Original Article

Boreholes on three bivalve species found on the sand beach at Sagot Cape, Baengnyeongdo, Korea

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ABSTRACT

Circular to subcircular boreholes were found on the surfaces of three different bivalve shells (*Mactra chinensis*, *Felaniella usta*, and *Nuttallia japonica*) that were pushed onto the sand beach at Sagot Cape, Baengnyeongdo, Korea. The boreholes are characterized by beveled holes that are parabolic in cross section. The boreholes are classified into the ichnospecies *Oichnus paraboloides*, probably drilled by a naticid gastropod *Glossaulax didyma didyma* living in the Baengnyeong tidal flat. In the case of *Mactra*-shells, boreholes are observed more or less evenly on left and right valves, and 96% of boreholes are located on the umbo. This may suggest that the life position of the Baengnyeong bivalves did not dictate the preference of *G. didyma didyma* in the Baengnyeong tidal flat ecosystem. The clustered distribution of the boreholes in the umbo area indicates a strong site selectivity for boreholes that is quite a common phenomenon in many naticid gastropods.

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Introduction

The predator–prey relationship is a commonly encountered biological interaction in nature where one organism (predator) consumes another (prey). In marine ecosystems, predators which feed on bivalves use a variety of foraging methods such as boring, drilling, rasping, and scraping (e.g. Dietl 2004). In the course of predation, predators often leave various traces (e.g. boreholes and tunnels) on prey shells, which provide quantifiable data on the predator–prey interaction (e.g. Kelley and Hansen 1993; Kitchell 1986; Peitso et al 1994). As a consequence, many researchers have used traces left on prey shells to approximate the specific predator–prey interactions, particularly when direct observations of prey shells with predators in nature are not feasible (Bromley 1981; Ceranka and Złotnik 2003; Kitchell et al 1981; Kowalewski 2004; Leighton 2002). In fact, studies on boreholes have increased our understandings of various aspects of predator–prey interactions in the modern benthic realm (Cintra-Buenrostro 2012; Hasegawa and Sato 2009) and in the fossil record (Chiba and Sato 2016; Kowalewski et al 1998).

The drill hole on bivalve shells is one of the most commonly encountered traces generated by predatory gastropods. Drilling on bivalves, however, is also caused by other animals such as nematodes (Steer and Semmens 2003) and octopods (Giovanni and Garassino 2012; Kelley and Hansen 2003; Kowalewski 2002) which leave similar-looking drill holes on their prey. Among them, naticid and muricid gastropods have been extensively studied as true drillers of some infaunal bivalves (Dietl and Kelley 2006; Guerrero and Reyment 1988; Harper 2003). In particular, naticid gastropods (family Naticidae) are known to leave a characteristic beveled borehole that is generally classified into an ichnospecies *Oichnus paraboloides* Bromley, 1981 (Bromley 1981; Zonneveld and Gingras 2014). In this paper, we first report the ichnospecies *O. paraboloides* found on the three modern bivalve species collected from the sand beach at Sagot Cape (Natural monument no. 391), Baengnyeongdo, Korea. We also discuss the taxonomy of the ichnospecies *O. paraboloides*, prey selectivity of naticid gastropods, and other aspects of prey (bivalves) and predator (gastropods) interactions.

Materials and methods

In October 2015, thousands of empty bivalve shells were pushed onto the sand beach at Sagot Cape, which is designated as "Natural

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Monument No. 391", Baengnyeongdo, Korea (Figure 1). The bivalve shells were scattered along the coastline of Baengnyeongdo (Figure 2A), and some of them were found as an aggregated assemblage (Figure 2B). We collected 200 shells (only shells with two valves attached) randomly by hand from a single site of the sand beach composed mostly of quartzite sediments (Lim et al 1998).

The specimens with drill holes were cleaned with commercial bleach, and then they were washed in distilled water. After careful removal of sediments and debris, drill holes of the valves were examined under a dissecting microscope. The shell height, the maximum distance from the umbo to the ventral margin, was measured with a digital caliper to evaluate the size of prey bivalves (Table 1). The position of the drill holes was also recorded. To evaluate the valve selectivity by predatory gastropods, drilled valves were recognized as right valve or left valve. The drilling frequency of each bivalve species was also calculated by dividing the number of drilled shells by the total number of shells collected. To observe the morphology of drill holes in detail, the drilled valves were cut into pieces after embedding in epoxy resin, mounted on aluminum stubs with double-sided tape, and then examined under an SU8220 (Hitachi) scanning electron microscope at Kyungpook National University. The outer borehole diameter (OBD) and inner borehole diameter (IBD) were recorded by measuring the maximum diameter of the borehole using scaled scanning electron microscope pictures, and the microstructure of the borehole surfaces was also examined.

All specimens were deposited in the collections of the Cultural Heritage Administration of Korea. Collection numbers of Cultural Heritage Administration of Korea were given to the selected 20 specimens of the drilled bivalves (NHCG 10930–1 to NHCG 10930–20). Taxonomy of the drilled bivalve shells was aided by several illustrated books of Korean mollusks (Choe et al 1999; Min and Lee 2005; Min et al 2004) and personal communication with Dr Min in Molluscan Research Institute.

Results

Three different bivalve species were identified among the 200 shells collected (Table 1): *Mactra chinensis* Philippi (162 specimens, 81%), *Felaniella usta* Gould (22 specimens, 11%), and *Nuttallia japonica* Deshayes (16 specimens, 8%) (for further taxonomy of bivalve shells, see Choe et al 1999; Min and Lee 2005). All three bivalves are known as rich species on the western and southern coasts of the Korean Peninsula (Min and Lee 2005). About half of the shells (92 specimens) bear circular to subcircular holes on the shell surfaces (Figure 3), which are known as boreholes drilled by predatory gastropods (Table 1). Almost all the boreholes are observed to be present on only one of two valves of the shells; only one shell of *N. japonica* has a borehole in both valves.

The boreholes found on the prey shells of three species (*M. chinensis*, *F. usta*, and *N. japonica*) are almost identical in morphology, but differ slightly in size and position of the drill holes (Figure 3, Table 1). They are circular to subcircular in plain view and parabolic in cross section, and, thus, the diameter of the outer borehole (OBD) is always larger than that of the inner borehole (IBD) (Figure 4B). Consequently, the depth to diameter ratio of the borehole is less than 1. The OBDs of all the boreholes collected range from 0.30 to 0.54 cm (mean 0.40 cm), whereas the IBD is from 0.23 to 0.04 cm (mean 0.27 cm) (Table 1). The OBD and IBD, however, differ slightly according to the species of prey shells; shells of *Mactra* have the largest outer borehole (0.440 ± 0.423 cm); whereas, the largest inner borehole is observed in the specimens of *Felaniella* (0.330 ± 0.033 cm). The shells of *Nuttallia* (Figure 3K) are characterized by the smallest OBD (0.334 ± 0.034 cm) and IBD (0.225 ± 0.007 cm) and, thus, have the steepest borehole slope among the three species.
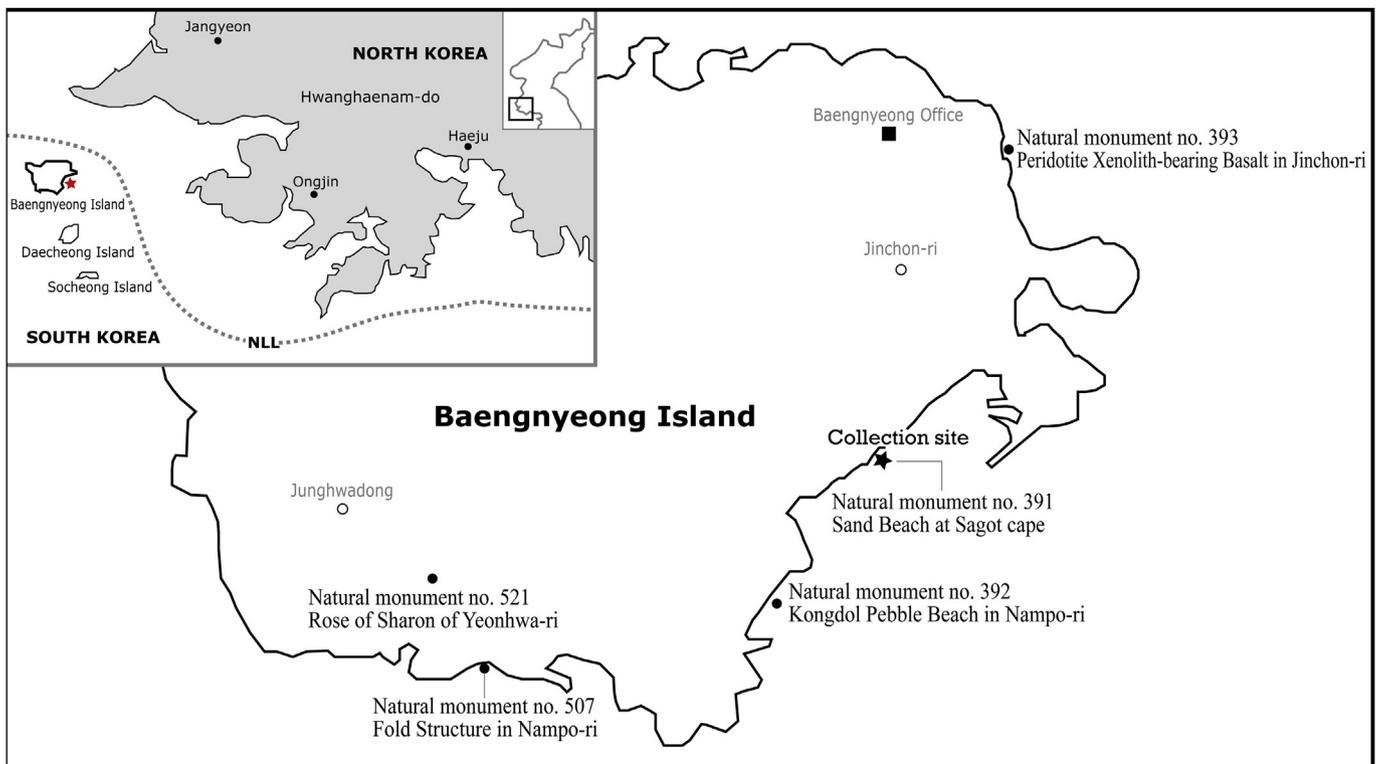
Figure 1. Location of the sampling area of drilled bivalves on Baengnyeongdo, Korea. The collection site (black star) of drilled bivalves is located on the sand beach at Sagot Cape.
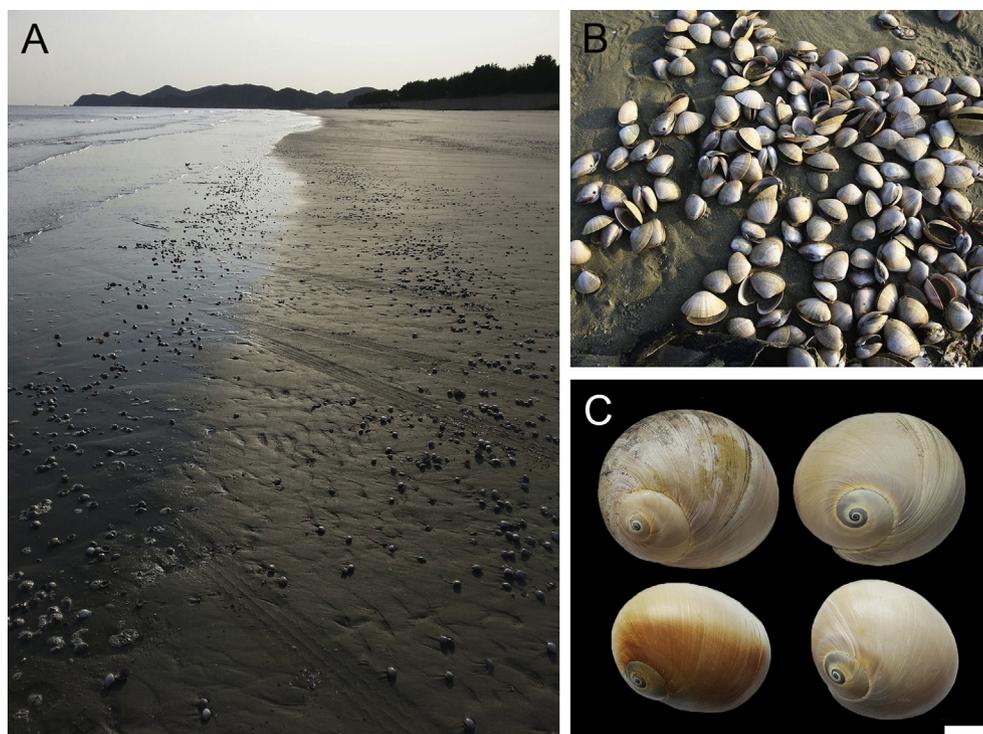
Figure 2. Mollusk shells that were pushed onto the sand beach at Sagot Cape in October 2015: A, bivalve shells scattered along the coastline of the Sagot sand beach; B, an aggregated assemblage of drilled bivalve *Mactra chinensis*; C, predatory naticid gastropod *Glossaulax didyma didyma*. Picture of *G. didyma didyma* was provided by Dr Min in Molluscan Research Institute. Scale bar in C represents 2 cm.

Table 1. Characteristics of drill holes found from the three bivalve species collected from the sand beach at Sagot Cape, Baengnyeongdo, Korea.

Bivalve species	Shell height (cm)	OBD (cm)	IBD (cm)	DF	Number of drilled shell	
					LV	RV
Mactra chinensis	2.795 ± 0.263	0.440 ± 0.423	0.260 ± 0.035	50.6% (82/162)	46	38
Felaniella usta	2.158 ± 0.115	0.430 ± 0.032	0.330 ± 0.033	22.7% (5/22)	3	2
Nuttallia japonica	2.840 ± 0.012	0.334 ± 0.034	0.225 ± 0.007	31.3% (5/16)	2	3

OBD = outer borehole diameter; IBD = inner borehole diameter; DF = drilling frequency (100 × number of drilled shells/total number of shells collected); LV = left valve, RV = right valve.

Description of drill holes

All boreholes collected from the sand beach occurred solitarily on the shell surfaces and were found more or less evenly on left valves and right valves: 46 left and 38 right valves in the shells of *Mactra*, three left and two right valves in the shells of *Felaniella*, and two left and three right valves in the shells of *Nuttallia* (Table 1). Such an occurrence suggests that there was no specific valve preference by drilling gastropods living in the Baengnyeong tidal flat. The borehole sites on the shells, however, differ in position depending on the bivalve species. For example, more than 96% of boreholes (80 out of 82 specimens) in the shells of *Mactra* are located on the umbo (Figures 3A–J), whereas the shells of *Felaniella* have more or less randomly distributed boreholes (Figures 3L–O).

Most of the parabolic forms are symmetric in terms of a borehole center; whereas, asymmetric paraboloids with a gentler angle toward the ventral margin are occasionally observed in the specimens of *Felaniella* (Figure 3M). The asymmetric paraboloids seem to be the result of oblique drilling by predatory gastropods (Klompmaker et al 2016). The edges of the outer borehole in the shell of *Mactra* are generally smooth and regular (Figures 5A and 5D), whereas those in shells of *Felaniella* and *Nuttallia* are characterized by sharp outlines (Figures 5B and 5C). A wavy outline of the outer borehole is observed in one specimen of *N. japonica* (Figures 5B and 5F). Unlike the edges of outer boreholes, those of inner boreholes are sharp, irregular, and often broken due to mechanical abrasion (Figures 5A and 5C). This is mainly because the edges of inner boreholes are very thin and thus fragile. Wall structures of boreholes in shells of *Mactra* are smooth and uniform without any specific structures (Figures 5A and 5E), whereas boreholes in the two other species (*F. usta* and *N. japonica*) show a concentrically stratified structure (Figures 5B, 5C and 5F). Such a structural difference may reflect the difference in the crystal structures according to the different bivalve species (e.g. Carriker 1978). No specific ornamentation is observed in the borehole walls of any of the three prey species.

IBD to OBD ratio of *Mactra* shells is approximately 0.59 (Table 1 and Figure 4B). According to Kitchell et al (1986), the boreholes of *Mactra* shells may be classified as functional boreholes because the IBD to OBD ratio is greater than 0.5. Although some researchers argued that this index may be different for different naticid species (Grey 2001; Hoffmeister and Kowalewski 2001), it is reasonable to conclude, if we consider the limited range of inner borehole size and height of the prey shell, that the inner borehole is large enough for the proboscis of drilling gastropods to perforate the shell of *Mactra*.

Incomplete boreholes, i.e. boreholes that did not penetrate the entire thickness of the valve, are occasionally observed only in
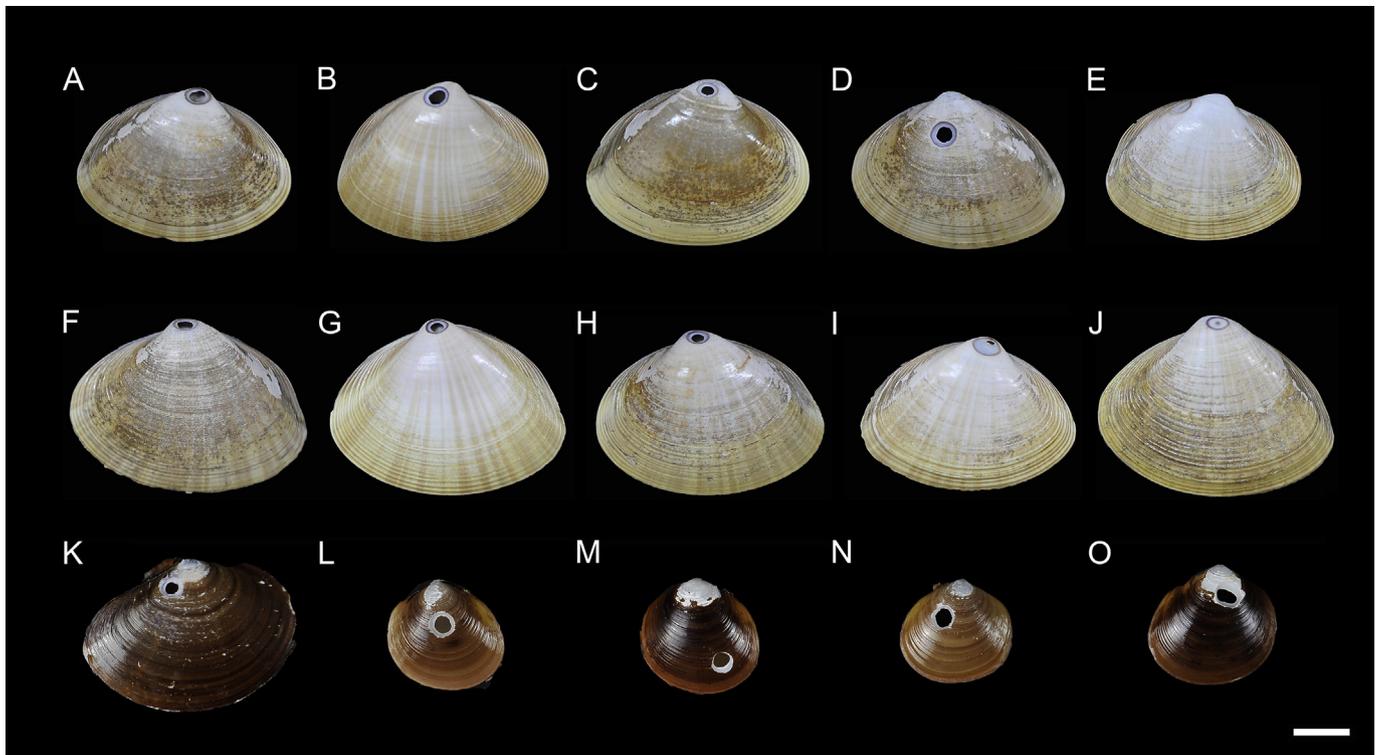
Figure 3. Ichnospecies *Oichnus paraboloides* Bromley found in three bivalve shells: A–J, *Mactra chinensis*; K, *Nuttallia japonica*; L–O, *Felaniella usta*; Note that most boreholes in the shells of *M. chinensis* are located on the umbo of the right valve (A–C) and the left valve (F–H). An abnormally placed borehole (D) and incomplete boreholes (E, I, and J) are also present. (A–O), NHCG 10930–1 to NHCG 10930–15, respectively. Scale bar represents 1 cm for all figures.

specimens of *Mactra*; three specimens out of 82 drilled shells of *Mactra* contain incomplete boreholes (Figures 3E, I and J). The incomplete boreholes are characterized by a flat bottom and a slightly raised central boss (Figure 5D), but no structural difference between the flat bottom and the central boss of incomplete boreholes is recognized.

Discussion

### Taxonomic consideration and predatory gastropods

The boreholes of the three bivalve species (species of *Mactra*, *Felaniella*, and *Nuttallia*) are almost identical in morphology, characterized by small beveled holes that are parabolic in cross section. These characters are typical and diagnostic features of the ichnospecies *O. paraboloides* (Bromley 1981; Kong et al 2015; Kowalewski 1993; Nielsen and Nielsen 2001; Pek and Mikulas 1996). As a consequence, they are, in this study, classified into the ichnospecies *O. paraboloides*, although several authors erected different ichnogenera (e.g. *Sedilichnus* Müller 1977; *Tremichnus* Brett 1985) from similar-looking boreholes. As Zonneveld and Gingras (2014) suggested, we agree in this paper that the ichnogenus *Oichnus* is a junior synonym of *Sedilichnus*. However, subsequent authors (Donovan and Novak 2015; Gendy et al 2015; Klompmaker et al 2014; Rojas et al 2014; Sebastian et al 2015) have continuously used ichnogenus *Oichnus* rather than *Sedilichnus*. Due to such an extensive usage by many authors, we use temporarily the ichnogenus *Oichnus* rather than *Sedilichnus* in this paper (for detailed systematics, see Kong et al 2015).

Three ichnospecies of *Oichnus* (*O. ovalis*, *O. simplex*, and *O. paraboloides*) found commonly on the modern and fossil bivalve shells are different in morphology, and thus, each of them were attributed to the drilling behaviors of different predatory

organisms (e.g. Bromley 1981). Different drillers (e.g. gastropods, worms and octopods), however, are known to produce similar (or even identical) drill holes to the *Oichnus* ichnospecies (Bromley 1993; Kabat 1990). For example, *O. simplex* characterized by cylindrical holes is known to be produced by muricid gastropods (Bromley 1981), but holes similar to *O. simplex* was also reported to be produced by octopods (Carriker and Gruber 1999; Harper 2002; Klompmaker et al 2014). Consequently, careful investigation is required to identify a specific predatory organism only by morphological characters of drill holes.

Oichnus paraboloides is characterized by beveled holes with a parabolic surface wall and is known to be produced by naticid gastropods (Dietl and Kelley 2006; Kelley and Hansen 2003). As a result, the beveled holes with a parabolic cross section (Figures 5A–C) and presence of incomplete boreholes (Figures 3J and 5D) with a raised central boss suggest that the Baengnyeong bivalves were drilled by naticid gastropods. Naticid gastropods (family Naticidae) live within the sediments usually preferring infaunal preys of bivalves, whereas epifaunal muricids (family Muricidae) tend to drill epifaunal preys (Herbert and Dietl 2002; Kelley and Hansen 2003; Kowalewski 2004). The abundance of naticid gastropods and scarcity of muricid gastropods in Baengnyeong tidal flat also support naticid gastropods as the major predator of Baengnyeong bivalves (Min and Lee 2005; Min et al 2004).

Naticid gastropods living within the intertidal sand shoal of Baengnyeongdo include *Lunatia fortunei*, *Glossaulax didyma didyma*, *G. didyma ampla*, *G. bicolor*, and *G. reiniana* (Choe et al 1999; Min and Lee 2005; Min et al 2004). *G. didyma didyma* among the five gastropod species is the most dominant naticid gastropod (Figure 2C). The exact identification of drillers at the species level may be impossible because we collected dead shells that were pushed onto the sand beach at Sagot Cape by waves. However, a frequent observation in the field by local people that *G. didyma*
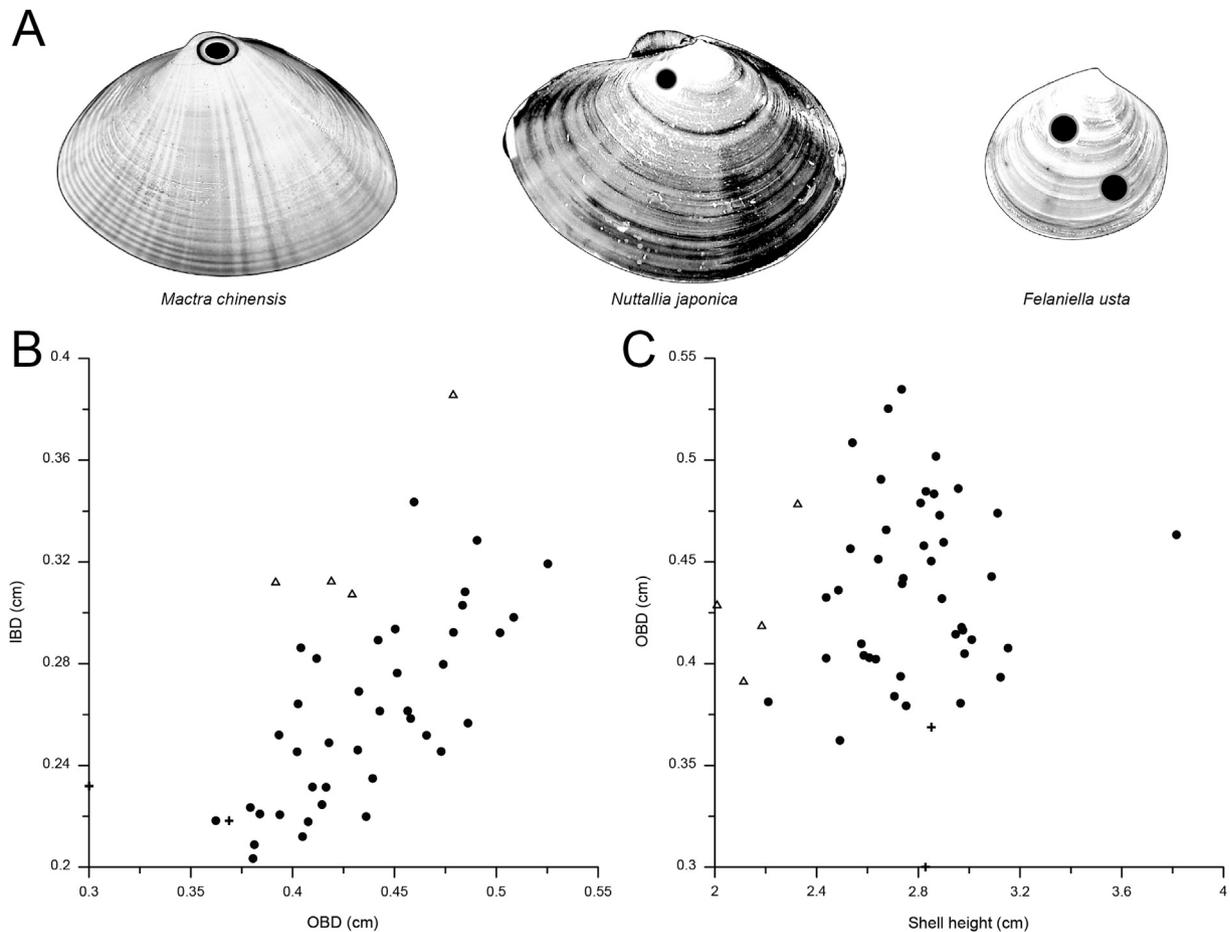
Figure 4. *Oichnus paraboloides*: A, position of *O. paraboloides* on three bivalve species; B, plots showing the relationship between outer borehole diameter (OBD) and inner borehole diameter (IBD); C, plots showing the relationship between outer borehole diameter and shell height; (*M. chinensis*, black circle; *N. japonica*, cross; *F. usta*; open triangle).

didyma are attacking trough shells (*M. chinensis*) may indicate that Baengnyeong trough shells collected were drilled by the naticid gastropod *G. didyma didyma*. In addition, the limited size variation of the OBD and IBD of all 92 drilled valves (Figures 4B and 4C) may further suggest that all Baengnyeong bivalves were drilled by same gastropod predator, *G. didyma didyma*. The incomplete boreholes observed in trough shells (Figures 3E, I and J) indicate a failure of the drilling attempt by the Baengnyeong gastropod *G. didyma didyma* (e.g. Chattopadhyay and Dutta 2013; Kowalewski 2002).

Prey selectivity

Several authors documented, on the basis of field observations and laboratory experiments, that some naticid gastropods (e.g. *G. didyma* and *Euspira fortunei*) have a significant preference for drilling the left valve rather than the right valve of bivalve preys (Hasegawa and Sato 2009; Hirayama et al 1996; Rodrigues et al 1987). Hasegawa and Sato (2009) argued that this preference is closely related to both predatory behavior and the life position of prey bivalves within the sediments. Drill holes in Baengnyeong specimens, however, are observed more or less evenly on left and right valves. In the case of *Mactra* shells, for example, 46 boreholes are located on the left valve and 38 boreholes on the right valve (Table 1). A specific valve preference was not recognized in all three species of Baengnyeong bivalves, although the statistical evaluation is not possible in the other two bivalve shells (*F. usta* and *N. japonica*) due to a low sample size. This observation may suggest that the life position of the three Baengnyeong bivalves did not

dictate the preference of the predatory gastropod, *G. didyma didyma* in Baengnyeong tidal flat ecosystem.

The concentration of boreholes in a specific region is observed in the prey shells of *Mactra*, showing that 81 boreholes out of 84 (96%) are located on the umbo (Figures 3A–J). Such a concentration of boreholes, on the other hand, cannot be estimated in the other two drilled species of *Felaniella* and *Nuttallia* because of the limited number of samples collected (Figures 3 and 5A). In the shells of *Mactra*, the clustered distribution of the boreholes on the umbo (Figures 3A–J) strongly indicates the site selectivity for a borehole. Such a stereotypical placement of boreholes is a quite common phenomenon in many predatory naticid gastropods. Indeed, the concentration of boreholes in a specific region has been widely reported from the bivalve shells drilled by naticid gastropods (Cintra-Buenrostro 2012; Dietl and Alexander 1995; Kelley 1991; Kingsley-Smith et al 2003), although the location of boreholes varies within and between bivalve species (Chattopadhyay and Dutta 2013). In particular, Peitso et al (1994) documented that 97% of prey littleneck clams (*Prothotaca staminea*) were drilled on the umbo when attacked by naticid snails (*Euspira*).

The concentration of boreholes in a specific region is known to be related to a gastropod's manipulation during handling of bivalve preys and the size of bivalve preys (Kitchell et al 1986; Peitso et al 1994). In the shells of *Mactra*, a high concentration (96%) of drill holes on the umbo is also likely to be associated with moon snail's easiness of prey handling (Ziegelmeier 1954) and the position of bivalve prey's body mass (Chattopadhyay and Dutta 2013). The predatory gastropods (*G. didyma didyma*) in Baengnyeong tidal flat
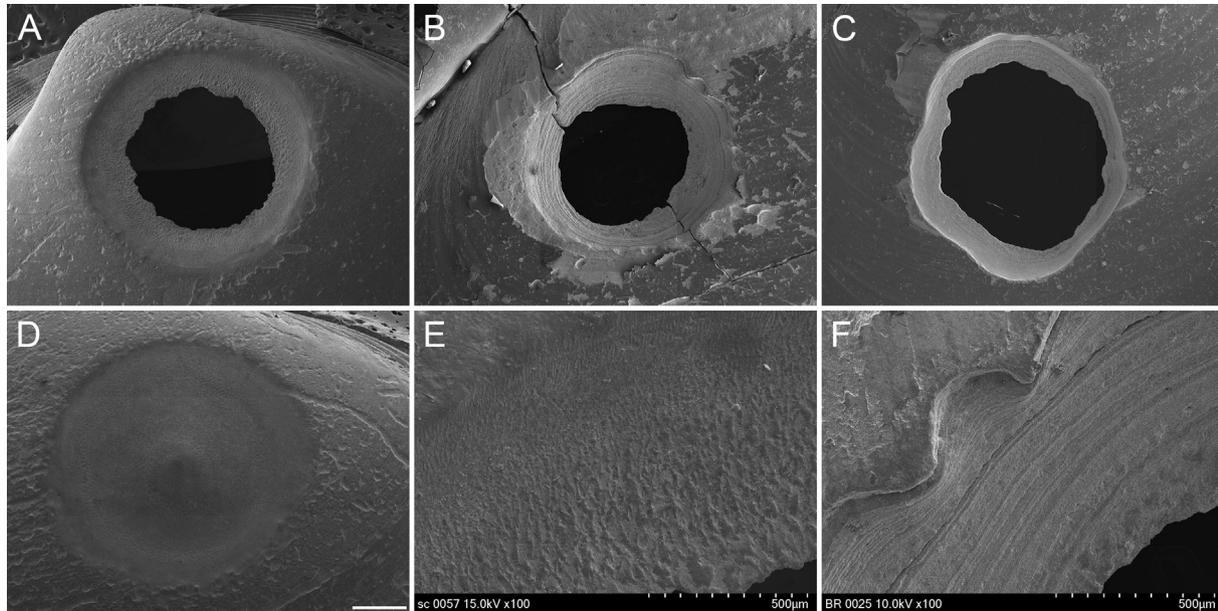
Figure 5. SEM pictures of borehole *Oichnus paraboloides*: A, *M. chinensis*; B, *N. japonica*; C, *F. usta*; D, incomplete borehole on *M. chinensis*; E, smooth wall structure of *M. chinensis*; F, concentrically stratified wall structure of *N. japonica*. Note that the boreholes are characterized by beveled holes that are parabolic in cross section and that two different wall types (smooth and stratified) are observed according to the bivalve species. Scale bar in (D) is 1 mm for (A)—(C).

seem to have manipulated their bivalve prey (*Mactra*) so that the umbo is closest to their mouth, mainly because the main body mass of the clam lies beneath the umbo. In our specimens (particularly in the shells of *Mactra*), however, the site selectivity is not likely to be influenced by the size of preys because no correlation between shell height and position of boreholes was observed (Figure 4).

The naticid gastropod is known to attack its preferred prey size classes (Chiba and Sato 2016; Kingsley-Smith et al 2003; Rodrigues et al 1987), and the size of the borehole (particularly OBD) drilled by the gastropod is also known to be correlated with the size of the individual naticid predator (Carriker and Van Zandt 1972; Kitchell et al 1981). More than 70% of the boreholes were found on prey shells of *Mactra*, and all drilled shells of the Baengnyeong specimens are very similar in size (2.795 ± 0.263 cm in height, Table 1). This may explain a specific size preference for *Mactra* by naticid gastropod *G. didyma didyma*. The higher drilling frequency (100 × number of drilled shells/total number of shells collected) of *Mactra* shells (50.6%) than that of the other two species (22.7% in *Felaniella* and 31.3% in *Nuttallia*) also supports this interpretation, all of which indicate that the bivalve of *M. chinensis* with 2.795 ± 0.263 cm in height is a major size-matched prey of predatory gastropod *G. didyma didyma* in the benthic community of the Baengnyeong tidal flat.

Conflicts of interest

The authors declare that there is no conflicts of interest.

Acknowledgments

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