Burrow utilization by the Japanese mitten crab *Eriocheir japonica* in the clay sediment of a freshwater river of Kyushu, Japan

Satoshi Kobayashi, Miguel Vazquez Archdale

**Abstract.**—This is the first record of the burrows of the Japanese mitten crab *Eriocheir japonica*. Morphologies of the burrows found in the clay sediment used by this crab were recorded by excavating them in a small freshwater river in Japan. Only *E. japonica* was found inside 2 of the 10 burrows examined (15 crabs and one crab, respectively), and the other 8 were empty. Crabs of various sizes (6.1–47.0 mm in carapace width) were collected from inside the occupied burrows. Burrow morphology ranged from single tunnels to complex burrows with multiple openings and tunnels. Openings (2–10 cm in diameter) were mostly located underwater. The single tunnels were 14–65 cm long. Considering the different digging habits of other burrowing animals found in this area, it can be concluded that *E. japonica* constructed these burrows. Burrows resembled those of the Chinese mitten crab *E. sinensis*, but were different in their location (freshwater vs. tidal), sediment type (clay vs. sand and silt), opening placement (mainly underwater vs. intertidal) and occupation rate (low vs. high). The low occupation rate suggests that *E. japonica* do not always rest in their burrows and rather prefer to hide beneath the riverbed’s large rocks. These results reflect the adaptation of *E. japonica* to the unstable environment of Japanese rivers.

**Key words:** crab burrows in riverbanks, burrow morphology, sibling mitten-crab species, freshwater burrowing animals, Japanese river environment

**Introduction**

The Japanese mitten crab *Eriocheir japonica* (de Haan, 1835) is a varunid crab widely distributed in eastern Asia, including Far-east Russia, eastern Korea, the whole of Japan except the Ogasawara Islands, western Taiwan and Hong-Kong (Guo et al., 1997; Komai et al., 2006). This crab is a large omnivorous benthic species, which often grows over 60 mm in carapace width (CW). The Japanese mitten crab is widely distributed along the rivers and seacoasts, because it is a catadromous species, i.e., migrating from freshwater rivers to the sea for reproduction (Kobayashi & Matsuura, 1991, 1995a,b). In many rivers in Japan and its neighboring countries, *E. japonica* have been exposed to strong fishing pressure as an important commercial crab species, especially for adult crabs during the season of their downstream migration. In the freshwater rivers where they reside, *E. japonica* increase in size until they attain maturity, and this period accounts for approximately 70–80% of their lifetime (Kobayashi, 2011a).

Our recent study has revealed the outline of *E. japonica*’s life mode in their freshwater habitat (Kobayashi & Vazquez Archdale, 2021), which can be summarized as follows. Small crabs (CW < 20 mm) crawl upstream aided by their relatively long ambulatory legs, which are adapted to crawl against the strong currents they encounter (Kobayashi, 2002). They have an evident positive rheotaxis and basically pre-
fer to spend their time in this rapid water flow environment (Kobayashi, 2012a); small crabs actively move and do not stay in the same place for a long time. Therefore, small crabs can widely disperse upstream along the course of rivers. These moving habits gradually weaken as they grow, and when they become adult crabs, they eventually lose their positive rheotaxis. Consequently, adult crabs can move freely within a stream unit (reach, interval between meanderings) that are repeated with different river bed environments (pools, riffles and runs). Adult crabs use pools as their resting site, and can wander between pools around various sites while searching for food. Riffles and runs act as connecting passages between pools. Food preference of *E. japonica* is biased towards herbivory, but they increase their carnivorous characteristics when approaching sexual maturation (Kobayashi, 2009). They are basically deposit feeders and scavengers, but because they need animal protein, and these animal foods are rarely found on the river substrate, they need to wander searching for it. After accumulating enough energy by this active foraging for protein and lipid rich animal foods, adults finally develop a negative rheotaxis and begin their downstream migration towards the tidal river area. Most crabs spend approximately 2–3 years of their lives in this freshwater phase (Kobayashi, 2011b).

The Japanese mitten crab has a congeneric species, *E. sinensis* H. Milne-Edwards, 1853 (Chinese mitten crab), which is also catadromous and an important fishery species, and is originally distributed in middle-northern China and western Korea. Recent studies have revealed that this species is genetically close to *E. japonica* and that it evolved during the Pleistocene from a common ancestor while adapting to the large rivers and estuarine environment formed in the vast plains of the continental area (Xu et al., 2009; Kobayashi, 2012b).

While examining the literature of *E. sinensis*, we noticed that this crab has a characteristic of habitat engineering; there are reports of construction of burrows with elongated tunnels along the riverbanks of their native and introduced ranges (Peters & Panning, 1933; Rudnick et al., 2005). For this reason, we decided to investigate if this burrowing habit is also common in *E. japonica*, and to see if there is a difference in their ecological niche between the two species. In Japan, *E. japonica* can be easily collected from the gaps found beneath rocks underlying river channels (Kobayashi, 2003, 2012a), but up to this date there has been no record of their burrowing habit in their natural habitat. Thus, the purpose of this survey was to search for possible burrows along a small freshwater river in south-eastern Japan, and if any could be found to clarify their function and to compare their architecture and materials with those documented for *E. sinensis*.

**Materials & Methods**

The study site was selected within the lower freshwater area of the Saigo River, extending 1–1.5 km upstream from the rivermouth (33°45′45″N, 130°28′55″E, Fig. 1). The main stream of the Saigo River is nearly 6 km in length, running through paddy fields and the residential areas of Fukutsu City into the open coast of the Genkai-nada Sea, which is located in the western edge of the Sea of Japan. Surveys on growth, distribution and migration of *E. japonica* have been carried out for several years in this river (Kobayashi, 2003, 2006, 2012b); and *E. japonica* is widely distributed along its course as far as 5 km upstream from the river mouth. Megalopae of *E. japonica* settle and metamorphose into 1st-instar crabs (approximately 2 mm in CW) in the upper tidal river (nursery ground; nearly 500 m from the river mouth that is located just downstream from a tide-stopping weir). Juvenile crabs grown up to approximately >5 mm CW and actively migrate upstream into the freshwater area aided by their long walking legs through a
The burrows observed in the clay sediment were found in the lower freshwater area of this river (Fig. 1b, c). The survey area is located further upstream from the tidal area (area indicated by arrows, Fig. 1c), and it is a complete freshwater area that is not affected by the tides, even if there is no tide-stopping weir present in this area. The clay was strictly defined from the fineness of its grains, but it could be easily discriminated from the other sediments (sand, mud and silt) by its adhesive and solid nature. In this study site, the clay substrate can be easily confirmed because the evenly gray-colored hard stratum is exposed.

In the study site, river channels are ordinarily 5–10 m wide and flow meandering naturally within the floodplain, where a dense riparian vegetation grows. Artificial levees have been constructed outside the floodplain, which is approximately 20 m wide. The flow rate of this river is comparatively stable even during the drier season (less rainfall from December to February), but the water level can occasionally spillover the banks and flood the floodplain completely, so that the water mass reaches the levees during the flood season (June and July). Within each stream unit (defined as half a pitch of the meander); one run, one riffle, and one pool emerge alternately (see Fig. 1c). The distribution of burrows within this stream unit was roughly observed.

The survey of the burrows was conducted in an area extending approximately 30 m along the channel in the afternoon (13:00–16:00) of June 15, 2002. To examine the morphology of the burrows, casting plaster or resin into them was deemed inappropriate in the present environment, especially in the riffle area. Thus, the shape of the burrows was directly determined.
by excavating the clay sediment slowly with a bended steel wire that was inserted within the tunnel. The clay sediment was comparatively stable and the morphology of the burrows could be easily understood from their profile. The large and small diameters of the openings, length of tunnels (total length for single linear ones, and distances between folding points in the case of complex ones), and water depth of the edge of the burrows were measured to the nearest cm using a tape measure and a ruler, and their rough shapes were sketched onto a notebook. The bended steel wire was also used for the measurement of the total length of the burrows by inserting it into the tunnels. Although nearly 15 burrows were damaged in the process, 10 burrows were found intact and could be successfully excavated around the edges; these ones were selected for recording their features.

When *E. japonica* were found inside their burrows during the excavating, they were collected by hand. Their maximum carapace width (CW) was measured to 0.1 mm using a vernier caliper. They were sexed by the shape of their abdomen, but young crabs of CW $\leq$ 10 mm, which were difficult to sex accurately by the naked eyes, were scored as unsexed juvenile crabs. The presence of other burrowing animals was also examined within the burrows and around the clay sediment in the lower freshwater area.

**Results**

The burrowing site was limited to the clay sediment (Fig. 2), but varied within the stream unit. Burrows were abundantly found in the banks around riffles and pool areas. The clay sediment was exposed in some pools where the substrate had been washed away deeply, especially at the meandering site of the current (approximately 50–120 cm deep). Generally, pools of this type are created by large hard bedrocks which make the water flow meander, but in the lower reaches of the Saigo River, the clay sediment plays the same role of the bedrocks. The burrow openings were found in this exposed clay substrate. This clay substrate continues into the riffle area. In a large part of the riffle area (ca. 5–30 cm deep), numerous rocks were distributed on the coarse sand, but here the sand and stones were washed out from the slippery clay surface, and the impermeable clay stratum was exposed in the bottom, where some burrow openings could be found. In addition, the clay stratum was exposed as a belt less than 1 m wide in the profile of the banks in some of the pools (approximately 40–80 cm deep). In these banks, burrows were selectively dug in the clay stratum, while none were found in any other strata. In this clay sediment, several cm deep shallow dents, which were incomplete burrows, could also be observed.

Most burrow openings were positioned under the water and around the banks; no burrows were found in the mid-channel area. Some burrows opened above the water in the banks, but all the tunnels extended under the water in their inner part (Fig. 2d). Burrow morphology varied from single straight or curved tunnels to highly complex burrows with multiple openings and tunnels (Fig. 3). The length of tunnels with a simple structure ranged from 14–65 cm (Fig. 3b, c, d, g, h, i). The water depths of the openings examined were 7–22 cm below the water surface. Most tunnels were oriented slightly sloping downwards towards their deepest point 30 cm under the water level, and tunnels were dug within 12 cm in a vertical direction. In one simple burrow, the tunnel curved in its middle section and inverted its slope from downward to upward (Fig. 3i). The openings of the burrows were nearly round or oval and the smallest opening was 2 cm $\times$ 3 cm while the largest one was 8 cm $\times$ 10 cm. Chambers with wide distinctive open spaces could not be recognized in any of the burrows examined. The inner surface of the burrows was rough and had many crab claw scratches;
which suggests that *E. japonica* does not make any alterations to the inner surface of the burrows (Fig. 2e). No burrows were found within the study site with closed openings (burrows with no openings) or with traces of having been closed with clay sediment.

The density of these openings varied from 0–1 to 10–15 per 0.25 m$^2$. In the widely exposed clay layers, burrow openings were concentrated in large numbers in some areas.

Fig. 2. Photographs of the burrows of *Eriocheir japonica* dug in the clay sediment. a, burrows with relatively simple structure; b–d, burrows with complex structure and multiple openings; e, profile of a burrow showing its inner surface.
These openings created a pitted uneven clay surface (Fig. 2b, c, d). These burrow openings were in many cases those of highly complex burrows, and tunnels were connected with each other along their inner parts (Fig. 3a, e). In contrast, there was an area where the burrow opening was very rare (<1 per 0.25 m²); single tunnels were present in this area (Fig. 2a).

During the survey, no *E. japonica* was detected moving actively around the collection site; however, they could be collected only from 2 (burrows “a” and “i”, Fig. 3) of the 10 burrows examined and the remaining ones were found vacant. No other animals were found in or

---

**Fig. 3.** Diagram showing the morphologies and sizes (length and long and short diameters in cm) of *Eriocheir japonica*'s burrows dug in the clay sediment in the freshwater area of the Saigo River. The number in parenthesis is water depth in cm at each point.
around the burrows. Fifteen mitten crabs, including young unsexed juveniles of 6.1–8.8 mm CW and middle and large sized males of 18.0 mm and 39.2 mm CW, were collected from a burrow with complex tunnels and multiple openings (Figs. 3a & 4a). A large male of 47.0 mm CW was found inhabiting one simple burrow with a single opening (Figs. 3i & 4i).

Presence of burrows with such a complex structure and multiple openings may cause weakening of the clay sediment riverbanks to some degree when found at high densities, but this sediment is rigid and stable compared to other soft sediments. The clay in which the burrows were dug was hard and could not be easily broken by handling with the bare hands.

**Discussion**

**Confirmation of the burrows of E. japonica**

After examining the evidence found in the present study, we can propose that the burrows surveyed were those used only by *E. japonica*. The possibility that they could have been previously dug and inhabited by other freshwater burrowing animals (such as sesarmid crab *Orisarma dehaani* (H. Milne-Edwards), red swamp crawfish *Procambarus clarkii* (Girard), or Japanese eel *Anguilla japonica* Temminck & Schlegel) can be rejected according to the existing information on the habitat preference and features of the burrows made by these animals, and their distribution pattern in the present survey area. *Orisarma dehaani* inhabit the wetland above the water (floodplain) rather than the banks along the river edge. They dig J-shaped burrows or complexes of deformed J-shaped tunnels in the soft mud found above the clay layer; their burrows avoid the clay sediment and are curved in a horizontal direction when they come into contact with the clay layer. In addition, the inner surface of their burrows does not show scratches, except at some of their curving points (Hashiguchi & Miyake, 1967; Utashiro & Lebensspuren Research Group, 1969). In the lower reaches of the freshwater area adjacent to the tidal area of the Saigo River, abundant *O. dehaani* co-occurred with *E. japonica* during the survey period. However, they normally occurred in the wetland above the water (floodplain), and they dug their burrows on the terrestrial environment.

![Carapace width frequency distribution of Eriocheir japonica collected from burrows (burrows "a" and "i", from Fig. 3) dug in the clay sediment.](image)
apart from the river banks. *Procambarus clarkii* prefer the lentic environment and dig burrows in a mud bottom which has often dried up, such as found in rice fields, following mostly a vertical direction (Correia & Ferreira, 1995; Hirakoso, 2001). In the Saigo River, *P. clarkii* occurred underwater in the freshwater area of this river, but they prefer a muddy substrate, where water velocity becomes very slow or disrupted, and where ponds are formed in the floodplain. *Anguilla japonica* also inhabit the lotic environment in the river, but they dig their burrows in the soft mud substrate with two openings, which include a large main tunnel parallel to the axis of the water flow (mostly horizontal) (Aoyama et al., 2005). In the survey area, *Anguilla japonica* were found hiding themselves under large stones or within large vinyl-chloride (or steel) pipes in the channels similarly as *E. japonica*, but they were not found inside any of the burrows surveyed in the present study. Considering that the burrows surveyed in our study were located in the clay sediment and basically found underwater, and that none of the above mentioned animals were found around any of these burrows, it can be concluded that they must have been constructed by *E. japonica*.

**Comparison of *E. japonica* and *E. sinensis* burrows**

In the case of *E. sinensis*, juvenile crabs dig burrows in the soft-sediment found along the banks of the intertidal portions of streams (Peters & Panning, 1933; Rudnick et al., 2005). In Europe and North America, this burrowing activity has been regarded as one of the most serious negative economic and ecological impacts brought by the establishment of this invasive alien crab, because there were no other species digging such burrows there before (Dittel & Epifanio, 2009). This digging habit of *E. sinensis* has been linked to the harmful effects of erosion and river bank collapse when their burrows become too dense (Peters & Panning, 1933; Rudnick et al., 2005). This crab’s burrows have been found in the tidal river area, between the high and low tide lines, and contained at least a downward-sloping tunnel and a saturated terminal chamber. Burrow morphology ranged from single tunnels with one terminal chamber containing a single crab, to highly complex burrows with multiple surface openings and tunnels containing multiple crabs. The type of sediment found in areas where the burrows were dug was dominated by sand and silt.

Burrow characteristics share certain similarities between these two *Eriocheir* species. However, the following different points are noteworthy. First, no burrows of *E. japonica* have been found yet in a tidal river, and their openings are generally located beneath the water surface. Probably this is because the tidal river environment where crabs are distributed after they settle is different between the Japanese small and steep rivers and the large and slow flowing rivers that flow through the Chinese continental plains. Second, the mixture of saltwater/freshwater in the tidal rivers occurs differently in these locations. It can be pointed that many small Japanese rivers have large saltwater intrusions flowing into them, where the saltwater hardly mixes or only mixes slightly with freshwater. On the other hand, in the large continental rivers, saltwater and freshwater tend to mix well in the lower region, and the salinity gradient is clear along the tidal river course; and high salinity is limited to the lower tidal area even during the flow tide (McLusky & Elliot, 2004). Therefore, the settlement of young *E. sinensis* tends to occur in the middle area within the long tidal river (the uppermost area reached by saline water) and many young crabs grow up in the tidal rivers (e.g., the River Thames; Clark et al., 1998). In contrast, young crabs of *E. japonica* settle on the upper limit of the tidal river, their megalopae are delivered to the uppermost tidal river area aided by the invasion of saltwater wedges (Kobayashi & Vazquez Archdale, 2015), and
soon these juveniles migrate upstream and disperse into the freshwater area (Kobayashi, 1998). Thus, the habitat of *E. japonica* in tidal rivers is very narrow in many Japanese rivers and their residence time is short when compared to those of *E. sinensis*. Third, *E. japonica* digs burrows in comparatively hard sediment, not in soft sediments like sand and silt favored by *E. sinensis*. Probably clay is the most stable sediment, except for very large rocks. The clay sediment is rigid, but has plasticity, and the long and sharp claws of *E. japonica*’s walking legs (especially of juvenile crabs), which are adaptive to clinging to the substrate against the strong current (Kobayashi, 2002), are very suitable tools that can be used for digging their burrows. Because large rocks are rare and the river’s surface has a low complexity in these sites, crabs may use and modify the shallow dents found in the clay substrate by digging them deeper to turn them into burrows they can use to shelter themselves.

Furthermore, this crab prefers hiding in the gaps found beneath the large rocks lying within the river channels. Juvenile crabs tend to concentrate at high densities in this microhabitat environment in the riffle area of the channels during the daytime (> 15 per 0.25 m² in May in the Saigo River; Kobayashi, 2012a). Though *E. japonica* probably has a habit of digging and disturbing the substrate with their legs, it has not developed the skill necessary to plaster and harden the soft walls of its burrows with its chelipeds, as shown by the scratched marks that the crabs left on the inner surface of their burrows, nor has the ability to close the tunnel openings.

Even though *E. japonica* has the ability to dig burrows in the clay sediment, they are not always used as their residential nests, and their occupation is most likely to be low and temporary, as shown in the present data. Probably, the unoccupied burrows remain standing for a long time without collapsing because of their rigid and stable sediment material, and this may further reduce their occupancy rate.

Compared with the environment of the large continental rivers where *E. sinensis* resides, which flow slowly and have a stable sedimentation of fine-grained soft sediment (habitat of *E. sinensis*), in the Japanese short and steep river environment where *E. japonica* has evolved, the flow rate of sediment is large and the riverbed fluctuation is substantially dynamic (Takahashi, 2008; Yoshimura et al., 2005). Actually, when the Saigo River is flooded, soft sediment is frequently washed away and the route of the channels shifts, except where it is located on clay substrate. In such an unstable riverbed environment, it is more adaptive for *E. japonica* to shelter itself temporarily in the gaps found beneath large rocks than to waste energy digging specific burrows in the soft river sediment, and more especially for the migrating juveniles.

When juvenile and adult *E. japonica* were reared in captivity in aquaria, we could observe them sheltering themselves inside vinyl-chloride pipes of several sizes lying on the bottom as their shelter (Kobayashi, 2012c). Judging from the results of this long-term rearing experiment, the possibility of their burrow utilization could be expected. Meanwhile, *E. japonica* frequently tried to escape from their rearing enclosures, and this suggests that because of their restfulness, they do not manage to settle in or around their burrows in the wild, but prefer to wander about along the riverbed (Kobayashi, 2012c). The low occupancy of the burrows found in the present survey may reflect this behavioral tendency.

However, our present results were obtained during the summer, when crabs are moving actively stimulated by the warmer water temperature and larger river flow rate that results under large rain precipitation (Japan Meteorological Agency). While in winter, they reduce their locomotive activity and the number of crabs collected under rocks in the channels evidently decreases (Kobayashi, 2003). *Eriocheir japoni-
ca’s use of the burrows may increase during winter, but this still needs to be confirmed. On the other hand, high occupancy of burrows (about 1/4–3/4) was recorded in *E. sinensis*, and a higher rate was found during the summer and autumn rather than in winter (Rudnick et al., 2005). Although there are also reports about *E. sinensis* juveniles sheltering in the gaps found beneath rocks in the river channel (Gilbey et al., 2008), they may actively utilize their burrows in contrast to *E. japonica*.

As for the physical impact of *E. japonica*’s burrows on the riverbanks, damage may be very small compared to that caused by *E. sinensis* in the countries where it has invaded, because the former’s burrows are dug in a stable clay substrate within the river channel (underwater) that is far away from the levees, and are always exposed to the river flow. *Eriocheir japonica*’s habitat engineering is within the range of fluctuations of riverbed disturbance in the river channels. In the first place, the situations are very different from each other; as there are many other burrowing animals living on the banks and flood plain in Japanese rivers (e.g., *Orisarma dehaani* and some grapsid crabs), and the distribution of these burrowing crabs is considered normal in this river ecosystem and has not been regarded as a disaster prevention problem in the Japanese river management policy.

**Utilization of clay sediment burrows by *E. japonica***

*Eriocheir japonica* residing in the burrows included those of various life stages; not only middle or large crabs, but also young juveniles, which are on the course of their upstream migration and dispersion. Araki & Nakanishi (2013) studied artificial shelter use of *E. japonica*, and found that their modal preferred height of gaps beneath rocks could be calculated as 3 × body thickness of crabs (BT, BT = 0.47 × CW in mm – 1.22). If this calculation method is applied to the burrows found in our survey, the recorded diameter of the smallest opening (2–3 cm) fits nicely within the range of the preferred values calculated for the juvenile crabs of 10–20 mm CW. The various sizes of burrow opening found, including large ones with 10 cm in long axis (burrows “g”, “h” and “i”), suggest that the large adult crabs (approximately CW > 40 mm) dig and use these burrows in a similar way to the small juvenile crabs (10–20 mm CW). Although the preference of habitat environment and locomotive traits are different between the small juvenile crabs and the large adults (Kobayashi & Vazquez Archdale, 2021), their habit of using burrows as shelter may be similar.

The presence of the unsexed juvenile crabs of 6.1–8.8 mm CW inside burrow “a” (Figs. 3a & 4a) indicates that they occurred in burrows with a large open space available relative to their small body size. Although these young crabs probably do not dig such large burrows, they might have shared those already constructed by large elder crabs, at least as their resting sites together with elder and larger crabs. A similar behavior can be observed beneath large rocks in the stream channels, where *E. japonica* aggregate in large numbers, and small juveniles often occupy the same space together with large adults (Kobayashi, 2012a). *Eriocheir japonica* do not occupy exclusively their individual territories.

Among many burrowing crab species (in most cases intertidal or terrestrial), the environmental factors which determine the distribution of the burrows are sediment type, salinity, water content and vegetation (Teal, 1958; Ono, 1965; Saigusa, 1978; Mouton & Felder, 1996). In the case of *E. japonica*, the most critical factor might be sediment type (clay), but its background is different from that found in other cases (e.g., ocypodid and grapsid crabs). Some crab species are restricted to the specific substratum conditions not only for the site of the burrows but also for their home range, including their foraging site (Murai et al., 1982).
Their population density is strongly affected by the distribution of each substrate. While in the case of *E. japonica*, they occur in various water environments because of their migratory habit (Kobayashi, 2012a), and are not restricted to living around their burrowing area alone. They use the burrowing site only as one of their available resting places, and they can still live even in those rivers where the clay sediment is not exposed along the bank.

The present study is the first to record the burrows of *E. japonica* in their natural habitat, but it was derived from minimal data collected only during a brief survey carried out in one season. We still need to conduct an additional detailed survey for around a year, to be able to compare our findings precisely with the burrowing habit of *E. sinensis*.

**Literature Cited**

Aoyama, J., Shinoda, A., Sasai, A., Miller, M. J., & Tsukamoto, K., 2005. First observations of the burrows of *Anguilla japonica*. Journal of Fish Biology, 67: 1534–1543.

Araki, A., & Nakanishi, R., 2013. Artificial shelter preference by the Japanese mitten crab *Eriocheir japonica*. Journal of National Fisheries University, 62: 39–45. (In Japanese)

Clark, P. F., Rainbow, P. S., Robbins, R. S., Smith, B. D., Yeomans, W. E., Thomas, M., & Dobson, G. 1988. The alien Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura), in the Thames catchment. Journal of the Marine Biological Association of the United Kingdom, 78: 1215–1221.

Correia, A. M., & Ferreira, Ó. 1995. Burrowing behavior of the introduced red swamp crayfish *Procambarus clarkii* (Decapoda: Cambaridae) in Portugal. Journal of Crustacean Biology, 15: 248–257.

Dittel, A. I., & Epifanio, C. E. 2009. Invasion biology of the mitten crab *Eriocheir sinensis*: a brief review. Journal of Experimental Marine Biology and Ecology, 374: 79–92.

Gilbey, V., Attrill, M. J., & Coleman, R. A. 2008. Juvenile Chinese mitten crab (*Eriocheir sinensis*) in the Thames estuary: distribution, movement and possible interactions with the native crab *Carcinus maenas*. Biological Invasions, 10: 67–77.

Guo, J. Y., Ng, N. K., Dai, A., & Ng, P. K. L. 1997. The taxonomy of three commercially important species of mitten crabs of the genus *Eriocheir* De Haan, 1835 (Crustacea: Decapoda: Brachyura: Grapsidae). Raffles Bulletin of Zoology, 45: 445–476.

Hashiguchi, Y., & Miyake, S. 1967. Ecological studies of marsh crabs, *Sesarma* spp. II. Habitats, copulation and egg-bearing season. Scientific Bulletin of Faculty of Agriculture Kyushu University, 23: 81–89. (In Japanese)

Hirakoso, S. 2001. Burrows of *Procambarus clarkii* (Girard)(Decapoda: Cambaridae) -observations in the rice field of fallow state-. Earth Science, 55: 227–239. (In Japanese)

Japan Meteorological Agency. Climate Statistics. http://www.data.jma.go.jp/obd/stats/data/en/index.html. Accessed in Sep. 2017.

Kobayashi, S., 1998. Settlement and upstream migration of the Japanese mitten crab *Eriocheir japonica* (de Haan). Ecology and Civil Engineering, 1: 21–31.

Kobayashi, S., 2002. Relative growth pattern of walking legs of the Japanese mitten crab *Eriocheir japonica*. Journal of Crustacean Biology, 22: 601–606.

Kobayashi, S., 2003. Process of growth, migration and reproduction of middle- and large-sized Japanese mitten crab *Eriocheir japonica* (de Haan) in a small river and its adjacent seacoast. Benthos Research, 58: 87–104.

Kobayashi, S., 2006. Environmental condition in the settlement area and nursery ground of the Japanese mitten crab *Eriocheir japonica* (de Haan) in the tidal river area. Ecology and Civil Engineering, 8: 133–146. (In Japanese)

Kobayashi, S., 2009. Dietary preferences of the Japanese mitten crab *Eriocheir japonica* (de
Haan) in a river and adjacent seacoast in north Kyushu, Japan. Plankton and Benthos Research, 4: 77–87.

Kobayashi, S., 2011a. Growth patterns of the Japanese mitten crab *Eriocheir japonica* (de Haan) in the river phase in Fukuoka Prefecture, Japan. Journal of Crustacean Biology, 31: 653–659.

Kobayashi, S., 2011b. Invasive biology of the mitten crab *Eriocheir* spp.-I. Classification of *Eriocheir*: invasive alien species *E. sinensis* (Chinese mitten crab) and Japanese native species *E. japonica* (Japanese mitten crab). Biological Science (Tokyo), 63: 42–54. (In Japanese)

Kobayashi, S., 2012a. Microhabitat utilization pattern of the Japanese mitten crab *Eriocheir japonica* in the lower reaches of rivers. Ecology and Civil Engineering, 15. (In Japanese)

Kobayashi, S., 2012b. Invasive biology of the mitten crab *Eriocheir* spp.-III. Possibility of invasion of *Eriocheir sinensis* into Japan and interaction with native species. Biological Science (Tokyo), 63: 175–189. (In Japanese)

Kobayashi, S., 2012c. Molting growth patterns of the Japanese mitten crab *Eriocheir japonica* (de Haan) under laboratory conditions. Journal of Crustacean Biology, 32: 753–761.

Kobayashi, S., & Matsuura, S. 1991. Longitudinal distribution of the Japanese mitten crab *Eriocheir japonicus* De Haan in the Kaminokawa River, Kagoshima. Nippon Suisan Gakkaishi, 57: 1029–1034. (In Japanese)

Kobayashi, S., & Matsuura, S. 1995a. Reproductive ecology of the Japanese mitten crab *Eriocheir japonicus* (De Haan) in its marine phase. Benthos Research, 49: 15–28.

Kobayashi, S., & Matsuura, S. 1995b. Maturation and oviposition in the Japanese mitten crab *Eriocheir japonicus* (De Haan) in relation to their downstream migration. Fisheries Science, 61: 766–775.

Kobayashi, S., & Vazquez Archdale, M. 2015. Migration process of megalopa of the Japanese mitten crab *Eriocheir japonica* (De Haan) from open sea to tidal river. Estuaries and Coasts, 39: 846–854.

Kobayashi, S., & Vazquez Archdale, M. 2021. Habitat preference and locomotive traits of the Japanese mitten crab *Eriocheir japonica* within the stream unit of the freshwater river environment. Limnologica, 88: 125870.

Komai, T., Yamasaki, I., Kobayashi, S., Yamamoto, T., & Watanabe, S., 2006. *Eriocheir ogasawaraensis* Komai, a new species of mitten crab (Crustacea: Decapoda: Brachyura: Varunidae) from the Ogasawara Islands, Japan, with notes on the systematics of *Eriocheir* De Haan, 1835. Zootaxa, 1168: 1–20.

McLusky, D. S., & M. Elliot, 2004. The Estuarine Ecosystem: Ecology, Threats and Management. Oxford University Press, Oxford. 222 pp.

Mouton, E. C., & Felder, D. L., 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. Estuaries, 19: 51–61.

Murai, M., Goshima, S., & Nakasone, Y., 1982. Some behavioral characteristics related to food supply and soil texture of burrowing habitats observed on *Uca vocans vocans* and *U. lactea perplexa*. Marine Biology, 66: 191–197.

Ono, Y., 1965. On the ecological distribution of ocypodid crabs in the estuary. Memoir of Faculty of Science Kyushu University Series E (Biology), 4: 1–60.

Peters, N., & Panning, A., 1933. Die chinesische Wollhand Krabbe in Deutschland. Zoologischer Anzeiger Suppliment, 104: 1–180. (In German)

Rudnick, D. A., Chan, V., & Resh, V. H., 2005. Morphology and impacts of the burrows of the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards (Decapoda, Grapsoidea), in South San Francisco Bay, California, U.S.A. Crustaceana, 78: 787–807.

Saigusa, M., 1978. Ecological distribution of three species of the genus *Sesarma* in winter.
season. Zoological Magazine, 87: 142–150.
Takahashi, H., 2008. River Engineering (new
version). Tokyo University Press, Tokyo, pp.
282–292. (In Japanese)
Teal, J. M., 1958. Distribution of fiddler crabs in
Georgia salt marshes. Ecology, 39: 185–193.
Utashiro, T., & Lebensspuren Research Group,
1969. Ecology and burrows of Sesarma
(Holometopus) dehaani: biological studies
in "Lebensspuren" part XI. Memoir of Taka-
da Branch Niigata University, 14: 219–239.
(In Japanese)
Xu, J., Chan, T., Tsang, L., & Chu, K., 2009.
Phylogeography of the mitten crab Eriocheir
sensu stricto in East Asia: Pleistocene isola-
tion, population expansion and secondary
contact. Molecular Phylogenetics and Evo-
lution, 52: 45–56.

Yoshimura, C., Omura, T., Furumai, H., & Tock-
ner, K., 2005. Present state of rivers and
streams in Japan. River Research and Appli-
cations, 21: 93–112.

Addresses
(SK) Hakozaki 3–36–36–401, Higashi-ku,
Fukuoka 812–0053, Japan
(MVA) Fisheries Resources Sciences Division,
Faculty of Fisheries, Kagoshima University,
Shimoarata 4–50–20, Kagoshima 890–0056,
Japan

E-mail address of corresponding author
(SK) mokuzuz@fb3.so-net.ne.jp