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BIOGEOGRAPHIC SHELL SHAPE VARIATION IN *TROPHON GEVERSIANUS* (GASTROPODA: MURICIDAE) ALONG THE SOUTHWESTERN ATLANTIC COAST

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ABSTRACT: Broad-scale latitudinal morphological trends in gastropods along the southwestern Atlantic coast are scant, since the majority of studies have focused on local scales. Here, we evaluate biogeographic shell shape variation in the marine gastropod *Trophon geversianus* across most of its distributional range, covering 14 degrees of latitude. Samples come from death assemblages which have the potential to unveil biogeographic patterns along spatio-temporal scales and are not affected by short-term volatility in comparison with living assemblages. We performed morphometric analyses on shells from death assemblages, and compared shape variation between mid-Holocene and modern shells from one southern site. Multivariate analyses identified two morphotypes matching the biogeographic regions of the Argentine Sea that segregates a warm-temperate from a cold-temperate zone. The Magellan province morphotype is characterized by a larger shell, lower spire height, and higher aperture length than the Argentinean province morphotype. This change in shell shape is significantly correlated to sea surface temperature, even after accounting for spatial autocorrelation, which could be indirectly influencing intraspecific morphoclines via shifts in growth rates. On the other side, shell size and shape variations were also detected (size increase over recent geological time) between mid-Holocene and modern specimens at the Beagle Channel, which could be attributed to paleoenvironmental changes and to shifts in predator-prey relationships. Our study illustrates the usefulness of death assemblages for revealing large-scale patterns of shell-shape variability in mollusk species, and highlights the spatial coincidence of intraspecific morphological differentiation with the transition zone between biogeographic provinces of the Argentine Sea.

INTRODUCTION

Shell shape in gastropods is a key trait that reflects phylogenetic history and life habits (Signor 1982; Reid et al. 1996); morphological studies are therefore of major interest because they allow interdisciplinary work between ecology and paleontology (Jablonski and Shubin 2015). At a biogeographical scale, numerous studies have analyzed morphological variations in terms of evolutionary factors, the relative importance of genetic differentiation, phenotypic plasticity, and their interdependence (e.g., Vermeij 1978; Parsons 1997; Trussell and Etter 2001; Irie 2006; Lee and Boulding 2010).

Following the 'morphometric revolution' that took place two decades ago (Rohlf and Marcus 1993), multiple studies have been published applying morphogeometric techniques to evaluate size and shape changes across diverse taxa. Although geometric morphometrics is a powerful tool for the study of morphological variation because it possesses numerous advantages over the more traditional approach based on linear measurements, several studies have pointed out that both approaches lead to very comparable conclusions (Maderbacher et al. 2008; Breno et al. 2011; Fontoura and Morais 2011; Navia et al. 2015). The advantage of traditional morphometrics is that some simple measurements or angles can have direct

and clear functional-mechanistic meaning which is not necessarily true with landmarks or outlines (see Vermeij 1973; Stanley 1988). In the last few decades, morphometrics has become a powerful tool for: (1) discerning taxonomic problems (Carvajal-Rodríguez et al. 2006; Van Der Molen et al. 2013); (2) identifying different morphotypes within a single species (Gustafson et al. 2014; Márquez et al. 2015); and (3) documenting phenotypic patterns through space and time (McShane et al. 1994; Gordillo et al. 2011a; Boretto et al. 2014; Bayer et al. 2015; Morán et al. 2018).

The Argentinean coast, located in the southwest Atlantic, is an excellent study area for marine biogeographic aspects given its vast latitudinal expanse with strong variation in oceanographic conditions (Malvé et al. 2018). In addition, this coast encompasses two major biogeographic provinces: the Argentinean and the Magellan (Balech and Ehrlich 2008) (Fig. 1). The different physiographic characteristics allow the distinct comparison of movable sandy bottoms in the former and gravel bottoms where large algae grow in the latter. Climatic differences explain the prevalence of northern winds in the Argentinean province, where warm and temperate-cold coastal waters alternate, while in the Magellan province strong westerly winds with a predominance of subantarctic waters from the Malvinas Current (Balech and Ehrlich 2008) prevail. These factors account for the faunal composition differences between the provinces: the

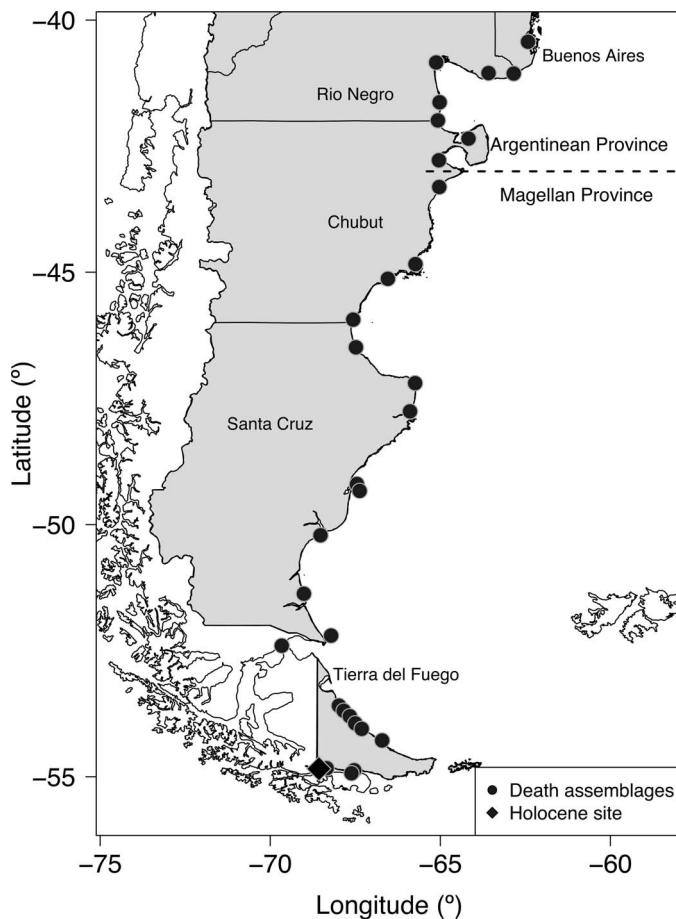


FIG. 1.—Map of the study area, showing the collecting sites of *Trophon geversianus* shells in death assemblages and in a mid-Holocene site. The boundary between the Argentinean and Magellan marine biogeographic provinces is also shown.

Argentinean is characterized by considerable heterogeneity of its components, and the Magellan by homogeneity of components and endemic taxa (Balech and Ehrlich 2008).

The boundary between these provinces has not been clearly established, as it varies seasonally between 41°S and 43°S due to northward fluctuations of the cold Malvinas Current in winter (Balech and Ehrlich 2008). The boundary is defined by the detailed analysis of the fauna composition of both provinces using benthic organisms (echinoderms, crustaceans, and mollusks) and nektonic organisms (fishes) (Balech and Ehrlich 2008). Like most places in the world, determination of biogeographical regions and provinces has been largely based on species range boundaries for individual taxa together with characterization of oceanographic/environmental conditions (Wieters et al. 2012). In the case of Argentina, these limits appear to follow discontinuities in oceanographic characteristics, namely the convergence of the Brazil-Malvinas currents, which produce extreme temperature gradients (Boschi 2000; Liuzzi et al. 2011). However, other authors have associated the biogeographic provinces with changes in productivity and habitat features (Gorny 1999).

This boundary has long been controversial because of the ambiguity and fuzziness associated with its spatio-temporal variability, so in order to adopt a conservative approach, we established the southern limit of the Argentinean province to be 43°S (e.g., Martinelli et al. 2013; Archuby et al. 2015). The dominance of different water masses in these two provinces

cause water temperatures to be lower in the Magellan Province (3.5°C to 11°C; Boltovskoy 1979) than in the Argentine Province (18°C to 24°C; Boltovskoy 1979). The water temperature difference is one of the main determinants of the molluscan fauna composition of these two regions (Gordillo 1998b; Pastorino 2000). In addition, chlorophyll *a* has a much more variable pattern along the study area, with lower values observed around mid-latitudes (2 mg*m⁻³) and increasing towards the north (up to 5 mg*m⁻³) and south (2–5 mg*m⁻³) (Malvé et al. 2018). The Argentine Patagonian coast also provides an opportunity to collect and examine mollusk shell assemblages due to their relative abundance and high preservation potential (Gordillo et al. 2014). Empty shells, mostly bivalves and gastropods, are found along the coast in the active beach and in adjacent deposits in marine terraces (Feruglio 1950; Gordillo 1998b; Martinelli et al. 2013).

Trophon geversianus (Pallas 1774, Gastropoda: Muricidae) is a conspicuous predatory snail inhabiting intertidal and subtidal habitats (up to 56 m) along the Southwestern Atlantic and Southeastern Pacific (Pastorino 2005). On the southwest Atlantic coast, this species is reported from 35°S to 56°S (including the Malvinas/Falkland Islands), while on the southeast Pacific coast, it ranges from 42°S to 56°S (Griffin and Pastorino 2005; Pastorino 2005). *Trophon geversianus* is dioecious, with internal fertilization and intra-capsular embryonic development (Zaixso 1973; Penchaszadeh 1976). Planktonic larvae are unknown in this genus (Pastorino 2005), there is no evidence of external sexual dimorphism, and the sex ratio is different from 1:1 (with a bias towards females) (Cumplido et al. 2010). *Trophon geversianus* is a shell-boring gastropod that inhabits rocky and sandy bottoms and preys on epifaunal and semi-infaunal mollusk species (Gordillo 1998a). Shell size (up to 100 mm) is extremely variable, as can be appreciated from the abundance of names proposed for the different morphological variants of this species (Pastorino 2005).

Although *T. geversianus* is the most studied species of the genus (Pastorino 2005), available information about its biology and ecology is fragmentary and mostly unpublished (Andrade et al. 2009), and studies of large-scale patterns of ecological and life-history traits are virtually absent. However, this species exhibits marked morphological variability, ranging from smooth to profusely ornamented specimens depending on the area of collection (Pastorino 2005). Márquez et al. (2015) detected the existence of intertidal and subtidal morphotypes of *T. geversianus* at Golfo Nuevo, Northern Patagonia. They found more globose individuals in the intertidal, and fusiform shells in the subtidal. A recent study by Malvé et al. (2018) showed that *T. geversianus* exhibits strong geographic variability in shell size, which slightly increases towards higher latitudes and is coupled with seawater pH. Different studies have shown that shell form (e.g., shape, thickness, ornamentation) in gastropods vary across large-scale latitudinal gradients, in response to abiotic (e.g., sea temperature, wave action, calcification potential) and biotic (i.e., predation pressure) factors (Grauss 1974; Vermeij 1978; Trussell and Etter 2001; Watson et al. 2012). Nevertheless, the existence of latitudinal changes in the shell morphology of *T. geversianus*, and the possible underlying factors, remains unstudied.

This study aims to evaluate variations in the shell shape of *T. geversianus* along an extensive latitudinal gradient in the southwestern Atlantic coast using modern death assemblages. Morphometric analyses were carried out taking into account a set of shell characteristics from two distinct biogeographic regions. Furthermore, a comparison between modern versus fossil shells was performed at the southern tip of South America. Given the strong clines in oceanographic conditions along with latitudinal changes in predation pressure and shell production cost observed in the study area, we hypothesize the existence of marked geographic changes in the shell shape of *T. geversianus* within this study area.

TABLE 1.—Details of the 31 study sites. Key: A=Argentinean province (n = 518); M=Magellan province (n = 339); *—the Transition Zone (41°S–43°S) between the Argentinean and Magellan biogeographic provinces; †=the fossil site.

Sites	Latitude (°)	Longitude (°)	Specimen size (mean SL ± S.D.)	Range size (minimum SL– maximum SL)	Sample size	Biogeographic province
Los Pocitos	-40.43	-62.42	35.02 ± 4.96	(31.51 - 38.53)	2	A
Piedras Coloradas	-40.84	-65.12	20.30 ± 4.03	(15.64 - 22.66)	3	A
El Cóndor	-41.06	-62.84	35.22 ± 12.02	(20.87 - 50.60)	6	A*
Caleta de los Loros	-41.05	-63.58	44.92 ± 8.77	(18.05 - 64.68)	89	A*
Playas Doradas	-41.63	-65.02	38.34 ± 13.21	(11.86 - 62.99)	21	A*
Puerto Lobos	-41.99	-65.07	22.69 ± 4.98	(10.59 - 41.00)	304	A*
Puerto Pirámides	-42.35	-64.17	19.56 ± 4.36	(11.72 - 31.59)	37	A*
Puerto Madryn	-42.78	-65.04	17.91 ± 5.93	(8.07 - 39.37)	56	A*
Playa Unión	-43.31	-65.03	22.67 ± 5.99	(15.23 - 29.52)	5	M
Playa Elola	-44.84	-65.73	32.95 ± 10.76	(19.38 - 54.94)	22	M
Bahía Bustamante	-45.13	-66.54	32.72 ± 5.82	(24.61 - 45.47)	15	M
Rada Tilly	-45.94	-67.56	31.75 ± 8.56	(17.20 - 60.80)	22	M
Caleta Olivia	-46.49	-67.48	36.80 ± 6.70	(22.72 - 52.00)	31	M
Cabo Blanco	-47.20	-65.74	28.38 ± 4.31	(23.00 - 33.50)	4	M
Puerto Deseado	-47.76	-65.89	40.81 ± 1.63	(39.65 - 41.96)	2	M
San Julián	-49.20	-67.45	39.54 ± 0.00	(39.54 - 39.54)	1	M
Makenke	-49.33	-67.37	21.91 ± 6.08	(10.97 - 35.84)	59	M
Monte León	-50.21	-68.52	33.92 ± 6.15	(22.12 - 40.26)	8	M
Punta Loyola	-51.37	-69.01	22.23 ± 3.28	(18.18 - 28.61)	23	M
Faro Vírgenes	-52.20	-68.21	36.05 ± 14.34	(29.37 - 53.08)	12	M
Estrecho de Magallanes	-52.40	-69.66	48.25 ± 21.10	(16.66 - 78.68)	20	M
Río Chico	-53.59	-67.98	28.46 ± 7.97	(16.66 - 44.02)	11	M
Cabo Domingo	-53.69	-67.84	22.02 ± 6.65	(15.66 - 30.64)	4	M
Río Grande	-53.80	-67.66	24.62 ± 5.79	(15.55 - 35.47)	13	M
Punta María	-53.94	-67.50	28.92 ± 4.53	(23.71 - 31.94)	3	M
Auricosta	-54.05	-67.31	32.66 ± 7.43	(15.63 - 46.47)	36	M
Cabo San Pablo	-54.28	-66.71	38.35 ± 5.64	(25.29 - 47.92)	15	M
Bahía Golondrina	-54.83	-68.33	49.31 ± 8.71	(34.60 - 73.70)	29	M
Bahía Brown	-54.87	-67.53	60.33 ± 7.65	(51.50 - 65.00)	3	M
Puerto Williams	-54.93	-67.61	61.10 ± 0.00	(61.10 - 61.10)	1	M
Río Ovando †	-54.50	-68.35	33.14 ± 13.62	(13.70 - 72.81)	30	M

MATERIALS AND METHODS

Collection of Specimens

Shells were collected from 31 sites along the study area (Table 1), which encompasses 14 degrees of latitude (~ 1600 km) and covers most of the geographic range reported for *T. geversianus* along the southwestern Atlantic coast. Representative quadrat samples were used for modern shells. The molluscan death assemblage at each beach was sampled from the high-water mark every 10 m using 0.5 × 0.5 m quadrats. Paleontological material from the Holocene marine terrace in the Beagle Channel was obtained using volumetric samples which consisted of 10 dm³ bulk sediment; samples were sieved in the field using 1 mm and 0.05 mm sieves to reduce the volume. Next, specimens were separated and counted. Holocene shells were recovered from sandy sediments and are interpreted as belonging to shallow, subtidal and cold-temperate environments (Gordillo 1999) (for further details see methodology in Cárdenas and Gordillo 2009). Death assemblages typically include specimens spanning from a few years to hundreds of years (i.e., they are time-averaged, Kidwell 2002, 2013; Archuby et al. 2015), which allows us to include multiple cohorts. In addition, death assemblages are also spatially averaged, and include shells from different types of habitat. Altogether, the use of time-averaged death assemblages can increase the robustness of the analyses despite the short-term volatility of living assemblages.

Taphonomic processes such as fragmentation, dissolution, abrasion, and bioerosion can affect a shell's traits (Aguirre and Farinati 1999; Zuschin et al. 2003). However, most of the shells collected retain their normal

ornamentation, thus suggesting that abrasion and bioerosion were negligible. Other taphonomic attributes were taken into account and minimized whenever possible, such as fragmentation, since only whole (undamaged) shells were used in the analyses. All studied specimens are stored in the mollusk collection of the repository at the Research Center on Earth Sciences, Ciudad Universitaria, Córdoba (CICTERRA, CONICET-UNC).

Morphometric Measurements

Taking into account various reference works (Chiu et al. 2002; Pizá and Cazzaniga 2003; Madec and Bellido 2007), seven morphometric characteristics were selected (Fig. 2). Shell length was measured along an axis passing through the apex to the bottom of the siphonal canal. Shell width is the maximum width perpendicular to the shell length measurement. Aperture length is the length from the beginning of the first suture to the bottom of the aperture. Aperture width is the maximum width of the aperture. Spire height was measured from the beginning of the first suture to the apex of the shell. Shell thickness was measured in the middle of the aperture. All characteristics were measured to the nearest millimeter with a digital caliper. We also registered shell mass using a digital scale (0.01 g of precision). Some of these traits have a functional significance. For instance, aperture form correlates positively with foot shape in most gastropods, and foot shape in turn, correlates moderately well with substrate preference (McNair et al. 1981). On the other hand, shell thickness of intertidal gastropods varies among intertidal shores, in part because of differential predation by crabs (Trussell 1996).

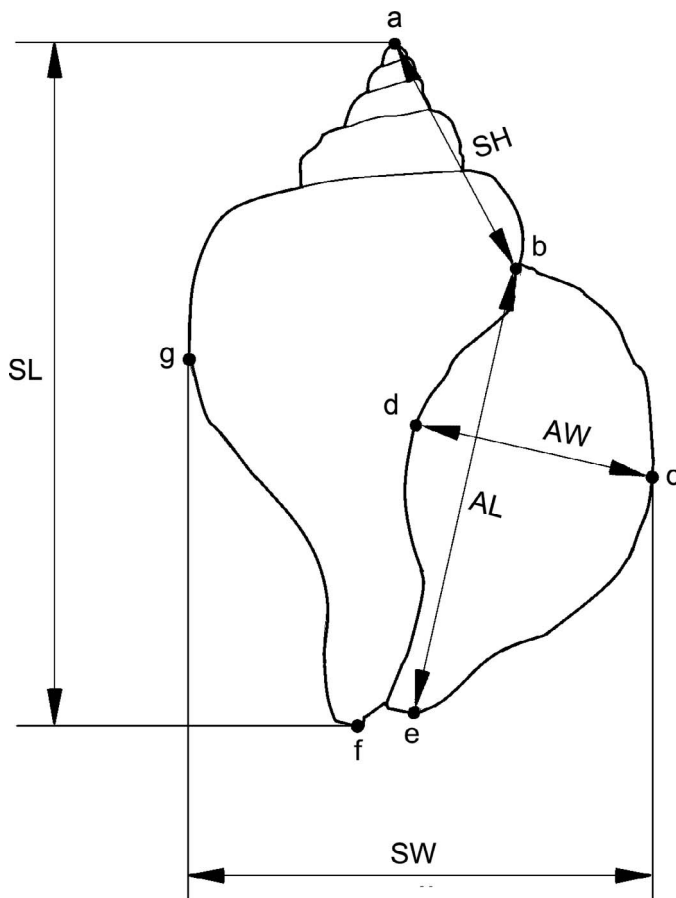


FIG. 2.—Shell measurements of *Trophon geversianus*: shell length (SL), shell width (SW), aperture length (AL), aperture width (AW), and spire height (SH).

Data Analyses

For the morphometric analyses, 857 empty shells were used (518 from the Argentinean province and 339 from the Magellan province). In addition, we compared 30 modern shells and 30 fossil shells from the Beagle Channel at the southern tip of South America. Because most of the quantitative traits vary according to body size, comparisons between individuals and populations can be complicated; thus, body size variations must be eliminated from the morphometric analyses (Lleonart et al. 2000; Bartels et al. 2011). One of the most recommended ways of carrying out allometry corrections is by applying Thorpe's size normalization (Thorpe 1975). This technique eliminates the effects of body size from any trait, independently of its relation to body size, according to the following expression (Lleonart et al. 2000):

$$Y^* = Y_i(X_o/X_i)^b$$

Where Y^* is the normalized trait, Y_i is the original trait, X_i is the individual body size, X_o is the mean body size, and b is the slope of the ordinary least squares regression between Y_i and X_i (after log-transformation).

To characterize the spatio-temporal variation of shells, Principal Component Analyses (PCA) was performed based on correlation matrices. The first two axes of the PCA were used to visualize groups. To corroborate differences between groups, we conducted a multivariate comparison analysis using Hotelling's T^2 test (Hammer and Harper 2006). Differences were also evaluated for individual PCA axes using a t-test. To assess the possible role of environment shaping spatial changes in shell morphom-

TABLE 2.—Loadings of the morphometric characters associated with the first two components of both Principal Component Analyses. The measurements of the two highest values associated to PC1 and PC2 are highlighted in bold.

	Geographic variation		Temporal variation	
	Axis 1	Axis 2	Axis 1	Axis 2
SW (shell width)	0.5104	0.0715	0.5944	0.1337
SH (spire height)	-0.0957	0.7110	-0.0785	-0.0164
AL (aperture length)	0.3899	-0.5106	0.3984	-0.4665
AW (aperture width)	0.4933	-0.0810	0.5194	-0.3301
ST (shell thickness)	0.4043	0.2844	0.1614	0.7190
SM (shell mass)	0.4141	0.3758	0.4314	0.3719

etry, we tested for correlation between each of the first two principal components and mean annual sea surface temperature estimated for each site using the BioOracle database (Tyberghein et al. 2012; climatologies from grid cells with ~ 9.2 km resolution, available at <http://www.oracle.ugent.be/>). The residuals of ordinary least-squares regressions between PC1 and PC2 versus sea surface temperature were analyzed to evaluate the existence of spatial autocorrelation using Moran's standardized index (Dormann et al. 2007). All analyses were carried out in R v.3.5.0 (R Team Core 2018).

RESULTS

Biogeographic Variation

The PCA revealed that 63.5% of total shape variation is expressed by the first (37.4%) and second (26.1%) axes (Fig. 3). Magellan and Argentinean morphologies overlap in the PCA morphospace but show a weak differentiation along PC2 (Fig. 3). The separation between these two groups is confirmed by the result from the Hotelling's T^2 ($P < 0.001$). Analyses of single components showed that biogeographic differences are significant only along PC2 (t-test, $P < 0.0001$), but not along PC1 (t-test, $P = 0.12$). The variables mostly affecting variation along PC1 were shell width and aperture width, whereas PC2 was mostly attributable to spire height and aperture length (Table 2). Specimens from the Magellan province were characterized by having shells with shorter spires and higher aperture length than individuals from the Argentinean province (Fig. 4, 5C, 5D). PCA axes showed different latitudinal trends (Fig. 5A, 5B); PC2 varied negatively with latitude ($r = -0.68$, $P < 0.0001$), whereas PC1 showed no significant latitudinal trend ($r = -0.21$, $P = 0.27$). Aperture length and spire height also showed significant latitudinal trends increasing ($r = -0.62$, $P < 0.0001$, Fig. 5C) and decreasing ($r = 0.68$, $P < 0.0001$; Fig. 5D) towards higher latitudes, respectively. Sea surface temperature was not correlated to PC1 ($r = 0.01$, $P = 0.97$; Fig. 6A), but the correlation was positive and significant for PC2 ($r = 0.56$, $P < 0.002$; Fig. 6B). Spatial autocorrelation test were not significant in either case (Moran's I, $P > 0.05$; Fig. 6A, 6B).

Shape Variation between mid-Holocene and Modern Specimens

In a similar way to testing for biogeographic variation, a PCA was performed comparing morphologies from active beaches and Holocene marine terraces from the Beagle Channel. The first two axes of the PCA explained 62.5% of total morphological variation (Fig. 7). Hotelling's T^2 test showed highly significant shape differences between biogeographic provinces ($P < 0.001$), whereas these differences were mostly observed along PC2 (t-test, $P < 0.004$) rather than along PC1 (t-test, $P = 0.44$). The variables most related with PC1 were shell width and aperture width,

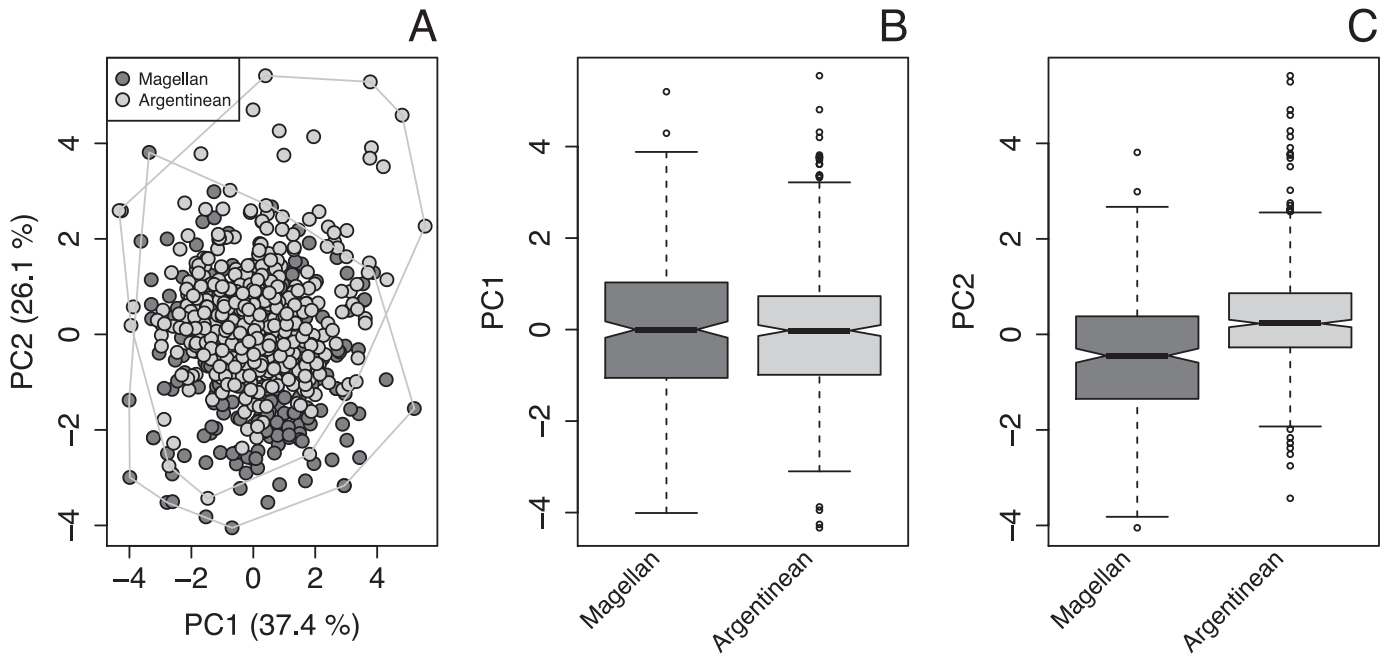


FIG. 3.—Principal Component Analysis of the shell measurements of *Trophon geversianus* according to biogeographic region. A) PC1 versus PC2. B) Boxplot of Magellan and Argentinean morphotypes along PC1. C) Boxplot of Magellan and Argentinean morphotypes along PC2.

whereas shell thickness and aperture length contributed more to PC2 (Table 2). Modern individuals exhibited thicker shells and slightly longer aperture lengths than mid-Holocene specimens (Fig. 7).

DISCUSSION

Our results show that *T. geversianus* exhibits a marked variability in shell shape at a biogeographical scale between distant regions (extending

over 1600 km) and encompassing two biogeographic provinces. This study reports a spatial coincidence of intraspecific morphological differentiation with the provincial boundary, where this species does not remain the same morphologically along the study area. The fact that the provincial boundary closely coincides with different morphotypes may indicate that the processes underlying provinciality and the patterns that allow morphological differences are shared. For example, an environmental

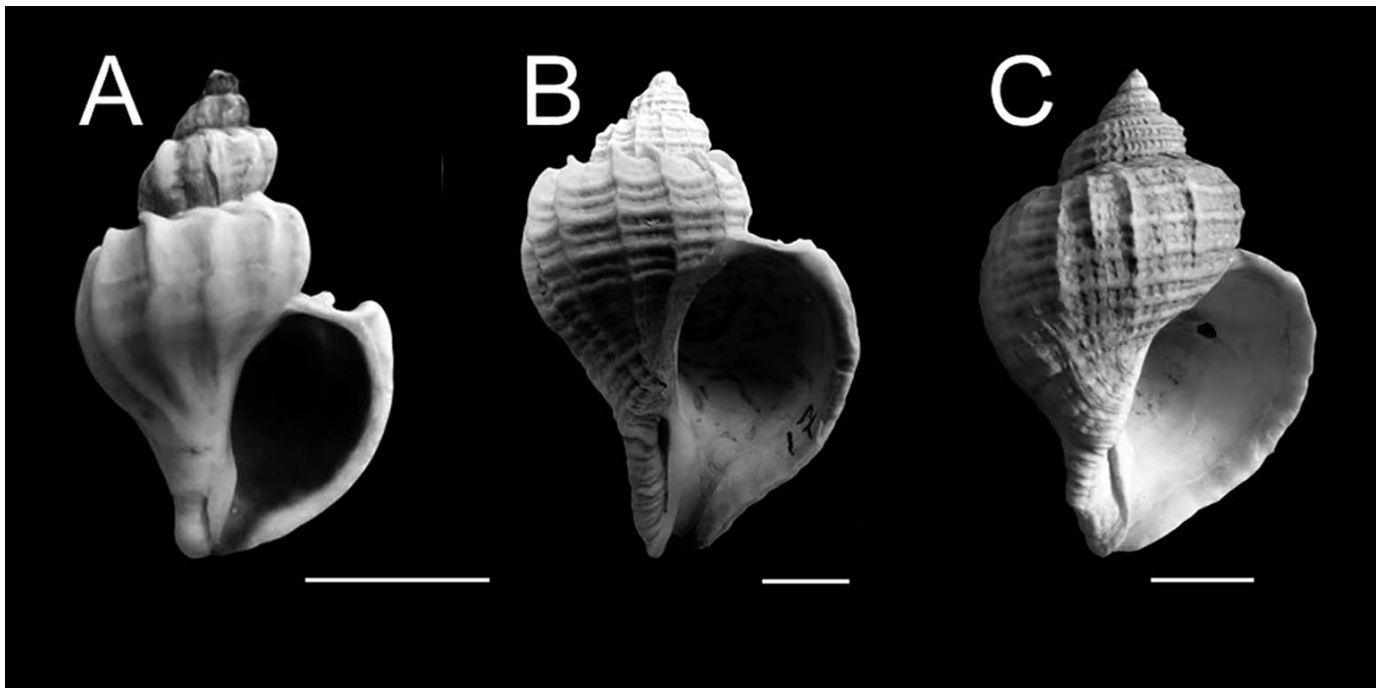


FIG. 4.—Illustrative representation of morphotypes. A) Morphotype of the Argentinean province. B) Morphotype of the Magellan province. C) Fossil specimen from the Beagle Channel. Scale bar in all cases is 1cm. Specimens illustrated are stored under numbers CEGH-UNC 27224, 27225, and 27226.

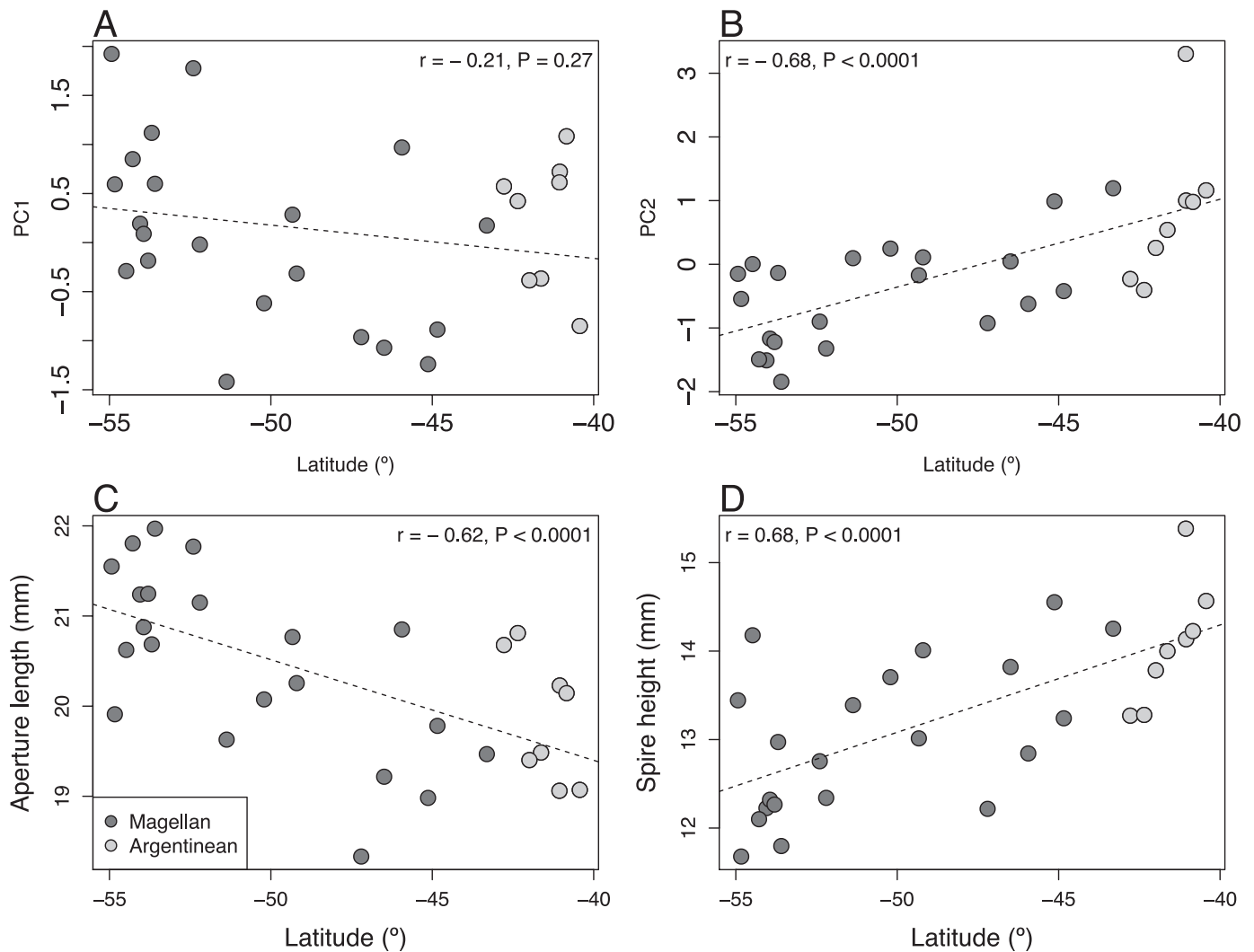


FIG. 5.—Latitudinal pattern of variation in shell shape of *Trophon geversianus*. A) PC1 as a function of latitude. B) PC2 as a function of latitude. C) Aperture length as a function of latitude. D) Spire height as a function of latitude.

boundary may provoke dispersal to be less likely and/or require significant ecophenotypic or genetic intraspecific changes for a single species to go through the transition zone.

The morphotype of the Magellan province is characterized by larger shells, with shorter spires and higher aperture length than the morphotype from the Argentinean province. Previous studies have shown marked spatial differences in shell morphology of marine gastropods in different parts of the world, for example the southwestern Atlantic coast (Teso et al. 2011; Avaca et al. 2013), the North Atlantic coast (Trussell and Smith 2000), the northeastern Pacific coast (Lee and Boulding 2010), the Indian and West Pacific Oceans (Irie 2006), and the east coast of South Africa (Teske et al. 2007). In South America, Sepúlveda and Ibáñez (2012) reported the existence of morphological clinal variation in the intertidal muricid snail *Acanthina monodon* along the southeastern Pacific coast. Similar to our study, they showed two morphotypes to the north and south of 41°S, coinciding with a major biogeographic boundary. These authors suggest that the morphotypes reported are the result of site-specific ecophenotypes responding to local variation.

The question whether morphological variation in *T. geversianus* is driven by phenotypic plasticity or genetic differentiation cannot be answered at present due to the lack of phylogeographic studies on the

species. In a previous study, Márquez et al. (2015) revealed local-scale morphological variability in *T. geversianus* between intertidal and subtidal habitats probably attributed to phenotypic plasticity, since phylogenetic analysis of COI gene fragments showed no consistent differences among individuals sampled in both habitats. These authors found two ecomorphs of *T. geversianus* as a response to physically stressful conditions on intertidal rocky shores (as opposed to lower physical stress but higher predation pressure in subtidal habitats). This finding corroborates those of Pastorino (2005) on the extremely variable nature of *T. geversianus* shells, not only from north to south but also from intertidal to subtidal environments.

However, several studies have shown a correspondence between phylogeographic and biogeographic breaks in marine gastropods, especially in species with restricted dispersal potential (Haye et al. 2014). A strong genetic differentiation cannot be ruled out because of the limited spatial dispersal induced by the lack of planktonic larvae in *T. geversianus*. Nevertheless, there are well-documented cases of enhanced spatial dispersal of marine invertebrates due to rafting on floating objects (Thiel and Haye 2006; Gordillo 2006; Gordillo and Nielsen 2013). If genetic flow is unrestricted across the species' geographic range, the observed morphological differences should emerge as a response to the strong

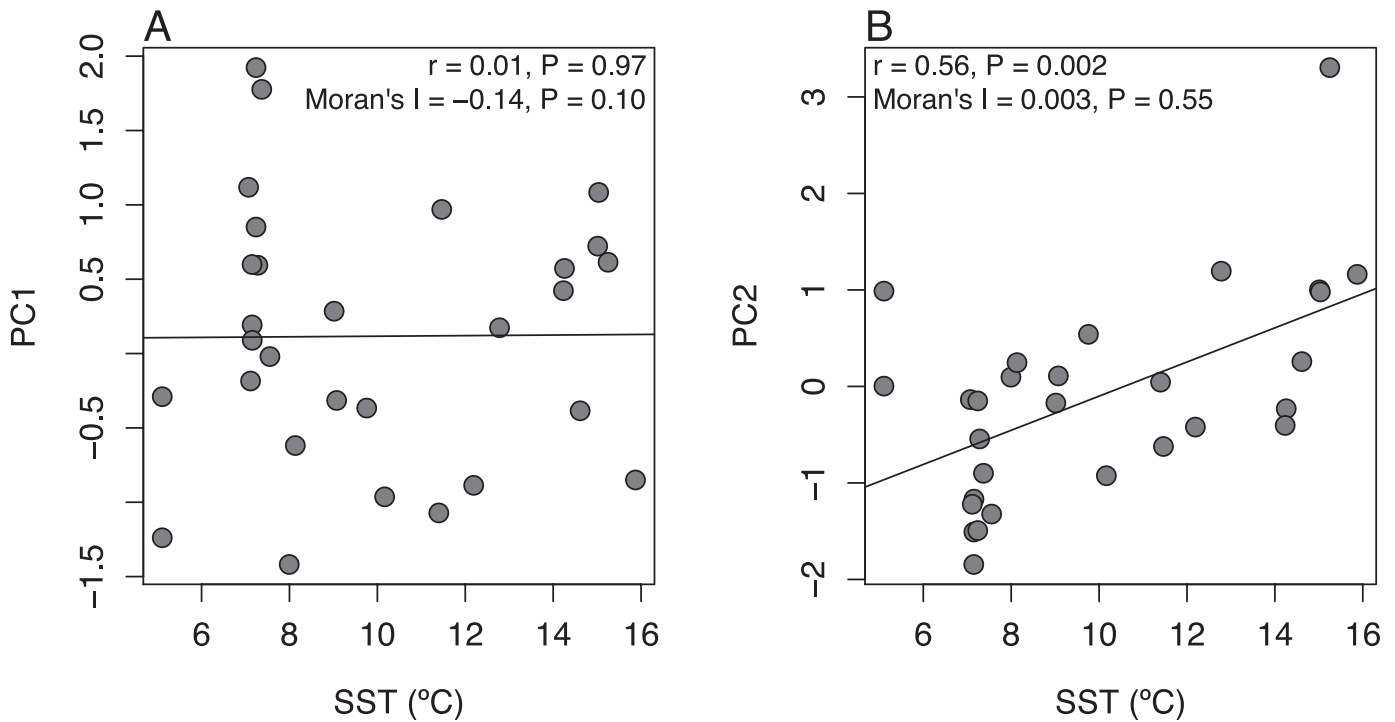


FIG. 6.—Correlation between sea surface temperature and shape variation in *Trophon geversianus*. **A**) PC1 as a function of temperature. **B**) PC2 as a function of temperature. Moran's I values indicate a lack of spatial autocorrelation in the residuals of both principal components.

environmental (i.e., oceanographic) variation across the study area. For instance, sea surface temperature varied twofold, decreasing by around 7°C along the latitudinal gradient, from the northern sites (15°C) to the southern ones (7°C) (Malvé et al. 2018). Indeed, the morphological variation described by PC2 is strongly associated with sea surface temperature, a relationship that holds even after accounting for spatial

autocorrelation. At least in some gastropods, latitudinal differences in water temperature are known to contribute to the biogeographic variation in shell shape (Trussell and Etter 2001). The relationship between shell shape and sea temperature could be associated to latitudinal changes in the growth rate induced by sea temperature. Poikilotherms in general tend to grow faster at higher temperatures (Brown et al. 2004). Since low growth

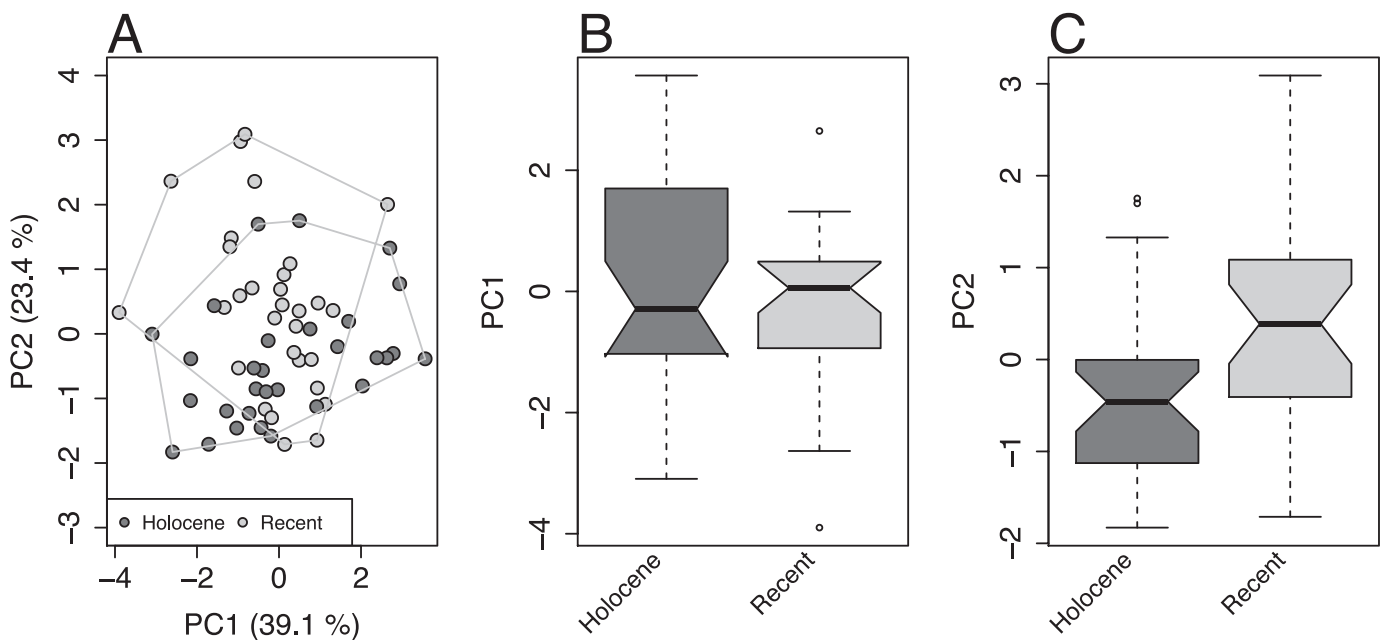


FIG. 7.—First two axes of a Principal Component Analysis of the shell measurements of *Trophon geversianus* regarding shape variation between Holocene and modern shells. **A**) PC1 versus PC2. **B**) Boxplot of Holocene and modern shells along PC1. **C**) Boxplot of Holocene and modern shells along PC2.

rates in gastropods are associated with shells exhibiting small spires and elongated apertures (Kemp and Bertness 1984; Urdy et al. 2010), then the decrease in growth rate at lower temperatures may control changes in shell shape, but ecophysiological and sclerochronological studies are needed to validate this hypothesis. However, other factors such as calcification potential, wave action, and predation pressure (see below) may also affect the variation in shell shape (Grauss 1974; Vermeij 1978; Trussell and Etter 2001; Watson et al. 2012) and need further investigation.

We also found differences in shell morphology between samples from mid-Holocene and modern deposits of the southern tip of South America (Fig. 1), although interpretations are preliminary due to the smaller sample size and spatial extent included. Paleoenvironmental reconstructions suggest different conditions for the mid-Holocene, characterized by warmer waters and higher inputs of freshwater (Gordillo et al. 2011b, 2015). Interestingly, the thickening of *T. geversianus* shells from the mid-Holocene to the present is associated with an increase in the body size of the clam *Tawera gayi*, a common prey of *T. geversianus* (Gordillo et al. 2011b). Attaining a larger size provides *T. geversianus* the opportunity to attack larger prey, thus maximizing the amount of food obtained in a single, long, and energetically expensive event of drilling (Gordillo and Archuby 2012). However, further studies centered on predator-prey relationships will be essential to understand whether the morphological changes in *T. geversianus* and *Tawera gayi* are coupled over the past few thousands of years and may be due to microevolutionary changes or econophenotypic processes. In any case the covariation between the size of predator and prey is highly informative and worth pursuing.

The SW Atlantic coast constitutes a dynamic mosaic of sub environments (Bayer et al. 2016) in which the interplay between physical and biological factors varies greatly according to its latitude. For example, the presence of imposex in Northern Patagonia is slightly affecting *T. geversianus* and is known to affect gastropod shell shape (Bigatti et al. 2009; Primost et al. 2015). On the other hand, the invasive potential of the voracious European green crab (*Carcinus maenas*) along Chubut province may also induce shell changes over short time scales as previously reported in the Gulf of Maine (USA) between 42.5–45°N in the Atlantic Ocean (Trussell 2000). In that study, marine snails exposed to predatory crab effluent in the field increased shell thickness rapidly compared with controls, indicating that predator-induced phenotypic plasticity may explain broad-scale geographic and temporal phenotypic variation (Trussell 2000). At the same time on exposed shores, the abundance of crabs decreases with strong wave action, while gastropod shells become thinner and have longer apertures that allow the presence of a bigger foot to better attach to the substrate. In wave-exposed environments, it is important to remain attached to the substratum, and disturbed snails have to emerge quickly from their shell in order to reattach (Johannesson 2016; Leighton et al. 2016). Notably, the greater aperture length of the Magellan morphotype matches the higher wave action of the Magellan province coasts in comparison with the Argentinean province (Malvé et al. 2018).

This study illustrates the usefulness of death assemblages, in which shells are time and space averaged, allowing the collection of individuals from broader spatiotemporal scales, unlike the composition of snapshot-like living assemblages (i.e., sampled at a single time). In this respect, *T. geversianus* is one of the most abundant gastropods along the southwestern Atlantic coast and offers a clear example of shell variability through space and time. Moreover, our results highlight the value of classic (i.e., non-geometric) morphometric analyses, which allow faster data acquisition of large sample sizes (> 850 shells). Future studies should be aimed at understanding the joint spatial and temporal variability in shell morphology and deciphering the relative role of ecological and evolutionary drivers influencing shell traits.

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