

## **Cannibalism in Holocene muricid snails in the Beagle Channel, at the extreme southern tip of South America: an opportunistic response?**

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### **ABSTRACT**

This work documents the occurrence of drillholes on muricid *Trophon geversianus* shells from a Holocene raised marine deposit in the Beagle Channel, located on the extreme southern tip of South America (~ 55°S). Based on drillhole morphology and previous data under laboratory conditions these predatory holes are attributed to conspecifics, thus suggesting cannibalism. It appears that when food is scarce and the alternative prey (*Tawera gayi* and other clams) is not available, *T. geversianus* may increase the frequency of cannibalism in order to compensate for the loss of bivalve prey. Cannibalism therefore developed at ca. 4000 yr. BP as a response to the lack of clams, which would have disappeared during a sudden hydrological local event that affected the filter feeders.

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### **INTRODUCTION**

Cannibalism is not only widespread in the animal kingdom, it is actually important in the ecology of many species of aquatic and terrestrial communities (Fox, 1975; Polis, 1981). This intraspecific interaction has the potential to alter the functional relationship of predator-prey interactions (Rudolf, 2008).

In the fossil record cannibalism has been identified during the Cambrian, as seen in priapulids from the Burgess Shale; and, as modern priapulids are also known to be cannibals, this feeding behavior has remained remarkably similar for 530 million years (Brett and Walker, 2002).

Cannibalism in fossil marine gastropods has been often considered in naticids. For example, Kelley (1991), and then Dietl and Alexander (2000) examined cannibalism by Miocene-Pleistocene

naticid gastropods from Maryland. More recently, Martinell et al. (2010) investigated confamilial predation in Pliocene naticids from southern France, and Serralta (2010) described cannibalism in *Polinices marambioensis* from the La Meseta Formation (Eocene) in Antarctica.

Although research on cannibalism in fossil muricid gastropods is extremely scarce, Spanier (1987) attributed drillholes in the Holocene muricid snail *Chicoreus ramosus* from the Red Sea to conspecifics, and Dávid (1997) found signs of cannibalism in the Oligocene of Hungary through muricid boring observed on the shells of muricid gastropods.

The ecological significance of cannibalism has been discussed in previous research on naticids (see Kelley, 1991). On the one hand, cannibalism is seen as evidence of predator ineptitude, or an absence of bivalve prey (Stanton and Nelson, 1980; Polis, 1981). On the other hand, cannibalism is considered the result of selective predation in order to maximize energy gain per unit foraging time, as shown by cost-benefit ratios (Kitchell et al., 1986; Kelley, 1991; Kelley and Hansen, 2007), thus suggesting that it is sometimes more beneficial for naticids to prey upon themselves rather than bivalves. In relation to muricids, Spanier (1986, 1987) associated cannibalism of snails from the Red Sea with the absence of an alternative food.

The objective of this work is to document the occurrence of intraspecific predation in specimens of the muricid *Trophon geversianus* of ca. 4000 years BP from the Beagle Channel, and to discuss the ecological reasons behind this occasional phenomenon.

### Muricid Gastropods and Cannibalism

Muricid gastropods are a diverse family of predator snails, comprising around 1,600 living and 1,200 fossil Cenozoic species (Barco et al., 2010; Merle et al., 2011). They are common members of shallow marine benthic communities in most areas of the world, mainly preying on bivalves and barnacles, leaving a recognizable drillhole on the skeleton of their victims. Thus drilling is preserved in the fossil record and can be used to determine patterns of predation in the past (Vermeij, 1980; Kelley and Hansen, 2003).

In southern South America, the most common living drilling muricid along the sea and channel shores is the whelk *T. geversianus*, and predation by this species appears to be an important cause of mortality in epifaunal mussels and semi-infaunal

venerid clams (Gordillo, 1994; Gordillo and Archuby, 2012). In the Beagle Channel, *T. geversianus* inhabits the rocky and gravelly shores, which are mainly covered by mussels (Ingólfsson, 2005), but this snail is also associated with *Tawera gayi* clams, which live in soft substrates (Lomovasky et al. 2005).

This species has also been recovered from Holocene and Pleistocene marine deposits located in southern Argentina and Chile (Gordillo, 1999; Gordillo and Isla, 2011; Gordillo et al., 2011). Previous research showed the ability of this predator to capture and subdue mobile prey under laboratory conditions. In this region, *T. geversianus* drills holes primarily in the clam *T. gayi*, or the mussel *M. chilensis*, depending on which one is dominant in the substrate, while other species would only be occasional food items (Gordillo and Amuchástegui, 1998; Andrade and Ríos, 2007; Gordillo et al., 2011; Gordillo and Archuby, 2012).

In muricids, intraspecific predation (cannibalism) has been shown to take place in living gastropods (e.g., Paine, 1966; Spanier, 1986; Rilov et al., 2004; Vasconcelos et al., 2012), although very little information is available for the snail *T. geversianus*. Osorio (2002) first reported cannibalism in *T. geversianus* under aquarium conditions, and more recently Cumplido et al. (2011), studying the embryological development of this species, observed drilling attempts in a prehatching embryo of *T. geversianus*, thus also suggesting cannibalism.

### Muricid Drillholes

To excavate a drillhole, muricids penetrate the shell of their prey by a mechanical scraping action of the radula, together with chemical activities of carbonic anhydrase, chelating agents and enzymes secreted by the ABO (accessory boring organ) situated in the foot (Carriker, 1981). More recent studies also showed that muricids can produce different secretions to paralyze their prey (Andrews et al., 1991; West et al., 1994; Roseghini et al., 1996). After extracellular digestion, muricids take their food in fluid form; and given that they suction the nutrient-rich fluids of the prey's body tissues, they really are liquid feeders (Crothers, 1985) and also feed on suspended and soluble organic nutrients (Lau and Leung, 2004).

The drilling mechanism in *T. geversianus*, including the drilling and the feeding phase, is a very slow process. Under laboratory conditions, it mostly takes between 6-10 days (Gordillo and

Amuchástegui, 1998; Andrade and Ríos, 2007; Gordillo and Archuby, 2012).

Predation patterns and bore holes by *T. geversianus* on different prey have been described in previous papers (Gordillo, 1994, 1998; Gordillo and Amuchástegui, 1998; Gordillo and Archuby, 2012, in press). Other drilling predators from the Beagle Channel are the muricids *Xymenopsis muriciformis* and *Acanthina monodon*. Drillholes produced by *X. muriciformis* resemble a cylinder and are relatively smaller than those produced by *T. geversianus* (Gordillo, 1998). *A. monodon* only lives on rocky substrates where it feeds on mussels and barnacles, leaving different types of predation damage (Gordillo, 2001; Gordillo and Archuby, 2012). In any case *A. monodon* seems to bore less frequently since it normally uses a labral spine to open the mussels *Mytilus chilensis* and *Aulacomya atra* and barnacles, but also this species was able to drill cylindrical holes on *Brachidontes purpuratus* under laboratory conditions.

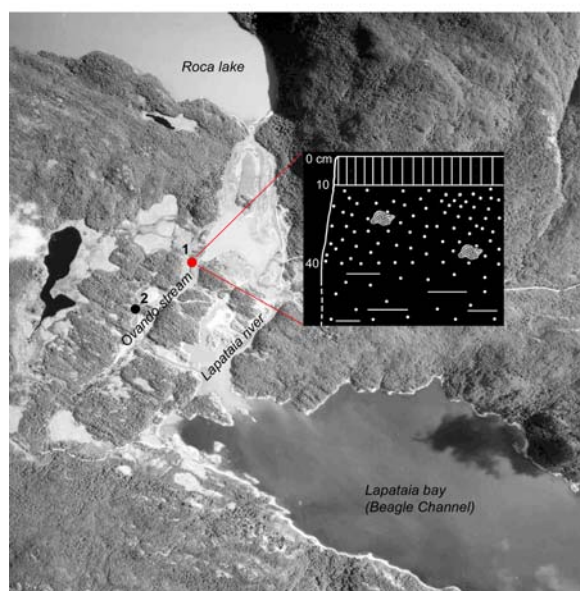
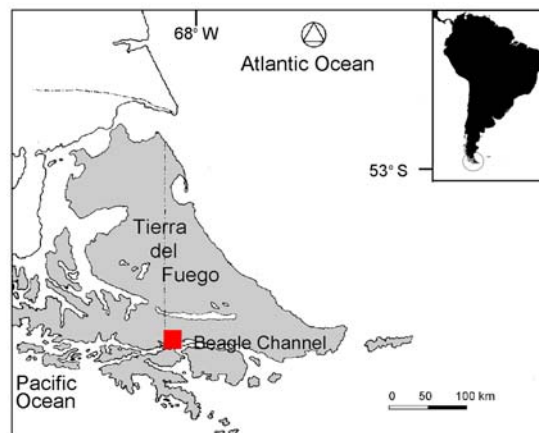
Muricid holes can usually be distinguished from those made by naticids by their size and shape; in general, muricid holes tend to be smaller and more cylindrical (Kelley and Hansen, 2003), although holes drilled by *T. geversianus* may vary from conical to cylindrical depending on the prey species drilled (Gordillo and Amuchástegui, 1998).

Finally, and given that *T. geversianus* drillholes look more like the classical description of naticid drillholes, it is important to point out that naticids (although present in the Beagle Channel) are practically absent in the studied area. Furthermore, there is also no evidence indicating that naticids from the Beagle Channel produce holes in the shells of their prey; and there is even a possibility that they ingest their prey without drilling.

## MATERIALS AND METHODS

The material considered in this study comes from a raised marine outcrop located in southern Tierra del Fuego, on the northern coast of the Beagle Channel (Figure 1). *T. geversianus* specimens with drillholes were collected from the upper part of Site 1 (Figure 1.2). A second site (Site 2; Figure 1.2) previously studied is mentioned here because it will be a reference for comparisons.

As indicated by previous geomorphological and paleontological studies (Rabassa et al., 1986; Gordillo et al., 1993; Gordillo et al., 2005; Rabassa et al., 2009), it is an environmentally complex area (Figure 2). During the last Pleistocene glaciations this area was covered by ice, but around 12 kyr. BP the ice disappeared from the Beagle Channel.



**FIGURE 1.** Location map showing the sampling site situated on the northern coast of the Beagle Channel. 1. The maps on the left side show the position of the studied area in southern South America. 2. The aerial photography (1:20.000) shows the area affected by the Holocene marine transgression. Radiocarbon dates were previously performed for Sites 1 and 2. *Trophon geversianus* shells with drillholes were recovered from the left part in Site 1.

After that, during the early Holocene this area was a low energy freshwater environment (Figure 2.1), but during mid-Holocene times (ca. 7500-4000 yr. BP), this area became a marine archipelago (Figure 2.2), and today it is a freshwater environment flanked by the rivers Ovando and Lapataia (Figure 2.3).



**FIGURE 2.** Landscape evolution of the studied area during the Holocene. 1. Glacilacustrine conditions after deglaciation during the early Holocene. 2. Sea transgression/regression during the middle Holocene. 3. The landscape during the late Holocene. 4. Animated landscape evolution (using Blender 2.64) (available online).

### Site 1

All complete, unbroken *T. geversianus* shells (N=20) lying on a layer of sand over an exposed area of 20 x 20 m were collected. In this area, a radiocarbon date by Coronato et al. (1999) gave an age of 4160 $\pm$ 45 yr. BP (Site 1; Figure 1).

The low number of *T. geversianus* shells collected per unit area in Site 1 is consistent with the proportion of the species in living communities (0.52 ind. m<sup>2</sup>; Andrade et al., 2009). Ten *T. geversianus* shells (50% of the total shells) showed signs of incomplete or complete drilling attempts.

### Site 2

Another level from this area, with clams in life position, gave a radiocarbon age of 4425 $\pm$ 55 yr. BP (Rabassa et al., 1986; Site 2; Figure 1). The fauna of site 2 was previously studied (Gordillo, 1999) and is dominated by filter feeding bivalves *T. gayi* (63%) and *Hiatella* sp. (19%) among other taxa which contribute most to the biomass. Bivalves normally occur as whole joined valves, oriented in life position, or horizontally, randomly oriented within the bed. Gastropods represent a minor proportion, although exhibit the highest richness. The most common gastropods are *Pareuthria plumbea*, which feed on carrion and the drilling gastropods *T. geversianus* and *X. muriciformis* which prey upon bivalves.

After examination and taking into account previous studies centered on laboratory experiments, which include the analysis of the morphology of drillholes (see above Muricid drillholes section), predatory drillings on *T. geversianus* shells were attributed to conspecifics. Each specimen of *T. geversianus* was measured with a digital caliper (precision of 0.01 mm) to determine height, width and thickness in millimeters. In specimens exhibiting borings, for each drilling attempt, outer and inner drillhole diameters were measured. In addition, each shell with borings was divided into five uneven sectors as an approach for evaluating site selectivity. These sectors were: the spire (sector 1); the last whorl in ventral position (sector 2) and the last whorl in dorsal position, subdivided into upper (sector 3), central (sector 4) and lower (sector 5) zones. The last subdivision into three zones (sectors 3, 4 and 5) was made to better discriminate site selectivity in dorsal position, taking into account the life position of the species with the dorsal side upwards.

To determine prey effectiveness, the number of complete holes was compared to the total number of drilling attempts. To analyze size selectivity

and frequency of cannibalism, the proportion of bored versus unbored shells in relation to prey size was determined. Three size classes were considered: between 20.00 and 29.99 mm (class I); between 30.00 and 39.99 mm (class II) and between 40.00 and 49.99 mm (class III). To infer the relative amount of prey biomass as energetic value, the biovolume was calculated. As biomass in bivalves and gastropods is correlated with the volume of the body cavity within the shell we determined the relationships of size to biovolume. Powell and Stanton (1985) proposed an operational measurement of biovolume based on the conversion of measured shell parameters (i.e., length, height, width) into cubic form. However, in this paper we measured true biovolume as the paleontological analog of biomass. For this purpose, the biovolume consumed by the predator was constructed for *T. geversianus* and for *T. gayi*, its main prey in Holocene deposits in the area (see: Muricid gastropods and cannibalism section), as follows. From hundreds of modern specimens of these two species collected from the Beagle Channel we selected a subsample of 10 specimens for each species, covering all size ranges. In the case of *T. geversianus*, it was within the range of 13-75 mm in height and was between 7-50 mm in width. To calculate the biovolume, a graduated glass cylinder was used, and measurements were taken of the fluid displaced when introducing each specimen. With these data, an equation for each species was obtained. In *T. geversianus*, the cavity of the last whorl was filled with plasticine. In this way species-specific equations were used to generate biomass derived from data sets. These data were used in conjunction with shell thickness as a function of drilling time, to be interpreted in association with a cost-benefit analysis (Kitchell et al., 1981; Kidwell, 1991). To infer predator-prey size and cost-benefit relationships, equations were based on unpublished data obtained previously under laboratory conditions. To test the predator-prey size relationship, the predator size for each borehole diameter was calculated based on nine observations of three different *T. geversianus* specimens eating *T. gayi* clams under laboratory conditions. Borehole inner diameter was then regressed against prey shell size. Predator size for each bored shell of *T. geversianus* was then estimated using this equation. To test whether patterns of prey selection by *T. geversianus* is related to biomass and energetic profitability, two bored shells from each prey species (i.e., *T. gayi* versus *T. geversianus*) of the same thickness were compared in biomass.

As drilling time includes drilling action and ingestion time, the calculations discriminated between these two phases. In this respect, we considered data on predation time (in days) obtained under laboratory conditions with *T. geversianus* preying on *T. gayi*. For each bored specimen of *T. gayi* we took into account (1) the number of days taken by *T. geversianus* from when it was placed on the prey until it left, (2) the shell thickness (as a measure of borehole depth) and (3) biovolume measurements based on empty shells. We correlated predation time (a) with borehole depth in order to evaluate whether predation time would increase in direct proportion to the drilling action required to excavate the shell and (b) with biovolume to evaluate whether predation time would increase in direct proportion to the volume of shell material eaten.

As a comparison, the relative abundance of the predator *T. geversianus* with respect to its potential prey, in different fossil and modern sites located on the Beagle Channel was compiled. Data analyses were done in Microsoft Excel and with the software PAST 2.02 (Hammer et al., 2001).

## RESULTS

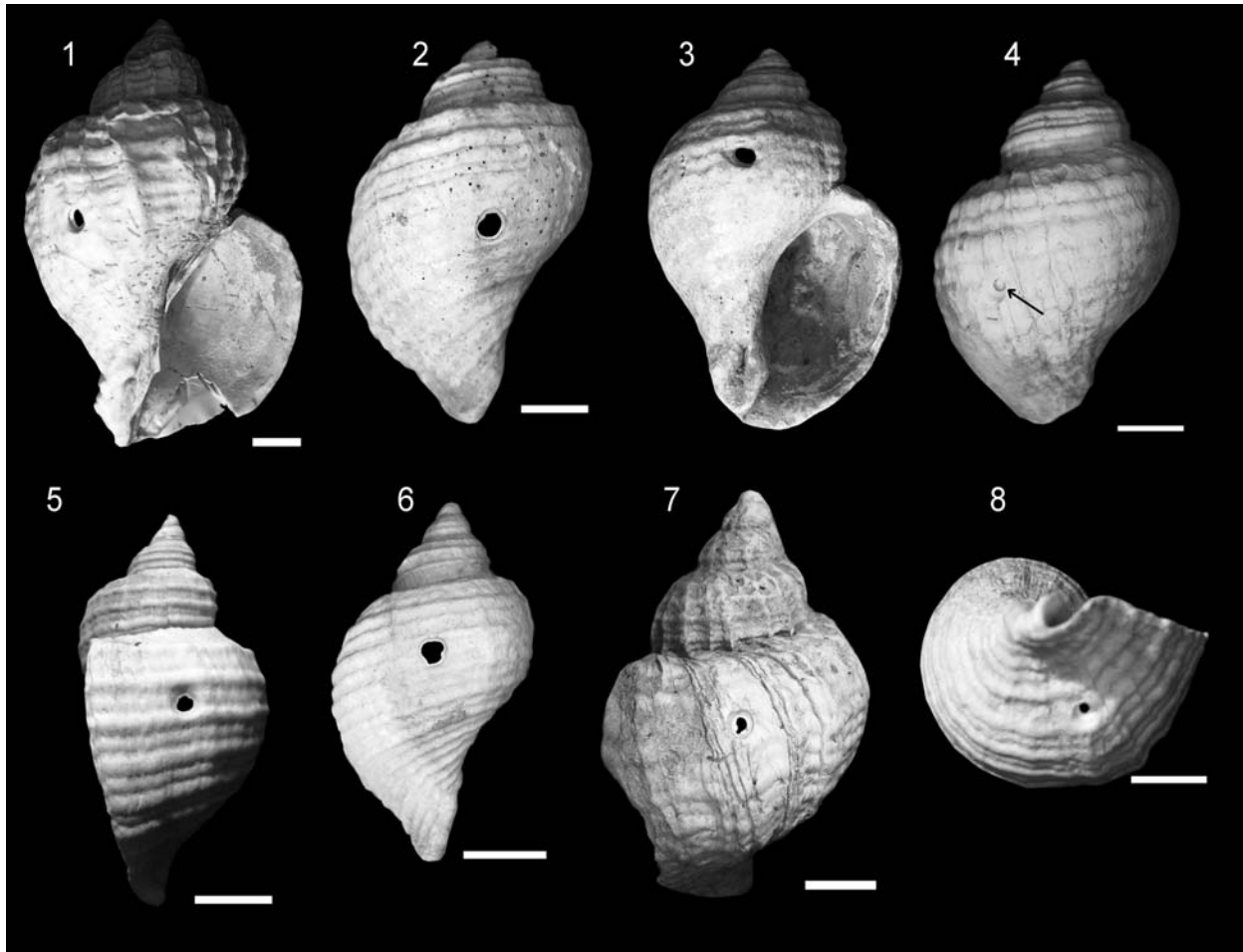
In relation to the age of fossil *T. geversianus* shells with drillholes, and since the exposed layer in which they were recovered is located at a relatively higher position with respect to both layers dated in ca. 4400-4100 yr. BP, it is highly likely to be younger (i.e., ca. 4000 years because after this age the sea retreated).

Figure 3 shows *T. geversianus* shells with predatory drillholes. In addition, Figure 4 provides a 3-D effect on the *T. geversianus* specimen illustrated as Figure 3.1.

These holes are circular to oval when seen from above, oriented to the shell surface and conical in cross section. All of them (100%) are located on the last whorl. Of these, 25% are in the ventral region (sector 2) and 75% in the dorsal region, distributed as follows: 25% in the upper zone (sector 3), 62.5% in the central area (sector 4) and 12.5% in the lower part (sector 5). The highest percentage in the dorsal area would relate to the life position of the snails, and not to a preference for a particular area.

*T. geversianus* completed drilling in eight out of 10 attempts (Prey effectiveness gave a value of 0.8), but as the incomplete borings are located on shells which also exhibit a second complete borehole (e.g., Figure 3.3-3.4), 100% of the specimens were eaten by the same or by another predator.





**FIGURE 3.** Holocene *Trophon geversianus* shells with drillholes attributed to conspecifics from the Cormoranes Archipelago (Beagle Channel). 1. CEGH-UNC 25410. 2. CEGH-UNC 25411. 3-4. CEGH-UNC 25412. 5. CEGH-UNC 25413. 6. CEGH-UNC 25414. 7. CEGH-UNC 25415. 8. CEGH-UNC 25416. Scales= 1 cm.

Thus, drilling was 100% successful. However, 20% of failed attempts still cost the predator time and energy without immediate gain.

Figure 5 shows that there is no complete overlapping in size between drilled and non drilled specimens of *T. geversianus* from the same assemblage. Specimens with drillholes tend to have larger size.

To estimate predator size, the height of *T. geversianus* was inferred by the inner diameter of boreholes excavated on *T. gayi* shells under laboratory conditions:  $\text{Ln } Y = 1.29 \text{ Ln } X + 0.13$ ; ( $R^2=0.72$ )

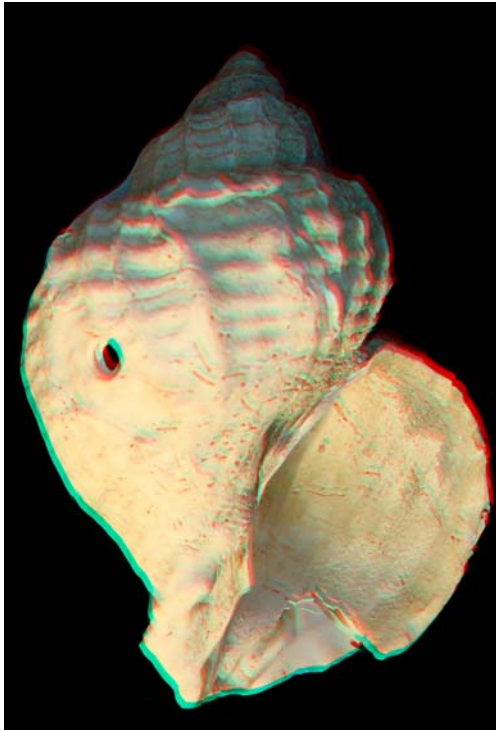
This equation was applied to each prey specimen with a complete borehole, and it was observed that predators appear to be smaller (specimens 2, 5, 6 and 7) or larger (specimens 1, 3 and 4) than their prey (Figure 6).

Taking into account that this is a mobile prey, it is more plausible that a small predator will find it

easier to eat for several days on the dorsal side of a larger victim than a smaller one. On the contrary, in the case of specimens 1, 3 and 4, the predators were apparently larger than their prey, and they probably manipulated their prey prior to making the hole in their victims. In the case of specimen 4, it appears to be considerably larger than its prey, which showed a borehole located on the ventral side, indicating that this specimen was perhaps manipulated and turned before being drilled.

To analyze the cost-benefit relationship an equation for each species was calculated based on modern specimens collected (Table 1).

These equations were applied in order to compare two boreholes of the same inner diameter (depth of 2.16 mm) excavated on valves of each of the two species: i.e., one *T. gayi* specimen of 33 mm long and one *T. geversianus* of 43.1 mm high. Similar values of biovolume were obtained for the two taxa, although slightly higher in *T. geversianus*:

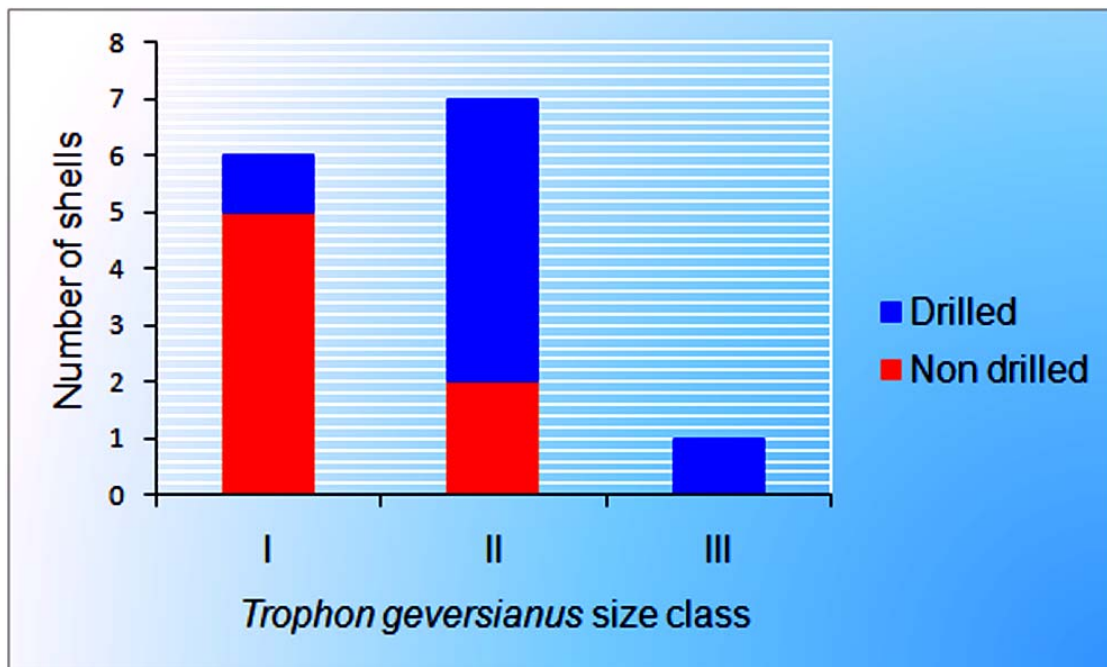


**FIGURE 4.** A *Trophon geversianus* specimen (See also Figure 3.1.) in 3D created using photoshop. The form of the drillhole is easier to interpret in 3D. This photograph was made using anaglyph techniques, which combine two photographs one in red and the other in cyan (blue+green) color. Three-dimensional red-cyan glasses are recommended to view this image correctly.

i.e., 7.27 for *T. gayi* and 8.56 for *T. geversianus*. These values indicate that for the same cost (to pass through the shell wall of *T. geversianus* or *T. gayi*), there is no benefit in one of these two food items, since the biomass of the two species is similar.

The relationships between predation time and shell thickness (borehole depth), and between predation time and biovolume (biomass) are plotted in Figures 7 and 8, respectively, showing a correlation coefficient of 0.88 in the first case and a lower value of 0.59 in the second graph. Thus there is a better relationship between the energy invested in excavating the drillhole and the borehole depth than the biomass obtained.

Finally, Table 2 shows great differences in the proportion of drilling predators and their potential prey in this study compared to other sites of different ages also located along the Beagle Channel. In addition to the different ratio, in the studied site this trophic interaction occurs within the same trophic level (intraguild), while in the other cases it involves a different trophic level (carnivorous and filter feeders) and organisms with a different mode of life (i.e., epifauna and semi-infauna), thus showing interguild predation. In this situation we have a competitive intraspecific interaction, since a cannibal can be cannibalized.



**FIGURE 5.** Drilled and non-drilled *Trophon geversianus* shells in three size classes. Size classes (shell width): I, 20.00-29.99 mm; II, 30.00-39.99 mm; III, 40.00-49.99 mm.

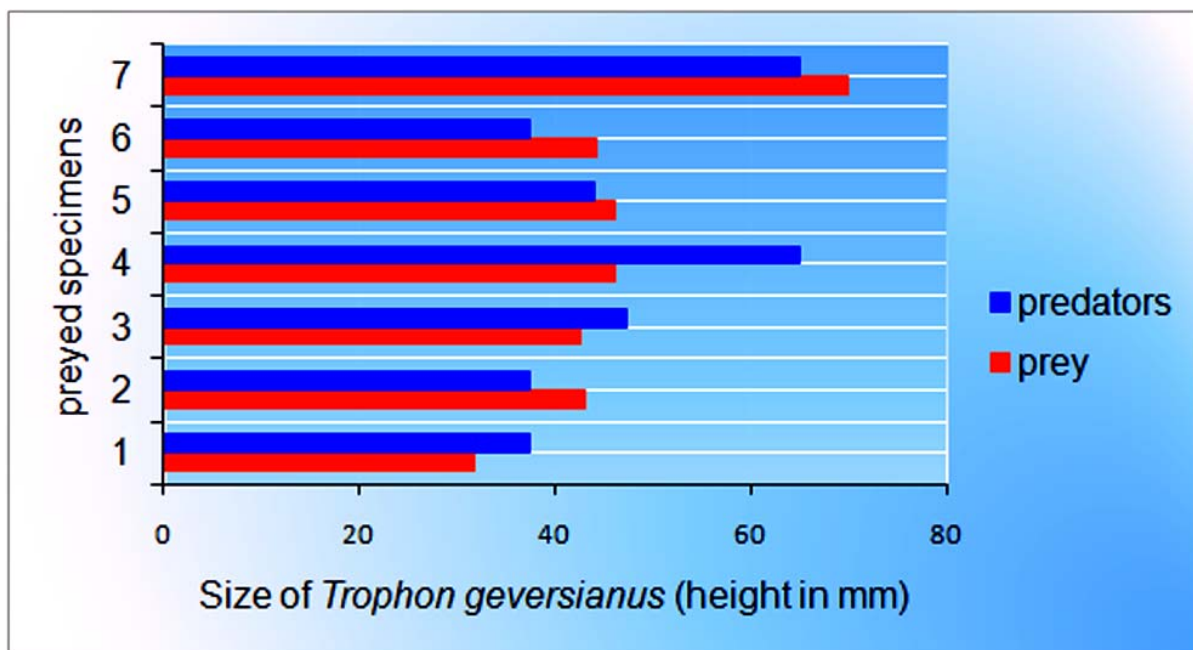


FIGURE 6. Larger and smaller predators with respect to their prey.

**DISCUSSION**

This study, while providing an ecological explanation of intraspecific predation in Holocene muricids from the Beagle Channel, also represents the first mention of cannibalism in Cenozoic fossil mollusks from South America.

Size frequency analysis in conjunction with the analysis of boreholes confirms that eaten specimens have a larger size, and that small specimens eat the larger ones. However, large specimens may also eat small prey if the predator initially manipulates the prey, or if the predator eats a dying or decaying specimen that offers no resistance. Although the number of *T. geversianus* recovered is relatively low, it is consistent with their relative abundance in modern and fossil communities in the region (Gordillo, 1999; Andrade et al., 2009; Gordillo and Archuby, 2012).

Several studies focused on naticid gastropods conclude that cannibalism results from selective predation in order to maximize energy gain, rather than from ineptitude of the predator or absence of bivalve prey (Kitchell et al., 1981; Kelley, 1991). More recently, Gould (2010) suggested that naticid

cannibalism is more likely in low competition environments in the presence of bivalve prey.

In contrast, few studies on muricids (Spanier, 1986) have shown that cannibalism only occurred in the absence of bivalve prey. The present study supports the view of the absence of bivalve prey, as described below.

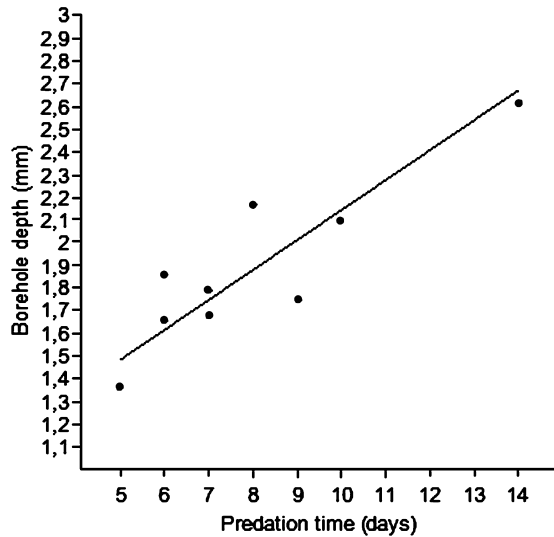
Polis (1981) in a classic study of intraspecific predation attributed cannibalism to the unavailability of alternative prey. As predicted by foraging theory, an animal may expand its diet beyond the normal limits of acceptable prey during periods of hunger or limited food supply (Polis, 1981), and cannibalism may enhance the survival of an individual during the transition time needed to discover common prey (Morton, 1987).

Taking into account previous studies in the region (Gordillo, 1993, 1999; Gordillo et al., 2011), it appears that prior to the onset of cannibal snails, the study area was inhabited by shallow benthic communities dominated by suspension feeder clams (site 2). Gordillo (1999) described two local benthic paleocommunities preserved in life position and composed of suspension feeders (80-90%),

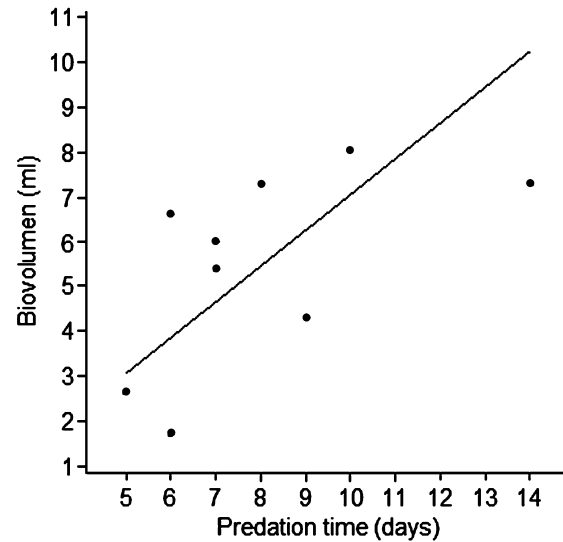
TABLE 1. Regression equations relating shell size (mm) to biovolume.

Species	Size (mm) vs. biovolume (ml)	r
<i>Tawera gayi</i>	Ln Y = 3,21 Ln X - 9,24; X= shell length	0.91
<i>Trophon geversianus</i>	Ln Y = 2,29 Ln X - 5,41; X = shell width	0.97





**FIGURE 7.** The relationship between predation time in days and borehole depth (thickness of the shell);  $r=0.88683$ ;  $p$  (uncorr)= 0.0014349



**FIGURE 8.** The relationship between predation time in days and biovolume as an indicator of biomass.  $r=0.58915$ ;  $p$  (uncorr)= 0.095.

grazers (5-10%) and carnivores (1-5%). The main suspension feeder is the venerid *T. gayi* and the muricid *T. geversianus* appeared as an important predator of the dominant clams (Gordillo et al., 2011). These assemblages were preserved in life position due to a phenomenon of mass mortality (Gordillo, 1993), attributed to abrupt changes in salinity conditions caused by the invasion of continental waters in areas hitherto occupied by sea water.

In this respect, it is believed that a sudden event, such as the increase in brackish water in

this area, produced a time-lag between the proportion of filter feeders and carnivores. In other words, these changes produced the mortality of filter feeders that did not adapt to sudden changes. This situation made the main prey (*T. gayi*) less available, which modified the relationship between filter feeders and predators, thus leading to cannibalism. It appears that when the main prey is not easily available, *T. geversianus*, as an opportunistic predator, may increase the frequency of cannibalism. It therefore follows that if prey abundance decreases

**TABLE 2.** Relative abundance of predators and their potential prey in different sites located on the Beagle Channel. *Trophon geversianus* specimens with drillholes were only found in site 1. In the other sites specimens with drillholes were always bivalves.

Sites	This study (site 1)	R.Ovando (site 2)	Gable (70 km east)	Ensenada (5 km east)
Age	ca. 4000 yr (Not dated)	4425+/-55	4790+/-100	Modern
Prey	35% <i>Trophon</i>	94% <i>Tawera</i>	96,38% <i>Tawera</i> , <i>Mytilus</i>	97,8% <i>Mytilus</i>
Predator	65% <i>Trophon</i>	6% <i>Trophon</i>	3,6% <i>Trophon</i> , <i>Xymenopsis</i>	2,2% <i>Trophon</i>
N	20	180	138	141
<i>Trophon</i> Predation	Intraguild	Interguild	Interguild	Interguild
Competition Regime	High	Low	Low	Low

then there are relatively more predators, and cannibalism increases.

Under this abrupt change in situation, the behavior of *T. geversianus* shifted from non-cannibal to cannibal, thus showing it to have flexible feeding behavior. This predator is therefore a generalistic, selective and opportunistic predator, and is occasionally cannibalistic.

Furthermore, given that small specimens of *T. geversianus* normally inhabit the intertidal zone, it is also plausible that when the sea level dropped (before this area was definitively disconnected from the sea), *T. geversianus* specimens living in the intertidal zone moved to the subtidal waters inhabited by larger specimens. Thus, a higher number of predators could also cause intraspecific predation. Too many predators and too little prey therefore results in cannibalism.

Cannibalism can be dangerous for organisms because the roles of predator and prey can easily switch, and the original cannibal can become cannibalized (Dietl and Alexander, 2000). However, occasional cannibalistic behavior may be beneficial when alternative prey is not available in order to compensate for the loss of food.

As *T. geversianus* specimens with drillholes only appeared as fossils in a layer of sediment, it is believed that cannibalism is a circumstantial situation which naturally would not have been much more common. Hence, it appears that this community was subject to a highly competitive regime only during a brief lapse of time within the Holocene (i.e., ca. 4000 yr. BP). It is also likely that after this event, the whole population died as this region was disconnected from the sea.

Interestingly, this particular situation of a highly competitive regime was apparently reversed in benthic communities living in the Beagle Channel, since cannibalism has not been mentioned, except for isolated (only two shells) modern and reworked shells of *T. geversianus* collected along the beach.

When ecologically comparing *T. geversianus* and *T. gayi* as prey, some differences can be seen. Although in both cases they are mobile prey, they differ because *T. gayi* is a semi-infaunal burrower, and can be buried completely below the sediment, while *T. geversianus* is an epifaunal mobile prey. In a comparison with the present, it was noted that bored *T. geversianus* shells are rare and modern *T. gayi* exhibit high levels of predation by *T. geversianus*.

Taking into account that *T. geversianus* exhibits a preference for dominant bivalves such as the mussel *M. chilensis* and the clam *T. gayi* it is considered that in this case cannibalism is opportunistic or occasional and is stimulated by other factors associated with nutritional stress and high conspecific density. This interpretation is reinforced with data on modern and other Holocene paleocommunities dominated by clams, in which no bored *T. geversianus* shell was found. Thus, *T. geversianus* did not prey on congeners when alternative prey is present.

Differences in size frequency distribution and predator size are explained as follows. Cannibalism as an event could be explained by variation in the predator/prey ratio as seen in Table 2. This new situation, unfavorable for predators, would cause high intraspecific competition. In this competition, larger individuals would have benefited, leaving the smaller ones the only option to feed on its own congeners. The latter is reinforced by the interpretation based on borehole size (to infer predator size), which showed that larger individuals were eaten by the smaller ones.

Thus, the existence of occasional cannibalism at ca. 4000 yr. BP suggests a change in the ecological interaction between *T. geversianus* and alternative prey. This intraspecific interaction arose due to abrupt changes in the density of interacting functional groups (a reduction of filter feeders in this case), which had local consequences (cannibalism), but it is unknown if this event had long-term consequences for the *T. geversianus* population. Perhaps this predator increased its range of food items.

In summary, occasional cannibalism in the muricid *T. geversianus* appears to be caused when the predator/prey ratio is disturbed for any reason which causes a decrease in their usual food, resulting in high intraspecific competition that causes intraspecific predation. More work in muricids under laboratory conditions is needed to reinforce and to extend these interpretations to other members of this family and to assess evolutionary implications of this occasional interaction.

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