Orsis, 7: 57-64 (1992)

Borehole site-selection in *Naticarius hebraeus* (Chemnitz in Karsten, 1769) (Naticidae: Gastropoda)?

Carles Calvet i Catà[1]

Departament de Biologia Animal (Invertebrats). Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona

1. Present adress: Cinto Verdaguer, 4. 08360 Canet de Mar (Spain)

Key words: Bivalve prey: Boreholes; Naticid gastropod; NE-Spain.

Abstract. It is commonly accepted that in cold-water naticids, a direct relationship between predator and prey size and borehole diameter exists, the latter being frequently situated near the umbus of bivalve shells. Aquarium observations of *Naticarius hebraeus* from NE-Spain show that this predator traps its prey at the ventral margin, so that its proboscis with the boring organs remain closer to the umbus, the larger the snail is. This agrees with the findings that borehole diameter is larger when closer to the umbus. Furthermore, this parameter is larger near the umbus in the larger bivalve *Glycymeris glycymeris*, than in the smaller *Spisula subtruncata*, indicating that specific selection could change in time as predators grow. Standard deviation of borehole diameter is larger in *Spisula*, further away from the umbus, indicating, in agreement with Vignali & Galleni (1986), that smaller predators probably bore more randomly on bivalve shells than larger ones. In agreement with Negus (1975), a learning process in small naticids could exist in order to produce more consistently defined or located boreholes in time. In any case, this site-selection seems not to be an active result of the snail's predation, as suggested in former papers, but passively due to the predator/prey size ratio or the bivalve's shell shape.

Resumen. *¿Selección del punto de perforación en* Naticarius hebraeus *(Chemnitz in Karsten, 1769) (Naticidae: Gastropoda)?* Se acepta comúnmente que en los natícidos de agua fría existe una relación directa entre el tamaño de depredador y presa y el diámetro de perforación, estando la perforación frecuentemente situada cerca del umbo del bivalvo. Las observaciones en acuario con *Naticarius hebraeus* han revelado que este depredador inmoviliza a sus presas por el margen ventral, de forma que la proboscis con los órganos perforadores quedan tanto más cerca del umbo cuanto mayor es el gasterópodo. Ello coincide con el hecho observado de que el diámetro de las perforaciones aumenta en dirección al umbo. Además, este parámetro es mayor cerca del umbo en *Glycymeris glycymeris*, un bivalvo grande, que en *Spisula subtruncata*, más pequeño, sugiriendo que la selección específica cambia en el tiempo al ir creciendo los depredadores. La desviación típica del diámetro de perforación es mayor en *Spisula* lejos del umbo, indicando, en concordancia con Vignaly & Galleni (1986), que los depredadores más pequeños probablemente perforan las conchas de los bivalvos de una forma más al azar que los congéneres más grandes. Según Negus (1975) podría existir un proceso de aprendizaje en los natícidos pequeños de manera que produzcan unas perforaciones más perfectamente definidas o localizadas con la edad. De todas formas, esta selección del punto de perforación no parece ser el resultado de una selección activa, tal y como fue sugerido en trabajos anteriores, sino más bien un fenómeno pasivo debido al tamaño relativo depredador/presa o a la arquitectura del bivalvo.

Introduction

Naticid gastropods use several strategies to feed on their prey, including most commonly conventional shell boring but also suffocation in snails with a large mesopodium (Ansell & Morton 1987), and non-boring predation as observed in razor clams (Schneider 1981). Among conventional boring strategies, side-boring seems to be the most common in European cold-water naticids (Kitchell et al. 1986; Ansell & Morton 1987).

Many statistical analyses have revealed that several measurable predator/prey parameters are frequently closely interrelated. The most significant relationships were found to occur between prey and predator size, borehole diameter and prey shell structure.

In this sense, the following findings have been recorded in the literature:

a) Borehole diameter: Bayliss (1986) found borehole diameter in *Polinices alderi* to be directly related to shell length, as well as Wiltse (1980), and Kitchell et al. (1981) in *P. duplicatus* - the former gastropod preying on the bivalve *Gemma gemma*. In 1986, Kitchell et al. found the outer borehole diameter to be a more reasonable parameter to be measured because it reflects the predator's size independently of prey handling time. And finally, Rodrigues (1986) found operculum size to be a better predictor to snail's body-size and to have a positive correlation with boreholes of *Neverita didyma*, feeding on the bivalve, *Ruditapes philippinarum*.

b) Predator/prey size: Broom (1982) found a direct relationship between mean sizes of *Natica maculosa* and its bivalve prey *Anadara granosa*, while Berry (1982), working with the same predator, found larger individuals to feed on more and larger *Umbonium vestiarium* snails as predators grow. Furthermore, Edwards & Huebner (1977) observed that large *P. duplicatus* feed also on large *Mya arenaria*, while small or non-selective predators feed on smaller prey. Finally, Penney & Griffiths (1977) found small *Natica tecta* to select preferently small mussels. According to DeAngelis et al. (1987), larger sized predators are less likely to select small prey, which provide only little energetic benefit relative to the investment of time.

c) Borehole position: Most of the published results show a steady preference of naticid predators to drill near the umbus of their bivalve prey, as Negus (1975) observed in *Donax vittatus*, Rosewater (1980) in several Periplomatidae, Vignali & Galleni (1986) in *Glycymeris insubricus* and *Spisula subtruncata*, and finally Ansell & Morton (1987) for the naticid, *Glossaulax didyma*. Furthermore, Negus (1975) indicated that smaller predators drill occasionally further away from the umbus, and Vignali & Galleni suggested that these small individuals drill more randomly on bivalve shells.

The author of this paper agrees completely with the above observations after having studied the feeding behaviour of the Mediterranian naticid, *N. hebraeus*,

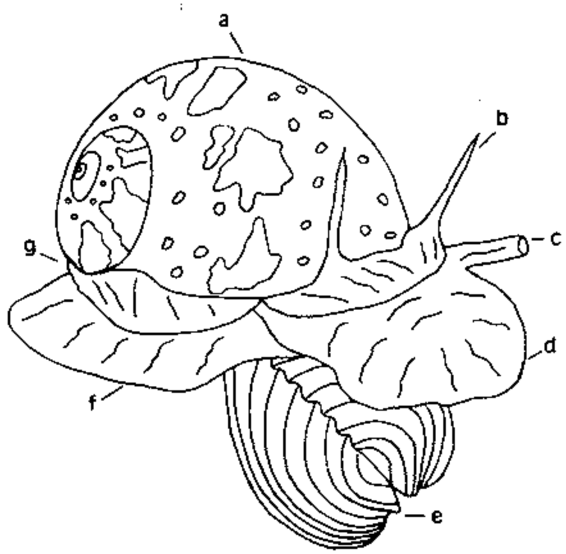

Figure 1. *Naticarius hebraeus* capturing a cardid bivalve. a) Naticid shell. b) Tentacles. c) Syphon. d) Propodium. e) Cardid prey. f) Mesopodium. g) Mesopodial fold.

and will discuss, with the aid of experimental data, some of the above mentioned findings which seem to indicate a direct relationship between predator and prey size and (outer) borehole diameter. Negus (1975), among other authors, revealed the importance of prey shell handling by the predator, so that for small predators, shell span seems to be too large to be bored near the umbus because naticids tend to trap their bivalve prey at a site opposite to the umbus.

Our experiments in aquaria revealed that *N. hebraeus* effectively traps its bivalve prey at the ventral margin, so that, for the same prey, its proboscis with the boring organs (radula + ABO [Accessory Boring Organ]) remain closer to the umbus, the bigger the snail is (Fig. 1).

Materials and methods

In order to evaluate these early observations made with *Naticarius* held in an aquarium, samples of drilled and undrilled, recently dead bivalve shells were obtained by diving on sandy shallow-water bottoms in several sampling stations (between El Garraf - Blanes) in the Mediterranian region of NE-Spain, between the 41°15'00" N - 1°54' 05" E and 41°39'59" N - 2°47'16" E co-ordinates.

In 1987 and 1988, a sample of 5375 empty shells was collected on these bottoms where *Naticarius* is the most abundant gastropod predator. Among these shells, only 412 showed the typical borehole of *Naticarius*, which was determined by the shape of boreholes obtained from this snail in the aquarium when fed with different bivalve preys. This sample includes only recently dead bivalves, while old and eroded shells were considered to have been long time transported by marine streams and did probably not correspond to the local *Naticarius* population. Other local naticids include the smaller *Lunatia alderi* (Forbes) and *L. guillemini* (Payraudeau), which drill also smaller prey and produce a more cylindrical borehole, while in *Naticarius*, the outer borehole diameter is visibly broader.

In order to evaluate complete and uncomplete shells together, it was assumed that a combination of two unbored valves corresponds to one non-preyed bivalve, while the combination of one bored and one unbored valve corresponds to one preyed bivalve. This method is analogous to that described by Vignali & Galleni (1986) and neither uncomplete nor multiple boreholes were observed in this area.

These 412 drilled shells were assigned taxonomically to specific bivalve species, being two of the most abundantly predated ones, *Glycymeris glycymeris* (Linneus) and *Spisula subtruncata* (Da Costa), which have been used in order to perform the current study due to their great abundance. In Calvet (1991) can be found data of less intensely preyed bivalves, diet composition, behaviour and biological rhythms.

Afterwards, measureable parameters, such as shell length, width and height, and outer borehole diameter were measured using a micrometrically equipped microscope, which allowed a high resolution at a magnification of x 64.

In order to assign each borehole to a consistent position on the bivalve shell surface, shells were divided into several zones, e.g. near the umbus, in the center and near the margins in a similar way to Vignaly & Galleni (1986) and Calvet (1989) as shown in Fig. 2, and for each borehole measured, the corresponding position on the shell was recorded.

Means and standard deviations were compared with t-Student test for means and F-Fisher-Snedecor test for variances.

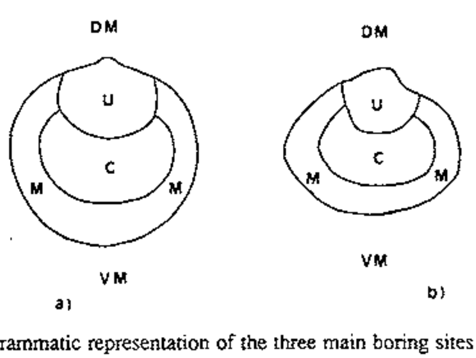

Figure 2. A diagrammatic representation of the three main boring sites on two different bivalve shells: a) *Glycymeris glycymeris*. b) *Spisula subtruncata*. Different positions include: U = near the umbus, C = near the center, and M = near the margins. Shell margins: DM = dorsal margin, VM = ventral margin (site where naticid predators place the foot and trap the shell).

Results and conclusions

In table 1, main results are represented, such as total number of intact collected shells, bored shells and the corresponding mean value and standard deviation of borehole diameter, which varies according to borehole position.

In *Glycymeris*, variances of boreholes are similar throughout the bivalve shell, although borehole diameter near the umbus is significantly larger than at the center - as can be concluded from the non-overlapping confidence limits in Table 1. At the center, this parameter is also significantly larger than at the margins ($t = 2.38$, $df = 66$, $P < 0.05$), so that borehole diameter decreases significantly in the following order: Umbus > Center > Margins.

These results enable us to assume in *Glycymeris* that large predators drill usually near the umbus, median ones near the center, while small ones drill normally at the margins. And the similar deviations throughout the shell suggest, that the predators' size range is not proportionally very different when comparing borehole locations throughout the shell's surface.

In *Spisula*, in contrast, standard deviation of borehole diameter in the central region and at the margins is significantly higher (respectively: $F = 2.57$, $df_1 = 6$, $df_2 = 21$; and $F = 1.85$, $df_1 = 30$, $df_2 = 29$) than near the umbus, which in agreement with Vignali & Galleni (1986) signifies that predators drilling near the center or the margins probably bore more randomly on bivalve shells.

Table 1. Measured bivalve prey parameters.

Species	*Glycymeris glycymeris*	*Spysula subtruncata*
N(D)	178	176
N(tot)	446	2151
BDU/SD (mm)	2.29/0.4914	1.94/0.4106
CL	(2.20;2.38) mm	(1.81;2.07) mm
N(U)	110	41
BDC/SD (mm)	2.00/0.4419	1.85/0.6660
CL	(1.86;2.14) mm	(1.68;1.99) mm
N(C)	40	86
BDM/SD (mm)	1.73/0.4893	1.75/0.5456
CL	(1.55;1.92) mm	(1.52;1.98) mm
N(M)	28	24

a) Collected total number of shells [N(tot)], bored shells [N(D)] – including: shells bored near the umbus (U), the center (C), and the margins (M), standard deviations (SD), and confidence limits (CL) for each bivalve analized at a 95% significance level.

b) N(D) = N(U) + N(C) + N(M).

c) In *Spisula*, 25 other boreholes were present, situated in the marginal region of the umbus (MU) [mean size = 1.74 mm; CL = (1.52;1.97)] and could not be properly compared with those in *Glycymeris*. Anyway, these 25 bores are not significantly different to those near the umbus, and their inclusion would only restrict the corresponding confidence limits thus giving the same results.

In addition, borehole diameter near the umbus in *Spisula* is significantly larger than at the margins ($t = 1.60$, $df = 63$, $P < 0.05$), though less different from values near the center.

In summary, in *Spisula* near the umbus, there are located bigger boreholes in a smaller size-range, while further away, there are smaller boreholes in a proportionally wider size-range. This could mean, in an analogous way to the above explanation, that larger snails tend to drill *Spisula* near the umbus, while smaller drill at the margins or the center. It may also mean that the size-range of smaller predators in the population is proportionally larger than that of bigger snails which could be defined as adult or old individuals, so that *Spisula* seems to be preferred by small naticids.

In any case, these results do not allow us to distingish whether the higher variability in small boreholes is due to the local snail-size distribution or to the individual borehole diameter variability. In agreement with Negus (1975), there could be a learning or improvement of drilling behaviour as naticids grow, in order to produce a more consistently defined or located borehole in time, so that adult snails' boreholes would be closer to a theoretically more optimal size or site than young snails' bores according to the cost-benefit model proposed by Kitchell et al. (1981).

Finally, average borehole diameter in the umbus region of *Glycymeris* is significantly larger than in *Spisula* as it can be observed by the non-overlapping confidence limits in Table 1, so that the average size of *Naticarius* predators is probably larger in the former case. Smaller snails seem to prefer *Spisula*, which is also a smaller bivalve, while larger snails seem to prefer *Glycymeris*, which is also a larger prey.

Discussion

According to D'Angelo & Gargiullo (1978) and our own observations, *Glycymeris* is a large clam reaching a size of 80 mm, while *Spisula* is much smaller and reaches only 25 mm shell length. While the former bivalve shows a quite constant borehole-size standard deviation all over its shell surface, this parameter is larger, further away from the umbus, in the latter. This specific difference might be due to the much larger local mean size of *Glycymeris* (18.22 mm [CL = 17.54; 18.90 mm]; N = 178), whose almost circular and large shell offers probably no hindrance to boring by predators of any size, and any predator's size probably corresponds neatly to a specific boring site on the bivalve shell.

In contrast, *Spisula*, which is locally significantly smaller (mean size =15.04 mm [CL = 14.73; 15.35 mm]; N = 176), might be bored unproblematically near the umbus by bigger snails, while smaller ones bore probably non-selectively near the central or marginal regions as it is suggested by the higher standard deviation of borehole diameter further away from the umbus. The same was suggested for similar Mediterranian bivalves by Vignali & Galleni (1986).

Observations in the aquarium revealed that *Naticarius* of any size tend to trap bivalve prey at the ventral margin with the aid of their large mesopodium, so that boring organs remain nearer to the umbus, the larger the snail is. This is a good explanation why boreholes are significantly larger in this region and smaller further away, and agrees with the above mentioned authors according to our own observations.

According to this feeding behaviour, there seems to exist no active borehole site-selection, but rather a passive prey handling action due to the relative predator/prey size. This allows to suggest the existence of, at least, two different kinds of selection:

— an active selection, performed through the predator's will, which is probably not the current case, and

— a passive selection, performed automatically by the naticid which could be due to the mentioned relative predator/prey size or to other facts such as shell structure, ornaments or even environmental conditionings such as streams, tides or other disturbances which could stress the predator's shell handling behaviour.

The reason why *Naticarius* traps its bivalve prey at the ventral shell margin is probably a consequence of the potential bivalves' escape behaviour. In our local Mediterranian region, several clams with a high mobility can be found, e.g. the Families Cardiidae and Veneridae, and particularly *Acanthocardia tuberculata* (L.) has a very muscular foot, by means of which, this bivalve skips away from the naticid after a first encounter. Therefore, these specific bivalves are less intensely preyed than expected. Consequently, naticids seem to have developed this offensive behaviour in order to reduce the risk of escape by the bivalve prey: By trapping the clam at the ventral margin, the naticid closes the shell, preventing the prey from withdrawing its foot, being consequently either suffocated or drilled by the predator. This behaviour is probably an evolutionary response of the naticid to the evolution of these bivalves' muscular foot.

Finally, the fact that larger naticids seem to prey preferentially on larger *Glycymeris*, while smaller ones do on smaller *Spisula* could indicate the existence of a change in the naticids' species-specific preferences in time, as the predator grows. In this sense, naticid diets could change significantly along different population size-classes, so that any diet composition should be related to a specific local naticid population size-class distribution.

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Manuscript received on March 1991