J. mar. biol. Ass. U.K. (1997), 77, 77-93
Printed in Great Britain

INTERSPECIFIC COMPARISONS OF GENETIC POPULATION STRUCTURE IN MEMBERS OF THE *JAERA ALBIFRONS* SPECIES COMPLEX

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Marked genetic differentiation in the intertidal isopod, *Jaera albifrons* (Crustacea: Isopoda) has been shown to occur on a scale of just a few metres on British shores. Allozyme electrophoresis at 21 enzyme-coding loci has been employed to examine genetic structure in other UK members of the complex (*Jaera forsmani*, *J. ischiosetosa*, *J. praehirsuta*), and explore the relationship between genetic diversity and perceived niche-width. Comparisons were made with the nonsibling species *J. nordmanni*. Three subpopulations of each species taken from each of two shores on Anglesey, UK (subpopulations N=30) were assayed for electrophoretic variability. Data from 11 polymorphic loci ($P_{0.95}$) demonstrated marked genetic differentiation in all populations of *J. albifrons* and *J. praehirsuta*, and on one shore for each of *J. ischiosetosa* and *J. nordmanni*, with *J. praehirsuta* (G_{ST}=0·207) and *J. albifrons* (G_{ST}=0·121) showing the highest genetic differentiation. In contrast, *J. forsmani* exhibited population homogeneity on both shores studied. Genetic diversity ranged markedly across species (H_o=0·165–0·040), with the two most widely distributed species, *J. albifrons* (H_o=0·135) and *J. ischiosetosa* (H_o=0·165) exhibiting the highest genetic variability, providing support for the niche-width variation hypothesis. Data indicate that although habitat fragmentation and direct development is associated with microgeographic differentiation in *Jaera* spp., localized factors such as habitat continuity and exposure to water movements determines the magnitude of such effects.

INTRODUCTION

Many intertidal invertebrates exercise strong habitat selection, either during their larval stages at settlement, or during subsequent phases of their life history (Newell, 1970). The combined effects of habitat preference and habitat fragmentation results in a typically patchy distribution of individuals, which, depending on dispersal capacity, subpopulation size and selection pressures may result in populations displaying varying degrees of genetic divergence (Ward, 1989). Although it is difficult to distinguish the relative roles of life history and environmental factors on population differentiation, such considerations are important when predicting responses to natural or man-made changes in the environment. Population subdivision is a major determinant of effective population size (Wright, 1978), which in turn may influence mating patterns, levels of genetic variability, and opportunities for localized adaptation.

One effective way of disentangling the effects of biotic and physical factors on population differentiation is to compare genetic structure in sibling species with similar life history strategies but differing ecologies. One such case is provided by the *Jaera albifrons* Leach species complex, which on British shores comprises four species of intertidal isopods, *J. albifrons*, *J. ischiosetosa* Forsman, *J. praehirsuta* Forsman and *J. forsmani* Bocquet (Naylor & Haahtela, 1966). Females of each species are morphologically indistinguishable, though differences in male secondary sexual characteristics and courtship behaviour secure a low incidence (<0·1%; Carvalho, 1989a; Piertney, 1994) of interspecific hybridization. All species display direct development, with release of brooded young in direct proximity to the mother. Life history and morphological similarity does, however, contrast with differences in habitat preferences and ecological distribution (Figure 1), both in terms of the substrate inhabited (rocks or algae) and the favoured tidal range. Such habitat selection and differing tolerances to salinity fluctuations (Jones, 1972a,b) results in characteristic distributions, with *J. albifrons* and *J. ischiosetosa* often displaying the largest population densities, occupying the broadest tidal ranges and range of shores (Naylor, 1972).

Previous single-species studies on British populations of *J. albifrons* (Carvalho, 1989b; Piertney & Carvalho, 1994, 1995a,b) have detected uniformly high levels of genetic diversity and microgeographic genetic differentiation, which has been related to low vagility, small effective population sizes of local 'rock populations', and the stochastic effects of localized extinctions and inbreeding (Knowlton & Jackson, 1993). Here, using allozymes we test whether similar patterns are found in other members of the group, and whether identifiable differences in the continuity and permanence of habitats and inferred niche breadth influence the levels and distribution of

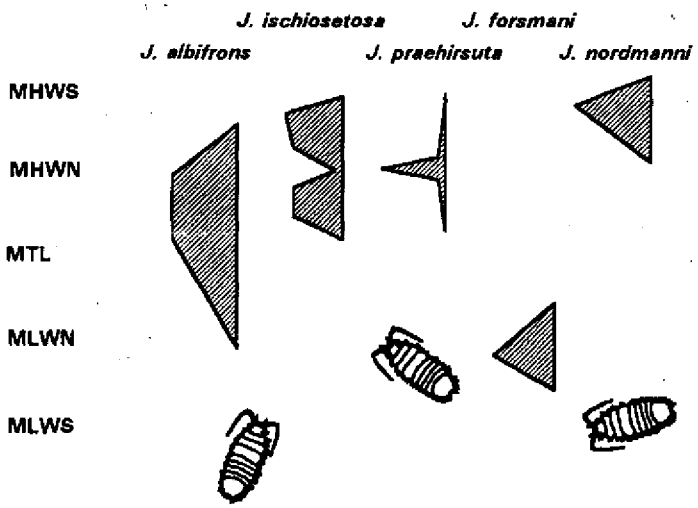

Figure 1. Average distribution and relative abundance of *Jaera* spp. in relation to tidal level. Schematic representation is based on a combination of information taken from Naylor & Haahtela (1966) and field collections of each species from UK shores (G.R.C. & S.B.P., personal observations). MHWN, mean high water neap; MHWS, mean high water spring; MLWN, mean low water neap; MLWS, mean low water spring; MTL, mean tide level.

genetic variability. Higher rates of gene flow in Danish populations of *J. albifrons* (Siegismund & Christensen, 1992) has, for example, been related to a more continuous distribution of microhabitats and subpopulations on respective shores, resulting in genetic homogeneity. Patterns within the *J. albifrons* complex are compared with the biologically distinct nonsibling species, *J. nordmanni* (Rathke), since the latter usually displays far lower levels of population patchiness, and occupies a markedly different type of intertidal habitat (Naylor, 1972).

MATERIALS AND METHODS

Sampling and species identification

Samples of *Jaera* spp. (N=29–50 per sample; mean 45 per sample; Table 1) were obtained from eight shores around Anglesey, UK (Figure 2) by collecting individuals randomly from the underside of rocks or amongst algae. Animals were returned to the laboratory, examined for male specific status according to Naylor (1972), and stored frozen until electrophoresis.

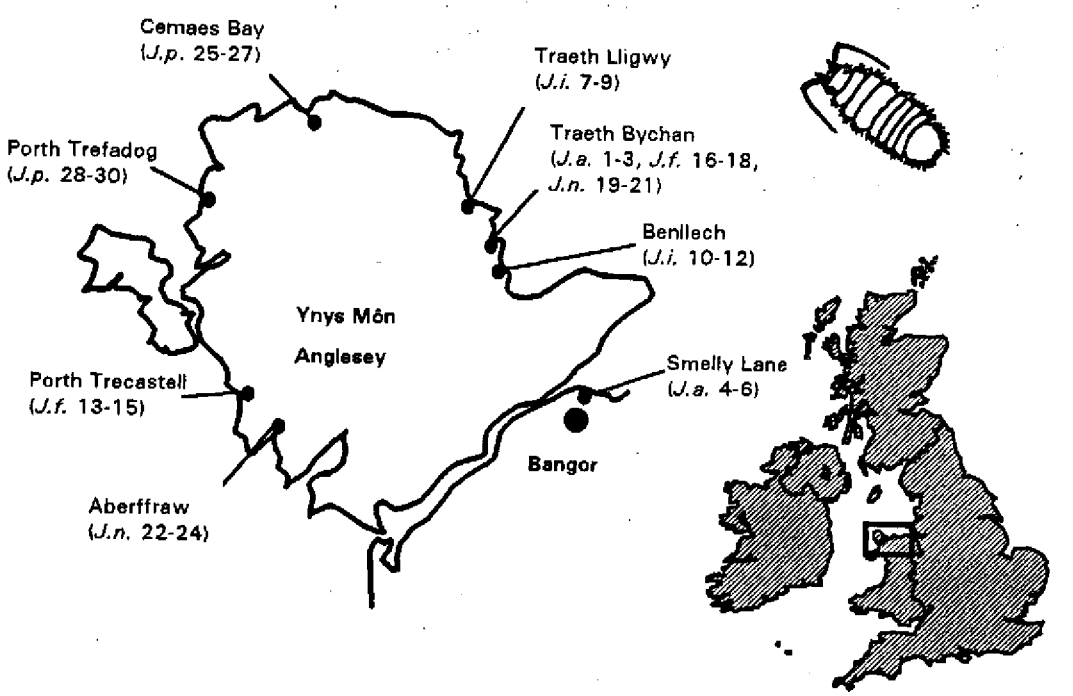

Figure 2. Sample sites for *Jaera* spp. collections. Six subpopulations of each species (1–30) were obtained from each of two shores around Anglesey, UK. J.a., *J. albifrons*; J.f., *J. forsmani*; J.i., *J. ischiosetosa*; J.p., *J. praehirsuta*; J.n., *J. nordmanni*.

Table 1. *Allele frequencies in thirty subpopulations of* Jaera *spp. Alleles are described by their anodal mobility relative to that of the most common allele which is set at 100.*

Locus	Allele	Population 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
	(N)	50	50	50	50	50	50	50	50	50	50	50	50	35	31	39	31	29	36	50	50	50	50	50	50	29	42	37	50	50	50
Apk	100	0·66	0·73	0·81	0·76	0·69	0·81	0·65	0·58	0·63	0·74	0·69	0·74	1·00	1·00	1·00	1·00	1·00	1·00	0·65	0·69	0·62	0·94	0·99	0·87	0·16	0·24	0·08	0·26	0·38	0·38
	86	0·34	0·27	0·19	0·24	0·31	0·19	0·35	0·42	0·37	0·26	0·31	0·26	-	-	-	-	-	-	-	-	-	-	-	-	0·85	0·76	0·92	0·74	0·62	0·62
	70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·35	0·31	0·38	0·06	0·01	0·13	-	-	-	-	-	-
Got	100	0·7	0·74	0·43	0·89	0·41	0·71	0·59	0·38	0·5	0·43	0·48	0·51	-	-	-	-	-	-	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	82	0·3	0·26	0·57	0·11	0·59	0·29	0·41	0·62	0·5	0·57	0·52	0·49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	75	-	-	-	-	-	-	-	-	-	-	-	-	0·3	0·34	0·32	0·18	0·12	0·18	-	-	-	-	-	-	-	-	-	-	-	-
	40	-	-	-	-	-	-	-	-	-	-	-	-	0·7	0·66	0·68	0·82	0·88	0·82	-	-	-	-	-	-	-	-	-	-	-	-
Hk	100	0·42	0·71	0·64	0·37	0·6	0·44	0·71	0·7	0·74	0·63	0·61	0·42	0·46	0·52	0·67	0·16	0·10	0·11	-	-	-	-	-	-	-	-	-	-	-	-
	95	0·58	0·29	0·36	0·63	0·4	0·34	-	-	-	0·37	0·39	0·58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	70	-	-	-	-	-	0·22	0·29	0·3	0·26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·03	0·14	0·20	0·32	0·38	0·19
	65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·97	0·86	0·80	0·68	0·62	0·81
	85	-	-	-	-	-	-	-	-	-	-	-	-	0·54	0·48	0·33	0·84	0·90	0·89	-	-	-	-	-	-	-	-	-	-	-	-
	90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·99	1·00	0·91	0·95	0·98	0·88	-	-	-	-	-	-
	80	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·01	-	0·09	0·05	0·02	0·12	-	-	-	-	-	-
Idh	100	0·84	0·7	0·78	0·94	0·72	0·22	0·06	0·11	0·04	0·06	0·11	0·09	1·00	1·00	1·00	1·00	1·00	1·00	0·88	0·92	0·87	0·73	0·69	0·7	0·97	0·76	0·89	0·96	0·97	0·98
	133	0·05	0·25	0·16	0·06	0·28	0·47	0·33	0·3	0·39	0·3	0·09	0·25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	64	0·11	0·05	0·06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	43	-	-	-	-	-	0·31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	150	-	-	-	-	-	-	0·61	0·59	0·57	0·64	0·8	0·66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	70	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·03	0·24	0·11	0·04	0·03	0·02
	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·12	0·08	0·13	0·27	0·31	0·3	-	-	-	-	-	-
Ldh	100	0·7	0·86	0·79	0·62	0·76	0·51	0·49	0·46	0·5	0·52	0·49	0·66	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00	1·00
	127	0·3	0·14	0·21	0·38	0·24	0·49	0·51	0·54	0·5	0·48	0·51	0·34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mdh	100	1·00	1·00	1·00	1·00	1·00	1·00	0·61	0·72	0·64	0·4	0·49	0·57	0·057	0·097	0·026	0·145	0·172	0·194	1·00	1·00	1·00	1·00	1·00	1·00	-	-	-	-	-	-
	68	-	-	-	-	-	-	0·39	0·28	0·36	0·6	0·51	0·43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·638	0·44	0·784	0·85	0·98	0·96
	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·362	0·56	0·216	0·15	0·02	0·04
	55	-	-	-	-	-	-	-	-	-	-	-	-	0·943	0·903	0·974	0·855	0·828	0·806	-	-	-	-	-	-	-	-	-	-	-	-
Mpi	100	0·84	0·64	0·73	0·85	0·69	0·15	0·52	0·48	0·47	0·39	0·32	0·42	-	-	-	-	-	-	1·00	1·00	1·00	1·00	1·00	1·00	0·19	0·321	0·243	0·08	0·22	0·11
	105	0·16	0·36	0·27	0·15	0·31	0·2	0·48	0·52	0·53	0·61	0·68	0·58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	80	-	-	-	-	-	0·65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·81	0·679	0·757	0·92	0·78	0·89
	70	-	-	-	-	-	-	-	-	-	-	-	-	0·314	0·242	0·295	0·226	0·276	0·222	-	-	-	-	-	-	-	-	-	-	-	-
	65	-	-	-	-	-	-	-	-	-	-	-	-	0·686	0·758	0·705	0·774	0·724	0·778	-	-	-	-	-	-	-	-	-	-	-	-
6Pgdh	100	0·39	0·67	0·55	0·64	0·71	0·86	0·39	0·4	0·4	0·61	0·59	0·54	0·871	0·935	0·91	0·839	0·897	0·792	0·2	0·31	0·25	0·31	0·16	0·28	0·155	0·274	0·095	1·00	1·00	1·00
	97	0·42	0·31	0·4	0·34	0·27	0·03	0·1	0·02	0·06	0·07	0·02	0·02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	108	0·19	0·02	0·05	0·02	0·02	0·11	0·51	0·58	0·54	0·14	0·2	0·26	-	-	-	-	-	-	-	-	-	-	-	-	0·845	0·726	0·905	-	-	-
	47	-	-	-	-	-	-	-	-	-	-	-	-	0·129	0·065	0·09	0·161	0·103	0·208	-	-	-	-	-	-	-	-	-	-	-	-
	55	-	-	-	-	-	-	-	-	-	0·18	0·19	0·18	-	-	-	-	-	-	0·8	0·69	0·75	0·69	0·84	0·72	-	-	-	-	-	-
Pgi-2	100	0·46	0·7	0·81	0·69	0·41	0·72	0·5	0·48	0·58	0·19	0·09	0·12	1·00	1·00	1·00	1·00	1·00	1·00	-	-	-	-	-	-	1·00	1·00	1·00	1·00	1·00	1·00
	170	0·54	0·3	0·19	0·31	0·59	0·28	0·5	0·52	0·42	0·81	0·91	0·88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	89	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·85	0·9	0·9	0·96	0·98	0·95	-	-	-	-	-	-
	120	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·15	0·1	0·1	0·04	0·02	0·05	-	-	-	-	-	-
Pgm-1	100	0·32	0·23	0·05	0·88	0·92	0·3	0·29	0·35	0·32	0·45	0·53	0·41	-	-	-	-	-	-	1·00	1·00	1·00	1·00	1·00	1·00	0·034	0·179	0·068	0·19	0·1	0·21
	78	0·25	0·16	0·38	0·02	0·02	0·22	0·71	0·65	0·68	0·55	0·47	0·59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	105	0·43	0·61	0·57	0·1	0·06	0·48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·966	0·821	0·932	0·81	0·9	0·79
	70	-	-	-	-	-	-	-	-	-	-	-	-	0·829	0·871	0·885	0·968	0·879	0·903	-	-	-	-	-	-	-	-	-	-	-	-
	55	-	-	-	-	-	-	-	-	-	-	-	-	0·171	0·129	0·115	0·032	0·121	0·097	-	-	-	-	-	-	-	-	-	-	-	-
Pgm-2	100	0·6	0·71	0·46	0·81	0·7	0·62	0·2	0·24	0·11	0·02	0·11	0·09	1·00	1·00	1·00	1·00	1·00	1·00	-	-	-	-	-	-	0·759	0·905	0·824	0·33	0·2	0·06
	64	0·4	0·29	0·54	0·19	0·3	0·38	0·54	0·44	0·55	0·33	0·41	0·29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	80	-	-	-	-	-	-	0·26	0·32	0·34	0·65	0·48	0·62	-	-	-	-	-	-	-	-	-	-	-	-	0·241	0·095	0·176	0·67	0·8	0·94
	140	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·76	0·7	0·72	0·4	0·34	-	-	-	-	-	-	-
	127	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0·24	0·3	0·28	0·6	0·66	-	-	-	-	-	-	-

To obtain estimates of genetic variation representative of each species, three subpopulations separated by an average distance of 20 m were obtained from two shores per species (N=30). Individuals for each sample were obtained usually from the underside of several proximate rocks or algal fronds, though with *J. forsmani* and *J. praehirsuta* it was sometimes necessary to gather animals from a wider area, though always within a 8 m radius.

As males only could be distinguished morphologically, particular care was taken to avoid the inclusion of different species within a population sample. Population purity of intraspecific samples was confirmed using diagnostic species-specific allelic arrays at several allozymic loci (Carvalho, 1989b; Piertney, 1994). Moreover, previous field surveys (G.R.C. & S.B.P., personal observations) had documented the distribution of males from each species on different shores, and sites were chosen that exhibited a population 'purity' (Jones & Naylor, 1971) of >94%. Previous studies (Carvalho, 1989b; Piertney, 1994) had recorded a uniformly low incidence of interspecific hybridization (<0·1%) among species on British shores. Only at Traeth Bychan were two member species (*J. albifrons* and *J. forsmani*) sampled simultaneously from the same shore, though even here, differences in microhabitat distribution resulted in similarly high levels of population purity at the sampled sites.

Allozyme electrophoresis

Standard horizontal starch gel electrophoresis (13% starch; Connaught Laboratories, Ltd) (Harris & Hopkinson, 1976) was used to assay 21 enzyme-coding loci using several buffer systems as described in Carvalho (1989b). Whole animals were homogenized in 10 µl of 0·1M Tris-HCl, pH 8·0, containing NADP (10 mg ml^{-1}), Triton X-100 (0·14 µl ml^{-1}) and β-mercaptoethanol (1 µl ml^{-1}). Alleles are described as having a percentage mobility relative to the common allele that was assigned an arbitrary value of 100.

Statistical analysis

Allele frequencies, Nei's (1978) unbiased estimate for expected heterozygosity (H_e), observed heterozygosity (H_o) and percentage of polymorphic loci were calculated for each population using the BIOSYS-1 program (Swofford & Selander, 1981). Deviation from Hardy-Weinberg expectations for panmixia was tested by a Markov chain method (Guo & Thompson, 1992) at each combination of locus and population. An exact test of Hardy-Weinberg equilibria was performed for loci and for populations (Louis & Dempster, 1987).

Fisher exact probabilities were calculated for population differentiation in situations where there are deviation from Hardy-Weinberg equilibria by GENEPOP using a Markov chain method (Raymond & Rousset, 1995b). Genetic diversity within and between subpopulations and between shores was determined by carrying out a gene diversity analysis of the polymorphic loci by Nei's method (1973), as extended by Chakraborty (1980) with the Nei & Chesser (1983) correction for small sample size and suspected deviation from Hardy-Weinberg expectations. This procedure is analogous to a nested analysis of variance (ANOVA) (Sokal & Rohlf, 1981), where the components of genetic diversity are partitioned according to a hierarchy which, in the present

study, consisted of three levels: (i) subpopulations; (ii) subpopulations within shores; and (iii) subpopulations from different shores.

Wherever significance testing occurred, the sequential Bonferroni technique was employed to eliminate false assignment of significance by chance (Rice, 1989).

RESULTS

Genetic diversity and genotypic distributions

Of the 21 enzyme-loci routinely assayed, 11 were polymorphic ($P_{0.95}$) overall, though with differences in the incidence of polymorphism among species (Table 1): within the species complex, *Jaera albifrons* and *J. ischiosetosa* exhibited the highest levels of polymorphism, and *J. forsmani* the lowest (Table 2).

Jaera nordmanni displayed the lowest proportion of polymorphic loci (0·24). Mean observed heterozygosity estimates (Table 2), (H_o) differed markedly among species showing similar among-species patterns as seen previously with the proportion of polymorphic loci; Mann-Whitney *U* testing (Sokal & Rohlf, 1981) revealed a clear and

Table 2. *Measures of genetic diversity for 30 subpopulations of* Jaera *spp.*

Subspecies	Population	Rock population	No. of alleles	Percentage polymorphic loci	H_o	H_e
J. albifrons	Traeth Bychan	1	1·6	45·5	0·135	0·211
				±0·2	±0·035	±0·053
	Traeth Bychan	2	1·6	45·5	0·141	0·192
				±0·2	±0·035	±0·047
	Traeth Bychan	3	1·6	45·5	0·125	0·194
				±0·2	±0·033	±0·048
	Smelly Lane	4	1·5	45·5	0·103	0·151
				±0·1	±0·03	±0·041
	Smelly Lane	5	1·5	45·5	0·141	0·187
				±0·1	±0·037	±0·047
	Smelly Lane	6	1.7	45·5	0·162	0·219
				±0·2	±0·042	±0·056
Mean values			**1·6**	**45·5**	**0·135**	**0·192**
				±0·2	**±0·035**	**±0·049**
J. ischiosetosa	Traeth Lligwy	7	1.6	50	0·182	0·249
				±0·2	±0·041	±0·055
	Traeth Lligwy	8	1·6	50	0·174	0·249
				±0·2	±0·039	±0·055
	Traeth Lligwy	9	1·6	50	0·164	0·246
				±0·2	±0·039	±0·054
	Benllech	10	1·7	50	0·169	0·236
				±0·2	±0·039	±0·052
	Benllech	11	1·7	50	0·14	0·23
				±0·2	±0·036	±0·053
	Benllech	12	1·7	50	0·162	0·235
				±0·2	±0·038	±0·053
Mean values			**1·7**	**50·0**	**0·165**	**0·241**
				±0·2	**±0·038**	**±0·054**

J. forsmani	Porth Trecastell	13	1·3	27·3 ±0·1	0·047 ±0·021	0·091 ±0·036
	Porth Trecastell	14	1·3	27·3 ±0·1	0·056 ±0·028	0·085 ±0·034
	Porth Trecastell	15	1·3	22·7 ±0·1	0·037 ±0·018	0·079 ±0·033
	Traeth Bychan	16	1·3	22·7 ±0·1	0·038 ±0·017	0·069 ±0·027
	Traeth Bychan	17	1·3	27·3 ±0·1	0·022 ±0·009	0·068 ±0·026
	Traeth Bychan	18	1·3	27·3 ±0·1	0·042 ±0·016	0·076 ±0·028
Mean values			**1·3**	**25·7 ±0·1**	**0·040 ±0·018**	**0·078 ±0·031**
J. praehirsuta	Cemaes Bay	25	1·4	22·7 ±0·1	0·034 ±0·019	0·086 ±0·031
	Cemaes Bay	26	1·4	36·4 ±0·1	0·082 ±0·025	0·127 ±0·039
	Cemaes Bay	27	1·4	36·4 ±0·1	0·042 ±0·016	0·09 ±0·029
	Porth Trefadog	28	1·3	27·3 ±0·1	0·046 ±0·019	0·094 ±0·034
	Porth Trefadog	29	1·3	22·7 ±0·1	0·034 ±0·015	0·086 ±0·035
	Porth Trefadog	30	1·3	22·7 ±0·1	0·03 ±0·015	0·07 ±0·029
Mean values			**1·4**	**28·0 ±0·1**	**0·045 ±0·018**	**0·092 ±0·033**
J. nordmanni	Traeth Bychan	19	1·3	22·7 ±0·1	0·061 ±0·026	0·075 ±0·031
	Traeth Bychan	20	1·2	22·7 ±0·1	0·06 ±0·028	0·074 ±0·033
	Traeth Bychan	21	1·3	27·3 ±0·1	0·065 ±0·026	0·084 ±0·033
	Aberffraw	22	1·3	22·7 ±0·1	0·048 ±0·025	0·073 ±0·033
	Aberffraw	23	1·3	13·6 ±0·1	0·044 ±0·023	0·057 ±0·029
	Aberffraw	24	1·3	27·3 ±0·1	0·055 ±0·023	0·085 ±0·034
Mean values			**1·3**	**21·8 ±0·1**	**0·056 ±0·025**	**0·075 ±0·032**

significant ($P<0·005$) hierarchy in the levels of H_o between species, with *J. ischiosetosa* > *J. albifrons* > *J. nordmanni* > *J. forsmani* = *J. praehirsuta*.

Examination of the frequency distributions of allozyme genotypes (Table 3) highlights that within the species complex, genotypic equilibria for panmixia was found only rarely at individual loci, and was absent from all species/population combinations when taken across loci. In all cases, deviation was caused by a deficiency of heterozygous genotypes. The outgroup comparison, *J. nordmanni*, also showed significant deviation from HW expectations, but to a lesser extent than in the species complex. The extent and nature of deviations from Hardy-Weinberg equilibrium were thus similar among members of the species complex.

Table 3. *Exact probabilities of Hardy-Weinberg equilibrium in each of 30 subpopulations at each locus.*

Subspecies	Population		*Apk*	*Got*	*Hk*	*Idh*	*Ldh*	*Mdh*	*Mpi*	*6Pgdh*	*Pgi-2*	*Pgm-1*	*Pgm-2*	χ^2	Df	Prob.
J. albifrons	Traeth Bychan	1	0·056	0·021	0·246	0·000	0·320	-	0·001	0·000	0·052	0·000	0·000	124·1	20	0
		2	0·303	0·269	0·298	0·001	0·039	-	0·034	0·000	0·021	0·000	0·298	87·4	20	0
		3	0·008	0·000	0·034	0·000	0·025	-	0·003	0·028	0·008	0·012	0·052	112·5	20	0
	Smelly Lane	4	0·003	0·007	0·068	0·005	0·033	-	0·007	0·005	0·507	0·010	0·055	81·8	20	0
		5	0·183	0·041	0·081	0·162	0·020	-	0·183	0·007	0·146	0·000	0·741	63·2	20	0
		6	0·008	0·298	0·000	0·001	0·094	-	0·000	0·035	0·036	0·001	0·033	133·4	20	0
J. ischiosetosa	Traeth Lligwy	7	0·549	0·384	0·298	0·027	0·094	0·388	0·164	0·000	0·012	0·001	0·001	80·4	22	0
		8	0·562	0·130	0·741	0·000	0·002	0·162	0·002	0·002	0·051	0·231	0·000	102·9	22	0
		9	1·000	0·405	0·269	0·000	0·405	0·130	0·000	0·000	0·003	0·000	0·000	142·8	22	0
	Benllech	10	0·269	0·147	0·545	0·005	0·002	0·020	0·150	0·000	0·001	0·097	0·002	125·8	22	0
		11	0·507	0·000	0·016	0·000	0·266	0·001	0·002	0·000	0·000	0·267	0·000	193·2	22	0
		12	0·001	0·266	0·019	0·001	0·528	0·147	0·246	0·000	0·126	0·000	0·000	153·3	22	0
J. forsmani	Porth Trecastell	13	-	0·037	0·087	-	-	0·086	0·007	0·004	-	0·000	-	57·1	12	0
		14	-	0·248	1·000	-	-	0·012	0·004	0·001	-	0·054	-	42·6	12	0
		15	-	0·000	0·070	-	-	0·013	0·007	0·000	-	0·003	-	68·2	12	0
	Traeth Bychan	16	-	0·029	0·000	-	-	0·093	0·145	0·146	-	0·016	-	43·3	12	0
		17	-	0·032	0·014	-	-	0·000	0·001	0·014	-	0·032	-	70·9	12	0
		18	-	0·061	0·040	-	-	0·012	0·000	0·146	-	0·275	-	52·5	12	0
J. nordmanni	Traeth Bychan	19	0·231	-	-	0·126	-	-	-	0·662	0·061	-	0·020	21·3	10	0·0188
		20	0·507	-	-	0·261	-	-	-	0·507	0·003	-	0·320	19·1	10	0·0389
		21	0·763	-	0·326	0·024	-	-	-	0·005	0·392	-	0·162	26·2	12	0·0099
	Aberffraw	22	0·005	-	0·099	0·303	-	-	-	0·001	0·000	-	0·247	51	12	0
		23	-	-	0·010	0·045	-	-	-	0·329	0·010	-	0·056	32·6	10	0·0003
		24	0·172	-	0·126	0·021	-	-	-	0·162	0·002	-	0·001	45·5	12	0
J. praehirsuta	Cemaes Bay	25	0·000	-	0·018	0·018	-	0·105	0·002	0·000	-	0·018	0·298	80·1	16	0
		26	0·032	-	1·000	0·198	-	0·004	0·012	0·045	-	0·097	0·001	55·2	16	0
		27	0·009	-	0·021	0·001	-	0·319	0·000	0·000	-	0·003	0·056	86·1	10	0
	Porth Trefadog	28	0·001	-	0·000	0·060	-	0·000	0·001	-	-	0·008	0·113	92	14	0
		29	0·001	-	0·000	0·030	-	0·010	0·006	-	-	0·003	0·000	112·6	14	0
		30	0·000	-	0·055	0·010	-	0·000	0·000	-	-	0·025	0·000	103·4	14	0
	Over all loci.															
	χ^2		169·9	129·0	237·8	263·6	70·9	157·0	286·2	440·7	160·5	270·3	276·6			
	Df		46	36	56	48	24	36	48	54	36	48	48			
	Probability		0	0	HS	HS	0	0	HS	HS	0	HS	HS			

HS, highly significant.

Genetic differentiation

As in previous single-species studies (Carvalho, 1989a,b; Piertney, 1994; Piertney & Carvalho, 1994, 1995a), significant levels of population differentiation were detected between subpopulations of *J. albifrons* (Table 4). However, such levels of divergence were not necessarily representative of the other members of the group. No localized population structuring was detected for *J. forsmani*, and *J. nordmanni* and *J. ischiosetosa* were deemed panmictic at Traeth Bychan and Traeth Lligwy respectively. Only *J. praehirsuta* displayed patterns similar to *J. albifrons* with consistent population divergence between subpopulations irrespective of sample site.

Table 4. *Fisher exact tests for population differentiation between three subpopulations on two shores for each* Jaera *spp.*

		Exact test		
		χ^2	df	Prob.
J. albifrons	Traeth Bychan	∞	20	HS
	Smelly Lane	∞	20	HS
J. ischiosetosa	Traeth Lligwy	26·6	22	0·21
	Benllech	57·3	22	HS
J. forsmani	Porth Trecastell	13·6	12	0·3
	Traeth Bychan	9·5	12	0·7
J. nordmanni	Traeth Bychan	21·3	12	0·0504
	Aberffraw	30·2	12	0·0028
J. praehirsuta	Cemaes Bay	∞	16	HS
	Porth Trefadog	∞	14	HS

HS, highly significant.

Gene diversities and coefficients of gene differentiation are presented in Table 5. For all species, the majority of the total genetic differentiation was attributable to differentiation within subpopulations (G_S=0·793–0·941), the remainder being due to differentiation between populations (G_{ST}=0·207–0·059). Comparison of G_{ST} values, estimates that are analogous to the F_{ST} coefficient of Wright (1965), for *J. praehirsuta* and *J. albifrons* (0·207 and 0·121 respectively), the only species showing divergence between all subpopulations, indicates that population divergence was considerably higher in the former. The relative ratios of G_{HT} and G_{SH} (Table 5) to the overall differentiation between subpopulations provides an estimator of the effects of gross habitat differences between the shore on population structure. Except for *J. albifrons*, $G_{HT}/G_{ST} > G_{SH}/G_{ST}$, suggesting that habitat structure on a shore does affect the degree of localized divergence.

Table 5. *Gene diversity analysis of six subpopulations for each* Jaera *spp.*

J. albifrons	H_T	H_S	D_{ST}	D_{HT}	D_{SH}	D_M	G_S	G_{ST}	G_{HT}	G_{SH}
APK	0·382	0·375	0·006	0·000	0·006	0·010	0·983	0·017	0·001	0·016
GOT	0·457	0·398	0·059	0·001	0·058	0·089	0·870	0·130	0·002	0·127
HK	0·530	0·491	0·039	0·005	0·033	0·058	0·927	0·073	0·010	0·062
IDH	0·461	0·373	0·088	0·013	0·075	0·132	0·809	0·191	0·028	0·164
LDH	0·415	0·388	0·027	0·012	0·015	0·040	0·936	0·064	0·028	0·036
MPI	0·507	0·387	0·120	0·020	0·101	0·181	0·763	0·237	0·039	0·198
6PGDH	0·503	0·462	0·041	0·017	0·024	0·062	0·918	0·082	0·034	0·048
PGI-2	0·465	0·423	0·042	0·001	0·041	0·063	0·910	0·090	0·003	0·088
PGM-1	0·626	0·454	0·172	0·096	0·076	0·258	0·725	0·275	0·154	0·121
PGM-2	0·455	0·431	0·024	0·007	0·017	0·036	0·948	0·052	0·016	0·036
Mean	0·480	0·418	0·062	0·017	0·045	0·093	0·879	0·121	0·032	0·090
G_{HT}/G_{ST}	0·260									
G_{SH}/G_{ST}	0·740									

J. ischiosetosa	H_T	H_S	D_{ST}	D_{HT}	D_{SH}	D_M	G_S	G_{ST}	G_{HT}	G_{SH}
APK	0·441	0·434	0·007	0·005	0·001	0·010	0·985	0·015	0·012	0·003
GOT	0·499	0·491	0·009	0·000	0·008	0·013	0·983	0·017	0·000	0·017
HK	0·527	0·441	0·086	0·077	0·009	0·129	0·837	0·163	0·145	0·018
IDH	0·501	0·486	0·015	0·007	0·008	0·023	0·970	0·030	0·014	0·016
LDH	0·499	0·491	0·008	0·003	0·006	0·013	0·983	0·017	0·005	0·012
MDH	0·490	0·468	0·021	0·014	0·007	0·032	0·956	0·044	0·030	0·014
MPI	0·491	0·482	0·009	0·006	0·002	0·013	0·982	0·018	0·013	0·005
6PGDH	0·613	0·563	0·049	0·046	0·003	0·074	0·920	0·080	0·076	0·005
PGI-2	0·440	0·362	0·078	0·075	0·004	0·118	0·822	0·178	0·170	0·008
PGM-1	0·477	0·463	0·013	0·010	0·003	0·020	0·972	0·028	0·022	0·006
PGM-2	0·603	0·566	0·037	0·029	0·008	0·056	0·938	0·062	0·048	0·013
Mean	0·507	0·477	0·030	0·025	0·005	0·046	0·941	0·059	0·049	0·011
G_{HT}/G_{ST}	0·821									
G_{SH}/G_{ST}	0·179									

J. forsmani	H_T	H_S	D_{ST}	D_{HT}	D_{SH}	D_M	G_S	G_{ST}	G_{HT}	G_{SH}
GOT	0·365	0·351	0·014	0·013	0·001	0·021	0·962	0·038	0·035	0·003
HK	0·446	0·349	0·097	0·089	0·008	0·146	0·782	0·218	0·199	0·019
MDH	0·204	0·196	0·007	0·006	0·001	0·011	0·964	0·036	0·030	0·006
MPI	0·387	0·385	0·002	0·001	0·002	0·004	0·994	0·006	0·002	0·004
6PGDH	0·220	0·216	0·005	0·002	0·003	0·007	0·980	0·020	0·009	0·012
PGM-1	0·197	0·194	0·003	0·002	0·002	0·005	0·982	0·018	0·008	0·010
Mean	0·303	0·282	0·021	0·019	0·003	0·032	0·944	0·056	0·047	0·009
G_{HT}/G_{ST}	0·842									
G_{SH}/G_{ST}	*0·161*									

Table 5. *(Continued).*

J. praehirsuta	H_T	H_S	D_{ST}	D_{HT}	D_{SH}	D_M	G_S	G_{ST}	G_{HT}	G_{SH}
APK	0·374	0·350	0·024	0·017	0·007	0·036	0·936	0·064	0·044	0·020
HK	0·334	0·308	0·026	0·014	0·011	0·038	0·923	0·077	0·043	0·034
IDH	0·144	0·133	0·012	0·005	0·007	0·018	0·918	0·082	0·032	0·050
MDH	0·348	0·277	0·071	0·048	0·023	0·106	0·796	0·204	0·137	0·066
MPI	0·313	0·300	0·013	0·007	0·007	0·020	0·958	0·042	0·021	0·021
6PGDH	0·485	0·139	0·346	0·341	0·006	0·519	0·286	0·714	0·703	0·011
PGM-1	0·226	0·218	0·009	0·003	0·006	0·013	0·961	0·039	0·012	0·027
PGM-2	0·500	0·284	0·216	0·200	0·016	0·324	0·568	0·432	0·401	0·031
Mean	0·341	0·251	0·090	0·079	0·010	0·134	0·793	0·207	0·174	0·033
G_{HT}/G_{ST}	0·842									
G_{SH}/G_{ST}	*0·157*									

J. nordmanni	H_T	H_S	D_{ST}	D_{HT}	D_{SH}	D_M	G_S	G_{ST}	G_{HT}	G_{SH}
APK	0.328	0.285	0.042	0.039	0.003	0.064	0.871	0.129	0.120	0.010
HK	0.092	0.088	0.004	0.000	0.003	0.006	0.958	0.042	0.005	0.037
IDH	0.322	0.304	0.018	0.017	0.001	0.026	0.945	0.055	0.052	0.002
6PGDH	0.377	0.370	0.006	0.000	0.006	0.009	0.983	0.017	0.000	0.017
PGI-2	0.142	0.138	0.004	0.003	0.001	0.006	0.972	0.028	0.023	0.005
PGM-2	0.643	0.519	0.124	0.063	0.061	0.185	0.808	0.192	0.098	0.094
Mean	0.317	0.284	0.033	0.020	0.013	0.049	0.923	0.077	0.050	0.028
G_{HT}/G_{ST}	0.644									
G_{SH}/G_{ST}	0.356									

Gene diversity: H_T, total diversity; H_S, within subpopulations; D_{ST}, between subpopulations; D_{HT}, between shores; D_{SH}, between subpopulations within shores; D_M, absolute differentiation between subpopulations. Coefficients of gene differentiation: G_S, within subpopulations; G_{ST}, between subpopulations; G_{HT}, between shores; G_{SH}, between subpopulations within shores.

DISCUSSION

Levels of genetic variability

Levels of genetic variability in the sibling species of *Jaera* differed markedly in the samples examined, ranging from H_o=0·165 in *Jaera ischiosetosa* to H_o=0·040 in *J. forsmani*, which not only represents highly significant differences, but is amongst the highest range observed among closely related species (Nevo, 1978; Lavie et al., 1993). Since the gene diversity analysis demonstrated that across loci the major proportion of genetic variability was contained within local subpopulations, the inclusion of six subpopulations of each species, including comparisons between two shores, suggests that the levels detected here are likely to be representative of electrophoretic variation within the complex. Moreover, other allozymic studies on British shores (Carvalho, 1989a; S.B.P. & G.R.C., personal observations) have detected similar ranges in heterozygosity among these species.

Although estimates of niche-width based on distribution patterns is subjective, it is reasonable to assume that such characteristics would vary among members of the complex depending on their occurrence at different tidal levels, as well as their overall geographic occurrence. In addition to spatial components, the niche of intertidal

animals will comprise a strong temporal element related to diurnal and tidal cycles; a species that occurs higher up the shore, for example, is likely to be more tolerant to fluctuating environmental factors such as temperature, salinity, oxygen levels, and so on, thus occupying a broader ecological niche. In a similar way, occupying a wide tidal range would result in habitation of a broader range of microhabitats and exposure to wider environmental variation. Based on such reasoning, *J. ischiosetosa* and *J. albifrons* would be predicted to possess broader ecological niches than either *J. forsmani* or *J. praehirsuta* due to residency of the former two species across a more extensive tidal range, and their higher abundances and wider geographic distribution on UK shores (Naylor, 1972, figure 1).

Explorations of correlations between niche-width and genetic variation were first formalized by Van Valen (1965) in the niche-width variation hypothesis, who suggested that selection for different alleles in different environments would result in a positive relationship between niche breadth and levels of genetic variability. Although it is undisputed that no single such association could account for all the heterogeneity in patterns of genetic variation observed among taxa (Nevo et al., 1984; Hedrick, 1986), there are several cases where such correlations have been found (Lavie & Nevo, 1981, 1986; Nevo et al., 1984; Noy et al., 1987; Lavie et al., 1993; Pavlicek & Nevo, 1995), providing indirect evidence for selective maintenance of a proportion of variability at polymorphic loci. Exceptions are, however, also evident (Somero & Soule, 1974; Schopf & Gooch, 1971; Ayala & Valentine, 1979).

The patterns observed in the present study certainly support the niche-width variation hypothesis in that the highest levels of electrophoretic variation were observed in *Jaera* spp. perceived to have the broadest ecological niches. Allozymic (Carvalho, 1989a) and behavioural data on ethological isolation (Solignac, 1978; Carvalho, 1989a) do indeed show *J. albifrons* and *J. ischiosetosa* to be the most closely related of the sibling species, demonstrating clear correspondence between genetic and ecological characteristics. The lower genetic diversity levels in *J. nordmanni* conforms also with expectations based on their shore distribution. A similar supportive association between genetic diversity and niche-width was most recently observed in a pair of cirripede species (Lavie et al., 1993), where the cosmopolitan *Chthamalus stellatus* exhibited significantly higher genetic diversity than the ecologically restricted *Euraphia depressa*. It is important to emphasize, however, that factors such as the subjective nature of niche-width estimation, differences in effective population size, gene flow, local selection pressures and habitat permanence (Carvalho, 1989a,b; Piertney & Carvalho, 1994; 1995a) are likely to confound correlations between ecological and genetic diversity.

Population structure and genotypic distributions

A major characteristic of all British *J. albifrons* populations studied hitherto (Carvalho, 1989a,b; Piertney & Carvalho, 1994; Piertney & Carvalho, 1995a) is the ubiquitous occurrence of deviations from Hardy-Weinberg equilibrium, due exclusively to a marked deficit of heterozygotes. Data presented herein strengthen these patterns, with genotypic disequilibria being the most typical pattern found, and thus the characteristic structure for the sibling species complex. It is therefore likely that common factors are operative in determining such distortions, including localized selection, nonrandom

mating, restricted gene flow and random genetic drift (Piertney & Carvalho, 1994, 1995a,b); factors most probably related to direct development, strong habitat selection and the resultant patchy distribution of individuals. Indeed, recent studies (Piertney & Carvalho, 1995b) have shown high genetic relatedness among intact assemblages of *J. albifrons* on the underside of rocks, suggesting that inbreeding contributes to the excess of homozygotes typical of some stable rock populations.

Patterns within the *J. albifrons* complex contrast with those found in the nonsibling *J. nordmanni*, where genotypic distributions were more frequently in equilibrium (Table 3). Although *J. nordmanni* and members of the complex share identical life histories, they differ in two pertinent ways; first, they occupy freshwater streams which are typically fast-flowing, at least during tidal surge, thereby increasing chances of dislodgement and passive dispersal; and secondly, their sex ratio is usually balanced, unlike the female dominance characteristic of the complex (Jones & Naylor, 1971; Piertney & Carvalho, 1996). Both such features are likely to promote dispersal and random mating, thus decreasing the chances of isolation and chance fluctuations in genotype frequency; characteristics that are in accord with the lower levels of population differentiation detected in *Jaera* spp. living out of freshwater runoffs or streams, or found low on the shore (Table 4).

Patterns of genetic differentiation

Single-species studies on *J. albifrons* from UK shores (Carvalho, 1989a; Piertney & Carvalho, 1994; Carvalho & Piertney, 1995a,b) have revealed uniformly high levels of microgeographic genetic differentiation (within populations G_{ST}=0·207–0·059), often on a scale of just a few metres. Temporal studies showing the persistence of allele frequency differences demonstrated that such features were not atypical products of localized or ephemeral conditions, but characteristic of the species. Such genetic heterogeneity does, however, contrast with patterns disclosed in Baltic populations of *J. albifrons*, where local populations exhibited genetic homogeneity (Siegismund & Christensen, 1992). The apparent panmixia was related to the more continuous distribution of rock habitats and associated higher rates of gene flow.

Significant microgeographic genetic differentiation was detected in most populations of all species studied here, except *J. forsmani* (Table 4), and on one shore for each of *J. ischiosetosa* and *J. nordmanni*, with the highest divergence found in *J. praehirsuta* (G_{ST}=0·207) and *J. albifrons* (G_{ST}=0·121). *Jaera forsmani* was unique within the complex in exhibiting no significant population differentiation among any of the studied subpopulations, which may in part arise from the increased continuity of *Fucus serratus* habitats on the lower shore, affording greater opportunities for movement of *Jaera* among rocks. Living on rocks within flowing waters (*J. ischiosetosa*, *J. nordmanni*) or on the lower shores (*J. forsmani*), also presumably offers greater chances for dislodgement and passive dispersal due to turbulence or wave action, though evidently not sufficient to ensure genetic homogeneity. Indeed, natural and laboratory observations on recolonization of rocks by *J. albifrons* (S.B.P. & G.R.C., personal observations), suggest behavioural and morphological adaptations to retain individuals at sites, presumably to reduce chances of predation or removal to unfavourable substrates.

Mark-recapture data (Carvalho, 1989a), the temporal persistence of allele frequency discontinuities (Piertney & Carvalho, 1995a), and the distribution of rare alleles (Carvalho, 1989a; Piertney & Carvalho, 1995a,b) indicate strongly that in *J. albifrons*, dispersal is normally restricted to just a few metres. Although comparable data are not available for other members of the complex, the described respective genetic structures support the existence of a similarly restricted vagility, though in *J. forsmani* localized gene flow may be higher; it remains to assess patterns in other populations to assess the generality of patterns found.

Data from gene diversity analyses were consistent with previous observations (Carvalho, 1989b; Piertney & Carvalho, 1994) showing the majority of genetic diversity to be contained within respective subpopulations, though when taken singly, some loci (Table 5) exhibited high levels of differentiation. A consistent pattern has been detected in *J. albifrons*, where marked spatial variation in *MPI* allele frequencies exhibits a strong association with the incidence of sewage contamination (Carvalho, 1989b; Piertney, 1994; Piertney & Carvalho, 1994). Such between-locus variation suggests that localized selection plays a role in shaping population structure.

Localized population divergence between neighbouring 'demes' caused by restricted gene flow and conforming to Levins' (1970) metapopulation model of population structure thus appears to be typical of many populations of the genus on UK shores, though data indicate some specific (*J. forsmani*) and localized (*J. ischiosetosa* and *J. nordmanni*) exceptions. Species conforming to Levins' (1970) model are prone to rapid changes in allele frequencies due to inbreeding, founder effect, genetic drift and localized selection, as suggestive of past (Carvalho, 1989b; Piertney & Carvalho, 1994, 1995a,b) and present studies on *Jaera* spp.

Thus microgeographic genetic differentiation appears typical of three members of the *J. albifrons* species complex; the patchy distribution of rocks and algae in the intertidal, together with direct development, has resulted in fragmentation of the gene pool, though habitat features such as water movements and habitat continuity do appear to determine the magnitude of effects. Exposure to increased water movements and a more continuous distribution of favourable substrates appear to promote genetic homogeneity, presumably through facilitating dispersal and gene flow. Although several factors will interact to determine local levels of genetic diversity, species occupying a wider range of microhabitats exhibited significantly higher heterozygosities, in line with the niche-width variation hypothesis. Direct comparative studies on the stability and dispersal of local rock populations of different *Jaera* spp., in combination with estimates of variation in physiological tolerance to environmental factors, would provide a fruitful empirical approach for the continued analysis and interpretation of population genetic structure in these sibling species.

We thank Professor E. Naylor for initial assistance with species identification and for additional financial support from the School of Animal Biology, (UCNW); Dr R.J. Lewis, Ms K.H. Loney and Mr J. Firth for assistance with field sampling. G.R.C. gratefully acknowledges receipt of a Research Fellowship from the Natural Environment Research Council (NERC) to conduct this study.

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Submitted 7 May 1996. Accepted 15 October 1996.