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No gene flow across the Eastern Pacific Barrier in the reef-building coral *Porites lobata*

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Abstract

The expanse of deep water between the central Pacific islands and the continental shelf of the Eastern Tropical Pacific is regarded as the world's most potent marine biogeographic barrier. During recurrent climatic fluctuations (ENSO, El Niño Southern Oscillation), however, changes in water temperature and the speed and direction of currents become favourable for trans-oceanic dispersal of larvae from central Pacific to marginal eastern Pacific reefs. Here, we investigate the population connectivity of the reef-building coral *Porites lobata* across the Eastern Pacific Barrier (EPB). Patterns of recent gene flow in samples (n = 1173) from the central Pacific and the Eastern Tropical Pacific (ETP) were analysed with 12 microsatellite loci. Results indicated that *P. lobata* from the ETP are strongly isolated from those in the central Pacific and Hawaii (F'_{ct} = 0.509; P < 0.001). However, samples from Clipperton Atoll, an oceanic island on the eastern side of the EPB, grouped with the central Pacific. Within the central Pacific, Hawaiian populations were strongly isolated from three co-occurring clusters found throughout the remainder of the central Pacific. No further substructure was evident in the ETP. Changes in oceanographic conditions during ENSO over the past several thousand years thus appear insufficient to support larval deliveries from the central Pacific to the ETP or strong postsettlement selection acts on ETP settlers from the central Pacific. Recovery of *P. lobata* populations in the frequently disturbed ETP thus must depend on local larval sources.

Keywords: central Pacific, Clipperton Atoll, Eastern Tropical Pacific, gene flow, microsatellite, *Porites lobata*

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Introduction

The geographic isolation of shallow-water tropical corals living in the eastern Pacific has stimulated interest in their origin and evolution. As elsewhere in tropical seas, habitats formed by these corals harbour a rich diversity of associated species and contribute to local economies via fisheries and reef-related tourism (Jameson & McManus 1995; Davidson *et al*. 2003). However, coral communities in the eastern Pacific often occur where environmental conditions for reef growth are marginal (Glynn 1984; Guzman & Cortes 1993; Cortes 1997). These precarious conditions have spurred interest in how these reef corals persist (Richmond 1985; Glynn *et al*. 1991; Glynn & Colgan 1992). Here, we assess one component of this persistence, the extent of gene flow between coral populations in the eastern Pacific and populations further west, to answer long-standing questions for marine biogeographers and provide critical information for the management of coral reefs.

The Eastern Tropical Pacific biogeographic zone (Fig. 1) stretches from the Sea of Cortez to the northern Pacific coast of Peru (Cortes 1997) and became isolated from the Caribbean *c*. 3 Mya with the closure of the Central American Portal (Duque-Caro 1990; Coates & Obando 1996). A 5000 to 8000-km deep-water barrier

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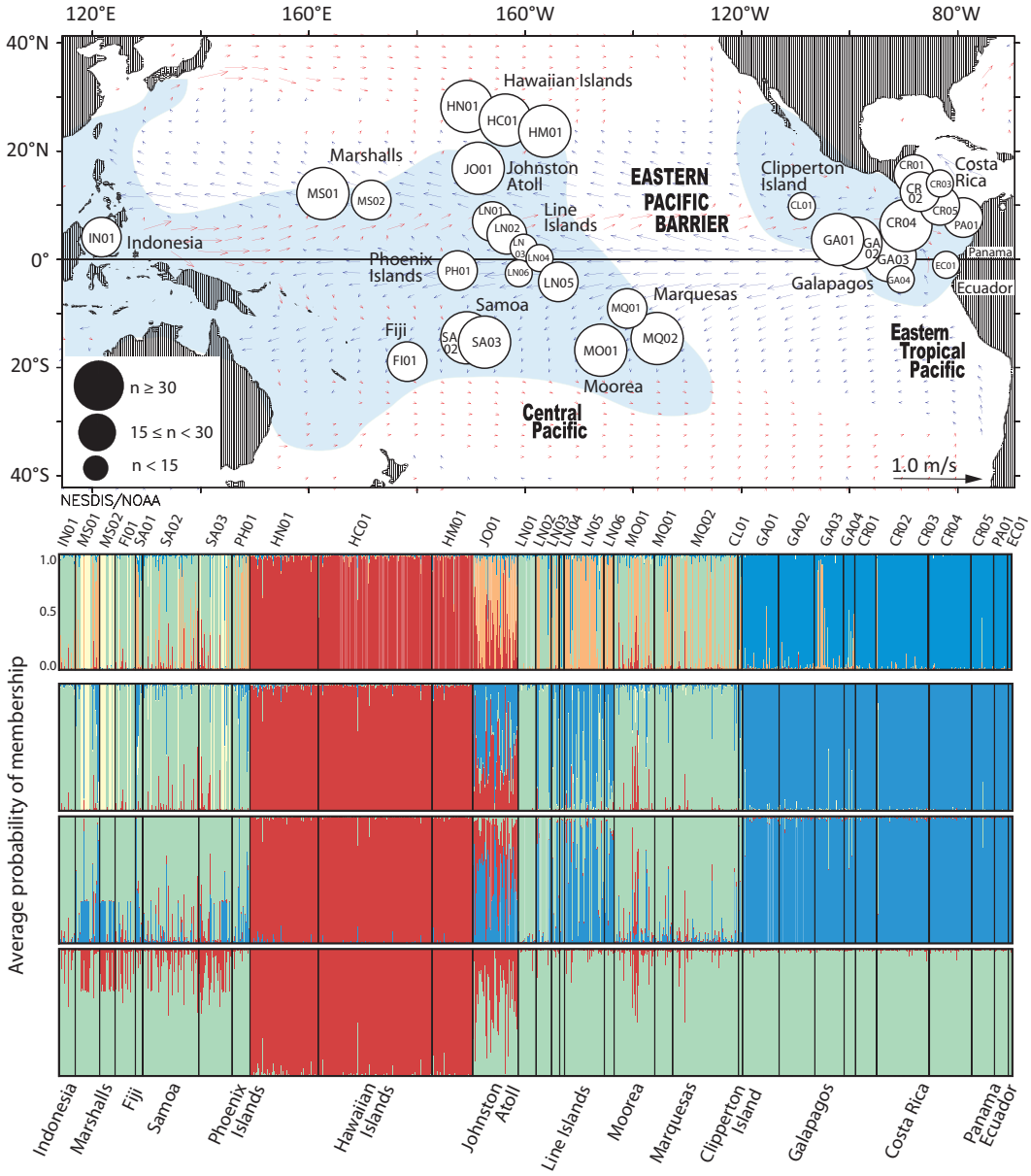

Fig. 1 *Porites lobata* population structure across the central and Eastern Tropical Pacific. The size of the circles is proportional to the sample size (*n*, chart inset) collected at each location. Bar graphs show the average probability of membership (*y*-axis) of individuals (n = 1173, *x*-axis) in K = 5 to K = 2 clusters (shown in descending order) as identified by STRUCTURE.

(Dana 1975; Grigg & Hey 1992) now separates Eastern Tropical Pacific biotas from the Indo-West Pacific region. Darwin (Darwin 1880, p. 317) regarded this eastern Pacific barrier (EPB) as 'impassable', and Ekman (Ekman 1953) concluded that it is the world's most potent [soft] marine barrier to larval dispersal.

The present-day eastern Pacific coral fauna has been viewed as a relict derived from pan-Tethyan, western Atlantic (Caribbean) species formerly connected via the shallow Central American corridor (McCoy and Heck 1976; Heck and McCoy 1978). After the closure of the Central American Portal, the eastern Pacific communities were modified by extinctions and evolutionary changes mediated by unfavourable climatic conditions during the late Pliocene and Pleistocene (Budd 1989, 1994).

In contrast, Dana (1975) [and later Glynn & Wellington (1983) and Cortes (1997)] argued that the eastern Pacific coral reef biota was established more recently (since Pleistocene low sea level stands) by dispersal from the other side of the EPB, chiefly via the North Equatorial Counter Current (NECC). These conclusions are based on the taxonomic affinities of reef-building

corals inhabiting the eastern Pacific and on their potential for dispersal, inferred from a combination of larval durations, rafting capabilities and trans-Pacific current patterns.

Glynn & Ault (2000) defined three main biogeographic provinces in the modern eastern Pacific based on presence/absence data of reef-building coral species. The Equatorial province, including mainland Ecuador to Costa Rica, the Galapagos Archipelago and Cocos Island, is the most species-rich with 17–26 species, followed by the Northern province (which includes mainland Mexico and the Revillagigedo Islands) with 18–24 species. The Island Group province (including Malpelo Island and Clipperton Atoll) is relatively species poor (7–10 species) and extends across the EPB to include some islands/atolls in the central Pacific.

In terms of ongoing connectivity, gene flow between central and eastern Pacific populations has been inferred in fish (Rosenblatt & Waples 1986; Lessios & Robertson 2006), sea urchins (Lessios *et al.* 2003) and seastars (Nishida & Lucas 1988), but little is known about the extent of gene flow across the EPB in reef-building corals. Comparisons of *P. lobata* between South Pacific Islands and the Galapagos detected moderate levels of genetic differentiation in the ITS-1 and ITS-2 regions (Forsman 2003). Restricted dispersal between the central and eastern Pacific was also evident based on ITS sequence data of *Pocillopora* spp. (Combosch *et al.* 2008); however, the taxonomy of the eastern Pacific pocilloporids is in flux (Pinzon & LaJeunesse 2011) complicating the interpretation of these results beyond problems inherent to interpretation of multi-copy markers like ITS.

The severe 1982–1983 El Niño Southern Oscillation (ENSO) event (Glynn 1988) forced the recognition that changes in Pacific circulation patterns and transport rates could greatly influence west-to-east dispersal routes. The 1982–1983 and 1997–1998 ENSOs resulted in extensive mortality of reef-building corals (Glynn 1997, Glynn & Ault 2000). Soon after, however, some Indo-West Pacific colonists arrived (Lessios *et al.* 1996, Reid and Kaiser 2001). Because these classic eastern Pacific ENSO events accelerate the rate and latitudinal extent of eastward flow along the North Equatorial Countercurrent (thus halving the transport time across the EPB), they should enhance the eastward transport of larvae across the EPB (Richmond 1990; Glynn *et al.* 1996).

The escalating magnitude and frequency of ENSO events since the mid-1970s (Trenberth & Hoar 1996; Rajagopalan *et al.* 1997) further suggests that the pattern of trans-Pacific gene flow between coral populations may have undergone recent changes. However, this change may be driven by the emergence of a new type of El Niño, the Central Pacific (CP) El Niño (Kao & Yu 2009; Kug *et al.* 2009; Lee & McPhaden 2010), in which the warm water anomaly associated with the sea surface warming event is shifted westwards to the central Pacific. Current models of global warming predict that the ratio of CP- to EP (eastern Pacific) – ENSO will continue to increase (Yeh *et al.* 2009). Thus, predictions regarding the effects of ENSO events on trans-EPB dispersal by corals remain unclear.

Porites lobata is an ecosystem engineer that builds the framework of reefs throughout the Pacific (Glynn *et al.* 1994). *Porites* spp. can become large (one giant measured 7 m tall and 41 m in circumference, Brown *et al.* 2009) and old (approaching 1000 years, Potts *et al.* 1985), and skeleton cores provide long-term temperature records, akin to tree ring data (Cole *et al.* 1993). *P. lobata* produces planktonic larvae via gonochoric broadcast spawning (Glynn *et al.* 1994). Eggs contain symbiotic algae (Glynn *et al.* 1994). Thus, larvae can obtain nutrition during their planktonic lives, thereby extending their dispersal potential (Richmond 1987), although the duration of their pelagic development is unknown. Phylogenetic and morphological analyses provide evidence for unrecognized species diversity within the genus (Forsman 2003; Forsman & Birkeland 2009; Forsman *et al.* 2010); however, only limited information is available on the population genetic structure of Pacific *Porites* species. Polato *et al.* (2010) showed that *P. lobata* follows an isolation-by-distance pattern along the Hawaiian Archipelago. Little gene flow connected the Hawaiian Islands and their closest neighbour, Johnston Atoll, 2500 km away.

Here we test the following hypotheses using multilocus genotypes generated from a set of polymorphic microsatellite markers: H_o) Samples of *P. lobata* from the central and eastern Pacific show evidence of population differentiation owing to low levels of ongoing gene flow; H_i) Isolated eastern Pacific atolls/islands in the Island Group of Glynn & Ault (2000, Clipperton) are connected to central Pacific atolls/islands (Line Islands, Johnston, Hawaii) in accordance with coral biogeographic patterns; H_{ii}) Populations within the Eastern Tropical Pacific are subdivided owing to limited gene flow between oceanic island and continental shelf populations.

Materials and methods

Sample collection

Samples were collected from locations in two regions, the central Pacific (CP) and the Eastern Tropical Pacific (ETP, Table 1, Fig. 1). Small fragments (~1 cm^2) were broken from colonies using a hammer and chisel and stored in 70% ethanol at −20 °C until DNA extraction

Table 1 *Porites lobata* samples (n = 1264) were obtained from three regions (CP = central Pacific West (W) and East (E), HI = Hawaii, ETP = Eastern Tropical Pacific) and 33 sites

Region	Subregion	Site	Site name	*N*	Ng	Ng/*N*	Latitude	Longitude
CP (W)	Indonesia	IN01	Kalimantan*	20	20	1.00	−1.10612	114.1439
	Marshalls	MS01	Kwajalein	30	30	1.00	9.200792	167.4228
		MS02	Majuro	20	19	0.95	7.115578	171.184
	Fiji	FI01	Fiji	33	25	0.76	−16.5782	179.4144
	Samoa	SA01	American Samoa	9	9	1.00	NA	NA
		SA02	Ofu/Olosega	78	69	0.88	−14.1528	−169.647
		SA03	Tutuila	46	41	0.89	−14.2928	−170.699
	Phoenix Islands	PH01	Enderbury	23	22	0.96	−3.13264	−171.089
	Hawaii North	HN01	Hawaii North†	84	84	1.00	28.14504	−177.006
HI	Hawaii Central	HC01	Hawaii Central‡	149	140	0.94	23.74846	−166.158
	Hawaii Middle	HM01	Hawaii Main§	53	50	0.94	20.82216	−156.341
CP (E)	Johnston Atoll	JO01	Johnston Atoll	58	56	0.97	16.74463	−169.526
	Line Islands	LN01	Kingman Reef	22	22	1.00	6.396564	−162.416
		LN02	Palmyra	19	19	1.00	5.881678	−162.085
		LN03	Teraina	10	10	1.00	4.683889	−160.38
		LN04	Tabuaeran	7	6	0.86	3.867286	−159.324
		LN05	Christmas	49	49	1.00	1.982039	−157.265
		LN06	Jarvis	12	12	1.00	−0.37941	−160.015
	Moorea	MO01	Moorea	50	50	1.00	−17.5261	−149.818
	Marquesas	MQ01	Hiva Oa	22	22	1.00	−9.76595	−139.008
		MQ02	Motane	82	81	0.99	−9.98589	−138.829
ETP	Clipperton	CL01	Clipperton	5	5	1.00	10.29989	−109.216
	Galapagos	GA01	Darwin	46	45	0.98	1.616525	−91.9733
		GA02	Wolf	45	44	0.98	1.336935	−91.806
		GA03	Marchena	38	36	0.95	0.318369	−90.4691
		GA04	Southern Galapagos¶	14	14	1.00	−0.72846	−90.059
	Costa Rica	CR01	Marino Ballena	32	26	0.81	9.104583	−83.7068
		CR02	Caño	79	64	0.81	8.71067	−83.8911
		CR03	Drake Bay	8	1	0.13	8.6713	−83.7267
		CR04	Gulfo Dulce	29	28	0.97	8.727433	−83.3863
		CR05	Cocos Island	55	52	0.95	5.534834	−87.0875
	Panama	PA01	Panama**	17	17	1.00	8.223265	−80.3817
	Ecuador	EC01	LaLlorona	20	5	0.25	1.476383	−80.7937
Total				1264	1173			
Mean				38.0	35.5	0.91		
SD				30.9	29.0	0.20		

Sites are arranged in approximately west-to-east and north-to-south order. Given are total sample size (*N*), the number of unique multilocus genotypes (genets; Ng = 139) and the ratio of genets over samples collected (Ng/N). GPS locations are in decimal degrees (WGS84).

*Krakatau, Bankga, Lembeh Strait, Komodo, Bali.

†Samples from Polato *et al*. 2010: Pearl and Hermes, Midway, Kure.

‡Samples from Polato *et al*. 2010: Maro, Necker, French Frigate Shoals, Nihoa, Gardener Pinnacles.

§Samples from Polato *et al*. 2010: Oahu, Hawai'i.

¶Santiago, Baltra, Champion.

**Uva, Contadora, Coibita.

could be performed. Genomic DNA was extracted using the Qiagen DNeasy 96 blood and tissue kit. Data for Hawaii and Johnston (n = 318) were published in Polato *et al*. (2010) but were generated in the same laboratory as data presented here.

Microsatellite analysis

A total of 12 microsatellite loci were used (Table S1): eight from Polato *et al*. (2010) and four additional loci (pl1370, pl1483, pl1868 and pl905) developed for this

study (Table S1). Briefly, PCRs using fluorescently labelled primers were performed in four multiplex reactions consisting of 2–4 primer pairs each and in one single-plex reaction (Table S1). Thermal cycling was performed in an MJ Research PT200 or an Eppendorf Mastercycler Gradient cycler with an initial denaturation step of 95 °C for 5 min followed by 35 cycles of 95 °C for 20 s; 52–56 °C (see Table S1) for 20 s and 72 °C for 30 s. A final extension of 30 min at 72 °C ensured the addition of a terminal adenine (Brownstein *et al.* 1996). Fragments were analysed using an ABI 3730 sequencer with an internal size standard (Genescan LIZ-500; Applied Biosystems). Electropherograms were visualized and allele sizes were called using GENEMAPPER 4.0 (Applied Biosystems). An allele calling error rate of 0.01 was determined based on repeated runs of 100 samples.

Samples that failed to amplify for more than 2 of 12 loci (n = 290 of 1554 or 18%) were excluded from all further analysis. The remaining individuals (n = 1264) thus sometimes contained missing data at one (n = 259) or two (n = 182) loci. In this data set, there was an overall average failure rate of 4% (SD 3%) and a per locus failure rate of <10% for each locus in the included samples.

Analysis of multi-locus genotype data

Unique multi-locus genotypes (MLG) were defined in GENALEX 6.4 by requiring complete matches at all loci. Considering missing data in the assignment resulted in the same number of unique MLGs (n = 1173) as ignoring the missing data. Only unique MLGs were used in subsequent analyses. Potential genotyping errors were detected with GENCLONE 2.0 (Arnaud-Haond & Belkhir 2007) and spurious allele calls were corrected by reexamining the allele calls in GENEMAPPER 4.0.

Unique MLGs were tested for conformation to Hardy-Weinberg expectations and linkage disequilibrium (LD) using Genepop on the Web (Raymond & Rousset 1995). We used the R-package FDRtool to adjust P-values for multiple testing (Strimmer 2008). Large heterozygote deficits are common in marine invertebrates (Addison & Hart 2005) including corals (Baums 2008). We attempted to distinguish among some of the possible causes by estimating null allele frequencies while accounting for inbreeding using INEST (Chybicki & Burczyk 2009) and distinguished between inbreeding and self-fertilization using RMES (David *et al.* 2007).

Because observed allelic diversity can be proportional to sample size (Leberg 2002), the program HP-RARE (Kalinowski 2005) was used to compute rarefied allelic richness. Nonparametric Kruskal–Wallis ANOVA was used to test for significant differences among diversity measures because of slight deviations from normality.

To inspect for a relationship between uncorrected F_{st} and geographic distance, Mantel's test for isolation by distance (IBD) was run in GENODIVE with 999 bootstrap permutations. Principal component analysis (PCA) was performed on a matrix of covariance values calculated from population allele frequencies (GENODIVE). CR03 was excluded from IBD and PCA analysis based on its small sample size (Ng = 1).

Population clustering

STRUCTURE v2.3.3 (Pritchard *et al.* 2000) was used to estimate the number of population clusters (K). STRUCTURE assigns genotypes to clusters by minimizing linkage disequilibrium and deviations from Hardy–Weinberg within clusters. Preliminary analyses showed that location priors did not increase resolution of population clustering in our data, so only runs without location priors are reported. Correlated allele frequencies and admixed populations were assumed based on previous work on this (Polato *et al.* 2010) and other broadcast spawning corals (Baums *et al.* 2006, 2010; Foster *et al.* online early). Changing these assumptions did not alter the outcome of the clustering (Fig. S1). Values of K = 1–33 were tested by running replicate simulations ($\geq$3) with 10^6 Markov Chain Monte Carlo (MCMC) repetitions each, and a burn-in of 10 000 iterations on the Bioportal of the University of Oslo (Kumar *et al.* 2009). The most likely value for K based on STRUCTURE output was determined by plotting the log probability [L(K)] of the data over multiple runs and comparing that with ΔK (Evanno *et al.* 2005) as implemented in STRUCTURE HARVESTER (Earl 2009). Results of the three STRUCTURE runs were merged with CLUMPP (Jakobsson & Rosenberg 2007) and visualized with DISTRUCT (Rosenberg 2004).

The robustness of the STRUCTURE results was tested using two other clustering programs with different algorithms and assumptions: INSTRUCT, which models inbreeding and does not assume Hardy–Weinberg equilibrium (Gao *et al.* 2007) and GENELAND (Guillot *et al.* 2005, 2008), which can account for null alleles but assumes uncorrelated allele frequencies (Gao *et al.* 2011), a condition likely violated by admixture here. In INSTRUCT, the model to infer population structure and inbreeding coefficients was run in three parallel chains with 5×10^5 MCMC repetitions and a burn-in of 10^5 iterations each. We estimated the number of clusters in GENELAND without specifying any priors. The number of iterations was 10^6, the thinning interval was 10^3, and the maximum number of populations K = 20. Convergence of the Markov Chain was checked by inspecting the log-likelihood posterior densities and by comparing the log-likelihood values of multiple independent runs (n = 3).

Analysis of molecular variance (AMOVA) (Excoffier *et al.* 1992) on F_{st} and F'_{st} (Meirmans 2006) as implemented in GENODIVE was used to test hypotheses based on both biogeography and on the clusters identified by STRUCTURE. Statistical analyses were performed at multiple scales (Table 1): by site, within regions (Hawaii, central Pacific, Eastern Tropical Pacific) and among regions. Site CR03 was excluded because of its low sample size ($N_g = 1$).

We were particularly interested in the genetic connection of Clipperton Atoll to the central and eastern Pacific. To inspect Clipperton's clustering, we assigned all multi-locus genotypes to their region of origin (central Pacific, Hawaii or Eastern Tropical Pacific) while treating the five Clipperton samples as unknowns. We did these runs using three replicates with 10^7 repetitions (10^6 discarded as burn-in), assuming correlated allele frequency and admixture. STRUCTURE then returned the assignment probability of each of the five Clipperton samples to one of the three regions. Further, multilocus genotypes that had a significantly lower assignment probability for the cluster they were sampled in than for one of the other two clusters were flagged as potential migrants in this analysis.

Results

Multi-locus genotyping

Our genetic analysis of 1264 sampled ramets yielded 1173 unique multi-locus genotypes (Tables 1 and 2). The median combined probability of identity was 8.7×10^{-11}. Thus, samples with identical multi-locus genotypes can be confidently ascribed to clonal reproduction. The high proportion of unique MLGs over the total number of samples collected (mean $Ng/N = 0.91 \pm 0.20$, Table 1) confirms earlier findings of limited asexual reproduction in *Porites lobata* (Polato *et al.* 2010). Populations ranged from almost entirely clonal (site CR03 in Costa Rica) to entirely sexual ($n = 14$ sites, Table 1), although detailed comparisons of clonal structure among sites would be misleading owing to variation in sampling effort. Repeated multilocus genotypes (i.e. exact matches at all loci) were always confined to a single sampling location (i.e. <2 km).

Tests of LD and deviation from HWE

Only 7.9% of 2178 tests rejected the null hypothesis of independence among loci after FDR correction (Strimmer 2008) when testing the 33 sites as defined by geography (Table 1), indicating that loci are largely in linkage equilibrium. Eighteen percent of 396 tests showed significant deviation from HWE after FDR correction when testing the 33 sites as defined by geography.

Conventional algorithms to estimate the frequencies of null alleles require *a priori* information on the level of inbreeding (van Oosterhout *et al.* 2006; Chybicki & Burczyk 2009). In the absence of such information, we used INEST (Chybicki & Burczyk 2009) to estimate the contribution of inbreeding and null alleles to heterozygote deficits (Table S2, Fig. 2). Individual inbreeding values were generally low ($F_{i\ mean} = 0.03$; CI 95 = 0.00–0.13, Table S1) and null allele frequencies ranged between 0.08 and 0.24 across loci and populations (Fig. 2). Interestingly, loci showed significant differences in the frequency of null alleles across the three regions (Fig. 2): each region had at least one locus with lower null allele frequency then other regions. In accordance with the findings of INEST, selfing rates were not significantly different from zero overall ($s_{all} = 0.01$, 95% CI95 = 0–0.26, $\chi^2 = -160.66$, DF = 1, $P = 1$) and selfing rates did not differ among populations ($s_{average} = 0.03$, CI95 = 0.01–0.06, $\chi^2 = 12.80$, DF = 16, $P = 0.69$).

The high frequency of null alleles at some loci and locations might lead to overestimation of the number of clusters K when running STRUCTURE (STRUCTURE documentation v. 2.3.3). We thus reran STRUCTURE using the same settings as previously on a data set excluding the four loci with the highest frequencies of nulls (PL1483, PL1556, PL1968, PL340). The remaining eight loci had null allele frequencies below 15%. The results (online Supporting information) are consistent with the findings using all 12 loci with respect to the most likely number of population clusters and patterns of population differentiation and IBD.

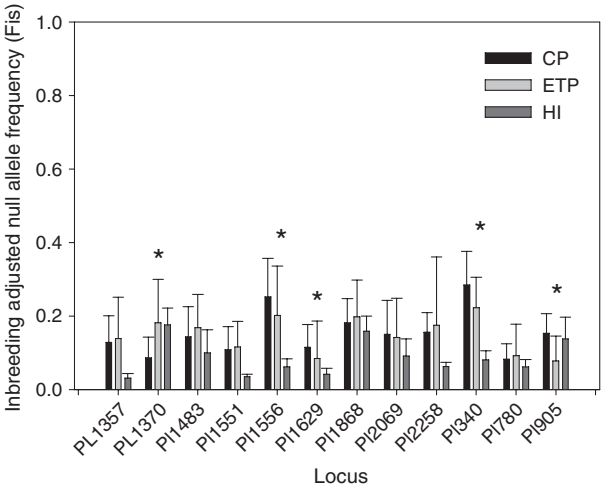

Fig. 2 *Porites lobata*: Frequency of inbreeding-adjusted null alleles (+1 SD) over 12 loci across the central Pacific (CP), the Hawaiian Archipelago (HI) and the Eastern Tropical Pacific (ETP). A Kruskal–Wallis one-way analysis of variance indicated differences in null allele frequency within loci across regions (asterisk, $P < 0.05$).

Genetic diversity and population structure

Sites in the central Pacific had higher average allelic richness (AR(20)) and private allele richness (AP(20)) compared with Hawaii and the Eastern Tropical Pacific ($P < 0.001$, DF 2, One-Way Kruskal–Wallis ANOVA) when rarefied to a sample size of three sites per region and 20 genes per site (Fig. 3). Similarly, the number of effective alleles (AE) averaged across sites was highest in the central Pacific ($AE_{mean} = 6.24$, 1.83 SD) followed by Hawaii ($AE_{mean} = 5.81$, 0.76 SD) and the Eastern Tropical Pacific ($AE_{mean} = 4.34$, 1.38 SD).

The signature of IBD was weak when the entire data set was considered (Fig. 4A, $r^2 = 0.07$; $P = 0.001$). Regionally, IBD was nonsignificant in the western portion of the central Pacific (Fig. 4B, $r^2 = 0.00$; $P > 0.1$), moderate in the eastern portion of the central Pacific (Fig. 4C, $r^2 = 0.35$; $P < 0.001$) and strong in the ETP (Fig. 4D, $r^2 = 0.43$; $P < 0.01$), but only when the most distant site (Clipperton) was included (Fig. 4D, $r^2 = 0.07$; $P < 0.01$ without Cl01). Polato *et al.* (2010) reported $r^2 = 0.32$ along the Hawaiian Island Chain [2500 km; comparable with the ETP in geographic scale (Fig. 4)].

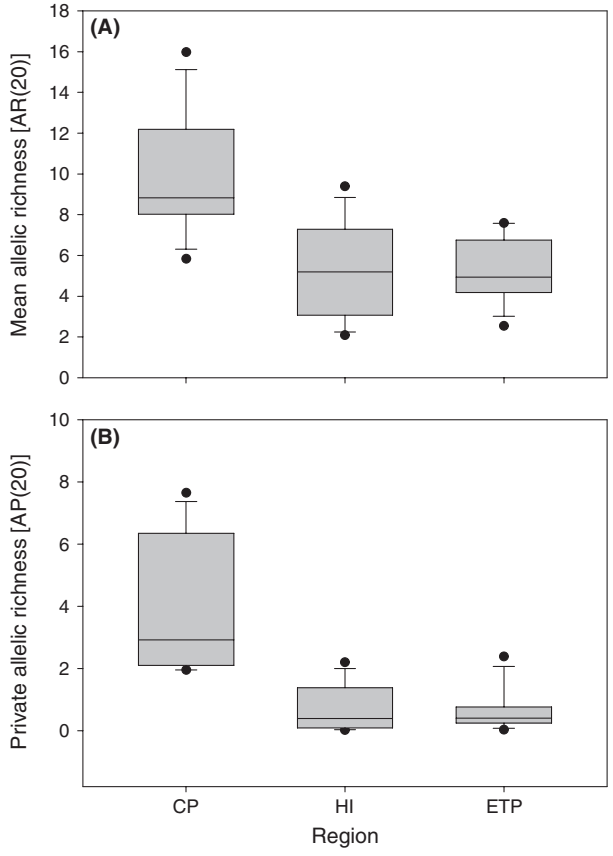

Fig. 3 *Porites lobata* mean allelic richness (AR(20)) and private allele richness (AP(20)) rarefied to a sample size of three sites per region and 20 genes per site. A Kruskal–Wallis one-way analysis of variance indicated differences across regions ($P < 0.01$) for both AR(20) and AP(20). CP = central Pacific, HI = Hawaiian Islands, ETP = Eastern Tropical Pacific.

Principal components analysis separated the Hawaiian Islands and the ETP from the remainder of the Pacific (Fig. 5). Interestingly, Clipperton Atoll grouped with the central Pacific, even though geographically it lies east of the Eastern Pacific Barrier. Johnston Atoll occupied a position equidistant from the centre of the other clusters (Hawaii, central Pacific and ETP).

Plots of ΔK (Evanno *et al.* 2005) and LnP(K) from STRUCTURE indicate that five is the most likely number of population clusters present in the full data set (Fig. 6 A, B). At $K = 2$, Hawaii formed a separate cluster from the remainder of the samples. At $K = 3$, the ETP and the northern Line Islands separated from the remainder of the CP and HI. At $K = 4$, a cluster with few members appeared in the Western CP. At $K = 5$, samples from the northern Line Islands that previously grouped with the ETP, now formed a separate cluster confined to the west of the Eastern Pacific Barrier (Fig. 1). The ETP appeared homogenous at this level of analysis (Fig. 1), with the exception of samples from Clipperton, five samples from the Galapagos and one sample from Costa Rica. Consistent with the PCA (Fig. 5), Johnston appeared admixed between Hawaii and the central Pacific.

INSTRUCT results (which consider potential inbreeding) agreed with those from STRUCTURE that five was the most likely value of K (not shown). GENELAND (which considers null alleles) estimated the number of clusters as seven under a model without prior information on spatial location or population membership of samples (not shown). One of the additional clusters in GENELAND separated the Marquesas (MQ1 and MQ2) from the Line Islands (also observable in STRUCTURE runs on central Pacific samples only at $K = 9$, not shown). The second additional cluster occurred at low frequency in the Line Islands, Phoenix, Marshalls, Fiji, Samoa and Moorea.

F_{st} values were significant in 58% of all pairwise comparisons (after FDR correction), with larger values observed between more distant sites (Table S3). F_{st} ranged from 0 to 0.27 (0–0.47 with Meirman's F'_{st} ; -0.14 – 0.76 with Jost's D), with maximum values detected between the Hawaiian sites and the remainder of the central Pacific (online Supporting information). There was significant among-population differentiation based on an AMOVA considering 32 populations ($F_{st} = 0.157$, SE 0.018, $P < 0.001$, $F'_{st} = 0.459$, Table 3A). Adding the level of 'region' to the AMOVA resulted in strong differentiation among regions ($F_{ct} = 0.145$, 0.02 SE, $P < 0.001$, $F'_{ct} = 0.464$, Table 3B) and a lower amount of differentiation among populations within regions ($F_{sc} = 0.063$,

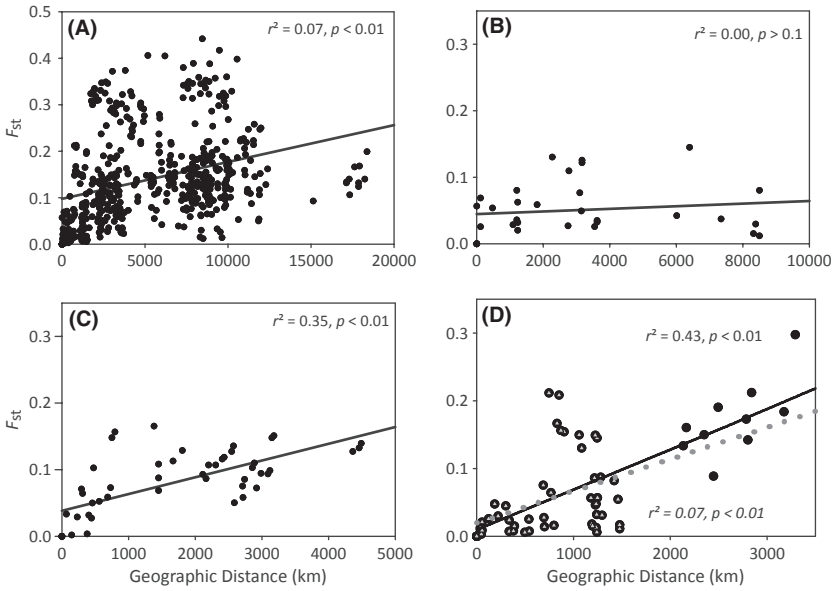

Fig. 4 Isolation-by-distance patterns in *Porites lobata*. Geographical distance explained 7% of the variation in genetic distance (F_{st}) across all sampling site, none of the variation in the western central Pacific (b), and 35% of the variation in the eastern central Pacific (c). Geographical distance explained 43% of the variation in genetic distance among all sites in the Eastern Tropical Pacific (d) black circles and regression line) and 7% of the variation when excluding Clipperton (d, grey triangles and dotted regression line). Note differences in axis scales among panels.

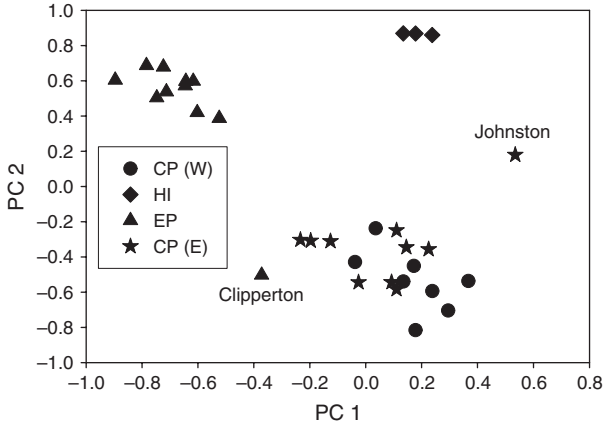

Fig. 5 Principal component analysis of allele frequency covariance in *Porites lobata* populations. 31 of 229 Principal component analysis (PCA)-axes were retained, explaining 100% of the cumulative variance. Plotted are the first two axes explaining 47.73% ($P < 0.05$) and 28.9% ($P < 0.05$) of the variance, respectively. central Pacific West [CP (W), circles], central Pacific East [CP (E), stars], Hawaii (HI, diamonds), eastern Pacific (EP, triangles).

0.00 SE, $P < 0.001$, $F'_{sc} = 0.197$, Table 3B) consistent with PCA and STRUCTURE analysis.

In STRUCTURE runs where all but the Clipperton samples were assigned *a priori* to their region of origin (HI, CP or ETP, Fig. 7), the Clipperton samples assigned with a higher probability to the central (average assignment probability CP = 0.74 ± 0.23 SD) than to the Eastern Tropical Pacific (average assignment probability ETP = 0.24 ± 0.23 SD). As expected, none of the Clipperton samples assigned to Hawaii (average assignment probability HI = 0.02 ± 0.00 SD). Considering the *a priori* assigned samples (all but those from Clipperton), STRUCTURE identified seven genotypes from the central Pacific (one from PH01, four from JO01, two from LN04, Fig. 7) and one genotype from the eastern Pacific (CR03, Fig. 7) as first generation migrants with high probability (>0.9, $P < 0.001$). All of JO01 migrants had likely ancestry in HI whereas the most likely origin of the PH01 and the 2 LN04 migrants was the ETP (Fig. 7). None of the genotypes from the Galapagos assigned to the CP in this analysis (Fig. 7). The origin of the migrant CR03 sample appeared to be the CP (Fig. 7).

Discussion

Our genetic data corroborate previous biogeographic hypotheses on the Eastern Pacific Barrier in the broadest sense: most populations of *Porites lobata* are presently isolated from those in the central Pacific. However, the data also suggested that Clipperton Atoll is genetically similar to populations in the central Pacific despite residing to the east of the Eastern Pacific Barrier and that gene flow between insular and continental populations within the ETP is quite high.

Table 2 Summary of per locus statistics based on 12 microsatellite markers for *Porites lobata*.

Locus	N_a	N_{eff}	H_o	H_s	H_t	H'_t	G_{is}	G_{st}	G'_{st} (Nei)	G'_{st} (Hed)	D_{est}
PL 0340	18	2.562	0.253	0.657	0.726	0.728	0.614	0.095	0.097	0.282	0.207
PL 0780	18	3.035	0.636	0.702	0.828	0.832	0.094	0.152	0.156	0.521	0.435
PL 0905	27	4.469	0.624	0.819	0.907	0.910	0.237	0.097	0.100	0.550	0.501
PL 1357	31	3.211	0.534	0.726	0.845	0.849	0.264	0.141	0.145	0.526	0.449
PL 1370	21	2.531	0.508	0.637	0.774	0.778	0.203	0.177	0.182	0.498	0.390
PL 1483	19	2.933	0.446	0.699	0.799	0.802	0.361	0.126	0.129	0.426	0.344
PL 1551	11	2.569	0.513	0.642	0.762	0.765	0.201	0.157	0.161	0.447	0.344
PL 1556	18	2.049	0.211	0.551	0.716	0.721	0.618	0.230	0.236	0.521	0.378
PL 1629	10	2.046	0.494	0.535	0.606	0.608	0.076	0.118	0.121	0.258	0.158
PL 1868	18	3.311	0.414	0.742	0.804	0.806	0.442	0.078	0.080	0.307	0.249
PL 2069	10	2.937	0.52	0.696	0.804	0.808	0.252	0.135	0.138	0.453	0.368
PL 2258	28	2.595	0.474	0.651	0.814	0.819	0.272	0.200	0.205	0.584	0.480
Mean	19.08	2.85	0.47	0.67	0.78	0.79	0.30	0.14	0.14	0.44	0.35
SE	1.99	0.19	0.04	0.02	0.02	0.02	0.05	0.013	0.01	0.03	0.03

N_a = number of alleles, N_{eff} = number of effective alleles, H_o = observed heterozygosity, H_s = heterozygosity within populations, H_t = total heterozygosity, H'_t = corrected total heterozygosity, G_{is} = inbreeding coefficient, G_{st} = fixation index, G'_{st} (Nei) = Nei's corrected fixation index (Nei 1987), all values are significant at $P < 0.01$, G'_{st} (Hed) = Hedrick's corrected fixation index (Hedrick & Goodnight 2005), D_{est} = Jost's differentiation index (Jost 2008). SE = Standard errors obtained through jackknifing over loci. All values calculated with GENODIVE (Meirmans 2006).

Table 3 Population differentiation among 32 sites (A) and 3 biogeographic regions (B) of *Porites lobata*.

Source of variation	Nested in	% var	*F*-stat	*F*-value	SE	*P*-value	*F*′-value
A)							
Within Individual	–	0.612	F_{it}	0.388	0.032	–	–
Among Individual	Population	0.231	F_{is}	0.274	0.037	0.001	–
Among Population		0.157	F_{st}	0.157	0.018	0.001	0.459
B)							
Within Individual	–	0.583	F_{it}	0.417	0.041	–	–
Among Individual	Population	0.219	F_{is}	0.274	0.041	0.001	–
Among Population	Region	0.054	F_{sc}	0.063	0.007	0.001	0.197
Among Region	–	0.145	F_{ct}	0.145	0.020	0.001	0.464

Based on an Analysis of Molecular Variance (AMOVA) calculated assuming an infinite allele model (equivalent to F_{st}). CR03 was excluded due to low sample size ($N_g = 1$). SE = Standard Error. F' is a standardized version of F_{st} (Meirmans 2006).

Is the EPB a barrier to corals?

The depauperate coral reef fauna in the Eastern Tropical Pacific experiences frequent large-scale disturbances in the form of ENSO warming events (Wyrtki 1975; Glynn & Colgan 1992; McPhaden 1999). ENSO can lead to widespread bleaching and mortality of corals (Glynn 1984; Glynn & Deweerdt 1991; Jimenez & Cortes 2001). However, recovery of reefs from ENSO events can be rapid, at least in some locations (Glynn & Colgan 1992; Glynn *et al.* 2009). Were recovering reefs reseeded via long-distance dispersal or were recruits derived from local sources? The vibrant coral reefs of the central Pacific (Veron 1995; Sandin *et al.* 2008; Edmunds *et al.* 2010) support large populations of the major eastern Pacific reef-builders, including *Porites lobata*, and thus might be a source for recruits. However, the broad stretch of deep water between the central and eastern Pacific (Darwin 1880) and the mostly westward current flow of the North Equatorial Current (NEC) (reviewed in Kessler 2006; Wyrtki *et al.* 1981) are formidable barriers to dispersal. During classic (EP) ENSO years, eastward flow in the NECC is warmer and faster (reviewed in Bonjean & Lagerloef 2002; Kessler 2006), providing a potential bridge to the eastern Pacific (Richmond 1990).

Our results suggest that the central and most eastern Pacific locations are presently isolated (Figs 1, 5, S1, S2 and S4, Table 3). The one exceptional location is Clipperton Atoll. Situated to the east of the EPB, it nonetheless groups genetically with the central Pacific (Table 3, Figs 1, 5 and 7). The most likely route for dispersing larvae or rafting adult corals from the central Pacific

(specifically the Line Islands) to Clipperton Atoll is the NECC, which skirts Clipperton Atoll even in non-ENSO years (Kessler 2006). Clipperton samples had a 0.74 ± 0.23 SD assignment probability to the central Pacific compared with a 0.24 ± 0.23 SD probability of belonging to the Eastern Tropical Pacific. Increased sample sizes from Clipperton would help confirm these findings, although STRUCTURE should deliver robust assignments for the five samples in hand given the comprehensive sampling of potential source populations (Falush *et al.* 2003).

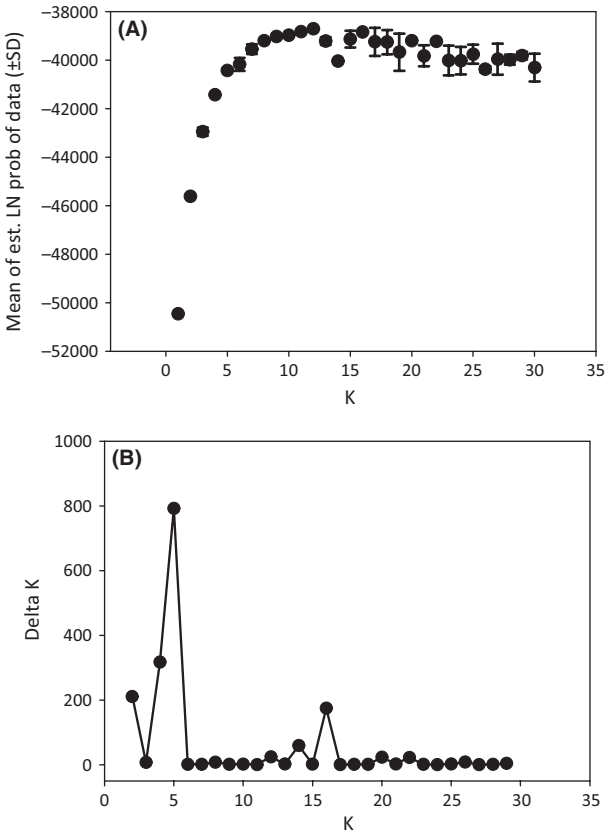

Fig. 6 Mean log-likelihood of K (a) and Delta K (b) values for STRUCTURE analysis of *Porites lobata* samples, pacific-wide.

The genetic clustering of *P. lobata* samples from Clipperton with the central Pacific concurs with biogeographical clustering based on the distribution of coral species (Glynn & Ault (2000). Their island group includes Clipperton Atoll and the central Pacific islands of Hawaii, Johnston and Fanning. While *P. lobata* samples from Clipperton grouped genetically with the central Pacific islands to which Fanning belongs (Figs 1, 5 and 7), Hawaiian *P. lobata* were differentiated from both the central Pacific and the ETP (Figs 1 and 5). Our sampling does not allow for complete overlap with the Glynn and Ault predictions: we were unable to secure samples from Malpelo (another ETP island biogeographically grouped with the CP), and *P. lobata* does not occur in their northern province (where it is replaced by *P. evermanni*, Boulay *et al.*, in prep.). However, the geographic restriction of *P. lobata* to the southern province indicates a lack of successful recruitment to the northern province, supporting Glynn and Ault's biogeographic clusters.

In model runs where each genotype (with the exception of Clipperton, see above) was assigned a priori to originate from the location it was sampled (Fig. 7), seven genotypes collected in the central Pacific and one genotype sampled in the eastern Pacific (CR03) were identified as first generation migrants with high probability (>0.9, $P < 0.001$) confirming very low levels of migration among regions consistent with the high among-region F_{st} value (0.145 ± 0.02 SE; F'_{st} = 0.465, Table 3B). Preliminary analysis showed that the flagged CR03 genotype harboured an unusual ITS – sequence (Forsman *et al.* 2009), indicating possible introgression from *Porites evermanni*. Thus, introgression within the

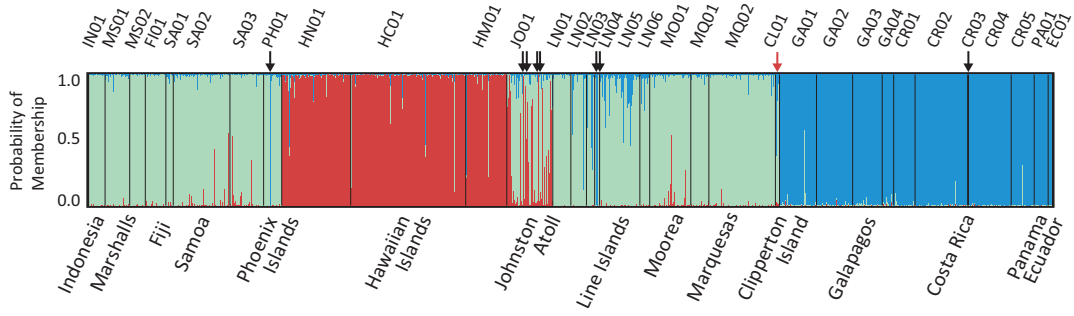

Fig. 7 When treated as genotypes of unknown origin, four Clipperton genotypes (red arrow) assigned with high probability (mean CP = 0.84 ± 0.09) to the central Pacific ($K = 3$) and one genotype appeared admixed between CP (assignment probability = 0.36) and EP (0.62). Structure identified seven genotypes from the central Pacific (one from PH01, four from JO01, two from LN04) and one genotype from the eastern Pacific (CR03) as first generation migrants (black arrows) with high probability (>0.9, $P < 0.001$). Model assumed admixed populations, correlated allele frequencies and $K = 3$.

EP and not migration from the CP might be the cause for the unusual genetic composition of this individual. Only two of the CP migrants were assigned to the EP and ITS sequences of CP migrants grouped within the *P. lobata* clade identified by (Forsman *et al.* 2009). Future work will explore the extent of introgression between *P. lobata* and *P. evermanni* in the ETP and elsewhere with the expectation that introgression rates between species will vary across their geographic range (Fukami *et al.* 2004; Ladner & Palumbi 2012).

Similar to findings for *P. lobata*, populations in the central/western Pacific and the eastern Pacific were differentiated in *Conus* snails (Duda & Lessios 2009), soldierfish (Craig *et al.* 2007) and lobsters (Chow *et al.* 2011). Limited gene flow was also reported between the Galapagos and South Pacific Island populations of *P. lobata* (Forsman 2003) and between central and eastern Pacific populations of *Pocillopora damicornis* (Combosch *et al.* 2008), in contrast to ongoing gene flow between urchin populations in Clipperton/Cocos Island and the central Pacific (Lessios *et al.* 1998). Further, of 20 fish species found on either side of the EPB, only two showed significant divergence between the central and eastern Pacific (Lessios & Robertson 2006).

The strong divergence among Hawaii, the central Pacific and the eastern Pacific, the occurrence of a well-supported but rare cluster within the western central Pacific (yellow cluster) and the co-occurrence of the orange and green cluster in the eastern central Pacific, raise questions about the level of taxonomic resolution addressed here. While we cannot exclude the possibility that each of the highly supported clusters constitutes a different species (Ladner & Palumbi 2012), we think this is unlikely for several reasons. First, markers designed for *P. lobata* often failed to amplify when used on other *Porites* species. We determined this by applying our markers to samples identified as other *Porites* species ($n = 37$; *P. latistella*, *P. compressa*, *P. duerdeni*, *P. lutea*, *P. panamensis*) by independent expert morphological analysis (Z. Forsman) and ITS sequencing (Forsman *et al.* 2009). In fact, we initially discovered that *Porites* samples from the northern EP are *P. evermanni* and not *P. lobata* based on patterns of amplification failure and fixed alleles with nonoverlapping size range at three loci in *P. evermanni* that are otherwise polymorphic in *P. lobata*. We have since substantiated this finding by describing habitat and ecological differences between the species (Boulay *et al.* in prep). Based on these findings, we conducted analyses on patterns of amplification failure across loci and found no further signal, that is, knowing that one locus failed did not help to predict amplification failure at any of the other 11 loci (see also Fig. 2). Second, phylogenetic analysis of sequences from six nuclear markers for samples of *P. lobata* from Hawaii (the type locality) and other closely related *Porites* agreed with our microsatellite and field identifications (Hellberg *et al.* in prep). Furthermore, ITS sequences of representative samples from clusters identified here fell within the clade previously described as *Porites lobata* by Forsman *et al.* (2009). Finally, the clusters identified by STRUCTURE might not present biological reality, although AMOVA (Table 3) and pair-wise F_{st} comparisons among sites (Supplements) are congruent with STRUCTURE results. Regardless of the level of taxonomic resolution, the conclusion of a general lack of gene flow across the EPB and isolation of Hawaii holds.

Patterns of gene flow within the central Pacific

Within the central Pacific, Hawaiian populations were strongly isolated from the remainder of the region, including their nearest neighbour Johnston Atoll, as in Polato *et al.* (2010). The near-linear arrangement of the Line Islands, the Marquesas, Moorea and Johnston Atoll (Fig. 1) lends itself to tests for IBD and indeed the correlation between genetic and geographic distance was moderately strong in this region (Fig. 4 C).

General patterns of population genetic differentiation among reef dwellers in this region of the central Pacific are yet to emerge. Restricted gene flow has been reported for corals (Magalon *et al.* 2005), oysters (Arnaud-Haond *et al.* 2004) and some reef fish (Gaither *et al.* 2010, Planes & Fauvelot 2002), with turbinid gastropods revealing endemic genetic clades in each archipelago (Meyer *et al.* 2005). In contrast, some other reef fish, even congeners of those mentioned previously (Gaither *et al.* 2010; Eble *et al.* 2011), show little structure across the central Indo-Pacific, and no population differentiation was observed between populations of the urchin *Diadema savignyi* from Moorea and Kiribati (Lessios *et al.* 2001).

Patterns of gene flow within the Eastern Tropical Pacific

With the exception of the differentiation of Clipperton Atoll from the remainder of the ETP, population differentiation was weak in this region (Fig. 1). Data on population genetic structure of corals in the ETP is sparse and complicated by difficult morphological species identification (Pinzon & LaJeunesse 2011). Genetically, three types (Type I–III) of *Pocillopora* spp. can be distinguished in the ETP (Pinzon & LaJeunesse 2011). *P. damicornis* Type I, the only type with sufficient samples sizes across the region to allow for population-level analysis, shows panmixia in the ETP (including the Mexican mainland, Revillagigedo Island, Clipperton

Atoll, the Galapagos and Panama) at seven microsatellite loci (Pinzon & LaJeunesse 2011). In contrast, Combosch & Vollmer (2011) found five distinct but co-occurring genetic clusters in varying proportions along the Panama coast. It is not clear whether those clusters correspond to any of the types identified in the Pinzon and LaJeunesse study. Using six allozyme loci Chávez-Romo *et al.* (2009) found three genetically distinct clusters along the Mexican coast, but again it is not clear whether those samples represented just one or multiple types described by Pinzon & LaJeunesse (2011).

Several other marine organisms show little population genetic structure within the ETP. Some that evince population genetic differences between the central/western Pacific and the eastern Pacific show no further structure within ETP samples (Craig *et al.* 2007; Duda & Lessios 2009; Chow *et al.* 2011). Similarly, no population structure was found among ETP sites in rocky intertidal snails and sea urchins (McCartney *et al.* 2000; Hurtado *et al.* 2007). In contrast, significant population structure often occurs between the Gulf of California and populations to the south (Riginos & Nachman 2001; Hurtado *et al.* 2007; Saarman *et al.* 2010).

Is the Eastern Tropical Pacific marginal?

Many reef-building corals occur over large geographic ranges and experience suboptimal and variable conditions at the margins of their distributions. Such marginal populations can provide insights into how corals might respond to climate change (Guinotte *et al.* 2003; Lirman & Manzello 2009; Hennige *et al.* 2010; Goodkin *et al.* 2011). For example, coral communities in the Eastern Tropical Pacific (ETP) already experience seasonal cold upwelling, El Niño Southern Oscillation warm events and reduced aragonite saturation states (Glynn & Colgan 1992; Fong & Glynn 2000). In fact, the eastern Pacific experiences some of the most severe stress exposures of any coral province worldwide (Maina *et al.* 2011). The conditions in edge habitats have spurred interest in how coral populations persist there, how they will react to a rapidly changing climate and what role they play in the evolution of coral species.

Moving out from the geographic centre of a species' range, physical isolation is expected to increase and population size is expected to decrease, often accompanied by losses in allelic diversity owing to lack of gene flow and increased levels of inbreeding (reviewed in Eckert *et al.* 2008; Sagarin & Gaines 2002). For *P. lobata*, sites in the central Pacific had almost twice as much allelic richness as sites in Hawaii and the ETP (Fig. 3), a higher number of effective alleles, and inbreeding was generally low (Table S2). Because corals can reproduce locally by asexual means (Highsmith 1982; Baums *et al.* 2006; Foster *et al.* 2007), reduced gene flow into marginal populations can result in increased clonality. Our sampling effort was not constant across sites, so genotypic diversity among them cannot be easily compared, but generally we find little evidence of asexual reproduction in *P. lobata* across its range. Although, congruent with the above-mentioned predictions, two of the eastern Pacific sites (CR03 and EC01) showed low genotypic diversity (Table 1).

Microsatellite heterozygosities generally decrease with increasing distance from the centres of coral diversity in the Pacific and Atlantic (Baums 2008). Examples of low heterozygosity in marginal locales include *P. damicornis* from Lord Howe Island (Miller & Ayre 2004), *Seriatopora hystrix* from Scott Reef in Australia (Underwood *et al.* 2007) and coral species from Japan (Adjeroud & Tsuchiya 1999; Ayre & Hughes 2004). In taxa that are connected via gene flow across the EPB, including 18 species of reef fish (Lessios & Robertson 2006) and a sea urchins (Lessios *et al.* 1998), no such reduction in genetic diversity across the EBP is apparent.

Conclusions

The Eastern Pacific Barrier isolates populations of the important ecosystem engineer, *Porites lobata*, in the central and Eastern Tropical Pacific. The exception to this generality comes from Clipperton Atoll, which we found to be most genetically similar to populations in the Line Islands and the Marquesas. Dispersal from the central Pacific to Clipperton Atoll likely occurs via the NECC, which reaches Clipperton even during non-ENSO years when the NECC is relatively weak. We had hypothesized that recurrent strengthening of the NECC during increasingly intense ENSO events may result in gene flow between the central and Eastern Tropical Pacific; however, very little exchange was evident in the data, nor did we find support for genetic differentiation between the oceanic island and continental shelf in accordance with biogeographic patterns (Glynn & Ault 2000).

Climate change is threatening coral reefs world-wide (Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007). Coral populations already growing in marginal habitats (Maina *et al.* 2011) can provide insights into how corals might respond to climate change (Guinotte *et al.* 2003; Lirman & Manzello 2009; Hennige *et al.* 2010; Goodkin *et al.* 2011; Cooper *et al.* 2012). Mounting evidence indicates that marginal coral populations harbour less neutral genetic diversity then more central populations (Fig. 3 (Adjeroud & Tsuchiya 1999; Ayre & Hughes 2004; Baums 2008; Miller & Ayre 2004; Underwood

et al. 2007), but little is known about the distribution of functional genetic diversity across the range of coral species. This should be a major focus of future research.

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I.B. performed the statistical analysis and wrote the paper. J.B. and N.P. developed methods and performed laboratory analysis. All authors collected samples, read, edited and approved the manuscript. I.B. and M.E. obtained funding and designed the study.

Data accessibility

Sampling locations, Structure input files and microsatellite data: DRYAD entry doi:10.5061/dryad.7gp1f.

Supporting information

Additional Supporting Information may be found in the online version of this article.

Fig. S1 *Porites lobata* population structure across the central and Eastern Tropical Pacific assuming no admixture among populations.

Fig. S2 *Porites lobata* population structure across the central and Eastern Tropical Pacific analyzed with eight of twelve loci.

Fig. S3 Mean log-likelihood (A) and Delta K (B) values of K for STRUCTURE analysis of *Porites lobata* samples Pacific-wide using only eight loci.

Fig. S4 Principal component analysis of allele frequency covariance in *Porites lobata* using only eight of the loci.

Table S1 Microsatellite loci for *Porites lobata*.

Table S2 *Porites lobata* null allele frequencies and individual inbreeding values.

Table S3 Pairwise F_{st} values (lower diagonal) and their significance (upper diagonal) among *Porites lobata* sampling sites.

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