Genetic variability in a population of antarctic brachiopods

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A number of researchers have suggested that the genetic variability of populations should vary in some systematic way with variations in environmental parameters. Perhaps the most common suggestion is that genetic variability should be highest in spatially and/or temporally variable environments (Levins, 1968). Although it is known that genetic variability is different in different populations, ranging from essentially none up to a heterozygosity level of 25 percent or more in the average individual, data on the environmental patterns of genetic variability are few. We have studied the antarctic brachiopod *Liothyrella notorcadensis* (Jackson, 1912) during a broad preliminary survey of genetic variability in a variety of marine invertebrate taxa from a wide range of environments.

In Arthur Harbor, Anvers Island, Antarctica, *L. notorcadensis* commonly occurs in clusters along submerged rock walls beneath a *Desmartia* canopy, especially at depths of about 17 meters, just above the horizon where the walls intersect bottom sediments. The figure shows this species *in situ*. A sample of 100 individuals was collected during January 1973 at several sites along a 90-meter transect at a depth of 17 meters. The live specimens were quick-frozen

A cluster of *Liothyrella notorcadensis* at a depth of 17 meters in Arthur Harbor, Anvers Island. The thread-like organism is a polychaete.

until thawed in our laboratory during analysis. The animals then were homogenized whole except for 22 individuals that were dissected for the following tissue samples: lophophore, mantle, gut, and adductor muscle. Homogenates of whole animals or tissues were centrifuged and a small amount of the supernatant was absorbed with filter paper. The remaining sample preparation techniques are as described by Ayala *et al.* (1973). The assays employed are described by Ayala *et al.* (1972), with modifications and additions as indicated in Ayala *et al.* (1973), plus this additional assay: glucose-6-phosphate dehydrogenase (buffer B, 6 hours at 25 volts per centimeter; stain, 20 milligrams NBT, 20 milligrams β-NAD+, 20 milligrams glucose-6-phosphate, in 100-milliliter Tris-HCL buffer, pH 7.1; incubate 1 hour at 37°C., add 5 milligrams PMS). Gels were fixed as described by Ayala *et al.* (1972). Three control samples of standard stocks of *Drosophila willistoni* were run in every gel.

We assayed 14 different kinds of enzymes and some additional proteins without known enzymatic activity. For seven enzymes, only one zone of activity was scored, while for the other seven enzymes and the other proteins, from two to six zones of activity were scored; well defined bands with repeatable characteristics were used. A total of 34 zones of activity were scored; each is assumed to be coded by one gene locus. Two or more bands were present in 11 of the 34 zones, and these band pattern configurations conformed to the expectations of Mendelian heredity and to the Hardy-Weinberg principle. Previous experience suggests that biases arising from our assumptions regarding the relation between loci and zones of activity are unlikely to substantially affect the interpretations. Gene loci and alleles are designated by a method described in Ayala *et al.* (1972, 1973).

No allelic variation was described at 23 of the 34 loci scored. Of the other 11 loci (table), eight are considered to be polymorphic because the second most common allele at these loci had a frequency greater than 0.01. The proportion of polymorphic loci, then, is 23.5 percent (eight out of 34 loci). If a locus is considered polymorphic when the most common allele has a frequency no greater than 0.95 (Ayala *et al.*, 1973)—a more restrictive definition—then the proportion of polymorphic loci falls to 11.7 percent (four out of 34).

The proportion of heterozygous loci per individual, averaged over all individuals, is 0.3865, with a variance of 0.3884. If mating were random the expected variance would be equal to the proportion of heterozygous loci per individual, or 0.3865; the difference between the expected and observed variance is not statistically significant (the probability that it is due to chance is between 0.40 and 0.60). Thus there is no evidence that this population is inbred or that we

have sampled two or more populations with different allele frequencies.

With an average heterozygosity of about 3.9 percent, *Liothyrella notorcadensis* clearly has only a small amount of genetic variability. By comparison, a brachiopod population from the deep sea (*Frieleia halli* from a depth of 1,244 meters off San Diego) (Valentine and Ayala, in press) has an average heterozygosity of 17 percent; other deep sea organisms have similarly high genetic variabilities (Ayala *et al.*, in press a; Ayala *et al.*, in preparation). The deep sea and Antarctica are somewhat similar in having rather low temperatures, low ranges of temperatures, and similarly high stability of most ecological parameters. The chief difference between them is that productivity is highly seasonal in Antarctica; trophic resource supplies (chiefly detritus at the base of the food chain) are far more stable in the deep sea. In shallow water there is a general correlation between the stability of trophic resource supplies and genetic variabilities, as far as they are known. The antarctic population has high resource instability and low genetic variability (this paper); temperate zone populations have intermediate resource instabilities and low to intermediate genetic variabilities (Selander *et al.*, 1970; Schopf and Murphy, 1974; Ayala *et al.*, in press a), while a tropical population has high resource stability and high genetic variability (Ayala *et al.*, 1973), like the deep sea.

Genetic variabilities in these populations do not correlate well with temperature levels or ranges, species fecundities, or other known environmental parameters, except with trophic resource stability and with the biological parameters (diversity and modal specialization) that commonly are positively associated with this factor (Valentine, 1971, 1973). We conclude that the hypothesis of positive correlation between genetic and environmental variabilities is not correct. Indeed, the best correlation is a negative one. A tentative explanation of this trend (Ayala *et al.*, in press b) is that populations in trophically unstable ecosystems tend to be flexibly adapted generalists, living in a variety of habitats and utilizing a variety of food sources, but that this flexibility is achieved by a harmoniously coadapted suite of optimal alleles that code for generalized functions (see Stebbins, 1950). Fitness is at a premium and therefore alternate alleles are eliminated by stabilizing selection, which is strong. In trophically stable environments, by contrast, specialization is favored and multiple alleles may be maintained at many loci so that each individual may be optimally adapted. This adaptation is not

Allelic variation detected at 11 loci in *Liothyrella notorcadensis*.

Locus	N	Allelic frequencies							Heterozygous individuals	
									Expected	Observed
Acph–1*	200	100 .995	102 .005						.010	.010
Adk–1	200	100 .990	103 .010						.020	.020
Est–1	200	100 .985	103 .015						.029	.030
Est–5	190	96 .021	100 .979						.041	.042
Idh	58	100 .889	104 .121						.215	.241
Lap–2	196	98 .005	100 .949	102 .046					.097	.102
Lap–4	200	98 .015	100 .600	103 .150	105 .085	108 .010	110 .120	112 .020	.595	.580
Me	138	100 .986	102 .015						.029	.029
Pt–2*	116	97 .009	100 .991						.017	.017
Pt–4*	156	95 .006	100 .987	104 .006					.025	.026
Tpi–2	178	98 .006	100 .860	103 .135					.233	.213
Average (including all 34 loci studied):	157 ± 8								.039 ± .019	.038 ± .018

* Not considered to be polymorphic since the frequency of their second most common allele is <0.01.

Key: N—the number of genes sampled at each locus; Acph—acid phosphatase; Adk—adenylate kinase; Est—esterase; Idh—isocitrate dehydrogenase; Lap—leucine aminopeptidase; Me—malic enzyme; Pt—protein; Tpi—triosephosphate isomerase.

to a generalized functional response but rather to a highly special part of the environmental mosaic; recombination assures a supply of slight functional variants that may fit into spatial variations in the environment, hand in glove. In this model genetic variability thus is employed to enhance specialization, while flexibility is best achieved by low genetic variabilities.

We are continuing studies on genetic variability in antarctic invertebrates, and in those from temperate and tropical regimes, to determine whether the trends observed to date are general and to subject the trophic resource hypothesis to further tests.

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Ecology of echinoderms from the Antarctic Peninsula

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During February and March of 1972 and 1973 large collections of echinoderms were obtained along the west coast of the Antarctic Peninsula by University of Maine personnel aboard R/V *Hero*. Stations were made primarily around Anvers Island and south along the coast to Adelaide Island. Depths of capture ranged from the intertidal zone to 750 meters. Details of field operations and personnel involved are reported in Dearborn *et al.* (1972, 1973).

During 1973 and 1974 considerable progress was made in identifying this material. Crinoids, asteroids, ophiuroids, and echinoids have been determined to genus and in most instances to species. Holothurians have not been of direct concern. They have been deposited in the U.S. National Museum of Natural History and will not be reported by us. Our initial sorting and subsequent identification work has been very time consuming because of the relatively large numbers of small and juvenile specimens present, particularly among asteroids and ophiuroids. This has meant that for several ecologically important species—like the brittle stars *Ophionotus victoriae, Ophioperla koehleri,* and *Ophiurolepis martensi*—specimens from tiny juveniles to large adults are available for investigations requiring size series (*e.g.,* considerations of morphological changes with growth and variations in food habits with increasing size).

As expected, the large, 20-armed comatulid *Promachocrinus kerguelensis* dominates the crinoid fauna of the Antarctic Peninsula at the depths sampled. *Anthometra adriani, Florometra mawsoni,* and *Iso-*