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Snails versus hermit crabs: a new interpretation on shell-peeling predation in fossil gastropod assemblages

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Abstract. We propose two new methods, an "endobiont method" and a "model method," to quantitatively evaluate shell-peeling predation against snails and hermit crabs in fossil gastropod assemblages. The endobiont method, based on the frequency of peeled and pagurized shells, provides the minimum and maximum estimates of predation against hermit crabs. The model method, based on the frequency distribution of shell repairs per shell in peeled and unpeeled shells, estimates directly the frequencies of predation against hermit crabs and snails. Our two methods were applied to a deep-water gastropod assemblage from the Pliocene Shinzato Formation, Okinawa, Japan. Results show that peeling predation, irrespective of the high frequency of repaired breaks (thought to be an indication of high predatory attacks on snails in previous studies), is mostly attributable to hermit crabs rather than to snails in elongate shells, whereas it is the reverse in spherical shells. The results suggest that the frequency of repaired breaks is strongly controlled by the abundance of elongate shells in fossil gastropod assemblages, and that the increasing evidence of peeling predation, irrespective of predation pressure, is also caused by the increase of elongate shells (e.g., caenogastropods) in gastropod assemblages since the mid-Mesozoic. The new methods could be used for the real understanding of the history of this unique biological interaction through geologic times.

Key words: gastropod, hermit crab, Mesozoic marine revolution, Okinawa, Pliocene, predation, taphonomy

Introduction

Shell-crushing predation by durophagous animals such as decapod crustaceans became an important cause of death and a pervasive component of natural selection during the course of gastropod evolution, and its fossil record has been cited as a major piece of evidence for the "Mesozoic marine revolution" and "escalation" hypotheses (Vermeij, 1977, 1983, 1987). Such predation leaves characteristic breaks on gastropod shells (represented by jagged fractures on the outer lip: = peeled breaks). The origin of the breaks in such shells (peeled shells), however, is difficult to determine, that is, whether they resulted from lethal attacks on snails (primary predation, or PP), from attacks to secondary occupants such as hermit crabs (secondary predation, or SP), or from accidental *postmortem* physical destruction (e.g., Shoup, 1968; Bertness, 1981; Vermeij, 1982; LaBarbera and Merz, 1992; Kowalewski, 2002). In addition, "mistaken predation" (accidental attacks on empty shells: Walker and Yamada, 1993) leaves similar breaks, which we regard as being in the SP category. To avoid this problem, previous studies ("the percent with scars method" and "the scars per shell method"; see Alexander and Dietl, 2003) have been analyzing unsuccessful, repaired breaks (represented by jagged lines in whorls) in fossil gastropod assemblages through geologic time, based on the assumption that the incidence of unsuccessful predation correlates with the proportion of an animal population killed by predators (see Vermeij, 1982). These studies have shown that the frequency of repaired breaks, although it can be biased by several factors, was very low in the Paleozoic and early Mesozoic, and has increased since that time with an apparent peak during the latest Cretaceous (Vermeij *et*

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al., 1981; Alexander and Dietl, 2003, and many references therein). The frequency of repaired breaks in gastropods, however, relies on the frequency of attacks by predators and the vulnerability of prey: a low frequency of repaired breaks suggests either that attacks were infrequent or highly lethal, whereas a high frequency of repaired breaks suggests either that attacks were frequent or not highly lethal (Alexander and Dietl, 2003; see Leighton, 2002 for other factors to the frequency). Therefore, elucidating the effect on gastropod evolution of such predation ideally depends on dealing directly with lethally attacked shells (i.e., PP).

Vermeij (1982) was the first to quantitatively evaluate PP and SP in gastropod assemblages by calculating the number of peeled and drilled shells divided by the number of drilled shells. This procedure is based on the assumption that peeled shells with a naticid or muricid drill hole are attributed to SP, because these predatory gastropods only attack living snails. This study provides the minimum estimate of SP because hermit crabs prefer undrilled shells (Pechenik and Lewis, 2000). We here propose two new methods to quantitatively evaluate the PP and SP values more in detail, based on material from the Pliocene Shinzato Formation, Okinawa, Japan, as a case study. We show that predation on hermit crabs may have been an important agent in the fragmentation of shells in fossil gastropod assemblages much more than previously thought and the new methods provide an insight into the study of this unique biological interaction through geologic times.

Materials

The fossil gastropods discussed here were collected from an exposure of the latest Pliocene Shinzato Formation on Miyagishima islet off Okinawa Island, southern Japan (locality 87-21 in Noda, 1988; Figure 1). The strata at this site consist of bioturbated sandy mud; the exposure is about 20 m thick and contains diverse upper-bathyal mollusks (200–400 fathoms according to MacNeil, 1960). The gastropod assemblage at this site can be considered to be allochthonous in origin, irrespective of no positive sign of shell transportation by currents, because the shells may have been mixed up together by the expected activities of hermit crabs. The gastropod shells from this site we used for the analysis are stout without noticeable signs of shell fragmentation by currents and sediment compaction, and are scattered abundantly in denudated residue under the subtropical climate prevailing in this area. Additionally, the sediment matrix is easily removed from the shells, so that even the delicate traces of epi- and endobionts are clearly seen under a binocular microscope. Specimens were collected by sieving the fossil-bearing residue with a 2-mm mesh and recovering and counting all complete and fragmented shells. We omitted severely fragmented and drilled shells in our analyses, and counted all the repaired and peeled breaks that appeared in the whorls for the model method. We follow the identification of gastropods of MacNeil (1960) and Noda (1980, 1988). The specimens are all deposited in the Department of Geology, the National Science Museum, Tokyo (NSM).

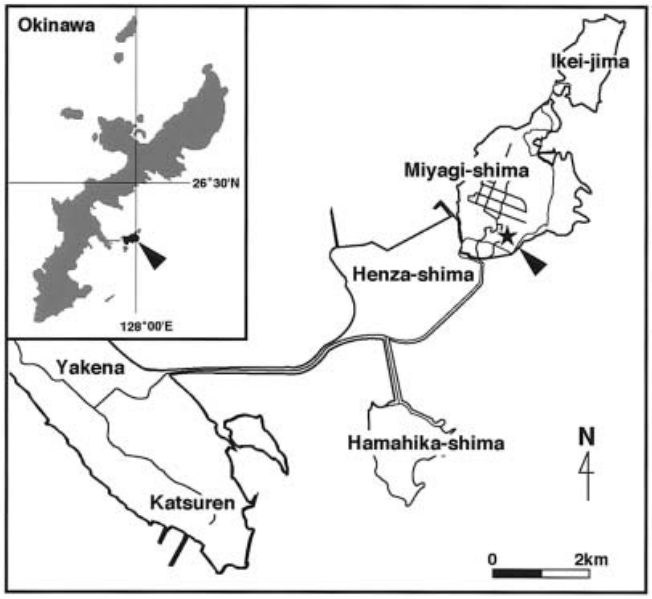


Figure 1. Map showing the sample locality.

Endobiont method

Figure 2 shows a taphonomic scenario for gastropods. When snails die, shells remain intact (Figure 2A) or are fragmented biologically by predators such as shell-drilling gastropods (Figure 2B) or crabs (Figure 2C), then incorporated into death assemblages. After being physically fragmented or not (Figure 2D, E), dead shells become a buried assemblage directly, or they are utilized by secondary occupants such as hermit crabs with or without commensal-biont infestation (Figure 2F, G). Hermitted shells are then incorporated into the buried assemblage, sometimes with biological (Figure 2H) and physical fragmentation (Figure 2J), the former of which occurs due to crushing predation against secondary occupants. Reworked shells from the buried assemblage can be

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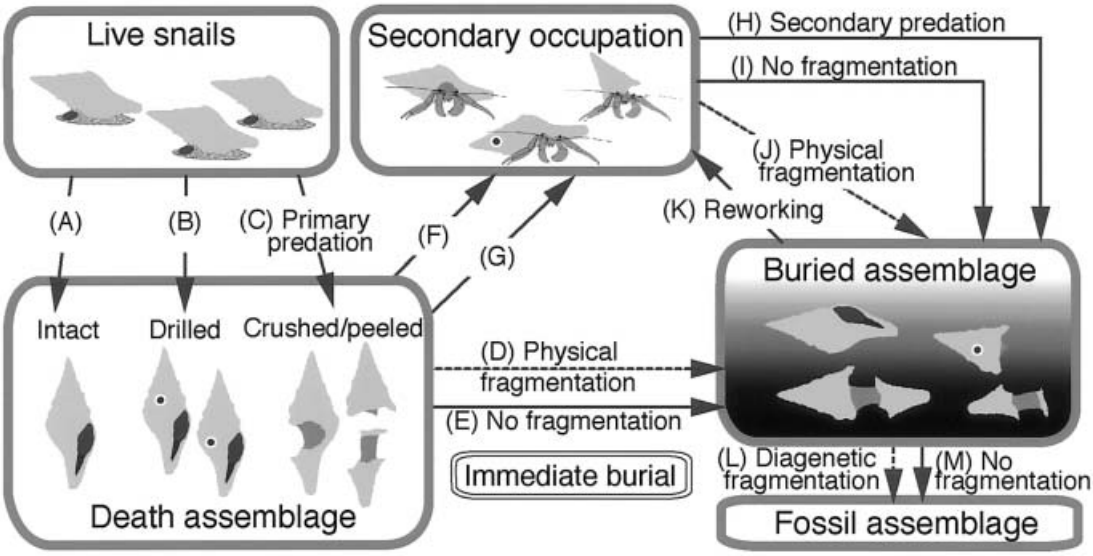


Figure 2. Taphonomic history of shell fragmentation.

reincorporated into the taphonomic process (Figure 2K). Finally, the buried assemblage turns into a fossil assemblage through diagenesis, with or without physical fragmentation (Figure 2L, M).

In this scenario, biological shell fragmentation occurs in two ways: predation against snails (PP) and against hermit crabs (SP). We are unable to distinguish PP and SP for peeled shells, because they are the same in appearance. However, trace-fossil commensals of hermit crabs are useful ''markers'' for detecting SP in the fossil gastropod assemblages. Here we deal with two kinds of domicile drill holes produced by spionid annelids, which are obligatorily commensals on hermit crabs. One is the ichnospecies *Helicotaphrichnus commensalis* that is a U-shaped burrow on the columella of gastropods, where the annelids benefit from filter feeding and receiving respiratory currents generated by the hermit crabs (Kern *et al.*, 1974; Kern, 1979; Figure 3). The other consists of small, round drill holes found only on apical whorls (we call this an ''apical drill hole'') (Williams, 2000; unpublished observation; Figure 3A, F). We follow Walker (1992) in using the terms ''hermitted'' and ''pagurized'' to denote shells occupied by hermit crabs and those with associated trace fossils or body fossils, respectively.

Such trace fossils tell us the various taphonomic histories of gastropod shells (Walker, 1988, 1989, 1992; Seilacher, 1969). Figure 4A schematically shows the distribution of PP and SP in pagurized, unpagurized, hermitted and unhermitted shells in dead and fossil gastropod assemblages. It shows that (1) peeled breaks in pagurized shells resulted from both PP and SP; (2) peeled breaks are due only to PP in unhermitted shells. The difference in frequency of peeled shells between pagurized and unpagurized shells can be regarded as the actual amount of SP when all the unpagurized shells were unhermitted (Figure 4B). However, unpagurized shells may include a certain number of hermitted shells, and hermitted, unpagurized shells include PP and SP to the same degree as do pagurized shells, because the domicile drill holes seem not to have affected predatory preference (Figure 4C). Consequently, the difference in frequency of peeled shells between pagurized and unpagurized shells is evidently smaller than the actual SP and therefore can be regarded as the minimum estimate of SP. Figure 4C shows an example of the calculation in *Gemmula cassinella*.

The frequency of pagurized specimens ranges from 0.05 (*Cancellaria yonabaruensis* and *Euspira* cf. *pallida*) to 0.88 (*Pseudolatirus yonabaruensis*) for the 15 species examined, and the pagurized shells bear peeled breaks more than do the unpagurized shells in 13 species, evidently suggesting that SP is involved (Table 1). An exception is *Naticarius* cf. *niasensis*, where the unpagurized shells bear peeled breaks more than do pagurized shells, most probably due to the small number of pagurized shells. The other exception is *Hindsia solida*, where the thick outer lip in adults seems to have prevented effective peeling by predators. The minimum estimate for SP by this method ranges from 0.01 (four species) to 0.35 (*Gemmula granosa*) (Table 1).

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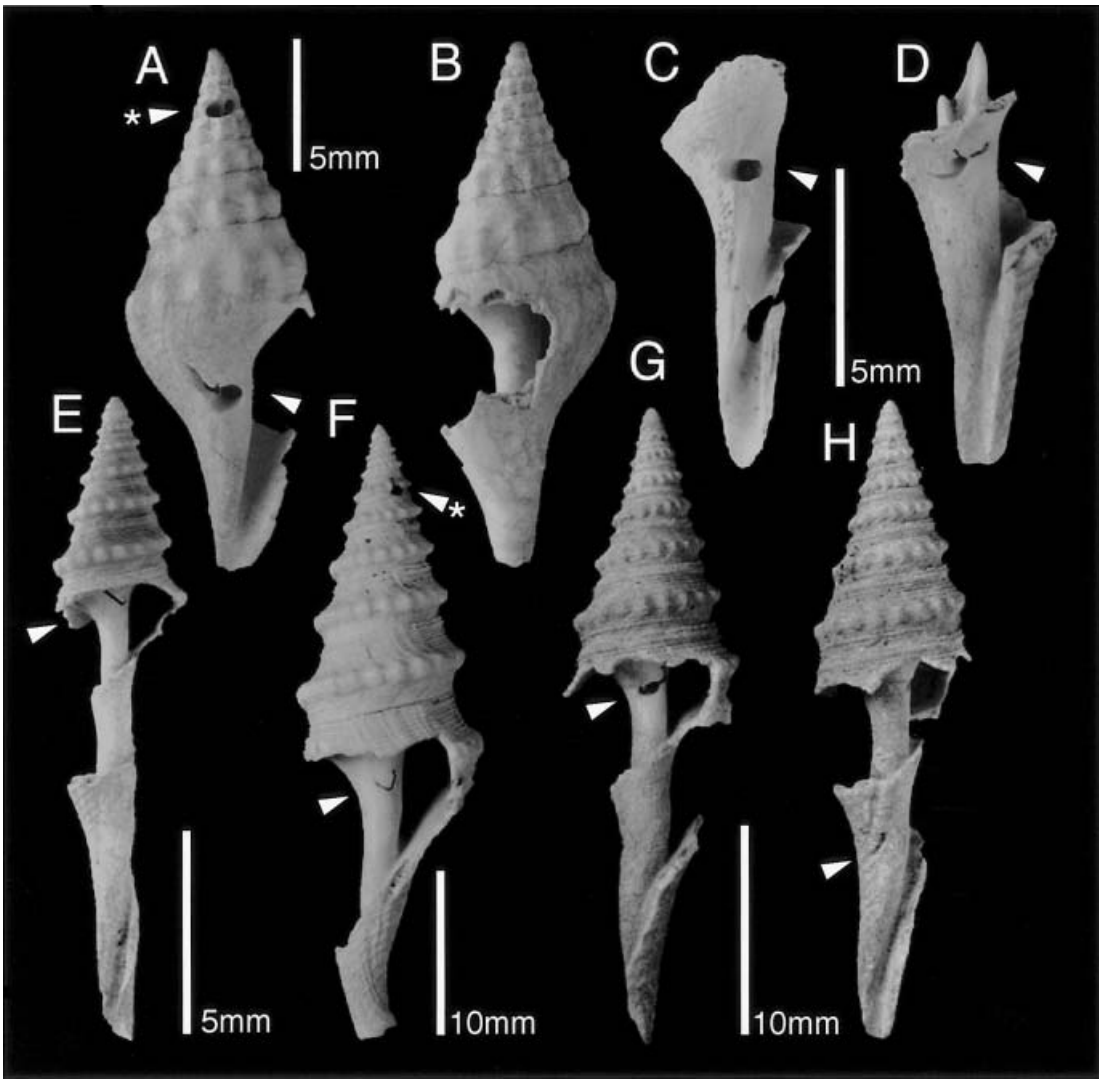


Figure 3. Trace fossils and shell fragmentation patterns for selected gastropods. Arrowheads indicate *Helicotaphrichnus commensalis*, and arrowhead with asterisk indicates ''apical drill hole.'' **A**, **B**. *Makiyamaia* sp. with *H. commensalis* and an ''apical drill hole.'' NSM PM14845. **C**, **D**. Severely broken turrid specimen with *H. commensalis* near original aperture. C, NSM PM14846; D, NSM PM14847. **E**, **F**. *Gemmula granosa* with *H. commensalis* on columella of newly generated aperture. E, NSM PM14848; F, NSM PM14849. **G**, **H**. *Gemmula granosa* with *H. commensalis* close to original and newly generated apertures. NSM PM14850.

Helicotaphrichnus commensalis is positioned in the inner lip or columella within the shell aperture (Figure 3A), and the presence of a deep peeled-break well behind the location of *H. commensalis* strongly suggests that it was due to predation against a hermit crab rather than a snail, because the aperture was likely intact when the shell was hermitted (Figure 3B). *H. commensalis* is sometimes present on the columella of a secondary aperture formed by destruction (Figure 3E–G), suggesting that the shell was hermitted after predation against its former resident(s) – either a snail or hermit crab(s). When *H. commensalis* is present on the columella close to both the original and secondary aperture, it suggests that the shells were hermitted at least twice, and that shell peeling was evidently performed against hermit crabs (Figure 3G, H). Even for severely broken shells, the presence of *H. commensalis* on the columella near the original aperture implies that the shells were intact when they were hermitted (Figure 3C, D).

The peeled breaks among the shells that bear *H. commensalis* on the columellas of the original aperture

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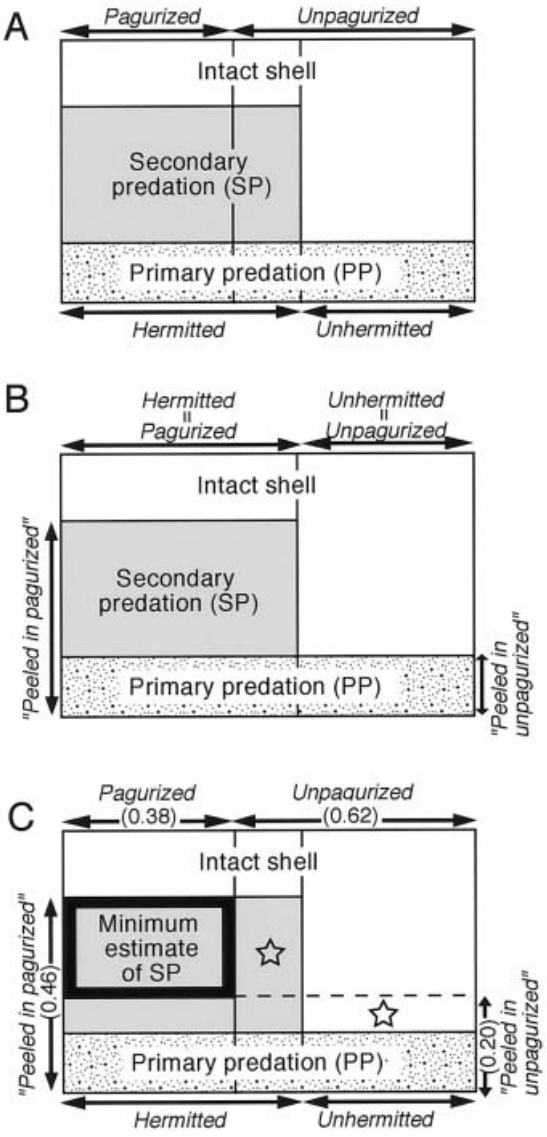


Figure 4. **A**. Schematic distribution of primary (PP) and secondary predation (SP) in pagurized and unpagurized shells. **B**. Schematic distribution of primary (PP) and secondary predation (SP) in pagurized and unpagurized shells when unpagurized shells are all unhermitted. In this case, difference in frequency of peeled shells between pagurized and unpagurized can be regarded as actual amount of SP and can be represented by shaded area: SP = ("peeled in pagurized" – "peeled in unpagurized") × "pagurized." **C**. Example of minimum estimate of SP in *Gemmula cassinella* (number in parentheses, see Table 1). Unpagurized shells can be expected to include hermitted shells, so that difference in frequency of peeled shells between pagurized and unpagurized can be regarded as minimum estimate of SP (area surrounded by thick line). Areas indicated by asterisks are same in size. For *G. cassinella*, minimum estimate of SP can be calculated as ("0.46" – "0.20") × "0.38."

only resulted from SP and their frequency can be regarded as the actual rate of SP when all the shells were hermitted. However, the fossil assemblage may contain shells buried immediately without being occupied by hermit crabs. Therefore, the actual SP frequency appears to be lower than this rate and can be regarded as a maximum value. The maximum estimate of SP by this method ranges from zero (three naticid species) to 0.60 (*Trochocerithium shikoensis*) (Table 1).

Model method

Our model, based on the frequency distributions of the number of repaired breaks per shell (Table 2), employs three parameters: (1) frequency that a snail encounters predation in its life span (predation intensity r); (2) lethality of predation (p); and (3) probability that a dead shell suffered SP at least once (α).

First, we treat time as discrete. This model assumes that, in the absence of predation, each snail survives for its intrinsic life span L. Our snails encounter predation with a probability a for each time interval. Here, ap and $a(1-p)$ give the probability that they encounter lethal and sublethal predation, respectively. The predation intensity r is defined as:

$$r = La \tag{1}$$

Suppose that our snail encounters sublethal predations x times during its life span, then the same number of repaired breaks will be left on its dead shell. If it survived predation $x-1$ times and the next predation was lethal, x numbers of scars will be left, but the last one will be unrepaired. We define the probabilities for the former and latter events as $\mathrm{sub}(x)$ and $\mathrm{let}(x)$, which are defined as:

$$\mathrm{sub}(x) = {}_L\mathrm{C}_x(1-a)^{L-x}\{a(1-p)\}^x \quad \text{for } x \geq 0 \tag{2}$$

$$\begin{aligned}\mathrm{let}(x) = {} & [1 + {}_x\mathrm{C}_{x-1}(1-a) + {}_{x+1}\mathrm{C}_{x-1}(1-a)^2 \\ & + \cdots + {}_{L-1}\mathrm{C}_{x-1}(1-a)^{L-x}]a^x(1-p)^{x-1}p \\ & \text{for } x \geq 1,\end{aligned} \tag{3}$$

Here, we consider a short limit for a discrete time step ($a \to 0$, $L \to \infty$, $r = La$). Since binomial distribution now can be asymptotically replaced by a Poisson's distribution, equations 2 and 3 can be expressed as a function of r instead of a and L:

$$\mathrm{sub}(x) \to \mathrm{e}^{-r}r^x(1-p)^x/x! \tag{4}$$

$$\begin{aligned}\mathrm{let}(x) \to {} & [1 - \mathrm{e}^{-r}\{1 + r + r^2/2 + \cdots \\ & + r^{x-1}/(x-1)!\}](1-p)^{x-1}p,\end{aligned} \tag{5}$$

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Table 1. Results of analyses and comparisons with previous methods for 15 gastropod species.

			Frequency (number of specimens)											
			Endobiont method						Model method				Previous Method	
Species	N*	Shell shape (W/H)	Peeled	Pagurized	Peeled in pagurized	Peeled in unpagurized	Minimum estimate of SP†	Maximum estimate of SP	Predation to hermit crabs (α)	Lethal predation to snails (PP)§	Predation lethality (p)	No. of attack through snail's life (r)	"Percent with scars"#	"Scars per shell"**
Trochocerithium shikoensis	137	.47	.22	.07	.33(9)	.21(128)	.01	.60(5)	.22	.00	.00	.90	.59	1.03
Splendrillia sp.	53	.31	.25	.72	.26(38)	.20(15)	.04	.21(19)	.05	.18	.20	1.00	.55	.73
Gemmula granosa	52	.33	.35	.77	.45(40)	.00(12)	.35	.35(23)	.35	.00	.00	.40	.32	.38
Gemmula cassinella	132	.33	.30	.38	.46(50)	.20(82)	.10	.30(20)	.28	.03	.10	.25	.20	.26
Daphnella ryukyuensis	91	.33	.24	.21	.32(19)	.22(72)	.02	.40(10)	.22	.00	.00	.30	.23	.30
Coronasyrinx takabanarensis	36	.35	.50	.53	.58(19)	.41(17)	.09	.42(12)	.42	.11	.22	.55	.33	.39
Makiyamaia coreanica	18	.42	.50	.83	.53(15)	.33(3)	.17	.50(14)	.30	.37	.48	.95	.56	.67
Pseudolatirus yonabaruensis	26	.31	.38	.88	.39(23)	.33(3)	.05	.25(12)	.15	.28	.25	1.30	.63	.94
Hindsia solida	64	.50	.31	.17	.27(11)	.32(53)	–	.25(8)	.30	.02	.02	.90	.57	.80
Hindsia takabanarensis	41	.48	.10	.68	.11(28)	.08(13)	.02	.08(12)	.06	.01	.02	.55	.41	.43
Cancellaria yonabaruensis	128	.60	.10	.05	.29(7)	.09(121)	.01	.25(4)	.16	.00	.00	.55	.43	.61
Euspira cf. *pallida*	152	.89	.14	.05	.29(7)	.13(145)	.01	.00(3)	.04	.10	.42	.25	.14	.15
Natica aff. *stellata*	18	.85	.17	.28	.20(5)	.15(13)	.01	.00(4)	.00	.17	.74	.25	.07	.07
Natica sp.	67	1.05	.28	.07	.60(5)	.26(62)	.03	–	.08	.23	.86	.30	.04	.04
Naticarius cf. *niasensis*	30	.98	.40	.07	.00(2)	.43(28)	–	.00(1)	.06	.33	1.00	.45	.00	.00

*Number of specimen without predatory drill holes.
†Frequency of SP (difference of peeled rate between pagurized and unpagrized) in total specimens.
§Sum of let(x) for the corresponding values of p and r.
#Frequency of shells with repaired scars in unpeeled shells.
**Mean frequency of repaired scars in unpeeled shells.

Table 2. Data for model method. Expected fractions of unpeeled specimen with x repair(s) and peeled specimen with $x-1$ repair(s) are given by function SUB(x) and LET(x), respectively.

		Number of shell repair(s) per shell											
		Unpeeled specimens						Peeled specimens					
Species	N	0	1	2	3	4	5	0	1	2	3	4	5
Trochocerithium shikoensis	137	44	34	18	6	3	2	11	8	6	4	1	0
Splendrillia sp.	53	18	15	7	0	0	0	8	4	1	0	0	0
Gemmula granosa	52	23	9	2	0	0	0	12	5	1	0	0	0
Gemmula cassinella	132	74	14	5	0	0	0	30	6	2	0	0	1
Daphnella ryukyuensis	91	53	12	3	1	0	0	12	8	1	1	0	0
Coronasyrinx takabanarensis	36	12	5	1	0	0	0	12	4	2	0	0	0
Makiyamaia coreanica	18	4	4	1	0	0	0	8	1	0	0	0	0
Pseudolatirus yonabaruensis	26	6	6	3	1	0	0	6	3	1	0	0	0
Hindsia solida	64	19	15	10	0	0	0	9	8	3	0	0	0
Hindsia takabanarensis	41	22	14	1	0	0	0	2	1	1	0	0	0
Cancellaria yonabaruensis	128	65	34	12	4	0	0	9	4	0	0	0	0
Euspira cf. *pallida*	152	113	17	1	0	0	0	19	2	0	0	0	0
Natica aff. *stellata*	18	14	1	0	0	0	0	3	0	0	0	0	0
Natica sp.	67	46	2	0	0	0	0	19	0	0	0	0	0
Naticarius cf. *niasensis*	30	18	0	0	0	0	0	12	0	0	0	0	0

Sum of the series in equation 5 can be further simplified as:

$$\mathrm{let}(x) = [1 - \Gamma(x,r)/\Gamma(x)](1-p)^{x-1}p, \qquad (6)$$

where $\Gamma(x)$ and $\Gamma(x,r)$ are complete and incomplete gamma functions, respectively. Now we have to incorporate the effect of SP. Since predation of hermit crabs in shells with repaired breaks produces new, unrepaired breaks, the probability distributions in shells with x number of repaired breaks ($=\mathrm{SUB}(x)$), and the $x-1$ number of repaired and one unrepaired breaks ($=\mathrm{LET}(x)$), are described as:

$$\mathrm{SUB}(x) = (1-\alpha)\,\mathrm{sub}(x) \qquad (7)$$

$$\mathrm{LET}(x) = \mathrm{let}(x) + \alpha\,\mathrm{sub}(x-1) \qquad (8)$$

Our data can be applied to these final expressions. We found the best-fit parameters by the least-squared method among three-dimensional parameter grids with steps of 0.05 from 0 to 1 for α and p, and from 0 to 10 for r. All computations were performed with Mathematica 3.0 software (Wolfram Research) on a standard PC. The p, r and α estimated from our data are shown in Table 1. Based upon equations 4 and 7, the shell repair frequencies obtained from the ''percent with scars method (F_1)'' and that from the ''scars per shell method (F_2)'' in previous studies can now be described as:

$$F_1 = 1 - e^{-r(1-p)} \quad \text{and} \qquad (9)$$

$$F_2 = r(1-p) \qquad (10)$$

This shows that the repair frequencies are simply generated as a function of r and p.

Discussion and conclusions

We employed the two methods to 12 species (*H. solida*, *Natica* sp. and *N.* cf. *niasensis* were not applicable for the endobiont method), and the incidence of SP by the model method falls within the range of SP by the endobiont method for 10 species (Table 1: *E.* cf. *pallida* and *Natica* aff. *stellata* are slightly out of this range, most probably due to the small sample size for the endobiont method), which suggests that our two methods are appropriate. However, the results of our analyses are still biased because the severely fragmented shells were not included. We assume that the SP is involved more than the results because the frequency of pagurized shell is higher in the severely fragmented shells (53%; we only examined shells with apical whorls) than in the counted shells (21%). Repeated occupation by hermit crabs and their inability in shell repair result in further accumulation of peeled breaks (SP) in dead gastropod shells. Additionally, hermitted shells (mostly surface dwellers) may have more potential for encounters with the predators than live, burrowing snails.

Our study, uncomplicated as it is, has expressed for the first time the importance of SP for the fossil gastropod assemblages and evaluated SP and PP quantitatively. In elongate shells (e.g., *T. shikoensis* and four turrid species), the shell peelings are largely attributed

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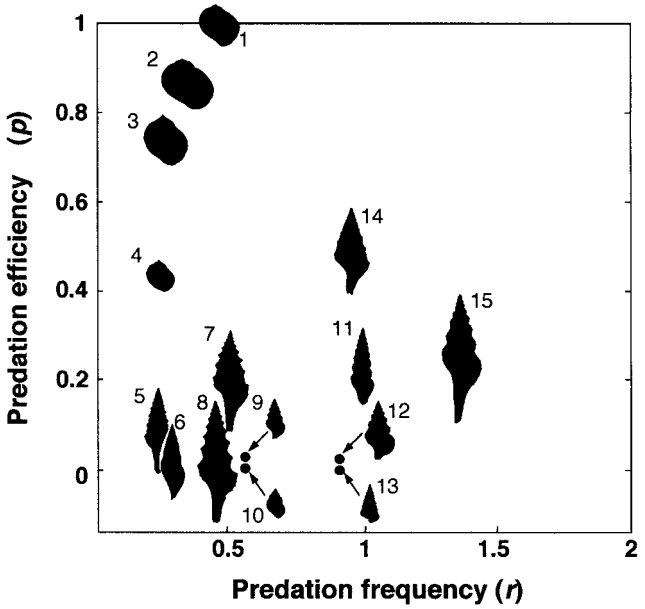


Figure 5. Predation efficiency (p) and predation frequency (r) for 15 gastropod species from Shinzato Formation. Data from Table 1. Abbreviations: 1, *Naticalius* cf. *niasensis*; 2, *Natica* sp.; 3, *Natica* aff. *stellata*; 4, *Euspira* cf. *pallida*; 5, *Gemmula cassinella*; 6, *Daphnella ryukyuensis*; 7, *Coronasyrinx takabanarensis*; 8, *Gemmula granosa*; 9, *Hindsia takabanarensis*; 10, *Cancellaria yonabaruensis*; 11, *Splendrillia* sp.; 12, *Hindsia solida*; 13, *Trochocerithium shikoensis*; 14, *Makiyamaia coreanica*; 15, *Pseudolatirus yonabaruensis*.

to predation on hermit crabs (SP) irrespective of the very high frequencies of shell repairs, whereas they are the reverse for four spherical naticid shells. The predation lethality (p values in the model method) is significantly correlated with shell elongation (Figure 5 and Table 1, $r^2 = 0.635$, $p < 0.005$), further supporting the notion that shell elongation is an anti-predatory adaptation in gastropods (e.g., Vermeij, 1987). This is evidently due to the fact that the elongate shells are less vulnerable to crab predation than the spherical shells, because of the deep retraction of the soft animal into the shell and the narrowness of the apertural opening that prevents the insertion of claws (e.g., Vermeij, 1987). Due to this effect, sublethal repaired breaks are greater in number on elongate shells than on spherical shells (Schindel *et al.*, 1982). This is shown well in *Daphnella ryukyuensis* (elongate) and *Natica* sp. (spherical), where both were equally attacked 0.30 time during their lifetime, but the incidence of repaired breaks for the former is nearly six or seven times greater than for the latter in the ''percent with scars method'' and ''scars per shell method,'' respectively (Table 1).

The results of this study strongly imply that the frequency of shell repair is also strongly controlled by the composition of shell morphotypes and their abundance in gastropod assemblages, and suggest reconsideration of the history of crushing predation based on shell repair. The more the number of species with elongate shells in gastropod assemblages, the higher the incidence of shell repair. The evolutionary history of gastropods shows that during the Paleozoic gastropod assemblages consisted mainly of species whose shell architectures are thought to be vulnerable to crushing predation, including uncoiling, planispiral, rounded and trochiform (i.e., ''archaeogastropods''), and that the elongate shells resistant to crushing predation (i.e., many caenogastropods) have increased gradually in proportion through geologic times (Sohl, 1977; Schindel *et al.*, 1982; Vermeij, 1987). It is therefore possible that the incidence of sublethal shell repair has increased gradually through geologic time due to the increase of elongate shells. To avoid the effects of shell architecture and to evaluate the history of crushing predation correctly, we should deal with changes in repair incidence by analyzing taxonomic groups with similar shell architectures. Such studies have been undertaken only on terebrids, turritellids, naticids, and conids (Vermeij *et al.*, 1980; Allmon *et al.*, 1990; Dietl and Alexander, 1998; Alexander and Dietl, 2003). These studies did not show any obvious trends in the repair frequency, which synchronize with one another.

We have not yet employed our methods rigorously to shallow marine, soft-bottom gastropod assemblages. We presume however that the SP is also dominant in such environments because hermitted shells are so common there (e.g., Simoyama, 1985). The endobiont method based on *H. commensalis* and the ''apical drill holes'' appears to be difficult to apply to shallow marine, soft-bottom gastropod assemblages because the two endobionts are usually uncommon in shallow marine soft bottoms than in deepwater bottoms (Ishikawa and Kase, unpublished data). However, the endobiont method appears to be applicable by detecting other endo- and/or epibionts common in shallow waters being useful for recognizing hermitted shells (Walker, 1992). In contrast, our model method is highly useful to evaluate the shell fragmentation even for shallow marine, soft-bottom assemblages if bulk material from outcrops unbiased by collectors is available. In this case, we can only evaluate the PP because the physical shell fragmentation is not ignorable under such high-energy environments (but see Oji *et al.*, 2003). A preliminary analysis of shell fragmentation in two cerithiid gastropods from an inter-

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tidal sand flat of Palau shows that *Clypeomorus petrosus* (N = 100) and *Rhinoclavis aspera* (N = 53) have unexpectedly low PP values (3% and 0%, respectively) in spite of the high frequencies of peeled shells (54% and 57%, respectively). This suggests that postmortem breakage is also an important agent for shell fragmentation in shallow-water gastropod assemblages as well as in deep-sea assemblages (Ishikawa and Kase, unpublished).

The fossil record of hermit crabs (Paguroidea) dates back to the early Jurassic (Briggs *et al.*, 1993) and the direct evidence of hermit crabs occupying gastropod shells dates from the late Cretaceous (Mertin, 1941). Crab predation on hermit crabs therefore may have occurred since the late Mesozoic. In conclusion, by applying our new methods, the predation intensity (r) and lethality of predation (p) can now be estimated as separate variables in fossil gastropod assemblages, which provides an insight into a more realistic view of the history of this unique biological interaction through deep time.

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