



Genetic structure of the scleractinian coral, *Pocillopora damicornis*, from the Mexican Pacific

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Abstract. Genetic structure was studied in the coral *Pocillopora damicornis* in three areas of coral development of the Mexican Pacific (MP). Specimens were collected from six localities: El Portugues and Punta Gaviotas located inside the Gulf of California (GC), Punta Arenas and Isla Redonda from the entrance of GC, and Las Dos Hermanas and La Entrega in the south of the MP. Exclusive genotypes were observed in the northern and southern populations. Genetic variation was similar along the MP, although slight higher variation was observed in the southern populations. Most of the populations presented significant deficits heterozygotes. These deficiencies could be due to the predominance of the asexual reproduction by fragmentation, localized sexual reproduction, inbreeding and/or Wahlund effect among localities, and different mortality events by natural disturbances. Cluster analysis based on genetic distance showed three groups by geographical proximity: two populations inside the GC, those ones located in the entrance of the GC, and two populations located at the south of the MP. Mean significant F_{ST} value ($F_{ST} = 0.153$) indicated a genetic structure. Differences in sexual and asexual reproduction among the localities coupled with local recruitment and currents patterns are possibly generating the genetic structure observed in the populations of *P. damicornis* in the MP.

Key words: Population structure, *Pocillopora damicornis*, Mexican Pacific, population genetics.

Introduction

The coral *Pocillopora damicornis* is one of the dominant coral species in reef systems of the eastern Pacific. This coral is distributed from the Gulf of California in Mexico to Ecuador, including all the nearby oceanic islands (Glynn and Ault 2000; Pérez-Vivar et al. 2006). This species is one of the most studied and widely distributed reef corals in the world. Examination by allozyme electrophoresis of this species has allowed determinate the genetic structure in coral populations throughout the Indo Pacific (Stoddart 1984; Ayre et al. 1997; Yu et al. 1999; Ayre and Hughes 2004; Smith-Keune and van Oppen 2006).

In the Mexican Pacific (MP), reproductive studies indicated that this species can reproduce both sexually (spawn gametes) and asexually (fragmentation) and presents a geographic variation in its reproductive mode along the Mexican Pacific (Chávez-Romo and Reyes-Bonilla 2007; Carpizo-Ituarte et al. 2009). In addition, there is not information about the genetic variation of *P. damicornis* in the MP. Genetic studies

realized in other coral species as *Porites panamensis* (Paz-García et al. 2009b) and *Pavona gigantea* (Saavedra-Sotelo 2007) have showed a genetic structure in their populations.

Our aim was to determine the genetic structure of the coral *P. damicornis* along of the Mexican Pacific. This study is relevant due the populations are in active recovery after bleaching and mortality caused by the 1997-98 El Niño event (Carriquiry et al. 2001; Reyes-Bonilla 2001).

Material and Methods

Sample Collection. We collected 22 to 48 fragments (2 m of depth) of *P. damicornis* from six localities along of the MP (Fig. 1): El Portugues (POR) and Punta Gaviotas (PGA) inside of the GC (GC); Punta Arena de la Ventana (PAV) and La Isla Redonda (IRD) in the entrance of the GC; and two localities from the south of MP, Las Dos Hermanas (LDH) and La Entrega (LET). The coral fragments were frozen in

liquid nitrogen and transported to the laboratory, where they were stored at -80°C .



Figure 1. Collection areas. Points indicate collected sites along the Mexican Pacific. **POR** El Portugues, **PGA** Punta Gaviotas, **PAV** Punta Arenas, **IRD** Isla Redonda, **LDH** Las Dos Hermanas and **LET** La Entrega.

Electrophoresis. We conducted a coral tissue extraction in Stoddard's buffer modification (Stoddard 1983, Weil 1992) using a sonic desmembrator. Homogenates were centrifuged at 2600 g for 10 min at 4°C , and the supernatants were stored at -80°C . We determine the concentration of total proteins from each sample by Bradford's method (Bradford 1976) and 25 to 50 μg of sample was used for the analysis of each enzyme system (Paz-García et al. 2009a). Allozyme analysis was carried out using vertical electrophoresis with 8%T polyacrilamide gels (Manchenko 1994). Four enzyme systems were used: Leucyl glycine glycine peptidase (LGG 1, E.C. 3.4.11.1) enzyme malic (ME 1&2, E.C. 1.1.1.40), glutamate dehydrogenase (GDH 1, E.C. 1.4.1.3) and esterase (EST 1&2, EC 3.1.1.1). Tris-Glycine Buffer was used in the electrophoresis. Alleles were assigned a value based on the ratio of their electrophoretic mobility relative to that of the most common allele.

Statistical analyses. Genetic variability was calculated for each population and the Hardy-Weinberg equilibrium (HWE) was tested by χ^2 analyses, using the Biosys-1 and GENPOP programs (Swofford and Selander 1981; Raymond and Rousset 1995). The magnitude and direction of departures from HWE at each locus were also assessed to each population. These departures were expressed as Wright's fixation index (f), where positive and negative values represented deficits and excesses of heterozygotes, respectively (Wright 1978). Unbiased genetic distance was used for cluster analysis, calculated in TFPGA software (Nei 1978; Miller 1997). Wright's F statistics were calculated to determine the degree of differentiation among populations (Weir and Cockerham 1984). We calculated pairwise F_{ST} estimates between each pair of populations. 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

Six loci were scored from four enzyme systems, one monomorphic and five polymorphic. Exclusive genotypes were observed in the northern (POR: LGG-1^{AB}; PGA: LGG-1^{AB} and LGG-1^{BC}) and southern (LDH: LGG-1^{AC}, LGG-1^{BC} and LGG-1^{CD}; LET: LGG-1^{AC} and LGG-1^{CD}) populations (Anexus I). Allelic diversity was 2.3 in the populations from inside and entrance Gulf of California and 2.5 in south of MP (Fig. 1a). Genetic variation was slight higher in southern populations (LDH and LET). All populations presented significant deviations of Hardy-Weinberg equilibrium in deficits of heterozygotes (Fig. 1b and Table 1).

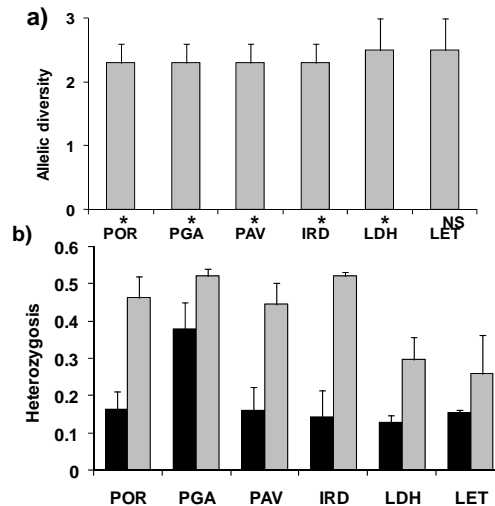


Figure 2. a) Allelic diversity (calculated with 5 loci polymorphic). b) Heterozygosis observed and expected, black and gray respectively, in six populations of *Pocillopora damicornis*. Error bars indicate (SE) variation among populations. Significant level after sequential Bonferroni correction ($p < 0.001$). NS: Not significant.

Table 1. Wright's fixation index (f) indicating heterozygote excess (negative number) or deficit (positive number) for each locus in populations of *P. damicornis* from the Mexican Pacific. Significant deviations from Hardy-Weinberg equilibrium after sequential Bonferroni correction ($*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

Population	POR	PGA	PAV	IRD	LDH	LET
Locus						
ME-1	0.672 ^{***}	-0.080	0.523 ^{**}	0.894 ^{***}	0.760 ^{**}	-0.077
EST-1	0.300	0.107	0.414	0.506	0.468	-0.100
EST-2	0.467 [*]	0.275	0.513 [*]	0.417	-0.077	-0.083
GDH-1	1.000 ^{***}	1.000 ^{***}	1.000 ^{***}	1.000 ^{***}	1.000 ^{***}	1.000 ^{***}
LGG-1	0.959 ^{***}	0.675 ^{***}	1.000 ^{***}	1.000 ^{***}	0.696 ^{***}	0.759 [*]

The UPGMA cluster analysis, based on Nei's (1978) unbiased genetic distance, showed three groups by proximity geographical: I) the populations from inside of the GC, II) two populations from the entrance of the gulf and III) the populations of the south of MP as other cluster (Fig. 2). The individual inbreeding coefficient (F_{IS}) and the total inbreeding coefficient (F_{IT}) were significantly different from zero in each locus and mean value (Table 2). F_{ST} values were statistically significant, except for locus EST-2, and ranged from 0.062 to 0.213. Mean significant F_{ST} value ($F_{ST}=0.153$) indicate a population structure of *P. damicornis* in the MP (Table 2).

F_{ST} values calculated between pairs of populations, ranged from 0.027 to 0.420 (Table 3). These comparisons showed a great genetic subdivision of the populations from LDH and LET with the other analyzed populations (Table 3).

Table 2. Wrights F -statistics calculated to each locus for *P. damicornis* from the Mexican Pacific. Significant level after sequential Bonferroni correction ($*p < 0.05$, $**p < 0.01$).

Locus	F_{IS}	F_{IT}	F_{ST}
ME-1	0.405**	0.447**	0.062*
EST-1	0.294**	0.429**	0.184*
EST-2	0.422**	0.443**	0.040 ^{NS}
GDH-1	1.000**	1.000**	0.213*
LGG-1	0.837**	0.866**	0.187*
Total	0.625**	0.682**	0.153*
Average Jackknife	0.632	0.691	0.155
Standard error	0.140	0.127	0.030
Bootstrap over loci 95% Confidence Interval	0.374-0.862	0.456-0.887	0.096-0.200

Table 3. Pairwise F_{ST} (below diagonal) and p values (above diagonal) in *P. damicornis* from the Mexican Pacific. Significant level after sequential Bonferroni correction ($*p < 0.01$). ^{NS}: Not significant.

Population	POR	PGA	PAV	IRD	LDH	LET
POR	—	0.039 ^{NS}	0.002 ^{NS}	0.025 ^{NS}	0.000*	0.000*
PGA	0.027	—	0.007 ^{NS}	0.004 ^{NS}	0.000*	0.000*
PAV	0.048	0.034	—	0.148 ^{NS}	0.000*	0.000*
IRD	0.057	0.065	0.034	—	0.000*	0.000*
LDH	0.361	0.244	0.362	0.420	—	0.014 ^{NS}
LET	0.232	0.135	0.188	0.265	0.148	—

Discussion

Allelic diversity in most populations of *Pocillopora damicornis* from the Mexican Pacific showed slight lower values (2.2-2.5; Fig. 2a), compared with those reported in six populations from Japan which ranged of 3.1 to 3.8 and six habitats from One Tree Island Reef, Australia with values from 3.5 alleles per locus (Adjeroud and Tsuchiya 1999; Sherman et al. 2005).

In addition, a declination of allelic diversity with increasing latitude (from 3.6 to 1.3) was observed in *P. damicornis* along the east of mainland Australia. This variation suggests a high genetic differentiation among the populations (Miller and Ayre 2008). Therefore, the observed values of allelic diversity suggest a lower genetic differentiation among the populations from the PM.

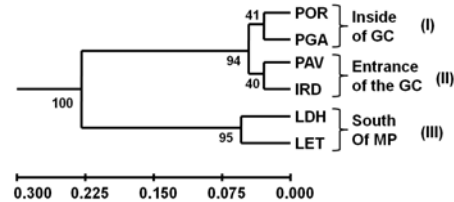


Figure 3. Cluster analysis based on Nei's (1978) unbiased genetic distances showing relationship among populations of *Pocillopora damicornis* from the Mexican Pacific. Bootstrapped values over 40% (based on 1000 randomizations) are shown next to corresponding nodes.

The slight higher genetic variation and exclusive genotypes found in the southern populations of *P. damicornis*, could be due to a larval dispersion coming from the populations from Central America (Panama, Costa Rica and Galapagos Islands). Possibly originated by a high genetic diversity in those populations that perhaps have a past genetic contribution of the populations from the Indo Pacific. In addition, recent studies realized in Panama, Clipperton Island and Hawaii, indicate that trans-Pacific gene flow in *P. damicornis* between the Central and Eastern Pacific is restricted; and the Eastern Pacific corals exist in relative isolation from their Central Pacific counterparts and interact with each other differently (Combosch et al. 2008).

The observed heterozygosity values ranged from 0.127 to 0.378 (Fig. 2b) and they are similar to six populations from Japan that present an asexual reproduction as main mode in the maintenance of their populations (ranged from 0.244 to 0.366; Adjeroud and Tsuchiya 1999). We detected significant deviations from HWE in each population (Table 1). Significant heterozygous deficit has been commonly observed in coral species (Adjeroud and Tsuchiya 1999; Nishikawa and Sakai 2005; Miller and Ayre 2008; Paz-García et al. 2009). These deviations has been associated to the predominance of the asexual reproduction by fragmentation, inbreeding and/or Wanhund effect among localities, as consequence of different events of recruitment of different cohorts and for different coralline communities, and different mortality events by natural disturbances (Ayre et al. 1997; Adjeroud and

Tsuchiya 1999; Sherman et al. 2005; Ayre and Hughes 2004; Constantini et al. 2007).

Cluster analysis based on Nei's (1978) unbiased genetic distance suggests that the populations of *P. damicornis* that are from inside the GC (POR and PGA), and the entrance (PAV and IRD) of the GC, possess slight genetic differences (Fig. 3). While the LDH and LET present high genetic differences with northern populations. This pattern suggests a subdivision among the populations of *P. damicornis* and coincides with the observed in *Porites panamensis* along the MP (Paz-García et al. 2009b). These results suggest that populations from inside and the entrance of GC may be a group genetically more homogeneous, while that southern populations showed a genetic differentiation that could be due to the high frequency of natural phenomenon that they are generally presented along the MP (e.g. hurricanes, storms, ENSO events, upwelling areas; Medina-Rosas et al. 2005; Paz-García et al. 2009b). Furthermore the values of the bootstrapped in the cluster analysis corroborate this differentiation in the most southern populations (Fig. 3) and it coincides with that found in other coral species studied in the MP as *P. panamensis* and *P. gigantea* (Saavedra-Sotelo 2007; Paz-García et al. 2009b).

Significant differences found in the individual inbreeding coefficient (F_{IS}) and the total (F_{IT}) of the populations (Table 2), indicate a heterozygote deficiency and a possible local recruitment in the populations of *P. damicornis* in the PM. F_{ST} values in the most loci and mean significant F_{ST} value ($F_{ST} = 0.153$) indicated a high genetic structure in the populations of *P. damicornis* in comparison with other coral species studied in the MP as *P. panamensis* ($F_{ST}=0.104$; Paz-García et al. 2009b) and *P. gigantea* (Φ_{ST} 0.10-0.20; Saavedra-Sotelo 2007). Previous studies in the GC and MP have found population subdivision in different marine invertebrates and fishes groups (De la Rosa-Vélez et al. 2000; Riginos y Nachman 2001; Valles-Jimenez et al. 2005; Paz-García et al. 2009b). Different factors can generate a population genetic subdivision in the MP, as biogeography, distance geographic, habitat discontinuities, temperature gradients and upwelling areas (De la Rosa-Vélez et al. 2000; Riginos and Nachman 2001; Halfar et al. 2005; Valles-Jimenez et al. 2005).

In addition, the genetic differentiation observed in populations of *P. damicornis* could be due to differences in sexual (spawning gametes) and asexual (fragmentation) reproduction among the localities of the MP (Chávez-Romo and Reyes-Bonilla 2007; Carpizo-Ituarte et al. 2009). Studies realized in Japan and Australia have been reported differences in the reproductive strategies of *P. damicornis* and the main

reference that the asexual reproduction contributes substantially in the genetic structuring and in the maintenance of established population of the species (Stoddart 1984a, b; Adjeroud and Tsuchiya 1999). Fragmentation has been observed as common reproductive strategy in the populations of the *P. damicornis* in the MP. Patches of this species easily colonize soft substrates (sand or gravel) after their branches become detached following cyclones; these branches attach themselves to the bottom and continue developing (Reyes-Bonilla 2003). However, recent studies show that the population of PGA present evidences of sexual reproduction (Chávez-Romo and Reyes-Bonilla 2007), which would explain because the populations of inside the GC have a close genetic relationship with the populations the entrance of the GC. Although previous studies mention that the population from IRD presents an asexual reproduction for fragmentation way (Carpizo-Ituarte et al. 2009).

Nevertheless, although the reproduction influences in the genetic differentiation, it is not considered to be the only factor. The local recruitment coupled with currents patterns may limit the larval dispersion and generate the genetic structure observed in the populations of *P. damicornis* in the MP. The possibility has been mentioned that the Coastal Current Costa Rica (CCCR), in direction south to north, transports coralline propagules from Central America until Oaxaca, for the likeness of coralline species among these areas (Glynn and Wellington 1983; Reyes-Bonilla and López-Pérez 1998). Also, dispersion may occur from Oaxaca to Bahia de Banderas and from there to the Gulf of California. However the exclusive genotypes found in the OAX populations (LDH: LGG-1^{AC}, LGG-1^{BC} and LGG-1^{CD}; LET: LGG-1^{AC} and LGG-1^{CD}) indicate that not all the coral species can be dispersed in the same way because different oceanic fronts exist to the south of Bahia de Banderas and the Gulf of California and that which coincides with that observed for *P. panamensis* along the MP (Reyes-Bonilla 2003; Paz-García et al. 2009b). Also, recent studies of the reproductive biology of *P. damicornis* in the population LET showed evidences that these reproduce in an asexual way (fragmentation; Carpizo-Ituarte et al. 2009), that which would support the fact that the genotypes found in LDH and LET were exclusive of these populations due a dispersion capacity doesn't exist toward the north. The dispersion could be limited between coral population with sexual reproduction by the existence of long sand barriers and mangroves communities localized along the MP (Glynn y Ault 2000; Reyes-Bonilla 2003). However, it is necessary to carry out other studies that analyze the ecology, reproduction and genetics of the populations of *P. damicornis* to

understand the relationship that exists among these ecosystems along Mexican Pacific.

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