Journal of the Marine Biological Association of the United Kingdom, 2010, 90(5), 947–952. © Marine Biological Association of the United Kingdom, 2010
doi:10.1017/S0025315410000214

Burrow morphology and associated animals of the mud shrimp *Upogebia yokoyai* (Crustacea: Thalassinidea: Upogebiidae)

KYOKO KINOSHITA[1,4], GYO ITANI[2] AND TAKASHI UCHINO[3]

[1]Faculty of Environmental and Symbiotic Sciences, Prefectural University of Kumamoto, 3-1-100 Tsukide, Kumamoto 862-8502, Japan, [2]Faculty of Education, Kochi University, 2-5-1 Akebono-cho, Kochi 780-8520, Japan, [3]Miyagi Prefectural Tajiri Sakura High School, 137, Aza-Nakaniibori, Tajirinumabe, Oosaki-shi, Miyagi 989-4308, Japan, [4]Present address: Research Center for Environmental Risk, National Institute for Environmental Studies, 16-2, Onogawa, Tsukuba, Ibaraki 305-8506, Japan

The burrow morphology of the mud shrimp Upogebia yokoyai *was investigated on a tidal flat in the Nanakita River mouth in north-eastern Japan using* in situ *resin casting. A total of 26 burrow casts were recovered, including those of 16 large shrimps and 10 small shrimps. Burrows of large shrimp were relatively simple and Y-shaped with depth exceeding 1.2 m. Although burrow diameter was related to shrimp size, correlation with other burrow measurements was low. Three large casts were connected to others via a narrow horizontal portion potentially reflecting mating behaviour of the shrimp. Burrows of small shrimp were more complex than those of the other upogebiids and were connected to large burrows. In 6.7% of cases, bopyrid isopods were present in the branchial chamber. Three species of gobies were found in the burrows. These data show that burrows of* U. yokoyai *serve not only as a recruitment site for conspecific shrimp, but also as habitat for other animals in the tidal flat.*

Keywords: burrow morphology, associated animals, mud shrimp, *Upogebia yokoyai*

Submitted 27 April 2009; accepted 29 November 2009; first published online 2 June 2010

INTRODUCTION

Thalassinidean mud shrimps are a dominant burrowing group in marine and estuarine sediments. Bioturbation by the shrimps during burrow construction as well as their feeding patterns have significant effects on the physical, chemical and microbiological characteristics of the sediment (Posey *et al.*, 1991; Ziebis *et al.*, 1996; Nates & Felder, 1998; Bird *et al.*, 2000; Kinoshita *et al.*, 2003a, 2008; Papaspyrou *et al.*, 2005). The structures of burrows of several thalassinidean shrimps have been previously described (see Griffis & Suchanek, 1991; Nickell & Atkinson, 1995 for reviews). Generally, upogebiid shrimp burrows are distinctly U-shaped or Y-shaped and are divided into an upper section, which is U-shaped, and a lower more vertical shaft (Dworschak, 1983; Hall-Spencer & Atkinson, 1999; Coelho *et al.*, 2000; Candisani *et al.*, 2001; Kinoshita, 2002; Kinoshita & Itani, 2005; Li *et al.*, 2008). The burrows of these shrimps often serve as habitats for other animals, such as copepods, phoronid worms, bivalves, crabs and gobies (MacGinitie 1930; Kato & Itani, 1995; Astall *et al.*, 1996; Itani *et al.*, 2002; Itani, 2002; Itoh & Nishida, 2002; Kinoshita, 2002; Santagata, 2004; Nara *et al.*, 2008). Thus, these shrimps play a major role in structuring the local benthic community.

Corresponding author:
K. Kinoshita
Email: kinoshita.kyoko@nies.go.jp

Upogebia yokoyai Makarov is a common member of the family Upogebiidae on tidal flats in Japan (Itani, 2004). The ecology of this species has been studied with respect to its life history in a local population in western Japan (Itani, 2001) and in relation to its trophic level (Kanaya *et al.*, 2007). *Upogebia yokoyai* was often confused with *U. major*. For example, some reports on the respiration characteristics (Mukai & Koike, 1984) and gill-cleaning mechanism (Batang & Suzuki, 2003) of *U. major* are in fact references to *U. yokoyai* (see Sakai & Mukai, 1991; Itani, 2004). Therefore, some aspects of the physiology and ecology of *U. yokoyai* are still poorly understood.

In this study, the burrow structure of *U. yokoyai* was investigated using *in situ* resin casting. The characteristics of the shrimp burrow are compared with those of other upogebiid species. Additionally, we report on associated animals found attached to the shrimp and in their burrows.

MATERIALS AND METHODS

The study site chosen was a tidal flat in Nanakita River mouth (38°15′N 141°00′E), Miyagi prefecture, in north-eastern Japan. The sediment was mainly sand (1.4% gravel, 97.4% sand and 1.2% silt–clay). The horizontal distance between the lowest spring tide line and the lower edge of the reed marsh was approximately 20 m. The mean number of burrow openings was 592 m^{-2}, reaching a maximum of 720 m^{-2} in some areas (Kinoshita, personal observation). Burrow casts were made in April 2000, using polyester resin

Table 1. Burrow dimensions of *Upogebia yokoyai* from resin casts. Connected casts are indicated with the same letters.

Cast No.	Total length (cm)	Burrow depth (cm)	Upper U-shaped section			Lower section		Mean burrow diameter (cm)	Surface area (cm^2)	Volume (cm^3)	Carapace length (cm)	Sex
			Depth (cm)	Width (cm)	Length (cm)	Depth (cm)	Length (cm)					
Large casts												
1	196.2	105.1	27.5	40.3	71.5	77.6	107.0	1.87	1,155	541	ND	UN
2[a]	185.1	97.0	32.5	13.5	84.2	64.5	81.0	1.95	1,135	555	2.10	M
3[b]	152.8	98.0	22.7	ND	47.8	75.3	105.0	1.75	838	366	1.89	F
4	157.6	109.4	28.3	ND	48.0	81.1	101.8	1.81	894	403	1.97	F
5[c]	174.9	110.3	30.5	10.2	77.4	79.8	97.5	1.72	947	408	1.88	F
6	172.2	115.2	27.6	29.0	74.6	87.6	97.6	1.75	945	413	1.93	F
7[d]	136.5	81.0	31.5	23.5	75.1	49.5	61.4	1.72	739	318	1.92	F
8[e]	166.9	108.3	25.1	ND	61.6	83.2	100.0	1.79	938	420	2.03	M
9[e]	130.9	104.6	22.8	ND	27.2	81.8	97.7	1.78	733	326	1.98	F
10[f]	168.8	77.5	28.5	ND	73.2	49.0	57.0	1.84	978	451	2.03	M
11[f]	ND	85.1	19.7	ND	ND	65.4	75.5	1.38	ND	ND	ND	UN
12	137.8	78.3	27.9	27.1	72.2	50.4	65.6	1.88	814	383	2.05	M
13[g]	180.8	112.8	38.3	ND	86.6	74.5	94.2	1.87	1,061	496	2.02	M
14[g]	172.7	97.4	46.3	ND	105.1	51.1	58.4	1.67	905	377	1.89	F*
15[h]	187.3	124.3	24.4	34.3	65.3	99.9	115.0	2.01	1,181	593	2.22	M
16	208.0	110.1	23.8	22.2	61.2	86.3	130.0	1.73	1,128	487	ND	F
Mean	168.6	100.9	28.6	25.0	68.7	72.3	90.3	1.78	944	420	1.99	
± SD	22.2	14.1	6.5	10.0	18.5	15.7	21.5	0.14	147	83	0.10	
Small casts												
17[a]	36.3							0.46	52	6	0.54	J
18[b]	83.4							0.95	249	59	1.18	F
19[b]	9.1							0.55	16	2	0.57	J
20[c]	31.3							0.64	63	10	0.77	F
21[d]	22.4							0.48	33	4	0.61	J
22[e]	46.4							0.47	68	8	0.59	J
23[g]	57.7							0.55	100	14	0.75	J
24[g]	47.5							0.55	81	11	0.68	J
25[h]	72.8							0.60	136	20	0.77	J
26[h]	52.2							0.51	83	11	0.64	J
Mean	45.9							0.57	83	12	0.71	
± SD	22.4							0.15	66	17	0.19	

ND, no data; M, males; F, females; J, juveniles; UN, sex unknown; *, parasitized specimens.

(Eporak® G-226P, Nippon Shokubai Co. Ltd, Japan), as recommended by Hamano (1990). Liquid resin was poured into frames that encompassed several burrows and the hardened casts were carefully removed from the sediment after 4 days. All shrimps appearing on the surface following removal of the casts were collected by hand. In the laboratory, casts were examined, photographed, and measured as recommended by Kinoshita & Itani (2005). Burrow depth was measured as the straight-line vertical distance from the top of the cast to the bottom. The length of each major section—the upper U-shaped and the lower shaft—was measured to the nearest 0.1 cm using a measuring tape. The distance between the burrow openings was alo measured (overall width of U-shaped section). Cast diameters were measured to the nearest 0.01 cm using a hand caliper, thereby enabling individual burrow surface area and burrow volume to be calculated from total length and mean burrow diameter. The number of turning chambers and branches per cast were also recorded.

Shrimps trapped in the cast were carefully removed and fixed with 10% neutralized seawater–formalin. Carapace length (CL) was measured from the tip of the rostrum to the rear edge of the carapace (nearest 0.01 cm) using hand calipers. Large shrimp (CL > 0.77 cm) were sexed by inspecting for the presence or absence of the first pleopods (present in females) while smaller shrimps were considered juveniles and were not sexed. All other animals caught during casting were identified.

RESULTS

A total of 26 burrow casts were recovered. Casts were separated into two size-classes (large and small) for the purpose of comparison; 16 large casts and 10 smaller casts were obtained (Table 1). The large burrows consisted of an upper U-shaped section and a lower shaft section, with or without turning chambers and branches (Figure 1A–C). The total burrow length ranged from 130.9 to 208.0 cm and the burrow depth ranged from 77.5 to 124.3 cm. Further, the depth of the U-shaped section ranged from 19.7 to 46.3 cm, and the length from 27.2 to 105.1 cm. Depth of the lower shaft ranged from 49.0 to 99.9 cm, and the length from 57.0 to 130.0 cm. The burrow surface area ranged from 733 to

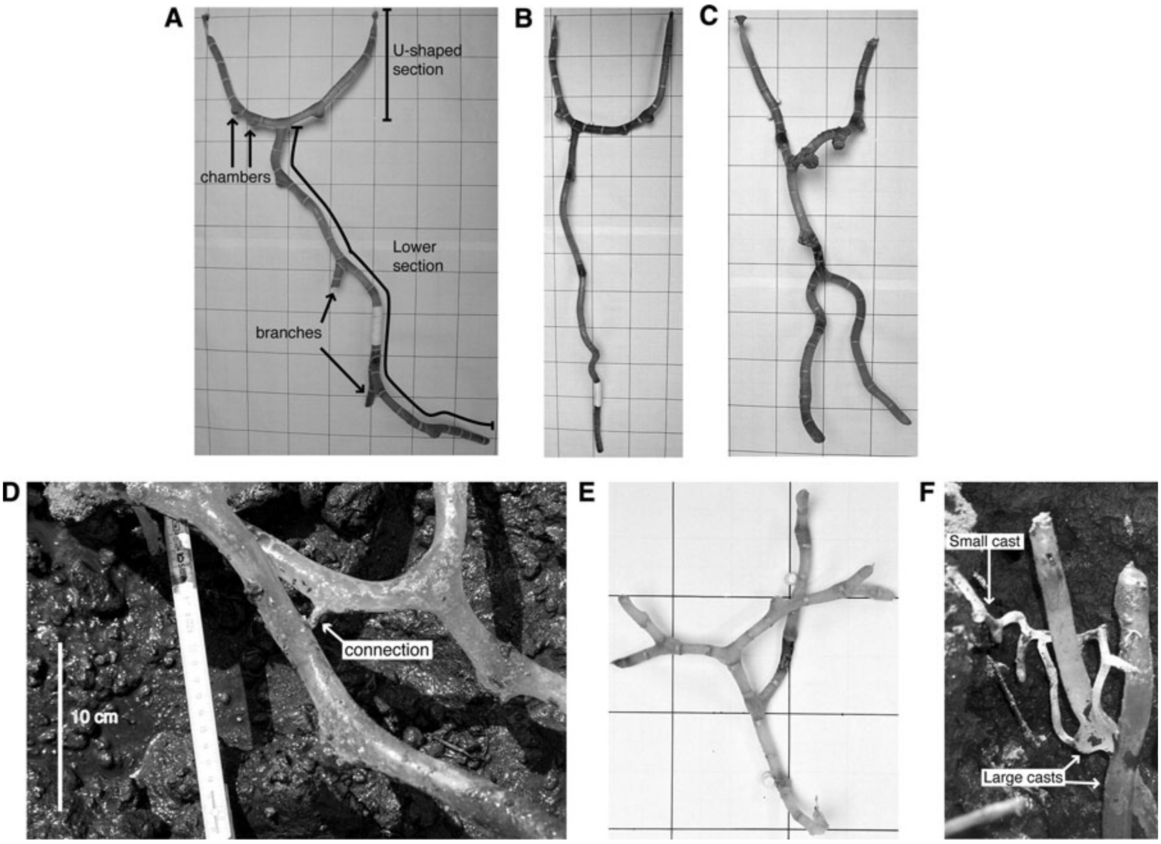

Fig. 1. Typical burrow casts (A–C, E) and close-up showing connection between casts (D, F). (A) Cast number 1; (B) cast number 6; (C) cast number 10; (D) cast number 13 (left) and 14 (right); (E) cast number 18; (F) cast number 22 (small cast, left), 9 (large cast, center) and 8 (large cast, right). Background squares (A–C, E) 10 cm × 10 cm.

1181 cm^2, and burrow volume ranged from 318 to 593 cm^3. Three pairs of large casts were connected through a narrow horizontal connection (Figure 1D). The small burrows were more complex in structure (Figure 1E) and were connected to the large burrows (Figure 1F). The total length of the small burrows ranged from 9.1 to 83.4 cm, the surface area ranged from 7.8 to 124.7 cm^2, and the burrow volume ranged from 2 to 59 cm^3. Each cast contained only a single shrimp. Carapace length measurements of the large shrimp ranged from 1.88 to 2.22 cm, and those of the small shrimp ranged from 0.54 to 1.18 cm. Mean burrow diameter of the large casts ranged from 1.38 to 2.01 cm, and from 0.47 to 0.95 cm for the small casts. Relationships between the CL of the shrimp and mean burrow diameter, total burrow length, burrow depth and depth of the U-shaped section are shown in Figure 2. Mean burrow diameter and total burrow length were related to CL ($r^2 = 0.996$ and 0.933), but no significant relationships were found with other burrow measurements ($r^2 < 0.5$). Total burrow length was not related to CL ($r^2 = 0.128$) for large casts. The number of chambers in the large casts ranged from 2 to 9, while that in the small casts ranged from 0 to 9. The number of branches in the large casts ranged from 0 to 3, while that in the small casts ranged from 1 to 6.

Three size-classes of shrimp could be identified in a total of 163 individuals of *U. yokoyai* collected (less than 0.8 cm CL, 1.1–1.3 cm CL, and over 1.5 cm CL; Figure 3). The sex-ratio of the shrimp with CL over 0.77 cm was 3:7 (male:female). Some shrimps (6.7%; 7 males and 4 females) showed branchial chambers occupied by the bopyrid isopod *Gyge ovalis*. Sizes of the affected shrimps were 1.53–1.90 cm CL (Figure 3). Four gobies (one *Chaneogobius macrognathos* and *Chaneogobius mororanus*; one each and two *Eutaeniichthys gilli*) were collected from the large burrow.

DISCUSSION

The burrow structure of *Upogebia yokoyai* is generally Y-shaped. This is the most common pattern observed among the family Upogebiidae (Nickell & Atkinson, 1995). However, these detailed features are different in each species. Kinoshita & Itani (2005) compared the burrow structure of *Austinogebia narutensis* and *Upogebia issaeffi* that lived in the same tidal flat. The burrow of *A. narutensis* tended to have a wider and shallower U-shaped section than those of *U. issaeffi* though the difference of each shrimp size was considered. The differences in the burrow structure of the two shrimps were due to potentially non-adaptive phylogenetic interspecific differences. The data show that mean burrow diameter and total burrow length of the burrow of *U. yokoyai* were related to shrimp size, but no significant relationships were found with other burrow measurements. Upogebiid shrimps tend to extend their burrow vertically, with linear or exponential increases in the upper U-shaped section and the lower section in association with the shrimp size (Dworschak, 1983; Coelho *et al.*, 2000; Kinoshita, 2002). Li *et al.* (2008) compared the burrow structures of *Austinogebia edulis* that lived on muddy shore and sandy shore, and suggested that the different sediment

https://doi.org/10.1017/S0025315410000214 Published online by Cambridge University Press

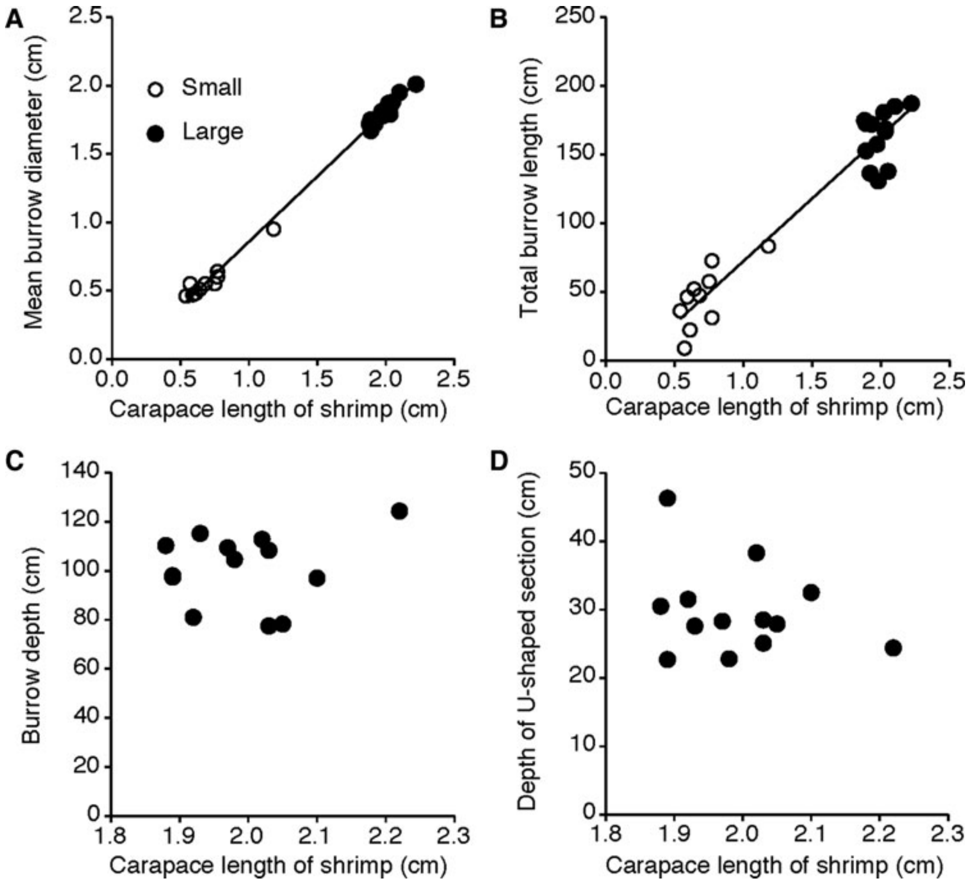

Fig. 2. Relationship between carapace length of shrimp and burrow measurement. (A) mean burrow diameter ($y = 0.95x - 0.10$, $r^2 = 0.996$, N = 23); (B) burrow total length ($y = 91.23x - 18.61$, $r^2 = 0.933$, N = 23); (C) burrow depth ($y = 28.50x + 44.26$, $r^2 = 0.035$, N = 13); D, depth of U-shaped section ($y = -17.10x + 63.82$, $r^2 = 0.064$, N = 13).

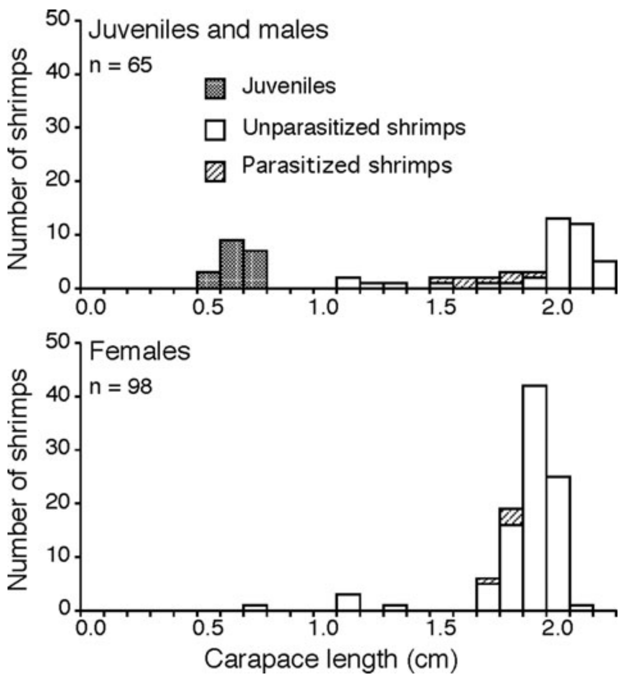

Fig. 3. Length–frequency histogram of juvenile and male *Upogebia yokoyai* sampled on Nanakita River tidal-flat (top) and female shrimp (bottom). Parasitization by the bopyrid isopod *Gyge ovalis* is also indicated.

property affected the relationship between burrow parameters (burrow depth and width of U-shaped section) and shrimp size. Therefore, the burrow structure in the present study might be influenced by not only this species characteristic but also the sediment property. An investigation of burrows in different environments should be made to better understand the burrow morphology of *U. yokoyai*. Burrows of small *U. yokoyai* were complex and always connected to large burrows. Juveniles of other thalassinidean shrimps have also been shown to use conspecific burrows as recruitment sites (Forbes, 1973; Frey & Howard, 1975; Tamaki *et al.*, 1992; Felder & Griffis, 1994; Candisani *et al.*, 2001). Juveniles of *N. harmandi* [= *Callianassa japonica*] use the adult burrows until they are able to construct their own, avoiding heavy bioturbation by adults (Tamaki *et al.*, 1992). In contrast, juveniles of *U. major* and *U. omissa* occupied their own independent simple U- or Y-shaped burrows (Coelho *et al.*, 2000; Kinoshita, 2002). At our study site, the physical disturbance caused by the water and tidal current is likely to be always present, but small *U. yokoyai* that use large conspecific adult burrows may have an advantage in terms of survival.

Our data show that *U. yokoyai* creates a quite deep burrow. Although the upper U-shaped section is generally less than 47 cm from the sediment surface, the lower shaft extends much deeper (maximum depth of 124 cm in this study). In most Upogebiid shrimps, burrow depth is less than 100 cm (Li *et al.*, 2008). Thus, *U. yokoyai* is one of the deep burrowers in this family along with *U. major* whose burrows reach the exceptional depth of 208 cm (Kinoshita, 2002). Upogebiid shrimps use the U-shaped section for filter feeding and irrigation activities (Dworschak, 1983; Allanson *et al.*, 1992), yet the function of the lower section is unclear (Astall *et al.*, 1997). Several authors suggest that the lower section may act as an anti-predator device (Astall *et al.*, 1997; Candisani *et al.*, 2001; Li *et al.*, 2008) and Kinoshita *et al.* (2003b) report that the vertical expansion of the lower section of the burrow of *U. major* provides refuge from predators and physical stress, allowing the shrimps to survive for a long time. We hypothesize that the lower section may also be used as a shelter when the U-shaped section breaks because of a physical disturbance caused by wave and tidal action. Even if the U-shaped section breaks, the shrimp can repair it using the lower section without emerging from the burrow. Further behavioural studies on these mud shrimp would be necessary to clarify this hypothesis.

We observed connections from three large burrows to other large burrows. These burrows appear to be purposely connected. Four casts with connections were inhabited by male–female pairs suggesting possible mating behaviour of the shrimp. Other upogebiid shrimps have also been found in inter-connected burrows (Coelho *et al.*, 2000; Candisani *et al.*, 2001; Li *et al.*, 2008) and Candisani *et al.* (2001) reported that burrows of *Upogebia noronhensis* with additional branches resulted from male searches for females during breeding.

Gobies are frequently found in thalassinid shrimp burrows (Kinoshita, 2002; Kneer *et al.*, 2008). Three species of gobies were collected when casting the burrow of *U. yokoyai*. These species are commonly found outside of the shrimp burrows (Kanou *et al.*, 2000) and the shrimp burrows may be used only temporarily when the mudflat is exposed. The relationship merits further investigation. The bopyrid isopod *G. ovalis* was found at a prevalence of 6.7% in shrimps less than 2 cm CL. Itani (2001) reported that bopyrid isopods were present in the branchial chamber of 10.1% of *U. yokoyai* on a tidal flat in Tonda River mouth in western Japan. While it is well known that the isopods exert a negative influence on the reproduction and metabolism of their hosts (Tucker, 1930; Hughes, 1940; Smith *et al.*, 2008), further investigation would be necessary to demonstrate such a negative effect on growth of *U. yokoyai*.

In conclusion, burrows of *U. yokoyai* are relatively simple and Y-shaped, but depths exceed 1.2 m. Burrow diameter and total burrow length were related to shrimp size, but no significant relationships were found with other burrow measurements on the Nanakita River tidal-flat. Small *U. yokoyai* create their own burrows which are connected to the burrows of large conspecifics. This strategy may help the small shrimps avoid physical or other stresses, but experimental work is required to test this. Some large casts were connected to other large casts through a narrow connection suggesting subterranean mating behaviour of the shrimp. One species of bopyrid isopod and three species of gobies that appear to be endoeketes were found to be associated with the shrimp. Thus both the shrimp body and its burrow provide a habitat for other animals in the tidal flat community.

ACKNOWLEDGEMENTS

We thank the following contributors for their superb cooperation, without which this paper could never have been completed. T. Sunobe graciously identified the gobies. T. Toya and S. Takagi assisted in the field observations. R. S. Lavin assisted in editing the English version of the manuscript. Thanks are also due to the Executive Editor and referees for providing valuable comments and suggestions.

REFERENCES

Allanson B.R., Skinner D. and Imberger J. (1992) Flow in prawn burrows. *Estuarine, Coastal and Shelf Science* 35, 253–266.

Astall C.M., Taylor A.C. and Atkinson R.J.A. (1996) Notes on some branchial isopods parasitic on upogebiid mud-shrimps (Decapoda: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom* 76, 821–824.

Astall C.M., Taylor A.C. and Atkinson R.J.A. (1997) Behavioural and physiological implication of a burrow-dwelling lifestyle for two species of upogebiid mud-shrimp (Crustacea: Thalassinidea). *Estuarine, Coastal and Shelf Science* 44, 155–168.

Batang Z.B. and Suzuki H. (2003) Gill-cleaning mechanisms of the burrowing thalassinidean shrimps *Nihonotrypaea japonica* and *Upogebia major* (Crustacea: Decapoda). *Journal of Zoology, London* 261, 69–77.

Bird F.L., Boon P.I. and Nichols P.D. (2000) Physicochemical and microbial properties of burrows of the deposit-feeding thalassinidean ghost shrimp *Biffarius arenosus* (Decapoda: Callianassidae). *Estuarine, Coastal and Shelf Science* 51, 279–291.

Candisani L.C., Sumida P.Y.G. and Pires-Vanin A.M.S. (2001) Burrow morphology and mating behaviour of the thalassinidean shrimp *Upogebia noronhensis*. *Journal of the Marine Biological Association of the United Kingdom* 81, 799–803.

Coelho V.R., Cooper R.A. and Rodrigues S.A. (2000) Burrow morphology and behavior of the mud shrimp *Upogebia omissa* (Decapoda: Thalassinidea: Upogebiidae). *Marine Ecology Progress Series* 200, 229–240.

Dworschak P.C. (1983) The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea): I. The burrows. *P.SZNI: Marine Ecology* 4, 19–43.

Forbes A.T. (1973) An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea) *Marine Biology* 22, 361–365.

Frey R.W. and Howard J.D. (1975) Endobenthic adaptations of juvenile thalassinidean shrimp. *Bulletin of the Geological Society of Denmark* 24, 283–297.

Griffis R.B. and Suchanek T.H. (1991) A model of burrow architecture and trophic modes in thalassinidean shrimp (Decapoda: Thalassinidea). *Marine Ecology Progress Series* 79, 171–183.

Hall-Spencer J.M. and Atkinson R.J.A. (1999) *Upogebia deltaura* (Crustacea: Thalassinidea) in Clyde Sea maerl beds, Scotland. *Journal of the Marine Biological Association of the United Kingdom* 79, 871–880.

Hamano T. (1990) How to make casts of the burrows of benthic animals with polyester resin. *Benthos Research* 39, 15–19.

Hughes T.E. (1940) The effects on the fat and starch metabolism of *Gebia* by the parasite *Gyge branchialis*. *Journal of Experimental Biology* 17, 331–336.

Itani G. (2001) Population characteristics of *Upogebia yokoyai* (Crustacea, Decapoda, Thalassinidea) at a tidal flat in southern Wakayama, Japan. *Nanki Seibutsu* 43, 1–5.

https://doi.org/10.1017/S0025315410000214 Published online by Cambridge University Press

Itani G. (2002) Two types of symbioses between grapsid crabs and a host thalassinidean shrimp. *Publications of the Seto Marine Biological Laboratoy* 39, 129–137.

Itani G. (2004) Distribution of intertidal upogebiid shrimp (Crustacea: Decapoda: Thalassidea) in Japan. *Contributions from the Biological Laboratory, Kyoto University* 29, 383–399.

Itani G., Davie P.J.F. and Takeda M. (2002) Taxonomic notes on *Acmaeopleura balssi* Shen, 1932 and *A. toriumii* Takeda, 1974 (Crustacea, Brachyra, Grapsidae) from Japanese waters. *Bulletin of the National Science MuseumSeries A (Zoology)* 28, 43–50.

Itoh H. and Nishida S. (2002) A new species of *Hemicyclops* (Copepoda, Poecilostomatoida) from burrows of the mud shrimp *Upogebia major* in an estuarine mud-flat in Tokyo Bay, Japan. *Hydrobiologia* 474, 139–146.

Kanaya G., Takagi S., Nobata E. and Kikuchi E. (2007) Spatial dietary shift of macrozoobenthos in a brackish lagoon revealed by carbon and nitrogen stable isotope ratios. *Marine Ecology Progress Series* 345, 117–127.

Kanou K., Koike T. and Kohno H. (2000) Ichthyofauna of tidelands in the inner Tokyo Bay, and its diversity. *Japanese Journal of Ichthyology* 47, 115–129.

Kato M. and Itani G. (1995) Commensalism of a bivalve, *Peregrinamor ohshimai*, with a thalassinidean burrowing shrimp, *Upogebia major. Journal of the Marine Biological Association of the United Kingdom* 75, 941–947.

Kinoshita K. (2002) Burrow structure of the mud shrimp *Upogebia major* (Decapoda: Thalassinidea: Upogebiidae). *Journal of Crustacean Biology* 22, 474–480.

Kinoshita K. and Itani G. (2005) Interspecific differences in the burrow morphology between the sympatric mud shrimps, *Austinogebia narutensis* and *Upogebia issaeffi* (Crustacea: Thalassinidea: Upogebiidae). *Journal of the Marine Biological Association of the United Kingdom* 85, 943–947.

Kinoshita K., Wada M., Kogure K. and Furota T. (2003a) Mud shrimp burrows as dynamic traps and processors of tidal-flat materials. *Marine Ecology Progress Series* 247, 159–164.

Kinoshita K., Nakayama S. and Furota T. (2003b) Life cycle characteristics of the deep-burrowing mud shrimp *Upogebia major* (Thalassinidea: Upogebiidae) on a tidal flat along the northern coast of Tokyo Bay. *Journal of Crustacean Biology* 23, 318–327.

Kinoshita K., Wada M., Kogure K. and Furota T. (2008) Microbial activity and accumulation of organic matter in the burrow of the mud shrimp, *Upogebia major* (Crustacea: Thalassinidea). *Marine Biology* 153, 277–283.

Kneer D., Asmus H. and Vonk J.A. (2008) Seagrass as the main food source of *Neaxius acanthus* (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutierei* (Thalassinidea: Callianassidae). *Estuarine, Coastal and Shelf Science* 79, 620–630.

Li H.Y., Lin F.-J., Chan B.K.K. and Chan T.-Y. (2008) Burrow morphology and dynamics of mud shrimp in Asian soft shores. *Journal of Zoology* 274, 301–311.

MacGinitie G.E. (1930) The natural history of the mud shrimp *Upogebia pugettensis* (Dana). *Annals and Magazine of Natural History, Series 10* 6, 36–44, plate I – III.

Mukai H. and Koike I. (1984) Behavior and respiration of the burrowing shrimps *Upogebia major* (De Haan) and *Callianassa japonica* (De Haan). *Journal of Crustacean Biology* 4, 191–200.

Nara M., Akiyama H. and Itani G. (2008) Macrosymbiotic association of the myid bivalve *Cryptomya* with thalassinidean shrimps: examples from modem and Pleistocene tidal flats of Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 261, 100–104.

Nates S.F. and Felder D.L. (1998) Impacts of burrowing ghost shrimp, genus *Lepidophthalmus* Crustacea: Decapoda: Thalassinidea, on penaeid shrimp culture. *Journal of the World Aquaculture Society* 29, 188–210.

Nickell L.A. and Atkinson R.J.A. (1995) Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Marine Ecology Progress Series* 128, 181–197.

Papaspyrou S., Gregersen T., Cox R., Thessalou-Legaki M. and Kristensen E. (2005) Sediment properties and bacterial community in burrows of the ghost shrimp *Pestarella tyrrhena* (Decapoda: Thalassinidea). *Aquatic Microbial Ecology* 38, 181–190.

Posey M.H., Dumbauld B.R. and Armstrong D.A. (1991) Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *Journal of Experimental Marine Biology and Ecology* 148, 283–294.

Sakai K. and Mukai H. (1991) Two species of *Upogebia* from Tokushima, Japan, with a description of a new species, *Upogebia trispinosa* (Crustacea: Decapoda: Thalassinidea). *Zoologische Mededelingen* 65, 317–325.

Santagata S. (2004) A waterborne behavioral cue for the actinotroch larva of *Phoronis pallida* (Phoronida) produced by *Upogebia pugettensis* (Decapoda: Thalassinidea). *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 207, 103–115.

Smith A.E., Chapman J.W. and Dumbauld B.R. (2008) Population structure and energetics of the bopyrid isopod parasite *Orthione griffenis* in mud shrimp *Upogebia pugettensis. Journal of Crustacean Biology* 28, 228–233.

Tamaki A., Ikebe K., Muramatsu K. and Ingole B. (1992) Utilization of adult burrows by juveniles of the ghost shrimp, *Callianassa japonica* Ortmann: evidence from resin casts of burrows. *Researches on Crustacea* 21, 113–120.

Tucker B.W. (1930) On the effects of an epicaridan parasite, *Gyge branchialis*, on *Upogebia littoralis. Quarterly Journal of Microscopical Science* 74, 1–118.

and

Ziebis W., Forster S., Huettel M. and Jørgensen B.B. (1996) Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature* 382, 619–622.

Correspondence should be addressed to:
K. Kinoshita
Research Center for Environmental Risk
National Institute for Environmental Studies
16-2, Onogawa, Tsukuba, Ibaraki 305-8506, Japan
email: kinoshita.kyoko@nies.go.jp