

# Predation by drilling gastropods and asteroids upon mussels in rocky shallow shores of southernmost South America: Paleontological implications

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To achieve a better understanding of predation pattern recorded in the fossil record it is essential to study predator-prey interactions in the modern seas. It includes the data collected from the field observations as well as from the experiments in captivity. Such an approach allows recognition of the bioeroders, its description and also provides quantification of these interactions. This work offers a case study of the traces of predation resulting from the predator-prey interactions between three mussels: *Mytilus chilensis*, *Brachidontes purpuratus*, and *Aulacomya atra*; and their five natural enemies: the gastropods *Trophon geversianus*, *Xymenopsis muriciformis*, and *Acanthina monodon*, and the asteroids *Cosmasterias lurida* and *Anasterias antarctica* living along the intertidal and/or subtidal rocky shores in Tierra del Fuego. The predatory damage to mussel shells varies according to the predator and prey species and techniques for attacking prey are highly specialized. *A. monodon* drills a hole in *B. purpuratus* but uses the outer lip of its shell as a wedge to open the valves of *M. chilensis* and *A. atra*. *T. geversianus* always makes holes, but while it drills the valve walls of *M. chilensis*, it prefers to drill the valve edges of *A. atra* and *B. purpuratus*, with different characteristic patterns. Usually the shells of mussels killed by *C. lurida* do not suffer from any mechanical damage, but some other shells were crushed or fractured along the margins. Comparatively, time required to successfully attack a prey was shorter in *C. lurida* (24 hours), followed by *A. monodon* (36 hours), and longer in *T. geversianus* (9 to 10 days). Traces of predation are not randomly distributed across size classes of mussel prey, reflecting selectivity for a particular size class. Also, drill holes are usually placed at specific sectors of the shell, indicating site selectivity. These observations offer some paleontological implications for investigating the pattern of predation in fossil record. They show that different patterns of shell damage can be due to different predator species (e.g., wall vs. edge drillings), although the same predator species can leave different marks when consuming different prey (e.g., *T. geversianus*). Most disconcerting for paleontologists are cases of predation which do not leave any marks on the prey shell detectable in the fossil record (e.g., predation by asteroids), or leave ambiguous marks (*A. monodon* when preying with the spine). In conclusion, besides the opportunity to identify some traces of predation by drilling gastropods in fossil mussels, this work gives criteria to address predation in some particular paleontological cases that would otherwise be dismissed by researchers.

Key words: Bivalvia, Gastropoda, Asteroidea, predation, prey selection, taphonomy, Tierra del Fuego, Argentina.

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## Introduction

This study focuses on predator-prey interactions between the mussels *Mytilus chilensis*, *Brachidontes purpuratus*, and *Aulacomya atra*, and their natural enemies, the gastropods *Trophon geversianus*, *Xymenopsis muriciformis*, and *Acanthina monodon*, and the asteroids *Cosmasterias lurida* and *Anasterias antarctica*. Using these organisms as a model system, this study combines experimental data with field observations and sampling to identify traces of predation. Our goal

is to recognize the bioeroders and describe and quantify predation patterns, to achieve a better understanding of the biotic interactions between these predators and the three mussel prey.

Mussel beds in shallow waters are present in both the northern and southern hemispheres and, as they are commercially important as part of bivalve cultures, their invertebrate predators, mainly gastropods, asteroids and crabs, have attracted the attention of numerous investigators in different parts of the world (e.g., Griffiths 1981; O'Neill et al. 1983;

Wickens and Griffiths 1985; MacKinnon et al. 1993; Dolmer 1998; Leonard et al. 1999; Urrutia and Navarro 2001; Soto et al. 2004). In addition, adequate recognition of shell damage types is even more important for paleontologists who cannot make direct observations of predation but encounter shells in the fossil record that have experienced predation (Kowalewski et al. 1997; Kowalewski 2002; Kelley et al. 2003).

In this regard, the goal of this paper is to describe recent advances in the study of this kind of predation in Tierra del Fuego, in the hope that this information may be useful as a basis for further studies on the functional morphology and biotic interactions of bivalve mussels in both Recent and fossil examples.

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

*Other abbreviations.*—H, statistic value of the Kruskal-Wallis test; n, number of individuals; p, the probability value of a statistical test; r, correlation coefficient; Z, approximation value of the Mann-Whitney U-test.

## Geographical and ecological setting

Tierra del Fuego (Fig. 1) is a large archipelago located in the southernmost part of South America, consisting of Isla Grande, the main island, and a great number of smaller islands, including Isla Hoste, Isla Navarino, and Isla de los Estados. It is separated from the South American continent and the South Chilean Archipelago by the Strait of Magellan, while the Beagle Channel separates Isla Grande from Isla Navarino.

The northern Beagle Channel coast exhibits a rugged rocky shoreline where pocket gravel beaches develop in the embayments, and which is subjected to a microtidal regime (1.1 m at Ushuaia). Tides in this region correspond to the unequal semi-diurnal regime with alternating small and large tidal cycles.

The Atlantic coast of Isla Grande is characterized by extensive and wide beaches composed of gravel and coarse sand. This coast line has a macrotidal regime (4.6 m at Cabo San Pablo), and is exposed to high energy Atlantic waves and intense westerly winds.

In Tierra del Fuego, the blue mussel *Mytilus chilensis* Hupé, 1854 is the most abundant species along the rocky and gravelly shores. Another mytilid, the small purple mussel *Brachidontes purpuratus* (Lamarck, 1819) is common in the midshore region, and a third species, the ribbed mussel *Aulacomya atra* (Molina, 1782), is also present but in low abundance (Zaixso et al. 1978; Ingólfsson 2005). At the intertidal-upper subtidal fringe, their predator species are the gastropods *Acanthina monodon* (Pallas, 1774), *Trophon geversianus* (Pallas, 1774), *Xymenopsis muriciformis* (King,

1832) and the asteroid *Anasterias antarctica* (Lütken, 1857) (Ojeda and Santelices 1984; Ingólfsson 2005). Another asteroid, the seastar *Cosmasterias lurida* (Philippi, 1858) inhabits subtidal benthonic marine communities (Castilla 1985; Mutschke and Ríos 2006), but is also observed in the lower intertidal, during the lowest half-monthly low-tides.

## Historical background

**Drilling predation.**—Drilling is a specialized form of predation in which a hole is made either through the shell wall or, in some bivalve prey, at the edge of the valve. Predation by muricaceans is well-known owing to the abundance of these carnivores in shallow seas, where they prey on epifaunal species such as barnacles and bivalves. Muricid gastropods use an accessory boring organ (Carriker 1981), which secretes an enzyme (carbonic anhydrase) that softens the shell, in conjunction with their tongue-like radula, to excavate a slightly cylindrical hole, through which the predator's proboscis is inserted (Vermeij 1993). Ausich and Gurrola (1979) found cylindrical boreholes in Mississippian brachiopods which resemble those made by drilling gastropods, but the earliest report of a muricoid is recorded from the Early Cretaceous (Kaim 2004). Previous studies on shell-drilling gastropods in Tierra del Fuego show that *Trophon geversianus* and *Xymenopsis muriciformis* excavate cylindrical or tronco-conical drill-holes, perpendicular to the shell surface of their prey (Gordillo 1998; Gordillo and Amuchástegui 1998). A third drilling gastropod, the whelk *Acanthina monodon*, can use the downwardly projecting spine on the outer lip alternatively as a wedge or a chisel to open mussels and barnacles (Gordillo 2001). Boreholes in fossil shells attributable to drilling gastropods have also been described for Holocene marine deposits along the Beagle Channel (Gordillo 1994).

**Predation by sea-stars.**—A close relationship between asteroids and bivalves is well established in the Recent fauna, and it is far too striking to be coincidental that a similar relationship occurs in many early fossil faunas (Carter 1968). It is known that asteroids, as potential predators in marine ecosystems, appeared during the Ordovician. They have occurred and been observed in the fossil record in apparent feeding position on a bivalve (Blake and Guensburg 1994), a characteristic behavior related to extraoral digestion, and with their stomachs distended with small gastropod prey (Spencer and Wright 1966).

Sea-stars are particularly common in the littoral zone where they feed on most available slowly moving and sessile animals. They search for prey by moving slowly over the surface of the substrate, using their tube feet. Among the asteroids, two broad types of feeding behavior may be distinguished: the extraoral and the intraoral feeding, but neither type inflicts consistent morphological damage on the prey animal (Carter 1968). In Tierra del Fuego, the sea-star *Cosmasterias lurida*, which inhabits coastal belts of giant kelp

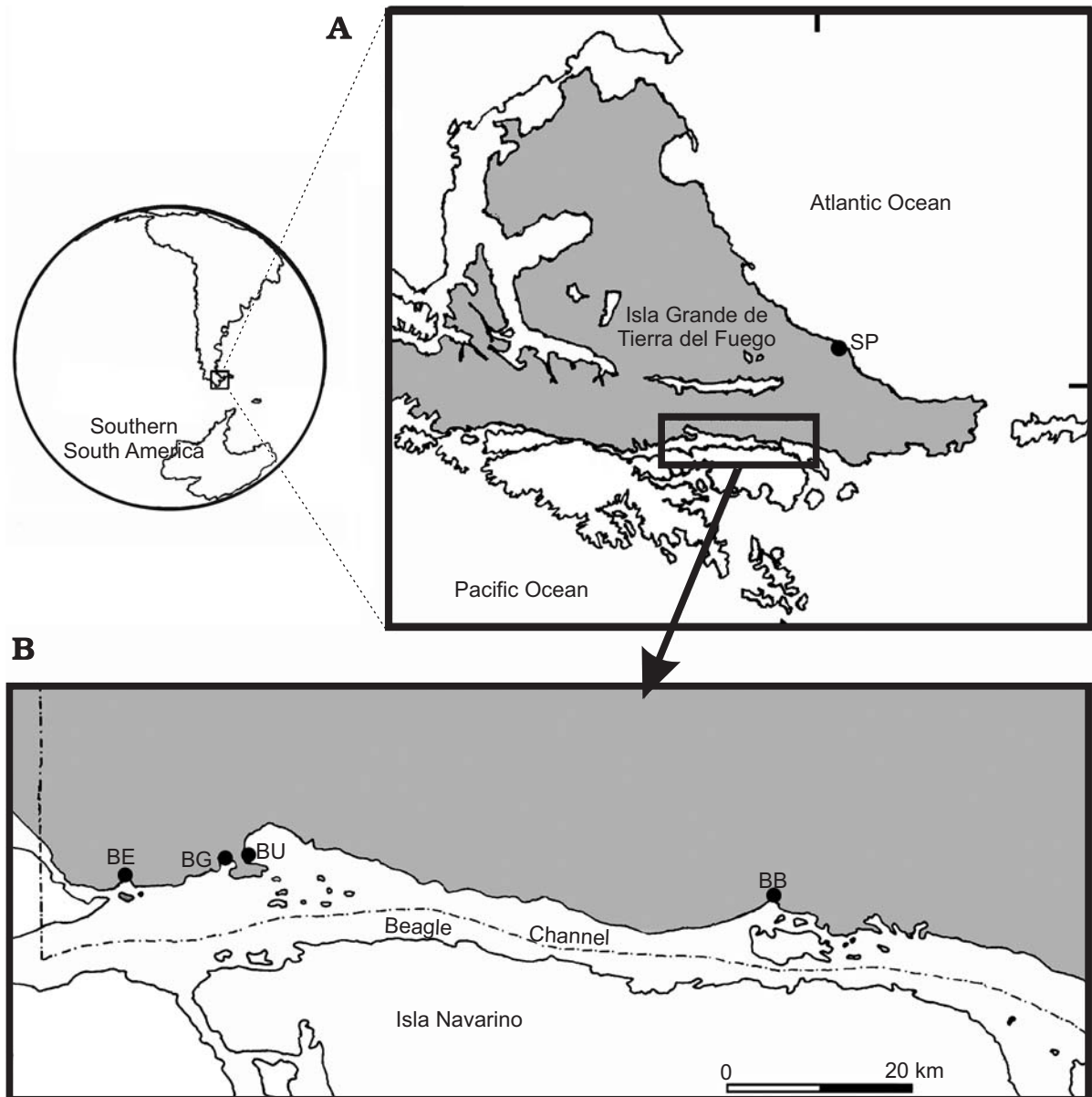


Fig. 1. Map showing sampling sites in Tierra del Fuego. **A.** Isla Grande de Tierra del Fuego. **B.** A sector of the Beagle Channel showing localities on the southern part of the island. Abbreviations: BB, Bahía Brown; BE, Bahía Ensenada; BG, Bahía Golondrina; BU, Bahía Ushuaia; SP, Cabo San Pablo.

*Macrocystis pyrifera* along the Beagle Channel, preys on different prey according to their local abundances (Castilla 1985). Both species included in this study (*Cosmasterias lurida* and *Anasterias antarctica*) capture prey using their tube feet and arms, and assume a humped feeding position to digest the prey extraorally.

## Material and methods

**Sampling of shell accumulations.**—Time-averaged shell assemblages occurring along two beaches, Bahía Golondrina and Bahía Brown (Fig. 1), were sampled and examined to evaluate frequency of drilling predation, and site and size se-

lectivity. These accumulations are time-averaged assemblages because remains of mollusks (shells) from different time intervals (in this case on the scale of years) co-occur in a single assemblage (Walker and Bambach 1971; Meldahl et al. 1997). They were sampled using a  $0.5 \times 0.5$  m square (a quadrat). All shells in the quadrats (36 quadrats in Bahía Golondrina, 21 quadrats in Bahía Brown) were collected for identification, counting, and further analysis in the laboratory.

**Experiments under laboratory conditions.**—Laboratory experiments were conducted with the aim of studying different aspects of the predation-prey interactions and the resultant traces left in the shells. For that purpose, *T. geversianus* and *A. monodon* individuals were fed with *M. chilensis*, while *C. lurida* individuals were provided with *M. chilensis*

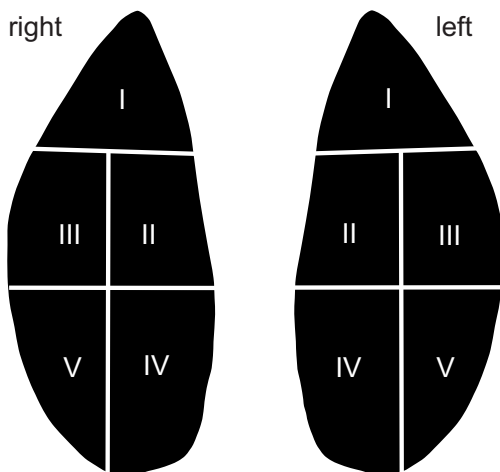


Fig. 2. Scheme of the surface of a mussel shell indicating 5 (I, II, III, IV and V) sectors used for the drill site preference analyses.

and *A. atra*. Both mussels and their predators were collected from the rocky intertidal/subtidal of Bahía Golondrina, Beagle Channel. This study was conducted at the Centro Austral de Investigaciones Científicas (CADIC, Ushuaia, Argentina) as part of a series of experiments.

Prey items, separated into three non-overlapping size classes of mussels according to their maximum shell length (small, medium, large), were used in the gastropod and sea-star experiments. In each experiment with mussels, 6 predators (12 with a replicate) were used and all size of prey was presented simultaneously to determine prey choice.

*Mytilus* size-categories were established in the following way: small, less than 30 mm; medium, between 30 and 50 mm, and large, more than 50 mm (normally less than 70 mm). *Aulacomya* size-categories were: small, less than 35 mm; medium, between 35 and 55 mm and large, between 55 and 75 mm. The amount of specimens was established following the criterion of offering equal weights (100 g) of every size class. Thus, there were more small individuals than medium and large ones and more medium individuals than large ones. Each predator (*T. geversianus*, *A. monodon*, and *C. lurida*) was housed in a 19-liter glass aquarium, divided by a transversal glass wall to provide two compartments for replicates. The tanks were kept in a cold room at 2–9°C.

Predation was monitored once a day during eight months. Mussels were replaced as soon as they were consumed. A second larger tank was used to keep the mussels used to replace preyed specimens.

To estimate the weight of mussels eaten in aquarium experiments, a correlation was calculated between their length and wet weight using previously collected living mussels of different sizes.

In other aquaria we offered mussel specimens to the gastropod and asteroid predators to observe quantitative patterns of attack and marks of predation. These experiments involved the pairs *T. geversianus*–*A. atra*, *T. geversianus*–*B. purpuratus*, *A. monodon*–*A. atra*, *A. monodon*–*B. purpuratus*, *X. muri-*

*ciformis*–*M. chilensis*, *X. muriciformis*–*A. atra*, *C. lurida*–*B. purpuratus*, and *A. antarctica*–*M. chilensis*.

**Predation intensity.**—Predation intensity was firstly assessed on the basis of evaluation of the number of prey items consumed per time unit under experimental conditions. Secondly, it was estimated from the frequency of drilled specimens found in beach shell accumulations. It was calculated as the number of valves (right+left) in the sample that contained at least one complete drillhole divided by 0.5 times the number of valves in the sample. Uncomplete drillholes were calculated separately since that they record failed predatory attacks.

**Analysis of selectivity.**—Empty mussel shells from experiments and beaches were examined to record selectivity for one of the valves (i.e., right versus left) and the position of drill holes on the shell surface of the prey. Right or left valve preference was evaluated using the Fisher's Exact test (Zar 1999). To evaluate the preference for particular sites on each valve, we divided the prey shell into five sectors as shown in Fig. 2. The resulting distribution of observed holes per sector was evaluated statistically using Chi-square goodness of fit test (Zar 1999). Expected frequencies were calculated as the proportion of the total number of specimens utilized in the analysis that is equivalent to the proportion of that sector in relation to the total surface. The null hypothesis was that the predator would not select the site of drilling and, hence, every place in the valve had the same probability of being attacked.

To evaluate size selectivity in transported shells we compared the size-frequency distribution of drilled specimens of a given prey against the size-frequency distribution of undrilled specimens of that prey in the same locality. The statistical difference was evaluated using Mann-Whitney U-test with Z approximation (Zar 1999). For this purpose similar amounts of drilled and undrilled shells were measured from two localities, Bahía Brown and Bahía Golondrina.

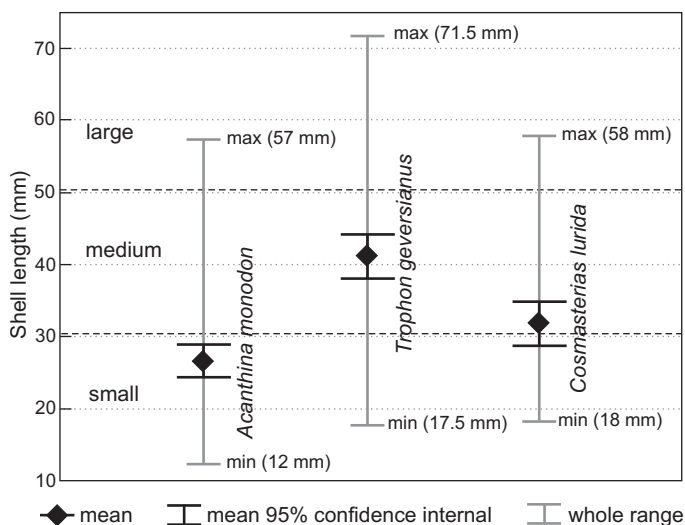


Fig. 3. Means with confidence limits of shell lengths of *Mytilus chilensis* Hupé, 1854 consumed by the three different predators included in aquarium experiments. Dashed lines separate size categories.



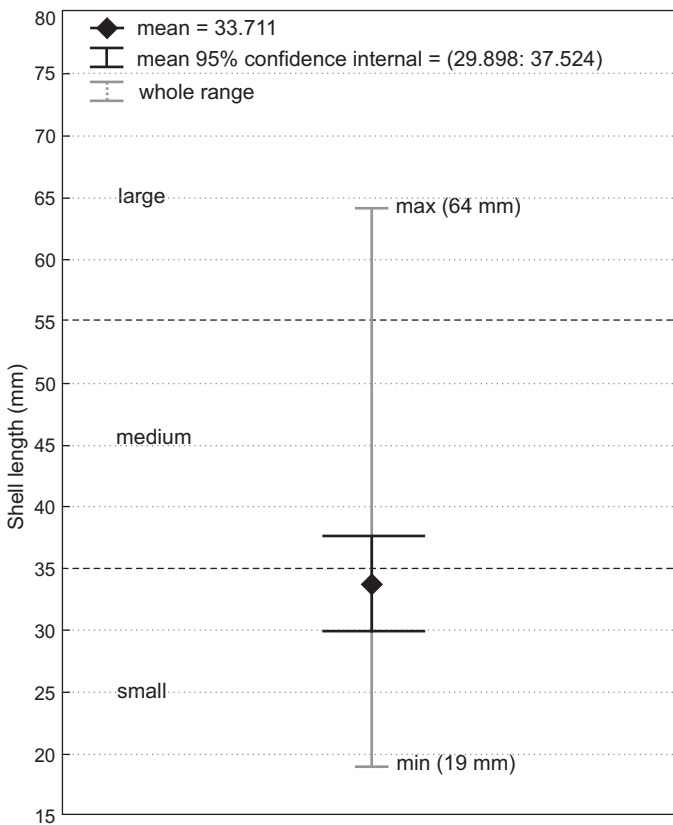


Fig. 4. Means with confidence limits of shell lengths of *Aulacomya atra* (Molina, 1782) consumed by *Cosmasterias lurida* (Philippi, 1858) in aquarium experiments. Dashed lines separate size categories.

Means and confidence intervals (95%) of prey size from aquarium experiments were plotted together with their maximum and minimum values in a chart that incorporates the three size categories. Size preferences of *M. chilensis* prey consumed by the three predators, as resulted from aquarium information, were compared using a non-parametric Kruskal-Wallis ANOVA. Post hoc tests were performed using Bonferroni corrected Mann-Whitney U-Test.

Statistical tests were performed with the software PAST 2.02 (Hammer et al. 2001). Null hypotheses with p-values lower than 0.05 were rejected.

**Field quantification of living taxa.**—Predator abundance in the intertidal mussel beds was estimated by counting all specimens included in five 100 × 100 cm quadrats at different months during a period of 18 months. Three localities were sampled (Fig. 1): a sheltered bay (Bahía Ushuaia) and a more exposed site (Bahía Golondrina) on the Beagle Channel, and a second exposed site (Cabo San Pablo) on the Atlantic coast. All living predators within each quadrat were identified and counted in the field, and their activity was recorded as feeding or not feeding.

Because *T. geversianus* inhabits the lower intertidal zones, we were unable to record the population density for this species in winter, as during winter months this area is not exposed during low tides in the daytime. For that reason, during winter

months (May and July) data were recorded at night with the help of a flashlight.

## Results

After 8 months of quantitative experiments in laboratory we observed that 12 *T. geversianus* snails ate a total of 85 *M. chilensis* prey specimens. Other 12 *T. geversianus* snails ate 77 *A. atra*. Three *A. monodon* ate 20 *B. purpuratus* prey and other 6 *A. monodon* snails ate 88 *M. chilensis* prey. A total of 86 mussels (42 *M. chilensis*, 44 *A. atra*) were preyed on by one specimen of *C. lurida*. The 3 specimens of *A. antarctica* collected for experiments did not eat and died after two months, so the corresponding test could not be performed.

In addition, qualitative data were recorded for other species of mussels that were eaten by drilling gastropods and asteroids both in laboratory experiments and in the field (Table 1). Table 2 lists other taxa that were also found as bored shells, either on the beach (Recent) or in Holocene (fossil) deposits along the Beagle Channel.

Table 1. Predator/prey records of other species based on field observations and/or laboratory experiments.

Predators	Other prey in situ and/or lab
<b>Gastropods</b>	
<i>Trophon geversianus</i>	<i>Tawera gayi</i> and cirripedes in Bahía Ensenada <i>Tawera gayi</i> in lab <i>Hiatella</i> sp. in lab
<i>Xymenopsis muriciformis</i>	<i>Tawera gayi</i> in lab <i>Hiatella</i> sp. in lab
<i>Acanthina monodon</i>	cirripedes in lab and in Bahía Golondrina
<b>Asteroids</b>	
<i>Cosmasterias lurida</i>	Chitons at Isla Redonda, in front of Bahía Ensenada
<i>Anasterias antarctica</i>	<i>Trophon geversianus</i> , chitons, and sea-urchins in Bahía Golondrina

Table 2. List of taxa with bored shells collected along the Beagle Channel.

Recent shells	Fossil shells ca. 4500–4000 years B.P.
<i>Mytilus chilensis</i> (Mytilidae)	<i>Mytilus chilensis</i> (Mytilidae)
<i>Brachidontes purpuratus</i> (Mytilidae)	<i>Venus antiqua</i> (Veneridae)
<i>Aulacomya atra</i> (Mytilidae)	<i>Tawera gayi</i> (Veneridae)
<i>Mulinia edulis</i> (Veneridae)	<i>Hiatella</i> sp. (Saxicavidae)
<i>Retrotapes exalbidus</i> (Veneridae)	<i>Pareuthria plumbea</i> (Buccinidae)
<i>Venus antiqua</i> (Veneridae)	<i>Trophon geversianus</i> (Muricidae)
<i>Tawera gayi</i> (Veneridae)	
<i>Hiatella</i> sp. (Saxicavidae)	
<i>Nacella deaurata</i> (Nacellidae)	
<i>Crepidula dilatata</i> (Calyptraeidae)	
<i>Pareuthria plumbea</i> (Buccinidae)	
<i>Trophon geversianus</i> (Muricidae)	
<i>Xymenopsis muriciformis</i> (Muricidae)	

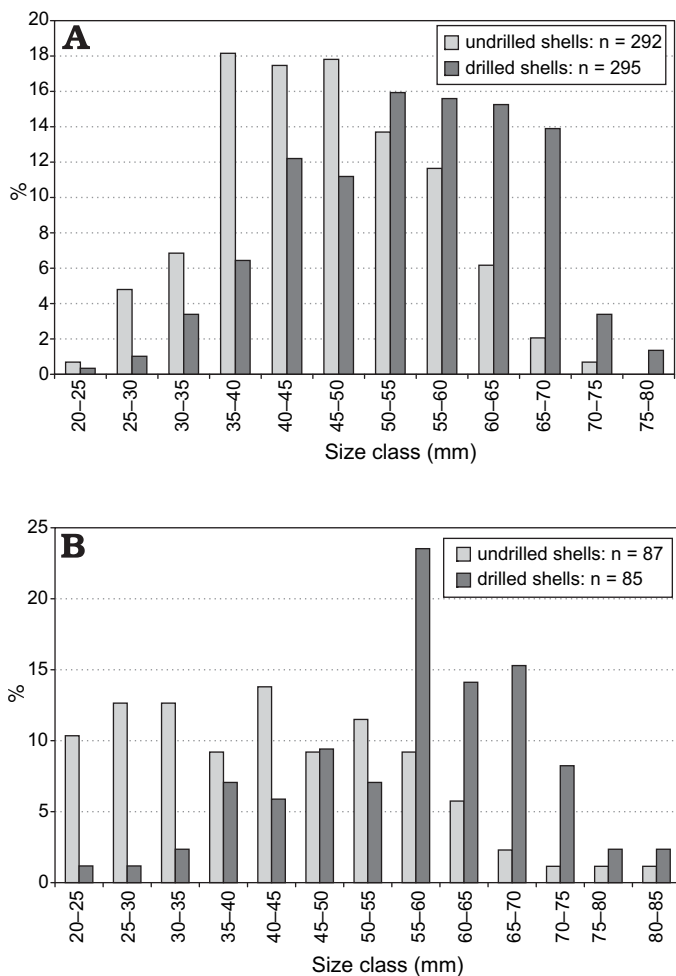


Fig. 5. Bar chart of size classes for drilled and undrilled shells collected in the field. Y axis is the frequency of each size class. **A.** Bahía Golondrina. **B.** Bahía Brown.

Predation frequencies estimated for Bahía Golondrina were: *M. chilensis*, 16.2%; *A. atra*, 11.7%. In the same locality, shells with incomplete holes on *M. chilensis* reached 1.7%.

**Predation and size.**—The three species preying upon *M. chilensis* differed significantly in the size of prey they consumed (Kruskal-Wallis  $H = 46.945$   $p = 0.000$ ; the three species significantly differed in prey size from each other, *A. monodon*–*C. lurida*,  $p = 0.003$ ; *A. monodon*–*T. geversianus*,  $p = 0.000$ ; *T. geversianus*–*C. lurida*,  $p = 0.001$ ). *A. monodon* selected *M. chilensis* prey of small size, *T. geversianus* preferred medium-sized mussels and *C. lurida* preyed upon medium to small-sized mussels (Fig. 3). *C. lurida* selected

*A. atra* prey of small to medium size (Fig. 4). The regression equations that relate shell length ( $x$ ) and neperian logarithm of weight for *M. chilensis* and *A. atra* for the three size categories are presented in Table 3.

The size of *T. geversianus* did not correlate with *M. chilensis* prey size ( $r = 0.06$ ,  $p > 0.05$ ,  $n = 83$ ). Larger *T. geversianus* consumed larger *A. atra* specimens ( $r = 0.54$ ,  $p < 0.05$ ,  $n = 75$ ). A similar pattern was observed in *A. monodon* consuming *M. chilensis* ( $r = 0.20$ ,  $p < 0.05$ ,  $n = 88$ ), but although significant, the association is weak.

Analysis of dead shells collected in the field indicated that the predators systematically selected larger shells in both sampled localities, Bahía Golondrina ( $Z = 8.656$ ;  $p = 0.000$ ) and Bahía Brown ( $Z = 6.34$ ;  $p = 0.000$ ). These differences are illustrated in Fig. 5 by means of bar charts.

**Site selectivity** (valve accumulations and experiments).—Drill-holes in *M. chilensis* shells collected in Bahía Brown were not located in a particular sector of the shell ( $p = 0.258$ ; Fig. 6A). However, in Bahía Golondrina, drill-site selection was significant ( $p = 0.000$ ; Fig. 6B). In this case, sectors I (anterior) and IV (posterior ventral) had frequency of holes lower than predicted by chance, while sector II (medial ventral) had more holes than expected. For *A. atra* collected from Bahía Brown, in 100% of cases the holes were on the edges, and 79% of them were on the posterior edge of the valve (sectors IV and V). These results have limited relevance, as two drilling gastropods were present in the same community and it is not possible to distinguish the species responsible for the drilling. Aquarium experiments allowed refining these observations. In the case of *T. geversianus* preying upon *M. chilensis*, significant selection in favor of sector III (medial dorsal) was recorded ( $p = 0.000$ ; Fig. 6C). Experiments of *X. muriciformis* consuming *M. chilensis* had a small sample size and did not allow statistical testing (Fig. 6D). In *A. atra* shells preyed upon by *T. geversianus* in aquarium experiments, borings were always located at the edge of the shells.

**Valve selection.**—Out of 295 consumed specimens of *M. chilensis* collected in Bahía Golondrina, 145 were drilled on the left valve while 150 had bores on the right one. There was no valve selection ( $p < 0.771$ ). Analysis of valve selection for *M. chilensis* from Bahía Brown yielded similar results (right valves: 34; left valves: 47;  $p < 0.149$ ).

**In situ field observations.**—From the field observations of feeding activities of *T. geversianus*, this predator's activity can be inferred to increase towards the summer (Fig. 7). The

Table 3. Regression equations relating shell length ( $x$ ) and wet weight in two mussel prey.  $x$  = length (mm);  $y$  = weight (g)

<i>Mytilus chilensis</i>	<i>Aulacomya atra</i>
Specimens between 10–29.9 mm: $\text{Ln } y = 0.139668x - 3.05498$ ; $r = 0.87$ ; $n = 56$	Specimens between 10–34.9 mm: $\text{Ln } y = 0.125102x - 2.64041$ ; $r = 0.94$ ; $n = 10$
Specimens between 30–49.9 mm: $\text{Ln } y = 0.068835x - 0.88935$ ; $r = 0.89$ ; $n = 68$	Specimens between 35–54.9 mm: $\text{Ln } y = 0.077299x - 1.34187$ ; $r = 0.95$ ; $n = 13$
Specimens between 50–69.9 mm: $\text{Ln } y = 0.047723x + 0.30508$ ; $r = 0.93$ ; $n = 40$	Specimens between 55–74.9 mm: $\text{Ln } y = 0.043295x + 0.519718$ ; $r = 0.94$ ; $n = 20$

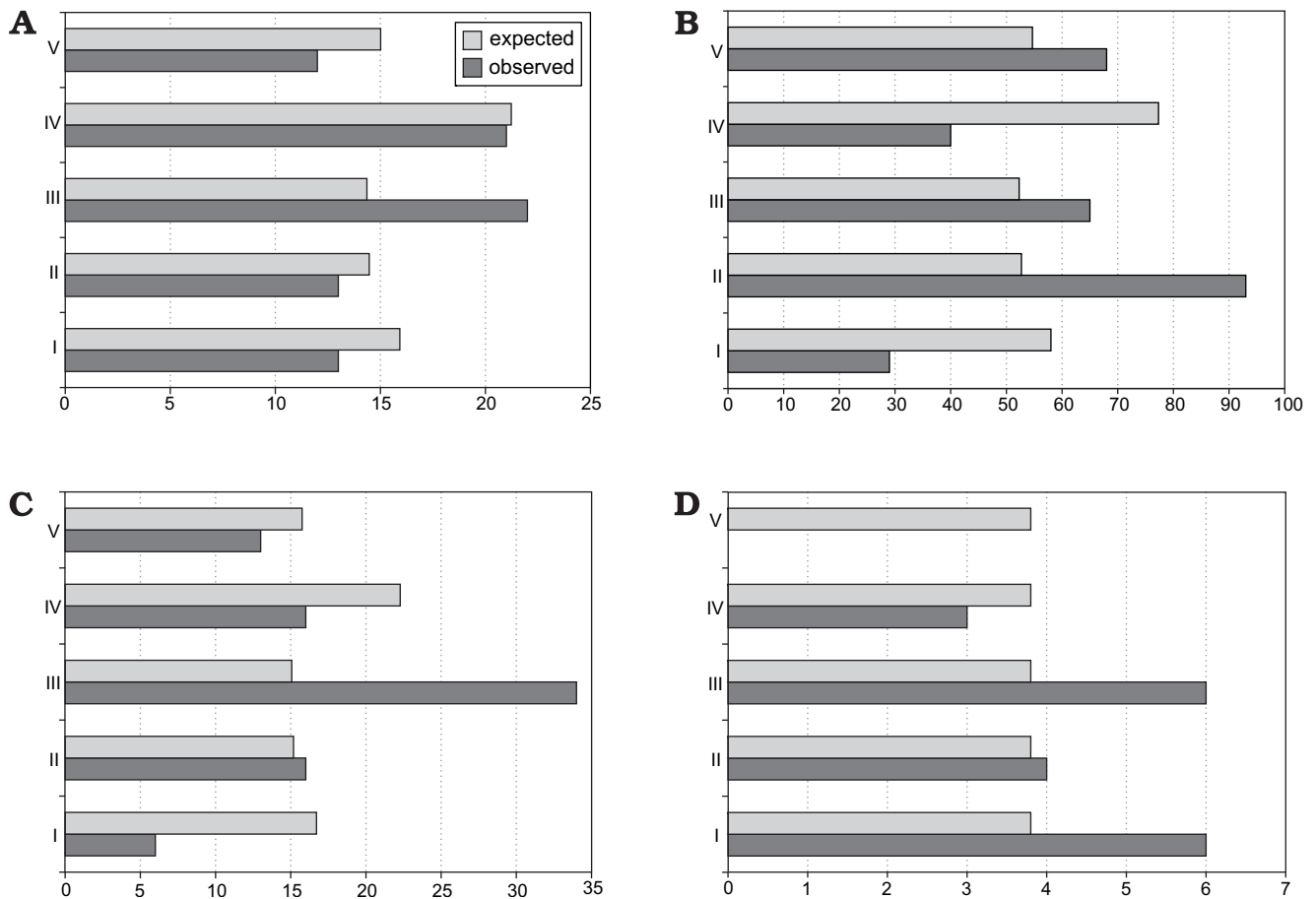


Fig. 6. Position of drill holes on *Mytilus chilensis* Hupé, 1854. Y axis: valve sector; X axis: frequency. **A.** Bahía Brown shell accumulations ( $n = 81$ ). **B.** Bahía Golondrina shell accumulations ( $n = 295$ ). **C.** Produced by *Trophon geversianus* (Pallas, 1774) under aquarium conditions ( $n = 85$ ). **D.** Produced by *Xymenopsis muriciformis* (King, 1832) under aquarium conditions ( $n = 19$ ).

presence of this species was occasionally recorded in May, but there were no specimens in July. Those specimens that occurred in May were never observed eating.

One characteristic of the population distribution of the predator *T. geversianus* with respect to the distribution of the mussel prey, which was observed in all localities, is that specimens of *T. geversianus* were rare in the range where mussels were more abundant (i.e., the middle intertidal zone), but they were common just below (i.e., in the lower intertidal zone), where mussels were few.

Regarding the asteroid predators, only *A. antarctica* was observed along the Atlantic coast and the Beagle Channel preying on the mussels *M. chilensis* and *B. purpuratus*. However, both asteroids were recorded feeding on chitons (Table 1). In addition, *A. antarctica* was found preying on *T. geversianus* and echinoids.

**Traces of predation.**—Different types of damage were caused by predator gastropods (Figs. 8–10). Damage by asteroids is less evident (Fig. 11), but some characteristics are mentioned.

On *M. chilensis*, *T. geversianus* (Fig. 8E) makes a circular hole located in central or subcentral position (Fig. 8A–D). The morphology of this borehole has been described in pre-

vious works (Gordillo 1998; Gordillo and Amuchástegui 1998), and it is characterized by important size differences between the inner and the outer diameters (Fig. 8D). On *B. purpuratus*, *T. geversianus* sometimes made boreholes in the surface of one of the valves (Fig. 8F–H), but the holes were mostly made in marginal position (Fig. 8I, J). On *A. atra*, in all cases, the holes were made on the edges (Fig. 8K, L). Interestingly, although *B. purpuratus* and *A. atra* exhibit boreholes on the edges, their structures are completely different. In *B. purpuratus* the borehole involves both valves (Fig. 8I, J). In *A. atra* the predator only drills one of the valves (right or left), while leaving a spot-like mark on the internal surface of the opposite valve (Fig. 8M).

The second predator, *X. muriciformis* (Fig. 9D), also makes circular holes on *M. chilensis* located in different sites of the shell surface (Fig. 9A–C, E, F). These boreholes, however, display lesser size difference between the inner and outer diameters, thus the holes are closer to a cylindrical shape (Fig. 9F).

The whelk *A. monodon* (Fig. 10G, H) adopts two different strategies depending on the prey, leaving different types of predation damage. In *B. purpuratus*, this predator drills a circular hole located in the central area of the valve (Fig. 10A), while failed attempts leaving incomplete holes are common (Fig. 10B, C). In the other two preys, *M. chilensis*

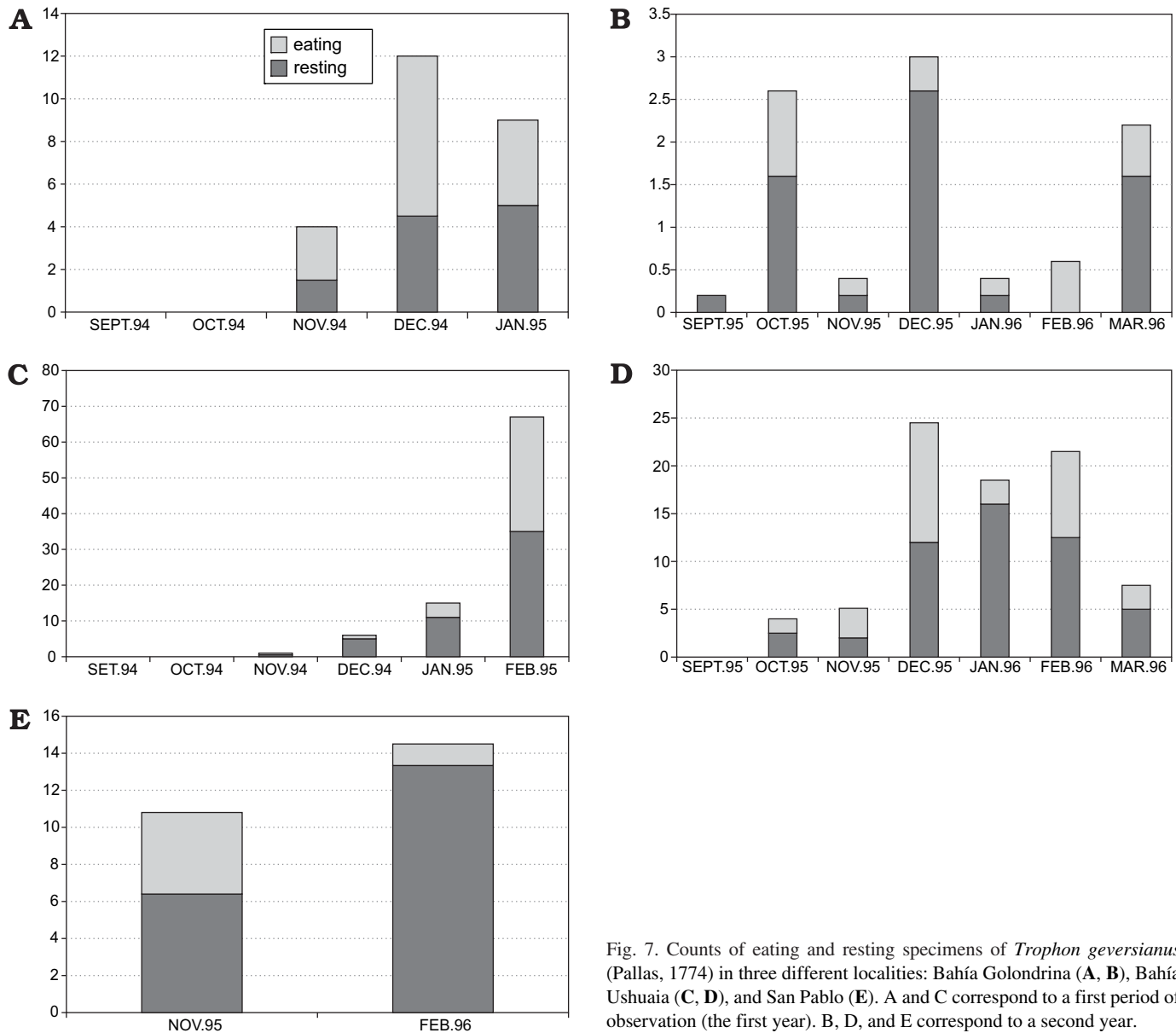


Fig. 7. Counts of eating and resting specimens of *Trophon geversianus* (Pallas, 1774) in three different localities: Bahía Golondrina (A, B), Bahía Ushuaia (C, D), and San Pablo (E). A and C correspond to a first period of observation (the first year). B, D, and E correspond to a second year.

and *A. atra*, this predator uses its long labral spine to apply pressure on the area of contact between the opposite valves. In the relatively fragile shells of *M. chilensis*, this mechanical action produces a characteristic pattern of cracks (chipping or pinching) on the edges (Fig. 10D–F, I–O). However, this action does not break the strong shell of *A. atra* (Fig. 10P–S), leaving a typical mark on the edges (marginal notches) only observable from the internal view (Fig. 10Q, S).

*C. lurida* (Fig. 11I) begins its attack by wrapping the prey with its arms. After the body of the mussel has been successfully consumed, its valves remain joined. Moreover, most of the successful predation was achieved without crushing the valves of the prey. However, after the attack of this predator, the periostracum (conchiolin layer) of the area around the byssus is removed by the action of acids discharged by the predator. No mechanical damage by this predator was detected in most of the shells (Fig. 11A–C, F–H), although some of them were fractured along the margins (Fig. 11D) or

crushed (Fig. 11E) during the attack. The resulting patterns of shell damage are indistinguishable from those caused by physical factors.

#### Time of prey consumption under laboratory conditions.

—*T. geversianus* needed 9.09 days (95% confidence intervals  $\pm 5.2$  days) to finish a successful attack on a *M. chilensis* and 10.03 days (95% confidence intervals  $\pm 6.9$  days) in the case of an *A. atra* specimen. *A. monodon* needed between one and two days to consume a *M. edulis* while *C. lurida* took only one day for the same task.

## Discussion

Drilling predation of mussels by muricid gastropods represents one of the very rare instances when quantitative evaluation of biotic interactions both in the modern seas as well as in



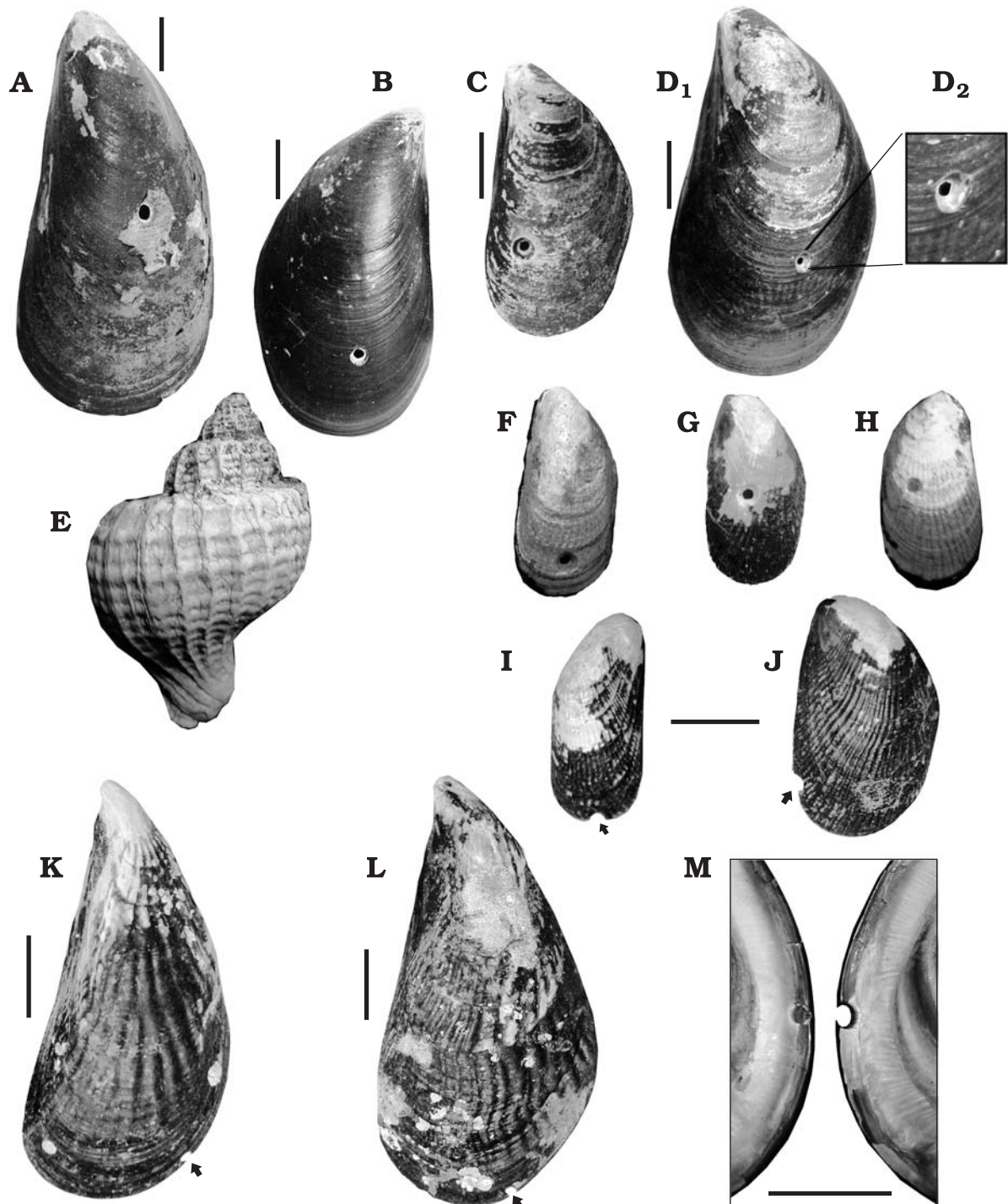


Fig. 8. Predation marks produced by *Trophon geversianus* (Pallas, 1774) in mussels under aquarium conditions. **A–D.** *Mytilus chilensis* Hupé, 1854. **A.** CEGH-UNC 25339, left valve in external view. **B.** CEGH-UNC 25340, right valve in external view. **C.** CEGH-UNC 25341, left valve in external view. **D.** CEGH-UNC 25342, left valve in external view (**D<sub>1</sub>**), detailed (**D<sub>2</sub>**). **E.** *Trophon geversianus* (Pallas, 1774), CEGH-UNC 25343, shell in dorsal view. **F–J.** *Brachidontes purpuratus* (Lamarck, 1819). **F.** CEGH-UNC 25344, left valve in external view. **G.** CEGH-UNC 25345, left valve in external view. **H.** CEGH-UNC 25346, right valve in external view. **I.** CEGH-UNC 25347, right valve in external view. **J.** CEGH-UNC 25348, left valve in external view. **K–M.** *Aulacomya atra* (Molina, 1782). **K.** CEGH-UNC 25349, left valve in external view. **L.** CEGH-UNC 25350, left valve in external view. **M.** detailed sector of marginal area of both valves of specimen CEGH-UNC 25349 in internal view. Arrows indicate marginal drillings. Scale bars 10 mm.

the geological record is possible. Although some researchers have studied drilling predation to much detail (Vermeij 1987; Kelley and Hansen 1993; Kowalewski et al. 1998; Kelley et al.

2003), nevertheless, the patterns of predation are still poorly investigated in the southern hemisphere. In this study we examined different sources of data and provided diagnostic tools

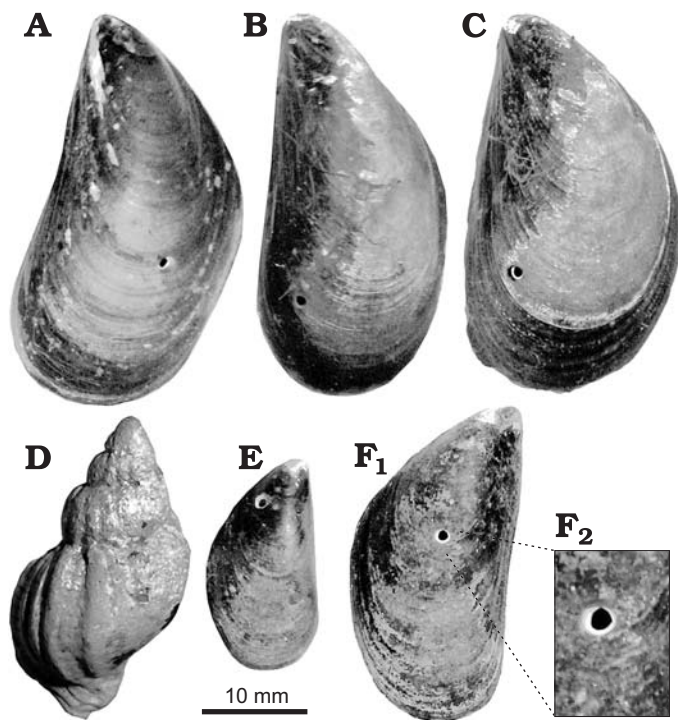


Fig. 9. Predation marks produced by *Xymenopsis muriciformis* (King, 1832) in mussels under aquarium conditions on *Mytilus chilensis* Hupé, 1854. A–C, E, F. *Mytilus chilensis* Hupé, 1854. A. CEGH-UNC 25351, left valve in external view. B. CEGH-UNC 25352, left valve in external view. C. CEGH-UNC 25353, left valve in external view. E. CEGH-UNC 25355, right valve in external view. F. CEGH-UNC 25356, right valve in external view (F<sub>1</sub>), close-up of the drill hole (F<sub>2</sub>). D. *Xymenopsis muriciformis* (King, 1832), CEGH-UNC 25354, shell in dorsal view.

to identify predator/prey relationships between mussels and their enemies.

Gastropod predation leaves a characteristic, easily recognizable pattern on the shell of their prey. The shape and location of the holes and other marks such as marginal chipping or marginal crushing can be used as diagnostic elements. Sea-star predation is less evident on mussel shells. One diagnostic element present on the bivalve shell after sea-star attack is a sector around the byssal area where the periostracum is destroyed by an acidic substance secreted by the predator. Therefore, both drilling gastropods and sea-stars yield diagnostic patterns of damage in mussel shells. However, the diagnostic pattern produced by sea-stars only affects the conchiolin layer of shells, a feature that is missing in majority of the fossil shells.

From an ecological point of view, this paper analyzes members of two groups (asteroids and gastropods) of predators of mollusks with generalist and opportunistic predation strategies. Asteroids are more generalist predators (Gil and Zaixso 2008) than drilling gastropods whose diet consist almost exclusively of shelled mollusks, especially bivalves (Gordillo 1994; 1998; 2001; Andrade and Ríos 2007; González et al. 2007). In the Beagle Channel, Castilla (1985) studied the diet of *C. lurida* and concluded that this generalist

species feeds on at least 25 prey species including gastropods, bivalves, cirripeds, amphipods, crabs, ascidians, brachiopods, echinoids, and notothenid fishes. This predator feeds on the mussels *B. purpuratus* and *A. atra*, and on the second-trophic-level carnivorous *Trophon* spp. snails (Castilla 1985). In our study *A. antarctica* was observed in the field eating both sessile and vagile prey belonging to different groups, including *M. chilensis*, *B. purpuratus*, *T. geversianus*, chitons, and echinoids, showing that this predator is also a generalist and/or opportunistic species.

Our results indicate that these gastropods and asteroids select the size of their prey. In the case of the gastropods, they can increase the range of preys by varying the position of the holes or adopting alternative strategies. An example of the former strategy is displayed by the predatory gastropod *T. geversianus* which, depending on its prey, is able to drill the hole on the surface of the valve or at its margin. Finally, as an example of the latter strategy is *A. monodon*, which is capable of drilling a hole or using the labral spine to open the valve of its prey depending on the species attacked.

## Paleontological implications

Predators that leave drill holes in marine invertebrate shells provide quantitative data on various aspects of prey-predator interactions and have produced one of the longest and richest fossil records of an ecological interaction (Kowalewski et al. 1998). Detailed investigations of Recent examples of predator-prey interactions, including experiments in captivity and field observation, and a description of the traces left on prey shells, is essential in improving interpretation of the patterns found in the fossil record. For instance, despite it is known that a complete drill hole on a mollusk shell most probably entails a successful attack, it has been proved that the opposite statement is not always true: a successful predation does not imply the presence of a complete drill hole. Some muricid gastropods can attack bivalves successfully without drilling (Kowalewski 2004) or after making an incomplete hole that reaches soft tissues, in the case of cirripedes (Palmer 1980, 1990; Hart and Palmer 1987; Rocha-Barreira et al. 2004). In the same way sea stars have not been documented leaving a trace on the valves after successfully consuming their prey. Thus, having a fair knowledge of the complexity of the pattern recorded in mollusk shells after predation activities is important to appreciate the uncertainty of what is observed in the fossil record.

In our study we demonstrated that, when present, drill holes are valuable tools allowing detection of the fine details of this biotic interaction, such as the preference for a certain prey size and site of boring. We also demonstrated that the same predator (*T. geversianus*) shows different behavior according to the prey species: it produces complete holes placed on the shell surface when drilling *M. chilensis*; or a majority of holes placed at the margins of the shells, but perforating both valves (*B. purpuratus*); or marginal

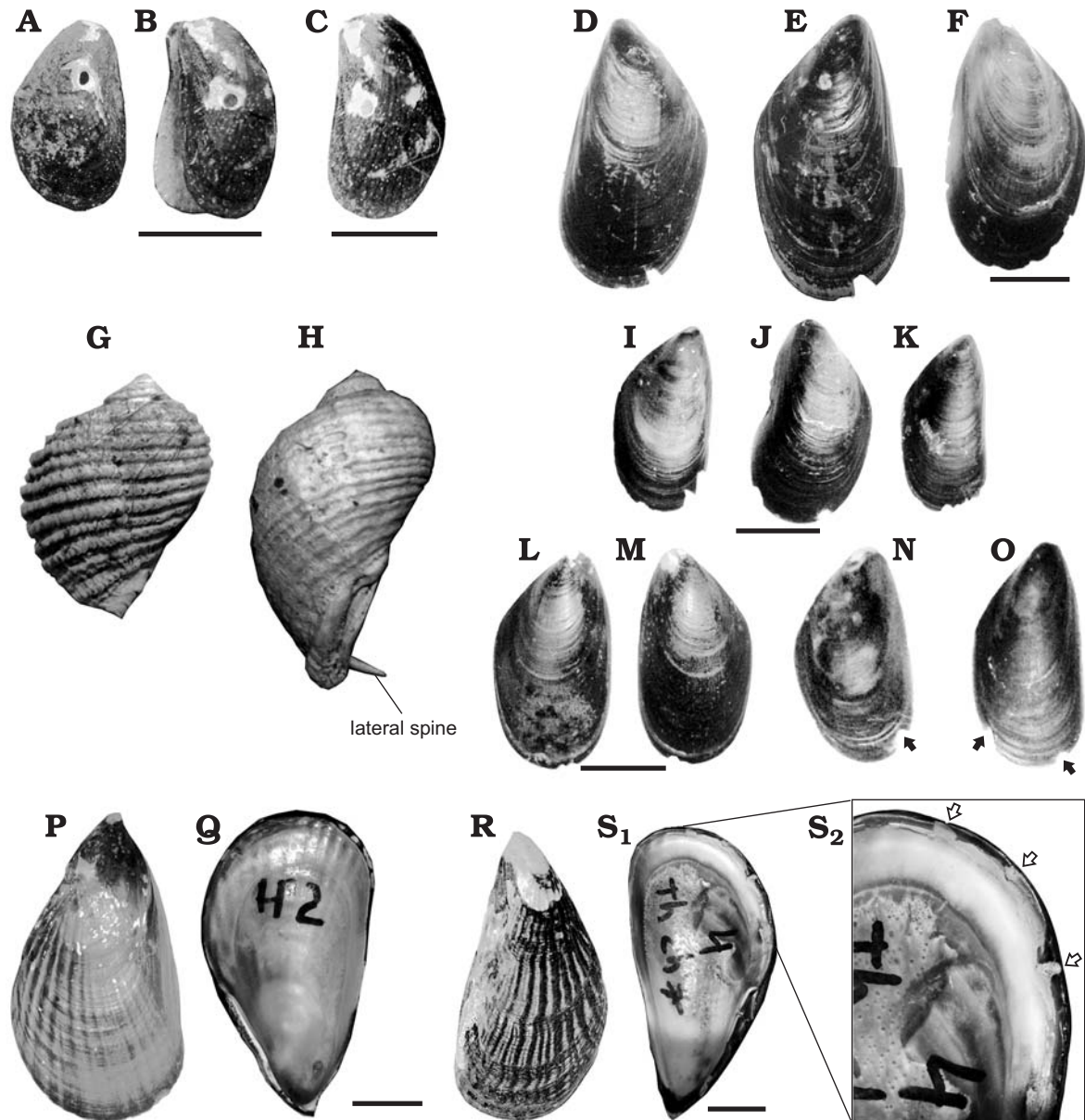


Fig. 10. Predation marks produced by *Acanthina monodon* (Pallas, 1774) in mussels under aquarium conditions. **A–C.** *Brachidontes purpuratus* (Lamarck, 1819). **A.** CEGH-UNC 25357, articulated specimen, external view of right valve. **B.** CEGH-UNC 25358, articulated specimen, external view of left valve. **C.** CEGH-UNC 25359, articulated specimen, external view of left valve. **D–F, I–O.** *Mytilus chilensis* Hupé, 1854. **D.** CEGH-UNC 25360, left valve in external view. **E.** CEGH-UNC 25361, right valve in external view. **F.** CEGH-UNC 25362, left valve in external view. **I.** CEGH-UNC 25365, right valve in external view. **J.** CEGH-UNC 25366, left valve in external view. **K.** CEGH-UNC 25367, right valve in external view. **L.** CEGH-UNC 25368, right valve in external view. **M.** CEGH-UNC 25369, left valve in external view. **N.** CEGH-UNC 25370, right valve in external view. **O.** CEGH-UNC 25371, right valve in external view. **G, H.** *Acanthina monodon* (Pallas, 1774). **G.** CEGH-UNC 25363, valve in dorsal view. **H.** CEGH-UNC 25364, valve in lateral view. **P–S.** *Aulacomya atra* (Molina, 1782). **P.** CEGH-UNC 25372, right valve in external view. **Q.** CEGH-UNC 25372, right valve in internal view. **R.** CEGH-UNC 25375, left valve in external view. **S.** CEGH-UNC 25375, left valve in internal view ( $S_1$ ), close-up of the notches ( $S_2$ ). Black arrows indicate chipping margins, white arrows indicate notches. Scale bars 10 mm.

drillings that affect one valve and leave a mark on the internal surface of the other (*A. atra*). Regarding to these differences, the two species with marginal drilling (*B. purpuratus* and *A. atra*) also coincide in that they have ribbed shells. It is likely that these ribs produce an irregular surface and/or are thickened, acting as an obstacle that will slow down the time it takes the predator to eat the prey (i.e., because the predator invests more time to drill the hole or looking for

another suitable site). On the other side, differences between *B. purpuratus* and *A. atra* are most probably related to the manner the predator manipulates two preys with different shell shape: the inflated shell of *B. purpuratus* and the compressed shell of *A. atra*.

Also, *A. monodon* drills a hole to prey upon *B. purpuratus* but opens *M. chilensis* and *A. atra* shells with its labral spine. Moreover, after the attack *B. purpuratus* shells are damaged



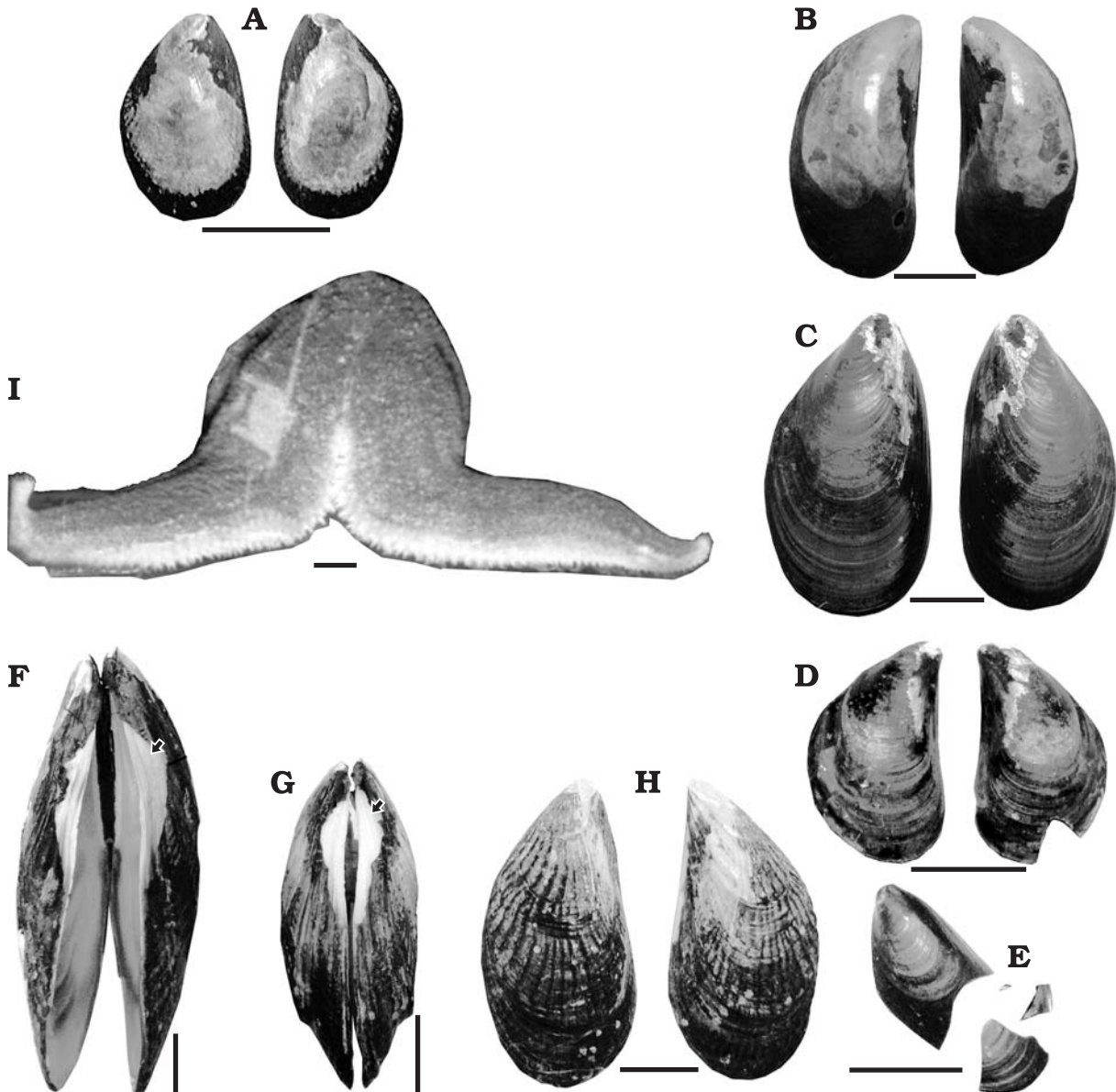


Fig. 11. Predation marks produced by *Cosmasterias lurida* (Philippi, 1858) in mussels under aquarium conditions. **A.** *Brachidontes purpuratus* (Lamarck, 1819), CEGH-UNC 25376, right and left valves in external view. **B–E.** *Mytilus chilensis* Hupé, 1854. **B.** CEGH-UNC 25377, right and left valve in external view. **C.** CEGH-UNC 25378, right and left valve in external view. **D.** CEGH-UNC 25379, right and left valve in external view. **E.** CEGH-UNC 25380, right valve in external view. **F–H.** *Aulacomya atra* (Molina, 1782). **F.** CEGH-UNC 25380, articulated specimen in ventral view. **G.** CEGH-UNC 25381, articulated specimen in ventral view. **H.** CEGH-UNC 25382, right and left valve in external view. **I.** Syn-vivo specimen of the sea star *Cosmasterias lurida* (Philippi, 1858). Scale bars 10 mm.

with relatively easily recognizable traces, but *A. atra* acquires subtle marks that are more difficult to detect in the fossils.

We also showed that the sea star *C. lurida* successfully consumes mussels without leaving traces in the calcareous layers of the shell, or in some cases producing a fracture indistinguishable from physical damage. This predation cannot be detected in the fossil record. However, in this study this species has been demonstrated to be an important predator on mussels based on the time needed to complete consumption of the prey and the amount of prey they can consume per unit time. Over several million years of activity, sea stars must have left an enormous amount of empty

shells that provide no clues for the paleontologists what was their fate.

*T. geversianus* and *C. lurida* showed size selectivity when preying upon mussels. Selectivity in *A. monodon* was demonstrated to be weak, probably due to the fact that this predator uses different strategies, thereby increasing its spectrum of probable prey sizes.

Optimal foraging theory suggests that a predator will select the most profitable prey (Pyke 1984), which is determined by energetic value, success rate, handling time and recognition time costs of the prey (Kitchell et al. 1981). In this regard, the fact that a single predator attacks in different ways the differ-



ent preys is probably related to lower energy consumption. The same with respect to size selection that comes from the experiments and the shells collected in the field.

New field and lab studies, centered on different potential predators of mussels, including crabs, are needed in the future; these will elucidate a more complete spectrum of the biotic interactions in Tierra del Fuego region. Biotic interactions shape community structure in modern marine ecosystems, and predation, although its role in evolution is quite controversial, has been thought to play an important role in the dynamics of evolutionary change in organisms and their biological surroundings (Vermeij 1987). In this regard, exploring the fossil record of drilling predation will contribute to a better understanding of the role of predation at different scales.

## Conclusions

The predator-prey interaction complex integrated by three species of mussels (prey) and three species of muricid gastropods and two of sea stars (predators) in the southernmost region of South America, Tierra del Fuego, was described from laboratory experiments, field observations, and study of Recent shell accumulations. The interaction was demonstrated to be complex in terms of predator behaviors and associated traces left in prey valves.

The time intervals needed to attack and completely consume a prey specimen were determined: between 9 and 10 days on average for *T. geversianus* consuming *M. chilensis* and *A. atra* respectively; 1–2 days for *A. monodon* with *M. chilensis* and nearly 24 hours for *C. lurida* with the same species.

The different predators differ in the size of prey of a given species that they consume. Drilled specimens in the field are larger than undrilled ones, indicating that whelks prefer to attack large-sized prey. Borings are usually placed at particular positions indicating that these muricid gastropods select the place where they drill.

*A. antarctica* is a generalist predator, which had previously been also concluded for *C. lurida*. None of the sea stars leave a trace that would be recognizable in the fossil record after consuming the mussel.

Traces of predation by muricid gastropods on mussels in Tierra del Fuego does not show a unique pattern. The same predator species develop different behaviors with different prey species and this variability is imprinted in the shell as different patterns of traces. As a general rule, traces underestimate the impact of predation on living communities.

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## References

- 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.
- 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.
- Blake, D.B. and Guensburg, T.E. 1994. Predation by the Ordovician asteroid *Promopalaeaster* on a pelecypod. *Lethaia* 27: 235–238.
- 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 bivalve mollusca. *Palaeogeography, Palaeoclimatology, Palaeoecology* 4: 29–65.
- Castilla, J.C. 1985. Food webs and functional aspects of the kelp, *Macrocystis pyrifera*, community in the Beagle Channel, Chile. In: W.R. Siegfried, P.R. Condy, and R.M. Laws (eds.), *Antarctic Nutrient Cycles and Food Webs*, 407–414. Springer-Verlag, Berlin.
- Dolmer, P. 1998. The interactions between bed structure of *Mytilus edulis* L. and the predator *Asterias rubens* L. *Journal of Experimental Marine Biology and Ecology* 228: 137–150.
- Gil, D.G. and Zaijso, H.E. 2008. Feeding ecology of the subantarctic sea star *Anasterias minuta* within tide pools in Patagonia, Argentina. *Revista de Biología Tropical* 56: 311–328.
- González, J., Daza, E., Vargas, C., Cortes, C., Guzmán, L., Miranda, H., Vargas, C., and Yannicell, B. 2007. *Diagnóstico para la administración y conservación del recurso caracol Trophon en Bahía Gente Grande, XII Región. Informe Final Proyecto FIP 2004-47*. 186 pp. Instituto de Fomento Pesquero, Valparaíso.
- Gordillo, S. 1994. Perforaciones en bivalvos subfósiles y actuales del Canal Beagle, Tierra del Fuego. *Ameghiniana* 31: 177–185.
- Gordillo, S. 1998. Trophonid 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. 2001. Marcas de la depredación de *Acanthina* Fisher von Waldheim, 1807 (Gastropoda: Muricidae) sobre Bivalvia. *Ameghiniana* 38: 55–60.
- Gordillo, S. and Amuchástegui, S. 1998. Estrategias de depredación del gastrópodo perforador *Trophon geversianus* (Pallas) (Muricoidea: Trophonidae). *Malacologia* 39: 83–91.
- Griffiths, R.J. 1981. Predation on the bivalve *Choromytilus meridionalis* by the gastropod *Natica (Tectonatica) tecta*. *Anton. Journal of Molluscan Studies* 47: 112–130.
- Hammer, O., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological Statistics software package for education and data analysis. *Paleontologia Electronica* 4 (1): 1–9.
- Hart, M.W. and Palmer, A.R. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. *Journal of Experimental Marine Biology and Ecology* 107: 101–120.
- Ingólfsson, A. 2005. Community structure and zonation patterns of rocky shores at high latitudes: an interoceanic comparison. *Journal of Biogeography* 32: 169–182.
- Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica* 62: 3–183.
- Kelley, P.H. and Hansen, T.A. 1993. Evolution of the naticid gastropod predator-prey system: An evaluation of the hypothesis of escalation. *Palaios* 8: 358–375.
- Kelley, P.H., Kowalewski, M., and Hansen, T.A. 2003. *Predator-Prey In-*

- teractions in the Fossil Record. 464 pp. Kluwer Academic/Plenum Publishers, 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.
- 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 lamellose* (Muricidae): Paleobiological and ecological implications. *Journal of Molluscan Studies* 70: 359–370.
- Kowalewski, M., Dulai, A., and Fursich, F.T. 1998. A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology* 26: 1091–1094.
- Kowalewski, M., Flessa, K.W., and Marcot, J.D. 1997. Predatory scars in the shells of a Recent lingulid brachiopod: paleontological and ecological implications. *Acta Palaeontologica Polonica* 42: 497–532.
- Leonard, G.H., Bertness, M.D., and Yund, P.O. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* 80: 1–14.
- MacKinnon, C.M., Gallant, R., and Gillis, B. 1993. Some observations on starfish predation on mussel spat collectors. *P.E.I. Department of Agriculture Fisheries and Forestry, Technical Reports Series* 208: 1–28.
- Meldahl, K.H., Flessa, K.W., and Cutler, A.H. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23: 207–229.
- Mutschke, E. and Ríos, C. 2006. Distribución espacial y abundancia relativa de equinodermos en el Estrecho de Magallanes, Chile. *Ciencia y Tecnología del Mar* 29: 91–102.
- Ojeda, F.P. and Santelices, B. 1984. Invertebrate communities in holdfasts of the kelp *Macrocystis pyrifera* from southern Chile. *Marine Ecology Progress Series* 16: 65–73.
- O'Neill, S.M., Sutterlin, A.M., and Aggett, D. 1983. The effects of size-selective feeding by starfish *Asterias vulgaris* on the production on mussels *Mytilus edulis* cultured on nets. *Aquaculture* 35: 211–220.
- Palmer, A.R. 1980. *A Comparative and Experimental Study of Feeding and Growth in Thaidid Gastropods*. 320 pp. Unpublished Ph.D. dissertation, University of Washington, Seattle.
- Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology* 71: 758–775.
- Pyke, G.H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523–575.
- Rocha-Barreira, C., Santana, I.C.H., and Franklin-Júnior, W. 2004. Predatory behavior *Thais haemastoma floridana* (Conrad, 1837) (Mollusca) in laboratory. *Thalassas* 20: 55–60.
- Soto, R.E., Castilla, J.C., and Bozinovic, F. 2004. Conducta de forrajeo del gastrópodo *Acanthina monodon* Pallas, 1774 (Gastropoda: Muricidae) en el intermareal rocoso de Chile central. *Revista Chilena de Historia Natural* 77: 157–175.
- Spencer, W.K. and Wright, C.W. 1966. Asterozoans. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part U, Echinodermata* 3, 4–107. Geological Society of America, Boulder.
- Urrutia, G.X. and Navarro, J.M. 2001. Patterns of shell penetration by *Chorus giganteus* juveniles (Gastropoda: Muricidae) on the mussel *Semimytilus algosus*. *Journal of Experimental Marine Biology and Ecology* 258: 141–153.
- Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life*. 527pp. Princeton University Press, Princeton.
- Vermeij, G.J. 1993. *A Natural History of Shells*. 207 pp. Princeton Science Library, Princeton.
- Walker, K.R. and Bambach, R.K. 1971. The significance of fossil assemblages from fine-grained sediments: time-averaged communities. *Geological Society of America, Abstract with Programs* 3: 783–784.
- Wickens, P.A. and Griffiths, C.L. 1985. Predation by *Nucella cingulata* (Linnaeus, 1771) on mussels, particularly *Aulacomya ater* (Molina, 1782). *Veliger* 27: 366–374.
- Zaixso, H.E., Boraso, A.L., and López Gappa, J.J. 1978. Observaciones sobre el mesolitoral rocoso de la zona de Ushuaia (Tierra del Fuego, Argentina). *Ecosur* 5: 119–130.
- Zar, J.H. 1999. *Biostatistical Analysis*. 663 pp. Prentice Hall, New Jersey.