Patterns of Meiofaunal Colonisation as an Indicator of Reforested *Rhizophora mucronata* Mangrove Recovery in Gazi Bay, Kenya

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Abstract—Meiofaunal recolonisation patterns were investigated in restored Rhizophora mucronata forests by assessing their density, community composition and diversity. This was done in five- and ten-year reforested mangroves, with natural and degraded controls. MDS and ANOSIM of meiofaunal community composition separated the natural and the ten-year reforested sites from the fiveyear reforested and degraded sites. Nematodes were the dominant meiofaunal taxon at all the sites, accounting for >90% of the meiofaunal densities. The natural and the ten-year reforested sites were rich in silt/clay sediments and organic matter, and had the highest meiofaunal (1201 ± 197 and 1379 ± 369 meiofauna.10 cm⁻² respectively) and nematode (1142 \pm 196 and 1320 \pm 341 meiofauna.10 cm⁻² respectively) densities. The degraded site had a significantly higher Shannon Diversity index than all the other sites, which was linked to the higher dominance by nematodes in the natural, five- and ten-year old reforested sites. The study showed that degradation of mangroves leads to changes in habitat with concomitantly impoverished meiofaunal communities in terms of their density and community composition. It was also evident that recovery of meiofaunal communities, particular of the nematodes, occurs after five to ten year's reforestation.

INTRODUCTION

Meiofauna comprise all sediment-dwelling metazoans which are retained on a 38 µm sieve (Vincx, 1996). They are ubiquitous in most marine ecosystems, from estuaries to the hydrothermal vents in the deep sea (Giere, 1993). Their abundance and species composition are controlled by several physical factors, including sediment particle size, temperature and salinity, as well as biochemical conditions fluxes of organic matter and oxygen (Giere, 1993). The role of meiofauna in carbon flows through benthic food webs in marine biotopes, including tidal mud flats and estuaries, is still a matter of debate (Bouillon et al., 2004a, b; Urban-Malinga & Moens, 2006). Some studies suggest that meiofauna may play an important role in trophic processes such as the breakdown of mangrove plant material to detritus and its mineralisation by micro-organisms (De Mesel, et al., 2003; Riera & Hubas, 2003; Chinnadurai & Fernado, 2007).

According to Tietjen and Alongi (1990) and Coull (1999), meiofauna may stimulate bacterial growth and hence contribute to nutrient generation in several ways such as: i) the mechanical breakdown of detrital particles which makes them more susceptible to microbial decomposition, ii) the excretion of nutrients which are used by the microbial community, iii) the production of slime and mucus that attracts and sustains bacterial growth and iv) sediment bioturbation with meiofauna acting as conveyors of biochemical substances within the sediments and between the sediments and overlying waters.

The wide range of feeding modes found in meiofaunal groups enables them to occupy several trophic levels which, coupled with their relatively high densities, may enhance the energy flow in the detrital system (Dye, 1983a, b). Meiofauna are preyed upon by juveniles of a large number of fish species and benthic macrofauna like shrimps, crabs, polychaetes and gastropods (Olaffson & Moore, 1990; Vincx, 1996). Many meiofaunal predators have an obligatory meiofaunal feeding stage with copepods as the major meiofaunal prey (Gee, 1989).

According to Gwyther (2003), fallen leaves in mangrove forests provide new patches of phytal habitat on the sediment surface, providing an opportunity to investigate successional, trophic and taxonomic changes in litter assemblages as the fallen leaves decay. Meiofaunal particulate food on leaf litter includes the surface biofilm, which comprises bacteria, microalgae, protozoa and fungi (Skilletter & Warren, 2000; Netto & Galluci, 2003). Gee and Sommerfield (1997) showed that the climax meiofauna on mangrove leaf litter were not influenced by the species of mangrove leaf. However, there is a shift in species composition over time which reflects meiofaunal successional changes associated with differential leaf litter decay.

Mangrove forests and their associated soft-sediments are common coastal habitats in tropical and warm subtropical latitudes. The majority of mangrove forests lie within the vicinity of coastal cities or other large human settlements. which makes anthropogenic disturbance a major factor that modifies the structure of mangrove communities (Kairo & Abuodha, 2001; Alongi, 2002). The need for fast economic development in the coastal zone has led to massive destruction of mangrove forests in many countries. The effects of eutrophication, unplanned coastal development, unsustainable exploitation of mangrove resources and aquaculture are common on tropical and subtropical coastlines (Netto & Galluci, 2003). Some of these activities involve cutting or clear felling of the mangrove trees, leaving some areas completely bare.

Although meiofauna are threatened by mangrove degradation which causes the loss of their habitat, very few studies have focused on meiofaunal assemblages, especially in degraded and restored mangrove forests, despite the crucial role they play in these systems. Most studies have focused on macrofaunal assemblages in mangroves (e.g. Fondo & Martens, 1998; Sasekumar and Chong, 1998). Furthermore, only a few studies have focused on mangrove restoration and meiofaunal recolonisation in restored mangrove ecosystems (e.g. Khalil, 2001; Mwojoria, 2007).

An understanding of the effects of habitat loss or restoration on the functioning of mangrove ecosystems necessitates elucidation of their faunal diversity. Meiobenthic and macrobenthic assemblages form a crucial component in mangrove ecosystems and, therefore, should be analysed together with their vegetation structure to determine the overall mangrove restoration process and success (Field, 1999). Studies of this nature have been undertaken on the ecology and distribution of meiofauna in various parts of the world such as Australia (Hodda & Nicholas, 1985; Alongi, 1987a, b, c; Gwyther, 2003), Tanzania (Olaffson et al., 2000), SE India (Chinnadurai & Fernado, 2007), Sudan (Khalil, 2001) and Brazil (Netto & Galluci, 2003). However, few studies that have been undertaken on mangrove degradation and/or reforestation along the Kenyan coast and have concentrated mainly on the macrobenthic assemblages (Fondo & Martens, 1998; Bosire et al., 2004). While Vanhove et al. (1992) and Schrijvers et al. (1995, 1997) have undertaken ecological studies on Kenyan mangrove meiofauna, only one study (Mwojoria, 2007) has focused on the effects of degradation and restoration of a Sonneratia alba mangrove ecosystem in this regard.

This study thus constitutes the first along the Kenyan coast which compares the meiofaunal community assemblages in natural, reforested and degraded (clear-felled) *Rhizophora mucronata* forests.

The objectives of the study were to:

- Determine the effect of mangrove forest degradation (clear-felling) on meiofaunal densities, community composition and diversity.
- Compare the meiofauna in *R. mucronata* forests at different stages of restoration.
- Relate patterns in the meiofaunal community structure to physical characteristics in the sediments.

These objectives were achieved by comparing the meiobenthos in two reforested *R. mucronata* areas of different age (five and ten years old) with those in a natural and fully degraded forest.

MATERIALS and METHODS

Study site

The study was conducted in Gazi Bay, 50 km south of Mombasa in Kenya, in a natural stand of *R. mucronata*, five- and ten-year old replantings, and a degraded forest (Fig. 1).



Figure 1. Map of Gazi Bay showing the study sites. 1 = Degraded site, 2 = Natural site, 3 = ten-year old reforested site and 4 = five-year old reforested site (adapted from Bosire *et al.*, 2004).

The natural (Nat), ten-year old reforested (Refo10) and degraded (Degr) sites were in inundation class 4 and were therefore flooded by tidal water during high spring tides, while the five-year old reforested site (Refo5) was in inundation class 2 and was covered by water during medium high tides (Hogarth, 1999).

Sampling and sample analysis

Three sampling plots measuring 15 x 15 m (225 m²) and 50 m apart were randomly selected at each of the above sites. Triplicate sediment cores (3.2 cm internal diameter, 5 cm long) were randomly collected from each plot and fixed in 5% formalin for meiofaunal analysis. Meiofauna were separated from the sediment by sieving through a 38 µm sieve with 2 mm and 0.5 mm pre-sieving to exclude debris and macrofauna. The meiofaunal fraction retained on the 38 µm sieve was centrifuged three times at 6000 rpm with magnesium sulphate (MgSO₄) of specific density 1.28 for 10 minutes (Heip et al., 1974, 1985) and re-sieved through the 38 µm mesh. The meiofauna were then rinsed in tap water and stained with Rose Bengal. Meiofauna were identified to the highest taxon and counted under a dissecting microscope following Higgins and Thiel (1992). Additionally, three sediment cores (6.4 cm \emptyset , 10 cm long) were randomly collected in each plot for total organic matter (TOM) and grain size analysis. The TOM samples were oven-dried at 80°C for 24 h to remove all the moisture. Thereafter, 10 g of the dried samples were ashed at 600°C for 6 h to obtain the ash free dry weight (AFDW); TOM was calculated as the percentage of the ashed material. Sediment grain size was analysed using the standard method of Buchanan and Kain (1971). Interstitial sediment water samples were collected for measurement of salinity and temperature in a 5-10 cm hole dug in the sediment. Salinity was measured using an Atago optical refractometer. Temperature was measured using a glass thermometer. Sampling was undertaken during low tide during the dry season (for ease of access) in September 2005.

Statistical analysis

Data were analysed using PRIMER (v. 5) and STATISTICA (v. 6). Principal Component Analysis (PCA) ordination using Euclidean distances was used to reveal variation between sites based on the sediment characteristics. Non-metric multidimensional scaling (nMDS) ordination of square root-transformed data using the Bray-Curtis similarity coefficient was used to reveal similarities between the study sites in terms of meiofaunal community composition. Variations in meiofaunal density between sites were tested using analysis of similarity (ANOSIM; Clarke & Gorley, 2001). The Shannon diversity index (H'), highest taxonomic richness (S) and species rarefaction (ES_a) were calculated using DIVERSE. SIMPER was used to determine which meiofaunal taxa contributed most to the similarities and dissimilarities, and between sites. Differences in environmental characteristics between sites, their meiofaunal density and diversity indices were analysed using ANOVA, while post hoc analysis was performed using Tukey's Honest Significant Difference test.

RESULTS

Environmental characteristics

Principal Component Analysis (PCA) based on TOM, silt/clay, salinity and temperature showed a clear separation between the sites (Fig. 2). Principal Components (PC) 1 and 2 explained 99% of the observed variability (PC 1; 87 %, PC 2; 12 %). The first principal component revealed that the natural and the ten-year old reforested sites had higher TOM and silt/clay and were separated from the fiveyear old reforested and degraded sites with high sand content. The five-year old reforested site showed a lot of variability in sediment composition which may be an indication of its transitional state. Separation along the second principal component was less pronounced, although it revealed differences between the natural site and the ten-year old reforested sites based on TOM.



Figure 2. PCA ordination showing the separation of natural, ten-year old reforested, five-year old reforested and degraded sites in Gazi Bay in terms of their physical sediment characteristics.

Meiofaunal densities and community composition

A total of 15 meiofaunal classes were recorded at all the sites. The natural and the ten-year old reforested sites had nine meiofaunal classes each, while the degraded and the fiveyear old reforested sites had eight and seven classes respectively. Nematoda comprised the dominant taxon at all the study sites, accounting for over 90% of the meiofauna.

Figure 3 illustrates the variation in total meiofaunal densities. The natural site had lower densities $(1201 \pm 197 \text{ meiofauna.10 cm}^2)$ than the ten-year old reforested site $(1379 \pm 369 \text{ meiofauna.10 cm}^2)$ (Fig. 3a). Significantly higher meiofaunal densities were recorded at the natural and ten-year old reforested sites than all the other sites (ANOVA, df = 3, F = 17.64, p < 0.05). However, both the degraded and five-year old reforested sites did not differ significantly in meiofauna densities.

Similarly, nematode densities (Fig. 3b) were highest at the ten-year old reforested site $(1320 \pm 341 \text{ meiofana.}10 \text{ cm}^{-2})$ and lowest at

the degraded site $(320 \pm 243 \text{ meiofana.10} \text{ cm}^{-2})$. As with the total meiofauna, the natural site had lower nematode densities $(1142 \pm 196 \text{ meiofana.10} \text{ cm}^{-2})$ than the ten-year old reforested site. The nematode densities recorded at the natural and ten-year old reforested sites were significantly higher than all the other sites (ANOVA, df = 3, F= 17.44, p < 0.05).

Non-Metric Multidimensional Scaling (nMDS) of the meiofaunal densities and community composition revealed no separation between the natural and the tenyear old reforested sites (Fig. 4). However, the five-year old reforested and the degraded sites formed separate clusters. The nMDS pattern was further confirmed by ANOSIM pair-wise comparisons which revealed no significant differences (R >0.5) between the clusters other than those containing the natural and the ten-year old reforested sites (R = -0.062). SIMPER analysis revealed that the dissimilarities observed between sites were mainly contributed to by the Copepoda, Oligochaeta and Nemertina.



Figure 3. Density (mean \pm SE) of a) meiofauna and b) Nematoda in the natural, ten-year old reforested, five-year old reforested and degraded sites in Gazi Bay (n=9).

Meiofaunal diversity

The meiofaunal taxonomic richness was highest at the ten-year old reforested site (4.6 ± 1.1) and lowest at the five-year old reforested site (3.3 ± 0.9) . The five-year old

reforested site also had the lowest Shannon diversity index and taxonomic rarefaction $(0.1 \pm 0 \text{ and } 1.4 \pm 0.3 \text{ respectively; Table 1})$. Due to the influence of species dominance on the Shannon diversity index (Maguran, 1991),



Figure 4. nMDS (Log_x+1) of meiofaunal community composition showing affinities between the natural, ten-year old reforested , five-year old reforested and degraded sites in Gazi Bay.

Table 1. Meiofaunal community diversity measures (mean \pm SD, n=9) in the natural, tenyear old reforested, five-year old reforested and degraded sites.

Sites	S	ES_{50}	H' \log_{e}
Natural	4.4 ± 1.4	2.2 ± 0.6	0.2 ± 0.1
Ten years reforested	4.6 ± 1.1	2.0 ± 0.2	0.2 ± 0.1
Five years reforested	3.3 ± 0.9	1.4 ± 0.3	0.1 ± 0
Degraded	3.9 ± 1.1	2.5 ± 0.3	0.4 ± 0.2

S = meiofaunal taxonomic richness; ES₅₀ = meiofaunal taxonomic rarefaction; H' \log_{a} = Shannon Diversity Index

the natural and the ten-year old reforested sites had low Shannon diversity indices due to the dominance of the meiofauna here by nematodes. However, due to the lower relative abundance of nematodes at the degraded site, its Shannon diversity index was the highest. There were no significant differences between sites in meiofaunal taxonomic richness, but the differences in taxonomic rarefaction (Kruskal-Wallis, df = 3, H = 16.43, p <0.05) and the Shannon diversity index (Kruskal-Wallis, df = 3, H = 18.72, p <0.05) were significant.

DISCUSSION

Vanhove et al. (1992) investigated the vertical distribution of meiofauna in sediments associated with five mangrove species (Avicenia marina, Bruguiera gymnorrhiza, Ceriops tagal, Rhizophora mucronata and Sonneratia alba) in Gazi Bay, Kenya, and identified 17 meiofauna taxa. The highest meiofaunal densities occurred in sediments of B. gymnorrhiza (6707 meiofauna.10 cm⁻²) followed by R. mucronata (3998 meiofauna.10 cm⁻²), A. marina (3442 meiofauna.10 cm⁻²), S. alba (2889 meiofauna.10 cm⁻²) and C. tagal (1976 meiofauna.10 cm⁻²), with nematodes accounting for 95% of the meiofaunal densities. Sediment granulometry and oxygen conditions proved to be the major factors influencing meiofaunal distribution. Schrijvers et al. (1995) investigated the human impact on meiofauna in partially impacted C. tagal and R. mucronata mangroves in Gazi Bay, Kenya. They established that impacted sites had lower densities of meiofauna and, in particular, nematodes. They linked this decrease to the loss of both organic matter and muddy sediments in cleared mangroves, resulting from increased tidal currents which lead to sediment re-suspension and eventual erosion.

In Gazi Bay, mangrove restoration programmes started 15 years ago. However, only Mwojoria (2007) has studied benthic meiofauna in restored S. alba mangrove forests. His findings indicated that there were no differences in meiofaunal densities at natural and reforested sites. The results of the present study show a clear separation of restored R. mucronata forest stands of different age (five and ten years), based on their sediment characteristics and also on their meiofaunal densities and community composition. However, the differences in meiofaunal community structure between the natural and the ten-year old reforested sites were not significant, despite their differences in sediment characteristics (especially TOM). This shows that the meiofaunal population is regulated by complex of factors.

The total number of taxa recorded was similar to that found by Vanhove et al. (1992), Schrijvers et al. (1997) at R. mucronata sites, and by Mwojoria (2007) at S. alba sites in Gazi Bay. However, the density of meiofauna encountered in the current study was different from the earlier studies. Vanhove et al. (1992) and Schrijvers et al. (1997) recorded higher densities of meiofauna at their R. mucronata sites (3998 and 6101 meiofauna.10 cm⁻² respectively), compared to the current study (1339 meiofauna.10 cm⁻²), while Mwojoria (2007) recorded almost similar densities of between 1576 and 1774 meiofauna.10 cm⁻² at the S. alba sites. Chinnadurai and Fernado, (2007) recorded far lower meiofaunal densities (max 474 meiofauna.10 cm⁻²) in R. apiculata stands in S Indian mangroves, while Netto and Galluci (2003) recorded a maximum of 1586 meiofauna.10 cm⁻² in Brazilian mangroves. Nevertheless, these meiofaunal densities fall within the same order of magnitude.

Differences in meiofaunal densities between the present and earlier studies in Gazi Bay can be related to the inundation class of the study sites as the latter were located in inundation class 1, while the sites in the current study were located in inundation class 4. Mangroves in inundation class 4 are covered by tidal water during high spring tides only, while those in inundation class 1 are covered by water during all high tides (Hogarth, 1999). Mangroves in inundation class 4 are exposed for longer periods, while those in inundation class 1 are covered by water during all tidal cycles. Tidal level thus appears to play a crucial role in benthic community dynamics since it determines the duration of elevated temperature and salinity stress during exposure. In this regard, Sasekumar (1994) recorded an increase in meiofaunal densities with decreasing tidal height in Malaysia, linked to reduced tidal exposure and environmental stress. Additionally, Alongi (1987a) recorded decreased nematode densities with reduced tidal exposure in Australian mangrove forests. The differences were linked to differences in physico-chemical parameters such as sediment granulometry, soluble tannins, temperature and disturbance as well as food availability.

Nematoda were the most abundant taxon in the current study, accounting for over 90% of the meiofaunal densities at all the sites. Meiofaunal dominance by nematodes has also been reported in earlier surveys of East African (Vanhove et al., 1992; Schrijvers et. al., 1997; Olaffson et al., 2000; Mwojoria, 2007), Indian (Sasekumar, 1994; Chinnadurai & Fernado, 2007), and South African mangroves (Dye, 1983a, b; Hodda & Nicholas, 1985). In the present study, the natural and the ten-year old reforested sites were characterised by complex pneumatophores, silty sediments (silt fraction >50%), the highest TOM content and the highest densities of meiofauna, especially nematodes. These factors, coupled with the availability of leaf litter and detritus, probably provided the meiofauna with suitable habitat at these sites.

Giere, (1993) noted that nematode community composition and diversity are largely determined by sediment structure, and probably by the levels of silt which limit their range. In similar vein, Netto and Galluci (2003) stated that sediment grain size and organic matter play a vital role in determining the patterns of meiofauna distribution. These parameters influence the availability of food for meiofauna via the detrital food web, as sediment infauna feed on microflora associated with decomposing detrital material (Skilletter & Warren, 2000). In this regard, Gwyther (2003) noted that detritus in different stages of decomposition harbours biofilms, creating microhabitats that harbour bacteria, microalgae, protozoa and fungi which constitute food for benthic fauna. These factors undoubtedly contributed to the high densities of meiofauna recorded at the natural and the ten-year old reforested sites.

Although the meiofauna community at the ten-year old reforested site equalled that of the natural site, the two sites differed in terms of TOM and sediment type. The former had a more diverse meiofauna than the natural site, as evidenced by its higher taxonomic richness. These results may indicate that the natural site harboured a climax community, while the meiofaunal community at ten-year old reforested site, being a developing system, was still developing as the habitat became more amenable.

A reduced mangrove canopy exposes the underlying sediments which causes environmental stress to benthic fauna (Sasekumar, 1994). Sediment salinity and temperature increase with exposure, negatively affecting the benthic microphytobenthos which constitute a food source for benthic fauna (Ingole & Parulekar, 1998). The elevated temperatures and salinities recorded at the degraded site suggest that environmental stress was high, which, in combination with the lower TOM content, would have impaired the meiofauna at this site.

This study has thus added to the body of information on meiofaunal communities in Kenyan mangroves, including restored *R. mucronata* mangroves for which this information was hitherto lacking. It has shown that degradation of mangrove forests leads to changes in the interstitial habitat, and is associated impoverishment of the meiofauna in terms of density and community composition. A slow recovery takes place in the meiofaunal community with improvement in the sediment habitat some years after reforestation, but some taxa like the nematodes only re-appear in naturally high densities more than five years after reforestation. Acknowledgements-Special thanks are due to Vlaamse Interuniversitaire Raad – Inter University Council - University of Nairobi (VLIR-IUC-UoN) programme for funding this research.

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