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Enzymatic and morphometric analyses in mediterranean populations of the rose shrimp, *Aristeus antennatus* (Risso, 1816)

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Abstract

Eleven samples of rose shrimp (*Aristeus antennatus*) from different areas of the Mediterranean Sea and adjacent Atlantic waters were subjected to morphometric and electrophoretic analyses. The object was to characterize possible population differences that would account for previously reported differences in behavioural patterns observed in commercial fishing activity. Genetic analysis of 27 enzyme systems yielded only fifteen useful loci of which fibre had allele variants, but only two of them were polymorphic within 95%. Morphometric analysis of nine body and appendage measurements revealed significant differences between sampling sites in scaphocerite length, uropodal length, and the length of the articles on the third walking leg. The samples analysed genetically could not be differentiated, but morphological differences were compared between different hydrographic regions of the Mediterranean Basin. © 1998 Elsevier Science B.V.

Keywords: Aristeus antennatus; Crustacea; Morphometrics; Genetics; Allozyme; Mediterranean Sea

1. Introduction

Aristeus antennatus (rose shrimp) is an important crustacean resource in the fisheries and ecology of the Mediterranean Sea (Tobar and Sardà, 1987; Cartes and Sardà, 1993; Demestre and Lleonart, 1993; Cartes, 1994). This species ranges from the adjacent Atlantic waters off Morocco and Portugal to Israel at depths between 300 and 2200 m

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(Cartes and Sardà, 1992; Sardà and Cartes, 1993). As a consequence of its broad depth distribution, this species has a highly characteristic and distinctive life history that differs from that of other deep-sea shrimps. Crosnier (1978) and Freitas (1985) also reported this species off Mozambique and eastern South Africa. The first papers dealt with fisheries aspects (Bas, 1960, 1966; Maurin, 1965; Massutí and Daroca, 1978). In the late 1980's several studies were carried out to elucidate spatio–temporal fluctuations in rose shrimp populations (Arrobas and Ribeiro, 1984, 1987; Tobar and Sardà, 1987; Sardà et al., 1994). Various workers have considered the species' general biology (Sardà and Demestre, 1987; Ribeiro, 1988; Demestre and Fortuño, 1992). Recent studies on local fishing grounds have highlighted different aspects of behaviour and population structure (sex ratio, abundance, size range) (Sardà et al., 1994). However, yields for this species vary around the Mediterranean, and the species fluctuate in certain areas at certain times of year (Relini and Orsi Relini, 1987). Furthermore, other results suggest significant differences in the biology of this species in different areas (Sardà, 1987; Bianchini and Ragonese, 1994). These patterns may suggest separate subpopulations or biological stocks, usually defined as self-sustaining subunits of a species, that are more or less reproductively isolated from one another. Functional morphometrics has been studied (Sardà et al., 1995) and has revealed the adaptive effects of certain body parts on the swimming and feeding behaviour of the different size groups and between the sexes, but no other studies on population differentiation have been carried out on the basis of morphometric changes. On the other hand, some biochemical genetic studies have been performed on penaeids (Lester, 1979; Hedgecock et al., 1982; Tam and Chu, 1993) but no electrophoretic data have been reported for the rose shrimp until now. This paper presents the first comparative morphometric and biochemical genetic study on *A. antennatus* in its distribution area in the Mediterranean Sea and the adjacent Atlantic Ocean region.

2. Methods

Samples for morphological and genetic studies were taken from Mediterranean and Atlantic waters (Table 1 and Fig. 1). In addition to samples from trawlers on commercial fishing grounds between 400 and 900 m deep, two samples were collected at depths between 1000 and 1200 m using special Otter Trawl Maireta System (OTMS) gear (Sardà et al., 1994), off Barcelona (D) and Marseille (d). All samples were stored in insulated containers with dry ice after capture and during transportation to the laboratory, where they were stored at -30°C pending analysis. Elapsed time from capture until arrival at the laboratory in no case exceeded 72 h. Because the sex ratio was highly skewed, with a preponderance of females, and because males were not only few in number but also small in size, only females were used in the analyses.

2.1. Morphometry

Nine specific morphometric length measurements were taken with a caliper (± 0.1 mm) in a total of 876 specimens (Table 1 and Fig. 2). The measurements were selected

Table 1
Geographical location of the sampling localities considered and number of individuals used in each type of analysis (–: insufficient data)

Region	Location	Morphological analysis	Genetic analysis
Atlantic	Portugal: Lisbon (P)	54	30
	Morocco: Larache (M)	91	57
Western Mediterranean	Spain:		
	Alicante (A)	90	30
	Barcelona (B)	133	30
	Barcelona (> 1000 m) (D)	48	30
	Palma (Balearic Islands) (C)	67	30
	France:		
	Marseille (F)	125	30
	Marseille (> 1000 m) (d)	–	30
Central Mediterranean	Italy:		
	Rome (R)	98	24
	Mazara (S)	103	46
Eastern Mediterranean	Israel: Haifa (I)	67	53
	Total	876	390

based on their functional role and their importance in the swimming and feeding behaviour (Sardà et al., 1995).

All measurements were standardized to a selected size (25 mm carapace length), previous logarithmic transformation, to avoid allometric effects according the procedure of Lombarte and Lleonart (1993). A data matrix was constructed, where the columns were the different measurements considered and the rows were sample location, and a correspondence analysis was performed (Benzecri, 1980). This made it possible to

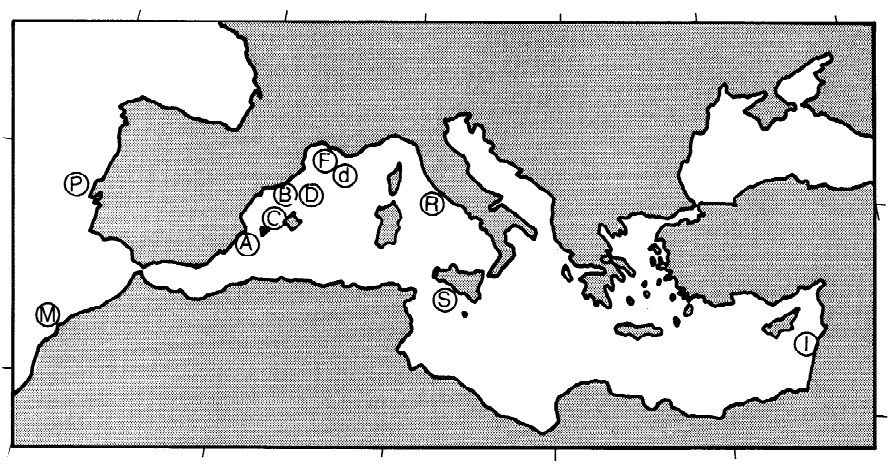

Fig. 1. Map of the Mediterranean Sea showing the sampling locations for *A. antennatus*: P, Lisboa (Portugal); M, Larache (Morocco); A, Alicante; B, Barcelona; D, Barcelona deep sample; C, Palma (Spain); F, Marseille (France); R, Rome; S, Mazara (Italy); I, Haifa (Israel).

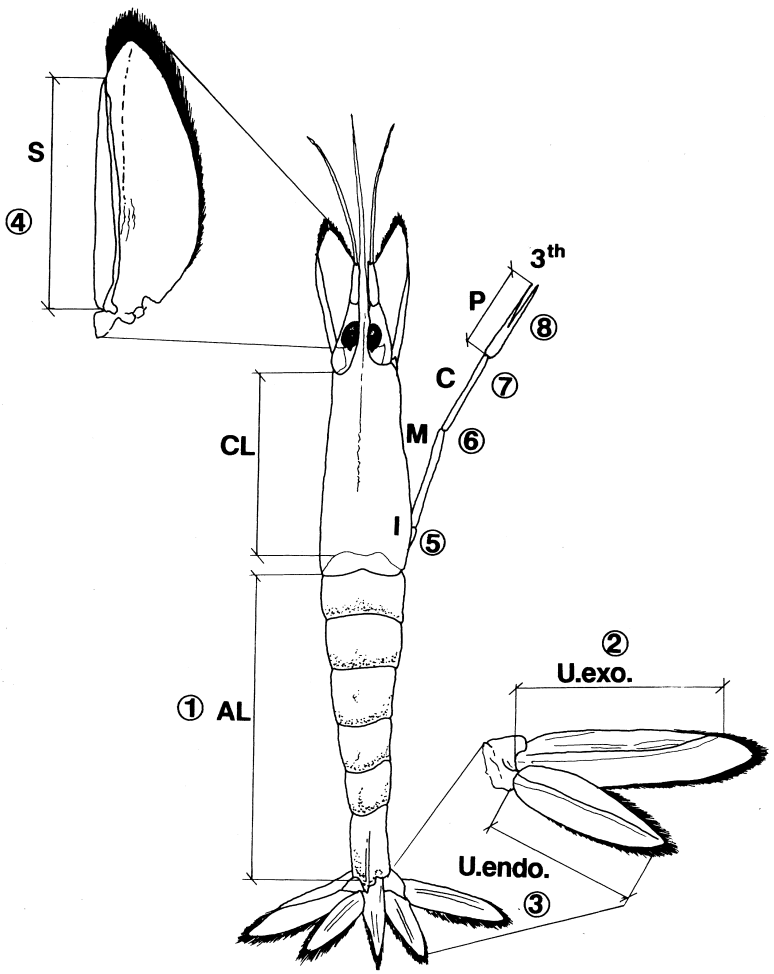

Fig. 2. Morphometric length measurements considered in the analysis: CL, carapace, AL, abdomen (1); U. exo., uropodal exopodite (2); U. endo.; uropodal endopodite (3); S, scaphocerite (4); I, ischium (5); M, merus (6); C, carpus (7); P, propodus (8).

represent the centroids for all the populations and all the length measurements on the same scale. Canonical correlation analysis was carried out as an objective test of the statistical significance of morphometric differences between populations (Cuadras, 1991). Bartlett's test demonstrated the homogeneity of the variance–covariance values. Use of these two forms of multifactorial analysis furnished two types of complementary information that both enabled the morphological length measurements to be associated with the populations considered and yielded a measure of their statistical significance.

Statistical differences of the length measurements in the different samples were tested by comparing the slopes of the regression lines for the data, following log transformation, applying an analysis of variance (ANOVA) to the relationship between each length measurement and carapace length, which was the independent variable. The function

was of the form $y = ax^b$. To simplify presentation of the data and results as much as possible, only the most extreme populations were selected, based on the multifactorial analysis results obtained using the methods described above: Israel (I) for the Eastern Mediterranean Sea, Portugal (P) and Morocco (M) for the Atlantic Ocean, Barcelona (B) and Sicily (S) for the Central Mediterranean Sea, and one of the deep samples (D). Comparison of these samples provided a basis for interpreting relative appendage size in the most distantly separated populations.

2.2. Protein electrophoresis

A total of 390 individuals was collected for electrophoretic analysis, and a few grams of skeletal muscle and the hepatopancreas were analysed. Horizontal starch gel electrophoresis was employed following the general procedure outlined by Aebersold et al. (1989). A total of 27 enzyme systems were assayed. Genetic interpretation of the banding patterns produced by the enzyme systems followed the principles explained by Utter et al. (1987). The genetic nomenclature used follows the proposals by Shaklee et al. (1990). A summary of the enzyme systems analysed in this study and the pertinent nomenclature is set out below: aspartate aminotransferase (AAT) (2.6.1.1); acid phosphatase (ACP) (3.1.3.2); alcohol dehydrogenase (ADH) (1.1.1.19); creatine kinase (CK) (2.7.3.2); diaphorase (DIA) (1.6.4.3); esterase (EST) (3.1.1.-); fumarate hydratase (FH) (4.2.1.2); glutamate dehydrogenase (GLUDH) (1.4.1.2); glyceraldehyde-3-phosphate dehydrogenase (GAPDH) (1.2.1.12); glycerol-3-phosphate dehydrogenase (G3PDH) (1.1.1.8); glucose-6-phosphate isomerase (GPI) (5.3.1.9); β-glucuronidase (βGUS) (3.2.1.31); L-iditol dehydrogenase (IDDH) (1.1.1.14); isocitrate dehydrogenase (IDHP) (1.1.1.42); L-lactate dehydrogenase (LDH) (1.1.1.27); lactoylglutathione lyase (LGL) (4.4.1.5); leucine aminopeptidase (LAP) (3.4.11.1); malate dehydrogenase (MDH) (1.1.1.37); malic enzyme, NAD^+ (MEP) (1.1.1.40); mannose-6-phosphate isomerase (MPI) (5.3.1.8); peptidase-LGG (PEP–LGG) (3.4.-.-); peptidase–LT (PEP-LT) (3.4.-.-); phosphoglucomutase (PGM) (5.4.2.2); phosphogluconate dehydrogenase (PGDH) (1.1.1.44); pyruvate kinase (PK) (2.7.1.40); tyrosine aminotransferase (TAT) (2.6.1.5); xanthine oxidase (XO) (1.2.3.2).

Statistical testing included the exact significance probabilities test (Fisher's exact test) for Hardy–Weinberg equilibrium (BIOSYS-1 computer program, Swofford and Selander, 1981), a contingency chi-square test (BIOSYS-1), Monte Carlo simulation (McElroy et al., 1992) and Fisher's exact test (GENEPOP, Raymond and Rousset, 1995) to measure heterogeneity of allele frequencies among samples. F_{ST} gene diversity analysis and genetic distance (Nei, 1973, 1978) were used to test the genetic structure of the rose shrimp population.

3. Results

3.1. Morphometry

Morphometric separation between Israel (I), Morocco–Portugal (M–P), the deep sample (D), and the rest of the samples [A, B, C, R, and S (see Table 1)] was evaluated

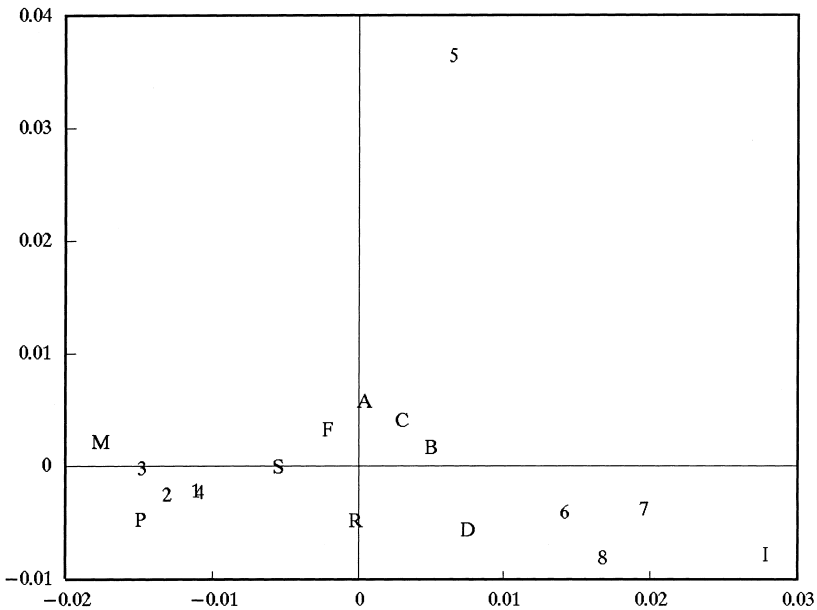

Fig. 3. Relative associations among the centroids of the different samples and length measurements, on the first and second axes from the correspondence analysis. Letters identify different samples: P, Lisboa (Portugal); M, Larache (Morocco); A, Alicante; B, Barcelona; D, Barcelona deep sample; C, Palma (Spain); F, Marseille (France); R, Rome; S, Mazara (Italy); I, Haifa (Israel). Numbers identify different morphometric length measurements: (1) abdomen; (2) uropodal exopodite; (3) uropodal endopodite; (4) scaphocerite; (5) ischium; (6) merus; (7) carpus; (8) propodus.

by means of correspondence analysis (Fig. 3). The first two axes explained 42.05% and 27.32% of the variance. The amount of variance explained by the third axis fell off sharply, to only 9.3%. The first axis accounted for a high percentage of the total variance and was associated with geographical longitude. Body measurements relating to swimming ability (1, 2, 3, and 4, see Table 2 and Fig. 3) were associated with the Atlantic Ocean samples (M and P), while third walking leg length (6, 7, and 8) was associated more closely with the deep sample (D) and Israel (I). Ischium size (5) was located some distance away from the cluster of data points and did not exhibit a clear relationship to any other measurement. This was probably due to the irregular shape of this article, which may have increased measurement error, or this article may present a degree of variance greater than the precision of the measurements. Canonical analysis was used to evaluate significant differences ($F = 24.99$, F-table $= 1.29$; $p < 0.05$, df $=$ 72 and 5232) (Fig. 4).

In Table 2, we compare different samples showing the values of the regression line slopes for those length measurements that were significantly different. In the interest of brevity, only the most widely separated geographic regions according to the results of the multifactorial analyses have been considered, as already explained above. The samples considered were thus the two Central Mediterranean samples (B and S) at different latitudes, the deep sample (D $>$ 1000 m in depth), the Atlantic Ocean samples

Table 2
Slope comparisons of the regression lines from the each morphometric length measurements versus carapace length between selected distant samples, based on ANOVA results

Samples compared	Morphometric measures								
	AL (1)	U.exo. (2)	U.endo. (3)	S (4)	I (5)	M (6)	C (7)	P (8)	N
Atlantic (M) and Central (S) Mediterranean versus Eastern (I) Mediterranean									
I	ns	0.702	ns	0.787	ns	ns	ns	ns	2
S		0.778		0.900					
I	0.681	ns	0.768	0.787	ns	1.015	1.157	1.109	6
M	0.643		0.694	0.739		0.796	1.025	0.765	
S	ns	0.778	0.796	0.900	ns	0.991	1.155	1.035	6
M		0.684	0.694	0.739		0.796	1.025	0.765	
Atlantic (M), Central (S) and Eastern (I) Mediterranean versus Deep (D) sample									
D	ns	ns	0.696	ns	ns	ns	ns	ns	1
I			0.768						
D	ns	0.677	0.696	0.808	ns	ns	ns	ns	3
S		0.778	0.796	0.900					
D	ns	ns	ns	0.808	ns	0.990	1.195	1.019	4
M				0.739		0.796	1.025	0.765	
Western (B) versus Atlantic (M) and Central (S) Mediterranean; Western (B) versus Deep (D) sample									
B	ns	0.747	ns	ns	ns	ns	1.126	ns	2
D		0.677					0.195		
B	0.748	0.747	0.732	0.789	ns	ns	ns	ns	4
S	0.651	0.778	0.796	0.900					
B	0.748	0.747	ns	0.789	ns	0.970	1.126	1.034	6
M	0.643	0.684		0.739		0.796	1.025	0.765	
Atlantic (between samples, P–M)									
P	0.697	0.757	ns	ns	ns	ns	ns	0.895	3
M	0.643	0.684						0.765	
n	4	7	5	7	0	4	6	5	

Numbers are slopes of the regressions with significant differences; ns, non-significant differences between slopes ($p < 0.01$); N: total number of significant differences between populations; n: total number of significant differences between length measurement values (length measurements: AL, abdomen; U. exo., uropodal exopodite; U. endo., uropodal endopodite; S, scaphocerite; I, ischium; M, merus; C, carpus; P, propodus).

(M and P), and the Eastern Mediterranean sample (I). Significant differences were observed for various length measurement values between the samples that were furthest apart longitudinally (I–M: six measurements; S–M: six measurements; and B–M: six measurements; see column N in Table 2). Specimens in the deep sample (D) were most similar to the specimens in the sample from off Israel (I–D: one significantly different length measurement) and to the specimens in the Central Mediterranean samples (B–D:

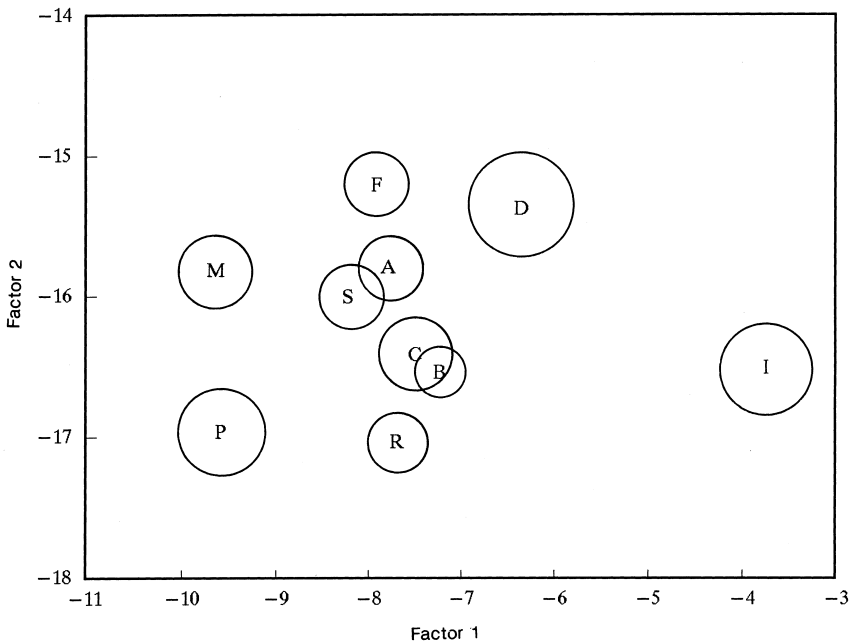

Fig. 4. Canonical analysis, plot of the results. Distance among letters are proportional to morphometrical differences observed. The circle perimeters are proportional to the confidence intervals. Letters identify different samples: P, Lisboa (Portugal); M, Larache (Morocco); A, Alicante; B, Barcelona; D, Barcelona deep sample; C, Palma (Spain); F, Marseille (France); R, Rome; S, Mazara (Italy); I, Haifa (Israel).

two significantly different length measurements; D–S: three significantly different length measurements). The Atlantic Ocean samples were also close (M–P: three significantly different length measurements).

Analysis of the slopes (b) of the regression lines for the different length measurements on carapace length (Table 2) showed that article lengths on the third walking leg were relatively larger in the Eastern Mediterranean population (I), particularly the pincer-shaped propodus ($b_{\mathrm{Pr}} = 1.109$) as compared to the Atlantic Ocean specimens (M: $b_{\mathrm{Pr}} = 0.765$). The specimens in sample M presented the smallest measurement values for third walking leg articles.

Turning to the swimming appendages (scaphocerite and uropodal endopodite and exopodite), the Central Mediterranean samples (B–S) presented significantly longer lengths ($b > 0.7$), while the Atlantic Ocean samples again exhibited the smallest lengths (P–M: $b < 0.7$). Comparison of all the aforesaid geographical populations with the deep sample indicated that the length measurement values for the deep-sea specimens were quite similar to those for the specimens in both samples I and S. On the whole, the measurement values tended to be intermediate between those of samples I and S, with few significant differences. Fig. 5 sets out a schematic representation of the significant

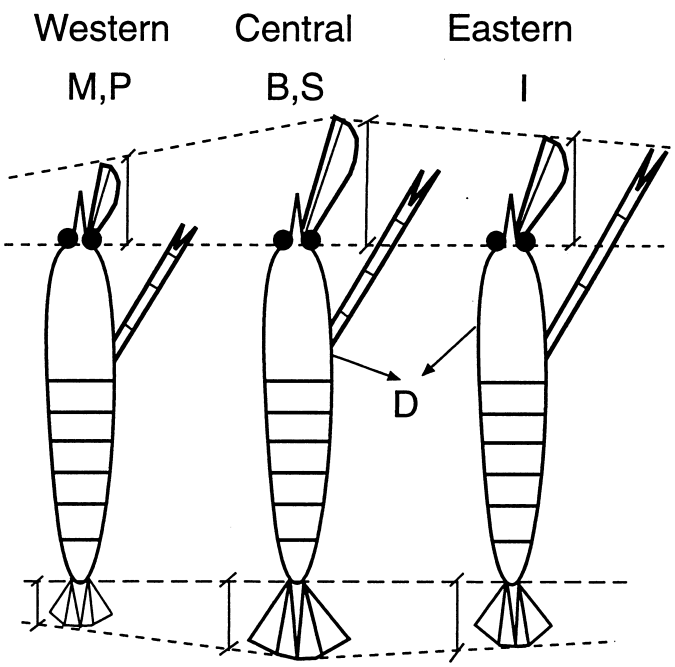

Fig. 5. Conceptual diagram of morphometric differences between *A. antennatus* samples (proportions not drawn to scale).

differences recorded for the morphometric analysis for a better conceptual understanding of the results.

3.2. Protein electrophoresis

Despite the high electrophoretic effort applied to the 27 enzyme systems, only fifteen loci useful in the population survey were identified. Ten of these fifteen loci were monomorphic, and the remaining five loci exhibited some allele variants (*GPI**, *IDHP**, *MDH-1**, *MDH-2**, and *PGM**) (Table 3). Two of these five loci (*GPI** and *PGM**) were polymorphic within 95% confidence limits. Fisher's exact tests were performed for allele frequencies at the five polymorphic loci. Only one of 35 tests for departure from Hardy Weinberg equilibrium was significant at the 5% level [Barcelona sample (B) for locus *GPI**]. This rejection was interpreted as reflecting the 5% random rejection expected at this level of significance (type I error) rather than as being biologically relevant.

The proportion of polymorphic loci (*P*, 95%) for the species ranged from 0.133 to 0.200, and expected heterozygosity ranged from 0.043 to 0.066. The three tests for heterogeneity of allele frequencies conducted, on the five polymorphic loci in all the

Table 3
Allele frequencies of the five polimorphic loci in all samples of *A. antennatus*

Locus	Samples										
	P	A	B	C	D	F	d	R	S	I	M
*MDH-1**											
N	30	30	30	30	30	30	30	24	46	53	57
*100	1.000	1.000	1.000	1.000	1.000	0.950	0.967	1.000	1.000	1.000	1.000
*120						0.033	0.033				
*180						0.017					
Fisher's test	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
*MDH-2**											
N	30	30	30	30	30	30	30	24	46	53	57
*100	1.000	1.000	1.000	0.983	1.000	1.000	0.967	1.000	0.978	0.981	0.982
*95				0.017			0.033		0.022	0.019	0.018
Fisher's test	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
*GPI**											
N	30	30	30	30	30	30	30	24	46	53	55
*100	0.667	0.550	0.633	0.600	0.500	0.517	0.617	0.583	0.500	0.557	0.536
*90	0.333	0.433	0.367	0.400	0.500	0.483	0.350	0.417	0.500	0.415	0.464
*120		0.017					0.033			0.019	
*70										0.009	
Fisher's test	ns	ns	$p < 0.05$	ns	ns	ns	ns	ns	ns	ns	ns
*PGM**											
N	30	30	30	30	28	29	30	24	46	50	55
*100	0.800	0.733	0.917	0.867	0.929	0.897	0.883	0.917	0.035	0.900	0.900
*95	0.050	0.133	0.017	0.050	0.036	0.086	0.017		0.022	0.020	0.045
*105	0.133	0.133	0.067	0.083	0.036	0.017	0.100	0.083	0.043	0.080	0.055
*80	0.017										
Fisher's test	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
*IDHP-1**											
N	30	30	30	30	29	30	30	24	46	53	57
*100	1.000	0.983	0.983	0.983	0.966	1.000	1.000	1.000	1.000	0.972	0.956
*53		0.017		0.017	0.034					0.009	0.009
*105			0.017							0.019	0.035
Fisher's test	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Fisher's exact test probabilities results to test Hardy–Weinberg equilibrium. *N*, sample size; ns, not statistically significance.

Table 4
Probabilities of contingency analysis of all *A. antennatus* samples at all loci

Locus	Contingency X^2	Fisher's exact test	Monte Carlo simulation
*MDH-1**	0.02489	0.00700[a]	0.0110
*MDH-2**	0.58996	0.77246	0.5900
*GPI**	0.51123	0.66892	0.5500
*PGM**	0.02406	0.03914	0.0090[a]
*IDHP-1**	0.22204	0.40876	0.1900

[a] Significant for Bonferroni procedure.

samples, gave similar results. Heterogeneity was detected at the loci *MDH-1** and *PGM**. When Bonferroni procedure is applied to the five loci, only the *MDH-1** locus remains significant for Fisher's test and *PGM** for the Monte Carlo test. Thus by applying the Bonferroni procedure rather weak evidence exist about genetic differentiation among samples (Table 4). The measures of genetic differentiation were: *D* maximum = 0.002 and $F_{ST} = 0.017$.

4. Discussion

Morphometric differences between several presumably separate populations of *A. antennatus* have been observed over the distribution area for this species, ranging throughout the Mediterranean Sea and into the adjacent waters of the Atlantic Ocean. The multifactorial analyses carried out indicated that geographical longitude was the main factor affecting morphological differentiation between the samples examined in this study. Morphometric differences were recorded for the relative proportions between swimming and walking appendages (abdomen, scaphocerite, uropodal exopodite and endopodite, and third walking leg articles). The scaphocerite, uropodal endopodite, and carpus on the third walking leg exhibited adaptive plasticity and were the main length measurements responsible for the significant differences observed.

The deep sample taken at below 1000 m (D) displayed characteristics relatively similar and intermediate to the Israeli and Central Mediterranean samples. Sardà et al. (1994) reported variations in the real structure (size range, sex ratio, and density) between populations dwelling at depths of less than and more than 1000 m, all year round. It seems plausible to attribute to the relatively higher environmental stability of the deep-sea habitat (ecologically, Gage and Tyler (1991) and oceanographically, Hopkins (1985)), which would exert less pressure on morphological plasticity in the species inhabiting those depths, a intermediate morphological position of deep sea sample D between the morphological characteristics of the Central and Eastern Mediterranean samples. The other shallower samples would be influenced by the different and strongest ecological conditions of the more superficial waters.

On the other hand, Dall et al. (1990) stated that genetic diversity in penaeids appears to be among the lowest of any recorded in animals. The heterozygosity values of from 0.043 to 0.066 in the *A. antennatus* samples obtained in the present study corroborate the low genetic variability already reported in penaeids (Lester, 1979; Nelson and Hedgecock, 1980; Tam and Chu, 1993). In addition, the very low values for F_{ST} and genetic distance provide evidence about no population structure among the samples. Comparison of allele frequencies by contingency tables indicated low levels of differentiation among samples. The most detailed test for heterogeneity of all pairs of population showed that heterogeneities at the loci *MDH-1** and *PGM** are associated with the Marseille (F) and Alicante (A) samples respectively. The life history of this species may account for the very high levels of genetic similarity among the sampling locations. Passive dispersal of individuals might also be a factor in maintaining genetic similarity between the samples (Table 4) so that the genetic analysis of population structure revealed no geographical subdivisions related to the morphometric results. At

this point is necessary to note that other marine species (e.g., hake, mussel and anchovy) exhibit a pattern of intraspecific genetic divergence in the same region of study, suggesting the action of common biogeographic processes (Roldan, 1995; Quesada et al., 1995; Magoulas et al., 1996). However, historical gene exchange in the recent past coupled with large effective population sizes of this species would obscure true divergence.

The morphological differences observed may be attributable to non-genetic growth responses to the differing habitats in the Mediterranean regions considered, arising from the oceanographic conditions and general current flow pattern in the Mediterranean Sea.

The surface structure of the Atlantic Ocean waters is more stable than that of the waters in the Western Mediterranean Basin (Wang et al., 1988; POEM Group, 1992; Özsoy and Ünlüata, 1993), with numerous branches and separate gyres and filaments causing disturbances in the submarine canyons on the middle slope. The Atlantic current is considerably spent by the time it reaches the Eastern region, where its flow takes the form of slow gyres with little turbulence. Logically, this contributes to the oligotrophic conditions prevailing in the Eastern region as compared to the more highly eutrophic Western systems and to the comparatively lower productivity, which declines sharply from the Atlantic Ocean side to the Eastern side.

The greater turbulence and productivity of the Western and Central Mediterranean waters could account for the adaptive trend towards the development of relatively larger swimming appendages (uropodal endopodite and exopodite and scaphocerite) to enhance swimming thrust and balance in the Western and Central Mediterranean populations as opposed to the Atlantic and Eastern Mediterranean populations. The progressive increase in the length of the articles on the third walking leg, in particular the pincer-shaped propodus, from the Atlantic region to the Eastern region would appear to be more closely related to a 'cropper' feeding strategy and to rooting in the substratum in search of food in the less productive, more highly oligotrophic Eastern region. This consideration is based on the findings of studies on the diet (Cartes and Sardà, 1989; Cartes, 1994) and functional morphology (Sardà et al., 1995) of *A. antennatus*.

To conclude, the morphometric analysis presented here provides a basis for postulating that the observed morphological differences in *A. antennatus* are the result of ecophenotypic adaptive morphology by this species in response to different habitats and oceanographic conditions in the Mediterranean Sea and adjacent Atlantic Ocean waters, without a genetic basis. The species' present adaptive capacity appears to be sufficient to keep *A. antennatus* populations stable over time. Based on these findings, additional genetic studies, possibly focusing on more sensitive DNA markers, would appear to be warranted to elucidate further the amount of genetic differentiation between rose shrimp populations.

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