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Ecophenotypic plasticity in shell growth direction of asari clam *Ruditapes philippinarum*

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Original Article

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Abstract

Asari clam (or Manila clam) *Ruditapes philippinarum* is an important bivalve for local fisheries. This species exhibits a large variation in shell morphology, and the shell roundness tends to be greater in more unsuitable habitats. To test whether the increments in shell size parameters (length, height and width) were affected solely by environmental conditions or by internal factors such as initial shell shapes or growth rate, a field caging experiment was conducted at two different sites of unsuitable and suitable habitats in Matsukawaura Lagoon, Japan, where shell shapes of wild clams were significantly different between the habitats. In the experiment, clams were released from the two sites to the same site or to the other site and were re-collected after 3, 6 and 12 months of caging. Caged clams originating from unsuitable habitats and released to suitable habitats showed a reduction in shell height relative to shell length, while clams from suitable habitats introduced to unsuitable habitats showed marked increases in both shell height and width. Generalized linear mixed models suggested that the increase in shell height was affected largely by the release habitat (environment) whereas the increase in shell width was affected largely by the individual growth rate. These results suggest that marginal growths in shell height and width respond differently to external and internal factors of clams, resulting in plasticity in their shell shapes according to the environments to which they are translocated.

Introduction

Bivalves often exhibit intraspecific morphological variation in shell shapes between localities (Holme, 1961; Eager *et al*., 1984; Márquez & van der Molen, 2011; Signorelli *et al*., 2013), habitat types (Zieritz & Aldridge, 2009) and latitude (Beukema & Meehan, 1985). Intraspecific shell shape variation can be used to discriminate populations or stocks (Palmer *et al*., 2004; Márquez *et al*., 2010, 2017). However, shell shape often varies within a population and can be a useful indicator for evaluating habitat suitability (Holopainen & Kuiper, 1982; Kakino, 1996). Variations in shell morphology often reflect environmental characteristics rather than genetic effects (Yokogawa, 1998; Kwon *et al*., 1999; Costa *et al*., 2008), suggesting phenotypic plasticity in shell shapes, as suggested for some species (Soares *et al*., 1998; Sousa *et al*., 2007; Zieritz *et al*., 2010; Inoue *et al*., 2013).

Asari clam *Ruditapes philippinarum* is a commercially important bivalve inhabiting tidal flats in Japan. Their shell sharpness and thickness vary among localities (Watanabe & Katayama, 2010; Caill-Milly *et al*., 2012, 2014). This morphological variation reflects the environmental adaptability of clams, as the shell height and width become greater in unsuitable habitats (Choe & Oshima, 1958; Kakino, 1996; Saito *et al*., 2007). However, it is unclear which external or internal factors cause different phenotypes. If external factors, equivalent to surrounding environments, largely govern shell shapes, individuals would respond similarly to the environment regardless of the variation in individual growth (internal factor). On the contrary, if the individual growth rate is the driver affecting shell shapes, the shell shape variation would be associated with individual growth even under the same environments.

This study aimed to: (1) confirm the ecophenotypic plasticity in clam shell shape, and (2) clarify which external or internal factors affect shell morphology. In asari clam, marginal shell growth can be used to explore the process of shell shape formation because it has been suggested that the direction of shell growth of transplanted clams is related to the environment rather than the shell shape at the time of transplantation (Choe & Oshima, 1958). In the present study, a cross-translocating experiment was conducted in the field. Clams from suitable and unsuitable habitats were released to both habitats, and the marginal shell growth and changes in shell shapes were compared between origins and destinations.

Materials and methods

Study site

Matsukawaura Lagoon, Fukushima, Japan (37°49′ N 140° 59′E) was chosen as the study site. This lagoon has an area of 6 km^2, and almost half of the lagoon is intertidal. The tidal range is ~1.5 m, salinity is usually above 25, and water temperature fluctuates seasonally from 5–27°C

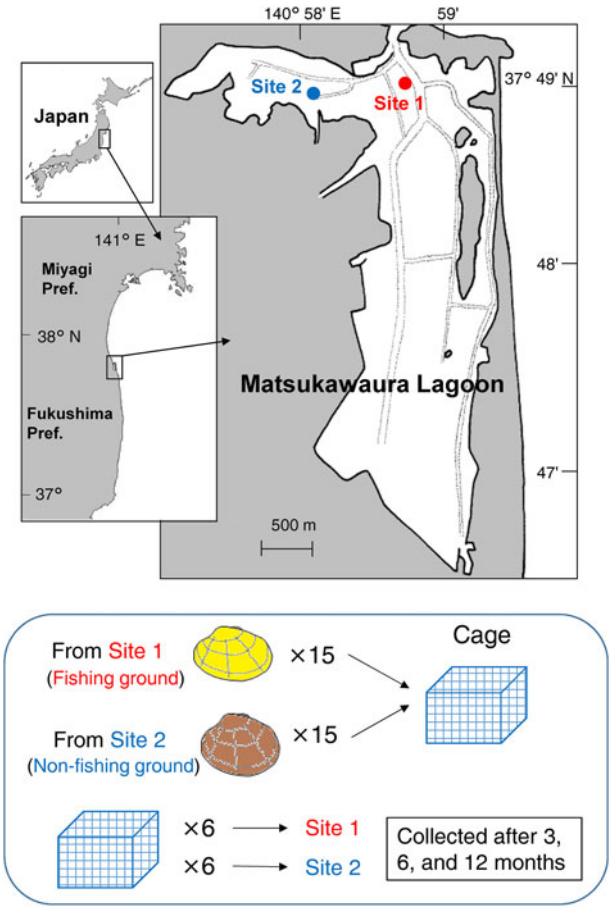

Fig. 1. Map of the study site and the schema of the field experiment.

(Tomiyama, 2016, 2018). The asari clam is the most dominant bivalve in this lagoon and is the target species for the clam fishery.

Two sites were selected for clam collection and a field experiment (sites were the same as Tomiyama, 2016). Site 1 (suitable habitat) was located near the mouth of the lagoon, which was connected to the open sea (Figure 1). This site is a fishing ground for the asari clam. The site had a sandy substratum (median grain diameter = 2.23 mm, average silt-clay content = 2.79%), and was densely inhabited by the clams at an average density of 296 individuals m^{-2}. Site 2 (unsuitable habitat) was located in the western part of the lagoon, ~700 m from Site 1. This site was a non-fishing ground, and the substratum at the intertidal zone was muddy sand (median grain diameter = 1.82 mm, average silt-clay content = 7.35%), whereas the substratum in the subtidal zone was mud. The clam inhabited only the areas in the intertidal zone at an average density of 93 individuals m^{-2}. Local fishers empirically recognized the relatively low soft body mass of clams at Site 2, and clams at this site were not harvested commercially.

Clam collection

To investigate the shell morphology for the field experiment, wild asari clams (N = 213 at Site 1; N = 209 at Site 2) were collected by digging the intertidal flat substratum and sieving through a 9 mm mesh at each site in May 2008. Additional subsamples of wild clams (N = 20 at Site 1; N = 11 at Site 2) were also collected in the same manner in August 2008.

For collected clams, the shell length (SL, mm), shell height (SH, mm), and shell width (SW, mm) were measured with a sliding caliper to the nearest 0.1 mm (Figure 2), following procedures developed by Watanabe & Katayama (2010). For clams collected in May 2008, 180 clams per site were subjected to a field experiment after the measurement.

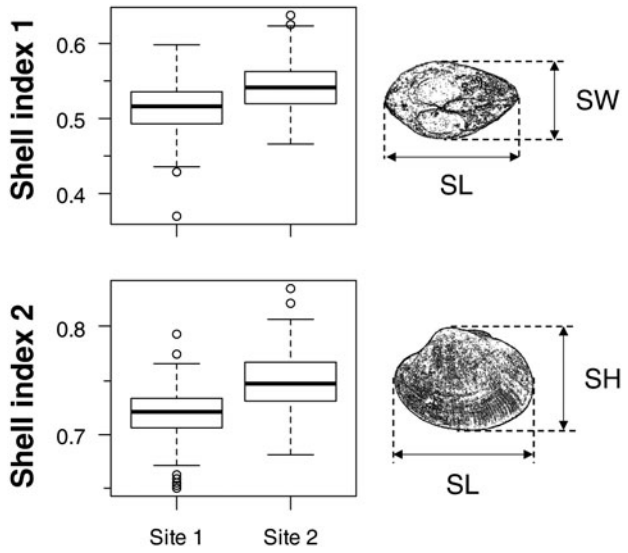

Fig. 2. Shell indices of wild asari clam collected from Sites 1 and 2. Shell indices 1 and 2 show the ratio of shell width (SW) or shell height (SH) relative to shell length (SL). Sample sizes were 233 and 220 for Sites 1 and 2, respectively. Boxes show the 25% and 75% quartiles and median, dashed vertical bars show the maximum and minimum values, and open circles show outliers. Significant differences were observed between sites (Mann–Whitney U test; SI1: $U = 14932$, $P < 0.001$; SI2: $U = 10826$, $P < 0.001$).

Field experiment

A field caging experiment was conducted at both sites until May 2009. A total of 360 asari clams of 26–48 mm SL were used. They were labelled by numbering their shells with a permanent marker. Clams were randomly divided into 12 groups consisting of 15 individuals per site per group, and a total of 30 clams from two sites were assigned to each group. Clams of each group were placed in a nylon-netting cage (25 × 25 × 15 cm, 6 mm mesh), and a total of 12 cages (6 cages per site) were buried at intertidal flats of Sites 1 and 2 in May 2008 (6 days after collection; Figure 1).

After 3, 6 and 12 months, two cages were collected from each site (one from the upper intertidal flat and the other from the lower intertidal flat) and brought to the laboratory. The surviving clams were subjected to post-experiment measurements of SL, SH and SW.

Analysis

To evaluate shell morphology, shell indices 1 and 2 (SI1 and SI2; following Watanabe & Katayama, 2010), determined by $SW \times SL^{-1}$ and $SH \times SL^{-1}$, respectively, were used. It has been suggested that both indices are negatively correlated with the nutritional condition in asari clams and that SH relative to SL (SI2) was more sensitive to the nutritional condition than SI1 (Watanabe & Katayama, 2010).

For wild clams (including caged clams before the field experiment, N = 453), SI1 and SI2 were compared between sites using the Mann–Whitney U test. Linear mixed models (LMMs) were constructed for SI1 and SI2 to explore the factors affecting shell shape variation. Initial explanatory variables were site and SL, and random variables were the month of collection and upper/lower intertidal flats. Models were fitted by maximum likelihood, and significant variables among both random and explanatory variables were selected by backward elimination.

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Table 1. Selected linear mixed models for shell indices in wild asari clam

Response variable	Analysis of deviance				Coefficients			
	Error source	df	χ^2	*P*	Parameter	Estimate	SE	*P*
SI1 (shell width × shell length^{-1})					Intercept	0.46	0.012	<0.001
	Site	1	73.90	<0.001	Site (Site 2)	0.037	0.003	<0.001
	SL	1	19.72	<0.001	SL	0.0014	0.0003	<0.001
SI2 (shell height × shell length^{-1})					Intercept	0.75	0.009	<0.001
	Site	1	148.45	<0.001	Site (Site 2)	0.027	0.002	<0.001
	SL	1	13.34	<0.001	SL	−0.0008	0.0002	<0.001

Analysis of deviance was carried out using the Type II Wald χ^2 test. All initial explanatory variables of the site and shell length (SL) were selected in both models. The coefficient of site (Site 2) was evaluated based on Site 1.

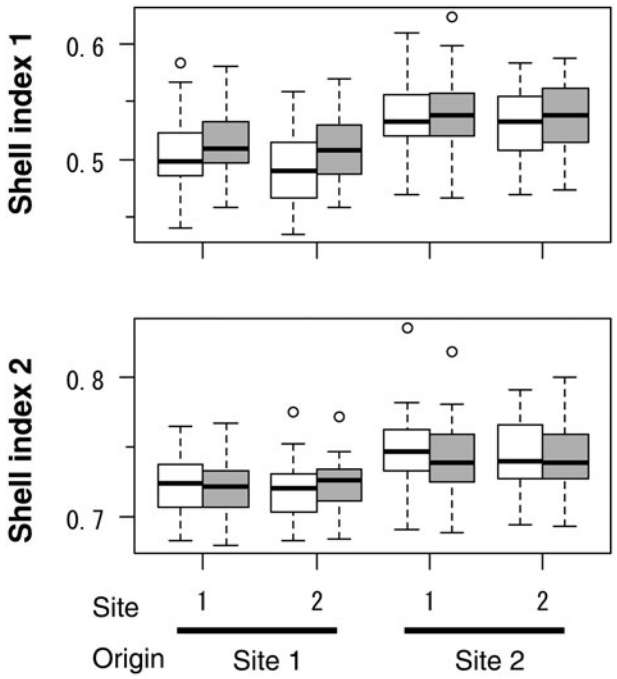

Fig. 3. Shell indices of caged asari clam in the field experiment. Data of survivors with growth of ≥0.5 mm shell length are shown. Open and solid boxes indicate values at the beginning and the end of the experiment, respectively. Site shows the location of caging, and origin shows the site where the clams inhabited before collection for the caging. Sample sizes were 53, 43, 51 and 36 for clams from Site 1 to Site 1, from Site 1 to Site 2, from Site 2 to Site 1, and from Site 2 to Site 1, respectively. Boxes show the 25% and 75% quartiles and median, dashed vertical bars show the maximum and minimum values, and open circles show outliers.

Three analyses were performed for caged clams (post-experiment). Initially, clams with low growth (<0.5 mm increase in shell length (ΔSL)) were eliminated from the analyses to avoid the influence of measurement errors and to evaluate the marginal shell growth patterns. A total of 96 and 87 individuals originating from sites 1 and 2, respectively, were used. First, LMMs were constructed for the SI1 and SI2 of clams at recapture. Initial explanatory variables were the origin site of clams, site of release, and beginning/end of the experiment to test whether the indices changed during the experiment. Cage, duration (3, 6 and 12 months), and the individuals were incorporated as random variables. The models were fitted by maximum likelihood, and both random and explanatory variables were selected by backward elimination.

Second, increases in SW and SH (ΔSW and ΔSH) relative to ΔSL were analysed by LMM to test whether ΔSW and ΔSH vary between sites and/or origins. The ΔSW and ΔSH were used as response variables, and the original site of clams, site of release, and ΔSL were used as initial explanatory variables. Cage and duration were incorporated as random variables. Models were fitted by maximum likelihood, and both random and explanatory variables were selected by backward elimination.

Third, to examine the factors affecting the direction of marginal shell growth, generalized linear mixed models (GLMMs) with Gaussian family and log-link function were constructed. The response variables were ΔSW and ΔSH. Initial explanatory variables were site, log-transformed individual growth rate (mm SL per 30 days), and log-transformed initial index of SI1 or SI2. The log-transformed ΔSL was incorporated as an offset term. The random variables were cage and duration. Models were selected based on the Akaike information criterion (AIC). To test whether the growth rates of clams vary between sites and/or origins, a LMM was constructed for the growth rate during each period, using the origin site of clams and site of release as explanatory variables and cage as a random variable. The model was fitted using the maximum likelihood and was selected.

All statistical analyses were performed using the R software (www.r-project.org) and packages 'lme4', 'lmerTest', 'MuMIn' and 'car'.

Results

Shell morphology of wild clams

Shell indices SI1 and SI2 of wild clams were both significantly greater at Site 2 than at Site 1 (Figure 2). In the LMM, clam SL positively affected SI1, whereas SL negatively affected SI2 (Table 1). Greater indices at Site 2 than at Site 1 were also observed in the model. SL was not significantly different between the sites (Mann–Whitney *U* test, $U = 24638$, $P = 0.48$).

Shell morphology of translocated clams

Shell index 1 was mostly greater at the end of the experiment than at the beginning (Figure 3), and the beginning or end was selected as an explanatory variable in the LMM (Table 2). The selected LMM showed that the origin of clams affected SI1: clams originating from Site 2 showed greater SI1. The contribution of beginning/end was greater than the origin of clams (Table 2). On the contrary, SI2 at the end of the experiment was lower than at the beginning (negative coefficient for 'end' in Table 2), and the variation in SI2 was largely governed by the origin (greater χ^2 in the 'origin' than 'beginning/end').

The site and origin were not selected in the LMM for ΔSW. In contrast, ΔSH was greater at Site 2 than at Site 1, and clams originating from Site 2 exhibited a greater ΔSH (Figure 4, Table 2).

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Table 2. Selected linear mixed models for shell indices in caged asari clam with ≥0.5 mm increase in shell length (ΔSL) in the field experiment

Response variable	Analysis of deviance				Coefficients			
	Error source	df	χ^2	*P*	Parameter	Estimate	SE	*P*
SI1 (shell width × shell length^{-1})					Intercept	0.50	0.003	<0.001
	Origin	1	58.78	<0.001	Origin (Site 2)	0.032	0.004	<0.001
	B/E	1	113.86	<0.001	B/E (End)	0.0098	0.0009	<0.001
SI2 (shell height × shell length^{-1})					Intercept	0.72	0.002	<0.001
	Origin	1	47.65	<0.001	Origin (Site 2)	0.022	0.003	<0.001
	B/E	1	11.79	<0.001	B/E (End)	−0.002	0.0007	<0.001
ΔSW (increment of shell width)					Intercept	0.20	0.058	0.003
	ΔSL	1	2358.9	<0.001	ΔSL	0.58	0.012	<0.001
ΔSH (increment of shell height)					Intercept	−0.14	0.051	0.009
	Origin	1	12.47	<0.001	Origin (Site 2)	−0.17	0.049	<0.001
	Site	1	28.28	<0.001	Site (Site 2)	0.24	0.046	<0.001
	ΔSL	1	4996.8	<0.001	ΔSL	0.74	0.010	<0.001

Analysis of deviance was carried out using the Type II Wald χ^2 test. The B/E and ΔSL indicate the beginning or end of the experiment and the increment of shell length, respectively. The coefficients of origin and site were evaluated based on Site 1.

The growth rate of clams did not differ between the sites but differed between origins (Figure 5). In the LMM for growth rate during each of 3, 6 and 12 months, the site was consistently eliminated and the origin was selected as an explanatory variable: clams originating from Site 1 exhibited greater growth rates. In the GLMM for the change in shell indices, ΔSW ΔSL^{-1} was governed largely by the individual growth rate, whereas ΔSH ΔSL^{-1} was driven by the site (Table 3). Slower-growing individuals tended to increase ΔSW ΔSL^{-1} more than faster-growing individuals, and clams released at Site 2 exhibited a slightly larger ΔSW. In contrast, clams released at Site 2 exhibited a greater ΔSH, but a small contribution of growth rate was also observed, although the effect of growth rate was positive.

Discussion

This study confirmed that clams exhibit ecophenotypic plasticity in marginal shell growth. Individuals transplanted from the unsuitable site (Site 2) to suitable habitat (Site 1) showed a decrease in SH relative to SL (SI2, Figure 3), whereas individuals transplanted from Site 1 to Site 2 exhibited an increase in both SW and SH. This result coincides with previous suggestions regarding shell morphological plasticity in this species (Choe & Ohshima, 1958; Kakino, 1996) and other species (Stirling & Okumuş, 1994).

The present study is the first to elucidate that shell shape varies not only by the environment (external factor) but also by individual growth rates (internal factor). ΔSW was primarily driven by the growth rate, whereas ΔSH was chiefly affected by the environment (site), suggesting that fast-growing individuals in unsuitable habitats exhibit relatively small ΔSW and large ΔSH. To our knowledge, such a different pattern in the marginal growth direction between width and height has been reported for the first time. The following observations support this pattern. The SW relative to SL (SI1) mostly increased in caged clams during the experiment, irrespective of the release site or the origin of the clams (Figure 3). This result indicates that clam growth was reduced, possibly due to the artificial caging effect. The SH relative to SL (SI2) increased in the clams originating from suitable habitat (Site 1) and released at unsuitable habitat (Site 2), whereas it decreased in the clams originating from Site 2 and released at Site 1.

Different directions for shell marginal growth between SW and SH were also observed in the experiment in 2009, in which clams were caged at various densities (Tomiyama & Sato, 2021). ΔSW ΔSL^{-1} was primarily explained by the individual growth rate, similar to the present study, whereas ΔSH ΔSL^{-1} was explained solely by the original SI2. No density-dependent effect was detected for either index. Thus, the different responses of marginal shell growth in SW and SH are likely.

For asari clams, the ratio of SW to SL (SI1) has been demonstrated to correlate with the nutritional condition of the clam (Watanabe & Katayama, 2010) or the current velocity of the habitat (Kakino, 2002). Although the relationships between either SI1 or SI2 and shell growth rate determined from the microstructure of shell sections were weak (Watanabe & Katayama, 2010), clams with low growth rates can be expected to exhibit relatively greater ΔSW and ΔSH. Our models showed that SI1 was regulated by growth, whereas SI2 was affected mainly by the environment. Such different patterns of relative growth were also observed in asari clams in a previous study (Cigarría & Fernández, 1998), in which clams in denser conditions showed smaller SH, whereas no difference in SW was observed between clams at various densities.

The mechanisms underlying the variation in the shell growth directions remain unclear. Environmental conditions do not affect the shell biomineralization process (Gizzi *et al.*, 2016). SW is related to shell thickness, and slow-growing individuals have thicker shells (Watanabe & Katayama, 2010). It is unclear why SH responds differently to SW response, although many studies have suggested the relevance of environmental factors to shell shape variations (e.g. reviewed by Costa *et al.*, 2008). Differences in environmental factors between sites, such as substratum (sandy at Site 1) and food supply (greater current velocity at Site 1), were probably related to habitat suitability of asari clams and would affect their shell shapes. However, variations in elevation or other environmental factors in microhabitats within each site may also affect the shell growth direction. Further studies are required to reveal the mechanisms regulating marginal shell growth patterns and shell morphology of clams.

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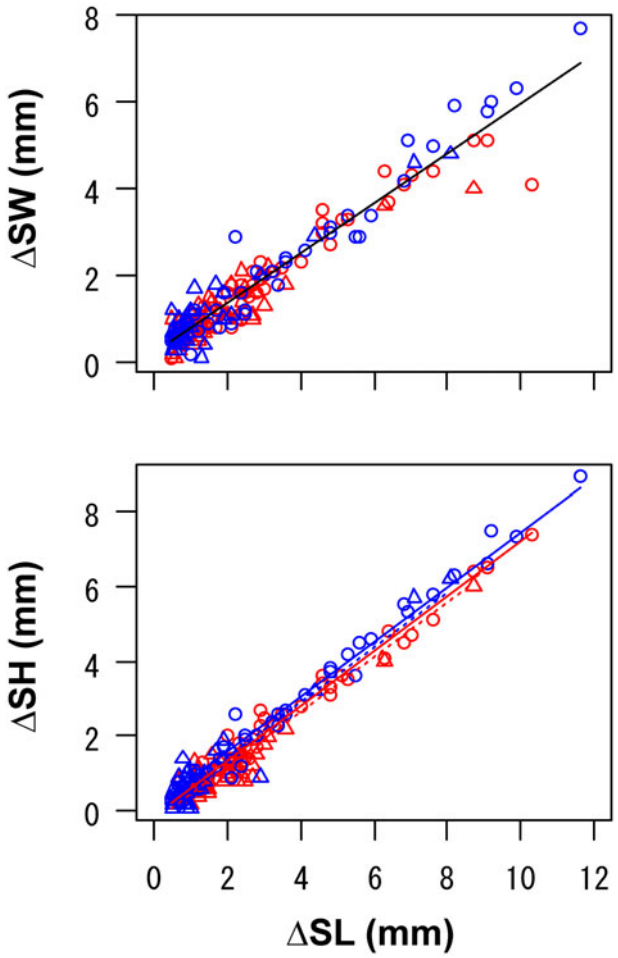

Fig. 4. Relationships between the increment of shell length (ΔSL) and that of shell width (ΔSW) or shell height (ΔSH) in caged asari clam in the field experiment. Data of survivors with increments of ≥0.5 mm in shell length are shown. Data were pooled for cages with different durations. Sample sizes were the same as Figure 3. Circles with solid lines and triangles with dotted lines show the origin of clams as Sites 1 and 2, respectively. Red and blue colours (in online version) show the sites for release (i.e. caging) as Sites 1 and 2, respectively. Lines show linear predictions derived from the linear mixed models (Table 2).

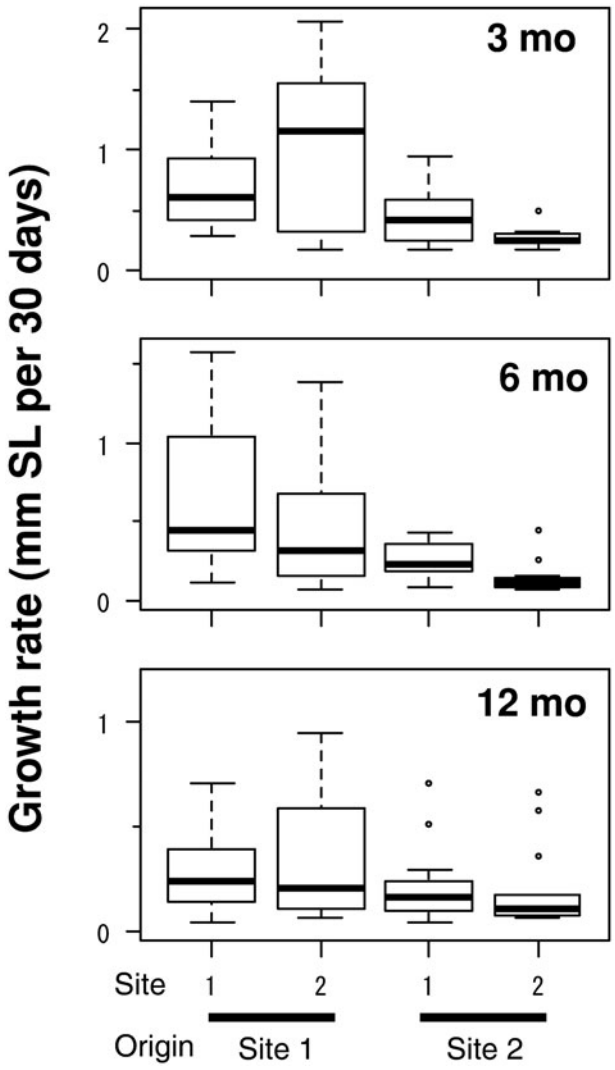

Fig. 5. Growth rate in shell length of caged asari clam in the field experiment. Data of survivors with increments of ≥0.5 mm in shell length are shown. Sample sizes were the same as Figure 3. Boxes show the 25% and 75% quartiles and median, dashed vertical bars show the maximum and minimum values, and open circles show outliers.

Table 3. Selected generalized linear mixed models (Gaussian family with log-link function) for shell shape in caged asari clam in the field experiment.

Response variable	Analysis of deviance				Coefficients			
	Error source	df	χ^2	*P*	Parameter	Estimate	SE	*P*
$\Delta SW \cdot \Delta SL^{-1}$ (Response variable = ΔSW, offset = log ΔSL)					Intercept	−0.86.	0.17	<0.001
	log ($SI1_0$)	1	3.06	0.080	log ($SI1_0$)	−0.42	0.24	0.080
	Site	1	4.67	0.031	Site (Site 2)	0.10	0.048	0.031
	log (GR)	1	32.78	<0.001	log (GR)	−0.14	0.024	<0.001
$\Delta SH \cdot \Delta SL^{-1}$ (Response variable = ΔSH, offset = log ΔSL)					Intercept	−0.60	0.13	<0.001
	log ($SI2_0$)	1	2.17	0.14	log ($SI2_0$)	−0.62	0.42	0.14
	Site	1	15.51	<0.001	Site (Site 2)	0.099	0.025	<0.001
	log (GR)	1	4.84	0.028	log (GR)	0.043	0.020	0.028

Analysis of deviance was carried out using the Type II Wald χ^2 test. The ΔSW, ΔSL, ΔSH, $SI1_0$, $SI2_0$, and GR indicate increments in shell width, shell length, and shell height, initial shell index 1, initial shell index 2, and growth rate (mm shell length per 30 days), respectively. The coefficient of site (Site 2) was evaluated based on Site 1.

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In conclusion, this study demonstrated the plasticity of clam shell shapes through a cross-transplantation experiment. Notably, shell growths in width and height relative to the length were possibly regulated by different mechanisms. The SW relative to SL was most closely related to the internal factor (growth rate), whereas SH relative to SL was related to external factors (site for transplantation). Such implications are expected to contribute to the understanding of the mechanisms of shell-shape plasticity in bivalves.

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