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Genetic structure of giant clam (*Tridacna maxima*) populations from reefs in the Western Coral Sea

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Abstract. Allozyme variation at six polymorphic loci was examined in 10 populations of *Tridacna maxima* from reefs in the Western Coral Sea, to test whether patterns of relatedness previously reported for foraminiferan populations reflected a fundamental structuring of the fauna in the region. Genetic distances (Nei's D) among populations of *T. maxima* ranged from 0–0.065 and increased with increasing geographical separation. No significant differences in gene frequencies were observed among populations within two groups of reefs identified by cluster analysis: the Great Barrier Reef (GBR), and among the offshore reefs excluding Lihou and Osprey. Significant genetic differences among these groups and the outliers Lihou and Osprey were consistent with the greater geographical separation of populations between areas than within areas. There was no evidence of differentiation along a north-south axis as reported for the foraminiferan *Marginopora vertebralis,* nor did populations from offshore reefs on the Queensland Plateau form a well-defined group that was genetically distinct from the GBR. The patterns observed for *M. vertebralis* do not appear to reflect a fundamental structuring of biota in the region. The differences in the pattern of genetic variation for *M. vertebralis* as compared with those for *T. maxima* may be due to several differences in the biological characteristics of the two species. The time of breeding in particular may influence the extent to which the divergence of the East Australian Current restricts larval dispersal among reefs in the central Queensland Plateau.

Introduction

Coral reefs on the submarine Queensland Plateau, approximately 300 km from the east coast of tropical Australia, are separated from the Great Barrier Reef (GBR), and from one or two isolated offshore reefs, by waters greater than 1000 m depth. These reefs are difficult to access, and little is known of the relationship between the fauna of the oceanic reefs to each other, and to those of the GBR, a large reef complex developed on the Australian continental shelf.

Given the greater geographical proximity of the reefs on the Queensland Plateau, and the likelihood that they share recent geological histories, a particularly close relationship of the faunas of these reefs to each other, and a more distant relationship to the isolated offshore reefs and the GBR might be expected. However, surveys of genetic variation in the benthic foraminiferan *Marginopora vertebralis* from Western Coral Sea reefs provided evidence for other patterns of relatedness (Benzie 1991). Populations of *M. vertebralis* from reefs on the Queensland Plateau did not form a related group that was genetically distinct from those on the Great Barrier Reef. Populations on isolated offshore reefs like Marion Reef formed genetic outliers, but so did Holmes Reef population situated close to other reefs on the Queensland Plateau. Reefs on the southern part of the Queensland Plateau were closely related to those on the GBR, and showed some genetic differentiation from reef populations on the northern part of the Queensland Plateau. The genetic disjunction of foraminiferan populations coincided with the southern limit of the divergence of the East Australian Current (EAC), and it was suggested that east-west dispersal parallel to the current was relatively easy compared with north-south dispersal perpendicular to the current (Benzie 1991).

Lack of genetic differentiation over large areas suggested some mechanism for long distance dispersal, but the dispersal mechanisms of *M. vertebralis* are unknown. Lack of knowledge of the biology of *M. vertebralis* and technical difficulties arising from small sample sizes for some enzymes assayed means further work is required to establish the generality of these results.

In order to test whether the genetic structure of foraminiferan populations reflected a fundamental structuring of populations in this region, we chose to examine the

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pattern of genetic relatedness among populations of a species with a known planktonic phase and likely to have a high dispersal capability. *Tridacna maxima* is particularly suited for this purpose as the species has a well-developed planktonic larval phase lasting 9 days (Lucas 1988). This giant clam also occurs commonly in coral reefs throughout the region and is known to have high levels of protein polymorphism (Ayala et al. 1973; Campbell et al. 1975).

The surveys also allowed the first analysis of regional patterns of connectedness of *T. maxima*. To date, genetic information has been obtained from only two widely-separated localities in the Pacific (Ayala et al. 1973; Campbell et al. 1975).

Methods

Field collections

Between 8 and 30 individuals of *T. maxima* were sampled from each of 8 reefs in the Coral Sea during July and August 1989 and 2 reefs from the GBR (Fig. 1). Clam tissue samples were obtained from more than one site on some reefs, but samples within a reef were pooled for analysis (Fig. 1). Scuba divers cut a small piece of tissue from the margin of the mantle using forceps and scissors, and placed the biopsy in seawater in a plastic bag. The shell was wedged open during the operation with a geological hammer to sample tissue without sacrificing the animals. The seawater was drained from the bag, the tissue snap-frozen in liquid nitrogen, and stored at −80° C until electrophoretic analysis.

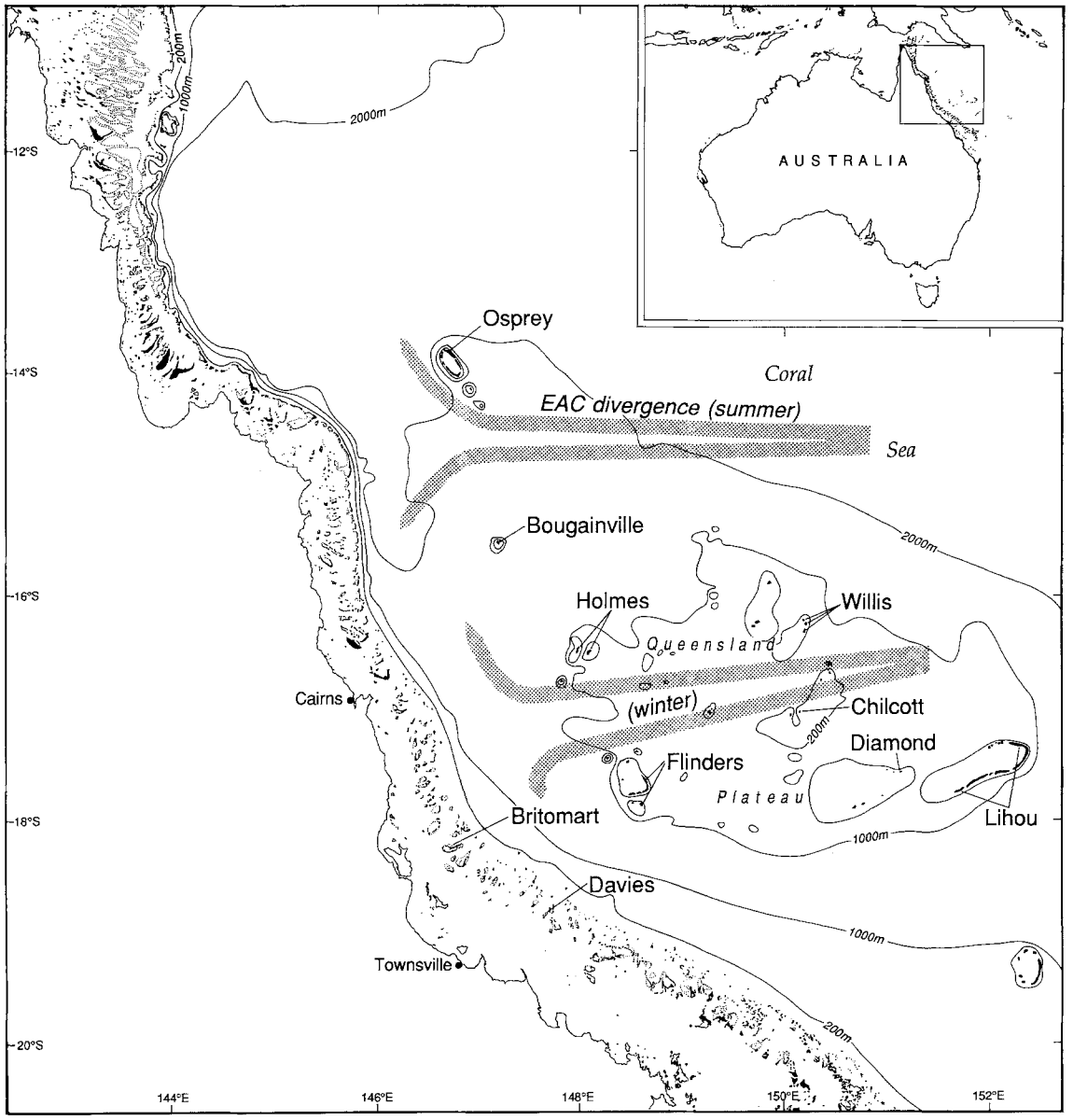

Fig. 1. Map of the reefs sampled in the Western Coral Sea and Great Barrier Reef. Multiple lines to Willis, Flinders, Holmes, and Lihou indicate the position of multiple sites sampled on these reefs. The arrows illustrate the general position of the East Australian Current divergence during the austral summer (about 14°S) and the austral winter (about 18°S)

Laboratory analyses

A piece of tissue 1 cm × 1 cm was crushed in 3 drops of an 0.04% aqueous solution of β-mercaptoethanol. Samples were kept on ice during crushing and prior to loading on gels. The lysate was absorbed onto filter paper wicks for starch gel electrophoresis (Shaklee and Keenan 1986).

Six enzymes could be assayed accurately from mantle tissue: lactate dehydrogenase EC 1.1.1.27 (LDH); malate dehydrogenase EC 1.1.1.37 (MDH); phosphoglucomutase EC 2.7.5.1 (PGM): diaphorase EC 1.6.*.* (DIAPH); peptidase using leu-gly-gly substrate EC 3.4.11/13.* (LGG); and glutathione reductase EC 1.6.4.2 (GSR). LDH, MDH, and LGG were run on Tris citrate pH 7.0 (TC 7.0) starch gels [12% w/v Sigma starch (S-4501) in buffer] at 200 volts for six hours. The gel buffer was 9.6 mM Tris, 3 mM citric acid, and the electrode buffer 135 mM Tris, 43 mM citric acid, both buffers adjusted to pH 7.0 using citric acid solution. GSR was run on Tris EDTA citrate pH 7.9 (TEC 7.9) at 200 volts for 6 h. The gel buffer was 8.5 mM Tris, 3 mM citric acid and 0.27 mM Na_2EDTA, and the electrode buffer 135 mM Tris, 43 mM citric acid and 4 mM Na_2EDTA, both buffers adjusted to pH 7.9 using citric acid solution. DIAPH and PGM were run on Tris EDTA borate pH 8.4 (TEB 8.4) and 200 volts for 6 h. The gel buffer was 48 mM Tris, 37 mM boric acid, and 1 mM Na_2EDTA, and the electrode buffer 150 mM Tris, 117 mM boric acid and 3 mM Na_2EDTA, both buffers adjusted to pH 8.4 using boric acid solution.

All zymograms were visualised using enzyme-specific stains following recipes in Harris and Hopkinson (1976). LDH, MDH, and GSR produced one-banded and three-banded patterns at one zone of activity consistent with dimer homozygotes and heterozygotes, together with one other zone of activity in LDH and MDH that could not be resolved. PGM, DIAPH and LGG produced two-banded and one-banded individuals consistent with monomer heterozygotes and homozygotes respectively. LGG also produced a second zone of activity with well-defined bands considered to be a second locus, but which did not stain reliably, and which was not scored. Bands at a locus were designated alphabetically with the fastest migrating band denoted "a", the second "b" and so on. The locus coding for the fastest migrating enzyme was designated "1" and slower migrating loci numbered consecutively. Cross correlations of alleles among populations confirmed allele identifications over the whole data set. *T. maxima* has dinoflagellate symbionts but com-

Table 1. Gene frequencies at six polymorphic loci screened in ten populations of *T. maxima* from the Western Coral Sea and Great Barrier Reef. Sample sizes (*n*) are given at the bottom of the table. Flinders $n=17$ for *Pgm, Gsr* and *Lgg-1* and 18 for all other loci

Locis/allele	Flinders	Willis	Lihou	Holmes	Chilcott	Diamond	Bougainville	Osprey	Britomart	Davies
Ldh-1										
a	–	–	–	–	–	–	0.040	–	–	–
b	–	–	–	0.026	–	–	–	–	–	–
c	1.000	1.000	0.944	0.974	0.972	0.972	0.960	1.000	1.000	1.000
d	–	–	0.056	–	0.028	0.028	–	–	–	–
Mdh-2										
a	–	–	–	–	0.028	–	–	–	–	–
b	1.000	1.000	1.000	0.974	0.972	1.000	1.000	1.000	1.000	1.000
c	–	–	–	0.026	–	–	–	–	–	–
Pgm										
a	0.029	0.095	0.056	0.026	0.111	0.083	0.040	0.017	–	–
b	0.441	0.405	0.333	0.658	0.444	0.528	0.520	0.517	0.750	0.633
c	0.500	0.357	0.333	0.263	0.444	0.333	0.340	0.383	0.188	0.333
d	–	0.024	–	–	–	–	–	–	0.063	–
e	0.029	0.095	0.167	0.053	–	0.056	0.100	0.083	–	–
f	–	0.024	0.111	–	–	–	–	–	–	0.033
Diaph										
a	–	–	–	–	–	–	–	–	–	–
b	0.028	0.024	–	–	–	0.028	0.040	0.017	–	0.033
c	0.028	0.024	–	–	–	–	–	0.017	0.063	–
d	0.444	0.310	0.167	0.474	0.333	0.528	0.400	0.283	0.188	0.400
e	0.444	0.571	0.778	0.500	0.611	0.389	0.440	0.650	0.625	0.567
f	0.056	0.071	0.056	0.026	0.028	0.056	0.120	0.017	0.063	–
g	–	–	–	–	0.028	–	–	0.017	0.063	–
Lgg-1										
a	0.029	0.048	–	–	–	0.028	0.020	–	–	–
b	0.471	0.357	0.333	0.447	0.611	0.556	0.540	0.250	0.688	0.633
c	0.412	0.548	0.667	0.526	0.389	0.361	0.380	0.583	0.313	0.367
d	0.088	0.048	–	0.026	–	0.056	0.060	0.167	–	–
Gsr										
a	0.029	0.024	0.056	0.026	–	–	–	0.017	0.063	–
b	–	–	–	–	0.139	0.028	–	–	–	–
c	0.235	0.214	0.111	0.158	0.167	0.139	0.160	0.050	0.313	0.167
d	0.059	–	–	0.026	0.028	0.083	0.080	0.050	–	0.167
e	0.559	0.524	0.556	0.447	0.556	0.528	0.580	0.383	0.500	0.367
f	0.029	0.095	0.056	0.079	0.056	0.139	0.060	0.383	–	0.067
g	0.059	0.095	–	0.079	–	0.083	0.020	0.033	–	0.067
h	0.029	0.048	0.222	0.184	0.056	–	0.100	0.083	0.125	0.167
n	18(17)	21	9	19	18	18	25	30	8	15

parison of patterns from symbiont free tissue (muscle) in preliminary tests identified the bands derived from clam enzymes. Symbiont derived bands, when present, occurred as additional smeared zones of activity that did not overlap with the zones of activity identified as clam.

Statistical analyses

In reefs where clams were obtained from more than one site, sample sizes at each site were usually small (<6). Preliminary statistical tests showed no significant differences in gene frequencies among sites within a reef, and the reef subsamples were pooled for further analyses.

Calculation of gene frequencies and population genetic statistics was carried out using the BIOSYS-1 package (Swofford and Selander 1981). F-statistics were calculated following Weir and Cockerham (1984) whose method explicitly takes account of differences in samples sizes among the populations tested. The statistical significance of F_{IS} (a measure of genetic differentiation within populations) and F_{ST} (a measure of genetic differentiation between populations) was calculated using the equations given in Waples (1987) to estimate chi-square. Chi-square tests for heterogeneity of gene frequencies used programs in BIOSYS-1. These did not offer the facility of pooling rare alleles, with degrees of freedom reflecting the product of the number of alleles minus one and the number of populations minus one summed over loci.

Results

Pgm, Diaph, Lgg-1 and *Gsr* were highly variable while *Ldh-1* and *Mdh-2* gene frequencies were dominated by the same allele in all populations (Table 1). In the more variable systems, a single allele predominated within most populations and other variants were present at relatively low frequency. Observed levels of polymorphism and the mean number of alleles per locus were not generally related to sample size even though sample sizes were small in some populations (Table 2). In all populations mean heterozygosity was similar to that expected under conditions of Hardy-Weinberg equilibrium and there were no significant deviations from Hardy-Weinberg equilibrium at individual loci in any population using exact probabilities (Elston and Forthofer 1977). When more than two alleles were present genotypes were pooled into three classes for this test – homozygotes for the most common allele, heterozygotes for the most common allele and one of the other alleles, and all other genotypes (Swofford and Selander 1981).

Genetic distances among the populations were generally small but those between Lihou and Osprey compared with all other populations were 2–4 times greater than the other pairwise comparisons, with Lihou and Osprey forming a group separate from all the other populations in the cluster analysis (Table 3, Fig. 2). Principal coordinates plots of the populations (not illustrated) demonstrated that Lihou and Osprey were as widely separated in multidimensional space as each was from a cluster consisting of all other populations. This indicated Lihou and Osprey did not constitute a well-defined, closely-related group, but were both outliers that fused together in the dendrogram before either was fused to the main group.

F-statistic analysis of the total set of populations, and of the major groups observed in the cluster analysis, revealed no structuring within populations, i.e. all F_{IS} values were non-significant (Table 4). This result is consistent with the conformance to Hardy-Weinberg found in each population in the exact tests described above. No significant differentiation was observed among populations from within the GBR, or among populations from within the Queensland Plateau reefs, either using heterogeneity chis-quare, or F_{ST}.

Table 2. Summary data on genetic variation in the 10 populations of *T. maxima* sampled. Standard errors are given where appropriate in parentheses. A locus is considered polymorphic if more than one allele was detected and the expected heterozygosity is Nei's unbiased estimate (Nei 1978)

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct-count	HDYWBG expected
1. Flinders	17.5	3.7	66.7	0.338	0.408
	(0.2)	(1.0)		(0.121)	(0.129)
2. Willis	21.0	3.8	66.7	0.389	0.425
	(0.0)	(0.9)		(0.127)	(0.136)
3. Lihou	9.0	3.0	83.3	0.352	0.401
	(0.0)	(0.7)		(0.113)	(0.124)
4. Holmes	19.0	3.5	100.0	0.439	0.406
	(0.0)	(0.8)		(0.127)	(0.117)
5. Chilcott	18.0	3.2	100.0	0.370	0.399
	(0.0)	(0.7)		(0.106)	(0.111)
6. Diamond	18.0	3.5	83.3	0.407	0.419
	(0.0)	(0.7)		(0.132)	(0.125)
7. Bougainville	25.0	3.5	83.3	0.400	0.423
	(0.0)	(0.7)		(0.121)	(0.122)
8. Osprey	30.0	3.7	66.7	0.328	0.396
	(0.0)	(1.0)		(0.105)	(0.128)
9. Britomart	8.0	2.7	66.7	0.292	0.360
	(0.0)	(0.7)		(0.115)	(0.120)
10. Davies	15.0	2.7	66.7	0.333	0.387
	(0.0)	(0.8)		(0.113)	(0.131)

Table 3. Matrix of Nei's unbiased genetic distance (Nei 1978) among all the *T. maxima* populations surveyed

Population	1	2	3	4	5	6	7	8	9	10
1. Flinders	–									
2. Willis	0.000	–								
3. Lihou	0.031	0.000	–							
4. Holmes	0.006	0.005	0.025	–						
5. Chilcott	0.000	0.004	0.019	0.013	–					
6. Diamond	0.000	0.009	0.053	0.000	0.003	–				
7. Bougainville	0.000	0.003	0.029	0.000	0.000	0.000	–			
8. Osprey	0.037	0.014	0.018	0.025	0.042	0.041	0.040	–		
9. Britomart	0.025	0.027	0.043	0.010	0.009	0.022	0.009	0.065	–	
10. Davies	0.007	0.018	0.040	0.000	0.003	0.000	0.000	0.040	0.000	–

Significant differences in gene frequencies were observed between populations from the GBR and the Queensland Plateau, between Lihou and Osprey, and among populations in the whole data set using chi-square (Table 4). *Gsr, Lgg-1* and *Pgm* contributed to this differentiation. *Lgg-1*^{d} and *Gsr*^{f} were found at high frequency in Osprey, *Gsr*^{h}, *Pgm*^{e}, and *Pgm*^{f} at high frequency in Lihou, and *Lgg*^{b} at low frequency in both Lihou and Osprey and Willis compared with the other populations (Table 1). On average *Gsr*^{c}, *Gsr*^{d} and *Gsr*^{h} were more abundant in the GBR populations than the average for the Queensland Plateau populations (Table 1). However, none of the F_{ST} values for these data sets was significant.

A potential explanation for the discrepancy between chi-square and the F-statistics is that the chi-square value may have been inflated by the inclusion of a number of cells with small values. Another explanation is that F_{ST} measures the average level of variation occurring among populations. When one population differs greatly from several others that do not differ from each other, the overall F_{ST} value may not be significant. Data from populations clustering in the major groups, and for which no differences in gene frequencies among populations had been detected within the group using chi-square, were therefore pooled and the resulting four populations subjected to F-statistic analysis.

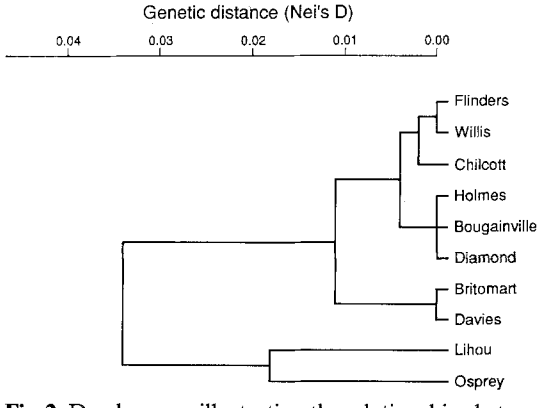

Fig. 2. Dendrogram illustrating the relationships between the populations sampled. Values of Nei's unbiased genetic distance (Nei's D) were clustered using the UPGMA algorithm. The cophenetic correlation of the dendrogram was 0.79

F_{IS} values were not significant for any locus and confirmed the pooled populations had not included populations that differed in gene frequencies from each other. The mean F_{ST} values demonstrated significant interpopulation variation among Lihou, Osprey, the rest of the Queensland Plateau and the GBR (Table 5). *Diaph, Lgg-1* and *Gsr* contributed to this pattern.

Table 4. Genetic differentiation among populations within the total data set, and among populations within the groups identified by the cluster analysis. ns = not significant

Population set	$X^2(df)$	Weirs F_{ST}	Weirs F_{IS}
All populations	351.6(225)**	0.011 ns	0.065 ns
GBR populations	19.5(15) ns	−0.016 ns	0.137 ns
Plateau populations (Total excluding Osprey, Lihou and the GBR)	141.5(125) ns	−0.002 ns	0.039 ns
Plateau and GBR populations	210.3(175)**	−0.001 ns	0.053 ns
Lihou and Osprey populations	30.4(18)*	0.015 ns	0.107 ns

* $P<0.05$
** $P<0.001$

Table 5. F-statistics analysis of the four populations derived from pooling reef populations within the four groups identified in the cluster analysis. It was established before pooling data that no significant differences in gene frequencies occurred between populations within the sets pooled. An unbiased estimate of F_{ST} was obtained by jack-kifing and 95% confidence limits calculated following Weir and Cockerham (1984). ns = not significant

Locus	F_{IS}	F_{ST}
Ldh-1	−0.010 ns	−0.003 ns
Mdh-2	0.003 ns	−0.011 ns
Pgm	0.021 ns	0.004 ns
Diaph	0.163 ns	0.026***
Lgg-1	−0.002 ns	0.054***
Gsr	0.150 ns	0.042***
Mean	0.054	0.019**
Unbiased estimate ±95% confidence limits		0.0188 ± 0.0023

** $P<0.01$
*** $P<0.001$

Genetic distances among populations increased with increasing geographical separation although there was a wide scatter (Fig. 3). The graph illustrates that the genetic distances between Lihou and Osprey and all other populations are consistent with their geographical separation from the other populations.

Discussion

The pattern of genetic differentiation among *Tridacna maxima* populations from the Western Coral Sea does not support the hypothesis that the pattern of variation reported for *M. vertebralis* (Benzie 1991) reflects a fundamental structuring of biota in the region. There was no evidence of differentiation along a north-south axis as described for the foraminiferan, and genetic differences among clam populations increased simply as a function of geographical separation.

The two outliers in the giant clam analysis, Lihou and Osprey, were at the southern and northern limits of the region sampled. If *T. maxima*'s dispersal capabilities were higher than those of *M. vertebralis*, differentiation on a north-south axis might only be demonstrated by sampling over a greater geographical region. It is possible that further sampling to the north and south of the outliers would reveal a north-south pattern of genetic differentiation, but this pattern would be very different to that reported for *M. vertebralis*.

A feature of the north-south genetic differentiation displayed by *M. vertebralis* was the distinction of populations in the northern half of the Queensland Plateau from those in the southern half related to the East Australian Current (EAC) divergence (Benzie 1991). Details of current flow among reefs on the Queensland Plateau are unknown and are likely to be complex, but generalised current patterns for the Western Coral Sea show a major divergence of the EAC which alters position with season and which ranges between 14°S and 18°S crossing the Queensland Plateau in the austral winter (Pickard et al. 1977; Church 1987; Andrews and Clegg 1989). The zone between the genetically differentiated groups of foraminiferan populations coincided with the southern limit of the divergence. This pattern was not observed in *T. maxima*.

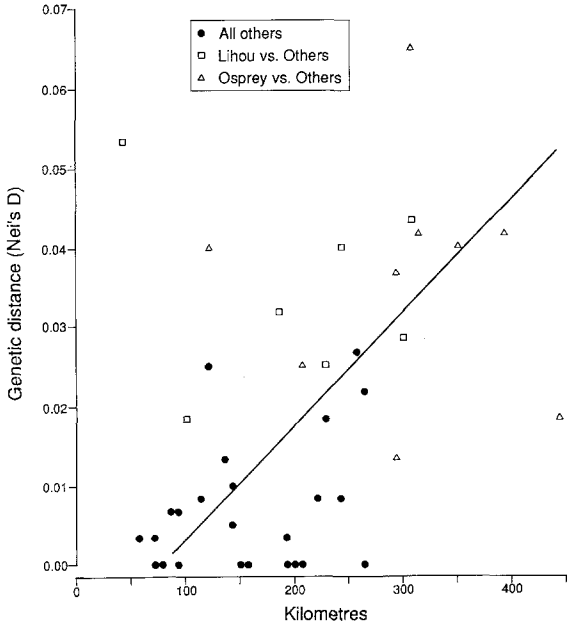

Fig. 3. Plot of the Nei's unbiased genetic distance (Nei's D) between pairs of populations as a function of their geographical separation. The shortest linear distance between sites measured to scale from a map was used to estimate geographical separation. Y (genetic distance) = 0.000085 X (geographical separation) – 0.00015. As not all points are independent r^2 and associated probabilities cannot be calculated

The genetic distances of both Lihou and Osprey populations to other populations were consistent with the general relationship between genetic distance and geographical separation observed in the total data set. There is, therefore, no evidence to suggest the genetic distinction of the Lihou or Osprey populations reflects anything other than their greater geographic separation from the other populations sampled. It is of interest to note that the genetic differences observed between Lihou, Osprey and the other group of reefs was similar to the minimum genetic distance estimated between a *T. maxima* population in the GBR and another on Enewetak Atoll in the Marshall Islands separated by several thousand kilometers (Campbell et al. 1975). It is emphasised that the data for the GBR versus Eniwetok is a minimum genetic distance and the true value could be greater. As a different, and smaller set of genes was sampled in the present study close comparison of distances with the previous study is inappropriate. Given the wide scatter of points in Fig. 3, it is not clear how strong the relationship is between genetic distance and geographical separation. F_{ST} values observed for *T. maxima* are similar to those observed for other widespread marine invertebrates with a similar larval life-span (Nishida and Lucas 1988; Benzie and Stoddart 1992).

There are two possible explanations for the difference in the patterns observed in *M. vertebralis* and *T. maxima*, both of which depend upon assumptions about the biology of *M. vertebralis*. The first is that *M. vertebralis* does not have as high a dispersal capability as *T. maxima*. The fact that *M. vertebralis* does not show marked genetic differentiation over large geographical scales would suggest otherwise. However, it is possible that the lack of differentiation among *M. vertebralis* populations results from low rates of populations divergence for other reasons such as low mutation rates. Population differentiation in this case would be slowed by relatively low levels of dispersal among populations.

Another possibility is that *M. vertebralis* might have young with high dispersal capacity but that these are produced at the time of year the EAC divergence crosses the centre of the Queensland Plateau (18°S during the austral winter) and that *T. maxima* breeds when the divergence is elsewhere. It is not known whether *M. vertebralis* has a defined breeding time, or when that time might be. However, all species of giant clams investigated from the GBR breed in the austral summer (Copland and Lucas

1988) when the divergence is to the north (14°S and closer to Osprey). If the divergence were to play an important role in determining the fate of planktonic larvae, all but one of the *T. maxima* populations surveyed occur in the southern half of the current at the time larvae are produced, and would not be expected to show marked genetic differences. One might expect Osprey to differ from the others but this population differed no more than might be expected on the basis of its geographical separation from the other reefs surveyed. The data provided no evidence in support of a strong effect of the divergence on the genetic differentiation of *T. maxima* populations.

The data obtained from the survey of genetic variation in *T. maxima* do not support the view that the pattern of variation observed in *M. vertebralis* reflects a fundamental structuring of the fauna in the regioin. However, *T. maxima* breeds at a time when the EAC divergence would be unlikely to give rise to the pattern of dispersal observed for the foraminiferan. Lack of knowledge about the biology of *M. vertebralis* prevents more definitive discussion. It will be important to obtain information on the genetic structure of other species whose biology is better known, to clarify the role of the EAC divergence in determining the genetic structure of organisms in the Western Coral Sea.

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