



Development and characterization of 148 SNP markers in the caribbean symmetrical brain coral *Pseudodiploria strigosa*

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Abstract

As coral reefs decline, restoring lost coral populations has been hampered due to the paucity of genetic information available for many coral species. In the Caribbean, the symmetrical brain coral *Pseudodiploria strigosa*, a prominent framework builder of the reef, has experienced an accelerated decline due to stony coral tissue loss disease (SCTLD). Colonies of *P. strigosa* gene-banked in response to the threat of SCTLD in Florida, USA, were sampled to develop 148 novel single nucleotide polymorphism (SNP) markers using genotyping-by-sequencing (GBS). The observed heterozygosity (H_o) and expected heterozygosity (H_e) ranged from 0.008 to 0.888 and 0.018 to 0.500, respectively. Deviations from Hardy–Weinberg equilibrium within populations, measured by the inbreeding coefficient index (F_{is}), ranged from -0.799 to 0.923. In total, 96 SNPs were found to deviate significantly from Hardy–Weinberg ($p < 0.05$). These SNPs can be used for genetic population analysis to assist management and restoration of *P. strigosa*.

Keywords *Pseudodiploria strigosa* · Single nucleotide polymorphism (SNP) markers · Genotyping-by-sequencing (GBS) · Genetic diversity

Coral reefs are in decline throughout the Caribbean and Western Atlantic, with significant reductions in live coral cover and diversity due to a combination of local and global impacts (Gardner et al. 2003; Sotka and Hay 2009; de Bakker et al. 2017). Originating in Southeast Florida in 2014, the stony coral tissue loss disease (SCTLD) outbreak has hastened the demise of more than 30 species of coral in the Florida Reef Tract and the wider Caribbean (Atlantic and Gulf Rapid Reef Assessment 2021; Walton et al. 2018). In response, the Florida Coral Rescue Project was developed to collect whole colonies of coral species susceptible to SCTLD and gene bank them in land-based facilities for future propagation and restoration to the reef (Florida Coral Rescue 2021). A total of 20 species have been prioritized for genetic marker development within the Florida Coral

Rescue Project, including the symmetrical brain coral *Pseudodiploria strigosa*, which is highly susceptible to the disease, and experiencing significant, whole-colony mortality on reefs impacted by SCTLD (Walton et al. 2018; Alvarez-Filip et al. 2019; Sharp et al. 2020; Brandt et al. 2021; Dahlgren et al. 2021; Kolodziej et al. 2021; Williams et al. 2021).

The development of standardized marker sets and common, cost-effective, efficient genotyping procedures for the prioritized suite of impacted coral species is critical to the objective of the Florida Coral Rescue Project. Corals reproduce both sexually and asexually; molecular-based clone (genet) identification is necessary to ensure genetic diversity preservation thresholds (50 genets per species) are met. Whereas more genets are secured where possible, the 50-genetic minimum is based on inbreeding avoidance (Jamieson and Allendorf 2012) and limiting large impacts of drift on natural selection (García-Dorado 2012), especially in situations where genetic-rescue interventions may become necessary (Hedrick and Garcia-Dorado 2016). Genet identifications and accompanying genotype data will also aid the curation of coral colonies within and between holding facilities, inform captive breeding efforts, and ultimately, facilitate restoration guidance and monitoring. To generate informative loci for *P. strigosa*, we used

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genotyping-by-sequencing (GBS), which sequences targeted fractions of the genome, to develop and characterize single nucleotide polymorphism (SNP) markers.

As part of the Florida Coral Rescue Project, 284 *P. strigosa* colonies were collected from 54 sites and placed into land-based aquaria. These colonies spanned a large area of the Florida Reef Tract (approximately 350 km), between Broward County in the north through the Dry Tortugas in the southwest. Sterile razor blades were used to collect 0.5 cm² of live tissue from each of the 284 *P. strigosa* colonies. Total DNA was extracted using the Qiagen DNeasy Kit (Qiagen, Valencia, California) under a modified protocol (Baums and Kitchen 2020). Sixteen samples were screened for quality and eligibility for GBS. In total, 10 libraries (8 single samples, 2 pools of 4 samples each) were constructed following digestion with the restriction enzyme *MslI*. Libraries were submitted for 150 bp paired-end GBS on an Illumina NextSeq 550. Raw sequencing reads were demultiplexed, adapter trimmed, and screened for restriction-enzyme cut sites. Reads were further assessed for quality using FastQC (Andrews 2010) and filtered accordingly using Trimmomatic software (Bolger et al. 2014). To ensure that the final reads would contain only coral DNA and not that of the endosymbiotic dinoflagellates (Symbiodinaceae), available genomes of the symbionts were used to filter out reads amplified from each of the genera *Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* (NCBI Accession GCA_003297005.1, GCA_000507305.1, GCA_003297045.1, and an unpublished *D. trenchii* genome provided by Mauricio Rodriguez-Lanetty, respectively) using BBDuk software (Decontamination Using Kmers) from the BBTools suite (Bushnell 2014). Raw total reads ranged from 1,455,624 to 4,561,912, with an average of 3,482,200 reads per sample. After all QC trimming, total reads ranged from 708,451 to 2,191,077, with an average of 1,671,189 reads per sample. Sequence clustering and SNP calling were performed in TASSEL using its reference-free UNEAK pipeline (Bradbury et al. 2007). A total of 28,016 raw SNPs were discovered, but after a minimum-call-rate filter of 80% and a minor-allele-frequency filter of 5% were applied, 8,913 SNPs remained. The remaining SNPs were further filtered to retain sites having a read depth between 45 and 250. Flanking sequences of the remaining SNPs were then examined to identify 64-mer sequences that contained the SNP site near their center, allowing adequate room for primer design. A total of 192 SNPs were selected to move to the next phase for KASPTM assay design (Biosearch Technologies, Petaluma, California). Screening of 284 samples via KASPTM assay genotyping resulted in the identification of 148 high-quality SNPs suitable for downstream analyses.

Using the 148 SNPs and all 284 *P. strigosa* samples, population genetic statistics were calculated for each locus

(Table 1). The observed (H_o) and expected heterozygosity (H_e), inbreeding coefficient index (F_{is}), and p value for Hardy–Weinberg equilibrium were calculated using the GenAlEx 6.5 software (Peakall and Smouse 2006, 2012). The observed and expected heterozygosity for each locus ranged from 0.008 to 0.888 and 0.018 to 0.500, respectively. Deviations from Hardy–Weinberg within populations, as measured by the F_{is} , ranged from -0.799 to 0.923 . In total, 96 SNPs were found to deviate significantly from Hardy–Weinberg ($p < 0.05$) (T1 Supplementary Material). Deviations could have resulted from inbreeding, population substructure, purifying selection, copy number variation, or genotyping error (Lee et al. 2008; Wang and Shete 2012; Graffelman et al. 2017).

These novel SNP markers in *P. strigosa* are a valuable tool for researchers studying the genetic structure of this species and for managers planning coral restoration in the Caribbean region.

Table 1 Characteristics of 148 new SNP loci developed for *Pseudodiploria strigosa*. Ho = observed heterozygosity; He = expected heterozygosity; Fis = inbreeding coefficient; HWE = results for Hardy–Weinberg equilibrium test, NS = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

| Locus ID | SNP type | Ho | He | Fis | HWE |
|-------------------|----------|-------|-------|--------|-----|
| TP10358_coralPSTR | C/T | 0.028 | 0.254 | 0.890 | *** |
| TP10489_coralPSTR | C/T | 0.113 | 0.159 | 0.288 | *** |
| TP1064_coralPSTR | G/A | 0.513 | 0.468 | -0.096 | NS |
| TP11053_coralPSTR | C/A | 0.430 | 0.499 | 0.138 | * |
| TP11134_coralPSTR | G/A | 0.387 | 0.403 | 0.040 | NS |
| TP11146_coralPSTR | A/G | 0.150 | 0.446 | 0.663 | *** |
| TP11321_coralPSTR | A/G | 0.357 | 0.371 | 0.037 | NS |
| TP11629_coralPSTR | C/T | 0.204 | 0.230 | 0.112 | NS |
| TP11725_coralPSTR | G/A | 0.158 | 0.279 | 0.433 | *** |
| TP11903_coralPSTR | A/G | 0.745 | 0.499 | -0.493 | *** |
| TP12079_coralPSTR | A/G | 0.483 | 0.383 | -0.261 | *** |
| TP12455_coralPSTR | T/C | 0.284 | 0.304 | 0.067 | NS |
| TP12520_coralPSTR | G/A | 0.040 | 0.187 | 0.787 | *** |
| TP12526_coralPSTR | A/T | 0.136 | 0.494 | 0.724 | *** |
| TP12901_coralPSTR | A/G | 0.344 | 0.454 | 0.242 | *** |
| TP1344_coralPSTR | A/G | 0.145 | 0.490 | 0.704 | *** |
| TP14155_coralPSTR | A/C | 0.630 | 0.432 | -0.460 | *** |
| TP1428_coralPSTR | A/G | 0.209 | 0.318 | 0.342 | *** |
| TP1437_coralPSTR | C/T | 0.133 | 0.152 | 0.128 | * |
| TP14440_coralPSTR | A/G | 0.148 | 0.150 | 0.020 | NS |
| TP14630_coralPSTR | T/C | 0.102 | 0.105 | 0.020 | NS |
| TP1471_coralPSTR | T/C | 0.239 | 0.307 | 0.222 | *** |
| TP15106_coralPSTR | G/C | 0.226 | 0.287 | 0.213 | ** |
| TP15161_coralPSTR | A/G | 0.365 | 0.393 | 0.071 | NS |
| TP15231_coralPSTR | T/C | 0.410 | 0.432 | 0.051 | NS |
| TP1548_coralPSTR | C/T | 0.116 | 0.465 | 0.751 | *** |
| TP15775_coralPSTR | G/A | 0.173 | 0.333 | 0.480 | *** |
| TP15858_coralPSTR | T/C | 0.304 | 0.482 | 0.371 | *** |
| TP1588_coralPSTR | A/G | 0.469 | 0.478 | 0.018 | NS |
| TP15934_coralPSTR | T/C | 0.392 | 0.406 | 0.036 | NS |
| TP16109_coralPSTR | T/C | 0.466 | 0.471 | 0.010 | NS |
| TP16422_coralPSTR | A/C | 0.316 | 0.433 | 0.272 | *** |
| TP1647_coralPSTR | T/G | 0.332 | 0.445 | 0.254 | *** |
| TP16622_coralPSTR | T/C | 0.290 | 0.475 | 0.390 | *** |
| TP17034_coralPSTR | A/G | 0.180 | 0.209 | 0.139 | * |
| TP17068_coralPSTR | A/G | 0.405 | 0.456 | 0.111 | NS |
| TP17123_coralPSTR | G/A | 0.353 | 0.376 | 0.062 | NS |
| TP17305_coralPSTR | A/G | 0.143 | 0.147 | 0.028 | NS |
| TP17373_coralPSTR | T/C | 0.212 | 0.285 | 0.258 | *** |
| TP17656_coralPSTR | A/C | 0.369 | 0.492 | 0.251 | *** |
| TP17661_coralPSTR | A/G | 0.313 | 0.322 | 0.031 | NS |
| TP17682_coralPSTR | T/C | 0.311 | 0.301 | -0.035 | NS |
| TP179_coralPSTR | A/G | 0.469 | 0.500 | 0.062 | NS |
| TP18006_coralPSTR | A/G | 0.121 | 0.171 | 0.289 | *** |
| TP18183_coralPSTR | T/G | 0.313 | 0.264 | -0.185 | ** |
| TP18260_coralPSTR | A/G | 0.833 | 0.489 | -0.704 | *** |
| TP18524_coralPSTR | C/T | 0.272 | 0.235 | -0.157 | * |
| TP186_coralPSTR | T/G | 0.238 | 0.490 | 0.515 | *** |
| TP18755_coralPSTR | A/G | 0.406 | 0.455 | 0.109 | NS |
| TP18865_coralPSTR | A/G | 0.252 | 0.291 | 0.133 | * |
| TP19012_coralPSTR | G/A | 0.164 | 0.254 | 0.354 | *** |
| TP19062_coralPSTR | G/A | 0.452 | 0.498 | 0.092 | NS |
| TP1918_coralPSTR | T/C | 0.233 | 0.489 | 0.523 | *** |
| TP19504_coralPSTR | T/C | 0.360 | 0.488 | 0.263 | *** |

(continued) Table 1

| Locus ID | SNP type | Ho | He | Fis | HWE |
|-------------------|----------|-------|-------|--------|-----|
| TP19716_coralPSTR | G/A | 0.248 | 0.499 | 0.504 | *** |
| TP19818_coralPSTR | T/C | 0.108 | 0.455 | 0.763 | *** |
| TP20098_coralPSTR | T/C | 0.030 | 0.096 | 0.684 | *** |
| TP20385_coralPSTR | T/C | 0.154 | 0.301 | 0.488 | *** |
| TP20519_coralPSTR | G/A | 0.357 | 0.393 | 0.092 | NS |
| TP20700_coralPSTR | C/T | 0.432 | 0.365 | -0.181 | ** |
| TP2072_coralPSTR | G/T | 0.236 | 0.221 | -0.067 | NS |
| TP20805_coralPSTR | G/A | 0.099 | 0.153 | 0.356 | *** |
| TP21046_coralPSTR | G/A | 0.241 | 0.319 | 0.246 | *** |
| TP21358_coralPSTR | A/G | 0.431 | 0.473 | 0.088 | NS |
| TP21388_coralPSTR | A/G | 0.229 | 0.443 | 0.483 | *** |
| TP21484_coralPSTR | G/A | 0.486 | 0.474 | -0.024 | NS |
| TP21522_coralPSTR | C/T | 0.009 | 0.061 | 0.853 | *** |
| TP2169_coralPSTR | C/T | 0.013 | 0.022 | 0.393 | *** |
| TP21704_coralPSTR | T/G | 0.135 | 0.302 | 0.552 | *** |
| TP225_coralPSTR | T/C | 0.198 | 0.266 | 0.256 | *** |
| TP22666_coralPSTR | C/T | 0.046 | 0.224 | 0.795 | *** |
| TP22727_coralPSTR | A/G | 0.378 | 0.481 | 0.214 | *** |
| TP23073_coralPSTR | G/A | 0.175 | 0.180 | 0.028 | NS |
| TP23099_coralPSTR | C/A | 0.253 | 0.274 | 0.076 | NS |
| TP23267_coralPSTR | T/C | 0.402 | 0.488 | 0.177 | ** |
| TP2328_coralPSTR | T/C | 0.356 | 0.450 | 0.208 | ** |
| TP23493_coralPSTR | C/T | 0.065 | 0.140 | 0.536 | *** |
| TP23545_coralPSTR | A/C | 0.189 | 0.171 | -0.105 | NS |
| TP2358_coralPSTR | T/C | 0.389 | 0.454 | 0.143 | * |
| TP23602_coralPSTR | T/G | 0.308 | 0.500 | 0.385 | *** |
| TP23612_coralPSTR | T/C | 0.341 | 0.487 | 0.301 | *** |
| TP2424_coralPSTR | A/C | 0.215 | 0.413 | 0.481 | *** |
| TP24257_coralPSTR | T/C | 0.123 | 0.209 | 0.413 | *** |
| TP24258_coralPSTR | A/G | 0.295 | 0.301 | 0.022 | NS |
| TP24331_coralPSTR | G/A | 0.030 | 0.061 | 0.518 | *** |
| TP25162_coralPSTR | A/G | 0.408 | 0.335 | -0.218 | ** |
| TP25333_coralPSTR | G/T | 0.248 | 0.434 | 0.429 | *** |
| TP25337_coralPSTR | T/C | 0.234 | 0.293 | 0.203 | ** |
| TP25449_coralPSTR | G/A | 0.477 | 0.499 | 0.043 | NS |
| TP25464_coralPSTR | T/G | 0.202 | 0.181 | -0.112 | NS |
| TP25548_coralPSTR | C/T | 0.153 | 0.458 | 0.665 | *** |
| TP25572_coralPSTR | G/A | 0.359 | 0.440 | 0.185 | ** |
| TP25640_coralPSTR | C/T | 0.255 | 0.286 | 0.108 | NS |
| TP26168_coralPSTR | C/A | 0.179 | 0.310 | 0.423 | *** |
| TP26204_coralPSTR | A/G | 0.184 | 0.295 | 0.376 | *** |
| TP26285_coralPSTR | C/T | 0.235 | 0.257 | 0.087 | NS |
| TP26319_coralPSTR | T/C | 0.112 | 0.189 | 0.408 | *** |
| TP26478_coralPSTR | G/A | 0.455 | 0.453 | -0.005 | NS |
| TP26773_coralPSTR | A/G | 0.189 | 0.467 | 0.595 | *** |
| TP27958_coralPSTR | T/C | 0.357 | 0.482 | 0.260 | *** |
| TP3181_coralPSTR | G/T | 0.866 | 0.491 | -0.763 | *** |
| TP3259_coralPSTR | G/A | 0.268 | 0.290 | 0.076 | NS |
| TP3466_coralPSTR | T/G | 0.127 | 0.148 | 0.141 | * |
| TP3477_coralPSTR | A/G | 0.358 | 0.367 | 0.022 | NS |
| TP3629_coralPSTR | G/T | 0.192 | 0.299 | 0.360 | *** |
| TP4003_coralPSTR | T/G | 0.411 | 0.458 | 0.103 | NS |
| TP4073_coralPSTR | A/G | 0.036 | 0.334 | 0.892 | *** |
| TP4221_coralPSTR | C/T | 0.723 | 0.486 | -0.489 | *** |

(continued) Table 1

| Locus ID | SNP type | Ho | He | Fis | HWE |
|------------------|----------|-------|-------|--------|-----|
| TP4483_coralPSTR | T/C | 0.352 | 0.360 | 0.022 | NS |
| TP4920_coralPSTR | T/C | 0.179 | 0.316 | 0.432 | *** |
| TP4970_coralPSTR | C/A | 0.288 | 0.332 | 0.131 | * |
| TP5379_coralPSTR | T/G | 0.449 | 0.494 | 0.092 | NS |
| TP5515_coralPSTR | C/T | 0.226 | 0.302 | 0.252 | *** |
| TP5696_coralPSTR | A/C | 0.418 | 0.443 | 0.055 | NS |
| TP5699_coralPSTR | A/G | 0.222 | 0.197 | -0.125 | NS |
| TP5707_coralPSTR | C/A | 0.158 | 0.166 | 0.050 | NS |
| TP5800_coralPSTR | T/C | 0.280 | 0.291 | 0.039 | NS |
| TP6011_coralPSTR | G/T | 0.136 | 0.127 | -0.073 | NS |
| TP6155_coralPSTR | T/C | 0.434 | 0.481 | 0.098 | NS |
| TP6417_coralPSTR | T/G | 0.149 | 0.232 | 0.358 | *** |
| TP6615_coralPSTR | G/T | 0.469 | 0.500 | 0.061 | NS |
| TP6687_coralPSTR | A/G | 0.455 | 0.483 | 0.058 | NS |
| TP6689_coralPSTR | G/A | 0.273 | 0.373 | 0.269 | *** |
| TP6837_coralPSTR | T/C | 0.045 | 0.091 | 0.498 | *** |
| TP6963_coralPSTR | A/G | 0.161 | 0.148 | -0.088 | NS |
| TP7061_coralPSTR | G/A | 0.519 | 0.492 | -0.054 | NS |
| TP7339_coralPSTR | T/C | 0.400 | 0.410 | 0.024 | NS |
| TP7449_coralPSTR | G/T | 0.172 | 0.391 | 0.560 | *** |
| TP7469_coralPSTR | T/C | 0.036 | 0.086 | 0.581 | *** |
| TP748_coralPSTR | T/G | 0.136 | 0.127 | -0.073 | NS |
| TP7499_coralPSTR | G/A | 0.227 | 0.344 | 0.340 | *** |
| TP7532_coralPSTR | T/G | 0.506 | 0.387 | -0.310 | *** |
| TP7706_coralPSTR | A/C | 0.516 | 0.407 | -0.266 | *** |
| TP8225_coralPSTR | T/C | 0.461 | 0.475 | 0.030 | NS |
| TP8254_coralPSTR | T/C | 0.230 | 0.229 | -0.008 | NS |
| TP8374_coralPSTR | T/C | 0.133 | 0.132 | -0.013 | NS |
| TP838_coralPSTR | A/C | 0.215 | 0.266 | 0.192 | ** |
| TP8382_coralPSTR | G/T | 0.336 | 0.387 | 0.132 | * |
| TP8526_coralPSTR | A/G | 0.411 | 0.439 | 0.065 | NS |
| TP8608_coralPSTR | G/A | 0.199 | 0.267 | 0.255 | *** |
| TP863_coralPSTR | C/T | 0.452 | 0.420 | -0.077 | NS |
| TP8657_coralPSTR | G/A | 0.191 | 0.498 | 0.616 | *** |
| TP8830_coralPSTR | G/A | 0.176 | 0.363 | 0.514 | *** |
| TP9_coralPSTR | C/T | 0.438 | 0.443 | 0.010 | NS |
| TP9155_coralPSTR | A/G | 0.383 | 0.440 | 0.129 | * |
| TP9573_coralPSTR | A/G | 0.871 | 0.492 | -0.771 | *** |
| TP9711_coralPSTR | C/T | 0.164 | 0.164 | 0.003 | NS |
| TP9785_coralPSTR | T/C | 0.281 | 0.288 | 0.025 | NS |

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12686-022-01294-z>.

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Declarations

Conflict of interest The authors declare that they have no competing financial interests.

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