protection (*i.e.*, authorized scientific research or managed non-extractive activities) to low protection (*i.e.*, artisanal fishing and recreational activities (Croquer *et al*. 2016; Cavada-Blanco *et al*. 2021). According to this zoning, human activities are mostly concentrated within the northeast main island, (Gran Roque) and nearby cays (Figure 1).

Abundance, distribution, and habitat

To determine the distribution and abundance of *Acropora cervicornis* in the MPA, visual censuses were conducted between April and November 2014, encompassing 127 sites across the archipelago. These sites were selected to cover the vast majority of potential and confirmed *A. cervicornis* habitats within the MPA. Several criteria were used during the selection, including (1) personal expertise and knowledge of the MPA, (2) anecdotal information gathered from local stakeholders (*e.g.*, diving operators, fishers, and homestay owners), and (3) observation of potential habitats from raster satellite images. With these criteria, the surveys included a suite of different habitats including windward (exposed) and leeward (protected) cays, fringing and barrier reefs, reef patches, mixed seagrasses, and sand habitats within the lagoon (Figure 1). From this data, we produced a distribution map for *A. cervicornis* at the scale of the entire MPA.

At each site, five observers conducted the visual surveys through free-diving following the reef contour along shallow to intermediate habitats (1–15 m depth). Twentymeter-wide belt-transects were surveyed ranging from 500 to 800 m in length following the procedures outlined in (Croquer *et al*. 2016). At each belt-transect, the start and endpoints were geo-referenced with a Garmin 60S GPS (location accuracy within 3-15m) and the presence/absence of *Acropora cervicornis* along each transect with basic descriptive variables of their habitat (*e.g.*, depth, level of wave exposure) was recorded.

Colony density and ramification within patches made colony differentiation too inaccurate to estimate abundance through the direct count of discrete colonies. Consequently, we used a qualitative approach to estimate abundance and health status following the IUCN Red List of threatened species guidelines for modular organisms (IUCN Standards and Petitions Committee 2019). We classified *A. cervicornis* patches into four different morphologies (Figure 2a-d): (1) continuous patches or thickets (*i.e.*, fields extending over 100 m), (2) dispersed patches (*i.e.*, fragmented patches separated to each other by less than 2 m and extending for 10 m), (3) scattered patches (*i.e.*, mixed patches composed of isolated and mingled colonies), and (4) isolated colonies (*i.e.*, patches composed of individual colonies smaller than 2m wide, and at least 5 m apart from each other). Each morphology type was then categorized according to their frequency of occurrence as abundant (76-100%), common (51-75%), uncommon (26-50%), and rare (0-25%). Patches distribution and abundance were later mapped using QGIS v3.16.4 (QGIS Development Team 2021).

Cover and health status

Using the distribution map of *Acropora cervicornis* obtained from the previous section, a total of 11 sites were randomly selected to describe the benthic community associated with these patches. In order to have a representation of the benthic cover of these patches across the entire archipelago, at least three sites were included in major geographic sectors of the MPA: (1) North-East (Madrizquí, Bajo de Medio 1 and Bajo del Medio 2), (2) Central-East (Noronquí, La Venada, and Rabusquí), and (3) Central-Southwest (Laguna de Espenquí, Isla Felipa, Isla Larga, Herradura Dos Mosquises, and Los Canquises). On each site, four 25 m-long transects were deployed systematically at depths that ranged be-

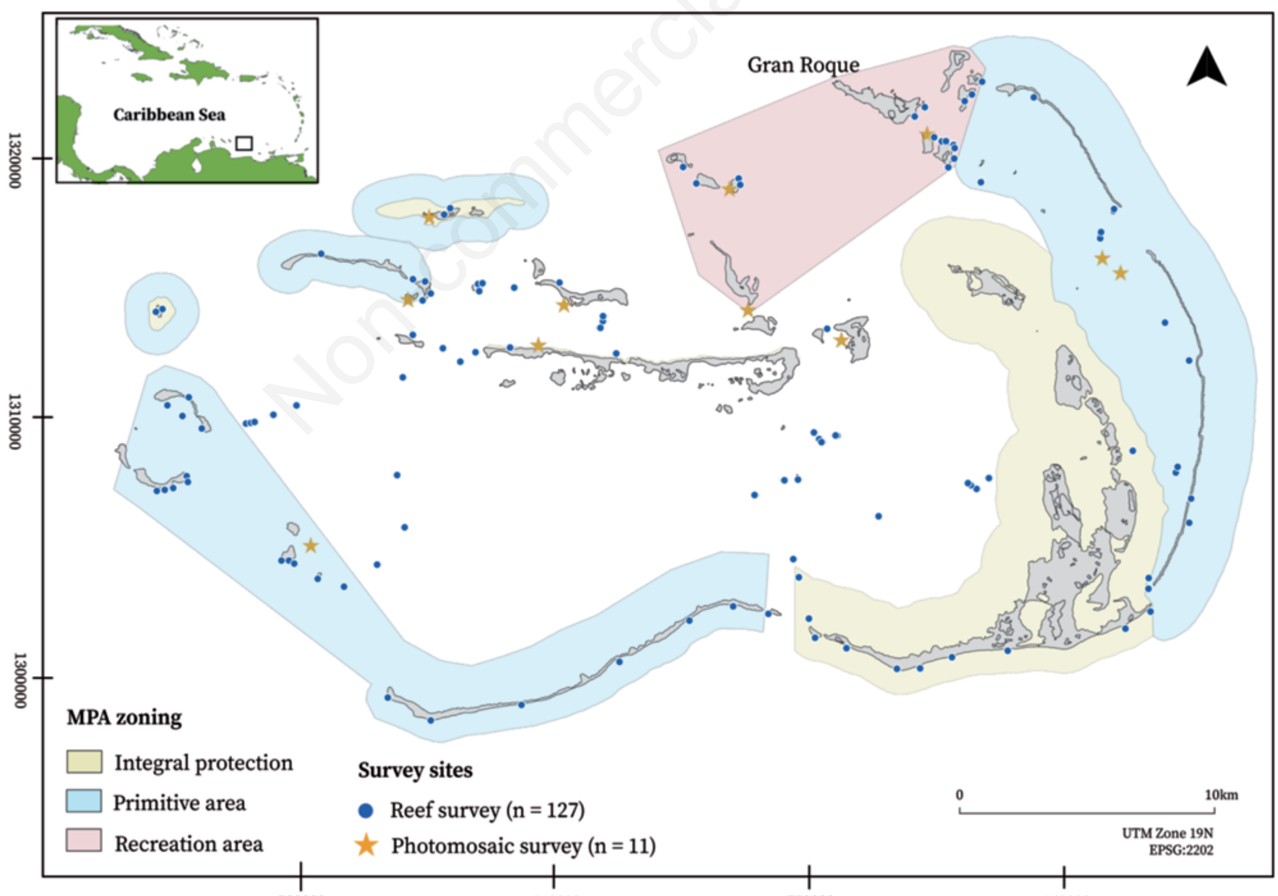

Figure 1. Archipelago Los Roques National Park (Los Roques) map showing survey locations and coastal-marine use zones.

tween 2-10 meters. Along each transect, high-resolution photos were taken ensuring an overlap of at least 30% to produce 25 m^2 photomosaics (Figure 2e). The photomosaics were built using Hugin (D'Angelo 2010), following the same methodology as in Agudo-Adriani *et al*. (2019) in a process that entailed three main steps. First, the identification of matching control points between images to estimate the relative position of an image in a sequence. Secondly, photo alignment and optimization of movement (tilt and balance), and position axes (*x, y, z*). Lastly, the stitching and blending of images using a rectilinear projection together with brightness and colour exposure corrections to produce a unique 25m-long photomosaic.

On each photomosaic, live cover of *Acropora cervicornis,* other biotic (*e.g*., sponges, octocorals, macroalgae, other coral species; see S.M.1), and abiotic substrates (*e.g.*, dead coral, sand, and coral rubble) were determined from 100 randomly overlayed points per mosaic using the software CPCe (Kohler and Gill 2006). We used 100 points based on species richness accumulation curves estimated from 20 random transects (see S.M.2). Disease frequency was determined by counting the number of branches bearing signs of white band disease (WBD) (Weil and Hooten 2008) in relation to the total number of branches overlapping with the 100 points. The frequency of old (*i.e.*, exposed skeleton covered by opportunistic organisms such as algae) and recent mortality (*i.e*., bared coral skeletons) was also determined (see S.M.3). The criteria for determining the previous vari-

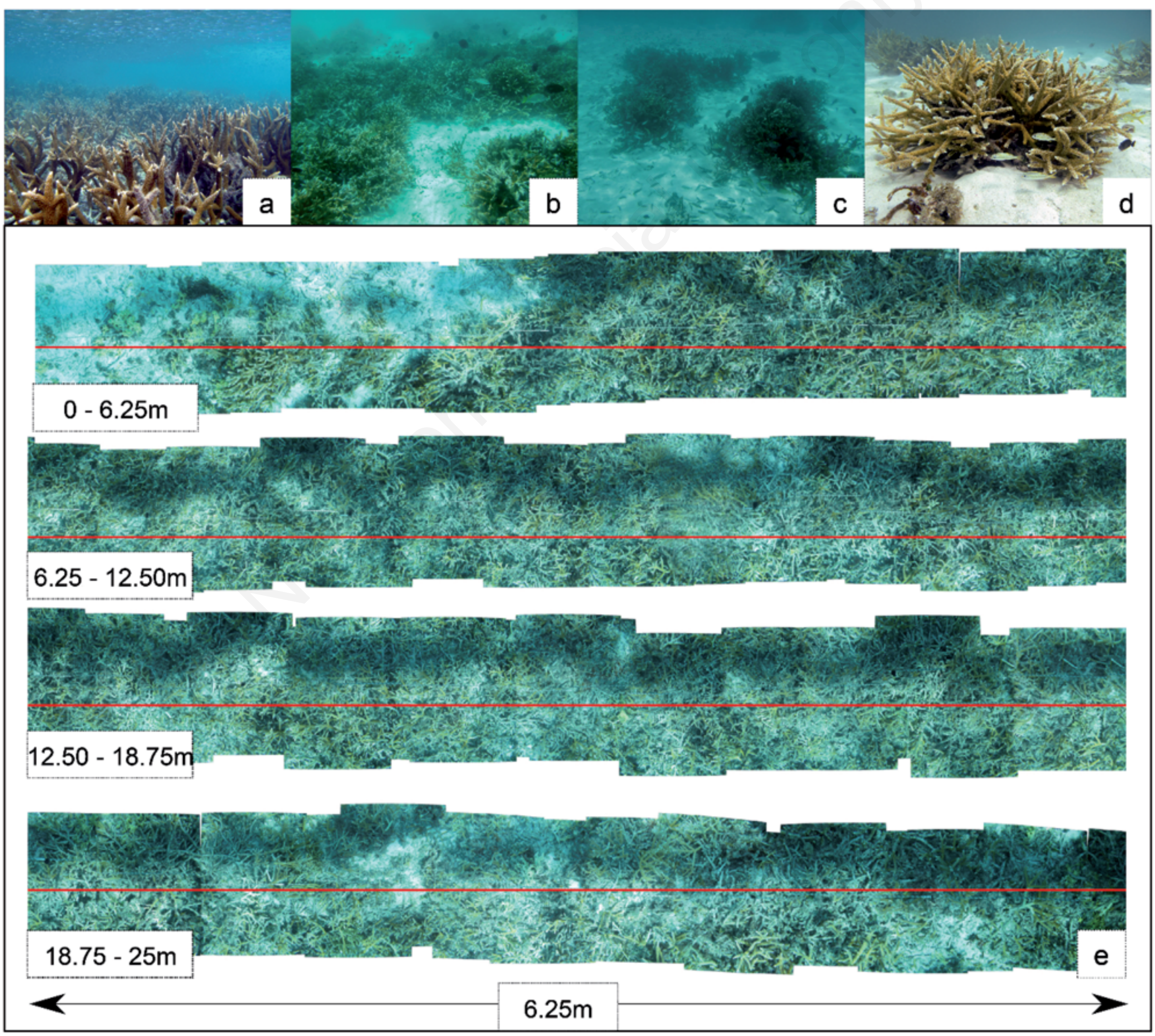

Figure 2. Photographs showing the four types of *Acropora cervicornis* patches morphology: (a) Continuous patch, (b) dispersed patches, (c) scattered patches, (d) isolated colonies. (d) Example of a reconstructed 25m long photomosaic, where the red line follows the transect line.

ables were based in the AGRRA protocol (Lang *et al*. 2010) and field standardization.

Statistical analysis

We aimed at identifying the variables that better explained differences in live cover of *Acropora cervicornis* across sites. For this, a distance-based linear model (DistLM; Legendre and Anderson 1999) was performed using *A. cervicornis* live cover as the response variable, using the following as predictor variables: distance to the biggest permanent human settlement and least protected zone in the MPA (Gran Roque Island), latitude and longitude coordinates to control for spatial correlations, patch morphology, habitat wave exposure (leeward, windward), and depth.

To test whether changes in the community structure associated with *Acropora cervicornis* patches and prevalence of WBD varied across locations and sites, two-way Analysis of Variance based on Permutations (PERMANOVA) were done using the *vegan* package (Anderson 2005; Oksanen *et al*. 2019). For these, similarity matrices were built using Bray-Curtis dissimilarities and Euclidean distances respectively, with geographic sector as a fixed factor (with three levels: North-East, Central-East, and Central-Southwest), and sites as a random factor nested within sectors. A SIMPER analysis was later performed to determine the variables that contributed to the most dissimilarity between geographical sectors and sites. Plots were made using the package *ggplot2* (Wickham 2009), implemented in R (R Core Team 2020; RStudio Team 2020). Source code material, and data matrices available at https://github.com/Stephanocoenia/cervicornisLR.

RESULTS

Abundance, distribution, and habitat

Out of the 127 sites surveyed, we found *Acropora cervicornis* in 37 (29%) sites; indicating that this species has a narrow and very restricted distribution in Los Roques (Figure 3a). The distribution of the four morphologies varied across the archipelago, with dispersed patches being the most frequent type (76% of sites were *A. cervicornis* was found). Isolated colonies and scattered patches were recorded in 70% and 43% of the sites, respectively. In terms of abundance, dispersed and scattered patches were common in most of the sites where these morphology types occurred (32% and 22% of occurrence sites, respectively; Figure 3a). Continuous and large patches were only observed in two sites (La Venada and Madrizquí; 5% of all surveyed sites); both within the least protection levels of the MPA zoning (recreation area; Figure 1).

As for habitat features, we found the majority of *A. cervicornis* patches were twice as frequent in leeward reefs regardless of patch morphology (Figure 3b), and more than 40% of the patches were frequent in shallow depths (0-5 meters; Figure 3c). The only two continuous patches were found in deeper reef zones (Figure 3c). Combined, these results indicate that larger patches of *A. cervicornis* are currently limited to a few sites in Los Roques; either because this species always had limited spatial distribution within the archipelago, or because its populations have declined in the past.

The DistLM analysis (Table 1) showed that only two (*i.e.*, patch morphology and depth) out of the seven variables included in the model, significantly explained live cover variations of *Acropora cervicornis* across sites. However, these two variables combined explained 49% of the variability in live coral cover recorded across sites.

Community structure within *Acropora cervicornis* patches

The average live cover of *Acropora cervicornis* across the surveyed (via photomosaics) sites was 26.9±14.2 % (Figure 4), with values above this recorded at La Venada (54.5±25.9%), Madrizquí (37.7±25.5%), Noronquí (35.7±10.5%), Isla Felipa (34.7±10.1%), Isla Larga (34.7±5.9%) and Bajo del Medio 1 (32.5±9.1%). Seven scleractinian species were also part of the coral community, but their live cover never exceeded 3% (*i.e*., *Orbicella annularis, Orbicella faveolata, Siderastrea siderea, Eusmilia fastigiata, Diploria strigosa*; Figure 5). Other

Table 1. Distance-based multivariate analysis for a linear model (DistLM) using *Acropora cervicornis* cover as the response variable. Predictor variables were site coordinates (latitude and longitude), distance of each location to Gran Roque, thicket morphology, habitat wave exposure, depth, and nearest neighbour relation. * Indicates p-values <0.05

Variable	Sum Squares	Pseudo-F	p-value	Prop
Longitude	490.730	1.3935	0.244	0.0321
Latitude	360.430	1.0146	0.325	0.0235
Distance to GR	359.970	1.0133	0.340	0.0235
Thicket morphology	5166.000	21.5400	0.001*	0.3380
Habitat	79.401	0.2194	0.622	0.0519
Depth	2288.900	7.3994	0.008*	0.1497
Nearest neighbour	600.210	1.7171	1.171	0.0393

organisms such as octocorals (*e.g.*, *Briareum asbestinum*, *Plexaura homomalla,* and *Pseudoplexaura porosa*), hydrocorals (*i.e.*, *Millepora complanata*), and sponges were ubiquitously found in these patches and occupying less than 2% of the substrate (Figure 4). The algae community was dominated by macroalgae, but never exceeded 10% of cover (Figure 4). Highest cover for abiotic substrates corresponded to sand (6.4±2.7-

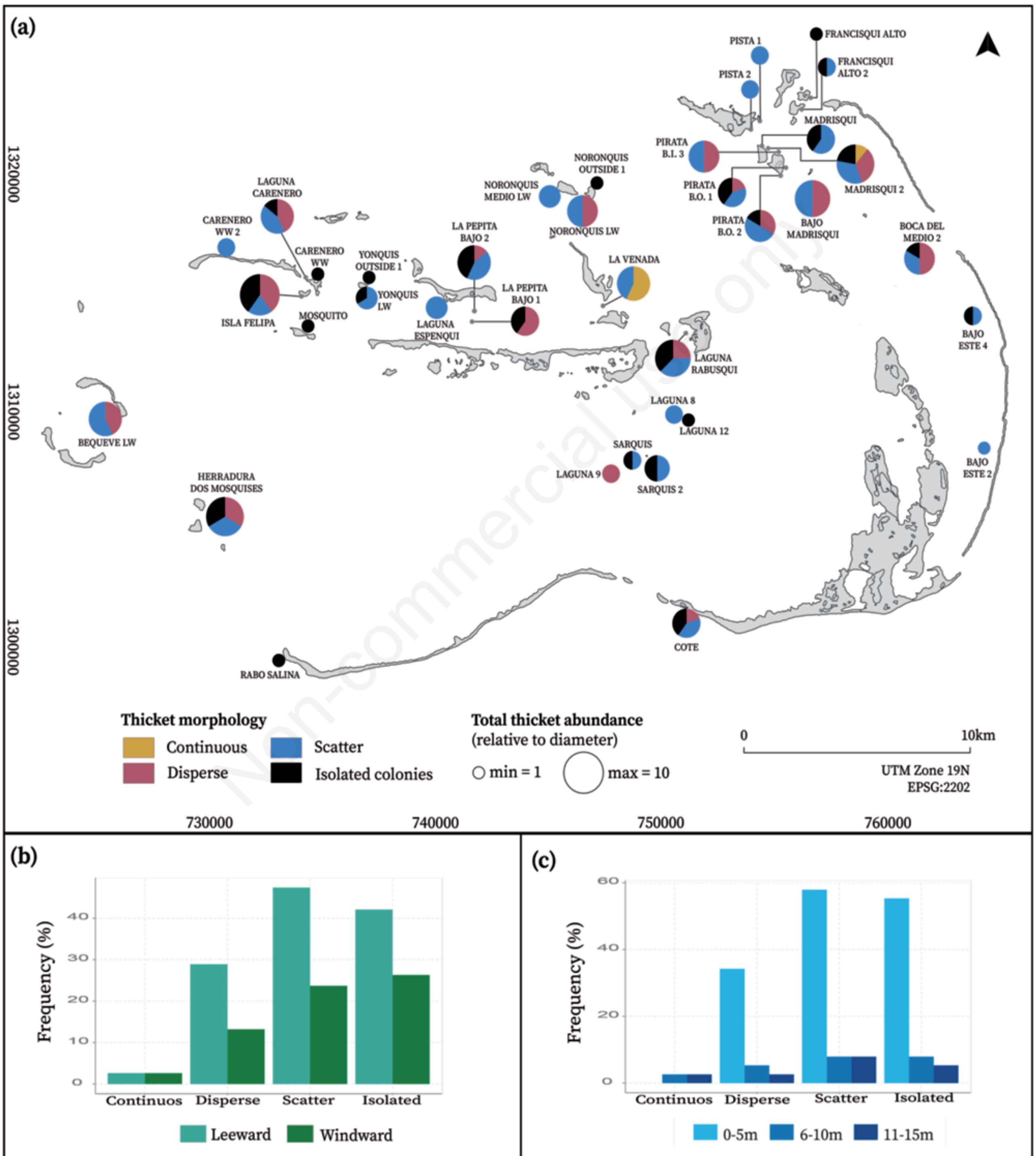

Figure 3. *Acropora cervicornis* patches abundance and distribution map in Los Roques (a), frequency of patches according to habitat exposure (b), and depth profiles (c).

52.3±16.1 %, Figure 4) and coral rubble (8.1±3.7-32.7±8.6%, Figure 4). The benthic community of *Acropora cervicornis* patches significantly varied at the scale of sites within sectors of the MPA, encompassing 52% of the total variation (Table 2). To a lesser extent, the geographical sector explained only 13% of this benthic variation (Table 2). Where 70% of this variability was due to differences in the cover of live *A. cervicornis*, macroalgae, *Pseudoplexaura porosa* tissue, as well as old coral mortality, sand, and rubble.

Health status

Dead branches were consistently found at every surveyed patch; however, old mortality was on average 10-

Table 2. PERMANOVA based using a Bray-Curtis dissimilarity matrix of benthic substrates across two factors: geographical sectors and sites. * Indicates p-values <0.05

Variation source	df	Sum of Squares	Mean Squares	F-Model	p-value	R2
Sector	2	0.51	0.26	5.96	0.001*	0.13
Sector: site	8	2.07	0.26	6.02	0.001*	0.52
Residuals	33	1.42	0.04			0.35
Total	43	4.01				1.00

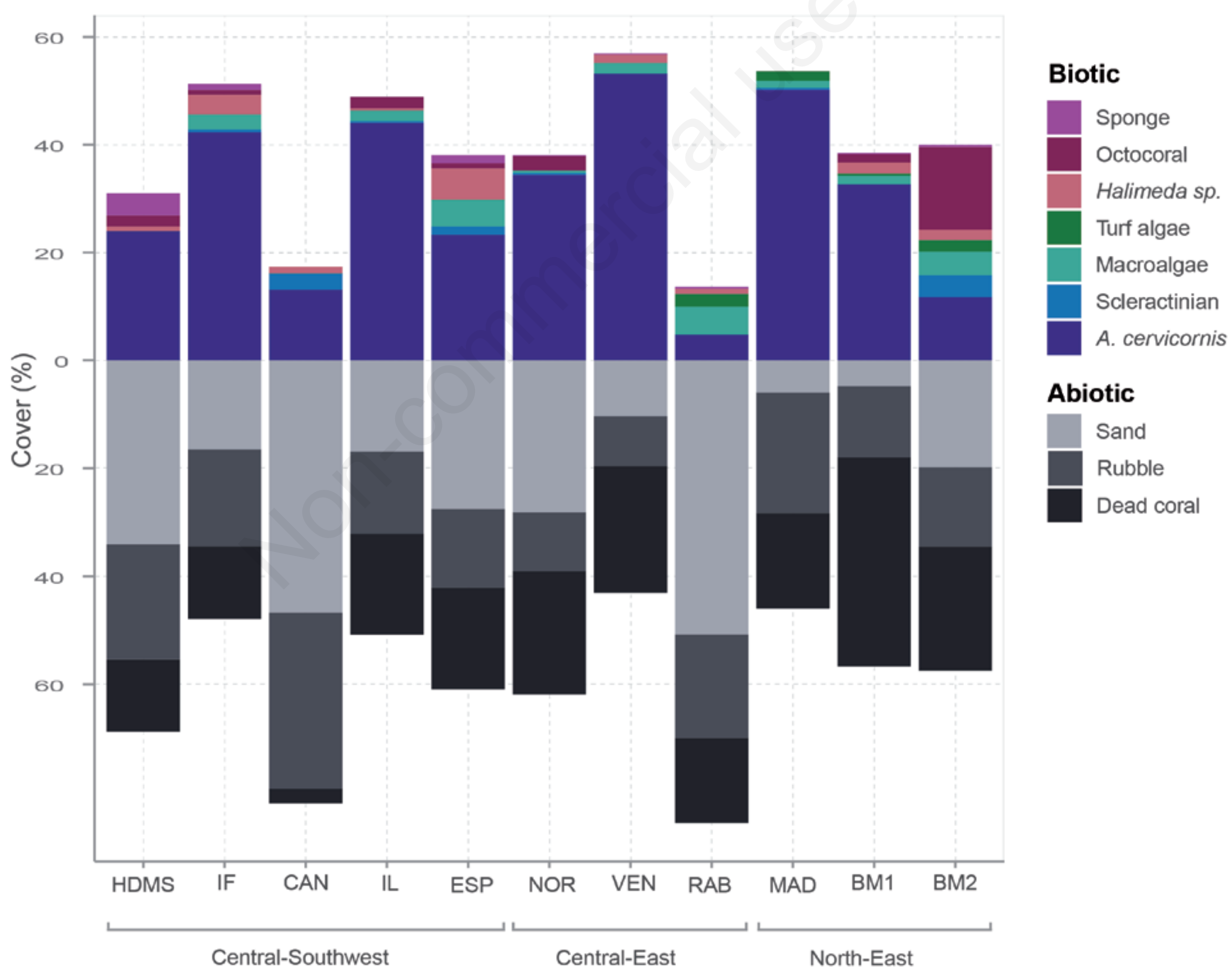

Figure 4. Average cover of biotic benthic community groups and abiotic substrates associated to *Acropora cervicornis* patches per location, and geographic sectors. Sponges, octocoral and scleractinian species were grouped into major categories. HDMS: Herradura Dos Mosquises, IF: Isla Felipa, CAN: Los Canquises, IL: Isla Larga, ESP: Laguna de Espenquí, NOR: Noronquí, VEN: La Venada, RAB: Rabusquí, MAD: Madrizquí, BM1: Bajo de Medio 1, BM2: Bajo del Medio 2.

fold higher compared to the frequency of recent mortality which seldom exceeded 2% across all sites (Figure 5a). The highest average of old mortality was recorded at the largest and more continuous patches, ranging from 27.7±7.9 in La Venada to 26.8±27.1 in Madrisquí. In Los Canquises, the farthest site from any recreational activity and human settlement point in the MPA, partial mortality was 12-fold lower compared to the previous sites (Figure 5a). Moreover, only two sites (Bajo del Medio 1, Bajo del Medio) presented higher mortality than live tissue. WBD prevalence ranged between 0.1% and 22%, significantly varying at the scale of sites and explaining 43% of the total variation among sites (Figure 5b, Table 3). Furthermore, prevalence above the average was only recorded at Boca del Medio 2 (19.0±16.0%), La Venada (17.5±11.9%), and Espenquí (12.2±11.3 %; Figure 5b).

Our results indicate that surveyed patches in the MPA showed a live cover of *A. cervicornis* above 10%, with low macroalgal abundance (<5%), predominance of old mortality (≤25%), and a WBD prevalence that never exceeded 10%.

DISCUSSION

This study represents the first systematic and comprehensive survey of *Acropora cervicornis* populations across Los Roques. Prior to our study, all available information was

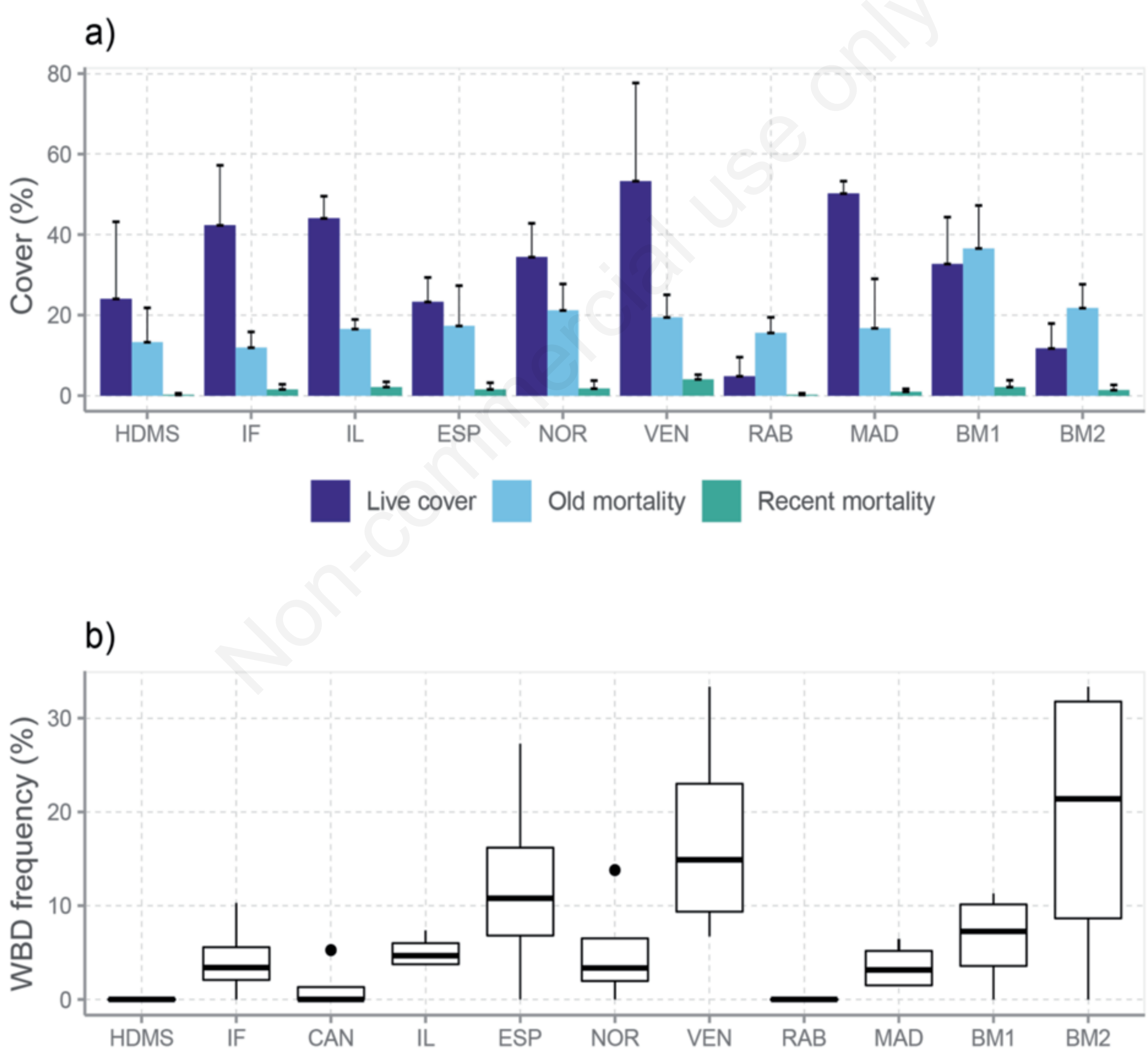

Figure 5. Health status of *Acropora cervicornis* in Los Roques. Live cover tissue *versus* old and recent mortality (a), and white band disease (WBD) prevalence (b) per location. HDMS: Herradura Dos Mosquises, IF: Isla Felipa, CAN: Los Canquises, IL: Isla Larga, ESP: Laguna de Espenquí, NOR: Noronquí, VEN: La Venada, RAB: Rabusquí, MAD: Madrizquí, BM1: Bajo del Medio 1, BM2: Bajo del Medio 2.

limited to a single site (Sandía and Medina 1987) or aimed to describe the benthic community structure at three points in time, as opposed to assessing the status of *A. cervicornis* (Villamizar *et al*. 2003; Weil 2003; Miyazawa *et al*. 2020). We found that *A. cervicornis* has a restricted distribution in Los Roques, where it was typically located on shallow and protected reefs, and mostly forming scatter and/or dispersed patches. Only two continuous and abundant patches of *A. cervicornis* were spotted in two surveyed sites located within the low protection zones of the MPA. Moreover, the prevalence of WBD and recent mortality was low (<10%) across the survey sites, and the cover of recently dead tissue did not surpass old mortality and live tissue.

The continuous *Acropora cervicornis* patches showing the highest live cover recorded within the MPA were only found in La Venada and Madrizquí (53.3±24.4 and 50.2%±3.1% respectively), both locations inside the lowest level protection zones. These islands are close to the biggest and most heavily populated island of Gran Roque Island, where various tourism and diving activities are permitted. In addition, the proximity to Gran Roque Island also increases the proximity to anthropogenic stressors such as pollution and sewage discharges (Croquer *et al*. 2016).

Within the MPA, *Acropora cervicornis* occupies habitats with highly specific features, consisting of leeward sandy bottoms protected from strong wave energy. The presence of sand as dominant substrate contrast with previous habitat descriptions from other parts of the species distribution range in the Florida Keys (Miller *et al*. 2008; D'Antonio *et al*. 2016) and other U.S. Caribbean territories (Wirt *et al*. 2015) where they report that this species occurs mostly on consolidated hardbottom, and rubble zones. However, the presence of most patches in leeward reefs is consistent with previous studies (Vargas-Angel *et al*. 2003; D'Antonio *et al*. 2016; Weil *et al*. 2020). Furthermore, we found that *A. cervicornis* cover in Los Roques was highly related to patch morphology and depth, where the species presence was seldom observed deeper than 5 m. This is consistent with previous findings indicating that *A. cervicornis* occurred at depths ranging from 15 to 25 m before their population collapsed, and now the species is regularly found in shallower habitats ranging from 5 to 14 m (Vargas-Angel *et al*. 2003; Miller *et al*. 2008). Even though previous population data of the species in the MPA is limited for comparison, the low occupancy, predominance of scatter patches, and in the occurrence in shallow areas could suggest that *A. cervicornis* has reduced its distribution habitats across the MPA. This evidence should prompt decision-makers to design specific actions to restore and/or to foster population recovery of this species in specific areas within the MPA. Such efforts are currently absent and have never been attempted in Los Roques.

The health status of *Acropora cervicornis* suggests that factors producing mortality in the archipelago are widespread across the MPA. The prevalence of WBD was commonly observed across the MPA distribution of the species, ranging from 0% to 33.3% (mean 6.8%±9.2%), which was similar to other reports across other large and continuous patches in the Caribbean (Lirman *et al*. 2010; Miller *et al*. 2014; Goergen *et al*. 2019). Also, the continuous patch in La Venada presented the second highest prevalence of WBD (mean 17.5%±11.9%) across survey sites. It has been previously observed that high-density patches are more susceptible to predation and diseases are less likely to be to persist through modern disturbances and conditions (Goergen *et al*. 2019). Therefore, highlighting the increased vulnerability of one of the biggest patches of *A. cervicornis* in the MPA.

Different studies have shown that Los Roques harbours healthy populations of other key and vulnerable scleractinian species such as *Acropora palmata* and *Dendrogyra cylindrus* (Zubillaga *et al*. 2005; Croquer *et al*. 2016; Cavada-Blanco *et al*. 2020; Cavada-Blanco *et al*. 2021). Most likely because the archipelago remains outside the main impact route of hurricanes and has not been subjected to coastal development (Zubillaga *et al*. 2005; Croquer *et al*. 2016). However, it is imperative to maintain constant surveillance across the whole MPA because *A. cervicornis* is known to be highly vulnerable to natural and anthropogenic disturbances such as diseases (Gladfelter 1982; Aronson and Precht 2001; Verde *et al*. 2016), recurrent epizootic events (Knowlton 1992; Williams and Miller 2005; Miller *et al*. 2014; Goergen *et al*. 2019), increase of storms frequency and habitat degradation (Hernández-Delgado *et al*. 2014; Goergen *et al*. 2019), and episodes of high thermal stress that can lead to loss of disease resistance (Quinn and Kojis 2008; Muller *et al*. 2018). Even in cases where the population's dynamic seems stable and without disturbances, the growth rate of patches is below equilibrium (Mercado-Molina *et al*. 2015).

Table 3. Univariate PERMANOVA using a Euclidean dissimilarity matrix of white band disease frequency. * Indicates p-values <0.05

Variation source	df	Sum of Squares	Mean Squares	F-Model	p-value	R2
Sector	2	204.14	102.07	1.80	0.216	0.06
Sector: site	8	1548.06	193.51	3.41	0.015*	0.43
Residuals	33	1874.41	56.80			0.52
Total	43	3626.61				1.00

The survey shows that Los Roques holds one of the few healthy and large *Acropora cervicornis* populations in the Southern Caribbean. *A. cervicornis* patches live cover and disease prevalence comparable to other continuous patches found in the region such as Fort Lauderdale-Florida (Vargas-Angel *et al*. 2003; Williams *et al*. 2008; Walker *et al*. 2012), La Parguera-Puerto Rico (Lucas and Weil 2016; Weil *et al*. 2020), Coral Gardens-Belize (Busch *et al*. 2016), Punta Rusia-Dominican Republic (Lirman *et al*. 2010), and Roatan-Honduras (Keck *et al*. 2005). This shows that even after the critical mass bleaching events of 2005 and 2010 (Villamizar *et al*. 2008; Bastidas *et al*. 2012), *A. cervicornis* populations were still found thriving in shallow and vulnerable habitats affected by sudden increases in water temperature. Thus, the results presented in this study show that there are still potential refugia for this species in Los Roques.

Multiple studies have shown that there are phylogeographical barriers (*e.g*., Mona Passage, Mesoamerican Barrier Reef) across the extent of the wider Caribbean for multiple coral species (Baums *et al*. 2005; Galindo *et al*. 2006; Vollmer and Palumbi 2007; Zubillaga *et al*. 2008; Baums *et al*. 2010; Foster *et al*. 2012; Rippe *et al*. 2017). Moreover, larvae dispersal and gene flow of *Acropora cervicornis* is limited when distances exceed 500 km (Vollmer and Palumbi 2007). In this sense, the populations in the MPA might represent reservoirs of genetic variation for the Southern Caribbean, where sexually produced larvae can be used to assist the restoration of populations that are not thriving well in the neighbouring areas. However, it is important to first assess the proportion of clones, reproductive success, and the population's genetic variability to further understand the population's dynamics within the MPA. Therefore, with appropriate local management, conservation, and protection of local source populations we can safeguard the future of the species in the area (Vollmer and Palumbi 2007; Weil *et al*. 2020).

Overall local and anthropogenic threats might be minimized due to limited access to the area, its MPA status, and low human populations. However, the latest evidence of the MPA's degradation due to parrotfish and other herbivores overfishing, changes in governance, and inadequate surveillance and law enforcement poses an imminent threat (Croquer *et al*. 2016; Agudo-Adriani *et al*. 2019; Cavada-Blanco *et al*. 2020; Cavada-Blanco *et al*. 2021). Thus, we suggest the urgent need to revise the MPA´s zoning and regulations, established in 1991, to protect these dense and extensive patches of *Acropora cervicornis*. Finally, information presented in this paper could be used to plan future restoration plans for this species based on sexual and/or asexual propagation as other Caribbean countries are currently implementing (Bayraktarov *et al*. 2020; Sellares-Blasco *et al*. 2021).

CONCLUSIONS

This paper represents the first baseline study showing the distribution and status of *Acropora cervicornis* in Los Roques. We showed this species is restricted to a limited number of sites within the MPA with dispersed and scattered patches prevailing upon continuous patches. However, most patches of *A. cervicornis* showed average live cover >30%, low prevalence of WBD, and macroalgal abundance, further suggesting that Los Roques represents a stronghold for staghorn corals as it still holds healthy populations. Nonetheless, the distribution of this species clearly overlaps with areas with low protection levels where fishing and tourism activities occur, and the largest human population is settled. This, along with an outdated MPA zonation, may severely hamper the persistence of *A. cervicornis* in Los Roques in the future.

ACKNOWLEDGEMENTS

This project was partially funded by an EDGE of Existence Fellowship awarded to Francoise Cavada-Blanco in 2013, and by the Laboratorio de Ecología Experimental (Universidad Simón Bolívar) through in-kind contributions. Field studies were authorized by the Ministerio del Poder Popular de Ecosocialismo, Hábitat y Vivienda (Approval number: 0323), and Territorio Insular Miranda (Approval number: 006). We would like to acknowledge our boat driver, fishers, dive operators and lodges for their time, and for providing information about the species in Los Roques. We also thank Luis M. Montilla for helping with data analysis, and Maria Zalm for proofreading the manuscript.

Corresponding author: Stephanie J. Martinez.
E-mail: jmartinez.sh@gmail.com

Authors' contributions: All the authors made a substantive intellectual contribution, performed part of the experiments. All the authors have read and approved the final version of the manuscript and agreed to be accountable for all aspects of the work.

Availability of data and materials: All data generated or analyzed during this study are included in this published article.

Conflict of interest: The authors declare no potential conflict of interest.

Keywords: Acropora cervicornis, MPA, Los Roques, staghorn coral.

Received: 5 December 2021.
Accepted: 29 December 2021.

Licensee PAGEPress, Italy
Advances in Oceanography and Limnology, 2021; 12:10005
DOI: 10.4081/aiol.2021.10005

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