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Phenotypic variation of south-western Atlantic clam *Mactra isabelleana* (Bivalvia: Mactridae)

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The phenotypic shell shape variation of Mactra isabelleana was tested using the geometric morphometric method. Four localities were sampled along the Rio de la Plata estuary and the coast of Buenos Aires province. Principal component analysis and canonical variates analysis of the first principal components were performed to reveal the shell variation and differences among localities, respectively. The specimens from different microhabitats mostly overlapped, although differences in shape were observed in the development of the umbo, the enlargement of the dorsoventral axes and the elongation of the posterior end. The ecological and physical parameters that could influence shell shape variation are discussed.

Keywords: Bivalvia, estuary, shell variation, Mactridae, d’Orbigny, geometric morphometric, landmarks

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INTRODUCTION

The family Mactridae Lamarck (1809) is a worldwide family represented almost in all seas (Keen, 1969). It dates from the lower Cretaceous of North America (Skelton & Benton, 1993). In the western Atlantic, after a taxonomic review of the whole family, Signorelli & Pastorino (2011, 2012) restricted to seven the species for the Magellanic zoological province and to seven for the Argentine provinces. Alcide d’Orbigny (1846) proposed from the Argentine province, four species, including *Mactra isabelleana*, described from Maldonado Bay, Uruguay. However, this species ranges from Rio de Janeiro (~22°S), Brazil to the San Matías Gulf (~41°S), Argentina (Signorelli & Pastorino, 2012, and literature therein). This is a burrowing species commonly sampled from muddy and sandy bottoms along the Buenos Aires coast and Rio de la Plata estuary. Its presence along the study area (around 20 degrees of latitude) suggests a tolerance to different environmental factors that could be influencing the shell shape. This variation was only recently mentioned by Scarabino *et al.* (2006).

The morphological analysis of the shell plays an important role in diverse fields such as taxonomy, evolution, functional anatomy, or fisheries management of molluscs. The shell is generally the most conspicuous part of the mollusc body and, to a large degree, also the most variable in shape. Because intra- and inter-specific variation in shell morphology is the result of the combined effects of genetic differentiation

and phenotypic plasticity, its study constitutes a key element (e.g. Stanley, 1970; Gould, 1971; Ackerly, 1992; Manuel & Dadswell, 1993; Gaspar *et al.*, 2002; Ubukata, 2003; Márquez *et al.*, 2011). The molluscs are restrained by different biological and environmental processes, which are recorded in the ontogeny (Palmer *et al.*, 2004; Krapivka *et al.*, 2007; Márquez *et al.*, 2010a). These processes change the external morphology of taxa. Modern morphometric methods could be an excellent way to quantify and study these changes. Traditional morphometric methods present difficulties for the assessment of shell shape variation (Sokal & Rohlf, 1995), because the results are very sensitive to the particular distances and ratios chosen. These measurements are highly correlated with size (Bookstein, 1991; Zelditch *et al.*, 2004) and make it difficult to obtain robust size-free shape variables. The more recently developed landmarks based method for morphometric analysis, the geometric morphometrics (GM) approach, provides an effective way to avoid confusion between size and shape by preserving shape variables throughout the analysis (Rohlf & Marcus, 1993; Adams *et al.*, 2004; Mitteroecker & Gunz, 2009). Several authors have worked with GM methods to report shell variation in molluscs (e.g. Chiu *et al.*, 2002; Carvajal-Rodríguez *et al.*, 2005; Márquez *et al.*, 2011; Teso *et al.*, 2011). Studies of intraspecific shell shape variation were mentioned in several species of bivalves (i.e. Crampton, 1995; Ubukata, 2003; Márquez *et al.*, 2010b; Gordillo *et al.*, 2011; Márquez & Van der Molen, 2011). Salinity, grain size, wave exposure, latitudinal gradient and depth have been proposed to explain intraspecific shell shape variation of bivalves (Olabarriá & Thurson, 2004; Aguirre *et al.*, 2006; Conde-Padín *et al.*, 2007; Krapivka *et al.*, 2007; Roopnarine *et al.*, 2008; Márquez *et al.*, 2011).

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The objective of this work is to compare the shell shape variation of *Mactra isabelleana* sampled along the Rio de la Plata estuary and open sea by using GM methodology.

MATERIALS AND METHODS

Fieldwork

The sampled localities are from south to north: Mar del Plata (MDP, $38^{\circ}00'32''S$ $57^{\circ}31'45''W$), San Clemente del Tuyú (SCle, $36^{\circ}23'52''S$ $56^{\circ}42'13''W$) and Río de la Plata estuary (E, $35^{\circ}38'45''S$ $56^{\circ}53'03''W$) in Argentina; and Buceo beach, Montevideo (MTV, $34^{\circ}54'02''S$ $56^{\circ}07'20''W$) in Uruguay (Figure 1). The samples from MDP and E were collected with a trawling net aboard the RV 'Puerto Deseado' in October 2009 and those from SCle and MTV by hand in the intertidal zone in November 2007.

Geometric morphometrics and statistical analyses

Fifteen specimens of *M. isabelleana* were randomly selected from each locality. All the specimens were cleaned of soft

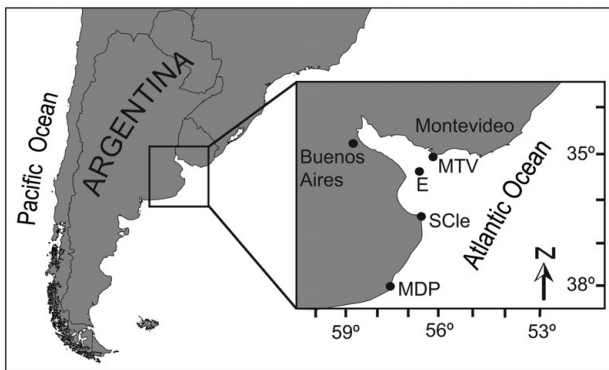


Fig. 1. Map of the study area showing the four sampling localities: Montevideo (MTV); Estuary (E); San Clemente del Tuyú (SCle) and Mar del Plata (MDP).

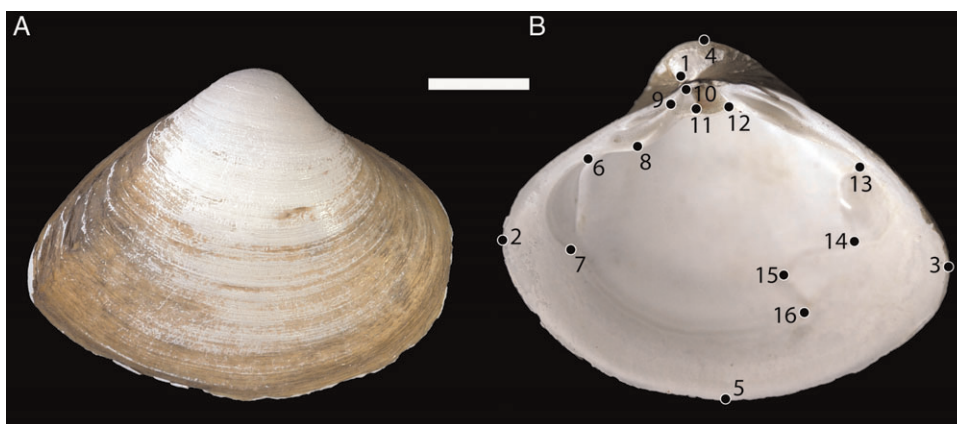


Fig. 2. (A) External view of *Mactra isabelleana* d'Orbigny, 1846; (B) internal view of right valves showing location of Type I and Type II geometrically homologous landmarks. These landmarks are: LM1, Umbo; LM2, anterior end; LM3, posterior end; LM4, dorsal margin; LM5, ventral margin; LM6, superior limit of the anterior adductor muscle scar; LM7, inferior limit of the anterior adductor muscle scar; LM8, distal limit of the dorsal anterior lateral tooth; LM9, inferior limit of the anterior cardinal tooth; LM10, superior limit of the anterior cardinal tooth; LM11, ventral limit of the posterior cardinal tooth; LM12, posterior limit of the resilifer; LM13, superior limit of the posterior adductor muscle; LM14, inferior limit of the posterior adductor muscle; LM15, internal limit of the pallial sinus; LM16, external limit of the pallial sinus. Scale bar = 1 cm.

tissues and the inner side of the left valves photographed with a Nikon D100 digital camera. The forms of individuals were captured by the Cartesian coordinates of a two-dimensional configuration of 16 anatomical landmarks. To improve the identification of points, all landmarks were painted with small points of a permanent marker after capturing them (Figure 2).

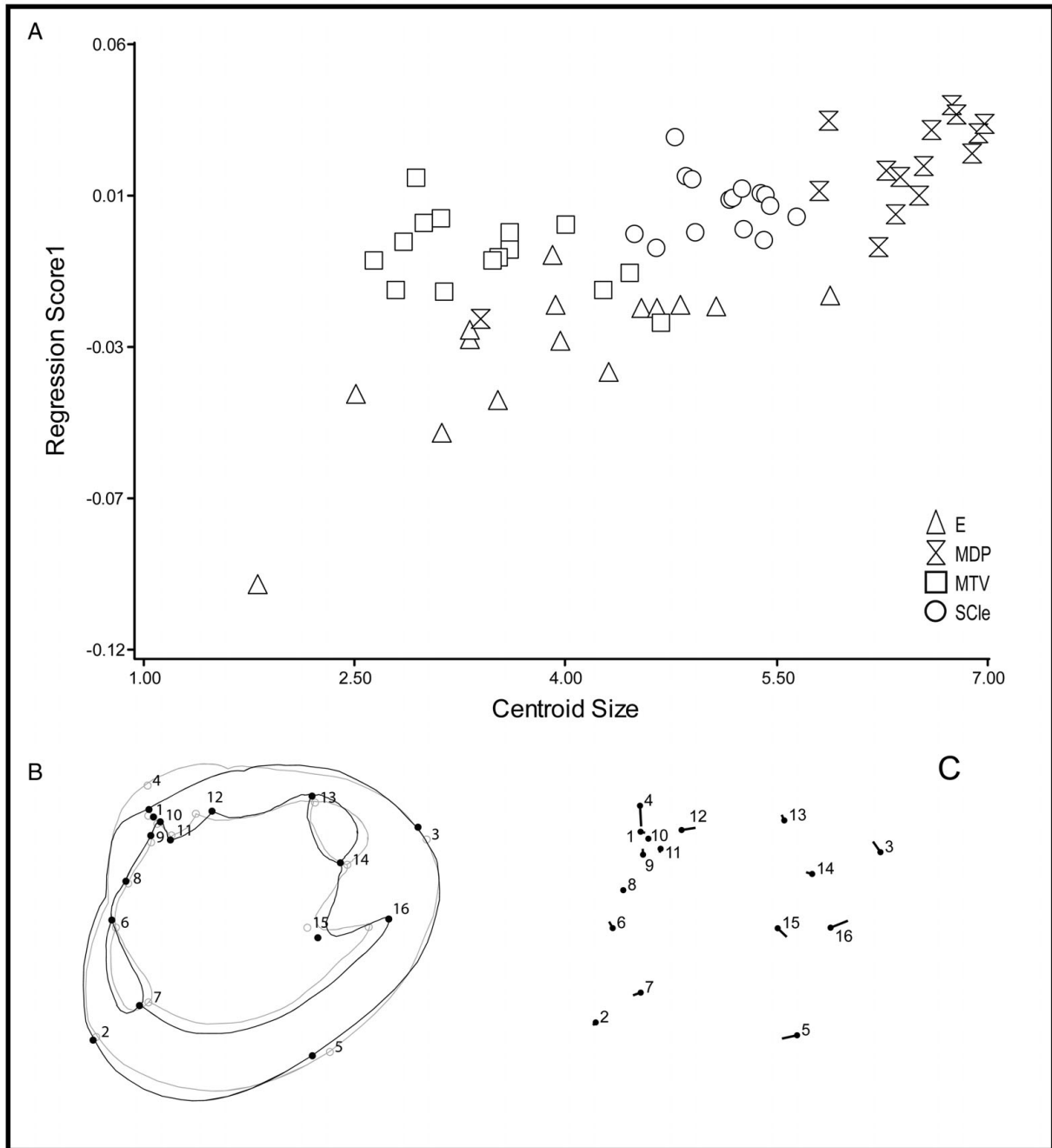
All specimens were digitalized with the software TPS dig2 (Rohlf, 1996) by one observer (J.H.S.). Landmark configurations were superimposed by generalized Procrustes analysis (Rohlf & Slice, 1990; Slice *et al.*, 1996). This procedure translates and rotates the landmark configurations to a common origin and scales them to unit centroid size. To assess and control putative allometric effects, we computed the multivariate regression of shape (Procrustes coordinates used as dependent variables) on size (independent variable). Klingenberg (2008) suggested that such regression is of utility to detect and remove the effect of size, age or environmental factors before shape comparisons between groups. To evaluate the independence between the shape and size variables, we carried out a permutation test with 10,000 rounds. The principal components of shape were calculated from a principal component (PC) analysis of the variance-covariance matrix of the Procrustes coordinates to display the major features of shape variation along the axes. The variable used for size normalization was the centroid size, 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).

We have computed a canonical variate analysis (CVA) on the first PCs in order to recover an axis of maximum discrimination among groups. Only the first, most informative, PCs were used in order to accomplish the 'rule of thumb' of discriminant analysis which indicates that the sample size of the smallest group (P , $N = 15$) needs to exceed by large amounts the number of predictor variables (16 2D landmarks = 28 shape variables or PCs). To test shape differences between localities we used an 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-MDGC:

127 Valdano & Di Rienzo, 2007; Márquez *et al.*, 2010b). This
 128 new method is a hybrid technique that combines a hierarchi-
 129 cal clustering based on Mahalanobis distances (Mahalanobis,
 130 1948) for hypothesis testing in multivariate cases. This
 131 method is successful in determining the number of groups
 132 in hierarchical cluster analyses. The graphical output of
 133 the MDGC test is a useful tool, since it shows a clear dis-
 134 tinction between statistically different shell shapes from
 135 each locality as well as their relationships (Márquez *et al.*,
 136 2010b).

RESULTS

Allometric growth, in which shape varies with size, was
 observed. The multivariate regression of shape on centroid
 size was highly statistically significant (permutation test with
 10,000 random permutations, $P < 0.0001$), and accounted
 for 11% of the total amount of shape variation (Figure 3).
 To describe the size-unrelated shell shape features, we per-
 formed a PC of the residuals from the regression of shape
 on centroid size (allometric correction). The first 8 PCs



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187 Fig. 3. Regression of shape onto size: (A) shape scores as a function of centroid size illustrating allometric growth of *Mactra isabelleana*. Shapes at the opposite
 188 extremes of the range of allometric variation are shown by using shell outlines (B), and displacement vector graphs (C); (B) the grey outline diagram shows average
 189 shell shape and the change from the grey circles to the black dots indicate the predicted landmark shift corresponding to an increase of centroid size by 7 scale
 factor; (C) the vector from the black dot diagram, indicates the predicted landmark shift corresponding to an increase of centroid size by 7 scale factor.

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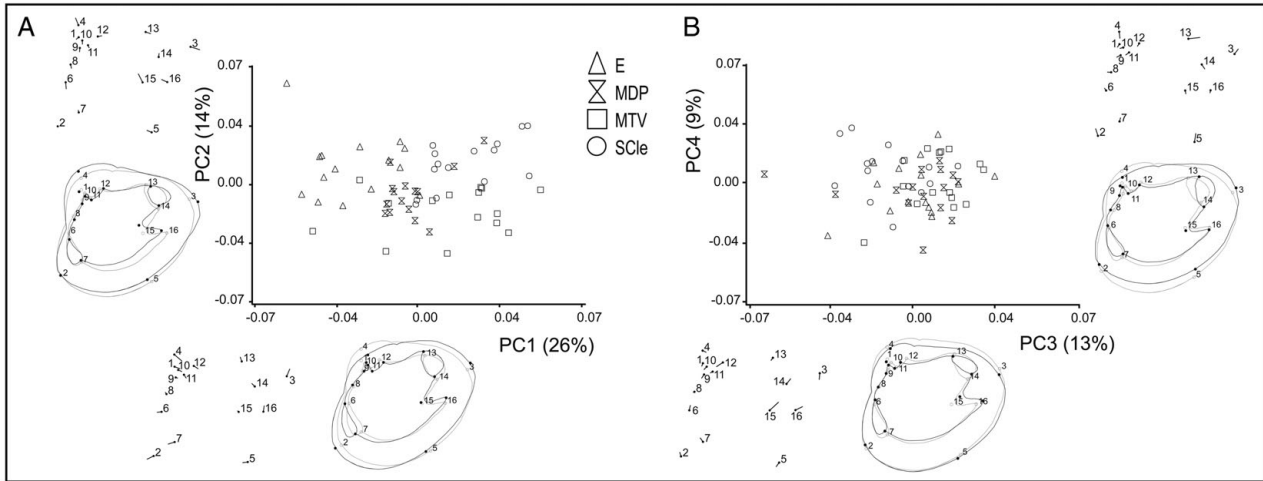


Fig. 4. Plot of the principal components (PCs) for *Mactra isabelleana* localities based on Procrustes distances. The figures represent the transformation and displacement vectors from the overall mean shape (light grey outline and black dot) to the positive extreme shape (black outline and vector) for 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. See Figure 1 for localities reference labels.

explained 82.5% of the total variation. The pattern of the shell shape variation is summarized in Figure 4 with scatterplots for the first four PCs of shape. The specimens from the four localities were mostly overlap. The geometrical interpretation of the positive extremes of PC1 was associated with an enlargement of the dorsoventral axis of the shell. The second PC axis was related to the development of the umbo shape and elongation of the posterior area (Figure 4A). The third PC showed a more circular shell shape and a shallower pallial sinus. Finally the fourth PC was associated with a posterior end elongation and less inflated umbo (Figure 4B).

The shell shape variations among the four localities sampled, were successfully discriminated using CVA of the residuals from the regression of shape on centroid size. The

first eight PCs explained collectively 83% of total variance. All them were used to compute a CVA with the smallest sample size ($P, N = 16$) being twice the shape variables used as predictors. The first 2 canonical axes (CV) explained 96% of the total variance. The greatest difference in CV1 was between the E and MTV localities (Figure 5A). The most evident shell shape variation along the CV1 was the difference in the development of the umbo and the elongation of the anterior end (Figure 5A). The CV2 was mostly associated with enlargement of the dorsoventral axis of the shell (Figure 5A) and this variation was observed between SCLE and the other localities.

The dendrogram calculated on the Mahalanobis distance matrix showed that, even though each locality had a

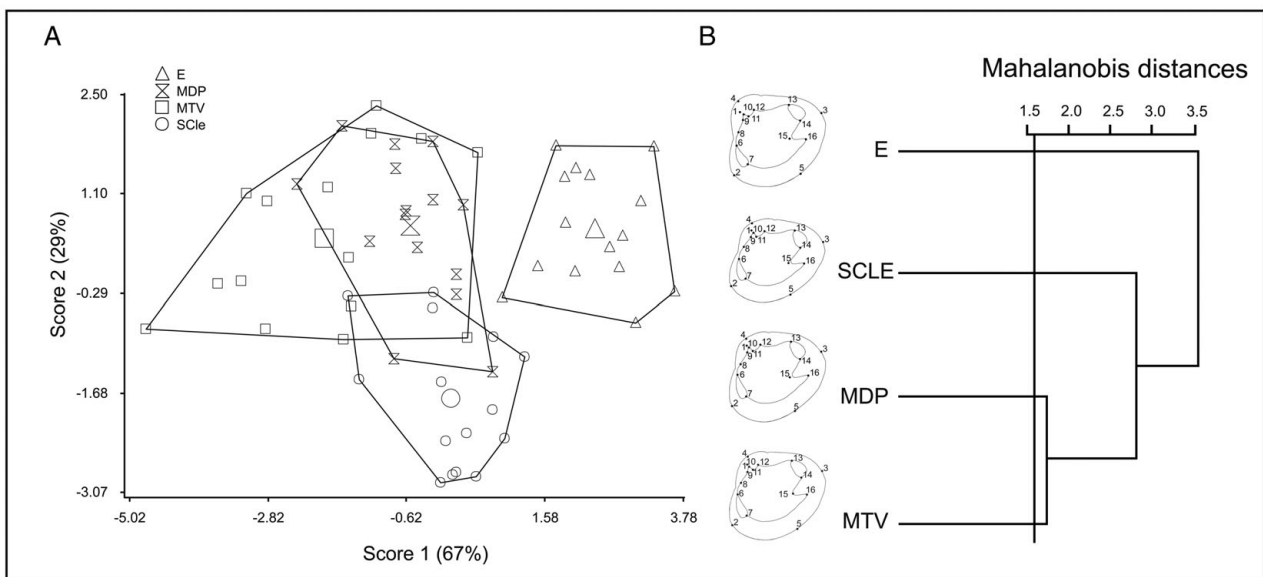


Fig. 5. Shell shape differences between localities: (A) analysis of the overall shell shape variation along the first two canonical axes. The largest symbols indicate the average for each locality; (B) Unweighted Pair Group Method with Arithmetic Mean dendrogram showing the relationships among localities, and the diagrams of the reconstructed consensus configurations of each sampled locality. The cut-off criterion ($P = 0.05$) obtained with the MDGC test is indicated with a horizontal line. Four statistically different groups of shell shapes were identified by this method.

characteristic shell shape with statistically significant differences ($P < 0.05$), similarities between sites grouped them in three principal groups. In the first level group are included the specimens from MTV and MDP. The specimens from SCLE were the most related and compounded the second group. Finally the specimens from E were the most divergent group in terms of their shell shape (Figure 5B).

DISCUSSION

In the GM method, the term shape is used to denote the geometric properties of an object that are independent of the object's overall size, position and orientation, whereas the form of an object comprises both its shape and size. The GM method allows testing separately the size and shape components of variations. In our paper, we study the shell shape variations but not shell form variation. The shape/size variation, called allometry, refers to a change in shape associated with size differences. The presence of allometry can account for a large and statistically significant proportion of morphological variation. We tested it by using a multivariate regression of shape onto size (Figure 3). The relation between size and shape was detected (allometry) which indicates that the shape variations were dependent on the size variation (Figure 3). The main shell form variation was related to the size and shape of umbo, chondrophore development and pallial sinus depth (Figure 3B, C). After this test we focused on the shell shape variation study of *M. isabelleana*. The unrelated-size shell shape variation observed was examined in four populations of Río de la Plata estuary and open sea. The use of the GM method revealed, with high resolution, the overall shell shape variations and significant differences between populations from different localities. The shell morphology of the specimens belonging to the MTV group was the most similar to that observed in the MDP group. The E locality was the most divergent population among the four localities sampled. The main variations in shell shape, evidenced by the PCs, were related to the enlargement of the posterior end and the development of the umbo. Both variations suggested a transition from trigonal to more elongated shells.

In natural systems, organisms face several ecological challenges and often respond with phenotypic shifts (Langerhans *et al.*, 2007). Thereby, the interaction between environment and genotype affects considerably the phenotype of the organisms. The results obtained in this study suggest, environmental similarities between MDP and MTV, intermediate in SCLE and exclusive in E. The adaptations to different environments are registered on the morphology of the species. There are several publications about the relationship between shell morphology and environmental factors such as latitude, temperature, currents, depth and type of sediment (e.g. Beukema & Meehan, 1985; Claxton *et al.*, 1998; Roopnarine *et al.*, 2008). In our study, the seasonal cycle of temperature, with cold and warm periods, affected similarly the four localities sampled (Guerrero *et al.*, 1997). The salinity effect over shell variation was also largely studied (e.g. Aguirre *et al.*, 2006; Krapivka *et al.*, 2007; Márquez & Van der Molen, 2011). Salinity apparently plays an important role over the morphology of *M. isabelleana*. This parameter is closely related to the oceanic currents and the type of sediment deposited by the basins of the Paraná and Uruguay Rivers (e.g. Stramma & Peterson, 1990; Guerrero *et al.*, 1997; Framiñan

et al., 1999; Simionato *et al.*, 2007). The bottom salinity values were similar in SCLE and MTV (25‰) while E presented the lower values (15‰) and MDP the highest values (36‰) (Guerrero *et al.*, 1997; Framiñan *et al.*, 1999; Acha *et al.*, 2003). The dispersion of the planktonic larvae in bivalves connects regional and local populations (Gaines *et al.*, 2007). Salinity and currents, among others causes, could affect this dispersion. However, in our study we observed that the specimens belonging to the E group are living in a muddy, anoxic substrate deposited by the basins of the Paraná and Uruguay Rivers while the other groups are burrowed in muddy to sandy substrates. These clearly divergent sediment conditions support our main hypothesis that the shell shape variation could be produced by different grain size existent along localities. In addition, the direction and speed of sediment, poured by the rivers' basins facilitate the connection between the E and SCLE groups, explaining the intermediate condition of the latter. The MDP and MTV groups were the most morphologically similar due to the grain size substrate where the organisms are living. In both localities sandy bottoms are dominant. (e.g. Carranza & Rodriguez, 2007; Haefen *et al.*, 2011). The SCLE group shows an intermediate morphology between the open sea and estuary morphotypes. This locality has a sandy soft bottom influenced by the pouring of mud sediments from the rivers (e.g. Lopez *et al.*, 2008). Finally the grain size sampled in the E locality is dominated by a fine mud substrate.

The shell shape variation among different populations of *M. isabelleana* studied was revealed using GM. The presence of this species in the Río de la Plata estuary and open sea is an excellent example to test the shell shape plasticity in burrowing species affected by the substrate where they are living.

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