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Distribution of intertidal upogebiid shrimp (Crustacea: Decapoda: Thalassinidea) in Japan

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ABSTRACT The distributions of six intertidal species of Upogebiidae were determined by collecting shrimp from 74 sites on tidal flats and boulder beaches in Japan, from northern Honshu (the main island of Japan) to the Ryukyu Archipelago (southwestern Japan). *Upogebia major*, *U. issaeffi*, and *Austinogebia narutensis* were not found in the Ryukyu Archipelago, whereas *U. carinicauda* and *U. pugnax* were collected only from the Ryukyus or warmer regions exposed to the Kuroshio Current. *Upogebia yokoyai* was collected all over Japan and was the most common species in this study. From the viewpoint of habitat, *U. yokoyai* and *U. issaeffi* were unique in that the former was distributed mainly on brackish tidal flats and the latter mainly on boulder beaches. The identity of the upogebiid shrimp in some reports was corrected.

KEY WORDS Thalassinidea / Upogebiidae / *Upogebia* / *Austinogebia* /distribution / tidal flat

Introduction

Mud shrimp of the family Upogebiidae are common burrowers in shallow waters worldwide (Dworschak, 2000). They construct U- or Y-shaped burrows in soft sediment and create water currents with their rhythmically stroking pleopods (Mukai and Koike, 1984; Dworschak, 1987; Nickell and Atkinson, 1995; Astall et al., 1997). Some upogebiids bore into sponges or corals, making U-shaped burrows (Scott et al., 1988; Griffis and Suchanek, 1991). Upogebiids feed mainly on suspended matter strained from the water using the setal basket formed from the first and second pereiopods (MacGinitie, 1930), but several species are also able to feed on deposits (Dworschak, 1987; Griffis and Suchanek, 1991; Coelho et al., 2000).

Fourteen species of Upogebiidae have been reported from Japanese waters (Sakai, 1982; Sakai, 1987; Sakai and Mukai, 1991; Sakai and Takeda, 1995; Komai et al., 1999). Irrespective of the high diversity of upogebiid shrimp in Japanese waters, most ecological studies of upogebiid shrimp have been confined to *Upogebia major* and *U. yokoyai* (see the Discussion for the identity of the shrimp in some reports). For *U. major*, studies have examined the life history (Lützen et al., 2001; Kinoshita et al., 2003a), histology of the testis (Ishikawa, 1891; Oka, 1941), larval development (Konishi, 1989), burrow morphology and its environment (Ohshima, 1967; Hamano, 1990; Kinoshita, 2002; Kinoshita et al., 2003b), and symbiotic animals (Shiino, 1937; Shôji, 1938; Shiino, 1939; Dotu, 1954; Kato and Itani, 1995; Sakai et al., 1995; Miya, 1997; Hayashi, 1998; Sato et

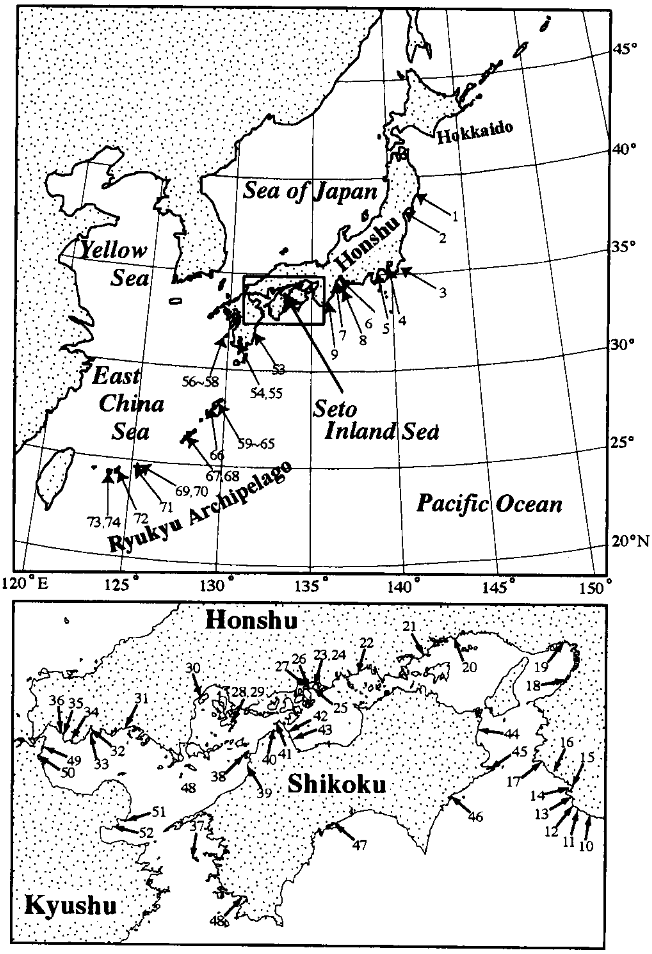

Fig. 1. Map of Japanese waters showing the collection sites of thalassinidean shrimps. The enlarged map shows the Seto Inland Sea.

al., 2001; Itani, 2002; Itani and Kato, 2002; Itoh and Nishida, 2002; Kinoshita, 2002). For *U. yokoyai*, studies have examined habitat (Sakai et al., 1988), the life history (Itani, 2001), gill cleaning (Batang and Suzuki, 2003), respiration (Mukai and Koike, 1984), the burrow environment (Koike and Mukai, 1983), the effect of bioturbation on community structure (Mukai, 1992), and symbiotic animals (Itani et al., 1996; Itani and Kato, 2002).

For the other upogebiid species, other than taxonomic studies, the only reports are on the internal asymmetry of *A. narutensis* (Imafuku, 1993) and animals symbiotic with *U. issaeffi*, *U. carinicauda*, *U. pugnax*, and *A. narutensis* (Shiino, 1958; Shiino, 1964; Kato and

Itani, 1995; Sakai et al., 1995; Kato and Itani, 2000; Itani and Kato, 2002; Itani et al., 2002). To better understand the biology of upogebiid shrimp in Japan, shrimp were collected from more than 70 sites. This study describes the distributions of six intertidal species and discusses the biogeography of these shrimp and their habitat characteristics.

Materials and Methods

Between January 1995 and March 2004, shrimp were collected from 74 sites on tidal flats or boulder beaches where burrows of thalassinidean shrimp were abundant (Fig. 1). Samples of thalassinideans were obtained by digging sediments and the shrimp were separated from the sediment in the field by sorting by hand and with a 1-mm mesh sieve. The amount of sediment processed in each digging trial was about 50 cm square by more than 40 cm deep in muddy or sandy flats and about 40 cm square by more than 30 cm deep in gravelly flats and boulder beaches. The sampling stations were selected randomly at each site; there were at least seven stations on muddy or sandy flats and at least four on gravelly flats or boulder shores. For the 13 sites denoted by asterisks in Table 1, less sediment was processed per digging trial and there were fewer digging trials than stated above. The sampling sites were characterized by substrate (muddy sand, sand, gravel, and boulder) and the water condition was represented by the geographic nature of the site (riverside and seashore).

Results

Six species of upogebiid shrimp were collected: *Upogebia major*, *U. yokoyai*, *U. issaeffi*, *U. carinicauda*, *U. pugnax* (sensu Sakai, 1995), and *Austinogebia narutensis*. *Upogebia major* and *A. narutensis* are larger species with carapace lengths exceeding 30 and 25 mm, respectively. *Upogebia yokoyai* and *U. issaeffi* are mid-sized species, about 20 mm in carapace length. *Upogebia pugnax* and *U. carinicauda* are smaller species, about 15 mm in carapace length.

Figures 2 and 3 show the collection sites where the six species of Upogebiidae were found. The name and habitat characteristics of each site are listed in Table 1. *Upogebia yokoyai* was collected from 29 localities, *U. major* from 11 localities, *U. issaeffi* from 10 localities, *U. pugnax* from 9 localities, *A. narutensis* from 5 localities, and *U. carinicauda* from 4 localities. The habitat characteristics of each species were represented as the frequency of occurrence (%) in a particular sediment type (Fig. 4a) or water condition (Fig. 4b). The sediment types of the 74 sampling sites included 35 sandy mud, 23 sand, 4 gravel, and 12 boulder sites. The water conditions included 49 seaside and 25 riverside sites. Figure 5 shows the boulder beaches where *U. issaeffi* was found.

No upogebiid shrimp were collected at localities not listed in Table 1, although callianassid or laomediid shrimp were collected elsewhere. The distributions of three

Table 1. Sampling sites where the six species of Upogebiidae were found.

No.	Locality	Sediment	Habi -tat[1]	Upogebiid species
Honshu				
1	Orikasa-gawa River, Yamada	muddy sand	r	*U. major, U. yokoyai*
2	Nanakitada-gawa River, Sendai	muddy sand	r	*U. yokoyai*
4	Obitsu-gawa River, Kisarazu	muddy sand	s	*U. major*
6	Fujimae-higata tidal flat, Nagoya	muddy sand	s	*U. major, U. yokoyai*
7	Tanaka-gawa River, Kawage	muddy sand	r	*U. yokoyai*
9*	Tamanoura, Nachikatsuura	boulders	s	*U. issaeffi*
10*	Susami-gawa River, Susami	gravels	r	*U. yokoyai*
11*	Kasabo Bay, Hikigawa	boulders	s	*U. issaeffi*
12	Tsubaki-onsen, Shirahama	boulders	s	*U. issaeffi*
13	Tonda-gawa River, Shirahama	gravels	r	*U. yokoyai*
14	Hatake-jima Is., Shirahama	boulders	s	*U. issaeffi*
15	Tanabe Bay, Shirahama	sand	s	*U. pugnax*
16	Kirime-gawa River, Inami	gravels	r	*U. yokoyai*
17	Hidaka-gawa River, Gobo	muddy sand	r	*U. yokoyai*
20	Chigusa-gawa River, Ako	muddy sand	r	*U. major, U. yokoyai*
21*	Oki, Ushimado	muddy sand	s	*U. major*
22	Osa, Yorishima	muddy sand	s	*U. major*
23	Rinkai, Mukai-shima Is.	sand	s	*U. issaeffi, A. narutensis*
24*	Rinkai, Mukai-shima Is.	boulders	s	*U. issaeffi*
25	Okajo, Mukai-shima Is.	muddy sand	s	*U. major*
26*	Tsubuta, Mukai-shima Is.	muddy sand	s	*U. major*
27*	Iwashi-shima Is.	sand	s	*U. issaeffi, A. narutensis*
28	Tainouchi Bay, Kurahashi-jima Is.	muddy sand	s	*U. issaeffi*
29	Tainouchi Bay, Kurahashi-jima Is.	muddy sand	r	*U. yokoyai*
30	Nakatsuoka-gawa River, Ohno	muddy sand	r	*U. yokoyai*
31	Shirodani, Tokuyama	boulders	s	*U. issaeffi*
32	Nagasawa-gawa River, Yamaguchi	muddy sand	r	*U. yokoyai*
33	Yamaguchi Bay, Yamaguch	muddy sand	s	*U. major, U. yokoyai, A. narutensis*
Shikoku				
39*	Shigenobu-gawa River, Matsuyama	muddy sand	r	*U. yokoyai*
40	Kyuouhama, Onishi	muddy sand	s	*A. narutensis*
42	Sakurai, Imabari	muddy sand	r	*U. yokoyai*
43	Kawaratsu, Toyo	sand	s	*A. narutensis*
44*	Yoshino-gawa River, Tokushima	muddy sand	r	*U. major, U. yokoyai*
45	Tsubaki-gawa River, Tsubaki	muddy sand	r	*U. yokoyai*
46	Kinme, Shishikui	sand	s	*U. pugnax*
47	Uranouchi Bay, Suzaki	muddy sand	s	*U. yokoyai*
48	Fukura-gawa River, Sukumo	muddy sand	r	*U. yokoyai*
Kyushu				
50*	Sone-higata, Kitakyushu	muddy sand	s	*U. major, U. yokoyai*
53	Oyodo-gawa River, Miyazaki	muddy sand	r	*U. yokoyai*
54	Hachiman-gawa River, Kiire	muddy sand	r	*U. yokoyai*
56	Kuwanoura Bay, Kamikoshiki Is.	gravels	r	*U. yokoyai*
57*	Kuwanoura Bay, Kamikoshiki Is.	sand	s	*U. pugnax*

58*	Urauchi Bay, Kamikoshiki Is.	boulders	s	*U. issaeffi*
Ryukyu				
59	Yanyu-higata, Amami-Ohshima Is.	muddy sand	s	*U. yokoyai, U. carinicauda*
60	Tatsugo Bay, Amami-Ohshima Is.	muddy sand	s	*U. carinicauda*
61	Akina, Amami-Ohshima Is.	muddy sand	s	*U. pugnax*
62	Naikai, Amami-Ohshima Is.	muddy sand	r	*U. yokoyai, U. pugnax*
63	Sumiyo River, Amami-Ohshima Is.	muddy sand	r	*U. yokoyai, U. pugnax*
64	Honohoshi, Amami-Ohshima Is.	sand	s	*U. yokoyai*
65	Ashiken, Amami-Ohshima Is.	muddy sand	s	*U. carinicauda*
66	Miura, Kakeroma-jima Is.	muddy sand	s	*U. carinicauda*
69	Oura Bay, Miyako Is.	sand	s	*U. pugnax*
70*	Yonaha Bay, Miyako Is.	muddy sand	s	*U. pugnax*
72	Kabira Bay, Ishigaki Is.	sand	s	*U. yokoyai*
74	Funaura Bay, Iriomote Is.	muddy sand	r	*U. yokoyai*

* Sites where sampling effort was minimal.
[1] r, riverside; s, seashore.

Nihonotrypaea species (*N. japonica, N. harmandi* and *N. petalura*) are well documented in western Kyushu (Tamaki et al., 1999; Wardiatno et al., 2003). For the taxonomy of callianassid shrimps in Japan, see Sakai (2001) and Tamaki (2003). *Callianassa bouvieri* was collected from sandy beaches in the Ryukyu archipelago. *Laomedia astacina* was collected from tidal rivers from Honshu to the Ryukyus.

Discussion

1. Geographic distribution

In this study, *Upogebia major* was collected from Honshu, Shikoku, and Kyushu, but not from the Ryukyu Archipelago, in southwestern Japan. Records of this species in Hokkaido, northern Japan, is reviewed by Komai et al. (1992). The southern limit of *U. major* in Japan might be the Yatsushiro Sea, where Lützen *et al.* (2001) studied the shrimp. There are records of this species from southern Russia (Vladivostok), Korea, and north China (Holthuis, 1991). The identity of *U. major* from Hong Kong (Morton and Morton, 1983) must be verified, since this species is not distributed at lower latitudes, *i.e.*, southern Japan (this study) or Taiwan (Lin et al., 2001).

The other species not collected from the Ryukyu Archipelago were *U. issaeffi* and *Austinogebia narutensis*. *Upogebia issaeffi* was collected from Honshu, islands in the Seto Inland Sea, and the Koshiki-jima Islands, west of Kyushu. The first record from Japan is that of Yokoya (1939), who collected this species from Onagawa, in Miyagi Pref., northeastern Honshu. The type locality and only record abroad is Vladivostok (Balss, 1913). Although *A. narutensis* was collected only from the Seto Inland Sea in this study, this species is distributed on the Pacific coasts of Honshu and Shikoku (Sakai, 1986; 1987) and Taiwan (Ngoc-Ho, 1994; Lin et al., 2001; Ngoc-Ho, 2001).

Upogebia yokoyai was found throughout Japan in this study. This species was

Fig. 2. The distributions of well-studied upogebiid shrimp in Japanese waters: a, *Upogebia major*; b, *U. yokoyai*. Solid symbols indicate collection sites in this study. Open symbols indicate major taxonomic records or study sites reported in major ecological surveys not visited in this study. The arrows indicate the references: 1, Ohshima, 1967; 2, Kinoshita, 2002; 3, Ito and Nishida, 2002; 4, Sakai et al., 1995; 5, Kato and Itani, 1995; 6, Shôji, 1938; 7, Lützen et al., 2001; 8, Yokoya, 1930; 9, Mukai, 1992; 10, Itani, 2001; 11, Sakai et al., 1988.

described from Mutsu Bay (Yokoya, 1930; Makarov, 1938), in the northernmost part of Honshu, but so far it has not been reported from Hokkaido, or neighboring countries. *Upogebia yokoyai* was the most commonly collected species, found at 29 localities (39% of the total collection sites). In many reports, this species has been confused with *U. major*. For example, *U. major* of Mukai and Koike (1984) collected from Yamada Bay (site 1 in this study) was actually *U. yokoyai* (Sakai and Mukai, 1991). The shrimp studied by Koike

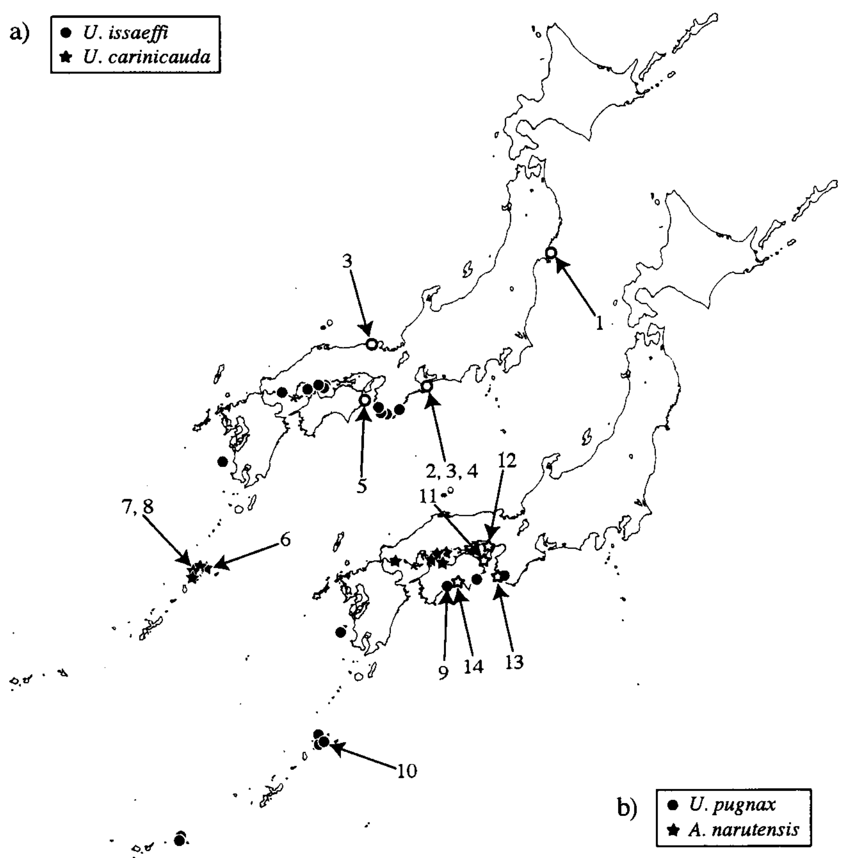

Fig. 3. The distributions of less-studied upogebiid shrimp in Japanese waters: a, *Upogebia issaeffi* and *U. carinicauda*; b, *Upogebia pugnax* and *Austinogebia narutensis*. Solid symbols indicate collection sites in this study. Open symbols indicate taxonomic records not visited in this study. The arrows indicate the references: 1, Yokoya, 1939; 2, Shiino, 1958; 3. Sakai, 1982; 4. Sakai, 1984b; 5. Sakai et al., 1995; 6, Sakai and Takeda, 1995; 7, Kato and Itani, 2000; 8, Itani and Kato, 2002; 9. Sakai, 1995; 10. Shiino, 1964; 11. Sakai, 1986; 12, Imafuku, 1993; 13. Miyake, 1982; 14. Sakai, 1987.

and Mukai (1983) was also *U. yokoyai* (Dr. H. Mukai, Hokkaido University, personal communication). Nevertheless, caution is necessary because *U. major* and *U. yokoyai* are sympatric in Yamada Bay. The identity of the upogebiid shrimp in Kagoshima Prefecture, southern Kyushu, used by Batang and Suzuki (2003) was *U. yokoyai* after examining two specimens that Dr. H. Suzuki (Kagoshima University) kindly sent.

The species collected only from the southern part of Japan were *U. carinicauda* and

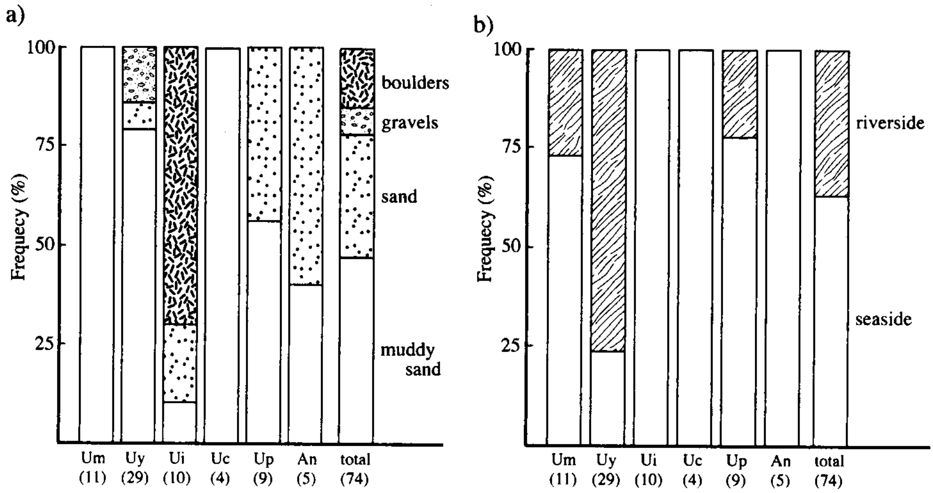

Fig. 4. Habitat characteristics of upogebiid shrimp in this study: a, sediment; b, water conditions. The frequency of occurrence (%) in a particular habitat is shown for each species. The numbers of collection sites are shown in parentheses. Um, *Upogebia major*; Uy, *U. yokoyai*; Ui, *U. issaeffi*; Uc, *U. carinicauda*; Up, *U. pugnax*; An, *Austinogebia narutensis*.

U. pugnax. *Upogebia carinicauda*, which is widely distributed in the tropical Indo-West Pacific (de Man, 1928; Sakai and Takeda, 1995), was found only on the Amami-Ohshima and Kakeroma Islands, despite vigorous sampling efforts at the other sites in the Ryukyu Archipelago. *Upogebia pugnax* was collected from warmer regions, along the Kuroshio Current. The type locality of this species and the only record abroad is Indonesia. Ngoc-Ho (1994) claimed that the Japanese populations are not *U. pugnax*, and described a new species *U. sakaii*, although Sakai (1995) disputed this. There is taxonomic confusion because the type specimen was a feminized young male parasitized by a sacculinid.

Table 2 lists the 14 species of Upogebiidae recorded from Japanese waters. In the list, the information for Sakai (1987) and Komai *et al.* (1999) has been revised. *Upogebia kyushuensis* was once assigned to *Wolffogebia* Sakai, 1982 (Sakai, 1987), but has since been excluded from the genus (Sakai, 1993; Ngoc-Ho et al., 2001). *Gebiacantha acanthochela* was included in the list, because the type locality is not the Yellow Sea, as mentioned in Sakai (1967b), but is the East China Sea, as indicated by the latitude and longitude (29°02'N, 125°25'E) of the paratype (Sakai, 1967b). In the Japanese abstract of the same paper, he stated that the specimens were collected from the East China Sea, not the Yellow Sea (Sakai, 1967b). The generic status of this species is highly controversial. Ngoc-Ho (1989; 2001) established and rediagnosed the genus *Gebiacantha*, but Sakai and Türkay (1995) believe that *Gebiacantha* should be treated as a synonym of *Upogebia*. Records of *Upogebia isodactyla* from the Seto Inland Sea (Nakazawa, 1927) might be misidentification (see Sakai, 1971; 1972) and it was excluded from the list.

2. Habitat

This study clearly shows the habitat characteristics for *Upogebia yokoyai* and *U.*

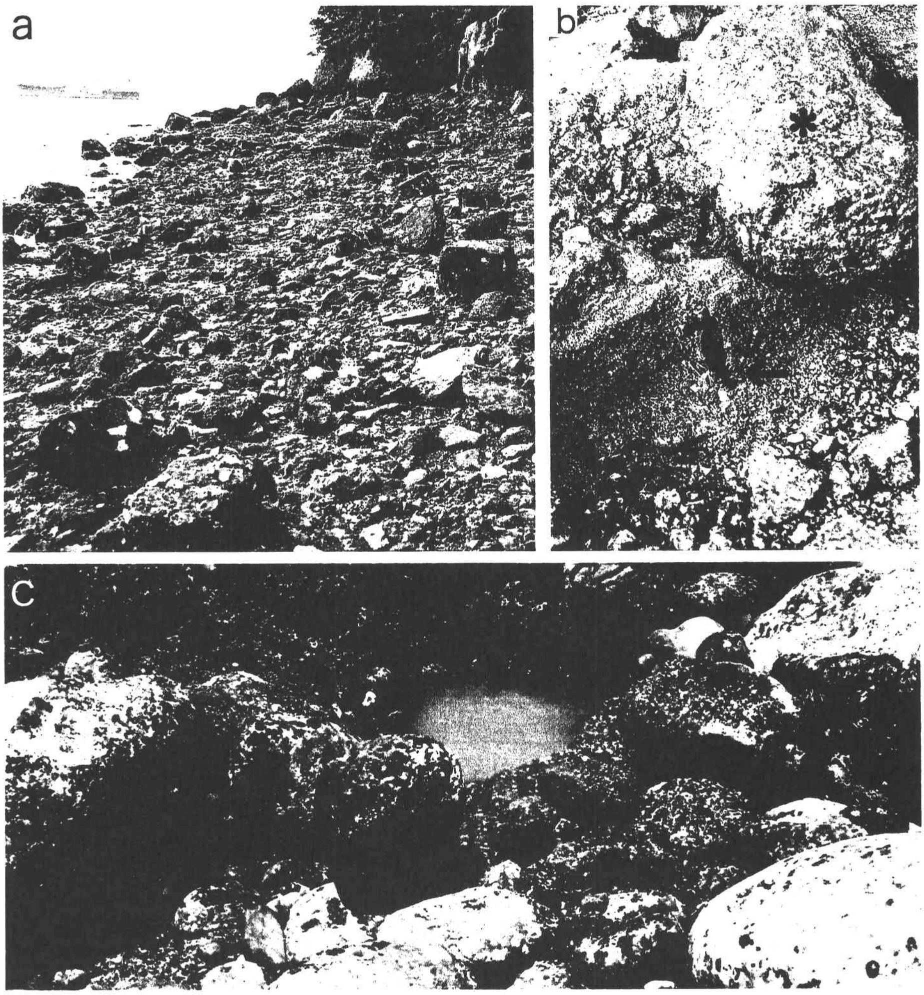

Fig. 5. The photographs of boulder beaches where *Upogebia issaeffi* was found: a, Mukaishima Is. (site 24); b, the same site, close-up of the burrow of *U. issaeffi* (arrow) where a boulder (*) was removed; c, Tsubaki-onsen (site 12), in the middle of a digging trial.

issaeffi. *Upogebia yokoyai* was most commonly found on riverside flats. The salinity of the surface water at site 13, situated at the mouth of the Tonda River, was 0 psu at low tide and 3 to 15 psu at high tide (Itani, 2001). At seaside sites 1, 6, 47, and 50, the tidal flat was influenced by a river flowing into the flat. At site 33, there was no river, but fresh ground water upwelled where *U. yokoyai* was abundant. Perhaps the salinity gradient dictates the distribution of *U. major* and *U. yokoyai* where they are sympatric in temperate mud flats. In the Yoshino River (site 44 in this study), Sakai *et al.* (1988) found that *U. major* was not distributed in the lower salinity area upstream, although both species were found at the mouth of the river. Nishimura (1981) postulated that the estuarine species that is distributed only in temperate East Asia originated from tropical Indo-West Pacific species that entered

Table 2. List of the species of Upogebiidae recorded from Japanese waters.

Genus Species	Type locality	Geographic range	Depth of occurrence
Upogebia Leach, 1814			
Upogebia major (de Haan, 1841)	Japan	Japan, Vladiostok to north China	intertidal
Upogebia carinicauda (Stimpson, 1860)	Hong Kong	tropical Indo-West Pacific	intertidal
Upogebia pugnax de Man, 1905	Sumbawa (Indonesia)	Indonesia, Japan	up to 36m (Indonesia), intertidal (Japan)
Upogebia issaeffi (Balss, 1913)	Vladivostok	Vladiostok, Japan	intertidal
Upogebia kyushuensis Yokoya, 1933	Kyushu (Japan)	Japan	106-192m deep
Upogebia yokoyai Makarov, 1938	Mutsu Bay (Japan)	Japan	intertidal
Upogebia miyakei Sakai, 1967	Ishigaki Is. (Japan)	Japan, Indonesia[1]	unknown
Upogebia imperfecta Sakai, 1982	Yellow Sea	Yellow Sea, Japan[2]	20-50m deep
Upogebia trispinosa Sakai & Mukai, 1991	Katsuura-gawa River (Japan)	Japan	intertidal
Acutigebia Sakai, 1982			
Acutigebia trypeta (Sakai, 1970)	Amami-Oshima (Japan)	Japan, Heron Island (Australia)[3]	intertidal, inside coral block
Neogebicula Sakai, 1982			
Neogebicula monochela (Sakai, 1967)	off Tomioka (Japan)	Japan	38m deep, shell and rocky bottom
Tuerkayogebia Sakai, 1982			
Tuerkayogebia kiiensis (Sakai, 1971)	Tanabe Bay (Japan)	Japan	20m deep
Gebiacantha Ngoc-Ho, 1989			
Gebiacantha acanthochela (Sakai, 1967)	East China Sea	Japan	100m deep
Austinogebia Ngoc-Ho, 2001			
Austinogebia narutensis (Sakai, 1986)	Naruto (Japan)	Japan, Taiwan[4]	intertidal to 20m deep

[1] Ngoc-Ho, 1990; [2] Komai et al., 1999; [3] Sakai, 1984a; [4] Ngoc-Ho, 1994.

a large estuary thought to exist in the East China Sea in the Late Pliocene. A future phylogeographic study might reveal the speciation and evolution of salinity tolerance in *U. yokoyai*.

Upogebia issaeffi was the only upogebiid shrimp found on boulder shores in Japan. Sakai *et al.* (1995) considered this species rare, which might be due to its special habitat. The habitat of *U. issaeffi* is similar to that of *Nihonotrypaea petalura* (Tamaki et al., 1999; Shimoda and Tamaki, 2004), which was collected with *U. issaeffi* at three localities (12, 24, 31). However, boulder shores were not the only habitat that *U. issaeffi* used. At localities 23, 27, and 28, *U. issaeffi* was collected from sandy beaches where *N. petalura* was also collected. Plasticity in the sediment type of the habitat was also found in *U. yokoyai*, *U. pugnax*, and *A. narutensis*. Some upogebiids are known to live in a wide range of substrates (for the European and Mediterranean species, reviewed in Ngoc-Ho, 2003). For example, *U. deltaura* is found in sediments ranging from fine mud to calcareous coarse gravel (Hall-Spencer and Atkinson, 1999).

Of the four upogebiid species distributed in the Seto Inland Sea, the habitat of *A. narutensis* was not characterized because of the small number of collection sites. This species was sympatric with *U. issaeffi* on sandy shores (sites 23, 27) and it was sympatric with *U. major* on a muddy shore (site 33). This species also occurs in subtidal sediment. Sakai (1987) collected many specimens of this species from Kochi, at depths of 15 m. Another record of the subtidal distribution of this species is a specimen from Tanabe Bay, at a depth of 20 m (Sakai, 1986), which Miyake (1982) erroneously called *U. major*. Imafuku (1993) studied the internal asymmetry of a upogebiid collected in a trawl net from shallow water in the eastern Seto Inland Sea. The shrimp was identified as *A. narutensis* after examining three specimens kindly sent by Dr. M. Imafuku (Kyoto University). According to an unpublished record of Dr. S. Yamato (Kyoto University), many upogebiid shrimp were distributed in the subtidal sediments off site 23, and the author identified these as *A. narutensis*.

In this study, the distributions of some of the intertidal upogebiid shrimp could be explained by salinity and particle size gradients. A quantitative measurement of environmental parameters in the tidal flats where two or more species are sympatric is needed to fully understand the distributions of upogebiids. Habitat preference experiments using adult and young shrimp may also be needed. Future research must examine how the sediment type affects the ecology and burrow morphology of thalassinidean shrimps.

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