Effects of contrasting patterns of larval dispersal on the genetic connectedness of local populations of two intertidal starfish, *Patiriella calcar* and *P. exigua**

Alison Hunt

Department of Biology, University of Wollongong, Locked Bag 8844, South Coast Mail Centre, Wollongong,
New South Wales 2521, Australia

ABSTRACT: The closely related intertidal starfish *Patiriella calcar* and *P. exigua* have markedly different dispersal capabilities. *P. calcar* is considered to have sexually produced planktonic larvae and hence the potential for wide dispersal. If this is the case local populations should be strongly interconnected and there should be little or no accumulation of genetic variation. Conversely, *P. exigua* has no known means of dispersal between local populations since development proceeds directly from egg masses laid on the rocky shore. Therefore, local populations of *P. exigua* may be less genotypically diverse than *P. calcar*, but should display marked genetic heterogeneity among local populations resulting from the accumulating effects of genetic drift and localised natural selection. To test these predictions genetic data were used to assess the genotypic structure and apparent connectedness of local populations of both species along 230 km of the southeast coast of Australia. Electrophoretic variation was surveyed for 5 loci. Single-locus genotype frequencies within all local populations of both species closely matched expectations for Hardy-Weinberg equilibria. This implies that local populations are maintained by recruitment of outcrossed sexually produced offspring, but as predicted, *P. exigua* had fewer alleles at each locus and fewer heterozygous individuals than *P. calcar*. Furthermore, it appears that these 2 species have vastly different levels of gene flow among local populations. The 6 local populations of *P. calcar* were genetically homogeneous [$F_{ST} = 0 \pm 0.001$ (SE)] and these populations were thus inferred to be strongly connected by larval dispersal. In sharp contrast, the 11 local populations of the directly developing *P. exigua* were highly genetically heterogeneous which is reflected in consistently high levels of genetic variance ($F_{ST} = 0.462 \pm 0.048$).

INTRODUCTION

Echinoderms are a conspicuous and important component of many marine environments (e.g. Paine 1966, Benzie & Stoddart 1992). This has provoked enormous interest in the great diversity of echinoderm life histories, and these have been shown to include species which are brooders (Chia 1966, Keough & Dartnall 1978), species which undergo asexual replication of sexually produced planktonic larvae (Bosch et al. 1989)

or asexual replication by fission or autotomy (Emson & Wilkie 1980), broadcast spawning of sexually produced gametes (Barker & Nichols 1983) and species which combine modes of reproduction and means of dispersal (Johnson & Threlfall 1987, McClary & Mladenov 1989).

Many recent studies have demonstrated the value of genetic data in determining local population structure and inferred dispersal distances for marine organisms (e. g. Koehn et al. 1976, Burton & Feldman 1981, Grosberg 1987, Ayre & Willis 1988, Hunt & Ayre 1989, Johnson & Black 1990) and echinoderms in particular (e.g. Kwast et al. 1990, Palumbi & Kessing 1991, Benzie

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& Stoddart 1992) and have often overturned predictions based solely upon histological or ecological data. Consequently, the present study uses genetic data to assess the mode of reproduction and apparent scale of dispersal of 2 species of co-occurring intertidal starfish, *Patiriella exigua* (Lamarck) and *P. calcar* (Lamarck). Both species are common and have similar geographic ranges along the southeastern coast of Australia (Dartnall 1971). *P. calcar* is believed to disperse via sexually produced planktonic larvae (Lawson-Kerr & Anderson 1978, Byrne 1991) which remain in the planktonic stage for ca 10 d (Lawson-Kerr & Anderson 1978). It therefore has the potential for wide dispersal. Conversely, dispersal of *P. exigua* is thought to be severely restricted as juveniles develop directly from egg masses deposited onto the rocky shore (Lawson-Kerr & Anderson 1978, Byrne 1991). Although the mating system of this species is unknown there is some evidence to suggest that *P. exigua* may be protandric and/or simultaneously hermaphroditic (Byrne 1991). Neither *P. calcar* or *P. exigua* is known to reproduce asexually.

Philopatry, or restricted dispersal, in the absence of selection, should result in both low levels of variability due to a reduction in the effective population size (Soulé 1976, Gallardo & Perron 1982), and genetic divergence of local populations, as the effects of drift and localised selection may accumulate each generation due to offspring remaining within the parental habitat (Wright 1968). Although this issue has been considered for many years (e.g. see Gooch & Schopf 1970) few studies have dealt directly with the effects of restricted dispersal on the genetic structure of populations (e.g. Burton & Feldman 1981, Kwast et al. 1990, Ward 1990, Johnson & Black 1991, Siegismund & Müller 1991), and none have looked at species from the southeast coast of Australia (Ayre 1990).

In contrast, high genetic diversity within local populations and genetic homogeneity among populations characterise a species with wide dispersal of sexually produced planktonic larvae. However, the wide dispersal of sexually produced planktonic larvae will typically only be possible by transport via ocean currents, and a species with planktonic larvae may experience quite restricted dispersal if the current flow is disjointed or unreliable. The unpredictable nature of the major current flow along the southeast coast of Australia, the East Australian Current, may strongly influence patterns of dispersal along this coastline. This current flows in a southerly direction along the eastern coast of Australia but is also composed of a complex set of eddies (Hamon 1965) before finally moving offshore to the east at the southeastern corner of Australia (Hamon et al. 1975). The use of genetic data is therefore essential as a means of inferring realised rather than potential dispersal distances.

This study examined the genotypic composition of local populations of the 2 species of intertidal starfish, *Patiriella exigua* and *P. calcar*, in order to infer their mode of reproduction and source of most recruitment. Gene frequencies were then used to investigate the consequences of philopatry and wide dispersal for the genetic connectedness of local populations.

METHODS

Collections of samples. Starfish were collected from stable intertidal rock platforms, over a total distance of 230 km, between Kurnell (34° 2' S, 151° 12' E) and Durras (35° 40' S, 150° 18' E) on the southeast coast of Australia. Samples of 29 to 48 individuals of *Patiriella calcar* and *P. exigua* were collected from each of 6 and 11 separate headlands (local populations) respectively, including 4 sites in which they co-occurred. Starfish were transported to the laboratory alive and then stored frozen at −80 °C pending electrophoretic analysis.

Electrophoresis. Tissue extracts were prepared for each individual by macerating a small portion of arm in a 10 % sucrose solution. Electrophoresis was carried out on horizontal starch gels (12 % w/v) using methods modified from Harris & Hopkinson (1976). Each species of starfish was assayed for 5 enzyme encoding loci: *Gpi*, *Pgm*, *Hk*, *Mdh* and *Sod* for *Patiriella calcar*, and *Gpi*, *Pgm*, *Hk*, *Lpp* and *Ltp* for *P. exigua*. *Gpi* was apparently dimeric in both species as was *Lpp* in *P. exigua*. *Mdh* appeared to be dimeric for 2 enzymes although only locus 1 could be consistently scored. All other enzymes in both species were assumed to be monomeric and encoded by 1 scorable locus. The electrophoretic buffers used were No. 5 for *Ltp*, *Lpp*, *Mdh*, *Sod* and No. 9 for *Gpi*, *Hk*, and *Pgm* as described and numbered by Selander et al. (1971). Alleles were labelled alphabetically in order of decreasing mobility and a 5-locus genotype was inferred for each individual.

Analysis of intra-population variation. Regardless of whether recruits are the product of widespread dispersal or direct development, the genotypic structure of local populations can be used to infer the mating system of the species. Allozyme data were used to assess the levels and patterns of genotypic diversity present within local populations. Departures of genotype frequencies from those expected under Hardy-Weinberg equilibria were estimated for all loci at all sites as well as an overall estimate for each species (F_{IS}). Deficits of heterozygous individuals relative to those expected under Hardy-Weinberg equilibrium are reflected in positive values and may indicate subdivision of the population on some scale due to inbreeding and Wahlund effects, whereas asexual repro-

duction can lead to both excesses and deficits. The statistical significance of the departures of the observed number of heterozygotes from those expected under Hardy-Weinberg equilibria were calculated by chi-square goodness of fit analyses with 2 categories, homozygotes and heterozygotes (Zar 1984, p. 42).

Although single-locus genotype frequencies may return to Hardy-Weinberg equilibrium after 1 generation of random mating, the association between alleles at different loci can persist for many generations (Waller & Knight 1989) and may reflect past episodes of inbreeding or asexual reproduction, random drift, selection, mutations or the mixing of genetically distinct populations (Crow & Kimura 1970, Hedrick et al. 1978). Therefore it was important to look at multi-locus genotype frequencies in order to provide a more sensitive test of the history of patterns of mating and recruitment. Hill's (1974) diallelic pairwise linkage disequilibrium measure was used to test for the presence of inter-locus associations. Although the sample sizes in this study are such that low intensities of disequilibrium will probably not be detected this test will allow relatively intense levels of disequilibrium to be detected (Brown 1975). For each comparison the most

locally common allele plus all other alleles at that locus were compared to all other loci within each local population. Chi-square analyses were used to determine the statistical significance of disequilibrium in each case.

Inter-population variation. The level of genetic differentiation of local populations provides an indication of the level of gene flow and can be estimated as the standardised variance in allelic frequencies, F_{ST}. F_{ST} was calculated among samples for each allele and each locus using the formulation of Wright (1978) (BIO-SYS-1 program; Swofford & Selander 1981). To provide a less biased estimate of the mean F_{ST} across all loci, a jackknife estimate of F_{ST} and its variance ($\theta \pm$ SE) was also calculated using the method of Weir & Cockerham (1984). For each locus the statistical significance of the inter-population variation in allelic frequencies was calculated by heterogeneity chi-square analysis. To ensure validity of these tests, rare alleles were pooled with the next most common allele for each locus to ensure that all chi-square cells contained expected values > 4.

The overall pattern of allelic frequency variation at polymorphic loci in *Patiriella exigua* was assessed by

Table 1 *Patiriella calcar.* Allelic frequencies for 5 enzyme-encoding loci for collections from local populations separated by 230 km on the southeast coast of Australia. Local populations listed from north to south. Sample size given in parentheses. –: allele absent

Locus Allele	Kurnnell (29)	Woonona (43)	Bellambi (39)	Nth Beach (45)	Ulladulla (41)	Durras (29)
Gpi						
a	0.018	0.035	0.026	0.033	0.037	–
b	0.052	0.186	0.115	0.089	0.146	0.018
c	0.483	0.337	0.397	0.478	0.341	0.362
d	0.310	0.302	0.269	0.300	0.268	0.414
e	0.103	0.128	0.179	0.100	0.159	0.172
f	0.034	0.012	0.014	–	0.049	0.034
Pgm						
a	0.017	0.046	0.051	0.056	0.037	–
b	0.897	0.884	0.872	0.900	0.951	0.897
c	0.086	0.070	0.077	0.044	0.012	0.103
Hk						
a	0.017	–	0.013	–	–	–
b	0.017	0.012	0.013	0.044	0.024	0.069
c	0.224	0.314	0.269	0.200	0.268	0.190
d	0.690	0.627	0.564	0.644	0.671	0.707
e	0.052	0.035	0.128	0.100	0.037	0.034
f	–	0.012	0.013	0.012	–	–
Mdh						
a	0.155	0.198	0.282	0.234	0.244	0.276
b	0.828	0.779	0.718	0.722	0.756	0.707
c	0.017	0.023	–	0.044	–	0.017
Sod						
a	–	–	0.013	–	–	–
b	1.000	1.000	0.987	1.000	1.000	1.000

Nei's (1978) unbiased measure of genetic identity. A dendrogram produced by the UPGMA clustering technique (Sokal & Sneath 1963) was used to summarise the genetic similarity of local populations.

RESULTS

Intra-population variation

The genotypic composition of samples from local populations of both *Patiriella calcar* and *P. exigua* were consistent with the genetic structure of local populations maintained by recruitment of sexually produced offspring. Four of the five loci examined for *P. calcar* were highly polymorphic with an average of 4.0 ± 0.3 ($\pm$ SE) alleles per locus and on average 1.6 ± 0.1 ($\pm$ SE) loci were heterozygous per individual (Table 1), however, the *Sod* locus was polymorphic in only 1 individual at Bellambi. Almost all individuals had unique 5-locus genotypes and genotype frequencies were in close agreement with expectations for Hardy-Weinberg equilibria for all loci and all local populations with only a slight overall deficit of heterozygotes (F_{IS} weighted mean = 0.065). None of the 13 deficits or 10 excesses of heterozygotes found proved to be significantly different from Hardy-Weinberg expectations. Additionally, no linkage disequilibrium (p > 0.05) was

found between any loci within the 6 local populations of *P. calcar*.

Similarly, genotype frequencies within local populations of *Patiriella exigua* typically provided a close fit to expectations for Hardy-Weinberg equilibria (Table 2) with only slight deficits of heterozygous individuals (F_{IS} weighted mean = 0.098). Only 2 of the 16 cases of deficits from Hardy-Weinberg equilibria were statistically significant and these were both at the *Ltp* locus in samples from Sandon Pt. (p < 0.05) and Kioloa (p < 0.001) but none of the 17 excesses. Furthermore, no cases of statistically significant linkage disequilibrium were detected (p > 0.05) in any of the 11 local populations. The 5 loci examined for *P. exigua* were less polymorphic than those of *P. calcar* and on average ($\pm$ SE) there were 1.8 ± 0.1 alleles per locus and 0.8 ± 0.0 loci heterozygous per individual. Nonetheless, all 5 loci could be considered polymorphic although variation at the *Hk* locus was only found at Pt Kembla where 6 individuals contained the alternate *Hk*[a].

Inter-population variation

Local populations of *Patiriella calcar* and *P. exigua* displayed markedly different levels of genetic differentiation.

Patiriella calcar showed no appreciable allelic varia-

Table 2. As in Table 1 but for *Patiriella exigua*

Locus Allele	Garie Beach (47)	Sandon Pt (36)	Woo-nona (35)	Bell-ambi (45)	Nth Beach (40)	Sth Beach (43)	Port Kembla (40)	Windang Is. (36)	Bass Pt (46)	Kioloa (48)	Durras (33)
Gpi											
a	0.957	1.000	1.000	0.556	0.762	0.477	0.200	–	0.054	0.917	1.000
b	0.011	–	–	–	–	–	–	–	–	–	–
c	0.021	–	–	0.444	0.238	0.523	0.788	1.000	0.946	0.083	–
d	0.011	–	–	–	–	–	0.012	–	–	–	–
Pgm											
a	0.021	–	–	–	0.125	0.035	0.038	0.014	0.065	–	–
b	0.979	1.000	1.000	0.967	0.875	0.965	0.962	0.986	0.935	1.000	1.000
c	–	–	–	0.033	–	–	–	–	–	–	–
Hk											
a	–	–	–	–	–	–	0.100	–	–	–	–
b	1.000	1.000	1.000	1.000	1.000	1.000	0.900	1.000	1.000	1.000	1.000
Lpp											
a	0.138	0.597	0.773	0.056	0.512	0.267	0.888	0.042	0.163	1.000	0.758
b	0.724	0.292	–	–	–	0.058	0.062	–	0.033	–	–
c	0.138	0.111	0.227	0.944	0.488	0.675	0.050	0.958	0.804	–	0.242
Ltp											
a	–	–	–	0.011	–	–	–	–	–	–	–
b	0.638	0.875	0.985	0.989	0.988	0.779	0.725	0.917	0.870	0.552	0.652
c	0.351	0.125	0.015	–	0.012	0.221	0.275	0.083	0.130	0.448	0.348
d	0.011	–	–	–	–	–	–	–	–	–	–

Table 3. *Patiriella calcar.* Allelic frequency variation for 5 enzyme-encoding loci among samples. F_{ST}: standardised variance (Wright 1978). $\theta \pm$ SE obtained by jacknife procedure (Weir & Cockerham 1984). Probability: heterogeneity chi-square analysis for each locus. NS: not significant at $p < 0.05$. nt: valid chi-square could not be tested

Locus	F_{ST}	Probability
Gpi	0.003	NS
Pgm	0.000	NS
Hk	0.001	NS
Mdh	0.000	NS
Sod	0.000	nt
$\theta \pm$ SE	0.000 $\pm$ 0.001	

tion among 6 local populations (F_{ST} = 0.000 $\pm$ 0.001) (Table 3). F_{ST} values for individual alleles, weighted averages for each locus, and across all loci, ranged from 0 for all alleles at 3 loci to 0.023 for the relatively rare *Gpi*[b]. Only *Gpi* and *Hk* had measurable, although not significant ($p > 0.05$), F_{ST} values of 0.003 and 0.001 respectively (Table 3).

In contrast, allelic frequencies for *Patiriella exigua* varied greatly among the 11 local populations (F_{ST} = 0.462 $\pm$ 0.048) (Table 4). All alleles, except for those which were extremely rare, had high genetic variances and these ranged from 0.020 for *Pgm*[c] to 0.607 for *Gpi*[c]. Variation at the *Gpi*, *Lpp* and *Ltp* loci was highly significant ($p < 0.0001$) and resulted in F_{ST} values of 0.601, 0.469 and 0.143 respectively. Low levels of polymorphism at *Pgm* and *Hk* are reflected in the lower, but still high, F_{ST} values of 0.036 and 0.080 respectively. The statistical significance of allelic heterogeneity for these 2 loci could not be tested because of small expected values. However, the differentiation of local populations was such that 4 of the 6 loci contained at least 1 allele that was unique to only 1 local population (Table 2). Furthermore, at both the *Gpi* and *Lpp* loci there was no allele which was the most common in all cases, and in fact all 3 alleles at the *Lpp* locus were the most common allele in at least 1 local population. There was no clear geographic pattern to this allelic variation for *P. exigua* (Fig. 1).

Table 4. As in Table 3 but for *Patiriella exigua*.

Locus	F_{ST}	Probability
Gpi	0.601	<0.0001
Pgm	0.036	nt
Hk	0.080	nt
Lpp	0.469	<0.0001
Ltp	0.143	<0.0001
$\theta \pm$ SE	0.462 $\pm$ 0.048	

North Beach	5
Woonona	3
Sandon Pt.	2
Kioloa	10
Durras	11
Garie Beach	1
Bellambi	4
South Beach	6
Windang Is.	8
Bass Pt.	9
Pt. Kembla	7

.3   .2   .1   0
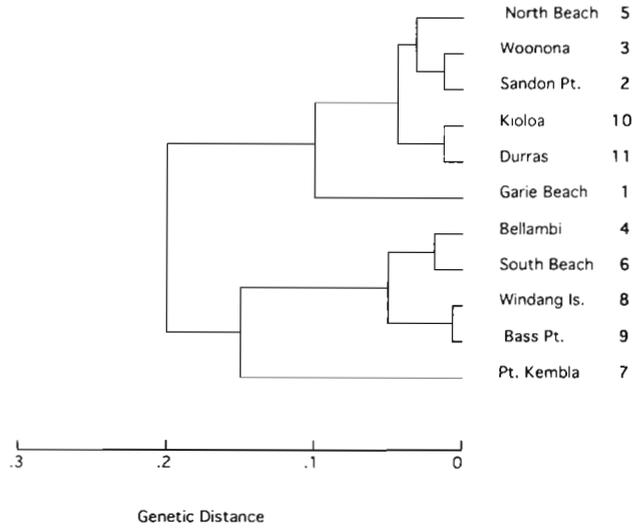
Genetic Distance

Fig. 1. UPGMA dendrogramm (Sokal & Sneath 1963) showing the genetic relatedness of 11 samples of *Patiriella exigua* collected over 230 km of the southeast coast of Australia as estimated by Nei's (1974) unbiased minimum genetic distance (D). Local populations are numbered from north to south

DISCUSSION

The genetic structure of local populations of *Patiriella exigua* and *P. calcar* are consistent with the predicted effects of recruitment via sexually produced offspring, although with very different patterns of dispersal.

Reproduction and recruitment

In contrast with several recent studies of other species of echinoderms (e.g. Emson & Wilkie 1980, Bosch et al. 1989, McClary & Mladenov 1989) there was no evidence to suggest asexual reproduction for either species as genotype frequencies within samples from each local population were in close agreement with expectations for Hardy-Weinberg equilibrium and the majority of individuals had unique 5-locus genotypes. The weighted average F_{IS} value of 0.065 for *Patiriella calcar* and 0.098 for *P. exigua* indicates an overall slight deficit of heterozygotes as compared with expectations for Hardy-Weinberg equilibria. However, only 2 local populations of *P. exigua* had significant deficits of heterozygotes and these were both at the *Ltp* locus. Such isolated departures are not attributable to the mode of reproduction as the breeding system of the organism affects all loci equally but may suggest selection favouring homozygosity at that locus. In fact, such a good fit to Hardy-Weinberg expectations is uncommon as a deficiency of heterozygous individuals tend to

characterise marine invertebrate populations (e.g. Koehn et al. 1976, Johnson & Black 1984, Foltz 1986, Kwast et al. 1990, Grant & Lang 1991) (but see Grant & Lang 1991).

Genetic connectedness

Differences in the dispersal capabilities of *Patiriella calcar* and *P. exigua* are reflected in the inter-population allelic variation. As was predicted, due to the presence of a planktonic larvae, local populations of *P. calcar* appear to be strongly interconnected. There was little detectable variation in allelic frequencies for populations separated by up to 230 km. The overall F_{ST} value of 0 ± 0.001 was well within the range expected for a sexually reproducing species with widespread dispersal (Levinton & Suchanek 1978, Johnson & Black 1984). Low levels of genetic variation among local populations have been demonstrated for other marine species (e.g. Koehn et al. 1976, Levinton & Suchanek 1978, Johnson & Black 1984, Hunt & Ayre 1989, Benzie & Stoddart 1992) and are thought to be the result of dispersal of sexually produced planktonic larvae.

In sharp contrast to the apparently panmictic breeding unit of *Patiriella exigua*, local populations of *P. exigua* appear to be, at most, only weakly connected with the majority of recruits coming from within local populations. There was marked inter-population variation in allelic frequencies at all loci for *P. exigua* ($F_{ST} = 0.462 \pm 0.048$), and unlike *P. calcar* in which only those alleles which were shared by all sites reached high frequencies, patchily distributed alleles reached high frequencies in a few localities of *P. exigua*. However, there was no apparent geographic pattern to this allelic variation. Such haphazard allelic variation and high frequencies of patchily distributed alleles are a predictable consequence of limited gene flow and increased genetic drift (Slatkin 1981, Grant & Utter 1988) and although there have been no comparable studies on the east coast of Australia, a few studies elsewhere have revealed similar patterns of variation for species with restricted dispersal (e.g. intertidal gastropods: Ward 1990, Johnson & Black 1991; starfish: Kwast et al. 1990; freshwater amphipod: Siegismund & Müller 1991; marine copepod: Burton & Feldman 1981).

A further consequence of restricted gene flow is that local populations will have lower levels of variability due to a reduction in effective population size, which consequently increases susceptibility to genetic drift and the accumulated effects of localised selection (Soulé 1976, Gallardo & Perron 1982) and this was the case for *Patiriella exigua* and *P. calcar*. *P. exigua* has fewer alleles at each locus and fewer heterozygous individuals than *P. calcar*

It would appear that local populations of *Patiriella exigua* do not regularly receive recruits from outside sources. Furthermore, the absence of intense linkage disequilibrium within populations suggests that they have not recently been subject to population bottlenecks or close inbreeding (Waller & Knight 1989) as has been demonstrated for some species with restricted dispersal (e.g. Foltz et al. 1982). Instead it would seem that these samples were taken from randomly mating, isolated local populations; however, further fine-scale sampling is required to confirm this. Conversely, local populations of *P. calcar* sampled in this study appear to form a large and undifferentiated panmictic group in which genetic exchange between local populations would prevent the effects of drift or selection from accumulating. Such strong interconnectedness must be a consequence of the southerly flow of the East Australian Current despite its unpredictability; this has been shown to be the case for 2 other marine species on the southeast coast of Australia, *Pyura stolonifera* (Killingly 1976) and *Oulactis muscosa* (Hunt & Ayre 1989). The East Australian Current may have important consequences for the genetic composition of southern and eastern populations of species along this coastline as there is some evidence to suggest that movement off the coast near the southeastern corner of Australia may effectively divide species into eastern and southern populations (Ayre et al. 1991). Further sampling will be required to assess the potential impact of the divergence of the East Australian Current on more southerly local populations of *P. calcar* and *P. exigua*.

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