

Shell shape variation of queen conch *Strombus gigas* (Mesogastropoda: Strombidae) from Southwest Caribbean

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Abstract: The endangered species *Strombus gigas* is a marine gastropod of significant economic importance through the Greater Caribbean region. In contrast to phenotypic plasticity, the role of genetics on shell variations in *S. gigas* has not been addressed so far, despite its importance in evolution, management and conservation of this species. This work used geometric morphometrics to investigate the phenotypic variation of 219 shells of *S. gigas* from eight sites of the Colombian Southwest Caribbean. Differences in mean size between sexes and among sites were contrasted by analysis of variance. Allometry was tested by multivariate regression and the hypothesis of common slope was contrasted by covariance multivariate analysis. Differences in the shell shape among sites were analyzed by principal component analysis. Sexual size dimorphism was not significant, whereas sexual shape dimorphism was significant and variable across sites. Differences in the shell shape among sites were concordant with genetic differences based on microsatellite data, supporting its genetic background. Besides, differences in the shell shape between populations genetically similar suggest a role of phenotypic plasticity in the morphometric variation of the shell shape. These outcomes evidence the role of genetic background and phenotypic plasticity in the shell shape of *S. gigas*. Thus, geometric morphometrics of shell shape may constitute a complementary tool to explore the genetic diversity of this species. *Rev. Biol. Trop.* 64 (4): 1585-1595. Epub 2016 December 01.

Key words: geometric morphometrics, phenotypic plasticity, phenotypic stocks, fishery management, Colombian Caribbean.

The queen conch *Strombus gigas* Linnaeus, 1758 is a large marine gastropod of significant economic importance through the Greater Caribbean region (Theile, 2005). In this endangered species, the genetic patchiness seems to characterize the natural populations since studies using neutral markers have shown both gene flow (Mitton, Berg, & Orr, 1989; Campton, Berg Jr, Robinson, & Glazer, 1992) and genetic structure either at isolated sites or at micro-scales across different Caribbean areas (Mitton et al., 1989; Tello-Cetina, Rodríguez-Gil, & Rodríguez-Romero, 2005; Márquez et al., 2013).

The morphometrics studies in *S. gigas* has been used to solve ecological questions of fisheries interest (Randall, 1964; Ávila-Poveda

& Baqueiro-Cárdenas, 2006). Thus, the measures based on shell length and lip thickness to estimate the size at sexual maturity are used as a parameter for management regulations and sustainability of fisheries (Wenner, Fusaro, & Oaten, 1974; Conand, 1981; 1989; Appeldoorn, 1988). However, the morphometric studies have not been used to define phenotypic stocks so far, this information allows to determine the way the stock responds to exploitation. This issue is relevant since the ontogenic rates influence many population attributes that are intimately related to population dynamics (Garrod & Horwood, 1984).

On the other hand, the morphometric studies have documented sexual size dimorphism in *S. gigas* shell (Randall, 1964; Galindo-Pérez,

2009) and other members of the genus *Strombus* such as *S. gibberulus*, *S. flammeus* (Abbott, 1949), *S. pugilis* (Colton, 1905; Galindo-Pérez, 2009), *S. canarium* (Cob, Arshad, & Idris, 2008), and *S. costatus* (Galindo-Pérez, 2009). Similarly, the sexual shape dimorphism in the shell has been reported in *S. gigas*, *S. costatus* (Galindo-Pérez, 2009), *S. pugilis* (Colton, 1905; Galindo-Pérez, 2009) and other no phylogenetically related snails like *Buccinum undatum* (Hallers-Tjabbers, 1979), *Nucella lapillus* (Son & Hughes, 2000), *Pomacea canaliculata* (Estebenet, Martín, & Burela, 2006) and *Buccinanops globulosus* (Avaca, Narvarte, Martín, & Van der Molen, 2013).

In addition, evolutionary studies of shell in *S. gigas* have evidenced plastic responses to environmental variations (Alcolado, 1976; Stoner & Davis, 1994; Martín-Mora, James, & Stoner, 1995) and to predators under controlled conditions (Delgado, Glazer, & Stewart, 2002). Likewise, the plastic responses to environmental variations have been found in other snail species (Pascoal et al., 2012; Kistner & Dybdahl, 2013; Gustafson, Kensinger, Bolek, & Luttbeg, 2014; Solas, Hughes, Márquez, & Brante, 2015). During ontogeny, these plastic responses to environmental heterogeneity constitute a key factor in the potential of species to colonize, survive and reproduce; abilities that allow them to persist under diverse environmental conditions and expand its distribution range (Stearns, 1989). However, it remains to address whether the variations in shell shape of *S. gigas* reflect genetic differences as well as it occurs in other gastropods (Johannesson & Johannesson, 1996; Conde-Padín, Caballero, & Rólan-Alvarez, 2009; Martínez-Fernández, Paes de la Cadena, & Rolán-Alvarez, 2010; Zieritz, Hoffman, Amos, & Aldridge 2010; Pascoal et al., 2012).

Thus, in this work, geometric morphometric analysis was used to address the effect of genetics and geographic origin on *S. gigas* shell size and shape across a broad area in the Colombian Southwestern Caribbean (San Andrés archipelago). In this area, the spatial phenotypic variation of *S. gigas* shell

is unknown, although this information may complement the genetic studies in this region (Márquez et al., 2013). The genetic control of the shell shape cannot be overlooked in populations of *S. gigas* from Colombian San Andrés archipelago because they are structured in three genetically different groups. Furthermore, both the bathymetry of San Andrés archipelago (Andrade, 2001) that limit the queen conch dispersion among sites, as well as the environmental and fishing variable conditions, may induce phenotypic differences in the queen conch shells.

MATERIALS AND METHODS

Specimens and study area: A total of 219 shells of adult individuals of *S. gigas* were assessed using geometric morphometric analysis. These samples were collected at different sites in the San Andrés archipelago, which are separated by depths ranging from 100 to 1 500 fathoms that impede the dispersal of juveniles and adults among these sites (Fig. 1). In this area, the population genetics of *S. gigas* shows a moderate genetic structure among three regions of the San Andrés archipelago: Southern (South-South-West and East-South-East atolls); Northern (Roncador, Queena and Serrana atolls) and most Northern, near to Jamaica (Serranilla atoll, Alice shoal and Bajo Nuevo atoll) (Márquez et al., 2013). On the other hand, the fishing pressure is differential among the sites because some of them are subjected to artisanal (South-South-West and East-South-East atolls, Roncador, Serrana) and industrial fisheries (Queena, Serranilla atoll, Alice shoal and Bajo Nuevo atoll).

Geometric morphometrics: Ten landmarks of type II (Bookstein, 1991) were identified on digital photographs of shells (Fig. 2). To reduce peripheral optical distortion, each shell was photographed in the centre of the visual field, and landmarks were digitized twice on the set of 219 shells. Digital precision was estimated by using the “Repeatability” index (individual variance / total variance) in a model

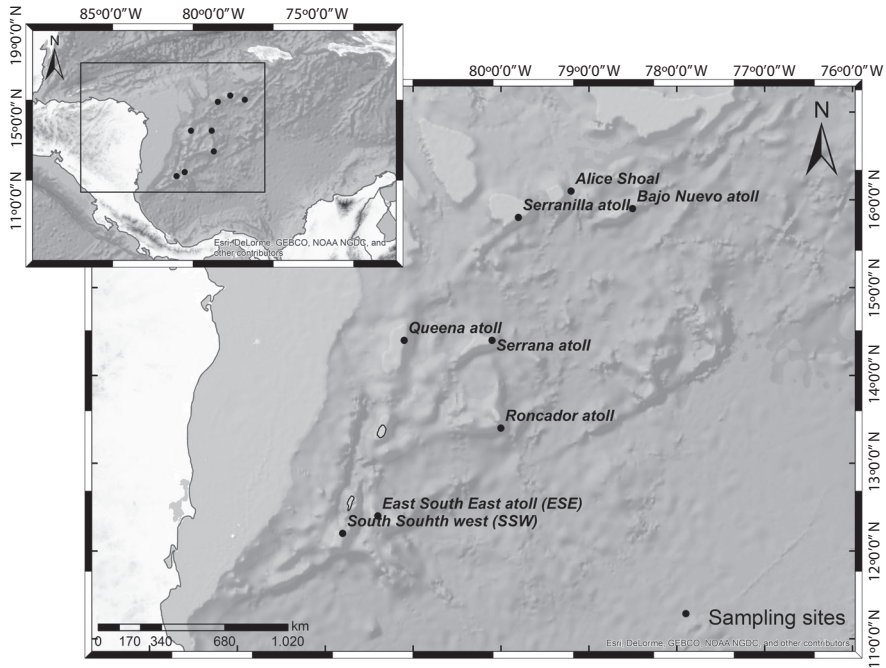


Fig. 1. Sampling sites of queen conch *S. gigas* from San Colombian Andrés archipelago, Southwest Caribbean.
Fig. 1. Sitios de muestreo de *S. gigas* en el archipiélago colombiano de San Andrés, Caribe suroccidental.

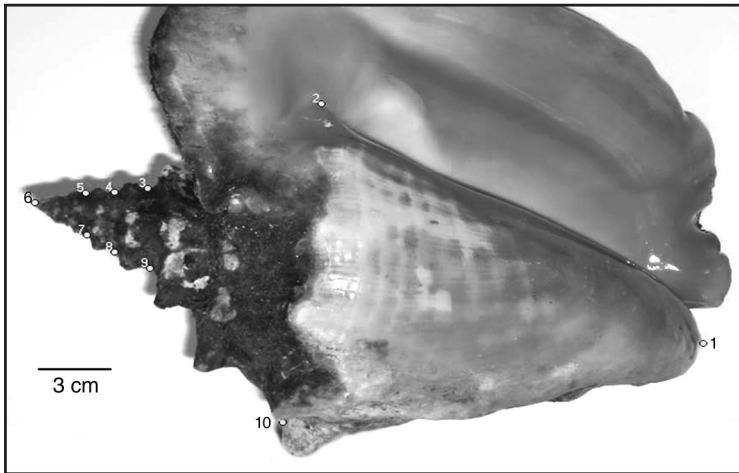


Fig. 2. Ten landmarks type II measured as coordinates of *S. gigas* shells. Numbering on the landmarks denotes the arrangement followed during digitization.
Fig. 2. Diez puntos anatómicos de referencia tipo II empleados como coordenadas para las conchas de *S. gigas*. La numeración de los puntos de referencia denota el arreglo seguido durante la digitalización.

II one-way ANOVA on repeated measures (Arnqvist & Mårtensson, 1998) using VAR module of the software CLIC V.70 (Dujardin, 2013). Raw data of coordinates were submitted to Generalized Procrustes analyses to generate “partial warp” scores and uniform components (Rohlf, 1990; Rohlf & Slice, 1990) as shape variables, using the modules COO and MOG of the software CLIC V.70 (Dujardin, 2013).

Size variation: The isometric estimator known as centroid size was extracted from coordinates and used for size comparisons of the shell. Centroid size is defined as the square root of the sum of the squared distances between the centre of the configuration of landmarks and each individual landmark (Bookstein, 1990). First, the principal effect of sex on centroid size was investigated by a one-way ANOVA in samples from three sites for which data were available (Serranilla atoll, Alice shoal and Bajo Nuevo atoll). To avoid bias depending upon the type of measure of size, the analysis was also performed using siphon longitude as a measure of size. Second, the centroid size among eight sites was compared using one-way ANOVA. All ANOVAs were performed after verified that the assumptions of normality and homoscedasticity were satisfied. *A posteriori* Bonferroni tests were then conducted to test pairwise treatment comparisons. Finally, to detect correlations between size variation and genetics and geographic position, a multiple regression was performed using the centroid size as a dependent variable and the mean observed heterozygosity previously published (Márquez et al., 2013), latitude and longitude as the independent variables. The method Variance Inflation Factor (VIF) was used to estimate the multicollinearity among independent variables. In residuals, the normality was estimated by Lilliefors test, homoscedasticity by studentized Breusch-Pagan test and autocorrelation by Durbin-Watson. Finally, the Hierarchical Partitioning method was used for calculating the contribution of all independent variables to the regression model. Analysis

were conducted in R 2.15.2 (www.r-project.org) and RWizard (Guisande, 2015).

Shape variation: The effect of sex (Serranilla atoll, Alice shoal and Bajo Nuevo atoll) and geographic origin on shell shape of *S. gigas* from San Andrés archipelago was explored by using principal component analysis. Statistical significance between pair-wise Euclidean distances was assessed using 1 000 permutations and multiple comparisons were adjusted by Bonferroni Test (Sokal & Rohlf, 1995). The residual relationship between shape and size variables was explored by multivariate regression and permutation test procedure for statistical significance (Good, 2000). Using MANCOVA (with size as a covariate), we also investigated the model of an allometric trend common to different population and the statistical significance was obtained by the Wilks statistics. The Euclidean distances derived from the first five principal components, which explained 97 % of total variation, were used to construct a UPGMA tree (Mega v.6.0; Tamura, Stecher, Peterson, Filipksi, & Kumar, 2013). Finally, the relationship among Euclidean distances and heterozygosity differences was evaluated by a Mantel test.

RESULTS

Repeatability: Congruence between two sets of measures from the same set of 219 shell photographs showed fairly good agreement for CS ($R = 0.999$), as well as for the five relative warps (RW1, RW2, RW3, RW4 and RW5, with $R = 0.905, 0.809, 0.817, 0.935, 0.794$ respectively) representing most of the shape variation (97 %).

Size variation: Centroid size (Shapiro-Wilks: 0.992, $P = 0.982$; Barlett Test: 1.000, $P = 0.948$) and siphon longitude (Shapiro-Wilks: 0.987, $P = 0.864$; Barlett Test: 1.000, $P = 0.887$) showed normal distribution and variance homogeneity. Both size measures were not significant between sexes (all $P > 0.05$). In contrast, the differences of size among sites

were significant ($F_{(8, 246)} = 52.63$; $P = 0.000$) showing a gradient from South (smallest individuals) to North (largest individuals) (Fig. 3). On the other hand, the multiple regression showed that the variables heterozygosity and latitude explain the 62.9 % of the observed variance in the centroid size ($r^2 = 0.629$; $P < 0.001$). These variables did not show multicollinearity ($VIF = 1.593$) and residuals satisfied the assumptions of normality (Kolmogorov-Smirnov: 0.056; $P = 0.085$) and absent of autocorrelation (Durbin-Watson: 1.821; $P = 0.072$) although they did not show homoscedasticity (Breusch-Pagan: 0.795; $P = 0.033$).

Shape variation: Sexual shape dimorphism was not significant in all the studied sites ($P > 0.160$ after Bonferroni correction). However, since the allometric effect was significant ($p = 0.000$), the variation of shape after correcting for size was evaluated because the hypothesis of a common allometric model was accepted (λ Wilks: 0.3869; $F_{(80,414)}: 1.1271$; $P = 0.230$). Without allometric effect, the sexual shape dimorphism was significant in Alice shoal (Euclidean distance: 0.028; $p = 0.000$) and Bajo Nuevo atoll (Euclidean distance: 0.027; $P = 0.000$) but it was non-significant in Serranilla, after Bonferroni correction (Euclidean distance: 0.019; $P = 0.028 > 0.003$). However, both sexes showed the same topology of the tree according to the geographic origin (Fig. 4). The Euclidean distances among regions and

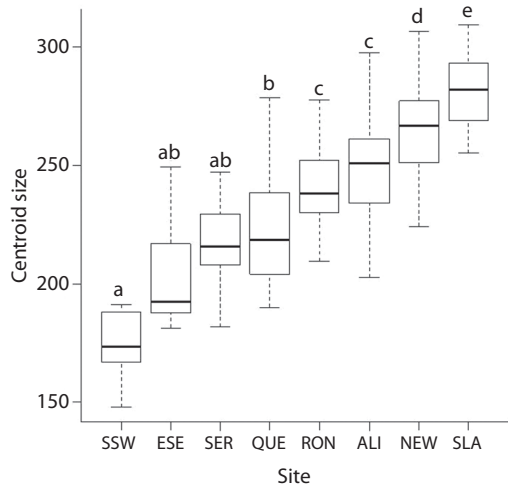


Fig. 3. Centroid size (mm) variation of *S. gigas* shells from Colombian Caribbean. SSW: South South West, ESE: East South East, SER: Serrana, QUE: Queena, RON: Roncador, ALI: Alice shoal, NEW: Bajo Nuevo atoll, SLA: Serranilla. Different lowercase letter on the box denotes statistical significance.

Fig. 3. Variación del tamaño centroide (mm) de las conchas de *S. gigas* del Caribe colombiano. SSW: South South West, ESE: East South East, SER: Serrana, QUE: Queena, RON: Roncador, ALI: Alice shoal, NEW: Bajo Nuevo atoll, SLA: Serranilla. Diferentes letras minúsculas en las cajas denota significancia estadística.

sites were highly significant (Table 1). Additionally, the UPGMA tree clustered the samples in three main groups (Fig. 5): (1) Alice shoal, Serranilla and Bajo Nuevo atolls, (2) Serrana atoll and (3) South-South-West, East-South-East, Queena and Roncador atolls. On the

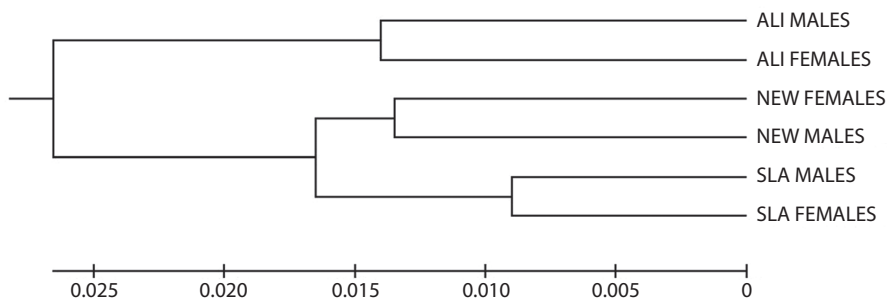


Fig. 4. UPGMA tree based on Euclidean distance derived from five principal components that explain the 97 % of the total variation of the shell. Alice shoal (ALI), Bajo Nuevo atoll (NEW) and Serranilla (SLA) atolls.

Fig. 4. Árbol UPGMA basado en las distancias euclidianas derivadas de cinco componentes principales que explican el 97 % de la variación total de la concha. Alice shoal (ALI), Bajo Nuevo atoll (NEW) and Serranilla (SLA) atolls.

TABLE1
Euclidean distances (Ed) and statistical significance (P) of *S. gigas* shell shape among regions and sampling sites

CUADRO 1
Distancia euclidiana (Ed) y significancia estadística (P) de la conformación de la concha de *S. gigas* entre regiones y sitios de muestreo

Pairwise comparisons		Ed	P
Among regions			
Southern region	Northern region	0.036	0.037*
Southern region	Most Northern region	0.109	0.000*
Northern region	Most Northern region	0.120	0.000*
Within regions-among sites			
Southern region			
SSW	ESE	0.056	0.025*
Northern region			
QUE	RON	0.073	0.000*
QUE	SER	0.129	0.000*
RON	SER	0.098	0.000*
Most Northern region			
ALI	NEW	0.029	0.000*
ALI	SLA	0.055	0.000*
NEW	SLA	0.038	0.000*

*Denotes statistical significance. / *Denota significancia estadística.

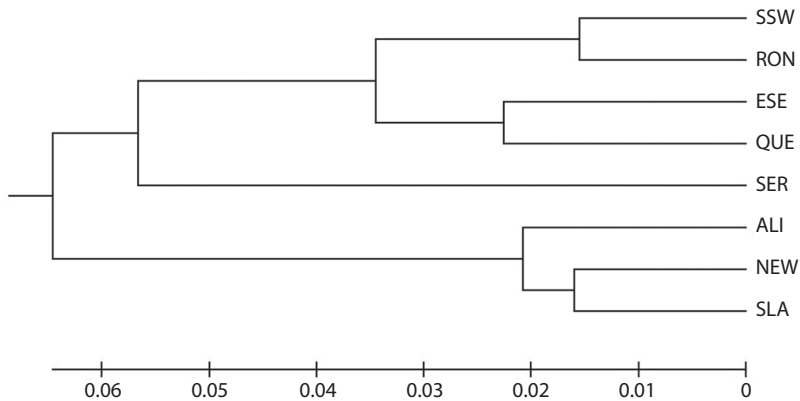


Fig. 5. UPGMA tree based on Euclidean distance among sites derived from five principal components that explain the 97 % of the total variation of the shell. South South West (SSW), East South East (ESE), Queena (QUE), Roncador (RON), Serrana (SER), Alice shoal (ALI), Bajo Nuevo atoll (NEW), Serranilla (SLA).

Fig. 5. Árbol UPGMA basado en las distancias euclidianas derivadas de cinco componentes principales que explican el 97 % de la variación total de la concha. South South West (SSW), East South East (ESE), Queena (QUE), Roncador (RON), Serrana (SER), Alice shoal (ALI), Bajo Nuevo atoll (NEW), Serranilla (SLA).

other hand, the shell shape variation was not correlated with variations in heterozygosity (r : -0.074; t : -0.348; P = 0.364).

DISCUSSION

The use of three moderate differentiated genetic groups in this work allowed us to assess the role of genetics and geographical origin on shell size and shape of *S. gigas*. Non-significant sexual size dimorphism of *S. gigas* found in this work contrasts with previous studies of this species in other Caribbean regions (Randall, 1964; Avila-Poveda & Baqueiro-Cárdenas, 2006; Galindo-Pérez, 2009) but it is concordant with results found in *S. pugilis* (Galindo-Pérez, 2009). This suggests that the sexual size dimorphism may vary among sites, corroborating that the degree of sexual size dimorphism in gastropods may differ among localities as well as found in *S. gibberulus* and *S. flammeus* from Indo-Pacific (Abbott, 1949). In other taxa, changes in sexual size dimorphism may result from sexual differences in phenotypic plasticity (Stillwell & Davidowitz, 2010; Márquez & Saldamando-Benjumea, 2013). This may explain the results found in *S. gigas* because the shell of queen conch is a plastic trait (Alcolado, 1976; Stoner & Davis, 1994; Martín-Mora et al., 1995; Delgado et al., 2002; Clerveaux, Danylchuk, & Clerveaux, 2005) and the habitat exert a high influence on the morphology of juvenile and adults (Martín-Mora et al., 1995).

On the other hand, the sexual shape dimorphism in *S. gigas* shell is concordant with previous studies in *S. gigas*, *S. costatus* (Galindo-Pérez, 2009), *S. pugilis* (Colton, 1905; Galindo-Pérez, 2009) and other snails like *Buccinum undatum* (Hallers-Tjabbers, 1979), *Nucella lapillus* (Son & Hughes, 2000), *Pomacea canaliculata* (Avaca et al., 2013). Such variations cannot be explained by allometry since the sexual shape dimorphism was significant after size correction. However, the degree of sexual shape dimorphism varied across sites (it was non-significant in Serranilla) suggesting that this trait may also be plastic.

Geographical comparisons of the size showed that shells of queen conch were significant different among sites. This result is concordant with those found in samples from Puerto Rico (Appeldoorn, 1994), Bahamas (Stoner & Ray-Culp, 2000) and Turks and Caicos (Clerveaux et al., 2005). Furthermore, queen conchs from archipelago displayed an increasing gradient of size from South to North atolls. The size gradient may result from food competition related to population density, which has been reported in other Caribbean areas (Cala de la Hera, De Jesús-Navarrete, Oliva-Rivera, & Ocaña-Borrego, 2011) but our results do not show the expected inverse relationship among shell size and population density. Here, largest snails were found in high population density sites, whereas smallest snails were in low population density sites.

Alternatively, the gradient in the shell size may result from fishing pressure. Such decreasing of body and sexual mature size as a result of fishing has been previously described in *S. gigas* (De Jesús-Navarrete, Medina-Quej, & Oliva-Rivera, 2003; De Jesús-Navarrete & Valencia-Hernández, 2013). However, this explanation seems unlikely because the size of *S. gigas* shells were inversely related to the fishery pressure: largest snails were in the sites subjected to industrial fishery, whereas the smallest snails were in the sites subjected to artisanal fishery.

Instead, the size pattern may result from differences in food quality/availability as well as genetic background. A previous study established that the quality and availability of food may affect the growth rate and thus, the total longitude of the *S. gigas* shell (Alcolado, 1976). Such explanation suggests a gradient of food quality and availability among the atolls likely related to the influence of marine currents since largest individuals are influenced by the Caribbean Central Currents, whereas smallest ones are influenced by the anticyclonic gyre. However, the lack of information about these parameters does not permit to contrast this hypothesis. Additionally, the selective extractions of largest individuals may favour

the reproductive success of smallest snails. This explanation is likely since the variation in shell size was directly correlated with the latitude and the levels of heterozygosity of the populations.

On the other hand, the differences in shell shape among sites are consistent with genetic differences and low dispersion of snails among atolls. Morphometric differences are concordant with genetic differences evidenced previously by microsatellites (Márquez et al., 2013) among populations near to Jamaica (Serranilla atoll, Alice shoal and Bajo Nuevo atoll) and the North of Archipelago (Roncador, Queena and Serrana atolls) and between South-South-West and East-South-East atolls. However, morphometric differences were also found among genetically similar populations (Serranilla versus Queena and Roncador) corroborating the role of phenotypic plasticity in the variation of *S. gigas* shell (Alcolado, 1976; Stoner & Davis, 1994; Martín-Mora et al., 1995; Delgado et al., 2002).

The role of genetic background as well as phenotypic plasticity on the shell shape has been evidenced in other snails such as *Littorina saxatilis* (Johannesson & Johannesson, 1996; Conde-Padín et al., 2009; Martínez-Fernández et al., 2010), *Unio pictorum* (Zieritz et al., 2010) and *Nucella lapillus* (Pascoal et al. 2012). The influence of both factors on the *S. gigas* shell shape would explain the lack of correlation between genetic diversity measured by neutral markers and the phenotypic variation, likely submitted to different evolutionary forces. This different behavior of genetic markers was also used to explain the divergence between genetic and morphometric data in other taxa (Márquez, Jaramillo-O, Gómez-Palacio, & Dujardin, 2011).

In conclusion, the results of this study support the idea that the variation of the shell of *S. gigas* may be explained by phenotypic plasticity to environmental variation as well as the genetic background. It has been proposed that these two factors may maximise fitness when the environmental circumstances became uncertain by unpredictable changes in local

or long distance dispersal (Pascoal et al. 2012). For the fishery stock assessment, groups with different growth or reproduction dynamics should be modelled and managed separately, regardless of genetic homogeneity (Cadrin, Friedland, & Waldman, 2005). Thus, the geometric morphometrics of shell of queen conch may represent a valuable complementary tool in the management and conservation regulations.

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RESUMEN

Variación de la conformación de la concha del caracol reina *Strombus gigas* (Caenogastropoda: Strombidae) del Caribe suroccidental. La especie en peligro, *Strombus gigas*, es un gastrópodo marino de importancia económica en la región del Gran Caribe. En contraste con la plasticidad fenotípica, el papel de la genética en la variación de la concha en *S. gigas* no ha sido abordado hasta ahora, a pesar de su importancia evolutiva, manejo y conservación. Este trabajo utilizó la morfometría geométrica para investigar la variación fenotípica de la concha de *S. gigas* en ocho sitios del suroeste del Caribe colombiano. Las diferencias en el tamaño promedio entre sexos y sitios se contrastaron mediante análisis de varianza. La alometría se evaluó mediante regresión multivariada y la hipótesis de pendientes similares se contrastó mediante un análisis multivariado de covarianza. Las diferencias en la conformación de las conchas entre sitios se exploraron mediante análisis de componentes principales. El dimorfismo sexual en el tamaño no fue significativo, mientras que el dimorfismo sexual en la conformación fue significativo y variable entre los sitios. Las diferencias en la conformación de la concha entre sitios fueron concordantes con diferencias genéticas basadas en microsatélites, lo cual apoya su base genética. Además, las diferencias en conformación de la concha entre poblaciones genéticamente similares sugieren un papel de la plasticidad fenotípica en la variación

morfométrica de la conformación de la concha. Estos resultados evidencian el papel de la genética y la plasticidad fenotípica en la conformación de la concha de *S. gigas*. Por lo tanto, la morfometría geométrica de la conformación de la concha puede constituir una herramienta complementaria para explorar la diversidad genética de esta especie.

Palabras clave: morfometría geométrica; plasticidad fenotípica; stocks; manejo pesquero; caribe colombiano.

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