Variation in distribution of Sudanese mangroves and their ecological significance for benthic fauna

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Variation in distribution of Sudanese mangroves and their ecological significance for benthic fauna

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Dedication

To my daughter Dilara,

my parents, and

to the memory of my grand mom Fatima and uncle Mamon

Who left when we need them the most

You left fingerprints of grace on our lives

You shan't be forgotten

Summary

SUMMARY

The ecological and socioeconomic importance of mangroves has been recognized worldwide. Mangroves along the Sudanese coast, despite their small extent being at their climatological limits of geographical distribution, are believed to have significant ecological roles similar to other tropical mangrove systems. However, they are possibly subjected to degradation due to climate change as well as activities caused by rapid growth and development of coastal communities. These activities, especially mangrove clearance and deforestation, may impair the ecological functions that mangroves are providing, such as being a habitat for a variety of fauna. Moreover, the management of mangroves in Sudan is hindered by the lack of information on the distribution and status of mangroves as well as on the impact of human disturbances such as mangrove clearance on both the environment and the fauna that are inhabiting this valuable ecosystem. This PhD study, therefore, aimed at investigating the spatio-temporal dynamics of mangrove stands along the Sudanese coast and at exploring their ecological significance as habitat for infauna. The specific aims of this study were to:

I. Investigate the spatio-temporal distribution of mangroves along the Sudanese Red Sea coast.
II. Provide insight into the ecological importance of these mangroves as habitat provider for the associated benthic communities by comparing the meio- and macrofauna of three different coastal habitats including an intact mangrove, a cleared mangrove and a bare sand flat.

The assessment of the spatio-temporal distribution of mangroves covered the whole Sudanese Red Sea coast (21° 16' 48"'N, 37° 6' 36"E to 18° 0''N, 38° 34'E). An additional analysis of change detection at a local scale targeting an area of shrimp farming and an undisturbed mangrove was carried out at the sites, Mersa Atta and Mersa Ashat, respectively. To assess the importance of mangrove as a habitat provider for benthic fauna, structural and functional community characteristics of meio- and macrofauna were compared for three contrasting sites situated in the area south of Suakin city along the Sudanese Red Sea coast. These sites consisting of a bare sand flat, a cleared mangrove, and an intact mangrove, were representing a varying degree of mangrove removal. Three stations, corresponding to different seasonal water levels, were established at each site to assess the variability within each study site related to distance from the summer low water line.

All three habitats differed in terms of sediment composition and organic matter. The intact mangrove sediment was on the average characterized by a high mud content (clay and silt; 63.6%), finer particles (median grain size; 91.7 µm) and very poorly sorted sediment. Relative to the other habitats, it was more enriched in terms of organic content as shown by the higher percentage of total organic carbon (TOC;4.6%). However, the organic matter was of low quality (C/N ratio of 44.5). The sediment of the bare sand flat was characterized by a higher sand content (70.4%), coarser particle sizes (271µm), poorly sorted sediment and lower TOC concentrations (1.4%) but of higher quality (C/N ratio was 26.1), as compared to the intact mangrove. The cleared mangrove habitat showed intermediate sediment characteristics between the bare sand flat and the intact mangrove, especially in terms of sediment grain size with an average mud and sand content of 50% each, poorly sorted sediment, a low quantity of TOC (1.2%) and of low quality as indicated by the average C/N ratio (54.6). Samples were collected to assess the differences in macro- and meiofauna densities and biomass, composition, and taxonomic diversity at higher taxa level for both size groups and at genus levels for the nematodes.

Chapter one gives an overview of mangrove biology in general, it explores the general functional significance of mangroves in coastal environments, discusses the threats to Sudanese mangroves in general and specifically the impacts of clearance on mangrove ecosystems, and explains the broad framework and key features of this Ph.D.

Chapter two investigates the spatio-temporal pattern of mangrove stands along the Sudanese coast between the years 1984 and 2013 based on multi-temporal Landsat data and using remote sensing and GIS techniques. The distribution of mangroves during the study period was highly variable ranging from 329 to 721 ha. However, further ground-truthing is required to validate the remote sensing observations, to identify to what extent the variability can be attributed to factors such as meteorology or geographical suitability, and to asses if anthropogenic impact is important too. To further assess the human impact on mangroves in the area, a more detailed change detection study was performed in two sites representing a human impacted mangrove from a salt pan construction and shrimp farming, and a non-human impacted mangrove. The areal distribution of the impacted mangrove showed a continuous increase from 1990 to 2010 suggesting that increased nutrient supply from these activities may have been beneficial for mangrove growth. On the other hand, the mangrove distribution in the non-impacted mangrove was highly variable during the study period, which could be linked to the variability in rainfall.

Chapter three compares the three study sites representing different degrees of mangrove clearance (intact mangrove, cleared mangrove and bare sand flat) in terms of macrofauna densities, biomass, taxonomic diversity and trophic diversity. The latter was examined using carbon and nitrogen stable isotope analysis and community-wide metrics based on these stable isotope values.

Macrofauna standing stock, composition and diversity differed between the three habitats. The intact mangrove, relative to the other habitats, had higher biomass, taxa evenness and diversity. These differences between sites were more pronounced for the high- and mid-water stations; at these stations, the macrofauna from the intact mangrove showed significantly higher abundance and taxon richness compared to the cleared mangroves. Macrofauna in the intact mangrove was characterized by a complex trophic structure of taxa that occupy a wide range of trophic positions (higher $\delta^{15}N$ range) and utilized a wide range of food sources (higher $\delta^{13}C$ range) available within mangrove habitats. Macrofauna in the bare sand flat, and the cleared and intact mangroves was dominated, respectively, by bivalves (35%), polychaetes (46%) and decapod crabs (25%). The abundance of mangrove keystone taxa (decapods and gastropods) in the cleared mangrove was significantly lower than in the intact mangrove. The divergence in macrofauna characteristics between the cleared and intact mangroves can be attributed to differences in sediment characteristics likely resulting from mangrove clearance.

Chapter four compares the same three sites representing different habitats in terms of meiofauna and nematode community structure. There were significant differences in meiofauna and nematode characteristics between habitats. In comparison to the cleared mangrove, the intact mangrove had significantly lower meiofauna and nematode abundances, whereas the values of the measured diversity indices were higher. The difference in meiofauna composition between the cleared and intact mangroves was governed by the taxa Acarina and Copepoda, and the nematode genera *Onchium*, *Terschellingia*, *Haliplectus*, *Syringolaimus*, *Spirina* and *Sphaerolaimus*, which were found only in the intact mangrove, whereas genera such as *Daptonema*, *Theristus* and *Ethmolaimus* attained much higher abundances in the cleared mangrove. The intact mangrove showed higher functional and trophic diversity as indicated by higher values of the maturity index, and higher trophic diversity estimates. Results from the analysis of ecological quality status (EQS) for habitats using nematode-based indices suggested that the intact mangrove in general had a high/good EQS, while the cleared mangrove and the bare sand flat displayed a moderate/poor EQS. Differences between the cleared and intact mangrove may be partly due to the differences in sediment characteristics resulting from the removal of mangrove trees.

Chapter five analyses differences in nematode biomass characteristics between the three sites representing different coastal habitats. The difference in biomass was assessed using various graphical representations such as biomass size spectra (NBS) and the abundance biomass comparison method (ABC). Results revealed significant difference between sites for nematode individual biomass, with higher values observed in the intact mangrove compared to the

other habitats, and for total biomass, with higher values in the intact mangrove as compared to the bare sand flat, but comparable to the values in the cleared mangroves. The habitats were also different in community composition based on nematode biomass. There were clear differences in the nematode biomass size spectra (NBS) and abundance/biomass curves (ABC) between sites. The cleared mangrove showed a bimodal nature of biomass spectra compared to the bare sand flat and intact mangrove which showed a unimodal biomass distribution. The bimodality in the cleared mangrove site can be explained by the presence of few larger omnivores/predators and epigrowth feeders, and the higher proportional abundances of a small-bodied non-selective deposit feeders. The ABC curves suggested that the cleared mangrove was moderately to grossly disturbed. It seemed that clearance has caused a shift in sediment composition resulting in a change in biomass size spectra and abundance/biomass curves.

Chapter six presents a synthesis in which the findings of the preceding chapters are combined to make statements about the general status of the Sudanese mangrove ecosystem. The Driver-Pressure-State-Impact-Response framework (DPSIR) was used to connect the driving forces, the pressures on mangroves along the Sudanese coast, including activities other than mangrove clearance, and their impact on the state of mangroves, and the societal response in form of regulatory laws or management plans. At the end of this chapter, a number of recommendations are given.

Samenvatting

SAMENVATTING

Het ecologische en socio-economische belang van mangrovebossen is wereldwijd erkend. Mangrovebossen langs de Soedanese kust hebben een kleine omvang aangezien deze regio nabij de klimatologische grens van het spreidingsgebied van mangroves gelegen is. Toch wordt aangenomen dat de Soedanese mangroves, net zoals andere tropische mangrovesystemen, een significante ecologische rol vervullen. Deze systemen zijn mogelijks bezig aan een achteruitgang omwille van klimaatsverandering en activiteiten die gepaard gaan met de snelle groei en ontwikkeling van kustgemeenschappen. Deze activiteiten - en met stip houtkap en ontbossing - kunnen de ecologische functies van mangrovebossen, waaronder de voorziening van habitat voor een verscheidenheid aan fauna, belemmeren. Daarenboven wordt het beheer van mangrovebossen in Soedan bemoeilijkt door gebrek aan informatie over de tijdruimtelijke spreiding en toestand van mangrovebossen, en over de impact van menselijke activiteiten, zoals houtkap, op de omgeving en fauna in dit waardevolle ecosysteem. Dit doctoraatsonderzoek had bijgevolg als doel de tijdruimtelijke dynamiek en het ecologische belang als habitat voor infauna van mangrovebossen langsheen de Soedanese kust, te exploreren. De specifieke doelstellingen van deze studie waren:

i. Het onderzoeken van de tijdruimtelijke spreiding van mangrovebossen langs de Rode Zee kust in Soedan;
ii. Meer inzicht verwerven in het ecologische belang van deze mangroves als voorziener van habitat voor de geassocieerde benthische gemeenschappen. Dit werd bewerkstelligd door de meio- en macrofauna van drie verschillende habitats, i.e. een intact mangrovebos, een gekapte mangrove en een onbegroeide zandvlakte, te vergelijken.

De studie van de tijdruimtelijke distributie van mangroves besloeg de volledige Rode Zee kust (21° 16' 48"'N, 37° 6' 36"E to 18° 0''N, 38° 34'E). Een bijkomende analyse van veranderingsdetectie op lokale schaal werd uitgevoerd in de gebieden Mersa Atta, waar garnalen worden gekweekt, en voor een onverstoord mangrovebos in Mersa Ashat. Om het belang na te gaan van mangrovebossen als habitatverschaffer voor benthos, werden de structurele en functionele eigenschappen van meio- en macrofaunagemeenschappen vergeleken tussen drie contrasterende gebieden ten zuiden van Suakin city. Deze gebieden, nl. een zandvlakte, een gekapte mangrove, en een intacte mangrove, vertonen een verschillende graad van houtkap. In elk gebied werden drie stations, gekenmerkt door verschillende seizoenale waterniveaus, gekozen,

om voor elk gebied de variabiliteit na te gaan gelinkt aan de afstand tot de laagwaterlijn in de zomer.

Het sediment in de drie gebieden verschilde in samenstelling en percentage organisch materiaal. Het sediment in het intacte mangrovebos was over het algemeen gekenmerkt door een hoog sibgehalte (klei en silt; 63.6%), fijnere sedimentpartikels (mediane korrelgrootte: 91.7 µm), en erg slecht gesorteerd sediment. Het sediment was relatief rijk in organisch materiaal zoals bleek uit het hogere percentage van totale organische koolstof (TOC; 4.6%). Niettegenstaande bleek het organische materiaal van lage kwaliteit (C/N ratio was 44.5). Het sediment van de zandvlakte had een hoog zandgehalte (70.4%), grovere sedimentkorrels (271 µm), slecht gesorteerd sediment en lagere TOC concentraties (1.4%). De zandvlakte was wel gekenmerkt door sediment van hogere nutritionele kwaliteit (C/N ratio bedroeg 26.1) dan dit in het intacte bos. Het gekapte mangrovebos vertoonde eigenschappen intermediair tussen deze van de zandvlakte en het intacte mangrovebos. Dit was voornamelijk het geval voor de korrelgroottedata met een gemiddelde slib- en zandconcentratie van elk 50%, slecht gesorteerd sediment, een laag gehalte aan TOC (1.2%) en laag kwalitatief organisch materiaal, zoals blijkt uit de hoge gemiddelde C/N ratio (54.6). Stalen werden verzameld om verschillen te bepalen in densiteit, biomassa, samenstelling en diversiteit voor macro- en meiofauna. Diversiteit werd geëvalueerd op hoger taxonniveau voor meio- en macrofauna, en op genusniveau voor nematoden.

Hoofdstuk één geeft een algemeen overzicht van mangrovebiologie, verkent het functioneel belang van mangrovebossen in kustsystemen, en behandelt de bedreigingen, waaronder houtkap, voor Soedanese mangrovebossen, en hun impact op het mangrove-ecosysteem. Op het einde van dit hoofdstuk worden het algemene kader en de voornaamste aspecten van dit doctoraatsonderzoek uit de doeken gedaan.

Hoofdstuk twee onderzoekt het tijdruimtelijke patroon van mangrovebossen langs de Soedanese kust tussen 1984 en 2004 op basis van Landsat data, met behulp van *remote sensing* en GIS technieken. De omvang van de mangrovebossen varieerde erg sterk in deze periode, en schommelde tussen 329 en 721 ha. Verdere verificatie op het terrein is echter wel vereist om deze *remote sensing* data te valideren en om na te gaan of deze variabiliteit gerelateerd kan worden aan meteorologische gegevens of geografische geschiktheid, en of antropogene invloeden een rol hebben gespeeld. Om de menselijke impact op mangroves in de regio verder te evalueren, werd een meer gedetailleerde veranderingsdetectiestudie uitgevoerd in een door mensen verstoord (door de constructie van een zoutziederij en een garnalenkwekerij) en een niet-verstoord mangrovebos. Tussen 1990 en 2010 vertoonde het verstoorde mangrovebos een gestage toename in omvang. Dit suggereert dat de toegenomen aanvoer van nutriënten, veroorzaakt door menselijke activiteiten, voordelig was voor de groei van mangroves. De spreiding van mangroves in het pristiene mangrovebos was erg variabel in deze periode, hetgeen gelinkt kon worden aan de variabele regenval.

Hoofdstuk drie vergelijkt de densiteit, biomassa, taxonomische diversiteit en trofische diversiteit van de macrofauna in de drie studiegebieden. De trofische diversiteit werd onderzocht met behulp van koolstof en stikstof stabiele isotoopanalyse en gemeenschapsindicatoren berekend op basis van deze stabiele isotoopwaarden. Macrofauna biomassa, samenstelling en diversiteit verschilde tussen de drie gebieden. Het intacte mangrovebos vertoonde een hogere abundantie, een grotere taxongelijkmatigheid en hogere diversiteit ten opzichte van de andere gebieden. Deze verschillen tussen de gebieden waren het meest uitgesproken voor de hoog- en midwater stations; op deze stations was de macrofauna in het intacte mangrovebos abundanter en rijker in taxa dan de gekapte mangroves. De macrofauna van het intacte mangrovebos was gekarakteriseerd door een complexe trofische structuur met taxa die een brede waaier aan trofische posities bekleedden (grotere spreiding van $\delta^{15}N$) en die een breed gamma aan voedselbronnen (grote spreiding van $\delta^{13}C$) consumeerden. De macrofauna van de zandvlakte, het gekapte mangrovebos, en het intacte mangrovebos werden gedomineerd door, respectievelijk, bivalven (35%), polychaeten (46%) en krabben (25%). De abundantie van mangrovebos-sleuteltaxa (decapoden en gastropoden) was beduidend lager in het gekapte dan in het intacte mangrovebos. De verschillen in macrofauna tussen de gekapte en intacte mangrovebossen zijn te wijten aan verschillen in sedimenteigenschappen veroorzaakt door houtkap.

In **Hoofdstuk vier** vergelijken we de structuur van de meiofauna- en de nematodengemeenschap tussen dezelfde drie gebieden. Er waren significante verschillen in meiofauna- en nematodeneigenschappen tussen de habitats. In het gekapte mangrovebos was de abundantie van meiofauna en nematoden lager dan in het intacte bos, maar het eerste habitat werd gekenmerkt door een hogere diversiteit. Het verschil in meiofaunasamenstelling tussen het intacte en gekapte mangrovebos werd voornamelijk veroorzaakt door de taxa Acarina en Copepoda die enkel aanwezig waren in het intacte bos. Verschillen tussen gebieden in de samenstelling van nematodengemeenschappen waren voornamelijk te wijten aan, enerzijds, *Onchium*, *Terschellingia*, *Haliplectus*, *Syringolaimus*, *Spirina* and *Sphaerolaimus*, die enkel teruggevonden werden in het intacte mangrovebos, en, anderzijds, *Daptonema*, *Theristus* and *Ethmolaimus,* die een veel hogere relatieve abundantie kenden in de gekapte mangrovebossen. Het intacte mangrovebos vertoonde een hogere functionele en trofische diversiteit zoals blijkt uit de hoger waarden voor de maturiteitsindex en trofische diversiteitsindex. De analyse van de ecologische status (EQS), gebaseerd op nematode indices, toonde aan dat het intacte mangrovebos een hoge EQS heeft, terwijl het gekapte bos en de onbegroeide zandvlakte een matige/slechte EQS vertonen. Deze verschillen tussen de intacte en gedegradeerde mangrovebossen kunnen deels te wijten zijn aan verschillen in sedimentkarakteristieken ten gevolge van de verwijdering van mangrovebomen.

Hoofdstuk vijf analyseert verschillen in nematodenbiomassa tussen weerom dezelfde drie gebieden. Hiertoe werden verscheidene grafische technieken gebruikt zoals het opstellen van biomassa-grootte-spectra (NBS) en de abundantie-biomassa-vergelijkingsmethode (ABC). Er werden significante verschillen gezien in individuele nematodenbiomassa tussen gebieden, waarbij nematoden in het intacte mangrovebos hogere waarden vertoonden dan deze van de onbegroeide zandvlakte. Totale biomassa in het intacte mangrovebos was hoger dan op de zandvlakte, maar gelijkaardig aan deze in het gekapte mangrovebos. Er waren duidelijke verschillen in de NBS en ABC curves tussen de gebieden. Het gekapte bos vertoonde een bimodaal NBS patroon, terwijl de zandvlakte en het intacte bos een unimodale biomassaspreiding kenden. De ABC curves gaven aan dat de gekapte mangrovebos matig tot zwaar verstoord was. Blijkbaar had de houtkap een verschuiving in sedimentsamenstelling teweeggebracht welke resulteerde in een verandering in abundantie/biomassa curves.

Hoofdstuk zes presenteert een synthese over de algemene toestand van het Soedanese mangrove-ecosysteem op basis van de resultaten van de voorgaande hoofdstukken. De *Driver-Pressure-State-Impact-Response* framework (DPSIR) werd gebruikt om een verbinding te maken tussen de drijfkrachten, de bedreigingen voor de Soedanese mangroves (waaronder ook andere activiteiten dan houtkap), en de respons van de maatschappij, onder de vorm van wetten of beheersplannen. Op het eind van dit hoofdstuk worden een aantal aanbevelingen gedaan.

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General Introduction

Chapter 1

General Introduction

This study aims to investigate the spatio-temporal dynamics of mangrove stands along the Sudanese coast and explore their ecological significance as habitat provider for benthic fauna. In this chapter, we first give background information on the physical, climatic and oceanographic setting of the Red Sea in general and, more particular, the Sudanese Red Sea. Secondly, we introduce mangrove ecosystems along the Sudanese coast and explain their major biological and ecological characteristics, as well as their threats. Further, we elaborate on the use of remote sensing as tools for mangrove mapping. We also explain the most characteristic features of the benthos, a major component of various soft bottom marine ecosystems, including mangroves, and often used as indicator for the status of marine ecosystems. At the end, a general description of the study area is provided.

1.1. Description of the Sudanese Red Sea

1.1.1. Geomorphology

The Red Sea is a semi-enclosed, elongated and narrow-shaped basin that extends SE-NW between 12° N, 43° E and 30° N, 32° E, and covers a distance of approximately 2,000 km (Fig. 1.1). The coastal plains of the Red Sea are in general bordered by high mountains rising about 1000 m in the north and more than 3500 m in the south. The coastal plains are generally narrow with a width of 5-35 km in the north which increases to about 50 km in the south. However, the break in the Red Sea hills at Tokar, Sudan has resulted in a low and broad coastal plain. Finally, one of the most important characteristic geomorphologic features of the Red Sea region is the marginal sabkha flats and evaporites. Sabkha flats are typical supratidal areas that emerge at arid coastal flats as a result of high rates of evaporation coupled with tidal mechanisms (periodic flooding), resulting in the accumulation of windblown sediments and evaporites including gypsum, calcium carbonate, and salts. The Sudanese Red Sea is characterized by the presence of numerous sheltered bays (mersas) and several khors. Khors are seasonally flash flooded depressions that transport water and alluvium, originating from the Red Sea hills during rains, across the relatively wide coastal plains. The water is eventually drained either into lagoons or to the seaward end of extensive basins.

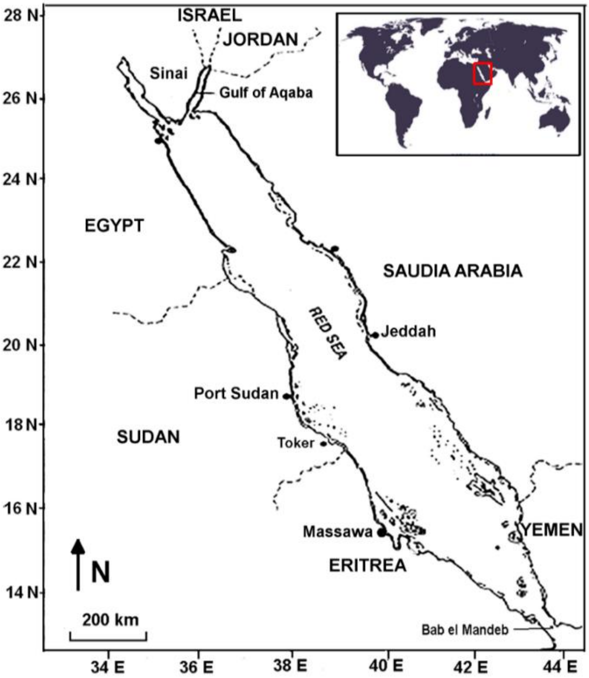


Figure 1.1. Geographical location of the Red Sea. From Behairy *et al.* (1992).

1.1.2. Climate

The climate of the Sudanese Red Sea is characterized by high summer temperatures and aridity throughout the year due to its geographical position within the subtropical high pressure belt. Descending air is adiabatically warmed as it loses altitude and is consequently dried. This leads to the formation of semi-permanent high pressure zones with a divergent circulation that suppresses cloud cover and precipitation, except when this pattern is disturbed by incursions of rare storm centers from outside. This normally occurs in the winter months when low pressure storm centers enter from the Mediterranean region. In this sense the climate regime is more Mediterranean exhibiting a clear division into hot and cool seasons with rainfall confined almost exclusively to the cool period from October to April (Fig. 1.2a). The mean monthly air temperature ranges from 20 to 38 °C. The mean maximum temperature ranges between 35 to 45 °C in summer, while the mean minimum temperature ranges between 18 and 31 °C in winter (Fig. 1.2b). Interannual variability in temperatures in not abnormal. However, since mid of 1990th the

Red Sea has been relatively warmer, with temperatures higher than the global averages, as shown by the annual temperature anomalies, which report more frequent warmer episodes than colder ones (Raitsos *et al.*, 2011).

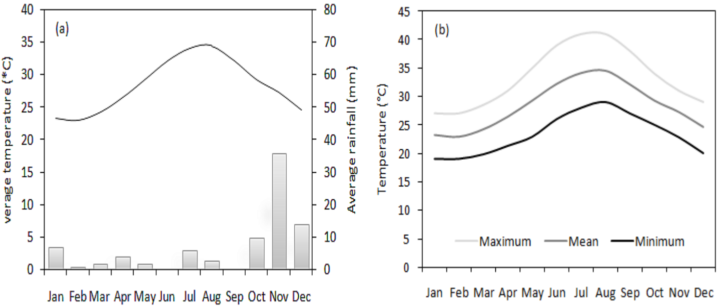


Figure 1.2. Climate diagram for the Sudanese Red Sea coast with mean temperature and rainfall (source: http://en.climate-data.org.) and (b) Monthly mean, minimum and maximum temperatures along the Sudanese Red Sea coast (Database recorded at Port Sudan station)

Rainfall over the Red Sea and its coasts is very sparse (averaging 60 mm/year) and often very localized. Raining occurs spasmodically i.e. mostly in the form of showers of short spells, often associated with thunderstorms and occasionally with dust storms. The rainy season at the Sudanese coast occurs in winter, with maximum rainfall in November (El Tom, 1991; Musa, 1991). The average annual rainfall has changed from over 400 mm in the late nineteenth century to less than 250 mm after the 1970s due to intensified aridity in the region (Musa, 1991). The coast, nevertheless, receives higher rainfalls (averaging 70 mm/year, Fig. 1.2a) than the other parts of the central Red Sea, as it is the area where the northern and southern air masses meet (Fouda & Gerges, 1994).

1.1.3. Oceanography

Surface water temperature in the Red Sea increases from north to south showing wide variability between different seasons. The annual mean sea surface temperature ranges between 24 °C in the Gulf of Aden and 30 °C in the north of the Red Sea, while the seasonal surface temperature varies between 22 and 30 °C in winter, and 29 and 30 °C in summer (Fig. 1.3b,c). Along the Sudanese coast, the recorded annual mean sea surface temperature ranges from 28 to 30 °C (Fig. 1.3a), while the mean seasonal surface temperature ranges between 26 and 29 °C in winter and the corresponding figures for summer season are 30 to 33 °C (Fig. 1.3b,c).

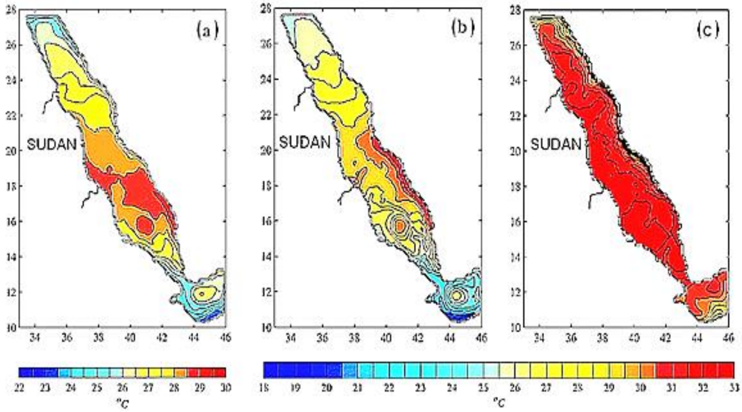


Figure 1.3. Annual (a), and seasonal (b) November-March and (c) June-September sea surface temperature distribution in the Red Sea from MICOM simulation (average over the last 9 years of simulation). From Sofianos and Johns (2003).

The average salinity (PSU) in the Red Sea ranges between 36 at Bab el Mandeb in the south and 41 in the north (Fig. 1.4a), and can reach values of up to 45 PSU in some areas. These high salinities are due to intense evaporation (averaging 200 cm/year) and a minimal fresh water input through rainfall. Along the coast of Sudan, the average annual salinity ranges from 39 in the south to 40.5 in the north (Fig. 1.4b,c).

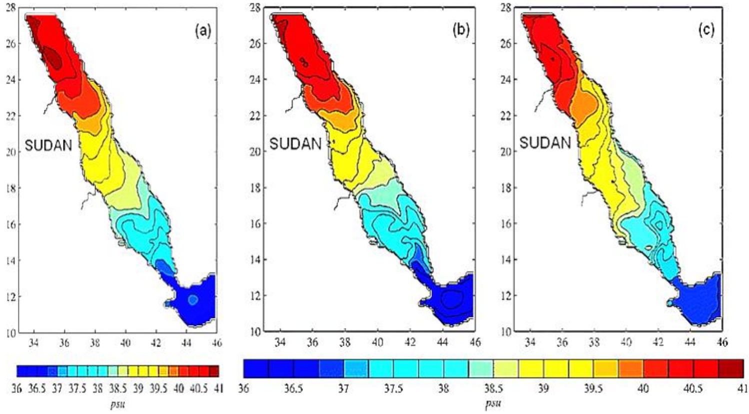


Figure 1.4. Annual (a), and seasonal (b) November-March and (c) June-September sea surface salinity distribution in the Red Sea from MICOM simulation (average over the last 9 years of simulation). From Sofianos and Johns (2003).

Tides in the Red Sea are local oscillatory tides of a small amplitude and a semi-diurnal pattern which results in high water at one end of the sea, when it is low water at the other end. Tidal ranges change widely from north to south, with the greatest values of 1.5-1.8 m in the north and only 0.9 m in the south. Along the coast of Sudan, there is no appreciable semi-diurnal tide compared to southern and northern parts (0.1-0.5 m). However, the seasonal sea level regularly moves up and down throughout the year (Abdel Karim & Babiker, 1991). The fluctuation of the sea level strongly varies between seasons, being about 1.0 m higher in winter and around 0.45 m lower in summer (Taylor & Reid, 1984; Eltaib, 2010). These seasonal tides are driven partly by greater evaporation in the summer and freshwater fluxes in winter. However, the surface current in Bab el Mandeb, which flows into the Red Sea in winter and partly blows outward by strong winds in summer, appears to be the main factor in determining the seasonal rise and fall of the sea water (Sheppard *et al.*, 1992).

Most of the Red Sea water has been considered as oligotrophic and deficient in several major nutrients including nitrate, ammonium, phosphate, and silicate (Raitsos *et al.*, 2013), with the exception of small areas off the Sinai Peninsula and the southern transition area between the Red Sea and the Indian Ocean (Thiel *et al.*, 1986). The low concentration can be attributed to the fact that no rivers are entering the Red Sea, except for small seasonal water courses or khors, and the low rainfall in the area. Typical concentrations of nitrate and phosphate in the open Red Sea water are 1.0 µmol/l and 0.2 µmol/l. High levels of nitrite and ammonia have been recorded in the upper water, which can be considered as an indicator of high bacterial activities. Near the coast of Sudan, phytoplankton productivity (measured as Chl-a concentrations) ranges between 0.1-.0.2 mg/m³ and can be up to 5.0 mg/m³ in some areas (Raitsos *et al.*, 2013), while nutrient concentrations are very low ranging between 1.5-4.0 and 0.06-1.0 µmol/l for nitrate and phosphate (Dowidar, 1984; Nasr *et al.*, 1987).

1.1.4. Coastal biodiversity

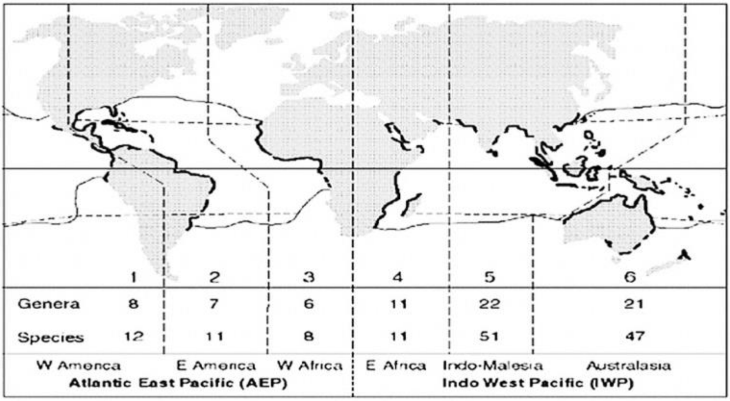
A number of different habitats, consisting of various biotopes such as: halophytic vegetation, saltmarshes, algal beds, sandy beaches and mud flats, rocky shores, sabkha and hyper-saline pools, seagrass beds, and coral reefs are present along the Sudanese coast. Among the halophytes, mangrove represent a very important component that closely interlinks all these biotopes through various biotic and abiotic fluxes.

1.2. Biology and ecology of mangroves

The term “*mangrove*” is often ascribed to both the plants and the forest ecosystem. As a plant, mangrove refers to an ecological group of woody halophytic trees or shrub species, generally exceeding half a meter in height. They normally grow above mean sea level in the upper intertidal zone of marine coastal environments at the interface between land and sea. As an ecosystem, mangrove is a type of intertidal wetland ecosystem that constitute of trees as described above and associated microbes, fungi, algae, animals, of which the synergy is driven by specific abiotic factors (Kathiresan & Bingham, 2001; Alongi, 2002; Luther & Greenberg, 2009).

1.2.1. Mangrove distribution and structure

The global distribution of mangroves indicates a tropical dominance with major latitudinal limits (between 30° north and 30° south) relating best to major ocean currents and the 20°C seawater isotherm in winter. Northern extensions of this limit occur in Japan (31°22’N) and Bermuda (32°20’N); southern extensions are found in Australia (38°45’S), New Zealand (38°59’S), and on the East Coast of South Africa (32°59’S), (Fig. 1.5; Alongi, 2002). The Sudanese mangroves extend in a coastline of about 500 km long, from 23°09'N, 35°37'E to 18°01'N, 38°35'E, covering an area of about 500 ha. This means that they exst close to the uppermost latitudinal limit of mangrove distribution and that they are marginally located with respect to the preferred climatological zones of mangroves (Alongi *et al.*, 2009).



	1	2	3	4	5	6
Genera	8	7	6	11	22	21
Species	12	11	8	11	51	47
	W America	E America	W Africa	E Africa	Indo-Malesia	Australasia
	Atlantic East Pacific (AEP)			Indo West Pacific (IWP)		

Figure 1.5. Global distribution of the world’s mangrove forests and their biogeographic provinces. Forests are designated as heavy lines. The number of mangrove trees genera and species within each province are noted below the map. From Alongi *et al.* (2009).

In general, mangrove distribution is confined to soft sediments that are protected from extreme wave action such as found in the deltas of large rivers and estuaries, and on the leeward side of barrier islands (Alongi, 2002; Luther & Greenberg, 2009). The structure of mangrove forests varies at global, regional and local scales and over different time scales (Duke *et al.*, 1998). At the global scale, mangroves are ultimately limited by temperature, but at the regional scale differences in mangrove structure may be explained by coastal geomorphology, which appears to be more important in determining the physical and chemical conditions of mangrove development. Mangroves exhibit different local distribution patterns in a number of different geographic regions, which often results in monospecific bands of vegetation occurring parallel to the shoreline (Smith, 1992). This indicates that the floristic composition of mangrove communities varies substantially across the intertidal zone and among geographic regions. In arid climates, woody plants are excluded from the landward fringe due to a high salinity and as a result salt marshes and tidal pans cover the area. Wet climates, on the other hand, tend to be more hospitable to a wide variety of plant species because the salt concentration in the landward soil is lower, and thus, terrestrial tree species intermingle with mangrove species (Luther & Greenberg, 2009). At the local scale, occurrence of species may differ across an estuary and species tend to segregate into monospecific patterns (known as *physiognomy*), which are apparently strongly related to differences in tidal height, water salinity, range of salinity of the soil, and aeration of the soil (Macnae, 1968; Lugo & Snedaker, 1974; Chapman, 1975; Duke, 1992).

Mangroves have been classified based on tidal and hydro-period characteristics into six physiognomic mangrove forest types. These include: (i) over-wash mangrove: patches, islands, or promontories (raised masses of land, declined abruptly from only one side) that are entirely covered by water at high tide, with the effect that there is little leaf litter accumulation; (ii) fringing mangrove: relatively narrow strips tracing a shoreline, a lagoon or the more steeply shelving part of an estuarine or deltaic channel; (iii) basin mangrove: typically present in a very shallow depression, away from the water’s edge (there is no wave action and mangroves may only be infrequently inundated); (iv) riverine mangrove: these mangroves grow along flowing waters such as tidal rivers and creeks which are flooded during the highest tides and which dry up at the lowest tides; (v) hammock mangrove: similar to basin mangrove, but existing in more elevated sites; and (vi) dwarf mangrove: limited to the flat coastal fringe. In Sudan we find mainly three physiognomic forest types: over-wash, fringing and basin mangroves (see also further).

1.2.2. Factors affecting mangrove forest development and structure

In general, the establishment, development and structural characteristics of mangrove forests, such as canopy height, tree density, and biomass accumulation are defined by a number of abiotic factors. Among these factors, the following are considered to be the major determinants for mangrove distribution:

i. *Climate*: The latitudinal limits of mangroves distribution vary depending on air and water temperature. Both factors are important in regulating several internal physiological processes such as salt regulation and excretion (Krauss *et al.*, 2008). A very extensive mangrove occurs only when the average winter temperature is 20° C and when the seasonal temperature range does not exceed 10° C. Mangrove growth declines if the temperature progresses towards the colder limits. However, the effect of climate factors on mangrove growth and development varies among and within species (Mendelssohn & McKee, 2000). Nevertheless, temperature alone is not enough to define the distribution and development of mangroves at the latitudinal limit, because of the large variation in both average air and sea surface temperature (Quisthoudt *et al.*, 2012).

ii. *Salinity*: Salinity is important for germination, survival, growth and distribution of mangrove species (Krauss *et al.*, 2008). The growth of mangroves in relation to salinity is species specific (Ball, 1988a), since mangrove species are either obligate halophytes or facultative halophytes. Freshwater is a physiological requirement, while salt water is an ecological requirement for their growth. The former prevents excess respiratory losses while the latter prevents invasion and competition from non-halophytes (Jayatissa, 2008; Wang *et al.*, 2011). Mangroves, in general, prefer a brackish water environment and in extreme saline conditions stunted growth is observed.

iii. *Tidal inundation*: Tidal fluctuation indirectly plays an important role in mangrove growth and development through the provision of salt, exchange of nutrients and the renewal of water. While it increases nutrient levels it also reduces sulfur compounds. It excludes most other vascular plants and by this reduces competition. Tides also flush the soil and decrease soil salinity in areas with high evaporation (Macnae, 1968; Golley *et al.*, 1975).

iv. *Geomorphological suitability and wave energy*: Although mangroves are able to grow on sand, peat and coral, they luxuriantly grow in alluvial soils (i.e. loose, fine-textured mud or silt, rich in humus) with low wave energy (Tomlinson, 1986). This form of substrate allows for colonization and succession of mangrove trees (Chaudhuri & Choudhury, 1994), while low wave energy allows for propagule establishment and accumulation of fine sediment (Feller & Sitnik, 1996). In addition, the slope of the intertidal area, which is constrained by topography and accretion rate, will influence the establishment of mangroves higher in the intertidal area.

v. *Nutrient availability:* Many mangrove soils have extremely low nutrient availability (e.g., Lovelock *et al.,* 2005); however, nutrient availability varies greatly between mangroves and also within a mangrove stand (Feller *et al.,* 2003a). Nutrient availability has been found to be one of the dominant factors influencing mangrove productivity (e.g., Onuf *et al.,* 1977; Boto & Wellington, 1984; Feller *et al.,* 2003b; Reef *et al.,* 2010), and vegetation performance (Ukpong, 1997). It also affects the growth of *Avicennia* seedlings, which showed a logarithmic pattern in relation to the availability of organic matter. This means *Avicennia* seedlings have limited capability on utilizing organic matter for growth (Gleason & Ewel, 2002). N and P were both considered as limiting factors for mangrove growth in general (Lovelock *et al.*, 2004; Elser & Hamilton, 2007), while N was observed to limit the growth of *A. marina* in South Africa (Naidoo, 2009) and New Zealand (Lovelock *et al.,* 2007a). The limitation of P and N for the growth of mangroves also showed latitudinal pattern, indicating differing nutritional requirements in relation to latitude, with N found to be more limiting at the higher latitudes (Lovelock *et al.,* 2007b). It was also suggested that forests fringing the ocean i.e. ‘open’ systems are N limited while those internal to the islands and permanently flooded i.e. areas with low exchange rates with the oceans are P limited (Smith, 1984; Medina *et al.*, 2010).

However, not one of the above listed factors is exclusively determinant for the distribution of mangroves, because some of these factors can greatly influence each other. For example, the availability of nutrients to mangrove plant production is controlled by a variety of biotic and abiotic factors such as tidal inundation, soil type, redox status and microbial activities of soils, plant species, litter production and decomposition. On the other hand, topographic factors such as elevation, determine the frequency and duration of tidal inundation, which subsequently affects the salinity, oxidation state and nutrient availability of the soil, resulting in complex patterns of nutrient demand and supply that contribute to the variable structure of mangrove forests.

It is rather exceptional that mangroves are able to grow in the arid environment of Sudan and the Red Sea area in general, unless in other areas where winter rains occur. The diversity of the mangroves in Sudan is very low, with monospecific stands of *Avicennia marina* (Mohammed, 1984; Untawale *et* *al.*, 1992; PERSGA, 2004; Kathiresan & Rajendran, 2005). Nevertheless, other species such as *Rhizophora mucronata* and *Bruguiera gymnorhiza* were earlier found in the country but are not recorded recently anymore (Andrews, 1950; Kassas, 1957; .Zahran, 1965; Kassas & Zahran, 1967).

The distribution of the Sudanese mangroves is constrained by all of the above mentioned factors, including the absence of diurnal tides. While the precipitation does not exceed 150 mm/year (Musa, 1991), the seasonal ranges of air and water temperatures (Section 1.1.2 and 1.1.3) are exceeding the seasonal range required for the extensive development of mangroves (less than 10°C). This suggests that the limiting condition for mangrove distribution is not only a climatic factor, but that the development of mangroves in Sudan can be explained by the combination of temperature and aridity (Quisthoudt, 2013). As mentioned before, salinity along the Sudanese coast is considerably high and can be considered as an important factor in determining the distribution of the mangroves too. The high salinity also may have influenced mangroves by reducing the diversity of trees to only one salt-tolerant species. Also the local topography of the Sudanese coast, being in a narrow coastal plain with a small slope in addition to the absence of permanent rivers that can bring alluvial soils, may have influenced the distribution pattern of mangroves. *A. marina* stands are found only along the shore-line, on near-shore islets and fringing tidal inlets or creeks, which extend landwards along depressed areas of various sizes, locally known as “mersa”. The density and size of the *A. marina* stands increases towards the southern coast, especially at the mouths of khors that enter the sea from mountains, and that support muddier substrates and receive more freshwater influx from surface run-off. These khors are mostly dry except during the occasional rain storms that supply freshwater and sustain mangrove life. Nevertheless, at some localities in the northern parts, the better oxygenated, sandier substrate and considerable underground freshwater seepage may favor growth of *Avicennia* trees to a greater height and “Girth at Breast Height (GBH) or circumference or diameter usually measured at 1.4 m from ground level”, (PERSGA, 2004). Low phytoplankton productivity and low nutrient concentrations (phosphate, nitrate and nitrite) along the Sudanese coast suggest that the growth of mangroves is limited by the availability of these nutrients too.

1.3. Mangrove ecosystem functions

1.3.1. Mangrove forest production

Mangrove trees are the foundation species in mangrove ecosystems (Ellison *et al.*, 2005). Although early scientists regarded mangrove forests as unimportant transitional communities with a low productivity, today, their productivity is viewed as rather high and important for supporting mangrove and adjacent coastal food webs, as well as for the stability of mangrove-fringed coasts. The productivity of mangrove forests is, however, highly variable over both large (latitudinal) and smaller (hydrological) scales (Bouillon *et al.*, 2008; Alongi, 2009). Variation in the primary productivity of mangrove forests emerges from a wide range of biotic and abiotic factors and results in highly variable environments for seedlings and other plants and fauna (Feller *et al.*, 2010). Net primary productivity (NPP) of forests, determined by the balance of the total CO_2 fixed by the forest and total plant respiration, has been generally underestimated in the past (Bouillon *et al.*, 2008, Alongi, 2009). The estimated net primary production based on light attenuation for different mangrove forests in Papua New Guinea and northern Australia, ranges from 18 to 34 kg C/ha. However, estimates of the productivity of mangrove forests based on photosynthesis rates on the west coast of Peninsular Malaysia were nearly 10 times greater than previous production estimates (Clough *et al.*, 1997; Alongi, 2009). These estimates indicate that, on an areal basis, mangroves are usually more productive than salt marshes, seagrass, macroalgae, coral reef algae, microphytobenthos, and phytoplankton (Alongi, 2002). The productivity of the Red Sea mangroves in general is relatively low, despite the fact that few quantitative studies have been attempted (Por *et al.*, 1977; Dor & Levy, 1984; Crossland *et al.*, 1987). Gross productivity of the poorly-developed mangroves on the northern side of the Red Sea is probably less than 0.5 $kg.cm^2$/year, whereas in the well-developed mangals of the southern Red Sea, it can be 1 $kg.cm^2$/year (Sheppard *et al.*, 1992; Fouda & Gerges, 1994).

Other primary producers living in mangrove ecosystems that are usually not considered in NPP estimates include the phytoplankton in tidal waters, benthic cyanobacterial and microalgal mats, algal turfs, and distinctive root epiphytic algal communities (the Bostrychietum) that adheres to aboveground roots and stems. These components are highly productive, contributing up to 15% to the forest gross primary productivity (Dawes *et al.*, 1999). Nevertheless, their contribution to the overall primary production of the ecosystem is highly variable, depending on factors such as climatic variation (e.g. light) and their relative proportions compared to vascular plants (Ong & Gong, 2013). These components may be more important than their absolute contribution to NPP because they may be preferentially decomposed and consumed (Bouillon *et al.*, 2008) and thus potentially play a key role in nutrient cycling (Lee & Joye, 2006).

1.3.2. Carbon and nutrient cycling

The estimated photosynthetic carbon fixed by mangroves in excess of ecosystem requirements approaches 40% of the net primary production (Duarte & Cebrian, 1996). This implies that the produced carbon is either stored in the wood which is eventually decomposed within the system, accumulated in sediments, or exported to the adjacent coastal habitats.

Mangrove average carbon budget estimates indicate that, 9% is consumed by herbivores, 30% is exported, 10% is stored in sediments, and 40% is decomposed and recycled within the system (Duarte & Cebrian, 1996). However, the values listed above are closely linked to the studied systems and, therefore, cannot be generalized.

Nutrient cycling in mangrove forests reflects a balance between nutrient inputs, availability, and internal cycling, which in turn are intimately linked to microbial mediated carbon turnover in mangrove soils (Lee *et al.*, 2008). Decomposition of the litter contributes to the production of dissolved organic matter (DOM) and the recycling of nutrients both in the mangal and in adjacent habitats. The nutrient cycling begins when leaves fall from the mangroves and are subjected to a combination of leaching and microbial degradation (Lee *et al.*, 1990; Chale, 1993). Leaching alone removes a number of substances and can produce high levels of DOM (Benner *et al.*, 1990). Microbial degradation alters soil nutrient concentrations and nutrient cycling through the processes of denitrification, which reduces inorganic nitrogen concentrations and, thus, limits the plant production (Joye, 2002); and through microbial nitrogen fixation, which increases nitrogen available for plant production (Joye & Lee, 2004). The rate of litter decomposition can be affected by a number of factors, including species, latitude, environmental variables (e.g. tidal height), rainfall and temperature, and feeding activities of invertebrates, which accelerates breakdown and decomposition of mangrove litter. For example, litter decomposition rates vary between mangrove species (Lu & Lin, 1990; Tam *et al.*, 1990). Kristensen *et al.* (1995) found that *Avicennia* spp. leaves decompose faster than *Rhizophora* spp. because they are thinner, sink faster and contain lesser tannins. In subtropical mangrove forests, senescent leaves of *R. mucronata* and *C. tagal* decompose substantially faster during the rainy season (Woitchik *et al.*, 1997). Mackey and Smail (1996) found significantly faster decomposition of *A. marina* debris in the lower intertidal zone with greater inundation. They also found an exponential relationship between leaf decomposition rate and latitude. Leaves decomposed more rapidly at lower latitudes, and they attributed the observed pattern to temperature differences. According to Camilleri (1992) the decomposition rate of mangrove litter is greatly affected by the feeding activities of marine invertebrates, which breakdown and process large volume of mangrove litter.

Mangroves contribute to around 15% of the organic carbon globally accumulating in marine sediments (Twilley *et al.*, 1992; Jennerjahn & Ittekkot, 2002) and to about 10% of the terrestrial dissolved organic carbon (DOC) exported to the ocean (Dittmar *et al.*, 2006). Most data on material exchange involve estimates of export of particulate organic carbon mainly as litter (about 40% of total mangrove litter) from mangrove estuaries (Dittmar *et al.*, 2006).

DOC exported from mangroves has a unique chemical signature, derived from degradation products of mangrove detritus incorporated into the soil and often seeping out of the porewater. The origin of the DOC is often deduced from a clear tidal signature, with mangrove DOC leaving the estuary and DOC of marine origin entering the estuary. DOC is often transported further offshore. However, interactions among productivity, geomorphology, and hydrology influence material exchange with tidal waters via outwelling and inwelling, thus also impacting the services provided by mangrove ecosystems within larger and connected coastal ecosystems (Alongi, 2009). The amount of organic detritus originated from mangrove and potentially available for export strongly depends on local conditions, which varies enormously among mangrove habitats. These include net forest primary production, tidal range, the ratio of mangrove to watershed area, lateral trapping, high salinity plugs, total mangrove area, frequency of storms, amount of rainfall, and extent of activities of crabs and other litter-feeding fauna (Twilley *et al.*, 1992; Alongi, 2009).

1.3.3. Food Webs and Energy Fluxes

Mangroves are transitional habitats between land and sea, thus, they play a central role in connecting both environments through transferring organic matter and energy fluxes across ecosystems. However, their contribution to the food web appears to be localized (Fleming *et al.*, 1990) since trophic analyses in mangrove habitats failed to provide convincing evidence that mangrove organic production is the basis of near shore secondary production, except in some restricted circumstances (Lee, 2005).

Mangrove forests have been described as detritus-based ecosystems where primary consumers play a minor role (Tomlinson, 1986). Mangrove detritus is probably more important as a substrate for microbial activity and nutrient regeneration (Kathiresan, 2012) and largely appears as a trophic dead end, so the carbon from the detritus is not transferred up the food chain, at least not in significant quantities (e.g. Bouillon *et al.*, 2004a). However, recent studies have shown that herbivory in mangroves is comparable to that of other temperate and tropical forests (Cannicci *et al.*, 2008). Similar to their role in other ecosystems, mangrove herbivores play important ecological roles that include increasing habitat and community complexity, creating light gaps, interfering with internal nutrient cycling, and increasing nutrient losses (Feller, 2002).

Mangroves may have strong trophic linkages with epibenthic invertebrates and fish living in the mangal and in nearby habitats (e.g. seagrass beds). For example, macrobenthic consumers of fresh mangrove leaf litter perform a role intermediate between the shredders in low order streams and the deposit-feeders in subtidal marine environments in terms of their contribution to organic matter flow and food generation for other consumers in the adjoined habitats (Lee, 2008). On the other hand, mangrove detritus may contribute significantly to the nutrition of some invertebrates living in tidal creeks (e.g. juvenile *Penaeus merguiensis* from Malaysian and Australian mangroves). These juveniles prawn feed directly on mangrove detritus, on other small detritivores invertebrates, on benthic microalgae growing in the mangal, on a variety of cyanobacteria and microalgae that live on submerged portions of the mangroves and on leaf litter (e.g. Newell *et al.*, 1995; Sheridan, 1991; Farnsworth & Ellison, 1995). However, many macrobenthos species apparently do not utilize mangrove detritus but other sources (see e.g. Bouillon *et al.,* 2004b). Mangroves apparently contribute little to the carbon assimilation of most fish; with the exception of syngnathid fish (pipefish) in the Negombo Estuary of Sri Lanka which feed primarily on mangrove litter (Pinto & Punchihewa, 1996). It was also found that wet-dry tropical estuarine mangroves, where fresh water is intermittent, are the most important contributors to the diet of fish species *Leiognathus equulus* (Abrantes *et al.*, 2015).

1.3.4. Connectivity

The ecosystems of mangroves, seagrasses and coral reefs are functionally linked. This linkage is, however, not well enough understood to support management practices. The health and productivity of individual habitats existing in the coastal zone are dependent on a number of complex interactions, which are classified into five major types: (1) physical processes, (2) transfer of dissolved organic matter (3) particulate organic matter, (4) animal migration and (5) human impacts (Kathiresan & Alikunhi, 2011). Among the above mentioned interactions the exchange of nutrients (organic matter) and animal migration are of particular importance. Exported mangrove litter is an important source of detritus in seagrass ecosystems (Alongi,, 1989; Bouillon *et al.,* 2004b). The nutrients released from the microbial decomposition of mangrove litter enhance the microbial planktonic populations. The organic matter associated with microbes is transferred to adjacent coral reef ecosystems through seagrass beds. In this respect, mangroves contribute significantly to the marine food web through the indirect pathway and create interconnected coastal ecosystems (Fig. 1.6; Kathiresan & Alikunhi, 2011).

Mangrove ecosystems are important for fish production. They serve as nursery, and feeding and breeding grounds for many fishes and shellfishes. Nearly 80% of the fish catches are directly or indirectly dependent on mangrove and other coastal ecosystems worldwide (Kjerfve & Macintosh, 1997). Mangroves and seagrass beds are vital nursery areas for many important coral reef fishes (Mumby *et al.*, 2004; Unsworth *et al.*, 2008; Nagelkerken *et al.*, 2014). Mumby and Hatings (2008) showed that mangrove-based ontogenetic migrations of parrotfish may, through a trophic cascade on macroalgae, enhance the recovery rate of mid-shelf reefs from hurricanes. Therefore, they are interlinked with coral reefs through animal migration and dispersal. Inter-habitat migrations occur within invertebrate (Hiddink, 2003) and vertebrate fauna (Law & Dickman, 1998; Nagelkerken *et al.*, 2000a,b).

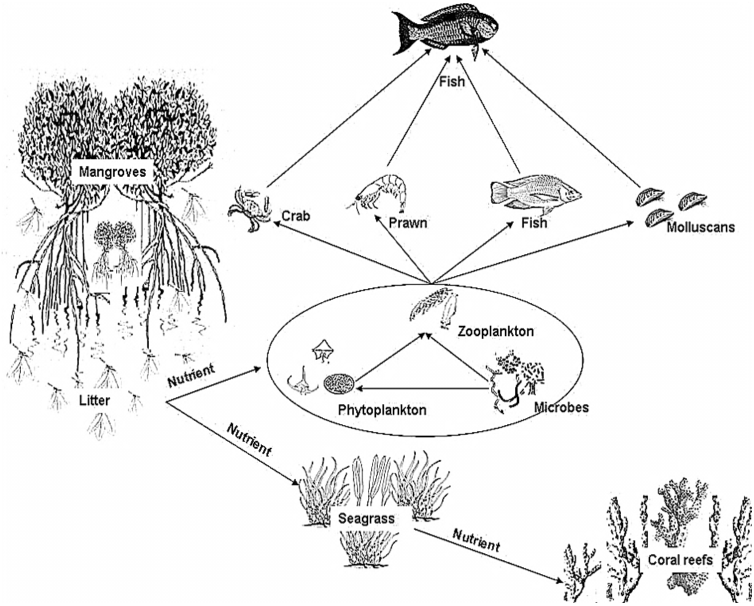


Figure 1.6. Schematic diagram representing trophic and functional linkages among coastal ecosystems. From Kathiresan and Alikunhi (2011).

Mangroves can also be connected to the seagrass bed and coral reefs through other provided services such as trapping of sediment, and thus acting as sinks to the suspended sediments to keep good quality water for seagrass and coral reefs (Woodroffe, 1992; Wolanski *et al.*, 1992; Wolanski,, 1995; Furukawa *et al.*, 1997). Disappearance or removal of mangroves can alter the connectivity between different components of the marine environment and, thus, can have negative consequences such as decrease in fisheries production (.e.g. Primavera, 1997) and deterioration of other coastal habitats (e.g. Koch *et al.*, 2009).

The Sudanese mangroves, despite their small areal extension and marginal location, are also considered important for the ichtyofauna and some macro-invertebrates, although evidence is limited only to few studies (El Hag, 1978; Brandford, 1980; Khalil, 1994; Khalil & Krupp,1994). These studies, which were carried out in mangrove areas and associated lagoons, as well as in the open shore in the southern part of the Sudanese coast, have reported that mersas and associated mangrove stands are considered as breeding grounds and nurseries for several fish and shrimps species, and important habitats for a number of commercial shrimp species in the Tokar Delta area including the species *Penaeus semisulcatus, Penaeus latisulcatus, Penaeus japonicus, Penaeus monodon, Penaeus indicus, Metapenaeus monoceros* and *Metapenaeus stebbingi* (El Hag, 1978; Brandford, 1980). Khalil (1994) described the relations of fish species to mangroves in the Sudanese Red Sea and identified three main categories:

I. True residents, which spend their entire life cycle in the mangroves. This category includes the fish species *Aphanius dispar*, *Gerres oyena* and some gobiids.
II. Closely associated species, which are found in the mangroves as juveniles or juveniles and sub-adults. These species apparently utilize the mangroves as nursery and feeding grounds and include the fish species *Acanthopagrus berda*, *Chanos chanos*, *Crenidens crenidens*, *Hypoatherina temminckii, Leiognathus equulus, Terapon jarbua, Pomadasys commersonni* and some *Mugilidae* spp.
III. Loosely associated species, which occur in the mangroves as occasional visitors entering there searching for food or protection e.g. *Sillago sihama, Thryssa baelama*.

Most of the extensive mangrove stands are located at the mouth of khors, which bring a lot of sediment load during the rainy season. By trapping these sediments, mangroves provide good quality water for both the seagrass bed and coral reefs and protect them from deterioration.

1.3.5. Translation of ecological benefits into direct human benefits

The economic value of natural products and ecosystem services generated by mangrove forests is generally underestimated (Barbier, 1994). As a consequence, mangrove ecosystems have become prime candidates for conversion into large scale development activities such as agriculture, aquaculture, forestry, salt extraction and other infrastructure. Evaluation of the importance of mangroves for society requires insight into the flow of products and services within the social system of coastal communities, and how they are linked and influenced by domestic and international markets and institutions. It also requires insight into the biophysical links within and between mangroves and other ecosystems for the generation of natural products and ecological services. The economic benefits provided by an environmental good or service is the sum of what all members of society would be willing to pay for it. Therefore, it is misleading to characterize all ecosystem services as ‘‘benefits’’ (Barbier *et al.*, 2011). Mangroves provide a number of directly or indirectly derived highly valued human benefits including goods (such as raw material and food) and services including coastal protection, erosion control, water purification, supporting of fisheries, carbon sequestration, tourism, recreation, education, and research.

Of the ecosystem services listed above, three have received most attention in terms of determining their value to coastal populations. These include: (1) their use by local coastal communities for a variety of products, such as fuel wood, timber, raw materials, honey and resins, and crabs and shellfish; (2) their role as nursery and breeding habitats for offshore fisheries; and (3) their propensity to serve as natural ''coastal storm barriers'' to periodic wind and wave or storm surge events, such as tropical storms, coastal floods, typhoons, and tsunamis. For example, in Thailand, the net present value (NPV) arising from the net income to local communities from collected forest and other products and shellfish was estimated in 1996 between US$ 484/ha and US$ 584/ha. In addition, the Net Present Value (NPV) of mangroves as breeding and nursery habitat in support of offshore artisanal fisheries ranged from US$ 708/ha to US$ 987/ha, and the storm protection service was estimated between US$8966 and US$10821/ha (Barbier, 2007). Such benefits are considerable when compared to the average incomes of coastal households. Coastal protection measured by the ability of mangroves to attenuate and/or dissipate waves and wind energy was estimated at US$8966 to US$10821/ha (Barbier, 2007). Erosion control services provided by sediment stabilization and soil retention in vegetation root structure was estimated at US$3679/ha/year (Sathirathai & Barbier, 2001). Support for fisheries by providing suitable reproductive habitat and nursery grounds and sheltered living space was estimated at US$708 to US$987/ha. Carbon sequestration generated by biological productivity, biogeochemical activity, and sedimentation was estimated at US$30.50/ha/year (Chumra *et al.*, 2003).

1.4. Mangrove system analysis

The coupling of mangroves to coastal food webs has been analyzed using a number of approaches including energy flux and ecosystem mass balance, and abundance of natural isotopes (Twilley, 1995). On the other hand, conceptual and simulated models are important in system ecology because they can assist in understanding the relative importance of the food sources to different marine fauna and can be very useful in explaining the contrasting findings of the contribution of mangroves to the coastal food web generated by stable isotope approaches. They can especially be used to highlight the gaps in our knowledge and indicate the impact of human disturbances on the ecosystem.

1.4.1. Energy flux and ecosystem mass balance

Mangrove ecosystems have been modeled in terms of energy and material fluxes by Odum and Heald (1975) and others. They reported that the major energy flow is via the detritus food chain and not the grazing food chain demonstrating, as mentioned earlier, that particulate organic matter is exported from mangrove forests to adjacent waters, while mangroves may serve as a nutrient sink for importing inorganic nutrients. The outcome of this model, however, appeared highly variable when compared between different mangrove sites (Robertson & Alongi, 1992).

1.4.2. Stable isotope analysis

More recent, stable isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) are used as integrators and tracers of ecological processes (Robinson, 2001). They provide ecological information across a range of spatio-temporal scales i.e. from cell to ecosystems and across time scales of seconds to millennia (Dawson *et al.*, 2002). Over the last few decades, the use of stable isotope ratios in ecological studies has increased greatly, most notably in the area of trophic ecology and food webs (Peterson & Fry, 1987; Fry, 2006). However, applications of stable isotopes in food web studies have been mostly qualitative to date, prompting the recent development of quantitative approaches to investigate different aspects of trophic ecology and food web structure using stable isotope data (e.g., Bearhop *et al.*, 2004; Newsome *et al.*, 2007; Schmidt *et al.*, 2007).

Stable isotope analysis offers one of the possible approaches to study the incorporation of different carbon sources into food webs on the condition that there is a sufficiently large difference in the isotopic composition of the different primary carbon sources (terrestrial material, phytoplankton, benthic microalgae). Therefore, they have been used to study benthic food webs in a variety of ecosystems (e.g. Dauby, 1990; Riera *et al.*, 1999; Yoshii *et al.*, 1999; Lepoint *et al.*, 2000). Several quantitative stable isotope studies have been carried out in mangrove ecosystems as well (e.g. Rodelli *et al.*, 1984; Newell *et al.*, 1995; Loneragan *et al.*, 1997; Marguillier *et al.*, 1997; Dehairs *et al.*, 2000; Hsieh *et al.*, 2002; Lee, 2000; Bouillon *et al.*, 2002a). They have substantially increased the knowledge on mangrove food webs since the publication of the work of Odum and Heald (1975), and potentially provide indications of the origins and transformations of organic matter (e.g. Newell *et al.*, 1995; Bouillon *et al.*, 2008).

Despite the extensive studies on estuarine food webs, the importance of contributions from mangrove litter to the diet of marine fauna has not been resolved yet. The general conclusion resulting from many studies concerning the benthic communities in the aquatic environment adjacent to mangrove forests is that mangrove carbon is only used in a very restricted zone in and near mangrove forests, but its role is rapidly taken over by phytoplankton (Rodelli *et al.*, 1984; Zieman *et al.*, 1984; Fleming *et al.*, 1990; Primavera, 1997; Loneragan *et al.*, 1997; Lee, 2000; Hsieh *et al.,* 2002; Bouillon *et al.*, 2002b; Macia, 2004), except in some restricted circumstances (Lee, 2005). While some studies indicate that there is only little direct contribution of mangrove to the diet of benthic macro-invertebrates (e.g. Tue *et al.*, 2012) and fish (e.g. Nyunja *et al.,* 2009; Laura *et al.*, 2014; Shahraki *et al.*, 2014), some other studies confirmed the importance of mangrove leafs to the diet of fish (Zagras *et al.*, 2013) and mangrove derived carbon for fish and prawn (Sheaves *et al.*, 2012; Al-Maslamani *et al.*, 2013 ; Abrantes *et al.*, 2015).

Community-wide metrics based on stable isotope representations of species' niches have been introduced by Layman *et al.* (2007a) as an additional tool to describe the trophic structure at species or community level. Since then, they have been used to quantify trophic niche width collapses following aquatic ecosystem fragmentation (Layman *et al.*, 2007b), hydrological changes (Delong *et al.*, 2011), or the introduction of exotic species (Jackson *et al.*, 2012), and to identify patterns in food web structure in saline lakes (Cooper & Wissel 2012) or estuaries (Abrantes *et al.*, 2014).

As mentioned earlier, the geophysical processes and the landscape setting are very important in the development and functioning of mangrove forests. Twilley *et al.* (1998) proposed geomorphic and topographic elements to be used to characterize different mangrove systems, based on the environmental setting hypothesis (Twilley, 1995), as a useful framework to summarize food web patterns in estuaries and coastal waters as well as other ecosystem functions of mangroves. Twilley *et al.* (1998) classified mangrove geomorphic types based upon the degree of terrigenous input and position of the mangrove forest relative to this input into delta, lagoon, delta/lagoon, or estuarine mangroves (Fig. 1.7). The ecogeomorphic classifcation of mangroves describes the nature of geophysical processes of coastal environments that along with ecological processes account for the biological and functional diversity of mangrove wetlands (Thom, 1984; Woodroffe, 1992; Twilley, 1995; Twilley *et al.*, 1996; Twilley, 1997). According to this classification, there will be variability in ecosystem dynamics resulting from the differential act of the geophysical processes, forcing functions or stressors that dominate coastal processes including soil type, salinity, tidal amplitude, rainfall, nutrients, hydro-period, cyclones, drought, and salt accumulation; with structural complexity and productivity increasing from dwarf to riverine types (Lugo & Snedaker, 1974). The increase of geophysical energies in a coastal region will promote greater mangrove biomass and productivity, forest regeneration rates, landscape ratios (mangrove to open water area), and exchange of nutrients and organic matter with coastal waters (Fig. 1.7). Thus the quantity of detritus export from mangrove wetlands depends on the type of environmental setting (Twilley, 1998). Changes in the environmental settings that regulate the exchange of water, energy and materials across coastal landscapes can control levels of biological diversity as well as primary and secondary productivity (Risser, 1995; Carter *et al.*, 1994).

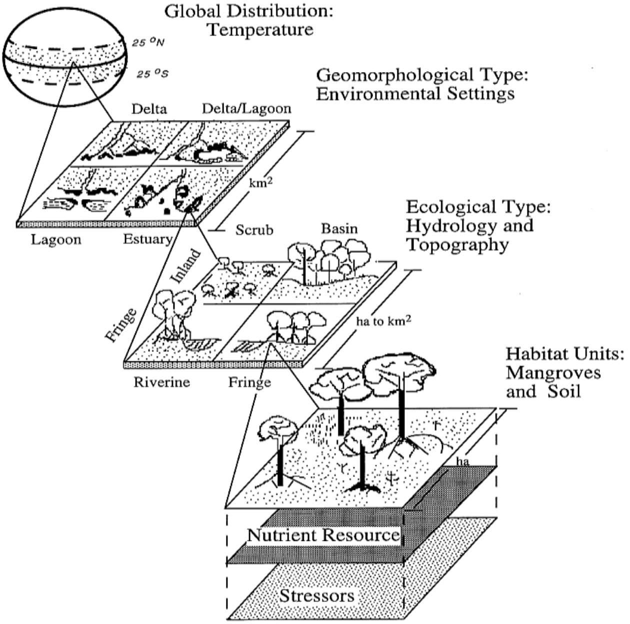


Figure 1.7. Hierarchical classification system to describe different patterns of mangrove structure and function based on geomorphological and ecological factors and stressor along gradients from fringe to more inland locations. From Twilley *et al.* (1998).

1.5. Mangrove destruction and fragmentation

Fragmentation, in general, is defined as the loss and isolation of natural habitats (Meffe & Carroll, 1997). Ecosystem or habitat loss refers to the disappearance of an ecosystem, an assemblage of an organism, or to the alteration of the physical environment in which they exchange energy and matter to the point that it is rendered unfit to support the species dependent upon it as their home territory (Fahrig, 2003).

The survival of mangroves, throughout their range, is at risk due to destruction and fragmentation. The global mangrove forest has decreased by 35% of its total area over the past 30 years. This equals a total loss rate of 2.1% or around 3000 square kilometers of mangroves per year (Valiela *et al.*, 2001). If the destruction of mangroves continues, they may likely be totally lost within 100 years or at best prediction forests might be reduced to relic patches too small to support the diversity of organisms that depend on them (FAO, 2003; Duke *et al.*, 2007; Luther & Greenberg, 2009).

Mangroves commonly occur in discrete patches and are thus naturally fragmented. However, their integrity may become more fragmented due to natural forces acting over a long time frame of thousands or millions of years such as climate change (*e.g*. glaciations, changes in rainfall, sea level rise) or over short periods (decades or months) such as cyclones, El Niño-Southern Oscillation, tsunamis, and diseases. In addition, many human activities that emerge from population expansion and intervention such as resource extraction in terms of felling for wood products, mangrove clearing for agriculture and pond aquaculture, urban development (*e.g*. construction of buildings, roads etc.), change of tidal and hydrological regimes, and industrial development are the chief causes of mangrove destruction and fragmentation (Alongi, 2002; Laverty & Gibbs, 2007).

1.5.1. Impact of mangrove fragmentation and destruction

Loss and fragmentation of ecosystems are tightly coupled processes as the pattern of loss affects the degree of fragmentation. Fragmentation is a consequence of loss (Haila, 1999), in which mangroves degrade to its lowest quality, and is best thought of as the subdivision of a formerly contiguous mangrove into fragments that lack an effective ecological connectivity. It is often difficult to distinguish between the effects of these two processes, since they often happen simultaneously (Laverty & Gibbs, 2007). Loss of habitat impacts species principally by reducing available resources and microenvironments. On the other hand, fragmentation has additional consequences by reducing continuity and interfering with species dispersal and migration, thereby isolating populations and disrupting the flow of individual plants and animals (and their genetic material) across a landscape (Laverty & Gibbs, 2007). In addition to the abovementioned effects, fragmentation and the resulting isolation of a forest can have a variety of physical impacts on the forests by affecting temperature, light, wind, and water conditions (Saunders *et al.*, 1991). Generally, habitat loss is of far greater consequence to biological diversity than habitat fragmentation (Fahrig, 2003).

1.5.2. Impact of mangrove clearing

The characteristics of mangrove wood being of high calorific value and rich in phenols, and hence, highly resistant to deterioration, make them highly suitable for charcoal and firewood, chipboard industry, and quality paper. Mangrove clearance is the process of the instance clearing of mangrove trees' green and woody parts, resulting in complete eradication of the mangrove forest. Therefore, it is different from mangrove destruction and fragmentation where damage is partly caused to the mangrove trees or forest. Clearance of mangroves due to overexploitation of resources and habitat conversion for aquaculture are the main drivers behind mangrove loss (UNEP, 2006). In Sudan, mangroves were cleared mainly for coastal development such as building of new harbors or expanding of the existing ones. Recently, about 2 ha of mangrove area were cleared in 2012 to establish a new harbor for export of livestock. In addition, mangroves have been destroyed by the poor design of an outfall access road and recreational areas, and by salt works construction; i.e. saltwater access canals and banks which were cut through mangrove stands. Mangrove clearance and change in land use can predominantly affect mangroves ecosystems and alter the functions which they provide. At global scale, loss of mangrove may have a significant impact on global carbon budgets, because mangroves fix and store significant amounts of carbon (Cebrian, 2002). At a local scale, harvesting and clearance of mangroves, even at a small scale, reduce the live stem, above-ground biomass and increase the canopy gaps between less dense and smaller trees (Alongi & de Carvalho, 2008). Mangrove eradication can cause changes in the sediment from a muddy to a sandier environment (Alfaro, 2010). It can promote concentrations of dissolved sulfide, metals, and ammonium in the interstitial due to enhanced soil desiccation, declined solute uptake, and O_2 translocation to live roots (Alongi & de Carvalho, 2008). Mangrove clearance can also lead to reduction in bacterial diversity and nitrogen fixation rates, to formation of anaerobic soil, and changes in sediment organic carbon and other related biochemical/microbial parameters. The decline in live roots and the microbial metabolic activities can also result in shifts in composition of microbial communities (Sjöling *et al.*, 2005; Alongi & de Carvalho, 2008; Dinesh & Ghoshal Chaudhuri, 2013). Moreover, clearance can result in an increase in algal biomass and richness with dominance of specific groups of algae, such as cyanobacteria, due to change in abiotic factors (Granek & Ruttenberg, 2008), and ultimately leads to changes in faunal distribution. Other effects of mangrove clearance include a decrease in the availability of fish and prawns, increase in coastal erosion, and eventually reduction of seagrass and coral reefs (Fondo & Martens, 1998).

1.6. Benthic fauna

1.6.1. Mangrove as a habitat for benthic fauna

Benthic invertebrate communities in mangroves are generally separated into two major size classes. The meiofauna, generally defined as animals passing through a 1 or 0.5 mm sieve but being retained on a 42 or 38 µm mesh, and the macrofauna which are greater than 1 mm. Both groups often show marked zonation patterns, and colonize a variety of specific micro-environments within mangrove habitats (Nagelkerken *et al.*, 2008). While some species dwell on the sediment surface (epifauna) or reside in burrows or live beneath the surface of the sediment-water interface (infauna), others live on pneumatophores and lower tree trunks or prop-roots; they burrow in decaying wood, while some species can even be found in the tree canopies (Sasekumar, 1974; Ashton, 1999). Nematodes and harpacticoid copepods usually are the dominant meiofaunal taxa found in mangrove sediments. Other meiofauna taxa commonly found include some species of polychaetes, ostracods, oligochaetes, turbellarians and bivalves. Mangrove macrofauna, on the other hand, are represented by epifauna and infauna. The distinction between infauna and epifauna is, however, not always straightforward and related to the organisms' functional role. For example, many sesarmid crabs create extensive burrow systems, while others appear to find refuge in crevices from decaying wood or root structures, or their burrowing status is unknown (Gillikin & Kamanu, 2005).

1.6.2. Factors affection the distribution of benthic fauna

Studies on meiofaunal and macrofaunal communities within mangrove sediments have highlighted the importance of a number of physicochemical factors in regulating their distribution and abundance including tidal height, salinity, temperature, dissolved oxygen, organic content, sediment grain size, sediment-associated tannins, depth of the redox potential discontinuity (reducing) layer within the sediments, and distribution along the intertidal-subtidal gradient in estuarine environments (Somerfield *et al.*, 1998; Coull, 1999). In addition, these biotas represent an important food source for many other larger taxa, while competition both among individuals within a species as well as among species, can also play a major role in limiting faunal abundances and distribution. The combined effect of the above mentioned physicochemical factors, and the predation and competition effects resulted in very complex spatial and temporal patterns in the structure of these assemblages (Kennish, 1986; Levinton, 1995; Valiela, 1995).

Meiofaunal distributions are patchy, and vary seasonally (Alongi & Christoffersen, 1992), leading to widely varying estimates of abundance. The majority of individuals are concentrated near the sediment surface, especially in muds (Somerfield *et al.*, 1998), while in relatively oxic sandier sediments more specimens are found below the sediment surface (Vanhove *et al.*, 1992; Nagelkerken *et al.*, 2008). Mangroves are characterized by depositional fine sediments, often with high organic content. Nematodes, harpacticoid copepods and Turbellaria usually constitute the most dominant taxa in mangrove. Besides some meiofauna taxa that survive in sulphidic environments based on chemosynthetic symbiosis, such as the genus *Parastomonema*, family Siphonolaimidae, are known to occur in mangrove sediments (Somerfield *et al.*, 1998; Kito & Aryuthaka, 2006).

Macrofaunal communities in mangrove habitats consist mainly of gastropods, bivalves and brachyuran crabs. Gastropods occupy a wide range of ecological niches (Cantera *et al.*, 1983; Plaziat, 1984) and they can be found in various habitats within mangroves, such as on stems and roots and in the sediment. Gastropods can attain very high species diversity in some mangrove ecosystems and can even reach higher densities and biomass than brachyuran crabs in some cases. A number of gastropod genera (e.g. *Ellobium, Enigmonia*) and species (e.g. *Littorariascabra* and *T. palustris*), known fom tropical and sub-tropical areas of the Indo-Pacific, appear to occur exclusively in mangrove systems. Bivalves are often considered to be confined to a narrow seaward zone, due to feeding and larval settlement restrictions (Nagelkerken *et al.*, 2008 and the references therein). Ocypodid crabs (*Uca spp.* and *Macrophthalmus spp.*, or *Ucidescordatus*) in Central and South American mangroves and grapsid crabs (Sesarminae, *Metopograpsus spp.*, *Metaplax spp.*) in the Indo-Pacific, Thailand, Australia and Singapore, usually dominate the crab fauna and species often exhibit marked horizontal and vertical zonation patterns.

The fact that different mangrove plants have different environmental niches and affect their surroundings differently, may affect the distribution of benthic communities. It has been suggested that the difference in the distribution and the composition of meiofaunal and macrofaunal communities may be attributed to differences in tree root structure, the presence of specific tree species or tree diversity, and the physical and chemical nature of the leaf litter (Lee, 1998; Ellison *et al.*, 1999; Dahdouh-Guebas *et al.*, 2002). It also appears that the presence or absence of mangrove vegetation is relatively unimportant in determining the composition of meiofaunal communities (Nagelkerken *et al.*, 2008). However coarsening of sediments as a consequence of mangrove clearing will affect both the meio- and macrofauna since their assemblage structure strongly depends on the sediment composition too.

1.6.3 Functional role of benthic fauna in mangrove ecosystems

Despite the abundance and ubiquity of meiofauna, knowledge about their interactions and their role in the functioning of mangrove ecosystems is lacking. Macrofauna play a very important functional role by modifying the physical and chemical properties of mangrove sediments (Cannicci *et al.*, 2008). Although molluscs occupy all levels of the food web, as predators, herbivores, detritivores and filter feeders, their overall ecological role and the effects they exert within the mangrove ecosystem are far from clear (Cannicci *et al.*, 2008).

Crabs and gastropods exert extraordinary influence on a wide variety of mangrove processes (Lee, 1998; 1999; Kristensen, 2008). Through their consumption of mangrove leaf litter (e.g. Decapod: grapsid crab; Gastropoda: *Terebralia*), they significantly reduce the amount of detritus available for export, thus enhancing retention and recycling of nutrients and organic matter internally (Leh & Sasekumar, 1985; Micheli *et al.*, 1991; Emmerson & McGwynne, 1992; Lee, 1997; Cannicci *et al.*, 2008). Their wastes can support coprophagous organisms, further ensuring conservation of materials within the forest. Since propagule recruitment supports natural regeneration of mangrove forests, determining in the long term the structure and functioning of mangrove ecosystems, seed, seedling and propagule predation has been considered an important factor determining seedling distribution patterns in many mangrove stands (Cannicci *et al.*, 2008; Dahdouh-Guebas *et al.*, 2011; Van der Stocken *et al.*, 2012; Van Nedervelde *et al.*, 2012; Nayar *et al.*, 2012). Crabs are the main actors in this process, but our understanding of the strong impact of gastropods, by means of high and differential consumption of propagules, has greatly developed recently (Fratini *et al.*, 2001; Fratini *et al.*, 2008). Additionally, their selective consumption of mangrove propagules (e.g. Decapod: sesarmid crabs and hermit crabs; Gastropod: *T. palustris*) affects forest structure by reducing the recruitment and relative abundance of tree species whose propagules are preferentially consumed (Fratini *et al.*, 2004; Lindquist & Carroll, 2004; Bosire *et al.*, 2008). Bioturbation by crabs results in changes in soil texture and chemistry, surface topography, degree of anoxia, and abundance of meiofauna while stimulating microbial production. The presence of crab burrows enhances the flow of tidal water through the forest floor, speeding up not only the flow of water but also the exchange of the associated dissolved and particulate material between forests and adjacent waterways (Ridd, 1996; Cannicci *et al.*, 2008). A similar important effect is exerted by large mobile gastropods through destabilization of the sediment due to the tracks left by their heavy shells. The presence of adult individuals of *T. palustris* induces mud surface rearrangement, affecting the abundance of meiofauna communities (decreasing density) and of the cyanobacteria carpet (complete disappearance). Overall, this induces a general modification of the biological, chemical and physical parameters of the mangrove soil surface (Carlen & Olafsson, 2002)

Crabs and gastropods, therefore, represent keystone species in mangrove ecosystems. Recent work has focused on clarifying the trophic role of crabs, especially on the positive feedback loops and interactions with trees and other flora and fauna in relation to food availability (Ashton, 2002; Kristensen & Alongi, 2006), and their reproductive and life history strategies in relation to tree composition and environmental factors (Lee & Kwok, 2002; Koch *et al.*, 2005; Moser *et al.*, 2005). It has been found in mescosm experiments that the presence of the fiddler crab, *Uca vocans*, stimulated the growth and development of *A. marina* saplings but depressed the abundance and productivity of microalgal mats at the soil surface (Kristensen & Alongi, 2006).

1.6.4. Benthic fauna as bioindicator

Bioindicators are organisms or assemblages of organisms of which responses to change in the environment are considered to be representative to evaluate the quality of the environment (or a part of the environment). They have particular requirements with regard to a known set of physical or chemical variables. As such, changes in presence/absence, numbers, morphology, physiology or behavior of those organisms indicate that the given physical or chemical variables are outside their preferred limits. Positive indicators, also named opportunistic species such as some polychaete worms (Méndez *et al.*, 1997), tend to increase in abundance in disturbed areas, outcompeting original species. Negative indicators are usually key species in the environment that tend to decrease in biomass and show reduced growth rates after change (e.g. Crouau & Moia, 2006; LeBlanc, 2007; Amara *et al.*, 2009). They are efficient indicators of disturbance due to a general reallocation of resources favoring tolerance to stress, by combating against contaminants, low oxygen levels or repairing damage (Diaz & Rosenberg, 1995; Wu, 2002).

Benthic macroinvertebrates have been used to monitor the human environmental impacts on water quality since the early 1900s (Wallace *et al.,* 1996). Despite the primary limitation of the use of macrofauna in biomonitoring, i.e. their patchy distribution and high sampling variability, and the taxonomic difficulties associated with their identification, they are ideally suited for assessing environmental quality, because of their well-established ecological roles in the function of aquatic ecosystem and their importance in the aquatic food web (Clements, 1997). On the other hand, the use of meiofauna as a biological indicator is a more recent development than the utilization of macrofauna in monitoring aquatic ecosystems (Coull & Chandler, 1992). The advantages of the former are numerous and strongly emphasized by Kennedy and Jacoby (1999), while some of the arguments traditionally advanced against their use underline difficulties in identification, the high rate of sampling frequency and the microscopic size of these organisms. However, new technologies and tools, such as standardized methodologies, electronic identification keys, molecular approaches and the creation of new indices, currently allow for and promote the use of meiofauna in ecological studies (Giere, 2009).

Effects of disturbances on communities can be divided into two categories: structural and functional. Structural responses are typically associated with community-level measures and generally include measures such as total abundances, species richness, diversity, and community composition; while functional traits mostly refer to such as trophic diversity. The changes in these measures are very important for better monitoring of ecosystem health. Recently the establishment of standardized methods appeared to be a worldwide priority since the assessment of the ecological quality status of an ecosystem became very important. The Water Framework Directive (WFD; EC, 2000) has suggested the use of biological, hydro-morphological, chemical and physico-chemical elements as indicators of good quality. Among the biological indicators, the use of benthos, phytoplankton, macrophytes, phytobenthos and fish fauna was highly recommended. Following the recommendations of WFD's, a number of community-based indices using macrobenthos as biological indicator of the quality of marine sediments such as AMBI, BENTIX, and BOPA were developed and have proven their usefulness in identifying the quality status of the sites studied. However, the use of meiobenthos and marine free-living nematodes is still at its initial stages (Borja *et al.*, 2000; Gómez-Gesteira & Dauvin, 2000; Simboura & Zenetos, 2002; Rosenberg *et al.*, 2004; Salas *et al.*, 2006; Borja *et al.*, 2008; de-la-Ossa-Carretero *et al.*, 2009; Moreno *et al.*, 2011). If new indices can be applied based on taxonomic data, particularly at genus level, they can be candidates to serve in monitoring environmental quality. They can especially assist in understanding the effect of natural and human impact on mangrove ecosystems.

1.7. Mangrove mapping

Mangroves have significant ecological and economical values. Therefore, up-to-date information with regard to the extent and condition of mangrove ecosystems is an essential aid to conservation and restoration measures, management policy and decision-making processes. Typical mangrove habitats are temporarily inundated and often located in inaccessible regions. Consequently, traditional field observation and survey methods are extremely time-consuming and cost intensive. To address these issues, large-scale and long-term monitoring, and cost-effective tools, which are available by means of remote-sensing technology (Blasco *et al.*, 1998; Mumby *et al.*, 1999) for mapping mangrove extent and distribution (Aschbacher *et al.*, 1995; Green *et al.*, 1998; Manson *et al.*, 2001), classification (Wang *et al.*, 2008), and their sustainable management (Dahdouh-Guebas, 2002) are required.

1.7.1. Methods

Conventional space-borne satellite sensors have played an important role in mapping mangrove distribution at both global (Spalding *et al.*, 1997; 2010; FAO, 2003; 2007; Giri *et al.*, 2011) and regional scales (e.g. Semeniuk, 1983; Giesen *et al.*, 2007; UNEP, 2007; Giri *et al.*, 2008). However, differences in sensors used, methods applied, the location of the research sites (which exhibit varying environmental conditions and plant biodiversity), and the purpose of each study make it extremely difficult to compare the success of the applied methods and their results. Data most commonly used stems from Landsat (MSS, TM and ETM+), SPOT XS, Ikonos, QuickBird, radar and aerial photography (Green *et al.*, 1998; Blasco *et al.*, 1998; Neukermans *et al.*, 2008; Dahdouh-Guebas *et al.*, 2005; Nascimento *et al.*, 2013).

There are two different approaches that are used to make classification maps based on remotely sensed data: the pixel based approach, which uses pixels as the fundamental unit of information; and the object-based approach, which uses the information about the spectral signature of each pixel and its spatial information (Wang *et al.*, 2004). In the first approach, a pixel is assigned to a category taking into account the spectral information of the pixel without noticing the neighboring pixels, while in the second approach the fundamental units of information are objects created by clustering pixels that have a similar spectral signature, shape, position and texture (Khorram *et al.*, 2012; Wang *et al.*, 2004). Mangroves in different regions of the world were successfully mapped using both approaches (see Table 1.1)

Table 1.1. List of studies used pixel and object based approaches for classification of mangroves in different regions of the world

Approach	Region	Author
Pixel based	Sri Lanka	Dahdouh-Guebas *et al.* (2005)
	Mexico	Hernandez Cornejo *et al.* (2005)
	United States	Everitt *et al.* (2008)
	Kenya	Neukermans *et. al.* (2008)
	New Zeland	Gao (2010)
	Global	Giri *et al.* (2011)
	Malaysia	Satyanarayana *et al.* (2011)
	Africa	Fatoyinbo & Simard, (2013)
Object based	Senegal	Conchedda *et al.* (2008)
	Thailand	Myint *et al.* (2008)
	Brazil	De Oliveira Vasconcelos *et al.* (2011)
	Brazil	Nascimento *et al.* (2013)
Both approaches	Panama	Wang *et al.* (2004)
	Australia	Kamal and Phinn (2011)

1.7.2. *Mangrove characteristics in Optical Remotely Sensed Data*

Mangroves grow at the land-sea interface, and therefore, the major features contributing to the pixel composition in remotely sensed imagery are vegetation, soil, and water. Any mixture of the individual surface appearance is also influenced by seasonal and diurnal intertidal interactions. These circumstances greatly affect the spectral characterization of the image components (Kuenzer *et al.*, 2011). Textural and spectral characteristics of the canopy and leaves are the main features used to distinguish among mangrove communities (Ramsey & Jensen, 1996). Their structural appearance, partially more homogeneous or heterogeneous, depends on several factors, such as species composition, distribution pattern, growth form, density growth, and stand height. The spectral variation of the canopy reflectance is a function of several optical properties, such as leaf area index (LAI), background reflectance, and leaf inclination. The spectral signature of a single species is defined by age, vitality, and phenological and physiological characteristics. Periodic climatic changes that influence the leaf dynamics of foliation and leaf senescence such as seasonal rainfalls may also have an impact on the spectral response (Blasco *et al.*, 1998; Díaz & Blackburn, 2003; Wang *et al.*, 2008; Kuenzer *et al.*, 2011). The spectral-response signal also depends on the internal leaf structure as well as the number of cell layers, intercellular spaces, air–water interfaces, and cell size. Additionally, intertidal effects and the soil type influence the spectral signal of plant communities (Blasco *et al.*, 1998; Díaz & Blackburn, 2003). Mangroves with lower-stand density are significantly affected by intertidal effects; the sparser the vegetation canopies, the greater the influence of the ground surface. For example, in medium-resolution imagery, the reflection of mudflats in the background may result in a spectral signal that can easily be confused with urban residential areas (Gao, 1998).

1.7.3. *Application of the remotely sensed data in mangrove research*

Medium-resolution imagery not only provides multispectral surface information on global and regional scale, but they also serve a multitude of applications including: (i) change-detection, which enables the evaluation of subtle changes over a long period of time (trends) as well as the identification of sudden changes due to natural or dramatic anthropogenic impacts such as tsunami destruction or conversion to shrimp farms (e.g. Seto & Fragkias, 2007; Giri *et al.*, 2008; Bao *et al.*, 2013; Kirui *et al.*, 2013; Carney *et al.*, 2014; Kuenzer *et al.*, 2014; Myint *et al.*, 2014; Xin *et al.*, 2014); (ii) assessment of the ecological status of mangroves by discriminating age, density, and species (Aschbacher *et al.*, 1995); and (iii) assessment of rehabilitation and plantation sites on previously degraded or non-degraded areas (Selvam *et al.*, 2003; Shuman & Ambrose, 2003; Klemas, 2013; Manik *et al.*, 2013; Monsef *et al.*, 2013).

1.8. Status of mangroves in Sudan

In Sudan mangroves are protected by Central Forestry and the Provincial Forestry Acts of 1932, Public Health Act 1973, the Forests Act of 1989. They are specifically protected under the Forests National Corporation Act of 1986, Environment Protection Act of 2000, issued by the Higher Council for Environment and Natural Resources (HCENR), the Environmental Protection Act (18 of 2001) and the Forests and Renewable Natural Resources Act (11 of 2002).

There are 19 mangrove stands distributed along the Sudanese coast. Their areal coverage was roughly estimated between 1.5 and 6 km² (Fig.1.8), which represent up to 0.02% of the total African mangrove, in different inventory studies published between 1980 and 2013. Thirteen of these mangroves were identified by FAO in 1995 as highly productive ecosystems that may play an important role in maintaining of biodiversity of the coastal habitats.

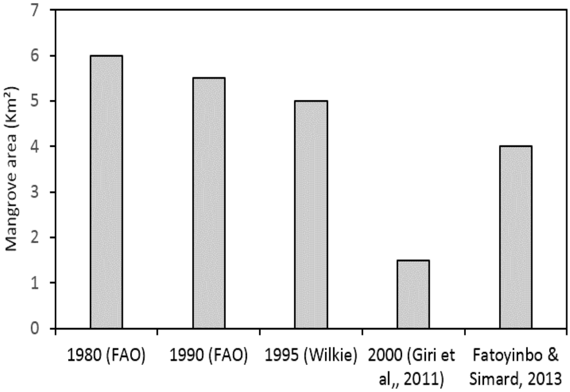


Figure 1.8. Mangrove areal coverage (km²) along the Sudanese Red Sea coast. The estimates by Giri *et al.* (2011) and Fatoyinbo and Simard (2013) are for the year 2000.

Despite their ecological values, the survival of the Sudanese mangroves is seriously threatened. Apart from mass mortality caused by increased temperature and decreased precipitation as a result of climate change, mangroves are also affected by various human activities such as camel grazing, cutting and removal of the mangroves, damming of freshwater from rain due to the lack of perennial rivers and the arid climate, diverting tidal water to feed salt pans, and shrimp farming (Mohammed, 1984; Untawale *et al.*, 1992; PERSGA, 2004). In addition, other human activities caused by rapid development and growth of coastal communities were also reported to have negative impacts. These include: coastal construction and urbanization of rural areas, changes in land use, oil shipping and production, coastal industrial development, oil or direct chemical and industrial inputs to the mangrove areas, marine dumping, tourism, boating and recreational fishing (PERSGA, 2004).

The prominent effects of these activities encompass considerable reduction in the green parts of the trees, dryness of the uppermost and outermost parts of the grazed branches, limiting mangrove growth to stunted multi-stemmed bushes, destruction of the seedlings and pneumatophores under the feet of camels, increased intrusion of saltwater leading to hyper-saline habitats unfavourable for mangrove growth, decline in the alluvium and sediment load deposited at the khor mouths, leading to shrinkage of the area occupied by mangroves, increased sand infilling and deposition of sand from land obstructing tidal inlets and channels through which tidal flow regularly floods the mangrove forests, organic enrichment from shrimp farms and pollution from oil spills and leakages into the adjacent mangroves (PERSGA, 2004).

1.9. Rationale of the study

Despite the relatively small areal coverage of mangroves in Sudan, they still hold characteristics and plenty of services that make them functionally and economically unique and valuable ecosystems. At present, increasing human but also natural stresses pose threats to the undisturbed mangroves and may cause rapid shrinkage of mangroves worldwide. There are nineteen mangrove stands found along the Sudanese coast line. The vast majority of them lack any legal protection. However, three out of these stands are about to be included within established marine protected areas or reserves. Given the absence of clear coastal zone management plans, the presence of numerous stakeholders, and the growth of coastal developments in the country, mangroves may be subject to further loss and degradation impacts resulting from changes in land use, in combination with climate change effects. Due to the major gaps in our knowledge about the physical environment of mangroves, their ecological functions and their associated faunal communities; short and long-term effects of natural and human induced impacts are still poorly understood. Therefore, there is a pressing need for applying ecosystem-based research that entails both basic fundamental and problem-oriented research, in order to understand community structure and functions in the complex framework of both biotic and abiotic interactions. This knowledge will allow to further develop guidelines for sustainable utilization and protection of the resources.

1.10. Objective

The aim of this study is to investigate the spatio-temporal dynamics of mangrove stands along the Sudanese coast and explore their ecological significance as habitat provider for infauna. The study will answer the following questions:

1. What is the recent historical and current extent of mangroves in Sudan?
2. Do Sudanese mangroves, as a marginal habitat, provide significant ecological services by supporting benthic communities?

The specific aims of this study were to:

i. Investigate the spatio-temporal distribution of mangroves along the Sudanese Red Sea coast.
ii. Provide insight into the ecological importance of these mangroves as habitat provider for the associated benthic communities represented by meiofauna and macrofauna.

The first objective is achieved by remote sensing, while the second objective is based on meio- and macrofaunal analyses.

1.11. Study site

The selected study area for the spatio-temporal distribution of mangrove covers the area that lies between 21°16'48"'N, 37°6'36"E to 18°0''N,38°34'E along the Sudanese coastline (Fig. 1.9). All sites were compared over the period between 1984 and 2013.

For a detailed study on mangrove change detection by remote sensing technique two sites were selected (Fig. 1.9). The first site Mersa Atta (19° 18’N, 37° 18’E), represents an area where shrimp farming takes place in the vicinity of the mangrove. The mangroves at this site are the most dense and extensive on the coast and located between the two main ports in the country, Sudan and Suakin. They grow along the mainland shore and on several small islets enclosing a shallow, wide, muddy lagoon. There are two mangrove stands: the northern and a southern stands, both extend as a narrow strip fringing the shore. The inner stands on the facing islets are dense and are made up of five patches which are separated from each other by narrow shallow channels, and from the shoreline mangroves by the deep and wide lagoon. A major threat to the existence of these mangroves is a saltpan which was established after July 1985 and which was expanded after the year 2000 to include a shrimp farm. However, no mangrove deforestation was associated with the construction of the shrimp ponds. Additionally, these mangroves suffer from heavy browsing and felling of trees before 2000, although since the establishment of the shrimp farm, access to this site by people from local communities for camel grazing and felling was banned.

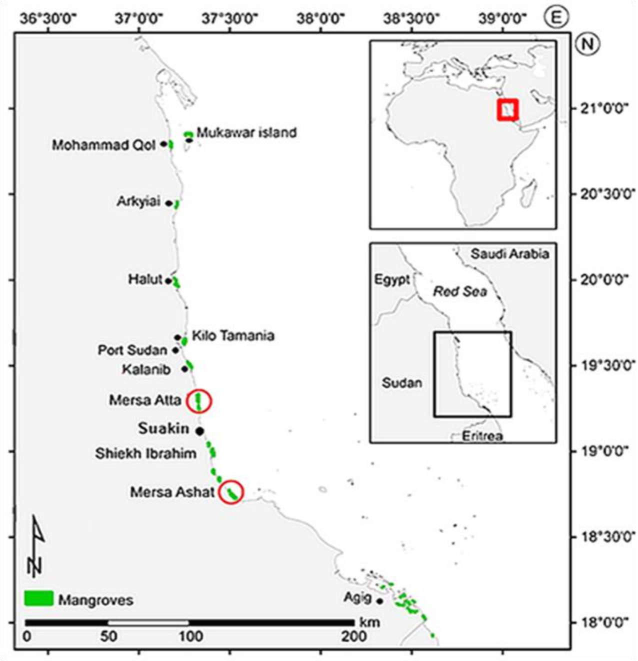


Figure 1.9. The spatial distribution of mangroves along the Sudanese coast. Red circles indicate the location of the change detection study sites at mersa Atta and mersa Ashat). Source: Flanders Marine Institute (VLIZ).

The second site Mersa Ashat (18° 45’N, 37° 30’E), represents a natural mangrove located in the southern part of the Sudanese coastline. The area has three stands: the northern and southern stands bend round the northern edge to enclose a large inlet. A third stand is located seaward on an elongated islet, forming the inner bank of the inlet. The rich mangrove stand at this site recieves considerable seasonal freshwater and alluvium during the rainy season. Compared to other mangrove areas in the country, the forests cover a wider area, well above 500 m width. However, this mangrove area has suffered from extensive mass mortality, especially the landward belt, during the period of 1997-2000 resulting from a prolonged period of declined annual rainfall and the effects of the 1997/98 El Niño. In addition, clear cutting of mangroves at this site occurred during the period of 2004-2007 (fishermen personal comments in 2010 and 2011, pers. comm.). The small scale cutting and the collection of dry limbs and tree trunks for fuel took place in the landward belt

(PERSGA, 2004) and was associated with the active commercial exploitation and processing of holothurians (sea cucumbers) collected from shallow waters around mangrove areas (UNEP, 2007; Samoilys, 2011). However, fishing for sea cucumber was prohibited in this area since then (Laverdiere, 2009). During the period of 2000-2004, the mangrove vegetation in this site had partly recovered (PERSGA, 2004).

The importance of mangroves for benthic fauna were assessed based on the selection of three sites representing three different habitats: a bare sand flat, an area with sparse, mainly dead mangrove trunks and an intact mangrove (Fig. 1.10). The bare sand flat and the cleared mangrove are both located at Mersa Ashat, at only 1.2 km distance apart (S1 and S2). The Sheikh Ibrahim intact mangrove (S3; 18° 59’N, 37° 24’E), is located about 26 km north to the cleared mangrove site and is characterized by the presence of *A. marina* stands. They consist of a narrow outer belt comprised of low-growing trees of 3-5m in height and 15-50 cm Girth at Breast Height (GBH). The inner zones consist of well-grown trees reaching up to 6-8 m in height and 35-70 cm GBH.

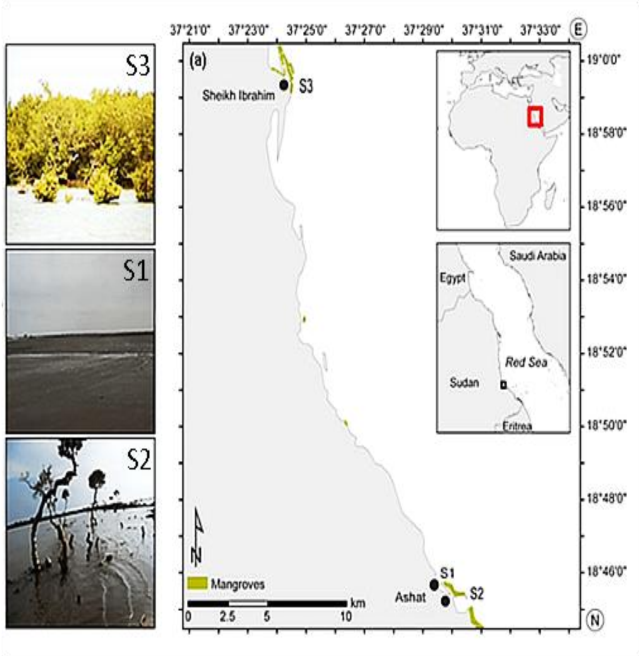


Figure 1.10. Location of the sampling for the study sites of potential effect of mangrove clearance (S1: bare sand flat, S2: cleared mangrove, S3: intact mangrove) south of Suakin city, Sudanese Red Sea coast. Source: Flanders Marine Institute (VLIZ).

Sampling for benthic fauna took place in December 2010. As explained before (see1.1.3.), there is no appreciable tidal regime in our study area (0.1-0.5 m). However, the seasonal sea level regularly moves up and down throughout the year, being about 1 m higher in winter than the average. Because samples were taken in winter when the water level was increased to about 50 cm high. Samples were collected from 3 zones referring to the seasonal water levels and further indicated as upper high water, mid water and low water levels as shown in Figure 1.11. This means that the high-water station (HW) was just below the water line mark during the high-water level in winter; the mid-water station (MW) was the area with remnants of mangrove trunks in the cleared mangrove habitat, and with mangrove stands in the mangrove habitat, or in the middle part of the bare sand flat; and the low-water station (LW) was just above the water line mark at summer low water level. The width of each zone from high to low water was about 40 m, 45 m and 15 m, respectively.

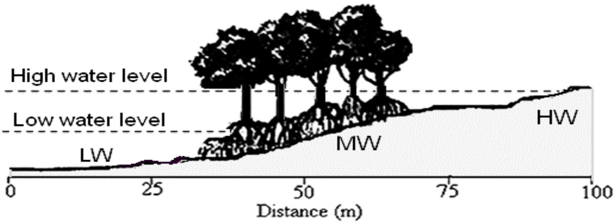


Figure 1.11. A diagram showing the position of the sampling station within each of the sampling sites in relation to seasonal water level. The low level refers to summer water levels, the high level refers to the winter situation.

1.12. Thesis outline

In the present research, we analysed the mangrove ecosystems along the Sudanese coast considering the importance of mangrove habitat for benthic fauna, compared to other coastal habitats. Each chapter of the thesis covers a stand-alone topic. However, some overlap in the method sections occurs in chapter 3, 4 and 5 although different benthic fauna components are focused on.

The study is organized into 6 chapters as shown in Figure 1.12. A brief background description of the study area, the rationale of the study, the overall objective, and an overview of the general aspects related to the thesis topic were presented in **Chapter 1**. In order to accomplish the objectives of the study, two main components of the mangrove ecosystem in Sudan, the vegetation and benthic fauna, were investigated.

The first component, the vegetation aspects in terms of temporal variation in mangrove extent and the factors that may affect their distribution is discussed in **Chapter 2**. Multi-temporal Landsat images covering the period from 1984 to 2013 were used to create the classified maps, and to estimate the areal coverage of mangroves as well as their fragmentation (based on various patch indices). To investigate the effect of human impact on mangroves, a change detection study based on post classification change detection matrix was performed in two sites representing a human-impacted site by shrimp farming and non-impacted mangrove forests.

The second component assesses, in three separate chapters, the ecological importance of mangrove to benthic macrofauna and meiofauna in terms of biodiversity, compared to other habitats. In **Chapter 3**, the spatial distribution and community composition of macrofauna was investigated in three study sites, i.e. a bare sand flat, a cleared mangrove and an intact mangrove, as well as in three stations established at each sites representing high-, mid- and low-water levels. Stable isotope-based community metrics (using dual isotopes of carbon and nitrogen) were also used to investigate patterns in trophic structure in these habitats. Habitats were compared in terms of community structure, standing stock, and structural and trophic diversity to evaluate the importance of the Sudanese mangrove as habitat provider for benthic macrofauna. This paper was published as: Sabeel R. A. O., Ingels J., Pape E., Vanreusel A. (2014) Macrofauna along the Sudanese Red Sea coast: potential effect of mangrove clearance on community and trophic structure. Marine Ecology, doi: 10.1111/maec.12184.

In **Chapter 4**, the meiofauna spatial distribution and community composition was investigated in a similar way as the macrofauna to evaluate if there is in difference in meiofauna and nematode assemblages between the three sites representing three different habitats. We further looked into the nematode assemblages by investigating their abundances, composition, structural and functional diversity. Data from various indices of structural and functional diversity were used to assess the quality of these habitats using the ecological quality status approach. The aim was to provide an insight on the spatial distribution and composition of meiofauna and nematode communities and to investigate the role of environmental variables. This work is submitted and currently under review for the Journal of marine biological association UK as: Sabeel R. A. O. and Vanreusel A. Determining the potential impacts of mangrove clearing on community structure and functional traits of meiofauna along Sudanese coast.

Chapter 5 assesses the patterns of nematode biomass using graphical methods such as the Abundance/Biomass Curve (ABC) and Nematode Biomass Size Spectra (NBSS). We aimed at comparing the ABC and NBSS patterns for nematode genera in the different studied habitats. Links between the sediment properties and patterns in nematode biomass NBSS were also examined. This manuscript was published as: Sabeel R. A. O. and Vanreusel A. (2015) Potential impact of mangrove clearance on biomass and biomass size spectra of nematode along the Sudanese Red Sea coast. Marine Environmental Research 103, 46–55.

Chapter 6 provides a general discussion, the findings of the previous chapters were incorporated into the DPSIR (Driving forces-Pressures-State-Impacts-Responses) framework. concluding remarks on the status of the Sudanese mangroves were drawn and management recommendations were suggested.

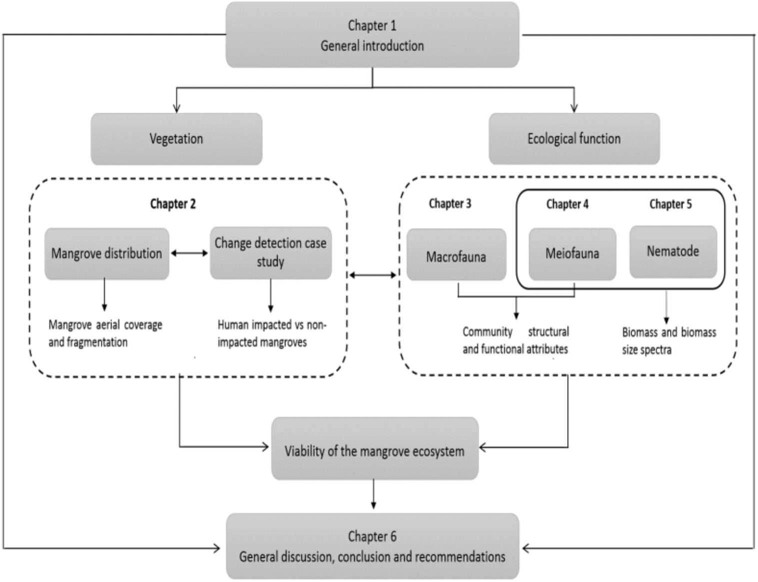


Figure 1.12. Schematic diagram outlining the structure of the thesis.

2

Distribution of the Sudanese mangroves

Chapter 2

Spatio-temporal distribution of mangroves on Sudanese Red Sea coast using multitemporal Landsat image

Abstract

The spatio-temporal distribution of mangroves along the Sudanese Red Sea coast was assessed using multi-temporal Landsat images from 1984 to 2013. Mangroves were classified using the Spectral Angle Mapper (SAM) technique. A post classification change detection matrix study was performed in two sites representing a human-impacted area by shrimp farming and a non-impacted mangrove area. Various patch indices for assessing mangrove fragmentation were compared. The total Sudanese mangrove area ranged between 329 and 721 ha. In this analysis mangrove spatial extent increased during 1984-1990 and decreased sharply during the period 1995-2000, possibly due to severe droughts caused by El Niño-SO events in 1997/98. Between 2000 and 2010, a large increase in the mangrove area was observed, which could be attributed to increased rainfall conditions after the droughts. A high fragmentation in mangroves was observed in 2005 most probably due to increased human activities in the coastal area in close proximity to the present mangroves. While the detected changes in the non-impacted mangroves followed the pattern of rainfall, the mangrove areal extent close to the shrimp farm showed a continuous increase till 2010 independently of the meteorological conditions suggesting a large positive effect of the farm through a decrease in soil salinity and an increase in nutrients promoting the growth of mangroves during that period. However, since 2010 the area of this impacted mangrove forest is decreasing.

2.1. Introduction

Mangroves are a predominant form of intertidal coastal vegetation that occurs worldwide in the tropic and subtropics. Despite their low contribution to the world's forest cover, they were reported to account for 11% of the total input of terrestrial carbon into the ocean (Jennerjahn & Ittekot, 2002; Alongi, 2014a), and for 10% of the terrestrial dissolved organic carbon (DOC) exported to the ocean (Dittmar *et al.*, 2001; 2006). They serve as carbon sink with a high carbon sequestration rate (Duarte *et al.*, 2005; Donato *et al.*, 2011; 2012; McLeod *et al.*, 2011; Hopkinson *et al.*, 2012). Mangroves function synergetically with adjoining habitats in sustaining fisheries through the export of detrital material depending on hydrodynamics and trophic linkage (e.g. Lee, 2004; Mumby *et al.*, 2004; Meynecke *et al.*, 2008; Nagelkerken *et al.*, 2008; 2014; Sheaves *et al.*, 2012; 2014; Davis *et al.*, 2014; Lee *et al.*, 2014). Thus, they are not only crucial for biodiversity conservation, but they also play a critical role in the livelihood of coastal communities, e.g. as a source of wood for fuel and construction, and by supporting about one third of the global fisheries production (Naylor *et al.*, 2000).

The naturally resilient mangrove forests are currently being subjected to a variety of natural and human pressures. About 35% of the mangroves worldwide have disappeared since 1980s at a rate of 1 to 2% per year (Valiela *et al.*, 2001; Alongi, 2002; Duke *et al.*, 2007; Polidoro *et al.*, 2010). A particularly important fact is that the loss of mangroves, with a rate of up to 8% (FAO, 2007), continues to accelerate in the developing countries through human population growth in the coastal areas (Alongi, 2014b). Mangrove fragmentation is a landscape-level process in which a contiguous mangrove forest stand is progressively subdivided into smaller and more dispersed patches. Fragmentation affects mangroves by reducing the continuity of habitat. This can affect species dispersal and migration if populations get isolated and if the propagule flow of individual plants and of animals is disrupted across the landscape. A number of indices to measure landscape patterns (Hargis *et al.,* 1997, 1998; Tischendorf, 2001) and to characterize habitat loss and fragmentation have been developed mostly for the terrestrial environment. Some of these metrics have been successfully applied to mangroves to detect the extent of fragmentation and understand the ecological changes for effective management of these ecosystems (e.g. Manson *et al.*, 2003; Seto & Fragkias, 2007; Li *et al.*, 2013; Vaz, 2014).

The loss and fragmentation of mangrove ecosystems present a challenge to conservation management, given that both the resulting patterns and their effects on different ecological processes vary considerably over time and at varying rates (Turner *et al.,* 2001). Hence, accurate and reliable continuously updated data on their distribution and condition are required for proper management and sustainable use of the forest. Remote sensing techniques using high resolution systems such as Landsat are considered as one of the major applications that can provide data of repetitive coverage and consistent image quality at short intervals. Application of remote sensing allows also for monitoring the spatio-temporal dynamics of mangrove forests. At regional scale, a wide range of satellite images such as Landsat, SPOT XS data, high spatial resolution airborne multispectral and SIR-C radar data were used in the East African region for studies on mangrove status (Gang & Agatsiva, 1992; Dahdouh-Guebas *et al.*, 2004a), composition of mangrove species (Neukermans *et al.*, 2008), management purposes (Fatoyinbo *et al.*, 2008; Ferreira *et al.*, 2009), selection of mangrove plantation sites (Elsebaie *et al.*, 2013), change detection and human impact (Dahdouh-Guebas *et al.*, 2004b; Obade *et al*., 2004; Kirui *et al.*, 2013). Landsat has also been used by several authors for mangrove mapping at both small scales (e.g. Zahran & Willis, 2009; Kumar *et al.*, 2010) and large scales (e.g. Liu *et al.*, 2008; Giri *et al.*, 2008, 2011).

Mangroves in Sudan are situated in an arid climate and close to the northernmost extent of their latitudinal limit. They comprise of monospecific stands of *Avicennia marina* that rarely exceed 9 m in height (Mohammed, 1984; Untawale *et al.*, 1992; PERSGA, 2004; Kathiresan & Rajendran, 2005). Although mangroves in Sudan have a small coverage, they are still ecologically important. Their ecological roles include trapping of runoff sediments and thus protecting the adjacent seagrass beds and coral reefs. They may consolidate shore habitats and provide nursery and shelter for a number of marine organisms. They may also provide nesting, roosting and breeding sites for several birds, and enrich the marine food web in the surrounding oligotrophic waters (Khalil, 1994; Khalil & Krupp, 1994; Wilkie, 1995). Beside the limited information on the rate of mangrove degradation or fragmentation, the available statistical data on the extent of the mangrove forest are inconsistent across time making the available quantitative information unreliable. There is an urgent need to identify and understand general patterns of mangrove loss and fragmentation, particularly those resulting from human activities.

In the present study multi-temporal Landsat imagery was used to map and calculate the change of mangrove cover through comparison between multi-temporal pairs of classified maps. This study will answer the following questions: What is the current extent of mangroves in Sudan? Were mangroves in Sudan changing over the last three decades and if so what is the trend of the change? Since an increasing number of planned shrimp farms along the Sudanese coast are anticipated to create environmental problems in the future, especially those in close proximity to mangroves in the southern part of the coastline, we also tried to understand the effect of shrimp farming on the mangrove areal extension. Using multi-temporal satellite images covering the last three decades we specifically aimed at: (1) exploring the feasibility of using Landsat imagery in mapping the small fragmented mangroves in Sudan; (2) quantifying the spatio-temporal dynamics of mangrove extent; (3) assessing the temporal mangrove fragmentation pattern; and (4) exploring the possible effect of shrimp farming on mangroves by comparing respectively a mangrove site close to a shrimp farm and a non-impacted mangrove site. This study will give insight into the overall status of Sudanese mangroves and thus will provide base line information essential for policy-making and coastal management planning.

2.2. Materials and methods

2.2.1. Study area

The study area covers the entire Sudanese Red Sea coastline (21°16'48"'N, 37°6'36"E to 18° 0''N, 38°34'E), (Fig. 2.1). Mangroves (*A. marina*) are the most noticeable woody vegetation component that occurs along the coastline in the form of four major classes i.e. off-shore islet forest, shore-line forest, small aggregations of mangroves, and relict thin mangrove (Mohammed, 1984). The change detection study was conducted on the two most extensive and dense mangrove sites in an economical hotspot area at the central part of the Sudanese coast. Most of the major industrial activities are concentrated in this area including the two major ports Port Sudan and Suakin, both with oil terminals, a duty free zone area, a shrimp farm, salt pans, desalination plants, electrical power stations, and a refinery. The first site is the human impacted mangrove site at mersa Atta, located only about 22 km north of Suakin city. A major threat to the sustenance of these mangroves is a salt-evaporating pan, established after July 1985, on a saline bare area at 500 m distance behind the mangrove, which was then expanded after the year 2000 to include a shrimp farm. However, no mangrove clearance was associated with the construction of the salt pans or the shrimp ponds. The area is characterized by a semi-diurnal tidal flow of 0.1-0.5 m. Even these small tidal fluctuations cause periods of ebb and flood in the mangrove during the summer season due to the flat topography of the area. The flat area behind the mangrove is seasonally inundated and periodically filled with crusts of white salt. In winter, the sea water level increases by about 1 m more than in the summer, while the freshwater supply usually increases due to the input of seasonal rainwater received by the area through khors or wadis such as khor Batra and khor Aklahok (personal observation). These khors are also important for recharging the groundwater flow in the area. The second site, the non-impacted mangrove, is represented by mangroves at mersa Ashat located 42 km south of Suakin city. The area has three stands, with the northern and southern stands bending over the northern edge to enclose a large inlet. A third stand is located seaward on an elongated islet, forming the inner bank of the inlet. Compared to other mangrove areas in the country, the forests cover a wider area, well above 500 m width in parts.

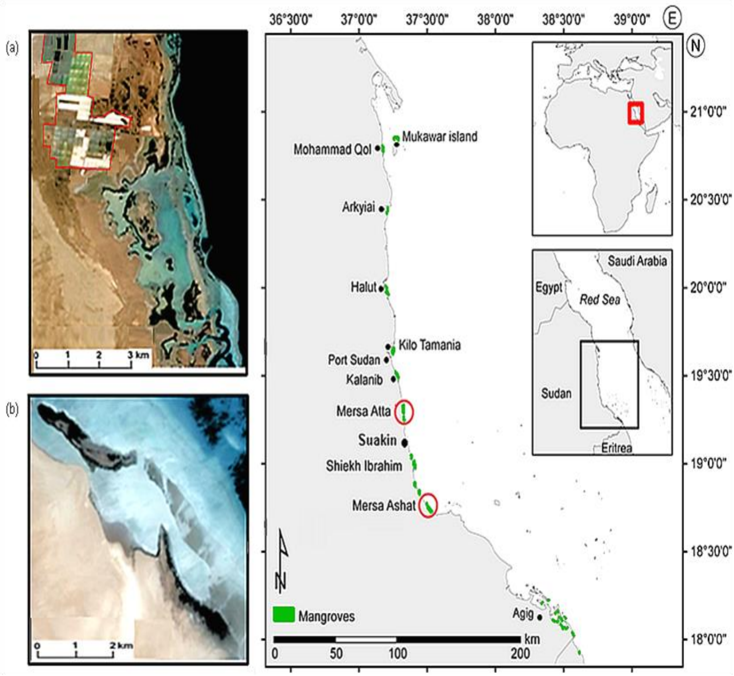


Figure 2.1. A map showing the spatial distribution of mangroves (in green) along the Sudanese coast. The locations indicated with a red circle represent the impacted mangrove by saltpan and the shrimp farm at mersa Atta (upper panel, (a)) and the non-impacted mangrove at mersa Ashat (lower panel, (b)). The marked area in the upper panel represent the location of the salt pan and the shrimp farm. Images are from Google Earth.

2.2.2. Climate and physical setting

Data on the average year-round temperature and precipitation in the study area were obtained from the U.S. National Oceanographic and Atmospheric Administration (NOAA) and Jeddah Regional Climate Center (JCC). The climate of the Red Sea in general is a typical desert and semi-desert climate, characterized by high summer temperatures and aridity throughout the year, due to its geographical position within the subtropical high pressure belt. The recorded maximum air temperature during the study period reached up to 50 °C, while the mean air temperature ranged between 18 °C in winter and 40 °C in summer. The mean monthly temperature ranged from 25 to 40 °C (Fig. 2.2a). The number of days with a temperature higher than 32 °C also varied during the study period with a higher number of warm days (170-200 days/year) in the period 1983-1990, in 1999-2001, and in the period 2006-2009 (Fig. 2.2b).

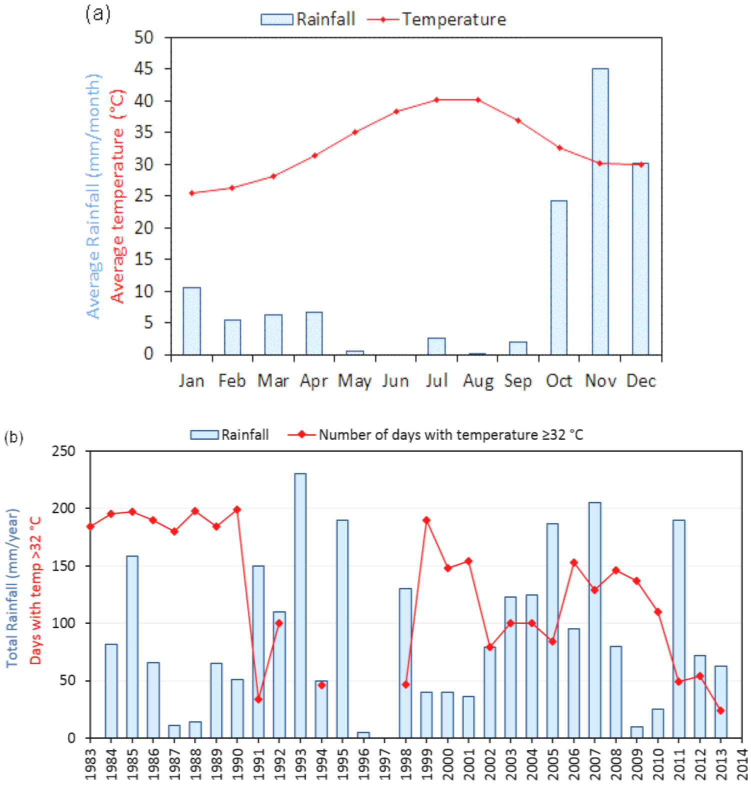


Figure 2.2. Time series showing (a) mean monthly temperature and precipitation, and (b) annual average precipitation and total number of days with temperature higher than 32 °C along the Sudanese Red Sea Coast for the period from 1982 to 2013. Data recorded by climate station at Port Sudan (626410, HSSP; Latitude: 19°6' N, Longitude: 37°2'; Altitude: 3) were obtained from NOAA and JCC. Complete data on to total number of days for 1993 and 1995-1997 are not available.

The rainfall along the Sudanese Red Sea coast is extremely low and mostly in the form of showers of short spells. The mean monthly rainfall during 1983-2014 ranged from 3 to 45 mm (Fig. 2.2a), while the mean annual precipitation over the 32-year study period ranged between 0 and 230 mm/year (Fig. 2.2b). The trend in precipitation was characterized by three drier phases, where average rainfall was lower than the overall mean annual rainfall (136 mm), for the periods 1983-1990, 1996-2002 and 2012-2014 (with the exception of high rain fall in 1999), and two wet phases for the periods 1991-1995 and 2003-2011 (with the exception of the drier years 1994, 2008 and 2009). The Red Sea is in general one of the most saline water bodies in the world, owing to a high evaporation and a lack of permanent rivers or streams draining into the sea. The Sudanese Red Sea coast is characterized by a high salinity (39-40.5 PSU) with minimal seasonal variation. Tides at the Sudanese Red Sea coast show diurnal amplitudes with a small range of 0.1-0.5 m (Eltaib, 2010). The seasonal variation in mean water level being nearly a meter higher in winter than in summer is therefore more significant (Abdel Karim & Babiker, 1991).

2.2.3. Data acquisition and pre-processing

Landsat images (Multispectral Scanner (MSS), Landsat Thematic Mapper (TM), Landsat Enhanced Thematic Mapper Plus (ETM+), and Landsat 8 Operational Land Imager (OLI) covering the entire Sudanese coastline were acquired from the U.S. Geological Survey (USGS) Center for Earth Resources Observation and Science (EROS) website (www.glovis.usgs.gov). Description of band designations for the Landsat satellites image used in this study is shown in Table 2.1. A set of 3 images was required to cover the entire coastline. Simultaneous free cloud images collected within the same season (dry season) or, if not possible, within the same year over a five years span between 1985 and 2013, were used for mapping and detecting changes in mangroves (Appendix 1).

Because the geo-referenced Landsat images were obtained by different sensors (i.e. MSS, LT4-5, ETM+, and OLI), their radiometric performance, solar illumination conditions, atmospheric scattering and absorption were different. To allow a comparison and mosaic of these different satellite images and to improve the classification results, all images were subjected to radiometric correction. This process involves two steps: (i) conversion of images from Digital Numbers (DN) to the physical measure of Top Of Atmosphere reflectance (TOA, NASA, 2011), and (ii) application of a simple atmospheric correction using the Dark Object Subtraction method (DOS1) in QGIS (GRASS-tool (i.atcorr)). Landsat 7 (ETM+) images have wedge-shaped gaps on both sides of each scene due to the failure of the Scan Line Corrector (SLC), which compensates for the forward motion of the satellite, resulting in approximately 22% data loss. Thus, images of the years 2005 and 2010 were further processed for gaps filling using Geospatial Data Abstraction Library (GDAL) “fill-no data” tool.

Table 2.1. Summary and band description of the used Landsat imagery

Satellite	Sensor	Date	Band No.	Wavelength (µm)	Spatial resolution (m)
Landsat 5	MSS	1984	Band 1	0.5-0.6	60
			Band 2	0.6-0.7	
			Band 3	0.7-0.8	
			Band 4	0.8-1.1	
Landsat 4-5	TM	1990	Band 1	0.45-0.52	30
		1995	Band 2	0.52-0.60	
			Band 3	0.63-0.69	
			Band 4	0.76-0.90	
			Band 5	1.55-1.75	
			Band 7	2.08-2.35	
Landsat 7	ETM+	2000	Band 1	0.45-0.52	30
		2005	Band 2	0.52-0.60	
		2010	Band 3	0.63-0.69	
			Band 4	0.77-0.90	
			Band 5	1.55-1.75	
			Band 7	2.09-2.35	
Landsat 8	OLI	2013	Band 2 – Blue	0.45 - 0.51	30
			Band 3 - Green	0.53 - 0.59	
			Band 4 - Red	0.64 - 0.67	
			Band 5- NIR	0.85 - 0.88	
			Band 6 - SWIR1	1.57 - 1.65	
			Band 7 - SWIR2	2.11 - 2.29	

For the interpretation of mangroves in the image, the classification input was identified by creating a false color composite image (near infrared composite) using band 3, 2, and 1 for Landsat MSS; band 4, 3 and 2 for Landsat 4-5 and 7, and band 4, 5, and 3 for Landsat 8. This band combination allows for identification of vegetation and reflects a large part of the incident light in the near-infrared wavelength. Eight classes, i.e. (1) mangrove, (2) salt marshes (3) salt, (4) saline soil, (5) muddy and sandy soil, (6) urban area, (7) shallow water, and (8) deep water were identified based on their distinctive appearance in the different false color composite images (Table 2.2; Horning, 2004). No systematic ground truthing was done during this study; however, during our fieldwork in the non-impacted site (mersa Ashat), the number and nature of different classes were noted. Therefore, the false composite images for this site were generated first and then compared with composite images from different sites and years to assess if there is any inconsistency or if there is any mixture in the appearance of different classes. Moreover, the false composite images generated from Landsat image since 2000 were also compared with their corresponding image from Google Earth. This step was followed by the creation of regions of interest (ROI) shape files, i.e. the training sample (polygons) of all input classes, using a region growing algorithm. This algorithm allows extraction of map individual pixels in the input image to a set of similar pixels through image segmentation (Adams & Bischof, 1994).

Table 2.2. Description of the appearance of each class in the false color composite image (RGB band combinations) of the different used Landsat

Class	Appearance and interpretation
Mangrove	Denser mangroves appear in a deep red color. Sparse mangroves appear in brown and yellow or lighter red
Salt marshes	Reddish
Salt	White
Saline soil	Light cyan or grey
Muddy and sandy soil	Dark to light Brown
Shallow water	Shades of lighter blue
Deep water	Very dark blue to black

2.2.4. Image classification and post-processing

All pre-classification, classification and post-classification processes were performed in QGIS 2.2.0 software (Quantum GIS Development Team, 2013). Image classification was performed using the Spectral Angle Mapping classification algorithm provided by SAGA tool in Semi-Automatic Classification Plugin (version 2.5.2) for QGIS. The Spectral Angle Mapper (SAM) is a supervised classification technique that uses the n-D angle to match pixels to reference spectra (in this case the selected training sample of each class). This technique also creates groups of pixels (i.e. clusters) based on information of the input data (classes), provided by the user and the spectral properties of each class (Khorram *et al.*, 2012). The algorithm determines the similarity between two reflectance spectra by calculating the ‘spectral angle’ between them, treating them as vectors in a space with dimensionality equal to the number of bands (Jensen, 2005). The image reflectance spectrum is then assigned a correlation factor between 0 (low correlation) and 1 (high correlation) relative to the reference reflectance spectral library or end-members (Kamal & Phinn, 2011). The spectral angle is the angle between any two vectors with a common origin. The magnitude of the angle specifies the degree of dissimilarity between material and reference. The smaller angle correlates to a more similar spectral reflectance signature (Borengasser *et al.*, 2008). The SAM matches the spectra of all image pixels to the end-members spectral reflectance, and classifies each class within a certain angle threshold. Thus, if the derived end-members were correct representatives of object classes, the SAM classification result would accurately represent the distribution of those classes in the map (Kamal & Phinn, 2011). The advantages of the use of SAM over other pixel-based algorithms are the following: (i) the production of accurate class polygons with only few unclassified pixels (Kamal & Phinn, 2011); (ii) SAM does not require the data to be normally distributed; (iii) topographic illumination and atmospheric effects are likely less problematic allowing for collecting the reference spectra from different scenes and different imaging systems to be used for image classification; (iv) SAM is insensitive to data variances and to the size of the training data set as well; and (v) SAM performs consistently well in different eco-regions including biotic communities in semi-arid desert areas (Sohn & Rebello, 2002).

The change detection process was performed using post-classification comparison techniques, which involved comparative analysis of the classification results for the time periods between 1984-1990, 1990-1995, 1995-2000, 2000-2005, 2005-2010, and 2010-2013. This approach may generate a source of uncertainty due to (i) semantic differences in class definitions between maps and (ii) classification errors. To minimize the semantic differences in class definitions, the same number of classes for all images was used. The minimum mapping unit used in this study was 0.09 ha.

2.2.5. Accuracy assessment

Accuracy assessment is often required for evaluating the quality of land-cover classification results. In this study, the accuracy assessment of the class “mangrove” was conducted for each classification result and estimated using user’s accuracy (UA), and producer’s accuracy (PA). The overall classification accuracy (OCA) and Kappa coefficient (KC) were also reported. They are both discrete multivariate techniques and are appropriate for accuracy assessment because remotely sensed data are discrete rather than continuous (Jensen, 2005). This is achieved by comparison of the land-cover classification and the ROIs shape file as ground truth (theoretically, image pixels belonging to a certain ROI should be classified as that ROI's class). Validation of the classification was done using a different ROI shape file based on 10% randomly selected pixels for each land-cover class. The overall classification accuracy, the user’s accuracy, and the producer’s accuracy were used to assess the accuracy of the change detection based on a post classification change matrix function (Foody, 2002).

A simple approach for accuracy assessment that focuses on two components of disagreement between maps in terms of the quantity and spatial allocation of categories, namely quantity disagreement and allocation disagreement proposed by Pontius and Millones (2011), was also used to assess the accuracy of the classification and land-cover changes for the change detection study. Quantity disagreement calculates the amount of difference between the reference map and a comparison map that is due to the less than perfect match in the proportion of the categories, whilst allocation disagreement is defined as 'the amount of difference between the reference map and a comparison map that is due to less than the optimal match in the spatial allocation of the categories, given the proportions of the categories in the reference and comparison maps' (Pontius & Millones, 2011). The quantity disagreement, allocation disagreement, user's accuracy, producer's accuracy were calculated using Pontius's error matrix with classes classification and validation data for classification accuracies, and time 1 and time 2 map data for change detection.

2.2.6. Mangrove fragmentation

Mangrove fragmentation was assessed using various indices such as class area, edge, shape complexity, and aggregation metrics. Metrics were first computed at landscape class level (mangrove) using Fragstats v. 4.2 (McGarigal *et al.*, 2012). Metrics were then subjected to correlation analysis to screen out the redundant indices using Spearman rank correlation coefficient in Statistica v.7. This process was followed by a selection of indices that best address the spatial characteristics of mangroves and their changes during the last three decades. The description of these indices and their behavior are shown in Table 2.3.

Table 2.3. Description of the landscape pattern metrics used for the assessment of mangrove fragmentation and their potential ecological application (McGarigal and Cushman, 2002; Rutledge, 2003).

Metric	Index (units)	Abbreviation	Range	Description and behaviour	Ecological application
Area	Mean patch size (ha)	MPS		Average area of a patch of a particular class. The lower the patch size the more fragmented the mangroves are.	Patterns of associated animal species abundances
	Largest Patch Index (%)	LPI	0 < LPI≤ 100	Percentage of total landscape area comprised by the largest patch and thus it is a measure of dominance. Decrease as a result of fragmentation.	Habitat quality especially for migratory fauna
Shape	Mean Shape Index	MSI		A measure of shape complexity. Increase denote more complex patch shape.	Patterns of associated animal species abundance; species diversity within the patch; re-vegetation
	Contagion Index (%)	CI	0 < CI ≤100	The physical continuity of a patch type (or a habitat) across the landscape. The lower the values, the more disaggregate and higher fragmented the habitat.	Age and physical structure: of mangrove forest and associated animal species composition
Aggregation	Number of Patches	NP	NP ≥ 1, without limit.	Number of patches in the landscape class, index of spatial heterogeneity. Increase of the index signifies the spatial heterogeneity of a class.	Stability of associated animal species interactions and competition; propagation of disturbances across a landscape
	Mean Euclidean nearest-neighbour distance (m)	ENN	ENN > 0, without limit	Distance to the nearest neighbouring patches of the same type. Quantifies patch isolation and habitat quality. Decreased with increasing fragmentation.	Population dynamics; associated animal species distribution, and interactions, immigration
	Aggregation Index (%)	AI	0 ≤ AI ≤100	A measure of isolation and compactness. The lower the values the more disaggregated and fragmented the patch.	Habitat quality; associated animal species distribution
	Proximity Index	PI	PI ≥ 0	Number of patches of same type within specified area. Quantifies the spatial context of a habitat patch in relation to its neighbours. A larger index value denote more contiguous and/or closer patches	Habitat quality; animal related species distribution

2.3. Results

2.3.1. Mangrove distribution and areal extent

The classification derived from Landsat scenes (Appendix 2a,b) had an overall accuracy of 87-97%. The mangrove UA ranged between 78.49% and 95.02%, and mangrove PA falls between 75.70% and 88.76%, while the kappa coefficient for mangroves ranged between 0.75 and 0.95 (Table 2.4).

The Sudanese mangroves showed high variability in areal coverage over time. The lowest estimate was about 329 ha in 2000 and the highest was 721 ha in 2010 (Table 2.4).

Table 2.4. Areal coverage and classification accuracy of mangroves along the Sudanese Red Sea coast during the period from 1984-2013, derived from classifying multi-temporal Landsat scenes.

Year	Mangrove area (ha)	UA (%)	PA (%)	KC	OA (%)
1984	455	78.49	75.70	0.75	87
1990	603	95.02	88.76	0.94	97
1995	575	92.54	88.52	0.92	94
2000	329	92.86	85.53	0.96	96
2005	545	93.47	87.60	0.94	92
2010	721	92.96	87.23	0.94	93
2013	433	93.10	86.78	0.95	89

* UA: user accuracy, PA: producer accuracy, KC: kappa coefficient, OA: over all accuracy.

The largest extent, representing between 80-90% of the total mangrove area, was found extensively in the central and the southern part of the country at the mouth of khors. The mangrove coverage did not correlated neither with the average rainfall nor with the longer periods of higher temperature as measured by the number of days with temperature higher than 32 °C ($R^2=0.08$ and 0.03, respectively; $P > 0.05$; Fig. 2.3).

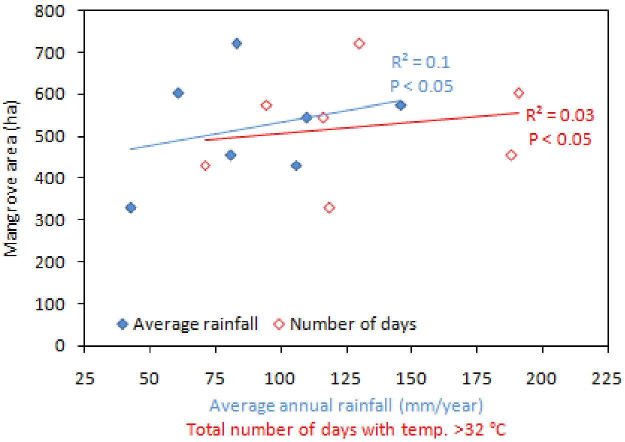


Figure 2.3. A simple linear regression of average annual rainfall (blue line) and the period with temperature higher than 32 °C (red line) versus the estimated areal distribution of mangroves during the period of 1982-2013.

2.3.2. Patterns of mangrove fragmentation

The aggregated results of the patch area, edge, shape complexity and aggregation indices reflected a varying fragmentation pattern of mangroves during the study period (Fig. 2.4). The number of patches (NP) were 220 and 238 in 1990 and 1995, respectively. It dropped significantly in 2000 and 2010-2013, and increased abruptly in 2005. Mean patch size (MPS) increased slightly in 2000, decreased sharply to a minimum size of 0.57 in 2005 and showed a proliferation during 2010.

Largest Patch Index (LPI) ranged between 4% and 12% of the total mangrove with the lowest and highest value recorded in 2005 and 2010, respectively. The Mean Shape Index (MSI) and Proximity Index (PI) gradually decreased from their maximum in 1990 to their minimum values in 2005, then sharply increased during 2010-2013. Both the CI, the ENN_MN and AI showed a very narrow range of variation throughout the period from 1990-2013 with a slight increase of CI and AI in 2013. The values of the patch indices for the year 1984 were higher for all indices except for LPI and NP which showed lower values compared to other years.

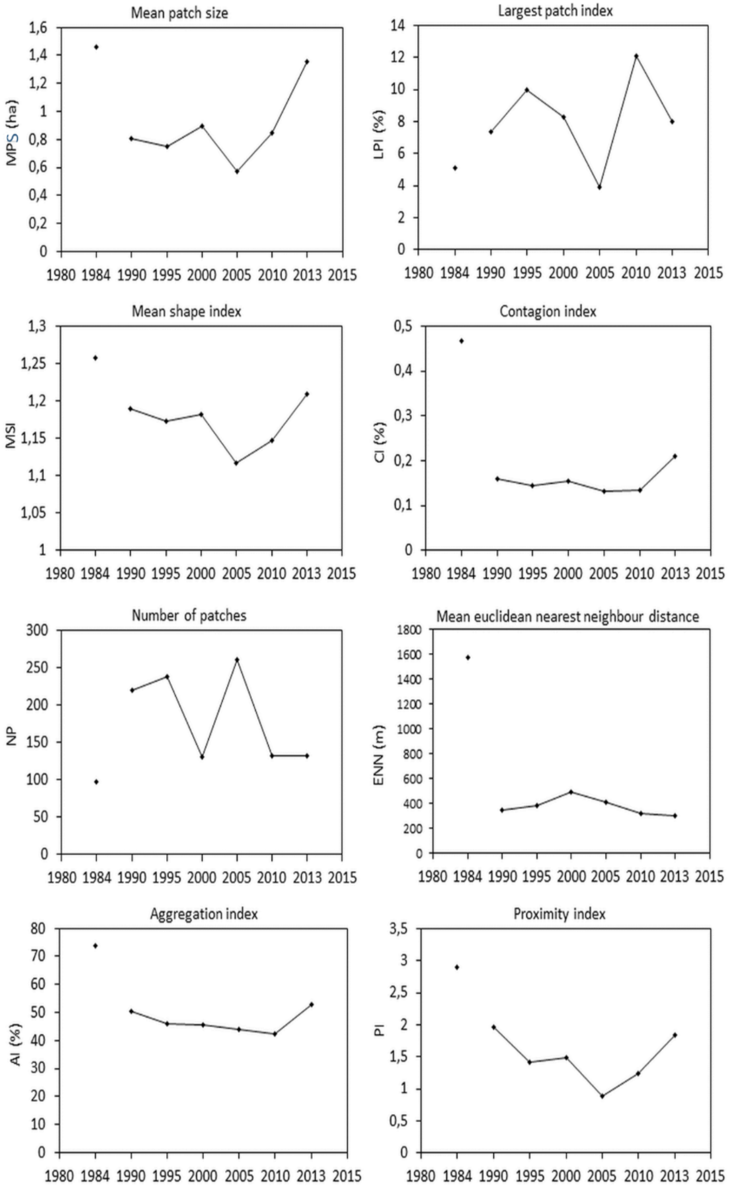


Figure 2.4. Landscape metrics of mangrove derived from Landsat for the period between 1984-2013 measuring Sudanese mangrove area, shape complexity, and aggregation.

2.3.3. Change detection case study

2.3.3.1. Classification accuracy

The accuracy of mangrove classification in both the impacted and non-impacted mangrove sites over the study period is shown in Figure 2.5 and Table 2.5. The overall accuracy ranged between 79% and 100% in the impacted mangrove and between 51% and 84% in the non-impacted mangrove (Fig. 2.5a). Although the overall accuracy was lower in the non-impacted mangroves, the quantity and allocation disagreements values, which ranged from 2 to 13% and 0 to 11%, respectively, were lower than in the impacted mangrove (Fig. 2.5b, c). The user's and producer's accuracies of the mangrove class, listed in Table 2.5, were very high (>85%). Mangroves in the impacted site were accurately classified in 1990 and 1995 as indicated by the 100% user's and producer's accuracies, while in the non-impacted site were accurately classified in 1990, 2000, 2005 and 2010. The error in the user's and producer's accuracies for mangrove in the remaining years is due to confusion of mangrove with all other classes (Appendix 3a,b).

Table 2.5. User's and producer's accuracies of the classification of the impacted and non-impacted mangroves during the study period

Site	Year	User's accuracy (%)	Producer's accuracy (%)
Impacted mangrove	1984	100	85
	1990	100	100
	1995	100	100
	2000	100	93
	2005	86	93
	2010	100	96
	2013	100	81
Non-impacted mangrove	1984	89	100
	1990	100	100
	1995	100	94
	2000	100	100
	2005	100	100
	2010	100	100
	2013	100	96

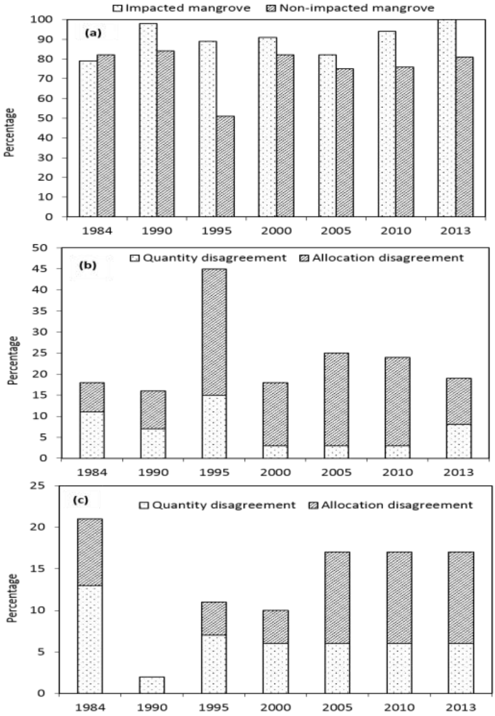


Figure 2.5. Overall accuracy of classification for impacted and non-impacted sites (a), and quantity and allocation disagreements of mangrove classification evaluated in (b) impacted mangrove and (c) non-impacted mangroves.

On the other hand, the overall accuracy of the change in the land-cover classes from the post-classification comparison maps showed lower values, ranging from 60 to 66% in the impacted mangrove and 30 to 70% in the non-impacted mangrove, compared to accuracy of mangrove classification (Fig. 2.6a). In contrast, the values of quantity and allocation disagreements showed higher values ranging from 10 to 33% and 13 to 25% in the impacted mangrove, and 11 to 68% and 19 to 32% in the non-impacted mangrove (Fig. 2.6b,c). The user's and producer's accuracies of change in classes showed that changes were less detected in mangroves compared to other classes as indicated by the lower values of user's accuracy (Appendix 2 and 3). The values of the user's accuracy ranged between 13 and 78% in the impacted, and between 18 and 47% in the non-impacted mangrove, while values of the producer's accuracy ranged between 23-97% in the impacted and 18-68% in the non-impacted mangrove (Table 2.6).

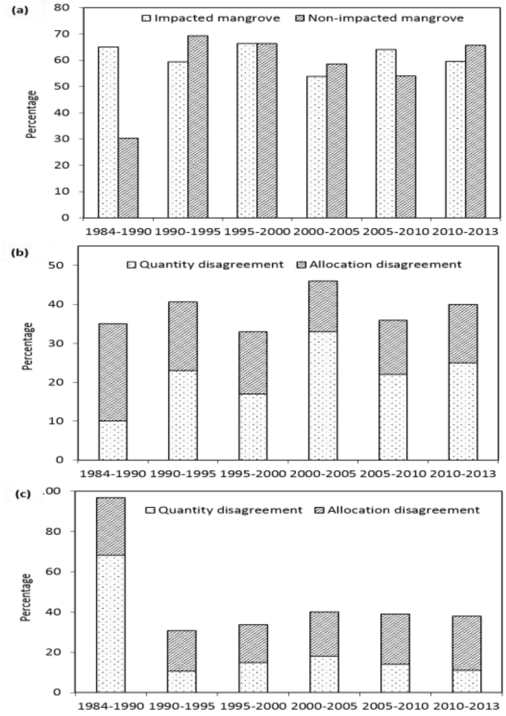


Figure 2.6. Overall accuracy of the change in land-cover classes (a), and quantity and allocation disagreements of mangrove change evaluated in (b) the impacted mangrove and (c) the non-impacted mangrove.

Table 2.6. User's and producer's accuracies of the change of the impacted and non-impacted mangroves during the study period

Site	Year	Producer accuracy (%)	User accuracy (%)
Impacted mangrove	1984-1990	50	76
	1990-1995	29	19
	1995-2000	89	13
	2000-2005	97	59
	2005-2010	23	78
	2010-2013	26	74
Non-impacted mangrove	1984-1990	68	18
	1990-1995	37	30
	1995-2000	18	33
	2000-2005	24	24
	2005-2010	51	27
	2010-2013	27	47

2.3.3.2. Mangrove change

The total area in the human impacted and non-impacted sites during the study period is shown in Figure 2.7. The change in mangrove area between 1990 and 2013 is shown in Table 2.7 and Figure 2.8.

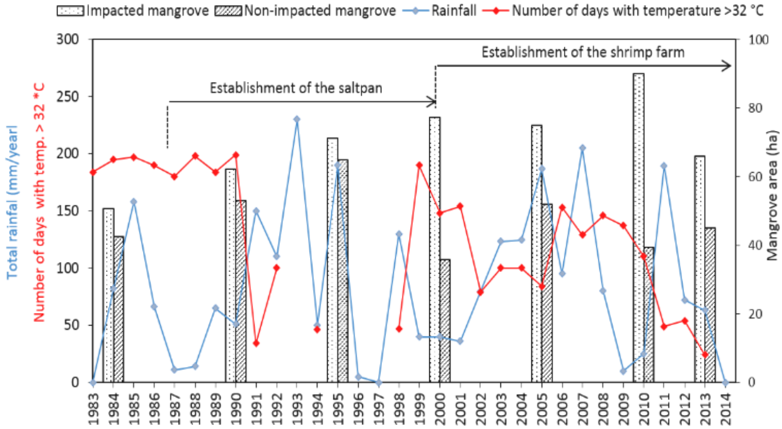
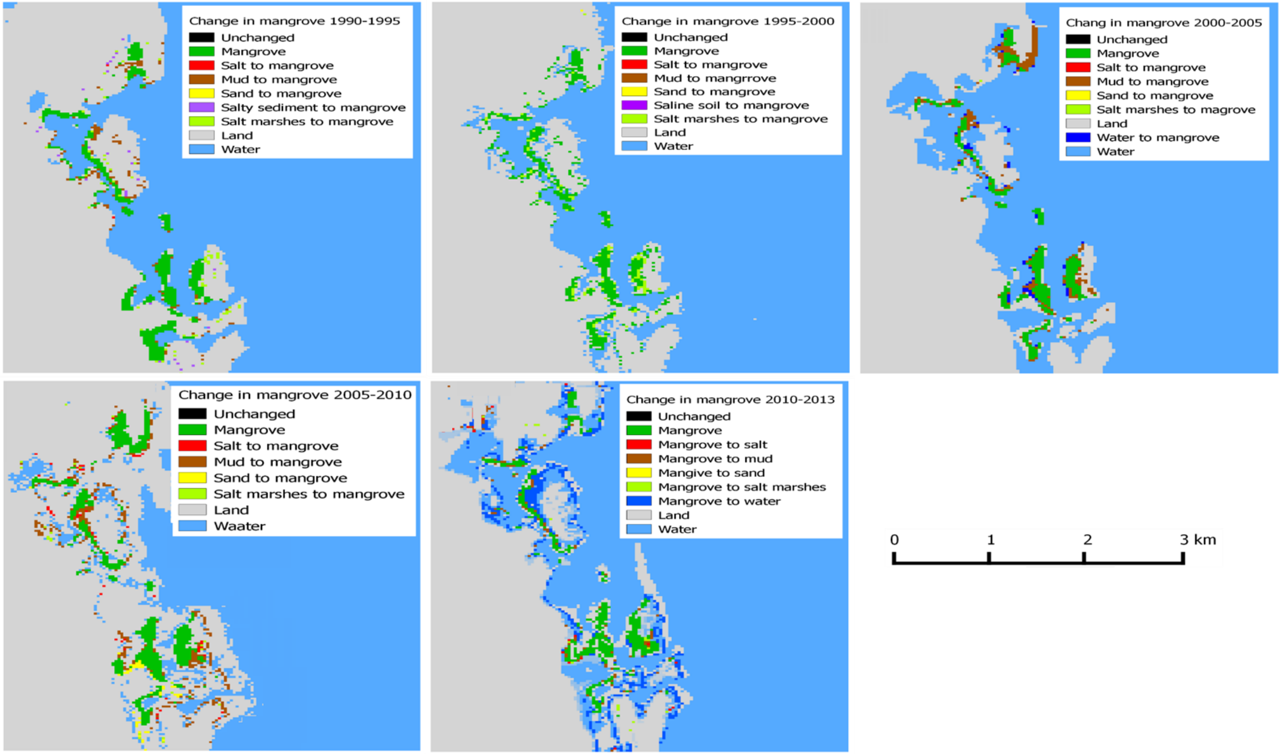


Figure 2.7. Total mangrove area (bars) for the human impacted and non-impacted sites, total precipitation (blue line) and number of days with temperature above 32 °C (red line) recorded at Port Sudan (626410, HSSP) during the period of 1984-2013.

Table 2.7. Change in mangrove area and rate of change during the study period.

Site	Period	Mangrove area (ha)	Mangrove change (ha)	Rate of change (%)
Impacted mangrove	1984-1990	62	12	23
	1990-1995	71	9	14
	1995-2000	77	6	8
	2000-2005	75	-2	-3
	2005-2010	90	15	20
	2010-2013	66	-24	-27
Non-impacted mangrove	1984-1990	53	11	25
	1990-1995	65	12	23
	1995-2000	36	-29	-45
	2000-2005	52	16	46
	2005-2010	40	-12	-23
	2010-2013	45	5	13

Both mangroves showed high variation in total areal extent. The trend in temporal change of mangroves at the impacted site showed continuous increase in coverage from 51 to 90 ha in the period between 1984-2000, with a rate ranging from 8 to 23%, and a slight decrease in 2000-2005 with a rate of -3%. Mangroves continued to increase to reach a maximum areal extent in 2005-2010 with an increment rate of 20%, while in 2013 mangroves decreased significantly to 66 ha with a change rate of -27%. The total area of mangrove at the non-impacted mangrove increased by about 50% during 1984-1995 as compared to 1984, followed by large loss during 1995-2000 to almost half of the existing area in 1995. The area of mangroves increased during 2000-2005 and 2010 -2013 with a rate of 46% and 13% respectively. Mangrove area showed a decrease by 23% during 2005-2010 (Fig. 2.7 and 2.8, Table 2.7).


Change in mangrove 1990-1995
Unchanged
Mangrove
Salt to mangrove
Mud to mangrove
Sand to mangrove
Salty sediment to mangrove
Salt marshes to mangrove
Land
Water
Change in mangrove 1995-2000
Unchanged
Mangrove
Salt to mangrove
Mud to mangrrove
Sand to mangrove
Saline soil to mangrove
Salt marshes to mangrove
Land
Water
Chang in mangrove 2000-2005
Unchanged
Mangrove
Salt to mangrove
Mud to mangrove
Sand to mangrove
Salt marshes to magrove
Land
Water to mangrove
Water
Change in mangrove 2005-2010
Unchanged
Mangrove
Salt to mangrove
Mud to mangrove
Sand to mangrove
Salt marshes to mangrove
Land
Waater
Change in mangrove 2010-2013
Unchanged
Mangrove
Mangrove to salt
Mangrove to mud
Mangive to sand
Mangrove to salt marshes
Mangrove to water
Land
Water
0
1
2
3 km

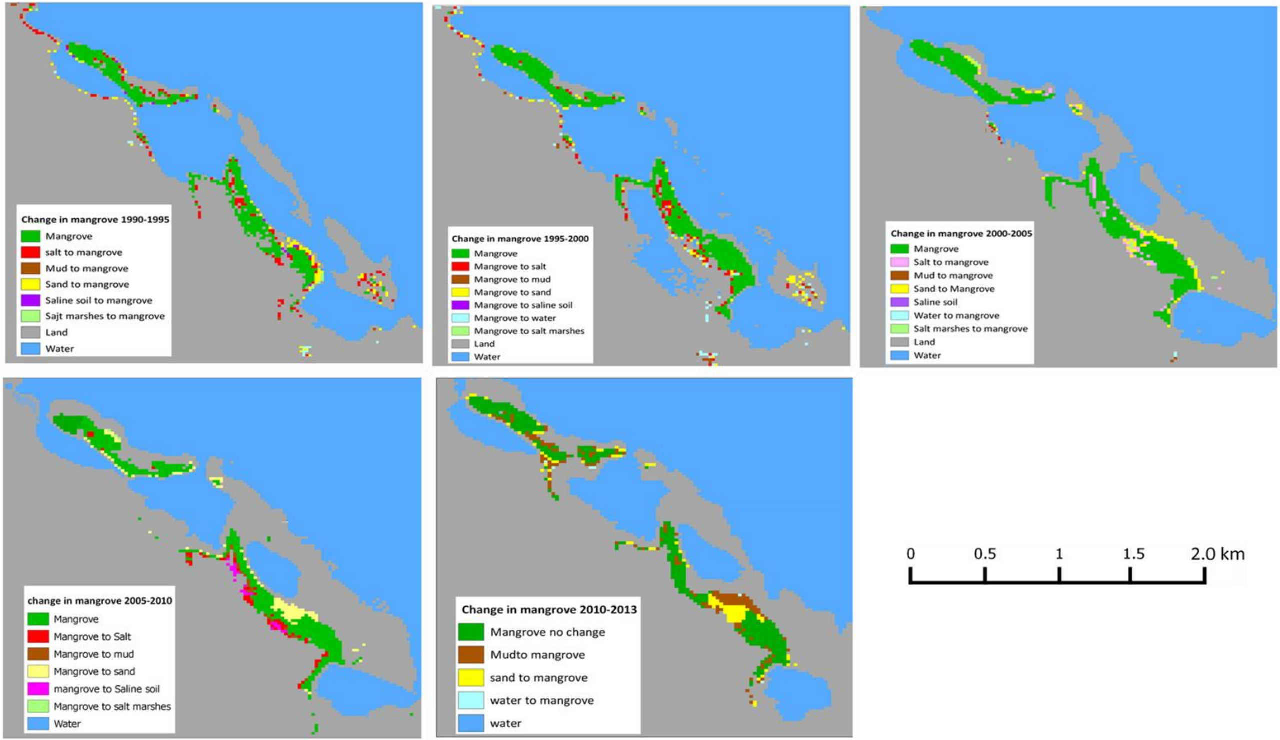


Figure 2.8. Change in mangrove distribution in (a) human-impacted mangrove and (b) non-impacted mangrove during the selected periods

With respect to meteorological conditions, the mangrove areas in the impacted site did not significantly correlated with average rainfall ($R^2 = 0.01$) or number of days with high temperature ($R^2 = 0,21$), whereas the area of mangroves in the non-impacted site significantly correlated with rainfall ($R^2 = 0.55$). Non-impacted mangroves did not correlate with long periods of temperature higher than 32 °C ($R^2 = 0.02$), (Fig. 2.9a, b).

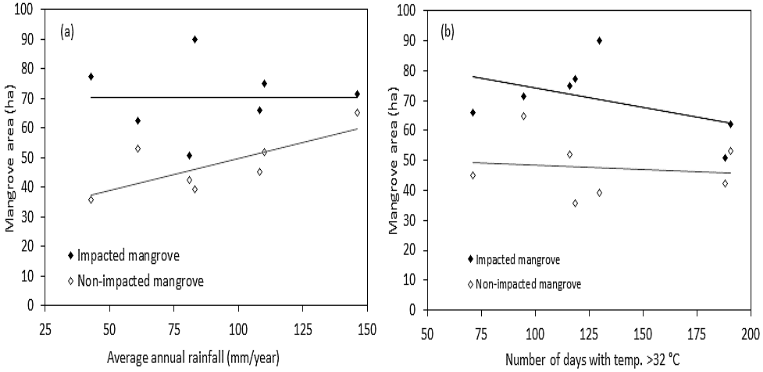


Figure 2.9. Simple linear regression for the relationship between mangrove coverage area and (a) average rainfall and (b) number of days with temperature higher than 32 °C in the impacted ($R^2 = 0.01$ and 0.21, respectively; $P > 0.05$) and non-impacted mangrove ($R^2 = 0.55$; $P < 0.05$; and 0.02, $P > 0.05$); respectively, during the period between 1984 and 2013.

In addition, the variation in the mangrove coverage area in both sites was associated with significant changes in the other land-cover classes. In the impacted site a decrease in saline soil (-68%), salt marshes (-18%), sand (-10%), and shallow water by 24% was observed during the period of 1984-2000, while an increase in muddy soils by 74% and 88% was observed in the period of 1984-1990 and 1995-2000, respectively. A decrease in saline and muddy soils by -73 and -71 %, and an increase in sand by 61% were observed during 2000-2005. Muddy and sandy soils were decreased by -57% and -17%, while saline soil was increased by 19% during 2005-2010. During 2013 the saline soil was increased by 34% since the year 2010, while salt marshes, mud and sand decreased between 5-7% each. The observed decrease in mangrove area in the non-impacted site during the periods 1995-2000 and 2005-2010 was associated with a remarkable decrease in salt marshes (54% and 11 %, respectively) and muddy soil (68% and 23%, respectively). An increase in sand and salt was also observed during 1995-2000 (97% and 44%) and 2005-2010 (22% and 46%). The increase in mangrove during 2000-2015 was associated with an increase in mud content (56%) and a decrease in sand and salt (-31% and -27%), (Appendix 4).

2.4. Discussion

2.4.1. Mangrove classification

The classification of mangroves derived from Landsat scenes resulted in a mangrove UA higher than 78%, PA higher than 75% and KC higher than 0.75. Landsat images used in this study were very useful for mapping the extent of mangrove and change detection with an acceptable percentage of classification accuracy. With respect to the change detection study, the accuracy of mangrove classification using cross validation techniques and the proposed error matrix by Pontius and Millones (2011) resulted in high overall accuracies of at least 79% at the impacted mangrove and 75%, except for the year 1995, in the non-impacted mangrove. This indicates that although the supervised semi-automatic pixel-based technique used in this study was useful in classification of mangroves with high classification accuracy (86-100% user's accuracy and 81-100% producer's accuracy), there was misidentification of mangroves and other classes. This is clearly shown by the higher values of the quantity and allocation disagreement, and thus low accuracy in terms of both quantity and allocation of pixels, which indicates a failure in discriminating between different classes. However, the main source of misidentification, which was mainly due to the confusion of mangroves with all other classes, was identified by comparing the classified map and the cross validated map using Pontius's error matrix. The user' and producer's accuracies were highly variable for different classes. They were remarkably lower for mangrove classes compared to other classes, which showed in some cases 100% accuracy especially at the non-impacted mangrove. This can be explained by the low comparability between mangrove and all other classes.

The accuracy of the classification in this study is constrained by the number of spectral bands and the coarser spatial resolution of the Landsat, which can produce an improvement of the accuracy as seen in the classification results based on Landsat ETM+ and OLI compared to MSS 1984. However, differences in the spatial resolution are not necessarily the only explanation for the low classification accuracy of mangroves, which can be mostly attributable to a number of other factors including: (i) the time during which the Landsat images were obtained. Although all of the images were obtained when the water is at its lowest level, the variation in light intensity and leaf water content which varies from date to date can affect the spectral behavior of mangroves (Adam *et al.*, 2010), and thus the classification accuracy; (ii) habitat heterogeneity across the study area, where the sparse mangroves represent a very small area surrounded by large areas of water and land (Diaz-Gallegos & Acosta-Velázquez, 2008; Wickham *et al.*, 2010); (iii) mangrove conditions and stress. The differences in spectral reflectance resulted from mangrove conditions e.g. healthy and poor conditions, which may affect the level of chlorophyll content, nitrogen and water content (Zhang *et al.*, 2012; 2013; Flores-de-Santiago *et al.*, 2013). In addition, in arid and semi-arid areas where mangroves are under considerable stress due to hypersaline conditions, resulting from the climate, temporal changes in leaf pigments content can be induced which may affect the strength of the reflectance of spectral characteristics of mangroves (Zhang *et al.*, 2014).

2.4.2 Mangrove temporal change

The mangrove area ranged between 431 and 721 ha. Our estimates of total mangrove area indicated a net loss of about 250 ha between 1995 and 2000 followed by an increase by about 390 ha between 2000 and 2010. Earlier estimations of the extent of mangrove cover along the Sudanese coast varied between 100 ha (Giri *et al.*, 2011) and 93700 ha (Spalding *et al.*, 1997) as shown in Table (2.8). The later estimate is based on an analysis of a map with a scale of 1:1 000 000, which is too small to provide a reliable estimate. Our estimates of mangrove extent are close to the estimates by Wilkie (1995) and Fatoyinbo and Simard (2013). However, they varied considerably compared to the estimates from other studies listed in Table 2.8. The variation in the estimated areal extent of mangroves was most probably due to the wide variation in the used assessment methods, measurement scale, classification approaches and classification systems, or definition of the true mangrove species.

Table 2.8. A comparative account of the historical extent of mangrove forest along the Sudanese coast reported by various authors

Year	Mangrove area (ha)	Assessment method	Author
1980	605		FAO, 2003
1990	535		FAO, 2003
1992	93700	Analysis were based on regional sketch map in Sheppard *et al.*(1992). Scale 1:1 000 000	Spalding *et al.*, 1997
1995	500	Field combined with satellite imagery	Wilkie, 1995
2000	500		FAO, 2007
2000	584	Remotely sensed imagery	Dawelbait *et al.*, 2006
2000	1000	Map analysis. Scale 1:200,000	Spalding *et al.*, 2010
2000	100	Satellite imagery.	Giri *et al.*, 2011
2002	400	Satellite imagery.	Fatoyinbo & Simard, 2013
2005	500		FAO, 2007

*The estimates from Dawelbait *et al.*, 2006 and Spalding *et al.*, 2010 were based on Africover dataset (Landsat(TM), scale: 1:1:100,000 ; FAO, 2003).

*The estimates from FAO for 1980, 1990, 2000 and 2005 have been calculated applying the FRA 2000 (FAO, 2001) annual forest cover change rate for 1990-2000 (-1.4 percent) to the most recent, reliable figure.

2.4.3. Mangrove fragmentation

While measures of area are the most common descriptors of habitat distribution, other metrics such as edge and shape can be used to describe the spatial patterns and the degree of fragmentation of habitats. In general, fragmentation of an ecosystem is often characterized by (i) a decline in the total area and size of fragments; (ii) increased in number of patches and isolation of fragments from similar habitats; and (iii) increased total amount of patch edges (Rutledge, 2003). In our study, mangrove fragmentation delineated by the measured indices unveils inconsistent patterns over time. As shown by the results, mangroves in 1984, despite their lower surface area, were less fragmented as compared to the other studied years. However, the results from the year 1984 are not comparable to the other years, because the 1984 Landsat has a coarser spatial resolution (60 m) compared to other Landsat images used in this study. It is well known that the patch indices are greatly related to the spatial resolution of the study. Increasing resolution will decrease the smallest patch size (e.g. one can detect smaller patches) and probably increase the number of patches (Turner *et al.,* 1989). The low image resolution will also affect measurement of patch area and patch edge, thus affecting many landscape indices, particularly those related to shape (Benson & MacKenzie, 1995) such as the contagion and the aggregation indices. The aggregated analysis of the all measured indices, except for the NP, for the period of 1990 to 2013 showed consistently lower values in 2005 indicating that the highest degree of fragmentation experienced by the Sudanese mangroves during the study period was in 2005. The behavior of the indices during the following period (2010-2013) revealed a varying degree of recovery, indicating high aggregation of these mangroves. However, the results also delineated that the Sudanese mangroves are naturally fragmented habitats as clearly shown by the low value of the indices throughout the study period. Fragmentation from natural causes does not greatly affect mangroves, however, forest fragmented by anthropogenic sources is at higher risk of further fragmentation and increases their patchiness. For example, mangroves in 2000 had a similar fragmentation pattern to mangroves in 1995 and were less fragmented than in 2005, notwithstanding they were smaller by about 250 ha than in 1995 and 2005. Mangroves in 2005 were also more fragmented than in 1995 in spite of their similar areal extent. This fragmentation pattern has two implications: (i) the loss of about 250 ha that occurred in 2000 possibly as a result of the drought caused by El Niño-SO, might not necessarily have increased mangrove fragmentation as shown by the relatively higher values of the fragmentation indices compared to 2005; and (ii) despite the increase in area in 2005 the mangroves fragmentation was higher suggesting that the cause of fragmentation of mangroves in 2000, which was a natural phenomenon, is different from that in 2005 pointing to the increased human activities in the area.

Habitat loss and fragmentation can have a devastating impact on some ecological processes (Goodwin and Fahrig, 2002; Turner, 2005; Laurance *et al.*, 2008; Obade, 2009; Bennett and Saunders, 2010), and will negatively impact the faunal communities associated with these habitats. The differential responses to certain disturbances such as clear cutting for timber and loss of wetlands (mangroves) will restructure the benthic communities within patches. Some changes will result from intraspecific processes responding to changes in abiotic conditions. Other changes will result from adjustments in interspecific interactions. Examples of abiotic conditions affected by fragmentation include light, moisture, wind, and soil regimes (Saunders *et al.,* 1991; Didham, 1998). The consequences of fragmentation on biota are based on four intraspecific population processes of growth, reproduction, mortality, and dispersal and the corresponding interspecific processes (Rutledge, 2003), which will result in a decline in biological diversity, change in dominance and the likelihood of occurrence, and immigration (O'Neill *et al.*, 1997). For example, the mass mortality of mangrove at mersa Ashat as a result of drought associated with El Niño 97/98 followed by clear cutting of dry limbs resulted in different values for abundance, diversity, dominant species and functional groups of benthic fauna compared to intact mangroves in the area (Sabeel *et al.*, 2014; Sabeel and Vanreusel, 2014). Similar results on the effect of mangrove loss on macrofauna (Alfaro, 2010) and mangrove fragmentation on fish fauna (e.g. Layman *et al.*, 2004; Valentine-Rose *et al.*, 2007; Abrogueña *et al.*, 2012) were reported elsewhere.

2.4.4. Factors limiting mangrove areal extent and distribution

2.4.4.1. Climate

In general, the variability in the areal extent, structural development and stand distribution of the Sudanese mangroves can be partly attributed to extreme climatic conditions found in arid environments namely the combination of the aridity (low rainfall) and extreme higher temperature (Quisthoudt, 2013). In our study, no relationship was detected between rainfall or longer periods of higher temperature and the mangrove areal extent during the study period. However, the loss of mangroves that occurred between 1995 and 2000 could be explained by 1997/98 El Niño-SO during which a mass mortality of mangrove occurred as a result of the combined effect of low rainfall and longer period of high temperature. The improved weather condition, the higher precipitation and the low temperature may explain the expansion of mangroves during the following periods, which may be related to reduced salinity as a result of increased freshwater inputs via runoff. It is expected that since the Sudanese mangroves are marginal, they are fragile, and that any change in their climatic setting can seriously affect their distribution. However further evidence is required from ground truthing.

2.4.4.2. Salinity

The relationship between growth of mangroves and salt concentrations can be shown by a classic curve reflecting concentrations which are deficient, saturating and toxic to growth (Ball, 1988a,b). The growth of mangroves is typically enhanced under low to moderate salinities (Ball, 2002). However, the interspecific differences in seedling survival under high or low salinities may reflect interspecific differences in requirement for, and tolerance of, different salt (NaCl) concentrations (Ball, 1996). As mentioned earlier (in Sec. 2.2.2), the Sudanese coastline is characterized by high salinity, due to absence of rivers and estuaries, with minimal variation throughout the year. Therefore, mangroves developed in high-lying rather than in low salinity areas, but their extensive distribution is limited to areas with freshwater flushes such as in the mouth of khors. Salt concentration in particular may also explain the low diversity of mangroves at the Sudanese coast. *A. marina* has been reported as the only mangrove species growing in the country (Mohammed, 1984; Untawale *et al.*, 1992; PRESGA, 2004; Kathiresan & Rajendran, 2005), even though older surveys reported the presence of *Bruguiera gymnorrhiza* and *Rhizophora mucronata* occurring in the south of the Sudanese coastline (Andrews, 1950; Kassas & Zahran, 1967). This denotes that *Bruguiera* and *Rhizophora*, which are less halo-tolerant and unable to withstand hypersaline conditions, were replaced either by *Avicennia*, which is better adapted to high salinity (Patela *et al.*, 2010; Reef *et al.*, 2010).

2.4.4.3. Geomorphology and tidal inundation

Temperature and salinity are among the most important drivers in mangrove establishment and early development (e.g. Ball, 2002; Krauss, 2008). However, factors such as geomorphologic setting, suitable substrate and the tidal inundation may play an important role in limiting their distribution along the Sudanese coast. The Red Sea is, in general, characterized by narrow coastal plains and the coastline frequently protrudes out in the form of rocky headlands. Furthermore, the coastline and the outlying fringing reefs are incised at irregular intervals by creeks. These creeks are typically drowned streamed valleys. The beach rock is usually overlain with sediment, even in most sheltered areas. Based on the abovementioned geomorphological features and the classification by Thom (1984), mangroves along the Sudanese coast are typical drowned bedrock valley mangroves found in creeks, which are dominated by terrigenous sediments, and mangroves in carbonate settings, which can be seen in oceanic islands, coral reefs and carbonate banks. The mangrove belonging to drowned bedrock valleys can be specifically found at the mouth of khors, while the carbonate setting types are found (i) in the fringe area of some of the islands, where wave energy and wind speed is less and brackish water is present due to mixing of seawater with the margin of the freshwater lens, ii) in between two islands, where the water is shallow and there is accumulated deposits of sediments, iii) along the borders of a lagoon that is connected to the sea, and iv) along the borders of a lagoon that has lost connection to the sea but receives seawater periodically. Freshwater enters into all these types of mangroves through surface runoff and underground seepage. These areas normally receive limited amount of terrestrial sediment but they are rich in calcareous sediment or lime mud.

On the other hand, tidal inundation and surface drainage patterns have often been used to describe mangrove development and species zonation. However, in Sudan, where mangroves exhibit little topography, tidal inundation is ineffective. The Sudanese coast experienced a low range of tidal flooding, caused by the local topography form of the Sudanese coast, which is relatively flat, and much of the mangrove forested areas are in fringing or basin form. The low tidal range is also limiting the encroachment and development of mangrove forest further inland. In addition, the typical zonation of mangrove trees is mainly linked to the pattern of tidal flooding. The low tidal range is, therefore, may partly explain the presence of only monospecific stands of the grey mangrove (*A. marina*) in the area, while *Rhizophora mucronata* were reported in Djibouti, Egypt, Saudi Arabia and Yemen, where the tidal range is relatively higher than in Sudan.

2.4.5. Mangrove change detection

The high variability of the mangrove area in both the impacted and non-impacted mangroves can be primarily attributed to the variability in the accuracy of classification for different years. The high values of the quantity and allocation disagreements indicated that there is some misidentification among the different classes. However, the high values of the user’s and producer’s accuracies in both mangroves indicate that the misidentification occurred in other land-cover classes. This allowed us to proceed confidently with the change detection study for the mangroves.

2.4.5.1. Impacted mangrove

In addition to the environmental and geomorphological factors that can affect the distribution of mangrove, other human related activities and changes in land use can be the primarily driving forces for the change in the areal extent and fragmentation of mangroves in Sudan. Previous surveys conducted along the Sudanese coastline (e.g. Mohammed, 1984; PRESGA, 2004) have reported various human activities such as excessive camel grazing, deforestation and felling, shrimp farming, saltpans, freshwater damming, urbanization, oil and industrial pollution, coastal construction, and changes in land use, that may have adversely affected the extent and health of mangroves. These induced effects were mainly through the modifications of the topography of the coastal area, dredging and infilling on the shore, increased intrusion of saltwater leading to hypersaline habitats, and reception of herbicides, pesticides and fertilizers. The overall impact of these practices involves reduction in tree cover and mass mortality of mangroves. In general, the negative impact of human activities are of higher magnitude than those of natural disturbances and appear to synergistically amplify the negative effects of natural disturbances (e.g., droughts, storms, El Niño-SO events) thus extending the time for ecosystem recovery (Calderon-Aguilera *et al.*, 2012).

The human impacted site showed a perpetual increase in mangrove coverage from 1984-2010. Hence, neither the change in weather conditions nor the anthropogenic activities in the surroundings of this mangrove forest resulted in a netto decrease of the forest area. The increase can be attributed to changes in coastal morphodynamic setting. The increase in mangrove during 1984-2000 was associated with an increase in muddy soils, and a decrease in saline soil, salt marshes, and sandy soils. These changes, especially the decrease in saline soil, occurred after establishment of a salt pan in 1987 suggesting that the construction of channels to fuel the salt pan has resulted in less accumulation of salt on soils adjacent to mangroves. Consequently, the saline soil were converted to muddy soil which allowed for further colonization of this new established habitat by mangroves. The increase in mangrove during 2000-2010 was accompanied with an increase in area occupied by other habitat such as saline soil, salt marshes, and sand. This condition occurred after the saltpan was expanded to include a shrimp farm situated about 1 km far from the mangrove forest. The greater expansion of these mangroves with a high increment rate (20%) suggests that the effluent from the farm, which often disposed directly into the mangrove area, and/or the lower soil salinity possibly stimulated mangrove development. Mohammed (2006) investigated the production from this shrimp farm at its earliest stages in 2003-2004. He found that the amount of phosphate, nitrite and nitrate amount in the discharged water from two ponds, stocked with a density of 120000 and 30000 individuals/ha and fed with artificial feed, are 13.69 µmol/l, 21.69 µmol/l and 2.14 µmol/l, respectively. Considering the low nutrients concentrations (0.06-1.0, 1.5-4.0 and 0.1-0.40 µmol/l for phosphate nitrate and nitrite, respectively) within the euphotic zone in the northern Red Sea (Dowidar, 1984; Nasr *et al*, 1987; Qurban *et al.*, 2014), effluents from the shrimp farm may have enriched the water surrounding the mangrove with particulate and dissolved organic and inorganic nutrients. This may have enhanced the nitrogen uptake by mangrove and promoted seedling growth and faster mangrove expansion (Gautier, 2002; Primavera *et al.*, 2007). Moreover, *A. marina* is the most tolerant mangrove species to large abiotic fluctuations (MacFarlane & Burchett, 2002; Joshi & Ghose, 2003) and, therefore, it is not surprisingly that they may sustained the chemical content from farm effluent and assimilated the excess nutrient into mangrove biomass. Wong *et al.* (1995), Trott and Alongi (2000) and other studies have all concluded that nutrient enrichment can be beneficial for mangrove growth and ecosystem health. However, evidence is mounting that eutrophication can also have negative consequences for mangrove growth. A Red Sea study demonstrated that *A. marina* grown under sewage pollution stress showed stunted morphology and that mortality rates within the effected mangrove strand were high, probably due to the loss of pneumatophores and soil anoxia (Mandura, 1997). This may partly explain the significant decline in this mangrove during 2010-2013 with a rate of -27% from 90 to 66 ha. Nutrient enrichment can also increase sensitivity to drought and hyper-salinity because nutrient-induced increases in allocation to canopy rather than roots can indirectly increase mortality rates due to enhanced susceptibility to water deficits (Lovelock *et al.*, 2009). This suggests that nutrient and salt concentrations significantly elevated in the effluents, as the farm was expanded and the shrimp production was intensified, beyond mangrove tolerance levels (Vaiphasa *et al.*, 2007). This adversely affected mangrove growth either due to eutrophication (Thomas *et al.*, 2010) or salinization (Primavera, 2006). The later condition was observed during the period of 2010-2013 when saline soil was increased by 34%, which may indicate that soil contained enough soluble salts to interfere with the growth of mangroves. It is also worth to mention that the combination of the human activities and the environmental conditions, being drier during 2010-2013, may adversely affect the mangroves by decreasing their cover. In general, the health of mangrove trees, especially those growing along the mainland shore where the effluents from the shrimp farm are disposed, appear to be adversely affected over time. This is clearly shown by their appearance in the composite image (appendix 5), which changed from deep red (1990), suggesting the broad leaf and/or healthier mangrove, to light red (2005), signifying sparsely or weak mangrove leaves.

2.4.5.2. Non-impacted mangrove

Mangroves at the non-impacted site showed a small areal extent (36-65 ha) during the study period. A significant relationship was observed between mangroves areal extent in this site and the rainfall. The decrease in mangroves between 1995 and 2000 can be explained by the prolonged period of droughts caused by 1997/98 El Niño-SO (ENSO; Allan *et al.*, 1996; Drexler & Ewel, 2001), during which reductions in rainfall over the central Red Sea are well below normal fluctuations (<0.5 mm/day; Hafez & El Rafy, 2008). However, the effect of 97/98 El Niño-SO covered the whole region, i.e. the human impacted site was also affected by El Niño-SO, but the magnitude of impact was more pronounced in the non-impacted site. The stagnation and absence of freshwater combined with high evaporation may have created hypersaline conditions, whereby the saline soil area increased 5 times more in 2000 than in 1995. Decline in rainfall may also have a role in changing coastal morphodynamics by increasing the infilling and deposition of sand. Martinho *et al.* (2010) found that dune fields, along the southern coast of Brazil, increase their width as the precipitation decreases and the sand supply increases in the area. Kitheka *et al.* (2002) found that heavy supply of terrigenous sediments during the El Niño-SO of 1997–1998 led to the huge deposition of sediments in mangrove wetland. We found that sand in 2000 increased by 2.5% compared to 1995, hence, this increase may be due to drought during 1997-1998. Sand infilling and sand deposition can inhibit the seedling establishment (Thampanya *et al.*, 2002; Balke *et al.*, 2011; 2013), and influence the forest structure (Lovelock *et al.*, 2010) by causing a massive destruction of the mangroves (Kitheka *et al.*, 2002). Deposition can also obstruct the tidal inlet and channels through which tidal flow regularly floods the mangrove forests. Insufficient runoff may also cause a decrease in the alluvium and sediment load deposited at the mouth of khor Ashat, a seasonal watercourse flow from the nearby mountains, at the non-impacted mangrove. All these conditions collectively created unfavorable conditions for mangrove growth resulting in shrinkage of the area occupied by mangroves. Similar results were found in Puerto Rico (Cintron *et al.*, 1978) and Senegal (Isupova & Mikhailov, 2008). This period is also characterized by mangrove die back, due to insufficient runoff to neutralize the effects of decreased rainfall, followed by expansion of mangroves as rainfall increase as observed during the period 2000-2013. During this period mangrove were partly regenerated; however, recovery of the mangroves did not take place in some parts of the area affected by the mass mortality. About 80% of the dry limbs and tree trunks of the mangrove of the outer belt (4.68 ha) has been collected by fishermen for fuel wood for processing their catch of sea cucumber (Laverdiere, 2009). However, since 2007 fishing for sea cucumber is prohibited in this area.

2.5. Conclusion

This study has described the distribution and temporal change of mangroves over the entire Sudanese Red Sea coast during 1984-2013. Two sites, representing impacted and non-impacted mangroves, were used to investigate the potential effect of human activities in terms of shrimp farming on mangroves. To our knowledge this study represents a first attempt to provide quantitative assessment on the temporal distribution and change detection of mangroves along the Sudanese red sea coast. The spectral angle mapper (SAM) classification method used in this study performed consistently well in the classification of mangroves considering the aridity of the area which might interfere with the spectral signal strength of this vegetation. However, the accuracy of the classification was limited by the lack of systematic ground truthing. There was a high variability in mangrove areal extent during the study period. A set of landscape metrics was used to assess the fragmentation of mangroves during 1984-2013. Apparently, acceleration in fragmentation of mangroves occurred during the period 2000-2005, followed by a gradual deceleration in fragmentation during the period 2005-2013. The fragmentation of an ecosystem is a complex process that acts on a complex system and results in a wide arrangement of spatial patterns. The use of landscape metrics to describe these patterns is useful, particularly those that result from human activities. However, the foundation to derive such metrics must always be in harmony with the purpose of relating those metrics with ecological processes in order to understand the causes and consequences of spatial heterogeneity and how they vary with scale in order to influence management of both natural and human dominated habitats. The growth of mangroves appear to be positively enhanced after the construction of the salt pan and the shrimp farm, while non-impacted mangrove showed mortality and expansion of mangrove forests in response to climatic events, such as El Niño-SO and increased rainfall in this arid area. We suggest that studies on effluents from the shrimp farm, their chemical content and the effect of these chemicals on the survival of mangroves in addition to monitoring of the mangrove distribution for management purpose should be carried out in the area on a regular basis.

3

Importance of Sudanese mangroves to macrofauna

Chapter 3

Assessement of the importance of the Sudanese mangroves as a habitat for benthic macrofauna

Adapted from: Sabeel R. A. O., Ingels J., Pape E., Vanreusel A. (2014) Macrofauna along the Sudanese Red Sea coast: potential effect of mangrove clearance on community and trophic structure. *Marine Ecology.*doi: 10.1111/maec.12184

Abstract

Mangroves along the Sudanese Red Sea coast are under continuing anthropogenic pressure. To better understand the influence of mangrove clearance on the intertidal benthic community, we investigated composition, biodiversity and standing stock of the macrofauna communities at high-, mid- and low-water level in three contrasting habitats: a bare sand flat, a cleared mangrove, and an intact mangrove. In addition, a community-wide metric approach based on taxon-specific carbon and nitrogen isotope values was used to compare the trophic structure between the three habitats. The habitats differed significantly in terms of macrofaunal standing stock, community composition and trophic structure. The high- and mid-water levels of the intact mangroves showed a distinct macrofaunal community characterized by elevated densities and biomass, largely governed by higher decapod and gastropod abundances. Diversity was similar for cleared and intact mangrove, but much lower for the bare sand flat. Community-wide metrics indicated highest trophic diversity and community niche breadth in the intact mangrove. Differences between the cleared and intact mangroves can be partly attributed to differences in sediment characteristics resulting from mangrove clearance. These results suggest a significant impact of mangrove clearance on the macrofaunal community and trophic structure. This study calls for further investigations and management actions to protect and restore these habitats and ensuring the persistence of this ecologically valuable coastal ecosystem.

3.1. Introduction

Tropical mangroves represent unique and significant productive ecosystems. They provide a number of essential services for human wellbeing and survival, including food provision, coastal protection, waste absorption, climate regulation, recreation and education (Qureshi, 1990; Nagelkerken *et al.*, 2008). Despite their relatively simple forest structure on a macroscale, mangroves are believed to play an important role in supporting the estuarine and coastal food webs by creating a complex environment on a meso- and micro-scale for a variety of mainly, benthic organisms. The biodiversity associated with mangroves is important from a functional point of view since mangroves may provide food and shelter for different organisms including socio-economically important macro-invertebrates and fish species. The benthos plays a vital role in mangrove productivity by altering the physical habitat (e.g. increase aeration of the sediment as a result of burrowing activities) and by stimulating nutrient turnover through organic matter retention and bioturbation activities (Smith *et al.*, 1991). In addition, most macrofaunal taxa (>1 mm) may provide a trophic linkage to various benthivorous marine consumers entering the mangroves during their occasional or regular feeding migrations (Bouillon *et al.*, 2002a,b; Lee, 2008). Also dissolved organic carbon (DOC), and dissolved inorganic nitrogen (DIN) originating from the excretion and biomass degradation of macrobenthos can stimulate bacterio-plankton production (Hutchings, 1998; Dittmar *et al.*, 2006). Furthermore, the community composition of the macrobenthos can be considered as a biological indicator of the ecosystem's health and functionality because of its response to anthropogenic impacts (Brown *et al.*, 2000; Hatje *et al.*, 2008).

The Sudanese Red Sea coast is characterized by about 19 distinct mangrove stands (mainly comprising the grey mangrove tree (*Avicennia marina)* extending from north to south. Despite their fragmented nature and small size compared to those from other tropical coasts (PERSGA, 2004), they are considered to play similarly important ecological roles (Khalil & Krupp, 1994). The total area of mangrove stands along the Sudanese coast was about 605 ha in 1980, but according to FAO, has shown an annual loss of 7 ha since then (www.fao.org/forestry/mangroves). Most mangrove stands appear to be under threat and are very likely to disappear in the coming decade as a result of increasing human activity in the coastal area in addition to threats from climate change. The main causes of mangrove degradation include over-grazing by camels, wood cutting for fuel wood, construction of dams (mainly constructed by salt extraction companies) that reduce the flow of fresh water to the mangroves, highway construction, and building of dykes to collect fresh water. Another cause of the degradation of mangroves in Sudan is linked to the activity of fishermen fishing for holothurians, who collect firewood from mangrove forests to process their catch (Laverdiere, 2009*)*. The available knowledge on the benthic communities of the Red Sea mangroves is scant. Therefore, improving our understanding of their ecology, community structure, and role in energy flows is of crucial importance in a conservation context. Such studies are imperative to move towards a sustainable management of these ecosystems.

This study examines the spatial variability of the macrofauna in three habitats along the Sudanese Red Sea coast: a bare sand flat, a cleared former mangrove and an intact mangrove also referred to as relict mangrove. This sampling design may help to understand community changes due to mangrove clearance. It also allows predicting further assemblage changes if a cleared mangrove is, overtime, converted to less complex habitat such as a bare sand flat. Despite the lack of replication of habitat types, the comparison can provide insight into the potential changes in habitats and associated fauna due to clearance, since the sites were chosen based on their similarity in environmental properties, notably, the topography. The aim of this study is to compare between the three habitats: (i) community structure, abundance, biomass and diversity of the macrofauna communities, and (ii) food web structure of the macrofauna, in terms of its complexity, based on community-wide metrics. This study is a first step in the evaluation of the importance of the Sudanese mangroves as a provider for temporary or permanent habitat for marine fauna. It will also contribute to our understanding of the potential impact of mangrove habitat loss on higher trophic levels, since the macrofauna is considered to be a direct link in the energy flow between primary producers and larger consumers (Edgar & Shaw, 1995).

3.2. Materials and methods

3.2.1. Study sites

The Sudanese Red Sea coast (23°6’N, 35°59’E; 17°59’N, 38°35’E) is about 750 km long. It is nearly tideless, with a mean spring tide of 0.1 m. Seasonal water level changes, being up to 0.5-1.3 m higher in winter as a result of intense rainfall, are greater than lunar tidal changes (Musa, 1991). The rainy (winter) season is from November to April with mean annual precipitation of 164 mm at Suakin city. The present study was carried out at three sites representing three different habitats along the Sudanese Red Sea coast. The first two sites, the Ashat bare sand flat (site 1) (18° 45’N, 37° 30’E), and the Ashat cleared mangrove (site 2) (18° 45’N, 37° 30’E) are located about 40 km south of Suakin city (19° 06’N, 37° 20’E); while the Sheikh Ibrahim intact mangrove (S3; 18° 59’N, 37° 24’E), is located about 30 km south of Suakin (Fig. 3.1a).

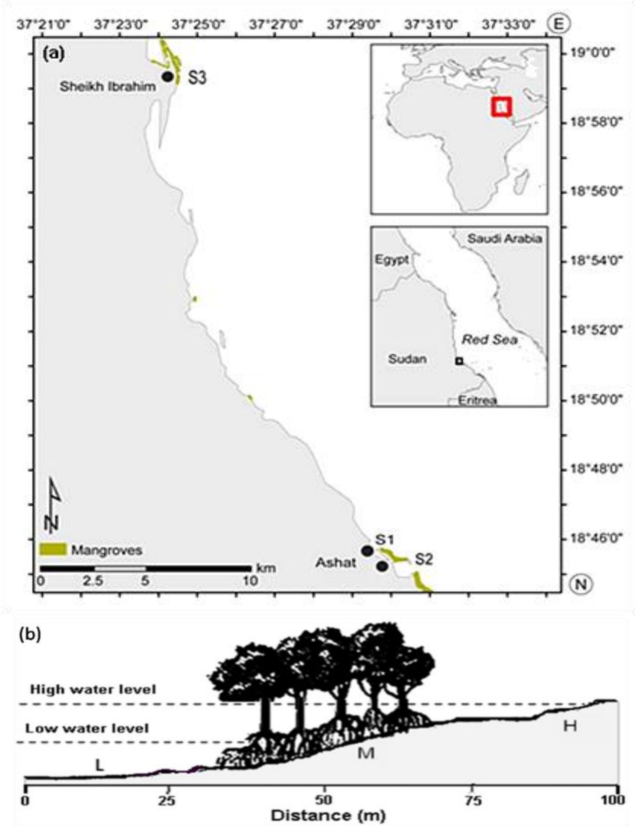


Figure 3.1. (a) Location of the study sites (S1: bare sand flat habitat, S2: cleared mangrove habitat, S3: intact mangrove habitat) sampled along the Sudanese coast south of Suakin, and (b) Profile of transect with sampling stations (H: high-water, M: mid-water, L: low-water) along the gradient of seasonal water level. Source: Flanders Marine Institute (VLIZ).

The gradual clearance of the outer belt of the mangrove at Ashat is linked to fishermen who were fishing for sea cucumbers from the subtidal areas around the mangrove, and collecting firewood from mangrove forests to process their catch (fishermen personal comments in 2010 and 2011, pers. comm.). Site 3 (intact or relict mangrove) is characterized by the presence of *A. marina* stands. Three stations were established at each site parallel to each other along a water level gradient of about 100 m length (Fig. 3.1b). These stations were referred to as: (i) high-water level station (H), which is just below the water line mark during the high-water level and about 30-40 m far from the outer edge of the mangrove; (ii) mid-water level station (M) without mangrove stand at the bare sand flat habitat but with remnants of mangrove trunks in the cleared mangrove habitat, and with mangrove stands in the mangrove habitat, and; (iii) low-water level station (L) which is just above the water line mark at lower water level and about 10-15 m far from the inner edge of the mangrove at the intact mangrove site. Samples were collected between the 19th and 26th of December 2010. At the time of sampling, the mean water temperature averaged 20 °C at the sand flat and the cleared mangrove, and 22 °C at the intact mangrove.

3.2.2. *Sediment characteristics*

Three replicate sediments cores (Ø6 cm, 5 cm depth) were taken from each water level station at each site to assess grain size distribution and organic content. Sediment fractions were analyzed using a Laser Particle Size Analyzer (Malvern Mastersizer 2000 laser diffractometer, Malvern Instruments Ltd., UK). Median grain size and grain size classes (clay <4 µm, silt (4-63 µm) and sand (>63µm) were determined and classified following Wentworth (1922). The sorting coefficient and sorting classes were calculated and described after Folk and Ward (1957). For the determination of total organic carbon (TOC) and total nitrogen (TN) content of the sediment, subsamples of 5 mg of fine-ground sediment were analyzed using a CN analyzer (FLASH 2000 Series Nitrogen and Carbon analyzer).

3.2.3. Macrofauna analysis

3.2.3.1. Community analysis

A rectangular metal frame (36x20 cm) was used to collect macrofauna in all habitats and water level stations. Since the frame could only be inserted down to 5 cm sediment depth in the mangrove stand due to the presence of roots, this sampling depth was kept in the other habitats. Three replicate samples were sieved through a 1 mm mesh and fixed immediately in 4% seawater-buffered formalin. All individuals were counted, weighed and identified to family level. Biomass samples were dried at 60 °C for 48 h, and weighed (dry weight). Next, samples were combusted in a muffle furnace for 2 h at 500 °C, and re-weighed (ash weight). Individual biomass (g) was determined as ash free dry weight (AFDW; dry weight minus ash weight). Total taxon biomass was determined as average individual biomass multiplied by the total number of individuals per taxon.

3.2.3.2. Stable isotope analysis

Samples for carbon and nitrogen isotope measurements for macrofauna taxa, identified to family level, were collected from all water levels at all site. One to

3 individuals per taxon were used for the analysis. Whole individuals of small macrofauna individuals (or pooled individuals of small taxa when the amount of dry material of a single specimen was insufficient) and muscle tissue of large macrofauna were used for stable isotope analysis, while hard-shelled organisms were acidified with diluted HCl (10%) to remove carbonates. As acidification may affect $\delta^{15}N$ (Bunn *et al.*, 1995; Kolasinski *et al.*, 2008), $\delta^{15}N$ samples were not acidified. In addition, samples for potential basal resources accessible to macrofauna, including fresh mangrove (*A. marina*) leaves collected from the intact mangrove site, seagrass leaves, epiphytes, macroalgae, sediment organic matter (SOM) and suspended particulate organic matter (SPOM) were also collected from each site. All samples were oven dried at 60 °C for 24 hrs to determine $\delta^{13}C$ and $\delta^{15}N$ isotope signatures.

C and N isotope analyses were performed using an elemental analyzer interfaced to a PDZ Europa ANCA-GSL continuous flow isotope ratio mass spectrometer (IRMS) (UC Davis, University of California, USA). Stable isotope values were expressed relative to the international standards V-PDB (Vienna PeeDee Belemnite) and Air for carbon and nitrogen, respectively, and calculated as:

$$\delta X\ (‰) = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000$$

where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

The analytical precision of this method is 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Stable isotope samples comprised of 1 individual each. For some taxa, replicates were measured.

3.2.3.3. Measures for trophic structure

Community-wide indices, characterizing the food web structure based on the average isotopic composition of the consumers, were calculated according to Layman *et al.* (2007a). The following indices were computed from $\delta^{13}C$–$\delta^{15}N$ bi-plot space as: (1) $\delta^{13}C$ range (CR), which is the horizontal distance between the most enriched and most depleted $\delta^{13}C$ values, (2) $\delta^{15}N$ range (NR), which is the vertical distance between the most enriched and most depleted $\delta^{15}N$ values; (3) total convex hull area (TA), encompassed by all consumers in the bi-plot space, indicating the total amount of niche space occupied, (4) the average Euclidean distance of each species to the $\delta^{13}C$–$\delta^{15}N$ centroid (CD), (5) the mean Euclidean distance to each species' nearest neighbor in the bi-plot space (NND), and (6) the standard deviation of the nearest neighbor Euclidean distance (SNND), a measure for the evenness of species packing in the bi-plot space. The first four metrics are community-wide measures of the total extent of spacing within the $\delta^{13}C$-$\delta^{15}N$ bi-plot. Larger NR and CR suggest more trophic levels and the presence of multiple basal resources with distinct $\delta^{13}C$, respectively. Greater values of TA and CD imply greater spacing of species in the $\delta^{13}C$-$\delta^{15}N$ bi-plot. The last two metrics (NND and SNND) reflect the relative positions within niche space and thus these can be used to estimate the extent of trophic redundancy. Smaller NND indicates a larger fraction of species with similar feeding strategies, while lower SNND suggests a more even distribution of trophic niches. The isotopic ranges of the macrofauna identified by the convex hull in each habitat were compared to the theoretical ranges of the benthic secondary producers of the theoretical trophic pathways in the estuarine food web on the basis of an average 2.5‰ and 3.4‰ of nitrogen isotopic fractionation for primary and secondary consumers, respectively (Eggers & Jones, 2000; Post, 2002).

3.2.4. Statistical analysis

All analyses were conducted in Primer v6 using the PERMANOVA + add-on (Anderson *et al.,* 2008). Macrofaunal diversity was expressed as taxon richness (S) and Shannon-Wiener taxon diversity (H'), both calculated from raw abundance data with the DIVERSE routine (Clarke & Warwick, 2001). Differences in macrofaunal communities between and within sites (=habitats) and water level stations were tested using a 2-way crossed non-parametric permutational ANOVA (PERMANOVA) design with fixed factors Habitat (Ha) and Water Level station (WL), and the interaction term Ha x WL. Univariate analyses were performed on Euclidean distance-based resemblance matrices of untransformed, univariate diversity, abundance and biomass data; multivariate analysis was done using the Bray-Curtis distance based resemblance matrices of square root-transformed community composition data. Prior to the PERMANOVA test, homogeneity of multivariate dispersion was tested for using a non-parametric dispersion test (PERMDISP; Anderson *et al.*, 2008) based on Bray-Curtis similarity measure on square root transformed data. PERMDISP results revealed no difference in dispersion for the density and biomass data neither between habitats (F=1.26, P=0.43 and F=1.49, P=0.36; respectively), water level stations (F= 0.98, P=0.47 and F= 2.46, P=0.15; respectively), nor for the interaction factor Ha x WL (F=5.80, P=0.16 and F=20.99, P=0.07; respectively). Thus, the null hypothesis of homogeneity of multivariate dispersion was accepted for all factors. Pairwise tests were executed following significant interaction or main effects (the latter in case there was no significant interaction effect) in the full model. A non-metric multidimensional scaling (MDS) on square root transformed taxon abundance data was carried out to visualize spatial variability in macrofaunal community composition (Clarke, 1993; Clarke & Warwick, 2001). A 2-way crossed SIMPER (similarity percentage analysis) routine was run (Clarke, 1993; Clarke & Warwick, 2001) to determine taxon contributions to compositional differences within and between habitats and water level stations.

Principal components analysis (PCA) was performed to compare environmental variables between sites and water level stations. Distance-Based Linear Modeling (DISTLM) was used to analyze and model the relationship between environmental variables and macrofaunal community attributes. This routine allows for predictor variables (here: silt, clay, sand, sediment sorting, median grain size, TN, TOC, and C/N) to be fitted on ordination axes based on biological data to test and quantify the variation explained by one or more environmental variables. Predictor variables were selected based on draftsman plots and Pearson correlation coefficients. Variables with a correlation coefficient of ≥ 0.9 were considered collinear and so only one of these was retained in the analysis (Anderson *et al.,* 2008). The fitting of the best model was done using a step-wise selection procedure and adjusted R^2 as a selection criterion. The model was visualized in multi-dimensional space using Distance Based Redundancy (dbRDA) analysis.

3.3. Results

3.3.1. Sediment characteristics

Sediment characteristics for all habitats and water level stations are presented in Table 3.1 and visualized in Fig. 3.2. Overall, the intact mangrove (site 3) had finer, more poorly sorted sediments with higher C/N ratios and higher TOC and TN values compared to the other habitats. Results of the univariate PERMANOVA indicated a significant interaction effect between sites and water levels for all sediment characteristics, except for C/N ($P < 0.05$, Table 3.2). The pairwise tests showed that significant differences were between the intact mangrove site and the other two sites, and between the bare sand flat and the other two habitats. However, these differences depended on the water level considered. At the high-water level, the bare sand flat had a significantly lower mud content, sediment sorting, TN and TOC, but median grain size was higher compared to the intact and cleared mangrove. The intact mangrove showed a significantly higher mud content and sediment sorting coefficient at the mid-water station, while the cleared mangrove had a significantly higher median grain size, and the bare sand flat had lower TOC values. At the low-water level station, the sorting coefficient and TN were higher in the intact mangrove, while sediments were on average coarser at the cleared mangrove site ($P < 0.05$, Table 3.2).

Table 3.1. Mean±SE values for sediment environmental variables at the different water level stations (H: high-water level, M: mid-water level, L: low-water level) in each habitat.

site	Water level	Clay (%)	Silt (%)	Sand (%)	Median grain size (µm)		Sediment sorting Coefficient		TOC (%)	TN (%)	C/N
Bare sand flat	HW	3.7±0.4	22.3±2.7	74.0±2.6	273.0±10.1	MS	1.3±0.1	PS	0.1±0.0	0.00±0.0	3.9±3.9
	MW	3.6±0.3	16.8±1.1	79.6±1.3	310.0±6.3	MS	0.9±0.0	MS	0.2±0.0	0.01±0.0	8.7±4.4
	LW	6.0±1.2	36.3±7.4	57.7±8.5	230.0±22.1	FS	3.1±0.2	VPS	3.9±0.6	0.10±0.0	65.6±20.4
Cleared mangrove	HW	17.6±2.0	69.8±1.2	12.7±2.7	27.0±3.8	MSi	2.6±0.0	VPS	0.8±0.1	0.04±0.0	21.0±2.5
	MW	3.0±1.1	19.5±7.1	77.5±8.1	183.0±32.9	FS	1.1±0.1	PS	1.0±0.2	0.03±0.0	52.6±21.3
	LW	4.9±0.1	34.0±1.5	61.1±1.6	90.0±3.7	VFS	1.5±0.1	PS	1.7±0.2	0.02±0.0	90.1±10.6
Intact mangrove	HW	11.8±1.3	59.6±6.1	28.6±7.1	49.0±6.0	CSi	3.0±0.1	VPS	0.6±0.1	0.04±0.0	16.4±2.2
	MW	16.4±3.6	66.1±5.4	17.6±8.9	30.0±6.5	MSi	3.0±0.1	VPS	3.4±1.0	0.20±0.1	20.0±1.6
	LW	6.6±0.6	30.4±2.7	63.1±3.3	196.0±20.0	FS	4.9±0.1	EPS	8.7±0.5	0.90±0.0	97.2±21.0

MSi: medium silt; CSi: coarse silt VFS: very fine sand; FS: fine sand; MS: medium sand; PS: poorly sorted. MS: moderately sorted. VPS: very poorly sorted. EPS: extremely poorly sorted; TN: total nitrogen, TOC: total organic carbon,. C/N: carbon nitrogen ratio.

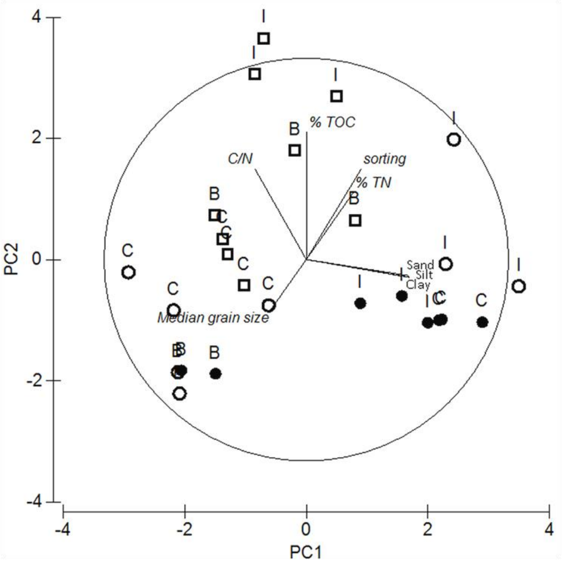


Figure 3.2. Principal component analysis (PCA) ordination of water level stations (filled circle: high-water level, open circle: mid-water level, open square: low-water level) and habitats (B: bare sand flat, C: cleared mangrove, I: intact mangrove). Eigenvectors (environmental variables) were superimposed (TN: total nitrogen, TOC: total organic carbon, C/N: carbon-nitrogen ratio).

3.3.2. Macrofauna

3.3.2.1. Abundance

Total macrofaunal densities varied greatly between and within the three habitats (Fig. 3.3a). Highest average abundances were recorded at the low-water level of the cleared mangrove. Generally, numbers increased towards the sea at the bare sand flat and at the cleared mangrove site, whereas the opposite trend was observed for the intact mangrove. PERMANOVA results indicated a significant interaction effect of water level and habitat on macrofaunal abundance ($P < 0.05$, Table 3.2). Pairwise tests showed that at the high-water level, the intact mangrove area exhibited higher densities than the cleared mangrove and the bare sand flat ($P < 0.05$). At the mid-water level, the intact mangrove harboured significantly greater macrofaunal density than the bare sand flat, whilst the opposite was observed for the low-water level stations ($P < 0.05$; Table 3.2).

3.3.2.2. Biomass

Overall, macrofaunal total biomass averaged 9.19±1.49 g (AFDW)/m^{2}, with highest biomass recorded at the mid-water level station of the intact mangrove habitat (Fig. 3.3b). PERMANOVA results revealed a significant interaction between habitat and water level station ($P < 0.05$, Table 2). Pairwise tests indicated no general significant differences between water levels in all habitats, except for the low-water station at the bare sand flat where biomass was significantly higher compared to the low-water level station at the cleared and intact mangrove site ($P < 0.05$, Table 3.2).

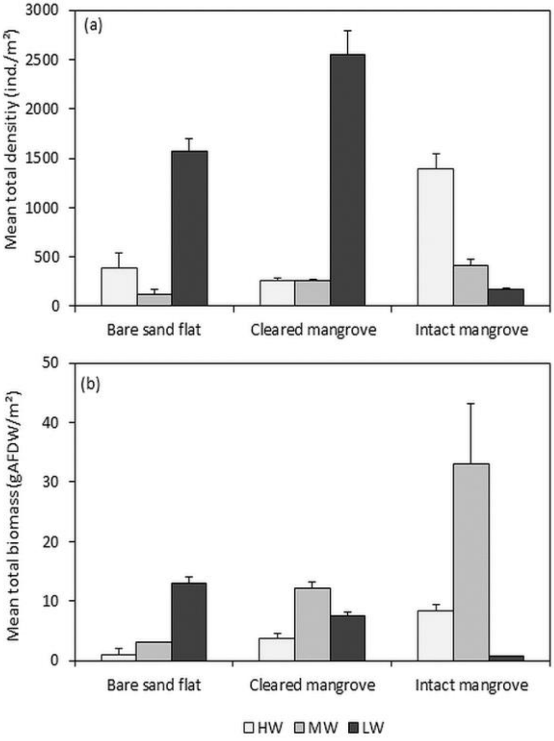


Figure 3.3. Mean values (±SE) for macrofaunal (a) abundance and (b) biomass at each water level (H: high-water, M: mid-water, L: low-water) within the three habitats. Values were averaged over replicates (n≤1-6).

Table 3.2. Results of the Univariate PERMANOVA analyses to test for differences in sediment characteristics (TN: total nitrogen, TOC: total organic carbon, C/N: carbon-nitrogen ratio) and macrofaunal characteristics (total abundance, total biomass, taxon richness (S), Shannon-Wiener taxon diversity (H'), δ13C and δ15N) for factors Habitat (B: bare sand flat, C: cleared mangrove, I: intact mangrove) and Water Level (H: high-water, M: mid-water, L: low-water), and the interaction between Habitat and Water Levels (significant P values (<0.05) in bold italic). NS: not significant.

Variable	Main tests									Pair-wise test					
	Habitat			Water level			Habitat x Water level			Habitat	WL	Ha x WL (Site factor)		Ha x WL (Station factor)	
	df	F	P	*df*	*F*	*P*	*df*	*F*	*P*						
Sediment environmental variables															
Mud Content	2	27.08	***0.0001***	2	13.88	***0.0006***	4	22.18	***0.0001***	I>C>B	H>M, L	H	C,I>B	1	NS
												M	I>C,B	2	H>M,L
												L	NS	3	L<H,M
Median grain size	2	428.07	***0.0001***	2	45.00	***0.0001***	4	89.38	***0.0001***	B>C,I	H<M, L	H	B>I> C	1	M>L
												M	C>B> I	2	M>L>H
												L	I,B> C	3	L>H>M
Sediment sorting coefficient	2	23.32	***0.0001***	2	11.20	***0.0014***	4	4.91	***0.0064***	I>B,C	L>H>M	H	B<C<I	1	L>M
												M	I>C,B	2	H>M,L
												L	I>C	3	L>H,M
TN	2	7.76	***0.002***	2	2.66	0.0855	4	3.44	***0.0227***	I>B,C	NS	H	B<I,C	1	NS
												M	NS	2	H>L
												L	I>C	3	L>H
TOC	2	46.38	***0.0001***	2	77.65	***0.0001***	4	17.98	***0.0001***	I>B,C	L>H,M	H	B<I,C	1	L>H,M
												M	B<I,C	2	L>H,M
												L	I>B>C	3	L>M>H
C/N	2	3.84	***0.0384***	2	25.80	***0.0001***	4	0.75	0.5773	B<C	L>H,M	NS			NS
Macrofauna community attributes															
Total Density	2	0.86	0.4454	2	3.91	***0.0305***	4	4.04	***0.0145***	NS	M<H,L	H	I>B>C	1	L>H,M
												M	B< I,C	2	NS
												L	I<C,B	3	H>M,L
Total Biomass	2	29.99	0.061	2	0.91	0.423	4	32.53	***0.041***	NS	NS	H	NS	1	L>M>H
												M	NS	2	NS
												L	B>I,C	3	NS
Community composition	2	6.3724	***0.0001***	2	6.4958	***0.0001***	4	3.6882	***0.0001***	B≠C≠I	H=M, L≠H,M	H	B=C, IM≠ B, C	1	H=M, L≠H,M
												M	C≠I, B=C,I	2	H=M, L≠H,M
												L	B=C, I≠B,C	3	H≠M≠L
Taxon richness (S)	2	1.45	0.2499	2	13.89	***0.0002***	4	4.19	***0.0108***	B<C,I	L>H,M	H	I >B	1	L>H,M
												M	I> B	2	NS
												L	B>I	3	NS
Shannon-Wiener diversity (H)'	2	6.55	***0.0072***	2	13.79	***0.0001***	4	7.84	***0.0003***	B<C,I	L>H,M	H	I,C>B	1	L>H,M
												M	I>B	2	NS
												L	B>C	3	H,M,L
Macrofauna trophic attributes															
$\delta^{13}C$	2	3.167	***0.0455***	2						I>C					
$\delta^{15}N$	2	0.9454	0.3946	2						NS					

3.3.2.3. Taxon diversity and community composition

A total of 31 macrofauna families belonging to 4 phyla and 7 classes were identified (Table 3.3). Figure 3.4 shows the relative abundance of each taxon at the different water level stations in each habitat. Polychaetes were most abundant in the cleared mangrove, whereas decapods and gastropods were most common in the intact mangrove. The bare sand flat was mostly dominated by bivalves and poriferans. Amphipods were found only at the low-water level station at the cleared mangrove site.

Table 3.3. List of the taxa found in each station (H: high water-level, M: mid water-level, and L: low water-level) within the three habitats (i.e. intact mangrove, cleared mangrove and bare sand flat) sampled along the Sudanese Red Sea coast. Numbers indicate the average density of individuals identified per sample (ind./713 cm²)

Taxa	Bare sand flat			Cleared Mangrove			Intact mangrove		
	H	M	L	H	M	L	H	M	L
Porifera	3	2	6	3	3	4	3	5	1
Bivalvia									
Mytilidae	0	0	21	2	1	8	5	1	1
Tellinidae	0	0	11	0	0	3	0	0	1
Semelidae	0	0	2	0	0	2	0	0	4
Mactridae	0	0	2	0	0	0	0	0	0
Veneridae	0	0	1	0	0	0	0	0	0
Cardiidae	0	0	2	0	0	1	0	0	0
Petricolidae	0	0	0	0	0	1	0	0	0
Solemyidae	0	0	0	0	0	0	0	1	1
Cultellidae	0	0	1	0	0	1	0	0	0
Gastropoda									
Batillaridae	0	0	17	3	1	9	73	6	2
Cancellaridae	0	0	1	0	0	0	0	2	1
Trochidae	0	0	1	0	0	0	0	0	0
Marginellidae	0	0	4	1	1	2	3	2	0
Decapoda									
Diogenidae	0	0	3	0	0	3	5	3	1
Leucosiidae	0	0	2	0	0	0	1	0	1
Grapsidae	0	0	0	0	0	0	0	2	0
Ocypodidae	0	0	1	3	3	1	1	1	1
Amphipoda	0	0	0	1	0	1	0	0	0
Polychaeta									
Opheliidae	0	0	0	0	0	1	0	0	0
Nereididae	0	0	9	0	3	93	0	0	1
Chaetopteridae	0	0	0	0	0	1	0	0	0
Spionidae	0	0	1	1	1	14	0	0	0
Cirratulidae	0	0	0	0	0	5	0	0	0
Phyllodocidae	0	0	0	0	0	1	0	0	0
Lumbrineridae (*Eunicidae)*	0	0	0	1	1	1	0	0	0
Serpulidae	0	0	1	0	0	1	0	0	1
Aphelochaeta	0	0	0	0	0	0	0	0	1
Oweniidae	0	0	0	0	0	4	0	0	0
Maldanidae (*Euclymene*)	0	0	0	0	0	4	0	0	0
Orbiniidae (*Scoloplos)*	0	0	1	3	9	2	0	0	0
Others	7	4	0	2	4	30	2	6	1

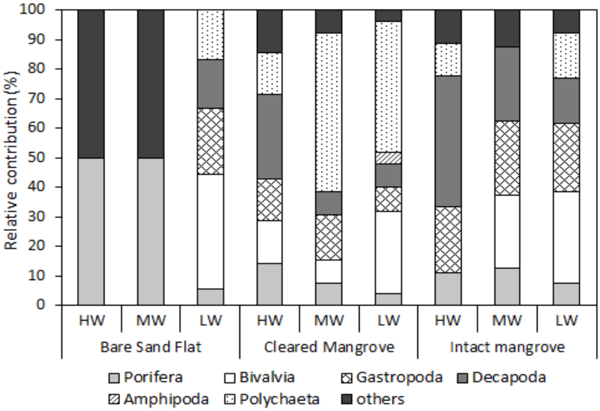


Figure 3.4. Relative abundance of macrofaunal taxa at each water level station (H: high-water level, M: mid-water level, L: low-water level) in each habitat.

Although the MDS (Fig. 3.5) did not show a clear separation of habitats or water levels, the main PERMANOVA test revealed a significant interaction effect between habitats and water levels ($P < 0.0001$). Results from the SIMPER routine indicated that the average dissimilarity (based on abundance data) was highest between the intact mangrove and the degraded mangrove habitats, i.e. the bare sand flat and the cleared mangrove (88.94% and 84.75%). The average dissimilarity between water levels was highest between the low- and both the high-and mid-water levels (90.84% and 87.76%). The taxa that contributed most to the differences observed between habitats and water levels are listed in the table provided in Appendix 5.

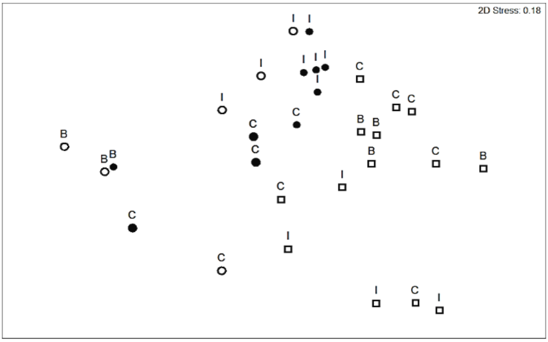


Figure 3.5. Non-metric multidimensional scaling (MDS) ordination of square-root transformed macrofauna abundances. Symbols indicate water level (filled circle: high-water level, open circle: mid-water level, open square: low-water level); letters indicate habitats (B: bare sand flat, C: cleared mangrove, I: intact mangrove).

Taxon richness (S) and Shannon Wiener taxon diversity (H’) varied greatly between and within habitats. PERMANOVA results revealed a significant interaction effect of habitat and water level on both H’ and S ($P < 0.05$, Table 3.2). The pairwise test showed significantly higher S values at the high- and mid-water level of the intact mangrove compared to the bare sand flat, but the opposite was observed for the low-water level station ($P < 0.05$, Table 3.2). H’ followed a similar trend, being elevated at the high- and mid-water level stations in the intact and cleared mangrove, and being lower at the low-water level of the cleared mangrove site compared to the bare sand flat ($P < 0.05$; Table 3.2). The analysis failed to detect any significant differences in H’ between the intact and cleared mangrove. The intact mangrove is on average richer in taxa (higher values of S), but less diverse (lower values of H’) than the cleared mangrove for the high-water level station. The opposite is true for the low- and mid-water level with lower S, but higher H’ values in the intact mangrove relative to the cleared mangrove (Table 3.2).

3.3.2.4. Trophic structure

Ranges of the $\delta^{13}C$ and $\delta^{15}N$ values of the potential macrofauna food sources are shown in Figure 3.6. There was no significant variability between and among sites in the $\delta^{13}C$ and $\delta^{15}N$ values of potential basal sources (t-test; $P > 0.05$).

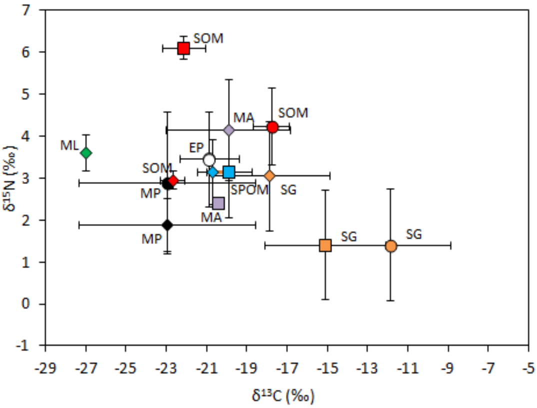


Figure 3.6. Plot of δ13C and δ15N (Mean±SD) values of different macrofauna food sources, represented by different colours (green: mangrove leaves (ML), orange: seagrass (SG), white: epiphytes (EP), black: macrophytobenthos (MP), violet: macroalgae (MA), blue: suspended particulate organic matter (SPOM), red: sediment organic matter (SOM)), sampled in the three habitats (square: bare sand flat, circle cleared mangrove, diamond: intact mangrove).

The $\delta^{13}C$ values of the macrofauna taxa collected in the three habitats ranged between -18.5 and -8.7‰, whilst the $\delta^{15}N$ ranged between 2.1 and 11.6‰ (Appendix 6). Taxa sampled in the intact mangrove showed a wider range of $\delta^{13}C$ and $\delta^{15}N$ values compared to the cleared mangrove and the bare sand flat (Fig. 3.7). The univariate PERMANOVA on the other hand showed significant differences between habitats in terms of $\delta^{13}C$ ($P < 0.05$, Table 3.2), but not in terms of $\delta^{15}N$. Pairwise comparisons indicated that these differences were primarily due to the difference in macrofaunal isotopic signature between the cleared and intact mangrove ($P < 0.05$, Table 3.2). The inspection of mean values of $\delta^{15}N$ indicated that the intact mangrove had higher values compared to the cleared mangrove. In the intact mangrove, bivalves and polychaetes were the most depleted in ^{15}N and ^{13}C, indicating that they are probably detritivores. Decapods were most enriched in ^{15}N, implying these taxa have a higher trophic position (Fig. 3.7).

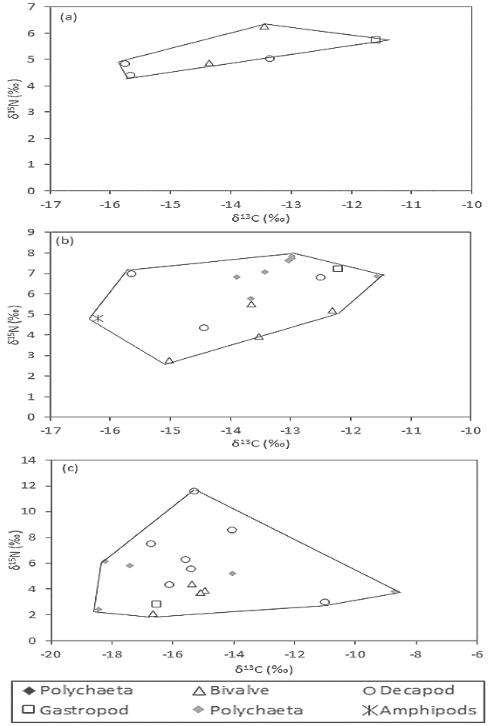


Figure 3.7. $\delta^{13}C$ and $\delta^{15}N$ of macrofauna collected from the three different habitats, i.e. bare sand flat (a), cleared mangrove (b), and intact mangrove (c). Each point represents the mean value of δ13C and δ15N of each measured taxon (see graph legend). The polygons represent the convex hulls used to calculate total area (TA). The convex hulls also delineate the extent of the consumers' trophic pathways as represented by the range of $\delta^{15}N$. Note the different scaling of the axes.

The community-wide metrics for the three habitats are shown in Table 3.4. Compared to the cleared mangrove and the bare sand flat, the intact mangrove has a much higher trophic diversity as suggested by the higher values of the community-wide indices. The intact mangrove is characterized by more trophic levels (NR), more basal resources with distinct $\delta^{13}C$ signals (as illustrated by both the resource $\delta^{13}C$ data shown in the table in Appendix 6, and by CR), and more divergent feeding strategies (TA, CD) which are more equally divided over the different macrofaunal taxa (NDD, SDNDD). TA and NR are higher in the cleared mangrove than at the bare sand flat, whilst the opposite is true for NDD and SSND.

Table 3.4. Community-wide metrics for macrofaunal trophic structure in the three habitats. NR: $\delta^{15}N$ range, CR: $\delta^{13}C$ range, TA: total area, CD: mean distance to centroid, NDD: mean nearest neighbor distance, SDNDD: standard deviation of nearest neighbor distance

Habitat	NR	CR	TA	CD	NDD	SDNDD
Bare sand flat	4.16	5.08	15.02	0.83	1.09	0.61
Cleared mangrove	5.07	4.65	24.99	1.10	0.49	0.54
Intact mangrove	9.30	16.84	80.78	1.76	0.87	0.63

3.3.3. Relationship between environmental variables and macrofaunal communities

Percentages of clay, silt, sand, and median grain size were strongly correlated ($R \geq 0.9$), and consequently clay and sand were omitted from the sequential tests, but they were retained in the marginal tests of the DISTLM analyses. The marginal DISTLM tests (Appendix 7) indicated that the variability in macrofaunal taxon composition and taxon Shannon-Wiener diversity (H’) was strongly correlated to all environmental variables, except for TN in case of composition and for silt, clay, sand in case of diversity (H’), which individually explained between 8.3-43.9% ($P < 0.05$). The marginal tests further showed that median grain size alone could explain 10.9% of the total variation in macrofauna total biomass. Median grain size explained also most of the variability in taxon richness (S) followed by C/N (27.5 and 19.7%, $P < 0.01$). None of the environmental variables could individually explain a significant part of the variation in total macrofauna abundance.

The sequential DISTLM tests (Appendix 6) revealed that the variation in total macrofaunal abundance could be partly explained by TOC (13.5%, $P < 0.05$), while the variability in total macrofauna biomass could be explained by median grain size (10.9%, $P = 0.05$). The total variation in macrofaunal diversity (H’) and taxon richness (S) was largely explained by median grain size (43.9 and 27.5%, P < 0.01). Median grain size also contributed the most to total compositional variation (17.6%), followed by C/N (12.0%) and TOC (6.8%) (P < 0.01; Appendix 6).

A dbRDA ordination plot was constructed to visualize the variability in macrofauna composition in relation to environmental variables (Fig. 3.8). This plot illustrates the importance of TOC and C/N to distinguish between the low-water level, on the one hand, and the mid- and high-water level stations, on the other hand. For the mid- and high-water levels, a separation can be seen between the intact mangrove and the other two habitats (i.e. the bare sand flat and cleared mangrove), which seems to be mainly driven by silt content and median grain size.

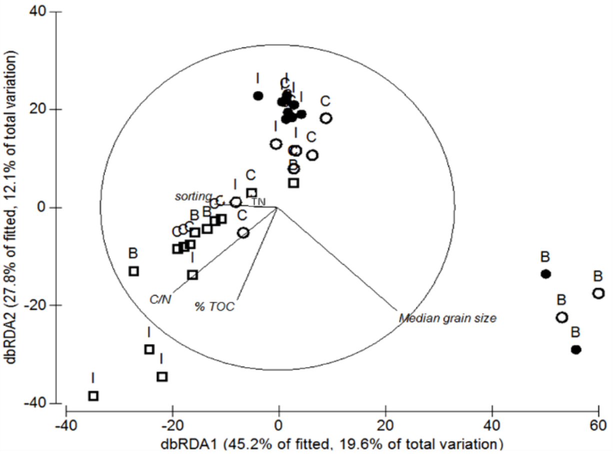


Figure 3.8. Distance based redundancy analysis (dbRDA) ordination of the fitted model of the macrofaunal community composition in relation to environmental variables (TN: total nitrogen, TOC: total organic carbon, C/N: carbon-nitrogen ratio). Symbols indicate water level (filled circle: high-water, open circle: mid-water, open square: low-water), whilst letters indicate habitats (B: bare sand flat, C: cleared mangrove, I: intact mangrove).

3.4. Discussion

3.4.1. Relationship between environmental variables and macrofauna community attributes

Our results suggest that the difference in macrofaunal communities between the three habitats can be linked to the divergent environmental conditions. Sediment grain size and biogeochemical sedimentary characteristics differed significantly between habitats and water levels. Both types of abiotic characteristics are known to be related to the spatial distribution of macrofaunal assemblages (Snelgrove & Butman, 1994; Chapman & Tolhurst, 2007). The intact mangrove showed higher mud and organic matter content than the bare sand flat and the cleared mangrove. This suggests that finer silt particles were retained better in the mangrove stand, indicating a fine sediment-retention effect of mangrove trees. It is therefore likely that differences in macrofauna between the intact and the cleared mangrove habitats (i.e. the cleared mangrove and the bare sand flat) can be attributed indirectly to the presence/absence of mangroves (Granek & Ruttenberg, 2008; Alfaro, 2010).

Deposition of organic detritus may be expected in areas with reduced water flow, and hence in areas where finer sediments dominate. The high total organic carbon (TOC) values in the intact mangroves, particularly at the lower water level, may have resulted from the decomposition of mangrove foliage and other vegetative remains in the sediments (Ramanathan, 1997), although terrestrially derived and suspended organic inputs cannot be excluded. However, the low carbon-nitrogen (C/N) ratio at the mid-water level station in the intact mangrove, compared to the cleared mangrove, may indicate that sediment detritus in the former habitat is richer in nitrogen mainly due to the enhanced nutritional value of the mangrove leaves as a result of fragmentation by crabs (Lee, 2008). Therefore, our study is, in that respect, in general agreement with previous studies (e.g. Pearson & Rosenberg, 1978; Mannino & Montagna, 1997; Ysebaert & Herman, 2002; Ramey & Snelgrove, 2003; Chapman & Tolhurst, 2007), which have suggested that sediment characteristics are important in structuring the macrofauna.

3.4.2. Macrofauna standing stock

Alongi (1989) suggested that mangrove macrofauna is much less abundant compared to the fauna associated with other coastal habitats. However, other studies (e.g. Schrijvers *et al.*, 1995a; Bosire *et al.*, 2004) reported much higher macrofaunal densities in mangrove forests compared to adjacent bare areas. The variation in spatial distribution of macrofauna in the intertidal is linked to various factors like the presence of microalgae (Connor & Edgar, 1982), grain size composition and quality of the organic content of the sediments (Dauwe *et al.*, 1998; Lee, 1999), sediment stability and carbohydrates (Underwood & Paterson, 1993), in addition to tidal dynamics (Barry & Dayton, 1991; Peterson, 1992).

Along the Sudanese Red Sea coast, the macrofaunal densities in the intact and recently cleared mangrove site were higher than those reported for various other tropical intertidal habitats (Alongi, 1989, 1990; Dittmann, 2002, Schrijvers *et al.*, 1995a; Bosire *et al.*, 2004). Also average total biomass of macrofauna recorded in the present study was similar or even higher than that reported from other tropical estuaries and lagoons (Alongi, 1990; Ricciardi & Bourget, 1999). The high densities recorded at the high- and mid-water level of the intact mangrove and at the low-water levels of the cleared mangrove compared to the other two habitats are consistent with Fondo & Martens (1998) and Alfaro (2010). The biomass at the high- and mid-water levels followed a similar trend as densities, being higher in the intact mangrove, which can be linked to the presence of some larger Grapsid crabs. The high macrofaunal standing stock at the high- and mid-water level in the intact mangrove may be further attributed to the higher availability of high quality food in the sediment as indicated by the lower C/N ratios, the moderate concentrations of sediment organic matter (Pearson & Rosenberg, 1978; Dauwe *et al.*, 1998), and the high sedimentary mud content (Ysebaert & Herman, 2002; Thrush *et al.*, 2003; Anderson, 2008). The high levels of organic matter associated with fine sediments may fuel detritivores in mangrove sediments (Dye, 1986; Bouillon *et. al.*, 2003; Bouillon *et. al.*, 2008). Some larger macrobenthic detritivores have developed the ability to consume refractory mangrove leaf litter, turning it into a form that is more conducive to further consumption by themselves and other animals (Lee, 2008). Grapsid crabs shred and consume large amounts of fresh mangrove litter, and consequently produce faecal material with an increased surface area to volume ratio, which facilitates microbial colonisation (Lee, 1997; Werry & Lee, 2005). In contrast, the lower macrofaunal density at the mid-water level station in the cleared mangrove may be ascribed to the lower mud content and low food quality. The lower mud content at this water level station is most likely the result of the removal of finer sediment particles and organic matter by accelerated erosion. In addition, sediment coarsening due to mangrove clearance can result in lower sediment stability with subsequent changes in the associated benthic communities (Probert, 1984; Underwood & Paterson, 1993; Defew *et al.*, 2002). Although sediment and food quality at the high-water level station of the cleared mangrove are still comparable to that in the intact mangrove, macrofauna standing stock is lower at the former site. These findings suggest that the above mentioned environmental drivers do not work independently from other processes like disturbance due to clearing. Possibly, the disturbance is not yet reflected in environmental characteristics such as sediment composition and food input (Probert, 1984; Thrush & Dayton, 2002).

The relatively low densities and biomass of the macrofauna at the low-water level of the intact mangrove are possibly linked to the elevated sedimentary TOC levels (8.7% at the intact mangrove versus 1.7 and 3.9% at the cleared mangrove and the bare sand flat, respectively). Mangrove leaf litter is a rich source of carbon but is poor in nitrogen (evidenced by the high C/N ratio). Furthermore, a high concentration of TOC and mangrove-derived organic matter may depress species richness, abundance and biomass owing to the production of toxic substances, such as tannins, from mangrove roots and leaf litter (Pearson & Rosenberg, 1978; Alongi, 1987). Hyland *et al.* (2005) quantified the relationship between TOC and species richness and showed that TOC values exceeding 3.5%, as observed for the low-water level station in the intact mangrove, can impair benthic assemblages.

3.4.3. Macrofauna composition and diversity

Compared to most other tropical intertidal habitats, mangrove forests are characterized by low species richness (Dittmann, 2002). A total of 31 families were recorded in this study, which is similar to values recorded for mangroves worldwide (Ditmann, 2000; Schrijvers *et al.*, 1995a; Bosire *et al.*, 2004). The cleared mangrove harboured more taxa (24 taxa) than the bare sand flat (20 taxa) and the intact mangrove (16 taxa). The low taxon richness of mangrove fauna is not only linked to the poor nutritional quality of the leaf litter, but also to other factors, including the age of the mangrove stand (Morrisey *et al.*, 2003; Alfaro, 2006), elevation and salinity (Lui *et al.*, 2002), the negative effects of polyphenolic acids (tannins) derived from trees, low microphytobenthos densities, and the harsh physical conditions induced by tidal cycles of exposure and inundation (Alongi & Christoffersen, 1992). Mangrove macrofauna assemblages are therefore dominated by a few species that are adapted to these conditions (Lee, 2008).

The fauna composition in the intact mangrove, especially at the high- and mid-water level station, diverged significantly from that in the other habitats. This divergence was governed by the gastropods and decapods, which tended to be dominant in or restricted to the intact mangrove habitat. Several studies (e.g. Ashton *et al.*, 2003; Skilleter & Warren 2000) have proposed the use of the mangrove crab or gastropod community structure as an indicator for the status of the mangrove forest, as these species do not move over large distances and several crab species are relatively long-living. In our study, Batillaridae gastropods were dominant at the high-water levels of the intact mangroves where the sediment was muddier. The Grapsidae (decapods), which are known to be common in mature mangrove forests (Sasekumar & Chong, 1998), and which feed on mangrove leaves (May, 1999) or scavenge on different types of organic matter (Alfaro, 2006), were restricted together with Solemyidae (bivalves) to the intact mangrove. Both taxa can survive high organic matter concentrations and low oxygen levels, and their spatial distribution reflects their tolerance to the prevailing harsh environmental conditions. The elevated densities of polychaetes in the cleared mangrove relative to the intact mangrove are likely related to the high food quality, as indicated by the lower C/N values, and sediment properties, notably the coarser sediment and lower mud fraction (Dittmann, 2000; Sarkar, 2005). The distribution of the bivalve families Tellinidae and Semelidae in all low-water level stations is in agreement with several other studies on the distribution and zonation of soft-sediment fauna along tropical shores (Sasekumar, 1974; Warwick & Ruswahyuni, 1987; Schrijvers *et al.*, 1995a; Dittmann, 2000), and was probably linked to the high sand content. The presence of Diogenidae (hermit crabs) in the high- and low-water level at the cleared and intact mangrove site suggests that the spatial distribution of this taxon is driven by the preference for fine sediment over sandy bottoms (Lowery & Nelson, 1988) or for sediment with high organic content (Mantelatto *et al.*, 2004).

In general, faunal composition in the three habitats seems to rely not only on sediment characteristics, such as sediment grain size and food quality, but it also reflects a complex association of physico-chemical factors and biological interactions between members of the community operating over time (Pearson & Rosenberg, 1978; Snelgrove & Butman, 1994).

3.4.4. Macrofaunal trophic structure

Most studies so far that have investigated the impact of mangrove clearance on the benthic ecosystem were based on faunal community analyses, such as taxonomic diversity indices or dominance analysis (Macintosh *et al.*, 2002; Bosire *et al.*, 2004, 2008). The usage of community-wide metrics based on stable isotopes is an alternative tool which may help to comprehend the structural and functional heterogeneity within an ecosystem. This approach differs from traditional food web metrics by providing different information on the food web structure as well as by facilitating the link with species richness and ecosystem function measures (Layman *et al.*, 2007a).

In the present study, we examined the food web structure of the three habitats by calculating six community metrics for macrobenthos based on carbon and nitrogen stable isotopes. The isotope signatures of the dominant taxa varied strongly between habitats. Most of the taxa from the bare sand flat and the cleared mangrove were at the base of the food web, while the intact mangrove showed a more complex food web in terms of basal resource utilization and trophic diversity.

The macrofauna displayed a great range of $\delta^{13}C$ values (between -18.5 and -8.7‰), which exceeds the average of the potential primary food sources, when $\delta^{13}C$ fractionation is considered, indicating the importance of different basal resources to these consumers (Layman *et al.*, 2007a). The very similar CR in the bare sand flat and the cleared mangrove (0.43‰, Table 3.4) indicates that a similarly wide range of resources are utilized by benthic consumers in both habitats. In contrast, the intact mangrove displayed a wider CR range (i.e. 16.84‰, Table 3. 4) which reflects the inclusion of additional food sources with distinct isotope signatures for consumers (detritivores or predators) at the basal and higher trophic levels. Thus, a higher degree of niche differentiation (Layman *et al.*, 2007b) was observed in this site due to the presence of taxa which are more depleted in ^{13}C like bivalves (e.g. Semelidae) and more enriched in ^{13}C, such as decapods (e.g. Grapsidae)

The intact mangrove displayed highest trophic diversity as shown by the greater total area (TA) and $\delta^{15}N$ range (NR), resulting in a clear separation between major trophic pathways. The TA and NR in the cleared mangroves are higher than those in the bare sand flat pointing to more energy transfer to higher trophic levels (higher trophic diversity), mainly because of the presence of taxa like decapods (e.g. Ocyptidae) and polychaetes (e.g. Opheliidae and Nereididae) which have high $\delta^{15}N$ values. However, the decrease in NDD and SNND suggests that the elevated trophic diversity in the cleared mangrove as compared to the intact mangrove is only due to an increase in trophic redundancy i.e. an increase in the number of species at different trophic levels that utilize different proportions of an existing basal food source in both habitats (Layman *et al.*, 2007a). This can be explained by an increased abundance of grazers, filter feeders, or omnivores which utilize different parts of macroalgae or suspended organic matter.

Furthermore, observations based on the NR and the average fractionation of the food sources indicated that the intact mangrove is characterized by the presence of several taxa showing different trophic niches and a more distinct trophic position (at least 4 different trophic groups), compared to the cleared mangrove (2 trophic groups: deposit feeders and filter feeders) and the bare sand flat (1 trophic group: filter feeders). This is directly related to the presence of detritivore and predator groups which are missing from the other systems.

Hence, it can be expected that the removal of mangroves has an effect on the trophic structure of the associated fauna. In agreement, the removal of salt marshes resulted in a significant shift in the associated benthic communities because of their role in regulating algal and animal communities (Whitcraft & Levin, 2007). Layman *et al.* (2007b) even reported the collapse in niche width of a top predator resulting from modified physicochemical conditions and nutrient cycles. The collapse was mainly due to the reduction in the basal resources supporting the food web, as well as to the variation of trophic level among organisms.

3.5. Conclusion

This study has shown that macrofauna can be a sensitive indicator of changes in dynamic intertidal ecosystems resulting from human disturbance. Clearing mangroves may alter sediment characteristics, possibly resulting in reduced macrofaunal standing stock. Habitat change is generally recognized as a major threat to biodiversity, and the removal of mangroves may also result in the loss of trophic complexity and functional attributes inherent to mangroves through the loss of higher trophic levels. These results provide valuable information on the ecological importance of the mangroves along the Sudanese coast despite their small size. Therefore, management units need to consider better tools for mangrove conservation and restoration.

4

Importance of Sudanese mangroves to meiofauna

Chapter 4

Assessement of the importance of the Sudanese mangroves as a habitat for benthic meiofauna

Adapted from: Sabeel R. A. O. and Vanreusel A. (Submitted) Determining the potential impacts of mangrove clearing on community structure and functional traits of meiofauna along the Sudanese coast. Journal of marine biological association UK.

Abstract

Meiofauna was investigated in three contrasting sites along the Sudanese coast with the aim of identifying to what extent meiofauna of natural mangrove stands are different from cleared mangrove and bare sand flat habitats. Differences in meiofauna taxa and nematode genera assemblages among and within sites were evaluated using various quantitative and qualitative measurements for structural and functional attributes. The physical and biogeochemical composition of the sediment significantly varied between habitats in association with significant differences in characteristics of the meiofauna community. As compared to the intact mangrove, the cleared mangrove showed elevated meiofaunal and nematode abundances. The meiofauna taxa Acari and Copepoda, and the nematode genera *Onchium*, *Terschellingia*, *Haliplectus*, *Syringolaimus*, *Spirinia* and *Sphaerolaimus* were absent in the sediment of the cleared mangrove, whereas *Daptonema*, *Theristus* and *Ethmolaimus* occurred with largely highest abundances in this site. The structural and functional diversity estimates were lower in the cleared mangrove compared to the intact mangrove. Differences in community composition between the cleared and intact mangrove are at least partly explained by differences in sediment characteristics. These results highlighted that variation in the characteristics of the meiobenthic community between the intact mangrove and the other habitats, when assessed by various taxonomic and functional attributes, concomitant with changes in sediment properties, can be helpful in understanding the ecological value of this habitat.

4.1. Introduction

Mangrove ecosystems are important transitional environments which act as a buffer between the land and the sea. They are characteristic of tropical regions, subject to the action of tides, and consist of woody tree species adapted to fluctuations in salinity. Although mangroves make up less than 1 percent of tropical forests and less than 0.4 percent of the global total forest, they are a valuable ecosystem that also fulfils many important ecosystem services (Kathiresan, 2012). Mangroves form the foundation of a complex marine food chain by providing sources of food and shelter for a diverse animal community that inhabits both the forest interior and the adjacent coastal waters (Odum & McIvor 1990; Middleton & McKee, 2001). Other ecological benefits of mangroves include creation of critical habitats for fisheries and coastal bird populations by providing nurseries, hatcheries and roosting sites, stabilization of the sediment and protection of shorelines from erosion, and reduction of pollutant concentrations and preservation of water quality (e.g. Nagelkerken *et al.*, 2008; Kathiresan, 2012).

Mangrove ecosystems are susceptible to a variety of disturbances whether they are natural, such as storms, tsunamis and fluctuations in precipitation and temperature, or human induced resulted from climate change, pollution, organic enrichment and clearing (Alongi, 2002; Gilman *et al.*, 2008 and references therein). In general, disturbance can directly disrupt the affected ecosystem, community, or population structure, but its effect can also be indirect by changing the food resources and substrate availability, or the physical and biochemical properties of the sediments (Zajac & Whitlatch, 1982; White & Pickett, 1985; Suding & Hobbs, 2009; Thrush *et al.*, 2009; Hooper *et al.*, 2012). In the case of mangroves, disturbances can directly affect the forest composition and structure by the removal of trees or by changing physico-chemical conditions of the sediment required for tree regeneration (Hauff *et al.*, 2006; Alongi & de Carvalho, 2008; Obade *et al.*, 2009). The extent of damage and the speed of recovery are function of the intensity, frequency, periodicity of forest disturbance, and the type of forest (Jiménez *et al.*, 1985; Sousa, 2001). Apart from their damaging effects on the vegetation, disturbances are also considered an important source for temporal and spatial heterogeneity in the structure and dynamics of the associated fauna, such as the benthos living in mangrove sediments (e.g. Probert, 1984; Sousa, 1984; Hall, 1994). Mangroves along the Sudanese coast face various human practices, such as cutting of trees, camel grazing and removal of mangrove stands for coastal development, in addition to other climatological effects, such as El Niño/Southern Oscillation (ENSO), which cause mangrove degradation and may threaten their existence.

Meiofauna are the numerically dominant metazoans that occupy sediments of a variety of habitats. It has an important ecological role in estuarine sediments as they are closely associated with physical and biochemical characteristics of the sediment, which makes them a good bioindicator of anthropogenic disturbance in aquatic ecosystems (e.g. Schratzberger *et al.*, 2004a,b; Steyaert *et al.*, 2007; Moreno *et al.*, 2008a,b). In any ecosystem, it is difficult to detect the effect of disturbances on community structure because of the temporal and spatial variability in natural communities. In addition, it requires data on the nature of the community before and after disturbance, which are usually unavailable. Although before-after-control-impact (BACI) approaches are highly recommended, they are often not possible due to the lack of pre-impact data. This problem can only be partly overcome by using after-control/impact designs (ACI), which have been widely used in environmental impact studies (Chapman *et al.,* 1995, Roberts 1996, Lardicci *et al.,* 1999, Guidetti *et al.,* 2002). When using ACI, it is generally not possible to attribute causation to any particular event, therefore, this approach can only detect the effect of human interventions by simultaneously examining differences between disturbed and undisturbed control locations, takin into account the limitation that the observed differences may partly be due to other factors (Underwood, 1992; 1993; 1994).

In this study, meiofauna was investigated in three contrasting sites along the Sudanese Red Sea coast. Sites were selected based on their similarity in general topography, with respect to water level, while they represent different stages of mangrove clearance: an intact mangrove, a cleared mangrove, and a bare sand flat (Sabeel *et al.*, 2014). By comparing these sites, we tested the null hypothesis that meiofauna and nematode assemblages, including measures for the ecological quality status (EQS), do not differ between habitats. The aims of the present study were to: (1) describe the spatial variability in meiofauna/nematode community structure and functional traits among the three different habitats; (2) describe links between environmental variables and variation in meiofaunal/nematode community structure, (3) provide an insight into how mangrove clearing potentially affects the structure and function of the benthos.

4.2. Material and Methods

4.2.1. Study Site

The study was conducted at the southern part of the Sudanese coastal line. The area is characterized by a semi-arid climate with a mean annual precipitation of 164 mm, and a mean daily temperature of 29 °C in winter and 42 °C in summer (El Tom, 1991; Musa, 1991). Tides in the area are unusual with a mean spring tide of 0.1 m. The seasonal variation in water levels are up to 0.5-1.3 m higher, results from intense rainfall during winter months (Musa, 1991). Three sites representing three different habitats were sampled for meiofauna (Fig.4.1a), (Sabeel *et al.*, 2014). Site 1 is a bare sand flat, site 2 is an area gradually cleared from mangrove trees, over a period of 3 to 5 years before sampling in 2010, and site 3 is an intact mangrove (*Avicennia marina*) stand. Distance between site 1 & 2 is about 1.2 km, while distance between site 1 & 3 is 8.8 km, and between site 2 & 3 about 26 km. Three stations corresponding to different seasonal water levels were established at each site. These stations were referred to as: (i) high-water (HW), which is just below the water line mark during the high-water level; (ii) mid-water (MW) with remnants of mangrove trunks in the cleared mangrove habitat, and with mangrove stands in the mangrove habitat, or in the middle part of the bare sand flat; and (iii) low-water (LW), which is just above the water line mark at lower water level. The width of each zone from high to low water was about 40 m, 45 m and 15 m, respectively.

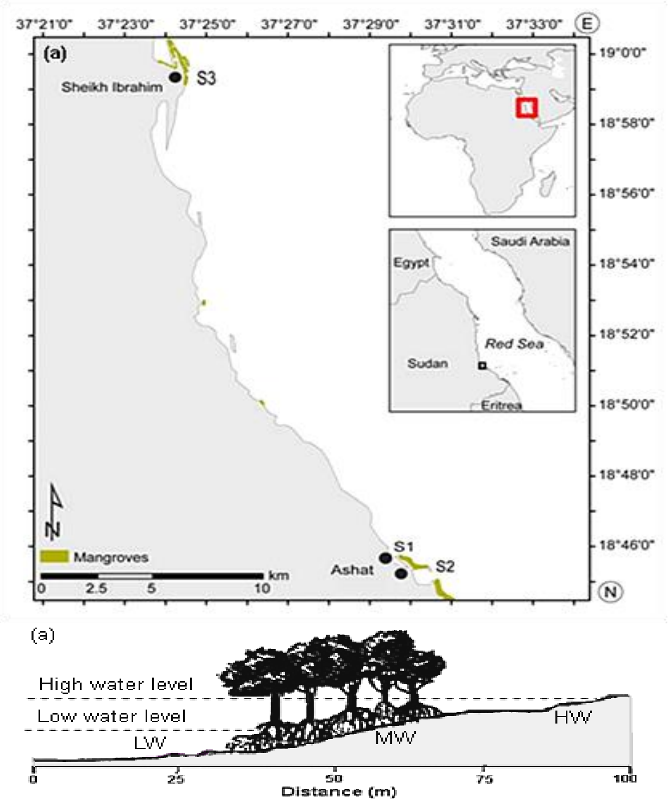


Figure 4.1. (a) Location of the three sampling sites S1: bare sand flat habitat, S2: cleared mangrove habitat, S3: intact mangrove, south of Suakin city, Sudanese Red Sea coast and (b) Profile of transect with sampling stations(H: high-water, M: mid-water, L: low-water) along the seasonal water level gradient. Source: Source: of the map Flanders Marine Institute (VLIZ).

4.2.2. Sampling methods

For meiofauna analysis, a maximum of 3 sediment samples were collected at each station at all sites using cylindrical hand corers with an internal diameter of 5.64 cm (25 cm² surface area) to a sediment depth of 5 cm. The complete sediment columns were immediately fixed in 4% neutral formaldehyde filtered seawater solution. In the laboratory, organisms were extracted from the sediment by centrifugation with Ludox (Heip *et al.*, 1985). All animals passing a 1mm sieve and retained by a 32 µm mesh were stained with Rose Bengal of 1% concentration, counted and sorted into the major taxa under a stereomicroscope. At each water level, 3 additional core samples were taken for granulometry and organic matter analysis. Sediment fractions were analyzed using a Laser particle size analyzer (Malvern Mastersizer 2000 Laser difractometer, Malvern Instrument Ltd., UK), while the determination of the sedimentary total organic matter (TOC), and total nitrogen (TN) was done using a CN analyzer (FLASH 2000 Series Nitrogen and Carbon analyzer).

4.2.3. Nematode community analysis

The abundance of nematodes was determined by counting all nematodes in each sample, using a stereomicroscope with 100x magnification, and converted to abundances per 10 cm². A total of one hundred nematodes per sample (or all if less than 100 present) were picked out randomly, transferred to glycerol through two series of ethanol-glycerol solutions and mounted in glycerin slides (De Griesse, 1969). Nematodes were subsequently identified to genus level under a compound microscope (1000× magnification) using the pictorial key to nematode genera (Warwick *et al.*, 1998), and the NeMys online identification key (Vanaverbeke *et al.*, 2015).

To assess the structural diversity at each sampling station, nematode diversity indices (taxa richness (S), evenness (Pielou index, J') and the Shannon-Wiener diversity index (H')) were calculated using PRIMER v6.0 software (Clarke & Gorley, 2006). All diversity indices were determined at nematode genus level. In addition, all individuals were assigned after Wieser (1953) to one of the four trophic groups: selective deposit feeders (1A), non-selective deposit feeders (1B), epistrate (diatom) feeders (2A), and predators/omnivores (2B). The trophic diversity (ITD) was then calculated as the value of trophic index according to the formula given by Heip *et al.* (1985):

$$ITD = \sum_{i=1}^{n} \theta_i^2$$

Where θ is the relative contribution of the number of individuals of each trophic group to the total number of individuals, and n is the number of trophic groups. ITD ranges from 0.25 (highest trophic diversity; i.e. each of the four trophic guilds account for 25% of the nematode density) to 1.0 (lowest diversity; i.e. one trophic guild accounts for 100% of nematode density).

The life history strategy or the maturity index (MI) was computed as the weighted average of the individual genus c–p values according to the following formula (Bongers, 1990; Bongers *et al.*, 1991; 1995):

$$MI = \sum_{i=1}^{n} v(i).f(i)$$

Where v(i) is the c-p value of the taxon i and f(i) is the frequency of that taxon in a sample. By placing nematode on a *c-p* scale ranging from 2 (originally 1) for “colonisers” to 5 for “persisters”, the MI allows to measure the impact of disturbance and to monitor the structural and functional changes of nematode communities in disturbed habitats. Genera classified as colonisers have short lifecycles, high reproduction rates, high colonisation ability and are tolerant against various types of disturbance (r-strategist). Genera classified as persisters have comparatively long lifecycles, low colonisation ability, few offsprings and are more sensitive to disturbance (K-strategists). The MI varies from 2, under extremely disturbed conditions, to ≥3 under undisturbed conditions.

The ecological quality status (EQS) of the studied sites was assessed using the approach proposed by Moreno *et al.* (2011), in which different nematode-based indices are compared to threshold values as recommended by Long *et al.* (1995) and Marin *et al.* (2008). The values obtained for different taxonomical and functional diversity indices were compared to the proposed thresholds values, which allowed assigning different sites/stations to one of the predefined 5 quality classes (high-good-moderate-poor-bad).

4.2.4. Data analysis

All data analyses were performed using the software package PERMANOVA + add in PRIMER 6 (Anderson, 2005; Anderson *et al.*, 2008). To test for the spatial heterogeneity of sediment and biological data (for meiofauna higher taxa and nematode genera) between sites and between stations, non-parametric univariate and multivariate permutational ANOVA analyses (PERMANOVA; Anderson, 2005; Anderson *et al.*, 2008) were performed. This required a two-way crossed design (factor “site” with 3 levels, fixed: bare sand flat, cleared mangrove, intact mangrove and factor “water level” with 3 levels, fixed: HW, MW, LW). Euclidean distance-based resemblance matrices on untransformed data were used for univariate analysis and Bray-Curtis similarity-based resemblance matrices on square root-transformed data.

To test for the pattern of dispersion of meiofauna and nematode samples, a non-parametric multivariate dispersion test (PERMDISP; Anderson *et al.*, 2008) based on a Bray-Curtis similarity matrix on square root-transformed abundance data was performed. The results revealed no difference in dispersion between habitats in terms of both meiofauna and nematodes in the factors site (F = 2.2375, P = 0.1067 and F = 1.1672, P =0.404), water level (F = 0.70334, P = 0.6015 and F =2.1675, P = 0.1927) or the interaction factor (F = 2.3958, P = 0.839 and F = 2.6654, P = 0.6769). When required, the main-factor test was followed by pair-wise comparisons to investigate significant interaction effects in the full-model test. Multidimensional scaling plot (MDS) derived from Bray-Curtis similarity matrices on square root-transformed data was used to visualize the differences in the structure of meiofauna and nematode communities following the procedure described by Clarke and Warwick (1994). A two-way crossed similarity percentages (SIMPER) analysis (factors: site and water level) was performed to identify the main taxa of meiofauna and nematode genera responsible for the observed multivariate community patterns.

A detailed description of the collection, analyzing procedures and the results of the sediment environmental variables, Including clay, silt, sand, median grain size, sediment sorting, total organic carbon (TOC) and total nitrogen (TN), are presented in Sabeel *et al.* (2014); Chapter3. These data were used as well to test for their relationship with data from meiofauna taxa and nematode genera assemblages, using Distance-Based Linear Modeling (DISTLM) routines based on coupled individual cores, as also described in Sabeel *et al.*(2014). The fitting of the best explanatory environmental variables in the DISTLM models were constructed using step-wise as selection procedure and adjusted R^2 as a selection criterion.

4.3. Results

4.3.1. Meiofaunal community composition

Average total meiofauna densities are shown in Table 4.1. Results revealed a significant interaction effect of site and water level on meiofauna community (PERMANOVA, $P < 0.001$;Table 4.2). Total abundances of meiofauna were significantly higher in HW and MW at the cleared than at the intact mangrove, but abundance was still higher at the intact mangrove compared to the bare sand flat. At LW abundances were significantly higher at the intact mangrove compared to the other habitats ($P < 0.05$).

Table 4.1. Mean±SE values for meiofaunal density (ind./10 cm²) and diversity indices (S: taxa richness, J': taxa evenness, H': Shannon- Wiener diversity) measured in different water levels (HW: high-water, MW: mid-water, LW: low-water) at each site.

Site	**Water level**	**Total density**	**S**	**J'**	**H'**
Bare sand flat	HW	18.0±9.5	3.0±0.0	0.26±0.02	0.29±0.02
	MW	86.4±15.5	4.0±0.0	0.25±0.00	0.34±0.00
	LW	69.0±32.5	6.0±1.0	0.54±0.02	0.95±0.06
Cleared mangrove	HW	372.0±71.1	4.0±0.0	0.08±0.01	0.12±0.02
	MW	281.1±41.8	6.0±0.6	0.40±0.03	0.70±0.04
	LW	309.2±54.4	6.7±0.3	0.41±0.05	0.76±0.07
Intact mangrove	HW	268.4±32.9	10.0±0.0	0.21±0.02	0.49±0.05
	MW	173.8±25.4	10.7±0.5	0.51±0.03	1.20±0.06
	LW	420.4±55.8	12.0±0.0	0.55±0.02	1.37±0.05

A total of 15 major taxa were found in the three sites, with 15, 11 and 6 taxa counted in the intact mangrove, the cleared mangrove, and bare sand flat sites, respectively. Nematodes were the dominant taxon at all sampling sites (40–98%) followed by Copepoda Including nauplii (2– 33%), Polychaeta and Turbellaria (1-14%) (Fig. 4.2). The contribution of both Acarina and Ostracoda did not exceed 6% each, whereas the remaining taxa including Oligochaeta, Holothuroidea, Gastrotricha, Gastropoda, Gnathostomulida, Amphipoda and Isopoda represented collectively about 2-13% of the total meiofauna. Results indicated a significant interaction effect on meiofauna composition and taxon richness (PERMANOVA, $P < 0.01$ and 0.05; respectively). Meiofauna composition, based on abundance data, was significantly different (Fig. 4.3) and taxon richness was significantly higher at all water levels of the intact mangrove compared to the cleared mangrove and the bare sand flat (PERMANOVA, $P < 0.05$; Table 4.2).

Table 4.2. PERMANOVA results for total meiofauna abundances, taxa composition, taxa richness (S), taxa evenness (J'), and taxa diversity (H') measured in different water level station (WL) at each site (S). HW: high-water, MW: mid-water, LW: low-water and BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove. Significant values of the P-values obtained by permutation are indicated in bold italic.

Meiofaunal characteristic	Factor	Main test			Pair-Wise comparison
		df	Pseudo-F	P	
Total abundance	S	2	101.81	***0.0003***	BSF<IM=CM
	WL	2	10.42	***0.0027***	M<H, L
	S × WL	4	10.39	***0.0007***	HW: CM>IM>BSF
					MW: CM>IM>BSF
					LW: IM>CM>BSF
Taxa composition	S	2	101.63	***0.0001***	BSF≠ IM≠ CM
	WL	2	55.93	***0.0001***	HW≠ MW≠ LW
	S × WL	4	42.65	***0.0385***	HW: IM≠CM≠BSF
					MW: CM≠IM≠BSF
					LW: IM≠CM≠BSF
Taxa richness (S)	S	2	89.51	***0.0001***	IM> CM> BSF
	WL	2	11.23	***0.0017***	HW < MW< LW
	S × WL	3	75.83	***0.004***	HW: IM>CM>BSF
					MW: IM> CM
					LW: IM> CM=BSF
Taxa evenness (J')	S		6.2028	***0.019***	IM> BSF > CM
	WL		17.748	***0.0003***	LW> HW=MW
	S × WL		1.6953	0.2119	NS
Taxa diversity (H')	S	2	23.094	***0.0002***	IM> CM=BSF
	WL	2	10.316	***0.0009***	LW> HW=MW
	S × WL	3	1.8058	0.1918	NS

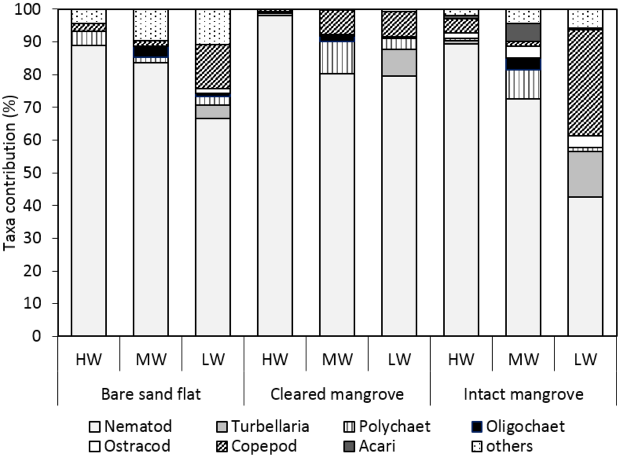


Figure 4.2. Percentage contribution of taxa to the total meiofauna abundance found at each water level (HW: high-water, MW: mid-water, LW: low-water) at the three sites

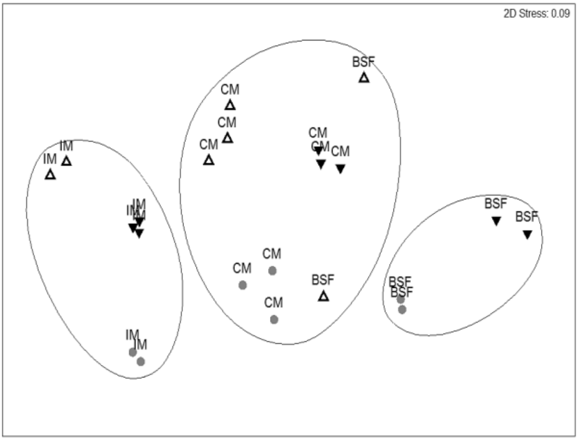


Figure 4.3. Non-metric multidimensional scaling (nMDS) ordination of square root transformed meiofauna abundance data. Symbols indicate different water level (filled triangle: high-water, filled circle: mid-water, open triangle: Low-water) at different sites; BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove. Lines represent similarity at 60%.

The SIMPER analysis identified the taxa that are responsible for the differences in community structure between and within different sites (Appendix 8a). Among the taxa causing dissimilarities, Acarina, Gastrotricha and Gnathostomulida were confined to the intact mangrove, while Ostracoda and Copepoda were more abundant in the intact mangrove than in the other two sites. Gastropoda was found in low abundances in the intact and cleared mangroves, while Turbellaria and Polychaeta were relatively more abundant in these sites than in the bare sand flat. Values of taxon evenness (J'), and Shannon-Wiener diversity (H') were in general low and increased from HW to LW levels (Table 4.1). Results showed that values for both indices were significantly different between sites and water levels (Table 4.2). The values of J' and H' were significantly higher in the intact mangrove than in the cleared mangrove (PERMANOVA, $P \leq 0.05$). Comparing the stations, only LW showed significantly higher values of these indices compared to HW and MW ($P \leq 0.01$).

4.3.2. Nematode Community Analysis

4.3.2.1. Abundance and community composition

Significant differences in total nematode abundances were detected for the interaction between site and water level (PERMANOVA, $P < 0.05$, Table 4.3). This can be explained by significantly higher nematode abundances found at HW and MW stations of the cleared mangrove compared to the intact mangrove and the bare sand flat, while abundances at the LW were only different between the cleared mangrove and the bare sand flat (PERMANOVA, $P < 0.05$, Table 4.3, Fig. 4.4).

A total of 35 nematode genera belonging to 20 families were identified (Table 4.4). The most abundant families were Xyalidae, Ethmolaimidae, Linhomoeidae and Microlaimidae. Results from main and pair-wise tests on community composition revealed a significant effect for the interaction factor between sites and water levels (PERMANOVA, $P = 0.0001$ and $P < 0.05$, respectively; Table 4.3). The MDS plot, based on abundance data of nematode genera, visually reflected the spatial distribution of nematode assemblages in sites and along the water level gradient (Fig. 4.5). Nematode communities at each site were separated and within each site clear shifts in community composition for different water levels were observed.

Table 4.3. PERMANOVA results for total nematode abundances, assemblage composition, genera richness (S) genera evenness (J'), genera diversity (H'), maturity index (MI), and trophic diversity (ITD) measured in different water levels (HW: high-water, MW: mid-water, LW: Low-water) at the three sites (BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove). The P-values obtained by permutation and significant values are indicated in bold italic.

Nematode characteristic	Factor	Main test			Pairwise comparison
		Df	Pseudo-F	P	
Total abundances	S	2	48.43	***0.0001***	CM>IM>BSF
	L	2	4.23	***0.0399***	HW> MW, LW
	S × WL	4	3.41	***0.0425***	HW: CM>IM>BSF
					MW: CM>IM>BSF
					LW: CM>IM
Genera composition	S	2	28.31	***0.0001***	BSF≠IM≠CM
	WL	2	9.95	***0.0001***	HW≠MW≠LW
	S × WL	4	7.69	***0.0001***	HW: IM≠CM≠BSF
					MW: IM≠CM≠BSF
					LW: IM≠CM≠BSF
Genera richness (S)	S	2	5.60	***0.0005***	IM> CM, BSF
	WL	2	2.00	***0.0022***	HW < MW, LW
	S × WL	3	2.90	***0.0002***	HW: IM>CM, BSF
					MW: IM>CM, BSF
					LW: NS
Genera evenness (J’)	S	2	7.90	***0.0022***	IM> CM, BSF
	WL	2	1.30	***0.0174***	LW>HW, MW
	S × WL	3	2.70	***0.0098***	HW: IM>CM, BSF
					MW: IM> CM
					LW: NS
Genera diversity (H')	S	2	17.11	***0.0001***	IM>CM, BSF
	WL	2	3.12	***0.0001***	HW< MW, LW
	S × WL	3	5.2	***0.0003***	HW: IM>CM, BSF
					MW: IM>CM, BSF
					LW: NS
Maturity index (MI)	S	2	15,59	***0.0004***	CM<RM, BSF
	WL	2	6,35	***0.0102***	MW< HW, LW
	S × WL	4	5,01	***0.0131***	HW: NS
					MW: IM>CM
					LW: IM, BSF>CM
Index of tropic diversity (ITD)	S	2	13.80	***0.0034***	IM<CM<BSF
	WL	2	0.65	0.6887	NS
	S × WL	3	1.61	0.0726	NS

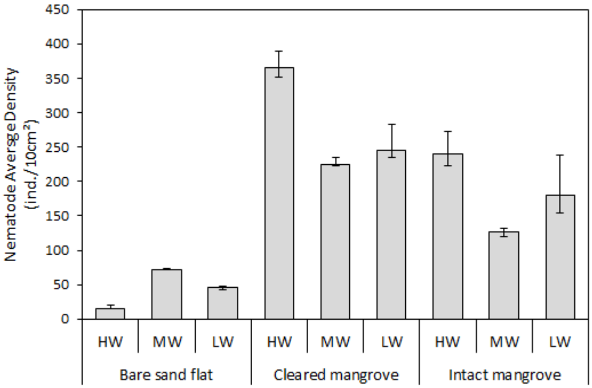


Figure 4.4. Mean nematode abundance assessed in each water level (HW: high-water, MW: mid-water, LW: Low-water) at different sites. Error bars denote the SE of mean abundance values per water level station.

Dissimilarity in genus composition, based on SIMPER analysis, was highest between the intact mangroves and both the cleared mangrove and the bare sand flat (70 and 86%), while dissimilarity between water levels was highest between the HW and both the MW and LW stations (63 % and 67%) (Appendix 8b). The genus *Chromadorina* was only found in the bare sand flat, while the genera *Onchium*, *Spirinia*, *Haliplectus*, *Synonchium*, and *Sphaerolaimus* were confined to the intact mangrove. The genera *Aegialoalaimus*, *Axonolaimus*, *Procamacolaimus,* *Molgolaimus*, *Draconema*, *Epsilonema*, *Dolicholaimus*, *Leptolaimus*, *Prooncholaimus*, *Oxystomina*¸ and *Halalaimus* occurred at very low abundances exclusively in the cleared mangrove. The genera *Daptonema* and *Theristus* were found nearly throughout all water levels at the three sites.

Table 4.4. Family, genus, abundance (ind./10 cm²), c-p values and feeding group for all nematode genera collected at the three sampling sites. Generic frequency is expressed as percentage of occurrence. Family and genus abundances are expressed as percentage of total numbers.

Family	Genus	c-p value	Feeding grup	Bare sand flat			Cleared mangrove			Intact mangrove			Frequency (%)	Genus (%)
				HW	MW	LW	HW	MW	LW	HW	MW	LW		
Aegialoalaimidae	*Aegialoalaimus*	4	1A	0	0	0	0	0	4	0	0	0	5	0.27
Axonolaimidae	*Axonolaimus*	2	1B	0	0	0	2	0	0	0	0	0	5	0.11
Camacolaimidae	*Onchium*	3	2A	0	0	0	0	0	0	0	0	6	5	0.27
	Procamacolaimus	3	2A	0	0	0	1	1	1	0	0	0	14	0.27
Chromadoridae	*Chromadora*	3	2A	0	0	1	0	3	0	0	0	0	14	0.29
	Chromodorina	3	2A	0	0	2	0	0	0	0	0	0	9	0.09
	Spilophorella	2	2A	0	0	3	3	7	19	0	0	0	41	2.21
Cyatholaimidae	*Paracyatholaimus*	2	2A	0	3	0	0	18	0	0	15	0	27	2.14
Desmodoridae	*Desmodora*	2	2A	0	0	0	0	23	30	0	5	11	36	4.53
	Molgolaimus	3	2A	0	0	0	0	0	3	0	0	0	5	0.22
	Metachromadora	2	2A	0	0	0	9	0	0	13	0	0	23	1.57
Draconematidae	*Draconema*	3	1A	0	0	0	0	1	0	0	0	0	68	0.08
Ethmolaimidae	*Ethmolaimus*	3	2A	0	3	4	192	15	0	33	5	0	5	17.72
Epsilonematidae	*Epsilonema*	3	1A	0	0	0	0	0	4	0	0	0	32	0.29
Haliplectidae	*Haliplectus*	2	1A	0	0	0	0	0	0	52	7	26	5	5.24
Ironidae	*Dolicholaimus*	4	2B	0	0	0	0	0	3	0	0	0	50	0.22
	Syringolaimus	2	2B	6	10	13	0	0	0	15	12	0	14	2.99
Leptolaimidae	*Leptolaimus*	3	1A	0	0	0	7	0	7	0	0	0	45	0.99
Linhomoeidae	*Terschellingia*	2	1A	0	2	1	0	0	0	18	15	28	27	3.5
	Metalinhomoeus	3	1B	0	4	0	0	8	12	0	0	0	9	1.65
	Spirinia	4	2A	0	0	0	0	0	0	0	0	60	5	2.84
Microlaimidae	*Microlaimus*	2	2A	0	0	0	0	16	33	28	2	0	45	5.6
	Bolbolaimus	3	2A	0	0	0	0	0	11	18	2	0	27	2.16
Monhysteridae	*Monhystrella*	2	1B	0	44	2	6	1	11	19	4	0	59	5.07
Oncholaimidae	*Viscosia*	3	2B	0	0	2	0	0	11	8	10	9	55	2.35
	Prooncholaimus	2	2B	0	0	0	0	8	0	0	0	0	9	0.6
	Oncholaimus	4	2B	0	0	5	10	0	0	0	8	6	32	1.66
Oxystominidae	*Oxystomina*	4	1A	0	0	0	0	0	3	0	0	0	5	0.22
	Halalaimus	4	1A	0	0	0	0	0	4	0	0	0	5	0.3
Selachinematidae	*Synonchium*	3	2B	0	0	0	0	0	0	1	0	0	5	0.08
Sphaerolaimidae	*Sphaerolaimus*	3	2B	0	0	0	0	0	0	1	5	0	14	0.26
Xyalidae	*Daptonema*	2	1B	8	3	10	111	100	77	49	21	26	100	27.37
	Theristus	2	1B	1	2	4	22	24	12	21	2	0	77	6.04
	Stylotheristus	2	1B	0	0	0	1	0	0	0	0	9	14	0.52
	Paramonhystera	2	1B	0	0	0	0	0	1	3	0	0	9	0.28

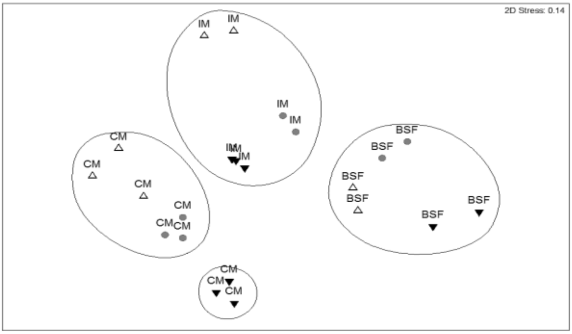


Figure 4.5. Non-metric multidimensional scaling (MDS) ordination plot of square root transformed abundance data of nematode genera sampled at each water level station. Symbols indicate different water levels (filled triangle: high-water, filled circle: mid-water, open triangle: Low-water) at different sites; BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove. Lines represent similarity at 60%.

Figure 4.6 illustrates the feeding group distribution in all water levels at the sampled sites. Proportion of selective deposit feeders (1A), epistrate feeders (2A) and non-selective deposit feeders (1B) showed a significant interaction effect between sites and water levels, while the proportion of predators/omnivores (2B) was only significantly different between sites (PERMANOVA, $P < 0.05$, Table 4.3). The intact mangrove exhibited significantly higher proportions of 1A and lower proportions of 1B at all water levels as compared to the cleared mangrove, whereas the HW in the cleared mangrove showed significantly higher proportions of 2A than in the intact mangrove ($P < 0.05$). The proportion of 2B was significantly lower in the bare sand flat as compared to the intact and cleared mangroves.

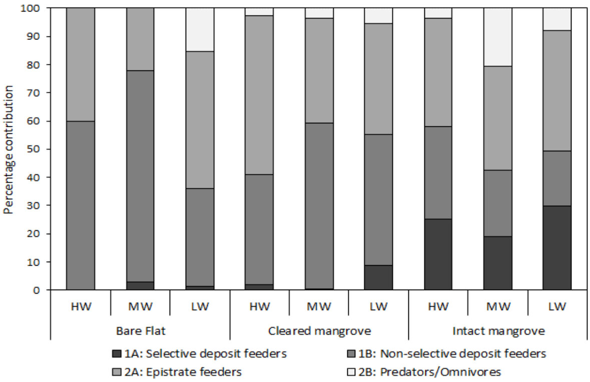


Figure 4.6. Relative abundance (%) of nematode feeding groups in different water levels; HW: high-water, MW: mid-water, LW: low-water, at each site.

4.3.2.2. Taxonomic and functional diversity

Univariate tests for differences in diversity indices detected a significant interaction effect based on nematode genera on all diversity indices (PERMANOVA, $P \leq 0.05$; Table 4.3). As compared to the intact mangrove, the HW and MW station at the cleared mangroves exhibit significantly lower genus richness, diversity H' and the least even distribution of abundances among nematode genera, as shown by Pielou's evenness ($P < 0.05$; and Table 4.5). No significant differences in these indices were detected at the LW of all sites. Values for the maturity Index (MI) were significantly lower in the MW and LW at the cleared mangrove compared to the other sites indicating the dominance of colonizers at this site. The pair-wise comparison revealed significantly lower values of ITD in all water levels of the intact mangrove, indicating the higher trophic diversity at the intact mangrove as compared to the cleared mangrove ($P < 0.05$; Table 4.3 and 4.5).

Table 4.5. Mean values (±SE) for nematode diversity indices (averaged over replicates) calculated for different water-levels (HW: high-water, MW: mid-water, LW: low-water) in all sites.

Site	Water level	Genus richness (S)	Genera evenness (J')	Genera diversity (H')	Maturity Index (MI)	Index of Trophic Diversity (ITD)
Bare Sand	HW	3.00±0.00	0.76 ± 0.04	0.84±0.05	2.88±0.35	0.53±0.03
Flat	MW	8.00±0.00	0.64 ± 0.08	1.33±0.16	2.34±0.13	0.61±0.12
	LW	10.50±0.50	0.87 ± 0.00	2.06±0.05	2.76±0.02	0.54±0.06
Cleared	HW	7.00±0.71	0.60 ± 0.09	1.18±0.22	2.54±0.14	0.53±0.08
Mangrove	MW	10.00±0.71	0.81 ±0.04	1.77±0.08	2.1±0.03	0.42±0.03
	LW	9.00±1.41	0.86 ±0.03	1.97±0.08	2.23±0.03	0.38±0.02
Intact	HW	12.00±0.00	0.91 ± 0.01	2.25±0.03	2.58±0.06	0.33±0.01
Mangrove	MW	12.00±0.50	0.93 ±0.01	2.36±0.08	2.6±0.04	0.25±0.03
	LW	8.00±1.00	0.89 ±0.0	1.83±0.11	2.71±0.01	0.31±0.01

4.3.3. Relation between meiofauna and nematode community characteristics, and environmental variables

The marginal DISTLM test showed that meiofaunal composition, richness, and diversity were explained by all environmental variables, except clay and sorting, in addition to CN in case of richness and median grain size in case of diversity (H'). Meiofauna total abundances was explained only by median grain size and sorting, while taxa evenness was explained only by TOC and C/N. ($P < 0.05$; Appendix 9). In terms of nematodes, clay, silt, sand and TN contributed significantly in explaining variability in total abundances, whereas organic matter (TOC, TN, C/N) and sorting could explain the variability in composition. The variability in nematode functional diversity could be partly explained by sediment sorting, while none of the environmental variables could explain the variability in genera richness, evenness, diversity H' or ITD. ($P < 0.05$; Appendix 9).

The sequential DISTLM test showed that meiofauna composition and evenness was explained by TOC, C/N, silt in addition to median grain size in case of composition, and TN in case of evenness (appendix 9). TOC and C/N explained 74.9 % of the variation in diversity, while only TN and median grain size explained the variation in richness and abundance (51.3% and 28.0%, $P < 0.05$). silt and TOC explained the variability in nematode total abundance (25.7% and 12.7%, $P \leq 0.05$), while sorting explained the variability in MI (36.9 %, $P< 0.01$). Variability in nematode genera richness, evenness, Shannon Wiener and trophic diversity could be partly explained by C/N (14.9%), TOC (13.9%), sorting (13.3%) and silt (20%), respectively. Sediment sorting alone explained 36.9% of the total variation in MI ($P < 0.01$).

4.3.4. Ecological quality status (EQS)

The results of EQS using nematode-based indices (Tables 4.6 and 4.7) suggested that the intact mangrove in general had a high/good EQS with the lowest variability between stations, while the cleared mangrove and the bare sand flat displayed a moderate/poor EQS, with the cleared mangroves showing a very high within habitat variability (Table 4.7).

Table 4.6. Thresholds for the evaluation of the ecological quality status after Moreno *et al.* (2011).

Status	Namatode Genera richness (S)	Maturity index (MI)	c-p	Diversity index (H’)	Index of trophic diversity (ITD)	Sensitive/Tolerant genera (>10%)
High	>12	>2.8	c-p 2 ≤ 50% and c-p 4 > 10%	>4.5	0.25	*Desmoscolecidae, Microlaimus, Richtersia, Oncholaimus, Pomponema, Epacanthion (sensitive group to chemicals and organic enrichment)*
Good		2.8 ≤ MI < 2.6	c-p 2 ≥ 50% and c-p 4 > 10%	3.5 < H’ < 4.5	0.25 < ITD ≤ 0.4	*Halalaimus, Setosabatieria, Ptycholaimellus (sensitive genera)*
Moderate	4–12	2.6 ≤ MI < 2.4	c-p 2 ≥ 50% and 3 < c-p 4 < 10%	2.5 < H’ < 3.5	0.4 < ITD ≤ 0.6	*Anticoma, Desmodora, Spirinia, Marylynia, Prochromadorella*
Poor	<4	2.4 ≤ MI < 2.2	c-p 2 > 60% and c-p 4 < 3%	1 < H’ ≤ 2.5	0.6 < ITD ≤ 0.8	*Daptonema/Theristus, Paralongicyatholaimus, Parodontophora, Odontophora (tolerant to reduced and oxygen-depleted sediments).*
Bad		≤2.2	c-p 2 > 80%	0 < H’ ≤ 1	1	*Paracomesoma, Terschellingia, Sabatieria (Tolerant group to high organic matter)*

Table 4.7. Results of EQS evaluated in different stations (HW: high-water, MW: mid-water, LW: low-water) at different sites (BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove).

		Genera richness	Average MI	c-p	H'	ITD	Sensitive/Tollerant genera (>10%)
Bare Sand Flat	Overall Site	7.2	2.7	🟥	1.4	0.6	*Terschellingia, Oncholaimus, Daptonema, Theristus*
	HW	3.0	2.9	🟥	0.8	0.5	*Daptonema, Theristus*
	MW	8.0	2.3	🟥	1.3	0.6	*Terschellingia, Daptonema, Theristus*
	LW	10.5	2.8	🟩	2.1	0.5	*Oncholaimus, Daptonema, Theristus*
Cleared Mangrove	Overall Site	8.3	2.3	🟧	1.6	0.4	*Desmodora, Microlaimus, Oncholaimus, Halalaimus, Daptonema, Theristus*
	HW	6.5	2.5	🟧	1.2	0.5	*Oncholaimus, Daptonema, Theristus*
	MW	9.5	2.1	🟥	1.8	0.4	*Desmodora, Microlaimus, Daptonema, Theristus*
	LW	9.0	2.2	🟨	2.0	0.4	*Desmodora, Microlaimus, Halalaimus, Daptonema, Theristus*
Intact Mangrove	Overall Site	11.3	2.6	🟩	2.1	0.3	*Desmodora, Spirina, Terschellingia, Microlaimus, Oncholaimus, Daptonema, Theristus*
	HW	12.0	2.6	🟩	2.3	0.3	*Terschellingia, Microlaimus, Daptonema, Theristus*
	MW	12.0	2.6	🟩	2.4	0.3	*Desmodora, Terschellingia, Microlaimus, Oncholaimus, Daptonema, Theristus*
	LW	10.0	2.7	🟨	1.8	0.3	*Desmodora, Spirina, Terschellingia, Oncholaimus, Daptonema, Theristus*

High= dark green, good= light green, moderate = yellow; poor = orange; bad = red (A color for the sites was assigned if two of the three stations have fallen into this category)

4.4. **Discussion**

Mangroves usually exhibit a degree of stability, being resilient to certain natural perturbations and human disturbances, while the inhabiting fauna may be tolerant to certain degrees of disturbances (Alongi, 2009). However, mangrove clearance causes major changes in the physical and biochemical habitat of the associated endofauna, with possible major consequences for the structural and functional composition of the benthos. In this study, we report on the potential consequences of mangrove clearance in the Sudanese Red Sea coast by comparing three different habitats. Within each habitat, three different water levels were also investigated to estimate the variability within sites. Our study was limited by the possible regional and local differences due to varying distances between sites and the lack of replication of habitat types at different locations, which may limit the certainty of the effect of clearing and may not allow these results to be generalized. However, the comparison of these sites, since they were chosen for their similarity in topography, which is expected to affect other environmental factors such as sediment grain size and nutrients available for benthos, provided an insight into the potential changes in habitats and associated fauna by linking differences in the present benthic communities to well established environmental drivers (e.g. Alfaro, 2010). The comparison of sites also allows predicting assemblage changes when a mangrove is cleared by natural processes or human activities and if a cleared mangrove is further converted over time to a less complex habitat such as a bare sand flat (Gladsone & Schreider, 2003; Bosire *et al.*, 2004; Mutua *et al.*, 2014; Sabeel *et al.*, 2014).

Although mangrove forests have great influence on coastal ecosystems, only few studies have reported on the consequences of their clearance on abiotic and biotic processes including the increase in the sedimentation rate at the seaward side as a result of the increased amount of fine-grained (<63 µm) sediment load, but also the shift of the sediment from a muddy to a sandier nature, the decrease in organic content, the increase in light intensity and temperature, and the increase in algal biomass and generic richness (Granek & Ruttenberg, 2008; Alfaro, 2010; Ellegaard *et al.*, 2014). Our results indicated that the measured environmental variables significantly varied between sites suggesting that sediment characteristics at the cleared mangrove were modified as a result of mangrove clearance (Sabeel *et al.*, 2014). Evidence for this modification was most pronounced at the mid-water station, which showed an intermediate situation between the bare sand flat and the intact mangrove. Mangroves are generally known for being depositional sites for sediment and associated carbon and nutrients (Alongi & de Carvalho, 2008; Yang *et al.*, 2014). Above-ground root systems and stems enhance sediment deposition by increasing friction and reducing tidal current velocities, which results in settling of fine sediments (Yang *et al.*, 2014). Removing mangrove forests will, thus, alter this process and fine sediments will be removed. The presence or absence of mangroves likely explains the differences in environmental variables, which in turn may affect meiofaunal and nematode assemblages by changing their structure and community composition. Results from DISTLM analysis showed that the investigated sediment variables, especially silt and median grain, contributed with varying degree, to the total variation in meiofauna and nematode community characteristics and composition. Sediment grain size is a primary factor for determining the abundance and species composition of meiofauna in general and nematodes in particular (Heip *et al.*, 1985; Steyaert *et al.*, 1999; Vanaverbeke *et al.*, 2002; Raes *et al.*, 2007; Semprucci *et al.*, 2010, Fonseca *et al.*, 2014). Sediment grain size affects the burrowing and the interstitial behavior of organisms directly, but also indirectly by affecting the physico-chemical properties of the sediment (Vanaverbeke *et al.*, 2011).

Meiofaunal abundances at the intact mangrove were lower than those recently recorded from mangroves in the north of the Red Sea (Pusceddu *et al.*, 2014) and from other regions worldwide (Sahoo *et al.*, 2013, and the references therein). However, abundances reported from the cleared mangrove site are comparable to those found in an earlier study from similar habitats, including partially cleared and cleared-cut mangroves, at the Sudanese Red Sea coast (Khalil, 2001). The higher abundances in the HW and MW of the cleared mangrove compared to the intact mangrove are not unexpected. Previous studies have shown that sediments of disturbed mangrove forests, e.g. by trampling or removal of mangrove trees, have higher benthic abundances relative to undisturbed forests possibly due to increased ability of species to exploit resources such as space and food, resulting from loss of the root mat, or due to change in the properties of the sediment(e.g. Dye**,** 2006; Alfaro, 2010; Sabeel *et al.*, 2014). This observation suggests that other environmental factors are strongly associated with the increase in abundances among which: (i) resource availability and quality (De Troch *et al.*, 2006), (ii) local biochemical conditions such as oxygen availability (Vanreusel *et al.*, 1995a; Steyaert *et al.*, 2007) or tannin concentrations (Alongi, 1987), (iii) organic enrichment associated with a higher silt/clay composition (Ansari *et al.*, 2014), and (iv) species interactions such as facilitation or the lack of competition or predation by species from the macrobenthos (Van Colen *et al.*, 2009; Braeckman *et al.*, 2011; Maria *et al.*, 2011; Ingels *et al.*, 2014). Our study suggests that the lack of interference or competition with the macrofauna and the availability of resources may explain the increased abundances in the cleared mangroves. Schrijvers *et al.* (1995b) showed by means of exclusion experiments that, when macrofaunal epifauna was excluded, the abundance of the most common predatory and microalgae-feeding nematodes tended to increase in the surface layers, together with the amount of detritus and pigment concentrations. A study on the macrofauna from the same sites and stations (Sabeel *et al.*, 2014) showed significantly lower abundances of macrofauna, especially decapod crabs and gastropods, in the cleared site compared to the mangrove, supporting our suggestion that the lower interaction with the macrofauna is an important factor in structuring the nematode community especially in the HW and MW stations of the cleared mangrove, where higher meiofauna densities were found. The decrease in mangrove-derived tannin, resulting from the removal of mangrove trees, may also be important in the increase of meiofauna in the high and mid water stations at the cleared mangrove by reducing the negative effect of tannin on meiofauna (Alongi, 1987, Sahoo *et al.*, 2013). However, the higher meiofauna abundances at the cleared mangrove can also be explained by the increased availability of high quality food resources, which is possibly resulting from higher microalgal and cyanobacterial biomass (Moens & Vincx, 1997) primarily due to greater light penetration compared to the intact mangrove (Granek & Ruttenberg, 2008). The low abundances at the bare sand flat is associated with coarser sediments and low TOC values pointing to low food input. An interesting finding is that Turbellaria was numerical dominant in the intact and cleared mangrove in agreement with Alongi (1989) who found that they made up 60% of all meiofauna in mangrove sediment, while in exposed sand and mud the species number decrease, but their abundance remain relatively high. Their relatively high abundance may be related to the rich food supply such as diatoms and bacteria.

The difference in meiofauna composition between sites is attributed to the lower abundance or absence of some meiofaunal groups such as Acarina, Ostracoda, and Gastropoda in the cleared mangrove. Similarly nematode composition in the cleared mangrove showed three major differences in nematode diversity and community structure compared to the intact mangrove. Firstly, several genera present in the intact mangrove of this study such as *Onchium*, *Terschellingia, Haliplectus*, *Syringolaimus*, *Spirinia* and *Sphaerolaimus*, some known as characteristic for mangrove sediments (e.g., Gee & Somerfield, 1997; Khalil, 2001; Zhou, 2001**;** Torres Pratts & Schizas, 2007; Pinto *et al.*, 2013), were absent from the cleared mangrove. Secondly, some genera which occurred in all sites, such as *Ethmolaimus*, *Daptonema*, and *Theristus*, showed elevated abundances in the cleared mangrove. Finally, several genera from the cleared mangrove site, although present in low abundances, were not found in the other two sites, e.g. *Aegialoalaimus*, *Axonolaimus*, *Procamacolaimus*, *Molgolaimus*, *Draconema*, *Epsilonema*, *Dolicholaimus*, *Leptolaimus*, *Prooncholaimus*, *Oxystomina,* and *Halalaimus*. Moreover, meiofauna taxa and nematode genera were more diverse in the intact mangrove compared to the cleared mangrove. In general, our results did not confirm the expected positive relationship between sediment grain size and diversity (Heip *et al.*, 1985; Giere, 1993), since the communities from the muddy mangrove sediments were more diverse than those from the other sites with coarser grain sediment. There is also high variability in diversity among stations with a similar grain size (e.g., the HW in the cleared and intact mangrove) supporting previous observations that other factors which are co-varying with the sediment granulometry such as food and oxygen availability, and organic enrichment are also important in structuring meiofauna and nematode communities (Fonseca *et al.*, 2014).

Differences in nematode community composition also resulted in shifts in functional attributes of the nematodes, as reflected in the feeding type distribution. The cleared mangrove showed a remarkably lower abundance of the selective deposit feeders at all three stations, and a higher abundance of the epistrate feeders at the HW station when compared to the intact mangrove. The reduced proportion of the selective deposit feeders (1A) in the cleared mangrove is associated with the absence of *Terschellingia* and *Haliplectus*. The abundance of *Terschellingia* is known to be considerably affected by physical and biological disturbance (Austen *et al.*, 1998; Schratzberger & Warwick, 1998; Schratzberger *et al.*, 2009), and mangrove clearance (Khalil, 2001). Moreover, *Terschellingia* and *Haliplectus* were found to be abundant in mangroves worldwide. *Haliplectus* is more abundant in mangrove leaf litter (Alongi, 1987; Torres Pratts & Schizas, 2007), whereas *Terschellingia* is typical for anoxic, organically enriched soft sediments (Schratzberger *et al.*, 2000; Steyaert, 2007). Therefore, a decrease of selective deposit feeders and the increase in non-selective deposit feeders might be partly attributed to the lower organic matter concentrations (detritus and the increase in diatoms and algal mats (Moens & Vincx, 1997) when mangroves were cleared.

The index of trophic diversity was significantly higher at the cleared mangrove and the bare sand flat suggesting that the feeding type diversity and, thus, the trophic complexity, in these two habitats was lower as compared to the intact mangrove. The higher trophic diversity in the intact mangrove was mainly due to increased proportions of the selective deposit feeders (1A) such as *Terschellingia,* which are classified as bacterial feeders. They are highly abundant in silt and clay sediments due to their physiological characteristics and ability to tolerate the excessive organic content and the adverse conditions of mangrove sedimentary environment, and the plasticity of their diet, which allows them to consume different food items of various sizes. On the other hand, the low trophic diversity in the cleared mangrove was primarily due to increased dominance of the opportunistic genera such as non-selective deposit feeders (1B), which are adapted to rapidly recolonize disturbed areas and establish a large population within a relatively short time. The lower trophic diversity at the cleared mangrove is also associated with the high density of feeding type 2A, which may be the result of the observed overgrowth of diatoms and cyanobacteria especially at the high-water station (personal observation). Environmental variables, such as water depth, granulometry, distance from the source of pollution (Maurer *et al.*, 1999), and factors related with physical disturbance of the seabed (Schratzberger *et al.*, 2009) have been reported to significantly influence the ITD. Similar effects might be expected when mangroves are cleared which results in a change in sediment granulometry, from finer to coarser as observed in the mid-water station, low bacterial biomass and altered chemical conditions. The life history characteristics as presented by the maturity index (MI) showed an opposite pattern to ITD, especially in the cleared mangrove, confirming the dominance of trophically similar genera with low c-p value (mainly colonizers). About 50% of genera present in the cleared mangrove were indeed classified as ‘’colonizers’’ or “opportunistic” (c-p = 2). Generally, under disturbed conditions, the abundance of opportunistic species is expected to increase (Ferris *et al.*, 2001). Their abundance is also expected to respond positively after the increase of green algal blooms at the soil surface. Similarly, the increased supply of resources to the food web through direct herbivory is indicated by the increase in the more r-selected plant-feeding nematodes (Ferris & Bongers, 2006). A close look in the relationship between the feeding type and the MI, showed a significant increase in the dominance of the non-selective deposit feeders (1B, about 1-3 fold) and low MI values in the cleared mangrove compared to the intact mangrove. This may in general imply that the disturbances that cause a low MI will result in the high abundance of the 1B feeding type. On the contrary, a stable environment that shows higher MI may show a higher trophic diversity.

The EQS approach based on different nematode-based indices was used to evaluate the ecological quality of the studied habitats following Moreno *et al.* (2011). The indices S, MI, c-p values and ITD resulted in different EQS categories for the different sites. In agreement with Alves *et al*. (2013) and Moreno *et al.* (2011), the percentage composition of c-p values highlighted the different environmental conditions and, thus, allowed for better classification of the habitats, than MI. In contrast to what was observed by the aforementioned authors, ITD allowed for a clear separation of the intact mangrove (classified as good EQS) from the cleared mangrove (classified as moderate). It is noteworthy that it makes no sense to reserve the classification of “high quality” based on a single specific value (for instance based on the ITD criterion) which has only a very small chance to occur. We, therefore, propose, based on studies on mangroves, to use a range of values between 0.25-0.3 as a threshold for the “high quality” classification. If this range is applied, then the mid water station of the intact mangrove will fall within this category. The remaining indices did not allow for a classification of the sites especially the diversity index (H'), despite the higher values in the intact mangrove compared to the cleared mangrove and the bare sand flat, and the sensitive/tolerant genera, which classified the intact mangrove to have a poor EQS. However, when sites' EQS were evaluated using the H' thresholds values as recommended by Marin *et al.* (2008), small differences in the classification of the sites was noted, with the intact mangrove classified as having a moderate EQS, the cleared mangrove as moderate/bad, and the bare flat classified as bad. This indicates that the range of the threshold values of H' suggested by Moreno *et al.* (2011) are too narrow to detect any differences between sites. Moreover, the sensitive/tolerant genera classified the intact mangrove to have a poor/bad EQS due to the dominance of the genera *Daptonema/Theristus* and *Terschellingia*, which are naturally present in the mangrove as they are more tolerant to stressful conditions, such as anoxia, that occurred in the mangrove sediments. The selection of the reference thresholds for diversity (H') and species richness were based on the extended data matrices available for the Eastern Mediterranean ecosystems, while the selection of the sensitive/tolerant genera was based on the correlation with the sedimentary TOM concentration. Most of the studies on nematode diversity in mangroves from different places in the world have reported H' values ranging between 0.47 and 4.34 (e.g. the present study; Olafsson, 1995; Schrijvers, 1996; Xuan *et al*., 2007 and the references therein; Pinto, 2013). These values are lower than the range proposed by Moreno *et al.* (2011) for both the high and bad quality categories. Since the diversity in mangrove sediments is low compared to other intertidal habitats due to adverse environmental conditions we also suggest that the threshold values of diversity (H') for the high quality category should be lowered to e.g. >4.0. Therefore, we argue that the EQS approach developed by Moreno *et al.* (2011) can be applied as such to mangrove ecosystems provided that other indicative genera are identified. In addition, sand flats are naturally disturbed ecosystems and, therefore, falsely classified as poor. This showed that EQS concept is too context-specific to be of any use for making generalizations and is of limited relevance in areas where it has not been developed for. Different ecosystems should therefore be evaluated differently which, however, reduces the strength of the EQS approach.

4.5. Conclusion

This study illustrates differences in sediment characteristics and associated meiobenthic communities when comparing three contrasting sites, including cleared and intact mangroves in addition to a bare sand flat. The intact mangrove habitat was characterized by low abundances, but diverse meiobenthic communities. The after-control/impact approach (ACI) used in this study, though more limited in establishing cause-effect relationships between mangrove clearance and responses of meiofauna populations, was useful in detecting the consistent and significant differences in sediment characteristics (Sabeel *et al*., 2014), and in the structural and functional diversity of the meiofauna community between the different sites. Application of functional trait indices combined with sufficient taxonomic information may deliver additional ecological information related to the effect of mangrove disturbance (clearance) and thus, to ecosystem health if modified for mangrove system.

5

Nematode biomass and biomass spectra

Chapter 5

The use of nematode biomass and biomass spectra for the assessment of disturbance in Sudanese mangroves

Adapted from: Sabeel R. A. O. and Vanreusel A. (2015) Potential impact of mangrove clearance on biomass and biomass size spectra of nematodes along the Sudanese Red Sea coast. Marine Environmental Research, 103, 46-55.

Abstract

The potential effect of mangrove clearance on total nematode assemblage biomass, Nematode Biomass spectra (NBS) and abundance/biomass curves (ABC) was investigated by studying three sites, each representing a different degree of mangrove clearance. Results revealed significant differences between the three sites in sediment and nematode characteristics. Although both the cleared and intact mangrove sites had comparable total nematode biomass values, clear differences in biomass size spectra and abundance biomass curves were observed. The results suggested that the variation in the sediment characteristics affected the nematode community composition and biomass spectra. In contrast to the unimodal nematode biomass size spectra that were found at the intact mangrove and the bare sand flat site, the cleared mangrove site showed a bimodal biomass size spectrum, owing to higher numbers of smaller-bodied opportunistic non-selective deposit feeding nematodes, but at the same time large epistratum feeders and omnivores/predators were present too. The ABC method classified the cleared mangrove as moderately to grossly disturbed.

5.1. Introduction

Mangrove forests constitute 0.7% of tropical forest areas (Giri *et al.*, 2011). They are ecologically important as they provide habitat for a rich biodiversity (Nagelkerken *et al.*, 2008). However, during the past century they experienced massive destruction from natural disturbances, including cyclones and other storms, lightning, tsunami and floods, and human disturbances such as wood harvesting, trees felling, aquaculture and pollution. The estimated world's original mangrove forest is less than half of what it once was (Spalding *et al.*, 2010), primarily due to human disturbance (Field *et al.*, 1999).

As a pristine habitat, mangroves are generally considered well-structured ecosystems inhabited by species representing a wide range of ecological strategies, but when this habitat is disturbed, a deviation from balanced conditions and pronounced changes in the ecosystem usually may occur. A variety of human disturbances, notably clearing of mangrove for agriculture, aquaculture, and urban and coastal development (Alongi, 2002; Giri *et al.*, 2008), can devastate and profoundly affect mangroves, by changing the average environmental conditions and eventually altering the associated faunal and floral communities. Consequently, they reduce mangrove habitat complexity (Dye, 2006) and diminish their values as a provider of a number of ecosystem services, such as feeding and nursery habitats for benthic invertebrates and fish, maintaining biodiversity, carbon export/sequestration, recycling nutrients, filtering pollutants, and assimilating waste (Barbier *et al.*, 2011; Lee *et al.*, 2014).

Meiofauna represent an important component of the benthic ecosystem. They play an important role in ecosystem processes, by stimulating organic matter degradation and nutrients recycling (Austen, 2004), and by linking the smaller (e.g. bacteria) and larger organisms (e.g. macrofauna) in the marine benthic food web (Moens *et al.*, 2005; Danovaro *et al.*, 2007; Giere, 2009). Their unique characteristics, being small in size, highly diverse, with high turnover rates, and the absence of larval dispersion (Heip *et al.*, 1985; Higgins & Thiel, 1988) allowed for their use as biological indicator of anthropogenic disturbance (Heip *et al.*, 1988; Warwick, 1988; Moreno *et al.*, 2008a). Nematodes in particular are more sensitive and able to respond rapidly to disturbances of varied nature, frequency and quantity (Schratzberger & Warwick, 1998; 1999) making them a useful tool to detect changes in marine sediments. They have been used as an early indicator of the changing in environmental conditions, reflecting the effects created by natural or anthropogenic disturbance (e.g. Schratzberger *et al.*, 2004; Steyaert *et al.*, 2007; Moreno *et al.*, 2008b; Liu *et al.*, 2011) and to assess the overall system quality (e.g. Marin *et al.* 2008; Moreno *et al.*, 2011, Alves *et al.*, 2013, Semprucci *et al.*, 2013).

In addition to a number of taxonomic and trait-based indices, such as taxonomic diversity, maturity index and trophic diversity (e.g. Bongers *et al.*, 1991; Heip *et al.*, 1985), non-taxonomic approaches, such as the comparison of abundance-biomass curves (ABC) and biomass spectra (BS) were developed to study the structural and functional biological response to changes in the environment (Schwinghamer, 1981; Warwick, 1986; Warwick *et al.*, 1987). The latter have especially been presented as advantageous over other methods and are widely used to describe the structure of marine ecosystems. Biomass spectrum were investigated including all benthic size classes (Schwinghamer, 1981; Warwick, 1984; Drgas *et al.*, 1998), or exclusively within the meio- or macrofauna, or even on selected taxa such as nematodes (Vanreusel *et al.*, 1995b; Vanaverbeke *et al.*, 2003). In addition, many authors have tested whether or not BS of benthic communities comprising all sizes from bacteria to macrofauna conformed to a bimodal pattern (Schwinghamer, 1981; Warwick, 1984; Drgas *et al.*, 1998; Duplisea, 2000), and to what extent a bimodal distribution pattern can be explained by abiotic factors such as sediment grain size (Duplisea & Drgas, 1999; Duplisea, 2000; Leaper *et al.*, 2001). Biomass spectra are highly recommended for monitoring changes in ecosystems particularly because of their relation to metabolism and energy transfer through the community and because of their relative simplicity (Turnbull *et al.*, 2014). According to Vanaverbeke *et al*. (2003), nematode biomass spectra (NBS) is a valuable tool to assess functional changes in nematode communities as a result of a changing environment, since this is less time consuming and can be performed by non-specialists.

The ABC method is based on the comparison of abundance and biomass distributions of the present species within a size category or taxon in a sample (Warwick, 1986; Warwick *et al.*, 1987) and may illustrate the differential performance of those distributions in response to specific environmental conditions (Warwick, 1986; McManus & Pauly, 1990; Meire & Dereu, 1990; Warwick & Clarke, 2001). Therefore, this method may allow identifying to what extent communities are affected by disturbances. With increasing disturbance, it is expected that slow-growing species cannot cope with the change, while the system is increasingly dominated by r-selected species (fast-growing, small, opportunistic). Consequently, the biomass curve will be lower than the abundance curve. An advantage of the method is that it does not require a spatial or temporal control against which to compare the index (Clarke & Warwick, 2001).

Despite the potential ecological importance of Sudanese mangroves, they face a number of threats including, but not limited to, mangrove clearing. In addition to the limited information on their ecology, there is a lack of understanding on how specific activities such as clearing can impact specific components of these ecosystems. By relating nematode biomass structure, and environmental variables at three different coastal habitats, including an intact and a cleared mangrove, and a bare sand flat, valuable information on the conditions of at least part of the benthic ecosystem regarding disturbance may be drawn.

The specific aims of this study were to: (i) compare the patterns of nematode biomass, NBS and ABC curves in three different habitats along the Sudanese coast; and (ii) evaluate the relationships between environmental properties and patterns in nematode biomass. The resulting assessment may be useful for detecting the ecological change using nematode biomass as a descriptor of anthropogenic disturbance (including clearance) on mangrove ecosystems.

5.2. Material and Methods

5.2.1. Study Site

The study was performed at the southern part of the Sudanese coastal line. The area is characterized by a semi-arid climate with a mean daily temperature of 29 °C in winter and 42 °C in summer. Annual rainfall averages 164 mm. Tides in the area are unusually small with a mean spring tide of 0.1 m. The seasonal variation in water levels is up to 0.5-1 m higher, as a result from intense rainfall during winter months (Musa, 1991). Three sites representing varying degrees of mangrove clearance were sampled for nematodes at 3 water levels (Fig. 5.1a). The granulometric properties of the sediment measured in all sites and water levels are shown in Chapter 2, Table 3.1. and discussed in detail in Sabeel *et al.* (2014). Site 1 is a bare sand flat, characterized by a high sand content (57-80%), larger median grain size (87-122 µm), and moderately to very poorly sorted sediments. Site 2 is recently cleared from mangrove trees (3-5 years before sampling event). The sediment has a sand content of 12-77%, a median grain size between 19-138 µm, and poorly to very poorly sorted sediments. Site 3 is an intact mangrove, with *Avicennia marina* stands. It has a high mud content (37-82%), a finer median grain size (23-125 µm), and very poorly sorted sediments. Distance between site 1 and 2 is about 1.2 km, while the distance between site 2 and 3 is about 26 km. To include the spatial variation within sites related to seasonal water levels, three stations corresponding to these water levels were established at each site (Fig. 5.1b). These stations were referred to as: (i) high-water (HW), which is just below the water line mark during the winter high-water level; (ii) mid-water (MW) without mangrove stand in the bare sand flat habitat, with remnants of mangrove trunks in the cleared mangrove habitat, and with mangrove stands in the intact mangrove habitat; and (iii) low-water (LW), which is just above the water line mark at summer low water level. The width of each zone from high to low water was about 40 m, 45 m and 15 m, respectively. (Figure 1b). Sites were chosen based on their topographic similarity to facilitate the comparison between sites.

5.2.2. Sampling and sample processing

In each water level at each site, a maximum of three sediment samples to a depth of 5 cm were collected using cylindrical hand corers (5.64 cm Ø, 25 cm² surface area). The complete sediment columns were immediately fixed in 4% neutral formaldehyde filtered seawater solution. Nematodes were extracted from the sediment by centrifugation with Ludox (Heip *et al.*, 1985). All nematodes retained by a 32 µm sieve were stained with Rose Bengal of 1%

concentration. At each water level 3 additional core samples coupled with the samples of nematodes were taken for sediment properties. Detailed description of the collection and the analysis procedures of the environmental data are presented in Sabeel *et al.* (2014) (**Chapter 3**).

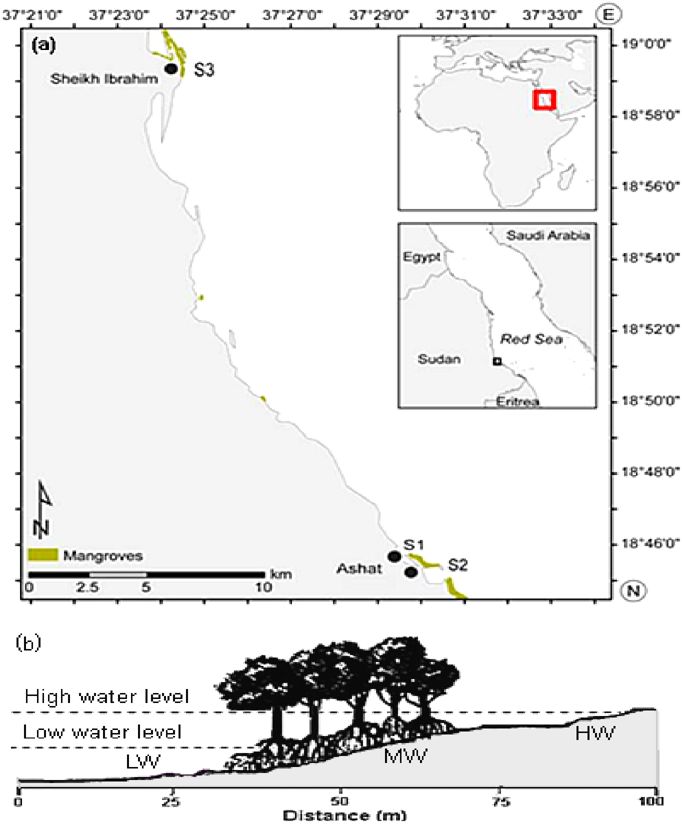


Figure 5.1. (a) Location of the three sampling sites (S1: bare sand flat, S2: cleared mangrove, S3: intact mangrove) at the Sudanese Red Sea coast, and (b) Profile of transect with sampling stations (H: high-water, M: mid-water, L: low-water). along the seasonal water level gradient (From Sabeel *et al.*, 2014)

Nematodes were sorted and identified to genus level at high magnification under a binocular stereomicroscope (Leica DLMB, magnification 100x) and a compound microscope (1000 × magnification) using the pictorial key to nematode genera (Warwick *et al.*, 1998), and the NeMys online identification key (Vanaverbeke *et al.*, 2015). The abundance of nematodes was determined by counting all nematodes in each sample and converted to abundances per 10 cm². Nematode dry biomass (dwt) was calculated by measuring the maximum length (L), excluding the filiform tails, and the maximal body width (W) of nematodes using an image analyser (Leica DMR compound microscope and Leica LAS 3.3 imaging software). Individual biomass was then calculated using Andrassy's formula for body mass (Andrássy, 1956) with the adaptation of Feller & Warwick (1988) assuming a dry to wet weight ratio (r) of 0.25 and specific gravity (sgr) of 1.13.

$$dwt = L \times W^2 \times 1600000 \times sgr \times \mathrm{r}$$

Nematode total biomass for each water level was then calculated as the product of averaged individual genus biomass, and the total number of nematodes per sample, and their corresponding average abundances.

In addition, all individuals were assigned after Wieser (1953) to one of the four trophic groups, selective deposit feeders (1A), non-selective deposit feeders (1B), epistrate (diatom) feeders (2A), and predators/omnivores (2B); and placed on a *c-p* scale ranging from 2 (originally 1) for "colonisers" to 5 for "persisters" (Bongers, 1990; Bongers *et al.*, 1991; 1995).

5.2.3. Construction of nematode biomass spectra (NBS)

The biomass size spectra (NBS) were constructed using $\log_2$ grouping of nematode dry weight (µg) on the x-axis and the total dry weight biomass (µg) per size class on the y-axis. Each $\log_2$ size class represents the sum of the dry weight of all organisms within that class, e.g. size class 0 represents the sum of the biomass of all organisms in the dry weight range $\geq 2^0$ to $<2^1$, which means a biomass ≥ 1 to < 2 µg (Vanaverbeke *et al.*, 2003). The NBS were constructed after pooling biomass measurements of all replicates for each water level station.

5.2.4. *Construction of the abundance/biomass comparison plots (ABC)*

The ABC plots were constructed for each water level (after pooling replicates) as proposed by Warwick (1986). This method involves the plotting of separate k-dominance curves for species abundances and species biomasses on the same graph and making a comparison of the forms of these curves. The species are ranked in order of importance in terms of abundance or biomass on a logarithmic scale (x-axis) against percentage dominance on a cumulative scale (y-axis). The relative position of these curves has been suggested as a measure of the degree of disturbance. In an undisturbed environment, the biomass curve overlies the abundance curve for its entire length as an indication of the dominance of a few large species (K-selected species). In a disturbed environment, the abundance curve overlies the biomass curve as a result of numerical dominance of a few species with small body sizes (r-selected species). The degree and direction of the separation of these curves, which is represented by the area between the two curves is given by the W-statistic (Clarke, 1990) and expressed as:

$$W = \sum_{i=1}^{S} (B_i - A_i)/[50(S-1)]$$

Where B_i is the relative biomass of the ith-species, A_i is the relative abundance of the ith-species, and S is the number of species. The W-statistic can show values in the range of -1 to 1 with W close to 1 for undisturbed conditions. It points to equal abundances across species while the biomass is dominated by K-selected species. Therefore, the biomass curve lies above the abundance curve. When W is close to -1, mainly k-selected species declined, whereas smaller *r*-selected species became dominant, both numerically and in terms of biomass. Therefore, the biomass curve lies below the abundance curve suggesting a more disturbed community. The W values close to zero are considered to characterize a moderately disturbed community.

5.2.5. Data analyses

To investigate the differences in nematode biomass (mean individual and total) and composition (using biomass values per taxonomic group) between sites and water levels, non-parametric univariate and multivariate permutational ANOVA analyses were performed based on a two-way crossed design (factor “site” (3 levels, fixed) and the factor “water level” (3 levels, fixed)). Euclidean distance based resemblance matrices on untransformed nematode biomass data were used for univariate analysis, and Bray-Curtis similarity resemblance matrices based on fourth root transformed biomass data were used for multivariate analysis. The patterns of dispersion (variability), by testing the null hypothesis of no effect of dispersions of samples on small scale (within sites) and large scale (among sites), were examined using a non-parametric multivariate dispersion test (PERMDISP; Anderson, 2008) based on the Bray–Curtis similarity measure on the fourth-root transformed data. The test revealed no dispersion effect in the factor site (F = 3.4509, P = 0.0896) and the interaction factor (site × station; F =19.173, P =0.0695). However, significant differences in dispersion for the factor station were detected with greater variability in nematode assemblages observed between the mid- and the low-water stations. Thus, the null hypothesis of the homogeneity of dispersions was retained only for the factors site and interaction (site × station). When significant effects were detected by PERMANOVA ($P < 0.05$) for these factors, differences between levels within groups were identified comparing all possible pair combinations (i.e. post-hoc pair wise comparisons). Multidimensional scaling plots (MDS) derived from Bray-Curtis similarity matrices on transformed biomass data were used to visualize the differences in the structure of nematode assemblages following the procedure described by Clarke and Warwick (1994). All the above mentioned analyses were performed using software package PRIMER 6+ PERMANOVA (Anderson, 2005; Anderson *et al.*, 2008). To test for significant differences in the distribution of NBS in each of the water levels at each site, a Chi-square (χ^2) goodness-of-fit test was computed in STATISTICA (StatSoft Inc., 2004).

The relationship between environmental variables (namely: silt, median grain size, sediment sorting, TN, TOC, and CN) and nematode biomass (total, individual and composition) was tested using Distance-Based Linear Modeling (DISTLM) routines, based on sediment cores coupled with cores for nematode analysis. This test was performed using the software package PRIMER 6+ PERMANOVA (Anderson, 2005; Anderson *et al.*, 2008). DISTLM models were constructed using a step-wise selection procedure and adjusted R^2 as a selection criterion to enable the fitting of the best explanatory environmental variables in the model.

5.3. Results

5.3.1. Nematode biomass

Mean individual nematode biomass ranged between 0.34 µg dwt/10 cm^2 in the HW at the bare sand flat and 4.67 µg dwt/10 cm^2 in the HW at the intact mangrove, and the total nematode biomass ranged from 2.16 to 66.13 µg dwt/10 cm^2 (Table 5.1). Results revealed significant differences in mean individual biomass for the interaction factor between sites and water levels, with higher values in the MW of the intact mangrove than in the cleared mangrove and the bare sand flat (PERMANOVA, $P < 0.05$; Table 5.2). Mean total nematode biomass was only significantly different between sites (PERMANOVA, $P < 0.01$; Table 5.2), with higher biomass values noted in the intact and cleared mangroves compared to the bare sand flat (PERMANOVA, $P < 0.05$; Table 5.2).

Table 5.1. Total biomass (µg dwt/10cm²) per nematode genus, c-p values (Bongers,1990) and feeding groups (Wieser, 1953) assignments for all nematode genera averaged per station (HW: high water, MW: mid water, LW: low water) at the three sampling sites.

Family	Genus	c-p values	Feeding group	Bare sand flat			Cleared mangrove			Intact mangrove		
				HW	MW	LW	HW	MW	LW	HW	MW	LW
Aegialoalaimidae	*Aegialoalaimus*	4	1A	0	0	0	0	0	0.25	0	0	0
Axonolaimidae	*Axonolaimus*	2	1B	0	0	0	1.3	0	0	0	0	0
Camacolaimidae	*Onchium*	3	2A	0	0	0	0	0	0	0	0	3.65
	Procamacolaimus	3	2A	0	0	0	0.02	0.02	0.02	0	0	0
Chromadoridae	*Chromadora*	3	2A	0	0	0.17	0	0.4	0	0	0	0
	Chromodorina	3	2A	0	0	0.17	0	0	0	0	0	0
	Spilophorella	2	2A	0	0	0.16	0.49	1.3	5.52	0	0	0
Cyatholaimidae	*Paracyatholaimus*	2	2A	0	4.25	0	0	2.06	0	0	8.05	0
Desmodoridae	*Desmodora*	2	2A	0	0	0	0	7.15	6.98	0	0.82	1.96
	Molgolaimus	3	2A	0	0	0	0	0	0.19	0	0	0
	Metachromodora	2	2A	0	0	0	0.43	0	0	7.56	0	0
Draconematidae	*Draconema*	3	1A	0	0	0	0	0.22	0	0	0	0
Ethmolaimidae	*Ethmolaimus*	3	2A	0	0.13	0.43	27.48	2.15	0	5.34	0.2	0
Epsilonematidae	*Epsilonema*	3	1A	0	0	0	0	0	0.57	0	0	0
Haliplectidae	*Haliplectus*	2	1A	0	0	0	0	0	0	3.5	0.49	1.89
Ironidae	*Dolicholaimus*	4	2B	0	0	0	0	0	0.23	0	0	0
	Syringolaimus	2	2B	0.97	1.37	0.9	0	0	0	0.53	0.74	0
Leptolaimidae	*Leptolaimus*	3	1A	0	0	0	0.7	0	0.37	0	0	0
Linhomoeidae	*Terschellingia*	2	1A	0	0.07	0.07	0	0	0	2.38	0.61	3.21
	Metalinhomoeus	3	1B	0	0.1	0	0	0.39	0.69	0	0	0
	Spirina	4	2A	0	0	0	0	0	0	0	0	29.73
Microlaimidae	*Microlaimus*	2	2A	0	0	0	0	0.81	1.43	0.3	0.04	0
	Bolbolaimus	3	2A	0	0	0	0	0	0.89	0.69	0.03	0
Monhysteridae	*Monhysterilla*	2	1B	0	1.07	0.07	0.34	0.02	0.22	0.79	0.14	0
Oncholaimidae	*Viscosia*	3	2B	0	0	2.91	0	0	5.4	13.36	4.39	3.33
	Prooncholaimus	2	2B	0	0	0	0	3.05	0	0	0	0
	Oncholaimus	4	2B	0	0	12.33	16.01	0	0	0	12.98	8.65
Oxystominidae	*Oxystomina*	4	1A	0	0	0	0	0	0.16	0	0	0
	Halalaimus	4	1A	0	0	0	0	0	0.1	0	0	0
Selachinematidae	*Synonchium*	3	2B	0	0	0	0	0	0	0.79	0	0
Sphaerolaimidae	*Sphaerolaimus*	3	2B	0	0	0	0	0	0	0.06	9.9	0
Xyalidae	*Daptonema*	2	1B	1.12	1.73	1.7	16.13	24.11	14.52	8.71	3.2	4.31
	Theristus	2	1B	0.07	0.3	0.57	2.86	1.59	0.84	1.51	0.35	0
	Stylotheristus	2	1B	0	0	0	0.37	0	0	0	0	2.37
	Paramonhystera	2	1B	0	0	0	0	0	0.15	0.12	0	0
Average individual biomass per station				0.34	1.32	2.63	1.59	1.20	1.54	2.91	4.67	1.56
Average total biomass per station				2.16	9.03	19.48	66.13	43.06	38.53	45.62	41.94	59.09

Table 5.2. PERMANOVA results for mean individual biomass, mean total nematode biomass, and assemblage composition based on biomass data measured in different water levels (HW: high-water, MW: mid-water, LW: low-water) at the sampled sites (BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove). The P-values obtained by permutation and significant values are indicated in bold italic.

Nematode characteristic	PERMANOVA main test						PAIR-WISE TESTS		
	Source	df	SS	MS	Pseudo-F	P(perm)	Site/water level		P(perm)
Average individual biomass	Site	2	12.1	6.0	5.6	***0.0158***	IM>CM, BSF		≤0.05
	Station	2	2.2	1.1	1.0	0.3868	NS		
	Sitexstation	4	13.9	3.5	3.2	***0.0478***	H	NS	
							M	IM>CM, BSF	<0.05
							L	NS	
Total biomass	Site	2	6563.1	3281.6	9.0	***0.004***	CM,IM>BSF		<0.05
	Station	2	237.62	118.8	0.3	0.7265	NS		
	sitexstation	4	1695.1	423.8	11.7	0.3672	NS		
Community composition	Site	2	16582.0	8290.9	20.5	***0.0001***	IM≠CM≠BSF		≤0,001
	Station	2	10503.0	5251.7	13.0	***0.0001***	HW≠MW≠LW		≤0,001
	sitexstation	4	11622.0	2905.5	71.901	***0.0001***	H	IM≠CM≠BSF	<0.01
							M	IM≠CM≠BSF	<0.05
							L	IM≠CM≠BSF	<0.05

Significant spatial differences in nematode composition based on biomass per genus were detected for the interaction between sites and water level (PERMANOVA, P =0.0001; Table 5.2). A clear spatial segregation of the three sites with also a clear shift in community composition for different water levels were observed (Fig. 5.2).

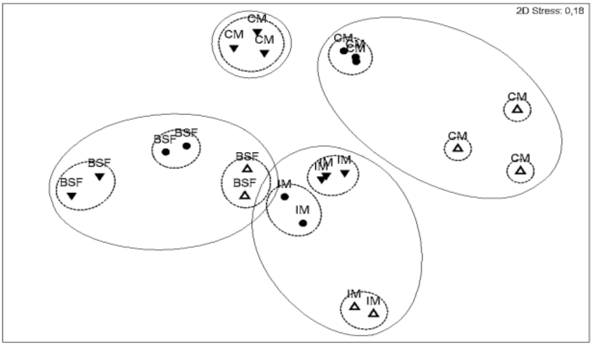


Figure 5.2. Non-metric multidimensional scaling (MDS) ordination of square root transformed nematode biomass data from different water levels as indicated by symbols (filled triangle: high-water, filled circle: mid-water, open triangle: low-water) at different sites (BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove). The continuous and dotted lines represent similarity at 60 and 80%, respectively.

5.3.2. Relationship between nematode biomass and environmental variables

The best fitted models, based on environmental variables that explain the individual and total biomass per station, as well as the community composition based on biomass data are shown in Table 5.3. Result from marginal DISTLM test showed that individual and total nematode biomass were explained by clay, silt and sand content contributing between 24.4% and 29.1% (P < 0.05). All tested environmental variables, except median grain size (MGS), contributed individually to the total variation in nematode composition by explaining between 7.4% and 14.8% each (P < 0.05).

The sequential DISTLM test indicated that part of the variation in mean individual biomass could be explained by silt content (29.18%, P < 0.01). Silt and median grain size contributed significantly to the variation in mean total biomass by 25.95 % and 21.62%, respectively (P < 0.05). The variation in nematode composition based on biomass was explained by sediment sorting (14.76 %, P < 0.001), C/N (12.28 %, P < 0.01), and median grain size (10.60 %, P < 0.01).

Table 5.3. Results of Distance-based linear modeling (DISTLM) testing for relationships between selected sediment characteristics (MGS: median grain size, Sort: sediment sorting, TOC: total organic carbon content, C/N: total carbon-nitrogen ratio) and nematode community attributes patterns in marginal tests (variation explained by single variables) and in sequential tests (variation explained by adding new variable each time to get the optimum fit criterion) using the stepwise selection procedure: on the basis of the adjusted R² selection criterion (significant P values in bold italic).

Nematode characteristic	MARGINAL TESTS					SEQUENTIAL TESTS						
	Variable	SS (trace)	Pseudo-F	P	Proportion (%)	Variable	Adjusted R^2	SS (trace)	Pseudo-F	P	Proportion (%)	Cumulative (%)
Average individual biomass	Clay	10.87	7.12	***0.0136***	26.24	+Silt	0.26	12.09	8.2392	***0.0063***	29.18	29.18
	Silt	12.09	8.24	***0.0083***	29.18	+MGS	0.31	3.54	2.6073	0.1206	8.55	37.72
	Sand	12.07	8.22	***0.0071***	29.13							
	MGS	6.81	3.93	0.0636	16.43							
	Sort	2.87	1.49	0.2432	6.92							
	% TOC	0.44	0.21	0.6754	1.05							
	C/N	0.00	0.00	0.9966	0.00							
Total biomass	Clay	3233.30	6.48	***0.0193***	24.48	+Silt	0.22	3427.40	7.0096	***0.0161***	25.95	25.95
	Silt	3427.40	7.01	***0.0151***	25.95	+MGS	0.42	2855.30	7.8352	***0.0096***	21.62	47.57
	Sand	3458.00	7.09	***0.0177***	26.18	+C/N	0.44	571.84	1.6205	0.2227	4.33	51.90
	MGS	1324.50	2.23	0.1531	10.03							
	Sort	1503.90	2.57	0.1229	11.39							
	% TOC	753.31	1.21	0.2993	5.70							
	C/N	425.32	0.67	0.4341	3.22							
Community composition	Clay	5391.10	2.20	***0.0281***	9.93	+sort	0.10	8015.50	3.4631	***0.0004***	14.76	14.76
	Silt	5588.90	2.29	***0.0183***	10.29	+C/N	0.19	6667.10	3.197	***0.0035***	12.28	27.04
	Sand	5599.60	2.30	***0.0217***	10.31	+ MGS	0.27	5758.10	3.0605	***0.0054***	10.60	37.64
	MGS	4034.50	1.61	0.1182	7.43	+Silt	0.30	3224.00	1.7887	0.0955	5.94	43.58
	Sort	8015.50	3.46	***0.0005***	14.76	+TOC	0.33	3037.50	1.7606	0.1004	5.59	49.17
	% TOC	7103.90	3.01	***0.0047***	13.08							
	C/N	6942.80	2.93	***0.0025***	12.79							

5.3.3. Nematode biomass spectra (NBS)

NBS for the different water levels in each site are shown in Figure 5.3. Water levels and sites differed in shape and modi of the NBS. The bare sand flat and intact mangrove showed mainly a unimodal distribution, while CM showed a bimodal distribution of NBS at all water levels. In the HW, the bare sand flat showed a very low biomass without any noticeable peak, while in the intact mangrove the spectrum peaked at class -3 with a total biomass of 25.06 µg dwt. In the MW and LW stations, the bare sand flat showed an abrupt increase in biomass, which peaked at class 0 with a total biomass of 11.44 µg dwt and 8.80 µg dwt, respectively; whereas at the intact mangrove, the spectra peaked at class -1 with a total biomass of 7.71 µg dwt and 20.88 µg dwt, respectively. At the cleared mangrove, biomass in the HW and MW peaked at -3 with a total biomass of 16.23 µg dwt and 12.83 µg dwt, respectively, while in the LW the spectrum peaked at class -2 with a total biomass of 10.58 µg dwt. After these initial peaks, biomass in the cleared mangrove dropped rapidly each time, but showed also a second peak at size class 2 for the HW with a total biomass of 5.24 µg dwt, and at size class 0 for the MW and LW with a total biomass of 7.64 and 16.39 µg dwt, respectively. Results from the chi-square test indicated significant differences in size class distribution between sites, except for the HW at the cleared and the intact mangroves, and within sites except between the HW and both MW and LW levels at the bare sand flat, and between the MW and both HW and LW levels at the cleared mangrove ($P < 0.01$, Table 5.4).

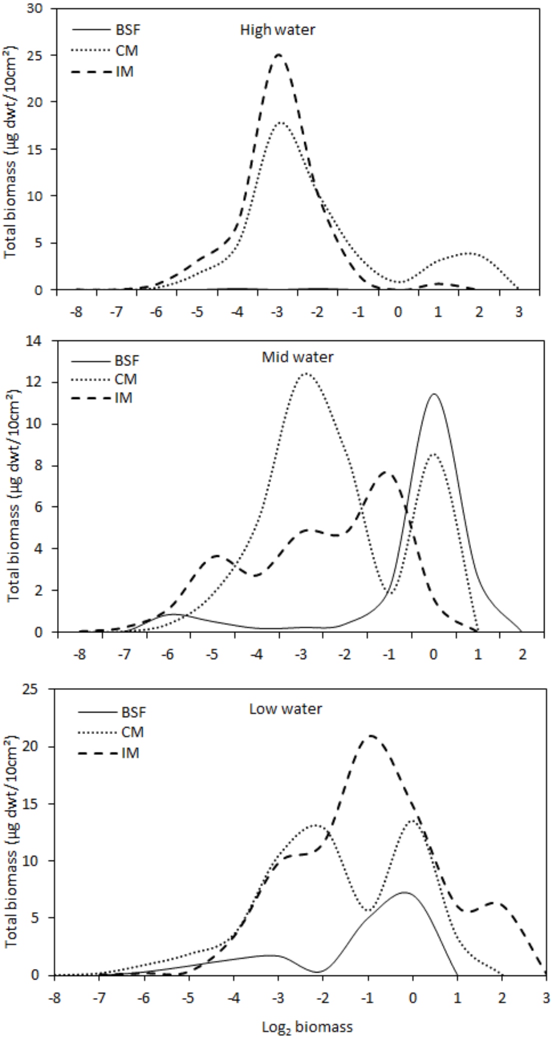


Figure 5.3. Nematode biomass size spectra of different water level stations at different sites: The continuous lines represent the bare sand flat, the dotted lines represent the cleared mangrove and the dashed lines represent the intact mangrove.

Table 5.4. Results from Chi-square for the differences in nematode biomass size classes between water level station (HW: high-water, MW: mid-water, LW: Low-water) and sites(BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove). df indicates thedegrees of freedom and *P* indicates the P-values, significant P-values are indicated in bold italic

Comparison			Chi-Square	Df	*P*
Site	High-water	BSF, CM	1082.51	10	***0.0001***
		BSF, IM	2512.56	10	***0.0001***
		CM, IM	11.62	10	0.3112
	Mid-water	BSF, CM	1013.55	10	***0.0001***
		BSF, IM	138.35	10	***0.0001***
		CM, IM	25.73	10	***0.0041***
	Low-water	BSF, CM	217.98	9	***0.0001***
		BSF, IM	151.75	9	***0.0001***
		CM, IM	41.01	10	***0.0001***
Water Level	Bare sand flat	HW, MW	1.02	10	0.9998
		HW, LW	16.58	9	0.0557
		MW, LW	29.31	9	***0.0002***
	Cleared mangrove	HW, MW	13.89	10	0.178
		HW, LW	76.49	10	***0.0001***
		MW, LW	14.40	10	11.555
	Intact mangrove	HW, MW	33.57	10	***0.0002***
		HW, LW	283.76	10	***0.0001***
		MW, LW	99.81	10	***0.0001***

5.3.4. Nematode abundance biomass curve (ABC)

ABC curves obtained for all stations at all sites, together with the associated W values are presented in Figure 5.4. All water levels, except for HW at the cleared mangrove, showed a more even distribution of abundance than of biomass as indicated by the positive W values. According to the model, the HW station at the cleared mangrove is classified as grossly disturbed due to a negative W value, resulting from the fact that the abundance curve is lying largely above the biomass curve and that both curves are crossing. The LW station at the bare sand flat and both the HW and MW stations at the intact mangrove can be classified as undisturbed based on the fact that the biomass curve always lies above the abundance curve resulting in higher W values. The remaining stations are classified as moderately disturbed, as reflected by the low, but still positive values and by the coinciding biomass and abundance curves.

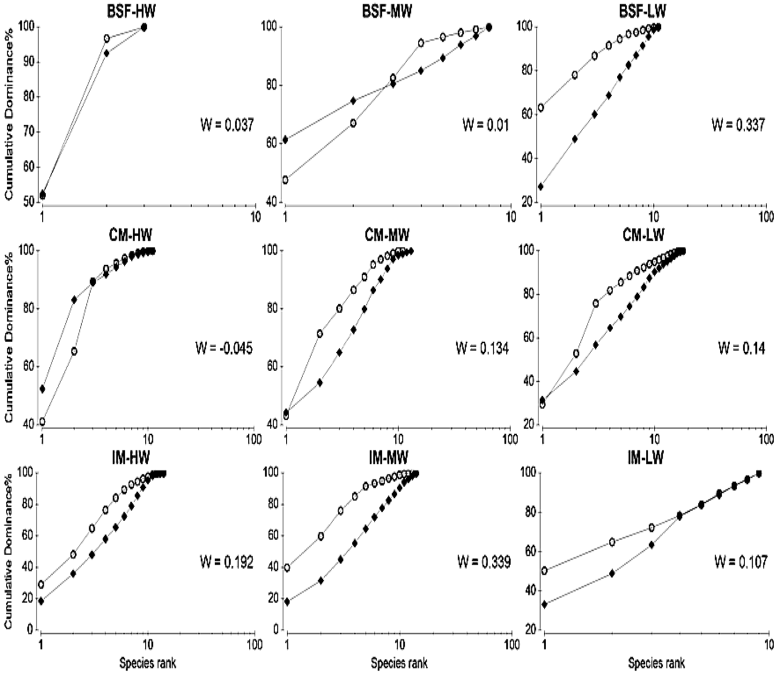


Figure 5.4. ABC curves and W values obtained for each water level (HW: high-water, MW: mid-water, LW: low-water) at each sampling site (BSF: bare sand flat, CM: cleared mangrove, IM: intact mangrove). Lines with filled diamonds represent abundance; lines with open circles represent biomass.

5.4. Discussion

The results of the different analyses clearly demonstrate the high variability between sites with regard to both univariate and multivariate comparisons of nematode biomass indicating the distinct nematode assemblages inhabiting these sites. Total and individual biomass, and also nematode biomass spectra significantly differed between sites, whereas ABC curves showed different patterns. Also the analysis of the sediment characteristics (Sabeel *et al.*, 2014) indicated a clear spatial heterogeneity between sites but also between the stations for each site. Both the intact and cleared mangroves showed an elevated individual and total biomass as compared to the bare sand flat. It is well known that nematode biomass is largely a function of food availability and physical properties of the sediment (e.g. Schwinghamer, 1983; Udalov *et al.*, 2005; Schratzberger *et al.*, 2008). In our study, the variation in the total and individual biomass can be explained by the different content of silt and median grain size as shown by the results from the DISTLM analysis. Total biomass increases with increasing percentage of silt, in agreement with Quang *et al*. (2014), while the individual biomass was lower in the sediment with higher percentage of sand, as reported by Tita *et al*. (1999). On the other hand, the variation in nematode composition is mainly attributed to the spatial variation in sediment sorting, grain size and C/N. Sediment grain size is a primary factor for determining nematode genera composition by affecting the burrowing and the interstitial behavior of organisms directly or indirectly, but also by affecting the sediment related environmental characteristics such as quality of organic matter, which may also play an important role in the functional structure of nematode assemblages (Schratzberger *et al.*, 2007). In general, the fauna burrows in sediments with a mean particle size of <125 µm, whereas sediment with larger grain sizes tend to be dominated by interstitial fauna (Coull, 1999).

The IM and the BSF in general showed single NBS peaks, while the CM showed a bimodal spectrum with a shift towards smaller and larger size classes, especially compared to the intact mangrove. The presence of a relatively high unimodal spectrum in the MW and HW at the bare sand flat, despite the lower biomass values, indicates that the community is dominated by few size classes, in comparison to the intact mangrove spectrum shape which was more gradual, suggesting a better distributed community among the various size classes. The cleared mangrove showed a bimodal distribution of the NBS indicating the presence of both small and large bodied specimens. Many authors have attempted to interpret the variation in nematode body size in relation to grain size distribution, especially in terms of interstitial space, and nematode life style (e.g. Schwinghamer, 1981; Heip *et al*., 1985; Giere, 1993; Tita *et al*.; 1999; Udalov *et al.*, 2005). In general, large nematodes dominate silty anoxic sediments, while in sandy sediments with large interstitial space smaller nematodes prevail, although also long and slender nematodes inhabit these coarse sediments. This interpretation may partly explain the pattern noted in the HW and LW at the bare sand flat, where sediments are coarser compared to the sediments in the other sites. However, this did not fully conform to the pattern noted in the other sites, especially at the cleared mangrove, implying that the change in size spectrum seems not equivocally related to sediment composition (e.g. Duplisea & Drgas, 1999; Duplisea, 2000; Leaper *et al.*, 2001) and may interrelate with other biogeochemical conditions of the sediments, such as oxygen availability, organic load and its quality, which are extremely critical and only indirectly related to granulometry, suggesting that the variation in the size spectra is mainly attributed to the functional adaptation of nematodes to the changing environmental conditions (Vanaverbeke *et al.*, 2003).

The bimodal distribution of the NBS in the cleared mangrove, where fine sand sediments with significant portions of silt are dominant as compared to other habitats, resulted from the presence of few larger omnivores/predators (*Oncholaimus, Prooncholaimus, Viscosia*) and epigrowth feeders (e.g. *Desmodora*), the higher proportional abundances of a small-bodied non-selective deposit feeder (*Daptonema*), and a lower abundance of the selective deposit feeders, mainly *Terschellingia* and *Haliplectus*, which belong to size class -3. The alteration in nematode community composition can be attributed to changes in sediment characteristics as a result of mangrove removal. However, it is difficult to relate these changes to a single factor. While Williams (1972) relates the distribution of nematode species directly to pore-space, more recent studies suggest that the shift in size class is more likely the response of organisms to other sediment-related chemical and physical factors such as oxygen concentration (Snelgrove & Butman 1994; Steyaert *et al.* 2007), abundance of microalgal biomass (Schwinghamer, 1983) and sediment disturbance (Vanaverbeke *et al.*, 2003). Since the cleared mangroves showed the presence of opportunistic nematodes species, such as *Daptonema,* which is considered as colonizers i.e. individuals that show rapid growth, and early reproduction (Vanaverbeke *et al.*, 2003), but also large sized omnivores/scavengers resulting in a bimodal size spectrum, this may point to consequence of disturbance resulting from mangrove clearance. However, further experimental evidence is required.

According to the ABC method, the cleared mangrove was moderately to highly disturbed from LW to HW. This is in contrast to the intact mangrove which was only moderately disturbed at the LW station, while the bare sand flat was moderately disturbed at the HW and MW stations. The ABC method is based on the assumption that increasing disturbance shifts communities from a dominance by large bodied species with low turnover rates toward dominance by small-bodied species with high turnover rates, the so called opportunistic or r-strategist species, represented by a large numbers of individuals. This appears to be confirmed in this study, as a shift in composition of life-history strategy towards the dominance of smaller nematodes (colonizers and intermediate with c-p 2 and 3) was observed in the cleared mangrove as compared to the intact mangrove, possibly pointing to a higher stress level. The increase in number of colonizers (opportunistic genera) was more pronounced in the cleared mangrove and is probably associated with the increase in the availability of high quality food, pointing to the higher levels of algal growth (pers. obser.) most likely as a result of mangrove clearance which allows for greater light penetration in the cleared than in the intact mangrove (Granek & Ruttenberg, 2008).

5.5. Conclusion

Our results indicate clear spatial variability in biomass, biomass size spectrum and abundance-biomass curves of nematode assemblages at different sites. The cleared mangrove showed a bimodal mode of NBS distribution, and was classified as moderately to grossly disturbed based on the ABC conditions as compared to the intact mangrove. Nematode biomass and size spectra seem strongly influenced by sediment characteristics such as grain size composition suggesting that the differences in nematode community parameters resulted from changing sediment conditions following clearing. The graphical representation of nematode assemblage biomass size spectra and the abundance biomass comparison method showed a promising tool for detecting the impact of clearance on mangrove and thus identifying its effect on the benthos

6

General discussion

Chapter 6
General Discussion

Introduction

The ecological role of Sudanese mangrove has been acknowledged by several authors since mid of the 20th century (e.g. Andrews, 1950; Kassas, 1957; Zahran, 1965; Kassas & Zahran, 1967; Mohammed, 1984). Nevertheless, these mangroves face a number of natural and anthropogenic threats that interfer with their ecological functions. Among these threats, mangrove clear cutting and removal has the most devastating effect on both the mangroves and the adjacent coastal habitats. The development of management strategies in response to the public opposition to mangrove conservation is, however, hindered by the lack of supportive scientific data that highlight the physical and the ecological consequences of their removal. The increase of the local human populations and the ongoing coastal development in the proximity of mangroves will inevitably further increase their loss if no immediate action is taken. This study aimed to investigate the temporal distribution of mangroves along the Sudanese coast and assess their importance as a habitat provider for benthic faunal communities. The following sections outline and integrate the key findings from each chapter discussed within the context of this PhD thesis.

6.1. Mangrove benthic fauna

Mangrove macrofauna and meiofauna are important components of mangrove ecosystems because of the important role they play in recycling nutrients and preserving the energy in the form of carbon and nitrogen mainly through breaking down leaf litter (Nordhaus *et al.*, 2009). The burrowing activities of macrofauna enhance the sediment properties and biochemical processes by increasing the porosity and water flow through the sediment, assisting in flushing toxic substances, and promoting nutrient recycling (e.g. Kristensen *et al.*, 2008). Meiofauna, on the other hand, are the most abundant fauna in mangrove sediments, and are also suggested to play an important role in litter degradation and thus in nutrient recycling. Furthermore, studies suggest that some taxa are part of the diet of commercially important fish (Coull *et al.*, 1995) and crustaceans (Dittel *et al.*, 1997). To our knowledge, there are no adequate studies that have been undertaken on the benthic assemblages and species of mangrove forests in Sudan. Here, benthic macro-and meiofauna, with special reference to nematodes, were studied in three different habitats representing a vegetated site (intact mangrove) and two non-vegetated sites (bare sand flat and cleared mangrove) along the Sudanese coast.

The initial aim of the study was to investigate the impact of mangrove clearance and the response of benthic communities to this disturbance. The ideal design to study such an impact is to apply a Before After Impact Control design (BACI), which was not possible to be implemented in our study because the clearance of the mangrove was not planned and took place about 5 years before sampling. Therefore, the sampling design adopted in this study was based on the after impact control design, which is limited by the lack of replication of the habitat type, in addition to temporal replication. Other factors than habitat type may be responsible for the observed differences between sites. Furthermore, mangrove clearance is a complex process that involves various stages of changes in physical characteristics of the sediment. In addition, it is not unusual for benthic communities to exhibit temporal variance in different locations, while temporal interactions among places are also not uncommon (Underwood, 1994). Therefore, the applied design is more subjective and only allows for highlighting the difference in sediment characteristics and benthic communities between the studied habitats since the sites were chosen for their similarity in topography. Considering the patchiness typical for mangrove sediments (Todd, 2001) the number of replicate samples taken (maximum 3 replicates) was rather small. Despite the aforementioned constrains and the limited logistics in the study area, this study can still provide a valuable insight into the variability of benthic communities between habitats as we identified a significant part of the local variation by sampling three stations per site.

6.1.1. Global comparison of the habitats

A global comparison of the vegetated and non-vegetated habitats in terms of benthic fauna characteristics, and therefore an integration of Chapter 3, 4 and 5, is discussed below. Overall, the cleared mangrove had the highest faunal abundances for both meio- and macrofauna. The intact mangrove, on the other hand, had higher meiofaunal and nematode abundances, and similar macrofauna abundances as compared to the bare sand flat. Previous studies on abundances of mangrove macrofauna (Schrijvers *et al.*, 1998; Dittmann, 2001; Alfaro, 2006) and meiofauna, particularly nematodes (Alongi, 1990), have reported assemblages with lower or similar densitiest than the adjacent habitats such as seagrass meadows and open sand/mudflats. However, higher meiofauna densities than usually found in mangrove (500 ind./10 cm^2; Alongi, 1989) have been recorded in some African tropical mangroves (e.g. Dye, 1983; Vanhove *et al.*, 1992; O´lafsson, 1995; O´lafsson *et al.*, 2000). The intact mangrove in Sudan encompasses a number of structurally and functionally distinct benthic assemblages and diverse phyla, as compared to the adjacent intertidal habitats, which is in agreement with other mangrove systems (Skov *et al.*, 2002; Lee, 2008; Nagelkerken *et al.*, 2008). In terms of the composition, the intact mangrove was dominated by decapod crabs (macrofauna), copepods and nematodes (meiofauna), and more specifically the nematode genera *Haliplectus* (Haliplectidae), *Terschellingia* and *Spirina* (Linhomoeidae), and *Daptonema* (Xyalidae), which are in general associated with mangrove habitats. The cleared mangrove was dominatedby polychaetes (macrofauna) and the nematode genera *Desmodora* (Desmodoridae), *Ethmolaimus* (Ethmolaimidae), *Microlaimus* (Microlaimidae), *Daptonema* and *Theristus* (Xyalidae), while the bare sand flat was dominated by bivalves (macrofauna) and the nematode genera *Monhystrella* (Monhysteridae), and *Syringolaimus* (Irononidae). The structural diversity in the intact mangrove showed a more even distribution of the benthos, and a higher Shannon Wiener diversity (H') and taxa/genera richness, except for macrofauna, compared to both other habitats. Most invertebrate groups within a given mangrove forest area are represented by only a few to ≤50 species (Alongi *&* Sasekumar, 1992) with the highest diversity most often found among the crustaceans (Kathiresan *&* Bingham, 2001). Studies on mangrove macrobenthos have generally reported assemblages with lower species richness than the adjacent coastal habitats such as open mud/sand flats. This may be explained by the trophic limitation of mangroves, being of poor nutritional quality, together with the physical environmental stresses which may have limited the proliferation of benthic species. The benthos is therefore dominated by larger populations of only a few species that are adapted to these limitations (Lee, 2008). In term of biomass, the intact mangrove had higher macrofaunal total biomass and nematode individual biomass, and similar total nematode biomass as compared to the cleared mangrove habitat (**Chapter 3 and 5**). The nematode biomass spectra (NBS) differed significantly between habitats and mainly demonstrated a unimodal distribution in the intact mangrove (at smaller size classes) and the bare sand flat (at bigger size classes), while a bimodal distribution of NBS was observed in the cleared mangrove (**Chapter 5**).

Food webs have already been studied widely in several mangrove ecosystems, with respect to trophic biodiversity, community composition and dynamics, food chain length or predator-prey interactions (e.g. Sheaves & Molony, 2000; Lepoint *et al.*, 2000; Abrantes & Sheaves, 2009). Stable isotope analysis has been used to study the incorporation of different carbon sources into benthic food webs in a variety of ecosystems, on the condition that there is a sufficiently large difference in the isotopic composition of the different primary carbon sources (Bouillon *et al.*, 2004a). In our study, trophic diversity was assessed using different methods for macrofauna (stable isotope analysis and community wide metrics approach) and nematodes (feeding groups and index of trophic diversity). As compared to the non-vegetated habitats, the intact mangrove is characterized by the highest trophic diversity for macrofauna, as indicated by more trophic levels (higher range of $\delta^{15}N$), more basal resources (higher range of δ^{13}C) and more divergent feeding strategies (higher TA and CD) which are more equally divided over the different macrofaunal taxa (lower NDD and higher SDNDD) (**Chapter 3**). Nematodes in the intact mangrove had also more even proportions of the 4 trophic groups and thus higher trophic diversity (lower ITD). However, mangrove litter as such was far less important as a food source for both benthic communities. The range of values of δ^{13}C and δ^{15}N in the bare sand flat and cleared mangrove are smaller, indicating that macrofauna in both habitats are less diverse with lower trophic levels (2-3) as compared to the intact mangrove. When a variety of food sources are available, mangrove fauna shows a remarkable diversity in their resource utilization patterns of the different sources, with different faunal groups occupying each a different trophic niche (Bouillon *et al.*, 2002b). On the other hand, the length of the food chain is determined by a number of factors such as ecosystem size and species richness, and can help to quantify trophic structure (Vander Zanden *et al.*, 1999; Post *et al.*, 2000; Vander Zanden & Fetzer, 2007). We identified 4 trophic levels in the intact mangrove, in agreement with Bouillon *et al.* (2002a) and Abrantes and Sheaves (2009), and 2 to 3 trophic levels in the cleared mangrove and the bare sand flat.

Some of the differences in benthic communities between habitats were partly attributed to the variability in sediment characteristics. The differences in sediment characteristics between the intact and the cleared mangrove in particular, may have resulted from removal of mangrove trees. The intact mangrove had sediment that on average was predominated by a high mud content, finer particles, very poorly sorted sediment and was more enriched in terms of organic content as shown by the higher percentage of TOC; however, the organic matter is of low quality as the C/N ratio is very high. This was expected since the main source of organic matter in mangroves is the leaf litter which is a rich source of carbon while the nitrogen is nutritionally poor. The sediment of the bare sand flat on the other hand is characterized by a high sand content, coarse particle sizes, poorly sorted sediment and high quality of the organic matter present as indicated by the low C/N values, although of low quantity as indicated by the low TOC values. The cleared mangrove habitat showed intermediate sediment characteristics between the bare sand flat and the intact mangrove, especially in terms of sediment grain size with equal mud and sand content, poorly sorted sediment, and low quantity and quality of organic matter. The high mud content in the intact mangrove is mainly due to the presence of the root systems which assist in the slow water flow, facilitating the deposition of terrigenous sediment carried by freshwater runoff. When this feature is absent, mangroves lose their buffering capacity against erosion and the fine sediment will be carried further to the adjacent shallow water, resulting in a higher sand content in the sediment. The high organic content in the intact mangrove resulted from the accumulation of organic matter from leaf litter. In contrast, the cleared mangrove site lacks the mangrove cover, resulting in resuspension of organic matter which subsequently is washed away by tidal currents leaving the area with low organic content. The removal of the vegetation cover also can increase the light penetration leading to higher algal growth which may explain the higher C/N in this site.

In agreement with other studies, our results suggest that the differences between the investigated ecosystems are at least partly linked to mangrove clearance, which are largely resulting from the loss of biological functions due to the alteration of physical and biological processes commonly associated with mangrove forests (e.g. Granek & Ruttenberg, 2008; Alfaro, 2010; Ellegaard *et al.*, 2014). It is well known that benthic fauna are highly dependent on the sedimentary biotopes. Sediment type and organic matter may influence meiofauna, especially nematode assemblages, 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), while grain size and percentage of TOC may influence both meio-and macrofauna. The availability of leaf litter provides enhanced resource availability, but it may also increase the amount of toxic material such as tannins which adversely affect macrofaunal communities by decreasing their taxa richness. Although temperature, salinity and temperature were not measured in this study, it is expected that sediment in the cleared mangrove would have higher temperature and salinity as a result of the higher evaporation rate than in the intact mangrove. Both temperature and salinity may be strongly related to pattern in the benthic communities; salinity in particular acts as a limiting factor in the distribution of living organisms and its variation caused by dilution and evaporation is likely to influence the distribution of macrofauna by reducing their diversity and composition (Sasekumar, 1994). The spatial variation in meiofauna or nematode assemblages on the other hand may also be linked to salinity. Changes in meiofauna community structure relating to salinity in tropical mangroves has been reported by Somerfield *et al.* (1998) and Alongi (1987b). However, the influence of some other factors such as temperature and granulometry (e.g. Xuan Quang *et al*., 2013) can override the effect of salinity (Austen & Warwick, 1989). Micro-algal biomass may increase, when mangroves are cleared, possibly as a result of change in temperature and light intensity (Granek & Ruttenberg, 2008). This impact was not actually quantified in this study; however, the presence of micro-algal mats was observed in the cleared mangrove, but not in the intact mangrove. In terms of benthic fauna, mangrove clearance has caused remarkable changes in the standing stock of macrofauna and nematode. In agreement with Alfaro (2010) and Sweetman *et al.* (2010), the study also suggest that community structure of benthic fauna, sediment characteristics, and carbon dynamics in the habitats where mangroves have been cleared can remain fundamentally different from intact mangrove and the bare sand flat until at least 5 years after clearance.

6.1.2. Benthic fauna as bioindicator of mangrove disturbance

Benthic invertebrates are useful bioindicators, providing a more accurate understanding of changing aquatic conditions than chemical and microbiological data (Ravera, 1998; Vaghela *et al.*, 2010). Therefore, they are used in monitoring to determine whether the community is changing over time due to natural- or human-caused impacts. Their community characteristics such as abundance, biomass, richness, diversity, evenness, and community composition in aquatic ecosystems can be influenced due to anthropogenic disturbances (e.g. Schrijvers *et al.*, 1995; Gray, 2000; Geetanjali *et al.*, 2001; Simboura & Zenetos, 2002; Schratzberger *et al.*, 2004a; Ikomi *et al.*, 2005; Steyaert *et al.*, 2007; Cannicci *et al.*, 2009; Semprucci *et al.*, 2010; Vaghela *et al.*, 2010; Alves *et al.*, 2013). In our study, the differences in the patterns of benthic fauna between the cleared and intact mangroves, as assessed by different multivariate analyses and diversity indices, suggest the usefulness of the benthic fauna as a potential tool to study the effect of disturbance on mangroves in Sudan. Removal of mangrove trees resulted in a decreased amount of leaf litter and an increase in the availability of other food sources for macro- and meiofauna, such as microalgae (Granek & Ruttenberg, 2008). This caused a shift in the trophic composition which is a good indicator for changes in ecosystem functions. For example as shown in (**Chapter 2**), Ocypodidae (decapods) had similar $\delta^{13}C$ signature in the cleared and intact mangrove indicating that they feed on the same food sources in both sites. Their abundance, however, was higher in the cleared mangrove which may indicate that there was a higher quantity of food available for them in the cleared than in the intact mangrove. On the other hand, the Nereididae (polychaete) showed more enriched $\delta^{13}C$ as well as higher abundances in the cleared mangrove than in the intact mangrove, signifying a shift in their role as primarily substrate feeders (bacteria and detritus) in the intact mangrove to more enriched food sources (probably benthic microalgae) in the cleared mangrove (Amaral *et al.*, 2009; Geist *et al.*, 2011). An interesting observation is that the isotopic signature of Diogenidae (decapods) in the intact mangrove showed more depleted $\delta^{13}C$ values in the mid-water station (-16.7‰) and more enriched $\delta^{13}C$ values in the low water station (-15.0‰). However, in the cleared mangrove Diogenidae were only found in the low water with individuals having a $\delta^{13}C$ value similar to those in low water of the intact mangrove (-14.4‰ and 4.3‰). This may indicate that the disappearance of Diogenidae in the mid water locations at the cleared mangrove is related to low availability of food as a result of mangrove clearance.

6.1.3. *Impact of clearance on mangrove ecosystem functioning*

Mangrove ecosystems provide a wide range of ecological services that are widely recognized (e.g. Rönnbäck, 1999; Kathiresan & Bingham, 2001; Kathiresan, 2012; Lee *et al.*, 2014). They are known as highly productive intertidal forests (Borges *et al.*, 2003; Dittmar *et al.*, 2006; Alongi, 2007; Bouillon *et al.*, 2008; Kristensen *et al.*, 2008; Donato *et al.*, 2011) that provide a feeding and foraging habitat for a wide range of fauna. The litter from trees, the subsurface root growth, and probably a range of other sources, such as autochthonous production by benthic or epiphytic micro-/macroalgae and phytoplankton provide significant inputs of organic carbon to mangrove sediments (Bouillon *et al.*, 2004a; Kristensen, 2007). The plant material that is not exported by tidal action enters the local sediment and significantly contributes to the sedimentary organic carbon after being decomposed (Kristensen *et al.*, 2008). The spatial distribution of nutrients as such is controlled by external and internal loadings, whereas vertical distribution is largely driven by the in situ microbial activities (Prasad *et al.*, 2008). Moreover, mangroves enhance sediment accretion by damping currents, attenuating waves and altering patterns of water flow. The structure of mangrove trees, especially the presence of the aerial roots, reduces the water velocity and encourages the settling of fine silts, clays and organic-rich sediments, which are either transported into the system or produced in situ from the mangrove plants (Furukawa *et al.*, 1997).

Given that most of the above mentioned ecological roles have not yet been sufficiently studied in the Sudanese mangroves, many services including their function as a feeding ground and habitat for a variety of terrestrial and benthic marine fauna, have been hypothetically ascribed to Sudanese mangroves. In the arid Red Sea region, there is no permanent flow of fresh water to the sea. The leaf litter and detritus brought to the marine ecosystem by tidal flushing of coastal mangrove areas, where these exist, is the only source of nutrients from the terrestrial zone during the dry season. This further magnifies the role of mangroves in the marine food web. In Sudan, such a role is considered to be a crucial function of the narrow mangrove fringe found along parts of the Red Sea coast (Wilkie, 1995).

Benthic macrofauna and meiofauna are important components of mangrove ecosystems because of their role in the recycling of the organic matter within the mangrove ecosystem. The number and composition of these faunal components play a crucial role in the functioning of a system (e.g., Hooper *et al.*, 2005), while trophic structure is one of the factors that drives the functioning of benthos in an ecosystem. Our study gave an insight into the trophic and benthic community structure in Sudanese mangroves (**Chapter 3 and 4)**. Mangrove ecosystems have detritus-based food webs, based on decaying plant tissue, and the direct consumption of mangrove litter by few taxa appear to be an exception. In general, mangrove-derived material contribute to complex food webs and important energy transfers by making a localized contribution to the food web, with little exportation of organic matter to adjacent habitats (Meziane &Tsuchiya, 2002; Kieckbusch *et al.*, 2004; Alfaro *et al.*, 2006), through the direct utilization of mangrove detritus by benthic fauna. The Sudanese mangroves are not different and have also detritus-based food webs, based on decaying plant tissue (leaf litter and coarse woody debris). Overall, a complex benthic food web consisting of four trophic levels of consumers with predominance of sub-surface deposit feeders, basically detritivores and scavengers, is found in the intact mangrove (**chapter 3 and 4**). To investigate the effect of mangrove clearance at higher trophic level, a study on fish community associated with mangroves and other intertidal habitats was among the initial aims of this research, but due to some logistic and time limitations the proposed study did not take place within the framework of this study as planned. However, other studies (e.g. El Hag, 1978; Brandford, 1980; Khalil, 1994; Khalil & Krupp, 1994) suggest that Sudanese mangroves may also have strong trophic linkages with adjacent habitats, by serving as feeding ground and nursery habitat for a number of epibenthic invertebrates and juvenile fish. These species, especially detritivorous fishes and their juveniles, may feed directly on a protein-rich detritus built up by microorganisms in the decomposing organic matter (Rajendran & Kathiresan, 2004, 2007), on benthic microalgae growing in the mangal, and/or indirectly on other small detritivorous invertebrates (Newell *et al.*, 1995; Kathiresan, 2012). Mangrove litter is found to be the most important contributor to the diet of *Leiognathus equulus* in Australian wet-dry tropical estuarine mangroves, where freshwater inflow is intermittent (Abrantes *et al.*, 2014). This species is one of the most dominant fish species that are closely associated with mangroves in Sudan, suggesting that Sudanese mangroves may also contribute significantly to the diet of this species.

Several studies confirmed that mangroves are important, serving as an intermediate nursery habitat, by providing food and shelter that may increase the survivorship of young fish. They strongly influence the community structure of fish on neighbouring seagrass and coral reefs, and increase the abundance and biomass of several commercially important species (e.g. Nagelkerken *et al.*, 2000a, 2001; Dorenbosch *et al.*, 2004, 2007; Mumby *et al.*, 2004; Verweij *et al.*, 2006; Shibuno*et al.*, 2008; Unsworth *et al.*, 2008; Vaslet *et al.*, 2010). This indicates that there is strong connectivity between mangroves and the adjacent habitats such as seagrass beds mainly through trophic linkages (Kathiresan, 2014; Lee *et al.*, 2014). For example, **Chapter 3** of this study demonstrates that motile macrofauna (decapod crab) from the intact mangrove showed $\delta^{15}N$ values that ranged between 2.95‰ and 11.55‰, occupying different trophic niches (four trophic levels; Bouillon *et al.*, 2002a) indicating that they probably feed on detritus, microphytobenthos, macroalgae, or on other fauna (Meziane *et al.*, 2002; Bouillon *et al.*, 2004b). Some of these crabs (e.g. swimming crabs: Leucosiidae), on the other hand, showed enriched $\delta^{13}C$ values of -11‰, typical for macrofauna from the adjacent seagrass habitats, indicating an interaction or connectivity between mangroves and their adjacent habitats. These species probably use the mangroves only as a refuge and feed on food items from the adjacent habitats.

The ecological functions of mangroves as habitat for specific benthic fauna, as supported by our results, have been substantially impaired by the loss of mangrove trees. When mangroves are cleared, it results in a shift towards a simpler food web consisting mainly of surface-feeders such as grazers (e.g. polychaetes) and scrapers in addition to some opportunistic feeders which are highly adaptable to changing food availability. The cleared mangrove is also characterized by the loss of the trophically basic species that are energetically linking the mangrove production to many other species in the food web. Thus, removal of mangrove result in the loss of the base of the food web (leaf litter) and loss of species at lower trophic level, which will consequently lead to the rapid loss of species at higher trophic level. This is particularly important in terms of fish populations especially of the species that depend directly on mangrove habitats. Although fish communities were not studied within the context of this PhD, it is likely that clearance will reduce the abundance, species diversity and the trophic diversity of the detritus and benthic-crustacean feeders, while the abundance of the zooplankton feeders is likely to increase (Shinnaka *et al.*, 2007). Eventually, the affected mangrove system will remain inhospitable to juvenile fishes.

Mangroves also serve as fine sediment trapper and prevent soil erosion. This process helps in the supply of clean and nutrient-rich water for the adjacent ecosystems such as coral reefs, seaweeds and seagrass beds upon which many of the living marine resources depend (Kathiresan, 2012). The removal of mangroves increases the silt deposition in the seaward areas indicating that sediment becomes loose and that fine particles are remobilized and taken further towards the adjacent habitats and may in long term lead to degradation of these habitats.

The pathways of mangrove leaf litter in the benthic food web, as shown by our study, and the utilization of leaf litter as suggested by El Hag (1978) and Khalil (1994) is shown in a schematic diagram in Figure 6.1.

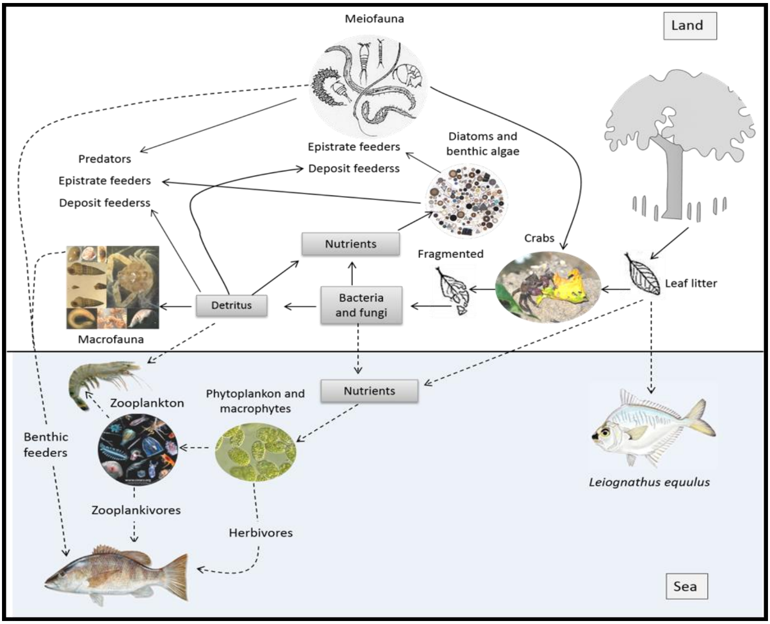


Figure 6.1. Schematic diagram showing the pathways of mangrove leaf litter in mangrove sediment (based on this study (solid lines) which support mangrove benthic food web and the speculated pathways (dotted lines) of the leaf based on other studies in Red Sea (El Hag, 1978; khalil, 1994) and other mangrove areas (e.g. Abrantes *et al.*, 2014) which may potentially support the aquatic (low-water) detritus based food web through some degree of carbon export, pelagic, mixed detritus.

6.2. Mangrove distribution along the Sudanese coast

6.2.1. Mangrove Mapping

The temporal distribution of mangroves along the Sudanese coast was assessed during the period of 1984-2013 based on remote sensing and Geographic Information Systems (GIS) techniques, using multi-temporal Landsat imagery and semi-supervised classification of the land cover classes by the Spectral Angle Mapper (SAM) technique. Remote sensing and GIS have been globally used as a technique to map mangroves (e.g. Giri *et al.*, 2011; Fatoyinbo & Simard, 2013). The pixel-based approach on the other hand uses pixels as the fundamental unit of information. Analysis of the spectral signatures of reflectance enables to evaluate the spectral differentiation of different land cover categories based on the patterns of various spectral signatures of different classes in an optical image. It allows to distinguish vegetation due to its unique spectral signature. Various heterogeneous patches, distinctly relevant to the various land cover classes, were visually identifiable in the false color composite images. Chlorophyll contents in mangroves reflect high in the Near Infra-Red (NIR) band and low in the red and green region of the electromagnetic spectrum (Carter & Miller, 1994; Carter & Knapp, 2001). Hence, mangroves could be distinguished from other land cover types by bright or deep red color pixels, if they are densely distributed, or brown, yellow and lighter red, if sparsely distributed. In contrast, water bodies show the lowest reflectance in the NIR band and higher reflectance in the visible bands. Other features like built-up land, mudflats, and sandy areas give lower reflectance in the NIR band and a greater reflectance in the green band. It is likely that the classification method used in this study has created a type of error most probably due to brightness of the soil caused by the aridity of the area. These errors can be linked to: (i) small patches of mangroves that were indicated in the classified map but were not identified neither on the composite image nor on Google Earth; (ii) small patches of mangroves that had been overlooked in the composite image or Google Earth and that are not indicated on the classified map; or (iii) isolated pixels in land or water where mangroves are unlikely to be present. These types of error can impair the classification accuracy causing an under/over estimation of the extent of the mangroves especially because the mangrove distribution estimated in this study was limited by the lack of ground truth data. It is also possible that there was a difficulty in distinguishing fine ecological divisions between certain vegetation classes in some areas, e.g. the border between mangroves and its adjacent salt marshes. Therefore, the results of this study needs to be considered as a preliminary estimation of mangrove distribution and possible change over time. It is still possible to map these mangroves using remote sensed data for monitoring purposes; however, for management purpose it is recommended that the estimated area should be validated by collecting adequate ground truth data to confirm the observed remote sensing based patterns.

Mangroves along the Sudanese coast are characterized by a uniform type of evergreen trees with habitats being associated with creeks, coastal lagoons and khor inlets. They are found as small areas or as narrow and elongated strips along the coastline and include communities that grow on soft-bottom and hard bottomed substrates, with the latter being more prevalent. Although three other mangrove species are known in the Red Sea costal area, only *A. marina*, which can grow in both types of substrates and tolerate the high salinities and extreme water temperature associated with this region, is found in Sudan. This is a typical characteristic of mangroves found at the latitudinal limits of naturally occurring mangrove ecosystems (Körner & Paulsen, 2004; Quisthoudt, 2013) as found along the Red Sea (27-28°N). Based on ecological features and the extent and distribution of mangrove stands, the coastal area in Sudan may be divided into three stretches:

(i) the northern part which includes the coastal area from the Egyptian border in the north to Port Sudan in the south;
(ii) the central part including the coastal area from Port Sudan in the north to Suakin town in the south, and
(iii) the southern part which includes the coastal area between Suakin and the Eritrean borders in the South.

Based on our estimations, the areal extent of Sudanese mangroves was highly variable during the study period of 1984-2013. Mangroves had the lowest areal extent of 329 ha in 2000 and the highest extent of 721 ha in 2010. The total area of individual mangrove stands in 2013 ranged from 0.4 to 203.5 ha (Fig. 6.2).

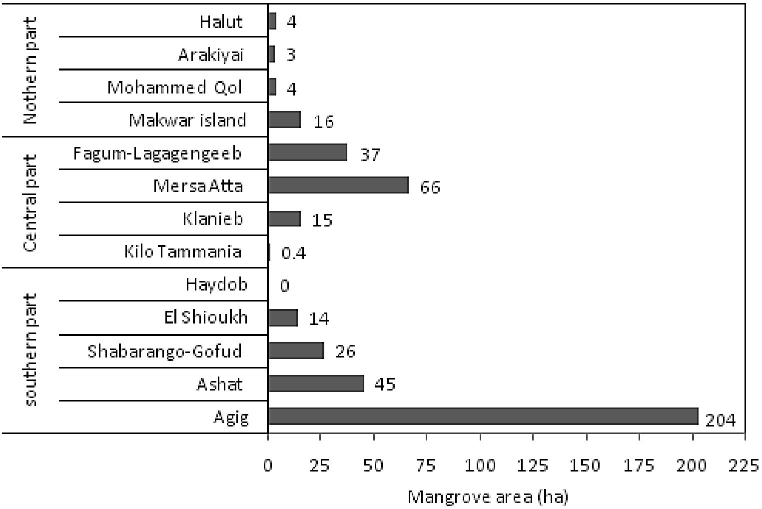


Figure 6.2. Areal distribution (ha) of mangroves along the Sudanese Red Sea coast (from north to south) in the year 2013 as estimated by this study.

The acceleration in fragmentation of mangroves occurred during the period 2000-2005, followed by a gradual deceleration in fragmentation during the period 2005-2013. In general, the change in the pattern of mangrove distribution in Sudan might be partly attributed to climatic (weather) changes. The spatial relationships between mangrove distribution and climate, especially the influence of precipitation and temperature, are well known (Duke *et al.*, 1998). However, the combination of the aridity and temperature (Quisthoudt *et al.*, 2012) as well as the combination of a number of other factors including salinity, the lack of geomorphologic suitability and tidal inundation (Quisthoudt, 2013) may explain the spatial distribution of mangroves along the Sudanese coast. However, change in mangrove distribution might also be attributed to human activities.

6.2.2. Change detection case study

Since we assumed that in addition to climate effects, change in the distribution of mangroves was also caused by human activities, we compared the temporal extent of mangroves in two selected sites representing human impacted and non-impacted mangroves. Our results suggest that catastrophic events such as El Niño can cause mass destruction of mangroves within short periods. The non-impacted mangrove at Mersa Ashat was reduced by 45% (29 ha) during 1995-2000. The partial recovery of these mangroves, showing 46% increase in area (16 ha) during 2000-2005, provides evidence that even after such devastating effect, mangroves are able to regenerate naturally if anthropogenic activities are kept to a minimum. On the other hand, the growth of mangroves at the impacted site seemed to be promoted by the construction of a salt pan and shrimp farm, possibly due to reduction in salt accumulation and most probably by the enrichment of the water with nutrients from farm effluents.

As indicated earlier, the low nutrient availability due the lack of perpetual rivers in the Red sea, may have contributed to limit the growth of mangroves in the region. Mangroves in the southern USA have been shown to suffer both N and P limitation when experimentally exposed to low nutrient conditions (Lin *&* Sternberg, 1992; Koch, 1997; Feller *et al.*, 2003b). Similarly, both the growth of trees and seedling establishment process in mangroves in Bocas del Toro, Panama, were found to be limited by the same factors (Lovelock *et al.*, 2004). This analysis showed that N has consistent advantage on *Avicennia* growth while P tends to be more dynamic i.e. early development of mangroves are driven by N availability, while P roles in stimulating growth of leaves and branches (Kathirean & Bingham, 2001). In Belize, both N and P limitation were observed, depending on the location within the forest (Feller *et al.*, 2003a). Nitrogen has been observed as the nutrient that limits the growth of mangroves most frequently in the Indo-Pacific and the African continent (Lovelock *et al.*, 2007a), and the growth of *A. marina* in South Africa (Naidoo, 2009) and New Zealand (Lovelock *et al.*, 2007b). As summarized above, nutrient additions can stimulate mangrove growth and the nutrient enrichment from the shrimp farm effluent can be beneficial for mangrove growth and ecosystem health (Trott *&* Alongi, 2000). This potentially means that not all human activities, in the short run, are destructive to mangroves. However, evidence is mounting that in the long run, eutrophication can also have negative consequences for mangrove growth. Therefore, the benefits of pond based aquaculture could be balanced with the benefits of mangrove preservation by taking into account the different elements of the productivity of mangrove-estuarine ecosystems, in addition to the negative effects of shrimp farming. Therefore, for effective mangrove management, further site specific research to determine the direct effects of shrimp farming on mangroves is needed.

6.3. The DPSIR framework

Management of mangrove ecosystems has highlighted the need for resource management with a holistic perspective. For this to take place, multidisciplinary approaches are required for the description of environmental problems by establishing a connection between ecological data on one hand and the needs of decision-making environmental managers on the other (Maxim *et al.*, 2009). The DPSIR (Drivers-Pressures-State-Impact-Responses) framework is one of these approaches, which provides a heuristic framework for the analysis of cause-effect relationships in complex systems which are subject to human action (Brandt, 2000). The general idea behind the DPSIR concept is that the **Driving** forces, which are the human activities, exert a certain **Pressure** on the natural resources, leaving it in a certain **State**. This will create a certain environmental **Impact**, which usually require societal reaction and **Responses** to those changes. The response, which is usually in form of regulatory laws or rehabilitation plans, depending on the situation in hand (Bidone & Lacerdo, 2004; Maxim *et al.*, 2009; Omann *et al.*, 2009; Atkins *et al.*, 2011), can run across different segments of the society including the political sphere, but also socio-economic, and purely economic sectors (Mateus & Campuzano, 2008). The DPSIR frame therefore allows managers and scientists to highlight issues that must be prioritized with regard to management of natural systems.

The DPSIR framework was used here to explore its utility with regards to two issues relevant to the Sudanese mangroves (Fig. 6.3): firstly to examine the effect of the specific pressure (i.e. mangrove clearance) on mangroves as based on our study; and secondly, the effect of other potential pressures in the area defined by several other studies (e.g. Mohammed, 1984; Abu Bakr, 1995; Elhag & Abdel Gadir, 1998; Abdel Latif, 1993; Suga, 1999; Wiktelius *et al.*, 2003; Karrar, 2003, 2011; PRESGA, 2004).

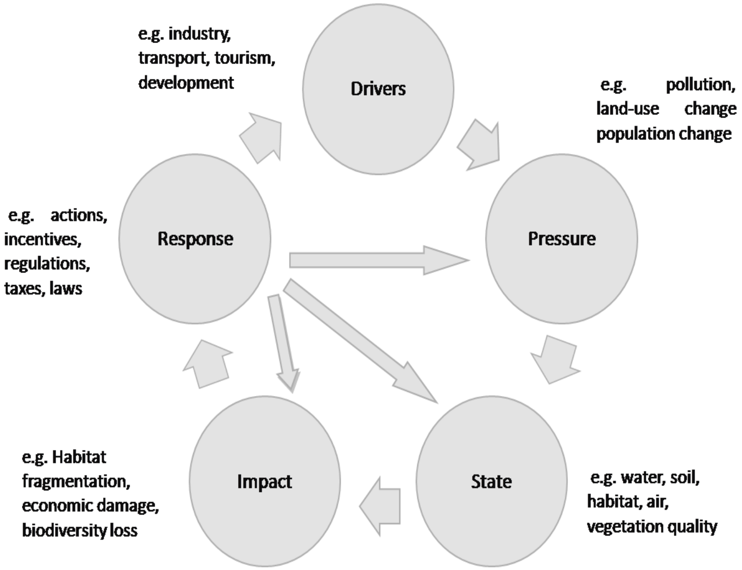


Figure 6.3. The DPSIR assessment framework

The **driving forces** of the change, degradation or loss of mangrove ecosystem and services in Sudan can be natural or anthropogenic. The direct drivers for change include climate change, external inputs and change in land use and land cover. In general, there are some indications that a number of ecological changes experienced in the Red Sea region during the last decades are probably linked to climate change. With regards to the Sudanese mangroves, the increased frequency and duration of drought episodes such as during the 1998 El Niño is the major driver for the changes.

Mangroves along the Sudanese Red Sea coast may also been affected by land use/land cover change, which can result in severe negative impacts on ecosystems and associated fauna and flora. Mangrove ecosystems are indeed vulnerable to various coastal development practices such as road building, construction of new ports and expansion of existing ones, such as in the Port Sudan and Suakin areas. Limited subsistence agriculture and horticulture that is practiced by some inhabitants for their livelihood along and close to the mouth of khors, where the land is flat and most of the extensive mangroves stands are found, can result in the degradation of these mangroves through the excessive use of fertilizers and pesticides. Other indirect drivers that may affect Sudanese mangroves and which emerge from human activities include demographic developments, physical alteration of the coastal area by activities such as urbanization, coastal development (e.g. building of harbors, dredge and fill operations) and industries such as salt production, mining, oil/gas exploration and production, power and desalination plants, refineries and shrimp farming. Population density of the Red Sea state has increased with a rate of +4.8% per year, from 684,271 in 1993 to 1,396,110 in 2010 (6.4 inhabitants per km²), with the majority of them being pastoralist and agro-pastoralist. More than 70% of the urban and rural communities, as well as the pastoral and agricultural activities are found in a coastal strip of 20-50 km width. This is mainly due to the harshness of the physical environment in the Red Sea State, which has had a direct influence on the distribution pattern of the population and the adopted transhumance (Babiker & Pantuliano, 2006).

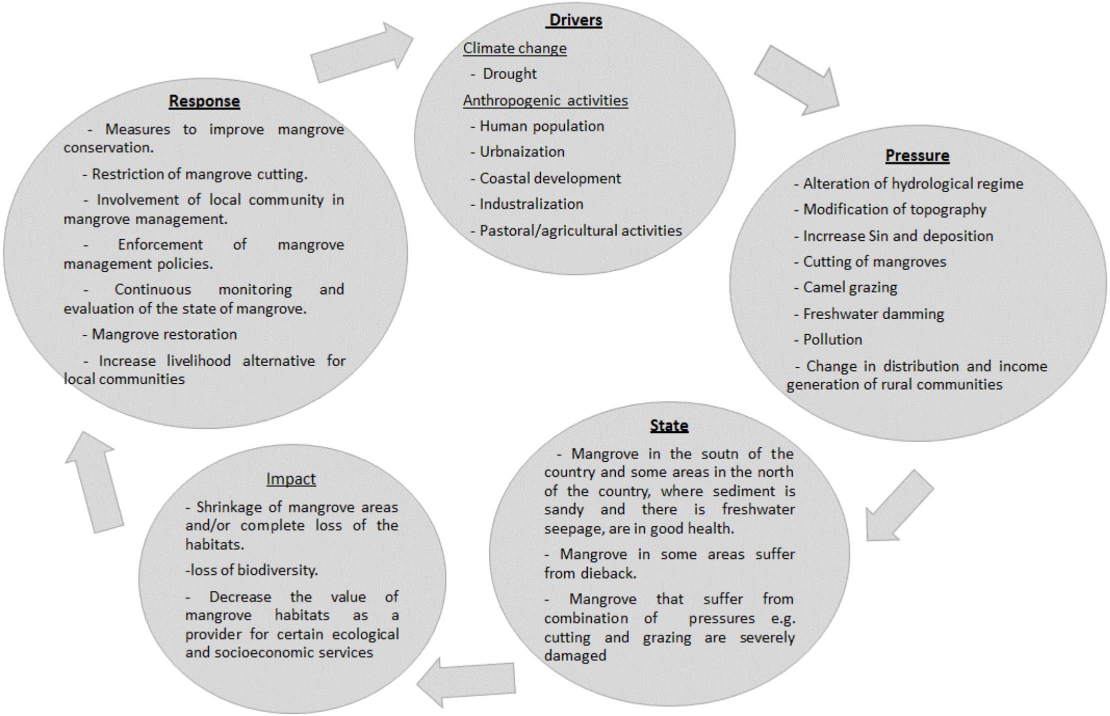
The climate change and the disastrous effect of the prolonged period of drought during mid-1980s and the subsequent effect of 1998 El Niño caused a serious **pressure** on mangrove areas. This resulted in a reduced amount of run-off reaching the mangrove area, increased sand deposition in the khors' channels and mouths and alteration of the hydrological regime. Climate change has also a profound effect on infrastructure and social systems, by influencing the income of rural and urban communities since most of them are pastoralist and agro-pastoralist. This generates another pressure on mangroves, especially from rural communities that live in a close proximity to mangroves. Cutting and removal of the mangroves, and camel grazing were reported to increase in the country (Karrar, 2011) most probably as a consequence of land and heritage loss, the decline in ecosystem services (e.g. agriculture and fisheries), property rights issues, and change in general socioeconomic patterns in the coastal zone (PRESGA). For example, land degradation and the urban demand for fuel has generated an increase in the price of firewood and charcoal and as a consequence more people, who are engaged in other livelihood practice such as pastoralization, have been attracted to this activity. Practices that related to coastal land uses such as freshwater damming to compensate for the decrease in water supply, and land filling and dredging, which is usually carried out in near-shore and shallow coastal waters, are increasing in the area too. Pollution caused by effluents from industrial activities, oil waste, organic pollutants, heavy metals, heated brine and cooling water, discharge of untreated domestic and shrimp farm waste sewage, and the extensive use of pesticides, insecticides and herbicides for agricultural purposes mainly at Delta Tokar at the southern coast (Abu Bakr, 1995, Elhag & Abdel Gadir, 1998; Wiktelius *et al.*, 2003) also represent potential threats to mangroves.

Both climate change and direct human activities left most of the mangroves in varying **state**. Most of the stands in the northern part have average mangrove tree height ranging from 2.0 to 8.0 m, while in the central and southern parts it ranges from 0.35 to 7.0 m and 0.6 to 9.0 m, respectively. The Girth at Breast

Height (GBH) ranges from 10.0 to 125.0 cm in the north, 5.0 to 80.0 cm in the central part, and 5.0 to 195.0 cm in the south. Mass mortality, top dying, and loss and wholesale destruction of mangroves have been recorded in a number of mangrove stands due to clearing or coastal industrial development (PRESGA, 2004). The remaining mangrove stands vary in their status between degraded and fragmented to relatively good state, depending on the type and intensity of pressure they face. Especially mangrove stands in the southern part of the country and some stands in the northern and central parts are dense and considered of a good state due to the minimal pressure they received. In areas where severe cutting or where a combination of overgrazing and over-cutting is observed (e.g. Mersa Hydob), mangroves are severely degraded. In stands suffering from grazing, cutting, and felling, especially those which are easily accessible from land (e.g. Kilo-Tammania, Shiokh and Halout), mangroves are lightly to moderately degraded (e.g. Abdel Latif, 1993; Suga, 1999). The combined effect of natural and human activities may eventually result in complete degradation or extinction of mangroves (e.g. the outer belt of mangrove at Mersa Ashat, Karrar; 2003). The degradation of mangroves is attributed to the modification of hydrological regimes, increased intrusion of saltwater leading to hypersaline habitats unfavourable for mangrove growth, increased sand infilling and deposition of sand from the sea obstructing tidal inlets and channels through which tidal flow regularly floods the mangrove forests. However, apparently good natural regeneration in most of the stands is taking place, since a considerable number of healthy seedlings are observed growing in the inner fringes and some denuded areas of most of the mangrove stands (PRESGA, 2004).

The above discussed pressures can have a profound **impact** on the physical environment, the mangrove community, the associated flora and fauna, and subsequently on the nearby communities who depend on mangroves in their livelihood. The overall impact on mangroves is the considerable loss of the habitat and overall degradation and fragmentation. Drought may have already impacted Sudanese mangroves by reducing their abundance and development. In many stands, cutting and felling can affect the forest by decreasing the number of trees, limiting the tree growth to stunted multi-stemmed bushes, and increasing the denuded patches within mangrove forests, while over-grazing can affect mangrove forests by reducing the green parts of trees and dryness of the uppermost and outermost parts of the grazed branches. In areas where the effect of these practices are severe, vegetation cover is reduced and mangroves become very sparse or even disappeared. The increase in the level of organic carbon in domestic and shrimp farm sewage may promote the growth of mangroves, but in the long run reduces soil redox potential and may, therefore, lead to retardation of mangrove growth causing additional stress on mangroves and their associated fauna. The unsustainable use and the destructive practices have resulted in loss and degradation of mangrove habitat in the Sudanese coast, reducing their ability to provide their key ecological services as a habitat provider for associated faunal communities and threatening biodiversity (**Chapter 3-5**). Mangrove habitats are tightly interlinked to the other marine habitats, so that the loss of one habitat can have flow-on effects that degrade and reduce the services provided by these linked habitats. In Sudan, mangroves provide permanent or temporary feeding habitats and nursery areas for a number of fish from adjacent seagrass bed and coral reefs (Khalil, 1994), suggesting that the removal of these mangroves can interrupt these linkages and cause biodiversity loss and lower productivity in reef and seagrass habitats.

The degradation of the Sudanese mangroves and the demand for their services highlight the need for a local, **response**. A range of options exists to respond to the challenges that the degradation of ecosystems is posing (for example, implementation of regional and global agreements or stakeholder participation and capacity development). Addressing uncertainties such as basic knowledge of biodiversity and ecosystem processes, and elaborating trade-offs among uses of ecosystem services. In Sudan, mangroves are protected under numerous environmentally related laws, legislations and regulations including the Sudan Environmental Protection Act 2001, the Environmental Public Health 1975, the Regulations for the protection of the Environment 2007 (amended 2005), the Wildlife Protection and National Parks Act. 1986, and the Forests and Renewable Natural Resources Act 1989 (amended 2002). However, despite these numerous laws for mangrove protection, enforcement has been virtually absent, and mangrove destruction still occurs widely.



Drivers

Climate change
- Drought

Anthropogenic activities
- Human population
- Urbnaization
- Coastal development
- Industralization
- Pastoral/agricultural activities

Pressure
- Alteration of hydrological regime
- Modification of topography
- Incrrease Sin and deposition
- Cutting of mangroves
- Camel grazing
- Freshwater damming
- Pollution
- Change in distribution and income generation of rural communities

State
- Mangrove in the soutn of the country and some areas in the north of the country, where sediment is sandy and there is freshwater seepage, are in good health.
- Mangrove in some areas suffer from dieback.
- Mangrove that suffer from combination of pressures e.g. cutting and grazing are severely damaged

Impact
- Shrinkage of mangrove areas and/or complete loss of the habitats.
- loss of biodiversity.
- Decrease the value of mangrove habitats as a provider for certain ecological and socioeconomic services

Response
- Measures to improve mangrove conservation.
- Restriction of mangrove cutting.
- Involvement of local community in mangrove management.
- Enforcement of mangrove management policies.
- Continuous monitoring and evaluation of the state of mangrove.
- Mangrove restoration
- Increase livelihood alternative for local communities

Figure 6.4. Summary of DPSIR framework for the mangrove forests along the Sudanese Red Sea coast.

6.4. Management of mangroves in Sudan

Mangrove management and conservation in Sudan is limited by the lack of basic knowledge on their extent, their status and the linkages to other ecosystems. The lack of integrated planning and management resulted from uncontrolled expansion and development of coastal areas, in addition to the lack of understanding of certain ecological processes, such as El Niño/Southern Oscillation and marine biodiversity in general. According to Macintosh and Ashton (2002) a comprehensive information database on mangroves in each country is necessary to monitor their status, and realize its economic potential. Economic arguments carry the greatest weight in conservation and management of mangroves (Macintosh & Ashton, 2002). However, the true economic value of mangrove diversity and natural resources is difficult to measure, and important ecological processes and functions are undervalued. The importance of mangroves in Sudan is not recognized by the current policies, knowing that these policies are also weak or widely lacking. The existing policies and legislations still lack consistent implementation and enforcement because funding, political will, and human resources are lacking. In fact the destruction of mangrove areas in Sudan can be directly attributed to policy failure. Mangroves, according to legislation, belong to the state property regime which is responsible for their guarding and protecting their areas. However, they become open-access to anyone who wishes to encroach upon them. An example is provided by the commercial shrimp farming which has been recently started in Sudan. Because shrimp farming has high market value compared to mangrove ecosystem, the governmental policy tends to be prejudiced or biased towards the promotion of shrimp culture. Thus, the economic value of shrimp farming is usually overestimated and the total economic value of mangrove is underestimated, while estimation of the social cost and benefits from its environmental services are often neglected. The result is that more and more shrimp farms are proposed and planned to be established in close proximity to mangrove areas. Our finding from the change detection study (**Chapter 2**) suggests that shrimp farming by itself do not pose any environmental threat, given that certain measures for treatment of the effluent from the farm before release into mangrove areas are adopted. It becomes a problem when mangrove trees are cleared for establishing these farms.

In the long-term, destruction and degradation of mangroves will seriously affect marine fisheries, increase coastal erosion and the impacts of the sea on land, and lead to degradation of adjacent habitats (coral reefs, seagrass beds) upon which many of the living marine resources depend. Such losses are far greater, in the long run, than any profits to be gained from commercial and industrial projects causing mangrove degradation. Therefore, before policy can be appropriately designed, it is necessary to correctly assess the foregone benefits of mangroves and compare them with the actual returns from other land use activities. The economic valuation of the mangrove should include the estimation of the direct use value based on local use (e.g. timber, fuelwood, wood, birds, crabs), which can be estimated from the net income generated by the locals; the indirect use value determined by the contribution of resources in terms of their environmental and ecological services to support current production and consumption (e.g. support to off-shore fishery, serving as a nursery ground, coastline protection and stabilization, carbon sequestration, erosion control), non-use value (tourism, recreation, education, and research), and benefit analysis of alternative land uses such as shrimp farming.

6.5. Conclusion

Mangroves along the Sudanese coast are located in an area characterised by an arid climate, at the northern limits of their geographical ranges. They are overall in relatively good health with only isolated degraded sites (UNEP, 2007). However, as Sudanese mangroves are predominantly small, thin,and growing in a very harsh environment, any additional natural pressure or human interference, such as clear cutting or changes in land use in the surrounding coastal areas, form a significant threat. Such interference will ultimately create changes in the coastal environment that will affect mangroves and other natural coastal habitats. Some land use activities such as shrimp farming can be beneficial for Sudanese mangroves by increasing their areal distribution as a result of enriching the surrounding water with nutrients from farm effluent. However, restricted measures for the treatment of the effluent to minimize the nutrient load before release to the mangrove must be adopted. Mangrove ecosystems in Sudan are dynamic and spatially variable in their environmental conditions on a small scale. Clear differences in benthic macro- and meio-fauna attributes was observed between habitats. Mangrove associated benthic fauna is naturally adapted to survive in these conditions especially with the variability in food availability. However, mangrove clearance may cause fundamental changes to these habitats, and forms a threat to these communities by changing their structural and functional attributes as a result of the loss of biodiversity and trophic linkages within the mangrove. These changes are linked to changes in sediment characteristics as a result of removal of trees. Since these mangroves are fragile and very sensitive, they might not recover from changes. This was shown by our study, where after several years since mangrove trees had been cleared, still there is a pronounced difference in sediment and fauna characteristics. In fact, the cleared mangrove site had characteristics more or less similar to those observed in the bare sand flat signifying its gradually evolvement towards becoming a bare sand flat. The observed differences in benthic communities between vegetated and non-vegetated habitats, such as the higher abundance of decapods crab (e.g. grapsidae) and gastropods (macrofauna), copepdes and acarina (meiofauna), and the nematode genera *Onchium*, *Terschellingia*, *Haliplectus*, *Spirina* in the intact mangrove, which are considered typical organisms for mangrove systems, suggest their potential use as a tool to study human impact on mangrove ecosystems. They may also be applied to identify the effects of other driving forces partly emerging from human activities acting on mangroves such as climate change and pollution.

6.6. Future research

To understand the impact of mangrove clearance, any future study should make the following considerations:

i. The result from mangrove mapping can be improved by exploring other available algorithms such as maximum likelihood, by using a combination of pixel-and object base approaches, or by exploring other classification methods such as Short-wave infrared, SAR or hyper spectral data to provide more details and increase the spectral differences between mangroves and other types of vegetation.
ii. Temporal studies on sediment geochemistry and mangrove decomposition pathways, as well as in algal biomass and benthic communities, in the cleared site are needed to track changes and recovery of the cleared mangrove. This is especially crucial in order to assess the time required by these mangroves to recover from such disturbance.
iii. The study of other consequences of mangrove clearance, such as sedimentation and erosion on the adjacent costal habitats, are also needed.
iv. Since some mangrove stands suffer from multiple pressures such as cutting and grazing, any further studies should consider the combination of these stressors.
v. More shrimp farms are planned to be established in the Sudanese coast, therefore, future studies should investigate the long term effect of the effluent from shrimp farming on mangrove and evaluate the spatial relation of mangro ves with aquaculture ponds.
vi. To determine the value of intact mangroves along the Sudanese coast to fishes and the effect of mangrove removal on fish inhibiting mangroves, empirical data on both structural and trophic composition of associated fish assemblages from mangroves and adjacent undisturbed/disturbed sites are needed.
vii. Studies on the effect of mangrove and seagrass patchiness and habitat connectivity on fisheries production need to be carried out. This is of particular importance for the designation of marine protected areas or the design of networks of no-take fishing reserves. It is also, of course, of general significance for conservation of marine habitats.

7

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8

Appendices

Appendices

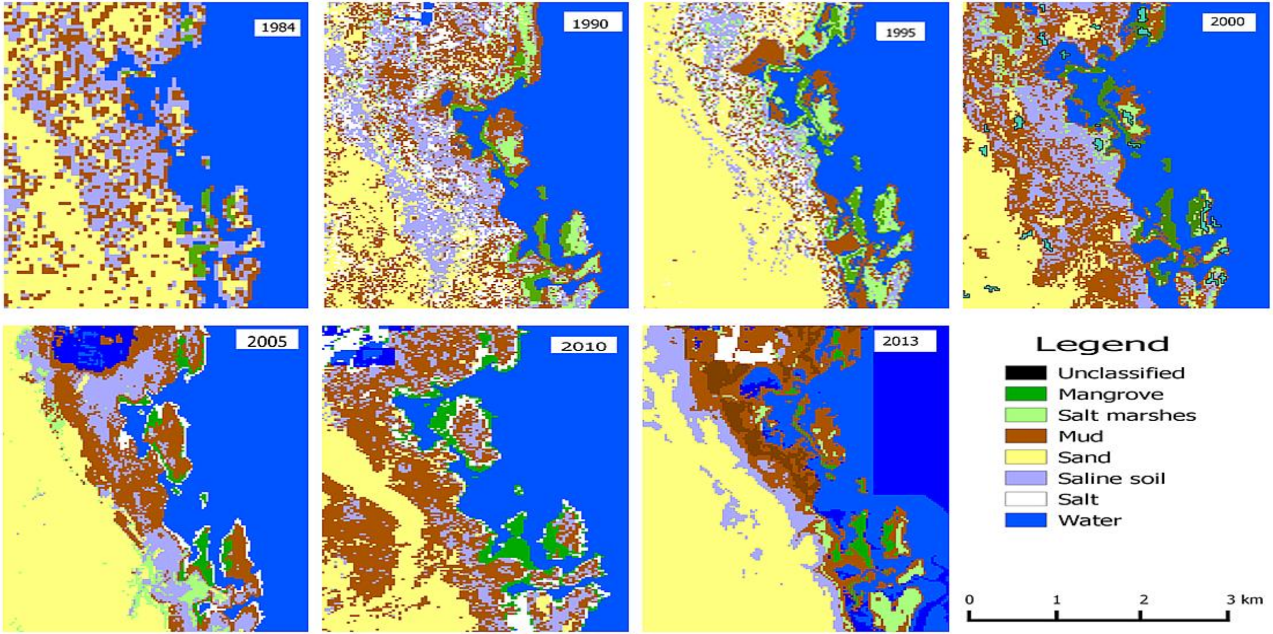
Appendix 1

Landsat imagery used to create mosaics

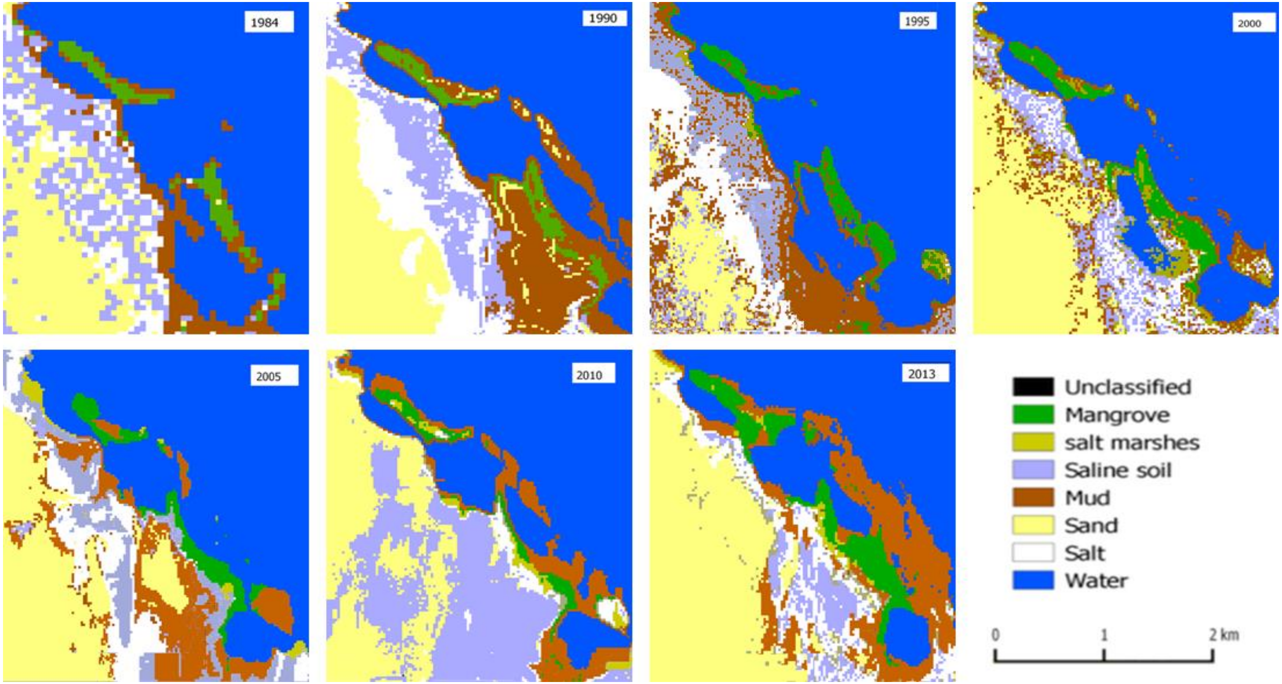
Year	Mosaic	Satellite	Date	Path/ Row
1984	MSS	Landsat 5	Jun 13, 1984	171 / 046
	MSS	Landsat 5	Jun 13, 1984	171 / 047
	MSS	Landsat 5	Jun 06, 1984	170 / 047
1990	TM	Landsat 4	Apr 03, 1990	171 / 046
	TM	Landsat 4	May 21, 1990	171 / 047
	TM	Landsat 4	Nov 06, 1990	170 / 047
1995	TM	Landsat 5	Mar 24, 1995	171 / 046
	TM	Landsat 5	Mar 24, 1995	171 / 047
	TM	Landsat 5	May 20, 1995	170 / 047
2000	ETM+	Landsat 7	Jun 17, 2000	171 / 046
	ETM+	Landsat 7	Jun 01, 2000	171 / 047
	TM	Landsat 5	Sep 22, 2000	170 / 047
2005	ETM+	Landsat 7	Sep 19, 2005	171 / 046
	ETM+	Landsat 7	Sep 19, 2005	171 / 047
	ETM+	Landsat 7	Sep 28, 2005	170 / 047
2010	ETM+	Landsat 7	Oct 03, 2010	171 / 046
	ETM+	Landsat 7	Sep 17, 2010	171 / 047
	ETM+	Landsat 7	Apr 03, 2010	170 / 047
2013	OLI	Landsat 8	Jun 29, 2013	171 / 046
	ETM+	Landsat 7	Jun 21, 2013	171 / 047
	OLI	Landsat 8	Jul 8, 2013	170 / 047

Appendix 2

(a) Classification maps for the impacted mangrove by shrimp farming at Mersa Atta



(b) Classification maps for the non-impacted mangrove at Mersa Ashat



Appendix 3

(c) Error matrices for the change analysis in the impacted mangrove site generated based onpost-classification comparison techniquesof different classified maps. Numbers denote pixels.

1984-1990: Overall accuracy 65%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	346	430	536	74	69	12	1467	50	76
Saline soil	74	1603	6829	1814	295	53	10668	66	85
Mud	86	1792	10599	3383	574	100	16534	57	36
Sand	40	556	5453	5092	208	20	11369	51	55
Shallow water	16	77	356	0	5944	2237	8630	32	31
Deep water	130	294	673	13	1689	28122	30921	8	9
Total	692	4752	24446	10376	8779	30544	79589		

1990-1995: Overall accuracy 60%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	560	0	37	0	21	7	67	692	29	19
Saline soil	2	1571	2035	0	819	1	327	4755	92	67
Mud	95	13452	5166	3302	1449	73	958	24495	49	79
Sand	11	3948	1213	4348	30	0	894	10444	43	58
Shallow water	13	21	62	0	8253	372	71	8792	37	6
Deep water	3	0	3	0	1733	29301	3	31043	2	6
Salt marshes	108	756	1546	9	782	9	793	4003	75	80
Total	232	19748	10025	7659	13066	29756	80486	84224		

1995-2000: Overall accuracy 66%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	608	15	43	9	5	14	98	792	34	23
Saline soil	2	4781	10629	3818	233	104	181	19748	44	76
Mud	103	2924	4673	837	357	230	938	10062	75	54
Sand	3	159	1658	5838	0	1	0	7659	49	24
Shallow water	81	288	676	7	10066	1873	96	13087	9	23
Deep water	42	0	14	0	244	29463	0	29763	7	1
Salt marshes	80	305	1190	918	98	92	430	3113	75	86
Total	311	8457	18840	11418	10998	31763	81787	84224		

2000-2005: Overall accuracy 55%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	460	0	25	0	22	20	14	541	50	15
Saline soil	76	386	619	68	802	238	63	2252	95	83
Mud	317	2919	3359	278	837	652	1051	9413	82	64
Sand	12	2157	8414	8469	266	59	68	19445	26	56
Shallow water	0	24	50	2	248	25	11	360	98	31
Deep water	10	45	119	7	8284	30611	36	39112	4	22
Salt marshes	44	2941	6297	2603	544	172	500	13101	71	96
Total	919	8472	18883	11427	11003	31777	1743	84224		

2005-2010: Overall accuracy 65%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	415	685	639	71	29	150	124	2113	23	80
Saline soil	6	276	3795	5130	8	242	4509	13966	88	98
Mud	100	640	932	103	206	85	213	2279	90	59
Sand	0	19	1633	12906	0	240	1873	16671	34	23
Shallow water	2	135	20	1	54	7510	0	7722	85	99
Deep water	17	343	321	0	63	30652	0	31396	22	2
Salt marshes	1	154	2073	1234	0	233	6382	10077	51	37
Total	541	2252	9413	19445	360	39112	13101	84224		

2010-2013: Overall accuracy 60%

Land-cover class	Mangrove	Saline soil	Mud	Sand	Shallow water	Deep water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	550	186	242	0	780	244	111	2113	74	26
Saline soil	34	4913	3639	3105	978	193	1104	13966	65	58
Mud	96	282	284	1	1201	247	168	2279	88	97
Sand	2	3905	2833	9671	21	19	220	16671	42	39
Shallow water	3	33	10	0	5712	1960	4	7722	26	54
Deep water	20	4	55	0	3400	27912	5	31396	11	9
Salt marshes	37	2375	3055	3030	434	61	1085	10077	89	60
Total	742	11698	10118	15807	12526	30636	2697	84224		

(d) Error matrices for the change analysis in the non-impacted mangrove site generated based on post-classification comparison techniques of different classified maps. Numbers denote pixels.

1984-1990: overall accuracy 30%

Land-cover class	Mangrove	Mud	Sand	Saline soil	Shallow water	Deep water	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	313	6	24	92	0	14	313	67	30
Salt	0	38	35	13	14	198	0	99	96
Mud	2	878	108	14	1584	1001	2	42	76
Sand	41	351	324	133	109	624	41	69	80
Saline soil	0	120	0	0	1691	29	0	51	8
Water	604	130	559	982	19	267	604	87	90
Total	961	1526	1054	1236	3422	2139	961		

1990-1995: overall accuracy 70%

Land-cover class	Mangrove	Salt	Mud	Sand	Saline soil	Water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	483	75	0	53	0	2	74	687	37	30
Salt	142	342	14	94	0	12	473	1077	78	68
Mud	12	227	789	454	4	543	46	2075	64	62
Sand	88	523	0	58	0	139	943	1751	96	97
Saline soil	16	18	1178	613	1349	18	82	3274	0	59
Water	15	304	202	264	1	886	138	1810	45	51
Salt marshes	9	34	0	0	0	0	11435	11478	13	0
Total	765	1523	2183	1536	1354	1600	13191	22152		

1995-2000: overall accuracy 66%

Land-cover class	Mangrove	Salt	Mud	Sand	Saline soil	Water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	313	90	37	11	0	0	0	451	21	31
Salt	0	14	354	0	23	302	6	699	98	98
Mud	0	0	0	0	1774	29	0	1803	100	100
Sand	76	327	477	105	2	38	16	1041	96	90
Saline soil	0	0	0	0	2000	0	0	2000	56	0
Water	0	0	58	0	732	1455	10	2255	23	35
Salt marshes	8	485	468	2252	13	61	10616	13903	0	24
Total	397	916	1394	2368	4544	1885	10648	22152		

2000-2005: overall accuracy 60%

Land-cover class	Mangrove	Salt	Mud	Sand	Saline soil	Water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	295	25	0	0	1	27	49	397	56	26
Salt	65	336	137	21	73	185	99	916	86	88
Mud	0	163	596	29	310	284	12	1394	95	95
Sand	302	351	128	342	220	74	951	2368	12	26
Saline soil	0	22	749	3349	325	99	0	4544	93	96
Water	0	236	786	54	68	740	1	1885	100	100
Salt marshes	16	55	0	0	0	0	10577	10648	99	89
Total	678	1188	2396	3795	997	1409	11689	22152		

2005-2010: overall accuracy 55%

Land-cover class	Mangrove	Salt	Mud	Sand	Saline soil	Water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	310	66	0	0	3	0	47	426	51	27
Salt	26	129	631	930	457	385	0	2558	94	95
Mud	112	1166	2	0	0	40	609	1929	100	100
Sand	25	229	584	1961	432	494	1	3726	46	47
Saline soil	92	273	189	2	11	136	64	767	99	99
Water	3	106	0	0	0	1	10130	10240	100	100
Salt marshes	59	307	761	716	281	373	9	2506	100	100
Total	568	1969	1406	2893	903	1056	10851	22152		

2010-2013: overall accuracy 66%

Land-cover class	Mangrove	Salt	Mud	Sand	Saline soil	Water	Salt marshes	Total	User's accuracy (%)	Producer's accuracy(%)
Mangrove	264	33	0	65	0	2	0	364	47	27
Salt	2	294	44	35	57	114	14	560	74	59
Mud	41	228	19	136	6	99	30	559	99	99
Sand	176	97	14	699	0	24	349	1359	100	100
Saline soil	0	64	1284	1	1799	1173	0	4321	36	18
Water	0	85	202	35	3263	412	1	3998	100	100
Salt marshes	18	66	0	480	0	0	10427	10991	100	98
Total	501	867	1563	1451	5125	1824	10821	22152		

Appendix 4

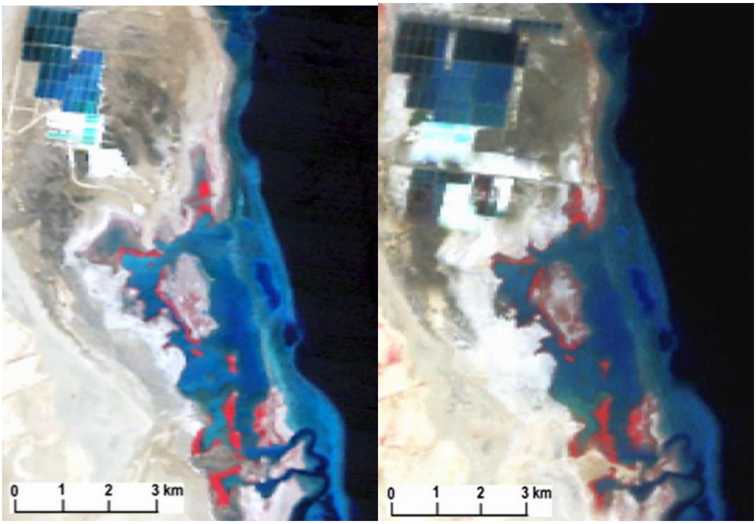
(a) Rate of change in land-cover classesin impacted mangrove non-impacted mangroveduring the period of 1984-2013

Site	Land-cover class	1984-1990	1990-1995	1995-2000	2000-2005	2005-2010	2010-2013
Impacted mangrove	Salt marshes	11	0	-29	76	-8	-7
	Saline soil	8	-112	36	-73	19	34
	Mud	74	-124	88	-71	-57	-6
	sand	-7	33	-36	61	-17	-5
	shallow water	0	-9	33	-11	1	38
	deep water	-1	7	-4	24	-25	-2
Non-impacted mangrove	salt marshes		0	-54	24	-11	-5
	Saline soil	-5	-67	20	-20	-150	81
	Mud	-7	9	-68	56	-23	-42
	Sand	-10	44	97	56	22	14
	water	3	-90	17	-31	-3	7
	salt	1	-15	44	-29	46	-3

*Rate of change in mangrove was shown in Table 2.8.(b) Percentage of land-cover classes change during the study period

Appendix 5

Composite image of mangrove impacted by shrimp farming at Mersa Atta showing the difference in the appearance of mangrove between1990 (left) and 2005 (right)



Appendix 6

SIMPER analysis of raw abundance and biomass data showing the percentage contribution (cumulative) of each taxon to the average Bray-Curtis dissimilarities between the three habitats.

	Species	Average abundance		Average dissimilarity	Dissimilarity/ SD	Contribution %
		Bare sand flat	Cleared mangrove	(Average dissimilarity = 78.71%)		
Habitat	Neredidae	4.63	40.86	18.47	0.8	23.47
	Orbiniidae	0.38	4	10.96	0.5	13.92
	Mytilidae	10.63	4.07	9.57	0.81	12.16
	Turridae	8.5	5.14	9.41	0.79	11.96
	Ocypodidae	0.38	1.79	5.78	0.53	7.34
	Porifera	4.38	3.14	4.74	1	6.03
	Spionid	0.38	6.14	4	0.85	5.09
	Tellinidae	5.63	1.29	3.23	0.75	4.11
	Marginellidae	1.75	1.43	3.11	0.83	3.95
	Cirratuilidae	0	2.14	1.41	0.34	1.8
	Diogenidae	1.38	1.29	0.95	0.72	1.2
		re sand flat	Intact mangrove	(Averagedissimilarity = 88.94%)		
	Turridae	8.5	32.42	35.84	1.14	40.3
	Mytilidae	10.63	2.33	13.02	0.84	14.64
	Porifera	4.38	2.83	7.3	0.81	8.2
	Tellinidae	5.63	0.25	5.55	0.89	6.24
	Diogenidae	1.38	3 .08	5.33	1.08	5.99
	Neredidae	4.63	0.25	4.51	0.93	5.07
	Marginellidae	1.75	1.83	4.15	0.91	4.66
	Cancellaridae	0.25	0.75	1.98	0.44	2.22
	Ocypodidae	0.38	1.08	1.81	0.94	2.04
	Grapsidae	0	0.58	1.29	0.25	1.45
		d mangrove	Intact mangrove	(Averagedissimilarity = 84.75%)		
	Turridae	5.14	32.42	28.51	1.02	33.64
	Neredidae	40.86	0.25	17.99	0.65	21.23
	Orbiniidae	4	0	5.31	0.53	6.27
	Porifera	3.14	2.83	4.82	0.68	5.69
	Diogenidae	1.29	3.08	4.4	1.16	5.2
	Mytilidae	4.07	2.33	4	0.95	4.72
	Spionidae	6.14	0	3.46	0.58	4.09
	Ocypodidae	1.79	1.08	2.85	0.77	3.37
	Marginellidae	1.43	1.83	2.27	0.96	2.67
	Semelidae	0.64	1.33	1.66	0.46	1.96
	Cirratuilidae	2.14	0.08	1.6	0.3	1.88
Water level		High level	Mid water	(Average dissimilarity = 63.22%)		
	Turridae	34.18	2.56	28.35	1.04	44.85
	Orbiniidae	1.09	3.78	8.66	0.61	13.7
	Porifera	2.64	3.33	6.47	0.47	10.24
	Ocypodidae	1.64	1.56	4.28	0.66	6.78
	Mytilidae	2.64	0.78	3.73	0.93	5.9
	Neredidae	0.18	1.22	2.69	0.41	4.26
	Marginellidae	1.82	1.11	2.09	0.93	3.31
	Diogenidae	2.36	1	1.53	0.55	2.42
		High level	Low water	(Averagedissimilarity = 90.84%)		
	Turridae	34.18	9.29	31.82	1.06	35.03
	Neredidae	0.18	42.79	19.66	0.71	21.65
	Mytilidae	2.64	9.57	7.71	0.67	8.49
	Spionidae	0.18	6.07	3.58	0.6	3.94

	Diogenidae	2.36	2.21	3.48	1	3.83
	Porifera	2.64	3.86	3.43	0.88	3.77
	Tellinidae	0	4.71	3.31	0.67	3.65
	Semelidae	0	2.43	3.27	0.99	3.6
	Marginellidae	1.82	1.86	2.62	0.93	2.88
	Ocypodidae	1.64	0.64	2.38	0.54	2.62
	Orbiniidae	1.09	0.93	2.29	0.34	2.52
		Mid water	Low water	(Averagedissimilarity = 87.76%)		
	Neredidae	1.22	42.79	22.91	0.82	26.1
	Turridae	2.56	9.29	10.27	0.91	11.71
	Mytilidae	0.78	9.57	8.19	0.65	9.34
	Porifera	3.33	3.86	6.89	0.81	7.85
	Orbiniidae	3.78	0.93	5.25	0.47	5.98
	Semelidae	0	2.43	4.96	0.89	5.65
	Spionidae	0.22	6.07	4.14	0.67	4.72
	Tellinidae	0	4.71	3.99	0.75	4.54
	Diogenidae	1	2.21	3.82	1.13	4.35
	Ocypodidae	1.56	0.64	3.12	0.67	3.56
	Marginellidae	1.11	1.86	3.02	0.86	3.44
	Cirratuilidae	0	2.21	1.98	0.35	2.26
	Cancellaridae	0.67	0.43	1.66	0.49	1.89

Appendix 7

Average values of stable carbon and nitrogen isotope signatures of (a) potential food sources and (b) macrofauna collected from different water levels (H: high-water level, M: mid-water level, l: low-water level) at the three studied sites.

(a)

Potential food sources	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bare sand flat		
Seagrass	-15.1±3.0	1.4±1.3
Epiphytes	-20.9±1.5	3.4±1.1
Macroalgae	-20.4±3.1	2.4±1.2
Suspended particulate organic matter (SPOM)	-20.7±0.53	3.1±0.53
Sediment organic matter (SOM)	-22.1±1.1	6.1±0.3
Cleared mangrove		
Seagrass	-11.9±3.0	1.4±1.3
Epiphytes	-20.7±2.1	3.5±1.6
Microphytobenthos	-23.0±0.1	2.9±0.1
Macroalgae	-20.4±4.4	2.4±1.7
Suspended particulate organic matter (SPOM)	-20.7±0.8	3.1±0.7
Sediment organic matter (SOM)	-17.8±0.8	4.2±0.9
Intact mangrove		
Mangrove (fresh leaves)	-27	3.6
Seagrass	-17.9±3.0	3.05±1.3
Macroalgae	-19.9±4.4	4.15±0.6
Microphytobenthos	-22.9±3.1	1.88±1.2
Suspended particulate organic matter (SPOM)	-19.7±1.1	3.14±1.1
Sediment organic matter (SOM)	-22.7±0.6	2.95±2.2

(b)

Site/water level	Taxon	Family	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bare sand flat				
Low water	Decapoda	Diogenidae	-15.8	4.8
Low water	Decapoda	Ocyptidae	-15.7	4.4
Low water	Decapoda	Leucosiidae	-13.3	5.0
Low water	Bivalvia	Mytilidae	-14.4	4.9
Low water	Bivalvia	Tellinidae	-13.4	6.3
Low water	Gastropoda	Batillaridae	-11.6	5.7
Cleared mangrove				
Mid water	Gastropoda	Batillaridae	-12.5	6.8
Mid water	Decapoda	Ocyptidae	-15.6	6.9
Mid water	Polychaeta	Nereididae	-13.0	7.6
Low water	Gastropoda	Ocyptidae	-12.2	7.2
Low water	Bivalvia	Tellinidae	-13.7	5.5
Low water	Bivalvia	Mytilidae	-12.3	5.2
Low water	Bivalvia	Semelidae	-15.0	2.8

Low water	Bivalvia	Petrcelidae	-13.5	3.9
Low water	Decapoda	Diogenidae	-14.4	4.3
Low water	Polychaeta	Ophelidae	-13.0	7.8
Low water	Polychaeta	Nereididae	-13.0	7.7
Low water	Polychaeta	Spoinidae	-13.7	5.8
Low water	Polychaeta	Cirratuilidae	-13.4	7.1
Low water	Polychaeta	Oweniidae	-13.9	6.8
Low water	Polychaeta	Euriciodae	-11.6	6.9
Low water	Amphipoda		-16.2	4.8
Intact mangrove				
High water	Bivalvia	Mytilidae	-15.0	3.7
High water	Decapoda	Leucosiidae	-11.0	3.0
High water	Decapoda	Diogenidae	-16.1	4.3
High water	Decapoda	Diogenidae	-16.7	2.1
High water	Decapoda	Grapsidae	-15.3	11.6
High water	Decapoda	Ocypodidae	-14.0	8.5
High water	Gastropoda	Batillaridae	-16.5	2.8
Low water	Polychaeta	Aphelochaeta	-8.7	3.8
Low water	Polychaeta	Neredidae	-17.4	5.8
Low water	Polychaeta	Serpula	-18.5	2.4
Low water	Polychaeta	unclassified	-14.0	5.2
Low water	Decapoda	Ocyptidae	-15.4	5.6
Low water	Decapoda	Leucosiidae	-16.7	7.5
Low water	Decapoda	Diogenidae	-15.6	6.3
Low water	Bivalvia	Mytilidae	-15.0	3.9
Low water	Bivalvia	Semelidae	-18.2	6.1
Low water	Bivalvia	Tellinidae	-15.4	4.4

Appendix 8

Results of Distance-based linear modeling (DISTLM) testing for relationships between selected sediment characteristics (MGS: median grain size, SS: sediment sorting, TN: total nitrogen content, TOC: total organic carbon content, C/N: total carbon-nitrogen ratio) and macrofaunal community attributes patterns in marginal tests (variation explained by single variables) and in sequential tests (variation explained by adding new variable each time to get the optimum fit criterion) using the stepwise selection procedure: on the basis of the adjusted R² selection criterion (significant*P* values in bold italic)

Macrofauna attributes	MARGINAL TESTS					SEQUENTIAL TESTS						
	Variable	SS(trace)	Pseudo-F	P	Proportion	Variable	R²	SS(trace)	Pseudo-F	P	Proportion	Cumulative
Total abundance	Clay	3810.8	0.68	0.4218	2.1	+C/N	0.0589	15979	3.0653	0.0903	0.0874	0.0874
	Silt	18.615	0.00	0.9576	0.0	+% TOC	0.1728	24773	5.4068	*0.0235*	0.1355	0.2229
	Sand	111.33	0.02	0.8926	0.1	+Silt	0.2024	9495.7	2.1493	0.1502	0.0520	0.2749
	MGS	14050	2.66	0.0816	7.7	+% TN	0.2027	4471.4	1.0125	0.2887	0.0244	0.2994
	SS	2488.2	0.44	0.5229	1.4							
	% TN	4718.2	0.85	0.3191	2.6							
	% TOC	2738.3	0.49	0.4975	1.5							
	C/N	15979	3.0653	0.0887	8.7	3.0653	0.0887					
Total biomass	Clay	0.00008	0.010	0.921	0.0	+ MGS	0.0803	0.0261	3.7954	*0.0502*	0.1091	0.10908
	Silt	0.00047	0.061	0.8015	0.2	+ SS	0.0985	0.0110	1.6275	0.2087	0.0458	0.15492
	Sand	0.00022	0.029	0.8672	0.1							
	MGS	0.02609	3.795	*0.05*	10.9							
	SS	0.02511	3.636	0.0696	10.5							
	% TN	0.02144	3.052	0.0883	9.0							
	% TOC	0.01027	1.390	0.2502	4.3							
	C/N	0.01059	1.436	0.2437	4.4							
Taxon richness	Clay	4.358	0.25	0.6177	0.8	+ MGS	0.2527	152.23	12.157	*0.0016*	0.2753	0.27531
	Silt	0.868	0.05	0.821	0.2	+C/N	0.2961	35.104	2.9765	0.0958	0.0636	0.3388
	Sand	0.068	0.00	0.9513	0.0							
	MGS	152.230	12.16	*0.0019*	27.5							
	SS	18.314	1.10	0.3043	3.3							
	% TN	9.451	0.56	0.4792	1.7							
	% TOC	26.198	1.59	0.2173	4.7							
	C/N	108.980	7.85	*0.008*	19.7							
Diversity (H’)	Clay	0.11	0.225	0.64	0.7	+ MGS	0.4214	6.5923	25.038	*0.0001*	0.4390	0.4390

	Silt	0.20	0.435	0.5076	1.3	+% TOC	0.4695	0.9416	3.9003	*0.0546*	0.0627	0.5017
	Sand	0.18	0.391	0.5349	1.2							
	MGS	6.59	25.038	*0.0001*	43.9							
	SS	1.95	4.778	*0.0383*	13.0							
	% TN	1.81	4.373	*0.0369*	12.0							
	% TOC	2.94	7.798	*0.0092*	19.6							
	C/N	2.79	7.303	*0.0109*	18.6							
Taxon composition	Clay	5575.4	2.15	*0.0357*	6.3	+ MGS	0.1500	15569	6.8217	*0.0001*	0.1757	0.17572
	Silt	7386.1	2.91	*0.0062*	8.3	+C/N	0.2507	10666	5.3017	*0.0001*	0.1204	0.2961
	Sand	7014.3	2.75	*0.0094*	7.9	+TOC	0.3008	6049.7	3.2226	*0.0022*	0.0683	0.36438
	MGS	15569	6.82	*0.0001*	17.6	+TN	0.3135	2861.3	1.5523	0.1414	0.0323	0.39667
	SS	8330.5	3.32	*0.0031*	9.4	+SS	0.3324	3264.6	1.8212	0.0798	0.0368	0.43352
	% TN	4477.5	1.70	0.0919	5.1							
	% TOC	11422	4.74	*0.0001*	12.9							
	C/N	13319	5.66	*0.0001*	15.0							

Appendix 9

SIMPER analysis of (a) meiofaunal and (b) nematode average abundance data per core showing the average dissimilarity, dissimilarity standard deviation (SD) and percentage contribution of each taxon to the average Bray-Curtis dissimilarities between the three habitats

(a)

	Species	Average abundance		Average dissimilarity	Dissimilarity SD	Contribution %
		Bare sand flat	Cleared mangrove	(Average dissimilarity = 78.71%)		
Habitat	Nematoda	4.6	6.5	8.7	1.3	25.1
	Turbellaria	0.6	2.2	6.4	1.5	18.6
	Copepoda	1.8	3.4	6.3	2.0	18.2
	Polychaeta	1.4	3.0	5.5	1.7	16.0
	Ostracoda	0.3	0.9	2.5	1.0	7.3
	Holothuroidea	0.7	0.1	1.5	0.6	4.3
	Gastropoda	0.0	0.5	1.5	0.7	4.2
		Bare sand flat	Intact mangrove	(Average dissimilarity = 88.94%)		
	Ostracoda	0.3	2.8	7.3	2.8	14.1
	Acarina	0.0	2.2	6.7	2.4	12.9
	Copepoda	1.8	3.6	6.0	1.7	11.5
	Nematoda	4.6	6.2	5.5	1.3	10.6
	Gastrotricha	0.0	2.0	5.4	2.9	10.4
	Turbellaria	0.6	2.3	4.8	1.5	9.3
	Gastropoda	0.0	1.4	4.3	1.7	8.3
	Gnathostomulida	0.0	1.5	4.1	1.5	7.8
	Polychaeta	1.4	2.6	3.7	1.8	7.2
		Cleared mangrove	Intact mangrove	(Average dissimilarity = 84.75%)		
	Acarina	0.0	2.2	5.4	2.6	17.6
	Ostracoda	0.9	2.8	5.1	2.1	16.5
	Gastrotricha	0.0	2.0	4.4	2.8	14.4
	Copepoda	3.4	3.6	3.7	3.2	11.9
	Gnathostomulida	0.0	1.5	3.4	1.5	11.0
	Gastropoda	0.5	1.4	3.3	1.6	10.8
	Turbellaria	2.2	2.3	1.5	1.6	4.7
	Polychaeta	3.0	2.6	1.3	1.6	4.1
Water level		High level	Mid water	(Average dissimilarity = 63.22%)		
	Oligochaeta	0.0	2.5	8.5	3.1	25.7
	Polychaeta	1.5	3.3	6.2	2.1	18.5
	Copepoda	2.2	2.6	4.6	2.4	13.9
	Turbellaria	1.5	0.3	3.4	1.4	10.2
	Nematoda	5.9	5.8	3.4	1.0	10.1
	Ostracoda	0.9	1.3	2.9	1.5	8.8
	Gastropoda	0.7	0.6	1.1	0.7	3.3
		High level	Low water	(Average dissimilarity = 90.84%)		
	Copepoda	2.2	4.3	6.8	2.0	20.6
	Turbellaria	1.5	3.7	6.7	2.3	20.4
	Polychaeta	1.5	2.6	3.7	1.6	11.3
	Ostracoda	0.9	1.8	3.1	1.1	9.5
	Holothuroidea	0.0	0.7	2.6	0.6	7.9
	Gastropoda	0.7	0.7	2.1	1.0	6.5

	Nematoda	5.9	5.8	2.0	1.0	6.0
	Amphipoda	0.0	0.7	1.9	1.3	5.7
	Gastrotricha	0.4	0.9	1.2	0.7	3.7
		Mid water	Low water	(Average dissimilarity = 87.76%)		
	Turbellaria	0.3	3.7	8.4	4.0	26.6
	Oligochaeta	2.5	0.2	5.8	3.4	18.5
	Copepoda	2.6	4.3	3.6	1.1	11.6
	Polychaeta	3.3	2.6	2.4	2.3	7.8
	Ostracoda	1.3	1.8	2.3	1.0	7.4
	Holothuroidea	0.0	0.7	2.3	0.7	7.4
	Gastropoda	0.6	0.7	1.5	0.9	4.7
	Amphipoda	0.2	0.7	1.4	1.0	4.4
	Gnathostomulida	0.0	0.8	1.2	0.5	3.9

(b)

Species		Average abundance		Average dissimilarity	Dissimilarity SD	Contribution %
		Bare sand flat	Cleared mangrove	(Average dissimilarity = 90.95 %)		
Habitat	*Daptonema*	7.2	96.1	27.2	3.1	29.9
	Ethmolaimus	2.3	68.8	18.7	0.7	20.6
	Monhystrella	15.5	6.0	6.7	1.1	7.4
	Theristus	2.5	19.2	5.8	1.6	6.3
	Microlaimus	0.0	16.2	5.6	1.0	6.1
	Desmodora	0.0	17.7	5.5	0.8	6.0
	Syringolaimus	9.5	0.0	3.1	2.1	3.5
	Spilophorella	0.9	9.7	2.7	0.9	3.0
	Metalinhomoeus	1.4	6.8	2.3	0.7	2.5
	Paracyatholaimus	1.1	5.9	1.9	0.6	2.0
	Leptolaimus	0.0	4.6	1.6	0.5	1.7
	Oncholaimus	1,73	3,47	1,51	0,92	1,66
		Bare sand flat	Intact mangrove	(Average dissimilarity = 85,67%)		
	Haliplectus	0.0	42.4	12.1	2.0	14.1
	Daptonema	7.2	45.6	11.9	3.5	13.9
	Monhystrella	15.5	9.4	9.1	1.0	10.6
	Terschellingia	0.9	32.2	8.8	2.2	10.2
	Spirinia	0.0	42.6	8.6	0.6	10.0
	Ethmolaimus	2.3	15.8	5.5	0.7	6.5
	Microlaimus	0.0	12.9	4.6	1.0	5.3
	Viscosia	0.7	12.9	4.0	3.2	4.6
	Theristus	2.5	9.5	3.4	1.2	4.0
	Bolbolaimus	0.0	8.3	2.9	1.0	3.4
	Syringolaimus	9.5	9.8	2.7	2.6	3.1
	Desmodora	0.0	9.2	2.2	1.0	2.6
	Oncholaimus	1.7	6.4	2.0	0.9	2.3
		Cleared mangrove	Intact mangrove	(Average dissimilarity = 70,46%)		
	Daptonema	96.1	45.6	12.0	1.3	17.1
	Ethmolaimus	68.8	15.8	11.4	0.8	16.2
	Haliplectus	0.0	42.4	6.5	2.0	9.3
	Spirinia	0.0	42.6	6.1	0.6	8.6
	Terschellingia	0.0	32.2	5.4	1.7	7.7
	Microlaimus	16.2	12.9	4.4	3.1	6.3
	Theristus	19.2	9.5	2.9	1.0	4.1

	Desmodora	17.7	9.2	2.7	0.9	3.9
	Syringolaimus	0.0	9.8	2.0	1.4	2.8
	Viscosia	3.5	12.9	1.9	2.1	2.7
	Oncholaimus	3.5	6.4	1.9	1.4	2.6
	Bolbolaimus	3.6	8.3	1.8	1.3	2.6
	Monhystrella	6.0	9.4	1.8	1.2	2.5
	Spilophorella	9.7	0.0	1.6	0.9	2.2
	Metalinhomoeus	6.8	0.0	1.2	0.7	1.7
Water level		High level	Mid water	(Average dissimilarity = 63.32%)		
	Ethmolaimus	84.3	8.8	17.3	1.2	27.3
	Monhystrella	9.7	14.2	12.3	0.6	19.5
	Daptonema	62.2	49.6	7.0	2.0	11.1
	Haliplectus	19.5	1.9	3.6	0.7	5.7
	Paracyatholaimus	0.0	12.9	3.4	2.0	5.4
	Microlaimus	10.7	7.5	3.4	1.3	5.3
	Theristus	16.2	11.4	2.5	1.4	3.9
	Desmodora	0.0	11.3	2.3	1.3	3.6
	Metachromodora	8.3	0.0	1.8	1.2	2.9
	Metalinhomoeus	0.0	4.8	1.7	0.9	2.6
	Oncholaimus	3.9	2.4	1.5	1.1	2.4
	Bolbolaimus	6.8	0.6	1.2	0.6	2.0
		High level	Low water	(Average dissimilarity = 66.62%)		
	Ethmolaimus	84.3	1.1	17.9	1.2	26.8
	Daptonema	62.2	54.7	6.6	1.3	9.9
	Spirinia	0.0	42.6	6.4	0.7	9.5
	Microlaimus	10.7	13.9	3.8	1.5	5.7
	Theristus	16.2	6.5	3.4	1.9	5.1
	Desmodora	0.0	20.7	3.3	0.9	4.9
	Oncholaimus	3.9	5.5	3.1	1.0	4.6
	Syringolaimus	7.2	3.6	2.8	0.7	4.1
	Terschellingia	6.9	20.2	2.5	0.7	3.7
	Monhystrella	9.7	5.2	2.4	1.6	3.5
	Spilophorella	1.1	8.9	2.1	0.9	3.1
	Viscosia	3.2	11.4	2.0	2.3	3.1
	Bolbolaimus	6.8	4.6	1.6	1.1	2.4
	Metachromodora	8.3	0.0	1.3	1.2	2.0
	Stylotheristus	0.5	6.3	1.1	0.8	1.6
		Mid water	Low water	(Average dissimilarity = 59.06%)		
	Monhystrella	14.2	5.2	9.9	0.7	16.8
	Daptonema	49.6	54.7	6.3	1.4	10.6
	Spirinia	0.0	42.6	6.2	0.5	10.4
	Desmodora	11.3	20.7	3.9	1.1	6.5
	Paracyatholaimus	12.9	0.0	3.3	1.5	5.7
	Theristus	11.4	6.5	2.8	1.1	4.7
	Terschellingia	5.0	20.2	2.6	0.6	4.5
	Haliplectus	1.9	18.3	2.3	0.5	3.9
	Ethmolaimus	8.8	1.1	2.2	1.8	3.7
	Microlaimus	7.5	13.9	2.1	0.9	3.6
	Metalinhomoeus	4.8	5.1	2.0	1.1	3.4
	Viscosia	3.0	11.4	2.0	2.9	3.4
	Spilophorella	3.1	8.9	2.0	0.9	3.3
	Oncholaimus	2.4	5.5	1.6	0.8	2.7
	Syringolaimus	6.2	3.6	1.3	0.7	2.3
	Bolbolaimus	0.6	4.6	1.2	0.7	2.0
	Prooncholaimus	3.6	0.0	1.0	0.6	1.7
	Stylotheristus	0.0	6.3	0.9	0.5	1.6

Appendix10

Results of Distance-based linear modeling (DISTLM) testing for relationships between selected sediment characteristics (MGS: median grain size, Sort: sediment sorting, TN: total nitrogen content, TOC: total organic carbon content, C/N: total carbon-nitrogen ratio), and meiofauna and nematode communities attributes patterns in marginal tests (variation explained by single variables) and in sequential tests (variation explained by adding new variable each time to get the optimum fit criterion) using the stepwise selection procedure: on the basis of the adjusted R² selection criterion. SS(trace): portion of sum of squares relative to the analysed predictor variable; pseudo-F: statistic; P: significance level obtained by permutation. Significant P-values are shown in bold italic

Characteristic		**MARGINAL TESTS**					**SEQUENTIAL TESTS**						
		Variable	**SS (trace)**	**Pseudo-F**	**P**	**Proportion (%)**	**Variable**	**Adjusted R²**	**SS (trace)**	**Pseudo-F**	**P**	**Proportion (%)**	**Cumulative (%)**
Meiofauna	Total abundance	Silt	55098	3.26	0.0848	14.02	+MGS	0.43	18140	17.15	***0.0005***	0.4616	46.16
		MGS	18140	17.15	***0.0003***	46.16							
		Sort	32954	1.83	0.1913	8.39							
		TN	27435	1.50	0.2415	6.98							
		TOC	32283	1.79	0.2013	8.21							
		C/N	23203	1.25	0.2693	5.90							
	composition	Silt	1350.5	1.78	0.1483	8.18	+MGS	0.30	5507	10.01	***0.0001***	0.3335	33.35
		MGS	5506.9	10.01	***0.0001***	33.35	+TN	0.43	2494	5.57	***0.0019***	0.1510	48.45
		Sort	2768.3	4.03	***0.0134***	16.76	+ Sort	0.58	2554	7.72	***0.0001***	0.1547	63.92
		TN	4134.6	6.68	***0.0013***	25.04	+C/N	0.63	1055	3.66	***0.0165***	0.0639	70.31
		TOC	3206.6	4.82	***0.0073***	19.42	+Silt	0.64	341	1.20	0.3146	0.0207	72.37
		C/N	2562.6	3.67	***0.0227***	15.52							
	Taxa richness (S)	silt	12.6	1.49	0.2403	6.94	+ TN	0.49	93	21.06	***0.0002***	0.5129	51.29
		MGS	53.8	8.44	***0.0072***	29.67	+MGS	0.54	12.5	3.14	***0.0886***	0.0691	58.2
		Sort	49.2	7.44	***0.0119***	27.12							
		TN	93.0	21.06	***0.0001***	51.29							
		TOC	65.5	11.32	***0.0022***	36.15							
		C/N	12.3	1.45	0.2544	6.78							
	Taxa evenness (J')	silt	0.08	3.43	0.0774	14.64	+TOC	0.46	0.26	19.05	***0.0001***	0.4878	48.78
		MGS	0.03	1.33	0.2682	6.25	+Silt	0.54	0.05	4.62	***0.0437***	0.1003	58.81
		Sort	0.04	1.52	0.2361	7.04	+TN	0.64	0.05	6.07	***0.0250***	0.1039	69.19

		TN	0.13	6.81	***0.0164***	25.40	+C/N	0.77	0.06	10.62	***0.0046***	0.1185	81.04
		TOC	0.26	19.05	***0.0001***	48.78							
		C/N	0.21	13.35	***0.0025***	40.03							
	Taxa diversity (H')	silt	0.09	0.60	0.4467	2.90	+TOC	0.64	2.02	37.57	***0.0001***	0.6526	65.26
		MGS	0.54	4.25	***0.0491***	17.54	+TN	0.66	0.12	2.42	0.1375	0.0393	69.19
		Sort	0.55	4.28	***0.0529***	17.64	+C/N	0.75	0.30	8.22	***0.0110***	0.0966	78.85
		TN	1.51	18.99	***0.0004***	48.70	-TOC	0.76	0.01	0.26	0.6308	0.0030	78.55
		TOC	2.02	37.57	***0.0001***	65.26	+Silt	0.85	0.26	11.78	***0.0032***	0.0848	87.03
		C/N	1.12	11.32	***0.0039***	36.14							
Nematode	Total abundance	Silt	71053	6.92	***0.0185***	25.72	+Silt	0.22	71053	6.92	***0.0164***	0.2572	25.72
		MGS	45448	3.94	0.0669	16.45	+C/N	0.25	17837	1.81	0.1892	0.0646	32.17
		Sort	2126.7	0.16	0.6938	0.77	+TOC	0.36	35004	4.13	***0.0544***	0.1267	44.84
		TOC	3317	0.24	0.6278	1.20	+MSG	0.39	16392	2.05	0.1751	0.0593	50.78
		C/N	612.5	0.04	0.8264	0.22							
	Composition	Silt	4128.1	1.94	0.0664	8.84	+TOC	0.10	6468.4	3.22	***0.0037***	0.1385	13.85
		MGS	2998.9	1.37	0.2112	6.42	+C/N	0.19	5877.1	3.25	***0.0068***	0.1258	26.43
		Sort	5931.6	2.91	***0.0084***	12.70	+Silt	0.29	5736.2	3.61	***0.0040***	0.1228	38.72
		TOC	6468.4	3.22	***0.0045***	13.85	+ Sort	0.29	1696.6	1.07	0.3788	0.0363	42.35
		C/N	4659.4	2.22	***0.0365***	9.98							
	Genera richness (S)	Silt	15.4	2.10	0.1609	9.50	+Silt	0.05	15.39	2.10	0.1647	0.0950	9.5
		MGS	11.6	1.54	0.2268	7.16	+C/N	0.16	24.12	3.74	0.0686	0.1489	24.39
		Sort	11.8	1.57	0.2251	7.29	+TOC	0.18	8.04	1.27	0.2676	0.0497	29.36
		TOC	1.7	0.21	0.6592	1.04							
		C/N	9.6	1.26	0.2706	5.92							
	Genera evenness (J')	Silt	0.0	0.01	0.9430	0.03	+ TOC	0.10	0.05	3.22	0.0713	0.1388	13.88
		MGS	0.0	0.01	0.9312	0.04							
		Sort	0.04	2.64	0.1212	11.67							
		TOC	0.05	3.22	0.0750	13.88							
		C/N	0.04	2.70	0.1116	11.90							
	Genera diversity (H')	Silt	0.24	0.99	0.3396	4.73	+Sort	0.09	0.69	3.09	0.0917	0.1337	13.37
		MGS	0.14	0.55	0.4579	2.66	+C/N	0.12	0.38	1.76	0.2020	0.0735	20.72
		Sort	0.69	3.09	0.0890	13.37	+MGS	0.17	0.44	2.16	0.1636	0.0850	29.22
		TOC	0.42	1.77	0.1906	8.11	- Sort	0.21	0.02	0.11	0.7471	0.0044	28.78

		C/N	0.68	3.03	0.0955	13.16							
	Maturity index (MI)	Silt	0.15	1.52	0.2256	7.08	+Sort	0.33786	0.79226	11.716	***0.0017***	0.3694	36.939
		MGS	0.07	0.70	0.4107	3.39	+C/N	0.37229	0.13443	2.0968	0.1627	0.0627	43.207
		Sort	0.79	11.72	***0.0031***	36.94	+MGS	0.39912	0.11343	1.8484	0.1949	0.0529	48.496
		TOC	0.22	2.24	0.1531	10.06							
		C/N	0.01	0.10	0.7549	0.49							
	Trophic diversity (ITD)	Silt	0.02	2.03	0.1648	9.23	+Silt	0.05	0.02	2.0327	0.1714	0.0923	9.23
		MGS	0.02	1.58	0.2287	7.30	+C/N	0.11	0.03	2.43	0.1355	0.1029	19.52
		Sort	0.01	0.86	0.3674	4.14							
		TOC	0.00	0.19	0.6754	0.95							
		C/N	0.01	0.71	0.4024	3.41							