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TEMPORAL PATTERN OF NATICID PREDATION ON *GLYCYMERIS YESSOENSIS* (SOWERBY) DURING THE LATE CENOZOIC IN JAPAN

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ABSTRACT

No temporal trend in the intensity of drilling by naticids on *Glycymeris yessoensis* can be recognized during the late Cenozoic. Drilling sites shifted from the umbo to the center of the valve during the late Cenozoic. This shift might reflect the change of predators from *Glossaulax* in the Miocene to *Cryptonatica* or *Euspira* in the Pleistocene. Borehole sites in the middle Pleistocene were more stereotyped than in the early Pleistocene population despite the same predators. Edge drilling, which is a faster drilling method, first appeared in the population showing high drilling intensities in the early Pleistocene. Because a prediction of the hypothesis of escalation is that changes in predators' behavior developed through time, these changes in drilling location may be the results of escalation. In contrast with the stereotypic trend of borehole sites, correlation coefficients of predator-prey size decreased from the early to the middle Pleistocene.

INTRODUCTION

Based on the hypothesis of escalation proposed by Vermeij (1987), predators respond evolutionarily to their own enemies, such as other predators or competitors, not to prey. According to this theory, predation behavior is expected to become efficient for reducing the chance of injury by the predator's enemies through time. Predatory drill holes are the only certain indicators of predation because other durophagous features sometimes are difficult to separate from taphonomic breakage (Harper et al., 1998). In order to test the hypothesis of escalation, it is necessary to examine the temporal pattern of drilling predation (see Kelley and Hansen, 2003). Naticids are adequate for this examination because they make characteristic parabolic holes on their prey (Kitchell et al., 1981; Kabat, 1990).

Several studies have focused on the temporal pattern of drilling predation on genera or faunas from the Cretaceous to Recent (Dudley and Vermeij, 1978; Vermeij, 1980; Allmon et al., 1990; Kelley and Hansen, 1993, 1996a, b; Kelley et al., 2001). When Thomas (1976) studied the

temporal pattern of naticid predation on two clades of *Glycymeris* from the lower Miocene to Pliocene of the North American Atlantic Coastal Plain, no temporal trend in the drilling frequency was found, but a shift of drilling site away from umbones was noted. Hagadorn and Boyajian (1997) observed little change in the frequency of naticid predation on *Turritella* from the Atlantic and Gulf Coastal Plains, USA, during the Neogene. These studies showed that drilling frequency increased in the Cretaceous or early Cenozoic and stabilized in the late Cenozoic. Drilling frequency also varies with environmental conditions (e.g., Alexander and Dietl, 2001). Thus, it is necessary to examine the temporal pattern of drilling predation at the species level in order to evaluate the hypothesis of escalation. Other than Tull and Böning-Gaese (1993), no study to date has focused on this topic at the species level.

Tull and Böning-Gaese (1993) compared drilling patterns on two species of *Turritella* from the Recent with those from the upper Pleistocene in the Gulf of California region. They found no temporal trends of drilling predation on the species by naticids. However, to confirm the stability of drilling pattern during the late Cenozoic, more long-term data are needed.

The purpose of this paper is to elucidate the temporal pattern of drilling frequency, drilling site, and predator-prey size relationship in *Glycymeris yessoensis*. The genus *Glycymeris* Da Costa, 1778 is a common bivalve living in temperate and tropical waters. *Glycymeris yessoensis* (Sowerby, 1889) is a species that occurs in the boreal water in northern Japan, Primorie, the Okhotsk Sea, and Kamchatka (Higo et al., 1999), and has a long life span, often more than 45 years (Tanabe et al., 2004). Numerous fossil occurrences are known from Neogene and Quaternary deposits in northern Japan (Matsukuma, 1986). The oldest record of this species is from the lower middle Miocene Ausinskaya Formation in southwestern Sakhalin (Ilyina, 1954; Zhidkova et al., 1968). Thus, this species is well suited for examining the long-term pattern of drilling predation during the late Cenozoic.

MATERIALS AND METHODS

Nine specimens of *Glycymeris yessoensis* were collected from the lower middle Miocene Ausinskaya Formation in Sakhalin; however, it is very

TABLE 1—Fossil localities, formation, age, number of total specimens (N) and number of articulated valves (AN) of *Glycymeris yessoensis*.

No.	Loc.	Formation	Age	N	AN
1	Okada in Fukushima Pref.	Kubota F.	early late Miocene	72	0
2	Awasegai in Akita Pref.	Tentokuji F.	Pliocene	363	4
3	Osuga in Niigata Pref.	Nadachi F.	Pliocene	125	0
4	Futatsunuma in Fuykushima Pref.	Tomioka F.	Pliocene	106	0
5	Omma in Ishikawa Pref.	Omma F.	early Pleistocene	51	0
6	Shichiba in Niigata Pref.	Sawane F.	early Pleistocene	360	0
7	Shichiba R. in Niigata Pref.	Sawane F.	early Pleistocene	56	0
8	Chikagawa R. in Aomori Pref.	Hamada F.	early Pleistocene	53	0
9	Kaikozawa in Hokkaido	Uzura F.	early Pleistocene	36	0
10	Inashibetsu R. in Hokkaido	Osarushinai F.	early Pleistocene	115	0
11	Wakimoto in Akita Pref.	Shibikawa F.	middle Pleistocene	243	0
12	Anden in Akita Pref.	Shibikawa F.	middle Pleistocene	481	0
13	Otohama in Fukushima Pref.		Recent	78	0
14	Shimokita in Aomori Pref.		Recent	146	43

difficult to examine drilling predation in these specimens because of poor preservation. For this reason, Miocene material used in this study is restricted to museum specimens from the early late Miocene Kubota Formation at Okada, Fukushima Prefecture (Table 1, Fig. 1). These specimens are housed at the University Museum of University of Tokyo (UMUT) and the Saito Ho-on Kai Museum in Sendai (SHM). In addition, specimens of *G. yessoensis* collected from three Pliocene, seven early Pleistocene, and two middle Pleistocene localities in northern Japan that are housed at Joetsu University of Education (JUE), and Recent specimens from Fukushima and Aomori Prefectures housed at the National Science Museum (NSM) were used in these analyses.

In order to evaluate drilling predation, prey size, drilling intensity, prey effectiveness, drilling site, and relationship between predator and prey size were measured and calculated. Almost all fossil specimens are disarticulated except for four articulated specimens from Locality 4 (Table 1). While all Recent specimens from Locality 13 are disarticulated, 43 specimens from Locality 14 are articulated.

The drilling intensity (DI) was calculated as in the formula:

$$D/(0.5*DV+AV)$$

where D=valves with completely drilled holes; DV=disarticulated valves; and AV=articulated valves (see Hoffmeister and Kowalewski, 2001; Kowalewski, 2002).

The prey effectiveness (PE) is calculated as the ratio of the number of valves with incomplete holes divided by the total number of predation attempts (Vermeij et al., 1989). Kitchell et al. (1986) argued that naticid nonfunctional holes are those in which the ratio of inner diameter (IBD) to outer diameter (OBD) of holes is less than 0.5. However, their argument was based on only one species. Grey et al. (2005) demonstrated that various IBD:OBD ratios of functional holes were drilled by different naticid species. Only four specimens with IBD:OBD ratio <0.5 were found from the Pliocene Tentokuji Formation (Locality 2). In this paper, these specimens were treated as completely drilled.

Borehole sites and the predator-prey size relationships were examined

TABLE 2—Associated predatory naticid species with fossil *Glycymeris yessoensis*. Recent predatory naticid species are unknown because museum samples were used. Number in parentheses shows number of individuals. * = After Suzuki and Nojo (1991).

Age	Formation	Loc.	*Cryptonatica*	*Euspira*	*Glossaulax*	*Mammila*
e. l. Miocene	Kubota F.	1	*janthostoma* (6)		*didyma coticazae* (19)	
Pliocene	Tentokuji F.	2	*janthostoma* (48)	*pila* (57)	*didyma didyma* (21)	
	Nadachi F.	3	*clausa* (10)		*vesicalis* (2)	sp. (1)
	Tomioka F.	4	*janthostoma* (26)	*pila* (1)	*didyma didyma* (1)	
e. Pleistocene	Omma F.	5	*janthostoma* (2)	*pila* (2)	*reiniana* (1)	
	Sawane F.	6	*clausa* (1)	*pallida* (1)		
	Sawane F.	7	sp. (1)			
	Hamada F.	8	*janthostomoides* (1)			
	Uzura F.	9	*janthostomoides**			
	Osarushinai F.	10		*pila* (1)		
m. Pleistocene	Shibikawa F.	11	*clausa* (1)	*pila* (2)	sp. (1)	
	Shibikawa F.	12	*clausa* (2)			

TABLE 3—Frequency of complete boreholes distributed among the nine sectors of a valve (see Figure 3), and evenness (J′) of borehole site for five localities where more than 30 drilled specimens were collected. Low evenness means the holes are stereotyped in any sector.

Age	Formation	Loc.	n	I	II	III	IV	V	VI	VII	VIII	IX	J′
e. l. Miocene	Kubota F.	1	20		18					1	1		0.358
Pliocene	Tentokuji F	2	68		18	1	2	37		5	5		0.689
e. Pleist.	Sawane F.	6	108		9	1	6	46	13	2	23	8	0.781
m. Pleist.	Shibikawa F	11	38	2	2		1	24	3		7		0.671
	Shibikawa F	12	42		2		2	28	3	1	4	2	0.620

TABLE 4—Mean, maximum size of bored and unbored valves, predation intensity, prey effectiveness, existence of edge-drilled specimens, and correlation coefficient of predator-prey regression line.

|	Age	Mio.	Pliocene		
Index of predation	Location	1	2	3	4
Mean shell length (mm) of unbored valves		25.5 (n = 52)	25.1 (n = 299)	35.5 (n = 120)	32.2 (n = 103)
Maximum shell length (mm) of unbored valves		72.4	49.3	46.5	59.8
Mean shell length (mm) of valves with competely drilled holes		21.1 (n = 20)	18.4 (n = 68)	27.6 (n = 5)	42.6 (n = 3)
Maximum shell length (mm) of drilled valves		61.2	41.1	34.7	50.4
Mean shell length (mm) of total valves		24.3	23.9	35.2	32.5
Drilling intensity (DI)		0.56	0.35	0.08	0.06
Number of incompletely drilled specimens		0	2	2	0
Prey effectiveness (PE)		0.00	0.03	0.29	0.00
Edge drilled specimens		0	0	0	0
Correlation coefficient of predator-prey regression line		0.886	0.887		
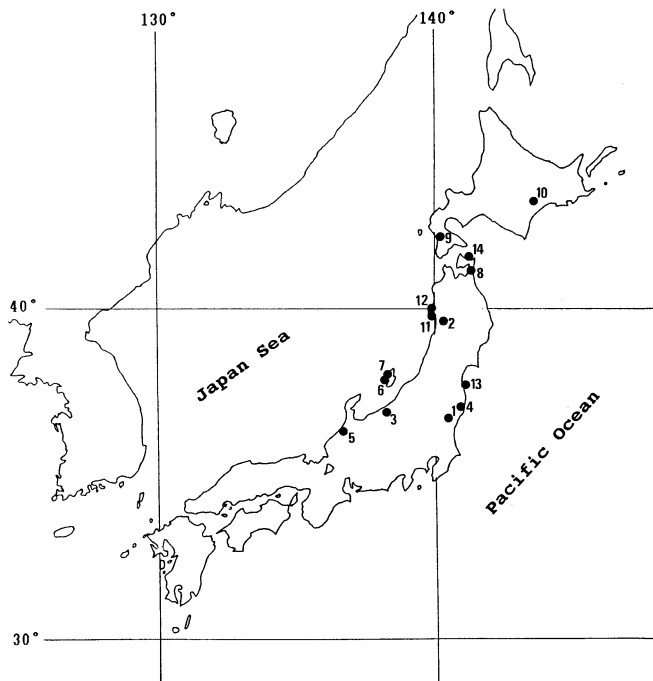
FIGURE 1—Locality map of fossil and Recent *Glycymeris yessoensis* used in this study (see also Table 1).

in populations that include more than 30 drilled specimens. These populations were obtained from 1 Pliocene, 1 early Pleistocene, and 2 middle Pleistocene localities. Twenty bored specimens from the Miocene Kubota Formation also were included. The first appearance of edge-drilled specimens (Fig. 2) also was determined.

To determine the borehole site, each bored valve is subdivided into nine sectors (I–IX; Fig. 3) following Kelley (1988). Pielou's J' index (=H'/H'max: Shannon-Weaver index $H' = -\Sigma \ n_i/N \ log_2 n_i/N$, where n_i=number of boreholes in each site and N=total number of boreholes) was calculated for evaluating stereotypy (after Dietl et al., 2001). Regressions between prey length (prey size) and outer diameter of holes (predator size) also were examined.

In this study, prey length was measured as the width between the anterior and posterior ends of shells. Correlation coefficients of regression lines were compared to evaluate flexibility in prey-size selectivity for naticids at each locality.

RESULTS

A large difference is recognized between early late Miocene and early Pleistocene naticid faunas (Table 2). In the early late Miocene, *Glossaulax didyma coticazae* (Makiyama, 1926) was the predominant species in the fauna. Nomura and Hatai (1936) recorded both *G. didyma coticazae* and *Cryptonatica janthostoma* (Deshayes, 1839) from the lower upper Miocene Kubota Formation, but Iwasaki (1970) described only *G. didyma coticazae*. In total, 19 specimens of *G. didyma coticazae* and 6 specimens of *Cryptonatica janthostoma* were identified with *Glycymeris yessoensis* when these collections were examined.

In contrast, *Cryptonatica* spp. or *Euspira pila* (Pilsbry, 1911) were common in the early Pleistocene faunas. The southernmost population at Locality 5 also includes the warm-water species *Glossaulax reiniana* (Dunker, 1877). Other populations did not include any species of *Glossaulax*. *Cryptonatica janthostoma* (Deshayes, 1839), *Glossaulax didyma didyma* (Röding, 1798), and *Euspira pila* (Pilsbry, 1911) are known from the Pliocene Tentokuji Formation at Locality 2 in about equal numbers. In other Pliocene faunas, *Cryptonatica* spp. is the dominant species, with *Glossaulax* and *Euspira* present.

Associated with the change in predators, the site of boring shifted from the umbonal part to the central part of shell. If the hypothesis of escalation is correct, borehole sites will become more stereotyped through time for more efficient predation. When the calculated J' value is low, the stereotypy of boreholes is high because the holes are concentrated in one area or sector. In the late Miocene fauna, boreholes primarily are located on the umbonal part (Sector II), and the stereotypy of holes is high (J'=0.358; Table 3). In contrast, most boreholes are recognized on the central (Sector V) or ventral (Sector VIII) site in the early to middle Pleistocene faunas. In the Pliocene Tentokuji fauna, many holes are drilled both on the umbonal and central parts. The stereotypy of holes decreased (J'=0.620–0.781) in the Plio–Pleistocene faunas as compared to the Miocene. Edge-drilling first appeared in small specimens (shell length <17.3 mm) in the early Pleistocene populations (Table 4). No edge drilling was found in the Miocene and Pliocene samples, despite the presence of small individuals.

When they examined drill holes of Recent and Pleistocene *Glycymeris yessoensis*, Tanabe et al. (2004) pointed out a tendency for higher predation intensity in younger specimens. However, no significant correlation between prey size (mean shell length of drilled specimens) and drilling intensity (DI) was found in this study (Fig. 4; Table 4; $p > 0.05$). Thus, the temporal trend of drilling intensity can be examined without concern for the size difference between populations. While the drilling intensity at one locality is relatively high (0.56) in the Miocene, it decreased slightly in the Pliocene (DI=0.06–0.35). On the other hand, drilling intensities in two middle Pleistocene (DI=0.18–0.32) and two Recent populations

TABLE 4—Extended.

	Early Pleistocene						M. Pleist.		Recent	
5	6	7	8	9	10	11	12	13	14
47.9	19.3	30.0	23.0	41.9	25.6	25.6	23.0	36.5	37.6
(n = 44)	(n = 252)	(n = 48)	(n = 38)	(n = 33)	(n = 109)	(n = 204)	(n = 439)	(n = 61)	(n = 100)
57.3	51.6	52.6	41.8	52.3	54.3	41.4	35.4	52.4	49.0
40.1	16.6	27.6	18.0	35.6	21.3	22.2	18.8	32.8	32.8
(n = 7)	(n = 108)	(n = 8)	(n = 15)	(n = 3)	(n = 6)	(n = 39)	(n = 42)	(n = 17)	(n = 3)
54.0	40.4	46.6	33.1	47.2	36.4	35.8	31.6	44.4	44.6
46.9	18.5	29.7	21.5	41.3	25.4	24.1	22.7	35.7	37.5
0.27	0.61	0.29	0.57	0.17	0.10	0.32	0.18	0.44	0.04
0	3	0	0	0	0	2	4	1	0
0.00	0.03	0.00	0.00	0.00	0.00	0.05	0.09	0.06	0.00
0	1	1	2	0	0	0	1	1?	0
	0.750					0.679	0.328		
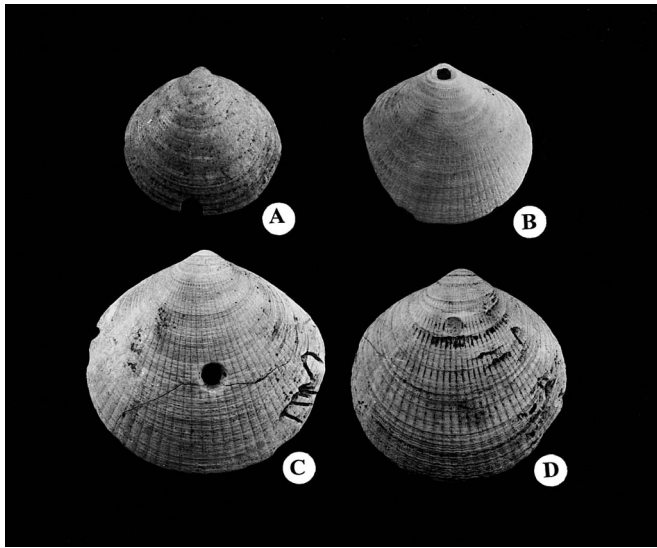
FIGURE 2—Drilled specimens. (A) Edge-drilled specimen, length=13.5 mm, Locality 12, middle Pleistocene Shibikawa Formation. (B) Completely bored specimen at the umbonal part, length=28.1 mm, Locality 3, Pliocene Nadachi Formation. (C) Completely drilled specimen at the central part of disc, length=40.2 mm, Locality 2, Pliocene Tentokuji Formation. (D) Incompletely bored specimen, length=35.1 mm, Locality 2, Pliocene Tentokuji Formation.

(DI=0.04–0.44) vary in intensity. However, geographical variation of DI during the early Pleistocene (0.10–0.61; see also Amano, 2003) encompasses almost the total range in drilling intensity throughout the interval studied. Prey effectiveness usually is low (PE<0.09), except in the Nadachi population (0.29).

If the hypothesis of escalation is correct, correlation of predator-prey size relationships is expected to increase over time. The correlation coefficient between predator size and prey size among the five populations that include more than 30 drilled specimens is high and positive in the Miocene, Pliocene, and early Pleistocene populations (0.750–0.887; Fig. 5; Table 4). The Pliocene population has the highest coefficient (0.887), while the middle Pleistocene populations are lower (0.328–0.679). The lowest coefficient (0.328; Anden population; Locality 12) differs statistically from older populations (Table 5).

DISCUSSION

Museum specimens from the lower upper Miocene Kubota Formation (Locality 1) and the Recent northeastern coasts (Localities 13, 14) were used in this study. The Kubota specimens originally were collected for analyzing the fauna and communities. Because shell length in these specimens ranges from 7.0 mm to 70.6 mm, the specimens seem to have been collected randomly, showing no sampling bias. The shell length of Recent specimens from Locality 13 also ranges from 19.8–52.4 mm, which shows no sampling bias. In contrast, the Recent sample from Locality 14 has narrower range of shell sizes (20.3–49.0 mm), and includes many articulated specimens. Because these specimens might have been collected selectively, the lowest drilling intensity observed in this study (0.04) may be due to this sampling bias.

An increasing trend of drilling intensity in early Pleistocene *Glycymeris yessoensis* was found from Honshu to Hokkaido (Amano, 2003). The low drilling intensity in the southernmost population at Locality 5 is an exceptional case, which was interpreted as the result of heavy drilling by commensal polychaetes, *Polydora glycymerica* (see Amano, 2003). In contrast, no temporal trend in the intensity of drilling during the late Cenozoic has been found. Excluding the lowest drilling intensity at Locality 14 because of its sampling bias, the geographical variation of DI during the early Pleistocene (0.10–0.61) includes almost the total range in drilling intensity from the early late Miocene to the Recent. This result
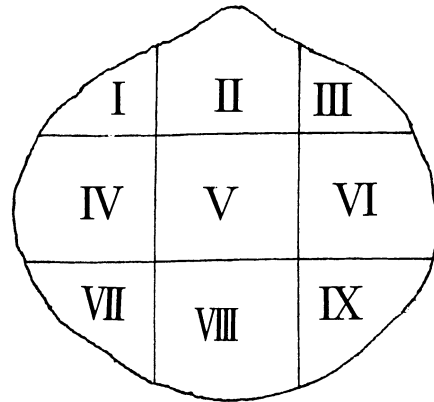

FIGURE 3—Sector designations for right valve (see also Kelley, 1988).

at the species level is concordant with those of Thomas (1976) and Hagadorn and Boyajian (1997) in the generic or clade level, and is consistent with the results of Tull and Böning-Gaese (1993) for the species level, but for a shorter time interval.

Prey effectiveness of *Glycymeris yessoensis* is low (PE of 0.09 or less, other than in the Nadachi specimens), and shows no temporal variation throughout the time interval. This result is concordant with those found at the assemblage level from the Cretaceous to the late Pleistocene (Kelley and Hansen, 1993, 1996a; Kelley et al., 2001).

However, it has become clear that a shift in borehole sites and the first appearance of edge-drilled specimens occurred in the early Pleistocene. Moreover, the correlation coefficient of predator-prey size decreased in the middle Pleistocene. The shift in drilling sites on the shell is consistent with a predator change from *Glossaulax didyma coticazae* in the Miocene to *Cryptonatica* spp. or *Euspira pila* in the Pleistocene. This predator change has been attributed to the adaptation of *Glycymeris yessoensis* to climatic cooling from the Miocene warm-temperate to the Plio–Pleistocene mild- or cool-temperate zone (see Ogasawara, 1994).

According to Matsukuma (1977) and personal observations, *Glossaulax didyma didyma* makes parabolic boreholes near the umbo of Recent *Glycymeris albolineata* (Lischke, 1872) and *Glycymeris vestita* (Dunker, 1877). If *Glossaulax didyma coticazae* drills holes near the umbo of *Glycymeris yessoensis*, like *Glossaulax didyma didyma*, it is easy to explain why the borehole sites are concentrated near the umbo. In the early late
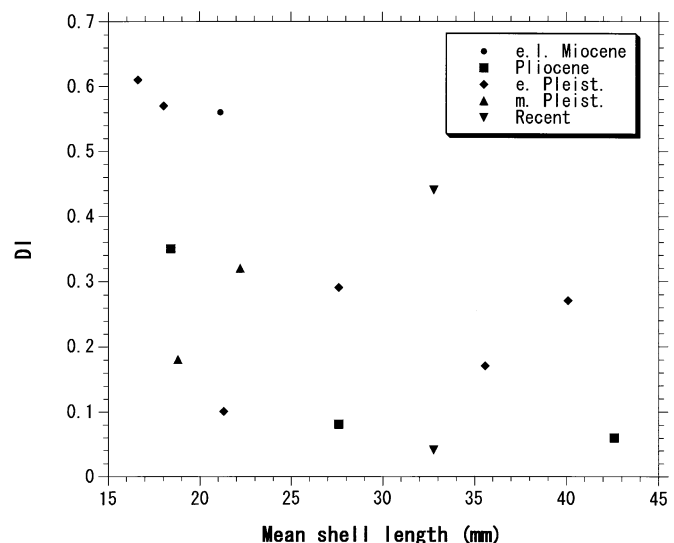
FIGURE 4—Relationship between the mean shell length of completely drilled valves at each localities and drilling intensity (DI). No significant correlation is found.
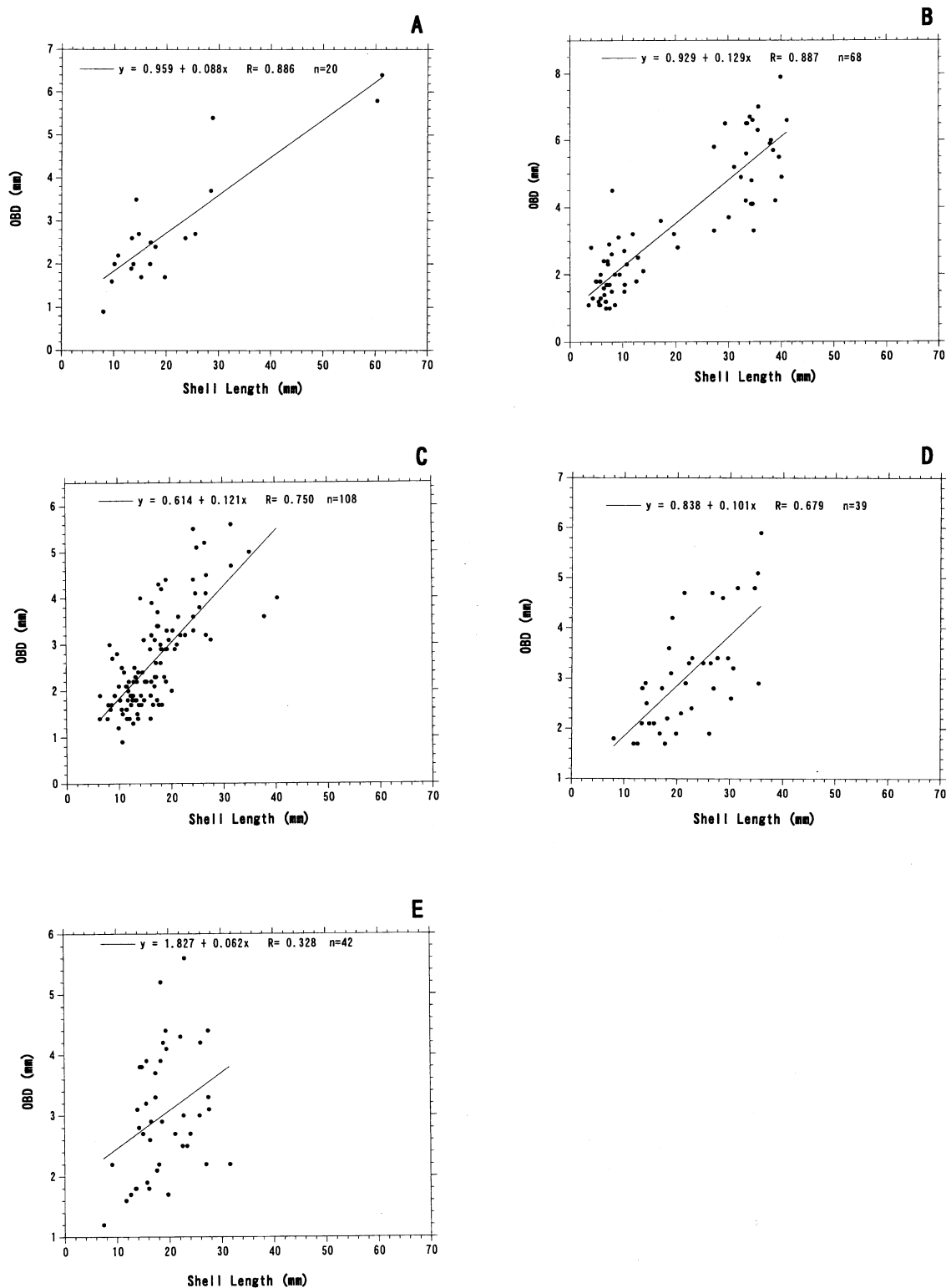
FIGURE 5—Regression of outer borehole diameter (OBD) (=predator size) for complete boreholes on shell length (=prey size) at five localities where more than 30 bored specimens were obtained. (A) Early late Miocene Kubota Formation (Locality 1). (B) Pliocene Tentokuji Formation (Locality 2). (C) Early Pleistocene Sawane Formation (Locality 6). (D) Middle Pleistocene Shibikawa Formation (Locality 11). (E) Middle Pleistocene Shibikawa Formation (Locality 12).

Miocene, *Glossaulax didyma coticazae* was a main predator, and might have drilled near the umbo, which shows high stereotypy (J'=0.358). In contrast, *Cryptonatica janthostomoides* (Kuroda and Habe, 1949) drills in the central part of the shell (Kosuge, 1967). Because *Glossaulax*, *Cryptonatica*, and *Euspira* coexisted as predators of *Glycymeris yessoensis* in

the Pliocene, the main borehole site moved to the umbonal and central area of shells. Thus, the stereotypy of borehole sites is lower (J'=0.689 at Locality 2) than in the early late Miocene.

After the early Pleistocene, *Cryptonatica* and *Euspira* were the main drillers, and drilled the central to ventral part of the shell. Why stereotypy

TABLE 5—Comparison of correlation coefficients (R) of regression lines on predator-prey size for five localities from where more than 30 drilled specimens were collected.

Loc. Loc.	1 e. l. Miocene	2 Pliocene	6 e. Pleist.	11 m. Pleist.	12 m. Pleist.
1	—	0.07	1.77	1.95	3.64*
2		—	2.70*	2.77*	5.20*
6			—	0.75	3.33*
11				—	2.09
12					—

* $p < 0.01$.

of borehole sites in the early Pleistocene was the lowest (J'=0.781; Locality 6) is unknown, especially given that there was a decrease in the number of predatory species. However, it is noteworthy that the site of the middle Pleistocene was more stereotyped (J'=0.620–0.671) than that of the early Pleistocene populations. At the assemblage level, an increasing trend of stereotypy has been found from the Miocene to Pliocene, and Pleistocene to Recent, in spite of the same predators (Dietl et al., 2001). The results of this study support Dietl et al.'s (2001) conclusions, which may be related to escalation.

Edge drilling is a faster method of drilling a hole in prey in warm-temperate or tropical waters (Vermeij, 1993; Dietl and Herbert, 2005). Moreover, this behavior is expressed only when competition between the predators is high (Dietl et al., 2004). Although edge drilling by probable parasites is known in some Paleozoic brachiopods (Deline et al., 2003), Vermeij and Roopnarine (2001) pointed out that this method of drilling became common in thick-shelled venerids in the latest Neogene to Recent of both coasts of tropical America. Edge-drilled specimens of *Glycymeris yessoensis* first appeared in a few, small specimens in the early Pleistocene population. These data on edge drilling in *G. yessoensis* are consistent with Vermeij and Roopnarine's (2001) results. Furthermore, as the climate cooled in northern Japan, edge drilling appeared in populations in Honshu (Localities 6–8, 12, 13), but not in Hokkaido. When the climate cooled after the late Pliocene, competition between predators might have been greater in the Honshu populations, which had a few warm-water species (see also Amano, 2003). Edge drilling is thought to be restricted to small specimens because adult shells of this species have a very thick ventral portion of the shell that would be difficult to edge drill.

The correlation coefficient between predator size and prey size is the highest in the Pliocene population (0.887), while the middle Pleistocene populations are lower (0.328–0.679). This decreasing trend of the correlation coefficient is consistent with Dietl and Alexander's (2000) results on naticid confamilial predation from the mid-Atlantic. They claimed that predator-prey mismatches may occur frequently when juvenile to subadult naticids become more profitable prey according to a cost-benefit analysis. However, their results differ from results presented here because of cannibalism.

According to Dietl and Alexander (1997), *Euspira heros* (Say, 1822) and *Neverita duplicata* (Say, 1822), with the same body-whorl diameter, make different size boreholes. Hagadorn and Boyajian (1997) found correlation coefficients of predator-prey size relationships are higher in the Pliocene than in the Miocene. However, they did not mention the species name of the naticids, and lumped several species of *Turritella* together as the prey species. In this study, the predator species in the Miocene (*Glossaulax didyma coticazae*) is different from the Pleistocene (*Cryptonatica* spp. and *Euspira pila*). It is difficult to determine whether the difference of coefficients between the two time periods is due to a real difference in predator-prey size relationships. However, the early Pleistocene population (Locality 6) shows a higher coefficient than the middle Pleistocene populations (Localities 11, 12) despite *Cryptonatica clausa* and *Euspira* spp. being the main predators in all three localities, and the difference between Localities 6 and 12 is statistically significant (Table 5). After the end of the early Pleistocene, most shallow-water species of

the Japan Sea borderland became extinct because of reduction of salinity during the glacial age (see Amano, 2004). Because middle Pleistocene predator and prey populations represented in the Shibikawa Formation might have reinvaded the Japan Sea after local extinction, it is possible that the newly invaded predators did not escalate enough to select their preferable size of victims. However, it is difficult to explain the stereotypic trend of borehole sites from the early to middle Pleistocene. Further examination is necessary to settle this contradictory problem.

CONCLUSIONS

This study, which examined temporal variation of drilling predation at the species level from the Miocene to Recent in the northern Pacific region, reached five main conclusions:

(1) No temporal trend in the intensity of drilling on *Glycymeris yessoensis* by naticids or the prey effectiveness of predation can be recognized during the late Cenozoic. In most populations, prey effectiveness by naticids was very low.

(2) Drilling sites shifted from the umbo to the center of the valve during the late Cenozoic. This change of site might be consistent with a predator change from *Glossaulax* in the Miocene to *Cryptonatica* or *Euspira* in the Pleistocene.

(3) Borehole sites from the middle Pleistocene were more stereotyped than in the early Pleistocene population despite nearly the same predators.

(4) Edge drilling first appeared in early Pleistocene populations with few warm-water species, consistent with the findings of Vermeij and Roopnarine (2001).

(5) Correlation coefficients of predator-prey size are highest in the Pliocene and lowest in the middle Pleistocene.

The above conclusions mainly are consistent with those from studies of clades, assemblages, or faunal-level analyses for Neogene molluscs. However, this study has revealed that the shift in borehole sites occurred along with a change in predators. Furthermore, for elucidating escalation, it also is important that the stereotypy of borehole sites is higher in the middle Pleistocene than in the early Pleistocene, and that edge drilling first appeared in the early Pleistocene, which was nearly same timing as in American faunas.

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