MICROMORPHY OFFERS EFFECTIVE DEFENSE AGAINST PREDATION: INSIGHTS FROM COST-BENEFIT ANALYSES OF THE MIOCENE MICROGASTROPOD PREDATION RECORD FROM KERALA, INDIA

BY

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Abstract — Predation, an important driver of natural selection, is studied in the fossil record using quantifiable traces like drill holes produced by gastropods and repair scars produced after durophagous attacks. Despite the abundance of such records in molluscan prey, predation records of micromolluscs (<5mm) remain largely unexplored. Using a Miocene assemblage of microgastropods from the Quilon Limestone, India, we established the predator-prey dynamics with the help of cost-benefit analyses. The overall predation intensity, measured by drilling frequency (DF) and repair scare frequency (RF) is low (DF = 0.06, RF= 0.04). The predation intensity does not depend on the relative abundance of prey families suggesting a non-random prey selection regardless of the encounter frequency. Predation is selective as revealed by higher predation observed in prey of specific family identity, ornamentation, and body size. The smallest size class has the lowest DF and RF supporting a negative size refugia. Higher frequency of incomplete drill holes (IDF) among prey in larger size classes and ornamented groups implies morphological defenses that result in higher failure. Microgastropods show a lower predation intensity than macrogastropods of the same family in a global comparison of coeval records. Results of the cost-benefit analyses explain this difference; the net energy gain from predatory drilling is found to increase monotonically with increasing prey size making the small prey less beneficial. Because the predators try to maximize net energy gain from a predatory attack, the microgastropod prey characterized by relatively low net energy yield would not be preferred in the presence of larger prey. Micromorphy, therefore, appears a viable strategy for the prey group to adopt as an evolutionary response against predation, especially in resource-limited conditions that fail to support large body size.

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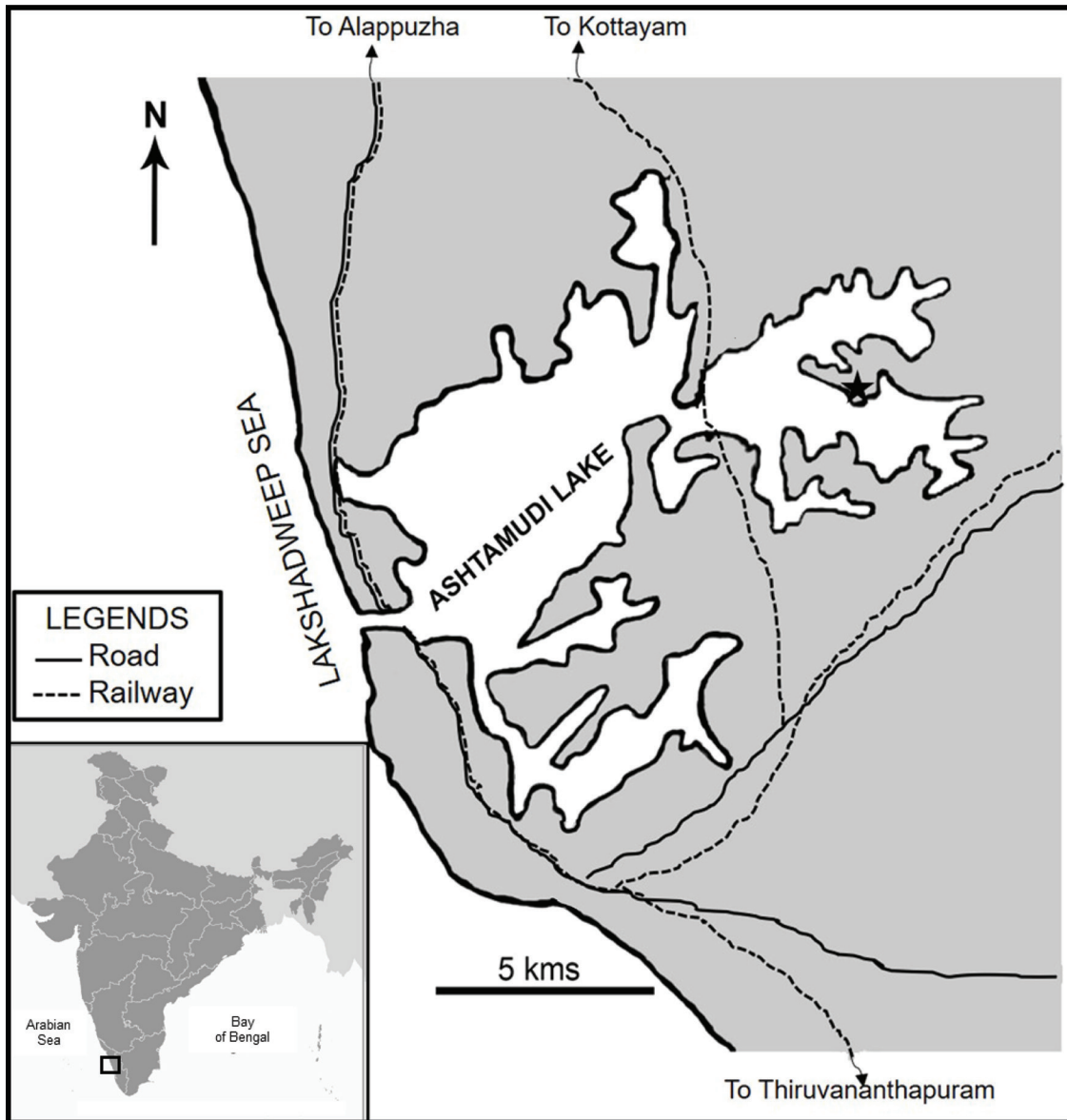
FIGURE 1 — Location of the studied locality with the map of India (inset). The star represents the location of the Quilon Limestone bed (Kerala). Modified after Chattopadhyay et al. (2020: Fig. 1.)

INTRODUCTION

Predation is an important ecological interaction and one of the major drivers of natural selection (Kitchell, 1986; Vermeij, 1987; Kelley and Hansen, 1993). It also plays a vital role in shaping community structure (Hines et al., 1990; Barnes et al., 2010). Direct evidence of predation events in the fossil record, such as the ones "caught in the act" are rare. Trace fossils like predatory drill holes and repair scars are common evidence of predation that can be studied quantitatively (Kelley et al., 2003). Complete drill holes represent a lethal attack in contrast to the traces of non-lethal attacks such as incomplete drill holes (but see Kowalewski, 2002) and repair scars. These traces reveal various aspects of predation (including the predator's identity, prey preference, and success rate) (Klompmaker et al., 2019). The fossil record of predatory traces proved crucial in understanding the evolution of marine invertebrates and restructuring of marine ecosystems as a response to biotic interactions (Vermeij et al., 1981; Huntley and Kowalewski, 2007).

The relative size of the prey and its predator often determines the outcome of a predatory interaction and plays an important role in shaping the evolutionary trajectory of the prey groups (Vermeij, 1987; Klompmaker et al., 2017).

In drilling predation, the prey size preference is primarily governed by the energy maximization of the predator for each attack (Kitchell et al., 1981; Chattopadhyay and Baumiller, 2009). Patterns like size refugia are common among the molluscs where prey greater than a specific size class are seldom attacked; the larger prey tend to be more difficult to capture and subdue (Leighton, 2002; Harper et al., 2009). Small prey is not always the most preferred size class either. Recent rhynchonelliform brachiopods from the Southern Hemisphere and tropical Northern Hemisphere demonstrated a lower intensity of shell-breaking predation among micromorph species that dominate the tropics (Harper and Peck, 2016). A fossilized assemblage of microbivalves (<5mm) also revealed a lower intensity of drilling predation in the smaller size class (<1mm) supporting the existence of a negative size refugia (Chattopadhyay et al., 2020). Such predation resistance among extremely small shelled invertebrates, such as molluscs and brachiopods, points to a complex relationship between size and predation intensity. To understand whether small size is an evolutionary response to predation, the predation record of micromolluscs needs to be explored. Except for the microbivalves, the predation record of microfossils primarily constitutes of taxa such as foraminifera (Culver and Lipps, 2003) and ostracods (Maddocks, 1988; Rayment and Elewa, 2003); microgastropods (<5mm) have not been studied extensively for their predation record.

Here we studied the microgastropod assemblage from the early Miocene Quilon Limestone bed from southwest India (Quilon, Kerala) (Harzhauser, 2014) to address the following questions:

1. What controls selectivity of microgastropod prey?

2. Is predation of microgastropods viable from the cost:benefit perspective?

3. Are predator-prey dynamics significantly different in microgastropods in comparison to macrogastropods?

MATERIALS AND METHODS

Locality and Collection

The field locality is situated on the cliffs along the shores of Ashtamudi Lake, near Padapakkara village, Kerala, India (N 08° 58'36", E 076° 38'08"; Fig. 1). The collection protocol has been described in detail in Chattopadhyay et al. (2020)

From the collected bulk sample, 371.8g of the sample was processed. The bulk sample was soaked in normal water for 5–6 days to loosen the sediments and subsequently, wet sieved using an 18μm sieve to remove the sedimentary particles. The remaining sediments were then dried, sieved, and classified into different size classes using a set of five sieves (mesh sizes 63, 60, 35, 25, 18μm). We studied the processed samples under the microscope and identified specimens up to the family level using the detailed study by Dey (1961) and Harzhauser (2014). The identified specimens were categorized into three size classes, small (less than 1mm), medium (1–2mm), and large (greater than 2mm).

The specimens were also classified into two groups based on ornamentation: the ones with smooth shells were classified as non-ornamented (Buccinidae, Eulimidae, Marginellidae, Naticidae, Phasianellidae, Scaliolidae, and Turbinidae) and rest as ornamented.

Specimens with any visible signs of predation (complete drill hole, incomplete drill hole, repair scar) were separated. Complete drillholes were further categorized into naticid drilling characterized by their parabolic shape, bevelled edges and muricid drill holes are cylindrical (Kabat, 1990; Kelley and Hansen, 2003). We used two protocols for characterizing the location of drill holes. In the first protocol, the gastropod shell was divided into two equal zones radially (apertural and abapertural) and each drill hole site was characterized using this scheme. In the second protocol, the gastropod shell was divided into three sectors vertically (top, central, basal) from the apex. Considering the total height of a specimen, the sectors were assigned based on the relative distance from the apex as the top (33% at the top), basal (33% at the base), and central (remaining 33% at the centre). We took detailed photographs of drilled specimens using a Nikon D700 attached to an Olympus SZX16 microscope. We processed the images using Image J to measure the size of the specimens and drill holes. The undrilled specimens were categorized into size-bins based on the mesh size of the sieve. For detailed imaging, representative specimens were imaged using an EVO LS10 Scanning Electron Microscope (SEM) (Carl Zeiss, Germany) where specimens were mounted on an aluminium stub using conductive carbon adhesive tape and imaged directly with low EHT (2–3 kV).

Drilling predation on Miocene macrogastropods from the same biogeographic region (Goswami et al, 2020) and other localities (Hoffmeister and Kowalewski, 2001; Kelley and Hansen, 2006; Sawyer and Zuschin, 2011) were compiled for comparative analysis. The family-specific predation matric is computed using the raw data if it is not reported in the published record.

Analysis

Drilling frequency (DF), a measure of successful predation attempts, is calculated by dividing the number of specimens with complete drill holes by the total number of specimens.

$$DF = \frac{N_D}{N} \quad (1)$$

Where, N_D = number of specimens with complete drill hole

N= Total number of specimens.

The incomplete drilling frequency (IDF), also referred to as "prey effectiveness" is calculated by dividing the total number of incomplete drill holes by the total number of drilling attempts (Chattopadhyay & Dutta, 2013).

$$IDF = \frac{N_I}{(N_I + N_D)} \quad (2)$$

Where, N_D = number of specimens with complete drill hole

N_I = number of incomplete drill holes

To estimate the intensity of repair scar (RF), the total number of specimens with repair scar was divided by the total number of individuals.

$$RF = \frac{N_R}{N} \quad (3)$$

Where, N_R = number of specimens with repair scar

N = Total number of specimens

To estimate the occurrence of multiple predation traces, we calculated MULT as the total number of holes in the specimens with multiple drill holes, divided by the total number of drilling attempts (Kelley and Hansen, 1993).

$$MULT = \frac{N_m}{(N_I + N_D + N_{msp})} \quad (2)$$

Where, N_m = total number of drillholes on the specimens with multiple drill holes

N_D = number of specimens with complete drill hole

N_I = number of incomplete drill holes

$N_{msp} = N_m$ – number of specimens with multiple drillholes

We used the Spearman correlation test to evaluate the correlation of predation intensity with abundance and size. We used two-tailed chi-square test to evaluate the variation in predation attempts (DF, IDF, and RF) between different size classes. For the site preference of drilling a chi-square test of goodness of fit was done. All the statistical tests were conducted using the R programming environment (R development core team, 2007).

Cost-Benefit Analyses

We reconstructed the size of the predator (Lpd) from the drill hole size (OBD) using the following equation proposed by Klompmaker et al. (2017).

$$log(OBD) = -1.09 + 0.94 * log(Lpd) \quad (4)$$

Where, OBD = Outer borehole diameter (mm)

Lpd = Length of gastopod predator (mm)

The cost-benefit analysis was done for the microgastropods by adapting the equation suggested by Kitchell et al., (1981), along with a few modifications. The total benefit is calculated using the ash-free dry weight (Wpr) of gastropod prey with a specific size (Lpr). We used the formula for the genus *Polinices* for all the species. The relation is given as (Edwards and Huebner, 1977)

$$log Wpr = -3.6201 + 2.5969 * log Lpr \quad (5)$$

Where, Wpr = Ash free dry weight of the prey (g)

Lpr = Length of the gastopod prey (mm)

The calculated ash-free dry weight (Equation.5) is then multiplied by the energetic conversion factor, 21.46kJ/g (Kitchell et al., 1981) to obtain the benefit.

$$benefit = 21.46 * Wpr \quad (6)$$

The cost is calculated as a product of metabolic rate and time taken to drill the prey species. The drilling time (t) is found to be directly related to the thickness of the shell (T). The shell thickness (T) is calculated as (Avery and Etter, 2006)

$$Log T = 1.49 + 1.30 * log(Lpr) \quad (7)$$

Where, T = Thickness of the shell (µm)

Lpr = Length of the gastropod (mm)

Using the thickness (T), we calculated the time (t) required to produce the drill hole (Kitchell et al., 1981)

$$t = (T + 0.068)/0.026 \quad (8)$$

Where, T = Thickness (mm)

t = drilling time (hours)

The metabolic rate of the predator is estimated through a series of steps. Using the OBD, the length of the predator (Lpd) is calculated (Equation 4).

Later the ash-free dry weight is calculated using the following relationship:

$$Log Wpd = -3.6201 + 2.5969 * log Lpd \quad (9)$$

Where, Wpd = Ash free dry weight of the predator (g)

Lpd = Length of the gastopod predator (mm)

The ash-free dry weight (Equation 9) is then used to find the metabolic rate in terms of the amount of oxygen consumed per hour (Harper and Peck, 2003)

$$M0_2 = 2.23 + 29.8 * Wpd \quad (10)$$

Where, $M0_2$ = Amount of oxygen consumed (µg)

Wpd = Ash free dry weight of the predator (g)

According to Harper and Peck (2003), 18.6µg of oxygen/hour is equivalent to 13µl of oxygen/ hour. This relation is used to calculate the amount of oxygen consumed in litres. Using standard conversion factors, we obtain the metabolic rate in kJ/hour.

$$Mpd = M0_2 * 13.9 \quad (11)$$

Where, Mpd = Metabolic rate of predator (kJ/hours)

The cost is estimated as

$$cost = Mpd * t$$

Using Equation 6, the net enegy gain is estimated from the following expression:

$$benefit/cost = (21.46 * Wpr) / (Mpd * t) \quad (13)$$

TABLE 1 — Overall abundance and summary of drilling predation of microgastropods from Quilon Limestone bed.

Family	Total specimens	Completely drilled specimens	Drilling frequency (DF)	Specimens with incomplete drilling	Incomplete drilling frequency (IDF)	Specimens with repair scars	Repair scar frequency (RF)	Frequency of multiple drillholes (MULT)
Cerithiidae	717	34	0.047	4	0.105	13	0.018	0.095
Pyramidellidae	195	12	0.061	2	0.143	21	0.108	0.125
Scaliolidae	117	1	0.008	0	0.000	2	0.017	0.000
Rissoinidae	103	23	0.223	3	0.115	3	0.029	0.133
Eulimidae	28	1	0.036	1	0.500	2	0.071	0.000
Naticidae	27	3	0.111	0	0.000	2	0.074	0.000
Obtortionidae	26	1	0.038	3	0.750	2	0.077	0.000
Phasianellidae	23	3	0.13	1	0.250	2	0.087	0.000
Turbinidae	18	1	0.056	0	0.000	3	0.167	0.000
Buccinidae	13	1	0.077	0	0.000	0	0	0.000
Marginellidae	11	0	0	0	0.000	0	0	0.000
Olividae	9	2	0.222	0	0.000	0	0	0.000
Raphitomidae	9	1	0.111	0	0.000	0	0	0.000
Horaiclavidae	8	1	0.125	0	0.000	1	0.125	0.000
Triphoroidae	8	0	0	0	0.000	0	0	0.000
Turritellidae	5	0	0	0	0.000	0	0	0.000
Mangellidae	2	0	0	0	0.000	0	0	0.000
Columbellidae	2	0	0	0	0.000	1	0.5	0.000
Borsoniidae	1	0	0	0	0.000	0	0	0.000
Cerithiopsidae	1	0	0	0	0.000	0	0	0.000
Epitoniidae	1	0	0	0	0.000	0	0	0.000
Torchidae	1	0	0	0	0.000	0	0	0.000
Tornidae	1	0	0	0	0.000	0	0	0.000
Pseudomelatomidae	1	0	0	0	0.000	0	0	0.000
Ringiculidae	1	0	0	0	0.000	0	0	0.000
Total	1328	84	0.063	14	0.143	52	0.039	0.097

RESULTS

A total of 1328 microgastropod specimens in our study represent 39 species, 35 genera, and 25 families. Cerithiidae is the most abundant family, represented by 718 individuals, followed by Pyramidellidae and Scaliolidae. A total of 150 individuals from 14 families show the signature of predation yielding an overall DF of 0.063 and RF of 0.039 (Table 1, Fig. 2, 3).

Eleven families, represented by more than ten individuals each, are considered for subsequent predation analyses (Fig. 2, 3, Table 1).

Among the eleven abundant families, we find ten with complete drillings (Fig. 2, 3B, 4A), six with incomplete drill holes (Fig. 2, 3C), and nine with repair scars. Rissoinidae and Obtortionidae have the maximum DF (0.22) and IDF

(0.75) respectively. The majority of the drill holes correspond to naticid drilling (76.5%) and the rest corresponds to muricid drilling (Fig. 3B). The overall incidence of multiple drillhole is low (MULT=0.097) and only three families (Rissoinidae, Cerithiidae, and Pyramidellidae) showed them (Fig. 4B).

The overall RF is 0.039 and Turbinidae has the highest RF (0.18). There is no significant correlation between the overall abundance of a family and the observed predation matric (DF, IDF, and RF) (Table 2, Fig. 5A–C). There is no significant difference in median DF or median RF between families with and without ornamentation (Fig. 5D–F); however, the ornamented shells show a significantly higher median IDF (p= 0.03; Fig. 5E).

RF and IDF are significantly higher in the larger size (Table 3, Fig. 6); DF shows a similar but non-statistically significant pattern (Table 4). The median size of the incompletely drilled

TABLE 2 — Results of Spearman correlation test between relative abundance and predation matrices for abundant families. *DF,* drilling frequency; *IDF*, incomplete drilling frequency; *RF*, repair frequency.

	Spearman rho	p-value
DF	0.045	0.90
IDF	0.286	0.39
RF	0.114	0.74

TABLE 3 — Predation intensity in terms of drilling frequency, incomplete drilling frequency and repair frequency with respect to size.

Size class	DF	IDF	RF
Small (< 1mm)	0.05	0.07	0.02
Medium (1–2 mm)	0.06	0.15	0.04
Large (>2 mm)	0.09	0.32	0.11

specimens is larger than the complete and undrilled specimens; however, the difference is not statistically significant (Fig. 7A).

The apertural placement of complete drill holes is significantly more common compared to the abapertural placement (Chi-square test, p=0.01); apertural placement is least favored for incomplete drilling (Fig. 7B). The central region of the shell records the highest incidences of drill holes (79%; Fig. 7C). There is a strong positive correlation between the OBD and the prey size (Spearman rho = 0.79, p=2.2e^{-16}), especially for naticid predation (Spearman rho= 0.81, p= 1.23e^{-13}; Fig. 8A). The overall prey-predator size ratio for microgastropods falls between 0.4 and 1.2 (Figure 8B). However, 'small' microgastropods have a higher prey-predator ratio compared to 'medium' and 'large' ones (Fig. 8). The cost-benefit analysis demonstrates a benefit: cost > 1 for all the successful predation (Fig. 8C–E) and this ratio increases with an increase in the size of the prey. The naticid drillings yielded a higher benefit: cost ratio than muricid drilling (Wilcox test, p=0.04; Fig. 8D, E).

When compared to other drilling predation observed in macrogastropods of Miocene age (Table 5), DF of the Quilon Limestone assemblage is lower compared to the other locations, except for Kutch (Goswami et al., 2020; Table 5, Fig. 9).

The benefit-cost ratio is significantly higher for the macro gastropods of Kutch than the micro gastropods from Kerala (Wilcox test, p<<0.01; Fig. 8D–E). The family-level global comparison also shows a low DF for microgastropods in contrast to macrogastropods, except for the Rissoinidae family (Fig. 10A). Family-level comparison of RF demonstrates similar low-frequency in microgastropods (Fig. 10B).

DISCUSSION

Drilling predation on molluscan prey is the most common fossil record of predation followed by repair scars (Klompmaker et al., 2019). Temporal and spatial patterns of predation have been established for molluscs (Kelley and Hansen, 1993; Kelley and Hansen, 2006; Klompmaker et al., 2017) using a variety of approaches including controlled experiments (Chattopadhyay and Baumiller, 2007; Chattopadhyay et al.,

2014a, Das et al., 2015), ecological surveys (Mondal et al., 2014; Chattopadhyay et al., 2014b, 2015; Pahari et al., 2016) along with documentation of fossil ecosystems. Despite such a large breadth of research on molluscan predation, micromolluscs are largely ignored. Individuals of ostracods and foraminifera that are comparable to micromolluscs in size are known to be preyed upon by drilling gastropods (Reyment et al., 1987; Culver and Lipps, 2003; Reyment and Elewa, 2003). It is, therefore, expected that micromolluscs will also be targeted by predators. Chattopadhyay et al. (2020) documented the drilling predation on microbivalve prey from the Quilon Limestone and demonstrated the selective nature of drilling predation in micromolluscs for the first time. Although there have been studies on the evolution (Weigand et al., 2013) and habitat preferences (Olabarria et al., 2002) of microgastropods, there has only been a few studies on the predation patterns in microgastropods (Ortiz-Jeronimo et al., 2021) and none focussing on the cost-benefit analyses. The present study attempts to fill this gap.

Predator Identity

Naticid predators are responsible for the majority (76.5%) of the drill holes in the Quilon microgastropods as affirmed by their parabolic shape (Kabat, 1990). The presence of individuals of the naticid family in our sample and the reported presence of multiple naticid genera (*Tanea, Natica*) in the assemblage (Harzhauzer, 2014) confirms the identity of the naticid predators. Some of the naticid drill holes from the assemblage were as small as 0.035 mm, implying a shell size of approximately 0.4 mm; these could be juvenile naticids because the shells were extremely thin and lack any strong mineralization. The non-naticid drill holes had a straight cylindrical boundary indicating muricid predation (Hoffman et al., 1974; Carriker, 1981 Kabat, 1990). Although we did not find any muricid specimens in our sample, the presence of muricid family (*Triplex* and *Dermomurex*) in the same locality (Harzhauzer, 2014) reveals the identity of the muricid drilling predator.

Repair scars are primarily produced after non-lethal breakage often due to a failed predation attempt by fishes and crabs. The presence of Xanthid crabs in our sample and presence from the same locality (Verma, 1977) points towards
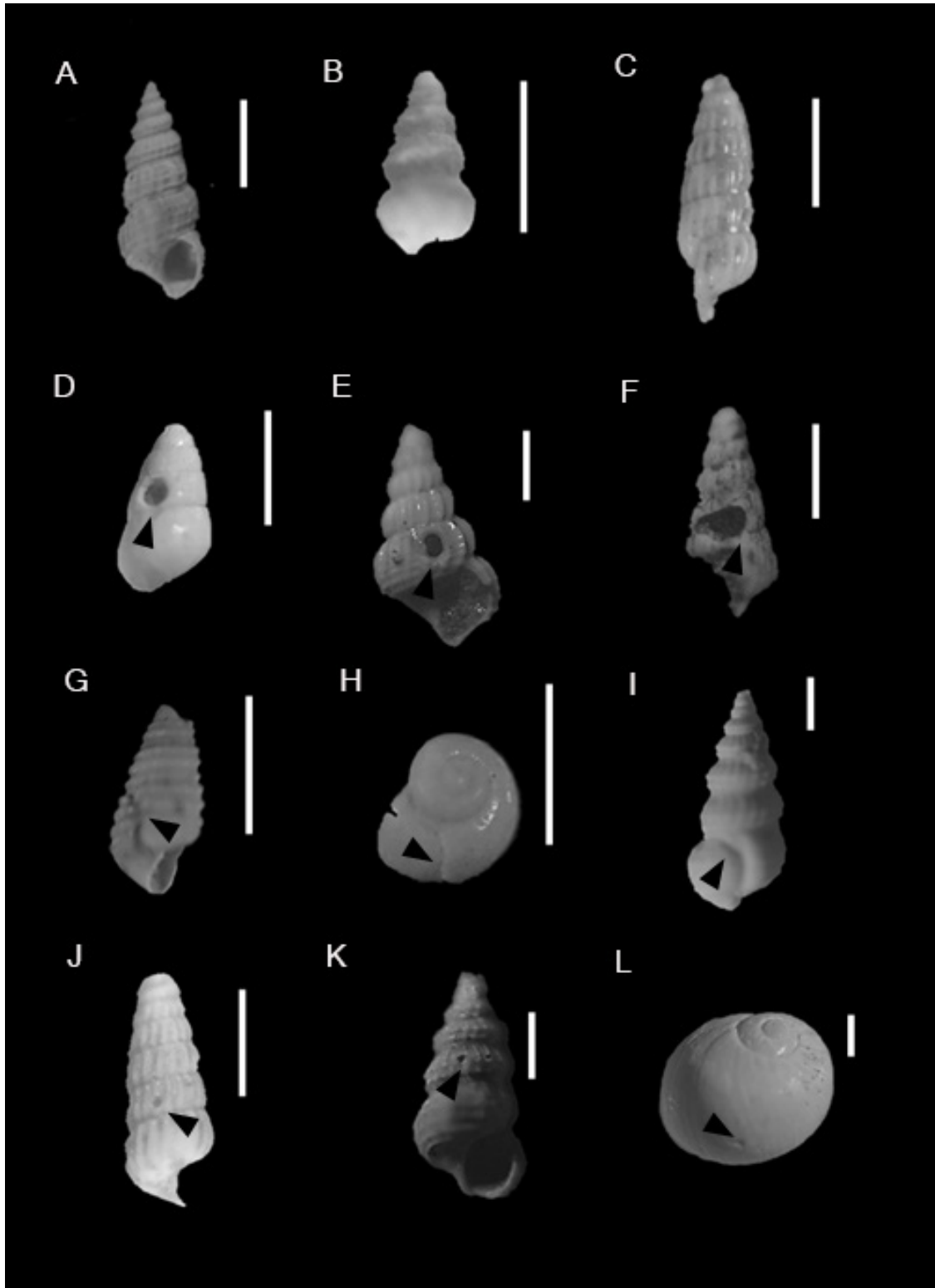
FIGURE 2 — Common gastropod families **A**, Cerithiidae, **B**, Scaliolidae and **C**, Pyramidellidae. Specimens with complete drill hole representing, **D**, Phasianellidae, **E**, Rissoinidae, **F**, Pyramidellidae. Specimens with repair marks representing **G**, Pyramidellidae, **H**, Turbinidae, **I**, Cerithiidae. Specimens with incomplete drill hole representing **J**, Pyramidellidae, **K**, Cerithiidae, and predator **L**, Naticidae. The scale corresponds to 1 mm.
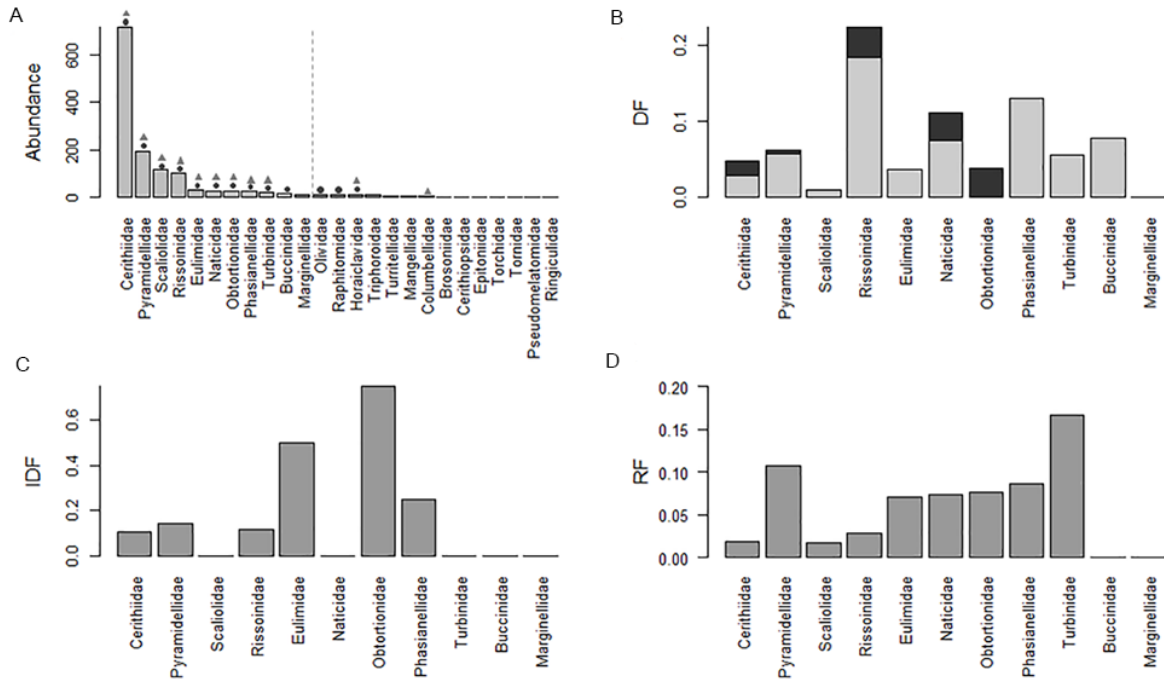
FIGURE 3 — Bar chart representing the **A**, abundance of all families. The dotted line separates the abundant (represented by more than ten individuals) and non-abundant families. The circles and triangles mark those families with drill holes and repair marks, respectively. Histograms representing the **B**, drilling frequency (DF) (the darker represents muricids and the lighter naticids), **C**, incomplete drilling frequency (IDF) and **D**, repair frequency (RF) of the eleven abundant gastropod families
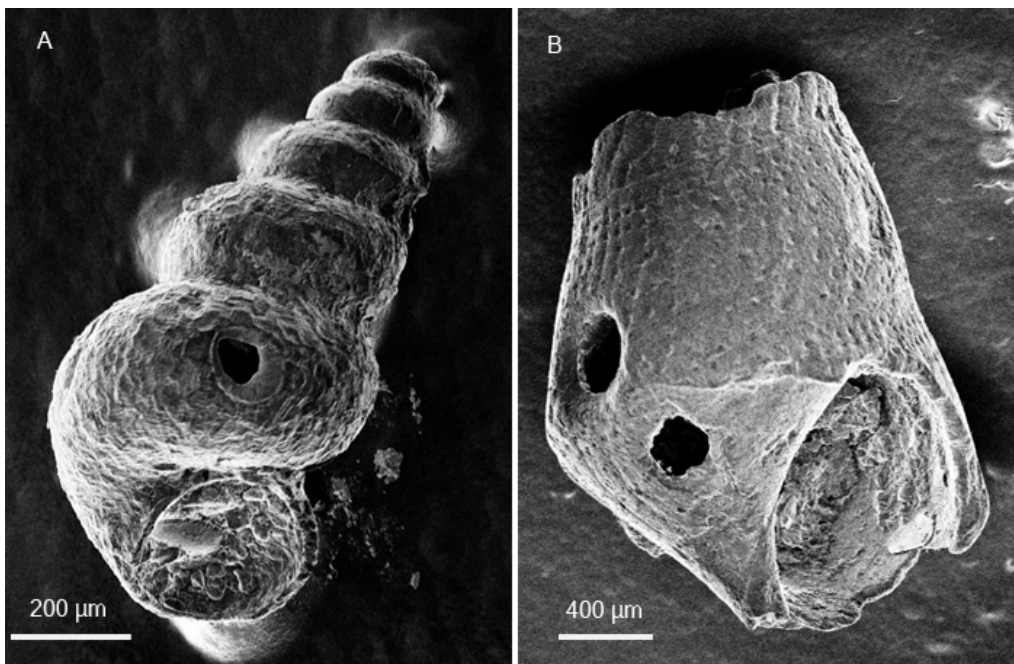
FIGURE 4 — SEM images of **A**, Complete drill hole in Scaliolidae, **B**, multiple drill hole in Pyramidellidae
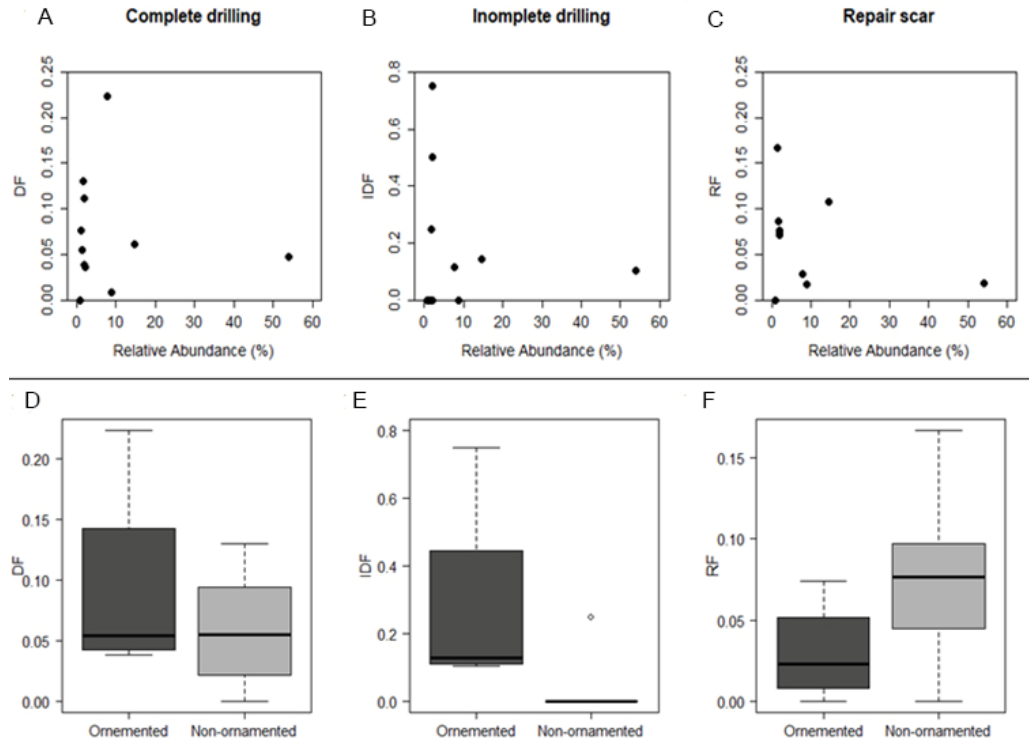
FIGURE 5 — The variation of predation marks with the relative abundance of family (**A–C**) and nature of ornamentation (**D–F**). The frequency of complete drillhole, incomplete drillhole and repair scars are represented by panels from the left to right. The boxes in the bottom panel are defined by 25th and 75th quantiles; thick line represents the median value.
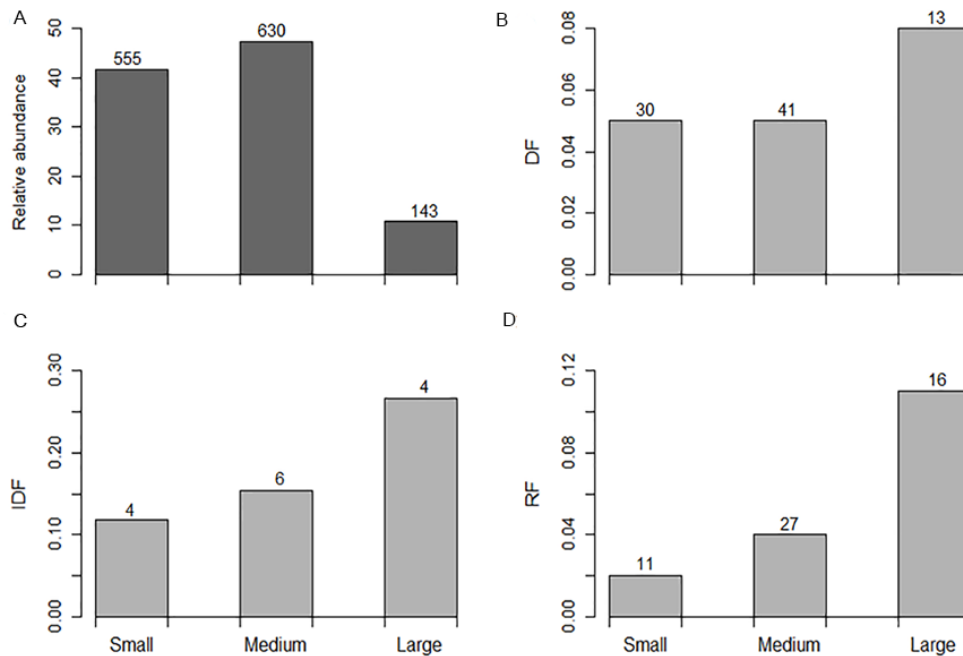

FIGURE 6 — Histogram showing the size class distribution of **A**, drilled and undrilled specimens, **B**, drilling frequency (DF), **C**, incomplete drilling frequency (IDF), and **D**, repair frequency (RF).
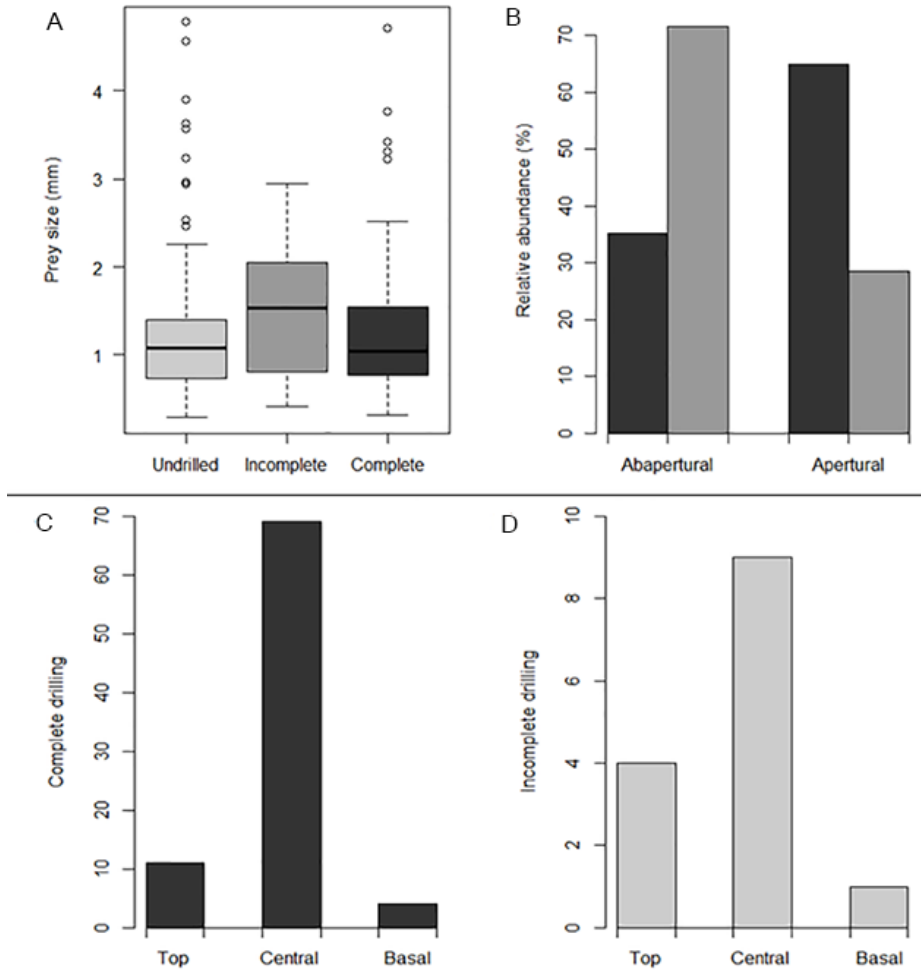
FIGURE 7 — Plot representing the variation in **A**, prey size and **B**, site selection between successful and unsuccessful predation attempts. The boxes in **A**, are defined by 25th and 75th quantiles; thick line represents the median value. The bar plots in **B**, represent relative abundance of specimens with complete drillhole (dark grey) and incomplete drill holes (light grey).

TABLE 4 — The results of the chi square tests done to evaluate the significance of variation in predation intensity interns of complete drilling, incomplete drilling, and repair scars (significant results are marked in bold).

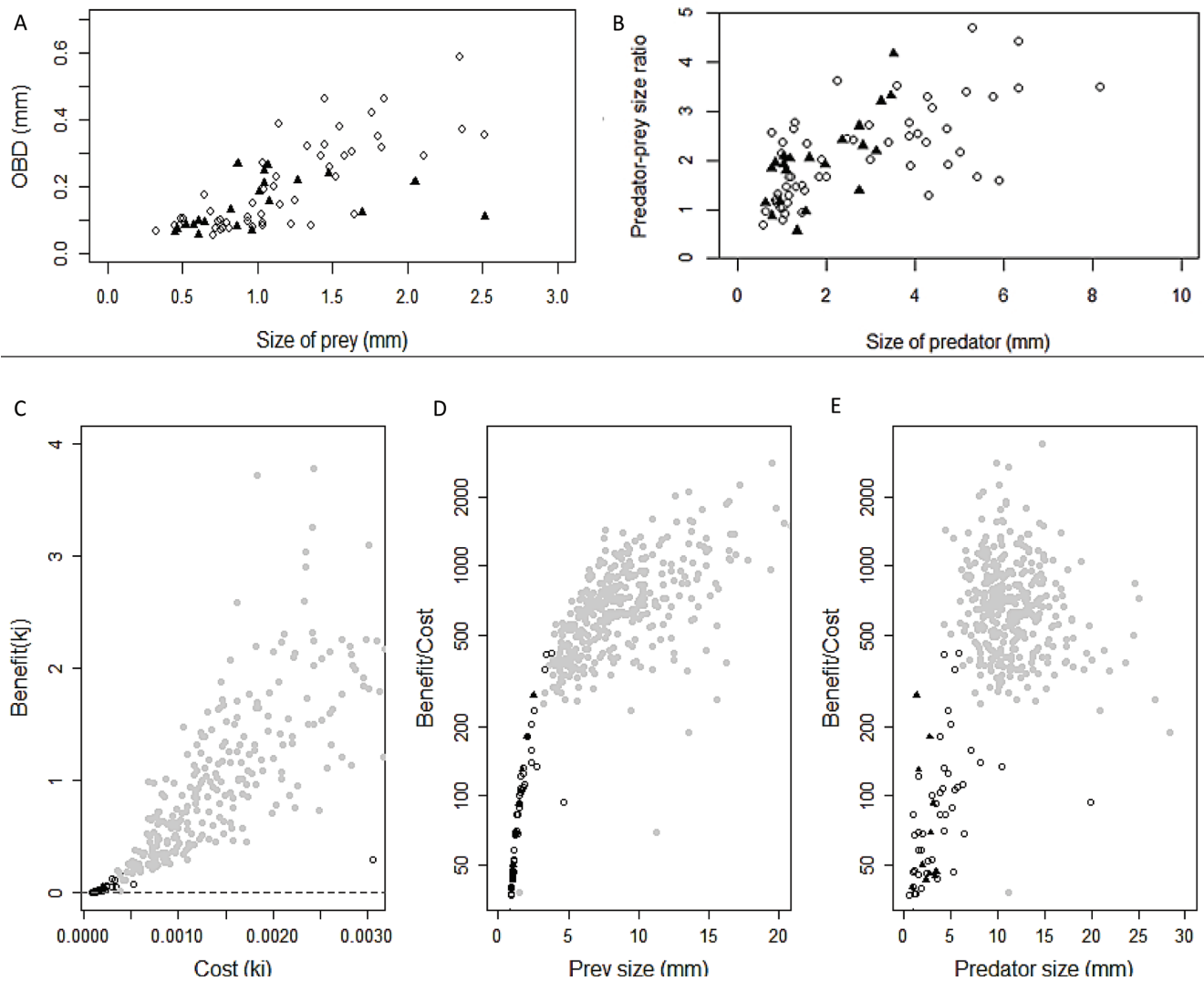| Size class	Chi square value for DF	p-value for DF	Chi square value for IDF	p-value for IDF	Chi square value for RF	p-value for RF
Small-Medium	0.009	0.926	0.196	0.658	5.041	**0.025**
Medium-Large	3.075	0.079	4.688	**0.030**	10.572	**0.001**
Small-Large	2.771	0.096	6.188	**0.013**	25.919	**0.000**

FIGURE 8 — Plot showing the relationship between **A**, size of the prey and the outer borehole diameter, **B**, the size of the predator and the prey-predator size ratio. Open circles represent naticid drilling and the closed triangles represent the muricid drilling. Cost – benefit relation for the micro gastropods, **C**, indicates the benefit gained by the predator species for a particular cost, **D**, scatter plot representing the relation between prey size and the benefit / cost ratio, **E**, relation between the inferred predator size and the benefit / cost ratio. The grey circles in the bottom panel represent data from Kutch and the dotted line in C indicate the minimum requirement for a successful predation (benefit = cost).

a potential durophagous predator. The higher number of repair scars among the 'large' microgastropods indicates a non-random predatory attack.

Factors Guiding the Prey Choice

The relative abundance of prey species is a good representation of the encounter frequency assuming the same lifespan of all the species, and studies have suggested that the predation intensity may be linked to prey availability (Leighton, 2002, 2003). However, taxon-specific DF, IDF, and RF in our study are not correlated to relative abundance (Fig. 6A–C) — a pattern consistent with findings for macro molluscs, both in the past and present ecosystems (Beu and

Maxwell, 1990; Kelley et al., 2003; Mallick et al., 2014; Pahari et al., 2016). A lack of correlation between predation intensity and relative abundance indicates a predator's preference towards a particular prey species, even if it is not the most abundant; such prey is often preferred by the predator due to certain morphological traits and highlights a selective behavior demonstrated by the predator. Our specimens show a highly selective nature of prey choice for both drilling and durophagous predation primarily guided by the morphological characters of the prey, including size and ornamentation.

Size.— The size of an individual often dictates if it is targeted by a particular predator and determines the outcome of a predatory interaction. The reliable reconstruction
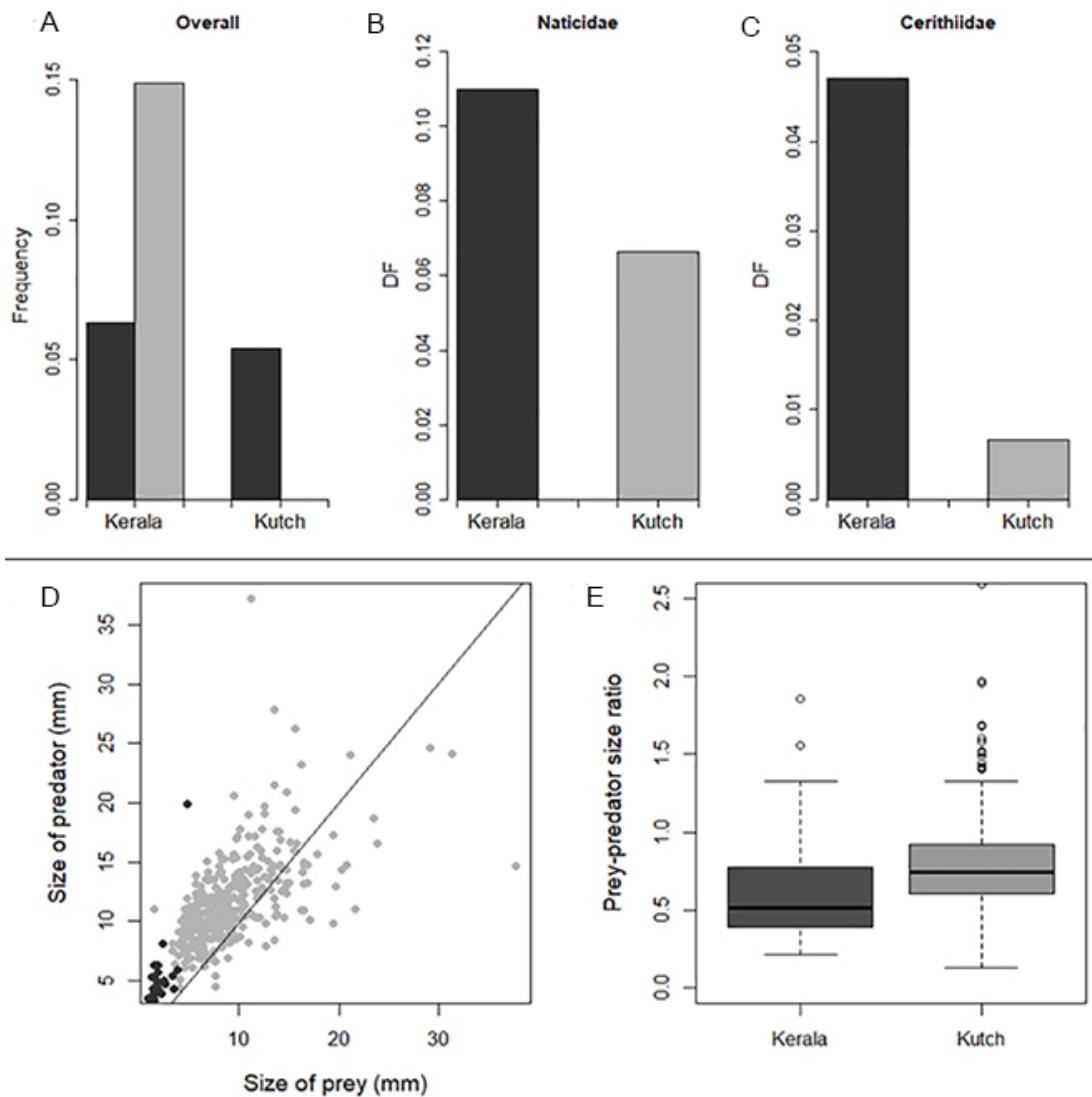
FIGURE 9 — Predatory patterns in Kerala and Kutch, India **A**, comparison of drilling frequency (DF) and incomplete drilling frequency (IDF), variation in DF for the common families **B**, Naticidae and **C**, Cerithiidae **D**, Relation between inferred size of the predator and size of the prey, grey represents Kerala specimens and black represents Kutch, **E**, boxplot representing the variation of prey predator size ratios.

of predator size is possible for drilling predation where experimental studies confirmed a strong positive correlation between the OBD and the size of the predator for specific families (Kitchell et al., 1981; Carriker and Gruber, 1999; Kowalewski, 2004; Klompmaker et al., 2017). The validity of the relationship has never been demonstrated for microgastropods. The inferred sizes of naticid and muricid predators from drill holes in the microgastropod assemblage are comparable to the size of corresponding specimens found from the locality, pointing to the validity of the approach.

Prey larger than a specific size are often avoided by predators due to difficulty in handling (Vermeij, 1987). Smaller prey are thought to offer low energetic gain and hence, not selected. Consequently, the predator targets medium-sized prey to maximize energy gain (Kitchell et al., 1981; Boggs et al., 1984; Kelley, 1988; Pahari et al., 2014; Chattopadhyay et al., 2020). The low DF in the smallest size class (although not statistically significant; Table 3) in our sample is consistent with this conclusion and suggests that the smaller size class is less likely to be attacked, providing refuge from predation. However, the higher IDF and RF in the larger size class suggest that the larger prey is efficient in escaping the predator once
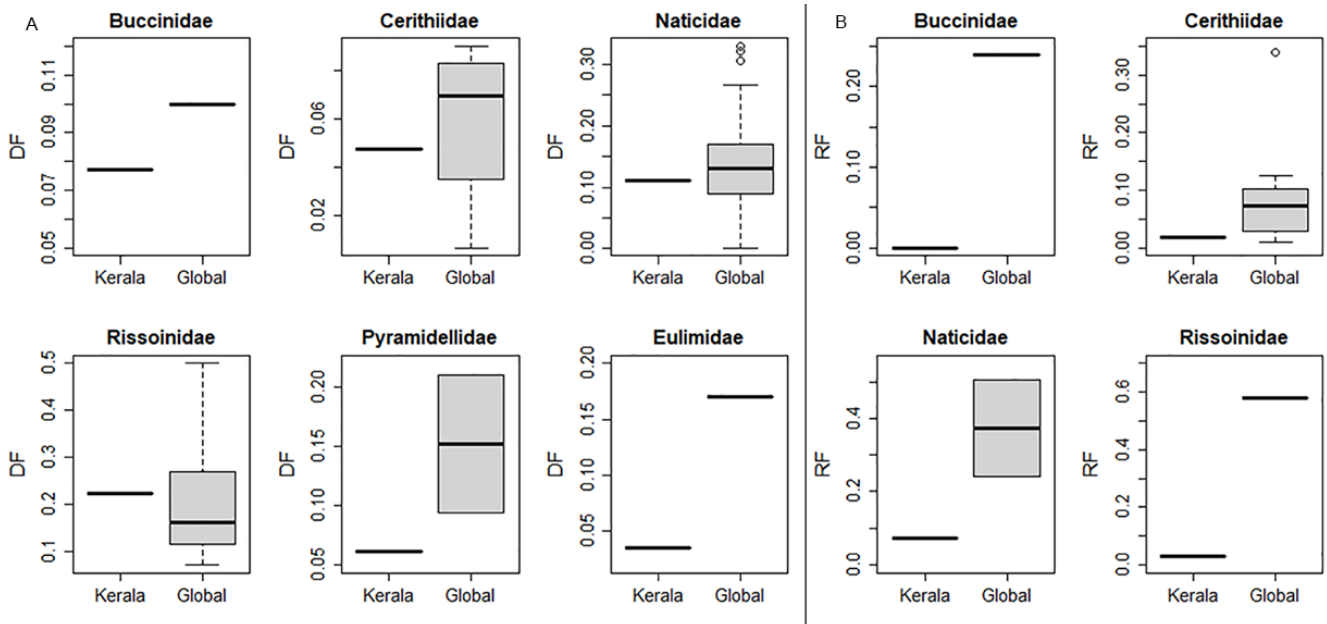
FIGURE 10 — Family-specific comparison in predatory patterns between Kerala and the other 628 coeval formations worldwide for **A**, drilling frequency (DF) and **B**, repair frequency (RF).

it is attacked. This result suggests complex prey-predator dynamics where the smaller size class is not preferred and larger prey are more successful in escaping from predators. Among two families of drilling predators, the naticids show a significant positive correlation between individual predator size and prey size demonstrating a strongly size-selective behavior (Fig. 9A–B). Because muricids do not envelope the prey within the foot unlike the naticids, muricid predators often do not show strong size-selectivity in their prey choice. The absence of size-selectivity of muricid predation not unique to micro gastropods and has been reported from macro gastropods (Tull and Böhning-Gaese, 1993).

Ornamentation.— Surface ornamentation plays an important role in determining the outcome of a predatory encounter. The ornamentation increases the effective thickness of the shell, making it more difficult to drill through. The presence of surface ornamentation such as coarse concentric ribs was found to reduce the incidence of successful drilling in bivalves (Klompmaker and Kelley 2015). Although the difference was not significant for DF and RF, the IDF was significantly higher in microgastropods with ornamentation, suggesting that ornamentation increases the probability of drilling failure. The two non-ornamented families (Eulimidae and Phasainallidae) with higher IDF have a smooth shiny surface that is hard to grab (Vermeij, 1987). Moreover, Eulimidae are parasitic and often associated with echinoderms, the defence strategies of echinids, for example the presence of spines makes them less vulnerable to predators that protect them from predators (Waren, 1983). A slightly higher, although not statistically significant, RF was found among the non-ornamented specimens, supporting the effect

of ornamentation producing failures in durophagous attacks. The highest RF, however, is found in a non-ornamented microgastropod family — the Turbinidae. The small size and the smooth shell may have helped them to escape from the durophagous attacks.

Taxon.— Both drilling and durophagous predators are known to demonstrate taxon selectivity (Alexander and Dietl, 2003; Chattopadhyay and Dutta, 2013; Chattopadhyay et al., 2015). Our study suggests that some prey taxa are preferred and the preference cannot be completely explained by the lack of morphological defense, such as the Rissoinidae family. They also have ornamentation such as ribs increasing their effective thickness, which should have acted against the predatory attacks. The abundance does not explain such higher rates always; families such as Scaliolidae and Cerithiidae have a larger relative abundance yet have a lower DF. In the absence of obvious high encounter frequency or morphological weakness, their behavioral traits may have contributed to such increased predation pressure.

Individual predatory families also show distinct selective patterns. Muricids are found to prey heavily upon Obtorionidae. Kitchell et al. (1981) have found that muricids are capable of drilling deeper holes, enabling them to prey on molluscs with a thicker shell or stronger ornamentation, such as the Obtortionidae. Because the deeper drill holes require longer drilling time, the probability of interruption by other predators and prey escape increases leading to higher frequency of incomplete drillings. This interpretation is also supported by the high IDF observed among Obtortionidae (Fig. 3C, Fig. 5B). In contrast to the overall dominance of naticid drilling, the assemblage demonstrates a low incidence

TABLE 5 —. Spatiotemporal comparison of drilling predation data on gastropods from other major Miocene assemblages.

Formation/place	Age	Number of specimens	Number of drilled specimens	Drilling frequency	Source
Calvert, Maryland, USA	Middle Miocene	594	---	0.202	Kelley & Hansen, 2006
Choptank, Maryland, USA	Middle Miocene	2323	---	0.272	Kelley & Hansen, 2006
St. Marys, Maryland, USA	Middle to Late Miocene	8637	---	0.38	Kelley & Hansen, 2006
Eastover, Maryland, USA	Late Miocene	67	---	0.209	Kelley & Hansen, 2006
Boreal, central Europe	Early to Middle Miocene	1159	284	0.245	Hoffmeister & Kowalewski, 2001
Paratethys, central Europe	Early to Middle Miocene	599	84	0.14	Hoffmeister & Kowalewski, 2001
Southeastern North Atlantic, France	Middle Miocene	67	22	0.328	Hoffmeister & Kowalewski, 2001
Karpatian and Serravalian, Central Parathethys, Europe	Early to Middle Miocene	22294	1596	0.072	Sawyer & Zuschin, 2011
Chassra, Kutch, India	Early to Middle Miocene	15891	---	0.0541	Goswami et al 2020

of naticid cannibalistic behavior. Out of 64 naticid drillings, only two are cannibalistic and both of them are found in the small size class of prey supporting the experimental findings of a higher frequency of cannibalism among smaller prey (Chattopadhyay et al., 2014a).

Predator Preference for Drill Hole Site

Naticid predators often show stereotypic behavior in selecting the drilling site (Dietl and Alexander, 2005). The majority of the complete naticid drill holes are located in the central region of the microgastropods (48.6%; Fig. 7C). Similar stereotypic behavior is known from macro molluscs (Allmon et al., 1990; Hagadorn and Boyajian, 1997; Goswami et al., 2020). When a prey individual is alarmed, it withdraws the soft parts inside the shell, up to nearly its central region (Kitchell, 1986; Hansen and Kelley, 1995). The drill holes in the central region ensure access to the soft tissue. A similar pattern is present among muricid drill holes suggesting a stereotypical behavior even of the muricid predators.

Our results show that drill holes are concentrated on the apertural side, mostly between the first (top) and the fourth sectors. The position of the drill hole is also dependent on the size and the morphology of the prey and the predator (Ansell, 1960; Sohl, 1969; Negus, 1975; Kabat, 1990). During naticid predation, the predator completely covers the prey with its foot to restrict its movement and it is often seen that they release a chemical that numbs the prey (Carriker and Gruber, 1999). Dietl and Alexander (2000) have explained that in confamilial predation in naticids they observe a significant number of drilling near the umbilicus, which would help the predator to immobilize a relatively "dangerous" prey, by

covering the aperture using the foot. This pattern was observed even when the prey is significantly larger and mobile. The higher intensity of naticid drill holes on the ventral side of the shell in our data thus suggests a stereotypical behavior by the predator to effectively immobilize the prey.

Prey Effectiveness and Repair Frequency

The presence of incomplete drill holes, multiple drill holes, and repair scars demonstrate the prey's ability to escape and/or the inability of the predators to complete an attack due to an interruption (Kelley et al., 2003). Incomplete drill holes do not always indicate prey's escape, because there are cases that reported the suffocation of the prey prior to the completion of drilling, thus resulting in death (Hutchings and Herbert, 2013) although rare in natural conditions (Visaggi et al., 2013). The results indicate a significant increase in IDF and RF with size. This may suggest that the shell thickness of the larger prey might be slightly higher, making it less desirable. These higher rates represent prey's physical defense mechanism acquired over its lifetime to escape predation. Chattopadhyay and Baumiller (2007) showed that the presence of secondary predators may result in the abandonment of the prey by the predatory gastropods, leading to the development of incomplete drilling. In such cases, RF is proportional to IDF and inversely proportional to DF (Chattopadhyay and Baumiller, 2010). The microgastropod assemblage, however, does not show any significant correlation (p = 0.43 for DF-RF, and p = 0.92 for IDF-RF) between the family-specific valued of these three indices suggesting limited involvement of predatory abandonment in producing an incomplete drill holes.

A high RF of an assemblage may indicate more predators, higher failure due to inefficiency of the predators or prey with stronger defenses (Vermeij et al., 1981). We have standardized the RF for both prey size and taxon. For the size standardized calculation, two reasons could account for the higher RF in the large size class: a) larger prey are usually older and, hence, accumulate scars over multiple attacks during ontogeny, b) larger prey are more likely to survive an attack in comparison to smaller prey and hence carry the signature of non-lethal attack. Multiple drill holes and incomplete drilling are not uncommon in the assemblage. Lower IDF and MULT values from macrogastropod assemblages of Miocene have been interpreted as the signature of highly efficient predation (Fortunato, 2007). The relatively higher values of IDF (14.3%) and MULT (9.7%), compared to the Kutch assemblage (0% and 0.70%) (Goswami et al., 2020) along with lower DF indicate that micro gastropods have an effective way of escaping predation.

The Energetics of Predation

The non-random prey selection is explained by the cost-benefit principle (DeAngelis and Kitchell, 1985). The cost is the invested energy by the predator in finding, capturing, and consuming the prey; the benefit is the energetic value of the prey tissue to the predator. The principle suggests that a predator selects prey to maximize the net energy gain, i.e., the difference between the benefit and cost. This principle has been shown to operate in prey selection by both naticids (Kitchell et al., 1981) and muricids (Chattopadhyay and Baumiller, 2009) on macromolluscan prey. Cost-benefit analyses confirm that selection of micromolluscan prey is non-random and each of the successful attacks yielded a positive net energy gain (Fig. 9C). The microgastropod prey yield higher energetic gain with increasing size primarily because of the increase in soft tissue volume and a negligible increase in thickness of the prey (Fig. 7A, D). This results in the exponential increase in benefit: cost ratio with prey size. This explains why smaller sizes among microgastropods are not the preferred prey confirmed by the lower DF in comparison to larger size classes (Fig. 9C–E). It is also important to note that none of the individuals below 0.35mm are drilled. This result also confirmed that a "negative size refuge" exists in microgastropods similar to microbivalve prey (Chattopadhyay et al., 2020). The cost-benefit analysis also confirms that micromorphy may act as an effective defense strategy by making the smaller sizes less preferred.

The cost-benefit analysis also brings out interesting behavioral attributes of the predator. Although the prey-predator size ratio decreases with predator size (Fig. 9B), the net energy gain increases. This implies that smaller predators, despite their selection of relatively larger prey, do not benefit energetically due to a disproportionately higher metabolic cost. When compared between two families of drillers, naticid drillings are more beneficial than muricids; the naticids are found to have a significantly higher net energy gain compared to muricids.

A Comparison to Macrogastropods

Low values of drilling frequency in microbivalves in comparison to coeval global averages have been used to establish the effectiveness of micromorphy against drilling predation (Chattopadhyay et al., 2020). Our study confirms this finding for both drilling and durophagous predation of microgastropods. The low predation intensity in family-level comparison with macrogastropods indicates the predation resistance of microgastropods (Fig. 10). Such lower intensity among the microgastropods is probably driven by their low energetic yield which makes them less preferred as demonstrated by the cost-benefit analyses. This conclusion is also supported by the higher benefit-cost ratio, observed among the macro gastropods from Kutch (Fig. 10C–E). However, there might be other factors that could affect the intensity of predation.

The studied section is interpreted to represent a seagrass environment (Reuter et al., 2011). Seagrass environments are often found to provide a natural refuge from predators (Irlandi, 1997; Wall et al., 2008) where leaf blades diminish the mobility of the predators and also makes it hard to detect the prey visually (Heck and Thoman, 1981; Irlandi, 1997). The roots also prevent digging, limiting the activity of infaunal predators (Wall et al., 2008). Since many of the predators (muricids, xanthid crabs) are epifaunal, the effect of the seagrass cannot completely explain the low predation intensity of the Quilon microgastropod assemblage.

Differential preservation of the macro-and microgastropods may also contribute to the observed low predation intensity of microgastropods. Generally, the smaller gastropods, especially juveniles, are rarely preserved in the fossil record (Kidwell, 2001; Cooper et al., 2006;) often leading to a difference in observed predation intensity across size classes (Chattopadhyay et al., 2016). One of the taphonomic biases thought to influence the inferred DF is the differential shell strength of drilled and undrilled shells (Roy et al., 1994; but see Zuschin and Stanton, 2001, Kelley, 2008, and Dyer et al., 2018). Drill holes reduce the shell strength and make the drilled shells more susceptible to point-load compression-induced breakage potentially leading to a reduced DF (Roy et al., 1994). However, the difference in breaking load between drilled and undrilled shells is more pronounced in larger shells (Fig. 3; Roy et al., 1994) — a pattern that is more likely to lower DF in macromolluscs. Moreover, the lighter shells of microgastropods are likely to be carried as suspension load in contrast to the macrogastropods that travel as bed load and get reworked in the process (Reuter et al., 2011). Most microgastropods in our collection retained their original structure without any breakage pointing to the limited role of compaction-induced breakage in developing the assemblage. Apart from this, the difference in hydrodynamic properties of drilled and undrilled shells are also known to create assemblages with reduced DF (Chattopadhyay et al., 2013a, b). However, the difference is more pronounced for larger size classes (Fig. 5; Chattopadhyay et al., 2013b). Both the taphonomic attributes

(compaction, hydrodynamics) that are known to reduce DF are more likely to affect macrogastropods and do not explain the observed low predation intensity in microgastropods implying a relatively negligible role of taphonomy in creating the pattern.

The relative abundance of predatory species is known to explain the predation intensity of a region (Allmon et al., 1990; Kardon 1998; Sawyer and Zuschin, 2011). In the recent study by Goswami et al. (2020), the low drilling intensity of macrogastropods from Kutch is explained by the low abundance of predators. Because of the low abundance of muricid gastropod in their assemblage, most muricid-like drill holes have been attributed to naticid. The microgastropod assemblage of the Quilon Limestone is characterized by a lower relative abundance of potential drillers (2.04%) in comparison to the reported values from other Miocene assemblages, such as Kutch (2.27 – 4.55%; Goswami et al., 2020). Muricid drilling is present in our collection and muricid specimens have been reported from the same locality (Harzhauser, 2014). However, the absence of muricid gastropod specimens in our documented collection is a probable indicator of their lower abundance.

Apart from the relative abundance of predators, the absence of preferred prey may also result in low predation intensity. The Quilon assemblage reports few turritellids – a family known to be a preferred prey with high DF (Kojumdjieva, 1974; Fortunato, 2007; Goswami et al., 2020). The absence of this group may have contributed to the overall lower DF of the Quilon assemblage. The availability of other preferred prey may also contribute to the lower predation intensity among microgastropods. Chattopadhyay et al. (2020) have reported a similar drilling frequency (DF = 0.06) among the microbivalves from the same locality, suggesting that microbivalves were unlikely to be a preferred prey over microgastropods. Other potential prey of this size class include ostracods and foraminifers. The thin shells of ostracods might lower the energy for drilling making them desirable prey (Reyment et al., 1987; Culver and Lipps, 2003; Reyment and Elewa, 2003). Although we do not have any direct evidence of predation from these groups, abundant ostracods (Yasuhara et al., 2020) and foraminifera (Rögl and Briguglio, 2018; Briguglio and Rögl, 2018) have been reported from the Quilon assemblage, supporting the availability of alternate prey types. This also opens the possibility for future studies to explore the predatory interactions in these groups to understand predator-prey dynamics at extremely small size classes.

CONCLUSIONS

Predation on molluscan communities from recent and past ecosystems, has been studied in-depth, with the exception of micromolluscs. The present study attempted to fill this gap by studying the predation signature in microgastropods from the Quilon Limestone of Kerala. The predation intensity of this assemblage is quite low for drilling (DF= 0.06) and durophagous (RF=0.04) predation. Also, the repair frequency (RF) and the incomplete drilling frequency (IDF) are found to be lower for the Quilon microgastropods in comparison to family-specific values of global reports of macrogastropods. These results support the previous findings of micromorphy acting against drilling predators with low drilling predation intensity as shown among microbivalves (Chattopadhyay et al., 2020). The small size of the prey species is a good defense against predation, and inverse size refugia are observed among microgastropods. However, the larger prey is found to escape predation more efficiently as demonstrated by a higher IDF among large size class. The physical features of the gastropod prey affect the intensity of predation rather than their abundance. The lower intensity of predation in this size range might be a result of multiple factors that includes a lower abundance of predators, the seagrass environment, and the presence of other prey species. Finally, the cost-benefit analysis suggests an increasing benefit to cost ratio with increasing prey size explaining the potential reason for preferring macrogastropods over microgastropods leading to the low predation intensity observed among micromolluscs.

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