

Life history characteristics and burrow structure of the mud shrimp (Decapoda: Upogebiidae)

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Abstract: Burrow-dwelling shrimps, formerly known as “thalassinids,” are attracting the attention of researchers as ecosystem engineers. This review focuses on the ecology of upogebiid shrimps worldwide, especially their life history and burrow traits. The mud shrimp has a larval period consisting of three to four zoeal stages with one decapodid stage. The time required for maturity and longevity has been estimated to be 1–3 years and 3–5 years, respectively. However, data on shrimp lifespan may be updated with the development and application of age determination methodologies. The structure of the shrimp burrow is mainly U- or Y-shaped and is similar among species but with some interspecific differences. Mud shrimps are filter feeders due to the ventilation activity in the U-shaped structure, and inhabit burrows with an inner diameter that fits their body. Burrow connections were recorded between burrows of males and females. Some juvenile mud shrimps may branch off from adult burrows to create their own burrows. This review discusses the response of shrimp populations in areas affected by the 2011 Great East Japan Earthquake. Owing to long maturation times, the recovery of these populations was slow in habitats affected by tsunamis. These results highlight the future effects of climate change on shrimp populations.

Key words: burrowing, ecosystem engineer, Gebiidea, larva, tsunami

Introduction

Mud shrimps of the family Upogebiidae (infraorder Gebiidea) dig and inhabit burrows in the substrate. Previously, they were included in the infraorder Thalassinidea along with ghost shrimps (Callianassidae; current infraorder Axiidea) (Shen et al. 2013, Poore et al. 2014), which also create deep burrows. Most mud shrimps dig burrows in substrates such as mud, sand, gravel, corals, and sponges (Dworschak 2000, 2015). The shrimps' activities have a variety of impacts on the abiotic environment of their habitat (Kinoshita et al. 2003a, 2008, Sasaki et al. 2014, Das et al. 2017) and can affect local benthic communities (Pillay & Branch 2011), creating spaces for other organisms (MacGinitie 1935, Atkinson & Taylor 2005, Dworschak et al. 2012, Tseng et al. 2019). Such burrow inhabitants are well studied in Japan (Sato et al. 2001,

Itoh & Nishida 2002, Itani & Kato 2002, Itani et al. 2002, Kinoshita 2002, Henmi & Itani 2014, 2021, Henmi et al. 2014, 2017, Shiozaki & Itani 2020, Seike & Goto 2020). Information on thalassinid burrow-dwelling shrimps is particularly abundant (Atkinson & Eastman 2015), as mud shrimps contribute to fishery resources. Large shrimp are a delicacy in western Japan, Korea, Taiwan, and Vietnam (Sato 2000, Ngoc-Ho 2001, Hong 2013, Das et al. 2017) and are used as bait in western Greece and South Africa (Hodgson et al. 2000, Conides et al. 2012). Juveniles serve as food resources for predators such as eels (Kaifu et al. 2013). Mud shrimps have ecological, environmental, and economic importance.

This review characterizes the ecology of upogebiid mud shrimps, especially their life history and burrow structure. Current knowledge of mud shrimp biology aids in the conservation of its symbiotic species, local ecosystems, and fisheries. The impact of climate change on the ecology of shrimps is also discussed based on shrimp distribution in areas affected by the 2011 Great East Japan Earthquake. As

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mud shrimps are mainly distributed in coastal waters, such as tidal flats and estuaries (Dworschak et al. 2012, Kornienko 2013, Dworschak 2015), there are concerns regarding the impact of human-induced sea level rise and floods on mud shrimp habitats.

1. Life history

Larval stage

The life history of the 16 species of mud shrimp (shown in Table 1), similar to that of many other crustaceans, consists of planktonic (larval) and benthic (juvenile-adult) stages (Fig. 1). Larval forms of the mud shrimp include zoea and decapodid (megalopa) stages. Although both zoea and decapodid are nymphoid, their athletic performance is different. The zoea swim using pleopods, whereas decapodids can also walk on the ground using pereopods (Anger 2006). The most common larval development pattern of upogebiid shrimp is three to four zoeal and one decapodid stage, except for *Austinogebia edulis* (Ngoc-Ho & Chan 1992), with two zoeal stages (Shy & Chan 1996), *Upogebia kempfi* Shenoy, 1967, with two decapodid stages (Shenoy 1967), *Upogebia paraffinis* Williams 1993, with five zoeal stages (Melo & Brossi-Garcia 2000), and *Upogebia savignyi* (Strahl 1892), with one zoeal stage and no decapodid stage (Gurney 1937). Development patterns of five to eight zoeal stages have been reported in larvae of other gebiidean (genus *Axianassa*, *Jaxea*, *Laomedia*, and *Naushonia*) and axiidean species (Pohle et al. 2011). Upogebiid shrimp larvae in the laboratory take 12–19 days to develop from hatching to three to four zoeal stages and one decapodid stage (Siddiqui & Tirmizi 1995, Konishi 1989, Kornienko et al. 2012). The egg diameter of mud shrimp is typically less than 1 mm; however, two species with short larval periods (*A. edulis* and *U. savignyi*) have eggs that are 1 mm or more in diameter (Gurney 1937, Shenoy 1967, Tunberg 1986, Dworschak 1988, Dumbauld et al. 1996, Shy & Chan 1996, Kinoshita et al. 2003).

Some decapod larvae exhibit lecithotrophic behavior but major larvae, including those of the mud shrimp, feed after hatching (Anger 2001, Maszczyk & Brzeziński 2018). Upogebiid larvae ingest diatoms, flagellates, ciliates, picoplankton, and nanoplankton (Fileman et al. 2014, Kornienko & Golubinskaya 2018), but do not feed on potentially toxic dinoflagellates (Fileman et al. 2014). For benthic animals, larval dispersal helps with genetic exchange and the colonization of new habitats, but it is also necessary to return to their original habitat to replenish the population (Bashevkin et al. 2020). Larval dynamics are influenced by physical factors (such as flow, light intensity, temperature, and salinity) and biological factors (such as food and predators) (Wooldridge & Loubser 1996, Cowen & Sponaugle 2009). Larvae are not only passively transported by these factors, but also change their dispersal distance in response to their behavior (Shanks 2009, Morgan & Fisher, 2010).

The distribution of mud shrimp larvae appears to be related to their natal origin. In some estuarine decapods, larvae that prefer brackish water (such as *Carcinus maenas* (Linnaeus 1758)) (Nagaraj 1993) are known to migrate to coastal areas at early stages, avoiding the estuarine environments of their progenitors. The larvae of the estuarine *Upogebia africana* (Ortmann 1984) and *Upogebia pusilla* (Petagna 1792) have been shown to exhibit this migration strategy (Emmerson 1983, Paula et al. 2001, Faleiro et al. 2012, Pires et al. 2013). Salinity appears to be a major limiting factor for survival of upogebiid larvae (Paula et al. 2001, Faleiro et al. 2012). The distribution of mud shrimp larvae appears to be related to their natal origin. Mud shrimp larvae in both estuarine and coastal areas remain within 30 km of the coastline, but their dispersal patterns vary (Pires et al. 2013). Mud shrimp and ghost shrimp live sympatrically, and their larvae are likely to exhibit similar migratory patterns (Golubinskaya & Korn 2020). For these reasons, mud shrimp larvae have the potential to be regularly dispersed over a moderately long larval period while selectively feeding.

Reproductive cycles

Many aquatic invertebrates, including crustaceans, undergo seasonal reproduction cycles. Some mud shrimps have distinct seasonality during the breeding season (Table 1), but others, such as *Upogebia omissa* Gomes Corrêa, 1968 breed perennially (Costa et al. 2020). Sexual dimorphism in shrimps suggest that females of many species of shrimp are iteroparous (Table 1) (Dworschak 1988, Hanekom & Baird 1992, Kevrekidis et al. 1997). *Upogebia major* (De Haan 1841) in Tokyo Bay (central Japan) produces only one brood during the breeding season, but some ovigerous females develop additional gonads (Kinoshita et al. 2003b). Golubinskaya & Korn (2020) suggest that *U. major* in Vostok Bay (Russia) has a long breeding period and repeatedly produce larvae during the breeding period under certain conditions.

Upogebia africana exposed to thermal pollution from thermal power stations have been shown to alter the initiation or duration of the breeding season, or exhibit precocious maturity (Hill 1977). Discussions about the reproductive cycle of aquatic invertebrates need to account for the environment of the planktonic and benthic stages (Anger 2001). For example, the breeding season for *U. major* in Tokyo Bay is from December to May (Kinoshita et al. 2003b), while the breeding season for mud shrimp in Russia is from April to May (Selin 2017). In Hokkaido, ovigerous *U. major* females were obtained in June (Konishi 1989). According to Golubinskaya et al. (2016), the difference between the breeding seasons of mud shrimp found in Japan and Russia is likely to be determined by the characteristics of larvae with low optimum water temperatures. *Upogebia major* larvae appear from March to May in Japan and from May to September in Russia (Kinoshita et al. 2003b, Golubinskaya et al. 2016, Golubinskaya & Korn

Table 1. Life history of Upogebia species of the world. The breeding season was mainly defined in terms of the occurrence of the ovigerous females.

Species	Larval stage	Breeding season/ Month or period	Maximum size of CL or TL (mm), female/male	Size of ovigerous female CL or TL (mm)	Maturation	Longevity	Locality	Reference
<i>Austinogebia edulis</i>	2Z+1D	Mar, May*	NA	NA	NA	NA	Western Central Taiwan	Shy & Chan 1996
<i>Upogebia affinis</i>	NA	Aug*	75.0/68.5 (TL)	NA	NA	NA	Beaufort coast, USA	Pearse 1945
	4Z (plankton sample)	NA	NA	NA	NA	NA	Chesapeake Bay, USA	Sandifer 1973
<i>Upogebia africana</i>	NA	Jul–Mar (mainly)	NA	10 (CL)	NA	NA	South Africa	Hill 1977
	NA	Jul–Mar (mainly)	24.8/24.4 (CL)	12–17 (CL)	1.5 years	4 years	South Africa	Hanekom & Baird 1992
	3–4Z+1D	NA	NA	NA	NA	NA	South Africa	Paula et al. 2001
<i>Upogebia darvini</i>	3Z+1D	Aug*	NA	11 (CL)	NA	NA	Phuket Is. Thailand	Ngoc-Ho 1977
<i>Upogebia delataura</i>	NA	May–Aug	21.8/23.6 (CL) 65.7/65.3 (TL)	15–21 (CL)	NA	NA	Western Sweden	Tunberg 1986
	4Z+1D	NA	NA	NA	NA	NA	Algarve, Portugal	Pires et al. 2013
<i>Upogebia issaeffi</i>	4Z+1D	Jul*	NA	NA	NA	NA	Vostok Bay, Russia	Korrienko et al. 2012
<i>Upogebia kempi</i>	4Z+2D	NA	NA	NA	NA	NA	Bombay, India	Shenoy 1967
<i>Upogebia major</i>	3Z+1D	Jun*	NA	NA	NA	NA	Hokkaido, Japan	Konishi 1989
	3Z+1D	Dec–May	34.4/35.6 (CL)	25.1–34.4 (CL)	over 2 years	NA	Tokyo Bay, Japan	Kinoshita et al. 2003b
<i>Upogebia omissa</i>	NA	Apr–May	117/116 (TL)	73 (TL)	over 2 years	4 years	Vostok Bay, Russia	Selin 2017
<i>Upogebia paraffinis</i>	5Z+1D	year-round	11.77/12.91 (CL)	6.33 (CL)	one year	3–4 years	Casa Caiada Beach, Brazil	Costa et al. 2020
<i>Upogebia pugettensis</i>	NA	Jun–Oct	13.5/14.5 (CL)	NA	NA	NA	Paranagua Bay, Brazil	Melo et al. 2004
	NA	Oct–May	33 (CL)	20–30 (CL)	mainly 3 years	3–5 years	Willapa Bay, USA	Dumbauld et al. 1996
	3Z+1D	Dec–Feb, late spring/ early summer	NA	NA	NA	NA	Friday Harbor, USA	Puls 2001
<i>Upogebia pusilla</i>	4Z+1D	Mar–Sep	60/66 (TL)	36 (TL)	2–3 years	3–5 years	Northern Adriatic Sea, Italy	Dworschak 1988
	NA	Apr–Aug	106/82 (TL)	39 (TL)	one year	3 years	Aegean Sea, Greece	Kevrekidis et al. 1997
	4Z+1D	May*	NA	NA	NA	NA	Mira Estuary, Portugal	Dos Santos & Paula 2003
	NA	NA	54/58 (TL)	NA	NA	4 years	Western Greece	Conides et al. 2012
	NA	May–Aug	NA	36 (TL)	NA	NA	Arcachon Bay, French	Pascal et al. 2016
<i>Upogebia quaddusiae</i>	NA	Apr–Jul	59.4 (male, TL)	32–40 (TL)	NA	NA	Slovenia	Jugovic et al. 2017
<i>Upogebia savignyi</i>	3Z+1D	Oct, Nov*	NA	NA	NA	NA	Sonari & Pacha, Pakistan	Siddiqui & Tirmizi 1995
<i>Upogebia vasquezii</i>	1Z	Feb*	NA	35 (TL)	NA	NA	Red Sea, Egypt	Gurney 1937
	3Z	Dec–Jul (except Apr)	61.5 (female, TL)	NA	NA	NA	Northern Brazil	Oliveira et al. 2012
	(plankton sample)	NA	NA	15.44 in mean (CL) 52.05 in mean (TL)	NA	NA	Marapanim Estuary, Brazil	Oliveira et al. 2014
<i>Upogebia yokoyai</i>	NA	Aug–Oct	12.14/11.75 (CL)	11.62, 11.65 (CL)	NA	NA	Wakayama, Japan	Itani 2001
	3–4Z+D (imperfect)	May–Aug	NA	35–52 (TL)	one year	NA	Kochi, Japan	Yamasaki et al. 2010
	3–4Z+D (imperfect)	May–Sep	63.2 (male, TL)	50–87 (TL)	one year	NA	Hiroshima, Japan	Yamasaki et al. 2010
	4Z+1D	NA	NA	NA	NA	NA	Vostok Bay, Russia	Korrienko et al. 2013

NA, not available. Z, zoeal stage. D, decapodid (megalopa) stage. CL, carapace length. TL, total length. * Not a year-round survey.

2020). For mud shrimp larvae, temperature conditions are not as restrictive as salinity (Paula et al. 2001, Faleiro et al. 2012), but if temperatures increase beyond the tolerance of the species, survival and development may be compromised. We have not yet fully learned the environmental clues that regulate the reproductive cycle of mud shrimps.

Maturity and longevity

In the case of mud shrimp, there is not enough existing information to discuss maturity and longevity due to the difficulty in collecting large, mature individuals. The age at maturity of mud shrimp is one year for *U. omissa* (Costa et al. 2020), 1.5 years for *U. africana* (Hanekon & Baird 1992), 2–3 years for *U. major* (Kinoshita et al. 2003b), and 3 years for *Upogebia pugettensis* (Dana, 1852) (Dumbauld et al. 1996). *Upogebia pusilla* and *U. yokoyai* had 1–3 years of intraspecific variation in maturity between different habitats (Dworschak 1988, Kevrekidis et al. 1997, Itani 2001, Yamasaki et al. 2010). The longevity of mud shrimp is 3–4 years for *U. omissa* (Costa et al. 2020), 3–5 years for *U. pusilla* (Dworschak 1988, Kevrekidis et al. 1997), and *U. pugettensis* (Dumbauld et al. 1996), and 4 years for *U. africana* (Hanekom & Baird 1992) and *U. major* (Selin 2017). According to Vogt (2019), average lifespan of decapod crustaceans in seawater and brackish water is approximately 6 years, but there is little research on aging and longevity of decapod crustaceans. In comparison, age determination in bivalves, sea urchins, and fish has been widely studied because it can be determined by examining hard tissues (shells, rotula, vertebrae, scales, and otoliths) on which growth bands are deposited (Panfili et al. 2002, Watanabe & Natsukari 2008, Bodnar 2009, Gimenez et al. 2020). Age determination in crustaceans is primarily based on analysis of size frequency distribution and life history data, which are often combined with growth models (Vogt 2012, Kilada & Driscoll 2017). Size frequency dependent growth models have been widely applied to wildlife populations, not just crustaceans, but are less definitive in long-lived species (Hartnoll 2001). Methodologies such as growth band analysis and the lipofuscin method have been developed that differ from traditional size frequency distribution approaches (Kilada & Driscoll 2017, Vogt 2019). Kilada & Driscoll (2017) validated the annual pattern of bands deposited in the eyestalks of known-age Antarctic krill (*Euphausia superba*) and determined their absolute age. The lipofuscin method quantifies the pigment lipofuscin, which accumulates in the brain regions of decapods as they age, and is used as an indicator for age determination (Sheehy 1992). The longevity of mud shrimp is currently thought to be approximately 3–5 years, but it may be updated with the development and application of these methods.

2. Burrow Structure

Most species dig burrows in mud, sand, and gravel.

A few species inhabit corals, such as *Acutigebia trypeata* (Sakai 1970), *Pomatogebia operculata* (Schmitt 1924) (Scott et al. 1988), and *Upogebia amboiensis* (De Man 1888) (Kleemann 1984), and sponges, such as *Upogebia darwinii* (Miers 1884) (Ngoc-Ho 1977) and *Upogebia* sp. (Scott et al. 1988). Casting of burrows with polyester resin or polyurethane foam enables understanding of the burrow structure of many shrimps (Hamano 1990, Dworschak et al. 2012, Sepahvand et al. 2014). In particular, casts with clear structures—because the hard smooth walls of upogebioid burrows prevent the casting material from penetrating the burrow—have been reported (Pearse 1945, Li et al. 2008). The basic burrow is a U-shaped structure with two openings, and burrows with a structure extending vertically from the bottom of the U-shape are known as Y-shaped burrows (Table 2) (Astall et al. 1997). Chambers and short branches are often found in these structures (Figs. 1–2) (Kinoshita 2002), and shrimp use them to reorient themselves within the burrows (Dworschak 1987). The cross section of the burrow is circular, and its diameter is dependent on shrimp size (e.g., Dworschak 1983). Nickell and Atkinson (1995) categorized burrow types based on the feeding habits of thalassinidean shrimps. Feeding occurs through the intake of suspended particles in the burrow (Dworschak 1988). Other mud shrimps such as Laomedidae and Axianassidae are deposit feeders and have more

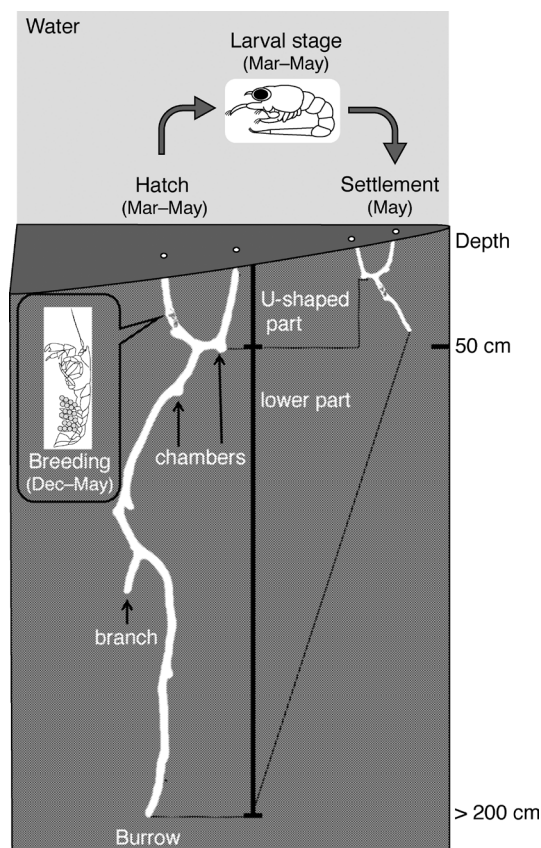


Fig. 1. Schematic life history of *Upogebia major* in Tokyo Bay. Modified from Kinoshita (2002) and Kinoshita et al. (2003b).

Table 2. Burrow structure of Upogebia species.

Species	Sediment types	Burrow structure	Maximum burrow depth (cm)	Burrow width (cm)	Burrow diameter (cm)	Carapace length of inhabitant shrimp (cm)	Locality	References
<i>Austinogebia edulis</i>	sand mud	Y-shaped Y-shaped, single oblique shaft	50 110	11 26	NA NA	1.00–2.00 0.64–2.35	Hong Kong Taiwan	Li et al. 2008 Li et al. 2008
<i>Austinogebia narutensis</i>	sand and mud	Y-shaped	73	NA	NA	NA	Taiwan	Tseng et al. 2019
<i>Pomatogebia operculata</i>	sand	Y-shaped	50	50	1.68–2.36	2.01–2.36	Japan	Kinoshita & Itani 2005
<i>Upogebia affinis</i>	sand coral mud	J-, U- and Y-shaped multiple U multiple U, single oblique shaft	47 6 >50	81* 11 >200*	2.0–2.5 0.5–1.2 NA	NA NA NA	Japan Barbados and Jamaica USA	Seike et al. 2020 Scott et al. 1988, Griffis & Suchanek 1991 Frey & Howard 1975, Griffis & Suchanek 1991
<i>Upogebia amboinensis</i>	coral	multiple U	6	11	1.0–1.2	NA	Australia	Kleemann 1984, Griffis & Suchanek 1991
<i>Upogebia carinicauda</i>	sandy mud and limestone bedrock	U- and Y-shaped, multiple U	30	37*	1.0–1.3, 1.2–1.7	NA	Iran	Sepahvand et al. 2014
<i>Upogebia deltaura</i>	calcareous gravels	multiple U	55	NA	1.8–2.47	1.71–2.20	Scotland	Hall-Spencer & Atkinson 1999
<i>Upogebia issaeffi</i>	sand	U- and Y-shaped	60	18	1.14–1.39	1.32–1.75	Japan	Kinoshita & Itani 2005
<i>Upogebia major</i>	mud	Y-shaped	207	38	0.54–2.99	0.31–3.31	Japan	Kinoshita 2002
<i>Upogebia omissa</i>	sand with gravel and shell fragments	Y-shaped, single oblique shaft (tunnel)	30	15	0.4–1.3	1.0–1.3	Brazil	Coelho et al. 2000
<i>Upogebia pugettensis</i>	sand	Y-shaped	90	70	NA	NA	Canada	Swinbanks & Murray 1981, Griffis & Suchanek 1991
<i>Upogebia pusilla</i>	mud	Y-shaped, multiple U	48	39	NA	NA	Italy	Dworschak 1983
<i>Upogebia stellata</i>	mud	Y-shaped, multiple U (incomplete)	26	NA	1.18, 1.39	NA	Scotland	Nickell & Atkinson 1995
<i>Upogebia tipica</i>	sandy mud	U- shaped	16	5	1.4–1.5	NA	Italy	Atkinson et al. 1998
<i>Upogebia yokoyai</i>	sand	Y-shaped	124	46	0.57–1.78	0.54–2.22	Japan	Kinoshita et al. 2010

NA, not available. "Burrow width" refers to U-shape width, but it is shown as horizontal extension in the marked studies (*).

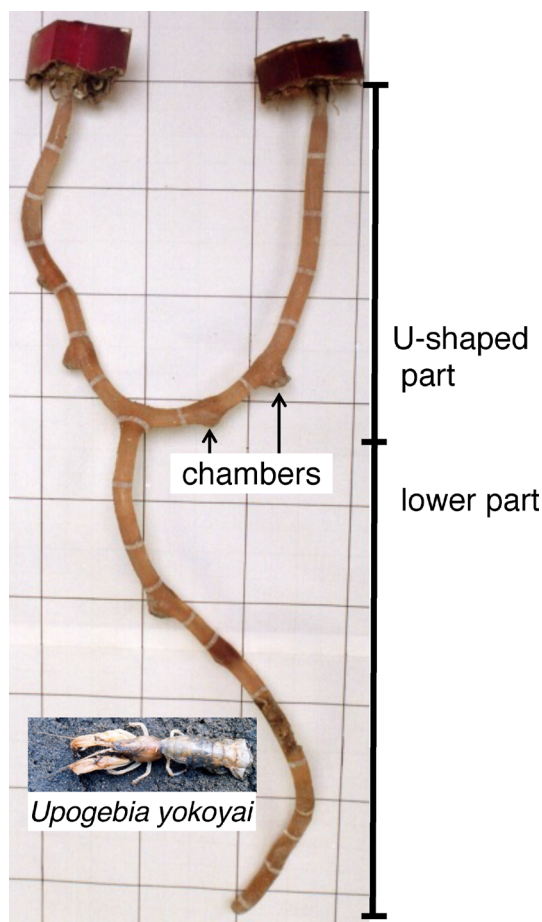


Fig. 2. Typical Y-shaped burrow cast, *Upogebia yokoyai*. Background squares 10 cm×10 cm. The original data is from Kinoshita et al. (2010).

complex burrow structures than upogebiids (Atkinson & Taylor 2005). Though the burrows of upogebiids appear similar, individualities in different burrows have also been reported. Most upogebiid shrimp burrows are less than 1 m deep, while *A. edulis* and *U. yokoyai* burrows are deeper than 1 m, and *U. major* burrows reach a depth exceeding 2 m (Table 2) (Hamano 1990, Kinoshita 2002, Li et al. 2008, Kinoshita et al. 2010). Burrows of *Upogebia affinis* (Say 1818) are branched, extending at least 2 m laterally (Frey & Howard 1975). Burrows of *Austinogebia narutensis* (Sakai 1986) are characterized by their wide, shallow U-shaped structure (Kinoshita & Itani 2005).

Upogebiid shrimp dig their own independent burrows, and cases of inter-connected burrows have been reported in males and females or juveniles and adults (Frey & Howard 1975, Coelho et al. 2000, Candisani et al. 2001, Li et al. 2008, Kinoshita et al. 2010, Sepahvand et al. 2014). Observations of *U. noronhensis* in aquaria by Candisani et al. (2001) showed that male shrimp dig additional tunnels extending from their own burrows to connect to female burrows as a mating strategy. It is also known that in Callianassidae (current infraorder Axiidea), *Nihonotrypaea harmandi* (Bouvier 1901) copulate in their burrows (Somi-

ya & Tamaki 2017) and juvenile shrimp burrows have been found to emerge from adult burrows (Frey & Howard 1975, Candisani et al. 2001, Kinoshita et al. 2010). Juveniles of *Kraussillichirus kraussi* (Stebbing 1900) and *Nihonotrypaea japonica* (Ortmann 1891) have also been shown to use conspecific burrows as recruitment sites (Forbes 1973) and to avoid heavy bioturbation by adults (Tamaki et al. 1992). Forbes (1973) indicated that *K. kraussi* have a short larval period (3–5 days) and can metamorphose in adult burrows. Many juvenile mud shrimps may also inadvertently use adult burrows due to their long larval periods. In contrast, two mud shrimps, *U. major* and *U. omisssa*, have their own independent burrows from the juvenile stage itself (Coelho et al. 2000, Kinoshita 2002). To the best of our knowledge, differences in the behavior of juvenile mud shrimps have not been discussed.

3. Future Effect of Climate Change on Mud Shrimp; Based on Lessons from the Great East Japan Earthquake

Little is known about the effect of climate change on the life history and habitat of benthic animals (Birchenough et al. 2015). The tsunami caused by the 2011 Great East Japan Earthquake greatly damaged the northwestern Pacific Ocean coastal area of Japan. Out of 13 species of *Upogebia* recorded in Japan (Komai 2020), three species—*Upogebia issaeffi* (Balss 1913), *U. major*, and *U. yokoyai*—were found in areas affected by the 2011 tsunami (Yokoya 1939, Sakai 1982, Itani 2004, Biodiversity Center of Japan 2007). Mud shrimp disappeared from the tidal flats affected by the disaster, but slowly reappeared in several areas (Kanaya et al. 2012, Kinoshita & Matsumasa 2016, Biodiversity Center of Japan 2016). It was expected that *U. major* would settle on the tidal flats of disaster-hit areas earlier than *U. yokoyai*, as the juvenile *U. major* creates independent burrows (Kinoshita 2002) but juvenile *U. yokoyai* use adult shrimp burrows to create burrows (Kinoshita et al. 2010). However, the earliest mud shrimps found in affected areas were *U. yokoyai* in the Orikasa River, Iwate prefecture (Kinoshita & Matsumasa 2016). The deep-burrowing decapods (*U. yokoyai* and *N. japonica*) were less resistant to disturbances arising from changes in the characteristics of sediments as a result of the tsunami in the tidal flats in Gamo Lagoon, Miyagi prefecture (Kanaya et al. 2015). It is possible that *U. yokoyai* in the Orikasa River survived tsunami disturbance by chance. Kanaya et al. (2015) reported that the rate of benthic animal recovery after heavy disturbance depends closely on their life-history traits. Mud shrimps, which tend to mature slowly, are among benthic animals whose populations recover slowly from physical disturbances.

Global tidal flats have been lost at a rate of approximately 0.55% per year over the last 30 years (1984–2016) (Murray et al. 2019). This is caused by human activities such as coastal development but also the effects of climate

change, such as rising sea levels, coastal erosion, and reduced sediment flux from rivers (Cazenave & Le Cozannet 2013, Murray et al. 2014). The establishment of protected areas (PAs) is a major tool for habitat and biodiversity conservation management (Hanawa 2002, Barr et al. 2011). However, PAs alone are unlikely to be sufficient to prevent ongoing tidal flat loss, as tidal flats within PAs are also being lost (Hill et al. 2021). Mud shrimps that inhabit tidal flats are also distributed in the neritic zone (e.g., Golubinskaya & Korn 2020, Seike et al. 2020), but the decrease in the tidal flats leads to a reduction in their distribution.

Creating alternative tidal flats is an effective means of conserving benthic communities on tidal flats. The tsunami and subsidence caused by the 2011 earthquake created new intertidal habitats for benthic animals including mud shrimps (Kinoshita & Matsumasa 2016, Matsumasa & Kinoshita 2016, Yuhara et al. 2019) but these new habitats have been reduced or lost by the reconstruction of seawalls. A tidal flat restoration project (Environmental Restoration Project on Enclosed Coastal Seas) using fallow fields was demonstrated in Ago Bay, Mie Prefecture, central Japan (Matsuda 2010, Kokubu & Yamada 2011). To achieve complementary tidal flat regeneration, knowledge of the current state of tidal flat ecosystems is necessary before the effects of climate change become serious.

This review showed that changes in seawater temperature affect the life history of shrimp and that physical disturbances can make it difficult to maintain the shrimp population. I hope that this report will help predict how global climate change will affect shrimp in the future.

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