



Morphometrics approaches to studying phenotypic plasticity in *Pomacea canaliculata* (Golden apple snail)

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ABSTRACT

Morphometrics can be used to quantify a trait of ecological significance by detecting phenotypic plasticity responses. *Pomacea canaliculata* (golden apple snail), an invasive agricultural pest, is an ideal model for demonstrating the organism's capability to morphologically transform in answer to environmental changes because of its slow mobility and known resilience to different ecological conditions. This study aims to explore a case of phenotypic plasticity, specifically a case of agro-ecotype, in geographically isolated, rice field populations of *P. canaliculata* from Mindanao, Philippines through the use of traditional and geometric morphometrics methods. Relative warp scores of the landmarked aperture, dorsal and whorl shapes of *P. canaliculata*, as well as some conchological measurements were subjected to Correlation Analysis Based on Distances (CORIANDIS) software, a tool which can visualize congruence and disparity of multivariate traits. Significant phenotypic variation is revealed among *P. canaliculata* populations, to which females exhibit greater plastic responses than males. This variability could be due to geographical isolation, as well as varying agricultural practices to counter-attack snails since these said practices can also affect some of the physico-chemical factors that influence *P. canaliculata* morphology. Evaluating these variations can therefore aid in understanding the very nature of this pest and consequently support integrated pest management control. This study has also revealed the efficiency of morphometrics and CORIANDIS in describing an organism's morphological variations.

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1. Introduction

Phenotypic plasticity refers to the potential of an individual's genotypes to produce different phenotypes when exposed to diverse environmental conditions. Variations in phenotypes among the individuals in a population could result from both genetic and environmental sources, specifically biotic-abiotic trait interplay (Gilbert, 2010). When the environments with which a genotype is confronted are heterogeneous, the resulting development of alternative phenotypes is often an adaptive strategy to minimize loss of fitness in a harsher environment or to maximize fitness in a favorable environment (Relyea, 2002; Madjos et al., 2015). Miner et al. (2005) stressed that phenotypic variation in morphometric traits is widespread in nature which may often be an adaptive mechanism

reflecting the environmental effects in the ecological niches of a population. Furthermore, according to Robinson and Parsons (2002), evolution of population-specific norms of reaction is more remarkable if there is low dispersal among populations.

Pomacea canaliculata, commonly known as golden apple snail, is an excellent model in eco-evolutionary genetics because of its slow mobility and known resilience to varying environmental conditions. Considered as one of the "100 worlds' worst invasive species, it has remarkably developed suitable phenotypes as a form of adaptive mechanism and has the potential to be ecologically damaging especially in agricultural fields. Several studies such as size determination at reproductive maturity, developmental stages assessment, growth rate evaluation (Demetillo et al., 2015; Taguing, 2015) together with recent phenotypic variation analysis on population structure (Torres et al., 2011; Mahilum and Demayo, 2014a,b; Moneva et al.,

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2012a,b,c; Galan et al., 2015; Madjos et al., 2015) have strengthened the hypothesis of agro-ecotypes in *P. canaliculata*, a case of modification in the expressed phenotype of a genotype as a function of the environment especially in agricultural ecosystems.

Whilst traditional morphometrics are useful in the studies of growth, geometric morphometrics are equally significant in demonstrating phenotypic plasticity in morphometric traits (Ginter et al., 2012; Addis et al., 2010). Variation in the traditional non-landmark data (length, width and number of whorls) and geometric morphometrics data (aperture, dorsal, whorl view) can be subjected to Correlation Analysis based on Distances (CORIANDIS) software, a tool which can visualize congruence and disparity of multivariate traits (Anies, 2015; Tabugo et al., 2010; Márquez and Knowles, 2007). Thus, this present study sought to demonstrate phenotypic plasticity among geographically-isolated rice field populations of *P. canaliculata* in Mindanao, Philippines through the use of the above-mentioned morphometrics tools. Evaluating these conchological variations can therefore aid in evaluating the very nature of this pest and support integrated pest management control as this organism is believed to have evolved into a complex of morphologically divergent populations in response to ecologically diverse habitats.

2. Materials and methods

2.1. Collection of samples and sampling sites

P. canaliculata was handpicked purposively along the three geographically-isolated rice fields in Mindanao, Philippines, with the following geographical position system readings: Butuan City - 08°56.747 N and 125°28.407 E; Iligan City - coordinates 08°11.954 N and 124°13.606 E; and Pagadian City - coordinates 07° 50' N and 123° 26' E.

Environmental factors that could possibly affect phenotypic variation aside from geographical isolation were also measured such as water depth, temperature and pH. Water depth was measured by using a meter stick, temperature with a laboratory thermometer, and pH with a pH meter. The data taken were the average of three trials. In each sampling site, thirty (30) males and 30 females were randomly chosen as a representative of each population, having a total of 180 specimens.

Sex identification was based on the works of Torres et al. (2011) and Yanes et al. (2010) wherein the female's aperture accordingly curves inward while the male shell curves outward.

2.2. Traditional morphometrics

Vernier caliper was used to obtain the conchological non-landmarked character measurements such as the length and the width. The length was taken from the apex of the shell to the

base of the aperture. The width was measured at the widest part of the shell when the shell is oriented so that aperture faces the observer; specifically measured from the side of the body whorl to the outermost side of the aperture. In counting the number of whorls, a complete turn indicates a whorl (Galan et al. 2015).

2.3. Geometric morphometrics

Geometric morphometrics are quantitative representation and analysis of morphological shape which uses geometric coordinates instead of the usual measurements used in traditional morphometrics. In coordinate acquisition, each snail from each population was photographed on its aperture, dorsal, and whorl view parts using WG1 Pentax camera (14 megapixels, optical zoom 10x). Images of the shell were oriented in the same position with the columella at 90° of the x-axis in the aperture view or in the orientation in which the apex is visible. The digital photographs were then processed using tpsdig 2.10 software (Rohlf, 2006) for landmark acquisition. Geometric morphometrics analysis captures shape differences in populations of organisms by subjecting landmark data to a method called Procrustes-fitting (Dryden and Mardia, 1998; Rohlf, 2001; Goodall, 1991). Fig. 1 shows the landmarks acquired in the 3 different views of the shell.

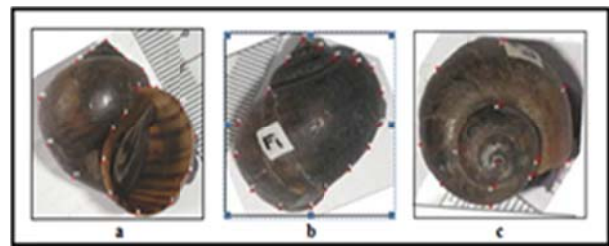


Fig. 1: Landmark acquisition of (a) aperture, (b) dorsal and (c) whorl of *P. canaliculata*.

Twenty-one (21) landmarks were identified on the aperture part; seventeen (17) landmarks on the dorsal part; and thirteen (13) landmarks on the whorl part of *P. canaliculata*.

2.4. Transformation and multivariate analyses

Each set of co-ordinates were submitted separately to a Generalized Procrustes Analysis (GPA) available in the tpsRelw software (Rohlf, 2007). This procedure translated, rotated and scaled the original configurations in order to achieve the best superimposition of all shapes. The size of each specimen is represented by the "centroid size", a measure that is able to estimate the size in all directions in a body better than is possible by using univariate measures such as maximum length.

After this superimposition, the software breaks down the morphological difference into a series of non-uniform components, described as partial warps. The scores of the specimens on the partial

warp axes constituted the shape variables that were used in the subsequent statistical analyses. The software was used to introduce shape variables into a Principal Component Analysis (PCA), and to visualize the warping associated with the various principal components (PCs). These components represent relative warps in the context of a TPS (thin-plate spline) approach (Burela and Martin, 2011) to provide a graphical representation of shape and to compare the sets of data (Addis et al., 2010).

Differences in the centroid sizes among populations were tested using Multi-Variate Analysis of Variance (MANOVA).

2.5. Correlation analysis based on distances (CORIANDIS)

Correlation analysis based on distances (CORIANDIS) was also applied. This integrates all the six characters (landmarked aperture, dorsal, whorl and non-landmarked length, width and number of whorls) in order to observe underlying differences and sources of variability among groups in terms of congruence among characters (Tabugo et al., 2010,

Anies et al., 2015). CORIANDIS software version 1.1 beta by Márquez and Knowles (2007) has been used to determine associations among multivariate datasets, trait variance or disparity, congruence and multivariate covariance measure on how similar the interspecific locations of characters of the species or populations. The option "Projections on compromise space" will plot all the specimens/groups and traits in the same space. The squared distances of each group to the origin are then computed for each of the shape data sets, and plotted in a stacked bar graph to give an overall impression of the differences between the populations of *P. canaliculata* (Tabugo et al., 2010).

3. Results and discussion

Most of the morphological variations of *P. canaliculata* are accordingly due to the effects associated with the environment, either phenotypic responses (plasticity) or particularly those which act during ontogenetic development (Benítez, 2013). Table 1 shows the mean data on the conchological features measured traditionally.

Table 1: Mean data on shell morphometrics of *P. canaliculata* in the three geographically-isolated ricefields in Mindanao, Philippines

Sites	<i>P. canaliculata</i> Sex	Mean morphometric data of <i>P. canaliculata</i> collected from the three sampling sites		
		Length(in cm)	Width (in cm)	# of whorls
Butuan	Male	12.48	7.66	4.06
	Female	13.85	10.38	4.13
Iligan	Male	31.87	15.73	3.93
	Female	33.00	18.37	4.23
Pagadian	Male	30.90	27.10	4.23
	Female	32.57	29.23	4.37

These differences in the mean traditional morphometrics supports phenotypic plasticity phenomenon since *P. canaliculata* were taken from different geographical regions, thus different environment made them varied from one another (Miner et al., 2005). According to ESSC (2002), the topology and the evolution of the geological land masses are some of the factors in the variability of both floral and faunal species. Among the three sites,

Butuan has different geologic evolution which was formed as a deltaic plain from the deposition of river sediments flowing through the Agusan River, the third longest river of the Philippines. On the other hand, Iligan and Pagadian were part of the mainland of Mindanao. Table 2 shows the physico-chemical factors of the three sampling sites known to affect the shell morphometrics of *P. canaliculata*.

Table 2: Physico-chemical factors of the three sampling sites in Mindanao, Philippines

Sites	Physico-chemical parameters (mean value)		
	Water depth (in cm)	Water Temperature (in °C)	Water pH
Butuan	51.00	28.87	4.50
Iligan	28.00	28.33	7.33
Pagadian	32.00	29.10	7.00

The physico-chemical parameters also vary so with the practices to counter-attack snails based on interviews from the local farmers. Accordingly, Butuan rice fields are treated with strong molluscicides while Pagadian rice fields are treated with biological measures by inducing ducks before seedling transplantation. Iligan rice fields are treated with both cultural and biological practices. These practices could be a factor in contributing to the snail's population phenotypic diversity since these

practices can also affect some of the physico-chemical factors that influence *P. canaliculata*.

In several experiments, an increase in the aperture and width expansion was found to be adaptive responses to their burrowing mechanism when exposed to strong molluscicides, high temperatures, low water depth and unfavorable water pH. In other certain instance, changes are often accompanied by a change in spire height and aperture size; high, narrow spires and small apertures may reduce predation (Chiba, 2009;

Lagesson, 2011), while low spires and large apertures may reduce dislodging and damage during tumbling (Haase, 2003). Furthermore, geometric

morphometrics data reveals the confirmatory statistics values of the phenotypic variations exhibited by *P. canaliculata* (Table 3).

Table 3: Confirmatory statistics values of the phenotypic variations exhibited by *P. canaliculata* using multivariate analysis of variance (MANOVA) from geometric morphometrics data

Sex	View	Pairwise Comparison	P-value	Remarks
Male	Aperture	Butuan vs. Iligan	3.2×10^{-5}	Extremely significant
		Butuan vs. Pagadian	5.2×10^{-11}	Extremely significant
		Iligan vs. Pagadian	4.1×10^{-14}	Extremely significant
	Dorsal	Butuan vs. Iligan	0.0010	Very significant
		Butuan vs. Pagadian	1.40×10^{-8}	Extremely significant
		Iligan vs. Pagadian	6.33×10^{-13}	Extremely significant
	Whorl	Butuan vs. Iligan	5.47×10^{-11}	Extremely significant
		Butuan vs. Pagadian	3.07×10^{-12}	Extremely significant
		Iligan vs. Pagadian	4.1×10^{-14}	Extremely significant
Female	Aperture	Butuan vs. Iligan	1.05×10^{-10}	Extremely significant
		Butuan vs. Pagadian	5.86×10^{-20}	Extremely significant
		Iligan vs. Pagadian	9.2×10^{-25}	Extremely significant
	Dorsal	Butuan vs. Iligan	8.96×10^{-17}	Extremely significant
		Butuan vs. Pagadian	6.88×10^{-19}	Extremely significant
		Iligan vs. Pagadian	1.02×10^{-29}	Extremely significant
	Whorl	Butuan vs. Iligan	8.96×10^{-17}	Extremely significant
		Butuan vs. Pagadian	6.88×10^{-19}	Extremely significant
		Iligan vs. Pagadian	1.02×10^{-29}	Extremely significant

Most of the views (aperture, dorsal and whorl) in both male and female *P. canaliculata* from different rice field locations exhibit extremely significant phenotypic variations. Using CORIANDIS software in integrating traditional and geometric morphometrics data, variations were detected in multiple data sets of characters and correlated evolution of these multivariate traits was determined for possible demonstration of phenotypic plasticity (Márquez and Knowles, 2007). Fig. 2 shows the plot of the principal components of “compromise” space axis accounting for 40.55%, 31%, 23.8%, 14.63%, 11.17%, 9.854% of the total compromise variance. The quality of the compromise is 66.86%.

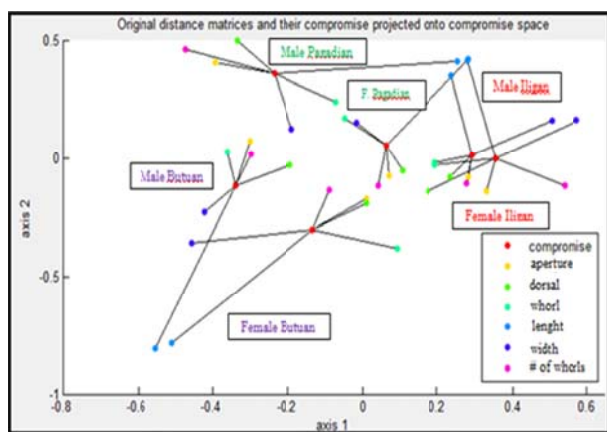


Fig. 2: Plot of the principal components of “compromise” space axis of the *P. canaliculata* populations

The plot indicates the congruence and multivariate measure on how related the interspecific locations of traits/characteristics (represented as colored points) are in this space. If two traits tend to be consistently different or similar between pairs of species, they are said to be

(positively) congruent, and will show in this plot as a general tendency to cluster together within species (Tabugo et al., 2010; Anies et al., 2015). The result shows a general tendency for each population of *P. canaliculata* to cluster out together implying great differences between the six populations with regards to six shell shape datasets (aperture, dorsal, whorl, length, width and number of whorls), except for a slight overlapping between male and female Iligan *P. canaliculata* populations. Female and male Butuan populations set out considerably from other species, although this seems to be largely a function of traits number 3 (landmarked whorl) and number 4 (length).

Finally, in evaluating the extent of variation, computation of codisparities was done and Pearson correlation coefficient was chosen to measure correlation. Codisparity measures the degree to which two traits tend to contribute similarly or proportionally to the divergence of the population. Squared distances to centroid for individual sets, which are the quantities used to compute codisparities shows the resulting disparity plot indicating the relative contribution of different characters to *P. canaliculata* population’s divergence (Fig. 3).

The total height of the stacked bar chart results from the addition of the squared distances of each trait separately (a measure of trait disparity). This shows how much each population differs from the rest by interpreting such differences in terms of individual character (Tabugo et al., 2010). This chart can therefore be interpreted as a decomposition of species distinctness from other species in terms of specific traits (Anies et al., 2015).

Results show that the heights of the stacked bar graphs were different between populations of *P. canaliculata*, implying morphological differences in

its shell shape. It can also be seen that the Butuan female *P. canaliculata* populations departs considerably from the other populations, to which the landmarked whorl and the non-landmarked length character traits largely contribute to its disparity. Notable also is the slight difference between the Pagadian female and Iligan male groups, a function of the width shape and of the number of the whorl traits. The Iligan female population has more elongated aperture opening aperture-narrower width ratio and more number of whorls than other female populations of *P. canaliculata* in Pagadian and Butuan (Madjos et al., 2015).

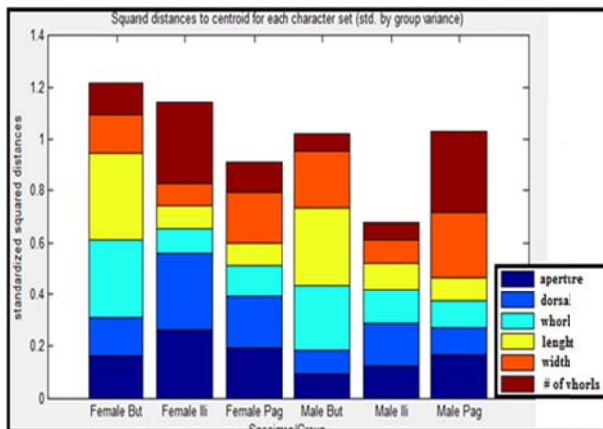


Fig. 3: Stacked bar graphs showing disparity among the 6 ricefield populations of male and female *P. canaliculata* with regards to 6 characters (aperture, dorsal, whorl, length, width and number of whorls)

Between sexes within the geographical location, greater variations can be accounted most in the height and whorl in all populations. While the 6 traits are equally advancing in Iligan male population, aperture (trait number 1) and dorsal (trait number 2) shape departs considerably for Iligan female group. Significant expanded width and wider aperture are evident in the latter than in the former group. The Butuan male population has somewhat elongated height and wider width ratio compared to Iligan male and Pagadian male groups. Width (trait number 5) and number of whorls (trait number 6) contribute similarly or proportionally to the divergence of the populations of male and female *P. canaliculata* in Pagadian. The observed sex-differences in all *P. canaliculata* populations could be products of a lot of factors such as (a) sexual selection mechanisms, (b) maternal patterns of inheritance of traits and (c) sex-influenced traits as females might have characters that are important for reproduction.

In applying the context of agro-ecotype, evolving variation in the expressed phenotype of a genotype as a function of the agricultural environment is suggestively demonstrated by *P. canaliculata*. As this invasive species spread through a new agricultural environment, they encounter novel selection pressures and challenges which permit population differentiation expressed as variability in morphology and genetic characteristics (Burela and

Martin, 2011; Tabugo et al., 2010; Chiba, 2009). Traditional and geometric morphometrics approaches to studying phenotypic plasticity therefore provides a good model for inferring the mechanisms behind population differentiation, especially in agro-ecotype perspective since this organism is believed to be comprised of complex morphologically divergent populations that occur in ecologically diverse habitats. Thus, phenotypic plasticity evolves as a great strategy for *P. canaliculata* to successfully invade changing environments (Hollander and Butlin, 2010).

4. Conclusion

This study have shown that traditional and geometric morphometrics analysis coupled with CORIANDIS are useful in describing variations among the populations based on individual and combined analysis of characters (landmarked aperture, dorsal and whorl and non-landmarked length, width and number of whorls). Overall results showed that *P. canaliculata* shell varies in shape, where geographic distance is not the only contributing factor in shaping the structure of the populations. It might also indicate phenotypic plasticity which allows the population to develop alternative phenotypes in response to fluctuating environments (with varying counter-attack practices and physico-chemical parameters). This study supports that variability is the raw material of adaptability and long-term survivability, hence making this agricultural rice pest *P. canaliculata* very invasive. Awareness of this variability is important if effective management strategies are to be developed in the agricultural ecosystems.

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