Colour polymorphism and genetic variation in *Idotea baltica* populations from the Adriatic Sea and Baltic Sea

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Abstract

Phenotypic and genetic variation was studied in two of the four European subspecies of the marine isopod *Idotea baltica;* the Mediterranean *I. b. basteri* and the Baltic *I. b. baltica.* Spatial and temporal patterns of colour polymorphism were analysed in northern Adriatic and western Baltic Sea populations. Pronounced differences in phenotype composition were observed between populations of both subspecies as seen in the distribution of various colour variants bilineata, lineata, flavafusca and several combined forms). Compared with Adriatic samples, western Baltic Sea populations show higher phenotypic diversity. To obtain an estimate of the degree of genetic divergence between the subspecies, 12 gene-enzyme systems were investigated electrophoretically. The results obtained indicate a relatively high level of genetic variation; *I. b. basteri* from the nothern Adriatic tends to be more polymorphic and more heterozygous than *I. b. baltica* from the western Baltic. Both subspecies share identical electrophoretic mobilities of the homologous enzyme proteins examined; however, in allelic composition they exhibit significant differences at approximately half the number of loci scored. The genetic distance (Nei's $\overline{D}$) measured at the subspecific level was 0.04. Amounts and geographical patterns of variation, observed both in colour phenotype and electrophoretic variation, are considered.

Introduction

Idotea baltica Pallas is a widely distributed, fairly cosmopolitan isopod occurring in subtidal and intertidal habitats of marine and brackish-water environments. Commonly associated with macrophytes, surface drift weed and floating debris, this euryhaline crustacean represents an important member in the food web of littoral communities. Hence, several studies have been made of its general biology and ecology (e.g. Naylor, 1955; Salemaa, 1979b).

European populations of *I. baltica* comprise four allopatric forms which are considered to be subspecies or geographical races: *I. b. baltica* Dahl, *I. b. tricuspidata* Desmarest, *I. b. basteri* Audouin and *I. b. stagnea* Tinturier-Hamelin. These subspecies can be distinguished by differences in morphological characters, growth allometries, rates of sexual development and geographic distribution (Tinturier-Hamelin, 1963a). *I. b. tricuspidata* and *I. b. basteri* are inhabitants of marine environments; the former is distributed in the Atlantic area, whereas the latter occurs in the Mediterranean Sea. *I. b. baltica* and *I. b. stagnea* inhabit brackish waters over a wide range of salinities; the former is restricted to the Baltic Sea, whereas the latter lives in certain coastal localities of the French Mediterranean.

Individuals of *I. baltica* exhibit considerable variation in body colour. This polychromatism has been examined in several investigations carried out from morphological, ecological, physiological and genetical points of view (e.g. Remane, 1931; Pea-

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body, 1939; Suneson, 1947; Koepcke, 1948; Salemaa, 1978, 1979a, b).

The patterns of colour variation observed have a hereditary background but the intensity of pigmentation may be affected by several factors such as food, moulting and colour of the environment. The ability to respond to the latter factor is under central nervous and hormonal control. *I. baltica* is able to change reversibly the intensity of integumental coloration in a way which depends on alterations of the dispersion of pigments located in the chromatophores. This physiological colour change, which is a reaction to visual stimuli, enables the species to merge with its immediate background and thus may have a protective significance.

The genetically determined and partially sex-linked pattern of colour variation has been extensively studied by Tinturier-Hamelin (1963a, b). Within the four *I. baltica* subspecies, she has distinguished the following six major phenotypes: uniformis, albafusca, flavafusca, maculata, bilineata and lineata. Irrespective of physiological colour change, these phenotypes are clearly distinguishable. Moreover, various combinations of these colour morphs may occur. As noticed by Tinturier-Hamelin, some differences exist in the distribution of the phenotype patterns. Investigations carried out on numerous northern Baltic Sea populations revealed considerable spatial variation and diversity in the phenotype composition associated with some seasonal changes in the relative frequencies of the colour morphs observed (Salemaa, 1978, 1979a).

The present paper attempts to assess the geographic separation of the subspecies *I. b. basteri* and *I. b. baltica* in terms of differences in phenotype composition and genetic structure. It provides further data on the distribution of colour morphs, occurring in various populations of the northern Adriatic Sea and western Baltic Sea. In addition, comparisons are made, based on electrophoretically detected enzyme variation at specific gene loci, to quantify the genetic divergence between the two subspecies concerned. An additional objective of this study was to look for any evidence of correlations between colour phenotype expression and allozymic variation.

Material and methods

Study areas and sampling

Two of the sampling stations chosen in the northern Adriatic Sea were located in the area of Venice: Station Santo Spirito in the Lagoon of Venice and Station Lido on the Lido Island (Italy) which is exposed to the open Adriatic Sea (Fig. 1a). Both localities are characterized by fluctuations in temperature and, within the lagoon, in salinity. In

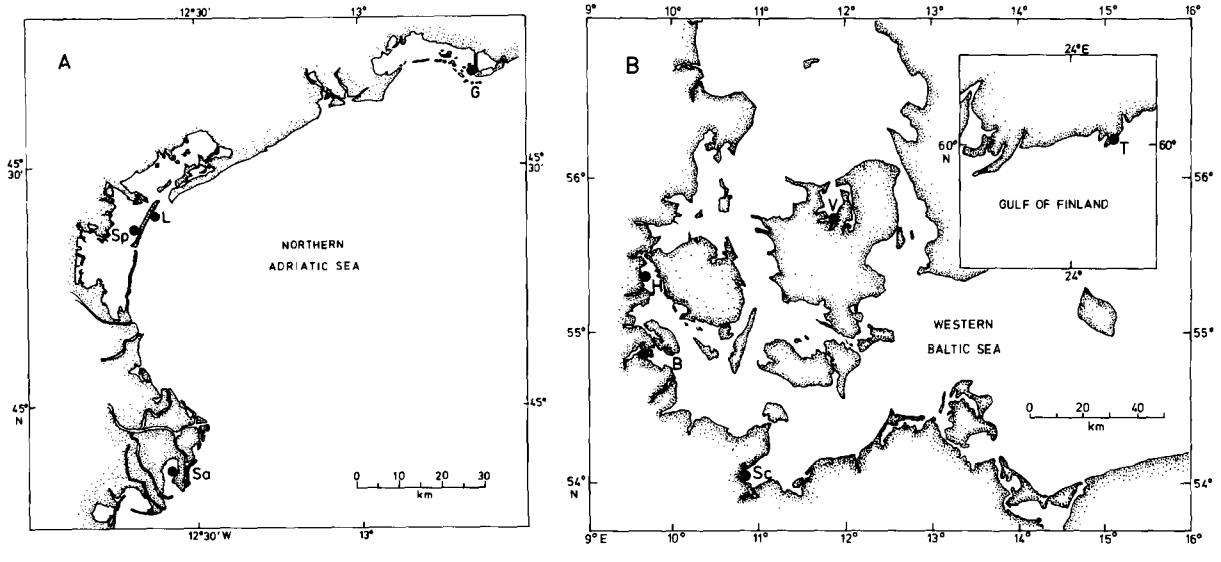

Fig. 1. Location of collecting sites. Abbreviations: Sa = Sacca di Scardovari, Sp = Santo Spirito, L = Lido, G = Grado, Sc = Scharbeutz, B = Bockholmwik, H = Hejlsminde, V = Vellerup Vig, T = Tvärminne.

surface water, seasonal temperatures range from about 5° to 25 °C. In the lagoon, salinity fluctuates between 27 and 36‰. Daily variations of these abiotic factors, resulting from a tidal range of about 1 m, may be more than 3 °C and 2‰ S. Details of the physical and chemical characteristics of the lagoonal environment are given by Franco (1962) and Comaschi and Voltolina (1973).

Two additional sampling stations, Grado (near the mouth of River Isonzo) and Sacca di Scardovari (Po delta), were selected for surveying colour variation in *I. b. basteri* populations. These localities are characterized by environmental conditions similar to those described above.

In the western Baltic Sea, *I. baltica* was collected in shallow water above sandy ground at the following localities (Fig. 1b): Scharbeutz (Lübeck Bay, FRG), Bockholmwik (Flensburg Bay, FRG), Hejlsminde (Jylland, Denmark) and Vellerup Vig (Isefjord, Denmark). Some complementary studies restricted to analysis of variation in selected allozymes were made using a sample taken from a rocky shore in the northern Baltic Sea at Tvärminne (Gulf of Finland).

Details of hydrographical and biological features, particularly of the western Baltic Sea including Danish coastal areas, are given by Muus (1967), Rasmussen (1973) and Magaard and Rheinheimer (1974). Some data referring to the northern Baltic Sea are presented by Salemaa (1979b).

The Baltic Sea, an enclosed basin with limited water exchange from the North Sea, is characterized by lowered salinity levels, which decrease progressively towards the northern part. Moreover, pronounced salinity and temperature stratifications exist in deeper waters, exhibiting regional and seasonal differences. Tidal influence is minimal or negligible.

Except for the Isefjord (Rasmussen, 1973), continuous measurements of fluctuations in the intensity of the environmental variables have not been made at the western Baltic collecting sites considered here. In these areas, salinity of surface water generally ranges between 15 to 20‰ S. Seasonal variations in salinity levels may occur depending on the amount of freshwater influx. Annual temperature fluctuations in shallow water range between 0° and 20 °C approximately. In surface waters at Tvärminne the range is between 0° and 16.5 °C and 6‰ S (summer) to 1‰ S (winter) (Salemaa, 1979b). This area is near the distribution limits of *I. b. baltica* in the Baltic, restricted by the 3–4‰ S-isohaline.

The idoteids were collected from sublittoral algal beds and eelgrass meadows at a depth of 0.5–1.5 m. The plants (particularly *Ulva rigida* and *Gracilaria confervoides* in the Adriatic, *Fucus vesiculosus* and *Zostera marina* in the Baltic Sea) were removed from the water in order to sample the adhering animals. Living individuals were examined with regard to colour phenotype. Since juveniles were included in this survey, sex was not discriminated in all samples.

Phenotypic diversity (H') was measured by use of the Shannon function $H' = -\Sigma p_i \cdot \ln p_i$ (p_i denotes the frequency of each phenotype observed).

Electrophoresis and enzyme assays

The isopods collected at the sampling sites were maintained, until used for electrophoresis, in aerated aquaria filled with water of the same salinity as that of the natural habitat. Whole animals were mechanically homogenized with equal volumes of 0.1 M Tris-HCl buffer at pH 8.0. The homogenates were centrifuged at 20 000 × g for 4 min. Horizontal (Shandon system) and vertical (Buchler Instruments) starch gel electrophoresis of the supernatant fraction was accomplished at 4 °C using 11–12.5% starch gels (Sigma and Connaught starch-hydrolyzed).

Two buffer systems, designated B and C and prepared according to Ayala *et al.* (1972) were utilized: B gel and electrode buffer: 87 mM Tris, 8.7 mM boric acid, 1 mM EDTA and 1 mM β-NAD^+, pH 9.0. C gel buffer: 9 mM Tris, 3 mM citric acid, pH 7.0; electrode buffer: 135 mM Tris and 45 mM citric acid.

For horizontal electrophoresis Whatman filter paper wicks were saturated with the supernatant and inserted into a slice made across the gel about 4 cm from the cathodal end. During vertical electrophoresis 20 µl of the supernatant was filled into each slot of the gels. Electrophoretic runs lasted 7–8 h at 20 V/cm (buffer B) and 4 h at 13 V/cm (buffer C). A cooling layer composed of a box filled with ice was placed on top of the gel. Vertical electrophoresis was terminated after 15 h at 8 V/cm (buffer B) and 5 V/cm (buffer C). Following electrophoresis gels were sliced horizontally to provide 3 slices.

Table 1. Gene-enzyme systems examined, numbers of alleles resolved, and electrophoretic systems employed.

Enzyme	Genetic locus	No of alleles		Electrophoretic system
		Adriatic populations	Baltic	
Arginine phosphokinase	*APK*	3	1	B
Glutamate oxalacetate transaminase	*GOT*	3	1	B, C
Gluconate pyruvate transaminase	*GPT*	2	3	B
Glycerol-3-phosphate dehydrogenase	*G3PD*	2	1	C
Malate dehydrogenase-1	*MDH-1*	1	1	C
Malate dehydrogenase-2	*MDH-2*	1	1	C
Malic enzyme	*ME*	2	1	B, C
Mannose-6-phosphate isomerase	*MPI*	6	5	B
6-Phosphogluconate dehydrogenase	*6PGD*	4	1	C
Phosphoglucose isomerase	*PGI*	5	4	C
Phosphoglucomutase	*PGM*	6	6	C
Pyruvate kinase	*PK*	1	1	C

Table 1 lists the enzymes assayed, the buffer systems used and the number of alleles resolved. Staining techniques followed Brewer (1970) and Ayala *et al.* (1972) with slight modifications. Further staining procedures were as described for APK (Bulnheim & Scholl, 1981), GPT, MPI, PK (Harris & Hopkinson, 1976), GOT and PGI (Scholl *et al.*, 1978).

The agar overlay method following Scholl *et al.* (1978) was applied to detect the following enzymes: APK, GPT, MPI, PK, PGI, PGM, and 6PGD. The latter two enzymes were stained in combination. Best results were obtained for PGM from horizontal and for GPT and MPI from vertical electrophoresis.

The electrophoretically detectable allelic variants were designated by the relative differences in anodal mobility of their protein products; the most frequent electromorphs observed at polymorphic loci were designed '100'. The mode of inheritance in allozyme variation could not be verified by progeny studies. However, breeding experiments indicated Mendelian inheritance patterns of allozymic variants in other malacostracan crustaceans (e.g. Hedgecock *et al.*, 1975; Sassaman, 1979). The genetic interpretations of the enzyme patterns visualized following electrophoresis were supported by the close agreement between expected and observed proportions of genotypes according to Hardy-Weinberg expectations. Nevertheless, the probability of errors by the application of this genetic model must be taken into account. As demonstrated by Fairbairn and Rolf (1980), this is true of random phenotypic variation, isozyme variants generated by posttranslational modification of protein structure and segregation of 'silent' alleles, particularly when sample sizes are <200. Deficiency or excess of heterozygotes was estimated by the parameter $D = (H_o - H_e)/H_e$. H_o and H_e are the heterozygotes (%) observed and expected assuming Hardy-Weinberg equilibrium (cf. Koehn *et al.*, 1976). Levels of heterogeneity in allele frequencies between samples were tested by application of the genic χ^2 test (Workman & Niswander, 1970). The mean genetic identity ($\bar{I}$) and genetic distance ($\bar{D}$) between populations were measured according to Nei (1972).

Results

As outlined by Tinturier-Hamelin (1963a), the four *Idotea baltica* subspecies can be distinguished by several characteristics. Among these, the shape of the pleotelson is of primary relevance for morphological distinction. The apical border of the pleotelson is tridentate in both forms considered here, but it reveals a more pronounced median process, depending on the size of the animal, in *I. b. baltica* (Fig. 2).

Experimental hybridisation, performed with some of the four subspecies (Tinturier-Hamelin, 1963a), has been carried out between individuals from the western Baltic Sea and northern Adriatic Sea. These interbreeding experiments were successfully accomplished in the laboratory, thus indicating the interfertility of the two subspecies concerned.

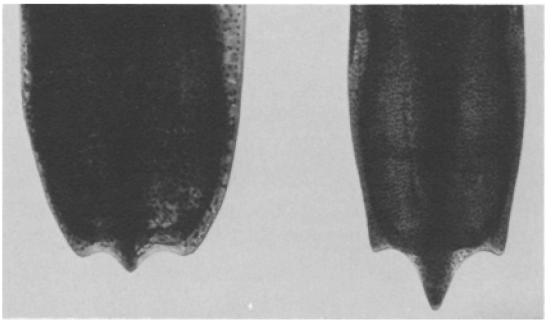

Fig. 2. Pleotelson of ♂♂ (body length: 20 mm) from *Idotea baltica basteri* (left) and *I. b. baltica* (right); magnification: ×8.

Colour polymorphism

As mentioned above, the following basic types of colour patterning are distinguishable in *Idotea baltica:* uniformis, lineata, bilineata, albafusca, flavafusca and maculata. In addition, various combinations of these phenotypes may occur (see Table 2). Illustrations of the major colour morphs are given by Tinturier-Hamelin (1963a) and Salemaa (1978).

To some extent the colour morphs flavafusca, albafusca and maculata exhibit sex-linked inheritance in the female line. Females are heterogametic, possessing W and Z chromosomes. The W chromosomes carry the alleles which determine the above phenotypes. Since sex determination also appears to be affected by autosomal genes, intersexes as well as sex inversions may occur (Tinturier-Hamelin, 1963a; Legrand & Legrand-Hamelin, 1975). Thus, sex determination and phenotype expression are correlated to a certain degree.

Table 2 provides the data on the proportions of the various phenotypes in the *I. b. basteri* and *I. b. baltica* populations obtained from 4 localities in the northern Adriatic Sea and 4 localities in the western Baltic Sea. In all samples examined, uniformis was the most frequent phenotype, comprising approximately 50 to 60% of the individuals. Compared with northern Adriatic populations, the variants lineata, albafusca and various hybrids were more frequently found in western Baltic populations. The presence of bilineata is significantly more pronounced in northern Adriatic populations which, however, lack the phenotype flavafusca. In our samples, the phenotype lineata includes the variant pseudolineata distinguished by Tinturier-Hamelin (1963b) from lineata.

Among the combined colour patterns which generally occur at low frequencies, three phenotypes are common in both subspecies: bilineata-lineata, albafusca-bilineata, and albafusca-bilineata-lineata. Other hybrids not found in *I. b. basteri* but represented by *I. b. baltica* populations include albafusca-maculata, bilineata-maculata, lineata-maculata, and albafusca-lineata. When compared with each other, using the Shannon function, North Adriatic Sea samples exhibit lower phenotypic diversities than western Baltic Sea populations. The relatively highest diversities were observed in the population from Bockholmwik (Table 2).

It is interesting to note that the frequencies of the phenotype bilineata-lineata, as observed from our data and from the results presented by Salemaa (1978, table 2, pp. 172–173), exceed in most cases the expected frequencies, these being calculated as the product of the probabilities of the two independent characters. As revealed by the application of the G-test, the difference is statistically significant ($P < 0.05$) in the four Adriatic collections (Scardovari and S. Spirito: May 1978, June 1979; Lido: September 1978), while it is highly significant ($P < 0.01$) in the western Baltic populations examined, with the exception of that from Vellerup.

These findings suggest the presence of a selective advantage, probably due to a better camouflage conferred by this phenotype on certain algae and, in particular, on *Zostera marina.* Compared to its distribution in Adriatic areas, this seagrass appears to be more abundant in the western Baltic Sea.

In addition to the investigations performed on the geographical variation of phenotype composition, some observations were made on temporal variations in the distribution patterns of the colour morphs concerned. At the Lido and S. Spirito localities slight seasonal fluctuations in the frequencies were established during the limited period of observation, from spring to fall (Table 2); however, no general trend of this variation is evident.

At Scharbeutz, the occurrence of the colour morphs was studied by means of samples taken over a three- to four-year period. In this population too, phenotype structure remained fairly stable.

Gene-enzyme variation

Twelve enzyme systems were investigated in *Idotea baltica basteri* and *I. b. baltica.* The respec-

Table 2. Distribution of colour phenotypes in *Idotea baltica*. N = number of individuals examined; H′ = index of phenotype diversity.

Phenotypes	Site, date							
	Grado		Scardovari Lido					
	III 76	V 76	V 76	IX 77	III 78	VI 78	IX 78	IX 79
uniformis	0.614	0.657	0.570	0.561	0.582	0.663	0.639	0.619
lineata	0.043	0.063	0.008		0.029	0.008	0.015	0.006
bilineata	0.270	0.084	0.320	0.262	0.276	0.271	0.230	0.275
albafusca	0.037	0.126	0.008	0.033	0.004	0.029	0.028	0.013
maculata				0.014	0.025		0.009	0.025
bilineata-lineata	0.037	0.028	0.086	0.014	0.015		0.039	0.025
albafusca-bilineata		0.035	0.008	0.117	0.062	0.029	0.039	0.038
albafusca-bilineata-lineata		0.007			0.007			
N	163	143	128	214	275	240	457	160
H′	1.032	1.171	1.013	1.159	1.157	0.871	1.083	1.047

Phenotypes	Site, date								
					S. Spirito				
	III 78	V 78	IX 78	II 79	VI 79	IX 79	II 80	VI 80	IX 80
uniformis	0.540	0.667	0.675	0.526	0.629	0.648	0.636	0.627	0.569
lineata	0.017		0.016		0.004	0.016	0.012	0.012	0.019
bilineata	0.293	0.241	0.227	0.336	0.290	0.210	0.255	0.277	0.318
albafusca	0.017	0.005	0.012	0.004		0.016	0.018	0.012	0.003
maculata	0.023	0.014	0.020	0.017	0.033	0.031	0.042	0.020	0.013
maculata-bilineata								0.008	
bilineata-lineata	0.046	0.023	0.004	0.034	0.024	0.021	0.006	0.016	0.010
albafusca-bilineata	0.057	0.051	0.043	0.078	0.020	0.058	0.030	0.028	0.068
albafusca-bilineata-lineata	0.006		0.004	0.004					
N	174	216	255	232	245	381	165	249	311
H′	1.254	0.938	0.978	1.131	0.954	1.095	1.030	1.038	1.062

Phenotypes	Site, date						
		Scharbeutz			Bockholmwik	Hejlsminde	Vellerup
	X 77	XI 78	X 80	IV 81	X 79	V 79	XI 79
uniformis	0.501	0.488	0.545	0.489	0.433	0.476	0.514
lineata	0.182	0.208	0.205	0.155	0.124	0.074	0.250
bilineata	0.053	0.027	0.037	0.066	0.082	0.119	0.048
albafusca	0.106	0.107	0.060	0.109	0.059	0.112	0.058
flavafusca	0.013	0.003		0.022	0.005	0.010	0.014
maculata	0.032	0.054	0.039	0.026	0.099	0.076	0.034
maculata-lineata	0.013	0.015	0.008	0.009	0.022	0.018	0.019
maculata-bilineata	0.001	0.003		0.003	0.005	0.010	
bilineata-lineata	0.075	0.069	0.096	0.107	0.135	0.074	0.029
albafusca-lineata	0.006	0.006	0.005	0.007	0.001		0.014
albafusca-bilineata	0.005	0.009	0.002		0.011	0.024	0.005
albafusca-bilineata-lineata		0.006		0.003	0.007		0.014
albafusca-maculata	0.008		0.002		0.008	0.006	
other hybrids	0.006	0.006	0.002	0.006	0.008		
N	1 061	336	616	699	741	498	208
H′	1.600	1.588	1.400	1.525	1.798	1.718	1.499

tive numbers of alleles per locus observed are given in Table 1. Several additional (probably polymorphic) enzymes encoded by particular loci could not be adequately resolved (e.g. esterase, hexokinase, lactate dehydrogenase, alkaline phosphatase). Interpopulation differences in electrophoretic resolution became apparent in glucose-6-phosphate dehydrogenase. Parallel runs demonstrated that individuals of Adriatic populations exhibit three clearly distinguishable alleles, whereas the enzyme stain gave a diffuse reaction in Baltic individuals. A positive reaction was observed for the aldolase stain in *I. b. basteri,* but not in *I. b. baltica.* When compared with Adriatic samples, Baltic idoteids, particularly representatives of the Tvärminne population, displayed poorly stained bands in the assay for PGM.

Allele frequency data obtained from those enzyme systems which provided reliable results, are listed in Table 3, including the number of heterozygotes observed and heterozygotes expected from Hardy-Weinberg distributions. Parallel runs on gels showed that the two subspecies share identical electrophoretic mobilities for all enzymes considered in this study.

Arginine phosphokinase

Three alleles were observed at the *APK* locus. Among these, two rare alleles were seen only in Adriatic populations. By contrast, the three Baltic

Table 3. Distribution of allele frequencies at polymorphic loci in *Idotea baltica* populations. Allelic variants are designated numerically. N = number of individuals examined; H_o = heterozygotes observed; H_e = heterozygotes expected; D = deficiency or excess of heterozygotes.

Locus	Site	Date	N	Allele frequencies				H_o	H_e	D
APK				*92*	*96*	*100*	*104*			
	Lido	IX 78	160	0.003		0.969	0.028	0.063	0.061	+0.033
	S. Spirito	V 79	166			0.985	0.015	0.030	0.030	
	Scharbeutz	VIII 78	96			1.0				
	Bockholmwik	X 79	95			1.0				
	Tvärminne	IX 79	44			1.0				
GOT				*94*	*100*	*106*				
	Lido	VI 78	159	0.016	0.984			0.031	0.031	
		IX 78	180	0.019	0.981			0.039	0.038	+0.026
	S. Spirito	V 78	120		1.0					
		IX 78	140	0.004	0.989	0.007		0.021	0.021	
		II 79	160	0.025	0.972	0.003		0.056	0.055	+0.018
		V 79	166	0.012	0.979	0.009		0.042	0.042	
	Scharbeutz	VIII 78	123		1.0					
	Bockholmwik	X 79	73		1.0					
	Tvärminne	IX 79	40		1.0					
GPT				*97*	*100*	*103*				
	S. Spirito	IV 80	52	0.010	0.990			0.019	0.020	-0.050
	Scharbeutz	X 80	82	0.018	0.604	0.378		0.402	0.492	-0.183
	Bockholmwik	V 80	39	0.026	0.705	0.269		0.436	0.430	+0.014
	Hejlsminde	V 79	75	0.047	0.587	0.367		0.413	0.519	-0.204
	Vellerup	XI 79	53	0.038	0.642	0.321		0.415	0.483	-0.141
	Tvärminne	IX 79	46	0.065	0.609	0.326		0.478	0.519	-0.079
G3PD				*100*	*110*					
	Lido	IX 77	66	0.636	0.364			0.333	0.463	-0.281
		III 78	150	0.577	0.423			0.407	0.489	-0.168
		VI 78	120	0.575	0.425			0.533	0.489	+0.090
		IX 78	166	0.569	0.431			0.524	0.491	+0.067
	S. Spirito	III 78	86	0.640	0.361			0.558	0.461	+0.210
		V 78	141	0.606	0.394			0.475	0.477	-0.004
		IX 78	133	0.609	0.391			0.511	0.476	+0.074
		II 79	147	0.592	0.408			0.476	0.483	-0.014
		V 79	159	0.632	0.368			0.409	0.465	-0.120
	Scharbeutz	VIII 78	47	1.0						

Table 3. (Continued)

Locus	Sites	Date	N	Allele frequencies						H_o	H_e	D
ME				*95*	*100*							
	Lido	VI 78	170	0.279	0.721					0.347	0.403	-0.139
		IX 78	178	0.272	0.728					0.388	0.397	-0.023
	S. Spirito	V 78	134	0.254	0.746					0.343	0.379	-0.095
		IX 78	139	0.277	0.723					0.353	0.401	-0.120
		II 79	147	0.235	0.765					0.306	0.359	-0.148
		V 79	165	0.288	0.712					0.430	0.410	-0.049
	Scharbeutz	VIII 78	79		1.0							
	Vellerup	XI 79	43		1.0							
MPI				*88*	*91*	*94*	*97*	*100*	*103*			
	S. Spirito	IV 80	52	0.010	0.019	0.096	0.269	0.481	0.125	0.596	0.671	-0.112
	Scharbeutz	X 80	90		0.011	0.028	0.356	0.578	0.028	0.444	0.537	-0.173
	Bockholmwik	V 80	76			0.040	0.243	0.691	0.026	0.434	0.461	-0.059
	Hejlsminde	V 79	26			0.135	0.289	0.558	0.019	0.462	0.587	-0.213
	Vellerup	XI 79	94		0.005	0.037	0.282	0.654	0.021	0.404	0.491	-0.177
	Tvärminne	IX 79	40			0.100	0.300	0.500	0.100	0.575	0.640	-0.102
6PGD				*90*	*95*	*100*	*105*					
	Lido	IX 77	99	0.020		0.955	0.025			0.091	0.088	+0.034
		III 78	196	0.005	0.018	0.957	0.020			0.087	0.084	+0.036
		VI 78	177	0.028	0.006	0.938	0.028			0.107	0.119	-0.101
		IX 78	180	0.019	0.025	0.928	0.028			0.139	0.138	+0.007
	S. Spirito	III 78	121	0.025	0.008	0.938	0.029			0.107	0.119	-0.101
		V 78	159	0.038		0.937	0.025			0.126	0.120	+0.050
		IX 78	178	0.011	0.011	0.955	0.023			0.090	0.087	+0.034
		II 79	160	0.028	0.013	0.922	0.038			0.156	0.150	+0.040
		V 79	163	0.022	0.003	0.954	0.022			0.092	0.089	+0.034
	Scharbeutz	VIII 78	121			1.0						
	Bockholmwik	X 79	44			1.0						
PGM				*88*	*92*	*96*	*100*	*104*	*108*			
	Lido	IX 77	98	0.015	0.056	0.321	0.475	0.128	0.005	0.684	0.652	+0.049
		III 78	196	0.008	0.084	0.339	0.452	0.112	0.005	0.561	0.661	-0.151
		VI 78	177	0.011	0.088	0.325	0.466	0.107	0.003	0.672	0.658	+0.021
		IX 78	180	0.014	0.103	0.322	0.453	0.097	0.011	0.689	0.671	+0.027
	S. Spirito	III 78	120	0.021	0.088	0.292	0.483	0.113	0.004	0.700	0.661	+0.059
		V 78	159	0.013	0.076	0.318	0.415	0.160	0.019	0.667	0.695	-0.040
		IX 78	180	0.003	0.089	0.292	0.497	0.108	0.011	0.739	0.648	+0.140
		II 79	160	0.016	0.094	0.291	0.503	0.094	0.003	0.625	0.645	-0.031
		V 79	164	0.012	0.082	0.335	0.488	0.079	0.003	0.567	0.637	-0.110
	Scharbeutz	VIII 78	86	0.035	0.058	0.302	0.424	0.174	0.006	0.581	0.694	-0.163
	Bockholmwik	X 79	88	0.011	0.085	0.244	0.352	0.261	0.046	0.750	0.739	+0.015
	Hejlsminde	V 79	26	0.019	0.019	0.250	0.442	0.212	0.058	0.539	0.693	-0.222
	Vellerup	XI 79	58		0.112	0.293	0.362	0.216	0.017	0.621	0.724	-0.142
PGI				*92*	*96*	*100*	*104*	*108*				
	Lido	III 78	97		0.041	0.933	0.026			0.134	0.127	+0.055
		VI 78	177	0.003	0.005	0.986	0.006			0.028	0.028	
		IX 78	180	0.003	0.014	0.964	0.011	0.008		0.072	0.071	+0.014
	S. Spirito	III 78	58		0.026	0.939	0.026	0.009		0.085	0.115	-0.261
		V 78	160	0.006	0.022	0.963	0.009			0.063	0.073	-0.137
		IX 78	140	0.021	0.004	0.957	0.011	0.007		0.086	0.084	+0.024
		II 79	160		0.022	0.959	0.013	0.006		0.081	0.079	+0.025
		V 79	166	0.006	0.015	0.967	0.009	0.003		0.054	0.065	-0.169
	Scharbeutz	VIII 78	160		0.044	0.953	0.003			0.094	0.090	+0.044
	Bockholmwik	X 79	163		0.049	0.945	0.006			0.098	0.105	-0.067
	Hejlsminde	V 79	113		0.053	0.934	0.013			0.115	0.125	-0.080
	Vellerup	XI 79	101		0.064	0.916	0.020			0.168	0.156	+0.077
	Tvärminne	IX 79	86		0.052	0.901	0.035	0.006		0.198	0.184	+0.076

populations examined were monomorphic at this particular locus.

Glutamate oxalacelate transaminase

Two zones of enzyme activity which are apparently determined by two gene loci were noted for GOT. One zone of extremely low anodal mobility was not scorable and is not considered here. The more anodally migrating zone of GOT activity exhibited a rather low level of allelic variation in both Adriatic populations. Three alleles were observed in specimens from S. Spirito and two in individuals from Lido, whereas Baltic populations were strictly monomorphic.

Gluconate pyruvate transaminase

One locus segregating for 3 alleles was demonstrated for GPT. Nearly all individuals from S. Spirito were homozygous at this particular locus. However, all Baltic populations studied were polymorphic. Low frequencies were noted for the slowly migrating allele (GPT^{97}) and moderate frequencies for the fast migrating allele (GPT^{103}).

Glycerol-3-phosphate dehydrogenase

Two common electrophoretic variants were observed at the *G3PD* locus. The slower migrating allele ($G3PD^{100}$) was common in both Adriatic populations. By contrast, the Baltic population from Scharbeutz is monomorphic for the slow allele.

Malate dehydrogenase

Two MDH systems were scored as monomorphic for both subspecies; MDH-2, which migrates only a short distance anodally from the origin, can be clearly distinguished from the faster migrating MDH-1. The former is probably of mitochondrial and the latter of cytoplasmic origin.

Malic enzyme

The levels of allelic variation as well as the electrophoretic pattern of ME are similar to those stated for G3PD. The fast allele is the more common in both Adriatic populations, whilst it is fixed in the Scharbeutz population.

Mannose-6-phosphate isomerase

MPI is encoded by six alleles. The differences observed between the S. Spirito and the Baltic populations are slight and only expressed by a relatively higher frequency of one allele (MPI^{88}). Compared with each other, Baltic samples show similar allelic diversity.

6-Phosphogluconate dehydrogenase

Four alleles were observed at the *6PGD* locus. Three of these electromorphs were present at fairly low frequencies in the two Adriatic populations. In the Baltic population from Scharbeutz, however, the most common allele is fixed.

Phosphoglucose isomerase

PGI was scored as polymorphic in all populations studied. Five alleles were observed in the subspecies *basteri* and four alleles in the subspecies *balthica*. The frequencies of the three most common alleles were similar in all samples examined.

Phosphoglucomutase

Six alleles were distinguished at the *PGM* locus in all populations studied. An overall similarity in allelic diversity can be seen at this particular locus, when both subspecies are compared. Levels of heterozygosity are extraordinarily high in all samples investigated.

Pyruvate kinase

Comparable to MDH, PK was scored as monomorphic for samples from both S. Spirito and Scharbeutz.

From the observed banding pattern a monomeric enzyme structure is indicated for APK, GPT, MPI and PGM and a dimeric structure for GOT, G6PD and PGI. A more complex structure is suggested for G3PD and ME.

The data presented above indicate that pronounced differences exist between Adriatic and Baltic populations in allelic compositions at the *G3PD, GPT* and *ME* loci. Significant differences ($P < 0.05$) in allelic compositions were also found at the *MPI, 6PGD, PGI* and *PGM* loci, when populations from S. Spirito (pooled data) and Scharbeutz were compared. As inferred from the 12 loci scored, 5 (8)* are polymorphic in *I. b. basteri* and 4 (4)* in *I. b. baltica*. For both subspecies the average number of alleles per locus was estimated, based on

* Loci were considered monomorphic when the frequency of the most common allele was ≥ 0.95 (numbers given in brackets are for ≥ 0.99).

data obtained from all populations studied (see Table 3). It amounts to 3.00 ± 1.86 (Adriatic populations) versus 2.17 ± 1.85 (Baltic populations).

Further measures of genetic variation were obtained by comparing the population from S. Spirito in the Lagoon of Venice with the Scharbeutz population from the Baltic Sea. The samples collected at both sites share the highest number of loci scored. For the computations, pooled data were used from samples taken repeatedly. Mean heterozygosity ($\overline{H}$) was calculated from observed and expected heterozygote proportions in each population assuming Hardy-Weinberg equilibrium. The respective values and their standard errors are: for the S. Spirito population $\overline{H}_o = 0.197 \pm 0.073$ ($\overline{H}_e = 0.205 \pm 0.077$) and for the Scharbeutz population $\overline{H}_o = 0.127 \pm 0.062$ ($\overline{H}_e = 0.151 \pm 0.075$). Thus, from these samples, *I. b. basteri* is more polymorphic and more heterozygous than *I. b. baltica* although the differences are not statistically significant. However, this conclusion must be considered with reservation because of the relatively low number of loci examined.

Further, the two populations were compared by calculating mean genetic identity ($\overline{I}$) and distance ($\overline{D}$) according to Nei (1972). These measures, commonly used to quantify the degree of genetic divergence between populations or taxa, gave $\overline{I} = 0.961$ and $\overline{D} = 0.0398$, respectively. Compared with computations made for several dipterans, these figures are at the level of genetic differences between populations. Subspecific differentiation estimated in the *Drosophila willistoni*-complex (Ayala *et al.*, 1974) gave average genetic identity values below 0.8. In contrast, for the morphologically and behaviourally distinct species *Drosophila silvestris* and *D. heteroneura*, $\overline{I}$ was calculated as 0.94 (Sene & Carson, 1977). To our knowledge, comparable estimates at the subspecific level are not yet available for other crustaceans. However, in the brine shrimp *Artemia franciscana*, although strict systematic differentiation into subspecies is not apparent, a recent electrophoretic study (Abreu-Grobois & Beardmore, 1982) has demonstrated significant genetic differentiation between conspecific populations with mean $\overline{I} = 0.899$ ($\overline{D} = 0.106$) over all populations. We suggest that the data obtained for *Idotea baltica* could underestimate the true biochemical subspecific divergence when taking into further account the differences described above regarding resolution and staining intensity of several enzyme systems.

In the two Adriatic populations a wide degree of interlocality homogeneity of allele frequencies was noted. Likewise, the Baltic Sea populations, obtained from a wider geographic range, exhibit relatively uniform allelic compositions and similar levels of heterozygosity as seen in the polymorphic *GTP, MPI, PGI* and *PGM* loci. Considering all samples studied in both subspecies, patterns of allelic diversity are similar for *MPI, PGI* and *PGM*.

Electrophoretic analysis was performed for several gene-enzyme systems on samples collected during different seasons from S. Spirito and Lido. These data provide evidence of slight temporal variations in allele frequencies and levels of heterozygosity, particularly at the *G3PD* locus. However, no significant differences are revealed when the genic contingency χ^2 test is used to examine heterogeneity of allele frequencies between samples.

In general, genotype frequencies at the polymorphic loci were in agreement with Hardy-Weinberg expectations, although the *MPI* locus and – to some extent – the *GPT* locus exhibit deficiencies of heterozygotes.

So far it has not been possible to find any evident correlation between patterns of colour morphs and genetic structure in terms of specific allozyme variations. A more detailed analysis of samples in which the same animals could be examined for sex, colour and electrophoretic variation is in progress.

Discussion

Phenotypic variation

Various euryhaline isopods, particularly members of the genera *Idotea, Sphaeroma* and *Jaera* represent suitable organisms for investigations on colour polymorphisms and for the identification of the factors acting on natural populations in marine and brackish-water environments. Several studies, concerned with the genetic background of polychromatism, have contributed to an understanding of the ecological significance of this variation (for references, see Gooch, 1975 and Salemaa, 1978, 1979). A detailed analysis of spatial and temporal patterns in relation to abiotic and biotic conditions is therefore required in order to formulate general

interpretations. Nevertheless, attempts to distinguish which evolutionary factors may cause patterns of genetic and phenotypic differentiation within a given species have often provided ambiguous results.

With regard to the distribution of the various colour morphs observed, some differences within the four *Idotea baltica* subspecies have been documented by Tinturier-Hamelin (1963a). As confirmed by this investigation, the phenotype flavafusca was not found in *I. b. basteri.*

From an analysis of numerous *I. b. balthica* populations, inhabiting the northern Baltic Sea, Salemaa (1978) provided evidence for the absence of the phenotypes lineata and pseudolineata in this area. Flavafusca which is similar to albafusca but lacking leucophores could not be clearly distinguished either. In total, northern Baltic populations include four major and six combined colour variants; uniformis was shown to be the most frequent morph, generally followed by albafusca, maculata and bilineata. Salemaa (1978) found extensive local variations in the proportions of the different colour morphs. The highest levels of variation were noted in the frequencies of albafusca and maculata, whilst the proportions of bilineata and of combined phenotypes were relatively stable. As reflected by the predominance of the uniformis variant in marginal populations, phenotype diversity decreases near the distribution limits of *I. b. baltica* at 3.5‰ S. Salemaa's results indicate that phenotype compositions appear to be correlated with the biotic diversity and substrate mosaicisms of littoral habitats: on exposed rocky and stony shores phenotype diversity was lower than in sheltered environments. In addition, the selective values of the phenotypes observed seem to be determined by the camouflage advantages they confer in each micro-habitat on a potential prey to predatory fish.

The four western Baltic Sea populations surveyed show a relatively homogeneous phenotype structure. Obtained from sheltered or moderately exposed habitats on sandy shores, they exhibit considerably more phenotypic variation than the northern Baltic populations for which Salemaa estimated $H' < 1.0$ in general. This correlates with the salinity-dependent species diversity in animal and plant communities which increases towards the western Baltic Sea.

It is interesting to note that samples taken from this area contrast with the phenotypic composition of northern Baltic populations in the presence of the colour morphs lineata (including pseudolineata) and flavafusca found at moderate or low frequencies, respectively. Thus, Baltic populations display remarkable overall phenotypic variation.

Compared with the Adriatic populations surveyed, differences in phenotype structure are expressed particularly by the low morph frequencies of lineata (including pseudolineata), relatively high frequencies of bilineata (including its combinations), and the absence of flavafusca. However, in most cases, phenotypic diversities of the samples from the northern Adriatic are greater than respective estimates made for northern Baltic populations (cf. Salemaa, 1978).

As far as it has been examined in this study, temporal variation of colour polymorphism appears to indicate a fairly stable equilibrium, suggesting a balanced nature of the polychromatism. This corresponds to the findings made by Salemaa (1979a) on the Finnish coast. They demonstrate that the genetic structures of successive generations do not undergo alterations, although seasonal fluctuations of phenotype compositions may occur.

Gene-enzyme variation

The results of the present investigation indicate relatively high levels of genetic variation in *Idotea baltica.* It must be emphasized, however, that the data obtained should be interpreted with caution owing to the relatively small number of loci scored and the absence of formal genetic analysis of the progeny from mated pairs.

Many crustaceans in aquatic habitats exhibit low to moderately low levels of heterozygosity when compared with other invertebrates (cf. Nevo, 1978). This was demonstrated for decapods (e.g. Gooch, 1977; Nemeth & Tracey, 1979; Mulley & Latter, 1980; Nelson & Hedgecock, 1980) and stomatopods (Redfield *et al.,* 1980). Gooch (1977) argued that low genetic variability is a phylogenetic character of decapod crustaceans. In euphausiids a trend in genetic variability from low in high latitudes to high in low latitudes (Ayala & Valentine, 1979) suggests a relationship to trophic resource availability.

To date, respective data from other marine crustacean taxa are scarce. Depending on the environment occupied, various species of the copepods

Tisbe and *Tigriopus* were shown to be polymorphic at ca. 50% (marine forms), 40% (brackish forms) and less than 20% (rock-pool forms) of the loci scored; in the amphipod *Gammarus insensibilis* this proportion amounts to approximately 20% (Battaglia *et al.*, 1978).

A relatively high level of genetic variability was reported from the cavernicole freshwater isopod *Asellus brevicauda,* exhibiting three colour morphs: 9 of 11 loci examined proved to be polymorphic (Steiner *et al.*, 1977). The variability is strongly colour-dependent with fixed differences established at two loci (*α-GPD-1* and *α-GPD-2*), while at a third locus *(PGI)* the difference is almost fixed. However, such allelic variation correlating with colour polymorphism could not be verified for the structural gene loci studied in *I. baltica.* Heterozygosity values similar to those reported for *I. baltica* were estimated by Sbordoni *et al.* (1980) in other aquatic isopods, comprising three cavernicole *Monolistra* and two marine *Sphaeroma* species. On the other hand, from an electrophoretic study of the terrestrial isopod *Armadillidium vulgare,* Beck and Price (1981) reported a low level of heterozygosity comparable to that found in various decapods.

Considering the general picture that emerged from this biochemical genetic analysis, we may conclude that Baltic Sea populations tend to be less polymorphic and less heterozygous than northern Adriatic Sea populations. An overall estimation made by averaging the H′ values from each study area gave the following figures (± standard deviation): northern Adriatic Sea $H' = 1.06 \pm 0.096$; western Baltic Sea, (a) Bay of Lübeck (Scharbeutz) $H' = 1.53 \pm 0.092$ and (b) fjord coast (Bockholmwik, Hejlsminde) $H' = 1.76 \pm 0.057$. The differences between Adriatic and Baltic Sea populations are significant in both cases (t-test: $P < 0.001$).

As far as phenotypic diversity and degree of heterozygosity can be considered comparable measures for characterizing the genetic structure of *Idotea* populations, the difference in genetic diversity assayed between colour genes and genes coding for enzymes is striking. The data obtained do not allow a general interpretation as yet. They may indicate that the forces acting on the two types of genes are different in Adriatic and Baltic Sea populations. At present, however, a precise definition of these forces cannot be given, unless, as an alternative explanation, the electrophoretically demonstrable protein polymorphism is considered selectively neutral (Kimura & Ohta, 1971).

During recent years, several theories have been discussed dealing with the relationship of genetic variability to habitat heterogeneity and to the adaptive strategies of the organisms concerned. Nelson and Hedgecock (1980), for example, have made an approach to correlate polymorphisms of gene-enzyme systems (differentiated into central metabolic, substrate-specific enzymes and less substrate-specific enzymes functioning in peripheral metabolic pathways) with various organismic and environmental characters in a multitude of decapod species. Whether or not the data so far presented on genetic variation in *Idotea* fit into such models cannot be ascertained until broader comparisons including populations from other geographic areas, especially from the Mediterranean and Atlantic have been made. As far as the investigated samples of the two *Idotea* subspecies are concerned, a relationship between the level of polymorphism and environmental structure could not be deduced. Both northern Adriatic populations studied, though living in different habitats, display a widely homogeneous allelic composition. Probably, continuous gene exchange between the two neighbouring locations prevents more marked genetic differentiation.

The present study shows that the extent and pattern of gene-enzyme variation do not exhibit pronounced differences in the Baltic Sea populations surveyed. This finding contrasts with the distribution of colour morphs which displays considerable spatial differences in phenotype compositions between northern and western Baltic populations. In this context, reference must also be made to the observation of Salemaa (1978), indicating an increase of phenotypic diversity in colour from fully exposed to sheltered habitats in the northern Baltic. But one must bear in mind that in this area ambient salinity levels and biotic diversity are very low.

Comparable to the observation made in *I. b. baltica,* a low degree of electrophoretically detectable genetic differentiation was also documented for *Gammarus zaddachi* and *G. salinus* populations obtained from various localities of the Baltic Sea (Bulnheim & Scholl, 1981). The genetic continuity observed is consistent with the relatively constant abiotic conditions prevailing in the Baltic Sea; except for temperature, there are no fluctuating environmental variables in the areas surveyed. Ap-

parently, within the limits of its salinity tolerance, these conditions do not restrict the dispersal of *I. b. baltica* and consequently, interregional mixing. But in view of its rather low propensities for locomotion and the lack of larval dispersal stages, large-scale migrations are not likely to occur. On the other hand, passive transportations by drifting seaweeds and other floating materials to which idoteids frequently are attached may contribute to a gene flow between local populations, at least over limited distances. Presently it is difficult to assess the importance of these factors for the dynamics of the population structure, since experimental studies on this subject are lacking.

From the viewpoint of geological time scales the Baltic is a recent sea. Following the last Ice Age, the Baltic has changed into a freshwater lake twice. Some 7000 years ago, it gradually attained a brackish character (cf. Magaard & Reinheimer, 1974). Subspecific differentiation in northern *I. baltica,* following invasion through the Danish sounds must, therefore, have occurred after this event. Hence, there is reason to believe that gene exchange with Mediterranean idoteids via Atlantic populations must have ceased for a considerable length of time, thus contributing to the subspecific divergence through geographic separation.

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References

Abreu-Grobois, F. A. & Beardmore, J. A., 1982. Genetic differentiation and speciation in the brine shrimp Artemia. In: Mechanism of speciation. Proceedings of a Symposium organised by the Accademia dei Lincei, Rome, 1981. Liss, New York. (In press).

Ayala, F. J., Powell, J. R., Tracey, M. L., Mourão, C. A. & Pérez-Salas, S., 1972. Enzyme variability in the Drosophila willistoni group. IV. Genic variation in natural populations of Drosophila willistoni. Genetics 70: 113–139.

Ayala, F. J., Tracey, M. L., Barr, L. G., McDonald, J. F. & Pérez-Salas, S., 1974. Genetic variation in natural populations of five Drosophila species and the hypothesis of the selective neutrality of protein polymorphisms. Genetics 77: 343–384.

Ayala, F. J. & Valentine, J. W., 1979. Genetic variability in the pelagic environment: A paradox? Ecology 60: 24–29.

Battaglia, B., Bisol, P. M. & Fava, G., 1978. Genetic variability in relation to the environment in some marine invertebrates. In: Marine Organisms. Genetics, ecology and evolution, eds B. Battaglia and J. A. Beardmore. Plenum Press, New York: 53–70.

Beck, M. L. & Price, J. O., 1981. Genetic variation in the terrestrial isopod, Armadillidium vulgare. J. Hered. 72: 15–18.

Brewer, G. J., 1970. An introduction to isozyme technique. Academic Press, London, 186 pp.

Bulnheim, H.-P. & Scholl, A., 1981. Genetic variation between geographic populations of the amphipods Gammarus zaddachi and G. salinus. Mar. Biol. 64: 105–115.

Comaschi, A. & Voltolina, D., 1973. Hydrological data from the surface waters of the lagoon of Venice. Atti Ist. Veneto Sci. 131: 35–58.

Fairbairn, D. J. & Roff, D. A., 1980. Testing genetic models of isozyme variability without breeding data: Can we depend on the χ^2? Can. J. Fish. Aquat. Sci. 37: 1149–1159.

Franco, P., 1962. Condizioni fisiche e chimiche delle acque lagunari nel porto-canale di Malamocco. Arch. Oceanogr. Limnol. 12: 226–255.

Gooch, J. L., 1975. Mechanisms of evolution and population genetics. In: Marine Ecology. 2. Physiological mechanisms. Ed. O. Kinne. Wiley, London, pp. 349–409.

Gooch, J. L., 1977. Allozyme genetics of life cycle stages of brachyurans. Chesapeake Sci. 18: 284–289.

Harris, H. & Hopkinson, D. A., 1976. Handbook of enzyme electrophoresis in human genetics. North-Holland, Amsterdam.

Hedgecock, D., Nelson, K., Shleser, R. A. & Tracey, M. L., 1975. Biochemical genetics of lobsters (Homarus). II. Inheritance of allozymes in H. americanus. J. Heredity 66: 114–118.

Kimura, M. & Otha, T., 1971. Protein polymorphism as a phase of molecular evolution. Nature, Lond. 229: 467–469.

Koehn, R. K., Milkman, R. & Mitton, J. B., 1976. Population genetics of marine pelecypods. IV. Selection, migration and genetic differentiation in the blue mussel Mytilus edulis. Evolution 30: 2–32.

Koepcke, H.-W., 1948. Über das Zeichnungsmuster einiger Idotea-Arten (Isopoda). Zool. Jb. (Physiol.) 61: 413–450.

Legrand, J.-J. & Legrand-Hamelin, E., 1975. Déterminisme de l'intersexualité et de la monogénie chez les Crustacés Isopodes. Pubbl. Staz. Zool. Napoli 39 (Suppl.): 443–461.

Magaard, L. & Reinheimer, G., 1974. Meereskunde der Ostsee. Springer, Berlin, 145 pp.

Mulley, J. C. & Latter, B. D. H., 1980. Genetic variation and evolutionary relationships within a group of thirteen species of penaeid prawns. Evolution 34: 904–916.

Muus, B. J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Medd. Danmarks Fisk. - Hav. (Ny Ser.) 5: 1–316.

Naylor, E., 1955. The ecological distribution of British species of Idotea (Isopoda). J. Anim. Ecol. 24: 255–269.

Nei, M., 1972. Genetic distance between populations. Am. Nat. 106: 283–292.

Nelson, K. & Hedgecock, D., 1980. Enzyme polymorphism and adaptive strategy in the decapod Crustacea. Am. Nat. 116: 238–280.

Nemeth, S. T. & Tracey, M. L., 1979. Allozyme variability and relatedness in six crayfish species. J. Hered. 70: 37–43.

Nevo, E., 1978. Genetic variation in natural populations: Patterns and theory. Theor. Pop. Biol. 13: 121–177.

Peabody, E. B., 1939. Pigmentary responses in the isopod, Idothea. J. exp. Zool. 82: 47–83.

Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1–507.

Redfield, J. A., Hedgecock, D., Nelson, K. & Salini, J. P., 1980. Low heterozygosity in tropical marine crustaceans of Australia and the trophic stability hypothesis. Mar. Biol. Letters 1, 303–313.

Remane, A., 1931. Farbwechsel, Farbrassen und Farbanpassung bei der Meeresassel Idothea tricuspidata. Verh. Deutsch. Zool. Ges.: 109–114.

Salemaa, H., 1978. Geographical variability in the colour polymorphism of Idotea baltica (Isopoda) in the northern Baltic. Hereditas 88: 165–182.

Salemaa, H., 1979a. Seasonal variability in the colour polymorphism of Idotea baltica (Isopoda) in the northern Baltic. Hereditas 90: 51–58.

Salemaa, H., 1979b. Ecology of Idotea spp. (Isopoda) in the northern Baltic. Ophelia 18: 133–150.

Sassaman, C., 1979. Genetics of the malate dehydrogenase isozymes of the isopod Porcellio scaber. J. exp. Zool. 210: 507–513.

Sbordoni, V., Caccone, A., de Matthaeis, E. & Sbordoni, M. C., 1980. Biochemical divergence between cavernicolous and marine Sphaeromidae and the Mediterranean salinity crisis. Experientia 36: 48–49.

Scholl, A., Corzilius, B. & Villwock, W., 1978. Beitrag zur Verwandtschaftsanalyse altweltlicher Zahnkarpfen der Tribus Aphaniini (Pisces, Cyprinodontidae) mit Hilfe elektrophoretischer Untersuchungsmethoden. Z. zool. Syst. Evolutionsforsch. 16: 116–132.

Sene, F. M. & Carson, H. L., 1977. Genetic variation in Hawaiian Drosophila. IV Allozymic similarity between D. silvestris and D. heteroneura from the island of Hawai. Genetics 86: 187–198.

Steiner, W. W. M., Lisowski, E. A. & Osterbur, D., 1977. Biochemical differences in sympatric color morphs of an aquatic isopod (Asellus brevicauda). Comp. Biochem. Physiol. 56 B: 371–374.

Suneson, S., 1947. Colour change and chromatophore activators in Idotea. K. fysiogr. Sällsk. Handl. N. F. 58: 1–34.

Tinturier-Hamelin, E., 1963a. Polychromatisme et détermination génétique du sexe chez l'espèce polytypique Idotea balthica (Pallas) (Isopode valvifère). Cah. Biol. mar. 4: 473–591.

Tinturier-Hamelin, E., 1963b. Définition et analyse génétique du phénotype pseudolineata de l'isopode valvifère Idotea balthica (Pallas). Crustaceana 5: 133–137.

Workman, P. L. & Niswander, J. D., 1970. Population studies on southwestern Indian tribes. II. Local genetic differentiation in the Papago. Am. J. Hum. Genet. 22: 24–49.

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