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Author for correspondence:
Kohei Oshiro, E-mail: oshiro.k.pdbk@gmail.com

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Patterns of shell utilization and preference in two sipunculan genera, *Phascolion* and *Aspidosiphon*

Kohei Oshiro[1], Akihiro Yoshikawa[2], Akira Asakura[1] and Ryutaro Goto[1]

[1]Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, 459 Shirahama, Nishimuro, Wakayama 649-2211, Japan and [2]Coastal Marine and Social Science Section, Atmosphere and Ocean Research Institute, The University of Tokyo, 1-19-8 Akahama, Otsuchi, Iwate 028-1102, Japan

Abstract

Sipunculans are non-segmented marine worms with an anterior retractable introvert, which are commonly included in Annelida based on molecular phylogenetic and phylogenomic analyses. They generally burrow in the soft sediments or live inside the crevices of hard substrata (e.g. calcareous/coralline rocks). However, members of some sipunculan genera (mainly *Phascolion* and *Aspidosiphon*) are known to have a peculiar habit of dwelling in vacant shells of gastropods or scaphopods. In this study, we investigated the shell utilization and preference pattern of the species of *Phascolion* and *Aspidosiphon* in Japan. We collected 302 sipunculans, comprising 273 and 29 individuals in *Phascolion* and *Aspidosiphon*, respectively, from 57–800 m depth of three study sites in the Pacific coast of Honshu Island, Japan. The species of *Phascolion* were found in vacant shells of 38 genera of 27 families of gastropods and six genera of four families of scaphopods, whereas the species of *Aspidosiphon* were found in 11 genera of 11 families of gastropods and one genus of scaphopod. These results suggest that members of each genus use a wide range of gastropod and scaphopod shells. The body size of the sipunculans was positively correlated with the shell size, suggesting that they change the shells as they grow. Furthermore, we investigated the shell preference of *Phascolion* species by comparing morphological characteristics of shells occupied and unoccupied by sipunculans. Generalized linear mixed model (GLMM) analyses suggest that the species of *Phascolion* tend to use long and narrow shells. Such shells likely fit well the elongated trunk of sipunculans.

Introduction

The vacant shells of molluscs (mainly gastropods) are often used as shelters by diverse animal taxa, including hermit crabs (Reese, 1969), tanaids (Kakui, 2019), polychaetes (Hylleberg, 1975), sipunculans (Cutler, 1994) and fishes (Bose *et al.*, 2020). In addition, the shells used by hermit crabs and sipunculans are known to be inhabited by a variety of symbiotic animals (Gage, 1968, 1979; Kristensen, 1970; Williams & McDermott, 2004; Goto *et al.*, 2007; Igawa *et al.*, 2017; Yoshikawa *et al.*, 2018; Jimi *et al.*, 2021; Herrán *et al.*, 2022). The vacant shells are thus considered to play an important role in engineering the ecosystem and maintaining the biodiversity in the sea bottoms, as suggested in Gutiérrez *et al.* (2003). However, despite the importance of the role of the vacant shells, studies of their ecological aspects remain scarce, except for hermit crabs (Hazlett, 1966, 1972; Wada *et al.*, 1999).

Sipunculans are a group of marine worms commonly included in Annelida based on molecular phylogenetic and phylogenomic analyses (e.g. Struck *et al.*, 2007, 2011; Weigert *et al.*, 2014; Rouse *et al.*, 2022). They comprise about 160 species in 16 genera and six families (Kawauchi *et al.*, 2012; Schulze & Kawauchi, 2021) and are morphologically characterized by an unsegmented body trunk, an anterior retractable introvert and the lack of the chaetae (Schulze & Kawauchi, 2021). Most sipunculans inhabit burrows in soft sediments or live in crevices in hard substrata (e.g. rocks, shells, corals and woods) (Cutler, 1994; Ferrero-Vicente *et al.*, 2016; Schulze & Kawauchi, 2021), whereas some of them are known to dwell in the vacant shells of gastropods or scaphopods (Hylleberg, 1975; Rice *et al.*, 1983; Cutler, 1994; Ferrero-Vicente *et al.*, 2011, 2012, 2013; Maiorova & Adrianov, 2013; Schulze & Kawauchi, 2021).

Shell-dwelling sipunculans are known from four genera; *Phascolion* (~20 spp., 5 subgen., 0–6000 m depth; Golfingiidae), *Nephasoma* (~23 spp., 3 subgen., 0–5000 m depth; Golfingiidae), *Apionsoma* (~5 spp., 2 subgen., 0–4000 m depth; Phascolosomatidae), and *Aspidosiphon* (~19 spp., 3 subgen., 0–200 m depth; Aspidosiphonidae) (Cutler, 1994).

Shell utilization pattern of sipunculans has been relatively well studied in species in the Atlantic Ocean. In the western coast of Sweden, *Phascolion* (*Phascolion*) *strombus strombus* (Montagu 1804) used more frequently the shells of the gastropods *Littorina littorea* (Linnaeus 1758) and *Turritella communis* (Risso 1826) and the scaphopod *Dentalium entalis* (Linnaeus 1758) than other shells (Hylleberg, 1975). In addition, a significant positive linear correlation was detected between the body weight of *P. strombus strombus* and the length of the shells used by them (Hylleberg, 1975). Hylleberg (1975) suggested by laboratory experiment data that *P. strombus strombus* swap shells when in those too small for them. In the

Indian River Lagoon of Florida, *Phascolion* (*Lesenka*) *cryptum* Hendrix, 1975 were commonly found in shells of five species of gastropods and most frequently in shells of *Cerithium muscarum* Say, 1832 (Rice *et al.*, 1983). Furthermore, *P. cryptum* was observed to always move to intact shells when their original shells were artificially reduced in size by being partially broken (Rice *et al.*, 1983). In the western Mediterranean Sea, five species of sipunculans were identified as shell-dwelling species (Pancucci-Papadopoulou *et al.*, 1999; Coll *et al.*, 2010). Among them, *Aspidosiphon* (*Aspidosiphon*) *muelleri* (Diesing 1851), *P. strombus strombus* and *Phascolion* (*Phascolion*) *caupo* (Hendrix 1975) used both gastropod shells and empty polychaete tubes as shelters (Ferrero-Vicente *et al.*, 2011, 2012, 2013). In addition, a significant linear correlation was detected between the trunk width of *A. muelleri* and the inner diameter of the tube used as the shelter (Ferrero-Vicente *et al.*, 2013). However, to understand the shell utilization patterns of sipunculans in more detail, a further quantitative study, especially in species in other geographic localities and sea depths, is needed.

In this study, we investigated shell utilization patterns of sipunculans collected from 57–800 m depth at three localities along the Pacific coast of Japan. Then, we examined the relationship between the shell size and body size of sipunculans and also the shell shapes preferred by species of the genus of *Phascolion.*

Materials and methods

Sampling

We collected shell-dwelling sipunculans from 14 stations of the following three study sites along the Pacific coast of Japan by dredge or beam trawl: (1) Shimoda (Station 1, off Shimoda, Shizuoka Prefecture, 200 m depth) (2) Kumanonada (Stations 2, 6–11, Kumano Sea, Mie Prefecture, 57–289 m depth) and (3) Tanabe (Stations 3–5, 12–14, off Tanabe Bay, Wakayama, Prefecture, 87–800 m depth) (Figure 1; Table 1). In three stations of Tanabe site (Stations 12–14), we collected not only the shells occupied by sipunculans, but also those occupied by other animals and unoccupied vacant shells. All the specimens were fixed with 99.5% ethanol and deposited in Seto Marine Biological Laboratory, Kyoto University.

Observation and measurements

Sipunculans

We removed the ethanol-fixed specimens of sipunculans from the shells by breaking them open with a small vise and then measured the following parameters of sipunculans with a calliper: trunk length (TL) and maximum trunk width (TW) (Figure 2A). The specimens were photographed after measurement. It was difficult to identify most sipunculan specimens to the species level or subgenus level because the internal structures that are diagnostic characters were substantially shrunken due to the fixation by ethanol. Thus, we used only genus-level identification for the analysis in this study. The identification was basically based on the keys described in Cutler (1994).

Vacant shells of gastropods and scaphopods

All the shells were photographed and most of them were identified to the genus level. However, some shells were highly degraded and thus difficult to identify to the genus level. The following parameters of the shells were measured with a caliper: shell length (SL), shell width (SW) and shell aperture length (SA) (Figure 2B, C).

Statistical analyses

Size correlation between sipunculans and their shells

We used Pearson's product-moment correlation coefficient (r) to check whether there is a significant relationship between the shell size and the body size of the sipunculans. This test was conducted using the 'cor.test' function of R ver. 3.5.3 (R Core Team, 2019).

Preference for gastropod shell shape in Phascolion

To determine which shell characteristics can influence the shell selection by *Phascolion* spp., we performed generalized linear mixed model (GLMM) analyses. In this analysis, the presence of *Phascolion* individual (presence = 1, absence = 0) was used as the response variable, and the following three factors were incorporated as factorial explanatory variables: (1) shell length, (2) shell width and (3) shell aperture length. Then, the family of shells was selected as a random factor. We used the specimens collected from three stations (Stations 12–14) of Tanabe site for the analyses.

Shells collected from these stations belonged to 23 gastropod families and were utilized by individuals of sipunculans (*Phascolion* spp. and *Aspidosiphon* spp.), hermit crabs (*Catapagurus* sp.) and other crustaceans (*Bubocorophium* sp.) (Figure S1). Among shell dwellers, *Phascolion* spp. were most abundant (Figure S1). In these stations, the sipunculans with scaphopod shells were scarce (N = 2) and thus not included in the analysis.

GLMM analyses were conducted using the glmmML function of R ver. 3.5.3. After the maximum-likelihood estimation, the parametric values that maximized likelihoods were obtained by using the glmmML function. Then, the AIC value between each model was compared using the dredge function of the statistical package R. The model with the lowest AIC value was adopted and the factor that affects the shell selection of the species of *Phascolion* discussed. Also, we performed logistic regression for each of the explanatory variables used in GLMM analyses to evaluate correlations between them and thereby facilitate the interpretation of the results.

Results

Composition of sipunculans genera among shells

A total of 302 individuals of sipunculans, including 273 individuals of *Phascolion* and 29 individuals of *Aspidosiphon*, were collected (Figure 3). Each sipunculan individual was solitary. *Phascolion* was more abundant than *Aspidoshion* in all three study sites at all depths except for the 200–300 m depth range at the Kumanonada site (Figure 4).

Diversity of molluscan shells used by sipunculans

The vacant shells used by *Phascolion* species contained 38 gastropod genera of 27 families and six scaphopod genera of four families (Table S1; Figure 5). On the other hand, the vacant shells used by *Aspidosiphon* species contained 11 gastropod genera of 11 families and one scaphopod genus (Table S2; Figure 5). The gastropod shells most frequently used by *Phascolion* species were those of Turridae (N = 47), Cerithiidae (N = 22) and Orectospiridae (N = 19), whereas the scaphopod shells most frequently used by *Phascolion* species were those of Entalinidae (N = 51), Gadilinidae (N = 15) and Gadilidae (N = 8) (Table S1; Figures 5, 6A–F). The gastropod shells most frequently used by *Aspidosiphon* species were those of Turridae (N = 12), Pseudomelatomidae (N = 4) and Nassariidae (N = 3), whereas the scaphopod shells used by *Aspidosiphon* species were only that of Gadlinidae (N = 1) (Table S2; Figures 5, 6G–J).

The gastropod shells most frequently used by *Phascolion* species were those of Cerithiidae (N = 2) at Shimoda, Turridae

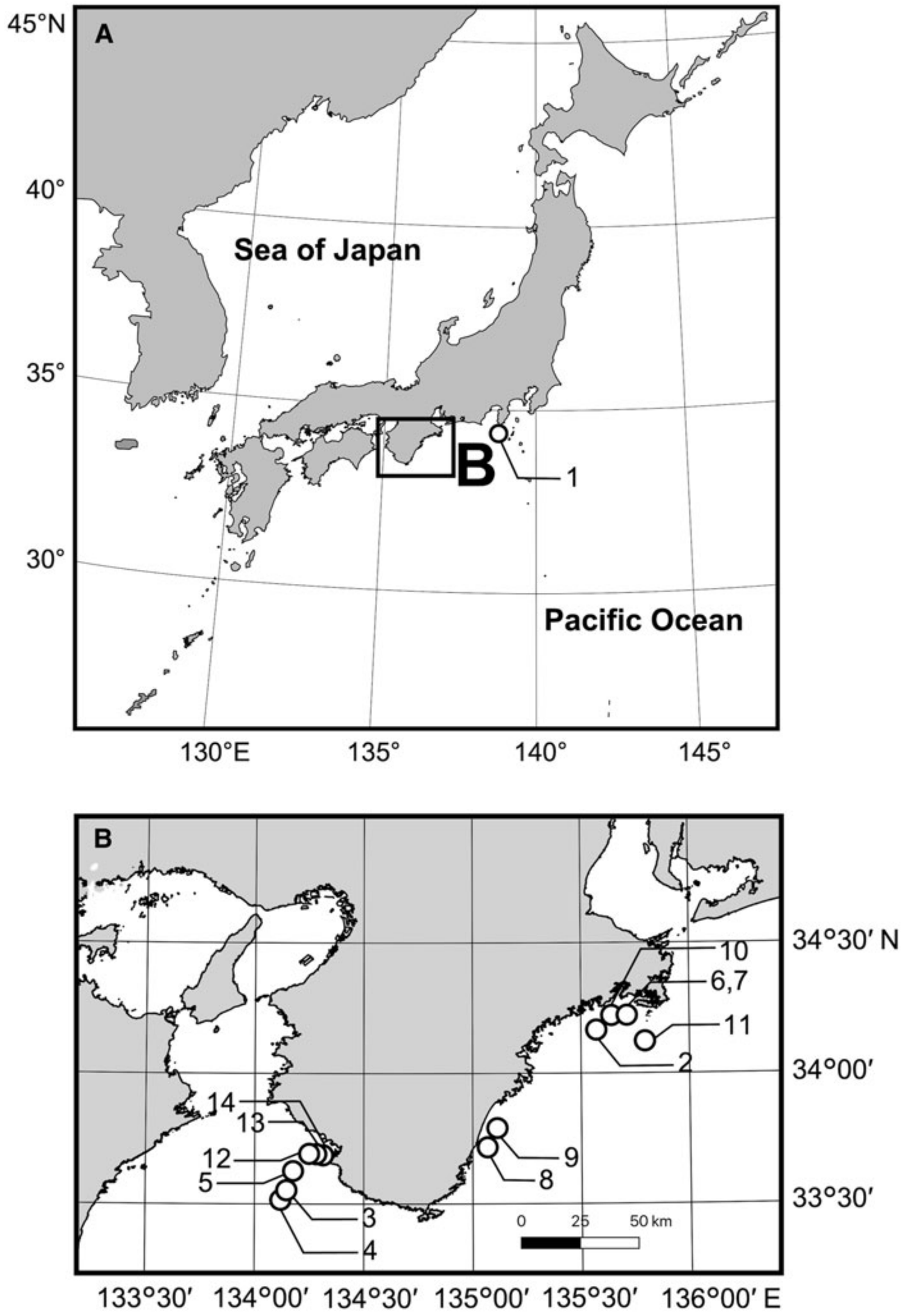

Fig. 1. Sampling localities. Circles indicate sampling stations: (A) Japanese Archipelago; (B) Kii Peninsula, Japan. Shimoda (Station 1), Kumanonada (Stations 2, 6–11), Tanabe (Stations 3–5, 12–14).

(N = 29) at Kumanonada and Orectospiridae (N = 18) at Tanabe (Table S1; Figure 7), whereas the scaphopod shells most frequently used by them were those of Entalinidae (N = 25) at Kumanonada and Entalinidae (N = 26) at Tanabe (Table S1; Figure 7). At Shimoda, scaphopod vacant shells used by shell-dwelling sipunculans were not found.

On the other hand, the gastropod shells most frequently used by *Aspidosiphon* species were those of Turridae at Kumanonada (N = 7) and at Tanabe (N = 5), whereas the scaphopod shell most frequently used by them was those of Gadilinidae (N = 1) at Kumanonada (Table S2; Figure 7). *Aspidosiphon* species with scaphopod vacant shells were not found at Tanabe (Figure 7C). *Aspidosiphon* species was not collected at Shimoda (Figure 7A).

Relationship of size between sipunculans and their shells

There was positive linear correlation between the body size of *Phascolion* individuals and the size of gastropod vacant shells collected at Shimoda, Tanabe and Kumanonada (Tables S3 and S4; Figure 8). Except for Shimoda, where no scaphopod shells occupied by sipunculans were found, there were positive linear correlations between the body size of *Phascolion* individuals and the size of scaphopod vacant shell collected at Tanabe and Kumanonada (Tables S3 and S4; Figure 9).

There were positive linear correlations between the body size of *Aspidosiphon* species and the size of gastropod vacant shell collected at Kumanonada (Tables S5 and S6; Figure 10).

Shell-shape preference of Phascolion

The results of GLMM analysis are shown in Table 2. The best fitted model with the lowest AIC was the one that includes 'shell length' and 'shell width' as factorial explanatory variables (AIC = 73.2) (Tables 2 and 3). The other selected models were summarized in Table 2. Among the explanatory variables, only the shell length was suggested to be significant (Table 3; Figure 11).

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Table 1. Sampling information

Station No.	Locality	Latitude	Longitude	Method	Depth
St 1	Shimoda	34°39′8″N	138°43′38″E	Dredge	200
St 2	Kumanonada	34°10′0″N	136°35′9″E	Beam trawl	185
St 3	Tanabe	33°35′2″N	135°9′4″E	Beam trawl	421
St 4	Tanabe	33°32′2″N	135°8′1″E	Beam trawl	800
St 5	Tanabe	33°38′0″N	135°10′9″E	Dredge	219
St 6	Kumanonada	34°13′3″N	136°42′7″E	Dredge	82
St 7	Kumanonada	34°13′3″N	136°42′7″E	Dredge	82
St 8	Kumanonada	33°44′7″N	136°4′2″E	Dredge	57
St 9	Kumanonada	33°48′0″N	136°6′0″E	Dredge	59
St 10	Kumanonada	34°13′7″N	136°39′1″E	Dredge	92
St 11	Kumanonada	34°7′3″N	136°48′8″E	Dredge	289
St 12	Tanabe	33°40′36″N	135°16′6″E	Dredge	90
St 13	Tanabe	33°40′40″N	135°16′23″E	Dredge	87
St 14	Tanabe	33°24′24″N	135°9′50″E	Dredge	87

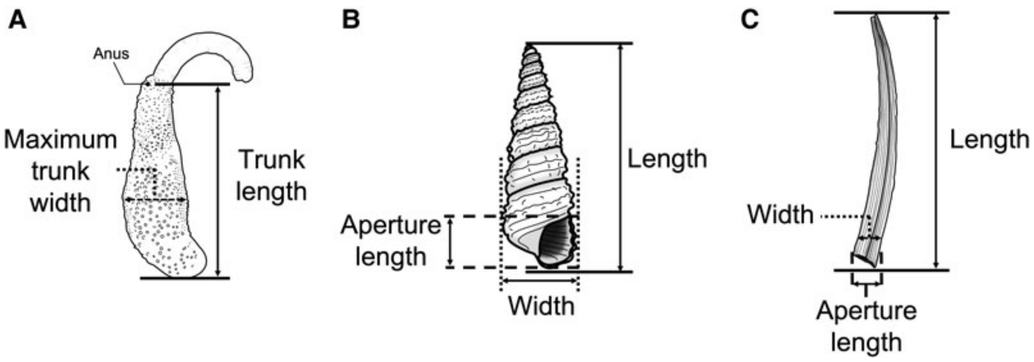

Fig. 2. Size measurements of shell/tube-dwelling sipunculans and their snail shells: (A) Sipuncula, (B) Gastropoda, (C) Scaphopoda.

Fig. 3. Shell-dwelling sipunculans. Sipunculans belonging to *Phascolion* (A, B) and *Aspidosiphon* (C, D). (A, C) Individuals inhabiting shells. (B, D) Individuals removed from their dwelling shells. Each panel shows a different individual. Scale bars = 4 mm.

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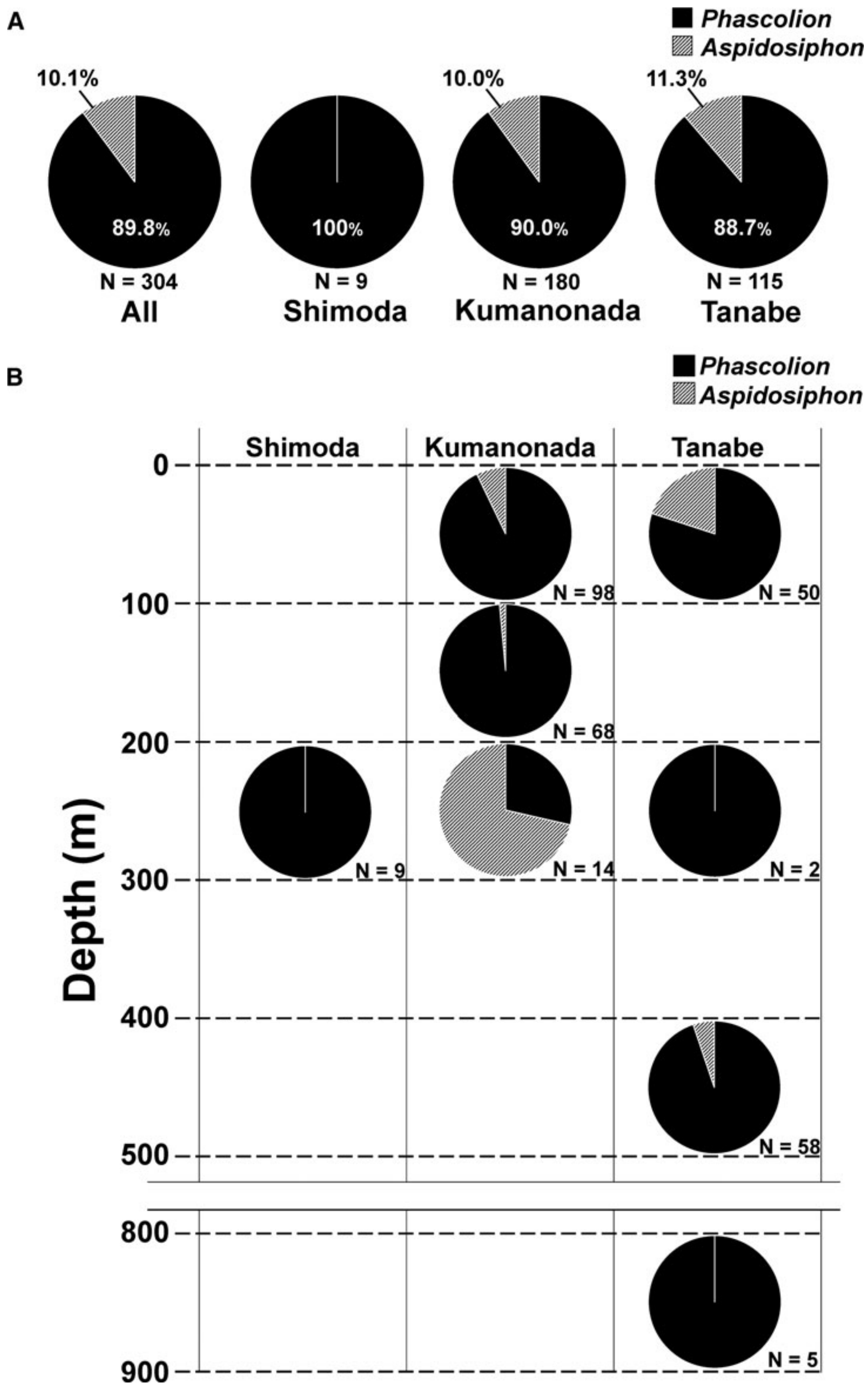

Fig. 4. The ratios of *Phascolion* to *Aspidosiphon* in each sampling site and depth. Black = *Phascolion*; Stripe = *Aspidosiphon*: (A) Each sampling locality, (B) Each sampling depth.

Discussion

Generic composition of sipunculans

The species of *Phascolion* and *Aspidosiphon* were found to occur sympatrically across a wide range of depth from 57–800 m along the Pacific coast in this study, and shells utilized by *Phascolion* species were more abundant than those shells utilized by *Aspidosiphon* species in all sampling sites and depths, except at a depth of 200–300 m in Kumanonada. However, dominance of *Aspidosiphon* species among shell-dwelling sipunculans was also reported in other sea areas. For example, *A. muelleri* is known to be dominant in the western Mediterranean Sea among shell-dwelling sipunculans (Açik *et al.*, 2005; Ferrero-Vicente *et al.*, 2011, 2013). Various factors, such as habitat preference, geographic region, depth and interspecific competition, likely play a role of determining the dominant shell-dwelling sipunculan species (or genus) and their community structure, although they remain not well studied. The studies in the Mediterranean Sea were mainly conducted in shallow water depth (6–45 m) of the Atlantic Sea, whereas the present study was carried out in the deeper area of the Pacific. Such differences in the geographic region and sea depth may be associated with differences in the community structure of shell-dwelling sipunculans.

It has been reported that the demand for shells by hermit crabs often exceeds the supply by snails (Hazlett, 1981), and thus they rob shells used by other individuals to obtain shells that fit their

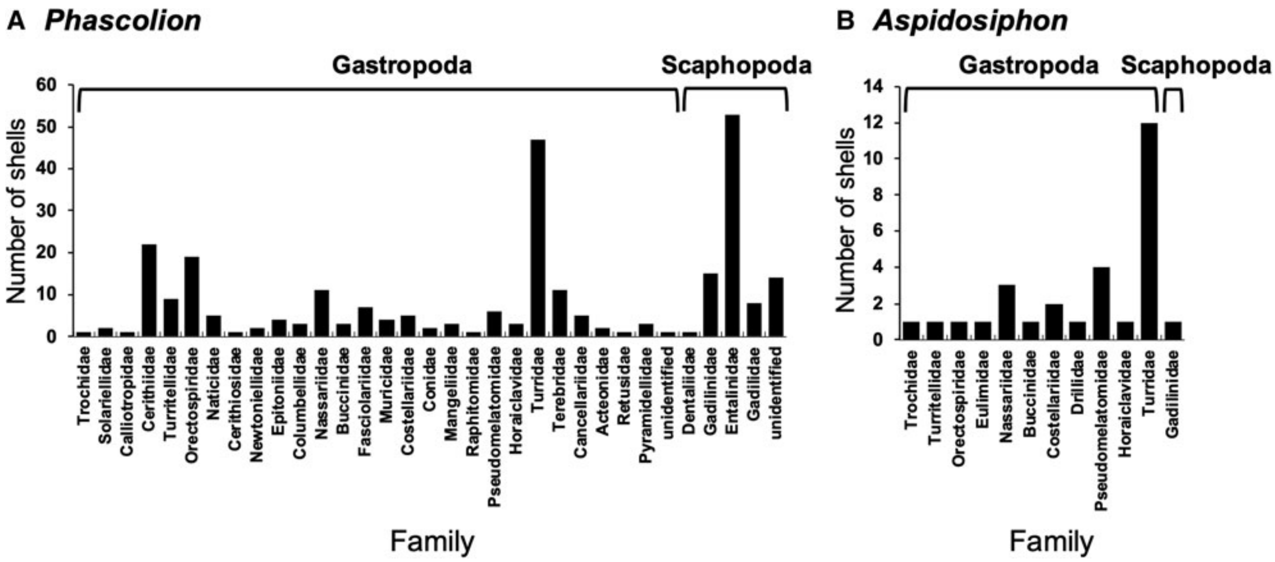

Fig. 5. Total number of individuals of shell families used by *Phascolion* and *Aspidosiphon* species. (A) *Phascolion*, (B) *Aspidosiphon*.

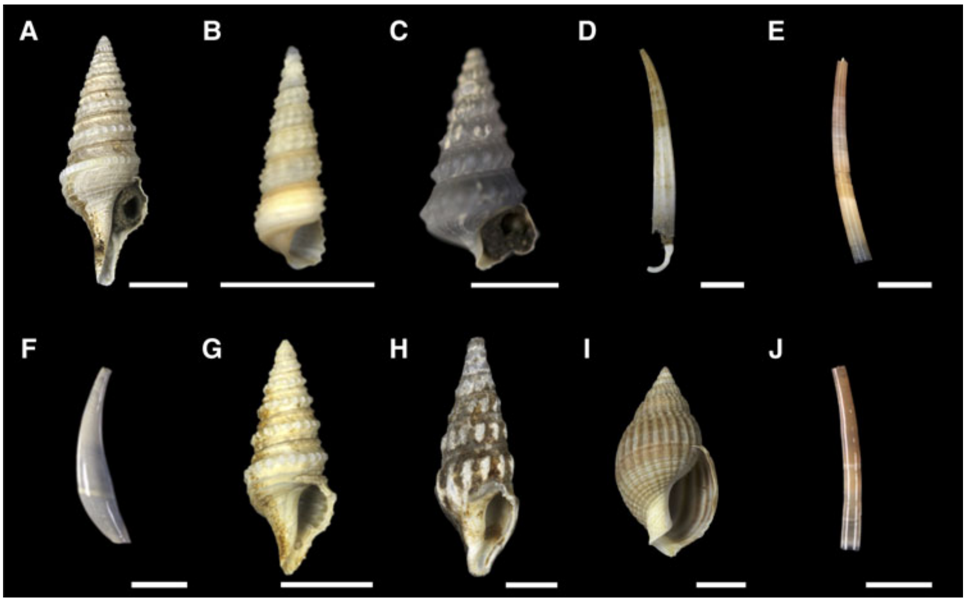

Fig. 6. Vacant shells most frequently used by species of *Phascolion* (A–F) and *Aspidosiphon* (G–J): (A) Turridae, (B) Cerithiidae, (C) Orectospiridae, (D) Entalinidae, (E) Gadilinidae, (F) Gadilidae, (G) Turridae, (H) Pseudomelatomidae, (I) Nassariidae, (J) Gadilinidae. Scale bars = 4 mm.

body size better (Asakura, 1984). This is probably the case with the shell-dwelling sipunculans. If such competition occurs, the abundance of the less competitive species is expected to be smaller than the other. This may be the reason why *Phascolion* spp. are more dominant than *Aspidosiphon* spp. in almost all the study sites. However, it remains unclear whether shell-dwelling sipunculans deprive other individuals of the shells. A further experimental verification may be necessary to clarify this.

Diversity of molluscan shells used by sipunculans

The species of *Phascolion* used a wide range of gastropod and scaphopod shells as shelters in this study. In the western coast of Sweden, *P. strombus strombus* used all the shells available in the study area (Hylleberg, 1975). Similarly, in the Indian River Lagoon of Florida, *P. cryptum* was also found in all of the most commonly occurring shells (Rice *et al.*, 1983). Furthermore, it is known that *Phascolion* in the Mediterranean Sea used not only the gastropod shells but also the tube of the polychaete *Ditrupa arietina* (Müller 1776) (Ferrero-Vicente *et al.*, 2011, 2012, 2013). Taken together, these results suggested that *Phascolion* species could potentially utilize a wide range of sea shells and also morphologically shell-like shelters.

The species of *Aspidosiphon* also used a wide range of gastropod and scaphopod shells as shelters in this study. However, the number of gastropod and scaphopod families of the shells used by *Aspidosiphon* species were fewer than those of *Phascolion* species. Although this result may be simply due to the collection of more specimens of *Phascolion* species, it is possible that *Aspidosiphon* species have a more strict shell preference than *Phascolion* species.

Turridae is the only family whose shells were collected at all sampling sites and frequently used by both *Phascolion* and *Aspidosiphon* spp. The results may imply that *Phascolion* and *Aspidosiphon* spp. prefer to use the shells of Turridae, although they are apparently able to utilize a wide variety of shells as mentioned above. In this study, the identification of shell-dwelling

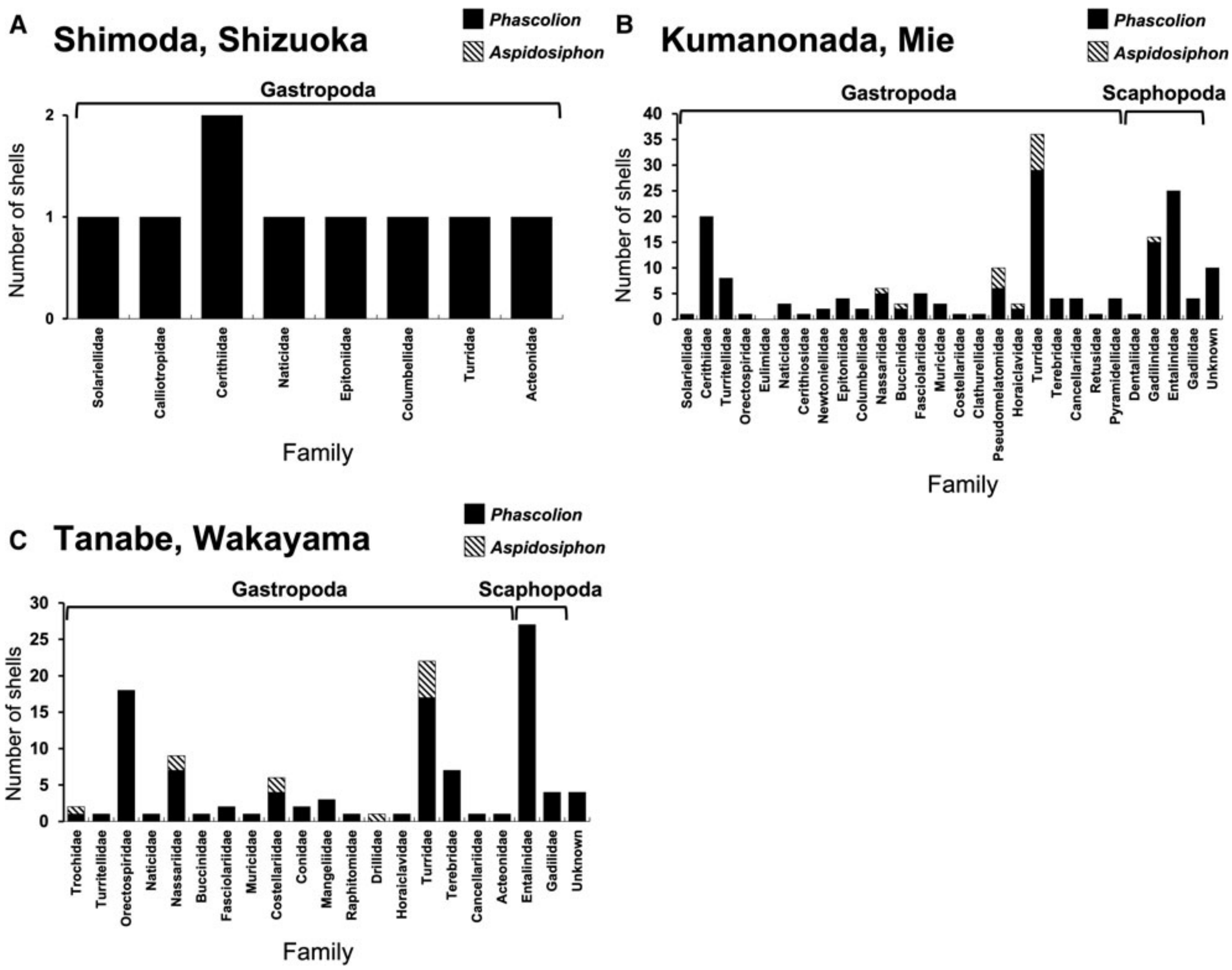

Fig. 7. Number of individuals of shell families used by *Phascolion* and *Aspidosiphon* species at each sampling locality. Black bars = *Phascolion,* Stripe bars = *Aspidosiphon.* (A) Shimoda, Shizuoka, Japan, (B) Kumanonada, Mie, Japan, (C) Tanabe, Wakayama, Japan.

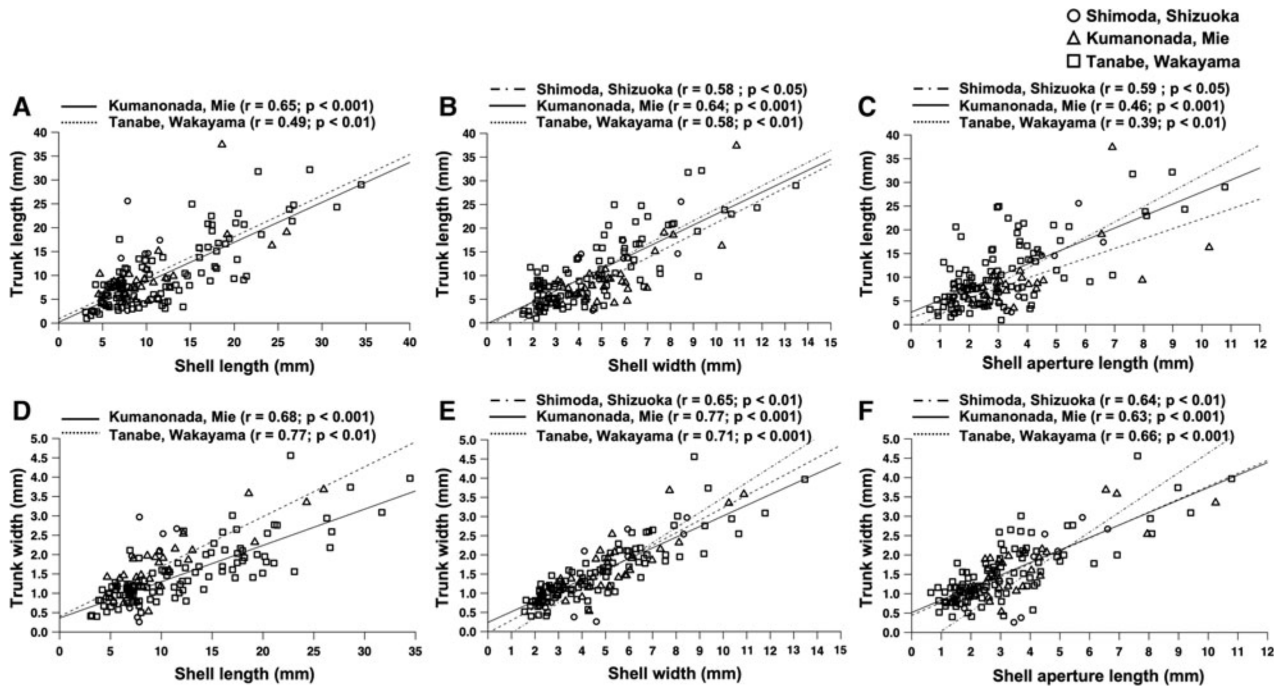

Fig. 8. Correlation equations between the body size of *Phascolion* species and their gastropod shell size: (A) trunk length and shell length, (B) trunk length and shell width, (C) trunk length and shell aperture length, (D) trunk width and shell length, (E) trunk width and shell width, (F) trunk width and shell aperture length.

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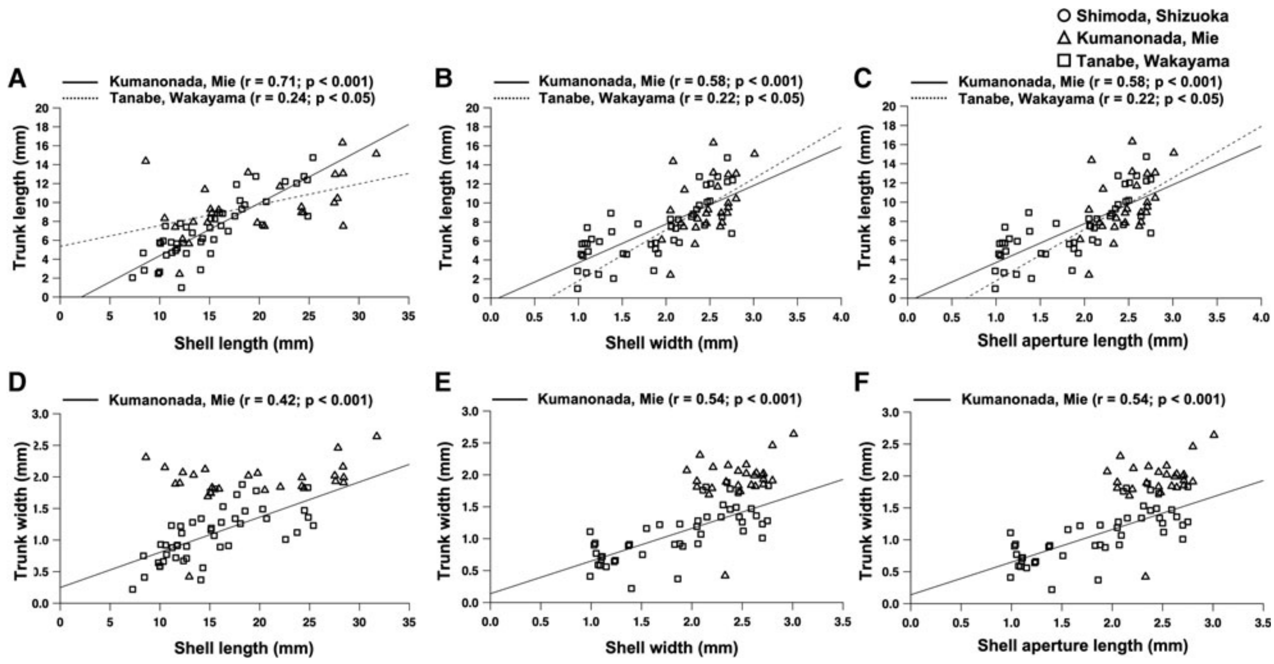

Fig. 9. Correlation equations between the body size of *Phascolion* species and their scaphopod shell size: (A) trunk length and shell length, (B) trunk length and shell width, (C) trunk length and shell aperture length, (D) trunk width and shell length, (E) trunk width and shell width, (F) trunk width and shell aperture length.

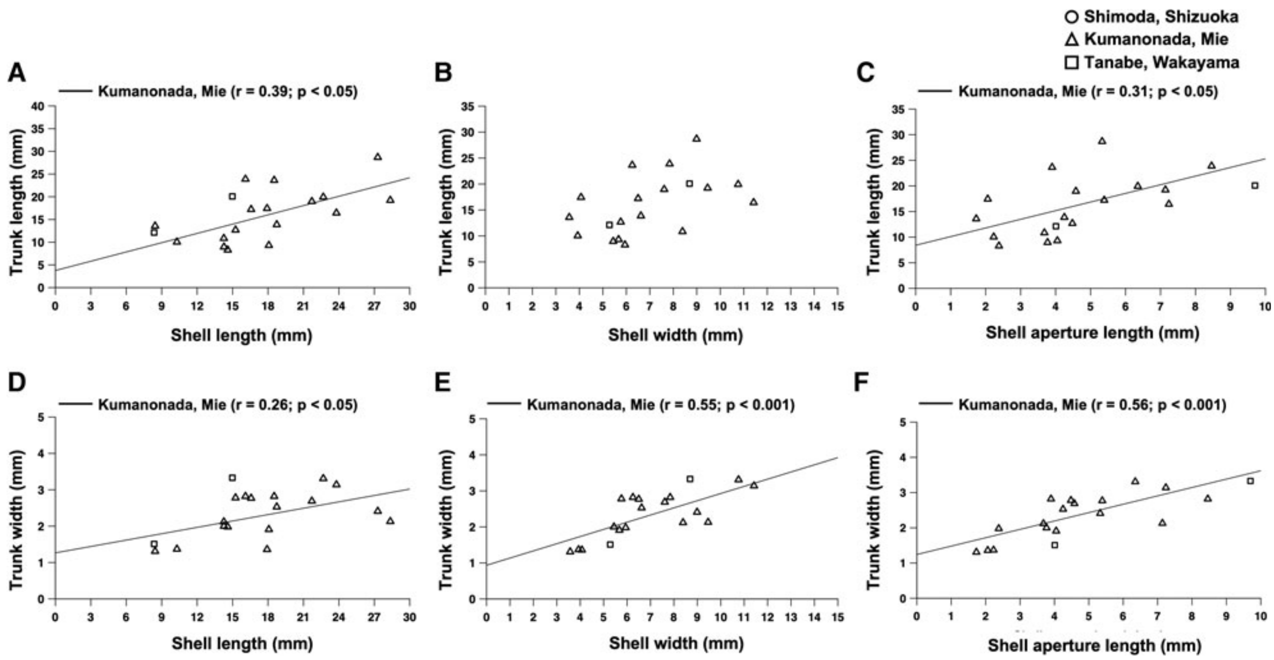

Fig. 10. Correlation coefficient and regression line between the body size of *Aspidosiphon* species and gastropod shell size: (A) Trunk length and shell length, (B) Trunk length and shell width, (C) Trunk length and shell aperture length, (D) Trunk width and shell length, (E) Trunk width and shell width, (F) Trunk width and shell aperture length.

Table 2. Results of each model of the generalized linear mixed model analysis with AIC value ordered by decreasing AIC

Intercept	Shell aperture length	Shell length	Shell width	df	loglik	AIC	delta	weight
−3.536		0.4963	−0.3372	4	−32.608	73.2	0	0.381
−3.772	−0.3708	0.6071	−0.2383	5	−31.814	73.6	0.41	0.311
−3.769	−0.5497	0.5254		4	−33.238	74.5	1.26	0.203
−3.885		0.3298		3	−34.993	76	2.77	0.096
−0.3395				2	−38.963	81.9	8.71	0.005
−0.4982	0.03987			3	−38.946	83.9	10.68	0.002
−0.258			−0.01333	3	−38.957	83.9	10.7	0.002
−0.4049	0.0652		−0.03183	4	−38.922	85.8	12.63	0.001

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Table 3. Results of a generalized linear mixed model for the shell-shape preference of *Phascolion* species

Factor	coef	se(coef)	*z* value	*P* value
Intercept	−3.5355	1.7059	−2.073	$P < 0.05$
Shell length	0.4963	0.1665	2.981	$P < 0.05$
Shell width	−0.3372	0.2425	−1.391	$P = 0.164$

sipunculans was limited to the genus level. Therefore, identification at the subgenus or species level may lead to different views or clearer tendencies in terms of shell preferences.

Relationship of size between sipunculans and their shells

The result of linear regression in this study indicates that, as shell size increases, so does the size of *Phascolion* in the shell. Two

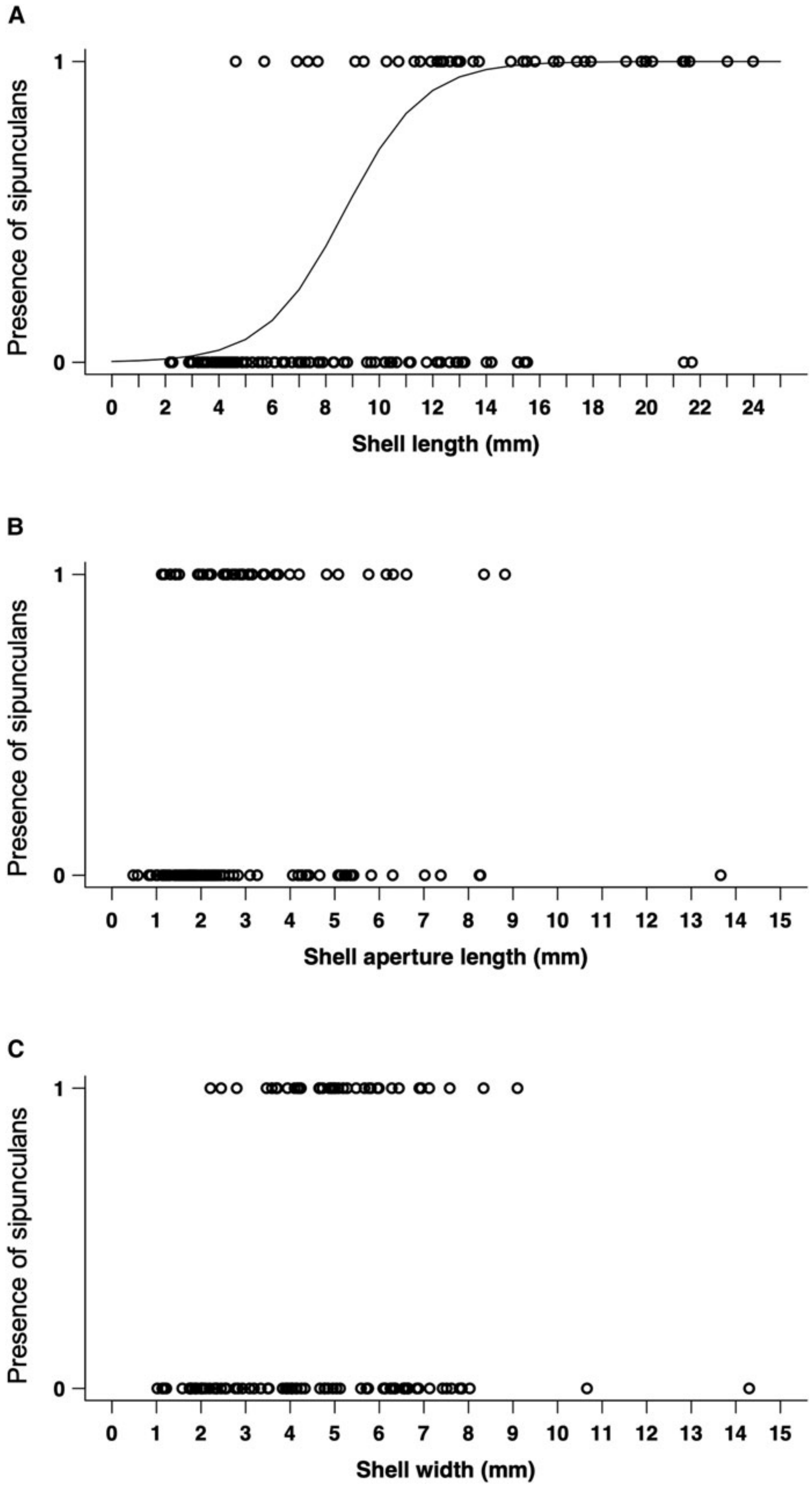

Fig. 11. Logistic regression for each factor. Scatter diagram and correlation matrix diagram of each factorial explanatory variable: (A) Shell length, (B) Shell width, (C) Shell aperture length.

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hypotheses can explain the correlation detected in this study. The first hypothesis is that sipunculans do not move across shells and that the size of the shells that the sipunculans first settle on determines the upper limit of their growth. In this case, small individuals of *Phascolion* species in large shells are supposed to be observed. However, such individuals were not found in this study. Thus, this hypothesis is unlikely to explain the findings of the present study. The second hypothesis is that sipunculans move across shells as they grow, like hermit crabs. Hylleberg (1975) conducted an experiment in the laboratory to determine whether *P. strombus strombus* performed a shell-exchanging behaviour. In his experiment, *P. strombus strombus* was kept in a 1 ml syringe and the free space in the syringe was reduced by 0.05 ml every other day. As a result, when it filled out the space of the syringe, *P. strombus strombus* left the syringe and entered the vacant shell of *Turritella*. Rice *et al.* (1983) observed in the field that immature juveniles and adults of *P. cryptum* were found in smaller and larger shells, respectively. Furthermore, their laboratory experiments showed that *P. cryptum* move to intact shells when their original shells are partially broken and artificially decreased in size. These results suggest that the species of *Phascolion* can exchange the shells as they grow. If *Phascolion* species in our study also exchange their shells as they grow, it can explain the positive correlation of size between sipunculans and their shells.

Shell shape preference of Phascolion

Although *Phascolion* were collected from a wide range of gastropods, GLMM analysis suggested that they tend to use long and narrow shells. Especially, the shell length was suggested to be the most significant factor in the shell selection of *Phascolion* spp.

Phascolion species in this study often used the vertically long shells of Turridae. Similarly, the gastropod shells of Cerithiidae and Orectospiridae, which were most frequently used by *Phascolion* species at Shimoda and Kumanonada, respectively, are also long vertically. The body of sipunculans, including *Phascolion*, is slender and anteroposteriorly long (Cutler, 1994). Thus, long shells apparently can fit the sipunculan body better and provide them ample inner space inside the shells to escape when they encounter predators.

The reason why *Phascolion* species use narrow shells may also due to their morphological characteristics. *Phascolion* species have a small thorn-like structure (namely, holdfast papillae) on the trunk, which are thought to prevent their body from being pulled out of the shell (Hylleberg, 1975; Cutler, 1994). For this structure to function effectively, sipunculans need to live in shells with an inner diameter close to the width of the trunk. In an experiment, *P. strombus strombus* given a glass tube as a shelter did not use the tube if its inner diameter was larger than its own body width, but stayed inside the tube if it was slightly smaller or equal in size (Hylleberg, 1975).

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