MURICID DRILLING PREDATION AT HIGH LATITUDES: INSIGHTS FROM THE SOUTHERNMOST ATLANTIC

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ABSTRACT

Drilling predation is frequently studied in the fossil record. Less information is available from recent environments, however. Previous studies have indicated that drilling predation is usually higher in the tropics but little research has been undertaken in high latitudes. To address this hypothesis, we examine muricid-drilling predation along a 1,000 km transect in southern South America. Drilling frequencies ranged between 3% and 36%, and they were not correlated with the abundance of the predator (*Trophon geversianus*) or the abundance of its preferred prey. The only locality with exceptionally high predation (36%) was a heavily anthropogenically impacted site. *Trophon* exhibited different drilling strategies on different prey, and edge drilling represented 27%–56% of the drill holes in mytilids. Drilling frequencies were not correlated with latitude or water temperature. Our results, however, show that drilling frequencies are indeed lower at high latitudes compared to the tropics, and these data provide a recent baseline to compare and interpret spatial variability in muricid drilling predation from past environments. The fact that dead-shell assemblages seem to be recording human-related impacts in this system strengthens their relevance as potentially valuable conservation tools.

INTRODUCTION

Predation is central to ecology as predators affect the distribution and abundance of their prey and this impacts community structure (Chapin et al., 1997; Meyer and Byers, 2005; Begon et al., 2006). In marine paleoenvironments, drilling gastropods from the families Naticidae and Muricidae are well studied (e.g., Dudley and Vermeij, 1978; Hansen and Kelley, 2003; Klompmaker, 2009) as they leave a drill hole (an excavation of a characteristic shape, Kabat, 1990) in the shell of their prey. Given that these traces are easy to recognize and quantify, they have been widely used to study predation on evolutionary and ecological scales (e.g., Sohl, 1969; Vermeij, 1980; Hansen and Kelley, 1995; Hoffmeister and Kowalewski, 2001; Kosnik, 2005), and latitudinal differences in predation intensity in recent and fossil environments have been suggested (Vermeij, 1993; Hansen and Kelley, 1995; Kelley and Hansen, 2007). For instance, drilling by naticids on recent *Turritella* from high latitudes—e.g., Canada, the Shetlands, and New Zealand—resulted in frequencies of 0% (sample n = 29), 2.9% (n = 34), and 2% (n = 50), respectively (Dudley and Vermeij, 1978). In contrast, low-latitude localities (Mexico and the Philippines) had drilling frequencies of 19% (n = 68) and 68% (n = 138), respectively (Dudley and Vermeij, 1978). For fossil *Turritella* from high latitudes, frequencies of predation by naticids were 20% (n = 519, Paris, Eocene) and 28% (n = 101, United States, Miocene). Low-latitude drilling frequencies on species from the same genus were higher, ranging between 27% (n = 263, Nigeria, Eocene) and 62% (n = 60, Panama, Miocene). Despite these differences, a clear relationship between

drilling predation and latitude has been hard to establish (Schemske et al., 2009), possibly due to the fact that most of the available information comes from the Northern Hemisphere and a few tropical islands; and also because methodological differences between studies may hinder the interpretation of results. For example, naticid drilling frequencies for the Eocene in the United States were higher in Virginia than in the Gulf coast, potentially indicating an equator-ward decrease in predation intensity (Hansen and Kelley, 1995). The number of samples for each area was different (4 vs. 11 respectively), however, and so were the environments the samples came from (inner shelf vs. open ocean). European Miocene gastropods also showed a decrease in drilling frequencies from higher to lower latitudes, but this result was only found for some habitats (Hoffmeister and Kowalweski, 2001). Studying recent bivalves from the east coast of the United States, Alexander and Dietl (2001) found higher naticid drilling frequencies in Florida than in New Jersey when comparing two species. Another contribution looking at recent shell assemblages from Maine to Florida failed to find any clear monotonic trend as naticid drilling predation increased in the Carolinian Province and decreased both to the north and to the south (Kelley and Hansen, 2007). Overall, differences in drilling predation with latitude have been documented for past and recent environments, yet no clear conclusions can be drawn. Moreover, since efforts have not been equally distributed across regions and across drilling predators, more data is needed from high latitudes (Hansen and Kelley, 2003), and from muricid predators.

Despite an extensive coast with variability in water temperature and mollusk composition (Gordillo, 1998b; Balech and Ehrlich, 2008), very few studies concerning drilling predation have been conducted in the South Atlantic. In this regard, the Argentine coast provides an interesting study case given its extension to poleward latitudes and the presence of two distinct biogeographic provinces (Balech and Ehrlich, 2008). These are the Magellan (43°S to 55°S) and Argentine (30°S to 43°S) provinces. The boundary between these provinces has not been clearly established as it varies seasonally between 41°S and 43°S with northward fluctuations of the cold Malvinas current in the winter (Balech and Ehrlich, 2008). In order to be conservative, for this study we establish the southern limit of the Argentine Province to be 43°S. The dominance of different water masses in these two provinces causes water temperatures to be lower in the Magellan Province (3.5 °C to 11 °C, Boltovskoy, 1979) than in the Argentine Province (18 °C to 24 °C, Boltovskoy, 1979). These water temperature differences are one of the main determinants of the molluscan fauna composition of these two regions (Gordillo, 1998b; Pastorino, 2000). In this regard, differences in water temperature could have significant effects on predation rates of marine low-intertidal organisms. Local changes of 3° have been found to decrease predation rates in the Northern Hemisphere muricid *Nucella* (Sanford, 2002). Whether temperature affects predation rates in the South Atlantic remains an open question as the only available information on drilling predation comes from Tierra del Fuego (e.g., Gordillo, 1994, 1998a, 2001; Gordillo and Amuchástegui, 1998; Gordillo and Archuby, 2012a), a paper from

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Buenos Aires (Pastorino and Ivanov, 1996), and two from Patagonia (e.g., Borzone, 1988; Zaixso and Bala, 1995). Interestingly, a muricid (*Trophon geversianus*) seems to be the dominant drilling predator in this area (Gordillo, 1994, and references therein). This muricid dominance provides a novel setting as previous work on spatial variability in drilling predation has focused on naticid predators (e.g., Vermeij, 1980; Allmon et al., 1990; Hansen and Kelley, 1995; Alexander and Dietl, 2001; Kelley and Hansen, 2007).

The information available on water currents indicates that local water temperature decreases toward the south. On a regional scale, this would be observed as a monotonic decrease in water temperature from the Argentine to the Magellan Province. In this context, we put forward the hypothesis that drilling predation will be lower in the Magellan Province (high latitude) than in the southern part of the Argentine Province (intermediate latitude, Fig. 1). Regionally this would be observed as a decrease in drilling frequencies coupled with a decrease in temperature. To test this, we analyze this biotic interaction along a gradient that stretches for 1,000 km in the Patagonian coast. As predators are expected to have a stronger impact on species rather than on communities (Harper, 2003), questions were addressed at the assemblage and species levels. We investigated whether locality and species-specific drilling frequencies (DFs) differed for the Argentine and Magellan provinces. Four localities were sampled from the Argentine Province (Puerto Lobos, Puerto Pirámides, El Doradillo, Puerto Madryn) and seven localities were sampled from the Magellan Province (Playa Unión, Playa Elola, Bahía Bustamante, Rada Tilly, Caleta Olivia, Cabo Blanco, Puerto Deseado). In addition, to better characterize *Trophon* as a predator we also seek to answer the following questions. (1) Do locality and species drilling frequencies show a positive correlation with the abundance of the gastropod? (2) Is the percentage of preferred species in a locality a good proxy for the percentage of drilled fauna? Valve-specific predation and edge drilling were also analyzed in detail for three prey species. Preference for right or left valves was calculated for the bivalves *Brachidontes purpuratus, Aulacomya atra*, and *Venus antiqua*. Preference for either of the valves would be an indicator of the bivalves' life mode (i.e., if it rests on the right or left valve), and we expect this to be manifested by differential drilling frequencies on either valve. Other choices such as wall or edge drilling can help characterize the drilling strategies used by the muricid. Experiments have found that edge drilling reduces the drilling time to a third and that this mechanism is important where potential enemies are abundant (Dietl and Herbert, 2005). As this behavior has been previously recorded for *T. geversianus* (Gordillo and Archuby, 2012a), we quantified it for the mytilids *B. purpuratus* and *A. atra*. Additionally, incomplete and multiple drill holes were calculated for *V. antiqua* and *Crepidula* cf. *onyx,* two prey species that were very abundant in specific localities.

MATERIALS AND METHODS

Geographic Location and Sample Collection

In April 2010, molluscan dead-shell assemblages were sampled at 11 beaches in Argentina (42–48°S), spanning approximately 1,000 km in the Argentine and Magellan Provinces (Fig. 1, Table 1). The area is mostly dominated by hard substrates, and affected by a strong macrotidal regime (Balech and Ehrlich, 2008; Servicio de Hidrografía Naval, 2012) and southwestern winds (45–140 km/h, Camacho, 1979; Bertness et al., 2006). Water temperature values for the localities were obtained from Servicio de Hidrografía Naval (Table 1), and the mean minimum water temperature was correlated with drilling frequencies, as low temperatures have been suggested to decrease feeding rates in invertebrates (Sanford, 2002).

The molluscan death assemblage at each locality was characterized using a minimum of 200 unbroken individuals sampled from the high-
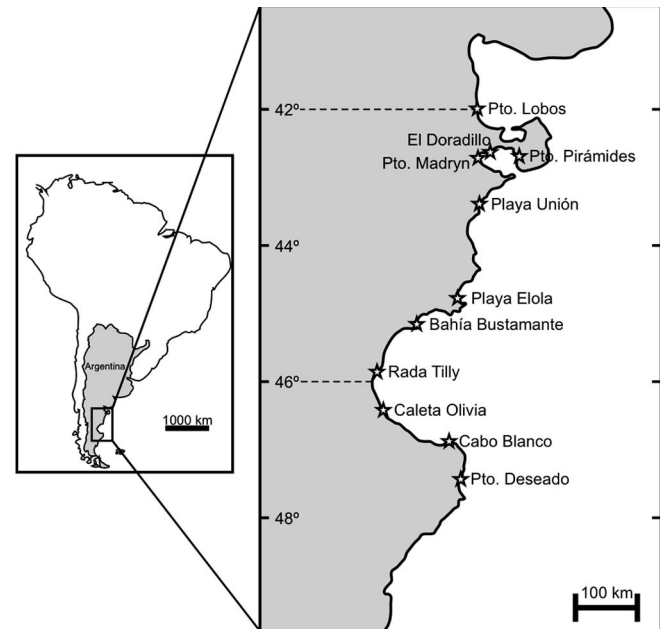

FIGURE 1—Location of studied sites along the coast of Argentina.

tide line. The reasoning behind this quota was to obtain a sample size that would be representative of the dead assemblage species composition and representative for statistical analyses. The high-water mark was sampled every 10 m using 0.5×0.5 m quadrats. Shells were collected from the sediment surface, and in some cases up to 10 cm deep if the beach was pebbly. Depending on density, shells from 10 to 20 quadrats were combined to obtain the 200-individual quota.

Identification of Drill Holes and Calculation of DFs

Samples were wet sieved using nested 10 mm and 1.0 mm sieves. Bivalves and gastropods were identified to the species level whenever possible using published literature (Pastorino, 1994; Núñez Cortés and Narosky, 1997; Aguirre and Farinati, 2000; Forcelli, 2000; Valdovinos and Rüth, 2005; de Aranzamendi et al., 2009; González Wevar et al., 2010). Each gastropod shell with at least a preserved apex was counted as one individual (fragmented or not). Left and right bivalve valves were independently counted and the larger of these plus the number of articulated valves was considered as the minimum number of individual bivalves. Any right or left valve with a drill hole was considered a drilled individual.

Predatory drill holes were identified using the following criteria: (1) holes of a circular shape and regular outline, (2) holes perpendicular to the shell, and (3) in the case of articulated valves, holes that go through only one of the valves (Kelley and Hansen, 2003; Yanes and Tyler, 2009; Sawyer and Zuschin, 2010). Since muricid holes can sometimes resemble naticid ones (Gordillo, 1998a), the identity of the driller was inferred from the presence and abundance of predators in the samples (Klompmaker, 2009). The large majority of drill holes observed, however, were cylindrical in shape (see Gordillo and Archuby, 2012a, and Gordillo and Archuby, 2012b), for a detailed examination of the morphology of drill holes produced by *T. geversianus* on different prey species).

Drilling frequencies were calculated using only unfragmented shells to avoid underestimating the number of drill holes (Yanes and Tyler, 2009). We estimated drilling frequencies for each locality, and each species in each locality using the formula from Kowalewski (2002). The drilling frequency is the number of individuals with at least one predation trace divided by the total number of individuals (excluding fragmentary shells). In the case of species-specific analyses, drill holes

TABLE 1—Sampled localities with their abbreviation, latitude, characterization of substrate type and water temperature (mean annual minimum and maximum values). Data taken from different sources (Boltovskoy, 2010; Helbling et al., 2010; and personal observations, 2010).

Locality	Locality abbreviation	Latitude	Substrate characteristics	Water temperature (°C)
Argentine Province				
Puerto Lobos	PL	41° 59′ 54.2″	Hard substrates of conglomerate and tuff. Sectors with fine sand beaches.	9.7–17.9
Puerto Pirámides	PP	42° 34′ 43.6″	Bottoms with sand and mud, some hard substrates. Sandy beaches. Cliffs.	9.6–16.9
El Doradillo	ED	42° 39′ 27.7″	Bottoms with sand and mud, some hard substrates. Sandy beaches.	9.7–16.9
Puerto Madryn	PM	42° 46′ 56.6″	Bottoms with sand and mud, some hard substrates. Sandy beaches.	9.8–16.9
Magellan Province				
Playa Unión	PU	43° 18′ 31.5″	Beaches with pebbles. Gravel and sand in the inferior horizons. Limestone rockgrounds.	8–18
Playa Elola	PE	44° 50′ 17.5″	Beaches with sandy gravel, hard substrates with basalt; some sandy and muddy.	6.4–16.1
Bahía Bustamante	BB	45° 07′ 42.5″	Rockgrounds alternating with sandy beaches, pebbles, and gravel. Hard and soft bottoms.	7.1–18
Rada Tilly	RT	45° 56′ 37″	Beaches with fine sand, tuff rockgrounds. Infralittoral with muddy and sandy bottoms.	6.5–15.5
Caleta Olivia	CO	46° 29′ 29.6″	Beaches with coarse sand and pebbles. Some rockgrounds in the midlittoral area.	5.2–14
Cabo Blanco	CB	47° 12′ 09.8″	Beaches with gravel and pebbles. Areas with hardgrounds with tidal forests of macroalgae.	4.2–12.9
Puerto Deseado	PD	47° 45′ 24.2″	Gravel beaches, some cliffs with sandy beaches, and sectors with hardgrounds.	4.9–13.5

were recorded as present on either right or left valves, and the position in the valve (wall vs. edge) was also documented. We represent these drilling frequencies as percentage of drilled individuals.

Subsampling Methods

Given the variability in the sample sizes (n = 218 to n = 2117), localities were standardized to the smallest sample size (n = 218, excluding fragmented shells), and resampled 10,000 times without replacement (Efron and Gong, 1983) using the R statistical software (R Development Core Team, 2012). A mean value and 95% confidence intervals were calculated for the locality and *Brachidontes purpuratus* drilling frequencies.

RESULTS

Mollusc Diversity and Abundance

A total of 12,680 individuals were sampled from 11 localities in the Argentine Patagonia. In total, 41 mollusk species were recognized, 21 gastropods (13 families), and 20 bivalves (9 families) (Supplementary Data 1[1]). Local species richness ranged from 10 to 23; Puerto Lobos, Puerto Pirámides, El Doradillo and Puerto Madryn were the localities with the highest values (Table 2). Gastropods were more abundant in the center of the sampled region, while bivalves (mytilids mainly) increased in abundance toward the northern and southern extremes.

TABLE 2—Richness, number of individuals found at each locality (N), and drilling frequencies per shell assemblage (DFs).

Locality	Richness	N	DFs (%)
Argentine Province			
Puerto Lobos	23	1,940	7
Puerto Pirámides	18	1,355	4
El Doradillo	20	1,053	5
Puerto Madryn	19	4,077	3
Magellan Province			
Playa Unión	11	834	36
Playa Elola	13	466	9
Bahía Bustamante	14	830	19
Rada Tilly	14	380	11
Caleta Olivia	11	669	10
Cabo Blanco	11	327	4
Puerto Deseado	10	751	3

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The majority of the molluscs came from the 10 mm sieve fraction, therefore, the drilling predation results that we present are only representative of specimens larger than that size fraction.

Three drilling predators were found in our samples: two muricids and one naticid (Table 3). Single *T. geversianus* individuals were found drilled at two sites. The naticid *Notocochlis isabelleana* was present at two sites in very low abundance.

Spatial Variability in Muricid Predation along a Temperature Gradient

Locality Drilling Frequencies.—Drilling frequencies ranged from 3% at Puerto Madryn to 19% at Bahía Bustamante (Table 2). Playa Unión had an unusually high drilling frequency of 36%. The drilling frequencies for the Argentine and the Magellan groups did not differ significantly (Wilcoxon rank sum test, $p = 0.185$, W = 6.5, no. sites = 11, Fig. 2B). The locality drilling frequencies of the Magellan Province displayed a higher variance than the ones from the Argentine Province (Fig. 2B).

No significant correlation was found between mean low water temperature and locality drilling frequencies (Spearman rank order correlation, $p = 0.906$, r = −0.04). Drilling frequencies, however, were higher (DF: 20%–36%) at mid-temperatures (~7–8 °C), and lower (DF: 3%–4%) at both higher (~10 °C) and lower (~4 °C) water temperatures (Fig. 3B).

Preferred Taxa and Predator Abundance.—The percentage of mytilids (*B. purpuratus*, *A. atra, Mytilus edulis chilensis*, and *Mytilus edulis platensis*) at each locality was not correlated with the percentage of drilled species at a site (Spearman rank order correlation, $p = 0.529$,

TABLE 3—Number of individuals of the potential drilling predators found at each locality.

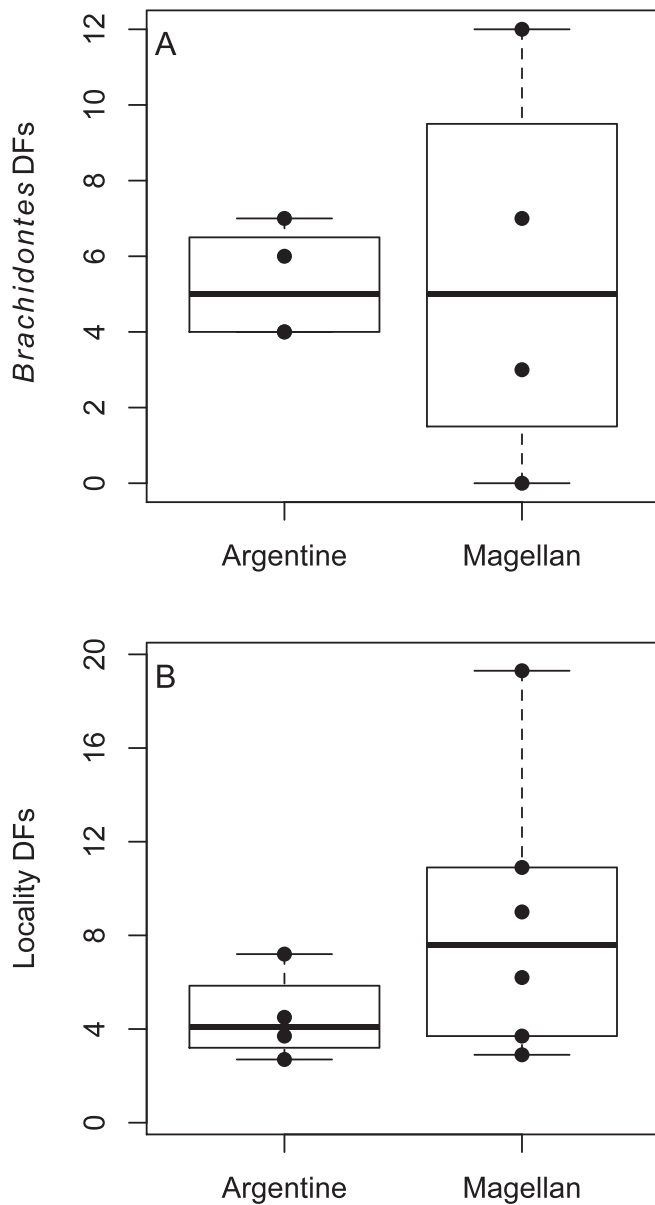| Locality	Trophon geversianus	Trophon plicatus	Notocochlis isabelleana
Argentine Province			
Puerto Lobos	146	-	2
Puerto Pirámides	18	-	-
El Doradillo	17	-	-
Puerto Madryn	122	-	9
Magellan Province			
Playa Unión	9	3	-
Playa Elola	18	-	-
Bahía Bustamante	20	-	-
Rada Tilly	11	-	-
Caleta Olivia	33	-	-
Cabo Blanco	7	3	-
Puerto Deseado	4	-	-

FIGURE 2—Boxplots showing A) *B. purpuratus* drilling frequencies (DFs expressed as %) for the Argentine and Magellan Provinces, B) locality drilling frequencies (DFs expressed as %) for the Argentine and Magellan Provinces. Horizontal bars represent median values, boxes enclose the 25th to 75th percentiles, and whiskers indicate the minimum and maximum values.
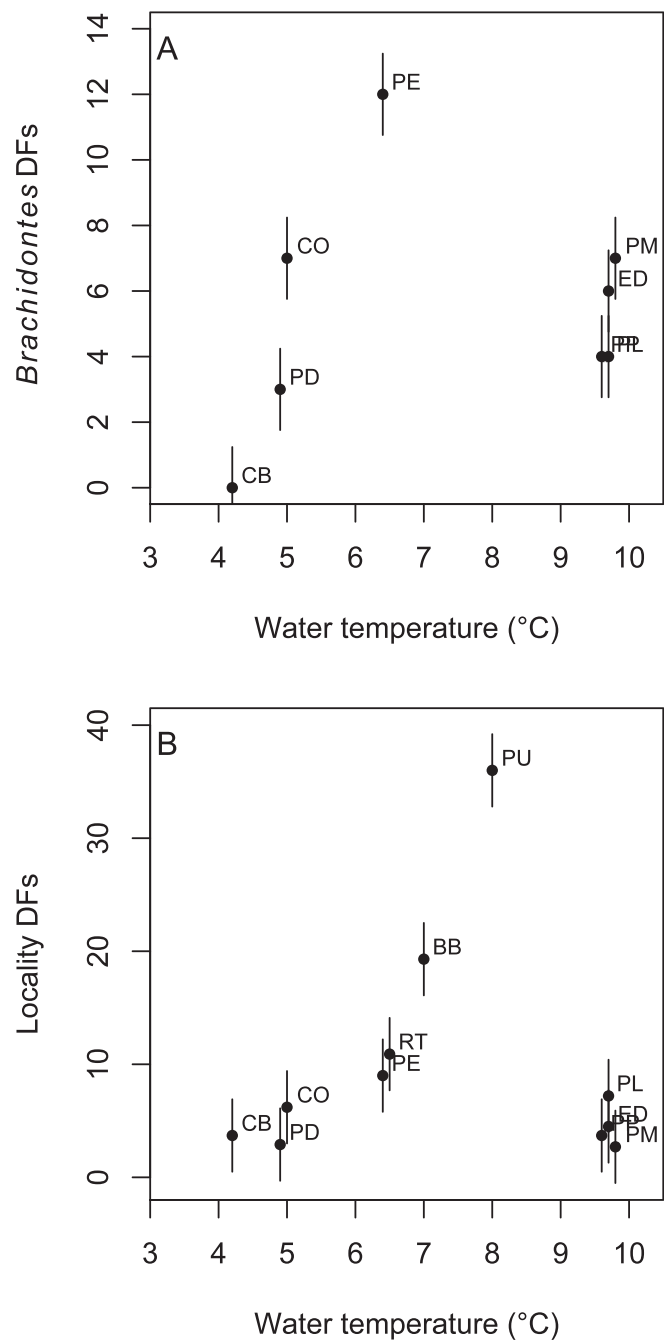

FIGURE 3—Scatter plot showing A) *B. purpuratus* drilling frequencies (DFs expressed as %) and mean minimum water temperature, B) locality drilling frequencies (DFs expressed as %) and mean minimum water temperature. Sites are organized from south (Magellan Province) to north (Argentine Province); locality abbreviations as in Table 1.

r = 0.242, Fig. 4). Additionally, no significant correlation was found between the relative abundance of *T. geversianus* and the drilling frequency at the site (Spearman rank order correlation, $p = 0.257$, r = 0.396).

Species Drilling Frequencies.—Across all localities 16 species were drilled. Puerto Madryn, with the largest sample size, had the highest number of drilled species (9), whereas Playa Unión and Cabo Blanco had the lowest (2) (Supplementary Data 2[1]). In some localities drill holes were seen exclusively on mytilids (Cabo Blanco and Puerto Deseado), and the only site where mytilids were not found drilled was Playa Unión. The species that were drilled in most localities were: *Brachidontes purpuratus* (in 8 out of 11 sites); *Aulacomya atra* (7 sites); *Crepidula dilatata* (5 sites); *Mytilus edulis chilensis* and *Tegula (A.) patagonica* (4 sites); *Mytilus edulis platensis, Brachidontes rodriguezii, Nacella magellanica, Venus antiqua,* and *Siphonaria lessoni* (3 sites); *Crepidula* cf. *onyx, Buccinanops globulosus*, and *Trophon geversianus*

(2 sites). The remaining species were consumed only once: *Nacella delicatissima, Fissurella* spp. and *Olivella tehuelcha.*

As *B. purpuratus* was the most abundant prey species across all sites, drilling frequencies based on standardized resampling data were calculated. Predation intensities ranged between 0% (Cabo Blanco) and 12% (Playa Elola) (Table 4). Similarly to what was found for locality-level DFs, no significant differences were found for the Argentine and Magellan groups (Wilcoxon rank sum test, $p = 1$, W = 8.5, no. sites = 8), and the variance in DFs from the Magellan was higher than the one from the Argentine Province (Fig. 2A).

No significant correlation was found between mean low water temperature and *B. purpuratus* drilling frequencies (Spearman rank
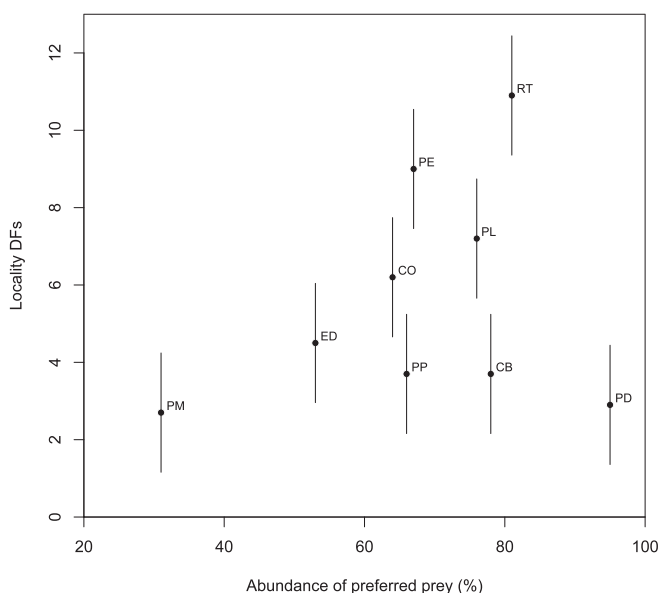
FIGURE 4—Scatter plot showing drilled individuals per locality (DFs expressed as %) and mytilids per locality (%). Locality names as in Table 1.
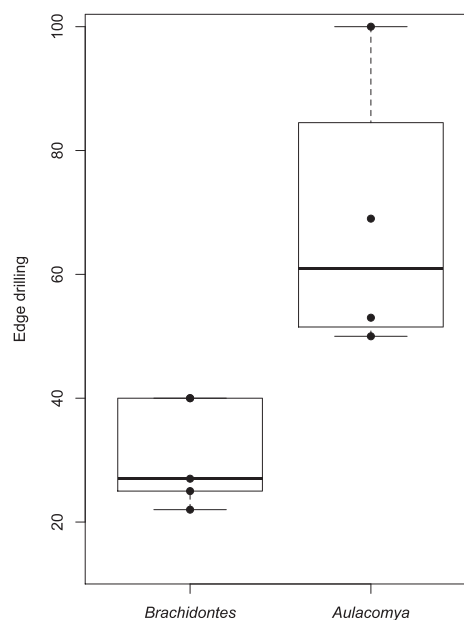

FIGURE 5—Boxplot showing edge drilling (%) for *B. purpuratus* and *A. atra*. Bars, boxes, and whiskers as in Figure 2.

correlation, $p = 0.223$, r = 0484). A similar tendency as the one observed for locality-level drilling frequencies was observed: drilling frequencies were higher (DF: 12%) at mid-temperatures ($\sim 6.5\ °C$), and lower (DF: 0%–5%) at both higher ($\sim 10\ °C$) and lower ($\sim 3\ °C$) water temperatures (Fig. 3A).

Drilling Strategies of the Predator on Specific Prey

Complete Drill Holes.—Four prey species were studied in more detail in order to better understand *Trophons*' drilling behavior. The predator exhibited no valve specific predation on the mytilid *Brachidontes purpuratus* (Wilcoxon rank sum test, $p = 1$, W = 31.5, no. sites = 8) or on *Aulacomya atra* (Wilcoxon rank sum test, $p = 0.751$, W = 14.5, no. sites = 6). Edge drilling accounted for 27% of the drill holes recorded in *B. purpuratus*. In contrast, for the mytilid *A. atra*, 56% of the drill holes were edge drilled (Fig. 5, Table 5). Valve-specific predation in *Venus*

TABLE 4—Drilling frequencies for *Brachidontes purpuratus*, and number of individuals found at each locality (N). 1 = Drilling frequency for *Tawera gayi* from Tierra del Fuego, shells collected using our same methodology (Gordillo, 1994). 2 = Drilling frequency for *Mytilus edulis chilensis* from Tierra del Fuego, shells collected using our same methodology (Gordillo and Archuby, 2012a). 3 = Drilling frequency for *Mytilus edulis chilensis* from Tierra del Fuego; shells were collected randomly by hand along the high-water mark (Gordillo, 1994, unpublished data).

Locality	N	DFs (%)
Argentine Province		
Puerto Lobos	774	5
Puerto Pirámides	473	4
El Doradillo	81	6
Puerto Madryn	358	7
Magellan Province		
Playa Unión	3	0
Playa Elola	170	14
Bahía Bustamante	0	0
Rada Tilly	29	17
Caleta Olivia	191	8
Cabo Blanco	58	0
Puerto Deseado	344	3
Canal Beagle[1]	543	22
Bahía Golondrina[2]	295	16
Cabo San Pablo[3]	300	26

antiqua, was not significant ($p = 0.09$, $\chi^2 = 2.9$), but right valves were drilled twice as often as left valves (9% left versus 19% right).

Incomplete and Multiple Drill Holes.—There was no significant difference between the distribution of incomplete drill holes on the valves of *V. antiqua* ($p = 0.13$, $\chi^2 = 2.3$, Table 5). For the gastropod *Crepidula* cf. *onyx*, incomplete drill holes represented 9% of the total drill holes, and multiple drill holes accounted for 10% of the total (Table 5).

DISCUSSION

Contrary to expectation, no difference in drilling frequencies was found between northern (Argentine Province) and southern (Magellan Province) localities. Locality drilling frequencies were usually <10% in the studied sites with the exception of Playa Unión (36%). Mytilids were the most abundant prey, and the drilling frequencies for *B. purpuratus* ranged from 0% to 12%. No difference in muricid predation between Argentine and Magellan Provinces was found for this species either. Neither predator abundance nor percentage of preferred prey species were verified as predictor variables of drilling frequencies. The predator used different strategies for the different prey species studied.

Muricid Predators

Comparing the abundance of the Naticidae and the Muricidae in our samples, muricids are clearly dominant in Patagonian shallow marine habitats. A recent review of naticids from Patagonia only mentions 13 species, and states that naticid diversity is not as high as it is in other regions (Pastorino, 2005a). In contrast, muricids from the genus *Trophon* are highly diverse (46 species reviewed by Aldea and Troncoso, 2010) and abundant in South America. *T. geversianus* is the most widespread species (Pastorino, 2005b), and the dominant predator in our samples (Table 3). *T. geversianus* and other species of this genus are important predators in Magellan and Antarctic systems based on experimental and field studies (Gordillo, 1994, 1998a; Zaixso and Bala, 1995; Gordillo and Amuchástegui, 1998; Harper and Peck, 2003; Andrade and Ríos, 2007; Andrade et al., 2009). In addition, muricids are expected to be better represented than naticids, which are typical of soft sediment habitats (Kabat, 1990), given that our samples were mostly dominated by epifaunal rocky-shore fauna (mytilids). These

TABLE 5—Valve-specific predation, edge drilling, incomplete (incomplete drill holes/total drill holes) and multiple drilling for the most abundant prey species.

| Species | Valve-specific predation | | Edge drilling | | | Incomplete drilling | | | Multiple drilling (%) |
	Selectivity?	No. sites	Mean (%)	Range (%)	No. sites	Mean (%)	Range (%)	No. sites	
Brachidontes purpuratus	No, *p* = 1	8	27	5–40	6	10	0–23	9	–
Aulacomya atra	No, *p* = 0.75	5	56	7–100	6	6	0–19	6	–
Venus antiqua	No, *p* = 0.09	1 (BB)	–	–	–	3	–	1 (BB)	–
Crepidula cf. *onyx*	–	–	–	–	–	9	–	1 (PU)	10

observations led to the conclusion that most of the drill holes are likely the work of *T. geversianus,* the most abundant drilling predator in this part of South America.

Drilling Frequencies in High Latitudes

Drilling gastropod predation traces were found in all 11 localities, indicating that it is a generalized phenomenon in this area. The predation levels found in this study are similar to those found by Dudley and Vermeij (1978), in which naticid drilling frequencies were calculated from recent *Turritella* museum specimens for several high-latitude localities. Labrador Peninsula in Canada (DF: 0%–2.9%), Alaska (DF: 3.7%), and New Zealand (DF: 2%–19.3%) had predation values comparable to the ones found in this study. Kelley and Hansen (2007) calculated naticid-drilling frequencies of 0% to 3%, and 5% for samples from the Virginian and Nova Scotian Provinces respectively. Similarly, Alexander and Dietl (2001) obtained naticid drilling frequencies of 4% for New Jersey. Our results for drilling predation in Patagonia are also consistent with frequencies obtained for other prey attacked by *Trophon* in Tierra del Fuego (Table 5). These values suggest that muricid predation in the Southern Hemisphere is similar to what has been previously found for high-latitude predation by naticids from the Northern Hemisphere.

Scales of Variability along a Temperature Gradient

Our results show that drilling frequencies are lower at high latitudes (lower temperature) than at lower latitudes (higher temperature). The role of temperature at smaller scales (regional and local) is not clear, however, and local factors may have a stronger incidence in the activity of predators. Even if temperature decreased along the gradient, the expected regional monotonic decrease in drilling frequencies coupled with water temperature was not observed. Looking at each Province in detail, predation did not differ between the Argentine and Magellan Provinces (*p* = 0.122, Fig. 2). The variance in drilling frequencies was lower for the Argentine Province, yet this is not surprising as there were four sites (Puerto Lobos, Puerto Pirámides, El Doradillo and Puerto Madryn) versus seven sites from the Magellan Province (Playa Unión, Playa Elola, Bahía Bustamante, Rada Tilly, Caleta Olivia, Cabo Blanco, and Puerto Deseado). A tendency found both for locality-level and species-specific analyses (*B. purpuratus*) was that drilling frequencies were lower at the lowest and highest temperature values. At mid-temperature, drilling frequencies were approximately three times higher (*p* <0.001, χ^2 = 17.3, no. sites = 10, Fig. 3). This is possibly not directly linked to temperature, as the dominant species at this locality (Bahía Bustamante, DF = 19%) was a semi-infaunal venerid (*V. antiqua*), which may be preferred over mytilids.

On a local level, environmental factors such as water temperature can affect drilling frequencies by altering the physiology and metabolism of marine benthic predators (Sanford, 2002). Within the tolerance limits of an organism, an increase of 4 °C in water temperature could cause biological rates to be 30%–55% higher (Sanford, 2002). Although this remains to be tested experimentally, local differences in temperature do not seem to affect the predatory activity

of *Trophon*. Previous investigations in Tierra del Fuego, where water temperature is lower (average minimum temperature is 2.3 °C, Servicio de Hidrografía Naval, 2012) found drilling frequencies similar to the ones documented here (10%–26%, Gordillo et al., 2011; Gordillo and Archuby, 2012; Table 5). Given the southern origin of this genus (Pastorino, 2005b), this predator may have adapted to cold water temperatures and thus shows no decrease in predatory activity with changes in local temperature toward the south of its distribution. The lack of differences between provinces and of a decrease in DFs on a regional level could be a manifestation of this adaptation. Thus, at least for *Trophon,* the effect of water temperature on DFs at different scales (regional and local) is not as straightforward as predicted.

Is Anthropogenic Impact Recorded on Predation Rates?

The relevance of dead-shell assemblages as tools for conservation and prediction of anthropogenic-related changes in ecosystems has been previously established (e.g., Kidwell, 2007; Dietl and Flessa, 2011). In this regard, one of our most significant findings was that Playa Unión, a site with strong eutrophication (Esteves et al., 1997; Helbling et al., 2010), was an outlier that displayed the highest drilling frequency (36%, Table 2), almost twice as high as the second highest (19%), and more than ten times higher than the lowest (2.7%). The most abundant species at the site (92% of the total specimens found), *Crepidula* cf. *onyx,* has been found to be favored by eutrophic environments (Zhao et al., 2003), and was present in only one site other than Playa Unión. This would be suggesting that the dominance of *Crepidula* is a consequence of a eutrophic environment. The link between this high abundance and high predation is straightforward as the predator is eating what is most abundant. In addition, and despite the low abundance of *Trophon* in the area (2%), the high abundance and low mobility of the prey could explain the high drilling frequency. A possible scenario could be that the species is attacked in high proportion given that it is an easy target as individuals attach themselves one on top of the other forming distinctive chains as part of their mating behavior (Gallardo, 1977). *Crepidula* females also undergo periods of temporary or permanent immobility during the time they are brooding their young (Chaparro et al., 1998); this could also increase their chance of being preyed upon. Finally, whether eutrophication in nutrient-rich marine environments favors higher consumption rates in predators needs to be addressed in future research.

Drilling Strategies of the Predator on Specific Prey

Complete Drill Holes.—Experimental studies carried out by Gordillo and Archuby (2012a) in Tierra del Fuego showed that *T. geversianus* exhibits different drilling behavior when attacking different mytilid prey species. These experimental results are in agreement with what we found in dead-shell assemblages. For the mytilids *B. purpuratus* and *A. atra,* no preference for left or right valves was found (Table 5). Edge drilling was the predominant strategy used by the muricid to feed on these bivalves, accounting for 27% and 56% of the drill holes in *B. purpuratus* and *A. atra* respectively (Table 5, Fig. 5). Gordillo and Archuby (2012a) suggested that the ribs on the shells of these species

may be the reason the gastropod chooses edge over wall drilling (especially for *A. atra*), as wall drilling would take longer due to the thick ribs. It is possible that the use of edge drilling reduces the time *Trophon* is exposed to potential predators, and it could also be a less energy-intensive strategy as well.

Two other prey species that were very abundant in only two sites were *V. antiqua* and *C.* cf. *onyx.* In *V. antiqua* drill holes always occurred on the walls, and not on the edges. Valve specificity analyses indicated no preference for right or left valves of the venerid (Table 5).

Incomplete and Multiple Drill Holes.—For *Crepidula,* incomplete drill holes represented 9% of the attacks and multiple drill holes 10% of the attacks. This pattern may reflect the lack of mobility in brooding females and the chain mating behavior previously mentioned (Gallardo, 1977; Chaparro et al., 1998).

Potential Biases in the Estimation of Drilling Frequencies

The Role of Other Consumers.—Drilling predation is only one of several types of predation in coastal marine systems. Sea stars, crustaceans, fish, and birds also consume mytilids and other molluscs. Thus, the role of predatory snails could depend on the predatory pressure by local sea stars, crabs, and fish that may be reducing their efficiency by density-dependent regulation. The activity of durophagous crabs has been known to lead to overestimations of drilling frequencies as the crushed shells will be lost from the death-assemblage (Vermeij et al., 1989). Given that there is insufficient information on crushing predators in Patagonia, the magnitude of this predation or its potential impact on our drilling frequency calculations is difficult to determine. Techniques like the Vermeij Crushing Analysis (Stafford and Leighton, 2011) could be used in the future to assess the impact of crushing predators in these environments.

Taphonomic Biases.—Preservational biases could be important if drilled and undrilled shells have different probabilities of being preserved or sampled. Roy et al. (1994) found that drilled valves are significantly more likely to undergo fragmentation than undrilled valves. To account for this variation, Roy et al. (1994) suggested considering the degree of fragmentation of the shell assemblages. If fragmentation is high, then drilling frequencies will likely be underestimated. In our case, fragmentation at the different localities varied between 14% and 47%. The degree of fragmentation was not correlated with drilling frequencies (Spearman rank correlation, $p = 0.95$, $r = 0.8$), so taphonomy is unlikely to be driving the observed pattern. Biased postmortem transportation can also affect the degree of representation of shells from different environments in the samples. As all of our samples come from different sites, the degree of preservation is expected to vary given varying local conditions; however, most of the species are found living on rocky shores, suggesting that these death assemblages are primarily representing the upper part of the intertidal community, and possibly there is an underrepresentation of the soft subtidal environments.

An added taphonomic bias is the presence of fossil assemblages along the coast of Patagonia, which could potentially mix with the samples we collected. Egidio Feruglio (1949) described most of these assemblages in a pioneering work on the molluscs from marine terraces in Patagonia. Several of the horizons he described were found during our sampling, therefore, we can be confident that the samples used in this study do not belong to fossil assemblages.

Implications for the Fossil Record of Drilling Predation

Drilling predation is the biotic interaction with the most well-known fossil record (Kowalewski et al., 1998). This is reflected by the fact that most contributions on this topic have been made by paleontologists or in a paleontological context (e.g., Allmon et al., 1990; Hansen and Kelley, 1995; Harper, 2003; Dietl et al., 2004; Klompmaker, 2009; among many others). Given that recent drilling predation is understudied, this

contribution offers a recent baseline that can be used to interpret patterns observed from high latitudes sites in the fossil record. The fact that the fossil record of drilling predation for muricids is less abundant than the one from naticids could limit the extrapolation of our results. Fossil muricids are abundant in Patagonia from the Oligocene onward, however (Griffin and Pastorino, 2005), and we think that rather than being a limitation, the study of muricid drilling predation in fossil and recent molluscs from Patagonia can provide novel insights that so far are not available from anywhere else in the world. Moreover, the fact that *Trophon* selected mytilid prey, and displayed different drilling strategies for the different species, sets a precedent for feeding preferences. Knowledge of this kind of behavior is lacking from the fossil record and it would be interesting to examine if it is limited to recent muricid genera or when it evolved.

CONCLUSIONS

1. We provide the first data on spatial variability for muricid predation in high latitudes of the Southern Hemisphere. Overall, drilling frequencies were generally lower than 10%, strengthening the idea that drilling frequencies for high-latitude environments are lower than those documented for low latitudes.

2. Our data also suggests that muricid predation varies spatially; however, this does not seem to be related to changes in water temperature along this gradient, as the Argentine and Magellan Provinces showed similar drilling predation values. Thus, there is not a clear relationship between water temperature and drilling predation at different scales.

3. A remarkably high drilling frequency in one site with high eutrophication may indicate that the impact of humans on recent marine environments can be recorded in dead-shell assemblages.

4. The drilling frequencies at locality or species level were not correlated with the abundance of the drilling gastropod, or with the abundance of the preferred prey.

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