Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008
Session number 14.490

Genetic variation in two morphotypes of *Porites panamensis* from the Gulf of California, Mexico

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Abstract. Genetic variation was analyzed to determine whether two morphotypes, a massive and columnar form, of *Porites panamensis* found together in the Gulf of California (GC) were genetically differentiated. Levels of genetic variation were similar between morphotypes and no fixed alleles were detected between them. Levels of sexual reproduction were high, as indicated by ratios N_G:N 0.76-1.00 and G_O:G_E 0.71-1.00 for both morphotypes. Analysis of Molecular Variation (AMOVA) indicated the greatest significant genetic variation within populations (97.85%) and among populations within morphotypes levels (2.63%), but not among morphotypes (-0.47%, p = 0.6826). Mean significant F_{ST} values for columnar (F_{ST} = 0.024) and massive (F_{ST} = 0.043) suggest that both morphotypes had moderate genetic structure within their populations. The number of migrants per generation (N_em) showed differences within morphotype populations (columnar 4.65-31 and massive 2.65-9.75). The lower genetic differentiation among morphotypes indicates that it is likely that they frequently interbreed. However, we observed a genetic differentiation among the populations of the morphotypes of *P. panamensis* in the north and central part of the GC, while in the south of the GC the populations of both the morphotypes are more similar and may constitute a population that is more genetically homogeneous. North-central coral communities from the GC are characterized by extreme temperature and nutrients conditions and adaptation to this stress environment may be reflected in our genetic data.

Key words: Species complex, genetic structure, Scleractinian coral, population genetics.

Introduction

The genus *Porites* Link 1807 has a cosmopolitan distribution and comprises around 60 of the world's main reef-building species (Veron 2000). It has proved difficult to efficiently delimit the taxonomic position of several species of this genus because of their considerable morphological diversity, resulting in overlapping of characters among taxa (Weil 1992; Garthwaite et al. 1994; Veron 2000). In the Gulf of California (GC), a complex of species presents this problem, involving the nominal taxon *Porites panamensis* Verrill 1866. This coral exhibits four colonial morphologies that were described originally as different species: massive (*P. panamensis, sensu stricto*), encrusting (*P. californica*), columnar (*P. nodulosa*) and branching form (*P. sverdrupi*). These nominal species were considered lately to be ecotypes of different depths and synonyms due the high morphological variation in the genus (Squires 1959; Wells 1983). However, morphometric and genetic studies indicate that at least the ramified form (*P. sverdrupi*) is a valid and endemic species of the GC (López-Forment 2003; López-Pérez et al. 2003; Forsman et al. 2006). The columnar and massive morphologies of *P. panamensis* have presented slight differences in the number of pali of their corallites (Ketchum and Reyes-Bonilla 2001). In field, differences between these forms were found in their susceptibility to algal colonization, which could mean that the columnar morphotype has a survival advantage over the massive (Paz-García and Reyes-Bonilla 2006). In vertical distribution, the massive morphology is from 1 to 30 m of depth and the columnar one is present from 1 to 5 m (López-Pérez et al. 2003; Paz-García and Reyes-Bonilla 2006). In addition, the massive morpotype is distributed from the GC to Colombia, while the columnar one is observed only inside the GC and Revillagigedo's islands (Ketchum and Reyes-Bonilla 2001; Paz-García and Reyes-Bonilla 2006). It is still unidentified if these differences between morphotypes are due the morphological plasticity or if they correspond to different species. Allozyme electrophoresis studies have been showed useful to distinguish species

boundaries in the genus *Porites* (Weil 1992; Garthwaite et al. 1994) and to assess the contribution of reproductive mode (sexual vs asexual) within the populations (Ng and Morton 2003; Nishikawa and Sakai 2005). Furthermore, the presence of different species or the morphology itself by means fragmentation could show differences between morphotype populations along the GC. The aims of this study were to (1) determine if the columnar and massive morphotypes of *P. panamensis* were genetically differentiated to clarify the taxonomic position of this group of morphospecies, (2) describe the genetic variation between the morphotype populations, (3) determine the contribution of reproductive mode (sexual vs asexual) within morphotype populations of *P. panamensis* in the GC.

Material and Methods

Field Work. In August of 2004, we collected 55 and 58 coral fragments for columnar and massive morphotypes, respectively, using SCUBA. The specimens were collected in one to three coral communities (1-9 m of depth and over an area of 400 m^2) within each collection area. The collection areas were in the GC, Mexico (Fig. 1): Bahía de Los Ángeles (BLA), Isla San Marcos (ISM), Bahía Concepción (BCO) and Sourth of Bahía de La Paz (BLP). The coral fragments were frozen in liquid nitrogen and transported to the Biochemistry Lab from the Centro de Investigaciones Biológicas del Noroeste at La Paz, BCS, Mexico where they were stored at –80°C.

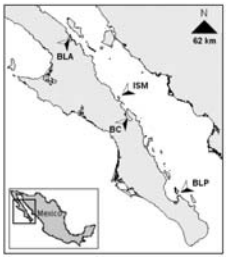

Figure 1: Map of Gulf of California showing four collection populations. **BLA** Bahía de Los Ángeles, **ISM** Isla San Marcos, **BCO** Bahía Concepción, **BLP** South of Bahía de La Paz.

Allozyme Electrophoresis. One or two ml of blastate was obtained with a gun of air pressure from SCUBA tank and rinsed with seawater. The blastate still contained zooxanthellae and although these possess own genetic material, in previous studies it has been observed that not affect the genetic analysis by allozyme on corals (Stoddart 1983; Willis and Ayre 1985). However, the microalgae symbionts were isolated of the host tissue by centrifugation to minimize the possibility of contamination (Stoddart 1983; Weil 1992). One milliliter of blastate was centrifugated at 2600 *g* for 4 min at 4°C. The supernatant was placed in vials and mixed with 40 µl of Stoddart's buffer modification (Stoddart 1983; Weil 1992). Zooxanthellae enzymes extracted from coral tissue did not appear on our gels. The concentration of total proteins from each sample was analyzed by Bradford's method (Bradford 1976) and 25 µg of sample was used for the analysis. Four enzyme systems were used: *Mdh* (E.C.1.1.1.37), *Leu-leu*, *Leu-tyr* and Leu-gly-gly peptidases (E.C.3.4.11). Allozyme analysis was carried out using the method of Polyacrilamide Gel Electrophoresis (PAGE) by discontinuous gel system in native conditions (Laemmli 1970; Manchenko 1994).

Statistic analysis. Genetic variability (Swofford and Selander 1981), $N_G{:}N$, and $G_O{:}G_E$ (see Table 1 legend) were calculated for each population of both morphotypes (Stoddart and Taylor 1988). Unbiased genetic distances (D) were used for cluster analysis (Nei 1978). We performed an analysis of molecular variance (AMOVA) to compare genetic similarity between the morphotype populations, P-values were calculated from a random permutation test with 16 000 replicates (Excoffier et al. 1992). The level of genetic heterogeneity and gene flow among morphotypes were estimated by F_{ST} and the average number of migrants per generation (*Nem*), respectively. We calculated pairwise F_{ST} estimates between each pair of populations (within and among population morphotypes). F_{ST} were tested for difference from zero permuting (10 000 replicates) alleles between samples with exact G-test (Goudet *et al*. 1996), as implemented in FSTAT v. 2.8 (Goudet 1995). We applied a sequential Bonferroni correction to reduce the chance of type I errors (Rice 1989).

Results

No fixed alleles were detected between morphotypes. The mean number of alleles per locus at each location ranged from 1.9 to 2.4 for the columnar morphotype and from 2.1 to 2.3 for the massive one (Table 1). The observed heterozygosities were slightly higher that the expected under Hardy–Weinberg equilibrium in all populations, ranging from 0.331 to 0.486 for columnar morphotype and 0.331 to 0.529 for massive morphotype (Table 1). The ratios $N_G{:}N$ (0.76-1.00) and $G_O{:}G_E$ (0.71-1.00) for both morphotypes indicate a high rate of sexual reproduction and that this strategy is the most important in the maintenance of their populations in the GC (Table 1). AMOVA indicated the greatest significant genetic variation within populations (97.85%, $p<0.001$) and among populations within morphotypes levels (2.63%, $p<0.001$), but not between morphotypes (-0.47%, $p = 0.6826$). The values of Nei´s (1978) unbiased genetic

distances within morphotype populations, ranged from 0 to 0.020 and 0 to 0.050 for columnar and massive morphotypes, respectively (Table 2). The values of genetic distance between samples of different morphotypes ranged from 0 to 0.047. Cluster analysis showed three groups by geographical proximity in the GC: one group included both northern morphotype populations, a second group formed by central massive populations, and center-south populations of the columnar with the southern population of the massive morphotype as another cluster (Fig. 2).

Table 1. Genetic variability and relative contribution of the sexual and asexual reproduction of populations of columnar and massive morphotypes of *P. panamensis* from the GC. *N* number of individual colonies at each population, N_G number of unique genotypes observed at each population, G_O and G_E observed and expected genotypic diversity, respectively. Population abbreviation as in Fig. 1. Standard errors in parentheses.

Morphotype	**Columnar**				**Massive**			
Population	*BLP*	*BCO*	*ISM*	*BLA*	*BLP*	*BCO*	*ISM*	*BLA*
N	13	14	14	14	13	14	17	14
Mean no. of alleles/locus	1.9 (0.1)	2.0 (0.0)	2.4 (0.2)	2.2 (0.1)	2.3 (0.2)	2.2 (0.1)	2.3 (0.2)	2.1 (0.2)
Observed heterozigosity	0.331 (0.05)	0.486 (0.04)	0.429 (0.02)	0.457 (0.05)	0.331 (0.05)	0.507 (0.03)	0.529 (0.03)	0.429 (0.07)
Expected heterozigosity	0.273 (0.04)	0.374 (0.02)	0.395 (0.02)	0.392 (0.04)	0.301 (0.03)	0.424 (0.02)	0.412 (0.02)	0.333 (0.05)
N_G:*N*	0.769	1.000	1.000	1.000	1.000	1.000	1.000	1.000
G_O:G_E	0.719	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 2. Nei´s unbiased genetic distance (below diagonal) and F_{ST} values (above diagonal) for the morphotypes of *Porites panamensis* from the GC. Population abbreviations as in Figure 1. *p<0.05, ***p<0.01 after Bonferroni correction.

	Population		1	2	3	4	5	6	7	8
1	Col	BLP	———	0.008	**0.023***	**0.051****	0.009	0.032	**0.066****	**0.045***
2	Col	BC	0.000	———	0.001	**0.031***	0.000	0.000	0.031	0.018
3	Col	ISM	0.005	0.000	———	0.032	0.013	0.000	0.022	**0.030***
4	Col	BLA	0.020	0.014	0.018	———	**0.053****	**0.034***	**0.071****	0.018
5	Mas	BLP	0.001	0.000	0.003	0.025	———	0.037	**0.070****	0.036
6	Mas	BC	0.007	0.000	0.000	0.019	0.014	———	0.000	0.025
7	Mas	ISM	0.029	0.014	0.011	0.047	0.036	0.000	———	**0.086****
8	Mas	BLA	0.015	0.003	0.013	0.005	0.014	0.008	0.050	———

Mean significant F_{ST} values after Bonferroni correction were observed for columnar (F_{ST}=0.024, p<0.01) and massive (F_{ST}=0.043, p<0.01) morphotypes. Pairwise F_{ST} estimates revealed no significant differences between the populations of both morphotypes in the same location, but significant differences were observed between the populations of BLA from both morphotypes and the rest of the GC (Table 2). N_em showed differences between morphotypes; the columnar presented higher values (4.65-31) among its populations in comparison with the massive (2.65-9.75). N_em between populations of different morphotypes ranged from 3.27 to 27.52.

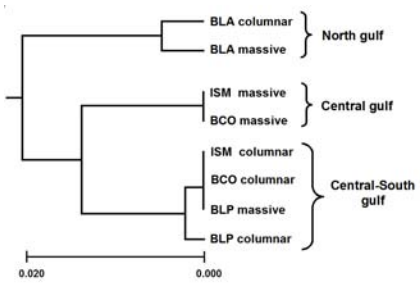

Figure 2: UPGMA dendrogram showing the populations of columnar and massive morphotypes of *P. panamensis* in the GC based on Nei´s (1978) unbiased genetic distance.

Discussion

No fixed alleles were detected between columnar and massive morphotypes of *P. panamensis* and AMOVA indicated that the variation was not significantly partitioned between morphotypes (-0.47, p=0.6826). In addition, the Nei´s (1978) unbiased genetic distance between morphotypes was 0.0009. These data suggest that both morphotypes interbreed frequently and are likely to be the same species. However, slight genetic differences were observed between morphotype populations. The columnar morphotype had lower genetic differentiation within populations (D <0.020) than the massive one (D <0.050). The values of genetic distance within populations of the columnar morphotype are similar to those reported in literature for populations with slight genetic differentiation, such as *Platygyra sinensis* (D <0.008; Ng and Morton 2003) and *Mydedium elephantotus* (D <0.015; Yu J-K et al. 1999). The values of genetic distance obtained within populations of the massive morphotype and among the populations of the morphotypes are more similar to the distances reported for those species that possess genetic structure in their populations such as *Goniastrea aspera* (D <0.040, Nishikawa and Sakai 2005) and *Pocillopora damicornis* (D < 0.066; Adjeroud and Tsuchiya 1999).

The dendrogram of Nei´s unbiased genetic distance showed three groups of populations clustering mostly by geographical vicinity (Fig. 2). This pattern showed the subdivision exists among the populations of the morphotypes of *P. panamensis* in the north part and central of the GC, while in the south of the GC the populations of both the morphotypes are more similar and may constitute a population that is more genetically homogeneous. Mean significant F_{ST} values observed in both morphotypes (F_{ST} > 0.024, p<0.01) suggest that those have a genetic structure within their populations along the GC. Genetic structure in both morphotypes can be explained by the

brooding larvae of *P. panamensis* that are recruited to some few meters of the parental colonies (Glynn and Ault 2000). Pairwise F_{ST} estimates revealed no significant differences between the populations of both morphotypes in the same location, but significant differences were observed between the populations of BLA from both morphotypes and the rest of the GC (Table 2). Studies carried out with diverse taxa have suggested the north area of the GC is a different biogeographic region; it has based on the pattern of distribution of species, salinity differences, temperature, tide, high eutrophic conditions, to the population subdivision and the reduction of the genetic flow in marine invertebrates and fishes (De la Rosa-Vélez et al. 2000; Riginos and Nachman 2001, Halfar et al. 2004). This difference may be due to combined effects of biogeography, geographical distances, and habitat discontinuity that could result in different evolutionary histories among populations (De la Rosa-Vélez et al. 2000; Riginos and Nachman 2001). In addition, the coral community of *P. panamensis* from Bahía de Los Angeles is characterized by temperatures extremes (ranging from 14°C to 30°C), lower penetration of light (-9m), the highest values average in chlorophyll in coral communities of high latitudes (2.2 mg Chl a/m), high content of phosphates (1.8 µmol/l) and nitrates (9.9 µmol/l) that affect the growth and coral development (Halfar et al. 2005). This community can be adapted to temperature stress and nutrients (Halfar et al. 2005), and may be reflected in our genetic data. The morphotypes showed differences in N_em in populations with separation of 750 km; the columnar form presents three times higher number of migrants within its populations in its maximum values in comparison with the massive one (4.65-31 vs 2.65-9.75). Similar values of migrants per generation have been estimated in populations with separation of 1700 km for broadcast spawners (4.8-24.8) and brooding species (1.4-19; Ayre and Hughes 2004). However, gene flow among populations is affected by diverse factors such as the reproductive mode of the studied species, overlapping generations, dispersal ability, habitat discontinuity, available space for recruitment, oceanographic conditions and isolation by distance (Stoddart 1983; Ayre and Hughes 2004).

Previous studies of allozyme electrophoresis in coral species have revealed populations that reproduce mainly sexually, asexually or with a mix of reproductive mode (Stoddart 1983; Yu et al. 1999; Nishikawa and Sakai 2005). Our data show that asexual reproduction (e.g. from fragmentation, budding, or fission) had little influence on the maintenance of the populations of *P. panamensis*, which is consistent with ecological studies (Glynn et al. 1994; Reyes-Bonilla and Calderón-Aguilera 1994). High ratios of N_G:N = 1 and G_O:G_E > 0.719 suggest that sexual reproduction in both morphotypes of *P. panamensis* is the most important means of maintaining their populations in the GC. These results are consistent with life history characteristics of the columnar morphotype in BLP, which can brood larvae over the whole year (Mora-Perez 2005). In addition, the population BLP of the columnar morphotype presented some clonal multilocus genotypes (Table 1). This suggests that this population is occasionally subject to reproduction via fragmentation, which is consistent with its colonial morphology and the incidence of hurricanes in the south of the GC. The absence of colonies with clonal multilocus genotypes in the massive morphotype is also consistent with its colonial morphology that is less likely to fragment. The generally high frequencies of unique multilocus genotypes in most populations of both morphotypes of *P. panamensis* may be due to diverse habitats and oceanographic conditions along the GC (López-Pérez et al. 2003; Halfar et al. 2005; Paz-García and Reyes-Bonilla 2006), to the high frequency of sexual reproduction and recruitment during the whole year (Mora-Perez 2005), or to the type and the frequency of moderate environmental disturbances (i.e. ENSO events and hurricanes) that may favor genotypic diversity in sexually reproducing coral communities (Coffroth and Lasker 1998). Our data suggest a higher sexual reproduction rate for massive morphotypes than columnar, however there are no reproductive studies of the massive morphotype in the GC. Studies carried out in Jalisco and Oaxaca showed that the massive morphotype reproduces during the warm months (May to September; Vizcaíno-Ochoa 2003; Rodríguez-Troncoso 2006). If this occurs in the GC, differences in the reproductive season among morphotypes (columnar whole-year vs massive warm season reproduction) could explain in part the genetic differences observed between the morphotype populations.

The observed differences among morphotype populations in the GC may be due to intrinsic factors (e.g. differences in expulsion times of sperm gametes and larvae, selective recruitment, differences in larvae dispersion), as it has been found in the members of the *Montastraea annularis* complex (Weil and Knowlton 1994; Knowlton et al. 1997). In addition, certain host genotypes from massive and columnar morphotypes were associated specifically with a particular *Symbiodinium* type and depth strongly influenced the frequency of occurrence of particular symbionts in populations of both morphotypes individuals (Paz-García et al. 2009). The possibility of host-symbiont co-evolution in *Porites panamensis* morphotypes is important due high or low light-

adapted symbiont may directly affect the differential success of larvae settling in deep or shallow environments. Further work should address to explain if the latitudinal genetic differentiation and genetic structure morphotypes depend on vertical distribution pattern, clade simbiont and/or intrinsic factors.

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