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Burrow morphology of three species of fiddler crab (*Uca*) along the coast of Pakistan

Naureen Aziz Qureshi[1] **& Noor Us Saher**[2,*]

[1] Department of Wildlife and Fisheries, Government College University, Faisalabad Allama Iqbal Road 38000, Faisalabad, Pakistan. Email: naureenaziz.qureshi@gmail.com.
[2] Centre of Excellence in Marine Biology, University of Karachi, Karachi 75270, Pakistan. Email: noorusaher@yahoo.com.

* Corresponding author: noorusaher@yahoo.com.

ABSTRACT. Burrowing by crabs is an important component of their functional role in mangrove biotopes. The Fiddler crab (*Uca*) is one of the more conspicuous burrowing organisms in the mangrove areas of Pakistan. To evaluate interspecific differences in burrowing behaviour between three species of *Uca* (*U. annulipes, U. chlorophthalmus* and *U. sindensis*), we compared vegetation cover, sediment composition and burrow morphology by using plaster of Paris casts. Five burrow morphology characters were measured (burrow number, depth, length, volume, and diameter of the burrow openings). Nearly all the morphological characters of the burrows differed significantly between species. The burrow morphology variations were correlated with the tidal level (distance from the water mark during low tide), porosity, percent organic matter, vegetation cover and structure of the sediments. The species-specific differences in the burrows cautions against generalizing regarding the functional role of fiddler crabs along the coast of Pakistan.

KEY WORDS: burrows, fiddler crab, ecosystem engineer, biotopes, burrow cast, tidal height.

INTRODUCTION

Fiddler crabs are semi-terrestrial organisms that may influence the sediment structure and other living communities mainly through their burrowing and feeding activities (Teal, 1958). Fiddler crabs construct their burrows actively in the intertidal zone from coarse beach sand to fine clay-rich marshy mud during low tide. The digging of burrows begins when the crabs are very small (Hyman, 1922; Herrnkind, 1968). The digging behavior of fiddler crabs has been described by various authors (Altevogt, 1955; Crane, 1975). These crabs are known to adjust their burrowing activities to a variety of conditions, such as stem density, root mat density, substratum, water, ground temperature, tidal periodicity, reproductive activity, threat by potential predators, seasons and mate display activities (Ringold, 1979; Bertness, 1985; Genoni, 1991). Faunally-mediated disturbances of the physical, chemical and biological structure of the sediment are known as 'bioturbation'. The bioturbation and fecal pellet production of fiddler crabs in mangroves have been described (Warren & Underwood, 1986; Dye & Lasiak, 1986; Skov et al., 2002; Bartolini et al., 2011). They result in increased growth of the cord grass, *Spartina alterniflora*, in salt marshes (Montague, 1980; 1984; Bertness, 1985). The resulting biogenic structures and the engineering processes involved in constructing and maintaining burrows generate complex interactions associated with trophic webs (Reise, 2002; Kristensen, 2008).

Burrows are important to fiddler crabs for a number of functions, allowing them to adopt a semi-terrestrial existence and avoid environmental stresses by behavioral means (Atkinson & Taylor, 1988). Fiddler crabs excavate burrows in the sediment, to avoid excessive wave action and obtain relief from hot and cold ambient temperatures and desiccation

(HYATT & SALMON, 1979; BERTNESS & MILLER, 1984; LIM & DIONG, 2003). Burrows provide a refuge from both aerial and terrestrial predators during exposed periods and from aquatic predators during flooding, water for physiological needs, and also sites for molting and reproduction (HYATT & SALMON, 1979; KATZ, 1980; CHRISTY, 1982; THURMAN, 1984; BERTNESS & MILLER, 1984; GENONI, 1991; LIM & DIONG, 2003; LIM, 2006; MILNER et al., 2010).

The architecture of the burrows plays an important ecological role in the life history of fiddler crabs as they are semi-terrestrial and active at low tide, returning to their burrows at high tide. Since the burrow is a place of refuge from predators, its structure must be advantageous to the crab when it is necessary to make a hasty retreat when pursued or threatened. Especially in anoxic sediments burrows have greater ecological significance as they help to improve the aeration of the sediments. Burrow morphology has been described by using plaster of Paris, rubber, or epoxy resin casts. General burrow morphology varies in diameter, depth, volume, and angle of the burrow with respect to the shoreline. General burrow design has been studied in several species of the fiddler crab including *Uca pugilator* (DEMBOWSKI, 1926; CHRISTY, 1982), *U. rapax* (GENONI, 1991), *U. pugnax* (GRAY, 1942; KATZ, 1980; BERTNESS & MILLER, 1984), *U. panacea* (currently synonymous with *U. pugnax* see POWERS, 1975), *U. longisignalis, U. spinicarpa, U. vocator, U. subcylindrica* (THURMAN, 1984), *U. tangeri* (WOLFRATH, 1992), *U. annulipes* and *U. vocans* (LIM & DIONG, 2003; LIM, 2006).

We hypothesized that the morphology of the burrows would vary between the three species of fiddler crabs, *U. annulipes, U. sindensis* and *U. chlorophthalmus,* as they prefer biotopes varying in tidal height, vegetation and sediment composition. There has been no previous comparative study of the burrow morphology of fiddler crabs along the coast of Pakistan. In the present study, we investigated differences in structural morphology and complexity of three species of fiddler crab burrows in their respective biotopes to identify the relationship of burrow morphology of *Uca* species according to their habitat found along the coast of Pakistan.

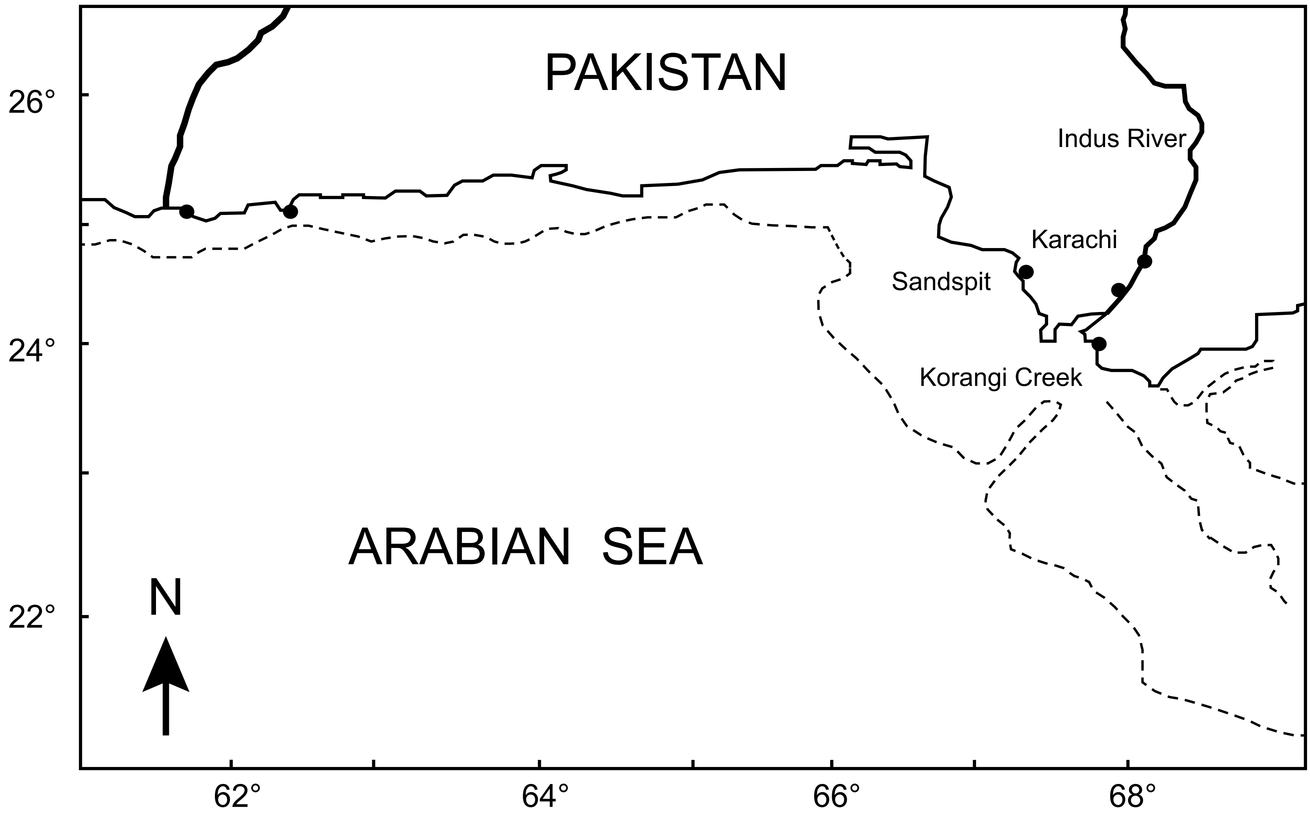

Fig. 1. – Coastline map of Pakistan showing the study sites i.e. Sandspit and Korangi creek mangrove areas.

MATERIAL AND METHODS

Study sites

Two sites, Sandspit and Korangi creek, were selected for the study based on the presence of separate patches of three species of fiddler crabs (Fig. 1). These sites differed markedly in terms of vegetation, tidal height and sediment properties, related to the habitat preferences of the respective species.

Site 1

The Sandspit backwaters mangrove area is located at (24^o50'N, 66^o56'E) south west of Karachi. The backwater is connected to the Arabian Sea through the Manora Channel. Sandspit beach is divided by a strip of dry land, with mud flats and mangrove vegetation found on the northern side. and sandy coast on its south. The dense vegetation comprises a monospecific stand of the mangrove species *Avicennia marina.*

Site 2

The second study site was located (24^o79'N, 67^o20'E) in the Korangi creek mangrove area near the salt works in the fishing village of Ibrahim Hyderi. The northernmost creeks of the Indus Delta are the Korangi and Phitti creeks of which Korangi creek is 12 km from Karachi Harbour and 9 km from Quaidabad. Korangi creek is connected at its northeastern end with Phitti and Kadiro creeks, while at its southwestern end, it connects with open sea and with Gizri creek, and the study area is bounded by extensive mangrove vegetation of *A. marina*.

Field Methodology

The identification of the burrow is an important issue in the study of burrow morphology of *Uca* species with sympatric distribution. For example, at a few sites *U. sindensis* coexists with *U. chlorophthalmus* whereas at other sites *U. chlorophthalmus* coexists with *U. annulipes*, and it was quite difficult to determine which burrow belonged to which crab species without identifying a pure distribution patch of each species. In this study the burrow cast data for *U. annulipes* and *U. chlorophthalmus* were collected from the two different stations of Sandspit and data for *U. sindensis* were collected from Korangi creek mangrove area. The plaster casts were found to be perfect for measuring the diameter, total length, total depth and volume of the burrows.

Burrow casts were made for the three species *viz*: *U. sindensis, U. chlorophthalmus* and *U. annulipes.* At selected sites, counts of open burrows were first conducted as these indicate the number of burrows present beneath the surface. The burrow-opening density within the distribution area of each species was estimated by randomly locating 0.25 m^2 quadrats (6 replicates). The total number of open burrows within each quadrat was counted. In each quadrat three or four burrows were randomly selected for casts.

Aqueous solution of plaster of Paris was poured into the selected crab burrows with the help of a syringe until the burrows were completely filled, then allowed to dry for 30 to 60 minutes (Warburg & Shuchman, 1978). If the crab emerged during this process, it was hand picked and placed in a marked poly bag for further analyses. The casts were then carefully dug up by hand, or with a spade in the case of hard substratum, then cleaned to remove as much sediment as possible from the surface of the cast. Each cast was separately placed in pre-marked poly bags and brought back to the laboratory for further analyses. After the casts were dug out, the area within each quadrat was excavated to a depth of 30 cm and the crabs were collected to calculate the relationship between the density of crabs and crab burrows. Three sediment cores (up to 30 cm in depth) were also taken adjacent to the casting area for each quadrat replicate, to analyse sediment properties. For each species, the different diameters of burrow openings (n = 45 at least) were also analyzed.

Crabs were caught within the burrows and at the mouths of their burrows. Burrow diameters were measured with vernier callipers and the following parameters of crabs recorded: sex, carapace width, carapace length (CL). The size (carapace length) of resident fiddler crabs can be determined for each species by using a linear equation expressing the relationship between CL and BD (burrow diameter). As a crab always enters its burrow sideways, (LIM & DIONG, 2003) carapace lengths have been used to study the relationship between resident crabs and their burrow diameters. The burrow diameter and crab length relationship was evaluated by the best fit regression line

$$\text{Carapace length (CL)} = a + b\,(\text{burrow diameter (BD)})$$

where a and b are coefficients to be estimated by the model. Data for males and females were pooled, as we observed no differences for the above parameters between the sexes during preliminary regression analysis.

LABORATORY ANALYSES

In the laboratory, sediment properties (percentage of organic matter and grain size) were analyzed. Percentage of organic matter was determined by the loss in mass after combustion in a muffle furnace, following SAHER & QURESHI (2010). Briefly, a 20-50 g sample of dry sediment was placed in a pre-weighed crucible, covered with a lid and combusted at 450 °C for 3 hrs. Grain size was analyzed by dry sieving methodology following FOLK (1974).

The morphology, size and structure of fiddler crab burrows were determined (Fig. 2). The parameters measured for each burrow cast were: burrow diameter (BD), total burrow length (TBL), total burrow depth (TBD), and burrow volume (BV). Volume was determined by weighing each cast (± 0.1g) and dividing the weight of the burrow cast by the density (2.2 g cm^{-3}) of plaster of Paris (CHAN et al., 2006). Only data for complete burrow casts were used for analyses.

Statistical analyses

Data for all burrow parameters studied and estimated were statistically analysed using Minitab (Version 15.0). A t-test was employed under the null hypothesis that the expected burrow densities were equal to the number of crabs. One-way analyses of variance (ANOVA) were used to test for differences between the species for density, total length, total depth, diameter and volume of burrows. Differences were accepted as significant at alpha = 0.05 for statistical analyses. Tukey's pairwise comparison tests were carried out when main effect ANOVA tests were significant for the burrow cast variables of the three species of *Uca* to relate variables to habitat. Pearson correlation coefficients were calculated to determine the relationship between burrow densities and sediment properties (percent organic and grain size).

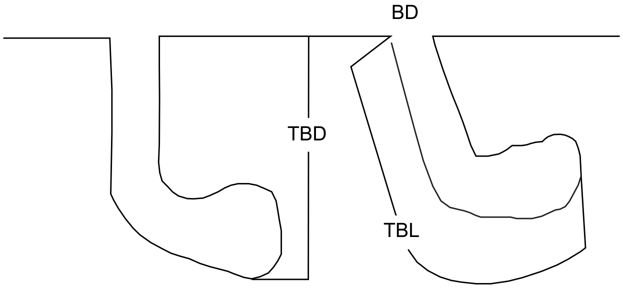

Fig. 2. – Burrow architecture parameters selected for analyses were BD: Burrow diameter (mm), TBL: Total burrow length (mm) and TBD: total burrow depth (mm).

RESULTS

There was a definite trend in the distribution area (biotope) of thèse three species of fiddler crabs. *U. chlorophthalmus* was the most frequently found species, mostly distributed from low tide level to mid tide level and to some extent up to high tide level of sandy and muddy areas. *U. sindensis* was mostly found at the high tide level of muddy and sandy areas. *U. annulipes* was mostly associated with fringing mangroves among pneumatophores.

TABLE 1

Summary of descriptive statistics for sediment properties (percentage organic, mean and median), burrows density and crab density from Sandspit backwater mangrove area and Korangi creek mangrove area during the study period.

Crab Species (Site)	Percentage organic	Mean (Φ)	Median (Φ)	Crab Density (m^{-2})	Burrow density (m^{-2})
Uca annulipes (Sandspit S1)	2.15±0.69 (1.28-3.56)	1.01±0.07 (0.88 -1.13)	0.95±0.06 (0.81-1.01)	28±12 (4-64)	74.5±31.0 (48 -144)
Uca chlorophthalmus (Sandspit S2)	1.85±0.67 (1.20–3.05)	1.29±0.16 (1.26-1.55)	1.35±0.06 (1.25-1.42)	45±16 (4-154)	145.1± 80.5 (56-252)
Uca sindensis (Korangi creek)	3.97±0.82 (2.60-4.29)	2.31±0.11 (2.14-2.47)	2.26±0.08 (2.13-2.36)	13±09 (2- 44)	98.7±52.5 (52 - 128)

Relationship between density (m^{-2}) of crabs and crabs burrows

The density of crabs and crab burrows varied considerably for all three species. The numbers of burrows were usually greater than the number of crabs. T- tests showed significant differences between the burrow and crab densities (Df = 11, T = 7.81, $P < 0.001$), (Df = 10, T = 4.78, $P < 0.001$) (Df = 11, T = 6.28, $P < 0.001$) for *U. sindensis, U. annulipes* and *U. chlorophthalmus*, respectively.

Relationship between carapace length of crabs and their burrow diameter

The relationship between carapace length of each resident crab (CL) and its burrow diameter (BD) was identified for each studied species by using simple linear regression. The data of male and female crabs were pooled as no significant intersexual differences were observed during preliminary analyses. Good correspondence and significant positive linear relationships were observed for all three species. Linear regressions for the different species of fiddler crab are:

U. sindensis: $CL = 2.212 + 0.591 * BD$ $r^2 = 0.713$
U. chlorophthalmus: $CL = 2.194 + 0.577 * BD$ $r^2 = 0.727$
U. annulipes: $CL = 5.118 + 0.419 * BD$ $r^2 = 0.586$

Sediment properties

The percentage of organic matter in all the biotopes of the three investigated species varied significantly. It was highest (3.92 + 0.87) for the *U. sindensis* biotope compared to biotopes of the other two species (Table 1). Grain size showed variation in sediment composition between biotopes of the three species (Fig. 3). The mean grain size (Mz) 2.31 Φ ±0.13 Φ can be classified as fine sand for *U. sindensis,* medium sand with Mz of sediments 1.35 Φ ±0.16 Φ for the site of *U. chlorophthalmus* and as coarse to medium sand ranging between 0.99 Φ ± 0.04 Φ phi for *U. annulipes* (Table 1).

Architecture of crabs burrows

A total of 148 casts were made for the three species of fiddler crabs during the study period: 58 for *U. chlorophthalmus*, 45 for *U. sindensis* and 45 for *U. annulipes*. Burrow casts generally varied in length and in the shape of closed ends (forming C, L, J, U, V and Y shapes) in vertical and complex branching morphologies with a single entrance, to complex interconnected burrow shafts with multiple entrances (Figs 4 & 5).

The burrow cast variables (TCL, TBD, BD and BV) varied according to species, their distribution according to tide levels, and biotope characteristics. Comparison of the size of burrow casts between the three species of *Uca* showed the mean TBL was 105.4±45.9 mm for *U. annulipes,* 128.0±34.2 mm for *U. chlorophthalmus* and 220.2±71.0 mm for *U. sindensis* (Table 2). The mean BD was 13.7±3.0 mm (*U. annulipes*),

TABLE 2

Summary of descriptive statistics for burrow morphological characters of three species *U. annulipes*, *U. chlorophthalmus* and *U. sindensis* from the two study sites.

Variable	Species	N	Mean + St.Dev	Min	Max
Total burrow length (TBL) in mm	*U. annulipes* *U. chlorophthalmus* *U. sindensis*	40 58 40	105.4 ± 45.9 128.0 ± 34.2 220.2 ± 71.0	45 62 110	210 205 335
Total burrow depths (TBD) in mm	*U. annulipes* *U. chlorophthalmus* *U. sindensis*	40 58 40	92.7 ± 36.5 95.7 ± 29.3 150.4 ± 62.0	32 46 70	145 165 244
Burrow diameter (BD) in mm	*U. annulipes* *U. chlorophthalmus* *U. sindensis*	40 58 40	13.7 ± 3.0 10.5 ± 3.8 12.8 ± 1.9	7 5 10	18 26 17
Burrow volume (BV) cm^3	*U. annulipes* *U. chlorophthalmus* *U. sindensis*	40 58 40	8.47 ± 5.87 6.69 ± 4.11 34.37 ± 16.94	1.84 1.92 16.61	23.04 22.47 82.39

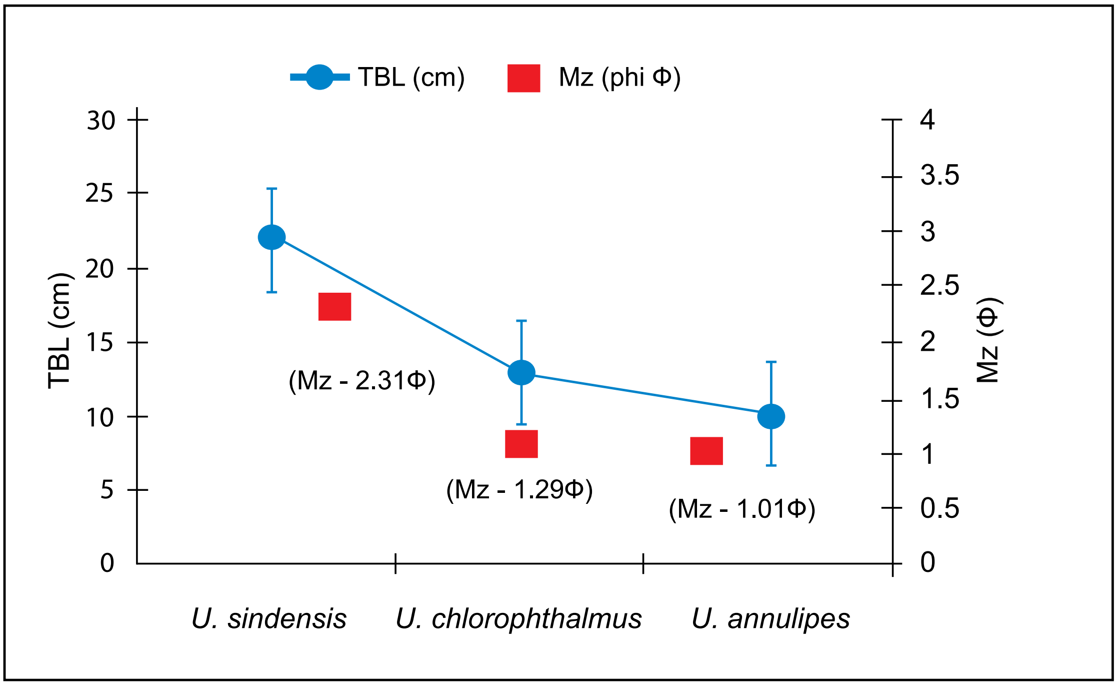

Fig. 3. – The average total burrow length (TBL) of three species of fiddler crab (*Uca sindensis, U. chlorophthalmus, U. annulipes*) in relation to mean sediment (Φ) grain size.

10.5±3.8 mm (*U. chlorophthalmus*) and 12.8±1.9 mm (*U. sindensis*) respectively. One-way ANOVA showed significant differences in TBL, TBD, BD and BV between the three species studied (Table 3). Also the density of burrow openings varied significantly ($F_{2, 17} = 24.79$, $P < 0.005$) between the three species (Table 3). *Post hoc* analysis showed that the density of burrow openings was significantly highest in *U. chlorophthalmus,* compared to *U. annulipes*, which was in turn significantly greater than *U. sindensis* (*U. chl.* > *U.ann.* > *U.sin.*) (Fig. 3).

Fig. 4. – The burrow structures of *Uca annulipes* (A) from Sandspit backwater mangrove area and *U. sindensis* (B) from Korangi creek mangrove areas during the study period.

Total burrow length, burrow depth and burrow volume were significantly greater in *U. sindensis* compared to the other two species (*U. sin.* < *U. ann.* ≈ *U. chl.*). The confidence interval for the TBL difference between the means of *U. sindensis* and *U. chlorophthalmus* extends from (4.122 to 11.654) to (-11.792 to -5.413) between the *U. annulipes* and *U. sindensis*. These ranges do not include zero, indicating that there was a statistically significant difference between the corresponding means.

The burrows of *U. annulipes* were less in volume with wider burrow openings. Burrow volume of *U. sindensis* was highest, with more winding shafts and usually only a single entrance observed (Fig. 4), whereas *U. chlorophthalmus* had multiple openings for a single burrow and variation in cast structure (Fig. 5).

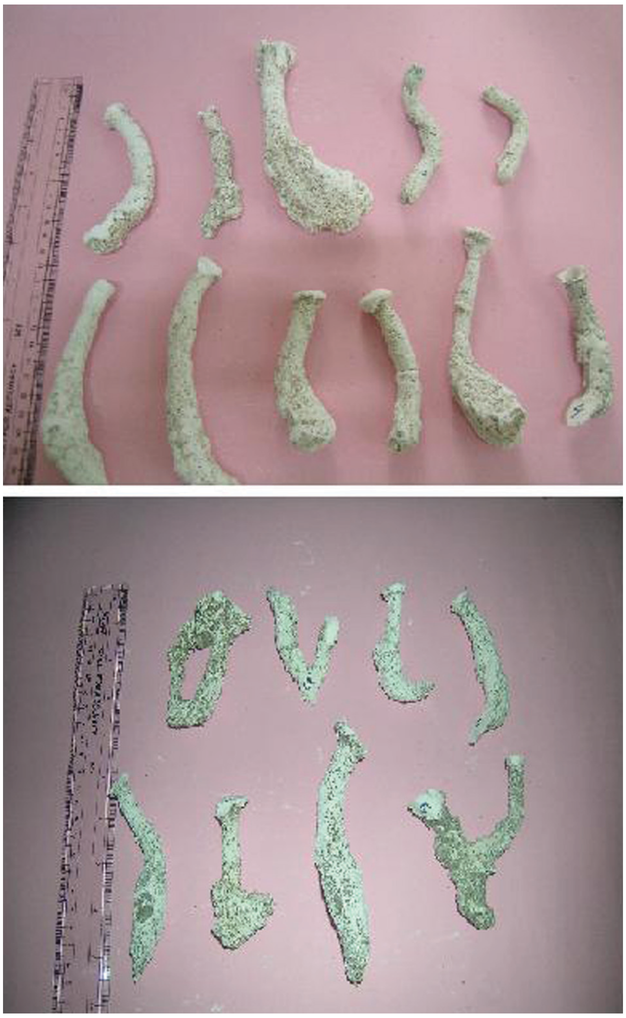

Fig. 5. – The burrow structures of *Uca chlorophthalmus* from Sandspit backwater mangrove area during the study period.

TABLE 3

Result of one way analysis of variance (ANOVA) comparing different burrow morphological characters of three species *U. annulipes*, *U. chlorophthalmus* and *U. sindensis*. (DF is degree of freedom, F is the F-statistics, and P is the probability level).

Variable	df1, df2	F	P	Significance	Tuckey's test
Total Number of burrows in m^2	2, 17	24.71	0.004	*	*U. ch.< U. an.< U. si.*
Total Burrow Length (TBL) in mm	2, 147	22.19	0	*	*U. si. < U. ch.≈U. an.*
Total Burrow Depth (TBD) in mm	2, 147	8.19	0.001	*	*U. si. < U. ch.≈U. an.*
Burrow Diameter (BD) in mm	2, 147	20.58	0	*	*U. si. < U. ch.≈ U. an.*
Burrow Volume (BV) in cm^{-3}	2, 147	24.84	0	*	*U. si. <U. ch. < U. an.*

DISCUSSION

Relationship between density of crabs and crab burrows

It is notoriously difficult to estimate the densities of fiddler crabs in relation to burrows. Burrow densities are related to surface activities, which are related to biotic functions such as feeding, availability of food, reproductive activities, agonistic behaviour, predation and recruitment. They are also related to abiotic features such as substratum preference, harsh conditions (rise and fall in temperature), tidal periodicity etc., and can result in spatial and temporal variability and over-estimates of crab densities (SKOV & HARTNOLL, 2001). The use of burrow densities as surrogate to crab densities has been established in the literature (ASPEY, 1978; MACINTOSH, 1984; GENONI, 1991; MOUTON & FELDER, 1995; DRAY & PAULA, 1998, NOBBS & MCGUINNESS, 1999). In the present study we observed higher densities of burrows than crabs in all three investigated species. We found a significant difference in burrow-opening density between the three species of *Uca* with the highest density in *U. chlorophthalmus* correlated with the lowest amount of organic matter. GENONI (1991) tested the effect of food availability through experimental studies, and found that fiddler crabs dig more burrows despite the presence of pre-existing unoccupied burrows. As fiddler crabs mostly feed around their burrow in a circular path on open mudflats (SAHER & QURESHI, in press), it is likely that additional burrows may increase feeding opportunities during periods of limited food availability and during the limited duration of low tide.

Burrows also serve other purposes such as providing escape routes from predators or fulfilling reproductive needs (WARREN, 1990; CHRISTY et al., 2001, 2002; SHIH et al., 2005). Crabs construct and maintain burrows that also provide refuge from both terrestrial predators during low tide and exposed periods when it is necessary to make a hasty retreat when pursued or threatened, and from aquatic predators when flooded (MONTAGUE, 1980; MORRISEY et al., 1999). In *U. chlorophthalmus*, which had burrows with more than one opening, the density of burrow openings did not give an accurate estimate of the burrows present under the ground. It is likely that burrow-opening counts are not an accurate indicator of burrows and crab abundance. In the present study *U. chlorophthalmus* crabs dug more burrows and burrow branches of lesser depth, probably to more quickly bring nutrient and rich organic sediments to the surface, as more organic matter is present in the sediments near the surface due to the fibrous mangrove root network. The multiple entrances may allow for easy escape from predators and also provide better nutrient exchange between water and the burrow environment during high tide, and better trapping of oxygen from air during the low tide period (MORISSEY et al., 1999).

Relationship between carapace length of crabs and burrow diameter

Larger-sized crabs had greater burrow diameter, larger burrow volume, and bigger chamber diameter than small- and medium-sized crabs. LIM (2006) compared sympatric populations of *U. annulipes* and *U. vocans* and found that burrow architecture was similar except for wider burrow diameters of *U. vocans* and related this to significantly large carapace length to carapace width ratios of *U. vocans*. She suggested that the difference in shape of the crab carapace required wider burrow diameter in *U. vocans* to enable the crab to move comfortably into the burrow.

Architecture of crabs burrows

The results of our one-way ANOVA showed significant differences in all burrow cast morphological characters between the three species *U. annulipes, U. chlorophthalmus* and *U. sindensis*. The morphology of burrows is mostly species-specific (GRIFFIS & SUCHANEK, 1991; WOLFRATH, 1992). However, given the wide variety of physical and chemical differences between different sediment types and vegetation, burrowing species might modify burrow architecture to adjust to a specific set of environmental parameters (GRIFFIS & CHAVEZ, 1988).

Literature on many *Uca* species is available; the general shape of the burrows has been described as either L or J-shaped (KATZ, 1980: *U. pugnax*; GENONI, 1991: *U. rapax*; MONTAGUE, 1980: *U. pugilator*) or even U-shaped (MONTAGUE, 1980: *U. pugnax*). MONTAGUE (1980) studied burrow morphology and observed that generally all *Uca* burrows were nearly vertical and straight, mostly unbranched with an enlargement at the terminal end. The morphology of the burrows of the three species of *Uca* examined in the present study showed considerable variation in shape, size, depth and complexity between species and ranged from single entrance shafts with no branches to interconnected shafts with multiple entrances.

Comparison of the size characteristics of burrow casts showed that the mean TBL and TBD were smallest for *U. annulipes,* and largest for *U. sindensis*. The corresponding burrow diameters were smallest for *U. chlorophthalmus* and largest for *U. sindensis*. LIM & DIONG (2003) found large-sized crabs made burrows with large diameters, volumes and chamber diameters: Crabs thus resided in spacious burrows, and significantly deeper burrows were found at high shore level than at mid and low shore regions. Deeper burrows might also be a way of maintaining lower burrow temperatures in areas that are exposed to sunlight for greater periods of time (POWERS & COLE, 1976; WOLFRATH, 1992; LIM & DIONG, 2003). We found the deepest burrows for *U. sindensis*, where the burrow area is covered during high spring tides and consists of open mudflats devoid of any vegetation, whereas the burrows of *U. annulipes* were found at shallow and intermediate depths and are regularly flooded by daily tides. This pattern found in the present study is consistent with that found for other crabs with deeper burrows in drier sediments (TAKEDA & KURIHARA, 1987; WOLFRATH, 1992; LIM & DIONG, 2003). THURMAN, (1984) showed that burrows of *U. subcylindrica* increase in depth with increasing distance from low water mark in Laguna Salado, Mexico, while WOLFRATH (1992) reported that burrows of *U. tangeri* were deeper at high tide levels of salt marsh than at lower levels near the water front. Burrows do not necessarily contain standing water but are usually only damp at low tides, and fiddler crabs have been observed to return to them every 10 to 30 minutes during feeding to renew the respiratory water lost both through evapo-transpiration and feeding activities (POWER, 1975; MONTAGUE, 1980; SAHER & QURESHI, in press).

LIM & DIONG (2003) further hypothesized that deeper burrows in the high intertidal areas might help fiddler crabs to maintain lower burrow temperature during ebb tides. They also observed that burrows in anoxic sediments had significantly shorter depths, which would help to improve aeration. Thus, a combination of temperature and moisture levels in the substratum could influence the burrow depth architecture for *Uca* species, playing an important ecological role in the life history of these species.

The surrounding vegetation and general sediment characteristics were found to be important factors influencing the burrow morphology of these species. Previous studies on ocypodid crabs found that crabs preferentially dug burrows near hard structures, such as plants and experimental enclosures, because these structures provided the burrows with some structural support (BERTNESS & MILLER, 1984; LIM & ROSIAH, 2007). The presence of vegetation has also been found to alter the stability of sediments (BERTNESS & MILLER, 1984). In the present study, the burrows of *U. annulipes* were distributed among pneumatophores and had thicker root matter in the burrow soil. Despite a comparative lack of vegetation, the burrows of *U. sindensis* were more winding and burrows of *U. chlorophthalmus* were wider than those of *U. annulipes*, which mostly consisted of straight shafts. In addition, many crabs can vary their burrowing behavior in response to the characteristics of the sediment (GENONI, 1991; EWA-OBOHO, 1993; KLASSEN & ENS, 1993). The sediments at sites of *U. annulipes* were coarser than at sites where we found *U. chlorophthalmus* and *U. sindensis*, and coarser sediments might have restricted deeper burrowing to some extent in *U. annulipes* as burrowing in coarser sediments is energetically more costly (GROW, 1982). The comparative lack of vegetation and fine sediments enabled *U. sindensis* to construct wide and deep burrows, winding below the surface to increase the space available inside the burrow within a limited depth (Fig. 4). The larger burrow volume and increased surface area would allow for a larger volume of air to aerate the water that collects in the burrow when submerged during high tide (LIM & DIONG, 2003). Finer sediments might provide a more stable substrate for larger, more complex burrows owing to their more cohesive nature (TAKEDA & KURIHARA, 1987; RUDNICK et al., 2005). Therefore, the presence of vegetation and the sediment properties in the present study could account for the differences observed in the patterns of burrow structure between all three species.

CONCLUSIONS

In conclusion, our results show that *Uca* species display significant interspecific variation in their burrow morphology in relation to the biotic and abiotic factors of their biotopes, such as sediment composition, substratum hardness and root-mat density of the surrounding vegetation. The sediment characteristics (percent organics, composition) and vegetation cover influence the morphology of fiddler crab burrows. The various combinations of sediment type and presence of vegetation as well as other environmental variables, such as inundation levels, result in burrows of different structure. More work is required to determine the extent of the impact of these environmental factors on burrow morphology. However, the spatial variation in burrow morphology found in the present study suggests that the varying burrowing activity of the investigated crabs in relation to vegetation and sediment composition is likely to be species specific and this should be further addressed in future studies.

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