

Shell shape variation in intertidal *Nerita undata* populations from southern Philippine Islands revealed by landmark-based morphometrics

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Abstract. Understanding intraspecific morphological variability is essential in revealing the ecological and evolutionary dynamics that shape marine gastropod populations. This study investigated the shell shape variation of *Nerita undata* collected from four islands in the Sulu Archipelago and Basilan, Philippines, using landmark-based geometric morphometrics. A total of 179 specimens were sampled from the islands of Balanguingui, Tapul, Lugus, and Malamawi. Standardized digital imaging captured the dorsal and ventral shell orientations, from which 39 landmark points were recorded. Relative warp analysis, thin-plate spline visualization, and multivariate statistics (multivariate analysis of variance and canonical variate analysis) were performed using TPS and PAST software. Results revealed significant differences in shape between populations, particularly in aperture size, spire height, and body whorl width. Ventral analysis showed that relative warp (RW1, 25.42%) captured variation in aperture width, while dorsal analysis indicated that RW1 (47.17%) explained variation in spire elevation. Canonical variate analysis further supported population-level shape divergence, albeit with overlapping patterns indicative of shared morphological traits. Environmental factors such as wave energy, habitat substrate, and microecological gradients were suggested to influence these patterns. The findings underscore the utility of geometric morphometrics in elucidating subtle morphological adaptations among intertidal gastropods. This study contributes to the growing knowledge of Philippine marine mollusk biodiversity and advocates for morphometric surveillance in marine monitoring programs.

Keywords: gastropods, geometric morphometrics, Sulu Archipelago, shell shape.

Introduction. Marine gastropods comprise a highly diverse group of mollusks that exhibit considerable ecological, morphological, and behavioral variability across habitats. Among their defining anatomical features, shell shape plays a central role in adaptation, predator defense, and locomotion (Vermeij 1973). The morphology of gastropod shells is influenced by both genetic and environmental factors, providing a robust system for studying evolutionary divergence, phenotypic plasticity, and local adaptation (Vermeij 1971; Rufino et al 2006). Within the intertidal zones, a dynamic ecological niche exposed to fluctuating salinity, temperature, and wave action, gastropods must develop structural features that confer survival advantages. As such, analyzing shell shape variation offers critical insights into the organism's response to ecological pressures and can serve as an indirect bioindicator of environmental variability (Jeafree et al 2025; Telesca et al 2018; Scalici et al 2016; Rufino et al 2013; Márquez et al 2015; Hallgrímsson 2005; Zelditch et al 2004).

Shell morphology has long been utilized in taxonomic delineation of marine gastropods. Traditional linear measurements, although still relevant, often fail to capture subtle and holistic variations in shape (Lai et al 2025; Martins et al 2024; Uba 2021; Johnson et al 2019; Verhaegen et al 2019; Doyle et al 2018; Jackson & Claybourn 2018; Walker & Grahame 2011; Johnson 2006). The advent of geometric morphometrics (GM) has revolutionized morphological studies by providing statistically robust, spatially explicit assessments of shape that preserve geometric relationships among landmarks (Bookstein

1991; Rohlf & Slice 1990). Landmark-based GM enables researchers to quantify shape in a two- or three-dimensional space using Cartesian coordinates, thereby overcoming the limitations of subjective morphological descriptions. In marine mollusk studies, GM has been applied to detect spatial and sexual shape variation (Madjos & Demayo 2018; Moneva et al 2012), document phenotypic plasticity (Camama et al 2014), and assess the impacts of anthropogenic activities on shell morphology (Krepski et al 2025; Ladas et al 2024; Whelan 2021; Zhao et al 2019; Mahilum & Demayo 2014).

Nerita undata (Linnaeus 1758) is a widely distributed intertidal gastropod in the Indo-Pacific region, characterized by a turban-shaped shell with distinct spiral ridges and a thickened aperture. It belongs to the family Neritidae, a lineage comprising over 150 species across 19 genera (Dangeubun & Uneputty 2005). Species within this family are notable for their shell coloration, sculpturing, and aperture dentition, which often vary in response to local environmental conditions (Tan & Clements 2008). *N. undata* typically inhabits rocky shores, reef flats, and mangrove root zones that are subjected to varying degrees of wave exposure, different substrate types, and desiccation stress. These environmental gradients are believed to influence shell development and phenotypic traits, such as spire height and aperture width (Veronika et al 2025; Musa et al 2023; Vorsatz et al 2021; Dangremond et al 2015; Lindegarth et al 2005; Perez et al 2009; Frey & Vermeij 2008; Vermeij 1973).

In the Philippine archipelago, *N. undata* has been frequently observed along the southern coastal provinces, particularly in the Sulu Archipelago and the neighboring island of Basilan. Despite its broad presence, comprehensive studies exploring its morphological variation across these islands are lacking. This knowledge gap persists despite the region's ecological significance—Sulu and Basilan are located within the Coral Triangle, a global hotspot of marine biodiversity (Carpenter & Springer 2005). Previous morphological investigations on gastropods in Mindanao and other regions of the Philippines, using GM tools, have uncovered significant shape differentiation even among geographically proximate populations (Torres et al 2011; Tabugo et al 2010). These patterns suggest potential microevolutionary divergence or phenotypic plasticity among *N. undata* populations inhabiting distinct coastal environments. Moreover, previous studies employing GM on related taxa such as *Pomacea canaliculata* and *Achatina fulica* have demonstrated the method's efficacy in discerning subtle morphological patterns and sexual dimorphic traits (Moneva et al 2012; Madjos & Demayo 2018). In these studies, variations were often linked to altitude, habitat complexity, or anthropogenic factors. Given the ecological variability of the Philippine intertidal zone, it is reasonable to hypothesize that the populations of *N. undata* from Sulu and Basilan experience unique selective pressures that manifest as shape divergence. For instance, wave energy, substrate hardness, and resource availability may influence shell thickness, curvature, and spire development (Gorr-Pozzi et al 2021; Bocxlaer et al 2020; Briones et al 2014; Yousif 2012; Vermeij 1971). These localized pressures can result in distinct morphological signatures detectable through GM.

The current study aims to investigate the shape variation of *N. undata* shells collected from four coastal sites in the Philippines: Balanguingui, Tapul, Lugus, and Malamawi. These locations were selected for their contrasting wave exposure, substrate types, and levels of anthropogenic disturbance. Using high-resolution digital imaging and landmark-based geometric morphometric analysis, we examined the ventral (aperture) and dorsal (spire) aspects of the shell to capture comprehensive shape descriptors. By applying relative warp analysis and multivariate statistics, we assessed both intra- and inter-population variation and visualized shape deformation using thin-plate splines. This study is novel in its geographic focus and methodological approach. It provides the first morphometric evidence of shell shape variation in *N. undata* across the Sulu-Basilan region using landmark-based techniques. This research builds on foundational morphometric studies of Philippine gastropods (Tabugo et al 2010; Moneva et al 2012; Torres et al 2011) and provides new data from a previously underexamined region. The implications of this research extend beyond taxonomy and ecology, as shell morphology can serve as a proxy for environmental health and evolutionary dynamics in intertidal communities (Alcaraz et al 2025; Lai et al 2025; Farré et al 2021; Vermeiren et al 2021;

Egan et al 2021; Kistner et al 2013; Márquez et al 2010; Rohlf 2008; Zelditch et al 2004). Furthermore, the findings of this study can inform conservation strategies by identifying morphologically distinct populations that may require site-specific protection.

In the broader context of climate change and habitat degradation, the application of GM to marine invertebrates offers an early-warning system for detecting phenotypic responses to environmental stressors (Poloczanska et al 2016; Ross et al 2016; Harvey et al 2014; Hajji 2024). Coastal ecosystems, such as those in Sulu and Basilan, are particularly vulnerable to anthropogenic threats, including sedimentation, coastal reclamation, and overharvesting. Subtle changes in shell shape may indicate ecological shifts before population declines become apparent. Thus, the application of GM in this study not only furthers scientific understanding but also enhances monitoring capacity in threatened coastal zones.

Material and Method

Study area and sample collection. This study was conducted in four distinct island sites located in the southern Philippines: Balanguingui, Tapul, Lugus (all within the Sulu Archipelago), and Malamawi Island (Basilan Province) (Figure 1). These sites were selected for their known populations of *Nerita undata* and for their varying environmental conditions, including wave energy, substrate type, and anthropogenic disturbance. All four sites are located within the Mindanao biogeographic region and feature characteristic rocky intertidal habitats. The collection was conducted manually by handpicking specimens during low tide between May and July 2023. A total of 179 mature individuals of *N. undata* were collected: Balanguingui (n=45), Tapul (n=44), Lugus (n=46), and Malamawi (n=44). The sample sizes per population (n=44–46) are within the recommended geometric morphometric sample sizes for shape data (Bookstein 1991; Adams et al 2013), which range from 30 to 50 specimens per group. While the sample sizes differed among sites, the sample was sufficiently balanced, thus any potential bias in the MANOVA (Multivariate Analysis of Variance) / CVA (Canonical variate analysis) statistics is unlikely to inflate type I error rates or affect the models' goodness of fit. The data met the key assumptions of multivariate analysis: approximately normal distribution of data, equal covariance matrices among groups, and no extreme outliers. The sample sizes were constrained by the availability of mature specimens at each site.

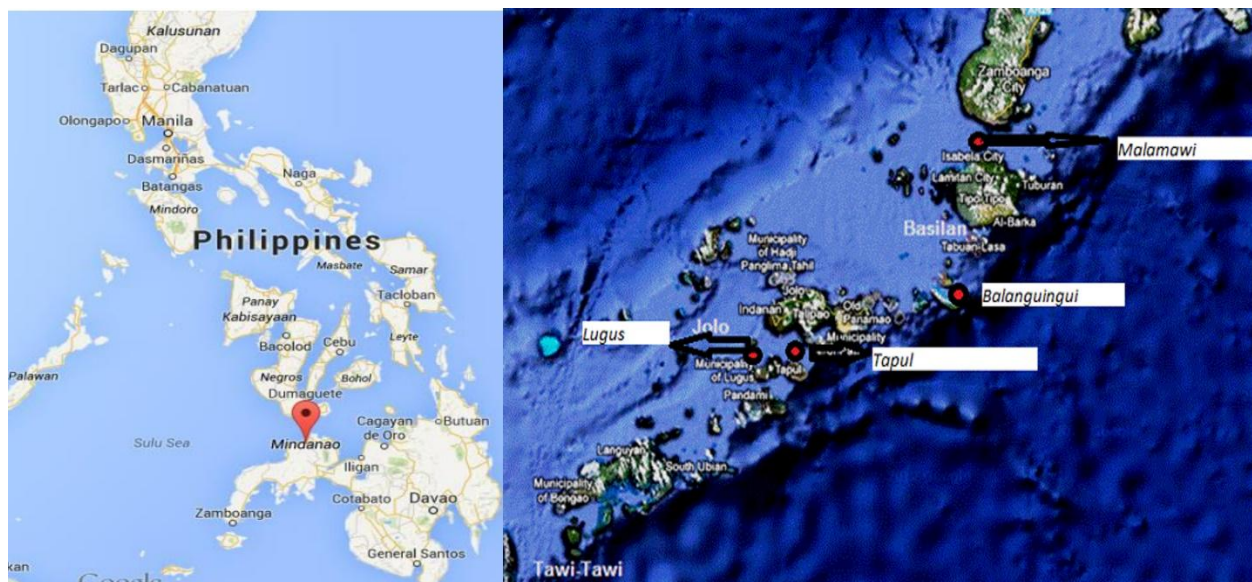


Figure 1. Study area-Sulu archipelago island-Balanguingui island, Tapul, Lugus, and Malamawi island of Basilan.

Specimen preparation and imaging. Specimens were thoroughly cleaned with tap water to remove debris and sediment. Soft tissues were extracted using pins, then washed repeatedly and air-dried for 48 hours. Each shell was then photographed in two

orientations: ventral (aperture-facing) and dorsal (spire-facing), using a Canon EOS 4000D digital camera mounted on a fixed tripod. The distance, focus, and lighting were standardized for all specimens, with shells stabilized on modeling clay to maintain consistent orientation. The images were saved as high-resolution JPEGs for morphometric analysis.

Landmark digitization. Landmarks were digitized using tpsUtil and tpsDig2 software (Rohlf 2004). For the ventral side, 23 homologous landmarks were placed along key anatomical structures of the aperture and columella, including the basal lip, inner and outer aperture edges, and columellar deck (Figure 2). For the dorsal view, 16 landmarks were positioned along the spiral cords, spire apex, and body whorl margins. Landmarks were chosen for their biological relevance and repeatability, ensuring consistent placement across specimens (Figure 3).

Table 1 presents a description of the anatomical landmark points identified on the ventral view of the *N. undata* shell, specifying their sequential positions along the aperture margin, basal lip, columella edge, inner lip, and outer aperture. Table 2 summarizes the anatomical landmark points on the dorsal view of the *N. undata* shell, outlining their distribution and positional relationships across the dorsal surface.

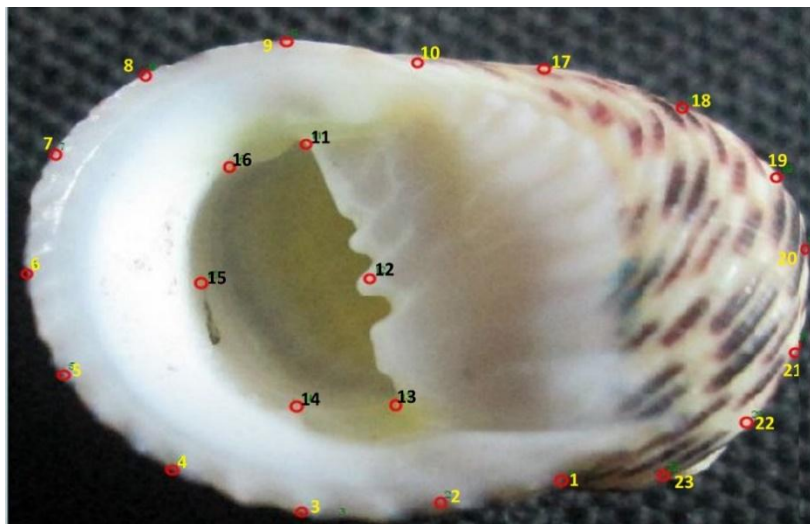


Figure 2. Ventral view of the snail showing assigned landmarks in *Nerita undata*.

Table 1
Descriptions of the anatomical landmark points on the ventral view of the *Nerita undata* shell

Landmark no.	Descriptions of landmark points
1	First LM in the aperture margin
2	LM in the aperture margin between LM 1 and 3
3	LM in the aperture margin between LM 2 and 4
4	LM in the aperture margin between LM 3 and 5
5	LM in the basal lip
6	LM in the basal lip between LM 5 and 7
7	LM in the aperture margin between LM 6 and 8
8	LM in the aperture margin between LM 7 and 9
9	LM in the aperture margin between LM 8 and 10
10	LM in the aperture margin between LM 9 and 11
11,12,13	LM's located at the columella edge
14,15,16	LM's located at the inner lip of the shell
17 to 23	LM's are located at the outer aperture of the shell

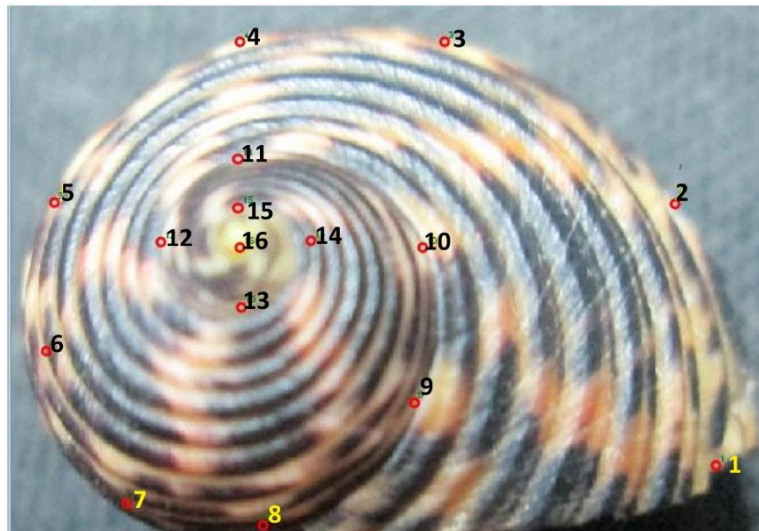


Figure 3. Dorsal view of the snail showing assigned landmarks in *Nerita undata*.

Table 2

Descriptions of the anatomical landmark points on the dorsal view of *Nerita undata* shell

<i>Landmark no.</i>	<i>Descriptions of landmark points</i>
1	First LM in the body whorl of the right border profile of the edge of shell
2	LM in the body whorl of the right border profile of the shell between LM 1 and LM 3
3	LM in the body whorl of the right border profile of the shell between LM 2 and LM 4
4	LM in the body whorl of the right border profile of the shell between LM 3 and LM 5
5	LM in the body whorl of the left border profile of the shell between LM 4 and LM 6
6	LM in the body whorl of the left border profile of the shell between LM 5 and LM 7
7	LM in the body whorl of the left border profile of the shell between LM 6 and LM 8
8	LM in the body whorl of the left bottom profile of the shell between LM 7 and LM 9
9,10,11,12,13,14,15	LM's positioned at the spiral cords of the shell
16	LM is located at the spire of the shell

Geometric morphometric analysis. All landmark coordinates were subjected to Procrustes superimposition to remove non-shape variation (i.e., differences due to size, position, and orientation). Subsequent analyses were performed using TPSRelw v1.48 (Rohlf 2008) to compute relative warp scores based on principal component analysis (PCA) of shape variables. Thin-plate spline (TPS) deformation grids were generated to visualize shape changes along the principal axes of variation (Bookstein 1991). The influence of allometry was assessed by regressing relative warp scores against centroid size.

Statistical analyses. Multivariate statistical tests were performed using the program PAST v1.91 (Hammer et al 2001). Shape variables were calculated from the sets of landmark coordinates defining the shape of the fins by the program PAST. These shape variables were analyzed after Procrustes superimposition (Bookstein 1991). The relative warp (RW) scores obtained from principal component analyses were used as the input variables for the multivariate tests. The first five relative warps explained 72.2% to 88.9% of the variation in shape in the specimens used in the tests. A multivariate analysis of variance (MANOVA) test was used to compare the shapes of the four species

studied, and a subsequent canonical variate analysis (CVA) was conducted to maximize between-group differences and provide a visual representation of the results. Multivariate assumptions were first checked prior to analyses. This was accomplished by assessing the shapes of distributions and residual plots for multivariate normality and performing Box's M test to determine if assumptions of homogeneity of covariance matrices had been met. Following verification of adequate fit, a MANOVA was performed on the data. Although group sizes were less than ideal, sample sizes (44–46 individuals/population) were sufficiently balanced such that potential biases associated with unequal sample sizes were probably minimal. Boxplots and histograms of the key relative warp axes illustrate the distribution of shape variation within and among populations as well as the magnitude of variation.

Ethical considerations. All specimen collections were conducted in accordance with the ethical guidelines approved by the local governing bodies and the Philippine Wildlife Act (RA 9147). Specimens were handled with minimal harm, and shells were retained for educational and scientific reference.

Results

Shell shape variation – ventral view. Geometric morphometric analysis of the ventral shell view, based on 23 landmark coordinates, revealed significant shape variability across the four *Nerita undata* populations sampled based on MANOVA analysis of RW scores (Table 3). Relative warp analysis showed that the first five axes accounted for most of the variation, with RW1 explaining 25.42%, RW2 15.97%, RW3 11.85%, RW4 10.10%, and RW5 7.66% (Table 4). Collectively, these warps captured approximately 71% of the total variation in shape.

Table 3
Results of the multivariate analysis of variance for the ventral portion of the shell

Populations	Balanguingui	Tapul	Lugus	Malamawi
Balanguingui	-	1.22E-07	1.12E-19	3.59E-24
Tapul		-	0.001964	6.31E-15
Lugus			-	1.34E-09
Malamawi				-

Table 4
Percentage variance of overall shell variation of the ventral portion of *Nerita undata* as explained by significant relative warp

Relative warp	% variance	The ventral portion of the shell
1	25.42	The first relative warp illustrates the differences between the shell samples. Those with low negative (left) RW1 scores have a broader aperture relative to the body whorl and a bigger size relative to the shell. On the contrary, those with high positive (right) scores along the first relative warp axis have narrower apertures and relatively smaller sizes, as indicated by the shell shapes.
2	15.97	Variation can be observed only in the apertural area, where samples at the negative axis tend to have wider apertures.
3	11.85	RW3 represents an observation that the positive scores have a narrower spire and a wider shell opening compared to the negative ones
4	10.10	At the positive extremes, shells have wider apertural openings and relatively longer bodies than at the opposing extremes.
5	7.66	Shells at the positive axis have a wider apertural area compared to those at the negative axis, where the aperture is narrower.

The first relative warp (RW1) highlighted the most conspicuous shape differences, particularly in the aperture's breadth and curvature. Specimens with strongly negative RW1 scores exhibited a broader, more rounded aperture, often extending posteriorly into the shell body. In contrast, those with positive RW1 scores exhibited narrower apertures and a more constricted columellar margin (Figure 4). RW2 primarily captured variation along the lower aperture lip and columellar deck, with more expansive basal lips in negatively scored specimens. RW3 to RW5 illustrated subtle differences in aperture elongation and outer lip curvature. Boxplots along the RW1 and RW2 axes showed apparent interpopulation variability. Notably, shells from Balanguingui exhibited wider apertures on average, whereas specimens from Malamawi and Tapul tended toward more elongated, constricted forms. Histogram overlays of RW1 also revealed bimodal distributions in the Tapul and Lugus populations, suggesting the presence of morphotypes within those locales. Figure 5 shows the results of the CVA analysis, in which the individual shells were distributed by shape. And population-specific trends can be observed.

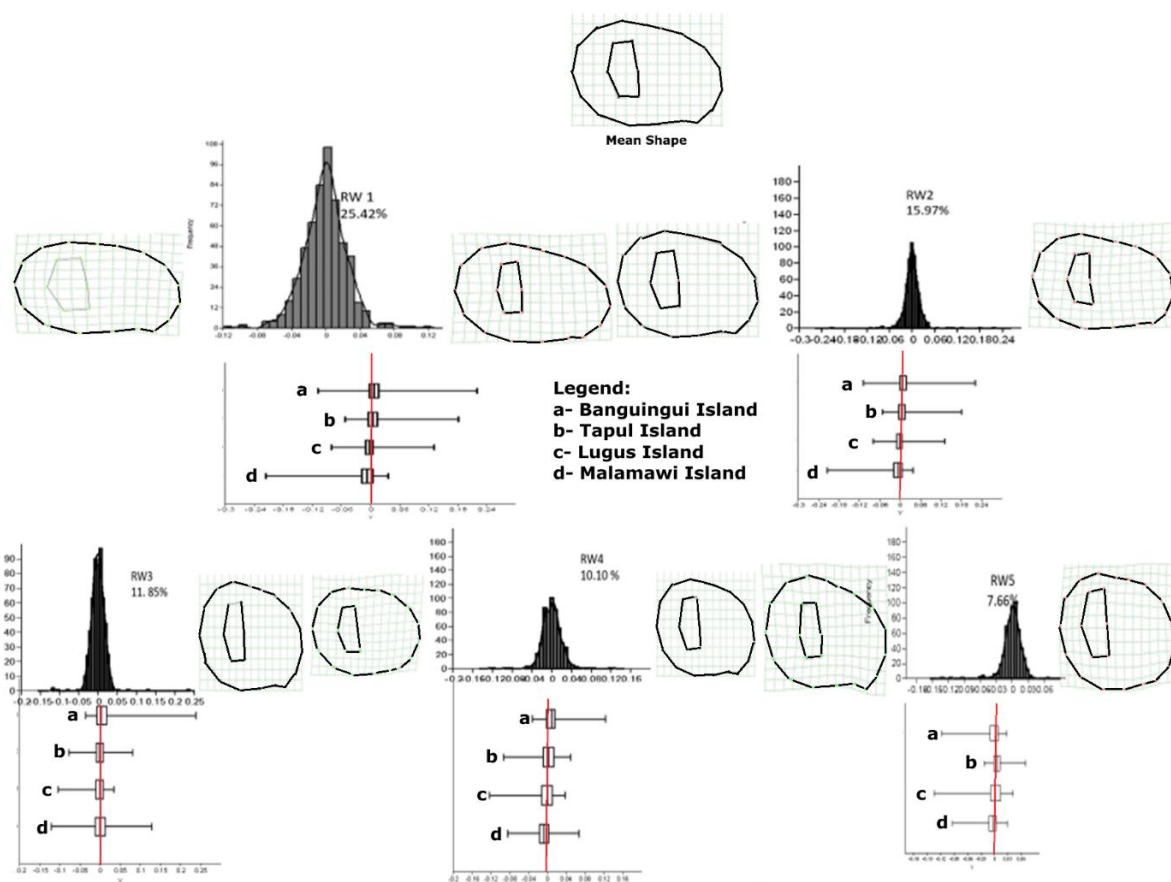


Figure 4. Relative warp box plot and histogram showing variations in the shape of the ventral shell portion of *Nerita undata* found in different areas. Percentage variance of overall shell variation of the ventral portion of *Nerita undata* as explained by significant relative warps.

CVA scatter plots were obtained from pooled individuals across different populations and displayed patterns of geographical variation.

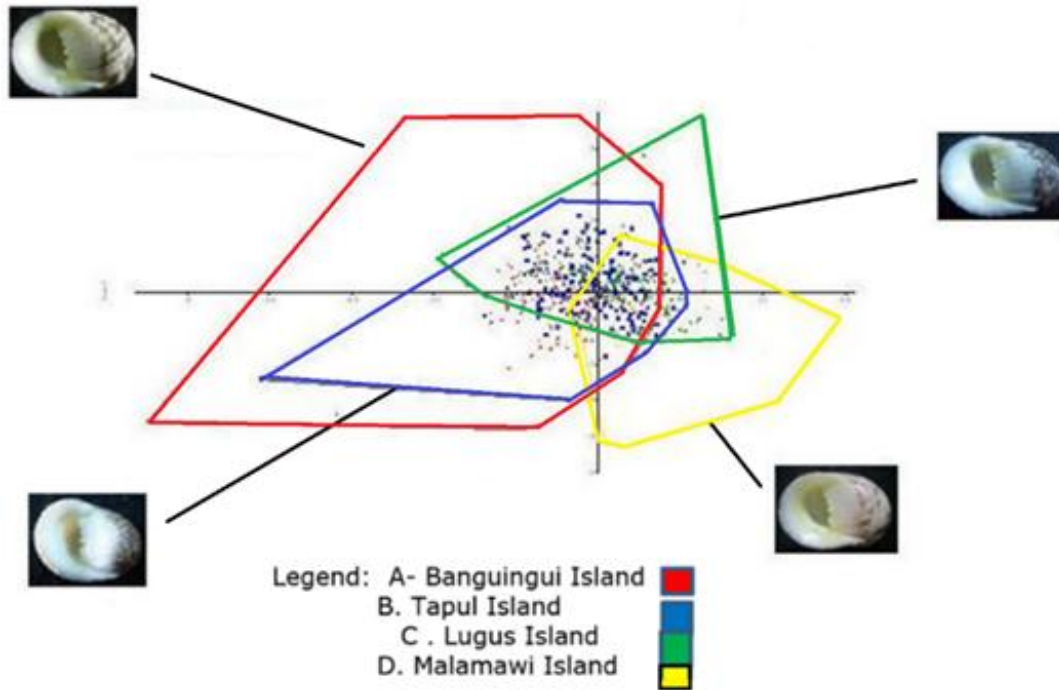


Figure 5. Canonical variate analysis (CVA) plots of relative scores of *Nerita undata*.

Shell shape variation – dorsal view. In the dorsal shell view, based on 16 landmarks, relative warp analysis indicated that RW1 alone explained 47.17% of the variation, with RW2 contributing 23.99%, RW3 10.17%, and RW4 5.17% (Table 5).

Table 5
 Percentage variance of overall shell variation of the dorsal portion of *Nerita undata*

RW	% of variance	Dorsal shell
1	47.17	RW1 indicates differences in the height of spires. Samples along the positive axis exhibit elevated spires, while samples along the negative axis show shorter spire lengths.
2	23.99	RW2 represents the total shape variation. Variation is evident at the body whorl. At the high positive axis, shells have short spire bases but a thinner body whorl width, compared to Low negative scores, which are broad.
3	10.17	Variation is evident at the body, whorl, and base of the shell spire. At the high positive end, shells have a short spire base but a narrower body whorl. On the other hand, samples at a low negative axis have a broader spire base and a wider body whorl.
4	5.17	At the low negative axis, shells have a short spire base but a narrower body whorl. In comparison, samples on the positive axis have a broader spire base and a wider body whorl.

Together, the first four axes captured 86.5% of dorsal shell shape variability. RW1 variation reflected pronounced differences in the spire height and whorl inflation. Specimens with high positive RW1 scores had elevated, prominent spires and narrower body whorls, while negatively scored individuals showed flattened spires and broader, more robust body whorls (Figure 6). RW2 emphasized differences in body whorl width and curvature, with more globose forms on the negative axis and elongated shells on the positive. RW3 and RW4 suggested finer-scale differences in spiral cord compression and whorl asymmetry. Population-specific trends emerged: Lugus shells generally showed higher spire heights, while Balanguingui specimens exhibited broader whorls and flatter

spires. Tapul and Malamawi individuals exhibited intermediate, overlapping morphologies. CVA scatterplots of dorsal morphology (Figure 7) showed partial clustering by location, with some overlap among groups, particularly between Tapul and Malamawi. Apparently, as all data points between four populations show their distribution pattern, an overlapping mean distribution can be observed, which generally accounts for shell-shape resemblances.

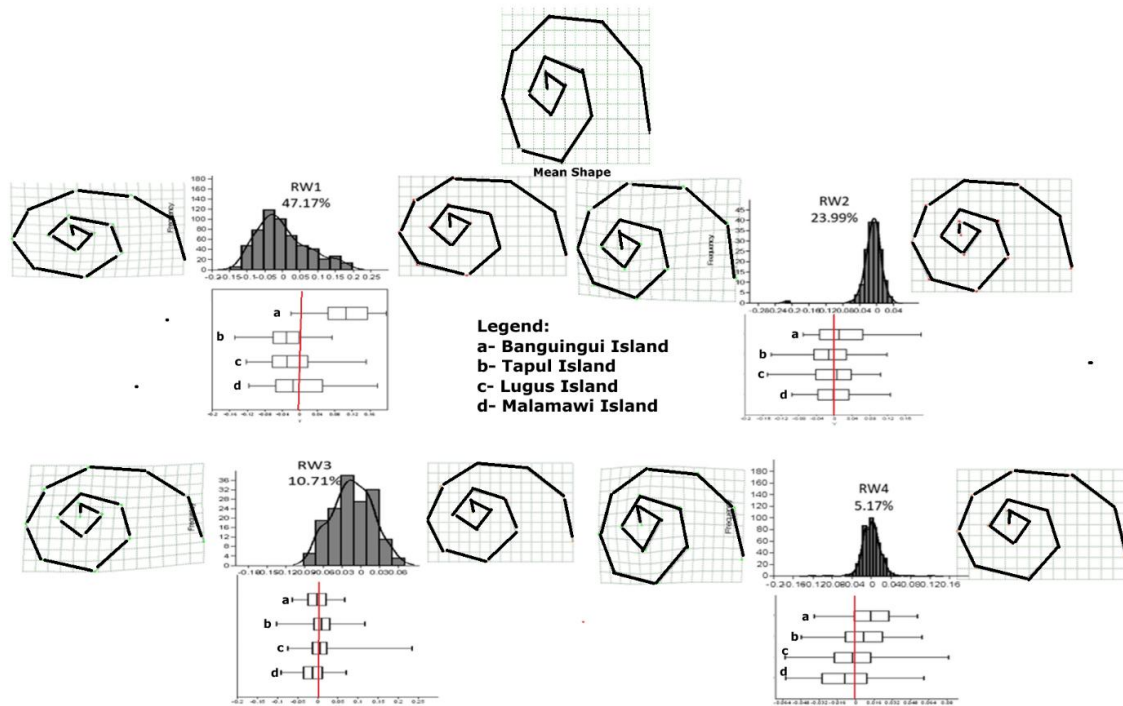


Figure 6. Consensus morphology visualization grid of the dorsal portion of *Nerita undata* shell shape pattern derived from significant four relative warps.

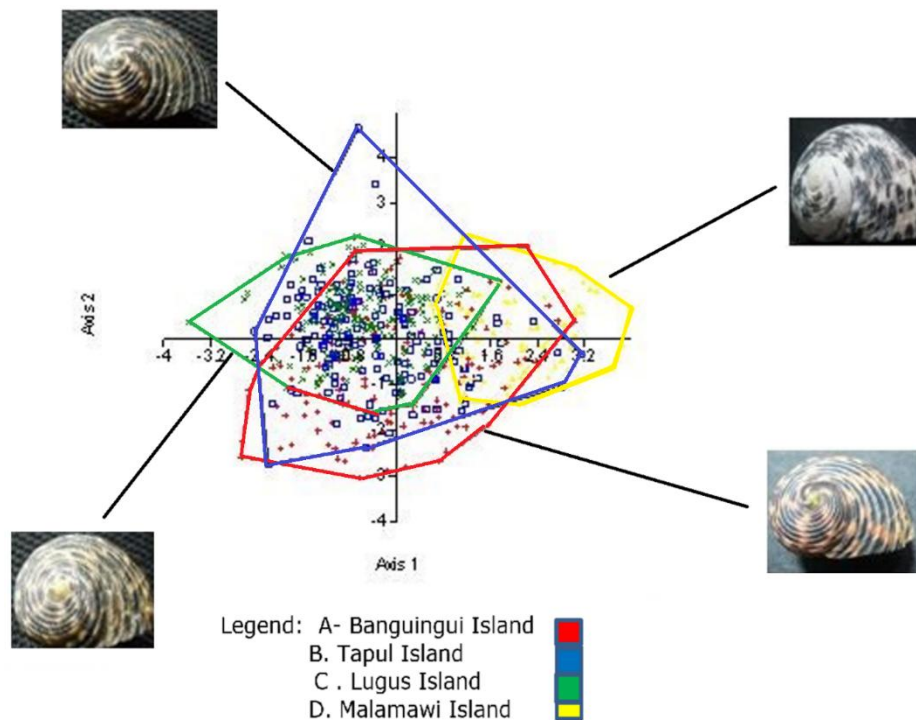


Figure 7. CVA scatter plot of *Nerita undata*'s dorsal portion.

Multivariate statistics. MANOVA results for both ventral and dorsal datasets confirmed significant shape differences between populations (Tables 4 and 6). All pairwise comparisons yielded p -values < 0.01 , indicating strong statistical support for population-level divergence in shell shape. For instance, ventral shape differences between Balanguingui and Malamawi were highly significant ($p = 3.59E-24$), as were dorsal differences between Tapul and Lugus ($p = 0.001964$).

Table 6
Results of the multivariate analysis of variance for the dorsal portion of the shell

Location	Balanguingui	Tapul	Lugus	Malamawi
Balanguingui	-	3.28772E-08	3.16895E-17	6.85081E-40
Tapul		-	0.00245181	3.12314E-43
Lugus			-	8.22605E-47
Malamawi ¹				-

CVA provided additional discrimination among shell morphologies. In the ventral CVA (Figure 5), Balanguingui and Lugus samples formed distinct clusters, while Tapul and Malamawi displayed overlapping CVA scores. In the dorsal CVA (Figure 7), clustering was more diffuse, suggesting a gradient of morphological transitions rather than strict segregation.

Overall morphological patterns. Overall, the geometric morphometric data revealed clear yet overlapping morphological trends among *N. undata* populations across Sulu and Basilan. Balanguingui shells were characterized by broader apertures and flatter dorsal spires, suggesting a possible adaptation to high-wave-energy environments, where low-profile, stable forms are advantageous. In contrast, Lugus shells exhibited narrower apertures and taller spires, traits often associated with calmer habitats or deeper crevices. Tapul and Malamawi shells exhibited a mix of both morphotypes, possibly reflecting transitional environmental gradients or gene flow between populations. The use of both ventral and dorsal perspectives proved essential for capturing the full scope of shell variation. Differences in aperture width and spire elevation were the most diagnostically informative traits across relative warps. These patterns suggest that environmental variation, microhabitat conditions, and possibly localized selection pressures influence *N. undata* shell morphology across islands.

Discussion. The present study utilized landmark-based geometric morphometric methods to assess shell shape variation in *Nerita undata* populations from four coastal sites in the Philippines: Balanguingui, Tapul, Lugus, and Malamawi. Our results revealed significant morphological differentiation within and among populations, supporting the hypothesis that shell shape in *N. undata* is responsive to local environmental conditions and may be shaped by microevolutionary processes (Venegas et al 2015; Gefaell & Galindo 2022; Abdelhady et al 2022; Starunova et al 2021; Bocxlaer et al 2020; Verhaegen et al 2019; Chiu et al 2002; Jablonski 2000). These findings are consistent with prior morphometric studies on gastropods that underscore the influence of habitat and ecological stressors on shell morphology (Lai et al 2025; Das et al 2025; Sempere-Valverde et al 2024; Catalan & de Chavez 2023; Matos et al 2020; Verhaegen et al 2019; Proćków et al 2018; Zelditch et al 2004; Vermeij 1971).

Shell morphology and environmental adaptation. Shell shape in marine gastropods is known to reflect adaptations to the physical environment, particularly in intertidal zones where organisms are exposed to extreme and fluctuating conditions such as wave force, temperature, salinity, and desiccation (Alcaraz et al 2024; Zhao et al 2023; Jan et al 2023; Briffa et al 2023; Janetzki et al 2021; Moisez et al 2020; Baharuddin et al 2019; Sousa et al 2018; Miller & Denny 2011; Vermeij 1973). Our analysis of the ventral view showed that aperture size was a key axis of variation (RW1=25.42%). This trait is ecologically relevant because it influences soft-tissue exposure, water retention, and

locomotor efficiency. Broad apertures, as observed in Balanguingui specimens, may facilitate stronger adhesion to substrates and allow more space for foot extension, which is advantageous in wave-exposed habitats (Vermeij 1973; Yousif 2012). Conversely, narrower apertures, found predominantly in Tapul and Lugus samples, may confer greater protection from predation and desiccation, particularly in shaded or more stable environments (Bocxlaer et al 2020; Moisez et al 2020; Baharuddin et al 2019; Verhaegen et al 2019; Avery et al 2006; McNair et al 1981). Similarly, dorsal-view analysis revealed that spire height and whorl width were critical dimensions for distinguishing populations. The dominance of RW1 (47.17%) in explaining variation in dorsal shape underscores the functional importance of spire height in ecological adaptation. Tall spires, such as those found in Lugus specimens, may increase shell volume and reduce exposure of vital organs to physical damage, although they may also increase the risk of toppling under high wave pressure (Tan & Clements 2008). Flat spires, more common in Balanguingui, may lower the center of gravity and enhance stability on rugged substrates, a hypothesis consistent with observed habitat wave-exposure gradients among the islands. These interpretations align with previous findings in gastropods and bivalves, in which morphological traits correspond to habitat types. For instance, Rufino et al (2006) demonstrated similar shape adaptations in *Chamelea gallina* populations subject to differing hydrodynamic regimes. Likewise, in *Pomacea canaliculata*, variations in aperture shape and shell height were linked to altitude and aquatic vegetation (Moneva et al 2012). These examples provide broader support for our interpretation that the shell shape variability in *N. undata* populations reflects ecological differentiation.

Statistical support for morphological divergence. The use of multivariate statistics, including MANOVA and CVA, strengthens the robustness of our morphological interpretations. All pairwise population comparisons yielded statistically significant differences in both ventral and dorsal datasets ($p < 0.01$), indicating that shell shape divergence is consistent across multiple axes of variation. The considerable overlap observed in the canonical variate space (Figures 5 and 7), particularly between Tapul and Malamawi, suggests shared environmental influences or ongoing gene flow. Nevertheless, the distinct clustering of Balanguingui and Lugus individuals affirms localized differentiation. Such patterns are commonly interpreted as evidence for incipient divergence within species under geographically structured selection (Zelditch et al 2004). The consistency of shape differences along both ventral and dorsal views further validates that the divergence is not random but localized and potentially functional. Similar analytical frameworks were employed by Camama et al (2014) and Madjos & Demayo (2018), who demonstrated that relative warp and canonical analyses are sensitive in detecting intraspecific variation and can reveal the influence of geographic and ecological structuring.

Implications for microevolution and population structure. While shell morphology is influenced by environmental pressures, genetic structure and phenotypic plasticity also play critical roles in shaping population-level differentiation. The Philippine archipelago, including the Sulu and Basilan islands, is known for its high degree of marine endemism and habitat fragmentation (Carpenter & Springer 2005). Such geographic isolation can lead to population divergence through genetic drift, local adaptation, or founder effects, especially in marine invertebrates with limited dispersal capability (Tampipi et al 2025; Kyriazis et al 2017; Brown et al 2013; Pazzaglia et al 1989; Hoeksema 1989). Although *N. undata* has a planktonic larval stage, the retention time and current flow in the Sulu Sea may limit dispersal between these islands, potentially leading to reproductive isolation and morphometric divergence over time. Moreover, environmental heterogeneity across the islands, such as differences in substratum, wave intensity, predation pressure, and anthropogenic disturbance, may exert localized selective pressures. For example, wave-exposed shores, such as those in Balanguingui, favor compact, low-spired shells. In contrast, more sheltered environments in Lugus may permit the development of taller spires and reduced aperture breadth. This pattern of eco-morphological differentiation has been observed in other tropical Neritidae species

(Tan & Clements 2008) and supports the idea of environmentally driven shape adaptation. These findings align with those of Johnson (2006), who reported that gastropod populations inhabiting different intertidal zones exhibited substantial variation in shell form despite taxonomic homogeneity (Lai et al 2025; Murley et al 2024; Catalan & de Chavez 2023; Lajtner et al 2021; Baharuddin et al 2019; Márquez et al 2015; Eschweiler et al 2009). Similarly, Mahilum & Demayo (2014) found that even small-scale environmental differences could drive significant morphological divergence among freshwater snails. The implication is that *N. undata* populations in the southern Philippines are likely undergoing localized adaptation, and their morphometric patterns could serve as indicators of microevolutionary processes in marine mollusks.

Utility of geometric morphometrics. The application of geometric morphometrics in this study proved effective in resolving subtle morphological differences that would likely have gone undetected with traditional linear measurements. Landmark-based GM retains spatial relationships among anatomical points, making it particularly suited for curved, irregular structures, such as gastropod shells (Bookstein 1991; Rohlf & Slice 1990). The ability to generate visual models using thin-plate splines adds an interpretive dimension to numerical results, facilitating a deeper biological understanding of shape deformation. Moreover, GM offers advantages in ecological monitoring and conservation biology. Shell shape changes, mainly when documented longitudinally, can serve as non-invasive indicators of environmental stress, habitat degradation, or population health. For instance, consistent flattening of spires or narrowing of apertures over time could reflect habitat hardening, increased predation pressure, or climate-induced changes in tidal patterns. Integrating GM with ecological, genetic, and environmental data would thus provide a holistic approach to biodiversity assessment in coastal systems (Mamat et al 2025; Leit et al 2025; Maqbul et al 2025; De & Dwivedi 2025; Chen et al 2024; Dwivedi et al 2023; Cruz et al 2022; Zelditch et al 2004; Márquez et al 2015).

Conclusions. Populations of *N. undata* from the Sulu Archipelago and Basilan showed appreciable variation in shape. The ventral and dorsal outlines of the shells of both populations showed considerable variation in shape characters, such as aperture width and spire height, with some variation being shared but much being population-specific. The shape of the shell was analyzed using multivariate methods (MANOVA, CVA). Results showed significant differences among the studied populations, indicating population level of divergence. However, overlap in morphospace among the studied populations is substantial, which likely indicates common environmental factors or gene flow among the localities. Variation in the morphology of *N. undata* shells across microhabitats was assessed using geometric morphometrics to test for shape differences among populations. The outcomes demonstrate the potential of shell morphology as an ecological indicator and contribute to knowledge of the ecological variation of intertidal organisms across the Philippine archipelago. Although some general insight into the functional basis for the form of intertidal *N. undata* on sandy versus rocky shores has been gained, the present study does not provide a quantitative assessment of environmental and genetic differences between groups. By employing a more rigorous, quantitative morphometric approach and extending the study to a broader geographic range, it may be possible to elucidate the relative importance of plasticity versus genetic differences in the formation of the hard parts of these ecologically important marine organisms and to compare them with their allogenic relatives. Ongoing environmental change and increasing human impact on coastal ecosystems demand continued monitoring of morphometric change in *N. undata* and other species, which can serve as valuable ecological indicators and inform the conservation and management of intertidal ecosystems.

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