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J. A. H. Benzie · A. Haskell · H. Lehman

Variation in the genetic composition of coral (*Pocillopora damicornis* and *Acropora palifera*) populations from different reef habitats

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Abstract The genetic structure of populations of the corals *Pocillopora damicornis* and *Acropora palifera* was examined in three habitats at One Tree Island during March and April 1993, using electrophoretically detectable variation at six allozyme loci. There were significant genetic differences among populations of *P. damicornis* within each of the reef crest, lagoon and microatoll habitats. The level of differentiation among populations was similar in each of the habitats. Differences between populations of *P. damicornis* from lagoon and microatolls were no greater than that within habitats, but genetic differentiation of these from crest populations was much higher. There was no difference in the genetic composition of *A. palifera* populations within or between the lagoon and microatolls, the only habitats where this species was found. Both coral species had observed:expected (G_O:G_E) genotypic diversity ratios >0.80, indicating predominantly sexual reproduction. These data, the high genotype diversity and general conformance of genotype frequencies to those expected under conditions of Hardy–Weinberg, suggested panmixis at each site. The high degree of sexual reproduction in the *P. damicornis* populations is unusual for a species where asexual reproduction has been the dominant mode of reproduction reported to date. Gene flow in both species was considerable between the lagoon and the closed microatolls. The genetic differences between populations of *P. damicornis* in these habitats and the reef crest may reflect the relative isolation of all populations within the closed One Tree Lagoon from those outside. However, local currents appear to offer effective means of dispersal between the habitats, suggesting that the genetic differences result from natural selection in the different environments within One Tree Lagoon and the reef crest.

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J. A. H. Benzie (✉)
Australian Institute of Marine Science, P.M.B. 3, Townsville M.C., Townsville, Queensland 4810, Australia

A. Haskell · H. Lehman
Southampton College, Long Island University,
239 Montauk Highway, Southampton, New York 11968, USA

Introduction

Coral reefs are a complex of habitats that differ in their physical and biological characteristics (Done 1982; Potts 1984). Variation in growth form of coral species occurring in more than one habitat has been thought to be a phenotypic response to environmental differences among habitats (Foster 1979; Veron 1986). This view implies that the genetic composition of coral populations in different habitats is likely to be the same, and that coral genotypes are likely to be broadly adapted to reef environments. However, surveys using biochemical markers have shown that the growth forms of at least one coral species, *Pavona cactus*, reflected the underlying occurrence of several clones, each of which had little phenotypic plasticity (Willis and Ayre 1985; Ayre and Willis 1988). Differences in the distribution of growth forms among habitats were accompanied, therefore, by differences in the genetic composition of populations among habitats.

Evidence that particular genotypes do not perform with the same degree of success in different habitats, even where there are no marked differences in growth form, has also been demonstrated in transplant experiments (Potts 1984). Fragments from the same colony of *Acropora palifera* did not survive and grow equally in all the habitats into which they had been introduced. Transplants from different colonies performed with varying degrees of success in given habitats. Slope and inner-flat habitats were difficult environments for all genotypes, and the outer-flat habitat was favourable for all genotypes (Potts 1984). Mortality in reef crest and lagoon habitats resulted from different processes, suggesting differential selection of genotypes. Differential selection would be likely to give rise to differences in the genetic composition of populations in different habitats.

The aim of the present study was to examine whether the genetic composition of *Pocillopora damicornis* and *Acropora palifera* populations differed among habitats at One Tree reef in the southern Great Barrier Reef (GBR). Reef crest and lagoon habitats were sampled because they are very different environments (Kinsey 1972; Potts 1984;

Potts and Swart 1984). The crest is characterised by strong wave surges and large ranges in water temperature, and is affected by oceanic water at high tide and reef-flat water at low tide. The lagoon is characterised by lower water movements, less variable water temperatures, and is not directly affected by oceanic water. Potts (1984) also showed that mortalities in his *A. palifera* transplants at Heron Island, close to One Tree, resulted from different processes in reef crest and lagoon habitats, and that genetic differences might be expected between populations in these two habitats.

One Tree reef is unique in the Great Barrier Reef in that it has a completely enclosed lagoon within which there are a number of microatolls. The walls of the microatolls are formed by large thickets of branching corals and reef matrix whose upward growth was constrained when their upper margins reached the water surface (Weins 1962; Woodroffe and McLean 1992). The upper parts of the colonies die as a result of exposure, but continued lateral growth and the erosion of dead material from the central area of the colonies leads to the development of an enclosed pool surrounded by a coral wall. In time, the region within the microatoll is colonised by other corals.

Although covered at high tide, water exchange between the enclosed pool in the microatoll and the rest of the lagoon is reduced. The environment within the microatolls is considered to have higher light intensity and higher temperatures than that in the lagoon (A. Steven unpublished data). Microatolls were sampled because, although similar to the lagoon relative to the crest habitat, they represent a special, isolated environment within the lagoon at One Tree.

Populations of *Pocillopora damicornis* and *Acropora palifera* were analysed for three reasons. Firstly, both species are common in a variety of reef habitats. Secondly, both species brood their young, and these might be expected to settle locally to a greater extent than the young of species which broadcast their gametes, so increasing the chance of detecting genetic differentiation among populations. Thirdly, methods for the detection of genetic variation using allozymes had already been developed for both taxa (Stoddart 1984 a; Ayre et al. 1991).

Acropora palifera had been the subject of the transplant experiments by Potts (1984). Although Potts considered that all his specimens belonged to *A. palifera* and not to the closely related *A. cuneata*, subsequent genetic work has shown that *A. cuneata* dominates reef crest and high-energy environments, while *A. palifera* dominates low-energy lagoon environments (Ayre et al. 1991). This finding does not invalidate the key conclusions of Potts' work, but it is possible that *A. cuneata* individuals were included in his material. In addition, it is possible that only *A. cuneata* may occur on the One Tree crest. *Pocillopora damicornis*, therefore, provided a taxon whose identification was likely to be unequivocal, for comparison of the reef crest and lagoon habitats.

Materials and methods

Field collections

Specimens of *Pocillopora damicornis* and *Acropora palifera* were obtained from three habitats at One Tree Island (23° 30′ S; 152° 06′ E) in the Capricorn–Bunker group of reefs in the southern GBR (Fig. 1) during late March and early April 1993. The habitats samples were the seaward side of the coral wall surrounding the closed One Tree reef lagoon on the lee side of the reef (reef crest), the outside walls and surrounds of the microatolls in the lagoon (lagoon), and the area inside the walls of closed microatolls (microatolls). All samples were obtained from depths < 3 m.

A total of three sites in each habitat including three different closed microatolls, was sampled. *Pocillopora damicornis* was obtained from all nine sites, but *Acropora palifera* only occurred in the six sites from the lagoon and microatoll. Collections of *A. palifera*-like specimens from the reef crest were all identified as *A. cuneata* as they possessed an allele at PGDH diagnostic of *A. cuneata* (Ayre et al. 1991).

Using a pipe cutter, biopsies 1.5 cm long were obtained from the growing tips of 45 to 50 individuals of each of the species occurring at a site. Chips from a given specimen were placed in small zip-lock plastic bag and kept in freshly changed seawater until they were processed. After cutting the coral tips into smaller tissue-bearing fragments (≃5 mm×5 mm), the fragments were transferred to individually labelled tubes and snap-frozen in liquid nitrogen. Samples were stored at –80 °C until analysis.

Laboratory analysis

A 5 mm×5 mm coral fragment was ground in two drops of an aqueous solution of 0.04% B mercapthethanol and 0.01% sucrose in a ceramic well using a stainless steel rod. A square of tissue paper (1 cm×1 cm) was placed over the crushed sample to act as a crude filter to prevent coral dust and mucus attaching to the Whatman No 3 chromatography paper wicks (3 mm×10 mm) that were used to soak up the exudate. The wicks were placed vertically in a cut made in a horizontal 12% starch gel.

Five polymorphic loci were scored from four enzyme systems in *Pocillopora damicornis*. The enzyme systems were: glucose phosphate isomerase EC 5.3.1.9. (GPI); peptidase using leucyl tyrosine as a substrate EC 3.4.11. – (LT); hexokinase EC 2.7.1.1. (HK); and phosphoglucomutase EC 5.4.2.2. (PGM). GPI and LT were run using a Tris citrate pH 8.0 (TC8) buffer. The gel buffer was 28 m*M* Tris and 11 m*M* citric acid, the electrode buffer was 172 m*M* Tris and 68 m*M* citric acid, and both buffers were adjusted to pH 8.0 using citric acid solution. Both electrode and gel buffers were diluted 1:1 with distilled water to achieve a half-strength TC8 buffer. HK and PGM were run using a Tris EDTA citrate pH 7.9 (TEC7.9) buffer. The gel buffer was 8.5 m*M* Tris, 3 m*M* citric acid and 0.27 m*M* Na_2 EDTA; the electrode buffer was 135 m*M* Tris, 43 m*M* citric acid and 4 m*M* Na_2EDTA; both buffers were adjusted to pH 7.9 using citric acid solution.

Five polymorphic loci were scored from enzyme systems in *Acropora palifera*. The enzyme systems were: malate dehydrogenase EC 1.1.1.37 (MDH); glucose phosphate isomerase EC 5.3.1.9 (GPI); glutamate dehydrogenase EC 1.4.1. – (GLUDH); and phosphoglucomutase EC 5.4.2.2(PGM). MDH and PGM were run using a TEC 7.9 buffer; GPI and GLUDH were run using a half-strength TC8 buffer. All gels were run at 200 V and ≃30 mA for 6 h in a constant-temperature room held at 3 °C.

*GPI** in both species, *LT-1** in *Pocillopora damicornis* and *MDH-1**, *MDH-2** and *GLUDH** in *Acropora palifera* produced one-banded and three-banded patterns consistent with dimer homozygotes and heterozygotes, respectively. *LT-2** in *P. damicornis* produced one-banded and thicker blocks of stain that could not be resolved clearly into more bands but were considered to represent homozygotes and dimer heterozygotes, respectively, where the three-bands were close enough together to fuse into a single block of stain.

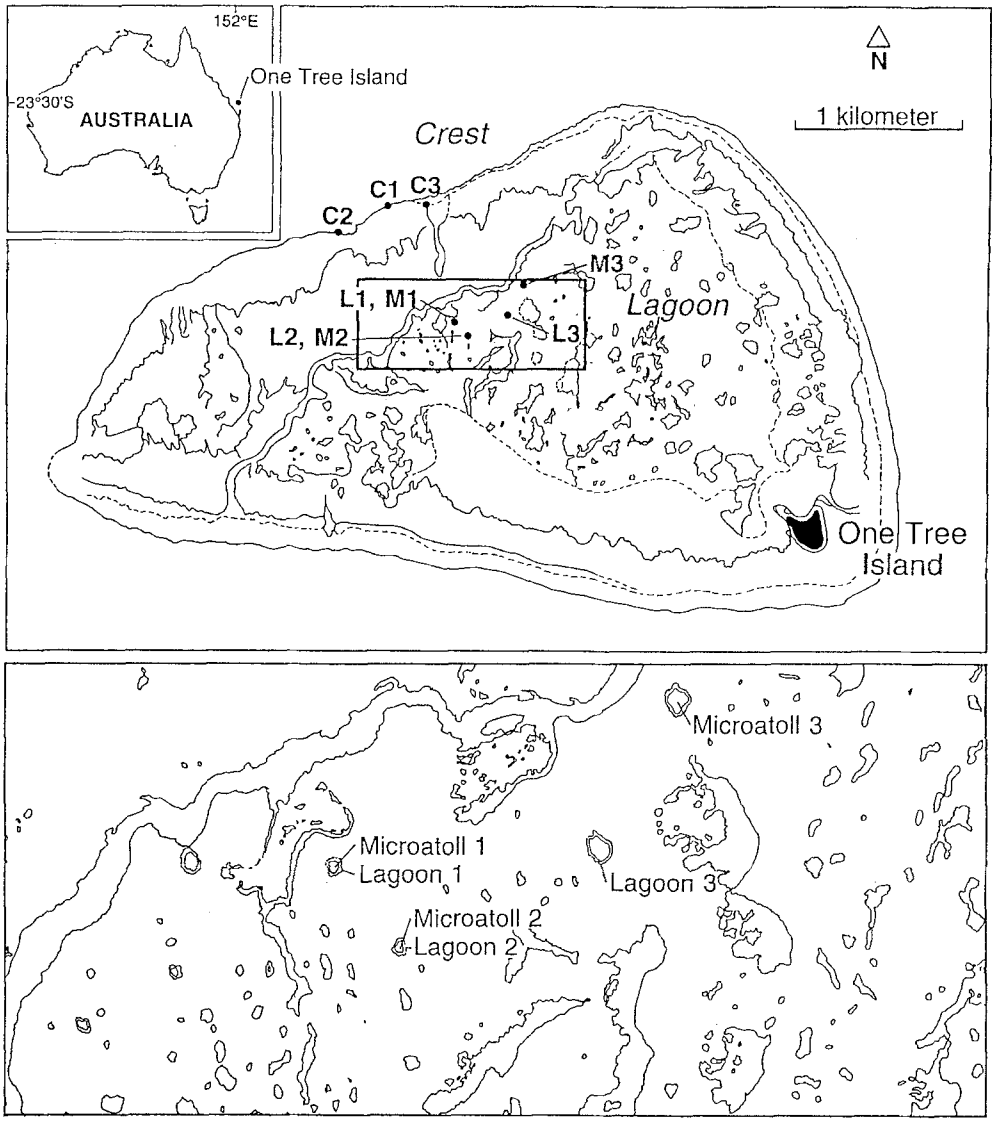

Fig. 1 Map showing locations of sample sites at One Tree Island, and position of One Tree island within Great Barrier Reef (*C1–C3*, *L1–3*, *M1–3* reef crest, lagoon and microatoll sites, respectively)

*HK** in *P. damicornis* had one-banded and two-banded patterns consistent with monomer homozygotes and heterozygotes, respectively. *PGM** in both species gave more complex banding patterns as a result of strong breakdown bands. In *P. damicornis* it was clear that homozygotes were two-banded and heterozygotes either four-banded when alleles migrated at sufficiently different rates, or three-banded when the breakdown band from the slower allele migrated to the same position as the faster allele, leading to a more darkly staining band at that position. Similarly, *A. palifera* homozygotes were all three-banded as a result of the presence of two strong breakdown bands, and heterozygotes were either five- or four-banded depending on the match in mobilities of one allele or its breakdown bands to those of the other allele.

All systems could be scored unequivocally and banding patterns were consistent on different gel runs of the same samples.

Statistical analysis

Gene frequencies, basic measures of genetic variability, genetic distance and cluster analyses were done using programs in BIOSYS (Swofford and Selander 1981). *F*-statistics were calculated using equations from Weir and Cockerham (1984) that specifically take account of differences in sample size. The significance of F_{ST}, a measure of genetic differentiation among populations, and of F_{IS}, a measure of genetic variation within populations, was calculated using equations given in Waples (1987) to estimate chi-square. Parallel analyses of Nei's gene-diversity statistic G_{ST} using bootstrap methods (Roff and Bentzen 1989) to calculate the statistical significance of the estimates provided almost identical results, confirming that the high number of rare alleles had not biased the chi-square estimates of significance of F_{ST} values using Waples (1987) equations.

Unbiased estimates of F_{ST} and of the variance in F_{ST} were obtained by jackknifing over loci following Reynolds et al. (1983) and Weir and Cockerham (1984). These estimates were used to calculate the average number of migrants per generation (Nm) being exchanged between populations using the equation $Nm=((1/F_{ST})-1)/4$. Observed genotypic diversity (G_o) was calculated as $1/\Sigma g_i^2$ where g_i is the frequency of the ith multilocus genotype in the population. The expected genotypic diversity (G_E) was calculated following Stoddart and Taylor (1988). Heterogeneity chi-square tests of genotype distributions used to test differences in gene frequencies between sites, and fits of genotype frequencies to Hardy–Weinberg expectations, used significance values corrected for multiple simultaneous tests (Miller 1966).

Table 1 *Pocillopora damicornis* and *Acropora palifera*. Gene frequencies for nine populations of *P. damicornis* and six populations of *A. palifera* collected from up to three different habitats at One Tree reef (*n* number of individual samples; *nd* no data; – zero)

	Reef crest			Lagoon			Microatoll		
	1	2	3	1	2	3	1	2	3
P. damicornis									
*GPI**									
280	–	–	0.010	–	–	–	–	–	–
250	0.031	0.030	–	–	–	0.010	0.010	–	–
230	–	0.010	0.020	–	–	–	0.010	–	–
200	0.063	–	0.010	–	0.020	–	0.010	0.011	–
190	0.052	0.010	0.050	0.020	0.030	0.010	0.070	0.033	0.020
150	0.229	0.240	0.230	0.240	0.210	0.250	0.230	0.189	0.180
100	0.604	0.600	0.620	0.720	0.720	0.720	0.660	0.767	0.800
50	0.021	0.110	0.060	0.020	0.020	0.010	0.010	–	–
*LT-1**									
113	–	–	–	–	–	–	0.020	–	0.020
106	0.042	0.070	–	0.010	0.050	0.270	0.280	0.044	0.310
100	0.656	0.540	0.610	0.270	0.290	0.380	0.380	0.322	0.480
94	0.260	0.300	0.300	0.410	0.510	0.210	0.270	0.500	0.150
88	0.042	0.090	0.090	0.190	0.080	0.100	0.050	0.133	0.020
80	–	–	–	0.120	0.070	0.040	–	–	0.020
*LT-2**									
114	–	–	–	0.020	0.030	0.010	–	–	–
107	0.010	0.140	0.240	0.090	0.180	0.170	0.100	0.133	0.090
100	0.771	0.630	0.420	0.660	0.510	0.490	0.560	0.511	0.420
93	0.125	0.190	0.280	0.180	0.240	0.300	0.260	0.256	0.310
86	0.094	0.040	0.060	0.050	0.040	0.030	0.080	0.100	0.180
*HK**									
100	0.708	0.710	0.710	0.370	0.490	0.380	0.420	0.422	0.460
92	0.271	0.290	0.290	0.570	0.510	0.610	0.530	0.578	0.520
85	0.021	–	–	0.060	–	0.010	0.050	–	0.020
*PGM**									
129	0.010	0.010	0.030	–	–	0.020	0.020	0.011	0.010
114	0.135	0.180	0.200	0.080	0.130	0.050	0.080	0.044	0.100
100	0.833	0.720	0.720	0.910	0.870	0.930	0.900	0.944	0.890
86	0.021	0.090	0.020	0.010	–	–	–	–	–
71	–	–	0.030	–	–	–	–	–	–
(*n*)	(48)	(50)	(50)	(50)	(50)	(50)	(50)	(45)	(50)
A. palifera									
*MDH-1**									
117				0.490	0.550	0.420	0.380	0.541	0.490
100	nd	nd	nd	0.510	0.450	0.580	0.620	0.459	0.510
*MDH-2**									
135				–	0.010	0.020	0.050	–	0.010
118				0.010	0.040	0.020	0.020	0.010	0.050
100				0.830	0.760	0.770	0.660	0.786	0.770
88				0.070	0.090	0.110	0.150	0.153	0.070
76	nd	nd	nd	0.090	0.100	0.080	0.120	0.051	0.100
*GPI**									
333				0.370	0.350	0.290	0.390	0.347	0.300
100				0.630	0.650	0.710	0.610	0.653	0.700
*GLUDH**									
170				0.060	0.040	–	0.020	–	0.020
100	nd	nd	nd	0.940	0.960	1.00	0.980	1.000	0.980
*PGM**									
123				0.020	0.020	–	–	–	0.010
113				0.010	–	–	–	–	–
100				0.960	0.980	1.000	0.980	0.990	0.990
87	nd	nd	nd	0.010	–	–	0.020	0.010	–
(*n*)	(–)	(–)	(–)	(50)	(50)	(50)	(50)	(49)	(50)

Table 2 *Pocillopora damicornis* and *Acropora palifera*. Nei's unbiased genetic distances (Nei 1978) between populations of *P. damicornis* within and between habitats at One Tree reef (below diagonal) and between populations of *A. palifera* within and between habitats at One Tree reef (above diagonal) (*nd* no data)

Population		1	2	3	4	5	6	7	8	9
Reef crest	1 (1)		nd	nd	nd	nd	nd	nd	nd	nd
	2 (2)	0.006		nd	nd	nd	nd	nd	nd	nd
	3 (3)	0.032	0.007		nd	nd	nd	nd	nd	nd
Lagoon	1 (4)	0.080	0.069	0.095		0.000	0.001	0.005	0.000	0.000
	2 (5)	0.075	0.049	0.053	0.008		0.002	0.007	0.000	0.000
	3 (6)	0.094	0.075	0.082	0.028	0.028		0.001	0.002	0.000
Microatoll	1 (7)	0.061	0.052	0.069	0.023	0.021	0.000		0.007	0.004
	2 (8)	0.086	0.068	0.072	0.005	0.000	0.021	0.017		0.000
	3 (9)	0.079	0.069	0.067	0.061	0.049	0.007	0.007	0.041	

Results

Gene frequencies in the *Pocillopora damicornis* populations from the reef crest habitat were markedly different from those in the lagoon and microatolls (Table 1). The frequencies of *GPI*100*, *HK*92* and *PGM*100* were higher, and that of *LT-1*100* lower, in the lagoon and microatolls. There were no obvious differences in gene frequencies between the lagoon and microatoll populations of either *P. damicornis* or *Acropora palifera*.

This result was reflected in the greater genetic distances between the reef crest populations of *Pocillopora damicornis* compared to those from other habitats, and the similarity of genetic distances among populations within and between the lagoon and microatoll habitats (Table 2). On average, the genetic distance between reef crest populations of *P. damicornis* and those from other habitats was 0.072, three to four times greater than that either within habitats (average 0.019) or between lagoon and microatoll habitats (average 0.021) (Table 3). Genetic distances among populations of *Acropora palifera* within (average 0.003) and between (average 0.002) lagoon and microatoll habitats were also similar, but approximately six times less than those between *P. damicornis* populations from the same habitats. The genetic similarity of lagoon and microatoll populations, and their distinction from the reef crest populations is clearly demonstrated in the dendrogram summarising their relationships (Fig. 2).

Genetic variability within each of the populations was high. The mean number of alleles per locus per population ranged between 3.4 and 4.0 for *Pocillopora damicornis*, and between 2.2 and 2.8 for *Acropora palifera*, and observed heterozygosities ranged between 0.425 and 0.504 for *P. damicornis* and between 0.212 and 0.300 for *A. palifera* (Table 4). The observed mean heterozygosities were not significantly different to those expected under conditions of Hardy–Weinberg equilibrium. Genotypic frequencies at each locus, in all populations of *P. damicornis* and *A. palifera*, were also shown to conform to those expected under conditions of Hardy–Weinberg equilibrium at each locus using the exact test, with one exception. A significant deficit of heterozygotes was observed in the Lagoon Site 2 population of *P. damicornis*. Fifteen **100/*94* heterozygotes were expected at *LT-1** but only five were observed, and three more **100/*100* and eight more **94/*94* homozygotes were recorded.

Table 3 *Pocillopora damicornis* and *Acropora palifera*. Nei's unbiased genetic distances among populations of *P. damicornis* and *A. palifera*, averaged within and between habitats at One Tree reef

Population	*P. damicornis*	*A. palifera*
Mean genetic distance within habitats		
reef crest	0.015 (0.006–0.032)	nd
lagoon	0.021 (0.008–0.028)	0.001 (0.000–0.002)
microatoll	0.022 (0.007–0.041)	0.004 (0.000–0.007)
Mean genetic distance between habitats		
reef crest-lagoon	0.075 (0.049–0.095)	nd
reef crest-microatoll	0.069 (0.052–0.086)	nd
lagoon-microatoll	0.021 (0.000–0.061)	0.002 (0.000–0.007)

The ratio of the number of genotypes observed (N_G) to the number of individuals samples (N_I) indicated that almost as many genotypes as individuals were found in all the *Pocillopora damicornis* populations irrespective of habitat (N_G:N_I>0.80) (Table 4). *Acropora palifera* had about half as many genotypes as individuals sampled in all habitats (N_G:N_I=0.47 on average). G_E:N_I provided an estimation of the proportion of the sample likely to be made up of unique genotypes and showed a good fit to the observed values of N_G:N_I for *P. damicornis*, where some 85 to 90% of genotypes occurred only once. Only ≈30% of the *A. palifera* genotypes were expected to occur once per sample.

G_O:G_E is a measure of the degree to which populations deviate from Hardy–Weinberg equilibrium and from linkage equilibrium, and can be used as a measure of the degree to which a population is reproducing sexually. The ratio of the observed genotypic diversity (G_O) to that expected under conditions of random mating (G_E) was high in both species suggesting high degrees of sexual reproduction. On average G_O:G_E=0.91 for *Pocillopora damicornis* and 0.93 for *Acropora palifera*.

However, the average for each habitat showed a trend of increasing G_O:G_E from the reef crest (G_O:G_E=0.85), through lagoon (G_O:G_E=0.92) to microatoll (G_O:G_E=0.96) populations of *Pocillopora damicornis*, and a similar trend from lagoon (G_O:G_E=0.84) to microatoll (G_O:G_E=1.02) populations of *Acropora palifera*.

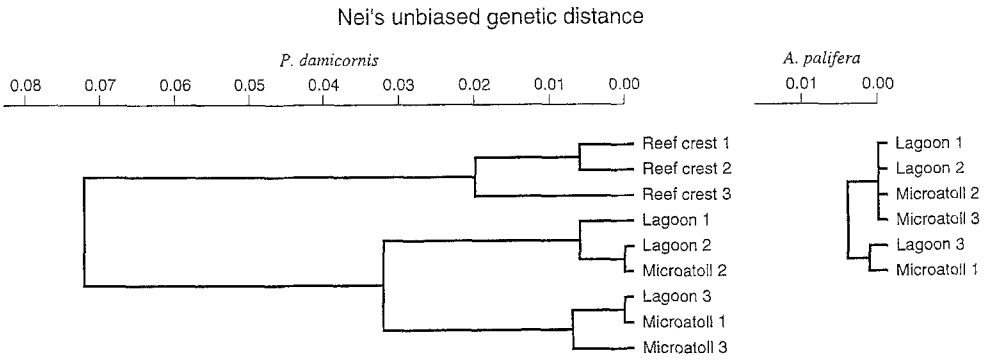

Fig. 2 *Pocillopora damicornis* and *Acropora palifera*. Dendrograms illustrating relationships between populations from three (*P. damicornis*) and two (*A. palifera*) habitats at One Tree Island. Nei's unbiased genetic distances (Nei's *D*) between populations were clustered using UPGMA (unweighted pair-group method of arithmetic averages) algorithm. Cophenetic correlations were 0.92 for *P. damicornis* dendrogram and 0.70 for *A. palifera* dendrogram

Table 4 *Pocillopora damicornis* and *Acropora palifera*. Genetic variability in nine populations of *P. damicornis* and six populations of *A. palifera* from different habitats at One Tree reef

Population		Mean no. of alleles per locus	% of loci polymorphic	Direct-count heterozygosity	Expected heterozygosity	No. of individuals (N_I)	Observed no. of genotypes (N_G)	$\frac{N_G}{N_I}$	Observed genotypic diversity (G_O)	Expected genotypic diversity (G_E)	$\frac{G_O}{G_E}$	$\frac{G_E}{N_I}$
P. damicornis												
reef crest	1	4.2 (0.5)	100	0.425 (0.058)	0.438 (0.050)	48	39	0.81	26.2	36.2 (5.7)	0.72	0.75
	2	4.0 (0.6)	100	0.492 (0.047)	0.520 (0.038)	50	48	0.96	46.3	45.5 (4.0)	1.02	0.91
	3	4.2 (0.9)	100	0.460 (0.052)	0.529 (0.049)	50	43	0.86	37.9	46.0 (3.8)	0.82	0.92
lagoon	1	4.0 (0.4)	100	0.504 (0.099)	0.475 (0.090)	50	45	0.90	41.7	43.4 (4.6)	0.96	0.87
	2	3.8 (0.7)	100	0.456 (0.081)	0.495 (0.078)	50	46	0.92	41.7	44.1 (4.5)	0.95	0.88
	3	4.2 (0.5)	100	0.468 (0.111)	0.485 (0.104)	50	45	0.90	37.9	44.0 (4.3)	0.86	0.88
microatoll	1	4.4 (0.7)	100	0.496 (0.077)	0.512 (0.088)	50	44	0.88	42.4	45.4 (4.0)	0.93	0.91
	2	3.4 (0.4)	100	0.449 (0.095)	0.453 (0.100)	45	39	0.87	34.3	36.8 (4.8)	0.93	0.82
	3	3.8 (0.6)	100	0.492 (0.103)	0.481 (0.095)	50	47	0.94	44.6	43.2 (4.6)	1.03	0.86
A. palifera												
lagoon	1	2.8 (0.5)	100	0.292 (0.094)	0.294 (0.088)	50	23	0.46	10.3	14.3 (3.1)	0.72	0.29
	2	2.6 (0.6)	100	0.300 (0.118)	0.297 (0.099)	50	22	0.44	10.5	15.5 (3.3)	0.68	0.31
	3	2.2 (0.7)	60	0.248 (0.106)	0.260 (0.107)	50	23	0.46	13.3	11.9 (2.4)	1.12	0.24
microatoll	1	2.6 (0.6)	100	0.288 (0.102)	0.313 (0.112)	50	32	0.64	21.6	18.8(3.8)	1.15	0.38
	2	2.2 (0.5)	80	0.212 (0.086)	0.268 (0.108)	49	21	0.43	13.4	11.8 (2.3)	1.14	0.24
	3	2.6 (0.6)	100	0.244 (0.103)	0.276 (0.102)	50	20	0.40	10.2	13.4 (2.9)	0.76	0.27

F-statistics analysis showed that significant differences in gene frequencies occurred between *Pocillopora damicornis* populations within each habitat (Table 5). Mean values of F_{ST} were similar for each habitat. More than one locus contributed to the effect in the lagoon and microatoll habitats, but only *LT-2** was responsible for the differentiation observed among reef crest populations. The total data set of all nine populations showed that all loci but *GPI** contributed strongly to the highly significant mean F_{ST} value. Upon pooling populations within each habitat and comparing habitat pairs, the reef crest was significantly differentiated from both the lagoon and microatoll habitats. The lagoon and microatoll populations were not significantly differentiated, with a mean F_{ST} of only 0.003. No significant differentiation was observed among *Acropora palifera* populations within or between the lagoon and microatoll habitats.

F_{ST} values were jackknifed over loci to provide variance estimates for F_{ST} (Table 6). These confirmed the similarity in the level of differentiation occurring among populations of *Pocillopora damicornis* within each of the habitats. The overall differentiation between lagoon and microatoll populations (0.005) was significantly less than that occurring between sites within each of these habitats (0.014 to 0.018) and one-tenth of that between the reef crest populations and those in the lagoon and microatolls. Jackknifed values of F_{ST} for *Acropora palifera* were all small, and significantly lower than the value for *P. damicornis*. The average number of migrants per generation was very high for populations of *A. palifera* within and between lagoon and microatoll habitats ($Nm > 44$). Gene exchange among *P. damicornis* populations was also high between pooled populations from these habitats. However, *Nm* was less within each habitat and was only one-tenth of this value

Table 5 *Pocillopora damicornis* and *Acropora palifera*. *F*-statistics describing degree of differentiation within (F_{IS}) and between (F_{ST}) populations in different habitats at One Tree reef

	F_{IS}				F_{ST}				Reef crest vs lagoon	Reef crest vs microatoll	Lagoon vs microatoll
	Reef crest	Lagoon	Microatoll	Total	Reef crest	Lagoon	Microatoll	Total			
P. damicornis											
*GPI**	-0.058^{NS}	0.041^{NS}	-0.043^{NS}	-0.024^{NS}	-0.005^{NS}	0.009^{NS}	0.017^{**}	0.011^{NS}	0.017^{**}	0.024^{***}	0.000^{NS}
*LT-1**	0.259^{***}	0.120^{NS}	0.100^{***}	0.147^{***}	0.001^{NS}	0.058^{***}	0.072^{***}	0.068^{***}	0.077^{***}	0.054^{***}	0.018^{***}
*LT-2**	0.001^{NS}	-0.078^{NS}	-0.088^{NS}	-0.057^{NS}	0.097^{***}	0.017^{**}	0.006^{NS}	0.034^{***}	0.002^{NS}	0.015^{***}	0.006^{**}
*HK**	-0.085^{NS}	-0.038^{NS}	0.028^{NS}	-0.032^{NS}	-0.009^{NS}	0.002^{NS}	-0.006^{NS}	0.071^{***}	0.156^{***}	0.130^{***}	0.000^{NS}
*PGM**	0.214^{**}	0.049^{NS}	-0.094^{NS}	0.100^{NS}	0.011^{NS}	0.001^{NS}	0.000^{NS}	0.042^{***}	0.062^{***}	0.069^{***}	0.000^{NS}
(Mean)	(0.066^{NS})	(0.019^{NS})	(-0.019^{NS})	(0.027^{NS})	(0.019^{**})	(0.014^{**})	(0.018^{**})	(0.045^{***})	(0.063^{***})	(0.059^{***})	(0.003^{NS})
A. palifera											
*MDH-1**		-0.112^{NS}	0.052^{NS}	-0.032^{NS}		0.009^{NS}	0.015^{NS}	0.009^{NS}			-0.003^{NS}
*MDH-2**		0.039^{NS}	0.212^{*}	0.133^{*}		-0.002^{NS}	0.013^{NS}	0.003^{NS}			0.000^{NS}
*GPI**		0.070^{NS}	0.115^{NS}	0.089		-0.004^{NS}	-0.003^{NS}	-0.004^{NS}			-0.003^{NS}
*GLUDH**		0.376^{***}	0.497^{***}	0.411^{***}		0.015^{NS}	-0.005^{NS}	0.010^{NS}			0.004^{NS}
*PGM**		-0.024^{NS}	-0.005	0.017		0.010^{NS}	-0.008^{NS}	0.001^{NS}			-0.002^{NS}
(Mean)	(nd)	(0.070^{NS})	(0.174^{*})	(0.117^{*})	(nd)	(0.005^{NS})	(-0.002^{NS})	(0.004^{NS})	(nd)	(nd)	(-0.001^{NS})

* $p<0.05$; ** $p<0.01$; *** $p>0.001$

between populations from the reef crest and those from other habitats ($Nm \leq 4$).

Discussion

Marked differences in the genetic composition of the crest populations of *Pocillopora damicornis* were observed relative to the lagoon and microatoll populations. This difference might reflect the effect of selection, but might also reflect isolation of the lagoon and microatoll populations from the crest populations. The lagoon at One Tree Island is completely encircled by a coral wall, and at low tide is almost completely cut off from the ocean. However, the identification of a means of larval transfer between the sites suggests that selection had some effect, if not a dominant role, in determining gene frequencies in these habitats.

At mid-flood tide, water spills over the crest into the lagoon from both the north-west and south-east rims but at all other times the flows are from the south-east, and at low tide there is a slow wind-induced circulation within the lagoon (Frith and Mason 1986). There is at least the potential for the distribution of larvae into the lagoon from the crest sites sampled, by means of the north-west currents at mid-flood tide. More important, the net volume flows from the south-east have the potential to transport larvae from the lagoon towards the north-west crest unless undescribed details of the lagoon circulation retain a high proportion of propagules. The net south-east flows are also likely to transport propagules released on the north-west crest away from the reef. The best alternative source of recruits from a crest habitat are the *Pocillopora damicornis* populations on the south-east crest. If these are effectively transported across the lagoon to the north-west crest, then so also would propagules produced by populations in the lagoon. This suggests that some selection would be required to maintain the gene frequencies observed in the north-west crest populations in the face of migration from the lagoon. Should the propagules carried from the south-east crest by the dominant south-east currents be entrapped by a lagoon circulation that prevents larvae produced in the lagoon reaching the north-west crest, then selection would be required to maintain the gene frequencies observed in the lagoon. The extent to which larvae are exchanged between habitats will depend upon the state of the tide when gametes or planulae are released. However, there appears to be an effective means of dispersal of gametes between the habitats, and no reason to expect a ten-fold reduction in the number of migrants per generation between the crest and the other habitats relative to that among the lagoon and microatoll populations.

The allozyme surveys of the *Pocillopora damicornis* and *Acropora palifera* populations provided no evidence that microatoll populations were genetically different from those in the lagoon. The similarity of the genetic composition of populations of both species in the two habitats suggests that similar selective regimes operate in the lagoon and microatolls, or that any effects of selection by

Table 6 *Pocillopora damicornis* and *Acropora palifera*. Jackknifed F_{ST} values together with 95% confidence limits (*CL*) and values for average number of migrants per generation (*Nm*) among populations within and between habitats on One Tree reef

	Reef crest	Lagoon	Microatoll	Reef crest vs lagoon	Reef crest vs microatoll	Lagoon vs microatoll
P. damicornis						
Jackknifed F_{ST}	0.019	0.014	0.018	0.063	0.058	0.005
(95% CL)	(0.013–0.025)	(0.010–0.024)	(0.014–0.022)	(0.055–0.071)	(0.052–0.064)	(0.004–0.006)
Nm	12.9	17.9	13.8	3.7	4.0	51.8
(95% CL)	(9.8–18.8)	(10.1–24.0)	(11.1–18.1)	(3.3–4.3)	(3.6–4.5)	(42.6–66.1)
A. palifera						
Jackknifed F_{ST}	nd	0.006	0.002	nd	nd	–0.001
(95% CL)		(0.004–0.007)	(0.001–0.004)			(–0.001–0.004)
Nm	nd	44.4	103.9	nd	nd	infinity
(95% CL)		(37.2–55.1)	(65.2–254.9)			(–)

the slightly different environment in the microatolls is overcome by gene flow between the habitats. Genetic divergence of the microatoll populations might also have been expected as a result of the isolation of the pool inside the microatoll from the rest of the lagoon. In such case, the degree of inter-population differentiation among microatoll populations would have been greater than the among populations within other habitats. This was not the case, and mixing of water over the microatoll wall at high tide appears sufficient to allow dispersal among populations. Panmixis, that is completely random mating, was inferred from observed gene frequencies among populations of *A. palifera* in the lagoon at One Tree Island, whether they occurred outside or inside the microatolls. Significant differentiation of *P. damicornis* populations within habitats was observed, but the levels of gene flow among populations of both species across the lagoon and microatoll habitats was high, and far greater than that required to prevent genetic differentiation of populations as a result of genetic drift.

All *Acropora palifera*-like samples obtained from the crest at One Tree Reef proved to be *A. cuneata*. All had an allele of PGDH characteristic of that species, as described by Ayre et al. (1991), and were therefore excluded from the present analyses. It is likely that Potts (1984) included some *A. cuneata* specimens in his transplant experiments at Heron Island. The marked differential mortality observed among transplants may have resulted in part from differences between these closely related species rather than among *A. palifera* clones. Nevertheless, the marked differences observed in gene frequencies of *Pocillopora damicornis* populations from the reef crest and lagoon habitats in the present study suggest that differential selection of coral genotypes may occur in these environments.

Both *Pocillopora damicornis* and *Acropora palifera* populations had genotype frequencies close to those expected under conditions of Hardy–Weinberg equilibrium suggesting random mating within local populations. Such a result was consistent with the known biology of *A. palifera* which, although it broods its young, produces them by fertilizing its eggs, using sperm in the surrounding water (Kojis 1986a). Planulae of *A. palifera* are produced year-round at low latitudes (Kojis 1986b) but at Heron Island Reef, close to One Tree Reef, gametes ripen only once a year and fertilisation occurs in only a few days in November. The restricted time for reproduction is also likely to enhance mixing of gametes, and therefore cross-fertilisation, among local populations.

In contrast, *Pocillopora damicornis* is thought to reproduce largely asexually (Stoddart 1984a, b) by means of brooded planulae whose mode of production appears independent of that of eggs and sperm (Stoddart 1983; Stoddart and Black 1985). *P. damicornis* can also reproduce asexually by means of fragmentation (Highsmith 1982), and this has been described as the dominant mode of reproduction in isolated populations in the eastern Pacific (Richmond 1987). Patterns of release of planulae by *P. damicornis* are extremely variable across the species range but predominate in winter in the north-central GBR (Harriot 1983).

The *Pocillopora damicornis* populations of One Tree differed considerably from those in previous reports in that reproduction was predominantly sexual. Genotypic diversity was high; G_O:G_E ratios ranged from 0.7 to 1.0 and averaged 0.9. Only one significant deviation of gene frequencies from those expected under conditions of Hardy–Weinberg equilibrium was encountered. Average G_O:G_E ratios were slightly less in the high-energy crest habitat, where fragmentation might be expected to occur more than in the low-energy lagoon environments. However, there was no evidence of major recruitment by this, or any other, asexual means.

Previous reports on the genetic structure of 25 *Pocillopora damicornis* populations from Australia showed low genotypic diversity and G_O:G_E ratios ranging from 0.07 to 0.61, but averaging only 0.40 (Stoddard 1984a, b). Many deviations of genotypic frequencies from those expected under conditions of Hardy–Weinberg equilibrium were observed, including heterozygote deficits and heterozygote excesses. Heterozygote deficits can be produced by a number of processes such as the Wahlund effect, where simple mixing of populations that differ in gene frequencies gives

rise to a deficit (Johnson and Black 1984), and by differential asexual reproduction among clones. The occurrence of heterozygote excesses among the deviations from Hardy–Weinberg confirmed that the deviations were the result of differential reproduction by clones, and not of a Wahlund effect.

The existence in some year-classes of novel genotypes that could only be produced by sexual recombination, the high levels of genetic variation in the total data set, and the concordance of clonal gene frequencies (i.e. gene frequencies calculated after pooling identical genotypes to estimate gene frequencies from a population of clones rather than a population of individuals) to those expected under conditions of Hardy–Weinberg provided evidence that sexual reproduction did occur in these populations (Stoddard 1984 a, b). However, asexual reproduction was the dominant mode of reproduction. It was considered to have been achieved by the asexual production of planulae and not by fragmentation. There was little direct evidence of fragmentation of colonies, and the distribution of clones was inconsistent with that mode of reproduction. The results from One Tree further confirm the variability in reproductive mode and timing of reproduction in *Pocillopora damicornis* throughout its range.

The occurrence of random mating within local populations of both *Pocillopora damicornis* and *Acropora palifera* simplify the interpretation of the results with respect to calculating gene flow among populations within and between habitats. Given the extent of water exchange among habitats, there are mechanisms for considerable exchange of genetic material among habitats. Although One Tree lagoon is relatively isolated from sites outside, it is not clear how this isolation should produce a ten-fold reduction in the number of migrants exchanged among populations. Transplant experiments are required to further test the hypothesis. However, it is suggested that differential selection between the crest and lagoon environments is responsible for the differences in gene frequencies observed among the populations of *P. damicornis* found in these habitats at One Tree reef.

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