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REPORT

Genetic differentiation in the mountainous star coral *Orbicella faveolata* around Cuba

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Abstract Caribbean coral reefs are biodiversity-rich habitats which provide numerous ecosystem services with both ecological and economical values, but nowadays they are severely degraded. In particular, populations of the major framework-building coral *Orbicella faveolata* have declined sharply, and therefore, understanding how these threatened coral populations are interconnected and how demographic changes have impacted their genetic diversity is essential for their management and conservation. Previous population genetic surveys showed that gene flow in this species is sometimes locally restricted in the Caribbean; however, little genetic data are available for Cuban populations. Here, we analyzed the variation at the mitochondrial DNA control region and six microsatellite loci from *O. faveolata* colonies from five distant localities representing most of the main coral reefs around Cuba. Both genetic markers showed evidence of genetic differentiation between the northwestern area (Colorados Archipelago) and the other reefs. Colonies from the Colorados Archipelago harbored the largest number of unique mtDNA haplotypes and microsatellite alleles, which suggests long-term large population size or gene flow from other areas of the Caribbean. These results indicate that the Colorados Archipelago area is particularly important for *O. faveolata* populations and it is well suited for reef management and restoration efforts.

Keywords Coral reefs · Genetic connectivity · mtDNA · Microsatellite loci

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Introduction

Across the Caribbean, coral cover has diminished around 60% in the past 30 years (Jackson et al. 2014), including Cuban reefs, which make up the largest reef area in the Caribbean (Duran et al. 2018). The coral *Orbicella faveolata* (Ellis and Solander 1786; Anthozoa: Merulinidae), a species that belongs to the *Orbicella* complex, is a framework-building species on Caribbean reefs, and was abundant on Cuban reefs (Duran et al. 2018; González et al. 2018). Forereefs dominated by *Orbicella* spp. have been associated with highest richness of species, processes and services (Mumby et al. 2008). Although *Orbicella* spp. are considered hermaphroditic broadcast spawners (Szmant 1991), asexual reproduction via fission or fragmentation is more common than previously thought on reefs with high

physical disturbance or limited possibilities of larvae settlement (Foster et al. 2007; Foster et al. 2013), yet still considered insignificant compared to sexual processes (Shearer et al. 2009; Rippe et al. 2017). While spawning and recruitment have decreased, declining populations of *Orbicella* spp. are widespread throughout the Caribbean (Dustan and Halas 1987; Hughes and Tanner 2000; Bruckner and Bruckner 2006; Edmunds and Elahi 2007; Levitan et al. 2014; Van Woesik et al. 2014), and particularly in Cuba (Duran et al. 2018; González et al. 2018). *Orbicella faveolata* is now listed under the Endangered category to the IUCN Red List of Threatened species as well as on the US Endangered Species Act.

A combination of ecological and genetic approaches is required to provide managers with tools that can help maintain the structure and function of marine ecosystems (Palumbi 2003). Genetic connectivity patterns among reef corals could be the guide for setting the scale of conservation and management strategies on Caribbean reefs (Vollmer and Palumbi 2007). Thus, efforts have been made to examine the genetic connectivity of *Orbicella* spp in the Caribbean. In the case of *O. faveolata,* populations are interconnected throughout the western Caribbean (Severance and Karl 2006; Rippe et al. 2017). However, complex patterns of gene flow restriction appear at the local scale at the Mesoamerican Barrier Reef System (MBRS) (Porto-Hannes et al. 2015; Rippe et al. 2017). Whereas biological factors such as pelagic larval duration, larval survival, settlement characteristics and larval vertical migration influence spatial genetic variation in sessile organisms (Sponaugle et al. 2002; Levin 2006; Mayorga-Adame et al. 2017), coral species with similar early life history traits present different connectivity patterns, likely due to abiotic factors such as fluctuating hydrodynamic patterns (Severance and Karl 2006). Further, the fact that larval transportation is unsteady and subject to many variables (Figueiredo et al. 2013) would also affect the genetic connectivity of marine populations. It has been suggested that coral population structure and coral life-history are considered as complex and likely influenced by numerous factors including geographic scale and physical characteristics at microscale and macroscale specific to individual reefs (Severance and Karl 2006).

While several studies have previously examined *O. faveolata* genetic connectivity through the Caribbean, none have included Cuban corals (Severance and Karl 2006; Porto-Hannes et al. 2015; Rippe et al. 2017). In this study, we sampled *O. faveolata* from five of the main reef localities around the Cuban archipelago. We assessed the population structure of *O. faveolata* using mitochondrial DNA (mtDNA) control region and six microsatellite loci. Our results show weak genetic differentiation among Cuban reefs, with Colorados Archipelago as the most differentiated reef. Moreover, we found the largest number of unique mtDNA haplotypes and microsatellite alleles within the *O. faveolata* colonies from Colorados Archipelago.

Materials and methods

A total of 116 *O. faveolata* colonies were sampled at five locations around Cuba (Fig. 1a) by scuba diving. Each reef was georeferenced (SupMat 1; see Fig. 1a for details on sampling sizes per locality), and adult colonies were morphologically identified. A coral fragment (2 cm^2) was cut from each colony (with hammer and chisel) and preserved in 70% ethanol. In order to reduce the likelihood of sampling clones, colonies were sampled at least 10 m apart. Sampling sizes largely depended on the size of the reef and abundance of the species.

Molecular procedures

Total genomic DNA was extracted using the NucleoSpin Blood and Tissue kit (Macherey–Nagel). Total DNA was quantified using a Qubit 3.0 Fluorometer (Invitrogen), and genomic DNA quality was assessed using agarose (1%) gel electrophoresis.

The mtDNA control region was amplified using the primers MNC1f and MNC1r (Fukami et al. 2004). Total genomic DNA, 5–100 ng, was used as template in a 30 µl PCR with one unit of GoTaq DNA polymerase (Promega), 0.2 µM of each primer, 0.2 nM of dNTPs and 1.5 mM of $MgCl_2$. The reaction started with denaturation at 94 °C for 180 s, followed by 40 cycles of denaturation for 45 s at 94 °C, annealing for 60 s at 50 °C and extension for 90 s at 72 °C, with 600 s at 72 °C used for the final extension. PCR products were purified using ExoSAP-IT (Affymetrix/USB) and used as templates for the ABI Prism BigDye terminator sequencing kit V.3 (Applied Biosystems) cycle sequencing, with the same primers used for PCR. Sequencing reactions were run in an ABI3100 automated sequencer (Applied Biosystems).

From the same *O. faveolata* DNA, six microsatellite loci specifically developed for this species and the species complex were analyzed. This included four loci described by Severance et al. (2004) (maMS8, maMS11, maMS2-4 and maMS2-8) and two by Davies et al. (2013) (Mfav5, Mfav7) (SupMat 2). PCRs were carried out in 9.0-µl volume using the following conditions: 5–20 ng of genomic DNA diluted in TE 1X buffer, 2.0 µM of each primer and 5.0 µl of Platinum™ Multiplex PCR Master Mix 2X (Applied Biosystems). Genotypes were scored using an ABI3130XL Genetic Analyzer with GS500-ROX size

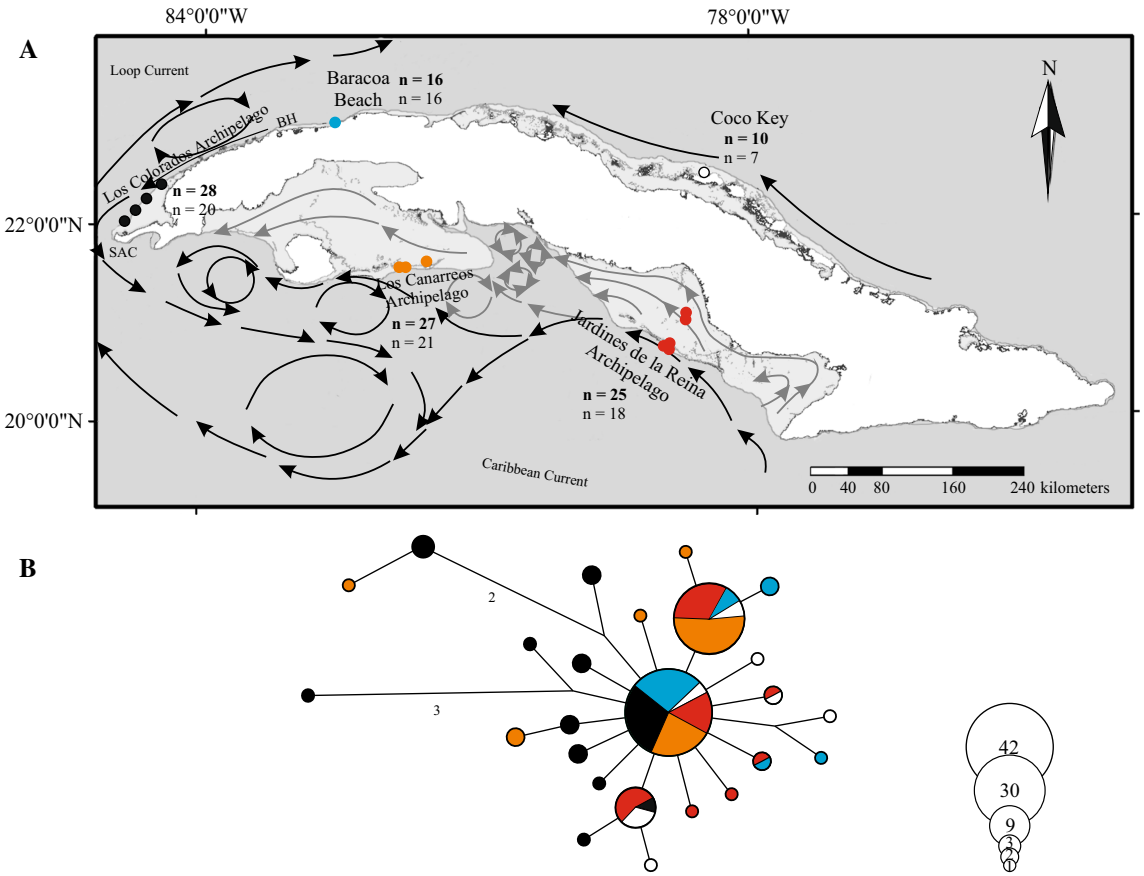

Fig. 1 **a** Sampling sites of *Orbicella faveolata* around Cuba. Arrows indicate major (black) and secondary (gray) oceanic and shelf circulation (Arriaza et al. 2012). Sampling sizes are indicated in each locality: in bold for mtDNA and regular font for microsatellite DNA. **b** mtDNA haplotype network. The size of circles is proportional to haplotype frequency (specified in the scale), and the color inside the circles matches the color of each locality in the map. Branches are proportional to the number of changes, when higher than one, number of changes is indicated. BH Bahía Honda. SAC San Antonio Cape

standard and the software Peak Scanner 2.0 (Applied Biosystems).

Data analysis

Individuals sharing identical nuclear and mtDNA genotypes (n = 7; three different clones in Canarreos and one in each of the other localities, two clone mates per clone) were removed as potential clones. Putative clone mates were only found within the same geographic site. Additionally, for three highly divergent sequences (more than 50 pb), BLAST search was used to verify similarity of the mtDNA control region with other species within the genus. The sequences were found more closely related to *O. franksi* than to *O. faveolata* and therefore removed for downstream analysis.

Mitochondrial DNA

Sequences were aligned with ClustalW using MEGA 7.0 (Kumar et al. 2016), with the alignment optimized by eye. A haplotype network was constructed to represent haplotype relationships using the median-joining network algorithm (Bandelt et al. 1999) and post-processed using maximum parsimony (Polzin and Daneschmand 2003) as implemented in Network 5.0 (Fluxus-engineering.com). Nucleotide diversity (π), haplotype diversity (h) (Nei 1987) and the number of haplotypes were estimated for each sampling locality and for pooled localities. The estimates were obtained with DnaSP v5.10.01 (Librado and Rozas 2009). Pairwise genetic differentiation between localities was estimated using Hudson's Snn (Hudson 2000) statistic calculated in DnaSP. p value correction for multiple comparisons was conducted with a 5% threshold using the Benjamini and Hochberg (1995) correction method implemented in R package stats (R Core Team 2018).

Microsatellite loci

Samples with missing data in more than two loci were discarded, leaving 82 unique genotypes for downstream analysis. Size range bins were assigned for each microsatellite allele with the software FLEXIBIN (Amos et al. 2007). To detect null alleles, large allele dropout and stuttering was employed the software Micro-Checker 2.2.3 (Van Oosterhout et al. 2004). All pairs of loci were tested for genotypic disequilibrium in FSTAT 2.9.3 (Goudet 2001) implementing the Bonferroni correction (Rice 1989). Deviations from Hardy–Weinberg equilibrium (HWE) were evaluated performing the *locus*-by-locality tests using Genepop 4.6 (Rousset 2008).

Allelic richness per locality was calculated as the locality mean of *locus*-specific allelic richness, using FSTAT (Goudet 2001). Expected and observed heterozygosities were calculated overall and by geographic locality, using FSTAT (Goudet 2001) and GenAlEx v6.502 (Peakall and Smouse 2006, 2012), respectively. Expected heterozygosity per site was calculated as unbiased expected heterozygosity as described by Peakall and Smouse (2012).

The global F_{ST} estimate was calculated in FSTAT (Goudet 2001) with 99% confidence intervals, obtained by bootstrapping over all loci. Pairwise F_{ST} values were calculated using GenAlEx (Peakall and Smouse 2006, 2012) but due to the high mutation rate of microsatellites, F_{ST} may underestimate population subdivision (Rousset 1996). To address this problem, G''_{ST} statistic (Meirmans and Hedrick 2011) was calculated between locality pairs and used to visualize the population structure in a principal coordinate analysis (PCoA), and both calculation and visualization were performed in GenAlEx (Peakall and Smouse 2006, 2012). Adjusted p values for multiple comparisons were calculated as previously mentioned. STRUCTURE software v2.3.4 (Pritchard et al. 2000; Falush et al. 2003, 2007) was used to infer genetic differentiation of the populations via Bayesian clustering method. For each potential K number of clusters (K number of populations, one to six), 20 independent replicate runs were performed with 10^6 MCMC repetitions after a burnin period of 500,000. We used the admixture model and LOCPRIOR, which use the sampling locations as prior information (Hubisz et al. 2009), and set $\alpha = 0.3$ following Wang (2017) suggestions for correcting the value of α prior. The most likely number of genetic clusters was then determined using: (1) the modal value of the statistic ΔK following the method of Evanno et al. (2005) implemented in STRUCTURE Harvester (Earl and vonHoldt 2012) and (2) Ln Pr[X|K] (the probability of obtaining the genotype data X given K) following the method of Pritchard et al. (2000). The program Clumpp v.1.1.2 (Jakobsson and Rosenberg, 2007) was then used to align individual posterior assignment probabilities from the 20 independent replicate runs with the best K. The program DISTRUCT v.1.1 (Rosenberg 2004) was used to graphically display the results produced by Clumpp.

Results

Mitochondrial DNA

The size of the mtDNA sequences was identical (930 bp) in the 106 individuals analyzed. A network shows the relationship among haplotypes (Fig. 1b), and presents many singletons and two haplotypes with relatively high frequencies present in most localities. The locality with the highest number of haplotypes ($n = 11$) was in Colorados Archipelago (Table 1), showing several exclusive singletons and low-frequency haplotypes. Overall, high haplotype diversity and low nucleotide diversity ($h = 0.79 \pm 0.031$, $\pi = 0.001 \pm 0.0002$) were observed. The highest diversity estimates were found in Colorados Archipelago ($h = 0.78 \pm 0.078$, $\pi = 0.002 \pm 0.0004$; Table 1) and Coco Key ($h = 0.91 \pm 0.077$, $\pi = 0.0019 \pm 0.0004$; Table 1).

Comparisons of pairwise sequence differentiation between localities (Hudson's Snn statistic) ranged from 0.56 to 0.77, and all were statistically significant ($p < 0.05$), except for Jardines de la Reina Archipelago-Coco Key and Jardines de la Reina Archipelago-Baracoa Beach comparisons.

Microsatellite loci

Six microsatellite loci were analyzed for 82 individuals of *O. faveolata*. After Bonferroni correction, no evidence for linkage disequilibrium (LD) was observed except from Canarreos Archipelago where eight of the 15 tests were significant ($p < 0.05$). No locus pairs were significantly associated in any other sampling site, indicating that the observed disequilibrium is not a result of physical linkage of the markers. Six out of 30 locus-by-locality Hardy–Weinberg equilibrium (HWE) tests showed heterozygote deficit, but no locus showed significant deficits in all populations. Consequently, since no evidence of null alleles was found, all loci were retained for further analysis.

The *O. faveolata* population with the highest number of unique alleles (13) was Colorados Archipelago. Overall observed and expected heterozygosity values (0.736 and 0.815, respectively) were relatively high. Per reef, observed heterozygosity values (*Ho*) and unbiased expected heterozygosity values (u*He*) ranged from 0.721 to 0.759 and from 0.788 to 0.856, respectively (Table 1). Mean allelic richness values were relatively low, ranging from

Table 1 Genetic diversity estimates of *Orbicella faveolata* in Cuba

Locality	mtDNA			Microsatellite *loci*			
	Hn	$h \pm$ SD	$\pi \pm$ SD	Allelic richness	Unique alleles	$H_o \pm$ SD	$uH_e \pm$ SD
Coco Key	7	0.911	0.00186	5.49	4	0.759	0.798
		±0.077	±0.00036			±0.089	±0.06
Baracoa Beach	5	0.667	0.00101	4.96	10	0.733	0.788
		±0.113	±0.00023			±0.081	±0.063
Colorados	11	0.780	0.00192	5.24	13	0.739	0.807
Archipelago		±0.078	±0.00038			±0.101	±0.089
Canarreos	5	0.647	0.00126	4.65	5	0.729	0.812
Archipelago		±0.060	±0.00034			±0.126	±0.067
Jardines de la Reina	7	0.777	0.00122	4.79	5	0.721	0.856
		±0.050	±0.00014			±0.112	±0.059

Hn number of haplotypes, *h* haplotype diversity, π nucleotide diversity, H_o observed heterozygosity uH_e unbiased expected heterozygosity, *SD* standard deviation

4.65 to 5.49 (Table 1). Unbiased expected heterozygosity was slightly higher in northern localities than in southern localities, albeit differences were not statistically significant (Student t test, $p > 0.05$).

The pairwise G''_{ST} estimates between localities (mean $G''_{ST} = 0.1068$, ranging from 0.000 to 0.221, Table 2) support Hudson's Snn statistic results showing statistically significant genetic differentiation ($p < 0.05$) in all comparisons involving Colorados Archipelago. Pairwise F_{ST} values are reported to allow contrast with previous studies (SupMat 3). Global F_{ST} was low but different from zero ($F_{ST} = 0.022$; 99% confidence interval: 0.011–0.037) and ranged between 0.019 (Jardines de La Reina vs Canarreos) and 0.051 (Colorados Archipelago vs Coco Key; SupMat 3).

A principal coordinates analysis based on pairwise G''_{ST} values produced two distinct clusters in opposite areas of the principal coordinate (PC) 1, explaining 79.19% of the variation in these data (Fig. 2). The population from Colorados Archipelago was distantly separated from populations from the other geographic sampling areas (Fig. 2). The remaining group includes all other localities, with moderate divergence along PC2, which explains 14.78% of variation. Baracoa Beach and Canarreos are in the opposite edges of this group.

The analysis with the program STRUCTURE shows that individuals are grouped into two main clusters ($K = 2$) following the Evanno et al. (2005) method (Fig. 3) or in three main clusters ($K = 3$) (Wilcoxon two-sample test $p < 0.05$ $K = 2$ vs. $K = 3$ and $p > 0.05$ $K = 3$ vs. $K = 4$)

Table 2 Pairwise comparisons of genetic differentiation between *Orbicella faveolata* sampling sites across Cuba. Statistic Snn (Hudson 2000) calculated using mtDNA sequences with 50,000 permutations is shown below the diagonal. Standardized F_{ST} (G''_{ST}, Meirmans and Hedrick 2011) estimates using microsatellite DNA are above the diagonal. Statistically significant values after using Benjamini and Hochberg (1995) correction method with 5% as threshold are in bold

Sampling site	Coco Key	Baracoa Beach	Colorados Archipelago	Canarreos Archipelago	Jardines de la Reina
Coco Key		0.088	0.221 $p = 0.014$	0.000	0.000
		$p = 0.17$		$p = 0.53$	$p = 0.83$
Baracoa Beach	0.68		0.165	0.110	0.050
	$p = 0.01$		$p = 0.006$	$p = 0.04$	$p = 0.16$
Colorados	0.72	0.68		0.179	0.213
Archipelago	$p = 0.02$	$p = 0.004$		$p = 0.003$	$p = 0.004$
Canarreos	0.77 $p = 0.000$	0.61	0.73		0.042
Archipelago		$p = 0.02$	$p = 0.000$		$p = 0.16$
Jardines de la Reina	0.58	0.57	0.70	0.56	
	$p = 0.42$	$p = 0.08$	$p = 0.000$	$p = 0.025$	

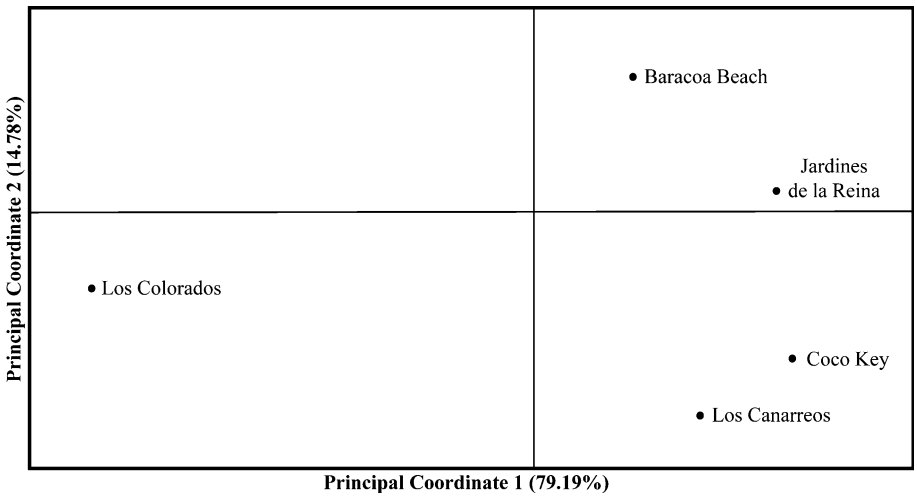

Fig. 2 Principal coordinates analysis (PCoA) using G′′ST (Meirmans and Hedrick 2011) pairwise estimates of genetic differentiation in *Orbicella faveolata*. Distance between points in ordinate space along each axis corresponds to genetic divergence. Percentages indicate the proportion of variation in the data explained by each axis

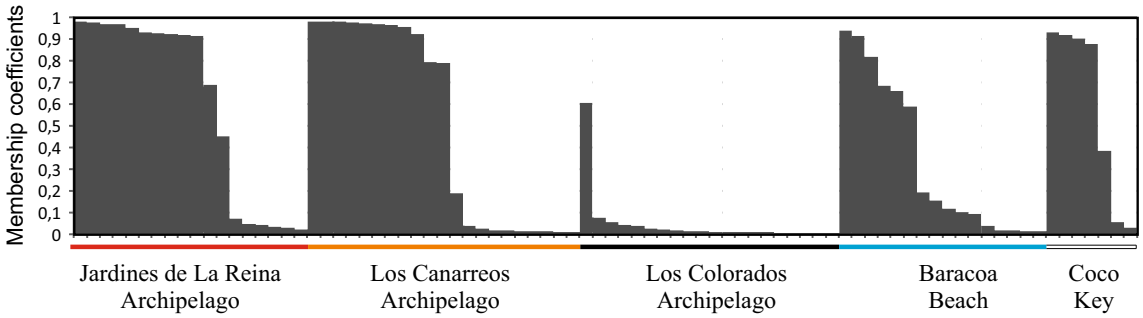

Fig. 3 Individual clustering analysis of *Orbicella faveolata* colonies obtained by STRUCTURE using microsatellite loci. Cluster assignment of individuals represented by vertical lines with estimated membership coefficients in each of the two defined clusters indicated by gray and white. Sampling regions are indicated by colors and presented following the direction of the main marine circulation around Cuba: from southeast to west and then from west to northeast

with Pritchard et al. (2000) method (SupMat 4). As with K =3, the third cluster is only represented by four colonies at the same geographic site (Canarreos Archipelago), we chose K = 2 as it is the smallest value of K that captures the major population structure and has a clear biological explanation: differentiation between Colorados Archipelago and the other localities (Fig. 3). Accordingly, the frequency of individuals assigned to the white cluster decreases from Jardines de la Reina and Coco Key to Colorados Archipelago (Fig. 3). In Colorados Archipelago, only one individual was mainly assigned to cluster gray, while in the other localities, both clusters are observed (SupMat 4).

Discussion

In the present study, we assessed the genetic structure of the reef building coral *O. faveolata* around Cuba. Microsatellite DNA results suggest two genetic clusters: on the one hand, the Colorados Archipelago and on the other hand, the other reefs. However, other patterns of genetic differentiation among populations are detected with mtDNA control region sequences. Moreover, the estimations of genetic diversity are among the lowest found in the region for scleractinian corals.

Genetic diversity

Low nucleotide diversity of mtDNA is common in scleractinian corals (Shearer et al. 2002) including the mtDNA control region (*Acropora cervicornis* π = 0.0057) (Caribbean-wide mean, control region), *A. cervicornis* π = 0.0050 (Puerto Rico, control region) (Garcia-Reyes and Schizas 2010). Yet, the values we observed in this study (overall π = 0.001 $\pm$ 0.0002) are among the lowest reported so far with some exceptions in branched corals as *A. palmata* in Puerto Rico (π = 0.00075; control region) and *A. palmata* in Bahamas (π = 0.00124; control region) (Garcia-Reyes and Schizas 2010). These findings contrast with the high overall haplotype diversity (h = 0.79 $\pm$ 0.031) as well as the high overall observed and expected heterozygosity values (0.736 and 0.815, respectively) revealed by the nuclear markers. Moreover,

allele richness of microsatellite loci (from 4.65 to 5.49) is also on the low side of the range previously described for the species (Shearer et al. 2009; Rippe et al. 2017). Reduced allelic diversity is usually related to recent bottlenecks or founder events followed by expansions, as allelic diversity is more sensitive to these events than heterozygosity (Allendorf 1986; Luikart et al. 1998; Greenbaum et al. 2014). Additionally, the combination of moderately high haplotype and low nucleotide diversity (leading to a star-like haplotype network) can also be a signature of a rapid population expansion from a small effective population size (Avise 2000; Allcock and Strugnell 2012). Historic demographic models for *O. faveolata* in the Caribbean revealed a twofold bottleneck around 1.28 millions of years (Mya) ago with an increment in population size starting around 0.17 Mya (Prada et al. 2016). Populations in Cuba could be reflecting a founder event since they are likely younger than 12 000 years (time when the mean sea level was about 40 meters below the current level; Khan et al. 2017) after the last glacial maxima (20–25 000 years ago) (Iturralde-Vinent, 2006), and most of the Cuban shelf was exposed (Steadman and Franklin 2017), leading to a stepping back along coastlines of all shallow-marine ecosystems.

In 30 locus-by-locality tests, six revealed heterozygote deficit, but no locus was consistently deviated from HWE. Patterns of locus-specific heterozygote deficiency in this species were previously attributed to introgressive hybridization and/or the inadvertent sampling of sibling species (Rippe et al. 2017). These deficiencies could also potentially be due to the predominance of asexual reproduction by fragmentation but massive corals as *Orbicella* spp. mainly reproduce sexually (Shearer et al. 2009; Rippe et al. 2017). Additionally, the sampling site with more statistically significant locus-by-locality test (Baracoa Beach, 2 tests) presented only one clone mate. We cannot completely discard any possible causes, since the three *Orbicella* species occur in sympatry throughout their range and exhibit low levels of mtDNA divergence and overlapping morphologies, particularly near the northern extent of their distribution (Fukami et al. 2004; Fukami and Knowlton 2005). However, we carefully morphologically identified colonies of *O. faveolata* and removed any sample with mitochondrial control region more similar to other *Orbicella* species than to *O. faveolata* (such as three divergent individuals from Jardines de la Reina with high similarity to putative *O. franksi* divergent lineage mtDNA (Fukami et al. 2004; Fukami and Knowlton 2005).

Hybridization has been described between *Orbicella faveolata* and other species within the genus (Szmant et al. 1997; Fukami et al. 2004). However, *O. faveolata* interspecific fertilization rates were lower than observed in within-species crosses (Szmant et al. 1997). Introgressive hybridization would produce heterozygote deficit when two species are able to hybridize, but still same-species mating is possible. However, the HWE departure signal produced by this event disappears after one generation of random mating in the absence of selection (Roques et al. 2001). Introgressive hybridization is also related to LD between loci pairs. Immediately after contact, LD will be high, then decaying in loosely linked loci due to recombination (Harrison and Larson 2014). Unless hybrids are less fit than parental species, a stable but marginal hybrid population is maintained (Barton and Hewitt 1985).

Population structure *F*-statistics and cluster analysis

Analysis using mtDNA sequences and microsatellite loci produced a consistent pattern of genetic differentiation for all comparisons involving Colorados Archipelago, but not for comparisons involving Canarreos Archipelago or among Baracoa Beach and Coco Key (significant only with mtDNA). Previous studies using microsatellite markers found *O. faveolata* populations to be mostly well mixed throughout the western Caribbean (Severance and Karl 2006; Rippe et al. 2017). However, at a smaller scale, genetic structure and restricted gene flow have also been observed at the Mesoamerican Barrier Reef System (MBRS) (Porto-Hannes et al. 2015; Rippe et al. 2017) and in the sibling species *O. annularis* in Jamaica and the MBRS (Foster et al. 2012). In Cuba, the latter showed evidence of gene flow with Belize, Jamaica (Drunkenmans Cay), Cayman Islands and Dominican Republic reefs (Foster et al. 2012). However, the study by Foster and colleagues (2012) lacked samples from Colorados Archipelago or Canarreos Archipelago and included samples from only two localities (Siboney and Bacunayagua) that fall into the geographic range of our study.

Genetic differentiation is observed with the mtDNA data between Canarreos Archipelago and other Cuban reefs. (Eight of 10 pairwise comparisons are significant with mtDNA, while only four are significant with microsatellite markers.) Discordance between mtDNA and nuclear markers is quite common and has been widely associated with either incomplete lineage sorting, mtDNA sorting more quickly due to smaller effective population size, introgression of mtDNA between closely related taxa, sex-biased dispersal or adaptive selection of mtDNA (Zink and Barrowclough 2008; Toews and Brelsford 2012; DeBiasse et al. 2014). Also, the high allele homoplasy characteristic of microsatellite markers (Estoup et al. 2002) may contribute to reduced population differentiation (i.e., Lu et al. 2001). Nonetheless, both microsatellite and mtDNA present congruent genetic differentiation patterns regarding Colorados Archipelago. In pairwise comparisons, both types of markers generally show differentiation between

Colorados Archipelago and Baracoa Beach, Coco Key, Jardines de la Reina or Canarreos Archipelago (Figs. 2, 3) and the STRUCTURE analysis show a gradient from western Colorados Archipelago (5% of assignment to the gray cluster) to northeast (59% of assignment to the gray cluster in Coco Key) and southeast (60% of assignment to the gray cluster in Jardines de la Reina), with Baracoa Beach (34% of assignment to the gray cluster) and Canarreos Archipelago (51% of assignment to the gray cluster) as transitional localities (Fig. 3). This transitional pattern suggests comparatively greater gene flow among others sampling sites than with Colorados Archipelago.

The high number of unique alleles and haplotypes diverging from the most common haplotypes supports the idea that Colorados Archipelago may represent a resilient *Orbicella* population, with long-term time-stability and unique diversification. However, there is no evidence of age difference (i.e., colony size) between reefs making this somewhat unlikely as the cause of the difference observed. A plausible alternative explanation could be the occurrence of historically different source populations for Colorados Archipelago and for the other reefs accompanied by limited gene flow that has prevented complete homogenization of alleles and haplotypes in Cuban populations.

Larval retention and self-recruitment could create a scenario of regionally structured populations (i.e., Brazeau et al. 2011; Timm et al. 2017). Paris et al. (2005) and Castellanos-Gell et al. (2016) conducted reef fish connectivity studies in the same (or nearby) Cuban reefs than here. The result of grouper larval drift simulations showed that the northwest spawning site (the closest site to Colorados Archipelago) received the lowest amount of recruits and was a poor source of larvae within and outside Cuba (Paris et al. 2005). Albeit in different manners, life history and currents shape connectivity around Cuba in three different reef fishes (Castellanos-Gell et al. 2016). Thus, panmixia was documented in *Acanthurus tractus*, a differentiation gradient following the direction of oceanic currents in *Stegastes partitus* and panmixia accompanied with a trend for a slight gradient of genetic differentiation in *Haemulon flavolineatum* (Castellanos-Gell et al. 2016). Coral planula larvae have poor swimming capacity compared to reef fish larvae (Hata et al. 2017). As a consequence the ability of coral larvae to navigate appears extremely limited, adversely affecting connectivity among reefs. Also around Cuba, genetic population structure prompted by local current patterns and habitat availability has been documented in the pink shrimp *Penaeus notialis* and the white shrimp *P. schmitti*, at a small geographic scale (20–50 km) (García-Machado et al. 2001; Borrell et al. 2004; Robainas-Barcia and García-Machado 2012).

Oceanographic currents and their seasonal variations are important elements determining gene flow and population connectivity in marine organisms (Cowen and Sponaugle 2009; White et al. 2010; Snyder et al. 2014). Small-scale oceanographic retention dynamics such as offshore eddies and countercurrents can limit the dispersal of larvae and can significantly increase their retention leading to self-recruitment (Cowen et al. 2006; Snyder et al. 2014). The Caribbean Current and the Loop Current are the main oceanic currents affecting Cuba (Fig. 1a) (Arriaza et al. 2012). Offshore, water flow following main oceanic currents prevails (to the east in the northwest, westward in the south and the northeast). Nevertheless, surrounding the shelf around the northwestern part of Cuba, marine current intensity values higher than 0.65 m/s correspond to countercurrents from east to west, from Bahia Honda to San Antonio Cape (Fig. 1a). Countercurrents form eddies in the region and affect local circulation, frequently as daily fluctuations of the main shelf water circulation during summer months (Arriaza et al. 2012). Around the same period (August, September or October depending on latitude), *Orbicella* spp. synchronously mass spawn once a year after a full moon (Szmant 1991; Levitan et al. 2011). More specifically, spawning in Cuban waters occurs in August, during the time of eddy formation, which could contribute to larval retention and self-recruitment in Colorados Archipelago. *Orbicella* spp. eggs accumulate in patchy distributions into visible surface aggregations during the first hours and develop into planula larvae within 24 h (Wellington and Fitt 2003). Hence, while on the surface, eggs are carried by the current and are more susceptible to stay in the eddy. Then, between 70 and 90 h after hatched *O. faveolata* planula larvae become positively geotactic and show exploratory behavior, and settle soon after that time (Vermeij et al. 2006).

Ocean currents are unlikely to fully explain the genetic differentiation of Colorados Archipelago, and other mechanisms may be influencing the region, such as a population of *O. faveolata* outside Cuban waters. In this case, significant gene flow between long-distance reefs has previously been documented, which is mediated by the flow of the Caribbean Current (Rippe et al. 2017). In the sibling species *O. annularis*, the high level of gene flow between Puerto Rico, Jamaica (Dairy Bull), Colombia and Nicaragua could not be explained by oceanographic models, especially when gene flow restriction was found between close Jamaican reefs (Foster et al. 2012). Foster and colleagues (2012) proposed that rare oceanographic events, such as hurricanes, could be the cause. Given that the tropical hurricane season in the Caribbean overlaps with the spawning season of Atlantic *Orbicella* spp. (Gardner et al. 2005; Lugo-Fernández and Gravois 2010), it is likely that these extreme climatic events contribute to coral dispersal. For instance, previous studies provided some evidence that hurricanes may increase genetic

exchanges among different areas (i.e., between Flower Garden Banks and Mexican reefs, Lugo-Fernández and Gravois 2010). Hurricane-mediated dispersal has also been mostly associated with increased fragmentation and short distance dispersal of colony's fragments inside the same reef, increasing clonal representation on reefs with greatest physical disturbance (Foster et al. 2007, 2012, 2013). Western Cuban reefs like Colorados have been the most affected reefs by hurricanes and cold fronts over the last 140 years within Cuba (Fig. 6 in Chollett et al. 2012; Sacasas-León 2013), but the number of clonal individuals found in this study was the same compared to less disturbed areas such as Jardines de la Reina Archipelago. Nevertheless, we cannot refute the stochastic and eventual influence of hurricanes and tropical storms on larvae dispersal.

Complex connectivity patterns as we found in Cuban *O. faveolata* populations, suggest that small-scale processes may significantly influence dispersal distances, shaping the connectivity of coral populations in the Caribbean Sea (Foster et al. 2012). In highly diverse systems such as coral reefs, full consideration of genetic diversity among a wide cross-spectrum of species with a multi-species approach is important to represent major parts of reef biodiversity and functions (Beger et al. 2014). In Cuba, efforts have been made (see García-Machado et al. 2018 for a review) but until this study, the coral genetic diversity of Cuba has not been studied. While the mechanisms driving genetic differentiation in Colorados Archipelago and Canarreos Archipelago reefs require further research, the genetic structure observed in *O. faveolata* deserves attention for local management actions. For instance, further research could clarify whether Canarreos Archipelago is particularly susceptible to hybridization between *Orbicella* spp. or more pronounced clonal reproduction. Indeed, reef slope or stochastic physical disturbance has been associated with more coral fragmentation, but scarcity of sexual recruits or lack of settlement surfaces has also been associated with more clonal reproduction in the species (Foster et al. 2013). In order to limit genetic erosion and loss of local adaptive characters, any effort of restoration and conservation as corals nurseries, coral greenhouses or coral planting should utilize knowledge of the genetic background and connection between coral populations. The results of this study provide new information indicating population structure along the Cuban platform, and suggest that at least the northwestern region reefs should be managed differentially. Consequently, further studies are necessary in other species to clarify if the patterns observed here are common to other species of Cuban corals.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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