



Genetic structure and diversity of the mustard hill coral *Porites astreoides* along the Florida Keys reef tract

Dominique N. Gallery^{1,2,3} · Michelle L. Green² · Ilsa B. Kuffner¹ · Elizabeth A. Lenz^{4,5} · Lauren T. Toth¹

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Abstract

Increases in local and global stressors have led to major declines in coral populations throughout the western Atlantic. While abundances of other species have declined, however, the relative abundance of the mustard hill coral, *Porites astreoides*, has increased. *Porites astreoides* is relatively resilient to some stressors, and because of its mixed reproductive strategies, its populations often recover quickly following disturbances. The ability for *P. astreoides* to continue as a potential “winner” in western Atlantic reefs relies on maintaining sufficient genetic variation within populations to support acclimatization and adaptation to current and future environmental change. Without high genetic diversity and gene flow within the population, it would have limited capacity for adaptation and the species’ competitive advantages could be short-lived. In this study, we determined the genetic relatedness of 37 *P. astreoides* colonies at four shallow reefs along the offshore Florida Keys Reef Tract (FKRT), a region particularly hard-hit by recent disturbances. Using previously designed microsatellite markers, we determined the genetic diversity and connectivity of individuals among and between sites. Our results suggest that the FKRT likely contains a single, well-mixed genetic population of *P. astreoides*, with high levels of gene flow and evidence for larval migration throughout the region. This suggests that regional populations of *P. astreoides* likely have a higher chance of maintaining resilience than many other western Atlantic species as they face current and future disturbances.

Keywords Population genetics · Connectivity · Scleractinians · Coral reefs · Reef resilience · Climate change

Introduction

Coral reefs provide a variety of important ecosystem services including supporting marine biodiversity (Harborne et al. 2006; Pratchett et al. 2014; Fisher et al. 2015), engineering habitat for marine organisms (Mumby et al. 2008; Pratchett et al. 2014), and transferring energy through trophic levels (Moberg and Folke 1999; Woodhead et al. 2019). For example,

coral reefs create complex, coastal geological structures (Moberg and Folke 1999; Spalding et al. 2014; Kuffner and Toth 2016) that can reduce wave energy and decrease erosion and storm damage on reef-lined coasts (Spalding et al. 2014; Storlazzi et al. 2019). With the effects of anthropogenic climate change exacerbating stressors acting on reefs (Hughes et al. 2017; Bruno et al. 2019), global coral cover has declined (Gardner et al. 2003; Bruno and Selig 2007), and this has impaired the ability of reefs to provide key ecological and geological functions (Kuffner and Toth 2016; Perry and Alvarez-Filip 2019).

In the western Atlantic, there have been major shifts in reef composition from dominance of large, reef-building corals, such as *Orbicella* and *Acropora* spp., to small non-reef-building “weedy” corals (Darling et al. 2012; sensu Knowlton, 2001) such as *P. astreoides* (González-Barrios and Álvarez-Filip 2018; Toth et al. 2019; Courtney et al. 2020) and other non-calcifying, benthic-dwelling organisms (Ruzicka et al. 2013; Lenz et al. 2015). There is evidence that shifts from reefs dominated by *Acropora* and *Orbicella* to weedy taxa can result in significant losses in community-wide calcification and reef rugosity (Alvarez-Filip et al.

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✉ Dominique N. Gallery
dgallery@utexas.edu

- ¹ US Geological Survey St. Petersburg Coastal and Marine Science Center, St. Petersburg 33701, USA
- ² University of South Florida, St. Petersburg 33701, USA
- ³ Department of Integrative Biology, The University of Texas at Austin, 78712 Austin, USA
- ⁴ Hawai’i Institute of Marine Biology, University of Hawai’i, Mānoa 96744, USA
- ⁵ Sea Grant College Program, University of Hawai’i At Mānoa, Mānoa 96822, USA

2013; Courtney et al. 2020). Without active and effective local and global management, the decline of the ecological and geological functions of coral reefs could continue into the future (Kennedy et al. 2013; Kuffner and Toth 2016; Perry and Alvarez-Filip 2019).

The Florida Keys Reef Tract (FKRT) has been especially hard-hit by disturbances over the last 50 years. Coral populations on these reefs began declining as early as the 1970s, primarily in response to major coral disease outbreaks and thermal-stress events (Dustan 1977; Precht and Miller 2007; Shinn and Kuffner 2017). By the late 1990s, coral cover on most reefs was <20% (Ruzicka et al. 2013; Toth et al. 2014), and currently, the average coral cover throughout the region is below 5% (Gilliam et al. 2017; Toth et al. 2019). Like many parts of the western Atlantic, coral loss on the FKRT has disproportionately affected reef-building species, which has led to relative increases in non-reef-building taxa (Ruzicka et al. 2013; Toth et al. 2014; 2019; Kuffner and Toth 2016). From 1974 to 1982, a change in the species composition of the scleractinian corals, from the dominance of large reef-building corals like *Acropora palmata* to small short-lived species like *Agaricia agaricites*, *Favia fragum*, and *Porites porites*, was observed in the northern Keys (Dustan and Halas 1987). Subsequent declines in reef-building *Orbicella* spp. corals between 1998 and 2011 also led to relative increases in the abundance of *Siderastrea* and *Millepora* spp. in some locations (Toth et al. 2014). A recent study comparing the modern composition of reefs in the FKRT to the geologic reef framework suggested that recent disturbances have also led to a relative increase in the abundance of the weedy coral *P. astreoides* over the last several decades that is without precedent in the last 8,000 years (Toth et al. 2019). Studies from other locations suggest that the relative abundance of *P. astreoides* has been increasing not just in Florida, but throughout the western Atlantic over the past several decades (Green et al. 2008; Edmunds 2010). Projections based on the population demographics of this species suggest that the relative increase in *P. astreoides* populations will likely continue in this region in the future (Edmunds 2010).

Porites astreoides is sensitive to bleaching and thermal stress (Wagner et al. 2010; Lirman et al. 2011; Colella et al. 2012; Grottoli et al. 2014; Manzello et al. 2015; Dias and Gondim 2016), which results in cascading effects such as impaired calcification (Manzello et al. 2015), photosynthesis (Kemp et al. 2011), and reproductive ecology (Ross et al. 2013). Additionally, Grottoli et al. (2014) reported reduced thermal tolerance in the species following recurring warming events. Rates of bleaching-related mortality are not as high for *P. astreoides* as some other species, however (Lirman et al. 2011, van Woesik et al. 2012), and the impact of bleaching on *P. astreoides* populations can be spatially variable (Lenz et al. 2021). For example, in the US Virgin

Islands, Smith et al. (2013) found limited mortality of *P. astreoides* following a region-wide bleaching event in 2005. The abundance of *P. astreoides* was also observed to have increased in the US Virgin Islands after that event (Smith et al. 2013), which may be a consequence of its ability to recover rapidly from disturbance due to its high fecundity (Bak and Engel 1979; Chornesky and Peters 1987; de Putron et al. 2017).

The relative success of *P. astreoides* has been attributed to multiple factors related to its life history and physiology. *Porites astreoides* has a complex life history, which includes a mixed-breeding system of hermaphrodites and female-only colonies, multiple reproductive cycles throughout the year, and fecundity positively correlated with colony age and size (Chornesky and Peters 1987; de Putron 2003). The size of coral colonies that are simultaneous hermaphrodite brooders is typically smaller at reproductive maturity than broadcast spawning colonies, possibly due to high mortality rates or cessation of growth with age (Szmant 1986). Corals with hermaphroditic brooding reproductive patterns are often referred to as “weedy” corals because they can rapidly recruit to open substrate after a disturbance, but they do not contribute as significantly to the ecological complexity of the reef as larger, broadcasting corals (Knowlton 2001, Darling et al. 2012). *Porites astreoides*’ multiple reproductive cycles per year, coupled with its parental care of offspring due to brooding, large planula larval size, and fast maturation (de Putron et al. 2017; Goodbody-Gringley et al. 2018), may contribute to the increasing dominance of this species following disturbance events (Baumann et al. 2016).

In addition to its resilience to bleaching, *P. astreoides* has been shown to have a relatively high tolerance to other disturbances that have impacted western Atlantic reefs since the 1970s. Resistance to most Caribbean coral diseases has been observed, including stony coral tissue loss disease (SCTLD), an ever-increasing threat to western Atlantic coral reefs that is currently decimating multiple species, especially *Dichocoenia stokesi*, *Meandrina meandrites*, and *Pseudodiploria strigosa* (Precht et al. 2016; Aeby et al. 2019; Gintert et al. 2019; Voss et al. 2019; Dahlgren 2020; Muller et al. 2020). *Porites astreoides* can also survive in waters with low pH, although ocean acidification may negatively impact its growth (Crook et al. 2012) and disrupt its larval settlement (Albright and Langdon 2011). Overall, the resilience of *P. astreoides* to multiple types of disturbances (van Woesik et al. 2012), its ability to acclimate to environmental variability (Kenkel et al. 2013; Kenkel and Matz 2016), and its increasing relative abundance in recent decades (Green et al. 2008; Toth et al. 2019) highlight the important role it will likely play on western Atlantic reefs in the future. The resilience of *P. astreoides* will ultimately depend on its ability to survive the regime of more frequent and intense thermal stress events expected in the future.

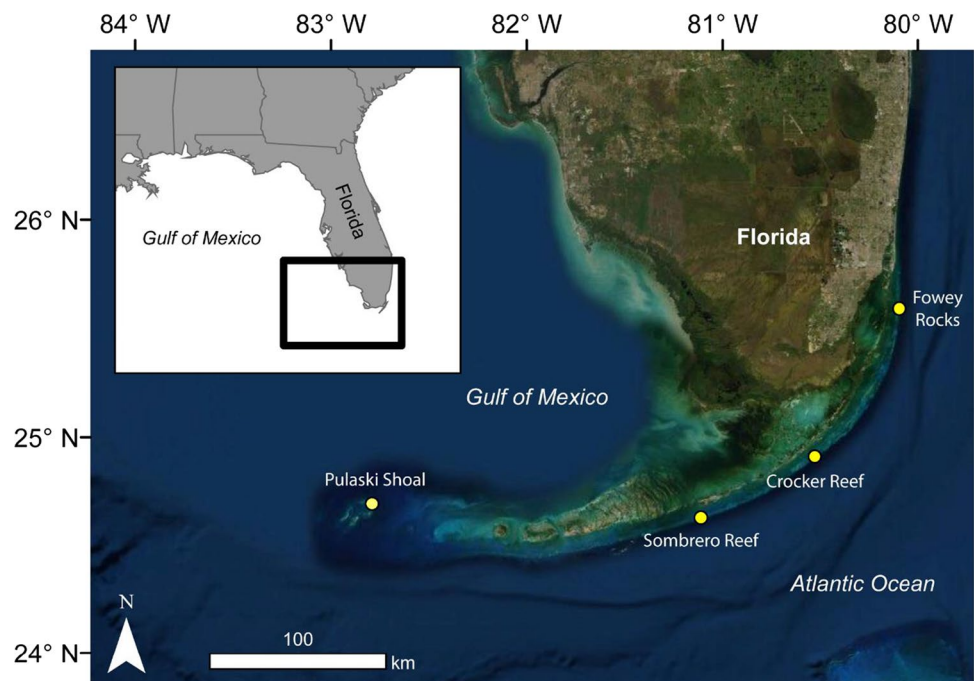
One way to assess the potential resilience of a species to environmental changes is through population genetics (Lacy 1988; O'Brien 1994; van Oppen and Gates 2006; Ouborg 2010; Ouborg et al. 2010; Holstein et al. 2016a). Previous genetic studies have shown that *P. astreoides* has high levels of gene flow, with dispersal distances of over 1700 km throughout the western Atlantic, which has led to genetic exchange spanning from the US Virgin Islands to the FKRT to Bermuda (Serrano et al. 2016). Brooding corals have traditionally been considered to have a high occurrence of asexual reproduction (Brazeau et al. 1998; Gleason et al. 2001), which could significantly reduce their genetic diversity (Herlihy and Eckert 2002; Ingvarsson 2002; Rausch and Morgan 2005); however, more recent studies have shown that inbreeding in brooding corals may be less common than previously thought (Smith et al. 2019). Increasing our current understanding of genetic variability of *P. astreoides* could help predict how populations of *P. astreoides* may respond to climate change and other anthropogenic disturbances in the future. By analyzing select microsatellites of *P. astreoides* collected from four sites throughout the Florida Keys—a subtropical location at the fringe of the species' range—we sought to expand on the findings of Serrano et al. (2016) to further evaluate the genetic relatedness of *P. astreoides* across the FKRT. We used this information to infer the regional genetic diversity and connectivity of *P. astreoides*, its most common reproductive mode, contemporary migration patterns, and how resilient the population is likely to be to future disturbances.

Materials and methods

Sample collection

Four study sites were selected along the Florida Keys reef tract (FKRT): Fowey Rocks in Biscayne National Park (25.59, –80.10), Crocker Reef in the Upper Florida Keys (24.91, –80.53), Sombrero Reef in the Middle Florida Keys (24.63, –81.11), and Pulaski Shoal in the Dry Tortugas National Park (24.69, –82.77) (Fig. 1). In 2015, ten colonies of *P. astreoides* were collected within a 100 to 200 m² area at each site, with individual colonies selected for sampling being no closer than approximately 20 m apart to reduce the probability of sampling clones (Kuffner et al. 2013). After collection, the corals were grown for 2 years (April 2015 to May 2017) on cinderblocks installed on the reef as part of the US Geological Survey calcification assessment project (Kuffner et al. 2013; Morrison et al. 2013). Coral colony condition was assessed and growth rates were monitored every 6 months during the study using the methods outlined in Kuffner et al. (2013; Lenz et al. 2021; data for the *P. astreoides* colonies examined here are presented in Kuffner et al. 2021). Upon completion of the 2 years of calcification assessments, 4-mm-wide sagittal sections (slabs) collected from the center of the colonies with a tile saw were brought to the US Geological Survey in St. Petersburg, FL, where host tissue was sampled for analysis of tissue health, reproduction, and coral-algal symbiont communities for an associated study (Lenz et al. 2021). The remaining live segments of

Fig. 1 Map of the Florida Keys reef tract. Yellow circles mark the offshore reef sites where *Porites astreoides* samples used in this study were collected ($n = 10$ per site): Fowey Rocks in Biscayne National Park, Crocker Reef, and Sombrero Reef in the Florida Keys National Marine Sanctuary, and Pulaski Shoal in Dry Tortugas National Park. Map image is the intellectual property of Esri and is used herein under license. Copyright 2020 Esri and its licensors. All rights reserved



the colonies were returned to the reef sites where they were originally collected and epoxied to the ocean floor.

DNA extraction

Prior to cutting with the tile saw, tissue samples were obtained from a 5 mm² section of the colony using a sterilized razor and placed in a 1% sodium dodecyl sulfate (SDS) DNA buffer solution (Lenz et al. 2021). One sample from Sombrero Reef was eliminated due to death prior to tissue sample collection. Genomic DNA was extracted from the remaining samples using the cetyltrimethylammonium bromide (CTAB) extraction protocol (Baker and Cuning 2016; Putnam et al. 2016). Samples were preserved in 500 µL 1% SDS followed by addition of Proteinase K to each sample. The samples were mixed with CTAB, then added to chloroform in an organic extraction process. Two ethanol precipitations and an ethanol wash were performed to extract purified DNA. Deviations from the CTAB protocol occurred during the SpeedVac steps of the ethanol precipitations and ethanol wash, with ethanol evaporation performed by leaving samples in the hood loosely covered with foil for 2 to 3 h until evaporation was complete. Extracted DNA was stored in a –20 °C freezer. Following extraction, quantification of DNA extracts was performed on a Qubit 3.0 Fluorometer (Life Technologies) following the manufacturer's protocols to quantify the extracted DNA and only samples with a minimum of 150 ng of DNA were used in polymerase chain reactions (PCRs). DNA quality was confirmed visually via gel electrophoresis on a 1.5% agarose.

Microsatellite selection and PCR amplification

Eleven microsatellites were targeted for population genetic analysis of the *P. astreoides* samples using eight PCR primers (Past_2, Past_3, Past_8, Past_10, Past_13, Past_16, Past_17, and Past_21) designed by Kenkel et al. (2013), and three (PaGA 7, PaGA24, and PaGA63) by Shearer and Coffroth (2004). PCR reactions for the microsatellites were amplified individually in 10 µL reactions using the Promega GoTaq Flexi system and included 10 ng of DNA, 1 µM fluorescently-labeled forward primer, 1 µM reverse primer, 0.2 mM dNTP, 2 µL 5X PCR GoTaq Flexi buffer, 0.25 U GoTaq Flexi polymerase, and 2 mM MgCl₂. Thermocycling was performed using a Bio-Rad T100 Thermocycler at the following settings: 1 × 95 °C for 5 min, 35–40 X (95 °C for 40 s, 58–60 °C for 60 s, 72 °C for 60 s), and 72 °C for 10 min (Supplementary Table 1).

Microsatellite analysis

PCR product from the microsatellites was transferred into 96-well plates, with negative controls, and sent to the University

of Illinois Urbana-Champaign (UIUC) Core Sequencing Facility for fragment analysis using an Applied Biosystems 3730xl DNA Analyzer and ROX1000 standards. The resulting microsatellite data, which are provided in (Gallery et al. 2021), were analyzed using GeneMapper software Version 5.0 (Applied Biosystems). Two samples from Fowey Rocks failed to amplify at more than four loci and were eliminated from further analysis. Three of the loci were excluded from analysis for all samples due to low amplification during PCR (PaGA 7, Past_2, Past_17). The remaining eight loci were examined for the presence of null alleles using Genepop software Version 4.7 (Dempsters EM and Brookfield methods) (Raymond and Rousset 1995; Rousset 2008), Cervus software Version 3.0.7 (Kalinowski et al. 2007), and Micro-checker software Version 2.2.3 (Oosterhout, Chakraborty, Brookfield 1 and Brookfield 2 methods) (van Oosterhout et al. 2004). Null alleles were initially found in three primer pairs: Past_3, Past_13, and PaGA 63; therefore, reamplification was performed using lowered annealing temperatures (Supplementary Table 1). Following reamplification and reanalysis for null alleles (Supplementary Table 2), only PaGA 63 consistently showed a high presence of null alleles across all testing methods; therefore, this locus was also eliminated from further analysis.

We used POWSIM Version 4.1 (Ryman and Palm 2006) to conduct a power analysis of our dataset. POWSIM can determine the α (type I error) and β (type II error) of a genotype dataset with a given number of individuals and loci. POWSIM was used to determine the minimum Nei's F_{ST} to provide β power of 0.8 using a chi-squared test and Fisher's exact test (after Ryman and Palm 2006). The R package "diveRcity" (Keenan et al. 2013) was used to calculate the pairwise Nei's F_{ST} for the power analysis.

Genetic diversity and population structure

The presence of clonal variants and probability of identity (PI), the likelihood of two unrelated individuals having identical genotypes, was determined using GenAlEx software Version 6.5 (Peakall and Smouse 2006, 2012). The seven loci that passed initial screening for null alleles were tested for Hardy–Weinberg equilibrium within groups (populations) using Arlequin software Version 3.5.2.2 (Excoffier and Lischer 2010). Hardy–Weinberg equilibrium was tested with two permutations: all sites grouped together and each site individually for a total of 35 tests (7 loci × 4 populations + all sites). FSTAT Version 2.9.4 (Goudet 2003) was used to calculate allelic richness for each of the seven alleles for the four populations and all sites combined. Additionally, FSTAT was used to calculate Nei's estimation of heterozygosity including observed heterozygosity, within-population gene diversity, overall gene diversity, and the amount of genetic diversity among the samples. Nei's genetic distance and genetic identity

Table 1 Results from Hardy–Weinberg equilibrium tests for the seven loci examined in *Porites astreoides* on the Florida Keys reef tract (after removal of the clones at Crocker Reef). N number of individuals, N_A number of alleles, H_{exp} expected heterozygosity, H_{obs} observed heterozygosity, p_{HWE} p values for tests of Hardy–Weinberg equilibrium, $s.d.$ standard deviation of observed heterozygosity. No loci were found to deviate significantly from Hardy–Weinberg equilibrium after Bonferroni adjustment ($\alpha=0.01$)

Population	Locus	N	N_A	H_{exp}	H_{obs}	p_{HWE}	$s.d.$
Fowey Rocks	Past_3	8	7	0.867	0.875	0.655	0.00055
	Past_8	8	7	0.792	0.625	0.088	0.00025
	Past_10	6	8	0.924	0.833	0.088	0.00026
	Past_13	8	5	0.725	0.750	0.425	0.00051
	Past_16	8	5	0.817	0.750	0.298	0.00046
	Past_21	6	5	0.818	0.667	0.030	0.00013
	PaGA 24	8	2	0.233	0.250	1.000	0.00000
Crocker Reef	Past_3	9	8	0.909	1.000	0.033	0.00016
	Past_8	9	6	0.680	0.667	0.148	0.00032
	Past_10	9	9	0.915	0.667	0.017	0.00010
	Past_13	9	7	0.895	0.889	0.877	0.00033
	Past_16	9	4	0.680	0.667	0.587	0.00046
	Past_21	9	7	0.830	0.889	0.397	0.00045
	PaGA 24	8	2	0.125	0.125	1.000	0.00000
Sombrero Key	Past_3	9	7	0.830	0.778	0.250	0.00041
	Past_8	9	6	0.804	0.556	0.075	0.00021
	Past_10	9	9	0.895	0.889	0.884	0.00033
	Past_13	9	6	0.824	0.667	0.066	0.00027
	Past_16	9	5	0.804	1.000	0.928	0.00026
	Past_21	8	7	0.867	0.750	0.656	0.00038
	PaGA 24	8	2	0.125	0.125	1.000	0.00000
Pulaski Shoal	Past_3	10	6	0.826	1.000	0.892	0.00033
	Past_8	10	6	0.737	0.700	0.721	0.00042
	Past_10	10	10	0.895	0.900	0.499	0.00048
	Past_13	10	7	0.847	0.900	0.698	0.00044
	Past_16	10	5	0.816	0.900	1.000	0.00000
	Past_21	10	7	0.642	0.800	1.000	0.00000
	PaGA 24	10	2	0.268	0.300	1.000	0.00000
All sites	Past_3	36	9	0.852	0.917	0.002	0.00005
	Past_8	36	12	0.765	0.649	0.152	0.00019
	Past_10	34	18	0.921	0.824	0.042	0.00012
	Past_13	36	10	0.848	0.806	0.030	0.00016
	Past_16	36	5	0.792	0.833	0.682	0.00048
	Past_21	33	11	0.821	0.788	0.664	0.00030
	PaGA 24	34	3	0.190	0.206	1.000	0.00000

were calculated with GenAlEx (Peakall and Smouse 2006, 2012).

For each site where the corals were collected, the inbreeding coefficient of individuals within each subpopulation (F_{IS}), the measure of population substructure (F_{ST}), and the overall inbreeding coefficient (F_{IT}), collectively known as the F-statistics, were determined using Arlequin. Arlequin was also utilized to test genetic differentiation and genetic distance among sites. Genetic differentiation among each population was calculated with analysis of molecular variance (AMOVA), and genetic distance was calculated via pairwise comparisons of F_{ST} values. Locus by locus AMOVA and locus by locus F-statistics were also analyzed.

Population structure within the FKRT was modeled after omitting clones to assess the number of potential genetic populations (K) from one to ten using Structure software Version 2.3 (Pritchard et al. 2000). Ten replicates for each K value were run with a burn-in of 100,000 and run lengths of 1,000,000 Markov chain Monte Carlo (MCMC) repetitions. An admixture model with no assumption of subpopulations based on sample location (LOCIPRIOR) and allele frequencies correlated was assumed for testing K values of one through ten. Structure results were analyzed for $L(K)$ and ΔK and visualized with Structure Harvester on the web v0.6.94 (Earl and vonHoldt 2012) using the Evanno method (Evanno et al. 2005). Because the minimum number of populations that can be detected using the Evanno

Table 2 Overall allelic richness and Nei's estimate in heterozygosity results from FSTAT (a program), FSTAT Version 2.9.4 for the seven loci examined in this study. AR allelic richness, H_O observed heterozygosity, H_S within-population gene diversity, H_T overall gene diversity, D_{ST} amount of gene diversity among samples

Locus	AR	H_O	H_S	H_T	D_{ST}
Past_3	5.982	0.913	0.854	0.852	-0.002
Past_8	5.372	0.637	0.760	0.767	0.007
Past_10	8.319	0.822	0.913	0.924	0.011
Past_13	6.286	0.801	0.824	0.846	0.022
Past_16	4.602	0.829	0.776	0.792	0.016
Past_21	5.611	0.776	0.790	0.821	0.032
PaGA 24	1.880	0.200	0.187	0.185	-0.002
Overall	—	0.711	0.729	0.741	0.012

method is two, StructureSelector (Li and Liu 2018) was also used to calculate the most likely number of populations using the Puechmaille method (Puechmaille 2016). The Puechmaille method employs four methods for calculating the number of populations: the median of medians (MedMed), the maximum of medians (MaxMed), the median of means (MedMean), and the maximum of means (MaxMean) (Puechmaille 2016). The method controls for the splitting of geographical populations, by limiting the membership coefficient threshold between 0.5 to 0.8, ensuring that each geographical population cannot belong to more than one cluster (Puechmaille 2016). Because the minimum threshold of 0.5 resulted in two different estimates of K , we increased the threshold to 0.51 so that all four methods resolved the same K value (Puechmaille 2016). Admixture bar graphs of Structure results were generated with StructuRly Version 0.1.0 (Crisuolo and Angelini 2020). The population structure of the subpopulations was visualized by ordinating the microsatellite data using a Principal Component Analysis (PCA) plot using the R Version 4.0.0 statistical software (R Core Team 2020). Contemporary migration movement between populations was analyzed with BayesAss Version 3.04 (Wilson and Rannala 2003) with a burn-in of 1,000,000, 10,000,000 MCMC iterations, and 1000 sampling intervals.

Results

Power analysis

The α error calculated for this study was 0.018 (χ^2) and 0.046 (Fisher's exact test), which indicates that the risk of false positives is less than 5%. The β power analysis (Supplementary Fig. 1) indicates that the minimum threshold of power needed to detect differentiation in Nei's F_{ST} values is 0.020. Nei's pairwise F_{ST} values (Supplementary Table 3)

Table 3 Matrix of Nei's genetic distance (above diagonal) and Nei's genetic identity (below diagonal) calculated with GenAlEx. Low values of genetic distance and high values of genetic identity indicate that pairwise populations are genetically similar due to genetic mixing between the four sites across the Florida Keys reef tract: Fowey Rocks (FWY), Crocker Reef (CRK), Sombrero Reef (SMK), and Pulaski Shoal (PLS)

Population	FWY	CRK	SMK	PLS
FWY	—	0.250	0.192	0.158
CRK	0.779	—	0.199	0.315
SMK	0.825	0.820	—	0.191
PLS	0.854	0.730	0.826	—

met this threshold in all but one pairwise comparison: Fowey Rocks and Pulaski Shoal. Therefore, comparisons between these two populations may be underpowered and not fully represent the potential genetic diversity and variation that is present. Overall, however, these results suggest that despite the relatively low sample size in our study, we had sufficient power to make general inferences about the genetic structure of populations of *P. astreoides* in the Florida Keys.

Presence of clones

Two *P. astreoides* colonies of 37 sampled at the four FKRT sites were potential genetic clones, representing approximately 2.7% clonality in the population. The clones were both samples from Crocker Reef. Probability of identity (PI) analysis of microsatellite markers at seven loci was extremely low, ranging from 1.1×10^{-7} to 2.3×10^{-7} , which indicates that the probability of misidentifying clones is low and that two individuals from Crocker Reef with identical genotypes are truly clones.

Hardy–Weinberg equilibrium

Of the 35 permutations of Hardy–Weinberg Equilibrium (HWE) tests that were run once the data for the clones at Crocker Reef were removed, none showed significant deviations from HWE (Table 1; Bonferroni-corrected $\alpha=0.01$). Prior to clone removal, Crocker Reef was found to have two loci outside of HWE, Past_3 and Past_10, which is likely due to the presence of a clone at that site. Because clones are indicative of non-random mating, deviations from HWE at the location with clonal presence are expected (Stoddart 1984).

Genetic variation

Overall allelic richness and Nei's estimates in heterozygosity (Table 2) show that the PaGA24 locus has lower diversity compared to the other 6 loci. The other loci have

comparatively higher allelic richness (4.602 and greater), within-population gene diversity (0.760 and greater), and overall gene diversity (0.767 and greater). Pairwise measurements of Nei’s genetic distance, which estimates the divergence between the populations, and Nei’s genetic identity, which estimates the similarity between populations (Table 3), indicate that there is likely little differentiation among populations in the FKRT.

Genetic differentiation was further analyzed with AMOVA locus by locus (Supplementary Table 4) and averaged with Arlequin. Percent variation among populations and among individuals was low—2.41% and 1.62%, respectively—and the percent variation between individuals was 95.97% (Table 4), indicating high levels of gene flow in *P. astreoides* throughout the FKRT. Overall, the results from our statistical analyses suggest that there is little genetic differentiation among the four sites, indicating panmixia of the populations throughout the FKRT. Pairwise F_{ST} estimates suggest no significant genetic distance between Fowey Rocks, Crocker Reef, Sombrero Reef, and Pulaski Shoal (Table 5); however, we reiterate that we may not have had sufficient power to definitively conclude that there is no differentiation between the populations of *P. astreoides* at the two geographic endmembers of our study: Fowey Rocks and Pulaski Shoal. Fixation indices (Table 6, Supplementary Table 5) also support the conclusion that there are low levels of genetic differentiation between populations, as well as low levels of inbreeding. F_{IS} and F_{IT} , the inbreeding coefficients of individuals within subpopulations and the total population, respectively, which can range from 0 to 1, were both low—0.017 and 0.024, respectively—suggesting

Table 4 Analysis of molecular variance (AMOVA) results from analysis of *Porites astreoides* population structure using number of different alleles among populations, among individuals, and between individuals. SSD sums of square deviations. V_a , V_b , V_c , V variance components. %V percentage of variation

	AMOVA results	Average
Among populations	SSD	11.006
	V_a	0.063
	%V	2.413
	p value	0.710
Among individuals	SSD	80.564
	V_b	0.042
	%V	1.619
	p value	0.309
Between individuals	SSD	80.000
	V_c	2.506
	%V	95.967
	p value	0.111
Total	SSD	179.570
	V	2.611

Table 5 Pairwise F_{ST} values for each of the four *Porites astreoides* populations excluding clones from Crocker Reef (CRK), which indicate the degree of genetic differentiation between populations. Populations are from four sites across the Florida Keys reef tract: Fowey Rocks (FWY), Crocker Reef (CRK), Sombrero Reef (SMK), and Pulaski Shoal (PLS). No values were statistically significant ($p < 0.05$). p values were calculated with Arlequin Version 3.5.2

Population	FWY	CRK	SMK	PLS
FWY	0.000			
CRK	0.029	0.000		
SMK	0.017	0.030	0.000	
PLS	−0.003	0.031	0.003	0.000

that inbreeding is uncommon on the FKRT. F_{ST} , the overall genetic divergence of subpopulations within the total population, was 0.040, which is well below the 0.150 threshold that would indicate significant genetic differentiation among subpopulations (Wright 1978; Frankham et al. 2002; Hartl and Clark 2007).

Population substructure

The highest mean log-likelihoods, $L(K)$, from the population structure analysis, were for a single population ($L(K) = -897.51 \pm 0.64$) or two populations ($L(K) = -899.81 \pm 1.99$), with the mean of the log-likelihoods decreasing and standard deviation increasing significantly after that point (Fig. 2a). Similarly, ΔK , (Fig. 2b) which peaks at the likely true value of K (Evanno et al. 2005), was the highest at $K = 2$. However, ΔK cannot be calculated for $K = 1$; therefore, other methods must be utilized to determine if there were more likely one or two genetic populations. Utilizing the Puechmaille method, StructureSelector indicated a $K = 1$ for MedMed, MaxMed, MedMean, and MaxMean, which suggests there is a single population throughout the Florida Keys (Fig. 2c, Supplementary Table 6). StructuRly bar graphs (Fig. 2d and e) show relatively even structure between $K = 2$ and $K = 3$ populations. The PCA indicates that while some genetic variability

Table 6 Average fixation indices for *Porites astreoides* using number of different alleles. F_{IS} is the inbreeding coefficient due to the inbreeding of individuals within subpopulations. F_{IT} is the inbreeding coefficient due to the inbreeding of individuals in the total population. F_{ST} is the amount of genetic differentiation among the subpopulations in relation to the total population

F-statistics	Average
F_{IS}	0.017
p value	0.309
F_{IT}	0.024
p value	0.710
F_{ST}	0.040
p value	0.111

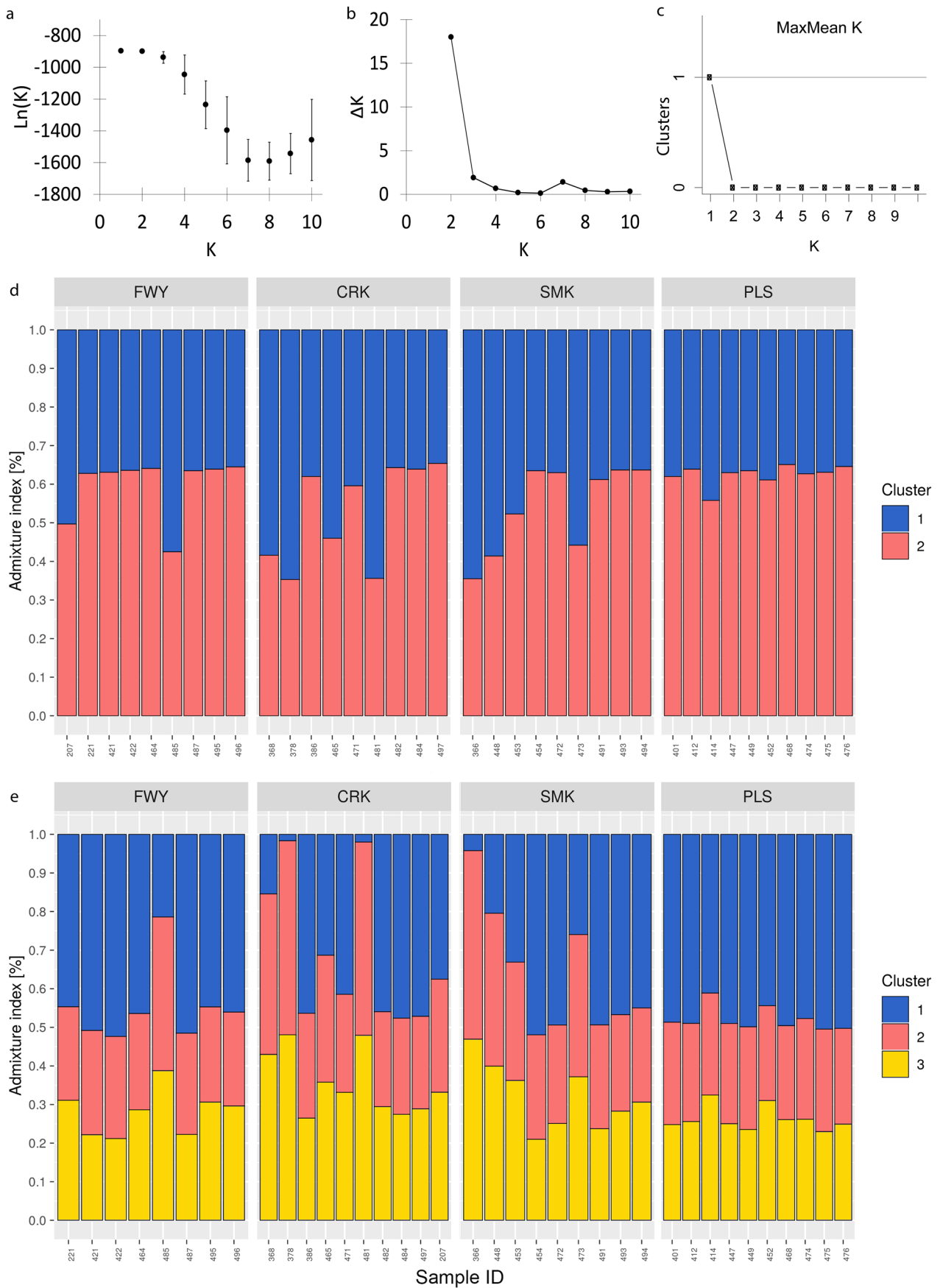


Fig. 2 Structure Harvester, StructureSelector, and StructuRly 0.1.0 analysis results of the number of potential populations (K) for $K=1-10$; **a** Mean natural log-likelihood of K ($L(K)$) with the error bars indicating standard deviation among replicates ($n=10$ for each K value). As K reaches the actual value, the mean natural log-likelihood peaks and the uncertainty are minimized; once K has passed, the true value log-likelihood decreases, and variance increases in simulations; **b** ΔK peaks at the actual value of K ; however, ΔK cannot be computed for one population. Therefore, other analyses must be performed to determine whether this is one or two populations (see the “Population substructure” section); **c** MaxMean K calculated using the Puechmaille method (Puechmaille 2016), which indicates a single genetic population (threshold=0.51); **d** Admixture bar plot with two populations; **e** Admixture bar plot with three populations. FWY = Fowey Rocks, CRK = Crocker Reef, SMK = Sombrero Reef, and PLS = Pulaski Shoal. Cluster refers to the inferred genetic breakdown on the population calculated by Structure software Version 2.3 (Pritchard et al. 2000)

among sites exists, with individual outliers from Crocker Reef and Pulaski Shoal, there is a clear genetic overlap among all four sites (Fig. 3). The aggregate of these results suggests that the actual number of genetic populations on the FKRT is most likely one; however, given our relatively low power, we cannot definitely rule out the possibility of more than one population.

Migration

Contemporary migration rates between the four sites were assessed with BayesAss Version 3.04 (Table 7). Of the twelve pairwise comparisons made, five showed migration rates over 10%: migration from Fowey Rocks to Crocker Reef (14.5%), from Crocker Reef to Fowey Rocks (11.4%), from Fowey Rocks to Sombrero Reef (14.6%), from Sombrero Reef to Fowey Rocks (10.9%), and from Sombrero Reef to Pulaski Shoal (22.4%).

Discussion

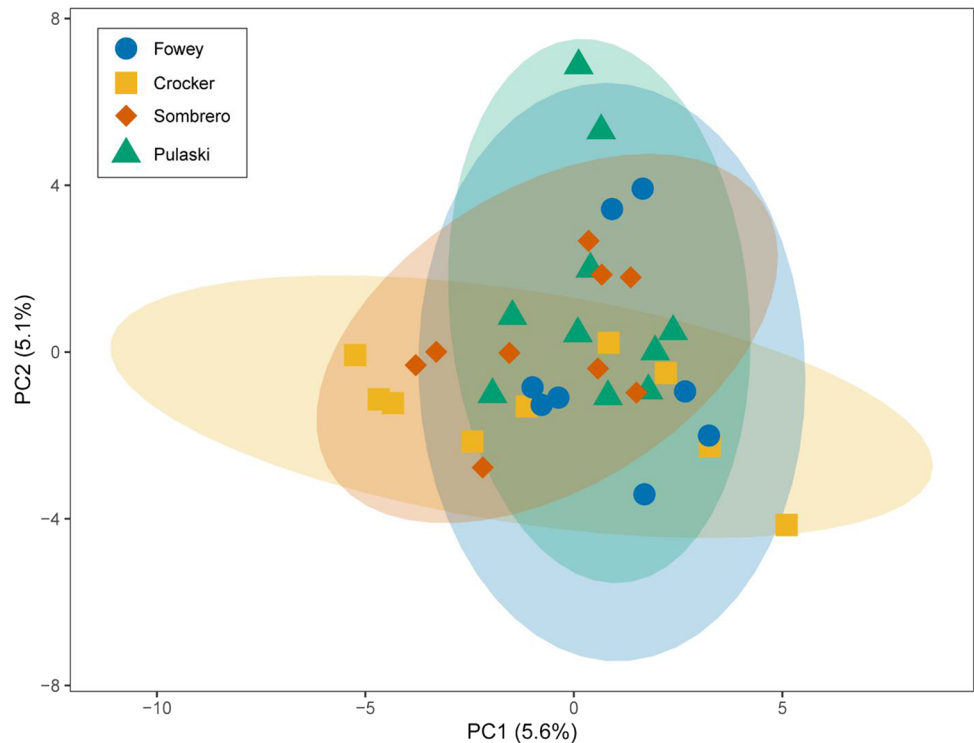
The relative success of *P. astreoides* populations in the Florida Keys and other western Atlantic locations in recent years (Green et al. 2008; Toth et al. 2019) suggests that this species has been a winner in the face of anthropogenic disturbances thus far. The continued ability of *P. astreoides* to provide live-reef habitat as disturbances increase and intensify (Hughes et al. 2017; Bruno et al. 2019), however, depends on its genetic diversity, which is the baseline requirement for resistance and resilience to future disturbances (Cardinale et al. 2012; Madin et al. 2016). Brooding, hermaphroditic corals, like *P. astreoides*, are at potential risk for self-fertilization (Brazeau et al. 1998; Carlon 1999; Gleason et al. 2001; Baums 2008) and inbreeding through related outcrossing (Carlon 1999). Although these reproductive strategies may contribute to the species' overall success, they can also

contribute to loss of genetic diversity over time (Woolsey 2012). A recent study of another brooding coral, *Pocillopora acuta*, suggested that sexual reproduction in brooding corals increases in prevalence as the density of the species increases (Smith et al. 2019). Therefore, the potential risks of inbreeding in *P. astreoides* will likely depend on its resilience and reproductive success, now and in the future. If the species does experience high amounts of inbreeding, the recent, relative population increases may only be a short-term gain with long-term evolutionary costs, possibly including reduced population fitness and inbreeding depression (Pekkala et al. 2014).

Inbreeding can cause adverse effects on reproductive fitness (Latter and Robertson 1962; Crnokrak and Roff 1999), loss of genetic diversity (Hedrick and Kalinowski 2000; Huisman et al. 2016), and higher risk of extinction (Lande 1994; Frankham 1995). Due to this increased extinction risk and the reduced capacity to adapt to environmental fluctuations (Bakker et al. 2010), measuring and monitoring inbreeding depression are of utmost concern for conservation biologists (Hedrick and Kalinowski 2000; Brook et al. 2002). We found, however, that the inbreeding coefficients, F_{IS} and F_{IT} , for *P. astreoides* on the FKRT were extremely low (0.017 and 0.024, respectively). While our findings counter previous predictions and observations of high inbreeding for this species due to selfing (Brazeau et al. 1998; Carlon 1999; Gleason et al. 2001; Baums 2008), our results corroborate Serrano et al. (2016), who also concluded that inbreeding of *P. astreoides* was uncommon throughout the western Atlantic.

We found 2.7% clonality in the population of *P. astreoides* on the FKRT. This is substantially lower than the level of clonality reported by Serrano et al. (2016), which was 12.4% in shallow Florida Keys reefs and approximately 10% throughout the western Atlantic. The difference in the level of clonality between this study and Serrano et al. (2016) is likely a result of differences in sampling methods and size. Whereas Serrano et al. (2016) haphazardly sampled approximately 660 *P. astreoides* colonies at a minimum distance of 1 m from one another, the 20 colonies we sampled were intentionally collected at least 20 m apart to avoid clones. The proximity of colonies in Serrano et al. (2016) would have led to a higher likelihood of sampling clones that had recruited near parent colonies (Baums et al. 2006, 2019). Another study that sampled *P. astreoides* from two locations in the Lower Keys found approximately 3.9% clonality (Kenkel et al. 2013), which is more similar to the level we observed; however, information on the distance between samples was not reported in that study. Relatively low levels of clonality in *P. astreoides* populations are further supported by a recent study which sequenced the complete genome of eight *P. astreoides* individuals collected from Carrie Bow Cay in Belize and found zero clones (Dimond and Roberts 2020);

Fig. 3 Principal component analysis (PCA) showing the genetic overlap of individual *Porites astreoides* coral colonies from each of the four reef sites: Fowey Rocks (blue circles), Crocker Reef (yellow squares), Sombrero Reef (red diamonds), and Pulaski Shoal (green triangles). Ellipses represent the standard deviation of the sample points on the plot for each subpopulation. The percent variation explained by each PC is given in parentheses on those axes. All sites show some degree of overlap indicating high gene flow and genetic connectivity of *P. astreoides* along the Florida Keys reef tract



however, individual colonies in that study were collected 1–30 km from each other, a distance that would greatly reduce the chance of finding clonal replicates. Together, these results suggest that while asexual reproduction and fragmentation can contribute to spatially clustered clones, the contribution of clones to *P. astreoides* populations over reef to regional scales is likely low on the FKRT and most other locations in the western Atlantic.

Our analyses of allelic richness, observed heterozygosity, within-population gene diversity, overall gene diversity, and amount of gene diversity among samples, collectively indicate high levels of genetic diversity within *P. astreoides* on the FKRT. Observed heterozygosity was greater than 0.50 in all loci, except PaGA24, which was 0.20 (Table 2). These values are higher than those reported for microsatellite markers in other brooding corals, including *Seriatopora hystrix* (Baums 2008; van der Ven et al. 2021) and *Pocillopora damicornis* (Yeoh and Dai 2010), but were similar to heterozygosity results found in other *P. astreoides* studies (Kenkel et al.

2013; Serrano et al. 2016). The low probability of inbreeding, low proportion of clones, and high genetic diversity we observed both within and between sites suggest that sexual outcrossing is likely the primary mode of reproduction of *P. astreoides* on the FKRT. This supports the conclusion of a recent study on another brooding coral, *Pocillopora acuta*, which indicated that sexual reproduction of brooding coral may be more dominant than previously thought (Smith et al. 2019). That study suggested that the observation of low sexual reproduction in brooding corals may have been an artifact related to the difficulty in observing sperm gametic release into the water column. We also found that all loci in our *P. astreoides* samples conformed to HWE, indicating that the major assumptions of the Hardy–Weinberg principle—a large population size, random mating, no net mutations, no migration between populations, and no net selection (Chen 2010)—have been met for this population. We conclude, therefore, that despite the potential for asexual reproduction, most reproduction of *P. astreoides* in the FKRT is likely random, sexual mating.

Table 7 Posterior mean \pm standard deviation of migration rates from BayesAss Version 3.04 (Wilson and Rannala 2003). Populations across the top of the table indicate the source population and populations along the left side of the table indicate the receiving population.

Population	FWY	CRK	SMK	PLS
FWY	—	0.114 \pm 0.056	0.109 \pm 0.053	0.059 \pm 0.050
CRK	0.145 \pm 0.056	—	0.062 \pm 0.043	0.048 \pm 0.041
SMK	0.146 \pm 0.076	0.071 \pm 0.069	—	0.043 \pm 0.041
PLS	0.040 \pm 0.040	0.033 \pm 0.031	0.224 \pm 0.047	—

Migration from Fowey Rocks (FWY) to Pulaski Shoal (PLS) was not significantly different from zero. Crocker Reef (CRK), Sombrero Reef (SMK)

The putative dominance of random, sexual reproduction of *P. astreoides* on the FKRT should support high regional genetic diversity given sufficient connectivity of populations. Compared with corals that reproduce by broadcast spawning, the larvae of brooding coral species like *P. astreoides* are thought to have relatively short larval duration periods (Fadlallah 1983; Szmant 1986). As a result, larval dispersal distances and, therefore connectivity, would be predicted to be lower for *P. astreoides* than for broadcast spawning taxa (Holstein et al. 2014); however, Serrano et al. (2016) found that long-distance dispersal of *P. astreoides* was relatively common in the western Atlantic, and gene flow within the FKRT and between the FKRT and nearby locations was high. Results from our BayesAss analyses indicated that with migration rates greater than 10% across all four sites in our study significant migration is occurring throughout the FKRT, further supporting the hypothesis of long-range larval dispersion in *P. astreoides*. These migration rates are comparable to those found in brooding coral *Helipora* spp. in Sekisei Lagoon, which ranged from 0.4 to 20.2% (Taninaka et al. 2019).

Other studies have also found evidence of relatively high vertical larval dispersal of *P. astreoides* and multigenerational connectivity, which may further increase the resiliency of the species (Holstein et al. 2016b). Larval size (~1 mm) upon release from parent colonies (Szmant 1986), vertical transmission of symbionts (Fadlallah 1983; Richmond and Hunter 1990), and high lipid and protein reserves (Fadlallah 1983; Richmond and Hunter 1990; Reich et al. 2017) should make *P. astreoides* larvae well-suited for long dispersal periods. For example, Torda et al. (2013) demonstrated that long-distance migration occurs in the brooding coral *Pocillopora damicornis*, attributing the success to larger, brooded larvae with zooxanthellae. Our study provides further support for high levels of gene flow throughout the FKRT. The low levels of variation among *P. astreoides* populations (2.4%) and individuals (1.6%) and the low F_{ST} value (0.040) reflect the low genetic differentiation among the four sites we sampled across 350 km of the FKRT (Fig. 2) and suggest that long-range larval dispersal is likely occurring between locations. Additionally, Nei's genetic distance showed that the pairwise distances between each population were relatively low, indicating that the four populations are likely experiencing panmixia and high levels of gene flow. Combined with the high genetic variation between individuals (95.97%), our results suggest high levels of genetic mixing and, therefore, high levels of regional gene flow (Uthicke and Benzie 2003). Furthermore, our analysis of the population structure suggests there is most likely a single, well-mixed breeding population of *P. astreoides* in the FKRT. It should be noted that due to the overall low resolution of the microsatellites and decreased power from low sample numbers in this study, there may be some genetic differences not captured; however, our conclusion of high levels of gene

flow for *P. astreoides* across the region is corroborated by other studies (Nunes et al. 2011; Serrano et al. 2016).

Currently, *P. astreoides* is one of the most abundant corals on the FKRT and our results suggest that its populations are likely to persist in the future. High levels of panmixia of *P. astreoides* throughout the FKRT demonstrate the population has withstood ongoing local and global stressors (i.e., disease outbreaks, temperature-induced bleaching, and hurricanes). Although relatively susceptible individuals within the population may succumb to disturbances, high genetic diversity creates a buffer from significant population declines (Sgrò et al. 2010). The high genetic diversity we observed in this study may explain the high within-site variability in bleaching response and recovery by the same *P. astreoides* individuals during thermal stress events in 2015 and 2016, as described by Lenz et al. (2021). That study found that although local accumulation of heat stress was the best predictor of bleaching response among sites, there was also high variability in bleaching severity and the recovery of individual corals within the most severely affected sites. Because Lenz et al. (2021) found that all of the corals hosted the symbiont genus *Symbiodinium* spp. (formerly Clade A), differences in bleaching susceptibility within sites were more likely related to the genetic and/or health-condition variability of the coral host interacting with the environment.

Although areas of the FKRT may provide refugia from some thermal stress events (Guest et al. 2018), it is likely that ocean warming will cause mortality of even the most resilient coral populations in the future (Hughes et al. 2017). For *P. astreoides*, however, high genetic diversity and high levels of gene flow throughout the FKRT and between the FKRT and other parts of the western Atlantic (Serrano et al. 2016) indicate large potential for natural selection and the opportunity for the population as a whole to withstand local sub-population collapses. For example, in 2010, many inshore, shallow reefs suffered high levels of mortality following a cold-water event and the impacts on *P. astreoides* were especially severe (Lirman et al. 2011; Colella et al. 2012); however, the relative abundance of *P. astreoides* increased following that disturbance (Kemp et al. 2016).

Overall, the genetic diversity and gene flow of *P. astreoides* on the FKRT suggest that compared with many of the reef-building species it has supplanted this species should continue to maintain relatively high resilience to future disturbance. Although *P. astreoides* cannot serve the same ecological and geological roles as its reef-building coral counterparts (Kennedy et al. 2013; Perry and Alvarez-Filip 2019; Toth et al. 2019), providing a live-coral covering of reef substrata, regardless of species, is important for creating cryptic habitat and preventing further erosion of remaining reef structures (Kuffner and Toth 2016). Therefore, the persistence of *P. astreoides* populations in the western Atlantic,

in combination with active management such as restoration of key reef-building taxa, could help maintain some reef function until the greater issues facing coral reefs (e.g., climate change and other anthropogenic impacts) are properly addressed.

Conclusion

Over the past 40 years, the relative abundance of *Porites astreoides* has increased throughout the western Atlantic; however, the species' potential to continue to play a significant functional role on reefs in the future depends on its genetic resilience to disturbance. In this study, we concluded that *P. astreoides* has high genetic diversity and little genetic population differentiation across 350 km of the FKRT, which suggests that despite being a brooding coral capable of high levels of asexual reproduction, its larvae are traveling throughout the region. Due to high levels of gene flow and high genetic overlap of the sites, there is likely only a single population of *P. astreoides* in the FKRT. Additionally, the low levels of inbreeding found in individuals, both within subpopulations and across the total population, suggest that sexual reproduction is the dominant reproductive mode for this species along the FKRT, as it was similarly shown across the western Atlantic. Sexual reproduction, in combination with high levels of gene flow, should allow this species to maintain high genetic diversity, which could help increase the species' ability to withstand stressors through adaptation. Overall, the regional population structure and life-history traits of *P. astreoides* suggest that the species will likely remain a dominant component of Florida's reefs in the future.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies The coral-relocation experiment was conducted under scientific permits from the Florida Keys National Marine Sanctuary (FKNMS-2013-024-A2 and FKNMS-2016-085-A1) and the National Park Service (BISC-2014-SCI-0020, BISC-2016-SCI-0003, DRTO-2015-SCI-0010, and DRTO-2016-SCI-0010), and coral samples are curated under NPS accession numbers BISC-228 and DRTO-274.

Data availability All data used in this study are published in a US Geological Survey Data Release (Gallery et al. 2021; <https://doi.org/10.5066/P9R8NZ2J>) with FGDC-compliant metadata.

Author contribution DNG, IBK, and LTT designed the study. Data was collected by DNG, MLG, IBK, and EAL and analyzed by DNG and MLG. DNG and LTT wrote the initial draft of the manuscript and all authors contributed to the final version.

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