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The effect of sewage discharge on the ecosystem engineering activities of two East African fiddler crab species: Consequences for mangrove ecosystem functioning

Fabrizio Bartolini [a,*], Filippo Cimò [a], Marco Fusi [a], Farid Dahdouh-Guebas [b,c],
Gil Penha Lopes [d], Stefano Cannicci [a]

[a] *Dipartimento di Biologia Evoluzionistica, Università degli Studi di Firenze, via Romana 17, I-50125 Firenze, Italy*
[b] *Laboratory of Complexity and Dynamics of Tropical Systems, Département de Biologie des Organismes, Faculté des Sciences, Université Libre de Bruxelles – ULB, CP 169, Avenue Franklin D. Roosevelt 50, B-1050 Bruxelles, Belgium*
[c] *Laboratory of Plant Biology and Nature Management, Mangrove Management Group, Faculteit Wetenschappen en Bio-Ingenieurswetenschappen, Vrije Universiteit Brussel – VUB, Pleinlaan 2, B-1050 Brussel, Belgium*
[d] *IMAR – Laboratório Marítimo da Guia, Centro de Oceanografia, Faculdade de Ciências da Universidade de Lisboa, Av. N.S. Cabo 939, 2750-374 Cascais, Portugal*

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ABSTRACT

A number of studies have suggested that mangrove forests and their faunal components may be pre-adapted to the impact of organic waste discharge, making them possible natural wastewater treatment wetlands. However, the results from recent research are contradictory. Some studies have shown that negative effects, sometimes subtle and difficult to observe, can be detected on specific biotic components of forests subjected to organic pollution. Therefore, the aim of the present study was to investigate possible alterations in the ecosystem engineering activities of a fiddler crab community dominating the landward belts of Kenyan mangrove forests. The total processed sediment produced by burrowing and foraging activities in a population from a peri-urban mangrove area receiving untreated domestic sewage was compared with that from a forest not affected by urban wastewater. The results showed how the peri-urban site hosted a higher biomass of crabs, which produced a significantly lower amount of processed sediment compared with the pristine site, resulting in a lower total top sediment mixing activity of the crabs. Thus, the present study showed a link between sewage exposure and top sediment reworking by crabs, which is potentially beneficial for mangrove growth and ecosystem functioning. This represents a possible example of cryptic ecological degradation in mangal systems.

1. Introduction

Our understanding of the role of the various biotic components involved in mangrove ecosystem functioning, as well as our knowledge about their strong ecological interconnections, has increased in recent years (Lee, 1999). Numerous studies have focused on the effects of mangrove benthic macrofauna, such as gastropods and crabs, on ecosystem functioning (Cannicci et al., 2008; Lee, 2008) and on the role of mangrove crabs as important ecosystem engineers (Kristensen, 2008; Lee, 1998). Among these, microalgal and bacterial feeding fiddler crabs (Ocypodidae, genus *Uca*) (Bouillon et al., 2002; France, 1998; Meziane and Tsuchiya, 2002) bioturbate the upper millimetres of sediment and produce feeding pseudopellets during their foraging activity (Dye and Lasiak, 1986). Dense fiddler crab populations can thus affect the surfaces of the forest floor (Skov et al., 2002). Their activities provide efficient top sediment mixing and they control micro- and macroalgal mat proliferation (Kristensen and Alongi, 2006).

Like many other mangrove crab species, fiddler crabs actively dig burrows for shelter during high tide periods, from predators and where they retire for moulting and mating (Jones, 1984). The substratum therefore appears heavily modified and this may affect, for example, the propagule dispersal of mangrove trees (Di Nitto et al., 2008). The presence of crab burrows also enhances sediment irrigation favouring the dilution of high quantities of segregated salts. This improves water uptake by mangrove roots, which is naturally auto-inhibited by the increase in salt concentrations in the sediment that results from salt-exclusion mechanisms at root level (Passioura et al., 1992; Stieglitz et al., 2000). Irrigation caused by burrow digging and burrow maintenance may also contribute to the removal of dissolved sulphide (Howes and Goehringer, 1994). In fact, the presence of burrows allows oxygen translocation to deeper layers of sediment, thus driving organic matter degradation

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* Corresponding author. Tel.: +39 0552288314; fax: +39 055222565.
E-mail addresses: fabrizio.bartolini@unifi.it (F. Bartolini), pipco82@hotmail.com (F. Cimò), marco.fusi@unimi.it (M. Fusi), fdahdouh@ulb.ac.be (F. Dahdouh-Guebas), gppenha-lopes@fc.ul.pt (G.P. Lopes), stefano.cannicci@unifi.it (S. Cannicci).

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pathways toward Fe(III) reduction and oxygen respiration, which inhibits sulphate reduction rates and consequently lowers the risk of free sulphide accumulation (Nielsen et al., 2003). Kristensen and Alongi (2006) observed that *Avicennia marina* in mesocosms had more pneumatophores and higher leaf production due to increased sediment mixing and aeration caused by the burrowing and foraging activities by *Uca vocans*.

The positive effects of crab bio-engineering on nutrient recycling, microalgal growth, sediment irrigation and, eventually, on the whole functioning of the mangrove forest can be important for tuning the effects of nutrient enrichment arising from sewage discharge, which is usually spatially localised (Wear and Tanner, 2007). From another perspective, however, sewage loadings in mangrove swamps, which are known to be nutrient limited systems, can produce an enrichment of available organic matter and nutrients, leading to an overgrowth of both aerobic and anaerobic bacteria, as well as of macroalgae, benthic diatoms (Meziane and Tsuchiya, 2002) and of larger trees (Mohamed et al., 2008). Hence, sewage represents a potential nutrient source that can support higher levels of primary and secondary production.

Recent studies (Cannicci et al., 2009) have shown how such a partially disturbed environment can sustain denser crab populations. Furthermore, behavioural observations on two *Uca* species dwelling in sewage-treated mesocosms, demonstrated a modification of the daily time budget of the crabs linked to the enhanced food availability (Bartolini et al., 2009). The importance of macrofaunal activities in coping with artificially enhanced nutrient availability was shown by Nielsen et al. (2003) studying the impact of fiddler crab activity under eutrophic conditions from coastal shrimp farming. In addition, crab burrows have been shown to be macrodetritus retention areas that reduce the amount of organic matter exported from the ecosystem (Botto et al., 2006).

The presence of crab fauna, particularly if combined with the presence of mangrove trees, increases total benthic metabolism which in turn accelerates the degradation of organic matter (Kristensen et al., 2000). Therefore, crabs seem to be a crucial ecological component in view of the recently proposed use of mangrove swamps for organic waste remediation (Boonsong et al., 2003; PUMPSEA, 2008; Yang et al., 2008).

The aim of this study was to investigate possible alterations in ecosystem engineering activities of fiddler crab communities directly linked to the impact of sewage loadings. We compared the bioturbation activity of two populations of the common fiddler crab species, *Uca annulipes* and *Uca inversa*, dwelling in the landward fringe of East African mangrove forests by quantifying the total sediment processed for burrowing and foraging activities. The populations studied dominated at two Kenyan sites, a peri-urban mangrove area receiving untreated domestic sewage and a forest not affected by urban wastewater.

2. Material and methods

2.1. Study area

The study was conducted in Kenya, where we compared a peri-urban mangrove area and a forest not affected by urban wastewater discharge. The first site, Mikindani (38° 38′ E, 4° 00′ S), is a forest placed on the banks of Tudor Creek, near Mombasa island, primarily affected by the sewage from the Mikindani residential estate and partly by the sewage discharge of the Mombasa Municipality (Mohamed et al., 2008; Mwangi et al., 1999) (Fig. 1). At this site, about 1200 kg of nitrogen and 5.5 kg of phosphorus are discharged via sewage into the mangrove system every day (Mohamed, 2008). The raw sewage runs freely from the inland through the mangrove forest, affecting primarily the landward fringe and eventually ending into the Tudor Creek waters (Mohamed, 2008). The sewage loadings decrease exponentially with distance from the sources, mainly due to the influence of the tidal cycles.

The second site, Gazi Bay (39° 30′ E, 4° 22′ S), is a mangrove area situated 47 km south of Mombasa without significant wastewater discharge and with large areas of relatively undisturbed forest apart from localised patches of tree logging.

At both sites, a typical East African mangroves zonation pattern is present, with a landward sandy belt dominated by *A. marina* and a seaward muddy belt dominated by *Rhizophora mucronata*. The landward mangrove belts of both sites were characterized by the presence of a conspicuous crab fauna, mainly belonging to the family Sesarmidae, represented by *Neosarmatium meinerti*, *Perisesarma guttatum* and *Chiromantes* spp. (Dahdouh-Guebas et al., 2002), and the Ocypodidae family, represented by two dominant species of fiddler crabs, *U. annulipes* and *U. inversa* (Cannicci et al., 2008), i.e., the objects of the present study.

To assess possible alterations in the bioturbation activities of the crab fauna, at both the peri- and non-urban site the fiddler crab populations inhabiting the landward belts, i.e. most exposed to sewage in Mikindani, were targeted. We used a stratified sampling design (Chapman and Tolhurst, 2004) as two different ecological settings in the landward zone, a vegetated and an almost vegetation-free belt, were clearly distinguishable in our study. The desert-like belt may be ascribed to that classified by Macnae (1968) as *Avicennia*-parkland. In particular, the unvegetated areas of Mikindani are continuous, due to heavy exploitation for wood extraction (Mohamed et al., 2008), and they form a true belt. On the other hand, the desert areas in Gazi have a more patchy distribution and represent a small fraction of the total forest area. The landward vegetated belts (hereafter called *Avicennia* belts) of the two sites were dominated by mature *A. marina* trees, where sesarmid crabs were abundant, together with a high density of *Uca* spp. which produce a large amount of burrows and feeding pseudopellets. Conversely, the desert-like areas (hereafter called desert belts) at both sites had almost no tree cover but a few shrubs of *A. marina*. Only large fiddler crab males can be recorded here, when they move to this area in large droves at the end of the low tide.

2.2. Abiotic and biotic environmental parameter sampling

2.2.1. Sediment granulometry and organic content

The sediment granulometry and organic content were determined from five sediment cores of 4 cm diameter and 15 cm depth, collected from two sub-areas in each belt (*Avicennia* and desert) at both the Gazi and Mikindani sites. Sediment texture was assessed by sieving 100 g subsamples through a series of sieves of 1000 μm to 63 μm mesh mounted on a mechanical shaker and graded according to the Wentworth scale. Samples were dried after sieving (75 °C for 48 h) and the mass of the sediment in each class was then weighed and expressed as percentage of the starting mass. The parameter $\Phi = -\log_2$(sieve mesh in mm) was used to plot the data from the different sites. Furthermore, the organic content was measured as the weight loss of 10 g dry sediment after combustion for three days in a muffle furnace at 350 °C.

2.2.2. Crab biomass and sediment bioturbation

Two temporal replicates were carried out at two consecutive spring tides, since this tidal phase is known to be the one at which the crabs show the maximal surface activity (see Kim et al., 2004). Two sub-areas inside each belt were chosen, about 300 m apart from each other, inside which two 50 × 50 cm frames were placed on the sediment at the beginning of the low tide. Following the observations of several authors concerning the activity patterns of fiddler crabs (Bartolini et al., 2009; Skov and Hartnoll, 2001), the

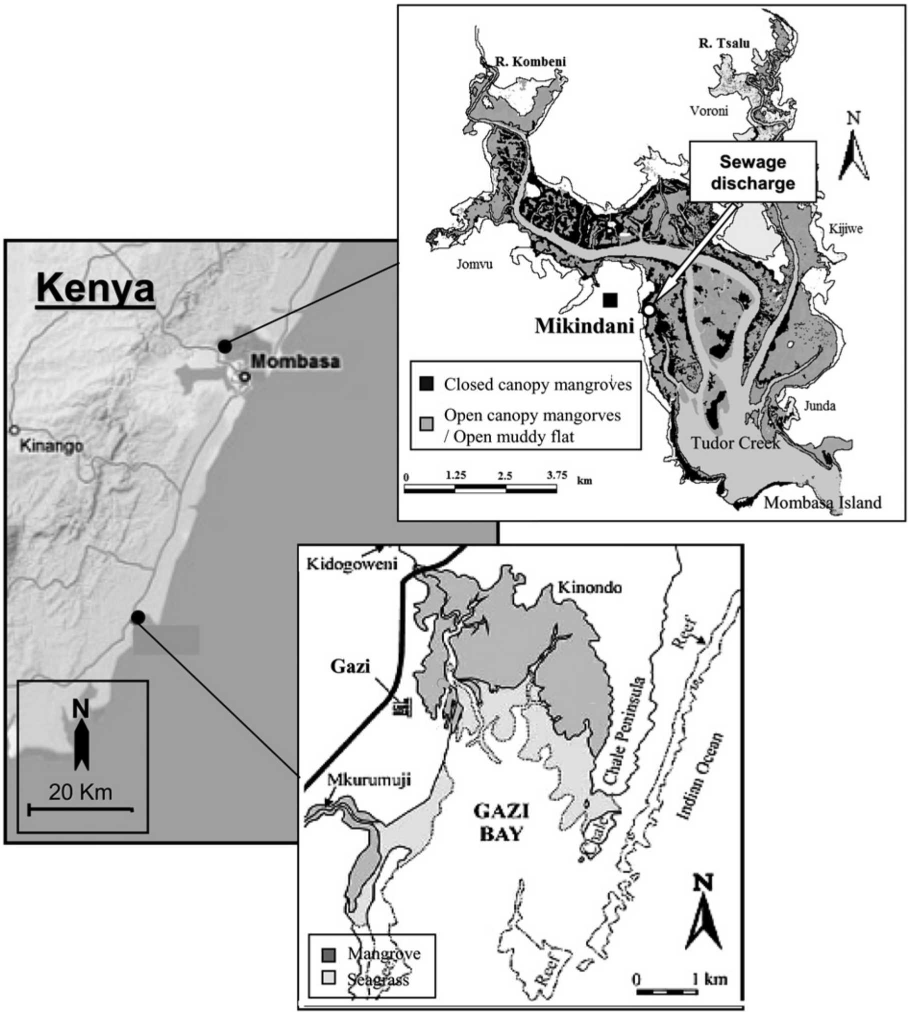

Fig. 1. Location of the two sampling sites along the Kenyan coast and the point of sewage discharge into Tudor Creek at Mikindani estate.

frames were left in place throughout the first three hours of the low tide. This time was enough to allow the crabs to perform their foraging activity, since they concentrate most of their foraging activity in the first low tide hours (see Eshky et al., 1995).

After three hours, the sediment processed by crabs in the form of pellets was gently collected by means of soft brushes and thin spatulas. We highlight that this was performed carefully avoiding picking up the unprocessed substrate below and separating the feeding pseudopellets from those produced as a consequence of burrow digging and maintenance. The former pseudopellets have diameters of 1–3 mm and have the same colour and grain size as the surrounding surface sediment; the latter are bigger, with a diameter of 5–7 mm, and they are characterized by a black-grey coloration typical of the subsurface anoxic sediment that sharply contrasts with that at the surface. After this operation, all the sediment within the frame was dug out with a shovel to a depth of 50 cm and sieved, to collect all the crabs trapped in the sediment. In the laboratory, both the pellets collected and the crabs, previously killed by keeping them for a few minutes in a freezer, were dried in an oven at 80 °C for 48 h and successively weighed to determine the total dry weight of both processed sediment and crab biomass in each quadrat.

2.2.3. Chlorophyll-a content of the sediment

In parallel with the biomass and bioturbation sampling, sediment samples of both unprocessed and processed sediment were collected to measure the Chlorophyll-a (Chl-a) content as an estimate of microalgal abundance. For each of the two sampled belts, we selected areas where crab activity was high and collected three samples of unprocessed surface sediment (depth < 1 cm), at the beginning of crabs foraging, and, in the same area, three samples of feeding pseudopellets collected three hours after the start of the low tide so as not to disturb the crabs during their activity. All samples were quickly brought to the laboratory for analyses. Sediment samples of about 1 g wet weight were extracted in 15 ml of 90% acetone for 24 h at 4 °C. Each sample was then spun down at 3000 rpm for 10 min and the supernatant analyzed for Chl-a content, which was calculated using the spectrophotometric equation from Parsons et al. (1984) and expressed in μg/g of sediment.

2.2.4. Burrow casting

Burrow casting was carried out in four 50×50 cm quadrats in each zone of each locality. Casts were obtained by pouring a polyester resin into the hole of an inhabited burrow and waiting for one hour to allow the resin to harden. The casts were then extracted from the sediment by means of a shovel and brought to the laboratory for measurement.

The volume of each cast was calculated by immersing it into a graduated recipient to measure the volume of water displaced. The surface of the cast was estimated by gluing stripes of tape of known area on the cast, until the gallery walls were completely covered. The actual depth reached *in situ* by the burrow was easily measured with a ruler by orienting the cast so as to keep the surface of the top of the cast horizontal. The surface orientation was easily seen because the resin spilled out of the burrow entrance and was deposited at the same level of the surrounding sediment. In order to accurately describe the topology of the burrows, the diameter of the each cast was measured at each 1 cm of linear length and these measures were standardised across casts by dividing them by the diameter of the burrow opening. Following Penha-Lopes et al. (2009) the various sections of the cast were classified as a "chamber" when the actual diameter/burrow opening diameter ratio was higher or equal to 1.45, and as a "funnel" section if the ratio was smaller than this value.

2.3. Statistical analysis

Principal Component Analysis (PCA) was performed on the sediment texture and organic content dataset and the null hypothesis of no difference in granulometry and organic content among sites/belts was tested by means of a three-way mixed model PERMANOVA (Anderson, 2001), based on a similarity matrix computed using Euclidean distances. The design considered the following factors: locality (fixed and orthogonal), belts (fixed and orthogonal) and sub-areas (random and nested in belt). Organic matter data was in percentage values which were arcsin transformed.

Due to the distribution of the data, a four-way mixed model PERMANOVA was applied to analyze the Chl-a concentration dataset considering the following factors: tide (full moon vs. new moon spring tide, random and orthogonal), locality (fixed and orthogonal), belt (fixed and orthogonal) and unprocessed vs. processed sediment (fixed and orthogonal).

For the analyses of fiddler crab biomass and of the masses of feeding and digging pellets, a four-way mixed design ANOVA on $x' = \sqrt{(x+1)}$ transformed data was utilised, with tidal phases (fixed and orthogonal), locality (fixed and orthogonal), belt (fixed and orthogonal) and subarea (random and nested in belts) as factors. The transformation was applied after the homogeneity of variances was assessed using Cochran's test.

A one-way PERMANOVA, based on a similarity matrix created on Euclidean distances among samples of normalized data, was used to test the null hypothesis that there were no differences among sites/belts of three morphometric parameters (depth, surface–volume ratio, relative size of burrow chamber) measured on the burrow resin casts. Principal coordinates analysis (PCO, Torgerson, 1958) was performed, based on a similarity matrix of the Euclidean distances among samples, to visualize the relations among the samples. Pearson correlation indexes were computed among the scores of the samples on each PCO axis with the related values of each of the variables considered and the resulting vectors superimposed on the PCO plot.

Student–Newman–Keuls (SNK) tests were used for multiple comparisons of means after the ANOVA had found significant differences, while post hoc pair-wise tests were applied after PERMANOVA. All tests were performed using GMAV 5 program (University of Sydney, Australia), PRIMER v. 6.1 (Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER routines (Anderson et al., 2008).

3. Results

3.1. Environmental parameters

3.1.1. Sediment granulometry and organic content

The mixed model PERMANOVA revealed significant differences only between the sediment characteristic of Gazi and Mikindani (Pseudo-$F = 18.39$; df = 1; $p = 0.019$). In fact, the box plot in Fig. 2A shows that samples from Mikindani have both a higher median Φ value and a greater variability in grain sizes, with a higher amount of large particle sizes, when compared with those from Gazi.

Thus, samples from the two sites appear well discriminated on the first Principal Component (61.8% of variability explained) which together with PC2 account for 84% of dataset variability (Fig. 2B). Samples from Gazi were mostly distributed along the negative quadrant of the PC1 axis, while the Mikindani samples were clustered at the positive one. The linear coefficients linking the original variables to the principal components revealed that the Mikindani samples were richer in fine ($Ø < 63\ \mu m$; $63\ \mu m < Ø < 125\ \mu m$) and coarse sand fractions ($Ø > 1000\ \mu m$). Gazi instead presents grain sizes falling more uniformly in the sand domain ($250\ \mu m < Ø < 500\ \mu m$). Organic content of the sediment was very low, 1.25 ± 0.27% and 1.34 ± 0.95% for Gazi and Mikindani respectively, and did not discriminate between the sites.

3.1.2. Chlorophyll-a content of the sediment

The PERMANOVA mixed design did not find consistent differences in Chl-a content between sites and belts. However a significantly

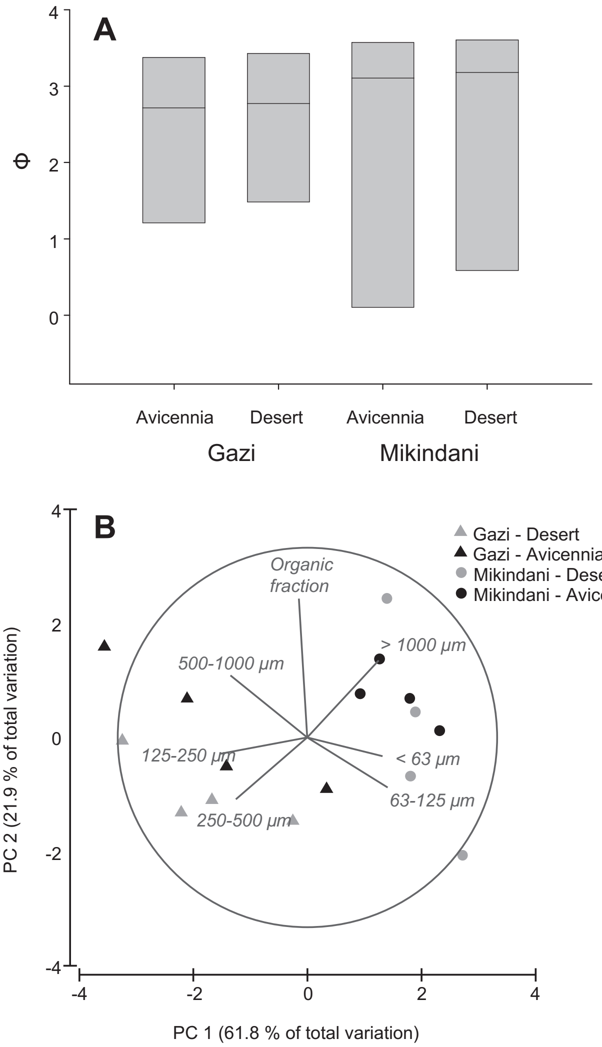

Fig. 2. Analyses of sediment characteristics at the *Avicennia* belts and desert areas, sampled at the peri-urban site of Mikindani and in the control mangrove forest at Gazi: (A) box plots constructed on the 25%ile and 75%ile values of Φ and its median values (lines internal to the boxes) and (B) two-dimensional scatter plot of the first and second principal components of sediment particle size and organic content. Vectors of the linear correlations with individual variables are superimposed on the graph.

higher content was found in the *Avicennia* belt of Mikindani during full moon tide (FMT) (interaction tide × belt, df = 1, pseudo-$F = 6.47$, $p = 0.013$; PERMANOVA test; Fig. 3). The FMT was characterized by high tide levels ranging only from 3.2 to 3.5 m, while the new moon tide (NMS) with higher tidal levels (3.4–3.7 m) showed no elevated Chl-a in the Mikindani desert belt (Fig. 3).

It is interesting that no differences were found in the Chl-a concentrations between pseudopellets and unprocessed sediment (3.25 ± 0.33 µg/g and 3.21 ± 0.39 µg/g, respectively), denoting an incomplete algal removal by fiddler crabs during the sorting activity, possibly followed by a subsequent re-growth of the phytobenthic populations within the pellets.

3.2. Crab bioturbation

3.2.1. Fiddler crab biomass and bioturbation

The presence of fiddler crabs in terms of dry biomass was always significantly greater in the *Avicennia* belt than in the desert belt at both localities (Fig. 4; Table 1, SNK test). A difference occurred between the *Avicennia* belts of the two sites as well, with the impacted one having greater crab presence. In contrast, there were few crabs in the desert belt at Gazi and no *Uca* specimens were collected sieving the soil of the sampling quadrats in the desert belt at Mikindani, although holes were present (Fig. 4).

The total mass of feeding pellets was much higher in Gazi where it was dependent on crab density (Table 1 and Fig. 4). This differs from the *Avicennia* belt of Mikindani where the bioturbation resulting from foraging activity was strongly depressed, despite the higher crab biomass (Fig. 4).

Although we could not sample any fiddler crab hiding in the burrows of the desert belt of Mikindani, the presence of few feeding pellets was recorded in the quadrats. These were most probably produced by the sporadic feeding activities of the large males observed wandering in droves into this area at the end of the low tide.

Regarding the bioturbation arising from burrow digging/maintenance, our data showed quite a high variability between the two temporal replicates so that no clear pattern emerged (Table 1).

3.2.2. Burrow casts

The burrow casts collected are not a complete set from all the ecological conditions studied because the characteristics of the sediment did not allow us to properly extract the casts at the *Avicennia* belt of Mikindani. Therefore only partial comparisons between the two sites were possible.

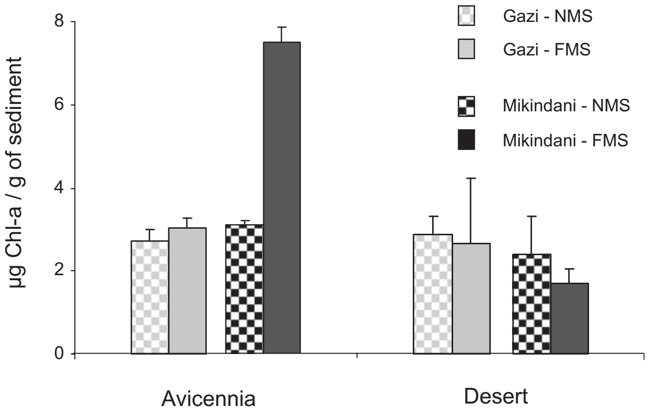

Fig. 3. Sediment Chlorophyll-a concentration for different site-zone conditions. NMS: New Moon Spring tide; FMS: Full Moon Spring tide. Error bars indicate SE.

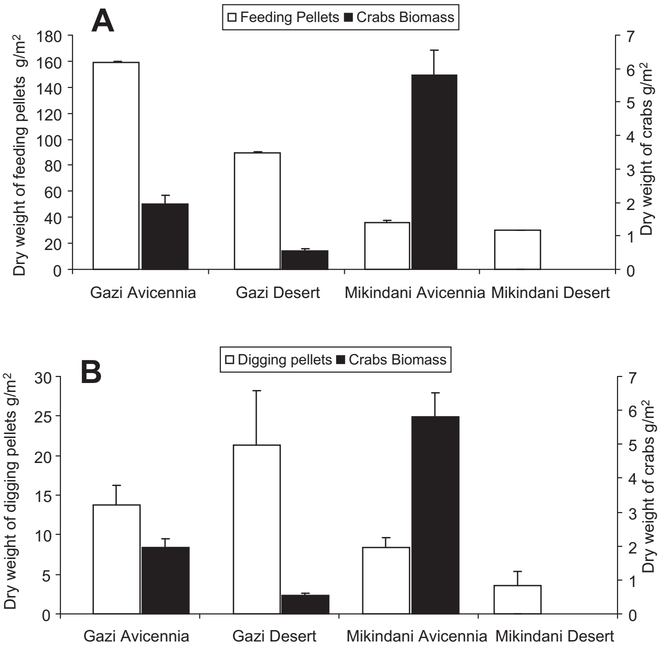

Fig. 4. Average *U. inversa* and *U. annulipes* dry weight biomass matched with average total feeding pseudopellets (A) and total burrow-maintenance pellets (B) produced for the different ecological conditions and localities studied. Error bars indicate SE.

Burrow structure was variable and quite different from the structure characterized by a bent funnel and a terminal sub-horizontal chamber observed by Lim and Diong (2003) for *U. annulipes* populations from Singapore (Fig. 5). The variations in general structure were numerous, particularly in the *Avicennia* zone of Gazi, where the funnel/terminal chamber scheme was difficult to detect and two-branched burrows or shelters with composite structures, consecutive funnel 1–chamber 1–funnel 2–chamber 2, were observed.

The general morphology of burrows at the different locations shows that the volumetric fraction of funnels was larger (60–80%) that that of chambers (Fig. 6). One-way PERMANOVA performed on three crab burrow parameters (% of chamber volume, depth,

Table 1
Results of 4-way ANOVAs for $\sqrt(x+1)$ transformed fiddler crab biomasses, feeding pseudopellets and digging pseudopellets. The factors are: Locality (two levels: Gazi, Mikindani), orthogonal and fixed, Belt (two levels: *Avicennia* belt, desert belt), orthogonal and fixed, Area (two levels), nested in Belt and random, Tide (two levels: full moon spring tide, new moon spring tide), orthogonal and fixed. The degrees of freedom, DF, variance, MS, and value of *F* ratio are shown. Number of replicates: $n = 2$.

Factors	DF	Crab biomass		Feeding pellets DW		Digging pellets DW	
		MS	*F*	MS	*F*	MS	*F*
Locality – loc	1	0.808	18.95*	233.766	70.650*	3.113	3.160
Belt – be	1	8.232	75.28*	35.932	5.860	7.351	8.850
Area (be) – ar	2	0.109	1.72	6.131	0.810	0.831	0.720
Tide – ti	1	0.520	6.70	28.885	1.510	8.167	14.650
loc × be	1	2.323	54.48*	6.978	2.110	0.377	0.380
loc × ar (be)	2	0.043	0.67	3.309	0.440	0.985	0.850
loc × ti	1	0.223	1.24	6.772	0.580	1.599	8.500
be × ti	1	0.808	10.41	0.161	0.010	0.101	0.180
ti × ar (be)	2	0.078	1.22	19.096	2.520	0.558	0.480
loc × be × ti	1	0.087	0.48	12.309	1.060	5.830	31.000*
ti × loc × ar (be)	2	0.179	2.82	11.619	1.530	0.188	0.160
RES	16	0.064		7.593		1.158	
TOT	31						

*$0.05 < p < 0.01$.

surface–volume ratio) found strong differences (pseudo-$F = 5.9447$, $\mathrm{df} = 2$, $p < 0.001$; PERMANOVA test) among the three different site-belt conditions studied (Gazi Avicennia belt, Gazi desert and Mikindani desert). In particular the pair-wise tests showed statistically significant differences for every comparison.

The two-dimensional scatter plot of principle coordinates (Fig. 7) shows that burrows from desert belt of Gazi were generally very shallow (see Fig. 5). In fact these samples are mostly distributed on the positive side of the PCO1 (56.9% of total variation explained) which is inversely correlated with burrow depth ($r = -0.83$). Furthermore, the samples from the desert belt at both sites appear to be distributed mostly on the negative portion of the PCO2 axis (28.1% of total variation explained) which is directly correlated with the relative proportion of burrow chamber ($r = 0.83$). This indicates an overall less cylindrical shape for the casts from the Avicennia belt of Gazi, which are more structured into a chambers and funnels system.

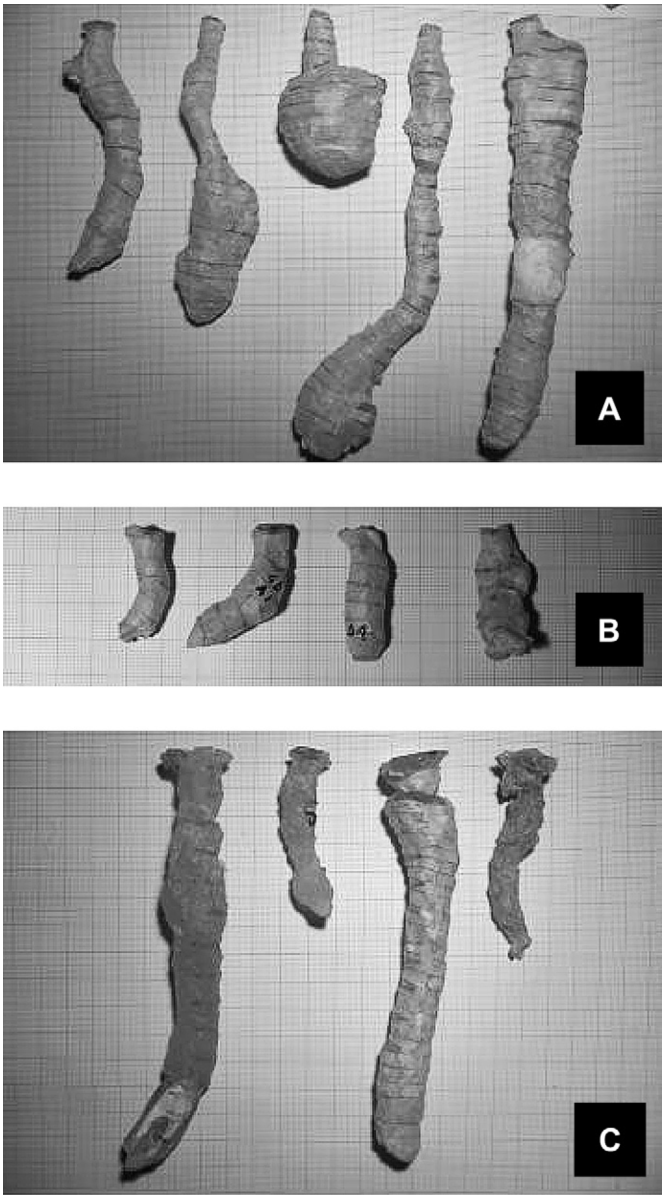

Fig. 5. Photographs of some of the burrow casts collected at the two sites and ecological conditions: A), Gazi *Avicennia* belt; B), Gazi desert belt; C), Mikindani desert belt.

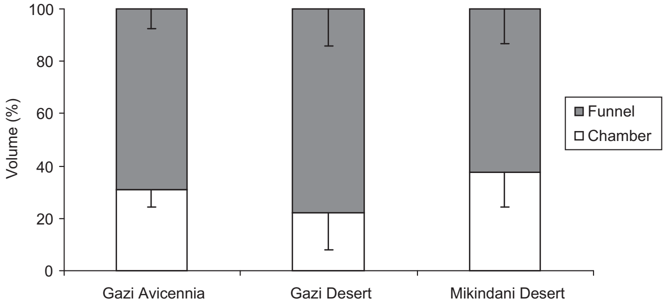

Fig. 6. Volumetric percentage of the two structural elements, funnel and chamber, that constitute the fiddler crab burrow. Gazi *Avicennia* belt, $n = 25$; Gazi desert belt, $n = 6$; Mikindani desert belt $n = 10$. Error bars indicate SE.

4. Discussion

The present study revealed two clear ecological patterns, which are of great relevance for the clarification of subtle but significant modification of relations among factors in human impacted mangrove areas. Firstly, the *Avicennia* belt at Mikindani has highest crab biomass, confirming the trends found by Cannicci et al. (2009) for East Africa. However, this increase in biomass was detected only in the vegetated areas near sewage outfalls, while in the desert belt affected by tree chopping, crabs were virtually absent. Secondly, a reduced production of feeding pellets was observed at the sewage affected Mikindani *Avicennia* belt, in contrast with the biomass trend. However, the present set of data also showed that sewage loading and tree chopping activities were not the sole ecological differences between the two study sites.

We also found differences in sediment texture between the two localities which was attributable to human impact. In fact, we found a bimodal distribution of granulometric classes, with a conspicuous presence of both coarse and fine particles at Mikindani, that Mohamed (2008) explained with the inland runoff due to agricultural practices. However, such a modification in granulometry cannot explain the enhanced crab biomass of the two *Uca* species. Moreover, because these species are specialised in sorting sandy particles (Icely and Jones, 1978), the presence of both fine and coarse sands would decrease their sorting efficiency, thus potentially causing an enhancement of feeding pellets production.

The large nutrient input at Mikindani would be expected to enhance the growth of microbenthic algae at this site (Tam, 1998). Although the Chl-a content of the sediment can only partially detect the actual algal growth, we found, during full moon tide, a peak of about 7.2 μg/g of Chl-a at Mikindani, which was never reached at the pristine site. However, a high degree of variability in Chl-a content of the sediment was found across time and sites, possibly due to quantitative and/or qualitative temporal differences in sewage outflow over time and to the dilution of the sewage by the tidal cycle. Further investigations and an increased number of replicates would help draw a more exhaustive picture of the effective biogeochemical dynamics caused by sewage contamination.

Our data suggest that the artificial nutrient enrichment of the Mikindani mangrove forest may result in an overgrowth of microalgae and bacteria, as demonstrated by several other studies (e.g. Meziane and Tsuchiya, 2002). These micro-organisms are known to be the main food source for fiddler crabs (Meziane et al., 2002) and their increase in biomass would result in the larger *Uca* populations observed at Mikindani with respect to Gazi.

The reduced feeding pellet production observed at Mikindani could be related to the enhancement in primary productivity. Although the peaks of a Chl-a recorded at Mikindani were not consistent through our temporal replicates, they suggest that the

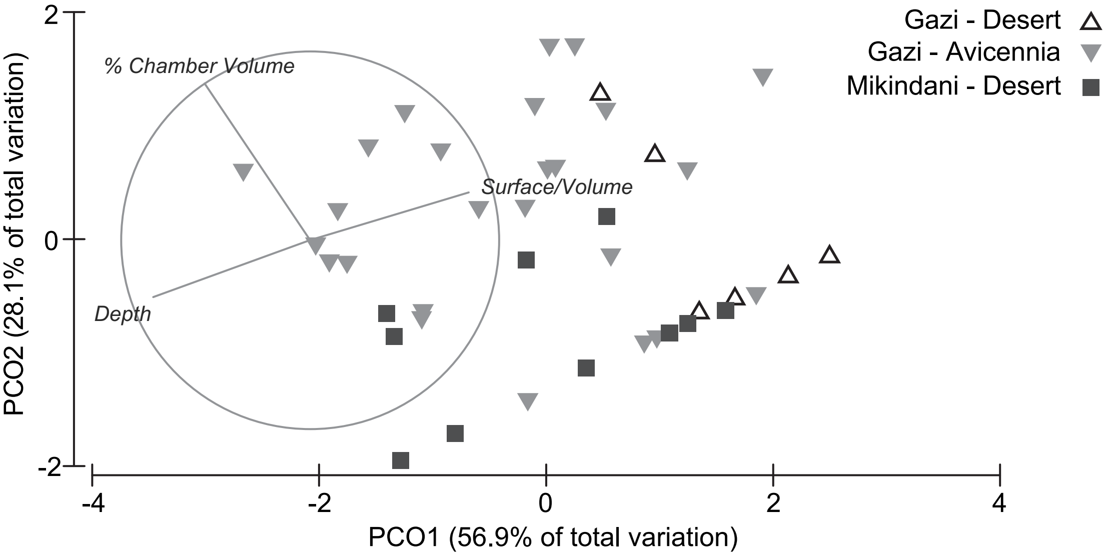

Fig. 7. Two-dimensional scatter plot of first and second principal coordinates axis of three morphometric parameters measured on crab burrow resin casts collected in the desert belts at Gazi and Mikindani and in the *Avicennia* belt at Gazi.

observed smaller pseudopellets production was a consequence of a large amount of trophic availability. Such a link appears quite reasonable when considering the results obtained by other authors. In fact, recently, Penha-Lopes et al. (2009) observed a similar reduction of feeding pellets production in mesocosms treated with sewage, in association with a strong enhancement of sediment Chl-a concentration.

Indeed, the surface activity of East African fiddler crabs is carried out during restricted intervals of time, represented by the diurnal low tides. During these favourable intervals, crabs exit their burrows and start a sequence of activities articulated in a clear hierarchical temporal series (see Eshky et al., 1995). Foraging is the main activity during the first hours (see Eshky et al., 1995; Weis and Weis, 2004) but its duration is related to the food availability (Bartolini et al., 2009), which in turn directly affects the amount of processed sediment. If *Uca* species are characterized by a maximum total intake per foraging interval, low amounts of processed sediment are expected whenever the concentrations of micro-organisms per unit of sediment volume increase. In such a scenario, an apparent positive effect of sewage dumping on the ecosystem, in terms of fiddler crabs abundance and biomass can hide an indirect, possibly negative, effect on the ecosystem functionality, through the reduction of the crabs sediment reworking activities, which proved to be beneficial for mangrove systems.

Another surprising result of this study is the similar Chl-a concentrations found in the feeding pseudopellets processed by the fiddler crabs and in the unprocessed sediment. Since the pseudopellets were collected only a few hours after their production, we may assume a natural and rapid re-growth of microalgae in pellets soon after the fiddler crabs' sorting activity. Anyway, sorting seems not to be highly efficient, as suggested by Icely and Jones (1978), at least not in terms of a complete removal of algal cells. Such a low sorting efficiency was, however, sufficient to allow all fiddler crabs reaching their maximum food intake capacity. The reduced amount of processed sediment by the crabs at Mikindani, in fact, shows that they did not feed *ad libitum* but simply stopped when they were satiated (Bartolini et al., 2009). A stimulating evolutionary hypothesis of this apparently low efficiency is that *Uca* spp. only partially deplete the microbenthic flora in the proximity of their burrows, in order to stimulate a fast recovery. Since the fiddler crabs are central place foragers (see Zeil et al., 2006), an almost total depletion of the algal biomass could, in fact, result in two scenarios. In the first scenario, crabs would be forced to feed progressively more distant from the burrow, with a high risk of predation and/or of burrow usurpation (Cannicci et al., 1999), and this is a possible explanation for the wandering behaviour performed by a minority of large males at the end of the low tide. The second result of a total algal depletion would be to permanently move to other areas, with the consequent risks and high costs of digging new burrows. Since the great majority of the fiddler crabs belonging to the studied populations remain within a few centimetres from their burrow through the entire tidal cycle, a sort of 'gardening' behaviour, i.e. an incomplete microalgae harvesting propitious to algal re-growth, would be an evolutionary stable strategy, providing that the food obtained is sufficient for the crab's requirements. Further studies are certainly needed to corroborate this intriguing hypothesis.

Feeding is not the only bioturbation activity performed by the crabs, since they also construct burrows and thus potentially the biogeochemistry of the top 10 cm of sediment (see Lim and Diong, 2003). However, in the present study the amount of pellets produced as a consequence of burrow maintenance showed a considerable heterogeneity among temporal replicates and sites, providing no supporting evidence of sewage effects.

Burrow structures were different from those observed by Lim and Diong (2003) for *U. annulipes* populations from Singapore. Moreover, burrows in the desert belt at Gazi, were shallower then those in the adjacent *Avicennia* area. We therefore hypothesise that these burrows could be temporary shelters dug to hide from the incipient high tide and used for only one or a few days. This hypothesis is confirmed by the low *Uca* spp. biomasses excavated from the Gazi desert area, that suggest that most of the crabs observed feeding in droves returned to their burrows in the neighbouring *Avicennia* zone. On the contrary, in the corresponding ecological condition at Mikindani we found burrows comparable to those observed in the *Avicennia* belt of Gazi (Mikindani desert, 10.6 ± 3.3 cm; Gazi *Avicennia*, 7.2 ± 3.8 cm) and corresponding to the average natural *U. annulipes* burrow depth (see Lim and Diong, 2003). However, the fact that no crabs were found in those burrows account of a temporary use of them, just like the one hypothesised for the desert belt of Gazi. The meaning of this difference could reside in the diverse origin of the two desert areas considered in the present study. At Mikindani, the desert areas have arisen *de facto* from the heavy wood extraction activities of the last four decades (Mohamed et al., 2008). From an environmental point of view, therefore, these areas can be seen as denuded *Avicennia* belts and not as natural salty tidal plains which is the case of those in the area studied at Gazi. Consequently, the presence of underground roots, stems and pneumatophores as residuals of recent chopping in the Mikindani area would explain the greater depth of the crab burrows (see Lim and Rosiah, 2007).

5. Conclusions

The present results support at least two interesting hypotheses, which are relevant for peri-urban mangrove areas management and rehabilitation, as well as in relation to the proposed potential use of mangrove forests as phytoremediating systems (Yang et al., 2008). At the present level of nutrient loading at Mikindani, a positive effect was evident in terms of fiddler crab population increase, but this effect masks a subtle indirect negative effect on the ecosystem functionality in the form of a reduction in the bioturbation activity, as a result of a decrease in the foraging activity of the crabs. In other words, there would be a contaminant-induced modification of the engineering role of the crabs which, by lowering their bioturbation activity, would stop the mixing of the first millimetres of sediment, that prove to be very important for mangrove seedlings (see Kristensen and Alongi, 2006). Indeed, this is another example of the concept of ‘cryptic ecological degradation’ *sensu* Dahdouh-Guebas et al. (2005). These authors originally pointed to ecological degradation (a loss of functional mangrove species) that is masked by an expansion of less important (less functional) semi-terrestrial species. Likewise, here, loss of bioturbation implies an ecological degradation, which is, however, masked by an increase in the size of the fiddler crab population.

In the long run, the modification of the engineering role of the crabs that we have shown, could presumably lower the sediment mixing and consequent oxidation. The results of this process will obviously be mangrove distress and an overgrowth of dense algal mats which can produce anoxic conditions in the environment (see Kristensen and Alongi, 2006). Thus, it is of utmost importance for the future, to concentrate efforts toward understanding how such ecological processes are triggered and to focus attention on the global effect they can exert on ecosystem dynamics. Further data are needed, for example, to test the effect of sewage exposure on mangrove propagule recruitment and survival over longer temporal intervals, as well as on the dynamics of macrobenthic communities and the fecundity of engineer species.

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