

Habitat-specific shape variation in the carapace of the crab *Cyrtograpsus angulatus*

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Keywords

salt marsh; rocky shore; geometric morphometrics; intraspecific variation; *Cyrtograpsus angulatus*.

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Abstract

Different environmental and sex conditions induce phenotypic responses (behavioural, morphological and physiological) in many species. The crab *Cyrtograpsus angulatus* inhabits contrasting intertidal habitats, such as rocky shores and salt marshes, where they are exposed to a wide diversity of predators. However, their anti-predator responses differ substantially between these two habitats: while crabs in the salt marshes use or built burrows or they simply hide by burying in the sediment into the tidal channels, on rocky shores they find shelter below rocks, inside crevices or under seaweeds in tidal pools. Considering that refuges in salt marshes can be adjusted by the crabs according to their size and the morphology, while in rocky shores they have to fit in the available refuges, we expect that the body shape differs between individuals from each intertidal habitat. In order to test this hypothesis, we collected male and female crabs from a salt marsh and a rocky shore, separated by 3 km, in San José Gulf, Patagonia, and compared the carapace shapes using geometric morphometric methods. The results showed that carapace shape variation is explained by the interaction between sex and habitats. In both sexes, the mean carapace shape on the rocky shore is more slender and more lengthened than in the salt marsh individuals. Furthermore, the posterior margin of the female carapaces was wider than that of male carapaces, which were slender and more rounded posterolaterally, independent of the intertidal habitat.

Introduction

Throughout their distribution range, members of the same species can inhabit very dissimilar environments (Mayr, 1963; Stearns & Hoekstra, 2000; and references therein). Physical conditions (e.g. habitat complexity, substratum type, salinity, temperature, among others) as well as ecological traits (e.g. competitive interactions, predation pressure and feeding behaviour) may differ among the different environments (Futuyma, 2005). As a result of this environment heterogeneity, notable phenotypic variation may exist among individuals with the same genotype from different sites (Miner *et al.*, 2005; Zhao *et al.*, 2010; Sánchez *et al.*, 2011). The species variability response of the same genotype according to the environment inhabited during ontogeny is a key factor for the potential of a species to colonize, survive and reproduce. In this way, the species can both persist under very diverse environmental conditions and expand their distribution range (Stearns, 1989; and references therein). Therefore, organisms that recruit in different environment conditions may exhibit behavioural, physiological and morphological differences (Pigliucci, 1996; Hollander *et al.*, 2006).

The grapsid crab *Cyrtograpsus angulatus* has a wide distributional range that includes very different habitats. Although

its main habitat is the rocky shore, it also occurs in soft-sediment habitats, such as salt marshes (Iribarne *et al.*, 2003). There are several important differences between the two principal environments inhabited by this species: salt marshes are characterized by the dominance of vascular plants such as tall cord-grasses that can ameliorate environmental conditions, reducing wave exposure and physical stress (Bertness, 1999). Potential predators also differ as do the refuges and the way in which crabs hide from predators. During high tide, crabs are mobile and active in the intertidal zone, while they are hidden during low tides. Crabs inhabiting salt marshes are able to use pre-existing burrows, build new burrows or simply dig into the sediment in the tidal channels (Martinetto *et al.*, 2007). However, on rocky shores they hide below rocks, inside crevices or under seaweeds in tidal pools. By doing so, crabs from soft bottom habitats can adjust the refuge to their shape and size, while crabs from hard bottom habitats have only minor possibilities to modify refuges, and consequently they have to fit into the existing refuges. Because of the importance of refuges as shelter against predators and stressful conditions, we hypothesized that substratum conditions (soft sediments or hard rock) affect the carapace morphology of *C. angulatus*, and that this effect would also be related to or mutually conditioned by the species' sexual dimorphism. Specifically, we

predict that there are differences between carapace shapes of crabs from the different intertidal types and sexes. To test our hypothesis, we used geometric morphometric (GM) methods to characterize the carapace shape of crabs. Landmark-based GM methods were preferred instead of classical measurement-based morphometrics because they present some advantages in the detection of subtle shape changes (Rufino, Abelló & Yule, 2004a; Márquez *et al.*, 2010). GM methods provide the most effective way to capture information about the size and shape of an organism, especially when combined with multivariate statistical procedures (Rohlf & Marcus, 1993; Adams, Rohlf & Slice, 2004; Zelditch *et al.*, 2004). Because the geometric nature implicit in the concept of shape is kept during the complete sequence of analyses, another important advantage of GM is that it allows to graphically visualize the results of any multivariate statistical analyses (Adams *et al.*, 2004). As crustaceans have hard exoskeletons and potentially numerous landmarks, they should constitute an ideal group for the application of GM methods (Rufino *et al.*, 2004a). There are several applications of GM to study different topics about crustacean size and shape variability. In Table 1, we summarized a review of such previous studies that applied landmark methods to extant crustaceans.

Materials and methods

In May 2010, a period that did not correspond to the reproductive stage of *C. angulatus* (Gavio, 2004), a total of 174 crabs (85 from rocky shore, 89 from salt marsh) were collected from different intertidal types of the Fracasso Beach (42°25'S, 64°07'W), on the coast of the San José Gulf, Patagonia, Argentina, and frozen (−20°C) soon after collection (Rufino, Abelló & Yule, 2004b). The intertidal sampling sites chosen were a rocky shore and a salt marsh separated by ~3 km of sandy beach (Fig. 1). Semidiurnal tides in the region have high amplitude (7–8 m).

Crabs were sexed based on morphology of the abdomen. Then, cephalothoraxes (henceforth carapaces) were dissected, carefully cleaned and, after drying, were numbered and photographed using a previously calibrated SONY digital camera (Sony Corporation of America, New York, NY, USA). Carapace length (CL) was measured as the straight line between landmark 1 and semi-landmark 15 (Fig. 2). In total, 41 males (CL: 1.76–3.45 cm) and 44 females (CL: 1.8–2.57 cm) from the rocky shore, and 38 males (CL: 1.04–3.71 cm) and 51 females (CL: 1.08–2.63 cm) from the salt marsh were sampled. Analyses of the carapace shape were performed using GM techniques based on landmark and semi-landmark configurations. During the last 2 decades, the use of GM became popular among biologists, anthropologists, physicians, etc., and has been widely validated as well. Details of these methods and its applications can be found in recent synthesis works (Adams *et al.*, 2004; Mitteroecker & Gunz, 2009; Lawing & Polly, 2010).

The shape of the individuals was captured by the Cartesian coordinates of a two-dimensional configuration of anatomical landmarks and semi-landmarks (Fig. 2). Because a homologous landmark falling on the sagittal symmetry axis is difficult

to detect on the posterior edge of *C. angulatus* carapace, we first defined it using seven semi-landmarks (Fig. 2a). For this purpose, we used TPSrelw software (Rohlf, 2003a) to calculate the algorithm that extends the thin plate splines and warp analysis to sliding semi-landmark points proposed by Bookstein (1996). In this method, the semi-landmark points are slid along the outline curve in order to minimize the bending energy of the configurations (Gunz, Mitteroecker & Bookstein, 2005; Klingenberg, 2008). After the detection of the sagittal axis, and the consequent definition of landmark 15 was made using the supplementary seven semi-landmarks, we discarded landmarks 16–19 to preserve only the left side of the carapace. This approach assumes bilateral symmetry on the studied specimens, and avoids the duplication of bilateral landmarks. This procedure is widely used as a way to avoid computational demands related to the degrees of freedom imposed by configurations made with numerous landmarks (Rufino *et al.*, 2004a).

All specimens were digitized by one observer (A. N.) using TPSdig2 software (Rohlf, 2003b). The resulting configuration of 15 landmarks (Fig. 2b) was then superimposed by generalized Procrustes analysis (Rohlf & Slice, 1990; Slice *et al.*, 1996). This procedure translates and rotates the landmark configurations to a common origin and scales them to unit centroid size.

The centroid size was used as proxy for carapace size and calculated for each specimen as the square root of the sum of the squared deviations of landmarks from the centroid (Bookstein, 1991; Zelditch *et al.*, 2004). The putative shape changes purely explained by variations in size (allometry) were assessed and controlled by computation of the pooled within-habitat and sex multivariate regression of shape (Procrustes coordinates used as dependent variables) on size (centroid size used as independent variable) (Bookstein, 1991; Monteiro, 1999; Klingenberg, Barluenga & Meyer, 2003; Klingenberg, 2011). To evaluate the independence between the shape and size variables, we ran a permutation test with 10 000 rounds (Good, 2000).

The principal components (PCs) of shape were calculated from a PC analysis of the variance–covariance matrix of the Procrustes coordinates in order to reduce the number of shape variables and to display the major features of shape variation along the axes (Zelditch *et al.*, 2004). Then, we performed a two-way multivariate analysis of variance (MANOVA) (Cuadras, 2008) to test for among sexes and/or habitat differences in carapace shape (PC that accounted 99% of total variations). To assess which groups were significantly different, we used the Multivariate Dirienzo Guzman Casanoves (MDGC) method, the extension to the multivariate case of a multiple comparison method based on cluster analysis generated using an unweighted pair-group method with arithmetic mean (UPGMA; Valdano & Di Rienzo, 2007; Márquez & Van der Molen, 2011). This novel method is a hybrid technique that combines a hierarchical clustering based on Mahalanobis distances (Mahalanobis, 1948) for hypothesis testing in multivariate cases. This method is successful in determining the number of groups in a hierarchical cluster analyses. The graphical output of the MDGC test is also a useful tool because it shows a clear distinction between statistically

Table 1 Studies showing examples of use of landmarks methods to modern crustaceans

Taxon	Anatomical structure used	Topic of variation	Number of landmarks and/or semi-landmarks used	Geometric morphometrics software used	Geographical data collection	References
<i>Uca</i> sp.	Carapace	Interspecific Intraspecific Allometry Interspecific	13 landmarks	TPS series	Atlantic and Gulf coasts of North America	Hopkins & Thurman, 2010
<i>Uca</i> sp.	Major and minor claws	Interspecific	6 landmarks	TPS series	Multiple museum and field around the world	Rosenberg, 2002
<i>Uca annulipes</i>	Carapace and claws	Geographical	12 carapace landmarks and 12 claw landmarks	TPS series	East African coast, Kenya, Tanzania, Mozambique, Flax Pond, USA	Silva, Mesquita & Paula, 2010
<i>Uca pugnax</i>	Major and minor claws	Intraspecific Allometry	6 landmarks	TPS series	Appendix 1 in the paper	Rosenberg, 1997
<i>Aegla araucaniensis</i>	Cephalothorax	Selection pressures	33 landmarks	TPS series	Rivers, Chile	Barría, Sepúlveda & Jara, 2011
<i>Aegla denticulata</i>		Interspecific				
<i>Aegla abtao</i>		Intraspecific				
<i>Aegla neuquensis</i>	Cephalothorax	Taxonomy	16 landmarks	TPS series	Rivers, Argentine	Giri & Loy, 2008
<i>Aegla riolimayana</i>		Sexual dimorphism				
<i>Aegla uruguayana</i>	Cephalothorax	Sexual dimorphism Interspecific	11 landmarks	TPS series	River, stream and lagoon, Argentine	Giri & Collins, 2004
<i>Aegla platensis</i>		Sexual dimorphism				
<i>Liocarcinus depurator</i> (L.)	Carapace	Digitizing technique Geographical	15 landmarks	TPS series	Alborán Sea and Mediterranean Sea, Spain	Rufino, Abelló & Yule, 2006
<i>Liocarcinus depurator</i> (L.)	Carapace	Sexual dimorphism	15 landmarks	TPS series	Iberian Mediterranean Sea, Spain	Rufino, Abelló & Yule, 2004a
<i>Liocarcinus depurator</i> (L.)	Carapace	Sexual dimorphism Preservation methods	15 landmarks	TPS series	Mediterranean Sea, Spain	Rufino, Abelló & Yule, 2004b
<i>Carcinus maenas</i>	Carapace and claws	Geographical	15 carapace landmarks and 9 claw landmarks	TPS series	Southwest English coast, England	Silva <i>et al.</i> , 2010b
<i>Carcinus maenas</i>	Carapace and claws	Geographical	15 carapace landmarks and 9 claw landmarks	TPS series	Portuguese coast, Portugal	Silva, Hawkins & Paula, 2009
<i>Pachygrapsus marmoratus</i>						
<i>Munida rugosa</i>	Claws	Sexual dimorphism Symmetry Allometry	6 landmarks	TPS series	Clyde Sea, Scotland	Claverie & Smith, 2010
<i>Munida rugosa</i>	Claws	Geographical				
<i>Cyrtograpsus affinis</i>	Claws Carapace	Sexual dimorphism Taxonomy	6 landmarks 15 landmarks	TPS series TPS series	Clyde Sea, Scotland South Atlantic ocean, Argentina	Claverie & Smith, 2007 Lezcano <i>et al.</i> , 2012
<i>Cyrtograpsus altmanua</i>		Geographical				
<i>Macrobrachium australe</i>	Carapace	Allometry Intraspecific	10 landmarks	TPS series	Rivers, Reunion Island	Zimmermann <i>et al.</i> , 2012
<i>Perisesarma guttatum</i>	Carapace	Geographical	12 landmarks	TPS series	East African coast, between Mozambique and Kenya Oahu, Hawaii	Silva, Mesquita & Paula, 2010 Claverie, Chan & Patek, 2010
<i>Gonodactylaceus fakatus</i>	Raptorial appendage	Modularity Functional morphology	Propodus/dactylus (3 landmarks and 42 semi-landmarks) and Merus (8 landmarks and 32 semi-landmarks)	TPS series		
<i>Eriphia verrucosa</i>	Claws	Sexual dimorphism Functional morphology	13 landmarks and 21 semi-landmarks	TPS series	Central coast of Portugal, Portugal	Silva <i>et al.</i> , 2010a
<i>Petrolisthes galathinus</i> complex	Sternal plate	Taxonomy Geographical	27 landmarks	TPS series	Multiple museum and field around the world	Hillier <i>et al.</i> , 2006

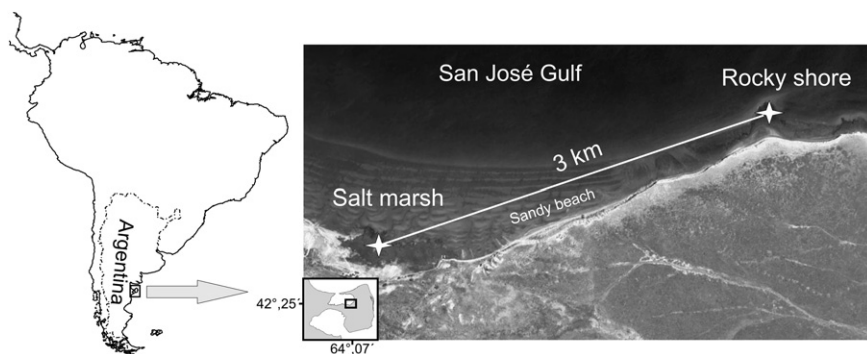


Figure 1 Map of the Fracasso Beach showing the sample collection sites on each intertidal type: salt marsh and rocky shore.

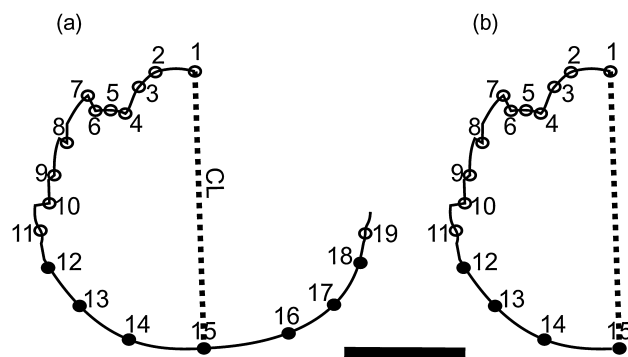


Figure 2 Diagram showing the position of the 12 landmarks and 7 semi-landmarks used to (a) calculate the posterior centre point of symmetrical axis and (b) define the carapace shape of crabs. These landmarks are: (1) the anterior edge of the carapace, (2) maximum curvature of the anterior edge, (3) maximum curvature of internal border of the ocular depression, (4 and 6) tips of the ocular depression, (5) maximum curvature of the ocular depression, (7) external border of the ocular depression, (8) first lateral teeth, (9) second lateral teeth, (10) third lateral teeth, (11 and 19) end point of the last teeth, and (12–18) semi-landmarks along the outline of posterior edge of the carapace. CL: carapace length (dotted line). Scale bar = 1 cm.

different shell shapes of mollusk bivalves from each locality, as well as their relationships (Márquez *et al.*, 2010; Signorelli, Márquez & Pastorino, 2012).

Finally, we have computed a canonical variate analysis (CVA) in order to recover an axis of maximum discrimination among groups. In addition, a matrix of Mahalanobis distances was calculated among all possible pairs of groups and the statistical significances of pairwise differences in mean shape were assessed after permutation tests (10 000 permutations per test). The data analyses were performed using MorphoJ v1.05a (Klingenberg, 2011), excepting the MANOVA analysis, which was performed using InfoStat software (Di Rienzo *et al.*, 2009).

Results

The pooled within-habitat and sex multivariate regression of shape on size was highly statistically significant (permutation

test with 10 000 random permutations, $P < 0.0001$), and accounted for 9.6% of the total amount of shape variation (Fig. 3). This suggests an allometric behaviour of the carapace of *C. angulatus*. The main carapace form variation related to bigger individuals (males from both intertidal types) was associated with the shape of the anterior edge, broadening of the anterolateral edge and shortening of the posterior part. For subsequent analyses, we used the regression residuals as new allometric-free carapace shape variables.

The allometric-free carapace shape variation is summarized in Fig. 4, consisting of scatter plots for the first four PCs of shape. The specimens from the four groups were mostly overlapped. The geometric interpretation of the positive extremes of PC1 is associated to the development of the posterior edge of the carapace, showing a triangular shape (e.g. with the anterior edge narrower than the posterior one). The second PC axis was related to the development of the anterior part of the carapace (ocular area and rostrum) and to an elongation of the posterior edge (Fig. 4a). The third PC showed a more laterally round shape of the carapace. Finally, the fourth PC was associated to an anterolateral broadening (Fig. 4b).

The two-way MANOVA analysis performed on the first 24 PCs (collectively accounting for a 99% of total variance) indicated a highly significant interaction between sexes and habitat for carapace shape (Table 2). The dendrogram calculated on the Mahalanobis distance matrix showed that each group had a carapace shape with statistically significant differences ($P < 0.05$), and even though sex was the main grouping factor, the habitat also behaved as an important discriminating factor (Fig. 5).

The among-groups carapace shape variation was successfully depicted using CVA. The first two canonical axes (CV) explained 84% of the total variance. As a general pattern, the CV1 was represented with sex while CV2 was associated with habitat. However, the greatest difference across the first CV was between females from the salt marsh and males from the rocky shore, being the last group represented by more slender and elongated carapaces (Fig. 6 and Table 2). The CV2 was mostly associated with narrowing and enlarging of the carapace (Fig. 6), and this axis of variation discriminates females of the rocky shore from males of the salt marsh. The among-groups comparison of mean shapes indicates that there are significant differences in carapace shape. Table 3 shows the

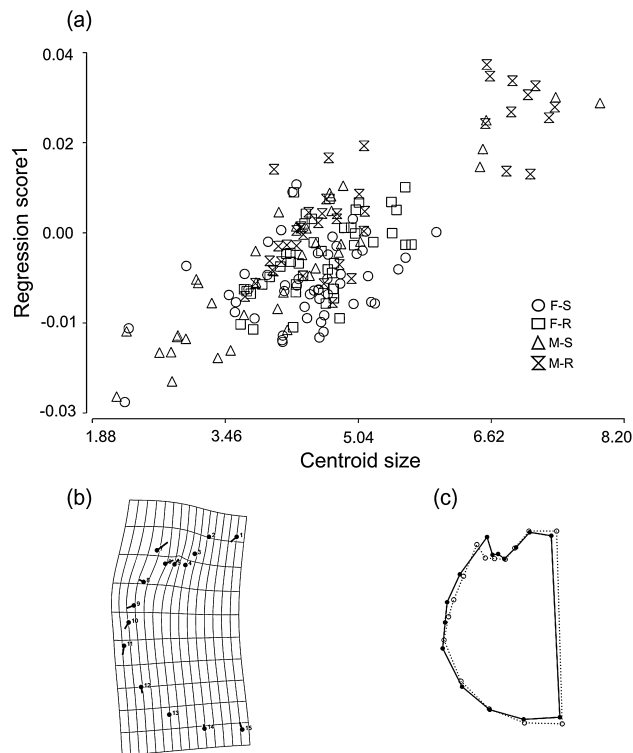


Figure 3 Pooled within-habitat and sex multivariate regression of shape onto size. (a) Shape scores as a function of centroid size illustrating allometric growth of the different *Cyrtograpsus angulatus* groups. Shapes at the opposite extremes of the range of allometric variation are shown by using transformation grids (b) and wireframes (c). (b) The transformation grids and the vectors from the black dot diagram (mean shape) indicate the predicted landmark shift corresponding to an increase of centroid size by 8 scale factor. (c) The wireframe shows the average shell shape and the change from the grey circles to the black dots indicates the predicted landmark shift corresponding to an increase of centroid size by 8 scale factor. Code for groups: F-S, female of salt marsh; F-R, female of rocky shore; M-S, male of salt marsh; M-R, male of rocky shore.

Table 2 Multivariate analysis of variance results showing Wilks’s statistic applied to the first 24 principal components (collectively accounted 99% of total variance) of carapace shape in *Cyrtograpsus angulatus*

	Statistic	F	d.f.	P
Sex	0.43	8.24	24	147 < 0.0001
Habitat	0.49	6.27	24	147 < 0.0001
Sex*habitat	0.69	2.82	24	147 < 0.0001

Mahalanobis distances among all possible pairs of groups and their P-values.

Discussion

Our results showed that differences in the carapace shape of *C. angulatus* are related to the interaction between the differ-

ent sexes and type of intertidal habitat. The refuge features on rocky shores and in salt marsh habitats could be the main environmental constraint to the carapace shape. The carapace shape may have high intraspecific variability during ontogeny such that crabs fit better in the refuges available in the two contrasting habitat types. Below we provide and discuss baseline information to facilitate the future design of experimental studies directed to accurately identify the exact factor or group of factors that determinate carapace shape variations.

The presence of allometry can account for a large and statistically significant proportion of morphological variation. Allometry in carapace shape was previously described in the other two species of the *Cyrtograpsus* genus by Lezcano *et al.* (2012). According to their results, we detected a very strong dependence of shape on size which suggests that the simple growing of the individuals introduces important shape variation across the ontogeny of this species. To explore the non-allometric shape variation, we controlled the static allometric effect by using the regression residuals as new size-unrelated carapace shape variables. However, further studies could characterize and discriminate ontogenetic carapace form changes (size + shape) of *C. angulatus* crab by means of GM techniques, and discuss their relationship with sex and habitat.

The use of GM analysis allowed us to characterize, with high resolution, the carapace shape variations of each group and to suggest associations between them. As expected, the carapace shape displays variations between sex and habitat. The major variations in carapace shape involve development of the posterior edge of the carapace and the anterior part (ocular area and rostrum). The carapace shape of the crabs was more similar between sexes than between habitat types. Surely this is related to the organisms that frequently develop specialized phenotypes adapted to local environmental conditions (Postma & Van Noordwijk, 2005). Predicting these results, we have chosen *a priori* the habitats where the study was carried out because they differ substantially in several major abiotic and biotic variables. For example, the site in the salt marsh was inside of a tidal channel that presented muddy sediment and high turbidity yet calm water. The water level fluctuations between tidal cycles are almost imperceptible within the channel because it remains water filled during low tides. On the other hand, on the rocky shore site the environmental conditions are more stressful for aquatic organisms due to the temperature variations, desiccation risk and wave exposure. For example, several intertidal mollusks on wave-exposed shores are typically smaller and flatter than those at sheltered sites (Prowse & Pile, 2005). Furthermore, trophic pressures are substantially different between the two habitat types. In the salt marsh, the principal predators are fishes, while on the rocky shore the situation depends on the tidal height (Quiroga, 2006). There, the principal predators on crabs are an octopus *Octopus tehuelchus* and fishes during high tide, while during the low tide there are also shorebirds and other opportunistic predators (Ré, 1998). Giri & Loy (2008) found that river specimens of *Aegla* are larger in size and have a carapace that is more slender than in the specimens inhabiting the lakes they studied. They suggested that these differences are related to the fact that lakes are stable systems,

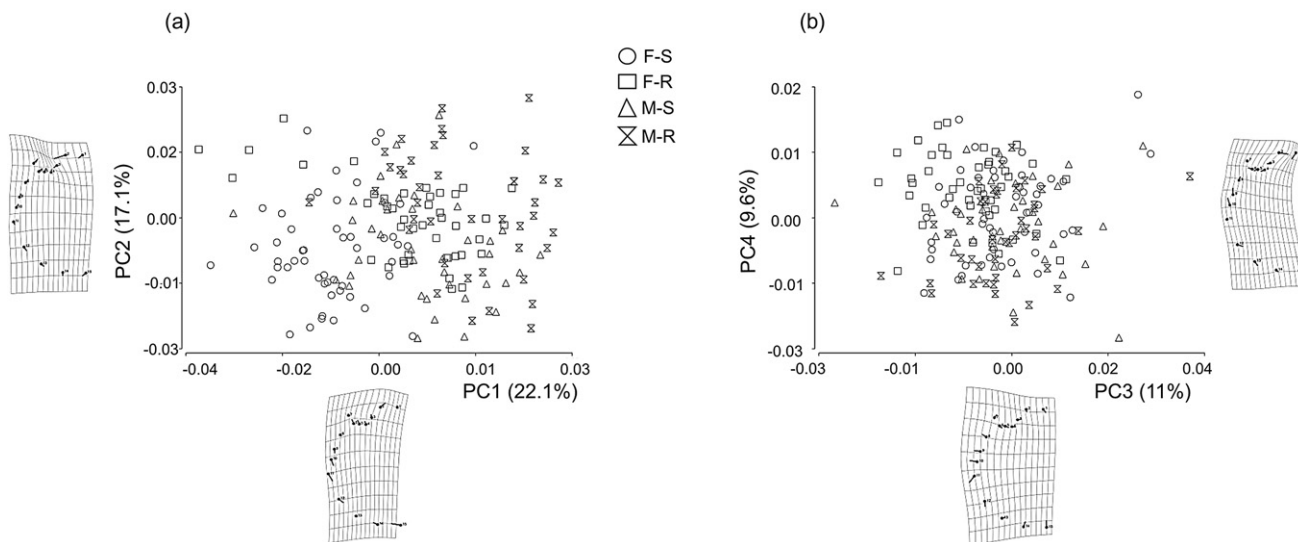


Figure 4 Plot of the principal components (PCs) for different habitat-sexes groups based on Procrustes distances. The figures represent the transformation grids and displacement vectors from the overall mean shape (black dot) to the positive extreme shape (vector) for each PC. Shape changes have been exaggerated (scale factor 0.1) in both types of graphic for better visualization: (a) PC1 versus PC2; and (b) PC3 versus PC4. Percentages of explained variance for each axis are in parentheses. Code for groups: F-S, female of salt marsh; F-R, female of rocky shore; M-S, male of salt marsh; M-R, male of rocky shore.

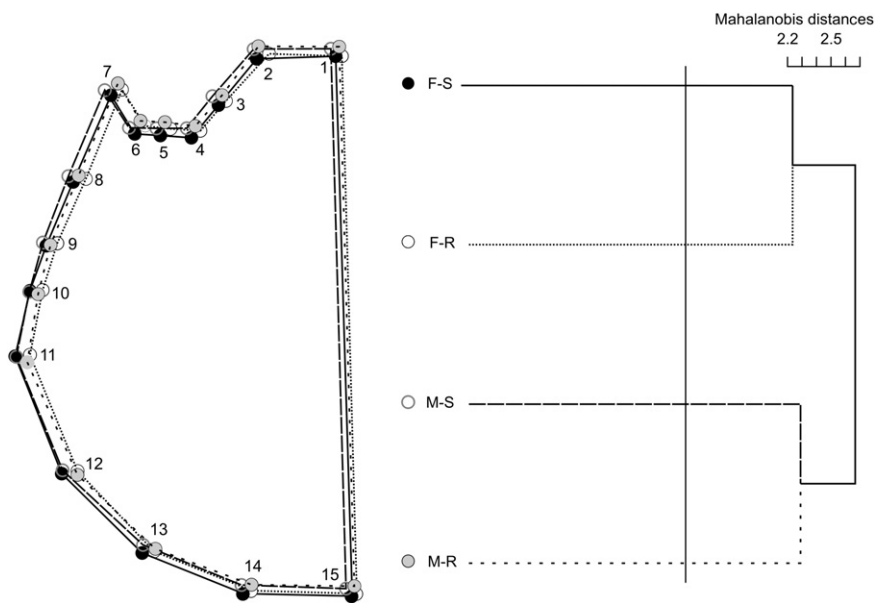


Figure 5 UPGMA (unweighted pair-group method with arithmetic mean) dendrogram showing the relationships between the groups of carapace shapes of *Cyrtograpsus angulatus* and the overlapped diagrams of the reconstructed consensus configurations of each sampled group. The cut-off criterion ($P = 0.05$) obtained with the Multivariate Dirienzo Guzman Casanoves (MDGC) test is indicated with a horizontal line. Four statistically different groups of carapace shapes were identified by this method. Code for groups: F-S, female of salt marsh; F-R, female of rocky shore; M-S, male of salt marsh; M-R, male of rocky shore.

varying in both resource availability and accessibility, current flow, and physical and chemical conditions. Our analyses revealed that rocky shore individuals have a more slender and lengthened carapace than the specimens inhabiting the salt marsh. Lakes such as salt marsh channels represent calm environments in which the conditions are more homogeneous over space and time, while in rivers and on rocky shores the organisms are more exposed to waves and currents. However, we

consider that the main difference between *C. angulatus* individuals from both intertidal habitats is that on rocky shores crabs can find refuge under rocks or cavities, or behind algae in tidal ponds where the water turbidity is low, while in salt marshes they are able to use and modify pre-existing burrows or build their own refuges.

Although body shape is a complex trait generally influenced by multiple environmental variables in addition to other evo-

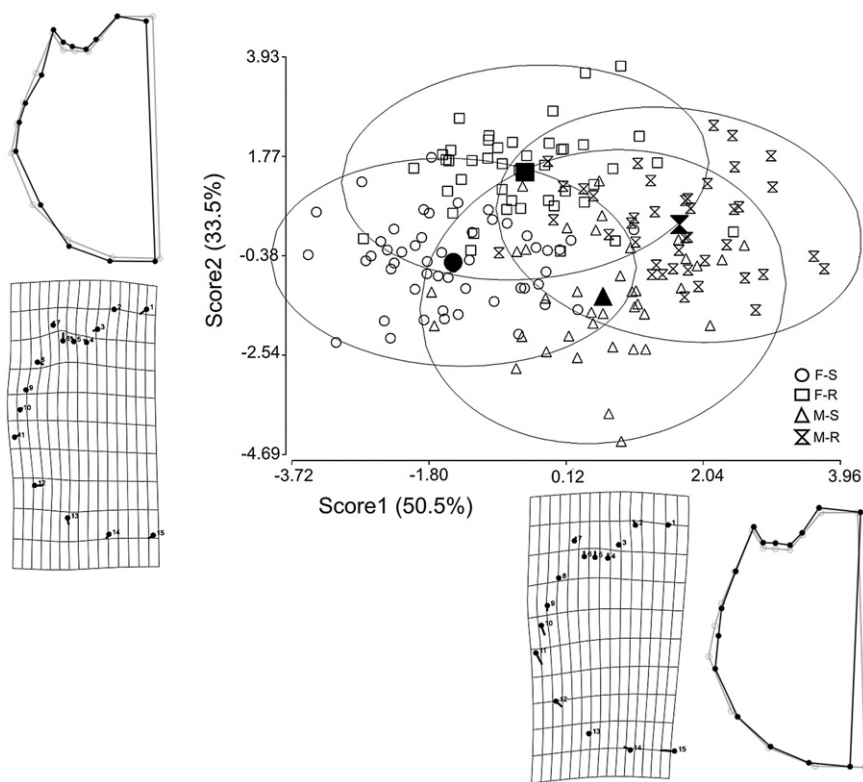


Figure 6 Carapace shape differences between groups. Canonical variate analysis of overall carapace shape variation along the first two canonical axes. Transformation grid diagrams show shape changes from mean shape (black dot) to the positive extreme (scale factor 10) in both axes. The largest symbols indicate the average for each group. Percentages of explained variance for each axis are in parentheses. Code for groups: F-S, female of salt marsh; F-R, female of rocky shore; M-S, male of salt marsh; M-R, male of rocky shore.

Table 3 Mahalanobis distance matrix for carapace shape (below the diagonal) and *P*-values (above of the diagonal) for all pairwise tests

Group	F-S	F-R	M-S	M-R
F-S	–	<0.0001	<0.0001	<0.0001
F-R	2.46	–	<0.0001	<0.0001
M-S	2.64	2.92	–	<0.0001
M-R	3.27	2.76	2.47	–

Code for groups: F-S, female of salt marsh; F-R, female of rocky shore; M-S, male of salt marsh; M-R, male of rocky shore.

lutionary factors (Langerhans, Chapman & Dewitt, 2007), our results support the hypothesis that the principal environment constrain is the habitat substrata, that it could be dictated by the need for suitable refuges against predators. However, more research is needed including other populations to make a generalization of this hypothesis.

On the other hand, we found sexual differences in the carapace shape of *C. angulatus*. Many crab species are dimorphic in particular characters, being usually the most evident the chelipeds (Thiel & Duffy, 2007). For example, the fiddler crabs (genus *Uca*, Ocypodidae), one of the most characteristic groups of crabs associated with intertidal soft bottoms, are characterized by strong sexual dimorphism and male cheliped asymmetry (Christy, 2007). Female crabs have two small feeding chelipeds, while males have a small minor claw used for feeding, such as females, and a large major

claw used for display and male–male agonistic interactions (Rosenberg, 2002; Silva, Mesquita & Paula, 2010). Furthermore, there are other features that differ between sexes in crabs that may be less perceptible at first sight, specially the dimorphism in the abdomen morphology, which is reported for many decapod species (Giri & Collins, 2004). GM studies showed sexual dimorphism on carapace shape in freshwater crabs (Giri & Collins, 2004; Giri & Loy, 2008). As a general pattern, it seems that females are smaller in size and are broader at the posterior end of cephalothorax (Barria, Sepúlveda & Jara, 2011). However, there are only few studies based on the sexual dimorphism in the carapace shape of the marine crabs’ species. For example, Rufino *et al.* (2004a) found that *Liocarcinus depurator* females had a longer base of the abdomen, which is also more concave, while males had broader carapaces related to their length, and also the carapace teeth are bigger. Our results agree with the referred freshwater and marine studies, showing that the carapace of female *C. angulatus* was wider in their posterior margin than that of males, which were slender and more rounded posterolaterally, independent of habitat type. These features represent an adaptation to increased fecundity by enlarging the relative volume for gonad space, while the male carapace is intended to be associated with stronger muscles employed during agonistic interactions (Rufino *et al.*, 2004a).

The major difference between the individuals from the two habitat types was that the posterior side of the carapace

from the rocky shore individuals was slender and more lengthened than in the salt marsh individuals, both in males and females. These changes in carapace shape are produced by the upward-pointing orientation of the anterior part of the carapace in salt marsh individuals. Therefore, two morphotypes can be distinguished in *C. angulatus* according to the habitat that it inhabits, confirming a high degree of intraspecific variability.

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