

Live-live and live-dead interactions in marine death assemblages: The case of the Patagonian clam *Venus antiqua*

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In this work we studied bioerosion and encrustation on dead shells of the shallow benthic clam *Venus antiqua* from Patagonia Argentina with the aim of understanding biotic interactions (live/live interaction) and postmortem encrustation (live/dead interaction). In this regard, drill hole analysis and epibiont distribution in shells from modern death assemblages were performed. Additionally, we analyzed crushing traces in the shells of the drilling gastropod *Trophon geversianus*, which were caused by another predator. The analysis of drill hole placement and epibiont distribution on *V. antiqua* shells show drill holes (75%) and the epibiont *Crepidula* spp. (70.91%) more concentrated in the upper sector of the valve, which might be explained by the vertical position and a semi-infaunal mode of life in this clam. Nevertheless, the presence of drill holes in the lower sector of the valve indicates that clams spent part of the time reclining on the sediment. There is also evidence that clams with *Crepidula* spp. as commensals are less frequently attacked by drilling gastropods. Besides, a high percentage of articulated clams (30.97%) show signs of attack by drilling gastropods, but incomplete drill holes (7.67%) also suggest failed attempts, resulting in a minimum of 23.30% of successful predation. These incomplete drill holes may suggest failed attempts due to another predator attack upon the snails consuming the clams thus interrupting the feeding activity: more than 60% of marks of crushing in *T. geversianus* shells could have been produced by other predators, such as crabs. The postmortem encrustation on *V. antiqua* shells (35%) was mainly produced by calcareous polychaetes, preferably located on the inner side of the valve indicating that the empty shells of *V. antiqua* served as cryptic environment before they become exposed on the beach. Finally our data show that drilling frequency is very low in Pleistocene assemblages, suggesting changes in burial depth dynamics of this suspension feeder.

Key words: Mollusca, Bivalvia, biotic interactions, drilling predation, crushing, epibionts, postmortem encrustation, Recent, Pleistocene, Patagonia.

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Introduction

Empty molluscan shells deposited along modern beaches are the remains of living organisms, but they are also records of post-mortem environments and taphonomic processes (Kidwell and Behrensmeier 1988). These death assemblages represent a first step towards the creation of a fossil assemblage. During this step, a large portion of the community (included some epibionts), is lost; these organisms make-up the non-preserved group. However, the skeletal

components of the remaining organisms are the preservable group subjected to different taphonomic processes such as fragmentation, dissolution, abrasion, bioerosion and such time-averaging processes as shell condensation (Cummins et al. 1986). These death assemblages do not necessarily correspond to animals living in a population or community simultaneously, but most probably reflect a temporal complex formed under various stochastic processes over a period of time (Fürsich 1978; Shimoyama and Fujisaka 1992). The living assemblage can vary from year to year due to vagaries of recruitment and mortality, so that the death assemblage

provides a better record of the organisms that usually inhabit an environment. Therefore, molluscan death assemblages capture a strong signal of relative abundance of living species (Kidwell 2002) and consequently serve to estimate the reliability of biological information in the fossil record. In this regard, studies focused on molluscan death assemblages, as detailed below, also provide signals for evaluating predation and other biotic interactions, and constitute an important tool for biological and paleontological studies.

Molluscan death assemblages provide direct evidence of biotic interactions offering quantifiable data on predator-prey relationships (Kowalewski 2002). Drill holes and crushing damage in shells are ubiquitous in the paleontological record and are most common and widely studied to evaluate predation.

As evidenced by previous works, predation in the marine realm can be quantified from traces by predators on skeletons of their prey (Kelley et al. 2003), and have even been used to test the coupling of predation and diversity throughout the Phanerozoic, from Ediacaran to Holocene (Huntley and Kowalewski 2007).

The fossil record yields abundant data on interaction between drilling predators and their shelled prey; thus, drilling predators and their prey are ideal for addressing questions about co-evolutionary processes or escalation (Kitchell et al. 1981; Vermeij 1987; Tull and Böhning-Gaese 1993; Kelley et al. 2003).

Drilling predation by gastropods involves mechanical rasping with the radula as well as secretions of the accessory boring organ (ABO) (Carriker 1981). Although it is known within several families of gastropods, most cases reported are produced by naticid and muricid gastropods. Drillholes produced by these gastropods, with some exceptions, are usually distinguishable (Kabat 1990; Kelley and Hansen 2003). Ausich and Gurrola (1979) found cylindrical holes in Mississippian brachiopods which resemble those made by drilling gastropods, but the earliest report of a drill hole attributed to muricid gastropods dates back to the Jurassic (Harper et al. 1998) though no safe muricid shells from the Jurassic are reported so far (Kaim 2004).

Shell breaking on marine bivalves and gastropods can also be the result of predation, and the dominant predators over geologic time include a varied array of clawed and jawed higher taxa (Alexander and Dietl 2003). For example, crushing damage by predators like crabs and fishes evolved during the Mesozoic, and experienced dramatic radiations in the Cenozoic (Walker and Brett 2002). Unfortunately most lethal fractures are often indistinguishable from non-predatory shell damage or abiotic shell destruction (Alexander and Dietl 2003), which makes most studies on shell breakage associated with predation are centered on sublethal gastropod and bivalve shell repairs. Recently, Stafford and Leighton (2011) refined a technique developed by Vermeij (1982), to estimate crushing predation in shelled prey, which can be performed on both modern and fossil shell assemblages, allowing the study of trends in crushing predation over both space and time. Using shells

bearing predatory drill holes, the “new old” method (Vermeij Crushing Analysis) proposed by Stafford and Leighton (2011) establishes a baseline for taphonomic damage in shell assemblage, and then estimates the frequency of predatory damage in comparison with that taphonomic baseline.

A further aspect to be considered in soft-bottom marine communities is that predator-prey interactions are complex due to the dominance of guilds of generalized predators capable of switching among diverse prey; in this regard, the analysis of trophic web can be simplified to a relative few strong interactions (Paine 1980; Eggleston et al. 1992).

Continuing with the biotic interactions in the marine realm, epibiosis is one of the few well-preserved biotic interactions in the fossil record dating back to the Early Paleozoic. It shows that the epibionts on shells (including bryozoans, tabulate corals, brachiopods, and extinct encrusting edrioasteroids) radiated by the Middle Ordovician (Lescinsky 2001) and that, during the Cenozoic, shell encrusters and other organisms able to settle on live and dead shells were very common. Curiously, published studies on Cenozoic fossil epibiosis are rare (see Taylor and Wilson 2003). Studying the spatial relationships among organisms that lived with each other provides insight into their community structure and environment. Epibiont composition is certainly informative for understanding patterns on live hosts, as they act as “discontinuous islands of substrate” within soft bottom environments. Besides, the study of epibiosis in death assemblages is useful to understand how a fossil assemblage differs from the living community from which it is derived, and to evaluate the correlation between living mollusks with Recent dead and fossil shells.

The Patagonia, Argentina provides an opportunity to collect and examine molluscan death assemblages. It is characterized by a huge coastline shaped by marine-terrace deposits accumulated throughout the Quaternary Period. Empty molluscan shells, mostly bivalves and gastropods, are found along the coast, both at the active beach and in adjacent marine-terrace deposits. In this regard, comparisons between modern and adjacent fossil shells are probably the most effective means for evaluating changes and reconstructing past environmental conditions during the Quaternary Period. But it is equally true that the knowledge of the Quaternary fossil record is essential for a better understanding of the origin of the modern biota from Patagonia. The abundance of mollusk shells over more than 2000 km of coastline facing the Atlantic Ocean has been noted by d’Orbigny (1834–1847) and Feruglio (1950), among other pioneer works.

One of the most common and widely distributed taxa in southern Patagonia are the clams *Venus antiqua* and its potential predator, the drilling gastropod *Trophon geversianus*. Both species have a wide distribution and are also well preserved in the fossil record, and that is why chose them for this study. *Venus antiqua* King, 1832 (= *Chione antiqua*, *Venus antiqua* or *Protothaca antiqua*; see remarks on systematics in Gordillo et al. 2008) is a typical element of the Magellan Province showing a wide area of distribution within the Atlantic and the Pacific oceans (Ríos 1994; Urban and Tesch 1996; Reid and

Osorio 2000). In Patagonia, Argentina, this clam is a common member of subtidal soft bottom communities (Verdinelly and Schuldt 1976; Escofet et al. 1978; Zaixso 1996) and preferably lives near the sediment-water interface, associated with medium-grained sand, and depths between 0 and 60 meters (Zaixso 1996). Fossil Pleistocene and Holocene *V. antiqua* is also very common along the Patagonian coast (Feruglio 1950; see a summary of fossil record of this species in Gordillo et al. 2008). The predatory gastropod *Trophon geversianus* (Pallas, 1774) also lives along the Atlantic coast between the provinces of Buenos Aires and Tierra del Fuego in continental Argentina, and up the Pacific coast of Chile to at least Chonos Archipelago (Griffin and Pastorino 2005). This is a very common muricid gastropod which inhabits both rocky and soft shallow bottoms. Muricids search for and drill prey epifaunally, although they may also dig up shallow infaunal prey (Kelley and Hansen 2003). In southern Patagonia, this muricid gastropod preys upon mytilids and venerid clams (Gordillo 1994, 1998; Andrade and Ríos 2007; Gordillo and Archuby 2012), depending on the predominant prey in the habitat in which it lives. *T. geversianus* is also mentioned as a very frequent species for Quaternary deposits in Patagonia (Feruglio 1950).

In this work we investigated biotic interactions (live/live interaction) including predation and epibionts, and postmortem encrustation (live/dead interaction) associated to *V. antiqua* shells preserved in molluscan death assemblages from Bustamante Bay, in Patagonia (Fig. 1). Our main aims are: (i) to test whether *V. antiqua* lives semi-infaunally, we evaluated the distribution of drill holes and marks of *Crepidula* spp. on shells; (ii) to test whether presence of *Crepidula* spp. on the clam shell represents an advantage against drilling predators (i.e., with *Crepidula* playing a protective role to the clams), the two interactions were analyzed together; (iii) to test whether failed attacks of *T. geversianus* on its prey are related to its own predators, we analyzed shell breaking patterns in shells of this snail; (iv) to test changes in drilling intensity through geologic time we compared drill frequency of modern and Pleistocene shells; and (v) to test whether the encrusters colonize shells after their death (postmortem encrusters) we analyzed calcareous polychaetes on the inner and outer surface of shells of *V. antiqua*.

Institutional abbreviations.—CEGH-UNC, Centro de Investigaciones Paleobiológicas, Universidad Nacional de Córdoba, Córdoba, Argentina.

Other abbreviations.—ABO, accessory boring organ; DF, frequency of drilling; PE, prey effectiveness; MIS, marine isotopic stage; VCA, Vermeij Crushing Analysis.

Material and methods

The study area, Bustamante Bay, is located in the San Jorge Gulf, Argentinean Patagonia (Fig. 2). This gulf is a semi-circular basin separated from the open sea by a mouth shal-

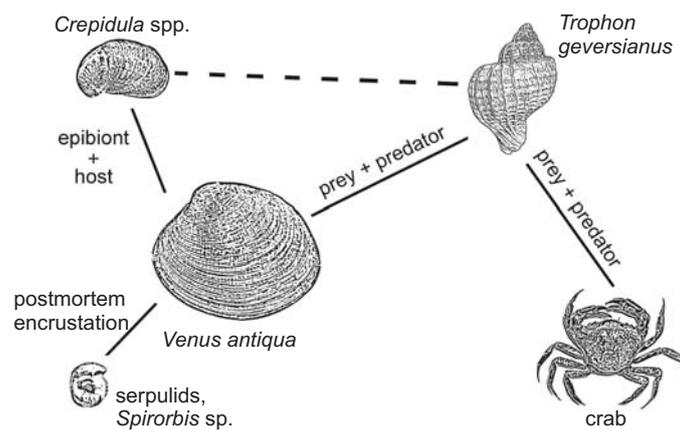


Fig. 1. Scheme showing biotic interactions (live/live interactions) and postmortem encrustation (live/dead interactions) associated with *Venus antiqua* King, 1832 shells preserved in molluscan death assemblages.

lower than the central part of the basin, which would have been a continental depression invaded by the sea (Cavallotto and Violante 2003). The Patagonian region is influenced by two major western boundary currents: Malvinas and Patagonian. Bustamante area is a well protected bay dominated by sandy bottoms, although wave-exposed and rocky bays are more common in Patagonia. This area was studied by Cionchi (1988), who described: a modern beach, currently evolving, and older units related to the sea-level highstands that formed during the Middle–Late Quaternary. Today, these raised marine units are clearly related to the marine oxygen isotope stages (MIS) as the Sangamonian highstand (Late Pleistocene, MIS 5e) commonly extended along the coast at an altitude of 16–20 m a.s.l. (Isla and Bujalesky 2008). In the same region, to the north, a higher raised marine level located close to Camarones probably belongs to MIS 7 (Schellmann 1998). Fossil material considered in this work was collected from both mentioned raised deposits.

Sampling was carried out in April 2010. Modern shells (Fig. 2) were collected using a square of 0.25 × 0.25 m. A representative sample was randomly taken from the active beach. This sample includes the material obtained in the surface from 20 squares randomly placed along the high intertidal level. Articulated and single valves of *V. antiqua* and *T. geversianus* shells were separated for further analysis. Shells were counted, and the height (maximum dorsal-ventral axis) and length (maximum anterior-posterior axis) of each articulated or disarticulated *V. antiqua* shell was also measured to the nearest 0.1 mm using vernier calipers.

For comparison with data on modern clams, Pleistocene shells were taken from bulk samples (50 cm³) randomly collected from two exposed marine sites: Bustamante and Camarones terraces (Fig. 2).

It is important to emphasize that the modern death assemblages analyzed in this work have not incorporated Quaternary reworked shells from the nearby area; contrary to the situation in other Patagonian sectors where fossil elements weathered out of the terraces have mixed with modern shells.

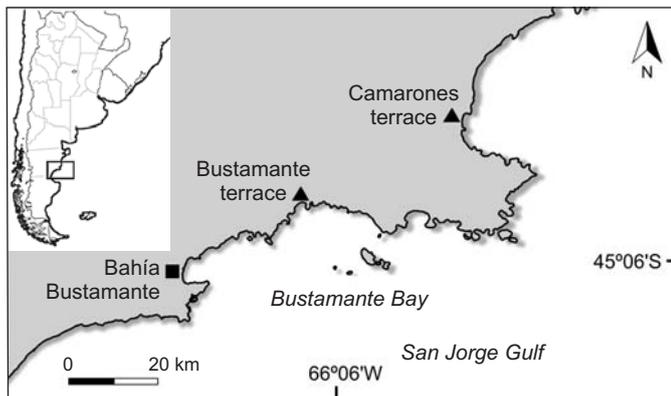


Fig 2. Map of a Patagonian sector showing sampled localities of modern (square) and Pleistocene (triangle) *Venus antiqua* King, 1832 shells.

To analyze holes produced by drilling gastropods we differentiated between predatory and non-predatory drill holes. In our study we considered only the first ones, which were easily separated from the others.

Predatory drill holes were classified as complete or incomplete drill holes. A complete drill hole is a circular hole oriented approximately perpendicular to the surface and an incomplete drill hole is a mark or a hole that does not penetrate to the interior of a shell.

Complete holes drilled by *T. geversianus* vary from cylindrical to conical, and change their location, depending on the prey species drilled (Gordillo 1994, 1998; Gordillo and Archuby 2012). Predatory experiments previously conducted in aquaria with *T. geversianus* preying upon the venerid clam *Tawera gayi* (Gordillo 1994) that closely resembles *V. antiqua* in shape and mode of life, allow for the correct identification of the drill holes. They are circular in plan-view, oriented perpendicular to the shell surface and truncated-conical in cross-section due to the external side is wider than the internal one. Incomplete drill holes exhibit a concave or flat bottom surrounded by a circular edge, and micro-rasping marks made by the radula can be observed under stereoscopic microscope.

To measure how often the clams were attacked by drilling predators and to evaluate their effectiveness in avoiding being eaten we discriminated between articulated and disarticulated (right and left) valves. For each valve we counted complete and incomplete drill holes to discriminate between “eaten” and “not eaten” specimens.

To evaluate the distribution of drill holes on *V. antiqua* shells, the surface of the valve was divided into two zones (upper and lower sectors; Fig. 3), useful as guides to evaluate life position of clams while preyed. The sector-based approach is a widely used strategy to study site selectivity within-element (Kowalewski 2002).

To compare between modern and Pleistocene shells, we calculated drilling frequency (DF) as a measure of how often organisms are attacked by drilling predators. We implemented the same nomenclature developed by Vermeij (1987) and used by Sawyer and Zuschin (2010). We calculated fre-

quency of drilling (DF), defined as the number of drilled valves divided by half the total number of valves, and prey effectiveness (PE), defined as the number of incomplete drill holes divided by the total number of drill holes (complete as well as incomplete).

Size frequency distribution of drilled specimens of *V. antiqua* was used as a proxy of size selectivity. The statistical difference between the size frequency distributions of drilled versus undrilled specimens was evaluated using the non-parametric Mann-Whitney U-test (Zar 1999). For that purpose we compared the length, height, and geometric mean of these two measurements between attacked and non attacked shells. For these analyses we included articulated (each articulated pair represents an individual) and right valves.

To evaluate damage produced by potential predators (i.e., crabs) on the drilling gastropod *T. geversianus* we took as reference the results obtained by Stafford and Leighton (2011) who applied the Vermeij Crushing Analysis (VCA) to four gastropod species. In this regard, using VCA, certain types of damage (i.e., apex removal, deep aperture chips, major body whorl damage and columella damage) are indicative of crushing predation and not caused by taphonomic forces. It should be noted that in our samples, because drilled gastropod shells were scarce, we cannot apply directly the VCA method, but we compared the shell damage frequency with the baseline of the VCA method. For that purpose *T. geversianus* shells were classified in seven categories: shells with predatory drill holes, intact shells, shells with damage in the apex, shells with damage to shell aperture margin, shells with crack in aperture or in body whorl, shells with a major damage in last whorl, and shells with columella damage.

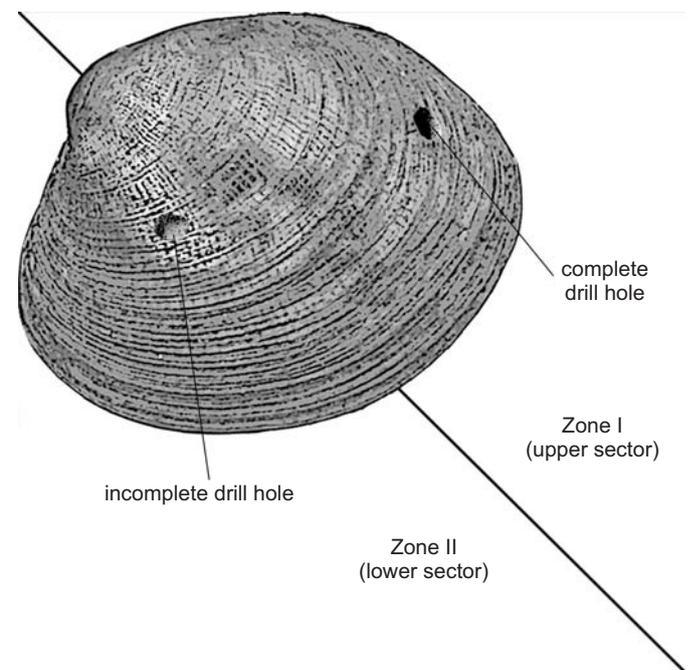


Fig 3. Diagram showing division of each valve into two zones.

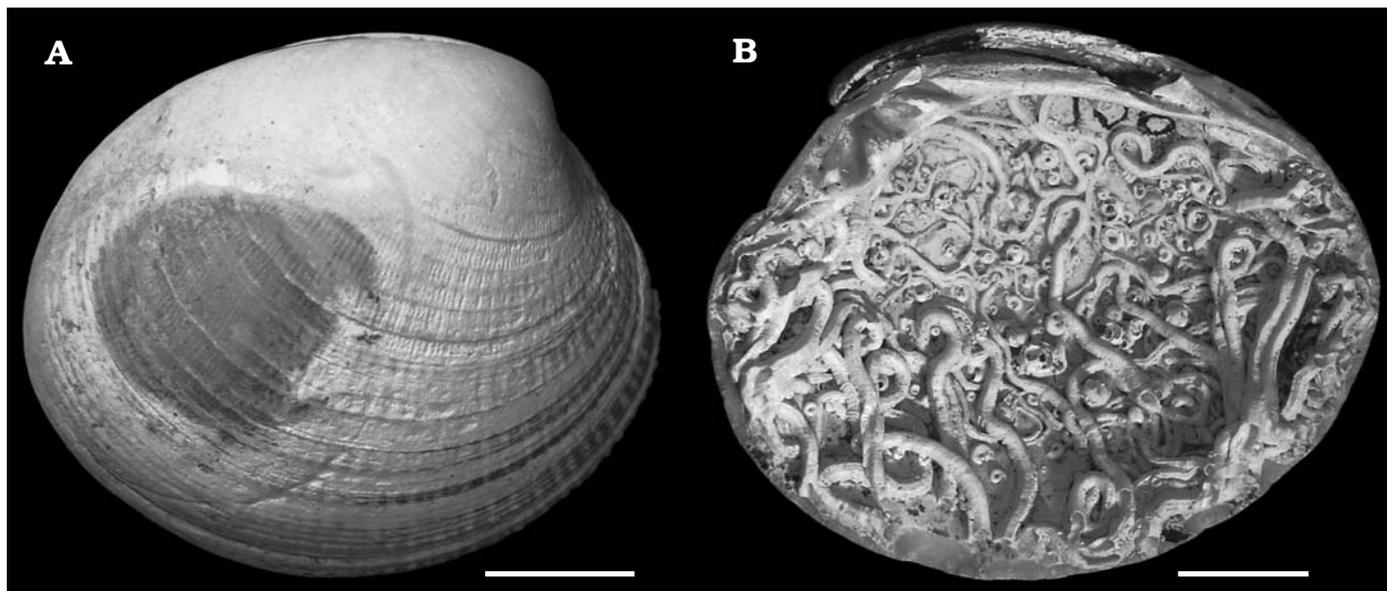


Fig. 4. Marks of epibionts on *Venus antiqua* King, 1832 shells, Recent, Bahía Bustamante. **A.** CEGH-UNC 25333, external view of a right valve with a mark that reproduces the basal outline shape of *Crepidula*. The central dark zone reproduces the rounded muscular foot of *Crepidula*. **B.** CEGH-UNC 25334, internal view of a right valve covered with calcareous tubes of tubicolous polychaetes. This figure also shows hinge ligament remains. Scale bars 10 mm.

To evaluate the non randomness of *Crepidula* spp. encrustations on *V. antiqua* shells, besides the upper and lower sectors that are shown in Fig. 3, we added a third zone (middle sector) for those cases with *Crepidula* spp. located across both sectors. Expected frequencies, which consider equal amount of encrustation in each sector, were contrasted against the observed frequencies with a chi-square goodness of fit test.

The presence of *Crepidula* spp. as an epibiont of *V. antiqua* was directly assessed by its presence or, if the shell of this species was found separated from the host, this epibiont was recognized through a mark (Fig. 4A) that reproduces the basal shape of the slipper snail.

Finally, tubicolous polychaetes were evaluated according to the presence of calcareous tubes (Fig. 4B) preserved on *V. antiqua* shells. To recognize postmortem encrustation and differentiate it from epibionts which settle on living clams, we analyzed epibionts on outer and inner shell surface separately. To evaluate covering, an arbitrary abundance scale (L or M) was also devised for calcareous polychaetes (i.e., *Serpula* and *Spirorbis*): L (less) with epibionts covering $\leq 50\%$ and M (more) with epibionts covering $> 50\%$. To compare between outer and inner surface, the abundance scale (surface covered) was only analyzed in disarticulated shells.

The null hypotheses that drill holes are randomly distributed between right and left valves and between upper and lower sectors of each valve were tested. For some statistical comparisons we used data from articulated plus right valves (slightly more abundant than left ones) to avoid counting same individual twice.

Statistical analyses were performed using the program PAST version 2.14 (Hammer et al. 2001). Null hypothesis is rejected when considering type I error of 0.05.

Results

Ratio of right/left valves

Table 1 shows that in the modern sample, the ratio of right/left valves of *Venus antiqua* is near 1:1. For the pooled sample disarticulated right valves sum 218 (50.7%) while left ones account for 212 (49.3%). This difference is not statistically significant (Yates' Corrected Chi Square = 0.02; $p = 0.89$).

Table 1. Number of articulated and disarticulated valves in modern sample from Bustamante Bay and total valves corrected to count bivalve abundance. Nmin, minimum number of specimens = articulated + left or right valves (choosing the most abundant of both sides); N, number of individuals calculated as articulated + (left+right valves)/2.

Modern sample	Total
Articulated valves	339
Right shells	218
Left shells	212
N (elements)	769
Nmin (individuals)	557
N (individuals)	554

Boreholes by *Trophon geversianus*:

Drilling predation

Based on borehole morphology (according to literature mentioned above), drill holes analyzed in this study were attributed to *Trophon geversianus*. Furthermore, with the exception of a single individual belonging to another muricid species (i.e., *Trophon plicatus*), the presence of naticids (present in other Patagonian beaches), which could be another group

Table 2. Details of incidence of drilling predation on Recent *Venus antiqua* shells from Bustamante Bay, Patagonia, Argentina.

Details of drilling predation	N	%
Articulated valves	339	100
Individuals with (complete and/or incomplete) drill holes	105	30.97
Individuals with at least one complete drill hole (eaten)	79	23.30
Individuals with only failed attacks. Not eaten.	26	7.67
Valves with multiple drill holes	19	5.6
Valves with complete drill holes in opposite valves	5	1.47
Valves with complete and incomplete drill holes in opposite valves	4	1.17
Left valves bored	50	14.75
Right valves bored	65	19.17
Individuals with drill holes in the upper sector	75	22.12
Individuals with drill holes in the lower sector	36	10.62
Disarticulated right valves	218	100
Right valves with drill holes	30	13.76
Right valves with complete drill holes	24	11.01
Right valves attacked on upper sector	26	11.93
Right valves attacked on lower sector	4	1.83
Disarticulated left valves	212	100
Left valves with drill holes	26	12.26
Left valves with complete drill holes	21	9.91
Left valves attacked on upper sector	24	11.32
Left valves attacked on lower sector	2	0.94

Table 3. Summary of drill holes data in Recent and Pleistocene samples. Abbreviations: BT, Bustamante terrace; CT, Camarones terrace; D, number of complete drill holes; DF, drill frequency; ID, number of incomplete drill holes; N, abundance; PE, prey effectiveness. Modern sample refers to all articulated specimens with at least one complete drill hole plus drill holes in disarticulated shells, the total being calculated as number of articulated + (number of left + right valves)/2.

Sample	N	D	ID	DF (%)	PE (%)
Modern sample	554	124	59	22.4	32.24
BT Pleistocene	30	1	1	6.7	50
CT Pleistocene	96	1	1	2.1	50

of potential predators of clams, in this area has not been registered.

Intensity of drilling predation.—A total of 105 individuals (30.97%), calculated from 339 articulated clams, showed drill holes; with 23.30% of them with at least one complete drill hole and 7.67% with only failed attacks (Table 2).

With the addition of disarticulated valves (339 + (218+212)/2) and, assuming that all disarticulated valves with drill holes are considered as belonging to different individuals, a total of 124 specimens (22.4%) have complete drill holes and are inferred to have been consumed. There is no statistically significant difference in the proportion of left and right valves (26 left, 30 right; Table 2) with attacks ($p = 0.54$). Thus, a value of 22.4% is a reasonably good estimator of prey consumption in this particular predator-prey relationship, though it slightly overestimates the predation rate

as in our material we found 1.5% of articulated valves with complete drill holes in both valves.

A similar calculation allows an estimation of 161 specimens (29.06%) attacked, and under the same calculation criterion we estimated 10.65% of individuals that have been unsuccessfully attacked or 7.76% if only articulated specimens are considered.

Finally, four articulated individuals (1.17%) were detected with a failed attack on one valve and complete hole on the other. In case these specimens became disarticulated, this pattern may lead to mistakenly interpret that valves with incomplete holes belonged to clams that survived the attack. This pattern is, fortunately, numerically small.

Modern versus Pleistocene shells.—Data on modern and Pleistocene shells are summarized in Table 3. Drilling frequency (DF) was higher in the modern sample (22.4%) than in the Pleistocene ones (between 2.1% and 6.7%). Prey effectiveness reaches a value of 32.24% in modern samples, but as only two drilled valves were found in each Pleistocene sample, effectiveness cannot be evaluated due to the small sample size.

Drill holes placement on shell surface.—There is a marked preference for the drill holes to be placed in the upper sector: 136 holes (75%) were in the upper sector of the valve, and 45 (25%) in the lower sector. This result allows rejection the null hypothesis that the two sectors are equally attacked (Yates' Corrected Chi Square = 23.3; $p = 0.000$). Finally, multiple drillings were observed in only 19 (5.6%) articulated valves, including complete and incomplete drill holes. These holes are mostly in opposite valves, but also in four cases they are in the same valve.

Regarding the differences between upper and lower sectors, we infer that holes on the lower sector were most probably made on individuals with shells in horizontal position. However, holes in the upper sector could have been made when the clam was in vertical or horizontal position. If we assume that when the clam is horizontal, it is equally likely to be attacked in both (upper and lower) sectors, then it is reasonable to think that 26.4% of holes were made with the clam in vertical position and 47.2% when it is in horizontal position. This speculation arises from considering that valves in horizontal position would be attacked approximately the same amount of times in both sectors, provided that the predator did not choose the place where it drills. Then, if 25% of the holes were made in the lower sector, one would expect a similar value in the upper one. The remaining upper borings would have been made with the clams in vertical position.

Size selectivity of drilling.—Drilled specimens are significantly smaller than undrilled ones (Mann-Whitney U-test; shell length, $p = 0.038$; shell height, $p = 0.009$; geometric mean, $p = 0.018$; Fig. 5). The highest frequency of drilling corresponds to the 30–45 mm (length) and 25–40 mm (height) size intervals. Despite the statistical significance, the difference is rather small: 1.26 and 1.34 mm for length

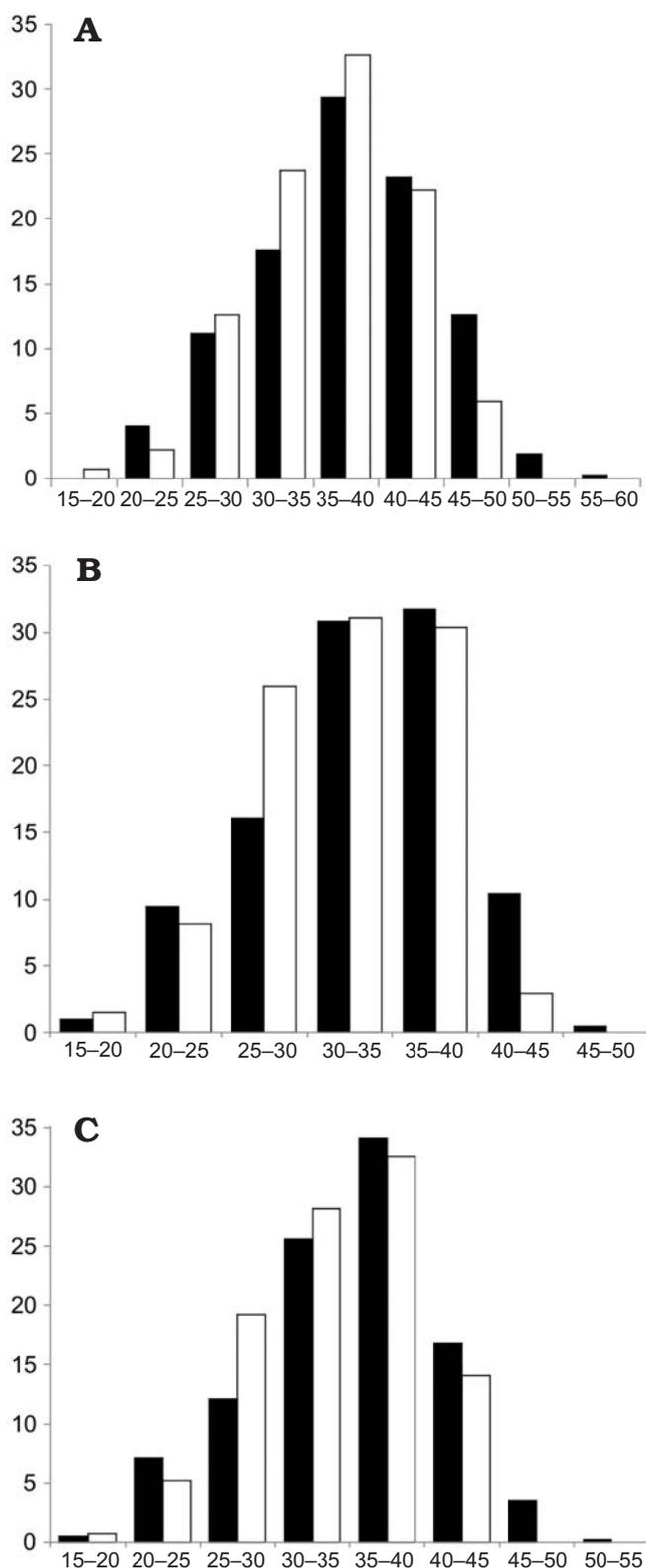


Fig. 5. Shell size frequency distribution of drilled (white bars) and undrilled (black bars) modern *Venus antiqua* King, 1832 shells. **A.** Shell length. **B.** Shell height. **C.** Geometric mean of shell length and height.

and height of the shells respectively. These differences do not exceed 4 % of the average of the three variables evaluated for the undrilled shells.

Damage on shells of the drilling gastropod *Trophon geversianus*.—This analysis was performed in connection with predatory failures recorded in our modern samples. In this regard, the failure of predators is not always related to effectiveness but to other external factors. For instance, the driller can be interrupted by its own predator (Kelley and Hansen 2003). According to our knowledge, we consider plausible that a drilling gastropod be attacked by crabs while eating a clam. It is widely known that crabs are potential predators of invertebrates in modern benthic environments. Moreover, this idea was strengthened further by confirming that *T. geversianus* from this region is a prey of crabs (Hidalgo et al. 2005).

Intact shells (Fig. 6B) represent the 11.8% of the total gastropods ($N = 34$). The most common types of shell damage are: gastropod shells with crack in body whorl (44.1%; Fig. 6D) or in aperture (20.6%; Fig. 6C), and a minor proportion of shells with a major damage in last whorl (8.0%; Fig. 6E) or shells with columella damage (8.0%; Fig. 6F).

In this regard, following the results by Stafford and Leighton (2011), more than 60% of marks in *T. geversianus* shells, including shells with crack in body whorl (44.1%) or in aperture (20.6%), and even intact shells (11.8%), could have been “potentially” produced by other predators and not caused by taphonomic forces. The latter is based in laboratory work by Edgell and Rochette (2009), who observed that predation by crabs produces also intact gastropod shells.

Association between *Venus antiqua* and *Crepidula* spp.—*Crepidula* spp. is present in 53 of 769 (6.89%) shells of *V. antiqua*. Similar to borings, there is a remarkable preference of *Crepidula* spp. for the upper sector (70.91%) of the valve of the host, with 14.55% and 14.55% in middle and lower locations (goodness of fit test, $\chi^2 = 34.95$, $p = 0.000$; Fig. 7).

When considering shells with marks of *Crepidula* spp., only 4 out of 53 (7.55%; Fig. 8) exhibit complete drill holes, a value that is lower than the 22.38% of complete borings described in this study. This result supports the hypothesis of *Crepidula* spp. preventing the host *V. antiqua* from being attacked by drilling predators (Yates' Corrected Chi Square = 6.51; $p = 0.011$).

Serpulid worm tubes and small spiral tubes of *Spirorbis* sp.—Of the 769 shells (articulated+left+right) of *V. antiqua* examined, 420 (54.6%) did not have evidence of encrustations. The remaining 349 (45.4%) did show epibionts of different types, including *Crepidula* spp. *Serpula* and *Spirorbis* tubes are present in 34.7% of the shells. Table 4 shows the distribution of *Serpula* and *Spirorbis* tubes in disarticulated *V. antiqua* shells, discriminating between left and right valves, as well as inner and outer surface. Results show that calcareous polychaetes fixed themselves preferably onto the inner surface of the empty *V. antiqua* shells. There was also showed greater abundance of shells partially-covered with respect to shells fully-covered with encrusters.

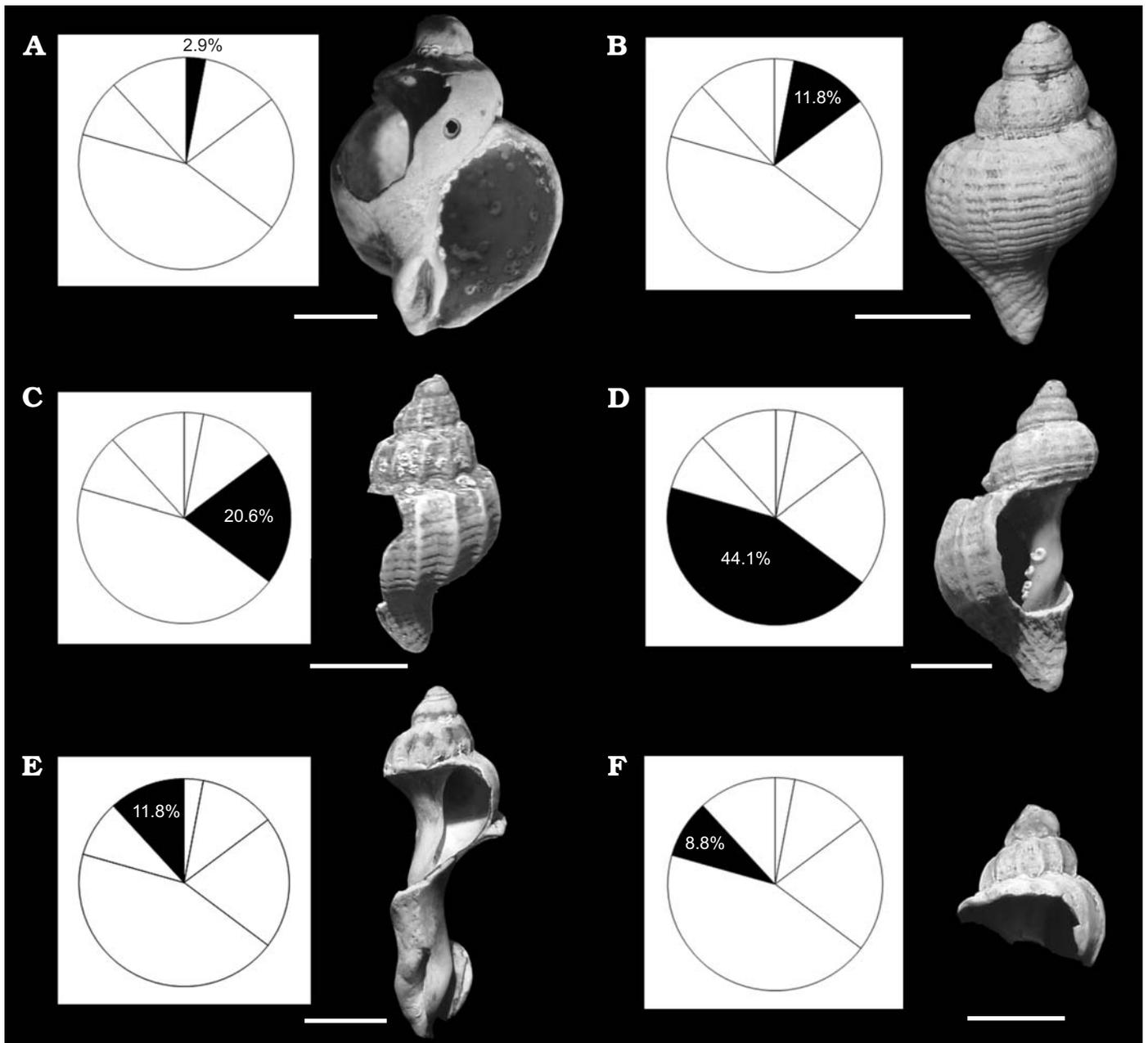


Fig. 6. Different types of damage recorded in modern *Trophon geversianus* shells collected from the same samples that the *Venus antiqua* King, 1832 shells, Bahía Bustamante. **A.** Shell with predatory drill hole. **B.** Intact shell. **C.** Shell with damage to shell aperture margin. **D.** Shell with crack in body whorl. **E.** Shell with a major damage in last whorl. **F.** Shell with columella damage. Pie charts show the proportion of snails (N = 34) with each type of damage, used here to infer crushing and drilling predation. Scale bars 10 mm.

Discussion

Venus antiqua shells from Patagonia bear abundant evidence of drilling gastropods attacks. The morphology of the holes, the higher abundance of *Trophon geversianus* with respect to other potential gastropod predators, as well as the results from previous experimental and in situ observations (Gordillo 1994, 1998; Gordillo and Archuby 2012) are all evidence that support the predation by this muricid on *V. antiqua*. The predator selects clams slightly smaller than the available size, and preferably drills on the posterior half of the valve.

Table 4. Coverage of calcareous polychaetes in *Venus antiqua* shells from Bustamante Bay.

Zone and area of covering	Right valves		Left valves	
	<i>Serpula</i>	<i>Spirorbis</i>	<i>Serpula</i>	<i>Spirorbis</i>
outer shell	>50%	1	–	1
	≤ 50%	8	11	10
inner shell	>50%	17	16	11
	≤ 50%	29	56	27
outer+inner	>50%	11	4	14
	≤ 50%	37	16	55

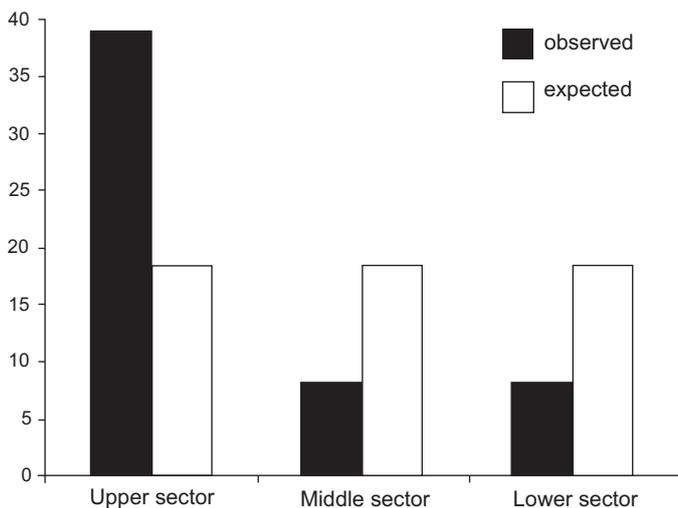


Fig. 7. Comparison between observed and expected frequencies of *Crepidula* spp. encrustations on *Venus antiqua* King, 1832 shells from Bustamante Bay.

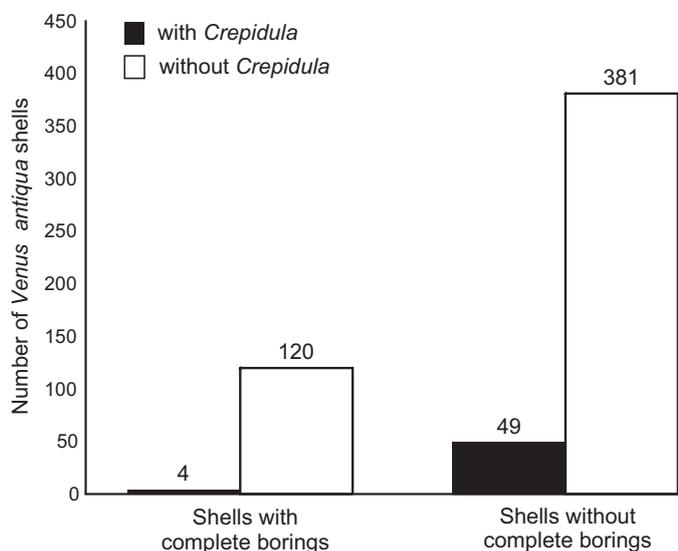


Fig. 8. Bar charts showing proportion of modern *Venus antiqua* King, 1832 shells exhibiting two different biotic interactions.

Besides, the position of drill holes provides information about different modes of life of *V. antiqua*, and unsuccessful attacks may, indirectly, give clues about other interactions. In addition, the presence of *Crepidula* spp. appears to represent a protection against drilling gastropods. Finally, postmortem encrusters fixed onto the inner shell surface represent a cryptic community inhabiting empty articulated *V. antiqua* valves. These aspects are discussed below.

Different modes of life of *Venus antiqua* is evidenced by drill holes.—The pattern of distribution of drill holes found in this study, preferentially located in the upper sector of the shell, might simply be the consequence of the restricted access to the lower areas of clams growing partially buried. However, the presence of drill holes in the lower sector is interpreted in a different way. It is known that during

storms, or windy events, clams can be washed out from their semi-infaunal or infaunal life positions and transported and deposited outside the sediment. Under this situation clams adopt a hydro-dynamically more stable horizontal orientation (Kondo 1997; Fig. 9A), but they would be more vulnerable to predators. In this regard, Thórarinsdóttir et al. (2009) noted that after the storms, still clams are easily attacked by other invertebrates and fishes. Thus, when a clam is lying in horizontal position both upper and lower sectors are equally accessible to the predators. A second position (Fig. 9B) is associated with the burrowing mechanism of clams described by Stanley (1970, 1975): when a clam starts burrowing, it adopts an erect position. Then, when it burrows into the sediment, the clam slides forward with each backward rotation instead of penetration downward. After that, the clam buries completely into the bottom (Fig. 9C), or stay partially buried (Fig. 9D). Once complete burial is achieved the clam is out of the reach of muricid gastropod attacks. Presumably, the prolonged semi-infaunal position also increases the frequency of drilling predation.

Prey effectiveness, incomplete drill holes and causes of interruption of drilling predation.—Results show that prey effectiveness in modern samples averages at 32.24%. The data given by Vermeij (1987) for Cenozoic bivalves indicate that 27% of the surveyed taxa showed an effectiveness of 30% or higher (close to the value obtained in our work) while the 73% remaining corresponds to lower values, mostly below 10%.

The number of failed attacks does not exceed 10%. An attack may be unsuccessful for a number of reasons, including inconsistency between morphology and/or size of a predator and the prey selected, interruption by physical events (e.g., storms) or interruption by biological reasons such as the prey escape or interference by other predators (Kelley and Hansen 2003). In addition, muricids are able to kill the prey without drilling, and sometimes, after a successful predation, they leave incomplete drill holes (Kowalewski 2004). For example the muricid *Thais clavigera* applies toxins to the edge of a limpet prey in order to immobilize the prey, so it can be consumed without drilling (Taylor and Morton 1996). In the case of naticid snails with a large mesopodium, they also include other strategy to feed, yielding incomplete holes despite a successful attack; i.e., sometimes they retain the prey until suffocation and if the prey gapes they feed before the drill hole is completed (Ansell and Morton 1987). Regarding the death assemblages studied here (although other possibilities are not entirely discarded), we hypothesize that many of the incomplete drill holes could result from the crab attack on the drilling gastropod. Crabs are well known predators of shelled mollusks, and available evidence indicates that shell breakage is a rapid method of subjugation (Vermeij 1987).

In Patagonia, the European green crab, *Carcinus maenas*, was recently introduced (Vinuesa 2005, 2007). This species was recorded for the first time in 2001 along the central coast of San Jorge Gulf (45°55'S) (Vinuesa 2005), and then, in 2003,

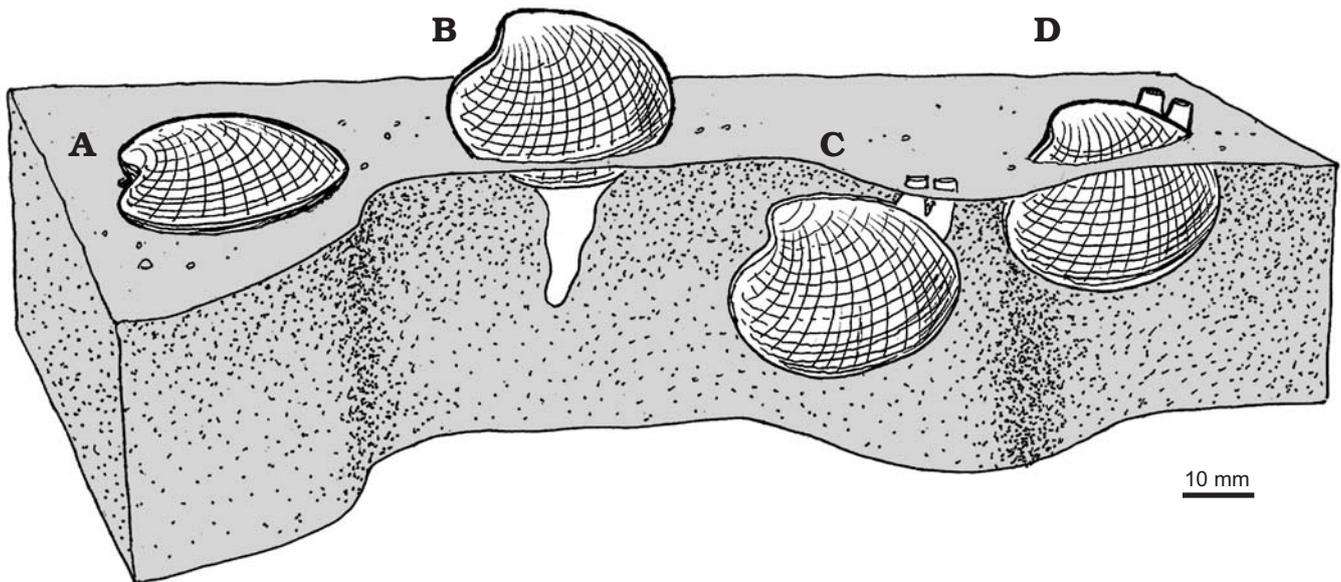


Fig. 9. Orientation of *Venus antiqua* King, 1832 in various situations. **A.** Reclining or reworked orientation. **B.** Erect probing orientation. **C.** Infaunal orientation. **D.** Semi-infaunal orientation.

in Camarones Bay, north to San Jorge Gulf (approximately 44°54'S) (Hidalgo et al. 2005). It is expected that the introduction of *C. maenas* in the Argentinean Patagonia will cause a large impact on shallow water communities as occurred in other parts of the world. For example, this crab invaded New England circa 1900 and appears to have caused the shell thickening in some native gastropods like the muricid *Nucella lapillus* to affiliate higher resistance to breakage (Vermeij 1982; Edgell and Rochette 2009; and references therein).

A recent experiment performed by Hidalgo et al. (2007) to evaluate potential predator-prey interactions for *C. maenas* and the native grapsid crab *Cyrtograpsus angulatus* living on Patagonian rocky shores showed that the invader crab was able to eat the snail *T. geversianus*, and other native shelled mollusks and crustaceans, while the native one had a low consumption rate on shelled prey, restricted to a small number of small mussels and barnacles.

During predation on hard-shelled preys *C. maenas* uses its crusher cheliped for cracking the shells, and its cutter cheliped to manipulate and reorient the preys (Elner, 1978; Preston et al. 1996). There is evidence obtained from experiments in aquaria that the crabs' shell-breaking behavior dominates in those predators fed with thin-shelled snails, whereas crabs fed thick-shelled snails mostly winkled flesh through the shell opening without damaging the shell itself (Edgell and Rochette 2009).

In our samples, the shells of *V. antiqua* have some skeletal features as crenulated margins, valve thickness and inflated shell making this species more resistant to the attack of crabs (Carter 1968); but also we did not find scars of sublethal damage as growth disruptions (Cintra-Buenrostro et al. 2005) or V-shaped indentation, both produced during failed attempts by crab predation. In contrast, the shells of the drilling predator *T. geversianus* exhibited different kind

of damage and many of them, as described above, could have been caused by crabs.

When gastropods are exposed to impact, the arched whorls and the apertures break first, and further mechanical destruction is determined by the shape and sculpturing of the shell. For example, this author pointed out that *Buccinum undatum* and *Littorina littorea*, which are frequently found along the Dutch coast, do have a hard aperture and they erode until the entire columella is exposed. There is no clearly identifiable pattern of crab attacks to the shell of prey. In any case, several questions arise and still need to be investigated.

One aspect that needs to be evaluated is the question why snails are more vulnerable to crabs while feeding on clams, which would be caused by chemical signals in the prey or visual signals in the crabs. In this regard, it is known that aquatic animals like snails, mussels, clams, crabs and barnacles, among other invertebrates, alter their behavior in response to chemical stimuli from predators (Rosen et al. 2009). For example, the rocky shore gastropod *Nucella lamellosa* can discriminate between the effluents of predatory and non-predatory brachyuran crabs (Marko and Palmer 1991). The drilling activity may cause the attraction of crabs that detect the substances released by the ABO of the snail. Considering that the drilling predator involved in our study needs several days to completely bore the prey shell and consume it (e.g., 9 days in the case of *T. geversianus* in Tierra del Fuego; Gordillo and Archuby 2012) they are exposed to the attack of crabs for a considerable period of time. It was also demonstrated under experimental conditions that *N. lamellosa* during the drilling activity releases the prey when a red crab is introduced into the aquarium (Chattopadhyay and Baumiller 2007). Irrespective whether the attack of a crab on a snail eventually takes place or not the bivalve shell is marked by an incomplete drill hole in consequence.

Finally, we noted only one specimen of *T. geversianus* with a drill hole, which bears also one *Crepidula* shell attached to its valve, and postmortem encrustation with calcareous polychaetes on its inner surface (Fig. 6A). This is an isolated case of a shell with different kinds of biotic interactions, including live-live and live-dead interactions, even showing a possible cannibalism behavior in *T. geversianus*. This last particular biotic interaction is at present being studied because drilled *T. geversianus* specimens attributable to conspecifics have been also found along the Beagle Chanel, in Tierra del Fuego (Table 2; Gordillo and Archuby 2012).

Are differences in drilling predation associated with environmental changes during the Quaternary?—Studies of drilling frequencies and relative effectiveness of predator and prey indicate significant changes in drilling gastropod predator-prey systems through time supporting the importance of biotic interactions in evolution (Kelley and Hansen 2003), but such changes were evaluated at a time scale much greater than a period of thousands of years considered in this work.

However, Tull and Böhning-Gaese (1993) analyzed prey shells from Pleistocene and Recent storm deposits from California, and no evidence of change in any aspect of drilling predation over the past 100 000 years was found. Also Amano (2006) observed no temporal trend in the intensity of drilling by naticids on *Glycymeris* during the late Cenozoic in Japan. On the other hand Key (2003), who analyzed drilling predation on *Crepidula* from United States coastal plain reported that naticid predation increased during the Pleistocene and the muricid predation decreased. This trend appears to be influenced by changes in competition (which favored naticids) correlated with environmental changes caused by the Plio-Pleistocene extinction event and affiliated the escalation.

In our work we found an increase in the intensity of predation from Pleistocene to Recent times. These differences were also observed elsewhere in Patagonia (e.g., Puerto Lobos, in northern Chubut). The Pleistocene shells are distinguished from the modern ones, because almost all of them are free of encrusters. The Pleistocene shells of *V. antiqua* are usually strong and exhibit very good state of preservation, so it is unlikely that lower Pleistocene drilling frequencies are biased due to taphonomic reasons.

The possible causes of these differences could be due to climatic and habitat changes during the Quaternary. Pleistocene shells were deposited: (i) prior to the Last Glacial Maximum (24 Kya; Rabassa 2008) when the sea level was 120 m below the present level, and (ii) prior to the formation of the San Jorge Gulf (15 Kya; Ponce et al. 2011). Based on these works we deduced that during the age of deposition of these Pleistocene shells (100–190 Kya; Schellmann 1998), the Patagonia coastline was a huge coastal plain, extending northwards to the Pampa, with a different hydrological regime, subject to storm effects and with rapid sedimentation rates, since it was more exposed to the open sea. Such geomorphological and sedimentological changes are likely to have influenced ecological patterns of benthic marine com-

munities. In this regard, the lack of epibionts and low drilling predation in Pleistocene shells is probably related to a deeper burial of these clams making them more difficult to attack by epifaunal muricid gastropods.

In addition, the studies performed by Lardies et al. (2001) on a living population of *V. antiqua* inhabiting a tidal flat in southern Chile showed that the burial depth dynamics of this suspension feeder species positively correlates with food availability in the water column. Also the presence of algal mats of *Glacilaria* or *Enteromorpha* in Bustamante Bay (Piriz and Casas 1996; Boraso and Zaixso 2007) affects the burial depth of *V. antiqua* due to chemical changes (sulphides, hypoxia) beneath the mat, as it was shown for the clam *Mya arenaria* in the Northern Hemisphere (Auffrey et al. 2004).

All these interactions need to be analyzed along with other indicators of food levels in the past such (as growth rates and/or adult size), and used together with sediment characteristics of Pleistocene deposits to help reconstruct relative patterns of paleoproductivity.

Influence of *Crepidula* epibiontism on the drilling predation.—*Crepidula* spp. is a group of gregarious species that monopolizes the space where it grows, impeding or restricting the settlement of larvae of other species as a side effect of space occupation (McGee and Targett 1989). Bustamante Bay bottoms are dominated by sand and hence, colonization of *V. antiqua* specimens as living substrates may be beneficial to epizoans which require hard bottoms, as *Crepidula* spp. does (Olabarria 2000). It is noticed that the two gastropods which interact with *V. antiqua* (i.e., *Crepidula* spp. and *T. geversianus*) are typical of hard substrates, denoting plasticity as they also form part of soft bottom communities.

Clams with *Crepidula* spp. attached are killed less frequently than those specimens that lack the epibiont. The epibiosis seems to represent a protection against predators instead of involving only a cost for the clam. This evidence a priori supports a mutualism between *Crepidula* spp. and *V. antiqua*. However, *Crepidula* probably is a defense character that increase survivorship of *V. antiqua* against *T. geversianus*, but probably it also makes it more vulnerable species to other predators as the crabs, because a clam with *Crepidula* has difficulties in burying.

The absence (at least among our samples) of *Crepidula* spp. encrusting the inner side of *V. antiqua* shells and the significant preference for colonizing the upper sector, all indicate that this epibiont colonized a living clam.

Postmortem guests: live/dead interactions.—In the marine realm, live hosts (e.g., clams) offer habitat for a great variety of organisms which encrust as epibionts, but dead shells exposed on the seafloor also act as hard substrate for any surface-dwelling organism, providing habitats for a diverse epizoan association of oysters, barnacles, serpulids, and sponges (see Kidwell and Jablonski 1983).

Our results showed that *V. antiqua* dead shells provide a substrate to tube-building polychaetes such as *Serpula* (probably *Serpula narconensis* Baird, 1865) and *Spirorbis* sp.

The preferential colonization of the inner valve suggests that the empty shells of *V. antiqua* serve as cryptic environment before they become exposed on the beach. Shells in soft-sediment environments can serve as important “benthic islands” for hard substrate communities (Taylor and Wilson 2003). Perhaps this habitat offers the possibility of avoiding predation or competition, or it provides shelter from physical disturbance, but it can also relate to physiological reasons. Cryptic suspension feeders capture and recycle particulate organic matter from surrounding environment (Enoch and Hockensmith 2008).

The calcareous polychaetes were found in still articulated specimens and disarticulated shells, with remains of the ligament. It suggests that these encrusters colonized the host soon after death. With respect to the abundance of tubicolous polychaetes, the fact that *V. antiqua* shells are partially covered with encrusters were more frequent than fully covered ones may denote a self-regulatory mechanism in this cryptic community.

Concluding remarks

This study shows that molluscan death assemblages in Patagonia retain strong signatures of the living benthic communities and biotic interactions. We demonstrated that the clam *V. antiqua* lives, at least part of the time, partially buried in the sediment or lying in horizontal position on the bottom. This semi-infaunal bivalve is frequently attacked and consumed by the muricid gastropod *T. geverianus* and the moderate number of recorded failed attacks is here interpreted as a result of the appearance of a second predator (most likely a crab) able to attack snails while they are eating clams. Furthermore, the presence of the epibiont *Crepidula* on *V. antiqua* appears to prevent the attack of drilling gastropods, and the calcareous polychaetes seem to constitute a cryptic community living inside the empty *V. antiqua* shells before they are exposed. Finally, differences in drill frequency between Pleistocene and modern shells suggest changes in predation through time, although the reasons are not clear enough for this region pending further research.

All these interactions constitute a complex system and multiple factors may influence the outcome of encounters between predator and prey, or the spatial relationships among organisms living in particular communities. At ecological time scales, these interactions are common processes that surely give rise to reciprocal adaptation between pairs of species involved, with one of them being likely to exert some selective pressure on the other (e.g., their predators) over the short term. In other words, microevolutionary processes that operate on ecological time scales may have macroevolutionary consequences (Dietl and Kelley 2002). Therefore, the studies of modern death assemblages to extract relevant ecological information on biotic interactions are essential in deciphering similar processes from the fossil record and indispensable to construct and test evolutionary hypotheses.

Finally, it should be noted that traces and remains of epibiont preserved on mollusk shells are a powerful tool both to paleontologists and ecologists.

Note added in proof

In a recently paper Pérez et al. (2013) conducted a systematic revision of the genus *Ameghinomya* Ihering, 1907 and its phylogenetic relationships were explored through a cladistic analysis based on morphological characters of extant and fossil species. Based on their results these authors proposed to assign the species *Venus antiqua* King, 1832 (extant, Southwestern Atlantic) to the genus *Ameghinomya*.

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References

- Alexander, R.R. and Dietl, G.P. 2003. The fossil record of shell-breaking predation on marine bivalves and gastropods. In: P.H. Kelley, M. Kowalewski, and T.A. Hansen (eds.), *Predator-Prey Interactions in the Fossil Record*, 141–176. Kluwer Academic/Plenum Publishers, New York.
- Amano, K. 2006. Temporal pattern of naticid predation on *Glycymeris yessoensis* (Sowerby) during the Late Cenozoic in Japan. *Palaios* 21: 369–374.
- Andrade, C. and Ríos, C. 2007. Estudio experimental de los hábitos tróficos de *Trophon geversianus* (Pallas 1774) (Gastropoda: Muricidae): selección y manipulación de presas. *Anales Instituto Patagonia (Chile)* 35: 45–53.
- Ansell, A.D. and Morton, B. 1987. Alternative predation tactics of a tropical naticid gastropod. *Journal of Experimental Marine Biology and Ecology* 11: 109–119.
- Auffrey, L.M., Robinson, S.M.C., and Barbeau, M.A. 2004. Effect of green macroalgal mats on burial depth of soft-shelled clams *Mya arenaria*. *Marine Ecology Progress Series* 278: 193–203.
- Ausich, W.I. and Gurrola, R.A. 1979. Two Boring Organisms in a Lower Mississippian Community of Southern Indiana. *Journal of Paleontology* 53: 335–344.
- Boraso, A.L. and Zaixso, J.M. 2007. Algas marinas bentónicas. In: D. Boltovskoy (ed.), *Atlas de Sensibilidad Ambiental de la Costa y el Mar Argentino*, 28. Fondo para el Medio Ambiente Mundial (GEF), Buenos Aires.
- Carriker, M.R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20: 403–422.
- Carter, R.M. 1968. On the biology and palaeontology of some predators of bivalved mollusca. *Palaeoecology, Palaeoclimatology, Palaeoecology* 4: 29–65.
- Cavallotto, J.L. and Violante, R.A. 2003. Late Pleistocene and Holocene

- transgressions in the northern Patagonian gulfs, Argentina. "Continental Shelves during the last Glacial Cycle" IGCP No. 464, Abstracts: 69. UNESCO/IUGS, Gdańsk. <http://tetide.geo.uniroma1.it/igcp464/Gdansk/Gdansk.htm#Abstracts>
- Chattopadhyay, D. and Baumiller, T.K. 2007. Drilling under threat: an experimental assessment of drilling behaviour of *Nucella lamellosa* in the presence of a predator. *Journal of Experimental Marine Biology and Ecology* 352: 257–266.
- Cintra-Buenrostro, C.E., Flessa, K.W., and Avila-Serrano, G. 2005. Who cares about a vanishing clam? Trophic importance of *Mulinia coloradoensis* inferred from predatory damage. *Palaaios* 20: 296–302.
- Cionchi J.L., 1988. Geomorfología de Bahía Bustamante y zonas adyacentes, Chubut. *Revista de la Asociación Geológica Argentina* 43: 51–62.
- Cummins, H., Powell, E.N., Stanton, R.J., and Staff, G. 1986. The rate of taphonomic loss in modern benthic habitats: how much of the potentially preservable community is preserved?. *Palaeoecology, Palaeoclimatology, Palaeoecology* 52: 291–320.
- Dietl, G.P. and Kelley, P.H. 2002. The fossil record of predator-prey arms races: coevolution and escalation hypotheses. In: M. Kowalewski and P.H. Kelley (eds.), *The Fossil Record of Predation. The Paleontological Society Papers* 8: 353–374.
- d'Orbigny, A.D. 1834–1847. *Voyage dans l'Amérique Méridionale. Mollusques, Vol. 5, Part 3*. 758 pp. Pitois-Levrault, Paris.
- Edgell, T.C. and Rochette, R. 2009. Prey-induced changes to a predator's behaviour and morphology: implications for shell-claw covariance in the northwest Atlantic. *Journal of Experimental Marine Biology and Ecology* 382: 1–7
- Eggleston, D.B., Lipcius, R.N., and Hines, A.H. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Marine Ecology Progress Series* 85: 55–68.
- Elner, R. W. 1978. The mechanisms of predation by the shore crab, *Carcinus maenas* (L) on the edible mussel, *Mytilus edulis* (L). *Oecologia* 36: 333–344.
- Enoch, I.C. and Hockensmith, G. 2008. Effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora damicornis*. In: *Proceedings of the 11th International Coral Reef Symposium*, 1368–1372. Ft. Lauderdale, Florida.
- Escofet, A., Orensanz, J.M., Olivier, S.R., and Scarabino, V. 1978. Bionología bentónica del Golfo San Matías (Río Negro, Argentina): metodología, experiencias y resultados del estudio ecológico de un gran espacio geográfico en América Latina. *Anales del Centro de Ciencias del Mar y Limnología* 5: 59–81.
- Feruglio, E. 1950. *Descripción Geológica de La Patagonia, Vol. 3*. 431 pp. Dirección General de Y.P.F., Buenos Aires.
- Fürsich, F.T. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia* 11: 243–250.
- Gordillo, S. 1994. Perforaciones en bivalvos subfósiles y actuales del Canal Beagle, Tierra del Fuego. *Ameghiniana* 31: 177–185.
- Gordillo, S. 1998. Trophic gastropod predation on recent bivalves from the Magellanic Region. In: P.A. Johnston and J.W. Haggart (eds.), *Bivalves: an Eon of Evolution. Paleobiological Studies Honoring Norman N. Newell*, 251–254. University of Calgary Press, Calgary.
- Gordillo, S. and Archuby, F. 2012. Predation by drilling gastropods and asteroids upon mussels in rocky shallow shores of southernmost South America: paleontological implications. *Acta Palaeontologica Polonica* 57: 633–646.
- Gordillo, S., Rabassa, J., and Coronato, A. 2008. Paleogeography and paleobiogeographic patterns of mid-Holocene mollusks from the Beagle Channel (southern Tierra del Fuego, Argentina). *Revista Geológica de Chile* 35 (2): 1–13.
- Griffin, M. and Pastorino, G. 2005. The Genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) in the Tertiary of Patagonia. *Journal of Paleontology* 79: 296–311.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaentologia Electronica* 4 (1): 1–9.
- Harper, E.M., Forsythe, G.T.W., and Palmer, T. 1998. Taphonomy and the Mesozoic Marine Revolution: preservation state masks the importance of boring predators. *Palaaios* 13: 352–360.
- Hidalgo, F., Baron, P.J., and Orensanz, J.M. 2005. A prediction come true: the green crab invades the Patagonian coast. *Biological Invasions* 7: 547–552.
- Hidalgo, F.J., Silliman, B.R., Bazterrica, M.C., and Bertness, M.D. 2007. Predation on the rocky shores of Patagonia, Argentina. *Estuaries and Coasts* 30: 886–894.
- Huntley, J.W. and Kowalewski, M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *PNAS* 104: 15006–15010.
- Isla, F.I. and Bujalesky, G.G. 2008. Coastal geology and morphology of Patagonia and the Fuegian Archipelago. In: J. Rabassa (ed.), *The Late Cenozoic of Patagonia and Tierra del Fuego. Quaternary Book Series*, 227–239. Elsevier, Amsterdam.
- Kabat, A.R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32: 155–193.
- Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaentologia Polonica* 62: 3–183.
- Kelley, P.H., Kowalewski, M., and Hansen, T.A. 2003. *Predator-Prey Interactions in the Fossil Record*. 464 pp. Kluwer Academic/Plenum Publishers, New York.
- Kelley, P.H. and Hansen, T.A. 2003. The fossil record of drilling predation on bivalves and gastropods. In: P.H. Kelley, M. Kowalewski, and T.A. Hansen (eds.), *Predator-Prey Interactions in the Fossil Record*, 113–139. Kluwer Academic/Plenum Publishers, New York.
- Key, H.M. 2003. *Temporal and Spatial Trends in Drilling Predation on Crepidula in the U.S. Coastal Plain*. 122 pp. Unpublished M.Sc. thesis, University of North Carolina, Wilmington.
- Kidwell, S. 2002. Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance. *Geology* 30: 803–806.
- Kidwell, S. and Behrensmeier, A.K. 1988. Overview: Ecological and evolutionary implications of taphonomic processes. *Palaeoecology, Palaeoclimatology, Palaeoecology* 63: 1–14
- Kidwell, S. and Jablonski, D. 1983. Taphonomic feedback: ecological consequences of shell accumulation. In: M.J.S. Tevesz and P.L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, 195–248. Plenum Press, New York.
- Kitchell, J.A., Boggs, C.H., Kitchell, J.F., and Rice, J.A. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology* 7: 533–552.
- Kondo, Y. 1987. Burrowing depth of infaunal bivalve—Observation of living species and its relation to shell morphology. *Transactions and Proceedings of the Palaeontological Society of Japan, N.S.* 148: 306–323.
- Kowalewski, M. 2002. The fossil record of predation: an overview of analytical methods. *Paleontological Society Papers* 8: 3–42.
- Kowalewski, M. 2004. Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): palaeobiological and ecological implications. *Journal of Molluscan Studies* 70: 359–370.
- Lardies, M.A., Clasing, E., Navarro, J.M., and Stead, R.A. 2001. Effects of environmental variables on burial depth of two infaunal bivalves inhabiting a tidal flat in southern Chile. *Journal of the Marine Biological Association of the United Kingdom* 81: 809–816.
- Lescinsky, H.L. 2001. Epibionts. In: D.E. Briggs and P.R. Crowther (eds.), *Palaebiology II*, 460–464. Blackwell Science Ltd., Malden, MA.
- Marko, P.B. and Palmer, A.R. 1991. Responses of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: Avoidance and attraction. *Biological Bulletin* 181: 363–370.
- McGee, B.L. and Targett, N.M. 1989. Larval and habitat selection in *Crepidula* (L.) and its effect on adult distribution patterns. *Journal of Experimental Marine Biology and Ecology* 131: 195–214
- Olabarria, C. 2000. Epibiont molluscs on neogastropod shells from sandy bottoms in the Pacific coast of Mexico. *Journal of Marine Biology Association of the United Kingdom* 80: 291–298.

- Paine, R.T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* 49: 667–685.
- Pérez, D., del Río, C.J., and Nielsen, S. 2013. Sistemática y filogenia del género *Ameghinomya* Ihering, 1907 (Bivalvia: Chioninae) del Cenozoico de Argentina y Chile. *Ameghiniana* 50: 354–374.
- Piriz, M.L. and Casas, G. 1996. *Macroalgas de interés comercial en las costas del sur de Chubut y norte de Santa Cruz. Informe Técnico N 26 del Plan de Manejo Integrado de la Zona Costera Patagónica*. 36 pp. GEF/PNUD/WCS/FPN CENPAT, CONICET, Puerto Madryn.
- Ponce, J.F., Rabassa, J., Coronato, A., and Borromei, A.M. 2011. Palaeogeographical evolution of the Atlantic coast of Pampa and Patagonia from the last glacial maximum to the Middle Holocene. *Biological Journal of the Linnean Society* 103: 363–379.
- Preston, S.J., Revie, I.C., Orr, J.F., and Roberts, D. 1996. A comparison of the strengths of gastropod shells with forces generated by potential crab predators. *Journal of Zoology, London* 238: 181–193.
- Rabassa, J. 2008. Late Cenozoic glaciations of Patagonia and Tierra del Fuego. In: J. Rabassa (ed.), Late Cenozoic of Patagonia and Tierra del Fuego. *Developments in Quaternary Science* 11: 151–204.
- Reid, D. and Osorio, C. 2000. The shallow-water marine mollusca of the Estero Elefantes and Laguna San Rafael, southern Chile. *Bulletin of the Natural History Museum of London, Zoology* 66: 109–146.
- Ríos, E. 1994. *Seashells of Brazil*. Second edition. 492 pp. Museu Oceanográfico da Fundação Universidade do Rio Grande, Rio Grande.
- Rosen, E., Schwarz, B., and Palmera, A.R. 2009. Smelling the difference: hermit crab responses to predatory and nonpredatory crabs. *Animal Behaviour* 78: 691–695.
- Sawyer, J.A. and Zuschin, M. 2010. Intensities of drilling predation from molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeography, Palaeoclimatology, Palaeoecology* 285: 152–173.
- Schellmann, G. 1998. Jungkänozoische Landschaftsgeschichte Patagoniens (Argentinien). Andine Vorlandvergletscherungen, Talentwicklung und marine Terrassen. *Essener Geographische Arbeiten* 29: 1–216.
- Shimoyama, S. and Fujisaka, H. 1992. A new interpretation of the left-right phenomenon during spatial diffusion and transport of bivalve shells. *The Journal of Geology* 100: 291–304.
- Stafford, E.S. and Leighton, L.R. 2011. Vermeij crushing analysis: A new old technique for estimating crushing predation in gastropod assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 305: 123–137.
- Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *The Geological Society of America Memoir* 125: 1–296.
- Stanley, S.M. 1975. Why clams have the shape they have: an experimental analysis of burrowing bivalves. *Paleobiology* 1: 48–58.
- Taylor, J.D. and Morton, B. 1996. The diets of predatory gastropods in the Cape d'Aguilar Marine Reserve, Hong Kong. *Asian Marine Biology* 13: 141–166.
- Taylor, P.D. and Wilson, M.A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth Science Reviews* 62: 1–103.
- Thórarinsdóttir, G.G., Gunnarsson, K., and Bogason, E. 2009. Mass mortality of ocean quahog, *Arctica islandica*, on hard substratum in Lonafjörður, north-eastern Iceland after a storm. *Marine Biodiversity Records* 2: 1–3.
- Tull, D.S. and Böhning-Gaese, K. 1993. Patterns of drilling predation on gastropods of the family Turritellidae in the Gulf of California. *Paleobiology* 19: 476–486.
- Urban, H.J. and Tesch, C. 1996. Aspects of the population dynamics of six bivalve species from southern Chile. *Archive of Fishery and Marine Research* 44: 243–256.
- Verdinelli, M.A. and Schuldt, M. 1976. Consideraciones preliminares sobre aspectos de la dinámica poblacional y reproducción de la almeja rayada *Ameghinomya antiqua* (King, 1831) (Chionidae) en Punta Loma, Golfo Nuevo-Chubut. *Revista del Museo de La Plata* 12: 183–202.
- Vermeij, G.J. 1982. Unsuccessful predation and evolution. *American Naturalist* 120: 701–720.
- Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life*. 527 pp. Princeton University Press, Princeton.
- Vinuesa, J.H. 2005. Distribución de crustáceos decápodos y estomatópodos del golfo San Jorge, Argentina. *Revista de Biología Marina y Oceanografía* 40: 7–21.
- Vinuesa, J.H. 2007. Molt and reproduction of the European green crab *Carcinus maenas* (Decapoda: Portunidae) in Patagonia, Argentina. *Revista de Biología Tropical* 55 (Supplement 1): 49–54.
- Walker, S.E. and Brett, C.E. 2002. Post-Paleozoic patterns of marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontological Society Papers* 8: 119–193.
- Zaixso, H.E. 1996. Distribución y abundancia de bivalvos de fondos blandos submareales del golfo San José y sur del golfo San Matías (Chubut, Argentina). *Medio Ambiente (Chile)* 13 97–113.
- Zar, J. 1999. *Biostatistical Analysis. 4th Ed.* 633 pp. Prentice Hall, New Jersey.