SHELL VARIABILITY IN *TROPHON GEVERSIANUS* (GASTROPODA: MURICIDAE) AT CALETA DE LOS LOROS (NORTHERN PATAGONIA, ARGENTINA) DURING THE LATE HOLOCENE: A STRONG LOCAL IMPRINT

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Abstract. Environmental change, such as variation in upwelling and the consequent fluctuation in marine primary productivity, may have profound effects on organisms. *Trophon geversianus* shells from Caleta de Los Loros (San Matías Gulf, Northern Patagonia, Argentina) were analyzed in order to compare morphological variability at different spatio-temporal scales. To do so, we performed morphometric analyses at three sites, two fossil deposits of different age from the late Holocene and one modern assemblage. In general, modern shells were thicker than fossil ones. A slight trend of size reduction is also observed over the time considered, since modern shells were, on average, smaller than fossil ones. Size variations of *T. geversianus* shells are explained on the basis of phenotypic plasticity as a response to the environmental changes recorded in the San Matías Gulf during the Holocene. These changes include variations in paleo-productivity, such as sea surface temperatures, salinities and water circulation changes, which would have modified nutrient availability. Furthermore, Caleta de Los Loros was validated as an outlier site along a latitudinal gradient. Shells from this peculiar place bear a closer resemblance to shells found in sites further south in the Magellan Province. Environmental conditions and oceanographic features related to the presence of upwelling events that were probably responsible for this pattern are discussed.

Key words. Death assemblages. Upwelling events. Latitudinal gradient. Outlier site. Morphometric analyses. Gastropod.

Resumen. VARIABILIDAD DE LA CONCHILLA EN *TROPHON GEVERSIANUS* (GASTROPODA: MURICIDAE) EN CALETA DE LOS LOROS (PATAGONIA NORTE, ARGENTINA) A LO LARGO DEL HOLOCENO TARDÍO: UNA FUERTE IMPRONTA LOCAL. Los cambios ambientales como la variación en los eventos de surgencia y la consiguiente fluctuación en la productividad primaria marina pueden tener profundos efectos en los organismos. En el presente trabajo, se analizaron conchillas de *Trophon geversianus* provenientes de Caleta de Los Loros (Golfo San Matías), con el fin de comparar la variabilidad morfológica a distintas escalas espacio-temporales. Para ello se realizaron análisis morfométricos en tres sitios, dos depósitos fósiles del Holoceno tardío y un ensamble moderno. En general, las conchillas modernas fueron más gruesas que las fósiles, observándose una ligera tendencia a la reducción de tamaño a través del tiempo considerado ya que las conchillas modernas fueron, en promedio, más pequeñas que las fósiles. La variación del tamaño de las conchillas de *T. geversianus* se explica sobre la base de la plasticidad fenotípica de la especie como respuesta a los cambios ambientales registrados en el Golfo San Matías durante el Holoceno. Estos cambios incluyen variaciones en la paleoproductividad, como la temperatura de la superficie del mar, salinidad y cambios en la circulación del agua, que habrían modificado la disponibilidad de nutrientes. Además, se validó Caleta de Los Loros como un sitio atípico a lo largo de un gradiente latitudinal. Las conchillas de Caleta de Los Loros se parecen más a aquellas encontradas en sitios más al sur en la Provincia Magallánica. Finalmente, se discuten las características ambientales y oceanográficas relacionadas con la presencia de eventos de surgencia que probablemente son los principales responsables del patrón observado.

Palabras clave. Ensambles de valvas. Eventos de surgencia. Gradiente latitudinal. Sitio atípico. Análisis morfométricos. Gasterópodo.
Marine gastropods are among the groups most frequently studied for interpreting drivers of morphological variation (e.g., Ramajo et al., 2013; Cazenave & Zanatta, 2016). For instance, shell shape variability has been evaluated in association with environmental gradients (Caley et al., 1995; Trussell, 2000; Trussell & Smith, 2000; Ramajo et al., 2013), thermal stress and wave forces (Trussell et al., 1993; Denny, 2006; Harley et al., 2009), tenacity, and shell thickness (Vermeij & Covich, 1978; Trussell et al., 1993), and even with paleoenvironmental changes (Gentry et al., 2008). Environmental change, such as variations in upwelling intensity and the consequent variation in marine primary productivity, may have profound effects on the morphology of calcareous organisms (Teusch et al., 2002); nevertheless, studies addressing this line of research are limited.

In a recent study, Malvé et al. (2018b) evaluated biogeographic shell shape variation in the marine snail *Trophon geversianus*, and recognized two morphotypes matching the biogeographic scheme of the Argentine Sea. In a previous study on the same species, Malvé et al. (2018a) also found that neither shell length nor relative shell weight showed any monotonic latitudinal trend, and the patterns of spatial variability were rather complex. These authors recognized a weak, non-significant, tendency of body size increase towards the south, with extremely large individuals at the northern end of the species’ geographic distribution at Caleta de Los Loros (Northern Patagonia), Márquez et al. (2015), the product of an intricate coastal to-
pography, which enables the establishment of local communities. High environmental heterogeneity, coupled with the presence of ecosystem engineer species such as matrices of scorched mussels (*Brachidontes rodriguezii* and *Perumytilus purpuratus*) (Prado & Castilla, 2006; Borthagaray & Carranza, 2007; Sueiro *et al.*, 2010) where *T. geversianus* partly inhabits, may be responsible for the great variability of intertidal communities over small spatial scales (sometimes in the order of meters) within the same area (Kelaher *et al.*, 2007).

This study focuses on fossil and modern shells collected at Caleta de Los Loros (San Matías Gulf) in order to further understand morphological variations of *Trophon geversianus* on a local scale, taking into account the peculiarity of this site in relation to a latitudinal gradient of 14 degrees along the southwestern Atlantic coast. This locality in Northern Patagonia is proposed and confirmed here for the first time as an outlier site. The specific goals were: i) to compare size variation between late Holocene and modern shells from Caleta de los Loros; ii) to compare size variation between Holocene and modern shells in the northern and southern Atlantic geographic distribution of the species; and iii) to validate Caleta de Los Loros as an outlier site along the Atlantic coast of Patagonia.

**GEOLOGICAL SETTING**

Caleta de Los Loros (located between 41° 01’ 25” S and 64° 06’ 20” W) is a Patagonian natural protected area with a wide variety of geographical features and environments such as dunes, rocky and sandy shores, cliffs, salt marshes, and beach ridges. Within these units there are three fossil spits of Holocene age indicating a growth pattern from east to west (Del Río & Colado, 1999; Sander *et al.*, 2018). Using optically stimulated luminescence (OSL) chronology, Sander *et al.* (2018) established surprisingly young ages in the Holocene evolution of Caleta de Los Loros. According to these studies, sedimentary successions in the distal part of the system formed prior to c. 2300 years BP, while the larger and more exposed western part of the system and the lagoon formed over the last c. 1000 years BP. Therefore, the oldest preserved lagoonal deposits formed in the protected inner part of the system, as is the case of H2 (see Fig. 1) and a younger deposit between c. 1000 and 500 years formed in the more exposed western part of the system as is the case of H1 (see Figure 1) (Sander *et al.*, 2018).

Caleta de Los Loros is a cove located in the San Matías Gulf, Argentina’s second largest gulf, in Río Negro province (Fig. 1), with an area of approximately 18,000 km². Being a semi-enclosed basin, the distribution of the physical properties and its evolution are basically governed by the interchange with the atmosphere and with the open ocean through the mouth of the gulf (Gagliardini & Rivas, 2004). Although the exchange with the open sea affects the physical conditions found inside the gulf, its particular geometry (shallow, with a pronounced sill that limits its mouth) means that the atmospheric forcing is of greatest importance (Rivas, 1990).

![Figure 1. Study area and sampling sites.](Image)
Additionally, cyclonic gyres have been documented near Caleta de Los Loros (Piola & Scasso, 1988), and these have important consequences for marine ecosystems. Cyclonic gyres result in the rise of deep waters (upwelling), involving the wind-driven motion of dense, cooler, and usually nutrient-rich water towards the surface, replacing the warmer, usually nutrient-depleted surface water. This increased availability of high concentrations of chlorophyll-a in upwelling regions results in high levels of primary productivity, thereby favoring fishery production in the zone where the cyclonic gyre occurred.

MATERIALS AND METHODS

Sampling and data sets. For the morphometric analyses of Caleta de Los Loros (see below), 198 empty *Trophon geversianus* shells were selectively collected from three sites, one modern (N=70) and two fossil (H1, N=73 and H2, N=55) assemblages in December 2016.

Paleontological material from Holocene marine terraces in the Beagle Channel (southern geographic distribution of the species) 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. These terraces correspond to Río Ovando site (54.50° S, 68.35° W) and are determined by ¹⁴C at 3839 yr BP (Gordillo *et al.*, 2015). The associated fauna of this assemblage includes macromollusks such as clams *Tawera gayi*, *Ameghinomya antiqua*, and the bivalve *Hiatella solida*. Among gastropods, the most common taxa are the muricid *Xymenopsis muriciformis* and one buccinid *Pareuthria plumbea*. These fossil shells from the Beagle Channel (southern tip of South America, 54.83° S) were compared with fossil shells from Caleta de Los Loros (northern Patagonia, 41.05° S).

To validate Caleta de Los Loros as an outlier site, we used a data set (Tab. 1) compiled by Malvé *et al.* (2018b), of 849 modern shells from 14 other sites throughout Argentinean Patagonia, which encompasses 14 degrees of latitude 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

| Site              | Latitude (°S) | Longitude (°W) | Biogeographic province | Sample size | Mean shell length (mm) | SD (mm) |
|-------------------|---------------|----------------|------------------------|-------------|------------------------|---------|
| Caleta de Los Loros (CL) | -41.05       | -63.58        | A                      | 100         | 44.42                  | 8.71    |
| Playas Doradas (PD)    | -41.63       | -65.02        | A*                     | 25          | 21.68                  | 7.04    |
| Puerto Lobos (PL)       | -41.99       | -65.07        | A*                     | 325         | 22.51                  | 5.05    |
| Puerto Pirámides (PP)   | -42.35       | -64.17        | A*                     | 39          | 19.60                  | 4.25    |
| Puerto Madryn (PM)      | -42.78       | -65.04        | A*                     | 59          | 18.14                  | 6.11    |
| Playa Elola (PE)        | -44.84       | -65.73        | M                      | 26          | 31.59                  | 10.45   |
| Bahía Bustamante (BB)   | -45.13       | -66.54        | M                      | 22          | 33.18                  | 5.70    |
| Rada Tilly (RT)         | -45.94       | -67.56        | M                      | 28          | 31.59                  | 8.88    |
| Caleta Olivia (CO)      | -46.49       | -67.48        | M                      | 37          | 36.51                  | 6.58    |
| Makenke (M)             | -49.33       | -67.37        | M                      | 76          | 20.8                   | 6.05    |
| Punta Loyola (L)        | -51.37       | -69.01        | M                      | 23          | 22.23                  | 3.28    |
| Strait of Magellan (MAG)| -52.40       | -69.49        | M                      | 22          | 47.29                  | 20.35   |
| Cabo Auricosta (A)      | -54.05       | -67.31        | M                      | 38          | 32.17                  | 7.23    |
| Bahía Golondrina (BG)   | -54.50       | -68.21        | M                      | 29          | 49.31                  | 8.71    |
x 0.5 m quadrats. 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 shell traits (Aguirre & Farinati, 1999; Zuschin et al., 2003). However, most of the shells collected retain their characteristic ornamentation, thus suggesting that abrasion, dissolution, and bioerosion were negligible. Other taphonomic attributes were taken into account and minimized whenever possible, as was the case with 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 Centro de Investigaciones en Ciencias de la Tierra (CICTERRA, CONICET-UNC), Córdoba, Argentina. Also, specimens illustrated are stored under numbers Cátedra de Estratigrafía y Geología Histórica (CEGH-UNC) 27423, 27424, and 27425.

**Morphometric measurements.** Seven morphometric characteristics were selected taking into account different reference studies (Chiu et al., 2002; Pizà & Cazzaniga, 2003; Madec & Bellido, 2007). Following the methodology used in Malvé et al. (2018b), all measurements were taken (Fig. 2). Shell length (SL) was measured along an axis passing through the apex to the bottom of the siphonal canal. Shell width (SW) is the maximum width perpendicular to the shell length measurement. Aperture length (AL) is the length from the beginning of the suture to the bottom of the aperture. Aperture width (AW) is the maximum width of the aperture. Spire height (SH) was measured from the beginning of the suture to the apex of the shell. Shell thickness (ST) was measured in the middle of the aperture between inner and outer layers with a caliper. All characteristics were measured to the nearest millimeter with a digital caliper. The total weight of each shell (without soft tissues) was also measured, using a digital scale (TW) (0.01 g of precision). See Supplementary Online Information for details on the morphometric data set.

**Data analyses.** For the morphometric analyses of Caleta de Los Loros, we compared the size variation of shells in three deposits: one modern (n=70, active beach), and two fossil deposits at different shore levels, H1 (Holocene 1; 41°0’51.33” S, 64°8’36.85” W; n=73; 5 m a.s.l) and H2 (Holocene 2; 41°0’52.6” S, 64°0.4’50.9” W; n=55, 31 m a.s.l). The different shore level between H1 and H2 may be interpreted as a proxy of age, thus the fossil assemblages are probably of different ages (see Sander et al., 2018), with H1 being a younger deposit than H2.

Given that T. geversianus exhibits allometric growth (Ostachuk, 2016), we applied 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):

\[ Y^* = Y_i \left( \frac{X_o}{X_i} \right)^b \]

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 $X_j$ (after log-transformation). To visualize differences in each measurement between sites, a one-way ANOVA followed by the Tukey test was carried out for each measurement.

To validate Caleta de Los Loros as an outlier site, we used box-plots to analyze different shell traits such as length, thickness and relative weight ($RW$, cubic root of shell weight/shell length) along a latitudinal gradient. A cluster analysis using the Bray-Curtis coefficient was also performed to visualize groups among the 14 localities. Only modern shells and sites with $n>20$ were used.

**RESULTS**

Size variation between late Holocene and modern specimens. ANOVA and the *a posteriori* Tukey test showed significant differences in only two of the seven variables considered: shell thickness ($ST$) (between H1 and the mod-

![Figure 3. Differences between each measurement for each site (San Matías Gulf) showing mean and standard deviation after Thorpe’s normalization. 1, SL= Shell length; 2, AL= Aperture length; 3, AW= Aperture width; 4, SH= Spire height; 5, TW= Total weight; 6, ST= Shell thickness; 7, SW= Shell width. Only TW and ST showed significant differences between sites. See details in text.](image-url)
ern assemblage, $F=6.22; p<0.002$), and total weight ($TW$) (between the modern assemblage and H1, and between H1 and H2, $F=12.38, p<0.001$) (Fig. 3). In general, H1 shells were thinner and lighter than the rest (Fig. 3). A slight non-significant trend of size reduction was also observed over the time considered, since modern shells were, on average, smaller than fossil ones (Figs. 3, 4).

Size variation between Holocene and modern shells at the northern and southern distribution of the species was opposite (Tab. 2). At the Beagle Channel (Magellan Province), modern shells were larger than fossil ones (t-test, $p<0.0001$), while no differences in size were found at Caleta de Los Loros (Argentinean Province) (t-test, $p>0.05$). Nevertheless, modern shells at Caleta de Los Loros were,

![Figure 4. Illustrative representation of specimens from Caleta de Los Loros. 1, modern shell from an active beach; 2, Holocene shell from H1 (younger deposit); 3, Holocene shell from H2 (older deposit). Specimens illustrated are stored under the following numbers: Catedra de Estratigrafía y Geología Histórica (CEGH-UNC) 27423, 27424, and 27425. Scale bar equals 1 cm.](image)

| Caleta de Los Loros (Argentinean province) | Beagle Channel (Magellan province) |
|-------------------------------------------|-----------------------------------|
| SL (mm) | Modern | H1 | H2 | Modern | Fossil |
| range | 45.46±9.11 | 47.41±7.49 | 48.64±6.57 | 49.31±8.71 | 33.14±13.62 |
| ST * (mm) | 1.55±0.50 | 1.27±0.43 | 1.40±0.54 | 1.66±0.42 | 1.25±0.47 |
| TW * (g) | 10.65±3.32 | 9.21±2.70 | 11.87±3.00 | 6.05±1.13 | 6.29±1.74 |
| N | 70 | 73 | 55 | 29 | 30 |
on average, smaller than fossil ones (see tendency of shell length in Figs. 3, 4 and Tab. 2). Range size in modern shells at Caleta de Los Loros was considerably wider compared to H1 and H2 (Tab. 2), while the reverse was observed between range sizes in modern and fossil assemblages at the Beagle Channel. On the other hand, modern shells were thicker than fossil ones irrespective of geographic location (t-test, p<0.001 for all cases) (Tab. 2).

**Caleta de Los Loros as an outlier site.** Shell length, shell thickness, and relative weight validate Caleta de Los Loros as an outlier site in comparison with sites nearby from the Argentinean biogeographic Province (Fig. 5). Cluster analysis showed the presence of two major groups that separates fairly well sites according to the biogeographic provinces (Fig. 6). Caleta de Los Loros is part of a well-defined group with sites located more than 1000 km southwards, such as the Strait of Magellan and Bahía Golondrina (Beagle Channel) at the southern tip of South America (Fig. 6). However, two localities from the Magellan Province (Makenke and Punta Loyola) showed shells with smaller sizes that grouped together with sites from the Argentinean Province.

**DISCUSSION**

*Size variation between fossil and modern shells.* Our results show a slight, non-significant trend of a decrease in size in modern samples compared with fossils at Caleta de Los Loros, contrary to previous reports (size increase over recent geological time) for the same species from the Beagle Channel (southern tip of South America) (Malvé *et al.*, 2018b). New samples taken along the study area would be
necessary to better elucidate this situation. However, why does this species show a different tendency of body size throughout the late Holocene along its geographic distribution? We suggest that the answer could be found in changes in primary productivity during the Holocene at Caleta de Los Loros. Recently, Boretto et al. (2014), Bayer et al. (2016), and Morán et al. (2018) proposed that shell size differences between fossil and modern assemblages of bivalve mollusks in Northern Patagonia are due to an increase in paleo-productivity and upwelling processes. In this respect, Teusch et al. (2002) also associated upwelling intensity with morphological variation between Pleistocene and Recent turritellid gastropods from Chile. These authors found that shells from the Pleistocene were on average 14 mm longer than modern shells from the same area, indicating that larger shell size is associated with more intense upwelling, and the increase in the amount of shell material secreted may be explained by increased availability of food associated with stronger upwelling.

Interestingly, Morán et al. (2018) also detected at Caleta de Los Loros that Holocene shells of *Ameghinomya antiqua* - a common bivalve predated by *T. geversianus* in the San Jorge Gulf (Gordillo & Archuby, 2014)- were rounder and larger than modern ones. The opposite trend was observed between *T. geversianus* and *Tawera gayi* (another common bivalve currently predated by *T. geversianus*) at the Beagle Channel, where both species increase their body size towards the present (Malvé et al., 2018b). In any case, the covariation between predator and prey sizes is highly informative and worth pursuing, especially when opposite trends were observed involving the same predator but different prey, along the northern and southern end of its geographic distribution in Argentinean Patagonia. Altogether, the results of this study could be explained either in the context of a predator-prey relationship, and as a response to the environmental changes registered in the San Matías Gulf during the late Quaternary. These changes include variations in sea surface temperatures, salinity, substrate, and also water circulation changes, which would have modified nutrient availability (Bayer et al., 2016).

At this point, we have the comparison between shell size variation between modern and Holocene shells at two sites (Beagle Channel and Caleta de Los Loros) with a completely different geological history (Rabassa et al., 2000; Ponce et al., 2011). Both sites are wave-protected areas and behave as outliers, taking into account the latitudinal gradient considered (Malvé et al., 2018b).

In this respect, Caleta de Los Loros evolved from an open coast subjected to wave action to a more restricted system, leaving a deep, narrow open sector (Del Río & Colado, 1999). Late Holocene assemblages were more exposed to wave action and the influence of tides. Nowadays, on exposed shores, strong wave action limits the abundance of crabs, hence gastropod shells become thinner and have longer apertures that allow the presence of a bigger foot to better attach to the substrate (Trussell & Etter, 2001). 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 re-attach (Johannesson, 2016; Leighton et al., 2016). On the contrary, on wave protected shores, crabs are more abundant and predation intensity is higher. So the fact that Holocene shells were thinner is in agreement with a higher energy habitat and with current theory on patterns of selection on gastropod shell morphology, although the taphonomic wear effect cannot be ruled out. It is already well known that shell shape in gastropods tends to be different on wave-exposed and wave-sheltered shores (Johannesson, 2016). The heavy surf on wave-exposed shores is thought to select for small size, whereas the high risk of shell-breaking predation on wave-sheltered shores is thought to select for increased shell size and thickness (Boulding et al., 1999; Pascoal et al., 2012).

In the near future, it would be extremely useful to begin a complete exploration of the latitudinal profile along the southwestern Atlantic to better elucidate shell size and shape evolution during the Late Quaternary in Patagonia. **Caleta de Los Loros as an outlier site.** At first sight, *Trophon geversianus* shells from this peculiar place located in the Argentinean Province bear a closer resemblance to shells found in sites further south (e.g., Magellan Province), a fact that was confirmed by a cluster analysis. Two sites from the Magellan Province (Makenke and Punta Loyola) are located in urban estuaries and were grouped with localities from the Argentinean Province. The smaller sizes of both sites may be explained by the physicochemical properties of brackish water from these environments that could influence shell traits.

Interestingly, outlier sites come from the southern and
northern extremes of the geographical distribution for this species on the Argentinean Patagonian coast. These three outliers (Caleta de Los Loros in northern Patagonia, and the Beagle Channel and Strait of Magellan in southern Patagonia) are sites characterized by protected shores, with calm waters, which are not directly exposed to the open sea. In northern Patagonia, upwelling events are predominant and the thermohaline front nearby provides very high concentrations of phytoplankton. In southern Patagonia, waters come from the Antarctic circumpolar current, which also has high primary productivity. Caleta de Los Loros, being a wave protected area, and an exceptional site situated in the northern sector of the mouth inside the San Matías Gulf, exhibits unusually large, thick shells for its geographic location. This situation could therefore be explained by the oceanographic features of the San Matías Gulf.

From an oceanographic point of view, Piola & Scasso (1988) pointed out the presence of a zonal front (Front of the San Matías Gulf) during a large part of the year situated near 41°50´S. These authors determined that the temperature difference between both regions reaches 3°C, although it becomes negligible in the winter. A mass of colder, nutrient-rich water coming from the continental shelf can also be clearly noted. This water mass comes from the south and goes round the Valdés Peninsula until it reaches the mouth of San José Gulf, interacting with local waters and those of the southern sector of the San Matías Gulf (Gagliardini & Rivas, 2004). Furthermore, Pisoni et al. (2014) found that sea surface temperature (SST) data reveals a narrow coastal band (~10 km) of relatively cold water extending ~100 km along the west coast of the San Matías Gulf. The SST in this band was 1.5°C lower than further offshore, suggesting that coastal upwelling is a dominant process controlling high-frequency temperature fluctuations near-shore.

Taking into account this oceanographic background, and considering that the upwelling of cooler, nutrient-rich waters towards the surface can trigger peaks in phytoplankton blooms, thus raising primary productivity, it is expected that grazer and filter-feeder populations (the main prey of *Trophon geversianus*) would thrive in the upwelling areas. Consequently, bivalves (*Ameghinomya antiqua*, *Brachidontes rodriquezii* and *Mytilus edulis*) are larger at Caleta de Los Loros than in nearby sites (Morán et al., 2018, and the authors’ personal observations). Larger sizes of *T. geversianus* in this area may be explained by the availability of larger prey via maximizing energy efficiency. Hence, attaining a larger size provides *T. geversianus* the opportunity to attack larger prey, thus increasing the amount of food obtained in a single, long, and energetically expensive event of drilling (Gordillo & Archuby, 2012).

Finally, oceanic fronts can generate barriers preventing larvae or adults from crossing. These fronts represent major barriers to gene flow and have a strong influence on the population’s genetic structure of some marine species (Galarza et al., 2009). Although a phylogenetic analysis of COI gene fragments in *T. geversianus* from Nuevo Gulf showed no consistent differences among individuals sampled in both intertidal and subtidal habitats (Márquez et al., 2015), so far, no genetic studies have been carried out on a regional scale.

**CONCLUDING REMARKS**

*Trophon geversianus* is a direct developer species (lacking free larvae), whose extreme shell variability generates highly different local morphs. This is the case of Caleta de Los Loros in which shells are unusually large, thick, and heavy according to its geographic location. Caleta de Los Loros and the Beagle Channel are both wave-protected shores that experienced a completely different geological history during the late Holocene; however these sites share, at present, high chlorophyll-α and calcite concentrations, and have lower pH values than the rest of the Atlantic coast (Malvé et al., 2018a). As a result, these sites showed the larger sizes of *T. geversianus* along the whole study area.

Finally, *Trophon geversianus* exhibits opposite trends of shell size variation between modern and late Holocene sites across its northern and southern geographic distribution. These trends could be explained on the basis of predator-prey interactions along with strong environmental and oceanographic conditions related to upwelling events.

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