Genetic Connectivity Patterns of Corals *Pocillopora damicornis* and *Porites panamensis* (Anthozoa: Scleractinia) along the West Coast of Mexico[1]

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Abstract: Genetic connectivity was studied in two scleractinian corals, *Pocillopora damicornis* (branching and broadcast spawner) and *Porites panamensis* (massive and brooding type), along the Pacific coast of Mexico. Allelic diversity between adults and juveniles, the latter recruited after the El Niño–Southern Oscillation (ENSO) 1997–1998 event, was determined, and level of genetic connectivity among populations was assessed. There were no significant differences in allelic diversity between adults and juveniles from the same location. Seascape spatial genetic analysis suggested two or three clusters, depending on the species: (1) Bahías de Huatulco, (2) south of the Baja California Peninsula and Bahía de Banderas, and (3) locations in the Gulf of California. The most important barrier to gene flow was detected between Bahía de Banderas and Bahías de Huatulco and corresponds with a major coastal stretch of sandy beaches and lagoons. Moderate to high gene flow was found inside and at the entrance of the Gulf of California ($N_em = 62–250$), possibly favored by seasonal circulation patterns and sexual reproduction. In contrast, low gene flow was observed between southern populations and the rest of coastal Mexico ($N_em < 1.7$) based on high local recruitment and habitat discontinuity. A close genetic relationship of corals from the southern part of the Baja California Peninsula and severely damaged Bahía de Banderas coral communities confirmed that exchange of propagules could have taken place between the localities after the ENSO 1997–1998 event. Despite different reproductive strategies, both species showed similar patterns, suggesting the importance of surficial currents and habitat discontinuity to predict connectivity among coral reefs.

In the eastern Pacific, coral communities have suffered mass coral bleaching and reduction of live coral cover by 50%–90% since the 1980s (Glynn 1990, Reyes-Bonilla et al. 2002). These losses are often attributed to El Niño–Southern Oscillation (ENSO) events

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(Glynn and Ault 2000). During the 1997–1998 ENSO event, coral reefs off the coast of Mexico suffered massive die-off of live coral cover exceeding 60% in Bahía de Banderas and Oaxaca, but only 18% in the Gulf of California (Carriquiry et al. 2001, Reyes-Bonilla et al. 2002, Reyes-Bonilla 2003). Differences in coral mortality in those areas during past ENSO events were attributed to hydrological barriers near the entrance of the Gulf of California that diminished the northern advance of warm water masses from the west (Fiedler 2002). The Gulf of California, therefore, could represent a reservoir or larval supply to damaged communities, such as Bahía de Banderas and other coastal locations (Carriquiry and Reyes-Bonilla 1997, Reyes-Bonilla et al. 2002, Chávez-Romo et al. 2009, Paz-García et al. 2009*a*). Studies of Bahía de Banderas and the coast of Oaxaca after ENSO 1997–1998 showed that surviving corals are able to maintain their reproductive activity and recruitment despite environmental disturbances (Medina-Rosas et al. 2005, López-Pérez et al. 2007).

The degree to which surviving corals contribute to regional resilience of reefs depends on the severity and extent of the damage and the level of connectivity among coral populations. The exchange of larvae from coral communities that have not experienced severe disturbances contributes to high genetic diversity and is crucial to recuperation of reefs after large-scale disturbances (Ayre and Hughes 2000, van Oppen and Gates 2006). Migrants may carry new alleles that will be integrated into the population, creating new gene combinations on which selection can potentially act (van Oppen and Gates 2006). Circulation patterns are one of the main factors that facilitate larval transport between healthy and damaged coral communities or act as a physical barrier to dispersal and generation of genetic differences of coral populations.

Some studies have been able to relate ocean currents to genetic similarity of coral populations (Benzie 1999, Yu et al. 1999), and others have reported genetic differences among sites presumably connected by ocean currents (Palumbi 2003). In the west coast of Mexico, ocean currents (see Figure 1) could represent one of the main mechanisms leading to population structure of corals and other invertebrate species (Valles-Jimenez et al. 2005, Chávez-Romo et al. 2009, Lin et al. 2009, Paz-García et al. 2009*a*).

Recently, studies have shown the importance of including adults and juveniles or recently recruited individuals in the analysis of genetic connectivity among populations and the role of biological (e.g., larval behavior and selection) and physical (e.g., environment and historical events) factors influencing present-day population structure (Palumbi 2003, Miller and Ayre 2004, Brazeau et al. 2005). New studies have combined information on geographical landscape features with analysis of genetic markers to understand how environmental factors affect the dispersal of individuals and to identify spatial patterns in the genetic structure and possible regions of discontinuous gene flow (Galindo et al. 2006, McInerney et al. 2009). From these studies has emerged a new discipline termed "landscape genetics" or "seascape genetics" in marine studies. Combining both sets of data has improved our ability to detect genetic structure in relation to oceanographic models and predict genetic patterns resulting from larval dispersal, such as in the Caribbean coral *Acropora cervicornis* (Baums et al. 2005, Galindo et al. 2006).

Pocillopora damicornis and *Porites panamensis* were chosen because these species are among the major coral reef builders and have a widespread distribution along the west coast of Mexico. In addition, these species may have different asexual reproductive strategies based on their colonial morphology (branching versus massive) and sexual reproduction (broadcast spawning versus brooding) along Mexico's Pacific coast (Chávez-Romo and Reyes-Bonilla 2007; H.E.C.-R., D.A.P.-G., F.C.-S., H.R.-B., A.L.-P., P.M.-R., and M.P.H.-C., unpubl. data).

The goals of this study were to: (1) determine the influence of ENSO 1997–1998 on the allelic diversity of *P. damicornis* and *P. panamensis*, (2) determine the effect of

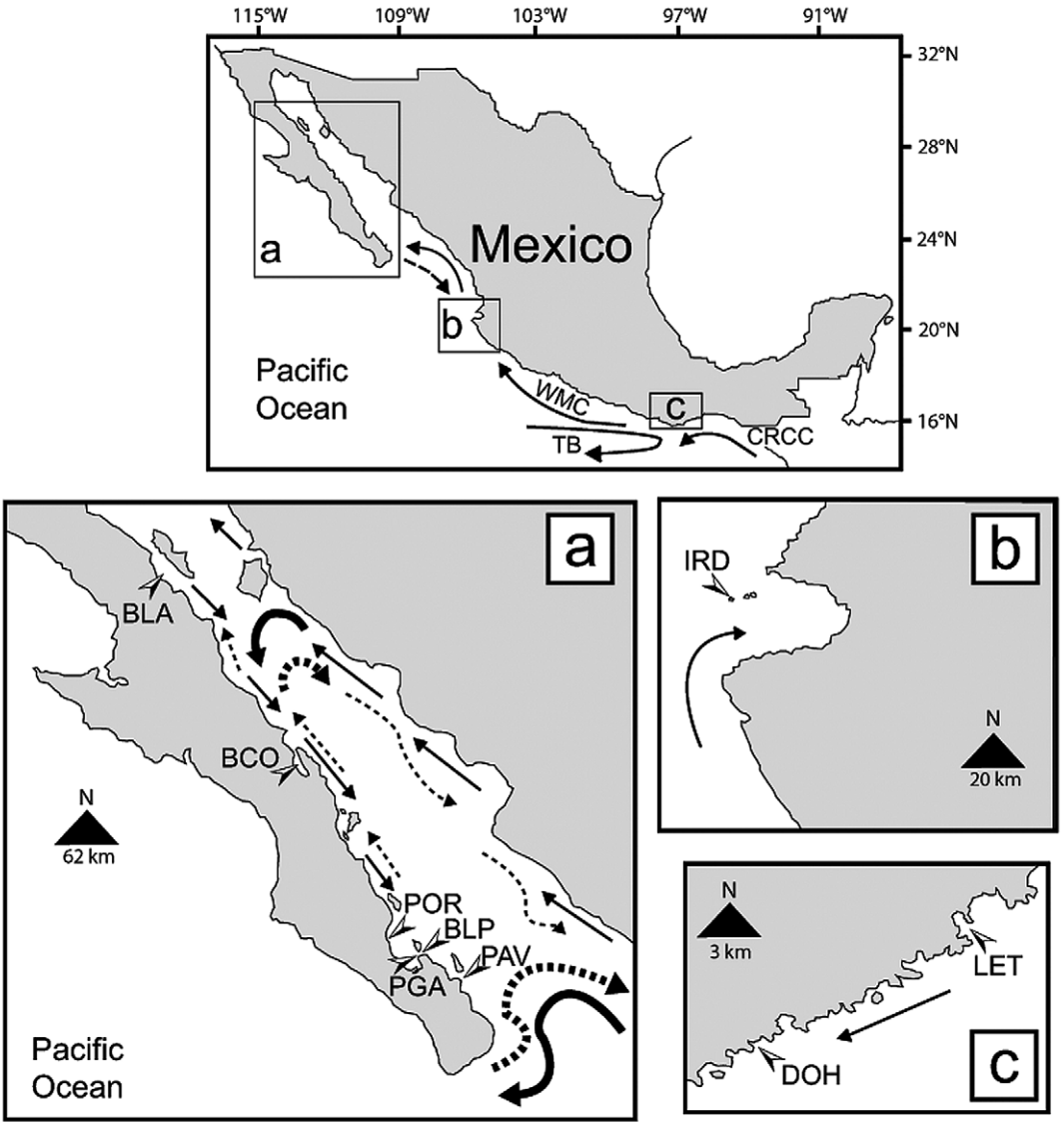

Figure 1. Locations sampled and general near-surface currents in the west coast of Mexico. Regions: (*a*) Gulf of California, (*b*) Bahía de Banderas, (*c*) Bahías de Huatulco. Locations: BLA, Bahía de Los Ángeles; BCO, Bahía Concepción; POR, El Portugués; PGA, Punta Gaviotas; BLP, south of Bahía de La Paz; PAV, Punta Arena de la Ventana; IRD, La Isla Redonda; DOH, Dos Hermanas; LET, La Entrega; WMC, West Mexican Current; TB, Tehuantepec Bowl; CRCC, Costa Rica Coastal Current. Solid lines in the Gulf of California in (*a*) indicate oceanic circulation in summer. Dashed arrows indicate a change of oceanic circulation in winter (Álvarez-Borrego 2002, Makarov and Jímez-Illesca 2003, Kessler 2006). Solid lines in (*b*) and (*c*) indicate general pattern of circulation.

larval recruitment and survivorship on genetic connectivity among coral populations along the west coast of Mexico, and (3) assess the level of genetic connectivity and discontinuities among coral populations along the west coast of Mexico, based on genetic and geographic information.

MATERIALS AND METHODS

Study Locations and Sample Collection

Pocillopora damicornis and *P. panamensis* were collected from three coastal regions (Figure 1). In the Gulf of California, two locations were sampled for *P. damicornis* (El Portugués, POR and Punta Gaviotas, PGA) and three areas for *P. panamensis* (Bahía de Los Angeles, BLA; Bahía Concepción, BCO; and the southern end of Bahía de La Paz, BLP). Both species were collected at Punta Arena de la Ventana (PAV) and La Isla Redonda (IRD), farther south and closer to the entrance of the Gulf of California. Along the mainland coast of Mexico in tropical waters, two locations were sampled for *P. damicornis* (Dos Hermanas, DOH and La Entrega, LET), and samples of *P. panamensis* were collected only at La Entrega. *Pocillopora damicornis* was collected from May through December 2006 and *P. panamensis* from August 2004 through December 2006.

To assess the influence of ENSO 1997–1998 on genetic diversity of *P. damicornis*, 10 to 48 adult colonies that survived that event (>15 cm branch length) and 6 to 18 juvenile colonies (<7 cm; colonies recruited after that event from 1999 through 2000) were collected at the same location. In addition, we collected 14 to 22 adult colonies (>10 cm, older than ENSO 1997–1998) and 6 to 12 juvenile colonies (<4 cm; colonies recruited from 2003 through 2004) of *P. panamensis* within the same location. All samples were collected at a depth of 1–9 m. Juvenile colonies of both species were sampled only at PAV, IRD, DOH, and LET. Heterogeneous sampling intensity among localities resulted from differences in local abundance. To avoid collecting samples with identical genetic fragments, samples were collected from individual colonies that appeared not to have originated from fragmentation and were separated by a minimum distance of 5 m. Coral samples were frozen in liquid nitrogen, transported to the laboratory, and stored at –80°C.

Allozyme Electrophoresis

Coral tissue extraction was conducted in Stoddart's buffer modification (Stoddart 1983, Weil 1992) using a sonic dismembrator. Two milliliters of blastate was centrifuged at 2,600 *g* for 10 min at 4°C. The resulting supernatant was placed in vials and stored at –80°C until analysis. To ensure homogeneous outcomes and avoid false negative results, concentration of proteins for each sample was determined, as described by Bradford (1976); 50 μg were used for the analysis of each enzyme system (Paz-García et al. 2009*c*). Prepared samples of allozymes were determined after protein separation by polyacrilamide gel electrophoresis at 4°C by a discontinuous gel system in native conditions (Manchenko 1994) using 8% acrylamide.

The genotype of each colony was determined for four enzyme systems revealing five polymorphic loci in both species, as described in two previous studies (Chávez-Romo et al. 2009, Paz-García et al. 2009*c*). These enzyme systems were leucine-glycyl-glycyl peptidase (*LGG-1*, E.C.3.4.11.1), malic enzyme (*ME-1*, E.C.1.1.1.40), glutamate dehydrogenase (*GDH-1 and GDH-2*, E.C.1.4.1.3), and esterase (*EST-1 and 2*, E.C. 3.1.1.1). Two loci were observed in the EST and GDH enzyme systems in *P. damicornis* and *P. panamensis*, respectively. Alleles at each locus were labeled alphabetically based on decreasing mobility from the origin.

Statistical and Seascape Spatial Genetic Analysis

Allelic diversity and observed (H_O) and expected (H_E) heterozygosities were calculated for each adult and juvenile location for both species, using GENALEX 6.2 (Peakall and Smouse 2006). Differences in allelic frequencies were tested between locations by the Markov chain method using GenePop 3.3 (Raymond and Rousset 1995). Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on unbiased genetic distance (Nei 1978) was used to assess the genetic similarity between adults and juveniles among the six areas for both species, as implemented in Tools for Population Genetic Analyses (TFPGA) (Miller 1997). Analyses were made by pooling adult and juvenile data for each species at each location; replicate multilocus genotypes were removed from

the data set to avoid upward bias in population differentiation measures (Baums et al. 2005, Whitaker 2006; H.E.C.-R., D.A.P.-G., F.C.-S., H.R.-B., A.L.-P., P.M.-R., and M.P.H.-C., unpubl. data).

Mean and standard deviations of θ (F_{ST}) and f (F_{IS}) (Weir and Cockerham 1984) were calculated by jackknifing over loci, and 95% confidence intervals were calculated by bootstrapping over loci. F_{IS} and F_{ST} estimations were performed in the Fstat program (Goudet 1995) and evaluated against 10,000 randomly permuted distributions. A sequential Bonferroni correction was applied to reduce the chance of type I error (Rice 1989). Pairwise F_{ST} values were estimated and used to calculate N_em under an island model ($N_em = (1/F_{ST} - 1)/4$ (Wright 1969) to estimate the magnitude of gene flow among locations. To test if there is a correlation between genetic divergence ($F_{ST} / [1 - F_{ST}]$) and geographical distance among populations (isolation by distance effects), a Mantel test was performed, comparing each pair of *P. damicornis* and *P. panamensis* locations. Mantel tests were carried out with 15,000 permutations using GenePop 3.3 (Raymond and Rousset 1995).

The statistical program Geneland was used to locate genetic discontinuities between populations, based on genetic and geographic information (Guillot et al. 2005). The program uses a Bayesian model that takes into account the spatial position of individual multilocus genotypes without prior information on the number of populations and degree of differentiation between them. All individuals from the same location were allocated the same GPS coordinates, because they were sampled within meters of each other. To infer the number of genetic clusters or populations (K) in the data set, 10 independent runs were made to check for convergence on K populations. Each run comprised 10^5 Markov chain Monte Carlo (MCMC) iterations with a thinning set at 100 and K genetic clusters varying from 1 to 10; the spatial and correlation models were considered. Once K was inferred, Geneland was run five times with this fixed value, 5×10^5 MCMC iterations, and the other parameters unchanged. These five runs were then postprocessed (with a burn-in of 1,000) to map posterior probabilities of population membership. Consistency of results across the five runs was visually checked.

The program Barrier (Manni et al. 2004) was used to identify shifts in gene flow based on geographic and genetic relationships among samples. To ensure that barriers were not identified by strong differentiation at only one or a few loci, the analyses were conducted using 100 matrices of θ values (Weir and Cockerham 1984) for each of the five polymorphic loci and using θ values based on all five allozyme loci. The robustness of barriers was proportional to the number of times each barrier was supported by the 100 data sets. Each data set supported a number of barriers of decreasing order, reflecting the relative strength of detected barriers.

RESULTS

Allelic diversity in both species was similar between adult colonies that survived ENSO 1997–1998 and recruits that settled after that event along the west coast of Mexico (Figure 2). The allelic diversity in adult and recruit locations for *P. damicornis* ranged from 1.6 to 2.1 and from 2.4 to 2.8 for *P. panamensis*. Recruits of both species from the southernmost locations showed slightly higher allelic diversity than adult colonies from the same location (Figure 2). Indeed, three *P. damicornis* recruits had private genotypes, two in DOH ($LGG\text{-}1^{AC}$ and $LGG\text{-}1^{CD}$) and one in LET ($LGG\text{-}1^{AC}$); only one adult colony showed the $LGG\text{-}1^{CD}$ genotype. Private genotypes were observed from LET for *P. panamensis* adults $EST\text{-}1^{AA}$ ($n = 9$) and $EST\text{-}1^{AB}$ ($n = 3$) and juveniles $EST\text{-}1^{AA}$ ($n = 6$).

The observed heterozygosis values ranged from 0.024 to 0.252 for *P. damicornis* and from 0.067 to 0.260 for *P. panamensis* (Table 1). Markov chain analyses indicated significant differences in allelic frequencies in most locations of both species (Tables 2, 3). Adult and recruit colonies from the same location did not differ significantly in the southern populations (DOH and LET) of either species. Recruit colonies of *P. damicornis* from IRD and PAV did not show allelic differentiation with adult colonies from POR and IRD (Table 2). PGA adult colonies and PAV recruits did not show differences. Finally, there were no sig-

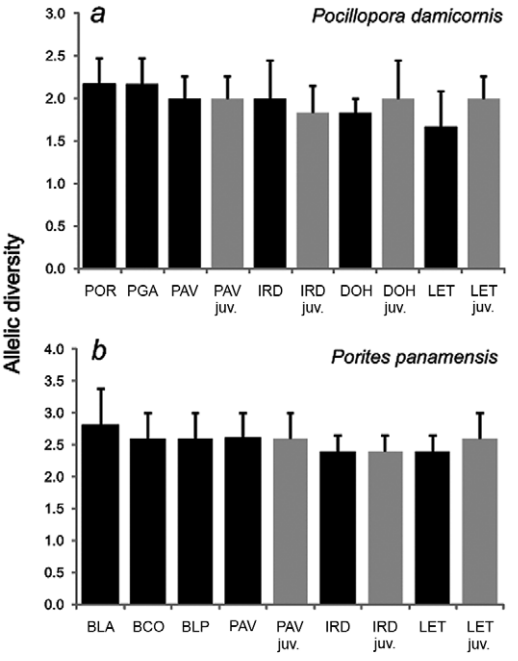

FIGURE 2. Allelic diversity in *Pocillopora damicornis* (*a*) and *Porites panamensis* (*b*). Adult colonies older than ENSO 1997–1998 shown in black and recruits after ENSO 1997–1998 in gray. Location abbreviations as in Figure 1. Bars indicate SE.

TABLE 1

Summary Statistics for *Pocillopora damicornis* and *Porites panamensis* at Each Location

Location	*N*	H_O	H_E	F_{IS}
Pocillopora damicornis				
POR	43	0.108	0.401	0.737
PAG	48	0.252	0.449	0.449
PAV	21	0.092	0.349	0.748
PAVj	10	0.133	0.358	0.659
IRD	14	0.116	0.391	0.727
IRDj	8	0.024	0.286	0.928
DOH	22	0.081	0.257	0.723
DOHj	18	0.095	0.204	0.560
LET	10	0.074	0.221	0.698
LETj	6	0.131	0.218	0.484
Porites panamensis				
BLA	20	0.260	0.569	0.561
BCO	20	0.180	0.548	0.687
BLP	20	0.190	0.539	0.662
PAV	22	0.127	0.477	0.744
PAVj	12	0.067	0.424	0.855
IRD	14	0.143	0.402	0.666
IRDj	6	0.133	0.411	0.726
LET	17	0.176	0.524	0.680
LETj	8	0.125	0.491	0.773

Note: Number of samples collected (*N*), average observed heterozygosities (H_O) and expected (H_E) at each location. Inbreeding coefficients (F_{IS}) (Weir and Cockerham 1984), averaged over all loci, were calculated using Fstat (Goudet 1995) and evaluated against 10,000 randomly permuted distributions. All F_{IS} values were significant ($P < .001$).

nificant differences between PAV adult colonies and IRD recruits and between recruit colonies of these locations in *P. panamensis* (Table 3).

Mean significant values of F_{IS} in both species (*P. damicornis* [$F_{IS} = 0.625$, $P < .01$] and *P. panamensis* [$F_{IS} = 0.686$, $P < .01$]) indicated reduction of heterozygous genotypes and high levels of local recruitment (Table 4). Cluster analysis (Nei 1978) of unbiased genetic distance showed three groups mainly by geographic proximity in both species for adults and juveniles (Figure 3): (1) inside the Gulf of California; (2) southeasternmost Baja California Peninsula and Bahía de Banderas; and (3) coast of Bahías de Huatulco.

Seascape spatial genetic analysis suggested two and three clusters along the west coast of Mexico for *P. damicornis* and *P. panamensis*, respectively (Figure 4). For *P. damicornis*, group contained populations from the Baja California Peninsula and Bahía de Banderas (Figure 4*a*). For *P. panamensis*, populations from inside the gulf and populations near the entrance of the gulf showed strong genetic discontinuity, forming two clusters in this region (Figure 4*c* and 4*d*). The last cluster was unequivocally from the southernmost locations (Bahías de Huatulco) for both species (DOH and LET) (Figure 4*b* and 4*e*). Two areas were indentified with shifts in gene flow by Barrier analysis (Figure 4). For both species, the first shift, in order of importance, was between Bahía de Banderas (IRD) and Bahías de Huatulco (DOH and LET) (Figure 4, I). The second barrier was detected only for *P. panamensis* from Bahía de La Paz (BLP) and the southern part of the peninsula (PAV) (Figure 4, II).

Mean significant values for F_{ST} in both species (*P. damicornis* [$F_{ST} = 0.072$, $P < .01$] and *P. panamensis* [$F_{ST} = 0.086$, $P < .01$]) indicate

TABLE 2

Allelic Differentiation Frequency in Adult and Juvenile Locations of *Pocillopora damicornis* along the West Coast of Mexico

Location	POR	PGA	PAV	PAVj	IRD	IRDj	DOH	DOHj	LET	LETj
POR	—									
PGA	***	—								
PAV	***	***	—							
PAVj	**	NS	**	—						
IRD	***	**	**	*	—					
IRDj	NS	*	*	NS	NS	—				
DOH	***	***	***	***	***	***	—			
DOHj	***	***	***	***	***	***	NS	—		
LET	***	***	***	***	***	***	***	*	—	
LETj	***	**	***	***	***	***	**	***	NS	—

NS, not significant; *($P < .05$); **($P < .01$); ***($P < .001$).

TABLE 3

Allelic Differentiation Frequency in Adult and Juvenile Locations of *Porites panamensis* along the West Coast of Mexico

Location	BLA	BCO	BLP	PAV	PAVj	IRD	IRDj	LET	LETj
BLA	—								
BCO	*	—							
BLP	*	***	—						
PAV	***	***	***	—					
PAVj	***	***	***	NS	—				
IRD	***	***	***	***	***	—			
IRDj	*	**	**	NS	NS	NS	—		
LET	***	***	***	***	***	***	***	—	
LETj	***	***	***	***	***	***	**	NS	—

NS, not significant; *($P < .05$); **($P < .01$); ***($P < .001$).

TABLE 4

Number of Alleles per Locus (Na) and F_{IS} and F_{ST} Values for *Pocillopora damicornis* and *Porites panamensis* in All Locations (Adults and Juveniles Pooled at Each Site, Where Applicable)

Pocillopora damicornis				*Porites panamensis*			
Locus	Na	F_{IS}	F_{ST}	Locus	Na	F_{IS}	F_{ST}
ME-1	2.000	0.405*	0.037^{NS}	ME-1	4.143	0.739*	0.101*
GDH-1	2.000	0.294*	0.099*	GDH-1	2.143	0.410*	0.024*
EST-1	2.000	0.422*	0.132*	GDH-2	2.000	0.004^{NS}	-0.035^{NS}
EST-2	2.714	1.000*	0.020^{NS}	EST-1	2.000	1.000*	0.291*
LGG-1	3.429	0.837*	0.061*	LGG-1	3.000	1.000*	0.056*
Over all loci		0.625*	0.072*	Over all loci		0.686*	0.086*
Mean (SD)	2.429 (0.639)	0.631 (0.137)	0.072 (0.019)	Mean (SD)	2.657 (0.929)	0.699 (0.163)	0.085 (0.058)
95% CI		0.378–0.860	0.037–0.104	95% CI		0.364–0.938	0.005–0.191

NS, not significant; *($P < .01$ after Bonferroni correction, except GDH-1 in *Porites* that was significant at $P < .05$); 95% CI, 95% confidence interval around the mean of F_{IS} and F_{ST}.

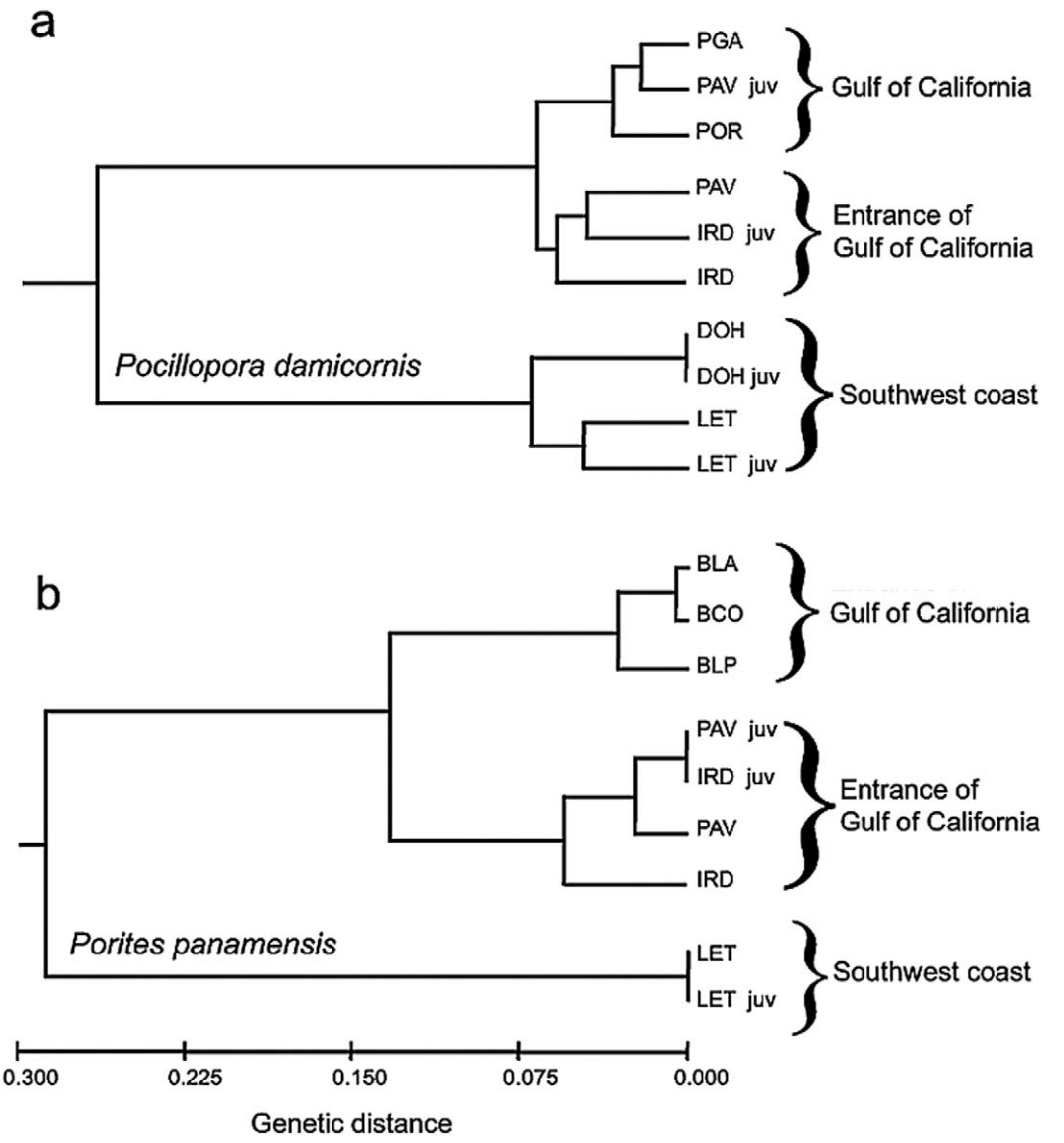

FIGURE 3. UPGMA cluster analysis based on unbiased genetic distance (Nei 1978) for adult and juvenile colonies of *Pocillopora damicornis* (*a*) and *Porites panamensis* (*b*) in the coastal areas off the west coast of Mexico. Location abbreviations as in Figure 1.

genetic structure in their populations along the west coast of Mexico (Table 4). Genetic differentiation in the Gulf of California, entrance to the gulf, and Bahías de Huatulco was also evident from significant pairwise F_{ST} estimates in both species (Tables 5, 6). Pairwise F_{ST} values ranged from 0.001 to 0.242 in *P. damicornis* and 0.001 to 0.167 in *P. panamensis* (Tables 5, 6). Two patterns of gene flow were observed in this study (Figure 5): (1) moderate to high gene flow between locations of Bahía de Banderas and Baja California Peninsula and (2) low gene flow among the Bahías de Huatulco populations.

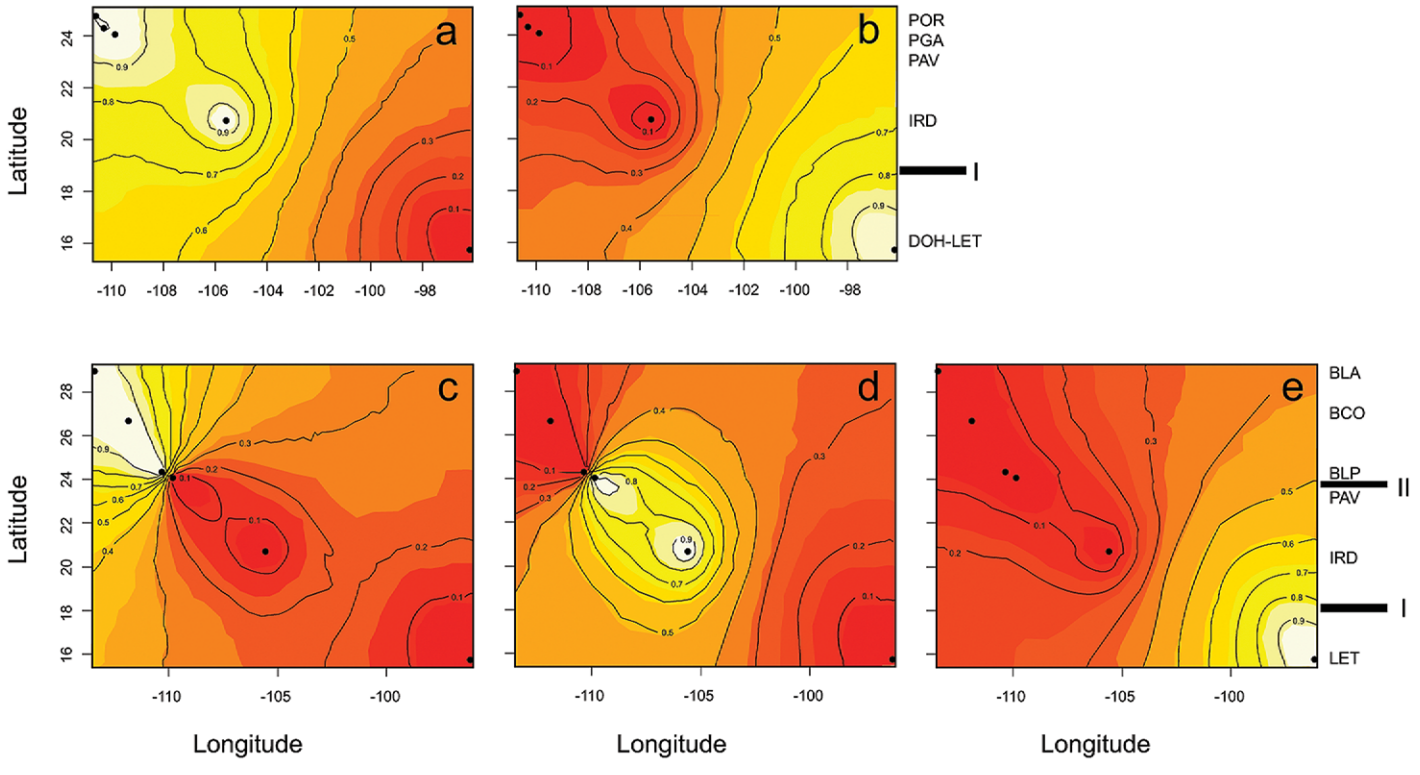

FIGURE 4. Map of posterior probabilities of population membership, spatial location of genetic discontinuities for populations of *Pocillopora damicornis* (*a–b*) and *Porites panamensis* (*c–e*), and major shifts in gene flow as identified by Barrier software. The highest membership values are in white, and the level curves illustrate the spatial changes in assignment values and spatial position of genetic discontinuities between locations. Main barriers to gene flow by order of importance shown in roman numerals. Location abbreviations as in Figure 1.

TABLE 5

Pairwise F_{ST} Values of *Pocillopora damicornis* Locations along the West Coast of Mexico

Location	POR	PGA	PAV	IRD	DOH	LET
POR	—					
PGA	0.012	—				
PAV	0.018	0.016	—			
IRD	0.004	0.023	0.001	—		
DOH	0.224**	0.165**	0.197**	0.242**	—	
LET	0.200**	0.132*	0.134*	0.235*	0.012	—

*($P < .05$); **($P < .001$).

TABLE 6

Pairwise F_{ST} Values of *Porites panamensis* Locations along the West Coast of Mexico

Location	BLA	BCO	BLP	PAV	IRD	LET
BLA	—					
BCO	0.001	—				
BLP	0.001	0.014	—			
PAV	0.038*	0.072*	0.070*	—		
IRD	0.081**	0.086*	0.141**	0.018	—	
LET	0.124**	0.129**	0.167**	0.159*	0.154*	—

*($P < .05$); **($P < .001$).

The highest gene flow in *P. damicornis* occurred in Bahía de Banderas and the peninsular locations ($N_em = 62–250$) (Figure 5); a moderate amount of gene flow was detected between the southwest populations (DOH versus LET, $N_em = 21$). The highest gene flow in *P. panamensis* was found in the northern part of the Gulf of California (BLA versus BCO, $N_em = 156$), and similar gene flow was detected between BLA and BLP ($N_em = 146$) (Figure 5). Moderate gene flow was observed among Bahía de Banderas and peninsular locations ($N_em = 1.5–14$) in this species. The lowest gene flow in both species was detected between southwest populations and the other locations ($N_em < 1.7$) (Figure 5), indicating strong barriers to gene flow in this region. N_em among locations ranged from 0.8 to 250 in *P. damicornis* and 1.2 to 156 in *P. panamensis* (Figure 5). Concurrently, a Mantel test was performed to measure the relationship between genetic divergence ($F_{ST}/[1-F_{ST}]$ values) and geographical distance among coral populations along the coasts of Mexico (Figure 6). There were significant relationships between these variables in *P. damicornis* ($R^2 = 0.638$, $P = .048$) and *P. panamensis* populations ($R^2 = 0.527$, $P = .025$), suggesting that genetic divergence among coral populations is associated with geographic distance in the case of *P. panamensis* and possibly in combination with other factors in *P. damicornis*.

DISCUSSION

Effect of ENSO 1997–1998 on Allelic Diversity in Coral Communities

Differences in allelic diversity were not found between adult colonies that survived the ENSO 1997–1998 and recruits in locations of *P. damicornis* and *P. panamensis* along the west coast of Mexico. Two possible explanations are (1) genetic diversity could have been equal before and after the ENSO event; however, this is unlikely because of large differences in mortality and live coral cover along the coast (Carriquiry et al. 2001, Reyes-Bonilla et al. 2002), and (2) genetic diversity was higher be-

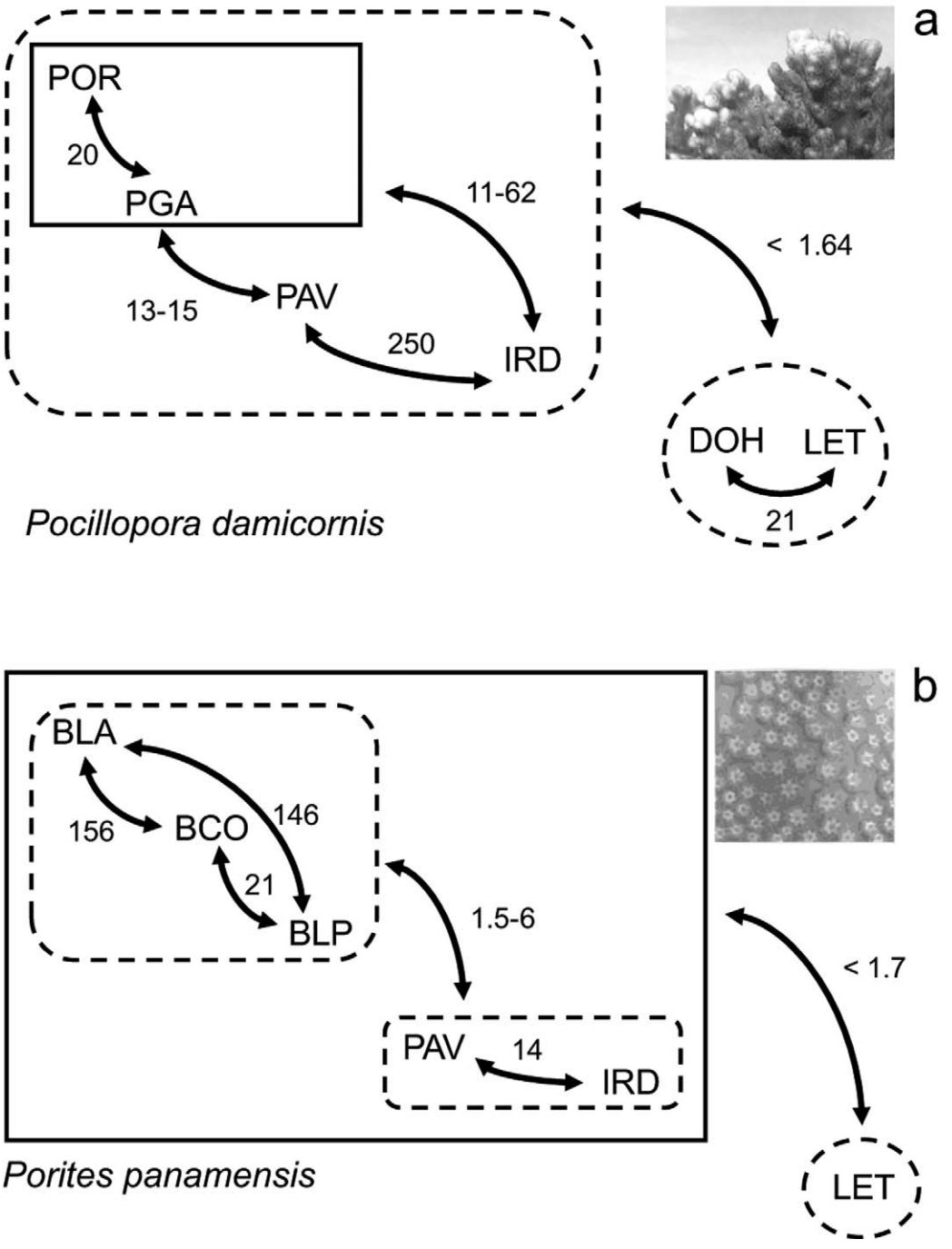

FIGURE 5. Estimates of gene flow (N_em) for *Pocillopora damicornis* (*a*) and *Porites panamensis* (*b*) in the west coast of Mexico. Locations inside the rectangles indicate gene flow among these locations with another location. Dashed lines indicate genetic groups obtained from seascape spatial analysis.

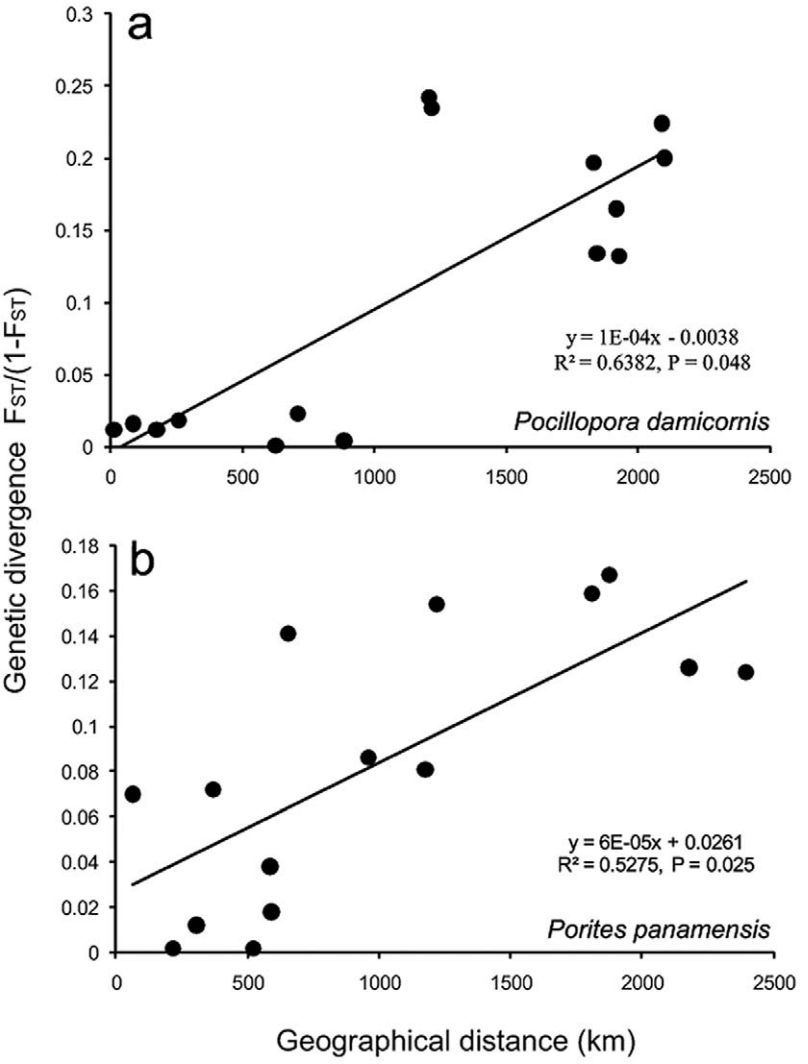

FIGURE 6. Isolation by distance test for *Pocillopora damicornis* (*a*) ($R^2 = 0.638$, $P = .048$) and *Porites panamensis* (*b*) ($R^2 = 0.527$, $P = .025$) populations from the west coast of Mexico. Mantel test with 15,000 permutations.

fore the ENSO 1997–1998 event, and recruits reflect the genetic diversity of the surviving adult colonies at these locations.

Although differences between adult and juvenile colonies were not significant, juvenile individuals along the southern coast (DOH and LET) had slightly higher allelic diversity than adult colonies (Figure 2), and some locations showed private genotypes. The presence of private genotypes in juveniles of both species could indicate immigrants from southern coral communities (Chávez-Romo et al. 2009, Paz-García et al. 2009*a*).

In this study, significant values for the F_{IS} statistics were observed. This heterozygous deficit is commonly observed in coral species (Adjeroud and Tsuchiya 1999, Miller and Ayre 2008). Several explanations were proposed, including inbreeding caused by high local recruitment, predominance of asexual

reproduction by fragmentation, lack of population mixing (Wahlund effect), and different mortality events from natural disturbances (Ayre et al. 1997, Ayre and Hughes 2004, Sherman et al. 2006, Constantini et al. 2007).

Coral communities experienced severe mortality during the ENSO 1997–1998, along with an impact on heterogeneity among localities of live coral cover along the west coast (Carriquiry et al. 2001, Reyes-Bonilla et al. 2002). Coral communities in the Gulf of California were less affected by the ENSO 1997–1998; perhaps upwelling zones diminished the effects on coral reefs by mixing cold and warm water (Carriquiry et al. 2001, Reyes-Bonilla et al. 2002).

Colonies of *P. damicornis* in Panama that are subjected to upwelling (temperatures < 20°C) show higher vulnerability to thermal stress at high temperatures than coral genotypes from nonupwelling locations (D'Croz and Maté 2004). Moreover, significant differences in allelic diversity of *P. panamensis* in Panama were present in upwelling and nonupwelling locations (Weil 1992). Upwelling zones may be an important mechanism explaining allelic diversity by promoting selection of genotypes adapted to cooler temperatures; thus, there is increasing susceptibility to bleaching during strong ENSO events. Of the areas with seasonal upwelling, the most important are located in the southern Gulf of California (close to Isla Cerralvo, between BLP and PAV), the northern part of the Bahía de Banderas, and the Gulf of Tehuantepec (Makarov and Jímez-Illesca 2003, Reyes-Bonilla 2003). Susceptibility to bleaching seems closely associated with the frequency of stress events and stress resistance of the hosts and symbionts among the coral communities, and this influences the genetic structure observed in our study.

Previous studies at the same localities have shown that *P. damicornis* and *P. panamensis* harbor different symbiont types that tolerate conditions of high turbidity, nutrients, seasonal upwelling, and bleaching events (LaJeunesse et al. 2008, Paz-García et al. 2009*b*). However, severe environmental stress associated with the ENSO 1997–1998 affected a greater proportion of *Pocillopora* colonies, during which only the most tolerant genotypic host-symbiont combinations survived in locations from Bahía de Banderas to Oaxaca (LaJeunesse et al. 2010). *Porites panamensis* was less affected than *P. damicornis* during the ENSO 1997–1998, and 10 different *Symbiodinium* types are associated with this species in the Gulf of California, Bahía de Banderas, and Oaxaca (LaJeunesse et al. 2008, Paz-García et al. 2009*b*; T. C. L., J. P., T. P., P.M.-R., A.L.-P., H.R.-B., M. W., and D.A.P.-G., unpubl. data). Combining genetic studies of host and symbiont before, during, and after ENSO events could help us understand how coral communities will survive during global warming.

Patterns of Connectivity along the West Coast of Mexico

Studies of connectivity levels and gene flow among populations are important in the evolutionary context. Moderate to high gene flow was observed inside and near the entrance of the Gulf of California, with a separation of 65–850 km among *P. damicornis* and 65–1,300 km in *P. panamensis*. The gene flow is probably from near-surface currents and cyclonic and anticyclonic eddies in the Gulf of California (Figure 1*a*) (Álvarez-Borrego 2002, Makarov and Jímez-Illesca 2003). Clustering of adults and juveniles from these areas (Figure 3) and Geneland analysis demonstrated a close genetic relationship between the southern Gulf of California and Bahía de Banderas coral communities (Figure 4), indicating that reefs in the southern Gulf of California export propagules to Bahía de Banderas coral communities as previous studies have suggested (Carriquiry and Reyes-Bonilla 1997, Carriquiry et al. 2001). Work by Saavedra-Sotelo et al. (2011) on ribosomal genes in *Pavona gigantea* (rDNA: ITS1-5.8S-ITS2) supports the close genetic relation between the two areas. In addition, this close genetic relation is favored by the frequency of sexual reproduction of coral species. Locations in the southern Gulf of California show sexual reproduction in *P. damicornis* in the warm season and frequent reproduction in *P. panamensis* (Chávez-Romo and Reyes-Bonilla 2007, Paz-García

et al. 2009*a*). Thus, these locations support genetic variation by sexual reproduction in both species and export larvae to damaged communities. This characteristic of a large population can generate moderate to high connectivity among locations from the Gulf of California, compared with the other populations (Figure 5).

Moderate gene flow in *P. damicornis* between reefs from Bahías de Huatulco (DOH versus LET, $N_em = 21$) represents the closest locations analyzed in this study (~10 km) and a genetic-geographical clustering; therefore, this close genetic variation was expected. Otherwise, low gene flow was observed in the southern coastal locations (DOH and LET) and the rest of the populations, with a separation of 1,200–2,100 km for *P. damicornis* and 1,210–2,500 km for *P. panamensis*.

Dispersion along the coast could be facilitated by the Costa Rica Coastal Current (CRCC) and local currents flowing from south to north that are close to the coast of Central America and Mexico (Figure 1) (Roden 1971, Glynn and Ault 2000). Several authors have suggested that the CRCC transports propagules from Central America to Oaxaca, as reflected by the close relation of coral species in this area (Glynn and Ault 2000, Reyes-Bonilla 2003). The colonies with private genotypes in Oaxaca could represent migrants from southern populations (Chávez-Romo et al. 2009, Paz-García et al. 2009*a*). However, recent observations indicate that anticyclonic flow around a shallow depression, the Tehuantepec Bowl, produces a strong southeastward near-surface current along the coast of Oaxaca into the Gulf of Tehuantepec that cuts off the CRCC, forcing it to turn offshore (Figure 1) (Kessler 2006). This current could represent one of the main barriers to gene flow in the southwest coast of Mexico. Population genetics studies that include Oaxaca and Central America are necessary to test if migration of coral species is possible between these regions.

Cluster analysis and Geneland analysis showed adults and juveniles of both species at the southern coastal locations as one isolated group (DOH and LET) (Figures 3 and 4). This indicates a high frequency of local recruitment and limited gene flow between these locations. Histological and genetic studies in these locations showed asexual reproduction by fragmentation mainly in *P. damicornis* and sexual (with a reproductive season of only 5 months) and asexual reproduction in *P. panamensis* (López-Pérez et al. 2007; H.E.C.-R., D.A.P.-G., F.C.-S., H.R.-B., A.L.-P., P.M.-R., and M.P.H.-C., unpubl. data). Moreover, high larval recruitment rates seem to be related to the coral cover of *P. panamensis* among the southern coast localities, suggesting limited dispersion (López-Pérez et al. 2007).

In addition, a significant relationship between genetic divergence and geographic distance for *P. panamensis* locations separated by 1,210–2,500 km (Figure 6) supports isolation by distance for this species. Several studies have suggested that the brooded larvae of *P. panamensis* have limited dispersion (Glynn and Ault 2000, López-Pérez et al. 2007, Paz-García et al. 2009*a*), and the results of our study confirmed this. Effects of isolation by distance are observed in other brooding coral species in populations separated by 20–50 km for *Seriatopora hystrix* (Maier et al. 2005) and *Balanophyllia elegans* (Hellberg 1996), respectively. In *P. damicornis*, effects of isolation by distance represent ~30% of the variation in coral communities in Australia (Sherman et al. 2006). In our study, Mantel tests revealed isolation by distance in both species (Figure 6). The model of isolation by distance indicates that gene flow is more common among close populations and diminishes among distant populations (Hellberg 1996, Palumbi 2003). Genetic differences between populations should accumulate if dispersal is geographically restricted. Therefore, this relationship can be increased by several factors that can limit gene flow: near-surface circulatory patterns, discontinuity of habitats, and frequency of sexual reproduction (Stoddart 1983, Palumbi 2003). These factors cannot be discounted in our results. For example, local near-surface circulation patterns in Bahía de Banderas and Bahías de Huatulco are complex and may have an effect on larval dispersion. In addition, major barriers of larval dispersion along the coast are located in that area (see

later in this section) (Glynn and Ault 2000, Reyes-Bonilla 2003). *Pocillopora damicornis* has an extremely low rate of sexual reproduction in Bahías de Huatulco. Colonies of this species did not recruit on tiles in Bahía de Banderas (Medina-Rosas et al. 2005, López-Pérez et al. 2007). Nevertheless, differences in genetic variation and gene flow were observed among populations of both species.

Cluster analysis and seascape genetic analyses confirmed genetic differentiation in two areas of the coast, depending on the coral species (Figures 3 and 4). Although *P. damicornis* and *P. panamensis* could have different strategies in sexual (broadcast spawning versus brooding) and asexual reproduction (fragmentation in branch versus massive colonies) along the coast (H.E.C.-R., D.A.P.-G., F.C.-S., H.R.-B., A.L.-P., P.M.-R., and M.P.H.-C., unpubl. data), both species showed mean significant F_{ST} values indicating genetic structure (Table 4). Moreover, a genetic study using nuclear genes in *Pavona gigantea* indicated significant genetic differentiation ($\Phi st = 0.159$, $P < .001$) among the same locations analyzed in this study (Saavedra-Sotelo et al. 2011). Previous studies have reported population subdivisions in coral species (Chávez-Romo et al. 2009, Paz-García et al. 2009*a*), other marine invertebrates, and fishes in coastal areas in the Gulf of California and the west coast of Mexico (Riginos and Nachman 2001, Valles-Jimenez et al. 2005, Lin et al. 2009). Our results indicate that different factors are influencing genetic structure, independent of species or reproductive mode but may, in response to geographic scale (physical and historical factors) and limited dispersion of larvae, produce high local recruitment in some locations (Chávez-Romo et al. 2009, Paz-García et al. 2009*a;* this study).

Barrier analysis shows two areas where gene flow is limited (Figure 4). The first barrier, in order of importance, occurs between Oaxaca and Bahía de Banderas and corresponds with major barriers or biofilters in dispersion of larvae. This includes many sandy beaches that fragment the habitats for reefs. Most important are sand bars along the coast of Colima, south to Oaxaca. Corals can gradually cross these barriers by colonizing small rocky patches (Glynn and Ault 2000, Reyes-Bonilla 2003), but our study showed extremely low gene flow. In addition, there are roughly 70 lagoon systems with mangroves as the main surrounding vegetation. These ecosystems can discharge high quantities of organic matter, nutrients, and freshwater to the coast and neighboring locations (200 times the annual volume of the lagoon and can vary from 100 to 400 times [CONABIO 1998, United Nations Environment Programme 2006]). These ecosystems probably limit dispersion of larvae.

The second barrier, in order of importance only in *P. panamensis*, occurs between Bahía de La Paz and the Baja California Peninsula (BLP and PAV) to its south. This is likely a result of a vicariant event caused by an ancient seaway across the peninsula. This seaway across the Isthmus of La Paz isolated the southernmost part of the peninsula as an island during the Pliocene (Aguirre-Léon et al. 1999, Riddle et al. 2000). A study of *Acanthemblemaria crockeri* (browncheek blenny) showed a high level of divergence between two morphotypes (Gulf form versus East Cape form) based on COI sequences, comparable with species-level differences in other fishes (Lin et al. 2009). Other studies confirm this only for terrestrial organisms, such as lizards and rodents (Aguirre-Léon et al. 1999, Riddle et al. 2000). This barrier might restrict gene flow and generate high genetic differentiation in marine organisms between locations separated by 30 to 60 km (Lin et al. 2009; this study).

The results of our study demonstrated that, possibly despite the different reproductive strategies of *P. damicornis* and *P. panamensis*, both showed a similar pattern of genetic structure and gene flow. Moderate to high gene flow and close genetic relation between adults and recruits from the far southern part of the coast of the Baja California Peninsula and severely damaged Bahía de Banderas populations support a propagule exchange after the ENSO 1997–1998 event. This indicates that several factors, near-surface currents, seasonal sexual reproduction, habitat discontinuity, and episodes of bleaching of coral populations, are as

important as reproductive strategy and larval type to predict connectivity among coral reefs.

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