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Population genetic studies of the crown-of-thorns starfish, *Acanthaster planci* (L.), in the Great Barrier Reef region

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Abstract. Seven populations of the crown-of-thorns starfish, *Acanthaster planci,* were compared genetically using starch gel electrophoresis in order to investigate the extent of genetic exchange throughout the Great Barrier Reef (GBR) region. These populations extended from Lizard Island in the north to One Tree Island in the south, a distance of approximately 1300 km. Thirteen of 36 enzymes assayed were genetically interpretable, and 10 (77%) of these were polymorphic. Mean heterozygosity over all loci was 0.225. An analysis of the gene frequency heterogeneity between the populations using Wright's F_{ST} statistic gave an overall F_{ST} of 0.019. The mean unbiased value of Nei's genetic distance between the populations was 0.009. These values indicate a homogeneous genetic composition throughout the range, and are consistent with the hypothesis that gene flow between these populations is high, and that *A. planci* throughout the GBR region are members of a single, effectively panmictic population. Within this group, the Green Island population was most distinct genetically because of differences in allele frequencies at the MDH-1 locus. Although there is no rigorous method for determining the selective basis for such differences, it is argued that the differences observed in the Green Island population were the result of selection. The basis for selective differences was possibly food availability since, at the time of sampling, the Green Island *A. planci* were the remnants of a large, high-density population that caused extensive coral mortality, and suffered severe population decline as food became scarce. These findings are consistent with observations of a relatively ordered sequence of outbreaks from north to south along the GBR, suggesting that all outbreaks but the first are secondary. Control measures, both on the GBR and elsewhere, have been unsuccessful except on a very small scale. Unless a vulnerable part of the *A. planci* life cycle can be identified, it would seem that the greatest chance for successful control would be to identify and control the causes of the primary population outbreak.

Introduction

The crown-of-thorns starfish, *Acanthaster planci* (L.), occurs widely throughout the Indo-Pacific region, including the Great Barrier Reef (GBR). It feeds on corals, and has caused severe damage to coral reefs in some areas (Chesher 1969; Pearson and Endean 1969). In the GBR region, *A. planci* first rose to prominence in the early 1960s when large numbers were observed feeding on the scleractinian coral at Green Island (Pearson and Endean 1969). Observations throughout the region suggested a southward spread of outbreaks (Pearson 1972; Pearson and Garrett 1975, 1976, 1978; Kenchington 1977); this is consistent with the known southward movement of surface water currents in the summer months in the GBR region (Walker and Collins 1982, 1985; Williams et al. 1984), when *A. planci* is known to spawn (Lucas 1973).

Unless this succession of outbreaks was caused by a series of primary outbreaks triggered independently, it is likely that the outbreaks south of Green Island were secondary, and arose as a result of enormous output of eggs from the primary outbreak population. If this is so, then gene flow throughout the GBR *A. planci* population is extensive, and the degree of genetic similarity between all reef populations will be high.

Large numbers of *A. planci* were again observed at Green Island in 1979/80 (Nash and Zell 1981), and the reported spread of outbreaks in a southward direction since then (Moran 1986) would appear to confirm the southward spread of secondary outbreaks.

This study addresses the question of genetic relatedness between *A. planci* populations throughout the GBR.

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If the apparent sequence of outbreaks throughout the central GBR region was fact, then the extensive gene flow should result in *A. planci* throughout the GBR region comprising a single panmictic population. This prediction was very largely confirmed.

Materials and methods

Specimens of *Acanthaster planci* were collected from the following localities within the GBR region: Lizard Island, Eyrie Reef, Yonge Reef, Green Island, Broadhurst Reef and One Tree Island (Fig. 1). *A. planci* was collected from two localities within the Lizard Island lagoon: (i) from the reef extending from North Point to Granite Bluff; and (ii) from the reef approximately midway between Lizard Island and Palfrey Island. These two collections were treated separately throughout this study. Abbreviations for each of these sites are given in Fig. 1, and are used throughout the text. Collections were made at Lizard Island, Eyrie Reef and Yonge Reef in June 1981. The Green Island and One Tree Island populations were sampled in July 1981, and the Broadhurst Reef population in October 1981.

Starfish were collected, using either snorkel or SCUBA, and placed into large bins containing flowing seawater until measured and dissected.

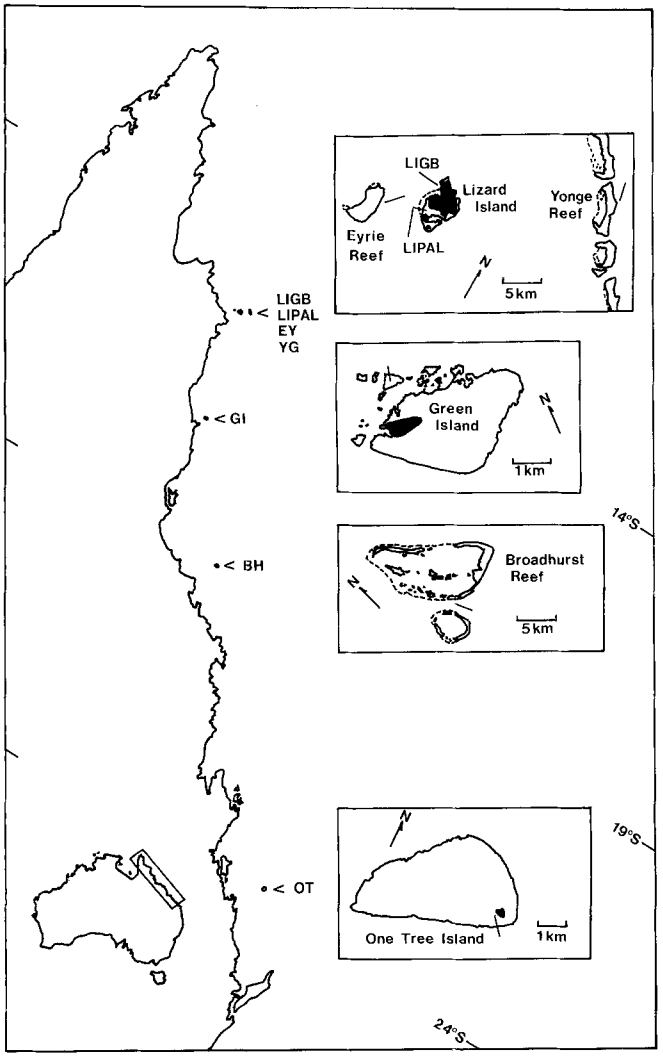

Fig. 1. Localities where *A. planci* was collected. LIGB = Lizard Island (Granite Bluff); LIPAL = Lizard Island (Palfrey Island); EY = Eyrie Reef; YG = Yonge Reef; GI = Green Island; BH = Broadhurst Reef; OT = One Tree Island. Collection sites are arrowed

Samples were frozen with dry ice (−79 °C) until transfer to the laboratory.

Electrophoretic procedures

Routine electrophoretic assays were of pyloric caecum; assays of other tissues (stomach, tube feet, gonad) showed that all enzyme loci for which genetically interpretable results could be obtained were found in pyloric caecum. Pieces of caecum were thawed, homogenized with one or two volumes of grinding buffer (10 mM solution of Tris, containing 1 mg/l NADP, adjusted to pH 6.8 with 1N HCl), and centrifuged at 27,000 g for 15 min at 4 °C. The supernatant was decanted and used immediately for electrophoresis, or stored at −79 °C for up to 5 days before use. Electrophoresis was carried out using 12% (w/v) Connaught starch. Genetically interpretable results were obtained for thirteen of thirty-six enzymes screened. These were routinely assayed using buffer systems A, B and C of Redfield and Salini (1980).

The histochemical staining procedures used are similar to those of Shaw and Prasad (1970), Ayala et al. (1974) and Redfield and Salini (1980).

Analytical procedures

Both the observed (H_O) and the expected (H_E) proportions of heterozygotes at each locus in each population sample were calculated. H_E was calculated as $H_E = 1 - \Sigma x_i^2$, where x_i refers to the frequency of the i-th allele.

The genotypic frequencies observed in each of the populations were compared with those predicted by Hardy-Weinberg assumptions (absence of selection, random mating) using a χ^2 goodness-of-fit test. To avoid problems of rare genotypes (<5 individuals), rare alleles were pooled until the expected value of the allelic classes was >5.

Heterogeneity of allele frequencies among populations at each polymorphic locus was tested for statistical significance with a χ^2 contingency test. When significant heterogeneity ($P<0.05$) was found, those populations which were the main contributors to this significance were identified by selectively excluding populations, either singly or in combination, from the χ^2 test. Using this procedure, it was possible to determine whether there was a general heterogeneity among populations at a locus, or whether a single population differed significantly from the rest. From sampling theory, standard errors of allele frequencies were calculated as $\sqrt{V}$, where $V = p_i(1-p_i)/2N$, p_i is the frequency of the i-th allele, and N is the number of individuals compared.

Genetic distance and genetic identity were calculated using the method of Nei (1978).

Genic heterogeneity between and within *A. planci* populations was investigated using Wright's (1943, 1951, 1965) F statistics. F_{IS}, the within-sample departure from Hardy-Weinberg proportions, was calculated for each locus by averaging F_i, the fixation index, over all subpopulations (Eanes and Koehn 1978). F_i was not corrected for bias caused by finite sample size as this is considered unnecessary when $N>10$ (Brown 1970). A weighted mean of F_{IS} over all loci was calculated according to Schaal (1975). The overall fixation index, F_{IT}, was computed from the equation

$$F_{IT} = 1 - H_T/(1 - \Sigma \bar{x}_i^2),$$

where H_T is the total proportion of heterozygotes in all population samples, and $1 - \Sigma \bar{x}_i^2$ is the expected proportion of heterozygotes based upon the mean allele frequencies of the entire population sample.

The amount of differentiation among populations was calculated by the standardized genetic variance statistic F_{ST}. F_{ST} values were calculated for each allele and for each locus. In addition, a mean F_{ST} over all loci was obtained, for each subpopulation, and for the entire GBR population, using the method of Wright (1980). F_{ST} was corrected for sampling error by the method of Nei and Imaizumi (1966) and Cavalli-Sforza and Bodmer (1971). The modified method of Weir and Cockerham (1984) for calculating the F statistics was not employed because of the unrealistic assumptions on which this method is based (Nei 1986).

Results

Ten of the thirteen genetically interpretable enzyme banding patterns were polymorphic. Genetic variability was not detected at three loci: EST (4-methylumbelliferyl acetate substrate), HK-2 and SOD-1. Two electrophoretic mobility classes could be seen at the SOD-2 locus, but the resolution was too poor for reliable identification. Nearly all of the 23 poorly resolved enzymes which could not be interpreted genetically exhibited electrophoretic variability.

Allele frequencies for each of the polymorphic loci studied are shown in Table 1. A deficiency of heterozygotes existed at most loci. These deficiencies reached significant levels ($P<0.05$) at the APH locus in the Lizard Island (Palfrey) population; at the 6PGD locus in the Lizard Island (Granite Bluff), Eyrie Reef, Yonge Reef and One Tree Island populations; at the PGM locus in the Green Island population; and at the MDH-1 locus in the Green Island population.

F_{IS} values (Table 2) give an average measure of heterozygote deficiency across all 10 loci. They are very heterogeneous, ranging from -0.0472 at PGI to 0.2663 at 6PGD. Positive values signify a deficiency of heterozygotes. The mean value of F_{IS}, 0.1566, is reasonably high, and suggests a consistent deviation from panmixia within most populations.

The total fixation index, F_{IT}, for each locus ranges from -0.0441 for TPI to 0.4419 for MDH-1 (Table 2).

The variation in allele frequencies between populations, measured by F_{ST}, is shown in Table 2. Correction for sampling error can result in negative values; these were replaced by zero, since F_{ST} can not be negative. Corrected values of F_{ST} range from zero for PGI and TPI to 0.1503 for MDH-1, with a mean over all loci and populations of 0.0191. With the exception of the MDH-1 locus, corrected F_{ST} values range from 0 to 0.0303.

The *A. planci* populations were analysed by a χ^2 test for heterogeneity of allele frequencies, at each locus, between the populations (Table 3). Significant deviations from homogeneity were found at 5 of the 10 polymorphic loci (Table 3 A). There is a great deal of heterogeneity among χ^2 values for individual loci, suggesting that selection is acting differently among the loci. Each locus was re-analysed by χ^2 with one or more populations selectively excluded, in order to estimate the relative contribution of each population towards the χ^2 value initially obtained (Table 3 B). At the APH locus, the main contributor to the strong deviation from homogeneity was the LIGB population. Particularly noteworthy here is the big difference in allelic composition between the two Lizard Island populations, LIGB and LIPAL. These two sampling sites were only about 4 km apart, so such differences were not expected.

Exclusion of the LIGB population from the analysis of IDH resulted in a non-significant χ^2 value, although the difference was not great. Exclusion of the YG or OT populations had little effect. The LIGB population is thus the main contributor to heterogeneity at the IDH locus.

At the MDH-1 locus, the χ^2 value became non-significant ($P>0.10$) when the GI population was excluded.

No single population appears to be contributing to the heterogeneity at the 6PGD locus; the exclusion of any one of LIGB, GI, or OT results in a non-significant χ^2 value (Table 3 B), suggesting that a general heterogeneity among the populations exists. At the PGM locus, on the other hand, the significance is largely due to the OT population, and to a lesser extent to LIPAL. When both LIGB and OT are excluded, the χ^2 value becomes non-significant ($P>0.50$).

In summary, the χ^2 analysis shows that there is significant local differentiation at 5 of the 10 loci examined.

Estimates of genetic distance (D) are shown in Table 4. Interpopulation genetic distances ranged from 0.0 to 0.0180, with a mean of 0.0094. Highest values were found with comparisons involving the Green Island population, which was attributable primarily to large differences in MDH-1 allele frequencies in this population.

In order to assess whether closely adjacent *A. planci* populations were more closely related genetically than more geographically distant ones, the genetic distance between each pair of populations (Table 4) was plotted against the geographical distances between them (Fig. 2). It can be seen that there is no consistent tendency for genetic distance to increase as the geographical distance increases, which might be expected if gene flow were limited or unifying selection were occurring (Kendall rank correlation; $P>0.20$).

Discussion

The results of this study show that *Acanthaster planci* is a highly genetically variable species, and is one of the more variable echinoderms studied to date. Higher levels of genetic variability have been found for few species (Nevo 1978; Ritte and Pashtan 1982).

Heterozygote deficiency has been commonly observed in marine invertebrates (review of Berger 1973; Ayala et al. 1973, 1974; Tracey et al. 1975; Koehn et al. 1976), but no convincing explanation has been offered. Possibly, related larvae travel in current-driven water masses together, settle together, and fertilize each others gametes, causing a degree of inbreeding.

Using Wright's F_{ST} and Nei's (1978) genetic distance D, the seven GBR *Acanthaster planci* populations sampled showed very little genetic differentiation. The mean F_{ST} value of 0.0309 found here is quite low when compared with the values obtained for many outbreeding animals (Eanes and Koehn 1978). However, very low F_{ST} values between populations thousands of kilometres apart have been reported in some marine species, including the milkfish *Chanos chanos* (Winans 1980), mussels (Levinton and Suchanek 1978) and limpets (Johnson and Black 1984). In a study of the population genetic structure of *Acanthaster planci*, Nishida and Lucas (in press)

Table 1. Allele frequencies at 10 variable loci in seven natural populations of *Acanthaster planci* on the Great Barrier Reef. H_O, H_E = observed and expected frequencies of heterozygous individuals, respectively. N = no. of genes sampled (twice the no. of individuals)

Locus	Alleles	LIGB	LIPAL	EY	YG	GI	BH	OT	Total[a]
APH	N	144	76	92	40	102	76	80	610
	93	0.063	0.184	0.120	0.175	0.167	0.079	0.138	0.123
	100	0.861	0.632	0.772	0.675	0.667	0.711	0.588	0.720
	107	0.076	0.184	0.109	0.150	0.167	0.211	0.275	0.157
	H_O	0.194	0.368	0.261	0.400	0.412	0.368	0.425	0.328
	H_E	0.249	0.533	0.378	0.491	0.500	0.445	0.560	0.442
HK-1	N	150	74	94	40	102	76	78	614
	100	0.927	0.932	0.936	1.000	0.931	0.987	0.936	0.943
	104	0.093	0.068	0.064	0.000	0.069	0.013	0.064	0.057
	H_O	0.093	0.135	0.085	0.000	0.098	0.026	0.077	0.081
	H_E	0.136	0.126	0.119	0.000	0.128	0.026	0.120	0.108
IDH	N	148	74	92	40	90	72	72	588
	89	0.007	0.014	0.000	0.000	0.000	0.042	0.014	0.010
	100	0.899	0.824	0.804	0.675	0.678	0.708	0.778	0.789
	115	0.095	0.162	0.196	0.325	0.322	0.250	0.208	0.201
	H_O	0.149	0.189	0.217	0.250	0.289	0.389	0.278	0.235
	H_E	0.183	0.294	0.315	0.439	0.437	0.434	0.351	0.337
MDH-1	N	148	76	94	40	100	76	82	616
	100	0.980	0.961	0.957	0.900	0.650	0.921	0.976	0.907
	113	0.020	0.039	0.043	0.100	0.350	0.079	0.024	0.093
	H_O	0.041	0.079	0.043	0.200	0.220	0.105	0.049	0.094
	H_E	0.040	0.076	0.081	0.180	0.455	0.145	0.048	0.168
MDH-2	N	148	76	94	40	100	76	82	616
	79	0.122	0.171	0.223	0.100	0.090	0.079	0.073	0.125
	100	0.878	0.829	0.766	0.900	0.910	0.908	0.915	0.870
	112	0.000	0.000	0.011	0.000	0.000	0.013	0.012	0.005
	H_O	0.216	0.289	0.383	0.100	0.180	0.132	0.122	0.224
	H_E	0.214	0.284	0.363	0.180	0.164	0.169	0.158	0.228
MPI	N	148	76	90	40	90	74	80	598
	93	0.169	0.250	0.244	0.350	0.233	0.176	0.188	0.216
	100	0.831	0.750	0.756	0.650	0.767	0.824	0.813	0.784
	H_O	0.203	0.289	0.222	0.400	0.289	0.243	0.275	0.258
	H_E	0.281	0.375	0.369	0.455	0.358	0.290	0.305	0.338
6PGD	N	148	72	88	34	86	68	76	572
	85	0.095	0.069	0.045	0.088	0.105	0.074	0.026	0.074
	100	0.439	0.389	0.364	0.382	0.326	0.397	0.289	0.375
	115	0.419	0.417	0.489	0.353	0.337	0.382	0.487	0.417
	120	0.047	0.125	0.102	0.176	0.233	0.147	0.197	0.134
	H_O	0.459	0.472	0.432	0.529	0.581	0.588	0.342	0.482
	H_E	0.620	0.655	0.616	0.690	0.715	0.669	0.640	0.662
PGI	N	136	68	88	36	78	70	82	558
	95	0.037	0.029	0.034	0.028	0.026	0.029	0.037	0.032
	100	0.860	0.897	0.886	0.861	0.846	0.900	0.939	0.884
	115	0.103	0.074	0.080	0.111	0.128	0.071	0.024	0.084
	H_O	0.235	0.206	0.227	0.277	0.282	0.200	0.122	0.219
	H_E	0.248	0.189	0.207	0.246	0.267	0.184	0.116	0.211
PGM	N	144	66	92	36	102	74	78	592
	78	0.181	0.106	0.185	0.167	0.225	0.270	0.333	0.211
	89	0.014	0.000	0.022	0.000	0.000	0.000	0.026	0.010
	100	0.806	0.894	0.793	0.833	0.775	0.730	0.641	0.779
	H_O	0.264	0.152	0.261	0.222	0.216	0.324	0.410	0.267
	H_E	0.317	0.190	0.336	0.278	0.349	0.394	0.477	0.349
TPI	N	148	76	94	40	88	72	78	596
	100	0.980	1.000	0.979	0.975	0.966	1.000	0.974	0.982
	104	0.020	0.000	0.021	0.025	0.034	0.000	0.026	0.018
	H_O	0.041	0.000	0.043	0.050	0.068	0.000	0.051	0.037
	H_E	0.040	0.000	0.042	0.049	0.066	0.000	0.050	0.036

[a] The total allele frequencies were calculated by pooling the data for all populations sampled. The expected frequencies of heterozygotes for the total sample were calculated according to Nei (1978)

Table 2. *F* statistics of *Acanthaster planci*

Locus	F_{ST} per locus	F_{IS}	F_{IT}
APH	0.0222	0.2334	0.2579
HK-1	0.0056	0.2074	0.2425
IDH	0.0303	0.2622	0.3035
MDH-1	0.1503	0.1642	0.4419
MDH-2	0.0158	0.0571	0.0579
MPI	0.0113	0.2281	0.2396
6PGD	0.0039	0.2663	0.2714
PGI	0.0	−0.0472	−0.0388
PGM	0.0228	0.2182	0.2343
TPI	0.0	−0.0305	−0.0441
F_{ST}[a]	0.0191		
F_{ST}[b]	0.0258		

[a] $F_{ST}=\sum S_p^2/\sum\bar{p}(1-\bar{p})$ (summed over all loci and populations)
[b] $\sum F_{ST}/10$ (mean F_{ST} per locus)

found a mean F_{ST} of 0.072 between populations spanning the entire Pacific Ocean.

Similarly, the values of Nei's *D* are also small when compared with the interpopulation distance levels in other starfish (Tuttle and Lindahl 1980) and in echinoids (Marcus 1977; Lessios 1979, 1981; Rosenberg and Wain 1982).

Low genetic distances over wide geographic ranges have been found in other marine invertebrates. For example, Selander et al. (1970) found a mean genetic distance of 0.01 between four populations of the horseshoe crab, *Limulus polyphemus*, from the Atlantic and Gulf of Mexico coasts of North America, and a comparison of populations of the clam *Tridacna maxima* from the GBR and Enewetak Atoll, nearly 4000 km apart, gave a mean genetic distance of 0.033 (Ayala 1975).

Table 3. χ^2 test of significance of allele frequency differences at each polymorphic locus, among all populations **A** with all populations included; **B** with one or more populations selectively excluded from those loci with significant differences. See Fig. 1 for population abbreviations. a = 0.05; *df* = degrees of freedom; *ns* = not significant

A				**B**			
Locus	*df*	χ^2	*P*	Locus	*df*	χ^2	*P*
APH	12	37.562	**	*APH* (-LIGB)	10	13.917	ns
				APH (-OT)	10	24.634	**
				APH (-LIGB, OT)	8	8.498	ns
HK-1	6	6.445	ns				
IDH	12	33.522	**	*IDH* (-LIGB)	10	17.216	ns
				IDH (-YG)	10	29.731	**
				IDH (-LIGB, YG)	8	14.573	ns
MDH-1	6	97.400	**	*MDH-1* (-GI)	5	8.183	ns
MDH-2	12	19.069	ns				
MPI	6	8.388	ns				
PGI	12	7.269	ns				
6PGD	18	31.235	*	*6PGD* (-LIGB)	15	16.139	ns
				6PGD (-GI)	15	21.877	ns
				6PGD (-OT)	15	24.102	ns
PGM	12	21.211	*	*PGM* (-LIPAL)	10	14.315	ns
				PGM (-OT)	10	12.205	ns
				PGM (-LIPAL, OT)	8	7.081	ns
TPI	6	3.277	ns				

* = $P<0.05$
** = $P<0.01$

Table 4. Genetic distance between pairs of *Acanthaster planci* populations

	LIGB	LIPAL	EY	YG	GI	BH	OT
LIGB	–						
LIPAL	0.0036	–					
EY	0.0012	0	–				
YG	0.0079	0	0.0018	–			
GI	0.0180	0.0116	0.0013	0.0029	–		
BH	0.0044	0.0027	0.0005	0	0.0061	–	
OT	0.0102	0.0055	0.0027	0.0057	0.0132	0.0006	–

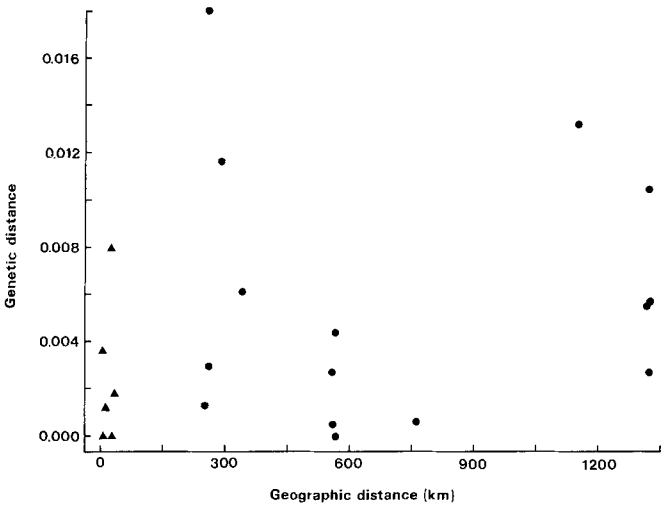

Fig. 2. Relationship between genetic distance and geographical distance between the study populations. ▲ = northern populations (Lizard Island, Eyrie Reef, Yonge Reef); ● = all other populations

High levels of genic similarity between populations often appear to be associated with high levels of mobility, whether in the adult or larval stages. In a review of patterns of population differentiation among species of marine invertebrates, it was shown (Burton 1983) that high levels of differentiation exist between population of species with limited dispersal capacity. The converse (low levels of gene differentiation in species with long planktonic larval durations) does not necessarily hold, however. The extent to which the potential for wide dispersal in the latter group is realized depends on such factors as local hydrographic conditions and larval behaviour.

The dispersal ability of *A. planci* larvae was demonstrated by Yamaguchi (1977), who found a correlation between larval geotactic behaviour and geographic distribution of four asteroid species: negative geotaxis was associated with pan-oceanic distributions, whereas positive geotaxis was associated with distributions around continental margins. The fact that *A. planci* occurs in the Hawaiian islands (Branham et al. 1971) and the eastern Pacific (Glynn 1974) also demonstrates its high dispersal capability.

In the light of the known duration of the planktonic larval phase of *A. planci* (Lucas 1973, 1975) and the movement of wind-driven surface water currents in the GBR region (Walker and Collins 1982, 1985), the high degree of genic similarity among the *A. planci* populations is not unexpected. The prevailing winds on the Queensland coast blow from the southeast. In summer, when *A. planci* spawns, these winds blow the least, and it has been shown (Walker and Collins 1982, 1985) that at such times, surface water flow is to the south and southeast. The pattern of *A. planci* outbreaks during the 1960s and early 1970s suggested a southward spread of populations, from both field observations (Pearson 1972) and from an analysis of the size structure of populations (Kenchington 1977). If a southward spread of *A. planci* outbreaks did in fact occur, then this could be due to one of two possible causes: (1) the initial outbreak may have occurred in the Cairns region (or further to the north), followed by secondary infestation of reefs to the south of Cairns by the pelagic dispersal of their larval progeny; (2) the triggering mechanism itself may have occurred in a chronological sequence from north to south. The lack of marked genetic differentiation between *A. planci* populations and the known dispersal characteristics of the larvae are consistent with the first hypothesis.

When interpreting the low genetic distances between populations, it should be borne in mind that small migration rates (a few individuals per generation) can keep populations from drifting apart in gene frequency (Allendorf and Phelps 1981). Thus, the low genetic distances between the GBR *A. planci* populations found in this study do not, in the absence of other information, provide conclusive evidence that migration between the populations is extensive.

There are two possible explanations for the significant heterogeneity of allele frequencies observed at five of the 10 polymorphic loci studied (Table 3). Firstly, there may be a common larval pool encompassing the entire region of this study, with differential selection occurring between the populations of relatively sedentary post-larval juveniles and adults. Secondly, there may be a proliferation of localized populations following colonization from elsewhere, with consequent incomplete gene flow; local populations would then be largely self-sustaining (self-recruiting) following the initial colonization. Depending on which of these explanations is correct, genetic differences between populations could be caused by either differential selection or the founder effect.

The second of these alternatives seems unlikely, given the high potential capacity for larval dispersal, as discussed above. Evidence in support of the first hypothesis comes from the fact that genetic distance is as great on a scale of 5 to 30 km between the northern study populations (the two Lizard Island sites, Eyrie Reef and Yonge Reef) as between northern and southern populations, spanning a distance of approximately 1300 km (Fig. 2).

It is also possible that populations could be genetically similar because they are subject to similar selection pressures. If some loci are neutral while others are subject to selection one would expect the F_{ST} values to differ from one locus to the next (Lewontin and Krakauer 1973). In our data the larger genetic distances and heterogeneity of F_{ST} which occur in comparisons involving the Green Island population are due to the high frequencies of MDH-1^{113} in the population. Although no rigorous significance test is available, this suggests that the difference in MDH-1 gene frequencies between Green Island and the other populations is due to selection.

The only known difference between the Green Island population and the others is that it was in an immediately post-plague phase when sampled. The extreme paucity of live hard coral at Green Island, and the drastic reduction of the *A. planci* population there, because of either migra-

tion, or death from starvation, strongly suggests that strong selective pressures were acting on this population. Many of the starfish collected at Green Island were feeding on a species of the soft coral *Sinularia,* and one was observed with its stomach everted over the silty bottom at the edge of the reef (unpublished observations). Thus, the few starfish remaining at Green Island at the time of collecting were survivors of very stressful conditions. It therefore is not surprising that some differences existed between this population and the rest. Whether the differences in MDH-1 allele frequencies found in the Green Island population are a consistent, characteristic response to extreme scarcity of food can only be determined by monitoring other populations as they undergo similar population peaks and crashes as occurred at Green Island. At the same time, it would be informative to measure change in MDH-1 in *A. planci* at Green Island after regrowth of hard coral there. It should be borne in mind that selection may not be acting on the MDH-1 locus itself, but on a locus closely linked to it and in linkage disequilibrium with it (Maynard Smith and Haigh 1974).

These results have implications for the management of *A. planci*, and for populations of marine species in general. The findings of this study are consistent with the observation that *A. planci* outbreaks have occurred in a relatively ordered sequence from north to south along the GBR, so that all outbreaks but the first are presumably of a secondary nature. Since the control of large *A. planci* outbreaks by poisoning or manual removal is impossible, as demonstrated at Green Island at the peak of the infestation (P. Tibbs personal communication 1980) and in Japan (Yamaguchi 1986), it is apparent that, unless novel control methods are devised, infestations cannot effectively be checked until the cause(s) of the initial outbreak are identified and controlled.

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