Biodiversity and Conservation 13: 1059–1074, 2004. © 2004 Kluwer Academic Publishers. Printed in the Netherlands.

Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay

J.O. BOSIRE^{1,2,*}, F. DAHDOUH-GUEBAS¹, J.G. KAIRO^{1,2}, S. CANNICCI³ and N. KOEDAM¹

¹Vrije Universiteit Brussel, Laboratory of General Botany and Nature Management, Mangrove Management Group (MMG), Pleinlaan 2, B-1050 Brussels, Belgium; ²Kenya Marine and Fisheries Research Institute (KMFRI), P.O. Box 81651, Mombasa, Kenya; ³Dipartmento di Biologia Animale e Genetica 'Leo Pardi', Universita degli Slodi di Firenze, Via Romana 17, I-50125 Firenze, Italy; *Author for correspondence (fax: +254-11-475157; e-mail: jbosire@kmfri.co.ke; bosire98@yahoo.com)

Received 2 October 2002; accepted in revised form 3 April 2003

Key words: Crabs, Environmental variables, Kenya, Recolonisation, Restored mangroves, Sediment-infauna

Abstract. Recolonisation by crab species and sediment-infauna taxa (at class level) in artificially regenerated mangrove stands of Avicennia marina, Rhizophora mucronata and Sonneratia alba (5 yr old) were studied using respective bare sites (open without mangroves or denuded) and natural sites (relatively undisturbed) as controls. The controls were chosen based on site history, physical proximity and tidal inundation class in reference to the particular reforested mangrove stand and samples randomly taken. A number of environmental variables were measured; interstitial water salinity and temperature (measured at low tide) were lower, whereas sediment organic matter content was higher in the areas with mangrove cover, with the natural sites having the highest content. The bare sites were generally sandier, whereas the areas with mangrove cover had higher proportions of clay and silt. Generally, there was a higher crab density in the reforested sites than in the bare sites, whereas crab species diversity (Shannon diversity index) did not vary from one site to another for any of the mangrove species. In terms of crab species composition, the reforested sites were more similar (Sørensen similarity coefficient) to the natural sites and less to the bare controls. For sediment-infauna, the reforested sites had a significantly higher density than the respective bare controls, while the natural sites had the highest density. The number of sediment-infauna taxa in both the reforested and natural sites of all the mangrove species was similar and higher than in the comparable bare sites. The results suggest that the reforested sites are supporting more faunal recolonisation, and therefore becoming more akin to the natural mangrove sites in terms of the investigated functional indicators. The findings seem to support the use of artificial mangrove regeneration (in areas where natural regeneration has been impeded by physical conditions or otherwise) as an effective management tool in the restoration and conservation of the functional integrity of degraded mangrove habitats.

Introduction

Mangrove fauna are an important and integral component of the mangrove ecosystem (Macnae and Kalk 1962; Macnae 1968; Ahmad 1984; Macintosh 1984; Robertson and Duke 1990; Ngoile and Shunula 1992; Aksornkoae 1993; Dahdouh-Guebas et al. 1997; Sheridan 1997; Ronnback 2001) and serve in determining the structure and functioning of the ecosystem as a whole (Macintosh 1984; Smith 1987; Sasekumar et al. 1992; Schrijvers et al. 1995; Dahdouh-Guebas et al. 1997; Lee 1997, 1998; Slim et al. 1997; Steele et al. 1999). Globally a lot of effort has been made in the restoration of mangroves in many countries, including, among others, Thailand (Aksornkoae 1996), Pakistan (Qureshi 1996), Australia (Saenger 1996), Bangladesh (Siddiqi and Khan 1996), Sri Lanka (SFFL 1997) and Kenya (Kairo 1995). The focus of restoration has been the return of the forest, while little is known about the re-establishment of ecosystem structure and function normally expected of undisturbed mangroves (Ellison 2000).

Schrijvers et al. (1995) studied the macrobenthic infauna of mangroves and surrounding beaches in Gazi Bay, Kenya and identified 16 taxa (at taxonomic class level), with macrobenthic densities ranging between 265 and 6025 indiv.m⁻². Fondo and Martens (1998) investigated the effects of mangrove deforestation on macrofauna densities and identified 13 infauna taxa (also at class level), with nematodes being numerically dominant. They compared variation in macrofauna densities in a deforested mangrove area with a natural mangrove area and found that higher densities of epifauna occurred in the natural mangrove area, whereas the presence of mangroves did not seem to influence infauna densities. Crabs play a significant role in the turn-over of mangrove litter (Macintosh 1984; Steinke et al. 1993; Dahdouh-Guebas et al. 1997; Lee 1998) and through their feeding activities, large proportions of organic matter production (mangrove leaves) are recycled within the forest and this initial retention of production reduces tidal export from the mangroves. Other important detritivores of mangroves are gastropods, sipunculids and polychaetes (Schrijvers et al. 1995), shrimps and penaeid prawns (Ngoile and Shunula 1992; Sasekumar et al. 1992) and fish, of which especially the young stages are prominent detritivores of the aquatic community.

The objective of this study was to investigate macrobenthic fauna (crabs and sediment-infauna) recolonisation of reforested mangrove areas at Gazi Bay, Kenya as a functional indicator of ecosystem functioning, because of the role played by this faunal component in the mangrove ecosystem. The hypothesis that was set for this study therefore, was that mangrove reforestation leads to recovery in ecosystem functioning in terms of increased faunal recruitment into the replanted stands as compared to bare sites.

Study area

Environmental settings

The study was conducted at Gazi (Maftaha) Bay (Figure 1), located at the south coast of Kenya about 50 km from Mombasa in Kwale district ($4^{\circ}25'$ S and $39^{\circ}30'$ E). The Bay is sheltered from strong waves by the presence of the Chale peninsula to the east and a fringing coral reef to the south. The mangrove is not continuously under direct influence of fresh water, because the two rivers (Kidogoweni in the north and Mkurumji in the south) draining into the bay are seasonal depending on the amount of rainfall inland. Groundwater seepage is also restricted to a few points (Tack and Polk 1999). Generally freshwater influx via rivers and direct rainfall in the Bay accounts for a volume of 305 000 m³ yr⁻¹ of which 20% is lost due to evapotranspiration, which is also responsible for a salinity maximum zone of 38



Figure 1. Map of the Kenyan coast showing the study site (Gazi Bay) and the location of the bare, reforested and natural sites of the R. mucronata, A. marina and S. alba forests (basic features redrawn by Slim 1990; Ruwa 1997 and adopted from Dahdouh-Guebas et al. 2002). Key: dark grey areas are mangroves, while the light areas are seagrasses. 1. R. mucronata bare site, 2. R. mucronata natural site, 3. R. mucronata reforested site, 4. S. alba bare and reforested sites, 5. S. alba natural site, and 6. A. marina bare, reforested and natural sites.

PSU in the upper region of the Bay covered by mangroves (Kitheka 1997). All the nine mangrove species occurring in Kenya are found in this Bay: Avicennia marina (Forsk.) Vierh., Bruguiera gymnorrhiza (L.) Lamk., Ceriops tagal (Perr.) C.B. Rob., Heritiera littoralis Dryand., Lumnitzera racemosa Willd., Rhizophora mucronata Lamk., Sonneratia alba J. Smith, Xylocarpus granatum Koen. and X. moluccencis (Lamk.) Roem. (nomenclature after Tomlinson 1986).

Site history

The mangrove forests of Gazi have been exploited for many years, especially for wood used for industrial fuel (in the calcium/chalk and brick industries in the 1970s) and building poles (Rawlins 1957; Kairo 1995), which left some areas along the coastline completely denuded. Experimental reforestation in these areas was carried out between 1991 and 1994 (Kairo 1995) and the local people were involved in the replanting of saplings of *R. mucronata*, *B. gymnorrhiza*, *A. marina*, *S. alba* and *C. tagal* in monospecific stands. The monospecific reforested (for *R. mucronata*, *S. alba*) and afforested (for *A. marina*) stands used in this study were covered by planted *R. mucronata* (6.74 ha), *S. alba* (0.4 ha) and *A. marina* (0.25 ha), which were all 5 yr old.

Three criteria were used in the selection of controls so as to minimise environmental variation and maximise on paired matching. The *S. alba* sites (reforested and controls) were of the same inundation class I (Watson 1928) flooded during all high tides and adjacent to each other, whereas all *R. mucronata* and *A. marina* sites were of inundation class II flooded at medium high tides. The respective sites of the latter two mangrove species were also adjacent to each other, except for the *R. mucronata* bare (denuded) site which was about 1 km away from its respective reforested and natural sites, but it was the closest one of the same inundation class and history (previously this site had *R. mucronata* and it was logged in the 1970s) as the comparable sites. The reforested sites had the same history as the bare controls. The *S. alba* bare control was logged in the 1970s (same time as the reforested site) and has not had any natural regeneration so far, whereas the *A. marina* planted site also did not have mangroves before.

Materials and methods

Environmental factors

Sediment interstitial water samples were randomly collected by digging a hole into the soil of 10–15 cm (depending on the inundation class; 10 cm for class I and 15 cm for class II). Salinity was measured using an optical refractometer (Atago brand), whereas temperature and pH were taken using a pH meter (WTW pH 320/ set-1). Three subsamples were taken per quadrat for three 10 m×10 m quadrats randomly chosen per site. The same experimental protocol was repeated for the controls (bare and natural sites). All measurements were taken at low tide.

Sediment samples were taken down to a depth of 5 cm using a hand corer of 6.4 cm diameter. Three replicates were taken per site (one replicate per quadrat). These samples were oven-dried at 80 °C for about three days until constant dry weight was obtained for granulometric analysis. About 20 g was weighed for each sample and transferred into prelabeled beakers. The organic matter in the samples was removed by digestion using 30% diluted technical H_2O_2 as an oxidising agent, after which the samples were rinsed with demineralised water until a more or less stable suspension was obtained (Wartel et al. 1995). The samples were then re-dried for 24 h at 105 °C and weighed. The difference in weight gave an estimate of the organic matter content. Grain size analysis was done using a combination of dry sieving and the sedigraph method as outlined by Wartel et al. (1995). The sedigraph determines the size distribution of particles dispersed in a liquid assuming settling of particles according to Stokes' law (Arnold 1986). For grain size ranges, the unified soil classification system was used (Robert et al. 1997).

Crabs

In the 10 m \times 10 m quadrats described above, three sub-quadrats of 1 m \times 1 m were randomly taken and measured at low tide per site (bare/denuded, reforested and natural) for all the mangrove species considered. All the crab species within each quadrat were identified and counted using a pair of binoculars. The binoculars allowed zooming in on the crabs for ease of identification. Species identification was done using dichotomic identification keys by Cannicci et al. (1997).

Sediment fauna

Nine sediment samples per site (bare, reforested and natural) were randomly taken (three per quadrat for the quadrats described above) using a hand corer of diameter 6.4 cm to a depth of 5 cm into the soil at low tide. The samples were fixed with 8% formalin in the laboratory before washing with a gentle jet of tap water over a set of 0.5 mm and 2 mm mesh sieves to separate fauna from sediments and detritus. All animals which remained on the sieves were picked with a forceps and put into the respective sieved samples. The animals were stained with Rose Bengal for ease of identification and counting under a dissecting microscope. Counting and identification were done to taxonomic class level using keys by Day (1974) at magnification $25 \times$.

Statistical analysis

Differences in macrofaunal densities and environmental parameters between sites within forests were determined using two-way ANOVA (fixed effect with replication), while *post hoc* analysis was done with Tukey's Honest Significant

| Variable | Source | df | MS | F | р |
|----------------|------------|----|---------|-------|------|
| Organic matter | Туре | 2 | 957.94 | 13.05 | 0.00 |
| • | Stand | 2 | 559.33 | 7.62 | 0.00 |
| | Stand×Type | 4 | 214.75 | 2.93 | 0.05 |
| Salinity | Туре | 2 | 82.51 | 9.05 | 0.00 |
| - | Stand | 2 | 28.40 | 3.11 | 0.07 |
| | Stand×Type | 4 | 26.84 | 2.94 | 0.05 |
| Temperature | Туре | 2 | 33.75 | 32.92 | 0.00 |
| * | Stand | 2 | 2.12 | 2.06 | 0.16 |
| | Stand×Type | 4 | 1.31 | 1.27 | 0.32 |
| pН | Туре | 2 | 0.07 | 1.53 | 0.24 |
| 1 | Stand | 2 | 1.09 | 25.24 | 0.00 |
| | Stand×Type | 4 | 0.24 | 5.53 | 0.00 |
| Clay | Туре | 2 | 582.17 | 4.12 | 0.03 |
| | Stand | 2 | 1821.14 | 12.90 | 0.00 |
| | Stand×Type | 4 | 92.50 | 0.66 | 0.63 |

Table 1. Summary of a two-way ANOVA (fixed effect with replication) analysis table of the sediment characteristics in *A. marina, R. mucronata* and *S. alba* forests (stands). The different sites (bare, reforested and natural) were used as treatments.

Difference (HSD) test. Crab species diversity was calculated using the Shannon diversity index (Begon et al. 1996), while differences in diversity between sites were analysed using the Student t-test. Sørensen's similarity coefficient (Kent and Coker 1992) was used to calculate similarity in crab species composition between sites.

Results

Environmental factors

With the exception of the *S. alba* forest, the bare sites in the other forests had higher interstitial salinities (p < 0.05) than the corresponding reforested and natural sites (Tables 1 and 2). Salinity was similar in all sites of the *S. alba* forest, whereas pH did not vary significantly between sites in all the forests. In *A. marina* and *R. mucronata* forests, interstitial temperature was highest (p < 0.05) at bare sites and lowest at natural sites. However, in the *S. alba* forest, the bare and reforested sites showed similar (p > 0.5) and higher temperatures than the natural site. The bare sites had the lowest organic matter content in all the forests. The bare sites had higher proportions of sand than the reforested and natural sites, though the clay content was not significantly different between sites.

| Table 2. Site averages (mean \pm SE) of sediment characteristics in plots with matched natural and reforested stands as well as bare controls for A. marin |
|---|
| mucronata and S. alba forests. Presented are also Tukey multiple comparisons within each forest. Sites within forests bearing the same letters were not signific. |
| different, whereas those bearing different letters were significantly different. pH and clay did not differ significantly among sites within forest stands, hence no le |
| were assigned to them. |

| Table 2. Site average mucronata and S. alba different, whereas those were assigned to them. | s (mean ± SE) forests. Presente e bearing differe | of sediment chi ed are also Tuke; art letters were si | aracteristics in y multiple com gnificantly diffe | plots with matc parisons within e srent. pH and cla | hed natural and each forest. Sites ay did not differ a | reforested stand within forests b significantly amo | s as well as ba learing the same ong sites within | re controls for <i>A</i> letters were not forest stands, her | . <i>marina, R</i> . significantly ice no letters |
|--|---|---|---|---|--|---|---|--|---|
| Parameter | | A. marina | | | R. mucronata | | | S. alba | |
| | Bare | Reforested | Natural | Bare | Reforested | Natural | Bare | Reforested | Natural |
| Salinity (PSU) | $^{a}43 \pm 1$ | $^{\mathrm{b}38}\pm1$ | $^{c}35\pm0.7$ | $^{a}44\pm3$ | $^{\mathrm{b}34}\pm0.6$ | $^{\mathrm{b}35}\pm0.6$ | $^{a}35\pm0.5$ | $^{a}36\pm0.4$ | $^{a}35\pm0.4$ |
| Hd | 7 ± 0 | 7 ± 0 | 7 ± 0.1 | 7 ± 0.1 | 7 ± 0.1 | 7 ± 0.1 | 8 ± 0.1 | 8 ± 0.1 | 7 ± 0 |
| Temperature (°C) | $^{\mathrm{a}}30\pm0.4$ | $^{ m b27}\pm0.1$ | $^{c}26\pm0.3$ | $^{a}30\pm0.6$ | $^{ m b}$ 27 \pm 0.2 | $^{ m c26}\pm0.1$ | $^{\mathrm{a}}30\pm0.3$ | $^{\mathrm{a}29}\pm0.7$ | $^{ m b}$ 27 \pm 0.1 |
| Organic matter (%) | $^{a}3\pm0.2$ | $^{\mathrm{b}19}\pm8$ | $^{ m b25}\pm11$ | $^{ m a4}\pm$ 0.1 | $^{ m b}$ 20 \pm 4 | $^{ m c40}\pm2$ | $^{a}1\pm0.3$ | $^{\mathrm{b}11}\pm2$ | $^{ m b5}\pm1$ |
| Clay (%) | 7 ± 3 | 23 ± 13 | 20 ± 9 | 17 ± 4 | 37 ± 8 | 42 ± 9 | 0 | 5 ± 2 | 5 ± 2 |



Figure 2. The density of crabs (no. m^{-2}) in the bare, reforested and natural sites of (a) *R. mucronata*, (b) *S. alba*, and (c) *A. marima*.

Table 3. Summary of a two-way ANOVA (fixed effect with replication) analysis table of the crab and soil-infauna densities and the number of sediment-infauna taxa in *A. marina, R. mucronata* and *S. alba* stands. The different sites (bare, reforested and natural) were used as treatments.

| Variable Source | | df | MS | F | р | |
|-----------------|------------|----|----------|-------|------|--|
| Crab density | Site | 2 | 120.04 | 3.26 | 0.06 | |
| | Stand | 2 | 427.15 | 11.59 | 0.00 | |
| | Stand×site | 4 | 136.09 | 3.69 | 0.02 | |
| Soil-infauna: | | | | | | |
| Density | Site | 2 | 43043.34 | 26.13 | 0.00 | |
| | Stand | 2 | 18817.24 | 11.42 | 0.00 | |
| | Stand×site | 4 | 22371.88 | 13.58 | 0.00 | |
| Taxa richness | Site | 2 | 13.20 | 21.97 | 0.00 | |
| | Stand | 2 | 17.81 | 29.65 | 0.00 | |
| | Stand×site | 4 | 1.23 | 2.05 | 0.13 | |

Crabs

For the *R. mucronata* forest (Figure 2a; Table 3), there was no significant difference (p > 0.05) in crab density between the reforested and bare sites and the natural and bare sites, respectively. There was, however, a significant difference (p < 0.05) between the reforested and natural sites with the former having a higher density. There was no significant difference (p > 0.05) in crab density between the reforested and bare sites of the *S. alba* forest (Figure 2b). The natural site, however, had a significantly higher (p < 0.05) crab density than the bare and reforested sites. The reforested site of *A. marina* forest (Figure 2c) had a higher crab density, compared to the respective bare and natural sites (p < 0.05). There were no significant differences (p > 0.05) in crab species diversity between all the sites within each respective mangrove forest (Table 4) considered, except for the *S. alba* site, where

Table 4. Analysis of differences in crab species diversity (Shannon–Wiener) and similarities between the bare, reforested (Ref.) and natural sites of *R. mucronata, S. alba* and *A. marina* using the Student t-test and the Sørensen similarity coefficient (S_s), respectively.

| Site | R. mucronata | | S. alba | | | A. marina | | | |
|---------------------|--------------|------|---------|------|------|-----------|------|------|--------|
| | t | р | Ss (%) | t | р | Ss (%) | t | р | Ss (%) |
| Ref. versus bare | 1.86 | 0.31 | 23 | 1.94 | 0.12 | 40 | 2.35 | 0.38 | 43 |
| Ref. versus natural | 1.83 | 0.34 | 45 | 1.90 | 0.34 | 48 | 2.35 | 0.19 | 50 |
| Natural versus bare | 1.90 | 0.43 | 27 | 1.90 | 0.02 | 38 | 1.95 | 0.13 | 43 |



Figure 3. Crab species which were found in the bare, reforested and natural sites of (a) *A. marina*, (b) *R. mucronata*, and (c) *S. alba*. Intersection points show species that occurred in two or three (as the case may be) of the indicated sites. Key: 1 = Uca annulipes; 2 = Neosarmatium meinerti; 3 = Sesarma ortmanni; 4 = S. longipes; 5 = N. smithi; 6 = U. urvillei; 7 = U. vocans; 8 = Metopograpsus thukuhar; <math>9 = M. oceanicus; 10 = S. leptosoma; 11 = Macrophthalmus bosci; 12 = S. guttatum; 13 = U. chlorophthalmus; 14 = Eurycarcinus natalensis, 15 = Selatium elongatum; 16 = U. inversa; and 17 = Ocypode ceratophthalmus.

the natural site had a significantly higher species diversity (p < 0.05) than the bare site. The reforested sites in all forests were more similar (Table 3; Figure 3a–c) to the natural sites and less to the bare sites in terms of crab species composition. With the exception of the *A. marina* (Figure 3a) sites, the reforested and natural sites of the other mangrove forests (Figure 3b, c) had more crab species in common. New species of crabs had also been recruited into the reforested sites, which did not occur in the comparable bare sites but were found in the respective natural sites. Typical examples are *Sesarma guttatum* A. Milne Edwards, *S. leptosoma* Hilgendorf and *Eurycarcinus natalensis* Krauss; species that occurred mainly in the reforested and natural *R. mucronata* sites (Figure 3b).

Sediment-infauna

There were highly significant differences (p < 0.05) in the densities of sedimentinfauna between all the sites of the mangrove species considered, with the bare sites having the lowest density, whereas the natural sites had the highest density (Figure



Figure 4. The density of sediment-infauna (no. m^{-2}) in the bare, reforested and natural sites of (a) *R. mucronata*, (b) *S. alba*, and (c) *A. marina*.



Figure 5. The number of sediment-infauna taxa found in bare, reforested and natural sites of (a) *A. marina*, (b) *R. mucronata*, and (c) *S. alba*. Intersection points show taxa which occurred in two or three (as the case may be) of the indicated sites. Key: 1 = Polychaeta; 2 = Oligochaeta; 3 = Nematoda; 4 = Amphipoda; 5 = Turbellaria; 6 = Bivalvia; 7 = Ostracoda; 8 = Isopoda; 9 = Copepoda; 10 = Cumacea; 11 = Gastropoda; 12 = Insecta; 13 = Crustacea; and 14 = Others.



Figure 6. The number of sediment-infauna taxa in the bare, reforested and natural sites of (a) *R. mucronata*, (b) *S. alba*, and (c) *A. marima*.

4a, b; Table 3) except for the *A. marina* forest (Figure 4c) where the reforested site had the highest density. New taxa of sediment-infauna had been recruited into all the reforested sites of all the mangrove species (Figure 5a–c), which also occurred in the corresponding natural sites. Some new sediment-infauna taxa, however, occurred strictly in the reforested sites. All the taxa that occurred in the bare sites were also found in the respective reforested and natural sites. Reforested and natural sites in the three forests had a similar (p > 0.05) number of taxa, which was highly significant compared to the corresponding bare sites (Figure 6a–c; Table 3).

Discussion

Higher crab densities in the reforested sites of *A. marina* and *R. mucronata* forests suggest that mangrove reforestation is encouraging crab recolonisation. Frith et al. (1976) found that the presence of mangrove trees and associated microhabitats accounted for the high abundance of grapsid crabs. They observed that within the forests these crabs occupied many microhabitats in addition to dwelling within the substratum, such as beneath dead wood, among rotting vegetation, on prop roots and tree trunks. These crabs feed on food items such as mangrove leaves, mangrove seedlings and fine plant and animal detritus (Macnae 1968; Michelil et al. 1991; Robertson 1991; Cannicci et al. 1996; Vannini et al. 1997; Dahdouh-Guebas et al. 1999, 2001; personal observation on *S. leptosoma*). Macnae and Kalk (1962) noted that a number of genera seek mangroves because there they find the right consistency of substrate for permanent burrows, the protection of a sheltered shore and the shade of a dense plant canopy.

A total of 13 sediment-infauna taxa were recorded in the present study, which is close to that recorded in previous studies conducted in the same area (Schrijvers et al. 1995; Fondo and Martens 1998). The density of sediment-infauna for all the three mangrove species considered was always significantly higher in the natural site, followed by the reforested site, whereas the bare site had the lowest density. The number of taxa in the reforested sites of the three mangrove forests was significantly higher than in the bare site, but always similar to that found in the natural site (with no significant difference between the reforested and natural sites within each mangrove forest). This suggests that mangrove reforestation has led to recovery of ecosystem functioning in terms of habitat provision for the sedimentinfauna, which play an important role in the mangrove ecosystem. Schrijvers et al. (1995) noted that denuded stations showed a low organic matter content. They noted that these areas, which were more open, do not slow down the incoming tide and have less of the fine grain size component and organic deposition. Macnae (1968) mentions the existence of a causal association between fauna and the type of mangrove. He also observed a clear relationship between the fauna and environmental variables such as substrate type, salinity, oxygen, water table level, presence of microorganisms and organic material. Their findings of mangrove stations having higher macrofaunal densities than open areas are consistent with observations in the present study, because organic matter content was higher in both the natural and reforested sites than in the bare sites of the studied mangrove forests. Harkantra et al. (1982) concluded that faunal abundance in relation to sediment type showed that loose sand sheltered substrates supported rich fauna, whereas fine textured substrata were relatively impoverished. Although it was not the objective of the present study to compare macrobenthic fauna densities between different mangrove species, it was apparent that the *S. alba* sites, the substrata of which were predominantly sandy, had the highest abundance and number of sediment-infauna taxa compared to the respective sites of the other mangrove species.

Some species/taxa in this study were found to occur either in all comparable sites, in only two sites or in some cases only in one respective site. Except for the A. marina sites, where there were no crab species strictly found either in the natural site, reforested site or in both, the converse was true of the other two mangrove species. Except for the species shared between the three sites, there were no crab species, for instance, which were shared between the natural and bare sites of R. mucronata and S. alba, implying that these two sites were quite different functionally, save for the species occurring commonly in the three sites. However, the reforested and natural sites of these two forests had a number of species in common. Apart from the species that occurred commonly in the three sites of these mangrove forests, some crab species were strictly found either in the reforested and natural sites or both, suggesting that these species are normally inhabitants of forested mangrove areas, which is consistent with the above mentioned studies. Of the new crab species recruited into the reforested sites, most of them were sesarmids, which play an important primary role in litter degradation (Malley 1978; Micheli et al. 1991; Micheli 1993; Lee 1997; Slim et al. 1997) in mangroves, hence initiating and enhancing the detrital based food webs by shredding the litter and returning it to the environment as faecal material in a more finely divided state. Subsequent degradation of this litter by microbes significantly contributes to the high nutrient enrichment in the mangrove ecosystem. With respect to sediment-infauna, there were no taxa found strictly in the bare sites, but whichever taxon or taxa occurred in the bare sites, the same taxon was also represented in the respective reforested and natural sites. The latter two sites, however, had a significantly higher number of taxa than the former. The reforested and natural sites of all the three mangrove forests had a number of taxa in common which did not occur in the comparable bare sites, besides those which were shared between all the three respective sites. Since all the sediment-infauna taxa found in the bare sites were also represented in the comparable reforested and natural sites, it is very likely that these taxa are universal in their occurrence and thus are not limited to areas with mangrove cover in the mangrove ecosystem. The bare sites were in all cases more impoverished than the comparable sites with mangroves, which stresses the ecological consequences of severe extractive human pressure on this ecosystem. This calls for rational mangrove exploitation and extended reforestation of other degraded sites so as to conserve the ecological functioning of the ecosystem, among other benefits. If co-occurrence of taxa in different sites is a reflection of functional ecological semblance or equivalency, then the reforested sites were more akin to the respective natural sites, emphasising the importance of mangrove cover in determining ecosystem structure and function.

In conservation biology, ecological restoration or nature management, one of the fundamental objectives is to maintain ecosystem functioning. In tropical coastal ecosystems, this comprises the functioning of many biocomplex relationships (Dahdouh-Guebas 2002) between ecosystem elements and also among interrelated ecosystems (mangrove forests, seagrass beds and coral reefs). This therefore implies that disturbance of one such ecosystem, depending on the scale, is likely to disrupt functional equilibrium within itself and in related ecosystems. Investigation of concomitant natural developments (e.g. floristic and faunistic recruitment and even biogeochemistry) in reforested sites is thus necessary to gain more insight into the impact of artificial regeneration in ecological conservation.

The modification of mangrove habitats by humans, especially through deforestation, results in the loss of the functional attributes inherent in mangroves, in this case the support of rich densities and taxa of the investigated fauna, which subsequently may alter the structure and functioning of the ecosystem. This was apparent from the impoverished macrobenthic densities in the bare sites, whereas the reforested sites had significantly higher densities and were richer, especially in the number of sediment-infauna taxa recruited. In fact, in terms of faunal densities and taxa/species composition, the reforested sites generally departed significantly from the respective bare controls and seemed to be functionally developing towards the original natural forests. The results therefore suggest that reforestation has had a positive impact as far as macrofaunal recruitment is concerned, hence supporting artificial mangrove regeneration as a management tool of restoring degraded mangrove ecosystems where natural regeneration has otherwise not been successful. More similar studies are, however, necessary in the future to augment these findings and monitor any evolving patterns of recolonisation.

Acknowledgements

Special thanks go to Prof. Daro for her assistance in the field, the Royal Belgian Institute of Natural Sciences through Prof. Wartel and F. Francken for assistance in grain size analysis and all the colleagues at KMFRI who assisted in both the sampling and lab work to make this study a success. The second author is a Postdoctoral Researcher of the Fund for Scientific Research (FWO – Vlaanderen). The research was financed by the Fund for Scientific Research (Flanders, Belgium) and the European Union and the results were presented at the Estuarine Research Federation Conference (ERF '99) and Mangrove Macrobenthos Meeting (MMM) of E. Africa (2000).

References

Ahmad N. 1984. Some aspects of economic resources of Sundarban mangrove forest of Bangladesh. In: Soepadimo E., Rao A.N. and Macintosh D.J. (Eds.), Proceedings of the Asian Symposium on Mangrove Environment, Research and Management. University of Malaya, Kuala Lumpar, Malaysia, pp. 644–651. Aksornkoae S. 1993. Ecology and Management of Mangroves. IUCN, Bangkok, Thailand, 176 pp.

- Aksornkoae S. 1996. Reforestation of mangrove forests in Thailand: a case study of Pattani province. In: Field C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society of Mangrove Ecosystems (ISME), Okinawa, Japan, pp. 52–63.
- Arnold K. 1986. Methods of Soil Analysis. Part 1: Physical and Mineralogical Methods. 2nd ed. American Society of Agronomy, Madison, Wisconsin, 1159 pp.
- Begon H., Harper J.L. and Townsend C.R. 1996. Ecology: Individuals, Populations and Communities. 3rd ed. Blackwell Science, Oxford, UK, 1068 pp.
- Cannicci S., Ritossa S., Ruwa R.K. and Vannini M. 1996. Tree fidelity and hole fidelity in the tree crab Sesarma leptosoma. Journal of Experimental Marine Biology and Ecology 196(1–2): 299–311.
- Cannicci S., Dahdouh-Guebas F., and Montemagno L. 1997. Field Keys for Kenyan Mangrove Crabs. Museo Zoologico 'Leo Pardi' of the University of Florence, Florence, Italy.
- Dahdouh-Guebas F. 2001. Mangrove vegetation structure, dynamics and regeneration. Ph.D. Thesis, Vrije Universiteit Brussel, Belgium. 317 pp.
- Dahdouh-Guebas F. 2002. The use of remote sensing and GIS in the sustainable management of tropical coastal ecosystems. In: Dahdouh-Guebas F. (Ed.), Remote Sensing and GIS in the Sustainable Management of Tropical Coastal Ecosystems. Environment, Development and Sustainability 4: 93–112.
- Dahdouh-Guebas F., Giuggioli M., Oluoch A., Vannini M. and Cannicci S. 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bulletin of Marine Science 64: 291–297.
- Dahdouh-Guebas F., Verneirt M., Cannicci S., Kairo J.G., Tack J.F. and Koedam N. 2002. An exploratory study on grapsid crab zonation in mangrove forests in Kenya. Wetlands Ecology and Management 10: 179–187.
- Dahdouh-Guebas F., Verneirt M., Tack J.F. and Koedam N. 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347: 83–89.
- Day J.H. 1974. A Guide to Marine Life of South Africa Shores. 2nd edn. Balkema, Capetown, South Africa, 300 pp.
- Ellison A.M. 2000. Mangrove restoration: Do we know enough? Restoration Ecology 8: 219-229.
- Fondo E. and Martens E. 1998. Effects of mangrove deforestation on macrofaunal densities in Gazi Bay, Kenya. Mangroves and Salt Marshes 2: 75–81.
- Frith D.W., Tantanasiriwong R. and Bhatia O. 1976. Zonation and abundance of macrofauna on a mangrove shore, Phuket Island, Southern Thailand. Phuket Marine Biology Center Research Bulletin 10: 1–37.
- Frith D.W. and Frith C.B. 1977. Observations on fiddler crabs (Ocypodidae: Genus Uca) on Surin Island, Western Peninsular, Thailand, with special reference to *Uca tetragonon* (Herbst). Phuket Marine Biology Center Research Bulletin 18: 1–14.
- Harkantra S.N., Rodrigues C.L. and Parulekar A.H. 1982. Macrobenthos of the shelf off North Eastern Bay of Bengal. Indian Journal of Marine Science 11: 115–121.
- Kairo J.G. 1995. Community participatory forestry for rehabilitation of deforested mangrove areas of Gazi Bay (Kenya). 'A first approach'. Final Technical Report, 59 pp.
- Kent M. and Coker P. 1992. Vegetation Description and Analysis: A Practical Approach. Wiley, New York, 363 pp.
- Kitheka J.U. 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. Estuarine Coastal and Shelf Science 45: 177–187.
- Lee S.Y. 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. Marine Ecology Progress Series 159: 275–284.
- Lee S.Y. 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. Marine Freshwater Research 49: 335–343.
- Macnae W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo West Pacific region. Advances in Marine Biology 6: 73–270.
- Macnae W. and Kalk M. 1962. The ecology of the mangrove swamps at Inhaca Island, Mozambique. Journal of Ecology 50: 19–34.
- Macintosh D.J. 1984. Ecology and productivity of Malaysian mangroves crab populations (Decapoda: Branchyura). In: Soepadimo E., Rao A.N. and Macintosh D.J. (Eds.), Proceedings of the Asian

Symposium on Mangrove Environment, Research and Management. University of Malaya, Kuala Lumpar, Malaysia, pp. 354–377.

- Macintosh D.J. 1988. The ecology and physiology of decapods of mangrove swamps. Symposium of the Zoological Society London 59: 315–341.
- Malley D.F. 1978. Degradation of mangrove leaf litter by the tropical sesarmid crab Chiromanthes onychophorum. Marine Biology 49: 377–386.
- Micheli F. 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. Journal of Experimental Marine Biology and Ecology 171: 165–186.
- Micheli F., Gherardi F. and Vannini M. 1991. Feeding and burrowing ecology of two East African mangrove crabs. Marine Biology 111: 247–254.
- Ngoile M.A.K. and Shunula J.P. 1992. Status and exploitation of the mangroves and associated fishery resources in Zanzibar. In: Jaccarini V. and Martens E. (Eds.), The Ecology of Mangroves and Related Ecosystems. Hydrobiologia 247: 229–234.
- Qureshi M.T. 1996. Restoration of mangroves in Pakistan. In: Field C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society of Mangrove Ecosystems (ISME), Okinawa, Japan, pp. 126–142.
- Rawlins S.P. 1957. The East-African mangrove trade. Unpublished manuscript #51 of the National Museum of Kenya, Nairobi, Kenya.
- Rönnbäck P. 2001. Mangroves and Seafood Production. The Ecological Economics of Sustainability. Akademitryck AB, Edsbruk, Sweden.
- Robertson A.I. 1991. Plant–animal interactions and the structure and function of mangrove forest ecosystems. Australian Journal of Ecology 16: 433–443.
- Robert L., Morlang A. and Gorman L. 1997. Monitoring the coastal environment Part II: Sediment sampling and geotechnical methods. Journal of Coastal Research 13: 308–330.
- Ruwa R.K. 1997. Zonation of burrowing crabs in the mangroves of the east coast of Kenya. In: Kjerfre B., de Lacerda L.D. and Diop E.H.S. (Eds.), Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, France, pp. 316–324.
- Saenger P. 1996. Mangrove restoration in Australia: a case study of Brisbane International Airport. In: Field C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society of Mangrove Ecosystems (ISME), Okinawa, Japan, pp. 36–51.
- Sasekumar A., Chong V.C., Leh M.V. and D'Cruz R. 1992. Mangroves as a habitat for fish and prawns. In: Jaccarini V. and Martens E. (Eds.), The Ecology of Mangroves and Related Ecosystems. Hydrobiologia 247: 195–207.
- Schrijvers J., Van Gansheke D. and Vincx M. 1995. Mangrove benthic infauna of mangrove and surrounding beaches at Gazi Bay, Kenya. Hydrobiologia 306: 55–66.
- SFFL 1997. Performance Report for the Years 1994, 1995 and 1996. Small Fisheries Federation of Lanka, Pambala, Kakkapalliya, Sri Lanka.
- Siddiqi N.A., and Khan M.A.S. 1996. Planting techniques of mangroves on new accretions in the coastal areas of Bangladesh. In: Field C.D. (Ed.), Restoration of Mangrove Ecosystems. International Society of Mangrove Ecosystems (ISME), Okinawa, Japan, pp. 143–159.
- Slim F.J., Hemminga M.A., Ochieng C., Jannink N.T., Cocheret de la Moriniere E. and van der Velde G. 1997. Leaf litter removal by the snail *Telebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). Journal of Experimental Marine Biology and Ecology 215: 35–48.
- Smith III T.J. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68: 266–273.
- Steele O.C., Ewel C.K. and Goldstein G. 1999. The importance of propagule predation in a forest of non-indigenous mangrove trees. Wetlands 19: 705–708.
- Steinke T.D., Rajh A. and Holland A.J. 1993. The feeding behaviour of the red mangrove crab Sesarma meinerti De Man, 1887 (Crustacea: Decapoda: Grapsidae) and its effect on the degradation of mangrove litter. South African Journal of Marine Science 13: 151–160.
- Stromberg H., Petterson C. and Johnson R. 1998. Spatial variations in benthic macrofauna and nutrient dynamics in a mangrove forest subject to intense deforestation: Zanzibar, Tanzania. Ambio 27(8): 734–739.

- Tack J.F. and Polk P. 1999. The influence of tropical catchments upon the coastal zone: modelling the links between groundwater and mangrove losses in Kenya, India and Florida. In: Harper D. and Brown T. (Eds.), Sustainable Management in Tropical Catchments. John Wiley and Sons Ltd, London.
- Tomlinson P.B. 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, UK, 419 pp. Vannini M., Oluoch A. and Ruwa R.K. 1997. Tree climbing decapods of Kenyan mangroves. In:
- Kjerfre B., de Lacerda L.D. and Diop E.H.S. (Eds.), Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, France, pp. 325–338.
- Wartel S., Barusseau J. and Cornand L. 1995. Improvement of grain size analyzes using the automated SEDIGRAPH 5100. Studiedocumenten van het K.B.I.N. 28 pp.
- Watson J.G. 1928. Mangrove Forests of the Malay Peninsula. Malay Forest Records Vol. 6. Fraser and Neave, Singapore, 275 pp.