

CHARACTERISTICS, DISTRIBUTION PATTERNS, AND IMPLICATIONS FOR ICHNOLOGY OF MODERN BURROWS OF *UCA (LEPTUCA) SPECIOSA*, SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Fiddler crabs (Brachyura: Ocypodidae: *Uca*) are important bioturbators globally in protected tropical and temperate marine intertidal to supratidal, muddy to sandy environments. Their burrow distribution patterns vary with specific substrate. The study area is a saltwort (*Salicornia virginica*) meadow in a high intertidal to supratidal zone bordered by mangroves on the northern end of Pigeon Creek, a slightly hypersaline lagoon on San Salvador Island. Here the mostly carbonate sand substrate is heavily burrowed by *Uca (Leptuca) speciosa* (Ives, 1891). Three micro-habitats were differentiated according to variations in vegetation cover and depth to groundwater, as follows: 1) a meadow wetland, commonly flooded during spring high tides and with dense, luxuriant *S. virginica* and intermediate substrate firmness values, which has the highest density of burrows and the widest range of burrow diameters with mid-range values in burrow depth and length – maintaining the best conditions for fiddler crabs that include individuals of different ages; 2) dryland with slightly more subaerial elevation and sparse vegetation with the highest substrate firmness values and lowest density of burrows, the burrows being deeper, longer, and exhibiting the lowest range of diameters – with less favorable burrowing conditions for only fully mature adults; 3) wetland with sparse vegetation in the high intertidal zone with lowest firmness values, lowest number of burrows, smallest burrow diameters, and shallowest and shortest burrows – favoring colonization mainly by juveniles. If burrows similar to those of this study were preserved as trace fossils, they should be assigned to the ichnospecies *Psilonichnus tubiformis* Fürsich, 1981. When ichnological features such as burrow densities and dimensions, along with sedimentological and stratigraphical data, are taken into account in ways similar to those of this neoichnological study, interpretations of paleoenvironmental conditions and burrowing crab paleopopulation distributions could be significantly improved.

KEY WORDS: Bahamas, burrows, control factors, fiddler crabs, substrate, *Uca (Leptuca) speciosa*

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INTRODUCTION

Fiddler crabs (Brachyura: Ocypodidae: *Uca*) are common intertidal to supratidal burrowers along protected muddy to sandy marine shorelines of tropical to temperate regions around the world (Crane, 1975; Lim, 2006). Most species of fiddler crabs produce and maintain burrows mainly as a refuge from predation and as a buffer from harsh environmental conditions such as excessive wave action, temperature and/or salinity changes, etc., and occasionally for molting, reproduction, or food storage (Kristensen, 2008; Qureshi and Saher, 2012, and references therein). The morphology of fiddler crabs burrows typically is simple; usually consisting of a more or less permanent shaft extending 10 to 40 cm into the substrate, with a J- or L-shaped ending and terminal chamber (Koretsky et al., 2002; Lim, 2006; Kristensen, 2008; de Gibert et al., 2013). However, beyond this general burrow shape, differences in morphology (diameter, volume, total depth, burrow neck height, curved burrow length, among others) both within the burrows of a given species and between species of fiddler crabs have been recognized and correlated with tidal level, temperature, oxygenation, porosity, percent organic matter, vegetation cover,

and structure of the substrate (Lim and Diong, 2003; Lim, 2006; Lim and Rosiah, 2007; Qureshi and Saher, 2012).

As mobile, endobenthic invertebrates, the distribution patterns of *Uca* are clearly affected by the salinity regime of the environment and by substrate characteristics, including sediment grain size and stability (firmness), levels of pore-water oxygenation, concentrations of organic matter, and vegetation cover (Teal, 1958; see review in Warren and Underwood, 1986), as reflected by burrowing activities and burrow features. Fiddler crab burrowing activity results in modification of sediment-substrate properties (chemical, physical, and biological) and of benthic community structure, as demonstrated in earlier background papers (Allen and Curran, 1974; Katz, 1979) and in more recent literature (Re-traubun et al., 1998; Botto and Iribarne, 2000; Gribsholt et al., 2003; MacCraith et al., 2003; Smith et al., 2009; Wang et al., 2010, and references therein). In this sense, fiddler crabs have been considered as ecosystem engineers in mangrove areas, altering the physical state of the habitat and affecting distribution patterns of other species (Reise, 2002; Kristensen, 2008; Bartolini et al., 2011). Different species of fiddlers are adapted to conditions spanning a wide range of

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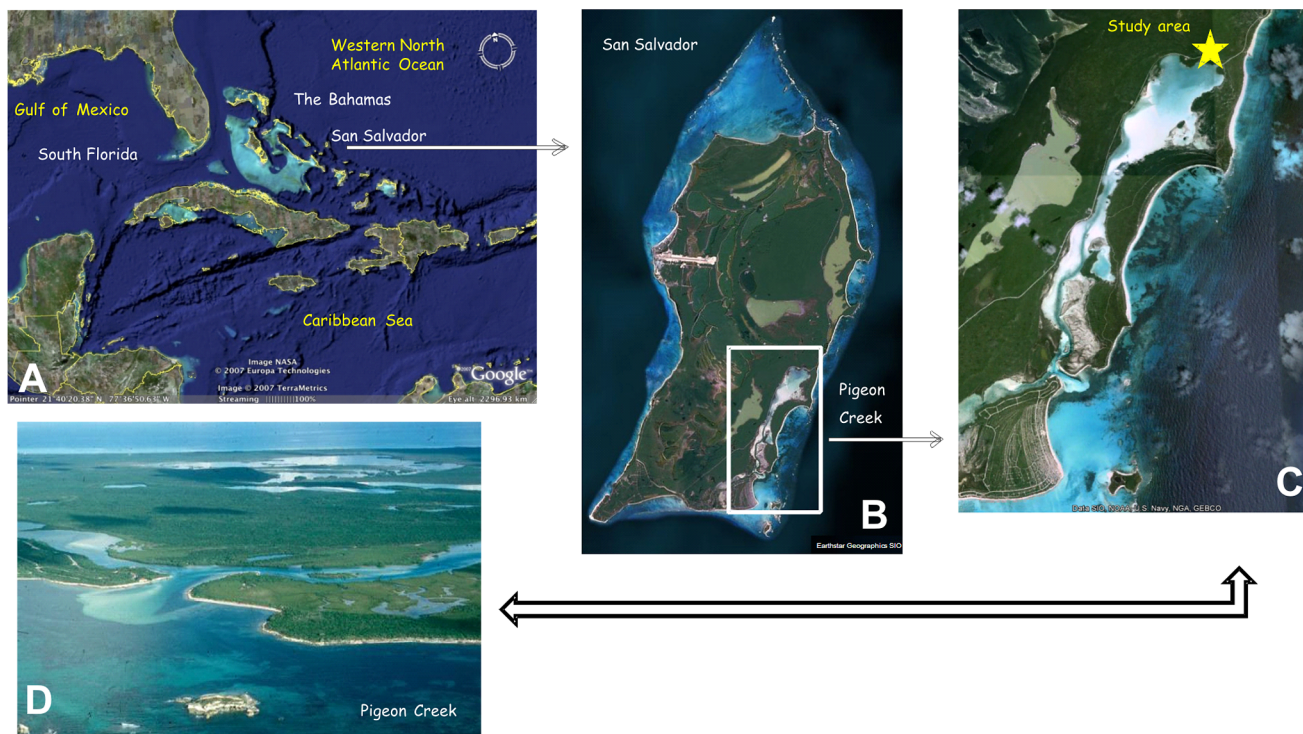


Fig. 1. Location of the study area. A, San Salvador Island in The Bahamas; B, Pigeon Creek on the southeast coast of San Salvador; C, the fiddler crab study area (yellow star); D, oblique aerial view of Pigeon Creek inlet connection to the Atlantic Ocean. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

environmental parameters, such as temperature, salinity, and relative humidity, and depending on the species, can be successful burrowing in clay-rich marsh muds to coarse beach sand (Mouton and Felder, 1995 for a review). However, specific factors, such as food availability or vegetation cover, can have a major influence on burrowing activity and burrow characteristics, including depth of burrowing and formation of branches (Genoni, 1991; Lim and Diong, 2003; Lim, 2006; Lim and Heng, 2007).

Recently, a detailed ichnological study of the burrowing activities of *Uca tangeri* (Eydoux, 1835), the only species of *Uca* that inhabits the coasts of Europe, quantified the influence of some physico-chemical parameters, e.g., sediment texture, grain size, firmness and groundwater level, on the burrowing behavior and burrows of this species (Rodríguez-Tovar et al., in press). This study and the present investigation provide guidance for how an analysis of fossil burrows attributed to fiddler crabs might be used to recognize paleoenvironmental controls in a stratigraphic context.

On a relative basis, fiddler crabs have been extensively studied, with their burrowing behavior now well characterized among the Decapoda, and their burrow features generally well known (see de Gibert et al., 2013, for a recent review). However, conclusive statements about precisely how environmental conditions influence burrow activity are few in number due to the variability of local features, i.e., ocean/atmosphere dynamics, tidal range, topography of the inhabited areas, and heterogeneous substrate characteristics. One approach to solving this problem is to analyze the burrows of a relatively small area that contains closely spaced but different micro-habitats. Our study area on North Pi-

geon Creek, San Salvador Island (Fig. 1A), presents an ideal site to study the burrows and bioturbation effects of a modern sub-tropical to tropical fiddler crab species. Along the supratidal margin of this hypersaline lagoon, inland from the zone of fringing mangroves, the burrowing activity of *Uca (Leptuca) speciosa* (Ives, 1891) is important and complete burrows are numerous. Associated with the effects of tidal range and lateral extension with flood tides, this area is characterized by variation in substrate characteristics and vegetation cover that manifests over short distances. The main goals of our research are to evaluate the influence of these environmental factors on burrow distribution and burrowing activity of the resident population of *U. speciosa*, based on a detailed quantitative analysis of burrow and substrate characteristics in the different, closely spaced micro-habitats of this study area. In addition, this investigation is one of only several previous studies to consider fiddler crab burrows from sandy, all-carbonate sediment settings (Curran and Martin, 2003; Knaust et al., 2012 and references therein). The form and variations in form of the modern burrows of *U. speciosa* are points of emphasis to facilitate comparison with similar burrows preserved in the fossil record.

MATERIALS AND METHODS

Pigeon Creek is a large, shallow, tidally (semi-diurnal) influenced, and slightly hypersaline lagoon on the southeast coast of San Salvador (Fig. 1B-D). The general characteristics of Pigeon Creek and its all-carbonate sediments were described by Mitchell (1987), and the ichnology of the complex decapod burrows that occupy the open intertidal sand flats seaward of mangroves that border the lagoon were studied in detail by Curran and Martin (2003). In a physiologic study of osmoregulation by fiddler crabs, Thurman et al. (2010) recorded the occurrence of four species of *Uca* in the

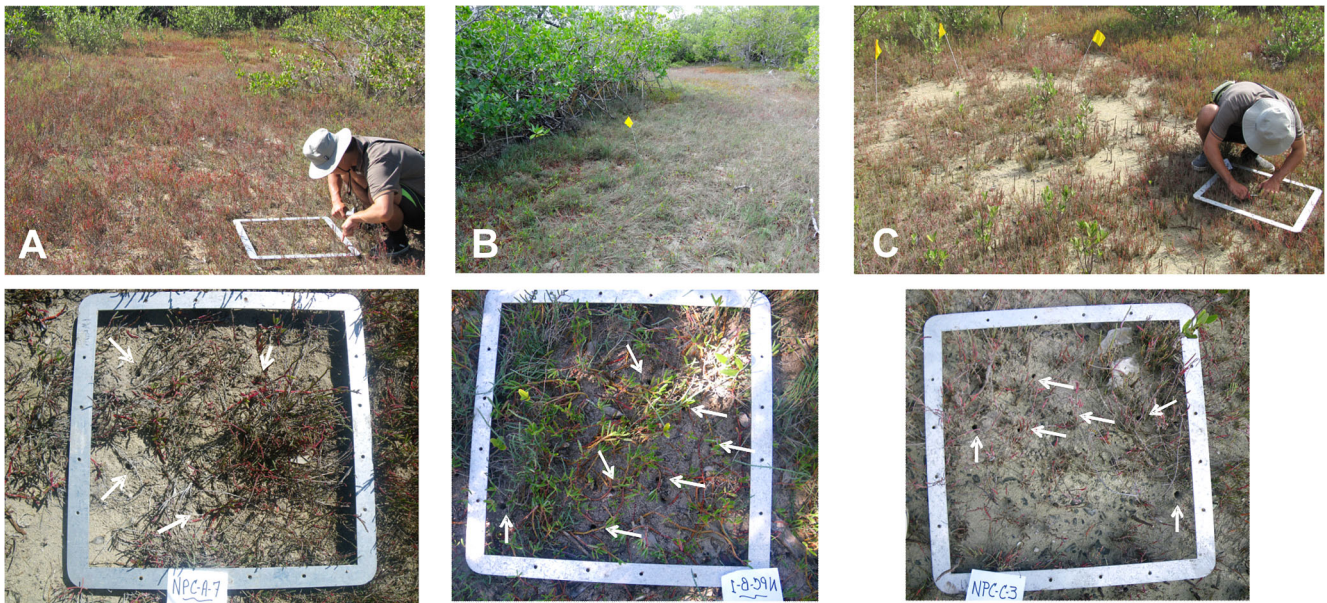


Fig. 2. Views of the study area micro-habitats (general view above and corresponding quadrats below). A, NPC-A, dryland with sparse vegetation (*Salicornia*), subaerial in fair-weather conditions, and characterized by saline groundwater about 30 cm below the surface; B, NPC-B, wetland with a stand of more luxuriant and somewhat denser *Salicornia*, with some regions occasionally subaquatic; C, NPC-C, wetland with sparse vegetation; this area is in the high intertidal zone (part of area ponded with salt water at full high tide), with *Salicornia* merging with black mangrove pneumatophores. Note: Standard quadrant area = 0.25 m²; yellow flags used to mark location of burrows where casting resin was poured; white arrows indicate *Uca speciosa* burrow openings. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

Pigeon Creek area, including *U. speciosa*, the burrower investigated in this study.

Our study area is located at the north end of Pigeon Creek (Fig. 1C), close to the intertidal margin of the lagoon and just off an unimproved land-survey road that connects to the main highway (Queen's Highway) of San Salvador. Here a *Salicornia* meadow (*S. virginica*) wetland area lies in the supratidal zone, bordered by red and black mangroves on the intertidal lagoon side. The selected area exhibits multiple features of interest for the purposes of this research, including: a) occasional influence of the tides onshore, beyond the intertidal margin of the lagoon, b) closely spaced lateral variations in depth to groundwater and vegetation cover, and c) significant bioturbation by the fiddler crab *U. speciosa*. Even though spring tide and storm supratidal influence is present, the distance of separation of several meters of the study area from the active, day-to-day intertidal zone facilitates burrow formation and preservation.

The organic-rich, fine to medium skeletal, peloidal carbonate sand substrate of the *Salicornia* meadow is heavily burrowed by *U. speciosa*. In this area, the three survey sites (micro-habitats) were differentiated according to variations in vegetation cover and depth of groundwater (Fig. 2). These sites lie in close proximity to each other, on the south side of the land-survey road, immediately adjacent to the water's edge of Pigeon

Creek, as follows: a) NPC-A (GPS: 24°00.626'N, 74°27.580'W), dryland with sparse vegetation (*Salicornia*); subaerial in fair-weather conditions and characterized by saline groundwater approx. 30 cm below the surface; b) NPC-B (24°00.637'N, 74°27.583'W), wetland with a stand of more luxuriant and somewhat denser *Salicornia*, locally with surface water; thus some parts of the area are occasionally and locally subaquatic; and c) NPC-C (24°00.621'N, 74°27.584'W), wetland with sparse vegetation, located in the high intertidal zone (part of area ponded with salt water at full high tide), with the *Salicornia* interspersed with black mangrove pneumatophores.

Fieldwork was performed in February 2013 in the three closely spaced micro-habitats (NPC-A to C) within the supratidal margin of Pigeon Creek. Research in our study area on public land was conducted with approval via a Permit to Conduct Scientific Research in The Bahamas issued to the authors on 17 December 2012 by The Bahamas Environment, Science & Technology (BEST) Commission of the Ministry of The Environment and Housing.

Ichnological features including burrow density, diameter of apertures, and counts of the number of burrow chimneys were measured. Burrow density was determined by counting the number of apertures present within 50 × 50 cm quadrat (0.25 m²) sampling areas (Figs. 2 and 3). In all

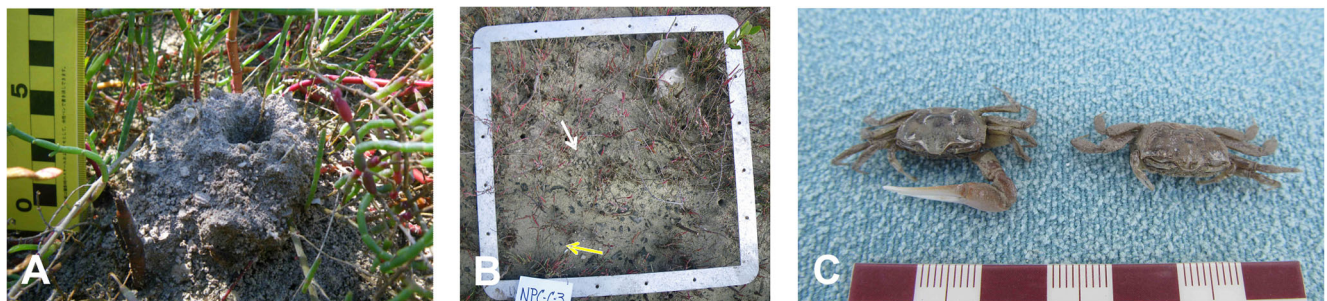


Fig. 3. Burrow features and trace maker. A, close-up view of *Uca speciosa* burrow chimney from micro-habitat NPC-B. Note different components of construction, including shell fragments; B, pellets (white arrow) and scratch marks (yellow arrow) surrounding the entrances of burrows in micro-habitat NPC-C; C, specimens of *U. speciosa* from the study area; crab with large claw is a male, the other female. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

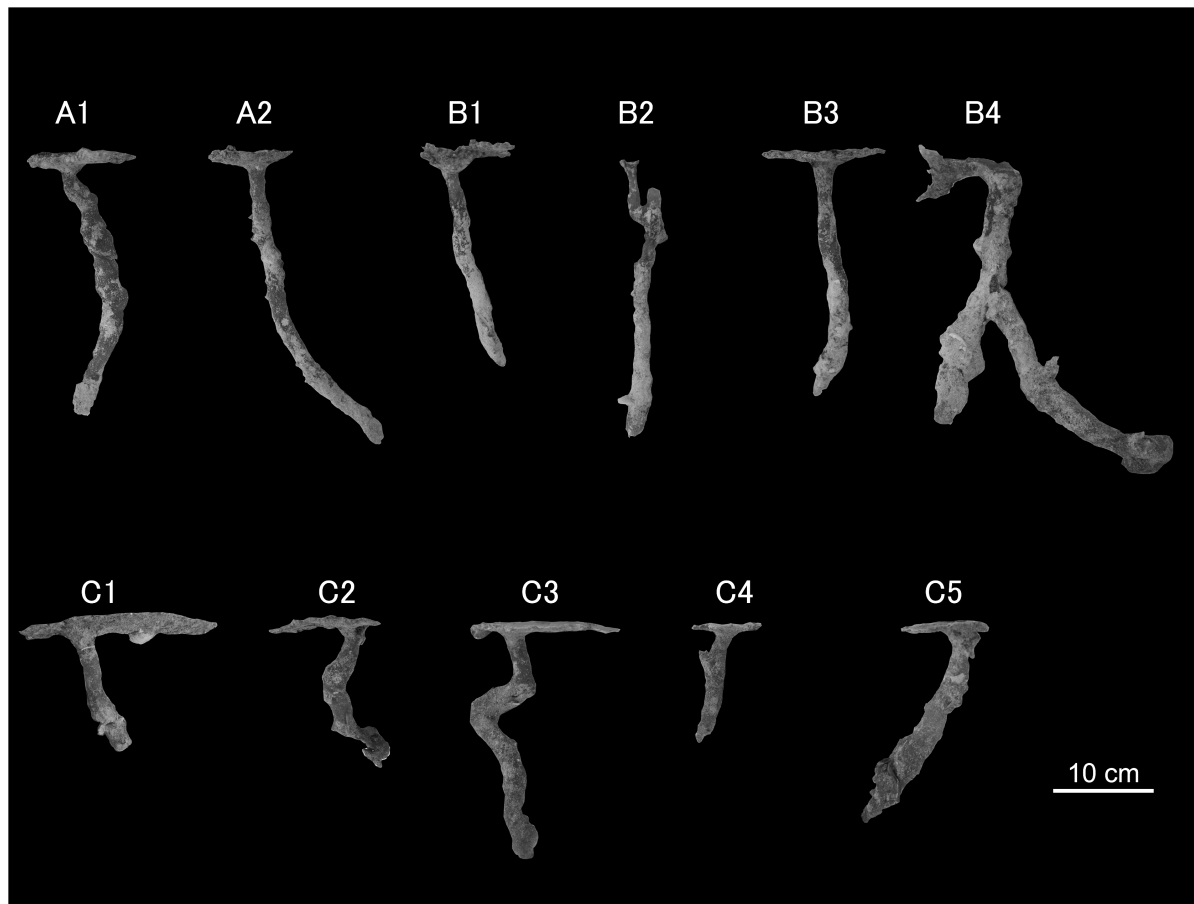


Fig. 4. Burrow casts from the studied micro-habitats. A1-A2 from the dryland (NPC-A); B1-B4 from the wetland with luxuriant vegetation (NPC-B); and C1-C5 from the wetland with sparse vegetation (NPC-C). Note: burrow cast B4 is not included in Table 2 because this burrow was made by a crab other than *Uca speciosa*.

three micro-habitats, and to be as objective as possible, 10 quadrats were randomly selected for analysis and data recording, except for NPC-C where lateral restrictions permitted data collection for only 5 quadrats. Mean burrow density per quadrat was calculated for each subenvironment. Burrow aperture diameter was measured with a caliper (in cases of slightly elliptical apertures, the maximum diameter was recorded) to the nearest millimeter. Pairwise Wilcoxon Rank Sum Tests were used to assess differences in burrow density and burrow aperture size between subenvironments. Statistical analyses were conducted using the program 'R' (version 3.0.2).

Casts of the burrows of *U. speciosa* were made *in situ* in each of the three micro-habitats, following the standard procedure of mixing polyester resin with hardener in the field and pouring the liquid down each burrow (Shinn, 1968; Seike and Nara, 2008; Seike et al., 2012). The resin was left to harden *in situ* for at least a period of 24 hours. Then each cast was carefully excavated using a spade and hand trowel; the ground was repaired after removal of casts. A total of 11 casts were obtained (Fig. 4); 2 casts in NPC-A, 4 in NPC-B and 5 in NPC-C. Measurements of the casts were made in the laboratory to complete the inventory of burrow morphology characteristics: 1) cast diameter was measured to the nearest millimeter at three points (upper, middle, and lower) along the main shaft using a hand calliper, 2) cast total length was measured to the nearest centimeter using a measuring tape (only one example with branching off the main shaft was cast; B2 in Fig. 4), and 3) depth of each burrow was measured to the nearest centimeter as the vertical, straight-line distance from the ground surface to base of the burrow. Other observations, such as the presence/absence of bioglyphs, also were made. Sediments were collected from each sampling site. In the laboratory, median grain size (d_{50}) and mud content (%) were determined for these samples using conventional sieving methods. Substrate firmness values were calculated by measuring the shear strength of the "soil" surface with a Torvane test instrument (Rodríguez-Tovar and Delgado, 2001, 2006;

Rodríguez-Tovar, 2007). Fiddler crabs were observed to be present around burrows in all three of the micro-habitat sites, and voucher specimens were collected and preserved for later identification.

RESULTS

Density and Diameter of Burrow Apertures

The wetland area NPC-B with its stand of more luxuriant and somewhat denser *Salicornia* exhibited by far the highest burrow density (mean \pm SD of 23 ± 8 /quadrat). This was followed by the wetland with sparse vegetation (NPC-C) with 10.4 ± 1.95 burrows per quadrat. The dryland with sparse vegetation (NPC-A) exhibited the lowest burrow density (7.7 ± 4.5 /quadrat). Burrow density between NPC-A and NPC-B, and NPC-B and NPC-C differs significantly ($p < 0.001$), whereas that between NPC-A and NPC-C showed no significant difference ($p > 0.05$; Fig. 5A).

NPC-B exhibited the widest range of aperture diameters (5-31 mm; Fig. 5B, Table 1) with a mean \pm SD of 13.2 ± 4.5 mm. NPC-C had the lowest burrow aperture diameter mean (11.5 ± 2.5 mm); range (6-16 mm). NPC-A showed a range of burrow aperture diameters of 7-23 mm and a mean of 13.6 ± 3.3 mm. Burrow diameters differed significantly ($p < 0.01$) between NPC-A and NPC-C. There was no significant difference in burrow diameter between NPC-A and NPC-B, and NPC-B and NPC-C ($p > 0.05$).

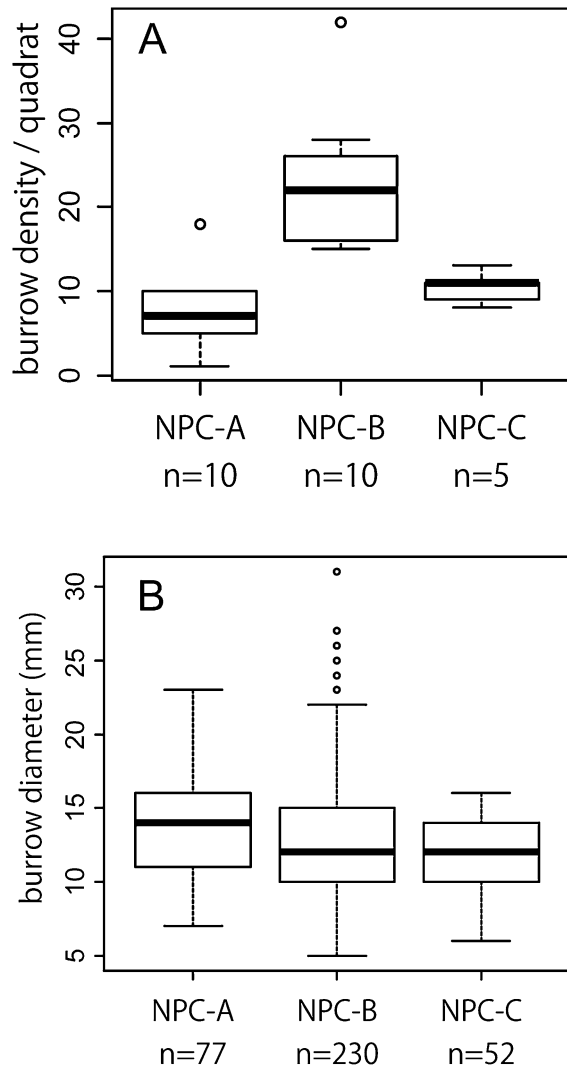


Fig. 5. Box plots in the studied micro-habitats using standard 50 × 50 cm quadrat (0.25 m²). A, burrow density; B, burrow diameter. Pairwise Wilcoxon Rank Sum tests were used to construct these plots. Note: the box plots show median values (line), 25 and 75% quantiles (box), 5 and 95% quantiles (whiskers), and outliers (dots).

Area NPC-B was characterized by the highest number of chimneys (10, one being 7 cm in height) and the greatest abundance of excavation and feeding pellets surrounding the burrow entrances, indicating a high level of daily activity in this area as compared to areas NPC-A and NPC-C with

3 and 1 chimneys, respectively, and relatively few pellets (Fig. 3A, B).

Burrow Cast Measurements

Important differences also were recognized when comparing the *Uca speciosa* burrow cast measurements from the three micro-habitats (Fig. 4; Table 2). Overall, the dryland with sparse vegetation (NPC-A) exhibited deeper and longer burrows (25 and 26 cm deep, and 23 and 30 cm long). Burrows here also had a noticeable increase in diameter in their middle and lower parts with respect to the upper part.

Area NPC-B with high vegetation cover had middle values in burrow depth (20-23 cm) and length (20-29 cm) and intermediate mean burrow diameter. As previously, some increase in burrow diameter in middle and lower parts of the burrows as compared to the upper parts was observed. Cast B2 is the only one with a branch, which was 2 cm in length.

With its sparse vegetation, area NPC-C was characterized by a reduction in burrow depth (12-17 cm) and length (13-29 cm) when compared to those of the other two micro-habitats. In contrast, burrows here had the highest mean diameter (16.5-23.3 cm), mainly due to an increase in diameter found in the lower parts of the burrows of this area.

Sediment Grain Size

The all-carbonate sediment of the study area consists primarily of fine to medium skeletal-peloidal sand with intercalated organic material. The median grain size (d_{50}) of NPC-A, NPC-B and NPC-C deposits was 0.29, 0.31 and 0.26 mm, respectively. Mud content for each site was 0.69% (NPC-A), 2.00% (NPC-B) and 2.29% (NPC-C).

Substrate Firmness

The firmness data (Table 3) showed clear variation between micro-habitats. NPC-A had the highest mean value of 604 Pa (range 390-784 Pa). NPC-B was intermediate at 245 Pa (range 196-314 Pa), and the surface of NPC-C was least firm, with a mean of 176 Pa (118-274 Pa).

DISCUSSION

Our results reveal differences between the three closely spaced micro-habitats of the study area with respect to both the ichnological features of the *U. speciosa* burrows and the physical characteristics of the area. Accurate recognition of such differences as they relate to populations of similar fossil burrows could aid significantly to achieving better interpretation of paleoenvironments. Vegetation cover, depth

Table 1. Basic statistics for burrow aperture diameters of *Uca speciosa* using a standard 50 × 50 cm quadrat (0.25 m²). NPC-A, dryland with sparse vegetation (*Salicornia*); NPC-B, wetland with a stand of more luxuriant and somewhat denser *Salicornia*; NPC-C, wetland with sparse vegetation.

| | NPC-A | NPC-B | NPC-C |
|------------------------|------------------|-------------------|-----------------|
| Number of observations | 77 (10 quadrats) | 230 (10 quadrats) | 52 (5 quadrats) |
| Mean ± SD | 13.6 ± 3.3 | 13.2 ± 4.5 | 11.5 ± 2.5 |
| Median | 14 | 12 | 12 |
| Mode | 15 | 10 | 14 |
| Minimum | 7 | 5 | 6 |
| Maximum | 23 | 31 | 16 |

Table 2. Basic statistics for burrow cast features of *Uca speciosa*.

| Site | Burrow cast | Burrow depth (cm) | Burrow length (cm) | Mean diameter (mm) | Burrow diameter (mm) | | |
|-------|-------------|-------------------|--------------------|--------------------|----------------------|-------------|------------|
| | | | | | Upper part | Middle part | Lower part |
| NPC-A | A1 | 23 | 25 | 17.6 | 14.9 | 21.2 | 16.8 |
| | A2 | 26 | 30 | 14.9 | 13.0 | 15.1 | 16.7 |
| NPC-B | B1 | 20 | 20 | 14.9 | 13.4 | 14.9 | 16.3 |
| | B2 | 23 | 29 | 11.4 | 6.8 | 15.6 | 11.9 |
| | B3 | 23 | 23 | 16.9 | 14.0 | 14.9 | 21.7 |
| NPC-C | C1 | 12 | 13 | 17.2 | 13.4 | 19.0 | 19.1 |
| | C2 | 13 | 15 | 16.5 | 15.4 | 15.8 | 18.4 |
| | C3 | 17 | 29 | 17.2 | 15.8 | 19.4 | 16.5 |
| | C4 | 16 | 22 | 23.3 | 17.0 | 21.4 | 31.5 |

to groundwater, and substrate firmness all act as controls on burrow density, diameters of burrow apertures, and other burrow features. Intra- and interspecific variations in burrow morphology of fiddler crabs have been related to biotic and abiotic environmental factors, such as oxygenation, temperature, sediment composition, substratum firmness, percent organics, and vegetation cover (Lim and Diong, 2003; Lim, 2006; Lim and Rosiah, 2007; Qureshi and Saher, 2012). In the North Pigeon Creek setting, sediment grain size (dominantly very fine to medium sand) did not show any important variation between micro-habitats of the study site, so this parameter does not have any real influence on burrow characteristics and distribution patterns for *U. speciosa*.

The wetland micro-habitat area NPC-B has a stand of more luxuriant and somewhat denser *Salicornia*, locally with less saline water over the saline groundwater table during high tides, and with intermediate firmness values. This micro-habitat is characterized by the greatest density of burrows, widest range of diameters, middle values in burrow depth and length, and clear increase in burrow diameter in the middle and lower parts of the burrows with respect to the upper parts. This area also includes burrows with the highest number of chimneys, and occasionally non-*Uca* crabs were observed (evidenced by burrow cast B4 in Fig. 4). In sum, this area presents the best conditions for endobenthic colonization and population development, including individuals of different sizes/ages.

Less favorable conditions for burrowing for *Uca* were manifested in the dryland (NPC-A), with its subaerial location under fair-weather conditions, sparse vegetation, and highest firmness values. The lowest number of burrows occurred here, but these burrows are deeper and longer and have the lowest range of diameters. These characteristics

indicate limitations on colonization, affecting mainly the smaller juvenile members of the population; only adult crabs can colonize this area, where they form deep and large burrows. The NPC-C wetland area, with sparse vegetation in the high intertidal zone and ponded with salt water at full high tide, exhibited the lowest substrate firmness values. Here also ontogenetic restriction in the population can be interpreted. The substrate characteristics appear to favor colonization mainly by juveniles, as revealed by the low numbers of burrows, smallest burrows diameters, and shallowest and shortest burrow depths and lengths. The soft substrate here undoubtedly impedes construction of large and deep burrows by adult fiddlers.

Our results confirm the importance of substrate features, including firmness, depth of groundwater, and vegetation density, in controlling the construction and characteristics of the burrows of *U. speciosa*. These environmental parameters also exert an important influence on population structure within broader areas occupied by the population.

Paleontological Perspective

The research presented here, together with previous studies on modern fiddler crab bioturbation (Korestky et al., 2002; Skov et al., 2002; Lim and Diong, 2003; Lim, 2006; Lim and Rosiah, 2007; Kristensen, 2008; Milner et al., 2010; Bartolini et al., 2011; Qureshi and Saher, 2012), opens new ways to apply neoichnological data to paleoichnological research, in this case with data on substrate features as they relate to fiddler crab population dynamics. One difficulty for this application could be the ability to achieve definitive recognition of fossil fiddler crab burrows. The oldest record of *Uca* is from the Lower Miocene (Brito, 1972; de Gibert et al., 2013). However, matching comparisons between modern burrows of *Uca* and their fossil counterparts are few, in part due to the difficulty of conclusive fossil burrow assignment as produced by *Uca*, especially when crab body fossils are not found in association with the burrows in question. De Gibert et al. (2013) presented a detailed comparison between modern burrows of *U. tangeri* in Spain and Upper Pliocene fossil counterparts from nearby outcrop areas. The fossil burrows were assigned to the ichnospecies *Psilonichnus tubiformis* Fürsich, 1981 (cf., Muniz et al., 2010), based on similar burrow morphologies.

A worldwide comparison of burrow morphologies for extant *Uca* confirmed the predominance of simple, mostly un-

Table 3. Basic statistics for substrate shear strength (Pa).

| | NPC-A | NPC-B | NPC-C |
|------------------------|-------|-------|-------|
| Number of observations | 25 | 25 | 25 |
| Mean | 604 | 245 | 176 |
| Median | 580 | 255 | 176 |
| Mode | 580 | 255 | 196 |
| Minimum | 390 | 196 | 118 |
| Maximum | 784 | 314 | 274 |

branched and unlined, J-shaped morphologies, along with recognition of the difficulty for definitive tracemaker identification of fossil burrows in the absence of associated body fossils (de Gibert et al., 2013). However, when burrow architectures are similar, our research indicates that integration of other ichnological features, such as density of traces, burrow dimensions (diameter of apertures, length, and depth), together with sedimentological and stratigraphical data, can be used to enhance interpretation of paleoenvironmental conditions and fossil fiddler crab population dynamics, including assessment of variable ontogenetic responses to substrate controls.

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