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Effects of recruitment on genetic patchiness in the urchin *Echinometra mathaei* in Western Australia

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Abstract

Enzyme polymorphisms in the sea urchin *Echinometra mathaei* were examined to test the relative influences of population turnover and patchiness in recruitment on genetic heterogeneity. We found that the total variance in allelic frequency among three populations separated by approximately 4 km at Rottnest Island, Western Australia (collected in February 1985) is as large as that among five additional samples collected over a distance of 1 300 km along the Western Australian coast in August 1987. This suggests that the forces causing genetic differentiation act on a local scale and occur in a single generation. A comparison of sites with different histories of recruitment indicates that the observed genetic differences among age groups are the result of pre-recruitment effects, and that differences among sites reflect their individual histories of recruitment.

Introduction

Many intertidal marine animals have planktonic dispersal of larvae and a sedentary adult stage. These characteristics have contrasting genetic consequences. Planktonic dispersal promotes gene exchange among spatially isolated populations, whereas a sedentary adult stage is subject to localised selection, which may produce genetic differences among local populations. In addition, the spatial subdivision of sedentary adult populations will preserve any within-generation genetic patchiness resulting either from selection or recruitment.

Several studies have examined the patterns of genetic subdivision in such species. Both the limpet *Siphonaria jeanae* (Johnson and Black 1982, 1984a) and the seastar *Acanthaster planci* (Nash et al. 1988, Nishida and Lucas 1988) showed a pattern of little geographic variation, but significant localised genetic heterogeneity. Such fine-scale genetic variation could result from either post-settlement selection or spatial heterogeneity in the genetic composition of the supply of recruits.

Post-recruitment selection has been shown to contribute to the genetic patchiness of a number of species (e.g. Koehn et al. 1982). For species with planktonic larvae, however, effects of localised selection cannot be transferred between generations and therefore are not cumulative through time. For species which have planktonic larvae and a sedentary adult stage, the genetic composition of the recruits, and not the adults, will have the major influence on the genetic composition of the population. Depending on the rate of population turnover, this influence may be either ephemeral, as shown for the short-lived limpet *Siphonaria jeanae* (Johnson and Black 1984b), or persistent in the case of a longer lived species. Hence, spatial heterogeneity in the genetic composition of the larval supply may have a greater influence than post-settlement selection on the extent of genetic patchiness in a species. The implication is that different rates of population turnover and different degrees of patchiness of recruitment should be reflected in the degree of localised genetic heterogeneity.

The sea urchin *Echinometra mathaei*, which has sedentary adults and pelagic larvae, is a suitable species on which to test this hypothesis. This species is abundant on shallow reefs throughout the Indo-Pacific region and is near the southern limit of its distribution at Rottnest Island, Western Australia. The populations of *E. mathaei* at Rottnest Island have been observed for many years and a number of sites are known to have different histories of recruitment. Furthermore, *E. mathaei* is long-lived, so that the adults generally represent an accumulation of many groups of recruits which have reached maturity. Having a different scale of population turnover to that of *Siphonaria jeanae*, which was also studied at Rottnest Island, and known recruitment histories at a number of sites, the population of *E. mathaei* at Rottnest Island provides an opportunity to test the influence of recruitment histories on the degree of genetic heterogeneity among local populations.

Materials and methods

Size structure and life expectancy of *Echinometra mathaei*

Three sites at Rottnest Island (32°S; 115°30′E) with reasonably understood histories of recruitment and separated by about 4 km were chosen for this study: Strickland Bay, Radar Reef and Cape Vlamingh. *Echinometra mathaei* has been continuously present at both Radar Reef and Cape Vlamingh at least since the studies of Pearse and Phillips (1968). In contrast, the population of urchins at Strickland Bay is the result of recent recruitment. There were no *E. mathaei* present at this site from at least 1974, until the first recruits were noted in August 1982 (R. Black personal observation).

At Rottnest Island, individuals of *Echinometra mathaei* with mature gametes can be found throughout the year (Pearse and Phillips 1968); however, recruitment is not continous and has been observed to occur over an extended season (R. Black, J. Prince personal communication). As a result of this seasonal recruitment, it has been possible to recognise distinct cohorts for up to two years at some of the sites, including the sites chosen for this study. The size structure of *E. mathaei* at these three sites was determined in February 1985 by measuring the maximum diameter of the test of each urchin in 19 haphazardly thrown 0.25 m^2 quadrats. Of these quadrats, six were from Strickland Bay, six from Radar Reef and seven from Cape Vlamingh. Based on the observation of distinct modes in the size-frequency distribution, three groups of urchins were identified (Fig. 1). We refer to these groups as recruits, subadults, and adults, corresponding to increasing test size. The term "subadults" refers only to the relatively small size of these individuals, many of which have mature gonads. Each of the three size groups was present at the three sites, and the size-frequency diagram was drawn from pooled data from all three sites. Although the mode in the size-frequency diagram which identifies the recruit group is small, the recruits were visually distinct in the field. The small number of recruits in the sampled quadrats may be due to their patchy spatial distribution.

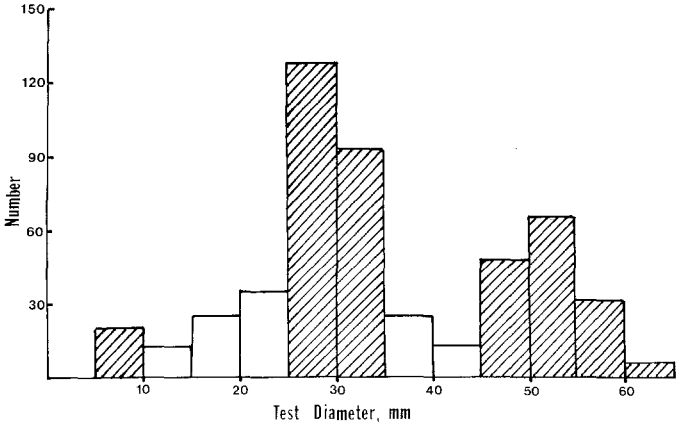

Fig. 1. *Echinometra mathaei.* Size-frequency distribution in combined quadrat samples from Rottnest Island in February 1985. Hatching indicates size groupings sampled for electrophoresis

Evidence from two sources suggests that *Echinometra mathaei* is a long-lived sea urchin. Firstly, Ebert (1982) examined the annual survival rates in 17 sea urchin species, including *E. mathaei,* from the Indo-west Pacific region. Based on his data, it is possible to estimate that for *E. mathaei* the expectation of further life of an individual of any age ($1/Z$) is 6.9 yr. Because recruitment was highly variable during his study, and estimates of $1/Z$ are highly sensitive to such variation, Ebert states "that the value of Z is probably too high" and therefore the value of $1/Z$ would underestimate the expectation of further life.

The second estimate of longevity is based on two experiments conducted by R. Black at Rottnest Island. By following the yearly size increment of a cohort of urchins that settled at Strickland Bay in 1982, he found that it takes approximately 5 yr for an urchin to attain a test diameter of 50 mm (unpublished data). Furthermore, 50 large urchins were transplanted in 1979 from Cape Vlamingh to another site at Rottnest Island, Fish Hook Bay, where there were no *Echinometra mathaei* existing at that time. In 1980, 17 of these were killed by heat during summer, but it was not until December 1984 that all the original 50 had disappeared. Therefore, even in an area where conditions may not be ideal, it has been shown that adult *E. mathaei* can live a further 4 yr. These two experiments provide a rough estimate of life expectancy for *E. mathaei* which is very similar to that calculated by Ebert (1982).

On this basis, the adults at the Strickland Bay site in 1985 most probably represent a single cohort, whereas the adults at Radar Reef and Cape Vlamingh should include many cohorts.

Population samples

Samples of approximately 100 individuals from of each of the three size groups were collected from each of the three sites at Rottnest Island for electrophoresis. The size-categories for this sampling were: ≤ 10 mm for recruits; 25 to 35 mm for subadults; ≥ 45 mm for adults (Fig. 1). Restriction of samples to these size ranges minimised the chance of mixing individuals from different age groups.

To determine the geographical scale of variation, samples of approximately 50 adult *Echinometra mathaei* were collected during August 1987 from five additional sites between Rottnest Island and North West Cape, a distance of approximately 1 300 km. The sites were Mandu Mandu (22°08′S; 113°52′E), Coral Bay (23°09′S; 113°36′E), Point Quobba (24°39′S; 113°24′E), and The Vee (28°44′S; 113°42′E) and Jon Jim Island (28°59′S; 113°58′E) from the Abrolhos Islands.

Electrophoresis

Samples of jaw muscle from each individual were stored at −70 °C, pending electrophoresis. Enzymes were extracted by grinding 1 vol of tissue in 2 vol of 10% (w/v) sucrose con-

taining 0.1% (v/v) mercaptoethanol and 0.1% (w/v) bromophenol blue. Electrophoresis was carried out in horizontal starch gels. A preliminary survey revealed four polymorphic enzymes which could be scored efficiently using one buffer (Tris-maleate buffer of Selander et al. 1971): glutamate oxaloacetate transaminase (EC 2.6.1.1; *Got* locus); malate dehydrogenase (EC 1.1.1.37; *Mdh* locus); phosphoglucose isomerase (EC 5.3.1.9; *Pgi* locus); and phosphoglucomutase (EC 2.7.5.1; *Pgm* locus). At each locus, alleles were labelled alphabetically, in order of decreasing electrophoretic mobility of their corresponding allozymes.

Analysis

Departures of genotypic frequencies from Hardy-Weinberg equilibrium for each locus in each sample are presented as values of D, where $D=[H_o-H_e]/H_e$, where H_o is the observed number and H_e the expected number of heterozygotes. Statistical significance of departures was tested with a goodness-of-fit chi-square. Variation of the proportion of heterozygotes within and between sites was tested with a contingency chi-square.

Variation of allelic frequencies among samples at each locus was quantified using F_{ST}, the standardised variance in allelic frequencies, calculated by the method of Weir and Cockerham (1984). Alleles with an overall average frequency of less than 0.05 were grouped for this analysis. To test the significance of these F_{ST} values, contingency chi-square values were calculated from F_{ST} using the method of Workman and Niswander (1970).

To enable a comparison of genetic variation on different geographical scales, F_{ST} was calculated among samples for the whole coastline, representing large-scale variation, and among samples from Rottnest Island to measure fine-scale variation. To maximize the geographic spread of the large-scale study while at the same time avoiding overrepresentation of one area, we used only one sample from Rottnest Island in the calculation of F_{ST} for the whole coastline. We randomly chose the adult cohort from Cape Vlamingh for this purpose. To examine the source of variation among the Rottnest Island populations, F_{ST} was calculated among sites for each cohort and among cohorts at each site for each of the four loci.

Results

The genetic composition of the Rottnest Island samples at each locus is summarised in Table 1. Considering that the sample sites at Rottnest Island are separated by small geographical distances, allelic frequencies were quite variable among the adult samples of *Echinometra mathaei*. The heterogeneity among sites for the adults, as measured by F_{ST}, was statistically significant ($P<0.05$) at both the *Got* and *Pgm* loci (Table 2). At the *Got* locus, the adult sample from Radar Reef was significantly different from both the Strickland Bay adult sample and the Cape Vlamingh sample, whereas the Strickland Bay and Cape Vlamingh samples were not significantly different from each other. At the *Pgm* locus, the allelic frequencies for each of the pairs of sites were significantly different from each other (chi-square test; $P<0.05$ for each pair of samples).

The subadults and recruits showed less variation among sites. For the subadults, there was significant heterogeneity in allelic frequencies only at the *Pgm* locus. The recruits showed no significant variation in allelic frequencies among sites at any of the four loci. Similarly, significant differences in the observed proportions of heterozygotes within groups among sites (Table 1) were found only for the adults, for the *Got* and *Pgi* loci. The observed heterogeneity at each of these loci is due to differences between Strickland Bay and the other two sites.

Comparisons among size groups within sites revealed significant differences in both allelic frequencies and heterozygosity. At each of the three sites the size groups had different allelic frequencies for at least one locus (Table 2). Examination of allelic frequencies at the significant loci shows that the observed differences are not due to any particular size group. Each size group in the Rottnest Island sites was tested separately for departures from Hardy-Weinberg equilibrium. Out of a total of 36 tests, there were three significant deviations from the expected genotypic distribution (Table 1), which is at a frequency not significantly different to that expected by chance alone. Of these three significant deviations, the recruits from Strickland Bay showed an excess of heterozygotes at the *Got* locus, and the Strickland Bay subadults and the Cape Vlamingh recruits showed significant deficits of heterozygotes at the *Pgm* locus. Whilst there is no overall pattern to these three significant departures, there is a general pattern of lower values of D for the adults than for the recruits. That is, for ten out of the twelve possible comparisons (3 sites, 4 loci) there is a greater deficit of heterozygotes in the adults than in the recruits (Table 1). In addition, adults at Strickland Bay have a smaller average deficit of heterozygotes over all loci ($D=-0.018$) than found at either Radar Reef ($D=-0.065$) or Cape Vlamingh ($D=-0.048$).

In summary, at Rottnest Island there is a pattern of increasing genetic differences among sites with age of the urchins, such that the majority of the observed differences are among the adults. The Strickland Bay adults were found to be responsible for the observed heterogeneity in proportions of observed heterozygotes. Superimposed on this pattern is an overall genetic heterogenity among age groups at all sites.

The genetic composition of the five additional geographic samples collected from along 1300 km of the Western Australian coastline (Table 3, Fig. 2) makes clear the significance of the local variation observed at Rottnest Island. With few exceptions, all alleles were found in each population. Among the exceptions, the highest allelic frequency in any population was only 0.033, indicating that the absence of one of these alleles from a sample is most likely due to the size of the samples, and does not indicate genetic distinctiveness of that population. Given the large distances between

Table 1. *Echinometra mathaei.* Allelic frequencies, heterozygosity (Het), and departures from Hardy-Weinberg genotypic frequencies (*D*) for four polymorphic enzymes in samples from Rottnest Island. Alleles with an overall average frequency of <0.05 are grouped as "other".–: allele absent; (*n*): sample size

Locus and allele	Strickland Bay			Radar Reef			Cape Vlamingh		
	adults	subadults	recruits	adults	subadults	recruits	adults	subadults	recruits
(*n*)	(99)	(96)	(36)	(86)	(94)	(57)	(92)	(93)	(85)
Got									
a	0.041	0.063	–	0.062	0.012	0.009	0.022	–	0.018
b	0.281	0.396	0.476	0.431	0.411	0.355	0.371	0.398	0.355
c	0.633	0.542	0.524	0.462	0.565	0.636	0.607	0.593	0.627
other	0.015	–	–	0.046	0.012	–	–	0.008	–
Het	0.428	0.625	0.762	0.600	0.524	0.564	0.596	0.508	0.464
D	−0.111	0.139	0.491*	0.000	−0.018	0.190	0.199	0.030	−0.063
Mdh									
a	0.066	0.057	0.028	0.064	0.064	0.059	0.043	0.081	0.034
b	0.899	0.906	0.931	0.919	0.931	0.924	0.929	0.909	0.925
other	0.035	0.037	0.041	0.027	0.005	0.017	0.028	0.010	0.041
Het	0.192	0.177	0.139	0.151	0.138	0.152	0.119	0.140	0.136
D	0.022	0.007	0.041	−0.011	0.063	0.057	−0.114	−0.172	−0.034
Pgi									
b	0.101	0.052	0.014	0.070	0.032	0.070	0.060	0.065	0.059
d	0.525	0.505	0.639	0.512	0.521	0.491	0.473	0.500	0.535
f	0.333	0.406	0.319	0.366	0.388	0.386	0.434	0.382	0.376
other	0.041	0.037	0.028	0.052	0.059	0.053	0.033	0.053	0.030
Het	0.677	0.562	0.611	0.523	0.617	0.544	0.505	0.581	0.588
D	0.119	−0.029	0.233	−0.129	0.070	−0.107	−0.139	−0.033	0.031
Pgm									
c	0.141	0.130	0.189	0.180	0.207	0.189	0.279	0.151	0.229
d	0.020	0.016	0.019	0.012	0.016	0.019	0.025	0.022	0.048
e	0.515	0.526	0.528	0.453	0.457	0.547	0.426	0.570	0.476
f	0.030	0.016	0.014	0.145	0.027	0.047	0.025	0.032	0.024
g	0.227	0.214	0.153	0.110	0.168	0.113	0.123	0.134	0.127
other	0.067	0.098	0.097	0.100	0.125	0.085	0.122	0.084	0.072
Het	0.596	0.489	0.638	0.639	0.587	0.604	0.623	0.570	0.566
D	−0.101	−0.258**	−0.039	−0.121	−0.177	−0.076	−0.138	−0.099	−0.195**

*, **: Departures from Hardy-Weinberg expectation, significant at $P<0.05$; and $P<0.01$, respectively

Table 2. *Echinometra mathaei.* Comparison of standardised variance in allelic frequencies (F_{ST}) among samples at Rottnest Island. Significance of F_{ST} was assessed by chi-square test

Comparison	*Got*	*Mdh*	*Pgi*	*Pgm*
Among sites				
adults	0.0251***	0.0004	0.0040	0.0210***
subadults	0.0010	0.0024	0.0001	0.0078*
recruits	0.0095	0.0021	0.0065	0.0006
Among groups				
Strickland	0.0215***	0.0015	0.0093*	0.0002
Radar	0.0148**	0.0031	0.0017	0.0090*
Vlamingh	0.0010	0.0032	0.0009	0.0130***

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

sites, the variances in allelic frequencies among these samples are comparatively small at all four loci. The average F_{ST} for the whole range of samples is 0.013 (Table 4), indicating that there is little genetic divergence over this large distance. In fact, the larger-scale variance in allelic frequencies is no greater than the variance among sites only 4 km apart at Rottnest Island (mean F_{ST} also 0.013). There is no obvious patterning, such as clines or geographic groupings, to the genetic differences among populations.

All five geographic samples were tested at each locus for departures from Hardy-Weinberg equilibrium. Out of a total of 20 tests (5 sites, 4 loci) there were no significant deviations from the expected genotypic distribution (Table 3).

Discussion

The fundamental finding of this study is that, although there is significant genetic heterogeneity among populations of *Echinometra mathaei* on a local scale, there is little additional large-scale geographic variation. The low value of F_{ST} among samples collected over a distance of 1 300 km is consistent with extensive gene flow over large geographic distances. This supports the findings of a number of studies which indicate that planktonic dispersal homogenizes allelic

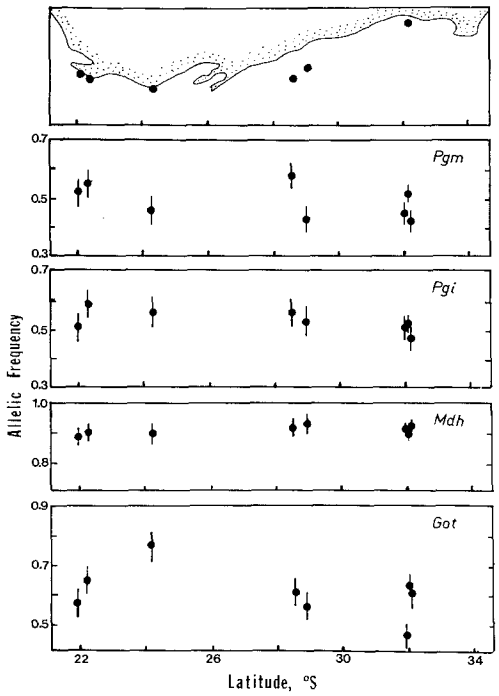

Fig. 2. *Echinometra mathaei.* Sample sites and frequencies of most common alleles at four polymorphic loci for the three Rottnest Island populations and for five sites along approx 1 300 km of Western Australian coastline; vertical lines indicate standard errors. Points for the three Rottnest Island samples (32°S; 115°30'E) are slightly offset for clarity

frequencies over large distances (Scheltema 1971, Berger 1973, Winans 1980, Johnson and Black 1984a, Waples 1987). The average F_{ST} for *E. mathaei* is comparable to those for a number of marine shore fishes (Waples 1987) and sedentary marine invertebrates with planktonic larvae (e.g. Nishida and Lucas 1988, Johnson and Black 1984b, 1990). It is even smaller than the value of 0.07 found for the crown-of-thorns seastar *Acanthaster planci* (Nishida and Lucas 1988), and similar to the average values for five species of venerid clams in Shark Bay, Western Australia, which range from 0.004 to 0.011 (Johnson and Black 1990). In contrast, species in which there is no planktonic dispersal of eggs or larvae have much greater geographic variation. For example, F_{ST} is 0.444 in the marine livebearing fish *Embiocta jacksoni* (Waples 1987), and 0.354 and 0.241, respectively, for the demersally egg-laying fishes *Menidia beryllina* and *M. peninsulae* (Johnson 1974).

The small amount of geographic variation in *Echinometra mathaei* is emphasised by the observation that the total variance in allele frequencies among populations collected from over a distance of 1 300 km is no larger than that among the Rottnest Island populations which are separated by a distance of approximately 4 km. The implication is that the forces causing genetic differentiation are acting on a local scale and occur within a single generation.

The absence of spatial genetic variation in the recruits of *Echinometra mathaei* among sites at Rottnest Island, combined with significant genetic heterogeneity among the samples of adults, suggests a pattern of increasing genetic differences among sites with increasing age of cohorts. There are two possible contrasting explanations for this pattern of genetic variation, which place the source of genetic differences at different stages of the life cycle. One explanation is post-recruitment selection, which may occur throughout the lifetime of a group of recruits and the effects of which would be expressed increasingly with age. Alternatively, the genetic heterogeneity may be due to different sites having different histories of recruitment combined with the effects of pre-recruitment selection. This second alternative is the genetic

Table 3. *Echinometra mathaei.* Allelic frequencies, heterozygosity (Het), and departures from Hardy-Weinberg genotypic frequencies (*D*) for four polymorphic enzymes in samples from Western Australian coast. Alleles with overall average frequency of <0.05 are grouped as "other"–: absent; (*n*): sample size

Locus and allele	Mandu Mandu	Coral Bay	Point Quobba	The Vee	Jon Jim Island
(*n*)	(45)	(50)	(46)	(49)	(46)
Got					
a	0.071	0.063	0.088	0.048	0.122
b	0.329	0.250	0.147	0.333	0.147
c	0.571	0.646	0.765	0.607	0.561
other	0.029	0.042	–	0.012	–
Het	0.629	0.521	0.471	0.619	0.585
D	0.107	0.001	0.202	0.181	0.015
Mdh					
a	0.085	0.070	0.071	0.060	0.056
b	0.890	0.900	0.898	0.920	0.933
other	0.024	0.020	0.010	0.020	–
Het	0.122	0.200	0.204	0.160	0.089
D	−0.396	0.073	0.074	0.059	−0.301
Pgi					
b	0.052	0.051	0.052	0.030	0.043
d	0.510	0.592	0.563	0.560	0.532
f	0.354	0.276	0.313	0.340	0.362
other	0.084	0.081	0.072	0.070	0.063
Het	0.583	0.490	0.562	0.580	0.511
D	−0.047	−0.143	−0.041	0.014	−0.133
Pgm					
c	0.167	0.120	0.174	0.071	0.109
d	0.033	0.080	0.033	0.031	0.141
e	0.522	0.550	0.457	0.582	0.435
f	0.056	0.110	0.130	0.112	0.120
g	0.156	0.090	0.163	0.102	0.120
other	0.066	0.050	0.043	0.102	0.075
Het	0.467	0.640	0.587	0.633	0.630
D	−0.311	−0.034	−0.189	−0.004	−0.167

Table 4. *Echinometra mathaei.* Comparison of standardised variance in allelic frequencies (F_{ST}) among samples from different geographical scales

Samples	Scale (km)	*Got*	*Mdh*	*Pgi*	*Pgm*	mean F_{ST}
W. Australian coastline	1 300	0.0206	0.0039	0.0064	0.0202	0.0127
Rottnest Island	4	0.0251	0.0004	0.0040	0.0210	0.0126

expression of "supply-side ecology" (Underwood and Fairweather 1989), which emphasizes the importance of variability in recruitment.

Either of these explanations might apply to *Echinometra mathaei*. The adults have been exposed to the effects of localised selection for the longest amount of time, and it is this group which has the greatest genetic differences among sites. Such post-recruitment selection has been observed most clearly in *Mytilus edulis* (Koehn et al. 1976, 1982). In principle, however, there are limits to this explanation, because the potential for selection is greatest during the period immediately following settlement and metamorphosis, during which heavy mortality is most likely to occur (Keough and Downes 1982). If post-recruitment selection were the major force acting on the populations of *E. mathaei* at Rottnest Island, and selection pressures were assumed to be relatively constant at a particular site through time, one would expect a directional pattern of change in allelic frequencies from the recruits to the adults. Such an orderly pattern is evident at the *Got* locus for both the Strickland Bay and Radar Reef sites (Table 1). The *direction* of the trend is different at the two sites, however, with the *Got*-c allele decreasing with age at Strickland Bay and increasing at Radar Reef. The population at Cape Vlamingh shows neither pattern, and none of the populations show coherent trends in the differences among age groups for the *Pgm* locus (Table 1). Therefore, it is possible that post-recruitment selection may be occurring, but it does not explain in any simple way the observed genetic variation among sites at Rottnest Island.

The evidence is more convincing that the genetic heterogeneity at Rottnest Island is due at least partly to the genetic history of the recruits. Under this view, the genetic differences between age groups may result from pre-recruitment effects, and differences between sites may result from the different histories of recruitment at those sites. The homogenising effect of planktonic mixing can result in genetically similar groups of larvae settling a different sites over reasonably large distances. In the absence of post-recruitment selection, it is possible that this genetic identity may be retained throughout the lifespan of the group. Such an effect has been shown for the limpet *Siphonaria jeanae* (Johnson and Black 1984b). The absence of variation among *Echinometra mathaei* recruits and the limited genetic heterogeneity among the subadults at Rottnest Island (Table 2) suggest that these are cohorts which are generally genetically homogeneous over the distances studied, and that the effects of post-recruitment selection on these groups are small. Furthermore, the observed differences among age groups at each site (Table 2) suggests that there is temporal heterogeneity in the genetic composition of the settling larvae.

The different recruitment histories of sites at Rottnest Island provide a clearer test between the alternative explanations for the genetic heterogeneity of *Echinometra mathaei*. As *E. mathaei* is long-lived and has been present at Radar Reef and Cape Vlamingh for a long time, during which recruitment has been observed to occur often, then the adult groups at these sites represent combinations of individuals from many years of recruitment. In contrast, Strickland Bay has an unusual history of recruitment, and the adult group represents a single cohort. If recruitment history is the major influence on the observed genetic composition of *E. mathaei* at Rottnest Island, then we can predict that the genetic composition of the Strickland Bay population should reflect its peculiar history.

The predictable characteristics are clearest for heterozygosity. Mixtures of genetically different cohorts should display a deficit of heterozygotes compared with Hardy-Weinberg expectations, as an expression of the Wahlund effect. Thus, if the history of recruitment underlies the basic patterns of genetic divergence of *Echinometra mathaei* at Rottnest Island, two predictions are possible. First, the adults at Radar Reef and Cape Vlamingh, which are mixtures of many cohorts, should have a greater deficit of heterozygotes than the adults at Strickland Bay, which represent a single cohort. Such a trend is apparent, as the average D across the four polymorphic loci is -0.018 at Strickland Bay, compared with -0.065 at Radar Reef and -0.048 at Cape Vlamingh. The second prediction from consideration of the Wahlund effect is that recruits should have a smaller deficit of heterozygotes than the adults, since the latter represent greater mixing of cohorts. This prediction was fulfilled in ten of the possible twelve comparisons, providing strong support for the view that the history of recruitment underlies the local-scale genetic patchiness.

It is noteworthy that the observation of smaller deficits of heterozygotes in recruits than in adults is contrary to many other examples. A common finding in marine molluscs, in particular, is a deficit of heterozygotes in young individuals, with a reduction of that deficit in adults (e.g Koehn et al. 1973, 1976, Tracey et al. 1975, Zouros et al. 1980, Johnson and Black 1982, Zouros and Foltz 1984). Such a pattern is most probably due to greater post-recruitment viability of heterozygotes. In contrast, post-recruitment selection is unlikely to produce an increased deficit of heterozygotes in adults, such as found in *Echinometra mathaei*.

Our conclusion is that the observed genetic heterogeneity among the adult groups of *Echinometra mathaei* is more probably due to the differences in recruitment histories of the sites than to post-recruitment selection. A similar conclusion was reached for the limpet *Siphonaria jeanae*, another species in which genetic differentiation among sites at Rottnest Island is as great as that over large distances along the Western Australian coast (Johnson and Black 1984b). The similarity could reflect relatively small environmental gradients on this coastline, which might reduce the intensity of localised selection, thereby increasing the importance of gene flow and patchiness of recruitment in determining the genetic makeup of local populations of adults. Although similar in some respects, the results for the two species studied at Rottnest Island differ in others, the most important of which is the increase in heterozygote deficits found in adult *E. mathaei*, contrasting with the decrease in *S. jeanae*. This difference is easily explained by the greater longevity of *E. mathaei*, which increases the potential for a Wahlund

effect through the mixing of cohorts. Thus, even if recruitment has an overriding influence on the genetics of local populations, the expression of that influence depends upon the demography of those populations. The implication is that studies of population genetics of marine species must take into account patterns of recruitment and population turnover.

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