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Journal
Marine Biology, 27(1)

ISSN
0025-3162

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Publication Date
1974-10-01

DOI
10.1007/bf00394760

Marine Biology 27, 51-57 (1974)

Genetic Variability in the Cosmopolitan Deep-Water Ophiuran *Ophiomusium lymani**

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Abstract

A population of the cosmopolitan deep-sea ophiuran *Ophiomusium lymani* was studied by gel electrophoresis, and proved to be highly variable genetically; about 53% of the 15 loci studied are polymorphic, and the average individual is heterozygous at about 17% of the loci. This is approximately the same genetic variability displayed by other species, belonging to other phyla or classes, from the same deep-sea trawl. A similarly high level of genetic variation occurs in deep-sea organisms in general, and in a shallow-water tropical species. Both the deep-sea and the tropics are trophically stable environments. On the other hand, low genetic variabilities have been found in marine species from trophically unstable environments. These data suggest that any phylogenetic effects on genetic variability are secondary, and that the trophic regime may be of major importance in determining genetic strategies of adaptation.

Introduction

During a broad preliminary survey of genetic variability among marine invertebrates, we have trawled for deep-sea species and have recovered a sample of *Ophiomusium lymani* from moderately deep water off San Diego. Ophiurans are among the more common types of deep-sea organisms. While they are not as diverse among the deep-sea benthos as some other groups, they represent a high percentage of individuals at many stations, and their deep-water species tend to be unusually widely distributed (Hyman, 1955). *O. lymani* is perhaps the most common and widely distributed of all the deep-sea ophiurans (Clark, 1941). It is recorded from all oceans except in very high latitudes, and has a wide bathymetric range recorded — from 70 to 1,588 fathoms (Clark, 1911). *O. lymani* has been figured by McClendon (1909) and Koehler (1922).

We have determined the genetic variability of this population of *Ophiomusium lymani* by techniques of gel electrophoresis. These techniques allow estimating, at least to a first approximation, the amount of genetic variation over the whole genome of a population or a species. Our study of *O. lymani* stems from an interest in the general question of genetic variability of species living in the relatively monotonous deep-sea environment. This is the first study of genetic variability based on a large population of ophiurans and, furthermore, *O. lymani* is the most widely-distributed species for which genetic variation has been surveyed at a moderately large number of loci.

Materials and Methods

The Ophiuran Sample

A large number of *Ophiomusium lymani* were recovered by otter trawl in the San Diego Trough from 1,244 m, on a mud bottom. Trawling was carried out from the R.V. "Oconostota" on April 16, 1973 from 117°31'W; 32°35'30" N; one run was made for about 750 m NNW from that station, and then a parallel return run to the SSE about 1 km west of the first track. The two samples were very similar, being dominated by ophiurans and holothurians with abundant brachiopods and occasional bivalves and asteroids.

Specimens of *Ophiomusium lymani* have been taken previously off San Diego (McClendon, 1909), and this species has been studied and photographed there *in situ* from a bathyscaphe (Barham *et al.*, 1967). *O. lymani* occurs in densities averaging about 8 to 9 individuals/m^2. In living position, the rays are arched, lifting the oral surface of the disc free of the substrate, and individuals appear to be relatively immobile. However, C.L. Hubbs has caught them on baited hooks (Barham *et al.*, 1967). Therefore, Barham *et al.* suggest that these ophiurans may be suspension feeders in part, but that an omnivorous habit is not unlikely. *O. lymani* is highly variable morphologically (Clark, 1941), and the specimens in our samples exhibit considerable amounts of phenotypic variability.

Methods

Immediately after recovering the trawls, the ophiurans were frozen in dry ice and were thus transferred to our laboratory, where they were

*This study is no. 5 of a series of reports on the results of "Expedition Quagmire".

kept at -70°C until prepared for electrophoresis. A sample of soft tissue from each specimen was homogenized in about 2 volumes of distilled H_2O while submerged in an ice-water bath. The homogenates were centrifugated in a refrigerated high-speed centrifuge at 17,000 revs/m for 20 min. A small quantity of supernatant, absorbed in a 4 x 9 mm wick of Whatman no.3 filter paper, was placed into a starch gel slab for horizontal electrophoresis. Samples from about 18 individuals were placed in each gel, together with 3 controls. As controls we used standard stocks of *Drosophila willistoni* flies. These stocks and the mobility of the *Ophiomusium lymani* enzymes relative to the controls are available upon request from the first author.

We have described elsewhere our techniques for gel preparation, the specifications for the electrophoretic runs, and the assays used (Ayala *et al.*, 1973, and in press, b, c). We assayed 11 different enzymes in *Ophiomusium lymani*, using 3 buffer systems symbolized as A,B, and C. These buffers are the same as those used by Ayala *et al.* (in press, b). A total of 15 different zones of enzymatic activity could reliably be scored, although several more could be detected in our gels. The enzymes assayed, the buffer system used for each enzyme, and the number of zones of activity scored are shown in Table 1.

A total of 257 specimens of *Ophiomusium lymani* were studied electrophoretically; 62 from the first trawl, 195 from the second, although not every individual was assayed for every enzyme.

Table 1. *Ophiomusium lymani*. Enzymes assayed and buffer systems used in the study of genetic variation

Enzyme	Abbreviation	Buffer system	Number of loci scored
Alkaline phosphatase	Aph	A	1
Esterase	Est	A	4
Hexokinase	Hk	C	1
Leucine aminopeptidase	Lap	A	2
Malate dehydrogenase	Mdh	A	1
Malic enzyme	Me	C	1
Phosphoglucomutase	Pgm	C	1
Phosphoglucose isomerase	Pgi	C	1
Tetrazolium oxidase	To	B	1
Triose phosphate isomerase	Tpi	B	1
Xanthine dehydrogenase	Xdh	B	1

Results

Variation was detected in 11 of the 15 zones of enzymatic activity studied in *Ophiomusium lymani*. The patterns observed in these variable zones conform to those expected for diploid organisms according to the rules of Mendelian heredity; the frequencies of the various patterns agree with the expectations derived from the Hardy-Weinberg principle for a random mating population. Therefore, we have assumed that each of the 11 variable zones of enzymatic activity is controlled by a polymorphic gene locus. No variation could be detected in 4 of the 15 zones of enzymatic activity scored in our gels; we have assumed that each of the invariant zones is controlled by a single gene locus, without allelic variation in this population of *O. lymani*.

Table 2 lists the 11 polymorphic loci, and gives for each locus the sample size, the allelic frequencies, the frequency of heterozygotes, and whether the locus is polymorphic or not. The results from the two trawl samples have been pooled together since, as we shall justify later, the two samples are genetically very similar. The abbreviations for the enzymes given in Table 1 are used to symbolize the gene loci — hyphenated numerals are added to identify the various zones of activity when several could be detected in a single enzyme assay. The number of genes sampled is twice the number of individuals. Alleles at a locus are represented by the first set of numbers, such as 96, 98, 100, etc. in Table 2; these numbers are arbitrary, except that the difference between any two within a locus refers to the difference in millimeters between the distances migrated by the enzymes coded by the alleles. For each locus, the observed frequency of heterozygotes is given, as well as the expected frequency, assuming Hardy-Weinberg equilibrium. Two criteria are used to decide whether a locus should be considered polymorphic, based on the frequency, P, of the most common allele: (1) when $P \leq 0.990$; (2) when $P \leq 0.950$.

A summary of the genetic variation found in our study is given in Table 3, where the data for the two trawl samples are shown separately. Clearly, the two samples are about equally polymorphic. The greater number of alleles observed in Sample II is simply due to the larger number of individuals studied from this sample. The two samples are similar not only in the amount but also in the kind of genetic variation; that is, both samples have essentially the same alleles in the same frequencies. Evidence of the genetic similarity of the two populations comes from various sources. First, from the agreement for the total sample between the observed and the expected number of heterozygotes, at each locus (Table 2) and for all loci (last column of Table 3). If the two samples had different sets of allelic frequencies, the expected frequencies of heterozygotes in the total sample would be greater than the observed frequencies due to the "Wahlund effect". Differences between the observed and expected numbers of heterozygotes are

Table 2. *Ophiomusium lymani*. Allelic frequencies at 11 polymorphic loci in a deep-sea population. N: number of genes (twice number of individuals) sampled at each locus. Two criteria are used to decide whether a locus is polymorphic, on the basis of the frequency, p, of the most common allele: (1) P ≤0.990; (2) P ≤0.950

Locus[a]	N	Allelic frequencies				Frequency of heterozygotes		Is locus polymorphic?	
						Observed	Expected	(1)	(2)
Est-6	506	96 0.008	98 0.012	100 0.893	102 0.087	0.202	0.194	yes	yes
Est-7	504	96 0.006	98 0.032	100 0.863	102 0.099	0.242	0.244	yes	yes
Hk	510	97 0.075	100 0.569	103 0.043	106 0.251				
		112 0.049	118 0.014			0.557	0.604	yes	yes
Lap-1	510	98 0.037	100 0.904	102 0.055	104 0.004	0.176	0.179	yes	yes
Lap-2	500	98 0.018	100 0.950	102 0.032		0.100	0.096	yes	yes
Me	306	96 0.003	100 0.948	104 0.049		0.092	0.099	yes	yes
Pgm	510	88 0.010	94 0.051	100 0.896	104 0.041				
		108 0.002				0.161	0.192	yes	yes
Pgi-2	510	94 0.004	97 0.002	100 0.971	103 0.022				
		106 0.002				0.051	0.057	yes	no
To	458	80 0.002	84 0.236	90 0.271	94 0.013				
		100 0.415	104 0.044	110 0.017	114 0.002	0.725	0.696	yes	yes
Tpi	270	96 0.015	100 0.952	104 0.033		0.081	0.093	yes	no
Xdh	510	99 0.006	100 0.951	101 0.024	102 0.018				
		104 0.002				0.098	0.095	yes	no

[a]For explanation of abbreviations see Table 1

not statistically significant at any individual locus, nor for all loci together. Further evidence of genetic differentiation between the two samples comes from the calculation of genetic similarity, I, and genetic distance, D, between the samples. The values of these parameters, obtained according to the method of Nei (1972), are I = 0.997, and D = 0.003. We may, then, conclude that our two samples come either from two populations genetically nearly identical, or from a single population. The similarity between the observed and the expected frequencies of heterozygotes suggests also that the organisms sampled approximate random mating equilibrium. This suggestion is further sup-

Table 3. *Ophiomusium lymani*. Summary of genetic variation in two deep-sea samples

Parameter	Sample I	Sample II	Total
Number of loci	15	15	15
Number of individuals	62	195	257
Genes sampled per locus	111±6	366±15	476±20
Alleles per locus	2.73±0.37	3.60± 0.53	3.67±0.53
Polymorphic loci	0.733	0.733	0.733
Polymorphic loci with P≤0.95	0.667	0.400	0.533
Frequency of heterozygotes:			
average of individuals (observed)	0.168±0.013	0.163±.006	0.164±0.005
average over loci (observed)	0.173±0.055	0.163±.055	0.166±0.054
average over loci (expected)	0.171±0.050	0.168±.056	0.170±0.054[a]

[a]Calculated according to expectations of Hardy-Weinberg equilibrium after pooling allelic frequencies for both samples

ported by the distribution of heterozygous loci per individual shown in Fig. 1. This distribution does not significantly differ from a normal distribution, with mean = 0.164 and standard deviation = 0.080, the observed heterozygosity values for the average over individuals (Table 3). It should be pointed out that two population samples of the brachiopod *Frieleia halli*, recovered from the same two trawls, proved also to be genetically essentially identical to each other (Valentine and Ayala, in press).

Table 3 shows that a great deal of genetic variation exists in *Ophiomusium lymani*. The proportion of polymorphic loci in our sample of 15 gene loci is either 73.3 or 53.3%, depending on whether a less or a more restrictive criterion of polymorphism is used. The number of alleles detected by electrophoresis ranges from 1 at each of the four monomorphic loci, to 8 at the *To* locus; for all 15 loci the average is 3.67.

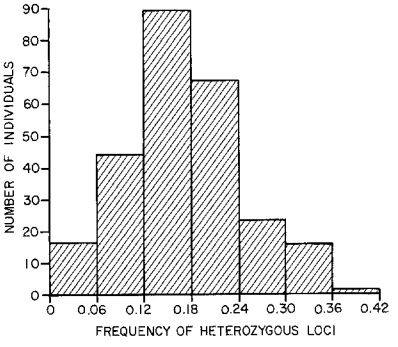

Fig. 1. *Ophiomusium lymani*. Distribution of 257 individuals according to proportion of heterozygous loci per individual

The most precise measure of genetic variation in outcrossing, sexually-reproducing organisms is the average heterozygosity. We have estimated this parameter in three ways: (1) by averaging over all individuals the proportion of heterozygous loci per individual; (2) by averaging over all loci the observed frequency of heterozygous individuals per locus; (3) by averaging over all loci the expected frequency of heterozygous individuals per locus. The mean values of (1) and (2) should be the same whenever every individual is studied at every locus. Such is not the case in our study; nearly every individual has been studied at all loci except *Me* and *Tpi*, for which only about half the individuals were sampled. The variances of (1) and (2) are not expected to be the same; in our case, as in general for outcrossing organisms, the variance of (2) is greater than the variance of (1). This is because the distribution of individual heterozygosities is normal (Fig. 1), while the distribution of loci heterozygosities is widely scattered with a single mode at one extreme of the distribution (the 4 loci with zero heterozygosities). Table 3 shows that, independent of how it is calculated, the mean heterozygosity for *Ophiomusium lymani* is about 17%. That is, on the average, about 17% of all *O. lymani* individuals are heterozygous at a locus, or 17% of the loci are heterozygous in an individual. This is a very high level of genetic variation, but similar to the levels observed in other deep-sea organisms (see below).

It may be worthwhile to point out that the most polymorphic locus in our samples of *Ophiomusium lymani* is *To*, at which 72% of 229 individuals studied are heterozygotes. The *To* locus is also the most polymorphic one in another deep-sea organism studied by us, the asteroid *Nearchaster aciculosus* (Ayala *et al.*, in press), in which the frequency of heterozygotes at this locus is 71%. It is tempting to speculate that there may be some physiological reason why the enzyme tetrayolium oxidase should be very polymorphic in organisms living at great depths under water. However, if such reason exists it is not general, since no allelic variation was detected at the *To* locus in another deep-sea organism studied by us, the brachiopod *Frieleia halli* (Valentine and Ayala, in press).

The question needs to be raised whether the genetically controlled protein variation detected in our study is adaptively significant or not. Recently, it has been suggested (for example, by Kimura and Ohta, 1971) that protein variation may be adaptively neutral; if such were the case, levels of genetic variation would be related to population size and to mutation rates, but not to the environmental regime or any other adaptively relevant parameter. This question can only be briefly discussed here. The most important point is that substantial evidence now exists supporting the notion that genetic variation detected at the molecular level by techniques such as gel electrophoresis is subject to natural selection, and thus is adaptive in character (for a recent summary see Ayala *et al.*, in press, a). Direct evidence supporting this conclusion can also be obtained from our data of protein variation in *Ophiomusium lymani*, as well as in 4 other deep-sea species whose protein variation we have studied — one brachiopod, *Frieleia halli* (Valentine and Ayala, in press) and 3 asteroids (Ayala *et al.*, in press, d), all collected from the San Diego Trough. The distribution of loci heterozygosities in all these deep-sea organisms is shown in Fig. 2. The date for the various species have been pooled, since the distribution of loci heterozygosities has the same configuration in all of them. It follows from the hypothesis of adaptive neutrality that the loci heterozygosities should be approximately normally distributed, since approximately the same level of heterozygosity is expected for all neutral loci in a given population. In contrast, the distribution observed in *O. lymani* (Table 2) as well as in the other deep-sea organisms (Fig. 2) is far from normal; rather, it is scattered over a broad range of values, with a large proportion of loci having little or no heterozygosity. As Ayala *et al.* (in press, a) have shown, if the mean heterozygosity is about 17% (as it is for all these deep-sea species, see Table 3), and if the variation is adaptively neutral, the probability of loci with zero or near-zero heterozygosities is vanishingly small; yet we find a large proportion (about one-third) of the loci with essentially no allelic variation.

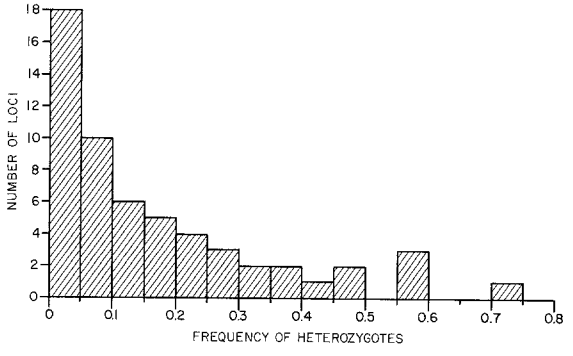

Fig. 2. Distribution of 57 gene loci according to proportion of heterozygous individuals per locus. Loci include 15 loci studied in *Ophiomusium lymani*, 16 loci studied in the deep-sea brachiopod *Frieleia halli*, and 24 loci studied in 3 deep-sea asteroids. Mean proportion of heterozygotes per locus is the same, 17%, in all these organisms

Discussion

The finding of high genetic variability in *Ophiomusium lymani* is of interest in several respects. It further confirms the discovery that genetic variability in the deep sea is generally high. Indeed, 5 other species recovered from the same trawls that yielded our sample of *O. lymani* have been studied electrophoretically (Ayala *et al.*, in press, d; Valentine and Ayala, in press; and Table 4 of present study). These species included 1 brachiopod and 4 asteroids. All are highly variable. Relatively few asteroid specimens were found, so that the data from all asteroid species are pooled in Table 4. In fact, however, the more abundant species (*Nearchaster aciculosus*) has an average heterozygosity of about 21%, apparently higher than the others. The lower variabilities detected in the rarer species may well be due, at least in part, to their small sample sizes. The close similarities of the frequencies of heterozygotes listed in Table 4, from the asteroids, from the brachiopod species, and from *O. lymani*, must be partly fortuitous, considering the errors inherent in sampling genetic variation by electrophoretic methods (Ayala *et al.*, 1970). Nevertheless, the genetic variabilities are indeed so similar that they cannot be distinguished by the present methods, even though three classes in two phyla are involved.

Ophiomusium lymani has been studied previously by electrophoretic techniques. Gooch and Schopf (1972) studied 8 loci in an average of 12 specimens per enzyme system from material dredged in the northwestern Atlantic Ocean. They estimated that two loci were polymorphic, and another two were scored as provisionally polymorphic. Since no allelic frequencies are given, there is no way to estimate average heterozygosities; in any case, the samples are too small to give reliable estimates. Doyle (1972) also studied *O. lymani*, but

Table 4. Genetic variation in deep-sea organisms from San Diego Trough

Parameter	*Ophiomusium lymani*	Asteroids[a]	*Frieleis halli*	Average
Number of loci studied	15	24	16	18.3±2.8
Genes sampled per locus	476±20	54±1	100±13	210±134
Alleles per locus	3.67±.53	3.21±.39	2.50±.29	3.13±.34
Polymorphic loci	0.733	0.833	0.750	0.772±0.031
Polymorphic loci with P≤0.95	0.533	0.583	0.563	0.560±0.015
Frequency of heterozygotes[b]:				
observed	0.166±0.054	0.176±0.035	0.169±0.043	0.170±0.003
expected	0.170±0.054	0.164±0.032	0.169±0.046	0.168±0.002

[a] Includes four species: *Nearchaster aciculosus*, *Pteraster jordani*, *Diplopteraster multipes*, and *Myxoderma sacculatum extenes*

[b] Calculated by averaging over all loci the frequency of heterozygous individuals at each locus

only at one polymorphic esterase locus (judging by the allelic frequencies given by Doyle, the locus studied by him may have been either our *Est-6* or *Est-7*). Previous electrophoretic studies of deep-sea species by Gooch and Schopf (1972), while based on relatively few individuals, nevertheless indicate considerable genetic variability in species from this environment, in agreement with our results.

Although no shallow-water ophiurans have yet been examined electrophoretically, a shallow-water brachiopod (*Liothyrella notorcadensis* from Antarctica; Ayala *et al.*, in press, c) and two shallow-water species of the asteroid *Asterias* (*A. forbesi* and *A. vulgaris* from the northwestern Atlantic Ocean; Schopf and Murphy, 1973) have been studied. These species all proved to have low genetic variability (3.9, 1.1, and 2.1% average heterozygosity, respectively). Since species of different phyla and classes from the same environment tend to have similar levels of genetic variability, while species of the same phyla and classes from different environments have very different levels of genetic variability, there appear to be no important phylogenetic controls on genetic variability in these forms.

On the other hand, environmental controls seem possible. In general, we have found that species in environments with the more stable trophic resource supplies, such as the tropics and the deep sea, have high genetic variabilities, while those in shallow water in temperate latitudes, where productivity is more seasonal, tend to be much lower. In very high latitudes, where productivity is extremely seasonal, essentially stopping during winter months, genetic variability is quite low (Ayala *et al.*, in press, c). The main exceptions to this trend are found in some temperate species that are less variable than expected (the two species of *Asterias* studied by Schopf and Murphy, 1973). This exception may be explicable as a result of the (geologically) recent history of these species, which may have fluctuated unusually in population size. Otherwise, the correlation has held, and *Ophiomusium lymani* fits very well the general trend previously observed — a positive correlation of genetic variability with environmental stability. This trend is opposed to the trend often predicted by theoretical population models, which postulate a negative correlation between genetic and environmental stability (e.g. Levins, 1968). Our findings are also in contradiction to the specific predictions of Grassle and Sanders (1973) and Grassle (in press) that deep-sea organisms should have low genetic variabilities.

One way of explaining the observed trends is to infer that individuals which live where there is greater fluctuation in trophic resources must tend to be more flexible and generalized in both feeding and habitat tolerances and requirements (Valentine, 1971, 1973). Favorable gene combinations that produce organisms flexibly adapted to such environments would tend to be strongly selected, as individual fitness would be at a premium. Thus, a few "optimal" genotypes — flexible ones — are found everywhere, alternate alleles are generally selected against, and populations tend to have low genetic variabilities. In trophically stable environments, however, where specialization is common, genetic variability is employed to adapt

members of the population to a variety of spatial variations in the environment (see Ayala *et al.*, in press, c, for more extended discussion).

A final observation on the variability in *Ophiomusium lymani* is that, although the genetic variability is high, it has not proven exceptional compared with that of other deep-sea species (3 asteroids and 1 brachiopod) that we have studied. Yet *O. lymani* has a far greater geographic range than the other deep-sea forms, and a very broad bathymetric range as well. The other deep-sea species are chiefly restricted to the far northern and northeastern Pacific Ocean; one ranges from near San Diego to Japan, and some may spread through the Arctic Ocean. Thus, although they are not narrowly restricted, they are far from cosmopolitan. The large differences in distribution range between *O. lymani* and the other 4 deep-sea species are not reflected in their genetic variabilities.

Acknowledgements. We thank J.C. Avise, C.A. Campbell and G.S. Zumwalt, all of the University of California, Davis (USA), and also the captain and crew of the R.V. "Oconostota", for their help in collecting the deep-sea samples. Dr. R.R. Hessler, Scripps Institution of Oceanography, arranged ship time and provided other courtesies, for which we are grateful. J. Branstrator, Department of Geology, University of California, Davis, verified the identification of *Ophiomusium lymani*. D. Hedgecock, University of California, Davis, helped with the statistical calculations.

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Date of final manuscript acceptance: June 7, 1974. Communicated by O. Kinne, Hamburg