

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science



journal homepage: www.elsevier.com/locate/ecss

Coastal exposure and artificialization: Drivers of shell shape variation in intertidal limpets

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ARTICLE INFO

Keywords: Patella aspera Patella crenata Limpets Intertidal Shell shape Local adaptation Wave exposure Coastal artificialization Geometric morphometrics Conservation

ABSTRACT

The level of exposure and the degree of coastal urbanization are key environmental and human-related factors that significantly affect the spatial distribution of species in different environments. Intertidal species show morphological adaptations to these influences, but little research has been done on how shell shape varies due to the island effect, including factors like island orientation and substrate type. This study aims to analyze the dorsal shell phenotypic variability of the limpets Patella aspera and Patella crenata, in response to island orientation (North vs. East) and different substrate types (Natural: platform and rocks; Artificial: wave breakers), on the island of Gran Canaria, using geometric morphometric analysis. Our findings support the hypothesis that these limpet species exhibit phenotypic plasticity in response to wave exposure influenced by island orientation and coastal artificialization. Oval shapes with wider and flattened shells, displaying greater shell lengths, on waveswept shores may be explained by the need for a larger foot to ensure attachment to substrate, thereby increasing resistance to dislodgement by wave action. In contrast, more rounded shapes with taller and narrower shells in sheltered environments can accommodate a smaller foot as an adaptation against thermal and desiccation stress. The substrate plays a secondary role in influencing the shell morphology, as slight variations were observed between natural and artificial substrates, particularly in body size, regardless of wave exposure. This phenotypic plasticity may lead to spatial segregation, enabling the species to exploit diverse habitats and reduce intraspecific and interspecific competition. The present study emphasizes the need to conserve intertidal species, particularly along the northern coast of Gran Canaria, by accounting for local responses, implementing targeted monitoring and protection efforts, and preserving the diverse phenotypic traits and plasticity of limpets on both protected and full-access shores amidst coastal sprawl and anthropogenic global change.

1. Introduction

Human activity is increasingly altering coastal environments, with over 40% of the global population living within 100 km of the coast, a figure expected to grow significantly in the coming decades (Tibbetts, 2002; Reimann et al., 2023). This growth is driving extensive infrastructure development and accelerating "ocean sprawl"—the expansion of artificial structures like seawalls and breakwaters that are expected to impact millions of square kilometers of seascapes by 2028 (Bugnot et al., 2021). The addition of hard, artificial substrates along coastlines disrupts natural habitats and ecological connectivity by altering physical and chemical conditions such as turbidity, water flow, and sediment deposition (Dafforn et al., 2015; Bishop et al., 2017). Unlike natural rocky substrates, artificial structures often offer less surface complexity, reducing biodiversity and limiting the genetic and phenotypic diversity of native species able to thrive there (Airoldi et al., 2015; Bulleri and Chapman, 2010). These structures also provide habitats for epibiontic

https://doi.org/10.1016/j.ecss.2025.109344

Received 7 January 2025; Received in revised form 4 April 2025; Accepted 4 May 2025 Available online 21 May 2025

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organisms typically found on natural rocky shores, such as limpets and macroalgae, which can establish stable populations on artificial surfaces (Moschella et al., 2005; Ostalé-Valriberas et al., 2023). However, by disrupting ecological connectivity, artificial structures impact local and regional biodiversity and promote the establishment of opportunistic and non-native species (Airoldi et al., 2015; Bulleri and Chapman, 2010). A crucial aspect of artificial habitats is their proximity and accessibility to human coastal populations (Airoldi et al., 2015). Typically, increased human interaction (e.g., shellfish harvesting and trampling), decreases the diversity and abundances of populations in both natural and artificial habitats (Airoldi et al., 2005; Sousa et al., 2019b). However, recent studies have shown that certain intertidal species, like limpets, can maintain substantial populations on artificial coastal structures built in open sea areas with severe hydrodynamic conditions, such as breakwaters and piers, where public access is restricted or less accessible (García-Gómez et al., 2015; Shabtay et al., 2018). These conditions enable these structures to function as smallscales reservoirs of biodiversity. For example, the breakwaters of the Strait of Gibraltar and Alboran Sea harbors host the largest population densities of the endangered limpet Patella ferruginea (Gmelin, 1791) (García-Gómez et al., 2011: Ostalé-Valriberas et al., 2022).

Limpets play important ecological roles as key herbivores and ecosystem engineers in rocky intertidal habitats (Burgos-Rubio et al., 2015; Sempere-Valverde et al., 2024). However, their populations are experiencing decreasing levels of abundance and diversity due to the alteration of coastal areas and unregulated harvesting (Espinosa et al., 2021). This decline is evident across various islands in the NE Atlantic Ocean, such as the Azores and the Webbnesia ecoregion (Madeira, Canary Is., and Selvagens) (Freitas et al., 2019), where limpets face a critical situation due to high levels of exploitation (Riera et al., 2016; Sousa et al., 2019b). Historically, limpet harvesting was minimal by the 1980s, primarily for self-consumption (Martins et al., 2017). However, with increasing human populations and the rising commercial value of limpets, exploitation has surged, leading to the collapse of their stocks (Sousa et al., 2019a). The intensity and consequences of this exploitation vary among the different islands of Webbnesia, depending on the human density (Martins et al., 2008). This has led to the establishment of laws and regulatory plans on some islands, such as the Canary Islands, where harvesting of commercial limpet species is prohibited from November 1st to April 30th during their reproductive period. During the rest of the year, limpet collection (above the established minimum sizes per species) is permitted outside protected areas with a daily maximum of 3 kg per person (Order 18th May 2011, Boletín Oficial de Canarias, 2011). However, these restrictions are sometimes not effective enough, as seen in the case of the limpet Patella candei candei d'Orbigny 1840, which now exists only in isolated populations in Fuerteventura, after becoming extinct in the rest of the Canary Islands (González-Lorenzo et al., 2015; Núñez et al., 2003).

These regulations have also been applied for other over-harvested species such as Patella crenata Gmelin, 1791 (previously known in the Canaries as P. candei crenata Gmelin, 1791 sensu A. d'Orbigny, 1840) and P. aspera Röding, 1798 (Faria et al., 2017). In recent decades, a constant decrease in their populations has been observed due to the selective harvesting of larger specimens for commercial purposes (Riera et al., 2016; Sousa et al., 2019a). Both species inhabit the mid-lower natural (e.g., platform, pebbles, and cliffs) and artificial (e.g., breakwaters and piers) intertidal rocky shores along the coast of the Canary Islands (Ramírez et al., 2008). However, P. crenata is typically found higher up in the intertidal than P. aspera, making it more exposed to air during low tides (Navarro et al., 2005). P. aspera has a conical shell with numerous radial ribs forming a very serrated edge, often covered with algae, and a yellowish foot, hence its common name "white limpet". Similarly, P. crenata has a conical shell with wider radial ribs alternating large and small, forming a lobulated edge, and is known as the "black limpet" due to its dark feet (Ramírez et al., 2008). Variations in limpets shell shape and morphometric parameters

(length, weight, and height), can serve as indicators of environmental changes and human impacts, as they exhibit a high phenotypical plasticity in response to their habitat (Vasconcelos et al., 2021). Furthermore, phenotypic plasticity is considered an important mechanism for environmental adaptation (Lande, 2009), speciation (Crispo, 2007) and evolution (Price et al., 2003). Therefore, analyzing shell shape variations using techniques such as geometric morphometrics, which examine curvature patterns in each specimen, is a valuable approach to understanding the impact of both abiotic (e.g., wave exposure, orientation, and substrate type) and anthropogenic factors (e.g., artificialization and harvesting) (Faria et al., 2017; Sempere-Valverde et al., 2024; Zelditch et al., 2012).

Numerous studies have elucidated significant morphological adaptations among intertidal species in response to these environmental variations (Harley et al., 2009; Battelli, 2016; Bensaâd-Bendiedid et al., 2022; Bouzaza and Mezali, 2018; Sempere-Valverde et al., 2024). Nonetheless, limited attention has been directed towards exploring variations in body size and shape associated with the island effect. which refers to the unique environmental gradients and selective pressures that islands exert on species, including spatial orientation, substrate types, and varying degrees of exposure to wave action. On islands like Gran Canaria, these factors can result in distinct morphological patterns along different coasts and substrate types due to differences in hydrodynamic forces and habitat availability. This study aims to assess the impacts of (i) coastal exposure linked to island orientation, (ii) coastal artificialization on the shell morphology of limpets (P. aspera and P. crenata) on Gran Canaria, and (iii) to quantify phenotypic variability among substrates at each orientation to inform conservation strategies for these intertidal species, in the context of increasing environmental change. Using geometric morphometric analysis, we examined dorsal shell shape variations. We hypothesize that shell morphology responds to orientation (North vs. East) and substrate type (platforms, rocks, wave breakers): limpets on northern shores, exposed to stronger waves, may have larger shells for stability and adhesion, while eastern limpets may develop taller shells for better water retention. Additionally, artificial substrates might drive irregular or taller shell shapes compared to natural rocks.

2. Material and methods

2.1. Data collection

In this study, 211 specimens of Patella crenata and 156 of Patella aspera, were collected between September 2023 and February 2024 from rocky shores in three coastal settlements on the Island of Gran Canaria: Puerto de Taliarte (East coast), and El Puertillo and El Altillo (North coast) (Fig. 1). Collection sites were selected in areas where shellfish harvesting is permitted (Order 18th May 2011, Boletín Oficial de Canarias, 2011). These habitats exhibited differences in exposure to wave action, with the North locations being more exposed and the East location more sheltered (Supplementary Figure S1). Attempts to sample southern locations were unsuccessful due to unsuitable sandy substrate. Each site included natural substrates-platforms (horizontal, flat rocky surfaces typically exposed during low tide) and rocks (irregular formations of varying sizes and shapes)-as well as artificial substrates, specifically wave breakers composed of large, angular boulders designed to mitigate wave energy. These artificial structures introduce heterogeneous habitats with crevices that can support diverse marine communities, including limpets.

For *P. aspera*, 66 of the 156 specimens were collected from the East coast (platform = 33, rocks = 33) and 90 from the North coast (platform = 38, rocks = 31, wave breakers = 21). For *P. crenata*, 102 specimens were collected from the East coast (platform = 31, rocks = 36 and wave breakers = 35) and 109 from the North (platform = 41, rocks = 32, wave breakers = 36). Due to seasonal conditions (winter season),



Fig. 1. Maps displaying the three sampling locations in Gran Canaria for *Patella aspera* and *P. crenata*: El Altillo and El Puertillo on the North coast, and Puerto de Taliarte on the East coast. Panels A–D show the spatial distribution of the sampling sites at different scales: (A) the location of Gran Canaria within the northeastern Atlantic; (B) the entire island of Gran Canaria highlighting the sampling sites; (C) a zoomed-in view of the northern coast with El Altillo and El Puertillo; (D) a zoomed-in view of the eastern coast with Puerto de Taliarte. Panel E presents wave rose diagrams for each sampling site, illustrating wave direction and height intervals (0–1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m, and > 5 m) for a two-year period (2022–2023), obtained from the PORTUS system by Puertos del Estado.

wave exposure, and the lower intertidal position of *P. aspera*, it was not possible to obtain specimens from wave breakers at Puerto de Taliarte.

For all specimens, total shell length (SL), shell width (SW), total limpet height (LH), and shell height (SH) were measured using a Goobay digital caliper (accuracy: 0.01 mm).

2.2. Morphometric analysis

A Pearson correlation analysis (*PerformanceAnalytics* R package v.2.0.4; Peterson and Carl, 2020) was conducted to assess relationships among *SL*, *SW*, *HL* and *SH*. Due to a high correlation between *SL* and the other variables (detailed in Results section), a normalization procedure

was applied to remove the effects of allometric growth. This adjustment prevents essential shape structures from being masked by size-related variance. Each specimen was scaled to a standard size and adjusted to the shape it would exhibit under allometric growth, following the method described by Lleonart et al. (2000) (see also Vasconcelos et al., 2021). After standardizing all variables, we checked data normality with the Shapiro–Wilk test (*broom* R package v.1.0.6; Robinson et al., 2023) and tested variance homogeneity using Levene's test (*car* R package v.3.1-2; Fox and Weisberg, 2019). For normally distributed data, Welch's Two Sample t-test (WT) with Bonferroni correction (*stats* R package; R Core Team, 2024) was used to examine morphometric differences between orientations. When normality was not met, we



Fig. 2. Ventral view of the shell of *Patella crenata* showing the selection method and position of landmark 2 (A). Dorsal views of the shells of *Patella aspera* (B) and *Patella crenata* (C), with white circles indicating landmarks (1 and 2) and *semilandmarks* (3–37). The apex of the shell was identified as the landmark 1 (LM1), while landmark 2 (LM2) was identified as the foremost point along the shell border aligning with the midpoint of the area occupied by the organism's head in ventral view. The remaining 35 *semilandmarks* (3–37) were determined as the intersections between the fan, characterized by evenly spaced axes (10°), and the shell border.

applied the Mann–Whitney U test (U-test). The Kruskal Wallis rank sum test (KW-test) assessed differences between substrates (platform, rocks, wave breakers) at each location, followed by pairwise Dunn's tests with Bonferroni adjustment (PD; *dunn.test* R package v.1.3.6; Dinno, 2024).

2.3. Geometric morphometric analysis

The dorsal surface of each shell was photographed with an iPhone X mounted on a KAISER RS 1 copy stand, using an RA 1 camera arm and RB 5000 DL system to ensure standard positioning and avoid image distortion. For geometric morphometric analyses, homologous landmarks and non-homologous semilandmarks were selected mainly along the shell edge (Fig. 2). Semilandmarks were used where specific structural details could not be defined by landmarks, capturing shell shape and curvature without requiring strict developmental homology (Bookstein, 1997; Gunz and Mitteroecker, 2013). In the dorsal view, landmark 1 (LM1) marked the apex, and landmark 2 (LM2) represented the shell's most anterior border, aligning with the center of the head area in ventral view (Fig. 2A). Using a 10°-spaced fan alignment, each shell was oriented so that LM1 was at the fan center and LM2 aligned along the fan's anterior line. The 35 semilandmarks were placed at intersections between the fan axes and shell border (Fig. 2B,C). Landmark and semilandmark coordinates (x and y) were collected using the Stereomorph R package v.1.6.7, producing TPS files for each specimen (Olsen and Westneat, 2015).

A Generalized Procrustes Analysis (GPA) was conducted to remove orientation, position, and scale effects while extracting size variables (Rohlf and Slice, 1990; Zelditch et al., 2012). This process centered and standardized the landmark configurations to a unit 'centroid size' and rotated them to minimize the Procrustes distances between homologous landmarks, producing aligned Procrustes coordinates (shape variables) and centroid size as size variables (Angeles et al., 2014). To test for allometric effects, a Procrustes ANOVA with 1,000 random iterations assessed the impact of centroid size on shape. Significant allometry was found for both species (detailed in the results), so residuals from this regression served as 'size-free' Procrustes coordinates for subsequent analyses (Klingenberg, 2016). Next, a Nested Multivariate Analysis of Variance (MANOVA) on the size-free Procrustes coordinates, also with 1,000 random iterations, was tested for significant shape variation by orientation and substrate type.

A Principal Component Analysis (PCA) was then performed with the *Geomorph* R package v.4.0.7 (Baken et al., 2021; Adams et al.,

2024), based on the covariance matrix of size-free Procrustes coordinates to capture shape variance along principal component (PC) axes (Rohlf and Marcus, 1993; Mitteroecker and Gunz, 2009; Zelditch et al., 2012). PCs explaining up to 95% of total variation were retained (Budinski et al., 2015; Vasconcelos et al., 2020). Thin-plate spline deformation grids (Bookstein, 1997) were employed to visualize the shape variation along the PC axes (Morpho R package v. 2.12; Schlager, 2017). Morphological disparity (MD) was also estimated to quantify the phenotypic variability between substrates in each orientation (Zelditch et al., 2012). A Canonical Variate Analysis (CVA) was performed (Geomorph R package v.4.0.7; Baken et al., 2021; Adams et al., 2024) on the reduced PCA matrix to identify mean shape variation among groups (orientation and substrate), maximizing their separation in morphospace (Linde et al., 2004; Zelditch et al., 2012). Classification accuracy was assessed with leave-one-out crossvalidation (Lachenbruch and Mickey, 1968) and Cohen's Kappa (k) coefficient, which evaluates classification improvement over chance (values from 0 to 1, with 1 indicating perfect agreement) (Wieckowska et al., 2022; Titus et al., 1984). All analyses were conducted in R (v.4.3.1; R Core Team, 2024).

3. Results

3.1. Morphometric analysis

The largest specimens of both *Patella crenata* and *Patella aspera* were found on wave breakers along the North coast (Supplementary Table 1). Shell length (SL) was greater in *P. crenata* (43.64 \pm 6.23mm) than in *P. aspera* (40.05 \pm 4.92mm). Due to the high correlation between *SL* and other measured variables (Supplementary Figure 2), a normalization procedure was applied to remove the effects of allometric growth. After size adjustment, the standardized variables (*SWi, HLi, SHi*) were mostly normally distributed (*P* > 0.05) in both species. Additionally, Levene's test revealed no significant variance differences (*P* > 0.05) across orientations or substrate types.

When analyzed by orientation, only *SWi* showed significant differences between island orientations for both species (Supplementary Figure 3). In the North orientation, *P. aspera* exhibited a decrease in *SWi* (*t*-test = 2.73, *P* = 0.007; Supplementary Figure 3A), while *P. crenata* showed an increase (*t*-test = -2.68, *P* = 0.008; Supplementary Figure 3D). Substrate-specific analyses revealed that, on wave breakers, *P. aspera* exhibited the highest *SWi* (KW-test: H = 12.89, P = 0.002; Supplementary Figure 4D) and *SHi* (H = 4.62, P = 0.100; $PD_{Platform-W aveBreakers}$: P = 0.032; Supplementary Figure 4F), whereas *HLi* was greater on platforms and rocks (H = 14.37, P = 0.001; Supplementary Figure 4E). For *P. crenata* in the East orientation, natural substrates supported higher *HLi* (H = 28.41, P < 0.001; Supplementary Figure 5B) and *SHi* (H = 20.05, P < 0.001; Supplementary Figure 5C) compared to artificial wave breakers. In contrast, *SWi* did not differ significantly across substrates (H = 0.39, P = 0.824). In the North orientation, platforms exhibited lower *SWi* (H = 6.10, P = 0.047; Supplementary Figure 5D) for *P. crenata*, while other variables showed no significant substrate-related differences.

3.2. Geometric morphometry analysis

To remove the effect of total shell length on shape (*P. aspera*: F = 2.71, P = 0.001; *P. crenata*: F = 3.78, P = 0.001), residuals from the regression served as 'size-free' variables for subsequent analysis. MANOVA analysis revealed significant shape differences in *P. aspera* based on orientation (F = 8.77, P = 0.01) but not substrate type (F = 1.21, P = 0.26). For *P. crenata*, significant differences were observed for both orientation (F = 12.17, P = 0.01) and substrate (F = 2.08, P = 0.01).

For P. aspera, the first 20 principal components (PCs) explained 95.5% variance, with PC1 (42.1%) distinguishing of substrate-associated shapes by orientation. Eastern shells had a wider anterior region (positive PC1 scores), while Northern shells showed a broader posterior (negative PC1) (Fig. 3A) . PC2 (22.1%) captured lateral shape variations, indicating a tendency for shells to expand either on the left (positive PC2) or right (negative PC2) sides. For P. crenata, the top 25 PCs accounted for 95.3% of variance, with PC1 (31.2%) and PC2 (22.6%) distinguishing between orientations. Eastern specimens exhibited a wider left-lateral part (positive PC1), while Northern ones had a broader right-lateral region (negative PC1) (Fig. 3B). PC2 reflected width variation in posterior (positive PC2) vs. anterior (negative PC2) shell sections.

In both species (Fig. 4), the first canonical variate (CV) axis explained all variance in mean shape due to orientation, with PC1 strongly and positively correlated with this axis. In P. aspera, shape differences were linked to the anterior and posterior shell regions (Fig. 4A), whereas in P. crenata, they were associated with left-right shell variation (Fig. 4B). Orientation-based classification was consistent across both species, with a 63.0% accuracy rate and a 37.0% misclassification rate. Cohen's kappa indicated a 23.2% and 25.9% improvement over chance for P. aspera and P. crenata, respectively (Table 1). For P. aspera, the first CV axis explained all variance in mean shape among East substrates (100%; Fig. 5A), highlighting subtle contour asymmetry (notably PC17). In the North, the first CV axis accounted for 59% of variance and the second for 41% (Fig. 5B). North-platform shells were shorter and wider from the mid to posterior region with more pointed anterior shapes (PC5), while shells from rock and wave breaker substrates showed less deviation (PCs 19 and 16, respectively). Substrate classification accuracy was higher in the North (64.4%, Cohen's k = 0.442) than the East (50.0%, Cohen's k = 0), with platform substrates showing greater accuracy in both orientations (East = 54.5%, North = 76.3%; Table 1). In P. crenata, the first CV axis explained 64.4% of variance in the East, where platform shells had broader left sides (PC1), and wave breakers showed shorter, laterally wider, and straighter posteriors (PC6; Fig. 5C). In the North, the first two CV axes accounted for 65.5% and 34.5% of variance, respectively (Fig. 5D). Platform and rock shells were more rounded, with rock shells flattening in the anterior and posterior (PC12, PC3). Wave breaker shells were narrower on the right and wider on the left side (PC1). Classification accuracy was higher in the East (74.5%, Cohen's k =0.617) than the North (64.2%, Cohen's k = 0.459), with East wave breakers showing the best accuracy (77.1%).

Morphological disparity analysis highlighted the platform substrate as having the greatest phenotypic variability in the North for *P. aspera* (MD = 0.005) and in both orientations for *P. crenata* (MD = 0.003). On the contrary, wave breakers displayed the lowest variability in *P. crenata* across both orientations (MD = 0.0027 for East; MD = 0.0023 for North).

4. Discussion

The present findings support the hypothesis that Patella aspera and Patella crenata exhibit a degree of phenotypic plasticity, influenced by island orientation and coastal artificialization. Notable differences in body size and dorsal shell shape were observed between orientations, with shells in the North being more oval and wider, while those in the East were rounder and narrower for both species. Slight variations were also noted between natural and artificial substrates, with specimens on artificial substrates showing a trend similar to those in more exposed environments (oval shape). Environmental factors such as wave energy, substrate type, thermal amplitude, and desiccation strongly influence shape and body size, determining functional limits and species distribution along environmental gradients (Etter, 1988; Trussell et al., 1993; Keough et al., 1997; Harley et al., 2009; Miller et al., 2009; Livore et al., 2018). For example, laboratory-controlled experiments on Fissurella latimarginata revealed that limpets from exposed environments developed flatter, wider shells, larger feet, and greater resistance to dislodgement under higher wave velocities compared to those from sheltered areas, which had more laterally compressed, peaked shapes and lower dislodgement resistance (Vasconcelos et al., 2021). In our study, both the North coast, more exposed to wave action due to prevailing oceanic currents and winds from the north-northeast (Riera and Delgado, 2019), and artificial substrates, typically built above the mean low water mark in severe hydrodynamic conditions for structural defense (Morris et al., 2018; Schoonees et al., 2019), exhibited similar morphological traits. Specimens from these environments showed greater shell width and oval shapes, with flattened shells that are wider at the posterior and pointed at the anterior. These traits, observed in both natural and artificial shores with severe hydrodynamic conditions, enhance attachment strength and resistance to dislodgement by waves (Carvajal-Rodríguez et al., 2005; Márquez et al., 2015; Sempere-Valverde et al., 2024; Vasconcelos et al., 2020, 2021). In wave-exposed environments, limpets expend significant energy maintaining adhesion, which can slow growth rates. These slower growth rates, in turn, influence shell architecture by modulating the extent of morphological adaptations to hydrodynamic forces (Denny, 2000; Denny and Blanchette, 2000; Jenkins and Hartnoll, 2001). Ultimately, the interplay between waveinduced mechanical stress and growth rate variability determines the observed patterns of shell morphology. This pattern aligns with findings from other intertidal limpets, including Fissurella latimarginata, Patella rustica, and Patella caerulea (Vasconcelos et al., 2021; Sempere-Valverde et al., 2024).

In contrast, specimens from the sheltered eastern regions and those on natural substrates exhibited more rounded shells with taller, blunter, and narrower shapes. This morphology is likely an adaptive response to higher thermal and desiccation stress (Branch, 1981; Harley et al., 2009; Vermeij, 1973). In these environments, species may prioritize shell height over width and length to enhance water retention, with taller shells possibly representing a strategy for faster growth under stressful conditions (Moore, 1934; Vermeij, 1973; Denny, 2000; Amer et al., 2018). This results in a more circular shell base and a centered apex (Bensaâd-Bendjedid et al., 2022; Sempere-Valverde et al., 2024), as observed in our study. The increased height accommodates a larger body and smaller foot, reducing contact with the substrate, which helps minimize heat loss on hot, dry surfaces and limits water loss through the shell during low tides (Vermeij, 1973; Queiroga et al., 2011). While wave exposure plays a role in shaping shell form through mechanical pressures, intrinsic factors like food availability, and growth



Fig. 3. Principal component analysis plots of PC1 vs. PC2 conducted on specimens of *Patella aspera* (A) and *P. crenata* (B) collected from the East and North orientations of the island of Gran Canaria. Additionally, the thin-plate spline deformation grids are represented to illustrate the shape variation along the PC axes (blue shape) with respect to the mean shape (red shape). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rates are also crucial in determining shell morphology and structural resilience (Steffani and Branch, 2003; Saura et al., 2012). For example, high-spired shells are known to regulate body temperature more effectively under thermal stress, keeping specimens cooler (Harley et al., 2009). In line with our findings, previous studies on limpets such as Patella depressa (Hines et al., 2017), Patella rustica (Amer et al., 2018; Bensaâd-Bendjedid et al., 2022; Sempere-Valverde et al., 2024), Patella caerulea (Battelli, 2016; Bouzaza and Mezali, 2018; Sempere-Valverde et al., 2024), and Cymbula nigra (Rivera-Ingraham et al., 2011) have demonstrated similar morphological patterns. For instance, P. rustica, which spends most of the day out of the water, developed taller, more rounded shells to retain water against desiccation. In contrast, P. ulyssiponensis, exposed only at low tide, exhibited flatter shells, making them more prone to water loss from increased wave action. Similarly, P. intermedia and P. vulgata showed a positive correlation between desiccation stress in the upper intertidal zone and increased shell height. These observations align with Vermeij's model (Vermeij, 1972), suggesting that shell height increases along a vertical intertidal gradient, with high intertidal species, like *P. crenata*, exhibiting more rounded shells due to harsher desiccation conditions compared to lower intertidal species such as *P. aspera* (Branch, 1981; Lowell, 1984; Ramírez et al., 2008). Furthermore, habitat homogenization in upper intertidal areas, where wave action is reduced, results in less morphological variation, as noted in *Phorcus sauciatus* (Vasconcelos et al., 2020). This may explain why *P. crenata* exhibits a generally more rounded shell shape, with slightly wider shells in the North and narrower shells in the East. While, *P. aspera* specimens, subject to higher wave exposure, show more pronounced morphological adaptations, with an oval shell shape in the North and a more rounded shape in the East.

In terms of substrate types, variations in body size and shape were evident between natural and artificial substrates in both species, with



Fig. 4. Canonical variate analysis (CVA) outcomes displaying the mean canonical scores and the magnitudes of the structure coefficients associated with orientation (North vs. East) for specimens of *Patella aspera* (A) and *P. crenata* (B) from the island of Gran Canaria. The direction and length of the vectors provides information on how each variable contributes to the separation of groups. A long vector indicates a significant influence on the separation between groups. Upward vectors indicate a positive correlation between the original variable and the canonical variable. Vectors pointing in similar directions are positively correlated with each other in the context of the canonical variable. Additionally, thin-plate spline deformation grids are provided, illustrating shape variations between East (pink shape) and North (blue shape) orientations with respect to the mean shape (black shape). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

more oval shells in artificial substrates to withstand harsh hydrodynamic conditions (Sempere-Valverde et al., 2024). However, regarding shell shape variations, only specimens of *P. crenata* exhibited slightly rounded shells in natural sheltered shores and oval in artificial waveswept shores. In contrast, these variations were not discernible in *P. aspera* specimens, likely because individuals from artificial substrates in the East were unavailable for this study. Most artificial substrates were located in less accessible areas like harbors, where most of the structures were submerged, and due to the harsh winter sea conditions, safe harvesting was not possible. Consequently, the absence of *P. aspera* individuals from wave breakers did not adequately explain the variability between natural and artificial substrates. Therefore, as observed in other studies, substrate type has a secondary effect on shell morphology, as variations in shell shape are primarily driven by adaptation to local hydrodynamic regimes (Vasconcelos et al., 2020; Sempere-Valverde et al., 2024). Both Vasconcelos et al. (2021) and Le Pennec et al. (2017) conducted studies using an experimental approach in a water flow flume to test this hypothesis. The results demonstrated

Table 1

Results of canonical variate analysis for Patella aspera and P. crenata shells depending on orientation and substrate. In bold, the assignation percentage of each actual group membership with its right predicted group.

Species	Factor/Actual group		Predicted group membership (%)		Correct classification (%)	Cohen's kappa
	Orientation	East	North	-		
P. aspera	East	53.0	47.0	-	62.8	0.232
	North	30.0	70.0	-		
P. crenata	East	60.8	39.2	-		
	North	34.9	65.1	-	63.0	0.259
	Substrate East	Platform	Rocks	Wave breakers		
P. aspera	Platform	54.5	45.5	-	50.0	0
	Rocks	54.5	45.5	-		
P. crenata	Platform	74.2	12.9	12.9	74.5	0.617
	Rocks	8.3	72.2	19.5		
	Wave breakers	8.6	14.3	77.1		
	Substrate North	Platform	Rocks	Wave breakers		
P. aspera	Platform	76.3	10.5	13.2	64.4	0.442
	Rocks	29.0	64.5	6.5		
	Wave breakers	28.6	28.6	42.8		
P. crenata	Platform	70.7	12.2	17.1	64.2	0.459
	Rocks	15.6	68.8	15.6		
	Wave breakers	30.5	16.7	52.8		



Fig. 5. Canonical variate analysis (CVA) results showing the canonical scores for the groups defined by the term as points and the canonical structure coefficients as vectors from the origin for specimens of *Patella aspera* (A and B) and *P. crenata* (C and D) collected from the substrate types Platform (light green circles), Rocks (dark green triangles) and Wave breakers (purple squares), across the East (A and C) and North (B and D) regions of the island of Gran Canaria, Spain. Bold shapes indicate class centroids per sampled site (each individual was allocated to the group with the nearest centroid). The direction and length of the vectors provides information on how each variable contributes to the separation of groups. Longer vectors indicate stronger correlation between the original variable and the canonical variables. Additionally, thin-plate spline deformation grids are provided, illustrating shape variations between Platform (light green shape), Rocks (dark green shape) and Wave breakers (purple shape) substrates with respect to the mean shape (red shape). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that morphological variations indeed respond to the hydrodynamic conditions, regardless of other environmental factors.

Moreover, the highest morphological variability was observed on natural platforms in the North for P. aspera and in both orientations for P. crenata, while the lowest was found on artificial substrates for both species. This may be explained by the fact that, although artificial substrates can provide novel habitats for the establishment of stable limpet populations (Airoldi et al., 2005; Moschella et al., 2005; Ostalé-Valriberas et al., 2023), their structure and composition reduce substrate complexity (Hall, 2018), and consequently, species phenotypic diversity (Bishop et al., 2017). Furthermore, recent studies suggested that artificial substrates, particularly those on severe hydrodynamic shores, are less accessible to humans, resulting in lower harvesting pressures and higher abundances (García-Gómez et al., 2015; Shabtay et al., 2018). Hence, artificial substrates exhibit lower phenotypic diversity but higher abundances than natural substrates (Moschella et al., 2005; Firth et al., 2013; Sanabria-Fernandez et al., 2018). Therefore, specimens on artificial substrates could serve as potential sources of limpets for other parts of the island, as shown for the endangered limpet Patella ferruginea in the Mediterranean Sea (García-Gómez et al., 2011; Ostalé-Valriberas et al., 2022). Furthermore, future eco-engineering modifications on these substrates should aim to increase their structural complexity by incorporating design elements that enhance habitat heterogeneity, such as ECO seawall panels-an innovative bio-enhancing concrete mix (Perkol-Finkel et al., 2018)-and structures replicating natural topographies to promote biodiversity (Evans et al., 2021). Such design enhancements have been shown to increase habitat value, promote biodiversity, and support ecological communities, thereby allowing these structures to function as reservoirs of both diversity and abundance (Perkol-Finkel et al., 2018; Sempere-Valverde et al., 2024). Nevertheless, conservation efforts should prioritize preserving natural substrates, where specimens exhibit higher phenotypic diversity and local adaptability, as observed here in the northern platforms of Gran Canaria. However, platforms are less exposed to wave action compared to artificial substrates, making them more accessible (Airoldi et al., 2005; Sousa et al., 2019b). Recent studies suggested that even in No-take areas, where harvesting is prohibited, illegal harvesting still occurs due to their settlement in highly accessible sites (Faria et al., 2024). Hence, effective conservation strategies demand proactive monitoring and engagement with local communities (Villaseñor-Derbez et al., 2022). While maintaining and monitoring the current no-take coastal areas in Gran Canaria is crucial to ensure the protection of these intertidal species (Order 18th May 2011, Boletín Oficial de Canarias, 2011), the distinctive environmental and anthropogenic conditions of each island highlight the need to expand such efforts across the Canary Archipelago. We recommend that similar studies be conducted on other islands to inform tailored conservation measures that address their unique ecological dynamics.

In conclusion, our findings support the hypothesis that P. aspera and P. crenata exhibit phenotypic adjustments to distinct environmental characteristics along the shores of Gran Canaria. These phenotypic variations, particularly in shell size and shape, are primarily influenced by responses to the severe hydrodynamic conditions typical of wave-swept shores like the North coast and artificial substrates. Slight variations between natural and artificial substrates were noted, mainly in body size, irrespective of wave exposure. These phenotypic traits may lead to spatial segregation, thereby allowing these species to explore a variety of habitats and reduce both intra- and interspecific competition. A proper conservation approach for these species along the coast of Gran Canaria, especially on the northern coast, including both protected and full-access shores, should focus on maintaining the populations of these intertidal species. This approach should account for their local phenotypic variations and ensure ongoing monitoring and protection efforts to preserve their diverse traits and potential for phenotypic flexibility. Further geometric morphometric studies should incorporate substrate types and other variables to enhance the assessment of the mechanisms driving variations in shell shape and size in other limpet and intertidal gastropod species, especially in the context of coastal sprawl and anthropogenic global change.

CRediT authorship contribution statement

Olivia Martínez-Ruiz: Writing – original draft, Methodology, Formal analysis, Data curation. **Rodrigo Riera:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Víctor M. Tuset:** Writing – review & editing, Validation. **Joana Vasconcelos:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Joana Vasconcelos reports financial support was provided by Foundation for Science and Technology. Joana Vasconcelos reports financial support was provided by Government of Gran Canaria. Joana Vasconcelos reports financial support was provided by University of Las Palmas de Gran Canaria. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to express our gratitude to Ministry of Agriculture, Livestock, Fisheries, and Food Sovereignty, Directorate of Fisheries of the Government of Gran Canaria for granting permission to collect limpets from September to October 2023 and January to March 2024. Our sincere thanks also go to Dr. Jose A. Sanabria-Fernandez for his generous assistance with the wave height plotting data. This work was supported by the Portuguese national funds through the Fundação para a Ciência e a Tecnologia I.P. (FCT) (grant numbers EXPL/MAT-APL/0262/2021, UIDB/04292/2020, UIDP/04292/2020, LA/P/0069/ 2020); and the Government of the Canary Islands [grant number VIERA Y CLAVIJO-2022-CIENCIAS-1].

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109344.

Data availability

Data will be made available on request.

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