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Interspecific differences in the burrow morphology between the sympatric mud shrimps, *Austinogebia narutensis* and *Upogebia issaeffi* (Crustacea: Thalassinidea: Upogebiidae)

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The morphology of burrows constructed by the upogebiid mud shrimps *Austinogebia narutensis* and *Upogebia issaeffi* was studied using resin castings of burrows *in situ* on Mukaishima Island, Seto Inland Sea, Japan, where the two species occurred sympatrically. The burrow structure of both shrimps is a relatively simple Y-shaped pattern, which is typical of the family Upogebiidae. Total burrow length, and length and overall width of the U-shaped section of *A. narutensis* were greater than those of *U. issaeffi*, possibly because *A. narutensis* is the larger species. When the ratios of the burrow measurements to the mean burrow diameter were compared to exclude possible size effects, the burrows of *A. narutensis* had a wider and shallower U-shaped section than those of *U. issaeffi*. Because the casts were made where the two species occurred sympatrically, the differences in the burrow morphology were not due to the differences in environmental factors but to the difference in the shrimp species, whether they are adaptive or not.

INTRODUCTION

Thalassinidean mud shrimps of the family Upogebiidae are common burrowers in shallow marine sediment (Dworschak, 2000). Upogebiid shrimps create water currents in the burrows and feed mainly on suspended matter strained by the setal basket formed by the first and second pereiopods (MacGinitie, 1930). Recent studies based on the burrow morphology, mouthpart morphology, and observations in aquaria, however, showed that the shrimp can resuspension feed and deposit feed as well (Dworschak, 1987; Nickell & Atkinson, 1995; Coelho et al., 2000a,b). In addition to feeding, these burrows also serve to protect the mud shrimp from desiccation and predation, and provide a habitat for many symbiotic animals and bacteria (e.g. MacGinitie, 1930; Anker et al., 2001; Itani, 2002; Itani et al., 2002; Kinoshita et al., 2003). Thus, research on the burrows of the mud shrimp is important to help understand the ecological characteristics of not only the shrimp but also the benthic community in marine sediments.

The burrow structure of the mud shrimp is typically Y- or U-shaped, that is, the U-shaped section with/without the lower I-shaped section (e.g. Dworschak, 1983; Nickell & Atkinson, 1995; Candisani et al., 2001). Inter- and intra-specific variation in burrow structure is also known, for example highly branched tunnels in *U. deltaura* (Hall-Spencer & Atkinson, 1999), a long and deep shaft in *U. major* (Kinoshita, 2002), and absence of the U-shaped part in some individuals of *U. omissa* (Coelho et al., 2000a). Such variation in burrow structure is supposed to be attributable to differences in the ecology of the shrimp such as feeding mode (Coelho et al., 2000a) or might be due to environmental factors such as sediment type, as has been examined for callianassid shrimps (Griffis & Chavez, 1988; Berkenbusch & Rowden, 2000). However, a non-adaptive, phylogenetic effect might also explain interspecific differences in burrow morphology as suggested by Dworschak & Ott (1993). So far little is known about the role of phylogenetic inheritance as opposed to functional needs in the burrow morphology of upogebiid shrimps.

The objective of the present study is to describe and compare the burrow structure of the upogebiid mud shrimps *Austinogebia narutensis* (Sakai, 1986) and *Upogebia issaeffi* (Balss, 1913) based on the analysis of resin casts *in situ*. In Japan, *A. narutensis* is distributed in lower intertidal to subtidal sandy to muddy shores, whereas *U. issaeffi* is distributed in mid-intertidal boulder shores and sandy to muddy shores (Itani, 2004). At the study site on Mukaishima Island in the Seto Inland Sea, the two species overlapped in their distribution, which enables the burrow morphology of the shrimp to be compared without any complicating effect of environmental condition.

MATERIALS AND METHODS

The study site chosen was at a small tidal flat ($\sim$200 m^2 in area) at Tachibana on a southern coast of Mukaishima Island, Hiroshima Prefecture, Japan (34°2′N 133°12′E), where *Austinogebia narutensis* and *Upogebia issaeffi* occurred sympatrically. Sediment consisted mainly of medium sand (12.2% gravel, 87.3% sand and 0.5% silt–clay). Spring tidal range is as high as 3.5 m.

Burrow casts of the mud shrimp were made from May to July in 1999, using polyester resin (U-PiCa, Japan U-PiCa Company Ltd), which was mixed with a peroxide catalyst (2% by volume) and was poured into the burrows.

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After one or two days, the hardened casts were carefully removed from the sediment. In the laboratory, the depth of each major section, i.e. the upper U-shaped section and the lower section, was measured to the nearest 1 cm as the straight-line vertical distance from the top to the bottom (Figure 1). The distance between the burrow openings (overall width of U-shaped section) was also measured. The entire length of each section, excluding the length of the side branch, was measured to the nearest 1 cm using a measuring tape. The diameters of the cast were measured to the nearest 0.01 cm at six points (four from the U-shaped section and two from the lower section) using a hand caliper. The number of turning chambers and side branches per cast were recorded. The polyester resin was transparent. Each shrimp trapped in a cast was carefully removed and its carapace length was measured to the nearest 0.01 cm using a hand caliper. All individuals were sexed by inspecting for the presence or absence of the first pleopods (present in females) and identified to species.

The differences in burrow measurements between the two species were analysed using the Mann–Whitney *U*-test. To exclude the effect of shrimp size, the ratios of burrow measurements to the mean burrow diameter of each cast were also compared between species. Mean diameter of the burrow was used instead of carapace length of the shrimp, since some specimens had a broken carapace and could not be measured.

RESULTS

Eleven nearly complete burrow casts were recovered for each upogebiid species. Typical burrow casts of *Austinogebia narutensis* and *Upogebia issaeffi* are shown in Figure 2. Measurements of the casts are summarized in Table 1. Casts of both upogebiid species showed similar features. The basic structure of the burrow consisted of the upper U-shaped section and the lower section, with turning chambers and with/without short side branches. The surface of the tunnels was smooth, suggestive of the presence of a burrow lining, but, in two casts of *A. narutensis* and four casts of *U. issaeffi*, a small amount of resin seeped out from the tunnel into the interstices of the surrounding sediment (arrow in Figure 2B), indicating that in these places the tunnel wall was unlined. Tunnels were circular in cross-section and were often constricted at the burrow openings. There was no mound or funnel-shaped part at the burrow openings. In spite of the dense patches of the sea grass *Zostera marina* in the lower intertidal to subtidal area, no plant fragments were found associated with the burrow-cast wall.

Each cast contained a single shrimp. Carapace length of *A. narutensis* ranged from 2.01 to 2.68 cm, and of *U. issaeffi* from 1.30 to 1.75 cm. Mean diameter of the burrows was smaller than the carapace length of the inhabiting shrimp. Sex ratio was not significantly different from 1:1

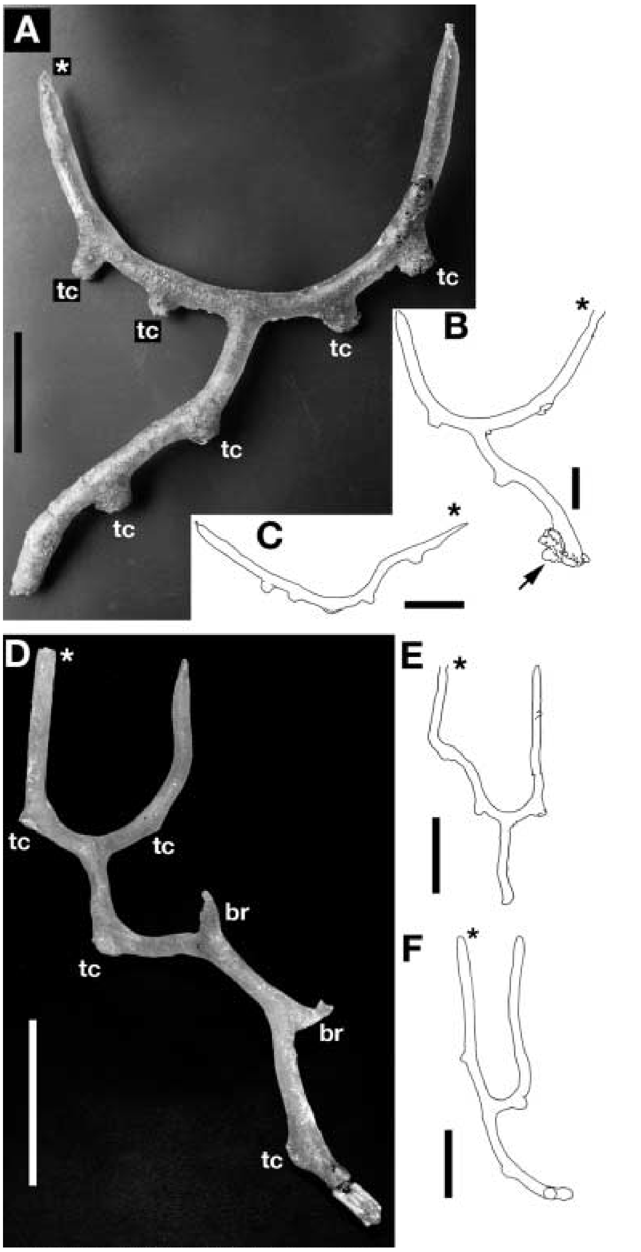

Figure 2. Burrow morphology of *Austinogebia narutensis* and *Upogebia issaeffi*. (A) Cast no. 1 of *A. narutensis*; (B) Cast no. 2 of *A. narutensis*; (C) Cast no. 10 of *A. narutensis*, lacking lower section; (D) Cast no. 4 of *U. issaeffi*; (E) Cast no. 6 of *U. issaeffi*; (F) Cast no. 5 of *U. issaeffi*. The asterisks indicate the burrow openings where resin was poured. tc, turning chamber; br, side branch. Scale bars: 10 cm.

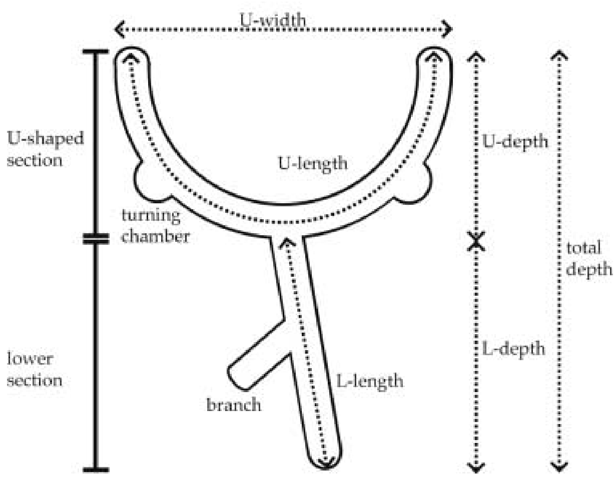

Figure 1. Schematic burrow of upogebiid shrimp indicating dimensions recorded.

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Table 1. *The burrow measurements of* Austinogebia narutensis *and* Upogebia issaeffi *determined from resin casts at Mukaishima Island.*

Cast no.	Burrow depth (cm)	Total length (cm)	Upper U-shaped section Depth (cm)	Upper U-shaped section Width (cm)	Upper U-shaped section Length (cm)	Lower section Depth (cm)	Lower section Length (cm)	No. of turning chambers	No. of side branches	Mean burrow diameter (cm)	Carapace length (cm)	Sex
A. narutensis												
1	49	98	24	35	62	25	36	6	0	2.07	2.28	♀
2	50	118	27	50	72	23	46	5	0	2.36	2.68	♀
3	40	87	14	38	55	26	32	3	1	2.11	2.30	♂
4	39	80	24	25	61	15	19	4	2	1.68	2.01	♂
5	34	72	13	40	50	21	22	2	0	2.05	n.d.	♀
6	37	82	18	33	52	19	30	4	0	1.94	2.09	♀
7	22	54	7	19	33	15	21	3	0	1.94	2.29	♀
8	41	102	21	44	71	20	31	4	0	2.08	n.d.	♂
9	24	68	24	42	68	0	0	4	0	2.17	2.43	♀
10	26	73	26	46	73	0	0	5	0	1.92	2.19	♂
11	26	66	17	40	55	9	11	2	0	2.02	2.20	UN
Mean	35.3	81.8	19.5	37.5	59.3	15.7	22.5	3.8	0.3	2.03	2.27	
U. issaeffi												
1	22	48	22	14	48	0	0	3	0	1.39	1.50	♀
2	35	72	13	4	29	22	43	4	2	1.21	n.d.	♂
3	21	58	13	13	36	8	22	4	1	1.24	1.38	♂
4	31	68	13	9	33	18	35	4	2	1.20	1.32	♂
5	39	79	26	8	57	13	22	4	1	1.22	1.35	♀
6	33	70	21	13	56	12	14	3	0	1.14	1.32	♂
7	60	123	31	10	75	29	48	3	2	1.71	1.75	♀
8	21	45	17	11	40	4	5	2	1	1.19	1.30	♂
9	18	47	13	18	41	5	6	1	3	1.27	1.44	♂
10	18	37	12	11	31	6	6	3	0	1.29	1.47	♂
11	21	45	14	12	37	7	8	3	0	1.15	1.35	♀
Mean	29.0	62.9	17.7	11.2	43.9	11.3	19.0	3.1	1.1	1.27	1.42	
P	n.s.	*	n.s.	**	*	n.s.	n.s.	n.s.	*	**	**	

UN, sex unknown; n.d., no data; *P*, level of significance (Mann–Whitney *U*-test); **, $P<0.01$; *, $P<0.05$; n.s., not significant ($P>0.05$).

for each species (binomial tests; $P>0.05$ in each species). Relationships between mean burrow diameter and carapace length of shrimp, total burrow depth, depth of U-shaped section, and overall width of U-shaped section are shown in Figure 3.

Depths of the burrows were not significantly different between the two species, 35.3 cm on average in *A. narutensis* and 29.0 cm on average in *U. issaeffi*. The deepest burrow (60 cm) was that of *U. issaeffi*. Total lengths of the burrows, and lengths and overall widths of the upper U-shaped section were greater in *A. narutensis*. The number of turning chambers was 3.8 on average in *A. narutensis* and 3.1 on average in *U. issaeffi*, showing no statistical difference. The number of turning chambers in the U-shaped section was not also significantly different (2.8 on average in *A. narutensis* and 2.5 on average in

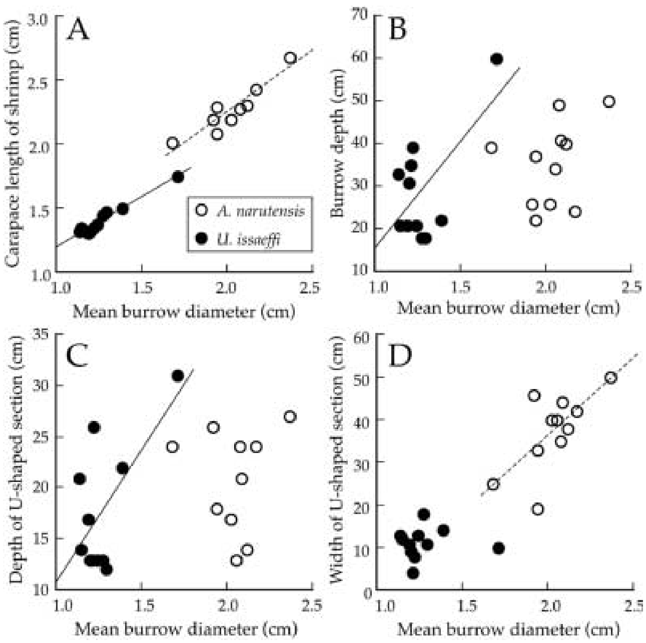

Figure 3. Relationship between mean burrow diameter of *Austinogebia narutensis* (open circle) and *Upogebia issaeffi* (closed circle) and burrow dimensions. Significant regression lines of *A. narutensis* (broken line) and *U. issaeffi* (solid line) are shown. (A) Carapace length of shrimp (*A. narutensis*, $y=0.96x+0.33$, N=9, $R^2=0.865$, $P<0.001$; *U. issaeffi*, $y=0.78x+0.41$, N=10, $R^2=0.950$, $P<0.001$); (B) total burrow depth (*U. issaeffi*, $y=50.0x-34.7$, N=11, $R^2=0.403$, $P<0.05$); (C) depth of U-shaped section (*U. issaeffi*, $y=25.8x-15.2$, N=11, $R^2=0.419$, $P<0.05$); (D) overall width of U-shaped section (*A. narutensis*, $y=36.4x-36.4$, N=11, $R^2=0.463$, $P<0.05$).

Table 2. *The ratios of burrow measurements to the mean diameter (MD) in* Austinogebia narutensis *and* Upogebia issaeffi.

	Burrow depth		Total length		Upper U-shaped section: Depth		Upper U-shaped section: Width		Upper U-shaped section: Length		Lower section: Depth		Lower section: Length	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Austinogebia narutensis	17.4	±4.6	40.2	±7.8	9.7	±3.2	18.3	±3.8	29.3	±5.9	7.7	±4.4	11.0	±6.6
Upogebia issaeffi	22.5	±7.8	48.9	±14.5	13.8	±4.1	8.8	±2.6	34.3	±8.7	8.7	±6.0	14.7	±12.0
P	n.s.		n.s.		*		**		n.s.		n.s.		n.s.	

P, level of siginificance (Mann–Whitney *U*-test); **, $P<0.01$; *, $P<0.05$; n.s., not significant ($P>0.05$).

U. issaeffi). The number of side branches was 0.3 on average in *A. narutensis* and 1.1 on average in *U. issaeffi*, showing a significant difference between the species.

The ratios of burrow measurements to the mean burrow diameter of each cast were compared between the species (Table 2). The width of the U-shaped component of the burrow was significantly wider in *A. narutensis* but its depth was deeper in *U. issaeffi*, indicating that the U-shaped section was wider and shallower in *A. narutensis* than in *U. issaeffi*.

DISCUSSION

The burrow morphology of *Austinogebia narutensis* and *Upogebia issaeffi* is a relatively simple Y-shaped pattern, which is typical of the family Upogebiidae (e.g. Dworschak, 1983; Nickell & Atkinson, 1995; Coelho et al., 2000a). The burrow structure of thalassinidean shrimps has been discussed in relation to the feeding mode (Griffis & Suchanek, 1991; Nickell & Atkinson, 1995). According to the approach of Nickell & Atkinson (1995) when considering a functional interpretation of burrow structure, *A. narutensis* and *U. issaeffi* may be suspension-feeders, as indicated by the features 'the U- or Y- shaped burrow construction' and 'circular tunnel cross section'. Compared with the burrow of *U. major* that is deeper than 2 m (Kinoshita, 2002), burrows of *A. narutensis* and *U. issaeffi* are not so deep. 'Deep burrow' may be indicative of sediment processing for feeding (Nickell & Atkinson, 1995), and in Upogebiidae, the lower section of the burrow of *U. omissa* was associated with deposit-feeding (Coelho et al., 2000a). Deep sediment may not be the primary nutritional source in *A. narutensis* and *U. issaeffi*.

Interspecific differences in the burrow morphology of upogebiid shrimp have not been well illustrated, probably because the structure is more or less a simple U- or Y-shaped pattern, and because the structure might be variable in response to spatially and temporally different environmental conditions. Researches conducted on callianassid thalassinidean shrimps have shown that larger burrows were created in mud than sand (Griffis & Chavez, 1988) and that burrows were smaller in winter (Berkenbusch & Rowden, 2000).

In the present study, some measurements of the burrows of *A. narutensis*, i.e. total length of the burrow and width and length of the U-shaped section, were greater than those of *U. issaeffi*, possibly because *A. narutensis* is the larger species. In contrast, the burrows of *A. narutensis* had a wider and shallower U-shaped section than those of *U. issaeffi* when the ratios of burrow measurements to the mean burrow diameter of each cast were compared. Because the burrow casts were made on the shore where the two species occurred sympatrically, the differences were not in response to environmental factors.

It is possible that the interspecific variation in the upper U-shaped section of the burrows would reflect ecological differences between the two shrimps, such as feeding and anti-predatatory mechanisms. The wide and shallow U-shape of the upper burrow component of *A. narutensis* is a result of oblique tunnels (Figure 2B,C), which might indicate surface access by the shrimp when the burrow is interpreted according to the functional approach of Nickell & Atkinson (1995). In this scenario, *A. narutensis* might sometimes enlarge the constricted burrow openings and gather surface sediment, rich in silt and organic content, for feeding and reinforcement of the burrow wall. However, the burrow of *U. pusilla* does not have oblique tunnels in the upper U-shaped section, although the shrimp is known to come out of its burrow to take surface sediment both in aquaria and *in situ* (Dworschak, 1983, 1987). Thus, oblique tunnels might not be necessary for upogebiid shrimps to access to the sediment surface. Behavioural observations of *A. narutensis* in aquaria are needed to examine how the shrimp uses its burrow.

Upogebiid shrimps are often found in the gut content of fish, for example, in Japan, the dogfish *Mustelus manazo* (Komai et al., 1999) and the eel goby *Taenioides cirratus* (Itani & Uchino, 2003). Because upogebiid shrimps spend considerable time irrigating and/or feeding in the U-shaped section (Dworschak, 1987; Astall et al., 1997), depth of the U-shaped section might be related to anti-predation. For the smaller shrimps, *U. issaeffi*, in particular, a proportionally deeper U-shaped section might reduce the risk of predation.

Side branches were more often found in *U. issaeffi* than in *A. narutensis*. Many side branches might show the feature 'chambered burrows' that indicates deposit feeding (Nickell & Atkinson, 1995). In the case of *U. omissa*, side branches were used to dispose of coarse particles disused in deposit-feeding or burrowing activity (Coelho et al., 2000a). On the other hand, Astall et al. (1997) observed that *U. deltaula* and *U. stellata* used side branches as sites for moulting and depositing exuvia, and, once ecdysis was finished, the branches were closed off. Accordingly, the function of side branches might be associated with two behavioural patterns, and we cannot conclude whether *U. issaeffi* use side branches for one of the two purposes or both purposes, or for another unknown purpose.

Another explanation of the interspecific differences in the burrow morphology is phylogenetic (Dworschak & Ott, 1993). The genus *Austinogebia* is diagnosed by presumably nonadaptive characters, such as the infraorbital spines, the knob on the proximal shoulder of the uropod exopod, and so on (Ngoc-Ho, 2001). The burrow morphology of *Austinogebia* may also be characterized by several nonadaptive features and is different from those of the sympatric *Upogebia*.

In conclusion, the differences in the burrow morphology of the sympatric upogebiid shrimp detected in the present study will be due to the difference in the shrimp species, whether they are adaptive or not. To better understand the function of the burrow morphology, future studies must examine ecological differences between the two species, such as particle-size analyses of the gut contents and functional morphology of the feeding appendages, as well as behavioural observation of the shrimp in aquaria. Investigations of environmental plasticity of the burrow morphology may also be fruitful.

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