Size-related changes in predatory behaviour of naticid gastropods from the Middle Miocene Korytnica Clays, Poland

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The analysis of shell-drilling predation by naticid gastropods on molluscs from the Korytnica Clays (Middle Miocene, Holy Cross Mountains, Central Poland) has focused on the bivalve *Corbula gibba* and gastropods *Natica tigrina* and *Hinia restitutiana*. The results indicate that predatory behaviour of naticids varies depending on the size of the predator. When drilling corbulids, large naticids displayed higher site-selectivity than smaller naticids. Also, large naticids drilled energetically attractive prey (*Hinia restitutiana* and *Natica tigrina*) more frequently than small naticids. Preferential drilling displayed by large naticids from the Korytnica Clays increases the net energy gain for the predator and in result allows it to drill more effectively.

Key words: Naticidae, Corbulidae, drill holes, predation, predatory behaviour, Middle Miocene.

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Introduction

The family Naticidae is a well known group of predatory gastropods that drill holes in shells of their prey (mostly molluscs) to access their internal soft tissues. This paper deals with some aspects of the predatory behaviour of naticids preying on the bivalve member of the family Corbulidae, *Corbula gibba* (Olivi, 1792) from the Korytnica Clays (Middle Miocene, Badenian, Holy Cross Mountains, Central Poland). The analysis focuses on relationship between the size of the predator and the site of the attack. An unusual distribution of naticid drillings in corbulid valves and its probable causes are described and analysed. In addition the distribution of drill holes and the relationship between the size of the predator and the success of the attack are analysed for the gastropods *Natica tigrina* Röding, 1789 and *Hinia restitutiana* (Fontannes, 1879) from the same locality.

Drilling activity of naticids from the Korytnica Clays has been described by Hoffman *et al.* (1974) and Kowalewski (1990). However, the relationships described here were not examined in those studies. Moreover, despite many detailed studies concerning naticid predation on corbulids (Taylor 1970; Adegoke & Tevesz 1974; Hoffman *et al.* 1974; Levy & Samtleben 1979; De Cauwer 1985; Kelley 1988, 1989; Kowalewski 1990; Anderson *et al.* 1991; Anderson 1992; Kelley & Hansen 1993; Harper 1994), the topics of this study have not been explored previously. In general, very few papers dealing with naticid predation investigated the relationship between the size of the predator and the choice of the drilling site (Berg 1976; Guerrero & Reyment 1988).Their results are either opposite (Berg 1976) to the ones presented here, or, if similar, reveal a less distinct pattern (Guerrero & Reyment 1988).

Materials and methods

Samples were collected from the Korytnica Clays, a unique facies deposited in the terminal part of a shallow bay that developed in the Miocene along the dismembered rocky shore on the southern slopes of the Holy Cross Mountains, Central Poland (see Radwański 1969; Bałuk & Radwański 1977). Two samples were obtained for the analysis. Sample 1 from the Korytnica-Plebania locality, sample 2 – two hundred meters north of Łysa Mountain (see Radwańska 1992: fig. 2A). All fossils larger than 1 mm were picked and counted. Length of all complete specimens of *Corbula gibba* was measured with the precision of 0.05 mm, and the diameter of drill holes was measured with the precision of 0.025 mm under a binocular microscope. Specimens of *Natica tigrina* and *Hinia restitutiana* collected from the Korytnica Clays over many years by other workers served as a comparative material.

The diameter of a hole is considered a very good proxy for the predator's size because of a direct correlation between the two variables (Kitchell *et al.* 1981). Holes exceeding 1 mm will be considered here as recording 'large' naticids, whereas those smaller than 1 mm as recording 'small' naticids. The term 'successful drill holes' refers to complete perforations with the ratio of inner to outer diameter exceeding 0.5 ('complete' *sensu* Kitchell *et al.* 1986), whereas the term 'unsuccessful' drill holes refer to perforations with the ratio lower than 0.5 ('incomplete' or 'non-functional' *sensu* Kitchell *et al.* 1986). Only successful drill holes enable consumption of prey (see Kitchell *et al.* 1986).

The pattern of distribution of holes on *C. gibba* shells was analysied by plotting the positions of drill holes on schematic diagrams of left and right valves (Fig. 1A–D). The right valve is divided by a dashed line into two regions. The area above the line will be referred to as the apical-dorsal, and the one below as the centro-ventral region. The centro-ventral and apical-dorsal regions occupy 40 and 60% of the right valve surface, respectively.

Distribution of naticid drillholes on shells of *C. gibba* and other attacked molluscs is used here to evaluate predatory behaviour of the Naticidae. It is also assumed that differences in frequency of mollusk shells belonging to different species reflect the

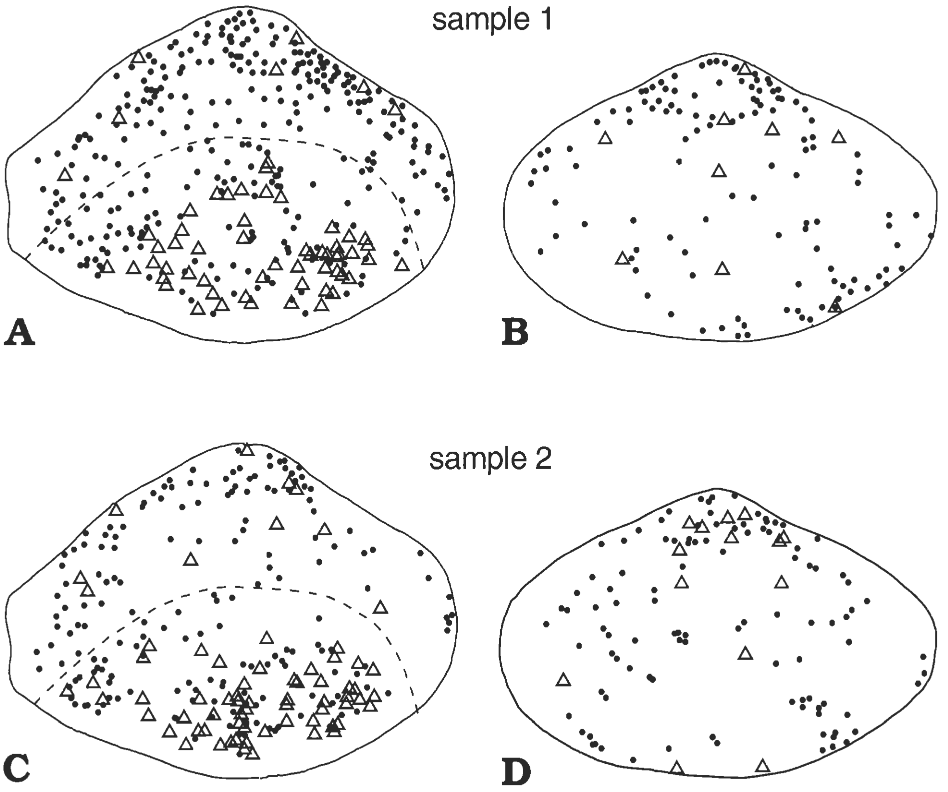

Fig. 1. Distribution of naticid drill holes on *Corbula gibba* valves. Right valves (**A**, **C**), left valves (**B**, **D**). Explanations: triangles, drill holes over 1 mm in diameter; dots, drill holes below 1 mm in diameter; the region located below the dashed line is the centro-ventral region of the right valve (ca. 40% of the total valve area); the region located above the dashed line is the dorso-apical region of the right valve (ca. 60% of the total valve area).

real differences in original communities. Such approaches can be justified if we assume that time-averaging and taphonomic processes were limited and did not bias the original ecological information recorded by drill holes in any substantial manner. The shape (high leptokurtosis and skewness) and strong interspecific variation of mollusc size-frequency distributions indicates that Korytnica assemblage is, at most, weakly time-averaged (Kowalewski & Miśniakiewicz 1993). Influence of taphonomy in the case of the Korytnica assemblage can also be neglected, as the remains of organisms from the Korytnica Clays were not altered substantially by post-mortem transportation or dissolution (Kowalewski 1990).

Results

Predation on *Corbula gibba*. — The relative number of *C. gibba* exceeds 70% of the total number of invertebrates in the analysed samples, while attacked individuals comprise 17–20% of the *C. gibba* specimens. These proportions are typical for the

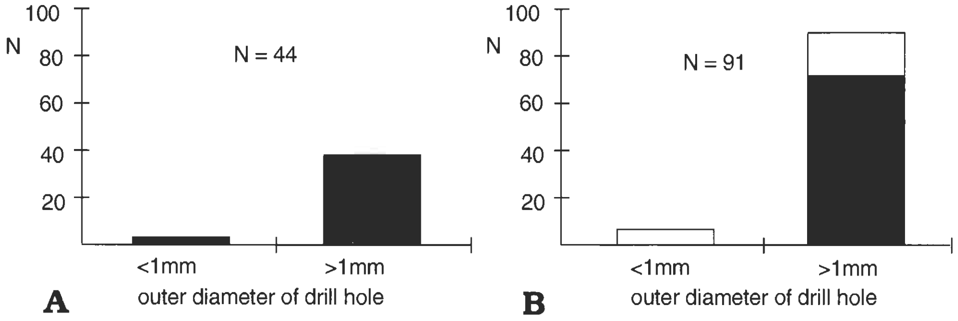

Fig. 2. Diagrams presenting number of drill holes with respect to their size. **A**. Drill holes in shells of *Hinia restitutiana*. **B**. Drill holes in shells of *Natica tigrina*; N, number of drill holes; white area, unsuccessful drill holes; black area, successful drill holes.

Korytnica Clay fossil assemblage (Hoffmann *et. al.* 1974; Kowalewski 1990). Distribution of drill holes on *C. gibba* shells is presented on Fig. 1A–D and numerical data are summarised in Table 1.

In general, drill holes below 1 mm are more frequent than those that exceed 1 mm. The distribution of drillings reveals three interesting patterns. First, on right valves, drill holes below 1 mm are distributed more or less evenly on the whole shell surface, while drillholes over 1 mm are concentrated in the centro-ventral region (see Fig. 1A, C and compare fq_{LC} with fq_{SC} in Table 1). Second, naticid drill holes occur more frequently in the right valve than in the left valve. Finally, drillings below 1 mm in size occur relatively more frequently on the left valve than drillings above 1 mm in size (see Fig. 1A–D and compare fq_{LL} with fq_{SL} in Table 1).

Predation on *Hinia restitutiana* and *Natica tigrina*. — In the Korytnica Clays *H. restitutiana* and *N. tigrina* are common. *N. tigrina* comprises between 2.6 to 3.0%, while *H. restitutiana* between 8.0 and 8.9% of the total number of invertebrates from investigated samples.

A total of 1.826 large specimens of *N. tigrina* (height of shell exceeding 8 mm) and 620 large specimens of *H. restitutiana* (height of shell exceeding 8 mm) previously collected from the Korytnica Clays were analysed. 5% of *N. tigrina* and 7% of *H. restitutiana* were drilled, respectively. The diagram on Fig. 2A shows that 87% (39 out of 44) drillings in *H. restitutiana* shells exceed 1 mm in diameter. All drill holes are successful. The diagram on Fig. 2B shows that 90% (70 out of 84) drill holes on shells of *N. tigrina* exceed 1 mm in diameter. 85% (72 out of 84) of these drill holes are successful. In contrast, all of the few drill holes smaller than1 mm are unsuccessful.

Disscusion

Potential borers. — Among many gastropod groups described from the Korytnica Clays (Pusch 1837; Hörnes 1856; Friedberg 1911–1928; Kowalewski 1930; Bałuk 1975, 1995, 1997), Muricidae, Naticidae, Marginellidae, Capulidae, Nassaridae and Cassidae are potential borers, capable do drill in mollusc shells. Thus, the observed

Table 1. Frequency of naticid drill holes on *Corbula gibba* valves.

No	n	fq_R [%]	N	N_R	N_L	fq_{NR} [%]	N_{LR}	N_{LL}	N_{SR}	N_{SL}	fq_{LC} [%]2	fq_{SC} [%]	fq_{LL} [%]	fq_{SL} [%]
1	2809	47.0±1.8	472	342	130	72.5±3.9	61	9	281	121	85.2±8.8	34.2±5.5	12.8±7.8	30.0±4.5
2	1801	51.1±2.3	360	243	117	67.5±4.9	69	14	174	103	84.0±8.6	47.1±7.5	16.9±8.0	37.2±5.7

No, number of sample; n, number of *C. gibba* valves, fq_R, percentage of right valves; N, number of drill holes; N_R, number of drill holes on right valves; N_L, number of drill holes on left valves; fq_{NR}, percentage of drill holes on right valves N_{LR}, number of drill holes over 1 mm in outer diameter on right valves; N_{LL}, number of drill holes over 1 mm (outer diameter) on left valves; N_{SR}, number of drill holes below 1 mm on right valves; N_{SL}, number of drill holes below 1 mm on left valves; fq_{LC}, percentage of drill holes over 1 mm in centro-ventral region of right valves; fq_{SC}, percentage of drill holes below 1 mm in centro-ventral region of right valves; fq_{LL}, percentage of drill holes over 1 mm on left valves; fq_{SL}, percentage of drill holes below 1 mm on left valves. Numbers following the '±' sign are confidence intervals computed from the following formula (Łomnicki 1995) $p \pm 1{,}96\sqrt{\frac{p(1-p)}{n}}$ where p denotes the proportion of one kind of fossil (such as left valves) observed in the collection of *n* specimens.

differences in distribution of small and large drill holes may reflect different drilling behaviour of predators belonging to different families.

Drilling behaviour and morphology of resulting drill holes were described for Recent marginellids (Ponder & Taylor 1992), capulids (Matsukuma 1978), cassids (Hughes & Hughes 1981) and nassarids (Morton & Chan 1997). Drill holes present in mollusc shells from the Korytnica Clays do not possess features that typify marginellid, capulid or cassid drillings (see Hoffman *et al.* 1974: pls. 1–4; Bałuk & Radwański 1977: pls. 3–5). Moreover, cassids drill mostly in echinoid tests and very rarely (if at all) in bivalve shells (see Hughes & Hughes 1981).

Nassarids can also be rejected as potential borers due to the following reasons. First, boreholes of recent nassarids described by Morton & Chan (1997) and these observed in collected material are perfectly differentiated in size. All drill holes observed in shells of *Hinia restitutiana* and *Natica tigrina* as well as great majority of the drill holes (97%) occurring in *Corbula gibba* shells collected from the Korytnica Clays are 0.3–2 mm in diameter. In contrast, drill holes of Recent nassarids do not exceed 0.25 mm in diameter because only juvenile (post-larval) individuals reveal drilling behaviour (Morton & Chan 1997). In Morton & Chan's (1997) experiments on adult nassarids, there has never been any evidence of shell boring either in the field or the laboratory.

Second, nassarids examined by Morton & Chan (1997) in laboratory tests were deprived of food. The latter authors suggest that drilling behaviour of studied nassarids was forced by hunger (Morton & Chan 1997). Third, although Morton & Chan's (1997) preliminary studies indicate that nassarids can drill in mollusc shells, most representatives of the Nassaridae are herbivores or scavengers obtaining the food without drilling (Davitashvili & Merklin 1968; Savazzi 1989). Thus, the only substantial question is how to distinguish naticid and muricid drill holes.

Many workers used morphological features of Naticidae and Muricidae drillholes to distinguish them (Reyment 1966; Carriker & Yochelson 1968; Bromley 1981; Kowalewski 1993). These are, however, considered by the author as unsatisfying. First of all, the drilling mechanism of naticids and muricids is extremely alike (Carriker

1981), and furthermore, too many factors not directly connected with the mechanism and anatomy of gastropod borers can influence drill hole morphology (for review see Kowalewski 1993). Therefore, statistical criteria are applied in this paper.

Sample 1 yielded 184 specimens of naticids and only one specimen of a muricid (*Murex friedbergi* Cossmann & Peyrot, 1924). Sample 2 yielded 120 specimens of naticids but no muricids were found in the material. The large differences in abundance between naticids and muricids strongly suggests that muricid drillings are very rare in shells of molluscs from the Korytnica Clays. Predominance of naticid drillings may have been further enhanced by the fact that naticids drill slightly faster than muricids (see laboratory tests by Kitchell *et al.* 1981). Consequently, all gastropod borings in shells of *Corbula gibba*, *Natica tigrina*, and *Hinia restitutiana* are assumed here to be of naticid origin. From a statistical point of view, the insignificant number of muricid drillings that may be included in the data should not affect notably the results.

Naticids from the Korytnica Clays are represented by seven species belonging to six genera (Bałuk 1995). This may hamper any behavioural interpretations because different naticids may have had different drilling behaviour, and it is almost impossible to identify a naticid on the basis of drill holes (Hoffman *et al.* 1974; Bromley 1981; Taylor *et al.* 1983; Kowalewski 1990). Fortunately, the dominant species in the collected samples, *Natica tigrina*, represents 95% of all specimens of naticids. Most likely, a majority of the analysed drillings were made by this species.

Naticid predation on *Corbula gibba*. — *C. gibba* is a bivalve with a very low mobility (Yonge 1946) and defends itself passively, clenching the valves and forcing the predator either to drill or crush its shell or, as is the case for some starfishes (Massé 1975 *fide* Vermeij 1978), to swallow articulated, intact shells. Such passive defence does not force the predator to seek a particularly elaborate strategy of attack. It is, therefore, not surprising that drillings are distributed over the almost entire surface of the shell. The only exception (i.e., the lack of drillings on the part of the right valve beyond the commissura) reflects most likely the fact that such drillings would be ineffective: they would not penetrate into the shell interior. This exception was also noted by Taylor *et al.* (1983) in their analysis of drillings in Cretaceous corbulids from Blackdown Greensand.

Results presented in the previous section suggest that naticids changed their behaviour with size. Large naticids prefered the centro-ventral region of the right valve of *C. gibba*, while small ones drilled more or less evenly on the whole shell surface, but penetrated left valves relatively more frequently than large naticids.

The most likely explanation for the preferential distribution of drill holes on the right valve may be connected with the variable thickness of shell and/or with the occurrence and thickness of conchiolin layers (Fisher 1963; Hoffman *et al.* 1974; Levy & Samtleben 1979; Kitchell *et al.* 1986; Harper 1994). The layers to a large degree hinder drilling of shell by predator and are often considered to be a crucial defensive adaptation of corbulids (Levy & Samtleben 1979; Harper 1994, but see also, Maslin 1989, Anderson 1992). Thickness of shell may considerably limit the success of naticid predation due to the following reasons. First, time required for drilling its positively correlated with the thickness of the shell (Kitchell *et al.*1981; Boggs *et. al.* 1984). Second, predators can be thickness-limited due to mechanical constrains on the depth of borehole penetration (Kitchell *et al.* 1981).

Corbula gibba shells (Yonge 1946) as well as shells of most bivalves are thickest in the apical region. However, conchiolin layers are thinnest there (Levy & Samtleben 1979: fig. 3). Thus, variable thickness of *C. gibba* shell seems to be responsible for observed preferential drill hole distribution. Avoiding the apical region is advantageous for the predator, as time required for drilling is much shorter and /or probability of failure due to the mechanical limitations decreases (see Kitchell *et al.* 1981). This is well supported by the distribution of unsuccessful drillings on *C. gibba* shells from the fossil material collected by Harper (1994). Almost all unsuccessful drill holes reported by Harper were concentrated within the apical-dorsal region. The specimens described by Harper were also similar in that they were collected from Miocene deposits and the drillings were made by gastropods from the family Naticidae.

Unfortunately, the number of unsuccessful drill holes recorded in the samples collected in this study is not sufficient for a statistical analysis. This is caused by a very high rate of succesful attacks by naticids (over 90% in each sample). The thinnest, centro-ventral region of the bivalve shell is also preferred as a borehole site by recent naticid *Natica alderi* (Forbes) preying on bivalve *Venus striatula* (da Costa) (Ansell 1960).

The other explanation for unusual drill hole distribution is a manipulation limit, forcing the large predator to drill in centro-ventral area of right valve. Ziegelmeier (1954) demonstrated that larger naticids turn their prey around with the foot until it is suitably positioned to be drilled. During the drilling process special folds of the foot extended over and around the bivalve holding it securely. One could suggest that the preferred holding position is the hinge so that drillings would be mostly on ventral part of the shell. In contrast, small predators are probably not able to hold their prey with the foot. Instead they must crawl around the shell surface and drill wherever it seems appropriate to them thus causing a distribution pattern that covers the entire shell surface.

Laboratory studies of Recent naticids confirm that the position of borehole reflects the behaviour involved in prey capture, manipulation and positioning for boring (Berg & Porter 1974). Preferential drilling in centro-ventral region of a bivalve shell by Recent naticid was described by Ansell (1960). On the other hand Berg's (1976) investigations clearly show that small Recent naticids can successfully prey on bivalve mollusks, which are 3–5 times larger than predator so that naticid is unable to hold the prey with the foot. Therefore, the manipulation limit hypothesis seem to be acceptable. However, Recent naticids may also prefer anterior or apical part of the bivalve shell as a borehole site (Negus 1975). This is because the borehole site depends on both the prey and the predator species (Berg & Porter 1974).

Regardless of their size, the Korytnica naticids drilled more frequently right valve of *C. gibba.* The preferential drilling of right valves of corbulids by naticids has been noted by many authors (Fischer 1963; Taylor *et al.* 1983; Kowalewski 1990) and typically linked with the inequivalve nature of shells of corbulid shells: the larger area of the right valve and the fact that the right valve envelopes the left valve making the latter less accessible. The preference is not likely to be related to the position of *C. gibba* in the sediment, as the bivalve lives in an upright position rather than lying on one of the valves (Yonge 1946).

The two samples analysed here (Fig. 1, Table 1) not only confirm the well known preference but also show that large naticids attacked the left valve considerably less frequently than small naticids.

The preferential drilling of the centro-ventral region of the right valve may have been advantageous to the predator for several reasons. First, with the increase of the drilling time the risk of failure increases because the predator may be attacked and forced to abandon its prey. Many naticid shells from Korytnica Clays bear traces of cannibalistic attacks, such traces have been observed in the samples analysed here as well as in previous studies (Hoffman *et al.* 1974; Kowalewski 1990). Second, drilling in the pre-apical region being more time-consuming, decreases the net energy gain for the predator.

Naticid predation on *Hinia restitutiana* and *Natica tigrina*. — The small naticids attacked large individuals of *H. restitutiana* less frequently than the large naticids. However, the small drill holes, despite their scarcity appear to have been successful. Therefore, the scarcity of holes drilled by small naticids is probably not related to the shell thickness of the prey, but rather reflects the mobility of prey. Recent representatives of the genera *Hinia* and *Natica* are mobile gastropods foraging both within as well as on the sediment (Davitashvili & Merklin 1968; Savazzi1989). Most likely, large individuals of *H. restitutiana* moved much quicker than small naticids, thus avoiding the attack (see also Vermeij 1982).

Small naticids attacked large individuals of *N. tigrina* much less frequently, and when this attack took place it was unsuccessful. All unsuccessful drillings below 1 mm in diameter have a depth comparable to their outer diameter. Their inner diameter decreases drastically with depth. This shape suggests that attacks were unsuccessful due to the thick shell of the prey (see Kitchell *et al.* 1981). The efficiency of attack on *N. tigrina* distinctly differs from the efficiency of attack on *H. restitutiana*. Nevertheless, shells of large *N. tigrina* are distinctly thicker than those of *H. restitutiana.* Because *N. tigrina* can be both the prey as well as the predator, the diagram in Fig. 2B presents in reality cases of a confamilial cannibalism. The low frequency of attacks by small naticids and the high rate of failed attacks both indicate that naticids are much less vulnerable to the attack by other naticids with increased size.

Ratio of attacks by small versus large naticids. — Large naticids less frequently drilled *Corbula gibba* than small ones. In contrast, small naticids less frequently drilled large individuals of *Hinia restitutiana* and *Natica tigrina.*

In the Korytnica assemblage *H. restitutiana* and *N. tigrina* attain much larger dimensions than *C. gibba*. The largest specimens of *H. restitutiana* and *N. tigrina* in the samples were 17 and 37 mm long, respectively. In addition, Recent representatives of the genera *Hinia* and *Natica* have a large, fleshy foot (Ziegelmeier 1954; Davitashvili & Merklin 1968). This organ is a potential food source for predators. In contrast, shells of *C. gibba* reach only 7 mm in length. Recent representatives of this species have a short foot as well as a short siphon (Yonge 1946). According to the cost-benefit model proposed by Kitchell *et al.* (1981), *H. restitutiana* and *N. tigrina* should have been more attractive prey than *C. gibba*. This results from differences in size and anatomical features of species. In the light of Kitchell's model there is no doubt that large naticids preyed more effectively.

Conclusions

Predatory behaviour of the naticids preying on *C. gibba* varied depending on the size of the predator. When drilling corbulids, larger individuals were more site-selective than the small ones. Also, large specimens drilled more energetically attractive (*H. restitutiana* and *N. tigrina*) prey more frequently. Cost-benefit analysis presented by Kitchell *et. al.* (1981) predicts that such preferential drilling as that of larger naticids from the Korytnica Clays increases the net energy gain for the predator and in result allows it to drill more effectively.

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Zmiany w rozwoju osobniczym drapieżniczych zachowań ślimaków z rodziny Naticidae ze środkowomioceńskich iłów korytnickich

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Streszczenie

Przedstawiono analizę rozkładu drążeń Naticidae na muszlach małża *Corbula gibba* (Olivi, 1792) oraz ślimaków *Hinia restitutiana* (Fontannes, 1879) i *Natica tigrina* Röding, 1789 pochodzących ze środkowomioceńskich iłów korytnickich. Wykazano, że drapieżnicze zachowania Naticidae były uzależnione od wielkości drapieżcy. Duże Naticidae drążyły głównie w środkowobrzusznym obszarze prawej skorupki *C. gibba*. Drążenia małych naticidów są zaś na tej skorupce rozmieszczone mniej lub bardziej przypadkowo (patrz Fig. 1A, C oraz porównaj fq_{LC} z fq_{SC} w Tabeli 1). Ponadto, małe Naticidae drążyły na skorupce lewej częściej niż duże (patrz Fig. 1A–D oraz porównaj fq_{LL} z fq_{SL} w Tabeli 1). Wielkość drapieżcy miała również wpływ na wybór gatunku ofiary. Duże Naticidae znacznie częściej niż małe atakowały *H. restitutiana* i *N. tigrina* (Fig. 2A, B), natomiast małe Naticidae częściej niż duże atakowały *C. gibba* (patrz Fig. 1A–D oraz porównaj sumę N_{LR} i N_{LL} z N_{SR} i N_{SL} w Tabeli 1). Wydaje się, że sposób umiejscawiania drążenia oraz wybór gatunku ofiary dokonywany przez duże ślimaki z iłów korytnickich mogły znacząco wpływać na zwiększenie efektywności polowania – prawa skorupka *C. gibba* jest bowiem w rejonie środkowobrzusznym najcieńsza. Drapieżnik atakujący ten obszar muszli potrzebował więc mniej czasu na jej przewiercenie. *H. restitutiana* i *N. tigrina* stanowiły zaś, ze względu na swoje rozmiary i budowę anatomiczną (duża mięsista noga), potencjalnie obfitsze źródło pożywienia niż *C. gibba*.