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Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands?

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ABSTRACT

The effect of different organic-rich sewage concentration (0%, 20% and 60% diluted in seawater) and absence or presence of mangrove trees on the survival, bioturbation activities and burrow morphology of fiddler crabs species was assessed. After 6 months, males of both species always showed higher survival (~80%) when compared to females (~20%). Crabs inhabiting pristine conditions achieved higher survival (67–87%) than those living in sewage-exposed mesocosms (40–71%). At 60% sewage loading, fiddler crabs processed less sediment (34–46%) during feeding and excavated slightly more sediment (45–80%) than at pristine conditions. While percent volume of the burrow chambers increased (13–66%) at contaminated mesocosms for both vegetation conditions, burrows were shallower (~33%) in bare cells loaded with sewage. The results show that fiddler crabs presented moderate mortality levels in these artificial mangrove wetlands, but mainly in sewage impacted cells. However, they still function as ecosystem engineers through bioturbation activities and burrow construction.

1. Introduction

Constructed freshwater wetlands are now a worldwide accepted technology for water pollution control, mainly due to low running cost (low energy consumption and training requirements) and high filtration efficiency (Crites et al., 2006) Mangrove forests have recently shown a potential as natural wastewater treatment facility in China, by removing nutrients and organic matter efficiently (Wong et al., 1997a; Yang et al., 2008). Growth and productivity in natural and pristine mangrove forests are usually nutrient limited (Hogarth, 2007). Consequently, discharge of moderate sewage loadings results in enhanced growth of trees (Mohamed et al., 2009) as well as stimulation of benthic primary producers and microheterotrophs (Tam, 1998; Meziane and Tsuchiya, 2002). The effect on macrofauna biomass and diversity seems to be dependent on the degree of contamination, proximity to the effluent and sensitivity of the species (Yu et al., 1997; Wear and Tanner, 2007; Cannicci et al., in press).

The benthic fauna in mangrove forests is typically dominated by burrowing decapods, such as fiddler crabs (*Uca* spp.). These crabs establish dense populations on intertidal flats (Skov and Hartnoll, 2001; Skov et al., 2002) making them important grazers on microalgae and bacteria (Bouillon et al., 2002; Reinsel, 2004), as well as key ecosystem engineers (Kristensen, 2008). The effects of *Uca* spp. on mangrove habitat characteristics have been extensively studied (for a review see Cannicci et al., 2008; Kristensen, 2008). Their crawling and foraging activities process a significant amount of the top 2 cm sediment layer during a single low tide period (Dye and Lasiak, 1986). As a consequence, they disturb the microbenthic primary producers and meiofauna communities in the top sediment (Ólafsson and Ndaro, 1997; Kristensen and Alongi, 2006). In addition, these crabs actively dig and maintain burrows in the sediment which function as a refuge from predation and adverse environmental conditions (e.g., high tide), provide water for the crabs' physiological needs (at low tide), and are used for moulting and reproduction (Crane, 1975). These biogenic structures may easily reach and pass 10 cm depth for adult mangrove fiddler crabs (Lim and Heng, 2007). Through their crawling, foraging and burrow construction and maintenance activities, *Uca* species increase sediment drainage, soil redox potential, translocate sediment, organic matter and nutrients, change sediment erosion threshold, and increase the sediment surface area (Wolfrath, 1992; Botto and Iribarne, 2000; Kristensen, 2008). Consequently, they stimulate microbial metabolism, organic matter degradation and nutrient cycling, as well as flora productivity (Gribsholt et al., 2003; Nielsen

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et al., 2003; Kristensen and Alongi, 2006), which may also potentially counteract adverse effects of anthropogenic eutrophication (Nielsen et al., 2003; McHenga and Tsuchiya, 2008).

Stimulation of microalgal and bacterial growth in sewage contaminated mangrove environments has apparently no effect (Yu et al., 1997) or increases fiddler crab abundance and/or biodiversity when compared to pristine mangrove areas (Cannicci et al., in press). This is probably caused by an enhanced reproductive performance of crabs due to the surplus of food availability (Penha-Lopes et al., submitted for publication), particularly in areas where environmental conditions (such as wind and water currents) restrict offshore dispersion of the pelagic larvae (Paula et al., 2001). However, under poor hydrodynamic conditions or in closed wastewater wetlands, organic enrichment above the ecosystem capacity may lead to eutrophication and consequently hypoxic conditions (Gray et al., 2002). Low oxygen levels can result in faunal migration to normoxic zones, lower survival and activity, and smaller burrow structures of marine benthic organisms. As a consequence, a decrease in the ecological role of bioturbation is observed (Diaz and Rosenberg, 1995). Among all benthic animals, crustaceans are considered one of the most sensitive species to hypoxia, only surpassed by fish. First their activity is decreased under hypoxia, and secondly exhibit high mortality if low oxygen concentrations are maintained for extended periods (Gray et al., 2002).

Knowledge on the ecological responses of mangrove associated fauna to urban sewage loadings is necessary. Understanding of direct and indirect effects of severe sewage contamination on crab survival and bioturbation activities is fundamental to comprehend the effects of organic discharge on mangrove forests and to develop sustainable mangrove wastewater wetlands. In this study, we addressed the effects of domestic sewage loading and vegetation type on (1) the survival, (2) bioturbation activity due to feeding and burrowing, and (3) burrow morphology of two fiddler crabs species, *Uca annulipes* (H. Milne Edwards, 1837) and *Uca inversa* (Hoffmann, 1874), in constructed mangrove mesocosms.

2. Materials and methods

2.1. Mesocosm set-up

Mangrove mesocosms were constructed in the upper intertidal zone of the Jangwani mangrove forest, Dar es Salaam, Tanzania. The system consisted of 27 cells (9 m^2 each) separated by 1-m tall cement walls and protected from tidal influence by a soil embankment. The sediment inside the cells was composed of the original sandy mangrove substratum from the area. Each cell was equipped with in- and outflow pipes for tidally simulated flooding and drainage with seawater or sewage mixtures. A daily tide with 12 h inundation (0.1 m water depth) starting at 23:00 and 12 h exposure starting 11:00 was applied. Sewage from a nearby hotel facility was subjected to primary treatment in a 86 m^3 storage pond before entering the mesocosm system. For complete details of the mesocosm construction and performance see PUMPSEA (2008).

The cells were either kept as unvegetated controls (bare), planted with *Rhizophora mucronata* Lam. or *Avicennia marina* (Forsk.) mangrove trees. These two species were chosen since they dominate mangrove areas along the Eastern African coast. Mangrove saplings were planted (at a density of 2.8 m^{-2}) on selected cells in early February 2006. Epifauna was introduced to all cells in late August, including males and females of two of the most abundant crab species in the area (*U. annulipes* and *U. inversa*) and the common mangrove gastropod, *Terebralia palustris* (Linnaeus, 1767). The fauna was randomly collected from the Kunduchi mangrove forest immediately prior to introduction. A density of 5 ind m^{-2} per sex and species were applied, except for *U. annulipes* females with only 3 ind m^{-2}. These are at the low range of natural densities in the area (Skov et al., 2002).

The mesocosm system was inundated exclusively with seawater from February to early October 2006. Subsequently, sewage loadings of 0, 20 and 60% mixed in seawater were applied. Three replicate cells were assigned for each sewage loading and vegetation treatment. The chosen sewage loadings are known to enhance growth of *A. marina* and *R. mucronata* (PUMPSEA, 2008). The chemical characteristics and biological oxygen demand (BOD) of sewage-seawater mixtures are presented in Table 1 and chlorophyll a concentration at the sediment surface is presented in Table 2.

2.2. Sediment oxidation level

The relative difference in Fe (III) and Fe(II) concentration is an excellent indicator of sediment oxidation level (Canfield et al., 2005). Two sediment cores were taken for solid phase Fe analysis from only one random cell per treatment due to logistic constraints. In the laboratory cores were sliced into the following depth intervals: 0–1, 1–2, 2–3, 3–4, 4–6, 6–8 and 10–12 cm before any further handling. Solid phase Fe was extracted by a modified version of the HCl technique of Lovley and Phillips (1987). Briefly, 100–300 mg subsamples were extracted in 5 ml of 0.5 M HCl for 30 min on a shaking platform. After centrifugation (1500 rpm) for 10 min, 50 μl of the supernatant were transferred to 2 ml Ferrozine solution for Fe(II) analysis and to 2 ml Ferrozine solution containing the reducing agent hydroxylamine (10 g l^{-1}) for total-Fe (Fe(II) + Fe(III)) analysis. The reactive amorphous Fe(III) oxide concentration was then operationally defined as the difference between total Fe and Fe(II).

2.3. Crab survival

The survival of crabs was checked 6 months after the start of sewage discharge into the mesocosm cells (end of March 2007).

Table 2

Sediment surface chlorophyll a concentration at different vegetation and sewage concentration treatments in April 2007 is shown ($N = 12$). Values are given as averages ± SE (adapted from PUMPSEA (2008)).

	Chl a (μg g^{-1})		
	0%	20%	60%
Bare	13.9 ± 3.9	12.5±6.1	23.1±9.4
A. marina	5.4±1.1	17.1±12.0	14.0±3.5
R. mucronata	8.1±2.7	10.1±4.0	14.7±7.0

Table 1

Chemical characteristics and oxygen uptake of the sewage-sea water mixtures used in the experimental mesocosms from October 2006 to April 2007. (DO: dissolved oxygen; BOD: biological oxygen demand) ($N = 45$). Values are given as averages ± SE (adapted from PUMPSEA (2008)). Different letters indicate significant difference – $p < 0.05$ – between sewage loading treatments.

Sewage loading (%)	Salinity (‰)	DO_{day} (μM)	DO_{night} (μM)	BOD (μM h^{-1})	NH_4^+ (μM)	NO_3^- (μM)	PO_4^{3-} (μM)
0	39.1 ± 0.6^a	308 ± 133	197 ± 17^a	5.1 ± 2.6^a	26 ± 2^a	3.6 ± 1.4	42 ± 4^a
20	24.5 ± 0.9^b	312 ± 227	10 ± 5^b	12.9 ± 2.9^a	123 ± 9^b	7.1 ± 2.9	109 ± 6^b
60	18.9 ± 1.4^c	225 ± 256	9 ± 1^b	21.3 ± 1.2^b	194 ± 17^{c42}	5.0 ± 1.4	206 ± 14^c

The density of crabs was determined by counting the number of active burrows in each cell. In addition, visual counting of active crabs on the surface of each cell was done to obtain the species and sex ratio (Skov et al., 2002). Although some crabs retreated into their burrows when the observer approached, the crab population on the surface was restored with normal activities after 5 min (Bartolini et al., accepted for publication). Counting was conducted early in the afternoon (after flushing out the cells) to obtain the maximum number of active crabs outside their burrows (Bartolini et al., accepted for publication). The counting procedure was replicated twice and the highest burrow and crab counts where used to estimate survival.

2.4. Bioturbation activities

Fiddler crabs feed at the sediment surface by sorting bacteria and microalgae from sediment grains placed in the mouth cavity by the minor chaela. The non-ingested particles are shaped into small (up to 3 mm) irregular balls, with colour and grain size similar to the surrounding surface sediment ('feeding pellets'). When crabs construct and maintain burrows, they form mounds (usually pellets with a diameter of 5–7 mm) near the opening. New mounds have a black-grey coloration typical of reduced sediment because they consist of sub-surface sediment ('burrowing pellets') extracted deep in burrows (Botto and Iribarne, 2000).

The two bioturbation modes performed by crabs (feeding and burrowing) were studied in only control (bare) and *A. marina* mesocosm cells at 0% and 60% sewage loadings due to logistical limitations. Since crabs were active until sunset (around 18:00) during emersion periods, all feeding and burrowing pellets produced were collected from around 19:00–23:00 in the haphazardly chosen cells. The sediment surface was smoothened when cells were flushed with water during inundation, at 23:00, which removed all irregularities and eliminated the bioturbation effects from the previous emersion period. This sampling procedure was repeated in two different tidal periods. Sampled sediment pellets were dried at 60 °C for 48 h and weighed (0.01 g). The amount of collected sediment due to bioturbation was correlated to the maximum number of surface active crabs in each sampled cell and compared between treatments.

About 30 random active crab holes were chosen in each examined cell for burrow resin casts. However, due to difficulties in obtaining complete casts, only between 8 and 28 were considered successful. The chosen burrow openings were, after 18:00, filled with a resin and hardening/catalyser solution until water started to emerge from the hole as an indication that the whole burrow was filled with resin. When the casts had solidified for about 2 h, they were dug up for subsequent measurement of burrow dimensions. Entrapped crabs in the burrow casts were identified to species and sexed when possible. However, due to the low number of identified casts, only data combining all burrows will be presented.

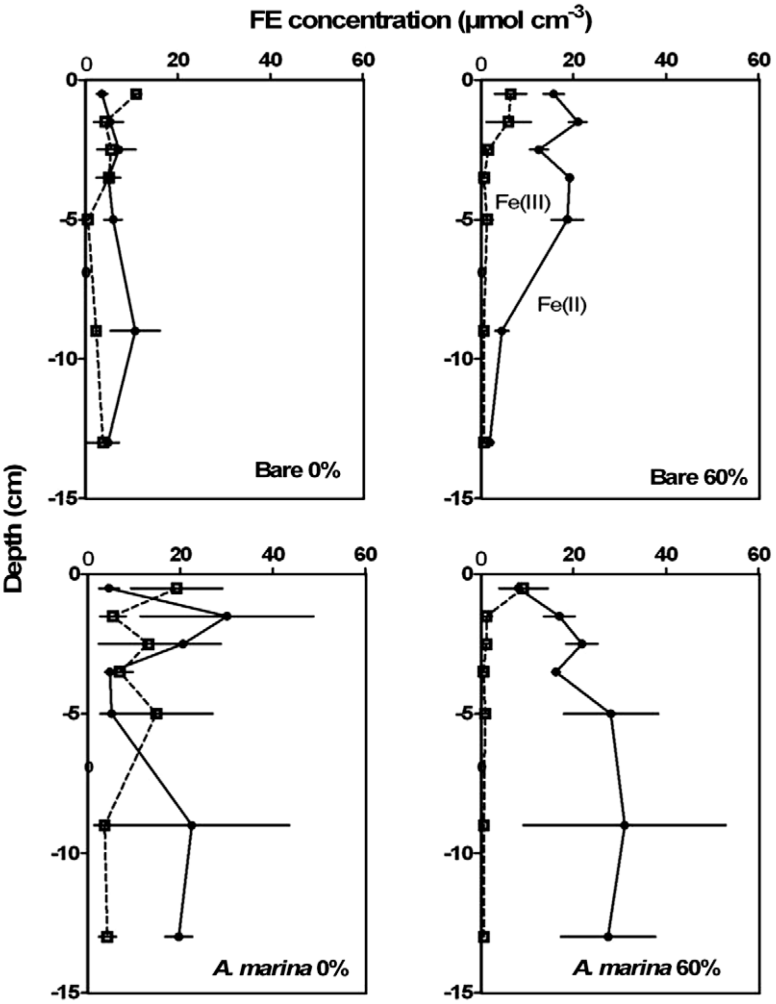

Fig. 1. Vertical profiles of solid phase iron in both vegetation and sewage loading conditions. Solid and dotter lines represent Fe(II) and Fe(III) concentration, respectively. Values are given as mean ± SE ($n = 2$).

Uca burrows are usually considered simple L or J shaped structures (e.g., Lim and Diong, 2003). However, for the present purpose we used a classification that divided burrows into 3 sections: an upper neck with entrance to the surface, a middle chamber and a deep extension leg. The distinction between the three sections were identified from the ratio between burrow (B_p) and surface opening perimeter (O_p): $R = B_p/O_p$. The chamber section was defined as burrow regions with $R > 1.45$, while the neck and extension leg were defined as burrow sections above and below the chamber, respectively, with $R < 1.45$.

Several additional burrow characteristics were also determined: total depth, wall surface area, total volume, volume of burrow sections, and angle of the different sections to horizontality. Total depth and angles were measured from lateral photographs of the burrow casts positioned with horizontal burrow entrance. The wall surface area was estimated from the length of tape with known width needed to cover the casts completely. The burrow volume was determined by dividing the weight of cast sections by the resin density (1.22 g cm^3). Although burrow depth, surface area and total volume was intended to be standardize to the burrow opening perimeter in order to minimize sampling bias due to differences in crab sizes, regression slopes were not different from zero and goodness of fitness (r^2) was always below 0.1. This way data was not standardized and even when data was standardized similar results were obtained (data not shown).

2.5. Statistical analysis

Differences in survival of the two *Uca* species between treatments were tested by a three-way ANOVA. A two-way ANOVA was applied to compare: pellet production by crab feeding and burrowing, burrow depth, surface area, total volume and percent volume of the 3 burrow sections between treatments (Vegetation vs. Sewage loading), as well as chlorophyll-a concentration. A one-way ANOVA was applied to compare salinity, oxygen levels and nutrients of seawater and sewage solution. Prior to analyses, the homogeneity of variances was assessed using Cochran's test and transformation of data was performed. While *Uca* survival data and percent volume of the burrows sections were transformed to $x' = \text{ArcSin}\ (x)$, *Uca* bioturbation data was transformed to $x' = \log\ (x + 1)$. When appropriate, Student–Newman–Keuls (SNK) tests were used as post hoc tests for multiple comparisons of the means.

3. Results

3.1. Mesocosms conditions

The sewage concentrations discharged into the contaminated mesocosms (20% and 60%) was lower in salinity, and higher in biological oxygen demand (BOD) than the seawater used to flush the pristine mesocosms (Table 1). As a consequence dissolved oxygen was low particularly during the night, while ammonium and phosphate concentrations were high in sewage treated cells. Chlorophyll a concentration in the top sediment tended to increase with sewage dosing and decrease with vegetation presence, although microalgae patchiness did not allow to find significant differences between treatments (Table 2).

Solid phase iron profiles differed among treatments (Fig. 1). Total iron (Fe(II) + Fe(III)) content was about twice as high in planted (0–14 cm depth integrated: ca. 250 μmol cm^{-2}) than in bare cells (0–14 cm depth integrated: 100–140 μmol cm^{-3}) and was independent of contamination level. Fe(II) always dominated over Fe(III) in contaminated cells. Fe(III) never exceeded 20 μmol cm^{-3} and was almost absent below 2 cm depth in 60% sewage treated cells, irrespective of vegetation. Fe(II) approached, and occasionally exceeded, 20 μmol cm^{-3} in these cells, except at depths below 5 cm in bare 60% cells. Fe(II) and Fe(III) did not change significantly with depth in pristine (0%) cells. In general, Fe(III) was higher and Fe(II) lower in these cells than those exposed to 60% sewage. Fe(III) was particularly high at all depths, and in the vegetated 0% cells presented concentrations ranging from 5 to 30 μmol cm^{-3}.

3.2. Crab survival

When active crabs are considered the only survivors in each cell (minimum estimate), male and female survivorship was estimated to 40% and 10%, respectively. However, from numbers of active burrows, male survivorship estimate increased to approximately, 80% and females to 20% (Fig. 2). While total survival was similar between species (males plus females), a significant decrease (Table 3) was observed in survival with increasing sewage loading, from 67% to 87% (0% sewage) to 40–71% (20% and 60% sewage). Vegetation, on the other hand, showed only a marginally significant positive effect on survival.

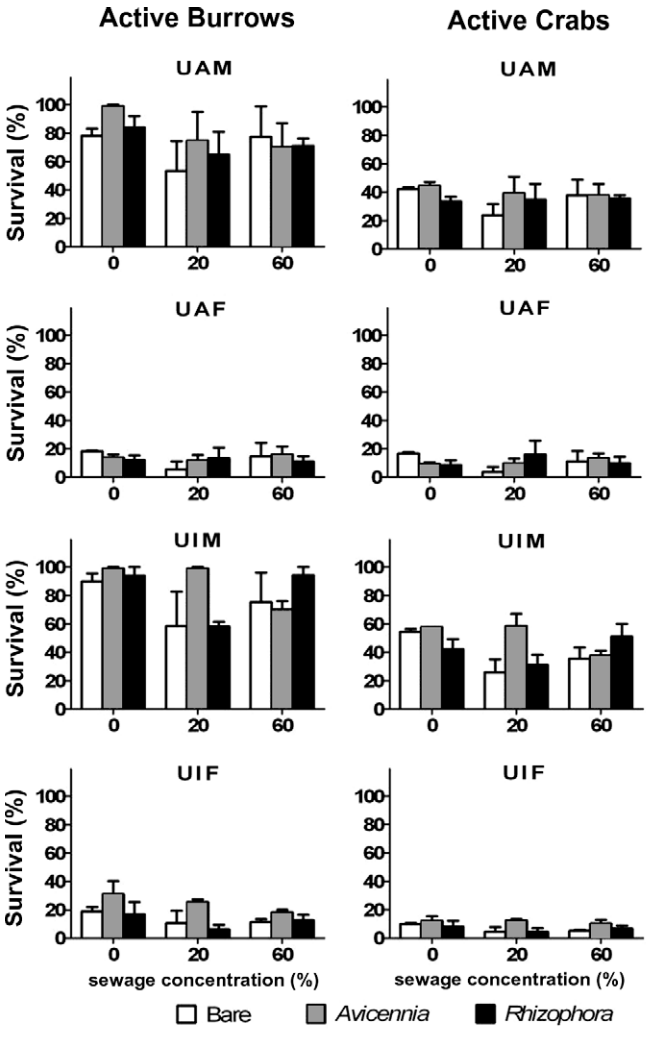

Fig. 2. Survival rates based on active burrows and active crabs of *U. annulipes* and *U. inversa* males and females after 6 months (April 07) for all vegetation factors and 0%, 20% and 60% sewage concentration treatments. Values are given as average (±SE), n = 3. UAM – *Uca annulipes* males; UAF – *U. annulipes* females; UIM – *U. inversa* males; UIF – *U. inversa* females.

Table 3
(A) Results of the 3-way ANOVA on genus *Uca* survival rates (October 06 to April 07) (Arcsin transformation). (B) 2-way ANOVA on sediment processed (expressed as DW) log $(x + 1)$ transformed for total sediment processed for feeding and during the burrow maintenance activity in different conditions. (C) 2-way ANOVA on crab burrow depth, total surface area and volume at both sewage load and vegetation type; and (D) 2-way ANOVA on volume (%) of neck, chamber and extension leg burrow sections at both sewage load and vegetation type (transformation Arcsen%). Factors: Species (fixed and orthogonal), Vegetation (fixed and orthogonal) and Sewage Concentration (fixed and orthogonal). The degrees of freedom, DF, Variance, MS, and values of *F* ratio are showed for each of the tests.

Factors	Survival rate (April 07–October 07)		
	Df	MS	*F*
Species (sp)	1	0.08	0.12
Vegetation (ve)	2	2.14	**3.39**[a]
Sewage (se)	2	3.92	**6.21**[b]
Species × vegetation	2	0.15	0.25
Species × sewage	2	0.09	0.14
Vegetation × sewage	4	0.99	1.57
sp × ve × se	4	0.37	0.59
Res	36	0.63	
Tot.	53		

(B)	DF	Feeding pellets		Burrow maintenance	
Source		MS	*F*	MS	*F*
Vegetation	1	2.95	0.09	3.70	0.02
Sewage	1	163.30	**4.91**[a]	767.10	3.47
Interaction	1	3.00	0.09	33.01	0.15
Res	20	33.22		221.30	221.31
Tot.	23				

(C)	DF	Depth		Surface area		Volume	
Source		MS	*F*	MS	*F*	MS	*F*
Vegetation	1	17.56	0.99	107.10	0.79	278.60	0.50
Sewage	1	79.29	**4.46**[a]	168.00	1.23	967.10	1.73
Interaction	1	67.04	3.77	47.14	0.35	30.80	0.06
Res	63	17.76		136.20		558.90	
Tot.	66						

(D)	DF	Vol. neck		Vol. chamber		Vol. extension leg	
Source		MS	*F*	MS	*F*	MS	*F*
Vegetation	1	0.10	1.59	0.14	2.37	0.00	0.02
Sewage	1	0.27	**4.31**[a]	1.10	**18.28**[b]	0.07	**4.89**[a]
Interaction	1	0.13	2.04	0.31	**5.15**[a]	0.01	0.53
Res	63	0.06		0.06		0.01	
Tot.	66						

[a] $p < 0.05$.
[b] $p < 0.001$.

3.3. Bioturbation activities

Each fiddler crab processed daily approximately 13 g dw during feeding in pristine (0%) cells, and showed a significant decrease by 34–46% at higher sewage concentration (Fig. 3, Table 3). Conversely, there was no significant effect of vegetation on the amount of feeding pellets produced. The amount of sediment handled by crabs for burrow maintenance under pristine conditions (17–20 g dw per active crab^{-1} day^{-1}) was of similar magnitude to that processed by feeding. Crabs exposed to 60% sewage handled 45–80% more burrow sediment (Fig. 3), but due to high variability among cells no significant differences were evident (Table 3). As for feeding activity, there was no apparent effect of vegetation on burrow maintenance.

Burrow morphology appeared visually affected by both vegetation and sewage loading (Fig. 4). However, only burrow depth and relative volume of burrow sections were affected significantly (Figs. 5 and 6, Table 3). Burrow surface area (22–29 cm^2), volume (34–48 cm^3), and section angles (neck: 64–72°; chamber: 42–56°; and extension leg: 52–55°), were similar under all vegetation and sewage treatments. Burrows in bare sediment were significantly 30% ($p < 0.01$) deeper under pristine than contaminated conditions (10.6 cm), while no such difference was evident in the presence of vegetation (~14 cm deep). While sewage also affected the relative volume of all three burrow sections significantly, no vegetation effect could be detected (Fig. 6 and Table 3). The volume of these sections was significantly ($p < 0.05$) greater (30%) in bare than planted cells under pristine conditions. About 38% larger chambers ($p < 0.001$) were found at sewage contaminated mesocosms than at pristine ones in the presence of trees. Sewage did not influence relative burrow chambers in bare cells. When chamber volume increased both neck and extension leg volumes tended to decrease (17–35%), although no significant differences were noted.

4. Discussion

4.1. Crab survival

U. annulipes and *U. inversa* can survive for at least 6 months under extreme conditions with respect to daily inundation periods of 12 h, low salinity and dissolved oxygen levels in the water column, as well as in sediments. However, some mortality occurred, mainly concerning females of both species. Although crab survival was negatively affected by sewage exposure, female survival was apparently always low even at pristine conditions. This indicates either that: (1) low activity of females on the sediment surface may underestimate their real abundance (Skov et al., 2002), which occurs particularly during the breeding season usually more strongly during the wet season when the sampling was performed (Litulo, 2005 and references therein), or (2) females are more sensitive than males to the artificial conditions of the wetland with respect to the long and constant inundation cycles.

Most studies on the effect of hypoxia on crabs have targeted mainly commercial and/or non-burrowing species. These have shown that most crabs do not survive more than a few hours or days, depending mainly on the species and hypoxia levels (Diaz and Rosenberg, 1995). Crabs do not possess efficient anaerobic metabolism and they are more dependent on their O_2 transport system than most other benthic invertebrates (Das and Stickle, 1993). However, both *U. annulipes* and *U. inversa* are known to inhabit and seal their burrows during immersion periods (De la Iglesia et al., 1994). They must therefore to some extent have the capacity to withstand the potentially hypoxic conditions that develop inside burrows for several hours. In our experiment, they adapted rapidly to the "artificial 12 h daily tides" used in the mesocosms, and remained inside burrows during immersion periods as under natural conditions. By doing so, they avoided hypoxia in the water column of contaminated cells, but had a higher risk of hypoxic exposure inside burrows. Under normal conditions they capture an air bubble inside while sealing their burrows, which provides sufficient oxygen for breathing until the next emersion period (De la Iglesia et al., 1994). The high organic matter availability and high microbial metabolism in contaminated mesocosms may be responsible for low oxygen levels in the water column and sediment (Canfield et al., 2005). The associated higher microbial oxygen consumption in burrow walls (Gribsholt et al., 2003; Nielsen et al., 2003) may augment hypoxia inside burrows and coupled with release of sulfide increase stress and may cause death by asphyxiation or drowning (Diaz and Rosenberg, 1995). The risk of a fatal outcome is higher during moulting as this oxygen sensitive process usually takes place inside burrows (Das and Stickle, 1993).

Also, fiddler crab males were observed to wander around for longer periods in contaminated mesocosms (Bartolini et al.,

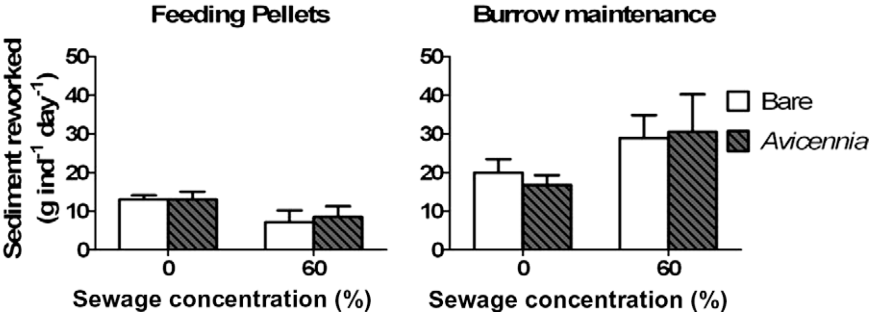

Fig. 3. Weight of sediment (g dw) processed by fiddler crabs feeding and burrowing activities at different sewage loadings and presence or absence of *A. marina* trees. Values are given as average (±SE), *n* = 3.

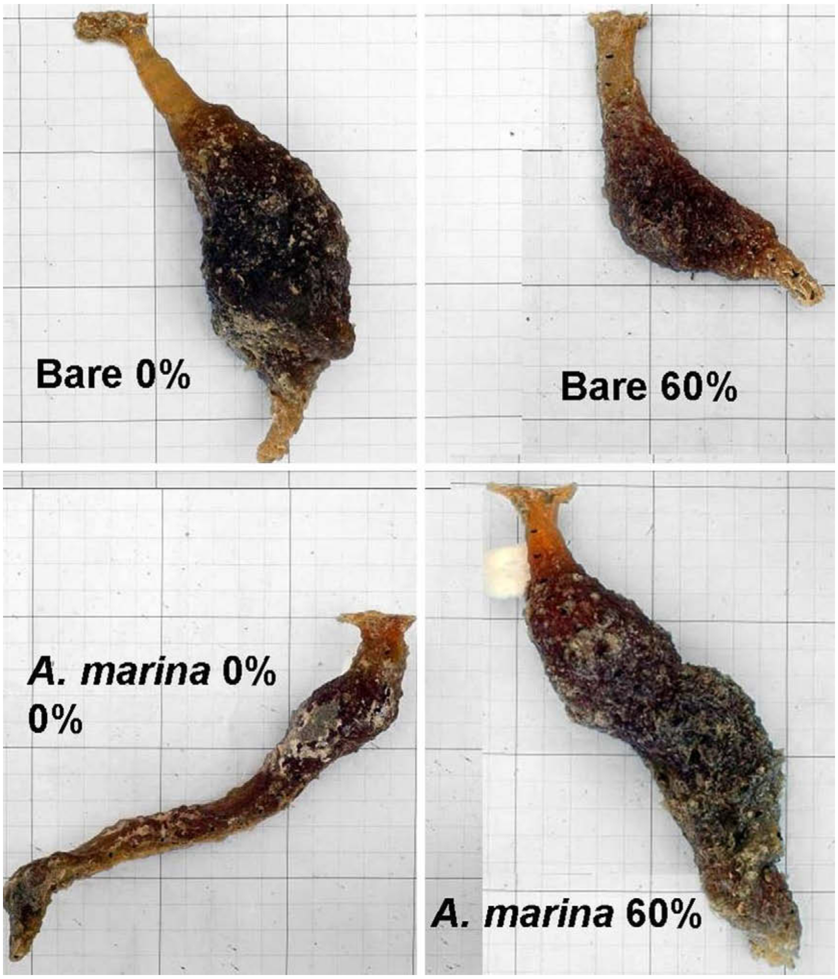

Fig. 4. Photos of illustrative burrow casts collected in all treatment types.

accepted for publication) and high agonistic interactions between males may have also been a factor increasing crab mortality. 'Hypoxic events are known to increase cannibalism in the crab *Callinectis sapidus*, leading to high mortality rates (Aumann et al., 2006).

The present survival results strongly depend on the approach to estimate abundance. A known number of individuals were introduced initially to the cells while the subsequent enumeration was done by indirect approaches. Some studies have found that fiddler crab burrows numbers overestimate (30%) the actual crab abundance while visual counting of active crabs, on the other hand, underestimates (40%) the real crab density (Skov and Hartnoll, 2001; Skov et al., 2002). If we correct our data according to these studies, we obtain similar survival using both methods (Table 4) at an average of 50% for males and 12% for females. This is a clear indication that crabs resist stressful conditions for extended periods of hypoxia, but conclusions must be taken with caution because this study was only performed for a 6-month period. The estimated low survival of females, coupled with chronic exposure to hypoxic conditions and toxic metabolites may lead to collapse of the crab population due to limited reproductive activity and larval development (Tankersley and Wieber, 2000; Wu, 2002; Bergey and Weis, 2008), which may jeopardize the fiddler crab sustainability in closed systems or heavily contaminated mangrove forests.

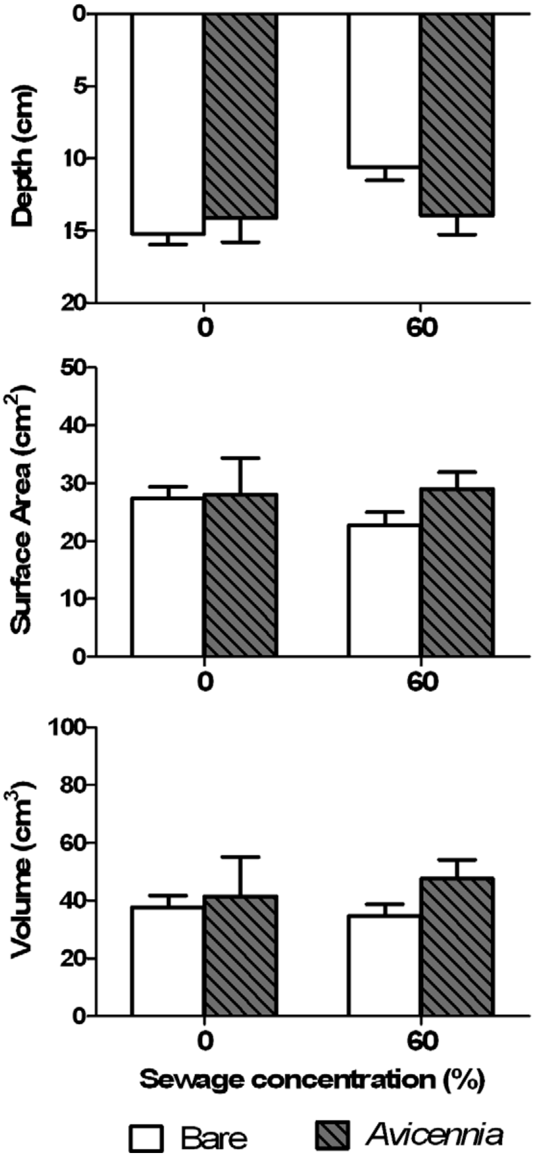

Fig. 5. Fiddler crab burrow depth, total volume and surface area for all active burrows for bare and *Avicennia marina* and 0% and 60% sewage loading treatments. Values are given as average (±SE) ($n_{B0} = 28$; $n_{B60} = 16$; $n_{A0} = 8$; $n_{A60} = 15$).

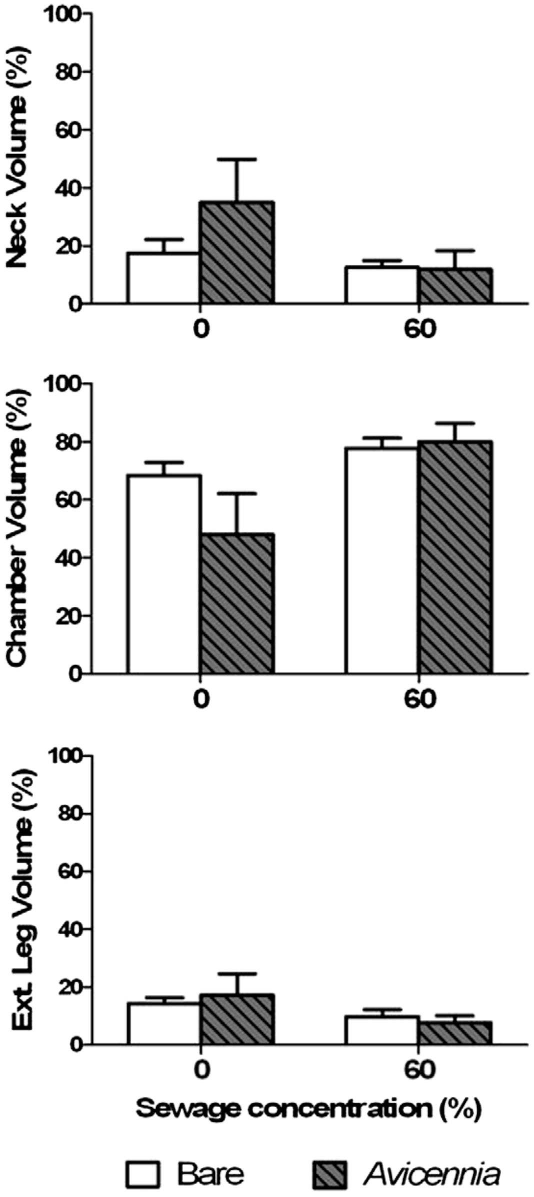

Fig. 6. Volumetric percentage of burrow neck, chamber and extension leg constituting fiddler crab's burrow for bare and *Avicennia marina* and 0% and 60% sewage loading treatments. Values are given as average (±SE) ($n_{B0} = 28$; $n_{B60} = 16$; $n_{A0} = 8$; $n_{A60} = 15$).

4.2. Bioturbation activities

The amount of sediment processed by crabs during feeding activities depends strongly on sewage loadings, while the presence of young trees has no significant influence. The effect of sewage concentration is probably caused by the higher nutrient availability in contaminated sediment and water, which enhances (>70%) microalgal production as a food source for these crabs (Bouillon et al., 2002; Meziane and Tsuchiya, 2002; Reinsel, 2004). The lack of effect by trees is probably due to the limited shading by the small canopy of young *A. marina* trees (107.8 ± 7.8 cm height), leading to similar microphytobenthos growth in both bare and planted cells. Foraging is the primary activity taking place during the first hours after crabs exit their burrows (Eshky et al., 1995) until they get satiated (Bartolini et al., accepted for publication) followed by a sequence of activities in a hierarchical temporal series (Eshky et al., 1995). If their intake efficiency remains constant the crabs need less time to be satiated at higher microalgae and bacteria densities in the sediment. Consequently, there is a decrease of the amount of feeding pellets produced and thus bioturbation potential. Alternatively, feeding rates can be lowered under hypoxic condition in the water column due to decreased metabolism of the crabs (Wu, 2002). A decrease in metabolic activity of more than 20% has been observed for important commercial crabs species (*Callinectes similis* and *C. sapidus*) under long-term (28 days) hypoxic conditions (Das and Stickle, 1993). However, a parallel behaviour study done at these mesocosms demonstrated that crab metabolism is not reduced but a significant modification of the period of the sequential activities is achieved (Bartolini et al., accepted for publication). The lesser time spent feeding allows the crabs to devote more time and effort on other behaviours, such as gallery construction and maintenance. We actually observed a slight increase in the amount of "deep" sediment brought to the surface under high sewage loadings. Other studies have shown the opposite effect, e.g. ghost shrimps, with a decrease of the burrowing activity and sediment turnover with increasing nutrient

Table 4
Total Survival and survival based on active burrows counts or active crabs counts corrected with previous studies (see discussion section for further explanation). Burrow counting overestimate in about 30% while visual counting underestimate in about 40%, so all raw data obtained was multiplied by 0.7 or 1.4, respectively. Values are given as averages ± SE. (*N* = 3).

	Sewage (%)	Total survival	UAM		UAF		UIM		UIF	
			Active burrows (corrected)	Active crabs (corrected)	Active burrows (corrected)	Active crabs (corrected)	Active burrows (corrected)	Active crabs (corrected)	Active burrows (corrected)	Active crabs (corrected)
Bare	0	67.3±3.6	54.7±6.2	59.1±1.8	12.8±0.4	23.3±1.5	62.9±4.1	76.2±2.7	13.3±2.1	14.0±0.9
	20	39.6±7.5	37.3±14.8	33.2±11.0	3.9±3.9	5.2±5.2	40.9±17.0	36.3±12.7	7.4±6.1	6.2±4.8
	60	59.2±11.5	54.1±15.1	52.9±15.3	10.2±6.8	15.6±10.4	52.8±14.5	49.8±10.9	8.0±1.4	7.3±1.0
Avicennia	0	87.6±5.7	69.3±0.7	62.2±3.6	9.7±1.5	13.0±1.5	69.3±0.7	80.9±0.0	21.8±6.5	17.1±4.5
	20	71.7±7.3	52.4±14.1	55.0±16.3	8.3±2.6	13.8±4.6	69.3±0.7	81.9±12.0	17.9±1.3	17.6±1.0
	60	55.0±6.4	49.2±11.8	52.9±11.2	11.2±4.0	19.0±4.6	49.2±6.9	52.9±4.8	12.8±1.3	14.5±3.7
Rhizophora	0	76.5±4.1	58.9±5.6	46.7±4.8	8.5±2.3	12.1±4.6	65.9±7.2	59.1±10.0	11.9±6.0	11.4±5.8
	20	49.8±7.1	45.5±11.1	48.7±15.3	9.5±5.1	22,5±13.5	40.9±3.9	43.6±10.0	4.4±2.3	6.2±3.6
	60	61.6±6.0	49.7±3.7	49.8±3.1	7.7±2.7	13.8±6.2	66.0±4.0	71.6±12.6	8.9±2.7	9.3±3.1

availability (e.g., Berkenbusch and Rowden, 1999). However, just as here, this was probably linked with lower demand to process sediment for obtaining food, as the burrowing activity of ghost shrimps is always linked to feeding.

The burrow structure of *U. annulipes* and *U. inversa* in our mesocosm cells was slightly different from the typical L or J funnel-bent chamber, as observed for *U. annulipes* populations in Singapore (Lim and Diong, 2003; Lim and Heng, 2007; Lim and Rosiah, 2007). The majority of burrows in our system exhibited an extra narrow elongation (extension leg) below the chamber. Otherwise, the general burrow morphology is within the dimensions already registered for fiddler crabs (Lim and Diong, 2003; Lim and Heng, 2007; Lim and Rosiah, 2007). The trend for shallower burrows with larger chambers in contaminated cells was probably a consequence of low redox conditions in the sediment (high Fe(II)). Shallow burrows are more likely to maintain oxic conditions by facilitating the diffusion of air between the gallery and atmosphere (Lim and Diong, 2003). Similarly, shallow *Uca pugnax* burrows have also been reported from oil contaminated salt marshes (Culbertson et al., 2007). The depth of crab burrows may therefore be a good proxy for environmental stress.

The decrease in burrowing depth as a consequence of hypoxia is usually not associated with concurrent change in burrow volume (Diaz and Rosenberg, 1995; Weissberger et al., 2009). Burrow volume therefore appears to be a key parameter that crabs need to keep constant to assure that sufficient air is trapped inside burrows to survive during immersion periods. Crabs seem to compensate shallower burrows by constructing larger chambers when reduced sediment conditions demand shallower burrowing depth. Consequently, the total burrow volume is maintained with minimum increase in burrow surface area, and thus sediment–air interfaces with potential for oxygen uptake (Gribsholt et al., 2003; Nielsen et al., 2003).

The similarity in burrow depth between pristine and contaminated planted cells indicates that mangrove trees compensate for the reducing effect of nutrient loading as observed in the bare cells. *A. marina* roots are known to translocate O_2 to deep sediment layers providing Fe(III) to iron reducers (Alongi, 2005; Kristensen and Alongi, 2006), which is clearly evident in planted pristine cells (Fig. 1). However, simultaneous exudation of labile DOC from roots also stimulates sulfate reducers forcing reduced conditions with high Fe(II) levels to prevail near the sediment surface (Kristensen and Alongi, 2006). This was actually what we observed in our planted cells. The presence of roots and pneumatophores therefore seems to have stabilized the sediments allowing deeper fiddler crab burrows when compared to unvegetated zones (Lim and Heng, 2007; Lim and Rosiah, 2007). It is puzzling, though, that this root induced stabilization in contaminated cells is not associated with higher Fe(III) concentrations in deep sediment. Except for the reducing effect of sewage, we have no explanation for this discrepancy.

4.3. Implications for wetland functioning

The role of mangrove wastewater wetlands is to remove, through biological, chemical and physical processes, organic matter and nutrients from sewage to acceptable levels before it is discharged into surrounding aquatic ecosystems (Yang et al., 2008). Bioturbation significantly influence the functioning of sediments, causing dramatic changes in nutrient dynamics and organic matter decomposition, and thus affect ecosystem health, productivity and filtration capacity (Kristensen and Kostka, 2005).

We found that fiddler crab survival, feeding intensity, reworking activity and biogenic structures were slightly affected by high sewage loadings. The observed decrease in feeding activity due to luxury growth of microalgae in contaminated sediments, may potentially lead to establishment of thick "algal mats" (Kristensen and Alongi, 2006), causing extended anoxia and sulfidic conditions in near-surface sediment (Kristensen and Alongi, 2006; Marsden and Bressington, 2009). However, through a simultaneous increase in deposition of excavated sediment on top of the microalgae at the surface, crabs prevent the development of algal mats and maintain higher benthic primary productivity (Blanchard et al., 2001). The activities of crabs may therefore improve mangrove system health and productivity (Kristensen and Alongi, 2006) and consequently its filtration capacity. Displacement of sediment from deep layers by crabs will also expose new surfaces to oxygen, increasing old and refractory organic matter degradation by efficient aerobic bacteria. At the same time, labile organic carbon is buried into anoxic layers full of starved anaerobic bacteria, that will degrade this fresh substrate easily and rapidly (Kristensen et al., 1995; Kristensen and Holmer, 2001; Kristensen and Kostka, 2005). In fact, the turnover time of an average burrow (volume $\sim$40 cm^3) when assuming a daily amount of 10 g excavated sediment per burrow is roughly 8 days. Furthermore, by creating juxtaposition of oxic and anoxic habitats, fiddler crabs have the potential to enhance nitrification–denitrification processes in the sediment and thus augment removal of fixed nitrogen from discharged sewage (Canfield et al., 2005).

A decrease in burrow depth at contaminated bare cells, could influence the sediment redox profile (Weissberger et al., 2009) and consequently carbon mineralization pathways in sub-surface sediment layers (Canfield et al., 2005). However, at planted cells (expected in a functional mangrove wetland) burrow depth was kept constant allowing the introduction of oxygen into sub-surface sediment and promoting conditions for oxic respiration and microbial Fe(III) reduction (Kristensen and Holmer, 2001; Kostka et al., 2002; Gribsholt et al., 2003). By not decreasing the average burrow wall surface area in contaminated conditions, sediment microbial metabolism might be enhanced and nutrient cycling continuously occur, promoting removal of nutrients from sediment exposed to organic waste contamination as has been shown for fiddler (Nielsen et al., 2003) and grapsid crabs (McHenga and Tsuchiya, 2008).

It must be emphasized, however that the low abundance of crabs used in the present experiment will not provide the optimal functioning and filtering capacity of mangrove wastewater wetlands (Nielsen et al., 2003). We only applied $\sim$10 crabs m^{-2}, while much higher densities (>100 m^{-2}) can easily be found in natural habitats (Skov et al., 2002). The increased impact of a crab population of 100 crabs m^{-2} in these wetlands can be stressed by the following scenario: the system reworking by feeding (10 g dw $crab^{-1}$ day^{-1}) and burrowing (25 g dw $crab^{-1}$ day^{-1}) of 100 crabs m^{-2} replaces the upper 0.3 cm every 6 days, instead of every second month as in the present situation. This also means that the sediment is reworked to $\sim$10 cm depth by fiddler crab burrows every 6 months at natural crab densities.

This study demonstrates that both fiddler crab species studied are efficient ecosystem engineers in sewage enriched mangrove sediment. However, the relatively high mortality of females renders their populations unstable and recruitment must be assured to maintain a sustainable system. The high bioturbation levels under contaminated conditions indicate that these crabs have the potential to enhance organic matter decomposition, as known for other macrobenthic species (see Kristensen and Kostka, 2005), and thus cause a rapid turnover and ultimate removal of organic and inorganic nutrients. While this study only examined one functional type of organism, it is important that future studies address the effect of multispecies epifaunal and infaunal assemblages, as well as their density and interactions on mangrove wastewater wetland biogeochemistry and filtration efficiency.

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