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REPORT

Phylogeography, population connectivity and demographic history of the Stoplight parrotfish, *Sparisoma viride* (Teleostei: Labridae), in the Greater Caribbean

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Abstract Few genetic studies that provide biological, ecological and evolutionary information have been conducted for parrotfishes, including *Sparisoma viride,* and none has covered the full geographic range of this species. Here, we examine the genetic patterns of the Stoplight parrotfish (*S. viride*) in the Greater Caribbean and its relationship with the recognized biogeographic provinces in the region. Phylogeographic, population and coalescent analyses were performed to examine the genetic structure and connectivity of *S. viride* populations throughout its entire range within the Greater Caribbean. Two mitochondrial (control region and *coxI*) and one nuclear (*RHO*) markers were used. The Stoplight parrotfish shows high haplotypic diversity (h) and low nucleotide diversity (π) in the control region, and low genetic diversity in *coxI* and *RHO*. No evidence of genetic structure was found, indicating a panmictic population throughout the Greater Caribbean with highly symmetrical migration rates among previously defined Caribbean biogeographic provinces. The demographic history estimates indicate events of bottlenecks followed by a population expansion dated at 80,000 years ago (kya) during the Pleistocene epoch. These

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results suggest that the contrasting environmental conditions that define the Greater Caribbean provinces are not barriers to gene flow for *S. viride*. The phylogeographic patterns of Stoplight parrotfish could be associated with the biological characteristics of the species (such as extensive pelagic larval duration and use of multiple habitats), historical demographic events and physical conditions of the Greater Caribbean, promoting the genetic homogeneity of the species in the region.

Keywords Biogeographical provinces · Environmental barriers · Genetic connectivity · Panmictic population · Reef fishes · Sudden demographic expansion

Introduction

Genetic structure and connectivity of reef-fish populations are driven by intricate processes associated with species life history; oceanographic, physical and environmental barriers; and historical process (Pelc et al. 2009; Limborg et al. 2012; Delrieu-Trottin et al. 2017). The barriers to gene flow among marine populations are usually classified as hard barriers—permanent and difficult to cross—such as the Isthmus of Panama and the Arabian Land Bridge, and soft barriers—semi-permeable boundaries that depend on specific environmental and biological circumstances—such as marine currents and contrasting physicochemical water conditions (Cowman and Bellwood 2013). Marine currents may function either as barriers or enhancers of gene flow (Pelc et al. 2009), while environmental factors, such as thermal variation, oceanographic and/or coastal conditions, could promote local adaptation, genetic structure and diversification processes in fish species (Rocha et al. 2005; Limborg et al. 2012; Teske et al. 2019; Sandoval-Huerta et al. 2019). Furthermore, the pelagic eggs and larvae of most coral reef fishes have the potential for widespread dispersal by local currents and gyres (Mora and Sale 2002). In some species, pelagic larval duration is correlated with the dispersal distance capacity (Bradbury et al. 2008), but in other species self-recruitment occurs (Jones et al. 1999), suggesting that other traits, such as the dispersal capability of adults and juveniles and broad environmental tolerance, could influence population connectivity (Luiz et al. 2012). Also, historical factors, such as ancient large-scale climatic fluctuations, are known to leave genetic signatures in contemporary populations (Ravago-Gotango and Juinio-Meñez 2010; DiBattista et al. 2012). The climatic oscillations of the last 2.6 My caused sea level changes associated with glacial and interglacial periods that promoted population contractions during sea level lowering and expansions when sea levels increased (Bard et al. 1990; Blanchon et al. 2009), resulting in cycles of genetic isolation and genetic exchange in reef-fish populations.

The Greater Caribbean (GC) represents the main hot spot of marine biodiversity in the tropical western Atlantic and harbors the highest number of species (814) and genera (150) of Atlantic marine fishes (Briggs and Bowen 2012; Robertson and Cramer 2014). Robertson and Cramer (2014) identified three biogeographic provinces in the GC based on distinctive fish faunas, and noted that there are environmental differences in temperature, nutrient availability and water transparency among the provinces, highlighting the importance of environmental conditions in the distribution of fish species. The three biogeographic provinces are as follows: (1) the northern Caribbean encompassing the Gulf of Mexico and the southeastern coast of the USA up to latitude 33° N, presents heterogeneous habitats, subtropical temperatures, eutrophic environment and low water transparency; (2) the central Caribbean includes the Antilles, Bermuda, the southwestern Caribbean islands and the Central American coast and is characterized by tropical temperatures, oligotrophic environment, high water transparency and abundant coral reef habitats; and 3) the southern Caribbean comprising the northern coast of South America up to latitude 7° N is characterized by tropical temperatures, eutrophic environment, low water transparency, an upwelling-effected area and has limited coral reef habitat (Fig. 1) (Robertson and Cramer 2014). This provincial subdivision matches the genetic structure previously found in some reef fishes (Jackson et al. 2014; Villegas-Sánchez et al. 2014), whereas in others, habitat partitioning, even in local scale, emerged as an explanation of the genetic differentiation (Rocha et al. 2005). In some other GC fish species, genetic discontinuities are associated with oceanographic currents (Taylor and Hellberg 2003, 2006; Eytan and Hellberg 2010) or show genetic patterns of isolation by distance (Puebla et al. 2009), but some species have panmictic populations with high genetic flow (Shulman and Bermingham 1995; Piñeros and Gutiérrez-Rodríguez 2017). However, for many Caribbean fish species, including iconic reef species such as the Stoplight parrotfish, little is known about the impact of biological, ecological and/or historical factors on population genetic patterns.

The Stoplight parrotfish, *Sparisoma viride,* is distributed across the GC (Robertson and van Tassell 2015). It is a protogynous hermaphrodite with two differential phases of coloration in adults (Reinboth 1968) and has an average life of 12 years (van Rooij and Videler 1997; Choat et al. 2003). It produces pelagic eggs, and larvae have a pelagic duration of ~ 47–80 days (Robertson et al. 2006; Robertson and van Tassell 2015). Adults rarely stray from coral reefs, although juveniles are common in sea grass beds (Böhlke and Chaplin 1993; Robertson and van Tassell

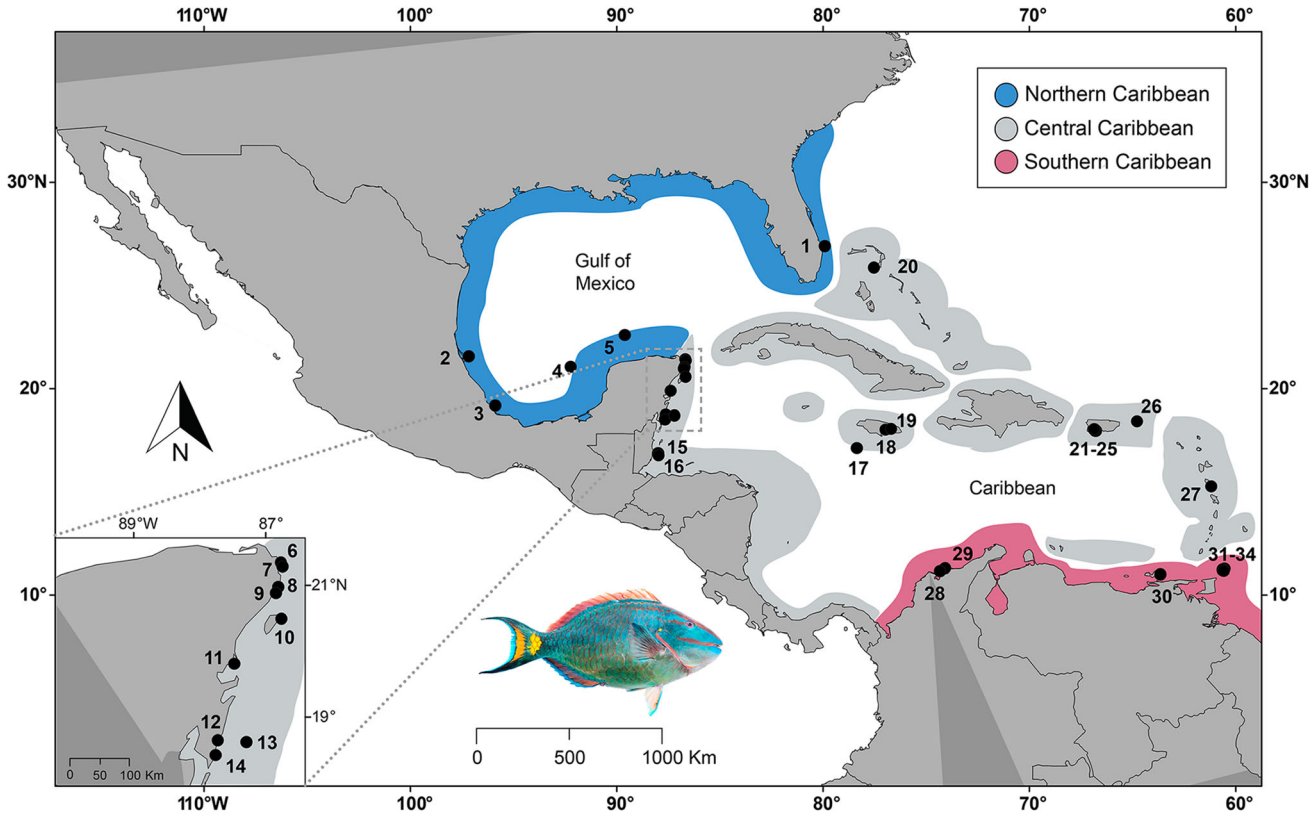

Fig. 1 Map showing collection sites of *Sparisoma viride* in the Greater Caribbean Sea for this study. The biogeographic provinces of Robertson and Cramer (2014) are indicated. Sampling localities of the Northern Caribbean: (1) Phil Foster Park, (2) Isla Lobos, (3) Antón Lizardo, (4) Cayos Sumergidos del Oeste, (5) Arrecife Alacranes. Sampling localities of the Central Caribbean: (6) Isla Mujeres, (7) El Faro, (8) Tanchacte, (9) Puerto Morelos, (10) Cozumel, (11) Punta Allen, (12) Mahaual, (13) Xcalak, (14) Banco Chinchorro, (15) Carrie Bow Cay, (16) Curlew Cay, (17) Pedro Bank, (18) Old Harbor, (19) Hunts Bay, (20) Hoffman Cay, (21) Playa la Jungla, (22) Playa Saila, (23) La parguera, (24) Old Busy, (25) Magueyes, (26) Brewers Bay, (27) Soufriere. Sampling localities of the Southern Caribbean: (28) El Morro, (29) Taganga, (30) Isla Margarita, (31) Arnos Vale beach, (32) Stor Bay, (33) Buccoo Reef, (34) Mount Irvine fish market

2015). The Stoplight parrotfish is a conspicuous element of coral reefs with large population sizes throughout the GC (Choat et al. 2003; Rocha et al. 2012; Hernández-Landa et al. 2014). Ecologically, it plays a key role as a herbivore in the control of macroalgae on Caribbean reefs, which are strong competitors of hard substrates with coral species (Bruggemann et al. 1994a, b; Mumby 2006; McManus and Polsenberg 2004). Currently, *S. viride* experiences exponential growth of commercial and artisanal fishing pressure in recent years (Picou-Gill et al. 1996; Matos-Caraballo et al. 2005).

A previous study using allozymes and RAPDs detected high genetic flow and low genetic structure among *S. viride* populations from five islands in the central and southern Caribbean (Geertjes et al. 2004). However, no previous study has investigated the geographic distribution of genetic variation in *S. viride* at a larger geographical scale to detect population genetic structure, as well as the associated evolutionary, ecological and biological processes. In this research, we used molecular markers with different rates of molecular evolution, mitochondrial DNA (*mt*DNA) and nuclear DNA (*n*DNA), to investigate the phylogeographic patterns in the Stoplight parrotfish in the GC to determine: (1) the distribution of *S. viride* genetic variation and its correlation with the three recognized biogeographic provinces within the GC, (2) the level of genetic connectivity and genetic structure among populations and (3) the influence of relevant historical demographic events. By comparing the results of different molecular markers and using previous information on the life history traits of *S. viride*, we constructed an integrated view of the genetic patterns of the species.

Materials and methods

Sample collections

We obtained samples of 243 individuals from 34 reefs covering the entire geographic distribution range of *S. viride* in the GC (Table S1, Fig. 1). To explore genetic variation across the Caribbean provinces as defined by

Robertson and Cramer (2014), we obtained samples from five reefs in the northern Caribbean (NC), 22 in the Central Caribbean (CC) and seven in the southern Caribbean (SC) (Table S1, Fig. 1). Some samples were captured with the help of fishermen, but most were caught with a hand net during night SCUBA diving and released alive after extracting a tissue sample. We took a fin-clip of each fish and preserved it in 95% ethanol and stored at -76 °C. Tissue samples were deposited in the fish collection of the Universidad Michoacana de San Nicolás de Hidalgo, México; Smithsonian Institution, USA; and Universidad de Puerto Rico, USA (Table S1). The sequences of *coxI* obtained from the Brewers Bay and Soufriere reefs were downloaded from GenBank with accession numbers JQ839594 and JQ839595, respectively (Table S1).

Laboratory procedures

We extracted total genomic DNA using the Phenol–Chloroform protocol (Sambrook et al. 1989). We amplified two *mt*DNA makers: control region (*CR*) and Cytochrome c oxidase subunit I (*coxI*) gene, and the Rhodopsin (*RHO*) *n*DNA gene. The PCR reactions were done in a final volume of 12.5 µl (for primer information and PCR conditions see Table S2). Resulting amplicons were purified with Exosap enzymes (Quiangen, Inc.) and sequenced in Macrogen, Seoul, South Korea.

Sequence alignment and molecular substitution model

Sequences obtained for each molecular marker were visualized, edited and aligned with the software MEGA v7.0.20 (Tamura et al. 2013). The *coxI* and *RHO* sequences were translated to amino acids to verify the alignment and the absence of stop codon. Also, for *RHO* sequences, heterozygotic individuals were identified through point mutation, and the alleles were separated using the PHASE algorithm with the software DNAsp v5.0 (Librado and Rozas 2009). Recombination of the *RHO* gene was analyzed with the phi test in SplitTree4 software (Huson and Bryant 2006), not showing recombination (Phi test P value = 0.95). We deposited all unique sequences in GenBank (accession numbers *coxI:* MT826786-MT826854, *CR:* MT833396-MT833638, *RHO:* MT846942-MT846990).

To determine which substitution model best fit the molecular data, we used the jModeltest v2.1.5 software (Darriba et al. 2012), on the corrected Akaike information criterion (AIC). Analyses were performed independently on each dataset for each molecular marker.

Genetic diversity and haplotype networks

We calculated *mt*DNA and *n*DNA genetic diversity for each reef, biogeographic province and all samples data. Although mitochondrial markers are inherited as a unit, we analyzed *CR* and *coxI* separately due to the large difference in substitution rates of the markers (Messmer et al. 2005). We calculated the number of haplotypes (*Hn*), haplotype diversity (h), nucleotide diversity (π), and number of polymorphic sites (S) in ARLEQUIN v3.5.1.2 (Excoffier et al. 2005). To analyze the genealogical relationships among the haplotypes and their geographic correspondence, we built a statistical parsimony network for each molecular marker using the software PopArt with the Median-Joining algorithm (Bandelt et al. 1999).

Population differentiation

Analyses of molecular variance (AMOVA) were performed to test the genetic differentiation. We pooled the samples into 1) Caribbean biogeographic provinces (Robertson and Cramer 2014), and 2) considering all the samples in a panmictic population. Also, we estimated population genetic differentiation by computing pairwise F_{ST} comparisons between reefs. These analyses were done in the software ARLEQUIN (Excoffier et al. 2005), each one with 1000 permutations to estimate the significance values.

We investigated patterns of isolation by distance (IBD) with Mantel tests using 10,000 permutations in IBDW v3.23 (Jensen et al. 2005). We used linearized F_{ST} ($F_{ST}/(1 - F_{ST})$) (Rousset 1997) pairwise values as genetic distances and we calculated geographic distances between reefs following the GC shoreline, using Google Earth v7.1.2.2041.

Migration estimates

Using the *CR* dataset, we estimated gene flow among the three GC biogeographic provinces (Robertson and Cramer 2014) in MIGRATE v3.6.2 (Beerli and Felsenstein 2001), which calculates long-term effective migration rates (Nm) using a Bayesian coalescent-based MCMC approach. We calculated Nm under a full migration model using 100 short (500,000 genealogies sampled) and four long replicates (20 millions of genealogies sampled) chains after discarding the first 2 million genealogies as burn-in.

Demographic history

We test evidence of historical changes in the demographic equilibrium of the Caribbean biogeographic provinces and across the entire data set for the three molecular markers.

We calculated the test of neutrality Tajima's D (Tajima 1989) and Fu's F_S (Fu and Li 1993) and assessed their significance with 10,000 permutations as implemented in ARLEQUIN. We also computed mismatch distributions and deviations of the observed mismatch distributions from those expected under a demographic expansion model using sum of squares deviations (SSD) and 1000 bootstrap replicates (Schneider and Excoffier 1999). Changes in population size through time were further estimated using a coalescent Extended Bayesian skyline plot (EBSP) approach as implemented in BEAST v1.8.4 (Heled and Drummond 2008). This analysis allows estimation of population size changes over time using a multi-loci approach. For EBSP analysis, one run of 200 million steps was performed, using the HKY substitution model estimated for the *coxI* and *RHO* and HKY + I+G for *CR*, an uncorrelated logarithmic relaxed clock method and ploidy of the markers was set accordingly. The mutation rate used for *CR* ranged from 2×10^{-8} (lower bound) to 5×10^{-8} (upper bound) per site per MY (Bowen et al. 2006a; Mach et al. 2011), for *coxI* ranged from 1×10^{-8} (lower bound) to 2×10^{-8} (upper bound) per site per MY and for *RHO* ranged from 4.5×10^{-9} (lower bound) to 5×10^{-9} (upper bound) per site per MY (Keith et al. 2011). Trees and parameters were sampled every 500 iterations, with a burn-in of 10%. Results were visualized using Tracer v1.7 (Rambaut et al. 2018) to confirm that convergence and stationarity had been reached, and that the effective sample size (ESS) was higher than 200. The plot of the EBSP result was drawn in R v3.5 (R Development Core Team 2011) following the script proposed by Trucchi et al. (2014).

Results

Genetic diversity

The *CR* dataset comprised 243 individuals with a maximum sequence length of 307 base pairs (bp), 48 polymorphic sites and 73 haplotypes. The *coxI* dataset contained 71 individuals with a maximum sequence length of 559 bp, eight polymorphic sites and eight haplotypes. After the PHASE and recombination analyses for 43 individuals, the *RHO* dataset comprised 86 sequences with a length of 822 bp, five polymorphic sites and six haplotypes. The *CR* dataset exhibited the highest values of haplotypic diversity ($h = 0.876 \pm 0.016$) and nucleotide diversity ($\pi = 0.0103 \pm 0.0003$), followed by *coxI* ($h = 0.214 \pm 0.065$, $\pi = 0.0004 \pm 0.0001$) and *RHO* ($h = 0.177 \pm 0.055$, $\pi = 0.0002 \pm 0.00008$), respectively. All genetic diversity indices showed little variation across biogeographic provinces. The highest haplotype diversity was found in the southern Caribbean for *coxI* and in the northern Caribbean province for *RHO* (Table 1; see Table S3 for genetic diversity results by collection site).

Haplotype networks

*mt*DNA and *n*DNA haplotype networks showed no significant overall phylogeographic structure. The *CR* network exhibited a mix of haplotypes of the three Caribbean biogeographic provinces, with the three most common haplotypes widely distributed and connected by few mutations to other low frequencies or unique haplotypes (Fig. 2a). The *coxI* and *RHO* networks presented a star-like pattern, with a central common and widely distributed haplotype connected to rare peripheral haplotypes from different biogeographic provinces (Fig. 2b, c).

Genetic structure and migration estimates

The results of the AMOVA for the three molecular markers did not show significant differences among the Caribbean biogeographic provinces or among sampled locations when the samples were pooled without a priori grouping (Table 2). The highest genetic variation was found within locations (*CR* ranged from 97.27 to 98.09%, *coxI* 98.93 to 100% and *RHO* 99.76 to 100%), with a smaller proportion found among locations (*CR* ranged from 1.62 to 2.73, *coxI* 0 to 1.07% and *RHO* 0 to 024%) (Table 2). The results of F_{ST} comparison of three molecular markers among locations were not significant (Table S4). There were no significant IBD patterns for three molecular markers (*CR*: $r = -0.066$, $P = 0.71$; *coxI*: $r = 0.005$, $P = 0.95$; *RHO*: $r = -0.01$, $P = 0.99$). Migration rates estimated between the biogeographic provinces of the Caribbean were high, and they showed similar numbers of migrants in all directions (range = 4.73×10^4 to 4.11×10^5).

Demographic history

The demographic history results for the *mt*DNA markers were consistent with sudden demographic expansion. For *CR*, Tajima's D values were negative and significant in all cases except for the southern province, while Fu's F_S was negative and significant for the central province and the global dataset (Table 3). The *coxI* data also produced negative values, but they were significant only for the central province and the global dataset in both estimators (Table 3). *RHO* showed negative but not significant values for both indexes (Table 3). Similar results were found in the Mismatch distributions analysis (Fig. S1), where SSD values revealed that the observed distributions did not deviate from those expected under a demographic expansion model (Table 3). EBSP for the multiple loci data sets

Table 1 Genetic diversity estimates of *mt*DNA and *n*DNA markers for *Sparisoma viride* in three Greater Caribbean provinces

Molecular marker	Biogeographic provinces	*n*	*Hn*	*S*	$h \pm$ SD	$\pi \pm$ SD
control region	Northern Caribbean	43	19	20	0.862 ± 0.044	0.0106 ± 0.0062
	Central Caribbean	174	60	61	0.881 ± 0.017	0.0115 ± 0.0065
	Southern Caribbean	26	15	17	0.876 ± 0.057	0.0116 ± 0.0068
	All samples	243	73	48	0.876 ± 0.016	0.0103 ± 0.0003
coxI	Northern Caribbean	18	2	1	0.111 ± 0.096	0.0001 ± 0.0003
	Central Caribbean	39	5	5	0.197 ± 0.084	0.0004 ± 0.0005
	Southern Caribbean	14	4	3	0.395 ± 0.158	0.0007 ± 0.0008
	All samples	71	8	8	0.214 ± 0.065	0.0004 ± 0.0001
RHO	Northern Caribbean	30	5	4	0.308 ± 0.107	0.0004 ± 0.0004
	Central Caribbean	36	3	2	0.109 ± 0.070	0.0001 ± 0.0003
	Southern Caribbean	20	2	1	0.100 ± 0.088	0.0001 ± 0.0002
	All samples	86	6	5	0.177 ± 0.055	0.0002 ± 0.0001

n, number of analyzed individuals. Diversity indices include number of haplotypes (*Hn*), number of polymorphic sites (*S*), and haplotypic (h) and nucleotide (π) diversity with their standard deviations (SD)

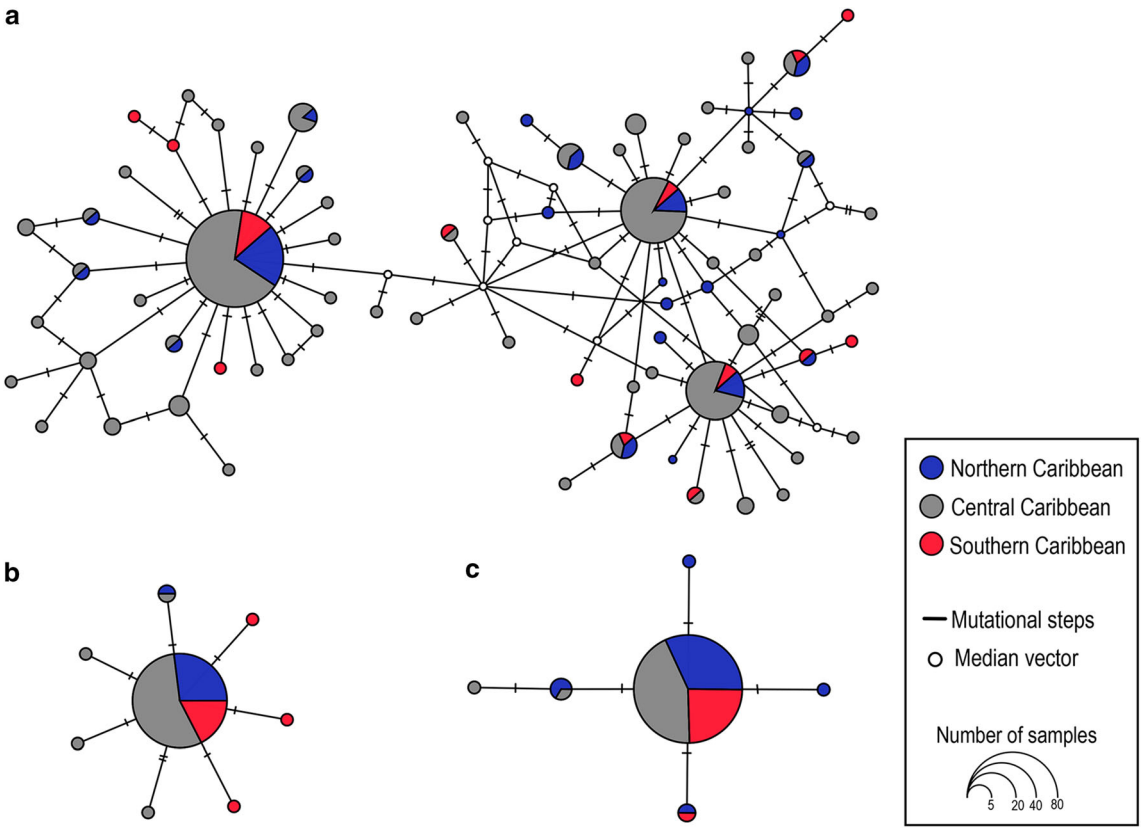

Fig. 2 Haplotype networks for the *mt*DNA markers: **a** control region and **b** the *coxI* gene, and **c** and the *n*DNA Rhodopsin gene (*RHO*). The colors are represented in each biogeographic province in accordance with the legend. The circle size is proportional to haplotype frequency

(*CR*, *coxI* and *RHO*) indicated a sudden increase in the effective population size in the last ~ 80,000 years (Fig. 3).

Discussion

Genetic variation patterns

The phylogeographic history of *Sparisoma viride* within the GC shows high values of haplotypic diversity that

Table 2 Results of the hierarchical analysis of variance (AMOVA) using *mt*DNA and *n*DNA sequences: (a) three genetic groups defined by the three Caribbean biogeographic provinces of Robertson and Cramer (2014); (b) a panmictic population

Genetic groups analyzed	Source of variation	Variation (%)	Fixation index	*P* value
Control region				
(a) Biogeographic provinces	Among biogeographic provinces	− 1.62	Φ_{CT} = − 0.016	0.978
	Among populations within biogeographic provinces	3.52	Φ_{SC} = 0.035	0.053
	Within populations	98.09	Φ_{ST} = 0.019	0.078
(b) Panmictic population (without grouping)	Among populations	2.73	Φ_{ST} = 0.027	0.080
	Within populations	97.27		
CoxI				
(a) Biogeographic provinces	Among biogeographic provinces	1.07	Φ_{CT} = 0.061	0.115
	Among populations within biogeographic provinces	0	Φ_{SC} = − 0.154	0.922
	Within populations	98.93	Φ_{ST} = − 0.084	0.825
(b) Panmictic population (without grouping)	Among populations	0	Φ_{ST} = − 0.111	0.822
	Within populations	100		
RHO				
(a) Biogeographic provinces	Among biogeographic provinces	0.24	Φ_{CT} = 0.012	0.673
	Among populations within biogeographic provinces	0	Φ_{SC} = − 0.057	0.721
	Within populations	99.76	Φ_{ST} = − 0.044	0.832
(b) Panmictic population (without grouping)	Among populations	0	Φ_{ST} = − 0.047	0.829
	Within populations	100		

Table 3 Demographic history of *Sparisoma viride* based on *mt*DNA control region and *coxI* gene markers and *n*DNA *RHO* gene for each Caribbean biogeographic province and the global dataset

Molecular marker	Biogeographic provinces	Tajima's *D*	Fu's *Fs*	SSD
Control region	Northern Caribbean	− 1.912*	− 1.476	0.0126
	Central Caribbean	− 1.907*	− 5.078**	0.0023
	Southern Caribbean	− 0.687	− 0.720	0.0109
	All samples	− 1.912*	− 4.681**	0.0033
CoxI	Northern Caribbean	− 1.165	− 1.612	–
	Central Caribbean	− 2.004*	− 3.546**	0.0110
	Southern Caribbean	− 1.670	− 2.255	–
	All samples	− 2.171*	− 4.049**	0.0091
RHO	Northern Caribbean	− 1.732	− 2.214	–
	Central Caribbean	− 1.284	− 1.083	–
	Southern Caribbean	− 1.164	− 1.648	–
	All samples	− 1.733	− 2.314	0.0190

Demographic history indices include Tajima's *D* test, Fu's *FS* and sum of squares deviations (SSD). A dash (–) indicated where calculations were not possible. *P* values consistent with demographic population expansions are indicate with *($P < 0.01$) and **($P < 0.001$)

contrast with low values of nucleotide diversity for *CR* sequences (Table 1). Similar results were found for several other reef-fish species from Atlantic to Indo-Pacific basins, including other parrotfishes (Dudgeon et al. 2000; Bay et al. 2004; Bowen et al. 2006b; Winters et al. 2010; DiBattista et al. 2012; Horne and van Herwerden 2013; Piñeros and Gutiérrez-Rodríguez 2017). Low genetic diversity values for both *coxI* and *RHO* (Table 2) could be an effect of the lower substitution rates expected for code regions as *coxI* and *RHO* when compared to those for the noncoding regions as *CR* (Lessios 2008; Eytan and Hellberg 2010).

The high genetic diversity found in this study could be related to large effective population sizes (Gyllensten 1985; Frankham 1996). High genetic diversity also has been reported for several other widely distributed marine fish species with large population sizes (Bagley et al. 1999; McCusker and Bentzen 2010). Ecological studies have

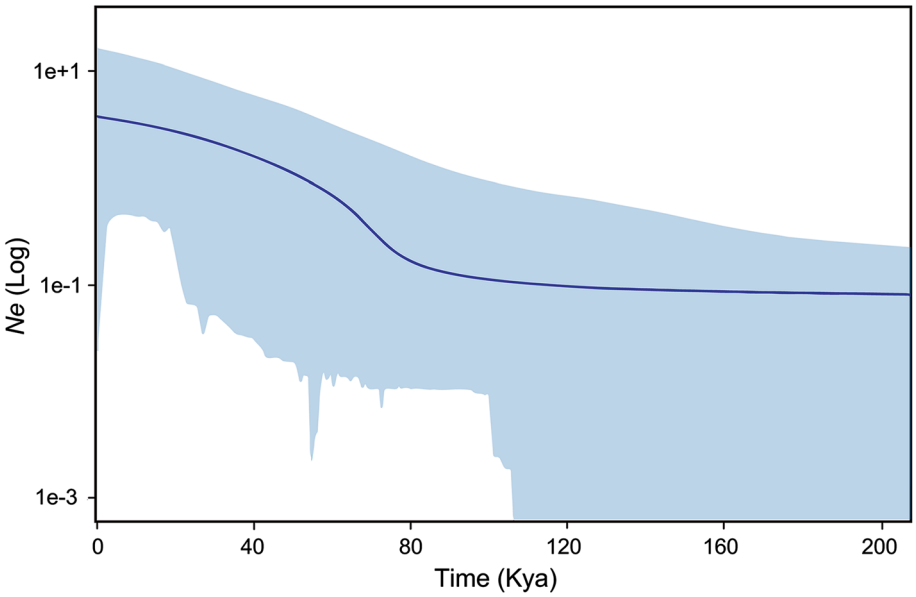

Fig. 3 Demographic history of *Sparisoma viride* estimated by Extended Bayesian skyline plots (BSP) for pooling the entire data sets of multilocus genetic data: the *mt*DNA control region and *coxI* gene markers, and *n*DNA *RHO* gene. The dark blue solid line represents the median effective population size estimates through time, the light blue shade highlights the upper and lower 95% confidence limits. The gray dotted line represents the date when began the population demographic increasing. The *x-axis* shows time in thousands of years ago (kya); the *y-axis* the effective population size (*Ne*) estimated as the log effective population size multiplied by generation time

shown that *S. viride* is one of the most abundant fish species of the GC (Hernández-Landa et al. 2014); for example, an estimated adult population of > 426,000 individuals occur in an area of 32 km^2 of protected coral reefs in Bonaire (Choat et al. 2003). A panmictic population size of millions of individuals of *S. viride* therefore is likely for the entire GC.

Genetic homogeneity through Caribbean biogeographical provinces

The mtDNA and *n*DNA results revealed high connectivity and no genetic differentiation among *S. viride* populations throughout the GC (Table 2, Table S4, Fig. 2). Similar results have been reported in a study that assessed the genetic structure of *S. viride* in a narrower portion of the species' geographic distribution—the Lesser Antilles (Geertjes et al. 2004), as well as in several other Caribbean reef fishes (Shulman and Bermingham 1995; Piñeros and Gutiérrez-Rodríguez 2017), and in numerous fish species inhabiting other oceanic basins (Lessios and Robertson 2006; Horne and van Herwerden 2013), including other labrid species (Dudgeon et al. 2000; Haney et al. 2007; Visram et al. 2010). The high genetic connectivity found for *S. viride* within the Caribbean Sea could be an outcome of the long pelagic larval duration (PLD), which can range from 47 to 80 days, with some individuals exhibiting PLDs over 90 days (Robertson et al. 2006). Long PLDs are usually associated with genetically homogeneous populations in widely distributed species (Waples 1987; Shulman and Bermingham 1995; Bonhomme and Planes 2000). This is in part because species with long PLDs (> 30 days) have high dispersal capabilities conducive to high levels of gene flow, which ultimately may result in panmictic populations (Riginos and Victor 2001; Mora and Sale 2002; Weersing and Toonen 2009). Our results suggest that the long PDL of *S. viride* could be invoked to explain its distribution among all GC provinces. Indeed, the long PLD of *S. viride* also has been used to explain the incipient genetic divergence found between this species and its sister species from the Brazilian coast—*S. amplum* (Robertson et al. 2006).

Another relevant factor that could be responsible for the genetic homogeneity among *S. viride* populations is broad habitat use. Although some labrid species of the genus *Halichoeres* showed population genetic structure attributable to differences between tropical and subtropical Caribbean habitats (Rocha et al. 2005), in general, reef fishes that have broad habitat use tend to have more homogeneous genetic structures than species with narrow habitat use because their ability to occupy different habitats may help them cross geographic barriers and/or persist in newly colonized areas (Rocha et al. 2002; Luiz et al. 2012; Palmerín-Serrano et al. 2020). *Sparisoma viride* is found in several types of tropical marine habitats characterized by different environmental conditions (e.g., different types of algae food supply and shelter habitats) during its different

life history stages (van Rooij et al. 1996a; Eggertsen et al. 2017). Early juvenile stages of *S. viride* (individual size < 5 cm) commonly occur in seagrass beds and mangroves, which are used as nursery habitats (Nagelkerken et al. 2000), and late juvenile stages (individual size < 15 cm) are associated with coral rubble (0–2 m depth) and flat reefs covered with octocorals (4–12 m depth) where they consume epilithic turf algae (Bruggemann et al. 1994a). Adults are usually found associated with dead coral and other types of hard-bottom habitats with a high amount of algal cover and endolithic algae and are distributed to 25 m depth (Bruggemann et al. 1994a, b; van Rooij et al. 1996a, b). Vertical distribution and the use of a diversity of reef habitats and substrates is correlated with a high degree of phenotypic plasticity in different life history phases of *S. viride*, (van Rooij et al. 1996b), rendering it a generalist species like other parrotfishes (Feitosa and Ferreira 2014; Eggertsen et al. 2017). Such marine habitats cover a substantial proportion of the GC shoreline (Robertson and van Tassell 2015), and they could promote a "stepping stone" dispersal mechanism among *S. viride* populations.

Population genetic homogeneity in *S. viride* also may be explained by highly symmetrical rates of genetic migration observed among populations. We estimated rates as high as hundreds of thousands of migrants, which suggest the presence of a single panmictic population widely spread across different Caribbean biogeographic provinces. Our results are in line with the high larval interchange rates previously reported for *S. viride* (Holstein et al. 2014). Highly connected populations have been reported for several other widely distributed Caribbean reef-fish species, including the Redlip blenny (*Ophioblennius atlanticus*), the French grunt (*Haemulon flavolineatum*), the Bluehead wrasse (*Thalassoma bifasciatum*), the Blackbar soldierfish (*Myripristis jacobus*) and the Sergeant major (*Abudefduf saxatilis*) (Shulman and Bermingham 1995; Bowen et al. 2006b; Piñeros and Gutiérrez-Rodríguez 2017). Environmental barriers that help maintain the three GC biogeographic provinces appear to have minimal influence in determining the patterns of gene flow in many reef fishes, including the Stoplight parrotfish.

Sequentially hermaphroditic fishes, like parrotfish, may have more significant potential to exhibit population structure than gonochoric species, mainly because the reduced effective population size in sex-changing species could increase the effect of genetic drift and genetic differentiation (Allsop and West 2004; Chopelet et al. 2009; Kazancioglu et al. 2009). Contrary to this expectation and to patterns of population genetic structure previously reported in some other parrotfish species (Kazancioglu et al. 2009), the Stoplight parrotfish shows no signals of population genetic structure despite being a protogynous hermaphrodite. The high connectivity among the Stoplight parrotfish populations and the large population size could counteract the genetic structure effects associated with sequential hermaphroditism.

Effect of Pleistocene climatic oscillations on the demographic history

The Pleistocene is characterized by dramatic climatic oscillations between glacial and interglacial cycles, which caused severe fluctuations in Caribbean Sea levels and consequently in marine populations. During glacial cycles, the sea level was as much as 120 m lower than it is today, and shorelines have shifted as much as 10–100 km horizontally (Jackson 1992; Greenstein et al. 1998). The resulting fragmentation and decrease of marine reef habitats caused the decline of marine populations, and in some cases triggered local extinctions in reef species (e.g., Siddall et al. 2003; Blanchon et al. 2009). In contrast, during interglacial cycles, sea level rose, increasing the shallow marine habitat coverage and promoting the demographic expansion of reef-fish populations (Bellwood and Wainwright 2003; Delrieu-Trottin et al. 2017). The Stoplight parrotfish inhabits shallow water (1–30 m) and is most abundant in the top 20 m (Hernández-Landa et al. 2014). This species was likely severely affected by the sea level fluctuations during the Pleistocene, experiencing several cycles of genetic isolation and secondary contacts—a processes mirrored by other fish species inhabiting shallow Caribbean reefs (Rocha et al. 2002; Taylor and Hellberg 2006; Piñeros and Gutiérrez-Rodríguez 2017). Population contractions during glacial periods promote extinctions of haplotypes with the consequent loss of the earlier population history, although the loss of genetic information does not necessarily imply strong population bottlenecks. Most species show meta-populations that experience local extinctions and colonization that maintained large population sizes, losing the genetic signal of the demographic drop (Grant 2015). Accordingly, the EBSP shows a constant population of *S. viride* through time with an increase during the late Pleistocene, around 80 kya (Fig. 3). This occurred during the Sangamon/Riss-Würm interglacial period, which was characterized by climatic warming and increased sea level (Bard et al.1990) and the consequent increasing of shallow marine habitat coverage. Although many factors can introduce error in expansion-time estimations of the EBSP analysis (see Grant 2015), our results are concordant with sea level rise and with dates of population expansion found in other reef fishes and coastal benthic organisms (Marko et al. 2010; Winters et al. 2010; Gaither et al. 2011; Horne and van Herwerden 2013; Delrieu-Trottin et al. 2017), including Caribbean fish species (Eytan and Hellberg 2010; Piñeros and Gutiérrez-Rodríguez 2017). Large sample population size, a high

number of molecular markers, and calculating the mutation rate of each molecular marker used for each species under study can improve the accuracy of the dating analysis.

Implications for conservation

The extent of genetic connectivity among marine populations has important implications for the management and conservations of marine resources (Palumbi 2003; Gaines et al. 2010; Green et al. 2015). Ecologically, the Stoplight parrotfish is a key species of Caribbean coral reefs that exhibits high genetic diversity and genetic connectivity across its geographic distribution range, likely indicating high resilience of the species to local population disturbances. In addition, the results of the historical demography analysis showed that *S. viride* was able to recover after historical disturbances, which could be a good indicator of the species' ability resilience in the face of ongoing disruptions to Caribbean reef systems. However, further research that includes high-resolution molecular markers to detect genetic structure in shorter time and finer spatial scales is needed to better understand genetic patterns of *S. viride* populations. Markers such as SNPs would allow estimates of the current genetic flow among populations and inferences regarding overall effects of overfishing and other ocean stressors such as habitat degradation on parrotfish genetic patterns.

In conclusion, our results show that the contrasting environmental conditions of biogeographic provinces in the Greater Caribbean are not an effective barrier to historical gene flow in *S. viride*, suggesting the presence of a highly homogeneous panmictic population across its geographical distribution. The high genetic connectivity found across the Stoplight parrotfish populations seems to be correlated with some of the species' intrinsic characteristics such as a long PLD, its ecological capability to use multiple habitats ontogenetically, and its large population sizes. The climatic dynamics occurring during the Pleistocene promoted the historical demographic expansion of *S. viride* around the Greater Caribbean region.

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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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