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Nematode Community Structure along the Continental Slope off the Kenyan Coast, Western Indian Ocean

key words: continental slope, marine nematodes, density, genera composition Kenyan coast

Abstract

Metazoan meiofauna and in particular nematode densities, diversity, community structure were studied in relation to water depth (20 m, 50 m, 500 m, 1000 m and 2000 m) along four bathymetric transects in the Western Indian Ocean off the Kenyan coast. Nematode densities ranged between 276–944 ind./10 cm^2, which is comparable to values from other oligotrophic areas in the world. Densities was correlated with oxygen concentrations in the overlying water, since they were lowest at mid-depth (500–1000 m) coinciding with the minimum oxygen level. Nematode community structure (at genus level) resembles communities found in temperate slope regions, which are also characterized by a low productivity. The community structure showed correlations with sediment composition, water depth and oxygen levels in the overlying water. Sediment composition was mainly important at the shelf where nematodes separated into a silty sediment-dwelling community with high abundances of *Daptonema, Dorylaimopsis, Terschellingia* and *Halalaimus,* and a sandy sediment-dwelling community characterised by high abundances of *Microlaimus* and *Halalaimus*. The genera *Monhystera*, *Acantholaimus*, *Sabatieria*, *Molgolaimus* and *Halalaimus* dominated the slope communities. The characteristic deep-sea taxa, the monhysterids and *Acantholaimus* increased in relative abundance with increasing depth, to become dominant at the lower slope (2000 m). The upper (500 m) and mid-slope (1000 m), which coincided with the lowest oxygen concentrations, were colonised by *Sabatieria*, a genus that is known to inhabit suboxic sediments. Diversity at the level of the genera showed an unimodal trend along the sampled gradient, with highest values at mid-depth (500 m). Although the oxygen minimum at mid depths is much less pronounced than in adjacent areas, the results of this study suggest an impact on the present communities.

1. Introduction

The Western Indian Ocean (WIO) off the Kenyan coast is an oligotrophic area (Semeneh *et al.*, 1995) with oxygen levels declining with depth along the upper slope down to a minimum at 1000 m. The study area lies partly in the Indian Ocean equatorial surface (0–500 m) water mass, which is influenced by the seasonally reversing monsoon gyres situated north of the 10 °S. At intermediate water depths (500–1500 m) along the Eastern African coast, the main water mass originates from the Red Sea. During the northern winter, low salinity (34.5 PSU), low temperature (0.1–2 °C) and low oxygen (2–3 ml/l) deep water replaces the high salinity (39 PSU) surface water at the Red Sea. This surface Red Sea water consequently flows to the Arabian Sea and can be detected here at 600–800 m, coinciding with the deep oxygen minimum layer (1.5 ml/l) in this area. The core of this Red Sea water progressively deepens to 1000 m off the Eastern African Coast. Therefore at intermediate depths off the Kenyan coast, Red Sea – Persian Gulf Water is present. The deep water mass (below

1500 m) consists of Circumpolar Deep Water, which is characterised by low temperature (0.1–2 °C), low salinity (34.7 PSU) and high dissolved oxygen concentrations (4.7 ml/l) (RAO and GRIFFITH, 1998).

The WIO off the Kenyan coast is located only a few degrees south of the well studied and highly productive Arabian Sea but it was only with the start of the Netherlands Indian Ocean Programme NIOP (1990–1995), investigating the effects of monsoons on coastal ecosystem (pelagic and benthic) in the WIO, that information on the productivity and the seasonality in relation to the monsoons was gathered from this area. One of the more specific objectives of this NIOP research programme was to find out, if the seasonally high productivity caused by up-welling also occurred along the Kenyan coast in a similar way it has been found off the Somalian coast.

Extending from 1° to 5° south of the equator, the Kenyan coast lies in a region characterised by a complex hydrodynamic regime. The seasonally reversing monsoon winds cause current reversal twice a year in the WIO (WAKWABI and NGULI, 1995). This current reversal causes upwelling along the Somali coast and, though to a lesser extent, along the northern part of the Kenyan coast. The Northeast monsoon winds blow from November to March and the Southeast monsoon from April to October with inter-monsoon periods in May and November. During the Northeast monsoon period, the main water currents are the predominantly north flowing East African Coastal Current and the southwards directed Somali current, which is still detectable at the northern part of the Kenyan coast. During Southeast monsoon the main water current is the equatorial counter current formed as a result of the meeting between these two currents (RAO and GRIFFITH, 1998).

Some results of the NIOP study already showed that during the Southeast monsoon, the surface water formed a homogenous surface layer overlying a main thermocline at 70–120 m water depth. During the onset of the northeast monsoon the homogenous layer was much shallower (50 m), since the thermocline shifted upwards by 30 m, and the water temperature was slightly higher (NGULI, 1995). It was also found that the primary productivity in the water column increased significantly from the southern most transect (< 100 mg $C/m^2 \cdot day$) to the northern most one (400 mg $C/m^2 \cdot day$). In addition, the productivity rates were higher during the onset of the northeast monsoon (November-December) (especially for the southern transects) compared to the southeast monsoon period (June/July) (KROMKAMP et al., 1995).

For this study sediment samples collected in 1992 along four parallel bathymetric transects (20 to 2000 m depth) off the Kenyan coast, were analysed for the meiofauna (defined as metazoan benthos smaller than 1 mm) with particular reference to the dominant group, the nematodes. Nematodes were identified to species level for the families Comesomatidae, Chromadoridae, Microlaimidae and the genus *Molgolaimus* and several new species from this area were described and published elsewhere (MUTHUMBI and VINCX, 1996; MUTHUMBI et al., 1997; MUTHUMBI and VINCX, 1997; MUTHUMBI and VINCX, 1998 a,b; MUTHUMBI and VINCX, 1999). Here, we report on the meiofauna density, the nematode composition and the diversity at the level of the genera. The aim of this study was to investigate the effect of oxygen, granulometry and food availability on the nematode density and community structure from the shelf down to mid slope depths.

2. Materials and Methods

2.1. Study Area

Four depth transects were sampled off the Kenyan coast in the Western Indian Ocean (WIO). From North to South these transects were named Kiwayu (K), Tana (T), Sabaki (S) and Gazi (G) (Fig. 1). At each transect up to six stations were sampled from the continental shelf (20 or 50 m) to the slope up to
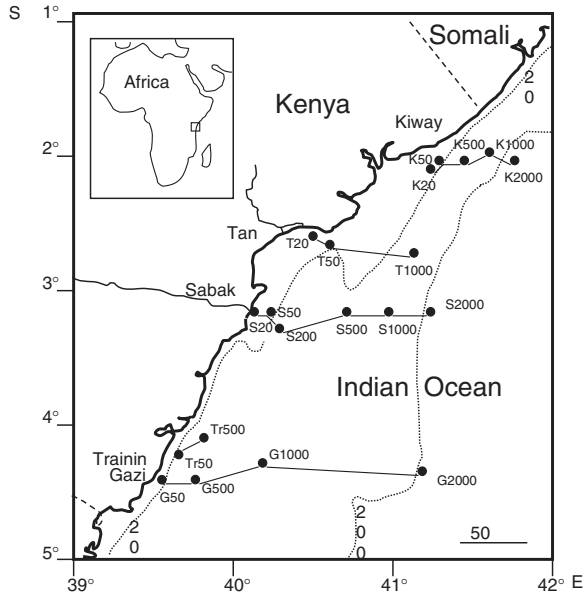
Figure 1.   Kenyan coast showing the sampling stations along 4 transects

a maximum of 2000 m depth (Table 1a, b). Sampling was performed during the southeast monsoon between 20th June and 4th July 1992 (KA1) and repeated during the onset of the Northeast monsoon between 20th November and 8th December 1992 (KA2). During the second campaign, the Tana transect was not sampled. Two extra stations were sampled within the vicinity of Gazi during a training programme conducted in November/December period referred here as Training (Tr) transect. Stations are referred to as the abbreviation for the transect, followed by its depth and the campaign number (1 or 2) (see Table 1a, b).

2.2. Sampling

Sediment samples were taken from the RV Tyro during the cruises KA1 and KA2 (NIOP 1992). Samples were collected with a modified box corer with a closing lid on top taking virtually undisturbed surface sediment. From each box core two sub-samples were taken up to a depth of 5 cm with a plastic core of 2.1 cm internal diameter and pooled. At most stations this procedure was repeated in order to get two replicate samples from separate box cores. Samples were preserved in 4% buffered formaldehyde solution. In the laboratory they were sieved over 1 mm and collected on a 32 μm sieve. They were centrifuged twice in Ludox and the supernatant stained overnight in rose bengal (Heip *et al.*, 1985).

2.3. Processing the Meiofauna

Metazoan meiofauna was identified up to higher taxonomic level using the meiofauna handbook of Higgins and Thiel (1988). Since the meiofauna densities from the first campaign were already published by Duineveld *et al.*, (1997), only nematode counts are repeated here for comparison with the second campaign.

Table 1a. Location and depth of the sampling stations for cruise KA1 (June/July 1992 – Southeast monsoon) (Station labels in brackets are as they were used during the campaigns).

Transect	Station	Latitude S	Longitude E	Depth (m)
Kiwayu	K20−1 (127)	02°03.61′	41°17.80′	24
	K50−1 (128)	02°03.16′	41°18.48′	55
	K500−1 (131)	02°00.27′	41°26.62′	500
	K1000−1 (132)	01°56.03′	41°31.54′	1000
	K2000−1 (133)	02°01.49′	41°46.96′	2015
Tana	T20−1 (120)	02°42.20′	40°31.18′	21
	T50−1 (121)	02°43.07′	40°33.89′	52
	T1000−1 (136)	02°40.05′	41°10.17′	992
Sabaki	S20−1 (108)	03°10.06′	40°10.06′	18
	S50−1 (111)	03°09.78′	40°14.41′	53
	S200−1 (114)	03°10.27′	40°17.02′	213
	S500−1 (117)	03°08.21′	40°41.80′	500
	S1000−1 (118)	03°08.46′	41°01.77′	1112
	S2000−1 (119)	03°10.67′	41°14.20′	2007
Gazi	G50−1 (103)	04°25.83′	39°33.58′	62
	G500−1 (105)	04°24.06′	39°45.99′	511
	G1000−1 (106)	04°20.35′	40°21.70′	1000
	G2000−1 (107)	04°21.83′	41°13.16′	2053

Table 1b. Location, depth, sediment organic carbon, sediment C/N ratio and fraction of fine sand and silt for cruise KA2 (November/December 1992 -onset of the Northeast monsoon).

Transect	Station	Latitude S	Longitude E	Depth (m)	org.C %	C/N	Silt %	Fine sand %
Kiwayu	K50−2 (528)	02°04.76′	41°17.40′	39	1.0	10.4	60.7	13.7
	K500−2 (531)	02°00.48′	41°37.56′	516	1.1	9.4	73	11.6
	K1000−2 (532)	01°56.02′	41°37.56′	904	0.9	9.1	65	13.5
	K2000−2 (533)	02°00.86′	41°47.71′	2027	0.6	8.7	83	7
Training	Tr50−2 (550)	04°11.96′	39°37.94′	51	0.2	6.8	12.6	53.6
	Tr500−2 (552)	04°07.71′	39°54.67′	500	0.4	8.4	44	26.6
Sabaki	S50−2 (511)	03°09.59′	40°13.94′	57	0.4	8.3	48.5	26.5
	S200−2 (514)	03°10.27′	40°17.34′	207	0.3	8.9	33.1	2.8
	S500−2 (517)	03°09.43′	40°41.25′	508	0.6	12.9		
	S1000−2 (518)	03°07.98′	40°59.96′	963	0.3	8.3	29.9	18.9
	S2000−2 (519)	03°09.28′	41°16.53′	2179	0.5	8.6	94.9	2.6
Gazi	G50−2 (503)	04°19.28′	39°35.56′	47	0.2	7.6	7.6	54.9
	G500−2 (505)	04°25.33′	39°45.21′	520	0.8	9.4	55.6	22.2
	G1000−2 (506)	04°19.45′	40°21.80′	1020	0.3	8.3	49.9	17.6
	G2000−2 (507)	04°21.31′	41°13.64′	2088	0.5	8.2	84.2	4.8

Nematodes (100 individuals randomly selected from each replicate sample) from both campaigns were identified to genus level using the pictorial key of Platt and Warwick (1988) and original species descriptions. Systematics was based mainly on Lorenzen (1981). The genera *Monhystera*, *Eumonhystera* and *Monhystrella* were in most cases referred to as monhysterids, although the largest fraction of this group consisted of *Monhystera,* while only a few specimens belonged to the other two closely related genera.

2.4. Environmental Data

Oxygen content in the water, and sediment chlorophyll *a* and phaeopigments concentrations were obtained from Duineveld *et al.*, (1997). Sediment grain size distribution was analysed for the November/December campaign only using a Malvern Particle size analyser 3600 Ec. Median grain size was calculated over the total sediment range and distinction was made between medium sand (< 500 μm), fine sand (< 250 μm), very fine sand (< 125 μm) and silt (< 63 μm) fractions. Sediment organic carbon and nitrogen were analysed using a Carlo-Erba (NA 1500) carbon-nitrogen analyser. Both elements were measured simultaneously from oven-dried samples from which inorganic carbon was removed by acidification with 25% HCl. These data were available from the second campaign only.

2.5. Data Analysis

Spearman Rank Order Correlation was used in order to assess the relationship between environmental and biotic variables. A correlation was considered significant at $p < 0.05$, and highly significant at $p < 0.001$. Multiple and single Linear Regression analysis was used to check if the nematode density and diversity could be explained by (linear) relationships with environmental variables such as oxygen concentrations in the overlying water column, food availability (org C, C : N ratio, chlorophyll *a* and phaeopigments from the sediment and the water) and sediment grain sizes. For most statistical analysis, the Tana transect was omitted while the Training transect was combined with the Gazi transect. An ANalysis Of VARiance (ANOVA) was used to test for significant effects between transects on environmental variables, nematode density and diversity distributions, if the data fulfilled assumptions for parametric analysis. If not, a non parametric Kruskal-Wallis test was performed.

The Two Way INdicator SPecies ANalysis (TWINSPAN) programme by Hill (1979) was used as multivariate approach for the nematode genera distribution data (Jongman *et al.*, 1987). This technique classifies the sites as well as the taxa by constructing an ordered two-way table from a sites-by-species matrix. In this case the data matrix consisted of relative abundances (%) of nematode genera from the different replicate samples. TWINSPAN has the advantage to yield indicator taxa characterising the delineated communities. In order to take the quantitative differences in relative abundances of the taxa into account, the programme defines the so-called pseudo-species. Pseudospecies cut levels 0, 2, 5, 10 and 20 were used for the equivalent relative abundances (%) of 0–2, 2–5, 5–10, 10–20 and >20 respectively to define pseudospecies 1, 2, 3, 4 and 5.

Nematode genus diversity was calculated using Hills diversity numbers of the orders 0 and 1 (Hill, 1973):

$$N_0 = \text{total number of species,}$$

$$N_1 = \exp(H'), \text{ the Shannon-Weaver diversity index, where } H' = -\Sigma p_i \ln(p_i)$$

(where p_i is the relative abundance of the ith genus)

The expected number of species (genera in this case) for 100 individuals was also calculated according to Sanders Rarefraction method (Sanders, 1968), modified by Hurlbert (1971).

3. Results

3.1. Environmental Characteristics

The sediments along the four depth transects mainly consisted of fine sand (2–55%) and silt (7–95%). There were no significant differences between transects for any of the granulometric characteristics. The silt fraction significantly increased with depth, with the

Table 2. Spearman rank correlations coefficients (R) between water depth, nematode densities, genus diversity and environmental variables (N = number of cases, ** $0.001 < p < 0.05$; *** $p < 0.001$; NS: not significant).

Environmental variables	N	Water depth	N	Nematode densities	N	Genus diversity
Depth	–	–	24	–0.54**	33	NS
Median grain size	14	–0.55**	11	NS	14	NS
Fine sand %	14	–0.61**	11	NS	14	0.71**
Silt %	14	0.67**	11	NS	14	–0.56**
Oxygen	23	–0.77***	22	0.70***	23	NS
Sediment Phaeopigments	24	–0.79***	24	0.63***	24	NS
Sediment Chl *a*	24	–0.85***	24	0.67***	24	NS
C/N	15	NS	12	NS	15	NS
Org C %	14	NS	11	NS	14	NS

sharpest increase at 2000 meter depth (> 85%), while both median grain size and the fine sand fraction decreased with depth (Table 2).

During the second campaign (KA2) the organic carbon content and the C/N ratio was measured (Table 1b). Values ranged between 0.2 and 1% for organic carbon while the C/N ratio varied from 6.8 to 12.9. Based on ANOVA a significant higher organic carbon content was found at the Kiwayu transect close to the Somalian coast ($F (3, 10) = 11.52$; $P = 0.001$). Organic carbon and the C/N ratio did not show any significant correlation with depth (Table 2).

Sediment chlorophyll *a* and phaeopigment concentrations decreased significantly with depth (Table 2), and thus also with distance offshore.

Oxygen (Fig. 2) decreased significantly with depth between the shelf stations and 1000 m depth (from 250 to 60 µM). At 2000 m however, oxygen increased again to values more or
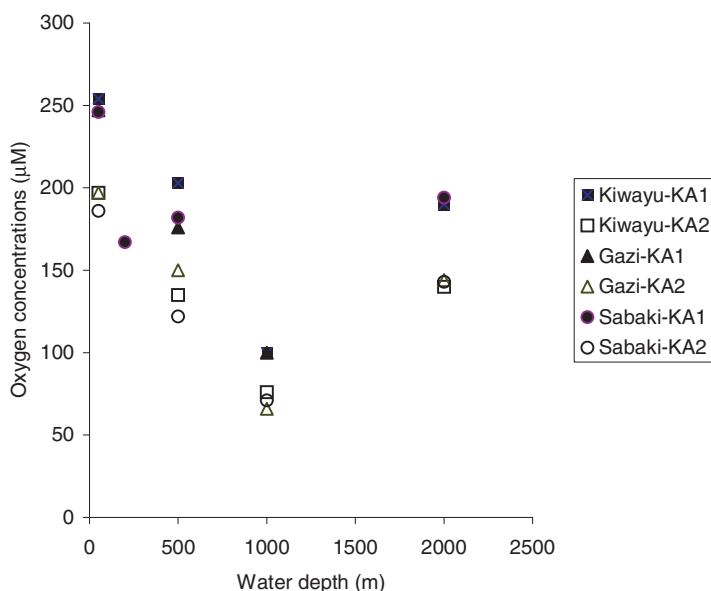

Figure 2. Oxygen concentrations (µM) in the overlying water in relation to depth with indication of the different transects and seasons (filled = southeast, open = northeast monsoon periods).

less similar as those at 500 m depth (between 130 and 200 μM). Oxygen did not differ significantly between transects.

In summary it was found that all transects were very similar except for the higher organic content in the northern Kiwayu transect, closest to the Somalian upwelling area. The sediment became finer (higher silt content) with depth. Sediment pigments (chlorophyll *a* and phaeopigments) were significantly higher at the shelf (50 m) compared to the slope (> 200 m), and also oxygen showed a significant higher value at the shelf and was significantly lowest at 1000 m water depth.

3.2. *Meiofauna Density*

Duineveld *et al.*, (1997) already showed meiofauna densities from the samples retrieved during the campaign KA1(June/July). Nematode densities from that study are shown together with the total meiofauna densities for November/December in Table 3. At all stations nematodes were the dominant taxon contributing to at least 80% of the total meiofauna community followed by harpacticoid copepods. Nematode densities showed a similar trend as the overall meiofauna: highest nematode densities were observed at the shallowest stations, generally decreasing with increasing water depth (Fig. 3). Conspicuously higher nematode densities were recorded at 20 m along the Sabaki (1928 ind./10 cm^2) and the Kiwayu (1324 ind./10 cm^2) transects which were sampled only in June/July 1992. At the other sites, densities ranged between 160–953 ind./10 cm^2 at 50 m and 251–635 ind./10 cm^2 at the deeper stations (Table 3). There were no significant differences between transects, although the mean nematode densities were higher along the northern most transect Kiwayu, compared to Sabaki and Gazi.
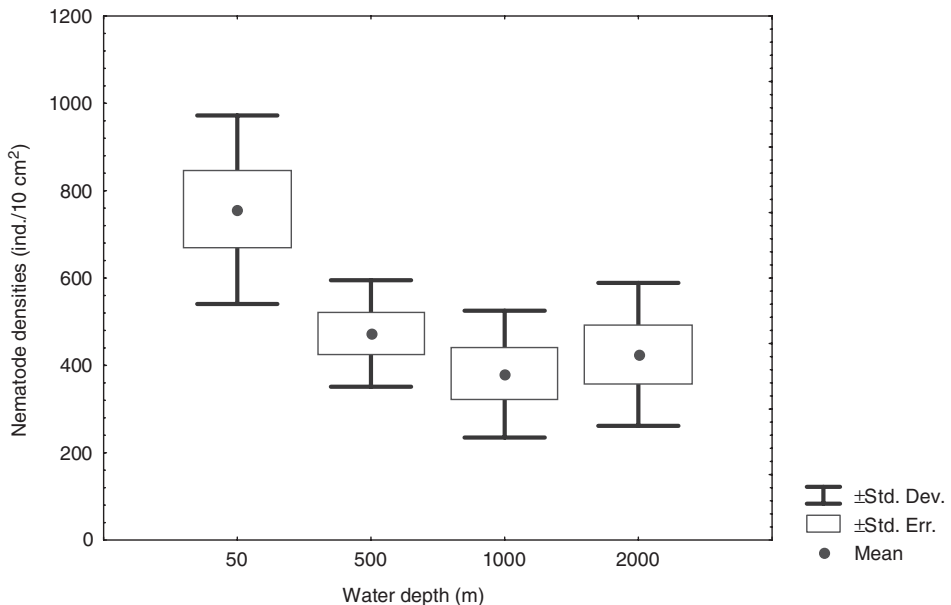

Figure 3.   Box whisker plots for nematode density per depth zone (20 m and 200 m stations not included).

Table 3. Meiofauna composition and total density (± std) (ind/10 cm^2) for November/December campaign and nematode density for June/July (from DUINEVELD *et al*., 1997).

	Depth (m)	Nema	Cope	Poly	Oligo	Others	Total	Nema
				Nov/Dec				June/July
Kiwayu	20							1324
	50	944	69	21	6	11	1052 ± 237	956
	500	453	51	2	3	7	516 ± 77	635
	1000	478	24	5	4	13	524 ± 189	285
	2000	696	40	3	2	11	752 ± 38	371
Tana	20							340
	50							160
	1000							301
Sabaki	20							1928
	50	559	26	36	1	6	629 ± 14	511
	200	507	49	44	17	29	646 ± 187	427
	500	411	36	11	2	11	471 ± 26	434
	1000	269	14	1	1	7	292 ± 11	632
	2000	514	19	2	1	6	541 ± 78	406
Training	50	814	59	22	4	11	910 ± 195	
	500	391	21	11	0	3	426 ± 169	
Gazi	50	614	54	32	7	40	746 ± 164	953
	500	317	24	5	0	10	356 ± 39	600
	1000	307	14	5	0	9	334 ± 17	307
	2000	276	17	0	0	1	295 ± 133	251

Nb: Nema = nematodes, Cope = copepodes, Poly = polychaetes, Oligo = oligochaetes

Nematode densities increased significantly with sediment-bound pigments, and oxygen levels. A multiple regression analysis in order to explain the variation in nematode densities revealed that only oxygen contributed significantly, whereas the pigments did not. Oxygen as such could explain 47% of the variability ($R^2 = 0.47$; $p < 0.05$) in nematode densities. Nematode densities increased with increasing oxygen levels in the overlying water (Fig. 4) suggesting that it was structuring the observed density trends along the bathymetric gradient. It should be noted that the shallowest stations with the highest densities were excluded from the regression analysis since no oxygen data were available.

3.3. Nematode Composition

In total 41 families were identified along the four transects. In June/July 1992, 41 families were counted, whereas only 37 families were present in November/December 1992. Only 15 families showed a relative abundance of 2% or more and contributed all together for 82% of the total population (Table 4). Most families occurred in similar proportions during both seasons. Among the most important families were the Xyalidae (12%), the Monhysteridae (12%), and the Comesomatidae (10%).
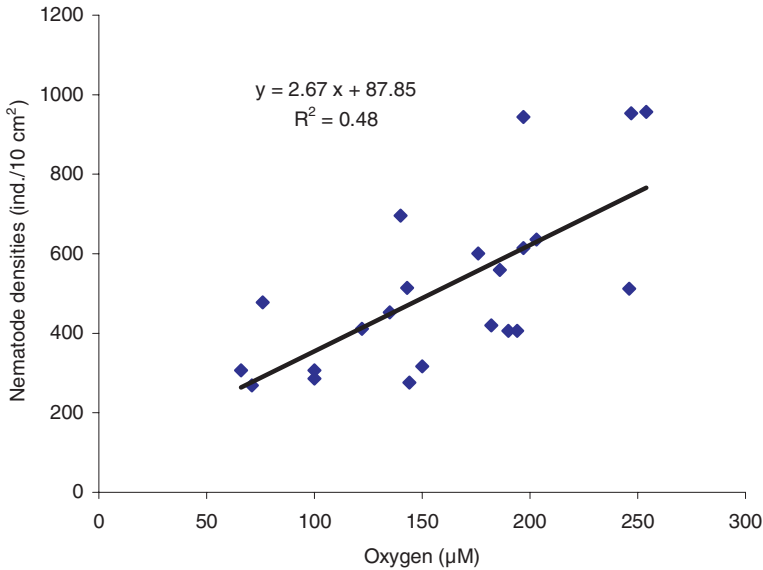
Figure 4.   Linear regression showing the relationship between nematode density and oxygen concentrations in the overlying water.

Table 4.   Relative abundance (%) of the dominant families in WIO.

Families	June/July	Nov/Dec	Mean
Xyalidae	11.7	12.4	12.1
Monhysteridae	11.3	12.3	11.8
Comesomatidae	11.6	9.3	10.5
Oxystomatidae	7.7	7.0	7.3
Chromadoridae	6.3	7.9	7.1
Desmodoridae	5.0	5.5	5.3
Microlaimidae	4.1	5.2	4.6
Linhomoeidae	5.6	3.4	4.5
Cyatholaimidae	4.0	4.8	4.4
Leptolaimidae	3.5	3.3	3.4
Desmoscolecidae	2.4	2.7	2.5
Selachinematidae	2.0	2.5	2.3
Diplopeltidae	1.7	2.6	2.2
Aegialoalaimidae	2.2	1.9	2.1
Ceramonematidae	1.8	2.4	2.1
Others	19	17	18

   In total 224 genera were identified from the four transects. In June/July 1992, 216 genera were identified, whereas in November/December of the same year, 188 genera were identified. Only 16 genera had a relative abundance of 1% or more and represented nearly half the total number of nematodes identified. Other genera were only poorly represented. The most dominant were the group monhysterid (mainly *Monhystera*) with 12%, followed by the genus *Halalaimus* (5.4%).

3.4. Nematode Communities

The multivariate analysis revealed the combined effect of depth and sediment composition on nematode community structure at the level of the genera (TWINSPAN based on relative abundances). There was no difference in genera composition between both seasons. Two nematode communities were identified (Fig. 5):

(I) A distinct shelf (20–200 m) nematode community (group A) separated on the basis of the high abundance of the genus *Daptonema* (pseudospecies 4) and further dominated by the genera *Halalaimus* (4.8%) *Terschellingia* (7.0%), *Dorylaimopsis* (4.8%) and *Microlaimus* (3.4%). A closer look at this group revealed that the more silty sediment of the Sabaki transect had a nematode community dominated mainly by the genera *Daptonema*, *Terschellingia* and *Dorylaimopsis,* while the Gazi and Training transects were dominated by the genus *Microlaimus*.

(II) A continental slope community characterised by the presence of *Acantholaimus* (1), *Syringolaimus* (1) and *Cyartonema* (1) and further made up of the genera *Halalaimus*, *Sabatieria*, monhysterids, *Cervonema,* and *Molgolaimus* (Fig. 6). The relative proportions of these genera varied with increasing depth resulting in differences between an upper slope (group B), a mid slope (group C) and a lower slope (group D) nematode assemblage. The

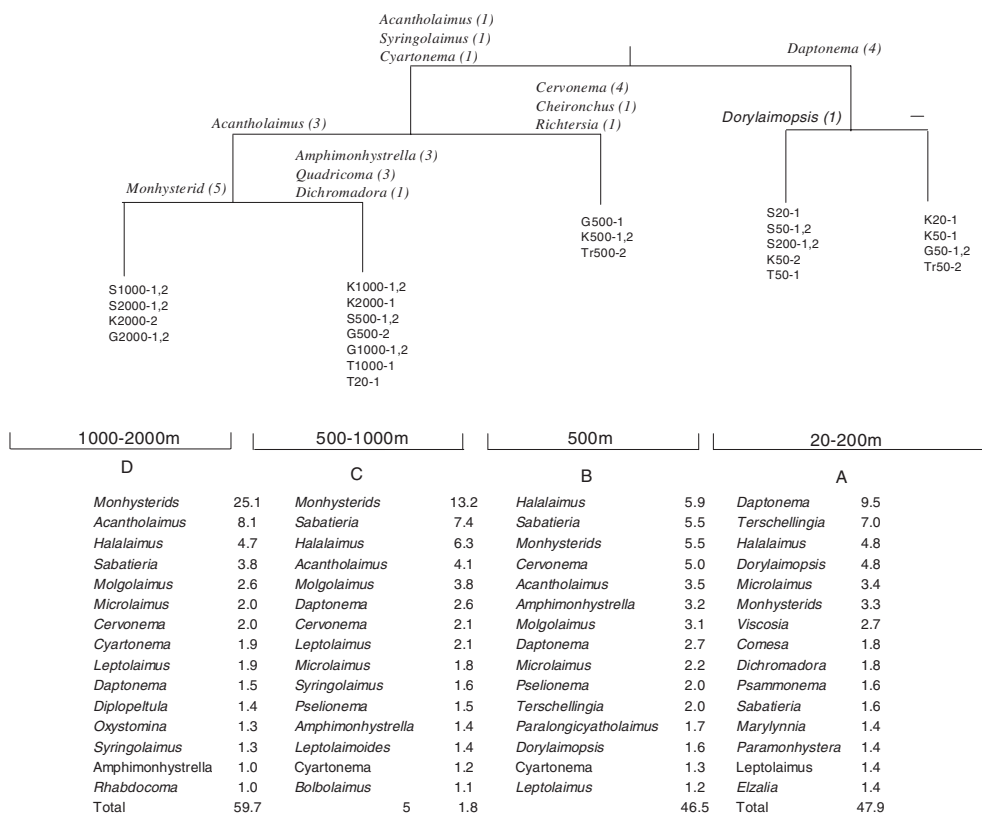| 1000-2000m		500-1000m		500m		20-200m	
D		**C**		**B**		**A**	
Monhysterids	25.1	*Monhysterids*	13.2	*Halalaimus*	5.9	*Daptonema*	9.5
Acantholaimus	8.1	*Sabatieria*	7.4	*Sabatieria*	5.5	*Terschellingia*	7.0
Halalaimus	4.7	*Halalaimus*	6.3	*Monhysterids*	5.5	*Halalaimus*	4.8
Sabatieria	3.8	*Acantholaimus*	4.1	*Cervonema*	5.0	*Dorylaimopsis*	4.8
Molgolaimus	2.6	*Molgolaimus*	3.8	*Acantholaimus*	3.5	*Microlaimus*	3.4
Microlaimus	2.0	*Daptonema*	2.6	*Amphimonhystrella*	3.2	*Monhysterids*	3.3
Cervonema	2.0	*Cervonema*	2.1	*Molgolaimus*	3.1	*Viscosia*	2.7
Cyartonema	1.9	*Leptolaimus*	2.1	*Daptonema*	2.7	*Comesa*	1.8
Leptolaimus	1.9	*Microlaimus*	1.8	*Microlaimus*	2.2	*Dichromadora*	1.8
Daptonema	1.5	*Syringolaimus*	1.6	*Pselionema*	2.0	*Psammonema*	1.6
Diplopeltula	1.4	*Pselionema*	1.5	*Terschellingia*	2.0	*Sabatieria*	1.6
Oxystomina	1.3	*Amphimonhystrella*	1.4	*Paralongicyatholaimus*	1.7	*Marylynnia*	1.4
Syringolaimus	1.3	*Leptolaimoides*	1.4	*Dorylaimopsis*	1.6	*Paramonhystera*	1.4
Amphimonhystrella	1.0	Cyartonema	1.2	Cyartonema	1.3	Leptolaimus	1.4
Rhabdocoma	1.0	Bolbolaimus	1.1	*Leptolaimus*	1.2	*Elzalia*	1.4
Total	59.7		5 1.8		46.5	Total	47.9

Figure 5.   TWINSPAN dendrogram based on relative abundances of nematode genera with indication of indicator genera and their cut levels and the dominant nematode genera per station (TWIN-)group (A, B, C and D).

upper slope (500 m) had a more or less equal distribution of the dominant genera among which were *Halalaimus* (5.9%), Monhysterids (5.5%), *Sabatieria* (5.5%), and *Cervonema* (5%). High abundances of *Cervonema* (4) and the presence of *Cheironchus* (1) and *Richtersia* (1) separated this assemblage from the deeper communities. The mid-slope community (mainly at 1000 m) was dominated by monhysterids (13.2%) *Sabatieria* (7.4%) *Halalaimus* (6.3%) and *Acantholaimus* (4.1%). However, *Amphimonhystrella* (3), *Quadricoma* (3) and *Dichromadora* (1) were selected as the indicator species by the TWINSPAN. The lower slope assemblage (mainly 2000 m stations) was characterised by the dominance of monhysterid (5) as well as *Acantholaimus* (8.1%) *Halalaimus* (4.7%) and to a lesser extent *Sabatieria* (3.8%).

The shift in importance in terms of relative abundances of certain genera with depth is clearly illustrated by this analysis. For instance, monhysterids and *Acantholaimus* became more important with depth, *Sabatieria*, *Cervonema* and *Molgolaimus* were important at upper and mid-slope while *Halalaimus* had more or less the same relative abundance (4.7–6.3%) at all depths (Fig. 6). On the other hand, shelf community genera like *Daptonema*, *Terschellingia*, *Dorylaimopsis* and *Microlaimus* became negligible with increasing depth.

3.5. Diversity at the Level of Genera

HILLS diversity numbers N_0 and N_1, and the expected number of genera for 100 individuals (Table 5) showed all similar trends, since they were highly correlated (R = 0.9; N = 11, P < 0.001). Lowest diversity numbers were found at 200 m, the highest at 500 m (ANOVA F (5,27) = 3; p < 0.05) (Fig. 7). No differences were found between transects.
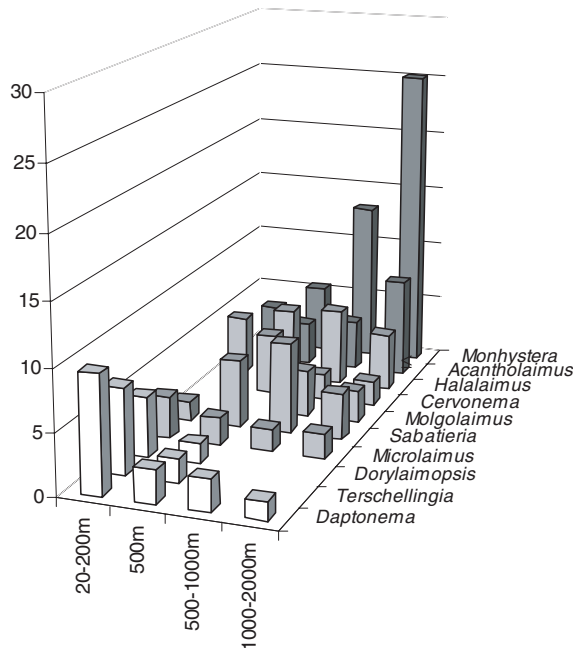

Figure 6.   Relative proportion of dominant nematode genera over the four depth groups resulting from the TWINSPAN (white bars: shallow water species; dark bars: deep-water species; grey bars: intermediate species).
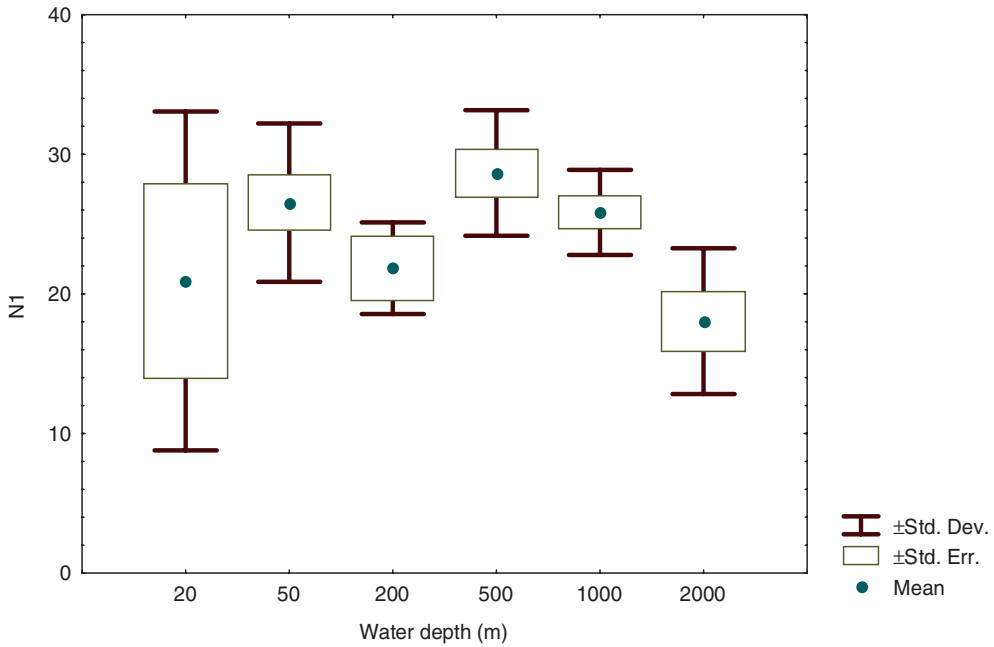
Figure 7.   Box whisker plots for nematode diversity (N_1) per depth zone.

Table 5.   Diversity indices at genus level per station (NA: Not available).

	N_0	N_1	$ES_{(100)}$		N_0	N_1	$ES_{(100)}$
K20−1	52,0	30.49	37,0				
K50−1	31,0	18.42	26,0	**K50−2**	49,0	21.14	32,0
K500−1	57,0	30.76	38,0	**K500−2**	56,0	28.27	37,0
K1000−1	56,0	26.29	37,0	**K1000−2**	55,0	27.4	
K2000−1	42,0	17.37	28,0	**K2000−2**	52,0	24.15	35,0
T20−1	48,0	25.02	33,0	**T20−1**	NA	NA	NA
T50−1	45,0	31.59	37,0	**T50−1**	NA	NA	NA
T1000−1	46,0	22.56	32,0	**T1000−1**	NA	NA	NA
S20−1	24,0	7.27	17,0	**S20−1**	NA	NA	NA
S50−1	40,0	20.33	29,0	**S50−2**	51,0	29	36,0
S200−1	40,0	19.52	29,0	**S200−2**	47,0	24.16	32,0
S500−1	48,0	21.62	33,0	**S500−2**	57,0	29.44	37,0
S1000−1	48,0	23.64	35,0	**S1000−2**	44,0	23.56	31.5
S2000−1	55,0	24.61	35.5	**S2000−2**	43,0	14.95	29,0
G50−1	59,0	28.3	39,0	**G50−2**	57,0	30.59	39.5
G500−1	63,0	35.39	41,0	**G500−2**	56,0	30.64	37,0
G1000−1	53,0	31.52	37,0	**G1000−2**	52,0	25.89	34.5
G2000−1	34,0	11.82	24.5	**G2000−2**	37,0	15.38	27.5
Tr50−2	NA	NA	NA	**Tr50−2**	55,0	32.9	39,0
TR500−2	NA	NA	NA	**TR500−2**	45,0	24.5	33,0

4. Discussion

4.1. Meiofauna Density

Total meiofauna densities in the Western Indian Ocean are comparable in both seasons varying between 292–1052 ind./10 cm^2 in November/December 1992 and 131–1189 ind./10 cm^2 in June/July 1992. These densities are nearly similar to densities (178–970 ind./10 cm^2) observed at the Goban Spur (NE Atlantic) at similar depths (VANAVERBEKE *et al.*, 1997a). Nematode densities in the WIO are further comparable to those from a transect in the Mediterranean and at North Carolina (Table 6). They are lower than the densities observed in the Pacific, most parts of the NE Atlantic, the Laptev Sea in the Arctic and the Weddell Sea in the Antarctic, but higher than the values observed in the Norwegian Sea and the tropical East Atlantic. Trends in nematode density along the continental margin have often been linked to surface primary production and water temperature (VINCX *et al.*, 1994). Water temperature influences the rate of organic degradation and thus the amount of available food reaching the sea floor. SEMENEH *et al.* (1995), observed that there was low nutrient concentration in the water column off the Kenyan coast and low uptake rates by phytoplankton, which could indicate that it concerns an oligotrophic area. This may explain the lower densities compared to the more productive temperate regions.

Table 6.   Nematode densities at various deep-sea sites.

Ocean	Place	Depth (m)	Density (ind/10cm^2)	Reference
W Atlantic	North Carolina	50–2500	33–1026	TIETJEN 1976
NE Atlantic	Goban Spur	206–2760	156–8989	SOETAERT *et al.*, (1997)
	Porcupine Sea Bight	1000, 2000	702–2385	PFANNKUCHE (1985)
	Bay of Biscay	190, 325	840, 779	VANREUSEL *et al.*, (1992)
	Norwegian Sea	970–2133	107–204	JENSEN 1988
Tropical E Atlantic	W. Africa	27–4601	13–888	SOLTWEDEL (1997)
Mediterranean		160–1220	336–637	SOETAERT *et al.*, (1991a)
Pacific Ocean	NE Japan	200–2000	473–1619	SHIRAYAMA and KOJIMA (1994)
Antarctic	Weddell Sea	211–2080	815–5122	VANHOVE *et al.*, (1995)
Arctic	Laptev Sea	65–3237	418–2683	VANAVERBEKE *et al.*, (1997b)
Indian Ocean	WIO	20–2000	160–1928	This study

Limited food resource and/or poor quality has been cited as the most important factor causing decreasing densities for meiobenthos with increasing water depth (JENSEN, 1988; VINCX *et al.*, 1994). The trends in nematode densities in the WIO were such that there was a decrease in densities with increasing depth down to 1000 m followed by a slight increase at 2000 m. SHIRAYAMA and KOJIMA (1994) observed a linear reduction of nematode densities with depth until 1500 m, after which it remained constant. In the Porcupine Sea Bight (500–4850 m), PFANNKUCHE (1985) observed a decline in meiofauna density with depth up to 4850 m. However, in the WIO no trends were observed in sedimentary C : N ratio that could suggest differential food availability with depth. Nutrient levels were generally low but they increased slightly with increase in depth away from the shallow stations suggesting that nutrients were largely of oceanic origin (NGULI, 1995). Although there were significant correlations between nematode densities and measures for food availability (sedi-

ment-bound pigments), regression analysis revealed the best regression with oxygen, explaining 47% of the variation in nematode densities. Although the oxygen levels in this study may not be considered as low compared to values in other oxygen minimum zones (OMZ) in the world, oxygen appears to have a negative relation with nematode densities. This is in contrast to the observation in the oxygen minimum zone (OMZ) from the Arabian Sea where nematode densities are unaffected by low oxygen (COOK *et al.*, 2000). In their study however, COOK *et al.* (2000) considered only the upper cm of sediment, while including the total vertical profile in the sediment can change the image. VANREUSEL *et al.* (1995) showed that in the surface sediments food availability is important in regulating meiofauna densities, whereas deeper in the sediments oxygen supply is often the limiting factor. In a study in the Tropical East Pacific LEVIN *et al.* (1991) observed that at low oxygen concentration, the abundance, composition and diversity of macrofauna was affected, but not the meiofauna abundance. Unlike, other areas where low oxygen levels in the intermediate waters are associated with high organic carbon input, low oxygen levels in WIO is due to the influence of the Red Sea water mass. This water mass flows from the Red Sea through the Arabian Sea at 600–800 m coinciding with the deep oxygen minimum (1.5 ml/l) layer of the Arabian Sea and is also detected between 500 and 1000 m (RAO and GRIFFITH, 1998) in our study area. Also THIEL (1966) observed low nematode counts at 1050 m water depth which corresponded with the OMZ in a deep transect in the North WIO. Deeper down at 1700 m, oxygen contents increased, but this obviously had no significant influence on the nematode densities.

There were no significant differences in nematode densities between transects, although the Kiwayu transect had significantly higher organic carbon contents and was considered as more productive (KROMKAMP *et al.*, 1995) because its close position to the Somalian upwelling area. This observation does not support the prediction that higher productivity in the (meio-)benthos results from upwelling which occurs in the northern part of the Kenyan coast (HEIP and DE BIE, 1995).

4.2. Nematode Composition

Multivariate analysis revealed two main nematode communities based on depth, *i.e.* a shelf and a slope community. The shelf community further subdivided into two assemblages based on the geographic position and the sediment grain size. Both *Terschellingia* and *Dorylaimopsis* have been found predominantly in silty and muddy sediments while the genus *Microlaimus* is often recorded in well oxygenated, sandy sediments (TIETJEN, 1976, 1977; VANAVERBEKE *et al.*, 1997a). The high amount of silt is deposited at the Sabaki transect mainly during the rainy season from April to October (KATWIJK *et al.*, 1994). At the coast off the southern transects, Gazi and Training, only seasonal rivers are found (OHOWA *et al.*, 1997) which have much less impact on the silt deposition on the shelf. Accordingly, the presence of a river plume may explain the difference in sediment composition and hence the nematode composition between both regions.

The nematode genera composition and distribution along the investigated depth transect in WIO were overall similar to those found in the temperate regions. The slope community at the WIO was dominated by the monhysterids (*Monhystera* and some closely related genera), and the genera *Acantholaimus, Halalaimus*, and *Sabatieria*. In other areas at similar depths some of these genera have been found dominant to sub-dominant (TIETJEN, 1976; VANREUSEL *et al.*, 1992; SOETAERT and HEIP, 1995). The genus *Acantholaimus* and the monhysterid group increased in relative abundance with increasing depth in many deep-sea areas (SOETAERT and HEIP, 1995) including the WIO. In the Western Indian Ocean, the genus *Sabatieria* that has been observed to inhabit anoxic or sub-oxic regions (SOETAERT and HEIP, 1995), was highly abundant at mid-depths (500–1000 m), which coincided with the oxygen

minimum layer. Another genus, *Molgolaimus* showing a relatively high abundance at this depth, has also been found to be important in the Antarctic in particular areas with intensive iceberg scouring (Vanhove *et al.*, 1999), and in the NE Pacific adjacent to hydrothermal vents (Vanreusel *et al.*, 1997). This may suggest that several species within this genus are adapted to withstand different kinds of disturbances, including physical and chemical changes. The abundance of *Halalaimus* was relatively high at all depths with a gentle shift in proportions from the shelf to the slope stations in the Western Indian Ocean. Similar distribution patterns were found in the NE Atlantic (Soetaert and Heip, 1995; Vanaverbeke *et al.*, 1997a), and the West Atlantic (Tietjen, 1976) whereas in the Arctic and the Antarctic the relative abundance of *Halalaimus* was rather low (Vanaverbeke *et al.*, 1997b; Vanhove *et al.*, 1995).

4.3. Diversity

Although the study area is characterised by a high number of genera (224), only a few genera are dominant while the majority are poorly represented. Diversity at the level of the genera showed a positive correlation with the amount of fine sand and a negative correlation with the silt fraction of the sediment. Heip and Decraemer (1974) stated that silty environments had lower spatial heterogeneity rendering such environments fewer niches and thus supporting fewer species compared to sandy sediments. Tietjen (1976, 1984) found a high species diversity in sediments with high sand content. Therefore, higher diversity at the most shallow stations along the Gazi transect compared to the other transects, is probably more linked to a higher sand and a lower silt fraction than to the proximity of the latter to upwelling effects.

Diversity at the level of the genus (Fig. 7) showed a more or less parabolic trend, being highest at mid-depth (500–1000 m) and lowest at the shallowest and the deepest stations. Such diversity trends have been observed in relation to depth for nematodes but also for other marine organisms in other parts of the oceans (Etter and Grassle, 1992; Boucher and Lambshead, 1995; Rex *et al.*, 1997).

The generally lower diversity at the shallow water stations and at the deepest stations, leaving mid-depths (which coincides with low oxygen levels) with high diversity, is in contrast with high productive regions with extreme low oxygen, where low diversities have been observed especially for the macrofauna (Levin *et al.*, 1991, 2000). The Kenyan coast is an oligotrophic area experiencing low oxygen levels at mid-depth not because of organic matter accumulation but because of the origin of its intermediate water mass (RSW). The nematode community here is not dominated by opportunistic species such as monhysterids. Furthermore, relatively high proportions of the genus *Sabatieria* which is known to colonise anoxic to sub-oxic sediments (Soetaert and Heip, 1995) were found at the 1000 m stations. We therefore suppose that in the WIO off the Kenyan coast a community has evolved that is adapted to the present oxygen gradient. Therefore the diversity correlates to depth as in other areas without organic carbon enrichment, showing an uni-modal or parabolic trend. In this context, Rogers (2000) pointed out that the high diversity observed at bathyal depths may be due to fluctuations in the atmospheric conditions in the past causing extinctions of the abyssal and shallow water fauna and leaving the bathyal depths as a source area for re-invasion.

Latitudinal trends in diversity have been shown for deep-sea bivalves, gastropods and isopods (Rex *et al.*, 1997) which show a cline from the tropics to the arctic. Vanhove *et al.*, (1999) compared deep-sea nematode diversity at the level of the genus from the Arctic, NE Atlantic, Mediterranean and the Antarctic, using various diversity indices and found no latitudinal trends. Comparing genus diversity (using Hills diversity numbers N_1) from WIO with these four regions, does not reveal any trends either. According to Rex *et al.* (1997)

and CALEY and SCHLUTER (1997), local diversity is directly related to regional diversity. Therefore, the diversity levels observed at the different regions is probably due to local environmental influence rather than their latitudinal location.

5. Conclusions

The higher productivity due to upwelling along the Somalian coast in the northern most transect, Kiwayu, was not reflected in significant higher densities. Higher nematode diversity was observed along the Gazi transect compared to the more northern transects. On the shelf, the most southern transects (Gazi and Training) were found different from the Northern transects based on their genera composition. This differentiation however was most probably linked to differences in sediment composition as a result of river influence rather than difference in productivity between all transects.

Nematode densities decreased with increasing water depth down to 1000 m, then slightly increasing again at 2000 m. Minimum densities coincided with the minimum oxygen concentration in the overlying water. This suggests that oxygen could have a direct or an indirect negative influence on densities. Nematode diversity at the level of the genera was highest at mid-depth (500 m). Unlike density, the generic diversity is not significantly correlated to oxygen level but instead showed a parabolic trend with a maximum at 500 m water depth.

6. Acknowledgements

7. References

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