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REPORT

The structuring role of microhabitat type in coral degradation zones: a case study with marine nematodes from Kenya and Zanzibar

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Abstract Nematode genus assemblages were identified from four locations in coral degradation zones (CDZs) along the African east coast: Watamu and Tiwi Beach (Kenya) and Matemwe and Makunduchi (Zanzibar). Three microhabitat types were distinguished: coralline sediment, coral gravel and coral fragments. Nematode community composition was comparable to that of other studies dealing with the same habitat. The presence of a common genus pool in CDZs was reflected in the considerable similarities between samples. The addition of coral fragments as a habitat for nematodes resulted in an increased importance of taxa typical for coarse sediments and large substrata. Local and regional turnover were of the same order of magnitude. The structuring effect of microhabitat type clearly overrode the effect on a local and regional scale. Differences in sediment characteristics were more important in structuring the nematode assemblages than differences between the coralline sediment and coral fragments. No effect related to the three-dimensional structure of coral fragments was found. Differences between nematode assemblages in the coralline sediment and on coral fragments were attributed to the exposed nature of the latter habitat, its large surface area and its microbial or algal cover. Differences in available food sources were reflected in nematode trophic composition.

Keywords Coral degradation zones · Nematodes · Microhabitats · Spatial turnover · Indian Ocean

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Introduction

Numerous studies have investigated the major factors that structure nematode community composition in coral reef associated sediments (Alongi 1986; Boucher and Gourbault 1990; Gourbault and Renaud-Mornant 1990; Tietjen 1991; Ólafsson et al. 1995; Boucher 1997; Ndaro and Ólafsson 1999; Netto et al. 1999; Kotta and Boucher 2001; de Jesús-Navarrete 2003). These efforts have produced a list of variables that are, at least potentially, determinant: (1) mean sediment grain size, (2) sediment clay-silt content, (3) sediment sorting, (4) sediment oxygen content, (5) position of redox potential discontinuity (RPD) layer in the sediment, (6) organic content of the sediment, (7) extent of bioturbation by macrobenthos, (8) macrofloral biomass, (9) water depth, (10) longitude, (11) latitude and (12) sampling scale. The vast majority of these factors is related to sediment characteristics.

Coral reef associated sediments can be found in all functional zones of the reef, e.g. the reef crest, reef flat, outer reef, reef pools, reef lagoon, etc. Most of the studies mentioned above have however focused on

lagoons, which separate the reef platform from the adjacent land mass. In this zone, dead coral material coming from the main reef or from scattered coral thickets in the lagoon itself (e.g. from patch reefs), is progressively degraded into smaller pieces (coral gravel) until it becomes coralline sediment. Because of the dynamic character of this functional zone, the term Coral Degradation Zone (CDZ) will be used throughout the text when referring to the lagoon between the reef and the coast. As a result of this gradual process of degradation, the CDZ sediment will obviously be mixed with coral fragments of different sizes and shapes. The presence of coral degradation products (dead coral fragments, coral gravel) on and in the sediment may have a profound effect on nematode assemblage structure on a local scale. So far, these coral degradation products have not yet been considered as an ecologically valuable habitat in tropical CDZs.

The present study contributes to the knowledge of nematode assemblages in CDZs of the Indian Ocean, a subject investigated in only a limited number of studies [Thomassin et al. 1976 (Madagascar); Ólafsson et al. 1995 (Zanzibar); Ndaro and Ólafsson 1999 (Zanzibar)].

Here, three distinct microhabitat types (i.e. coralline sediment, coral gravel and coral fragments) are distinguished. This unique approach makes it possible to investigate how changes in community composition resulting from the structuring role of microhabitat structure compares to the changes due to turnover on a local and regional scale. The key questions here are: (1) do CDZs harbour a typical nematode community? (2) how strong is turnover in taxonomic composition operating at local and regional scales? And (3) is microhabitat structure an additional source for variation in nematode community composition?

Materials and methods

Sampling sites, procedure and microhabitats

Meiofauna samples were collected in the CDZ of the fringing reefs stretching along the south coast of Kenya and along the east coast of Zanzibar Island (Unguja, Tanzania) (Fig. 1). In Kenya, samples were taken on two locations: Watamu, the northernmost location (03°23′S, 40°00′E; 27th February 2002), and Tiwi Beach, more to the south (4°14′S, 39°36′E; 22nd–23rd February 2002). In Zanzibar, samples were taken in Matemwe, located in the north of the island (5°52′S, 39°21′E; 24th August 2004 and 31st August 2004), and Makunduchi (6°28′S, 39°32′E and 6°25′S, 39°34′E; 15th August 2004 and 25th August 2004), located in the south of the island. Distance between both Kenyan locations is 104 km, between Tiwi Beach and Matemwe 183.5 km and between both Zanzibar locations 70 km.

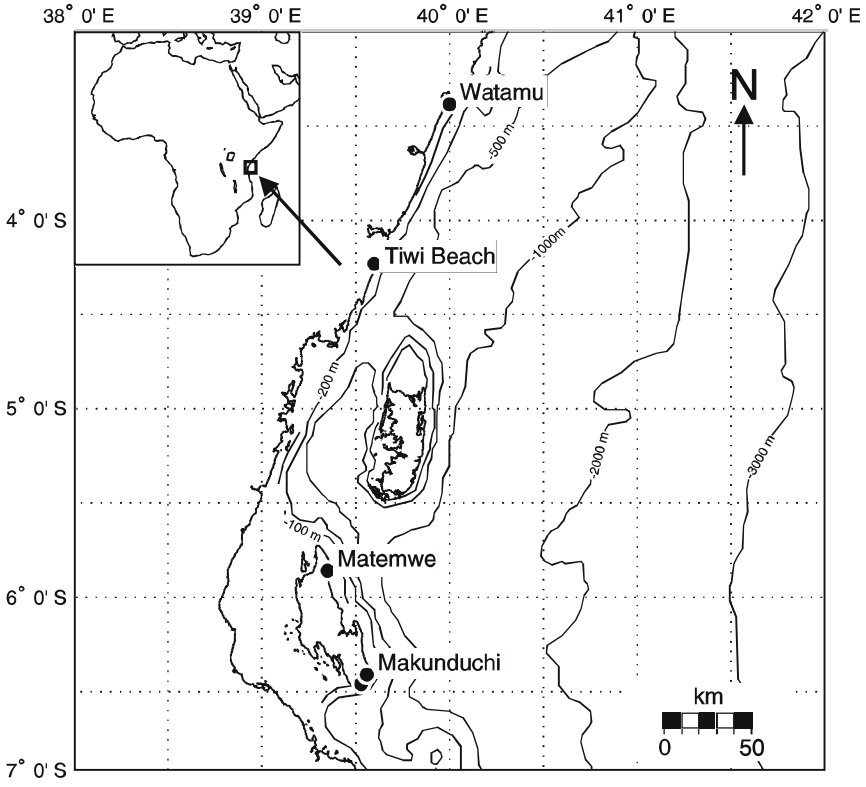


Fig. 1 Map of the study area; location of sampling sites is indicated. The northernmost island is Pemba, the southernmost island is Unguja (Zanzibar Island)

On each location, coralline sediment (six samples in both Kenya locations; two samples in both Zanzibar locations) and coral fragments (two samples in Watamu, three samples in Tiwi Beach and six samples in both Zanzibar locations) were collected. Coral gravel was collected in Watamu, Matemwe and Makunduchi (two samples in all three locations), but not in Tiwi Beach due to the absence of this microhabitat in the sampled area. Coral gravel can easily be distinguished from coralline sediment because small pieces of coral can still be recognised in this microhabitat, whereas this is no longer true for the sediment (Fig. 2). The dead coral fragments were either compact or branched, unaffected or eroded. In Zanzibar, different coral morphotypes were collected, which were identified as *Fungia*, *Goniastrea*, *Pocillopora*, *Tubipora* and *Porites*/*Stylophora*. *Porites* and *Sylophora* were considered as the same morphotype in this study, based on their robustness and branching morphology. All sampling was carried out under water. Sediment samples were taken with a Perspex sediment core (10 cm^2), coral gravel was gently scooped out with a spoon or sediment core and coral fragments were taken out manually. Coral gravel and coral fragments were put directly into firm plastic bags or buckets.

Laboratory analyses

Meiofauna extraction from coralline sediment and coral gravel was done by decantation with filtered seawater over a 1 mm and a 32 µm sieve and subsequent centrifugation. Coral fragments were rinsed off thoroughly, also with filtered seawater, over the same sieves. The material collected on the 32 µm sieve was then subjected to density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip et al. 1985; Vincx 1996). All material was fixed with 4% buffered formalin and stained with Rose Bengal. From each sample 200 nematodes (or all nematodes when less than 200 individuals were present in the examined sample) were randomly picked out. They were subsequently mounted onto slides using the formalin-ethanol-glycerol technique of Seinhorst (1959) and Vincx (1996), and identified up to the genus level, using Lorenzen (1994), Warwick et al. (1998), the Desmodoridae key in NeMys (Deprez et al. 2004), and original descriptions. The trophic composition of the nematode community was analysed according to the classification of Wieser (1953).

Statistical analyses

The PRIMER5 software (Plymouth Marine Laboratory; Clarke and Gorley 2001) was used to calculate Bray-Curtis (dis)similarities between all samples. Samples were grouped together in three ways, concordantly with three spatial scales: (1) the different regions (Kenya/Zanzibar: regional scale), (2) the different sampling locations (Watamu/Tiwi Beach/Makunduchi/Matemwe: local scale) and (3) the different habitats (coralline sediment/coral gravel/coral fragments: microhabitat scale). The obtained similarity matrix was used to produce non-metric multidimensional scaling two-dimensional plots (MDS). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low-stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke 1993). One-way, two-way crossed and two-way nested Analysis of Similarities (ANOSIM) were carried out to test for significant differences in the nematode community structure between different groups that were delimited beforehand. Similarity of Percentages (SIMPER) was used to investigate which genera were responsible for these differences. Due to differences in sample size, relative data were used per sample and these data were Log $(x + 1)$-transformed prior to the analysis.

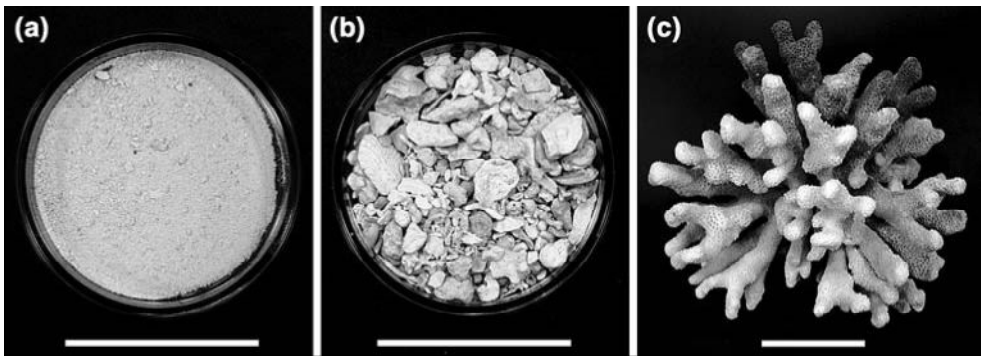


Fig. 2 The three microhabitats: **a** coralline sediment; **b** coral gravel; **c** coral fragment (*Porites*/*Stylophora* is given as an example). *Scale bars* 5 cm

The Pcord4 software (McCune and Mefford 1999) was applied to perform an Indicator Species Analysis (ISA) on the dominant genera (i.e. with a relative abundance >0.5%). Calculated indicator values were tested for statistical significance using a Monte Carlo test (Dufrêne and Legendre 1997). The same software was also used for TWINSPAN analysis, which is a divisive classification method (Hill 1979; Gauch Jr and Whittaker 1981). Calculated cut levels were 0.0; 0.5; 1.2; 3.0; 6.0; 53.0. For both ISA and TWINSPAN, relative data were used without transformation.

Parametric (one-way ANOVA) and non-parametric (Kruskal–Wallis ANOVA by ranks) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

Turnover on a regional, local and microhabitat scale is visualised in a ternary plot (Koleff et al. 2003). The values of a', b' and c' (i.e. the percentage of shared species a, the percentage of species exclusively present in the neighbouring sample b and the percentage of species exclusively present in the focal sample c) are plotted against a background of β_{sim}-values (Lennon et al. 2001). This technique has been used before to unravel nematode community turnover (G. Fonseca, personal communication).

Results

A total of 7,087 nematodes belonging to 149 different genera and 35 different families were included in the analysis. The coral gravel, coral fragments and coralline sediment yielded 89, 108 and 127 genera, respectively. A list of all encountered genera is provided in the Appendix.

Are there characteristic nematode communities for the different regions, locations and microhabitats? What is the structuring role of microhabitat structure?

The MDS biplot of all samples (Fig. 3a) shows both a separation of the samples from the two regions (dashed line) and a separation of the coral samples from the sediment samples (dotted line), although the separation between regions is not as clear-cut as the separation between the two microhabitats. Two-way crossed ANOSIM calculated significant assemblage differences between samples from Kenya and Zanzibar, irrespective of the microhabitat type ($R = 0.595$; $p = 0.001$). Differences between the nematode communities in different microhabitats, irrespective of the region where they occur, were also significant ($R = 0.484$; $p = 0.001$) and pairwise tests revealed significant differences between sediment and coral samples ($R = 0.648$; $p = 0.001$) and between coral gravel and coral samples ($R = 0.406$; $p = 0.01$). Significant differences were also found between communities from different microhabitats irrespective of potential differences between locations ($R = 0.552$; $p = 0.001$). In this analysis, pairwise tests again showed significant differences between sediment and coral samples ($R = 0.713$; $p = 0.001$) and between coral gravel and coral samples ($R = 0.479$; $p = 0.028$). There were no significant differences between sediment and gravel samples. The gravel samples are also found scattered between samples from both other microhabitats in the MDS plot (Fig. 3a). Therefore, the gravel samples were omitted in further analyses. On the MDS plot, the coral samples were clearly clustered more closely together than the sediment samples. Furthermore, it is clear from Fig. 3a that the two sediment samples in the top left corner of the plot, which originate from Matemwe (Zanzibar), have a community composition different from that of the other sediment samples.

No clear separation of groups of samples from the four different sampling locations could be observed from the plot (not shown). In agreement with this observation, two-way nested ANOSIM showed no clear separation of communities from different locations within each region ($R = 0.142$), although the p-level was significant ($p = 0.018$). The effect of locations on community structure, irrespective of the potential effect of microhabitats, was calculated per region to rule out the regional effect, and will be discussed below.

To define the most important structuring factor for the nematode communities, the effects of (1) regional forces within both microhabitats, (2) local forces within both regions, (3) local forces within both microhabitats per region, (4) microhabitat structure within both regions and (5) microhabitat structure within all locations were investigated with one-way (1, 3, 5) and two-way crossed (2, 4) ANOSIM (Table 1; Fig. 3b–e). Most effects were found to be significant. Especially the effect of microhabitat structure yielded well-separated groups. However, R-values indicated the occurrence of clearly different groups on both microhabitat, local and regional scales. There was no significant separation between the coral samples from Watamu and those from Tiwi Beach ($R = -0.3$), which is also obvious from Fig. 3b. A TWINSPAN dendrogram (Fig. 4) revealed that at a first level the two sediment samples from Matemwe (TWIN group 1) branch off from the other samples. *Richtersia* was specified as a TWINSPAN indicator genus for group 1. At a second level,

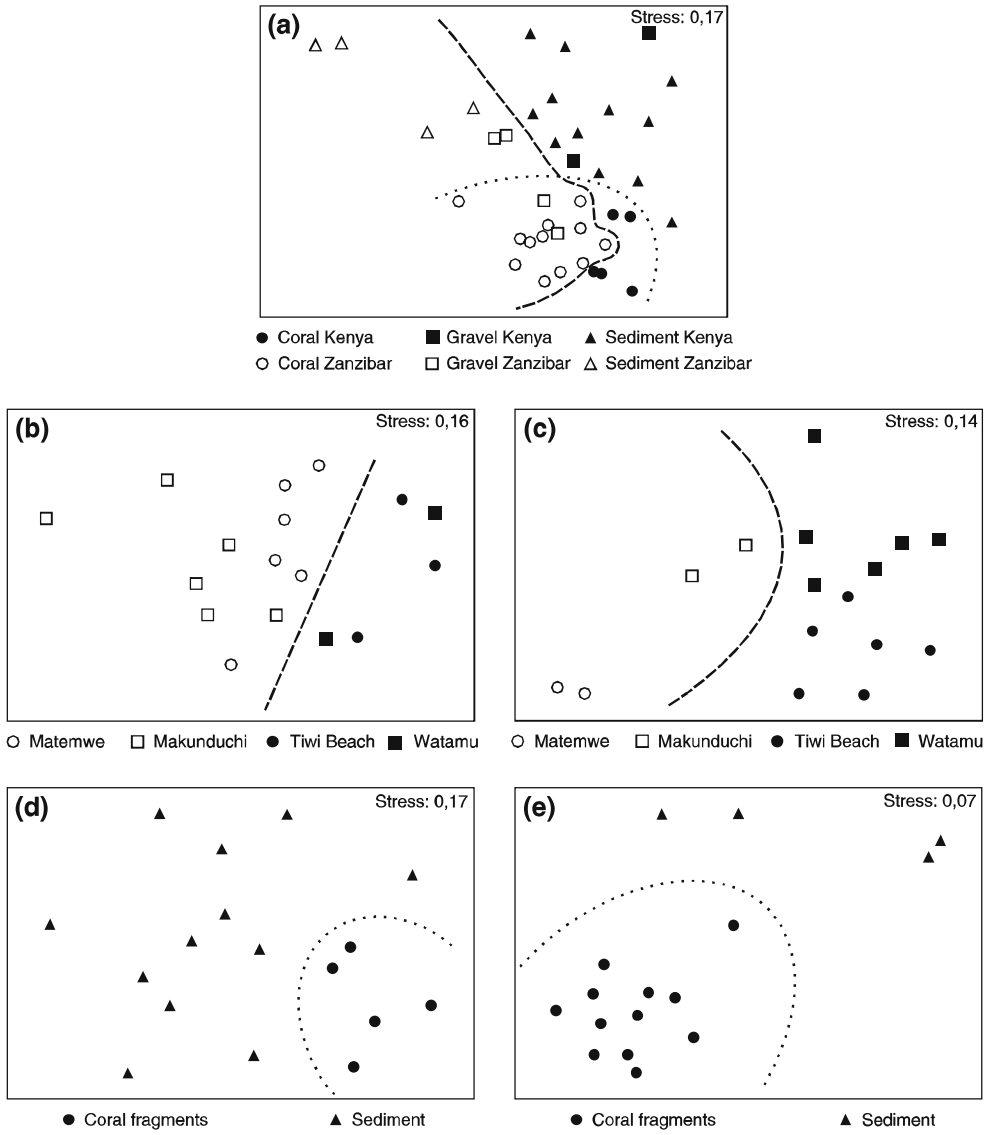


Fig. 3 Multidimensional scaling two-dimensional ordination plots. Stress values are indicated: **a** all samples; **b** coral samples; **c** sediment samples; **d** Kenya samples; **e** Zanzibar samples. The *dashed lines* separate samples from different regions (Kenya–Zanzibar); the *dotted line* separates sediment samples from coral samples

the other sediment samples (TWIN group 3) are separated from the coral samples (TWIN group 2). *Atrochromadora*, *Chromadora* and *Chromadorina* were specified as TWINSPAN indicator genera for group 2, whereas *Neochromadora* was specified as a TWINSPAN indicator genus for group 3.

The ternary graph (Fig. 5) shows that turnover (β_{sim}) between coral and sediment within the same location (grey squares) is generally higher than the turnover between locations within the same region (black circles) and between locations from different regions (white triangles). Due to a lower value for the turnover between the microhabitats in Watamu, these differences were not significant. Local and regional turnover are, however, clearly of the same order of magnitude, with a β_{sim}-value around 0.2.

An MDS plot (not shown) and subsequent two-way crossed ANOSIM analyses demonstrated the absence of an effect of the three-dimensional build-up of different coral morphotypes on the nematode community composition.

How unique and specific are the nematode communities in the different regions and microhabitats?

Even though the communities inhabiting coral fragments and coralline sediment in both regions are significantly different from each other, they do not make

Table 1 *R*-values and significance levels of the effects on different spatial scales, as calculated by one-way and two-way crossed ANOSIM (see text for details)

Selected samples		Effect		
		Regions	Locations	Microhabitats
Regions	Kenya		*R = 0.316; p = 0.007*	*R = 0.482; p = 0.009*
	Zanzibar		*R = 0.386; p = 0.002*	***R = 0.964; p = 0.001***
Locations	Watamu			*R = 0.188; p = 0.357*
	Tiwi Beach			*R = 0.747; p = 0.012*
	Matemwe			***R = 1.000; p = 0.036***
	Makunduchi			***R = 0.927; p = 0.036***
Microhabitats	Coral fragments	*R = 0.461; p = 0.004*		
	Coralline sediment	*R = 0.729; p = 0.001*		
Microhabitats per region	Kenya coral fragments		*R = –0.333; p = 0.900*	
	Kenya coralline sediment		*R = 0.391; p = 0.002*	
	Zanzibar coral fragments		*R = 0.354; p = 0.004*	
	Zanzibar coralline sediment		***R = 1.000; p = 0.333***	

Bold italics stands for well-separated groups ($R > 0.75$), italics underline for overlapping but clearly different groups ($0.75 \geq R > 0.5$), and italics double underline for the absence of clear groups ($R \leq 0.5$)

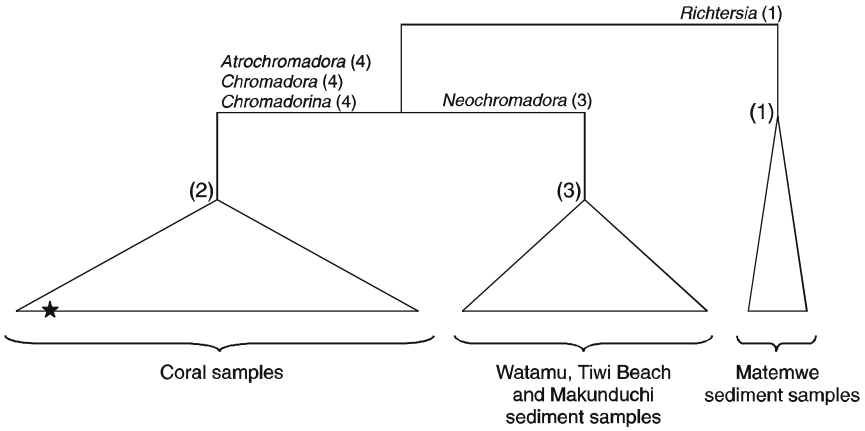


Fig. 4 TWINSPAN dendrogram based on relative abundances of nematode genera in each sample. Only sediment and coral fragment samples are considered. The *star figure* indicates a mismatched sediment sample in the coral samples TWIN group. TWINSPAN indicator *genera* for each TWIN group are indicated with their *signs*

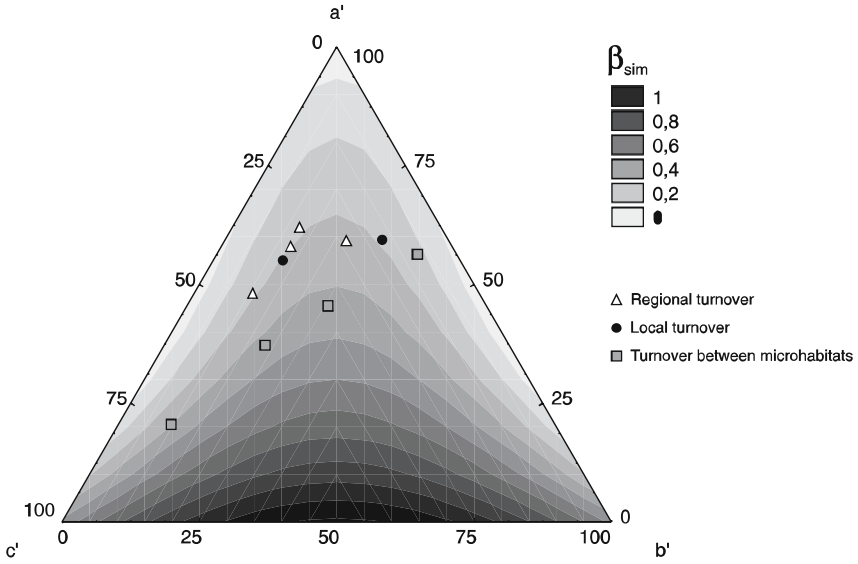


Fig. 5 Ternary plot representing species turnover between coral and sediment within the same location (turnover between microhabitats), between locations within the same region (local turnover) and between locations from different regions (regional turnover). *Shading* visualizes the values of β_{sim}

up distinct, clear-cut groups (Fig. 3a). Moreover, each group has at least half of its genera in common with other groups (Fig. 6). This effect is independent of the region. The lowest number of shared genera, as derived from the surface of the radar chart, was found for the sediment in Zanzibar, which was also characterised by

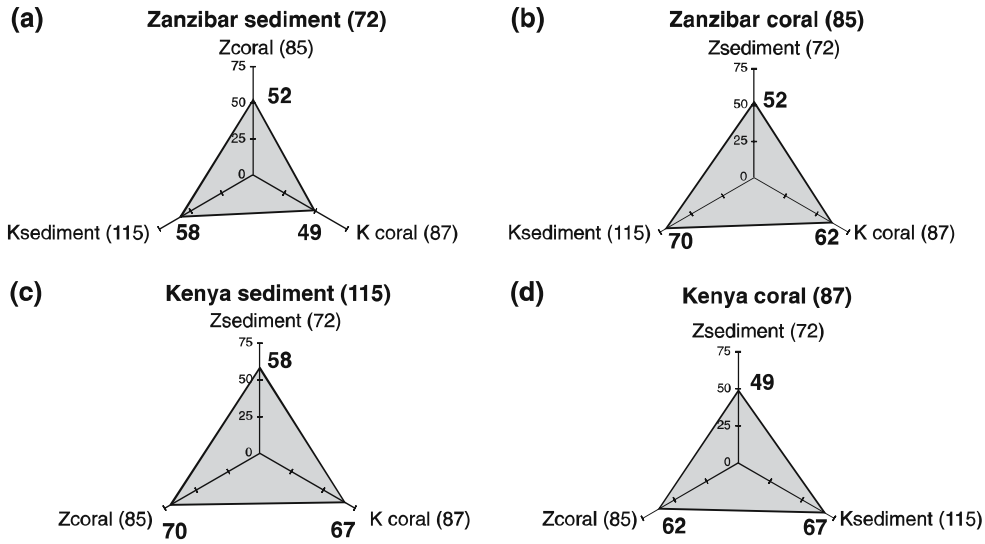


Fig. 6 Radar charts depicting the number of nematode genera shared between a certain microhabitat type in one of the regions (indicated above each graph) on the one hand and the other microhabitats in both regions (*Z* Zanzibar, *K* Kenya) on the other hand. The total number of genera in each microhabitat is indicated between *brackets*

the lowest number of genera (72) (Fig. 6a). The highest number of shared genera was found for the sediment in Kenya (Fig. 6c), which was characterised by the highest number of genera (115). Average dissimilarity (SIMPER analysis) between the four groups varied between 53.2% (Kenya coral-Zanzibar coral) and 82.8% (Kenya coral-Zanzibar sediment). Coral samples from both regions are relatively comparable in terms of associated nematode communities, whereas sediment samples from both regions are much more dissimilar from each other (average dissimilarity: 75.4%). On the other hand, the average similarity of samples within each group is relatively low: between 38.1% (Zanzibar sediment) and 52.9% (Zanzibar coral). Overall, average similarity of coral samples (50.2%) was higher than for sediment samples (33.9%).

The specificity of the nematode communities in the same four groups was evaluated in terms of uniqueness of genera, i.e. whether and how many genera are restricted to a certain microhabitat or region (Fig. 7). Although more stations were sampled for both Kenya sediment (12) and Zanzibar coral (12) (Fig. 7a), this was only reflected in a higher number of unique genera in the sediment from Kenya (Fig. 7b). The detailed distribution shows that most of the unique genera are restricted to 1 or, to a lesser extent, 2–3 samples within a group (Fig. 7c). Moreover, the number of unique genera corresponds well with the distribution of singletons (i.e. unique genera found in only one sample). There were no genera unique for Kenya and only three genera unique for Zanzibar. Within Kenya, 11 and 24 genera were unique for coral fragments and sediment,

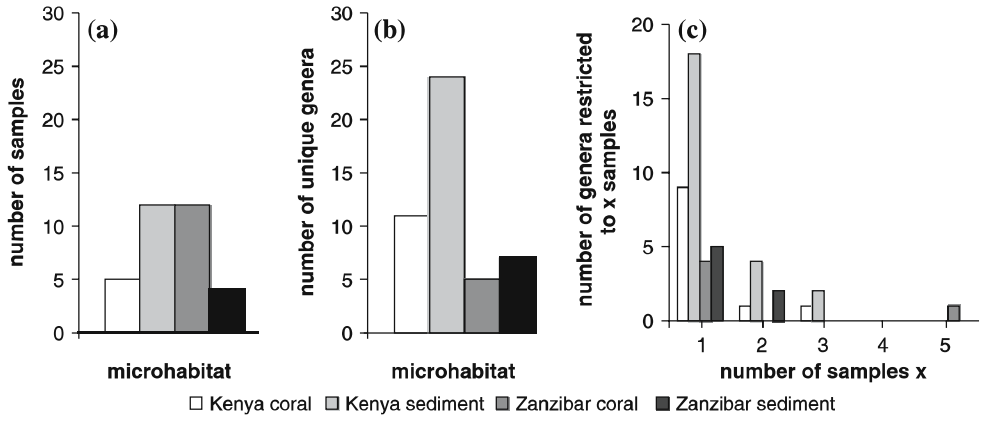


Fig. 7 Stacked columns depicting the number of nematode genera unique for a certain microhabitat type in one of the regions. **a** Comparison of sampling intensity; **b** Number of unique genera and **c** Detailed distribution of unique genera

respectively, whilst in Zanzibar 5 and 7 genera were restricted to coral fragments and sediment, respectively.

Characterisation of the nematode communities

An overview of the most abundant genera characteristic for coral and sediment samples from both regions is given in Fig. 8a, b, respectively. For the coral samples, all genera with a relative abundance >2%, calculated over all coral samples, and occurring in at least 75% of the coral samples were selected. For the sediment samples, all genera with a relative abundance of >2%, calculated over all sediment samples, and occurring in at least 50% of the sediment samples were selected. This difference in procedure is due to the low abundances of the dominant genera in the sediment samples. In this way 46.5, 50.5, 60.5 and 66.5% of the Zanzibar sediment, Kenya sediment, Zanzibar coral and Kenya coral communities is shown in the stack bars, respectively.

The three most abundant genera in the coral samples belong to the families Chromadoridae (*Atrochromadora*, *Chromadora*) and Epsilonematidae (*Epsilonema*), whereas those in the sediment samples are representatives of the families Desmodoridae (*Chromaspirina*, *Spirinia*) and Chromadoridae (*Neochromadora*). Strikingly, the five most abundant families for both microhabitats are the same: Chromadoridae, Cyatholaimidae, Desmodoridae, Epsilonematidae and Xyalidae. Chromadoridae is the dominant family on corals, with Desmodoridae the second most abundant. The opposite is the case in the coralline sediment.

All genera exhibiting significant indicator values are listed in Table 2. The highest indicator values and highest significance levels for the coral fragments are found in representatives of the family Chromadoridae (*Atrochromadora*, *Chromadorina*, *Chromadora*) and for the coralline sediment they are found in representatives of both Desmodoridae (*Eubostrichus*, *Metachromadora*, *Bolbonema*) and Chromadoridae (*Neochromadora*). For coral fragments, the same results were found within each region. Nine of ten genera featured in Fig. 8a are also indicator genera for coral fragments. This correspondence is not clear for the sediment samples. The four indicator genera for coralline sediment in Kenya belong to four different families, but none belongs to the Desmodoridae.

The list of genera that explain most of the average similarity within each of these four groups, as pointed out by a SIMPER analysis (not shown), corresponds well with the list of indicator genera (Table 2) and the genera provided in Fig. 8. Only for the overall coralline

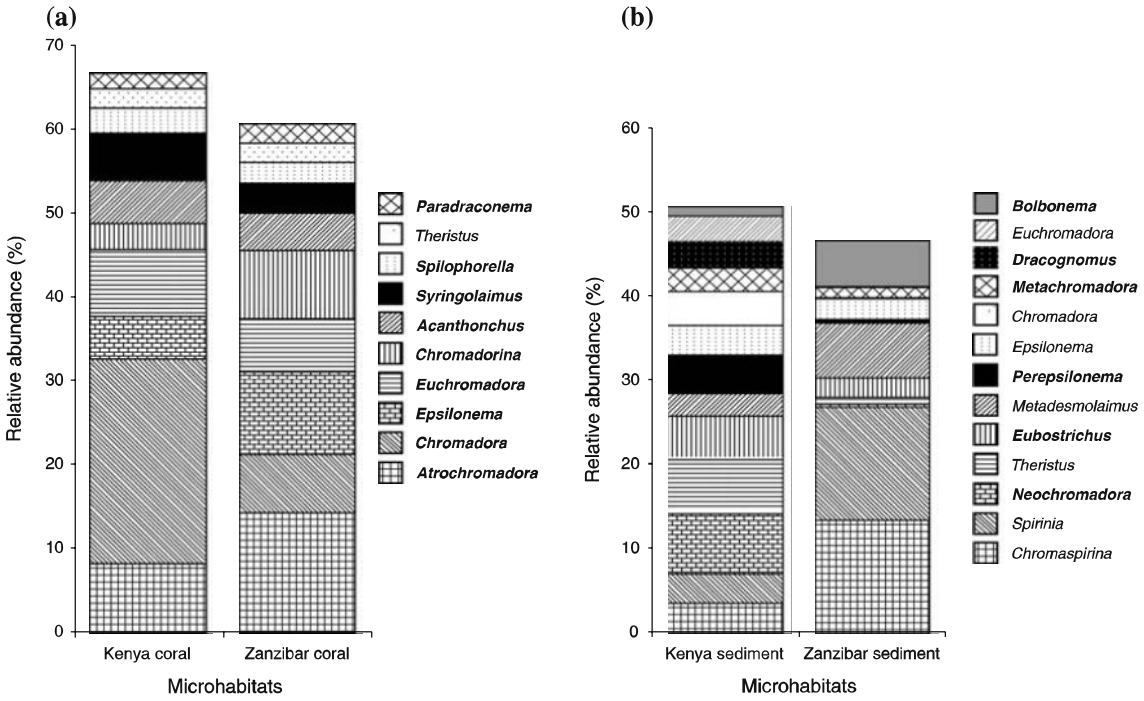


Fig. 8 Dominant nematode genera in coral and sediment samples from both regions. **a** Coral fragments: genera with a relative abundance >2% of the total coral community and occurring in at least 75% of the coral samples; **b** Sediment samples: genera with a relative abundance >2% of the total sediment community and occurring in at least 50% of the sediment samples. Indicator *genera* for either coral fragments or coralline sediment, as specified by an indicator species analysis, are printed in *bold* type

Table 2 Indicator genera for each separate microhabitat and for each microhabitat within a region, as specified by an indicator species analysis

Coral fragments		Coralline sediment	
Indicator genus	Indicator value	Indicator genus	Indicator value
Atrochromadora	89.2***	*Eubostrichus*	69.5**
Chromadorina	82.2***	*Neochromadora*	69.0**
Chromadora	79.8***	*Metachromadora*	56.7**
Paradraconema	72.6***	*Bolbonema*	53.3**
Daptonema	59.5***	*Perepsilonema*	56.1*
Euchromadora	74.7**	*Chromadorita*	56.0*
Acanthonchus	72.8**	*Ptycholaimellus*	52.0*
Epsilonema	72.5**	*Dracognomus*	46.0*
Spilophorella	69.6**	*Paracomesoma*	43.4*
Calomicrolaimus	54.8**		
Paracanthonchus	53.7**		
Syringolaimus	61.6*		
Halalaimus	48.3*		
Kenya coral		Kenya sediment	
Chromadora	68.6***	*Theristus*	49.6**
		Neochromadora	69.6*
		Perepsilonema	59.0*
		Dracognomus	56.0*
Zanzibar coral		Zanzibar sediment	
Chromadorina	64.0***	*Chromaspirina*	71.1***
Atrochromadora	58.4**	*Paracomesoma*	94.3**
Daptonema	56.9**	*Marylynnia*	71.1**
Halalaimus	51.7*	*Metadesmolaimus*	63.5*
Epsilonema	47.1*	*Molgolaimus*	52.1*
		Spirinia	51.5*

Only genera with a significant microhabitat preference are listed. Indicator values and significance levels are provided

***$p \leq 0.001$

**$0.001 < p \leq 0.01$

*$0.01 < p \leq 0.05$

sediment group, some considerable differences with the list of indicator genera were observed.

Marylynnia, *Metadesmolaimus*, *Paracomesoma* and *Molgolaimus* are the significant indicator genera for the sediment in Matemwe (Zanzibar). The importance of these genera in the distinction between the Matemwe sediment samples and all other samples is confirmed by a SIMPER analysis.

Epistratum feeders were the dominant trophic group in each microhabitat (65.6% in coralline sediment; 75.2% on coral fragments). No obvious structuring effect on either regional, local or microhabitat scale was found. However, some significant effects on the individual trophic groups were detected with an analysis of variance. For example, the relative abundance of non-selective deposit feeders (Wieser group 1b) was significantly higher in the sediment ($p = 0.01$) and the relative abundance of epistratum feeders (Wieser group 2a) was significantly higher on coral fragments ($p = 0.005$).

Discussion

Do coral degradation zones harbour a typical nematode community?

Desmodoridae, Chromadoridae, Xyalidae and Cyatholaimidae dominated both the sediment and coral fragments in the study area. This is consistent with most studies in tropical, reef-associated sediments (Grelet 1984; Renaud-Mornant and Gourbault 1984; Gourbault and Renaud-Mornant 1990; Boucher and Gourbault 1990; Tietjen 1991; Boucher 1997; Ndaro and Ólafsson 1999; Kotta and Boucher 2001). This general trend is also reflected in the genus composition of these sediments. A comparison with complete genus lists in similar environments (Alongi 1986; Gourbault and Renaud-Mornant 1990; de Jesús-Navarrete 2003) has shown that, respectively, 90, 80 and 77% of the genera encountered in Australia, French Polynesia and the Caribbean were also found along the East African coast. The total number of genera in these studies was rather low (35, 43 and 56). Nevertheless, these high percentages suggest similar (iso-) communities in CDZs all over the world. Moreover, the nematode communities in the sediments of lagoonal seagrass meadows (Ndaro and Ólafsson 1999; Fisher 2003; Fisher and Sheaves 2003) and on seagrass blades (Hopper and Meyers 1967) were also found to be comparable with the communities in the coralline sediment and on coral fragments of the present study, respectively. On the other hand, most taxa in lagoonal sediments belong to the same families and genera as those in most temperate, sublittoral sands (Boucher 1997), and especially Chromadoridae, Desmodoridae and Xyalidae become increasingly more important in gradually coarser sediments (Heip et al. 1985). Furthermore, very coarse sands yield high abundances of taxa belonging to the families Epsilonematidae and/or Draconematidae (Willems et al. 1982; Ndaro and Ólafsson 1999). The dominant families in the present study are thus explained solely by grain size and are not specific for this particular habitat.

Communities associated with the coral fragments in CDZs are considered for the first time in our study. This resulted in an increased importance of typical coarse sand/coarse substratum taxa such as Chromadoridae and Epsilonematidae.

There were no new families or genera found in our samples. This is consistent with the observation by

Inglis (1968) that in coral reef sediment samples from New Caledonia, all species were new to science, whereas all genera and families were already described. This was explained by the fact that genera at least tend to be cosmopolitan while species do not. This observation has been confirmed in the studies of Boucher and Gourbault (1990), Gourbault and Renaud-Mornant (1990), Tietjen (1991) and Boucher (1997). It can be concluded that CDZs do not harbour a typical community in terms of taxa restricted to this system or in terms of new taxa above species level.

Is microhabitat structure an additional source for variation in nematode community composition?

Microhabitat structure is the main factor structuring the nematode assemblages in CDZs along the east coast of Kenya and Zanzibar, as its effect on the nematode community structure overrides that of local or regional turnover. The nematode communities in CDZs seem to have a patchy distribution, determined by small-scale differences in microhabitat structure. The assemblages are even more affected by changes in sediment grain size than by the structural differences between sediment and coral fragments, which was evidenced by the separation of the Matemwe sediment samples from both the coral samples and the coarser sediment samples in the TWINSPAN dendrogram. A granulometric analysis of the Zanzibar sediment samples revealed that the sediment in Matemwe had a much smaller coarse sand fraction and a larger medium and fine sand fraction than the coarser Makunduchi sediment. Several studies have indeed shown that nematode assemblages in CDZs are mainly determined by sediment characteristics (Alongi 1986; Boucher and Gourbault 1990; Gourbault and Renaud-Mornant 1990; Tietjen 1991; Ólafsson et al. 1995; Boucher 1997; Ndaro and Ólafsson 1999; Netto et al. 1999; Kotta and Boucher 2001; de Jesús-Navarrete 2003). The explanation for the separation of the finer sediments at Matemwe may be related to food availability, oxygen availability and hydrodynamics: finer sediment is found in calm, undisturbed conditions, which are characterised by higher abundances of deposited food and a higher RPD layer, whereas coarser sediment is typically found in conditions characterised by strong hydrodynamic stress, resulting in removal of the phytodetritus on the sediment surface and better oxygenation. These three variables are known to influence nematode community composition in CDZs (Boucher and Gourbault 1990; Gourbault and Renaud-Mornant 1990; Tietjen 1991; Boucher 1997; Ndaro and Ólafsson 1999; Netto et al. 1999). In addition, the indicator genera for fine/medium Matemwe sediment have been recognised as typical taxa for fine, silty sediments (*Marylynnia*, Comesomatidae: Boucher and Gourbault 1990; Wieser and Hopper 1967) and oxygen depleted conditions (*Molgolaimus*: Boucher and Gourbault 1990).

Furthermore, the differences between the communities in the coralline sediment and those on the coral fragments were proven to be significant. Taking into account the TWINSPAN dendrogram, it can be concluded that there is (1) a principal distinction between fine/medium sediment communities and coarse habitat communities and (2) a distinction between coarse sediment communities and coral fragment communities on a secondary level. There are no significant differences between sediment and gravel samples and coral gravel is also significantly different from coral fragments.

It has been observed that the coral samples cluster more closely together in the MDS biplots than the sediment samples and that average similarity is higher between coral samples, whereas average dissimilarity is higher between sediment samples. This could either be explained by (1) differences between sediment samples due to variation in grain size or (2) a lack of structuring effect of the three-dimensional build-up of the coral fragments. The latter explanation has been confirmed in the present study despite of the considerable differences in surface structure of the finely branched *Pocillopora* compared to e.g. the solid surface of *Goniastrea*, the grooved surface of *Fungia* or the complex tubular habitus of *Tubipora*. Govaere et al. (1980) and Vanaverbeke et al. (2002) have demonstrated that slight differences in grain size, even within the same size class, can fundamentally influence nematode community composition. Moreover, as the majority of nematodes are typically slender, sediment-dwelling organisms (Giere 1993), which live in the interstitia between the sand grains, they are more prone to changes in sediment composition than to changes in the three-dimensional build-up of the substratum they are associated with.

The differences between coral associated communities and (coarse) sediment associated communities can be attributed to (1) the more exposed nature of the coral microhabitat, (2) differences in available surface area for epifaunal taxa and (3) the presence of a microbial biofilm and algal cover on the dead coral's surface. The fauna living on the surface and/or between the branches of the coral fragments, which lie relatively unprotected on the bottom and protrude from the sediment, is much more exposed to physical erosion by current activity than the fauna in the sediment. Hydrodynamic stress was indeed considerable on most sampling locations (M. Raes, personal observation). As a result, dead coral fragments are to be considered

preferable habitats only for those nematodes that are able to withstand the current's eroding effect, such as the epifaunal Epsilonematidae and Draconematidae. Representatives of these two nematode families are morphologically and ecologically well-adapted to physical disturbance (Willems et al. 1982; Raes and Vanreusel 2006). They are able to walk over different types of substratum like inchworms (Stauffer 1924; Lorenzen 1973), attaching themselves to the surface with specialised setae, adhesive tubes and/or caudal glands with specially adapted outlets (Raes et al. 2006). In accordance with this hypothesis, the genera *Paradraconema* (Draconematidae) and *Epsilonema* (Epsilonematidae) were recognised as indicator genera for coral fragments and both genera are also among the dominant genera on corals. Moreover, short, fat and heavily cuticularised nematodes such as Epsilonematidae are also more able to withstand different types of disturbance (Soetaert et al. 2002; Vanaverbeke et al. 2004).

The shift in dominance from Chromadoridae on corals to Desmodoridae in the sediment is at present not well understood, although the larger body size of desmodorids might be a limiting factor on coral fragments as larger animals tend to be washed away more easily from the coral surface. Trophic segregation might not play a role here as both Chromadoridae and most Desmodoridae are epistratum feeders according to Wieser (1953). The desmodorid *Eubostrichus* (subfamily Stilbonematinae), which is the most pronounced indicator genus for the coralline sediment, is known as a sediment-dweller carrying ectosymbiotic, sulphide-oxidising chemoautotrophic bacteria on its cuticle in order to survive in the deeper, oxygen depleted layers of the sediment (Ott 1995; Ott et al. 2005).

Epifaunal diatoms or an organic coating covers calcium carbonate structures such as coral fragments after the death of the living tissue (Suess 1968). The significantly higher relative abundance of epistratum feeders on coral fragments indicates the importance of these food sources on the coral surface, whereas the significantly lower abundance of non-selective deposit feeders in this microhabitat is attributed to the low amount of detrital material on the exposed coral fragments due to removal and resuspension by hydrodynamic activity. Epigrowth feeders and/or non-selective deposit feeders are generally the dominant trophic groups in subtidal coralline sediments (Alongi 1986; Gourbault and Renaud-Mornant 1989, 1990; Tietjen 1991; Ólafsson et al. 1995; Boucher 1997; Ndaro and Ólafsson 1999).

Next to the differences between communities in both microhabitats, the similarities between these assemblages are also considerable. The analysis of the number of shared genera has shown that at least 50% of the genera living in the sediment are also found on corals, even between different regions. The five most abundant families are also the same in both microhabitats. As already discussed above, this background community on family and genus level is typical for coarse, subtidal sands. The relatively low number of unique genera in each microhabitat also supports this idea. At least part of the similarity between coral fragments and the coralline sediment can be explained by sediment-trapping between the coral branches. It is clear that the different communities associated with corals and coralline sediments from Kenya and Zanzibar, respectively, are based in particular on different contributions of the genera that are present and not on the presence of unique, very specific genera restricted to a particular region or microhabitat.

How strong is the turnover in taxonomic composition operating at local and regional scales?

The extent of spatial turnover on a local and regional scale appears to be very much comparable, notwithstanding the separation of Zanzibar Island from the African mainland by the Zanzibar Channel. The only indication that a regional effect may be more important than a local effect lies in the absence of clear-cut groups in Fig. 3b and the low *R*-values for local effects within regions (Table 1). Nevertheless, differences in nematode community structure between regions are relatively small, given the high number of shared genera between the microhabitats of both regions and the absence or very low number of unique genera for Kenya or Zanzibar, respectively. This could be related to the cosmopolitan nature of nematode genera (see above). Considering the limited structuring effect of localities within regions, the low average similarities between samples within the same group (Zanzibar sediment, Kenya sediment, Zanzibar coral and Kenya coral) are attributed to patchiness.

High turnover on a regional scale has been observed by Kotta and Boucher (2001), with spatially closer regions having higher generic affinity. These regions (New Caledonia, Fiji, Moorea, Japan, Great Barrier Reef, Davies Reef, Guadeloupe, Indian Ocean and Red Sea) were however much more geographically distant from each other than the two regions in the present study. Turnover on a local (km) scale may have either a negligible (Heip et al. 1979) or a significant (Li et al. 1997; Netto et al. 2003) effect on nematode assemblage structure. Other studies also provide evidence for significant turnover between different areas or functional zones of a reef, i.e. on a scale of hundreds of meters to kilometers (Alongi 1986; Netto et al. 1999, 2003). These

differences were however attributed to different environmental conditions in the lagoon, the reef flat, reef crest, outer reef, reef pools and tidal flats. Kotta and Boucher (2001) also found that environmental variables such as grain size, silt content and water depth contributed most to the variability of nematode assemblages on a local scale, whereas variability on a regional scale was mainly determined by the geographical position of the sampling stations. Boucher (1997) and Kotta and Boucher (2001) observed that the extent of turnover between replicates often exceeded variability between regions and concluded that the pattern of nematode distribution is relatively homogeneous over tens of kilometers. This signifies that the variation in community composition within locations, due to small-scale differences in sediment characteristics and environmental conditions, exceeds the variation between localities on this scale.

The present survey showed that variations in the structure of the microhabitat and differences in environmental conditions occur on very small spatial scales and that these small-scale differences are the predominant factors determining the structure of nematode assemblages in CDZs.

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Appendix

Table 3

Table 3 List of identified genera. Taxonomy after Lorenzen (1994) and original genus descriptions

Acanthonchus (Cobb 1920)
Acanthopharynx (Marion 1870)
Actinonema (Cobb 1920)
Aegialoalaimus (de Man 1907)
aff. *Leptosomatum*
aff. *Nannolaimoides*
Alaimella (Cobb 1920)
Ammotheristus (Lorenzen 1977)
Anticoma (Bastian 1865)
Aphelenchoides (Fischer 1894)
Araeolaimoidea sp. 1
Araeolaimus (de Man 1888)
Atrochromadora (Wieser 1959)
Axonolaimus (de Man 1889)
Bathyepsilonema (Steiner 1931)
Bolbolaimus (Cobb 1920)
Bolbonema (Cobb 1920)
Calomicrolaimus (Lorenzen 1976)
Calyptronema (Marion 1870)
Camacolaimus (de Man 1889)
Cephalobidae gen. 1
Ceramonema (Cobb 1920)
Cervonema (Wieser 1954)
cf. *Aegialoalaimus*
cf. *Rhynchonema*
cf. *Rotylenchulus*
Cheironchus (Cobb 1917)
Chitwoodia (Gerlach 1956)
Chromadora (Bastian 1865)
Chromadorella (Filipjev 1918)
Chromadorina (Filipjev 1918)
Chromadorita (Filipjev 1922)
Chromaspirina (Filipjev 1918)
Comesomoides (Gourbault 1980)
Cricolaimus (Southern 1914)
Croconema (Cobb 1920)
Cyartonema (Cobb 1920)
Cyatholaimus (Bastian 1865)
Daptonema (Cobb 1920)
Dasynemoides (Chitwood 1936)
Desmodora (de Man 1889)
Desmodorella (Cobb 1933)
Desmoscolex (Claparède 1863)
Dichromadora (Kreis 1929)
Didelta (Cobb 1920)
Diodontolaimus (Southern 1914)
Diplopeltis (Cobb in Stiles and Hassal 1905)
Diplopeltula (Gerlach 1950)
Dolicholaimus (de Man 1888)
Dracognomus (Allen and Noffsinger 1978)
Dracograllus (Allen and Noffsinger 1978)
Draconema (Cobb 1913)
Eleutherolaimus (Filipjev 1922)
Enoplida gen. n. 1
Enoplida sp. 1
Enoploides (Ssaweljev 1912)
Enoplolaimus (de Man 1893)
Enoplus (Dujardin 1845)
Epacanthion (Wieser 1953)
Epsilonema (Steiner 1927)
Eubostrichus (Greeff 1869)
Euchromadora (de Man 1886)
Eurystomina (Filipjev 1921)
Gammanema (Cobb 1920)
Gomphionchus (Platt 1982)
Halalaimus (de Man 1888)
Halichoanolaimus (de Man 1886)
Innocuonema (Inglis 1969)
Laimella (Cobb 1920)
Latronema (Wieser 1954)

Table 3 continued

Leptepsilonema (Clasing 1983)
Leptolaimoides (Vitiello 1971)
Leptolaimus (de Man 1876)
Leptonemella (Cobb 1920)
Linhomoeus (Bastian 1865)
Litinium (Cobb 1920)
Longicyatholaimus (Micoletzky 1924)
Marylynnia (Hopper 1977)
Mesacanthion (Filipjev 1927)
Metachromadora (Filipjev 1918)
Metacyatholaimus (Stekhoven 1942)
Metadesmolaimus (Stekhoven 1935)
Metalinhomoeus (de Man 1907)
Metepsilonema (Steiner 1927)
Metoncholaimus (Filipjev 1918)
Microlaimus (de Man 1980)
Molgolaimus (Ditlevsen 1921)
Monhystera (Bastian 1865)
Monhystrella (Cobb 1918)
Nannolaimus (Cobb 1920)
Neochromadora (Micoletzky 1924)
Odontophora (Bütschli 1874)
Odontophoroides (Boucher and Helléouet 1977)
Omicronema (Cobb 1920)
Onchium (Cobb 1920)
Oncholaimus (Dujardin 1845)
Onyx (Cobb 1891)
Oxystomina (Filipjev 1921)
Papillonema (Verschelde Muthumbi and Vincx 1995)
Paracanthonchus (Micoletzky 1924)
Paracomesoma Home and Murphy 1972)
Paracyatholaimoides (Gerlach 1953)
Paracyatholaimus (Micoletzky 1922)
Paradraconema (Allen and Noffsinger 1978)
Paralinhomoeus (de Man 1907)
Paramesacanthion (Wieser 1953)
Paramonohystera (Steiner 1916)
Pareurystomina (Micoletzky 1930)
Parodontophora (Timm 1963)
Paroxystomina (Micoletzky 1924)
Perepsilonema (Lorenzen 1973)
Phanoderma (Bastian 1865)
Polkepsilonema (Verschelde and Vincx 1992)
Polygastrophora (de Man 1922)
Praeacanthonchus (Micoletzky 1924)
Procamacolaimus (Gerlach 1954)
Prochromadora (Filipjev 1922)
Prochromadorella (Micoletzky 1924)
Promonhystera (Wieser 1956)
Pseudochromadora (Daday 1899)
Pseudonchus (Cobb 1920)
Pternepsilonema (Verschelde and Vincx 1992)
Ptycholaimellus (Cobb 1920)
Rhabditis (Dujardin 1845)
Rhinema (Cobb 1920)
Rhips (Cobb 1920)
Rhynchonema (Cobb 1920)
Richtersia (Steiner 1916)
Sabatieria (Rouville 1903)
Southerniella (Allgén 1932)
Spilophorella (Filipjev 1917)
Spirinia (Gerlach 1963)
Steineria (Micoletzky 1922)

Table 3 continued

Stylotheristus (Lorenzen 1977)
Symplocostoma (Bastian 1865)
Synonema (Cobb 1920)
Syringolaimus (de Man 1888)
Terschellingia (de Man 1888)
Thalassironus (de Man 1889)
Thalassoalaimus (de Man 1893)
Theristus (Bastian 1865)
Trefusia (de man 1893)
Trichotheristus (Wieser 1956)
Tricoma (Cobb 1893)
Trissonchulus (de Man 1889)
Trochamus (Boucher and Bovée 1972)
Tubolaimoides (Gerlach 1963)
Viscosia (de Man 1890)
Zalonema (Cobb 1920)

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