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SEDIMENT BIOTURBATION POTENTIAL OF *UCA RAPAX* AND *UCA URUGUAYENSIS* AS A RESULT OF THEIR FEEDING ACTIVITY

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ABSTRACT

Bioturbation of mangrove sediments by *Uca uruguayensis* (Nobili, 1901) and *U. rapax* (Smith, 1870) was compared based on the grain-size composition and organic content in surface sediment around the burrow and feeding pellets in two mangrove zones of the São Vicente Estuary, state of São Paulo, Brazil. For each species, 25 burrows with active crabs were selected. All pellets within a 15-cm radius of each burrow were carefully collected; samples of substrate were taken; and the crab occupant was excavated, sexed, and measured for carapace width (CW). The number of spoon-tipped setae on the second maxilliped of each species was estimated; *U. uruguayensis* showed more of these setae than *U. rapax*. For both species, the sediment post-processed by feeding activity (feeding pellets) showed a similar increase of coarser fractions and a smaller organic content. However, *U. uruguayensis* was more efficient in removing organic matter (88.1%) from the sediment than *U. rapax* (37.5%). These results suggest that different numbers of spoon-tipped setae on the second maxillipeds of the fiddler crabs do not affect the potential for grain-size selection, but result in differing abilities to remove organic matter from the sediment.

KEY WORDS: feeding pellets, mangrove, sediment particle size, spoon-tipped setae, *Uca*

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INTRODUCTION

Mangrove ecosystems in tropical and subtropical estuaries are characterized by rapid organic decomposition and nutrient recycling (Twilley et al., 1986, 1997; Alongi, 1997; Sherman et al., 2003). Dissolved and particulate organic matter can be either retained or exported to adjacent environments (Lee, 1995; Jennerjahn and Ittekkot, 2002; Schwamborn et al., 2002; Kathiresan and Qasim, 2005). In these coastal systems, decapod crustaceans constitute an important part of the macrofauna (Macintosh, 1988), where fiddler crabs (*Uca* spp.) are common inhabitants and important sediment bioturbators (Kristensen, 2008). Their burrowing and feeding activities increase drainage, facilitate transport of organic nutrients, affect the redox potential, and alter erosion processes (Penha-Lopes, 2009).

Fiddler crabs feed avidly on the sediment, using their smaller claws (Christy, 1978; Caravello and Cameron, 1987). After it is brought to the mouth by the claw, the sediment is processed by the buccal appendages (Miller, 1961; Colpo and Negreiros-Fransozo, 2011) to remove organic matter, algae, small organisms, and bacteria, which are ingested as food, together with small inorganic particles (Miller, 1961; Maitland, 1990; Silva et al., 1994; Takeda and Murai, 2003). During the mouthparts sorting, the larger sediment particles are discarded around the entrance of the burrow as small pellets (Miller, 1961; Crane, 1975). In general, *Uca* live in dense populations and forage intensely in the immediate vicinity of the burrow (10-15 cm). At the end of a low-tide period, large numbers of feeding pellets can be found on the estuary bottom. Therefore, this fiddler crab activity can change the organic content and the granulometric features of the upper layer of sediment (Kristensen, 2008).

Species of *Uca* show differences in the mouthparts, especially in the numbers of spoon-tipped setae on the second maxilliped (Crane, 1975; Icely and Jones, 1978; Robertson and Newell, 1982b; Thurman, 1987; Costa and Negreiros-Fransozo, 2001; Lim, 2004; Colpo, 2005; Bezerra et al., 2006). Miller (1961) suggested that the spoon-tipped setae function to prevent the ingestion of coarser inorganic particles and to scrape the sediment grains, releasing the organic matter adhered on them. Therefore, fiddler crabs that have more spoon-tipped setae would be more able to manipulate larger-grained sediments than other species that have fewer of these specialized setae or lack them entirely; such species generally would be restricted to muddy sediments. Therefore, the number of spoon-tipped setae on the second maxilliped can affect the sediment grain-size sorting and the organic-matter extraction, resulting in different bioturbation potentials among fiddler-crab species.

Uca uruguayensis (Nobili, 1901) and *Uca rapax* (Smith, 1870), which have different numbers of spoon-tipped setae on their second maxillipeds (Colpo, 2005), were chosen to evaluate variations in the bioturbation potential during their feeding activity. We evaluated the mangrove substrate bioturbation by comparing the grain-size spectrum and the organic content, between the sediment around the burrow and the feeding pellets.

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MATERIALS AND METHODS

The study was carried out in the mangroves of Saponim Island (23°59′01″S, 46°24′15″W), near the Mar Pequeno Bridge, São Vicente, São Paulo State, Brazil (Fig. 1A). The predominant tree on the island is *Avicennia schaueriana*. Two sampling zones were established, one with a predominance of *U. uruguayensis* (Zone 1) and the other with *U. rapax* (Zone 2) (see Fig. 1B). In Zone 1, the sediment was sandy, with a strong tidal influence and sparsely covered by *Spartina alterniflora*, *Hibiscus tiliaceus*, and seedlings of *Laguncularia racemosa*. In Zone 2, the sediment was also sandy but with less tidal influence. The site was covered by medium-sized (<10 m in height) *A. schaueriana*, a few young *L. racemosa*, and *H. tiliaceus.*

To estimate the median number of spoon-tipped setae on the second maxilliped of these crabs, 78 individuals of *U. rapax* and 89 of *U. uruguayensis* were sampled. The right second maxilliped was removed and the number of spoon-tipped setae was counted under an optical microscope. The median numbers of these setae were compared between species by the Mann-Whitney test (Zar, 1999). The right second maxilliped of about four individuals of each species was removed under a stereomicroscope, cleaned by ultrasound, and fixed in 2.5% glutaraldehyde. Then, the maxillipeds were prepared for scanning electron microscopy (SEM) according to Felgenhauer (1987), to check the number of setae.

To estimate the bioturbation potential of *U. uruguayensis* and *U. rapax*, feeding pellets and sediment around the burrow were sampled during the first daytime low spring tide in July 2006. For each species, 25 burrows with actively foraging crabs, i.e., with feeding and burrowing pellets near the opening, were selected and the diameter of each entrance was measured. All feeding pellets within a 15-cm radius around the burrow were collected (Hemmi and Zeil, 2003). Only feeding pellets were carefully removed with tweezers and a small scoop. The samples of feeding pellets were placed in labeled plastic bags for analysis in the laboratory. Also within the 15-cm radius, sediment samples were collected with steel corers (5 cm in diameter and 2 cm in height), and placed in individual labeled plastic bags. The occupant fiddler crab was excavated, sexed and measured with a caliper (CW, carapace width).

Samples of sediment and feeding pellets from each burrow were placed in resistant containers and dehydrated in an oven (60°C for 72 h). Samples of substrate (10 g) and feeding pellets (5 g) were set aside for analysis of organic content by ash-free dry weight in a muffle furnace (500°C for 3 h), according to Pinheiro et al. (1996). The efficiency of each species in removing organic matter during the feeding process was assessed by differences in organic content (%) between the feeding pellets and the substrate around the burrow (Mann-Whitney test).

Other samples of substrate (30 g) and feeding pellets (5 g) were sorted for granulometric analysis, using differential sieving (Wentworth, 1922). For each species, the percentage of each granulometric fraction was compared by Mann-Whitney test, when the data did not show normal distribution (Shapiro-Wilk test) and equal variance (Levene test); or by Student's *t* test when the data were normal and homogeneous. These analyses allowed us to assess which grain-size classes were discarded or ingested by each species.

To assess possible changes in the substrate (sediment around the burrows) after processing by each crab species (pellets), a particle-size analysis was performed with pre- and post-processing substrate data, using the method of moments (McCammon, 1962). Calculations of mean grain size (ϕ), sorting, skewness and kurtosis were carried out in each case with the software SYSGRAN (Camargo, 2006), with the establishment of their classification. The sediment in each zone studied was also typified according to the

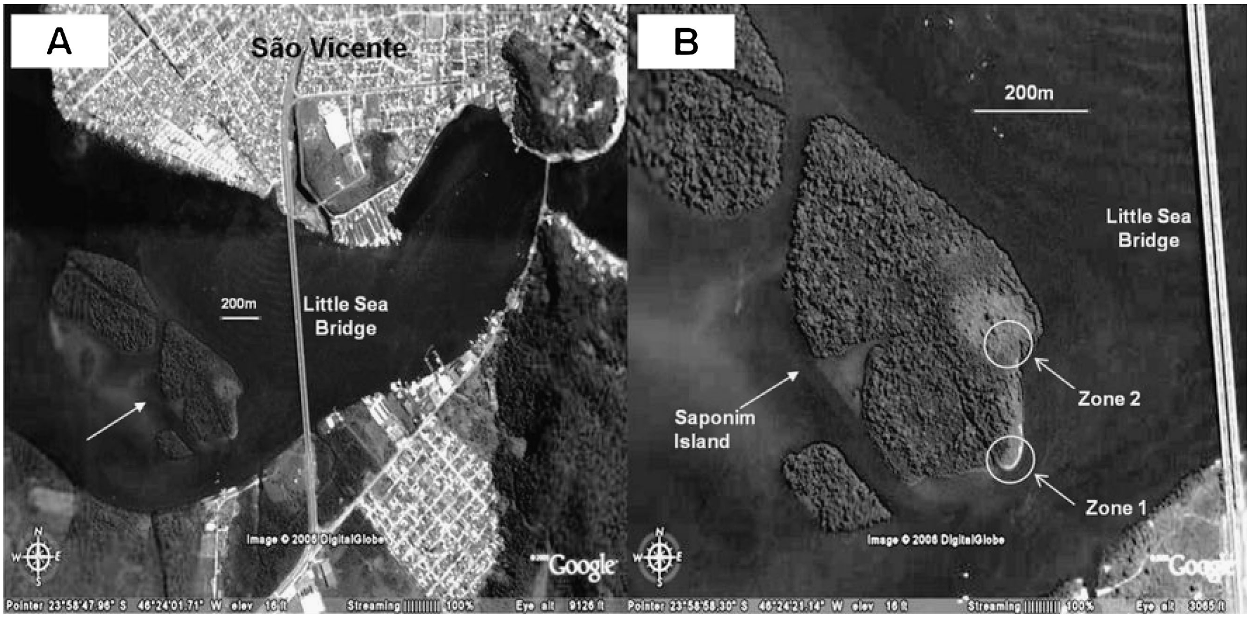

Fig. 1. General view of the São Vicente Estuary, São Vicente, São Paulo State, Brazil. A, With detail of Saponim Island; B, Showing the two sampling zones for *Uca uruguayensis* (Zone 1) and *Uca rapax* (Zone 2). (Modified from www.google.com.br.)

classifications of Shepard (1954) and Pejrup (1988), to estimate the texture and energy level, respectively, leading to the sediment deposition.

RESULTS

For *U. uruguayensis* (Zone 1), the diameter of the burrow openings ranged from 6.7 to 13.8 mm (10.7 ± 2.0 mm). For this species, 10 males and 15 females without eggs were collected, with sizes (CW) between 8.1 and 14.9 mm (11.4 ± 1.7 mm). The diameter of the burrow openings for *U. rapax* (Zone 2) ranged from 5.0 to 23.1 mm (11.0 ± 4.8 mm). We found 11 males and 16 females without eggs, totaling 27 crabs in 25 burrows of *U. rapax.*

Uca uruguayensis showed more spoon-tipped setae on the second maxilliped (156 ± 34.0) than *U. rapax* (87 ± 15.9) (Mann-Whitney test: $U = 3215.0$; $p < 0.0001$) (Fig. 2). Figure 3 shows a general view of the second maxilliped and the proportion of spoon-tipped setae on this appendage in each species.

The organic content of the sediment was similar between the zones (Student's t test: $t = 0.971$; $p = 0.336$). After the feeding process of both species, the organic-matter content decreased in the pellets. However, in Zone 1 (*U. uruguayensis*), the difference between the sediment and the pellets was greater (88.1%) (Mann-Whitney test: $U = 327.0$; $p < 0.0001$) than in Zone 2, where *U. rapax* extracted about 37.5% of the organic matter (Mann-Whitney test: $U = 535.5$; $p = 0.0489$). These results indicate a more efficient extraction of organic matter by *U. uruguayensis* than *U. rapax* (Fig. 4).

In Zone 1, for *U. uruguayensis*, the sediment contained mostly fine and very fine sand, whereas in the feeding pellets there was a significant reduction of the fine sand (Student's t test: $t = 3.06$; $p < 0.004$) and silt-clay fractions (Mann-Whitney test: $U = 813.0$; $p < 0.0001$). There was a significant increase in the very coarse, coarse, and medium sand fractions ($U = 363.5$, 339.0 and 389.0, respectively; $p < 0.0001$ for all) in the pellets. There was no significant difference between the amounts of the very fine sand fraction in the sediment and the feeding pellets ($U = 694.0$; $p = 0.277$) (Table 1 and Fig. 5). The sediment of Zone 1 showed a mean particle size (ϕ) of 3.098, ranking it as very fine sand, with a slight reduction of this value for the pellets (2.967), which changed its classification to fine sand. The sediment was moderately sorted, both before processing by the crabs (0.718) and after it (0.904); changing from approximately symmetrical (0.045) to a negative asymmetry after processing (−0.123); and with respect to kurtosis, increasing from platicurtic (0.744) to mesocurtic (0.967). According to Shepard's classification, the sediment of this estuarine zone was sandy-silt; while Pejrup's classification indicated a very highly hydrodynamic area (classification B-IV).

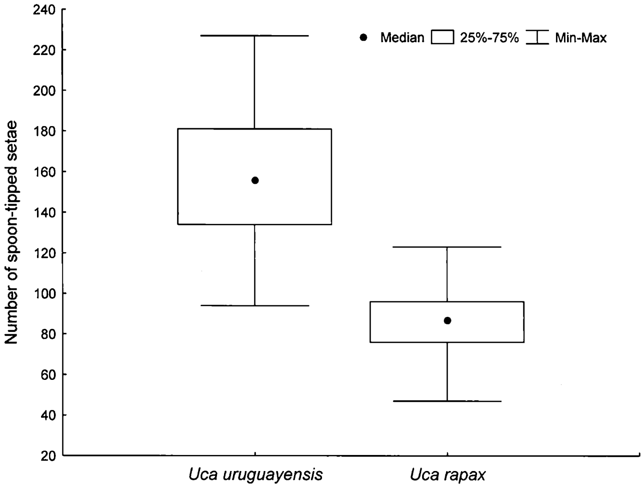

Fig. 2. Number of spoon-tipped setae on second maxillipeds of *Uca rapax* and *Uca uruguayensis* (Mann-Whitney test: $U = 3215.0$; $p < 0.0001$).

In Zone 2, for *U. rapax*, the sediment contained predominantly very fine and fine sand fractions. The amount of very fine sand and fine sand did not differ between sediment and pellets (Mann-Whitney test: $U = 644.0$; $p = 0.907$, and Student's t test: $t = 1.05$; $p = 0.301$, respectively). In the pellets, a significant increase of the medium and coarse sand ($U = 478.0$ and $t = 483.5$ respectively; and $p < 0.004$ for both) and very coarse sand fractions ($U = 483.5$; $p < 0.0001$) was recorded. The silt and clay fractions decreased in the feeding pellets after sediment processing by *U. rapax* ($U = 747.0$; $p = 0.034$) (Table 1 and Fig. 5). The sediment of Zone 2 (pre- or post-processing) was classified as very fine sand, with a mean particle size (ϕ) varying from 3.382 (sediment) to 3.301 (pellets), also moderately sorted both before and after processing by crabs (0.734 to 0.862, respectively); changed from negative asymmetry (−0.295) to very negative asymmetry (−0.398); and increased from platicurtic (0.856) to mesocurtic (1.072). The sediment was silty-sand according to Shepard's classification, and this zone was characterized as a very highly hydrodynamic area (classification C-IV) by Pejrup's method.

DISCUSSION

The potential for bioturbation of the sediment by *U. uruguayensis* and *U. rapax* during their feeding activity was similar in relation to grain-size composition, since both species return the larger mineral particles to the environment after the sorting process. The same occurs with organic matter removed from the substrate, but with more efficient extraction by *U. uruguayensis* than *U. rapax*, probably enabled by the larger number of spoon-tipped setae on the second maxilliped in the former.

During feeding, the mouthparts of fiddler crabs manipulate portions of sediment, sorting different particle sizes and scraping them to remove the organic matter. The larger, indigestible sand particles are deposited around the burrow opening in the form of tiny balls or feeding pellets (Crane, 1975), while the small grains are ingested together with organic matter. In some species, the feeding pellets are arranged in rows radiating from the opening, and can help the crab return home after foraging (path integration) (Zimmer-Faust, 1987; Zeil, 1998; Canicci et al., 1999; Layne et al., 2003).

The feeding pellets produced by both species were composed mainly of larger particles of sediment than the mean size of the sediment in the burrow surroundings. The proportion of fine particles (silt-clay, very fine and fine sand) in the

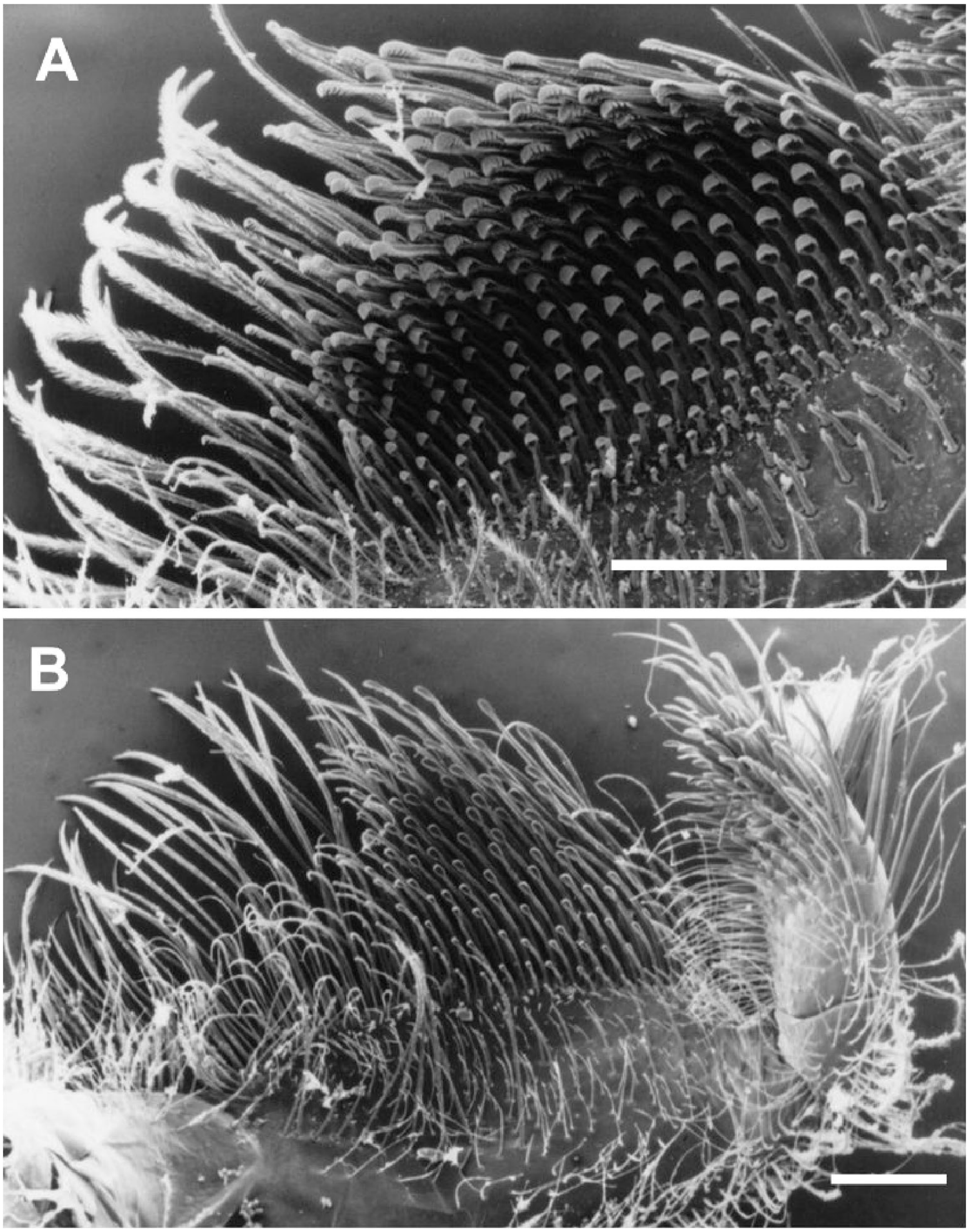

Fig. 3. Scanning electron micrographs of the second maxilliped, showing the larger number of spoon-tipped setae. A, *Uca uruguayensis*; B, *Uca rapax*. Bar scale in each photo is 0.5 mm.

pellets was lower than in the sediment around the burrow, suggesting that both species ingested smaller grains. However, the grain-size composition of the feeding pellets did not differ between *U. uruguayensis* and *U. rapax*. Similar results were reported by Robertson and Newell (1982a, b), Thurman (1987), and Colpo and Negreiros-Fransozo (2011). Mchenga (2007) observed bioturbation of mangrove sediments by increases of the particle diameter in areas post-processed by crabs, compared with areas without these crustaceans. However, Ribeiro et al. (2005) noted that the relationship between the feeding activity of fiddler crabs and changes in sediment characteristics may not be a direct cause-effect mechanism, but might also be an effect of external sources, e.g., local hydrology, which would explain the spatial variations of granulometry and organic-matter content, more than the foraging activity of crabs.

Fiddler crabs feed on interstitial organic elements in the sediment (diatoms, bacteria, other microorganisms, and debris) and the main role of the spoon-tipped setae on the second maxilliped is to scrape the sediment grains in order to release this adhered organic matter (Miller, 1961; Crane, 1975; Maitland, 1990; Silva et al., 1994; Botto and Iribarne, 2000). Therefore, it would be expected that species with more of these specialized setae clean the sediment particles more efficiently than species that have fewer setae or lack them. We found that both species remove organic

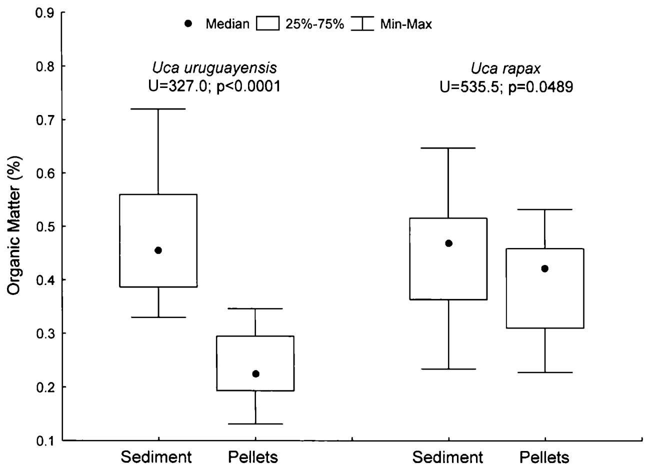

Fig. 4. Percentages of organic matter (%) in the sediment and feeding pellets in each sampling zone for the fiddler crabs *Uca uruguayensis* and *Uca rapax*.

Table 1. Comparison of the proportion of each particle size-class between pre-processed and post-processed sediment (feeding pellets) for areas with a predominance of *Uca uruguayensis* (Zone 1) and *Uca rapax* (Zone 2). *Data were compared by Student's t-test, since they satisfied the assumptions of homoscedasticity. Particle size classes: VCS, very coarse sand; CS, coarse sand; MS, medium sand; FS, fine sand; VFS, very fine sand; S + C, silt + clay.

		Median/mean*	U/t* value	p
Uca uruguayensis				
VCS	Sediment	0.007	363.5	<0.0001
	Pellets	0.106		
CS	Sediment	0.140	339.0	<0.0001
	Pellets	0.945		
MS	Sediment	0.639	389.0	<0.0001
	Pellets	1.678		
FS	Sediment	16.6*	3.06*	0.0036
	Pellets	14.0*		
VFS	Sediment	12.7	694.0	0.2772
	Pellets	11.7		
S + C	Sediment	0.062	813.0	<0.0001
	Pellets	0.036		
Uca rapax				
VCS	Sediment	0.067	450.0	<0.0001
	Pellets	0.240		
CS	Sediment	0.406	483.5	0.0029
	Pellets	0.694		
MS	Sediment	0.433	478.0	0.0020
	Pellets	0.726		
FS	Sediment	8.94*	1.05*	0.3008
	Pellets	8.10*		
VFS	Sediment	19.5	644.0	0.9073
	Pellets	19.5		
S + C	Sediment	0.727	747.0	0.0344
	Pellets	0.588		

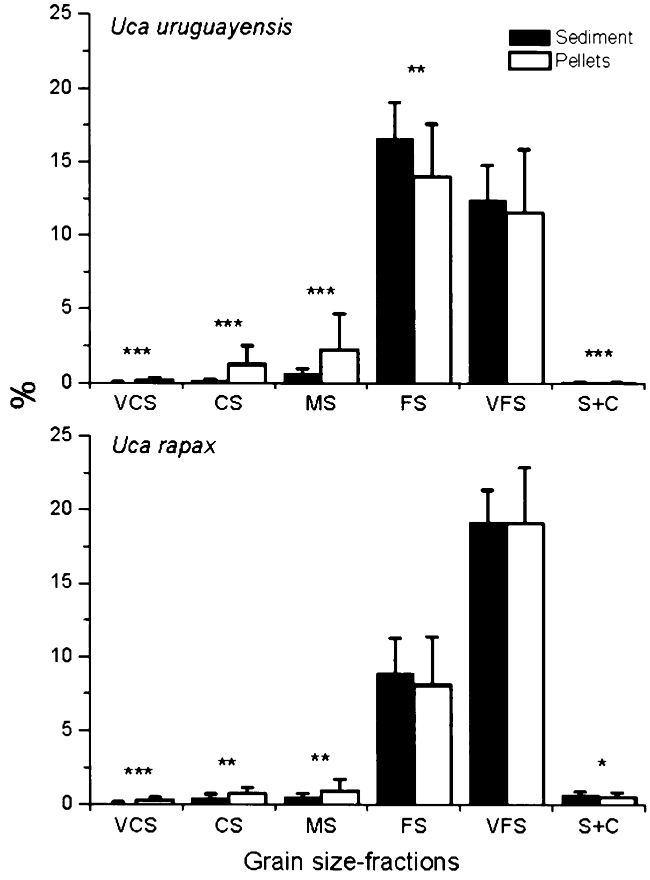

Fig. 5. Comparison of the percentage of each grain-size class between sediment and feeding pellets for each zone (Zone 1 = *Uca uruguayensis*; Zone 2 = *Uca rapax*; VCS = very coarse sand; CS = coarse sand; MS = medium sand; FS = fine sand; VFS = very fine sand; S + C = silt + clay) (* = $p < 0.05$; ** = $p < 0.004$; *** = $p < 0.0001$).

matter from the sediment, because the organic content in feeding pellets was lower than in the surrounding sediment. However, the interspecific differences in the amount of organic matter extracted in the pellets and the p values of the Mann-Whitney tests (% of organic content in sediment vs. in feeding pellets for each species) suggest that *U. uruguayensis*, which has many spoon-tipped setae, removes organic elements from the sediment more efficiently than *U. rapax*, which has fewer of these specialized setae. Therefore, our results support the hypothesis of a positive association between the number of spoon-tipped setae on the second maxillipeds of *Uca* spp., and their capacity to extract organic elements (food source) from the sediments (Miller, 1961; Crane, 1975; Thurman, 1987; O'Connor, 1990; Costa and Negreiros-Franzoso, 2001).

The number of spoon-tipped setae on the second maxilliped was previously used to explain the spatial distribution of the species of *Uca*: sand dwelling-crabs have large numbers of these setae, and mud-dwelling species have few or none (Crane, 1975; Icely and Jones, 1978; Thurman, 1987; Costa and Negreiros-Fransozo, 2001; Lim, 2005; Bezerra et al., 2006). Therefore, the differences in the number of spoon-tipped setae between *U. rapax* and *U. uruguayensis* suggest that their niches do not overlap. In subtropical mangroves of Brazil, *U. rapax* is found in areas with approximately 14.8% silt and clay, whereas *U. uruguayensis* occurs in sediments with 8.1% (Colpo et al., 2011). However, *U. uruguayensis* occurs in temperate mudflats (Spivak et al., 1997a, b; Daleo et al., 2003; Ribeiro et al., 2005) and Thurman et al. (2010)

showed that *U. rapax* occupies habitats with a wide range of substrates and osmolalities. Therefore, the distribution patterns of *Uca* species are affected by many environmental factors including substrate granulometric composition, organic-matter and water content, salinity, tidal exposure, vegetation, food availability, competition, etc. (Ewa-Oboho, 1993; Mounton and Felder, 1996; Bezerra et al., 2006). Therefore, in a few areas, these species can be sympatric.

Botto and Iribarne (2000) found that when feeding during low-tide periods, *U. uruguayensis* can remove about 680 g/m^2/day of sediment, which disintegrated during high tide in the surface layers. The authors suggested that this is caused by an increase of roughness/penetrability and establishment of erosion processes, with potential effects on sediment transport. For the congener *U. rapax*, which has the same ecological valence, this process should be identical, and could destabilize sediments and have a negative effect on suspension feeders, mainly in very highly hydrodynamic areas such as those studied here. The data obtained also indicate an edaphic change of post-processing sediment (pellets), mainly in relation to skewedness toward larger granules (negative or very negative), and a granulometric curve closer to normal (mesocurtic). No differences in grain sorting were evident between *U. uruguayensis* and *U. rapax*. Both species removed more small particles from the sediment, and left the coarser ones (fine sand).

We found evidence that the feeding activity of *U. uruguayensis* and *U. rapax* causes sediment bioturbation, changing the granulometric composition and the organic content. Despite the difference between these species in the number of spoon-tipped setae on the second maxilliped, the sediment sorting process was similar for both (amounts of fine and coarser sediment classes in the feeding pellets). However, the larger number of spoon-tipped setae in *U. uruguayensis* seems to allow a more efficient grain-cleaning process than in *U. rapax*.

The feeding activity of *U. uruguayensis* and *U. rapax* causes bioturbation in the mangrove sediments, changing the size-class composition and the organic content of the post-processed sediment. The different numbers of spoon-tipped setae on the second maxillipeds of these species did not affect their potential for grain-size selection, but resulted in different abilities to remove organic matter (food source) from the sediment. *Uca uruguayensis* (156 ± 34.0 spoon-tipped setae) is more efficient in cleaning sediment particles than is *U. rapax* (87 ± 15.9 spoon-tipped setae).

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