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GENETIC VARIABILITY IN THE PELAGIC ENVIRONMENT: A PARADOX?[1]

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Abstract. The pelagic environment is often regarded as rather homogeneous by comparison with shallow-water benthic environments. Species of krill of the pelagic genus *Euphausia* (Crustacea) display a trend in genetic variability from low in high latitudes to high in low latitudes, closely similar to trends displayed by shallow-water benthic invertebrates. We interpret the trends as genetic strategies, with few functionally-broad alleles in high latitude species or in species that range widely ecologically, and numerous functionally-narrow alleles in low latitude species that are narrowly restricted ecologically. The functionally-narrow alleles are maintained by forms of balancing selection and permit a high degree of specialization. Therefore the tropical krill species is highly sensitive to spatial heterogeneities within the pelagic zone, which does not appear homogeneous to selection.

Key words: adaptive strategies; Crustacea; Euphausia; *genetic strategies; genetic variation; krill; natural selection; pelagic environment.*

INTRODUCTION

Local patterns of spatial heterogeneity are associated with species diversity patterns. Diversity is lower in more homogeneous environments such as marine sand or mud flats than in more heterogeneous environments such as mixed rock and sand substrates along rocky shores. On the other hand, environments of similar spatial heterogeneities support different diversities in different regions. The latitudinal diversity gradient provides a classic example: rocky shores in low latitudes support more diverse faunas than those in high latitudes. Presumably in regions of higher diversity, species partition more finely an environment of any given spatial heterogeneity than do species in regions of low diversity. The process of regulation of the pattern of resource partitioning is in dispute but may well involve temporal environmental predictability or seasonality.

Some major environmental realms appear to be unusually homogeneous, at least by human perception. These include both the pelagic environment and the deep-sea floor. In each of these cases, writers have questioned whether spatial heterogeneity is great enough to permit resource partitioning among the faunas, which are diverse at least in some regions, or whether niches may be shared or diversity regulated through some other mechanism. The best-known statement of this question for the pelagic realm is by Hutchinson (1961), who presents the relatively high planktonic diversity in relatively homogeneous lake environments as a paradox. He suggests that temporal heterogeneities are associated with niche partitioning in those environments. The marine plankton is even more diverse and displays a strong latitudinal diversity gradient with rich biotas in low latitudes.

Other workers who have examined pelagic environments both in lakes and in the sea have concluded that they are more spatially heterogeneous than had been supposed (e.g., Margalef 1958, 1967, Richerson et al. 1970, Platt 1975, Richerson et al. 1975). Perhaps, then, niche partitioning may occur in the theoretically conventional manner so as to mitigate competition and permit the high diversities observed. Tappan and Loeblich (1973) have pointed out that low-latitude ocean waters of the euphotic zone are less mixed than in many high latitude regions and thus more stratified and heterogeneous. On the other hand, some high latitude water columns are rather stable (as in the Arctic Ocean, Dunbar 1968) but planktonic diversity therein is low. It is at any rate not necessary to postulate a gradient in spatial heterogeneity that matches the diversity pattern, but merely to establish that sufficient heterogeneity exists in regions supporting the diverse ecosystems, in order to escape the paradox of the plankton.

KRILL STRATEGIES AND GENETIC VARIABILITIES

From ecological and genetic principles, it has been widely held that genetic variability should be greater in populations inhabiting the spatially more heterogeneous environments (e.g., Levins 1968). This has proven to be true in a considerable variety of observational and experimental examples (review in Hed-

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rick et al. 1976). In order to extend the investigation of genetic variability patterns into the pelagic realm, we have studied 3 species of the krill genus *Euphausia* (Arthropoda: Crustacea) by techniques of gel electrophoresis. These techniques permit one to estimate, to a first approximation, the amount of genetic variation found in populations. The specific procedures used in our studies have been described elsewhere (Ayala et al. 1972, 1973). Briefly, tissue homogenates from the individuals to be examined are placed in starch gels and subjected to an electric current for several hours. The gels are then removed and placed in staining solutions that reveal the position of specific enzymes. Different migrating forms of a specific enzyme differ from each other in their amino acid sequences, and thus are products of different alleles of the gene locus coding for the enzyme. Allelic frequencies are in such a way obtained for each of many gene loci. The average amount of variation over all the loci studied provides an estimate of the amount of genetic variation in the population (Lewontin and Hubby 1966, Dobzhansky et al. 1977).

The 3 species we have studied are *E. superba* from circumantarctic waters, *E. mucronata* from the Peru–Chile current, and *E. distinguenda* from equatorial Pacific water off the Galapagos Islands (Fig. 1). The samples of *E. distinguenda* were collected at 7°32′N, 92°16′W (Population 1), and at 10°N, 93°45′W (Population 2).

Euphausia superba is relatively well known; it is a large form (length about 50–60 mm) which matures in 2 yr and lives slightly longer; it maintains high population densities and has a high reproductive potential.

The other species are less well known, though some of their properties may be inferred from general studies and reviews of krill biology and distribution (Brinton 1962, 1975, 1976, Mauchline and Fisher 1969). In the region inhabited by *E. mucronata,* krill densities are lower than for the circumantarctic and still lower in the region inhabited by *E. distinguenda* (Ponomareva 1966, map reproduced in Mauchline and Fisher 1969, page 377). Euphausid species tend to be smaller in lower latitudes; *C. mucronata* is about 17 mm long and *C. distinguenda* only about 8.5 mm long. Species for which data are available tend to mature earlier and die sooner in lower latitudes (1 yr is common in temperate forms). Krill ovaries carry proportionately fewer eggs as body size decreases, and the effect is so great that the reproductive potential of lower-latitude forms must be significantly smaller than for high-latitude forms, even considering their more frequent breeding (data summarized in Mauchline and Fisher 1969, especially Table 29). Evidently the 3 species we have studied form a sample of the major trends in population dynamics and strategies among krill.

The results of our electrophoretic study of *E. distinguenda* and *E. mucronata* are shown in Table 1. Similar data for *E. superba* have appeared elsewhere

FIG. 1. Geographic ranges of *Euphausia superba, E. mucronata* and *E. distinguenda*. X's indicate localities from which our samples were collected. Range data from Brinton (1962, 1975) and Mauchline and Fisher (1969).

(Ayala et al. 1976), where the enzymes coded by each of the gene loci listed in Table 1 are given. (The only exception is *Ldh,* which codes for lactate dehydrogenase, an enzyme not studied in *E. superba*.) For each locus the table gives the allelic frequencies and the observed frequency of heterozygous individuals. The alleles are named using the same criteria as for *E. superba* (Ayala et al. 1975). At each locus the most common allele in *E. superba* is named *100;* all other alleles are designated by reference to that standard, adding to or subtracting from 100 the number of millimeters by which the migration of the enzyme coded by each allele differs from the standard. The number of genes sampled (i.e., twice the number of individuals) at each locus is 130, 90, 100, respectively, for the 2 populations of *E. distinguenda* and for *E. mucronata,* except where noted in the table. The 2 populations of *E. distinguenda* are genetically very similar to each other, and therefore their data are given both separately and combined in Table 1.

The data for the 3 krill species are summarized in Table 2. The best single measure of genetic variation in a population is the expected frequency of heterozygous loci per individual, on the assumption of Hardy–Weinberg equilibrium. (See Dobzhansky et al. 1977; in the case of random mating populations, the observed and the expected heterozygosities should be very similar, as is the case for these krill populations.) Other, less precise, measures of genetic variation are the proportion of polymorphic loci and the number of alleles observed per locus.

As can be seen in Table 2, no matter what measure of variability is used, genetic variation is least in the circumantarctic species, intermediate in the temperate species, and greatest in the tropical species. For example, the expected frequency of heterozygous loci per individual is 21.3 ± 3.4 percent for *E. distinguenda,* 14.1 ± 2.5 percent for *E. mucronata,* and 5.7 ± 1.9 percent in *E. superba*. The results are not meaningfully different when only the 27 gene loci studied in all 3 species are used in the comparisons.

TABLE 1. Allelic frequencies at 30 gene loci in krill populations of the genus *Euphausia*. Dashes represent zero values, and blanks indicate that the locus has not been assayed. *H* is the observed frequency of heterozygous individuals at each locus (it has been omitted whenever $H = 0$ for all populations). The numbers of genes sampled at each locus are for most loci 130, 90, and 100 for Population 1, Population 2, and *E. mucronata* respectively; otherwise they are given as *N*

Gene	Alleles	*E. distinguenda*			*E. mucronata*
		Pop. 1	Pop. 2	Total	
Acph-1	82	. . .	.01	.005	.05
	84	. . .	. . .	. . .	.93
	86	.06	.02	.05	.02
	88	.85	.84	.85	. . .
	90	.09	.10	.09	. . .
	92	. . .	.02	.01	. . .
	H	.262	.244	.255	.140
Acph-2	86	.03	.02	.03	. . .
	90	.93	.94	.94	. . .
	94	.04	.03	.04	. . .
	100	. . .	. . .	. . .	.94
	102	. . .	. . .	. . .	.05
	104	. . .	. . .	. . .	.01
	H	.138	.111	.127	.120
Ald-2	92	. . .	. . .	. . .	.12
	96	.12	.38	.22	.81
	98	.05	.04	.05	.07
	100	.78	.58	.70	. . .
	102	.05	. . .	.03	. . .
	H	.400	.556	.464	.380
Ao-1	N	120	20	140	100
	98	.12	.10	.11	.07
	101	.01	. . .	.01	. . .
	103	.87	.90	.87	.93
	105	.01	. . .	.01	. . .
	H	.267	.200	.257	.140
Ao-2	N	120	20	140	100
	86	. . .	. . .	. . .	.01
	88	.98	1.00	.98	.97
	90	.03	. . .	. . .	.02
	92	. . .	. . .	.02	. . .
	H	.050	. . .	.043	.060
Aph-1	98	.18	.12	.16	.07
	100	.51	.51	.51	.93
	102	.31	.37	.33	. . .
	H	.554	.533	.545	.140
Aph-2	94	.02	.01	.01	. . .
	100	.98	.99	.99	1.00
	H	.031	.022	.027	. . .
Est-1	104	.14	.09	.12	.12
	106	.86	.89	.87	.87
	108	. . .	.02	.01	.01
	H	.246	.222	.236	.220
Est-4	96	.01	. . .	.004	. . .
	100	.02	.30	.14	.02
	102	.96	.68	.85	.06
	104	.01	.02	.01	.92
	H	.077	.422	.218	.160
Est-5	105	. . .	.111	.05	. . .
	107	. . .	.722	.30	. . .
	109	1.00	.17	.66	1.00
	H	. . .	.422	.173	. . .
Fum-1	97	.15	.10	.13	.01
	100	.82	.89	.85	.12
	102	.02	.01	.02	. . .
	103	. . .	. . .	. . .	.86
	105	. . .	. . .	. . .	.01
	H	.277	.200	.245	.280
Fum-2	N	90	90	180	
	102	1.00	1.00	1.00	
αGpd	N	90	90	180	100
	102	1.00	1.00	1.00	1.00
G3pd	102	1.00	1.00	1.00	1.00
G6pd-1	100	.02	.02	.02	.67
	102	.33	.39	.35	.33
	104	.64	.59	.62	. . .
	106	.02	. . .	.01	. . .
	H	.462	.489	.473	.480
Got	106	.01	. . .	.005	. . .
	111	.05	.02	.04	. . .
	114	.92	.93	.93	. . .
	116	.02	. . .	.01	. . .
	119	.01	.04	.02	.01
	121	. . .	. . .	. . .	.94
	125	. . .	. . .	. . .	.05
	H	.154	.133	.145	.120
Hk-1	N	130	50	280	
	96	.12	.08	.11	
	100	.88	.92	.89	
	H	.231	.080	.211	
Hk-2	N	130	50	280	100
	98	.01	. . .	.01	. . .
	100	.54	.60	.56	.20
	102	.37	.36	.37	.75
	104	.08	.04	.07	.05
	H	.646	.520	.611	.420
Lap	100	1.00	1.00	1.00	1.00
Ldh	N	60	20	80	100
	82	. . .	. . .	. . .	.01
	86	. . .	. . .	. . .	.01
	88	. . .	. . .	. . .	.88
	90	. . .	. . .	. . .	.10
	96	.02	. . .	.01	. . .
	98	.10	.10	.10	. . .
	100	.88	.90	.89	. . .
	H	.233	.200	.225	.240
Mdh-2	N	90	90	180	60
	106	. . .	. . .	. . .	.93
	108	. . .	. . .	. . .	.07
	116	.07	.06	.06	. . .
	118	.72	.76	.74	. . .
	120	.21	.19	.20	. . .
	H	.422	.400	.411	.133
Mdh-3	N	10	90	100	100
	114	. . .	.02	.02	. . .
	116	1.00	.98	.98	. . .
	124	. . .	. . .	. . .	1.00
	H	. . .	.044	.040	. . .
Me-2	96	.02	.02	.02	.03
	98	.05	.04	.05	.02
	100	.88	.89	.89	.81
	102	.05	.04	.05	.14
	104	.01	. . .	.005	. . .
	H	.231	.220	.227	.360
Odh	N	80	60	140	100
	88	. . .	.02	.01	. . .
	92	.95	.90	.93	.01
	94	.04	.08	.06	. . .
	96	. . .	. . .	. . .	.97
	98	.01	. . .	.01	.02
	H	.100	.133	.114	.060
6Pgd	96	.03	.03	.03	. . .
	98	.02	.04	.03	.04

TABLE 1 (CONTINUED)

Gene	Alleles	*E. distinguenda* Pop. 1	*E. distinguenda* Pop. 2	*E. distinguenda* Total	*E. mucronata*
	100	.92	.88	.90	.94
	102	.03	.04	.04	.02
	H	.123	.200	.155	.120
Pgi	N	128	88	216	100
	88	...	...	...	.01
	90	...	...	...	.06
	91	...	...	...	.89
	93	...	...	...	.01
	95	...	...	...	.01
	97	...	.02	.01	.02
	103	.01	...	.005	...
	105	.10	.05	.08	...
	106	.79	.83	.81	...
	109	.09	.10	.09	...
	111	.02	...	.01	...
	H	.297	.341	.315	.220
Pgm	117	...	...	...	.06
	119	.02	...	.01	.78
	120	...	...	...	.11
	121	.08	...	.05	.05
	123	.75	.06	.46	...
	125	.12	.02	.08	...
	127	.01	.19	.08	...
	129	.04	.71	.31	...
	131	...	.02	.01	...
	H	.400	.378	.391	.440
To-1	100	.99	1.00	.995	1.00
	102	.01	...	.005	...
	H	.015	...	.009	...
	N	80		80	80
To-2	114	1.00		1.00	1.00
Tpi	104	.03	.07	.05	...
	108	...	.01	.005	.97
	110	.97	.88	.93	.01
	114	...	.04	.02	.02
	H	.031	.200	.100	.060

TABLE 3. Genetic identity (I, above diagonal) and genetic distance (D, below diagonal) between 3 krill species of the genus *Euphausia*. The figures involving *E. distinguenda* are the average of the comparisons between each of the 2 *distinguenda* populations and the other species. Comparisons of the 2 *distinguenda* populations with each other give $I = 0.945$, $D = 0.056$

	distinguenda	*mucronata*	*superba*
E. distinguenda	...	.512	.358
E. mucronata	.669	...	.327
E. superba	1.030	1.117	...

The allelic frequencies given in Table 1 together with those given for *E. superba* in Ayala et al. (1975) make possible estimating the degree of genetic similarity between the various populations. The results are summarized in Table 3. Genetic similarity and genetic differentiation are measured using the statistics I and D (Nei 1972), where $D = -\log_e I$. The genetic distance, D, estimates the number of electrophoretically detectable allelic substitutions that have occurred in the separate evolution of the 2 populations under comparison. The genetic distance between the 2 populations of *E. distinguenda* is 0.056; this value is within the typical range observed between local populations of various sorts of organisms (Ayala 1975). The genetic distance between the species is comparable to what has been observed between congeneric species in other groups of organisms (review in Ayala 1975). For example, in the *Drosophila willistoni* group of species, the value of D is 0.581 between sibling (morphologically nearly indistinguishable) species, and 1.056 between morphologically clearly differentiated species.

The krill species we have studied are closely related members of the same species group of the genus *Euphausia* on morphological grounds, with *E. distinguenda* and *E. mucronata* being the most similar pair (Brinton 1975). Thus the morphological and electrophoretic indications of affinity are in harmony.

GENETIC VARIABILITY PATTERNS IN THE MARINE BENTHOS

The argument that spatial heterogeneity promotes genetic variability can be sustained for benthic marine

TABLE 2. Summary of genetic variation in 3 krill species of the genus *Euphausia*

Parameter	*E. distinguenda* Population 1	*E. distinguenda* Population 2	*E. distinguenda* Total	*E. mucronata*	*E. superba*
Gene loci sampled	30	29	30	28	36
Individuals sampled	65	45	110	50	127
Genes sampled per locus	116 ± 5	79 ± 4	195 ± 7	98 ± 2	243 ± 4
Alleles observed per locus	2.83 ± 0.26	2.69 ± 0.22	3.20 ± 0.28	2.54 ± 0.30	1.81 ± 0.14
Frequency of polymorphic loci*:					
$P \leq .990$	.733	.828	.800	.679	.361
$P \leq .950$	.600	.759	.700	.571	.139
Frequency of heterozygotes:					
average over individuals (observed)	0.201 ± 0.005	0.224 ± 0.014	0.211 ± 0.005	0.155 ± 0.010	0.058 ± 0.004
average over loci (observed)	0.188 ± 0.034	0.216 ± 0.034	0.201 ± 0.032	0.153 ± 0.028	0.057 ± 0.018
average over loci (expected)	0.188 ± 0.034	0.223 ± 0.035	0.213 ± 0.034	0.141 ± 0.025	0.057 ± 0.019

* P represents the frequency of the most common allele.

invertebrates, according to the data so far available. However, a similar argument has been made for temporal heterogeneity—that more temporally heterogeneous (unstable) environments promote genetic variability (references in Hedrick et al. 1976). Such an argument is contradicted by observations on patterns of genetic variability in benthic invertebrates (review in Valentine 1976). The more genetically variable species discovered to date live in the more stable environments, particularly in those environments (tropics, deep sea) with the greater trophic resource stabilities. This cannot be due to any systematic difference in spatial heterogeneity between the benthic environments involved; indeed the deep-sea benthic environment is relatively homogeneous (Hessler and Jumars 1974). Instead there must be some process associated with temporal environmental stabilities that regulates genetic variability independently of, and in addition to, spatial factors. The temporal variable that is most highly correlated with the genetic variability pattern is trophic resource stability.

We have used a selectionist argument to propose a model of genetic variability control (Ayala et al. 1975, Valentine 1976). In short, functionally flexible alleles are assumed to be favored in species that inhabit temporally variable environments or where individual organisms range widely through a variety of environments (these latter are commonly larger organisms); in the more extreme cases the species tend to be monomorphic for the most flexible alleles. In stable environments a variety of alleles, with narrower functional ranges, are found in the gene pools of species whose individuals have restricted environmental ranges. The multiple alleles are maintained by balancing selection which adapts the species to a variety of microhabitats within its habitat range. Each individual becomes a sort of specialist. Thus although the pelagic environment may differ from the benthic shelf environment in being physically more homogeneous on the average in higher latitudes, the trends of genetic variability are the same for krill and benthic invertebrates. Indeed the estimates of genetic variability for krill are quite comparable to those for benthic invertebrates from similar latitudes (Valentine 1976).

An alternative interpretation might be that the observed allelic variants are adaptively neutral and that the degrees of polymorphism simply reflect the balance between mutation rates and sampling drift (Kimura 1968, Kimura and Ohta 1971). However, the neutrality theory of protein polymorphism encounters serious difficulties (e.g., Ayala 1974). One difficulty, particularly noteworthy in the present context is that, according to the neutralist model, the amount of genetic variation is directly related to population size according to the formula

$$n_e = 4Nu + 1$$

or, for electrophoretic variation,

$$n_e = \sqrt{8Nu + 1}$$

where n_e is the effective number of alleles (i.e., the reciprocal of the expected frequency of homozygotes according to the Hardy–Weinberg principle), N is the effective size of the populations (i.e., approximately the number of breeding individuals), and u is the mutation rate per locus per generation for all neutral alleles. Thus, for closely related species, the larger the effective population size, the greater the amount of polymorphism—a prediction that is not verified at all in natural populations. Among the krill species discussed in this paper, *E. superba* undoubtedly has the largest population size by far; yet genetically it is the least polymorphic. This discrepancy could be accounted for, according to the neutrality theory, if *E. superba* would have gone through a severe bottleneck in population size in its recent history. The possibility that the members of *E. superba* may have consisted of only a few individuals in the recent past seems, however, most unlikely. We, therefore, favor a selectionist explanation of the degree of genetic variation found in different environments.

The Paradox of the Krill

Our interpretation of genetic strategies in the krill, to be consistent with that for benthic invertebrates, must be that only a few functionally-flexible alleles occur in the high latitude population and a wide variety of functionally-narrow alleles occur in the low latitude population, with the temperate population representing an intermediate condition. This trend is assumed to be due to the latitudinal differences in seasonality between the antarctic, temperate, and tropical environments. All our samples are from waters that are enriched by upwelling. However, circumantarctic waters have a longer period of extremely low light intensity; waters off the Antarctic Peninsula are essentially clear of autotrophs for several months each year. The waters of the Peru-Chile current are also seasonally productive, but light limitations vary less seasonally and the season of low productivity is shorter. In the tropical eastern Pacific, light intensities are rather equable year round and productivity, while subjected to perturbations due to upwelling, appears to be more equable than in the other regions (references in Valentine and Ayala 1976).

We infer that polymorphisms are chiefly maintained through forms of balancing selection. Thus the tropical pelagic environment must be spatially heterogeneous enough so that fitness varies from patch to patch for a great many alleles (all in the same pattern), creating an array of differential selection pressures that maintain allelic balances. Whereas traditional diversity theories require only that the pelagic environment be capable of being partitioned into enough niches to support the diversities acutally encountered, our model requires that the environment be so spatially het-

erogeneous that selection is sensitive to differences between numerous patches within the niches. Observers record various kinds of heterogeneities within the pelagic environment, but there is no way at present to know just what level is adequate to be consistent with the selectionist model of genetic variability.

We may, on the other hand, turn our argument around. If the neutralist hypothesis is rejected, then selection evidently is sensitive to spatial variations in the pelagic realm on a scale much finer than that of the niche. If selection is indeed this sensitive, then there is no longer any need to regard planktonic diversity as paradoxical, regardless of details of the results of quantification of pelagic heterogeneity. The same reasoning may be applied to the benthic fauna of the deep sea.

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