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Vertical Distribution of Gymnamoebae (Rhizopoda, Lobosea) in the Top Layer of Brackish-Water Sediments

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The paper reports on the distribution of amoebae in a vertical slice of sandy sediment from the brackish-water Nivå Bay (Baltic Sea, The Sound). The 24 × 20 mm slice 2 mm in thickness was gently cut from the top of sediment to a depth of 20 mm using coverslips, and further sectioned into 2 × 2 × 2 mm cubes. Each cube was inoculated into enrichment media to reveal the biodiversity of amoebae. The map of amoebae species distribution in the slice was drawn and analyzed. The results show patchy distributions of many amoebae species. Amoebae tend to form a band of maximum diversity within the depth interval 2–16 mm. Two mini-cores of sediment located close to the butt-ends of the slice were collected using cut 1 ml syringes. They were sliced and inoculated to reveal the biodiversity of amoebae at different depths. The distribution patterns of amoebae in the mini-cores were similar to the ones obtained in the slice, and show evident patchiness of some species. It seems that abundant species mostly form irregular patches 1–2 cm across, whereas many species are rare and appear in few number of specimens or in patches smaller than 2 mm.

Introduction

A characteristic feature of a boundary habitat is a stratification of the conditions and follow-up stratification of the biota. It is especially pronounced in the microbial communities populating a gradient environment, like the top layers of marine and freshwater sediments (Fenchel 1969, 1971; Finlay 1980). Mobile bacteria and protists follow the gradients, forming a changing pattern of the vertical distribution and abundance of species (Agamaliev and Bagirov 1975; Burkovsky 1971; Cleven 2004; Fenchel and Bernard 1996; Robertson and Kuenen 1999). In contrast, rhizopods are low mobile organisms and perhaps most of them cannot follow rapidly changing gradients. They are more tolerant to the changing environmental conditions (Alve 1994; Alve and Bernard 1995; Moodley et al. 1997; Smirnov 1999, 2001) and their distribution pattern probably reflects more conservative features of the environment. Best-studied rhizopods from this point of view are testate amoebae (e.g. Buttler et al. 1996; Charman and Warner 1992; Mitchell and Gilbert 2004) and foraminifera (e.g. Bak and Nieuwland 1989; Jorissen 1999; Jorissen et al. 1998). However there are scarce data on the distribution patterns of naked amoebae (Anderson 2002; Bischoff 2002; Smirnov 2002; Smirnov et al. 1998).

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Table 1. List of amoebae species isolated from the slice. Species, found only in 2003 are in bold. The species designated in Smirnov and Thar (2003) as "*Cochliopodium* sp. (4)" was found to represent a mixture of two species and divided into *Cochliopodium* sp. (3) and sp. (4). The species "*Vexillifera* sp." (op. cit.) now is called "*Vexillifera* sp. (1)". Average size is given from the cells measured in cultures and not from the species descriptions. Distribution pattern is estimated using Morisita's index of aggregation. Indexes exceeding 1.15 with the level of confidence >99.9% were believed to denote aggregated distribution. Species occurred in the numbers fewer than 8 ml^{-1} where not taken into account for the analysis of the distribution pattern.

Species	Size (μm)	Number of findings	MPN number, ml^{-1}	Distribution pattern
Vannella sp. (2)	20	77	97	Random
Cochliopodium sp. (3)	23	67	82	Random
Stygamoeba regulata	27	46	53	Aggregated
Cochliopodium gulosum	55	42	48	Aggregated
Cochliopodium sp. (4)	13	37	42	Aggregated
Thecamoeba orbis	20	17	19	Aggregated
Gocevia pontica	34	16	18	Aggregated
***Thecamoeba* sp. (1)**	10	14	15	Equally spaced
Mayorella kuwaitensis	50	12	13	Aggregated
Cochliopodium sp. (2)	30	11	11	Equally spaced
Vexillifera sp. (1)	13	8	8	Aggregated
Hartmannella lobifera	50	7	7	–
Platyamoeba plurinucleolus	20	6	6	–
Flabellula baltica	19	4	4	–
Hartmannella vermiformis	25	3	3	–
***Thecamoeba* sp. (2)**	37	3	3	–
Thecamoeba munda	40	3	3	–
Platyamoeba calycinucleolus	37	2	2	–
"Species A"	17	1	1	–
Korotnevella sp.	30	1	1	–
Vannella simplex	30	1	1	–
Saccamoeba sp.	35	1	1	–
***Vexillifera* sp. (2)**	43	1	1	–
Total number			439	

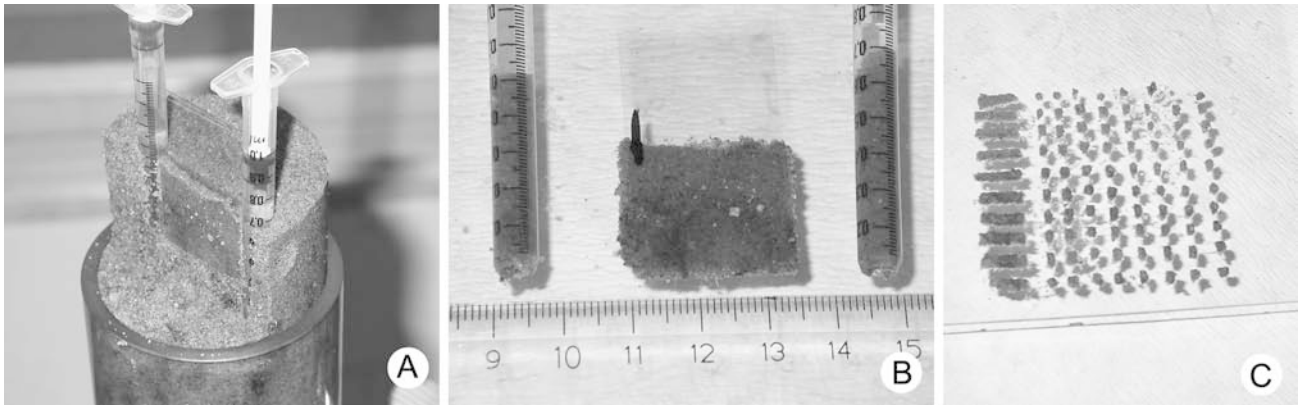


Figure 1. A. Studied slice of sediment bordered with two mini-cores. Half of the core is cut off. **B.** Studied slice of the sediments and mini-cores just before the final cut. **C.** Same slice cut into cubes 2 × 2 × 2 mm.

Our earlier study of the spatial distribution of amoebae in a horizontal slice of brackish-water sediment from the Nivå Bay at the depth interval of 3–5 mm (Smirnov and Thar 2003) revealed a complex pattern of amoebae species distribution with pronounced patchiness for some species and several "hot spots" of species diversity. We suggested that the patchiness is partly caused by the formation of microhabitats selectively occupied by amoebae species. In the present study, we examined the distribution of amoebae in a vertical slice from a sediment sample collected from the same location studied by Smirnov and Thar (2003). In addition, we investigated the vertical distribution of amoebae species in two mini-cores, collected with cut 1 ml syringes close to the butt-ends of the slice in order to compare the possible interpretations of the distribution pattern obtained with both sampling techniques.

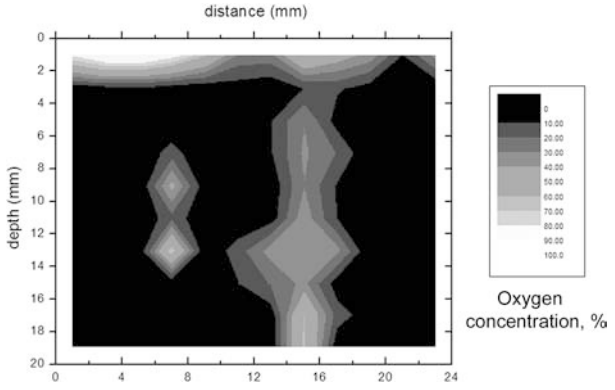


Figure 2. Map of the dissolved oxygen distribution in the slice based on the 24 vertical profiles. Oxygen concentration is indicated with the gray scale.

Results and Discussion

Species Diversity and Abundance

A total of 23 amoebae species were detected in the investigated slice of sediments. Among them, two species that we noted in August 2002 (Smirnov and Thar 2003), *Cochliopodium* sp. (5) and *Korotnevella nivo* were not isolated from the present slice (*Korotnevella nivo* was found in one of the mini-cores), whereas seven additional species were recovered (Table 1). All of them were low abundant, thus changes in the species composition are the results of the random sampling events. The average abundance of amoebae in the studied sediment slice in November 2003 was 439 ml^{-1}, while in August 2002

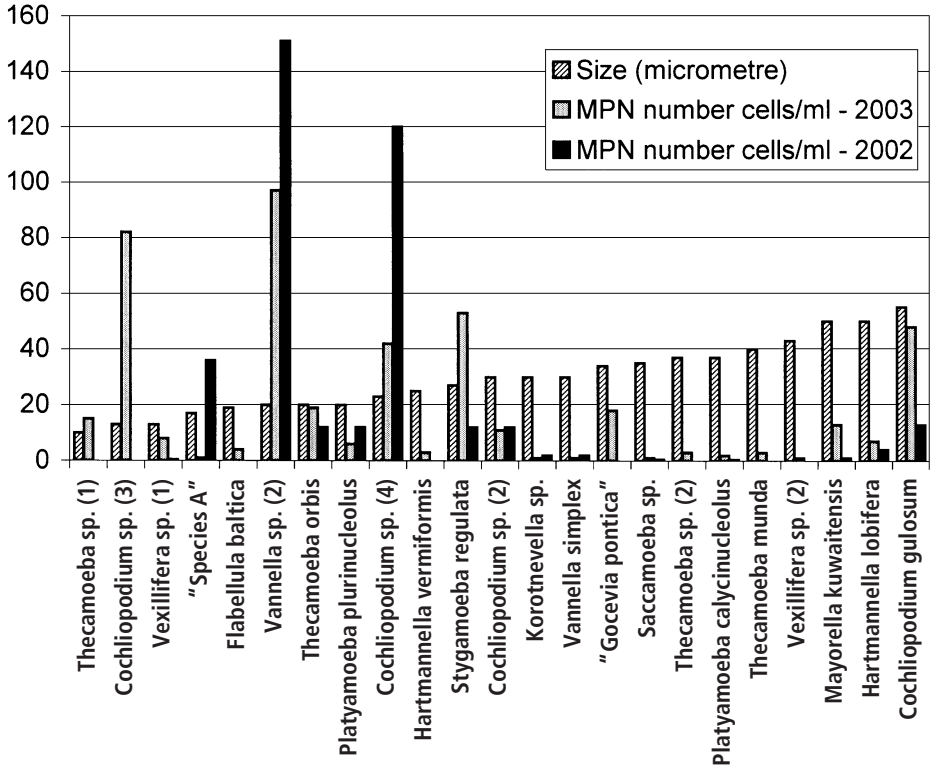


Figure 3. Average size and the number of findings of amoebae species in the sample in 2002 (Smirnov and Thar 2003) and in the present study. Species are ranged according to size.

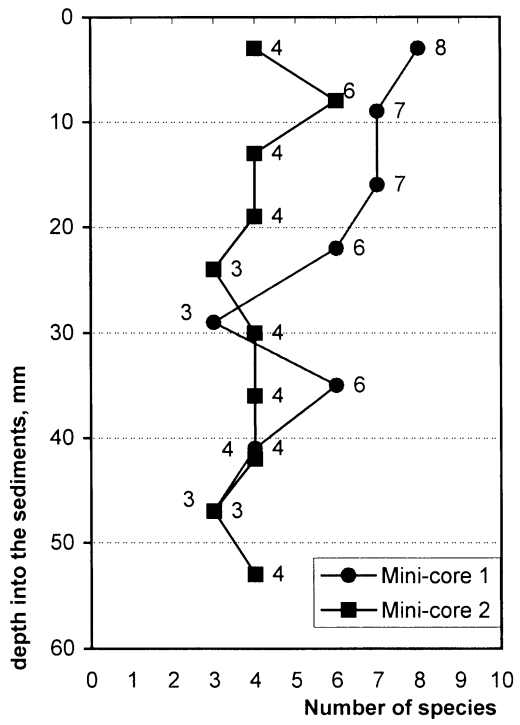


Figure 4. Number of amoebae species in the mini-cores at different depth.

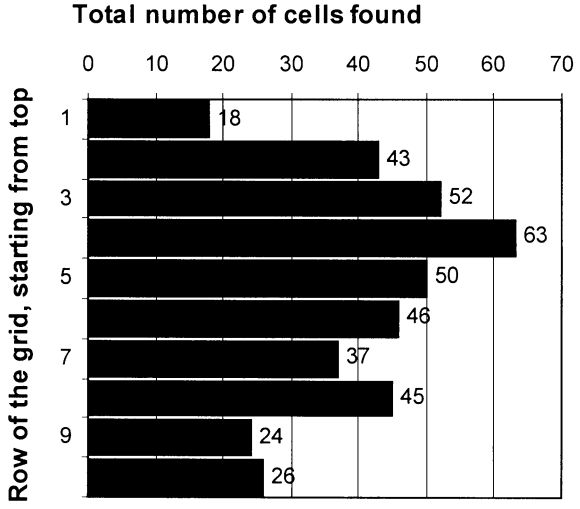
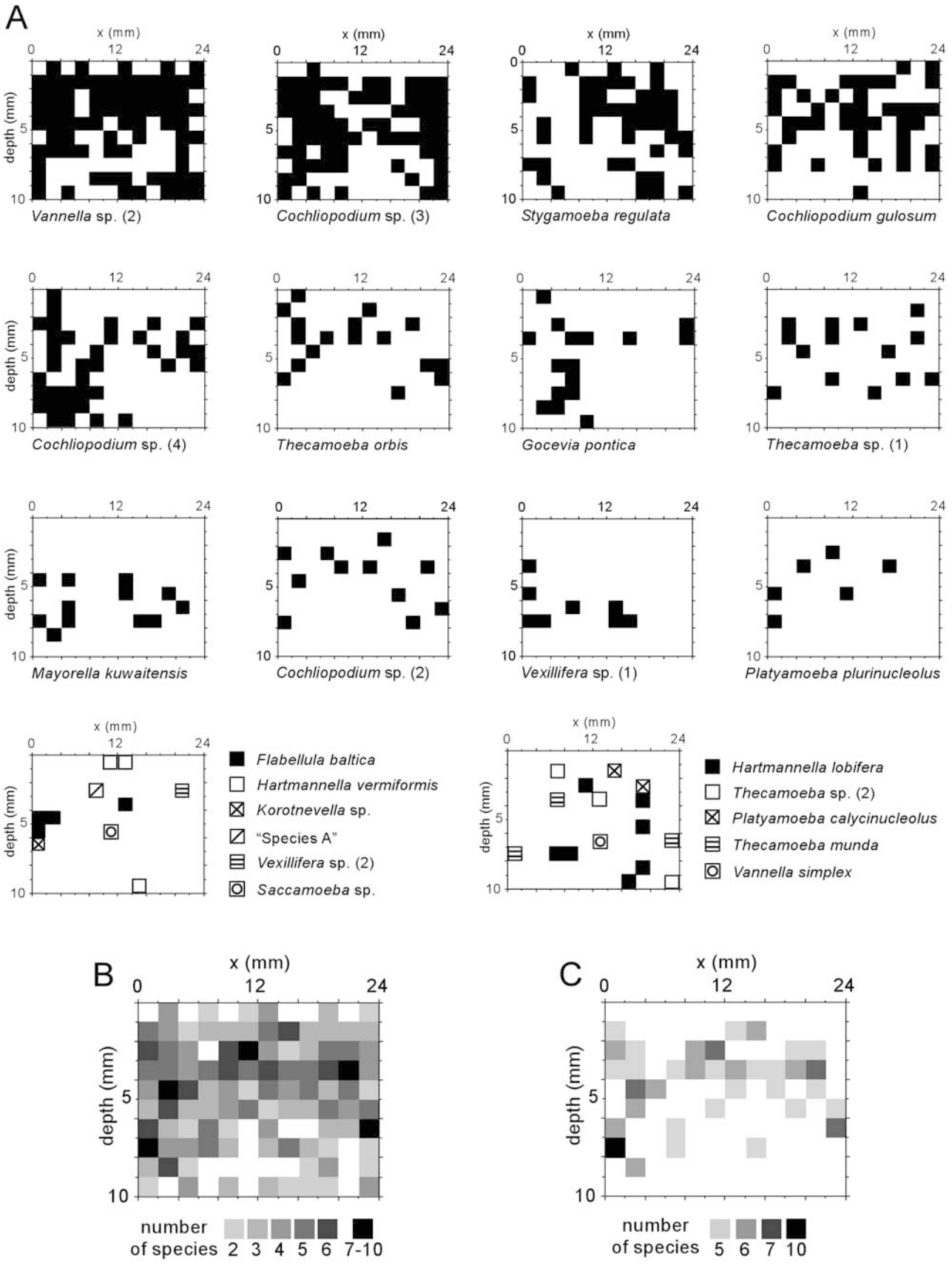


Figure 5. Total number of amoebae found in the sediment slice at different depths (each bar represents an overall number of amoebae in all cells within a horizontal row of the slice).

the abundance was 363 ml^{-1} and the species list contained 17 species. However, in November 2003 few species reached the maximal individual abundance, comparable with that noted in August 2002 or even exceeded it (Fig. 3). In 2002, two species were extremely abundant in the Nivå Bay sediments (151 and 119 ml^{-1}), whereas 14 species show an abundance of 0.5–12 ml^{-1}. In November 2003, the distribution of abundances was more even, and there was no clearly dominating species (Table 1, Fig. 3). However, the general tendency was the same: several relatively small species (average size ranged from 13 to 27 µm) were most abundant. The dominating species was the same in 2002 and 2003, *Vannella* sp. (2). The large species *Cochliopodium gulosum* (average size in our samples: 55 µm) ranked as no. 4 in abundance in 2003 (48 ml^{-1}), while in 2002, it was only no. 8 (8 ml^{-1}). In contrast, "Species A", which was highly abundant in 2002, was very rare in 2003.

Observations on the dynamics of amoebae species diversity and abundance in the natural habitats indicate the absence of pronounced regular diurnal, seasonal, or annual cycles (Anderson 1997; Butler and Rogerson 2000; Sawyer 1975; Smirnov and Goodkov 1996). Probably the abundance of the individual amoebae species and the general species diversity are both related to the diversity and abundance of available microniches (Smirnov and Thar 2003). During the winter period, Nivå Bay is exposed to strong winds, causing intensive exchange of the water in the bay and removal of remnants of sea grass and other organic material, causing deoxygenating of the sediments. Mats of purple sulfur bacteria, so common in this habitat during summer and often covering virtually the whole shore of the bay, never occur in autumn-winter-spring periods, when only the small patches of white sulfur bacteria and other kinds of bacteria occur (Bernard and Fenchel 1995; Fenchel 1969). Generally sediments in the bay are anoxic during the summer, while during winter they may be oxygenated to a considerable depth, with randomly distributed small anoxic patches inside the sediment. Of course, the distribution and abundance of microniches is not directly related with the general environmental conditions, but there is likely to be some dependence on general environmental factors, such as temperature and

Figure 6. A. Distribution maps of individual species ▶ within a sediment slice. **B.** Numbers of amoebae species found in the single cell, representing a 2 × 2 × 2 mm cube of a sediment slice. Number of species is indicated with the gray scale. **C.** Same as in B, only densely populated cells are included to reveal the "hot layer" of amoebae diversity


A
x (mm)
0
12
24
depth (mm)
5
10
Vannella sp. (2)
Cochliopodium sp. (3)
Stygamoeba regulata
Cochliopodium gulosum
Cochliopodium sp. (4)
Thecamoeba orbis
Gocevia pontica
Thecamoeba sp. (1)
Mayorella kuwaitensis
Cochliopodium sp. (2)
Vexillifera sp. (1)
Platyamoeba plurinucleolus
Flabellula baltica
Hartmannella vermiformis
Korotnevella sp.
"Species A"
Vexillifera sp. (2)
Saccamoeba sp.
Hartmannella lobifera
Thecamoeba sp. (2)
Platyamoeba calycinucleolus
Thecamoeba munda
Vannella simplex
B
C
number of species
2 3 4 5 6 7-10
5 6 7 10

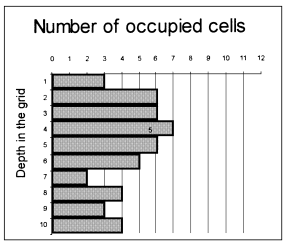
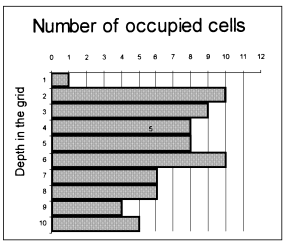
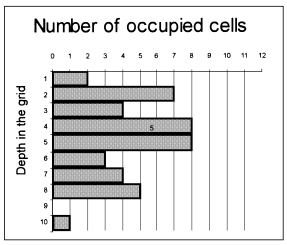
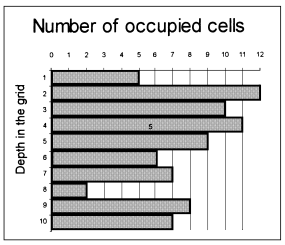
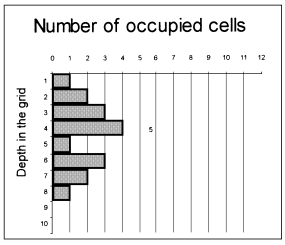
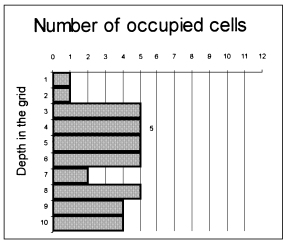
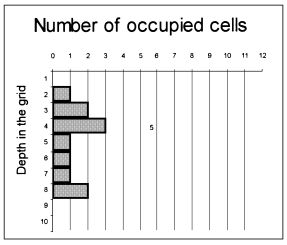
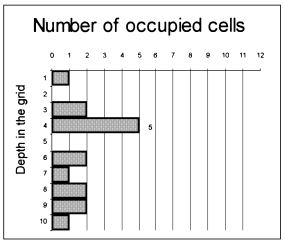
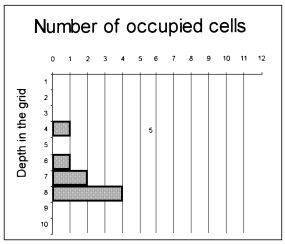
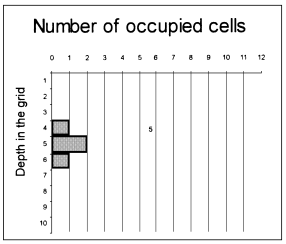
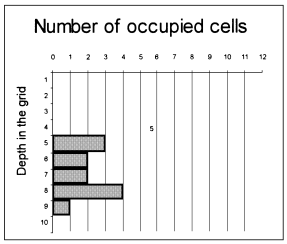
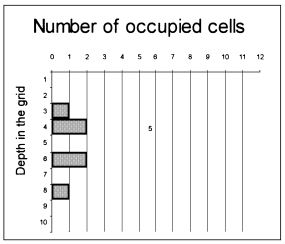
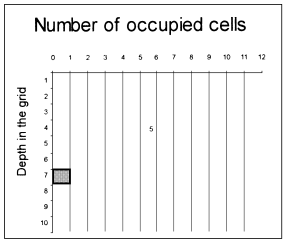
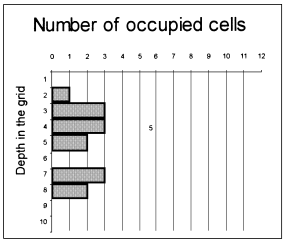
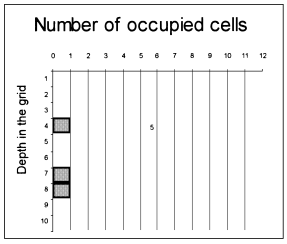
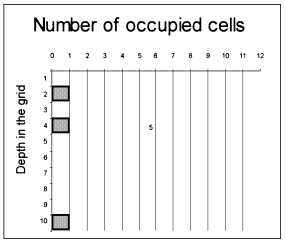
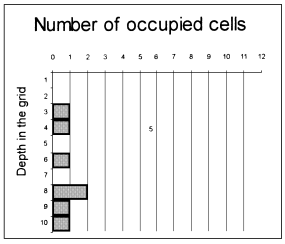
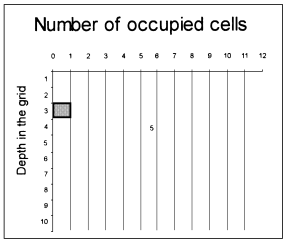
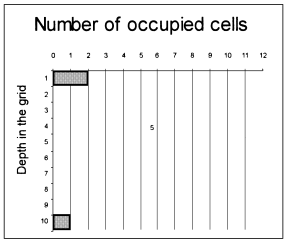
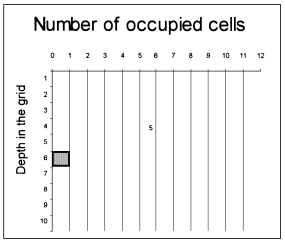
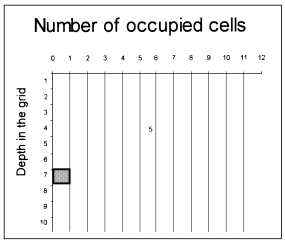
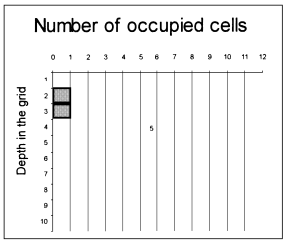
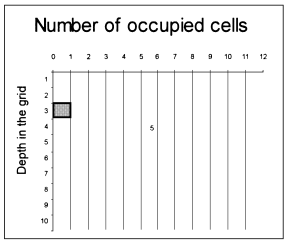
			
Stygamoeba regulata	*Cochliopodium* sp. (4)	*Cochliopodium gulosum*	*Vannella* sp. (2)
			
Thecamoeba orbis	*Cochliopodium* sp. (3)	*Cochliopodium* sp. (2)	"*Gocevia pontica*"
			
Vexillifera sp. (1)	*Flabellula baltica*	*Mayorella kuwaitensis*	*Platyamoeba plurinucleolus*
			
Korotnevella sp.	*Thecamoeba* sp. (1)	*Thecamoeba munda*	*Thecamoeba* sp.
			
Hartmannella lobifera	"Species A"	*Hartmannella vermiformis*	*Saccamoeba* sp.
			
Vannella simplex	*Platyamoeba calycinucleolus*	*Vexillifera* sp.(2)	

Table 2. Occurrence of species in the mini-cores at different depths.

Species	Mini-core 1								Mini-core 2									
Depth in sediment, mm	3	9	16	22	29	35	41	47	3	8	13	19	24	30	36	42	47	53
Cochliopodium sp. (4)	x	x	x		x	x	x	x	x	x			x				x	x
Cochliopodium sp. (3)	x	x	x	x		x	x	x								x		
Cochliopodium sp. (2)	x								x					x				
Cochliopodium gulosum		x	x	x	x	x	x		x	x	x	x		x				
Mayorella kuwaitensis	x	x																
Gocevia pontica	x		x					x		x				x	x			
Stygamoeba regulata		x	x	x						x		x	x		x			
Vannella sp. (2)	x	x		x	x	x			x	x	x				x			x
Thecamoeba sp. (1)	x			x			x				x				x	x		x
Platyamoeba calycinucleolus			x							x	x	x					x	
Korotnevella nivo						x												
Korotnevella sp. (1)		x																
Vexillifera sp. (1)			x	x														
Thecamoeba orbis												x		x			x	
Platyamoeba plurinucleolus						x												
Species "A"																x		x

oxygen content. Perhaps due to the lower water temperature and higher general oxygenation and water mixing in the late autumn–winter period, the diversity of the microniches available for amoebae increases, while no particular niche clearly dominates in the bay. The summer is characterized by more stable and homogeneous environmental conditions. Probably the general diversity of niches in summer is more limited, but certain kinds of niches are highly abundant.

There are observations to indicate that certain amoebae species in the North Atlantic may be found only during a specific period of the year, in particular in January (Sawyer 1975). Studies of freshwater amoebae at Valamo Island (Northwest Russia) clearly show a peak diversity in October, when the water is getting colder (4–7 °C) and reaches peak oxygenation, but before the lake is covered by ice (Smirnov and Goodkov 1996; Smirnov et al. 1998). However, and in contrast with our observation, Anderson (1997) found peak diversity of amoebae in a shallow water pond in July–August. Butler and Rogerson (2000) also noted that the species diversity of amoebae in the Clyde Sea area sediments was lowest in winter. Probably, the pattern depends on the particular conditions that are specific to a given type of habitat

The species diversity in the sediment mini-cores (Table 2) was less than that observed in the slice. A total of 16 species were found in the two cores. The total volume of both cores was about 1 ml, which is less than the total volume of the slice (1.92 ml). This observation supports the point that the volume of the sample is critical for revealing the biodiversity of amoebae because of the presence of low-abundant species (Smirnov 2002; Smirnov and Thar 2003). One core was richer in species than another (Table 2). This provides additional evidence of the highly heterogeneous species distribution at the distance of centimeters. The species *Thecamoeba orbis*, for example, was rather abundant in the slice, but found only in one of the cores. In both cores, the number of recovered species varied with depth (Fig. 4), showing a maximum in the upper 20 mm thick layer, which is in good agreement with the results obtained from the slice. It is interesting that the graphics, illustrating the individual species number at different depths (Fig. 7) in the mini-cores generally show the same tendencies as those obtained earlier from the much larger (15–20 cm) cores from Nivå Bay and other localities (Smirnov et al. 1998; Smirnov 2002). First of all, a common tendency is the very irregular distribution of species, as previously reported in the cores 1–2 by Smirnov (2002), and the presence of relatively well-pronouced vertical distribution patterns for some species. There are species occuring only in the upper sediment layer of sediments (e.g. *Mayorella kuwaitensis*); species occurring in various layers without evident preference to any of them (e.g. *Cochliopodium* spp. and *Thecamoeba* sp. (1), and randomly distributed rare species (e.g. *Flabellula baltica*) (Fig. 7). Partly the distribution patterns correspond to those in larger cores (Smirnov 2002); this

◀ **Figure 7.** Vertical distribution patterns of individual species within a slice.

may suggest that the distribution pattern determined with the presence of microniches is scale-independent because the size of the microniches is small compared to the size of the samples.

Spatial Distribution and Abundance of Amoebae

The vertical distribution of species was very heterogeneous. The number of species per cell of our grid (representing the cubical segment of the slice) varied from zero to ten species, which twice exceeds the maximal number of species that we have found in the cells of the horizontal slice during 2002 (Smirnov and Thar 2003, p. 366, Fig. 6). The distribution pattern of species in the vertical section shows a pronounced "hot layer" of the species diversity and abundance, similar to the "hotspots" of the species diversity noted in 2002. It was generally located at depths of 2–16 mm (Figs 5–6) right under the oxygenated zone of sediments. Perhaps its location may be partly explained by two factors that concurrently affect the amoebae: predation by molluscs and crustaceans, removing most of amoebae from the upper 1–2 mm of the sediment, and the decreasing O_2 content and increasing H_2S concentration with increasing depth, preventing trophozoites of most amoebae species from exploring deeper layers of sediments. However, other yet unexplored factors, such as the distribution of bacterial populations or the general organic flux through the sediments may influence this pattern as well.

Theoretically, smearing cells during the slicing of the core can violate the distribution pattern of amoebae. However, these violations, if they exist, seem to be negligible, otherwise we would have had no clear patchiness of species both in the horizontal (Smirnov and Thar 2003) and in the vertical sections (present paper), as well as no clear hot layer of amoebae diversity. The configuration of patches does not suggest the serious influence of smearing, as there are no pronounced "tales" in the distribution maps. Therefore, the observed pattern of amoebae distribution does not suggest considerable influence of smearing on the resulting distribution patterns. In addition, the use of coverslips as blades to cut sediments shows that they cause only minor violation of the sediment structure (as visible in Fig. 1A) during the cut and move down few sand grains.

Statistical treatment of the individual distribution maps for each species (Fig. 6) using Morisita's index of aggregation (Poole 1974) revealed two species showing random distribution and seven species with the tendency to form aggregates (Table 1). Species occurring in less than eight grid locations were not taken into account for the spatial distribution analysis due to the low reliability of statistical data. Two species show equally spaced distribution, but we believe that this is an artifact of the Morisita's index of aggregation. This algorithm reveals with sufficient level of confidence, the patches that are small compared with the overall size of the sample, but it can hardly reveal a patch, which is comparable in size with the entire sample. It seems that this index tends to consider low-abundant species that are randomly distributed within the hot layer of the species diversity though they are equally spaced distributed within the whole slice. For example, from Figure 6 it is evident that the species *Cochliopodium* sp. (2) and *Thecamoeba* sp.(1) are located predominantly within the hot layer of species diversity, while Morisita's index of aggregation treats them as equally spaced distributed because the populated cells of the grid are too distant from each other. For the data represented in Table 1 we accepted relatively low confidence limit for the index: 1.15.

As reported in 2002, the most abundant species generally show a random distribution. It may be the result of wide ecological tolerance of such species. Probably their microniches are so abundant that they actually merge in the sediments, forming a common niche and allowing amoebae of this species to explore the whole thickness of the studied sediment layer. Alternatively it may be related with the ability of these species to form resting stages. Maybe after the local bursts of abundance, they densely inoculate sediments with the resting stages when appropriate microniches decrease or disappear. In our enrichment cultures, we recover amoebae both from cysts and trophozoites, since both initiate amoebae population in the culture, and thus very high density of amoebae were recorded. However, the patchy distribution of many species shows that nonetheless some ecological preferences do exist and that there are areas in the sediments that species cannot (or do not) populate due to some reason. These areas apparently do not even contain cysts of certain species.

The analysis of the vertical pattern of the abundance of individual species (Fig. 7) generally confirmed the conclusions drawn from the data on minicores. We can easily suggest that the species, which regularly show peak abundances at certain depths, have relatively restricted ecological requirements, but their specific microniches are abundant at the moment of sampling. The upper few millimeters of the investigated sediment is characterized by steep physico-chemical gradients (Fenchel and Riedl 1970; Fenchel 1971). The microniches of such species may be specifically linked to certain areas in these gradients. From the same consideration, species showing more or less homogeneous distri-

bution patterns are perhaps universalists with wide ecological tolerance. Rare species and species distributed in patches may occupy rare microniches or rest in the sediment until appropriate niches appear.

Both, our earlier data (Smirnov and Thar 2003) and the present results (Fig. 6) indicate that if an amoebae species shows evident patchiness, the patches measure 5–15 mm across both in the vertical and the horizontal section. Thus, this size may correspond to the scale of individual microhabitats of some species, like *Mayorella kuwaitensis* or *Thecamoeba orbis.* Low-abundant species probably are represented with individual cells (trophozoites or cysts) or (theoretically) tiny aggregates of cells smaller than 2 mm across, while highly abundant ones populate nearly the entire top 1–2 cm of sediments. Vertical distribution pattern shows that amoebae form a densely populated layer in the top 1–2 cm of the sediments. The hot spots of amoebae diversity found in the horizontal section (Smirnov and Thar 2003) may be the locations where the sampled horizontal slice touched or transected the uneven "hot layer" of amoebae diversity in the sediments.

Methods

A submerged core of sandy bottom sediment from 30 cm depth was collected from the Nivå Bay (15 km South of Helsingør, Denmark) on November 11, 2003, then transported to the laboratory in approximately 30 min, mounted into a setup for microelectrode measurements and left to stabilize for 1 h. Oxygen measurements were performed as described in Smirnov and Thar (2003). To map the oxygen content, profiles down to 24 mm depth were collected on a 28 mm length line; at the end of the measurements, several control profiles were acquired at the starting area of the grid to make sure that oxygen distribution did not undergo changes during the time of measurements.

The area of measurements was marked and two coverslips, 20 × 60 mm in size, were gently pushed into the sediment cutting a vertical slice, 2 mm in thickness. Two 1 ml syringes were used to collect the mini-cores, bordering the slice from butt-ends (Fig. 1A). The core was gently pushed up until about 3 cm of sediment appeared over the edge of the plastic sampler. Sediments were gently sliced with a scalpel blade to isolate the slice, bordered by the coverslips. The slice was removed from the sediments, placed on the glass surface (Fig. 1B), and cut with coverslips (new coverslip for each cut) into 2 × 2 × 2 mm cubes (Fig. 1C). Each cube was inoculated into a 60 mm Petri dish. The medium used for inoculation was 0.01% filtered Cerophyl infusion in artificial seawater salinity 15 ppt (Weiner, Germany). All cultures of samples were incubated at room temperature. Negative controls (dishes undergoing all the same manipulations but not inoculated with the sediment) were incorporated. Mini-cores were sliced into 8 (core 1) and 10 layers (core 2) and each layer was similarly inoculated. Cultures were examined at days 8–9 and 23–24 of incubation using an inverted phase-contrast microscope. Each dish was screened under 100× and 400× magnification until the observation of at least two specimens of any recorded species. Data on Nivå Bay amoebae fauna (Smirnov 1999, 2001, 2002) were used to identify and distinguish species. Species names were given only for reliably identified amoebae, the rest were identified to genus. Designations of non-identified species correspond to those used by Smirnov (2001), Smirnov (2002) and Smirnov and Thar (2003). Trivial names like "Species A" were given to isolates that perhaps represent new taxa. Abundance of amoebae was calculated as described by Garstecki and Arndt (2000) – as MPN using Poisson series. Data were treated using the computer software Excel (Microsoft, USA), and Origin (OriginLab, USA), and analyzed by standard statistical and correlation analysis approaches (Poole 1974).

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