Short communication

The relationship between intertidal soil composition and fiddler crab burrow depth

Tung-Yun Chen [a], Gwo-Wen Hwang [b], Anderson B. Mayfield [c,d], Chang-Po Chen [e], Hsing-Juh Lin [a,e,*]

[a] Department of Life Sciences and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan
[b] Hydrotech Research Institute, National Taiwan University, Taipei 106, Taiwan
[c] National Museum of Marine Biology and Aquarium, Pingtung 944, Taiwan
[d] Living Oceans Foundation, MD 21403, USA
[e] Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan

ARTICLE INFO

ABSTRACT

Fiddler crab burrow morphologies in tidal flat ecosystems depend largely on physical characteristics of the soil. Herein, we aimed to examine the relationship between soil texture profiles and the burrow depths and morphologies of four fiddler crab species: *Tubuca arcuata*, *Gelasimus borealis*, *Xeruca formosensis*, and *Austruca lactea*. We found that the burrow depths of *T. arcuata*, *G. borealis*, and *A. lactea* (range = 8–50 cm) were strongly affected by surface soil composition; only the burrow depth of *X. formosensis* (which reached 100 cm in some cases) was influenced by the presence of deeper, clay-rich soils. Specifically, *X. formosensis* relied more heavily on fine soils, such as clay or silt, when they burrowed deeper into sand-covered mudflats. We hypothesize that deep burrowers, such as *X. formosensis*, may coat clay-rich soils on their burrow walls to impede flooding and to prevent burrow collapse, suggesting that surface soil composition does not necessarily determine the burrow depth and composition for all fiddler crab species.

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1. Introduction

Fiddler crabs are widely distributed in tropical and sub-tropical coastal intertidal zones (Crane, 1975 Wolfrath, 1992; Lim and Diong, 2003). With the exception of some species that live within hard substrates, most fiddler crabs live in coastal marshes, mangroves, or open tidal flats (Crane, 1975; Shih, 2015). Male fiddler crabs display lekking behavior; therefore, most species prefer vegetation-free tidal flats (Croll and McClintock, 2000). In these open tidal flats, burrows play integral roles in the lives of adult fiddler crabs. They provide shelter from excessive heat exposure during low tides, refuges during high tides, and protection from predators (Powers and Cole, 1976; Lim and Diong, 2003; Michaels and Zieman, 2013). Mating also occurs in such burrows during the breeding season (Ribeiro et al., 2010). The dense burrows can also improve aeration and aid in the local transport of nutrients within coastal tidal flats. Therefore, these crustaceans have been deemed "ecological engineers" or "bioturbators" (Kristensen and Alongi, 2006; Araújo et al., 2012).

Burrows are typically indicative of their builder, and species-specific burrow types are well documented (Crane, 1975; Shih et al., 2005). Previous studies have digitally characterized burrow morphology by documenting parameters such as depth, width, length, and branch number (Lim and Diong, 2003; Lim, 2006); such parameters are readily influenced by a number of environmental characteristics, most notably the degree of vegetation (Lim and Heng, 2007; Lim and Rosiah, 2007; Wang et al., 2014; Wang et al., 2015). Soil matrices in tidal flats are primarily composed of sand, silt, and/or clay, and the relative proportion of each determines the characteristics of the soil matrix. For instance, clay-rich soils have the strongest degree of cohesion between particles, making the matrices consisting of such soils the most difficult for water to penetrate (Christy, 1982; Morrisey et al., 1999; Wang et al., 2009). However, the relationship between local soil composition and fiddler crab burrow morphology has not been previously documented. For instance, do these crabs always simply use the most locally abundant soil to build their burrows or do they transport different soil types from nearby areas? As mentioned briefly above, the phys-

* Corresponding author at: Department of Life Sciences and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan.
E-mail address: hjlin@dragon.nchu.edu.tw (H.-J. Lin).

ical characteristics of different soils differ, meaning that certain soil types might serve as better burrow building material.

Most fiddler crab species living in tidal flats excavate 10–40 cm into the soil (Kristensen, 2008); however, *Afruca tangeri*, *Xeruca formosensis*, and *Leptuca subcylindrica* are known to burrow down to 90, 100, and 180 cm, respectively, below the surface (Thurman, 1984; Wolfrath, 1992; Shih et al., 2005). Soil texture may vary greatly across such depths, though the effects of soil texture profiles (i.e., the differences in soil texture amongst soil layers) have rarely been explored with regard to crab burrow formation. Soil composition could be hypothesized to particularly influence the burrowing of deep burrowers, especially if burrow-strengthening, low-penetrability, clay-rich soils are prevalent at certain depths and layers, but not in others. Herein, we aimed to examine the relationship between soil texture profiles and the burrow depths and morphologies of four fiddler crab species: *Tubuca arcuata*, *Gelasimus borealis*, *Austruca lactea*, and the deep burrower *X. formosensis*.

2. Materials and methods

2.1. Study sites and target species

Our study was conducted across five sites (n = 5-10 stations at each site) along the western coast of Taiwan; all sites (23°49′N–25°10′N, 120°13′E–121°27′E) are characterized by subtropical climate patterns. From south to north, these sites included Mailio (ML), Shenkang (SK), Xiangshan (XS), Zhuwei (ZW), and Wazihwei (WZ). The monthly average air temperature of all sites ranged from 15.6 to 29.6 °C, and precipitation ranged from 1148 to 1571 mm (Central Weather Bureau of Taiwan; www.cwb.gov.tw).

To prevent bias driven by differences in water levels amongst the five sites, we calculated the proportional submersion time for each station with the Weibull method (Chow et al., 1988), which is dependent upon both local elevation and sea level (Liao et al., 2008). The elevation of each station was precisely measured by a Real Time Kinematic system (GR-3, Topcon, USA), and sea level data of each site in 2014 were obtained from the Taiwan Typhoon and Flood Research Institute (TTFRI) database. We defined upper and lower intertidal zones as those whose submersion times were below and above 20%, respectively. The stations of SK and ZW were further divided into upper and lower intertidal zones (SK-U and SK-L, respectively, and ZW-U and ZW-L, respectively).

To minimize the influence of vegetation on crab burrow morphologies, all chosen sites were vegetation-free tidal flats, and all field work was conducted during low tide. The sampling times were the Fall of 2014 and from Spring to Fall in 2015; these seasons were chosen because the target fiddler crab species breed during these periods and so are especially active (Crane 1975; Hopkins and Thurman 2010; Shih, 2015). In total, all sites were visited four times, with the exception of ZW (two surveys only). The soil matrices observed did not change dramatically over time (data not shown); therefore, sampling time was not considered as a factor in the statistical analysis (described below).

2.2. Burrow resin casting

Burrow resin casts were made from unsaturated polyester resin (Tsai-Fu Industrial Co., Ltd, Taiwan) to quantify morphological parameters of the crab burrows. The sampling area at each station was an 8 m^2 quadrat. For each species, casting work was only conducted if there was a relatively high burrow density in the vicinity. After one hour of curing, resin casts (typically 3–25/site) were carefully unearthed and inspected to ensure that the resin reached the bottom of the burrow. The builder of the burrow could typically be determined by either its physical presence nearby or the type
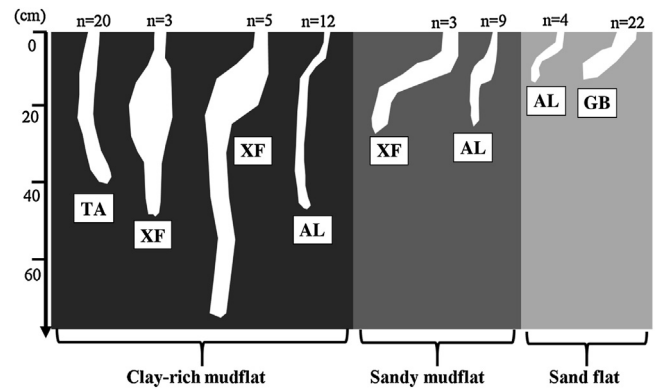
Fig. 1. A depiction of typical burrows of each of the four target fiddler crab species in different surface soil texture profiles: clay-rich mudflats (<100 μm), sandy mudflats (100–150 μm), and sand flats (150–250 μm). XF = *Xeruca formosensis*, TA = *Tubuca arcuata*, AL = *Austruca lactea*, and GB = *Gelasimus borealis*.

of specialized structure found around the burrow opening (e.g., chimney, hood; see Fig. 1). Burrow depth and sinuosity (width-depth ratio; unitless) were measured as described by Lim and Diong (2003).

2.3. Soil texture profile

To characterize the soil texture profile, two soil sub-samples were taken from each station within each of the five sites by a sampling instrument (LY082.1500, Zhen-Yong Industrial Co., Ltd, Taiwan), and the soil cores encompassed five *a priori*-assigned layers: 0–20 (surface), 20–40, 40–60, 60–80, and 80–100 cm. Then, we used PVC tubes (diameter: 2.6 cm; length: 5 cm) to extract the soil samples from the 322 cores. Soil texture analysis was performed by standard wet sieving (Hsieh and Chang, 1991), and the median grain size was calculated (Bale and Kenny, 2005).

2.4. Statistical analysis

The differences in burrow sinuosity and depth amongst the four species were analyzed by one-way ANOVAs, and Tukey's *post-hoc* tests were performed to test for individual mean differences (*p* < 0.05). All data were tested for homogeneity of variance using Levene's test. The relationships between burrow depth (natural log-transformed data) and median grain size were analyzed by linear regression analysis after having converted all data to Z-scores. All analyses were conducted with SigmaPlot ver. 12.0.

3. Results

3.1. Burrow morphologies of four Taiwanese fiddler crab species

The burrow structures of *X. formosensis* (n = 17 burrows), *T. arcuata* (n = 23), *A. lactea* (n = 27), and *G. borealis* (n = 25) are shown in the Electronic Supplemental Material (ESM). Coarse, smooth, and thin chimneys were typically located near the burrow openings of *X. formosensis*, *T. arcuata*, and *A. lactea*, respectively. However, there were no such specialized structures near the burrow openings of *G. borealis*. The burrows of *X. formosensis* were found in mudflats (Fig. 1). In clay-rich mudflats, the burrows of *X. fomosensis* had relatively enlarged chambers; moreover, they could be divided into shallow and deep burrows. Although the majority of burrows from the sandy mudflats also had slightly enlarged chambers, the burrows tended to be N-shaped. The burrows of *T. arcuata* were only found in clay-rich mudflats; they were typically straight, though slightly sinuous at the bottom. The burrows of *A. lactea* were observed in all
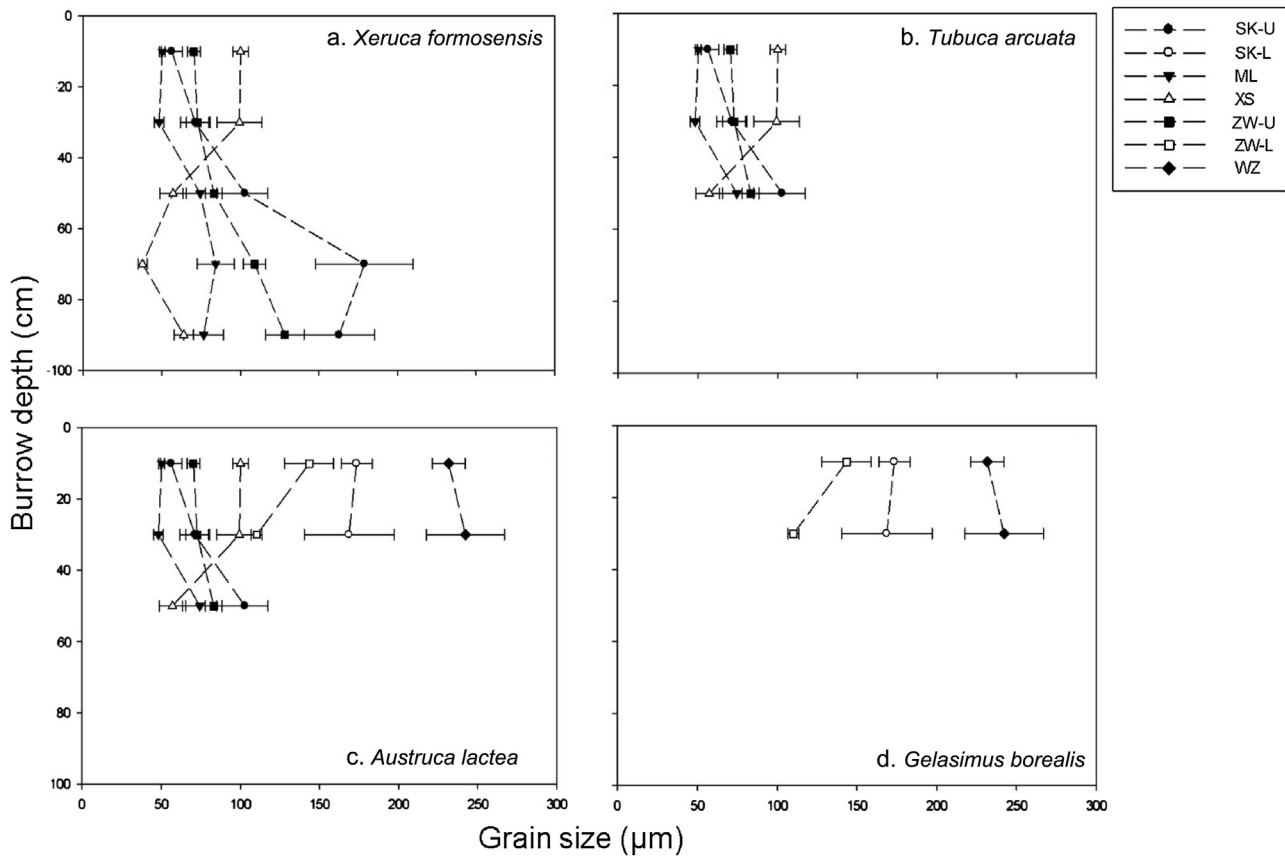
Fig. 2. Association between grain size (mean ± SE) and burrow depth for four species at five sites: (a) X. formosensis (burrow depth range: 0–100 cm), (b) T. arcuata (0–60 cm), (c) A. lactea (0–60 cm), and (d) G. borealis (0–20 cm). Mailio (ML), upper (SK-U) and lower (SK-L) intertidal regions at Shenkang, Xiangshan (XS), upper (ZW-U) and lower (ZW-L) intertidal regions at Zhuwei, and Wazihwei (WZ).

the three types of habitats. In the mudflats, the burrows of A. lactea were straight structures lacking chambers, while those in the sandy mudflats were generally J- or L-shaped with prominent chambers. The burrows of this species in sand flat ecosystems were thin, shallow, and devoid of chambers. Finally, the burrows of G. borealis were only found in the sand flats, and they were generally J-shaped.

There was a statistically significant effect of fiddler crab species on burrow sinuosity (one-way ANOVA, $F_{3,87} = 32.026$; $p<0.001$). Specifically, the burrows of G. borealis were the most sinuous of the four species (1.2 ± 0.4), and there were no significant differences amongst the other three species ($p>0.05$). There was also a significant effect of species on burrow depth ($F_{3,87} = 32.026$; $p < 0.001$); the burrows of X. formosensis and G. borealis were the deepest (47.8 ± 19.6 cm) and shallowest (7.9 ± 3.1 cm), respectively. All species, except G. borealis, readily penetrated the soil beyond 20 cm from the surface (Fig. 2). The burrows of X. formosensis, T. arcuata, and A. lactea in the upper intertidal zone (SK-U, ML, XS, and ZW-U) reached at least the third soil layer. In contrast, the burrows of A. lactea and G. borealis in the lower intertidal zones did not extend beyond the second layer.

3.2. Soil texture profiles for each species

Based on the grain size in the upper soil layer (top 20 cm), ML, SK-U, and ZW-U were classified as clay-rich mudflats (< 100 μm), XS was considered to be a sandy mudflat (100–150 μm), and SK-L, ZW-L, and WZ were classified as sand flats (150–250 μm). For the burrows of X. formosensis, there was a significant interaction effect between grain size and burrow depth (Fig. 2a), and only this species readily burrowed deep enough to encounter different grain sizes

from those of the surface soil. For this species, the vertical grain size distribution showed two predominant patterns: (I) increasing (SK-U, ZW-U, and ML) or (II) decreasing (XS) grain size with increasing burrow depth. For T. arcuata and A. lactea in the upper intertidal zones, there was also an interaction between grain size and burrow depth (Figs. 2b and c). For A. lactea and G. borealis in the lower intertidal zone (Fig. 2c and d), however, there was a significant difference in grain size between zones; the average grain size in the lower intertidal zone was coarser than in the upper intertidal zone.

3.3. The relationship between burrow depth and soil texture profile

The grain size data were partitioned into two groups according to burrow depths: 1) the top 20 cm of soil and 2) a finer soil layer deeper in the burrow (Fig. 3). When finer soils were considered in the inferior regions of the burrow, the burrow depth of X. formosensis was negatively correlated with grain size ($r^2 = 0.55$; $p < 0.001$). However, when only considering the grain size distribution in the top 20 cm of the soil matrix, there was no relationship between burrow depth and grain size ($p = 0.270$). No relationship was detected between the burrow depth of T. arcuata and soil grain size ($p = 0.512$). Although the burrow depth of A. lactea demonstrated a significant, negative relationship with grain size in the upper-layer ($r^2 = 0.52$; $p < 0.05$), the burrow depth of G. borealis was characterized by a significant, positive relationship with the grain size within the upper layer ($r^2 = 0.74$; $p < 0.01$).
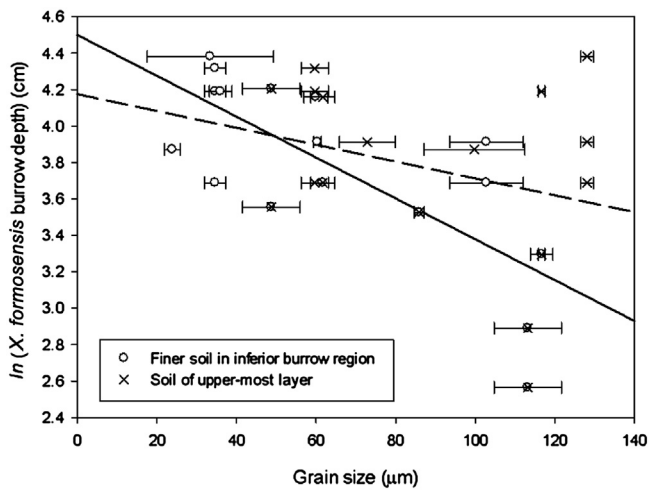
Fig. 3. The linear regression analysis between *Xeruca formosensis* burrow depth and grain size (mean ± SD) for two soil depth categories: the top 20 cm of soil (hatched line) and a finer soil layer deeper in the burrow (solid line; n = 17).
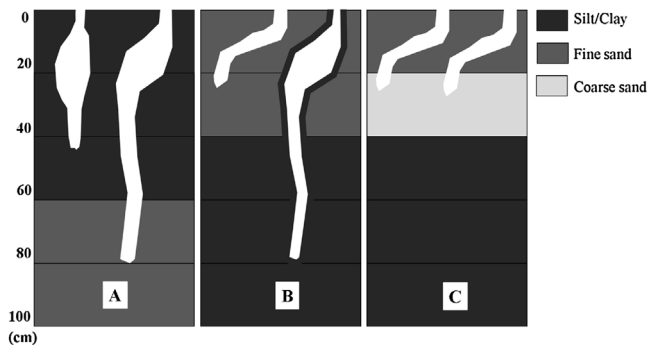
Fig. 4. A depiction of burrows of *Xeruca formosensis* within different soil texture profiles. Profile A burrows featured an upper, clay-rich layer and a lower sand layer and were common in upper intertidal mudflats of Shenkang and Zhuwei. Burrows of profiles B and C were characterized by upper sand layers and lower clay-rich layers and were common in mudflats of Xiangshan.

4. Discussion

For the widely distributed fiddler crab *A. lactea*, burrow depth changed across different soil grain size profiles. In contrast to the deep burrows of *T. arcuata* in the clay-rich mudflats, the burrows of *G. borealis* and *A. lactea* in the lower intertidal zone were not expected to be sturdy or deep when built within sand matrices. Indeed, their burrows were not readily maintained because tidewater frequently brought in sediments and flooded the burrows. This might be the reason why *G. borealis* built the most sinuous burrows; such could give them a better chance of avoiding being buried during flooding periods.

The burrows of *X. formosensis* appeared not only in clay-rich mudflats but also in sand-covered mudflats. This variation in soil profile preference might be linked to the ability of *X. formosensis* to burrow more deeply than the other target species. Amongst the three texture profile types documented for their burrows (Fig. 4), profile A burrows (e.g., those of SK-U and ZW-U) were composed of an upper clay-rich layer and a lower sand layer; in contrast, profiles B and C burrows (e.g., those of XS) were composed of upper sand layers and lower clay-rich layers, with profile C burrows having coarser sand in the second layer than profile B. Based on the burrow morphologies and soil texture profiles, profile A burrow builders normally constructed enlarged chambers, and they could continue burrowing beneath such chambers. Shallow, profile B bur-

rows tended to be N-shaped (Fig. 4); however, after entering the deeper layer, *X. formosensis* might have excavated deeper clay sediments in order to coat such water-impermeable soil particles on the burrow wall, including the wall surrounding the chamber; this could explain why clay-rich soils were found around the chamber even though such clay-rich soils were not necessarily the most common soil type in the proximate vicinity (Fig. 4). Meanwhile, the second layer of profile C was so coarse that it only allowed for the building of shallow, N-shaped burrows, rather than deeper ones (Fig. 4).

The hypothetical fine-soil coating behavior of *X. formosensis*, which was alluded to above, was not directly observed; however, some previous studies have mentioned the feasibility of similar compacting behavior by fiddler crabs, highlighting the potential of these crabs to serve as ecological engineers. Fiddler crabs can indeed directly change the vertical soil composition profile (McCraith et al., 2003). De (2015) found that *A. lactea* displays a type of fine-scale engineering by moving mud from under the surface sand (approximately 20 cm) to the surface to build mud mounds. Additionally, Huang et al. (2007) found that fiddler crabs in lower marsh regions can compact soil particles to strengthen their burrow structures. In theory, such coating behavior would be beneficial in terms of not only preventing the burrow from flooding, but it would, more generally, serve to strengthen the burrows. Therefore, we speculate that when the surface soil is relatively sandy, such as those profile B burrows of Fig. 4, deep burrowers, such as *X. formosensis,* may preferentially coat finer-textured soils on their burrow walls, or incidentally achieve this while moving soils out from the burrows, to impede flooding and to prevent burrow collapse. Future work should seek to further explore the possibility of complex burrow engineering by fiddler crabs, as well as other intertidal organisms whose abodes are routinely threatened by sea level changes.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2016.12.011.

References

Araújo Jr., J.M.C., Otero, X.L., Marques, A.G.B., Nóbrega, G.N., Silva, J.R.F., Ferreira, T.O., 2012. Selective geochemistry of iron in mangrove soils in a semiarid tropical climate: effects of the burrowing activity of the crabs *Ucides cordatus* and *Uca maracoani*. Geo-Marine Lett. 32, 289–300.

Bale, A.J., Kenny, A.J., 2005. Sediment Analysis and Seabed Characterization. Methods for the Study of Marine Benthos. Wiley-Blackwell, London, pp. 43–86.

Chow, V.T., Maidment, D.R., Mays, L.W., 1988. Applied Hydrology. McGraw-Hill, New York.

Christy, J.H., 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). Anim. Behav. 30, 687–694.

Crane, J., 1975. Fiddler Crabs of the World. Princeton University Press, Princeton.

Croll, G.A., McClintock, J.B., 2000. An evaluation of lekking behavior in the fiddler crab *Uca* spp. J. Exp. Mar. Biol. Ecol. 254, 109–121.

De, C., 2015. Burrowing and mud-mound building life habits of fiddler crab *Uca lactea* in the Bay of Bengal coast, India and their geological and geotechnical importance. Palaeontol. Electron. 18, 1–22.

Hsieh, H.L., Chang, K.H., 1991. Habitat characteristics and occurrence of the spionid Pseudopolydora sp. on the tube-caps of the onuphid Diopatra bilobata (Polychaeta: spionidae, Onuphidae). Bull. Inst. Zool. Acad. Sin. 30, 331–339.

Huang, K., Boudreau, B.P., Reed, D.C., 2007. Simulated fiddler-crab sediment mixing. J. Mar. Res. 65, 491–522.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51, 1557–1571.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30–43.

Liao, S.W., Chang, W.L., Lin, S.W., 2008. Status and habitat preferences for endemic inhabitants of fiddler crab *Uca formosensis* in Hsiang-Shan wetland, Taiwan. Environ. Monit. Assess 143, 203–214.

Lim, S.S.L., Diong, C.H., 2003. Burrow-morphological characters of the fiddler crab, Uca annulipes (H. Milne Edwards, 1837) and ecological correlates in a lagoonal beach on Pulau Hantu, Singapore. C rustaceana 76, 1055–1069.

Lim, S.S.L., Heng, M.M.S., 2007. Mangrove micro-habitat influence on bioturbative activities and burrow morphology of the fiddler crab, *Uca annulipes* (H Milne Edwards, 1837) (Decapoda, Ocypodidae). Crustaceana 80, 31–45.

Lim, S.S.L., Rosiah, A., 2007. Influence of pneumatophores on the burrow morphology of *Uca annulipes* (H milne edwards, 1837) (Brachyura, ocypodidae) in the field and in simulated mangrove micro-Habitats. Crustaceana 80, 1327–1338.

Lim, S.S.L., 2006. Fiddler crab burrow morphology: how do burrow dimensions and bioturbative activities compare in sympatric populations of *Uca vocans* (Linnaeus, 1758) and *U. annulipes* (H. Milne Edwards, 1837)? Crustaceana 79, 525–540.

McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh. J. Mar. Res. 61, 359–390.

Michaels, R.E., Zieman, J.C., 2013. Fiddler crab (Uca spp.) burrows have little effect on surrounding sediment oxygen concentrations. J. Exp. Mar. Biol. Ecol. 448, 104–113.

Morrisey, D.J., DeWitt, T.H., Roper, D.S., Williamson, R.B., 1999. Variation in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediment in New Zealand. Mar. Ecol. Prog. Ser. 182, 231–242.

Powers, L.W., Cole, J.F., 1976. Temperature variation in fiddler crab microhabitats. J. Exp. Mar. Biol. Ecol. 21, 141–157.

Ribeiro, P.D., Daleo, P., Iribarne, O.O., 2010. Density affects mating mode and large male mating advantage in a fiddler crab. Oecologia 164, 931–941.

Shih, H.T., Mok, H.K., Chang, H.W., 2005. Chimney building by male *Uca formosensis* Rathbun, 1921 (Crustacea: decapoda: Ocypodidae) after pairing: a new hypothesis for chimney function. Zool. Stud. 44, 242–251.

Shih, H.T., 2015. Uca (Xeruca), a new subgenus for the Taiwanese fiddler crab Uca formosensis Rathbun, 1921 (Crustacea: decapoda: Ocypodidae), based on morphological and molecular evidence. Zootaxa 3974, 151–169.

Thurman, C.L., 1984. Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. J. Crustacean Biol. 4, 665–681.

Wang, J.Q., Tang, L., Zhang, X.D., Wang, C.H., Gao, Y., Jiang, L.F., Chen, J.K., Li, B., 2009. Fine-scale environmental heterogeneities of tidal creeks affect distribution of crab burrows in a Chinese salt marsh. Ecol. Eng. 35, 1685–1692.

Wang, M., Gao, X., Wang, W., 2014. Differences in burrow morphology of crabs between *Spartina alterniflora* marsh and mangrove habitats. Ecol. Eng. 69, 213–219.

Wang, J.Q., Bertness, M.D., Li, B., Chen, J.K., Lü, W.G., 2015. Plant effects on burrowing crab morphology in a Chinese salt marsh: native vs. exotic plants. Ecol. Eng. 74, 376–384.

Wolfrath, B., 1992. Burrowing of the fiddler crab *Uca tangeri* in the Ria Formosa in Portugal and its influence on sediment structure. Mar. Ecol. Prog. Ser. 85, 237–243.