

How effective are ecological traits against drilling predation? Insights from recent bivalve assemblages of the northern Red Sea



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ABSTRACT

Biotic interactions, especially predation, have drawn considerable attention in recent times as an important agent of natural selection. Drilling predation is often used as a model system by paleobiologists to evaluate evolutionary and ecological effects of such predatory interaction on the composition of molluscan communities. Using drilling frequencies, it is possible to test quantitatively specific predictions that postulate the effectiveness of ecological traits against predation in present-day environments. The high frequency of drilling (DF) in a diverse recent bivalve assemblage from shallow water environments of the northern Red Sea enables us to test such evolutionary hypotheses, predicting low DF in large-sized bivalves, in infaunal bivalves, in siphonate and mobile bivalves, lower DF in byssally attached than in other epifaunal bivalves, and high DF in bivalves occurring in shallow habitats. We evaluate these predictions on the basis of more than 15,000 bivalve specimens collected at stations with meter-scale spatial resolution using three different methods to calculate DF, namely 1) per-species per-station DF, 2) per-species DF by pooling all stations, and 3) per-station DF by pooling all species. The results are not always consistent among these three methods. Among morphological attributes, we found size and shape of a species to be a good predictor of drilling frequency. However, life habit shows a pattern contrary to our prediction because infaunal groups show the highest DF. Although we did not find any significant correlation between predator abundance and DF at small spatial (station) scales, the dominance of naticid gastropods and low abundance of muricid gastropods at regional scales can explain the much higher DF observed in infauna than in epifauna. Characteristics of the siphon or mobility did not always play a major role in dictating the DF. Attachment type of epifauna does not always show a predictable pattern in deterring drilling predation; however, byssally attached bivalves sometimes show a slightly lower DF compared to cemented bivalves. Although water depth has no significant effect on DF, it might be influenced by the relatively narrow depth range of the stations. We did not find significant variation in DF between groups adapted to different habitats (i.e. substrate types); however, DF seems to differ between groups with different feeding mode. Our study demonstrates that some ecological traits (such as infaunalization or predator avoidance by choosing deeper habitat) that are claimed to be anti-predatory, do not offer effective defense against drilling predation in present-day environments—a result consistent with the idea of ever escalating predator-prey dynamics.

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1. Introduction

Biotic interactions, especially predation, are considered to be an important agency of natural selection (Vermeij, 1989; Thompson, 1998; Stanley, 2007) and can have significant effects on diversification (Huntley and Kowalewski, 2007; Blois et al., 2013). Detailed analysis of such interactions in recent communities give us valuable insights and provide opportunities for testing their contribution to the long term evolutionary dynamics (Kitchell et al., 1981; Chattopadhyay and Baumiller, 2007; Baumiller et al., 2008; Casey and Chattopadhyay,

2008; Sawyer et al., 2009; Sawyer and Zuschin, 2010). Predator-prey systems involving drilling predators are particularly relevant because they are one of the few instances where the predation trace survives the vagaries of fossilization (Kitchell, 1986; Kowalewski, 2002). Predatory drillings, therefore, attracted the attention of paleontologists and neontologists alike (Kelley and Hansen, 2003).

Thorough understanding of present-day predation is crucial to validate important evolutionary hypotheses such as coevolution and escalation. The escalation hypothesis states that enemy-related adaptation causes long term evolutionary trends in morphology, ecology and behavior of organisms (Vermeij, 1987, 1994). This hypothesis also claims that such adaptation favors the evolution of traits that limit the exposure of organisms to enemies (e.g., enhanced sensory system,

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high growth rate, and higher metabolic rate) and enhance their defense (e.g., armor, offensive weaponry, high locomotor performance, toxicity, crypsis and intimate association with well-defended species) (Vermeij, 1994). Among the morphological defenses, an increase in effective body size has often been used by molluscan prey against predation (Vermeij et al., 1980; Alexander and Dietl, 2001). The prey size selection by drilling gastropods has been studied and interpreted using cost-benefit analysis (DeAngelis et al., 1985; Kitchell et al., 1981; Chattopadhyay and Baumiller, 2009). These studies showed that prey size is selected by the predator to maximize the net energy gain, which is dictated by the balance between invested energy (through foraging, drilling and consumption) and energy gain (dependent on prey size and type). Kitchell et al. (1981) further demonstrated the existence of a handling limit for a specific size of naticid predator beyond which the attacks are more likely to fail. Vignali and Galleni (1986) argued that bivalve mortality decreases at larger size classes as vulnerability to attacks declines (i.e., size refuge).

It is possible that infaunalization strategies that ensure predator avoidance emerged along with intensification in epifaunal predation pressure (Stanley, 1968, 1974, 1977; Bambach, 1993). Moreover, Stanley (1986) claimed that siphonate bivalves evade predators more efficiently than non-siphonate bivalves. Whether bivalves infaunalized in response to predation is still an open question (Stanley, 1977; Thayer, 1979; Vermeij, 1987; McRoberts, 2001). Although we do not focus on the initial cause for infaunalization, we evaluate whether infaunalization correlates with reduced DFs in modern bivalves. Epifaunal bivalves vary in mobility and thus ought to differ in effectiveness as anti-predatory strategies. Thayer (1979) claimed that immobile epifauna declined significantly through time because of their inability to escape and survive the effects of grazing and predation on the sediment–water interface (e.g., LaBarbera, 1981). It has also been claimed that byssal attachment works as a deterrent against drilling predation; individuals from a colony of byssally attached individuals show a lesser degree of drilling intensity (Casey and Chattopadhyay, 2008). Moreover, Day et al. (1991) showed that clumps of mussels can attach themselves to drilling predator with their byssus threads thereby immobilizing the gastropods and causing them to starve. The shape of bivalves should also be a good correlate for vulnerability because life habits, mobility and type of attachment often correlate with the shape of bivalves (Stanley, 1970).

The escalation hypothesis also predicts that predation intensity is reduced in deeper water and in cryptic environments because predatory life strategies are energetically-demanding and are better supported in shallow, more-productive environments with a higher food supply (Vermeij, 1995). This view is supported by various studies on recent predation intensity along environmental gradients with a broad depth range (Hay et al., 1983; Hay, 1984; Oji, 1996).

Based on these claims, we test several predictions on the relationship between drilling incidence and the ecological and environmental attributes of prey that can be evaluated with interspecific analyses. We evaluate these hypotheses to assess the effectiveness of anti-predatory strategies against drilling predation using data from recent bivalve assemblages of the northern Red Sea.

1. Dependence on body size: Large body size can protect against predation as observed in various ecological guilds (Baskett, 2006; Mumby et al., 2006). The same is observed for drilling predation in recent (Edwards and Huebner, 1977; Franz, 1977; Vignali and Galleni, 1986) and in fossil molluscan assemblages (Kitchell et al., 1981; Kitchell, 1986; Kelley and Hansen, 1996; Chattopadhyay and Dutta, 2013; but see Harper et al., 1998; Kelley et al., 1997). Hence we expect to find a lower incidence of drilling in larger bivalves, assuming that there exists a size refuge. However, lack of such pattern might indicate that benefit increases at the same rate as drilling cost (DeAngelis et al., 1985; Kitchell, 1986; Kingsley-Smith et al., 2003a

& b) and therefore, a balance is maintained to keep the net energy gain constant.

2. Dependence on life habit: Infauna is less exposed to drilling predation compared to epifauna and semi-infauna. Even when infaunal prey is exposed to predators, the overall predation pressure is higher at the sediment/water interface because most top predators such as crabs, sea stars, fishes are epifaunal (Vermeij, 1977; Stanley, 1972). Although drilling predation is not fully equivalent to other forms of predation, it is still useful to assess whether infauna shows a lower incidence of drilling. More specifically, we also expect to see a higher incidence of drilling in infaunal bivalves that are non-siphonate because they are less likely to reposition themselves after disturbance (Stanley, 1986). We also expect to see a lower incidence of drilling among bivalves with higher mobility as they are expected to have a strong escape response.
3. Dependence on nature of attachment: We expect to see a lower incidence among byssally attached bivalves compared to other epifaunal bivalves because byssal attachment can deter drilling predation (Casey and Chattopadhyay, 2008).
4. Dependence on water depth: We expect to see a higher intensity of drilling predation in shallow, more productive habitats that support the energetically demanding life habit of predators (Vermeij, 1995; Hay et al., 1983; Hay, 1984).

2. Materials and method

2.1. Study area

The Northern Bay of Safaga is a coral-dominated, shallow-water area of approximately 75 km² (Zuschin and Oliver, 2005). It exhibits a highly structured bottom topography extending down to more than 50 m water depth. The annual water temperature ranges between 21 and 29 °C and salinity varies between 40 and 46‰, both without any obvious depth gradient due 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, 1994). Water energy is relatively weak, but a complex current pattern influences facies development (Piller and Pervesler, 1989) and bottom facies (identified during diving and mapping of the bay) and sedimentary facies (resulting from detailed sedimentological analyses of samples taken during the mapping work) generally show a good correspondence (Piller and Mansour, 1990; Piller, 1994).

2.2. Sampling

This study is based on quantitative and qualitative samples from stations with soft and hard substrata and in a depth range from intertidal to 52 m (for details see Chattopadhyay et al., 2014a). All shells used for this study stem from the sea floor or from the uppermost 30 cm of the sediment (i.e., the taphonomically active zone, Davies et al., 1989). All samples were evaluated with respect to their composition of bivalves and two major groups of drilling gastropods, naticids and muricids. Soft substrata molluscs were quantitatively studied from standardized bulk samples collected at thirteen stations by scuba diving (shallow subtidal to 40 m water depth) from all major sedimentary facies (Table 1). For more details on soft substrata samples, see Zuschin and Hohenegger (1998) and Zuschin and Oliver (2003a).

All major intertidal and subtidal hard substrata to a water depth of 40 m were quantitatively sampled for molluscs along transects using a 0.25 m² aluminium, square frame at 74 stations in Safaga Bay (Table 1). For more details on hard substrata stations see Zuschin et al. (2000, 2001) and Zuschin and Oliver (2003a).

Table 1

Taxonomic summary of drill hole data pooled across all samples for order, superfamily and families of bivalves.

Order	Superfamily	Family	Total valves	Drilled valves		DF
				Wall drilled	Edge drilled	
Arcida	Arcoidea	Arcidae	316	7	0	0.04
	Arcoidea	Glycymerididae	771	167	22	0.46
	Limopsoidea	Limopsidae	129	21	15	0.44
Cardiida	Arcticoidea	Trapezidae	4	0	0	0.00
	Cardioidea	Cardiidae	1115	40	0	0.07
	Chamoidea	Chamidae	177	0	0	0.00
	Cyamoidea	Sportellidae	6	1	0	0.33
	Galeommatoidae	Galeommatidae	4	0	0	0.00
	Galeommatoidae	Lasaeidae	5	1	0	0.40
	Gastrochaenoidea	Gastrochaenidae	0	0	0	0.00
	Glossoidae	Glossidae	2	0	0	0.00
	Mactroidea	Mactridae	10	0	0	0.00
	Mactroidea	Mesodesmatidae	5	0	0	0.00
	Tellinoidea	Psammobiidae	33	0	0	0.00
	Tellinoidea	Semelidae	266	10	0	0.08
	Tellinoidea	Solecurtidae	35	0	0	0.00
Tellinoidea	Tellinidae	1659	20	2	0.03	
Ungulinoidea	Ungulinidae	80	9	0	0.23	
Veneroidea	Veneridae	1700	176	22	0.22	
Carditida	Crassatelloidea	Carditidae	571	38	22	0.17
	Lucinoidea	Lucinidae	6151	687	81	0.24
Lucinida	Thyasiroidea	Thyasiridae	1	0	0	0.00
	Mytiloidea	Mytilidae	478	25	14	0.13
Nuculida	Nuculoidea	Nuculidae	2	0	0	0.00
Ostreida	Ostroidea	Gryphaeidae	240	14	0	0.12
	Ostroidea	Ostreidae	45	0	0	0.00
	Pinnoidea	Pinnidae	13	0	0	0.00
	Pterioidea	Malleidae	47	0	0	0.00
	Pterioidea	Pteriidae	49	0	0	0.00
	Anomioidea	Anomiidae	14	0	0	0.00
Pectinida	Limoidea	Limidae	77	3	0	0.08
	Pectinoidea	Pectinidae	95	0	0	0.00
	Pectinoidea	Spondylidae	91	14	1	0.32
	Plicatuloidea	Plicatulidae	4	0	0	0.00
Pholadida	Myoidea	Corbulidae	849	35	8	0.09
	Myoidea	Myidae	1	0	0	0.00
Poromyida	Cuspidarioidea	Cuspidariidae	1	0	0	0.00
Solemyida	Manzanelloidea	Nucinellidae	116	2	0	0.03
	Solemyoidea	Solemyidae	1	0	0	0.00
Solenida	Solenoidea	Pharidae	1	0	0	0.00
Thraciida	Thracoidea	Periplomatidae	1	0	0	0.00

Numerous qualitative samples (mostly surface collections from soft substrata) were taken all over the bay and these were evaluated in the present study (for details see [Chattopadhyay et al., 2014a](#)).

2.3. Life habit & environment

The species found in Safaga Bay were classified into five substrate tiers (epifaunal, infaunal, endobysate, boring, commensal) and four feeding guilds (suspension feeders, deposit feeders, chemoautotrophs, and others, represented by numerically rare carnivores and zooxanthellates). Epifaunal bivalves are further divided into byssally attached, cemented, crevice dwelling, and free lying bivalves. To characterize the bivalves based on characteristics of the siphon, we divided them into eight categories according to [Stanley, 1986](#): BuP (burrowing protobranch), EpB (epifaunal byssate), EpF (epifaunal freeliving), EpC (epifaunal cemented), En (endobysate), BuN (burrowing non-siphonate and non-protobranch), BuS (burrowing siphonate), and BoS (boring siphonate). In addition to the categories of [Stanley \(1986\)](#), we used the category EpS (epifaunal siphonate), which represents the highly specialized zooxanthellate tridacnids. We compared BuS with the rest of the categories to evaluate the role of siphon in avoiding the drilling predation. We also divided bivalves into four categories based on their mobility: groups with no escape response (fixosessile, most byssate species), weak response (most non-siphonate burrowers and burrowers with reduced siphon), strong

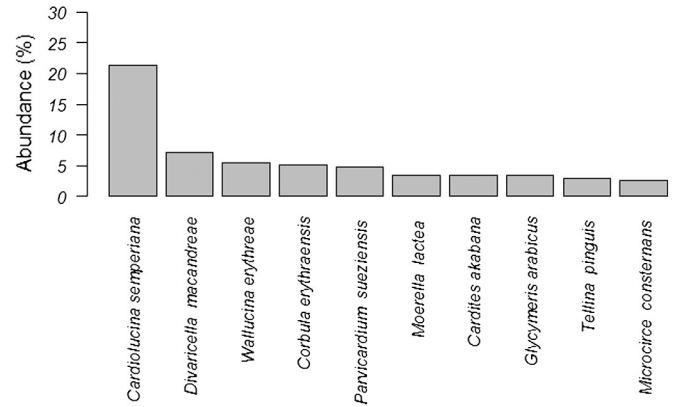


Fig. 1. Ten most abundant bivalve species in the studied assemblage.

response (most siphonate burrowers and some protobranch burrowers), and very strong response (tellinids and cardiids among siphonate burrowers). In order to evaluate the role of mobility, we simplified the categories to two groups and compare bivalves with poor (no or weak response) and good (strong to very strong response) escape ability.

We distinguished five environments, including fine-grained sediment (i.e. mud and muddy sand), coral sand, mangrove sand, reef and rock bottom. The depth of each station was recorded and used for analysis; stations with ≥ 10 m water depth are considered deep.

2.4. Predation traces, size and shape

Specimens were counted and studied for traces of drilling predation. Predatory drill holes were identified on the basis of the following criteria: circular in cross section with smooth sides, penetrated perpendicular to and from the outside of the shell surface, and penetrate one valve only in articulated shells ([Carriker and Yochelson, 1968](#); [Rohr, 1991](#); [Baumiller, 1996](#); [Kaplan and Baumiller, 2000](#); [Leighton, 2001](#)). The position of the drill hole was also noted as wall- or edge drilled. We considered a valve to be edge drilled only if the boundary of the hole intersected the commissural line. We did not differentiate between drill holes made by muricid and naticid gastropods.

We measured the size of specimens to test whether variation in prey size affects the frequency of drilling predation. We used the natural logarithm of the geometric mean of length and height that is considered to be the best available proxy of body size ([Kosnik et al., 2006](#)). We calculated the geometric mean of the anterior–posterior and dorsal–ventral length. We used the mean size of each species based on a small number (~5) of randomly chosen adult specimens sampled at each station. For

Table 2

Ecological summary of all drill hole data. N = total number of valves, D = total number of drilled valves.

	N	D	DF
<i>Bivalve life habit</i>			
Infaunal	12,746	1283	0.19
Epifaunal	1797	114	0.11
Seminafaunal/Endobysate	604	58	0.16
Commensal	17	2	0.24
<i>Epifaunal bivalve attachment</i>			
Byssally attached nestler	1131	85	0.12
Cemented	557	29	0.10
Crevice dweller/Cryptic	84	0	0.00
Free lying	25	0	0.00
<i>Bivalve feeding strategies</i>			
Suspension	6843	655	0.18
Chemoautotrophic	6269	770	0.23
Deposit	1996	32	0.03
Others	57	0	0.00

larger specimens, we measured the length using vernier calipers (± 0.1 mm). Smaller shells were examined under a LEICA MZ12 binocular microscope and measured using KS Run digitization software. Finally for each species at each station, we calculated the average geometric mean (averaged per station). The shape is approximated by the ratio of length and height (Huang et al., 2015).

2.5. Drilling frequency

The drilling frequency is calculated by dividing half of the number of bored valves by the total number of valves in the collection (Kowalewski, 2002). However, the general formula is not applicable for edge-drilling where both the valves are drilled (Chattopadhyay et al., 2014a). Therefore, we used the following modified equation to account for the presence of edge-drilled valves:

$$DF = (N_{\text{wall}} + (N_{\text{edge}} * 0.5)) / (N_{\text{Total}} * 0.5)$$

where,

N_{wall}	Number of wall-drilled valves
N_{edge}	Number of edge-drilled valves
N_{Total}	Total number of valves

We calculated DF at various taxonomic levels, for substrate tiers and feeding guilds, and across various environments. We used three scales of analyses to address the relationship between DF and various parameters.

First, per-species per-station DF was calculated for each species with a minimum number of 20 valves per station; we adopted this cut-off to avoid the influence of small sample size on drilling frequency (Vermeij, 1987). We analyzed the effect of size, shape, life habit and feeding mode on such per-species per-station DF. Second, per-species DF was calculated by pooling the data for each species from all the stations in the Safaga Bay. For this purpose, we analyzed the effect of size, shape, life habit and feeding mode using a minimum of 20 valves per species. Using this approach, we also computed total per-taxon DF at the order, superfamily and family level. Third, per-station DF was calculated by pooling all the species at a particular station. Again, using a minimum of 20 valves per station, we evaluated the effect of abundance of predators, life habit and water depth. Using the same method, we also evaluated the relation of per-station DF in infauna and epifauna.

2.6. Analyses

We used the Spearman rank order coefficient to measure the correlation of DF with size, shape and water depth (using the water depths of individual stations). We also estimated the effect of continuous variables (size, shape) and ordinal life habits (epifauna–1, semi-infauna–2, infauna–3) in per-species per-station method with simple (analyzing each predictor separately) and with multiple generalized linear models (GLMs) (analyzing all predictors simultaneously and evaluating their partial contributions to the total variation in DF) (Quinn and Keough, 2002). We used the logit-link function and quasibinomial variance functions suitable for modeling response variables represented by proportions (McCullagh and Nelder, 1989). Such models allow the response variables (DF) 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 under- or overdispersed relative to the variance expected from binomial processes. We used the Wilcoxon rank sum test to evaluate the difference in DF in various groups based on feeding, life habit, and attachment type of epifauna. All statistical analyses were performed in R (R Core Team, 2012).

3. Results

3.1. Basic structure of the Safaga Bay assemblage

A total of 15,615 valves of bivalve molluscs were collected, identified to species level and studied for drill holes. These shells represent 174 bivalve species from 41 families (Table 1). The five most abundant bivalve species account for 46.5% of the total bivalve assemblage and are heavily dominated by the chemosymbiotic lucinids, most notably *Cardiolucina semperiana* (Fig. 1). The pooled drilling frequency of the whole Safaga Bay assemblage is 23%; the wall-drilled individuals account for 21.5% and the edge-drilled individuals account for 1.5%. The details of the stereotypy of drill hole position are discussed in Chattopadhyay et al. (2014a). The bivalve assemblage is dominated by infauna (84%) and epifauna (12%). Semi-infauna and commensals contribute with less than 5% to the abundance (Table 2). Among epifauna, bivalves with byssal attachments show the highest abundance (63%), followed by cemented bivalves (31%). Trophic composition of bivalves is dominated by

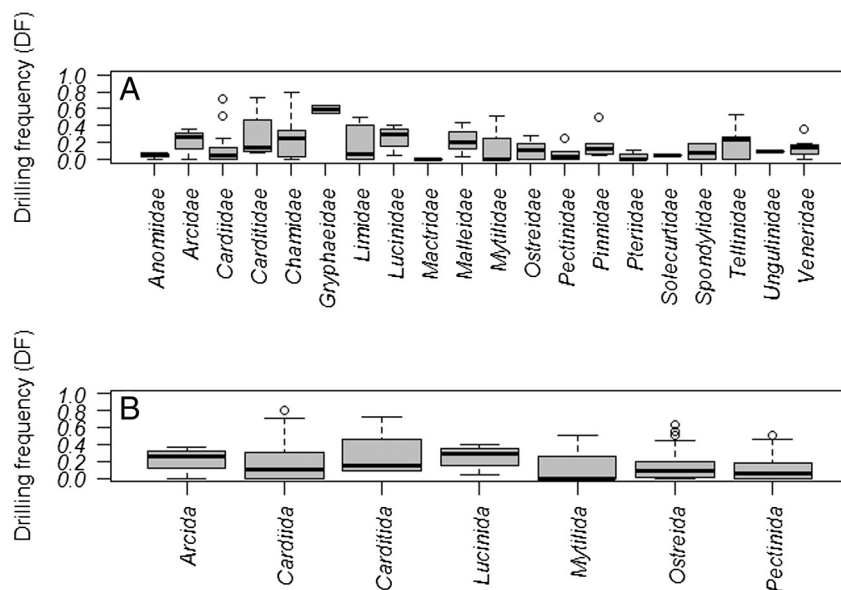


Fig. 2. Relationship between drilling frequency (DF) in various taxonomic groups for the “per-species” method. A. DF in families, B. DF in orders. The boxes are defined by 25th and 75th quantiles; thick line represents median value. The groups without any drilling have not been considered in the plot.

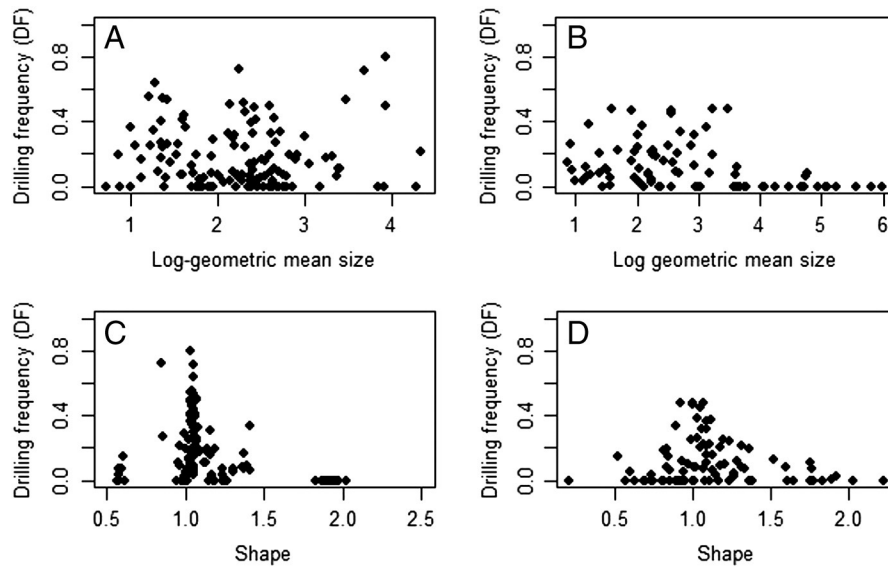


Fig. 3. Relationship between drilling frequency (DF) and various parameters. A. Size–DF relationship for “per-species per-station” method. B. Size–DF relationship for “per species” method. C. Shape–DF relationship for “per-species per-station” method. D. Shape–DF relationship “per-species” method. In C and D, the x-axis is the ratio of length/height.

suspension feeders (45%), closely followed by chemoautotrophs (41%) and deposit feeders (13%).

3.2. Drilling intensity among different taxonomic groups

Limopsis multistriata has the highest per-species DF (60%). The other species with higher than 50% DF are represented by the infaunal chemosymbiont species *LamelloLucina dentifera*, and the infaunal suspension-feeding species *Tucetona pectunculus* and *Glycymeris lividus*. Among the families, Gryphaeidae, Lucinidae, and Tellinidae have the highest per-taxon DF while Arcida and Lucinida have the highest per-taxon DF among the orders (Fig. 2A and B).

3.3. Predation pattern in size groups

There is no significant relationship between per-species-per-station DF and size (Fig. 3A) in either simple or multiple GLM (Table 4 A, B). Size, however, shows a significant negative correlation (Spearman rho = -0.4750601, p-value << 0.0001), with per-species DF implying a lower incidence of drilling in larger individuals (Fig. 3B).

3.4. Drilling intensity and shape

There is a slight negative relationship between shape and per-species per-station DF implying that elongated species are drilled more often than equi-dimensional species. The effect of shape on DF is

significant in both simple GLM and multiple GLM for per-species per-station DF (Table 4A, B) (Fig. 3C), i.e., DF decreases with increasing length/height ratio. However, this effect is insignificant for per-species DF (Spearman rho = 0.03, p = 0.78) (Fig. 3D).

3.5. Drilling intensity among bivalves with various life habits

Infauna shows higher DF with all three methods than in epifauna. Although the effect of life habit on DF is not significant in simple GLM, it becomes significant in multiple per-species per-station DF (Table 2 A, B) (Fig. 4A). The difference is significant for per-species DF (Fig. 4B) (Wilcoxon rank sum test, W = 463.5, p-value = 0.001) but not significant for per-station DF (Wilcoxon signed rank test, V = 38, p-value = 0.07) (Fig. 4C). However, correlation between the DF of infauna and epifauna within a single station is low and insignificant (Spearman rho = 0.03, p-value = 0.9, Fig. 4D). For some pairs of siphonal characteristic, we found significant differences in per-species per-station DF (EpB-BuN, BuN-BuS; Wilcoxon rank sum test, p < 0.05) (Fig. 5A.1), in per-species DF (EpB-BuN, EpB-BuS, BuN-BuS; Wilcoxon rank sum test, p < 0.05) (Fig. 5B.1), and in per-station DF (EpB-BuN; Wilcoxon signed rank test, p < 0.05) (Fig. 5C.1). We found a significantly higher DF in BuS than in other bivalves for per-species DF (Wilcoxon rank sum test, W = 1123.5, p-value = 0.0455); but the difference is not significant for per-species-per-station DF (Wilcoxon rank sum test, W = 1188, p-value = 0.2454) and per-station DF (Wilcoxon signed rank test, V =

Table 3
Distribution of drilled valves among various substrates. N = total number of valves, D = total number of drilled valves.

	N	D	DF
<i>Substrate</i>			
Fine-grained sediment	7042	763	0.20
Sandy sediment	6601	607	0.17
Reef	1313	92	0.13
Rock bottom	181	7	0.08
Mangrove sand	82	0	0.00
<i>Water depth</i>			
Deep	8463	856	0.19
Shallow	6755	614	0.17

Table 4
The results of GLM on the relationship between DF and various parameters for “per species per station” method. A. Simple GLM, B. Multiple GLM.

	Estimate	Std. error	t value	Pr(> t)
<i>A</i>				
Intercept	-1.73887	0.374422	-4.64414	8.20E-06
Log geometric mean size	0.058618	0.158926	0.368838	0.712844
Intercept	-0.59618	0.275821	-2.16146	0.032478
Shape	-0.80855	0.222499	-3.63394	0.0004
Intercept	-2.26144	0.622259	-3.63425	0.000399
Life mode	0.233713	0.216582	1.079097	0.282527
<i>B</i>				
Intercept	-2.27032	0.639977	-3.54749	0.000543
Log geometric mean size	0.098464	0.143387	0.686698	0.493506
Shape	-1.60099	0.431717	-3.70844	0.000309
Life mode	0.85355	0.244534	3.490524	0.00066

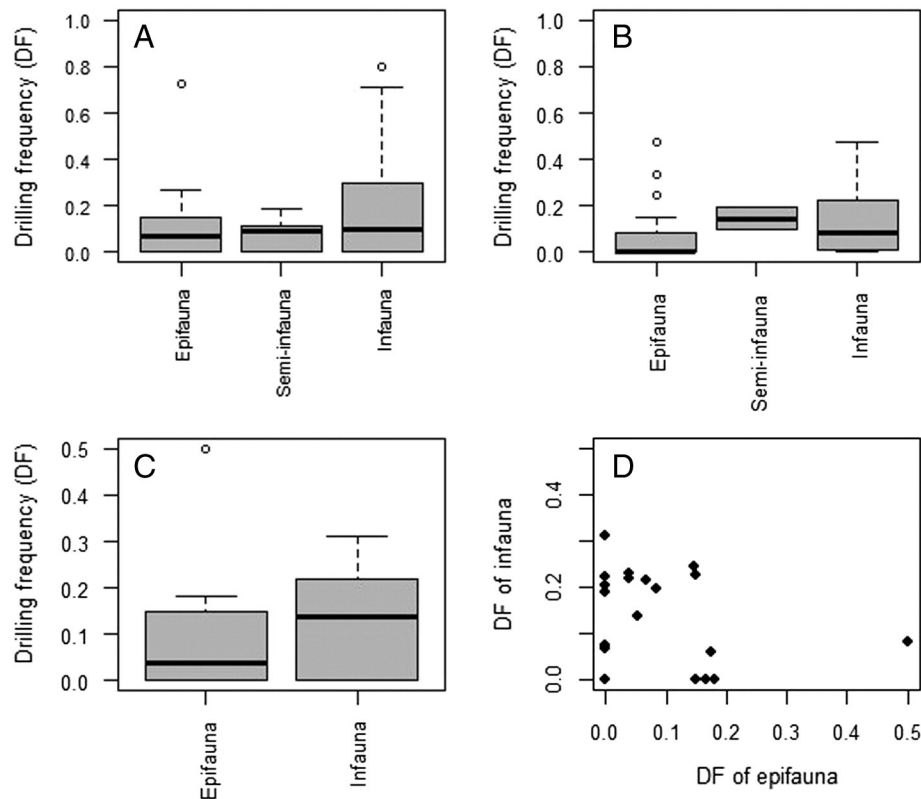


Fig. 4. Relationship between drilling frequency (DF) and life habit. A. Life habit–DF relationship for “per-species per-station” method. B. Life habit–DF relationship for “per-species” method. C. Life habit–DF relationship for “per-station” method. In A, B and C, the boxes are defined by 25th and 75th quantiles; thick line represents median value. D. The relationship between station specific DF in epifauna and infauna.

102, p -value = 0.7936) (Fig. 5A.2, B.2, C.2). The results of the comparison between BuS and the other bivalves does not change when tellinids and cardiiids (that have a very strong escape response) are excluded from the analysis. Per-species DF ranges from 24% (commensal) to 11% (epifaunal). However, commensals are represented by fewer than 20 individuals (Table 2) and therefore the high DF might be an artifact of low sample size.

The epifaunal bivalves are largely represented by bysally attached nestlers, followed by cemented epifauna, crevice dweller/cryptic bivalves, and free lying bivalves. Only the first two groups show per-species DF of ~10% while the remaining groups do not show any drill holes (Table 2). We did find a slightly higher per-species per-station DF in cemented bivalves compared to bysally attached ones (Fig. 6A, Wilcoxon rank sum test, $W = 2$, p -value = 0.03). However, the pattern is not significant for per-species DF (Fig. 6B, Wilcoxon rank sum test, $W = 85$, p -value = 0.4) and per-station DF (Fig. 6C; Wilcoxon signed rank test, $V = 13$, p -value = 0.9).

We found a significant difference between bivalves with poor and good escape response for per-species per-station DF (Wilcoxon rank sum test, $W = 3214.5$, $p < 0.001$) (Fig. 7A); but the difference is not significant for per-species DF (Wilcoxon rank sum test, $W = 569.5$, p -value = 0.91) (Fig. 7B) and per-station DF (Wilcoxon rank sum test, $W = 49.5$, p -value = 0.32) (Fig. 7C).

3.6. Drilling intensity among bivalves with different feeding modes

A difference between drilling frequency in chemoautotrophs and deposit feeders is evident (Fig. 8). This difference is significant for per-species per-station DF (Fig. 7A; Wilcoxon rank sum test, $W = 1060$, $p < 0.0001$) and for per-species DF (Fig. 7B; Wilcoxon rank sum test, $W = 126.5$, p -value = 0.001), but is not significant for per-station DF (Fig. 7C; Wilcoxon rank sum test, $W = 14$, p -value = 0.5).

3.7. Drilling intensity among habitats

The assemblage is dominated by inhabitants of fine-grained sediments followed by dwellers in or on sandy, reef and rock bottom and the pooled DF shows a similar pattern (Table 3). Individuals collected in mangrove sand do not have any drilled valves. The fine-grained sediments are showing a slightly higher incidence of drilling frequency compared to other substrate types (Fig. 8); however, the difference in DF between fine-grained sediments and reef is not significant for per-species per-station DF (Fig. 8A; Wilcoxon rank sum test, $W = 278$, p -value = 0.9) or for per-station DF (Fig. 8B; Wilcoxon rank sum test, $W = 6$, p -value = 0.5).

3.8. Drilling at different bathymetric levels

There is no correlation between DF and depth (Spearman rank order correlation, $\rho = 0.28$, $p = 0.2085$) (Fig. 9A) on the basis of per-station DF. The DF values of shallow and deep habitats are comparable (Wilcoxon rank sum test, $W = 21$, p -value = 0.09).

4. Discussion

4.1. Predator and prey

Among the drilling gastropods, both muricid and naticids occur in the Safaga Bay (Janssen et al., 2011 and unpublished data on neogastropods); nine species of Naticidae, ten species of Muricidae (six species of Muricinae and four species of Ergalataxinae) are known as drillers (Chattopadhyay et al., 2014a, Table 6). Naticidae are more abundant, are dominating in soft-substrata, and do not occur on hard substrata. Muricidae dominate on hard substrata, but also inhabit soft substrata. Therefore, we assume that the

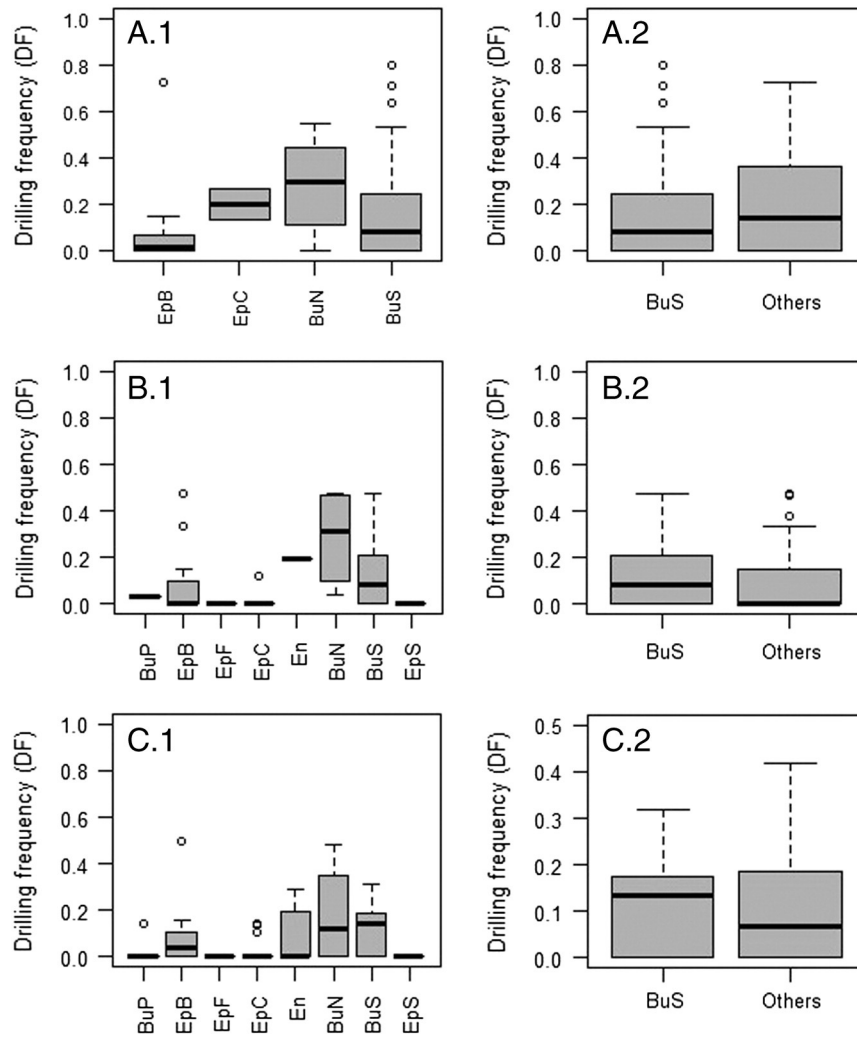


Fig. 5. Relationship between drilling frequency (DF) and siphon. A. Siphon–DF relationship for “per-species per-station” method. B. Siphon–DF relationship for “per-species” method. C. Siphon–DF relationship for “per-station” method. The right panel (A.2, B.2, C.2) represents analysis between two groups where BuS represents groups that are burrowing siphonate while the others comprise of BuP (burrowing protobranch), EpB (epifaunal byssate), EpF (epifaunal freeliving), EpC (epifaunal cemented), En (endobysate), BuN (burrowing non-siphonate and non-protobranch), and BoS (boring siphonate). In A, B and C, the boxes are defined by 25th and 75th quantiles; thick line represents median value.

majority of hard substrata drillings are made by Muricidae whereas the majority of the soft substrata drillings are probably made by Naticidae. The overall dominance of naticids in the Northern Bay of Safaga can explain the higher drilling frequency observed in in-fauna compared to epifauna. However, the variation in drilling intensity among stations (i.e., at small spatial scales) cannot be explained by the abundance of predators because the abundance of predatory groups does not correlate with per-station DF (Fig. 10B; Spearman $\rho = 0.25$, $p = 0.26$). The prey abundance does not explain the drilling intensity which is in contrast to the claim that DF can be affected by the encounter rate – a rate that is primarily controlled by prey abundance. We did not find any correlation between prey–species abundance and per-species DF (Fig. 10B).

4.2. Effectiveness of ecological attributes against drilling

4.2.1. Effect of size

Drilling predators are often size selective in their attack. Naticids drill larger prey as they grow larger (Edwards and Huebner, 1977; Kingsley-Smith et al., 2003a, b). Muricids, however, often do not show such a trend (Kowalewski, 2004; Casey and Chattopadhyay, 2008). Size selectivity has been examined using two different approaches in

previous studies: measuring drill hole diameters and comparing frequency distributions of drilled and undrilled specimens. In the first approach, size selectivity is established by studying the prey size and the corresponding predator size inferred from the drill hole diameter. In our study most naticids were small (in the range of few mm), whereas the muricids were comparatively large (mostly in the range of centimeters), but we did not measure drill hole size. While a number of studies found a positive correlation (Kitchell et al., 1981; Kelley and Hansen, 1996; Sickler et al., 1996; Kelley et al., 1997; Chattopadhyay and Dutta, 2013), others did not (Adegoke and Tevesz, 1974; Harper et al., 1998). Few other studies demonstrated size selectivity by comparing the frequency distributions of drilled vs. undrilled specimens, or drilled specimens vs. the total sample (e.g., Ansell, 1960; Allmon et al., 1990). Temporal pattern of size selectivity among drilling gastropods was presented as an indicator of predator–prey escalation. The majority of studies on Neogene to recent assemblages demonstrated size selectivity (Kojumdjieva, 1974; Kitchell et al., 1981; Hoffman and Martinell, 1984; Kabat and Kohn, 1986; Kelley, 1988, 1991; Anderson, 1992; Tull and Bohning-Gaese, 1993; Dietl and Alexander, 1995; Hagadorn and Boyajian, 1997; Dietl, 2000; Alexander and Dietl, 2001). Although our result of a negative correlation between size of the prey and per-species DF supports the “size refuge” hypothesis, this pattern is not found for per-species-per-station DF.

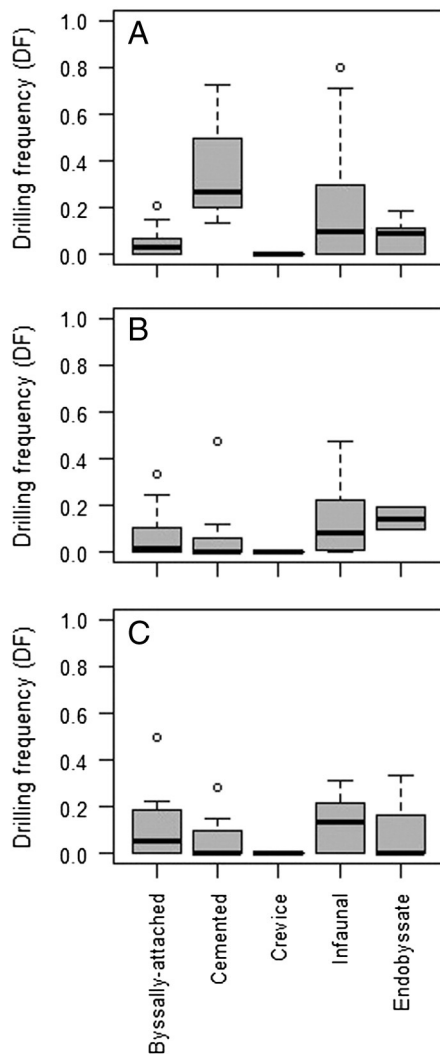


Fig. 6. Relationship between drilling frequency (DF) and attachment type. A. Plot for “per-species per station” method. B. Plot for “per-species” method. C. Plot for “per-station” method. The boxes are defined by 25th and 75th quantiles; thick line represents median value.

4.2.2. Effect of shape

The relationship between DF and shape has been observed before (Ansell, 1960; Stump, 1975; Kitchell, 1986) although the causal relationship is not clear. The bivalve shapes are often determined by their life habit and DF is most likely indirectly controlled by life habit: byssally attached bivalves are often elongated (Stanley, 1972; Heinberg, 1979; Savazzi, 1984). The relatively lower incidence of DF in elongated bivalves (with higher length vs height ratio) could therefore be a reflection of the preferential predation on some life habits (discussed later).

4.2.3. Effect of life habit

Vermeij (1987) attributed the increasing predation pressure during the Mesozoic as a driving mechanism for the infaunalization of bivalves. This view is also supported by Stanley (1986); however, he noted that siphonate bivalves evade predators more efficiently than non-siphonate ones. A lower DF is, thus, expected in infaunal compared to epifaunal groups and especially so in siphonate burrowers. Naticid gastropods typically prey upon infaunal bivalves and seldom hunt on the surface (Guerrero and Reymont, 1988; Dietl, 2002; but see Savazzi and Reymont, 1989). Muricids, on the other hand, search for and drill prey epifaunally; occasionally, they may dig up shallow-infaunal prey

(Kelley and Hansen, 2003). Such behavior is observed in the field of the present study (Fig. 11). This indicates that the position of a bivalve within the substrate largely controls the type of predator it is likely to encounter. Our results show that infauna has the highest of all DFs followed by semi-infauna and epifauna – a pattern contrary to the conventional prediction. This may contradict the above hypothesis of risk reduction by infaunalization, but is consistent with evolutionary increase of infaunal predation (Vermeij, 1987).

We also did not find significant differences between bivalves of dissimilar siphonal characteristics except for EpB (epifaunal byssate) and BuN (burrowing non-siphonate and non-protobranch). In all methods, BuN is showing a consistently high DF compared to EpB. The results of the DF comparison between BuS (Burrowing siphonate) and the other bivalves are not supporting the claim that siphonate bivalves are better protected. This implies that mobility of infaunal bivalves may play some role in their susceptibility to drilling predation; however, the pattern does not change even after the exclusion of highly mobile tellinids and cardiids with good escape responses. Mobility, when analyzed directly, does not support the claim of escape response. However, it is important to note that we get a slightly different pattern when the per-taxon DF is studied for the families; the highly mobile tellinids and cardiids tend to show lower DFs compared to the more sedentary lucinids and glycymeridids and venerids with moderate mobility show intermediate values of DF supporting the role of mobility (Table 1).

It is interesting to note that our results, especially the higher drilling in infauna, are contrary to the findings from recent assemblages from the Adriatic Sea (Sawyer and Zuschin, 2010) and the tropical Neogene of Panama and Costa Rica (Leonard-Pingel and Jackson, 2013). Our result is emphasizing that the dominance of a specific predator over the others determines the drilling frequency at larger spatial scales, i.e., at the scale of the Northern Bay of Safaga. Among the available predators, Naticidae have the higher abundance in the study area (Naticid: 105 shells – 9 species; Muricid: 15 shells – 6 species). The higher abundance and diversity of infaunal naticids is driving higher DF in infaunal bivalve population on which they prey. However, it is important to note that the variation in drilling frequency among stations is not determined by the predator abundance.

4.2.4. Effect of attachment type

It has been hypothesized that various attachment styles of epifauna could act differentially in deterring drilling attack. According to Harper (1991), multiple Mesozoic families of bivalves adopted cementation in response to increased predation pressure from grappling predators such as asteroids and crustaceans; a decrease in manipulability of cemented prey leads to reduced success for such predators. However, manipulability is only relevant for naticids among the drilling predators; muricids, on the contrary, rarely manipulate their prey (Carriker, 1981). Cementation should not play a major role in deterring drilling predation because naticids mostly prey on infaunal groups. In fact, Sawyer and Zuschin (2010) show that cemented bivalves possess very high DFs in the northern Adriatic Sea. Byssal attachment, in contrast, has been demonstrated as a deterrent for drilling predation. Controlled experiments demonstrated that clumping by mussels through byssal threads reduces drilling frequency (Casey and Chattopadhyay, 2008). Moreover, mussels can attach byssal threads to predatory gastropods and immobilize them with further byssal production (Petraitis, 1987; Day et al., 1991). Despite of these differences between cementation and byssal attachments, our study does not indicate significant difference between DF of cementing and byssally attached bivalves in all the cases and thus in deterring drilling predators.

4.2.5. Effect of feeding

Although there is no clear causal mechanism that connects feeding behavior of the prey and drilling patterns, predators may be expected to avoid chemosymbionts due to toxic reducing compounds in their tissues as documented by Kicklighter et al. (2004) on Vesicomidae, a

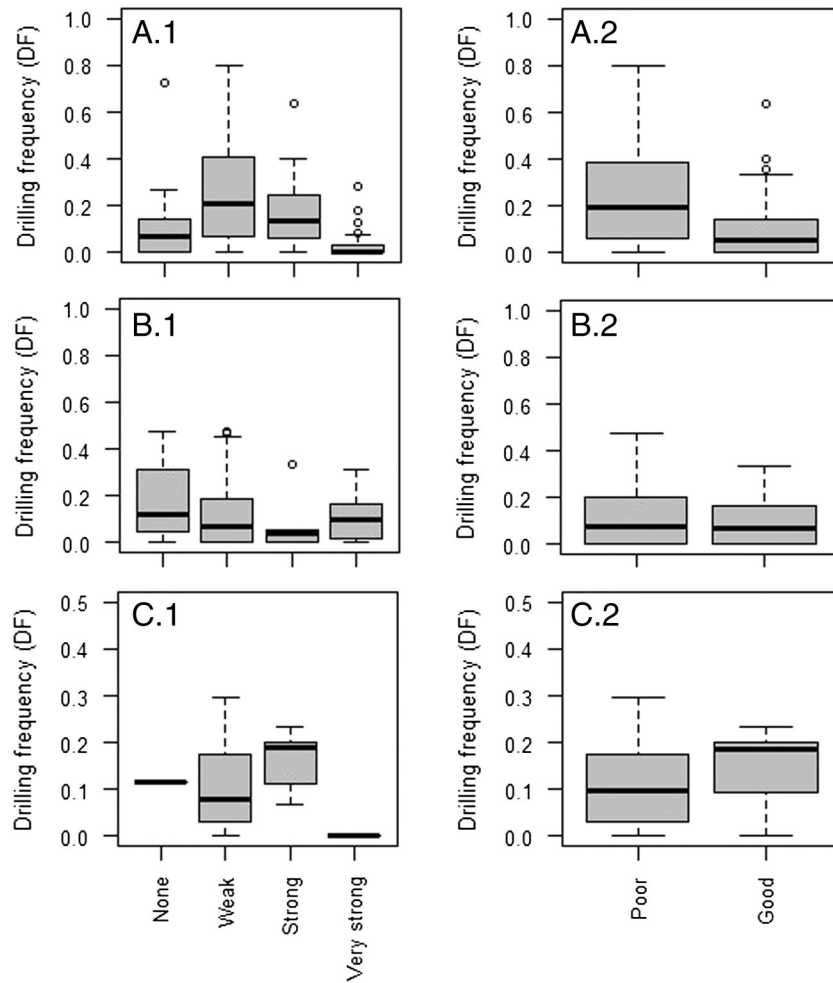


Fig. 7. Relationship between drilling frequency (DF) and mobility. Plot for “per-species per-station” method. B. Plot for “per-species” method. C. Plot for “per-station”. The right panel (A.2, B.2, C.2) represents analysis for two groups (poor = none + weak, good = strong + very strong). The boxes are defined by 25th and 75th quantiles; thick line represents median value.

highly specialized family of deep sea bivalves. Whether this result could be generalized for other chemosymbionts is a debatable issue. However, our results show an opposite pattern. Chemoautotrophs, in fact, show a higher DF compared to deposit feeders. Similar pattern of high DF in chemosymbionts are reported both from the recent northern Adriatic Sea (Sawyer and Zuschin, 2010) and northern Red Sea (Zuschin and Ebner, 2015) and from the fossil record (Kelley and Hansen, 1993, 2006).

4.2.6. Effect of depth and habitat

In contrast to several other studies (e.g. Sander and Lalli, 1982; von Rützen-Kositzkau, 1999; Walker, 2001; Tomašových and Zuschin, 2009) we did not find any negative relationship between depth and DF. One explanation is that, within this narrow depth range, the levels of predation do not vary significantly with depth. Hansen and Kelley (1995) found a difference in drilling between the inner/middle shelf and the outer shelf, with more drilling in the outer shelf. However, the drilling frequencies did not differ between the inner to middle shelf samples, a result comparable to those of the present study. Predation is also claimed to be 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). However, we did not find consistent differences in DF among different substrates. This lack of correlation of DF with depth and substrate could reflect the mosaic of habitats at the study area (Piller and Pervesler, 1989), potentially obscuring any correlation.

5. Implications

It is important to note that more often than not, the results of tests evaluating ecological predictions based on the evolutionary hypotheses are not consistent between the different methods that assess DFs at different spatial scales and at different taxonomic levels. This scale-dependency highlights the importance of the internal consistency of methods while comparing results from different studies for building a global database to evaluate temporal patterns.

In this study, we assessed the effectiveness of numerous ecological traits of the prey that have been claimed to be advantageous against predation. Various important ecological traits, such as infaunalization, being siphonate and mobile, or predator avoidance by choosing deeper-water habitats, fail to make a difference in DF in a modern subtropical bivalve assemblage. However, traits such as small size, specific shape and feeding style emerged as predictors for prey vulnerability against drilling predation. Whether such ecological traits were originally developed as a response to predation pressure or not, is a debatable issue. However, they definitely opened a new ecological niche. It is, therefore, pertinent to evaluate if, at all, they are effective against predation today. Although such studies are common for durophagous predation, it is quite rare in drilling predation. The study by Klompmaker and Kelley (2015) is one rare example where a similar line of questioning was investigated by assessing the effectiveness of shell ornamentation against drilling predation. In contrast to the claim of effective defense provided by ribbed ornamentation, they concluded that ribs are a likely

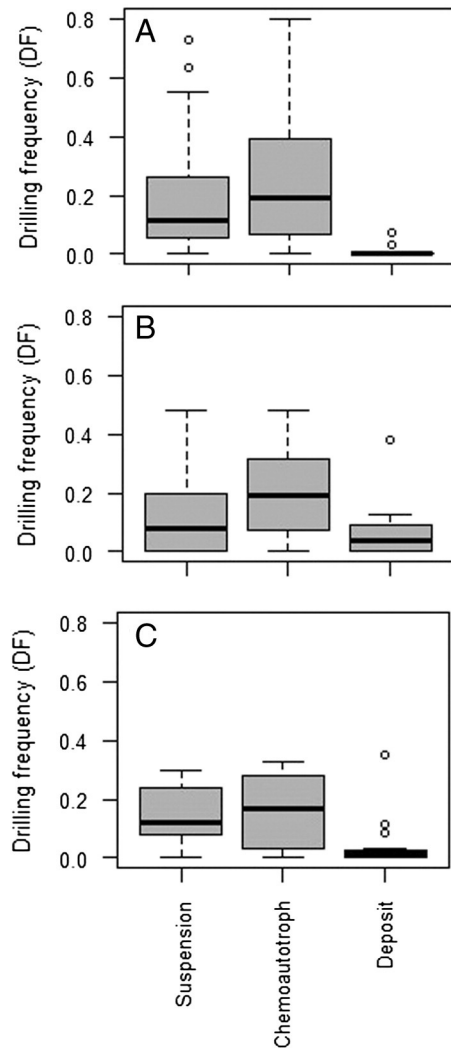


Fig. 8. Relationship between drilling frequency (DF) and feeding habit. A. Plot for “per-species per-station” method. B. Plot for “per-species” method. C. Plot for “per-station” method. The boxes are defined by 25th and 75th quantiles; thick line represents median value.

exaptation to drilling, because they serve also other purposes, for example stabilizing bivalves in the sediment.

There are two explanations for the observed lack of effectiveness of ecological traits in the studied ecosystem. The first one involves the specificity of anti-predatory strategies against a certain type of predator. One can argue that the ecological traits considered in this study are

effective against other kinds of predation such as durophagy. More comprehensive studies on comparative effects of types of predation on prey-groups are needed to answer this question. The second possibility is that the effectiveness of an anti-predatory defense is changing temporally; even a highly effective defense loses its edge with time against predators – a possibility that resonates with the idea of ever escalating predator–prey dynamics. A thorough examination documenting the continuous record of ecological traits and their effectiveness through time is needed to evaluate the second possibility.

6. Conclusion

In our study of drilling predation from a recent bivalve assemblage of the northern Red Sea, we evaluated specific evolutionary hypotheses predicting different levels of vulnerability of prey to drilling predation. Our evaluation was based on DF calculated by three different methods namely, 1) per-species per-station DF (sampled at meter-scale spatial resolution), 2) per-species DF by pooling all stations, and 3) per-station DF by pooling all species. The results are not always consistent among these three methods.

Among morphological attributes, we found size and shape of a species to be a good predictor of per-species DF and per-species-per-station DF respectively. Life habit plays an important role as documented by the higher DF in infaunal groups compared to epifauna. Although we did not find any significant correlation between predator abundance and DF at small spatial scales, the dominance of naticid gastropods and low abundance of muricid gastropods at the regional scale (Northern Bay of Safaga) can explain the difference between DF of infauna and epifauna. Character of the siphon and mobility do not always determine drilling frequency. Attachment type of epifauna does not explain differences in drilling frequency; bysally attached bivalves, however, sometimes show a slightly lower drilling frequency compared to cemented bivalves. We did not find significant variation in DF between groups with different water depth or habitat (substrate type). DF, however, shows strong differences between groups with different feeding mode and is particularly high in chemosymbiotic bivalves.

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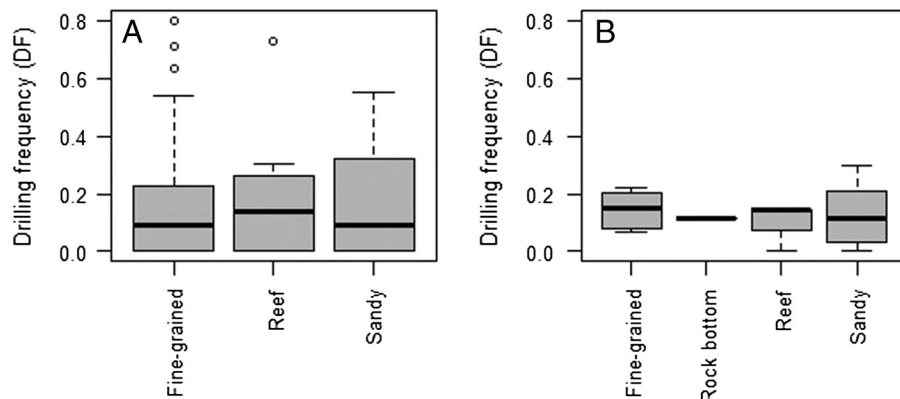


Fig. 9. Relationship between drilling frequency (DF) and habitat. A. Plot for “per-species per-station” method. B. Plot for “per-station” method. The boxes are defined by 25th and 75th quantiles; thick line represents median value.

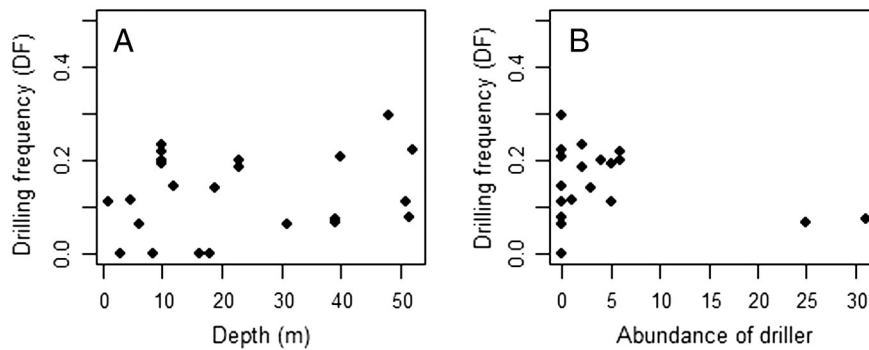


Fig. 10. Relationship between DF and various parameters for “per-station” method. A. DF–depth relationship. B. Relationship between DF and abundance of driller.

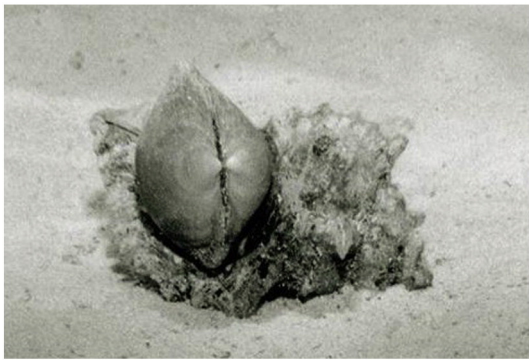


Fig. 11. A field photograph showing muricid (*Chicoreus*) drilling a *Glycymeris livida* on a sandy substrate.

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