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Genetic Connectivity among *Gorgonia ventalina* Linnaeus, 1758 (Cnidaria: Octocorallia: Gorgoniidae) Populations in the Caribbean Sea[1]

Luis R. Rodríguez Matos[2], Jason P. Andras[3], Ernesto Weil[2], and Nikolaos V. Schizas[2]

Abstract: The geographic partition of genetic variation, also known as population structure, is an essential attribute of a species' biology and a useful tool for resource managers to make informed decisions for the protection and long-term preservation of the species. Among the most severe deteriorations of coral reefs have been recorded in the Caribbean Sea and such biological knowledge from key species could assist stakeholders to construct sound management plans. The population structure of the iconic Caribbean Sea fan, *Gorgonia ventalina* Linnaeus, 1758, was estimated from DNA sequences of the mitochondrial marker MutS Like Homolog protein 1 (MSH1) and the nuclear marker Signal Recognition Particle 54 intron (SRP54). Samples encompassed most of the species' known distribution from Curaçao to Florida, the Lesser Antilles to Panamá, and Bermuda. Analysis of molecular variance revealed a significant amount of population differentiation between the eastern and western Caribbean with the MSH1 gene, however, no such signal was detected with the SRP54 intron. The Old Buoy and Mario reefs of western and southwestern Puerto Rico were the most genetically differentiated among all sites based on the MSH1 gene. Local current patterns at the reef level and low sample sizes are possible explanations for the observed patterns of genetic differentiation. Comparisons with other studies using microsatellites and SNPs, including a study with *G. ventalina* suggests that faster-evolving genomic areas are more appropriate markers for the detection of fine-scale population differentiation in *G. ventalina*.

Key words: mtDNA, soft corals, Puerto Rico, coral reefs, Caribbean Genome Center, population differentiation, MSH1, SRP54

Introduction

Coral reef organisms have shown resiliency throughout geological time (Stanley 2003), but nowadays, they face unprecedented stressors that threaten their survivorship. Climate change, overfishing, intense coastal use, and diseases have drastically changed the abundance and health of coral reef organisms

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(Hughes and Tanner 2000, Petes et al. 2003, Sokolow 2009, Weil et al. 2016). The remaining coral reefs are continuously threatened by one or more of the stressors mentioned above (Hughes et al. 2017).

In the Caribbean Sea, diseases have emerged as a significant stressor of corals and have reshaped the species composition in shallow reefs environments (Aronson and Precht 2001, Cróquer and Weil 2009). Coral cover has been reduced to 40% due to Caribbean-specific disease outbreaks in the last 30 years (Weil et al. 2006). The reduction of essential shallow scleractinian corals, *Acropora palmata* (Lamarck, 1816) and *Orbicella faveolata* (Ellis and Solander, 1786), because of these disease outbreaks (Cróquer and Weil 2009, Weil et al. 2016, Precht et al. 2016) along with the massive die-off of the key herbivore *Diadema antillarum* (Philippi, 1845) (Lessios 2005) characterize almost every Caribbean reef. The rate at which coral reef organisms die has necessitated advances in reef restoration and calls for a better understanding of the significant reef species' basic biology, such as studies on the genetic population structure. Incorporating life history information and genetic connectivity of important reef organisms is crucial for the improved design and management of Marine Protected Areas (MPAs) (Roberts 1997), which, together with science-based restoration efforts and reduction of global and local stressors, can provide the best chance for the recovery of the world's coral reefs. Species with great dispersal potential can cross geographical barriers and country borders; MPA implementations that do not consider the sources of larvae may reduce their effectiveness. Connectivity research that includes the comparison of distant and near populations can control for error and inherent noise in genetic data (Palumbi 2003).

Studies of important scleractinian species have shown that the presence of some oceanographic barriers and reproduction strategies might lead to genetic differentiation over time, separating populations from the western vs. the eastern Caribbean, despite the potential of these reef-building corals for high genetic exchange (Baums et al. 2005, 2006; Severance and Karl 2006; Vollmer and Palumbi 2007). Most connectivity studies target scleractinian corals due to their essential role in forming reefs through calcium carbonate deposition (Van Oppen and Gates 2006). In comparison, fewer studies target octocoral, although in the Caribbean, octocoral communities are the ones visually dominating most shallow reefs (Sánchez et al. 1998, Alcolado et al. 2008, Etnoyer et al. 2010).

Octocoral reef communities in the Caribbean are diverse (Sánchez et al. 1998, 2017), but studies on species identification are often impeded because of high amounts of phenotypic plasticity, often leading to species misidentifications (Yoshioka and Yoshioka 1991). Taxonomic errors by field scientists may have led to an underestimation or overestimation of how much genetic variability species harbor (Wirshing et al. 2005). Recently, studies have focused on quantifying how much genetic divergence exists between different species of octocorals (Sánchez et al. 2003a, b), but only a few studies have estimated the genetic population structure of gorgonians (Coffroth and Lasker 1998, Andras et al. 2013). Coffroth and Lasker (1998) showed that *Plexaura kuna* Lasker, Kim, and Coffroth, 1996 harbor low levels of genetic variability within a reef represented by two or three genets despite a large number of individuals. Smilansky and Lasker (2014) detected genetic structure in the commercially important species *Antillogorgia elisabethae* (Bayer, 1961) in scales less than one meter in 2010. Still, in other sampling years, 2009 and 2011, there was genetic structure in distances of 1000 m or more. Prada et al. (2008) showed that *Eunicea flexuosa* (Lamouroux, 1821) on the southwest coast of Puerto Rico has two distinctive morphologies that can be identified visually as shallow water and deep water morphotypes. The two morphotypes are genetically distinct, despite the ability to exchange genetic material (Prada et al. 2008). Prada and Hellberg (2013) extended the work with *E. flexuosa* in the Caribbean and showed that genetic structure could be found on a depth gradient in several areas of the Caribbean. The timing of spawning in this species plays an essential role as a barrier to reproductive isolation (Prada and Hellberg 2013).

Gorgonia ventalina Linnaeus, 1758 is one of the iconic and most frequently encountered octocoral species in shallow reefs around the Caribbean (Alcolado et al. 2008, Sánchez et al. 1998). In the past 30 years, sea fans have suffered significant mortality due to disease outbreaks of Red Band Disease (RBD), Black Band Disease (BBD) (Bruckner et al. 1997; Weil et al. 2000, 2017; Weil and Rogers 2011), aspergillosis (Nagelkerken et al. 1997; Flynn and Weil 2009; Weil et al. 2009, 2016) and predation by the snail *Cyphoma gibbosum* (Linnaeus, 1758) (Lucas et al. 2014). Sporadic population blooms of *C. gibbosum* have decimated up to 90% of the shallow water octocoral communities (Shäerer and Nemeth 2010). Since 1982, aspergillosis outbreaks have resulted in significant mortalities in *G. ventalina* and *G. flabellum* Linnaeus, 1758 in the southern Caribbean (Guzmán and Cortés 1985, Nagelkerken et al. 1997, Flynn and Weil 2009). An aspergillosis outbreak in 1995 in the leeward Antilles reduced the number of colonies of sea fans by 75% (Nugues and Nagelkerken 2006). Aspergillosis has the longest prevalence of all the diseases affecting *G. ventalina* (Nagelkerken et al. 1997, Petes et al. 2003, Weil et al. 2016); it kills large areas of tissue and affects reproduction (Nagelkerken et al. 1997, Petes et al. 2003, Flynn and Weil 2009). Reproductive effort decreases in a diseased colony and, in some instances, stops (Petes et al. 2003, Flynn and Weil 2009).

The dispersal potential of recruits of *G. ventalina* was once thought to be boundless, but research using microsatellite markers has shown that the lower limit of detecting genetic structure is less than 2 km (Andras et al. 2013). Petes et al. (2003) described briefly that *G. ventalina* is a gonochoric species and presumably a mass spawner, but there is no description of the gametogenesis and spawning period. *Gorgonia ventalina* develops after the larvae spend several days in the water column, then settle and grow perpendicular to the predominant wave current with fan height proportional to the orientation to the prevailing current (Wainweight and Dillon 1969). This research aims to quantify the genetic variability and estimate the Caribbean-wide population connectivity of *G. ventalina* using the mitochondrial marker MutS Like Homolog protein 1 (MSH1), a DNA mismatch repair enzyme homolog, and the nuclear marker Signal Recognition Particle 54 intron (SRP54).

Methods

Sample collection

Tissue samples (5 x 5 cm from each colony) of *G. ventalina* were collected from 2 to 24 widely separated colonies in each of 14 localities around the Caribbean Sea at depths between 5m and 25m using scuba gear (Tables 1, 2). Seven locations were sampled in Puerto Rico (Mona, Desecheo, Vieques, Old Buoy, Black Wall, Romero reef, El Mario reef), four locations in the Lesser Antilles (St. Croix, St. Kitts, Guadeloupe, and Grenada), one location in the leeward Antilles (Curaçao), one location on central Caribbean (Cayman Islands) and one in Bermuda. Samples were stored in 95% ethanol for tissue preservation. Additional tissue samples from Panamá, México, Belize, Bahamas, Florida, Tobago, and Barbados were supplied by Dr. Drew Harvell (Cornell University).

DNA extraction and PCR amplification

DNA was extracted using Qiagen DNeasy Blood and Tissue Kit, and the quality and quantity of DNA were verified with a NanoDrop Spectrophotometer. Two DNA markers were used, the mitochondrial MSH1 gene and the nuclear SRP54 intron. Amplification of MSH1 was accomplished using primers (MSHGventFORW 5'-GGGCTCAGAGGGGAATAGAC–3' and MSHGventREV 5'-ACTCCTAGTGGGCAACAAGC–3') modified from Sánchez et al. (2003a, b) (forward primer ND42599F 5’-GCCATTATGGTTAACTATTAC-3' and reverse primer Mut-3458R: 5’-TSGAGCAAAAGCCACTCC-3'. The amplification protocol began with a denaturation step at 95 °C for 3 min, followed by 35 cycles at 95 °C for 15 sec, 50 ° C for 30 sec, and 72° C for 1 min ending with a final extension step at 72° C for 5 min. Each PCR amplification was done using 12.5µl Biomix PCR reagent, which contained PCR buffer, Mg++, dNTPs, and Taq Polymerase), 1 µl of each primer, 9.5 µl of molecular grade H2O, and 1 µl of DNA with a concentration of 10-20 ng/µl. Amplification of the SRP54 intron was accomplished using primers (CrSRP54f 5’-CGAACTAAAATTAGAAGAAAACGAAG-3' and CrSRP54r 5’-TCATACATGTCTCTCTCAGCGTAAAC-3').

The amplification protocol began with a denaturation step at 95 °C for 5 min, followed by 35 cycles at 95 °C for 30 sec, 60 ° C for 30 sec, and 72° C for 1 min ending with a final extension step at 72° C for 5 min. The PCR solution contained 12.5µl Biomix PCR reagent, 1 µl of each primer, 9.5 µl of molecular grade H2O, and 1 µl of template DNA with a concentration of 10-20 ng/µl. The PCR products were processed with the Big Dye 3.1 Terminator Cycle Sequencing Kit, and the ethanol-precipitated products were sequenced into an ABI 3130xl 96-capillary Genetic Analyzer.

Data Analysis

DNA trace files were imported in CodonCode Aligner for base calling, quality assessment, contig assembly, visualization, and manual editing. Aligned sequences were imported to DnaSP 6 (Rozas et al. 2017) and were grouped based on their geographic location. Unphased genotype data of the nuclear marker were resolved in DnaSP by applying the PHASE v2.1 algorithm (Stephens et al. 2001), which assumes Hardy-Weinberg equilibrium and uses a coalescent-based Bayesian method to infer haplotypes. PHASE assumes that sampled sequences contain all the alleles found in a population; therefore, the more sampled individuals per population, the more accurate the phased alleles will be. An Arlequin file .arp (project file) and .hap (file with all haplotypes) were created through DnaSP for further population analysis in Arlequin 3.5.2.2 (Excoffier and Lischer 2010). The program modelTest-ng (Darriba et al. 2020) was used within raxmlGUI 2.0 (Edler et al. 2021) to estimate the best model of nucleotide substitution for the MSH1 and SRP54 haplotype alignment. All analyses in Arlequin were performed using the Jukes-Cantor (JC) nucleotide substitution model (Jukes and Cantor 1969) for MSH1 and Kimura-2-parameter (Kimura 1980) for SRP54. General statistical analysis, including the estimators of nucleotide diversity π and θ, and DNA neutrality tests [Tajima's D, Tajima (1989); Fu's (1996) Fs] to test for deviation from the neutral model of molecular evolution (Kimura 1968) were estimated in Arlequin.

We also performed a hierarchical analysis of molecular variance (AMOVA) test in Arlequin to test for differentiation between western and eastern Caribbean populations, as previous work has indicated the presence of such population demarcation in diverse marine species (Baums et al. 2005, Galindo et al. 2006, Andras et al. 2013). Previous work has supported the genetic relationship between Florida and Bahamas with the western Caribbean subpopulation together with Panamá and México (Baums et al. 2005). Therefore, we placed sequences from Florida and Bahamas in the western group for each gene. We also tested for genetic differentiation at a Caribbean wide scale by taking a “naïve” approach for the AMOVA design, with all sequences east of Mona Channel and east of the Dutch Antilles allocated to the eastern Caribbean group (i.e., Florida and Bahamas were placed in the eastern group) and similarly, all those sequences west of these locations allocated to the western Caribbean group. The rationale for this design is the variation of population structure in Caribbean coral species (Severance and Karl 2006, Hemond and Vollmer 2010, Mège et al. 2013), and extrapolations from one species to another species without testing is not a sound approach.

The statistical significance of Φ-statistics was assessed against the null hypothesis of panmixia by 10,000 permutations of groups and haplotypes. Population differentiation was estimated using pairwise Φ_{ST}s based on the average pairwise nucleotide differences within and among populations (Weir and Cockerham 1984) as implemented in Arlequin. The Bonferroni correction was used for multiple testing errors in population pairwise F_{ST} comparisons. Haplotype networks based on the parsimony method were constructed with PopART v. 1.7 (Leigh and Bryant 2015). All MSH1 sequences generated in this study have been submitted to GenBank (Accession Numbers OQ798039 - OQ798197). The short sequences of SPR54 are available in the Appendix, on the link to this paper in the website of the journal, and by contacting the authors.

Results

MSH1 gene

A portion of the mitochondrial gene MSH1 (441 bp) was obtained from 159 specimens from 16 locations in the wider Caribbean area (Table 1). Overall, 10 haplotypes were identified from the MSH1 sequences of *G. ventalina*. Most haplotypes (n = 4) were found in Florida and Cayman Island. *Gorgonia ventalina* MSH1 sequences exhibited few polymorphic sites; therefore, most genetic diversity values were close to 0. Overall, the genetic diversity of *G. ventalina* in the sampled region was very low. The nucleotide diversity indices π and θ were very low and similar for all locations, varying from 0.00041 to 0.00265 and from 0.00066 to 0.00285, respectively (Table 1).

The statistical tests Tajima's *D* and Fu's *F*s did not show significant departures from neutrality in any of the locations, except in Grenada for Fu’s *F*s (Table 1). The highest values of π and θ were found in *G. ventalina* at Old Buoy, western Puerto Rico, and Florida, respectively (Table 1). The lowest π and θ values of *G. ventalina* were found in Panamá and Curaçao, respectively (Table 1).

SRP54

An intronic region of the nuclear gene SRP54 (98 bp) was obtained from 197 specimens from 17 locations in the wider Caribbean area (Table 2). Nine unique haplotypes were derived from the sampled locations. *Gorgonia ventalina* exhibited few polymorphic sites in the SRP54 sequences, as expected from this short DNA segment, therefore most genetic diversity values were close to 0.

Similar with the MSH1 gene, the genetic diversity for *G. ventalina* based on SRP54 was low. The nucleotide diversity indices π and θ were similar and low for all locations, varying from 0.00524 (México) to 0.01202 (Desecheo) (Table 2).

Table 1. Location, locality's code, depth, global positioning system coordinates, and summary statistics of *Gorgonia ventalina* based on MSH1 sequences: n, number of samples; H, number of haplotypes; π, nucleotide diversity (standard deviation); θ, nucleotide diversity (standard deviation); Fu's *Fs*; and Tajima's *D*. Boldface indicates significance at $p < 0.05$.

Location	**Code**	**Depth**	**GPS coordinates**	**n**	**H**	**π (s.d.)**	**θ (s.d.)**	**Fu's *Fs***	**Tajima's *D***
Black Wall (Puerto Rico)	BWL	20 m	N17°53'05" W67°0'59"	5	2	0.00182 (0.00181)	0.00217 (0.00172)	1.04042	-0.97256
Old Buoy (Puerto Rico)	OLB	20 m	N17°53'17" W66°59'53"	4	3	0.00265 (0.00252)	0.00247 (0.00199)	-0.65789	0.59158
Desecheo (Puerto Rico)	DSH	20 m	N18°22' 57" W67°28'21"	2	1	0	0	0	0
Mario Reef (Puerto Rico)	MARIO	5 m	N17°57' 8" W67°3' 20"	11	2	0.00116 (0.00119)	0.00077 (0.00077)	1.02256	1.18560
Romero Reef (Puerto Rico)	ROM	5 m	N17°56'54" W66°58'59"	3	1	0	0	0	0
Saint Croix (US Virgin Islands)	STCX	20 m	N17°46'23" W64°48'41"	8	2	0.00057 (0.00081)	0.00087 (0.00087)	-0.18197	-1.05482
Saint Kitts	STKT	5 m	N17°15′ W62°40′	2	1	0	0	0	0
Guadeloupe	GUAD	5 m	N16°15′00″ W61°35′00″	12	2	0.00076 (0.00091)	0.00150 (0.00114)	0.43183	-1.45138
Grenada	GREN	20 m	N12°03′ W61°45′	12	3	0.00114 (0.00117)	0.00225 (0.00148)	-0.61396	**-1.62929**
Tobago	TCB	20 m	N11°11'24" W60°47'23"	14	1	0	0	0	0
Curaçao	CUC	20 m	N12°6'36" W68°58'11"	18	2	0.00083 (0.00094)	0.00066 (0.00066)	0.79606	0.48809
Panamá - Bocas del Toro - Punta Vieja	PAN1	20 m	N9°15'36" W82°7'12"	12	2	0.00069 (0.00086)	0.00075 (0.00075)	0.29736	-0.19492
Panamá- Bocas del Toro - Hospital Point	PAN2	20 m	N9°19'58" W82°12'35"	11	2	0.00041 (0.00065)	0.00077 (0.00077)	-0.40988	-1.1285
Cayman Island	CYM	20 m	N19°20′15″ W81°21′11″	24	4	0.00123 (0.00117)	0.00243 (0.00139)	-1.22537	-1.35652
Florida - Caryfort	FL8	5 m	N25°13'12" W80°12'35"	14	4	0.00180 (0.00155)	0.00285 (0.00169)	-0.92913	-1.22200
Bermuda	BER	5 m	N32°19'48", W64°40'12"	7	1	0	0	0	0

Table 2. Location, locality's code, depth, global positioning system coordinates, and summary statistics of *Gorgonia ventalina* based on SRP54 sequences: n, number of samples; H, number of haplotypes; π, nucleotide diversity (standard deviation); θ, nucleotide diversity (standard deviation); Fu's *Fs*; and Tajima's *D*.

Location	**Code**	**Depth**	**GPS position**	**n**	**H**	**π (s.d.)**	**θ (s.d.)**	**Fu's *F*s**	**Tajima's *D***
Bermuda	BER	5 m	N32°19'48" W64°40'12"	14	3	0.00611 (0.00618)	0.00963 (0.00626)	-0.00748	-0.95732
Bahamas - Lee Stoking Is. - Norman Cay	BAH1	5 m	N23°46'48" W76°7'47"	26	3	0.00935 (0.00745)	0.00802 (0.00507)	1.26676	0.40812
Florida-Caryfort	FL8	5 m	N25°13'12" W80°12'35"	30	3	0.00555 (0.00525)	0.00773 (0.00486)	0.23419	-0.66017
Florida - Sand key	FL1	5 m	N24°26'60" W81°52'12"	28	3	0.00637 (0.00574)	0.00787 (0.00496)	0.46604	-0.45642
Mona – Puerto Rico	MON	20 m	N18° 3'33" W67°51'49"	2	2	0.01020 (0.01443)	0.01020 (0.01020)	0.00000	0.00000
Desecheo – Puerto Rico	DSH	20 m	N18° 22'57" W67°28'21"	10	4	0.01202 (0.00950)	0.01082 (0.00719)	-0.53568	0.39804
Vieques – Puerto Rico	VQS	20 m	N18°04'21 W65°25'11"	22	3	0.00680 (0.00606)	0.00840 (0.00534)	0.42051	-0.49124
Saint Croix – US Virgin Islands	STCX	20 m	N17°46'23" W64°48'41"	24	3	0.00569 (0.00538)	0.00820 (0.0020)	-0.76831	0.12791
Grenada	GREN	20 m	N12°03′ W61°45′	24	4	0.01142 (0.00860)	0.00820 (0.00520)	0.45660	0.98999
Barbados	BAR	20 m	N13°10'12" W59°38'24"	28	3	0.00786 (0.00659)	0.00787 (0.00465)	0.92112	-0.00336
Tobago	TCB	20 m	N11°11'24" W60°47'23"	30	3	0.00866 (0.00702)	0.00773 (0.00486)	1.20469	0.28285
Curaçao	CUC	20 m	N12°6'36" W68°58'11"	24	4	0.00810 (0.00677)	0.0110 (0.00625)	-0.35598	-0.70896
México-Punta Allen	MBR6	20 m	N19°46'48" W87°25'48"	20	3	0.00731 (0.00638)	0.00863 (0.00551)	0.48973	-0.41004
México-Akumal Media Luna	MBR2	20 m	N20°23'60" W87°17'59"	30	5	0.00755 (0.00641)	0.01288 (0.00675)	-1.12808	-1.42276
México - Xcalak Doña Nica	MBR9	20 m	N18°17'24" W87°48'36"	26	4	0.00524 (0.00509)	0.01070 (0.00609)	-1.26720	-1.36199
Panamá-Bocas del Toro - Punta Vieja	PAN1	20 m	N9°15'36" W82°7'12"	28	3	0.01104 (0.00834)	0.00787 (0.00496)	1.76094	0.96867
Panamá-Bocas del Toro - Hospital Point	PAN2	20 m	N9°19'58" W82°12'35"	28	4	0.01055 (0.00808)	0.01049 (0.00595)	0.42105	0.01654

The Tajima's *D* and Fu's *F*s neutrality tests did not show significant departures from neutrality in any of the locations (Table 2). For the SRP54 gene, the highest values of π were found in *G. ventalina* at Desecheo, a small island off the west coast of Puerto Rico, and the highest values of θ at Akumal, Media Luna, México. The lowest values of π were found in the samples from Xcalat Dona Nica, México. Specimens from Tobago and Caryfort, Florida harbored the lowest values of θ (0.00773).

Haplotype Network Analysis (MSH1)

Ten distinct haplotypes (Hap) were derived from the MSH1 dataset (Figure 1). The parsimony network of *G. ventalina* based on MSH1 gene was characterized by a low number of haplotypes and was uninformative (Figure 1, Table 3). Hap 1 and Hap 5 were the most geographically widespread and most numerous of all mitochondrial haplotypes found in *G. ventalina.* Hap 1 was present in all localities sampled. Hap 9 was only present on Old Buoy and Hap 2 was shared between Old Buoy and Black Wall, both reefs are in the insular shelf edge of La Parguera, southwest Puerto Rico. Hap 5 was found in populations in Panamá, the Cayman Islands and Florida. Hap 6 and Hap 10 were only found in Florida and Panamá, respectively.

Haplotype Network Analysis (SRP54)

Nine haplotypes were derived from SRP54 sequences (Figure 2, Table 4). The parsimony network of *G. ventalina* based on SRP54 gene was characterized by a low number of haplotypes and it was uninformative (Figure 2). The network analysis suggested that the most common haplotype of *G. ventalina* was Hap 1. Hap 1, Hap 2, and Hap 3 are the most widespread geographically and most numerous of all haplotypes found in *G. ventalina.* There were some haplotypes present in only certain populations. Hap 4 was found only in Curaçao specimens and haplotypes 6, 7 and 8 only appeared in purple sea fans from México. Hap 9 was only detected in Panamá.

Analysis of Molecular Variance (AMOVA) MSH1

A hierarchical AMOVA test was applied to a total of 16 populations of *G. ventalina* across the wider Caribbean: Panamá (two reefs), Cayman Islands, Bermuda, Florida, Curaçao, Tobago, Grenada, Guadeloupe, St. Kitts, St. Croix, La Parguera (PR, four reefs) and Desecheo (PR), analyzed using MSH1 (Table 5). The 16 populations were allocated to the western and eastern Caribbean groups with Bermuda being a separate group. The two locations in Panamá, and Cayman Islands and Florida formed the western group and the remaining 11 formed the eastern group. As mentioned in the Materials and Methods, we also performed an AMOVA with Florida and Bermuda grouped in the eastern Caribbean.

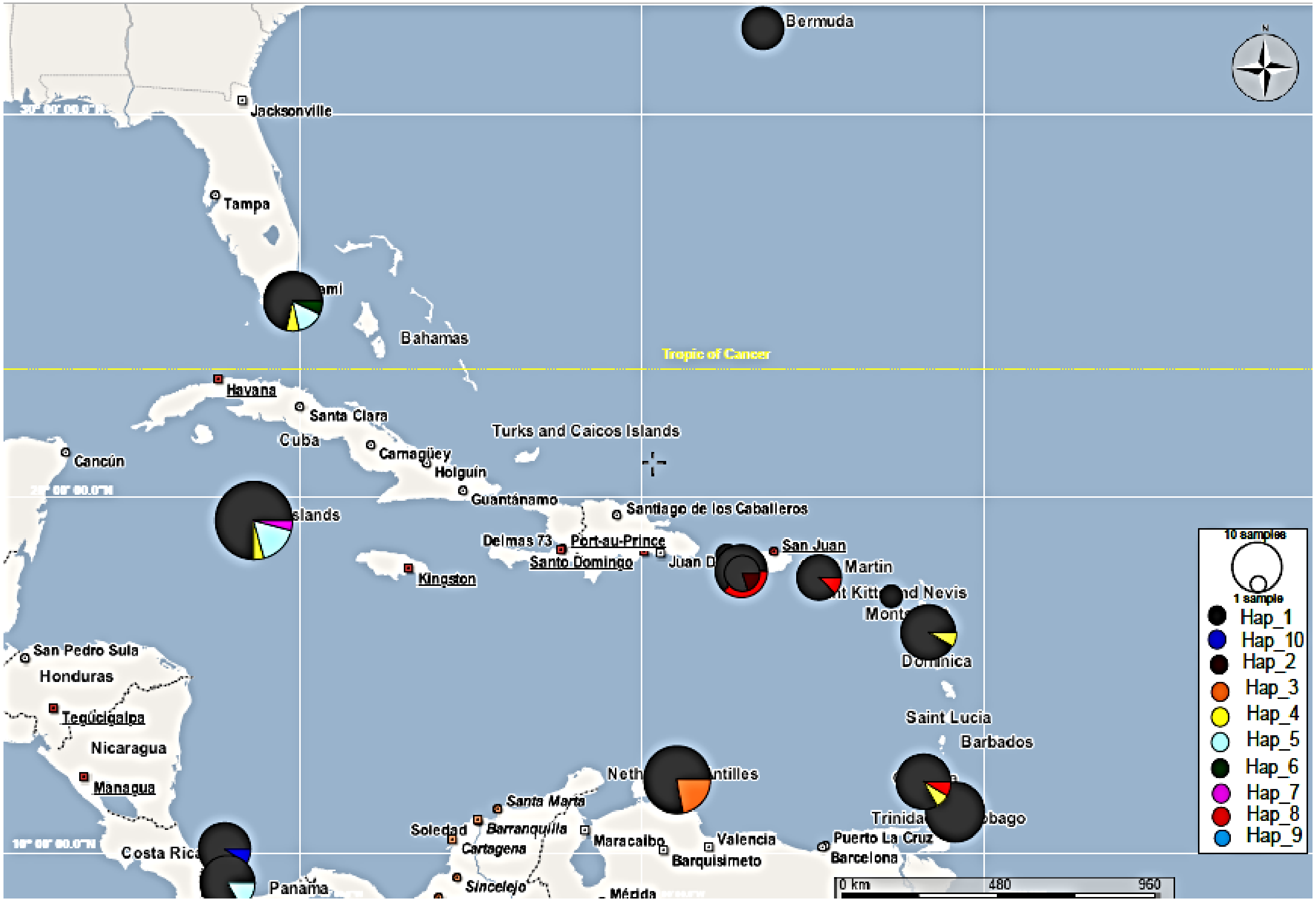

Figure 1. Haplotype network of *Gorgonia ventalina* populations based on MSH1 sequences.

Table 3. Haplotype frequencies in *Gorgonia ventalina* populations based on MSH1 sequences.

Haplotype (n)	Black Wall, Puerto Rico (5)	Mario, Puerto Rico (11)	Romero, Puerto Rico (3)	Old Buoy, Puerto Rico (4)	Desecheo, Puerto Rico (2)	St. Croix, US Virgin Islands (8)	St. Kitts (2)	Florida 8 (14)	Bermuda (7)	Guadeloupe (12)	Tobago (14)	Grenada (12)	Curaçao (18)	Cayman Islands (24)	Panamá 1 (12)	Panamá 2 (11)
Hap 1	4	7	3	1	2	7	2	10	7	11	14	10	14	18	10	10
Hap 2	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Hap 3	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Hap 4	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0
Hap 5	0	0	0	0	0	0	0	2	0	0	0	0	0	4	2	0
Hap 6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hap 7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hap 8	0	4	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Hap 9	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hap 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

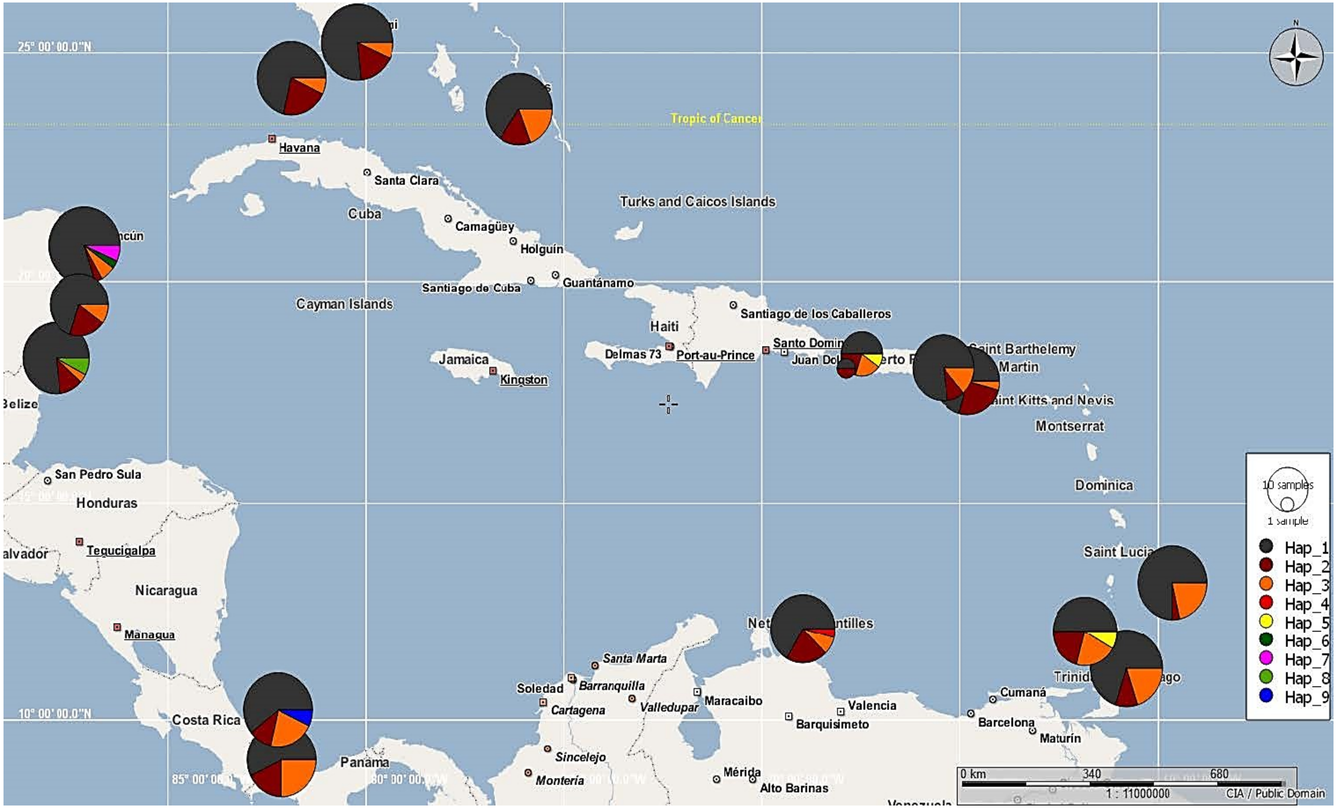

Figure 2. Haplotype network of *Gorgonia ventalina* populations based on SRP54 sequences.

Table 4. Haplotype frequencies in *Gorgonia ventalina* populations based on SRP54 sequences.

Haplotype (n)	Desecheo (10)	Mona, Puerto Rico (2)	Vieques, Puerto Rico (22)	St Croix, US Virgin Islands (24)	Bermuda (14)	Bahamas (26)	Florida 1 (28)	Florida 8 (30)	Grenada (24)	Tobago (30)	Barbados (28)	Curaçao (24)	Panamá 1 (28)	Panamá 2 (28)	México 2 (30)	México 6 (20)	México 9 (26)
Hap 1	5	1	17	17	10	17	20	23	12	21	21	16	16	17	24	14	20
Hap 2	2	1	2	6	3	4	6	5	5	3	1	5	5	3	1	4	3
Hap 3	2	0	3	1	1	5	2	2	5	6	6	2	7	6	2	2	1
Hap 4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hap 5	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Hap 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Hap 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Hap 8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Hap 9	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0

The AMOVA analysis, regardless the partition scheme, yielded a significant estimate of Φ_{ST} for the MSH1 gene (~86 and 87% of variation, $\Phi_{ST} = 0.136$ and 0.129, $p < 0.002$, Table 5) indicating the presence of population differentiation. The among populations, within groups percentage of molecular variance was also significant (~12 and 13% of variation, $\Phi_{SC} = 0.128$ and 0.136, $p < 0.004$). No significant differentiation was observed between the western and the eastern Caribbean groups.

Table 5. Analysis of Molecular Variance (AMOVA) based on MSH1 sequences indicating levels of genetic structure among three groups (Φ_{CT}), among populations within groups (Φ_{SC}), and within populations (Φ_{ST}). The western Caribbean group includes Panamá (2), Cayman Islands, and Florida. The eastern Caribbean group includes all others (Curaçao, Grenada, Tobago, Guadeloupe, St. Kitts, St. Croix, Black Wall, Romero, Mario, Old Buoy, and Desecheo) except Bermuda, the third group. Numbers in parentheses indicate AMOVA results when specimens from Florida and Bermuda were placed in the eastern Caribbean group.

Source of variation	**Degrees of freedom, d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among groups	2(1)	1.232(0.576)	0.00228(-0.00188)	0.99(-0.82)
Among populations within groups	13(14)	6.186(4.145)	0.02915 (0.04253)	12.65(13.71)
Within populations	143(143)	28.457(28.457)	0.19900(0.19900)	86.36(87.12)

Φ_{CT}: 0.00991; P=0.19366, (Φ_{CT}: -0.00822; p = 0.41238)

Φ_{SC}: 0.12777; P=0.00030, (Φ_{SC}: 0.13595; p = 0.00010)

Φ_{ST}: 0.13641; P=0.00119, (Φ_{ST}: 0.12885; p = 0.00089)

Comparisons of population pairwise F_{ST}s indicated that the southwestern reefs of Puerto Rico Maria and Old Buoy were the most differentiated of all locations (Table 6). The biggest differences were observed between St. Croix and Tobago ($F_{ST} = 0.78$). However, after we applied the Bonferroni correction (α /number of pairwise F_{ST} comparisons) to control for multiple testing, none of the pairwise F_{ST}s were significant at the $\alpha = 0.05$.

Table 6. Population pairwise F_{ST}s based on the Jukes-Cantor nucleotide model of substitution. 1: Panamá2, 2: Panamá1, 3: Cayman Islands, 4: Bermuda, 5: Black Wall, Puerto Rico, 6: Curaçao, 7: Desecheo, 8: Florida, 9: Grenada, 10: Guadeloupe, 11: Mario, Puerto Rico, 12: Old Buoy, Puerto Rico, 13: St. Croix, 14: Romero, 15: St. Kitts, 16: Tobago. All negative pairwise F_{ST}s have been converted to 0. Values in bold indicate significance at $\alpha = 0.05$, however, after the Bonferroni correction (α/number of comparisons), none of the pairwise F_{ST}s were significant.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0															
2	0.057	0														
3	0.028	0	0													
4	0	0.028	0	0												
5	0.092	0.096	0.070	0.073	0											
6	0.108	**0.136**	**0.114**	0.077	0.139	0										
7	0	0	0	0	0	0	0									
8	0.048	0	0	0.006	0.041	**0.121**	0	0								
9	0	0.037	0.013	0	0.032	**0.090**	0	0.011	0							
10	0	0.046	0.007	0	0.060	0.099	0	0.011	0	0						
11	0.240	**0.238**	**0.197**	0.230	0.176	**0.265**	0	**0.173**	0.088	**0.209**	0					
12	**0.648**	**0.609**	**0.553**	**0.654**	0.156	**0.619**	0.357	**0.461**	**0.531**	**0.592**	**0.558**	0				
13	0.006	0.047	0.019	0	0.048	0.096	0	0.029	0	0	0.032	**0.582**	0			
14	0	0	0	0	0	0	0	0	0	0	0.091	0.465	0	0		
15	0	0	0	0	0	0	0	0	0	0	0	0.357	0	0	0	
16	0.023	0.109	0.037	0	0.224	0.149	0	0.077	0.013	0.013	**0.340**	**0.780**	0.074	0	0	0

Analysis of Molecular Variance (AMOVA) - SRP54

An AMOVA test was applied to a total of 17 populations of *G. ventalina* across the wider Caribbean: Bahamas, Barbados, Bermuda, Florida (two reefs), Grenada, México (three reefs), Panamá (two reefs), St. Croix, Tobago, Desecheo

(PR), Mona (Puerto Rico), Vieques (Puerto Rico) and Curaçao analyzed using SRP54 (Tables 2, 7).

Table 7. Analysis of Molecular Variance (AMOVA) based on SRP54 sequences indicating levels of genetic structure among three groups (Φ_{CT}), among populations within groups (Φ_{SC}), and within populations (Φ_{ST}). The western Caribbean group includes Panamá (2), México (3), Florida (2) and the Bahamas. The eastern Caribbean group includes all others (Curaçao, Barbados, Grenada, Tobago, St. Kitts, St. Croix, Vieques, Mona and Desecheo) except Bermuda, the third group. Numbers in parentheses indicate AMOVA results when specimens from Florida, Bahamas and Bermuda were placed in the eastern Caribbean group.

Source of variation	**Degrees of freedom, d.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**
Among groups (western vs. eastern Caribbean)	2(1)	0.438 (0.338)	-0.00248 (-0.00076)	-0.62 (-0.19)
Among populations within groups	14(15)	6.835 (6.935)	0.00377 (0.00274)	0.94 (0.68)
Within populations	377(377)	150.700 (150.700)	0.39973 (0.39973)	99.68 (99.51)

Φ_{CT}:-0.00618, P=0.86406;(Φ_{CT}:-0.00189, p = 0.50129)
Φ_{SC}:0.00935, P=0.20604; (Φ_{SC}:0.00682, p = 0.24475)
Φ_{ST}:0.00323, P=0.27584; (Φ_{ST}:0.00494, p = 0.26921)

The 17 populations were allocated to the western and eastern Caribbean groups with Bermuda being a separate group. The locations in México, Panamá, Florida, and Bahamas formed the western group and the remaining eight locations formed the eastern group. Molecular variance analysis of *G. ventalina* indicated that 99.5% of the variation was allocated within populations (Table 7). The analysis yielded a low Φ_{ST} estimate of 0.003 (p = 0.276) and 0.004 (p = 0.269) for AMOVA design with the SRP54 gene, indicating no significant population differentiation among the groups. None of the other Φ statistics were significant, either. No differentiation was detected among the population pairwise F_{ST} comparisons in SRP54 (results not shown) except for Barbados vs. St. Croix (0.10651, p = 0.02277), Grenada vs. México 9 (0.08585, p = 0.03099), St. Croix vs. México 2 (0.06375, p = 0.03564) and México 9 vs. Panamá 1 (0.07934, p = 0.04069). When applied the Bonferroni correction to control for multiple testing, none of these comparisons were significant at the α = 0.05.

Discussion

Gorgonia ventalina MSH1

High levels of genetic similarity were detected among *G. ventalina* from most of the sampled locations. Nunes et al. (2009) suggested that species with immense dispersal potential carry a large amount of genetic diversity that may contribute to the species' resilience. Only 10 haplotypes were recovered from msh1, with Hap1 being the most abundant, comprising 81% of the sequences (Table 3). The other nine haplotypes appeared in 1% to 4% of the sampled populations. The high presence of one haplotype (Hap 1) in all locations with a few private haplotypes that are not very distant from the common one, suggests that *G. ventalina* has recently undergone a population reduction (bottleneck) and is now expanding. Mass mortality events have been reported for *G. ventalina* and its sibling species *G. flabellum* caused by diseases (Guzmán and Cortés 1985, Garzon-Ferreira and Zea 1992) that may have caused a population reduction in the wider Caribbean. Alternatively, this pattern of variation is indicative of under-sampling in some locations since the number of detected haplotypes depends on the number of sequences. Mitochondrial markers have been found to hold low levels of variation in anthozoans (Hellberg 2006). For scleractinian corals, Romano and Palumbi (1997) found low levels of molecular genetic differentiation on sequences of the mitochondrial 16S and COI genes. Medina et al. (1999) discovered the same pattern in sequences of COI in *Orbicella* species. In the genus *Acropora*, Van Oppen et al. (1999) reported low rates of genetic variation between species from the Caribbean and the Pacific using the cytochrome b marker. Genetic studies on octocorals have revealed that Caribbean octocorals follow the same pattern as scleractinian corals with low rates of molecular evolution in mitochondrial markers. France and Hoover (2002) found low levels of genetic variation within species using the COI on deep-sea octocorals. Shearer et al. (2002) pointed out that the within species genetic diversity of MSH1 on octocorals was close to 0%, however, the MSH1 marker has been used successfully to differentiate *Sarcophytum glaucum* from a Pacific reef in Japan into four clades (Aratake et al. 2012). The results of the current study agree with previous studies on octocorals using the same markers. In the Caribbean octocorals the MSH1 marker was used by Sánchez et al. (2003a, b) for phylogenetic analysis and found no significant differentiation between *G. ventalina* and *G. flabellum*. Low levels of molecular variation in the mtDNA have been associated with the Muts-like protein homologs in anthozoans that repair mismatches during DNA replication (Culligan et al. 2000). In soft corals, the use of mitochondrial genes is better suited for barcoding efforts (Morín et al. 2019) or phylogenetic reconstructions (e.g., Sánchez et al. 2021).

Gorgonia ventalina SRP54

The nuclear marker SRP54 also shows high genetic similarity among the sampled *G. ventalina*. Nine haplotypes were obtained with phased sequences, the most common haplotype (Hap 1) comprises 69% of all sequences, and the other common haplotypes were Hap 2 and Hap 3, comprising 14% and 13%, respectively. The AMOVA results (Table 7) showed no significant differences between populations with all the variation observed within populations. Mona Island is strategically placed in the middle of the biogeographic barrier of Mona Channel and SRP54 data provided us with the opportunity to test the affinities of *G. ventalina* to either western or eastern Caribbean. The AMOVA results were similar regardless of Mona placed within the western or the eastern Caribbean groups. The results were inconclusive most likely because of the small sample size and the low genetic variation of the marker. The SRP54 region was used by Concepcion et al. (2007), to detect cryptic species in the snowflake coral *Carijoa* and the gene was proposed as an alternative marker to the nuclear ITS ribosomal region. The SRP54 region was also used in the Xeniidae soft corals for genetic analyses and provided the resolution to distinguish between genera within the family but not to distinguish between morpho-species (Stemmer et al. 2012). Wirshing and Baker (2015) used SRP54 sequences to reconstruct the phylogenetic tree of *Pterogorgia* species to clarify the status of *Pterogorgia* morphospecies found in Saba. The resulting trees supported two primary clades but *Pterogorgia* morphospecies were grouped with *P. guadalupensis* and *P. citrina*. The same marker was used to investigate species boundaries in several closely related species of *Madracis* corals that hybridize but the marker was not a reliable diagnostic character compared to morphological characters (Frade et al. 2010).

Genetic connectivity

Gorgonia ventalina is connected throughout most of the Caribbean, as evidenced by our chosen markers and sampling design. Most of the genetic variation was found within populations with both genes (MSH1 = 87 %, SRP54 = 99.5%). Differentiation was detected using MSH1 mostly at two sites within Puerto Rico: Old Buoy and El Mario reef (Table 6). The pairwise F_{ST} comparisons between Old Buoy and El Mario Reef against several other locations were significant, but no obvious near-shore barrier is known between these sites. Population differentiation patterns stemming from our study suggest both restricted gene flow between reefs in close proximity (e.g., Mario Reef vs. Romero Reef) and extensive gene flow between reefs from the western and eastern edges of the Caribbean (Tobago vs. Panamá), a counterintuitive result. At reefs found in the La Parguera reef system, larval dispersal is likely influenced by the local oceanographic conditions and the geomorphology of individual reefs. Hydrodynamic forces caused by turbulent waters can affect recruitment patterns during larval settlement (Reidenbach et al. 2006) and lead to genetic differentiation between adjacent reefs. Water movement varies within and between reefs and depths in both the fore- and back-reef in La Parguera, adding to the complexity of larval transport (Appeldoorn et al. 1994, Williams et al. 2009) and potentially influencing local patterns and rates of gene flow. Garcia Reyes and Schizas (2010) discovered significant differentiation among reefs in La Parguera for *Acropora palmata,* with linear distances between reefs varying from 1.10 to 8.5 km. The number of samples and suitability of chosen markers was higher in the Garcia Reyes and Schizas' (2010) study, therefore genetic patterns could not be attributed to the experimental design as we suggest in the current study. At larger scales, the potential for a biphasic larva to be transported to other areas of the Caribbean by currents depends on the time spent in the water column before settling to the substrate (Roberts 1997). Duncan et al. (1982) described the current flow changes in a year, the changes in the direction may impact species differently depending on the breeding strategy and the time of the year they set off. Cowen and Sponaugle (2009) explained that for a population to exhibit high rates of genetic connectivity, the larval exchanges between populations have to be frequent enough to make a genetic impact on the receiving population. The lack of information on the dispersive planula stage of *G. ventalina* hinders our understanding of how distant populations interact. The AMOVA tests with MSH1 and SRP54 were designed to test for dispersal at large scales with samples throughout the distribution of *G. ventalina* and did detect differentiation at this geographic scale, albeit with MSH1 only. The SRP54 portion of the intron we analyzed was probably too short to contain enough genetic information to differentiate populations of *G. ventalina*.

On the large, distribution-wide scale, Andras et al. (2013) found that genetic differentiation was positively correlated with geographic distance and some populations of *G. ventalina* were different as near as 2 km from each other. They provided further evidence for a biogeographic break near Puerto Rico into western and eastern populations as well as other unique breaks in the Caribbean (e.g., the Yucatán Channel). Andras et al. (2011, 2013) recognized the importance of all biotic components of the holobiont and examined the signal correspondence between the genetic structure of Symbiodiniaceae and their *G. ventalina* host to address questions of concomitant genetic patterns between the host and the algal symbionts. connectivity patterns in the wider Caribbean. As in *G. ventalina*, the genetic patterns of Symbiodiniaceae were positively correlated with geographic distance and the Mona Channel did play a significant role in dividing the eastern and western Caribbean. Otherwise, the genetic patterns of the photosynthetic algae were somewhat incongruent from those of the purple sea fan host. There was much higher population differentiation in Symbiodiniaceae compared to the host.

The endosymbiotic algae exhibited population structure, broadly differentiating reefs from Mesoamerica, north, northeast, and southeast Caribbean (Andras et al. 2011) whereas in *G. ventalina,* differentiation was broadly observed among Mesoamerican reefs, Florida Keys, Bermuda, Puerto Rico+Bahamas+Curaçao, and east Caribbean (Andras et al. 2013). Both studies were conducted by employing microsatellite markers which provided sufficient variation to detect differentiation at large and small geographic scales. Microsatellite markers have revealed high levels of population structure in another Caribbean gorgonian across the Bahamas, *Antillogorgia* (e.g., *Pseudopterogorgia*) *elisabethae* (Gutiérrez-Rodríguez and Lasker 2004). In contrast, the markers used in the current study revealed genetic similarities across the Caribbean and did not match in sensitivity microsatellite markers to detect population differentiation. For the SRP54 marker, Hap 1, Hap 2, and Hap 3 were present in almost 100% of the localities suggesting high rates of genetic connectivity for the same marker that Concepcion et al. (2008) used to distinguish between cryptic species of the genus *Carijoa*. Stemmer et al. (2012) used SRP54 for the Alcyonacea family Xeniidae and found 25 distinct haplotypes in contrast with *G. ventalina* where we detected only nine haplotypes. The mitochondrial marker MSH1 also showed potentially high rates of genetic connectivity among some locations. For example, the MSH1 Hap 1 is present in all populations and comprises 81% of sequences of all samples. The findings in this study indicate a high realized dispersal potential for *G. ventalina* throughout the sampled region. Alternatively, our choices of molecular markers do not harbor enough genetic information that can be compartmentalized geographically.

The use of faster-evolving genetic regions such as microsatellites or genomic SNPs has been shown to provide the appropriate level of resolution to identify significant population differentiation in common, important Caribbean reef species. Population structure has been uncovered for several reef-building corals (e.g., Baums et al. 2005, 2006, Rippe et al. 2017) and *Gorgonia ventalina* (Andras et al. 2013) across the Caribbean. These studies successfully detected fine patterns of population structure by utilizing microsatellites. More recently, coral studies using SNP data have also been very successful in detecting population structure on fine geographic scale (e.g., Devlin-Durante and Baums 2017; Drury et al. 2017; García-Urueña et al. 2022). Population genomic studies with NGS applications such as RADseq are needed to improve our understanding of the fine- and wide-scale population structure in the iconic purple sea fan. Reproductive and larval development studies would further supplement our understanding of population connectivity in *G. ventalina*. We expect that population genomic studies in soft corals will uncover population structure patterns undetected by more traditional sequencing approaches such as ours.

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Appendix. A list of SRP54 sequences used in this study with acronyms of locations as listed on Table 2. At the end of each sequence name, "-1" and "-2" represent the two phased alleles of a sample. For example, BAH1_501-1 and BAH1_501-2 are the two alleles of specimen BAH1 from Bahamas. The entire list can be found in this link: https://blaypublishers.files.wordpress.com/2023/04/rodriguez-et-al._appendix_leb-103.docx . Readers can request a copy of the data file from the authors.

>BAH1_501-1
AACTAATAGGAAAATTGAAACATGGTAGGTTTTAATAGATTTGATTTTTTTT
GCACTGTACATGTGTACTTGTAATATTTTTTGTACTAAAGCCAAA

>BAH1_501-2
AACTAATAGGAAAATTGAAACATGGTAGGTTTTAATAGATTTGATTTTTTTT
GCACTGTACATGTGTACTTGTAATATTTTTTGTACTAAAGCCAAA

>BAH1_502-1
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GCACTGTACATGTGTACTTGTAATATTTTTTGTACTAAAGCCAAA

>BAH1_502-2
AACTAATAGGAAAATTGAAACATGGTAGGTTTTAATAGATTTGATTTTTTTT
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>BAH1_504-1
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>BAH1_504-2
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>BAH1_505-2
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>BAH1_507-2
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>BAH1_508-2
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>BAH1_510-2
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>BAH1_514-2
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>BAH1_515-2
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>BAH1_516-2
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>BAR_2335-2
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