

Effects of a high-risk environment on edge-drilling behavior: inference from Recent bivalves from the Red Sea

Devapriya Chattopadhyay, Martin Zuschin, and Adam Tomašovič

Abstract.—Edge-drilling is an unusual predation pattern in which a predatory gastropod drills a hole on the commissure between the valves of a bivalve. Although it is faster than wall drilling, it involves the potential risk of amputating the drilling organ. We therefore hypothesize that this risky strategy is advantageous only in environments where predators face high competition or predation pressure while feeding. The high frequency of edge-drilling (EDF, relative to the total number of drilled valves) in a diverse Recent bivalve assemblage from the Red Sea enables us to test this hypothesis, predicting (1) a low EDF in infaunal groups, (2) a high EDF in bivalves with elongated shape, (3) high incidence of edge-drilling in groups showing a high wall-drilling frequency, and (4) high EDF in shallow habitats. We evaluate these predictions based on >15,000 bivalve specimens. Among ecological attributes, we found substrate affinity and predation intensity of a species to be good predictors of edge-drilling incidence. Infaunal taxa with high length/width ratio have a low EDF, in accordance with our predictions. Predation intensity is also a significant predictor of edge-drilling; groups with high predation intensity show higher incidence of edge-drilling, confirming our prediction. Although water depth fails to show any significant effect on EDF, this analysis generally supports the high-risk hypothesis of edge-drilling incidence because shallow depths have considerable microhabitat variability. Classically the drill hole site selection has often been linked to predatory behavior. Our study indicates that prey attributes are also crucial in dictating the behavioral traits of a driller such as site selection. This calls for considering such details of the prey to fully understand predation in modern and fossil habitats. Moreover, this perspective is important for tackling the longstanding riddle of the limited temporal and spatial distribution of edge-drilling.

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Introduction

Predation is an important agent of natural selection, and studying predator-prey interactions in deep time helps evaluate its effect on the diversity, evolution and distribution of a group (Vermeij 1977, 1987; Roy 1996; Kelley et al. 2003; Huntley and Kowalewski 2007). Predator-prey systems involving drilling predators are especially relevant because the fossil evidence of predation can be analyzed quantitatively. Predatory drill holes have been studied in detail in Recent (e.g., Kitchell et al. 1981; Kabat 1990; Kelley and Hansen 2003; Sawyer and Zuschin 2010) and in fossil assemblages (e.g., Kabat 1990; Kowalewski et al. 1998; Kelley and Hansen 2003; Harper 2003, 2006; Huntley and Kowalewski 2007). Such studies have revealed that various aspects of the drill hole (such as size, shape,

position) provide important information about predator identity and behavior. One such aspect is the position of the drill hole (Kelley and Hansen 2003 for review).

The nonrandom distribution of drill holes on a prey shell is known as site-stereotypy of a drilling predator. Two of the five extant families of drilling predators, Muricidae and Naticidae, show some degree of site-stereotypy in bivalves (Hughes and Dunkin 1984; Kelley 1988; Roopnarine and Beussink 1999; Dietl et al. 2001; Chattopadhyay and Dutta 2013), gastropods (Berg and Nishenko 1975; Dietl and Alexander 2000), and in other invertebrate prey (Hart and Palmer 1987; Klompmaker 2011). Some authors have reported less selectivity by muricids than naticids (Stump 1975; Thomas 1976; Roopnarine and Willard 2001), which may reflect

differences in their drilling behavior. Naticids envelop prey in their foot and manipulate their prey much more than muricids do (Carriker 1981). Muricid gastropods search for and drill prey epifaunally, although they may also dig up shallow infaunal prey; following detection of prey, they select a site and produce a drill hole without enveloping the entire prey (Carriker 1981). These families of drilling gastropods appear in the Cretaceous (but see Bardhan et al. 2012a). Fossil evidence, however, shows that drilling gastropods evolved to select a specific site on the prey shell even before the Cretaceous (Kabat and Kohn 1986). Stereotypic behavior is most commonly reported from the Cenozoic (Kitchell et al. 1981; Kelley 1988; Kelley and Hansen 2003 and references therein), but has also been documented from the Paleozoic (Leighton 2001; Deline et al. 2003) and Mesozoic (Harper 2003; Chattopadhyay 2011; Bardhan et al. 2012b). It has often been argued that this site selectivity is guided by the cost-benefit ratio of an attack (Kitchell et al. 1981; Chattopadhyay and Baumiller 2009). Natural selection favors those predators that reduce drilling time because they are less susceptible to losing their prey to kleptoparasites, or to being eaten themselves by other predators (Morissette and Himmelman 2000; Ishida 2004). Drillers could reduce their predation time substantially by drilling a bivalve at the valve edge instead of drilling through a valve wall (Dietl and Herbert 2005). Hence, cost-benefit models predict that the bivalve edge is one of the best places to drill (Kitchell et al. 1981) and therefore should be chosen preferentially by drilling predators.

Edge-drilling is rare in the fossil record prior to the Cenozoic (Vermeij 2001), and detailed studies of drilling in Cenozoic assemblages frequently have reported an absence of edge-drilling (e.g., Anderson et al. 1991; Kelley and Hansen 1993, 1996, 2003; Hoffmeister and Kowalewski 2002; Chattopadhyay and Baumiller 2010; Sawyer and Zuschin 2011). However, edge-drilling is commonly observed in very shallow habitats in Recent assemblages (Taylor 1980; Vermeij 1980; Ansell and Morton 1987). The rarity of edge-drillings in the fossil record resulted in a

riddle from the cost-benefit perspective, and this phenomenon has thus invited contradictory views about its true implication for predatory behavior (Vermeij and Carlson 2000; Vermeij 2001; Vermeij and Roopnarine 2001; Dietl and Herbert 2005).

Edge-drilling has been reported as far back as the Mississippian (Deline et al. 2003), but it became quantitatively important only in the latest Neogene in warm-water seas (Vermeij 2001). Both parasites (capulid gastropods) and predators (muricid and naticid gastropods) produce such holes. Naticids are known to create edge-drills in bivalves such as lucinids and venerids (Vermeij 1980; Ansell and Morton 1987; Mondal et al. 2012). Muricids also produce edge-drills on diverse bivalve groups including mytilids and venerids (Wells 1958; Patterson Edward 1992; Morton 1994; Vermeij and Carlson 2000; Dietl et al. 2004; Gordillo and Archuby 2012; Martinelli et al. 2013).

It is argued that this strategy, although beneficial, involves some undesirable cost. The cost is the risk of amputation of the drilling organ while the prey closes its valves during a drilling attack (Burrell 1975; Roller et al. 1984). Accordingly, one hypothesis holds that this strategy is adopted only during times of high competition and/or high predation, when the gain from a quick and successful attack strongly outweighs the potential risk (Dietl et al. 2004). This view is supported by some neontological experiments and fossil data (Vermeij and Roopnarine 2001; Dietl et al. 2004; Mondal et al. 2012). Using behavioral experiments with a modern predator-prey system, Dietl et al. (2004) demonstrated that muricid drillers employ the edge-drilling strategy in the presence of conspecific snails ("high-risk" scenario). They also argued that the post-Pliocene decline in edge-drilling is caused by such a "low-risk" scenario; the population of drilling predators was smaller and weaker than their Pliocene counterparts, resulting in a reduced competitive stress.

Before evaluating such claims in deep time, however, it is important to validate the same in Recent assemblages. Besides conducting neontological experiments on Recent bivalves

in captivity, studies should also be conducted on specimens in their natural habitats because gastropods often behave differently in captivity (Kowalewski 2004). Moreover, the position of drill holes is dictated by prey-handling by the predator (Carriker 1981), which in turn may be influenced by prey size and shape (Ansell 1960; Stump 1975; Kitchell 1986). Nonetheless, factors such as these have never been critically documented for the incidence of edge-drilling. Moreover, recent studies documented that ecological attributes of prey (such as feeding habit and substrate preference) play an important role in predator-prey interactions (Sawyer and Zuschin 2010; Jackson and Leonard-Pingel 2011). Apart from the ecological attributes, the environment (such as bathymetry, habitat) can also play an important role in the dynamics of such interactions, as indicated by the spatial variance of drilling patterns (Hansen and Kelley 1995; Kelley and Hansen 2007). Nonetheless, the effects of prey-specific attributes and environmental factors on drilling stereotypy, and on edge-drilling in particular, remain poorly explored.

Using available experimental data (Ansell and Morton 1987; Dietl et al. 2004; Mondal et al. 2012), we have developed several predictions on the relationship between edge-drilling incidence and the ecological and environmental attributes of prey that can be evaluated with interspecific analyses. We evaluate these hypotheses using data from Recent bivalve assemblages.

1. Dependence on prey substrate affinity: Infauna is less exposed to predation compared to epifauna and semi-infauna. Even when infaunal prey are exposed to infaunal predators, the overall predation pressure is more at the sediment/water interface than inside the sediments (Vermeij 1977). Hence, we expect to find a lower incidence of edge-drilling in infauna ("low-risk environment"). Among epi- and semi-infauna, byssally attached individuals are not easily manipulated by their muricid drillers. We expect to see higher edge-drilling in those because it is difficult for the predator to access the central part of the shell.

2. Dependence on shape: Because the life habits of bivalves correlate with shell shape (e.g., Stanley 1972; Oliver and Allen 1980), we also expect a relationship between shape and edge-drilling frequency. Often bivalves that live in a colony by attaching themselves using byssal threads have an elongated shape. We expect to see a higher edge-drilling frequency in those.

3. Dependence on drilling predation pressure: Drilling predators face a "high-risk environment" when they pursue a prey that is most desirable by multiple individuals. Hence, an increase in drilling predation pressure should increase the incidence of edge-drilling.

4. Dependence on water depth: Predation is generally higher in shallow habitats (Vermeij 2001). We should, therefore, find a higher incidence of edge-drilling in shallower waters ("high-risk environment").

Materials and Methods

We used data from Recent bivalve assemblages sampled in their natural habitat, comprising more than 15,000 shells from a shallow water bay (max. depth 52 m) in the northern Red Sea (Zuschin and Oliver 2003, 2005).

Study Area

The Northern Bay of Safaga in the Red Sea is a coral-dominated, shallow-water area stretching approximately 10 km from north to south and approximately 7 km from east to west. It exhibits a complex bottom topography including islands, rock bottoms, reefs and various types of soft bottoms extending down to more than 50 m water depth (Fig. 1). The annual water temperature range is 21–29°C, and salinity is 40–46‰, both without any obvious depth gradient owing to complete water mixing. The tidal range is <1 m (Piller and Pervesler 1989). Terrigenous (thus nutrient) input occurs mainly along the coast and is due to fluvial transport during flash floods, local erosion of impure carbonate rocks and aeolian transport by the prevailing northerly winds (Piller and Mansour 1990). Water energy is relatively weak, but a complex current pattern influences facies

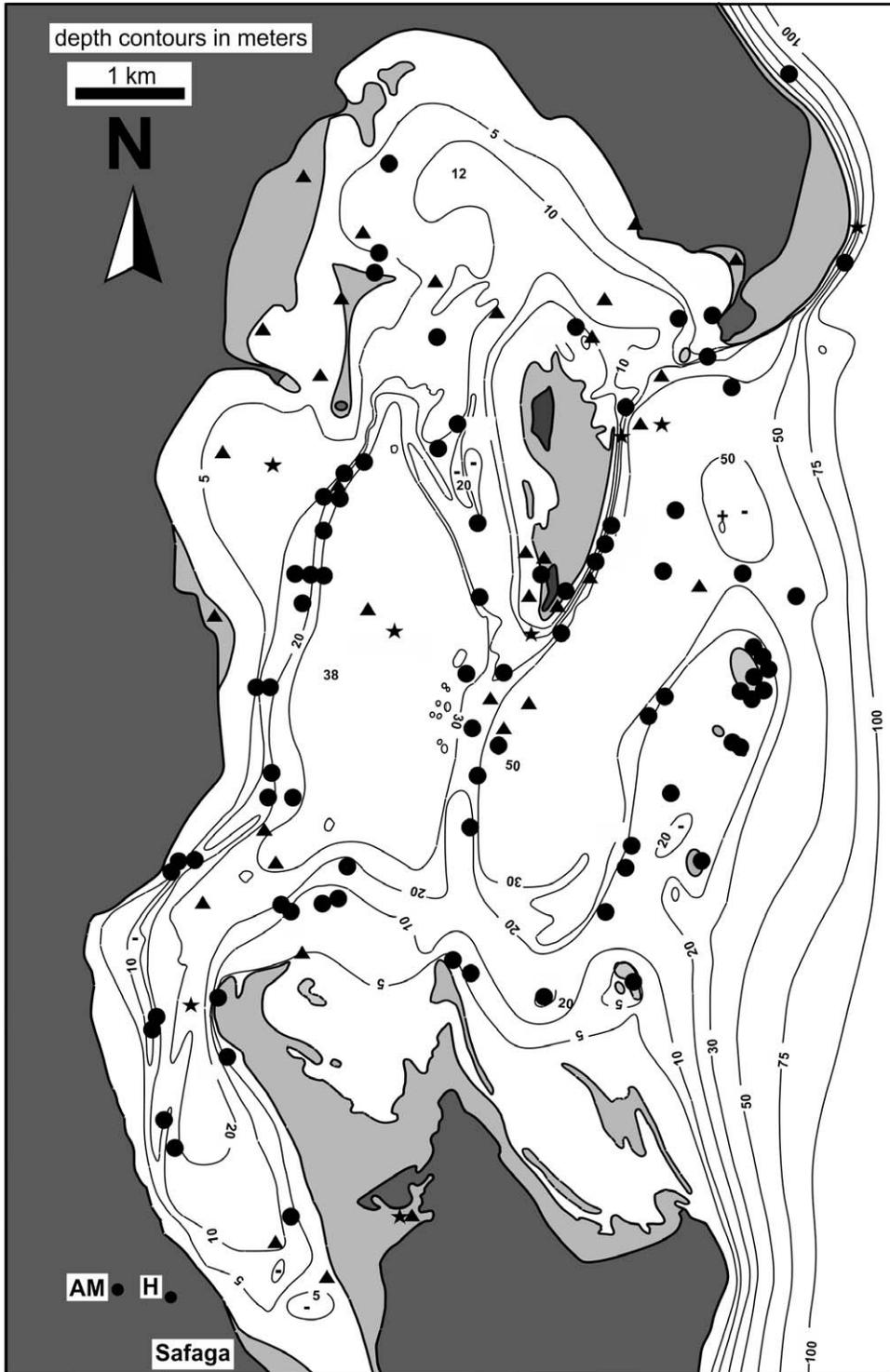


FIGURE 1. Map of study area showing sampling localities. Circles represent quantitative hard substrata samples, stars quantitative sediment samples, and triangles qualitative samples (mostly from soft substrata). AM, aerial mast; H, Safaga Hotel.

development. The sedimentary facies include mud, muddy sand, muddy and sandy seagrass, coral sand, and terrigenous sand of the mangrove channel (Piller and Pervesler 1989; Piller and Mansour 1990; Piller 1994; Zuschin and Hohenegger 1998).

Sampling

This study is based on three major sampling programs, which covered soft substrata and hard substrata and included both quantitative and qualitative samples taken from the intertidal to 52 m depth. All shells used for this study were collected from the sea-floor or from the uppermost 30 cm of the sediment, i.e., the taphonomically active zone (Davies et al. 1989). Actualistic studies suggest that most shells (especially the huge amount of juveniles) in this zone in carbonate environments are young (mostly in the range of decades), although significantly older shells can occur at such depths (Kidwell et al. 2005; Kosnik et al. 2009). The fauna in the soft substrata was strongly dominated by dead individuals, which are estimated to contribute >99% to total faunal composition (Zuschin and Hohenegger 1998). Although living molluscs dominated on the hard substrata (Zuschin et al. 2000), mostly dead individuals were collected and analyzed for the purpose of this study.

Quantitative Data from Soft Substrata.—For the quantitative analysis of bivalves inhabiting soft substrates, we studied 13 standardized bulk samples taken by scuba diving at eight stations (one with four samples, two with two samples, and five with one sample each). A steel cylinder with a diameter of 35 cm and a volume of 29 dm³ was pushed into the sediment and the uppermost 30 cm was sieved with a 1-mm-mesh net. (For more details on soft substrata stations referral is made to Zuschin and Hohenegger 1998 and Zuschin and Oliver 2003.) All sedimentary facies except the mangrove channel are represented by more than one station. Their water depth ranges from shallow subtidal to 40 m. Most of these stations (six stations; 46%) are located in water depths of 10 m or less, two stations (15%) in 11–20 m, two stations (15%) in 21–30 m, and three stations (23%) in 31–40m.

Quantitative Data from Hard Substrata.—Bivalves were studied in different intertidal and subtidal hard substrata at 74 stations in Safaga Bay with a 0.25 m² aluminum square frame. Samples were taken along depth-parallel transects. Living individuals within the frame were typically only counted, dead individuals were mostly collected, and only dead specimens were used in this study. Along the frame-transects, a mean of 4.4 m² (± 2.0) of seafloor was investigated per station, with a range of 1–11 m². For more details on hard substrata stations referral is made to Zuschin et al. (2000, 2001) and Zuschin and Oliver (2003). The sampling sites cover all major subtidal hard substrata, and the water depth of stations ranges from intertidal to 40 m. Most samples (50%) were taken at depths of 10 m or less (37 stations): 25 stations (8%) between 11 and 20 m, eight stations (8%) between 21 and 30 m, and four stations (5.4%) between 31 and 40 m.

Qualitative Samples.—During the initial mapping of bottom facies (Piller and Pervesler 1989), numerous samples (mostly from soft substrata) were taken from locations that were widely distributed across the bay. Additionally, shells were collected close to most of the quantitative hard substrata stations and during dives, from around (mostly deeper-water) soft substrata stations. The water depth of qualitative samples ranges from intertidal to 52 m. Again, most of the qualitative samples (49 samples, 47.1%) were taken in depths shallower than 10 m; 26 samples (25%) were taken between 11 and 20 m, 13 samples (12.5%) between 21 and 30 m, 12 samples (11.5%) between 31 and 40 m, 3 samples (2.9%) between 41 and 50 m, and 1 sample (1%) from below 50 m. All samples taken below 40 m are qualitative.

Ecological Guilds and Environment

The species found in Safaga Bay were classified into three life habits based on substrate relationship (epifaunal, semi-infaunal, and infaunal), seven finely subdivided substrate guilds (epibyssate, free-lying, cementing, endobyssate, crevice-dwelling, infaunal, and commensal), and four trophic guilds (suspension feeders, deposit feeders,

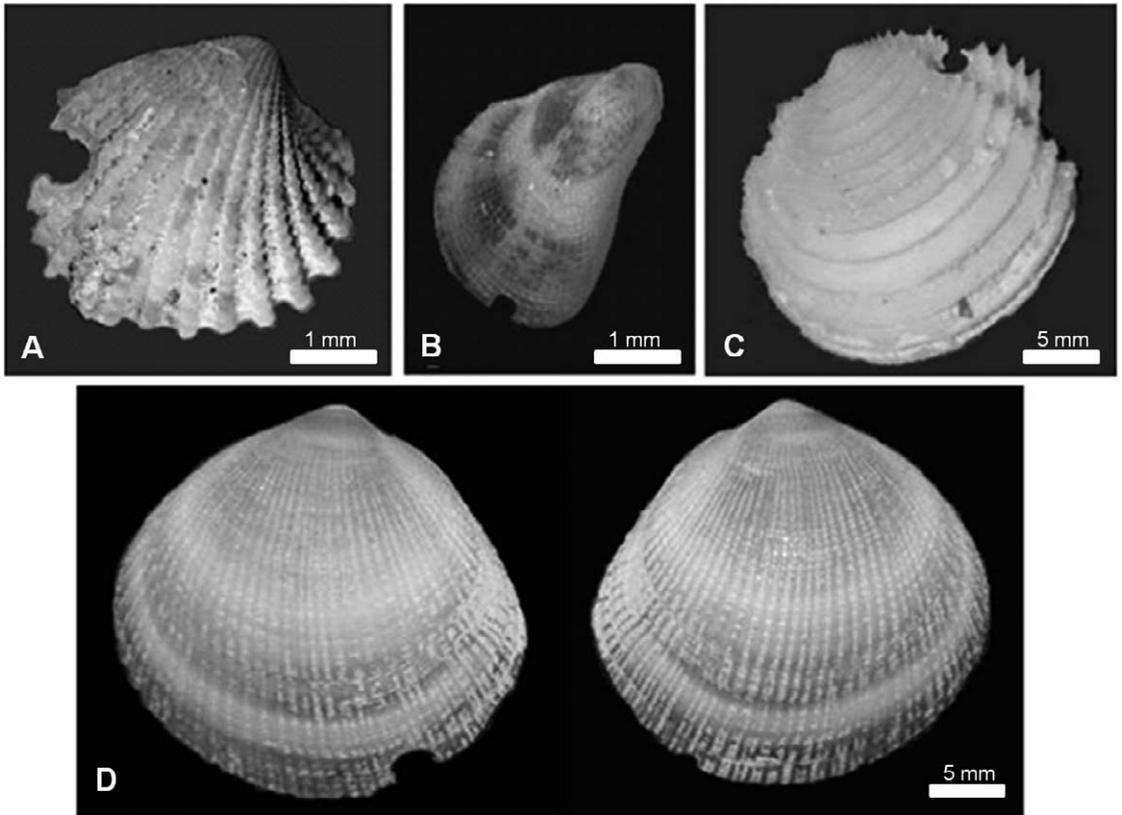


FIGURE 2. Incidences of edge-drilling in various bivalve species. A. *Cardites akabana*, B. *Septifer* sp., C. *Lamellolucina dentifera*, D. *Limopsis multistriata* (two valves of the same individual).

chemoautotrophs, and zooxanthellates). The samples were collected from five environments differing in substrate type and grain size: fine-grained bioclastic carbonate sediment, coral sand, mangrove sand, reef and rock bottom.

Detection of Predation Traces

Intact valves were counted and studied for traces of drilling predation. We considered a drill hole to be edge-drilled only if the boundary of the hole intersected the commissural line (Fig. 2). Although not all of the edge-drills affected the valves equally, we did not discriminate between different degrees of commissural interruption. The drill holes made by muricids are quite different from those of naticids in their morphology; whereas muricid drilling produces a cylindrical drill hole, naticid drill holes tend to be parabolic with a central boss visible in an incomplete hole (Kabat 1990). However, this difference is

quite difficult to recognize in many edge-drillings. Moreover, it was logistically challenging to identify the predator type for each drill hole for the entire collection. We therefore did not differentiate between muricid and naticid drillings while studying edge- or wall-drilled holes.

Shape and Size

We measured the length and height of those species represented by more than 20 specimens per station with the following protocol. The specimen size is represented by the binary logarithm of the geometric mean of length and height (Kosnik et al. 2006). We used three measures of per-station species size: (1) the maximum size of each species, based on the largest specimen sampled at each station; (2) the mean size of each species based on a small number (~5) of randomly chosen adult specimens sampled at each station; and (3) the minimum size of each species, based on

the smallest specimen among the five randomly chosen adult specimens. Therefore, for each species at each station, we calculated the maximum, mean, and minimum of logarithmic geometric mean size. The shape is approximated by the ratio of length (a) and height (b). For larger specimens, we measured the length and height using Vernier calipers (± 0.1 mm). Smaller shells were examined under a LEICA MZ12 binocular microscope and measured using KS Run digitization software.

Drilling Frequency

We defined the EDF as the proportion of half the number of edge-drilled valves relative to the sum of wall-drilled valves and half of edge-drilled valves. We measured EDF at various taxonomic levels. First, to investigate the effects of water depth on EDF, we pooled all specimens regardless of their species assignment, and computed the EDF for each station representing a unique depth. Second, to investigate the effect of size and shape on EDF, we calculated the species-specific EDF separately for each station. Similarly, we computed total EDF at the order, superfamily, and family level. Third, to evaluate the effect of substrate affinity, attachment strategies, feeding type, and habitat at broader spatial scales, we pooled all specimens into these groups, regardless of station and species assignment; later a per-region EDF for the whole Safaga Bay was computed for each category. In all cases, we studied the species represented by more than 20 individuals (40 valves) per sample.

In order to test the effect of drilling predation pressure on incidence of edge-drilling, we defined a measure of predation intensity as WDF; it is calculated as the number of wall-drilled valves divided by half of the sum of non-drilled and wall-drilled valves (Kowalewski 2002), thus excluding edge-drilled valves. Specimens are represented either by disarticulated valves or by shells. Our drilling frequency indices refer to the frequency of drilled individuals, not to the frequency of drilled specimens—they account for the effects of disarticulation and for the fact that wall-drilling affects just one valve where-

as edge-drilling affects both valves. The measure of edge-drilling incidence (EDI) for this specific test is defined as the number of edge-drilled valves divided by the sum of non-drilled and edge-drilled valves (the correction for the number of disarticulated valves is unnecessary in this case because edge-drilling usually leaves a signature in both valves). This measure is therefore independent of wall-drilling frequency. This measure might underestimate the true incidence if edge-drillings are asymmetric and much smaller in one of the valves because such valves are less likely to be distinguished as edge-drilled; such edge-drilling asymmetry is not frequent in our material. The total drilling frequency (TDF), measuring the number of edge-drilled plus wall-drilled individuals relative to all individuals, is computed as the sum of the number of wall-drilled valves and half of the number of edge-drilled valves, divided by half of the sum of all valves.

Analyses

We compared the EDFs among higher taxa and among ecological guilds by using the chi-square test. We used Spearman Rank correlation to measure the correlation of EDF with size, shape, and depth. We estimated the effects of continuous (size, shape, and WDF) and ordinal variables (epifauna – 1, semi-infauna – 2, and infauna – 3) on per-species per-station EDF in simple (taking each predictor separately) generalized linear models (GLM) and in multiple GLM (evaluating partial effects of all predictors simultaneously) (Quinn and Keough 2002). The effects of depth on per-station EDF (for all species and for selected families) were assessed in a simple GLM. We used the logit-link functions and quasibinomial variance functions suitable for proportions (McCullagh and Nelder 1989). Such models allow response variables (EDF) to range between 0 and 1 and errors to be not normally or uniformly distributed. The “quasi” function adds a parameter to the variance if data are underdispersed or overdispersed relative to the variance expected from binomial processes. All statistical analyses were performed in PAST 2.12 (Hammer et al. 2001) and R (R Core Development Team 2012).

TABLE 1. Taxonomic summary of drill hole data pooled across all samples for families of bivalves.

Order	Superfamily	Family	Total valves	WDF	EDF
Arcida	Arcoidea	Arcidae	316	0.04	0.00
		Glycymerididae	771	0.45	0.06
Cardiida	Limopsoidea	Limopsidae	129	0.37	0.21
	Arcticoidea	Trapezidae	4	0.00	0.00
	Cardioidea	Cardiidae	1115	0.07	0.00
	Chamoidea	Chamidae	177	0.00	0.00
	Cyamoidea	Sportellidae	6	0.33	0.00
	Galeommatoidea	Galeommatidae	4	0.00	0.00
		Lasaeidae	5	0.40	0.00
	Gastrochaenoidea	Gastrochaenidae	0	0.00	0.00
	Glossioidea	Glossidae	2	0.00	0.00
	Mactroidea	Mactridae	10	0.00	0.00
		Mesodesmatidae	5	0.00	0.00
	Tellinoidea	Psammobiidae	33	0.00	0.00
		Semelidae	266	0.08	0.00
		Solecurtidae	35	0.00	0.00
Tellinidae		1659	0.02	0.05	
Ungulinoidea	Ungulinidae	80	0.23	0.00	
Veneroidea	Veneridae	1700	0.21	0.06	
Carditida	Crassatelloidea	Carditidae	571	0.14	0.19
Lucinida	Lucinoidea	Lucinidae	6151	0.23	0.06
	Thyasiroidea	Thyasiridae	1	0.00	0.00
Mytilida	Mytiloidea	Mytilidae	478	0.11	0.18
Nuculida	Nuculoidea	Nuculidae	2	0.00	0.00
Ostreida	Ostreidea	Gryphaeidae	240	0.12	0.00
		Ostreidae	45	0.00	0.00
	Pinnoidea	Pinnidae	13	0.00	0.00
	Pterioidea	Malleidae	47	0.00	0.00
		Pteriidae	49	0.00	0.00
Pectinida	Anomioidea	Anomiidae	14	0.00	0.00
	Limioidea	Limidae	77	0.08	0.00
	Pectinoidea	Pectinidae	95	0.00	0.00
		Spondylidae	91	0.31	0.04
	Plicatuloidea	Plicatulidae	4	0.00	0.00
Pholadida	Myoidea	Corbulidae	849	0.08	0.10
		Myidae	1	0.00	0.00
Poromyida	Cuspidarioidea	Cuspidariidae	1	0.00	0.00
Solemyida	Manzanelloidea	Nucinellidae	116	0.03	0.00
	Solemyoidea	Solemyidae	1	0.00	0.00
Solenida	Solenioidea	Pharidae	1	0.00	0.00
Thraciida	Thracioidea	Periplomatidae	1	0.00	0.00

Results

A total of 15,615 valves of bivalve molluscs were studied, representing 174 bivalve species from 41 families (Table 1) from diverse ecological guilds (Table 2) and substrates (Table 3). The five most abundant bivalve species account for 46.5% of the total bivalve assemblage. The total proportion of edge- and wall-drilled individuals (TDF) of the fauna is 23%; the wall-drilled individuals account for 21.5%, the edge-drilled individuals for 1.5%.

Effect of Shape on EDF

EDF correlates negatively with shape (mean height/length ratio), with more elongated

valves being edge-drilled more often (Fig. 3A). The correlation is marginally significant (Spearman rank order correlation, $\rho = -0.19$, $p = 0.054$) and significant in a simple GLM (Table 4; slope = -1.43 , SE = 0.46 , $p = 0.0026$), although not in a multiple GLM (Table 5). Shape is significantly positively correlated with substrate affinity, so that higher L/H ratios are exhibited by semi-infaunal and infaunal species ($\rho = 0.52$, $p < 0.0001$). This correlation is not driven by relation between size and shape because generalized linear models do not show any significant effects of the three size measures on EDF in a simple GLM (Table 4; $p[\text{min size}] = 0.69$; $p[\text{mean size}] = 0.55$; $p[\text{max size}] = 0.37$) and in a multiple

TABLE 2. Ecological summary of all edge-drilling data. *n*, total number of valves; *e*, total number of valves with edge-drilling.

	<i>n</i>	<i>e</i>	EDF
Bivalve feeding strategies			
Suspension	6843	104	0.08
Chemoautotrophic	6269	81	0.055
Deposit	1996	2	0.03
Others	57	0	0
Bivalve substrate relationship			
Infaunal	12,746	135	0.055
Epifaunal	1797	31	0.135
Semi-infaunal/Endobysstae	604	21	0.18
Commensal	17	0	0
Epifaunal bivalve attachment			
Byssally attached nestler	1131	30	0.175
Cemented	557	1	0.015
Crevice dweller/Cryptic	84	0	0
Free lying	25	0	0

GLM (Table 5). Size has also no significant effects on EDF in simple GLM analyses that are performed separately on the three most frequent families (Mytilidae, Carditidae, and Corbulidae).

Edge-Drilling among Taxonomic Groups

Among species, *Limopsis multistriata* has the highest EDF (23%) followed by *Septifer forskali* and *Cardites akabana*. Among families, Limopsidae, Carditidae, and Mytilidae have the highest EDF (Table 1). Carditida has the highest EDF (37%) among orders.

Edge-Drilling among Bivalves with Different Substrate Affinities

Bivalve assemblages are dominated by infauna followed by epifauna. Semi-infaunal and commensal bivalves each contribute less than 5% to total abundance (Table 2). EDF differs significantly among these three groups (Fig. 3B). EDF of semi-infauna is higher than EDF of both epifauna ($\chi^2 = 3.925$, $p = 0.04$) and infauna ($\chi^2 = 63.49$, $p < 0.001$). EDF for epifaunal groups is also significantly higher than for infauna ($\chi^2 = 43.47$, $p < 0.001$). Epifauna largely consist of byssally attached nestlers, followed by cemented taxa. Crevice dwellers and free-lying groups do not show any edge-drilling. Byssally attached nestlers show a significantly higher EDF than the cemented epifauna ($\chi^2 = 20.6$, $p < 0.0001$). The relationship between EDF and substrate position is also significantly negative in a simple

GLM (slope = -0.65 , SE = 0.18, $p = 0.0004$) and in a multiple GLM (Tables 4, 5).

Edge-Drilling among Bivalves According to Feeding Mode

Bivalve assemblages are strongly dominated by suspension feeders followed by chemoautotrophs and then by deposit feeders. The suspension feeders show the maximum incidence of edge-drilling, followed by deposit feeders and chemoautotrophs. Although EDF differs among all groups, only the difference between suspension feeders and chemoautotrophs is statistically significant ($\chi^2 = 12.22$, $p < 0.0001$) (Table 2).

Edge-Drilling and Overall Predation Pressure

Wall-drilling frequency (WDF) has a significantly positive correlation with EDI (Fig. 3C; Spearman $\rho = 0.37$, $p = 0.0001$) and has significant positive effects on EDI in GLM analyses (Table 4; slope = -3 , SE = 0.59, $p < 0.0001$). This supports the hypothesis that predicts a positive relationship between predation pressure and edge-drilling frequency.

Edge-Drilling among Habitats

Bivalves analyzed in this study occur in habitats ranging from fine-grained muds to rock bottom (Table 3). The most abundant habitat is represented by fine-grained sediments, and the mangrove sand is the rarest. Calculated EDF for habitat type ranges from 14% to 0%. There is very little incidence of edge-drilling either from mangrove sand or from rocky bottom. The remaining three habitats have significantly higher EDF (χ^2 test,

TABLE 3. Edge-drilling frequency in various substrates. *n*, total number of valves; *e*, total number of valves with edge-drilling.

	<i>n</i>	<i>e</i>	EDF
Substrate			
Fine-grained sediment	7042	109	0.07
Coral sand	6601	71	0.06
Reef	1313	8	0.045
Rocky bottom	181	0	0
Mangrove sand	82	0	0
Water depth			
Shallow	6755	71	0.06
Deep	8463	117	0.07

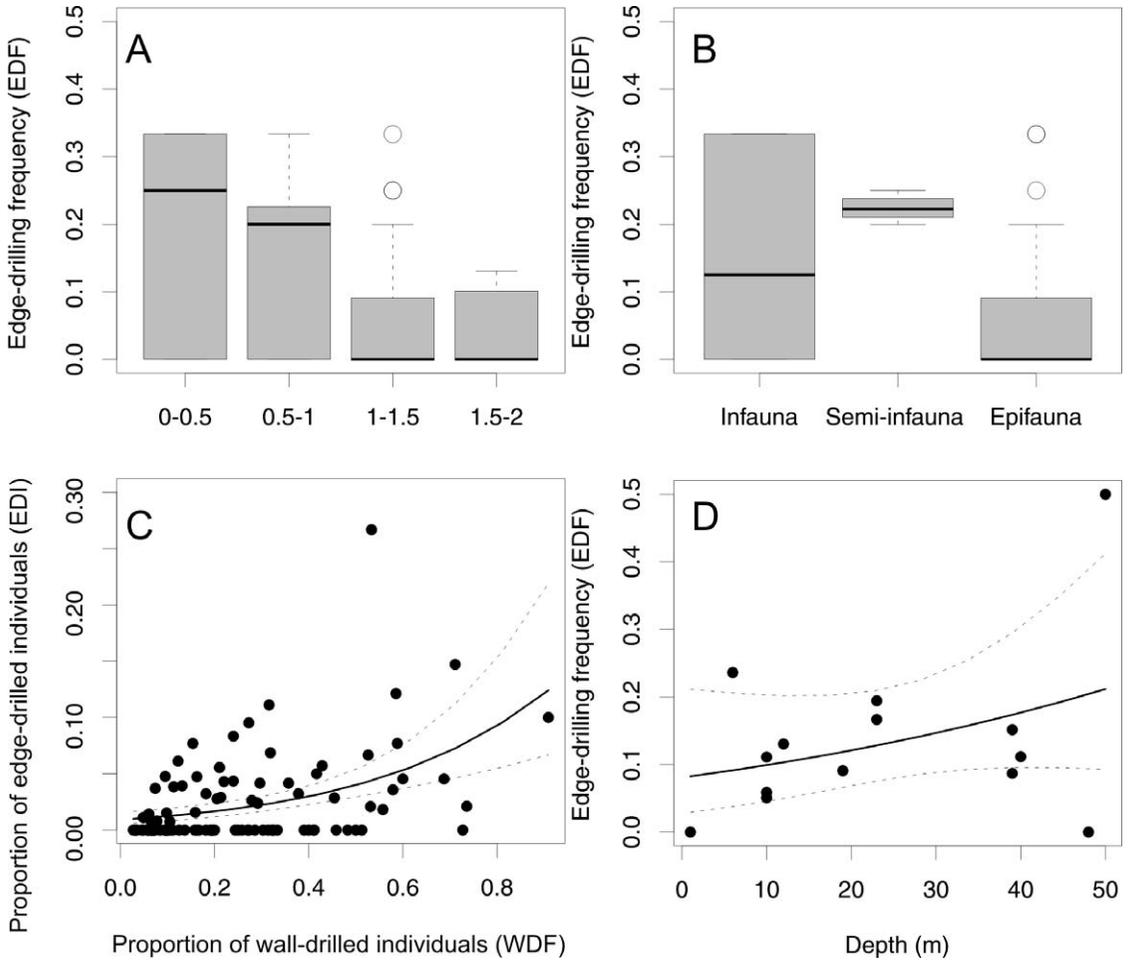


FIGURE 3. Relationship between edge-drilling and various parameters. A, The relationship between shape and EDF. The x-axis is the ratio length/height. The value of EDF is zero for commensal bivalves. B, The relationship between life modes and EDF. In A and B, the boxes are defined by 25th and 75th quantiles; thick line represents median value. C, The relationship between WDF and EDI. This shows the effect of predation pressure on edge-drilling incidence. D, Relationship between depth and the frequency of edge-drilling. In C and D, the solid line represents the slope of the line estimated by the generalized linear models and the dotted lines represent 95% confidence intervals around the slope.

$p < 0.05$), but are not significantly different from each other.

Effect of Depth on EDF

Deep habitat (>10 m) has a slightly higher EDF than the shallow habitat (<10 m), although the difference is not statistically significant ($\chi^2 = 1.9$, $p = 0.12$) (Fig. 3D). Depth has no significant effects when all species are pooled in a simple GLM (Fig. 3D; slope = 0.02, SE = 0.015, $p = 0.19$). There are also no significant depth effects on per-station EDF when individual families are analyzed separately.

Discussion

Identity of the Predators

The identity of drilling predators is generally determined from the morphology of a drill hole; however, the characteristic signature of a muricid or a naticid drilling is often obscured in an edge-drill. Hence, in this study, we did not identify the predator for each edge-drill. Instead, we studied the gastropod population known to produce drill holes from that area. Among drilling gastropods, both muricid and naticids are reported from the study area (Janssen et al. 2011 and unpub-

TABLE 4. The result of a simple generalized model showing the effect of variables on incidence of edge drilling. The effect is calculated using per-species per-station EDF for the first three variables (size, shape, and substrate). For assessing the effect of predation intensity, the relationship between EDI and WDF was evaluated. Per-station EDF was used for depth. The bold letters indicate a significant relationship.

	Estimate	SE	<i>t</i> -value	Pr(> <i>t</i>)
Size				
Intercept	-1.8	0.48	-3.77	0.0003
Size	-0.12	0.21	-0.59	0.55
Shape				
Intercept	-0.53	0.49	-1.05	0.29
Shape	-1.43	0.46	-3.09	0.0026
Substrate				
Intercept	-0.34	0.48	-0.72	0.475
Substrate	-0.65	0.18	-3.66	0.0004
Predation intensity				
Intercept	-4.68	0.27	-17.23	< 0.0001
WDF	-3.002	0.59	-5.006	< 0.0001
Depth				
Intercept	-2.42	0.46	-5.24	0.0002
Depth	0.02	0.015	1.39	0.19

lished data on neogastropods): nine species of Naticidae, six species of Muricinae, and four species of Ergalataxinae (Table 6). Two of the naticid genera, *Mammilla* and *Polinices*, are widely known to produce edge-drills (Vermeij 1980; Ansell and Morton 1987). Another muricid genus present in the area, *Chicoreus*, also produces edge-drills (Dietl and Herbert 2005). Only one genus of Ergalataxinae, *Morula*, is known to produce edge-drills, in oysters (Tan 2003). Considering the diversity of predators, naticids seem to be the major predatory group responsible for edge-drilling. Naticidae, however, dominate in soft substrata and do not occur on hard substrata. Muricidae, conversely, dominate on hard substrata but are also present in soft substrata. From this we can conclude that most hard substrata edge-drilling drillings are produced by Muricidae, whereas most of the soft substrata edge-drillings are probably produced by Naticidae.

Effect of Ecological Attributes on Edge-Drilling

Effect of Substrate Affinity.—The three bivalve families that show the highest EDF—Limopsidae, Mytilidae, and Carditidae—show no close phylogenetic relationship, but their life modes are very similar. All the genera we

studied from these families are either epi- or endobysate. We also found a significant effect of substrate affinity at the species level: semi-infaunal/endobysate species contribute most to EDF although this group contributes less than 5% to the total assemblage, and the significant effect of shape on EDF is related to the higher EDF on semi-infaunal groups. The second highest value comes from epifaunal bivalves, which represent less than 10% of the total assemblage. Although infaunalization protects bivalves from drilling attempts (Vermeij 1987; Stanley 1972; Sawyer and Zuschin 2010), its negative effect on edge-drilling cannot be linked to the same causal mechanism. We propose that the relationship is controlled by specific predatory behavior to tackle infaunal prey. Drilling activity completed infaunally exposes a driller to less risk than an attempt to drill an epifaunal or semi-infaunal prey. Attacking infaunal prey need not necessarily involve edge-drilling activity, which could account for the low incidence of edge-drilling among this group. Even when infaunal naticids hunt, they often capture prey from the sediment/water interface and subsequently move beneath the sediment (Carriker 1981). Among epifaunal bivalves, the byssally attached species bear the highest incidence of EDF, corroborating our findings about the preferred taxa for edge-drilling. These bivalves are generally attached to a substrate in an upright position with the commissure vertical (Stanley 1972) and are often preyed upon by epifaunal muricid predators. The shells are elongated, often with a flattened ventral surface, supporting and stabilizing the shell. They live in colonies and use clumping as an antipredatory defense against drilling (Casey and Chattopadhyay 2008). In such a configuration where the ventral part is inac-

TABLE 5. The result of a multiple generalized linear model showing the effects of three variables on per-species per-station EDF. The boldface represents a significant relationship.

	Estimate	Std. Error	<i>t</i> -value	Pr(> <i>t</i>)
Intercept	0.3	0.71	0.43	0.67
Size	-0.22	0.21	-1.01	0.32
Shape	-0.39	0.65	-0.6	0.55
Substrate	-0.56	0.29	-1.93	0.05

TABLE 6. A summary of predatory gastropod species and their abundance from the studied area.

Family	Species	Total shells
Naticidae	<i>Mammilla melanostoma</i>	2
	<i>Mammilla simiae</i>	2
	<i>Natica buriasiensis</i>	11
	<i>Naticarius onca</i>	3
	<i>Notocochlis gualteriana</i>	79
	<i>Tanea euzona</i>	1
	<i>Polinices flemingianus</i>	1
	<i>Polinices mammilla</i>	2
	<i>Sigatica mienisi</i>	4
	Muricinae	<i>Chicoreus virgineus</i>
<i>Pterynotus elongatus</i>		1
<i>Murex tribulus s.l.</i>		6
<i>Murex sp. 1 juv.</i>		3
<i>Murex sp. 2 juv.</i>		1
<i>Phyllocoma convoluta</i>		1
Ergalataxinae		<i>Morula chrysostroma</i>
	<i>Morula uva</i>	1
	<i>Morula granulata</i>	35
	<i>Muricodrupa fiscella</i>	1

cessible for attachment to the surface, the umbonal as well as the mid-region is protected by clumping; the commissural region, thus, becomes a likely position for drilling. Contrary to the pattern observed for life mode, feeding type does not influence the EDF. Nonetheless, the suspension feeders have a significantly higher EDF compared to chemoautotrophic bivalves. This difference probably reflects the fact that chemoautotrophs are all infaunal, whereas suspension feeders are composed of a mixed group (infaunal, semi-infaunal, and epifaunal).

Effect of Shape.—Bivalves with shapes elongated along the length dimension are more prone to edge-drilling (Fig. 3A). This relationship between EDF and shape is primarily determined by a high frequency of edge-drilling in byssate bivalves that are typically elongate, because elongation entails a reduced hinge, a dominantly anisomyarian nature, and reduced mobility (Stanley 1972; Heinberg 1979; Savazzi 1984).

Effect of Drilling Predation Intensity.—The positive relationship between drilling predation intensity (expressed by WDF) and incidence of edge-drilling (expressed by EDI) supports our third prediction, i.e., that there are more edge-drilled individuals with higher predation pressure. The semi-infaunal and epifaunal groups that are frequently wall-

drilled are often victims of edge-drilling. Predators attacking such “favorites” face a “higher-risk” scenario. Note, however, that both higher WDF and EDF are related to higher predation pressure. Therefore, higher EDF could also merely be an outcome of higher WDF. Although we have tested the hypothesis only for the intensity of drilling predation, it should be noted that other predators would also contribute in creating a “high-risk” scenario. Therefore, we might also expect a similar pattern of high EDF in habitats with a higher predation pressure in general. It is important to recognize that a higher EDF might not always result as a response to “higher risk.” It has been experimentally demonstrated that Recent muricid gastropods often produce incomplete drill holes in the presence of a predator (Chattopadhyay and Baumiller 2007). A similar phenomenon has been documented for naticids where the incomplete drilling frequency increases as a result of higher competition (Hutchings and Herbert 2013). In spite of the “high-risk” scenario, no edge-drill was produced in either case.

Effect of Environmental Attributes on Edge-Drilling

We have considered two major environmental attributes in this study, habitat and depth.

Effect of Depth.—Several studies documented a negative relationship between water depth and drilling predation (e.g., Sander and Lalli 1982; von Rützen-Kositzkau 1999; Walker 2001; Tomašových and Zuschin 2009), but we found no significant correlation between EDF and depth. One explanation is that, within this narrow depth range, the levels of competition and predation do not vary significantly with depth. Predation is also strongly controlled by habitat (Vermeij et al. 1981; Hansen and Kelley 1995; Cadée et al. 1997; Sawyer and Zuschin 2010; Jackson and Leonard-Pingel 2011); site stereotypy may therefore differ across different sublittoral substrates. However, we found no predictable difference among EDFs from different substrates. This lack of correlation of EDF with depth and substrate could reflect the mosaic of

habitats in the study area (Piller and Pervesler 1989), potentially obscuring any correlation.

Implications for the Fossil Record

Temporal change in stereotypy is often related to the hypothesis of escalation, which states that evolution is driven by enemies (Vermeij 1994). However, influence of the prey population on predatory behavior could lead to misdiagnosis of the escalation scenario because edge-drilling depends on the availability of suitable prey items (e.g., epifauna, byssally attached semi-infauna) as well as on the overall predation pressure on that group. Therefore, temporal studies using such stereotypy have to pay special attention to the ecology of the prey community.

This study also sheds light on the spatial distribution of edge-drilling. Predation pressure follows a latitudinal gradient and is highest near the tropics (Vermeij 1987). The same probably holds true for EDF because it seems to share a positive correlation with drilling predation intensity. The higher incidence of edge-drilling in tropical warm seas (e.g., Guam, Panama, New Guinea, and parts of the Caribbean) corroborates this claim (Vermeij 1980, 2001). Besides explaining the spatial distribution of edge-drilling, our findings also help explain the limited temporal distribution of edge-drilling, especially the event of the Neogene rise in edge-drilling frequency. The modern level of drilling predation intensity was not reached not until the Neogene, and edge-drilling was quantitatively insignificant until then (Vermeij 2001); edge-drilling started to increase once the overall drilling frequency reached the modern level. Our study thus shows that edge-drilling is closely related to predation intensity; i.e., it became common only in the Neogene, once predation intensity reached a certain threshold. This explanation of the Neogene rise in edge-drilling does not require the development of new predatory groups; it rather involves a behavioral shift among predators triggered by an ecological change. The predators responsible for such stereotypy might have been present even before the Neogene; however, they started to

engage in such a stereotypic drilling only in "high-risk" scenarios.

Conclusions

Prey handling by carnivorous gastropods influences the position of the drill hole, and the net benefit of an attack often depends on the selected drill hole site. Stereotypy of drill hole sites, largely a behavioral phenomenon, has rarely been linked to ecological and environmental attributes. Edge-drilling, however, presents a different scenario. Although beneficial, it poses a risk to the predator; hence, the strategy was thought to be used only during times of elevated ecological stress. This ecological interpretation of edge-drilling is extended to predict the effect of important ecological (shape, substrate affinity, predation intensity) and environmental (depth, habitat) attributes on its incidence. The prediction is a higher incidence of edge-drilling in elongated, non-infaunal (epifaunal, semi-infaunal) groups that are heavily preyed upon, as well as a lower edge-drilling incidence in deeper habitats. Our study partially supports these claims. Bivalve groups with elongate shapes were preferentially targeted for edge-drilling. We also found lower edge-drilling frequency in infaunal groups: an infaunal attack does not expose the predator to risky surroundings, reducing the likelihood of edge-drilling. Finally, byssal attachment apparently favors edge-drilling because individuals in byssally attached groups tend to expose only the commissural area for drilling. Such commissural exposure also explains the higher edge-drilling in semi-infaunal versus epifaunal groups. Groups that are heavily preyed upon show an elevated level of edge-drilling. Feeding habit has no apparent effect on edge-drilling.

The depth range studied here is fairly narrow and failed to indicate any difference in EDF between shallow and deeper habitats, in contrast to the predictions. Such lack of dependence partially reflects the mosaic pattern of shallow-water substrata, obscuring a potential trend.

This analysis supports the view that ecological and environmental details of the prey

affect traits such as stereotypy, which has traditionally been considered to be an intrinsically predator-driven trait. The results of this study call for considering the details of the prey to fully understand predation in modern and fossil habitats. This study also provides explanation for the limited spatial and temporal distribution of edge-drilling as a function of overall predation intensity. The higher incidence of edge-drilling of Recent assemblages results from the fact that the overall risk from all predators has greatly increased over time.

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