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ORIGINAL PAPER

Spatial Distribution of Gymnamoebae (Rhizopoda, Lobosea) in Brackish-Water Sediments at the Scale of Centimeters and Millimeters

Alexey Smirnov[a,b,1] and Roland Thar[a]

[a] Marine Biological Laboratory Helsingør, University of Copenhagen, Denmark
[b] Department of Invertebrate Zoology, Faculty of Biology and Soil Sciences, St. Petersburg State University, Universitetskaja nab. 7/9, 199034 St. Petersburg, Russia

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In order to study micro-spatial distribution of amoebae, an intact slice of sandy sediment from the brackish-water Nivå Bay (Baltic Sea, The Sound), 40 × 24 mm in size and 2 mm in thickness was gently sectioned into cubes, 2 × 2 × 2 mm in size. Each cube was inoculated into enrichment media to reveal the biodiversity of amoebae. Seventeen species of amoebae were recovered. The 2-D map of amoebae species distribution in the slice, consisting of 240 2 × 2 mm cells was drawn and analyzed. Results show heterogeneous distribution of amoebae at the scale of centimeters and millimeters and confirm the idea of the presence of microhabitats, selectively occupied by amoebae species. Three types of distribution patterns were found: random, aggregated and equally spaced. Microelectrode studies indicated that amoebae distribution was not related to the dissolved oxygen content in the sediment. The studied slice of sediment contained several pronounced "hotspots" of amoebae biodiversity, where up to four species co-occur in the same area. Seven species of amoebae numbered 1–4 specimens in the studied slice (i.e. there was 0.5–2 cell ml^{-1}). Analysis of the amoebae distribution map shows the high probability of undersampling rare amoebae species during faunistic studies.

Introduction

Natural habitats are heterogeneous. Any species populating a habitat has specific biological requirements and preferences allowing it to explore only a range of ecotopes within a habitat, and results in the aggregated distribution of organisms (Kotliar and Wiens 1990). Protists are not an exception, and the scale of their aggregates may range from kilometers (Sime-Ngando et al. 1992) to centimeters (Taylor and Berger 1980). Evidently, these are related to environmental conditions and gradients, but the particular factors causing aggregation of protists in most cases remain poorly understood (Patterson et al. 1989).

In the absence of chemical gradients or chemosensory behavior, the minimal possible size of aggregates in a homogeneous environment that still can maintain a stable protozoan population despite the loss of cells due to their random migrations was calculated to be about 20 cm for a ciliate population, and about 6 mm for bacteria (Fenchel 1987). Experimental studies show that numerous cases of protozoan aggregation occur at a much smaller scale.

[1] Corresponding author;
e-mail smirnov@home.rclph.spbu.ru

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Aggregates of ciliates measure from 1.5 to 4 cm (Taylor and Berger 1980), and aggregates of some protozoan species may measure less than 1 cm (Arlt 1973; Wiackowski 1981). Jørgensen (1977) suggested that micro-spatial heterogeneity might occur at scales as small as 100 µm. Thus, we can presume that small-scale aggregated distributions of protists reflect the micro-heterogeneity of the environment and are related to the chemosensory behavior and biology of particular species (Fenchel and Bernard 1986; Patterson et al. 1989). These facts bring us back to the idea of Bamforth (1963) who suggested the existence of "microhabitats" selectively occupied with protozoan species that can be "as small as few cubical centimeters" and favor different and special types of protozoan communities.

It has been shown that many protozoan species might be cryptic in the environment and require special efforts to be recovered (Fenchel et al. 1997; Smirnov 2001). A considerable proportion of the world-wide diversity of certain protist taxa can be found in a single local habitat with extensive sampling (Finlay and Clarke 1999). Some protozoan species may be recovered from apparently absolutely non-appropriate environments (Fenchel and Finlay 1995; Smirnov 1999). These and other facts lead to the idea of the global ubiquity of most protozoan species (Finlay 2002). It is logical to suggest that the observed ubiquity may be caused by the existence of very diverse and numerous microhabitats in any biogeocoenosis. The wide variety of microhabitats creates appropriate niches for a substantial fraction of known protozoan species. It explains both the aggregation of species (aggregates correspond to the microhabitats populated with a species) and the existence of cryptic species (they populate rare microhabitats, or microhabitats hardly reproducible in cultures).

The microhabitat model of the environment is rather complex because it must take into account temporary dynamics of the microhabitats, physical and chemical conditions causing the formation of specific microhabitats, the relationships between size, motility, and the activity range of a species, its biology and the scale of its microhabitat. From this consideration, the spatial distribution of relatively immotile species with simple life cycles, such as gymnamoebae, appears to be one of the promising indicators of the micro-structure of the environment.

A popular subject of investigation in this field is the microhabitat preferences of foraminifera (Jannik 2001; Jorissen 1999; Jorissen et al. 1998). There are some data on testate amoebae (Haman 1990; Meisterfeld 1991; Velho et al. 1990), but the naked rhizopods are almost completely omitted from such studies due to the methodological difficulties of species recovery. Anderson (2002) and Bischoff (2002) indicated that amoebae species distribution might be heterogeneous even at the scale of centimeters, reflecting the existence of "microbiogeocoenoses". Smirnov (2002) showed that the vertical distribution of amoebae in the brackish-water sediment is heterogeneous, with pronounced aggregation of some species. He suggested the existence of microhabitats, selectively occupied by amoebae species (Smirnov 1999, 2001, 2002). However, all suggestions are still based on the data from a few separate (even if closely located) integral samples, and to our knowledge, nobody has tried to investigate the micro-spatial distribution of amoebae within a single sample. The present paper reports on the study of amoebae distribution in a $40 \times 24 \times 2$ mm slice of the upper layer of sandy, brackish-water sediment using a homogeneous sampling grid with 2×2 mm cells (a total of 240 adjacent samples were studied).

Results and Discussion

3-D Distribution of Oxygen in the Core

The distribution of dissolved oxygen in the core was found to be highly heterogeneous. Vertical sections of the mapped area of sediments (Fig. 2) demonstrate the existence of pockets that show high (Fig. 2A, B) or low (Fig. 2E) oxygen concentrations, perhaps caused by the activity of burrowing animals. Super-saturation with the oxygen at the sediment surface was caused with the photosynthetic activity of diatoms and cyanobacteria, covering the sediment and inhabiting the top few millimeters of sand. Our observations confirm previous data on the heterogeneous distribution of oxygen in marine sediments caused by the activity of burrowing animals, photosynthesis in the top layers of sediments, and other reasons (Fenchel 1996; Fenchel and Glud 2000).

It is known that oxygen gradients are dynamically changing (Revsbech et al. 1980). Thus, we should hardly expect strong correlations of the distribution of relatively immotile protozoa with the oxygen concentration (Smirnov 2002). Vice versa, motile organisms that can actively relocate in the sediments are known to follow gradients in day-night and other cycles (Fenchel and Finlay 1990; Jørgensen 1982).

Species Diversity and Abundance of Amoebae

A total of 17 amoebae species were found in the investigated slice of sediments (Table 1). Their size

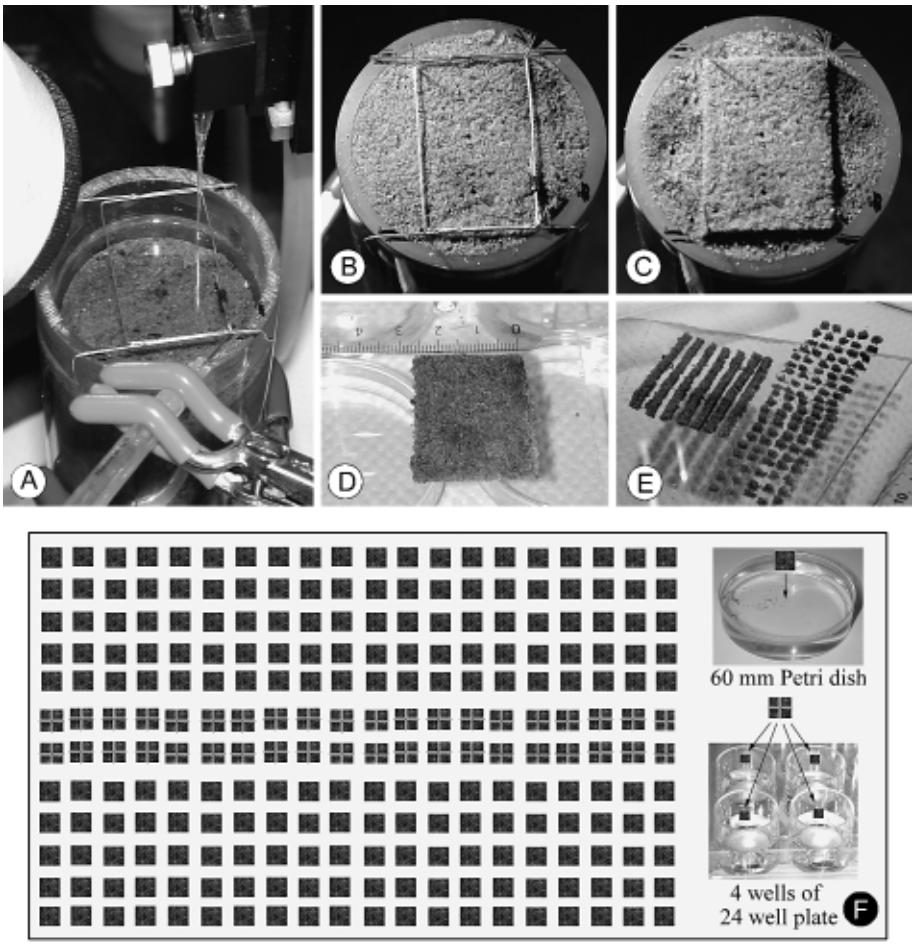

Figure 1. **A**: Microelectrode measurements in the core. **B**: Re-positioning of the frame after slicing off the top 1–2 mm of sediments. **C**: Studied slice of the sediments just before the final cut. **D**: Same slice after cutting, intact on the glass surface. **E**: Same slice, cut into the cubes $2 \times 2 \times 2$ mm. **F**: Scheme of the sectioning and inoculation of the slice.

distribution was rather uniform and an increment in the cell size generally corresponded to a decrement in abundance, with three exceptions (Fig. 3). Three small species (*Cochliopodium* sp. 4, *Vannella* sp. 2 and "Species A") were highly abundant in the sediments. We suggest that these are species that populated microhabitats that were most abundant in the sediment at the moment of sampling and/or are most easily reproducible in our cultures. The average number of amoebae in the studied slice of sediments was 259 ml^{-1} (MPA – minimal possible abundance) or 363 ml^{-1} (MPN – most probable number), which is in good agreement with the numbers of amoebae previously reported from various marine and brackish-water sediments (see Tab. 4 in Smirnov (2002) for comparative data). Note that the difference in MPA and MPN estimations of amoebae numbers is solely due to the high frequency of finding the three most abundant species.

Spatial Distribution of Amoebae

Spatial distribution of amoebae in the sample was found to be very heterogeneous (Fig. 4) and was not related to the actual oxygen concentration in the sediment (Fig. 5). Statistical treatment of the individual distribution maps for each species using Morisita's index of aggregation (Poole 1974) revealed three different patterns: species showing random distribution, species with the tendency to form aggregates, and species with equally spaced distribution (Tabs 1 and 2). Rare species occurring in less than 8 grid locations were not taken into account for the spatial distribution analysis.

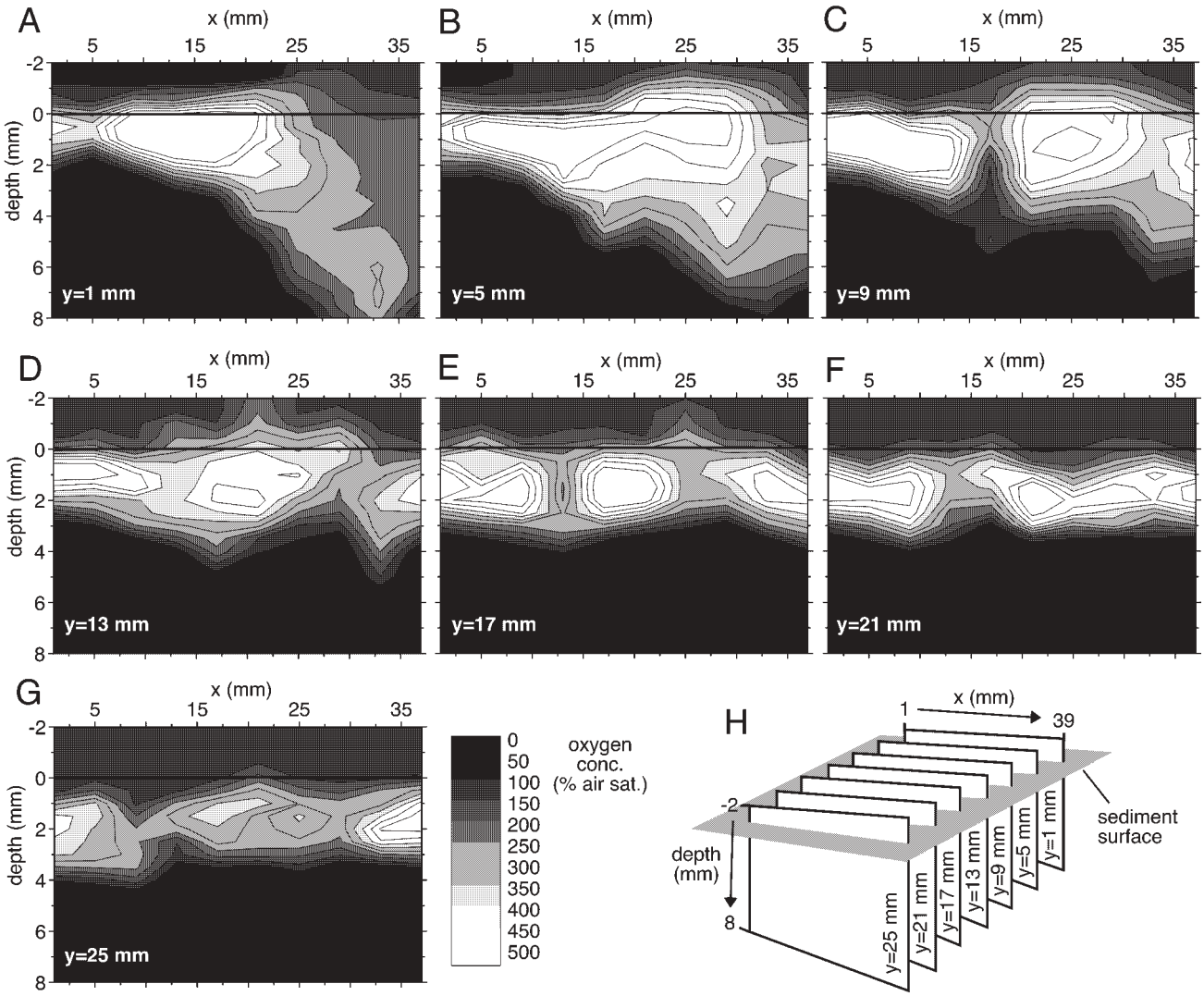

Figure 2. Dissolved oxygen distribution in the sediment core. **A–G**: Vertical sections of the sediment, located as shown in the figure. **H**. Oxygen concentration is indicated with the gray scale.

The three most abundant species (*Cochliopodium* sp. 4, *Vannella* sp. 2, "Species A") and *Thecamoeba orbis* show random distribution (Tab. 1). We must state the reservation that this may be an artefact of the statistical analysis related with the high frequency of occurrence of these species. A sampling grid with 2×2 mm cells may be too coarse to resolve these aggregates. However, a finer grid used for the two middle rows of samples (Fig. 1F) did not reveal any other pattern for these species, probably due to the destruction of the spatial structure of sandy sediments cut into such small portions. Five species (*Cochliopodium gulosum, Cochliopodium* sp. 2, *Cochliopodium* sp. 5, *Stygamoeba regulata* and *Hartmannella lobifera*) show pronounced aggregation (Tabs 1 and 2). A very interesting case is *Platyamoeba plurinucleolus* that shows statistically well-supported regular (namely, equally spaced) distribution (Tab. 2). We do not have a rational explanation for this phenomenon, which of course, may be just incidental.

In the studied grid, half of the species that were sufficiently abundant for statistical analysis show well-supported aggregated distribution (Tabs 1 and 2). It may be an indication for the presence of microhabitats selectively occupied by the amoebae species. The size of the aggregates differs and may reflect variation in size range of microhabitat for

Table 1. List of species found in the sample, average size (as recorded from our observations), abundance and distribution pattern for each species.

Species	Size (μm)	Number of findings	MPN number	Distribution pattern
1. *Vannella* sp.(2)	20	174	290	Random
2. *Cochliopodium* sp.(4)	23	146	230	Random
3. "Species A"[1]	17	62	69	Random
4. *Thecamoeba orbis*	20	23	23	Random
5. *Cochliopodium* sp. (2)	30	23	23	Aggregated
6. *Stygamoeba regulata*	27	23	23	Aggregated
7. *Platyamoeba plurinucleolus*	20	19	19	Equally spaced
8. *Cochliopodium gulosum*	55	15	15	Aggregated
9. *Hartmannella lobifera*	50	8	8	Aggregated
10. *Cochliopodium* sp. (5)	35	7	7	Aggregated
11. *Korotnevella* sp.	30	4	4	–
12. *Vannella simplex*	30	3	3	–
13. *Mayorella kuwaitensis*	50	2	2	–
14. *Korotnevella nivo*	60	1	1	–
15. *Vexillifera* sp.	13	1	1	–
16. *Saccamoeba* sp.	35	1	1	–
17. *Platyamoeba calycinucleolus*	37	1	1	–
Total abundance:		MPA: 513[2]	MPN: 720[3]	

[1]the designation "Species A" (not a systematic name!) was arbitrarily chosen to record a new species of small *Vannella*-like lobose amoeba that we cannot yet classify into any known amoebae genus due to its peculiar locomotive pattern.
[2]MPA (Minimal Possible Abundance) calculated as described by Smirnov (2002)
[3]MPN (Most Probable Number) of amoebae calculated as described by Garstecki and Arndt (2000), using Poisson series
"–" indicates that a species is too rare to make any conclusion about its distribution pattern.

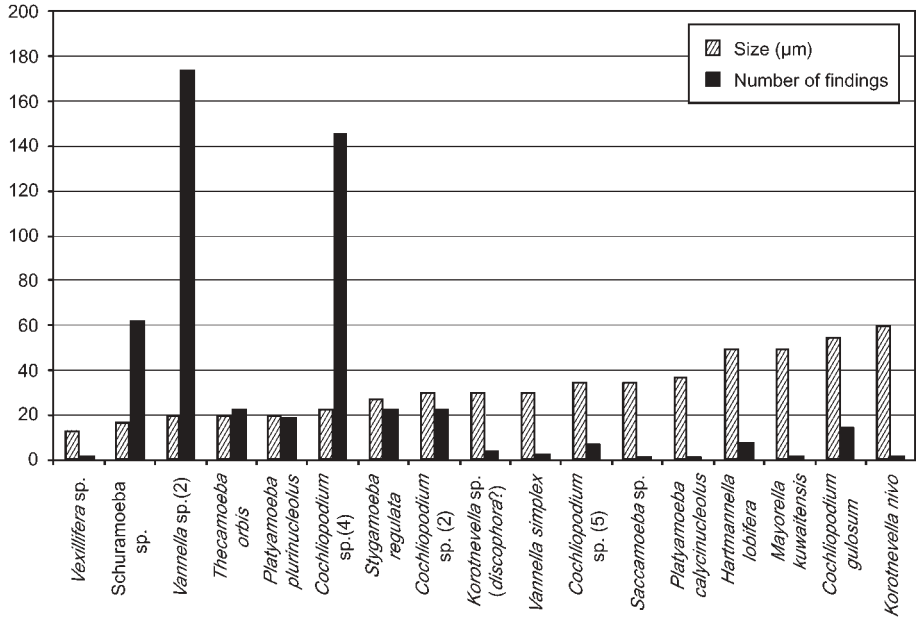

Figure 3. Average size and the number of findings of amoebae species in the sample. Note three species with unusually high frequency of finding.

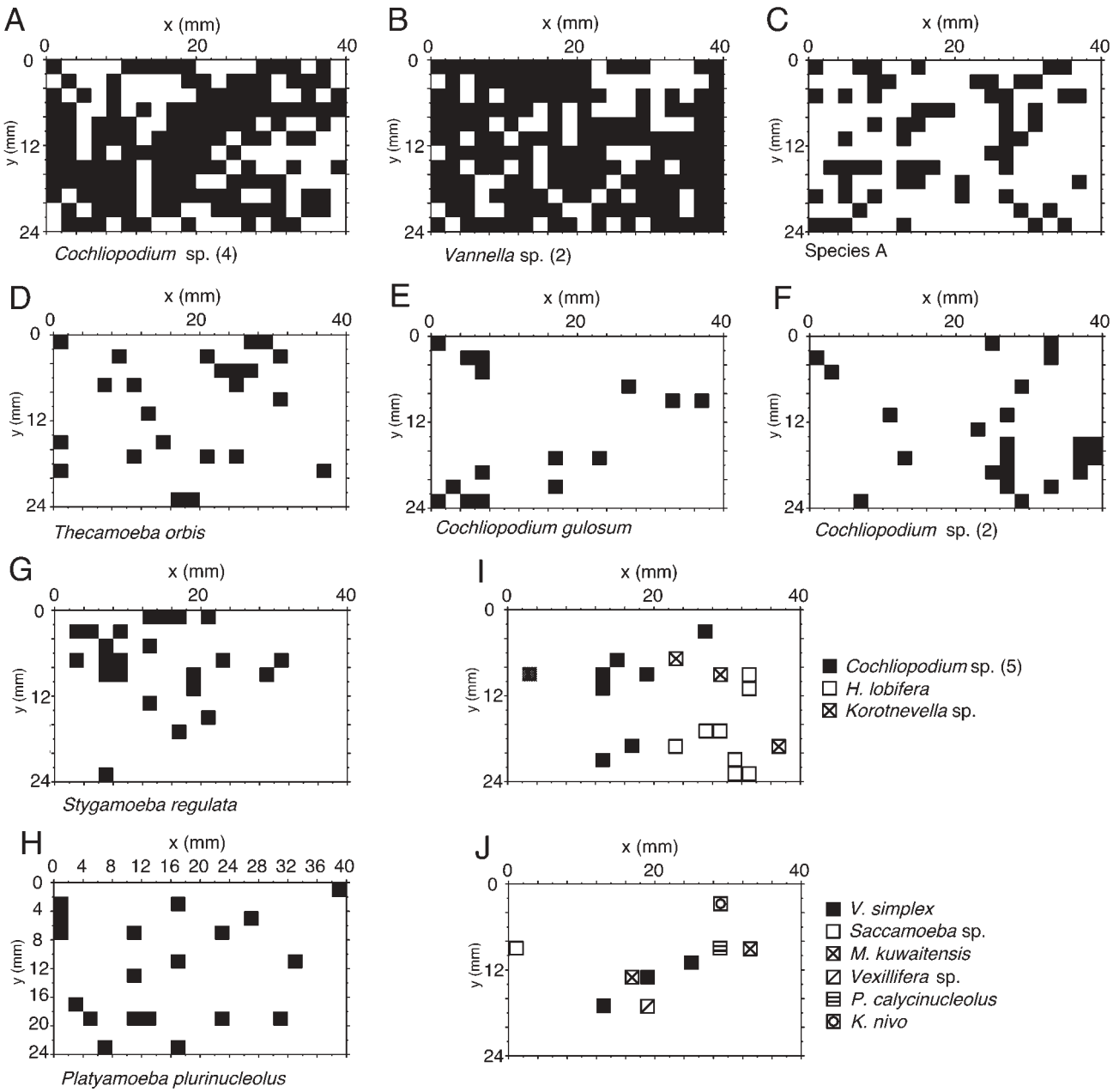

Figure 4. Spatial distribution of amoebae species in the sample. Grid maps with the cell size of 2 × 2 mm.

these species. In the future, it may be possible to estimate the size of microhabitats for different species by varying the scale of the grid in similar experiments. However, we must caution that we work only with a slice, whereas any aggregate has a 3-D structure that is not reflected in our scheme. We should also point out that the rare species might show some distribution pattern at lower resolution (e.g. grid consisting of 5 × 5 mm cells and with a bigger overall area).

Another reason of the occurrence of amoebae aggregates may be the "founder effect". Assuming 7amoebae were for some reason dispersed in the sediment and they then started to multiply, they will form aggregates, originating from a single or a few cells. However, the aggregation at such a local scale caused solely by the "founder effect" can take place either if the motility behavior of amoeba can be neglected or if the random re-dispersal of organisms due to bioturbation is very frequent. The first is not

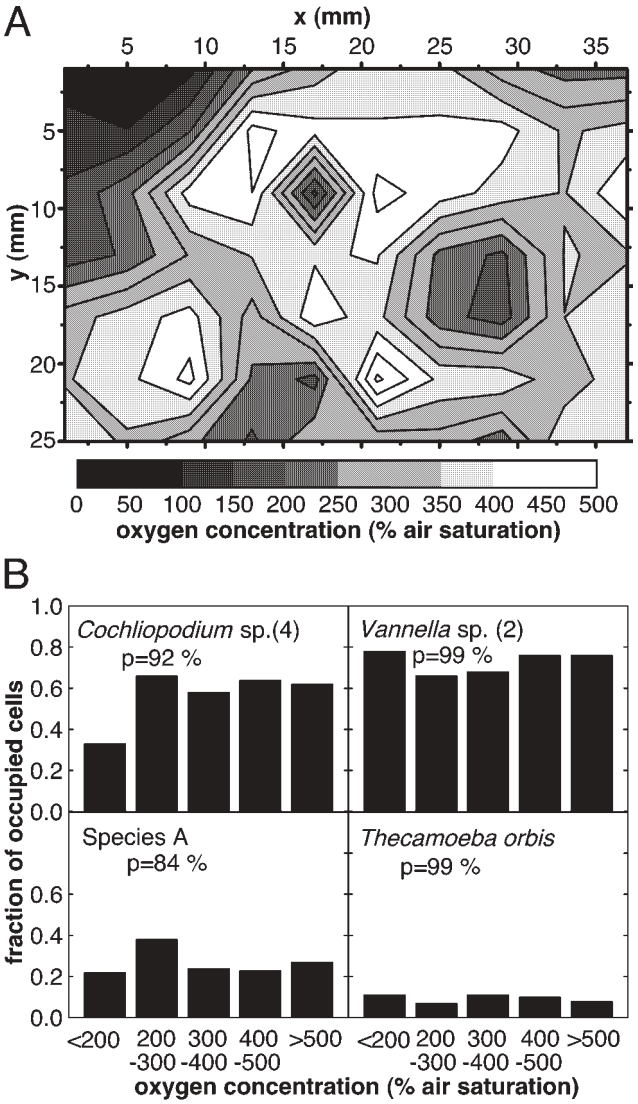

Figure 5. **A**: Actual oxygen concentration in the studied slice of sediments. **B**: Charts showing the number of amoebae found in the cell with given oxygen content. *p* denotes the probability that there is no correlation between the actual oxygen content and amoebae distribution as calculated by the "chi squared" method (Poole 1974).

the case for amoebae that normally move at 10–100 μm s^{-1} (e.g. Bovee and Sawyer 1979, Schaeffer 1926). The latter too, seems to be also not to be true; however, the question requires further studies. If, e.g. *Vannela ebro* is inoculated at a single spot on a sterile sediment surface, like the sand in the aquarium without noticeable water currents, it is able to explore an area of 20 × 30 cm within a week (Smirnov, unpublished observations). Secondly, frequent random re-dispersal due to bioturbation can also be excluded, as the sampled sediments were relatively well-structured. Thus, the observed aggregation patterns must be due to some tactic behavior that is already known for various amoebae species (Grebecki 1980; Grebecki and Wood 1994). *Euhyperamoeba fallax* shows complex feeding and other behavioral patterns that are not yet well understood (Seravin and Goodkov 1987). Altogether, both factors (i.e. both the "founder effect" and the tactic behavior) contribute to the formation of the observed distribution pattern. Perhaps random dispersal (due to wave action, activity of borrowing animals, etc.) is responsible for the occurrence of amoebae in appropriate microhabitats, whereas feeding and sensory behavior leads to the formation and maintenance of aggregates.

Three small species were found to be outstandingly abundant in the present experiment, but there were also very rare small species (Fig. 3). It may mean that perhaps some specific microhabitats are very common and easily reproducible in culture and some are rare in occurrence in our sample, or hardly reproducible in culture. Perhaps this explains why some amoebae species require specific media for lasting maintenance of pure cultures, but may be initially recovered in the most simple media (Page 1988). Probably, a certain number of microhabitats appropriate for such species appear in virtually any medium, and this it allows their recovery. However, continuous maintenance of species in culture requires these microhabitats to be stable and suffi-

Table 2. Results of the statistical test for the distribution pattern using Morisita's index of aggregation (Poole 1974). An index exceeding "1" denotes aggregated distribution; under "1" denotes equally spaced distribution. All species not listed in the table had Morisita's index close to 1.

Species	Morisita's index	Level of confidence	Distribution pattern
Cochliopodium gulosum	1.79	>99.9%	Aggregated
Cochliopodium sp. (2)	1.32	>99.9%	Aggregated
Cochliopodium sp. (5)	1.78	>99.9%	Aggregated
Stygamoeba regulata	1.56	>99.9%	Aggregated
Hartmannella lobifera	2.66	>99.9%	Aggregated
Platyamoeba plurinucleolus	0.72	>99.9%	Equally spaced

ciently abundant, which may be possible only in some specific medium.

Finally, it is possible to mark squares where four or more amoebae species were found (Fig. 6). These areas may be called "hotspots" of the biodiversity. These hotspots may correspond to the microhabitats formed around some "local edificator" (i.e. an object, determining the environmental conditions in its close surrounding) and providing niches for several species.

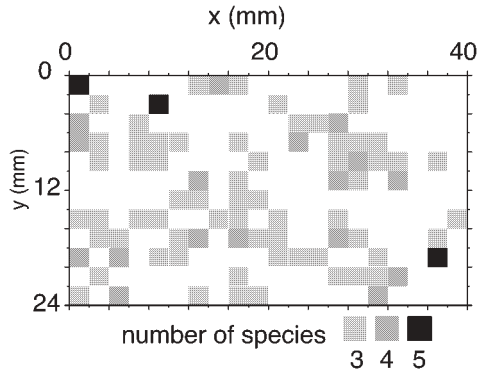

Figure 6. Map showing the "hotspots" of species diversity in the sample.

Methods of Sampling Heterogeneous Distribution of Amoebae

The data obtained on amoebae distribution can be utilized to estimate the probability of undersampling amoebae from the environment. For example, let us consider sampling with a core sampler 15 mm in inner diameter (corresponding to a cut 20 ml syringe). Within the area of 10 cm^2, it can be randomly placed in many ways. Some arbitrary chosen positions are shown in Figure 7A, B. It is evident that there is a likelihood of missing species with abundances of about 12 ml^{-1} and lower, i.e. 9 species from 17 noted in the slice of sediment studied in the present paper. When, sampling with a cut 1 ml syringe (inner diameter about 4.5 mm), it is possible to miss species showing abundances below 34 ml^{-1}, i.e. to recover only 3 species of 17, inhabiting the studied slice of sediments (Fig. 7C, D). These results easily explain the observed heterogeneity in the amoebae vertical distribution noted by Smirnov (2002), and confirm the data on heterogeneous amoebae distribution and aggregation of amoebae observed by Anderson (2002) and Bischoff (2002). The present data once more stress that lasting observation and extensive sampling are required for reliable studies on amoebae biodiversity from a local habitat.

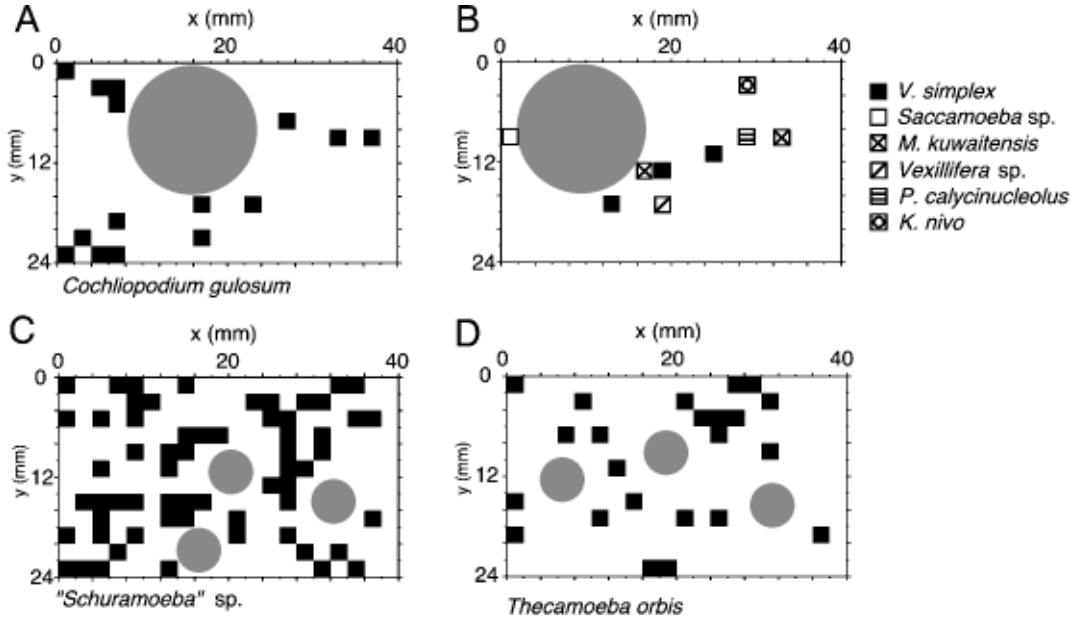

Figure 7. Several maps, showing the high chances to miss certain species during the sampling. **A, B**: Possible sampling with a 20 ml (15 mm inner diameter) syringe may result in missing species existing in less then 12 ml^{-1} in the sediments. **C, D**: Sampling with a 1 ml syringe (4.5 mm inner diameter) may result in missing species existing in less that 34 ml^{-1} in the sediments.

Methods

A core of sandy bottom sediment was collected from the Nivå Bay (15 km South of Helsingør, Denmark) on August, 2002. It was transported to the laboratory in approximately 30 min, mounted into a setup for microelectrode measurements and left to stabilize for 1 h. The sediment surface was illuminated with a fiber-optic halogen lamp (Schott KL2500 LCD, Germany). Illumination intensity and spectral composition were comparable to *in situ* conditions at the sampling site during daytime. To provide continuous mixing of the overlying water in the sediment core, the water surface was gently flushed with an air stream originating from a Pasteur pipette tip. Microelectrode measurements (Clark-type O_2 microsensors with a guard cathode, tip diameter of 10–20 µm, <2% stirring sensitivity) (Revsbech and Jørgensen 1986) of the oxygen profiles were performed using a computer-controlled micromanipulator and data acquisition setup (Unisense, Denmark). Oxygen profiles down to 8 mm depth were collected during 3.5 h on a regular 10 × 7 grid with 4 mm grid spacing; 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 were marked using a self-made frame (Fig. 1A), and the core was gently pushed up until 1–1.5 mm of sediment (the surface of core was not absolutely even) appeared over the edge of the grid. This layer was gently sliced with a scalpel blade and removed to make the surface of the core absolutely flat and smooth. The core was then pushed up for two more millimeters. The position of the frame was restored, and the area exactly corresponding to the region of oxygen measurements was cut with a blade on the top of the core (Fig. 1B, C). Thus, the examined 2 mm thick slice included sediments starting from the depths of 2–3 mm. It was gently sliced off with a blade and placed on the glass slide (Fig. 1D). The slice was further cut into portions for inoculation (Fig. 1E) using always new microscope coverslips to avoid cross-contamination as shown in the scheme (Fig. 1F). Each portion of the slice, representing a cube with approximately 2 mm sides was inoculated into the 60 mm Petri dish. Cubes from two central rows were further cut into four portions each and inoculated into 24-well tissue culture plates (Greiner, bio-one, USA). The inoculation medium was 0.01% filtered Cerophyl infusion in 15 ppt artificial seawater (Weiner, Germany). All cultures of samples were incubated under room temperature. Negative controls were incorporated.

Cultures in 24-well plates were examined at the10th and 20th day of incubation; cultures in 60 mm dishes – at 8–9th and 23–24th days 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). Trivial names were given to isolates that perhaps represent new taxa. Abundance of amoebae was calculated as described by Garstecki and Arndt (2000) using Poisson series (MPN) and Smirnov (2002) to calculate minimal possible number (MPA) of amoebae. 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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