

# Similar Patterns of Morphological Variation in Two Coastal Crab Species, *Carcinus aestuarii* (Decapoda: Portunidae) and *Pachygrapsus marmoratus* (Decapoda: Grapsidae), across the Biogeographic Transition Zone at The Siculo-Tunisian Strait

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**Abstract:** This study is the first to compare patterns of phenotypic polymorphism among populations of two sympatric species: the green crab *Carcinus aestuarii* and the marbled crab *Pachygrapsus marmoratus* across the Siculo-Tunisian Strait. For this purpose, 396 specimens, collected from nine sites along the Eastern and Western Mediterranean coasts of Tunisia, were examined for morphometric variability of nine morphometric traits for both species. Our results showed analogous dissimilarity patterns among locations as revealed by one-way analysis of similarities (ANOSIM), permutational multivariate analysis of variance (PERMANOVA) and multivariate regression analysis. At the regional scale, the *Hotelling's T-squared* test exhibited similar patterns of morphological differentiation in both species, showing a highly significant difference among Western and Eastern Mediterranean groups of populations for females and males. The similarity percentages analysis (SIMPER) revealed similar discriminative morphometric traits (carapace length and right and left chelae depth) in males of both crab species, accounting for morphological separation among examined locations and groups. The one-way analysis of covariance (ANCOVA) revealed similar trends in variation of these traits across locations in both species. Eastern Mediterranean crabs exhibited longer carapaces and deeper chelae. These results support the tendency that patterns of morphological diversity and polymorphism vary similarly in both crab species and suggest the involvement of several biotic and abiotic factors in shaping such morphological features.

**Key words:** Intertidal crabs, multivariate analyses, environmental heterogeneity, analogous morphometric dissimilarities, Tunisian coast

## Introduction

Species from phylogenetically disparate families, inhabiting common environments and similar niches, sometimes exhibit similarity in particular morphological elements as has been shown for the shells of different bivalve species (WATTERS 1994, CHECA & JIMÉNEZ-JIMÉNEZ 2003). Similar patterns of morphometric variations amongst species inhabiting similar environments at different geographical locations occur frequently when environmental factors exert strong selection pressure on the taxa in those environments, generating

similar phenotypic responses amongst them (LOSOS 1992, LOSOS *et al.* 1998, RÜBER *et al.* 1999, RÜBER & ADAMS 2001, MELVILLE *et al.* 2006, STAYTON 2006). Phenotypic responses in organisms at different spatial and temporal scales involve a wide range of factors, such as interspecific interactions, resource availability, climate and other environmental factors (MICHAUD & ECHTERNACHT 1995, MEIRI 2010).

Environmental heterogeneity across biogeographic barriers is known to yield similar patterns

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of genetic and morphometric variation amongst species inhabiting these areas. Comparative phylogeographical studies have often disclosed concordant patterns across unrelated species (AVISE 1998). Such common patterns are attributed to a shared history of fragmentation in the distribution of species, which causes long-term population subdivision followed by adaptation to specific abiotic features. Mounting evidence come from studies carried out across well-known phylogeographical boundaries such as the Strait of Gibraltar (BORSA *et al.* 1997, PANNACCIULLI *et al.* 1997, NACIRI *et al.* 1999, PEREZ-LOSADA *et al.* 1999, ZANE *et al.* 2000), the well-documented cases of the divide between the Gulf of Mexico and the Western Atlantic Coast (reviewed in AVISE 1994), and the separation between the Indian and the Western Pacific Oceans (WILLIAMS & BENZIE 1998).

The transition zone between the Eastern and Western Mediterranean basins, at the Siculo-Tunisian Strait, is considered as one of the most interesting Mediterranean barriers, and constitutes one of the well-documented biogeographical transitions in the marine environment (see ARNAUD-HAOND *et al.* 2007). The transition zone has been the subject of numerous phylogeographic studies of a wide variety of marine taxa including fish (BAHRI-SFAR *et al.* 2000, MEJRI *et al.* 2009, KAOUËCHE *et al.* 2011), bivalves (NIKULA & VAINOLA 2002, GHARBI *et al.* 2011), shrimps (ZITARI-CHATTI *et al.* 2008, 2009) and crabs (RAGIONIERI & SCHUBART 2013, DELI *et al.* 2014, 2015a, 2015b). While most of these studies have focused on intraspecific genetic polymorphisms, some authors report on pattern of intraspecific morphometric variation (DELI *et al.* 2014, 2015a). No comparative morphometric studies among populations of sympatric species across the region have been carried out so far.

The Tunisian shores, lying across both Mediterranean basins, are considered as excellent location to study comparative biogeographical processes. Indeed, the Tunisian littoral is characterised by habitats of different textures, with muddy and sandy habitats in the Eastern locations (those southward the Siculo-Tunisian Strait) and rocky habitats prevailing in the Western ones (those northward the Siculo-Tunisian Strait; DELI *et al.* pers. obs.). This, together with the notable difference in temperature and salinity among both Mediterranean basins (with the Eastern Mediterranean basin being warmer and more saline than the Western basin; SERENA 2005), could promote similar phenotypic response in marine invertebrate populations and, therefore, yield similar patterns of morphological diversity and polymorphism.

In this study, we aim to compare patterns of phenotypic polymorphism among populations of two sympatric species: the green crab *Carcinus aestuarii* (Nardo, 1847) and the marbled crab *Pachygrapsus marmoratus* (Fabricius, 1787). The two coastal crab species are widely distributed in the Mediterranean Sea (INGLE 1980, MORI *et al.* 1990, KOÇAK *et al.* 2011) and play an important role in structuring intertidal communities (BEHRENS YAMADA & HAUCK 2001, CANNICCI *et al.* 2002, CARLTON & COHEN 2003). They are very abundant across the Tunisian coast and occupy similar ecological niches. Previous studies showed a remarkable morphological differentiation among populations of each species analysed separately (DELI *et al.* 2014, 2015a). Furthermore, results of both studies suggest the existence of a striking similarity in pattern of variability between *C. aestuarii* and *P. marmoratus*. Both crab species exhibited similar biogeographic patterns across the Siculo-Tunisian Strait, with the existence of three morpho-groups that could be assigned to the two biogeographically different regions of the Western and Eastern Mediterranean basins. Accordingly, these interesting findings urged us to carry out a detailed examination of patterns of phenotypic polymorphism variation in populations of both species from similar sampling sites in order to seek for a possible interaction between species and sampling location. Thereby, we address the question whether specimens' morphology of the two species from the same sampling site and region varies in the same way under the impact of similar environmental conditions.

## Material and Methods

### Sample collection and morphometric measurements

Nine morphological measurements were used for the morphometric analyses in two crab species (*C. aestuarii* and *P. marmoratus*): carapace width (CW), carapace length (CL), carapace height (CH), right chela depth (RCHD), left chela depth (LCHD), right chela width (RCHW), left chela width (LCHW), propodus length (PL) and largest abdominal width (LABW). These characters were measured using vernier calipers to the nearest 0.01 mm. The width, length and height of the carapace were measured at the widest, longest, and deepest points respectively. Similarly, chela depth and width were measured at the deepest and widest points. Adult specimens of *C. aestuarii* (CW > 3 cm) and *P. marmoratus* (CW > 2 cm) were collected from nine sites in the littoral fringe off the Tunisian coast (Table 1). For com-

**Table 1.** Sampling information on the studied crab species *Carcinus aestuarii* and *Pachygrapsus marmoratus*, including regions, collection sites, geographic coordinates and the number of female and male specimens examined

Region	Collection site	Geographic coordinates	Number of examined specimens			
			<i>C. aestuarii</i>		<i>P. marmoratus</i>	
			Females	Males	Females	Males
Western Mediterranean	Tabarka	36°57'N 08°45'E	11	11	11	11
	Bizerte	37°16'N 09°52'E	11	11	11	11
	Korbos	36°46'N 10°32'E	11	11	11	11
	Kelibia	36°51'N 11°05'E	11	11	11	11
	Benikhiar	36°28'N 10°46'E	11	11	11	11
Eastern Mediterranean	Monastir	36°10'N 10°49'E	11	11	11	11
	Chebba	35°14'N 11°07'E	11	11	11	11
	Sfax	34°44'N 10°45'E	11	11	11	11
	Medenine	33°52'N 10°51'E	11	11	11	11

parison purposes, an equal number of specimens (11 males and 11 females) per location were examined for each crab species (Table 1).

**Statistical analyses**

Sexual dimorphism in morphological characters was tested prior to data analysis in order to decide whether to consider sex of specimens as an independent factor in the analysis. Multidimensional analyses based on permutation tests were performed to compare sex differences within and between the studied locations using the software PERMANOVA V.1.6 (ANDERSON 2005). As previous studies (based on our own analyses or inferred from earlier literature data) showed clearly the existence of sexual dimorphism in *C. aestuarii* (KOÇAK *et al.* 2011, DELI *et al.* 2014) and *P. marmoratus* (DELI *et al.* 2015a), female and male crabs were considered independently for statistical analyses in the present study.

Patterns of morphometric relationships can be influenced by the effect of allometric growth and size in species of undetermined age. Regressions, performed within the nine studied locations for the examined measurement of body dimensions (CL, CH, RCHD, LCHD, RCHW, LCHW, PRL, LABW) versus the carapace width (CW), used as an independent variable and considered as adjusted trait values (REIST 1985, DEBUSE *et al.* 2001), showed a positive and consistent allometry of each measured trait among populations, separately for females and males. Therefore, the effect of maximum carapace width ( $X$ ) variation on each measured trait ( $Y$ ) within each location was removed by using the allometric equation  $Y = aX^b$ . All measured traits were standardised using the equation:  $Y_i = Y_i (X_m / X_i)^b$  where  $Y_i$  is

the standardised measurement from the measured trait  $Y_i$  of the  $i^{th}$  specimen,  $X_m$  is the mean value of maximum carapace width for the examined location,  $X_i$  is the measured maximum carapace width of the  $i^{th}$  specimen and  $b$  is the standardising parameter obtained from the allometric equation (ANASTASIADOU & LEONARDOS 2008). Standardised values were then plotted against carapace width and arc-sinus/tangent-transformed to achieve normality, before being processed using multivariate analyses (CW was not considered since it was used to adjust all the remaining parameters).

The pattern of morphometric dissimilarities among locations for both crab species was assessed using non-parametric tests (one-way Analysis of Similarities, ANOSIM), implemented in the PAST software, V.2.17 (HAMMER *et al.* 2001), based on the Bray-Curtis distance (CLARKE 1993, ANDERSON 2001). The distances were converted to ranks. In a rough analogy with ANOVA, the test statistic  $R$  is based on comparing distances between groups with distances within groups. Large positive  $R$  (up to 1) signified dissimilarity between groups. The one-tailed significance was computed by permutation of group membership, with 9999 replicates. To assess the interaction between inter-location phenotypic polymorphism and the studied crab species for females and males, we used permutational multivariate analysis of variance (PERMANOVA), as implemented in the PERMANOVA software (ANDERSON 2005). The analysis was based on eight morphometric parameters, common to both surveyed species and carried out with the following design: the factor location was analysed as crossed fixed factor with nine levels

(Tabarka, Bizerte, Korbos, Kelibia, Benikhiar, Monastir, Chebba, Sfax, Medenine), while the factor species was analysed as crossed fixed factor with two levels (*C. aestuarii* et *P. marmoratus*). Pairwise comparisons of phenotypic polymorphism, between all pairs of locations, between the two sympatric crab species were done using PERMANOVA. These analyses were based on Bray-Curtis dissimilarities. Level of significance ( $P$ ) was inferred from permutation procedure. The number of used permutations was 9999.

In order to test for significant correlation between phenotypic polymorphism of both species and whether pattern of morphological differentiation varies similarly in the two crab species, the relationship between average dissimilarities (based on Bray-Curtis dissimilarities) among locations of *C. aestuarii* and those detected among *P. marmoratus* was assessed using the Linear, one independent, n dependent (multivariate regression) model, implemented in PAST. This model can fit each dependent variable separately to the independent variable using simple linear regression. We considered the dataset obtained for the green crab as an independent variable and the corresponding one for the marbled crab as a dependent variable. The “adjusted” correlation coefficient  $R^2$  associated with an overall MANOVA test of multivariate regression significance were provided. Variables, responsible for the eventual morphometric separation among locations, in both species, were identified using the Similarity Percentages (SIMPER) routine in PAST. One-way ANCOVA (Analysis of covariance), implemented in PAST, was used to test whether the patterns of traits variation across locations were similar for the two sympatric species. The analysis was based on the outcome of SIMPER analysis inferring similar contributors to the morphological differentiation among locations in both crab species. ANCOVA allows comparing one variable in two or more groups taking into account variability of other variables, called covariates. The analysis yielded a scatter plot and linear regression lines for all the groups. An  $F$ -test for the equality of regression slopes (as assumed by the ANCOVA) was also given. Non significant  $F$  meant that the hypotheses for equality of slopes could not be rejected.

Morphometric comparison among both species at the regional scale was carried out by assessing morphological differentiation among

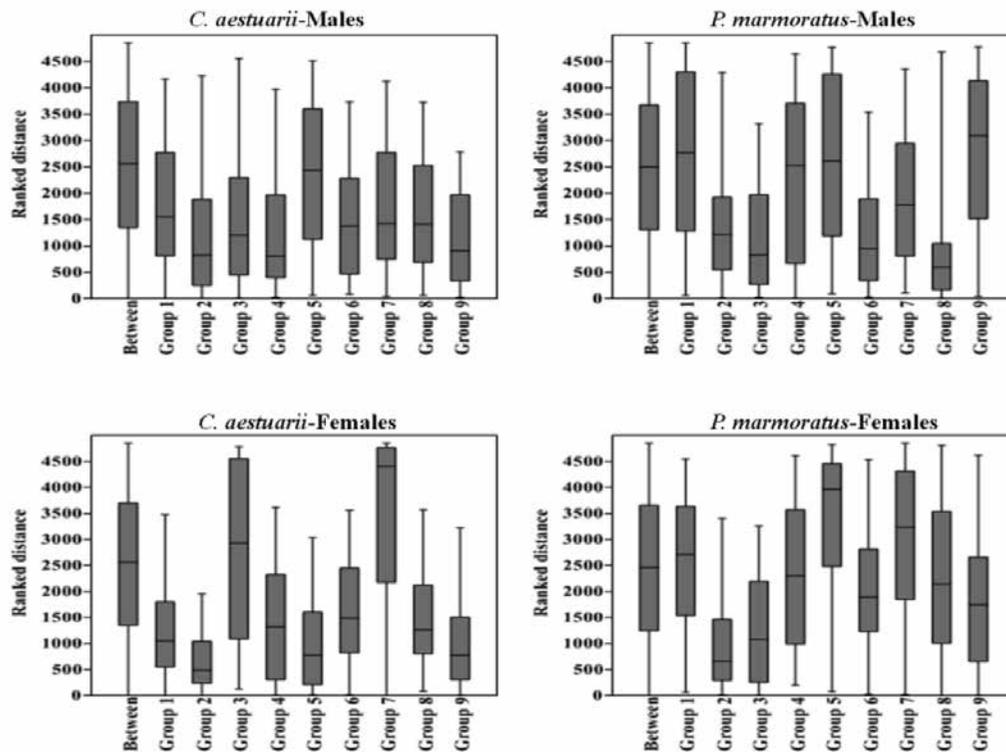
Western Mediterranean populations (Tabarka, Bizerte, Korbos, Kelibia, Benikhiar) and their Eastern Mediterranean counterparts (Monastir, Chebba, Sfax, Medenine). Discriminant/Hotelling analysis, implemented in PAST, was applied on the two sets of multivariate data for each crab species, for both females and males. Given the two sets of multivariate data, an axis was constructed so that it maximised the difference between the sets (DAVIS 1986). The two sets were then plotted along this axis using a histogram. Equality of the means of the two groups was tested by a multivariate analogue to the  $t$ -test, called *Hotelling's T-squared*, and a  $P$  value for this test was given to confirm or reject the hypothesis that the two groups were morphologically distinct. The SIMPER routine analysis was used to account for traits contributing to differences among Mediterranean basins, by species for each sex. Variation patterns of morphometric traits, contributing to morphological differentiation among basins in both crab species, were assessed in order to seek for similar trends.

## Results

### Inter-location morphometric comparison

One-way ANOSIM plots exhibited clear phenotypic differences among populations of the two crab species (Fig. 1). Statistical analyses revealed similar trends of morphological dissimilarities among female *C. aestuarii* ( $R = 0.362$ ;  $P < 0.001$ ) and female *P. marmoratus* ( $R = 0.112$ ;  $P < 0.001$ ). Similar tendency was shown for male crabs (*C. aestuarii*:  $R = 0.401$ ;  $P < 0.001$ ; *P. marmoratus*:  $R = 0.233$ ;  $P < 0.001$ ). PERMANOVA analysis showed the existence of highly significant interactions between the two factors, location and species, for both sexes (females:  $F_{\text{location} \times \text{species}} = 110.296$ ,  $P$  (permutation) = 0.0001; males:  $F_{\text{location} \times \text{species}} = 6144.920$ ,  $P$  (permutation) = 0.0001; Table 2). In addition, the results of the detailed analysis, comparing the pairwise phenotypic polymorphism between the two species, for females and males, confirmed this trend and revealed similarities in the significance level of morphometric difference for most studied comparisons (Table 3).

The multivariate regression analysis revealed highly significant correlation between average dissimilarities observed among *C. aestuarii* locations and those detected for *P. marmoratus* for both females ( $R^2 = 0.332$ ,  $P$  (regression) = 0.0002; Fig. 2A)



**Fig. 1.** One-way ANOSIM plots depicting inter-location morphometric variation for both sexes of *Carcinus aestuarii* and *Pachygrapsus marmoratus*. Group 1: Tabarka, Group 2: Bizerte, Group 3: Korbos, Group 4: Kelibia, Group 5: Benikhiar, Group 6: Monastir, Group 7: Chebba, Group 8: Sfax, Group 9: Medenine

**Table 2.** Summary of results of permutational multivariate analysis of variance (PERMANOVA) assessing the interaction between inter-location phenotypic polymorphism and the studied crab species for females and males

Females						
Source	df	SS	MS	F	P (Perm)	P (MC)
Location	8	228321.7012	28540.2126	876.1992	***	***
Species	1	3481.5592	3481.5592	106.8857	***	***
Location x Species	8	28741.1801	3592.6475	110.2961	***	***
Residual	180	5863.0943	32.5727			
Total	197	266407.5347				
Males						
Source	df	SS	MS	F	P (Perm)	P (MC)
Location	8	233637.1601	29204.6450	51714.2524	***	***
Species	1	3295.2225	3295.2225	5835.0296	***	***
Location x Species	8	27761.8220	3470.2277	6144.9209	***	***
Residual	180	101.6516	0.5647			
Total	197	264795.8562				

Notes: df represents degree of freedom, SS Sum of squares, MS Mean square, *F* morphometric distance inferred from Bray-Curtis dissimilarities, Perm permutation procedure, and MC Monte-Carlo asymptotic procedure. Number of permutations used is 9999. \*\*\* significant difference at  $P < 0.001$ .

and males ( $R^2 = 0.307$ ,  $P$  (regression) = 0.0004; Fig. 2B). The results supported the tendency that the pattern of morphological differentiation varies in the same way in both examined crab species. SIMPER analyses showed that carapace length (CL), right chela depth (RCHD) and left chela depth (LCHD)

contributed the most to the separation between male populations in both species, with a cumulative contribution of 56.43 % in *C. aestuarii* and 61 % in *P. marmoratus* (Table 4). For females, different patterns of parameters contribution were noted among the studied crab species with RCHD, RCHW and

**Table 3.** Pairwise comparisons of phenotypic polymorphism between the two sympatric crab species *Carcinus aestuarii* and *Pachygrapsus marmoratus*, for females and males based on Bray-Curtis dissimilarities

Comparison per population pairs/ Sex per studied species	Females		Males	
	<i>C. aestuarii</i> P (Perm)	<i>P. marmoratus</i> P (Perm)	<i>C. aestuarii</i> P (Perm)	<i>P. marmoratus</i> P (Perm)
Tabarka vs. Bizerte	***	***	***	***
Tabarka vs. Korbos	***	***	***	***
Tabarka vs. Kelibia	***	***	***	***
Tabarka vs. Benikhiar	***	***	***	***
Tabarka vs. Monastir	***	***	***	***
Tabarka vs. Chebba	***	***	***	***
Tabarka vs. Sfax	***	***	***	***
Tabarka vs. Medenine	***	***	***	***
Bizerte vs. Korbos	ns	***	ns	***
Bizerte vs. Kelibia	ns	***	***	***
Bizerte vs. Benikhiar	***	***	***	***
Bizerte vs. Monastir	***	***	***	***
Bizerte vs. Chebba	***	***	***	***
Bizerte vs. Sfax	***	***	***	***
Bizerte vs. Medenine	***	***	***	***
Korbos vs. Kelibia	**	**	***	ns
Korbos vs. Benikhiar	***	***	***	***
Korbos vs. Monastir	***	***	***	***
Korbos vs. Chebba	***	***	***	***
Korbos vs. Sfax	***	***	***	***
Korbos vs. Medenine	***	***	***	***
Kelibia vs. Benikhiar	***	***	***	***
Kelibia vs. Monastir	***	***	***	***
Kelibia vs. Chebba	***	***	***	***
Kelibia vs. Sfax	***	***	***	***
Kelibia vs. Medenine	***	***	***	***
Benikhiar vs. Monastir	***	ns	***	*
Benikhiar vs. Chebba	***	ns	***	ns
Benikhiar vs. Sfax	***	ns	***	ns
Benikhiar vs. Medenine	***	*	***	ns
Monastir vs. Chebba	ns	ns	ns	**
Monastir vs. Sfax	**	ns	***	***
Monastir vs. Medenine	ns	ns	*	ns
Chebba vs. Sfax	**	ns	***	*
Chebba vs. Medenine	ns	ns	*	*
Sfax vs. Medenine	*	ns	***	*

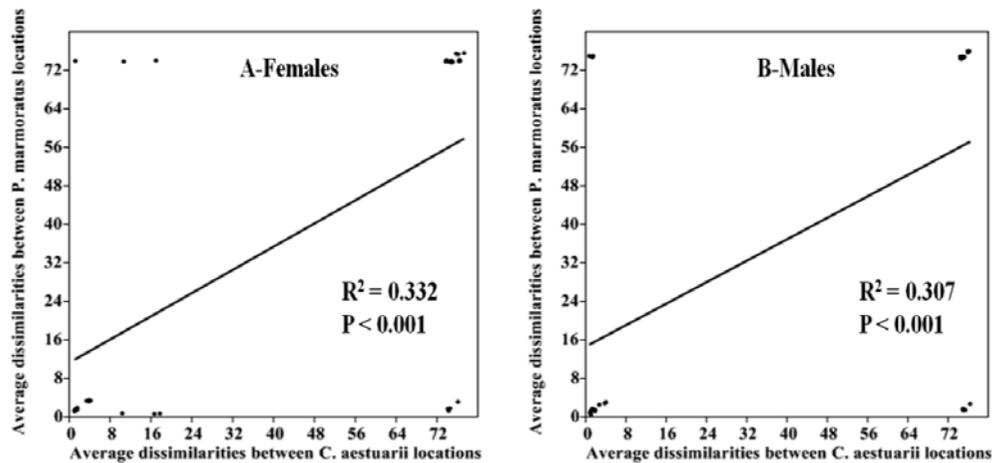
Notes: P (Perm) level of significance inferred from permutation procedure and deduced from permutational multivariate analysis of variance based on Bray-Curtis dissimilarities. Number of permutations used is 9999. \*  $P < 0.05$ , \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ , and ns  $P > 0.05$ .

LABW being the major contributors to the separation between *C. aestuarii* populations (cumulative contribution of 57.68 %). On the other hand, CL, LABW and CH were major contributors to the separation between *P. marmoratus* populations with a cumulative contribution of 76.43 % (Table 4). The

assumption that similar patterns of traits variation across locations could be observed in the two sympatric species was tested with one-way ANCOVA. Analysis, based on the three traits which contributed to the morphometric separation among males populations in *C. aestuarii* and *P. marmoratus* (CL,

**Table 4.** SIMPER analysis of traits contribution for differences, accounted among locations and basins for each sex of each species

Trait	Females						Males					
	<i>C. aestuarii</i>			<i>P. marmoratus</i>			<i>C. aestuarii</i>			<i>P. marmoratus</i>		
	Contribution %	Cumulative %	Trait	Contribution %	Cumulative %	Trait	Contribution %	Cumulative %	Trait	Contribution %	Cumulative %	
	Location											
RCHD	28.41	28.41	CL	35.68	35.68	RCHD	27.62	27.62	CL	40.75	40.75	
RCHW	14.99	43.40	LABW	32.57	68.25	CL	15.11	42.73	RCHD	10.26	51.02	
LABW	14.29	57.68	CH	8.17	76.43	LCHD	13.70	56.43	LCHD	9.98	61	
LCHD	11.02	68.70	PRL	6.68	83.11	RCHW	12.10	68.53	LABW	9.91	70.92	
CL	10.02	78.72	RCHD	5.74	88.86	LCHW	8.91	77.45	CH	9.35	80.27	
PRL	7.36	86.08	LCHD	5.02	93.89	PRL	8.04	85.49	PRL	7.40	87.68	
LCHW	7.19	93.28	RCHW	3.17	97.06	LABW	7.56	93.06	RCHW	6.40	94.08	
CH	6.71	100	LCHW	2.94	100	CH	6.94	100	LCHW	5.92	100	
	Basin											
RCHD	29.44	29.44	CL	36.44	36.44	RCHD	30.19	30.19	CL	40.46	40.46	
RCHW	14.71	44.16	LABW	31.96	68.40	LCHD	14.63	44.83	LCHD	10.41	50.88	
LABW	14.17	58.33	CH	8.08	76.49	CL	13.94	58.77	RCHD	10.35	61.23	
LCHD	11.24	69.57	PRL	6.57	83.06	RCHW	11.95	70.72	LABW	9.73	70.97	
CL	9.65	79.22	RCHD	5.68	88.74	LCHW	8.68	79.41	CH	9.32	80.29	
PRL	7.33	86.56	LCHD	5.03	93.77	PRL	7.24	86.65	PRL	7.38	87.68	
LCHW	7.19	93.75	RCHW	3.23	97.01	LABW	6.91	93.57	RCHW	6.34	94.02	
CH	6.24	100	LCHW	2.98	100	CH	6.43	100	LCHW	5.97	100	



**Fig. 2.** Multivariate regression analysis depicting correlation between average dissimilarities among *Carcinus aestuarii* and *Pachygrapsus marmoratus* locations, for both sexes

RCHD and LCHD), showed similar trends of the variation of each of the analysed morphometric traits across locations in both species (Figs. 3A, B, C). This was verified statistically by the homogeneity of regression slopes. Indeed, the slopes of the two regression lines (one for the green crab and the other for the marbled crab) were not significantly different (CL:  $F = 0.024$ ,  $P = 0.877$ ; RCHD:  $F = 1.885$ ,  $P = 0.191$ ; LCHD:  $F = 0.199$ ,  $P = 0.661$ ).

#### Inter-basin morphometric comparison

The *Hotelling's T-squared* test exhibited similar patterns of morphological differentiation in the two sympatric crab species, showing a highly significant difference among both groups of populations, corresponding to the Western and Eastern Mediterranean basins, for females (*C. aestuarii*: *Hotelling's T*<sup>2</sup> = 80.373,  $F = 9.321$ ,  $P < 0.001$ , Fig. 4A; *P. marmoratus*: *Hotelling's T*<sup>2</sup> = 98.469,  $F = 11.42$ ,  $P < 0.001$ , Fig. 4B) as well as for males (*C. aestuarii*: *Hotelling's T*<sup>2</sup> = 117.48,  $F = 13.625$ ,  $P < 0.001$ , Fig. 4C; *P. marmoratus*: *Hotelling's T*<sup>2</sup> = 101.26,  $F = 11.743$ ,  $P < 0.001$ , Fig. 4D).

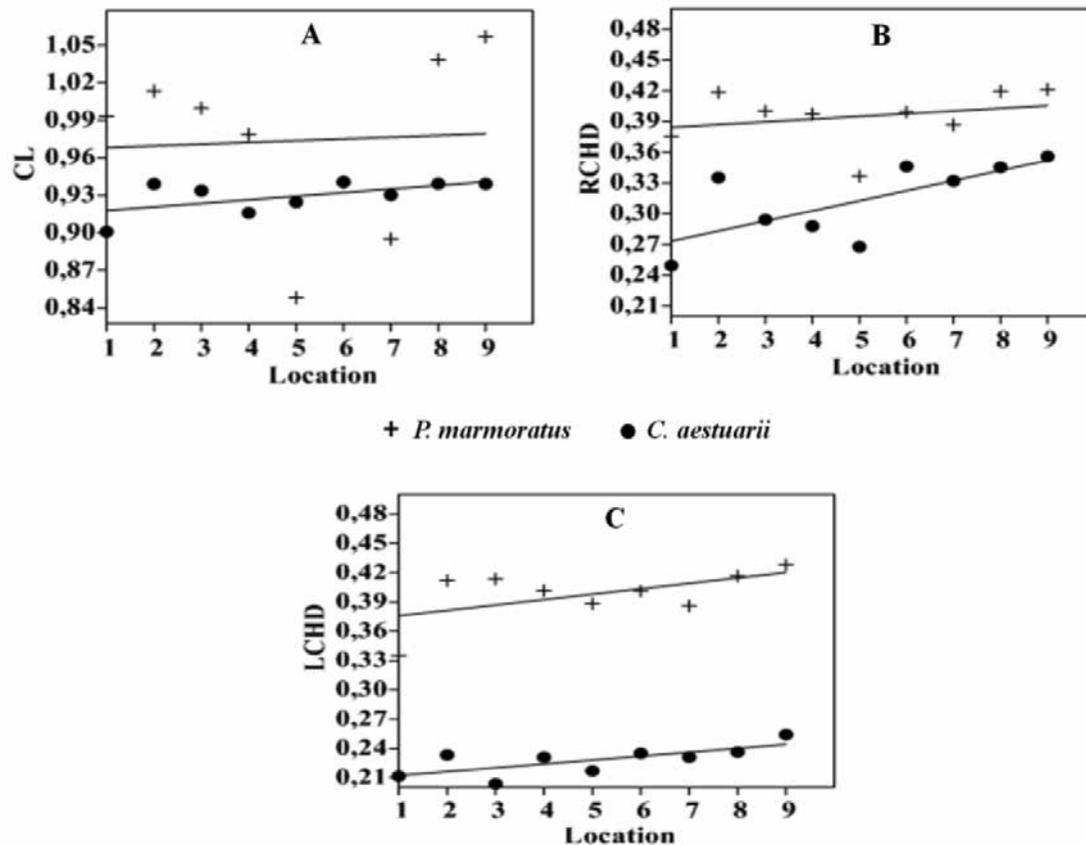
While no match was found between the females of the two sympatric crab species, regarding major contributors to the separation among the studied basins, SIMPER analyses of male groups, yielded similar results to that found for locations showing that CL, RCHD and LCHD contributed the most to the separation between males of both species, with a cumulative contribution of 58.77 % in *C. aestuarii* and 61.23 % in *P. marmoratus* (Table 4). Patterns of male contributors' variation among basins were similar for the two species (Fig. 5). The left and right chelae tended to be deeper in the Eastern Mediterranean specimens than those from the Western basin (Fig. 5B, C). In addition, carapaces of both crab species

from the Eastern Mediterranean were found to be longer than those from the Western Mediterranean (Fig. 5A).

## Discussion

The present study is the first to compare patterns of morphological variation in two sympatric crab species across the transition zone at the Siculo-Tunisian Strait. Our results showed similar patterns of morphometric differentiation among the studied locations and regions for both species. The present findings are consistent with those of HOPKINS & THURMAN (2010) for fiddler crabs (genus *Uca*) along the eastern shore of North America, where similar patterns of morphological variation were found in geographically separated populations in the Gulf of Mexico and the Atlantic Ocean. Comparable trends were shown for trans-Brazilian fiddler crab species, exhibiting similar patterns of morphological differences between their northern and southern populations, across the Ponta do Calcanhar biogeographical feature (HAMPTON *et al.* 2014). Common patterns of morphological variation were also found in other marine invertebrate sympatric species, such as the two intertidal littorinid gastropods *Littorina saxatilis* and *Melarhaphé neritoides* along the west coast of the Iberian Peninsula (QUEIROGA *et al.* 2011).

The results of the detailed PERMANOVA analyses, comparing morphometric differentiation among pairs of populations in the two species, revealed similar patterns of variation for females and males. This trend was confirmed by the results of a multivariate regression analysis showing significant correlation between average dissimilarities among

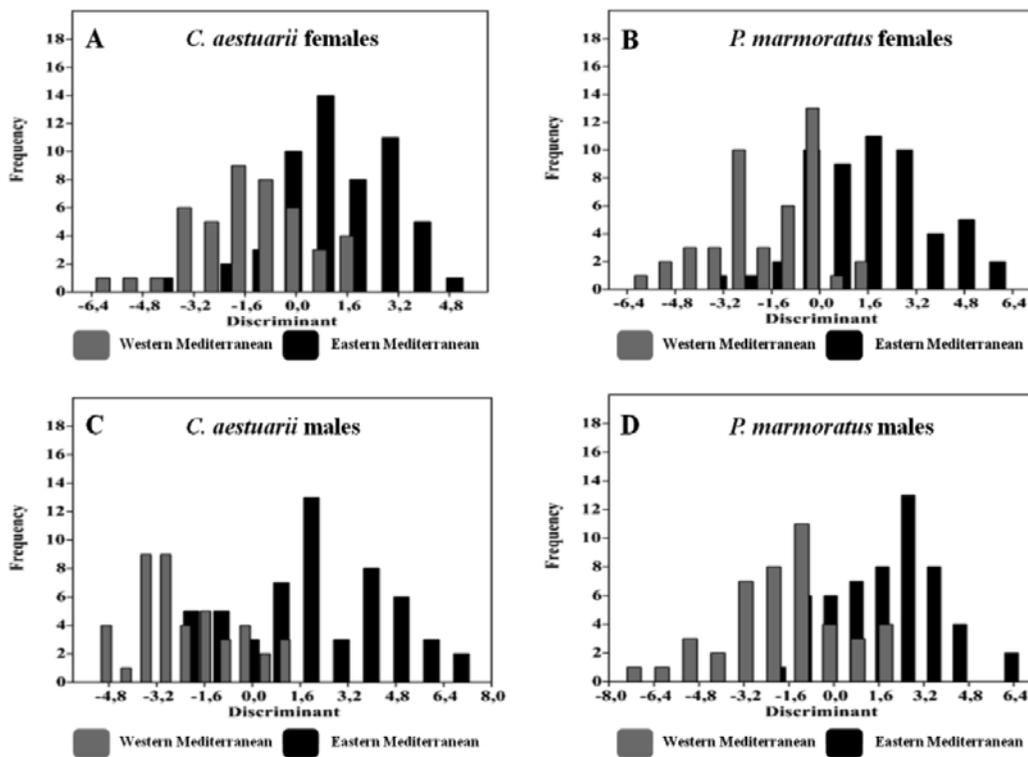


**Fig. 3.** One-way ANCOVA plots depicting patterns of carapace length (A), right chela depth (B) and left chela depth (C) variation across locations for both crab species. 1: Tabarka, 2: Bizerte, 3: Korbos, 4: Kelibia, 5: Benikhiar, 6: Monastir, 7: Chebba, 8: Sfax, 9: Medenine

locations for both sexes in *C. aestuarii* and *P. marmoratus* species. The outcome of these different analyses indicated alike dissimilarities patterns among locations, supporting the tendency that the pattern of morphological differentiation varies similarly in both crab species. This suggests that local adaptation may involve the selection of characters allowing crabs to use specific microhabitats (CROW *et al.* 2009). Because the samples were collected from the same locations, it is more likely that the two examined species are under the impact of similar selective pressures, leading to similar use of habitat and, therefore, to similar response to the environmental conditions at each site. In this sense, heterogeneous predation pressure across sampling sites could be one of the factors inducing similar levels of phenotypic differentiation among locations in *C. aestuarii* and *P. marmoratus*. Predation is often heterogeneous in its distribution and has been shown to impose strong evolutionary and plastic responses in the phenotypes of potential prey (KERFOOT & SIH 1987). For example, predator-induced mortality has been demonstrated to be a strong selective pressure capable

of driving rapid evolution in a suite of antipredator traits in insects (e.g., WHITMAN & AGRAWAL 2009), fish (e.g., WEBB 1986, REZNICK & GHALAMBOR 2001, O'STEEN *et al.* 2002) and lizards (e.g., IRSCHICK & LOSOS 1998, WARNER & ANDREWS 2002). Direct selection from predators can also induce similar plastic responses of the same traits in many species (e.g., HARVELL 1990, AGRAWAL 2001, STOKS *et al.* 2003, RELYEA & AULD 2005).

Alternatively, both crab species could exhibit adaptive plasticity in their morphology in response to changes in food quantity or type, across locations. For example, specialist crabs with a diet dominated by hard-shelled prey have been shown to develop more musculature when fed exclusively on that prey type instead of prey without hard exoskeletons (YAMADA & BOULDING 1998). Although we expected populations of both species to show local adaptation in behavioural, morphological and life-history traits, we also predicted that these same traits could exhibit some degree of plasticity in response to environmental conditions during development. Indeed, many studies have shown that the larvae of marine



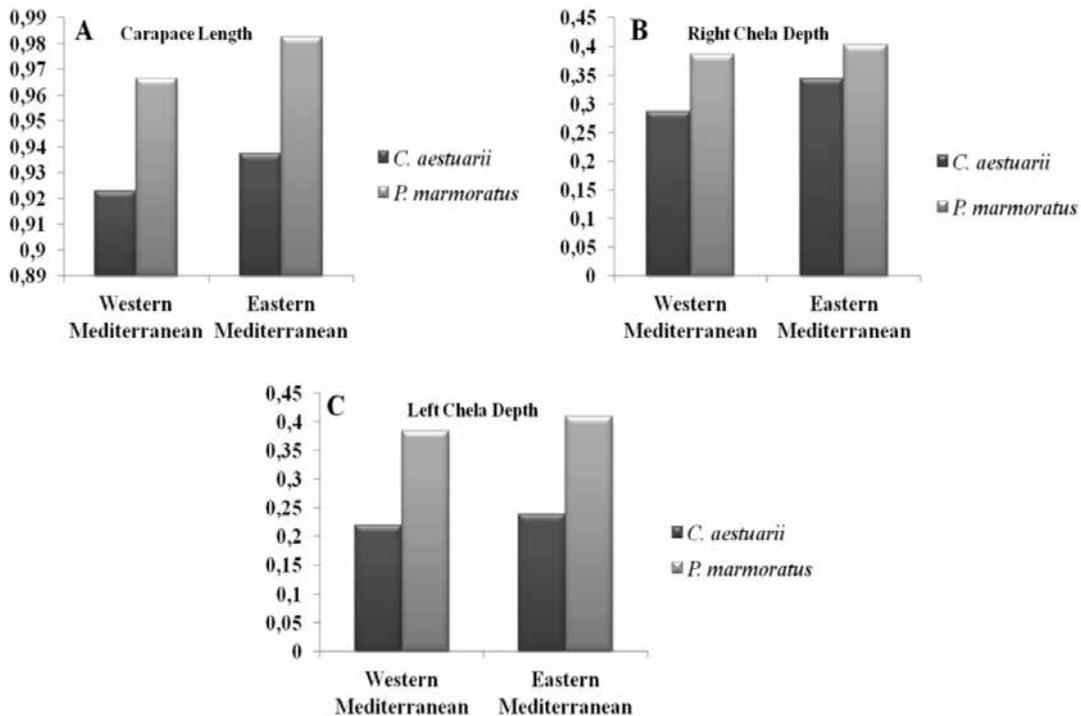
**Fig. 4.** Results of the discriminant/ Hotelling analysis applied on the two sets of multivariate data, for female (A) and male (C) *Carcinus aestuarii* as well as female (B) and male (D) *Pachygrapsus marmoratus*, corresponding to the Western Mediterranean (Tabarka, Bizerte, Korpos, Kelibia, Benikhiar – grey shading) and Eastern Mediterranean (Monastir, Chebba, Sfax, Medenine – black shading)

invertebrates are not totally passive and that even if they are carried away by currents, they require a suitable site to complete their metamorphosis (ECKMAN 1996, WEERSING & TOONEN 2009). At each larval stage, individuals are exposed to a wide variety of physical, chemical (salinity) and biological (inter- and intraspecific competition, nutrient availability, occurrence of predators) processes that affect the probability of transition from one stage to another (ECKMAN 1996, WING *et al.* 1995). In this context, the larvae of each species may show similar patterns of tolerance towards the habitat properties favourable to their metamorphoses. However, we do not have accurate and sufficient data to support this hypothesis. Further studies on the larval behaviour of each species are needed in order to understand the mechanisms that influence their dispersion and, therefore, the population dynamics.

SIMPER analysis showed similar set of traits (CL, RCHD, LCHD) contributing to the morphological differentiation among males' populations in both crab species, but not in females. The latter pattern in female crabs could be explained by the fact that the females of *C. aestuarii* and *P. marmoratus* exhibit disparate behaviour and interact differently with the environment they inhabit. Specific behaviour of

each crab's females might include life history traits, such as reproduction. ANCOVA analysis, based on the three traits which contributed to the morphometric separation among males' populations in *C. aestuarii* and *P. marmoratus*, showed similar trends of traits variation across locations in both species, highlighting a similar variation in carapace and chela morphology. Species with overlapping geographic ranges could exhibit character convergence (inducing similar trends in character variation) or displacement (favouring one character over the others) owing to several biotic (i.e. interspecific competition) and abiotic factors (i.e. species interaction with the environment). The distribution of alternative resources, when a limiting resource is unique and essential, might have a substantial influence on the effects of competition, with convergence being a possible result of selection on the competing species (ABRAMS 1987a, 1987b, FOX & VASSEUR 2008). Accordingly, owing to the fact that both species exploiting a common trophic niche, traits under selection might have responded similarly to those selective constraints (HERREL *et al.* 2008, VINCENT *et al.* 2009), reflecting overall adaptations to a shared environment.

Morphometric analysis at regional scale yielded similar morphological differentiation patterns in both



**Fig. 5.** Patterns of carapace length (A), right chela depth (B) and left chela depth (C) variation across Western and Eastern Mediterranean basins for both crab species.

crab species which could be attributed to either genetic differentiation or phenotypic plasticity. Recent studies by DELI *et al.* (2015a, 2015b) showed that the same surveyed locations, for both species, do differ in their genetic polymorphism. Indeed, while the Tunisian *P. marmoratus* showed genetic homogeneity, the green crab populations across the same surveyed geographic spectrum were shown to be structured and genetically differentiated. Accordingly, it is more likely that the concordance of phenotypic characters in defining two distinct groups, representing the Eastern and Western Mediterranean locations, might be a plastic response to divergent selection pressures between alternative environments. For instance, we can hypothesise that the similar pattern of morphological differentiation among both species groups could be the result of a regional adaptation to specific abiotic features, such as temperature and salinity. It is known that the Eastern Mediterranean basin is warmer and more saline than the Western with an average water temperature and salinity of 16-29°C and 39 ppt respectively; while the Western basin displays lower temperatures (12-23 °C) and salinity (36 ppt) (SERENA 2005). Furthermore, habitats of different textures characterise the sampling sites, with muddy and sandy habitats in the Eastern locations (those southward the Siculo-Tunisian Strait) and rocky habitats in the Western ones (those northward the Siculo-Tunisian Strait), which could also

promote similar phenotypic response in both species. THURMAN *et al.* (2013) showed that the two trans-Brazilian fiddler crabs species *Uca (Boboruca) thayeri* and *Uca (Leptuca) cumulanta*, exhibiting ecological similarities (similar salinity and substrate preferences), displayed a common pattern of morphological variation.

The most remarkable morphological differences among groups, which were common to both species as identified by SIMPER, were related to variation in carapace length and right and left chelae depth for male crabs. For these traits, the Eastern Mediterranean crabs exhibited longer and deeper proportions. This suggests the involvement of specific biotic and abiotic features that might have led to such morphological features.

Longer carapaces, characterising the Eastern Mediterranean crabs, might be an adaptation to the environment features of the region. It is known that the branchial region of the carapace overlying the gill chambers assures water conservation in intertidal crabs. Thus, enlarging carapace dimensions would likely serve as a safeguard against desiccation (JONES 1941). This seems advantageous for the Eastern Mediterranean specimens where the temperature tends to be higher (SERENA 2005). Fiddler crab species from arid regions in the western Gulf of Mexico showed similar adaptations (THURMAN 1998, HOPKINS & THURMAN 2010; THURMAN *et al.* 2013).

Carapace shape might also be related to the type of intertidal habitat as trophic pressures are substantially different between habitat types (QUIROGA 2006, IDASZKIN *et al.* 2013). Therefore, carapace shape of male crabs from Eastern Mediterranean muddy and sandy habitats may reflect feeding efficiency and food availability. VIJAYAKUMAR *et al.* (2000) showed that an increase in body dimensions (carapace width and carapace length) of the horseshoe crab *Tachypleus gigas* population could probably be due to increased availability of food. Broader carapaces, on the other hand, may play a role in the defence against predators or in agonistic encounters between males (GLASS & HUNTINGFORD 1988, REID *et al.* 1994).

Deeper chela, characterising the male crabs from the Eastern Mediterranean, could reflect a plastic response to differing environmental conditions such as prey-linked availability. Variations in the chela morphology have previously been linked to diet and prey resistance (SMITH & PALMER 1994, SMITH 2004). Therefore, claw morphology of Eastern and Western Mediterranean crabs can result from differing food availability on different shores. FERREIRA SILVA *et al.* (2009, 2010) showed a relationship between cheliped size and percentage of prey

intake in the two intertidal crab species *P. marmoratus* and *Eriphia verrucosa*, across shores of differing wave exposure. The authors found that larger claws corresponded to higher intake of hard-shelled prey, abundant on exposed shores. Claw morphology could also be affected by habitat feature of each Mediterranean basin. The study by ROSENBERG (2002) revealed the existence of a significant correlation between claw shape and habitat in fiddler crab species of the genus *Uca*. Sand-dwelling species were shown to have a relatively shorter manus and a longer chela than mud-dwelling species.

At last, the existence of similar patterns of phenotypic variation in the two sympatric crab species suggests the involvement of several biotic and abiotic factors which origin and effect require detailed investigations. The identification of selective pressures is currently required to explore local adaptation, probably linked to the ecology and habitat use (PLATH *et al.* 2007). Future studies of intra- and inter-specific phenotypic variation along experimental environmental gradients and predator regimes would allow understanding how coastal crabs can respond to environmental and climatic heterogeneity and help us predict responses to future changes.

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Received: 06.01.2016

Accepted: 12.10.2016