Hydrobiologia **462:** 41–73, 2001.

Nematode communities of Lake Tana and other inland water bodies of Ethiopia

Eyualem Abebe[1], Jan Mees[2] & August Coomans[2]
[1]*Institute of Cell, Animal and Population Biology, The University of Edinburgh, Ashworth Laboratories, King's Buildings, West Mains Road, Edinburgh EH9 3JT, Scotland, U.K.*
E-mail: eyualem@yahoo.com
[2]*Department of Biology, Ghent University, Ledeganckstraat 35, B-9000 Gent, Belgium*

Received 4 January 2001; in revised form 11 June 2001; accepted 11 July 2001

Key words: freshwater nematodes, nematode ecology, community ecology, Ethiopia, tropical lakes, rivers

Abstract

Free-living nematodes from littoral benthic sediments of four lakes, two rivers and a hot spring in Ethiopia are studied. Populations of nematodes encountered are identified to the species level. The general nematode (generic and species) composition of the lakes, rivers and hot spring are appraised by giving special emphasis to the nematodes from L. Tana, i.e. three sites where different environmental factors come into play were considered. Gelda is a site close to a river inlet (River Gelda), Gedero is a site exposed to strong wind action while Zegie is a secluded site protected by a land mass from any strong wind action. Nematode communities were identified using classification and ordination techniques. The identified communities are then characterised with respect to species composition, biomass, density, diversity, size structure, feeding type and maturity index. Also, the vertical distribution of nematodes is examined at the community and species level. An attempt has been made to associate these variations with the considered environmental factors viz. site, water depth, sediment depth, median grain size and percentage of mud in the sediment.

Median grain size and percentage of mud varied over the three sites with the lowest grain size and the highest percentage of mud in Gelda. The incoming river is regarded responsible for the high mud content at this site. The composition of the nematode communities from the lakes, rivers and hot spring by and large was typically freshwater. The highest number of species (40 species) was recorded from L. Tana (a lake relatively intensively sampled) whereas the lowest number was recorded from the saline lake, Abiyata (2 species). Both species in the latter belong to the genus *Monhystrella*. The complete dominance of species of this genus in L. Abiyata and its presence in the saline lakes and hot spring is argued to be associated with their opportunistic nature and their high temperature dependency and their capacity to withstand high osmotic stress conditions. The role played by salinity in the distribution of nematodes in inland water bodies is considered vital. The occurrence of two species of the genus *Udonchus* in River Abbay where an outlet of a waste disposal scheme of a textile factory is situated, and their absence in any other site coupled with the habitual presence of one of the two species in mineral waters are used to argue that the genus may be an indicator of some kind of environmental (chemical ?) stress. Five nematode communities are identified in L. Tana, viz. Gelda at 0.5 m, Gelda at 1.5 m, Zegie at 0.5 m, Zegie at 1.5 m and Gedero. The vulnerability of Gedero to strong wind action is maintained to be the main reason for the absence of a significant difference in nematode community at the two water depths at this site. The presence of few dominant species characterised four of the five communities. Factors that account for differences in species composition and abundance are discussed. Local conditions are thought to be important in the different communities in L. Tana. A strategy in niche partitioning is suggested to be the main driving force behind the composition of few most dominant species which (in L. Tana and other reviewed lakes) invariably was a combination of a deposit feeder(s) and an omnivore/predator(s) species. In general, nematode diversity in L. Tana was comparable to that found in oligotrophic and mesotrophic freshwater lakes. Nematode diversity varied over the different communities in L. Tana. The two communities in Gelda were less divers and were composed of smaller species than those communities in Zegie and Gedero, and this is explained by the muddy nature of the sediment in Gelda. Most of the difference in diversity among communities could be explained at the genus level. Density and biomass varied significantly over the five communities, density (m^{-2}) was in the range $91 \times 10^3 - 504.7 \times 10^3$ and biomass was in the range 0.02–0.33 g dry wt/m^2 (0.01–0.16 gC/m^2). Deposit feeders dominated in all communities followed by omnivore/predators. Epistrate feeders had the lowest abundance. In all sites, except Gelda at 0.5 m, a large proportion of the nematodes occurred in the uppermost sediment layer (0–1 cm). The number of species also decreased with increasing sediment depth. A relatively higher proportion of nematodes were found in the surface sediment at deeper water depth (1.5 m) than at shallower depth (0.5 m). The vertical profile of biomass followed that of density.

Introduction

Nematodes are ubiquitous and numerically the most important animal group in benthic aquatic habitats (Platt & Warwick, 1980; Heip et al., 1982, 1985; Pennak, 1988; Traunspurger, 1992, 1996a, b). While earlier works on aquatic nematodes concentrated on the taxonomy of the group, research done in more recent times are giving growing emphasis to their ecological aspects. The bulk of nematode research until very recently focused mainly on marine habitats, ignoring the inland water bodies of most parts of the world (Pennak, 1988). Studies on the marine environment have already gathered momentum and are now at a level of understanding the inter-relationships between the physico-chemical environment and the nematodes inhabiting it. Studies on nematodes from inland water bodies, however, are still largely at the taxonomical stage. Furthermore, at a global scale, taxonomic studies on inland water bodies can be considered at an extreme imbalance because relatively complete studies or surveys are concentrated mainly in the temperate region. Nematodes from African water bodies, except for South Africa, hardly received any attention to date. Especially those of ancient lakes are little known (Jacobs, 1984; Decraemer & Coomans, 1994). Information on the ecology of nematodes from inland water bodies is entirely restricted to the temperate region (Biró, 1968; Zullini, 1974, 1976; Prejs, 1977; Schiemer, 1978; Eder & Kirchengast, 1982; Prejs & Bernard, 1985; Prejs, 1986, 1987; Traunspurger, 1992, 1996a, b). Because of the highly variable nature of inland water bodies (Pennak, 1988) which are principally influenced by specific local conditions, patterns and generalisations from these nematological studies have not yet emerged. The problem is even further exacerbated by the inherent taxonomical confusion on the species involved. The only study on the ecology of nematodes from inland water bodies in the tropics (Ethiopia) was that of Tudorancea & Zullini (1989). In that study, however, the authors did not use the proper extraction methods to be able to use the data for generating wider generalisations, therefore that pioneer study remains considerably incomplete.

In the present work, we aim to assess aspects of the ecology (a.o. diversity, density, biomass patterns of horizontal and vertical distribution) of nematode species in some Ethiopian inland water bodies by giving emphasis to those of Lake Tana. The taxonomy of the collected nematodes has been investigated in a series of recent papers (Eyualem, 1996; Eyualem & Coomans, 1996a–f, 1997a, b). For all species recorded from the area we refer to, the species list presented in Table 3. Although we considered some environmental factors such as median grain size, proportion of mud in the sediment, water depth and site, the lack of detailed physico-chemical as well as biological data of the sediments in the studied sites makes our study more of a descriptive nature.

Materials and methods

Study area and sampling

The material studied was collected from three different environmental categories in Ethiopia, i.e. a hot spring, two rivers and four lakes. The investigated lakes are geographically of two types: three are located in the rift system (Lakes Abiyata, Shala and Ziway) while one is located out of the rift system (Lake Tana). The Ethiopian rift system has three main basins. The most northerly is the Ziway-Shala basin, which includes four interconnected lakes: Lakes Ziway, Abiyata, Shala and Langano (Fig. 1). Lake Ziway is situated in the northern part of the drainage basin, Lakes Abiyata and Langano in the middle region,

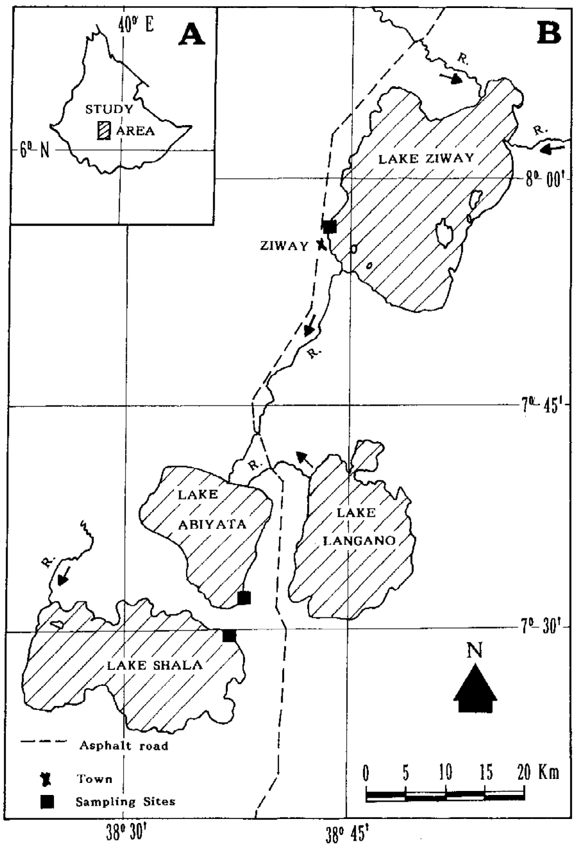


Figure 1. Lakes of the Ziway-Shala basin, (A) Location map; (B) Map showing sampling sites on Lakes Ziway, Abiyata and Shala.

and Lake Shala is the southernmost of the four lakes (Grove et al., 1975; Gasse & Street, 1978). Lake Langano was not sampled for this study. For a detailed description of the study areas, we refer to Eyualem & Coomans (1996a).

Lake Abiyata (7° 37′ N, 38° 35′ E) is a terminal lake with no apparent surface outlet. It is located at a lower altitude than Lakes Ziway and Langano with which it is connected through the rivers Bulbula and Horakalo, respectively. The water level in Lake Abiyata fluctuates with alternating wet and dry periods (Wood et al., 1978; Kassahun, 1982). Also, the lake is known to have a high degree of fluctuation in its ionic concentration, conductivity and salinity. Large bird populations, mainly flamingos, dwell on the lake and are reported to be a source of an appreciable amount of NH4$^+$ (Elizabeth et al., 1994; pers obs.). The sample from Lake Abiyata was collected at a littoral site on the southeastern part of the lake (Fig. 1). There was no vegetation cover and the sample was taken at 0.5m depth. It was a grazing site for flamingos, with a distinctive smell of their excreta. Lake Shala (7° 28′ N, 38° 30′ E) is the deepest lake in the country. Similar to Lake Abiyata, it has no apparent outlet but it receives inflow from several rivers, including mineral hot springs, which may contribute to the lake's high salinity (18.1 psu: Wood & Talling, 1988). At present, the lake is totally isolated from the other three lakes in the basin. The sample from this lake was taken at the northeastern side at 0.5 m depth where hot springs join the lake. An additional sample was collected at the cooler part of the biggest of all hot springs that flow into Lake Shala. The sample came from the northeastern part of the spring (41 °C, pH 8.62, conductivity 9800 mS cm^{-1}) about 15 m away from the lakeshore. This hot spring is easily identified in being situated at the most accessible site as one goes from the main asphalt road to the lake through the national park. Lake Ziway (7° 52′–8° 8′ N, 38° 44′–38° 55′ E) is the shallowest of the four lakes in the basin, with a mean and maximum depths of 2.5 and 7.0 m, respectively (Makin et al., 1975; Elizabeth et al., 1994). It is fed by two main rivers, Katar and Meki, and is connected to Lake Abiyata through the only outflowing river, Bulbula. The sample was taken on the western shore of the lake.

Lake Tana (11° 36′–12° 18′ N, 37° 00′–37° 37′ E) is the largest lake in Ethiopia with a surface area of about 3150 km^2, a maximum length of 78 km and a width of 64 km. It is located outside the rift system in an isolated basin (Fig. 2). The lake is estimated to have been formed approximately 2 million years ago at the Pliocene-Pleistocene transition when the flow of the River Abbay (the Blue Nile) was blocked by volcanic activity (Mohr, 1966; Baker et al., 1972). Many rivers and small streams feed the lake. The area receives on average 1200 mm annual rainfall between June and October (Wood & Talling, 1988). It drains south via the only outflow, River Abbay. Comprehensive studies on the primary and secondary productivity of Lake Tana are still lacking. The area around the lake is mainly farmland. Samples were collected from four sites: Gelda, Zegie, Gedero and a 10 m deep site (Fig. 2). Station 'Gelda' is situated on the southeastern part of the lake where the lake receives the relatively small River Gelda. The bottom was muddy, apparently deposited by the incoming river. It had very little littoral vegetation, but the water was well oxygenated (5 mg l^{-1}). Station 'Zegie' is situated on a secluded site on the south-western side of the lake and it is protected from strong wind action by a localised intrusion of landmass from its northern side. This sampling site

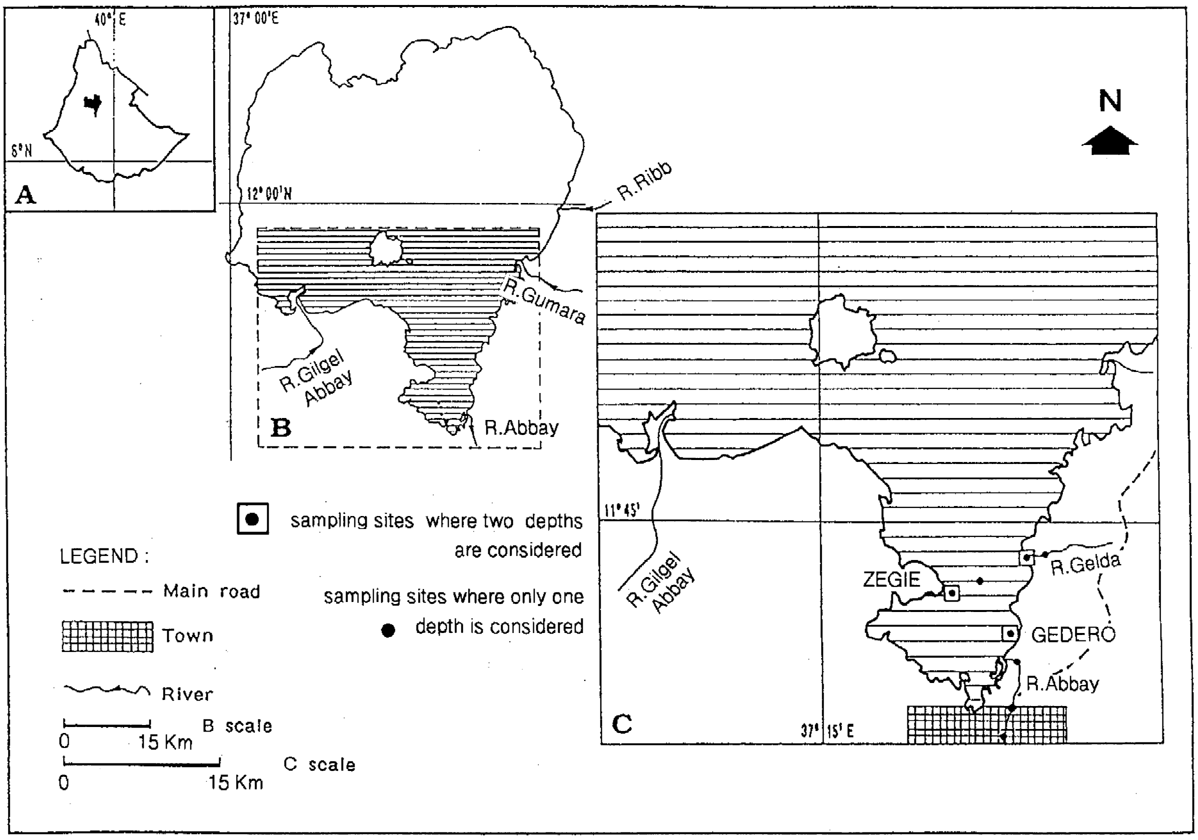


Figure 2. Map of Lake Tana, (A) Location map; (B) Map of Lake Tana and associated major rivers; (C) The southern part of Lake Tana, associated rivers and sampling stations.

was characterised by a predominantly rocky bottom covered with a thin layer of mud and with irregular muddy spots between rocks. For practical reasons, samples were collected from these muddy sites. Station 'Gedero', similar to Gelda, on its eastern side is bordered by an extensively farmed catchment area. It is exposed to strong wind action, especially in the afternoon and evenings, and has very little littoral vegetation. The bottom is muddy. The 'deep' site is situated approximately between Gelda and Zegie and has a depth of 10 m. The bottom was muddy.

River Abbay starts from the southern part of Lake Tana, passes through a town (Bahir Dar), and travels further south. Its flow is characterised by marked seasonal fluctuations: 80% of its annual flow occurs between August and October. Abbay is the main source of silt to the Nile. Samples from Abbay were collected at three sites (numbered as Abbay-1, Abbay-2 and Abbay-3). Abbay-1 was located approximately 1 km away from the lake and had a chiefly rocky bottom. Abbay-2 was a muddy site approximately 1 km south of Abbay-1. At this site on the western side of the river is located the outlet of a waste disposal scheme of a textile factory, with waste being discharged directly into the river. Chemical analysis of river water at the time of sampling (11:30 am) showed a higher nitrate concentration (25 mg l^{-1}) than was recorded for any site in Lake Tana or on the two rivers studied (undetectable in all). The third sample from the river was collected at a muddy site, Abbay-3, situated about 3 km further south from Abbay-2. Samples from all three sites were collected at a depth of 1 m, close to the riverbank. River Gelda travels west through an extensively farmed catchment to join the eastern shore of Lake Tana, the site Gelda (see above). The water as well as the bottom is muddy.

All samples were collected in triplicate during December 1993 and January 1994 using a 32 cm long Perspex cylinder with a 10 cm^2 surface area. In Lake Tana, each sediment core (three sites at two different depths) was divided into four slices: 0–1 cm, 1–3 cm, 3–5 cm and 5–10 cm. All samples were fixed

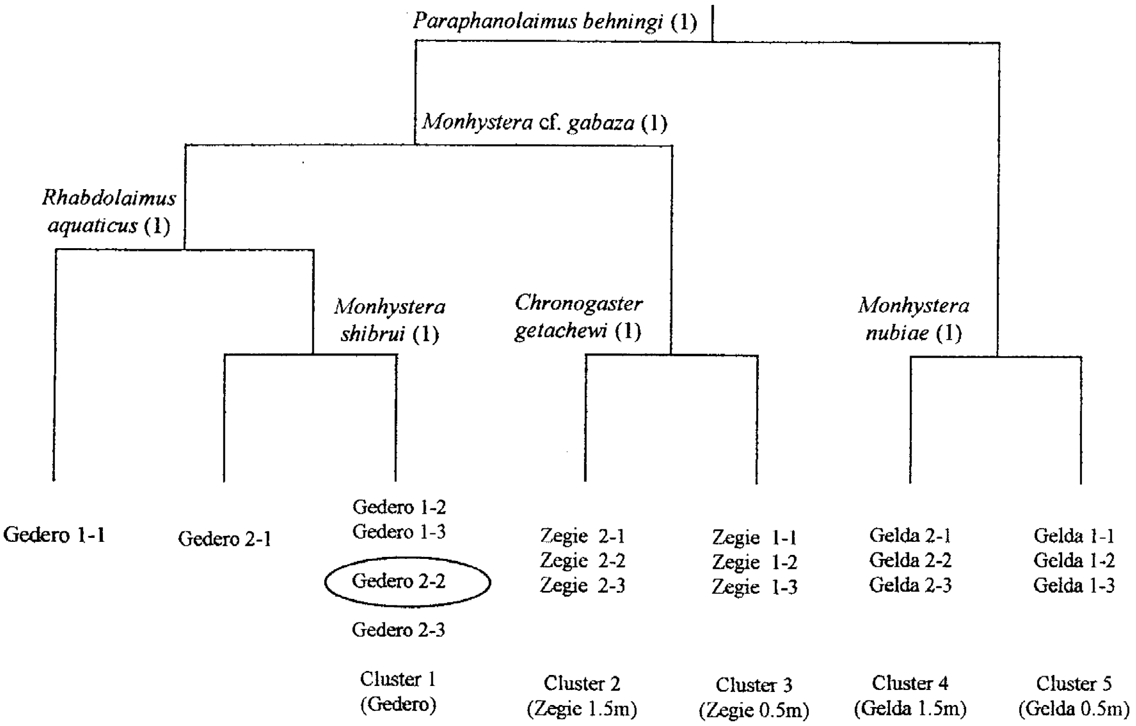


Figure 3. Result of TWINSPAN using transformed pooled data showing the different communities identified in L. Tana. Indicator species and pseudospecies cutlevels (in bracket) are given for each division. Unstable sample in group formation is marked out in oval.

using a hot (60 °C) formaldehyde solution, 4% final concentration. Nematodes were extracted using the centrifugal-floatation technique (Jenkins, 1964).

Water chemical and particle size analyses

Some chemical characteristics of the surface water were determined *in situ* for all localities except in Lakes Abiyata and Shala (only conductivity and pH were determined for Lake Shala). Ammonia, nitrite and nitrate were determined colorimetrically, while oxygen and total hardness were determined titrimetrically using Compact Laboratory for Water Analysis (Aquamerk model 11151). Conductivity and pH were measured using portable meters (HANNA instruments, conductivity using model HI 8733, and pH using model HI 9025). Particle size distribution of the sediment was determined in the laboratory by taking a spoonful from each sample. We used a COULTER LS 100 particle analyser (optical model FRAUNHOFER) attached to PC version 1.44.

Counting and identification of nematodes

All nematodes (i.e. adults and juveniles) except for members of the order Tylenchida, were picked, processed and identified to the species level in 66 out of the total 72 subsamples taken from the three sites of Lake Tana (Gedero, Gelda & Zegie). In the remaining 6 samples, 2 from Gedero and 4 from Zegie, only 200 nematodes were randomly picked for identification and from this the relative proportion of each species in each sample was established. The remaining nematodes in each of these 6 samples were counted under a dissecting microscope and the final number of each species in each sample was extrapolated based on the proportion established earlier. Members of the order Tylenchida Thorne, 1949 were encountered in many samples, but we did not attempt to identify them to the genus level or beyond. However, we have included them as a group when characterising different nematode communities and in the nematode biomass calculations.

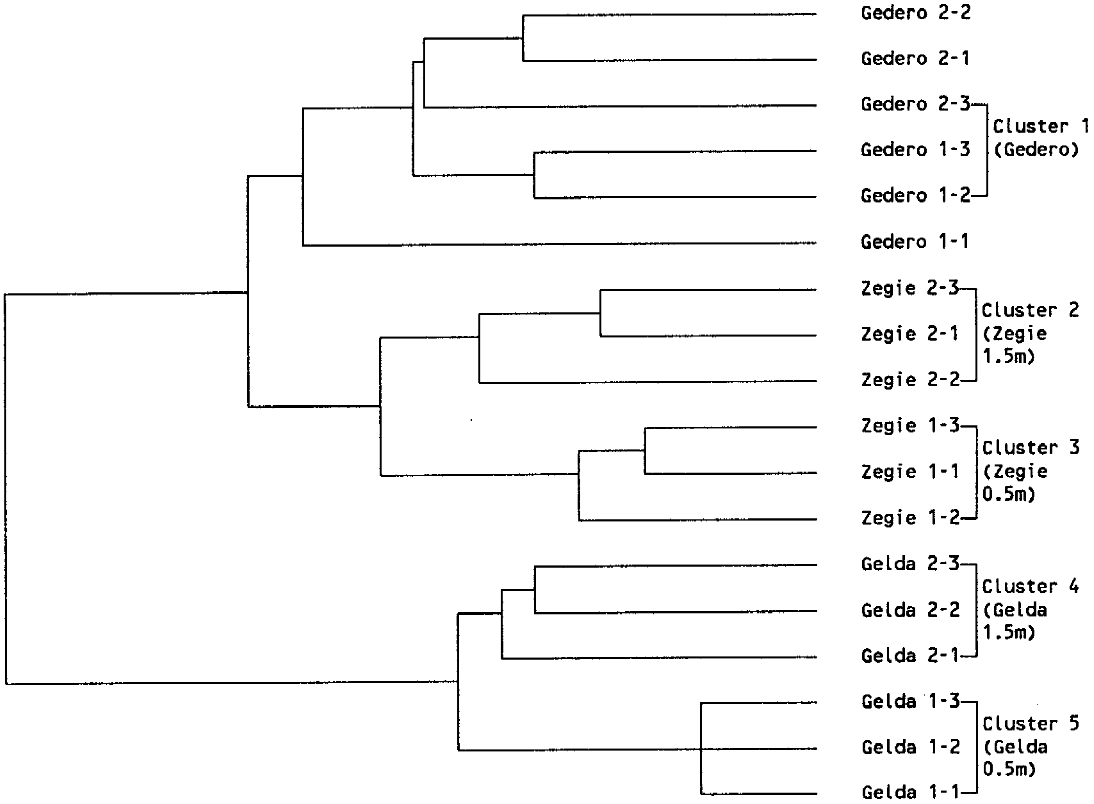
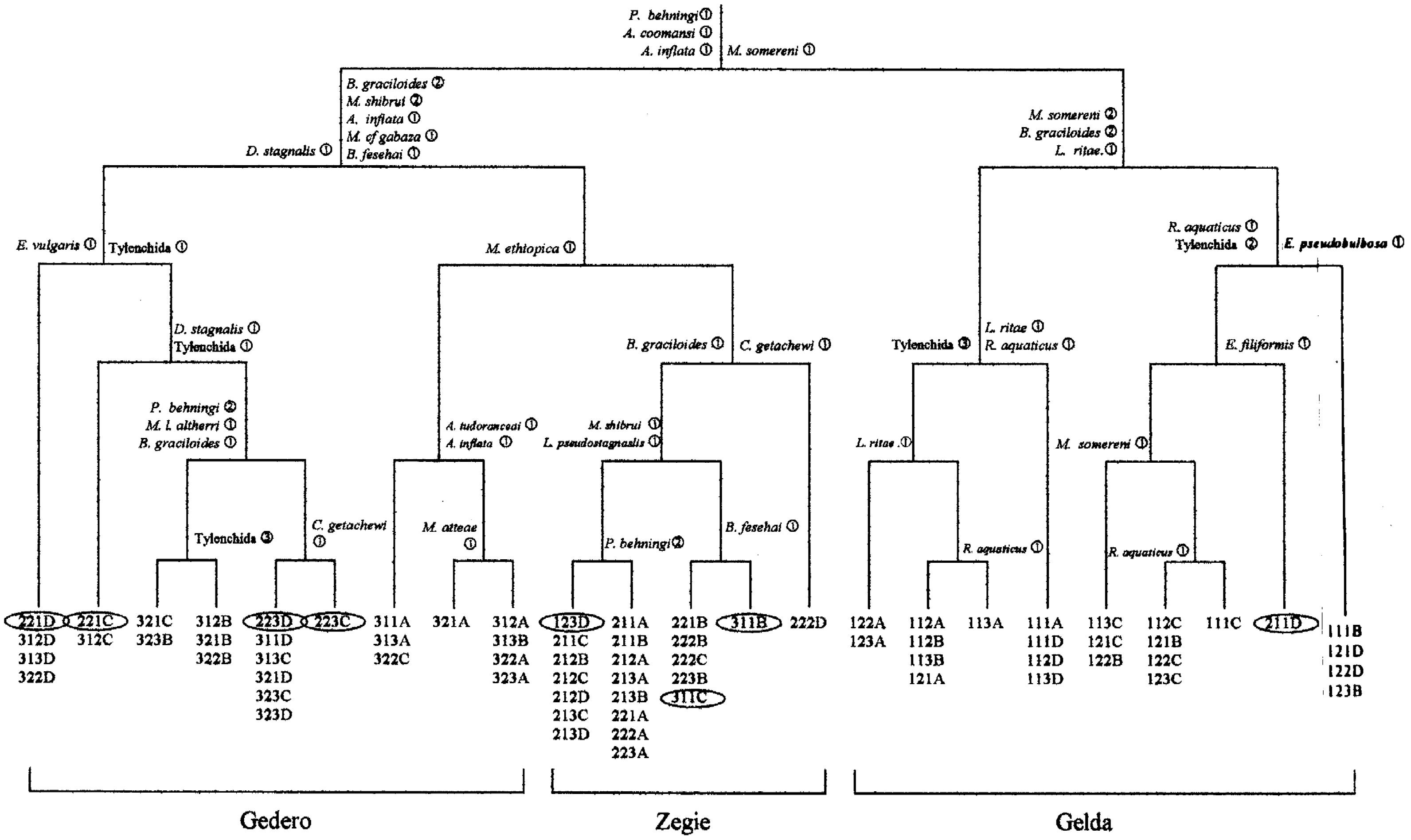


Figure 4. Result of cluster analysis using transformed pooled data showing the different communities identified in L. Tana.

Data analysis

Different multivariate techniques (classification and ordination) were used to identify nematode communities and to describe their structural characteristics (Heip et al., 1988). These analyses were done on matrices of densities and environmental variables. Density data were analysed both before and after fourth root transformation. Also, the density matrices were subjected to the analyses at two levels, i.e. (1) by considering each of the four slices separately (cf. the horizontal sectioning of the cores), and (2) by pooling the four slices of each core. Classification of the sampling sites according to their species composition was done with both divisive and agglomerative classification techniques: Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill, 1979) and Group Average Sorting cluster-analysis with the Bray–Curtis dissimilarity index (Bray & Curtis, 1957). The cut levels used were 0, 1, 3, 7, 15 and 25 for the untransformed data. An exploratory Correspondence Analysis (CA) was done to assess total community variability and to compare the scales of the species scores and the sample scores. We then used Canonical Correspondence Analysis (CCA) (Jongman et al., 1987; Ter Braak, 1988) to assess and visualise the relationship between species composition and environmental variables, i.e. study site, water depth, median grain size and percentage of mud in the sediment. Nematode communities were identified based on the results of the classification and ordination techniques described above.

Next, the following indices and methods were used to further characterise and compare nematode communities: (1) *Diversity*. Hill's diversity numbers of the order 0, 1, 2 and $+\infty$ were calculated (Hill, 1973). The lowest number gives the same weight to all species present, whereas the numbers of higher order give more and more weight to the more abundant species. N_0 is equal to the number of species present, $N_1 = e^H$ where H is the Shannon–Wiener diversity index, N_2 is the reciprocal of Simpson's dominance index, and N_∞ is the reciprocal of the relative abundance of the most abundant species. A hierarchical subdivision of diversity, for instance divisions into different levels



First number represents site, where 1 = Gelda, 2 = Zegie, 3 = Gedero;
Second number represents water depth, where 1 = 0.5m, 2 = 1.5m;
Third number represents the replicate core number;
Letter represents slice of the core, where A = 0-1cm, B = 1-3cm, C = 3-5cm, D = 5-10cm;
Number in circle following species' name is pseudospecies cutlevel.

Figure 5. Result of TWINSPAN using transformed slice data indicating the major site differences. Indicator species and pseudospecies cutlevels (in circle) are given for each division. Samples grouped out of their site are marked in oval.

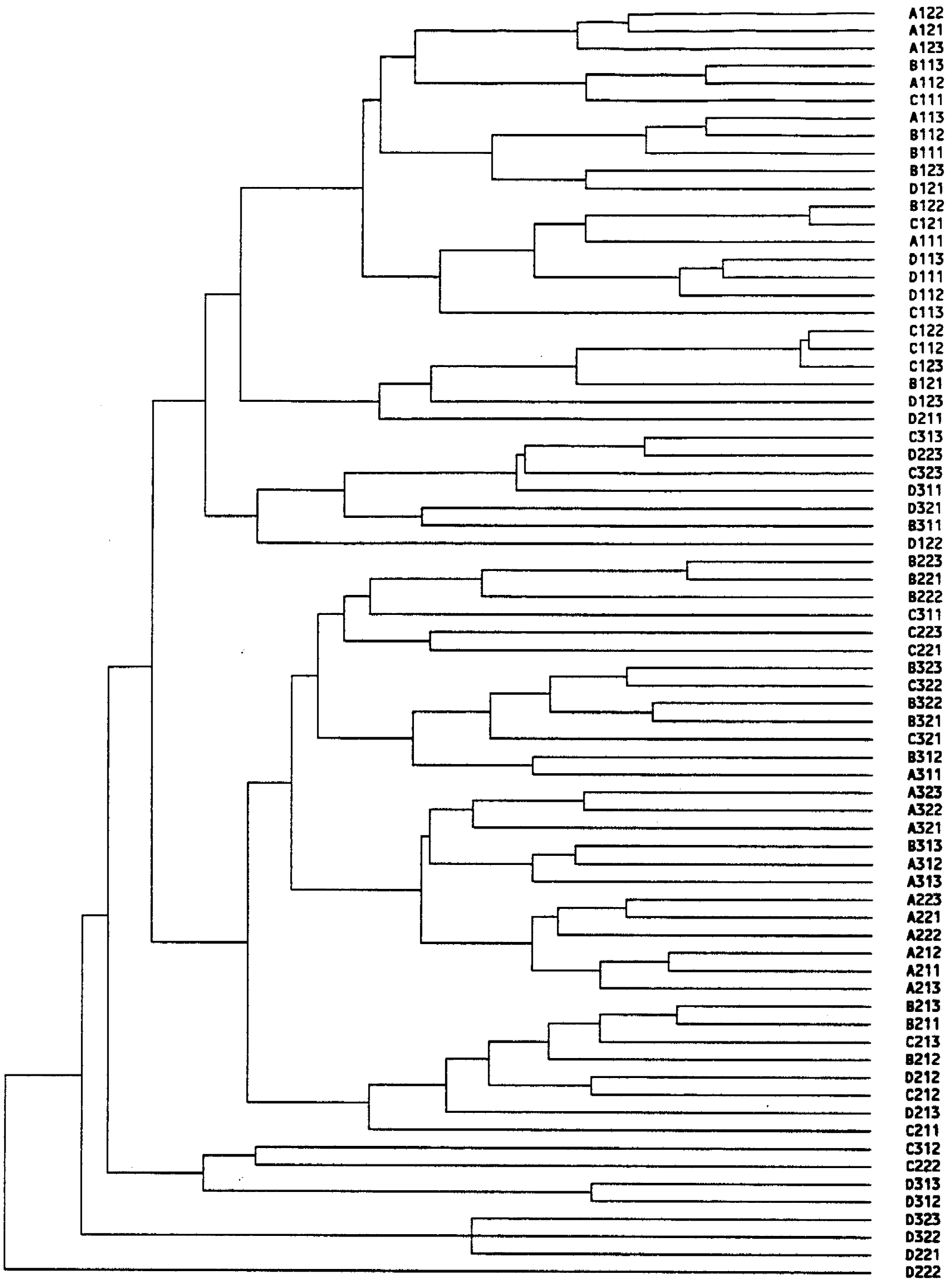


Figure 6. Result of cluster analysis using transformed slice data. Legend: Letter represents slice of the core, A = 0–1 cm, B = 1–3 cm, C = 3–5 cm, and D = 5–10 cm; Numbers represent as indicated in legend of Figure 5, first number represents site, second number represents water depth, and third represents replicate core number; for further detail refer to legend of Figure 5.

of taxonomic groups, trophic types etc., has been recommended by Heip et al. (1988) for a better description of the community in question, especially in cases where comparisons of communities are made. The Shannon–Wiener diversity index (H_T = total diversity) is divisible (Pielou, 1969 in Heip et al., 1988), a method we used to evaluate the between-genera diversity (H_g) and the average within-genus diversity (H_{wg}) as follows: $H_T = H_g + H_{\mathrm{wg}}$ where $H_g = -\Sigma q_i \mathrm{Ln}(q_i)$, with Σq_i = the proportional abundance of the genus *i,* and $H_{\mathrm{wg}} =_I \Sigma q_i$ $(-\mathrm{j}\Sigma r_{ij} \mathrm{Ln}(\mathrm{r}_{ij}))$, with r_{ij} = the proportional abundance of species *j* in genus *i.* We further used two methods to help visualise diversity. In *k*-dominance curves (Lambshead et al., 1983) the percentage abundance of the *k*th species plus the percentage abundance of all more dominant species (cumulative abundance) is plotted against the rank of the species *k*, in an order starting with the most abundant species and ending with the least abundant species. In species-abundance distributions, the number of species represented by *r* individuals is plotted against *r.* (2) *Biomass.* Biomass of individual nematodes was calculated according to Andrássy (1956). Males, females and juveniles were treated separately and the mean individual biomass was calculated for each species in every community where it occurred from measurements of at least five specimens. The total biomass of a species in a specific community was calculated by multiplying the number of males, females and juveniles by their respective mean individual biomass and adding up the products. The formula of Andrássy (1956) assumes that tail shape in nematodes is conoid. To be in agreement with this assumption, we only used the conoid part of the tail, excluding the filiform posterior part from the calculations. Dry weight and organic carbon were assumed to be 25% and 12.4% of the wet weight, respectively (Jensen, 1984). (3) *Maturity.* The Maturity Index (MI) is an index that indicates the condition of an ecosystem based on the composition of the nematode community (Bongers, 1990). We used *c-p* values as provided by Bongers (1990) and Bongers et al. (1995) for terrestrial and aquatic nematode families. Bongers et al. (1995) proposed a change of the *c-p* score for two families among which one is relevant to our study, the family Monhysteridae, based on a concept that subdivides opportunistic groups. They transferred this family from a *c-p* score of 1 to 2 based on the argument that they are general opportunists, i.e. they occur in food-poor conditions and do not form dauer larvae. Since Monhysteridae is one of the most dominant families in our samples with respect to density, results of calculations using the newly proposed value may produce values considerably higher than would be expected otherwise. Therefore, to show the impact of the change in *c-p* score, we have calculated maturity index values using both the old and recently proposed scores. Calculations using the initial value of 1 will undoubtedly make our MI values comparable with the literature while calculations using the later value of 2 can be used as reference for future comparison. (4) *Feeding types.* We employed Jensen's (1987a) classification scheme to assess the proportion of the feeding types. However, we used Wieser's (1953) earlier proposal of Group 2B, 'omnivore/predators', instead of Jensen's 'predator' group for the true predacious genera such as *Ironus* Bastian, 1865 as well as for those genera that are identified as omnivores by Yeates et al. (1993). Since the diet of nematodes is varied and often conclusions about food and feeding habits are based on limited observations (Yeates, 1979; Ferris & Ferris, 1989), we prefer to keep these groups together as omnivore/predators.

Results

Sediment particle composition

Median grain size and proportion of mud for the different sampling sites are given in Tables 1 and 2. In lake Tana, the sediment of the four sites ranged from silt (both water depths at Gelda) to fine sand (0.5 m water depth at Zegie) (nomenclature as in Holme & McIntyre, 1971). Median grain size increased significantly with water depth in Gedero and Zegie but did not change much in Gelda (ANOVA, $P<0.05$). The proportion of mud decreased significantly as water depth increased in Gedero and Zegie, but it remained more or less the same in Gelda (ANOVA, $P<0.05$). For River Abbay, sediment grain size increased while percentage of mud decreased away from the lake. The sediment in lake Shala and the hot spring was medium sand with a low mud percentage.

Species composition

A total of 51 species belonging to 6 orders, 15 families and 25 genera were identified from all sites (Table 3). Thirty-five species were recorded more than once. Twenty species (39%) were new to science and have been described elsewhere (Eyualem, 1996; Eyualem & Coomans, 1996a, b, c, d, e, f;

Table 1. Median grain size (μm) and proportion of mud (%) in the sediment of four sites of Lake Tana. Percentages of mud are given in parentheses

Water depth (m)	Sediment depth (cm)	Sites			
		Gedero	Gelda	Zegie	Deepest site
0.5	0–1	80.3 (30.6)	36.2 (97.0)	84.5 (36.4)	
0.5	1–3	71.3 (40.5)	31.8 (73.8)	81.9 (41.4)	
0.5	3–5	73.1 (38.8)	52.0 (89.1)	77.4 (41.9)	
0.5	5–10	64.1 (48.8)	14.6 (98.7)	117.9 (20.0)	
1.5	0–1	108.1 (13.6)	35.3 (67.9)	179.6 (8.4)	
1.5	1–3	112.8 (10.3)	27.3 (76.7)	172.5 (6.7)	
1.5	3–5	121.4 (12.8)	14.0 (99.9)	162.0 (4.7)	
1.5	5–10	92.8 (22.9)	46.2 (92.6)	139.4 (6.7)	
10					15.1 (90.0)

Table 2. Median grain size (μm) and proportion of mud (%) in the sediment of sites other than L. Tana

Sites		Water depth (m)	Median grain size	Proportion of mud
River Abbay	Abbay-1	1.0	21.4	77.8
	Abbay-2	1.0	76.9	46.3
	Abbay-3	1.0	123.0	40.9
River Gelda		1.0	88.1	44.1
Lake Abiyata		0.5	111.6	23.5
L. Shala		0.5	414.1	2.8
L. Ziway		0.5	70.7	45.5
Hot Spring		-	473.6	6.4

1997a, b) and three of the remaining species (*Aphanolaimus tudoranceai*, *Mesodorylaimus macrospiculum* and *Prodesmodora nurta*) were hitherto only recorded from Ethiopia. Eight species (*Chronogaster multispinatoides*, *E. mwerazii*, *Epitobrilus setosus*, *Ironus sphincterus*, *Ischiodorylaimus ugandanus*, *Monhystera* cf. *gabaza*, *Plectus (P.) galapagensis*, and *P. matoni*) were recorded for the first time out of their type localities. Twenty species belonged to the family Monhysteridae; the genus *Monhystrella* was represented by eight species. Sixteen genera were represented by a single species only. The highest number of species was recorded from Lake Tana (40 species) while the lowest number was recorded from Lake Abiyata (2 species). The only two species recorded from Lake Abiyata and three out of five species recorded from Lake Shala belonged to the genus *Monhystrella*. Despite their close proximity, Lake Shala and The hot spring shared only one species. Lake Tana shared most species recorded from River Abbay (10 out of 14) and River Gelda (4 out of 5). The four species that were found in River Abbay, but were absent from Lake Tana were *Eumonhystera geraerti*, *Prismatolaimus matoni*, *Udonchus merhatibebi* and *U. tenuicaudatus*. Similarly, *P. matoni* was only recorded from River Gelda. All four species found in Lake Ziway also occurred in Lake Tana. *Achromadora inflata* and *Eumonhystera vulgaris* were the most widely distributed species, followed by *Anonchus coomansi* and *Eumonhystera mwerazii*. The former two species were found in three

Table 3. List of species and their corresponding sites of occurrence

Species	Sites											
	L. Tana				R. Abbay			R. Gelda	L. Abiyata	L. Shala	Hot Spring	L. Ziway
	Gedero	Gelda	Zegie	Deepest site	Abbay-1	Abbay-2	Abbay-3					
1. *Achromadora inflata*	+	+	+		+	+	+					+
2. *Anonchus coomansi*	+		+	+		+	+					
3. *Aphanolaimus tudoranceai*	+		+	+	+							
4. *Brevitobrilus graciloides*	+	+	+		+							+
5. *Brevitobrilus fesehai*	+		+									
6. *Brevitobrilus tsalolikhini*	+		+									
7. *Chronogaster ethiopica*											+	
8. *Chronogaster getachewi*	+		+									
9. *Chronogaster multispinatoides*	+											
10. *Diploscapter coronatus*		+	+									
11. *Dorylaimus stagnalis*	+											
12. *Epitobrilus setosus*	+		+									
13. *Ethmolaimus zullinii*			+									
14. *Eumonhystera dispar*								+				
15. *Eumonhystera filiformis*	+	+	+									
16. *Eumonhystera geraerti*					+							
17. *Eumonhystera mwerazii*	+		+		+	+	+					
18. *Eumonhystera pseudobulbosa*	+	+	+	+								
19. *Eumonhystera vulgaris*	+		+	+	+	+	+	+				
20. *Ironus ignavus*	+			+								
21. *Ironus sphincterus*	+		+									+
22. *Ischiodorylaimus ugandanus*			+									
23. *Laimydorus ritae*		+										
24. *Laimydorus pseudostagnalis*			+									
25. *Mesodorylaimus macrospiculum*										+		
26. *Monhystera deleyi*			+	+								
27. *Monhystera* cf. *gabaza*			+									
28. *Monhystera nubiae*		+										
29. *Monhystera shibrui*	+	+	+									
30. *Monhystera somereni*		+	+									+
31. *Monhystera tanae*	+											
32. *Monhystrella arsiensis*											+	
33. *Monhystrella atteae*	+											
34. *Monhystrella ethiopica*	+				+		+					
35. *Monhystrella hoogewijsi*									+	+		
36. *Monhystrella jacobsi*									+	+		
37. *Monhystrella lepidura altherri*	+				+	+		+				
38. *Monhystrella macrura*										+		
39. *Monhystrella woitorum*			+									
40. *Mononchus truncatus*	+		+									
41. *Paraphanolaimus behningi*	+		+		+		+					
42. *Paraplectonema pedunculatum*			+	+		+	+					
43. *Plectus galapagensis*		+										
44. *Prismatolaimus matoni*					+		+					
45. *Prodesmodora nurta*			+									
46. *Rhabdolaimus aquaticus*	+	+	+							+	+	
47. *Rhabdolaimus* cf. *minor*	+							+				
48. *Rhabdolaimus terrestris*	+	+										
49. *Tripyla glomerans*			+									
50. *Udonchus merhatibebi*						+						
51. *Udonchus tenuicaudatus*						+	+					
Number of species at each site	**26**	**12**	**28**	**7**	**10**	**8**	**8**	**4**	**2**	**5**	**3**	**4**

sites in Lake Tana, the three sites of River Abbay, and in Lake Ziway, while the latter two species were present in three sites of Lake Tana, the three sites of River Abbay, and in River Gelda.

Identification of nematode communities in Lake Tana

The results of the TWINSPAN using the pooled and sliced data are presented in Figures 3 and 5. The first division separated Gelda from Gedero and Zegie. Indicator species for the latter community was *Paraphanolaimus behningi* and the second division in this cluster separated Zegie from Gedero with *Monhystera* cf. *gabaza* as indicator species for Zegie. The next division in the group of Gelda samples nicely divides the samples according to the two water depths considered, i.e. 0.5 m and 1.5 m. The indicator species for the deeper stations is *Monhystera nubiae*. The Zegie samples are also divided into a 0.5 m and a 1.5 m clusters. The indicator species for the deeper sites was *Chronogaster getachewi*. No distinction was observed with respect to water depth at Gedero. One of the four replicate cores of the Gedero cluster was a borderline member of the group and it showed instable behaviour in other analyses. With four replicates, the indicator species for Gedero was *Monhystera shibrui*, while it became *M. tanae* when the inconsistent replicate was excluded. Further divisions did not yield ecologically meaningful information. TWINSPAN allows for the identification of five nematode communities in Lake Tana, viz. Gelda 0.5 m, Gelda 1.5 m, Zegie 0.5 m, Zegie 1.5 m and Gedero.

The results of the cluster analyses are in general agreement with the TWINSPAN results: the five nematode communities can easily be distinguished (Figs 4 and 6). The communities at Zegie and Gedero were more similar to each other than to that of Gelda. Also, the difference between the two depth strata is evident in Zegie and Gelda but absent in Gedero.

The output of the CCA is shown in Figures 7–11. The inflation factors of the environmental variables ranged between 1.7 and 5.4. This is well below the critical value of 20, implying that no two environmental variables considered were strongly correlated. The eigenvalues for the first, second and third axes were 0.80, 0.37 and 0.33, respectively. Only the first ordination axis was significant (Monte Carlo permutation test over 99 permutations, p=0.01, F-ratio=4.92 for axis 1). The results are similar to those obtained with the classification techniques. In both ordination planes, the Gelda samples are located on the far right

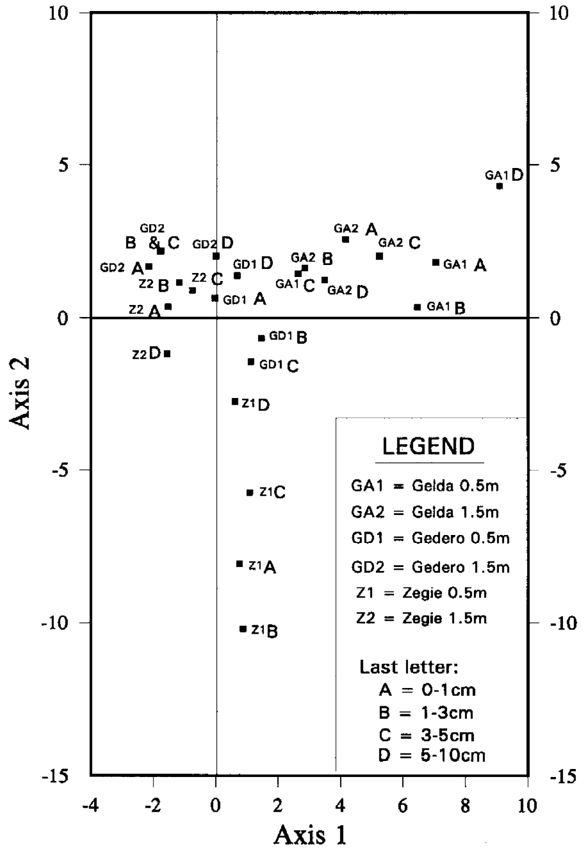


Figure 7. Result of Canonical Correspondence Analysis (CCA), biplot of sample scores using axes 1 & 2.

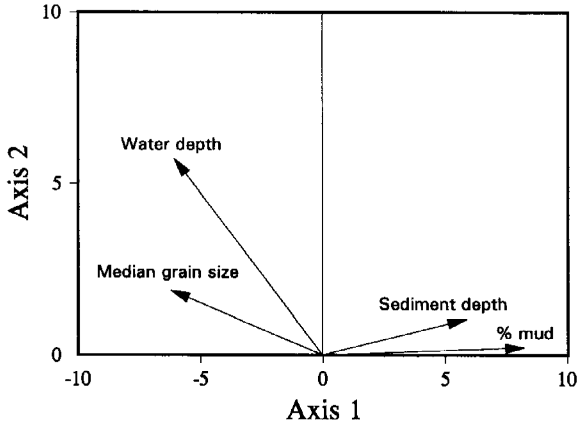


Figure 8. Result of Canonical Correspondence Analysis (CCA), biplot of environmental variables using axes 1 & 2.

side, clearly separated from the other two sites. Three of the four variables were significantly correlated with the species and sample plots (p=0.01and F-ratio=0.00 for percentage of mud; p=0.01 and F-ratio=2.7 for water depth; p=0.03, F-ratio=2.8 for median grain size). The longest arrow in the environmental biplot represents percentage of mud and almost parallels the first axis, separating the muddy Gelda samples from the less muddy samples of Zegie and Gedero. Percentage of mud and median grain size are negatively correlated. The ordination also separated the Gedero and Zegie samples but none of the environmental variables considered could explain the difference between them. Clusters of samples from the same depth strata can also be identified. In both planes, all Gedero 1.5 m and Zegie 1.5 m samples lie on the left side of the plot. The Gelda 1.5 m samples were found on the right side of the plane, but they were still situated further left than the 0.5 m samples from the same location. Moreover, in the ordination plane of the first and third axes the Zegie 1.5 m samples were distinctly separated from the rest in the upper left quadrant (Fig. 10). This separation was correlated with a higher median grain size and a lower percentage of mud. Deeper sediment layers (3–5 cm and 5–10 cm) tended to show more similarity than the upper sediment layer (0–1 cm and 1–3 cm) in the Gedero and Zegie samples. Still, sediment depth was not a powerful factor in the grouping of the samples. In the biplot of the species scores (first and second axes), a group of species characteristic for the muddy Gelda samples are situated in the upper right quadrant. Species characteristic for the Zegie and Gedero samples are situated close to each other in the left half of the plane (Fig. 9). In the ordination plane formed by the first and third axes (Fig. 11) two clusters of species are located on the left side of the diagram: the species in the upper quadrant characterise the Zegie 1.5 m samples, while the species in the lower quadrant characterise the Gedero 1.5 m samples. Species plotted close to the centre of the plane have a wide distribution and species occurring in the deeper sites of Zegie and Gedero are situated on the left side of the plane formed by the first and third axes.

In summary, we distinguish five communities: community 1 at Gedero, community 2 at Zegie 1.5 m, community 3 at Zegie 0.5 m, community 4 at Gelda 1.5 m, and community 5 at Gelda 0.5 m.

Characterisation of the nematode communities in Lake Tana

The species composition of the five communities, density, sex ratio, proportion of juveniles, vertical relative distribution of adults and juveniles of the dominant species (i.e. species constituting $>$3% of the total density) are shown in Figure 12 and Table 4. Both communities of Gelda and Zegie were dominated by a single species constituting about 40% of total density. In Gedero, the community was characterised by a lesser degree of dominance (about 20% for the first two species). This is also reflected in the K-dominance curves (Fig. 13) and Hill's diversity numbers (Table 5): diversity was highest in Gedero and lowest in Gelda. Most of the diversity in the nematode communities was due to between-genus diversity (79.5–88.6%, Table 5). The number of genera per 30 cm^2 ranged from 7 to 18, while only 1.28–1.53 species per genus were present. Species abundance plots show that most species were present in low densities, i.e. less than 5 individuals per 10 cm^2 (Fig. 14); 23, 12, 15, and 17% of the species were recorded with 0.33–1.00 individuals per 10 cm^2 in Gelda 1.5 m, Zegie 0.5 m, Zegie 1.5 m, and Gedero, respectively. Length–frequency distributions were comparable in all communities (Fig. 15). Most species were smaller than 2.0 mm. Larger species were only present in the Zegie and Gedero communities. The communities at the muddy sites (Gelda 0.5 m and 1.5 m) were not only less diverse, but they were also composed of smaller species.

Density and biomass were significantly different in the different communities (Table 5). Density ranged from 91 000 to 505 000 individuals per m^2; biomass ranged from 0.02 to 0.33 g dry weight per m^2 (0.01–0.16 gC per m^2). Density was lowest in Gelda (ANOVA, $p<0.01$) and highest in Zegie and Gedero community. Biomass at Gedero was significantly different from that of Gelda and Zegie. These differences were mainly due to the uppermost (0–1 cm) sediment layer (ANOVA, $p<0.01$); density and biomass in the lower sediment layers (1–10 cm) were not significantly different between sites. No significant differences in density and biomass were found between the two depth strata of the same site. Biomass varied significantly between the three sites and between the different sediment layers (ANOVA, $P<0.01$). Communities in deeper water (Gelda 1.5 m and Zegie 1.5 m) had a significantly different biomass in the uppermost (0–1 cm) sediment layer only (ANOVA, $P<0.05$).

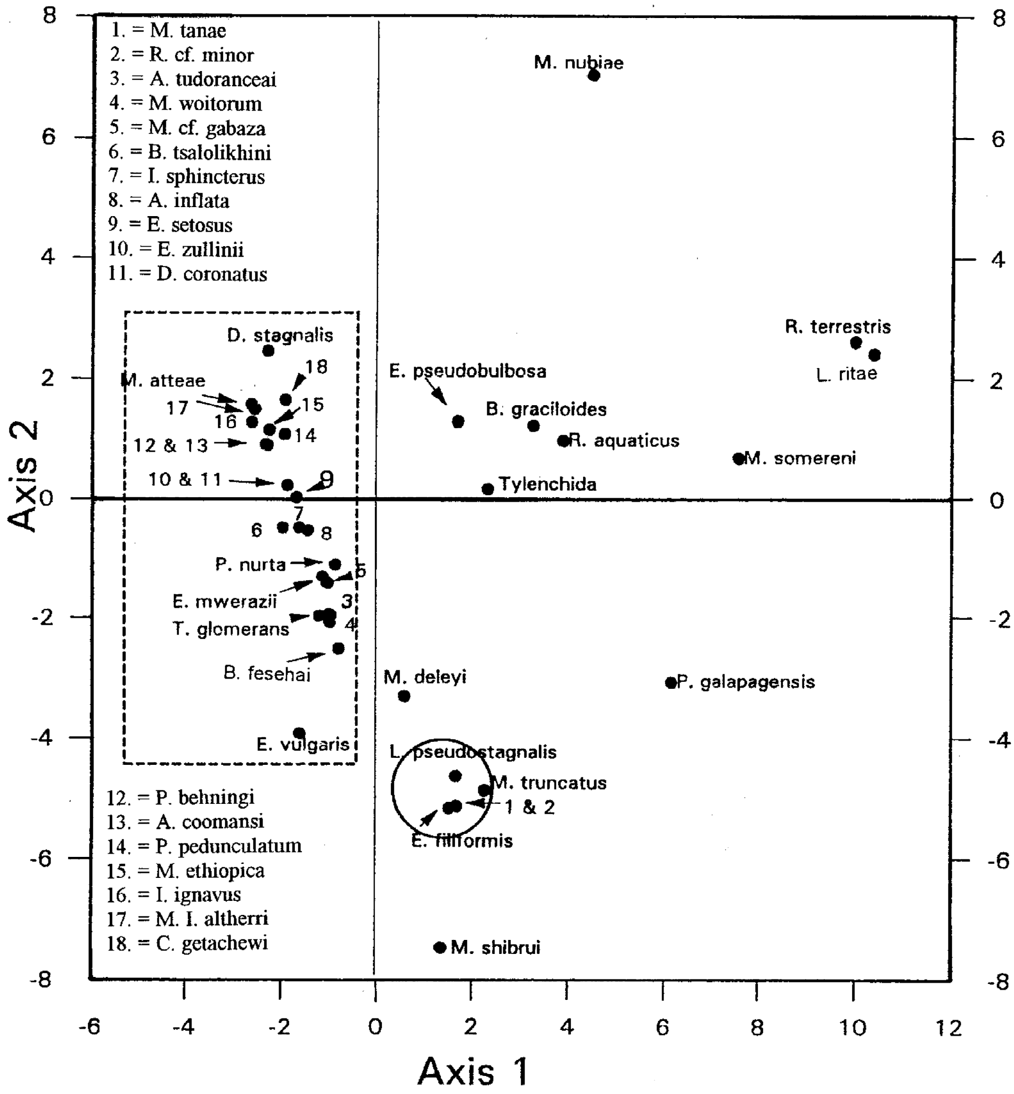


Figure 9. Result of Canonical Correspondence Analysis (CCA), biplot of species scores using axes 1 & 2.

The maturity index using a *c-p* score of 1 for the Monhysteridae shows that the community of Zegie 1.5 m (dominated by the persister genera *Anonchus*, *Paraphanolaimus*, *Brevitobrilus* and *Epitobrilus*) had the highest *c-p* value. The Gelda 1.5 m community (dominated mainly by the coloniser genus *Monhystera*) had the lowest *c-p* value (Table 5). The transfer of Monhysteridae from a *c-p* score of 1 to 2 increased MI values in the communities Gelda 0.5 m, Gelda 1.5 m, Zegie 0.5 m, Zegie 1.5 m, and Gedero by a factor of 1.13, 1.41, 1.26, 1.04 and 1.12, respectively. The maturity index doesn't seem to be correlated with diversity, density or biomass. Still, it is noteworthy that the Gelda 1.5 m community which was characterised by a low diversity and the lowest density and biomass is dominated by a coloniser genus.

Deposit feeders dominated all sites (Fig. 16). They constituted 48–70% of the entire community and generally their proportion tend to increase with water depth. The second dominant feeding type was the omnivores/predators. Their proportion decreased with water depth. Epistrate feeders had a very low abundance and their proportion increased with depth.

Vertical distribution

Vertical distribution profiles of the nematode communities of the different sites are depicted in Figures

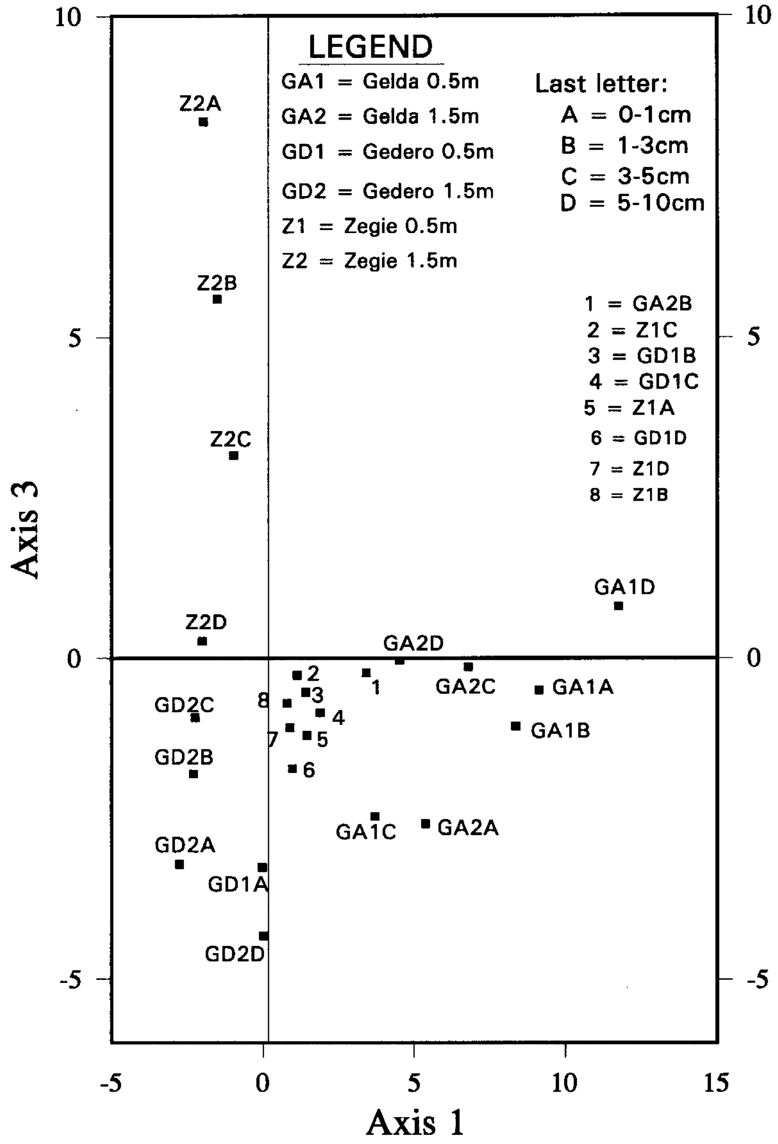


Figure 10. Result of Canonical Correspondence Analysis (CCA), biplot of sample scores using axes 1 & 3.

17–19. In all sites, except in Gelda 0.5 m, most nematodes (40–80%) were found in the uppermost sediment layer (0–1 cm). In Gelda 0.5 m, only 8% of the nematodes were found in the surface sediment layer; most (70%) occurred deeper in the sediment (5–10 cm). A lower proportion of nematodes was found in the upper sediment layers at a shallow water depth (0.5 m) than at a deeper water depth (1.5 m). Two patterns of vertical distribution were recognisable at the species level. Some species, e.g. *Laimydorus ritae*, tended to concentrate in the deeper sediment layers. Other species showed a preference for specific sediment layers depending on water depth: *Anonchus coomansi* was more or less evenly distributed at the shallow site Zegie 0.5 m, but they tended to concentrate in surface sediment layers at the deeper site Zegie 1.5 m. *B. graciloides* showed a similar pattern. At Gelda 0.5 m, the proportion and actual density of nematodes in the deeper sediment was high, but this was statistically insignificant (ANOVA, $P<0.05$) (Fig. 17). The vertical profile of biomass was in each site similar to that of the density. Biomass showed a significant vertical variation (ANOVA, $P<0.01$).

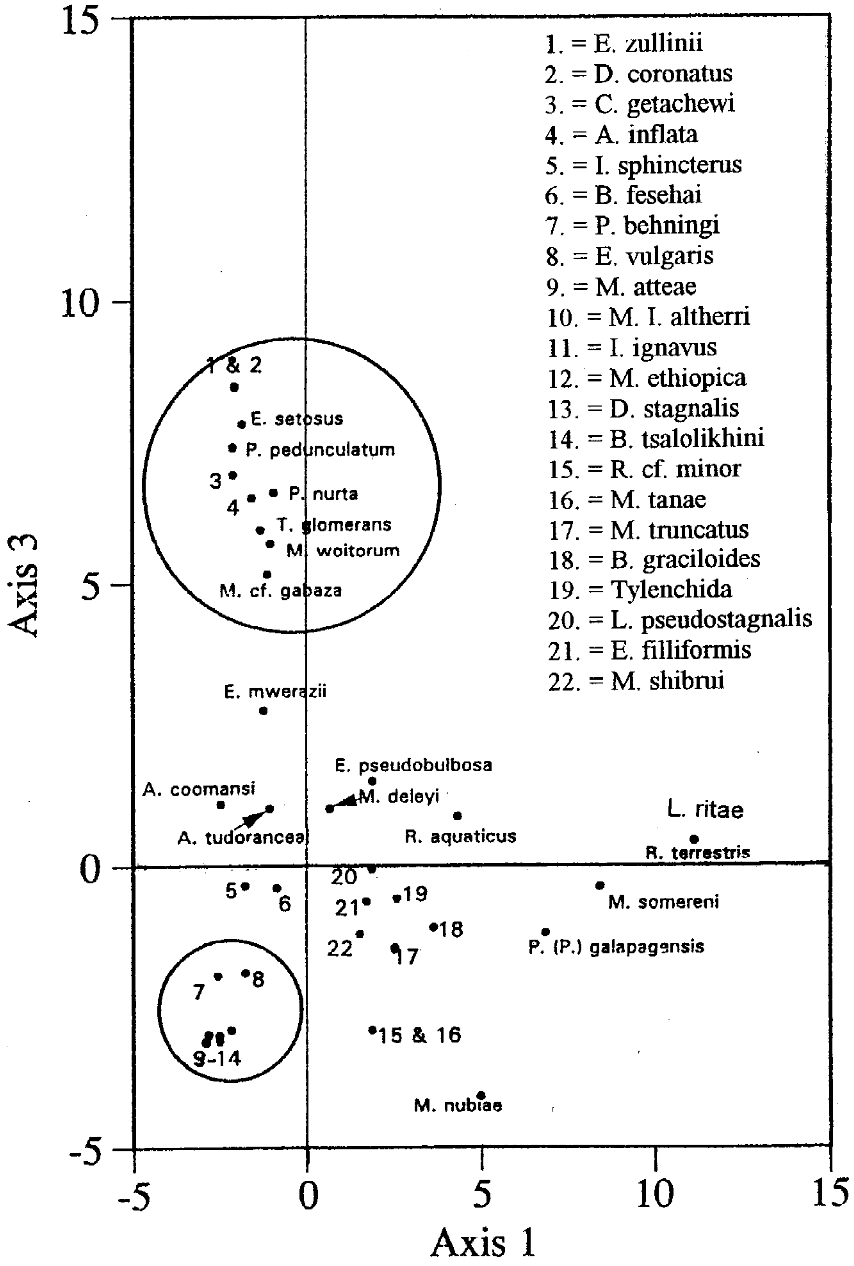


Figure 11. Result of Canonical Correspondence Analysis (CCA), biplot of species scores using axes 1 & 3.

The vertical distribution pattern of Hill's diversity numbers is shown in Figure 18. In all communities, the number of species (N_0) decreased with depth in the sediment. N_1 showed a similar trend except at Gelda 1.5 m where it increased with depth. N_2 and N_∞ showed little variation with depth at Zegie and Gelda, indicating that individuals in the deeper sediment layers were slightly more evenly distributed among the species than at the surface. For the Gedero community, N_2 and N_∞ were lower in the deeper sediment. Despite these tendencies, the *k*-dominance curves for the different sediment layers intersected for most communities (Fig. 13). Still, the *k*-dominance curves for the deeper sediment layers (5–10 cm) at Zegie 0.5 m, Zegie 1.5 m and Gedero were consistently higher than those of the surface sediment layers: the community

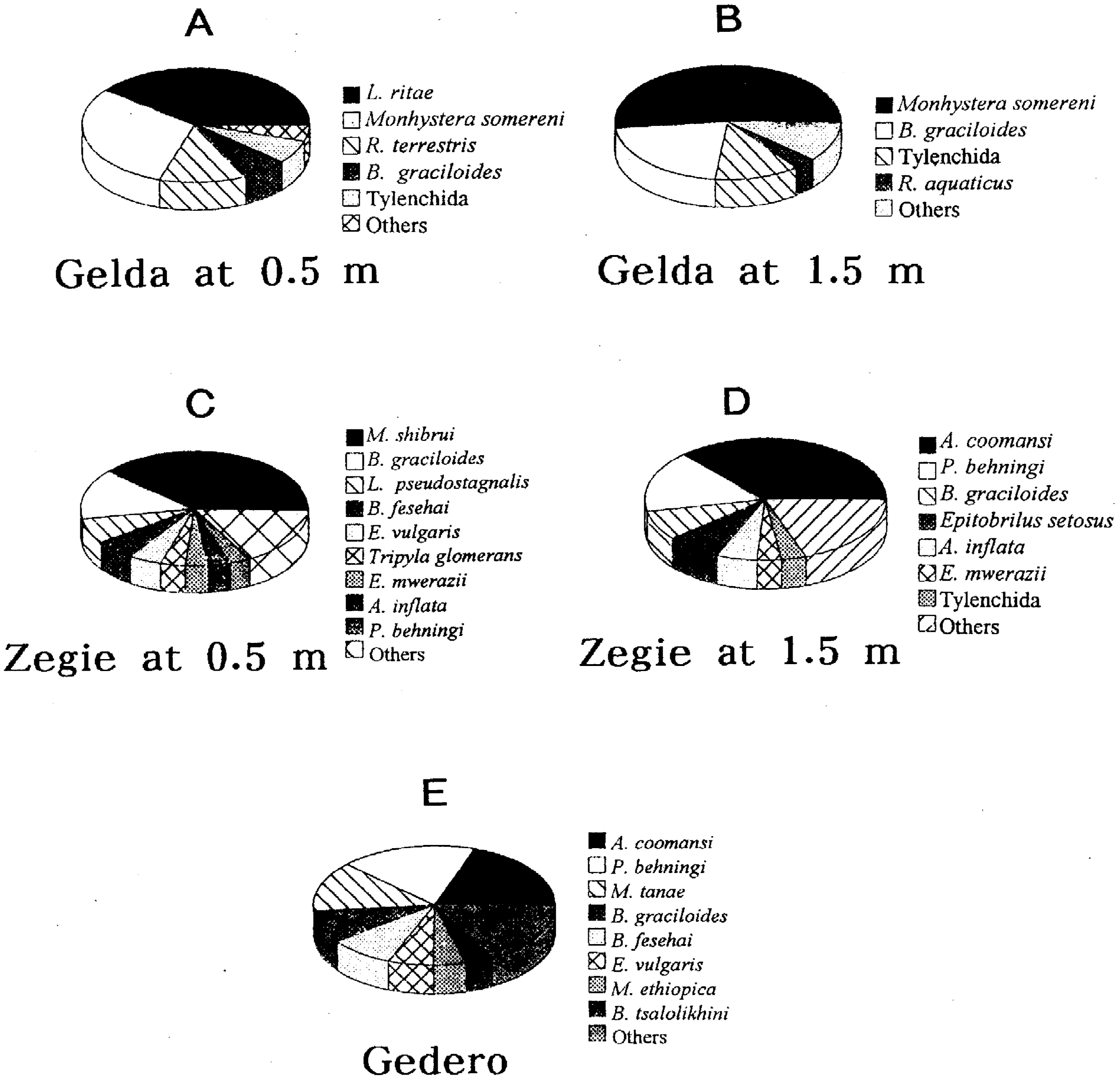


Figure 12. Species composition of the five communities identified in L. Tana. Species that have an abundance of <3% in their respective communities are included in 'Others'.

found at the surface was more diverse than that found in the deeper layers.

In the two shallow-water communities (Gelda 0.5 m and Zegie 0.5 m), the proportion of deposit feeders decreased and that of omnivore/predators increased from the surface to the deeper sediment layers (Fig. 16). The reverse trend was observed in Zegie 1.5 m and in Gedero. The vertical distribution of epistrate feeders did not show a clear pattern. Members of the order Tylenchida had a higher proportion in deeper sediment layers than at the surface. The length-frequency distribution showed no clear pattern with respect to sediment depth (Fig. 19). Still, larger species seemed to be absent from the deeper sediment layers in some of the deeper water sites.

Sex ratio

The sex ratios of species that constituted >3% of a community are given in Table 4. Most of the species encountered in this study (68.6%) were parthenogen-

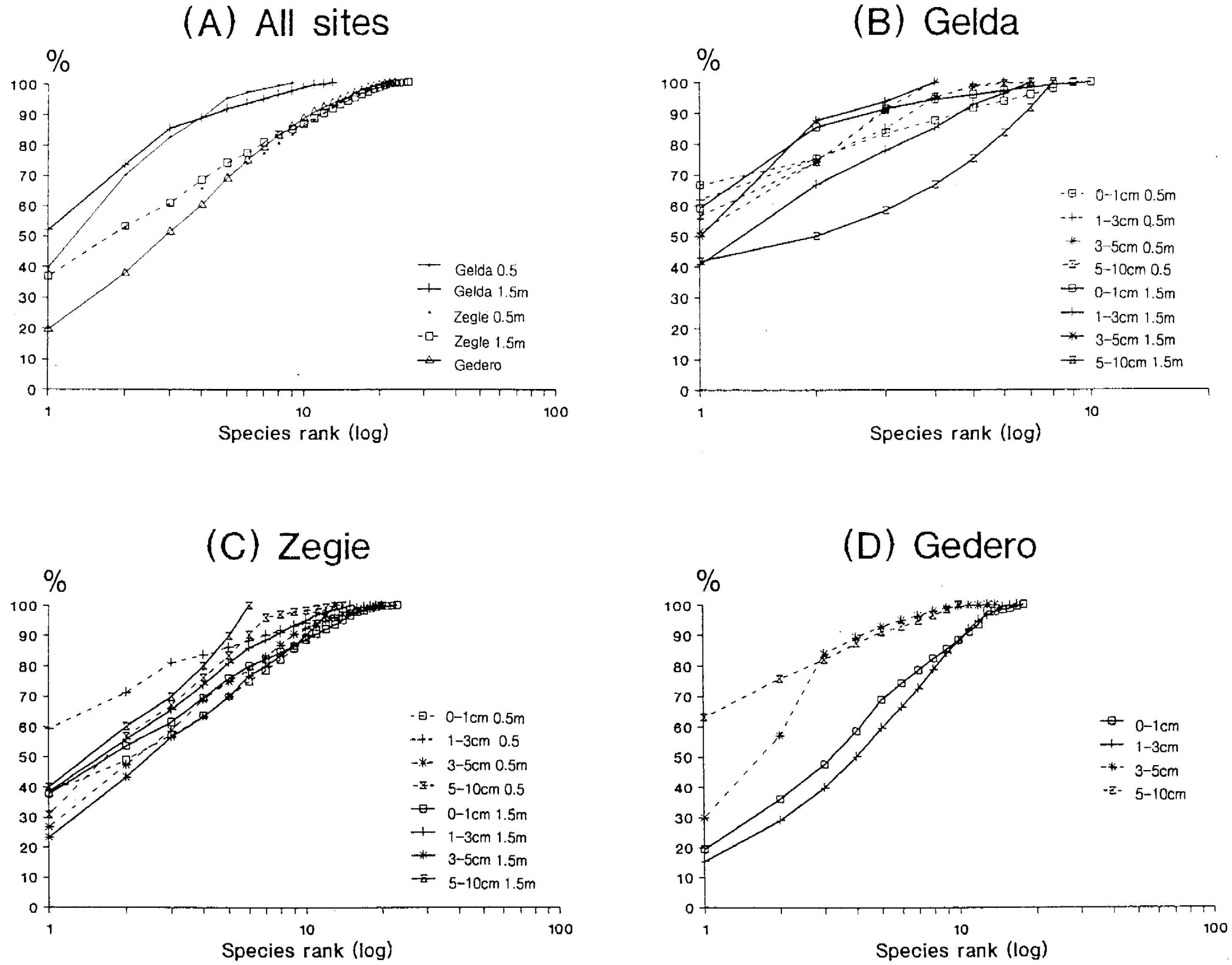


Figure 13. K-dominance curves, of the five communities in L. Tana (A), and of communities in each site separately (B–D).

Table 4. Population characteristics of the most dominant species (>3% at a specific water depth and/or site): number individuals per 10 cm^2 sediment, sex ratio at the specific water depth and/or site, proportion of juveniles (%) at the specific water depth and/or site, vertical relative distribution (%) of adults and juveniles together, and juveniles separately

Species	Site/Depth(m)	Mean no of individuals	Sex ratio Male:Female	Proportion of juveniles	Adults and juveniles together				Juveniles only			
					0–1 cm	1–3 cm	3–5 cm	5–10 cm	0–1 cm	1–3 cm	3–5 cm	5–10 cm
Achromadora inflata	Zegie/0.5	16	0:100	58.3	22.2	22.2	22.2	33.4	38.1	23.9	19.0	19.0
	Zegie/1.5	13	0:100	38.7	90.3	9.7	0.0	0.0	83.3	16.7	0.0	0.0
Anonchus coomansi	Zegie/1.5	85	38:62	59.5	71.8	24.0	2.1	2.1	62.1	30.9	2.6	3.4
	Gedero	37	61:39	56.8	56.8	33.7	7.4	2.1	57.4	33.3	5.6	3.7
Brevitobrilus graciloides	Gelda/0.5	13	33:66	74.4	74.4	25.6	15.4	48.7	0.0	20.7	17.2	62.1
	Gelda/1.5	19	40:60	56.7	56.7	1.7	0.0	0.0	100.0	0.0	0.0	0.0
	Zegie/0.5	73	50:50	72.7	72.7	23.3	30.8	24.6	20.0	22.4	30.4	27.2
	Zegie/1.5	18	50:50	71.4	71.4	42.9	0.0	0.0	55.0	45.0	0.0	0.0
	Gedero	17	72:28	55.3	55.3	17.0	0.0	0.0	80.8	19.2	0.0	0.0
Brevitobrilus fesehai	Zegie/0.5	29	80:20	83.1	83.1	52.5	13.6	1.7	32.7	35.1	12.2	2.0
	Gedero	16	66:34	80.0	80.0	32.0	0.0	0.0	67.5	32.5	0.0	0.0
Brevitobrilus tsalolikhini	Gedero	7	50:50	85.0	85.0	70.0	0.0	0.0	23.5	76.5	0.0	0.0
Epitobrilus setosus	Zegie/1.5	17	0:100	85.4	85.4	18.8	2.0	0.0	78.0	19.5	2.5	0.0
Eumonhystera mwerazi	Zegie/0.5	16	0:100	63.3	63.3	16.7	6.7	3.3	73.7	10.5	10.5	5.3
	Zegie/1.5	8	0:100	47.1	47.1	0.0	11.8	0.0	75.0	0.0	25.0	0.0
Eumonhystera vulgaris	Zegie/0.5	24	0:100	68.9	68.9	6.7	2.2	0.0	93.6	3.2	3.2	0.0
	Gedero	11	0:100	55.9	55.9	32.4	11.7	0.0	52.6	26.3	21.1	0.0
Laimydorus ritae	Gelda/0.5	8	34:66	79.5	79.5	0.0	0.0	99.6	0.5	0.0	0.0	99.5
Laimydorus pseudostagnalis	Zegie/0.5	35	53:47	53.0	53.0	4.8	27.7	60.3	13.6	9.1	34.1	43.2
Monhystera shibrui	Zegie/0.5	194	52:48	50.8	50.8	49.5	9.7	4.0	37.8	41.6	13.6	7.0
Monhystera somereni	Gelda/0.5	61	0:100	37.7	37.7	33.9	9.8	38.8	18.8	26.1	11.6	43.5
	Gelda/1.5	47	0:100	31.4	31.4	6.5	0.7	0.7	93.1	2.3	2.3	2.3
Monhystera tanae	Gedero	25	0:100	30.8	30.8	15.4	0.0	3.8	75.0	25.0	0.0	0.0
Monhystrella ethiopica	Gedero	8	0:100	50.0	50.0	25.0	0.0	0.0	60.0	40.0	0.0	0.0
Paraphanolaimus behningi	Zegie/0.5	15	50:50	74.1	74.1	9.7	6.5	3.2	82.6	8.8	4.3	4.3
	Zegie/1.5	38	50:50	84.5	84.5	25.0	8.3	1.2	62.0	26.8	9.8	1.4
	Gedero	34	40:60	77.3	77.3	28.4	6.8	5.7	52.9	30.9	8.8	7.4
Rhabdolaimus aquaticus	Gelda/1.5	3	0:100	0.0	0.0	22.2	66.7	11.1	0.0	0.0	0.0	0.0
Rhabdolaimus terrestris	Gelda/0.5	25	0:100	4.0	4.0	1.3	0.0	97.3	0.0	0.0	0.0	100.0
Tripyla glomerans	Zegie/0.5	18	50:50	31.8	31.8	9.0	45.5	41.0	7.1	7.1	35.8	50.0

etic, i.e. without males. Only about one third of the species were amphimictic. The proportion of amphimictic species in Lake Ziway, Zegie, Deepest Site, Gedero, Abbay-1, Gelda, Abbay-3, Abbay-2, and Lake Shala was 50.0, 42.9, 42.9, 40.7, 30.0, 25.0, 25.0, 20.0 and 12.5%, respectively. Amphimictic species were absent from the hot spring, Lake Abiyata and River Gelda samples. The proportion of amphimictic species was high in Lake Ziway, but note that there were only four species found. The sites with the highest proportion and number of amphimictic species were Zegie and Gedero.

Discussion

At the genus level, the nematode composition of the different sites in this study is by and large typical for freshwater habitats. Some of the genera (a.o. *Diploscapter*, *Dorylaimus*, *Mononchus*, *Plectus*, *Prismatolaimus* and *Rhabdolaimus*), however, have also been widely reported from terrestrial habitats.

The two saline lakes, Abiyata and Shala, shared two *Monhystrella* species. A species of the same genus was also found in the hot spring. High temperature dependency, the capacity to withstand high osmotic stress conditions and the occurrence of species of this genus in saline inland water bodies is well documented (Jacobs, 1987). The importance of salinity as a decisive environmental variable for the distribution of nematodes in inland water bodies can be demonstrated by the distinct species composition in these two saline lakes: all species found in these sites were absent from the freshwater bodies except for the ubiquitous *Rhabdolaimus aquaticus*. Furthermore, though the hot spring flows into Lake Shala, two of the three species found in the former locality were absent in the

Table 5. Some parameters of the five communities in L. Tana: Hill's diversity numbers (N_0, N_1, N_2 and N_∞), Shannon–Wiener index (total, between genera, and within-genus diversity), density (mean number/10 cm^2), biomass, maturity index (MI values calculated using a *c-p* score of 2 for Monhysteridae following Bongers et al. (1995) are indicated in parentheses), and the proportion of the different *c-p* scores (%)

		Gelda 0.5 m	Gelda 1.5 m	Zegie 0.5 m	Zegie 1.5 m	Gedero
Hill's diversity numbers						
	N_0	9	13	25	26.00	23.00
	N_1	7.17	4.55	9.92	9.86	11.92
	N_2	3.66	3.0	5.39	5.50	8.70
	N_∞	2.53	1.92	2.61	2.72	5.10
Shannon–Wiener index (bts/individual)						
Total	H_T	1.97	1.51	2.29	2.28	2.47
Between genera H_g		1.65	1.20	1.90	2.02	2.13
(% total)		85.8	79.5	83.0	88.6	86.2
Within-genus H_{wg}		0.32	0.31	0.39	0.26	0.4
Density		201.3	91.0	504.7	231.3	187.0
Biomass						
(mean dry weight μg/10 cm^2)		44.65	20.40	329.28	63.25	53.48
gC/m^2		0.022	0.010	0.163	0.030	0.027
Maturity index		2.54	1.45	1.97	2.67	2.38
		(2.87)	(2.04)	(2.49)	(2.79)	(2.67)
Proportion of						
	c-p score 1	0.00	0.18	0.00	0.05	0.00
	c-p score 2	23.80	58.42	41.70	8.40	21.42
	c-p score 3–5	76.20	41.40	58.30	91.10	78.42

latter. Lake Shala is characterised by a higher conductivity than the hot spring. Another factor that might explain the absence of species other than *Monhystrella* is the fluctuation of the water level in Lake Abiyata (see below). The three genera to which species found in the hot spring belong, i.e. *Chronogaster*, *Monhystrella* and *Rhabdolaimus*, are also known to have other species which commonly occur in hot springs (De Coninck, 1935; Meyl, 1954; Ocaña, 1991; Ocaña & Coomans, 1991; Ocaña, 1993), but *R. aquaticus*, the only hitherto known species of the genus found in the hot spring, was never reported from a similar habitat before.

Despite the close relation between River Gelda and Gelda in Lake Tana, it is interesting to note that they did not share a single species. The number of species shared by River Gelda and the three sites of River Abbay decreased with increasing distance from the source. Of the five species of River Gelda three, two and one also occurred in Abbay-1, Abbay-2 and Abbay-3, respectively. All species shared by these two rivers are ubiquitous. In addition, members of the genus *Prismatolaimus*, a genus present in both rivers but absent from Lake Tana, are known from wet terrestrial habitats.

Only three genera, i.e. *Aphanolaimus*, *Brevitobrilus* (reported as *Tobrilus stefanskii*) and *Eumonhystera*, are common to the nematofauna of the Ethiopian river Abbay and the Italian river Po (Zullini, 1974). Only *Eumonhystera* also occurs in River Gelda. Zullini (1976) also studied the nematodes of the Seveso river in Italy and more recently Eder & Kirchengast (1982) studied the nematode population of the polluted part of River Mur, Austria. Both studies

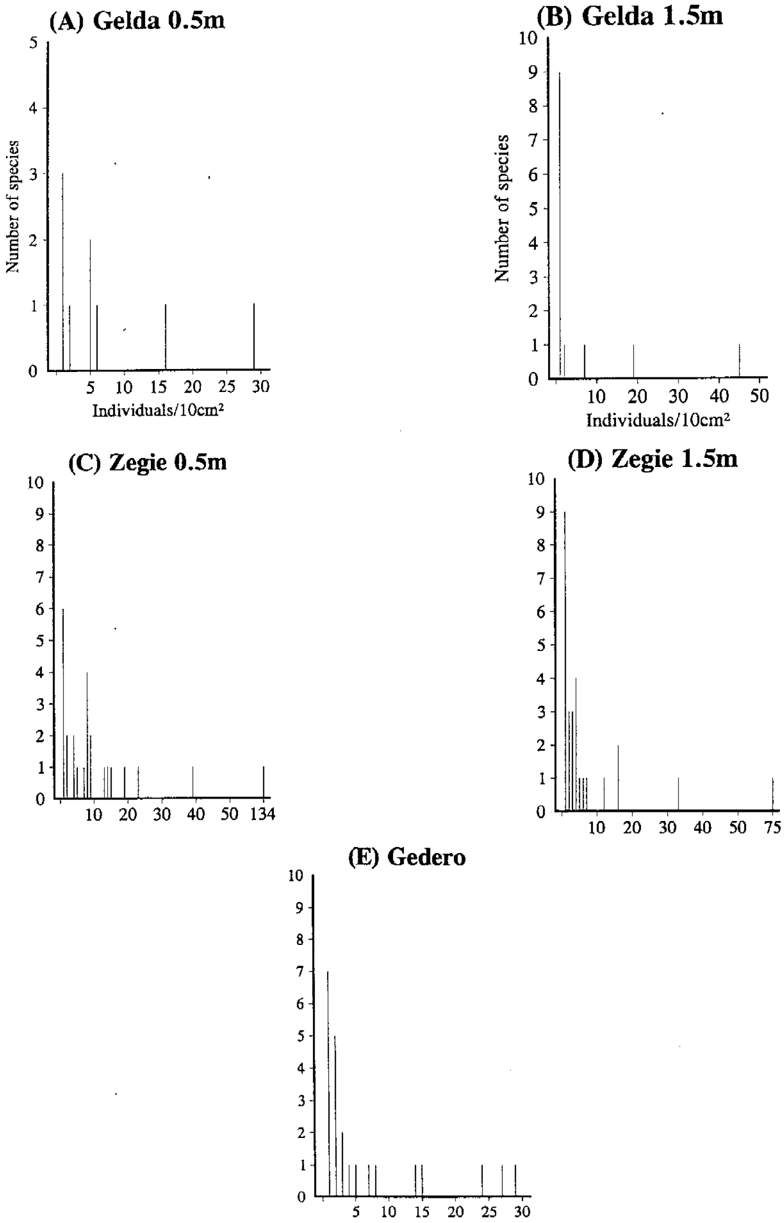


Figure 14. Species abundance distribution of each of the five communities in L. Tana.

showed that the Diplogasteroidea were the dominant group under medium and high pollution. The number of genera that occur in these European rivers as well as in the two Ethiopian rivers is very low. *Eumonhystera* (reported as *Monhystera filiformis* in Zullini, 1976) and *Prismatolaimus* are the only two genera common to all four rivers. *Achromadora* is also present in the two European rivers and in River Abbay. Both genera are known to be rather characteristic for wet terrestrial habitats than for freshwater bodies. At the species level, however, none of the 16 species found in the two Ethiopian rivers was reported in any of the European rivers.

The presence of two species of the genus *Udonchus* in River Abbay and their total absence in all other sites could be related to local conditions. The

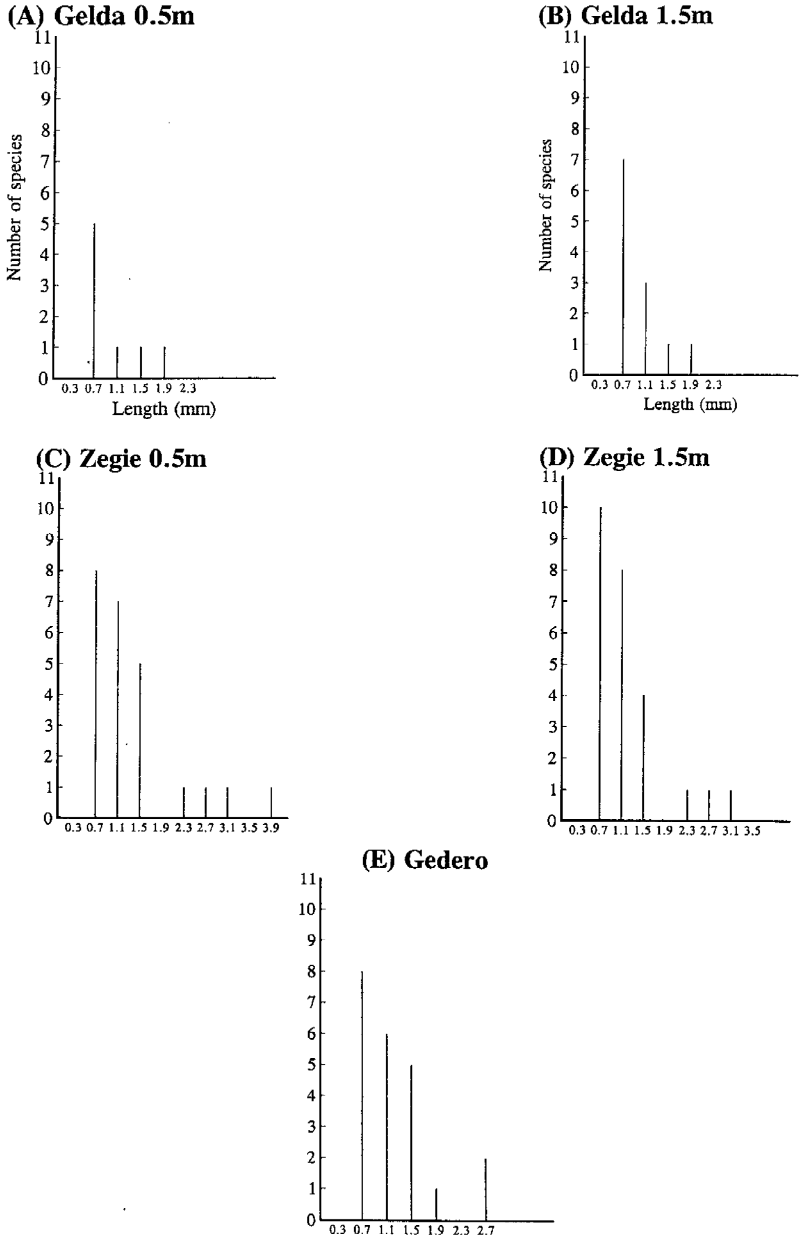


Figure 15. Size structure of adults only of each of the five communities in L. Tana.

genus constituted 67% and 51% of the nematode communities at Abbay-2 and Abbay-3, respectively. The outlet of a waste disposal scheme of a textile factory is located on the western side of the river at Abbay-2 and a higher concentration of nitrate was measured at the time of sampling. The type species of the genus *Udonchus* was reported from hot springs with a high salt content (Schneider, 1937; Schiemer, 1978; Ocaña et al., 1990; Ocaña, 1991). Ocaña (1993) also reported this species from a calcic bicarbonate spring, but it was absent in waste dumping sites for textile and ironware factories in the Seveso river, Italy (Zullini, 1976). The observed high density at the two sites could be associated to the effects of a presumable chemical pollution, but no detailed information is available at the moment. A notion that would make the genus an indicator of pollution should await further data generation and analyses. Nevertheless, our observation coupled with the

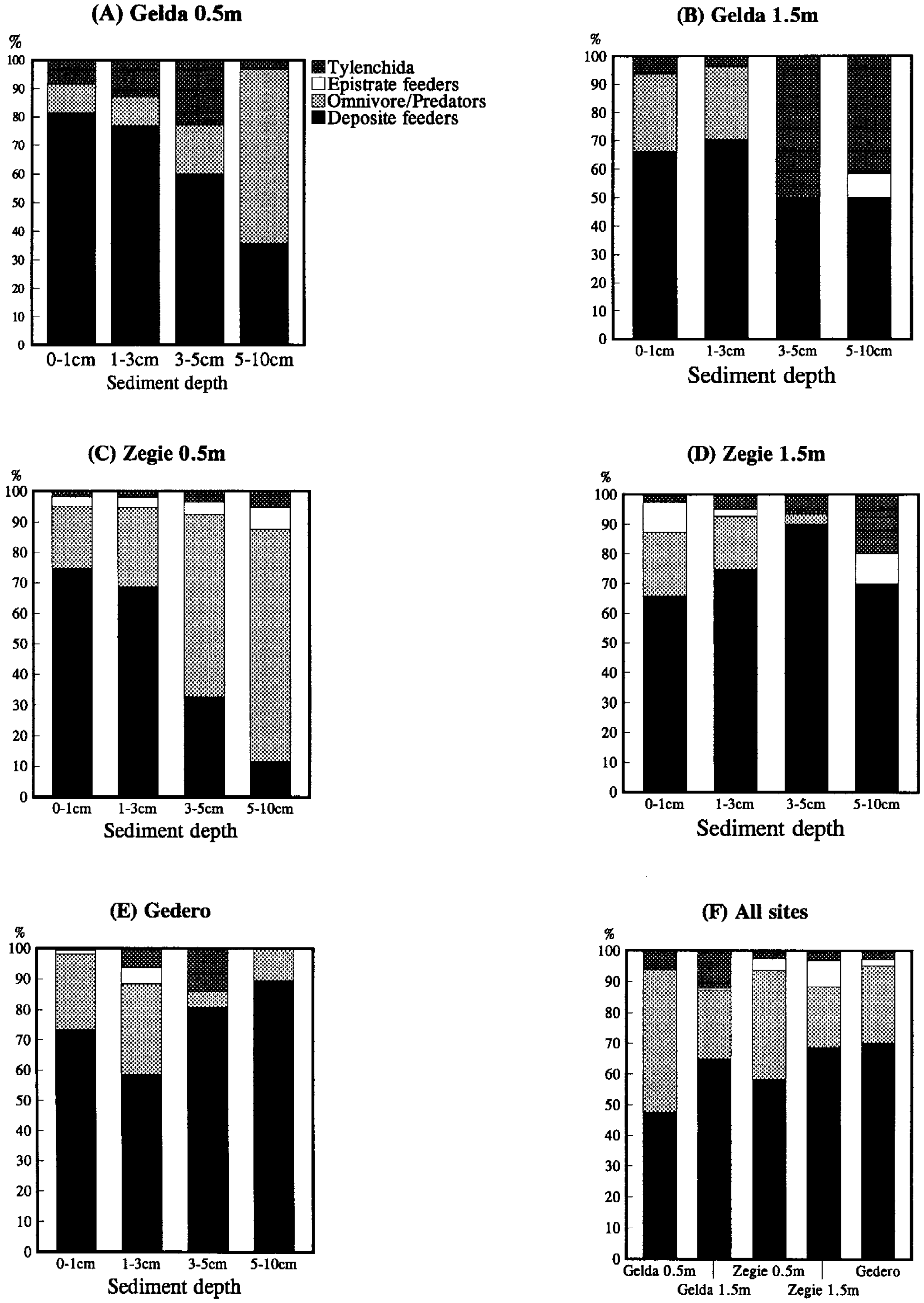


Figure 16. Relative proportion of feeding types with respect to sediment depth in each community (A–E), and in the five communities in L. Tana (F).

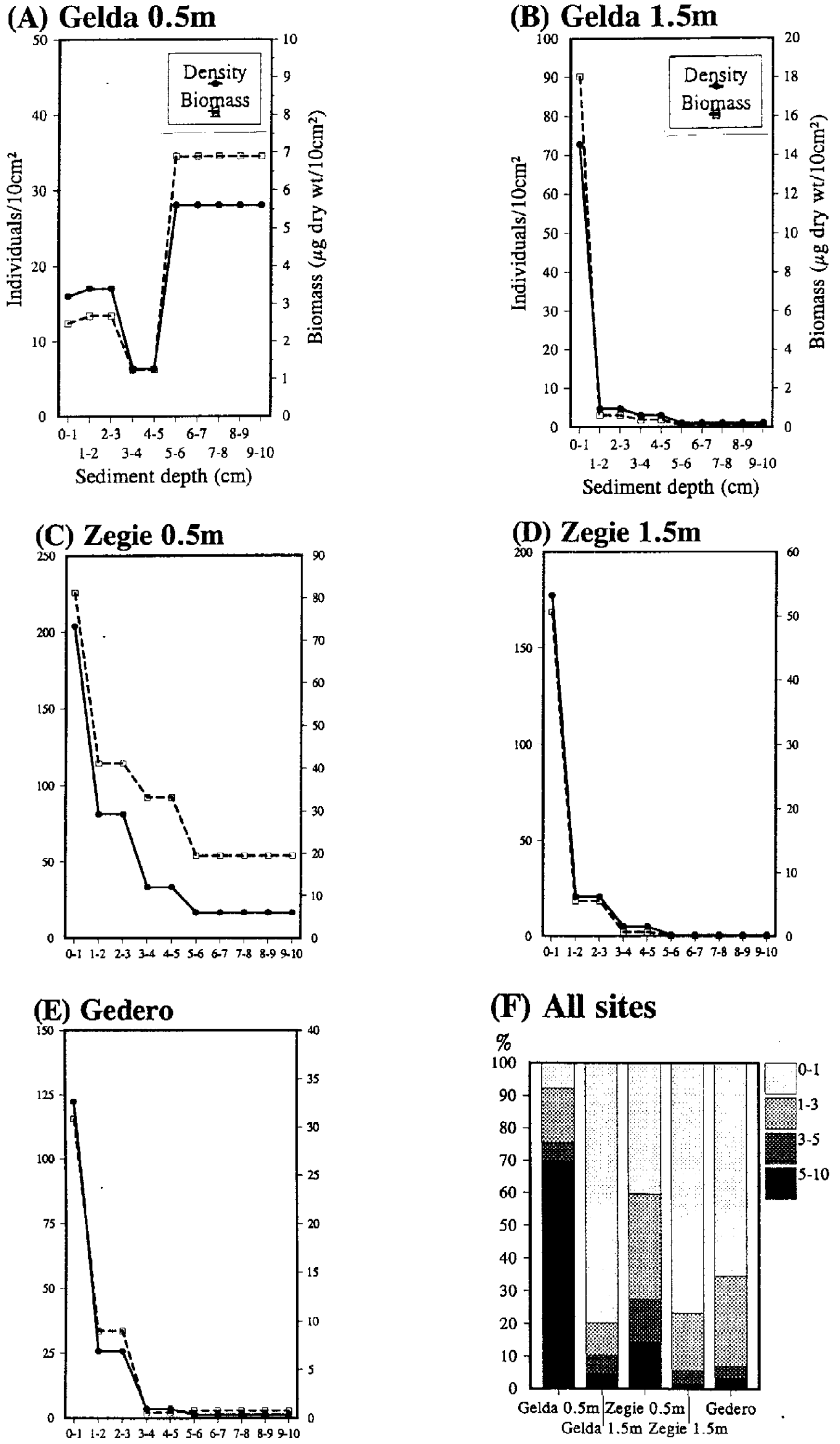


Figure 17. Vertical profile of average density (ind./10 cm^2) and biomass (g dry wt/10 cm^2) of nematodes in each of the five communities (A–E), and of total relative abundance in the five communities in L. Tana (F).

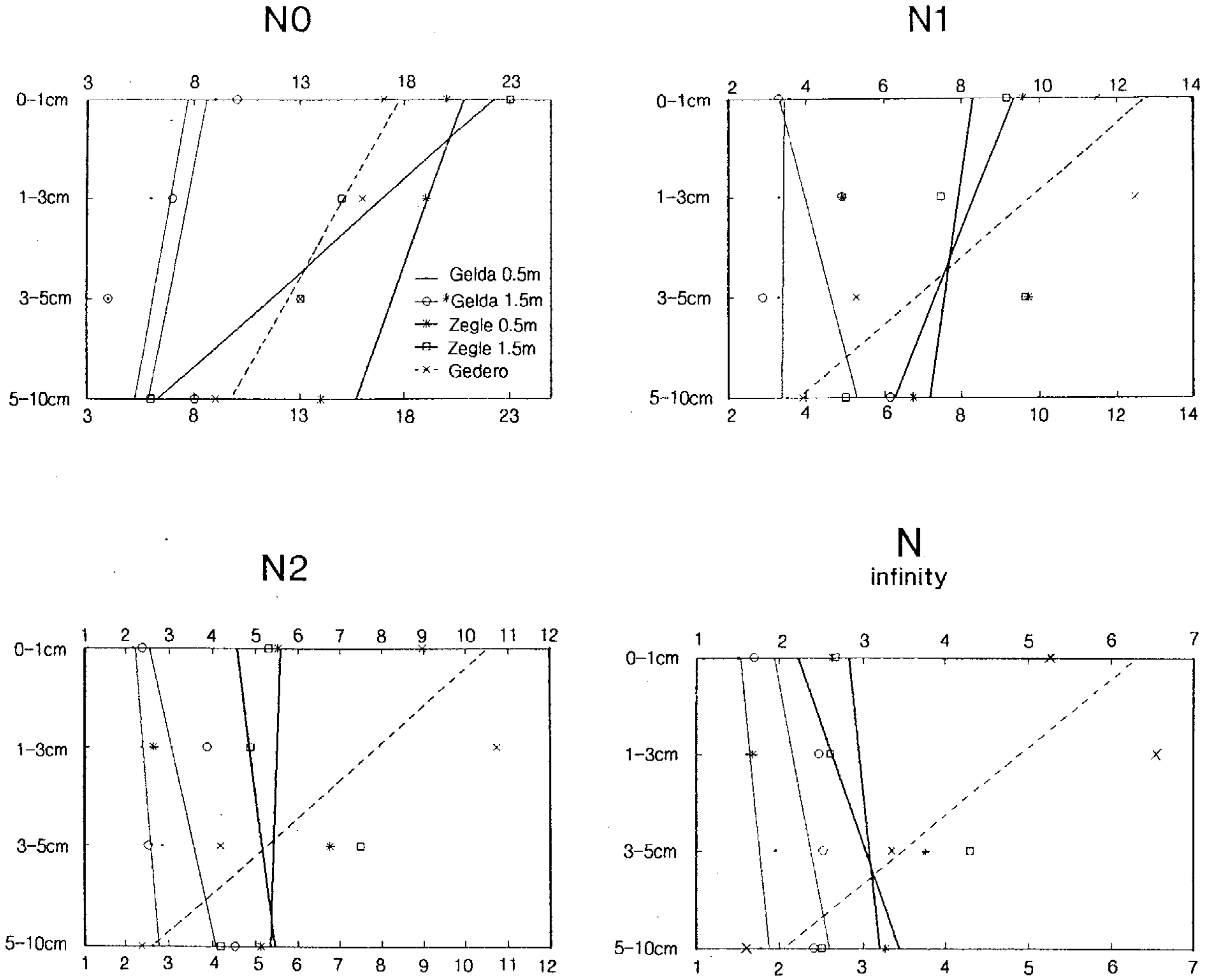


Figure 18. Vertical trends of Hill's diversity numbers, N_0, N_1, N_2, and N_∞ in the five communities in L. Tana.

habitual presence of the species in mineral waters may lead to a sound conclusion that the genus indicates the presence of some kind of environmental (chemical?) stress.

Filipjev (1931), Zullini (1988), Tudorancea & Zullini (1989) and Tsalolikhin (1992, 1993) studied nematodes of some inland water bodies in the southern part of Ethiopia. The species list reported by Tudorancea & Zullini (1989) was by far the most comprehensive. They reported 16 species, 6 of which were the ones described in Zullini (1988). In the present study, we only recorded 6 species from their list, and all except *B. graciloides* and *M. macrospiculum* were found from sites different from those indicated in previous studies. Tudorancea & Zullini (1989) sampled Lake Ziway more intensively than other sites and as a result found the highest number of species (12) there. Our list of species from the intensively sampled Lake Tana shows the presence of three times more species than reported for Lake Ziway, and five of these species also occur in Lake Ziway, viz. *B. graciloides* (as *Tobrilus africanus*), *A. tudoranceai*, *P. behningi*, *P. nurta*, and *T. glomerans*. Despite the higher number of bottom samples they studied from Lake Abiyata (12 samples), Tudorancea & Zullini (1989) reported a low number of species (only two), identical to our findings from only one sample. But, unlike our result, the two species they reported were not members of the genus *Monhystrella*. One striking detail in Tudorancea & Zullini's report is the absence of small sized genera especially the two Monhysterid genera common to many inland water bodies (*Eumonhystera* and *Monhystrella*). This can be explained by the method of extraction they used: the mesh they used was far too

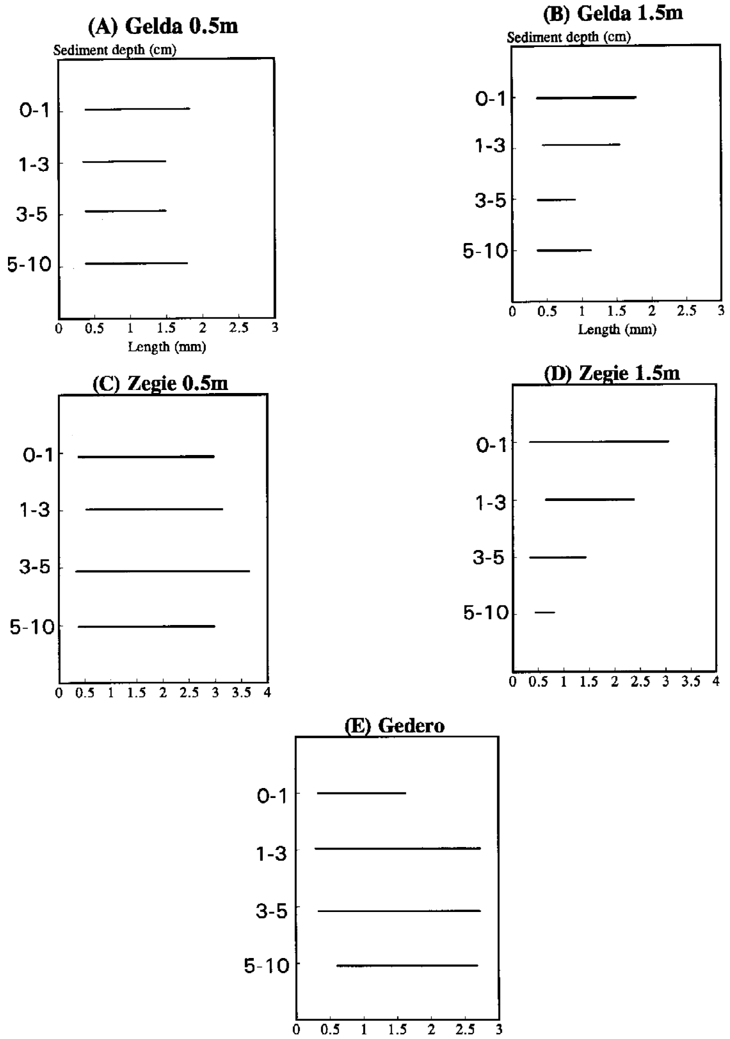


Figure 19. Vertical profile of size structure in the five communities in L. Tana.

wide (200 μm mesh size) to retain not only the small but also the reasonably large nematode species. As a standard it is recommended to use a mesh size of 38 μm to get a moderately high percentage of nematode extraction, but still a certain proportion of juveniles will be lost. Other possible reasons for the absence of the two big species in our samples but reported by them, are differences in sampling stations and time. Sampling stations in Lake Abiyata were not explicitly indicated in Tudorancea & Zullini (1989). With respect to time, though reported in 1989, the samples were collected in 1984–1985. The lake has since been subjected to more human interference by pumping its water for soda ash production, and the lake level is going down by the day. Subsequently this may gradually increase the surface area of the shallower part of the lake, which may be prone to extreme environmental fluctuations. A large amount of organic excrement of birds is added mainly in the shallower part of the lake. Moreover Tudorancea & Zullini (1989) reported the absence of nematodes in the deeper part (>3 m depth), maximum nematode density being found at 0.15 m water depth. In any case, the gradual narrowing of the lake diameter implies a drying up and therefore loss of a previously littoral part with its rich nematode community. Consequently, these changes might have favoured only opportunistic species with a wide range of environmental tolerance, thus the sole dominance of *Monhystrella* at present. Also, the number of species previously reported from Lake Shala is even lower than that for Lake Abiyata. Tudorancea & Zullini (1989) collected 11 samples but found only one species, *M. macrospiculum*. This can also be attributed to the reason mentioned above (extraction method), for the four species we additionally found (Table 3) are small and could not have been retained by the mesh size they used.

The higher number of genera and species recorded from Lake Tana, as compared to the other sites, could solely be due to the more intensive sampling on this lake. Decraemer & Coomans (1994) compiled lists of hitherto described species from ancient lakes: they indicated the number of non-tylenchid genera reported till recently from Lakes Malawi (Malawi), Kinneret (Israel), Titicaca (Peru), Tanganyika (Tanzania), Baikal (Russia) and Ohrid (Macedonia) to be 3, 7, 11, 14, 22 and 24, respectively. Among these genera Lake Tana shares 2, 6, 6 and 10 genera with Lakes Malawi, Baikal, Tanganyika and Ohrid, respectively. Lake Kinneret and Lake Tana did not even share a single genus. Likewise, Lake Tana shares 16 genera with Königssee (Germany) (Traunspurger, 1991), 10 with Neusiedlersee (Austria) (Schiemer, 1978), 10 with Loch Leven (Great Britain) (Bryant & Laybourn, 1974), and 5 with the Elbe estuary (Germany) (Blome & Faubel, 1996). Prejs (1977) studied the nematofauna of one Canadian, one Norwegian and 15 Polish lakes. The number of genera reported for these lakes was far lower (1–17 genera) than the number we found in Lake Tana. Lake Zielony Gasienicowy showed the highest similarity with Lake Tana in its generic composition with 7 genera being present in common in both lakes, while Lake Dgal Maly had a genus that was not found in Lake Tana.

At the species level, the similarity between the nematofauna of Lake Tana and other lakes is far less than at the genus level. The proportion of species not recorded from anywhere else before is high (34%) (Table 3). In spite of this high percentage, we prefer to refrain from conjecturing on endemicity of the nematofauna in this as well as other Ethiopian lakes. Species lists of the nematofauna from inland water bodies, especially in Africa, are incomplete which makes comparisons difficult and futile, and generalisations unreliable. Apart from those recorded for the first time, most nematode species recorded from Lake Tana have a wide distribution; 81% of the hitherto known species from the lake have also previously been reported from Africa (including Ethiopia) (Jacobs, 1984; Zullini, 1988). Among the already known species found in Lake Tana, only five were new records to Africa, and of these five species only two belong to typical freshwater genera, *Ironus* and *Epitobrilus*. The remaining three species belong to the genera mentioned above as widely inhabiting wet terrestrial habitats. These observations may indicate that nematodes in inland water bodies are probably easily dispersed. This could especially be true in a landmass like Africa where there are many long rivers, with their own tributary systems and catchment areas that travel across most parts of the continent.

Lakes Tanganyika and Malawi each shares only two species with Lake Tana: the former shares *B. graciloides* and *D. stagnalis* while the latter shares *B. graciloides* and *M. truncatus* (Decraemer & Coomans, 1994). Aside from these, the nematofauana of these lakes is quite different in species composition. Three species occur in both lakes Ohrid and Tana: *D. stagnalis*, *E. filiformis* and *P. pedunculatum*. The number of common species that occur in L. Tana and in Königssee, Neusiedlersee, and Elb estuary respectively are seven, five, and three. *D. stagnalis* is present in all but Königssee (Traunspurger, 1991; Blome & Faubel, 1996). Most of the Polish lakes studied by Prejs (1977) had a very poor nematofauna, composed only of few species that were not recorded from Lake Tana. The only two species that occurred in 6 of the 17 lakes and that were also present in Lake Tana are *E. filiformis* and *M. truncatus*. On the other hand, there is a remarkably strong similarity in species composition between Lake Tana and Lake Zegrzynskie (Poland): 10 of the species we found in the former were also reported in the latter (Prejs & Bernard, 1985). In spite of these similarities and differences, quantitative and qualitative comparisons of the nematofauna of inland water bodies remains difficult due to the incomplete lists of nematode species (see also below). An exception is Lake Baikal, whose nematofauna has been studied fairly well. The total number of free-living nematode species recorded is identical to what we found in Lake Tana. It is interesting to note that *D. stagnalis* is the only species common to the nematofauna of Lake Baikal and Lake Tana. The species composition in Lake Balaton is similar to that of Lake Tana in that it is dominated by monhysterids and leptolaimids (Biró, 1968). Most of the species of Lake Tanganyika are dorylaimids. According to Decraemer & Coomans (1994), this could be due to the more terrestrial origin of the nematofauna in the latter. The nematofauna of Lake Zegrzynskie has an equal proportion of monhysterids, leptolaimids and dorylaimids (Prejs & Bernard, 1985). In Königssee, however, it is the chromadorids that dominate the species composition (Traunspurger, 1992, 1996a).

In general, a discussion on the possible sources of variation in genus and species number and composition of the nematofauna in different lakes is, at present, premature for two reasons. Firstly, information on factors that play a role in the distribution of free-living nematodes in inland water bodies is still scanty, the best one can do at the moment is assume that those factors that influence the distribution of the relatively well studied marine nematodes also affect nematodes in inland water bodies. Secondly, a large proportion of the studies done on the nematofauna of inland water bodies do not go far beyond collecting a few samples for taxonomic purposes from a relatively small proportion of lakes and rivers. Moreover, as its invariable characteristic, detailed description of study sites in taxonomical studies on nematodes is wanting, making comparison of results of such studies with others cumbersome. The generally high variability of meiobenthos in freshwater habitats with respect to space and time (Pennak, 1988; Traunspurger, 1996a) also exacerbates the problem of comparison.

The classification and ordination techniques show that both the environmental factors and the nematode communities in the three stations of Lake Tana were clearly different. The smaller median grain size and the higher proportion of mud were the main factors separating the Gelda samples from the Gedero and Zegie samples. This is probably correlated with the load of silt deposited by the inflowing River Gelda. Most Ethiopian rivers are characterised by a marked seasonality: over-flooding occurs in the rainy season (June–September), particularly in highland areas, while very low water levels are recorded in the dry season (October–May). During the rainy season they typically wash and carry a significant amount of the topsoil, whence their characteristic reddish-brown colour. The amount of silt in the water gradually declines from October to November onwards. Still, at the time of sampling in January the water of River Gelda was brown, implying that silt was being deposited even after the rainy season was over. The structuring effects of sediment characteristics on nematode communities are well documented for marine habitats (Tietjen, 1977; Heip et al., 1982, 1985; Giere et al., 1988), but only a few studies have confirmed this for freshwater communities (Zullini, 1974; Schiemer, 1978; Tudorancea & Zullini, 1989).

In Gelda and Zegie, the 0.5 and 1.5 m depth strata were clearly characterised by different nematode communities. This pattern was not observed at Gedero. This is probably correlated with the exposed nature of this site: it is subject to strong wind action resulting in continuous mixing of the water column and resuspension of the sediments. The fact that nematode density and species composition varies with water depth is widely reported in inland water bodies (Prejs, 1977; Schiemer, 1978; Tudorancea & Zullini, 1989; Traunspurger, 1992, 1996a, b). Most studies revealed that densities are higher at shallower parts of lakes. Our findings confirm this generalisation.

P. behningi was absent at Gelda, but it was the second most dominant species in the deeper Gedero and Zegie communities. This may reflect its preference for less muddy sediments. The only other place where this species was reported to be dominant was in the deeper parts of Lake Balaton (Biró, 1968). *M.* cf. *gabaza* showed preference for the sheltered site, Zegie. All the indicator species of each of the three communities are species not recorded anywhere else before which are characterised by low density (Fig. 3); this fact coupled with the absence of detailed report on physico-chemical characteristics of the localities from where *P. behningi* and *M.* cf. *gabaza* have been described hinders the making of any generalisation about the relationships between species distribution and habitat.

The presence of few dominant species characterised four of the five communities (Fig. 13). The highest species dominance was observed in the two communities at Gelda. Tietjen (1977) noted that high species dominance is characteristic for shallow muds (deposit feeders being the predominant feeding type) and suggested that many species may be excluded through intense competition. In three communities, a member of the genus *Monhystera* was dominant in conjunction with either a dorylaimid (Gelda 0.5 m) or a tobrilid (Gelda 1.5 m and Zegie 0.5 m). A singular dominance of a *Monhystera* species or dominance in combination with a tobrilid has been reported for freshwater lakes repeatedly (e.g. Biró, 1968; Traunspurger, 1996b). In the other two communities in Lake Tana, deposit feeding leptolaimids (Zegie 1.5 m) or leptolaimids and monhysterids (Gedero) dominated the nematode communities. In the dominance hierarchy, these taxa are invariably followed by tobrilids (Fig. 12). Such combinations in dominance of deposit feeding monhysterids or leptolaimids with omnivorous/predatory tobrilids may rather be associated with niche partitioning than caused by tolerance to environmental factors. *R. terrestris* has been reported to be the most dominant species in the littoral of Königssee (Traunspurger, 1996a). We believe this author actually dealt with two species, *R. aquaticus* and *R. terrestris* (for a discussion see Eyualem & Coomans, 1996f). Although these species were not dominant, both reached quite high densities in Gelda, the former in the deeper and the latter in the shallower site.

Tudorancea & Zullini (1989) reported diversity values for some Ethiopian inland water bodies, but comparison with their results is difficult (cf. different extraction methods). Nematode diversity in Lake Tana is comparable to that reported for oligo- and mesotrophic freshwater lakes (Prejs, 1977) and estuaries, but it is much lower than that reported for deep-sea habitats (Tietjen, 1976; Heip et al., 1982; Soetaert et al., 1991; Blome & Faubel, 1996). The proportion of mud in the sediment has been shown to be negatively correlated with nematode diversity in marine environments (Heip & Decraemer, 1974; Soetaert et al., 1991): a muddy environment is homogeneous and has fewer microhabitats for nematodes. This may explain the low diversity observed in the two communities at Gelda, which were the muddiest sites studied. A high proportion of the Shannon–Wiener diversity (76–83%) in Lake Tana could be explained at the genus level. Soetaert et al. (1991) reported similar values (75–83%) in the Mediterranean deep-sea.

Size structures of nematode communities have been reported for some marine habitats, but no information is available for freshwater habitats. Size is an important aspect of nematode biology since it influences movement and biomass which in turn have impact on competition and predation at the community level (Soetaert & Heip, 1989, and references therein). Our results agree well with the generally accepted view that most nematodes of fine sediments are short burrowing forms, while in coarser sandy sediments the majority are interstitial, being either very small or very elongate and thin (Tietjen, 1976; Platt & Warwick, 1980; Heip et al., 1982). The absence of nematode species longer than 2 mm in the two communities at Gelda in Lake Tana could be correlated with the high mud content in the sediment.

Nematode density and biomass in freshwater bodies are generally in the lower range of those recorded from littoral marine habitats. Lake Tana has comparable nematode density and biomass as the littoral part of Königssee (Traunspurger, 1996a). All eutrophic and most oligotrophic lakes (except Char and Zielony Gasienicowy) studied by Prejs (1977) and the deeper part of L. Balaton (Biró, 1968) had a far lower nematode density than Lake Tana. The density we observed is comparable to ranges given for the limnic part of the Elbe estuary (Blome & Faubel, 1996) and adjacent sites in the Westerschelde estuary (Heip et al., 1982).

The maturity index can be used for monitoring environmental stress using nematode communities as an indicator (Bongers, 1990; Bongers et al., 1995). In Lake Tana, there is no apparent organic pollution, as shown by the absence of 'enrichment opportunists' in the nematode communities. The inorganic nutrient input is also expected to be negligible as the use of fertilisers by farmers in the area is limited. Still, our data suggest that the impact of seasonally fluctuating water levels on the biota can be detected. The maturity index can also indicate the degree of environmental stability.

As in L. Tana, deposit feeders are the most dominant feeding type in freshwater as well as marine nematode communities (Platt, 1977; Traunspurger, 1992; Soetaert & Heip, 1995; Traunspurger, 1996a, b). Even though the decisive factor(s) affecting nematode distribution in L. Tana is (are) not known for certainty, food availability may be one. Soetaert & Heip (1995) considered hydrodynamic stability to be important in the distribution of nematodes in enriched deep-sea environments, they failed to recognise an association between predatory and scavenging nematodes with sediment granulometry. A dominant species which is an algal feeder as an adult (*M. shibrui*) and the three epistrate feeding species were absent altogether or were represented by very few individuals in Gelda and Gedero communities. This may be an indicator that algal density could be lower at one site than at the other, nevertheless this idea is more of a speculation, for we cannot substantiate it, since data on algal distribution are not available in this lake.

The high relative proportion of omnivore/predators in Gelda 0.5 m was due mainly to the dominance by *Laimydorus ritae*. In Königssee also, food availability was claimed to be the main reason for the high relative proportion of omnivore/predators at 1 m water depth (19.1%) (Traunspurger, 1996a). Traunspurger, however, considered dorylaimids (which were as a whole insignificant in density) separate from omnivore/predators. He associated the density of his 'stylet-bearing group', i.e. mainly dorylaimids, which was represented by members of *L. flavomaculatus* with the high density of algae, *Chara*, at that depth. But, seen within the light of the wide ranging food habits of dorylaims in the aquatic environment and lack of a convincing proof on their parasitism on plants (Prejs, 1986, 1987), such a conclusion needs to be examined further.

Members of the order Tylenchida showed their highest relative proportion in Gelda. Members of this order are known to be transported by runoff from one site to the other and this could be the main reason for their relatively high proportion at this site (Faulkner & Bolander, 1970).

Vertical profile

Distribution

The universal fact that most nematodes in aquatic habitats tend to stay at the surface sediment layer (Fenchel et al., 1967; Tietjen, 1969; Bryant & Laybourn, 1974; Platt, 1977; Jensen, 1987b; Hendelberg & Jensen, 1993; Traunspurger, 1995, 1996a, b) has been confirmed by the results of this study. Without challenging this generally accepted view, some authors have revealed that population maxima of some species could be below the surface layer, implying that in some cases distribution could be species specific (Fenchel et al., 1967; Platt, 1977; Jensen, 1981; Traunspurger, 1996b), *Eudorylaimus andrassyi* is considered to be one such a species that could stand anaerobic conditions in muddy sediments (Por & Masry, 1968 in Jensen, 1995). Traunspurger & Drews (1996) also have reported the high proportion of *Laimydorus flavomaculatus* in Königsee. A community specific to the anaerobic sulphide system in marine habitats (referred to as the 'thiobios') was claimed by Fenchel & Riedl (1970) to be present in deeper sediment layers, but the idea has been challenged (Reise & Ax, 1979) in that meiofauna remains in close association with oxygenated layers or pocket areas within the sediment. Nonetheless some authors (Jensen, 1986, 1987b) considered the division of communities to aerobic and anaerobic as valid, thus the idea remains controversial. In any way, these discussions point out that singularly oxygen, though its effect on nematode may be less than on other meiofauna, is one of the most important factors that limit vertical distribution of nematodes (Fenchel et al., 1967; Platt, 1977; Heip et al., 1982; Hendelberg & Jensen, 1993). In addition to oxygen, Tietjen (1969) and Platt (1977) indicated that availability of food along the sediment profile could also play but a secondary role. Tietjen (1969) correlated the high density of nematodes at the surface sediment with a higher density of benthic diatoms at that sediment layer. The relatively high proportion of nematodes in deeper sediment layers in the Gelda 0.5 m community could be a species specific preference for that sediment layer for one of the above reasons, the community is dominated by *Laimydorus ritae*.

In temperate water bodies, the impact of seasonal fluctuation of temperature (with its consequences) has a pivotal impact on nematode communities, the proportion of nematodes in the upper sediment layer increases in warmer seasons while the reverse is true in colder seasons (Tietjen, 1969; Bryant & Laybourn, 1974; Hendelberg & Jensen, 1993; Traunspurger, 1996a, b). But, generally in the tropics, where a marked seasonal temperature difference is lacking, inland water bodies (especially shallow lakes and rivers) are mainly affected by the rainfall regime (water level) and by the extreme diurnal fluctuation of temperature (Payne, 1986). Some nematode species in tropical waters, therefore, may inhabit the deeper sediments at shallower sites which are exposed more to the extreme diurnal fluctuations but may concentrate only in the superficial layer in deeper and relatively protected sites, as we observed in L. Tana. An association between the rainfall regime and fluctuation of nematode communities in L. Ziway has already been demonstrated (Tudorancea & Zullini, 1989).

A decline in diversity with increasing sediment depth in the Mediterranean deep-sea was suggested to be associated with more conducive conditions at the superficial layer (Soetaert et al., 1991), analogous reasoning may also explain the difference in diversity of nematode communities at the uppermost and deeper sediment layer at Gedero and Zegie.

Size structure

Because of the bearing of reproductive cycle on juvenile production, the use of only adults for constructing size structure especially in momentary studies will have the advantage of being independent from reproductive activity for those species that do not reproduce continuously. For this reason, we have considered only adults (excluding members of the order Tylenchida) when constructing size structure.

In marine habitats, where size structure of nematodes with respect to sediment depth has been studied, longer nematodes occur in deeper layers while shorter nematodes inhabit the superficial sediment layer (Jensen, 1986, 1987b; Soetaert & Heip, 1989). Our findings in most sites were inconclusive on the relationship between nematode size and sediment depth, but what we observed in Gelda 1.5 m and Zegie 1.5 m was contradictory to what was reported for marine habitats. Jensen (1986, 1987b) reasoned that long body is an adaptation to life in anaerobic conditions where dissolved sulphide is high, he associated nematode size with physiological adaptation to get sufficient oxygen and/or dissolved food. On the other hand, Soetaert & Heip (1989) reflected on the physical ability of longer species to penetrate deeper into niches which may be inaccessible to smaller forms. Since these reasonings were made to explain an utterly contrary situation with what we observed in Gelda 1.5 and Zegie 1.5 m, it is highly improbable that they will be applicable here. Food availability, though never mentioned to be a factor affecting the vertical distribution of nematodes with respect to size, could be the main reason at least in L. Tana: unlike in the other sites, the long omnivore/predator species were present only in the surface sediment but were absent in the deeper sediment layers in these two sites.

Sex ratio

The variation of sex ratio of the species with time and water depth in Königsee was shown for *E. pratensis, M. paludicola* and *T. gracilis* (Traunspurger, 1996c, 1997, 1998).

Sexual reproduction has the evident advantage of conserving genetic variability over parthenogenetic reproduction. But, the production and maintenance of males that are not directly involved in progeny production is very costly. Therefore, in habitats where speedy invasion of an environment is required, as in the case of colonising a new site, parthenogeny has the benefits of directing all the available energy towards progeny production. Hence unstable habitats are more likely to be colonised now and then by parthenogenetic species than by amphimictic species, and vice versa. The absence of amphimictic species in L. Abiyata, The hot spring, R. Gelda and their low proportion in sites such as Gelda, Abbay-2, and Abbay-3 could be related to the relative instability (chemically or physically) in these habitats. Information on the reproductive capacity of the different species in these sites will help test this conjecture. In L. Tana, we did not observe any difference in the proportion of amphimictic species with respect to the different water depths and vertically with sediment depth.

Acknowledgements

We thank Prof. Dr M. Vincx for commenting on the manuscript. The first author thanks Ghent University (Belgium) for financial support. The technical assistance of Miss R. Vandriessche and Mr G. De Smet is gratefully acknowledged – the former for processing the samples and the latter for analysing the particle size distribution of the sediments. The second author acknowledges FKFO project 3G.0086.96 of the Flemish Science Foundation and contract BOF98-03, 12050398 of Ghent University.

References

Andrássy, I., 1956. Die Rauminhalts - und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. Acad. Sci.. Hungar. 2: 1–14.

Baker, B. H., P. A. Mohr & L. A. J. Williams, 1972. Geology of the eastern rift system of Africa. Geol. Soc. Amer., Special Paper 136: 67–89.

Biró, K., 1968. The nematodes of Lake Balaton. II. The nematodes of the open water mud in the Keszthely Bay. Annls. Inst. Biol. Hung. Acad. Sci. 35, 109–116.

Blome, D. & A. Faubel, 1996. Eulittoral nematodes from the Elbe estuary: Species composition, distribution and population dynamics. Arch. Hydrobiol., Supplement 110: 107–157.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83: 14–19.

Bongers, T., R. G. N. De Goede, G. W. Korthals & G. W. Yeates, 1995. Proposed changes of *c-p* classification for nematodes. Russ. J. Nematol. 3: 61–62.

Bray, J. R. & J. T. Curtis, 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 27: 325–349.

Bryant, V. M. T. & J. E. M. Laybourn, 1974. The vertical distribution of Ciliophora and Nematoda in the sediments of Loch Leven, Kinross. Proc. r. Soc. Edinb. 17: 265–273.

De Coninck, L. A., 1935. Contribution à la connaissance des nématodes libres du Congo belge. I. - Les nématodes libres des marais de la Nyamuamba (Ruwenzori) et des sources chaudes du Mont Banze (Lac Kivu). Revue Zool. Bot. Afr. 26: 249–326.

Decraemer, W. & A. Coomans, 1994. A compendium of our knowledge of the free-living nematofauna of ancient lakes. Arch. Hydrobiol. Beih. Ergebn. Limnol. 44: 173–181.

Digby, P. G. N. & R. A. Kempton, 1987. Multivariate analysis of ecological communities. Chapman and Hall Ltd., London: 260 pp.

Eder, R. & M. Kirchengast, 1982. The nematode-fauna (Nemathelminths, Nematoda) of a polluted part of the river Mur (Styria, Austria). Nematol. Medit. 10: 127–134.

Elizabeth, K., G.-M. Zinabu & I. Ahlgren, 1994. The Ethiopian Rift Valley lakes: chemical characteristics of a salinity–alkalinity series. Hydrobiologia 288: 1–12.

Eyualem Abebe, 1996. Aquatic nematodes from Ethiopia IV. The family Leptolaimidae Orley, 1880 *sensu* Lorenzen, 1981 (Chromadorida: Nematoda) with the description of *Anonchus coomansi* n. sp. Hydrobiologia 332: 1–26.

Eyualem Abebe & A. Coomans, 1996a. Aquatic nematodes from Ethiopia I. The genus *Monhystera* Bastian, 1865 (Monhysteridae: nematoda) with the description of four new species. Hydrobiologia 324: 1–51.

Eyualem Abebe & A. Coomans, 1996b. Aquatic nematodes from Ethiopia II. The genus *Monhystrella* Cobb, 1918 (Monhysteridae: nematoda) with the description of six new species. Hydrobiologia 324: 53–77.

Eyualem Abebe & A. Coomans, 1996c. Aquatic nematodes from Ethiopia III. The genus *Eumonhystera* Andrassy, 1981 with (Monhysteridae: Nematoda) with the description of *E. geraerti* n. sp. Hydrobiologia 324: 79–97.

Eyualem Abebe & A. Coomans, 1996d. Aquatic nematodes from Ethiopia V. Descriptions of *Achromadora inflata* n. sp., *Ethmolaimus zullinii* n. sp. and *Prodesmodora nurta* Zullini, 1988 (Chromadorida: Nematoda). Hydrobiologia 332: 27–39.

Eyualem Abebe & A. Coomans, 1996e. Aquatic nematodes from Ethiopia VI. The genera *Chronogaster* Cobb, 1913, *Plectus* Bastian, 1865 and *Prismatolaimus* de Man, 1880 with descriptions of *C. ethiopica* n. sp. and *C. getachewi* n. sp. (Chromadorida: Nematoda). Hydrobiologia 332: 41–61.

Eyualem Abebe & A. Coomans, 1996f. Aquatic nematodes from Ethiopia VII. The family Rhabdolaimidae Chitwood, 1951 *sensu* Lorenzen, 1981 (Chromadorida: Nematoda) with the description of *Udonchus merhatibebi* n. sp. Hydrobiologia 341: 197–214

Eyualem Abebe & A. Coomans, 1997a. Aquatic nematodes from Ethiopia VIII. Enoplids, with descriptions of *Brevitobrilus fesehai* n. sp. and *B. tsalolikhini* n. sp. (Enoplida: Nematoda). Hydrobiologia 345: 149–184.

Eyualem Abebe & A. Coomans, 1997b. Aquatic nematodes from Ethiopia IX. Descriptions of three dorylaimid species, *Mononchus truncatus* Bastian, 1865 and *Diploscapter coronatus* (Dorylaimida: Nematoda). Hydrobiologia 253: 121–138.

Faulkner L. R. & W. J. Bolander, 1970. Acquisition and distribution of nematodes in irrigation waterways of the Columbia basin in Eastern Washington. J. Nematol. 2: 362–367.

Fenchel, T. & R. J. Riedl, 1970. The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar. Biol. 7: 255–268.

Fenchel, T., B.-O. Jansson & W. von Thun, 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Öresund. Ophelia 4: 227–243.

Ferris, V. R. & J. M. Ferris, 1989. Why ecologists need systematics: Importance of systematics to ecological research. J. Nematol. 21: 308–314.

Filipjev, I., 1931. Report on Freshwater Nematoda: Mr. Omer-Cooper's Investigation of the Abyssinian Freshwaters (Hugh Scott Expedition). Proc. zool. Soc. Lond. 2: 429–443.

Gasse, F. & F. A. Street, 1978. Late quaternary lake-level fluctuations and environments of the Northern Rift Valley and Afar Depression (Ethiopia and Djibouti). Palaeogeography, Palaeoclimatology, Palaeoecology 24: 279–325.

Giere, O., A. Eleftheriou & D. J. Murison, 1988. Abiotic factors. In Higgins, R. H. & H. Thiel (eds), Introduction to the Study of Meiofauna. Smithsonian Institution Press, London: 61–78.

Goede, R. G. M. De, 1993. Terrestrial nematodes in a changing environment. PhD. Thesis. Wageningen University, Wageningen: 138 pp.

Grove, A. T., F. A. Street & A. S. Goudie, 1975. Former lake levels and climatic changes in the rift valley of Southern Ethiopia. Geogrl. J. 141: 177–202.

Heip, C. & W. Decraemer, 1974. The diversity of nematode communities in the southern North Sea. J. mar. biol. Ass. U. K. 54: 251–255.

Heip, C., M. Vincx & G. Vranken, 1985. The ecology of marine nematodes. Oceanogr. Mar. Biol. Ann. Rev. 23: 399–489.

Heip, C., M. Vincx, N. Smol & G. Vranken, 1982. The Systematics and Ecology of Free-living Marine Nematodes. Helminthological abstracts series B, Plant Nematology 51: 1–31.

Heip, C., P. M. J. Herman & K. Soetaert, 1988. In Higgins, R. H. & H. Thiel (eds), Introduction to the Study of Meiofauna. Smithsonian Institution Press, London: 197–231.

Hendelberg, M. & P. Jensen, 1993. Vertical distribution of the nematode fauna in a coastal sediment influenced by seasonal hypoxia in the bottom water. Ophelia 37: 83–94.

Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

Hill, M. O., 1979. A Fortran program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University, Ithaca, New York: 60 pp.

Holopainen, I. & L. Paasivirta, 1977. Abundance and biomass of the meiozoobenthos in the oligotrophic and mesohumic lake Pääjärvi, southern Finland. Ann. Zool. Fenn. 14: 124–134.

Holme, N. A. & A. D. McIntyre, 1971. Methods for the Study of Marine Benthos. International Biological Programme, Blackwell Scientific Publications, Oxford and Edinburgh, Handbook No 16: 334 pp.

Jacobs, L. J., 1984. The free-living inland aquatic nematodes of Africa – a review. Hydrobiologia 113: 259–291.

Jacobs, L. J., 1987. A redefinition of the genus *Monhystrella* Cobb (Nematoda, Monhysteridae) with keys to the species. Zool. Scr. 16: 191–197.

Jenkins, W. R., 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Pl. Dis. Reptr. 48: 692–703.

Jensen, P., 1981. Species distribution and a microhabitat theory for marine mud dwelling Comesomatidae (Nematoda) in European waters. Cah. Biol. Mar. 22: 231–241.

Jensen, P., 1984. Measuring carbon content in nematodes. Helgolanderwiss Meeresunters 38: 83–86.

Jensen, P., 1986. Nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico IV. Ecological aspects. Mar. Biol. 92: 489–503.

Jensen, P., 1987a. Feeding ecology of free-living aquatic nematodes. Mar. Ecol. Prog. Ser. 35: 187–196.

Jensen, P., 1987b. Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes. Oecologia 71: 564–567.

Jensen, P., 1995. Life history of the nematode *Theristus anoxybioticus* from sublittoral muddy sediment at methane seepages in the northern Kattegat, Denmark. Mar.Biol. 123: 131–136.

Jongman, R. H. G., C. G. F. Ter Braak & O. F. R. Van Tongeren, 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen: 299 pp.

Kassahun, W., 1982. Comparative limnology of Lake Abijata and Lake Langano in relation to primary and secondary production. M.Sc. Thesis, Addis Ababa University, Addis Ababa: 112 pp.

Lambshead, P. J. D., H. M. Platt & K. M. Shaw, 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. J. nat. Hist. 17: 859–874.

Makin, M. J., J. J. Kingham, A. E. Wadden, C. J. Birchall & T. Tamene, 1975. Development Projects in The Southern Rift Valley of Ethiopia. Land Resource study 21. Land Resources Division, Ministry of Overseas Development, England.

Meyl, A. H., 1954. Die bisher in Italien gefundenen freilebenden Erd- und Süsswasser-Nematoden. Archo. Zool. Ital. 39: 161–264.

Mohr, P. A., 1966. The Geology of Ethiopia. University College Press, Asmara: 268 pp.

Ocaña, A., 1991. A redescription of two nematode species found in hot springs. Nematol. Medit.19: 173–175.

Ocaña, A., 1993. Nematode fauna in calcic bicarbonate springs in the province of Granada (Spain). Nematol. Medit. 21: 199–206.

Ocaña A. & A. Coomans, 1991. Two *Chronogaster* species from Spain (Nematoda: Leptolaimidae). Nematologica 37: 38–43.

Ocaña, A., J. Picazo & F. Jimenez-Millan, 1990. First record of nematode species in continental water from Spain: taxonomic and ecological considerations. Nematol. Medit. 18: 179–188.

Payne, A. I., 1986. The Ecology of Tropical Lakes and Rivers. John Wiley & Sons Ltd., Chichester, 301 pp.

Pennak, R. W., 1988. Ecology of the freshwater meiofauna. In Higgins, R. H. & H. Thiel (eds), Introduction to the Study of Meiofauna. Smithsonian Institution Press, London: 39–60.

Pielou, E. C., 1969. An Introduction to Mathematical Ecology. John Wiley and Sons., New York: 286 pp.

Platt, H. M., 1977. Vertical and horizontal distribution of free-living marine nematodes from Strangford Lough, Northern Ireland. Cah. Biol. Mar. 18: 261–273.

Platt, H. M. & R. M. Warwick, 1980. The significance of free-living nematodes to the littoral ecosystem. In Price, J. H., D. E.G. Irvine & W. F. Farnham (eds), The Shore Environment, Volume 2: Ecosystems. Academic Press, London: 729–759.

Por, F. D. & D. Masry, 1968. Survival of a nematode and an oligochaete species in the anaerobic benthal of Lake Tiberias. Oikos 19: 388–391.

Prejs, K., 1977. The species diversity, numbers and biomass of benthic nematodes in central part of lakes with different trophy. Ekol. Pol.25: 31–44.

Prejs, K., 1986. Occurrence of stylet-bearing nematodes associated with aquatic vascular plants. Ekol. Pol. 34: 185–192.

Prejs, K., 1987. A field and laboratory study of the relation between some stylet-bearing nematodes and some aquatic vascular plants. Arch. Hydrobiol. 2: 237–258.

Prejs, K. & B. Bernard, 1985. Meiobenthos of man-made Lake Zegrezynskie. Ekol. Pol. 33: 499–509.

Reise, K. & P. Ax, 1979. A meiofaunal 'thiobios' limited to the anaerobic sulfide system of marine sand does not exist. Mar. Biol. 54: 225–237.

Schiemer, F., 1978. Verteilung und Systematik der Freilebenden Nematoden des Neusiedlersees. Hydrobiologia 58: 167–194.

Schneider, W., 1937. Freilebende Nematoden der Deutschen limnologischen Sundaexpedition nach Sumatra, Java und Bali. Archiv f. Hydrobiologie, Suppl.-Bd. (Tropische Binnengewässer VII.) 15: 30–108.

Soetaert, K., 1989. Ecology and systematics of meiofauna and nematode assemblages in the Western Mediterranean deep sea of Corsica. PhD. Thesis, University of Ghent: 345 pp.

Soetaert, K. & C. Heip, 1989. The size structure of nematode assemblages along a Mediterranean deep-sea transect. Deep Sea Res. 36: 93–102.

Soetaert, K. & C. Heip, 1995. Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean sea. Mar. Ecol. Prog. Ser. 125: 171–183.

Soetaert, K., C. Heip & M. Vincx, 1991. Diversity of nematode assemblages along a Mediterranean deep-sea transect. Mar. Ecol. Prog. Ser. 75: 275–282.

Ter Braak, C. J. F., 1988. CANOCO – a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agricultural Mat. Group. Wageningen, Ministry of Agriculture and Fisheries: 95 pp.

Tietjen, J. H., 1969. The ecology of shallow water meiofauna in two New England estuaries. Oecologia 2: 251–291.

Tietjen, J. H., 1976. Distribution and species diversity of deep-sea nematodes off North Carolina. Deep Sea Res. 23: 755–768.

Tietjen, J. H., 1977. Population distribution and structure of the free-living nematodes of Long Island Sound. Mar. Biol. 43: 123–136.

Traunspurger, W., 1991. Fischbiologie des Köningsee. Nahrungsangebot und Nahrungswahl, Forschungsbericht. 22: Band 1: 152pp.

Traunspurger, W., 1992. A study of the free-living freshwater nematodes of hard substrates in the littoral of the oligotrophic Königssee (National Park Berchtesgaden, F.R.G.). Spixiana 15: 233–238.

Traunspurger, W., 1995. Autecology of *Rhabdolaimus terrestris* de Man – a dominant freshwater nematode in an oligotrophic lake. Nematologica 41: 603–616.

Traunspurger, W., 1996a. Distribution of benthic nematodes in the littoral of an oligotrophic lake (Königssee, National Park Berchtesgaden, F.R.G.). Arch. Hydrobiol. 135: 393–412.

Traunspurger, W., 1996b. Distribution of benthic nematodes in the littori-profundal of an oligotrophic lake (Königssee, National Park Berchtesgaden, F.R.G.). Arch. Hydrobiol. 135: 557–575.

Traunspurger, W., 1996c. Autecology of *Monhystera paludicola* de Man, 1880 – Seasonal, bathymetric and vertical distribution of a free-living nematode in an oligotrophic lake. Int. Rev. ges. Hydrobiol. 81: 199–211.

Traunspurger, W., 1997. Distribution, seasonal occurrence and vertical pattern of *Tobrilus gracilis* (Bastian, 1865) and T. medius (Schneider, 1916). Nematologica 43: 59–81.

Traunspurger, W., 1998. Distribution and sex ratio of *Ethmolaimus pratensis* de Man, 1880 (Nematoda, Chromadorida) in an oligotrophic lake. Nematologica 44: 391–408.

Traunspurger, W. & C. Drews, 1996. Vertical distribution of benthic nematodes in an oligotrophic lake: seasonality, species and age segregation. Hydrobiologia 331: 33–42.

Tsalolikhin, S. J., 1992. Taxonomic notes on African species of the genus *Brevitobrilus* (Nematoda, Enoplida: Tobrilidae). Zoosyst. Rossica 1: 1–15.

Tsalolikhin, S. J., 1993. New and little-known free-living nematodes from Ethiopia. Zoosyst. Rossica 2: 37–40.

Tudorancea, C. & A. Zullini, 1989. Associations and distribution of benthic nematodes in the Ethiopian Rift Valley lakes. Hydrobiologia 179: 81–96.

Van Damme, D., R. Herman, J. Sharma, M. Holvoet, & P. Martens, 1980. Benthic studies of the Southern Bight of the North Sea and its adjacent continental estuaries. Progress report II. Fluctuations of the meiobenthic communities in the Westerschelde estuary. ICES. C.M./L. 23: 131–170.

Wieser, W., 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Ark. Zool. 4: 439–484.

Wood, R. B., M. V. Prosser & R. M. Baxter, 1978. Optical characteristics of the Rift Valley Lakes, Ethiopia. Sinet: Eth. J. Sci. 1: 73–85.

Wood, R. B. & J. F. Talling, 1988. Chemical and algal relationships in a salinity series of Ethiopian inland waters. Hydrobiologia 158: 29–67.

Yeates, G. W., 1979. Soil nematodes in terrestrial ecosystems. J. Nematol. 11: 213–229.

Yeates, G. W., T. Bongers, R. G. M. De Goede, D. W. Freckman & S. S. Georgieva, 1993. Feeding habits in soil nematode families and genera – An outline for soil ecologists. J. Nematol. 25: 315–331.

Zullini, A., 1974. The nematological population of the Po river.Boll. Zool. 41: 183–210.

Zullini, A., 1976. Nematodes as indicators of river pollution. Nematol. Medit. 4: 13–22.

Zullini, A., 1988. A new genus and five species of nematodes from Ethiopian lakes. Revue Nématol. 11: 279–288.