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MORPHOLOGICAL VARIATION AMONG POPULATIONS OF *ATYAEPHYRA DESMARESTII* (MILLET, 1831) (DECAPODA: CARIDEA: ATYIDAE) FROM FRESHWATER HABITATS OF NORTHWESTERN GREECE

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ABSTRACT

Multivariate statistical methods were employed to study the morphological variation of the freshwater shrimp (*Atyaephyra desmarestii*), sampled from four distinct freshwater habitats of northwestern Greece. Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA) were used in order to determine morphometrical differences among the biological categories (males, females and ovigerous females) and sampling sites. Statistical analysis of *A. desmarestii* morphometrical and population data showed that body heights and growth of appendages are correlated to biological category. Females found to have higher values for the measured body heights than males. On the other hand, morphometrical variables related mainly to body lengths such as rostral, telson and pleon lengths, were observed to be correlated to the study sites. Characters related to the swimming capacity, such as telson length, telson width, and pleon lengths, were generally found to have higher values in ovigerous females. Furthermore, among the four ecosystems, certain variables demonstrated higher values in the fluvial ecosystems and lower values in the lacustrine.

KEY WORDS: *Atyaephyra desmarestii*, Atyidae, Decapoda, freshwater habitats, Greece, morphological variation

INTRODUCTION

Atyaephyra desmarestii (Millet, 1831) is the unique representative of the monotypic genus *Atyaephyra* de Brito Capello, 1867. The species is a widespread natant decapod crustacean, whose range extends from the inland waters of Europe to North Africa and the Middle East as far as Iran (Bouvier, 1925; Holthuis, 1961; Karaman, 1972; Kinzelbach and Koster, 1985; Al-Adhub, 1987; Gorgin, 1996; d' Udekem d'Acoz, 1999; Fidalgo and Gerhardt, 2003; Anastasiadou et al., 2004). The first record of the decapod from Greece (Axios River) was made by Bouvier (1913). Holthuis (1961) reported the species from Lake Koronia (as *Atyaephyra desmarestii desmarestii*). Recent sampling, covering a dense station network of the Greek freshwaters, revealed the presence of *A. desmarestii* in the western and northern part of the mainland (Anastasiadou et al., 2004).

Bouvier (1913) discriminated the western from the eastern populations of *A. desmarestii* (*var. occidentalis* and *var. orientalis*, respectively). Following Bouvier (1913), Holthuis (1961), Karaman (1972), and Al-Adhub (1987) described distinct subspecies of *A. desmarestii* from different areas of its geographical distribution. Until recently, four subspecies of *A. desmarestii* have been known (*A. d. desmarestii*, *A. d. orientalis*, *A. d. stankoi*, and *A. d. mesopotamica*). However, the validity of the subspecies of *A. desmarestii* was questioned because of overlap in the currently used key morphological characters (Kinzelbach and Forest, 1985; Gorgin, 1996; Anastasiadou et al., 2004). Based on the hypothesis that "due to the geographical isolation, a complete examination of all morphological features will reveal real differences," Anastasiadou et al. (2006) redescribed the species in detail based on a topotypical French population. From this study, Anastasiadou et al. (2008) redescribe *Atyaephyra rosiana* De Brito Capello, 1867 from Portugal. Future comparative investigations of all morphological characters will reveal the existence of new species of the genus *Atyaephyra* from the different areas of its distribution.

From consideration of ecological and biological strategies, the genus shows a high degree of adaptability in colonizing new habitats (Fidalgo and Gerhardt, 2003) and a significant capacity of long distance migration (van den Brink and van der Velde, 1986). *A. desmarestii* is a phytophilous, eurythermal, and euryaline species, which prefers well oxygenated waters (Fidalgo and Gerhardt, 2003) and rich submerged aquatic vegetation (Fidalgo and Gerhardt, 2003; Anastasiadou et al., 2004). Nonetheless, it can also be found in lentic habitats with slow flowing waters, muddy substrates, and poor aquatic vegetation (Anastasiadou et al., 2005).

Functional morphometrics have been used in studies of natant decapods to compare geographically isolated populations (De Grave and Diaz, 2001; Tzeng, 2004; Tzeng et al., 2001), show intraspecific variation (De Grave, 1999; Kapiris and Thessalou-Legaki, 2001), and analyse the environmental interaction with species populations (Maynou and Sardá, 1997). The present study aims to elucidate potential intraspecific morphological variation, sexual dimorphism, and nuptial morphological changes of northwestern Greek *A. desmarestii* populations by applying morphometry and multivariate methods.

MATERIALS AND METHODS

Study Sites

Four major freshwater ecosystems of northwestern Greece (Figure 1), one lentic and three lotic, were selected for the purposes of the present study. The study sites met the following requirements: 1) either a riverine or

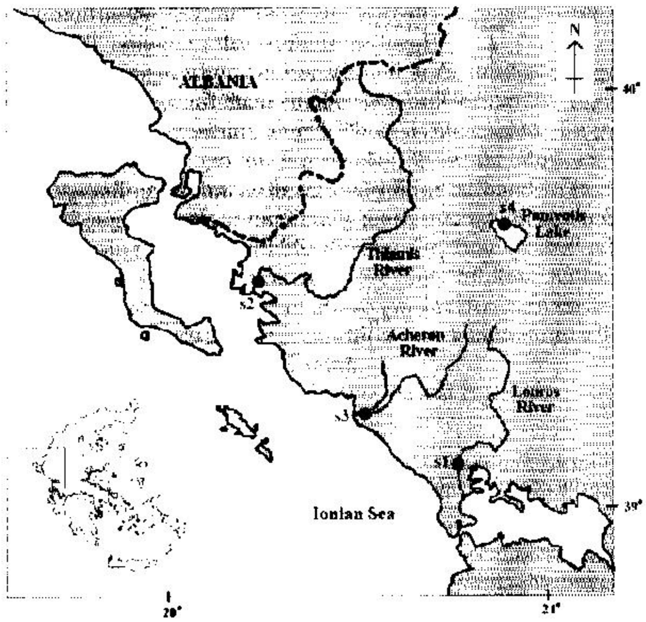

Fig. 1. Map indicating the study sites.

lacustrine profile 2) listed in Natura Special Conservation Areas (Habitats Directive EC, 92/43), and 3) exhibited high densities of *A. desmarestii* populations. The study was carried out to the following sampling sites: (1) s1, the Louros River (39°10′68″N, 20°53′23″E), (2) s2, the Thiamis River (39°33′47″N, 20°12′55″E), (3) s3, the Acheron River (39°13′96″N, 20°29′14″E) and (4) s4, Lake Pamvotis (39°41′48″N, 20°52′71″E) (Fig. 1). The main morphological characteristics, the trophic state, the aquatic vegetation, and the human activities for the four freshwater ecosystems are presented in Table 1.

Shrimp Sampling-Morphological Assessment

Shrimp sampling took place in the lacustrine and fluvial portions of each site, near the aquatic submerged vegetation. The specimens were collected by means of a hand net with a mesh size of 2 mm. The samples were collected during April 2004. The shrimps caught were preserved on site with 4% formalin solution. The sex was identified through stereomicroscopic inspection of the first and second pairs of pleopods. Eight morphometric measurements were made on each specimen (Fig. 2): total length (TL), carapace length (CL), carapace height (CH), rostral length (RL), second pleon segment height (SSH), sixth pleon segment length (SISL), telson length (TEL), and telson width (TEW). The body lengths were measured using digital calipers (± 0.01 mm). In order to study the sexual dimorphism and any nuptial differentiation, the ovigerous females were separated as a discrete biological category from general females. Furthermore, the juveniles were excluded from the morphological assessment, so that the state of maturity or other factors could not influence the observed differences.

Statistics

A total of 657 individuals were measured for this study. Analysis of Variance (ANOVA) (Zar, 1999) was first carried out in order to study the statistically significant differences of the carapace length compared to the other categories. Second, all the measurement values were transformed to $\log_{10}$ for normality. The allometric equation $Y = aX^b$ was used to remove the effect of carapace length (X) variation on characteristic length (Y), in each sample (Tzeng, 2004). All characteristics are standardized according to: $Yi^* = Yi \times (X/Xi)^b$. Where Yi^* is the standardized measurement length of the ith specimen, Yi is the measured length of the ith specimen, Xi is the measured carapace length of the ith specimen, and X is the mean value of the carapace lengths of the examined specimens. Furthermore, Analysis of Variance (ANOVA) was carried out in order to test the statistical significance of each measurement regarding site and biological category.

Table 1. Main morphological characteristics, trophic state, aquatic vegetation, and human activities for the four studied ecosystems. E-H, eutrophic to hypertrophic. [1]in situ observations; [2]according to Dafis et al. (1996); [3]according to Kagalou et al. (2003); [4]according to Kagalou et al. (submitted); [5]according to Romero et al. (2002); [6]according to Zalidis et al. (1994).

	Morphometric characteristics							Human usage and activities					
Ecosystem	Total length (km)[2,6]	Basin area (km²)[2,6]	Altitude (m)[2,6]	Mean flow (m³/sec)[2,6]	Mean depth (m)[1]	Trophic state[3,4]	Aquatic vegetation[2,5]	Urbanisation[1]	Agricultural activities[1,2]	Aquaculture[2]	Fishing[1,2]	Irrigation[1,2]	Dams[2]
Louros River	75	780	0-1400	23.8	2.5	—	*Typha angustifolia, Phragmites australis, Potamogeton* sp., *Myriophyllum* sp.	■	■	■	■	■	■
Thiamis River	115	1747	0-1300	57	2.7	—	*Typha angustifolia, Phragmites australis, Potamogeton* sp., *Polygonum* sp., *Ranunculus* sp.	■	■	■	■	■	■
Acheron River	50	—	0-1600		2	—	*Typha angustifolia, Phragmites australis*	■	■		■	■	
Lake Pamvotis	—	22.8	470	—	4.5	E-H	*Typha angustifolia, Phragmites australis, Nymphoides peltata, Lemna minor, Myriophyllum spicatum, Polygonum amphibium, Ranunculus trichophyllus, Phalaris arundinacea*	■	■		■	■	

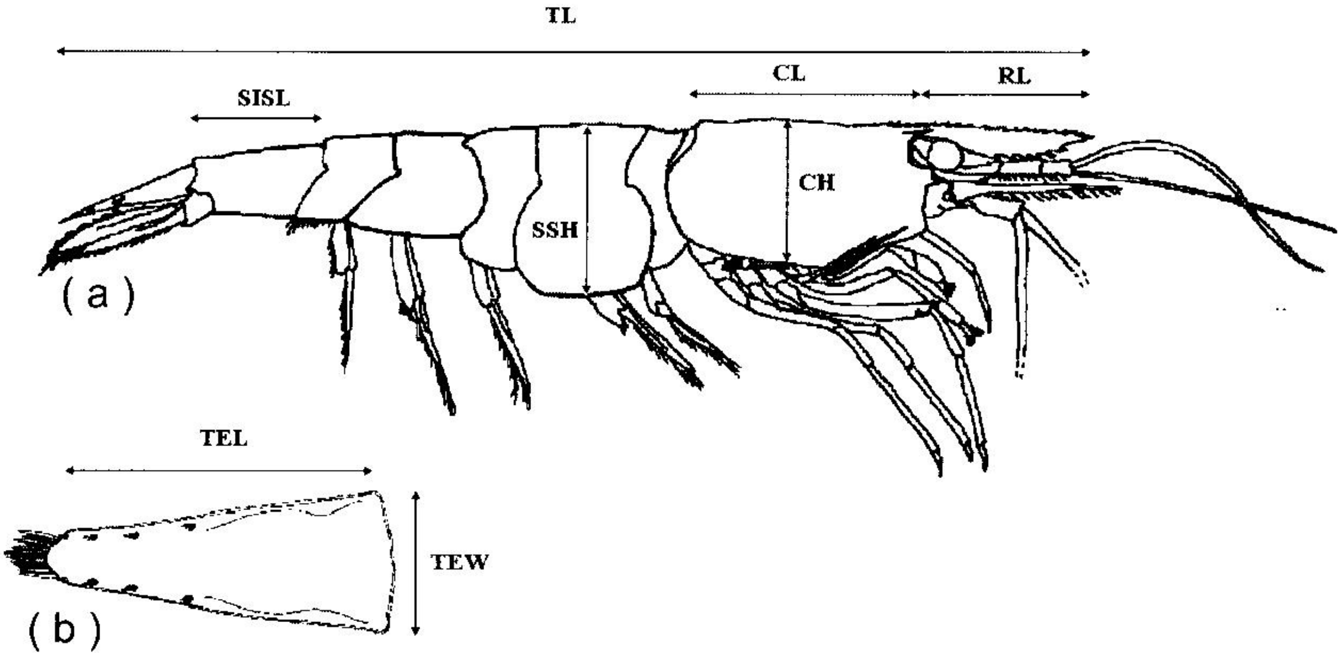

Fig. 2. Morphometric measurements taken on each individual of *Atyaephyra desmarestii*. a, lateral view of the specimen; b, dorsal view of telson. TL: total length, CL: carapace length, CH: carapace height, RL: rostral length, SSH: second pleon segment height, SISL: sixth pleon segment length, TEL: telson length and TEW: telson width.

Multivariate analyses [Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA)], were used to identify morphological differences among the biological categories and sampling sites, both of which are useful in analysing intraspecific variations (Thorpe, 1980). PCA was performed to detect the morphometrical differences among the biological categories and samples and to determine the contribution of each variable to the differentiation. The DFA was used to obtain a function for discriminating the known groups and was made with the stepwise method in which each variable was included in the analysis until the discriminant power was not further improved. The variables with F-value > 1 were considered to contribute to the DFA (Lu and Bernatchez, 1999; Saint-Laurent et al., 2003). A scatter plot of canonical scores in two-dimensional space was used for visual detection of groups. Differences among biological categories and samples were assessed with Wilk's λ and the associated F and P statistics. All statistical analyses were performed by the SPSS software (ver 15.0).

Results

Carapace lengths varied from 3.62 cm to 8.73 cm. Statistically significant differences were found in carapace length among the groups studied ($F = 669.3$; $P < 0.001$), sites ($F = 20.5$; $P < 0.001$), and their interaction ($F = 20.7$; $P < 0.001$). Ovigerous females had larger carapace length (CL = 6.81 ± 0.55) than non-ovigerous females (CL = 6.07 ± 0.79) and males (CL = 4.80 ± 0.48). Moreover, specimens collected from the Louros River had a longer carapace length than specimens collected from the other sites (Table 2). The males and females of the population of the Acheron River showed the lowest values of carapace length.

The two way Analysis of Variance revealed that the observed differences were statistically significant in reference to the biological category ($F = 269.8$; $P < 0.001$), to the sampling site ($F = 114.1$; $P < 0.001$), and their interaction ($F = 19.6$; $P < 0.001$). More specifically, the relative TL demonstrated higher values in males than females. Relative CH was found to have generally higher values in ovigerous females than in males and was also higher in specimens from the Thiamis River (Table 3). Relative RL showed a higher value in specimens from the Thiamis River and lower in the Acheron River. Relative SSH had higher values for ovigerous females in the Louros and Thiamis Rivers, while relative SISL and TEL exhibited higher values for ovigerous females in fluvial habitats (Louros, Thiamis, and Acheron Rivers) and lower values in the lacustrine habitat (Lake Pamvotis) (Table 3).

The PCA, after varimax rotation, extracted two PC factors with eigenvalues > 1, explaining 65.36% of the variance (Table 4). Accordingly, it can be assumed that PC 1

Table 2. Sampling site, sample size, means, standard deviation and ranges of carapace length (CL) (mm) by sex. Males, (M); non-ovigerous females, (F); ovigerous females, (OF); N, number of individulas.

			CL (mm)	
Sampling site	Sex	N	Mean (SD)	Range (Min-Max)
Louros River (s1)	M	48	5.23 (0.36)	4.30-6.03
	F	49	6.16 (0.39)	4.10-8.12
	OF	48	6.93 (0.89)	6.14-7.65
Thiamis River (s2)	M	100	4.81 (0.40)	3.92-5.97
	F	83	6.31 (0.78)	3.81-7.62
	OF	29	6.51 (0.52)	5.63-7.55
Acheron River (s3)	M	50	4.37 (0.49)	3.62-5.66
	F	50	5.38 (0.47)	4.50-7.29
	OF	50	7.07 (0.64)	5.81-8.73
Lake Pamvotis (s4)	M	50	4.79 (0.37)	4.10-5.53
	F	41	6.31 (0.41)	5.59-7.29
	OF	59	6.65 (0.46)	5.78-7.39

Table 3. Means and 95% Coefficient Interval (+/−) for the measured morphological features by site and biological category. M, males; F, non-ovigerous; OF, ovigerous females.

Characters	Sex	Louros River		Thiamis River		Acheron River		Lake Pamvotis	
		Mean	95% CI (+/−)	Mean	95% CI (+/−)	Mean	95% CI (+/−)	Mean	95% CI (+/−)
TL	M	3.41	0.01	3.45	0.01	3.45	0.01	3.45	0.01
	F	3.37	0.01	3.44	0.01	3.42	0.01-0	3.39	0.01-0
	OF	3.35	0.01	3.47	0.02-0.01	3.36	0.01	3.38	0.01
CH	M	2.48	0-0.001	2.51	0	2.49	0.01-0	2.45	0.01
	F	2.50	0.01	2.57	0-0.01	2.52	0.01	2.56	0-0.01
	OF	2.58	0.001-0	2.60	0.01	2.54	0.01	2.58	0.01-0
RL	M	2.63	0.01	2.70	0.01-0	2.59	0.01-0	2.62	0.01
	F	2.62	0.01	2.70	0.01	2.58	0.01	2.65	0.01
	OF	2.68	0.01	2.73	0.02-0.01	2.63	0.01-0	2.67	0.01
SSH	M	2.62	0.01	2.55	0-0.01	2.50	0.02-0.01	2.50	0.02-0.01
	F	2.65	0.01	2.63	0.01	2.57	0.01-0	2.60	0.01
	OF	2.67	0.01	2.73	0.02-0.01	2.64	0.01	2.67	0-0.01
SISL	M	2.48	0.01	2.48	0.01	2.51	0.01	2.49	0.01
	F	2.48	0.01	2.48	0.02-0.01	2.48	0.01	2.48	0.01
	OF	2.55	0.01	2.55	0.01	2.52	0.01-0	2.51	0.01
TEL	M	2.52	0.01	2.54	0.01-0	2.49	0.01	2.53	0.01
	F	2.50	0.01	2.56	0.01-0	2.48	0.01	2.58	0.01-0
	OF	2.58	0.01	2.57	0.02-0.01	2.53	0.01	2.57	0-0.01
TEW	M	1.97	0.01	1.98	0.02-0	1.95	0.01-0.02	1.99	0.01-0.02
	F	1.99	0.02-0	2.02	0.01	1.96	0.01	1.99	0.02-0.01
	OF	2.03	0.01	2.04	0.02	2.05	0.02-0.01	2.03	0.02-0

expressed characters mainly associated with the body heights (carapace height, second pleon height) and secondary with growth of appendages (telson length and width, sixth pleon length). PC II expressed variables exclusively associated with the body lengths, such as total length, telson length, and sixth pleon length. Rostral length is a morphological character that seems to participate to the two extracted factors with approximately the same loading. The PCs plots by sampling site for the different biological categories and the vector plot of the measured variables, for the two PCs are showed in Fig. 3. PC I exhibited higher values in non-ovigerous and ovigerous females, and was lower in males. Among the four distinct ecosystems, PC I showed the highest value in the Thiamis River and the lowest in the Acheron River. PC II in general, exhibited higher values in the male specimens, showing the highest value in the Thiamis River and the lowest in the Acheron River.

The position of group centroids after running the Discriminant Function Analysis is given in Table 5. Summary statistics demonstrated that for the males, the first function counted for 66.3% of the variance, while functions 2 and 3 accounted almost equivalently for 17.5% and 16.2%, respectively. Likewise, for the female specimens the first function accounted for 69.4% of the variance, the second for 19.3%, and the third function only for 11.3%. Finally, for the ovigerous females, first and second functions accounted rather highly for 53.3% and 36.3%, while third function only accounted for an additional 10.4%. The structure matrix for the measured variables (Table 6) revealed that some variables have strong correlation with the first and second discriminant functions. The scatter plots of the DFA scores in relation to the biological category and sampling site are presented in Fig. 4.

Table 4. Factor loadings of Principal Component Analysis (PCA) for each morphometric variable on the two extracted PCA factors after varimax normalized rotation.

Characters	PC I	PC II
Total Length	−0.246	0.888
Carapace Height	0.832	−0.049
Rostral Length	0.615	0.584
Second Somite Height	0.897	−0.102
Sixth Somite Length	0.547	0.389
Telson Length	0.726	0.214
Telson Width	0.677	−0.120

Discussion

The present study attempted to test the hypothesis whether populations of *A. desmarestii* occupying four different freshwater habitats could exhibit morphological differenti-

Table 5. Position of group centroids in Discriminant Function Analysis.

Sampling sites	Function 1	Function 2	Function 3
Males			
Louros R.	0.604	−0.702	1.124
Thiamis R.	1.269	0.392	0.326
Acheron R.	−1.99	0.821	0.351
L. Pamvotis	1.125	0.932	0.779
Non-ovigerous			
Louros R.	−1.783	0.688	−0.974
Thiamis R.	1.943	0.489	0.274
Acheron R.	−1.956	1.063	0.645
L. Pamvotis	0.583	−1.464	0.933
Ovigerous Females			
Louros R.	0.524	−1.987	0.523
Thiamis R.	2.752	1.864	0.520
Acheron R.	2.232	0.882	0.430
L. Pamvotis	0.113	−0.047	1.042

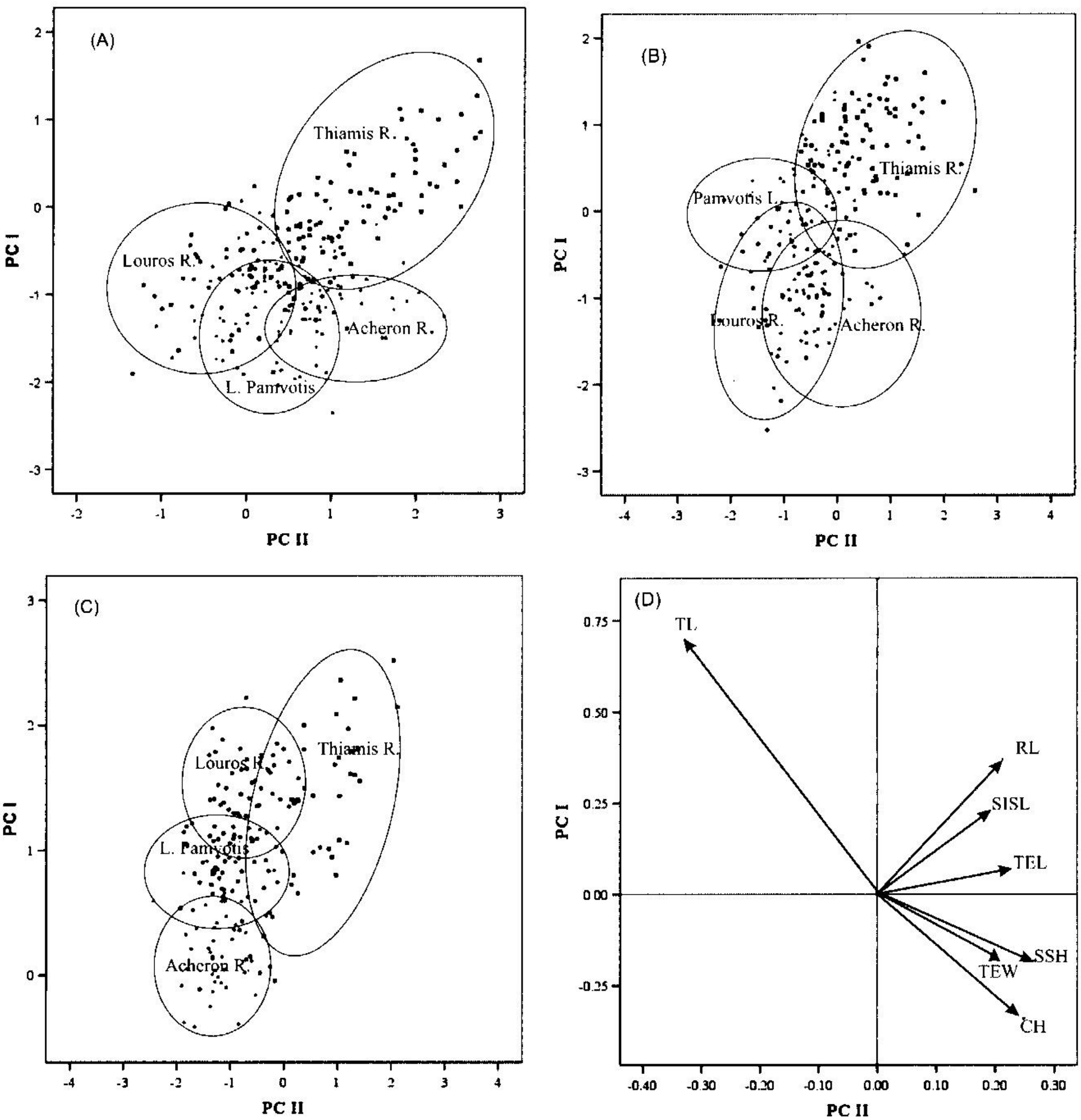

Fig. 3. A, PCs plot by sampling site for male specimens; B, PCs plot by sampling site for female specimens; C, PCs plot by sampling site for ovigerous female specimens; D, the vector plot of the measured variables, for PC I and PC II.

ation. Through minimization of additional variances by means of size standardization and data transformation, the statistical analyses discriminated the four populations of the freshwater shrimp *A. desmarestii*.

First of all, based on sexual dimorphism, non-ovigerous and ovigerous females were found to be larger than males in all studied populations. In previous studies (Bouvier, 1913; Holthuis, 1961; Al-Adhub, 1987; Fidalgo, 1989), it had been reported that females of *Atyaephyra desmarestii* were always larger than males.

Among the studied sites, the largest specimens were found in the Louros River and in Lake Pamvotis (Table 2). According to Tzeng (2004), allometric growth is affected by genetic and/or environmental factors. Since we inspected intraspecific variation, the observed body sizes could be possibly attributed to the environmental factors and especially to the trophic state and the nutrient loadings of the studied ecosystems.

For the standardized morphometric variables, relative body heights, e.g., height of carapace and pleomeres, and

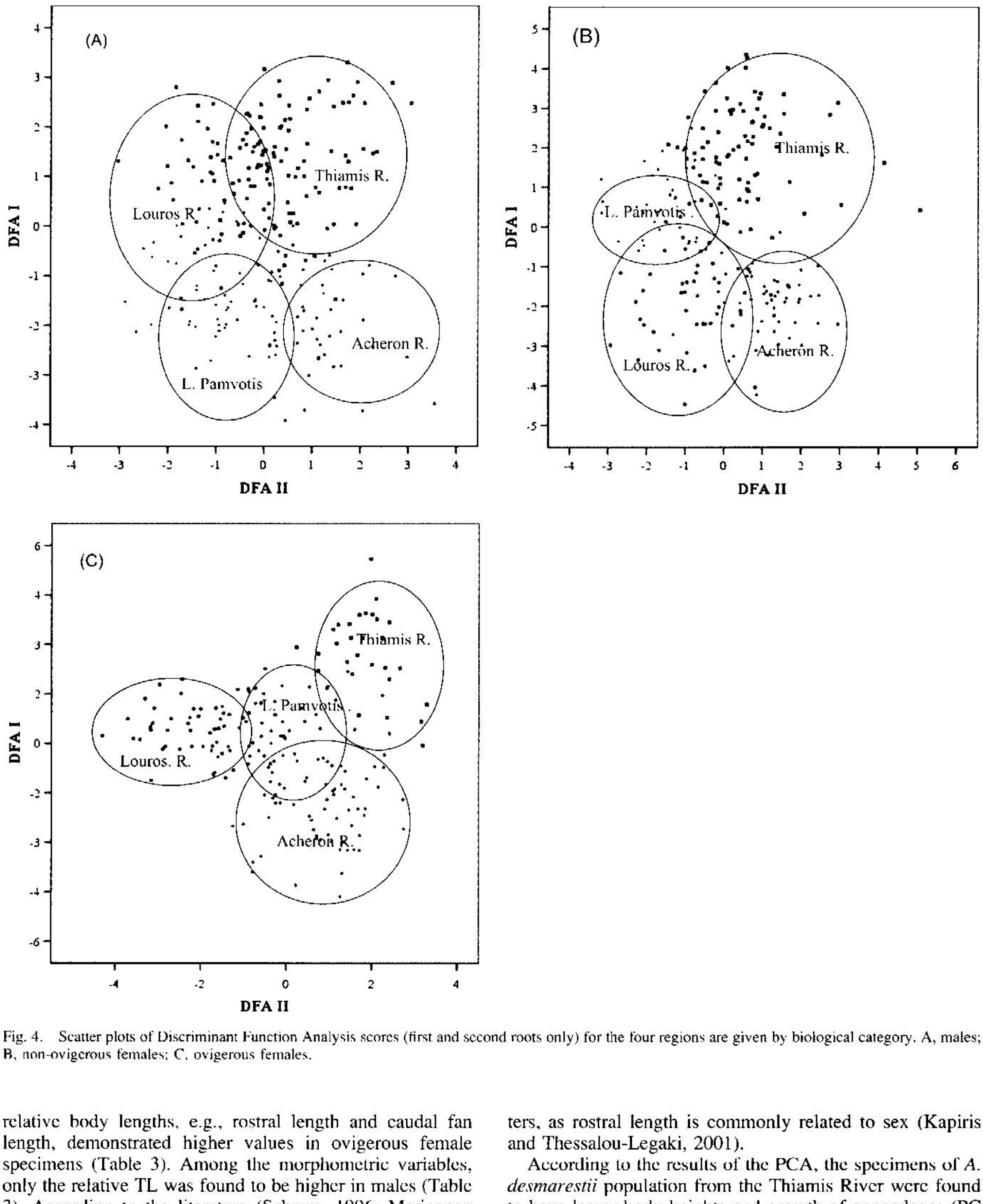

Fig. 4. Scatter plots of Discriminant Function Analysis scores (first and second roots only) for the four regions are given by biological category. A, males; B, non-ovigerous females; C, ovigerous females.

relative body lengths, e.g., rostral length and caudal fan length, demonstrated higher values in ovigerous female specimens (Table 3). Among the morphometric variables, only the relative TL was found to be higher in males (Table 3). According to the literature (Schram, 1996; Mariappan and Balasundaram, 2004), body heights of the natant decapods are related to sex due to the special configurations of the pleon of the female during the reproductive period. Furthermore, the variability of some morphometric characters, as rostral length is commonly related to sex (Kapiris and Thessalou-Legaki, 2001).

According to the results of the PCA, the specimens of *A. desmarestii* population from the Thiamis River were found to have larger body heights and growth of appendages (PC I). On the other hand, relatively higher values for total length and rostral length (PC II) were found in specimens from the Acheron River. Specimens from the Louros River and the Lake Pamvotis demonstrated almost the same values

Table 6. Discriminant Function Analysis on sexes separated. Structure matrix of discriminant loadings. All variables entered simultaneously, largest absolute correlation between each variable and any discriminant function indicated by an asterisk (*).

Characters	Function 1	Function 2	Function 3
Males			
TL	−0.068	0.417	0.578*
CH	0.309	0.633*	−0.189
RL	0.750*	0.273	0.543
SSH	0.536*	0.099	−0.238
SISL	0.029	0.415*	0.165
TEL	0.317	−0.238	0.449*
TEW	0.051	0.295	0.296*
Non-ovigerous Females			
TL	0.333	0.718*	0.175
CH	0.558*	0.065	0.443
RL	0.793*	−0.112	−0.490
SSH	0.602*	0.165	0.218
SISL	0.284*	0.277	−0.210
TEL	0.544*	−0.460	0.315
TEW	0.268	0.013	−0.321*
Ovigerous Females			
TL	0.568	0.669*	0.044
CH	0.448*	0.023	−0.235
RL	0.682*	0.019	0.039
SSH	0.636*	0.339	0.481
SISL	0.636*	−0.339	0.481
TEL	0.368	−0.368	0.380*
TEW	−0.036	0.088	0.238*

for PC I and PC II. This possibly could be attributed possibly to the trophic state of the habitats or to their distinct characteristics. In almost in all studied sites except the Thiamis River, males showed higher values for the relative TL than females. The relative TL reflects the pleon length after its standardization with carapace length. Relative body heights (CH, SSH) and RL showed the lower values in the Acheron River. The observed grouping of these characters may be explained as either special characteristics of the populations of this species, or as characteristics related to certain reproductive profiles.

Morphological characters such as SISL, TEL, and TEW revealed generally higher values in ovigerous females with greater body mass. During the reproductive period the ovigerous females migrate to the lower estuarine parts of the river and are generally vulnerable to predation (Agard, 1999). This sex-related morphometry could be related to the biological strategy of the species. In order to exceed the energetic cost of the reproductive migration and the predation risk, females form a powerful caudal fan (telson length, telson width, sixth pleon length). Such a caudal fan could aid in swimming or rapid escape from predators. Furthermore, the morphometric variables generally were found to have higher values in specimens collected from the fluvial ecosystems (Louros, Thiamis, and Acheron Rivers), where the shrimp must swim.

In reference to DFA, male specimens seem to be discriminated better by the first function, which is related to variables such as rostral length and second pleon height. Non-ovigerous and ovigerous females seem to be discriminated by variables referring to body heights and the growth of the appendages. Both groups of features are correlated to sex (Schram, 1996; Kapiris and Thessalou-Legaki, 2001; Mariappan and Balasundaram, 2004). Among the four ecosystems, the population from the Acheron River shows lower values for DFA I and higher values for DFA II. DFA II could be related to the swimming capacity of the specimens and seems to be more developed in specimens from the Acheron River. Conversely, specimens from the Louros and Thiamis Rivers show higher values to DFA I, which is related to rostral length and carapace height. Compared to the fluvial ecosystems, specimens from Lake Pamvotis show a morphological profile based equally on body lengths and body heights.

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