Response of Benthic Fauna to Mangrove Degradation and Restoration in Gazi Bay - Kenya

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Declaration

I declare that this thesis is my original work and has not been presented for a degree in any other university.

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Dedication

This work is dedicated to my late father, Peter Mutua Musango (1950 – 2004) and my mother, Elizabeth Mutindi to whom I owe so much.

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Abstract

The recovery towards a natural state of a restored *Rhizophora mucronata* mangrove ecosystem was investigated by assessing the sediment physical characteristics, densities, community composition and diversity of benthic macro-endofauna and meio-endofauna from a natural, a 10 years reforested, a 5 years reforested and a degraded (clear felled) mangrove ecosystem. The natural forest was used as a reference (baseline state) while the degraded site was to provide information on the effects of mangrove degradation on macro-endofauna. Samples for sediment physical characteristics and macro-endofauna were taken using a 6.4 cm diameter corer while meiofauna and nematode samples were taken using a 3.2 cm diameter corer. Nematode extraction was done by centrifuging using Magnesium Sulphate ($MgSO_4$) solution. There were significant differences (ANOVA, $p < 0.05$) between the study sites in Total Organic Matter (TOM), with the natural site recording the highest TOM levels (53.6 %). The 10 years reforested site was characterised by a significantly higher (72.9 %; ANOVA, $p < 0.05$) silt/clay fraction than the other sites. The natural site recorded significantly higher macro-endofauna densities (27,469 ± 11,189 Ind. /m^2) than all the other sites (ANOVA, $p < 0.05$). Oligochaeta was the dominant macrofauna taxon in the natural and the 10 years reforested sites, while Polychaeta and Nemertina dominated the 5 years reforested and the degraded sites respectively. The natural and the 10 years reforested sites recorded significantly higher (ANOVA, $p < 0.05$) meiofauna and nematode densities than the 5 years reforested and the degraded sites. Nematoda was the dominant meiofauna taxon in all the study sites. Both the natural and the 10 years reforested sites were characterised by high densities of the nematode genera *Terschellingia* and *Pierickia*, respectively, while the degraded site was dominated by the genera

Metachromadora. The index of Trophic Diversity (ITD) was low in all sites indicating that all nematode trophic groups were represented in almost similar proportions in all the sites. PCA and nMDS analysis together with ANOSIM using sediment physical characteristics and macro-endofauna taxa composition, respectively, gave a clear separation of all the sites. However, no separation of the natural and the 10 years reforested sites was observed based on meiofauna and nematofauna community assemblages. This shows that macro-endofauna is more sensitive to habitat modifications, and therefore, a better indicator of ecosystem recovery since the densities and community composition are not yet fully established to the natural state even after 10 years of reforestation. Inorder to understand the main source of organic matter (detritus) supporting meiobenthos re-colonisation of the reforested sites, a field experiment was done utilising mangrove leaves, sea grass leaves and diatoms as different food types. ANOSIM on meiofauna and nematode community composition gave a clear and significant separation ($R > 0.5$) of mangrove leaf litter from all the other food types, showing that mangrove leaf litter is the preferred source of detritus compared to sea grass and diatoms, for meiofauna within the studied mangrove ecosystems. This study shows that mangrove degradation leads to alterations in sediment physical characteristics, drastic declines in benthic-endofauna densities and changes in community composition. It is also evident that mangrove derived organic matter is the preferred source of detritus and greatly influences recolonisation of restored mangroves by benthic–endofauna. It further shows that the reforested mangrove ecosystems are evolving slowly towards ecosystems that are ecologically similar to the natural forests. However, the recovery may take more than 10 years before being fully realised as evidenced by the differences in TOM, macro-endofauna densities and community composition between the

natural and the 10 years reforested sites. The results of this study have clearly shown that artificial mangrove reforestation programmes should be initiated, encouraged and increased since they lead to recovery of the forest as well as the benthic community. This will lead to sustainability of the economic goods, ecological services and ultimately biodiversity conservation. From the results of this study, it is recommended that alternative building materials and energy sources like establishment of Casuarina plantations should be explored to reduce pressure (clear felling) on mangroves, which ultimately leads to deleterious effects in the benthic community. There is also need to analyse which aspect of the benthic community (density, community structure or diversity) is the best indicator of the recovery of the once degraded mangrove ecosystem.

Key words: Mangrove ecosystem, macrofauna, meiofauna, nematodes, recolonisation, ecosystem-restoration

CHAPTER ONE

Introduction and Literature Review

1.1 Introduction

Mangrove trees are a combination of woody trees and shrubs found in the tropics and subtropics along sheltered coastlines, which flourish in mangrove habitats. Mangrove habitats or mangals (=mangroves) are periodically inundated by sea water with rise in tides. Therefore, mangrove trees grow in substrates that are more or less permanently water logged, unstable and anoxic, whose salinity fluctuates and may be as high as that of the open sea or even higher. Since mangroves grow in sheltered tropical depositional and saline environments, the plants are exposed to saline conditions causing an expenditure of energy to conserve water (Hogarth, 1999). Therefore, mangroves and the associated vascular plants have xeric and halophytic adaptations which enable them survive in anaerobic, saline and frequently waterlogged sediments (Dawes, 1997).

According to Lugo and Snedaker (1974), mangroves can be classified as coastal fringes, overwash islands, riverine, basin, hammock and dwarf communities. Fringing mangroves occur along protected or sheltered shorelines, while overwash mangroves are low intertidal islands. Riverine mangroves occur along rivers and streams and often extend some distance inland. Mangrove trees are usually largest in riverine forests due to the availability of freshwater, nutrients and sediments (Hogarth, 1999). Basin mangroves occur in depressions or basins behind fringing mangroves or berms, and are connected to freshwater streams and coastal waters by tidal creeks. Since they are inland, basin mangroves tend to be smaller and have a more limited flora due to fluctuations in salinity

and prolonged periods of tidal exposure (Lugo & Snedaker 1974). Dwarf mangrove communities occur where abiotic conditions are severe due to limited exchange of water, which results in low nutrient levels, increased sediment salinities due to evaporation and water logging. Hammock mangroves occur in inland tropical wetlands and are isolated by freshwater. In sub tropical areas, hammock mangroves may be replaced by salt marshes due to low temperatures or frost (Lugo & Snedaker, 1974).

True or exclusive mangroves are those which only occur in the mangals, or only rarely elsewhere. Additionally, mangrove associates comprise a large number of plant species which typically occur on the landward margin of the mangal, and often in non-mangal habitats like coastal rain forests, salt marshes or lowland fresh water swamps. Several epiphytes like creepers, orchids, ferns which cannot tolerate saline conditions, only grow high up in the mangrove canopy (Hogarth, 1999).

Globally, mangrove forests cover about 181,000 to 198, 818 km^2, although restricted to (sub) tropical coastal areas (Spalding et al., 1997). Mangroves can grow on sand, peat, rock and coral substrates, though the most luxuriant forests are associated with muddy sediments found in deltaic coasts, lagoons and along estuarine environments. Climatic factors play a critical role in influencing the global distribution of mangroves, such that mangroves are almost exclusively tropical. Their geographical range or distribution is limited by temperature and although they can survive air temperatures as low as 5 ^{0}C, they are intolerant to frost. Mangroves distribution correlates closely with sea surface temperature such that they are delimited by the winter position of the 20 ^{0}C isotherm.

Consequently, the number of species tends to decrease as this isotherm is approached (Hogarth, 1999).

Mangroves have been described as both sinks and sources of nutrients under different situations. They offer many diverse habitats which, together with biochemical interactions, lead to an effective recycling of materials and the transformation of substances. Energy flow through mangrove ecosystems is mainly through detrital breakdown by a variety of detritivores and microbial decomposition pathways. This makes mangrove ecosystems to play an important role as the interface between land and the aquatic environment. Thus, any significant alteration in the integrity or function of mangrove forests affects the fauna and flora within these ecosystems, and also results in a similar alteration of the adjacent ecosystems (Stromberg et al., 1998; Hogarth, 1999).

Mangroves are among the most productive ecosystems and provide a wide range of goods and services. Mangrove ecosystem goods are the products which can be extracted from mangrove forests for direct or indirect human utilisation. These include seafood, timber, honey, fuel wood and medicines among others. Ecosystem services are the processes and conditions through which mangrove ecosystems and the associated fauna and flora support human needs (Daily, 1997). These services include nutrient recycling, sediment accretion and moderation of hydrological processes, which are indeed life supporting functions. Robertson and Alongi (1992) provide a detailed review of mangrove ecology, while Snedaker and Snedaker (1984) give a detailed account of research methods for studying mangrove ecosystems.

1.2 Literature Review

1.2.1 Value of mangrove ecosystems

Mangrove forests are precious resources for multiple socio-economic and ecological uses and cover vast areas of the world's coastlines (Field, 1999). They provide a nutritional base for a range of related fauna and a structural base for microhabitats used by other communities (Lee, 1998; Macintosh et al., 2002). Other ecological functions of mangrove ecosystems include: increasing species richness and/or biodiversity in estuarine and nearshore areas and acting as nursery grounds for various marine fauna. Similarly, they are also characterised by high organic production and act as nutrient traps, a function which reduces nutrient loads into the ocean waters, hence fostering the growth of sea grasses and corals. Additionally, mangroves play a role in shoreline stability by reducing excessive erosion (Hogarth, 1999; Alongi, 2002). There are a variety of traditional products extracted from mangrove trees. These include; tannins used for coating and preserving wood, nets and other fishing gear and dying of clothes. Honey and a variety of traditional medicines are also extracted from *Avicenia marina* in some areas (Alongi, 2002). Similarly, provision of livestock fodder has also been reported in several countries like Pakistan (Hogarth, 1999).

1.2.2 The mangrove community

A mangrove community not only consists of the assemblage of trees which are physiologically adapted to thriving in saline/brackish water, but also the heterogeneous community of organisms living in, on or around the mangrove trees and within the substrate. This community depends on the mangrove trees for attachment, shelter or

nutrients supply (Hogarth, 1999). The mangrove faunal community can be conveniently categorised as benthic, nektonic or planktonic depending on the areas they customarily inhabit. Those living on, in or near the sediment at any time during their life history constitute the benthos. Benthic organisms (= benthos) represent a major component of the mangrove environment, and are normally divided into three functional groups; the infauna or endobenthos living within the benthic substratum, epibenthos living on or near the surface of the substratum and hyper-benthos living just above the substratum, but still being dependent on the substratum for shelter and feeding. Benthic organisms can also be classified based on differences in sizes (Marbio, 1997; Pohle, 2003) as macrobenthos (=macrofauna; greater than 1mm) and include oligochaetes, polychaetes, crustaceans and molluscs. Meiobenthos (=meiofauna) are smaller benthos of intermediate size ranging between 38 µm and 1mm and mainly comprise nematodes and copepods. This study focuses on the infaunal macrobenthos (> 1 mm) and meiobenthos (between 38 µm and 1 mm) of *Rhizophora mucronata* mangrove ecosystems. In most benthic ecosystem types, nematodes are the dominant meiofauna group and represent 90 to 95 % of the total meiobenthos (Giere, 1993). Benthic organisms break down organic matter and act as a food source for many higher trophic levels mainly vertebrate species. They are also useful as indicators of environmental quality due to their varying levels of sensitivity to environmental degradation (Watson, 2003).

1.2.3 Macrofauna of mangrove ecosystems

Mangrove macrofauna are an important and integral component of the mangrove ecosystem (Macintosh, 1984; Ngoile & Shunula, 1992; Ronback, 2001) and play a role in

determining the structure and functioning of the ecosystem (Schrijvers et al., 1995; Lee, 1998). Among the dominant macrofauna in numbers and species are the crustaceans and molluscs (epifauna), oligochaetes and polychaetes (infauna) which form an important link between mangrove detritus at the base of the mangrove food web and the higher consumers including birds and commercial fish species (Macintosh, 1984). Macrofauna modify the physical environment and vegetation structure of mangroves through feeding and burrowing activities. Therefore, their diversity may reflect the status and functioning of mangrove ecosystems and serve as potential biological indicators of habitat change (Fratini et al., 2004). Sesarmid crabs and the gastropod mollusc, *Terebralia palustris*, are known to play an important role in mangrove ecosystems through litter degradation, which initiates and enhances the detrital based food webs by shredding the litter and releasing finer faecal material (Lee, 1997; Slim et al., 1997; Fratini et al., 2004). Through the burrowing and feeding activities of these larger macro-invertebrates, large proportions of organic matter production (mangrove leaves) are recycled within the forest. This initial retention of production reduces tidal export from the mangroves (Hogarth, 1999). Other important detritovores in the mangrove ecosystems include sipunculids and polychaetes (Schrijvers et al., 1995), shrimps and penaeid prawns (Ngoile & Shunula, 1992; Sesakumar et al., 1992) and fish, of which the juvenile stages are prominent detritivores of the aquatic community.

1.2.4 Meiofauna of mangrove ecosystems

Meiofauna (=meiobenthos) are an assemblage of mobile or hapto-sessile benthic invertebrates which are distinguished from macrobenthos by their small size. The size

boundaries of meiofauna are based on standardised mesh width of sieves with 1000 µm as upper and 42 µm as lower limits. Thus all benthic fauna passing the coarse sieve (1000 µm) but retained by the finer sieve (42 µm) during sieving is considered as meiofauna. However, deep sea meiobenthologists use a lower limit of 32 µm so as to retain the smallest meiofaunal nematodes (Giere, 1993). In the current study, a size boundary of 1000 µm and 38 µm was used, which is the commonly used size range for studying meiofauna of mangrove ecosystems (Giere, 1993).

Meiofauna occur in all types of marine sediments and occupy a wide variety of habitats. Mangrove meiofaunal groups include; nematodes, harpacticoid copepods, turbellarians, gastrotrichs, kinorhynchs, amphipods, isopods and insect larvae among others (Giere, 1993). Nematodes usually dominate all meiofauna samples both in abundance and biomass, and represent the most frequent metazoans. In meiofauna samples, 90 to 95 % of individuals and 50 to 90 % of biomass are usually made up of nematodes (Giere, 1993). All free living nematodes are of meiobenthic size. In contrast to the macrofauna, their role in the breakdown of organic material and in the production of detrital material is less well understood. However, evidence exists of their importance in recycling of nutrients hence enriching coastal waters to support marine benthic production (Fechel, 1970; Chinnadurai & Fernado, 2007). The wide range of feeding types found in meiofaunal groups enables them to occupy several trophic levels, which coupled with their relatively high densities, enhances the flow of energy in the detrital system (Dye, 1983a). Meiofauna are preyed upon by the juveniles of a large number of fish species

(Gee, 1989) and benthic macrofauna including shrimps, crabs, polychaetes and gastropods (Olaffson & Moore, 1990).

1.2.5 Benthic fauna and impact assessment

Benthic organisms, especially sediment infauna, have for a long time been used as bioindicators for water and sediment quality control and impact assessment because of their sedentary life styles. Bioindicators are a collection of organisms which give information about the environmental state, with effect variable being their presence or absence, population dynamics like abundance, diversity and age structure. Bioindicators are essential tools for monitoring the state of any ecosystem since they inform managers and policy makers of the effectiveness of strategies in achieving ecosystem sustainability. They are useful in coastal zone management as they may provide early warning of pollution or degradation of an ecosystem, alerting managers on mitigation of impacts before critical resources are lost. They also help to asses synergistic or additive relationships among impacts since most coastal ecosystems are affected by a combination of impacts (Linton & Warner, 2003). Examination of benthic community structure and function is a valuable tool for evaluating the condition of benthic habitats, monitoring rates of recovery after environmental perturbations and for providing an early warning of developing impacts to any ecosystem (Bilyard, 1987). USEPA (2002) cites several advantages of monitoring benthic infauna to determine the overall aquatic community health. These include;

a) Benthic infauna are typically sedentary and are, therefore, likely to respond to local environmental impacts.

b) Benthic infauna are sensitive to disturbances of habitat such that the communities respond fairly quickly with changes in species composition and abundance.
c) Benthic infauna are important components of the food chain and often transports not only nutrients but also toxicants to the rest of the system.
d) Monitoring benthic infauna provides an *in situ* measure of relative biotic integrity and habitat quality.
e) Among the biota, which is typically investigated for impact assessment, benthic infauna has the largest supporting database.
f) Many benthic organisms are resident year round, are naturally abundant, diverse and most are not fished or intentionally managed by man.

Due to their association and dependency on the sedimentary biotope, their high abundance, their exclusively sessile lifestyles (no pelagic life stage for dominant taxa) and short generation periods, meiobenthos (=meiofauna) have been widely used to determine the effects of disturbances in aquatic environments (Coull & Chandler, 1992; Schratzberger & Warwick, 1998). Their short generation periods, coupled with small sizes, implies that meiofauna can be maintained in small volumes of sediment such that changes in community structure can be analysed in short-term mesocosm experiments (Warwick, 1988a). A range of literature exists which assesses the effect of disturbances by different kinds of pollutants on meiofauna (Coull & Chandler, 1992; Austen et al., 1994). Many other studies have focused on the effects of biological disturbances by macrofauna on meiobenthos (White et al., 1980; Olaffson & Elmgren, 1991; Olaffson et

al., 1993; Schrijvers et al., 1997). The impacts of macrofauna on meiofauna can be direct through predation and competition or indirect through burrowing, movement and creation of sediment biotic structures like tubes. Physical biological disturbances like burrowing causes sediment resuspension which leads to sediment instability and changes in sediment chemistry by affecting the Redox Potential (Austen et al., 1998). The effects of physical disturbance depend on the nature of the disturbance, the disturbance frequency and intensity. In some microcosm experiments, Schratzberger and Warwick (1998) found that nematode assemblages from sheltered muddy sediments were less resilient to physical disturbance than those from mobile sandy sediments. These authors also found that nematodes from muddy sediments showed a graded change in community composition with increasing frequency of disturbance.

1.2.6 Methods used to assess effects of disturbance on benthic fauna

Moore and Bett (1989) suggested different attributes of meiofauna communities as tools for impact assessment such as the density of major taxa, species composition, abundance and diversity. Nematodes and copepods are the dominant meiofaunal groups and have mainly been used for impact related studies. Sediment organic matter and grain size control nematode abundance and need to be quantified during impact studies, if tangible conclusions have to be made. Copepods are more sensitive to perturbations, especially those influencing the levels and vertical distribution of sedimentary oxygen. Thus they are mainly confined to oxic layers of the sediment and are closely associated with sediment granulometry (Coull & Chandler, 1992).

In several assessment studies, both trophic diversity (the relative composition of feeding types) and species diversity have been used as indicators of disturbance on meiobenthos in particular nematodes (Olafsson, 1995; Schrijvers et al., 1997; Netto et. al., 1999). Wieser (1953) classified nematodes into feeding types based on the morphology of the buccal cavity. Four feeding types were identified which were categorised into two groups. Group 1 contains nematodes with an unarmed buccal cavity while Group 2 contains those nematodes with armed buccal cavity. Each group is further divided into two types; Type 1A contains those species with tiny or no buccal cavity and consists of selective deposit feeders. These nematodes selectively pick up small detrital material like bacteria. Type 1B contains those species with wide and unarmed buccal cavities and are non-selective deposit feeders relying on detrital material. Type 2A contains herbivorous nematode species with fixed teeth in the buccal cavity, while type 2B includes nematodes with wide buccal cavities and glands which open into large teeth, the so called omnivores or predators. Bongers et al., (1991) advanced the use of Maturity Index (MI) for nematodes as an indicator of enrichment. In this system, nematode families are ordered on colonizer-persister (cp) scale based on life history characteristics. These scales range from 1–5 with scale 1 representing early colonisers while scale 5 signifies persisters in undisturbed habitats. The rapid colonisers cp-1 are bacteria feeders, enrichment opportunists, have short generation periods, large gonad volumes, high rates of egg production and posses high mobility and metabolic activity. This class of nematodes show constant ingestion of sediment biofilm and usually enters a non-feeding, inactive ‘dauerlarva’ which is a survival stage when resources become limited or when the conditions are stressful. Hence they are, in a way, resilient to disturbance. There are two

types of nematode opportunists or colonisers; enrichment opportunists and general opportunists. Enrichment opportunists colonise food enriched conditions and are classified as cp-1 whereas general opportunists are classified as cp-2. Species in the higher cp classes have less pronounced productivity characteristics and bacteria are not the primary food source. They produce fewer eggs and are the most susceptible to environmental disturbance.

Pollution induces a shift in nematode community structure towards dominance by opportunistic nematode species. This results to a decrease in MI due to the disappearance of taxa higher in the cp scale. Therefore, pollution may lead to a decrease in nematode diversity as dominance by opportunistic species increases. Several other reviews on meiofauna and impact assessment exist. Raffaeli and Mason (1981) used the nematode copepod ratio to asses the impact of pollution and concluded that the ratio increased with increasing degree of pollution due to the reduction of the more sensitive harpacticoid copepods. Lambshead et al., (1983) used the k dominance method or the ABC method of Warwick (1986), which relates abundance to biomass. This method is based on the fact that in undisturbed biotopes, the k-selected specialists (persisters) account for high individual biomass though population abundance is usually low. However, in disturbed areas, communities of r selected generalists (colonisers) are numerous with low biomass.

Dye (2006) recorded increased densities of meiobenthos in trampled mangrove sediments compared to natural mangrove sites. This increase was linked to increased habitat complexity due to loss of root mat and increased food supply from the decomposing root

material. Benthic organisms may become abundant after disturbance through several mechanisms: Opportunistic species may colonise the disturbed patches, but be replaced by superior competitors in the later stages of recovery or they may respond to increased resources such as food and space. Meiobenthos may also increase in abundance as a result of release from predation, competition or release from the effects of bioturbation by macrobenthos (Schrijvers et al., 1997).

Benthic macrofauna have also become well established as useful bioindicators of ecological quality in coastal and estuarine environments. This is because they respond in a predictable, diverse and rapid manner to a variety of natural and anthropogenic stresses (Bilyard, 1987; Levin, 2000). Lu et al., (2002) documents that reclamation and restoration activities in estuarine and coastal waters, may seriously affect the marine environment, leading to increased water turbidity, enhanced sediment deposition as well as disturbance to biological groups. These authors recorded decreased macrofauna family numbers and abundance close to a reclaimed riverine area, which increased away from the reclaimed area. Community structure of the macrobenthos also changed over time with very few benthic taxa recorded near the reclaimed area. This decrease was linked to the loss of habitats, increase in suspended particulate matter which may impair the growth of sessile benthic organisms and burial of benthic organisms which were probably killed by smothering. The changes in community structure could also have been due to interspecific competition as sedimentation may facilitate growth of some tolerant species and inhibit the intolerant ones.

Cardoso et al., (2007) studied polychaete assemblages from a eutrophied and subsequently restored estuary and recorded a decline in polychaetes and overall macrofauna species richness, biomass and a replacement of herbivores by carnivores in the eutrophied estuary. However, after restoration projects were initiated, the total biomass and diversity of polychaetes, and overall macrofauna increased indicating that restoration leads to recovery of degraded ecosystems by improving habitat conditions for macrobenthos.

Calabretta and Oviatt (2008) studied the response of benthic fauna to anthropogenic stress (mainly urbanisation and related effects) in Narragansett Bay, Rhode Island and recorded low faunal diversity in sites near disturbance sources while relatively pristine sites away from the anthropogenic stressors recorded higher faunal diversity. This was linked to the fact that the species encountered close to a disturbance source are usually few, specialised and highly abundant opportunistic species. However, as the distance from the disturbance increases, stress decreases and the number of species and the relative abundance increase, ultimately leading to the steady state community.

1.2.7 Mangrove ecosystem degradation and restoration

Very few mangrove forests are pristine since most are, to some degree, affected by human activities. If exploitation is uncontrolled, the result is usually ecosystem deterioration followed by loss of biodiversity, reduction in the extent of the exploited forest and consequently a drastic reduction of the resource being exploited (Hogarth, 1999).

Mangrove ecosystem services have no direct economic value since they are not marketable. Therefore, for a long time, the value of mangroves has been perceived in terms of the goods which can be extracted, mainly wood products. This subjective perception has caused serious undervaluation of mangrove ecosystem functions (Costanza et al., 1997; Barbier & Cox 2002), leading to the consideration of mangroves as wastelands with low economic value. This subjective perception is also common in Kenya among communities living near mangroves, who consider mangrove forests as homes for monkeys which destroy their crops. Increased human pressure on mangroves coupled with the lack of appreciation of the true value of mangroves by policy makers, has led to a threat to mangrove ecosystem conservation efforts, leading to increased degradation of the ecosystems (Bosire, 2006).

The disappearance of most mangrove ecosystems is attributed to population pressure, wood extraction, coastal industrialisation and urbanisation, pollution, as well as land use changes or conversion of mangrove wetlands to other uses (Field, 1998, 1999; Alongi, 2002; Morrissey et al., 2003). Loss of biodiversity remains and will continue to be the severest impact on mangrove degradation since even the pristine mangroves are species poor compared to other tropical ecosystems (Alongi, 2002).

Along the Kenyan coast, the main causes of mangrove degradation has been the extraction of wood for building materials and as fuel wood, which has left some areas completely bare. However, there has been increased awareness of the true value of mangrove ecosystems, which has led to renewed efforts to protect and restore or

rehabilitate mangrove ecosystems (Kairo, 2001). In Gazi Bay, Kenya, restoration programmes started in 1994 and have proven successful as evidenced by structural developments of the mangrove stands (pers. obs).

Ecosystem restoration involves the process of converting a degraded ecosystem back into as nearly as possible its original condition (Field, 1998). The most important aspect in mangrove restoration is to restore ecosystem functions, which involves restoration of the vegetation structure and faunal community (Field, 1999). Though there are many mangrove restoration projects worldwide, very few have been documented to show ecosystem recovery of the replanted mangrove forests. Most of the available studies have been spot checks with no temporal assessments to determine ecosystem recovery. Therefore, there is need to define a criteria for determining whether mangrove ecosystems have been restored successfully, which should include vegetation structure and composition of the associated fauna (Field, 1998, 1999).

Field (1998) gives three main criteria for judging the success of mangrove rehabilitation programmes. These include the effectiveness and efficiency of the planting and the rate of recruitment of flora and fauna (recovery of ecosystem integrity). Similarly, the Society of Ecological Restoration International (SER) suggests that a restored ecosystem should have certain attributes like similar diversity and community structure in comparison with the reference sites, presence of indigenous species, presence of functional groups necessary for long term stability and the capacity of the physical environment to sustain reproducing populations (Maria et al., 2005). However, in most cases of mangrove

rehabilitation, the recruitment of fauna is rarely quantified. The focus of most restoration programmes has been to recover the forest, with little attention paid to the reestablishment of the ecosystem structure and function (Field, 1998). Ecological monitoring of reforested mangrove plantations is, therefore, of great importance, not only to evaluate structural developments of the forest stands, but also to understand the recolonisation patterns of the mangrove associated fauna. The reason for this approach is that mangrove vegetation generates a high habitat complexity which enhances the diversity of the associated fauna. Overall, biodiversity is important in maintaining genetic richness, ecological functioning and resilience of the ecosystem (Lee, 1998). Mangrove trees and the different plants of the forest under storey, combine to generate a particular benthic environment which interacts with the other biotic and abiotic components. A change in one of these basic components instigates changes in other aspects of the ecosystem, which ultimately have impacts on the benthic fauna (Hogarth, 1999). Therefore, as a management tool, it is important to understand the effects of mangrove deforestation and subsequent reforestation on the fauna they support.

1.3 Justification

Very few studies have looked at mangrove benthic macrofauna in relation to ecosystem degradation and restoration in Gazi Bay, Kenya. Similarly, studies dealing with the effects of mangrove forest clear felling and restoration on meiofauna and nematode community assemblages are completely lacking. In addition, the few studies on the impact of mangrove degradation and restoration on macrobenthos, such as Fondo and Martens (1998), Schrijvers et al., (1995) and Bosire et al., (2004) have been sporadic and

dealt with only one reforestation time regime. This is despite restoration efforts having been started more than 15 years ago (Kairo & Abuodha, 2001). It needs not be emphasised that benthos form a crucial component of the functioning of mangrove ecosystems and play a pivotal role in mangrove ecosystem restoration success (Field, 1999). Therefore, benthic infauna should be analysed together with vegetation structure inorder to determine the overall mangrove restoration process and success. Therefore, this study is the first to be conducted in Kenyan mangroves that compares benthic infauna community assemblages from natural, 10 years reforested, 5 years reforested and degraded *Rhizophora mucronata* forest stands. The aim was to investigate the effects of mangrove ecosystem restoration on the benthic infauna community structure. The study compares forests of different reforestation time regimes and focuses on the infaunal macrofauna and meiofauna, which had either not been adequately studied, or not studied at all in the reforested *R. mucronata* stands of Gazi Bay. The study further explores the sediment physical characteristics, which structure and influence benthic fauna recolonisation of mangrove sediments within the study sites. Finally, a high number of replicate samples were investigated per site, a sampling strategy which allowed full estimation of the high spatial heterogeneity which is typical for mangrove forests (Todd, 2001). The study will contribute to the management question whether reforestation of clear-cut mangrove areas can lead to complete recovery of ecosystem functions. The study will also assess the approximate time required for recovery by comparing the status of recovery in 5 and 10 years *R. mucronata* forest stands.

In addition, a field experiment was conducted inorder to understand the drivers (organic sources) of benthic fauna recolonisation of reforested mangroves. Several field colonisation experimental studies utilising mangrove leaf litter exist, and include: Zhou (2001); Gee and Somerfield (1997) and Somerfield et al., (1998). On the contrary, there is no study which has investigated the effect of different leaf litter types found in mangrove ecosystems on meiofauna and nematode colonisation. Inorder to design restoration programmes for mangrove ecosystems, it is essential to understand the influence that different sources of organic matter have on benthic communities. Therefore, the field experiments investigated the colonisation responses of total meiofauna, major meiofauna taxa and nematode community assemblages to different types of food sources (mangrove, sea grass, diatoms), different food quality additions (fresh versus partially decomposed) and sediment type (fine from natural mangrove forest versus coarse from a degraded forest). In addition, these experiments were set up to understand the actual drivers of meiofauna and nematode recolonisation in the reforested sites.

1.4 Research Questions

The study addresses the following research questions: (1) Does mangrove clear felling (degradation) lead to alteration of the sediment physical characteristics? (2) Does mangrove clear felling (degradation) lead to alteration of benthos (macrofauna, meiofauna and nematofauna) density, diversity and community composition? (3) Does the restoration of the *R. mucronata* mangrove ecosystem successfully create a benthic

community assemblage comparable in density, community composition and diversity to that of the original natural mangrove stand?

1.5 Aim and Objectives

The overall aim of this study was to provide a scientific explanation of the response of benthic fauna to mangrove reforestation and their recolonisation patterns in restored *R. mucronata* stands of different ages. The specific objectives were;

1. To determine the effects of mangrove forest degradation on the abundance, community composition and diversity of macro-endobenthos, meio-endobenthos and in particular nematodes.
2. To determine macro-endobenthos, meio-endobenthos and in particular nematode re-colonisation patterns of restored *R. mucronata* ecosystems.
3. To determine the relationship between the spatial patterns in benthos (macro-endofauna, meio-endofauna and in particular nematode community structure) and sediment physical characteristics.
4. To investigate the effect of different types of organic matter sediment type and diatoms on meiofaunal re-colonisation of mangrove sediments.
5. To investigate the effect of food quality (decomposition state) on meiofaunal re-colonisation of mangrove sediments.

CHAPTER TWO

General Materials and Methods

2.1 Study area: Environmental settings and history

The study was conducted at Gazi Bay (4^{o} $25^{/}$ S and 39^{o} $30^{/}$ E; Fig. 2.1a) located at the southern part of the Kenyan coast about 50 Km from Mombasa.

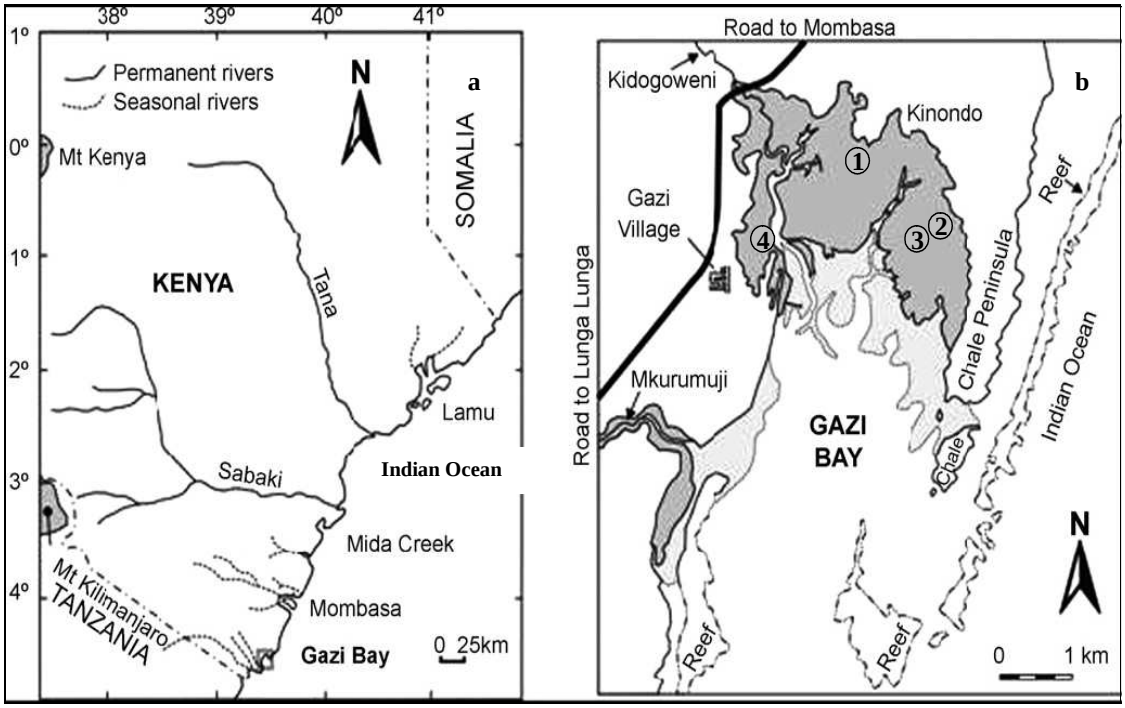

Figure 2.1. (a) Map of the Kenyan coast and (b) Gazi Bay, the study area. (**1**) Degraded site, (**2**) Natural site, (**3**) 10 years reforested site and (**4**) 5 years reforested site (Adopted from Bosire et al., 2004).

The bay is protected from strong wave energy by the Chale Peninsula to the east and a fringing coral reef to the south (Tack & Polk, 1999). The mangrove forests of Gazi Bay have been exploited for many years especially for industrial fuel wood used in the calcium carbonate industry and brick industries in the 1970s', and also for building poles (Kairo, 1995, Kairo et al., 2001). This unsustainable exploitation left some areas completely bare. However, experimental reforestation was started from 1991 and since then, several sites have been reforested with different mangrove species along the Kenyan coast (Kairo, 1995, Kairo et al., 2001).

Four of those *R. mucronata* reforested sites were selected for this study. Site 1 was the degraded forest; site 2 the natural forest; site 3 the 10 years reforested and site 4 the 5 years reforested (Figure 2.1b; Plate. 2.1). The sites were selected based on accessibility, similarity in tidal inundation and site history. The selected natural, 10 years reforested and degraded (bare) sites were in inundation class 4 and, therefore, flooded by tidal water during high spring tides. The 5 years reforested site was in inundation class 2 and, therefore, covered by water during all medium high tides (Hogarth, 1999).

The bare site was included so as to provide information on the impact of mangrove deforestation and associated changes in physical sediment conditions on macrofauna, meiofauna and nematofauna community composition. This site had no natural mangrove regeneration (pers. obs.) and was clear felled in 1970's (Kairo et al., 2001). The natural site acted as a control to identify the degree of recovery after reforestation.

a

b

c

d

Plate 2.1. The forest structure in **(a)** Natural site, **(b)** Degraded site, **(c)** 5 years forested site and **(d)** 10 years reforested site (Photos by Mutua, 2005).

2.2 Sampling design

In each sampling site, three sampling plots of 25 m^2 each were randomly selected. Within each of these plots, triplicate sediment cores were taken each time for sediment physical characteristics, macrofauna and meiofauna, giving a total of 9 replicate cores per sampling site. This sampling strategy allowed for the estimation of spatial heterogeneity which is

typical of mangrove forests (Table 2.1). Sediment samples for nematodes were taken randomly in triplicate from each sampling site during the dry season (July-September) in September 2004 and the wet season (October-December) in December 2004. Samples for sediment physical characteristics, macrofauna and meiofauna were collected during low spring tide in September 2005.

Table 2.1. A sampling plan showing the number of replicates taken for each parameter investigated.

Sites	**Natural**			**10 years Reforested**			**5 years Reforested**			**Degraded**		
3 Plots per site	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Total Organic Matter	3	3	3	3	3	3	3	3	3	3	3	3
Granulometry	3	3	3	3	3	3	3	3	3	3	3	3
Temperature	3	3	3	3	3	3	3	3	3	3	3	3
Macrofauna	3	3	3	3	3	3	3	3	3	3	3	3
Meiofauna	3	3	3	3	3	3	3	3	3	3	3	3
Nematoda	3 Wet season 3 Dry season			3 Wet Season 3 Dry Season			None			3 Wet Season 3 Dry Season		

2.3 Sampling and sample analysis

2.3.1 Environmental characteristics

The grain size and sediment total organic matter (TOM) samples were collected using a 6.4 cm diameter corer up to 10 cm depth. The TOM samples were kept in a cooler box in

the field and deep frozen immediately on arrival in the laboratory to arrest further microbial activity. The analysis of TOM was done by, first, drying the samples in an oven at 80 ^{0}C for 24 hours to remove all the moisture. The sample was then homogenised and 10 g of the dried sample was ashed at 600 ^{0}C for 6 hours, in a furnace, to obtain the ashed dry weight (ADW). Ash Free Dry Weight (AFDW) or TOM was then calculated as a percentage of the original dry weight of the sample.

Sediment grain size was analysed using the method described by Buchanan & Kain (1971). Sediment interstitial water samples for measurement of salinity and temperature were randomly taken by digging a hole into the sediment of 5-10 cm depth in each plot. Salinity was then measured using an optical refractometer (Atago brand), while temperature was measured using a glass thermometer. Samples for chlorophyll *a*, nitrogen and carbon were taken using a 3.2 cm corer up to 5 cm depth, sectioned at 1 cm intervals, kept in a cooler box in the field and stored in a deep freezer (-80 ^{0}C) upon arrival in the laboratory. Chlorophyll *a* was analysed by calorimetric method. Inorganic carbon was eliminated from the samples before organic carbon and nitrogen analysis by treating the samples with dilute hydrochloric acid. Afterwards, the amounts of carbon and nitrogen were analysed using a Carlo Erba element analyser, type NA-1500 (Nieuwenhuize & Mass, 1993-2002).

2.3.2 Macrofauna

Sampling for macrobenthos was done during spring low tide in September 2005. Three macrofauna core samples (6.4 cm internal diameter, 10 cm long) were taken at random

from each plot and immediately fixed in 5 % formalin for macrofaunal community analysis. Samples were sieved on a 0.5 mm sieve with a 2 mm sieve, on top, to trap large plant debris which were hampering the sorting process. The macro-endobenthos retained on the 0.5 mm sieve were analysed using a dissecting microscope. The various macrofauna taxa encountered were identified using Higgins and Thiel (1992) to class level, and counted.

2.3.3 Meiofauna

In each of the three plots per site, 3 sediment cores (3.2 cm internal diameter, 5 cm long) were taken at random and immediately fixed in 5 % formalin. In the laboratory, the samples were rinsed using tap water over 1 mm sieve to exclude macrofauna and any debris, and collected on a 38 µm sieve. The fraction retained on the 38 µm sieve was centrifuged three times at 6000 r.p.m. with Magnesium Sulphate ($MgSO_4$) of specific density 1.28, for 10 minutes and each time the supernatant was collected over 38 µm sieve. The supernatant was then rinsed in tap water and stained with Rose Bengal. The density of $MgSO_4$ is higher than that of meiofauna (1.08), which ensures that the meiofauna float on the $MgSO_4$, making it easy to decant (Heip et al., 1974, 1985). Meiofauna were identified and counted under a dissecting microscope to higher taxonomic class level following Higgins and Thiel (1992).

2.3.4 Nematodes

Sampling for nematodes was done seasonally between July-September (Dry season) in September and October-December (Wet season) in December 2004. From each of the

sampling sites, 3 sediment cores (3.2 cm internal diameter, 10 cm long) were taken at random, sectioned at 5 cm intervals and immediately fixed in 5 % formalin. In the laboratory, the samples were rinsed using tap water over 1 mm sieve to exclude macrofauna and any debris and collected on a 38 µm sieve. The fraction retained on the 38 µm sieve was centrifuged three times at 6000 r.p.m. with $MgSO_4$ of specific density 1.28 for 10 minutes. Afterwards the supernatant was sieved over 38 µm sieve to extract nematodes, rinsed with tap water to remove the $MgSO_4$ and stained with Rose Bengal. Then, nematodes were counted under a dissecting microscope and 200 and 100 individuals, picked randomly from the upper (0-5 cm) and lower (5-10 cm) sections respectively. Nematodes were fixed by transferring them from formalin to glycerol through a series of ethanol-glycerol solutions and mounted in glycerine slides (Warwick et al., 1998). Identification of the nematodes was done to genera level using the pictorial keys of Platt and Warwick (1983, 1988) and Warwick et al., (1998). They were assigned to trophic groups according to the scheme of Wieser (1953). According to this scheme, group 1 includes nematodes with an unarmed buccal cavity while group 2 are the nematodes whose buccal cavities are armed with one or more teeth and/or cuticular ridges, denticles or glands. Group 1A forms the selective deposit feeders with small or no buccal cavity. They feed on bacteria and small particles of detritus from the sediment. Group 1B includes the non-selective deposit feeding nematodes with a wider buccal cavity and consume detritus complexes including bacteria, diatoms, algae and macromolecules. Group 2A nematodes are the scrapers or epistrate feeders having smaller teeth in their buccal cavity. They scrape diatoms and algae off the surface of sand grains or pierce algal cells. Group 2B nematodes have wide buccal cavities with glands

opening in to the teeth and are omnivores or predators. They have variable feeding strategies including predation (Moens & Vincx, 1996). The length and maximal width of the nematodes were measured using an image analyser (Quantimet 500), while their biomass was calculated using Andrassy's formula (Andrassy, 1956) given as follows:

$$\frac{a^2 \times b}{16 \times 100000}$$

Where;

a = the greatest body width

b = body length

16 is a predetermined empirical value

2.4 Food type, food quality and diatom uptake field experiments

2.4.1 Experimental design

The *insitu* experiments for determining the effect of food type, diatom uptake, sediment type and food quality on meiofauna and nematode recolonisation were done at the natural site. The aim of the experiments was to investigate the effect of different food types, and decomposition state (quality), on meiofauna and specifically nematode recolonisation of mangrove sediments. In addition, the effect of sediment type on recolonisation was also tested. Therefore, a three factor experimental design was used for the food type experiment, with experimental treatments (factors) represented by 2 different food types, 2 sediment types and 4 incubation times. In addition, 2 controls (field and experimental) were added. The field controls consisted of meiofauna core samples taken from the experimental site at the beginning of the experiment, while the experimental controls

contained azoic sediments with no food type additions. The food type treatments were mangrove leaf litter (M) and seagrass leaf litter (S). The control samples were field controls (FC) and experimental controls (C). The field control was not included in the factorial design since it was sampled only once (at the beginning of the experiment), while the experimental controls were included since they were sampled during each incubation period. The different sediment types sediment from the natural forest (N) and sediment from the degraded forest (D). Each experimental treatment was a combination of the food type and sediment type. Colonisation rates of meiofauna and nematode genera, based on different stages of leaf litter decomposition, were determined by sampling the experimental treatments over time intervals of 1, 14, 30 and 60 days post-placement. Experimental control treatments containing no litter additions were included in the experiment for both natural and degraded azoic/organic free sediments. Each treatment was replicated four times.

A two factor experimental design was used for the food quality experiment with experimental treatments represented by different mangrove and sea grass leaf litter quality and time. The treatments were fresh mangrove leaves (MF), decomposed mangrove leaves (MD), fresh sea grass leaves (SF) and decomposed sea grass leaves (SD).

In the third experiment, ^{13}C labelled diatom treatments were added into the azoic and organic free experimental units so as to give an idea of the uptake rates of diatoms by nematodes.

2.4.2 Experimental sediment and leaf litter preparation

Surface sediments were collected up to a depth of 5 cm from the natural and degraded *R. mucronata* sites. After collection, the sediments were air dried for two days and combusted using a furnace at 600 ^{0}C for 6 hours in order to obtain azoic and organic free sediment. Yellowish senescent and ready to fall *R. mucronata* leaves were picked from the study site while sea grass leaves were collected along the beach in Gazi Bay. Senescent mangrove leaves were used instead of fresh green ones because they are the majority on the forest floor. The sea grass leaves were collected from the beach since these are the materials which are washed into the mangroves during tidal flooding. The leaves were air dried for 1 week and powdered into small grains using an electric grinder.

For the food quality experiment, some of the ground mangrove and sea grass leaves were buried in the experimental site for 4 days. This was meant to initiate bacterial decomposition and was used to test whether prior decomposition of detritus has any effect on meiofauna and nematode genera colonisation rates. This experiment was necessitated by the observation that within the degraded site, mangrove leaves, which were already decomposing, formed the main organic material deposited by incoming tides.

2.4.3 Estimation of organic content

Total organic matter (TOM) of natural *R. mucronata* sediment from the experimental site was determined by combusting 3 replicate dried (80 ^{0}C for 24 hours) sediment samples (20 g) at 600 ^{0}C for 6 hours. The method described by Buchanan and Kain (1971) was

used, which uses the percentage loss of dry weight as a measure of the sediment TOM. Organic matter levels of mangrove and sea grass leaves were obtained from literature. These values were used as standards to calculate the amount of leaf litter to be added to the experimental sediments.

2.4.4 Experiment preparation

Medical syringes with a capacity of 70 cc (3 cm diameter and 13.5 cm length) were used as experimental units. Circular windows measuring 2.5 cm diameter were cut on opposite sides of each syringe and covered with plastic nets of 2 mm mesh size (Fig. 2.2).

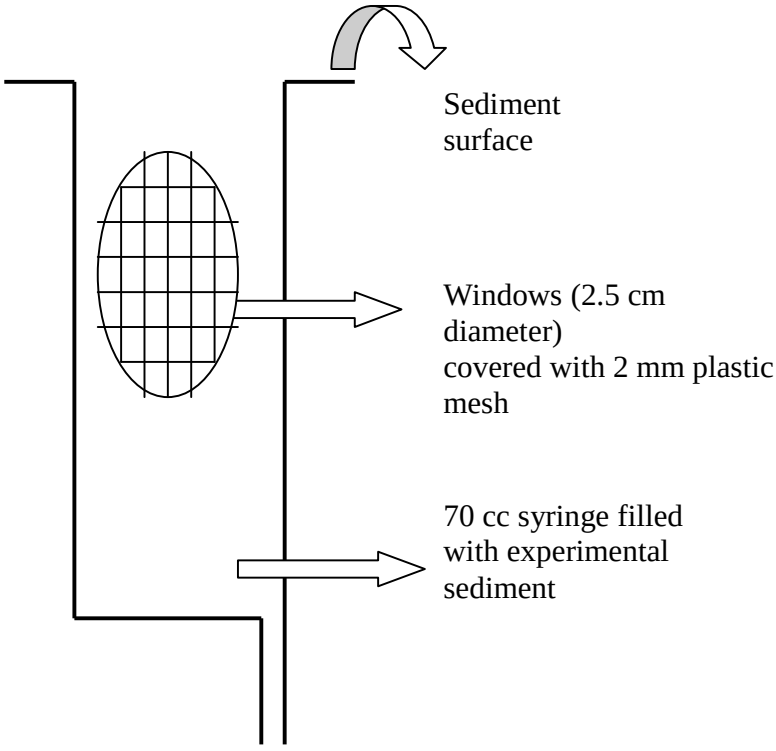

Figure. 2.2. Diagram showing the design of the experimental syringe (Adapted from Zhou, 2001).

These windows enabled the experimental sediments to exchange water with the surrounding natural sediment. The windows also enabled meiofauna to colonise the experimental sediments through horizontal migration in addition to vertical movement from the overlying water column. Azoic and organic free experimental sediments (see earlier) were put into the tubes and leaf litter added on top. The amount added was based on prior vertical analysis of TOM from the natural *R. mucronata* sediments where most organic matter was found to be concentrated on the top 5 cm. A small amount of moist experimental sediment was placed on top of the litter to prevent the litter from pouring during transportation to the field, in addition to preventing the litter from being washed away easily by tidal currents. The syringes were randomly embedded in the sediment and pushed till the syringe top levelled with the sediment surface. Each syringe carried a label indicating the food type/food quality, sediment type and day of sampling for easy recognition and retrieval during sampling. The syringes were fastened onto nearby roots or seedlings using nylon threads to avoid washing away by tidal currents. Four syringes per treatment were retrieved on day 1, day 14, day 30 and day 60 and immediately fixed in the field with 5 % formalin.

2.4.5 Laboratory sample extraction

In the laboratory, meiofauna samples were rinsed using tap water over a 1 mm sieve to exclude macrofauna and debris, and retained on a 38 µm sieve. The samples were then centrifuged three times at 6000 r.p.m with $MgSO_4$ (specific density 1.28) for 10 minutes. After centrifuging, the supernatant was poured onto a 38 µm sieve, rinsed in tap water and stained with Rose Bengal. Meiofauna were identified under a dissecting microscope

using Higgins and Thiel (1992) to higher taxonomic level and enumerated. From each sample, 50 nematodes were randomly picked, transferred from formalin to glycerol through a series of ethanol-glycerol solutions and mounted in glycerine slides according to Warwick et al. (1998). Nematodes were identified under a Leitz compound microscope to genus level using the pictorial keys of Platt and Warwick (1983, 1988) and Warwick et al. (1998) counted and assigned to trophic groups according to Wieser (1953).

2.5 ^{13}C uptake experiment

2.5.1 Diatom culturing

A culture of the benthic diatom species, *Seminavis robusta*, was obtained from the Laboratory of Parasitology and Aquatic Ecology (PAE, University of Ghent-Belgium). The diatoms were cultured in plastic bottles filled with 200 ml F/2 medium (artificial seawater with nutrients). To each bottle, 10 ml ^{13}C solution (0.336 mg ^{13}C/100 ml seawater) was added. To estimate the degree of enrichment (enrichment factor), diatoms were also cultured without the ^{13}C solution. After a period of 2 to 3 weeks of culturing, the diatoms were collected and rinsed, carefully, to remove the ^{13}C labelled medium. The diatoms were then freeze dried by lyofilisation. Salt crystals were removed by rinsing the diatoms over a filter. Afterwards, the diatoms were freeze dried again. In this way, only pure diatoms remained on the filter after rinsing. The freeze dried diatoms were weighed and put in equal proportions in different appendorfs for use in the field. Colonisation syringes were prepared as described earlier. Each syringe was filled with azoic inorganic sediment. On top of each sediment filled syringe, ^{13}C enriched diatoms were added. These syringes were finally embedded (planted) in the natural mangrove sediments in

triplicates and retrieved 1, 7, 14, 30 and 60 days post placement. The syringes were kept in a cooler box after retrieval in the field and stored in a deep freezer in the laboratory before analysis of the stable isotope content. In order to obtain ^{13}C background value for nematodes, sediment samples were picked from the experimental site, stored in a cooler box and kept in a deep freezer in the laboratory.

2.5.2 Sample preparation

Before processing the samples for further analysis, the frozen samples were diluted with 5 L distilled water and decanted over 38 µm sieve after defrosting. The decanting technique is based on the fact that meiobenthos are less dense than the sediment particles. Therefore, they stay longer in the supernatant (overlying water) making it possible to separate the meiofauna from the sediment. The decantation process was repeated 10 times ensuring that most (95 %) of the meiobenthos were extracted. The meiobenthos fraction was then stored in Milli-Q water. From each sample, 40 nematodes were picked out using a sterilised needle (rinsed with dilute Hydrochloric Acid) and washed in Milli-Q water to rinse off any remaining sediment particles and diatoms. The nematodes were then transferred into 3 x 6 mm aluminium cups containing a drop of Milli-Q water. To avoid contamination, the aluminium cups were stored at 550 ^0C for 24 hours before transferring the nematodes. The aluminium cups containing the nematodes were then dried at 60 ^0C in an oven for 12 hours. Afterwards the cups were closed and stored in sterile Multi-well Microtiter plates.

2.5.3 ^{13}C isotope analysis

The aluminium cups containing the nematodes (hereafter called monsters) were combusted at 980 ^{0}C so as to transform all organic carbon into carbon dioxide (CO_2). The CO_2 molecules were then determined using a mass spectrophotometer. In this process, the CO_2 molecules resulting from the oxidation were analysed with a continuous flow – isotope ratio mass spectrometer (Europa Tracermass, Crewe, England) which transforms CO_2 into an ion signal. The resulting ion signal is transformed into electrical pulses which are expressed as Volts and measured in milli Volts (mV). Ratios of ^{13}C:^{12}C were expressed as the relative per ml (‰) difference between the sample and the conventional standards (Pee Dee Belemnite carbonate). The isotope values are expressed in delta (δ) and calculated as follows;

$$\delta\,^{13}C = [(R_{monster}/R_{VPDB}) - 1] \times 10^{3}\ ‰$$

With $R = {}^{13}C/{}^{12}C$

$R_{VPDB} = 0.0112372$

VDPB = Pee Dee Belemnite which is the standard highly enriched reference material.

The treatments are expressed with respect to this highly enriched reference material. As most samples are normally less enriched (containing less ^{13}C), most of the delta values are negative. The rule is that the lower the delta value of the sample, the less heavy the isotopes are in the sample.

The measured $\delta\,^{13}C$ values ($\delta_{monster}$) are in fact the resultant of the $\delta\,^{13}C$ value from the organic material (δ_{org}) and the $\delta\,^{13}C$ value from the aluminium cup (δ_{cup}). This is given as follows:

δ_{org} x intensity org. = $\delta_{monster}$ x intensity monster – δ_{cup} x intensity cup

So… δ_{org} = ($\delta_{monster}$ x intensity monster – δ_{cup} x intensity cup) / intensity org

With intensity = amount of Carbon (µg)

The following values are calculated using the corrected delta values:

Carbon isotope-ratio (R)

$R = (\delta\,^{13}C/1000 + 1) \times R_{VPDB}$

^{13}C fraction (F)

$F = {}^{13}C / ({}^{13}C + {}^{12}C) = R / (R + 1)$

Excess ^{13}C (E)

The incorporation of ^{13}C is visualised by the excess relative to the background value for nematodes (without enriched food).

$E = F_{total} - F_{control}$

With $F_{control}$ = the ^{13}C fraction of the nematodes from the natural environment.

Total uptake of ^{13}C (I)

The incorporation of ^{13}C is expressed relative to the total uptake of ^{13}C, expressed in µg/sample.

$I_{total} = E \times intensity_{total}$

To get an idea about the ^{13}C that was taken up by a nematode, the total uptake was divided by the number of nematodes that were present in the analysed sample.

$I_{nematode} = I_{total}$ / number of nematodes

2.6 Statistical analysis

Data on physical sediment characteristics, macrofauna, meiofauna and nematode genera were analysed using Plymouth Routines in Multivariate Research (PRIMER version 5) and the software program STATISTICA (version 6). Principal Component Analysis (PCA) ordination using Euclidean distance was used to show patterns of variation between sites and between seasons based on physical sediment characteristics. Non metric multidimensional scaling (nMDS) ordination using Bray-Curtis similarity coefficient was used to show the patterns of (dis)similarities within and between the study sites on one hand and the (dis)similarities between seasons within sites on the other, in terms of the macrofauna, meiofauna and nematode community composition. Data for nMDS analysis were appropriately transformed when necessary. A measurement of the goodness-of-fit test (reliability of the analysis) of the nMDS ordination was given by the stress value. A low stress value (< 0.2) indicates a good ordination with no possibility of a misleading interpretation. Infact, it shows that the positions of the points in the nMDS are refined until they satisfy, as closely as possible, the dissimilarity relations between samples (Clarke, 1993). The variability in macrofauna taxa, meiofauna taxa and nematode genera community composition among sites and seasons was tested using analysis of similarity (ANOSIM; Clarke and Gorley, 2001). ANOSIM calculates the relatedness of samples (groups) based on a rank similarity matrix and is used to classify samples based on species

composition. The output is usually an R-value such that groups which are similar in fauna taxa composition have an R-value less than 0.5 and close to 0, while groups with different taxa composition have an R-value above 0.5 and close to 1. Species similarity percentages routine (SIMPER) was used to determine which benthic fauna taxa contributed most to the (dis)similarities between sites. Analysis of relative multivariate variability within each site was done using MVDISP (Multivariate Dispersion, Primer). This is a multivariate index for expressing within site variability. The Index of Multivariate Dispersion (IMD) lies between +1 and –1. It has a value of +1 when all variation within sites is lower than variation between sites, and a value of -1 when variation within sites is larger than variation between sites (Clarke and Warwick, 2001). Diversity indices Shannon diversity (H'), taxa richness (S) and taxa rarefaction, (ES_n) were calculated using DIVERSE (PRIMER version 5). Species richness gives the total number of species or taxa and is usually influenced by the sampling effort such that the higher the number of samples taken, the high the number of species likely to be encountered. Species rarefaction calculates the number of species expected in each sample if all samples were of a standard size. Shannon diversity index (H') assumes that individuals are randomly sampled from an infinitely large population and that all species are represented in the sample and takes into account richness and evenness (Maguran, 1988; Clarke and Warwick, 2001).

The differences between sites in environmental characteristics, macrofauna taxa, meiofauna taxa, nematode genera densities and diversity indices was analysed using ANOVA, with prior analysis of assumptions using Levens test for homogeneity of variances and the correlation between variances and means. In cases where the assumptions were fulfilled,

post hoc analysis was performed using Tukey's Honest Significant Difference (HSD) test. When assumptions for parametric testing were not fulfilled, the non-parametric Kruskal-Wallis test was used. Data were (logx+1) transformed for ANOVA when required.

Nematode trophic diversity was expressed by The Index of Trophic Diversity (ITD) which was calculated as follows: ITD = $\sum\theta^2$, θ is the contribution of the density of each trophic group to the total nematode density. ITD ranges from 0.25 (highest trophic diversity), where the four trophic guilds account for 25 % each to 1.0 (lowest trophic diversity), where one trophic guild accounts for 100 % of the nematode density; Heip et al. (1985). Results for the various aspects studied are presented, in chapters of this thesis as follows;

Chapter 3: Evidence of recovery of mangrove associated macro-endofauna after reforestation of *Rhizophora mucronata* mangrove in Gazi bay, Kenya.

Chapter 4: Patterns of colonisation of meiobenthos as an indicator of recovery of *Rhizophora mucronata* mangroves in Gazi Bay, Kenya.

Chapter 5: The Spatial and temporal variation of nematofauna of recovering tropical mangroves at Gazi Bay, Kenya.

Chapter 6: Meiofaunal response to different food type additions to azoic sediments in a tropical mangrove forest.

Chapter 7: Meiofaunal response to different food quality additions to azoic sediments in a tropical mangrove forest.

Chapter 8: General Discussion, Conclusions and Recommendations

CHAPTER THREE

Evidence of recovery of mangrove associated Macro-endofauna after reforestation of *Rhizophora mucronata* mangrove in Gazi bay, Kenya.

3.1 Introduction

Mangrove ecosystems, originally covering vast areas of the world's (sub) tropical coastlines, are precious resources for multiple socio-economical and ecological uses (Alongi, 1997). They provide a structural base for microhabitat diversity harbouring diverse associated communities, and a nutritional base for a wide range of fauna (Lee, 1998; Macintosh et al., 2002). In this way mangrove ecosystems increase the biodiversity of estuarine and nearshore areas and act as nursery and feeding grounds for various marine fauna (Alongi, 2002). Mangroves are also characterised by their high organic production as well as serving as nutrient traps (Alongi, 2002); a function which reduces nutrient loads into the ocean waters hence fostering the growth of sea grasses and corals. Additionally, mangroves play a role in shoreline stability by reducing excessive erosion (Hogarth, 1999; Alongi, 2002). There are a variety of traditional products for local use like tannins, honey, wood, charcoal, fodder and medicines which are extracted from mangrove trees (Ruitenbeek, 1992).

The benthic community is an important and integral component of mangroves (Macintosh, 1984; Ngoile & Shunula, 1992; Ronnback, 2001) and plays a significant role in the structure and function of the ecosystem (Schrijvers et al., 1995; Lee, 1998). Among the dominant macrobenthic taxa in terms of biomass in mangroves are the crabs and molluscs.

These two groups form an important link between mangrove detritus at the base of the mangrove food web, and the consumers including birds and commercial fish species (Macintosh, 1984; Bouillon et al., 2004). Sesarmid crabs and the gastropod mollusc (*Terebralia palustris*) are known to play an important role in litter degradation (Fratini et al., 2004) in East African mangrove ecosystems. Litter degradation by initial shredding and the subsequent release of finer faecal material initiates and enhances the detrital based food webs (Slim et al., 1997). Subsequent degradation of litter by micro-organisms, contributes to the high nutrient enrichment in the mangrove ecosystem, from which other small burrowing organisms may benefit (Skov & Hartnoll, 2002). Additionally, burrowing macrofauna also modify the physical and biogeochemical nature of the sediment which inturn impacts the vegetation structure (Fratini et al., 2004). Thus the structure and the diversity of the macro-endofauna communities may reflect the status and functioning of mangrove forest ecosystems, and serve as potential ecological indicators of habitat conditions.

Mangrove forests once occupied 75 % of the tropical coasts worldwide by area. However, anthropogenic pressures have reduced the global range to less than 50 % of their total original cover (Kairo et al., 2001). The disappearance of much of mangrove ecosystems can be attributed to population pressure, coastal industrialisation and urbanization, soil and water pollution, as well as conversion to coastal aquaculture (Field, 1998,1999; Alongi, 2002; Morrisey et al., 2003;). Along the Kenyan coast, mangrove degradation has been caused by the unrestricted extraction of wood for building materials and as fuel wood, which has left some areas completely bare (Kairo, 1995). However, increased awareness of the true value of mangrove ecosystems has led to renewed efforts to protect and restore or

rehabilitate them. Experimental mangrove reforestation along the Kenyan coast started between 1991 and 1994 (Kairo, 1995). These restoration projects have proven successful in some areas as shown by the vegetation structural developments of the restored mangrove stands (pers. obs.). However, for reforestation projects to be deemed successful, Field (1998) gives three main criteria for judging the success of mangrove rehabilitation programmes. These include the rate of recruitment of flora and fauna (recovery of ecosystem integrity), the effectiveness of the planting, and the efficiency of rehabilitation. Additionally, the Society of Ecological Restoration International (SER) suggests that a restored ecosystem should have certain attributes like similar diversity and community structure of the associated fauna and flora, the presence of indigenous species, the presence of functional groups necessary for long term stability and the capacity of the physical environment to sustain reproducing populations in comparison with the reference (natural) sites (Maria et al., 2005). However, in most case studies on mangrove rehabilitation, the recruitment of fauna is rarely quantified. The focus of most reforestation programmes has been to restore the forests as habitats, with little attention and knowledge about the reestablishment of the ecosystem structure and function (Field, 1999). Therefore, ecological monitoring of associated fauna of reforested mangrove plantations is of great importance, since mangrove vegetation contributes to the habitat complexity which enhances the diversity of the associated fauna. This biodiversity is especially important in maintaining genetic richness, ecological functioning and ecosystem resilience (Lee, 1998).

There are few studies which have investigated mangrove benthic fauna in relation to mangrove ecosystem degradation and restoration in Gazi Bay. These include Bosire et al. (2004) which found no differences in crab abundance and species diversity between

natural, 5 years reforested and bare stands of *R. mucronata*, *Sonneratia alba* and *Avicenia marina*. However, the bare sites recorded the lowest densities of sediment infauna mainly oligochaetes and nematodes, while the natural and reforested sites recorded the highest densities with no differences between the sites. Similarly, Fondo and Martens (1998), studied the effects of mangrove degradation on mangrove macrobenthos, and recorded very low densities in the bare sites compared to the natural sites. Both studies concluded that mangrove degradation leads to declines in macrobenthic densities due to changes in the sediment physical characteristics. However, these earlier studies mainly focussed on mangrove benthic epifauna with little emphasis on endofauna, and used only one reforestation time regime. The current study compares different reforestation time regimes and focuses on the endofaunal macrobenthos which hitherto had not been adequately investigated in the reforested *R. mucronata* stands. The study further explores the sediment physical characteristics, which structure and influence macro-endobenthic recolonisation of mangrove sediments within the study sites. Finally, a high number of replicate samples were investigated per site, a sampling strategy which allowed full estimation of the high spatial heterogeneity which is typical for mangrove forests (Todd, 2001).

3.2 Objectives

The objectives of this study were;

- To determine the sediment physical characteristics in the different mangrove forests.
- To determine the effects of mangrove forest degradation on macro-endofauna community composition.

- To determine macro-endobenthic recolonisation patterns of restored *R. mucronata*.
- To relate the spatial patterns in macro-endofauna community structure to sediment physical characteristics.

This was done by comparing the macro-endofauna and sediment physical characteristics in two reforested areas of different ages (5 and 10 years old) with those from a natural forest and a fully degraded (clear felled) site present in similar conditions at Gazi bay, Kenya.

3.3 Materials and Methods

The study site, macro-endofauna sampling, laboratory sample processing and identification have been described in Chapter 2 on materials and methods.

3.4 Results

3.4.1 Environmental characteristics

Figure 3.1 shows the variation in TOM within the studied sites The natural site showed the highest mean TOM levels (53.6 % ± 6) followed by the 10 years reforested site (29 % ± 6). The 5 years reforested and the degraded sites recorded the lowest levels (17.5 % ± 8 and 3.8 % ± 1, respectively). TOM was significantly different between all sites (ANOVA, df = 3, $F = 86.36$, $p < 0.05$). Pair wise Tukeys post hoc comparisons showed that all sites recorded significantly different TOM levels from each other ($p < 0.05$). Figure 3.2 shows the grain size distribution within sites. The highest sand content was recorded in the degraded and the 5 years reforested sites (79.3 % ± 4.7 and 59.4% ± 13.7 respectively). The 10 years reforested site recorded the lowest sand content (27.3 % ± 9), and consequently

the highest silt clay fraction (72.9 % ± 9) followed by the natural site (57.3 ± 5.5). Similarly, sand and silt/clay fractions showed significant differences between sites (Kruskal-Wallis, df = 3, H = 28.86, $p < 0.05$). These differences in TOM and grain size are related to the state of the forests since canopy cover plays a crucial role in determining these parameters.

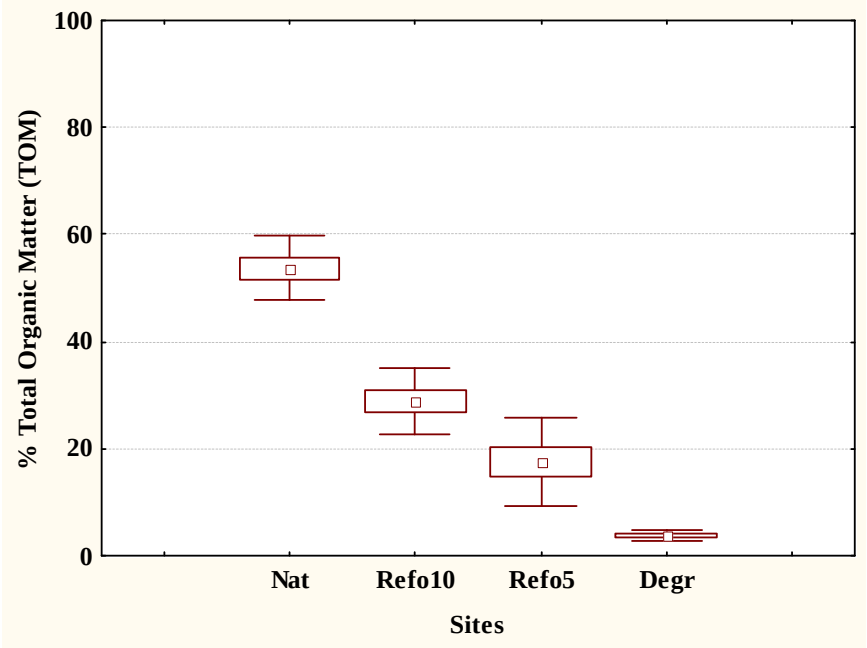

Figure 3.1. Variation in TOM (mean ± SD; n = 9) among the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and the degraded (Degr) sites.

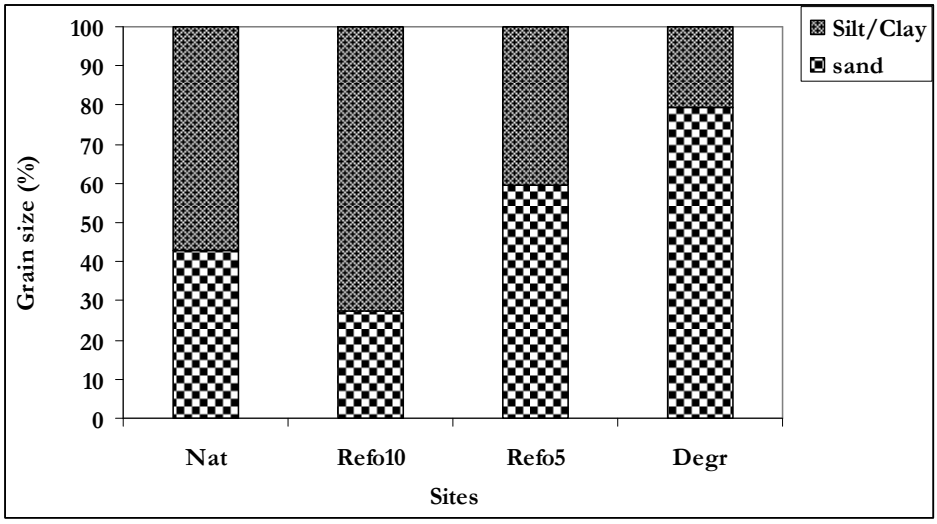

Figure 3.2. Variation in sand and silt/clay n=9) among the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and the degraded (Degr) sites.

The variations in temperature and salinity between sites are shown in figures 3.3. The degraded site recorded the highest temperature (33 $^{\circ}$C ± 1.4; Fig 3.3a) while the lowest was recorded from the 10 years reforested site (27.9 $^{\circ}$C ± 0.1). There were significant differences in temperature between sites (Kruskal-Wallis, df = 3, H = 30.44, $p < 0.05$). The natural and the 10 years reforested sites recorded lower temperatures than both the 5 years reforested and the degraded sites. However, no significant differences were observed between the natural and the 10 years reforested sites, and between the 5 years reforested and the degraded sites. The trends in Salinity (Fig. 3.3b), was more or less similar to that of temperature. The highest Salinity was recorded in the 5 years reforested site (47 PSU ± 1), while the natural site recorded the lowest (37 PSU ± 1.1).

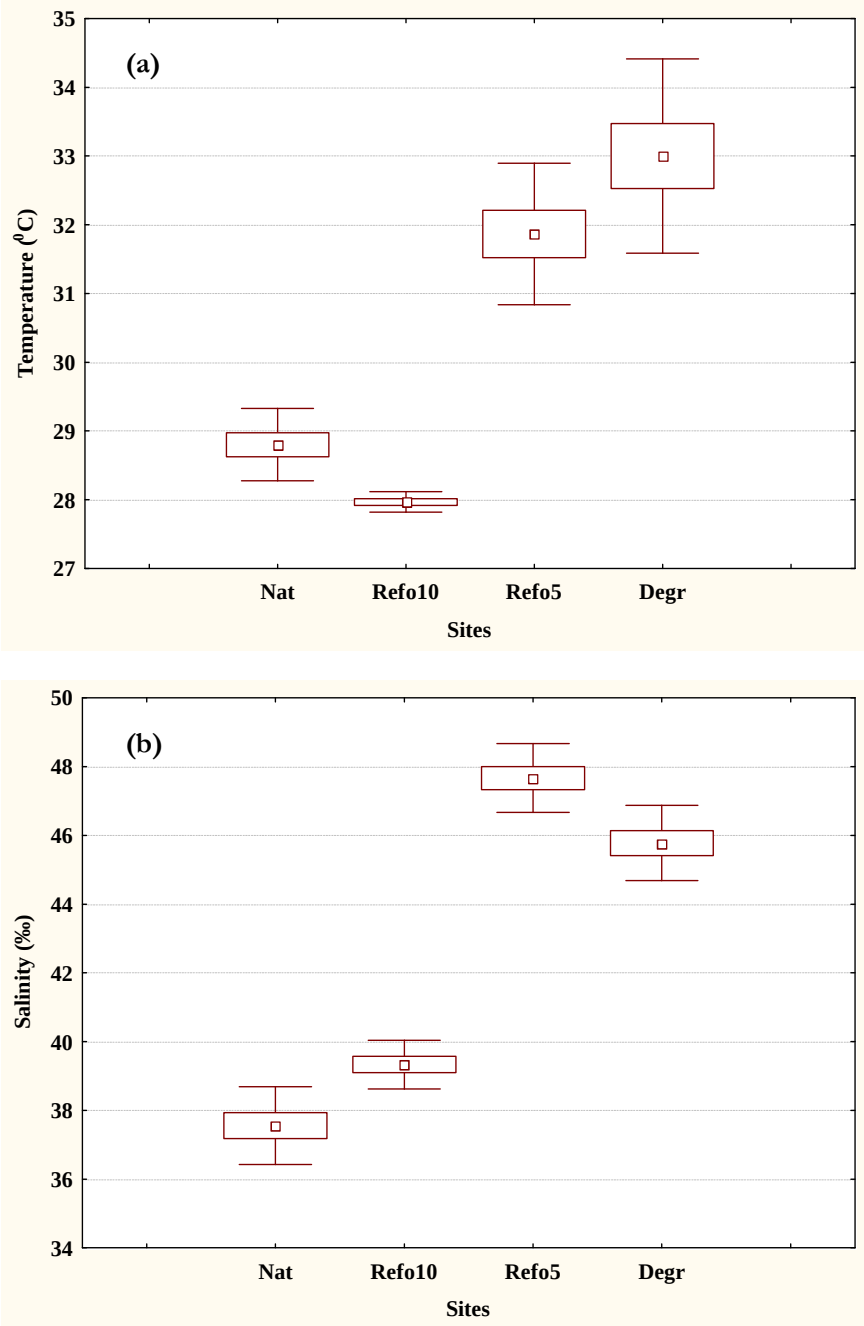

Figure 3.3a & b. Variation in (a) temperature and (b) salinity (mean ± SD, n = 9) among the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and the degraded (Degr) sites.

Salinity levels were significantly different between sites (ANOVA, df = 3, F = 217.17, $p < 0.05$). Tukeys Pair wise post hoc comparisons produced significant differences in salinity between the natural and the 10 years reforested sites on one hand, and the 5 years reforested and the degraded sites on the other.

The variations in sediment Chlorophyll *a* and C/N ratio are shown in figure 3.4. The natural site recorded the highest sediment Chlorophyll *a* (Fig. 3.4a) and C/N ratio (Fig. 3.4b) closely followed by the 10 years reforested site while the degraded site recorded the lowest levels of both variables. In all the sites, the highest chlorophyll *a* was recorded in the top 0-1 cm sediment section, while C/N ratio showed no differences between vertical sections. These differences in sediment physical characteristics are linked to differences in tree canopy cover.

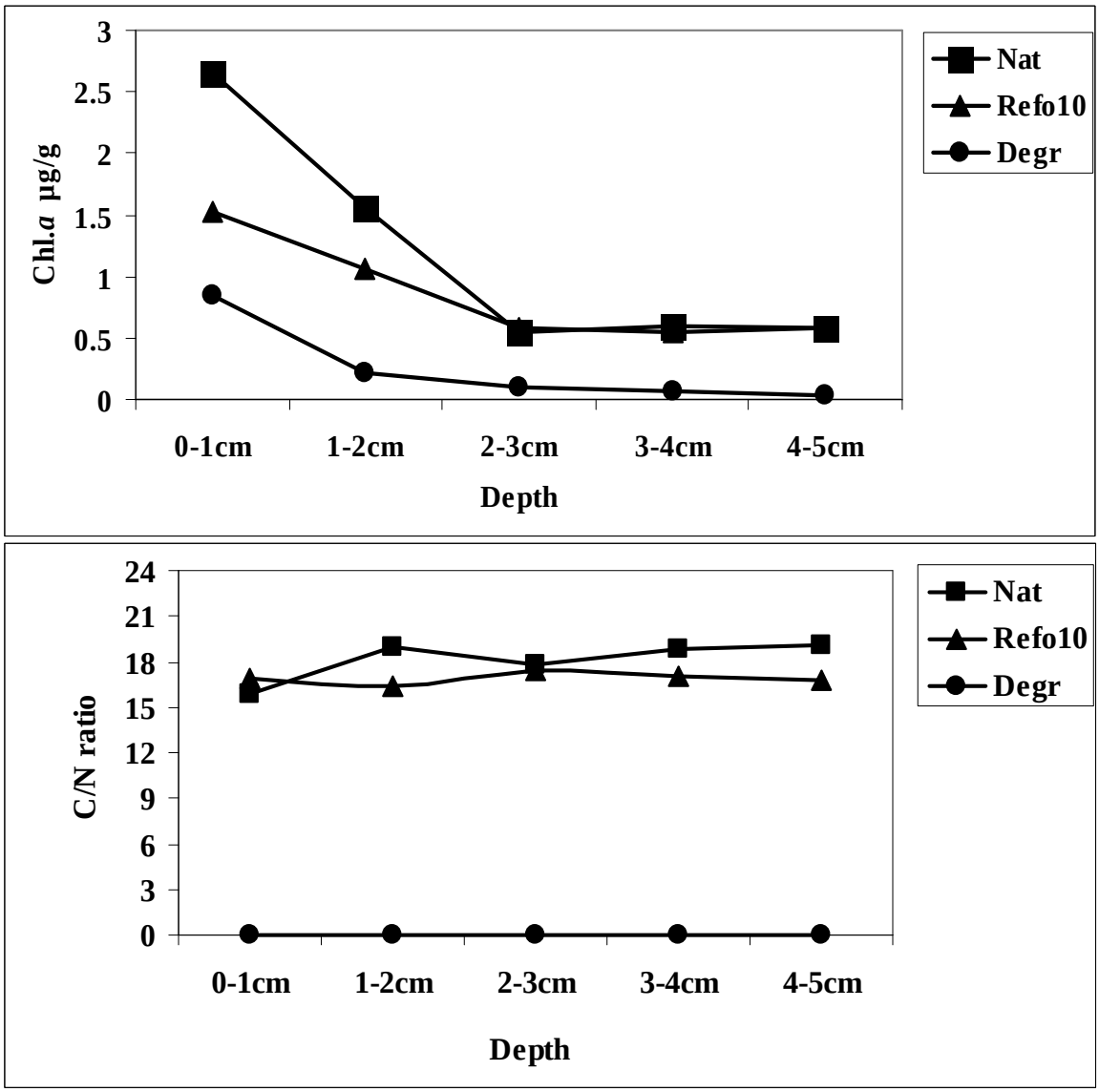

Figure 3.4a & b. Vertical profiles of (a) sediment chl. *a* and (b) C/N ratio within the natural (Nat), 10 years reforested (Refo10) and degraded (Degr) sites.

The ordination of sites (PCA) based on sediment physical characteristics data showed a clear separation of the 5 years reforested and the degraded sites from both the natural and the 10 years reforested sites (Fig. 3.5). Principal components (PC) 1 and 2 explained together 99 % of the variability (PC 1; 88 %, PC 2; 11 %). On the first principal component, the natural and the 10 years reforested sites with the highest TOM and silt/clay were separated from the 5 years reforested and the degraded sites having sandier sediments and low TOM. The separation of sites along the second principal component was less pronounced, and it separated the natural site from the 10 years reforested site based on TOM. The 5 years reforested site showed a lot of within site variation in abiotic factors as shown by the scattering of its replicates within the plot.

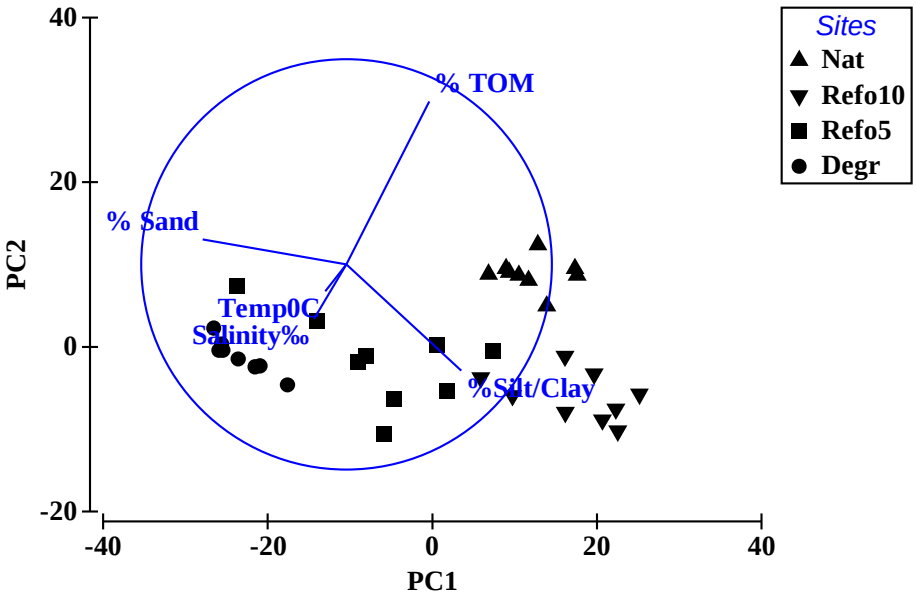

Figure 3.5. PCA ordination showing the separation of sites based on sediment physical characteristics. Natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and the degraded (Degr) sites.

3.4.2 Macrofauna densities and community composition

A total of 12 macro-endofauna taxa were recorded from all the sites (Table 3.1). The natural site recorded all the 12 taxa. The 10 years reforested site recorded 10 taxa while the 5 years reforested and the degraded sites recorded 7 taxa each. The highest macro-endofauna density was recorded in the natural site (27,469 ± 11,189 Ind./m²) while the 5 years reforested site recorded the lowest density (2,580 ± 946 Ind./m²). Oligochaeta was the most abundant taxon in the natural site (Fig. 3.6a) and the 10 years reforested site (Fig. 3.6b) accounting for 59 % and 60 % of the total densities, respectively.

The taxa Polychaeta and Nemertina were abundant in the 5 years reforested site (Fig. 3.6c) and the degraded site (Fig. 3.6d) accounting for 80 % and 79 % of the total densities respectively. The TOM rich silt/clay sediments recorded the highest macrofauna densities especially oligochaetes and nematodes. Nemertines seem to prefer sandy sediments while polychaetes seem to prefer sediments with almost equal proportions of sand and silt/clay. Thus the measured sediment physical characteristics influence the densities and type of macrofauna community.

Table 3.1. Macrofauna taxa densities (Ind. / m^2 ± SE, n = 9) in the different mangrove sites.

Macrofauna taxa	Natural	10 years reforested	5 years reforested	Degraded
Oligochaeta	16284 ± 9991	4617 ± 1628	123 ± 148	185 ± 271
Polychaeta	2346 ± 2106	1556 ± 630	2062 ± 557	99 ± 85
Nematoda	8099 ± 3229	1296 ± 209	25 ± 74	12 ± 37
Insect Larvae	123 ± 130	111 ± 30	111 ± 97	679 ± 737
Crustacea	235 ± 406	12 ± 37	37 ± 111	0
Arachnida	25 ± 42	49 ± 97	0	37 ± 64
Insecta	62 ± 42	25 ± 74	0	12 ± 37
Syncarida	160 ± 149	0	12 ± 37	0
Isopoda	62 ± 56	0	0	0
Copepoda	37 ± 37	25 ± 74	0	0
Nemertina	12 ± 21	12 ± 37	210 ± 263	3877 ± 1137
Amphipoda	25 ± 21	25 ± 74	0	0
Total ± SD	27469 ± 11189	7728 ± 2168	2580 ± 946	4901 ± 2764
Number of taxa	12	10	7	7

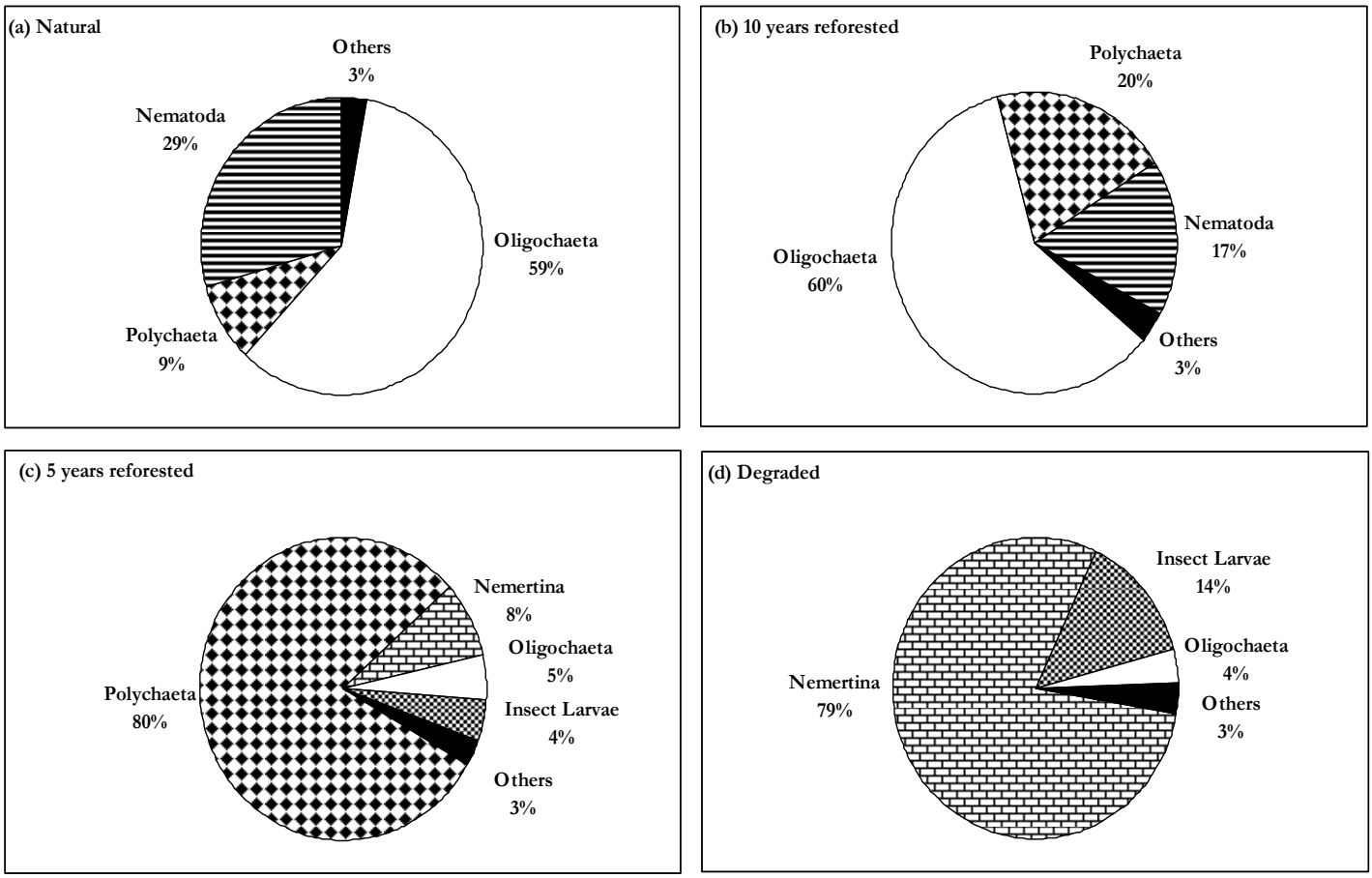

Figure 3.6a-d. Relative contributions (%) of the macro-endofauna taxa to the total macrofauna densities in the study sites.

Figure 3.7 show the variation in densities of macrofauna and the major macrofauna taxa. There were significant differences between sites (ANOVA, df = 3, F = 26.36, $p < 0.05$) in total macrofauna and major macrofauna densities. The natural site recorded significantly higher densities of macro-endofauna (Fig. 3.7a) than all the other sites (Tukeys HSD, $p < 0.05$). Similarly, the 10 years reforested site recorded significantly higher densities of macro-endofauna than the 5 years reforested site ($p < 0.05$). However, both reforested sites did not show significant differences in macrofauna densities with the degraded site.

Though Nematoda is a typical meiofauna group (< 0.5 mm), this taxon occurred in very high densities in the macrofauna fraction (> 0.5 mm) especially in the natural site. This occurrence was linked to the relatively large size of the nematodes that were retained on the 0.5 mm macrofauna sieve. Figure 3.7b shows total macrofauna densities with nematodes excluded, illustrating that macrofauna densities were still much higher at the natural site.

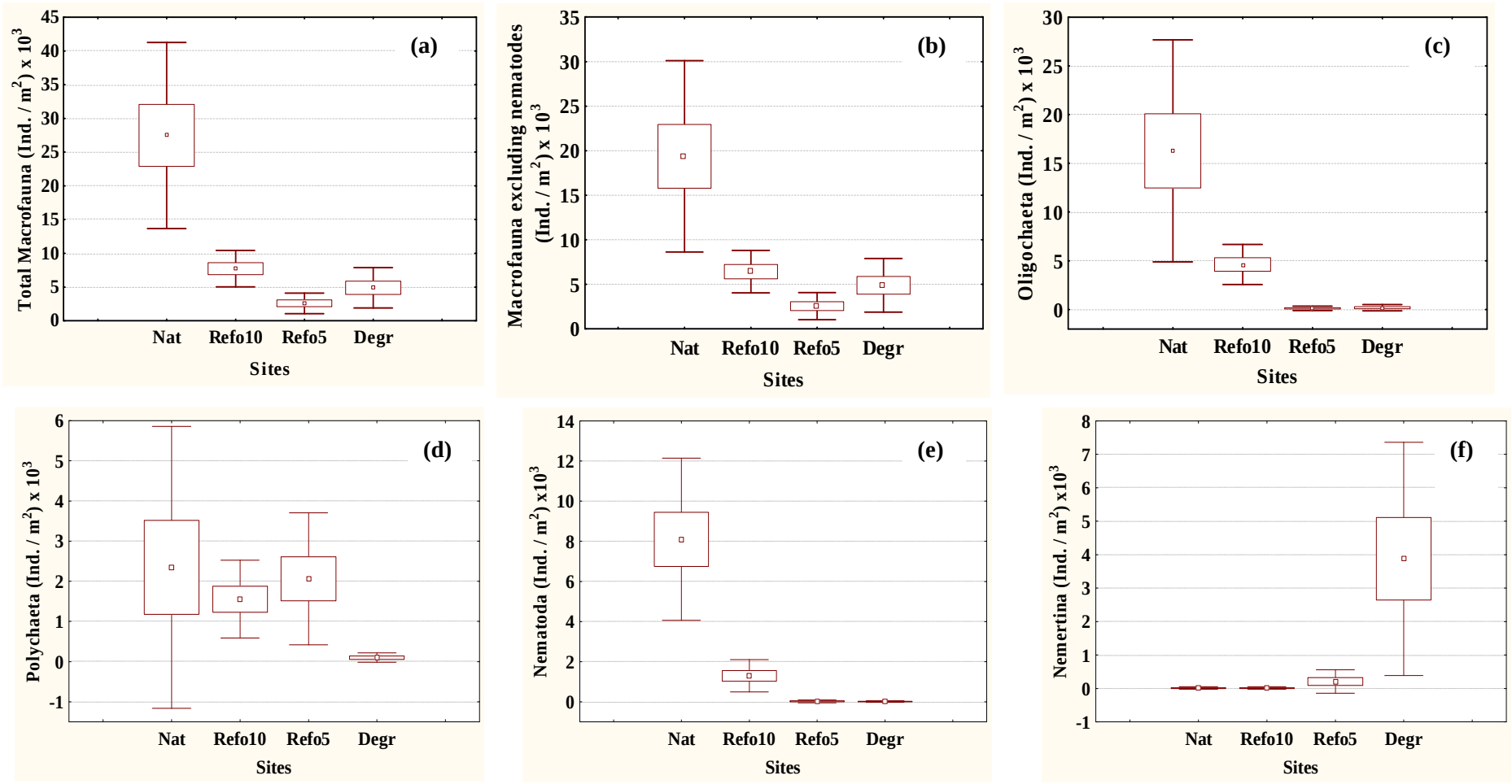

Figure 3.7a-f. The density (Mean ±SE; n = 9) of (a) Macrofauna (b) Macrofauna excluding nematodes (c) Oligochaeta (d) Polychaeta (e) Nematoda and (f) Nemertina in the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and degraded (Degr)sites.

The natural and the 10 years reforested sites also recorded significantly higher Oligochaeta densities (Fig. 3.7c) than the 5 years reforested and the degraded sites (Kruskal-Wallis, df = 3, H = 29.71, $p < 0.05$). The lack of significant differences between the natural and the 10 years reforested sites in Oligochaeta densities was due to the high variation of this taxon in the natural site.

Polychaeta densities were on average highest in the natural and both reforested sites, while the degraded site recorded the lowest (Fig. 3.7d). However, the variability within sites was so high that no significant differences were observed between sites.

Nematodes (Fig. 3.7e) occurred in very high densities in the natural site, with relatively lower densities recorded in the 10 years reforested site. They sporadically occurred in both the 5 years reforested and the degraded sites. Densities of Nematoda were significantly different between all sites (ANOVA, df = 3, F = 104.7, $p < 0.05$) except for the 5 years reforested and the degraded sites.

Densities of Nemertines were highest in the degraded site (Fig. 3.7f), with lower densities recorded in the 5 years reforested site and even much lower densities in the 10 years reforested and the natural sites. There were highly significant differences in densities of this taxon between the degraded site and all the other sites (Kruskal-Wallis, df = 3, H = 10.35, $p < 0.05$). The observed patterns of macro-endofauna and the major taxa distribution point to a link between sediment type, organic matter levels and the macro-endofauna densities.

An nMDS analysis showed that the four sites are different in terms of macro-endofauna community composition (Fig. 3.8). ANOSIM pair wise comparisons further confirmed that all sites were significantly different (Global R = 0.724; Table 3.2).

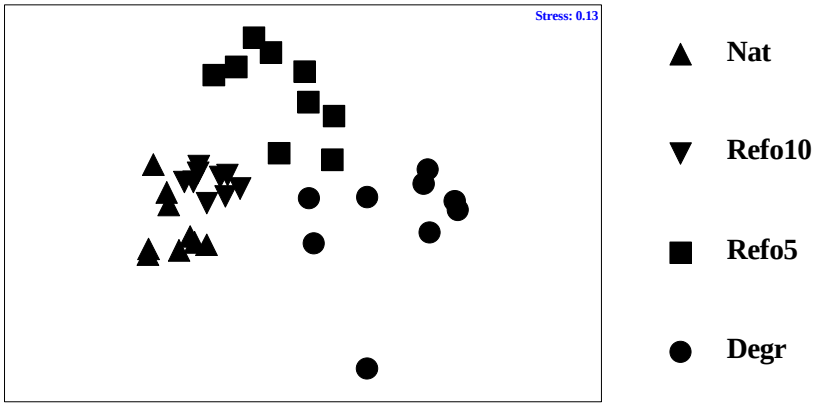

Figure 3.8. nMDS (√ transformed) on macro-endofauna community at higher taxon level showing affinities between the 9 replicates from the natural, reforested 10 yrs, reforested 5 yrs and the degraded sites.

Table 3.2. Pair wise ANOSIM comparisons between the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and the degraded (Degr) sites based on macro-endofauna community (Global R: 0.724).

Groups	**R-Value**
Nat, Refo10	0.671
Nat, Refo5	0.957
Nat, Degr	0.909
Refo10, Refo5	0.796
Refo10, Degr	0.803
Refo5, Degr	0.614

Similarity Percentage analysis (SIMPER, Similarities) showed that the taxa Oligochaeta, Nematoda, and to a lesser extent Polychaeta were responsible for the high average similarity (71 %) observed within the natural site. The high similarity (79 %) observed within the 10 years reforested site was mainly explained by Oligochaeta while Polychaeta was the major taxon responsible for the similarity within the 5 years reforested site. Nemertina and Insect larvae accounted for the similarity (though low) observed within the degraded site (Table 3.3).

Table 3.3. Relative percentage contribution (SIMPER) of macro-endofauna taxa (≥ 20 %) to similarities within the study sites. Natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and degraded (Degr).

Sites	**Average Sim. (%)**	**Macrofauna Taxa % contribution**				
		Oligochaeta	**Nematoda**	**Polychaeta**	**Nemertina**	**Insect Larvae**
Nat	71	45	36	14		
Refo10	79	49	23	25		
Refo5	54			86	5.4	
Degr	49			7	55	32

The macrofauna taxa responsible for the observed dissimilarities between sites were mainly Oligochaeta, Nematoda, Polychaeta and Nemertina. The dissimilarities between sites were very high (> 60 %) except for the natural and 10 years reforested sites (Table 3.4). These observations show that the taxa Oligochaeta and Nematoda dominated the organically rich and silty/clay sediments in the natural and the 10 years reforested sites. Nemertines were abundant in the organically poor and sandy sediments in the degraded site.

Table 3.4. Relative percentage contribution (SIMPER) of macro-endofauna taxa to dissimilarities between sites. Natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and degraded (Degr).

Sites	Average Dissimilarities (%)	Macrofauna taxa % contribution
Nat, Refo10	39	Nematoda (30), Oligochaeta (30), Polychaeta (11)
Nat, Refo5	76	Oligochaeta (41), Nematoda (32), Polychaeta (8)
Refo10, Refo5	62	Oligochaeta (44), Nematoda (24), Polychaeta (12)
Nat, Degr	87	Oligochaeta (33), Nematoda (26), Nemertina (15)
Refo10, Degr	80	Oligochaeta (30), Nemertina (24), Nematoda (17), Polychaeta (15)
Refo5, Degr	74	Nemertina (39), Polychaeta (29), Insect Larvae (16)

Analysis of relative multivariate variability within each site was done using MVDISP (Multivariate Dispersion, PRIMER). This is a multivariate index for expressing within site variability. MDISP showed that the 10 years reforested site was the least variable in macro-endofauna community, with an Index of Multivariate Dispersion (IMD) of 0.517. The natural site recorded an intermediate IMD value of 0.855, while the 5 years reforested and degraded sites were the most heterogeneous ecosystems in terms of macrofauna community composition (IMD = 1.3 each).

3.4.3 Macrofauna diversity

Taxa richness was significantly different between sites (ANOVA, $df = 3$, $F = 15$, $p < 0.05$). The natural site recorded significantly higher taxa richness (S), than all the other sites (Tukey HSD, $p < 0.05$). Similarly, the 10 years reforested site recorded significantly higher

taxa richness than the 5 years reforested site (Tukey HSD, $p < 0.05$), showing that the age of reforestation influenced the number of taxa recolonising the forests. However, the degraded site was not significantly different from the 5 years reforested site. The natural and 10 years reforested sites recorded significantly higher Shannon diversity index than the 5 years reforested and degraded sites (Kruskal-Wallis, $df = 3$, $H = 9.42$, $p < 0.05$). Similarly, both the natural and the 10 years reforested sites recorded significantly higher taxa rarefaction (Tukey HSD, $p < 0.05$) compared to the 5 years reforested and degraded sites (Table 3.5). These patterns of diversity indices are linked to the densities of the major taxa recorded from each site since both indices are highly influenced by the sample size.

Table 3.5. Macrofauna taxa diversity measures (mean ± SD; n = 9) in the study sites.

	Diversity measures		
Sites	**S**	**ES_{50}**	**H'(loge)**
Natural	5.9 ± 1.5	3.9 ± 0.6	0.9 ± 0.1
10 years reforested	4.3 ± 1.2	3.9 ± 0.9	1.0 ± 0.1
5 years reforested	2.6 ± 1.1	2.5 ± 1.1	0.6 ± 0.4
Degraded	3.0 ± 0.7	2.8 ± 0.7	0.5 ± 0.4

3.5 Discussion

Some previous studies have already documented the different community patterns of the benthos in natural, reforested and degraded mangroves in Gazi bay. Bosire et al. (2004) found similar crab species diversity and abundance between natural, 5 years reforested and bare sites of *Rhizophora mucronata*, *Sonneratia alba* and *Avicenia marina.* However, the

densities of sediment infauna were found to be different among the natural, 5 years reforested and bare sites of the three mangrove species. The bare sites had the lowest densities of sediment infauna whereas the natural site recorded the highest, except in *A. marina* where the 5 years reforested site had the highest densities. Crona and Ronnback (2005) found different shrimp densities between natural, replanted and degraded sites of *S. alba* in Gazi Bay. Additionally, Fondo and Martens (1998) researched on the effects of mangrove deforestation on macrobenthic densities by comparing macrobenthic densities from deforested and natural mangrove areas. They identified 13 classes of macrobenthos and recorded higher densities of epifauna in the natural mangrove area. These findings are similar to the results of the current study which recorded 12 taxa with the natural site recording the highest densities of macrofauna.

However, all the previous mentioned studies were based on a relatively small number of replicates per site (max 3), suggesting a risk for underestimation of the present small scale patchiness typical for mangrove sediments (Todd, 2001). The studies also considered only one reforestation time regime. Furthermore, characterisation of relevant environmental conditions should increase our insight on the structuring factors responsible for the differences in communities between reforested and natural sites.

Most of the measured sediment physical characteristics during this study did not only show differences between the forested and the degraded sites, but also among the reforested sites depending on the age of reforestation. The natural site still differed especially in terms of higher organic matter content and pigment concentrations from the 10 years reforested site. This 10 years reforested site was characterised by the highest silt/clay content, while the 5

years reforested site shared lower TOM, coarser sediments and higher salinity and temperature with the degraded site. The differences in silt/clay content between the natural and the 10 years reforested sites could be linked to the root network which plays a crucial role in slowing down tidal currents. Reduction of tidal currents leads to less resuspension and reduction in tidal erosion of fine sediment materials from the mangroves. Wave attenuation and the reduction of orbital water motion in waves within mangroves have been shown to be greater the closer the mangrove trees are to each other (Wolanski et al., 1992). The root network in the 10 years reforested site was observed to be more dense than in the natural site which is dominated by mature trees having big prop roots. These large sized prop roots, in the natural site, may not form an efficient trapping system compared to the smaller and dense root network observed in the 10 years reforested site. This may explain the observed differences in silt/clay content between the two sites.

The high levels of TOM in the natural site compared to the 10 years reforested site can be related to the high levels of peat which has accumulated over the years and the continuous supply of organic matter from falling mangrove leaves. It was observed that the samples from the natural site usually contained a section of undecomposed detrital material at the bottom of the core. Additionally, although young mangrove trees may be more leafy than the older ones hence dropping more leaves on to the forest floor, the observed dense aerial root network in the 10 years reforested site probably traps the leaves, preventing them from being buried in the sediments. The lower TOM levels recorded from the 10 years and the 5 years reforested sites compared to the natural site also shows the effect of forest age on TOM, with the older natural forest recording higher TOM levels. Indeed, Bosire et al. (2004) and Schrijvers et al. (1995) recorded similar trends in organic matter content in

natural, reforested and denuded mangrove sites. Denuded mangrove sites are usually more exposed due to lack of canopy cover, which makes them less efficient in slowing down incoming and outgoing tides. This leads to sediment resuspension and erosion of detrital material by tidal currents, resulting in coarser sediments and less organic matter.

The lower temperature recorded in the 10 years reforested site compared to the natural site may be related to the canopy aerial structure. It was observed that the 10 years reforested site formed a continuous canopy landscape as the trees were of similar height. This continuous canopy ensures effective shading of the sediments from solar radiation. However, in the natural site, gaps in the canopy were evident due to smothering of undergrowth by the big mature trees. These canopy gaps allowed penetration of solar radiation on to the sediment surface leading to relatively higher temperatures in the natural site. Similarly, evaporation from the degraded and the 5 years reforested sites is expected to be high due to lack of or reduced canopy cover. This is responsible for the high temperature and salinity recorded from these sites.

Sediment chlorophyll *a* concentration is an indication of sediment phytoplankton and bacterial abundance, while C/N ratio indicates the nutritional value of TOM and the associated microbial communities. The relatively cooler conditions in the natural and the 10 years reforested sites due to canopy cover, promote sediment phytoplankton and other microbial growth. These sedimentary phytoplankton and microbial communities are responsible for the observed high chlorophyll *a* and C/N ratio observed in these sites. However, canopy removal exposes the mangrove sediments to intense solar radiation

which leads to increased sediment temperature and salinity. This may not be favourable for sediment phytoplankton and microbial community growth. This explains the low Chlorophyll *a* and C/N ratio recorded from the degraded site. However, exposed sediments receive abundant solar radiation which may facilitate the growth of interstitial diatoms. This may explain the relatively higher chl. *a* recorded in the upper (0-1 cm) section than in the lower sections in the degraded site.

A total of 12 macro-endobenthic taxa were recorded during this study. This number of taxa is close to that recorded in previous studies conducted in the same area (16 taxa, Schrijvers et al., 1995; 13 taxa, Fondo & Martens, 1998; 13 taxa, Bosire et al., 2004). The density and number of macro-endofauna taxa were higher in the natural site than in all the other sites. This trend is similar to that recorded by Bosire et al. (2004), where natural *R. mucronata, S. alba and A. marina* sites recorded the highest sediment infauna densities compared to the reforested and degraded sites. The total number of taxa and average densities of macro-endofauna in the 10 years reforested site was also higher than in the 5 years reforested and degraded sites. This shows that the restoration of the mangrove forests has led to the recolonisation of sediment associated macro-endofauna, which may suggest ecosystem function recovery. However, this recolonisation seems to be forest age dependent and may take longer than 10 years for a complete similarity with the natural ecosystem to be achieved. A gradual change in the macrofaunal epifauna community structure with forest age has also been reported from the Ranong mangrove forest of Thailand (Macintosh et al., 2002), and from Matang mangroves in Malaysia (Sasekumar & Chong, 1998). Additionally, Morrisey et al. (2003) observed substantial differences in the abundance and composition of benthic fauna between young (3-12 years) and old (> 60 years) mangrove

forests. These differences were linked to higher organic matter content and leaf litter concentration with increasing forest age, which is similar to the results in this study.

Macrofauna patterns may vary in relation to sediment grain size and organic matter content (Hwey-Lian, 1995; Netto & Galluci, 2003). Their findings of high macrofauna densities in sites with high organic matter content are similar to the observations of the current study since organic matter content was high in the natural and the 10 years reforested sites, which also recorded the highest macro-endofauna densities. The complex prop root system in the forested mangrove sites, combined with the availability of leaf litter and detritus, provides enhanced resource availability for benthic fauna especially for nematodes and oligochaetes. However, mangrove derived detritus has been shown to be of low nutritional value due to their high tannin content (Alongi, 1987) and high C/N ratio (Skov & Hartnoll, 2002). Therefore, it seems that the food provision by mangrove detritus is mainly indirect via the detrital food web where detrivores like oligochaetes and nematodes may feed on the microflora associated with decomposing detrital material (Skilletter, 2000; Netto & Galluci, 2003).

Infact, according to Bouillon et al., (2004) sources of nutrients, especially carbon and nitrogen, for invertebrate communities in intertidal mangroves, do not only include local inputs from mangroves as litterfall or as part of the sediment organic pool, but also microbiota associated with detritus, a variety of epiflora and tidally imported sources like phytoplankton and seagrass derived organic matter. Additionally, even after intense microbial decomposition, mangrove and marsh derived detritus are refractory to digestion and poor in nutrients compared to phytoplankton, microphytobenthos and macroalgae

(Alongi, 1987). However, the microhabitats and substrates created by the large amounts of detritus in different degrees of decomposition play a role in the nutrition of benthic fauna. This nutritional input mainly comes from the surface biofilm which includes bacteria, microalgae, protozoa and fungi (Gwyther, 2003). Additionally, bacteria produce a heavy slimy layer on leaf litter during the initial stages of decomposition. This slimy layer acts as a matrix for accumulation of detritus, algae and fungal spores and ultimately the benthic fauna for which these materials are a prime food source (Fell et al., 1975; Moens & Vincx, 1997).

Physical environmental characteristics like sediment temperature, salinity and pH have also been shown to influence the abundance of mangrove benthic fauna (Tietjen, 1968; McLachlan, 1978; Ingole & Parulekar, 1998). Degraded mangrove areas are usually exposed to solar radiation due to lack of canopy cover. This exposure increases sediment temperature, which consequently reduces sediment water content and increases salinity. These changes, in sediment characteristics, negatively impact on the benthic fauna by increasing environmental stress (Sasekumar, 1994). Exposure also leads to desiccation which kills or limits the growth of microflora, removes water from floral cell cytoplasm in addition to changing the chemical status of organic materials, which are important media for microbial growth (Mfilinge et al., 2002). This explains the low densities on macro-endobenthos recorded in the 5 years reforested and degraded sites, which are more exposed and recorded the highest temperature and salinity.

The taxon Polychaeta dominated the 5 years reforested site which recorded a slightly higher sand fraction than silt/clay compared to the 10 years reforested and natural sites.

Hwey-Lian (1995) recorded high densities of Polychaeta from a subtropical mangrove in Taiwan characterised by a low silt/clay fraction but rich in organic matter. These more favourable sediment conditions for polychaetes colonisation of mangrove sediments, may explain the dominance of polychaetes in the 5 years reforested site, which recorded relatively higher sand than silt/clay and also relatively high organic matter content. Additionally, the dominance of polychaetes in the 5 years reforested site may also be due to faunal succession during the recolonisation process. This dominance by Polychaeta was also due to the low abundance of oligochaetes recorded in the 5 years reforested site.

Nemertines were abundant in the degraded site which also recorded the highest sand content and lowest TOM in association with the lack of vegetation. Most interstitial nemertines have been recorded from intertidal and subtidal zones subject to considerable current action, which facilitates sedimentation of relatively coarse sand and shell ash. Nemertines also prefer areas with low organic matter or silt (Higgins & Thiel, 1992). The physical conditions of the degraded site concur with the habitat preferences for nemertines, thus explaining the high densities recorded there.

Ecosystem restoration studies on created and recreated salt marshes, which are the temperate equivalents of mangroves in the tropics, have received much attention compared to mangroves worldwide. Minello and Zimmerman (1992), recorded higher organic matter levels in natural salt marshes compared to restored ones, which positively correlated with the density of sediment infauna and decapod crustaceans. Hampel et al. (2003) showed clear differences in nekton community composition, species abundance, biomass and detritus between a natural and 10 years old restored salt marsh in the Westerschelde

estuary. Similarly, Moseman et al. (2004) recorded higher macrofaunal densities and species richness in a natural salt marsh compared to a 19 month old restored salt marsh in California. These differences were linked to differences in salinity and organic matter content, which influenced the general succession of infauna. These results from salt marsh restoration studies concur with the results of the current study since the natural site recorded the highest TOM and also the highest density and taxa richness of macro-endobenthos. The results further support the fact that the restored mangrove forests have not yet attained a macro-endofauna community and sediment physical characteristics similar to the natural forest. This means that even after 10 yrs, the reforested site has not yet developed the optimum characteristics of a natural mangrove. The results have further shown the importance of mangrove sediment physical characteristics like organic matter and grain size in influencing the recolonisation and hence recovery of mangrove and salt marsh ecosystems' benthic communities.

3.6 Conclusions

The results of this study have shown that mangrove ecosystem degradation leads to detrimental changes in sediment physical characteristics, with consequent declines in macro-endobenthic densities and changes in macro-endobenthic community structure. It is also clear that the restored mangrove forests are gradually tending towards becoming ecologically similar to the natural forests. However, this may take longer than 10 years as shown by the differences in sediment characteristics, macro-endofauna densities as well as community composition between the natural and the reforested mangrove areas. Additionally, this study has contributed information that may assist in dealing with

questions on mangrove management and restoration, like whether young restored mangrove forests are ecologically similar to natural ones and how long restored mangroves may take to become similar to the natural ones.

CHAPTER FOUR

Patterns of colonisation of meiobenthos as an indicator of recovery of reforested *Rhizophora mucronata* mangroves in Gazi Bay, Kenya.

4.1 Introduction

Meiobenthos or benthic meiofauna are defined on a methodological basis as 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. Their abundance and species composition are controlled by several physical factors including sediment particle size, temperature and salinity, in addition to biochemical conditions related to organic matter input and oxygen availability (Giere, 1993). The role of meiofauna in carbon flows through the benthic food web, occurring in tidal mud flats and estuaries among other zones within the marine biotope, is still a matter of debate (Bouillon et. al., 2004; Urban-Malinga & Moens, 2006; Van Oevelen et. al, 2006). Some studies suggest that they 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) mechanical breakdown of detrital particles which makes them more susceptible to increased bacterial action, (ii) excreting nutrients which are used by the microbial community, (iii) production of slime and mucus that attracts and sustains bacterial growth

and (iv) sediment bioturbation where meiofauna act as vertical conveyors of biochemical substances within sediments and between the sediments and overlying waters. The grazing on bacteria by meiofauna may also keep them at their exponential phase of growth. The wide range of feeding types found in meiofaunal groups enables them to occupy several trophic levels. This, coupled with their relatively high densities, might enhance the flow of energy in the detrital system (Dye, 1983). Meiofauna are preyed upon by the 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 show an obligatory meiofaunal feeding stage where copepods appear to be the major meiofauna prey items (Gee, 1989).

According to Gwyther (2003), fallen leaves in mangrove forests provide new patches of phytal habitat on the sediment surface, which provides an opportunity to investigate successional, trophic and taxonomic aspects of litter assemblages as the fallen leaves decay. Particulate food resources for meiofauna on leaf litter comprise the surface biofilm, which comprises of bacteria, microalgae, protozoa and fungi (Skilletter, 2000; Netto & Galluci, 2003). Ecological studies on the community structure of the meiofauna of mangrove leaf litter in north-eastern Malaysia showed that the meiofauna climax community was not influenced by the species of mangrove leaf, although the community changed during the process of litter decay. However, the shift in species composition over time was a reflection of meiofauna successional changes associated with ageing leaves (Gee & Sommerfield, 1997). Free living marine nematodes are the most dominant group among the meiofauna of marine environments (Giere, 1993; Vincx, 1996). Their

great abundance, adaptation to a wide range of habitats and diverse morphological features suggest that nematodes play a major role in benthic ecosystems (Giere, 1993).

Mangrove forests and their associated soft-sediments are common coastal habitats in tropical and warm subtropical latitudes. The majority of mangrove forests are within the vicinity of coastal cities or other large human settlements, which makes disturbances from human activities to be considered as major factors that modify the structure of mangrove communities (Kairo & Abuodha, 2001; Alongi, 2002). The need for fast economic development has led many countries to massively destroy mangrove forests. Impacts related to eutrophication, unplanned coastal development, unsustainable exploitation of mangrove resources and aquaculture are frequent along the tropical and subtropical coastlines (Netto & Galluci, 2003). Some of these activities involve cutting/and or clear felling of the mangrove trees leaving some areas completely bare.

Although meiofauna are threatened by mangrove degradation, which leads to loss of their habitat, very few studies have focused on their assemblages especially in degraded and restored mangrove forests, despite the critical role they play as part of marine biodiversity. Most studies have focused on macrofaunal assemblages (Ruwa, 1988; Fondo & Martens, 1998; Sasekumar & Chong, 1998). Furthermore, only a few studies have focused on mangrove restoration and meiofaunal recolonisation of restored mangrove ecosystems which include Khalil (2001).

An important step for a comprehensive understanding of the effects of habitat loss or restoration on the functioning of mangrove ecosystems is the knowledge of faunal

diversity. It need not be emphasised that meiobenthic and macrobenthic assemblages form a crucial component of the functioning of mangrove ecosystems and, therefore, should be analysed together with vegetation structure, in order to determine the overall mangrove restoration process and success (Field, 1999). The few studies that have been undertaken in relation to mangrove degradation and/or reforestation along the Kenyan coast have mainly concentrated on the macrobenthic assemblages (Fondo & Martens, 1998; Bosire et. al., 2004).

Ecological studies on Kenyan mangrove meiobenthos are also very few and include studies by Vanhove et. al. (1992) and Schrijvers et al. (1995, 1997). Similarly, studies dealing with the effects of mangrove ecosystem degradation and restoration on meiobenthos community structure are completely lacking. Therefore, this study is the first along the Kenyan coast, which compares meiofauna community assemblages from a natural, a 10 years reforested, a 5 years reforested and a degraded *Rhizophora mucronata* forests. Additionally, the macrofauna community has also been analysed from the same study sites (Chapter 3) in order to contribute to the management question whether reforestation of clear-cut mangrove areas can be done and a complete recovery of ecosystem functions be attained.

4.2 Objectives

The objectives of this study were;

- To determine the effect of mangrove forest degradation (clear felling) on meiobenthos densities, community composition and diversity

- To investigate meiobenthos recolonisation patterns of restored *R. mucronata* forests
- To relate the spatial patterns in meiobenthos community structure to sediment physical characteristics

This was achieved by comparing the meiobenthos from two reforested areas of different ages (5 and 10 years old) with those from a natural forest and a fully degraded site.

4.3 Materials and Methods

The study site, meiobenthos sampling procedure, laboratory sample processing and identification have been described in detail in Chapter 2 on materials and methods.

4.4 Results

4.4.1 Meiobenthos densities and community composition

A total of 15 meiofauna taxa were recorded in all the sites. The natural and the 10 years reforested sites recorded 9 meiofauna taxa each, while the 5 years reforested and the degraded sites recorded 7 and 8 taxa, respectively. Nematoda was the dominant taxon in all the study sites accounting for over 90 % of the total meiofauna densities (Table 4.1). The 10 years reforested site recorded the highest meiofauna densities averaging 1379 ± 369 Ind. /10 cm^2, while the degraded site recorded the lowest densities (356 ± 248 Ind. /10 cm^2).

Table 4.1. Densities (mean ± SE; n = 9) of meiofauna taxa (Ind. /10 cm^2) in the natural, 10 years reforested, 5 years reforested and degraded sites.

	Natural	**10 years reforested**	**5 years reforested**	**Degraded**
Nematoda	1142 ± 61	1320 ± 285	788 ± 213	320 ± 247
Oligochaeta	43 ± 24	52 ± 32	3 ± 4	6 ± 5
Polychaeta	2 ± 1	2 ± 1	3 ± 2	1 ± 1
Nemertina	0	0	1 ± 1	27 ± 10
Bivalvia	1 ± 1	0	0	0
Gastropoda	1 ± 1	0	0	0
Amphipoda	0	1 ± 1	0	0
Copepoda	13 ± 12	3 ± 2	0	1 ± 1
Copepod nauplii	0	0	0	1 ±1
Foraminifera	0	1 ± 1	0	0
Cladocera	0	1 ± 1	0	0
Insecta	1 ± 1	1 ± 1	1 ± 1	1 ± 1
Insect Larvae	1 ± 1	1 ± 1	1 ± 1	1 ± 1
Arachnida	0	0	1 ± 1	0
Crustacea	1 ± 1	0	0	0
Mean ± SD	**1201 ± 123**	**1379 ± 130**	**796 ± 275**	**356 ± 67**
% Nematoda	**95**	**96**	**99**	**90**
No. of taxa	**9**	**9**	**7**	**8**

The variation in total meiofauna densities and the densities of the major meiofauna taxa are shown in figure 4.1. The natural site recorded relatively lower densities of meiofauna (1201 ± 197 Ind. /10 cm^2) than the 10 years reforested site (Fig. 4.1a). Total meiofauna densities showed significant differences between sites (ANOVA, df = 3, F = 17.64, $p < 0.05$). However, Tukeys HSD post hoc comparisons showed no significant differences ($p < 0.05$) between the natural site, the 10 years reforested and the 5 years reforested sites. The degraded site recorded significantly lower densities than the natural and the 10 years reforested sites ($p < 0.05$), but not different from the 5 years reforested site. The lack of significant differences between the 5 years reforested site and all the other sites was due to the high variation in meiofauna densities recorded in this site.

Similarly, nematode densities (Fig. 4.1b) were highest in the 10 years reforested site (1320 ± 341 Ind. /10 cm^2) and lowest in the degraded site (320 ± 243 Ind. /10 cm^2). Again, the natural site recorded lower nematode densities (1142 ± 196 Ind. /10 cm^2) than the 10 years reforested site. There were significant differences between sites in nematode densities (ANOVA, df = 3, F= 17.44, $p < 0.05$). Similar to total meiofauna densities, Tukeys HSD post hoc comparisons showed no significant differences between the natural, the 10 years reforested and the 5 years reforested sites, while the degraded site recorded significantly lower nematode densities than the natural and the 10 years reforested sites ($p < .05$), but not different from the 5 years reforested site. Just like total meiofauna densities, the lack of significant differences between the 5 years reforested site and all the other sites was due to the high variation in nematode densities recorded in this site. The observed trends in the densities of meiofauna and nematodes between sites reflect the differences in sediment physical characteristics. The silty/clay sediments rich

in TOM recorded the highest densities of meiofauna and in particular nematodes. This shows that sediment characteristics could be playing a role in influencing meiofauna, and in particular, nematodes recolonisation of the mangrove ecosystems.

The densities of oligochaetes (Fig. 4.1c) were highest in the 10 years reforested site (52 ± 28 Ind. /10 cm^2), while the 5 years reforested site recorded the lowest (3 ± 6 Ind. /10 cm^2). The natural site recorded 43 ± 26 Ind. /10 cm^2. The relative abundance of oligochaetes was 4 % in both the natural and the 10 years reforested sites. Both the natural and the 10 years reforested sites recorded significantly higher Oligochaeta densities than the 5 years reforested and the degraded sites (ANOVA, df = 3, F = 22.31, $p < 0.05$). The high densities of oligochaetes in the natural and the 10 years reforested sites could be related to the high relative proportions of silt/clay and high TOM recorded in these two sites.

Nemertines (Fig. 4.1d) were abundant in the degraded site (27 ± 23 Ind. /10 cm^2), while the 5 years reforested site recorded very low densities (1 ± 1 Ind. /10 cm^2). They were absent in the natural and the 10 years reforested sites. Nemertina was the second dominant taxon in the degraded site accounting for 8 % of the total meiofauna densities. Their relative abundance in the 5 years reforested site was, however, very low (< 0.5 %). Nemertines have been shown to prefer sandy sediments having low organic matter, which were characteristic of the degraded site.

The highest density of copepods (Fig. 4.1e) was recorded in the natural site (13 ± 18 Ind. / 10 cm^2), where they contributed only 1 % of the total meiofauna densities. The 10 years

reforested site recorded very low densities (3 ± 4 Ind. / 10 cm^2), while they were only occasionally present in the degraded site (1 ± 2 Ind. / 10 cm^2) and absent in the 5 years reforested site. Though copepods have been linked to sandy sediments which are well aerated, the degraded and 5 years reforested sites recorded the lowest densities, suggesting that other factors could be influencing their distribution in the studied sites.

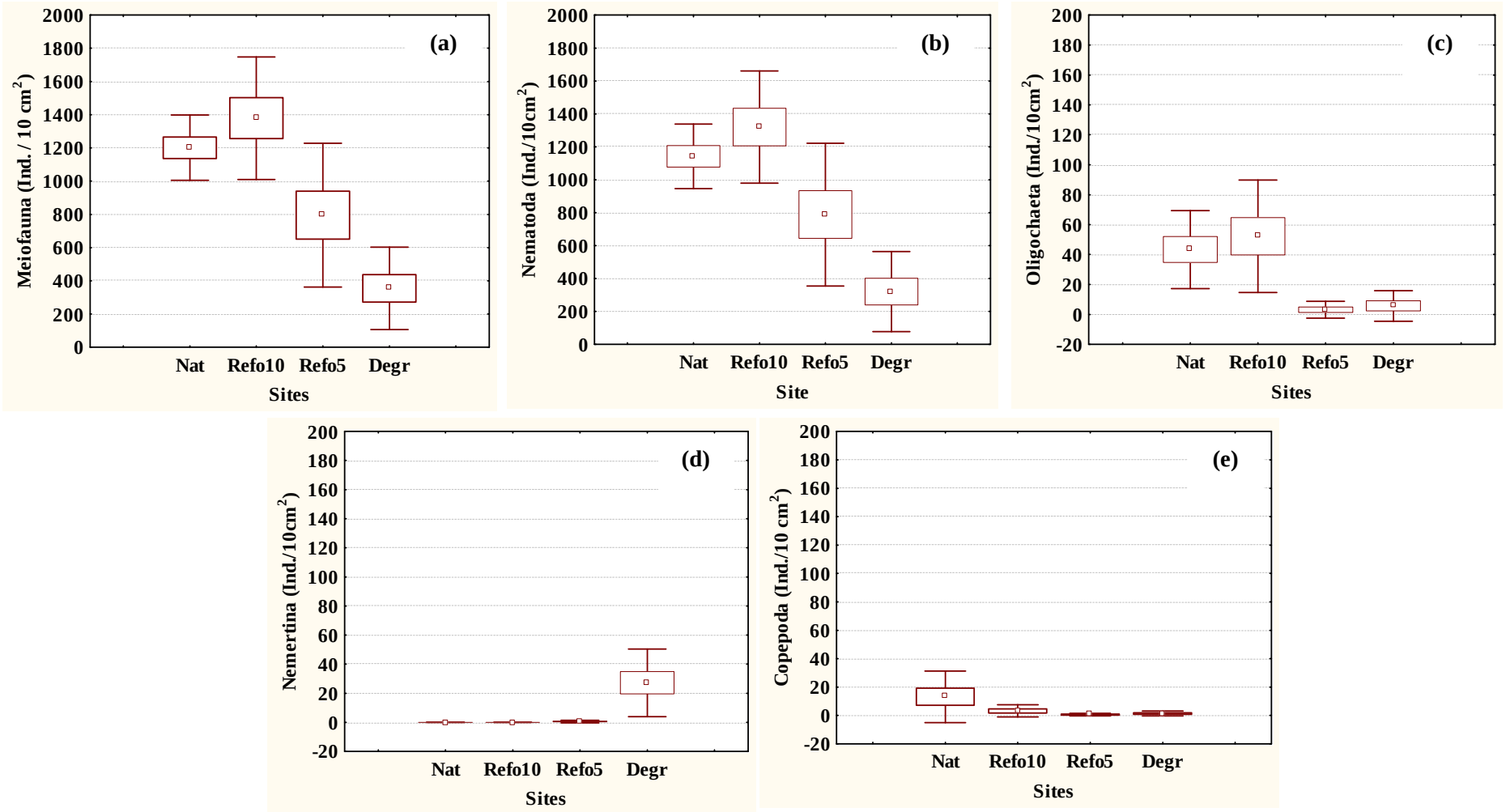

Figure 4.1a-e. Densities (Mean ± SD, n = 9) of (a) Meiofauna (b) Nematoda (c) Oligochaeta (d) Nemertina and (e) Copepoda in the natural (Nat), 10 years reforested (Refo10), 5 years reforested (Refo5) and degraded (Degr) sites.

Non-Metric Multidimensional Scaling (nMDS) on meiofauna densities and community composition showed no separation between the natural and the 10 years reforested sites (Fig. 4.2). However, the 5 years reforested and the degraded sites formed separate clusters.

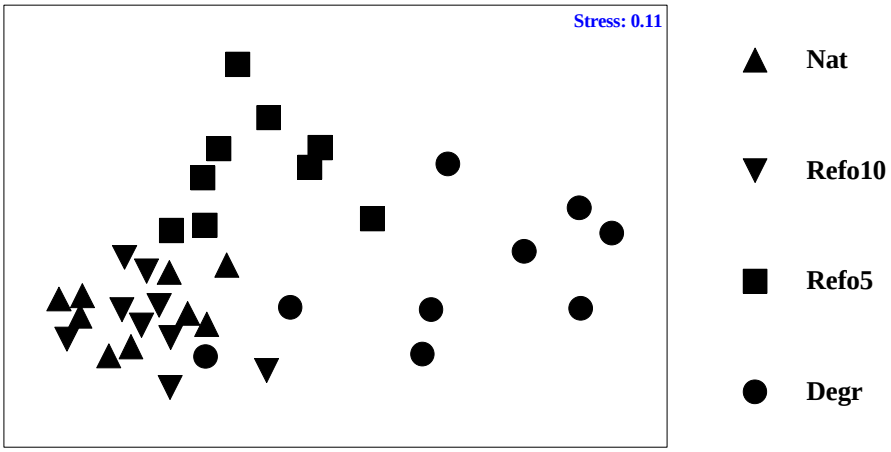

Figure 4.2. nMDS on (Logx+1) meiofauna community data showing grouping of sites. Natural site (Nat), 10 years reforested site (Refo10), 5 years reforested site (Refo5) and degraded site (Degr).

This pattern was further confirmed by ANOSIM pair wise comparisons (Table 4.2) which showed no significant differences between the natural and the 10 years reforested sites (R = -0.062) while all the other pairwise comparisons gave significant differences (R > 0.5). SIMPER analysis gave very high average similarities (> 70 %) within all sites. The taxa Nematoda, Oligochaeta and Nemertina were responsible for the high similarities observed within sites (Table 4.3). Additionally, the dissimilarities observed between sites

were mainly contributed by the taxa Copepoda, Oligochaeta, Nemertina and to a lesser extent Nematoda (Table 4.4).

Table 4.2. Pairwise ANOSIM comparisons between sites based on meiofauna community composition (Global R: 0.522).

Pairwise comparisons	**R Value**
Natural vs. 10 years reforested	-0.062
Natural vs. 5 years reforested	0.648
Natural vs. Degraded	0.704
10 years reforested vs. 5 years reforested	0.676
10 years reforested vs. Degraded	0.707
5 years reforested vs. Degraded	0.675

Table 4.3. Meiofauna taxa percentage contribution (SIMPER) to similarities within sites.

Sites	**Average Similarity**	**Meiofauna taxa contribution**				
		Nematoda	**Oligochaeta**	**Copepoda**	**Polychaeta**	**Nemertina**
Natural	83	61	27	8		
10 years reforested	82	62	28	4		
5 years reforested	78	87			8	
Degraded	72	63				29

Table 4.4. SIMPER lists showing the meiofauna taxa percentage contribution to dissimilarities between sites. Natural site (Nat), 10 years reforested site (Refo10), 5 years reforested site (Refo5) and degraded site (Degr).

Sites	**Average Dissimilarity**	**Meiofauna Taxa contribution to between sites similarities**
Nat vs. Refo10	17	Copepoda (31), Oligochaeta (18)
Nat vs. Refo5	30	Oligochaeta (40), Copepoda (23)
Refo10 vs. Refo5	30	Oligochaeta (43), Copepoda (13),
Nat vs. Degr	43	Nemertina (28), Oligochaeta (26), Nematoda (16), Copepoda (14)
Refo10 vs. Degr	43	Nemertina (28), Oligochaeta (27), Nematoda (17)
Refo5 vs. Degr	37	Nemertina (36), Nematoda (17),

Analysis of relative multivariate dispersion (MDISP), which is a measure of within site variability, showed that the natural and the 10 years reforested sites were the least variable with Indices of Multivariate Dispersion (IMD) of 0.737 and 0.752, respectively. However, the 5 years reforested and the degraded sites showed the highest within site variability (IMD = 1.11 and 1.4, respectively). These high IMD values recorded for the 5 years reforested and degraded sites show that these two sites were the most heterogeneous interms of meiofauna densities and community composition.

4.4.2 Meiofauna diversity measures

Meiofauna taxa richness was highest in the 10 years reforested site (4.6 ± 1.1) and lowest in the 5 years reforested site (3.3 ± 0.9). The 5 years reforested site also recorded the lowest Shannon diversity index and taxa rarefaction (1.4 ± 0.3 and 0.1 ± 0), respectively

(Table 4.5). Since Shannon diversity index is influenced by species dominance (Maguran, 1991), the natural, the 10 years reforested and the 5 years reforested sites recorded low indices due to the dominance by nematodes. However, due to the lower relative abundance of nematodes recorded in the degraded site, Shannon diversity index was highest here. There were no significant differences between sites in meiofauna taxa richness, while significant differences in taxa rarefaction (Kruskal-Wallis, df = 3, H = 16.43, $p < 0.05$) and the Shannon Wiener diversity index (Kruskal-Wallis, df = 3, H = 18.72, $p < 0.05$) were recorded.

Table 4.5. Meiofauna community diversity measures (mean ± SD, n=9) in the natural, 10 years reforested, 5 years reforested and degraded sites.

Sites	**S**	**ES_{50}**	**H' log_e**
Natural	4.4 ± 1.4	2.2 ± 0.6	0.2 ± 0.1
10 years reforested	4.6 ± 1.1	2.0 ± 0.2	0.2 ± 0.1
5 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

4.5 Discussion

There is limited quantitative information published on meiofauna of mangrove habitats in Kenya (Person. obs.). Studies on the distribution of meiofauna in mangrove sediments have been documented from various parts of the world such as Australia (Hodda & Nicholas,

1985; Alongi, 1987; Gwyther, 2003), Tanzania (Olaffson et al., 2000), S.E. India (Chinnadurai & Fernado, 2007), and Brazil (Netto & Galluci, 2003). Along the Kenyan coast, Vanhove et al. (1992) investigated the vertical distribution of meiofauna from sediments of five mangrove species (*Avicenia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal, Rhizophora mucronata and Sonneratia alba*) from Gazi Bay, Kenya, and identified a total of 17 meiofauna taxa. The highest densities occurred in sediments of *B. gymnorrhiza* (6707 Ind./10 cm^2) followed by *R. mucronata* (3998 Ind./10 cm^2), *A. marina* (3442 Ind./10 cm^2), *S. alba* (2889 Ind./10 cm^2) and *C. tagal* (1976 Ind./10 cm^2), with nematodes accounting for 95 % of the total densities. Sediment granulometry and oxygen conditions were the major factors influencing meiofauna distribution. Schrijvers et al. (1995) looked at the human impact on meiofauna in partially impacted *C. tagal* and *R. mucronata* mangroves in Gazi Bay, Kenya. In their study, impacted sites showed lower densities of meiofauna and nematodes, in particular. This decrease was linked to the loss of both organic matter and muddy sediments due to the clearing of mangroves, which increases tidal currents and sediment erosion. Exclusion experiments by Schrijvers et al. (1997) showed that meiobenthos, especially Oligochaeta and Nematoda, were influenced by resource competition with the epibenthos. The meiobenthos and epibenthos shared the same food source comprising of muddy detritus and microalgae.

Only Mwojoria (2007) studied benthic meiofauna in restored *S. alba* mangrove forests in Gazi Bay despite restoration programmes having being started 15 years ago. His study found no differences in meiofauna densities between the natural and reforested sites. Thus, this study forms the first account of meiofauna in restored *R. mucronata* mangrove forests

along the Kenyan coast. The results of the present study show a clear separation of the restored *R. mucronata* forest stands of different ages (5 and 10 years), based on environmental characteristics and also on the meiofauna taxa densities and community composition. The differences in meiofauna community between the natural and the 10 years reforested sites are not pronounced despite the differences in environmental characteristics (especially TOM) that are still present. This shows that meiofauna are controlled by a complex of factors within the studied mangrove environment.

Overall, 15 meiofauna taxa were recorded with the natural and the 10 years reforested sites recording 9 taxa each, while the degraded and 5 years reforested sites recorded 8 and 7 taxa, respectively. The total number of taxa recorded is similar to that observed by Vanhove et al. (1992), Schrijvers et al. (1997) from *R. mucronata* sites and Mwojoria (2007) from *S. alba* sites in Gazi Bay. However, the total density of meiofauna from the current study is different from those of earlier studies from Gazi Bay. Vanhove et al. (1992) and Schrijvers et al. (1997) recorded much higher densities of meiofauna from *R. mucronata* sites (3998 and 6101 Ind./10 cm^2, respectively), while Mwojoria (2007) recorded almost similar densities of between 1576 and 1774 from *S. alba* sites, compared to the current study (1339 ind/10 cm^2). From South Indian mangroves, Chinnadurai and Fernado, (2007) recorded far much lower meiofauna densities (max 474 Ind./10 cm^2) from *R. apiculata*, while Netto and Galluci, (2003) recorded a maximum of 1586 Ind./10 cm^2 from Brazilian mangroves.

The differences in meiofauna densities between the present and earlier studies from Gazi Bay can be related to the inundation class or tidal height of the study sites. The earlier study sites 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). This means that 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 plays a crucial role in benthic community dynamics since it determines the duration of high temperature and consequently salinity stress during low tides' exposure. Indeed, Sasekumar (1994) recorded an increase in meiofauna densities with decreasing tidal height in Malaysia, which he linked to minimal environmental stress since air exposure is reduced. Additionally, Alongi (1987) recorded decreased nematode densities with increased tidal height in mangrove forests in Australia. The differences were linked to differences in physical and chemical factors such as sediment granulometry, soluble tannins, temperature, disturbance and microbial food resources.

Nematoda was the most abundant taxon in the current study accounting for over 90 % of total densities in all the sites. Dominance by Nematoda 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; Hodda & Nicholas, 1985). The natural and the 10 years reforested sites having silty sediments (silt fraction > 50 %) in the present study, also recorded the highest TOM content and the highest densities of meiobenthos, especially

Nematoda. This shows that sediment type and sediment TOM levels influence the meiofauna distribution patterns observed. Giere, (1993) noted that nematode community composition and diversity, are largely determined by sediment structure and probably by the level of silt fraction, which limits their biotopical range. Sediments rich in TOM were recorded in the natural and the 10 years reforested sites with a complex system of pneumatophores. The complex system of pneumatophores in these sites, coupled with the availability of leaf litter and detritus provides an enhanced food source for benthic fauna. Netto and Galluci, (2003) noted that sediment grain size and organic matter content may play a vital role in determining the patterns of meiofauna distribution. This influence may act through the availability of food resources via the detrital food web, where sediment infauna feed on the microflora associated with decomposing detrital material (Skilletter & Warren, 2000). Additionally, Gwyther (2003), documents that the microhabitats created by the large amounts of detritus in different stages of decomposition harbours biofilms. These biofilms include bacteria, microalgae, protozoa and fungi which form food for benthic fauna. This explains the high densities of meiofauna recorded in the natural and the 10 years reforested sites which recorded high TOM levels, which could be providing several opportunities for meiofauna colonisation.

Exposure due to lack of mangrove canopy cover increases environmental stress to benthic fauna (Sasekumar, 1994). Increased sediment salinity and temperature may also negatively affect benthic microphytobenthos which act as food sources for benthic fauna (Ingole & Parulekar, 1998). The high temperature and salinity recorded in the degraded site suggests

that environmental stress was high, which in combination with the lower TOM content explains the low densities of meiofauna recorded in the degraded site.

Nemertines were abundant in the degraded site which also recorded the highest sand content and the lowest TOM levels. Most interstitial Nemertines have been recorded from intertidal and subtidal zones subject to considerable current action which facilitates erosion of fine sediments leaving relatively coarse sand. Nemertines also show preference to areas having low organic matter and/or low silt content (Higgins & Thiel, 1992). This explains the high densities of Nemertines recorded in the degraded site. It also shows that Nemertina is a taxon adapted to stressful environments.

Copepods occurred in very low densities in the current study with a maximum of 13 Ind./10 cm^2 in the natural site. These low densities can be related to sediment type since copepods are mostly correlated with coarser sediments which are more oxygenated than silty/clay sediments (Giere, 1993). Similarly, Wieser et al. (1974), stated that copepods especially Harpacticoid copepods are the most sensitive meiobenthic taxon to decreased oxygen levels. Copepods are usually restricted to the oxygen rich zones and tend to be found on or just beneath the surface of muds. However, their biotope extends deeper within sands and gravel to the level of the permanent water table (Wells, 1992). Although the degraded site had the highest sand content, it recorded very low Copepoda densities. This mainly shows that temperature and salinity stress due to exposure, did not favour Copepoda colonisation. Studies by Schrijvers et. al., (1995) in *R. mucronata* forests of Gazi Bay, however recorded much higher Copepoda densities (max 107 ± 38 Ind. /10 cm^2). These

sites were, however, located closer to the low water level hence are permanently wet. But in the current study, sampling sites were located closer to the high water mark where exposure is prolonged hence environmental stress is high due to increased temperature and salinity.

Unlike Nemertines which are purely confined to the degraded and the 5 years reforested sites, oligochaetes were recorded in all the sites with higher densities in the natural and the 10 years reforested sites. Mutua et al. (submitted) also recorded the same trend of oligochaetes in the macrofaunal size group. The occurrence of oligochaetes in the degraded and the 5 years reforested sites shows that this taxon is resilient to environmental stress. However, it remains to be investigated whether the species found in the natural and the 10 years reforested sites are the same as those from the degraded and the 5 years reforested sites.

Although the 10 years reforested site shows a similar meiofauna community structure with the natural site, the two sites still differ in terms of TOM and sediment type. The 10 years reforested site has not yet developed physical characteristics of a natural mangrove habitat. This was also reflected in the macrofauna community structure but not in the meiofauna. These differences were not only caused by both oligochaetes and polychaetes, but also by the large sized nematodes which were much more abundant in the natural site compared to the 10 years reforested site in the macrofauna size class. The 10 years reforested site recorded a more diverse meiofauna community than the natural site as evidenced by the relatively higher taxa richness. This could be reflecting the fact that the natural site has

already reached the climax community, while the 10 years reforested site being a developing system, still has its community growing as new habitat conditions become available. Contrally, the degraded site recorded a higher Shannon Diversity Index than all the other sites. This is because of the high densities of meiofauna and the higher dominance by Nematoda in these sites compared to the degraded site.

4.6 Conclusions

This study has added onto the existing information on mangrove meiofauna community assemblages along the Kenyan coast. It also provides new information on meiofauna assemblages from restored *R. mucronata* mangroves, which hitherto was lacking. It shows that degradation of mangrove forests leads to profound changes in the habitat conditions. These habitat changes lead to a strongly impoverished meiofauna community in terms of density and community composition. Despite the slow recovery of the habitat 10 years after restoration, as shown by depletion in the fine organic rich sediment fraction and macrofauna, the meiofauna densities and community composition have mainly re-established. It is also evident that recovery of the meiofauna community and in particular nematodes takes place between 5 and 10 years of reforestation. However, some taxa like Oligochaeta only re-appear in naturally high densities after more than 5 years following reforestation. This shows that complete recovery of ecosystem functions of the studied *R. mucronata* forests may take more than 10 years, though not all ecosystems aspects were investigated. This was also supported by the differences in sediment physical characteristics.

CHAPTER FIVE

The spatial and temporal variation of nematofauna of recovering tropical mangroves at Gazi Bay, Kenya.

5.1 Introduction

Mangroves are precious resources for multiple socio-economic and ecological uses. In the recent past, there has been a significant development in mangrove research, covering structure and function (Bosire et al., 2003, 2004, 2005; Bouillon et al., 2002; 2004; Mwashote & Jumba, 2002). This has provided a more comprehensive understanding of this ecosystem. However, increased economic developments, witnessed in many countries, have led to massive destruction of these vital ecosystems. Mostly, mangrove destruction is through eutrophication, unplanned coastal developments, unsustainable exploitation and conversion for aquaculture. These activities are frequent along the tropical and subtropical coastlines (Kairo & Abuodha, 2001; Netto & Galluci, 2003). Degradation of the floral component of mangrove ecosystems leads to direct impacts on the faunal structure and function (Fondo & Martens, 1998; Bosire et al., 2004; Mutua et al., unpublished). Among the marine benthos, Nematoda is a good taxon for use as ecological indicators for benthic environments (Schratzberger at. al., 2000). The reason for this is that they are the most abundant meiobenthic group and that small sample sizes can give enough animals for making concrete scientific conclusions. Nematodes also have a ubiquitous distribution, high diversity, short generation periods and continuous reproduction. They are also restricted to the sediments throughout life and have a wide range of adaptations, which enables them exploit, all littoral habitats (Higgins & Thiel,

1992; Kennedy & Jacobi, 1999). These traits ensure that the state and composition of nematode assemblages may be used to reflect the general health of the benthos (Kennedy & Jacobi, 1999). Moreover, Platt and Warwick (1980), argue that any general assessment of the ecology of intertidal habitats is incomplete if the nematofauna is not considered.

Nematodes are the most ubiquitous, abundant and diverse marine metazoan group in mangrove sediments (Alongi et al., 1992). According to Platt and Warwick (1980), they are of major energetic importance, form a significant part of the diet of many other organisms, play vital roles in facilitating decomposition as well as influencing the stability of sedimentary environments, and are potential indicators of environmental conditions. Their diverse morphologies and adaptation to a wide variety of habitats makes them major players in the benthic ecosystem (Giere, 1993). Differences in benthic physico-chemical characteristics including temperature, depth, mean grain size, salinity, mangrove forest productivity and food availability can be possible determinants of the development of different nematode communities among mangrove fringed estuaries (Alongi, 1987; Alongi & Sasekumar, 1992). Though sediment granulometry is mainly influenced by physical factors, macrofaunal bioturbation and disturbances due to feeding and locomotion can modify sediment structure leading to patchy distribution of meiobenthos and in particular nematodes (Giere, 1993).

Nematodes dominate the mangrove meiofauna, and several taxonomic descriptions have been made of mangrove nematodes from many parts of the world especially in Australia by Nicholas et al. (1991), Brazil by Netto and Galluci (2003) and in India by Sasekumar

(1994) and Chinnadurai and Fernado (2007). However, the Western Indian Ocean region, which includes the East African mangrove ecosystems, has received minimal coverage in meiobenthic and in particular nematofauna research. Although mangrove meiobenthic fauna have been documented along the Kenyan coast, for example, by Vanhove et al. (1992) and Schrijvers et al. (1995, 1997), only studies by Muthumbi (1994) and Mwojoria (2007) have researched on nematodes along the Kenyan coast. In addition, only Mwojoria (2007) has documented the nematode communities associated with degraded and restored *S. alba* in Gazi bay.

Therefore, no studies have related changes in nematode communities to *R. mucronata* mangrove degradation and restoration, despite restoration efforts having been started more than 15 yrs ago (Kairo & Abuodha, 2001). Only Mwojoria (2007) studied nematode distribution in natural, reforested and degraded *S. alba* forests. His study recorded relatively higher nematode densities from reforested *S. alba* compared to the natural site, though no significant differences between the two sites were found. The other few studies on the impact of mangrove degradation and restoration on benthos such as Fondo and Martens (1998), Schrijvers et al. (1995) and Bosire et al. (2004) have mainly focused on the macrobenthic assemblages in relation to mangrove degradation and restoration. This is despite the understanding that nematodes comprise a large fraction of marine benthic communities. They also form a crucial component of the functioning of mangrove ecosystems and play a pivotal role in mangrove ecosystem restoration success (Field, 1999). Therefore, to better understand the effects of mangrove habitat loss and restoration, studies on the nematofaunal diversity of these ecosystems are very crucial.

Therefore, this study is the first to be conducted in Kenyan mangroves that attempts to compare nematode community assemblages from natural, 10 years reforested and degraded *Rhizophora mucronata* forest stands, with a view to shed light on the effects of mangrove ecosystem degradation and restoration on nematode community structure. The study tried to answer the following questions: (1) Does mangrove clear felling (degradation) lead to alteration of nematode density and community composition? (2) Did the restoration of the *R. mucronata* mangrove ecosystem successfully create after 10 years, a nematode community assemblage comparable in density, community composition, diversity and biomass to that of the original natural mangrove stand? And (3) to what extent do nematode communities show seasonal variations?

5.2 Materials and Methods

5.2.1 Sampling and Sample processing

The detailed field sampling, laboratory sample processing and nematode identification procedures are also described in Chapter 2 on materials and methods.

5.3 Results.

5.3.1 Environmental characteristics

The spatial and temporal variations in sediment physical characteristics are shown in figures 5.1. Fig. 5.1a shows the spatial and temporal variations in TOM. Two-Way ANOVA showed significant differences between sites in TOM (ANOVA; $F = 856.63$, $df = 2$, $p < 0.05$). However, there was neither any seasonal differences within sites observed nor was the interaction between seasons and sites significant. The wet and dry seasons within

the natural site recorded significantly higher mean sediment TOM (48.1 % ± 6.6 and 48.4 % ± 5.4 respectively) than all the other sites. The lowest TOM levels (3.3 % ± 0.7 and 2.8 % ± 0.4) were recorded from the degraded site during both wet and dry seasons respectively. This trend in TOM shows the effect of forest age and clear felling on TOM. The natural mangroves being the oldest and not impacted have accumulated peat over time while the degraded site is not replenished with TOM as litter fall hence the low TOM levels.

The variations in sand between sites and between seasons are shown in Fig. 5.1b. There were significant differences between sites, between seasons within sites and the interaction between seasons and sites in sand content (ANOVA; $F = 185.36$, $df = 2$, $p < 0.05$; $F = 8.29$, $df = 1$, $p < 0.05$; $F = 7.37$, $df = 2$, $p < 0.05$ respectively). The degraded site recorded significantly sandier sediments (81.6 % ± 6.2 and 78.7 ± 1.8) during the dry and wet seasons, respectively, than the natural and the 10 years reforested sites.

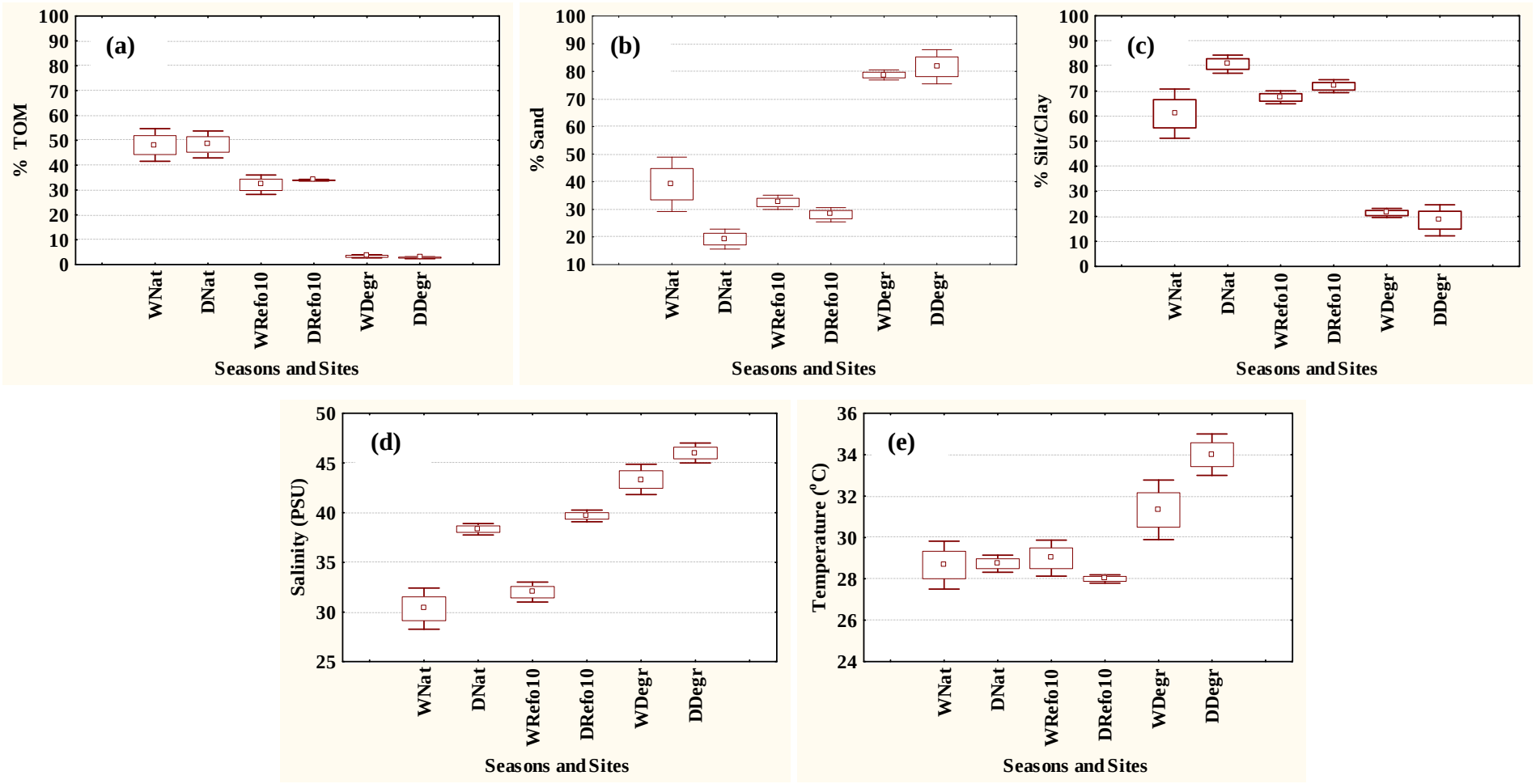

Figure. 5.1a-e. Spatio-Temporal variations in (a) TOM, (b) Sand, (c) Silt/Clay, (d) Salinity and (e) Temperature in the study sites. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

However, only the natural site recorded significant seasonal differences in sand content where the dry season recorded significantly lower sand content (19.2 % ± 3.6) than the wet season (39.1 ± 9.8) and than all the other sites ($p < 0.05$).

The proportion of silt/clay was significantly different between sites, between seasons and the interaction between seasons and sites was also significant (ANOVA; $F = 185.36$, $df = 2$, $p < 0.05$; $F = 8.29$, $df = 1$, $p < 0.05$; $F = 7.37$, $df = 2$, $p < 0.05$, respectively). Both the natural and the 10 years reforested sites recorded significantly higher silt/clay content ($p < 0.05$) during both seasons than the degraded site (Fig. 5.1c). Significant seasonal differences in silt/clay within sites were recorded within the natural site, where the dry season recorded significantly higher silt/clay fraction (80 % ± 3.6) than the wet season (60.9 % ± 9.8). The high sand content during the wet season in the natural site shows that surface runoff probably deposited sediments high in sand from the surrounding terrestrial systems. The wet and dry seasons within the degraded site recorded the lowest silt/clay content (21.3 % ± 1.8 and 18.4 % ± 6.2 respectively).

The level of salinity was significantly different between sites, between seasons and the interaction between sites and seasons was also significant (ANOVA; $F = 120.25$, $df = 2$, $p < 0.05$; $F = 108.4$, $df = 1$, $p < 0.05$; $F = 8.81$, $df = 2$, $p < 0.05$, respectively). The degraded site recorded significantly higher salinity ($p < 0.05$) during both dry and wet seasons (46 ± 1 and 43.4 ± 1.5 PSU, respectively) than the natural and the 10 years reforested sites, which recorded the lowest salinity during the wet season (30 ± 2.1 and 32 ± 1 PSU, respectively). Seasonal salinity differences were recorded from both the

natural and the 10 years reforested sites, where the dry season recorded significantly higher salinity ($p < 0.05$) that the wet season (Fig. 5.1d). There were significant differences in temperature (Fig. 5.1e) between sites and the interaction between seasons and sites (ANOVA; $F = 36.95$; $df = 2$, $p < 0.05$; $F = 5.95$, $df = 2$, $p < 0.05$, respectively). However, no significant differences between seasons within sites were observed. The degraded site recorded significantly higher temperatures ($34\ ^{0}C \pm 1$ and 31.3 ± 1.4) during the dry and wet seasons respectively ($p < 0.05$) than the natural and the 10 years reforested sites.

The ordination of sites and seasons within sites based on sediment physical characteristics data is shown in Fig. 5.2, and showed a clear separation of the degraded site from both the natural and the 10 years reforested sites. Principal components (PC) 1 and 2 explained 99 % of the variability (PC 1, 96 %; PC 2, 3 %). On the first principal component, the natural and the 10 years reforested sites, with the highest TOM and silt/clay, were separated from the degraded site having sandier sediments and low TOM. The separation of sites along the second principal component was less pronounced, though it separated the wet and dry seasons within the natural and the 10 years reforested sites, based on salinity and silt/clay fraction. The PCA output is in line with the ANOVA results which showed significant seasonal differences in sand, silt/clay and salinity only in the natural site. The degraded site having no canopy cover, experiences increased tidal erosion which reduces TOM and the silt/clay fraction.

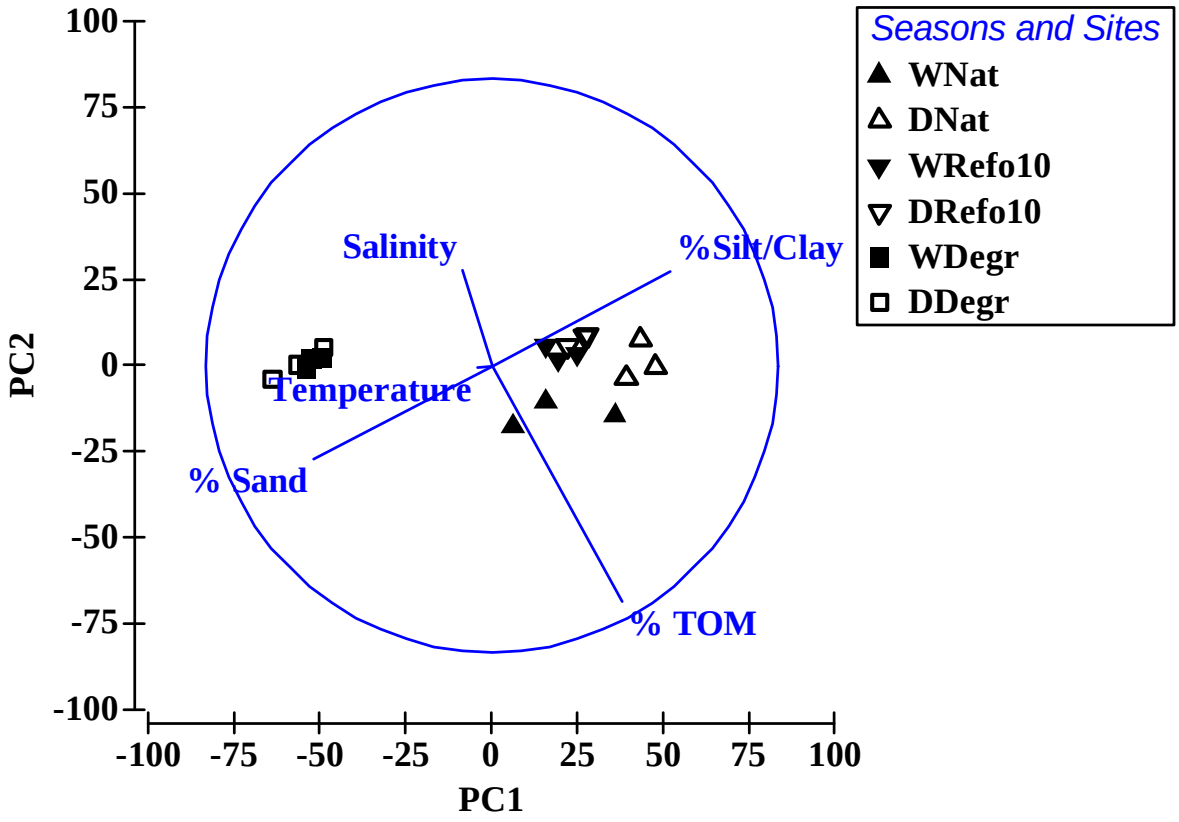

Figure. 5.2. Sediment physical characteristics: out put of Principal Component Analysis (PCA) on sites and seasons. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

5.3.2 Major nematode genera

Total nematode densities are shown in Fig 5.3. Total densities showed significant differences between sites (ANOVA; $F = 17$, $df = 2$, $p < 0.05$). The natural and the 10 years reforested sites recorded significantly higher densities than the degraded site. However, no seasonal differences were observed within sites. The high densities of nematodes in the natural and 10 years reforested sites shows the influence of food availability (TOM) and sediment type (silt/clay) on nematodes colonisation of mangroves.

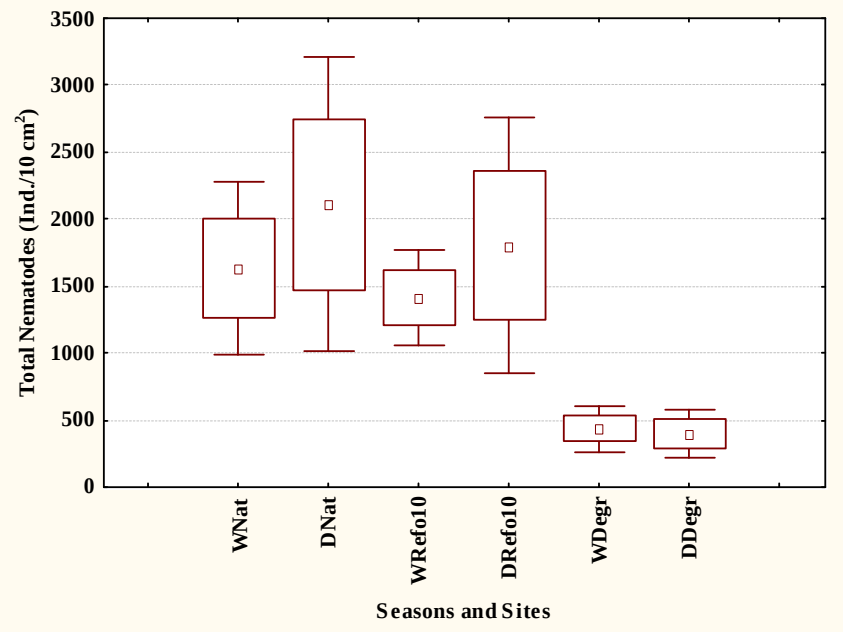

Figure 5.3. Spatial and temporal variations in nematode densities. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

Figures 5.4a-f shows the densities of the major nematode genera. Out of all the nematode genera identified and counted, *Terschellingia* (Fig. 5.4a) accounted for 22 % of the overall total density. It was the dominant genus in both the natural and the 10 years reforested sites, accounting for 25 % and 26 % of the total density, respectively. However, *Terschellingia* was totally absent from the degraded site. Densities of *Terschellingia* were significantly different between sites (ANOVA; $F = 245.3$, $df = 2$, $p < 0.05$) even though neither seasonal differences were observed in densities of *Terschellingia* within all sites nor was the interaction between seasons and sites significant.

The genus *Pierickia* (Fig. 5.4b) accounted for 11 % of the overall density. The densities were highest in the 10 years reforested site, where it accounted for 21 % of the total density. The natural site recorded intermediate densities with a relative abundance of 5 %. However, significantly lower densities of *Pierickia* (ANOVA; $F = 82.57$, $df = 2$, $p < 0.05$) were recorded in the degraded site, where it accounted for only 0.4 % of the total density. No seasonal differences within sites were observed, while the interaction between seasons and sites was also not significant.

The overall relative density of *Haliplectus* (Fig. 5.4c) was 4 %. The natural site recorded a relative density of 5 %, while the 10 years reforested and the degraded sites recorded relative densities of 4 % and 2 % respectively. The degraded site recorded significantly lower densities of *Haliplectus* (ANOVA; $F = 67.86$, $p < 0.05$) than both the natural and the 10 years reforested sites. Only the degraded site showed significant seasonal

differences in densities of *Haliplectus*, with the dry season recording significantly lower densities than the wet season (ANOVA; $F = 24.67$, $p < 0.05$). The observed significant differences between sites were caused by the extremely low densities of *Haliplectus* recorded during the dry season within the degraded site.

The genera *Trefusialaimus* contributed a relative abundance of 4 % to the overall density. In the natural site, it contributed 5 %, while in the 10 years reforested site, it accounted for 4 % of the total density. No *Trefusialaimus* was recorded in the degraded site, which was responsible for the observed significant differences between sites (ANOVA; $F = 92.13$, $df = 2$, $p < 0.05$). Neither were seasonal differences in densities of *Trefusialaimus* recorded nor was the interaction between seasons and sites significant (Fig. 5.4d).

The density of *Metachromadora* (Fig. 5.4e) was highest in the degraded site where it accounted for 24 % of the total density. However, in terms of the overall densities, it recorded a relative abundance of only 4 %. The densities of this genus were very low in the natural and the 10 years reforested sites, where relative abundances of 2 % and 0.5 %, respectively, were recorded. Due to the great variation in densities of *Metachromadora*, especially in the degraded site during the dry season, no significant differences between sites and between seasons within sites were observed.

The genus *Anoplostoma* (Fig. 5.4f) recorded an overall relative abundance of 3 %, with the degraded site recording the highest relative density of 14 %. The natural and the 10 years reforested sites recorded relative densities of 3 % and < 1 %, respectively. The 10

years reforested site recorded significantly lower densities of *Anoplostoma* (ANOVA; $F = 3.97$, $df = 2$, $p < 0.05$) compared to the natural and the degraded sites. No seasonal differences in the densities of *Anoplostoma* were observed. The observed differences between sites in the dominant nematode genera are possibly linked to the differences in sediment physical characteristics. The organically rich and silty sediments recorded high densities of the major genera especially the detrital feeders *Terschellingia* and *Pierickia*.

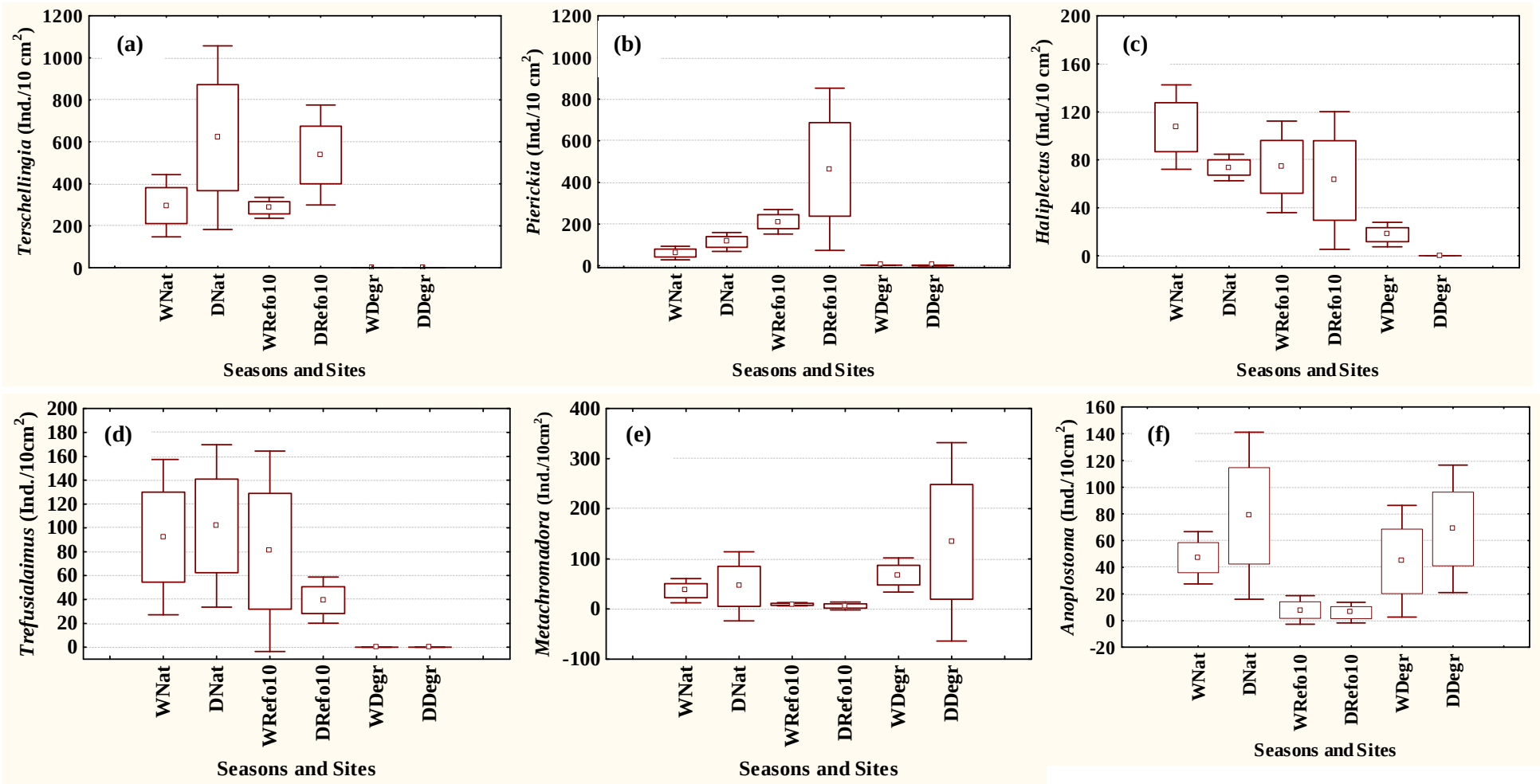

Figure. 5.4a-f. Spatial and temporal variation in numerical abundance of the major nematode genera; (a) *Terschellingia*, (b) *Pierickia*, (c) *Haliplectus*, (d) *Trefusialaimus*, (e) *Metachromadora* and (f) *Anoplostoma*. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10**;** Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

5.3.3 Nematode community assemblages

The nematode genera identified during the study are shown in Appendix 1. A total of 76 genera, belonging to 24 families were identified. Out of these, 62 genera belonging to 23 families were recorded from the 10 years reforested site, while 60 genera belonging to 23 families were recorded from the natural site. The degraded site recorded 33 genera belonging to 18 families. *Terschellingia* was the most abundant genus in the natural site contributing 25 % of the total nematode densities. Similarly, *Terschellingia* together with *Pierickia* were the dominant genera in the 10 years reforested site, contributing 26 % and 21 % of the total densities, respectively. The dominant genera in the degraded site were *Metachromadora* and *Anoplostoma*, which contributed 24 % and 14 % of the total densities, respectively.

The dominant families in the natural site were Linhomoeidae (31 %) and Desmodoridae (14 %). Linhomoeidae (32 %) and Comesomatidae (26 %) were the most abundant families in the 10 years reforested site, while Desmodoridae (29 %), Cyatholaimidae (15 %) and Anoplostomatidae (14 %) contributed the highest relative densities in the degraded sites. The number of genera is linked to the sediment physical characteristics with the detritus rich (high TOM) and silty sediments from the natural and the 10 years reforested sites recording the highest number of genera. The more stressful environment in the degraded site recorded the lowest number of nematode genera.

An nMDS analysis (Fig. 5.5) on nematode genera densities and community composition produced two clear clusters. The natural and the 10 years reforested sites formed one cluster which was separated from the degraded site. However, no clear separation of seasons within sites was observed.

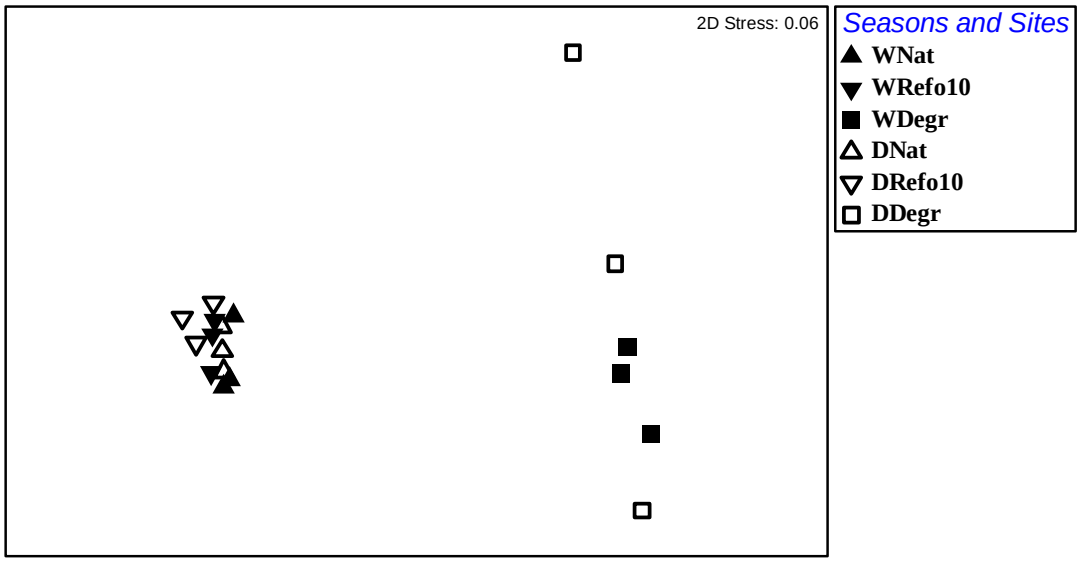

Figure. 5.5. Nematode genera community assemblage: Output of non-metric Multi Dimensional Scaling (nMDS) on square root transformed nematode genera densities data showing affinities between sites and between seasons within sites, WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years Reforested site; DRefo10; Dry season 10 years Reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

ANOSIM further confirmed the spatial patterns within the nMDS with the natural site being very similar to the 10 years reforested site irrespective of the season ($R < 0.5$) for all pair wise comparisons. The degraded site was significantly different from both the natural and the 10 years reforested sites in all seasons ($R > 0.5$) for all pair wise comparisons. In addition, ANOSIM showed no significant seasonal differences within sites ($R = -0.111$, 0.111 and 0.444) for the natural, the 10 years reforested and the degraded sites seasonal pair wise comparisons, respectively. The degraded site also showed the highest index of multivariate dispersion (1.2 and 1.7 for the wet and dry seasons, respectively, indicating that it's within site variability was very high.

SIMPER analysis showed that the genera *Terschellingia, Pierickia* and *Haliplectus* (Table 5.1) were among the genera responsible for the high similarity observed in both the natural and the 10 years reforested sites. The genera *Paracanthonchus* and *Metachromadora* contributed to the similarity observed within the degraded site. The degraded site recorded the lowest similarity which shows that there was high heterogeneity in nematode community composition. This was confirmed by MDISP analysis which showed the highest index of multivariate dispersion (IMD = 1.6) compared to the natural and the 10 years reforested sites which recorded an IMD of 0.7, each. The observed differences between the degraded site and both the natural and the 10 years reforested sites were mainly explained by the genera *Terschellingia, Pierickia,* and *Trefusialaimus* among others (Table 5.2). The degraded site recorded the lowest densities of these genera.

Table 5.1. SIMPER lists, showing the contribution percentages of the top five nematode genera to similarities within sites. Average similarity is shown in parenthesis.

Sites	**% Contribution**
Natural site (64)	*Terschellingia* (11) *Haliplectus* (7) *Trefusialaimus* (6) *Pierickia* (6) *Metalinhomoeus* (5)
10 years reforested site (65)	*Terschellingia* (15) *Pierickia* (11) *Halalaimus* (6) *Haliplectus* (5) *Hopperia* (5)
Degraded site (45)	*Paracanthonchus* (18) *Metachromadora* (15) *Anoplostoma* (14) *Theristus* (12) *Viscosia* (9)

Table 5.2. SIMPER lists, showing the percentage contributions of the top five nematode genera to dissimilarities between sites.

Sites	**% Contribution**
Natural and 10 years Reforested (40)	*Pierickia* (5 %) *Terschellingia* (5 %) *Spirinia* (4 %) *Anoplostoma* (3 %) *Trissonchulus* (3 %)
Natural and Degraded (74)	*Terschellingia* (10 %) *Trefusialaimus* (5 %) *Metalinhomoeus* (4 %) *Pierickia* (4 %) *Oxystomina* (4 %)
10 years Reforested and Degraded (78)	*Terschellingia* (11 %) *Pierickia* (8 %) *Paralinhomoeus* (4 %) *Trefusialaimus* (4 %) *Metachromadora* (4 %)

5.3.4 Nematode genera diversity

Nematode genus richness (S) ranged from 36 ± 0.2 in the natural site to 15 ± 5 in the degraded site (Fig. 5.6a). Similarly, genera rarefaction (Fig. 5.6b) was highest in the natural site (34 ± 7) and lowest in the degraded site (15 ± 5). The natural and the 10 years reforested sites recorded higher Shannon Diversity Index (3 ± 0.2 and 3 ± 0.4, respectively), than the degraded site (2 ± 0.4) (Fig 5.6c). The degraded site recorded significantly lower genus richness (ANOVA; $F = 47.89$, $df = 2$, $p < 0.05$), taxa rarefaction (ANOVA; $F = 41.07$, $df = 2$, $p < 0.05$) and Shannon diversity index ($F = 12.25$, $df = 2$, $p < 0.05$) than both the natural and the 10 years reforested sites. However, only the 10 years reforested site recorded seasonal differences, with the wet season recording significantly higher genera richness ($F = 8.19$, $df = 1$, $p < 0.05$), genera rarefaction ($F = 8.37$, $df = 1$, $p < 0.05$) and Shannon diversity index ($F = 9.29$, $df = 1$, $p < 0.05$) than the dry season. This could be related to the significant seasonal differences in sand and silt/clay. The allochthonous input of storm waters during the wet season brought in more sand which availed more habitat conditions for diverse nematode genera.

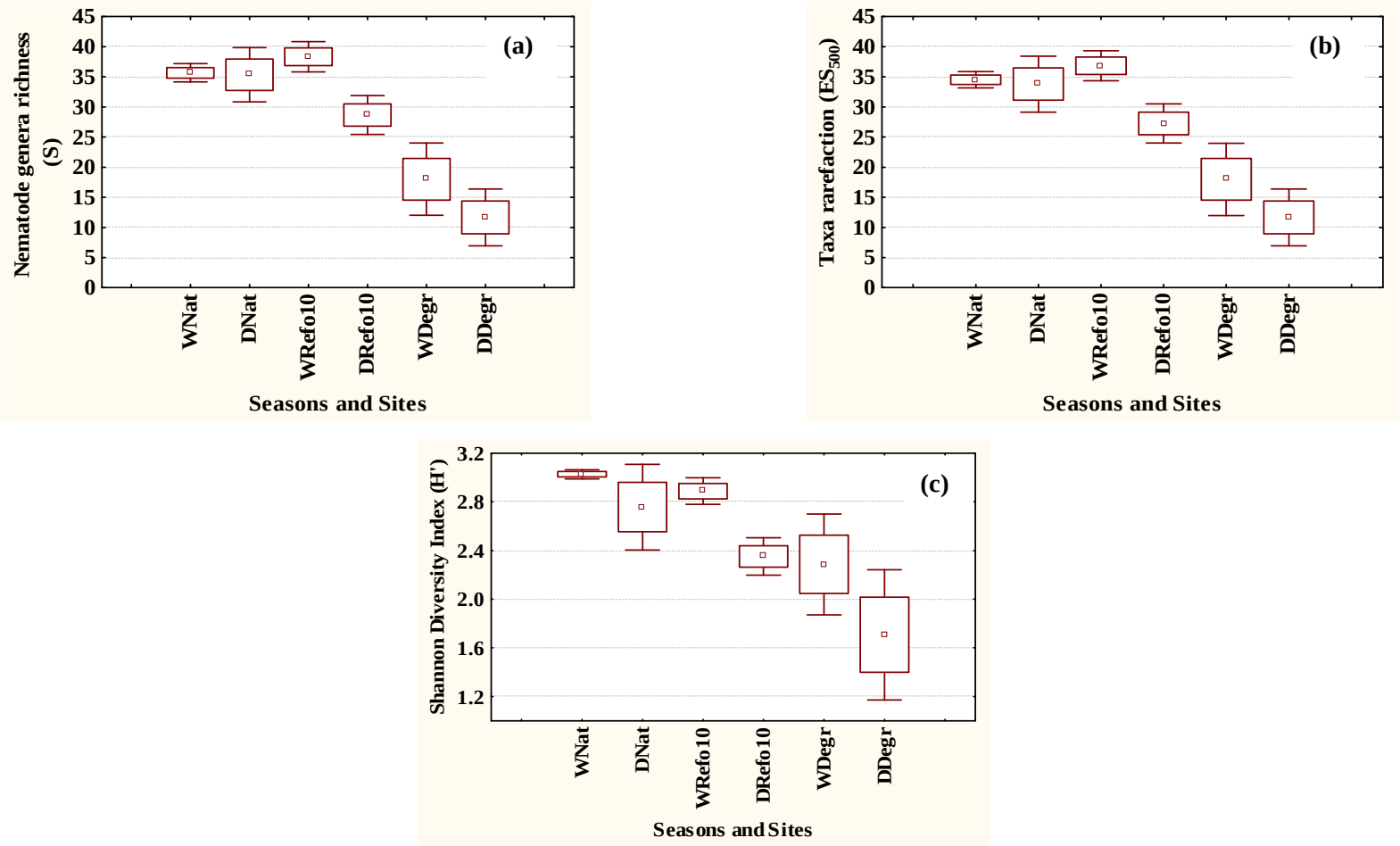

Figure. 5.6a-c. Spatial and temporal variations in; (a) nematode genus richness (S), (b) taxa rarefaction (ES_{500}) and (c) Shannon diversity index (H' Log_e). WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10**;** Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

5.3.5 Nematode ecological feeding groups

All the four ecological feeding groups described by Wieser (1953), were recorded in all the sampling sites and during all the seasons (Fig. 5.7).

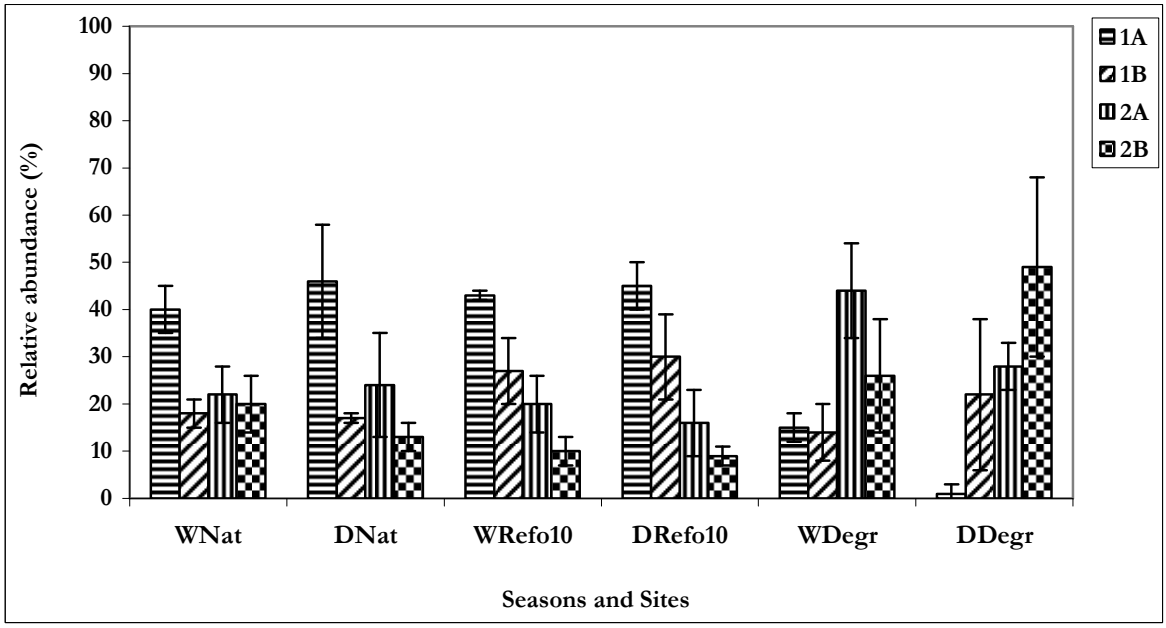

Figure 5.7. Relative abundance (mean ± SD; n = 3) of Wieser's feeding groups; **1A**; Selective deposit feeders, **1B**; Non-selective deposit feeders, **2A**; Epistrate feeders and **2B**; Omnivores or Predators. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

Selective deposit feeders (group 1A) dominated the natural and the 10 years reforested sites. This group recorded significant differences between sites in relative abundance (ANOVA; $F = 55.53$, $df = 2$, $p < 0.05$), with the natural and the 10 years reforested sites

recording significantly higher relative abundance of selective deposit feeders than the degraded site. Significant seasonal differences in selective deposit feeders were only observed in the degraded site (ANOVA; $F = 12.85$, $df = 1$, $p < 0.05$), where the wet season recorded a higher relative abundance. Non-selective deposit feeders (group 1B) were recorded in similar relative abundances between sites and between seasons within sites. Consequently, there were no significant differences between sites and between seasons within sites.

Epistrate feeders (2A), were significantly different between sites (ANOVA; $F = 8.64$, $df = 2$, $p < 0.05$), with the degraded site recording a significantly higher relative abundance of epistrate feeders than the natural and the 10 years reforested sites. No significant seasonal differences in epistrate feeders were observed within sites. However, a relatively higher relative abundance of this group was recorded during the wet season than during the dry season in the degraded site. Similarly, a significantly higher relative abundance of omnivores/predators (group 2B) was recorded in the degraded site (ANOVA; $F = 18.23$, $df = 2$, $p < 0.05$) compared to the natural and the 10 years reforested sites. No significant seasonal differences in omnivores/predators relative abundances were observed within sites. However, a relatively higher relative abundance of omnivores/predators was recorded during the dry season than during the wet season in the degraded site.

The genera *Terschellingia* and *Pierickia* were the dominant selective and non-selective deposit feeders in the natural and the 10 years reforested sites. The genera *Paracanthonchus* and *Metachromadora* dominated the epistrate and omnivore/predator trophic groups respectively in the degraded site (Table 5.4).

Table 5.3. Nematode genera percentage contribution to Wieser's feeding groups. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

Seasons and Sites	**Trophic groups**			
	1A	**1B**	**2A**	**2B**
WNat	*Terschellingia* (18) *Haliplectus* (7) *Trefusialaimus* (6)	*Metalinhomoeus* (5) *Pierickia* (4) *Anoplostoma* (3)	*Microlaimus* (6) *Spilophorella* (4) *Astomonema* (3)	*Trissonchulus* (6) *Sphaerolaimus* (4) *Sigmophoranema* (4)
DNat	*Terschellingia* (29) *Trefusialaimus* (5) *Oxystomina* (5)	*Pierickia* (5) *Anoplostoma* (4) *Metalinhomoeus* (3)	*Spirinia* (11) *Spilophorella* (5) *Microlaimus* (3)	*Trissonchulus* (4) *Sphaerolaimus* (3) *Metachromadora* (2)
WRefo10	*Terschellingia* (20) *Trefusialaimus* (6) *Haliplectus* (5)	*Pierickia* (15) *Paralinhomoeus* (3) *Metalinhomoeus* (2)	*Hopperia* (5) *Trissonchulus* (3) *Neochromadora* (3)	*Sphaerolaimus* (3) *Siphonolaimus* (3) *Halichoanolaimus* (1)
DRefo10	*Terschellingia* (30) *Leptosomatum* (4) *Haliplectus* (4)	*Pierickia* (26) *Paralinhomoeus* (4) *Metalinhomoeus* (1)	*Spilophorella* (5) *Pseudochromadora* (3) *Hopperia* (2)	*Sphaerolaimus* (4) *Siphonolaimus* (2) *Halichoanolaimus* (2)
WDegr	*Trefusia* (5) *Haliplectus* (4) *Molgolaimus* (3)	*Anoplostoma* (10) *Theristus* (5) *Pierickia* (0.5)	*Paracanthonchus* (17) *Microlaimus* (11) *Hopperia* (5)	*Metachromadora* (16) *Viscosia* (6) *Syringolaimus* (3)
DDegr	*Halalaimus* (1) *Oxystomina* (0.4)	*Anoplostoma* (17) *Theristus* (4) *Pierickia* (0.3)	*Paracanthonchus* (12) *Trissonchulus* (9) *Microlaimus* (2)	*Metachromadora* (34) *Viscosia* (11) *Syringolaimus* (3)

5.3.6 Nematodes' Index of Trophic Diversity (ITD)

ITD ranged from a high of 0.34 ± 0.25 in the natural site during the wet season, to a low of 0.33 ± 0.41 in the degraded site during the dry season (Fig. 5.8). The index of trophic diversity did not show any significant differences between sites neither were there significant differences between seasons within sites. The highest ITD (0.25) implies that all nematode trophic guilds are equally represented (25 %) in the total nematode density, whereas the lowest ITD (1) implies that one nematode trophic guild accounts for 100 % of the nematode density (Heip et al., 1985). Therefore, the results obtained show that all feeding groups were more or less equally represented in all the study sites, despite the dominance of some groups in some sites.

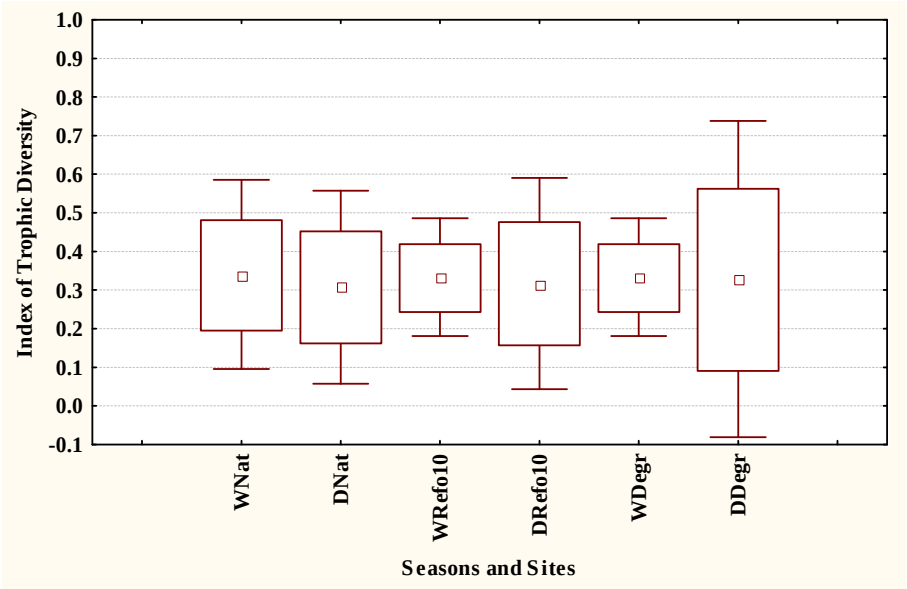

Figure 5.8. Variations in Index of Trophic Diversity (mean ± SD; n = 3). WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

5.3.7 Nematode Biomass

Nematode biomass was highest in the 10 years reforested site (2289 ± 454 µg/10 cm^2) and lowest in the degraded site (245 ± 66). The natural site recorded a relatively lower biomass 1944 ± 1552 µg/10 cm^2) than the 10 years reforested site (Fig. 5.9).

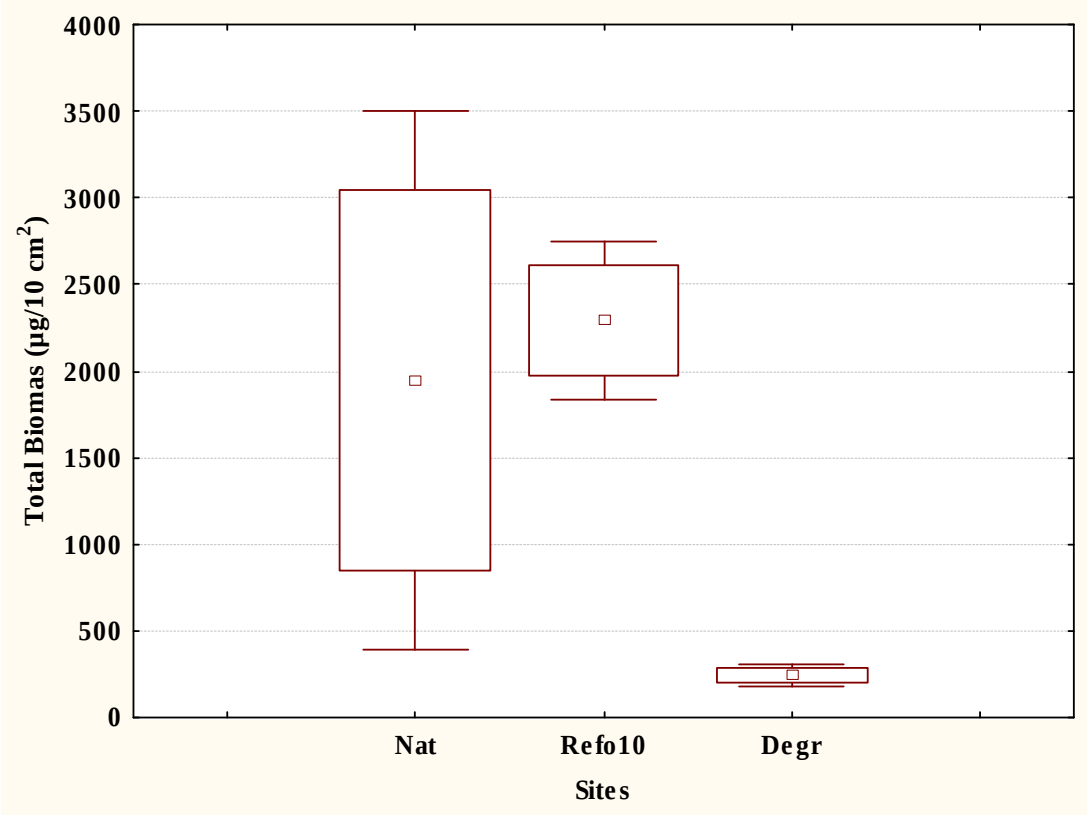

Figure 5.9. Total biomass of nematodes from the natural (Nat), 10 years reforested (Refo10) and degraded (Degr) sites.

Both the natural and the 10 years reforested sites recorded significantly higher nematode biomass than the degraded site (ANOVA; $F = 9.39$, $df = 2$, $p = 0.05$). The observed differences between sites in nematode biomass are linked to the observed nematode densities which were significantly low in the degraded site. The relatively higher biomass recorded from the 10 years reforested site compared to the natural site, was due to the larger nematodes and densities especially of the genus *Pierickia* (Family Comesomatidae).

The biomass of the main nematode genera is shown in Figure 5.10, while Table 5.5 shows the relative contribution of nematode genera and corresponding families to the total biomass. Biomass in the 10 years reforested site was mainly contributed by the family Comesomatidae (41 %) and Linhomoeidae (27 %). These families were represented by the genera *Pierickia* (37 %) and *Terschellingia* (19 %), respectively. The families Linhomoeidae (23 %) and Ironidae (23 %) contributed the highest biomass in the natural site. These families were represented by the genera *Terschellingia* (15 %) and *Trissonchulus* (23 %). Biomass in the degraded site was mainly contributed by the families Desmodoridae (51 %) and Ironidae (15 %). These families were represented by the genera *Metachromadora* (51 %) which contributed most of the biomass, and *Trissonchulus* (14 %), respectively.

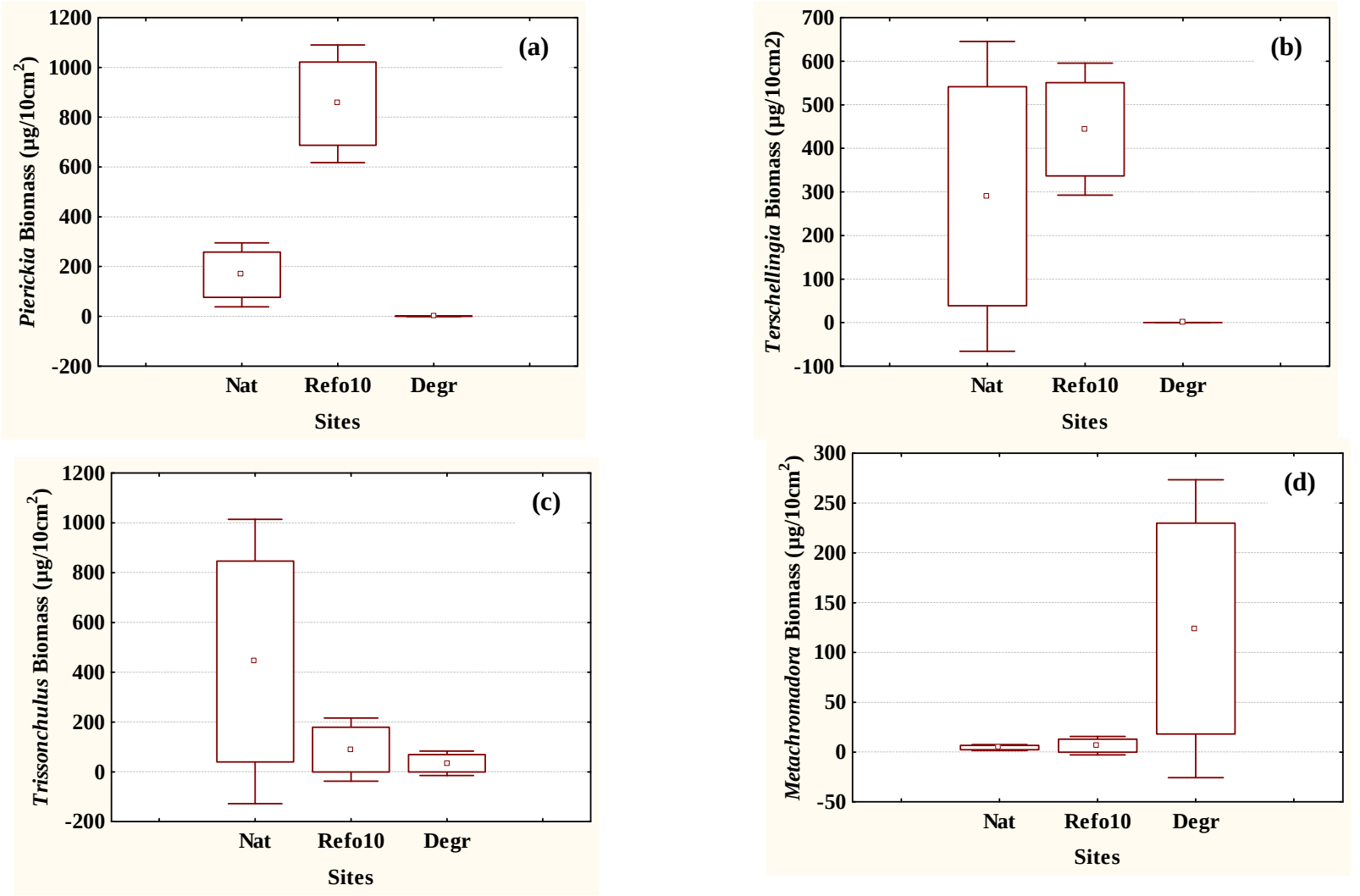

Figure 5.10. Individual biomass of nematode genera (a) *Pierickia* (b) *Terschellingia* (c) *Trissonchulus* and (d) *Metachromadora* from the natural (Nat), 10 years reforested (Refo10) and degraded (Degr) sites.

Table 5.4. Nematode biomass: percentage contribution of major families and corresponding genera from the study sites.

Site	Family and Corresponding genus			
Natural	Linhomoeidae	(23)	*Tershellingia*	(15)
	Ironidae	(23)	*Trissonchulus*	(23)
	Desmodoridae	(11)	*Spirinia*	(10)
	Trefusiidae	(11)	*Trefusialaimus*	(11)
	Comesomatidae	(10)	*Pierickia*	(9)
	Oxystominidae	(9)	*Oxystomina*	(8)
10 years Reforested	Comesomatidae	(41)	*Pierickia*	(37)
	Linhomoeidae	(27)	*Terschellingia*	(19)
	Anoplostomatidae	(8)	*Anoplostoma*	(8)
	Sphaerolaimidae	(5)	*Sphaerolaimus*	(5)
	Ironidae	(4)	*Trissonchulus*	(4)
Degraded	Desmodoridae	(51)	*Metachromadora*	(51)
	Ironidae	(15)	*Trissonchulus*	(14)
	Anoplostomatidae	(10)	*Anoplostoma*	(10)
	Cyatholaimidae	(8)	*Paracanthonchus*	(8)
	Oncholaimidae	(6)	*Viscosia*	(6)

5.3.8 Vertical distribution

The vertical distribution of nematode densities is shown in Figure 5.11. The overall densities of nematodes in the upper section (0-5 cm) were 1350 ± 662 Ind. /10 cm^2 in the natural site, 1220 ± 537 Ind. /10 cm^2 in the 10 years reforested site and 292 ± 123 in the degraded site. The densities were relatively low in the lower section (5-10 cm), being

highest in the natural site 523 ± 265. The 10 years reforested site recorded 387 ± 242 Ind. /10 cm^2, while the degraded site recorded the lowest densities 126 ± 57 Ind. /10 cm^2.

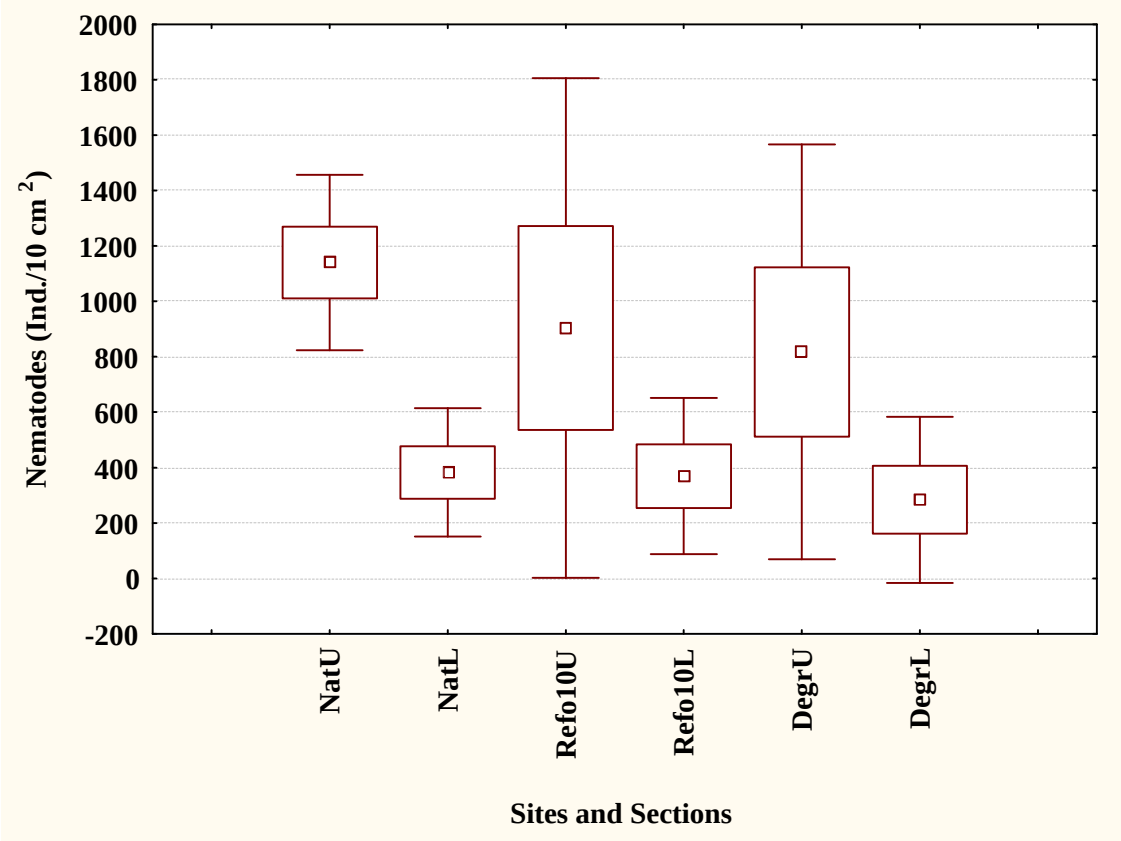

Figure 5.11. Densities of nematodes within the upper (0-5 cm) and lower (5-10 cm) vertical sections in the natural, 10 years reforested and degraded sites. NatU, Natural site Upper section; NatL, Natural site Lower section; Refo10U, 10 years Reforested site Upper section; Refo10L, 10 years Reforested site Lower section; DegrU, Degraded site Upper section and DegrL, Degraded site Lower section.

The differences in nematode densities between the upper and the lower sections were only significant in the natural site (ANOVA; $F = 18.2$, $df = 5$, $p < 0.05$). The 10 years reforested and the degraded sites recorded very high variations in nematode densities in the upper section, which explains the lack of significant differences between the upper and lower sections in these sites.

Figure 5.12 shows the vertical variation in densities of the major nematode genera. The genus *Terschellingia* (Fig. 5.12a) was dominant in both the upper and the lower sections of the natural site, contributing 14 % and 10 % of the total densities, respectively. The dominant genera in the upper section of the 10 years reforested site were *Pierickia* (Fig. 5.12b) and *Terschellingia*, contributing relative densities of 17 % and 16 %, respectively. However, in the lower section of the 10 years reforested site, *Terschellingia* contributed 9 % while *Pierickia* accounted for only 4 % to the total density. The upper section of the degraded site was characterised by the genus *Metachromadora* (Fig. 5.12c) which contributed 18 % of the total density. On the other hand, the genus *Anoplostoma* (Fig. 5.12d) was dominant in the lower section, contributing a relative abundance of 7 %. All the above major genera did not show significant vertical differences within sites.

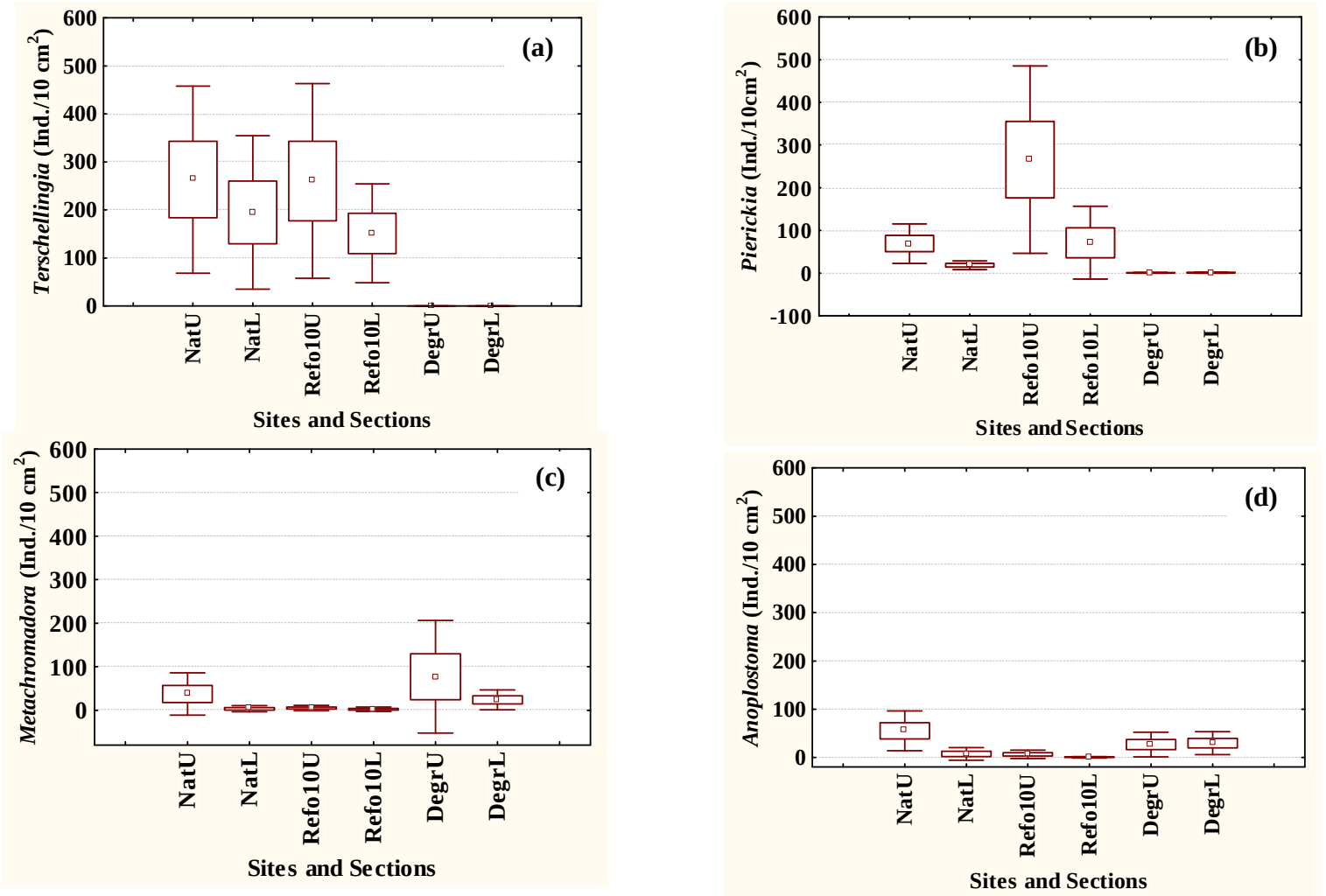

Figure 5.12a - d. Densities of (a) *Terschellingia* (b) *Pierickia* (c) *Metachromadora* and (d) *Anoplostoma* within the upper (0-5 cm) and lower (5-10 cm) sections in the natural, 10 years reforested and degraded sites. NatU, Natural site Upper section; NatL, Natural site Lower section; Refo10U, 10 years Reforested site Upper section; Refo10L, 10 years Reforested site Lower section; DegrU, Degraded site Upper section and DegrL, Degraded site Lower section.

An nMDS on log(x+1) transformed vertical distribution of nematode community composition data, showed a separation between the upper and lower sections in the natural and the 10 years reforested sites (Fig. 5.13).

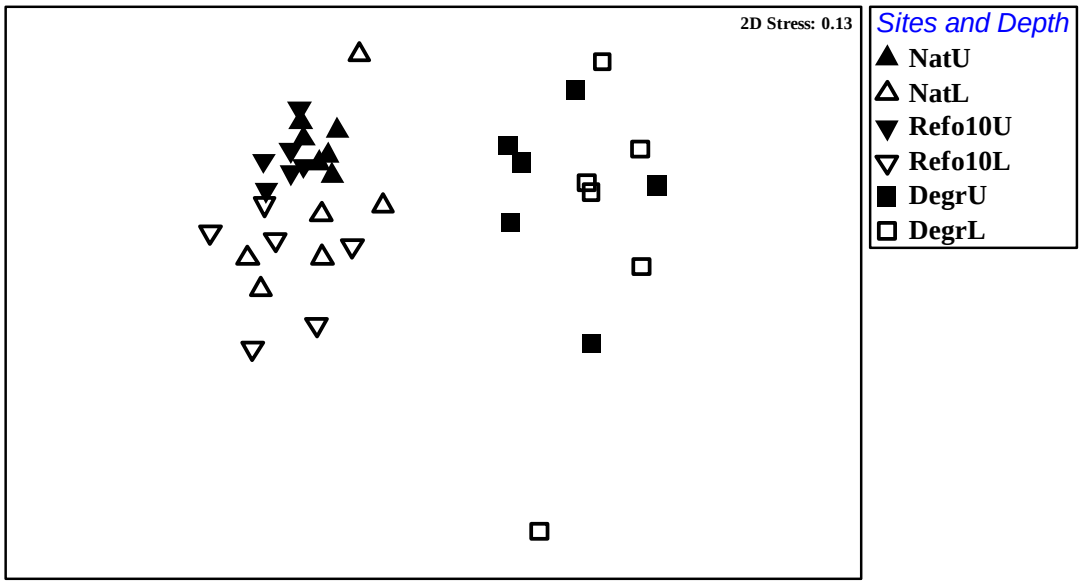

Figure 5.13. Nematode genera assemblages: Output of nMDS on (Logx+1) transformed data (n = 6) showing affinities between the upper (0-5 cm) and lower (5-10 cm) sections from the natural, 10 years reforested and the degraded sites (NatU, Natural site Upper section; NatL, Natural site Lower section; Refo10U, 10 years Reforested site Upper section; Refo10L, 10 years Reforested site Lower section; DegrU, Degraded site Upper section and DegrL, Degraded site Lower section).

This trend was further supported by ANOSIM (Global R = 0.589), with pair wise comparisons indicating a significant separation between the upper and the lower sections in the natural and in the 10 years reforested sites(R = 0.5 and 0.502, respectively). However, no clear vertical differences were observed in the degraded site (R = 0.041). The variation between sites in nematode community composition was re-emphasised within the vertical nMDS plot, with pair wise ANOSIM comparisons showing significant differences between the upper and lower sections in the natural and in the 10 years reforested sites on one hand, and both sections in the degraded site (R > 0.7).

SIMPER analysis for similarities within sites, showed that the genera *Terschellingia*, *Haliplectus* and *Pierickia*, were dominant in the upper section of the natural and the 10 years reforested sites. The lower sections of the two sites were characterised by *Terschellingia* and *Pierickia*. In the degraded site, *Paracanthonchus* and *Theristus* dominated the upper section, while *Metachromadora* and *Anoplostoma* were the dominant genera in the lower section (Table 5.6). The lower section in the natural and the 10 years reforested sites, as well as the upper and lower sections in the degraded site, recorded very low within section similarities (< 50 %). This is an indication of high variability in nematode community assemblages. This variability was further shown by MDISP, which gave very high indices of multivariate dispersion (IMD > 1) within these sections.

SIMPER analysis for dissimilarities between sections within sites (Table 5.7), showed the highest dissimilarity in the degraded site (59 %). The natural and 10 years reforested

sites recorded relatively lower dissimilarities (53 % and 54 %, respectively). The genera *Halalaimus*, *Oxystomina* and *Spilophorella* were among the genera responsible for the observed dissimilarity between the upper and lower sections in the natural and the 10 years reforested sites. The genera *Syringolaimus* and *Metachromadora* contributed most to the dissimilarities though not significant between sections in the degraded site.

Table 5.5. SIMPER lists, showing the percentage contributions of the top 5 genera to the similarities within sections. The percentage average similarities within the upper and lower sections respectively are shown in parenthesis.

Sites	**Upper Section (0-5cm)**	**Lower Section (5-10cm)**
Natural	*Terschellingia* (7)	*Terschellingia* (20)
(67, 47)	*Haliplectus* (6)	*Pierickia* (10)
	Trefusialaimus (6)	*Trissonchulus* (10)
	Oxystomina (6)	*Metalinhomoeus* (8)
	Spilophorella (6)	*Siphonolaimus* (7)
10 years Reforested	*Terschellingia* (9)	*Terschellingia* (22)
(63, 49)	*Pierickia* (8)	*Pierickia* (15)
	Halalaimus (7)	*Siphonolaimus* (10)
	Haliplectus (7)	*Halichoanolaimus* (8)
	Sphaerolaimus (6)	*Metalinhomoeus* (5)
Degraded	*Paracanthonchus* (18)	*Metachromadora* (25)
(48, 35)	*Theristus* (15)	*Anoplostoma* (20)
	Metachromadora (14)	*Paracanthonchus* (17)
	Anoplostoma (12)	*Viscosia* (16)
	Viscosia (9)	*Microlaimus* (7)

Table 5.6. SIMPER lists, showing the percentage contributions of the top 5 genera to the dissimilarities between sections within the sampling sites. Average percentage dissimilarity is shown in parenthesis.

Sites and Sections	% Contribution
Natural Upper section **Vs.** **Natural Lower section** (53)	*Halalaimus* (4) *Oxystomina* (4) *Anoplostoma* (4) *Paralinhomoeus* (4) *Spilophorella* (4)
10 years Reforested Upper section **Vs.** **10 years Reforested Lower section** (54)	*Spilophorella* (5) *Halalaimus* (4) *Haliplectus* (4) *Trefusialaimus* (4) *Sphaerolaimus* (4)
Degraded Upper section **Vs.** **Degraded Lower section** (59)	*Syringolaimus* (7) *Metachromadora* (7) *Anoplostoma* (6) *Paracanthonchus* (6) *Theristus* (6)

5.4 Discussion

5.4.1 Spatial variation

Mangroves are an important resource both ecologically and socio-ecomically because of the services and goods they provide. Along the Kenyan coast, mangroves have been clear cut in the past, to provide goods such as fuel wood and building materials, leading to loss of ecosystem services (Kairo & Abuodha, 2001). Reforestation efforts have been initiated in order to remedy the effects of forest loss. Monitoring studies on the recovery of these restored mangrove forests have mainly focused on vegetation structure. However, little is known about the ecological recovery of the reforested mangroves along the Kenyan coast. One of the main aspects of the evaluation of the success of an ecological restoration project, is to see how far all ecosystem components have re-established, and to what extent their functions have been put in place (Ellison, 2000). In this respect, only the study by Mwojoria (2007) has documented the most abundant and species rich metazoan taxon, the nematode communities, in degraded and reforested *S. alba* mangrove sediments in Kenya. Similarly, information on nematode colonisation of reforested mangrove ecosystems on a global scale is also rare and most studies have dealt with macrofauna and meiofauna up to higher taxa level (Khalil, 2001; Bosire et al., 2004). Therefore these results form the first account of nematodes associated with mangrove sediments in natural, reforested and degraded *R. mucronata* mangroves. It provides information on the impact of mangrove degradation and subsequent reforestation on nematode colonisation in previously deforested sites.

The results of this study show that nematodes are very diverse within the studied mangrove sediments, with a total of 76 genera belonging to 24 families that were recorded. Mwojoria (2007) recorded 72 genera belonging to 24 families, with densities ranging from 1638 to 1292 Ind. /10cm^2 from *S. alba* mangroves in Gazi Bay, which is similar to the results of the current study (1320 Ind./ 10cm^2). The total density of nematodes and number of genera recorded are also similar to those reported from other mangroves in India (Chinnadurai & Fernado, 2007), Brazil (Netto & Galluci, 2003) and Zanzibar (Ndaro & Olafsson, 1999). The density of nematodes was not different between the natural and the 10 years reforested sites, despite the different levels of TOM recorded in both areas. It has already been shown in Chapter 3 that these differences in TOM are related to the forest age in addition to the activity and behaviour of burrowing macrobenthos mainly crabs and the forest's root network. The similarities between the natural and the 10 years reforested sites in terms of nematode densities, can be linked to the fact that the supply of fresh organic material as food for the benthos, as reflected in chl. *a* concentrations and C/N ratio's is more or less equal in both the reforested and the natural sites. In addition, reforestation usually alters sediment physico-chemical conditions (Bosire et al., 2003) and is assumed to ultimately restore the functional importance of nutrient fluxes among other functions.

This study further shows that the 10 years reforested site is similar in nematode community assemblage to the natural site, but the two are very much different from the degraded site. Significant differences in physical sediment characteristics and nematode community between the natural and the 10 years reforested sites on one hand, and the

degraded site on the other were observed. This is a clear indication of the effect of human activities (clear felling) on the structure, function and biodiversity of mangrove ecosystems. Mangrove clear felling removes vegetation cover exposing the sediment to tidal erosion which leads to removal of the fine sediments and detritus, since these are easily resuspended by tidal currents. The dense root net work in the natural and the 10 years reforested sites ensures that tidal currents are slowed down and resuspension is reduced (Wolanski et al., 1992), leading to fine sediment and organic matter deposition. Fine sediments, rich in detritus, form the food for benthic fauna directly or indirectly by providing the medium which supports microphytobenthos growth, and in this way, forms essential food materials for benthic fauna (Snelgrove et al., 1997). Sediments, which are rich in mud and detritus, are characterised by high meiofaunal and, in particular, high nematode densities (Pavlyuk, 2004; Chinnadurai & Fernado, 2007).

In the present study, the percentage of silt/clay fraction was highest in the natural and the 10 years reforested sites, which also recorded the highest density, genera richness (S), genera rarefaction (ES_n) and Shannon diversity (H') of nematodes. The complex root system in these sites, coupled with the availability of detritus mainly derived from mangrove leaf litter, provides a suitable microhabitat for the nematodes. Mangrove derived detritus has been shown to be of low nutritional value (Bosire et al., 2005; Alongi & Christoffersen, 1992) and repellant to nematode colonisation due to high tannin content (Alongi, 1987). However, nematodes may excrete substances which stimulate soil micro-organisms, and produce exoenzymes which initiate decomposition of complex molecules from mangrove detritus (Ruess et. al., 2001; Ekschmitt et al., 1999). These

substances would promote the establishment and growth of bacterial populations that take over organic matter decomposition, ensuring that both nematodes and bacteria feed on the nutritious 'soup' of dissolved organic matter (DOM) and particulate organic matter (POM) released (Snelgrove et al., 1997; Riemann & Helmke, 2002).

The bacterial biomass associated with detritus may not be sufficient to meet detritivores' carbon and energy requirements (Blum et al., 1988). However, the presence of fungi, in substantial proportions in the detritus, increases the microbial detrital biomass sufficient to provide detritivores with their nutritional requirements (Blum et al., 1988; Snelgrove et al., 1997). This is in addition to the mangrove derived detritus whose nutritional value is increased through microbial decomposition (Skov & Hartnoll, 2002).

Total canopy removal by clear-felling, exposes mangrove sediments to intense solar radiation, which leads to increased interstitial water temperature and salinity. Bosire et al. (2003, 2004) recorded significantly higher interstitial water temperature and salinity in degraded *R. mucronata* sites compared to natural and reforested sites. The increased temperature and salinity impacts negatively on the benthic fauna due to increased environmental stress (Sasekumar, 1994). Salinity also affects the osmoregulation in meiofaunal species and hence could be a community regulator by determining the physiological activity of marine organisms (Ingole & Parulekar, 1998). Increased sediment temperature leads to desiccation, which kills or limits growth of microflora, removes water from plant cell cytoplasm and changes the chemical status of organic materials which are important media for microbial growth (Mfilinge et al., 2002). Sjoling

et al. (2005) recorded fewer bacterial species from degraded mangrove systems compared to relatively undisturbed systems in Kisakasaka, Tanzania. Higher bacterial diversity in the sediments of undisturbed mangroves may provide more diverse functional pathways for microbial nutrient cycling and, possibly a more stable ecosystem compared to the degraded sites. The lower Redox Potential and organic matter that were recorded in the above study, from deforested mangrove areas, shows that removal of mangroves and the consequent lack of roots, which promote oxidation in sediments, decreases the oxygen and organic matter input into the sediments. This leads to the disturbance of the vital root microbe interactions as well as the microbial food web (Holguin et al., 2001). Studies by Sjoling et al., (2005) indicate that low Redox Potential in degraded mangrove sediments due to lack of oxygen and ultimately accumulation of organic matter, also leads to increased anoxicity and high sulphide concentrations. This creates inhospitable habitats for most benthic fauna and ultimately leads to impoverished faunal abundances. This probably explains the low densities of benthic fauna recorded from the degraded site in the current study.

The high levels of TOM in the natural and the 10 years reforested sites is associated with high levels of detritus and associated micro-organisms. This explains the high relative abundance of deposit feeders recorded in these sites. The degraded site, which recorded the highest sand content, showed the highest proportion of epistrate feeders. The dominance of epistrate feeders in sandy sediments has also been recorded in other studies (Ndaro & Olafsson, 1999; Chinnadurai & Fernado 2007). Sediment granulometry influences the distribution of nematodes indirectly by controlling the interstitial spaces

and directly through individual grain surface areas which relate to biofilms and bacterial colonisation.

Generally, epistrate feeders dominate in larger grain size sediments whose interstitial spaces favours the growth of microphytobenthos, while deposit feeders dominate in fine sediments having high levels of detritus material (Giere, 1993). The low proportion of deposit feeders in the degraded site can also be explained by the lack of detrital material and the coarser sediment. In addition, the site also recorded very low TOM levels due to lack of canopy cover. The lack of canopy cover means that light was not limiting, a situation which favours the establishment of microphytobenthic communities like diatoms, which forms food for epistrate feeders. The seasonal differences observed in the relative abundance of selective deposit feeders in the degraded site were probably caused by the input of allochthonous detrital material through terrestrial runoff during the wet season. This input of allochthonous material may have provided the nematodes with a diverse food source from which to select from. The lack of significant differences in the relative abundance of the feeding groups between the natural and the 10 years reforested sites indicates that mangrove reforestation is returning the once degraded systems to the natural state within 10 years. This is through provision of microhabitats which are supporting similar trophic groups to the natural system.

Additionally, the Index of Trophic Diversity (ITD) was high in the natural site but not different from the 10 years reforested site. This shows that in both systems, the four trophic groups were equally represented. In addition to mangrove detritus, the high

Chlorophyll *a* and finer sediments in the natural and the 10 years reforested sites could point to a rich microphytobenthic community which is assumed to form food for the deposit feeders (Moens & Vincx, 1996). The genus *Metachromadora* was dominant in density and biomass in the degraded site which also recorded the highest sand content. Studies by Schratzberger et al. (2004) as well as those of Long and Othman (2005) have also documented high densities of *Metachromadora* in sandy sediments. Similarly, Mwojoria (2007) also recorded high densities of *Metachromadora* from degraded *S. alba* in Gazi Bay. These high densities were related to the ability of this genus to burrow hence has a better competitive ability especially in search of food. *Metachromadora* is also known to be eurytolerant to fluctuating environmental conditions, hence its high abundance in the exposed degraded site. The ability of this genus to survive tough environmental conditions and exposure to sunshine may also be linked to its thick cuticle.

Though the natural site recorded numerically higher densities of nematodes than the 10 years reforested site, total nematode biomass was higher in the 10 years reforested site compared to the former. This is attributed to the genus *Pierickia* which recorded the highest mean biomass within the study sites. This genus also recorded the highest density in the 10 years reforested site. The degraded site recorded the lowest biomass since it also recorded the lowest densities. The degraded site was also a stressful environment for faunal colonisation as shown by the low TOM, high interstitial temperature and salinity. According to Vanaverbeke et al. (2003), smaller species of nematodes seem to be resilient to disturbances like sediment removal, sediment resuspension and changes in overlying water currents. Therefore, the lower individual biomass recorded in the degraded site could also have been due to small sized nematodes,

which have adapted to frequent tidal sediment resuspension occasioned by canopy removal. The root network in both the natural and the 10 years reforested sites ensures minimal disturbance, which promotes sediment stability as well as ensuring colonisation by diverse nematode genera in high densities.

Due to limited information on the changes in benthic fauna in relation to mangrove restoration, a parallel is drawn with salt marshes which are the temperate equivalents of mangrove ecosystems in the tropics. Salt marshes, just like mangroves, fulfill several fundamental ecological functions like nutrient export to adjacent waters, filtering pollutants, prevention of shoreline erosion and acting as nurseries for a variety of fish and macro-crustaceans among other fauna (Odum, 1980). In the recent past, salt marsh creation and recreation has received global attention for mitigating wetland habitat losses due to agricultural and/or urban land reclamation and dike constructions. Natural and newly created marshes do not always represent similar habitat values for nekton and other estuarine organisms (Zedler, 1996).

Studies by Hampel et al., (2003) found no clear differences in species composition, density of major species of macro-crustaceans and environmental characteristics, but recorded differences in nekton community structure, biomass, species abundance, current regimes and detritus, between a natural and 10 years old restored salt marsh in the Westerschelde estuary. In addition, Minello and Zimmerman (1992) found that organic matter was higher in natural salt marshes than in restored marshes and correlated positively with the density of infauna and decapod crustaceans. Moseman et al. (2004),

recorded similar macrofaunal densities and species richness between a restored salt marsh (19 months) and a natural marsh in California, where percent organic matter positively correlated with insect densities. His study concluded that salinity and organic matter influenced the general succession of infauna.

Talley and Levin (1999), observed increasing similarity between a created and a natural salt marsh based on macrofauna assemblages and organic matter content over time. In this study, a 16 month old marsh exhibited the largest dissimilarity with the natural marsh. However, a 6 years and a 10 years old marsh recorded the highest similarity with the natural marshes. Organic matter correlated positively with macrofauna taxa abundance and diversity in the created marshes, indicating that detritus and live roots may provide food for deposit feeders, retain soil moisture and provide refuge from predators. These results from salt marshes restoration are in line with the findings of the current study, since the natural and the 10 years reforested sites, which were rich in organic matter, also recorded the highest densities, genera diversity and biomass of nematodes. The findings also support the fact that though nematode densities may be similar between the natural and the 10 years reforested *R. mucronata* ecosystems, differences in physico-chemical characteristics of the substrate still exist. The differences in sediment characteristics may explain the observed differences in nematode communities between the degraded site and both the natural and the 10 years reforested sites. The studies further emphasise the importance of sediments' physico-chemical characteristics like organic matter in faunal colonisation and hence recovery of restored mangroves and salt marsh ecosystems. In contrast to the macrofauna, the meiofauna and

nematode community assemblages are not different between the natural and the 10 years reforested sites. This shows that the differences observed in physico-chemical parameters between the natural and the 10 years reforested sites are no longer important at the meiofauna and nematode community level.

5.4.2 Vertical distribution

No earlier studies have documented the vertical distribution of nematode genera from Kenyan mangrove ecosystems. Only Vanhove et al. (1992) investigated the vertical distribution of meiofauna at higher taxa level in different mangrove species in Gazi bay, where no clear relationships between meiofauna densities and depth, except in *Bruguiera gymnorrhiza* sites were observed. However, Dye (1983a, 1983b) found a clear vertical distribution of nematode densities from Mngazana estuary, South Africa, which was linked to depth decreases in oxygen, food materials and increased Redox Potential. Due to progressive mineralisation, organic matter decreases with depth and the concentration of Hydrogen Sulphide (H_2S) increases while sediments get more anaerobic. According to Hodda and Nicholas, (1985), as depth increases, nematodes are limited by reduced food availability and the degree of reduction with depth. Muthumbi (1994) investigated the vertical migration of free living marine nematodes from *Ceriops tagal* mangroves in Gazi Bay. Her study found that the upper layers (0-5cm) have higher nematode densities than lower sections (5-10cm) which decreases during low tide though still higher than the deeper layers. The study further found that nematode species respond differently to tidal variations with some migrating downwards and others upwards with ebbing tide. These

differences are probably related to differences in their abilities to survive exposed conditions.

In the current study, nMDS on nematode densities and community assemblage's vertical distribution, did show a clear separation between the upper and the lower sections in nematode community composition in the natural and the 10 years reforested sites. However, no vertical differences were observed in the degraded site. The separation of the upper and the lower sections in the natural and the 10 years reforested sites can be attributed to the high levels of chlorophyll *a* and lower C/N ratio recorded from the upper section, which means that food availability in the upper section was high.

Other studies have documented differences in nematode densities between upper and lower sediment sections (Alongi, 1987; Nicholas et al., 1991), which were linked to food and oxygen availability. The upper sections are usually rich in TOM derived from mangrove leaf litter, and are relatively well aerated. This ensures that aerobic breakdown of organic matter and, consequently, nutrients release is efficient. Bioturbation was notably high in the natural and the 10 years reforested sites as evidenced by the presence of numerous crab burrows (personal observation). These burrows ensure that the surface sediment layers are effectively aerated, a situation which enhances aerobic decomposition of detrital material buried in the upper layers of the sediments. Although no vertical profiles of TOM, Oxygen and Redox potential were measured in the current study, Hodda et al. (1985) showed that the decrease in these parameters with depth usually

influences the vertical distribution of nematodes. Similar findings have also been documented by Dye (1983a, 1983b), Alongi, (1987a), Nicholas et al., (1991).

The genus *Terschellingia* is known to be a low oxygen consumer and is dominant in muddy sediments rich in organic matter (Schratzberger & Warwick, 1998a, 1998b). Therefore, its dominance in both the upper and the lower sections in the natural and the 10 years reforested sites reflect its ability to exploit organically rich but oxygen poor habitats. Similarly, lack of vertical profiles in *Terschellingia* has also been reported from Australian mangroves by Nicholas et al., (1991). The genera *Paracanthonchus* and *Metachromadora* were dominant in the upper and lower sections, respectively, in the degraded site. Being an epistrate feeder, the dominance of *Paracanthonchus* in the surface layers could be related to the availability of microphytobenthos especially diatoms. Olafsson and Elmgren, (1997) recorded increased densities of *Paracanthonchus* in sediment surface layers after a phytoplankton bloom. This occurrence was linked to increased reproduction of this genus which was stimulated by settling phytodetritus. *Metachromadora* on the other hand is an omnivore/predator and has been shown to burrow deeper especially in sandy sediments hence has a better competitive ability especially in search of food (Long & Othman, 2005).

5.4.3 Seasonal variation

Seasonal variations of plant and animal populations are the rule in nature and several abiotic and biotic variables may account for the temporal variation in benthos. Temperature and food availability have been cited as the main factors explaining seasonal

changes in the abundance of benthos (Olaffson & Elmgren, 1997). The absence of seasonal differences within sites in nematode densities and community composition in the present study, may be explained by the lack of seasonal trends in TOM (an indicator of food availability) and temperature which are key factors influencing nematode densities in mangrove sediments. Although sand and silt/clay showed significant seasonal variation in the natural site, they never influenced nematode densities. Lack of seasonal trends in nematode densities have been documented from mangroves in South Africa (Dye, 1983b). However, the genus *Haliplectus* showed significant differences between seasons in the degraded site, with higher densities recorded during the wet season. This difference may be linked to organic matter input from terrestrial runoff from the surrounding farmlands which flooded this site during the rainy season (personal observation). This genus is a selective deposit feeder hence may have been responding to the availability of diverse detrital material through flood waters.

The significantly higher sand content recorded in the natural site during the wet season could be linked to surface runoff from surrounding areas. Coral blocks harvesting was observed in the surrounding areas of the natural site. Therefore, the resulting small particles could have been washed by surface runoff water hence leading to the higher sand content.

5.5 Conclusions

The findings of the current study show that mangrove reforestation facilitates and influences nematode colonisation of the once degraded mangroves. This is through alteration of the physico-chemical conditions of the sediments by making organic matter available as mangrove leaf litter. Decomposing mangrove litter attracts bacteria, fungi and other microphytobenthos which have been suggested to provide food to benthic fauna especially nematodes. Reforestation also reduces sediment resuspension through the trapping ability of the established vegetation, thereby ensuring accumulation of silt/clay sediments which are favourable for benthic fauna colonisation. The established canopy cover also reduces surface sediments temperature and ultimately salinity through shading. This reduces environmental stress and, therefore, encourages faunal colonisation. The study also shows that mangrove clear-felling impairs nematode colonisation due to the resulting unfavourable conditions due to canopy removal. Although both the natural and the 10 years reforested sites showed no significant differences in nematode densities, community structure and the diversity indices, PCA based on sediment physical characteristics indicated clear differences between both sites especially in TOM.

The nematode community from the degraded site is different and impoverished in terms of densities and diversity compared to the natural and the 10 years reforested site. The reforested site is highly similar to the natural after 10 years in terms of nematode densities, biomass, community composition and trophic composition. The genera *Terschellingia* and *Pierickia* are typical of the natural and the 10 years reforested sites and hence describe a mature nematode community.

Thus the findings show that mangrove reforestation modifies sediment conditions leading to recovery of the systems ecological functions like faunal colonisation. However, recovery to the natural state in all aspects may take more than ten years. These findings further support mangrove reforestation efforts as this provides continuity of the systems ecological functions, which will ensure that there is sustainability of ecological services, economic benefits and ultimately biodiversity conservation.

CHAPTER SIX

Meiofaunal response to different food type additions to azoic sediments in a tropical mangrove forest.

6.1 Introduction

Meiofauna, particularly nematodes, occur on all substrata in the marine environment and the dynamic nature of phytal meiofauna assemblages have been shown on mangrove leaf litter by Gee and Sommerfield (1997), Zhou (2001) and Gwyther (2003). According to Findlay and Tenore (1982), detritus forms a major energy source for many marine benthic systems where detritally enriched marine habitats support a high abundance and diversity of meiofauna. Tietjen and Alongi (1990) have shown that although the nitrogen content of detrital material could be the best measure of its nutritional quality, mangrove leaf litter contains polyphenols like tannins, which may lead to complex relationships between the tannins, nitrogen content and age of the detritus. The interaction between these components influences the utilisation of mangrove detritus by meiofauna and, in particular, nematodes. According to Fell et al. (1975), mangrove leaves on the forest floor undergo an initial rapid leaching of dissolved organic matter (DOM). This leaching is followed by a slow decomposition of the remaining particulate organic matter (POM), facilitated by bacterial and fungal communities. These microflora condition the leaf litter for various invertebrate groups which utilise it as food. Gwyther (2003) indicated that particulate food sources for meiofauna on leaf litter comprise the surface biofilm, which includes bacteria, microalgae, protozoa and fungi. Krishnamurthy et al. (1984) recorded all types of nematode feeding groups on decaying mangrove leaves, an indication that

decaying litter consists of a variety of materials which can be used as food by meiofauna and, in particular, nematodes. Gee and Sommerfield (1997) showed that under similar sediment composition, salinity and tidal inundation, the initial chemical composition of mangrove leaves from different species, was responsible for the observed differences in meiofaunal communities during the decomposition process. These authors also showed that there exists a succession of meiofaunal communities during mangrove leaf litter decomposition process.

The energy supply for benthic consumers originates from a diversity of sources with the relative importance of different sources varying spatially and temporally (Peterson, 1999). Carbon isotope analysis has been used in ecological studies to determine the sources of the organic matter used by heterotrophic organisms based on the principle that 'you are what you eat' (Boschker & Middelburg, 2002). The natural ^{13}C isotope value is used frequently to investigate food webs for it is a marker for the food that is assimilated by a consumer. The use of natural stable isotope analysis provides insights on the source of organic matter that is actually assimilated over a long period of time, and is based on the close relationship between the stable isotope composition of a consumer and its food (Riera et al., 1996). The isotopic ratios C, N and S in producers and consumers of organic matter are useful in describing the organic matter flow and food web relationships in estuaries and coastal benthic communities (Peterson & Howarth, 1987).

Enrichment experiments are other techniques used to identify the importance of a specific labelled potential food source. In this way, cultures of diatoms or bacteria are grown in a

medium enriched with ^{13}C, ^{15}N or another stable isotope label. By offering this labelled food source over a certain period of time to potential consumers, the uptake and assimilation of the food can be measured and followed over time. This approach is used here to identify the importance of diatoms as a food source for nematodes in mangrove sediments.

Several field colonisation experimental studies utilising mangrove leaf litter have been done. These include: Zhou (2001) who looked at the responses of meiofauna taxa and nematode species to decaying mangrove leaf litter; Sommerfield et al. (1998) who looked at the relationships between meiofaunal communities and mangrove leaf litter diversity and Gee and Sommerfield (1997) who investigated the effects of mangrove diversity and leaf litter decay on meiofaunal diversity. However, there is no study which has investigated the effect of different leaf litter types in mangrove ecosystems on meiofauna and nematode colonisation. In order to design restoration programmes for mangrove ecosystems, it is essential to understand the influence that different sources of organic matter have on benthic communities.

The response to different food type and sediment additions was assessed in a *Rhizophora mucronata* mangrove forest. The experiments were performed between September and October 2005. This experiment was aimed at investigating the recolonisation responses of total meiofauna, major meiofauna taxa and nematode community assemblages in different types of food sources (mangrove, sea grass, diatoms), and sediment type (fine from natural mangrove forest versus coarse from a degraded forest). In an earlier study

(Mutua et al., unpublished; Chapter 4), meiofauna densities and nematode community assemblages were found to differ between a natural and a 10 years reforested sites on one hand and a 5 years reforested and a degraded *R. mucronata* sites on the other. The four types of forests were also found to differ in abiotic factors such as total organic matter (TOM), sediment granulometry, temperature and salinity. This experiment was therefore set up to understand the actual drivers of meiofauna and nematode re-colonisation in the reforested sites. Four main research questions were to be answered through this experiment:

- Does the availability of food (organic matter) affect meiofauna re-colonisation of mangroves?
- Does the type of organic matter (mangroves versus sea grasses) affect meiofauna re-colonisation of mangroves?
- Does the type of sediment (fine versus coarse) affect meiofauna re-colonisation of mangroves?
- Do diatoms form an important food source for nematodes within mangrove sediments?

6.2 Materials and methods

6.2.1 Study Site

The colonisation experiments were carried out in Gazi Bay-Kenya in a natural *Rhizophora mucronata* forest. An area of approximately 50 m^2 was demarcated in which the experimental syringes were placed. This site was chosen for the experiment since some other work was going on looking at the spatial patterns of macrofauna, meiofauna

and nematode community structure. The data obtained from this experiment will thus be useful in interpreting the observed spatial patterns. The detailed experimental design, experimental material preparation and laboratory analysis are given in Chapter 2 on materials and methods.

6.3 Results

6.3.1 Effect of food type on meiofauna re-colonisation

Thirteen meiofauna taxa were recorded. Seven taxa were recorded from the sea grass leaves, while the experimental control and mangrove leaves recorded 5 and 4 meiofauna taxa respectively. The field controls recorded nine meiofauna taxa. Nematoda was the most abundant taxon in relative abundance in all samples over all sampling days. Nematodes accounted for 99 % of the total meiofauna densities in the field control, 95 % in the experimental control and 93 % in both sea grass and mangrove leaf litter units. Oligochaeta was the second most abundant taxon accounting for 5 % of the total densities in the sea grass leaf litter, 3 % in the experimental control and mangrove leaf litter; and 1 % in the field control. The relative abundance of copepods was very low in the field control (< 1 %), but recorded relative abundances of 1 % in the experimental control, sea grass and mangrove leaf litter. Halacaroidea occurred in relatively high numbers in the mangrove leaf litter treatment accounting for 2 % of the total meiofauna densities.

Figure 6.1 shows the results from the food types compared to the field control for the natural sediments. Meiofauna colonised all the experimental units 1 day post placement (Fig. 6.1a).

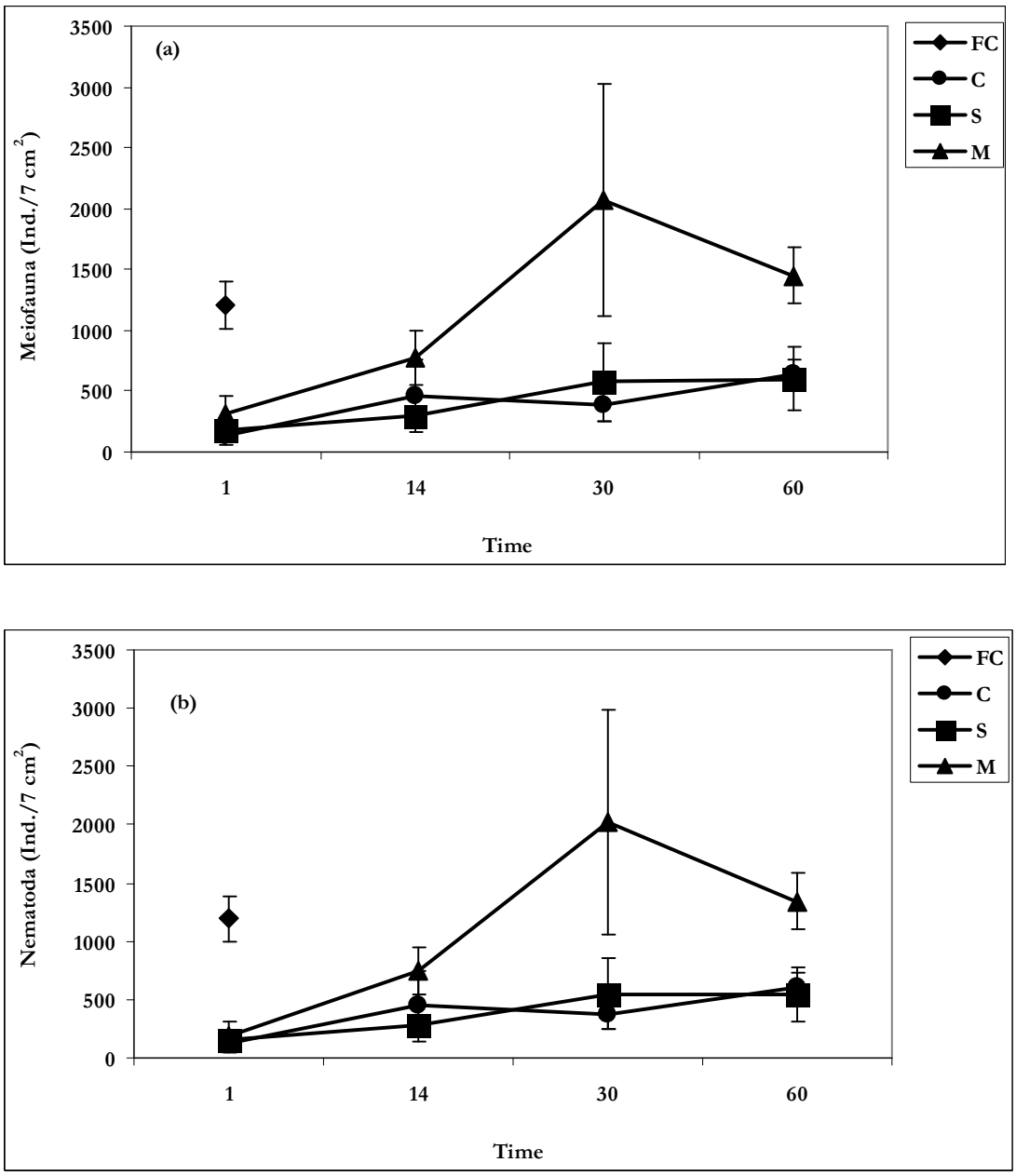

Figure 6.1. Colonisation rates expressed as densities (mean ±SD) of (a) Meiofauna and (b) Nematodes during the experimental period (days). FC, field control; C, experimental control; S, sea grass leaf litter and M, mangrove leaf litter.

The re-colonisation rate was higher in the organically enriched syringes (maximum 307 ± 160 Ind. /7 cm^2) compared to the organic free control (128 ± 75 Ind. /7 cm^2). However, compared to the field control, meiofauna initially re-colonised the different food types in very low numbers. The highest recolonisation of meiofauna on day 1 was recorded from the mangrove leaf litter treatment (307 ± 160 Ind. /7 cm^2) which was still much less than the densities from the field control (1209 ± 198 Ind. /7 cm^2). The slow rate of meiofauna re-colonisation of the experimental controls compared to the mangrove leaf litter treatments shows the importance of food (organic matter) in meiofaunal colonisation of mangrove sediments. Meiofauna densities increased during the course of the experiment especially in the mangrove leaf litter treatment. The increase in the experimental control was up to day 14 after which densities remained almost constant. Meiofauna densities from the sea grass treatment remained below those from the field control through out the experiment. The density of meiofauna from the mangrove leaf litter surpassed those from the field control on day 30 (2071 ± 958 Ind. /7 cm^2), and the densities remained higher than in the field control from day 30 up to the end of the experiment, although a decline was observed between days 30 and 60.

Since nematodes (Fig. 6.1b) were the dominant taxon in all the experimental units, they were responsible for the observed patterns of the total meiofauna. The highest nematode density was recorded in the mangrove leaf litter treatment on day 30, which surpassed that recorded from the field control (2017 ± 966 Ind. /7 cm^2). The densities remained higher than in the field control from day 30 up to the end of the experiment, although a decline was observed between days 30 and 60. These trends in meiofauna and nematode densities with time in the mangrove leaf litter treatment coincides with the low CN ratio

recorded on days 30 and 60 (Fig. 6.2a & 6.2b). Low CN ratio reflects a high nutritional value of the detritus. Therefore, this shows that after 30 days, mangrove leaves created better habitat conditions thereby enabling them to support higher meiofauna and nematode densities.

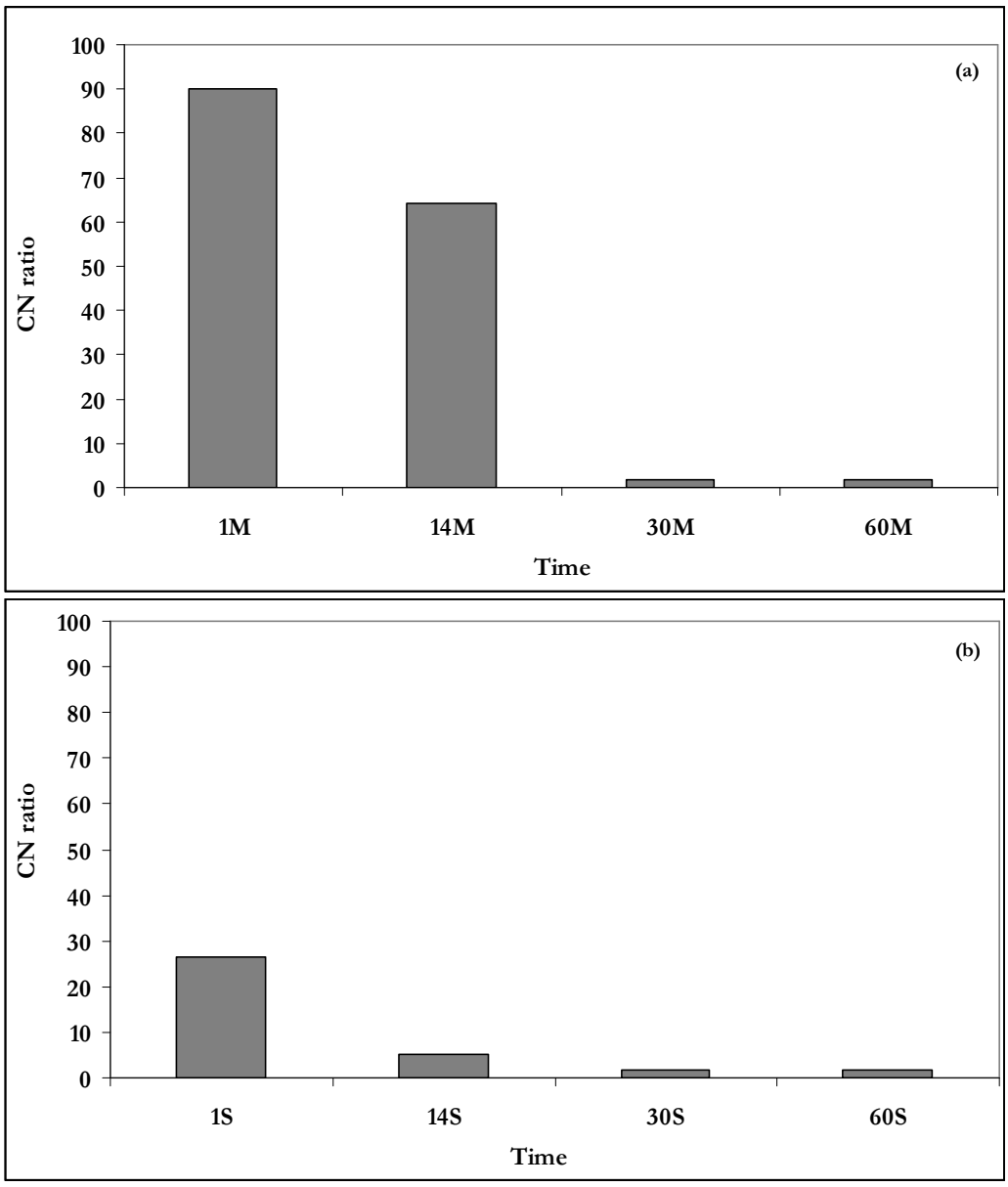

Figure 6.2. Variation in CN ratio with time (days) in (a) the mangrove leaf litter and (b) sea grass leaf litter.

6.3.2 Effect of food type on meiofauna densities and community composition

Two-Way ANOVA was used to investigate the effects of food type (mangrove, sea grass and experimental control) and time (1, 14, 30 and 60 days) on total meiofauna and nematode densities. As shown in Table 6.1, there were overall significant differences in total meiofauna (ANOVA; df = 2, F = 19.511, $p < 0.05$) and nematode densities (ANOVA; df = 2, F = 14.712, $p < 0.05$) between food types. However, Tukey HSD test showed no significant differences between food types on day 1 (Fig. 6.3a). On days 14, 30 and 60 (Figs. 6.3b, 6.3c & 6.3d), the mangrove leaf litter treatment recorded significantly higher meiofauna and nematode densities than the sea grass leaf litter and the experimental control treatments (ANOVA; Tukey $p < 0.05$). The fact that the mangrove leaf litter recorded significant differences with the other treatments over time indicates that mangrove leaf litter exerted a greater influence on meiofauna and nematode colonisation of the food types with time.

Table 6.1. Out put of Two-Way ANOVA showing the effects of food type, time and the interactions between food type and time

Variable	**Comparisons**	**df**	**F**	**p**
Log Total Meiofauna	**Food Type**	2	19.511	0.000
	Time	3	22.546	0.000
	Food Type * Time	6	1.179	0.3504
Log Nematoda	**Food Type**	2	14.712	0.000
	Time	3	26.595	0.000
	Food Type * Time	6	1.503	0.219

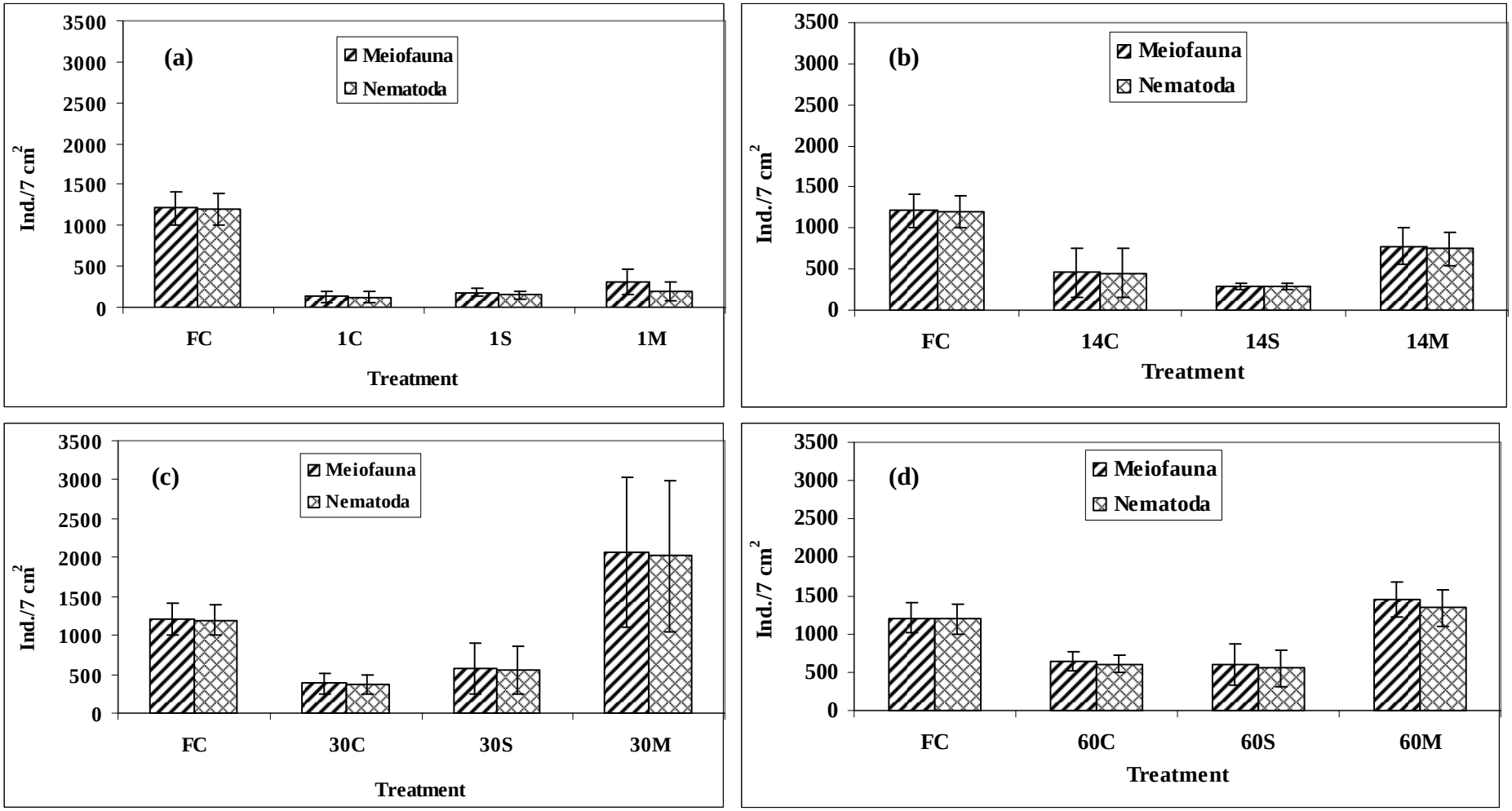

Figure 6.3. Densities of meiofauna and nematodes (Mean ± SD, n = 3) on (a) day 1, (b) day 14, (c) day 30 and (d) day 60 from the different food types compared to the field control. FC; field controls, C; experimental controls, S; sea grass leaf litter and M; mangrove leaf litter treatments.

An nMDS analysis (Fig. 6.4) and ANOSIM (Table 6.2) on meiofauna community composition from the different food type treatments including the experimental and field controls was performed for each experimental day separately.

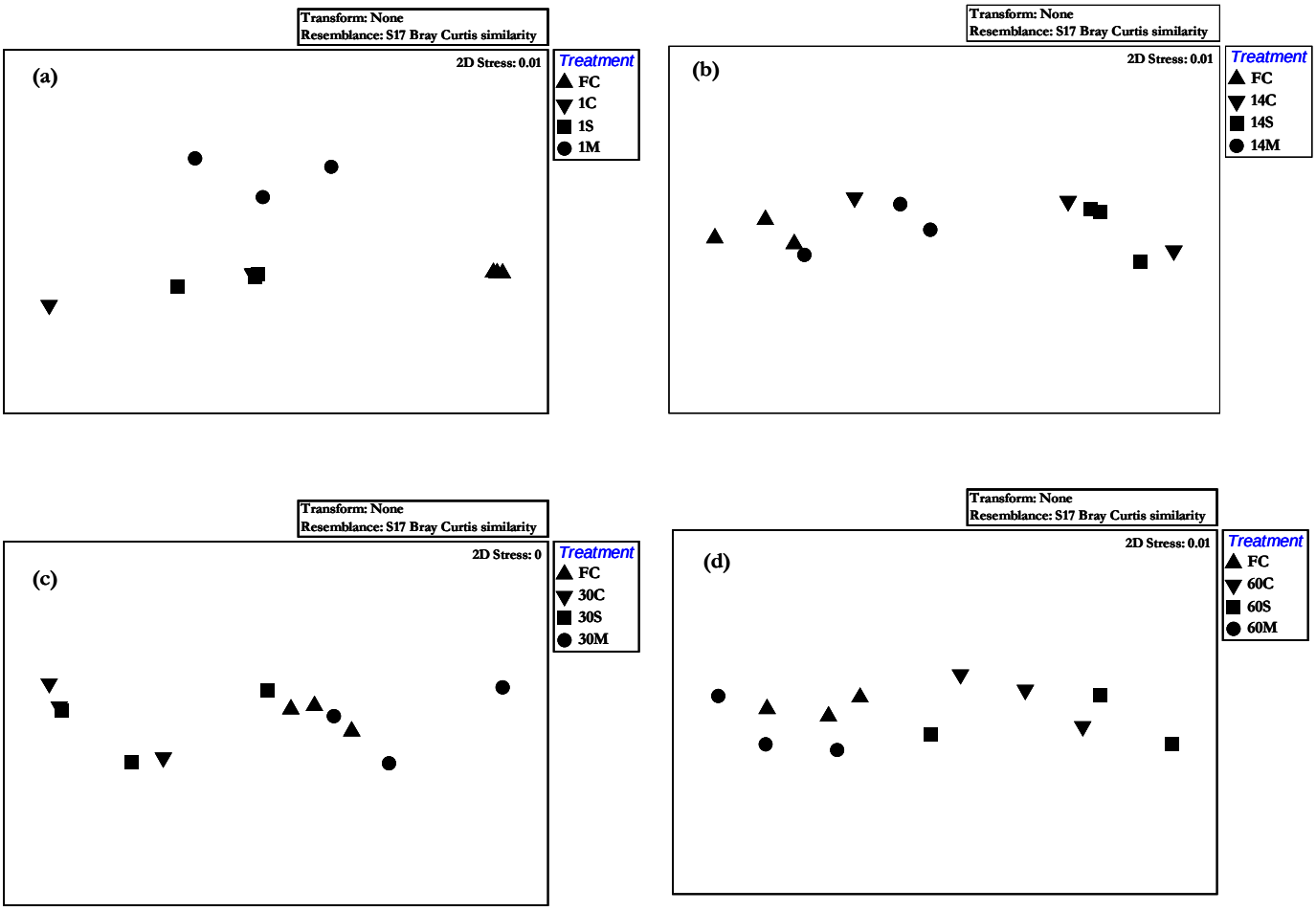

Figure. 6.4. nMDS ordination plot (non transformed data) of meiofauna community assemblage from the different food types on experimental on (a) day 1 (b) day 14 (c) day 30 and (d) day 60.

Table 6.2. ANOSIM output showing pair wise comparisons between food types on each experimental day. Global R is shown in parenthesis while * shows the significant comparisons.

Pairwise comparisons	**Experimental Days**			
	Day 1 (0.701)	**Day 14 (0.557)**	**Day 30 (0.552)**	**Day 60 (0.549)**
FC and C	1*	0.593*	1*	0.963*
FC and S	1*	1*	0.519*	0.667*
FC and M	1*	0.519*	0.111	0.037
C and S	0.111	0	0.148	0.074
C and M	0.333	0.185	0.963*	1*
S and M	0.704*	1*	0.667*	0.778*

The results, showed a separation and significant differences (ANOSIM; $R > 0.5$) between the mangroves and sea grass leaf litter on day 1 (Fig. 6.4a) and day 14 (Fig. 6.4b). The field control formed a distinct cluster and recorded significant differences from all the food types on days 1 and 14 (ANOSIM; $R > 0.5$). On day 30 (Fig. 6.4c) and day 60 (Fig. 6.4d), the mangrove leaf litter treatment was separated from both the experimental control and sea grass leaf litter (ANOSIM; $R > 0.5$), but not from the field control (ANOSIM; $R < 0.5$). The lack of significant differences between the field control and mangrove leaf litter treatment on days 30 and 60 is in line with ANOVA results for total meiofauna densities which showed no significant differences between the two treatments on these days. It also shows that after 30 days post placement, the mangrove leaves created habitat conditions which supported similar meiofauna communities to the surrounding sediments (field control).

6.3.3 Effect of time within food types on meiofauna densities and community composition.

Figure 6.5 shows the changes with time in meiofauna and nematode densities within the different food type treatments. There were significant time effects within the experimental control and mangrove leaf litter treatments in total meiofauna (ANOVA; df = 3, F = 22.546, $p < 0.05$) and nematode densities (ANOVA, df = 3, F = 26.595, $p < 0.05$).

Within the experimental control treatments (Fig. 6.5a), only day 1 recorded significantly lower meiofauna and nematode densities compared to days 14, 30 and 60 (ANOVA; Tukeys, $p < 0.05$). The sea grass treatment (Fig. 6.5b) recorded no significant time effects (ANOVA; Tukey, $p > 0.05$), between the different days. This might be partly due to the high variations observed on days 30 and 60. Experimental days 1 and 14 within the mangrove leaf litter treatment (Fig. 6.5c) recorded significantly lower meiofauna and nematode densities than days 30 and 60. Day 1 also recorded significantly lower meiofauna and nematode densities than day 14 (ANOVA; Tukey, $p < 0.05$). However, days 30 ad 60 recorded similar meiofauna and nematode densities (ANOVA; Tukey. $p > 0.05$). No significant interaction effect between food type and time in meiofauna and nematode densities was recorded.

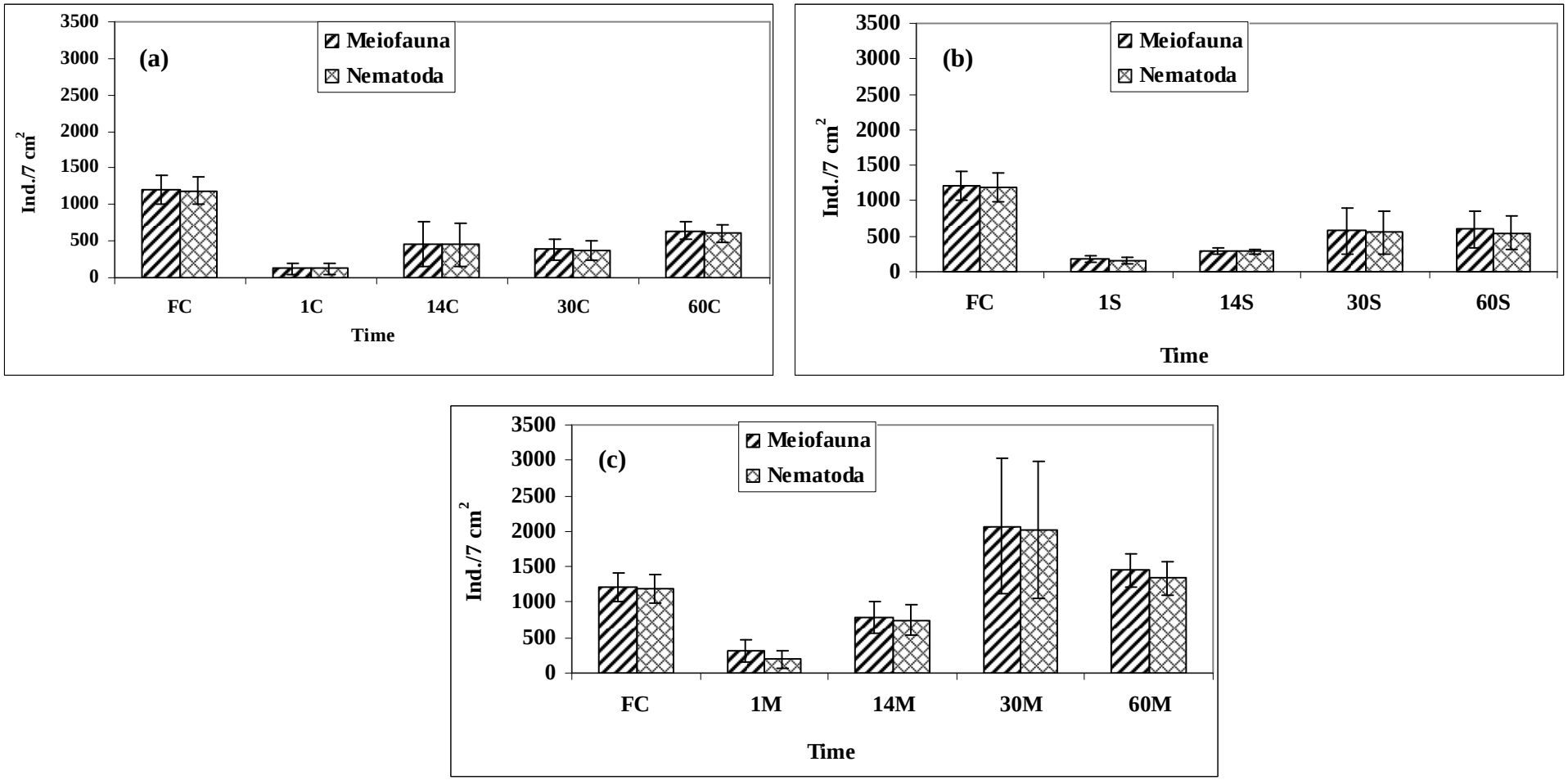

Figure 6.5a-c. Variations in total meiofauna and Nematoda within, (a) experimental control (b) sea grass and (c) mangrove treatments over the experimental period (days).

The sea grass and experimental controls recorded significantly lower densities of meiofauna (ANOVA, df = 12, F = 11.32, $p < 0.05$) and nematodes (ANOVA, df = 12, F = 11.85, $p < 0.05$) on all days ($\leq$ 778 and 747 Ind. / 7 cm^2, respectively) compared to the field control (1209 and 1192 Ind. / 7cm^2). However, on day 30 and day 60, the mangrove leaf litter recorded relatively higher, but not significantly different meiofauna and nematode densities than the field control. This shows that after 30 days, the mangrove leaf litter supported the same densities of meiofauna and nematodes as the field control.

An nMDS analysis (Fig. 6.6) and ANOSIM (Table 6.3) on meiofauna community composition over time for each food type (sea grass, mangrove leaves and experimental controls) separately, showed an overall significant time effect within all food type treatments (ANOSIM; $R > 0.5$). Within the experimental controls, day 1 was separated from days 30 and 60 (Fig 6.6a). The sea grass leaf litter treatment showed a separation of day 1 from all the other days (Fig. 6.6b), and day 14 from day 60 (ANOSIM; $R > 0.5$). Within the mangrove leaf litter treatment, day 1 was separated from all the other days, while day 14 was separated from days 30 and 60 (Fig. 6.6c). This pattern was further shown by ANOSIM ($R > 0.5$) for all pair wise comparisons.

The field control which was included in all three analyses showed differences with all the days within the experimental controls and sea grass treatments (ANOSIM; $R > 0.5$). However, within the mangrove leaf litter treatment, only days 1 and 14 were separated from the field controls, with ANOSIM recording significant differences ($R > 0.5$).

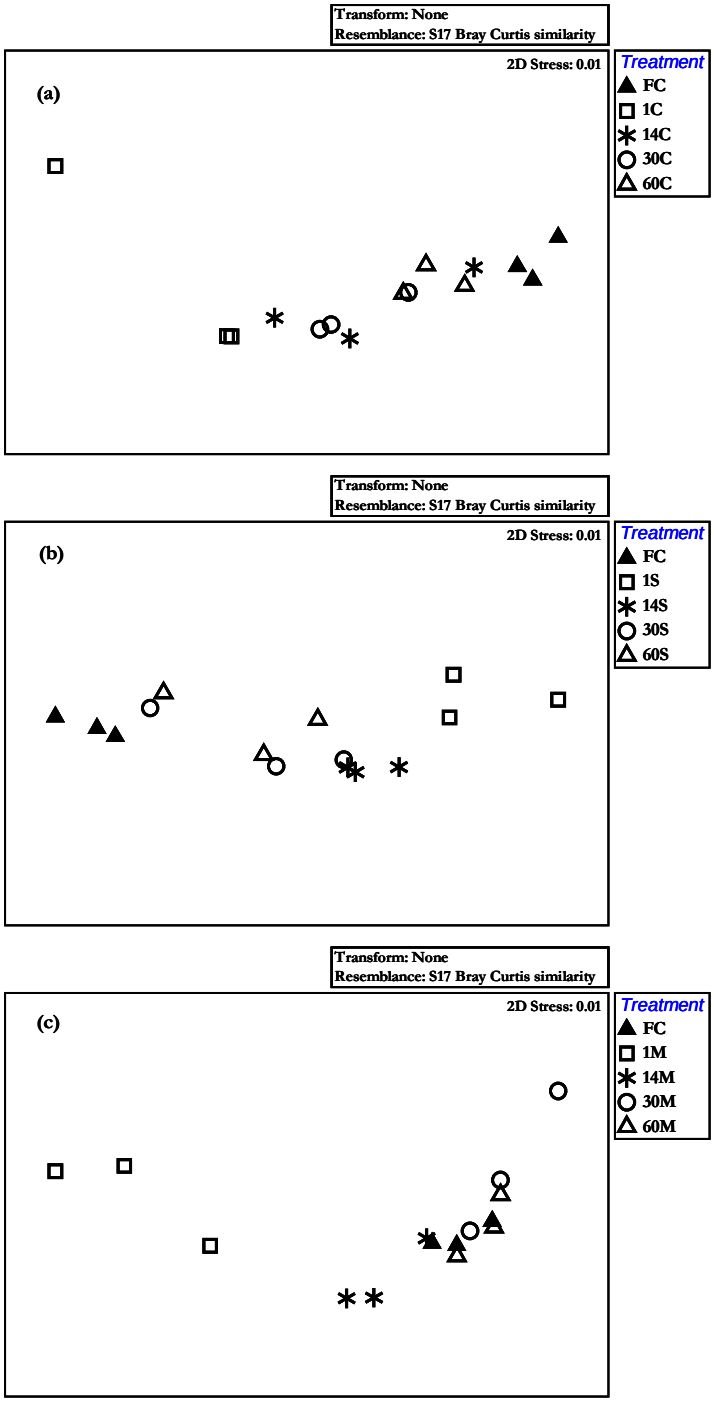

Figure 6.6a-c. nMDS ordination plot (non transformed data) of meiofauna community assemblage on all experimental days from (a) experimental controls, C; (b) sea grass leaf litter, S; and (c) mangrove leaf litter, M. FC denotes the field control.

Table 6.3. ANOSIM output showing pair wise comparisons between experimental days within food types. Global R in parenthesis while (*) shows the significant comparisons.

Pairwise Comparisons	**Food Types**		
	C (0.516*)	**S (0.63*)**	**M (0.492*)**
FC and Day 1	1*	1*	1*
FC and Day 14	0.593*	1*	0.519*
FC and Day 30	1*	0.519*	0.111
FC and Day 60	0.963*	0.667*	0.037
Day 1 and Day 14	0.333	0.778*	0.926*
Day 1 and Day 30	0.481*	0.852*	1*
Day 1 and Day 60	0.667*	0.926*	1*
Day 14 and Day 30	0.148	0.259	0.667*
Day 14 and Day 60	0.148	0.519*	0.667*
Day 30 and Day 60	0.37	0.333	0.074

6.3.4 Effect of food type on meiofauna diversity

Meiofauna diversity indices from the different food types and experimental days are shown in Figure 6.7. Over the entire experimental period, the highest meiofauna taxa richness (S) (Fig. 6.7a) and Shannon diversity index (H') (Fig. 6.7b) were recorded from mangrove leaf litter treatment (6.3 ± 1.8 and 0.38 ± 0.27), while the field control recorded the lowest (3 ± 1 and 0.07 ± 0.03).

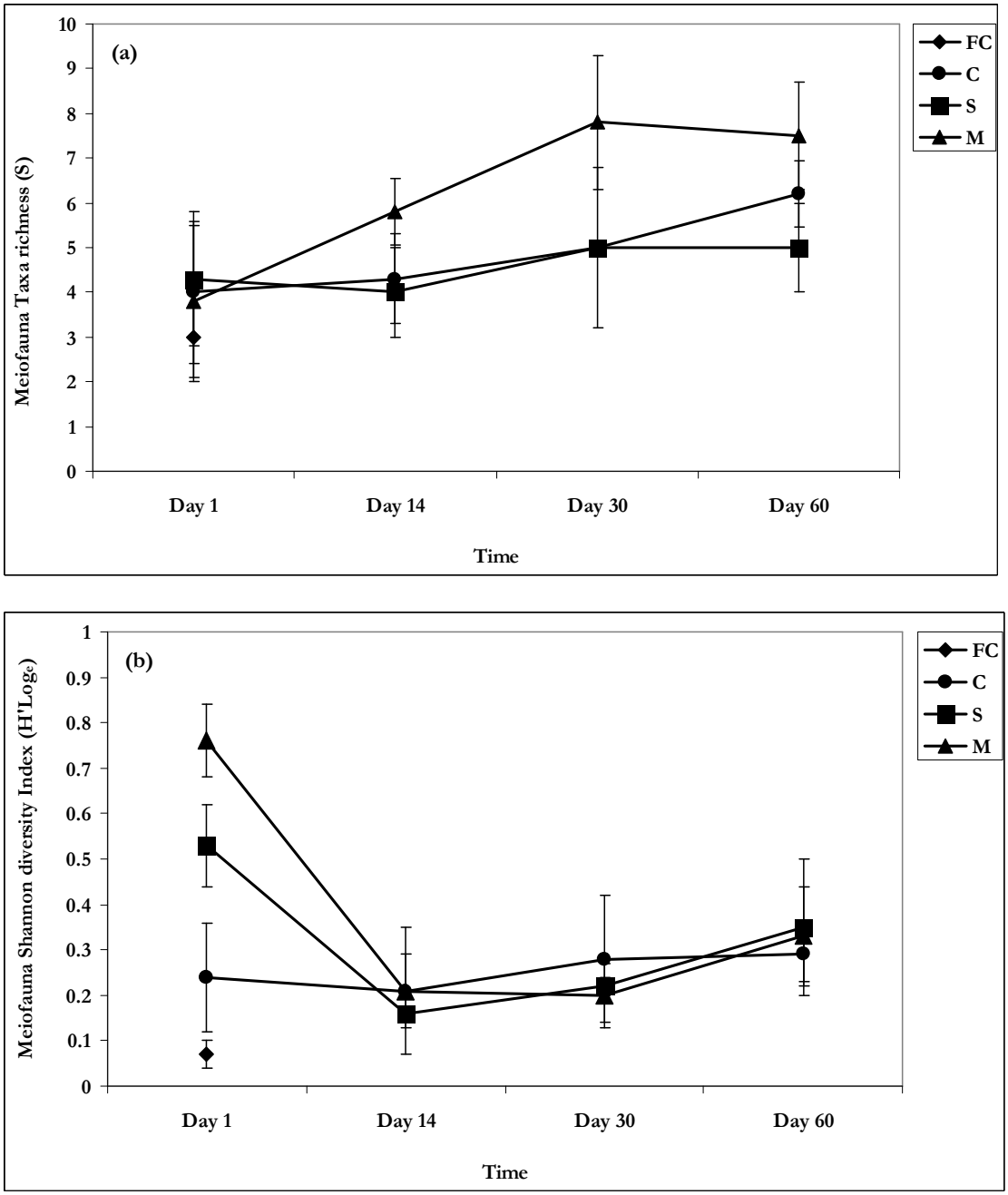

Figure 6.7. Changes in (a) meiofauna taxa richness and (b) Shannon diversity index with time (days). FC; field control, C; experimental control, S; sea grass leaf litter and M; mangrove leaf litter.

The field control recorded significantly lower taxa richness (ANOVA, df = 3, F = 5.742, $p < 0.05$) and Shannon diversity index (ANOVA, df = 3, F = 3.43, $p < 0.05$) compared to all the food type treatments. However, post hoc analysis showed that only the mangrove leaves treatment recorded significantly higher meiofauna taxa richness and Shannon diversity Index (ANOVA, Tukeys HSD, $p < 0.05$) than the field control over the entire experimental period.

There were significant differences in meiofauna taxa richness (ANOVA; df = 2, F = 9.24, $p < 0.05$) and Shannon Diversity index (ANOVA; df = 2, F = 8.1564, $p < 0.05$) between the different food types, on one hand, and the experimental control, on the other. A significant food type effect was recorded on day 30 where the mangrove leaf litter recorded significantly higher meiofauna taxa richness (ANOVA; Tukey's HSD, $p < 0.05$) than the experimental control. In addition, only the mangrove leaf litter recorded a significant temporal effect in meiofauna taxa richness, where day 1 recorded a significantly lower meiofauna taxa richness than days 30 and 60 (ANOVA; Tukey's HSD, $p < 0.05$). However, both mangrove and sea grass leaf litter treatments recorded significant temporal effects in Shannon diversity index, with day 1 recording a significantly higher index than days 14 and 30 in the sea grass leaf litter, and than days 14, 30 and 60 in the mangrove litter treatment (ANOVA; Tukey's HSD, $p < 0.05$). The fact that mangrove leaf litter recorded the highest taxa richness and Shannon diversity index indicates that mangrove leaf litter attracted a more diverse meiofauna community compared to the sea grass and experimental controls. The observed significant differences between food types show that meiofauna taxa responded differently to the various food

type additions. The increase in meiofauna taxa richness with time in the mangrove leaf litter probably reflects the changes in the chemistry and the microbial community associated with decomposing leaf litter. These changes created more diverse habitats thereby attracting more meiofauna taxa with time.

6.3.5 Effect of food type on nematode community composition

A total of 85 nematode genera were recorded during the entire experimental period. The experimental controls recorded 65 genera, the sea grass leaf litter 50 genera, mangrove leaf litter 47 genera and the field controls 30 genera. The relative abundances of the dominant genera in each food type treatments are shown in Table 6.4. Over the entire experimental period, the genera *Theristus, Dichromadora,* and *Diplolaimelloides* mainly characterised the nematode community within the mangrove leaf litter treatment. The sea grass leaf litter was dominated by the genera *Desmolaimus, Theristus* and *Terschellingia* during the course of the experiment. The experimental controls were dominated by the genera *Terschellingia*, *Viscosia* and *Halalaimus* while *Terschellingia* and *Pierickia* were the dominant genera in the field controls.

Table 6.4. Overall relative abundance of the dominant nematode genera (≥ 5 %) in each food type treatment. FC; field controls, C; experiment controls, M; mangrove leaves, S; sea grass leaves.

Treatments	Dominant nematode genera abundance per treatment
FC	*Terschellingia* (25), *Pierickia* (9), *Spirinia* (6), *Sphaerolaimus* (5)
C	*Terschellingia* (13), *Viscosia* (11), *Halalaimus* (6), *Daptonema* (6), *Dichromadora* (5), *Haliplectus* (5)
M	*Theristus* (12), *Dichromadora* (11), *Diplolaimelloides* (9), *Daptonema* (8), *Haliplectus* (7), *Terschellingia* (7)
S	*Desmolaimus* (14), *Theristus* (12), *Terschellingia* (7), *Haliplectus* (6), *Daptonema* (5)

nMDS analysis (Fig. 6.8) and ANOSIM on nematode community composition comparing the effect of the different food types including the field and experimental controls, was performed for each day separately. The ordination graph for day 1 (Fig. 6.8a) showed a separation of the field controls from all the food types, and the sea grass leaf litter from the experimental control and mangrove leaf litter. On day 14 (Fig. 6.8b), the mangroves and sea grass treatments were separated from each other and from the field controls. All the treatments were separated from each other and from the field controls on day 30 (Fig. 6.8c). On day 60 (Fig. 6.8d), no separation between food types was observed though one replicate of the experimental control was separated from the other treatments. These nMDS patterns were further shown by ANOSIM (Table 6.5) which produced overall significant differences (ANOSIM, Global R = 0.875 and 1) on days 1 and 30 respectively. These separations show that the different food types supported different

nematode communities which could be linked to the changes in habitat conditions with time.

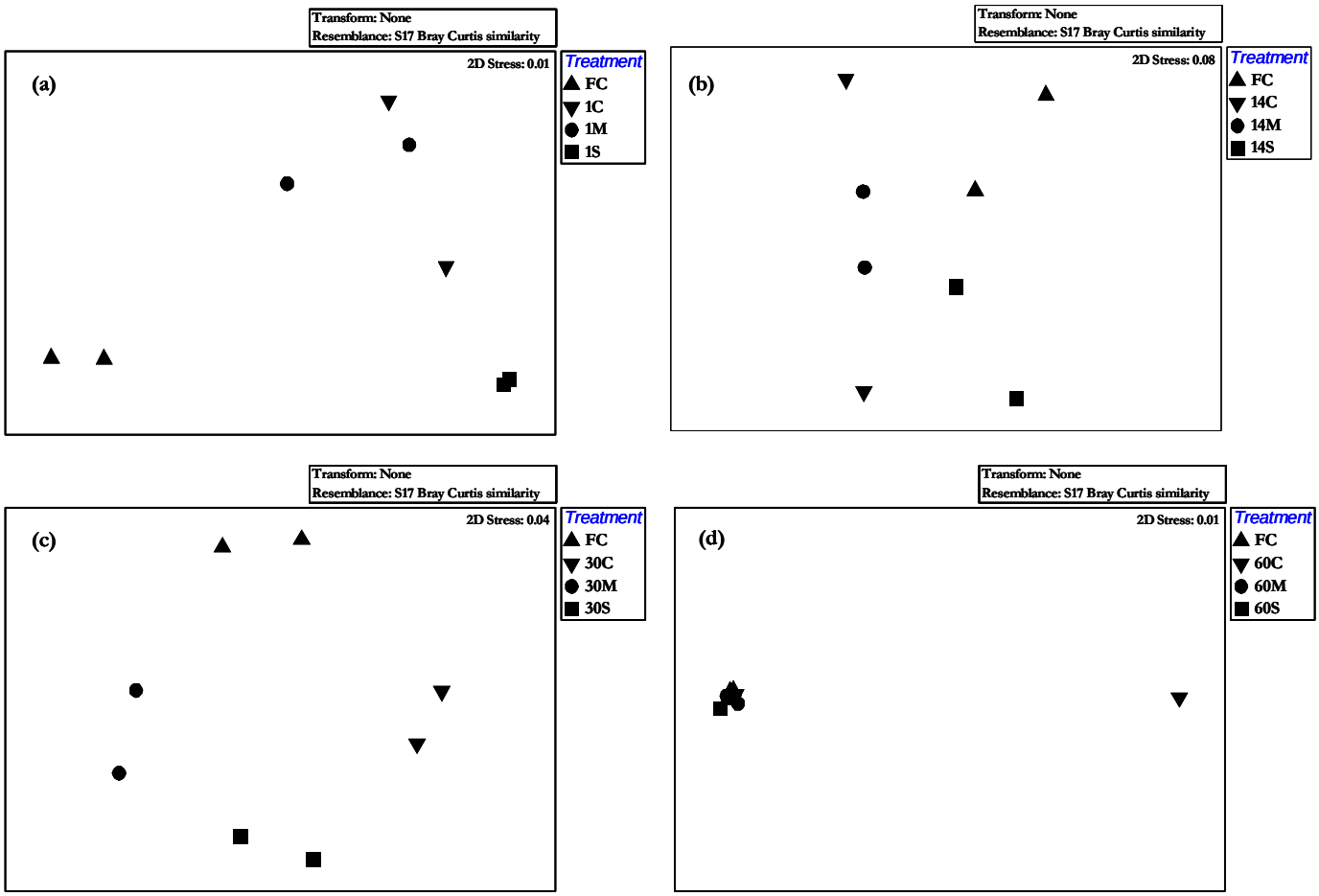

Figure. 6.8. nMDS ordination plot (non-transformed data) of nematode community assemblages from the different food types on days; (a) 1, (b) 14, (c) 30 and (d) 60.

Table 6.5. Results of ANOSIM global and pair-wise tests using Bray-Curtis similarity, showing the effect of food type (treatment) on nematode community structure during the experimental period. * represents significant differences.

Pairwise comparisons	**Day 1** (R = 0.875)	**Day 14** (R = 0.396)	**Day 30** (R = 1)	**Day 60** (R = 0)
FC & C	1*	0.25	1*	0.25
FC & M	1*	1*	1*	0
FC & S	1*	1*	1*	0.5*
C & M	0	0	1*	-0.25
C & S	0.5*	-0.25	1*	0.25
M & S	1*	0.5*	1*	-0.25

The observed dissimilarity between the field control and all the food types on day 1 was attributed to the high abundance of the genus *Terschellingia* in the field control (Table 6.6). Similarly, the observed dissimilarity between the field control, the sea grass and the experimental controls on day 30 was attributed to the high abundance of the genus *Terschellingia* in the field controls whereas the relative abundance of this genus was much lower in the sea grass and experimental control treatments. The genera *Theristus* and *Diplolaimelloides* were responsible for the observed dissimilarities between mangrove leaf litter and all the other treatments including the field control on day 30. The mangrove leaf litter recorded the highest density of the genera *Theristus* and *Diplolaimelloides* on day 30 (640 and 485 Ind. / 7 cm^2 respectively) whereas *Terschellingia* was only present in very low numbers (63 Ind. /7 cm^2).

Table 6.6. SIMPER list showing the three main genera contributing to the Bray-Curtis dissimilarity (%) between food types on each day. F, field control; C, experiment controls; M, mangrove leaf litter and S, sea grass leaf litter.

Treatments compared	**Day 1**	**Day 14**	**Day 30**	**Day 60**
FC and C	*Terschellingia* (23) *Pierickia* (9) *Spirinia* (5)	*Terschellingia* (20) *Viscosia* (10) *Pierickia* (8)	*Terschellingia* (23) *Pierickia* (10) *Spirinia* (6)	*Terschellingia* (15) *Pierickia* (8) *Molgolaimus* (5)
FC and M	*Terschellingia* (25) *Pierickia* (8) *Spirinia* (5)	*Terschellingia* (17) *Dichromadora* (8) *Pierickia* (7)	*Theristus* (15) *Diplolaimelloides* (13) *Terschellingia* (13)	*Terschellingia* (10) *Dichromadora* (8) *Paracanthonchus* (6)
FC and S	*Terschellingia* (24) *Pierickia* (9) *Spirinia* (5)	*Terschellingia* (23) *Pierickia* (9) *Spirinia* (6)	*Terschellingia* (23) *Pierickia* (8) *Theristus* (8)	*Terschellingia* (17) *Desmolaimus* (9) *Pierickia* (6)
C and M	*Oxystomina* (9) *Terschellingia* (7) *Pierickia* (5)	*Viscosia* (15) *Haliplectus* (13) *Dichromadora* (11)	*Theristus* (23) *Diplolaimelloides* (17) *Dichromadora* (8)	*Dichromadora* (8) *Terschellingia* (7) *Paracanthonchus* (7)
C and S	*Diplolaimelloides* (12) *Camacolaimus* (12) *Terschellingia* (9)	*Viscosia* (20) *Desmolaimus* (7) *Terschellingia* (6)	*Theristus* (26) *Terschellingia* (8) *Dichromadora* (5)	*Desmolaimus* (15) *Terschellingia* (18) *Molgolaimus* (6)
M and S	*Oxystomina* (10) *Diplolaimelloides* (9) *Camacolaimus* (9)	*Haliplectus* (18) *Dichromadora* (15) *Theristus* (10)	*Diplolaimelloides* (20) *Theristus* (16) *Dichromadora* (8)	*Desmolaimus* (10) *Dichromadora* (10) *Diplolaimelloides* (7)

6.3.6 Effect of time within food types on nematode community composition

In order to investigate nematode community succession within food types over the entire experimental period, nematode community assemblages were compared between experimental days for each food type (Fig. 6.9).

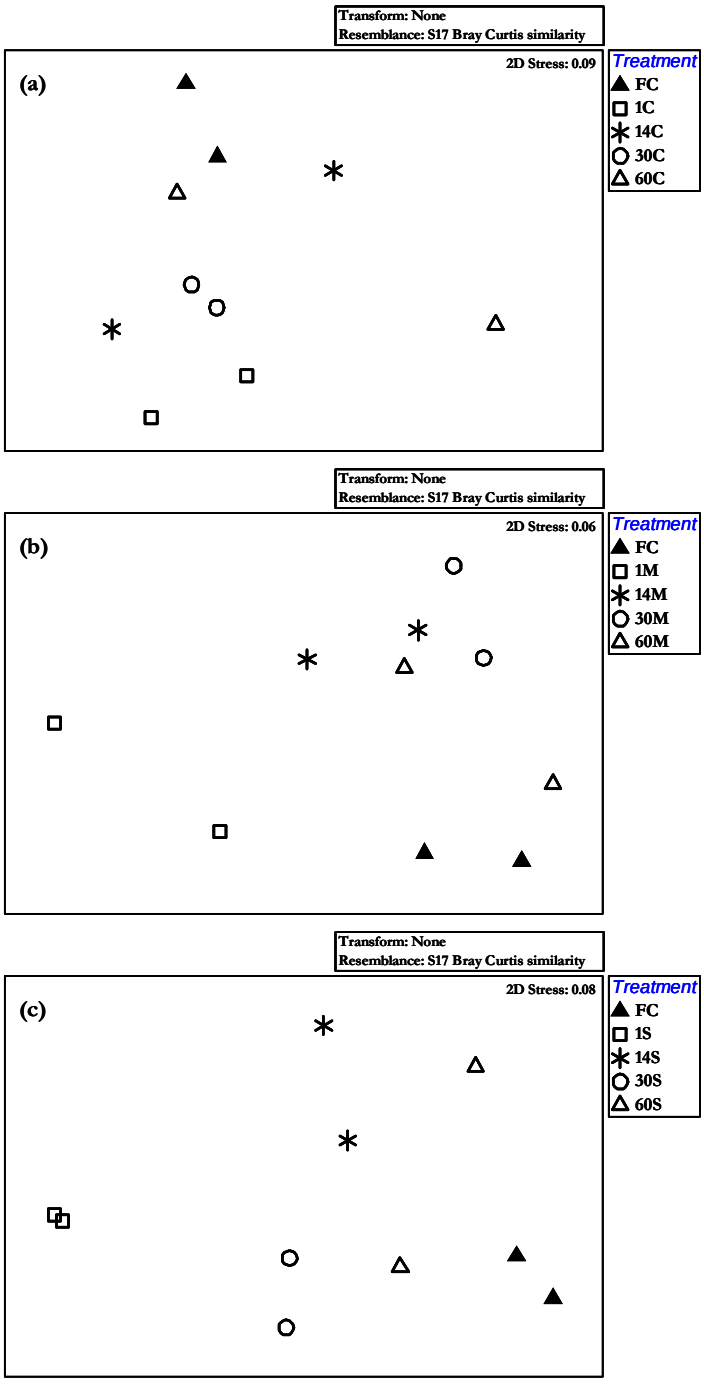

Figure 6.9. nMDS on nematode community assemblage showing the effect of time within (a) experimental controls, (b) mangrove leaf litter, (c) sea grass leaf litter.

In each of these analyses, the field control was also included. The experimental control (Fig 6.9a) did not show any overall significant temporal effect (ANOSIM, Global R < 0.5). Within the mangrove leaf litter treatment, day 1 was significantly separated (ANOSIM, R > 0.5) from all the other experimental days (Fig. 6.9b). The sea grass leaf litter treatment recorded significant temporal effects except for between day 14 and day 60 (Fig. 6.9c). The field controls were separated from days 1, 14 and 30 in the mangrove leaf litter, with days 1 and 30 in the experiment controls and with all the experimental days in the sea grass leaf litter. These temporal effects were confirmed by ANOSIM (Global R = 0.65 and 0.86) for the mangrove and sea grass leaf litter treatments respectively (Table 6.7). This temporal effect in nematode community assemblage is an indication of nematode community succession probably as the chemistry of the leaf litter changes with decomposition. The lack of significant time effects within the experimental controls shows that food availability is essential for the development of a diverse nematode community in mangrove sediments.

Table 6.7. Results of ANOSIM global and pair-wise tests using Bray-Curtis similarity, showing the effect of time on nematode community structure in each food type. Global R is shown in parenthesis while * shows significant comparisons.

Pairwise Comparisons	**Food Types**		
	C (R = 0.186)	**M (R = 0.65)**	**S (R = 0.86)**
FC & 1	1*	1*	1*
FC & 14	0.25	1*	1*
FC & 30	1*	1*	1*
FC & 60	0.25	0	0.5*
1 & 14	-0.25	1*	1*
1 & 30	0	1*	1*
1 & 60	0.25	1*	1*
14 &30	0	0.5*	0.75*
14 & 60	-0.5	0	0
30 & 60	0	0	0.5*

Table 6.8 shows the nematode genera succession within each food type and experimental controls during the experimental period. The genera *Dichromadora*, *Haliplectus*, *Theristus* and *Terschellingia* mainly characterised experimental days 1, 14, 30 and 60, respectively, within the mangrove leaf litter treatment. The sea grass leaf litter was characterised by the genera *Camacolaimus*, *Daptonema*, *Theristus* and *Desmolaimus*. The experimental control was dominated by *Halalaimus*, *Dichromadora* and *Terschellingia* while *Terschellingia* and *Pierickia* were the dominant genera in the field controls. The fact that different nematode genera were dominant on each experimental day from each

food type treatment is a reflection of nematode community succession with time. This could be as a result of changes in the chemistry and/or microbial communities and hence habitat conditions as decomposition progressed.

Table 6.8. SIMPER lists showing the percentage contribution of three main genera characterising each experimental day within each food type.

Food type	**Species contribution**			
	Day 1	**Day 14**	**Day 30**	**Day 60**
FC	*Terschellingia* (42)	*Terschellingia* (42)	*Terschellingia* (42)	*Terschellingia* (42)
	Pierickia (17)	*Pierickia* (17)	*Pierickia* (17)	*Pierickia* (17)
	Trissonchulus (6)	*Trissonchulus* (6)	*Trissonchulus* (6)	*Trissonchulus* (6)
C	*Halalaimus* (23)	*Dichromadora* (43)	*Terschellingia* (28)	*Terschellingia* (33)
	Leptolaimus (23)	*Procamacolaimus* (21)	*Daptonema* (11)	*Leptolaimus* (33)
	Dichromadora (15)	*Terschellingia* (14)	*Leptolaimus* (11)	*Camacolaimus* (33)
M	*Dichromadora* (15)	*Haliplectus* (25)	*Theristus* (34)	*Terschellingia* (22)
	Pierickia (15)	*Dichromadora* (21)	*Diplolaimelloides* (22)	*Dichromadora* (16)
	Halalaimus (10)	*Daptonema* (20)	*Dichromadora* (10)	*Halalaimus* (11)
S	*Camacolaimus* (28)	*Daptonema* (30)	*Theristus* (50)	*Desmolaimus* (32)
	Diplolaimelloides (23)	*Desmolaimus* (27)	*Dichromadora* (19)	*Theristus* (18)
	Dichromadora (13)	*Terschellingia* (13)	*Haliplectus* (11)	*Terschellingia* (9)

Similarly, several nematode genera were responsible for the observed dissimilarities between days within food types (Table 6.9). The genera *Theristus*, *Terschellingia* and *Diplolaimelloides* mainly contributed to the observed dissimilarities between experimental days in the mangrove leaf litter. The dissimilarities between experimental days in the sea grass leaf litter were mainly attributed to the genera *Desmolaimus* and *Theristus*. The genus *Terschellingia* recorded the highest densities in the field control and

was responsible for the dissimilarities between the field control and all the food types over the entire experimental period.

Table 6.9. SIMPER lists showing the three main genera contributing to the Bray-Curtis dissimilarity (%) between experimental days within each food type.

Days	**Species contribution**		
	C	**M**	**S**
1 & 14	*Viscosia* (23) *Terschellingia* (7) *Halalaimus* (6)	*Haliplectus* (16) *Dichromadora* (14) *Theristus* (10)	*Desmolaimus* (11) *Daptonema* (9) *Terschellingia* (8)
1 & 30	*Terschellingia* (8) *Trefusialaimus* (6) *Desmolaimus* (5)	*Theristus* (22) *Diplolaimelloides* (17) *Dichromadora* (8)	*Theristus* (31) *Haliplectus* (8) *Dichromadora* (6)
1 & 60	*Terschellingia* (14) *Molgolaimus* (12) *Haliplectus* (4)	*Terschellingia* (11) *Dichromadora* (9) *Paracanthonchus* (8)	*Desmolaimus* (21) *Theristus* (7) *Terschellingia* (7)
14 &30	*Viscosia* (22) *Terschellingia* (7) *Halalaimus* (6)	*Theristus* (19) *Diplolaimelloides* (18) *Leptolaimus* (5)	*Theristus* (25) *Terschellingia* (6) *Desmolaimus* (6)
14 & 60	*Viscosia* (15) *Terschellingia* (11) *Molgolaimus* (9)	*Paracanthonchus* (9) *Diplolaimelloides* (8) *Terschellingia* (7)	*Desmolaimus* (18) *Theristus* (8) *Haliplectus* (7)
30 & 60	*Terschellingia* (13) *Molgolaimus* (12) *Haliplectus* (4)	*Theristus* (19) *Diplolaimelloides* (10) *Terschellingia* (6)	*Desmolaimus* (20) *Terschellingia* (7) *Theristus* (7)

6.3.7 Effect of food type on nematode community diversity

Both the field and experimental controls recorded the highest nematode taxa richness (21 and 21.8, respectively; Fig. 6.10a) and also the highest Shannon diversity index (2.7 and 2.8, respectively; Fig. 6.10b). The sea grass leaf litter recorded the lowest nematode genera richness and Shannon diversity index (17.4 ± 2.4 and 2.5 ± 0.32, respectively). Overall, a significant food type effect was observed in both nematode genera richness (ANOVA; df = 3, F = 2.86, $p < 0.05$) and Shannon diversity index (ANOVA; df = 3, F = 3.28, $p < 0.05$). However, only day 1 recorded a food type effect in Shannon diversity index, with the sea grass leaf litter recording a significantly lower index than all the other food types (ANOVA; Tukey's HSD, $p < 0.05$). This means that after 1 day post placement, the colonisation by nematode communities of different food types was similar and that only the densities of the different genera may have changed with time. No significant differences in diversity indices were recorded between the field control and all the food type treatments (ANOVA, $p > 0.05$). Similarly, no significant time effect was observed in nematode genera richness (S) and Shannon diversity index (H') within all the food types. This lack of time effect in the diversity indices shows that the pioneer nematode colonisers persisted from day 1 up to day 60 in each food type treatment and that only the relative densities may have changed with time. The high nematode diversity recorded in the experimental control can be linked to the fact that these treatments contained no food additions, meaning that none of the nematode genera was able to dominate the experimental controls as food was limiting.

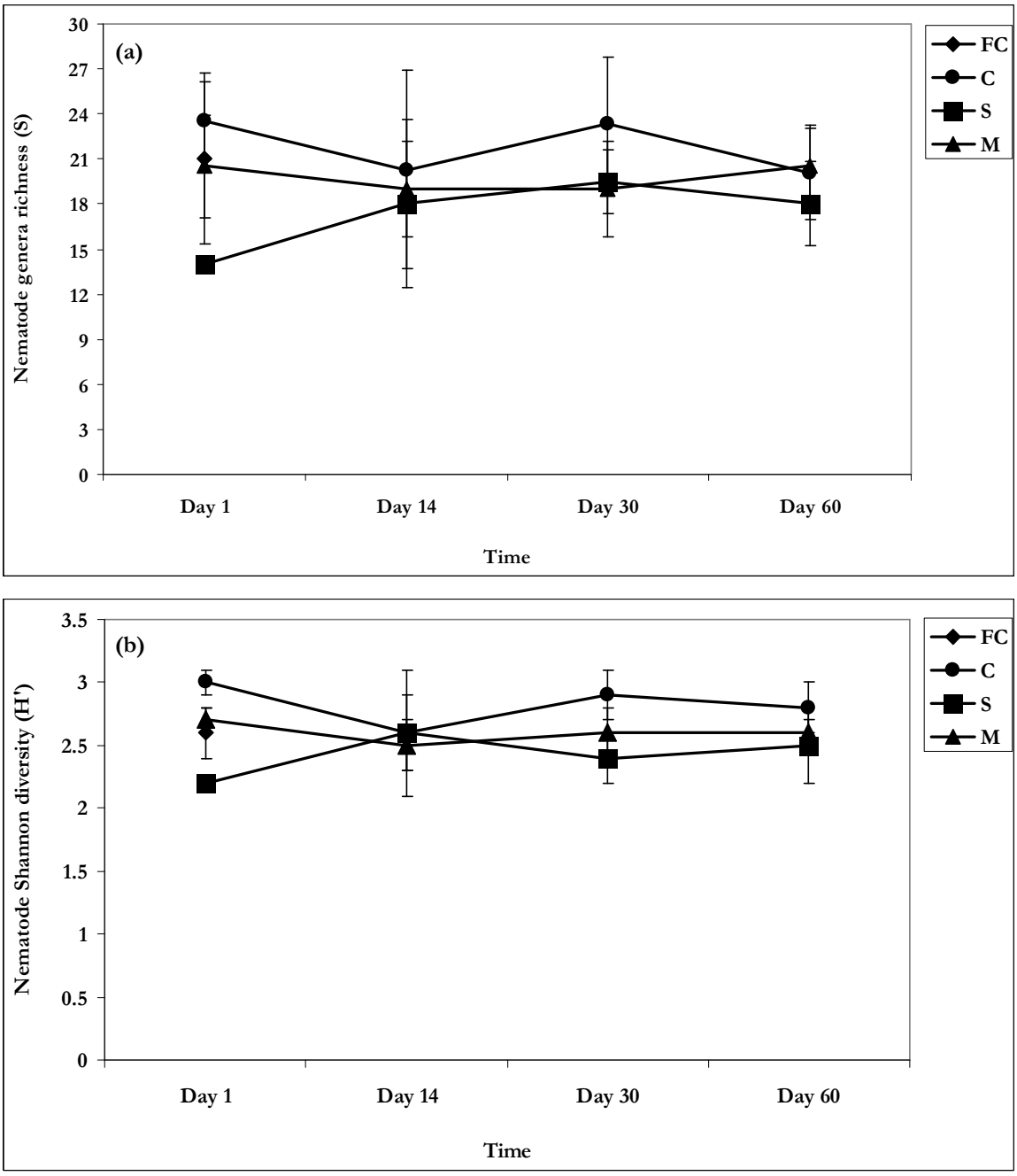

Figure 6.10. Changes in (a) nematode genera richness and (b) Shannon diversity index with time (days). FC; field control, C; experimental control, S; sea grass leaf litter and M; mangrove leaf litter.

6.3.8 Effect of food type on nematode community trophic structure

Nematode trophic structure was based on Wieser's (1953) classification scheme. The averaged trophic structure composition (Fig. 6.11) shows differences related to food type. Selective deposit feeders (1A) dominated the field and experimental controls. This feeding guild was mainly represented by the genus *Terschellingia.* Non-selective deposit feeders (1B) dominated the mangrove and sea grass leaf litter. The genera *Diplolaimelloides*, *Desmolaimus* and *Theristus* were the characteristic non-selective deposit feeders within the mangrove and sea grass leaf litter treatments.

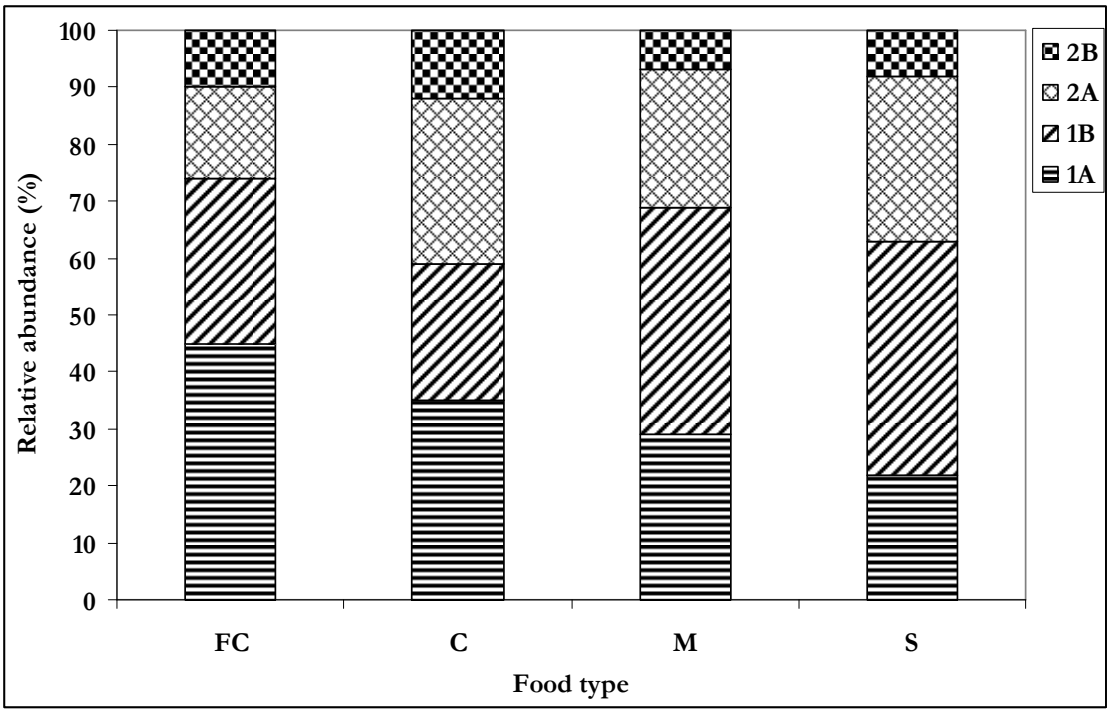

Figure. 6.11. Overall averaged relative abundance (%) of nematode trophic groups in the experimental control (C), mangrove (M), and sea grass (S) treatments over the entire experimental period against the field control (FC).

Figure 6.12 shows the succession in the relative abundance of nematode trophic groups within each food type. Epistrate feeders (2A) were abundant on days 1 and 14 whereas selective deposit feeders (1A) dominated days 30 and 60 within the experimental controls (Fig. 6.12a). Selective deposit feeders (1A) and epistrate feeders (2A) dominated mangrove and sea grass leaf litter treatments respectively on day 1. These trophic groups were replaced by non-selective deposit feeders (1B) over the remaining days of the experiment within both food types (Figs. 6.12b & 6.12c). These findings show that by the end of the experiment, only the experimental controls recorded similar dominant feeding group (1A) to the field control. The leaf litter additions of mangroves and sea grasses sustained more non-selective deposit feeders (1B) from day 14 to day 60. These differences in trophic structure between the field control and both the mangrove and sea grass leaf litter treatments could be linked to the availability of detrital material and possibly the microbial community associated with decomposing organic matter. The non-selective deposit feeders utilised both the leaf litter detritus and the microbial biomass associated with it.

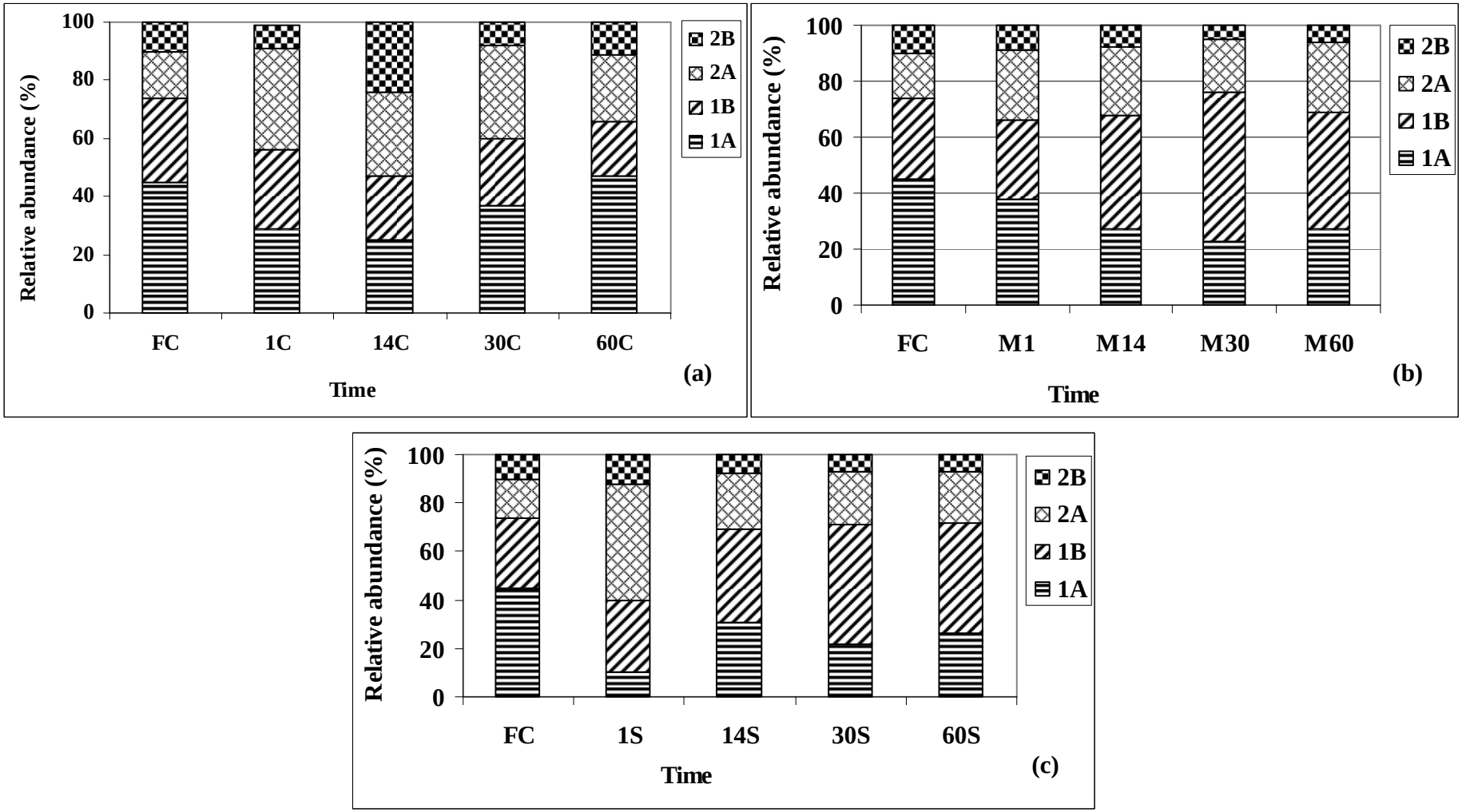

Figure 6.12. Variation in relative abundance of nematode trophic groups with time in (a) experiment control (b) mangrove leaves and (c) seagrass leaves over the entire experimental period against the field control.

6.3.9 ^{13}C uptake experiment

Mean $\delta^{13}C$ values of -34.5 ± 3.9 (Fig. 6.13) were recorded from the natural sediments. This value was less enriched compared to the diatoms $\delta^{13}C$ from all experimental enriched units. The highest average $\delta^{13}C$ values for the diatoms were recorded on day 7 (-13.5 ± 4.1) and day 30 (-12.9 ± 3). A significant depletion was recorded between day 30 and day 60 (ANOVA, df = 5, F = 3.34, p = 0.04). Though the natural sediments recorded a more depleted $\delta^{13}C$ value, it was not significantly different from the diatoms $\delta^{13}C$ for all incubation times.

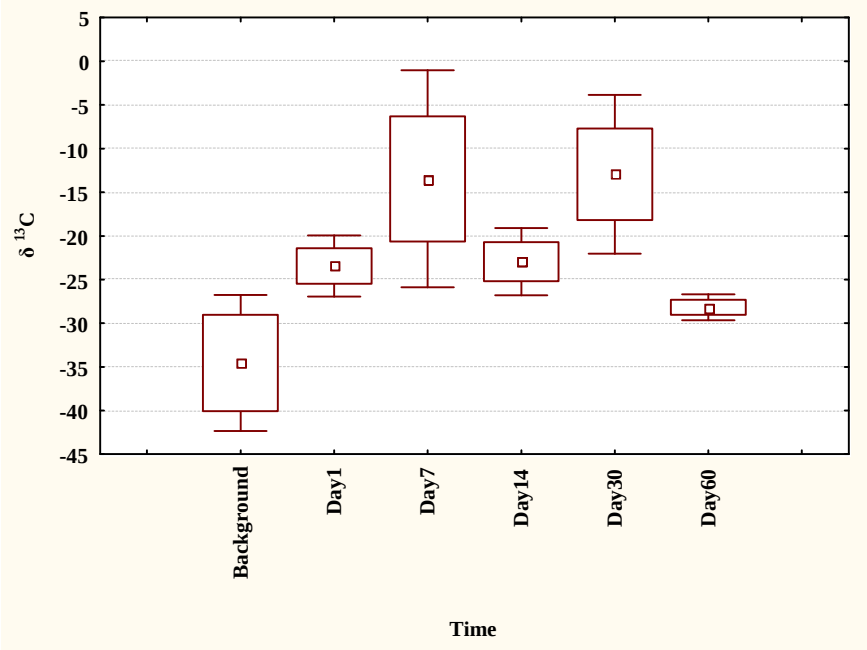

Figure 6.13. Variation in $\delta^{13}C$ (Mean ± SE, n = 3) from the natural sediment (Background) and from the labelled diatoms over the experimental period.

The specific uptake of $\delta^{13}C$ by nematodes (Fig. 6.14) showed very high variability within experimental days especially on days 1 and 14, while day 60 recorded the lowest specific uptake. The large variations within days led to lack of significant time effects in specific uptake of $\delta^{13}C$ by nematodes.

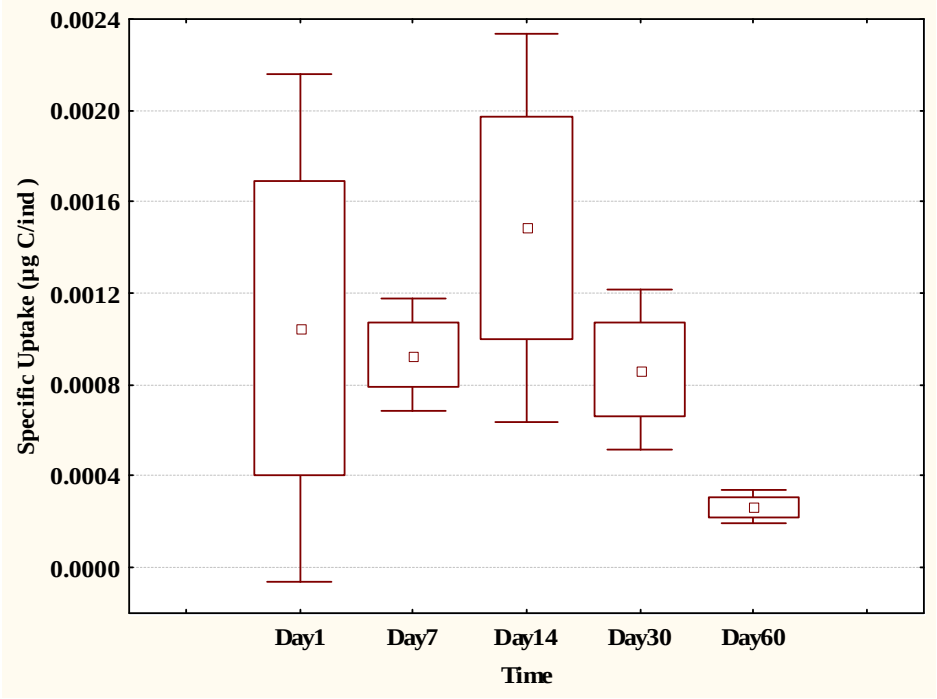

Figure 6.14. Variation in specific uptake of $\delta^{13}C$ (Mean ± SE, n = 3) over the experimental period.

The low rates of ^{13}C uptake by nematodes correspond to the low densities of nematodes recorded from the diatom food type treatment (Fig. 6.15). This probably is an indication that diatoms do not form an important food item within the studied mangroves.

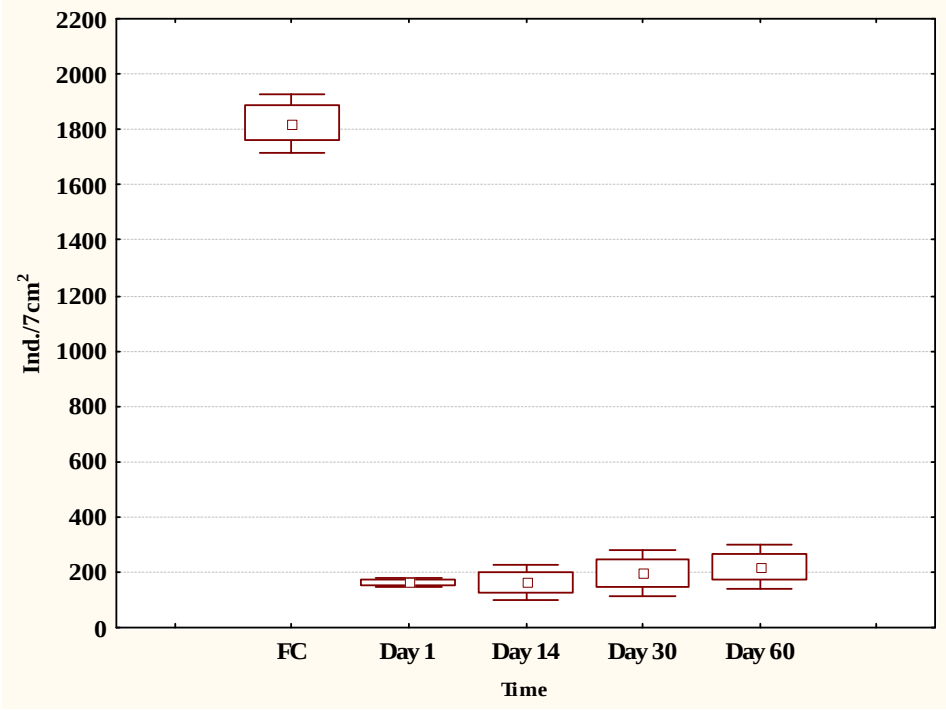

Figure 6.15. Densities of nematodes (mean ± SD, n = 3) from the diatom treatment over the experimental period compared to the field control (FC).

6.3.10 Effect of sediment type on meiofauna colonisation and densities

The degraded sediment treated with mangrove leaves recorded a faster meiofauna and nematode colonisation rates than the natural sediment. The densities of meiofauna (Fig. 6.16a) and nematodes (Fig. 6.16b) in the degraded sediment treated with mangrove leaves surpassed those from the field control from day 14, while the densities were higher than in the field control between day 14 and day 30 in the mangrove leaves treated with natural sediment. Meiofauna and nematode densities from the experimental control treated with natural and degraded sediments never surpassed those from the field control through out the experimental period. Three-Way ANOVA (Table 6.10) testing for the effect of food availability (mangrove leaves versus experimental control), the effect of time, the effect of sediment type (natural fine versus degraded coarse) and all possible interaction effects between a combination of the three factors, showed no significant differences between sediment types in total meiofauna (ANOVA; $df = 1$, $F = 0.001$, $p > 0.05$) and nematode densities (ANOVA; $df = 1$, $F = 0.105$, $p > 0.05$). However, an overall significant food availability effect in meiofauna (ANOVA, $df = 1$, $F = 61.39$, $p < 0.05$) and nematode densities (ANOVA; $df = 1$, $F = 43.16$, $p < 0.05$) was observed.

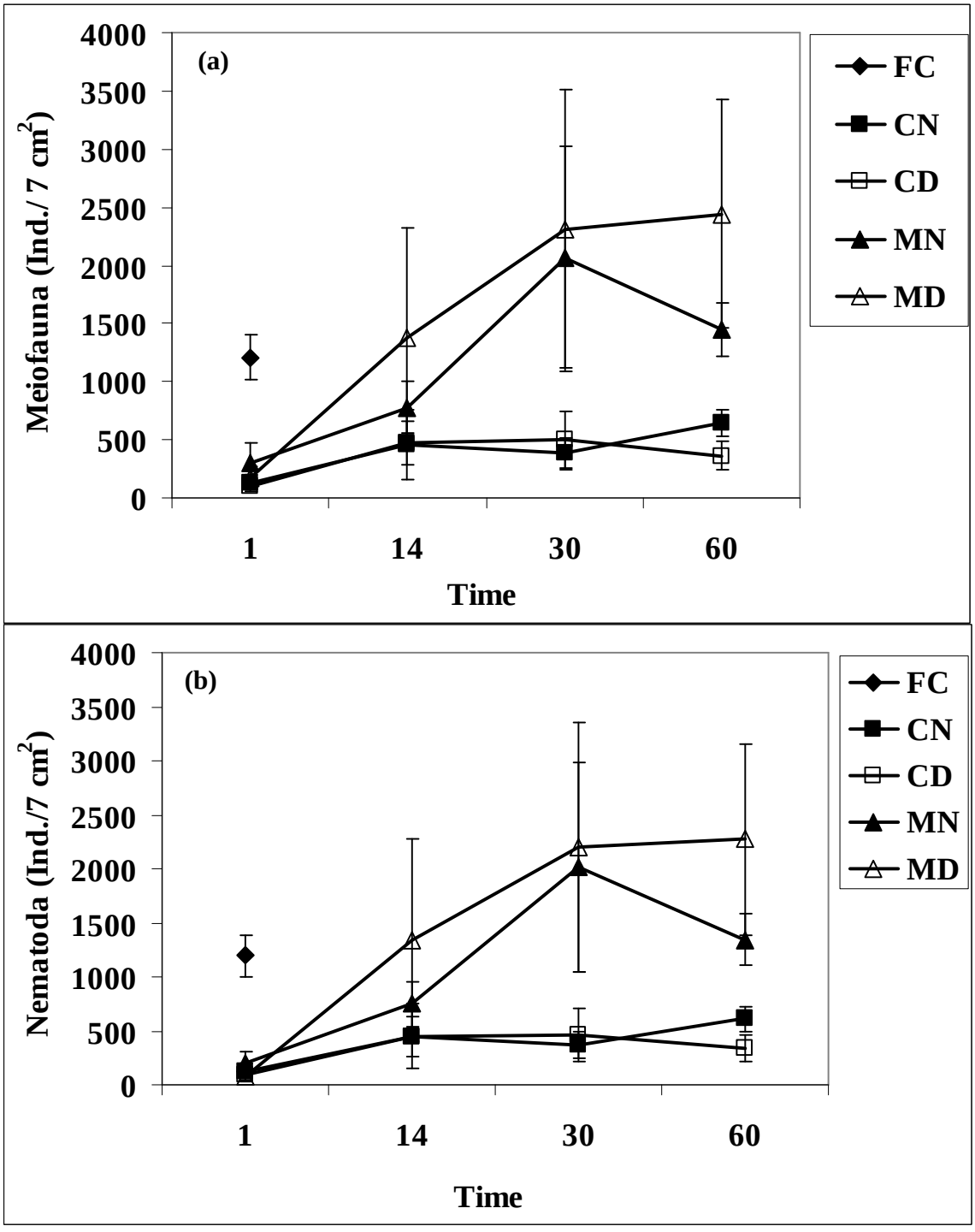

Figure 6.16. Colonisation rates of (a) Meiofauna and (b) Nematoda in the natural and degraded sediments of the experimental controls and mangrove leaf litter treatments over the experimental period (days).

Table 6.10. Out put of Three-Way ANOVA showing the effects of sediment type, food availability, time and the corresponding interaction effects. * represents significant effects ($p < 0.05$).

Variable	Comparisons	df	F	p
Log Total Meiofauna	**Sediment Type**	1	0.001	0.975072
	Food availability	1	61.398	0.000000*
	Time	3	38.135	0.000000*
	Time x Food availability	3	2.403	0.085784
	Time x Sediment type	3	0.901	0.451511
	Food availability x Sediment type	1	0.393	0.534936
	Time x Food x Sediment type	3	1.537	0.223754
Log Nematoda	**Sediment Type**	1	0.105	0.747563
	Food availability	1	43.186	0.000000*
	Time	3	47.373	0.000000*
	Time x Food availability	3	2.224	0.07756
	Time x Sediment type	3	1.235	0.313202
	Food availability x Sediment type	1	0.230	0.634724
	Time x Food x Sediment type	3	1.855	0.157095

Figure 6.17 shows the densities of meiofauna and nematodes from each sediment type on each experimental day. No food availability effect was recorded on day 1 (Fig. 6.17a) and day 14 (Fig 6.17b) (ANOVA; Tukey's HSD, $p > 0.05$). However, on day 30 (Fig 6.17c) and day 60 (Fig. 6.17d), the mangrove leaves treated with natural and degraded sediments recorded significantly higher meiofauna and nematode densities than the experimental controls (ANOVA; Tukey's HSD, $p < 0.05$). This confirms the earlier results on the effect of food type, that food availability is essential for meiofauna colonisation of mangrove sediments. All possible interaction effects between time, food type and sediment type were not significant.

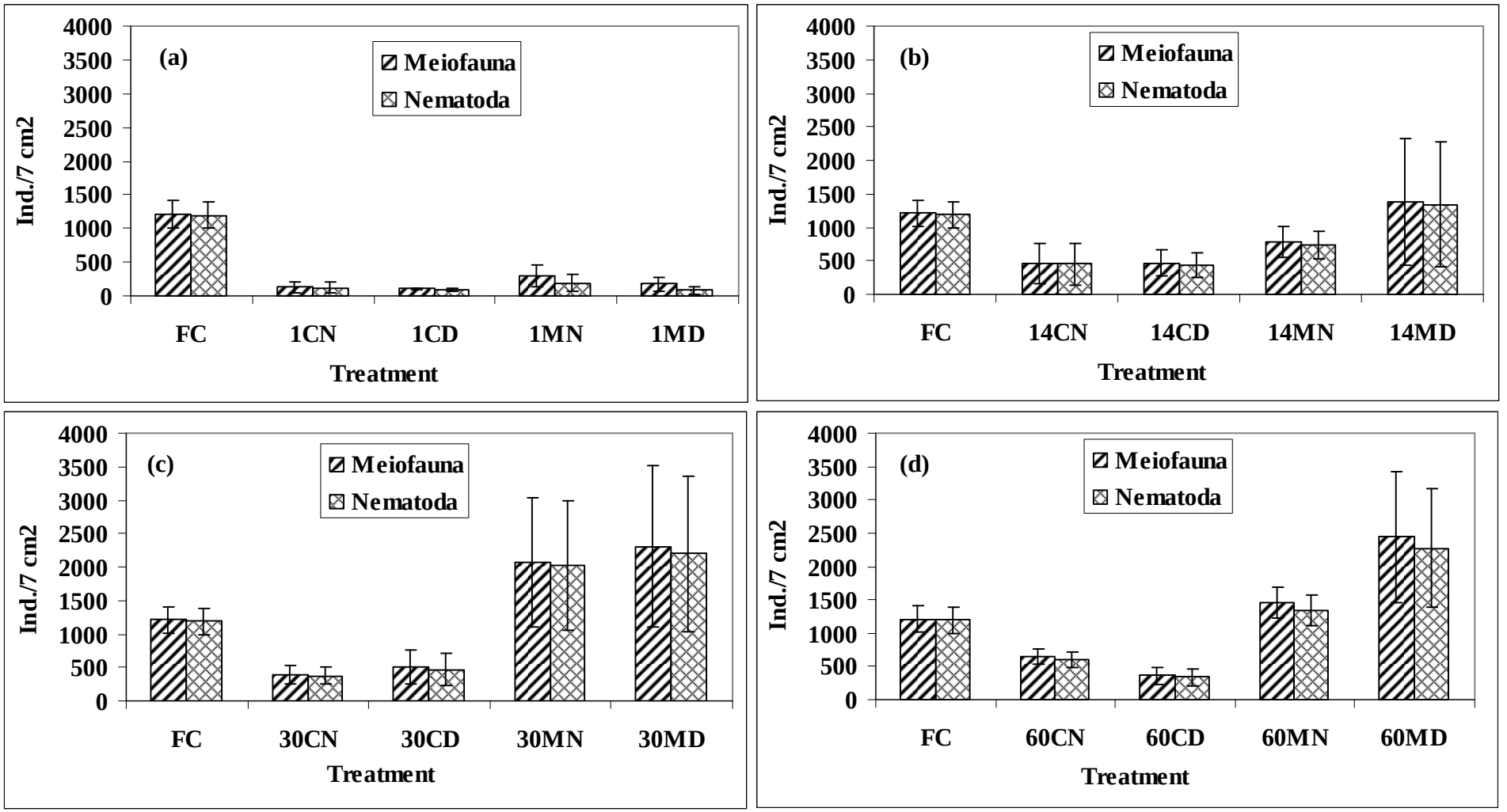

Figure 6.17. Sediment effect: variations in total meiofauna and Nematoda on (a) day 1, (b) day 14, (c) day 30 and (d) day 60. FC; field controls, C; experimental controls and M; mangrove leaf litter treatment.

6.3.11 Effect of sediment type on meiofauna community composition

The effect of sediment type on meiofauna community composition is shown in the nMDS analysis (Fig. 6.18a-d) and ANOSIM (Table 6.11). Both analyses showed no significant sediment effects (ANOSIM; $R < 0.5$) on meiofauna community composition on all days in the mangrove leaf litter treatments. Similarly, the experimental controls never recorded any significant sediment effect (ANOSIM; $R < 0.5$) on day 1 (Fig 6.18a), day 14 (Fig. 6.18b) and day 30 (Fig 6.18c). However, the experimental controls treated with degraded and natural sediments were separated on day 60 (Fig. 6.18d) and recorded significant sediment differences (ANOSIM; $R > 0.5$). Significant food availability effects within sediment treatments were also observed on days 30 and 60 for the natural sediment and on days 1, 30 and 60 for the degraded sediment treatments (ANOSIM; $R > 0.5$).

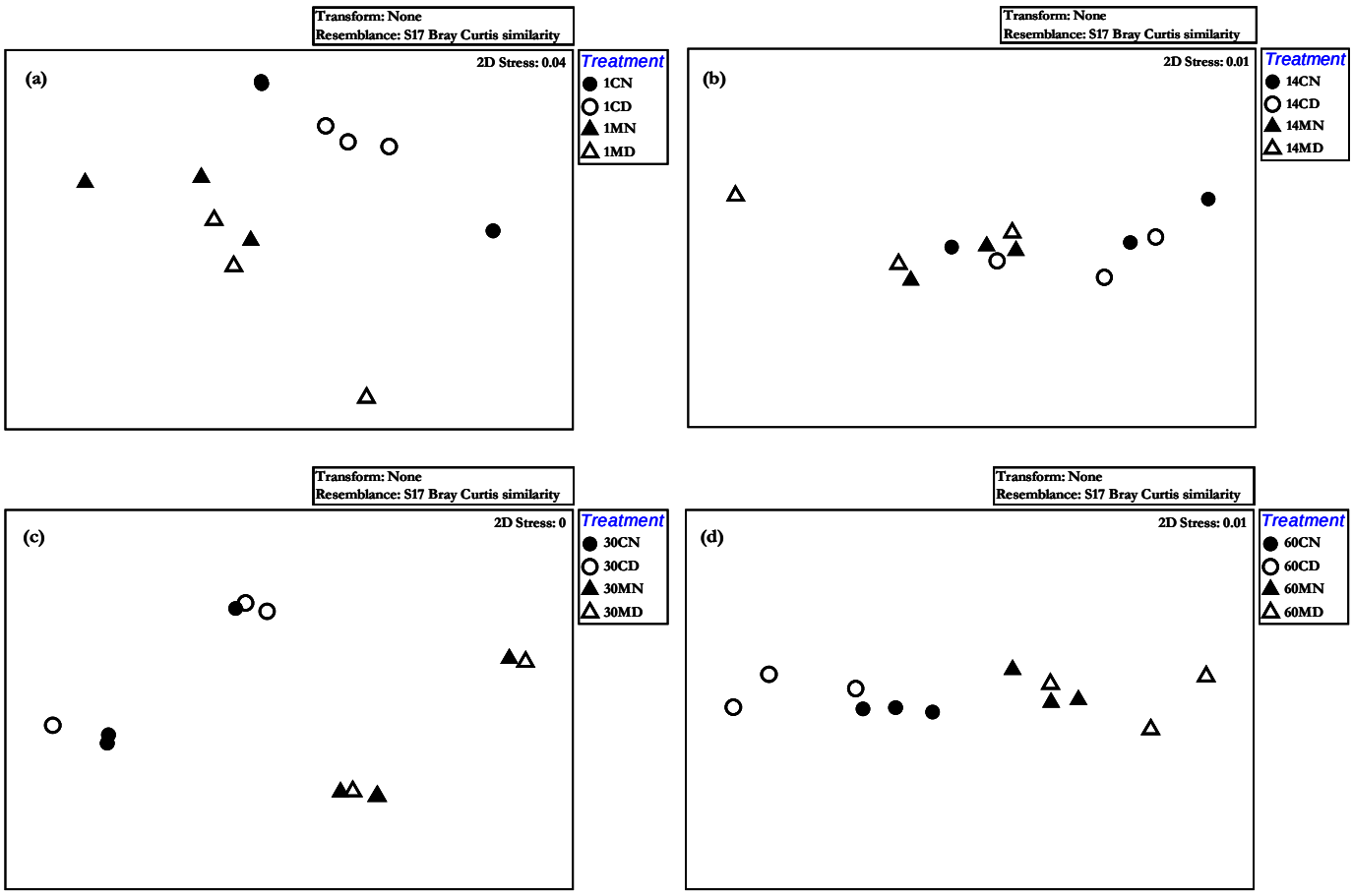

Figure 6.18. nMDS showing the affinities between the different sediment treatments within each food type on (a) day 1, (b) day 14, (c) day 30 and (d) day 60.

Table 6.11. ANOSIM output showing pair wise comparisons between sediment treatments on each experimental day. Global R is shown in parenthesis while (*) shows the significant sediment effects and food type interactions within the sediment treatments.

Pairwise Comparisons	**Experimental Days**			
	Day 1 (0.343)	**Day 14** (0.065)	**Day 30** (0.509)	**Day 60** (0.747)
CN and CD	0.259	0.296	0.037	0.556*
CN and MN	0.333	0.185	0.963*	1*
CN and MD	0.259	0.185	1*	0.926*
CD and MN	0.778*	0.259	0.667*	1*
CD and MD	0.556*	0.185	0.593*	1*
MN and MD	0.037	0.111	0.333	0.185

ANOVA and nMDS were also performed on the mangrove leaves and experimental controls treated with natural and degraded sediments separately, in order to see the changes in meiofauna densities and community composition over time within the different sediment treatments. There was a significant time effect within sediment treatments in meiofauna (ANOVA; $df = 3$, $F = 38.135$, $p < 0.05$) and nematode densities (ANOVA; $df = 3$, $F = 47.373$, $p < 0.05$). Generally, day 1 recorded significantly lower meiofauna and nematode densities (Fig. 6.19a & 6.19b) than all the other days (ANOVA; Tukeys HSD, $p < 0.05$) in the mangrove and experimental control treatments. An nMDS analysis (Fig. 6.20) and ANOSIM on meiofauna community assemblage also gave significant time effects within sediment treatments from both experimental controls and mangrove leaf litter treatments. Within the experimental controls, day 1 was separated from all the other days irrespective of the sediment type (Fig. 6.20a). Similarly, within

the mangrove leaf litter treatment (Fig. 6.20b), day 1 was separated from all the other days, while day 14 was separated from day 30 and day 60 irrespective of the sediment type. These patterns were confirmed by ANOSIM; R > 0.5) for all pairwise comparisons.

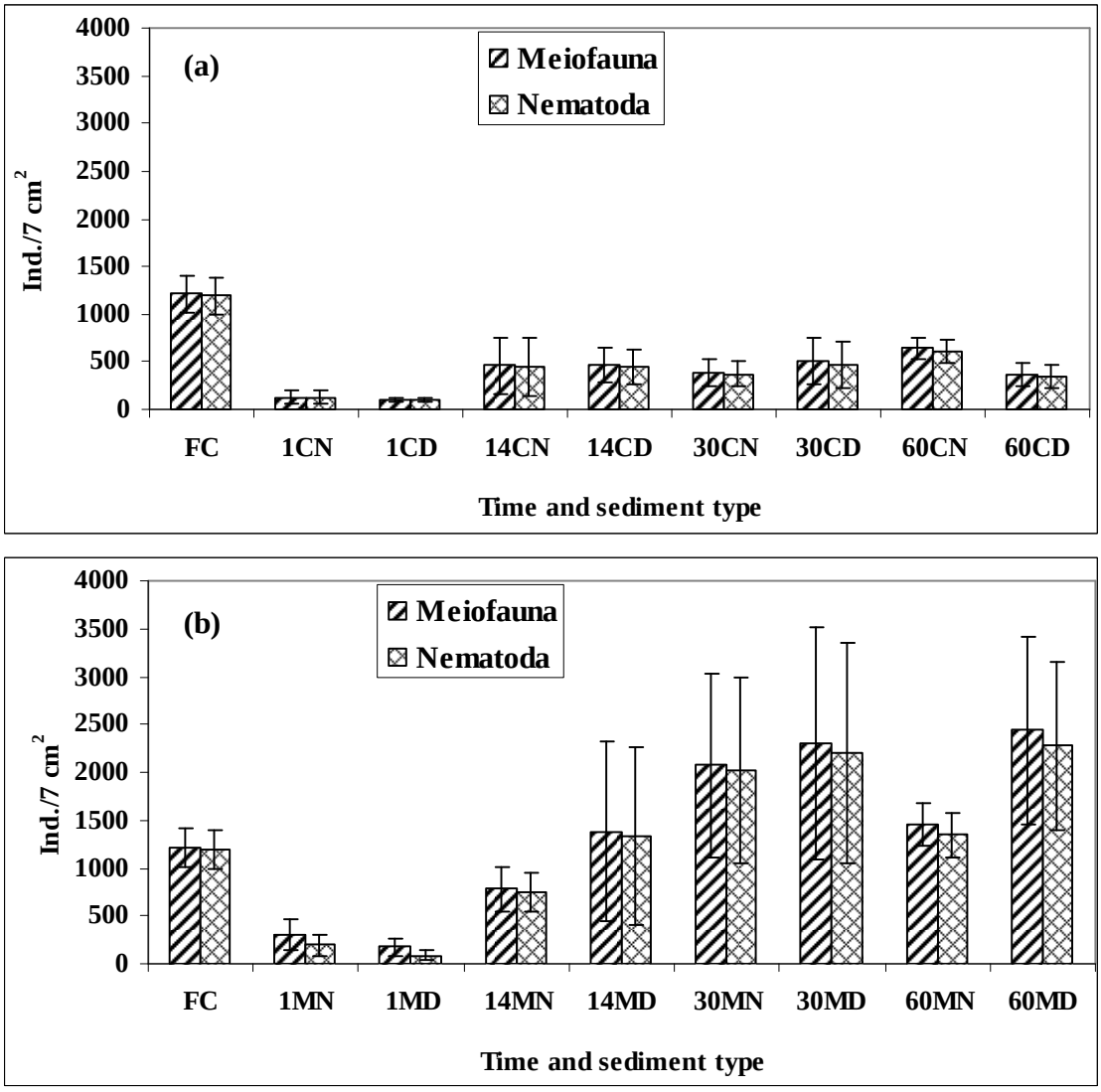

Figure 6.19. Effect of time (days) within sediment treatments on meiofauna and nematode densities from (a) experimental controls (b) mangrove leaf litter treatments.

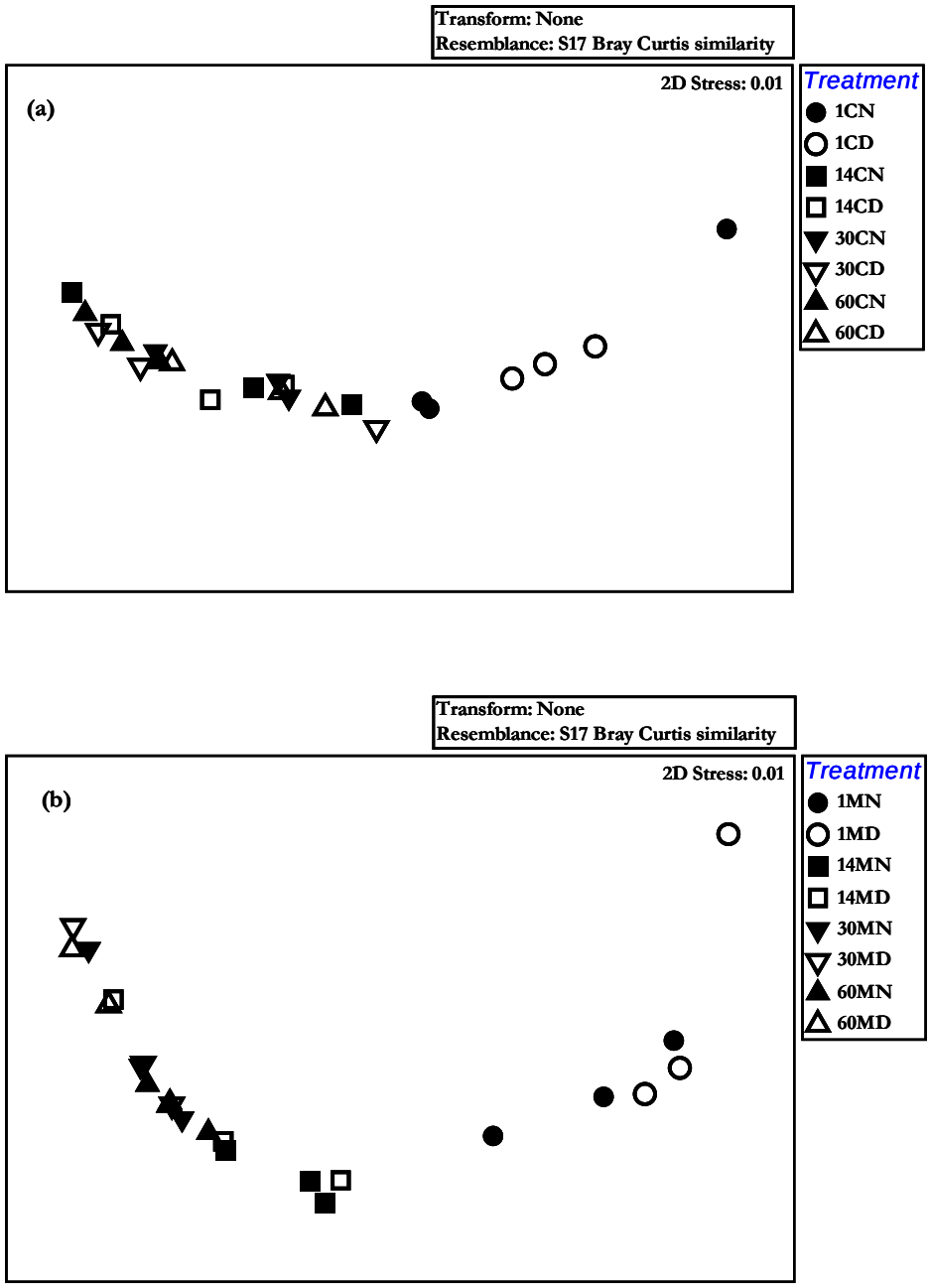

Figure 6.20. nMDS ordination plot (non transformed data) on meiofaunal community assemblage showing the effect of time within sediment treatments in (a) experimental controls (b) mangrove leaf litter treatments.

6.4. Discussion

The results have shown that meiofaunal re-colonisation of mangrove sediments is affected by the availability of food since in the presence of OM (as mangrove leaves) much higher densities were recorded compared to the experimental controls. Additionally, meiofaunal re-colonisation and nematode community structure, within mangroves, is affected by the type of food since mangrove leaves produced a much higher re-colonisation intensity than sea grass leaves. Meiofauna and nematode community composition also changed over time, which is possibly related to the decomposition process and the associated microflora. The type of sediment seems to have a minor or no effect on meiofauna re-colonisation while diatoms do not seem to form an important food source for nematodes within mangrove sediments as shown by the low nematode densities and $\delta^{13}C$ uptake rates.

There is scarcity of information on the influence of different detrital materials found within mangrove benthic ecosystems on meiofauna abundance and nematode community composition. Furthermore, no known field experiments have looked at meiofaunal re-colonisation of different types of detritus within mangrove ecosystems. The only available information on field colonisation experiments are based on single sources of organic matter. These include: Gwyther (2003) which looked at meiofauna assemblages from *Avicenia marina* leaf litter in a temperate mangrove forest in South-eastern Australia, Zhou (2001) which investigated the colonisation of different concentrations of *Kandelia candel* mangrove leaves by meiofauna in Hong Kong, and Gee and Sommerfield (1997) which investigated the effects of mangrove diversity on meiofaunal colonisation from a Malaysian mangrove. Therefore, this field experiment is the first to

investigate the influence of different sources of detritus in addition to the influence of sediment composition on meiofauna and nematode community structure within mangrove ecosystems.

In this study, it is shown that meiofauna and nematode re-colonisation of mangrove sediments is dependent on food type (detritus source) and that the preference for mangrove detritus by meiofauna is greater than for sea grass and diatoms. The study also shows that there is a succession of different nematode genera during the incubation of the experimental material, which is in parallel with the decomposition of the leaf litter.

The fact that meiofauna re-colonised the experimental controls devoid of organic matter one day post placement, indicates that meiofauna occupy any available space even in the absence of food. However, meiofauna densities within the experimental controls remained low through out the experimental period. These low densities recorded from the experimental controls compared to the field control and mangrove leaf litter treatments shows that organic matter plays an important role in influencing meiofaunal re-colonisation within mangrove benthic ecosystems.

The rapid colonisation of the experimental treatments one day post placement ranks among the fastest re-colonisation rates reported for meiofauna in field experimental studies. In similar experimental studies, Zhou (2001), recorded meiofaunal re-colonisation 1 day post placement, while Mirto and Danovaro (2004) and De Troch et al. (2005) recorded meiofaunal re-colonisation after 2 days.

6.4.1 The impact of mangrove leaves on meiofauna colonisation

The densities of meiofauna in the mangrove leaves enriched treatments were higher than in the experimental controls, and increased with time. This implies that decomposition enhanced the nutritional value of the detritus thereby attracting more meiofauna and specifically nematodes. Studies by Lugo and Snedaker (1974) and Lee (1995) show that macrophyte decomposition and detritus recycling are important in mangrove ecosystems, and contribute much of the nutrients for grazers and filter feeders, in addition to providing diverse habitats for colonisation by benthic fauna.

Although meiofauna colonisation was observed 1 day post placement, the rate of colonisation of mangrove leaf litter was initially slow and densities remained lower than in the field controls. This shows that there was a time lag before meiofauna could re-colonise the mangrove leaf litter and attain similar densities as in the field controls. Studies by Alongi (1987), show that mangrove derived polyphenic acids mainly tannins, correlate negatively with meiofauna in mangrove intertidal zones as they reduce the palatability of mangrove detritus. This author also recorded limited growth of *Terschellingia longicaudata* on *Rhizophora stylosa* detritus, which recorded the highest concentration of tannins compared to *Avicenia marina*. According to Zucker (1983) and Robbins et al. (1987), hydrolysable tannins impart a noxious taste on detritus, increase the acidity of plant materials, and precipitate plant proteins and gastrointestinal enzymes. Thus, these substances interfere with the feeding of benthic herbivores and detritovores. Additionally, according to Robertson (1988) and Tietjen and Alongi (1990), there is usually a rapid loss of tannins during the initial days of mangrove litter decay. The above

findings support the results of this study in that the low densities of meiofauna and nematodes recorded on day 1 could have been due to high tannin content of the mangrove litter. However, as the level of tannins decreased with decomposition, meiofauna and in particular nematode densities increased taking advantage of the increased palatability of the detritus. This effect of tannins may also explain the low meiofauna taxa richness recorded on day 1 and the dominance by selective deposit feeding nematodes recorded from the mangrove leaf litter. It is possible that the nematodes which re-colonised the mangrove leaf litter on day 1 probably selected the microflora associated with leaf litter but avoided the mangrove detritus due to its high tannin content. Similarly, Gee and Sommerfield (1997) showed that meiofaunal community development may be affected and controlled by the changes in leaf litter chemistry during decomposition and the subsequent successional development of the microflora community. Based on these earlier studies, it is evident that the mangrove leaf litter became more attractive to meiofauna as tannin concentration decreased with the decomposition process. This increased attractiveness can be supported by the decrease in CN ratio with time which was recorded from the mangrove leaf litter. A low CN ratio means that the nutritional value of the detritus increases as the nitrogen content is high (Skov & Hartnoll, 2002) and becomes more conducive as a food source or habitat for benthic organisms. The observed decrease in CN ratio further explains the observed increase in meiofauna and nematode densities with time.

6.4.2 The effect of mangrove leaves' decomposition on meiofauna

The densities of meiofauna and nematodes increased from day 1 up to the end of the experiment within the mangrove leaf litter treatments. However, the densities remained almost constant after day 14 within the experimental control and sea grass leaf litter treatments. This increase in meiofauna densities with time indicates that the attractiveness of mangrove leaf litter to meiofauna and nematodes increased as decomposition progressed. According to Heip et al. (1985), meiofauna play an important role in the decomposition process in temperate salt-marsh and other littoral macrophyte systems. This role is either directly by ingesting decomposing plant material, or indirectly by stimulating the growth of bacteria and fungi through grazing or nutrient enrichment of the microhabitat. Similarly, De Mesel et al. (2003) suggested based on experiments that meiofauna especially nematodes enhance organic matter decomposition through stimulation of microbial community. This stimulation may be through bioturbation which results in increased oxygen and nutrients, secretion of nutrient rich compounds like mucus, and grazing which keeps the bacterial community active and remineralising nutrients. These authors also argue that even though microorganisms may not provide the primary sources of carbon and energy to detritovores, they may be the major source of essential nutrients like fatty acids, amino acids, sterols, vitamins and other growth factors. Blum et al. (1988) and Robertson (1988) have also shown that bacterial abundance on decomposing *Rhizophora* leaves increases with the decomposition process. Additionally, Fell et. al. (1975) indicates that bacteria on leaf litter produce a slimy layer during the initial stages of decomposition. This slimy layer acts as a matrix for accumulation of detritus, algae and fungal spores and subsequently meiofauna which utilises these trapped

materials as a prime food source. According to Riemann and Helmke (2002), nematodes are believed to release hydrolytic enzymes in mucus which together with bacterial enzymes, breakdown chemical compounds like sugars. These hydrolysed compounds can be directly consumed by the nematodes yielding extra nutrients directly from the detritus. Therefore, the decrease in tannin concentration, the stimulation of microbial growth and the possible release of mucus by nematodes with time, explains the observed increase in meiofauna and nematode densities with time. This also explains the observed differences between day 1 and the other experimental days within the mangrove leaf litter.

The nematode community structure recorded from the mangrove leaf litter showed a link with time and consequently with leaf litter decomposition. This was indicated by changes in the dominant nematode genera and trophic structure with time. These changes in nematode community structure and trophic groups are associated with changes in leaf litter chemistry and/or microphyte community colonisation during the decomposition of mangrove leaves. Studies by Moens et al. (2005) have shown that free living aquatic nematodes produce mucus from ventral and caudal glands on which microbial growth has been observed. This has been interpreted as a mutualistic interaction, in which nematodes may feed on the micro-organisms that colonise the mucus rich tracks. With the help of a field experiment using different species of mangrove leaves, Gee and Sommerfield (1997) also found that the development of the nematode community is characterised by subtle shifts in the species composition colonising the leaves. These authors proposed that the observed changes in the meiofauna and nematode communities as decomposition progressed, may be linked to successional changes in the chemistry and hence microflora

of the leaf litter. Therefore, the changes in the mangrove leaf litter chemistry and the associated microbial growth as the detritus decomposed, explains the changes observed in nematode community assemblage with time. Infact, the CN ratio of the mangrove leaves decreased with time showing that the nutritional value of the litter increased as decomposition progressed. Increased nutritional value of the detritus availed more diverse microhabitats which led to the observed changes in nematode community composition.

Nematode genera composition was different between the experimental controls and the mangrove leaf litter. These differences especially on day 30 were linked to the rapid increase in the densities of the genera *Diplolaimelloides* and *Theristus* in the mangrove leaf litter. These genera were rare in the experimental controls. The density increase of these two genera could be linked to microbial growth on decomposing mangrove litter, and their presence could have also stimulated bacterial growth through mucus production, which inturn enhanced mangrove leaf litter breakdown. The microbes and detritus thus produced provided a source of food for these genera which are non-selective deposit feeders within mangrove ecosystems. The dominance by these two genera within the mangrove leaf litter also explains the low Shannon diversity index (H') recorded from the mangrove leaf litter compared to the experimental controls. Gwyther (2003) recorded a low nematode Shannon diversity index from Barwon mangroves-Australia which was linked to dominance by the genus *Tripyloides*.

The dominance of the epistrate feeder *Dichromadora* on day 1, the selective deposit feeder *Haliplectus* on day 14 and the non-selective deposit feeders *Theristus* and

Diplolaimelloides on day 30 in the mangrove leaf litter shows that there was a succession in nematode trophic groups. This shift in nematode trophic structure with time may be reflecting the changes in food resources available to nematodes within decomposing mangrove leaf litter. According to Ashton et al. (1999), the initial leaching of dissolved organic matter (DOM) from mangrove leaf litter is followed by a slow decomposition of the remaining particulate organic matter (POM) by bacteria and fungal communities, which develop rapidly on the leaves. Gwyther (2003) observed that particulate food sources on leaf litter are composed of the surface biofilm which includes bacteria, microalgae, protozoans and fungi. Therefore, the resulting mangrove detritus and associated microflora provided the food required by deposit feeders which dominated the mangrove leaf litter treatment. Similarly, the possible increase in microbial biomass and diversity with mangrove leaf litter decomposition may explain the shift in nematode feeding groups from selective deposit feeders on day 14 to non- selective deposit feeders (1B) on day 30. The dominance by deposit feeders within mangrove leaf litter during this experiment is similar to findings from other studies from Malaysian mangroves (Gee & Somerfield, 1997) and from temperate Barwon River mangroves-Victoria, SE Australia (Gwyther, 2003). The results of the current study show that deposit feeding nematodes (1A & 1B) form the pioneer colonisers and probably the main feeding groups associated with mangrove leaf litter.

By comparing the age of *Rhizophora stylosa* and *Avicenia marina* leaves with the population growth of two nematode species, Tietjen and Alongi (1990) recorded very low densities of *Monhystera* and *Chromadorina* (< 5 Ind. / leaf). These low numbers led to the conclusion that nematodes were unable to stimulate bacterial abundance hence may

not play a major role in cycling of organic matter in tropical mangrove forests. On the contrary, this experiment recorded much higher meiofauna and nematode densities (2442 and 2274 Ind. / 7 cm^2 respectively) and 901 Ind. / 7 cm^2 for the dominant genus *Theristus* within the mangrove leaf litter. Thus if the densities of meiofauna and nematodes is a reflection of their role in cycling of organic matter, then the high densities recorded during this experiment show that meiofauna and specifically nematodes play an important role in detritus cycling in tropical mangrove ecosystems.

6.4.3 The effect of diatoms on nematode colonisation

Previous studies have shown that diatoms and other micro-algae provide an important food source for many shallow water nematodes (Moens & Vincx, 1997; Gwyther, 2003). However, this study shows that diatoms are not the main food source for mangrove nematodes colonising azoic and organic free sediments. This is because nematode densities remained too low over the whole period of the re-colonisation experiment when diatoms were offered as a food source compared to other potential food sources. Secondly, it is also evident from the low $\delta^{13}C$ that diatoms do not form the main food source for benthic nematodes, since no significant differences were found with the background values. Riera et al. (1999) recorded $\delta^{13}C$ values of -14.4 for benthic diatoms from a *Spartina anglica* salt marsh while the value for nematodes was only -16.2. This value was so depleted that microphytobenthos were ruled out as a major food source for nematodes in this system. The value for non-enriched nematodes from mangrove sediments as recorded in this study was even lower (-34.5), already indicating that diatoms are not a major food item for the nematodes in the studied mangrove systems.

The large range in $\delta^{13}C$ suggests a high diversity of food sources for the nematodes. This diversity could also be explained by the fact that a nematode community consists of a mixture of species from different feeding guilds (Riera et al., 1999). Also, the low uptake by the nematodes of carbon as ^{13}C labelled diatoms in the enriched experiment is not unusual. Olaffson et al. (1999) recorded only 0.04 % of $\delta^{13}C$ label stored in meiobenthic tissue 1 month after incubation with labelled *Skeletonema costatum*. Similarly, Urban–Malinga and Moens (2006) showed that meiobenthos incorporate 0.48 % of average daily losses, with nematodes contributing for only 0.5 % to the total meiobenthic uptake. From Antarctic sediments, Moens et. al. (2007) observed that 0.0028 % to 0.023 % of the added ^{13}C was present in nematode biomass after 16 days. These earlier studies and the current results point to the fact that diatoms do not form an important food source for nematodes in natural mangrove sediments.

6.4.4 The importance of sediment type for meiofauna colonisation

Though no significant sediment effect was observed between the mangrove leaf litter treated with fine sediments from the natural and coarse sediments from the degraded forests, the degraded sediment recorded relatively higher densities of meiofauna and nematodes (1574 and 1473 Ind. /7 cm^2 respectively) compared to the natural sediment (1152 and 1075 Ind. /7 cm^2) over the entire experimental period. The lack of sediment effects may have been due to the high variation in meiofauna and nematode densities. However, the fact that the degraded sediment recorded relatively higher densities though not significant than the natural sediments implies that sediment type has little or no influence on meiofauna colonisation in mangrove forests.

6.5 Conclusions

The results have shown that meiofaunal re-colonisation of mangrove sediments is influenced by the presence and type of organic matter. Additionally, mangrove detritus is the main source of food either directly or indirectly within mangrove ecosystems. Nematoda is the dominant taxon within mangrove sediments and that the density of meiofauna increases with mangrove leaf litter decomposition. The succession in nematode community assemblage and trophic groups within the mangrove leaf litter is an indication of the changes in the utilisation of the litter as a source of food or a habitat by nematode genera. These changes reflect the changes in the leaf litter chemistry as shown by the changes in CN ratio, and/or microbial community. This experiment confirms the earlier studies which recorded differences in meiofauna densities and nematode genera assemblages between degraded and forested *R. mucronata* mangrove ecosystems. It ascertains that the differences observed are as a result of differences in organic matter levels and that this organic matter is mainly derived from mangrove leaves.

CHAPTER SEVEN

Meiofaunal response to different food quality additions to azoic sediments in a tropical mangrove.

7.1 Introduction

The same experiment as for the food type effect was repeated with an extra factor of food type freshness (quality) was added. The experiment used fresh mangrove and sea grass leaves as well as partially decomposed leaves (4 days decomposed). According to Fell et al. (1975), fallen mangrove leaves on the forest floor undergo an initial rapid leaching of dissolved organic matter (DOM). This leaching is followed by a slow decomposition of the remaining particulate organic matter (POM), facilitated by bacterial and fungal communities. These microflora condition the leaf litter for various invertebrate groups which utilise it as food. These microflora condition the leaf litter which is utilised by various invertebrate groups as food. It has been shown by Gwyther (2003) that particulate food sources for meiofauna on leaf litter comprise the surface biofilm comprising of bacteria, microalgae, protozoa and fungi. The diversity of food sources available on decomposing leaves was also shown by Krishnamurthy et al. (1984) who recorded all types of nematode feeding groups on decaying mangrove leaves. This was an indication that decaying litter consists of a variety of materials which can be used as food by meiofauna and in particular nematodes.

This food quality field experiment was necessitated by the observation that within the degraded site, mangrove leaves, which were already decomposing, formed the main organic material deposited by incoming tides. Some of the ground mangrove and sea grass leaves were buried in the experimental site for 4 days. This was meant to initiate bacterial decomposition and was used to test whether prior decomposition of detritus has any effect on meiofauna and nematode genera colonisation rates.

Therefore, the experiment was designed to test whether these already decomposing leaves would attract meiofauna in a similar way to the fresh leaves found in the natural mangrove forest sediments. This experiment was designed to answer the question; Does the state of decomposition of organic matter (fresh and 4 days decomposed mangrove and sea grass detritus) influence meiofauna re-colonisation of mangrove sediments?

7.2 Results

7.2.1 Effect of food quality on meiofauna colonisation

In this experiment, a total of 8 meiofauna taxa were recorded from all treatments over the entire experimental period. The decomposed mangrove leaves recorded all the 8 meiofauna taxa while the fresh mangrove leaves only recorded 5 meiofauna taxa. The decomposed and fresh sea grass leaves recorded 6 and 5 meiofauna taxa, respectively. The field and experiment controls recorded 4 and 5 taxa, respectively. Nematoda was the most abundant taxon accounting for a relative abundance of over 98 % in each treatment. Mangrove leaves were the preferred food type by meiofauna, with the decomposed leaves recording the highest densities of meiofauna and nematodes (maximum 3985 ± 2595 and

3955 ± 2597 Ind. / 7 cm^2, respectively). The decomposed sea grass leaves recorded the lowest densities (maximum 607 ± 16 and 596 ± 16 Ind. /7 cm^2, respectively). Figure 7.1 shows the colonisation rates where meiofauna (Fig. 7.1a) and particularly nematodes (Fig. 7.1b), colonised all treatments 1 day post placement.

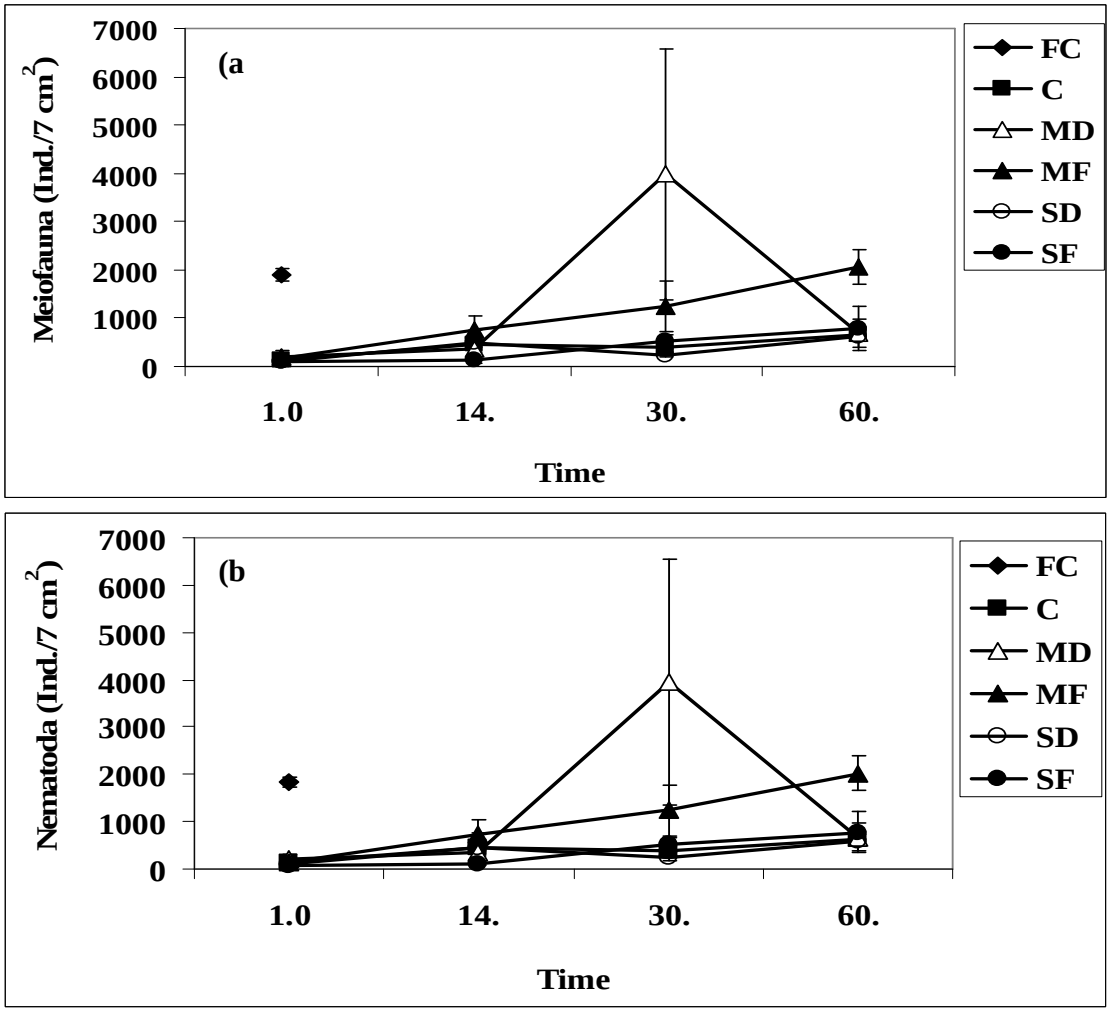

Figure 7.1. Colonisation rates of (a) meiofauna and (b) nematodes during the entire experimental period (days). FC, field control; MF, mangrove fresh leaves; MD, mangrove decomposed leaves; SF, sea grass fresh leaves and SD, sea grass decomposed leaves.

The initial meiofauna re-colonisation was, however, in very low densities (max. 207 Ind. /7 cm^2) from the decomposed mangrove leaves compared to the field control (1890 Ind. /7 cm^2). Total meiofauna and nematode densities surpassed those from the field control on day 30 and day 60 in the decomposed and fresh mangrove leaves treatments respectively. However, meiofauna and nematode densities from the sea grass leaves treatments never surpassed those from the field control. The peak in meiofauna and nematode densities was recorded on day 30 (3985 ± 2595 and 3955 ± 2597 Ind. / 7 cm^2, respectively) in the decomposed mangrove leaves and on day 60 (2059 ± 355 and 2014 ± 367 Ind. / 7 cm^2, respectively) in the fresh mangrove leaves. Re-colonisation by meiofauna and nematodes of the fresh mangrove leaves showed an increasing trend, while in the decomposed mangrove leaves, meiofauna and nematode colonisation drastically decreased after day 30, to densities below those from the field control. This probably indicates that the food/habitat conditions within the decomposed mangrove leaves became limiting after 30 days post placement. On the contrary, the food conditions provided by the fresh mangrove leaves were still conducive for meiofauna up to and may be beyond 60 days of the experiment.

7.2.2 Effect of food quality on meiofauna densities and community composition

Three Way ANOVA (Table 7.1) gave no overall food quality effects on meiofauna (ANOVA; df = 1, F = 0.009, p > 0.05) and nematode densities (ANOVA; df = 1, F = 0.001, p > 0.05).

Table 7.1. Out put of Three-Way ANOVA showing the effects of food quality, food type, time and the corresponding interaction effects. * shows the significant comparisons.

Variable	**Comparisons**	**df**	**F**	**p**
Log Total Meiofauna	**Food Quality**	1	0.009	0.926556
	Food type	1	50.576	0.000000*
	Time	3	50.307	0.000000*
	Time x Food quality	3	2.856	0.052495
	Time x Food type	3	4.423	0.010369*
	Food quality x food type	1	1.593	0.216076
	Time x Food quality x Food type	3	9.666	0.000108*
Log Nematoda	**Food Quality**	1	0.001	0.970513
	Food type	1	49.450	0.000000*
	Time	3	51.367	0.000000*
	Time x Food quality	3	2.946	0.047670
	Time x Food type	3	4.362	0.011018*
	Food quality x Food type	1	1.703	0.201203
	Time x Food quality x Food type	3	9.639	0.000110*

Similarly, Tukey's HSD test gave no significant food quality effects (ANOVA; Tukeys HSD, $p > 0.05$) for the mangrove leaves on day 1 (Fig. 7.2a), day 14 (Fig. 7.2b) and day 30 (Fig. 7.2c). However, on day 60 (Fig 7.2d), the fresh mangrove leaves recorded significantly higher meiofauna and nematode densities than the decomposed leaves (ANOVA; Tukey's HSD, $p < 0.05$). The fresh sea grass leaves recorded significantly lower meiofauna and nematode densities than the decomposed leaves on days 14, while on day 30, the decomposed sea grass leaves recorded significantly lower densities than the fresh leaves (ANOVA; Tukey's HSD, $p < 0.05$). Significant food type effects in meiofauna (ANOVA; $df = 1$, $F = 50.576$, $p < 0.05$) and nematode densities (ANOVA; $df = 1$, $F = 49.45$, $p < 0.05$) were however re-emphasised within the food quality treatments.

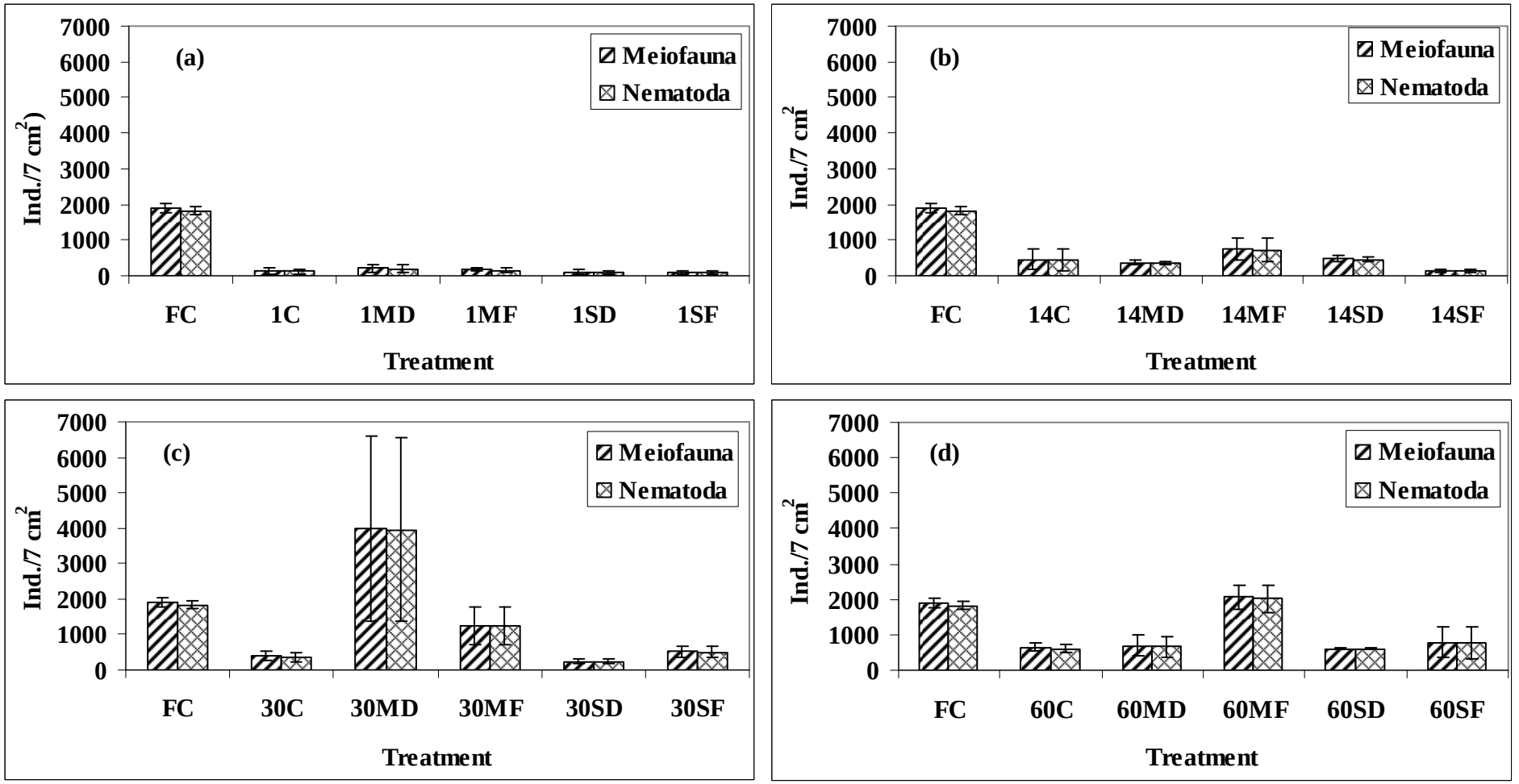

Figure 7.2. Densities (Mean ± SD, n = 3) of meiofauna and Nematoda within the different food quality treatments on (a) day 1, (b) day 14, (c) day 30 and (d) day 60.

An nMDS analysis (Fig. 7.3) and ANOSIM (Table 7.2) on meiofauna community composition comparing food quality on each day separately, showed a clustering of all food quality treatments on day 1, while the field controls were clearly separated from all the treatments (Fig. 7.3a). This trend was reaffirmed by ANOSIM which gave significant differences between the field control and all the other food quality treatments ($R > 0.5$). The separation of all food quality treatments from the field controls on day 1 shows that the treatments (detritus) attracted a different meiofauna community compared to the field controls. On day 14 (Fig. 7.3b) the field controls were also separated from all the food quality treatments, while only the seagrass leaves showed significant food quality effects (ANOSIM, $R > 0.5$). On day 30 (Fig. 7.3c), significant food quality effects (ANOSIM, $R > 0.5$) were also recorded for the sea grass leaves treatment, which were also separated from the field controls.

The mangrove leaves showed significant food quality differences (ANOSIM, $R > 0.5$) in meiofauna community composition on day 60 only (Fig. 7.3d). Significant food type effects were also evident within the food quality nMDS ordination plot on days 14, 30 and 60 (ANOSIM, $R > 0.5$) especially between the fresh mangrove and sea grass leaf litter.

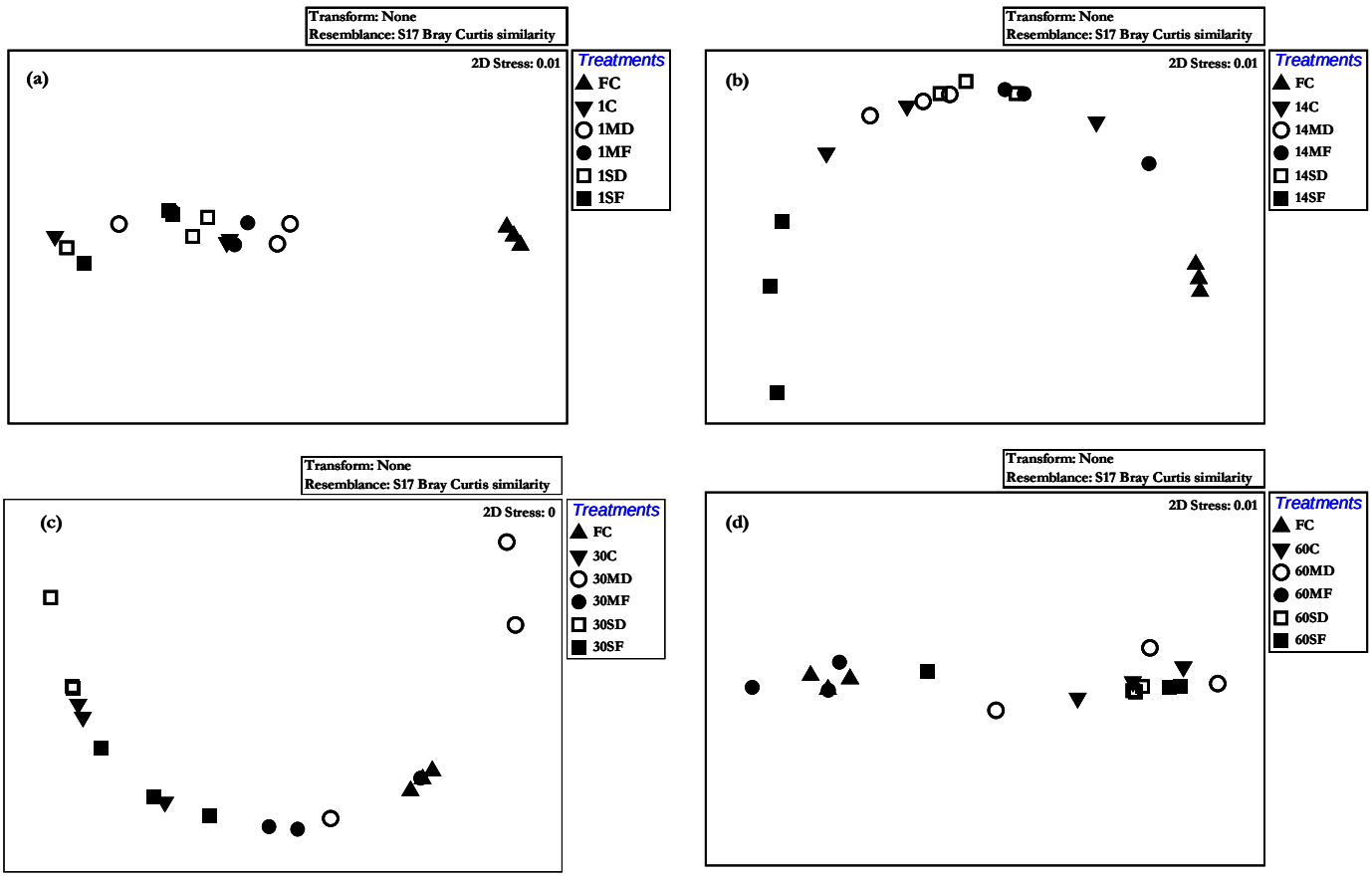

Figure 7.3a-d. nMDS on meiofauna community composition showing the affinities between food quality treatments on (a) day 1, (b) day 14, (c) day 30 and (d) day 60.

Table 7.2. ANOSIM pair wise comparisons between food quality treatments on each experimental day. FC; Field control, C; Experimental controls, MD; Mangrove decomposed leaves, MF; Mangrove Fresh leaves, SD: Sea grass decomposed leaves and SF; Sea grass fresh leaves. Global R in parentheses while * denotes significant comparisons.

Pairwise comparisons	**Experimental Day**			
	Day 1 R = 0.437	**Day 14** R = 0.63	**Day 30** R = 0.646	**Day 60** R = 541
FC and C	1	0.852*	1*	1*
FC and MD	1	1*	0.333	0.852*
FC and MF	1	0.778*	0.259	0.074
FC and SD	1*	1*	1*	1*
FC and SF	1*	1*	1*	0.778*
C and MD	0.037	0.111	0.852*	0.185
C and MF	0.037	0.037	0.815*	1*
C and SD	0.111	0.148	0.259	0.333
C and SF	0.037	0.519*	0.037	0.074
MD and MF	0.037	0.444	0.259	0.889*
MD and SD	0.037	0.037	0.926*	0.148
MD and SF	0.259	0.963*	0.741*	0.222
MF and SD	0.037	0.074	1*	1*
MF and SF	0.074	1*	0.593*	0.741*
SD and SF	0	1*	0.704*	0.333

7.2.3 Effect of time within food quality treatments on meiofauna densities and community composition

Figure 7.4 shows the effects of time within food quality treatments on meiofauna. There were overall significant time effects within the food quality treatments in meiofauna (ANOVA; df = 3, F = 50.307, $p < 0.05$) and nematode densities (ANOVA; df = 3, F = 51.367, $p < 0.05$). Both fresh and decomposed mangrove and sea grass leaves recorded significantly higher meiofauna and nematode densities on days 30 and 60 (ANOVA; Tukeys HSD, $p < 0.05$) compared to day 1 (Figs. 7.4a & 7.4b).

Similarly, nMDS analysis and ANOSIM on meiofauna community composition for each food treatment separately showed significant time effects (ANOSIM, $R > 0.5$) between day 1 and days 30 and 60 within the mangrove leaves treatment. The field control showed significant differences (ANOSIM, $R > 0.5$) with both fresh and decomposed mangrove leaves treatments on days 1 and 14 and with only the decomposed mangrove leaves on day 60 (Fig. 7.5a). The sea grass leaves (Fig. 7.5b) showed significant time effects between day 1 and days 14, 30 and 60 (ANOSIM, $R > 0.5$), while all experimental days were significantly different from the field control irrespective of the quality (ANOSIM, $R > 0.5$). These nMDS patterns show that after 60 days, only the fresh mangrove leaves could support a similar meiofauna community to that of the field control.

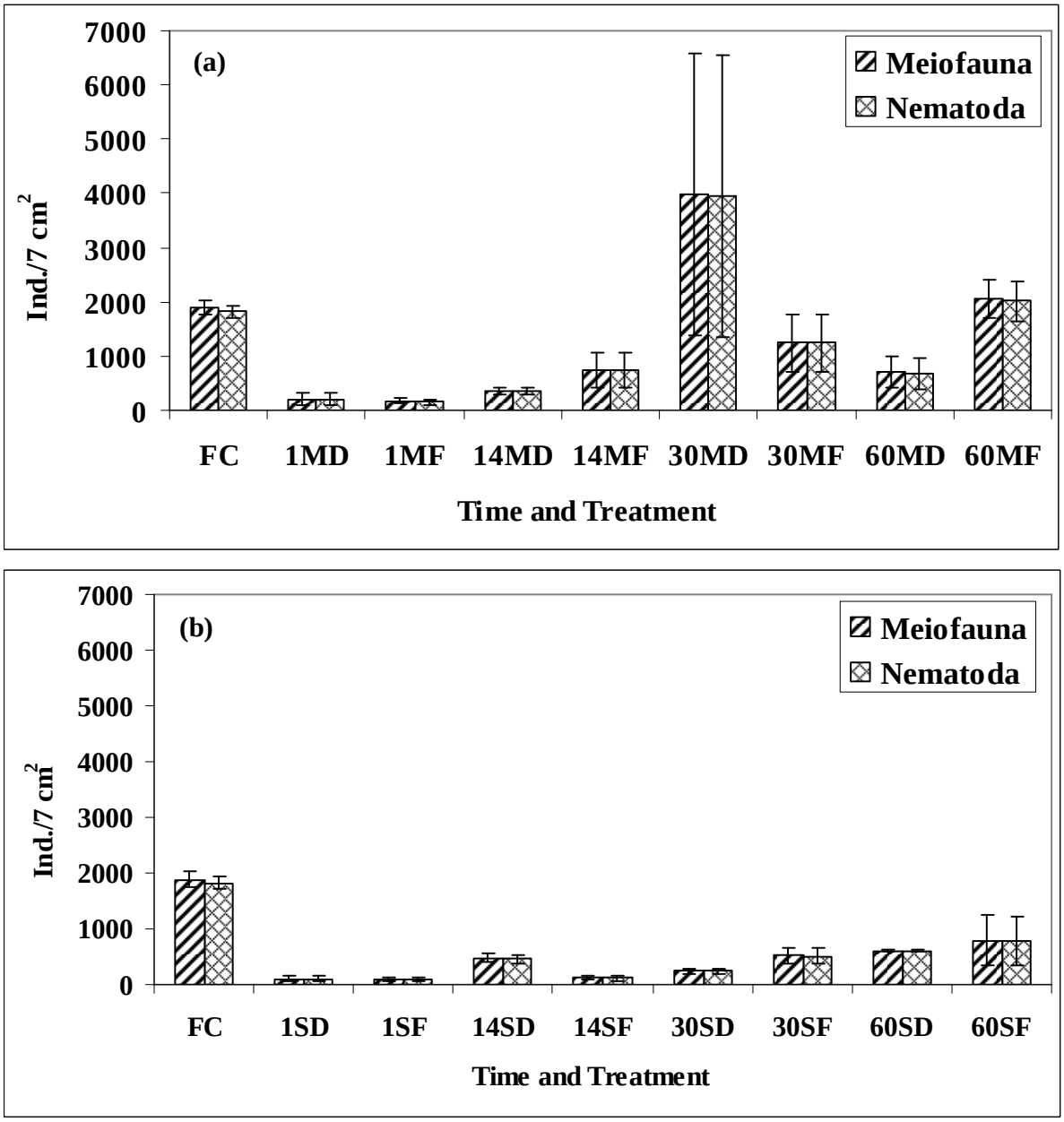

Figure 7.4. Densities (Mean ± SD, n = 3) of Meiofauna and Nematoda showing variations with time within food quality treatments from (a) mangrove leaf litter and (b) sea grass leaf litter treatments.

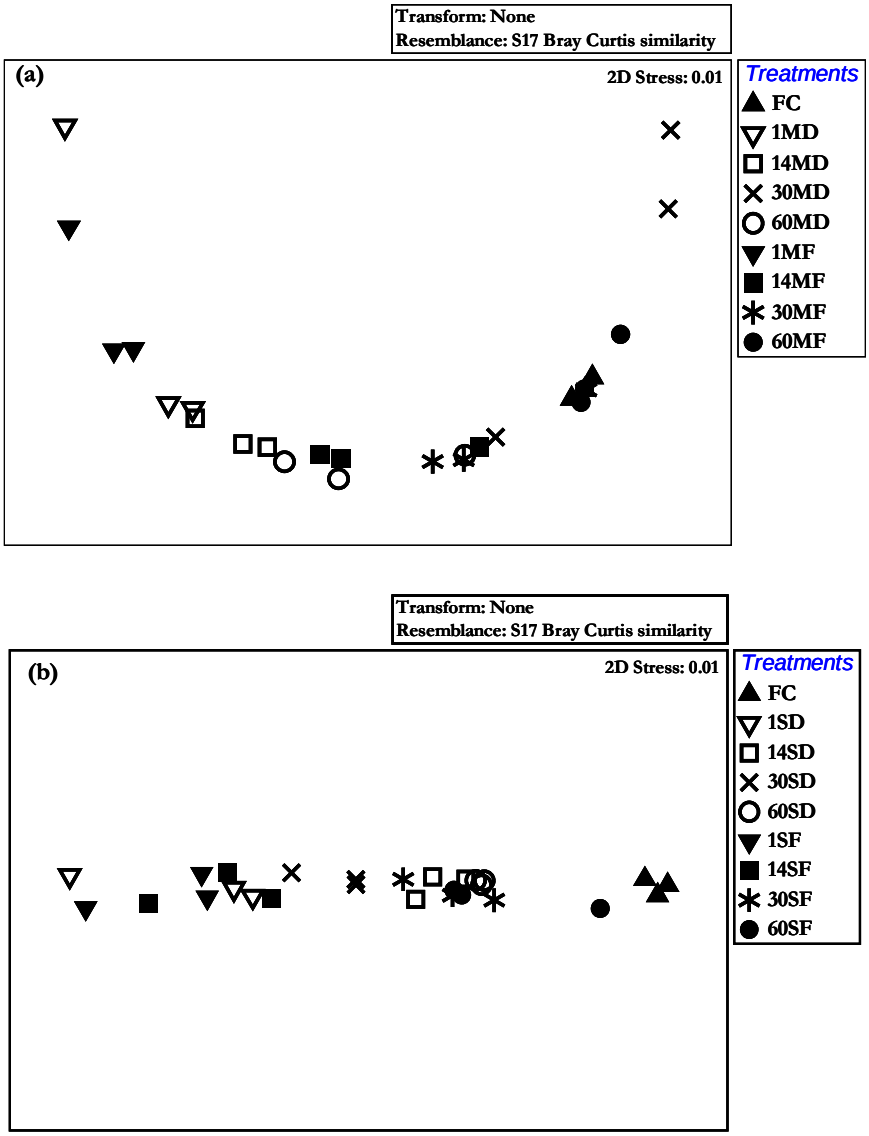

Figure 7.5. nMDS on meiofauna community showing the effect of time on the different food quality treatments in (a) mangrove leaf litter and (b) sea grass leaf litter treatments. FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed sea grass leaves.

7.2.4 Effect of food quality on nematode community assemblage

Table 7.3 shows the dominant nematode genera recorded from each treatment. A total of 90 nematode genera were recorded over the entire experimental period from all treatments. The decomposed mangrove leaves recorded 62 genera; the fresh sea grass leaves 55 genera, the decomposed sea grass leaves 52 genera and the fresh mangrove leaves 51 genera. The field controls recorded the lowest (28) nematode genera. The genus *Diplolaimelloides* was dominant in the fresh mangrove and sea grass leaves, while *Daptonema* dominated the decomposed mangrove and sea grass leaves. *Terschellingia* was the dominant genera in the field controls.

Table 7.3. Overall relative abundance of the dominant nematode genera (> 5 %) in each food quality treatment. FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves SF; fresh sea grass leaves and SD; decomposed sea grass leaves.

Treatments	**Dominant nematode genera abundance per treatment**
FC	*Terschellingia* (24 %), *Haliplectus* (11 %), *Halalaimus* (10 %)
MF	*Diplolaimelloides* (50 %), *Daptonema* (9 %), *Haliplectus* (7 %)
MD	*Daptonema* (25 %), *Diplolaimelloides* (10 %), *Terschellingia* (8 %), *Spilophorella* (8 %), *Halalaimus* (5 %), *Microlaimus* (5 %)
SF	*Diplolaimelloides* (19 %), *Daptonema* (14 %), *Theristus* (6 %), *Haliplectus* (6 %), *Terschellingia* (6 %), *Halalaimus* (6 %), *Spilophorella* (5 %)
SD	*Daptonema* (16 %), *Spilophorella* (12 %), *Haliplectus* (8 %), *Terschellingia* (6 %), *Diplolaimelloides* (5 %)

An nMDS analysis (Fig. 7.6) and ANOSIM (Table 7.4) showed no significant differences in nematode community assemblages between both fresh and decomposed mangrove and sea grass leaves (ANOSIM; $R < 0.5$) on day 1 (Fig 7.6a). However, significant differences in nematode community assemblages (ANOSIM, $R > 0.5$) were recorded between the fresh and decomposed mangrove leaves on day 14 (Fig. 7.6b), day 30 (Fig. 7.6c) and day 60 (Fig. 7.6d). The fresh and decomposed sea grass leaves only showed significant differences in nematode community assemblages on day 30 (ANOSIM, $R > 0.5$). The field control recorded significant differences in nematode community assemblages with all the food quality treatments on all experimental days (ANOSIM, $R > 0.5$).

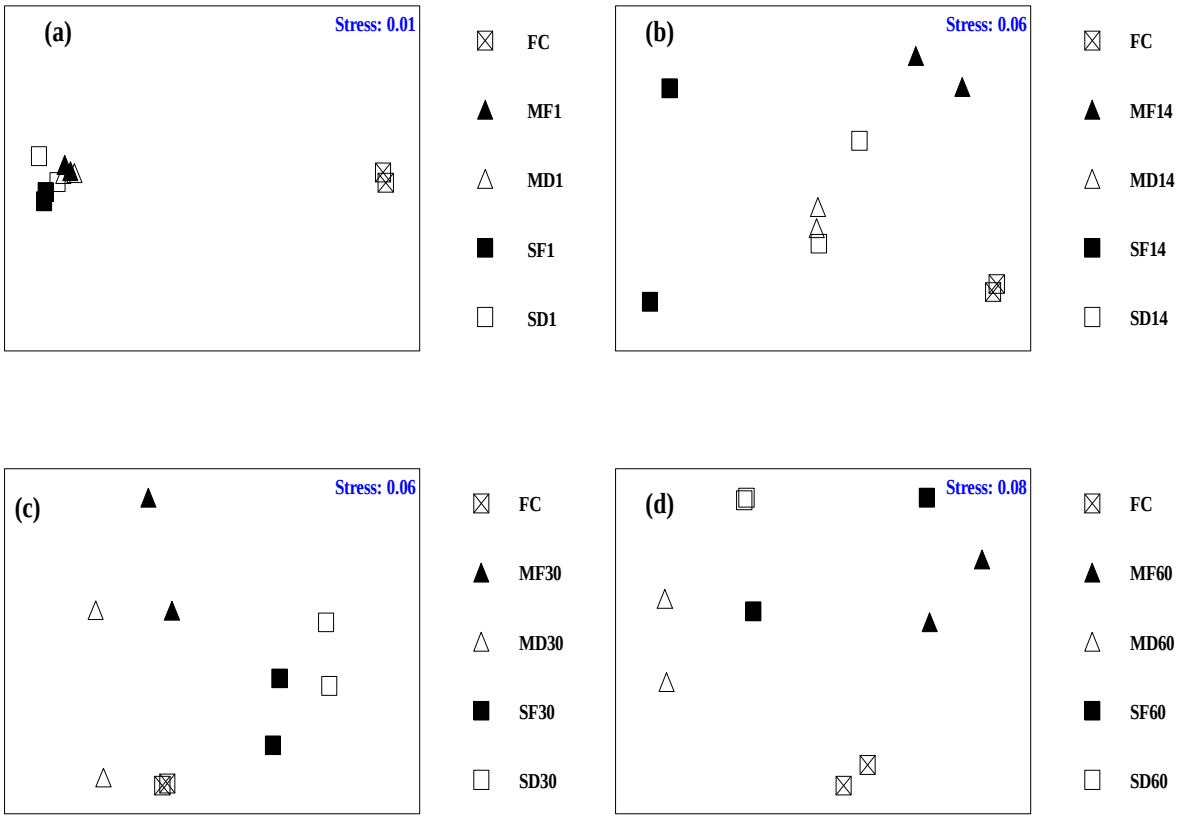

Figure 7.6. nMDS on non transformed nematode genera community assemblages data showing affinities between food quality treatments on (a) day 1, (b) day 14, (c) day 30 and (d) day 60. FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed seagrass leaves.

Table 7.4. Results of One-Way ANOSIM on nematode genera (Global R in parenthesis) using Bray-Curtis similarity between food quality treatments during the entire experimental period (Asterix (*) denotes significant differences, R>0.5). FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed sea grass leaves.

Pair wise comparisons	**Experimental days**			
	Day 1 (R=0.72)	**Day 14** (R=0.59)	**Day 30** (R=0.86)	**Day 60** (R=0.81)
FC and MD	1*	1*	0.5*	1*
FC and MF	1*	1*	1*	1*
FC and SD	1*	1*	1*	1*
FC and SF	1*	1*	1*	0.5*
MD and MF	-0.75	1*	0.5*	1*
SD and SF	-0.5	0.25	0.75*	0.25

SIMPER analysis (Table 7.5) showed that the dissimilarity between the fresh and the decomposed mangrove leaves on days 14 and 30 was mainly contributed by the genus *Daptonema* while the genus *Diplolaimelloides* contributed to the dissimilarities on day 60. The fresh mangrove leaves treatment recorded the highest density of *Daptonema* (101 Ind. /7cm^2) on day 14, while the decomposed mangrove leaves recorded the highest density (1237 Ind. /7 cm^2) on day 30. The fresh mangrove leaves treatment recorded the highest density of *Diplolaimelloides* (1193 Ind. /7 cm^2) on day 60. The dissimilarities between the sea grass leaves treatments on day 30 were attributed to the genera *Daptonema*, which was dominant in the fresh sea grass leaves (96 Ind. /7 cm^2) on day 30.

The dissimilarities between the field control and both fresh and decomposed sea grass leaves over the entire experimental period were explained by differences in abundances of the genus *Terschellingia*. Similarly, the dissimilarities between the field control and mangrove leaves on days 1 and 14 were explained by the genus *Terschellingia*. However, the genera *Daptonema* and *Diplolaimelloides* contributed to the discrimination between the field control and the mangrove leaves on day 30, while the genera *Terschellingia* and *Diplolaimelloides* were responsible for the differences on day 60. The genus *Daptonema* recorded the highest density (1237 Ind. /7 cm^2) in the decomposed mangrove leaves, while *Diplolaimelloides* recorded densities of 837 and 1193 Ind. /7 cm^2 on days 30 and 60 in the fresh mangrove leaves. No *Diplolaimelloides* was recorded in the field control, while *Daptonema* only recorded 3 Ind. /7 cm^2. The field controls recorded the highest density of the genus *Terschellingia* (439 Ind. /7 cm^2) compared to all the other food quality treatments. These differences in the dominant nematode genera between the different treatments point to the fact that they provided different habitat conditions/food for the nematodes.

Table 7.5. SIMPER lists showing the four main genera contributing to the Bray-Curtis dissimilarity (%) between treatments on each experimental day. FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed sea grass leaves.

Treatments compared	**Species contribution**			
	Day 1	**Day 14**	**Day 30**	**Day 60**
FC and MD	*Terschellingia* (24)	*Terschellingia* (25)	*Daptonema* (28)	*Terschellingia* (19)
	Haliplectus (10)	*Halalaimus* (10)	*Diplolaimelloides* (10)	*Haliplectus* (9)
	Halalaimus (9)	*Haliplectus* (7)	*Terschellingia* (5)	*Spilophorella* (9)
	Spilophorella (8)	*Spilophorella* (6)	*Spilophorella* (5)	*Halalaimus* (9)
FC and MF	*Terschellingia* (24)	*Terschellingia* (22)	*Diplolaimelloides* (33)	*Diplolaimelloides* (43)
	Haliplectus (10)	*Halalaimus* (9)	*Terschellingia* (16)	*Terschellingia* (12)
	Halalaimus (10)	*Spilophorella* (9)	*Halalaimus* (7)	*Halalaimus* (6)
	Spilophorella (8)	*Haliplectus* (6)	*Spilophorella* (6)	*Spilophorella* (4)
FC and SD	*Terschellingia* (24)	*Terschellingia* (24)	*Terschellingia* (23)	*Terschellingia* (23)
	Haliplectus (10)	*Halalaimus* (10)	*Haliplectus* (11)	*Haliplectus* (10)
	Halalaimus (10)	*Haliplectus* (7)	*Halalaimus* (10)	*Halalaimus* (8)
	Spilophorella (9)	*Spilophorella* (7)	*Spilophorella* (8)	*Spilophorella* (7)
FC and SF	*Terschellingia* (24)	*Terschellingia* (23)	*Terschellingia* (24)	*Terschellingia* (21)
	Haliplectus (10)	*Haliplectus* (11)	*Haliplectus* (10)	*Diplolaimelloides* (13)
	Halalaimus (10)	*Halalaimus* (10)	*Spilophorella* (9)	*Halalaimus* (8)
	Spilophorella (9)	*Spilophorella* (9)	*Halalaimus* (7)	*Spilophorella* (8)
MD and MF	*Spilophorella* (16)	*Daptonema* (12)	*Daptonema* (28)	*Diplolaimelloides* (53)
	Halalaimus (5)	*Microlaimus* (11)	*Diplolaimelloides* (14)	*Terschellingia* (5)
	Haliplectus (5)	*Spilophorella* (9)	*Terschellingia* (7)	*Haliplectus* (4)
	Subsphaerolaimus (4)	*Eumorpholaimus* (7)	*Spilophorella* (6)	*Daptonema* (4)
SD and SF	*Actinonema* (13)	*Haliplectus* (17)	*Daptonema* (12)	*Diplolaimelloides* (26)
	Spilophorella (10)	*Spilophorella* (13)	*Halalaimus* (11)	*Haliplectus* (8)
	Bathylaimus (7)	*Daptonema* (7)	*Sabatieria* (5)	*Theristus* (6)
	Theristus (6)	*Terschellingia* (6)	*Microlaimus* (5)	*Terschellingia* (5)

7.2.5 Effect of time within food quality treatments on nematode community composition

The ordinations of nematode communities' data with time are shown in Figure 7.7. Nematode community assemblages showed significant changes with time within food quality treatments.

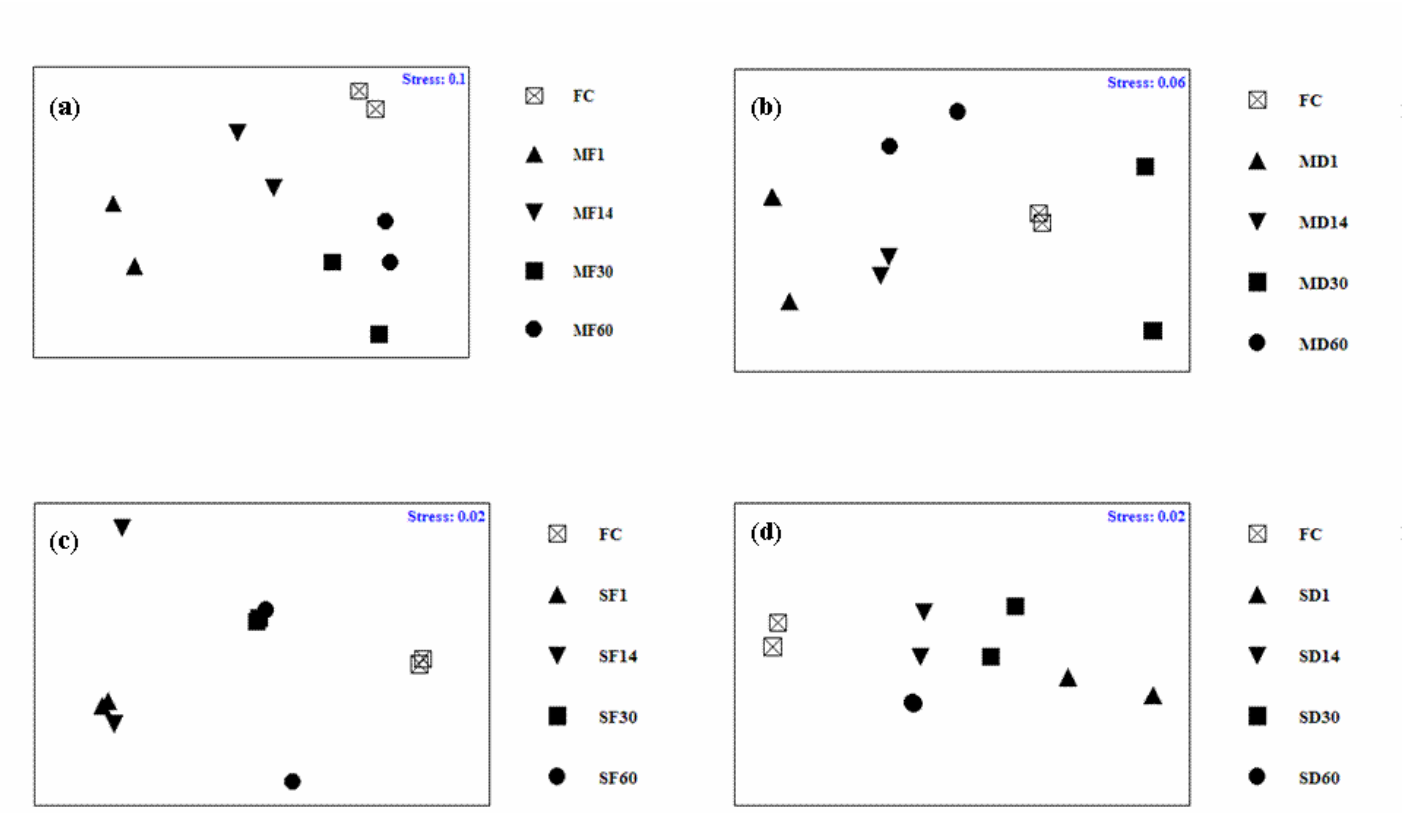

Figure 7.7. nMDS on nematode genera community assemblage from the different food quality treatments showing the affinities between time; (a) MF, (b) MD (c) SF and (d) SD on all experimental days. FC; field controls, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed seagrass leaves.

The fresh mangrove leaves (Fig. 7.7a) showed significant time differences in nematode community assemblage between all days except between days 30 and 60. The decomposed mangrove leaves (Fig. 7.7b) showed significant time effects in nematode community assemblage between all the experimental days. Only day 1 recorded significant time effects with days 30 and 60 in the fresh sea grass leaves (Fig. 7.7c), while all experimental days showed significant differences in nematode community assemblage in the decomposed sea grass leaves (Fig. 7.7d). These time effects within food quality treatments were confirmed by ANOSIM (Global $R > 0.5$; Table 7.6). The observed significant time effects in nematode community assemblages between all days in the decomposed mangrove and sea grass leaves treatments shows that these leaves probably offered a more diverse habitat for re-colonisation by nematodes compared to the fresh leaves. The lack of significant differences between day 30 and 60 in the fresh mangrove leaves confirms the earlier results on food type effects, which showed that after 30 days of the experiment, no new genera re-colonised the mangrove leaves.

The field controls showed significant differences in nematode community assemblage with all experimental days in the fresh and decomposed mangrove leaves and in the decomposed sea grass leaves (ANOSIM, $R \geq 0.5$; Table 7.6). However, the fresh sea grass leaves did not record a significantly different nematode community assemblage on day 60 from the field control (ANOSIM, $R < 0.5$). These differences between the field control and experimental days within each food quality treatment in nematode community assemblage, shows that leaf litter addition provided new and different habitats for nematode genera colonisation compared to the natural mangrove sediments.

Table 7.6. Results of ANOSIM on nematode community using Bray-Curtis similarity between experimental days within each food quality treatment. Global R values are shown in parenthesis while * denotes significant comparisons (R > 0.5). FC; field control, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed sea grass leaves.

Comparisons	**MF** (R = 0.86)	**MD** (R = 0.84)	**SF** (R = 0.55)	**SD** (R = 0.91)
FC and Day 1	1*	1*	1*	1*
FC and Day 14	1*	1*	1*	1*
FC and Day 30	1*	0.5*	1*	1*
FC and Day 60	1*	1*	0.25	1*
Day 1 and Day 14	1*	0.5*	0	1*
Day 1 and Day 30	1*	1*	1*	0.75*
Day 1 and Day 60	1*	1*	1*	1*
Day 14 and Day 30	1*	1*	0	1*
Day 14 and Day 60	1*	1*	0.25	0.5*
Day 30 and Day 60	-0.25	1*	-0.5	1*

SIMPER analysis (Table 7.7) showed that different nematode genera characterised experimental days within each food quality treatment. The fresh mangrove leaves were characterised by the genera *Spilophorella*, *Daptonema* and *Diplolaimelloides* while the genera *Spilophorella*, *Daptonema* and *Terschellingia* were the dominant genera in the decomposed mangrove leaves during the course of the experiment. The genera *Haliplectus*, *Daptonema* and *Theristus* characterised the fresh sea grass leaves, while *Terschellingia*, *Haliplectus* and *Daptonema* characterised the decomposed sea grass leaves over the experimental period.

Similarly, different nematode genera contributed to the observed dissimilarities between experimental days within each food quality treatments (Table 7.8). The differences between days within both fresh mangrove and seagrass leaves were contributed by the genera *Daptonema* and *Diplolaimelloides*, while the genera *Haliplectus*, *Daptonema*, *Microlaimus* and *Spilophorella* explained most of the differences between experimental days within the decomposed mangrove and sea grass leaves.

Table 7.7. SIMPER lists showing the two main nematode genera contributing to the Bray-Curtis similarity (%) within each food quality on each experimental day. FC; field control, MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed seagrass leaves.

Treatment	**Nematode genera contribution**			
	Day 1	**Day 14**	**Day 30**	**Day 60**
FC	*Terschellingia* (37) *Halalaimus* (14)			
MF	*Spilophorella* (26) *Terschellingia* (11)	*Daptonema* (21) *Microlaimus* (17)	*Diplolaimelloides*(89) *Terschellingia* (4)	*Diplolaimelloides*(71) *Paralinhomoeus* (9)
MD	*Spilophorella* (21) *Haliplectus* (16)	*Spilophorella* (36) *Haliplectus* (36)	*Daptonema* (48) *Terschellingia* (9)	*Terschellingia* (18) *Paralinhomoeus* (18)
SF	*Haliplectus* (10) *Spilophorella* (9)	*Daptonema* (23) *Subsphaerolaimus*(19)	*Daptonema* (15) *Halalaimus* (14)	*Theristus* (23) *Daptonema* (23)
SD	T*erschellingia* (12) *Spilophorella* (12)	*Haliplectus* (31) *Spilophorella* (28)	*Terschellingia* (25) *Spilophorella* (24)	*Daptonema* (24) *Spilophorella* (9)

Table 7.8. SIMPER lists showing the four main genera contributing to the Bray-Curtis dissimilarity (%) between experimental days within food quality treatments. MF; fresh mangrove leaves, MD; decomposed mangrove leaves, SF; fresh sea grass leaves and SD; decomposed seagrass leaves.

Pairwise comparisons	**Nematode genera contribution to dissimilarity**			
	MF	**MD**	**SF**	**SD**
1 and 14	*Daptonema* (12)	*Haliplectus* (22)	*Subsphaerolaimus* (5)	*Haliplectus* (17)
	Microlaimus (12)	*Spilophorella* (13)	*Terschellingia* (4)	*Spilophorella* (12)
	Haliplectus (9)	*Diplolaimelloides* (8)	*Deontolaimus* (4)	*Daptonema* (6)
	Eumorpholaimus (7)	*Terschellingia* (6)	*Spirinia* (4)	*Terschellingia* (6)
1 and 30	*Diplolaimelloides*(66)	*Daptonema* (31)	*Daptonema* (8)	*Daptonema* (15)
	Daptonema (11)	*Diplolaimelloides*(11)	*Halalaimus* (8)	*Terschellingia* (14)
	Haliplectus (6)	*Terschellingia* (8)	*Sabatieria* (5)	*Spilophorella* (6)
	Microlaimus (2)	*Spilophorella* (6)	*Microlaimus* (4)	*Actinonema* (6)
1 and 60	*Diplolaimelloides* (60)	*Microlaimus* (10)	*Diplolaimelloides*(14)	*Daptonema* (23)
	Paralinhomoeus (6)	*Terschellingia* (9)	*Daptonema* (8)	*Paracanthonchus* (8)
	Terschellingia (6)	*Paralinhomoeus* (8)	*Theristus* (6)	*Spilophorella* (6)
	Haliplectus (5)	*Pseudochromadora*(7)	*Haliplectus* (6)	*Diplolaimelloides* (6)
14 and 30	*Diplolaimelloides* (52)	*Daptonema* (32)	*Daptonema* (8)	*Haliplectus* (19)
	Daptonema (9)	*Diplolaimelloides* 11)	*Halalaimus* (7)	*Spilophorella* (9)
	Haliplectus (5)	*Terschellingia* (7)	*Microlaimus* (5)	*Daptonema* (6)
	Microlaimus (4)	*Halalaimus* (6)	*Sabatieria* (5)	*Terschellingia* (6)
14 and 60	*Diplolaimelloides* (55)	*Spilophorella* (10)	*Diplolaimelloides*(15)	*Daptonema* (17)
	Terschellingia (5)	*Microlaimus* (10)	*Theristus* (8)	*Haliplectus* (10)
	Paralinhomoeus (4)	*Haliplectus* (8)	*Daptonema* (7)	*Paracanthonchus* (7)
	Microlaimus (3)	*Paralinhomoeus* (8)	*Haliplectus* (7)	*Pseudochromadora*(4)
30 and 60	*Diplolaimelloides* (35)	*Daptonema* (31)	*Diplolaimelloides*(11)	*Daptonema* (17)
	Daptonema (10)	*Diplolaimelloides*(11)	*Haliplectus* (6)	*Paracanthonchus* (8)
	Paralinhomoeus (8)	*Spilophorella* (7)	*Theristus* (6)	*Terschellingia* (5)
	Terschellingia (8)	*Terschellingia* (6)	*Terschellingia* (5)	*Diplolaimelloides* (5)

7.2.6 Effect of food quality on nematode community diversity

Figure 7.8 shows the changes in nematode genera richness (Fig. 7.8a) and Shannon diversity index (Fig. 7.8b) with time. Over the entire experimental period, the decomposed seagrass leaves recorded the highest nematode genera richness and Shannon diversity index (20 ± 2 and 2.6 ± 0.1, respectively), while the fresh mangrove leaves recorded the lowest nematode genera richness and Shannon diversity index (16 ± 6 and 2 ± 0.8). However, no significant effect of food quality was observed in nematode genera richness (S) and Shannon diversity index (H') on all experimental days (ANOVA, $p > 0.05$). Similarly, no significant time effect was observed in all the food quality treatments (ANOVA, $p > 0.05$), neither was the interaction between food qualities and time significant. Additionally, the field control showed no significant differences in nematode genera richness and Shannon diversity with all the food quality treatments on each of the experimental days, and with time in each of the food quality treatments (ANOVA, Tukeys HSD, $p > 0.05$). This shows that the quality of the mangrove and sea grass leaves had no influence on the number of nematode genera recolonising the leaves on any experimental day. The lack of significant differences between the field control and all the food quality treatments shows that the nematode genera colonising the experimental units were from the surrounding mangrove sediments.

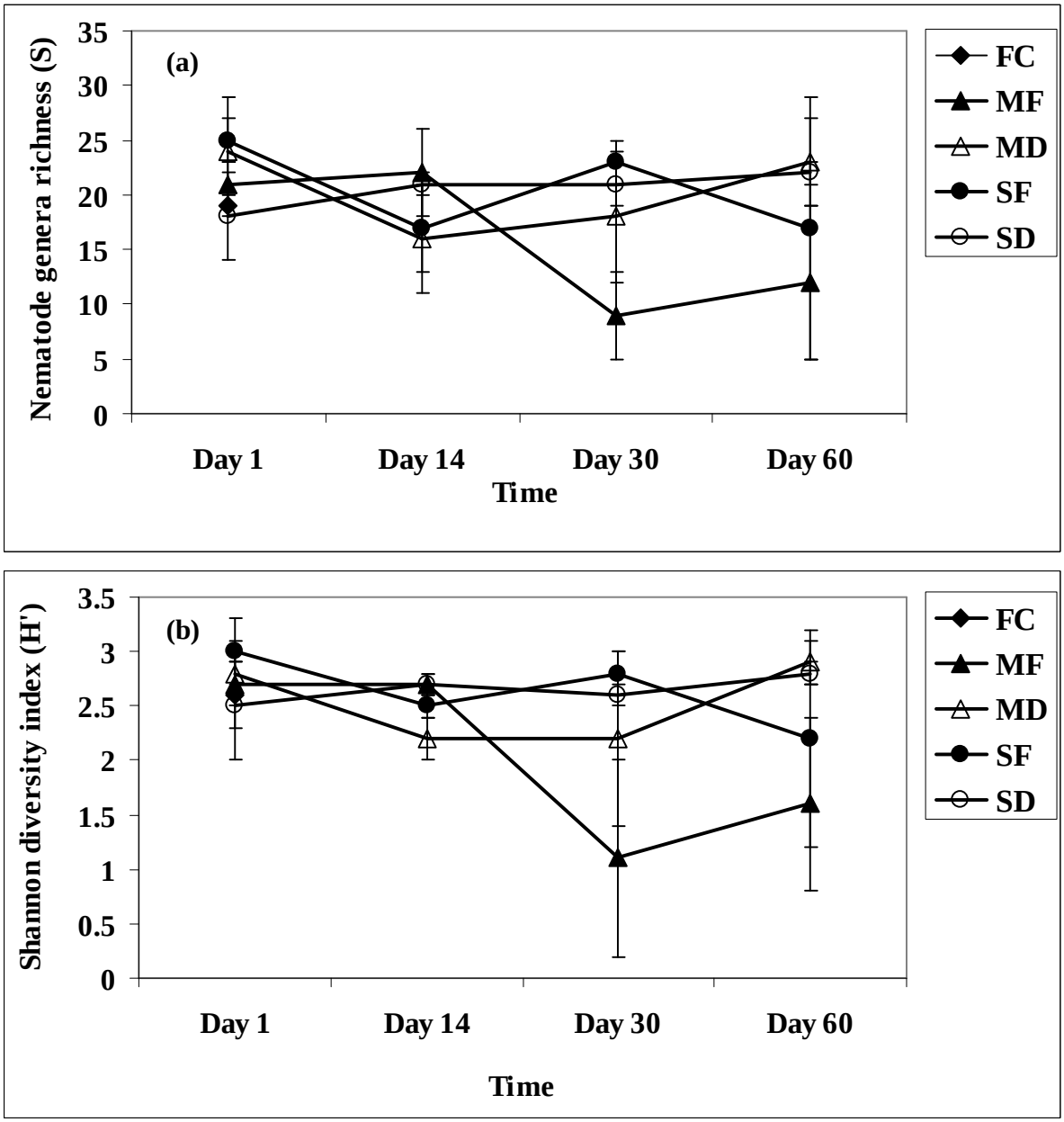

Figure 7.8. Changes in (a) nematode genera richness and (b) Shannon diversity index with time. FC; field control, C; experimental control, S; sea grass leaf litter and M; mangrove leaf litter.

7.2.7 Effect of food quality on nematode trophic structure

The quality of food showed an effect on nematode feeding groups over the entire experimental period (Fig. 7.9). Non-selective deposit feeders (1B) were the dominant feeding group in the fresh mangrove and seagrass leaves (55 % and 39 %, respectively). Epistrate feeders (2A) dominated the decomposed mangroves and seagrass leaves (34 % and 33 %, respectively).

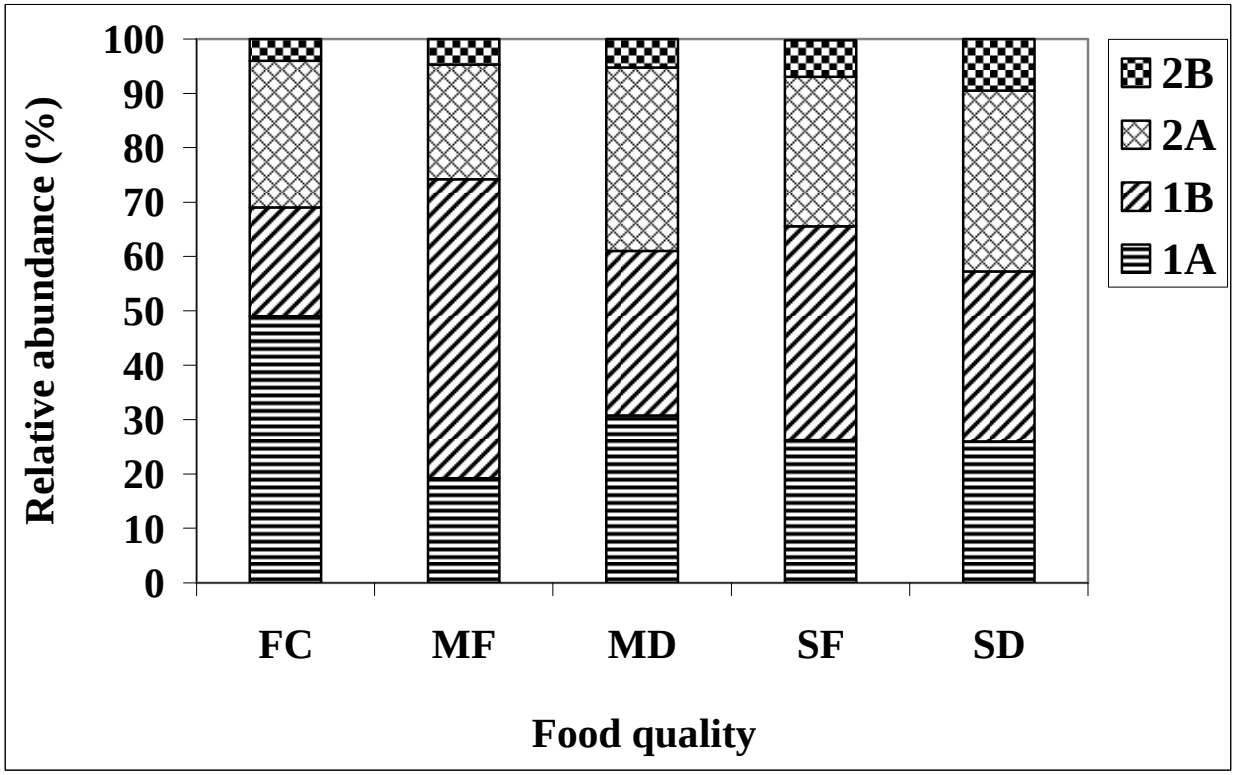

Figure. 7.9. Overall averaged relative abundance (%) of nematode trophic groups in the field control (FC), the fresh mangrove leaves (MF), decomposed mangrove leaves (MD), fresh seagrass leaves (SF) and decomposed sea grass leaves (SD).

Figure 7.10 shows the succession in nematode trophic groups with time within the different food quality treatments. Epistrate feeders (2A) were the dominant feeding group on day 1, while non-selective deposit feeders (1B) dominated the fresh mangrove leaves treatment from day 14 up to day 60 (Fig. 7.10a). Selective deposit feeders (1A) dominated the decomposed mangrove leaves on day 14, while non-selective deposit feeders (1B) and epistrate feeders (2A) were the dominant feeding groups on days 30 and 60 (Fig 7.10b). Epistrate feeders were most abundant on day 1 in the fresh sea grass leaves, while non selective deposit feeders characterised days 30 and 60 (Fig 7.10c). The decomposed seagrass leaves recorded more epistrate feeders on day 1, selective deposit feeders on day 14 and non selective deposit feeders on day 60 (Fig 7.10d). Selective deposit feeders (1A) were the dominant feeding group in the field control (49%). This succession in nematode feeding groups with time shows that there are changes in the habitat conditions provided by the different food quality treatments as decomposition progresses.

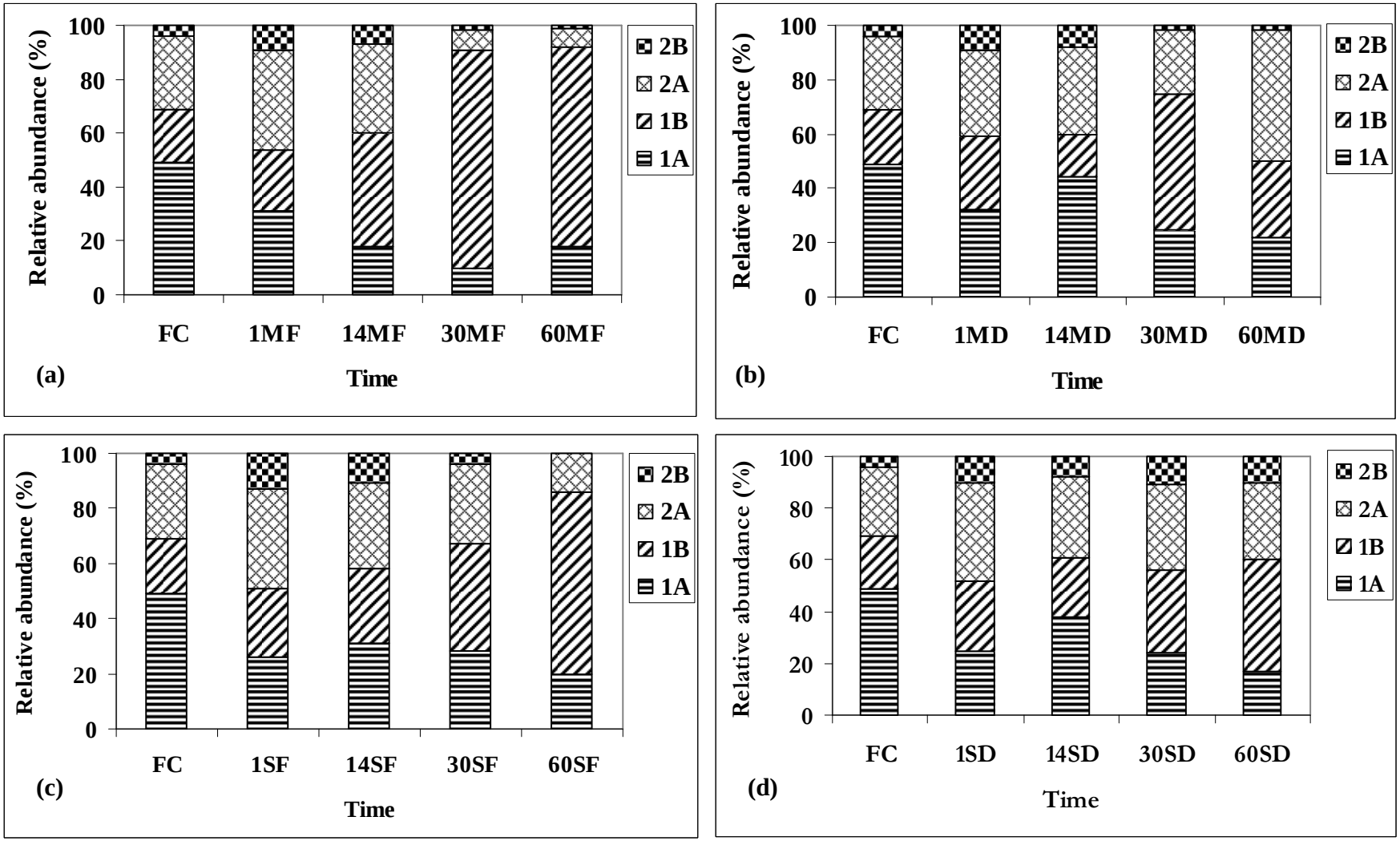

Figure 7.10. Variation in relative abundance of nematode trophic groups with time in (a) fresh mangrove leaves; MF (b) decomposed mangrove leaves; MD (c) fresh seagrass leaves (SF) and (d) decomposed seagrass leaves; (SD).

7.3 Discussion

The differences in meiofauna and nematode densities between the fresh and decomposed mangrove leaves were not pronounced. Infact, the effect of food type was re-emphasised in the analysis on food quality in the mangrove leaves. Similarly, nematode communities between the fresh and decomposed mangrove leaves were also not different. Though no significant differences between food quality was observed, the decomposed mangrove leaves recorded higher densities of meiofauna and nematodes compared to the fresh ones. This was however up to day 30 when the fresh mangrove leaves attracted higher densities of meiofauna and nematodes than the decomposed leaves. The experiment further reemphasizes that meiofauna and nematode re-colonisation of mangrove sediments is dependent on food type (detritus source) and that the preference for mangrove detritus by meiofauna is greater than for sea grass. The study also shows that there is a succession of different nematode genera during the incubation of the experimental material as shown by the different trophic groups recorded.

The lack of significant differences between the fresh and decomposed leaves means that the decomposition state of mangrove leaves may not influence meiofauna and nematode colonisation. However, this could have been due to the short duration (4 days) the leaves were decomposed at the start of the experiment by being buried in the sediment. Therefore, more work needs to be done especially employing mangrove leaves which have been decomposed for a longer period of time.

7.4 Conclusions

From the results obtained, meiofaunal colonisation of mangrove sediments is influenced by the presence and type of organic matter, and that mangrove detritus is the preferred source of organic matter within mangrove sediments. The quality of mangrove detritus may not have a great impact on meiofauna and nematode re-colonisation rates. Nematoda is the dominant taxon within mangrove sediments and that the density of meiofauna and nematodes increases with mangrove leaf litter decomposition. The succession in nematode community assemblage and trophic groups within the mangrove leaf litter is an indication of the changes in the utilisation of the litter as a source of food or a habitat by nematode genera. These changes reflect the changes in the leaf litter chemistry as shown by the changes in CN ratio, and/or microbial community. This experiment confirms the earlier studies which recorded differences in meiofauna densities and nematode genera assemblages between degraded and forested *R. mucronata* mangrove ecosystems. It ascertains that the differences observed are as a result of differences in organic matter levels and that this organic matter is mainly derived from mangrove leaves.

CHAPTER EIGHT

General Discussion, Conclusions and Recommendations

8.1 General Discussion

8.1.1 Sediment physical characteristics

The measured sediment physical characteristics did not only show differences between the forested and the degraded sites, but also among the reforested sites depending on the age of the forest. The high organic matter content (Fig. 3.1) in the natural site compared to the 10 years reforested site is as a result of undecomposed organic matter which has accumulated over the years. The lower TOM levels recorded from the 10 and 5 years reforested sites compared to the natural site shows the effect of forest age on TOM, with the older natural forest recording higher TOM levels. Denuded (deforested) mangrove areas are more exposed to wave energy due to lack of vegetation cover, which makes them less efficient in slowing down incoming and outgoing tides. This leads to increased sediment resuspension and erosion of detrital material by tidal currents, leading to reduced organic matter content of the sediments.

The differences in silt/clay (Fig. 3.2) content between the natural and the 10 years reforested sites is linked to the root network which reduces the energy of tidal currents and hence resuspension of fine sediment materials (Wolanski et al., 1992). The 10 years reforested site had a denser root network than the natural site which is dominated by mature trees having big prop roots. The degraded site lacking sediment holding structures recorded the highest sand content.

The continuous tree canopy observed in the 10 years reforested site ensures effective shading of the sediments from solar radiation. However, in the natural site, canopy gaps were evident due to smothering of undergrowth by the big mature trees. These canopy gaps allowed penetration of solar radiation on to the sediment surface leading to relatively higher temperatures in the natural site compared to the 10 years reforested site. Similarly, lack of or reduced canopy cover in the degraded and the 5 years reforested sites results in high evaporation, which explains the high temperature and salinity recorded from these sites. Similarly, the cooler conditions in the natural and the 10 years reforested sites due to canopy cover promotes sediment phytoplankton and other microbial growth, which are responsible for the observed high chlorophyll *a* and CN ratio observed in these sites. However, the exposure of sediments in the degraded and the 5 years reforested sites due to canopy removal, leads to increased temperature and salinity. This high temperature and salinity may not be favourable for microphytobenthic community growth and explains the low Chlorophyll *a* and CN ratio recorded from the degraded site.

8.1.2 Macrofauna

A total of 12 macro-endobenthic taxa (Table 3.1) were recorded during this study. The density and number of macro-endofauna taxa were highest in the natural site and lowest in the 5 years reforested and the degraded sites. Netto and Galluci (2003) have shown that the patterns of macrofauna densities and community assemblage in mangroves vary in relation to sediment grain size and organic matter content, with organic rich silty sediments recording the highest macrofauna densities. The complex prop root system in the forested mangrove sites, combined with the availability of leaf litter, provides enhanced resource availability for benthic fauna especially for nematodes and oligochaetes. However, the

degraded and the 5 years reforested sites which recorded organic matter poor and sandier sediments recorded the lowest macrofauna densities. Additionally, sediment temperature, salinity and pH also influence the abundance of mangrove benthic fauna (Ingole & Parulekar, 1998). Sediment exposure in deforested mangrove areas increases sediment temperature, which consequently reduces sediment water content and increases salinity. These changes increase environmental stress on the benthic fauna (Sasekumar, 1994) which kills or limits the growth of microflora in addition to changing the chemical status of organic materials, which are important media for microbial growth (Mfilinge et al., 2002). This explains the low densities on macro-endobenthos recorded in the 5 years reforested and degraded sites, which are more exposed and recorded the highest temperature and salinity. The total number of taxa and average densities of macro-endofauna in the 10 years reforested site was also higher than in the 5 years reforested and degraded sites. This shows that the restoration of the mangrove forests has led to the recolonisation of sediment associated macro-endofauna, which may suggest ecosystem function recovery. However, this re-colonisation seems to be forest age dependent and may take longer than 10 years for a complete recovery to the natural ecosystem state to be achieved.

8.1.3 Meiofauna

Overall, 15 meiofauna taxa were recorded during the current study (Table 4.1). The natural and the 10 years reforested sites recorded 9 taxa each, while the degraded and the 5 years reforested sites recorded 8 and 7 taxa, respectively. The natural and the 10 years reforested sites which recorded the highest silt/clay content (silt fraction > 50 %) and TOM also recorded the highest densities of meiobenthos especially Nematoda. The complex system

of pneumatophores in the natural and the 10 years sites, coupled with the availability of leaf litter provides an enhanced food source and habitat for benthic fauna. Sediment type and organic matter may also influence meiofauna through the availability of food resources via the detrital food web, where sediment infauna feed on the microflora associated with decomposing detrital material (Skilletter & Warren, 2000). These microflora include bacteria, microalgae, protozoa and fungi (Gwyther, 2003). This explains the high densities of meiofauna recorded in the natural and the 10 years reforested sites which recorded high TOM levels. The high TOM levels ensure that these sites provide several opportunities for meiofauna colonisation interms of food and habitats.

There have been no studies on the benthic meiofauna in restored Kenyan mangrove forests although restoration started 15 years ago. Thus this study is the first to document meiofaunal community assemblages in restored mangrove forests along the Kenyan coast. The study shows a clear separation of the restored *R. mucronata* forest stands of different ages (5 and 10 years), based on the meiofauna taxa community composition. However, the differences in meiofauna community assemblages between the natural and the 10 years reforested sites are not significant despite the differences in environmental characteristics (such as TOM). This shows that the differences in TOM, salinity and temperature may have no effect on the meiobenthos community composition between the two sites, and that meiofauna may be controlled a complex of parameters. It is also evident that meiofauna re-establish between 5-10 years of reforestation.

8.1.4 Nematofauna

Nematodes are very diverse within the studied mangrove sediments, with a total of 76 genera belonging to 24 families that were recorded (Appendix 1). The nematode density (Fig. 5.3) and community composition (Fig. 5.5) was not different between the natural and the 10 years reforested sites, despite the different levels of TOM recorded in both areas. These similarities between the natural and the 10 years reforested sites can be linked to the fact that the supply of fresh organic material as food for the benthos, as reflected in chl. *a* concentrations and CN ratio's (Fig. 3.4a&b), is more or less equal in both the 10 years reforested and the natural sites. The differences between the degraded site and both the natural and the 10 years reforested sites indicate the effect of human activities (mangrove clear felling) on the structure, function and biodiversity of mangrove ecosystems. Mangrove clear felling removes vegetation cover exposing the sediments to tidal erosion which results to removal of the fine sediments and detritus, since these are easily resuspended by tidal currents. The dense root network in the natural and the 10 years reforested sites ensures that tidal currents are slowed down and resuspension is reduced (Wolanski et al., 1992), leading to fine sediment and organic matter accumulation.

The high levels of TOM in the natural and the 10 years reforested sites is also associated with high levels of detritus and associated micro-organisms. This is responsible for the high relative abundance of deposit feeders recorded in these sites (Fig. 5.7). However, the degraded site which recorded the highest sand content, showed the highest proportion of epistrate feeders. Generally, epistrate feeders characterise larger grain size sediments

which favour the growth of microphytobenthos, while deposit feeders dominate in fine sediments having high levels of detritus material (Giere, 1993). Additionally, the natural site recorded the highest Index of Trophic Diversity (ITD) but not different from the 10 years reforested site. This shows that in both systems, the four trophic groups were represented in equal proportions.

The genus *Terschellingia* is a low oxygen consumer and is usually abundant in muddy sediments rich in organic matter (Schratzberger & Warwick, 1998a, 1998b). Therefore, its dominance in both the upper and the lower sections in the natural and the 10 years reforested sites (Fig. 5.12) show its potential to exploit organically rich but oxygen poor habitats. The genera *Paracanthonchus* being an epistrate feeder, was abundant in the degraded site and could be related to the availability of microphytobenthos especially diatoms. *Metachromadora* on the other hand is an omnivore/predator and has been shown to burrow deeper especially in sandy sediments hence has a better competitive ability especially in search of food (Long & Othman, 2005).

8.1.5 Effect of food type and quality field experiments

The field experiments have shown that food availability and the type of food (organic matter) affects meiofaunal colonisation of mangrove sediments since organically enriched sediments recorded much higher densities compared to the experimental controls. Additionally, mangrove leaves are the preferred detrital source within mangrove sediments as shown by the much higher colonisation intensity than in the sea grass leaves and the diatom treatments (Fig. 6.1). The type of sediment seems to have a minor or no

effect on meiofauna colonisation (Fig. 6.16), while diatoms do not seem to form an important food source for nematodes within mangrove sediments as shown by the low $\delta^{13}C$ uptake rates (Fig. 6.14) and low densities of nematodes in the diatom treatments (Fig. 6.15).

The study also shows that there is a succession of different nematode genera and nematode feeding groups during the incubation of the experimental material, which coincides with the decomposition of the leaf litter. Gee and Sommerfield (1997) showed that meiofaunal community development is affected and controlled by the changes in leaf litter chemistry during decomposition and the subsequent successional development of the microflora community. Therefore, decomposition may have increased the attractiveness of mangrove leaves, which can be supported by the decrease in CN ratio with time. A low CN ratio means increased nutritional value of detritus as the nitrogen content is high (Skov & Hartnoll, 2002). This makes the detritus become progressively more conducive as a food source or habitat for benthic organisms and notably diverse nematode genera.

8.2 General conclusions

The current study has shown that;

- Mangrove ecosystem degradation leads to profound changes in the habitat conditions in terms of sediment physical characteristics. These habitat changes lead to a strongly impoverished macrofauna, meiofauna and nematode community in terms of density, community composition and diversity.

- Mangrove reforestation modifies sediment conditions leading to partial recovery of the ecological functions such as faunal colonisation. This is through alteration of the physico-chemical conditions of the sediments by making organic matter available as mangrove leaf litter. Decomposing mangrove leaf litter attracts bacteria, fungi and other microphytobenthos which have been shown to provide food to benthic fauna.
- Reforestation also reduces sediment resuspension through the trapping ability of the established vegetation, thereby ensuring accumulation of silt/clay sediments which are favourable for benthic fauna colonisation. The established canopy cover also reduces surface sediments temperature and ultimately salinity through shading. This reduces environmental stress and therefore encourages faunal colonisation.
- Restored mangrove forests are gradually tending towards becoming ecologically similar to the natural forests. However, this may take longer than 10 years as shown by the differences in sediment characteristics as well as macro-endofauna densities and community composition between the natural and the reforested mangrove areas.
- Despite the slow recovery of the habitat 10 years after restoration, as shown by depletion in the fine organic rich sediment fraction and macrofauna, the meiofauna as well as nematode densities and community composition have mainly re-established. This shows that meiofauna and nematode community recolonisation takes place between 5-10 years post reforestation.
- The genera *Terschellingia* and *Pierickia* are typical of the natural and the 10 years reforested sites and hence characterise a mature nematode community, while the

genera *Paracanthonchus* and *Metachromadora* are characteristic of deforested mangrove areas.

- Deposit feeding nematodes are dominant in silty and organically rich sediments, while epistrate feeders and omnivore/predators are dominant in deforested areas having sandy and organically depleted sediments.
- Meiofauna and in particular nematode community colonisation of mangrove sediments is influenced by the presence and type of organic matter, and that mangrove detritus is the preferred source of organic matter within mangrove sediments.
- Nematoda is the dominant meiofauna taxon within mangrove sediments and that the density of meiofauna and nematodes increases with mangrove leaf litter decomposition.
- The succession in nematode community assemblages and trophic groups within mangrove leaf litter is an indication of the changes in the leaf litter chemistry and microbial community associated with decomposing mangrove litter.
- The differences observed between the forested and the degraded mangrove sites benthic fauna densities and community composition are as a result of the differences in organic matter levels and this organic matter is mainly derived from mangrove leaves.
- Additionally, this study has contributed information that may assist in dealing with questions of mangrove management and restoration, like whether young restored mangrove forests are ecologically similar to natural ones and how long restored mangroves may take to become similar to the natural ones.

- The findings further support artificial mangrove reforestation/regeneration efforts as they restore ecological functions, which ensure sustainability of ecological services, economic benefits and ultimately biodiversity conservation.

8.3 Recommendations

- Mangrove ecosystem degradation in particular clear felling should be discouraged since it leads to deleterious changes in habitat conditions for benthos. This ultimately leads to loss of biodiversity. Changes in biodiversity may negatively affect trophic linkages within mangrove ecosystems.
- Artificial mangrove reforestation programmes should be initiated, encouraged and increased since they lead to recovery of the forests and the benthic community.
- There is need for further research to ascertain which benthic community component (macrofauna, meiofauna or nematofauna) is the best indicator of ecosystem recovery.
- Additionally, there is need to further analyse which aspect of the benthic community (density, community structure or diversity) is the best for showing the recovery of the once degraded mangrove ecosystem.
- Policies governing mangrove ecosystem services exploitation should be put in place and or enforced to ensure sustainability of the resource.

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Appendices.

Appendix 1. Occurrence, distribution and relative abundance of nematode genera and families from the natural (Nat), the 10 years reforested (Refo10) and the degraded (Degr) sites. Shaded figures show the dominant (≥ 5 %) genera and families from each site.

Family	Genera	% Contribution per Genera			% Contribution per Family		
		Nat	Refo10	Degr	Nat	Refo10	Degr
Aegialoalaimidae	*Aegialoalaimus*	0.1	0.0	0.0	0.1	0.0	0.0
Anoplostomatidae	*Anoplostoma*	3.4	0.4	13.6	3.4	0.4	13.6
Chromadoridae	*Spilophorella*	4.1	3.9	0.7			
	Neochromadora	1.0	1.1	0.2			
	Actinonema	0.5	0.4	0.1			
	Ptychollaimellus	0.1	0.2	0.0			
	Spiliphera	0.1	0.0	0.0			
	Steineridora	0.0	0.0	0.2			
	Prochromadorella	0.1	0.0	0.0	5.9	5.6	1.3
Comesomatidae	*Pierickia*	4.7	21.0	0.4			
	Hopperia	0.4	3.4	3.0			
	Sabatieria	0.9	0.7	0.0			
	Vasostoma	0.2	0.2	0.3			
	Actarjania	0.0	0.1	0.0			
	Paracomesoma	0.0	0.1	0.0	6.1	25.5	3.6
Cyatholaimidae	*Paracanthonchus*	0.2	0.3	14.4			
	Paracyatholaimus	0.6	0.0	0.1			
	Longicyatholaimus	0.1	0.2	0.0			
	Metacyatholaimus	0.1	0.0	0.0			
	Metacylicolaimus	0.0	0.1	0.0	1.0	0.5	14.5
Desmodoridae	*Metachromadora*	2.2	0.5	24.2			
	Spirinia	6.4	0.3	2.3			
	Pseudochromadora	1.8	2.9	0.1			
	Sigmophoranema	2.2	0.1	0.4			
	Desmodora	0.7	0.1	0.0			
	Molgolaimus	0.2	0.0	1.7	13.5	3.9	28.7
Desmoscolicidae	*Desmoscolex*	0.0	0.1	0.0			
	Quadricoma	0.0	0.1	0.0	0.0	0.2	0.0

Family	Genera	% Contribution per Genera			% Contribution per Family		
		Nat	Refo10	Degr	Nat	Refo10	Degr
Diplopeltidae	*Southerniella*	0.2	0.3	0.0			
	Araeolaimus	0.1	0.2	0.6			
	Diplopeltula	0.2	0.0	0.0			
	Campylaimus	0.0	0.0	0.0	0.6	0.6	0.6
Enchelidiidae	*Belbolla*	0.5	0.5	0.0			
	Polygastrophora	0.3	0.1	0.0			
	Eurystomina	0.0	0.2	0.0	0.8	0.8	0.0
Haliplectidae	*Haliplectus*	4.8	4.3	2.1	4.8	4.3	2.1
Ironidae	*Trissonchulus*	4.5	1.7	4.7			
	Syringolaimus	0.2	0.3	3.4			
	Thalassironus	0.0	0.1	0.0			
	Pheronus	0.1	0.0	0.0			
	Dolicholaimus	0.1	0.0	0.0	4.9	2.2	8.1
Leptolaimidae	*Onchium*	0.5	0.7	1.7			
	Deontolaimus	0.0	0.7	0.8			
	Antomicron	0.1	0.0	0.0			
	Camacolaimus	0.0	0.0	0.0	0.6	1.4	2.5
Leptosomatidae	*Leptosomatum*	1.2	2.6	0.2	1.2	2.6	0.2
Linhomoeidae	*Terschellingia*	24.5	25.6	0.0			
	Metalinhomoeus	4.0	1.6	0.0			
	Paralinhomoeus	1.4	3.6	0.0			
	Eumorpholaimus	0.7	1.0	0.0			
	Linhomoeus	0.5	0.0	0.0			
	Desmolaimus	0.0	0.2	0.0			
	Eleutherolaimus	0.1	0.1	0.0			
	Megadesmolaimus	0.0	0.0	0.0	31.1	32.2	0.0
Microlaimidae	*Microlaimus*	4.0	0.9	6.8			
	Calomicrolaimus	0.0	0.1	0.0	4.0	1.0	6.8
Oncholaimidae	*Viscosia*	0.5	0.3	8.2			
	Metoncholaimus	0.0	0.0	0.2	0.5	0.3	8.5
Oxystominidae	*Halalaimus*	2.3	3.9	1.0			
	Oxystomina	4.0	1.9	0.2			
	Weiseria	0.0	0.1	0.0	6.4	5.9	1.3
Phanodermatidae	*Phanoderma*	0.1	0.0	0.0	0.1	0.0	0.0
Selachnematidae	*Halichoanolaimus*	0.5	1.6	0.7			
	Gammanema	0.0	0.0	0.5			
	Richtersia	0.0	0.1	0.0	0.5	1.7	1.3
Siphonolaimidae	*Siphonolaimus*	2.3	2.3	0.2			

Family	Genera	% Contribution per Genera			% Contribution per Family		
		Nat	Refo10	Degr	Nat	Refo10	Degr
	Astomonema	1.5	0.0	0.0	3.8	2.3	0.2
Sphaerolaimidae	*Sphaerolaimus*	3.6	3.4	0.1			
	Subsphaerolaimus	0.1	0.1	0.0			
	Doliolaimus	0.0	0.1	0.0	3.7	3.6	0.1
Trefusiidae	*Trefusialaimus*	5.2	3.7	0.0			
	Trefusia	0.2	0.2	2.6	5.4	3.9	2.6
Tripyloididae	*Bathylaimus*	0.1	0.0	0.0			
	Tripyloides	0.0	0.0	0.0	0.1	0.0	0.0
Xyalidae	*Theristus*	0.6	0.5	4.1			
	Daptonema	1.1	0.5	0.0	1.7	1.0	4.1
24 Families	**76 Genera**	**100**	**100**	**100**	**100**	**100**	**100**