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ORIGINAL PAPER

Assessment of regional and local biodiversity in tropical and subtropical coastal habitats in the East African Marine Ecoregion

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Abstract The transboundary networks of Marine Protected Areas (MPAs) project, TRANSMAP, assessed local turnover and regional biodiversity across the East African Marine Ecoregion, where inter-governmental co-operation has been working to connect local MPAs. The benthic fauna in the three most dominant habitats on this coastline—beaches, mangroves and seagrasses—were studied in two *Regions* (*Northern Region*, 10–13°S; *Southern Region*, 25–28°S). Meiofaunal taxa were used as the model faunal group owing to their diversity and abundance across habitat types and environmental conditions. Meiofaunal abundance averaged 2,500 individuals 10 cm^{-2} and was generally higher in mangrove and seagrass sediments than on the beaches, and was significantly different between *habitats* × *Regions*. In total, 18 taxa were recorded with highest diversity in the beach samples. Diversity indices and assemblage structure were significantly different between *habitats*, but also *Regions*. Specific granulometric 1Φ size classes,

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shore-height and number of rain days were the factors most significantly correlating with the observed assemblage patterns. Additionally, the size of a MPA and latitude (which correlated with MPA age, but not number of rain days), were the factors fitting best with meiofaunal assemblage patterns across the beaches, the habitat for which the most comprehensive data were generated. Sample diversity was higher in the *Southern Region*, and although within- and across-habitats diversity were similar across the *Regions*, the two *Regions* appeared to provide complementary habitats and supported different assemblages. Within the *Regions*, beaches (the only habitat for which more than one location was sampled) were significantly different between *Locations*, supporting the establishment of multiple protected locations of the same habitat within each transboundary MPA.

Keywords Beach · Benthos · Intertidal · East African Marine Ecoregion (EAME) · Mangrove · Meiofauna · Sand · Seagrass · Republic of Mozambique · Republic of South Africa · United Republic of Tanzania

Abbreviations

°C	Degrees centigrade
µm	Micrometres
ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
BDI	Beach Deposit Index
BI	Beach Index
EAME	East African Marine Ecoregion
EC	European Commission
GPS	Global Positioning System
HW	High water
INCO-DEV	International Co-operation for Development
km	Kilometres
L	Lower-shore
LW	Low water
m	Metre
M	Mid-shore
MHWN	Mean high water neap
MHWS	Mean high water spring
MLWN	Mean low water neap
MLWS	Mean low water spring
mm	Millimetres
MPA	Marine Protected Area
NHM	Natural History Museum, London
PERMANOVA	Permutational multivariate analysis of variance
PRIMER	Plymouth routines in multivariate ecological research
TRANSMAP	Transboundary networks of Marine Protected Areas for integrated conservation and sustainable development: biophysical, socio-economic and governance assessment in East Africa
U	Upper-shore
WWF	World Wide Fund for Nature
y/n	Yes/no

Introduction

Intertidal environments are transitional ecosystems that provide important environmental services and resources to local communities and adjacent ecosystems (Ewel et al. 2001). They are at risk from anthropogenic impacts such as pollution events, over-exploitation and sea-level rise resulting from global warming and are additionally vulnerable owing to low diversity resulting from extreme fluctuations in environmental conditions (Levin et al. 2001). Here we address regional biodiversity on the east African coast, from South Africa through Mozambique to Tanzania, where inter-governmental collaborations aim to create transboundary networks of Marine Protected Areas (MPAs). The study area covers the southern 18° of the 30° of latitude (approximately 4,630 km of coastline) within the WWF Global 200 East African Marine Ecoregion (EAME). It has a number of MPAs of various ages, sizes and enforcement levels which were established with the joint aims of sustainable resource management and socio-economic development, as well as basic biodiversity and habitat protection (Wells and Ngusaru 2004).

This research formed part of a larger EU TRANSMAP project (Transboundary networks of MPAs for integrated conservation and sustainable development: biophysical, socio-economic and governance assessment in East Africa), whose goal was the provision of robust data to support the creation of MPAs that *can maintain ecological functions, sustainable resource use and expected socio-economic development* (http://www.transmap.fc.ul.pt/index.asp?03pu). The TRANSMAP consortium partners were from both local African and European institutes, the NHM, London leading on the biodiversity workpackage. The biophysical objectives were principally to assess habitat and biological diversity, particularly macro- and mega-faunal resource diversity. Key intertidal habitats of beaches, seagrass meadows and mangrove forests were studied: seagrass meadows and mangrove forests are highly productive and provide important nursery grounds for migratory species, whilst mangroves also provide a key source of building material (Gullstrom et al. 2002; de la Torre-Castro and Ronnback 2004; Nagelkerken et al. 2008; Kristensen et al. 2008), and, although beach productivity varies with wave exposure, beaches also provide important nursery and nesting sites (Defeo et al. 2009).

Permanent meiofauna were studied owing to their numerical dominance and relatively high diversity over the spectrum of sedimentary habitats (Higgins and Thiel 1988; Giere 1993). Meiofauna assemblages are sensitive to sediment characteristics, salinity regimes, temperature and oxygen availability (Coull 1999; Soetaert et al. 1995; Attrill 2002; Vanaverbeke and Vincx 2008), and reflect changes in specific intertidal parameters such as interstitial drainage, intertidal morphology, and wave and tidal energy (Wieser 1959; Rodriguez et al. 2001; Moreno et al. 2006). Particularly, they maintain high abundance and species diversity relative to the macrofauna on tropical and sub-tropical beaches and in mangrove and seagrass sediments (McLachlan 1977a, b; Ansari 1984; Ansari and Parulekar 1994; Schrijvers et al. 1995; Netto and Gallucci 2003; Schlacher et al. 2008) and tend to exhibit diurnal vertical migration rather than the lateral migration seen in the macrofauna (McLachlan et al. 1977; McLachlan and Jaramillo 1995; Steyaert et al. 2001).

This study was the first of its kind in the region and consequently the primary objectives were an initial assessment of benthic biodiversity and to produce a baseline data set to enable future study. Additional objectives were to determine whether;

- differences occur between tropical and subtropical meiofaunal assemblages;
- meiofaunal higher-taxon assemblages differ between habitats;

- meiofaunal higher-taxon assemblages differ between different locations of the same habitat; and
- any observed assemblage patterns can be related to environmental parameters.

Materials and methods

Sites

Two *Regions* (1,000 km apart) were selected, a *Southern Region* (25–28°S) at the Mozambique–South Africa border and a *Northern Region* (10–13°S) at the Mozambique–Tanzania border (Fig. 1):

The *Northern Region* stretched from Mtwara in southern Tanzania to Mecufi (Pemba) in northern Mozambique, including Mnazi Bay-Ruvuma Estuary Marine Park, North Quirimbas Conservation Area, and the Quirimbas National Park. It has a humid tropical climate with an average rainfall of approximately 1 m per year (Kemp 2000) and falls within the Coral Coast subregion of EAME. It was divided into a Tanzanian site within the Southern Equatorial Current which experiences seasonal directional change in current flow and two Mozambique sites in the Mozambique Current (MC), a series of large, southward-flowing, anti-cyclonic oceanic eddies (Lutjeharms 2006). The region is a major down-welling area with a relatively low productivity (McClanahan 1988).

The *Southern Region* comprised the area from the Ilhas da Inhaca e dos Portugueses Faunal Reserve (southern Mozambique) to the Greater St. Lucia Wetland Park World Heritage Site (northeast South Africa). It has a sub-tropical climate with an average rainfall of approximately 0.75 m per year (Kemp 2000), and was divided into two South African sites within the Agulhas Current Large Marine Ecosystem and one Mozambique site located at the juncture where the MC and the East Madagascar Current join to form the Agulhas Current (Quartly and Srokosz 2003). The Mozambique and South African sites are potentially separated by inshore bedload-partitioning—currents flow north to Inhaca Island and south to St. Lucia (Lutjeharms 2006). Wave exposure at the beach sites is high owing to swell generated by the south-east trade winds of the Indian Ocean (Kalk 1995; Kemp 2000) and the region has high ocean productivity owing to local and irregularly timed upwelling (Lutjeharms 2006; Roberts et al. 2006).

Sampling sites were on the open coast, with the exception of Mocimboa in northern Mozambique, which was behind a series of barrier islands, and the seagrass and mangrove transects on Inhaca Island, southern Mozambique, which were on the leeward side of the island. Inhaca Island was the only barrier island in the study and the only site previously studied in detail. Its beaches are extensively exploited by the local community, principally for food resources, but no effect on the macro-benthic community has been found (de Boer and Prins 2002).

Habitat selection

Each *Region* encompassed an area >300 km and was divided into three *Locations* (100 km apart), which each included sandy, rocky, seagrass and mangrove shores and offshore coral reefs or islands. *Locations* were selected to provide comparable *Habitats* between *Regions*, based firstly on the occurrence of sandy beaches and then on the presence of adjacent mangrove forests and seagrass beds. All locations were within protected areas, with the

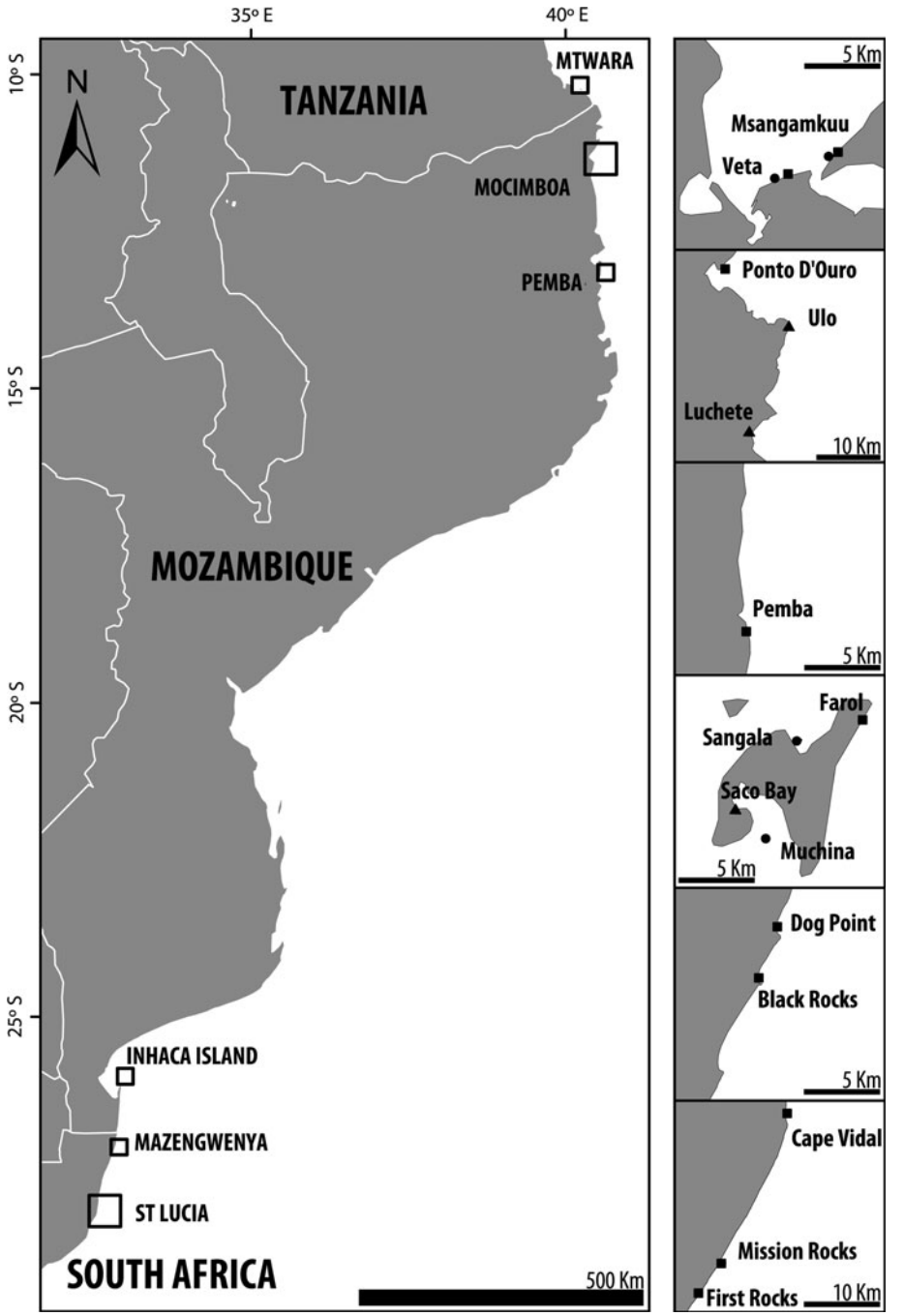


Fig. 1 The TRANSMAP sampling *Locations* on the east coast of Africa. The *Transects* sampled in each *Location* are detailed in the *insets*, from *top* to *bottom*: Mtwara, Mocimboa, Pemba, Inhaca Island, Mazengwenya, St. Lucia. Samples taken from beaches (*filled square*), seagrasses (*filled circle*) and mangroves (*filled triangle*)

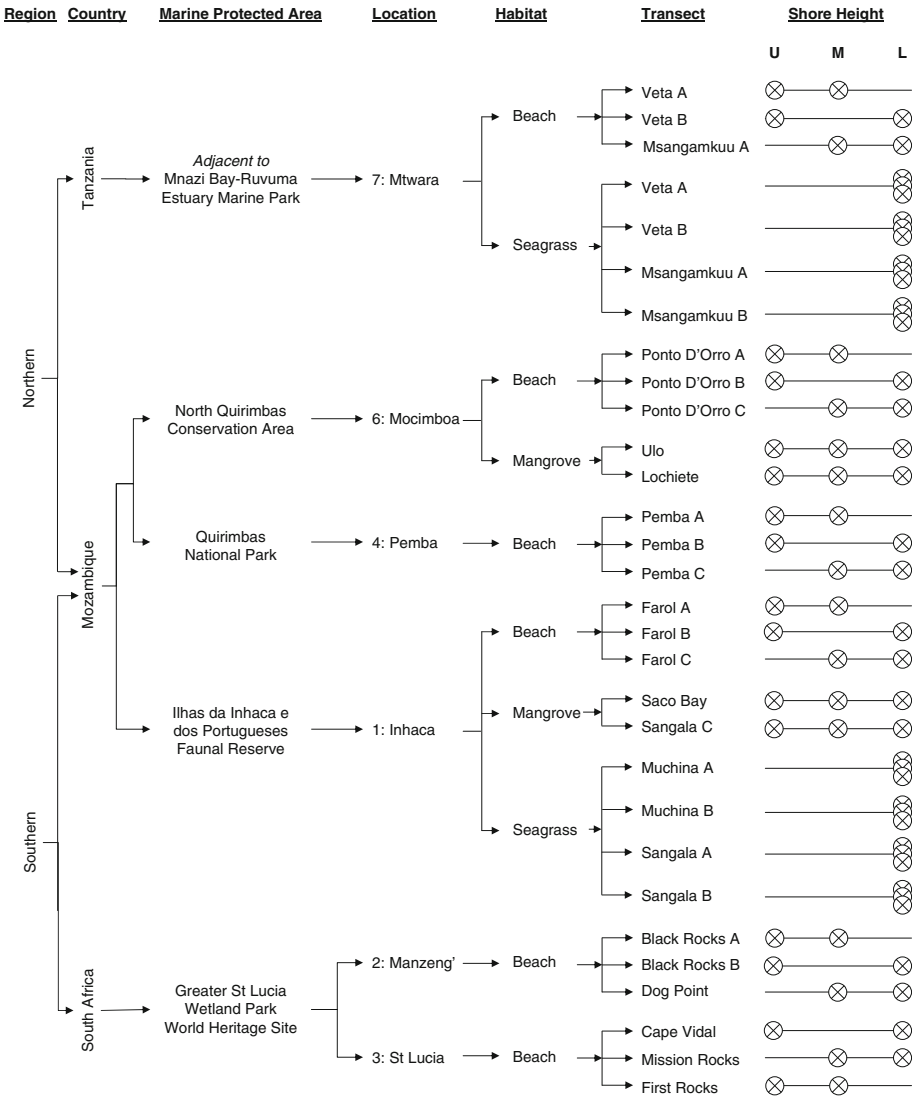


Fig. 2 Schematic showing the sampling strategy. Each symbol represents one sample. *U* Upper-shore, *M* mid-shore, *L* lower-shore, *Manzeng'* Mazengwenya

exception of Mtwara. In order to maximise sampling coverage, in each *Region* beaches were studied at three *Locations* and at one of these *Locations* mangroves and seagrasses were also studied. Beaches were sampled along three transects (1–20 km apart) and mangroves along two. Along these transects, both beaches and mangroves were sampled at three shore heights (lower-, mid- and upper-shore stations), with two replicates from each shore height across the three transects (Fig. 2): *Locations* were therefore taken as the functional experimental unit (six replicates in total), providing an initial assessment of regional biodiversity. Seagrass beds were sampled in two areas (10 s of metres apart), three replicate samples taken from each of two transects (10 m apart) in each area, making a

total of 12 replicate seagrass samples from each *Location*. See Fig. 1 for a summary of the sampling strategy and the numbers of replicates taken for each *Habitat*.

All beaches were clean, sandy and comprised material from both coastal erosion and coral-reef origin. Mangrove transects comprised three forest communities corresponding to shore height, in the *Northern Region* (Mocimboa, Mozambique) these were: *Sonneratia alba*, lower shore; *Rhizophora mucronata*, middle; *Avicennia marina*, upper. In the *Southern Region* (Inhaca, Mozambique) *Sonneratia alba* was not recorded and the mangrove transects were instead composed of *A. marina* on the upper and lower shores, and *R. mucronata* on the mid-shore. Seagrass sampling was restricted to *Thallasia hemprichii*-dominated patches, this being one of the most common species in the Western Indian Ocean (of thirteen known species in total) forming extensive beds usually in sheltered habitats or on intertidal flats (see Gullstrom et al. 2002 for review). Surprisingly, this will be one of only a few studies of [meiofaunal] assemblages in seagrass beds in the Southern Hemisphere (Boström et al. 2006; Edgar et al. 1994; Edgar 1999; De Troch et al. 2001, 2006; Paula et al. 2001).

Sampling methods

Meiofaunal sampling strategy and methods were designed by TJF. Sampling training following these protocols was provided by SCDH and was undertaken in Mozambique by SCDH and AM, in South Africa by DG, and in Tanzania by NJ, DJM and SY. All sampling was conducted during spring tides between May and September 2006, with the exception of the seagrass samples from the *Southern Region*, which were collected in June 2007. Cylindrical Perspex corers of approximately 5.7 cm internal diameter (25 cm^2 sampling surface), 30 cm length and with the bottom edge bevelled, were used to take 15 cm-deep sediment cores by hand. Samples were washed into storage pots with 4% formaldehyde buffered by excess borax.

Two additional core samples were taken from each station for granulometry and organic matter analysis. Also, where possible, a hand-held GPS device was used to record transect positions. The sampling sites were extremely inaccessible, limiting the amount of equipment and number of samples that could be safely carried, therefore, in some cases, environmental parameters which were not recorded at the time of sampling were estimated from other available data: GoogleEarth (http://earth.google.com/) was used to estimate habitat width (measured as extent of mangroves and seagrass beds along the coast and as distance between major headlands for beaches), maximum habitat elevation (measured at the most inland extent of mangroves and seagrass beds and as the highest sandy point on beaches), and true sampling height; rainfall and temperature data were taken from the World Weather Information Service (http://www.worldweather.org/), and the position of offshore coral reefs were taken from Reefbase (http://www.reefbase.org/).

In total 44 environmental parameters were collated: they are listed in Table 1.

Meiofaunal extraction

Meiofaunal sample extraction and enumeration methods were devised and developed by TJF and NB and undertaken by GMB, CL and NC. Sediment cores were washed over a 45 μm mesh sieve with filtered tap-water; no upper mesh limit was applied to ensure inclusion of adults of larger meiofaunal species. The beach samples were on the whole very 'clean' allowing for extraction by a series of ten decants in filtered tap-water with a stoppered 2-l cylinder. Some seagrass and mangrove samples, however, contained

Table 1 List of collated environmental parameters, sorted by sampling scale

Location	Transect	Station	Sample
Inside MPA (yes/no)	Habitat type	Sampling height, m	Gravel (>2,000 μm)
Age of MPA	Sampling date	Latitude (decimal)[b]	Very coarse sand (2,000–1,000 μm)
Total marine area of MPA (km^2)	Inland habitat type	Longitude (decimal)[b]	Coarse sand (1,000–500 μm)
Max. tidal range (MHWS-MLWS)	Sublittoral fringing habitat type		Medium sand (500–250 μm)
MHWS	Offshore habitat type		Fine sand (250–125 μm)
MHWN	Direction of shore (seaward/landward)		Very fine sand (125–63 μm)
MLWN	Rural, 0; town, 1		Mud (<63 μm)
MLWS	Total habitat width		Median sediment grain size, mm
Av. daily temp min °C (sampling month)	Elevation at HW, m		Sediment sorting
Av. daily temp max °C (sampling month)	Habitat depth, HW-LW, m		Sediment skewness
Mean annual rainfall, mm	Beach slope		Sediment organic matter, %
Mean air temp, °C	Log(1/beach slope)		bdi = (1/s) * (a/Mz)
Mean total rainfall (sampling month), mm			BI = log 10(Mz * TR)/S)
Mean no. rain days (sampling month)			
Offshore current[a]			
Current, seasonal direction change[a]			

[a] Location/transect

[b] Station/transect

low-density detritus and required both water decantation and Ludox (1.15 sg) centrifugation (de Jonge and Bouwman 1977; Platt and Warwick 1988). Centrifugation was repeated ten times to ensure 95% extraction efficiency, the supernatant poured-off, rinsed with distilled water and stored in 4% formaldehyde after each spin and retained sediment was then re-suspended before each repeat spin.

Samples were poured into 8 cm diameter Petri dishes with 4% formaldehyde and enumerated under a dissecting stereo-microscope (minimum 40× magnification). Where high abundance or detrital content prevented clear enumeration, samples were sub-sampled using an Äsko sample splitter (Elmgren 1973) or, in exceptional cases, by 20× dilution. Specimens were identified to meiofaunal phylum by GMB, CL and NC using Higgins and Thiel (1988). True meio-infaunal polychaetes and other polychaetes were counted separately as 'Archiannelida' and 'Polychaeta', respectively. Copepod and nauplii abundances were combined to give a total Copepoda abundance and this value was used in all analyses.

Sediment analysis

Particle-size analysis of sediment samples was undertaken following the methods of Buchanan (1984) by the local authors. Granulometry was analyzed by dry-weight into 1Φ sediment fractions (where $\Phi = -\log_2$ of the particle diameter in mm), and the standard parameters of median diameter (MDΦ), sorting (the spread of particle size around the median) as quartile deviation (QDΦ), and skewness (the bias of the deviation above or below the median) as Φ-quartile skewness (SKqΦ) were calculated by RNB.

Sediment organic content (as percentage loss-on-ignition at 540°C) was calculated for all *Habitats* in Mtwara (Tanzania, *Northern Region*) and for the seagrass beds at Inhaca (Mozambique, *Southern Region*) by the local authors.

An extensive number of indices have been suggested to assess intertidal sedimentary habitats based on physical and biogenic parameters (see for example de la Huz and Lastra 2008), and based on the available data we were able to calculate the Beach Deposit Index [BDI = (1/slope) * (1.03125, mm)/median grain size, mm] (Soares 2003 in McLachlan and Dorvlo 2005), the Beach Index [BI = log 10((median grain size, $\Phi + 1$) * (tidal range)/slope)] and log(1/beach slope) (McLachlan and Dorvlo 2005).

Statistical analysis

Diversity indices [Shannon–Wiener index (H') and Pielou evenness (J')] were calculated from the raw abundance data using PRIMER v5 (Clarke and Gorley 2001), and GraphPad PRISM 4 for Windows (GraphPad Software, San Diego, CA, USA) was used to produced graphs of those data and bar graphs of percentage abundances. Variability of meiofaunal abundance and diversity indices within *Habitats* was tested by the non-parametric Mann–Whitney test in GraphPad PRISM 4. Variability of the univariate indices was tested by [Multi-]factorial ANOVA with crossed and nested factors (GLM) in STATISTICA v8 (StatSoft.com). *Region* and *Habitat* were treated as a crossed factors and *Location* as a nested factor (in *Region*). The dataset did not provide enough power to undertake a GLM analysis of the univariate indices against the environmental data.

Variability of the meiofaunal assemblages was tested by multivariate ANOVA of the abundance data using PERMANOVA with Bray–Curtis dissimilarity (Anderson 2001; McArdle and Anderson 2001): This was tested within *Habitats* only owing to the unbalanced nature of the data, crossed and nested factors as before. Further multivariate analyses were conducted in PRIMER v5 (Clarke and Gorley 2001), namely Bray–Curtis similarity, cluster analysis, analysis of similarities (ANOSIM), and BIOENV (Spearman rank correlation, p_w) between-site similarities by species abundance data (Bray–Curtis) and by best-fitting environmental data (Euclidian distances). Particularly, BIOENV provides an insight into the correlation between environmental parameters and the biotic community: by comparing all combinations of environmental data with the biotic community by Spearman rank correlation (p_s), it determines an 'optimum' combination of environmental variable which provides greatest correlation with the biotic community.

All multivariate analyses of the biotic data were conducted on fourth-root transformed data to account for highly variable abundances between samples: environmental data were normalised before analyses (Clarke and Warwick 1994).

Results

Environmental parameters

All available environmental data are presented in Appendices 1–5. Sediments across the *Regions* and *Habitats* were generally sandy; the seagrass beds had the finest sediments and the beaches the coarsest (average median grain size 243 and 506 μm, respectively). Beach sediments were generally coarse clean sands, well-sorted with very low skewness, whilst the mangrove and seagrass sediments were less-well-sorted medium-fine sands. Exceptions were the beach and mangrove sediments at Mocimboa which had a greater proportion of fine sands and silt–clay, respectively, whilst the beach and seagrass sediments at Mtwara included a more significant coarse sand fraction.

Sediment organic content was generally low where recorded: On the beaches at Mtwara organic content ranged between 1–2%, whilst in seagrass bed sediments at Mtwara and Inhaca it ranged between 2.6–4 and 1.2–2.3%, respectively.

The values for BDI and log(1/slope) were both very variable between *Regions* and *Habitats* as well as within seagrass *Locations*, limiting the usefulness of these indices. BI, however, was more easily interpreted across *Habitat* types, indicating generally mesotidal reflective beaches (average BI = 1.8) and mesotidal dissipative mangroves and seagrasses (average BI = 2.9 and 3.3, respectively). The *Southern Region* beaches tended to be more reflective than those in the *Northern Region* (Average BI = 1.4 and 2, respectively), reflecting the greater wave exposure in the *Southern Region*. The mangroves and seagrasses in the *Southern Region*, however, tended to be more dissipative than those in the *Northern Region*, perhaps reflecting the position of these locations on the leeward side of Inhaca Island.

A draftsman's plot of the measured environmental parameters showed that some were highly correlated (Table 2), suggesting that super factors were subsuming the effects of specific factors. To avoid skewing the results of BIOENV analyses these were 'estimated' and excluded, for example, BI was selected over log(1/beach slope) owing to its greater suitability for studies over wide spatial scales and tidal ranges (McLachlan and Dorvlo 2005); Latitude was selected over longitude, and MPA age was excluded owing to its high correlation with Latitude. Noticeably, mean total rainfall in the sampling month and latitude were not correlated, highlighting a non-linear relationship between latitude and geographical province. In total the following parameters were excluded: Longitude, maximum tidal range, MHWN, average daily temperature minimum in the sampling month, mean number of rain days in the sampling month, age of MPA, log(1/beach slope) and habitat depth.

Meiofaunal abundance and diversity

Meiofaunal abundance ranged from 38.0 to 15714.4 individuals 10 cm^{-2} across the study, both values being recorded on sandy beaches (Fig. 3), although the majority of samples recorded abundances <5,000 individuals 10 cm^{-2}. The highest values were recorded in the upper-shore at Mocimboa beach (a result of the nematode, copepod and ostracod abundances) with abundance and diversity reducing to the lower shore. An opposite zonation was seen on Pemba beach and in the mangrove samples, whilst at Mtwara beach the mid-shore showed the highest abundance, and none of the *Southern Region* beaches exhibited a clear difference of abundance with shore height. Meiofaunal abundance in seagrass sediments was similarly variable within *Transects* and between *Regions*.

Table 2 Draftman's plot of environmental parameters—only factors with high correlation values are shown, significant correlation is highlighted in bold print

	Latitude	Beach slope	BI	MHWS	Av. daily temp max (sampling month)	Av. no. rain days (sampling month)	Longitude	Max. tidal range
Longitude	**0.99**	−0.29	0.05	0.80	0.85	−0.59	–	–
Age of MPA	**−0.92**	0.39	0.12	−0.54	−0.65	0.26	**−0.93**	−0.73
Habitat depth	−0.29	**0.93**	0.73	−0.06	−0.15	−0.17	−0.32	−0.18
Log(1/beach slope)	0.05	−0.76	**−0.97**	−0.11	−0.09	0.41	0.09	−0.02
Max. tidal range	**0.91**	−0.17	0.16	**0.97**	0.87	−0.80	**0.92**	–
MHWN	0.79	−0.06	0.26	**1.00**	0.85	**−0.90**	0.79	**0.96**
Av. daily temp min (sampling month)	0.87	−0.22	0.19	0.80	**1.00**	−0.79	0.84	0.85
Av. total rainfall (sampling month)	−0.73	−0.16	−0.52	−0.89	−0.83	**0.96**	−0.71	−0.85

Those factors in the left hand column were excluded from further analyses

A total of 18 taxa were recorded; Nematoda, Copepoda (Harpacticoida), Oligochaeta, Ostracoda, Tardigrada, Foraminifera (Hard), Polychaeta, Archiannelida, Halacarida, Turbellaria, Collembola, Kinorhyncha, Rotifera, Gastrotricha, Amphipoda, Isopoda, Mystacocarida and Nemertina. The latter four taxa were rare and grouped as 'others', the rest were found across the beaches, and Rotifera and Kinorhyncha were infrequently recorded: Rotifera were more common in seagrass beds and Kinorhyncha in mangrove sediments. Gastrotricha, Rotifera, Collembola and Archiannelida were not recorded from mangroves, whilst only the Collembola were absent from the seagrass samples.

Nematoda was the most dominant taxon, accounting for 49% of beach meio-infauna, 78% of mangrove meio-infauna, and 70% of seagrass meio-infauna (Fig. 4).

Multifactorial ANOVA of the univariate data identified differences across *Habitats*, *Habitat* * *Regions* and *Locations* (*Regions*), but the analysis did not have enough power (Table 3). The univariate results for each dependant variable were therefore examined: Abundance was significantly different across *Habitats*, *Habitat* * *Regions* and *Locations* (*Regions*) (ANOVA, $P < 0.01$ for each), but not *Regions*. The number of taxa per sample was significantly different between *Habitats* and *Locations* (*Regions*) (ANOVA, $P < 0.05$ for both), being highest on the beaches. Diversity and evenness were also significantly different between *Habitats* and *Location* (*Region*) (ANOVA, $P < 0.05$ for both), but not between *Regions*, and there was no interaction effect.

Beaches

On average, abundance was significantly higher on the beaches in the *Northern Region* than in the *Southern Region* (Mann–Whitney $U = 42.00$, $P < 0.001$), but none of the diversity indices indicated any significant difference between *Regions*. Taxon dominance was most variable within the beaches, with differences also between shore heights within *Locations*. On the beaches in the *Northern Region* nematodes dominated all shore heights at Mocimboa (Mozambique) and Mtwara (Tanzania), whilst at Pemba (Mozambique) copepods dominated the lower-shore and foraminiferans the mid-shore. On the *Southern Region* beaches copepods dominated the mid- and lower-shore at the Manzengwenya and

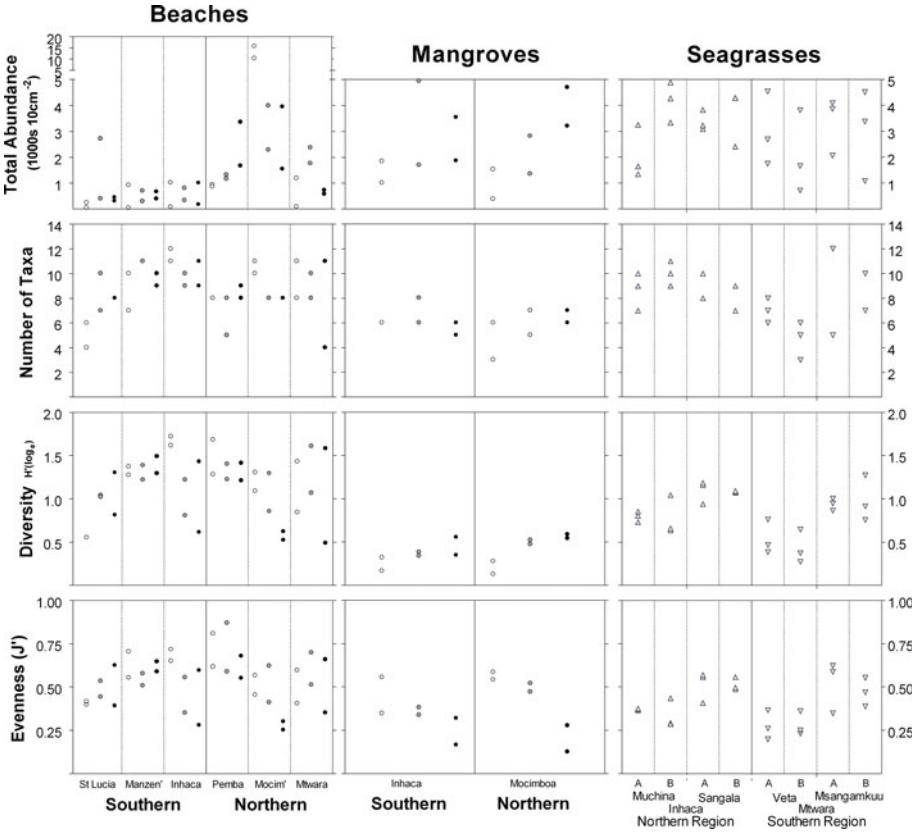


Fig. 3 Meiofauna abundance and diversity by *habitat*. *Open circles* upper-shore, *grey circles* mid-shore, *black circles* lower-shore, *open triangles* seagrass. Each replicate is shown, where less than two values are seen in a column, two replicates have the same value

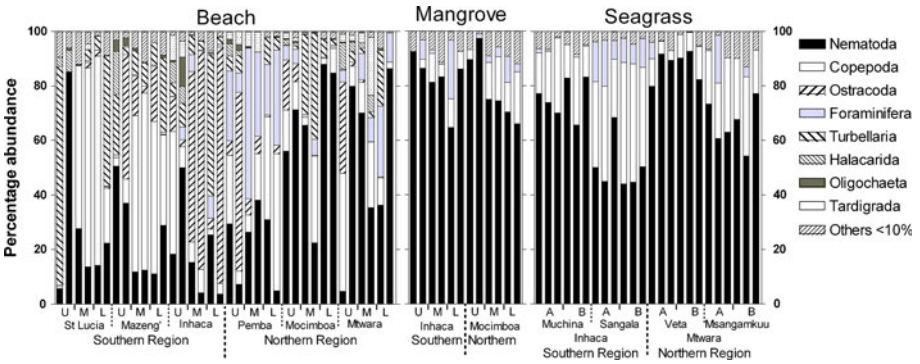


Fig. 4 Stacked column graphs of meiofaunal assemblage by percentage dominance. *U* Upper-shore, *M* mid-shore, *L* lower-shore, *A* station A, *B* station B, Manzeng' Mazengwenya

Table 3 Multivariate tests of significance, effect sizes, and powers for Wilks test

	Value	*F*	Effect	Error	*P*	Partial eta-squared	Non-centrality	Observed power ($\alpha = 0.05$)
Intercept	0.017	857.972	4	59.000	0.000	0.983	3431.888	1.000
Habitat	0.455	7.106	8	118.000	0.000	0.325	56.850	1.000
Region	0.958	0.640	4	59.000	0.636	0.042	2.560	0.197
Location (region)	0.436	3.534	16	180.886	0.000	0.238	56.542	1.000
Habitat * region	0.707	2.792	8	118.000	0.007	0.159	22.337	0.929

St. Lucia (South Africa), whilst at Inhaca Island (Mozambique) ostracods dominated the mid-shore. Generally, no trend could be identified for the upper-shore, and this was also the case for the lower-shore at Inhaca Island.

Mangroves and seagrasses

On average, meiofauna abundances in mangrove and seagrass beds were similar. The meiofaunal assemblages recorded in the mangroves showed no significant difference in abundance or diversity between the *Regions*. Nematoda accounted for >60% of abundance in all mangrove samples, with copepods being much less abundant (on average 8%), and only either Foraminifera, Turbellaria or Kinorhyncha (once) also representing >5% of samples. At Inhaca (*SR*) the mangrove assemblages tended to be denser than on the adjacent beach whilst at Mocimboa (*NR*) they tended to be less dense than the adjacent beach.

For the Seagrasses, the number of meiofaunal taxa, S, was significantly lower at Mtwara (*Northern Region*) than at Inhaca (*Southern Region*) (Mann–Whitney $U = 27.50$, $P < 0.05$), but abundance, diversity (H') and evenness were not significantly different. Nematodes were again most dominant (44–92% of individuals), followed by more abundant copepod populations (3–44% of individuals) than in mangroves, nematodes always comprised >50% of the assemblage at Mtwara, whilst copepods were more dominant in the *Southern Region*. Only the foraminiferans and polychaetes additionally represented >5% of individuals in some seagrass samples. At Inhaca, meiofaunal diversity in the seagrass beds and beach were similar, whilst at Mtwara the seagrass beds supported a less diverse meiofaunal assemblage than the adjacent beaches.

Multivariate analysis

The patchy distribution of taxa was such that meiofaunal assemblages varied significantly with *Region* and *Habitat* (ANOSIM, both $P < 0.01$: Table 4), although PERMANOVA analysis of the individual data sets (by *Habitat*) suggested that only the beach assemblages were significantly different between *Regions* (Table 5). Pair-wise a posteriori comparisons show that assemblages were significantly different between seagrass *transects* within *Regions* ($P < 0.01$), but beach *Locations* within-*Regions* were not significantly different ($P = 0.09$).

Table 4 Simple two-way crossed multivariate ANOVA (ANOSIM) of all meiofaunal assemblage data (data fourth-root transformed) to investigate differences between habitats and regions

	Sample statistic	Significance, *P*
Tests for differences between HABITAT groups (across all region groups)		
Global test	0.393	0.001
Pairwise tests		
Beach vs. mangrove	0.377	0.002
Beach vs. seagrass	0.417	0.001
Mangrove vs. seagrass	0.53	0.001
Tests for differences between REGION groups (across all habitat groups)		
Global test	0.319	0.001

Table 5 Results of multivariate PERMANOVA analyses used to investigate variability of meiofauna assemblages (data fourth-root transformed) within habitats between regions: results of three separate analyses undertaken on the beach, mangrove and seagrass data

Source	Beach		Mangrove	Seagrass	
	Region	Location (region)	Region	Region	Transect (region)
Degrees of freedom	1	4	1	1	2
Sum of squares	5496.25	4839.06	925.74	3016.97	2297.37
Mean squares	5496.25	1209.77	925.74	3016.97	1148.69
F	4.54	1.53	1.13	2.63	3.82
P (perm)	0.10	0.07	0.39	0.33	0.002
P (Monte Carlo)	0.01	0.09	0.35	0.14	0.004

Bray–Curtis Similarity of the individual samples showed that mangrove and seagrass assemblages were most similar and that the beach assemblages were divided by region with the those from *Southern Region* most distinct. For clarity, the group-average cluster-analysis of similarity is shown for the data averaged by *Location* and *Habitat* (Fig. 5). The two seagrass sites are shown to support different assemblages, the assemblage at the Mtwaran site being more similar to the adjacent beach and the Inhaca site more similar to the adjacent mangrove: This probably reflects the difference in the position of these beds, the Mtwaran seagrass beds being adjacent to the beach, extending into the intertidal, whilst the Inhacan seagrass beds were sheltered by the island and located at low-water, seaward of mangrove forests.

BIOENV analysis of the sample data indicated that the environmental parameters best correlating to the pattern of the meiofaunal assemblages (fourth-root transformed abundance data) were height of the sampling station, granulometry (percentage coarse sand) and mean number of rain days in the sampling month ($p_w = 0.51$). In addition, the maximum habitat elevation (as HW for beaches and mangroves and highest extent of seagrasses) was a key parameter (Table 6a).

Owing to its treatment of each sample as an independent data point, BIOENV analysis is a robust technique; however, the output from the analysis here is likely to be skewed by the greater number of beach samples. Indeed repeating the analysis for each *Habitat* in-turn

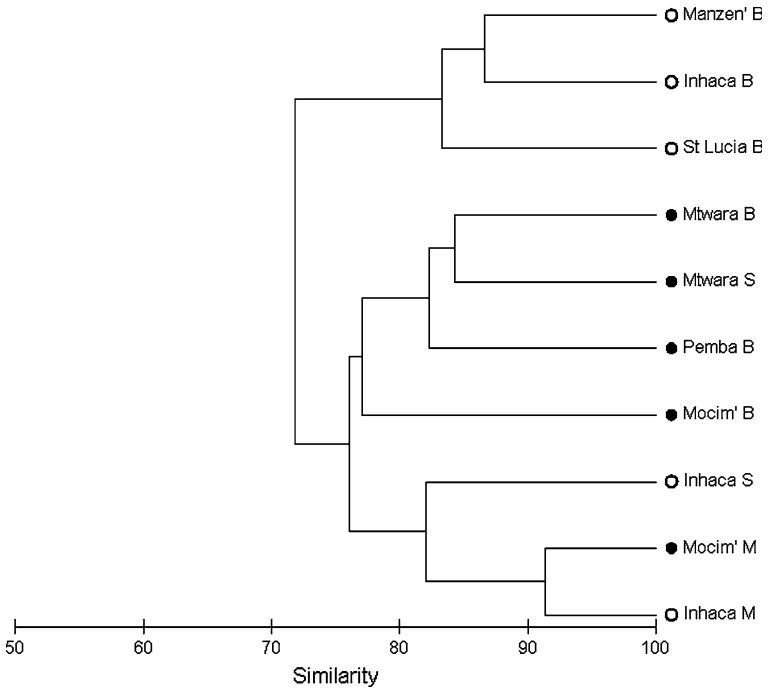


Fig. 5 Cluster analysis of Bray–Curtis similarity of meiofauna assemblages by location (four-root transformed data). Branches are labelled as '*Region_Location_Habitat*': *Solid circle* Northern Region, *open circle* Southern Region. Location abbreviations are *Manzeng'* Mazengwenya, *Mocim'* Mocimboa. Habitats are coded *B* beach, *M* mangrove, *S* seagrass

indicates this (Table 6b–d)—for beaches, the coarse-sand fraction and sampling height again contribute to the best fit parameters, but additionally so do latitude, maximum air temperature during the sampling month and size of the MPA ($p_w = 0.377$). For the mangroves, sampling height, coarse sand fraction and BDI were contributory ($p_w = 0.64$); whilst for seagrasses the assemblage pattern was best correlated to the fine and very fine sand fraction, latitude, habitat width and maximum habitat elevation ($p_w = 0.568$).

Discussion

Habitat conditions

All *Locations* and *Habitats* recorded sediment median grain diameter between 180 μm and 1 mm on average and more than 95% of sediment samples contained less than 5% silt/clay, indicating that sediments tended to suspend rarely and supported an interstitial fauna (Wieser 1959; Boaden 1968). Wieser (1959) first suggested a partition between interstitial and burrowing fauna at a median diameter of 2 mm. Later McLachlan et al. (1981) suggested that sediments with a median diameter greater than 3.3 mm would be dominated by harpacticoid copepods and that those with a median diameter less than 3.3 mm would be dominated by nematodes. However, we found that the dominant phyla show no correlation with this index of sediment type. At Pemba, for instance, sediment median diameter on the

Table 6 BIOENV analysis best fit parameters

	a. Across all habitats	b. Beaches	c. Mangroves	d. Seagrasses
No. of variables	3	5	3	5
Spearman's rank correlation, p_w	0.510	0.377	0.639	0.568
Contributing variables (single factor correlation, p_w)	Sampling height, m (0.420) Mean no. rain days (0.311) Coarse sand, % (0.223)	Latitude (0.288) Max. temp (0.255) Sampling height, m (0.223) Coarse sand, % (0.094) Size of MPA (0.155)	Sampling height, m (0.515) Coarse sand, % (0.259) BDI (0.200)	Fine sand, % (0.488) Very fine sand, % (0.322) Latitude (0.330) Habitat width (0.453) Max. habitat elevation (0.427)
Additional highly correlating single variables (single factor correlation, p_w)	Elevation at HW, m (0.310)	Very fine sand, % (0.283) MHWS (0.271) Mean no. rain days (0.218) MLWN (0.205)	–	Very coarse sand (0.408) Mud, % (0.394) Size of MPA (0.375) MHWS/MLWS/MLWN (0.375)

The environmental parameters providing the best Spearman's rank fit of site similarity with site similarity by meiofaunal assemblage (data fourth-root transformed). Abiotic data is transformed and standardised

beaches range between 0.3 and 0.9 mm, yet nematodes, copepods, foraminiferans and ostracods were each dominant in at least one sample.

The multivariate analyses never found median grain size to correlate with meiofaunal assemblages, nor sediment skew or kurtosis, suggesting that the use of these parameters to define habitat-type is too simplistic. BIOENV analyses consistently identified specific granulometric 1Φ size classes, in addition to latitude or rainfall and some parameter of wave exposure (e.g. shore height, maximum habitat height, slope, BDI, BI, tidal range). These finding appear to support the hypothesis of Moore (1972) that tropical intertidal assemblages are physically-controlled systems. They are also in agreement with data from Alongi (1987a), who found elevation and environmental parameters such as rainfall and sediment temperature to correlate with meiofaunal assemblages.

The BIOENV output also supports the hypothesis that beaches are predominantly controlled by physical forces related to wave exposure (McLachlan 1977a; Moreno et al. 2005; de la Huz and Lastra 2008). However, although our data indicate a strong correlation between the meiofauna assemblages and physical parameters, it does not include the biochemical or other [macro-/mega-fauna] biotic data to test these hypotheses directly.

Available data also suggest that low organic carbon content is the common state in intertidal sediments throughout both *Regions* and across *Habitats* and confirms the variability of these habitats. Organic carbon values recorded in seagrasses elsewhere range extensively, for example: 1.5–5.7%, De Troch et al. (2001); 2–15%, Paula et al. 2001; 0.3–0.5%, Monthum and Aryuthaka (2006). Equally, the sandy nature of the mangrove sediments here may indicate low organic carbon content, as recorded by others (e.g. 4–14%, Netto and Gallucci 2003; 2.7–22.5%, Alongi 1987a; 0–22%, Schrijvers et al. 1995). Although Schrijvers et al. (1995) found that sandier sediments were associated with mangroves in the high tide zone, or where mangroves were less dense or exploited, this

may also reflect distance to an organics/mud source and degree of shelter (Nybakken 1997).

Meiofaunal assemblages

Beaches

In both *Regions* meiofaunal abundance and the number of meiofaunal taxa recorded were generally similar to those found in similar habitats elsewhere (McLachlan 1977a, b; Pattnaik and Rao 1990; Rodriguez et al. 2001; Pinto and Santos 2006; Albuquerque et al. 2007). Abundance and distribution of intertidal sandy-beach meiofauna has been extensively studied and assemblage structure is generally attributed to physical forces related to wave exposure. These include sediment grain size and sediment structure, water circulation, oxygen content, and physical stability presenting 'physical-horizontal and chemical-vertical gradients' (Armonies and Reise 2000), which in turn influence food supply (McLachlan 1977b; Rodriguez et al. 2001; Moreno et al. 2005; Albuquerque et al. 2007; de la Huz and Lastra 2008).

Meiofaunal density was higher on the mid- and lower-shore at all but the Mocimboan *Location*, suggesting this was the only non-exposed site (McLachlan 1977a). Beach slope, tidal range and sediment-sorting at this *Location* did not differ significantly from the other *Locations*, however. The Mocimboan beach did record on average much higher densities per 10 cm^{-2}, which is indicative of reflective beaches (McLachlan et al. 1996; Rodriguez et al. 2001; Urban-Malinga et al. 2004). In fact all the beaches appear to be intermediate in state, but the various patterns of meiofaunal diversity and assemblage structure with shore height suggest that they experience different levels of wave exposure (McLachlan et al. 1996; Rodriguez et al. 2001).

Meiofaunal assemblage structure was very variable across the study. Generally nematodes were most abundant in the *Northern Region* and copepods in the *Southern Region*, probably reflecting greater dominance of copepods with increased perturbation by wave activity (McLachlan 1977a). However, ostracods, foraminiferans and turbellarians were also dominant in some samples, corresponding with the findings of other tropical and sub-tropical studies (e.g. Hulings 1974; Ansari et al. 1990; Rodriguez et al. 2001). Dominance of turbellarians at high water at St. Lucia was also noted by Dye et al. (1981). The dominant taxa on the mid- and lower-shore differed between our studies; possibly reflecting changes in environmental conditions with time (Gourbault et al. 1998; Pattnaik and Rao 1990; Hooge 1999; Gomes et al. 2002; Albuquerque et al. 2007).

On average, abundance was higher and diversity lower in the tropics (*Northern Region*) corresponding with other studies (see Table 7). That the sub-tropics (*Southern Region*) had a greater frequency and co-occurrence of the 'other' taxa emphasises this trend. However, other factors—primarily oligotrophic versus upwelling offshore waters, wave exposure and proximity to estuarine outflow—may confound our interpretation of these results with regard to latitude or geographical province.

Mangroves

Meiofaunal abundances recorded in the mangrove forest samples were within previously recorded ranges; Gomes et al. (2002) recorded in excess of 10,000 individuals 10 cm^{-2} on

Table 7 Comparison of meiofaunal diversity recorded in tropical and subtropical regions

Location	Latitude	Meiofaunal taxa, S	Total meiofauna average abundance	Grain size, mm		
				Median	Mean	Citation
Coroa do Aviao, Brazil	8 S	12	2950.0	0.22	0.24	Pinto and Santos (2006)
Mtwara, Tanzania	10 S	14	1115.5	0.51	–	This paper
Mocimboa, Mozambique	11 S	13	6272.2	0.46	–	This paper
Pemba, Mozambique	13 S	11	1546.5	0.58	–	This paper
Guadeloupe	16 N	13	–	0.36	–	Renaud-Mornant and Gourbault (1984)
Gopalpur, India	19 N	13	613.4	–	0.30	Pattnaik and Rao (1990)
Emirate	20 N	14	396.8	–	0.25	Kotwicki et al. (2005)
Inhaca, Mozambique	26 S	14	566.3	0.68	–	This paper
Mazengwenya, South Africa	27 S	14	502.0	0.42	–	This paper
St. Lucia, South Africa	28 S	13	683.9	0.39	–	This paper

some occasions in a tropical Brazilian mangrove, but the majority of studies record densities below 5,000 individuals 10 cm^{-2} (e.g. Dye 1983; Alongi 1987a; Netto and Gallucci 2003; Chinnadurai and Fernando 2003, 2006). No significant difference in abundance or diversity was found between the *Regions*. Yet, despite the low number of replicates, shore height was identified as a significant factor by the BIOENV analysis.

We found a clear trend of increasing abundance from high to low shore, in agreement with other authors (Olafsson 1995; Sasekumar 1994), and which was unrelated to mangal type as also found by Gee and Somerfield (1997). It is probable that site-specific abiotic factors such as wave and areal exposure and biotic factors such as grazing mask mangal-specific factors. For example, the rate of transport of litter away from the source tree or forest and the extent of sediment reworking are likely to vary between the locations (Mackey and Smail 1995; Day et al. 1996), whilst crab grazing may result in up to 100% leaf removal beneath *Avicennia marina* but 0% beneath *Sonneratia* (Olafsson et al. 2002). Where meiofaunal abundance has been found to directly correlate to mangal species (Vanhove et al. 1992), it probably reflects a longer residence time of dropped leaves: Mangrove leaf tannins (Alongi 1987b) and species-specific leaf nitrogen content and degradation rates (McKee and Faulkner 2000) inhibiting benthic fauna.

High dominance of nematodes is the common state recorded in mangroves, independent of sediment type. The general trend of increasing diversity down-shore, accompanied by decreasing nematode dominance, was comparable to other studies (Vanhove et al. 1992; Olafsson 1995; Sheridan 1997; Netto and Gallucci 2003), probably reflecting increasing submergence time.

Of the available environmental data, the pattern in meiofaunal assemblage structures in the mangroves was best described by sampling height, percentage coarse sand and BDI. Granulometry parameters are usually found to be important for mangrove meio-infaunal communities (as in other habitats), but additional factors identified vary with authors, partially depending on the parameters measured. These include oxygen content and redox potential (Dye 1983; Vanhove et al. 1992), salinity and photosynthetic pigments [as a proxy for food sources] (Gomes et al. 2002), sediment organic content (Olafsson et al. 2000), sediment temperature (Alongi 1987a), mangrove stand densities (Schrijvers et al. 1995; Dye 2006), mangrove-derived tannins (Alongi 1987b; Alongi and Christoffersen 1992) and sediment biochemistry (Ndaro et al. 1995). Most of these parameters are likely to interact with wave exposure and salinity, supporting the conclusion of Somerfield et al. (1998), that, "Meiofaunal communities in tropical soft sediment mangrove estuaries respond primarily to salinity and exposure gradients as in temperate non-vegetated estuaries". That other studies have not found salinity to be a key factor (e.g. Olafsson 1995; Olafsson et al. 2000), may suggest a split in meio-infaunal ecology between estuarine and non-estuarine mangrove forests. Salinity should be perhaps measured in terms of rate, duration and magnitude of change, if any, rather than as absolute values, similar to findings in non-vegetated estuarine/brackish water habitats (Attrill 2002; Barnes et al. 2008; Ferrero et al. 2008).

Seagrasses

Meiofauna abundances were generally high but very variable within the seagrass beds, but this appears to be a common state, and abundances were within the range recorded in other studies elsewhere, as were the number of taxa and the dominance of nematodes (Paula et al. 2001; De Troch et al. 2001, 2006; Monthum and Aryuthaka 2006). Meio-infaunal abundance has been shown to positively correlate with macrophyte biomass (Ansari and Parulekar 1994), but this is thought to reflect increased food supply [as detritus] rather than a structural influence (Edgar 1999; De Troch et al. 2001): Significant variation of grain size, pigments, nitrate, nitrite and organic matter has been reported within meadows (Paula et al. 2001; De Troch et al. 2001) and these parameters vary significantly with season (Danovaro 1996). This is in agreement with the BIOENV results reported here, with high within-bed variability of meiofaunal assemblages correlating with benthic parameters.

De Troch et al. (2001) found that meiofaunal assemblages were structured by physical factors in pioneer and intertidal seagrass meadows, but by biogenic parameters in climax and subtidal meadows. Certainly, the greater variability of abundance and diversity *within* sampling stations within meadows at the *Northern Location* may suggest an increased disturbance there (Warwick and Clarke 1993). Not only were the samples from Mtwara generally of lower meiofaunal diversity, but they also revealed assemblages more similar to the adjacent beach samples than other vegetated sites. This may result from disturbance by more frequent tidal exposure and/or greater ease of access to these intertidal stations in comparison to the infra-/sub-littoral stations in the *Southern Location*: Our BIOENV analysis identified that the meiofaunal assemblage patterns were most closely correlated with physical, wave and areal exposure-related parameters, total habitat width and latitude, which would support this conclusion.

Lower meiofaunal diversity in the seagrass beds within the *Northern Location* may also suggest a lower productivity here than the seagrass beds in the subtropical *Southern*

Location (De Troch et al. 2006), the latter being more dense. However, with only one *Location* representing each *Region*, it is not possible to state at which spatial scale these differences occur. It is probable that the differences recorded are local, reflecting influence of MPA status (the Mtwara site lies just outside an MPA) and physical disturbance, but biogeographical factors may be also important. Additionally, seagrass beds show considerable seasonal variability of environmental parameters (Paula et al. 2001) and therefore the time lag between sampling these two *Locations* restricts our conclusions further.

Comparison between habitats

Comparative studies of meiofaunal assemblages between adjacent habitats are rare and a consistent pattern has not been identified. Here we are able to consider interactions between beaches and mangroves, and beaches and seagrasses, across *Regions* and at one *Location* we were able to study all habitats.

BIOENV analysis did not find meiofauna assemblage patterns within *Habitats* to correlate with the type of adjacent intertidal or off-shore habitat, or with the occurrence of offshore islands. No consistent pattern of abundance or diversity was found between adjacent *Habitats*, and no consistent pattern of interaction between *Habitats* was identified. Also, although the *Habitats* supported distinct assemblages (when samples for each *Habitat* were pooled from each *Location*), only the seagrasses at Inhaca supported a consistently distinct assemblage. It is possible of course that the simple binary classification used here was too simplistic, and that distance to and type of adjacent flora, sediment or reef habitat might give different results.

It has been shown that mangrove, seagrass and beach habitats, being often recorded together, can exhibit interaction effects: For example, a significant fraction of litter in mangrove forests may be composed of fresh seagrass (Alongi and Christoffersen 1992). Conversely the more slowly decomposing mangrove litter (de Boer 2000) may be transported to seagrass beds (Hemminga et al. 1994) and adjacent bare sediments (Alongi et al. 1989). It is possible that the variability recorded in this study in diversity and assemblage structure with shore height on beaches between *Locations*/within *Regions* reflected occurrence/absence of adjacent vegetated areas and rates and type of litter deposited. For example, at the two South African beach *Locations* there was no adjacent marine vegetation, and at the exposed St. Lucia beaches diversity was low on the upper shore and tended to increase down shore but at Mazengwenya where off-shore rocks provide some shelter diversity was high and stable down the beach. Equally, at *Locations* where adjacent marine vegetation occurred a different pattern was recorded, at the Inhaca and Mocimboa beaches, where adjacent mangroves and seagrasses were recorded, a steep decline in diversity (and evenness) from the upper to lower shore was recorded, whilst at Mtwara where seagrasses and beaches were contiguous, diversity was very variable at all shore heights.

Beaches and mangroves

Meiofaunal diversity, but not abundance, showed a similar pattern between adjacent beaches and mangroves across the two *Regions*. Sample diversity was depressed in the

mangroves relative to the beaches, in agreement with macrofaunal studies (Sheridan 1997). Abundance, however, appeared to be more influenced by local levels of wave exposure and concomitantly sediment structures: On the mid- and lower-shore meiofaunal abundances were significantly higher in the mangroves than beach site at Inhaca, but were similar at Mocimboa. On the upper shore, sample abundances were similar between the two *Habitats* at Inhaca but much lower in the mangrove than beach samples at Mocimboa. This clearly shows the difficulties in extrapolating findings beyond a single study area.

Beaches and seagrasses

In all seagrass beds, meiofaunal density was on average higher but diversity similar or lower than in adjacent beaches at the same *Location*. This probably reflects the shelter and stability provided by seagrasses which results in the deposition of finer sediments than on the beaches. These results fall between those recorded elsewhere: Some studies have found a positive relationship between faunal abundance *and* diversity and the presence of seagrass beds (Siebert and Branch 2007 *and references therein*). Others have recorded reduced or equal meiofaunal abundance in seagrass beds relative to bare sediments relating this to hydrological or predation regimes (Decho et al. 1985; Siebert and Branch 2007). In the former case, seagrass beds are suggested to proved increased resource availability for meiofauna (Danovaro 1996; De Troch et al. 2006). In the latter it is thought they provide 'better' shelter for macrofauna and small megafauna, resulting in increased predation of the meiofauna (Decho et al. 1985). The higher density but lower diversity recorded here would therefore suggest that the seagrass beds studied are subject to a non-physical (chemical) disturbance and may be resource-limited (De Troch et al. 2006).

Conclusions

Meiofaunal higher taxon assemblage structure has been used to describe patterns over global (Kotwicki et al. 2005), regional (Kotta and Boucher 2001), and local (Moreno et al. 2006, 2008) scales. With the data collected here we were able to comment on regional and local scales and compare meiofaunal assemblages across habitats. The presence of on average 2,500 individuals 10 cm^{-2} (or 2.5×10^6 individuals m^{-2}) and a total of 18 permanent meiofaunal taxa indicates the validity of using meiofauna to assess relatively disparate habitats which may have only sparse or dissimilar macrofaunal assemblages. Thus enabling environmental, community and faunistic analyses without significant destructive sampling or deleterious interference of sensitive conservation-related habitats.

Careful selection of sampling *Locations* resulted in relatively comparable benthic habitats—with regard to sediment type, tidal range and Beach State Index—being studied across the *Regions*. Even at the higher taxonomic level it was possible to differentiate between *Habitats* and *Regions* with both univariate and multivariate data. Number of taxa per sample was on average higher in the subtropical *Southern Region* than the tropical *Northern Region*, contradicting latitudinal diversity gradient hypotheses (Hillebrand 2004;

McLachlan and Dorvlo 2007) but in agreement with other meiofaunal studies (Lambshead et al. 2002; Kotwicki et al. 2005).

The observed assemblage patterns appear to result from a combination of factors, but principally wave and areal exposure and geography which in turn influence other habitat parameters, including granulometry and presence/absence of marine vegetation. The different seasonal patterns between the two *Regions* (one rain period in the *Southern Region*, two in the *Northern Region*) may also prove important. Seasonal changes (in parameters such as beach topology, interstitial salinity, upwelling, temperature, desiccation, rainfall, wave action and food supply) may influence recorded faunal assemblages as actual peaks and troughs in abundance, reflecting reproductive rates, but also owing to species- and taxon-specific vertical migration into sediments beyond sampling depth (Harris 1972; Hulings 1974; Nicholas 2001; Steyaert et al. 2001).

Despite only six samples representing each beach *Location*, we recorded some of the highest meiofaunal higher-taxa (beta) diversity for sandy beaches. Yet it is likely that our data underestimate soft-bodied fauna such as the Turbellaria, and comparison with other meiofaunal studies remain difficult whilst researchers continue to enumerate different subsets of the size-class. In hindsight, our study would have been improved if all taxa were separately counted rather than the rare taxa being grouped as 'others' at such an early stage. Nonetheless, the data presented here are a good estimate of meiofaunal assemblages in sandy habitats over the two *Regions* and contribute to the currently limited understanding of intertidal meiofauna in the EAME region, extending the work of Schrijvers, De Troch and Vanhove (Ghent University) in Kenya, Olafsson (Stockholm University) in Zanzibar and McLachlan, Dye and others (University of Port Elizabeth) in South Africa.

We can conclude that, across the three habitats studied, the two Transboundary Regions provide complementary ecosystems and support different meiofaunal assemblages. Between *Habitats* we have shown that meiofaunal assemblages on beaches are distinct from those in mangroves and seagrasses, which support similar assemblages of meiofaunal major taxa, but that seagrass assemblages can be more similar to those on beaches when they are intertidal and/or under stress. Additionally, detailed data from the beaches highlight the importance of multi-location sampling to determine gamma diversity. Further year-round study is recommended, including non-sandy habitats and additional biochemical and physical measurements, in order to determine causality of the abundance patterns observed in the EAME benthos.

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Appendix 1 Environmental data across regions

Region	Country	Location	MPA's		Tides					Currents	
			Total area (km^2)	Age, years	Maximum range, m	MHWS, m	MHWN, m	MLWN, m	MLWS, m	Offshore current	Seasonal change (y/n)
Northern	Tanzania	Mtwara	200	n/a	3.2	3.6	2.6	1.4	0.4	EACC/SEC	y
	Mozambique	Mocim'	1,430	4	3.8	4.5	3.2	2	0.7	SEC/MC	n
		Pemba	230	4	3.6	4.1	2.8	1.7	0.5	SEC/MC	n
		Inhaca	20	41	2.4	3.2	2.3	1.7	0.8	MC	y
Southern	South Africa	Mazeng'	408	20	1.74	2.1	1.47	0.97	0.37	MC/AC	n
		St. Lucia	414	27	1.74	2.1	1.47	0.97	0.37	AC	n

Region	Country	Location	Air temperature			Rainfall		
			Annual mean air temperature, °C	Av. minimum, sampling month	Av. maximum, sampling month	Annual mean, mm	Mean total, sampling month	Mean no. of days, sampling month
Northern	Tanzania	Mtwara	25.65	18.2	27.7	1,164	15	3
	Mozambique	Mocim'	25.8	18.2	27.7	1,000	11.3	1.6
		Pemba	25.8	18.2	27.7	895	11.3	1.6
		Inhaca	24.9	16.8	26.4	884	31.9	2.8
Southern	South Africa	Mazeng'	26	12.5	22.8	1,200	62	7.1
		St. Lucia	26	12.5	22.8	1,200	62	7.1

Appendix 2 Environmental data across beach transects

Region	Country	Location	Transect	Rural, 0; town, 1	Seaward, 0; landward, 1	Total habitat width, km	Inland habitat				
							Dune	Forest	Rock	Mangrove	Scrub
Northern	Tanzania	Mtwara	Veta	1	0	3.6	0	0	1	0	1
			Msang'	1	0	3.7	0	0	1	0	1
	Mozambique	Mocimb'	Ponto D'Ouro	0	0	2.9	0	1	0	0	1
		Pemba	Pemba	0	0	39.0	1	0	0	0	1
		Inhaca	Farol	0	0	12.0	1	1	0	0	0
Southern	South Africa	Manzeng'	Black Rocks	0	0	3.3	1	1	0	0	0
			Dog Point	0	0	10.6	1	1	0	0	0
		St. Lucia	Cape Vidal	0	0	66.0	1	1	0	0	0
			Mission Rocks	0	0	32.0	1	1	0	0	0
			First Rocks	0	0	32.0	1	1	0	0	0

Region	Country	Location	Transect	Fringing habitat				Offshore habitat		
				sandbank	Seagrass	Rock	Reef	Reef	Islands	Sand/mudflats
Northern	Tanzania	Mtwara	Veta	0	0	0	1	0	0	0
			Msang'	0	0	0	1	0	0	0
	Mozambique	Mocimb'	Ponto D'Ouro	0	1	1	0	1	1	1
		Pemba	Pemba	0	0	0	1	0	0	0
		Inhaca	Farol	0	0	1	1	0	0	0
Southern	South Africa	Manzeng'	Black Rocks	0	0	1	1	0	0	0
			Dog Point	0	0	1	0	0	0	0
		St. Lucia	Cape Vidal	0	0	0	0	0	0	0
			Mission Rocks	0	0	0	0	0	0	0
			First Rocks	0	0	1	1	0	0	0

Appendix 3 Environmental data across beach samples

Region	Country	Location	Transect	Latitude (decimal)	Longitude (decimal)	Sampling date	Topography				
							Elevation at HW, m	Depth, HW-LW, m	Slope	Shore height	Station height, m
Northern	Tanzania	Mtwara	Veta A	−10.26	40.17	16/07/2006	7	170	24.3	U	7.0
										M	3.5
			Veta B	−10.26	40.17	15/07/2006	7	170	24.3	U	9.0
										L	0.0
			Msangamkuu A	−10.24	40.20	22/09/2006	9	350	38.9	L	0.0
										M	4.5
	Mozambique	Mocimboa	Ponto D'Ouro A	−11.33	40.38	08/07/2006	15	90	6	U	15.0
										M	7.5
			Ponto D'Ouro B	−11.33	40.38	08/07/2006	6	50	8.3	U	6.0
										L	0.0
			Ponto D'Ouro C	−11.33	40.38	08/07/2006	16	100	6.3	L	0.0
										M	8.0
		Pemba	Pemba A	−13.26	40.56	13/07/2006	4	115	28.8	U	4.0
										M	2.0
			Pemba B	−13.26	40.56	13/07/2006	4	115	28.8	L	0.0
										U	4.0
			Pemba C	−13.26	40.56	13/07/2006	4	115	28.8	L	0.0
										M	2.0

Appendix 3 continued

Region	Country	Location	Transect	Latitude (decimal)	Longitude (decimal)	Sampling date	Topography				
							Elevation at HW, m	Depth, HW-LW, m	Slope	Shore height	Station height, m
Southern	Mozambique	Inhaca	Farol A	25.98	32.99	12/05/2006	20	110	5.5	U	20.0
										M	10.0
			Farol B	−25.98	32.99	14/05/2006	19	120	6.3	U	19.0
										L	0.0
			Farol C	−25.98	32.99	14/05/2006	23	140	6.1	L	0.0
										M	11.5
	South Africa	Manzengwenya	Black Rocks A	−27.13	32.83	11/08/2006	11	100	9.1	U	11.0
										M	5.5
			Black Rocks B	−27.13	32.83	11/08/2006	11	100	9.1	U	11.0
										L	0.0
			Dog Point	−27.10	32.84	13/08/2006	9	90	10	M	4.5
										L	0.0
		St. Lucia	Cape Vidal	−28.12	32.56	10/08/2006	14	95	6.8	U	14.0
										L	0.0
			Mission Rocks	−28.33	32.45	09/08/2006	22	95	4.3	M	11.0
										L	0.0
			First Rocks	−28.28	32.49	14/08/2006	18	120	6.7	U	18.0
										M	9.0

Appendix 3 continued

Region	Country	Location	Transect	Granulometry				Beach state	
				Median mm	Sorting (QDΦ)	Skewness (SKqΦ)	Sediment organics, %	BDI	BI
Northern	Tanzania	Mtwara	Veta A	0.77	0.87	−0.17	1.02	0.11	−1.31
				0.37	0.28	−0.01	2.03	0.11	−0.92
			Veta B	0.59	0.61	−0.01	2	0.21	−1.18
				0.32	0.50	0.03	1.22	0.03	−1.20
			Msangamkuu A	0.76	0.82	−0.05	1.78	0.12	−1.72
				0.23	0.49	−0.07	2.24	0.09	−1.83
	Mozambique	Mocimboa	Ponto D'Ouro A	0.32	0.57	0.03	n/a	0.54	−0.69
				0.36	0.74	−0.01	n/a	0.48	−0.64
			Ponto D'Ouro B	0.46	0.58	−0.02	n/a	0.27	−0.68
				0.63	1.57	0.48	n/a	0.20	−0.54
			Ponto D'Ouro C	0.54	0.69	0.11	n/a	0.31	−0.48
				0.42	0.67	−0.10	n/a	0.39	−0.59
		Pemba	Pemba A	0.58	0.48	0.09	n/a	0.06	−1.14
				0.90	0.59	0.01	n/a	0.04	−0.95
			Pemba B	0.90	0.56	0.01	n/a	0.04	−0.95
				0.45	0.56	0.00	n/a	0.08	−1.25
			Pemba C	0.31	0.59	0.00	n/a	0.12	−1.41
				0.35	0.47	−0.01	n/a	0.10	−1.36

Appendix 3 continued

Region	Country	Location	Transect	Granulometry				Beach state	
				Median mm	Sorting (QDΦ)	Skewness (SKqΦ)	Sediment organics, %	BDI	BI
Southern	Mozambique	Inhaca	Farol A	0.63	0.58	0.26	n/a	0.30	−0.56
				0.76	0.38	−0.02	n/a	0.25	−0.48
			Farol B	0.60	0.41	0.08	n/a	0.27	−0.64
				0.72	0.32	0.01	n/a	0.23	−0.56
			Farol C	0.63	0.39	0.05	n/a	0.27	−0.60
				0.73	0.29	0.01	n/a	0.23	−0.54
	South Africa	Manzengwenya	Black Rocks A	0.41	0.46	−0.02	n/a	0.28	−1.11
				0.25	0.54	−0.08	n/a	0.45	−1.32
			Black Rocks B	0.27	0.50	−0.01	n/a	0.42	−1.29
				0.28	0.47	−0.02	n/a	0.41	−1.27
			Dog Point	0.54	0.64	0.01	n/a	0.19	−1.03
				0.78	0.63	0.01	n/a	0.13	−0.87
		St. Lucia	Cape Vidal	0.29	0.45	0.00	n/a	0.52	−1.13
				0.37	0.39	0.07	n/a	0.41	−1.02
			Mission Rocks	0.40	0.38	0.04	n/a	0.60	−0.79
				0.44	0.51	−0.02	n/a	0.54	−0.75
			First Rocks	0.30	0.36	−0.04	n/a	0.52	−1.11
				0.54	0.56	0.00	n/a	0.29	−0.85

Appendix 4 Environmental data across mangrove and seagrass transects

Region	Country	Location	Habitat	Transect	Rural, 0; town, 1	Total habitat width, km	Inland habitat					Fringing habitat			
							Dune	Forest	Rock	Mangrove	Scrub	sandbank	Seagrass	Rock	Reef
Northern	Tanz'	Mtwara	Seagrass	Veta	1	3.0	0	0	1	0	1	0	0	0	1
				Msangamkuu	1	2.4	0	0	1	0	1	0	0	0	1
	Mozambique	Mocimboa	Mangrove	Ulo	0	16.5	1	0	0	0	0	0	1	1	0
				Lochiete	0	8.3	0	1	0	0	1	0	1	1	0
Southern		Inhaca	Mangrove	Saco Bay	0	1.0	0	0	0	0	1	0	1	0	0
				Sangala	0	0.6	0	0	0	0	1	0	1	0	0
			Seagrass	Muchina	0	0.4	0	0	0	1	0	1	0	0	0
				Sangala	0	0.5	1	1	0	1	0	0	1	0	0

Region	Country	Location	Habitat	Transect	Offshore habitat			Seaward, 0; landward, 1
					Reef	Islands	Sand/mudflats	
Northern	Tanz'	Mtwara	Seagrass	Veta	0	0	0	0
				Msangamkuu	0	0	0	0
	Mozambique	Mocimboa	Mangrove	Ulo	1	1	1	0
				Lochiete	1	1	1	0
Southern		Inhaca	Mangrove	Saco Bay	0	1	0	1
				Sangala	0	1	1	1
			Seagrass	Muchina	0	1	1	1
				Sangala	0	1	1	1

Appendix 5 Environmental data across mangrove and seagrass stations

Region	Country	Location	Habitat	Transect	Latitude (decimal)	Longitude (decimal)	Sampling date	Topography				
								Elevation at HW, m	Depth, HW-LW, m	Slope	Shore height	Station height, m
Northern	Tanzania	Mtwara	Seagrass	Veta C	−10.26	40.17	28/09/2006	6.0	300	50	L	0.0
				Veta D	−10.26	40.17	28/09/2006	8.0	205	25.6	L	0.0
				Msangamkuu A	−10.24	40.20	28/09/2006	1.0		460	L	0.0
				Msangamkuu B	−10.24	40.20	28/09/2006	1.0	240	240	L	0.0
	Mozambique	Mocimboa	Mangrove	Ulo	−11.41	40.47	05/07/2006	5.0	400	80	U	5.0
											L	0.0
											M	2.5
				Lochiete	−11.56	40.42	06/07/2006	8.0	300	37.5	U	8.0
											L	0.0
											M	4.0
Southern	Mozambique	Inhaca	Mangrove	Saco Bay	−26.04	32.92	01/05/2006	3.0	700	233	U	3.0
											L	0.0
											M	1.5
				Sangala C	−25.99	32.94	26/05/2006	6.0	1,400	233	U	6.0
											L	0.0
											M	3.0
			Seagrass	Muchina A	−26.05	32.93	02/06/2007	1.0	160	160	L	0.0
				Muchina B	−26.05	32.93	02/06/2007	1.0	160	160	L	0.0
				Sangala A	−25.99	32.95	03/06/2007	1.0	2,300	2,300	L	0.0
				Sangala B	−25.99	32.96	03/06/2007	1.0	2,300	2,300	L	0.0

Appendix 5 continued

Region	Country	Location	Habitat	Transect	Granulometry				Beach state	
					Median, mm	Sorting (QDΦ)	Skewness (SKqΦ)	Sediment organics, %	BDI	BI
Northern	Tanzania	Mtwara	Seagrass	Veta C	0.23	0.50	−0.11	4.00	0.09	−1.83
				Veta D	0.25	0.54	−0.06	3.27	0.16	−1.51
				Msangamkuu A	0.23	0.55	−0.10	2.60	0.01	−2.80
				Msangamkuu B	0.23	0.53	−0.10	3.45	0.02	−2.51
	Mozambique	Mocimboa	Mangrove	Ulo	0.29	0.84	−0.22	n/a	0.04	−1.86
					0.27	1.53	−0.78	n/a	0.05	−1.89
					0.47	0.68	−0.12	n/a	0.03	−1.65
				Lochiete	0.27	0.60	0.00	n/a	0.10	−1.56
					0.29	0.76	0.03	n/a	0.09	−1.53
					0.22	1.24	−0.65	n/a	0.13	−1.65
Southern	Mozambique	Inhaca	Mangrove	Saco Bay	0.23	0.57	−0.14	n/a	0.02	−2.63
					0.34	1.11	−0.38	n/a	0.01	−2.46
					1.71	1.23	0.50	n/a	0.00	−1.75
				Sangala C	0.31	0.63	0.00	n/a	0.01	−2.50
					0.26	0.53	−0.02	n/a	0.02	−2.57
					0.38	0.75	−0.09	n/a	0.01	−2.41
			Seagrass	Muchina A	0.31	0.59	0.02	1.14	0.02	−2.33
				Muchina B	0.15	1.02	−0.25	1.23	0.04	−2.65
				Sangala A	0.18	0.43	0.02	1.79	0.00	−3.73
				Sangala B	0.36	1.09	−0.13	2.26	0.00	−3.43

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