



Morphometric variations of two patellid limpets between artificial breakwaters and natural reefs

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ABSTRACT

Artificial shorelines often differ from natural reefs in shape, composition, and habitat complexity. They promote higher accumulation of pollutants and increased physiological stress, which lead to changes in species distributions and ecosystem functioning. This can promote trophic shifts and reduced genetic diversity of gastropod populations inhabiting artificial shorelines and might promote morphological changes, which may influence behaviour, vulnerability to predation, feeding efficiency, sex ratios, reproductive development, and overall fitness. This study explores inter- and intraspecific shell morphometric variations in *Patella rustica* and *P. caerulea* between breakwaters (ripraps) and natural reefs in three sites of Ceuta (North Africa, Spain), including a physicochemical assessment of the studied locations: shore orientation, inclination and wave exposure, and substratum nature, heterogeneity and roughness. Limpets on artificial substrata had a slightly smaller extra-visceral cavity and flattened shell profile, which suggests that the desiccation and temperature stress driven by the lithological composition and roughness of the studied substrata might have influenced the registered shell shape variation. However, the high morphometric variation registered for both species across sites and substrata suggests that limpets' morphology might be responding to a complex interaction of environmental and ecological factors rather than solely rock type. The findings of this study highlight the complex interplay between rock type and local environmental conditions in shaping patellid limpets' shell morphology and provide insights into the adaptive mechanisms that drive shell shape variation in limpet populations in the face of coastal sprawl and anthropogenic global change.

1. Introduction

Coastal sprawl has dramatically altered intertidal ecosystems worldwide, resulting in changes in species distributions, community structure and ecosystem functioning (Connell and Glasby, 1999; Seitz et al., 2006; Bishop et al., 2017; Masucci and Reimer, 2019). Artificial structures are poor surrogates of natural ecosystems and often lack spatial heterogeneity at diverse spatial scales, causing an overall reduction in habitat complexity (Moschella et al., 2005; Firth et al., 2015; Cacabelos et al., 2018; Ostalé-Valriberas et al., 2018). At the intertidal level, surface orientation, inclination and heterogeneity determine the composition of the community and can determine the availability of refuge against desiccation and temperature stress, as well as grazing and predation pressure (Moreira et al., 2006; Bulleri and

Chapman, 2010; Aguilera et al., 2019; Amstutz et al., 2021). Moreover, roughness, along with other substratum characteristics, such as colour, shape, pH and lithology, could influence species settlement and the physical stress experienced by the communities inhabiting rocky surfaces (Rivera-Ingraham et al., 2013; Hanlon et al., 2018; Sempere-Valverde et al., 2023). Furthermore, faunal populations inhabiting artificial hard substrata can show higher accumulation of heavy metals and other pollutants, higher stress levels, shifts in the trophic niche and a reduced genetic diversity when compared to natural habitats (Sedano et al., 2020a, 2020c; Seitz et al., 2006; Espinosa et al., 2021). Due to these constraints, many local native species have trouble colonizing artificial substrata, which can lead to altered population structure and reduced genotypic and phenotypic diversity of marine organisms, promoting the fragmentation of native species populations and contributing

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to the loss of coastal biodiversity (Fauvelot et al., 2009, 2012; Firth et al., 2013, 2016; Bishop et al., 2017; Alter et al., 2020).

Limpets are common inhabitants of intertidal habitats and play important ecological roles in rocky intertidal communities as primary consumers and ecosystem engineers, influencing ecosystem dynamics (Burgos-Rubio et al., 2015). Due to their ecological importance and ability to respond to changes in habitat structure, limpets have been widely studied in the context of coastal urbanization and artificial substrata (e.g., Espinosa et al., 2009, 2011, 2021; Fauvelot et al., 2009; Chapman and Underwood, 2011). Although coastal structures always have a negative ecological impact because they replace natural habitats, the introduction of seawalls, breakwaters and jetties can have both positive and negative effects on limpet populations (e.g., Moreira et al., 2006; Rivera-Ingraham et al., 2011a; Bonnici et al., 2013; Cacabelos et al., 2016). Artificial substrata provide colonizable surfaces that might sustain high density of limpets, leading to increased population numbers for certain limpet species (Rivera-Ingraham et al., 2011a; Bonnici et al., 2013; Ostalé-Valriberas et al., 2023). However, artificial shorelines can also provide low-quality habitats, lacking refugia, causing trophic shifts and favouring non-indigenous species, which can negatively impact native limpets reproductive potential to the extent of not being able to sustain viable limpets' populations (Burgos-Rubio et al., 2015; Sedano et al., 2020a; Espinosa et al., 2021; Branch et al., 2023; Earp et al., 2023). Moreover, artificial substrata can lead to reduced genetic diversity within limpets' populations and an increased genetic differentiation from populations in natural areas, which suggests that artificial habitats may select for distinct and narrower range of genotypic traits than natural areas (Fauvelot et al., 2009, 2012). This would have conservational implications, as these limpets could be less resistant to environmental stressors and ecological impacts. Nonetheless, this reduced genetic diversity and increased differentiation could also be due to a founder effect, as the populations might be still settling on the recently deployed artificial habitat (Bishop et al., 2017 and references therein). In any case, the effects of substratum type and shape on limpet populations are complex and context-dependent, and further research is needed to better understand these effects and to develop effective management strategies for conserving limpet populations in urbanized coastal environments (Lima et al., 2016; Sedano et al., 2020a, 2020b; Espinosa et al., 2011, 2021; Fauvelot et al., 2012; Ostalé-Valriberas et al., 2022).

Gastropod shells are widely used as indicators of environmental changes in marine ecosystems, and limpets' shell parameters, such as height, thickness, and length, can be negatively affected by pollution stress (Nakhle, 2003; Márquez et al., 2011, 2017; Gharred et al., 2019; Harayashiki et al., 2020; Landro et al., 2021). Therefore, the analysis of shell shape can provide valuable insights into the overall health of marine ecosystems and the impact of abiotic and biotic stressors, such as urban proximity (Doyle et al., 2022; Maltseva et al., 2022). Overall, limpets' shell shape is determined by an interplay of genetic and environmental factors (Batelli, 2016; Nuñez et al., 2018; Nuñez and Fernández Iriarte, 2022), and limpets' shells are characterized by high phenotypical plasticity in shape, which has been linked to habitat adaptation (Puig, 2016; Bouzaza and Mezali, 2018, 2019; Echeverry et al., 2020; Vasconcelos et al., 2021; Belmokhtar et al., 2022). For example, limpets in higher tidal levels and warmer latitudes tend to have a taller shell profile, which reduces desiccation and temperature stress by reducing heat transfer from sunlight radiation and conduction with the substrate (Vermeij, 1973; Prusina, 2013). Similarly, a more centred shell apex and circular base increase adhesion strength to the substrate and could be an adaptation to areas with high wave action (Denny and Blanchette, 2000; Paulo Cabral, 2007; Bouzaza and Mezali, 2019). Varying urbanization pressure can also impact limpets shell shape (Gharred et al., 2019; Landro et al., 2021). For example, Tablado and Gappa (2001) described bigger panpulmonate limpets with higher shell profiles inside a harbour than nearby habitats exposed to wave action. It was hypothesized that the differences in size could be due to the

availability of longer foraging periods due to the absence of wave disturbance inside the port. Similarly, Landro et al. (2021) and Nuñez et al. (2012) found histological alterations, shells with globular malformations, decreased shell thickness and hardness, and a taller shell profile in areas under anthropogenic impact. In addition, the taller shell profiles detected inside harbours in these studies might be a response to lower wave action or to differences in substratum orientation and other environmental parameters of relevance for limpets that could have differed between the studied locations (Tablado and Gappa, 2001; Seabra et al., 2011; Nuñez et al., 2012; Landro et al., 2021). However, more research is needed to understand the adaptation of limpets to different habitats and how substratum type can influence limpets' morphology.

Geometric morphometrics can provide more insight into complex shape variation than classical techniques (Zelditch et al., 2012). Geometric morphometrics uses multivariate methods to identify subtle shape variations between populations and species by the analysis of intricate details, like curvature and sculpture patterns, which could help segregate species or understand ecological adaptations (Faria et al., 2017; Matos et al., 2020; Mamet et al., 2021). Using geometric morphometrics, this study aims to explore morphometric variations in limpet shell shape between artificial and natural substrata in different sites of Ceuta (N Africa, Spain) and the possible influence of a series of physicochemical variables in the observed shell shape patterns. To this end, the following alternative hypotheses have been tested. H1: the shell shape of *P. rustica* and *P. caerulea* vary between artificial breakwaters (ripraps) and natural rocky reefs; H2: this shell variation has the same change direction in different sites within the area of study; and H3: the shell form (shape + size) variation registered among sites and between substrata is coincident with differences in physicochemical parameters related to substratum type, wave exposure and spatial configuration of the studied sites and substrata.

2. Methods

2.1. Study area and species selection

The Strait of Gibraltar is a region of high biodiversity and ecological importance due to its location between biogeographical regions, making it key area for connectivity of populations that are vulnerable to impacts, and a priority area for conservation (Rivera-Ingraham et al., 2013; Ostalé-Valriberas et al., 2022). *Patella rustica* and *P. caerulea* are two common intertidal limpet species that are widely distributed throughout the Mediterranean Sea and the NE Atlantic Ocean. In Ceuta (Strait of Gibraltar), limpet species have been found in greater densities on artificial than natural substrata (see Ostalé-Valriberas et al., 2018, 2022). This is due to a reduced human collection pressure (fenced or hardly accessible), and higher shoreline heterogeneity on artificial than natural shorelines (Espinosa et al., 2009; Rivera-Ingraham et al., 2013; Ostalé-Valriberas et al., 2022, 2023).

Surveys were made in three Ceuta sites, each with dolomitic limestone r ripraps and natural rocky shores (less than 650 m apart) (Fig. 1. A). The ripraps studied in North Bay, Chorrillo, and Fuentecaballos were older than 16 years and were constructed in 1935, 1988, and 2006, respectively (Ostalé-Valriberas et al., 2018). Therefore, artificial substrata are expected to host climax benthic communities in terms of species composition and richness (Hawkins et al., 1983; Coombes, 2011; Dong et al., 2016). Additionally, these substrata are anticipated to support mature limpet populations, as the average lifespan of the studied species is less than 10 years (Espinosa et al., 2008; Henriques et al., 2012; Prusina et al., 2015).

2.2. Environmental study

The physicochemical description of the studied areas was carried out in July 2022 by haphazardly deploying two horizontal 10 m transects at

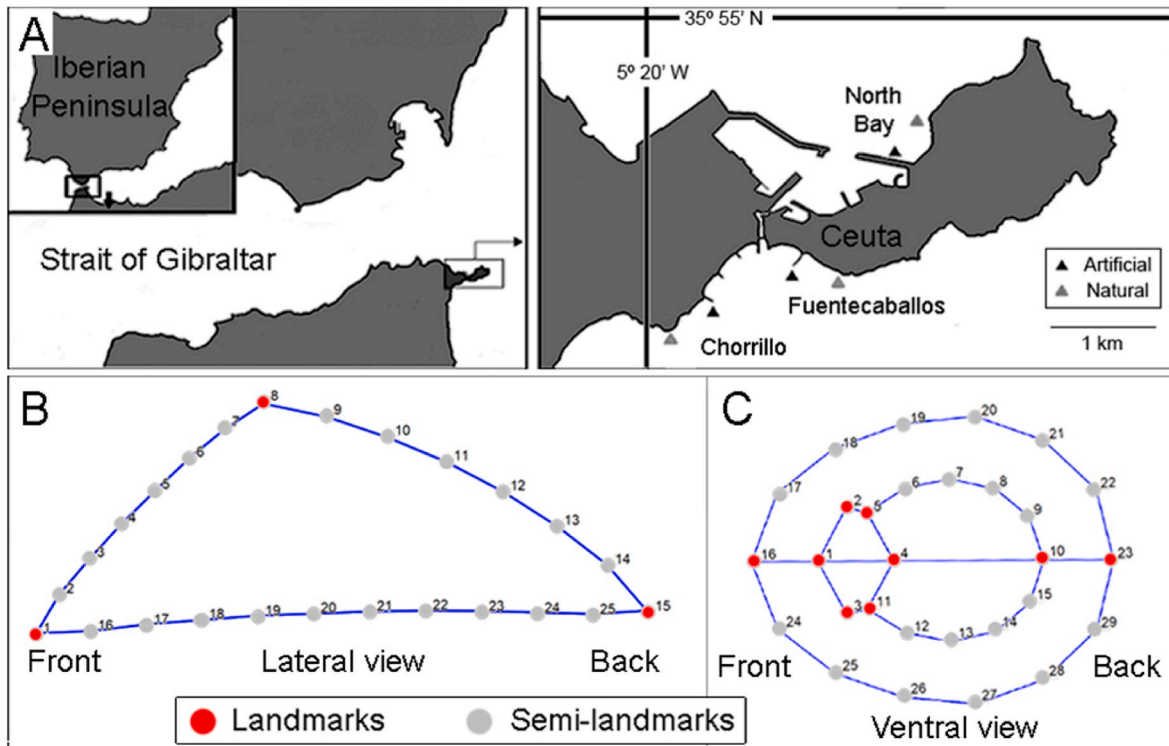


Fig. 1. A: Study sites, indicating the location of the sampled artificial and natural substrata in Ceuta (North Africa, Spain). B: Landmarks (LM) and semi-landmarks (S-LM) configuration for the lateral and ventral views depicting the consensus shape for all sampled individuals. The lateral view is a non-symmetric shape with LM1 located at the front end, LM8 on the apex and LM15 at the back end of the shell. These LM are respectively coincident with the LM16, LM 4 and LM23 of the ventral view. The ventral view is a symmetrical configuration with the axis of symmetry crossing LM16 (front of the shell), LM1 (front of the head), LM4 (apex), LM10 (posterior end of the hepatopancreatic cavity) and LM23 (back end of the shell). This LM and S-LM configuration was selected to reflect the shape contour of the border of the shell and the border of the hepatopancreatic cavity.

the upper midlittoral level in each of the studied sites and substrata (Fig. 1. A). Substratum inclination, heterogeneity and roughness were measured at each transect. Heterogeneity was calculated by horizontally deploying a flexible measuring tape along the upper midlittoral, following the rock contour (profile) along the whole length of the transect (10 m linear distance). Roughness and inclination were measured at the beginning, in the middle, and at the end of each transect. Roughness was measured following the same method as heterogeneity but along three horizontal 25 cm linear distance transects and using a profile gauge with 0.5 mm pins to obtain the rock profile (Frost et al., 2005). Both heterogeneity and roughness indexes were calculated by dividing the obtained profiles by the linear distance of the sampled transect (see Rivera-Ingraham et al., 2011b; Sedano et al., 2020b). Inclination was measured placing a 3 m stick on the rocky shore, perpendicular to the shoreline and spanning from the infralittoral to the supralittoral level, to measure the inclination angle of the stick with a digital clinometer.

The chemical and lithological composition of each transect rock was studied by collecting two rock chips per site and substratum. These were used to confirm the dolomitic nature of the artificial breakwater in the studied areas (see Ostalé-Valberas et al., 2023) and the information provided by the Geological and Mining Institute of Spain, which identifies the natural rock in the area as mainly metamorphic, with as gneisses (biotite schists), migmatites and porphyritic granitoids at North Bay, gneisses and migmatitic gneisses at Chorrillo, and phyllites and deformed conglomerates at Fuentecaballos (Pineda et al., 2013). Rock chips were milled and used to calculate the rock elemental composition by X-ray fluorescence (XRF) using an AXIOS spectrometer. Rock mineralogical composition was estimated by X-ray diffraction (XRD) using a powder diffractometer (Bruker D8 Advance) equipped with a high temperature chamber (Anton Paar XRK 900) and a fast

response/high sensitivity detector (Bruker Vantec 1) with radial Soller slits (Valverde et al., 2015).

Wave exposure and shore aspect (orientation) were obtained at each site and substratum with Google Earth. Wave exposure was quantified using the Fetch index, which has been successfully employed to predict intertidal community patterns (e.g., Burrows et al., 2008), and derives from an average between the maximum and effective fetch indices (Howes et al., 1994). Effective fetch (Fe) is calculated using the equation $Fe = [\sum(\cos \Theta_i) \times Fi] / \sum \cos \Theta_i$, with Θ_i representing angles between shore-normal and directions 0°, 45° left, and 45° right, and Fi as the distance in Km along the relevant vector, with a limit value of 1000 km conventionally used for open ocean. Maximum fetch is the maximum Fi recorded when calculating Fe . Finally, the wave exposure class of each coastline section is determined based on five categories: very protected (Fetch <1), Protected (1–10), semi-protected (10–50), semi-exposed (50–500), and exposed (>500) (Howes et al., 1994; Terrón-Sigler et al., 2016).

2.3. Morphometric study

Adult individuals of *Patella rustica* and *P. caerulea*, with sizes ranging from 1.5 to 4.0 cm (Frenkiel, 1975; Prusina, 2013), were randomly collected in May 2022 from two substrata: artificial limestone breakwaters and natural rock flats at three sites in Ceuta, Strait of Gibraltar, Spain (Fig. 1. A). At each site and substratum, a total of 25 individuals of each species were collected from the upper midlittoral (*P. caerulea*) and lower supralittoral (*P. rustica*) within a 25 m transect parallel to the shoreline (50 individuals per species and site). Limpets were collected ensuring that their shells were not excessively eroded to the extent of losing their original shape.

After collection, shells were cleaned and photographed from ventral

and lateral perspectives. The analysis of shell shape was performed using landmark-based (2D) geometric morphometric techniques. The apex, shell outline and hepatopancreatic outlines were captured from the lateral view using a non-symmetric configuration with 3 landmarks and 22 semi-landmarks (Fig. 1B), and from the ventral view using a symmetric configuration with 9 landmarks and 20 semi-landmarks (Fig. 1C). All specimens were digitized by the same observer (JS-V) using TpsDig2 v.2.17. The semi-landmarks used to capture contours were layered evenly along contour curves between landmarks and were homologated mathematically in an iterative process (sliding) using TpsRelw v.1.53. In this method, the S-LM coordinates are slid along the contour to minimize the bending energy of the landmark configuration (Slice, 2005). Then, a generalized Procrustes analysis was applied in which landmark configurations were rotated, translated to a common origin, and scaled to a unitary centroid size to obtain the Procrustes aligned coordinates, used as shape data (Rohlf and Slice, 1990).

2.4. Statistical analyses

Possible differences in shell size among sites and substrata for *P. rustica* and *P. caerulea* were tested using ANOVAs on centroid size data, after exploring the data for normality with a Kolmogorov-Smirnov test, and homoscedasticity with a Levene's test. These analyses were carried out using IBM SPSS Statistics 22. To account for allometry, multivariate regressions were performed in MorphoJ v1.06 b (Klingenberg, 2011) for both species and each species separately (Zelditch et al., 2012). The term "allometry," was used as defined by Mosimann (1970): the pattern of covariation among morphological traits or the relationship between shape and size components. MorphoJ regressions are computed and plotted after Drake and Klingenberg (2008), and originate from the regression equation $y = xb + e$, where y is the random vector of dependent variables, which in our case are the shape variables represented by the Procrustes coordinates (lateral view) and the symmetric component (ventral view), x is the random vector of independent variables, which in our case is the centroid size (shell size), b is the matrix of regression coefficients, and e is the random vector of error effects. The multivariate regression scores are then accounted with the variable $s_i = \mathbf{y}b_i^T(\mathbf{b}_i^T\mathbf{b}_i)^{-0.5}$, to obtain the shape score s_i , which is the shape variable that is most strongly associated with the i -th independent variable (x_i) (see Klingenberg, 2011). The statistical significance of the regression was tested with a permutation test (10,000 rounds) against the null hypothesis of independence. The presence of allometry was considered if the regression was significant (p -value < 0.05) and the regression coefficient higher than 5 %. In these cases, the vector of regression scores computed by MorphoJ for all the observations in the sample was visualized along with the shape variations represented by the multiple regression, which were plotted by reconstructing hypothetical forms of a wire frame connecting landmarks (wireframe plot). Whenever present, allometry component was eliminated during further analyses by working with the regression's residuals (Klingenberg, 2016; Outomuro and Johansson, 2017).

Shape data (PCscores) was used to perform conglomerate ordinations on Mahalanobis distances among species, sites and substrata using InfoStat (Di Rienzo et al., 2020). Subsequent ordinations and tests were made with MorphoJ software, using Discriminant Function Analyses with cross validation to explore variation between two groups of observations (species and substrata) and Canonical Variate Analyses as a general analysis to find the shape features that best distinguish among multiple groups of specimens (variation among sites) (Klingenberg, 2011 and references therein). Discriminant Function and Canonical Variate Analyses are classical techniques of multivariate statistics, and details can be found in most textbooks of multivariate statistics and morphometrics (e.g., Rohlf and Bookstein, 1990; Timm, 2002). In multivariate morphometrics, these are used to identify shape components that maximize the differences in shape between and among group of observations that are known a priori (Viscosi and Cardini, 2011). For

the resulting ordinations, shape differences between group means and along canonical axes were plotted using wireframe plots. Following these routines, differences between groups were analysed using permutation tests (10,000 permutations) on Procrustes distances (Mahalanobis distances) to calculate the Hotelling T-square statistic for the null hypothesis of equal group means.

3. Results

3.1. Environmental study

The physicochemical characterization of the sampling areas highlighted a higher macroscale heterogeneity and surface roughness of artificial substrata within all sites, except for roughness in Fuentecaballos (Table 1). Overall, shore aspect was similar for the artificial and natural areas of each site. At North Bay and Fuentecaballos, natural shores were slightly steeper than artificial shores; in contrast at Chorrillo the artificial shore was much steeper. Furthermore, all sites and substrata were semi-exposed according to Fetch index classification, although the sites facing south, particularly Chorrillo, were the most wave exposed site while North Bay site was the least exposed one. Finally, substrata had different elements and lithological composition, with artificial substrata being dolomitic riprap rocks, and natural rocks showing the profile of graphite, quartz and muscovite-rich metamorphic rocks (Supplementary Table 1).

3.2. Morphometric study

No individuals of *Patella caerulea* were found on the natural substratum in North Bay, so the morphometric study was carried out with a total of 275 individuals. The centroid sizes of *P. rustica* and *P. caerulea* followed a normal distribution for all sites and substrata (Kolmogorov-Smirnov: $P > 0.05$ in all test outputs) and were homoscedastic (Levene: *P. rustica*: $F_{5,269} = 0.57$; $P = 0.722$; *P. caerulea*: $F_{4,269} = 1.75$; $P = 0.143$). No differences in centroid size were found between substrata for *P. rustica* (ANOVA: $MS = 0.85$; $F_{1,269} = 2.31$; $P = 0.131$) and *P. caerulea* ($MS = 0.16$; $F_{1,269} = 0.40$; $P = 0.527$) and among sites for *P. caerulea* ($MS = 1.01$; $F_{2,269} = 2.55$; $P = 0.082$). However, centroid size was higher in North Bay than Fuentecaballos and Chorrillo for *P. rustica* ($MS = 6.88$; $F_{2,269} = 18.65$; $P < 0.001$) (see means and standard deviations at Supplementary Table 2).

Allometric changes in shell shape predicted less than 5 % of the overall shape variation when considering both species (Table 2). However, when considering species separately, allometric shell growth occurred in *P. rustica* lateral view, with shell height increasing more rapidly than length as size increased, and the ventral contour of *P. caerulea*, in which the inner contour grew more rapidly around the body than the head (Table 2; Supplementary Fig. 1). Therefore, allometry was considered present for *P. rustica* lateral view and *P. caerulea* ventral view and subsequent analyses were carried out with the residuals of these regressions, considered as new size-unrelated shell shape variables.

Overall, differences in shape between species were higher than their intraspecific variation for both lateral and ventral views, and higher for the lateral than the ventral view (see Fig. 2). On the lateral view, the mean shell shape of *P. rustica* is more conical, with the shell less projected on anterior-posterior axis, and more projected apex along the dorsal-ventral axis, than *P. caerulea* (Discriminant Function Analysis: $N = 275$; Mahalanobis distance = 4.28; T-square = 1248.5; P (perm) < 0.001 ; see Supplementary Table 3; Supplementary Fig. 2). On the ventral view, the shell contour of *P. rustica* was generally rounder, while *P. caerulea* had a more pentagonal shell contour shape, and the inner hepatopancreatic contour was slightly rounder, and the apex more displacement to the posterior part in *P. rustica* than *P. caerulea* ($N = 275$; Mahalanobis distance = 2.98; T-square = 757.7; P (perm) < 0.001 ; see Supplementary Table 3; Supplementary Fig. 2).

Table 1

Results for the environmental variables measured in each sampled location. * Rock type was inferred from the lithological results included at [Supplementary Table 1](#). Cell shading in the table is indicative of cell values, with darker shading applied to higher values.

Site	North Bay		Chorrillo		Fuentecaballos	
	Artificial	Natural	Artificial	Natural	Artificial	Natural
Heterogeneity	1.53	1.17	1.59	1.25	1.28	1.23
Roughness	32.80	29.60	32.41	31.17	31.37	31.78
Inclination	17.41°	21.11°	21.14°	13.44°	16.36°	18.79°
Fetch index	71.46	54.49	203.13	213.42	99.11	176.29
Shore aspect	N	NW	S	S	SE	S
Rock type*	Dolomite	Graphite	Dolomite	Quartz-muscovite	Dolomite	Muscovite

Table 2

Regressions results between centroid size as shell size (predictor variable), and the Procrustes coordinates (lateral view) and symmetric component (ventral view) as shape variables (response variables) to account for allometry, for all specimens (N = 275) and for each species separately: *Patella rustica* (n = 150) and *P. caerulea* (n = 125). SS = Total square sum; Residual = Residual square sum; % pred = regression coefficient. Bold values indicate the cases in which allometry is accepted (significant P-value and a regression coefficient higher than 5 %).

	Lateral view				Ventral view			
	SS	Residual	% pred	P-value	SS	Residual	% pred	P-value
All specimens	0.970	0.945	2.53	<0.001	0.536	0.511	4.79	<0.001
<i>P. rustica</i>	0.477	0.427	10.52	<0.001	0.243	0.235	3.43	<0.001
<i>P. caerulea</i>	0.357	0.346	3.17	0.010	0.233	0.220	5.76	<0.001

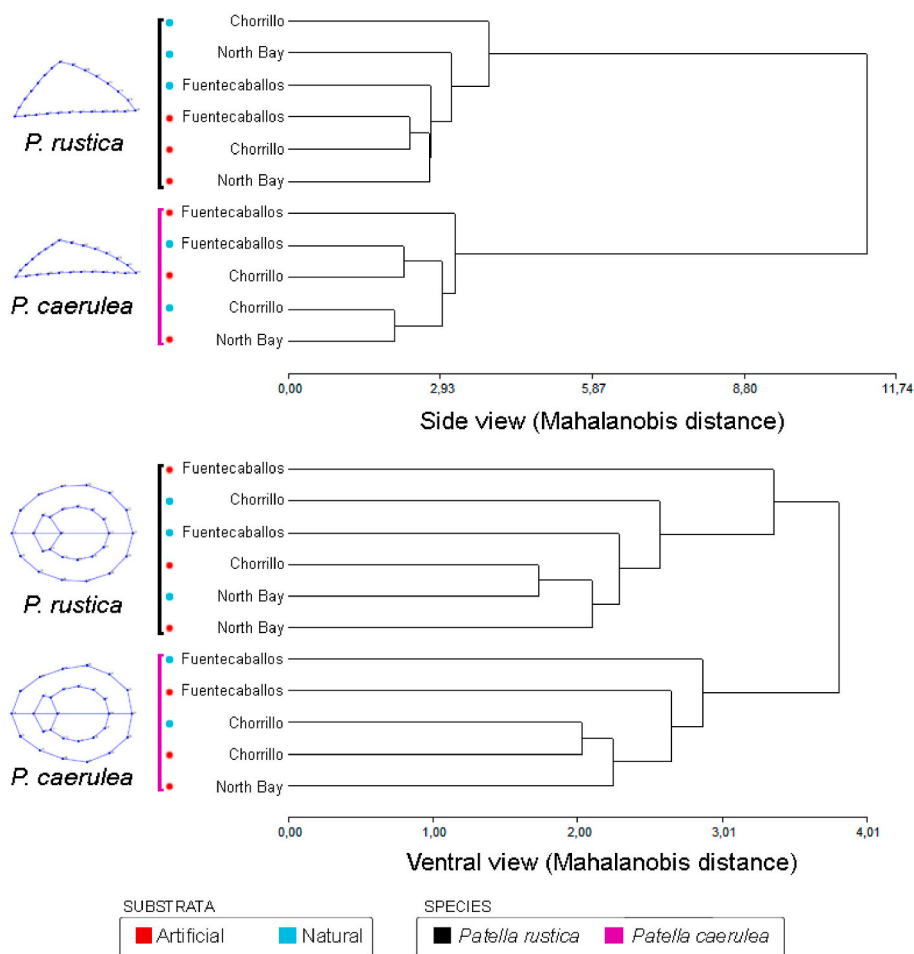


Fig. 2. Conglomerate ordinations depicting the Mahalanobis average distances among the sampling locations for all individuals (*P. rustica* and *P. caerulea*) using the lateral and ventral views shape data. The wireframes of the consensus shapes are included for *P. rustica* and *P. caerulea* along with their respective sample groups.

Table 3

Canonical Variate Analysis (CVA) on Procrustes coordinates, showing Mahalanobis distances (Md) and P-values from permutation tests (P (perm)) between pairs of sites for the lateral and ventral views of *P. rustica* and *P. caerulea*. NB = North Bay; Ch = Chorrillo; Fc = Fuentecaballos.

	Lateral view				Ventral view			
	Patella rustica		Patella caerulea		Patella rustica		Patella caerulea	
	Md	P (perm)	Md	P (perm)	Md	P (perm)	Md	P (perm)
NB vs. Ch	2.01	<0.001	2.68	<0.001	1.84	<0.001	2.22	<0.001
NB vs. Fc	1.88	<0.001	3.63	<0.001	2.08	<0.001	2.79	<0.001
Ch vs. Fc	2.01	<0.001	1.80	<0.001	2.12	<0.001	1.95	<0.001

Table 4

Discriminant analyses on Procrustes coordinates between substrata (artificial vs. natural) for the lateral and ventral views of *Patella rustica* and *P. caerulea*. M-distance = Mahalanobis distance; T-square = Hotelling's t-statistic; P (perm) = P-values from permutation tests.

	Lateral view			Ventral view		
	Mahalanobis distance	Hotelling's t-statistic	P (perm)	Mahalanobis distance	Hotelling's t-statistic	P (perm)
<i>P. rustica</i>	2.05	158.22	<0.001	1.44	77.54	0.001
<i>P. caerulea</i>	2.03	123.35	0.012	1.48	65.29	0.011

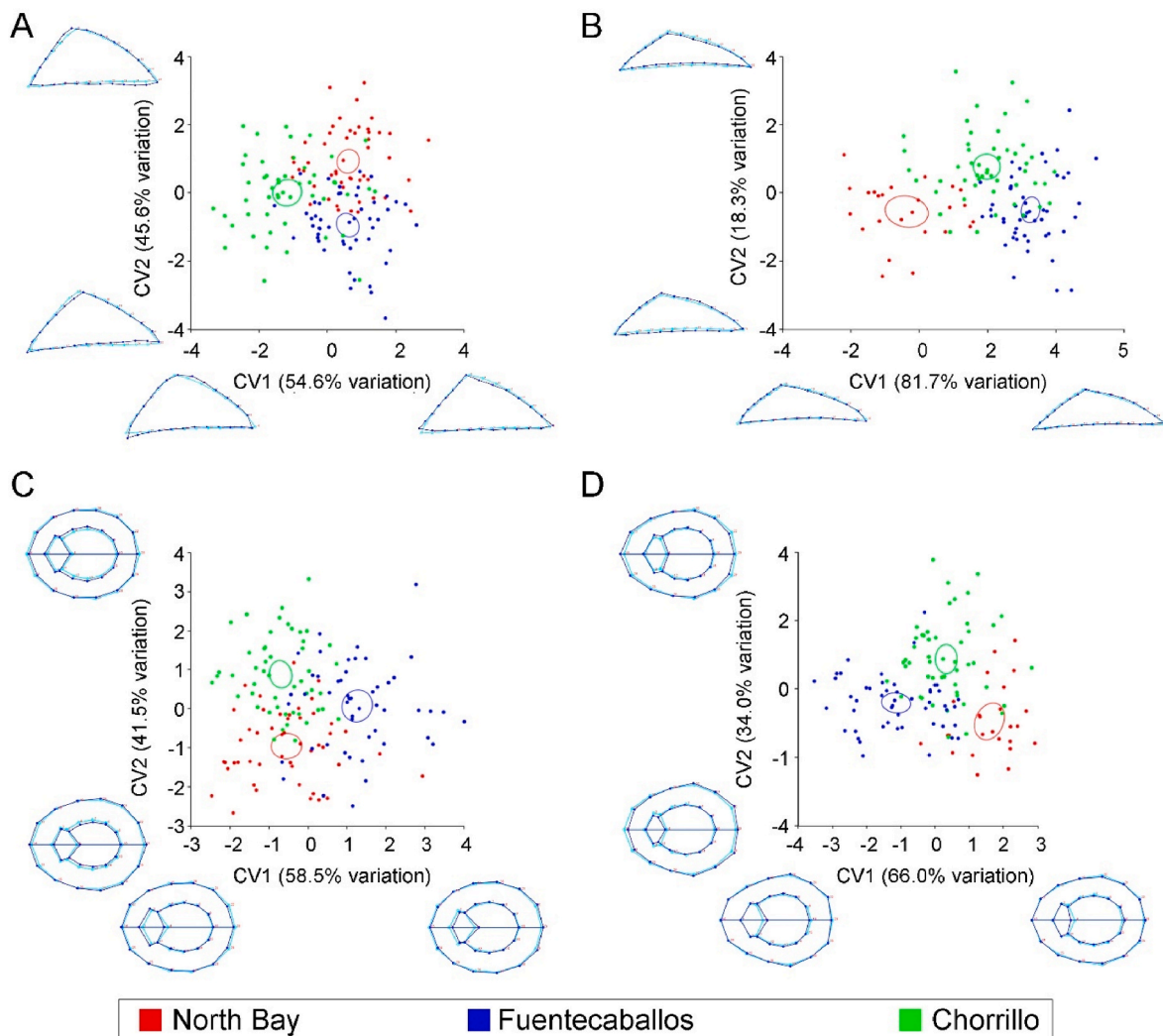


Fig. 3. Canonical Variate Analyses (CVAs) on Procrustes coordinates among sites for the lateral view of *P. rustica* (A) and *P. caerulea* (B) and the ventral view of *P. rustica* (C) and *P. caerulea* (D). The coloured circumferences in the CVAs represent 95 % confidence ellipses for the average of each site. The wireframe diagrams show the variation obtained in each CVA axis, showing both the positive and negative direction of the deformation, with a scale factor of ± 4 . Light blue indicates the consensus shape, while dark blue indicates the \pm shape extreme variations. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Mahalanobis distances among individuals revealed intraspecific differences among sites and substrata for both studied species (Table 3; Table 4). Overall, individuals had a specific shell shape at each site. These differences occurred for the lateral view in the position of the apex, which was closer to the centre of the shell at the sites in South Bay: Chorrillo and Fuentecaballos, and more displaced to the front of the animal in North Bay for both *P. rustica* (Fig. 3. A) and *P. caerulea* (Fig. 3. B). From the ventral view, the relative size of the hepatopancreatic contour around the head was smaller in Fuentecaballos and bigger in Chorrillo for both species (Fig. 3. C and D). In *P. caerulea*, the ventral shape varied from a rounder shell perimeter and elongated hepatopancreatic contour in North Bay to a more pentagonal outer shell perimeter and more globular inner contour in Fuentecaballos (Fig. 3. D).

Shell shape varied between artificial and natural substrata for *P. rustica* and *P. caerulea* (Table 4), although this variation was generally small and only *P. rustica* ventral view showed a clear distinction between substrata (Table 5). Nonetheless, both species showed a similar shell shape variation between substrata (Fig. 4). For the ventral view, *P. rustica* had a wider hepatopancreatic contour (inner contour) around the head and narrower around the body, which led to a wider space between the foot and the contour of the shell in natural than artificial substrata (Fig. 4). For the lateral view, *P. rustica* showed a higher shell in natural than artificial substrata. Seemingly, the relation between the hepatopancreatic contour around the body and the outer shell profile (outer contour) was also smaller and the lateral shell profile was slightly higher in natural than artificial substrata for *P. caerulea* (Fig. 4), which also led to a wider gap between the foot and the outer shell contour in natural than artificial substrata.

4. Discussion

A consistent morphological differences between artificial and natural substrata for both studied species and across sites (hypotheses H1 and H2) suggests that there is a common factor influencing shell morphology that segregates populations from natural versus artificial substrata. In the present study, rock lithology, heterogeneity and roughness were the environmental parameters that more clearly segregated natural and artificial substrata and could have influenced the observed differences in shell morphology (H3). These factors can influence the abundance and population structure of patellid limpets, particularly when comparing artificial and natural substrata (Espinosa et al., 2011; Rivera-Ingraham et al., 2011a; Batelli, 2016; Cacabelos et al., 2016; Ostalé-Valriberas et al., 2023). Nevertheless, rock type has a secondary role in structuring benthic communities (Cacabelos et al., 2016, 2019; Sempere-Valverde et al., 2023). Its effects on limpets' morphology are still poorly understood, and some authors found no differences in shell length and height when comparing different substrata (Batelli, 2016; Amer et al., 2018).

In this study, the artificial substrata (limestone boulders) could be promoting a lower desiccation stress than the natural metamorphic rocks. First, because the higher heterogeneity of artificial substrata (10 m scale) suggests that ripraps could have more nooks and crannies,

shadowed areas that limpets might be using to ameliorate desiccation and temperature stress during low tide (Prusina, 2013; Firth et al., 2015). Second, because a higher heterogeneity of the substratum surface at small scales (e.g., roughness) allows less heating and more water retention during low tide, even though heterogeneity in the field exists on many scales besides those tested in the present study (Aguilera et al., 2019; Sempere-Valverde et al., 2023; Ambrose et al., 2021). Third, because the differences in rock lithology determine their weathering rates, roughness, shape, texture, wettability and albedo, and can in turn influence desiccation stress during low tide (Sempere-Valverde et al., 2023 and references therein). Roughness differences are due in part to rock mineralogy and erosional history, to which intervene biological weathering coupled with bioerosion by endolithic algae bore into calcareous substrata through chemical processes (Schönberg and Wisshak, 2014; Sempere-Valverde et al., 2018; Ambrose et al., 2021). This might have contributed to an increased roughness of the studied calcareous rock in a microscopic scale and might provide an additional feeding resource for grazing organisms, in addition to microbial films on the surface (Hills and Hawkins, 1991), macro-algae (Della Santina et al., 1993) and macro-algal detritus (Notman et al., 2016). Moreover, calcareous rock types generally have a higher surface free energy than silica-rich ones, which results in a higher wetting (Callow and Fletcher, 1994; Ambrose et al., 2021). Finally, the calcareous artificial dolomite was lighter (higher albedo) than the natural rocks in the studied areas (JS-V pers. Obs.), which would imply lower thermal absorption by the former from sunlight. In conclusion, all these factors could have contributed to reduce the thermal and desiccation stress experienced on artificial substrata, influencing limpets' phenotype. It is interesting to note that earlier studies have suggested that artificial substrata could create hotter and drier conditions compared to natural substrata (Aguilera et al., 2019). This might be linked to the unique features of the surfaces examined in this study, as other artificial substrata, such as concrete, would not be as heterogeneous as the studied ripraps. Moreover, natural rock exhibits significant geographical heterogeneity, leading to a range of environmental conditions, while artificial substrates tend to show more uniformity across locations when compared to natural rock. Therefore, more research on different substrata and their effects across geographical scales would be needed before drawing conclusions about the ecological effects of substratum type.

Regardless of the high spatial and residual variability in *Patella rustica* and *P. caerulea*, which reflects the high phenotypical variability of both studied species (Belkhdja and Romdhane, 2012; Prusina, 2013; Bouzaza and Mezali, 2018), there was a common trend by both species towards a slightly increased shell height and a narrower hepatopancreatic contour on natural substrata. These are strategies adopted by limpets against thermal and desiccation stress (Vermeij, 1973; Harley et al., 2009). A taller shell has a smaller basal surface area per volume unit, which reduces temperature transfer by conduction with the substratum, reduces the area exposed to sunlight radiation, and might increase heat loss by convection (Harley et al., 2009). It also reduces the basal perimeter of the shell, which in turn minimizes water loss through

Table 5

Classification/misclassification tables for cross validation of discriminant functions between artificial and natural substrata for *Patella rustica* (n = 150) and *P. caerulea* (n = 125) lateral and ventral views.

Origin	<i>Patella rustica</i> Lateral view			<i>Patella rustica</i> Ventral view		
	Allocated to		Allocation accuracy	Allocated to		Allocation accuracy
	Artificial	Natural		Artificial	Natural	
Artificial	52	23	69.3 %	56	19	74.7 %
Natural	31	44	58.7 %	18	57	76.0 %
	<i>Patella caerulea</i> Lateral view			<i>Patella caerulea</i> Ventral view		
Artificial	52	23	69.3 %	52	23	69.3 %
Natural	22	28	56.0 %	23	27	54.0 %

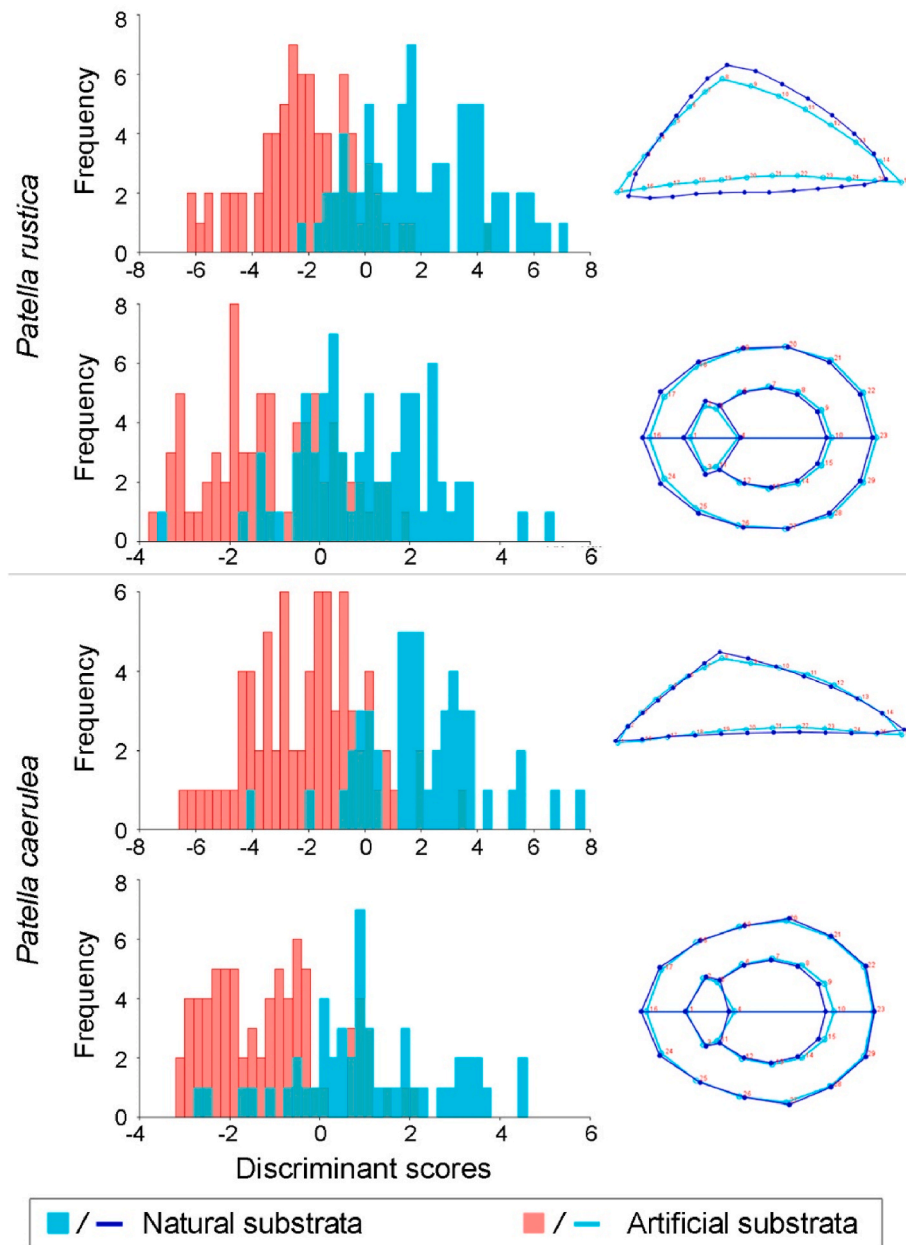


Fig. 4. Discriminant analyses on shell shape differences (Procrustes coordinates) for the lateral and ventral views of *P. rustica* and *P. caerulea* between natural and artificial substrata. The wireframe diagrams show the variation obtained along the discriminant scores, showing both the positive and negative direction of the deformation, with a scale factor of ± 3.0 . Therefore, the dark blue wireframe indicates a three-times exaggerated average shape on natural substrata, while the light blue indicates the same for artificial substrata. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the border of the shell during low tide (Vermeij, 1973). Moreover, a higher shell implies a higher lateral area in relation to basal area, which in turns increases the capacity of the extra-visceral cavity (Vermeij, 1973). This cavity is further increased by a narrower hepatopancreatic contour that increases the gap between the foot and shell perimeter and determines the amount of water that can be retained around the foot during low tide (Vermeij, 1973; Prusina, 2013). All this would help limpets better survive temperature and desiccation stress in the intertidal environment (Vermeij, 1973; Paulo Cabral, 2007; Harley et al., 2009), indicating that artificial substrata have lower temperatures and hence desiccation stress than those natural substrata in our study. Nevertheless, substratum type had a clear secondary role in influencing shell morphology, since shell shape variation is most likely determined by adaptation to the local environment. In field, environmental

conditions are determined by a complex interaction of factors that vary across sites and locations, such as shore aspect, inclination, local hydrodynamics, wave action, limited resources availability (e.g., food and refugia), as well as pollution, collection, competition and predation pressure (Denny and Blanchette, 2000; Tablado and Gappa, 2001; Rivera-Ingraham et al., 2011a; Amer et al., 2018; Bouzaza and Mezali, 2019; Vasconcelos et al., 2020; Espinosa et al., 2021; Ostalé-Valriberas et al., 2022, 2023). Therefore, further studies incorporating experimental manipulations would be necessary to further elucidate the underlying mechanisms driving patterns of shell variation in limpet species.

This study recorded the morphotypes that characterize *P. rustica* and *P. caerulea*, the high intraspecific variability in shell shape of these species, and their allometric growth patterns (Belkhodja and Romdhane,

2012; Prusina, 2013; Puig, 2016; Bouzaza and Mezali, 2018). Among intertidal limpets, there is a well-known inter- and intraspecific increase in shell height/basal area ratio with increasing shore level (Vermeij, 1973; Paulo Cabral, 2007; Rivera-Ingraham et al., 2011b). However, these changes can also occur throughout the ontogenetic development of these organisms. In the Mediterranean Sea, *P. rustica* shells exhibit allometric shell growth, with height increasing more rapidly than length, to reduce evaporative water loss (Paulo Cabral, 2007; Prusina, 2013; Amer et al., 2018), and with the shell base becoming more circular and the apex becoming more centred (Bensaâd-Bendjedid et al., 2022), which has been related to a faster and stronger adhesion to the substratum and might be an adaptation to a high hydrodynamic stress environment (Denny and Blanchette, 2000; Paulo Cabral, 2007; Bouzaza and Mezali, 2019). The same allometric growth, with the shell base becoming more circular and the apex becoming more centred, was found for *P. caerulea* in this study. In *P. caerulea*, Boukhicha et al. (2010) described an allometric increase in shell height, which along with a rounder basis would help to fight desiccation stress (Paulo Cabral, 2007). Finally, Boukhicha et al. (2010) described an allometric increase in radular length in *P. caerulea*, which has also been proposed as an adaptation to grazing higher shore levels, where algae are less abundant and more frequently encrusting (Paulo Cabral, 2007; Boukhicha et al., 2010). Finally, this allometric growth might as well be accompanied by a displacement of the home-scar to upper littoral levels, which are often inhabited by greater individuals of *P. Rustica* in the study area, while the small individuals are usually in lower tidal levels (JS-V Pers. Obs.). This shift in shore level between juveniles and adults occurs in other species, and it is frequent to find juveniles of limpets occupying different niches, such as tidepools and lower shore levels, than those inhabited by adults (Rivera-Ingraham et al., 2011b; Espinosa and Rivera-Ingraham, 2017; Livore et al., 2018; Seabra et al., 2020, 2023). Nonetheless, isometric growth and a negative allometric radular growth has also been recorded for *P. rustica* in the colder climate of NE Atlantic Portugal (Paulo Cabral, 2007), where the thermal and desiccation stress might be a less determinant factor for survival.

5. Conclusion

Our study highlights the complex interplay between rock type and local environmental conditions in shaping the morphology of patellid limpets and provide insights into the adaptive mechanisms that drive shell shape variation in limpet populations on substrata differing in heterogeneity, roughness and lithology. Coastal sprawl might have broad ecological and evolutionary implications on intertidal grazers, and it is important to understand the ecological impacts of coastal development on coastal ecosystems and in the ability of limpets to respond and adapt to changing environmental conditions (Espinosa and Rivera-Ingraham, 2017). Therefore, further research incorporating experimental manipulations, such as Vasconcelos et al. (2021), is needed to better understand the complex nature of limpets' morphological responses to environmental conditions. Given that artificial substrata might promote population isolation and trigger selective pressures in the long term, with different populations adapting to specific substratum characteristics (Nakano and Ozawa, 2005; Fauvelot et al., 2009; Rivera-Ingraham et al., 2011b; Sedano et al., 2020b; Espinosa et al., 2021), this study underscores the need for understanding the mechanisms that drive and maintain phenotypical and genotypical diversity as a basis for conserving such populations. Finally, the positive impact of artificial structures on limpet populations in this case study and others in the studied area, such as Rivera-Ingraham et al. (2011b), García-Gómez et al. (2014), and Ostalé-Valriberas et al. (2022, 2023), are geographically and structure-type (dolomitic breakwater) context specific, and they must not be used to advocate deployment of artificial substrata (Firth et al., 2020). Actually, coastal sprawl can have an overall negative impact on native biodiversity and may result in uniform selection pressures that negatively impact the limpet populations

inhabiting them (Moreira, 2006; Moreira et al., 2006; Fauvelot et al., 2009, 2012; Bulleri and Chapman, 2010; Burgos-Rubio et al., 2015; Bishop et al., 2017; Sedano et al., 2020a; Alter et al., 2020; Espinosa et al., 2021). In the Strait of Gibraltar there are some benefits of artificial structures for limpet populations and conservation of rare and endangered species (REF), but this is unlikely to always be the case.

CRedit authorship contribution statement

Juan Sempere-Valverde: Writing – original draft, Visualization, Formal analysis, Data curation. **Enrique Ostalé-Valriberas:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition. **Free Espinosa:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Federico Márquez:** Writing – review & editing, Validation, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be available at the University of Seville depository (<https://idus.us.es/>)

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Appendix A. Supplementary data

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