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Allometric differences on the shell shape of two scorched mussel species along the Atlantic South American Coast

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Abstract Scorched mussels (Bivalvia: Mytilidae) are an important component of rocky shore assemblages around the world. The mussel beds of the mid-intertidal coasts of the south-western Atlantic are composed of two species of scorched mussels, which dominate the physiognomy and structure of the rocky shore communities. The present study investigates the variation in the shell-shape allometric trajectories of both species of mussels throughout their distributional range in the southwestern Atlantic coast, from latitude 34°S to 53°S. Shells of *Brachidontes rodriguezii* were collected at two Uruguayan localities and four Argentinean localities, while shells of *Perumytilus purpuratus* were

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collected at six Argentinean localities. Shell shapes of the specimens were studied by geometric morphometrics using landmark and semi-landmark methods. Different evolutionary histories and thermal regimes characterize these two species. *Brachidontes rodriguezii* seems to have a long history in the region and is present in a restricted area, the warm temperate region of the south-western Atlantic, while *P. purpuratus* seems to have a recent history and is present in a wide thermal range, involving the cold-temperate regions of the south-western Atlantic and south-eastern Pacific and the warm-temperate region of the south-eastern Pacific. Based on these considerations, we prompt the hypothesis that allometric trajectories of *P. purpuratus* shell shape is more variable and adapted to a specific habitat than *B. rodriguezii*. The impact of allometry was larger in *P. purpuratus* than in *B. rodriguezii*. Graphical evidence was gathered, showing that these two species differ in allometric growth forms and that the allometric shell morphology changes reflect environmental constraints and adaptation. While the intertidal mussel beds of the South American coasts are ecologically similar in appearance, we found that the allometric variation of the scorched mussels occurs in response to diverging evolutionary processes such as phenotypic plasticity in *P. purpuratus* and canalization in *B. rodriguezii*.

Introduction

Comprehension about biological and physical factors triggering changes in phenotypic traits has been the main objective of evolutionary ecologists (Piersma and van Gils 2011). Evolutionary theory predicts a trade-off between environmental conditions and evolution generation, influencing the phenotypic and genotypic variations of populations and species (Wennersten and Forsman 2012). Changes in body form during growth are an important issue to study since many biomechanical, physiological, behavioral, and ecological variables are associated with allometry (that is, the proportion of shape changes that can be exclusively explained by variations in size). In general, the body grows allometrically through changes in character position as well as timing or rate of character´s development (Gould 1977; Zelditch and Fink 1996; Klingenberg and McIntyre 1998; Zelditch et al. 2000; Kimmel et al. 2008; Urdy et al. 2010a, b). Allometric growth within and among species is related to age-specific shifts in the variable environmental conditions, favouring attributes that optimize the individual survival (Gould 1977; among others). Phenotypic variability could be represented by several evolutionary components. However, phenotypic plasticity and canalization (Waddington 1942, 1957) are two opposed processes. Canalization refers to the buffering of development against environmental and genetic perturbations, while phenotypic plasticity is related to an adaptive change of the phenotype in reaction to the habitat´s particular heterogeneity (Pigliucci et al. 2006).

The shell is generally the most conspicuous part of the mollusk body and preserves the ontogenetic record of growth (Márquez et al. 2010; Urdy et al. 2010b). Therefore, the shell shape is a key morphological trait that reflects the phylogenetic history, function, and life-habit (Crampton and Maxwell 2000). Geometric morphometrics (GM) methods provide the most important tools that enable a clear mathematical separation between size and shape variation, whose variation can be analyzed separately, its relationships properly studied,

and the geometry of the structures under study can be visualized along every step of the statistical analyses (Zelditch et al. 2012). Such visualizations provide information about direction and magnitude of shape change. There are several GM applications aimed to study different topics about marine bivalves shell shape variations. An extensive review of previous studies that applied GM methods (landmarks and outlines) was made by Rufino et al. (2013). As far as we know, there is only one highly detailed ontogenetic allometric study of the shell shape changes (Márquez et al. 2010), and inter-specific analyses are absent to date. Comparative studies of the ontogeny play a crucial role in the understanding of the processes of morphological diversification.

There are two scorched mussel species (Mytilidae: Brachidontinae) occurring in the southern south-western Atlantic: *Brachidontes rodriguezii* (d'Orbigny 1842), restricted to the warm-temperate region (32°–43°S; Scarabino et al. 2006; Trovant et al. 2013) known as the Argentine Biogeographic province, and *Perumytilus purpuratus* (Lamarck 1819), that spans the warm-temperate region of the south-eastern Pacific (south of 3°S) and the cold-temperate region of the southern South America (north to 41°S on the Atlantic), respectively known as the Chile-Peru and Magellanic Biogeographic Provinces(Briggs and Bowen 2013). Trovant et al. (2015) showed that *Perumytilus* includes two genetically distinct clades. The North clade confined to the warm-temperate Chile-Peru Province, and the South clade to the cold-temperate Magellanic Biogeographic Province, the latter being the only brachidontin restricted to cold-temperate waters. Moreover, Trovant et al. (2015) hypothesized that differentiation of the cold-temperate clade originated from budding-off from range edge populations of the warm-temperate clade, adaptation to a colder thermal regime, and gradual expansion along the coasts of Patagonia. During the Quaternary glacial maxima, populations from southern Chile were likely extirpated, and populations from central Chile and the southwest Atlantic remained separated by long periods (the last culminating in the LGM) from those inhabiting non-glaciated eastern Patagonia. After ice receded, the range of the South clade presumably expanded back, a secondary contact zone being established between the two clades within a relatively narrow latitudinal range between Valdivia (39°48′S) and Concepcion (36°49′S). There is some evidence for the incipient speciation of these two clades in their genetic and sperm structure (Trovant et al. *op*.cit.; Briones et al. 2012). However, no morphological differences have been found between shell shape of both North and South clades. Northwards expansion of *P. purpuratus* into the warm-temperate region of the south-western Atlantic may have been constrained by high-density blocking involving interaction with *B. rodriguezii*. These two species occur sympatrically between 41° and 43°S in the south-western Atlantic, either of them dominating extensive intertidal beds respectively north and south of that latitudinal range (Adami et al. 2013), having a high level of genetic divergence and no evidence of hybridization among them (Trovant et al. 2013). In this context, Van der Molen et al. (2013) suggest that adult individuals of *B. rodrieguezzi* and *P. purpuratus* present different outline shell shapes in the transition zone and the use of geometric morphometrics provides an effective tool to identify species of little scorched mussels. As an extension of the latter study, and knowing that different evolutionary histories and thermal regimes characterize these two species, we consider that *B. rodriguezii* and *P. purpuratus* offer an excellent opportunity to study intra and inter-specific variations in response to different environmental conditions. They are interesting for a comparison of ontogenetic trajectories on the shell form as their uniform physiognomy (defined as the appearance of ecological communities; Whittaker 1962) consists of dense and extended monocultures, under different environmental conditions as salinity, temperature, substrate, pH, among other variables. The aim of this study is to compare the post- recruited ontogenetic processes of the

interspecific phenotypic diversity of two species of scorched mussel distributed along the south-western Atlantic Ocean. Due to the fact that *P. purpuratus* is distributed along warm and cold temperate regions of the south-eastern Pacific Ocean, as well as in the cold temperate region of the south-western Atlantic, we suggest that allometric trajectories of the shell shape can be potentially seen as adaptations to specific habitats that might have originated part of the significant differences with *B. rodriguezii*, which is restricted to the warm-temperate region. All in all, we predict smaller amounts of shell shape variation along the ontogeny of *B. rodriguezii* than in *P. purpuratus*.

Materials and methods

Study area

The study region extends over the warm and cold temperate regions of the south-western Atlantic, respectively known as the Argentine and Magellanic Biogeographic Provinces (Balech and Ehrlich 2008; and references therein). This region exhibits large topographical changes and climatic heterogeneity. Ph and the tidal amplitude increase with latitude, from basic to more basic (Tyberghein et al. 2012) and from microtidal to macrotidal (Servicio de Hidrografía Naval 2014), there is a declining trend in sea surface temperature mean with latitude (Tyberghein et al. 2012). Additionally, air temperature changes seasonally in response to variation in solar radiation (Piola and Falabella 2009).

In Patagonian shores, the intertidal ecosystem is exposed from mid to high energy flows during high tides. The extreme desiccation is an important feature of these intertidal mussel-dominated beds. Strong dry winds (45–140 km/h), combined with low rainfall probably make these shores one of the most physically demanding rocky intertidal systems in the world (Bertness et al. 2006). Significant ecological barriers (extensive sandy beaches and La Plata River estuary) separate rocky shores along warm-temperate region. However, the cold-temperate region includes extensive rocky shores formed by stretches of cliffs and abrasion platforms with pebble beaches (Schellmann and Radtke 2000; Cavallotto 2008).

Fieldwork

We collected specimens from 12 localities along a wide latitudinal gradient (19 south latitudinal grades, 2400 km straight-line), in the South Atlantic Ocean from Río Grande (53°44′S 67°43′W) in the south of Argentina to Punta del Diablo (34°02′S 53°32′W) in northern Uruguay (Fig. 1).

At each site, ontogenetic series were collected from natural populations, and individuals ranging from 1.6 to 31.0 mm were analyzed. They were invariably obtained randomly from the mid-intertidal rocky zone, aiming at the centroid of patches with 100% mussel cover developed over gently sloping ("horizontal") platforms. The density (ind 100 cm^{-2}) of each locality were registered. The following environmental variables: concentration of silicate, salinity, concentration of nitrate, concentration of calcite, pH, sea surface temperature and concentration of chlorophyll-a were obtained at each locality, based on data downloaded from a 9.2 km spatial resolution satellite image database (Tyberghein et al. 2012, available at http://www.oracle.ugent.be/).
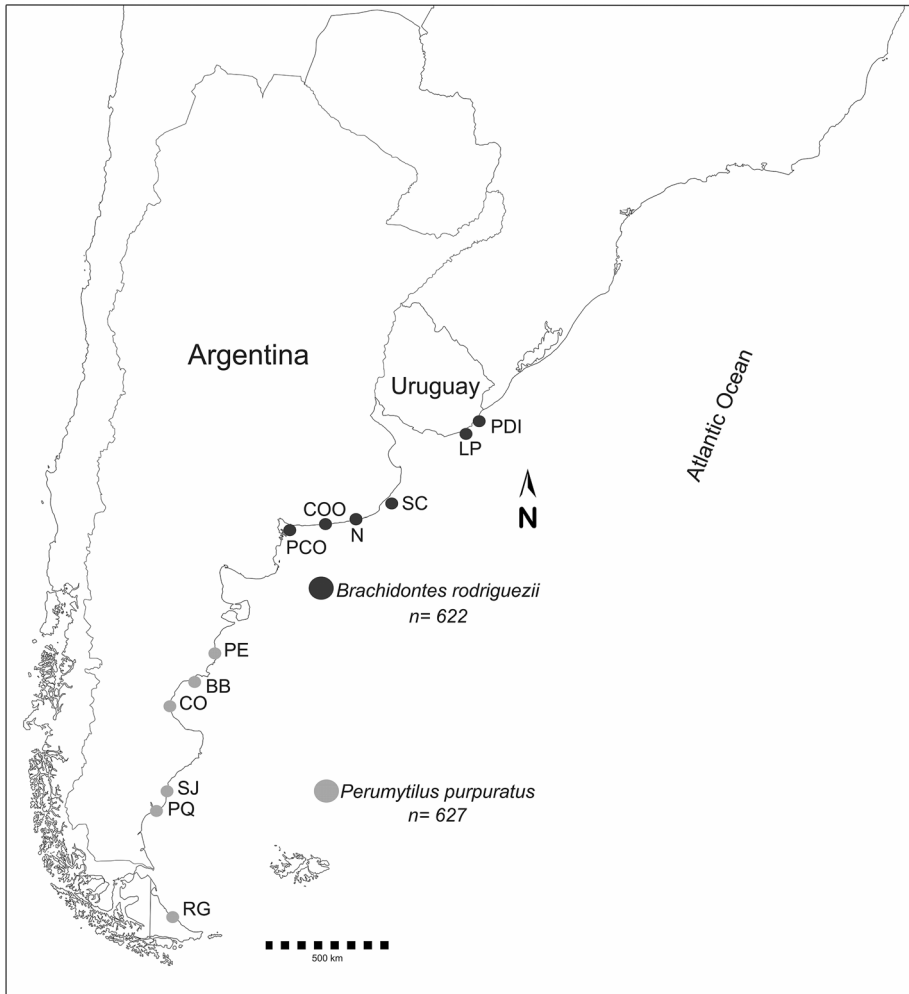
Fig. 1 Map of the South Atlantic Ocean shelf showing the 12 sampling localities. From South to North are: *RG* Río Grande, *PQ* Punta Quilla, *SJ* Puerto San Julián, *CO* Caleta Olivia, *BB* Bahía Bustamante and *PE* Punta Escondida, and *PCO* Pehuencó, *COO* Claromecó, *N* Necochea, *SC* Santa Clara, *LP* La Paloma, *PDI* Punta del Diablo

Geometric morphometric analysis

In all, 1249 specimens of the two species of mussels were analyzed. Around 100 individuals were randomly selected covering the ontogeny series from each site. Shell shape variables were generated from 4 anatomical landmarks and 40 semilandmarks to describe the overall outline form (for anatomical descriptions of the landmarks, see Fig. 2). Ten semilandmarks were pointed out on shell outline between landmarks 1, 2, 3 and 4. The exact location of semilandmark coordinates on the curve cannot be identified and hence it was mathematically estimated. Sliding was performed using the algorithm which optimizes the bending energy (Bookstein 1997; Gunz et al. 2005; Gunz and Mitteroecker 2013) to minimize the deformation between each specimen and the consensus shape (Procrustes

Fig. 2 Landmarks and semilandmark configurations on the outline of the scorched mussel shell *Brachidontes rodriguezii*. Landmarks (black dots) are: (*1*) umbo (anterior end), (*2*) tip of the posterior hinge ligament, (*3*) maximum posterior curvature, (*4*) projection at 90° of the vector formed between the landmark 1 and 2 on the outline of the shell. The semilandmarks (grey dots) (*5–14*) semi-landmarks along the boundary between the landmarks 1 and 2, (*15–24*) semi-landmarks between landmarks 2 and 3, (*25–34*) semi-landmarks between landmarks 3 and 4, and (*35–44*) semi-landmarks between landmarks 4 and 1. Scale bar = 1 cm
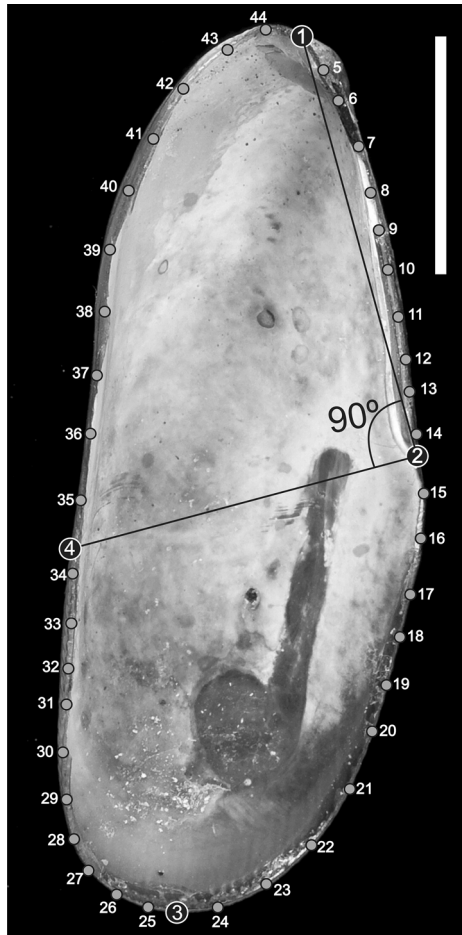
average of all specimens) in the TPSRelw software (Rohlf 2004). After sliding the semilandmarks, all the 44-landmark configurations were superimposed by a Generalized Procrustes Analysis (Rohlf and Slice 1990; Slice et al. 1996). This procedure translates and rotates the landmark configurations to a common origin and scales them to unit centroid size. The Procrustes coordinates of the aligned individuals were then used as shape variables to perform the multivariate statistical analyses. Only the left shells were digitized to avoid redundant information in symmetric structures.

Ontogenies analyses

In the present study, we understand "allometry" as the pattern of covariation among morphological traits or the relationship between size and shape components (Gould 1966; Mosimann 1970). To estimate the between-species allometry variation, we use a pooled species multivariate regression of the independent aligned Procrustes coordinates (the shape variables) on centroid size (the size measure, Monteiro 1999; Klingenberg 2016). To evaluate the differences on intra and inter-specific allometric trajectories, we used a

permutation MANCOVA test in R using Adonis function (Zelditch et al. 2012) to characterize how the ontogenies differ, testing the null hypothesis that the direction of ontogenetic change does no differ between species. After that, we study the direction of ontogenetic change throughout angle between allometric trajectory corporations. The aligned shape coordinates were used as dependent variables, species as the grouping variable, and centroid size as a covariate. If the interaction size x species is significant, then it follows that there are differences in the slopes. Moreover, we used angular comparisons of vector directions after the routine available in MorphoJ (Klingenberg 2011). This routine is used to compare the among-sites pairwise angular directions (both between and within-species), thus enabling the testing of the null hypothesis that the allometric vectors are no more similar than expected by chance. Angle between allometric trajectories is one of the most widespread methods to compare allometry trajectories among different groups (Klingenberg and Marugán-Lobón 2013). Mean angle refers to the (within-group) average trajectory. We used mean angle as a proxy to between-group variation in allometric trajectories. All morphometric analyses were conducted with the MorphoJ, version 1.06d software. Differences among inter and intraspecific mean angle were tested using ANOVA tests. Finally, we used the Mantel's simple test (Mantel 1967) to measure the degree of association between the angles and a matrix of environmental distances for each species independently: the Euclidean distances between localities based on the mean of eight environmental variables presented as supplementary material. When the variation patterns can be represented in matrix format, the Mantel test is one of the most widely used to assess matrix proportionality. Mantel test was used originally to evaluate the relationship between phenetic distances among local populations and their geographic distances (Sokal 1979). Since then, Mantel test has been used in several disciplines such as ecology (Fortin and Gurevitch 2001; MacDougall-Shackleton and MacDougall-Shackleton 2001; Wright and Wilkinson 2001), morphology (van Schaik et al. 2003; Márquez and Van der Molen 2011), and behaviour (Cheverud 1989), among others. Here we formalized among-group environmental and growth differences by obtaining Euclidian distances from raw environmental variables (Table 1 in supplementary material), and using the among-localities angles corresponding to allometric trajectories, respectively. Statistical analysis was run using Infostat software (Di Rienzo et al. 2009).

Results

Ontogenetic allometry

The relation between pooled within-species shape and size accounts for 31.2% of the variation in shape (Fig. 3a). Also, the permutation test indicates that such allometry is highly significant ($p < 0.0001$). The interspecific allometry shape changes were associated with the umbo position and the amplitude of the shell (similar to the relationship between height/length). Smaller specimens exhibit a rounded, sub-terminal umbo, and an expansion in anterior-dorsal and ventral direction, generating a rounded shell with anterior-dorsal and posterior–ventral curves slightly outward. Conversely, larger shells present a compression in dorsal–ventral direction, generating a terminal umbo with an elongated shell with an anterior–ventral convex curve (Fig. 3b). All localities of both species presented allometric growth (Table 1; Fig. 3c). Between-species and among-localities allometric trajectories were significantly different in term of their slopes (Table 2). The directions of all pairwise

Fig. 3 Allometric trajectories of the scorched mussel species of South American intertidal. **a** Pooled within-species regression. **b** Overlapped wireframes for shapes predicted by the multivariate regression of shape on size for *Brachidontes rodriguezii* (black vectors) and *Perumytilus purpuratus* (grey vectors) from the smallest (CS = 1) to largest specimens (CS = 70). **c** Pooled within-localities regression. Biggest circle indicates the centroid and the whiskers the standards deviations of two axes from each locality. Codes from South to North are: *RG* Río Grande, *PQ* Punta Quilla, *SJ* Puerto San Julián, *CO* Caleta Olivia, *BB* Bahía Bustamante and *PE* Punta Escondida, and *PCO* Pehuencó, *COO* Claromecó, *N* Necochea, *SC* Santa Clara, *LP* La Paloma, *PDI* Punta del Diablo

allometric trajectories were similar ($p < 0.001$), but the mean of between-species pairwise angle comparisons was greater than the within-species average (Table 2 in supplementary material).

Within-species comparisons showed that localities of *P. purpuratus* present more among-site angle dispersion than *B. rodriguezii* sites (Fig. 4). Finally, Mantel tests showed a significant correlation between the allometric angles and environmental (Table 1 in supplementary material) distances ($R = 0.55$; $p = 0.02$) in *B. rodriguezii,* whereas the same test provided non-significant results in *P. purpuratus* ($R = -0.17$; $p = 0.62$).

Discussion

This study used geometric morphometrics to compare the variation of the shell shape on the allometric ontogeny of *B. rodriguezii* and *P. purpuratus*, two small mussels from the south-western American coast. Also, we provide compelling graphical and analytical evidences that these species differ in allometric growth forms. We hypothesize that the allometries of the shell shape change reflect environmental constraints and adaptation. In fact, our results support the differentiation between the outline of *B. rodriguezii* and *P. purpuratus* shell shapes previously showed by Van der Molen et al. (2013) and Trovant et al. (2017), extending the difference to all the ontogeny. However, Aguirre et al. (2006) postulates no differences between *B. rodriguezii* and *P. purpuratus* shell shape, thus suggesting that *B. rodriguezii* could be considered a synonym of *P. purpuratus*. However, our results contradict this statement and suggest caution when assessing between-taxa relationships. The mytilids present morphological variations linked to geographical location and its position across the intertidal zone (Seed 1968; Briones and Guiñez 2005). Some environmental conditions, such as temperature, aerial exposure, and wave action have a major impact on the population dynamics of mussels, modifying their growth, reproduction, and shell morphology (Griffiths and Griffiths 1987; Hawkins et al. 1992; Seed and Suchanek 1992; Steffani and Branch 2003). Another potential modeler of the life-history pattern is the presence of predators (Reimer et al. 1995; Valladares et al. 2010). Here we show that the ontogenetic trajectories of *B. rodriguezii* and *P. purpuratus* deviate sharply from one another. During their ontogeny, *B. rodriguezii* follows a more conservative (more elliptical shape of the equal frequency ellipse) pattern through the morphospace than *P. purpuratus*, which present larger variation (larger minor axis of the ellipse, Fig. 3a). In the particular case of *B. rodriguezii,* the distribution of the variation on the allometric trajectory was restricted and presented a correspondence with the meso-scale environmental conditions. In spite of this, the ontogeny of the shell shape of *B. rodriguezii* presents a phenotype that arises as a balance between buffering development against perturbations and adaptive change in response to such perturbations or fluctuations. The biological robustness, defined here as the persistence of an organismal trait under perturbations (Félix and Wagner 2006), observed in the allometric trajectories exhibited by *B. rodriguezii*
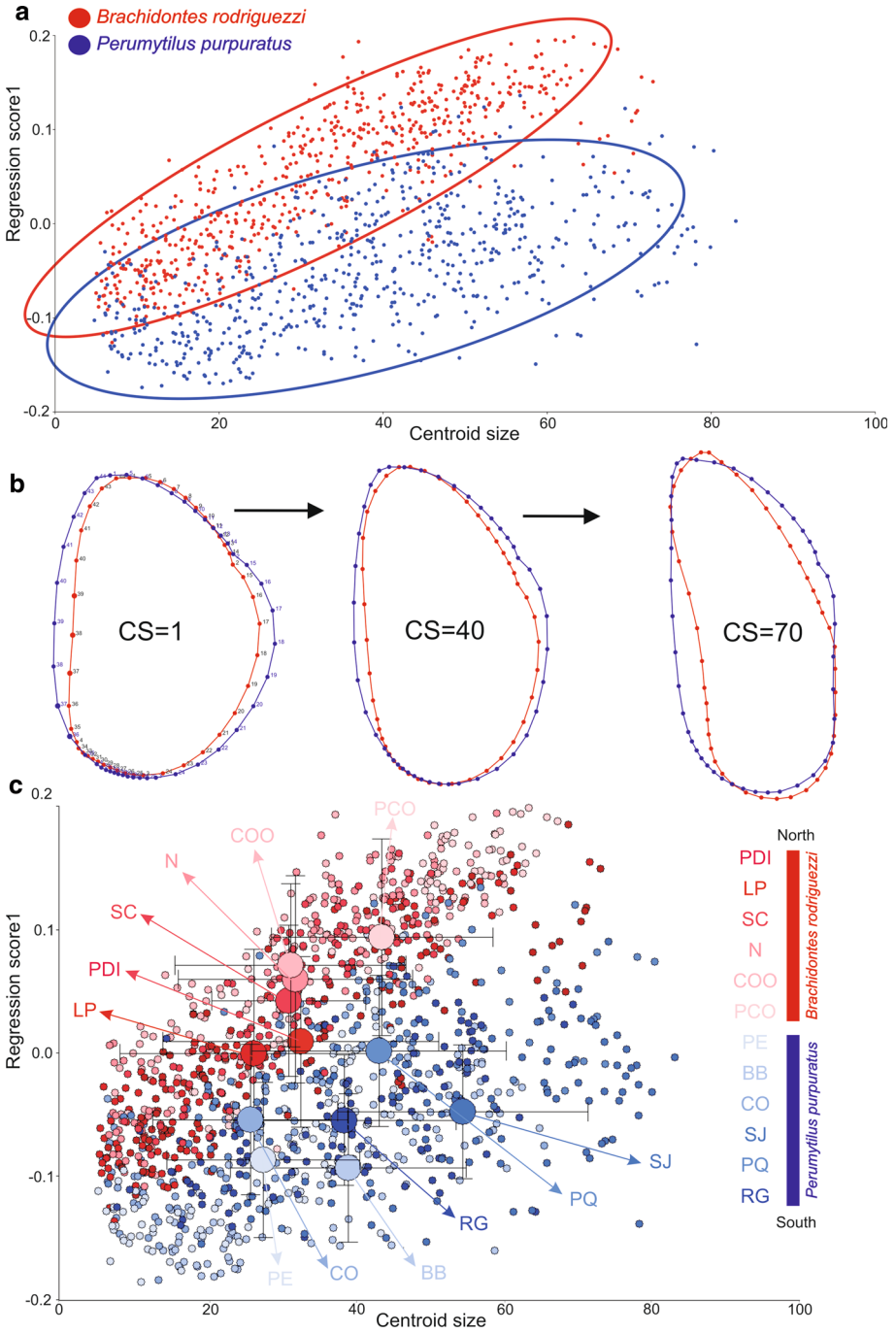
a
Regression score1
Brachidontes rodriguezzi
Perumytilus purpuratus
Centroid size

b
CS=1   →   CS=40   →   CS=70

c
Regression score1
Centroid size

North
PDI
LP
SC
N
COO
PCO   *Brachidontes rodriguezzi*

PE
BB
CO
SJ
PQ
RG   *Perumytilus purpuratus*
South

Table 1 Multivariate regression between shape and centroid size in scorched mussel species

Species	Localities	n	Sum of squares of Procrustes coordinates				
			% explained variance	Total	Predicted	Residual	*p* value
Perumytilus purpuratus	RG	108	20.83420	0.548.9	0.11425	0.434313	< 0.0001
	PQ	101	23.66210	0.53090	0.12562	0.40527	< 0.0001
	SJ	105	20.12170	0.61257	0.12326	0.48931	< 0.0001
	CO	100	42.21750	0.62472	0.26374	0.36098	< 0.0001
	BB	110	46.98240	0.65649	0.30844	0.34806	< 0.0001
	PE	103	42.84780	0.71873	0.30796	0.41077	< 0.0001
Brachidontes rodriguezii	PCO	90	71.88440	0.71147	0.51143	0.20003	< 0.0001
	COO	102	58.61300	0.63053	0.36957	0.26096	< 0.0001
	N	102	56.79770	0.98437	0.55910	0.42527	< 0.0001
	SC	108	47.24340	0.59787	0.28245	0.31542	< 0.0001
	LP	111	69.61210	1.00519	0.69973	0.30545	< 0.0001
	PDI	109	52.84130	0.80273	0.42417	0.37856	< 0.0001

Codes from South to North are: *RG* Río Grande, *PQ* Punta Quilla, *SJ* Puerto San Julián, *CO* Caleta Olivia, *BB* Bahía Bustamante and *PE* Punta Escondida, and *PCO* Pehuencó, *COO* Claromecó, *N* Necochea, *SC* Santa Clara, *LP* La Paloma, *PDI* Punta del Diablo

Table 2 MANCOVA in adonis(); inter-intra specific ontogenetic trajectories of scorched mussels

	Df	Sums of Sqs	Mean Sqs	F. Model	R2	Pr(> F)
Species						
CS	1	2.3275	2.3275	424.17	0.1651	0.001***
Specie	1	4.3975	4.3975	801.44	0.31193	0.001***
CS: specie	1	0.5467	0.5467	99.64	0.03878	0.001***
Residuals	1244	6.8259	0.0055	0.48419		
Total	1247	14.0976	1			
Perumytilus purpuratus						
CS	1	0.9477	0.94772	240.88	0.20005	0.001***
Localities	5	1.1528	0.23055	58.599	0.24333	0.001***
CS: localities	5	0.2212	0.04424	11.245	0.04669	0.001***
Residuals	614	2.4157	0.00393	0.50993		
Total	625	4.7374	1			
Brachidondes rodriguezii						
CS	1	2.9413	2.94132	956.06	0.49378	0.001***
Localities	5	0.9414	0.18828	61.2	0.15804	0.001***
CS: localities	5	0.2005	0.04009	13.03	0.03365	0.001***
Residuals	609	1.8736	0.00308	0.3143		
Total	620	5.9568	1			

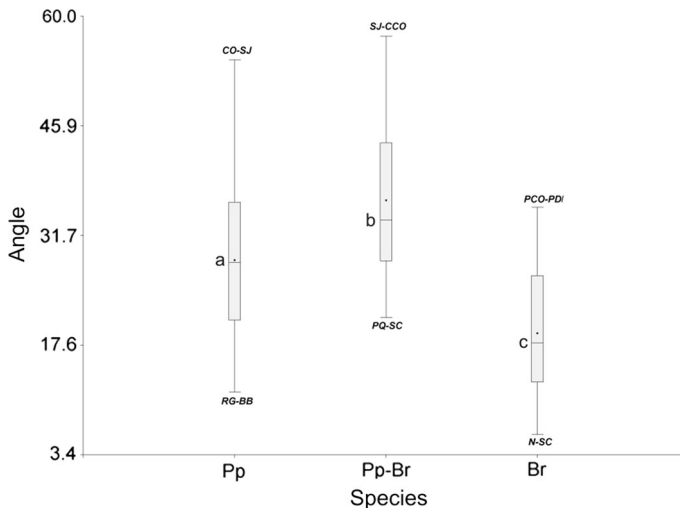The asterisks represent the statistical significance level

Fig. 4 Within and between-species angle variations. The central dot represents the mean; the median is showed as a central line; the limits of the box, the first and third quartiles, and the whiskers the 95% confidence interval. Different lowercase letters indicate significant differences ($p < 0.05$) in pairwise comparisons test. *CO–SJ* Caleta Olivia–San Julián, *RG–BB* Río Gallegos–Bahía Bustamante, *SJ–CCO* San Julián–Claromecó, *PQ–SC* Punta Quilla–Santa Clara, *PCO–PDI* Pehuencó–Punta del Diablo, *N–SC* Necochea–San Clemente

suggest environmental canalization (as defined by Wagner et al. 1997) of this species. Here we use canalization as defined by Willmore et al. (2007): a constraint on variability by restricting the scope of resultant variation expressed in the phenotype. On the other hand, the adaptation exhibited by *P. purpuratus* along its history of colonization of the South American coast can be the mechanism explaining the observed variation. Geographical expansion, from northern Chile to the Magellanic Biogeographic Province (Southern Chile and Southern Argentine), with a concurrent adaptation of marginal populations to a cold-temperate thermal regime, leading to incipient peripatric differentiation and the colonization of a new ecological niches (Trovant et al. 2015) is included in the adaptation *P. purpuratus*'s exhibited along the coast of South America. We found that *P. purpuratus* presents larger ontogenetic allometric variation than *B. rodriguezii*, thus being able to be more plastic in its phenotype. Therefore, phenotypic plastic responses to a new environmental variation along the ontogeny could help to expand the geographical distribution range via adaptation operating on a form to optimize the shell shape and buffering the environmental heterogeneity.

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