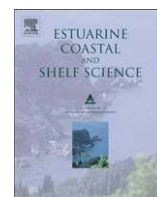




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Effects of urban wastewater on crab and mollusc assemblages in equatorial and subtropical mangroves of East Africa

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ABSTRACT

Mangrove forests are known to accomplish crucial ecosystem functions and services. They are nursery areas for fish, prawns and crabs, which provide coastal communities with a variety of food, timber and chemicals, and protect coasts from catastrophic events, such as tsunamis. Recently, a novel ecological service has been proposed for mangrove systems, namely natural wastewater treatment wetlands. This hypothesis was based on experimental data collected mainly in Chinese mangrove systems, which proved that mangrove soils were efficient in absorbing nutrients. Moreover, sewage loading seemed harmless to both plants and benthic communities in these systems. However, before promoting the use of natural mangroves as pollution buffers, or constructed mangrove wetlands as sewage treatment facilities, more data are needed on their overall tolerance to organic loading. Differences in macrobenthos patterns were thus investigated between peri-urban mangroves and sites not affected by sewage disposal in East Africa. We assessed differences in epifaunal assemblages, comprising crabs and molluscs, employing multivariate ACI unbalanced analyses to compare peri-urban mangrove swamps with those characteristic of non-urban mangroves with similar ecological traits. The sampling design was spatially nested, replicates being assessed at equatorial (southern Kenya) and subtropical (southern Mozambique) sites. The results manifested a consistent increase in crab biomass at the peri-urban sites in both Kenya and Mozambique. Moreover, the peri-urban systems were richer than the non-urban mangroves, both in terms of fiddler crabs (*Uca* spp.) which feed on benthic microalgae and bacteria, and sesamids, such as *Perisesarma guttatum* and *Neosarmatium meinerti*, which feed on both substratum and leaf litter. The abundance of gastropods, in contrast, decreased significantly, especially in Kenya, mainly due to the disappearance of the mud whelk *Terebralia palustris*. The results thus indicate that, in East African mangrove systems, domestic wastewater has detectable effects on crabs and molluscs, suggesting their usefulness as bioindicators of its effects in mangroves. Transformed benthic patterns at the peri-urban sites indicated the need for further study of the actual potential of natural mangrove forests to absorb pollution in sewage treatment.

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1. Introduction

Mangrove forests accomplish a number of ecosystem functions and services (Duke et al., 2007). Rates of net primary production in mangrove forests are the highest of any ecosystem ($> 2 \text{ t ha}^{-1} \text{ yr}^{-1}$), and vast amounts of carbon accumulate within their underlying litter (Alongi, 1998; Chmura et al., 2003). As a result, they play a key

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role in nutrient cycling in coastal ecosystems and global carbon cycling, and have been demonstrated to act both as nutrient sources and sinks (Kristensen et al., 2008). Carbon cycling and other ecosystem processes in mangroves provide crucial ecosystem services to estuarine habitats such as nursery areas for fish, prawns and crabs (Sheridan and Hays, 2003; Crona and Rönnbäck, 2005; Nagelkerken et al., 2008). Coastal human communities which live near mangrove areas also rely on the provision of a variety of food, timber, chemicals and medicines derived from mangrove forests (Ewel et al., 1998; Glaser, 2003; Walters et al., 2008). Their ecological function in coastal protection was demonstrated in the 2004 tsunami when mangroves in good ecological condition proved effective in this regard (Dahdouh-Guebas et al., 2005; Kathiresan and Rajendran, 2005). Last but not least, mangroves host a unique set of associated fauna, such as semi-terrestrial and tree-dwelling brachyuran crabs (Fratini et al., 2005; Cannicci et al., 2008) and insects (Cannicci et al., 2008), and, within soft-sediment habitats, they provide a unique hard-sediment substratum needed for a unique and diverse assemblage of benthos (Farnsworth and Ellison, 1996).

Apart from the above, some researchers have suggested that they have potential as natural wastewater treatment areas, a much-debated subject (Clough et al., 1983; Wong et al., 1995, 1997). Mangrove ecosystems and, in particular, their sediments are very efficient in absorbing nutrients, mainly phosphorous and nitrogen, derived from sewage (Tam and Wong, 1995, 1996a, b) and shrimp farming effluent (Trott et al., 2004). Moreover, in a field trial of two years in the Funtian Mangrove, P.R.C., Wong et al. (1997) found that sewage disposal had no harmful effect on the higher plant communities. Yu et al. (1997) detected no significant effects of wastewater on benthic biomass, density and community structure at the same experimental site, although they measured a significant decrease in the diversity and biomass of gastropods and interpreted this as a transient phenomenon followed by a recovery phase.

Although these studies of Chinese mangroves may suggest that they are tolerant to a degree of wastewater pollution, much concern still exists about the use of natural mangrove sites for sewage disposal. Kathiresan and Bingham (2001) suggest that the results obtained at Funtian Mangrove may not be applicable to other sites, since Indo-Pacific mangrove forests differ widely and their unique characteristics may lead to differences in tolerance to this perturbation. A second reason for caution relates to the effects of such organic loading on other crucial ecosystem processes and services provided by mangroves, such as the aforementioned functions as nursery grounds and a source of resources for coastal communities (Hogarth, 2007). The recent, extensive research on the use of constructed mangroves as wetlands for domestic wastewater treatment (Yang et al., 2008) could lead to the use of natural mangroves, which are being increasingly threatened by human activities, for this purpose.

The literature on the effects of sewage and peri-urban effluents on the faunal components of other shallow water ecosystems is not encouraging. In fact, although faunal assemblages in mangroves vary considerably spatially, which often confounds the results (Lindgarth and Hoskin, 2001; Chapman and Tolhurst, 2004), the macrofaunal distribution and diversity in peri-urban coastal systems have proven susceptible to a variety of pollutants and impacts, such as metals (Birch, 1996; Bergey and Weiss, 2008), pesticides (Garmouma et al., 1998), hydrocarbons (Siewicki, 1997; Inglis and Kross, 2000) and altered nutrient loads (Carpenter et al., 1998). Although it is often difficult to disentangle the specific effects of these many causes of disturbance, sewage disposal is surely one of the major causes of diversity loss in intertidal (Lercari and Defeo, 2003; Wear and Tanner,

2007) and subtidal coastal ecosystems (Roberts, 1996; Roberts et al., 1998). It appears difficult to hypothesise that wastewater dumping would not result in major changes in mangrove macrofauna.

Based on this background of concerns, the present study was designed to investigate the differences in macrobenthic patterns between peri-urban mangroves, impacted by sewage disposal, and non-urban sites with no evident wastewater disposal, in East Africa. We focused on key macrobenthic species, such as brachyuran crabs and molluscs that are heavily exposed to such perturbation, being strict residents of mangroves throughout their adult life (Skov et al., 2002; Fratini et al., 2004) that ingest sediment and leaf litter (Cannicci et al., 2008).

2. Methods

2.1. Study area and sampling design

To assess possible impacts of sewage on crab and mollusc assemblages, a multivariate ACI (After Control/Impact, Underwood, 1992, 1994) unbalanced design was followed, comparing the macrofaunal patterns found in a peri-urban mangrove swamp with those characteristic of two non-urban mangroves showing similar ecological traits. The unbalanced ACI sampling design was spatially replicated at equatorial (southern Kenya) and subtropical (southern Mozambique) sites. The mangroves selected for the study manifested distinctive zonation patterns in the dominance of their mangrove species, maintained by associated faunal assemblages (Macnae, 1968; Jones, 1984; Hartnoll et al., 2002; Skov et al., 2002; Dahdouh-Guebas et al., 2002). Thus, at each site, a stratified random sampling approach was applied. Two belts were considered: a landward sandy belt dominated by *Avicennia marina* (Forssk.) Vierh. trees, representing the zone flooded only during spring tides (hereafter the *Avicennia* belt); and a seaward muddy belt dominated by *Rhizophora mucronata* Lam. trees, flooded twice a day during high tides (hereafter the *Rhizophora* belt). At the Costa do Sol site (southern Mozambique) there is one wide *A. marina*-dominated area and, therefore only this belt was considered, comparing it with the corresponding *Avicennia* belts at the Mozambican control sites.

2.1.1. Kenya

All Kenyan sites were along its southern coast (Fig. 1). The impacted site was Mikindani, located on the banks of Tudor creek, within Mombasa harbour, while the two control, i.e. non-urban, sites were the mangroves of Gazi Bay, 47 km South of Mombasa (39°30' E, 4°22' S), and Shirazi Creek, 12 km South of Gazi Bay and about 60 km from Mombasa (39°25' E, 4°31' S). Although the geographical position of the two controls was not optimal for environmental monitoring (see Underwood, 1992, 1994), being south of the peri-urban site, they were selected because they were the most similar to the impacted site from an ecological point of view.

2.1.1.1. Gazi. Gazi Bay is a shallow water creek open to the Indian Ocean from the south and receives the inflow of two seasonal rivers, the Kidogoweni and the Kinondo. It is flooded twice a day to a maximum tidal height of about 4 m. The mangrove forest surrounding the bay is approximately 6 km² wide. All mangrove trees species found in East Africa are present: *Avicennia marina*, *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Rhizophora mucronata*, *Sonneratia alba* Sm., *Xylocarpus granatum* Koen and *Xylocarpus moluccensis* (Lamk.) Roem and the rare *Pemphis acidula* Forst.

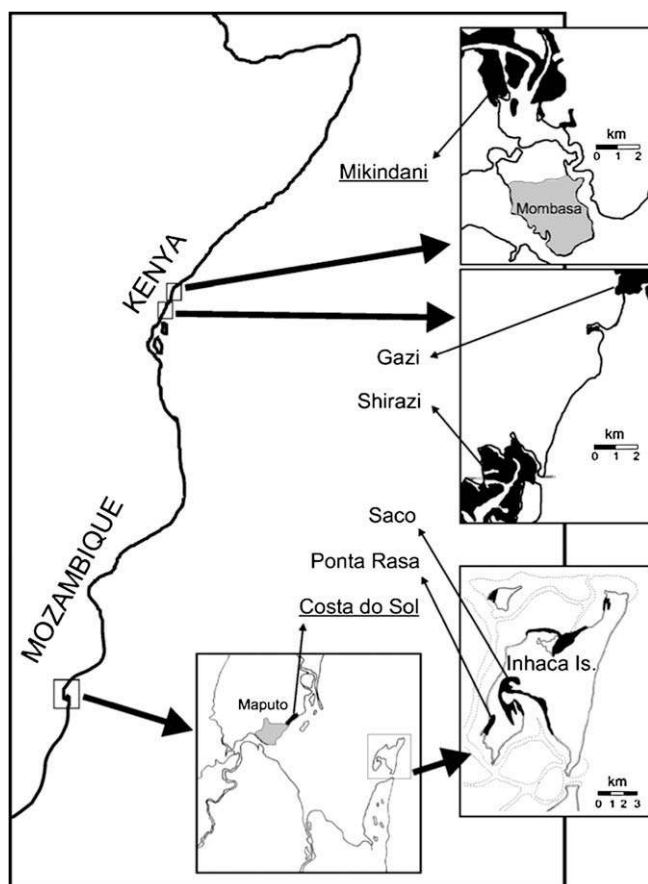


Fig. 1. Map of sampling locations along the East African coast. Underlined locations indicate peri-urban sites; mangroves are represented by the dark areas.

2.1.1.2. Shirazi. This mangrove swamp is located within the Funzi-Shirazi creek, where the Ramisi and Mwena Rivers enter the system through the Mamuja and Vikurani Creeks, respectively. The maximum tidal height is similar to the one recorded in Gazi and all the East African mangrove tree species are also present, with the exception of *P. acidula*.

2.1.1.3. Mikindani. This mangrove system is located within Tudor Creek, which surrounds the city of Mombasa, and has been exposed to sewage from both the Mikindani residential estate and Mombasa wastewater (Kitheka et al., 2003; Mohamed et al., 2008) for more than a decade. The sewage runs through the mangrove forest in canals, affecting the landward zone first which is dominated by *Avicennia marina*, and then flowing through the seaward *Rhizophora mucronata*-dominated belt to finally reach Tudor Creek. Mangroves here are flooded by sewage every tidal cycle and the loading is reduced exponentially with distance from source (Kitheka et al., 2003; Mohamed, 2008; Mohamed et al., 2008). About 1200 kg of nitrogen and 5.5 kg of phosphorous are discharged via sewage into the Mikindani system every day (Mohamed et al., 2008). Although this site is strongly dominated by *A. marina* and *Rhizophora mucronata* (a typical feature of Kenyan mangrove forests), all other East African mangrove species are present, with the exception of *Heritiera littoralis* and *Pemphis acidula*.

2.1.2. Mozambique

Sampling was conducted in three mangrove systems in the Maputo Bay area, in southern Mozambique. The peri-urban

mangrove, Costa do Sol, borders Maputo city (25°55' S, 32°35' E), on the mainland, while the two control sites, Saco and Ponta Rasa, are on Inhaca Island (26° S, 32°55' E). This island is located only 200 m from the northernmost tip of the Machangulo peninsula, which encircles Maputo Bay, and thus has the same physico-biological characteristics of the mainland surrounding Maputo Bay (Kalk, 1995) (Fig. 1). Thus, all these mangroves are located in a transitional region with a tropical to warm subtropical climate, characterised by a hot and rainy (September–March) and a warm and dry (April–August) season (Kalk, 1995). The only mangrove trees present in southern Mozambique are *Avicennia marina*, *Rhizophora mucronata*, *Bruguiera gymnorrhiza* and *Ceriops tagal* (Beentje and Bandeira, 2007).

2.1.2.1. Inhaca. Inhaca is located about 32 km east of Maputo. The maximum tidal amplitude is approximately 3.7 m. No rivers are present on the island, but there is a diffused and constant groundwater supply of freshwater to the mangrove systems, and the salinity decreases to around 30 in the surrounding water mass during the wet season (Paula et al., 1998). There are few human communities in the southern part of the island, and the absence of any domestic or industrial effluents contributes to the preservation of relatively pristine conditions compared to those around Maputo (Kalk, 1995; Omodei Zorini et al., 2004).

The Saco mangrove covers an area of 2.1 km² and is located in a small, enclosed and shallow bay in the south of the island (Fig. 1). *Avicennia marina* and *Rhizophora mucronata* dominate its vegetation (Kalk, 1995).

Ponta Rasa is the smallest mangrove system on the island, covering about 0.2 km², and is located on the southwest coast facing Maputo Bay (Fig. 1). The creek is dominated by *Rhizophora mucronata*, with sparser patches of *Ceriops tagal*, *Bruguiera gymnorrhiza* and *Avicennia marina* (Paula et al., 2003). Ponta Rasa has unique characteristics such as closure during neap tide due to the presence of a sill at the entrance of the creek, very sandy soils and a lower sediment fauna diversity and abundance than the Saco mangroves, but the same diversity in terms of the macrofaunal species (Kalk, 1995; Guerreiro et al., 1996).

2.1.2.2. Costa do Sol. This mangrove is characterised by a small and shallow seawater swamp located about 7 km North of the Maputo city centre, with a maximum tidal amplitude of about 3.5 m (Litulo, 2005). The seasonal river Quinhenganine discharges into the swamp after crossing the city. *Avicennia marina* and small patches of *Rhizophora mucronata* dominate its vegetation (Litulo, 2005; PUMPSEA, 2007). The system borders with a residential area which is now a part of the Maputo urban limits, and it has been receiving domestic sewage, aquaculture residues and solid waste of various sources over the last decades (PUMPSEA, 2007; Crona et al., 2009). Concentrations of nutrients, especially nitrates and nitrites, are significantly higher at Costa do Sol than at Saco and Ponta Rasa mangroves (Salvador, 2007; PUMPSEA, 2008).

2.2. Sampling methods

2.2.1. Sampling of natural assemblages

Two random transects (100–500 m apart) were selected in each of the two vegetation belts at each site following a nested design. In each transect, five 2 × 2 m quadrats were randomly sampled to assess the abundance and densities of the brachyuran and molluscan populations. At the peri-urban sites, care was taken to locate the transects close to the sewage dumping channels to obtain data on areas directly affected by the wastewater. The study was performed twice (factor “Time” in the analyses): a dry season in October 2005 in Kenya and in July–August 2005 in Mozambique,

Table 1
Results of the four-way PERMANOVA conducted on square root-transformed abundance data of 13 species of crabs and molluscs recorded at the three Kenyan sites.

Source	DF	Avicennia belt		Rhizophora belt	
		MS	F	MS	F
Time	1	3950.1	5.3*	13282.0	10.5**
Impact vs Controls	1	27,503.0	0.8	4414.7	0.3
Site (I vs C)	1	29,606.0	65.2**	14,720.0	16.8**
Time × I vs C	1	3938.2	5.3*	2114.0	1.7
Transect (site (I vs C))	3	454.1	0.6	876.9	0.7
Time × transect (site (I vs C))	3	746.6	1.2	1260.8	1.9
Res	49	616.3		680.8	
Total	59				

* $p < 0.05$; ** $p < 0.01$.

and a wet season in April 2006 in Kenya and in February 2006 in Mozambique.

Due to the complexity of the habitat and the differing behaviour of the study species, different sampling techniques were used to assess the abundances of the various groups of macrofauna:

(a) Molluscs: mainly represented by the gastropods *Terebralia palustris* (Fratini et al., 2004) and *Cerithidea decollata* (Vannini et al., 2006), and the oyster *Saccostrea cucullata* attached to the aerial roots of mangrove trees. Specimens were counted in the sampling quadrat.

(b) Fiddler crabs (genus *Uca*): represented by four species, *Uca annulipes*, *Uca inversa*, *Uca chlorophthalmus* and *Uca urvillei*. Following the suggestions of various authors (Nobbs and McGuinness, 1999; Macia et al., 2001; Skov et al., 2002), individuals were first counted visually at each site to assess the frequency of the different populations present in the quadrat. Secondly, crab burrows were counted in five random 50 × 50 cm subquadrats to avoid underestimation of specimens not active on the surface during the visual crab counts. The density of each species was estimated from the burrow counting data, calibrated with the species ratio obtained from the visual counting.

(c) Small sesamids: represented by *Chiromantes ortmanni*, *Chiromantes eulimene*, *Perisesarma guttatum*, *Parasesarma catenata*, *Parasesarma leptosoma*. These crabs were counted visually throughout the quadrat.

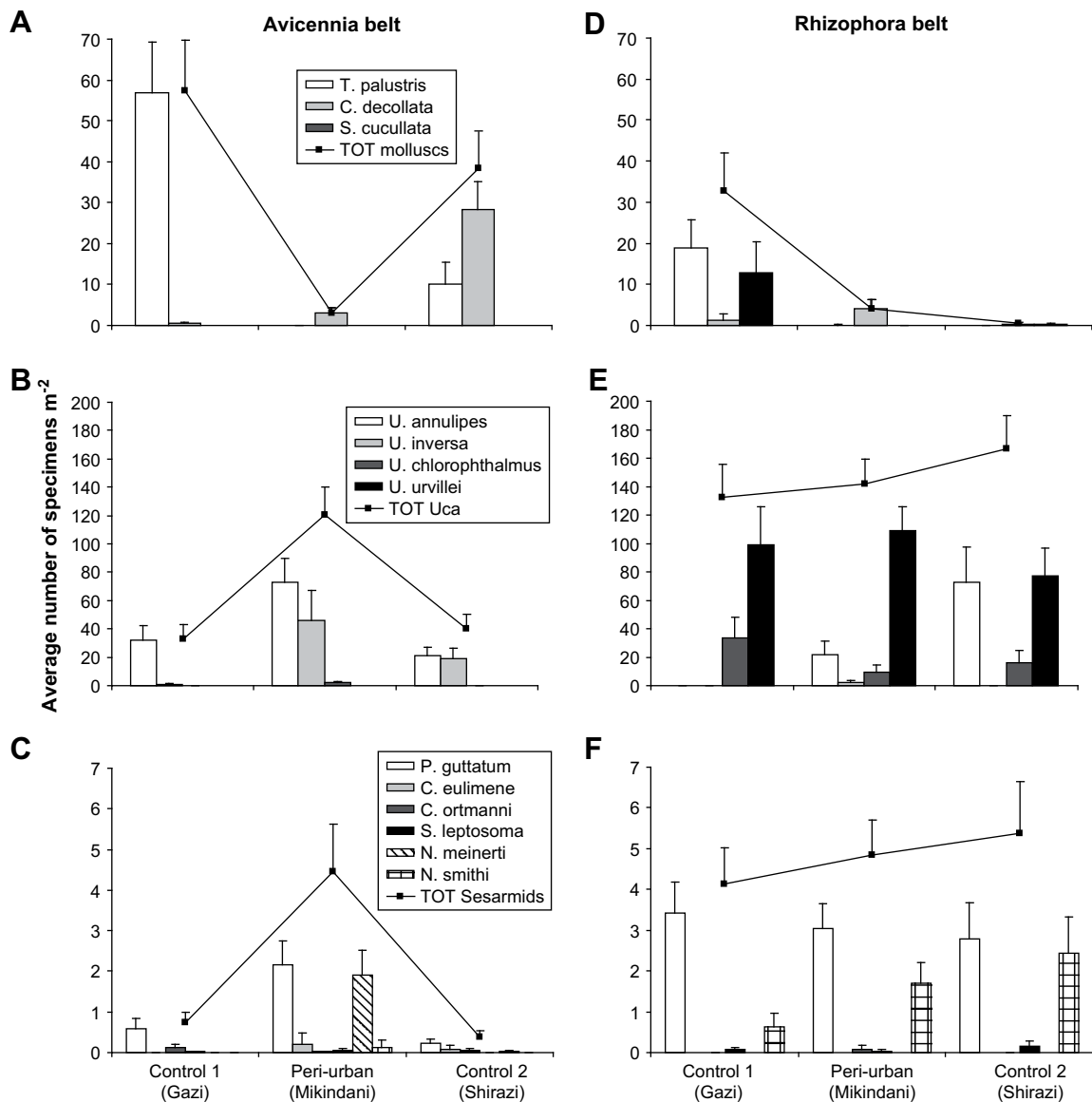


Fig. 2. Average abundance (±SE) of the most common species of molluscs (A and D), crabs of the genus *Uca* (B and E) and of the Sesamidae family (C and F) recorded in the *Avicennia* and *Rhizophora* belts at the three Kenyan sampling sites.

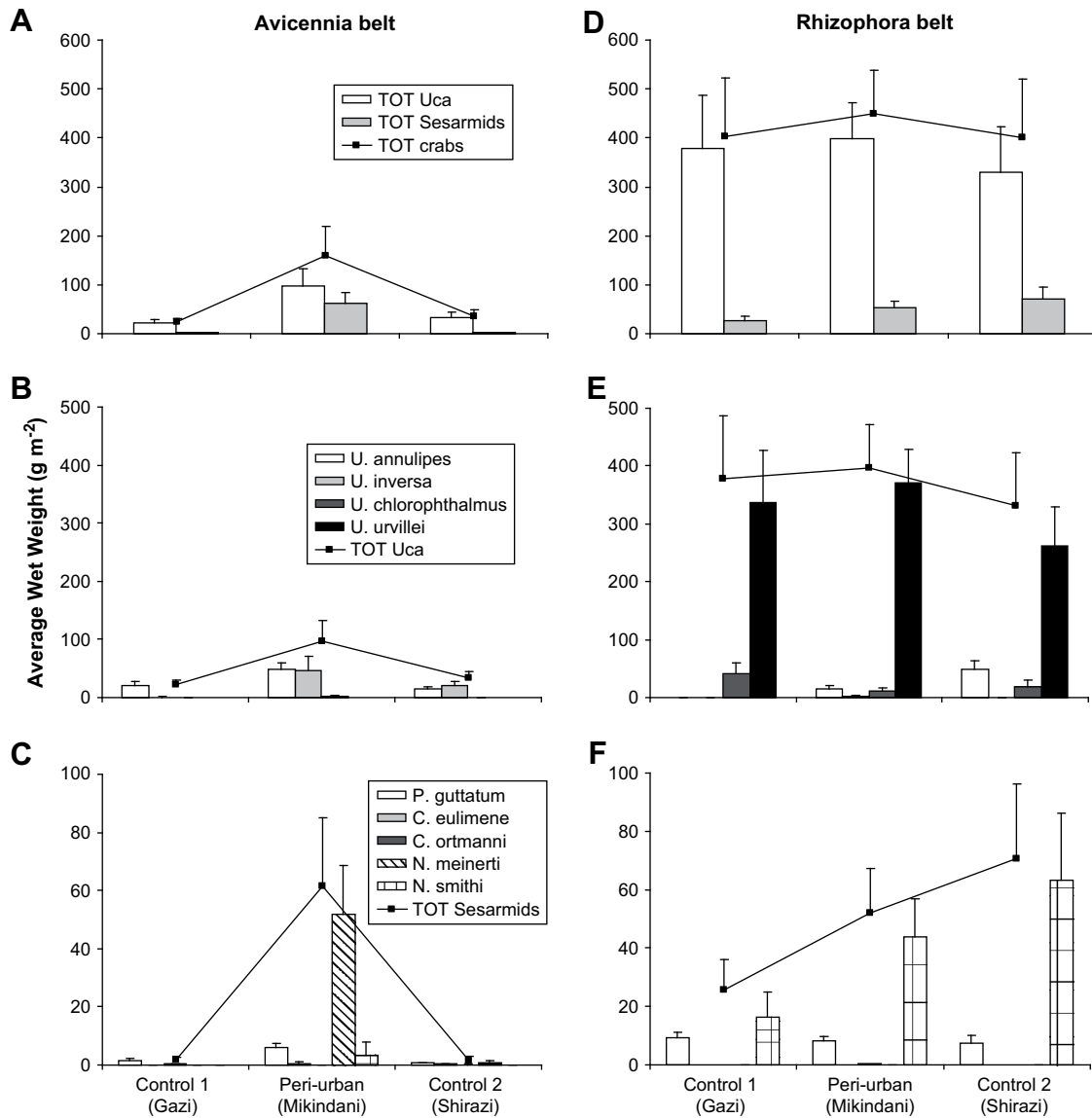


Fig. 3. Average biomass (expressed as Wet Weight \pm SE) of the most common taxa of crabs (A and D), the four species of the genus *Uca* (B and E) and the five species of Sesarmidae (C and F) estimated for the *Avicennia* and *Rhizophora* belts at the three Kenyan sampling sites.

(d) Large sesarmids: represented by *Neosarmatium meinerti* and *Neosarmatium smithi*. Their density was assessed by counting the operational burrows in the quadrats, since previous work from South Africa to Kenya has clearly shown that these refuges

are occupied by single crabs (Fratini et al., 2000; Emmerson, 2001; Skov et al., 2002; Berti et al., 2008).

Sediment was sampled at each replicated transect by collecting five cores 3.5 cm in diameter and 20 cm in depth. Standard weights (100 g)

Table 2

Results of the three four-way univariate PERMANOVAs conducted on biomass data (expressed as WW) for total crabs, crabs of the genus *Uca* and sesarmid crabs in the *Avicennia* belts at the three Kenyan sites.

Source	DF	Wet weight <i>Uca</i> spp.		Wet weight sesarmids		Wet weight crabs	
		MS	F	MS	F	MS	F
Time	1	678.3	0.2	1383.8	1725.5*	124.4	0.1
Impact vs Controls	1	65,390.0	6.7	47,555.0	66.8	22,4470.0	38.4*
Site (I vs C)	1	1388.6	0.3	0.9	0.1	1319.9	0.1
Time \times I vs C	1	8971.5	2.2	711.1	886.7**	4631.0	1.1
Transect (site (I vs C))	3	3521.1	4.4	2733.1	47.2*	11915.0	15.2*
Time \times site (I vs C)	1	3989.9	5.0	0.8	0.1	4103.8	5.2
Time \times transect (site (I vs C))	3	798.5	0.5	57.9	0.1	783.7	0.3
Res	48	1464.2		1484.0		2632.1	
Total	59						

* $p < 0.05$; ** $p < 0.01$.

Table 3
Results of the three four-way univariate PERMANOVAs conducted on biomass data (expressed as WW) for total crabs, crabs of the genus *Uca* and sesarmid crabs in the *Rhizophora* belts at the three Kenyan sites.

Source	DF	Wet weight <i>Uca</i> spp.		Wet weight sesarmids		Wet weight crabs	
		MS	F	MS	F	MS	F
Time	1	40,6380.0	5.8	52,322.0	10.4	750,330.0	19.8
Impact vs Controls	1	24835.0	2.2	207.7	0.3	29,584.0	3.9
Site (I vs C)	1	22,634.0	1.1	20,212.0	3.1	68.5	0.7
Time × I vs C	1	20,259.0	0.3	134.7	0.1	17,090.0	0.5
Transect (site (I vs C))	3	33,053.0	0.4	3844.8	0.5	47,881.0	0.9
Time × site (I vs C)	1	70,495.0	0.8	5021.5	0.7	37,887.0	0.7
Time × transect (site (I vs C))	3	93,679.0	2.9*	7684.8	6.8**	56,154.0	1.7
Res	48	32,790.0		1138.2		33,509.0	
Total	59						

* $p < 0.05$; ** $p < 0.01$.

of the different samples were dried at 105 °C in the laboratory. Sediment particles were separated according to grain size using a series of sieves of 2 mm to 63 µm mesh size mounted on a mechanical shaker and graded according to the Wentworth scale. The content of each sieve was weighed. Samples collected for the analysis of organic content were ignited at 550 °C for 3 h and cooled in a desiccator. The loss on ignition (LOI) was measured and the organic content expressed as a percentage of the dry weight (Heiri et al., 2001).

2.2.2. Crab biomass estimation

To estimate crab biomass at the different sampling stations, we collected a total of 463 crabs of the following species: *Chiromantes eulimene* (22), *Chiromantes ortmanni* (36), *Perisesarma guttatum* (73), *Parasesarma catenata* (36), *Uca annulipes* (117), *Uca inversa* (47), *Uca chlorophthalmus* (53), *Uca urvillei* (51), *Neosarmatium meinerti* (22) and *Neosarmatium smithi* (42). Carapace width (CW) and length (CL) were determined using vernier callipers, their wet weight (WW) of all specimens was measured using a precision balance and the sex was recorded. A strong positive correlation was found between crab dimensions and WW, and an average WW was calculated for the various populations. The total biomass of each species was then estimated by multiplying the average WW by the frequency observed of each species in the quadrats.

2.3. Statistical analyses

A PERMANOVA (permutational multivariate analysis of variance, Anderson, 2001) asymmetrical design was used to test the null hypothesis that there were no differences in the relative abundance of the different macrofaunal species, both among peri-urban and non-urban sites and within and between the two countries over time. Similarity matrices were computed using Bray–Curtis distance on square root-transformed data, since there were strong differences in the abundance of the different species. All analyses were based on 9999 permutations of residuals within a reduced model (Anderson and ter Braak, 2003) and Type III sums of squares to cope with the unbalanced design (Anderson et al., 2008). The PERMDISP (Anderson, 2006) technique was used to test the homogeneity of multivariate dispersions.

Principal Component Analysis was performed to visualise patterns in the granulometric characteristics of the soil and the organic content among the different sites. Finally, univariate PERMANOVA, based on similarity matrixes computed using Euclidean distances, was also employed to test the null hypothesis that there were no differences in crab biomass between the sites over time. Multivariate and univariate analyses were performed using PRIMER v. 6.1 (Clarke and Gorley, 2006) and the PERMANOVA+ for PRIMER routines (Anderson et al., 2008).

In particular, four-way multi- and univariate PERMANOVA tests were applied to determine whether there were differences in abundance and biomass within the two countries, with time (random and orthogonal), Impact vs Control (I vs C, asymmetrical, fixed and orthogonal), site (random and nested in 'I vs C') and transect (random and nested in site) as factors. For the Kenyan dataset, the four-ways design was applied separately for *Avicennia* and *Rhizophora* belts, given the *a priori* differences in faunal assemblages between the two belts.

Since a comparable *Avicennia* belt was present at all sites in both Mozambique and Kenya, we compared data from all non-urban and peri-urban sites to establish whether there are regional patterns in crab and mollusc abundance and biomass in East Africa as well as their variability in response to sewage stress. Two four-way PERMANOVA tests were applied to test for differences in abundance between the two countries, using Country (fixed and orthogonal), Impact vs. Control (I vs C, asymmetrical, fixed and orthogonal), site (random and nested in 'Country' and in 'I vs C') and transect (random and nested in site) as factors, in each sampling period. Differences in biomass between countries were tested using five-way multi- and univariate PERMANOVAs, with time (random and orthogonal), Country (fixed and orthogonal), Impact vs. Control (I vs C, asymmetrical, fixed and orthogonal), site (random and nested in 'Country' and in 'I vs C') and transect (random and nested in site) as factors.

3. Results

3.1. Kenya

3.1.1. Assemblages

The asymmetrical design of PERMANOVA revealed site differences in both the *Avicennia* and *Rhizophora* belts (Table 1), and the epifaunal assemblages differed markedly between locations and sampling periods. In the *Avicennia* belt,

Table 4

Results of the four-way permutational ANOVA conducted on square root-transformed abundance data for 10 species of crabs and molluscs recorded at the three Mozambican sites.

Source	DF	MS	F
Time	1	1868.7	4.8
Impact vs Controls	1	12,359.0	1.0
Site (I vs C)	1	6541.5	15.4**
Time × I vs C	1	6576.4	16.9**
Transect (site (I vs C))	3	425.4	1.1
Time × transect (site (I vs C))	3	389.6	1.4
Res	49	283.4	
Total	59		

* $p < 0.05$; ** $p < 0.01$.

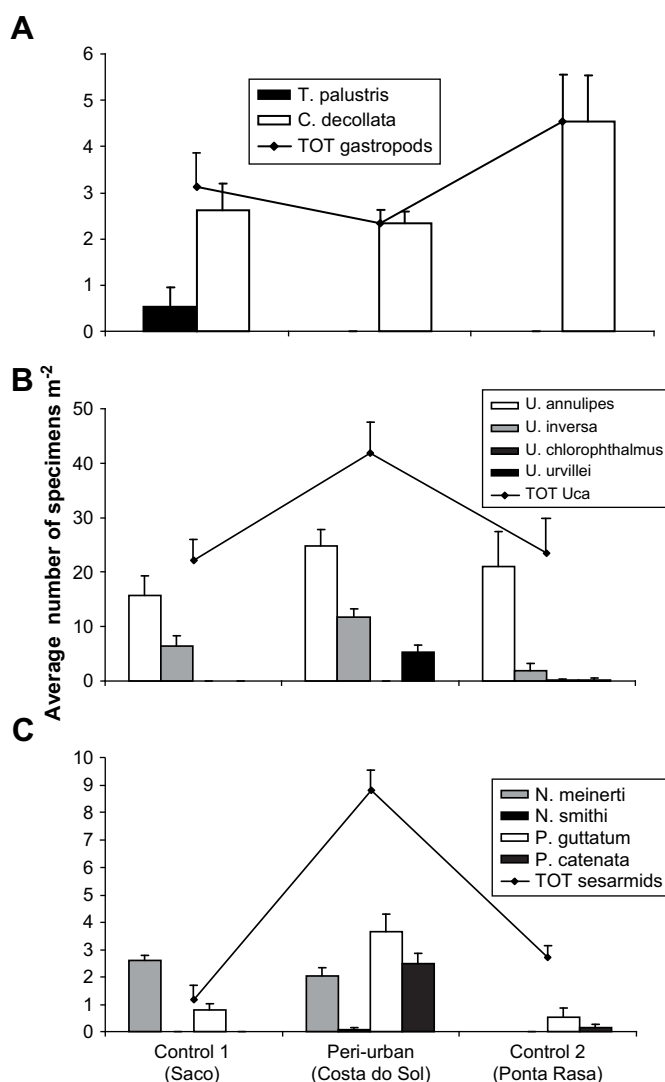


Fig. 4. Average abundance (\pm SE) of the most common species of molluscs (A), the most common species of the genus *Uca* (B) and of the Sesarmidae (C) at the three Mozambican sampling sites.

a significant interaction of time and I vs C emerged, testifying to temporal variability in differences between the two control sites.

There was a higher abundance and species diversity within the *Avicennia* belt at the impacted site than the control sites, where a higher abundance of both *Uca* species and sesarmids was recorded (Fig. 2B and C). Among the fiddler crabs, *Uca inversa* and *Uca annulipes* were particularly abundant at Mikindani compared to Gazi and Shirazi; *Uca chlorophthalmus* was also recorded (Fig. 2B). Sesarmid abundance was higher in the Mikindani *Avicennia* belt than that at Gazi or Shirazi. The density of *Perisesarma guttatum* and *Neosarmatium meinerti* in Mikindani was much higher than the corresponding habitats in Gazi and Shirazi (Fig. 2C). On the other hand, molluscs, especially the mud whelk *Terebralia palustris*, were less abundant in Mikindani than Gazi or Shirazi, (Fig. 2A). No patterns in epifaunal species abundance were detectable in the *Rhizophora* belts (Fig. 2D–F).

3.1.2. Biomass

The total crab biomass was always higher in the *Rhizophora* than in the *Avicennia* belts, regardless of site (Fig. 3). The results of the four-way PERMANOVA tests on *Uca* spp., Sesarmidae and total crab biomass are presented for the *Avicennia* and *Rhizophora* belts,

respectively, in Tables 2 and 3 and account for a higher homogeneity in the *Rhizophora* than *Avicennia* belts. In the *Rhizophora* belt, only the interaction between time and transect was significant for the *Uca* spp. and sesarmid biomass, but not for the total biomass (Fig. 3; Table 3). On the other hand, and although there were

Table 5

Results of the three four-way univariate PERMANOVAs conducted on biomass data (expressed as WW) for total crabs, crabs of the genus *Uca* and sesarmid crabs in the *Avicennia* belts at the three Mozambican sites.

Source	DF	Wet weight <i>Uca</i> spp.		Wet weight sesarmids		Wet weight crabs	
		MS	F	MS	F	MS	F
Time	1	1430.9	11.3	620.1	2.1	3934.9	4.8
I vs C	1	8519.4	15.0	39,793.0	1.8	85,137.0	3.9
Site (I vs C)	1	120.5	2.8	20,242.0	16.4*	17,239.0	12.0*
Time \times I vs C	1	454.7	3.6	2287.8	7.6	4782.3	5.9
Transect (site (I vs C))	3	56.2	0.1	989.9	1.0	720.1	0.6
Time \times site(I vs C)	1	126.3	0.3	300.2	0.3	816.0	0.7
Time \times transect (site (I vs C))	3	399.1	6.9**	974.7	2.0	1123.9	2.2
Res	48	57.8		481.4		502.1	
Total	59						

* $p < 0.05$; ** $p < 0.01$.

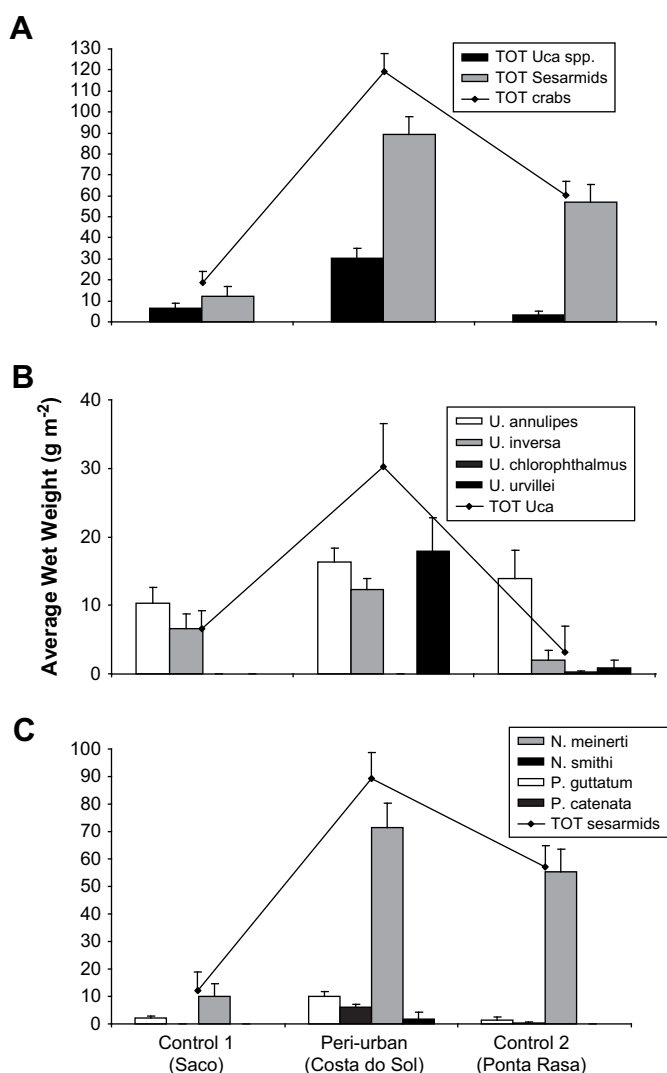


Fig. 5. Average biomass (expressed as Wet Weight ± SE) of the most common taxa of crabs (A), the four species of the genus *Uca* (B) and the four species of Sesarmidae (C) recorded at the three Mozambican sampling sites.

significant differences at the level of transects that accounted for considerable variability, the total crab biomass at the impacted sites in the *Avicennia* belt were consistently higher than in the two controls (Fig. 3; Table 2).

3.2. Mozambique

3.2.1. Assemblages

PERMANOVA revealed that the three Mozambique locations differed significantly from each other, although these differences were not consistent over time (Table 4). This result, again, confirmed the large temporal variability detected between the control sites.

While the differences found between the two sampling periods could be explained by seasonal differences at this subtropical location, the differences found between sites, and especially between Costa do Sol and the other two sites, were analysed further to provide an insight on changes in macrofaunal assemblages attributable to sewage impact. The data showed that the abundance of both major groups of mangrove crabs was higher at Costa do Sol than those at the control sites (Fig. 4B and C). This was particularly the case for *Uca* spp., attributable mainly to high densities of the

Table 6

Results of the four-way permutational ANOVA on square root-transformed abundance data for nine species of crabs and molluscs recorded in the *Avicennia* belts at the six Kenyan and Mozambican sites.

Source	DF	Time 1		Time 2	
		MS	F	MS	F
Country	1	8425.0	1.2	16,295.0	1.5
I vs C	1	9209.2	1.3	23,152.0	2.2
Country × (I vs C)	1	3675.1	0.5	10,951.0	1.0
Site (country × I vs C)	2	6874.4	18.6**	10,585.0	17.0**
Transect (site (country × I vs C))	6	368.8	1.3	623.0	1.0
Res	48	286.2		623.9	
Total	59				

* $p < 0.05$; ** $p < 0.01$.

most common species (*Uca annulipes* and *Uca inversa*) and to the presence of *Uca urvillei*, a species not found in the *Avicennia* belt at the non-urban sites (Fig. 4B). Similar patterns of differing abundance and species richness were observed for the Sesarmidae, with very high numbers of the two medium-size generalist species, *Perisesarma guttatum* and *Parasesarma catenata*, at the impacted site (Fig. 4C). No such patterns were detectable for gastropod abundance (Fig. 4A).

3.2.2. Biomass

The four-way PERMANOVA tests on Kenyan *Uca* spp., Sesarmidae and total crab biomass are presented in Table 5 and account for strong differences between sites, with significantly higher total crab and sesarimid biomasses at the impacted site of Costa do Sol (Fig. 5A, C) compared to the non-urban sites. The biomass of *Uca* spp. was very variable over time at the various sites, manifesting no consistent patterns (Fig. 5B, Table 5).

3.3. Kenya vs. Mozambique

3.3.1. Assemblages

The two four-way PERMANOVA tests revealed that the highest variability was at the level of sites in both countries (Table 6), thus showing no general patterns of change between the two peri-urban sites and the four controls.

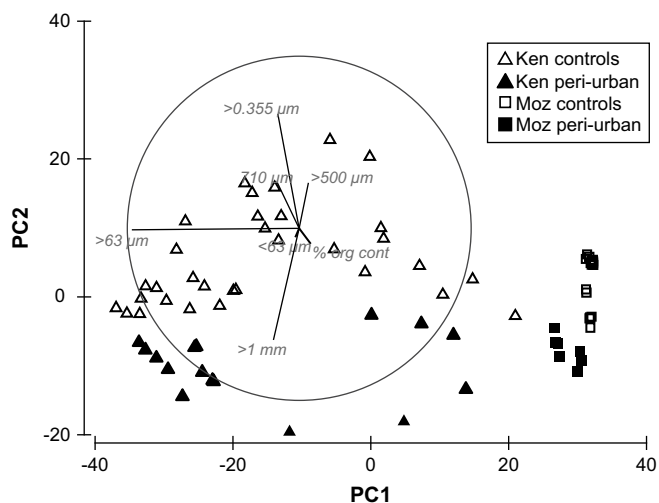


Fig. 6. Two-dimensional scatter plot of the first and second principal components of sediment particle size and organic content in *Avicennia* belts sampled at the peri-urban sites (Costa do Sol and Mikindani) and in the four control areas (Saco, Ponta Rasa, Gazi and Shirazi) in Mozambique and Kenya. Vectors of the linear correlations between individual variables are superimposed on the graph.

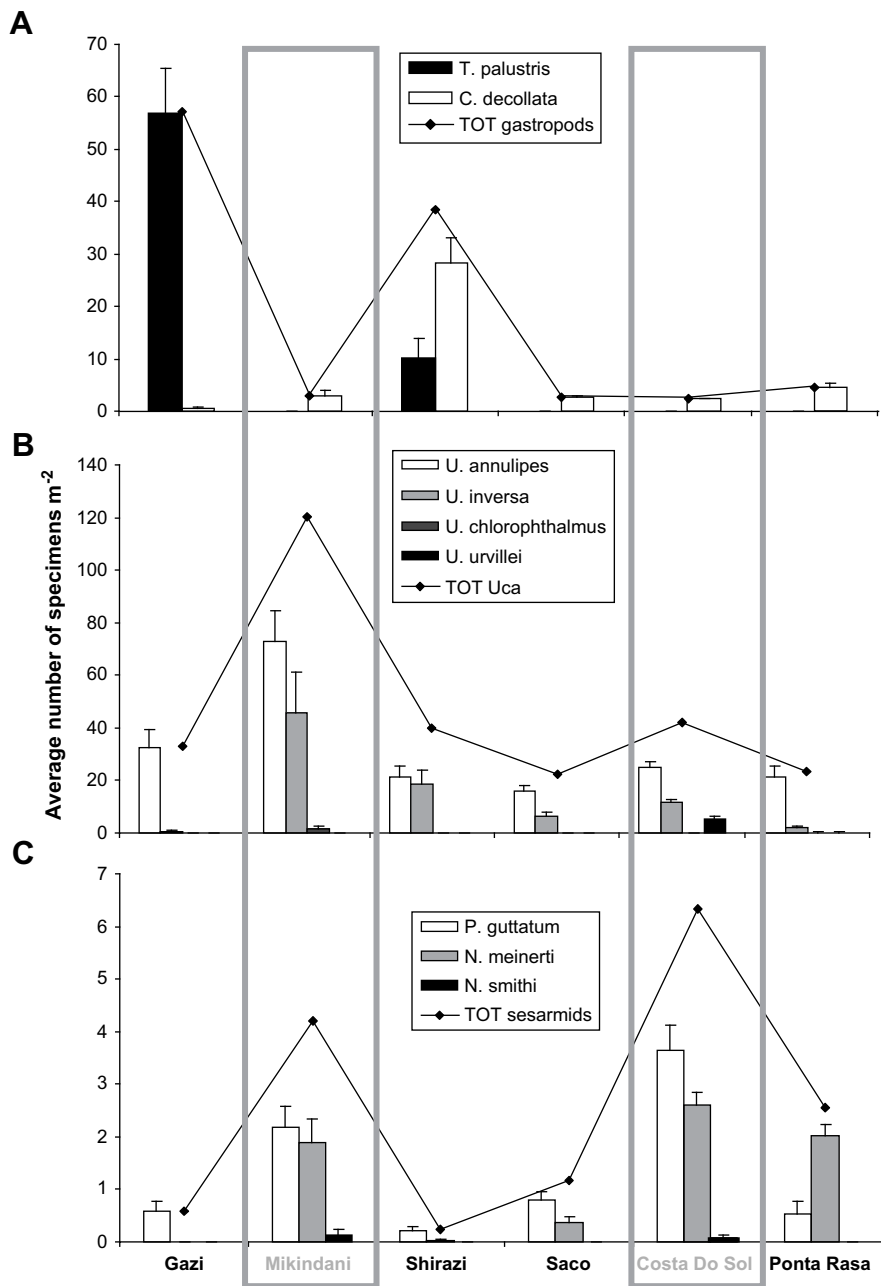


Fig. 7. Average abundance (\pm SE) of the most common species of molluscs (A), of the genus *Uca* (B) and of the Sesarmidae (C) at the three sampling sites in Kenya and Mozambique, respectively. The peri-urban sites are shaded in grey.

The PCA performed on the sediment particle sizes and organic content revealed that the Kenyan and Mozambican samples were markedly different (Fig. 6). Samples from Kenyan mangroves were mostly distributed along the negative quadrant of the I Principal Component (explaining the 81% of the total variability), while the Mozambican samples were clustered at the extreme I Component values (Fig. 6). The linear coefficients linking the original variables to the principal components revealed that the Kenyan samples were richer in fine sand than the Mozambican samples, regardless of their site of origin.

The changes in abundance of the different species among sites revealed strong tendencies (Fig. 7). Molluscs were scarce at both peri-urban sites (Fig. 7A), and scarce in all Mozambican *Avicennia* belts. Crab abundance was always higher at the peri-urban sites than at the respective control ones (Fig. 7B, C). The Kenyan peri-

urban site was characterised in particular by a higher density of fiddler crabs and sesarmids than Gazi and Shirazi. At Costa do Sol, only sesarmids manifested a clear increase in density (Fig. 7B, C).

3.3.2. Biomass

Results of differences in *Uca* spp., sesarmid and total crab biomass between non-urban and peri-urban sites tested by means of three five-way univariate PERMANOVA mixed designs are shown in Table 7. These account for a significant and consistent difference in total crab biomass, expressed as wet weight, between the peri-urban and the non-urban sites. The graphs in Fig. 8 show how the biomass recorded for both *Uca* spp. and sesarmids at the peri-urban sites was consistently higher than that recorded at the respective control sites (Fig. 8), although some differences between the equatorial and the subtropical systems were evident.

Table 7
Results of the three five-way univariate PERMANOVAs conducted on biomass data (expressed as WW) for total crabs, crabs of the genus *Uca* and sesarmid crabs in the *Avicennia* belts at the six Kenyan and Mozambican sites.

Source	DF	Wet Weight <i>Uca</i> spp.		Wet Weight sesarmids		Wet Weight crabs	
		MS	F	MS	F	MS	F
Time	1	69.4	0.1	1928.2	12.8	2729.4	1.1
Country	1	54,600.0	20.3	24,389.0	2.4	6005.8	0.8
I vs C	1	60,558.0	18.2	87,175.0	6.8	293,050.0	31.8**
Time × country	1	2039.8	1.0	75.6	0.5	1329.9	0.5
Time × I vs C	1	2693.4	1.3	2775.0	18.4*	0.6	0.1
Country × I vs C	1	13,352.0	2.1	172.8	0.0	16,563.0	1.0
Site (country × I vs C)	2	754.5	0.4	10,121.0	5.3*	9279.2	1.2
Time × country × I vs C	1	6732.7	3.3	224.0	1.5	9412.7	3.8
Transect (site (country × I vs C))	6	1788.7	3.0	1861.5	3.6	6317.7	6.6*
Time × site (country × I vs C)	2	2058.1	3.4	150.5	0.3	2459.9	2.6
Time × transect (site (country × I vs C))	6	598.8	0.8	516.3	0.5	953.8	0.6
Res	96	761.0		982.7		1567.1	
Total	119						

* $p < 0.05$; ** $p < 0.01$.

4. Discussion

Two major points must be emphasised in discussing the results of this study. The first is the high variability in macrofaunal assemblages, not only at small and large spatial scales, but also on a temporal scale, and the second is that, in spite of this variation, clear and consistent patterns between non-urban and peri-urban mangroves were detected, especially in terms of biomass.

The use of a stratified sampling design, adapted to the natural zonation of East African mangrove forests (Macnae, 1968; Kathiresan and Bingham, 2001; Dahdouh-Guebas et al., 2002), allowed us to compare relatively homogeneous areas in terms of vegetation cover and flooding regime. However, strong fluctuations in species abundance between sites, as well as between regions, were expected, for at least three reasons.

The first was the strong difference detected in soil characteristics, such as grain size, which clearly affect the distribution of fiddler crabs (Icely and Jones, 1978). The second was the wide geographical scale of our approach. Kenyan and southern Mozambican mangrove systems, although largely comparable in terms of dominant decapod and gastropod species, differ from each other in a number of aspects. The equatorial systems of Kenya have a higher ocypodid biomass compared to the subtropical Mozambican systems which are richer in terms of sesarmid biomass (Hartnoll et al., 2002). Moreover, some decapod species found, and even abundant, in Kenya are absent or scarce in Mozambique. This is the case with *Perisesarma samawati* (Gillikin and Schubart, 2004) and *Parasesarma leptosoma* (Emmerson et al., 2003), respectively. On the other hand, *Parasesarma catenata*, a southern African sesarmid, is abundant in the Maputo Bay area and absent in Kenya (Kalk, 1995).

However, the differences between the assemblages were not detected only at a large geographical scale. Indeed, a strong variability was also evident at the local scale, with the two non-urban forests in each country differing significantly from each other. However, this source of variability was anticipated from previous studies on mangrove macrobenthic infauna (Chapman, 1998; Kelaher et al., 1998; Chapman and Tolhurst, 2004) and other more general studies on spatial patterns of benthos in intertidal habitats (Thrush et al., 1994; Underwood and Chapman, 1998).

Infaunal species are considered to be key organisms in the detection of ecosystem changes as well as human impacts, due to their short life span and low mobility (Warwick and Clarke, 1993; Chapman, 2007). They are also known to be unpredictable and patchy in their distribution at small spatial scales and to undergo strong and unpredictable fluctuations in time (Underwood and

Chapman, 1996). In fact, in an Australian urbanised temperate mangrove system, Chapman and Tolhurst (2004) recently found strong differences in both benthic patterns and sediment characteristics even at the scale of meters and tens of meters, showing how the aforementioned parameters are only weakly correlated with each other. These authors suggested that the correlation between spatio-temporal ecological factors, such as sediment characteristics, microphytobenthos and leaf litter, and mangrove benthic abundance and distribution is complex. Successful analysis of these relationships requires nested sampling designs at various spatial and temporal scales, such as those utilised in this study, especially when the aim of the study is to disentangle natural variations from those attributable to human disturbance.

The present study not only accounted for random variability between experimental sites, but also revealed significant differences between the non-urban and peri-urban sites. Indeed, the high concentration of anthropogenic nutrients and pollutants introduced in the systems of Costa do Sol and Mikindani in urban sewage did not appear to stress the crab communities. At Mikindani in particular, different species abundances relative to control sites were only found in the *Avicennia* belts. These results are consistent with the observation that the dumping of sewage at Mikindani affects primarily the landward *Avicennia* belt, before flowing through the *Rhizophora* belt (Mohamed, 2008; Mohamed et al., 2008). Since both the soils and vegetation of this landward belt can efficiently assimilate the overload of nutrients (Tam and Wong, 1995; Wong et al., 1997), the landward mangrove belt at Mikindani probably acts as a first phytoremediation system, mitigating the effect of the wastewater.

In both countries, the number of crab species was higher at the peri-urban sites than at the corresponding control sites and the abundance and biomass of crab populations steadily and consistently increased. Interestingly, the data from this study not only confirm the shift in dominance from the Ocypodidae in Kenya to the Sesarmidae in Mozambique, found by Hartnoll et al. (2002), but they also show that their relative dominance is enhanced in the sewage dumping areas, with *Uca* spp. and Sesarmidae steeply increasing at Mikindani and Costa do Sol, respectively.

At the peri-urban sites, the high biomass of fiddler crabs may be directly linked to the enhanced nutrient concentrations from sewage loading due to the likely increase of benthic diatoms and bacteria upon which they feed (Meziane and Tsuchiya, 2002). These data are extremely important for the management of peri-urban mangrove areas, since fiddler crabs play a significant role in the control of algal mat growth in mangrove substrata and their bioengineering activities are fundamental for the growth of

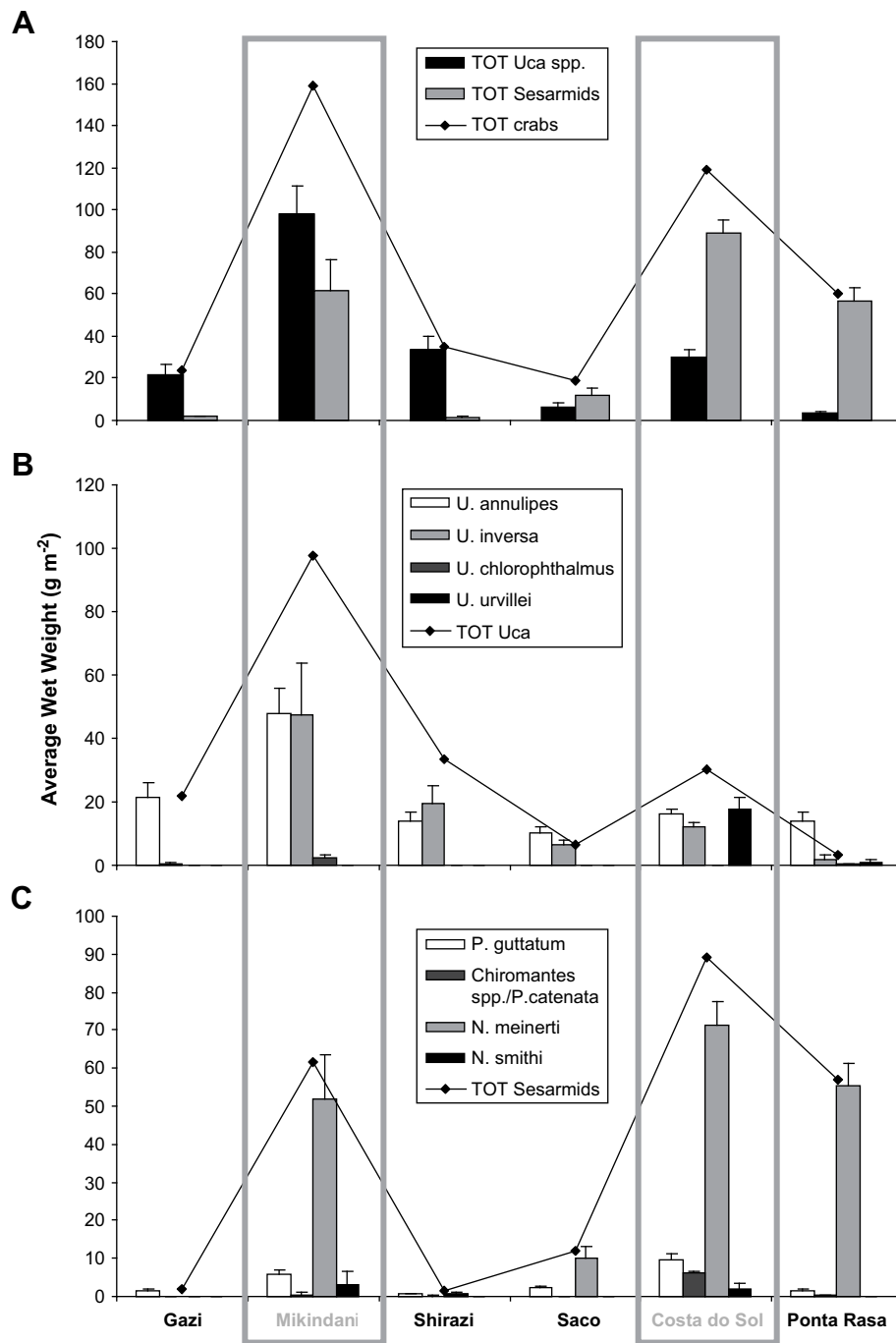


Fig. 8. Average biomass (expressed as Wet Weight \pm SE) of the most common taxa of crabs (A), the four species of the genus *Uca* (B) and the four species of the Sesarmidae (C) recorded at the three sampling sites in Kenya and Mozambique, respectively. The peri-urban sites are shaded in grey.

mangrove saplings and, eventually, for mangrove re-growth (Kristensen and Alongi, 2006; Kristensen, 2008).

Sesarmid crabs and, in particular, *Neosarmatium meinerti* and *Perisesarma guttatum*, also have a high tolerance to sewage and have been shown to utilise nutrient overloading at the waste disposal site at Maruhubi, Zanzibar (Machiwa and Hallberg, 1995; Skov and Hartnoll, 2002). A considerable shift in abundance also occurred in the mollusc species but, in this case, the wastewater had a negative impact on their populations. In fact, although *Cerithidea decollata* was far more variable in its abundance, making its spatial patterns difficult to interpret, *Terebralia palustris* totally

disappeared from the sewage disposal areas. A similar pattern of mollusc depopulation was observed by Yu et al. (1997) in Futian mangroves, P.R.C., experimentally treated with municipal wastewater. In that study, even at low sewage concentrations, the dominant gastropod species, *Melanoidea* spp. and *Assimidea nitida*, decreased dramatically after its introduction and the numbers remained significantly lower in the treated area relative to the control one. Another indication of a negative impact of sewage on *Terebralia palustris* populations is provided by a preliminary study on fauna distribution in the disturbed mangrove system of Maruhubi, Zanzibar (Machiwa and Hallberg, 1995). *T. palustris* proved to

be among the commonest mollusc species where *Avicennia marina* leaf litter was present, except in areas where sewage disposal occurred.

Terebralia palustris is by far the most important gastropod in terms of biomass in East African mangroves and it is known to feed on both the substratum as juveniles and leaf litter as adults, and to compete with sesarmid crabs for these resources (Fratini et al., 2000, 2004; Pape et al., 2008). Moreover, its congeneric, *Terebralia sulcata*, feeds mainly on bacteria, increasing in density in areas affected by wastewater (Meziane and Tsuchiya, 2002). However, while the competing crabs increased in density and biomasses at the sewage dumping sites, the gastropods nearly disappeared, suggesting a lower physiological tolerance to some of the altered conditions in the system, which should be addressed in future studies. For the moment, the present results suggest they have a role as key bioindicators for the detection of the severity of human sewage pollution in mangrove systems.

5. Conclusions

The present results show that East African mangrove crab and mollusc populations are significantly affected by domestic wastewater, in contrast to the findings of Yu et al. (1997) in the Futian Mangroves in the P.R.C. There were marked differences in benthic patterns at the peri-urban sites compared to the control sites, the crabs at the former being consistently higher in density and biomass at both the equatorial and subtropical locations. On the other hand, lower densities of gastropods were encountered at impacted sites, indicating that these organisms are not tolerant of this sort of pollution. Moreover, from an ecological point of view, the steady increase in crab biomass observed at the peri-urban sites did not indicate that the systems were healthier. Alterations of this nature in biomass of a crucial ecosystem component can lead to unsustainable alterations in ecosystem function (Duke et al., 2007; Cannicci et al., 2008), eventually causing a collapse of the system itself. In view of the ecological differences we found among mangrove assemblages and the low tolerance shown by some key taxa, we recommend that further studies be undertaken on wastewater impacts on mangrove benthos to further elucidate the potential of natural mangrove forests and wetland systems for sewage treatment.

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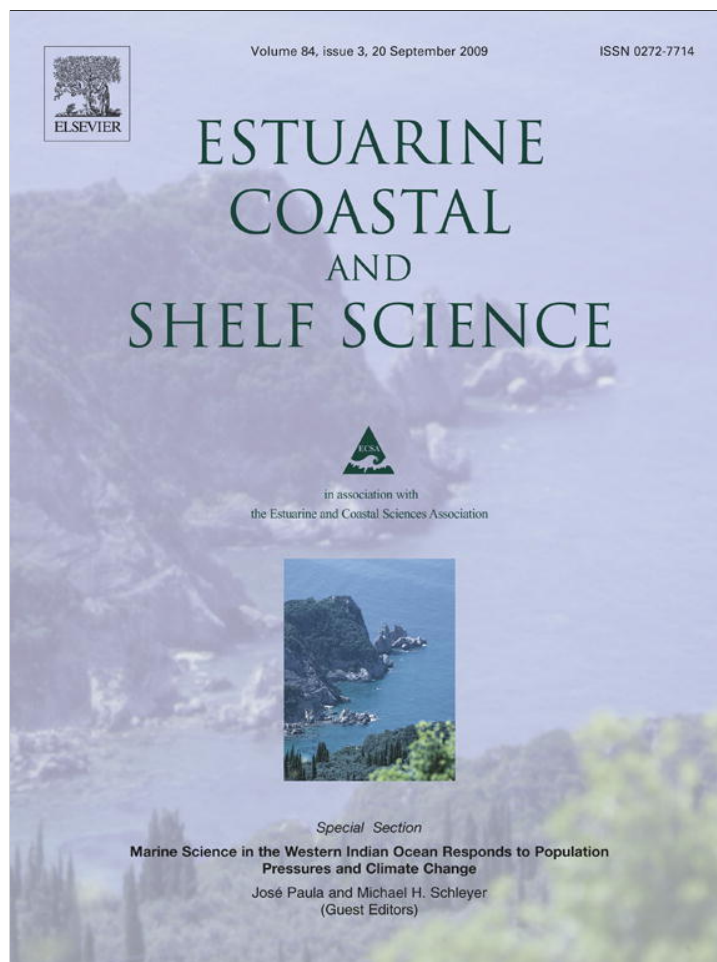
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