



## ***Lunella* shell damages and epibionts: what are inter-specific relations?**

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*Coastal Ecosystems*, 2018, vol 5, 1-13



# *Lunella* shell damages and epibionts: what are interspecific relations?

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## Abstract

The shells of *Lunella coronatus coreensis* (Récluz, 1853), which are commonly infested by different epibionts including in particular an alga *Pseudocladophora conchophora*, are often found to be physically damaged. There are basically two types of damages: (i) reduction of the peristracum and exposure of the inner layers, termed 'abrasion damage' herein, and (ii) perforation scars. Our study revealed that over 40% of individuals had abrasion damages at all four sampling sites in western Kyushu, while perforation scars occurred in <40% of individuals at these sites. Individuals with abrasion damages tended to be larger in size and had a significantly lower coverage of *Pseudocladophora* compared with those without abrasion damages. Similar trends were also observed when abrasion damages were categorized into different levels. In contrast, there was no significant difference in host size between groups with/without scar damages. *Pseudocladophora* coverage was significantly different among individuals with different levels of scar damage. Red algal biomass density was significantly higher in damaged than in non-damaged individuals. The result of GLM indicated that shell diameter and *Pseudocladophora* cover were strongly related to the levels of abrasion damage, and red algal biomass density might be related to increasing shell area with scar damages. The present study suggests linkages between high proportions of shell damages in natural *Lunella* populations and several biotic factors including infestation by epiphytes.

**Keywords:** bioerosion; interspecific interactions; intertidal stony shore; parasite; sessile organisms

## Introduction

Understanding interspecific relationships is one of the key themes in community ecology and evolutionary ecology. Epibiosis, in which two or more organisms grow on the other organism, is a ubiquitous form of interspecific relationship, especially in space-limited communities such as tropical rain forests and marine benthos (Dittman & Robles 1991). Epibionts could affect their hosts both positively and negatively. Host organisms may gain benefit in the form of protection against abiotic hazards such as desiccation and irradiation (Penhale 1977; Wahl 1996). Reduction in predation pressure is one of the most common positive effects attributed to epibionts (Bloom 1975; Vance 1978; Pitcher & Butler 1987). Some species of sponges effectively enhanced the escape ability of host scallops against predatory starfish by camouflaging or increasing their swimming efficacy by altering the shell surface textures (Bloom 1975). Laudien & Wahl (1999) revealed epibiotic hydrozoans and algae protected mussels from predation by reducing the palatability of host individuals compared with unfouled ones.

Epibionts are not always works amicable for host organisms, but also functioned as hindrances for the host organisms. Some epibionts are harmful to hosts as they reduce the hosts' mobility, growth and reproduction, and

increasing predation risks (e.g. Dittman & Robles 1991; Wahl 1996, 1997; Buschbaum & Reise 1999; Fernandez-Leborans *et al.* 2009; Hidalgo *et al.* 2010). Overgrowth of epibiotic barnacles decreased the crawling speed of intertidal gastropods (Buschbaum & Reise 1999), and macroalgal fouling over the mole crabs facilitate birds to find prey (Hidalgo *et al.*, 2010). Barnacles on mussel shells decrease the defensive behaviour of the host and increase its vulnerability to predation (Johansson 2010).

Host-epibiont relationship may also impact on ecological communities (Wahl 2008). Infestation by epibiotic bryozoans and bacteria decreased kelp's survivorship and facilitate the establishment of an invasive green algae *Codium fragile* under certain environmental conditions (e.g. Kupper *et al.* 2002; Levin *et al.* 2002). Epibiotic sponges on mangrove roots help nutrient supply and inhibit the colonization by isopods whose boring behaviour increases the risks of mangrove toppling in storms (Hay *et al.* 2004). Epibionts may also affect carbon cycling in estuarine systems by increasing the total annual primary production (Penhale & Smith 1977). While epibiont-host phenomena are widely observed, most are highly plastic and variable among species and local environments (Laudien & Wahl 1999; Fernandez-Leborans 2013) and the relationship is often described as a "non-symbiotic relationship" (Wahl 1989; Wahl & Mark 1999; Johansson 2010).

In marine benthos, the shells of gastropods and crustaceans are often used as valuable hard substrates by epibionts (e.g. Wahl 1989; Vasconcelos *et al.* 2007; Hidalgo *et al.* 2010; Johansson 2010). The shell of an intertidal gastropod, *Lunella coronatus coreensis* (Récluz 1853), for example, is used by several species of epibionts including an alga *Pseudocladophora conchopheria* (Sakai 1964). *P. conchopheria* is a filamentous green alga specific to the shell of *L. coreensis* (Matsuyama, Aruga & Tanaka 1999). Details of their relationship is still obscure due to a paucity of studies to date.

Recent field observation revealed that the majority of *L. coreensis* shells on rocky shores of southern Japan were physically damaged. These damages were of two types: 1) abrasion damage, loss of the peristracum and the exposures of inner layers, and 2) perforation scars. As these shell damages are possibly caused by epibiotic infestation, clarification of the relationships between epibionts and *L. coreensis* is likely to improve our understanding of the effects of epibiosis. In this study, we focus on an interspecific relationship between epiphytes and their host gastropods to clarify whether epibionts negatively affect *L. coreensis* by causing shell damages.

## Materials and Methods

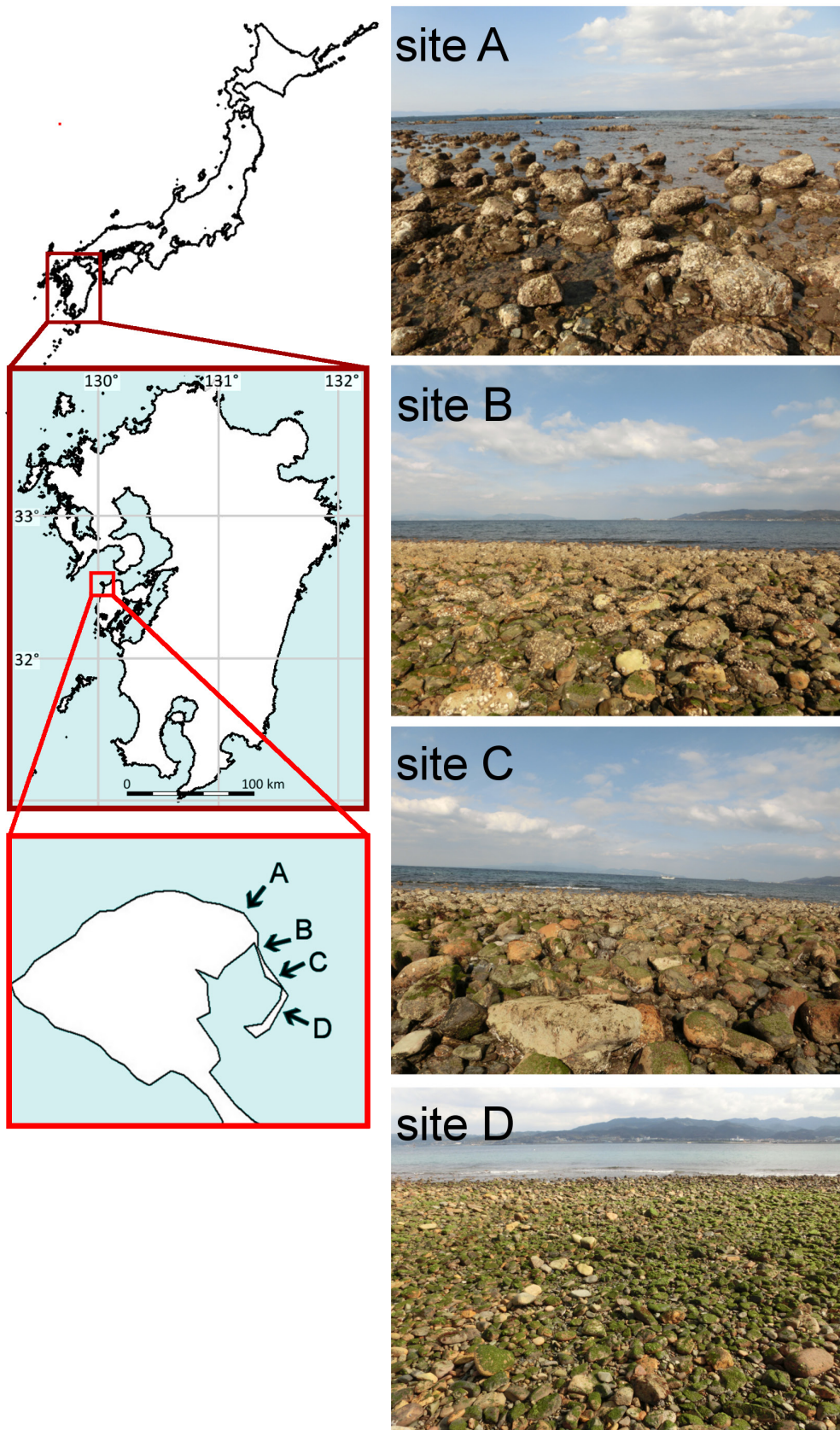
### Study organisms

*Lunella coronatus coreensis* (Récluz 1853) (hereafter *Lunella*) is an intertidal mollusc commonly observed in southern Japan. Their distribution extends to a wide area in the west Pacific including southern part of Hokkaido, Korea and even India (Yukihira *et al.* 1995).

*Pseudocladophora conchopheria* (Sakai 1964) (hereafter *Pseudocladophora*) is one of the miniscule species of Cladophorales with its total frond height <1 mm. The species ranges from the southern part of Hokkaido, through both the Pacific and Japanese Sea coasts to the Okinawa Islands. It was also reported from Korea (Sakai 1964; Kang 1966; Matsuyama, Aruga & Tanaka 1999). Although *P. conchopheria* has a wide distributional range, their occurrence is strictly restricted to the shell surface of *L. coreensis* (Sakai 1964; Matsuyama, Aruga & Tanaka 1999).

Other non-species-specific epibionts found on *Lunella* include sessile polychaetes (*Neodexiospira* sp. and *Pomatoleios kraussii*), *Amphibalanus* sp., some species





**Fig. 1** Map of (top to bottom) Japan, Kyushu, and the Tomioka peninsula of Amakusa-Shimoshima Island, with views of four sampling sites (site A-D indicated by arrows) on the Magarisaki spit. (Map created using the software "Hakuchizu KenMap ver. 9.1").

of red algal turfs like *Gelidium divaricatum* and *Gelidium pusillum*, crustose coralline algae, and some species of small limpets (*Hipponix conica* and juvenile of *Patelloida heroldi*). In this study, we focused on *G. divaricatum* and *G. pusillum*, because of their higher occurrence and coverage compared with other epibionts (Osawa, unpublished data).

#### Study site and sample collections

This study was conducted at the Magarisaki spit (32° 53'N, 130° 04'E) on Amakusa Shimoshima Island, Japan (Figure 1). This subtropical rocky/stony shore with sandy bottom is relatively sheltered and gently sloped, with the substrate stone sizes varying from 10–20cm (cobbles) to >70 cm (boulders). Intertidal communities on Magarisaki stony shores are dominated by several species of molluscan grazers including *Monodonta labio*, *Nerita japonica* and species of limpets (Takada & Kikuchi 1990, 1991; Tokeshi, Ota & Kawai 2000; Takada 2001).

Samples of *Lunella* were collected at four sites (A–D) along the shore (separated by 250–500m, Figure 1) during the spring tide in June 2014. Coastal currents run predominantly from site A to site D. Based on Keddy (1982),

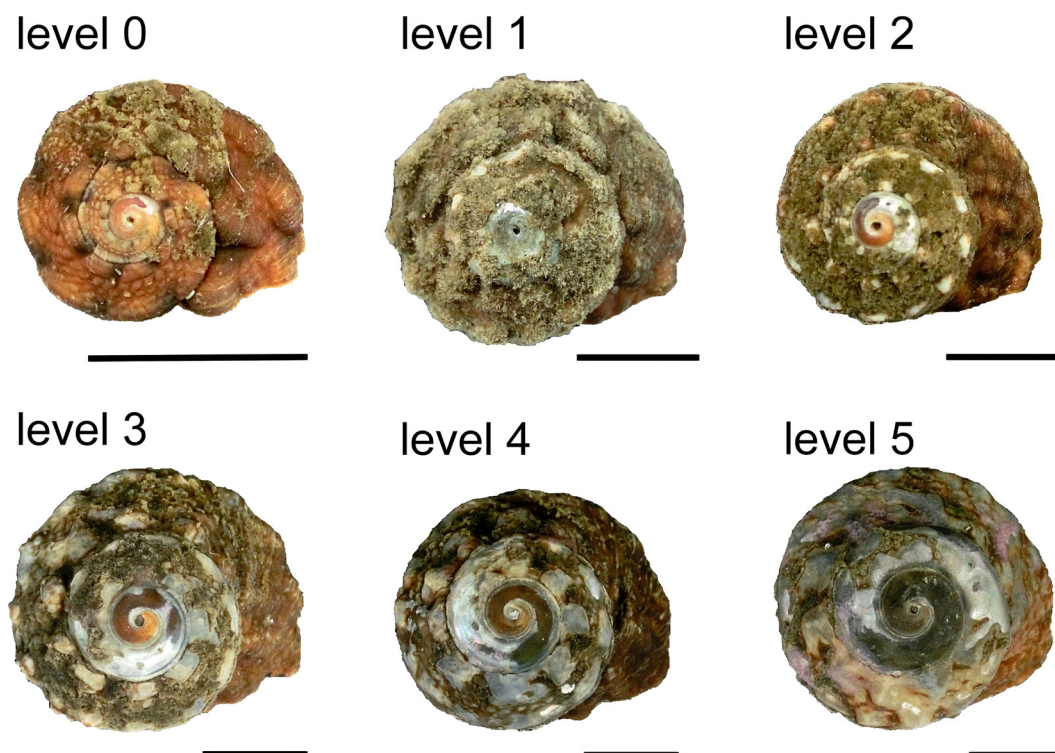
total fetch distance (hereafter fetch), the maximum length of open water that wind can travel, were calculated as the indicators of wave exposures of each sampling site. Site A had the longest fetch (354km) and site D the shortest (64km), indicating that A is in the most exposed condition and site D the least exposed. Site C had the second longest fetch (280km), followed by site B (127km).

More than 200 individuals of *Lunella* were randomly collected at each site at the fixed tidal level of 70–90cm. On return to the laboratory, individuals were separately fixed within the 10 % neutralized formalin seawater.

#### Measurements

Shell diameter of each *Lunella* individual was measured to the nearest 0.01 mm with digital callipers. Shell diameter referred to the longest linear distance from the side of the outer lip to the top of the body whorl on the opposite side. For individuals with protuberances on their shells, the first complete protuberance beside the outer lip was used as a starting point of measurement.

Photographs of all measured individuals were taken from the apical side for assessing damage levels and



**Fig. 2** Different levels of abrasion damage (0–5) with top (apical) views of *Lunella*. Bars are 1 cm.

**Table 1** Classification of abrasion damage levels, with reference to reduction in periostracum, and the conditions of apex and of tubercles. Apex; ○, no reduction of yellow or light-orange apex; △ some parts of apex reduced; ×, apex heavily damaged and mostly flattened. Tubercles; ○, no tubercles reduction in any part of the whorl; △ some parts of tubercles reduced; ×, tubercles heavily damaged and flattened. The positions of abraded tubercles were indicated in parenthesis.

Level	0	1	2	3	4	5
periostracum reduction	0%	< 10%	≤ 20%	< 50%	> 50%	> 80%
apex	○	△	△	×	×	×
tubercles	○	△ (penultimate whorl)	×	×	×	×
			(penultimate whorl)	(penultimate whorl and suture)	(penultimate whorl and suture)	(penultimate whorl and suture)

*Pseudocladophora* coverage. For individuals infested by red algae, *G. divaricatum* and *G. pusillum*, photographs were taken before and after the removal of red algae. The degree of shell abrasion damages was visually categorized into 6 levels based on the conditions of the whorl periostracum, tubercles and the apex (Table 1; Figure 2).

Existence of scar damages was determined only if the small holes were visually observable on the shell surface (Figure 3a). Because most of the scars were concentrated around the apical side, assessment of the damaged area was conducted using the top (apical) view photographs. The shell area on the apical side was separated into 9 sections (Figure 3b) (modified from Yamada, Wada & Ohno 2003). The sections with scars were noted and the total area with scar damages was used as a criterion for damage levels. The photographs after red algal removal were used for damage categorization. Individuals with abrasion damage level 0 but with holes on the shell surface and those with abrasion damage levels 1-5 but without holes indicated that these two types of damages separately occurred.

30 *Lunella* individuals were randomly selected from each site to quantify *Pseudocladophora* coverage. In the case of *Lunella* shells where red algae (*Gelidium* spp.) also occurred, *Pseudocladophora* cover was measured after the removal of red algae. *Pseudocladophora* were visually differentiated from shell layers on photographs by selecting the representative colours using GIMP 2 software. If the pixels of selected colours were less than 1% of the total shell pixels, they were excluded from *Pseudocladophora* pixels. *Pseudocladophora* coverage ( $P$ ) was calculated as

$$P (\%) = 100 \times \text{Pseudocladophora pixels} / \text{total shell pixels} \dots (\text{Eqn. 1})$$

Red algae were removed from shell surface, dried in an incubator (ESPEC Gravity Oven LG-122) for 12-24 hours at 70-80°C and weighed using a digital balance (Sartorius BP211D). Red algal biomass density ( $Rd$ ) was obtained as dry weight of red algae divided by shell surface area. Shell surface area ( $Sa$ ) was estimated using the following approximation (modified from Thomsen 2004, confirmed in [www.numericana.com](http://www.numericana.com): Surface Area of an Ellipsoid (<http://www.numericana.com/answer/ellipsoid.htm>), December 19, 2017) of a spheroidal surface with semi-diameter ( $Sd$ ) and semi-height ( $Sh$ ) (the axis of rotation), thus,

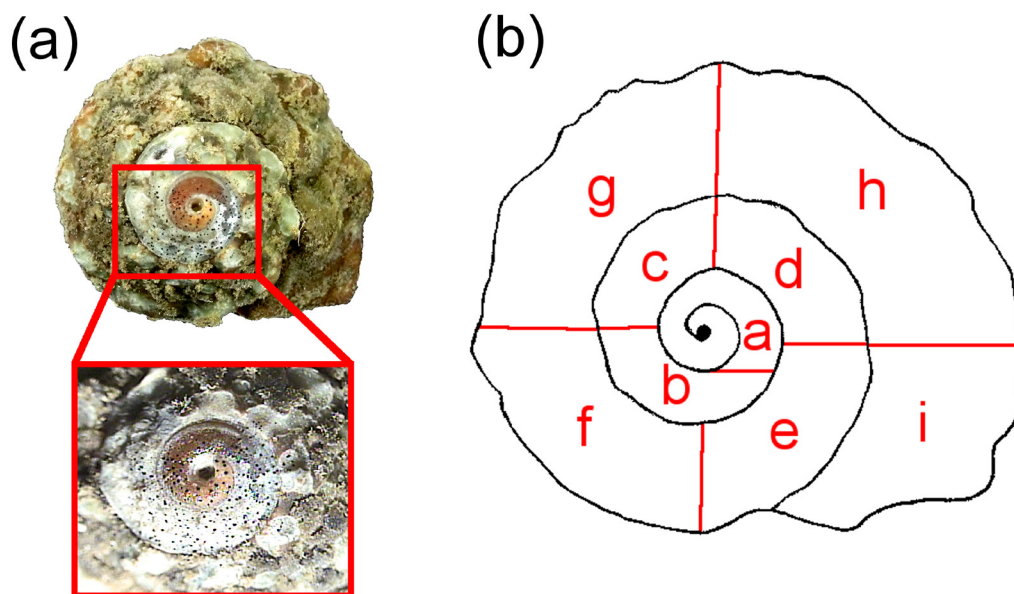
$$S_a \approx 4\pi \left( \left[ 2x(S_d Sh)^{1.6075} + S_d^{3.215} \right] / 3 \right)^{1/1.6075} \quad (\text{Eqn. 2})$$

#### Statistical analysis

The size differences of *Lunella* individuals from four sampling sites were tested using the Kruskal-Wallis rank sum test. Proportions of individuals with/without different damage types and the proportion of each damage level were enumerated per sampling site. Fisher's exact test was utilized to test whether categorized groups were proportionally different among sampling sites. Post-hoc multiple comparisons were conducted using extended pairwise comparisons for proportions, following Aoki (2010).

All collected specimens were pooled for comparison of shell diameter, *Pseudocladophora* coverage and the red algal biomass density ( $Rd$ ) between individuals with/without abrasion and scar damages. Mann-Whitney's U tests were used to test differences in size distributions. Host size differences, *Pseudocladophora* coverage and algal biomass density ( $Rd$ ) were compared among abrasion





**Fig. 3** (a) Example of an individual with scars, and (b) sections of shell areas for identifying scar positions.

damage levels and the scar damage levels. Homogeneity of variance was checked for every comparison using the Bartlett test. If homogeneity was rejected, Kruskal-Wallis rank sum test was employed; otherwise, one-way analysis of variances (ANOVA) was employed. Holm-adjusted pairwise comparisons using t-tests with pooled SD were conducted for the post-hoc multiple comparisons, only if the result of Kruskal-Wallis test and one-way ANOVA was significant. Categories with only one individual were excluded from the statistical analysis.

Models with different damage levels were constructed through generalized linear model (GLM) selecting an optimum model based on the Akaike Information Criterion (AIC; Akaike 1973) using R, ver. 3.1.2. Models with AIC difference from the smallest AIC ( $\Delta AIC$ ) being  $< 2.0$  were also included in the analysis. For model prediction of abrasion damages, the ranked factorial variable of “abrasion damage level (0-5) ( $A$ )” was used as a response variable. “Shell diameter” in mm ( $D$ ), “total fetch distances” ( $F$  km), as the indicator of geographical characteristic, “*Pseudocladophora* coverage” in % ( $P$ ), “red algal biomass density” in  $\text{mg}/\text{mm}^2$  ( $Rd$ ), and the “scar damage level (0-7)” ( $S$ ) as ranked factorial measure were included as explanatory variables. The binomial distribution and the logit function were assumed for the model,

$$\text{logit}(A) = \alpha_0 + \alpha_1 D + \alpha_2 F + \alpha_3 P + \alpha_4 Rd + \alpha_5 S \quad (\text{Eqn. 3})$$

Similarly, for the models of scar damages, “scar damage level” was used as the ranked factorial response variable ( $S$ ), and five variables (shell diameter ( $D$ ), fetch distance ( $F$ ), *Pseudocladophora* coverage ( $P$ ), red algal biomass density ( $Rd$ ), and abrasion level ( $A$ )) were incorporated as explanatory variables based on the logit link function with the binomial distribution, thus,

$$\text{logit}(S) = \beta_0 + \beta_1 D + \beta_2 F + \beta_3 P + \beta_4 Rd + \beta_5 A \quad (\text{Eqn. 4})$$

## Results

A total of 840 *Lunella* individuals from the four sites (A: 208, B: 208, C: 213, D: 211) were analysed. Mean shell diameter was significantly different among four sampling sites (Kruskal-Wallis rank sum test,  $\chi^2 = 319.28$ ,  $df = 3$ ,  $p < 0.001$ ). The largest mean shell size ( $21.9 \pm 2.0$  mm) occurred at site A, followed by site C and site B, ( $19.3 \pm 2.7$ , and  $18.4 \pm 2.5$  mm, respectively) (Figure 4). The smallest mean shell size was observed at site D ( $16.5 \pm 2.7$  mm).

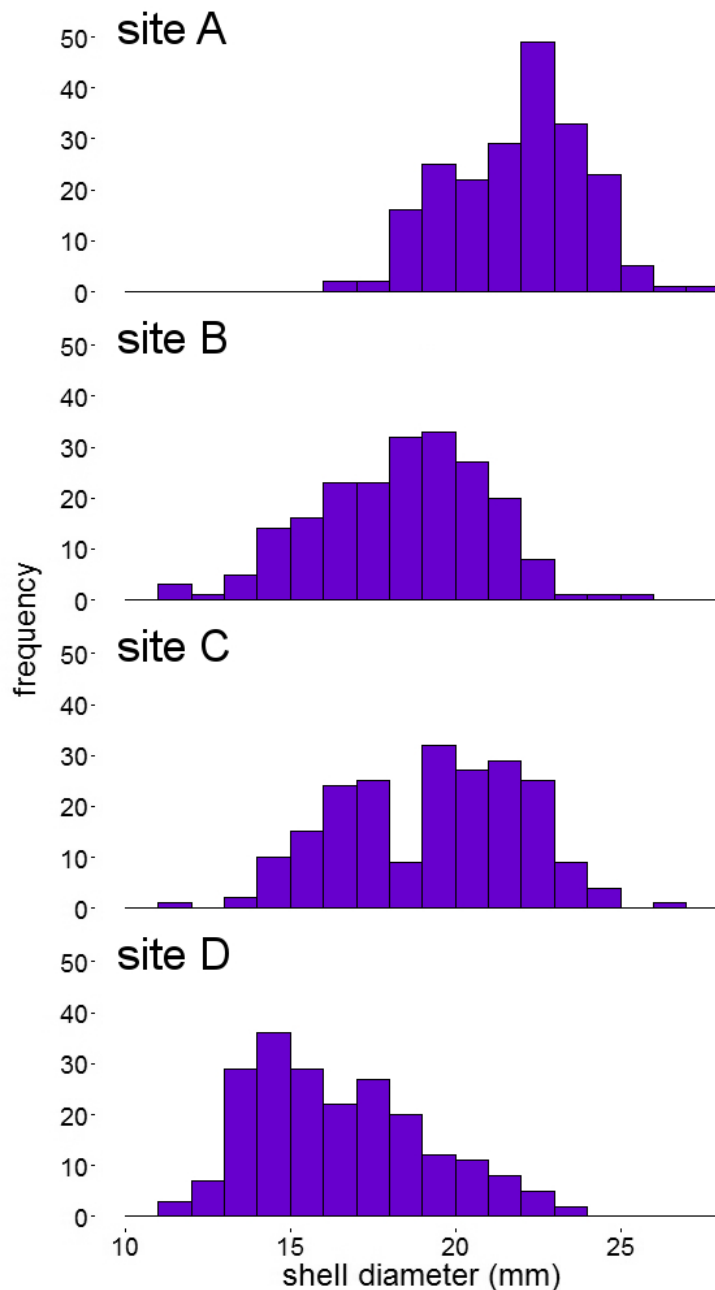


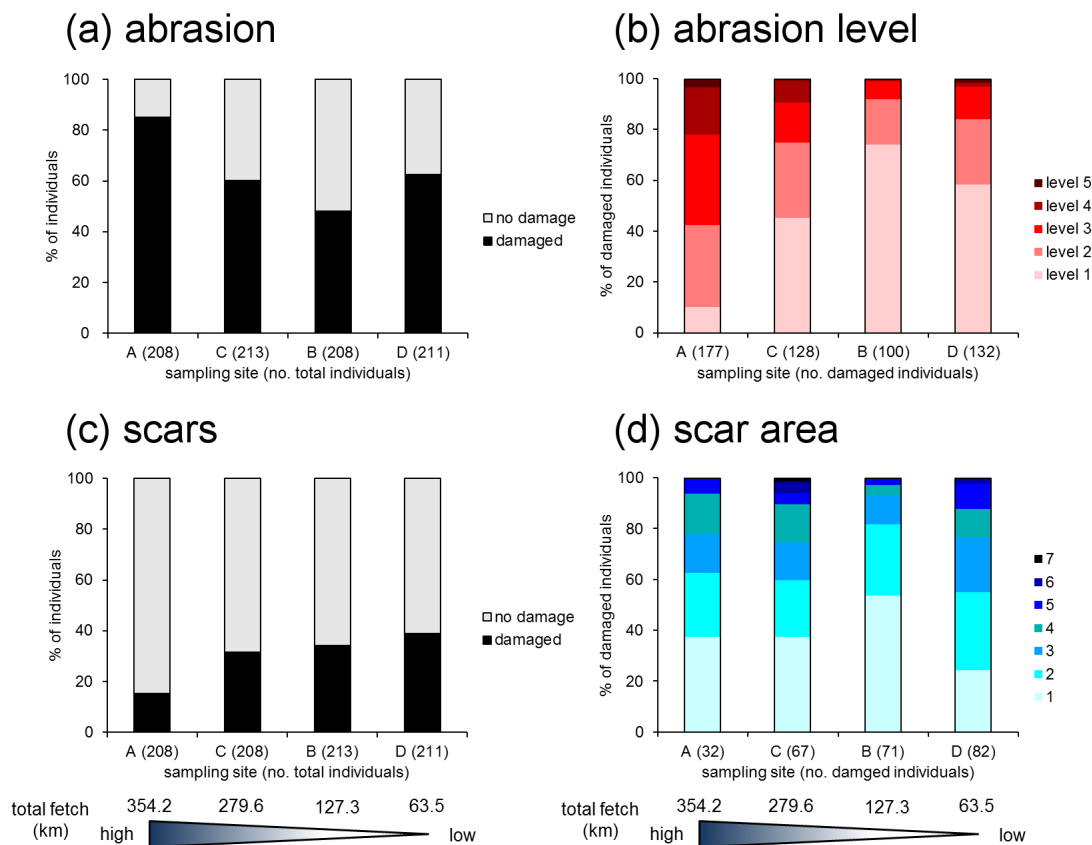
Fig. 4 Size frequency distributions of *Lunella* at sampling sites A - D.

The proportions of individuals with abrasion damages were more than 40% at all four sampling sites (Figure 5a). The highest proportion of damaged individuals was observed at site A (85.1%), and the lowest at site B (48.1%) with all site pairs showing significant differences except site C vs D (Fisher's exact test,  $p < 0.001$ ). The highest proportions of individuals with heavy abrasion damages (level 3-5) were observed at site A (49.0%), and the lowest at site B (3.9%) (Figure 5b). Less than 40% of individuals had scar damages at all sites (Figure 5c). Site D had the highest proportion of individuals with scars (38.9%), and site A the lowest (15.4%). The result of pairwise comparisons showed that site

A had a significantly lower proportion of individuals with scars than other sites (Fisher's exact test,  $p < 0.001$ ). There were no significant differences between sites B through D. The proportion of individuals with level 2 or above in scar damages was the highest at site D (75.6%) and the lowest at site B (46.5%) (Figure 5d).

Body size (diameter) of individuals with abrasion damages was significantly larger than those without (Mann-Whitney's U test,  $W = 33174$ ,  $p < 0.001$ ) (Figure 6a). For scar damages, though there was a significant difference between groups with/without damages (Mann-Whitney's U test,  $W = 67136$ ,  $p = 0.031$ ), the peaks occurred in 19-22 mm size



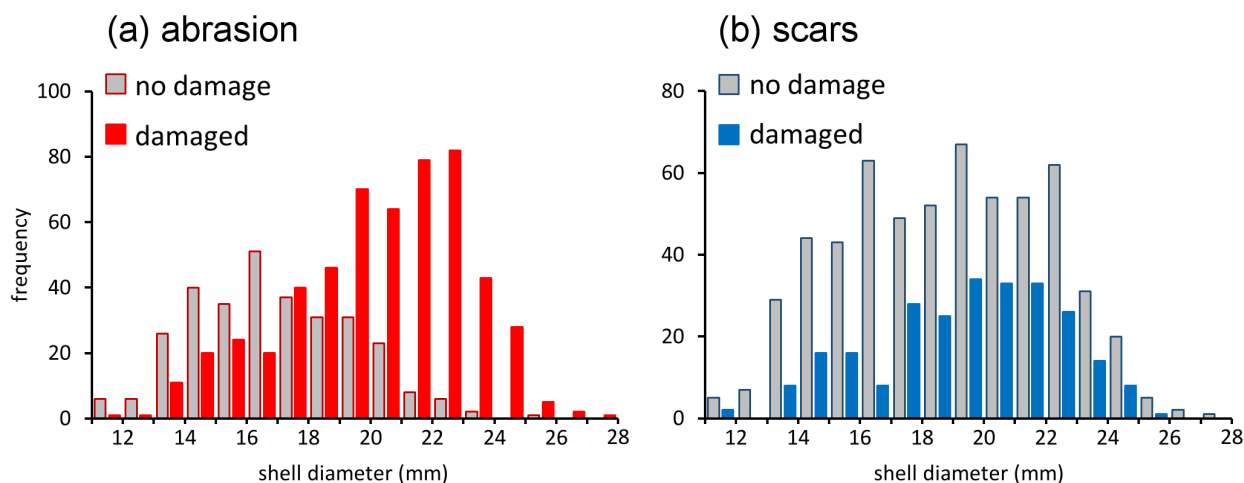


**Fig. 5** (a) Proportion of *Lunella* with (black)/without (gray) abrasion damage, and (b) proportions of individuals with different levels of abrasion damage (level 1-5 with light to dark red gradations). (c) Proportion of *Lunella* with (black)/without (gray) scar damages, and (d) proportions of individuals with different levels of scar damage (level 1-7 with light to dark blue gradations). Number in parentheses on the x axis in (a) and (c) is the total number of individuals captured at each sampling site. Number in parentheses on the x axis in (b) and (d) is the total number of individuals with damages. Horizontal axis is the four sampling sites in order of the size of total fetch (km).

class (Figure 6b).

The median shell diameter gradually increased with damage level (Kruskal-Wallis test,  $\chi^2=354.23$ ,  $df=5$ ,  $p<0.001$ ) (Figure 7a). The result of pairwise comparisons showed these differences were significant among all categories from level 0-4, except between levels 4-5. *Pseudocladophora* cover was significantly lower in individuals with abrasions (mean, 55.7%) than in those without damages (64.9%) (Mann-Whitney's U test,  $W = 4767.5$ ,  $p<0.001$ ). Further, *Pseudocladophora* coverage was highest in individuals with no abrasion damage and decreased with increasing damage levels (one-way ANOVA,  $F = 9.944$ , num.  $df = 5$ , denom.  $df = 176$ ,  $p<0.001$ ) (Figure 7b). Post-hoc multiple comparisons showed significant differences among all pairs except those of level 4-5. Mean red algal biomass density was not significantly different among abrasion levels (Kruskal-Wallis rank sum test,  $\chi^2 = 0.603$ ,  $df = 3$ ,  $p=0.896$ ) (Figure 7c).

Shell diameter of the individuals with scar damages was not significantly different among damage levels (one-way ANOVA;  $F=1.378$ , num.  $df = 6$ , denom.  $df = 832$ ,  $p = 0.221$ ) (Figure 7d). *Pseudocladophora* cover was slightly different among the scar damage levels (one-way ANOVA,  $F = 2.576$ , num.  $df = 4$ , denom.  $df = 175$ ,  $p=0.039$ ), but none of them were significant in pairwise comparisons (Figure 7e). Red algal biomass density (*Rd*) was significantly higher (mean,  $9.7 \mu\text{g mm}^{-2}$ ) in individuals with scar damages than in those without ( $3.0 \mu\text{g mm}^{-2}$ ) (Mann-Whitney's U test,  $W = 1473$ ,  $p<0.001$ ). Although *Rd* values heavily fluctuated among different damage levels, none of these differences were significant (Kruskal-Wallis rank sum test,  $\chi^2 = 3.050$ ,  $df = 5$ ,  $p=0.692$ ) (Figure 7f). These results suggest that the biomass of red algae was significantly greater in individuals with scar damages, but red algal biomass density did not scale with damage levels.



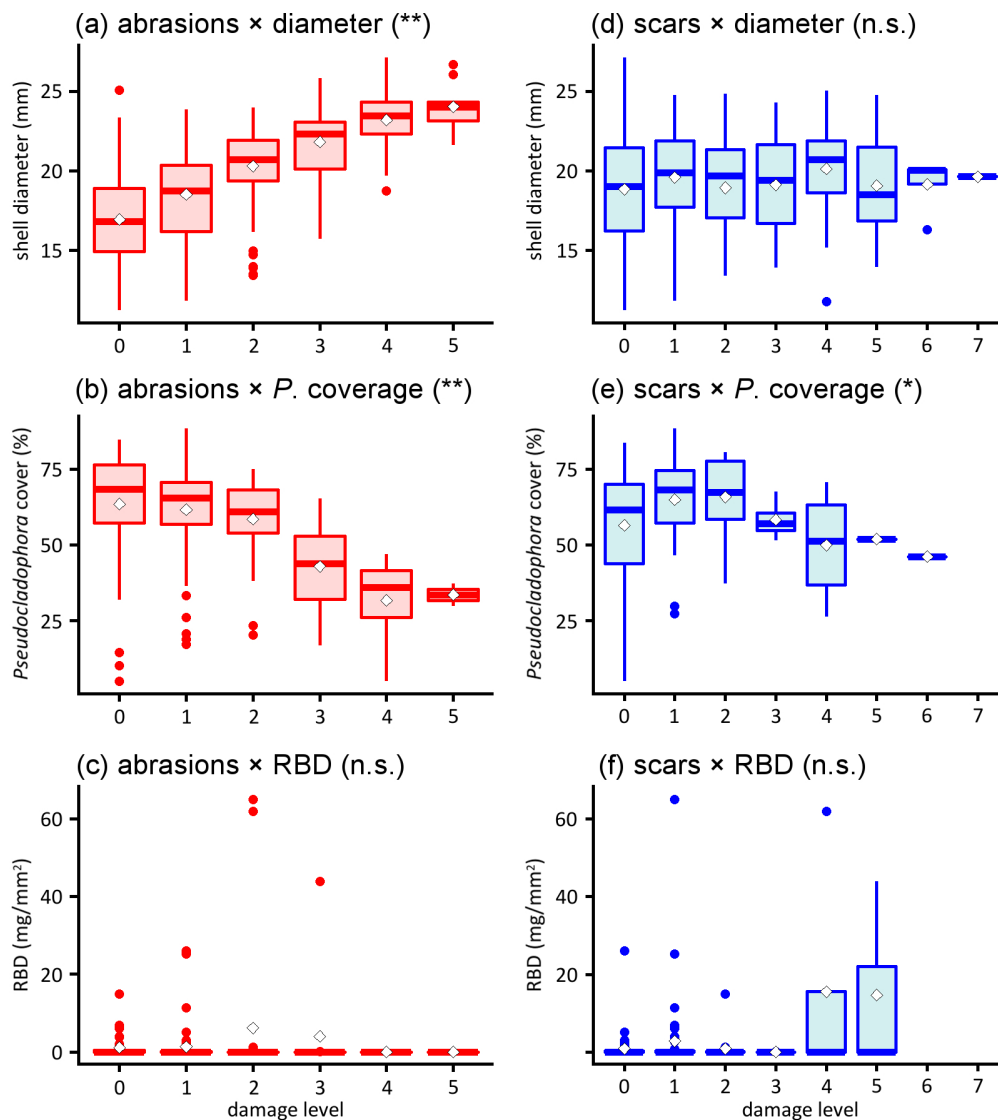
**Fig. 6** Size frequency distributions of *Lunella* individuals (a) with/without abrasion damages, (b) with/without scar damages.

A GLM analysis model with shell diameter and *Pseudocladophora* coverage (model  $D + P$ ) was selected as the minimum AIC model, plus three models with small values of  $\Delta$ AIC (Table 2a). Shell diameter and *Pseudocladophora* coverage were included constantly as explanatory variables of all selected models. Moreover, coefficients of those variables were significant in all models ( $Pr |z| < 0.05$ ), except for *Pseudocladophora* coverage in model  $D + P + Rd$ , indicating significant effects of shell diameter and *Pseudocladophora* coverage on the levels of abrasion damage. The directions of the effects toward the abrasion damage levels were different between the variables: the coefficients notably in the minimum AIC model ( $D + P$ ), shell diameter had a positive (0.514) while *Pseudocladophora* coverage had a negative effect (-0.055). For scar damages, the model with  $Rd$  as an explanatory variable was selected for the minimum AIC model (Table 2b). Other three models with *Pseudocladophora* coverage, shell diameter and total fetch distance as other explanatory variables, were selected as the second optimum models with  $\Delta$ AIC < 2.0 (Table 2b).  $Rd$  was the sole explanatory variable that was included in all selected models. Although  $Rd$  was selected as an effective explanatory variable compared with others, none of the coefficients of  $Rd$  was significantly different from zero.

## Discussion

Our results of GLM analysis indicated that the occurrence of two different types of shell damage might be influenced by different factors. For abrasion damages, host shell diameter was positively related and *Pseudocladophora* coverage negatively related to damage levels. These results imply that abrasion level increases with *Lunella* growth which in turn leads to a decrease in *Pseudocladophora* infestation. Yamada, Wada & Ohno (2003) observed newly-colonized *Pseudocladophora* on the growing margin of the shell lip and none around the apex. Additionally, the importance of the periostracum layers for continuous *Pseudocladophora* attachment and colonization has been suggested in several studies (Matsuyama & Aruga 1993; Matsuyama, Aruga & Tanaka 1999; Yamada, Wada & Ohno 2003). This points to a possibility that colonization by *Pseudocladophora* is restricted to the outer layer of *Lunella*, and it is prevented if the periostracum is removed. Morphological comparison of outer and inner layers of non-damaged individuals and the part of abrasion damages might clarify how *Pseudocladophora* colonization is limited with shell damages.

Our field study showed some relations between the environmental conditions and abrasion damages. Individuals at site A had abrasion damages heavily skewed towards higher levels compared to other sites. This may be due to environmental factors either directly causing more abrasion damages or indirectly increasing the proportion



**Fig. 7** Comparison among individuals with different damage levels. (a) Host shell diameter (mm), (b) *Pseudocladophora* coverage (%), and (c) red algal biomass density ( $\text{mg}/\text{mm}^2$ ) with different abrasion damage levels (level 0 – 5) and with different scar damage levels (level 0 – 7) in (d), (e), (f), respectively. Each box defines the 75% and 25% quartile and the median (horizontal bar, while diamond shows the mean); the upper and lower whiskers cover the values that extend the inter-quartile range by no more than 1.5 times. Outliers are shown as filled circles. \*\* $p < 0.01$ ; \* $p < 0.05$ ; n.s. no significant difference by Kruskal-Wallis rank sum test (a, c and f) and one-way ANOVA (b, d, and e).

of damaged individuals by influencing the size distribution of host gastropods. However, our GLM results showed a weak interaction between total fetch distance and abrasion damages. Differences in wave exposure among sites can strongly affect the local distribution of molluscs, as the attachment strength of smaller individuals might be weaker compared with larger individuals. Trussell (1997) revealed individuals of *Littorina obtusata* under wave-exposed environments have larger foot size and show greater

resistance against dislodgement compared with individuals from protected environments. Additionally, we found strong relations between abrasion damages and host shell size. These results suggest that the differences in damage occurrence among the sites might be related to variation in hydrodynamic forces causing non-homogeneous host size distributions.

Beside the importance of host size with respect to abrasion damages, heavy infestation by several epibionts



**Table 2.** Results of model selection with minimum AIC and the models with  $\Delta AIC < 2.0$  using the GLM, for (a) abrasion damage level, (b) total area with scar damages. Explanatory variables included in the models are shown with representative coefficient values. The models were in order with the smallest AIC. Intercept of the regression line is shown; *D*, shell diameter; *F*, total fetch distance of sampling site; *P*, *Pseudocladophora* coverage; *Rd*, red algal biomass density; *A*, abrasion level; *S*, total area with scars. \*\*  $Pr(>|z|) < 0.01$ , \* $Pr(>|z|) < 0.05$ , based on Wald statistics.

## (a) abrasion damage

model	Intercept	Explanatory variables					AIC	$\Delta AIC$
		<i>D</i>	<i>F</i>	<i>P</i>	<i>Rd</i>	<i>S</i>		
<i>D + P</i>	-5.937	0.514**		-0.055*			91.821	0
<i>D + F + P</i>	-5.561	0.555**	-0.005	-0.059*			91.845	0.024
<i>D + P + Rd</i>	-5.726	0.487**		-0.052	0.046		92.404	0.583
<i>D + F + P + Rd</i>	-5.460	0.527**	-0.004	-0.056*	0.033		93.123	1.302

## (b) scar area

model	Intercept	Explanatory variables					AIC	$\Delta AIC$
		<i>D</i>	<i>F</i>	<i>P</i>	<i>Rd</i>	<i>A</i>		
<i>Rd</i>	-0.485				0.081		97.386	0
<i>Rd + P</i>	-1.960			0.021	0.081		98.533	1.147
<i>D + Rd</i>	-2.556	0.105			0.079		98.734	1.348
<i>F + Rd</i>	-0.338		-0.001		0.078		99.328	1.942

could be another factor affecting abrasion damage. Large individuals tend to be heavily infested by several epibionts, which might increase the drag against water currents. The examples of morphological disturbances due to epibionts have been reported for several host species (Bronmark 1985; D'Antonio 1985; Oswald *et al.* 1984; Wahl 1989; Witman & Suchanek 1984; Vasconcelos *et al.* 2007). Reduction in periostracum layers was observed in dead *Lunella* infested by *Pseudocladophora* (Yamada, Wada & Ohno, 2003). Our results showed strong negative relations between *Pseudocladophora* coverage and abrasion damages, indicating a possibility that *Pseudocladophora* infestation may accelerate abrasion damages of host shells. This point requires further research.

Our GLM analysis indicates that host size had little or no effect on the occurrence of scar damages. For the scar damage levels, red algal biomass density was included as an effective explanatory variable in all selected models, but its coefficient was not significant. This suggests that the infestation of red algae might have some impact on the occurrence of scar damages. Boring sponges are another possibility of shell scars, as sponges of the family Clionidae is known to perforate mollusc shell and coral skeletons (Hartman 1958; Guida 1976; Vblayudhan 1983; Stefaniak, McAtee & Shulman 2005). In a study on the intertidal gastropod *Littorina littorina*, boring damages by

*Cliona* significantly decreased its shell strength and survival rate against predation (Stefaniak, McAtee & Shulman 2005). Other studies also reported the importance of shell properties against predators (Greenfield, Lewis & Hinke 2002; Le Rossignol *et al.* 2011).

Heavy epibiotic infestation can negatively affect hosts not only by inflicting physical damages but also by decreasing host fitness. In periwinkles, both growth rate and fertility were significantly lower in individuals with barnacles or artificial epibionts attached (Wahl 1996, 1997). This was considered to result from more energy being required for locomotion in those individuals. On the other hand, epibionts could operate positively to reduce predation risks for host organisms with chemical or visual camouflage, or being unpalatable (Bloom 1975; Feifarek 1987; Pitcher & Butler 1987; Wahl & Hay 1995; Laudien & Wahl 1999). Moreover, Penhale & Smith (1977) revealed the protective effect of epibionts against desiccation in some intertidal organisms. At this moment, we could not observe any positive effects of the epibionts of *Lunella*. However, if epiphytes function as shelters against predation/desiccation and these effects exceed the negative ones, *Lunella* and its epibionts might form a symbiotic relation. Additional field studies including predation/environmental effects may provide us with improved understanding of the relationships between the host gastropod and its epibionts.

## Acknowledgments

We thank Drs. Y. Serizawa and K. Serizawa from Faculty of Education and Human Sciences, University of Yamanashi, MN Aoki from Tohoku University, E. Titlyanov and T. Titlyanova from the Institute of Marine Biology, Russian Academy of Sciences, for providing us with information on *Pseudocladophora*, *Lunella* and *Gelidium* spp. We are also

grateful to Dr. Arakaki, the students and staff of Amakusa Marine Biological Laboratory, Kyushu University, for their support and valuable advice. This study was supported by the Sasakawa Scientific Research Grant from the Japan Science Society and a research grant from the Tokyo Institute of Technology.

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Published: 25 May 2018

Editorial note: this paper was first presented at the SCESAP Biodiversity Symposium in Bangkok 2015.