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ORIGINAL PAPER

A rapid response of testate amoebae and vegetation to inundation of a kettle hole mire

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Abstract Our palaeoecological study covers 73 years of history (1929–2002) of a kettle hole peatland inundated by water from a nearby, dammed lake. Testate amoebae, pollen and non-pollen palynomorphs (NPPs) were used to track the shift to wetter conditions in the peatland. Lead-210 was used to try and construct the chronology. We investigated how peatland testate amoebae communities changed since the damming of a nearby river. Furthermore, we evaluated how rapidly local vegetation responded to the increase in wetness, and how vegetation changes correlated with shifts in testate amoebae and NPPs. The Mukrza kettle hole provided palaeoecological

evidence of trophic state and hydrological changes since the lake filled with water in 1929. Three stages of development were revealed. The first two were associated with initial inundation, and the third was related to *Sphagnum* expansion and acidification. Quantitative reconstruction of groundwater level and pH, inferred using testate amoebae, confirmed our hypotheses about changes in hydrology and trophic state. Subfossil desmid remains lend qualitative support to the reconstruction. The ecology of several testate amoeba taxa is discussed in the context of succession and population establishment. There was complete species replacement since the time of inundation. Our investigation has two important applied aspects: (1) it enables prediction of the response of peatlands to a rise in water table on restored sites; and (2) it provides analogues for palaeoclimatological studies. The history of the Mukrza mire is an example of how palaeoecological studies can be used to assess the degree of change in peatlands transformed by human activities.

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Introduction

Testate amoebae are extremely useful in research on the hydrology and palaeohydrology of peatlands (Booth 2007; Charman et al. 2002; Lamentowicz and

Mitchell 2005b; Mitchell et al. 2008a, b). They have been used widely in palaeoecology, often in combination with other environmental proxies such as pollen and plant macrofossils (Blundell et al. 2008; Booth et al. 2008; Charman and Blundell 2007; Escobar et al. 2008; Lamentowicz et al. 2008b; Mitchell et al. 2008a, b; van der Linden et al. 2008). Existing quantitative palaeohydrological reconstructions are based on transfer functions that have been constructed for various regions of the world (Booth et al. 2008; Charman and Blundell 2007; Lamentowicz et al. 2008a; Lamentowicz and Mitchell 2005a; Payne and Mitchell 2007).

Peatland organisms react rapidly to water table increases (Weltzin et al. 2001). Wet shifts have been recognized in many palaeohydrological records across Europe (Amesbury et al. 2008; Hendon et al. 2001; Langdon and Barber 2005; Mauquoy et al. 2002; Roos-Barraclough et al. 2004; Sillasoo et al. 2007; Wilmshurst et al. 2002).

Peatlands are very sensitive to various human activities. Most of the Polish and European peatlands were transformed over the last 300 years (Tobolski 2003). A majority of them were exploited and damaged by human-mediated decreases in the water table (Joosten and Clarke 2002). The most important effect of such changes was associated with lowered water level and increased peat decomposition (Gorham and Rochefort 2003). The acrotelm was artificially deepened, which led to the disappearance of peat-forming plant species (Rydin and Jeglum 2006). Such changes have important implications for carbon turnover, as CO₂ is released to the atmosphere from peatlands that formerly played a role as carbon sinks (Belyea and Malmer 2004; Charman 2002; Laggoun-Défarge et al. 2008). Knowledge of processes in dried and rewetted peatlands is very important to understand wetland ecosystems, and is an important tool in conservation (Heathwaite and Göttlich 1993).

Most palaeoecological records of testate amoebae from peatlands have no associated historical background information. For example, the response of testate amoebae to water table fluctuation has not been tested against known wet shifts triggered by human activities. Hydrological fluctuations in peatlands may be caused by natural (i.e. climatic) phenomena or anthropogenic disturbances (Charman 2002). Palaeoecological data from sites where the timing of the disturbance is well known are particularly useful in that they enable the investigator to evaluate ecosystem

changes in response to a known, dated perturbation. It is then possible to assess how quickly protozoa react to abrupt wet shifts, or adjust to rapidly changing environmental conditions. Historically documented hydrological changes allow us to test transfer functions that employ testate amoebae as hydrologic proxies, and to further evaluate the utility of testate amoebae as environmental indicators.

The aims of this study were: (1) to determine how testate amoebae communities changed since artificial inundation of a peatland, which resulted from damming of a nearby river, (2) to assess how rapidly local vegetation responded to the increase in wetness and how such vegetation changes correlate with shifts in testate amoebae and NPPs, and (3) to evaluate the degree of change in the impacted peatland.

Study site

The study site is located in northern Poland, in the large Tuchola Forest (Bory Tucholskie) (Fig. 1). The forest is dominated by Scots pines (*Pinus sylvestris*) that grow on the outwash plain created during the Pomeranian phase of the last Vistulian (Weichselian) glaciation. The sandy sediment that underlies many lakes and peatlands in the Tuchola Forest is very permeable, so hydrological manipulations may affect them (Kowalewski 2003).

The present plant cover of the peatland is composed mostly of *Sphagnum riparium*, *S. fallax* and *S. fimbriatum*, accompanied by some vascular plants: *Vaccinium oxycoccos*, *Drosera rotundifolia* and *Eriophorum vaginatum*. The peatland margins are dominated by *Calla palustris*, *Typha latifolia*, *Lysimachia vulgaris*, *Juncus effusus*, *Carex rostrata*, *Solanum dulcamara*, and *Thelypteris palustris*. Dwarf pine trees are scattered on the peatland surface, while *Populus tremula*, *Alnus glutinosa* and *Frangula alnus* grow at the edge of the peatland.

The Mukrza kettle hole mire lies in a small (1 ha), but relatively deep basin (>15 m depth). The cross-section (13 cores) shows the site's stratigraphy (Fig. 2). The maximum cored depth was 14.25 m, but did not reach underlying mineral material, which in other cores was composed of sandur sands. In its initial phase, the basin was filled with water, which is documented by the presence of lake sediments. Next, telmatic conditions are recorded by the presence of true mosses (Bryopsida). The central part of the

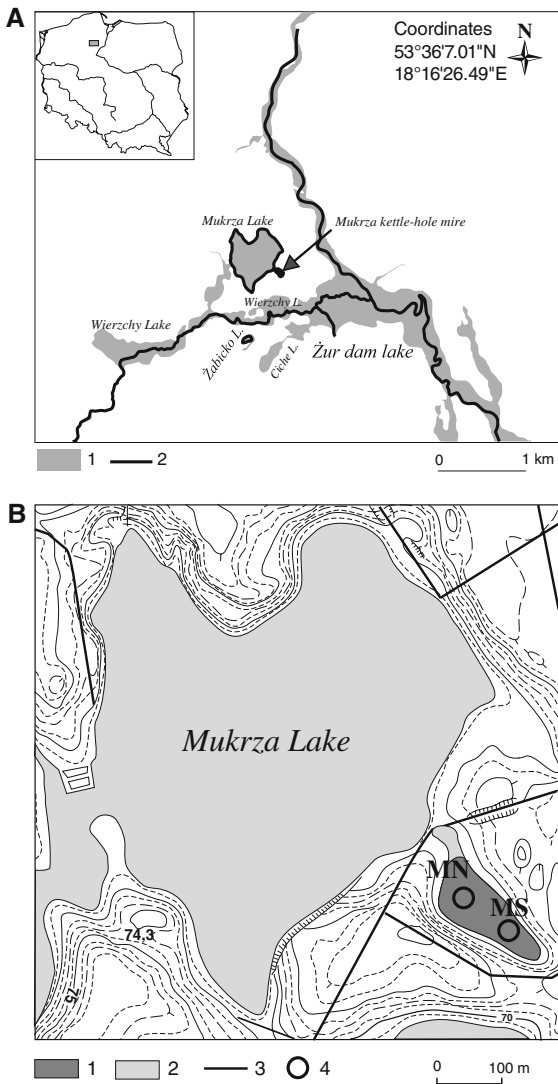


Fig. 1 Location of Mukrza lake. **a** Żur dam lake: 1 open water of Żur dam lake, 2 former river channel. **b** Mukrza lake with studied peatlands: 1 peatland, 2 open water, 3 path, 4 sampling sites

peatland (up to 7 m) is filled with a ‘plug’ composed of peat mosses (*Sphagnopsida*). *Sphagnum* peat does not contact the bottom of the basin, being isolated from it by true moss and herbaceous peat. There is a floating *Sphagnum* mat in the northern part of the mire, which has been disappearing gradually to the south.

Methods

A 50-cm-long core (MS) (Figs. 2, 3) was sampled from the *Sphagnum* mat that floats over the former

surface of the peatland. Seven bulk peat samples were taken for ²¹⁰Pb dating from core MS in 2002. Samples were dried at 105°C and then milled and homogenized. For polonium measurement, 1.2 g of material was used. Activity of ²¹⁰Po was measured by alpha spectrometry and ²¹⁰Pb was estimated from ²¹⁰Po activity, assuming the two radioisotopes were in isotopic equilibrium. The polonium was extracted from the samples with concentrated acids according to Flynn (1968). The CRS (Appleby 2001) model was used for ²¹⁰Pb age calculation. Measurements were carried out at the Institute of Geological Sciences of the Polish Academy of Sciences in Warsaw.

Samples (1 cm³) for pollen analysis were taken every 1 cm. Sample preparation followed standard laboratory protocols (Berglund and Ralska-Jasiewiczowa 1986). Before acetolysis, the peat material was boiled for 10 min in 10% KOH. The residue was then sieved over a 200 μm mesh. Pollen of trees and shrubs (arboreal pollen, AP) was counted to a total of 500, at 400× magnification. Pollen of aquatic and telmatic plants was excluded from the percentage calculation. Non-pollen palynomorphs (NPPs) *Pediastrum*, *Botryococcus*, *Coelastrum*, *Tetraedron* and *Scenedesmus*, spines of *Utricularia*, and charcoal were also counted. The identification of spores was based on the available literature (Erdtman et al. 1961; Faegri and Iversen 1989; Jankovská and Komárek 2000; Komárek and Jankovská 2001; Moore et al. 1991).

Samples for analysis of testate amoebae and other NPPs were taken at 2-cm intervals. Samples were prepared according to the sieving and back-sieving procedure described by Hendon and Charman (1997). Testate amoebae were identified and counted to a total of 150 individuals per sample at a magnification of 200–400×. Identification was based on the available literature (Charman et al. 2000; Clarke 2003; Groszpietsch 1958; Ogden and Hedley 1980).

To reconstruct quantitatively the water table depth and pH in the mire, we applied a training set consisting of 123 surface samples taken from natural *Sphagnum* mires in Pomerania (Lamentowicz et al. 2008c). The CANOCO program (ter Braak and Šmilauer 1998) was used for ordination analysis of the fossil testate amoebae data. Detrended correspondence analysis with square-root transformation was applied to visualize better the shift in testate amoebae communities. Other statistics were calculated in R-package (R Development Core Team 2006).

Fig. 2 Geological profile of Mukrza kettle-hole mire. MS—monolith described for this study

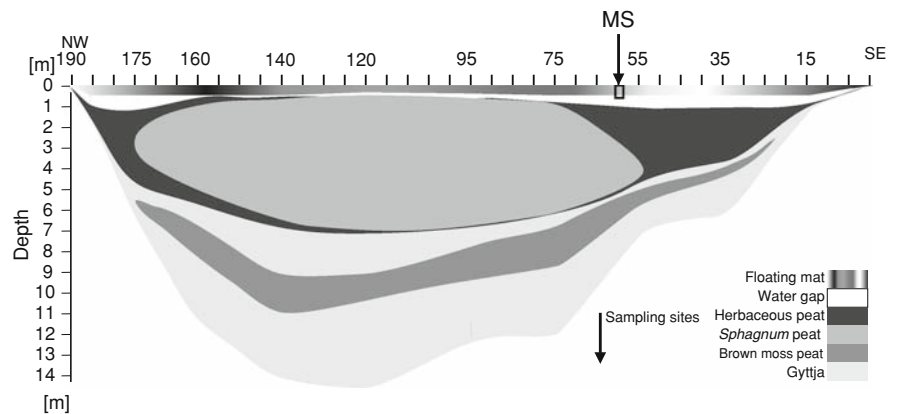
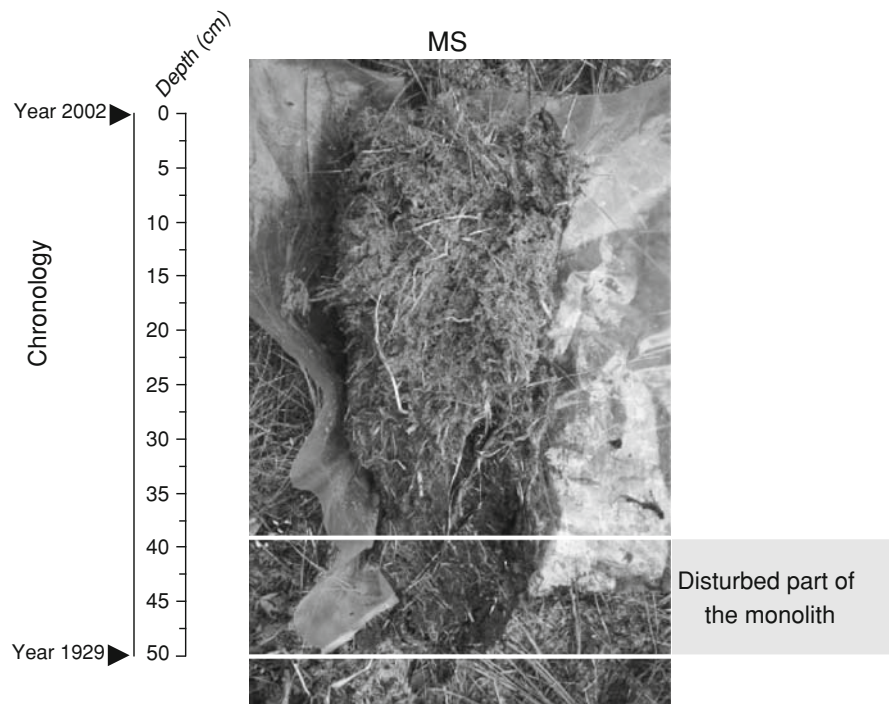


Fig. 3 Peat monolith MS sampled for the study



Stratigraphic diagrams were generated with Tilia Graph (Grimm 1992) and C2 (Juggins 2003). Zonation was constructed with the CONISS program (Grimm 1987) included in the Tilia-Graph package.

Results

Chronology

Lead-210 results from core MS displayed a non-monotonic decline in activity with depth, and large

uncertainties (Table 1). Consequently, the data were not used to develop a core chronology. Lead dating of recent peat has been described in the literature (e.g. Appleby et al. 1997; Shoty et al. 1996; Turetsky et al. 2004), but can be difficult or impossible (Payne and Pates 2009), especially if the peat has been disturbed. Dating problems may also occur if groundwater levels cause movement of the lead isotopes in peat profiles. This is the most probable explanation in Mukrza because samples from another core from this peatland, analysed the same way, provided satisfactory results. Because we were unable to construct an age-depth

Table 1 Results of lead dating of MS monolith

Depth [cm]	Activity (Bq/g)	Error (Bq/g)	Age ²¹⁰ Pb (years)	Error (years)
1	0.28	0.01	0	1.8
5	0.19	0.007	14	3
15	0.128	0.005	40	10
19	0.12	0.008	50	20
23	0.0966	0.0057	40	40
29	0.10	0.004	75	45
35	0.073	0.005	75	80

model for the core, we relied on two horizons of known age for dating, 1929, when the Wda River was dammed, and 2002, the date the core was collected.

Pollen and non-pollen palynomorphs (NPPs)

Domination of *Pinus* (up to 75%) pollen with a very low percentage of other tree taxa was typical for the MS core (Fig. 4). Pollen zones were determined as follows:

M-po-1 (50–38 cm)

This zone is characterized by a very high percentage of herbaceous plants (20%), including cereals (5%). *Utricularia* (represented by pollen or spines), *Potamogeton*, and *Lemna*. Cyperaceae, *Carex* type, *Typha latifolia* achieve the highest percentage among telmatophytes. *Sparganium* sp. and *Calla palustris* occur in small numbers.

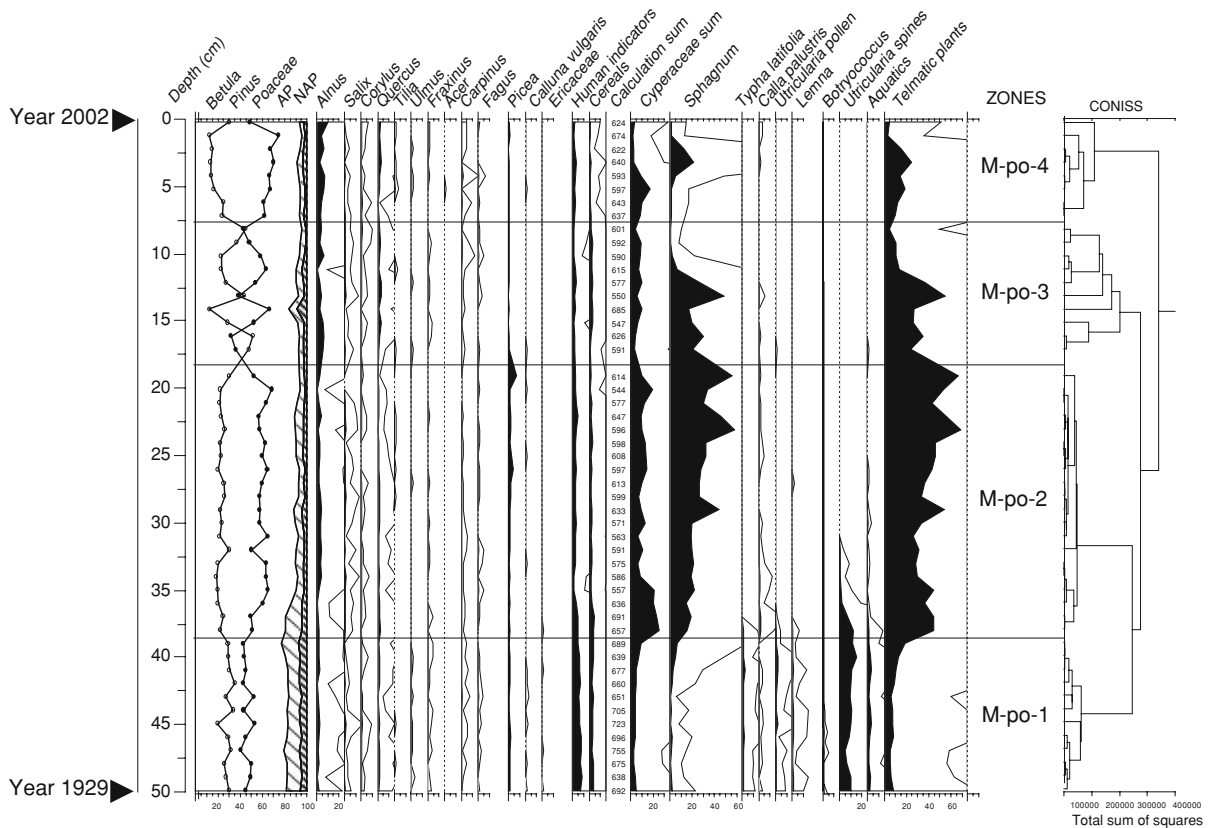


Fig. 4 Pollen percentage diagram with zonation

well known (Mitchell et al. 2008a, b). Chironomidae remains are recorded in this zone. The desmids *Cosmarium*, *Pleurotaenium* and *Euastrum*, very rare in the Quaternary deposits, reveal very wet conditions. Presence of mineral particles reflects soil erosion. The distance to water table (DWT) remains at 0 cm, which explains the presence of open-water indicators.

M-ta-2 (36–21 cm)

Chironomidae and diatoms are not present in this zone. *Pleurotaenium* is still present at the bottom of the zone, whereas *Cosmarium* and *Euastrum* are recorded throughout the zone. Mineral material is still present. *Diffflugia rubescens* and *Centropyxis aculeata* decline abruptly between 37 and 32 cm. Initially present in low percentages, *Nebela tincta* appears. *Cyclopyxis arcelloides*, *Hyalosphenia papilio* and *Assulina muscorum* suggest terrestrial and acidic conditions. Inferred pH decreases abruptly from 6 to about 4. *Sphagnum* remains are more common.

M-ta-3 (21–12 cm)

Testate amoebae (*Arcella catinus*, *Assulina muscorum*) indicate a gradual water table decrease. Increased percentage of *Centropyxis aculeata* suggests slight eutrophication. There are no desmids, diatoms or mineral particles in this zone.

M-ta-4 (12–0 cm)

Ground water gradually decreases to a maximum of 17.9 cm, indicated by a testate amoebae community dominated by *Assulina seminulum*, *Nebela militaris*, and *Physochila (Nebela) griseola*. *Hyalosphenia papilio* is a dominant taxon. Inferred pH varies around 4.

Ordination

Detrended correspondence analysis also confirmed the above-described zones that characterize the testate amoebae communities. Axis 1 represents moisture and trophic state. Reconstructed values of DWT and pH are correlated (Fig. 7), therefore the first axis of DCA might be interpreted as the gradient of wetness and trophic state. The line linking the samples (Fig. 6a) shows a path of succession linking

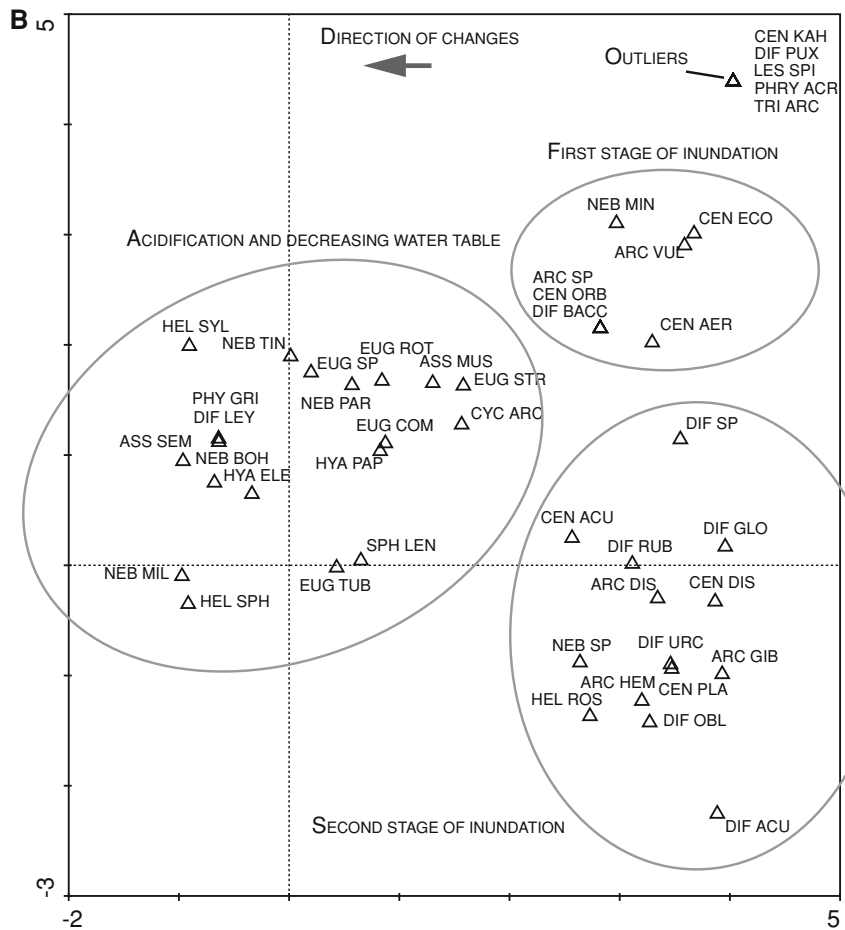
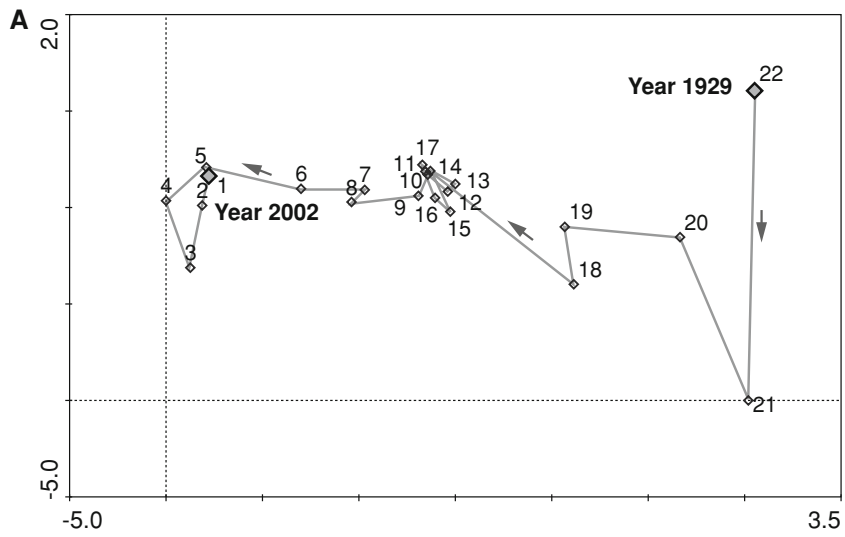
the particular assemblages. The DCA plot shows a complete replacement of species over time. Species structure in Fig. 6b shows testate amoebae that are wet indicators on the right side of the diagram, and dry indicators on the left side. The transition along the gradient is rather gradual. Sample 22 included an unusual species assemblage (*Diffflugia pulex*, *Phryganella acropodia* and *Trigonopyxis arcula*), probably transported from the former peatland surface, and was interpreted as an outlier. *Lesquereusia spiralis* is the taxon that is indicative of a flooded peatland surface. Two stages of the inundation are visible. The first one is represented by such taxa as *Arcella vulgaris* and *Centropyxis ecornis*, and the second consists of telmatic indicators like *Diffflugia rubescens* and *D. urceolata*. An assemblage dominated by *Hyalosphenia papilio* and *Assulina muscorum*, representing acidification and a decreasing trend in water table level, is well separated in the DCA plot.

Discussion

The present Mukrza peatland is an example of a peat-forming environment created by human activities. Our intention was to assess how the peatland responded to the well-known shift to wetter conditions caused by the Wda River damming. Artificial inundation led to a stable groundwater level, sustained by the Żur dam. This provided a unique opportunity to understand the local succession pattern under stable hydrological conditions. The material from Mukrza is exceptional because the exact time of the hydrologic change is known. The result of damming is even visible in the geological cross-section in the form of a ‘new’ peat stratum that formed over the former peatland surface (Fig. 2). Our detailed palaeoenvironmental study provides precise information about the pattern and timing of changes that took place from 1929 to 2002.

Pattern and timing of changes

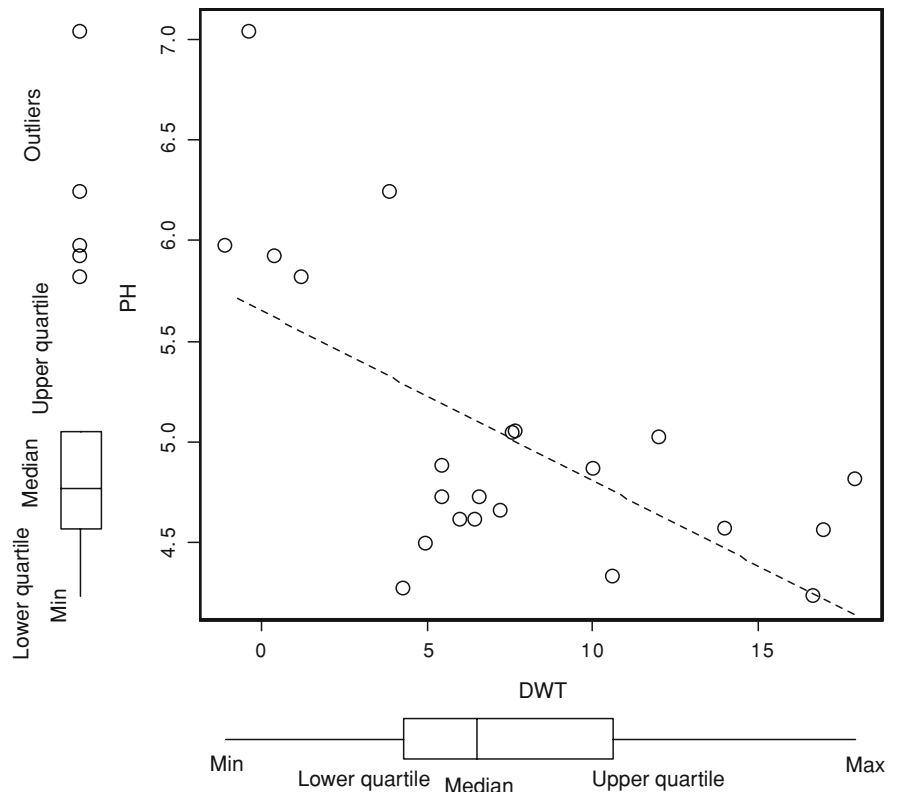
We reconstructed the complete hydrosere development that occurred under artificially wet conditions over 73 years. As much as 50 cm of peat accumulated since the dam was constructed, indicating the mean peat accumulation rate was very high (6.8 mm a^{-1}).



◀ **Fig. 6** Detrended correspondence analysis (DCA) plot. **a** samples: grey line follows the samples from the bottom to top of the monolith, grey arrows show direction of changes; **b** species: particular stages of the succession are marked, grey arrow shows direction of changes. Explanation of species names: ARC CAT *Arcella catinus*, ARC DIS *A. discoides*, ARC GIB *A. gibbosa*, ARC HEM *A. hemispherica*, ARC SP *A. sp.*, ARC VUL *A. vulgaris*, ASS MUS *Assulina muscorum*, ASS SEM *A. seminulum*, CEN ACU *Centropyxis aculeata*, CEN AER *C. aerophila*, CEN DIS *C. discoides*, CEN ECO *C. ecornic*, CEN KAH *C. kahlii*, CEN PLA *C. platystoma*, CEN ORB *C. orbicularis*, CYC ARC *Cyclopyxis arcelloides*, DIF ACU *Diffflugia acuminata*, DIF BACC *D. baccilifera*, DIF GLO *D. globulosa*, DIF LEY *D. leidyi*, DIF OBL *D. oblonga*, DIF PUX *D. pulex*, DIF RUB *D. rubescens*, DIF URC *D. urceolata*, DIF SP *D. sp.*, EUG COM *Euglypha compressa*, EUG ROT *E. rotunda*, EUG SP *E. sp.*, EUG STR *E. strigosa*, EUG TUB *E. tuberculata*, HEL ROS *Heleopera rosea*, HEL SPH *H. sphagnii*, HEL SYL *H. sylvatica*, HYA ELE *Hyalosphenia elegans*, HYA PAP *H. papilio*, LES SPI *Lesquereusia spiralis*, NEB BOH *Nebela bohemica*, NEB MIL *N. militaris*, NEB MIN *N. minor*, NEB PAR *N. parvula*, NEB SP *N. sp.*, NEB TIN *N. tincta*, PHY GRI *Physochila (Nebela) griseola*, PHRY ACR *Phryganella acropodia*, SPH LEN *Sphenoderia lenta*, TRI ARC *Trigonopyxis arcuata*

Both local vegetation and protozoa responded very rapidly to the inundation. Protozoa (testate amoebae), however, better reflect the particular stages of floating mat development. The bottom 10 cm was part of the floating mat, immersed in the water gap. Surprisingly, desmids were very well preserved. Aquatic and telmatic vegetation disappeared along with *Sphagnum* expansion. However, desmids existed up to 22 cm, indicating a very high water table. Testate amoebae communities tracked this rapid shift well, with a change from a *Centropyxis aculeata*-*Diffflugia rubescens* community to a *Cyclopyxis arcelloides*-*Hyalosphenia papilio* assemblage. Zone Ma-ta-3 represents a stable pH and DWT. The DWT and pH values inferred from testate amoebae are negatively correlated (Fig. 7), which suggests some minerotrophic influence, probably groundwater input. The Mukrza peatland records acidification above 36 cm, and it can be classified as a poor fen on the basis of vegetation and pH. The last stage (zone MA-ta-4) is associated with a lower water table, indicated by “dry” indicators such as *Nebela militaris*, *Nebela*

Fig. 7 Scatter plot of pH versus DWT with box plots characterizing each axis



tincta and *Assulina seminulum*. Such a sequence of changes was also observed in another study from the Tuchola Forest (Lamentowicz et al. 2007).

Palaeoecology and succession

Testate amoebae are increasingly used in palaeoenvironmental studies of peatlands (Mitchell et al. 2008a, b). However, we still do not know exactly how rapidly new communities are established in newly created habitats (Wanner et al. 2008). In the case of the Mukrza mire, a complete environmental change occurred within 1 year after the dammed lake filled with water. Records from Mukrza can be seen as an example of a wet shift under simplified, anthropogenic conditions.

Hydrological conditions in European peatlands are dependent on precipitation and temperature, which influence evapotranspiration (Charman 2002). Reconstruction of the above-mentioned climatic variables is therefore very difficult. Using subfossil testate amoebae, we were able to reconstruct a water table deficit during the growing season (Charman 2007). In the case of Mukrza, we are certain that the water table was influenced by the reservoir and that peatland vegetation changes are anthropogenic. For that reason, we were able to observe how the testate amoebae community gradually adjusted to the habitat. Such a pattern was also observed in long, Holocene records in which kettle holes became peatlands. Once a peatland reaches the terrestrialization threshold, it may become sensitive to climatic change. The decrease in the water table in Mukrza in recent times (MA-ta-4) might be related to climatic change. Because this peatland is not ombrotrophic, changes may be caused by alterations in local hydrology. More records from several sites in the region are needed to test this notion. There are, however, examples of minerotrophic peatlands that are sensitive to climatic changes (Booth et al. 2004).

We established the indicator status of some testate amoebae species that had been previously recorded in peats, for instance, *Diffflugia urceolata*, which was regarded as an indicator of flooding and eutrophication in a kettle hole mire in the Tuchola Forest (Lamentowicz et al. 2008c). In the Mukrza peatland, this species occurred in the first stage of inundation (Fig. 5, M-ta-1). This record supports our assumptions about the ecology of this species. *Arcella*

discooides is another intriguing taxon recorded in this study. It is usually regarded as a wet indicator. However, it is also found together with dry indicators in peatland palaeoecological studies (Blundell and Barber 2005; van der Linden et al. 2008). Lamentowicz et al. (2009) suggested that it should be regarded as a sign of disturbance and hydrological instability, as it rapidly colonizes new environments. In the Mukrza profile, it occurred only at the beginning of the flooding. This record also supports our former observations (Lamentowicz et al. 2009). Nevertheless, *A. discooides* may have a different ecological tolerance in other geographic locations. The lack of *Archerella flavum* in the Mukrza peat archive is surprising. In northern and western Poland, *A. flavum* occurs mainly in wet and acid *Sphagnum*. Considering other published peat profiles (Lamentowicz et al. 2008b, 2009), we can assume that *A. flavum* needs very oligotrophic and stable hydrological conditions. Protists are distributed mainly via wind, waterfowl, and other migrating animals (Weisse 2008). *A. flavum* had >50 years to immigrate into the newly created *Sphagnum* carpet. A possible explanation for its absence could be a complete lack of populations in the vicinity of the peatland.

Peatland management and human impact

The damming of a river may lead to various effects in its catchment. A GIS study by Kowalewski (2001) showed that the building of the Koronowski Reservoir resulted in similar processes as those observed in our study. That reservoir was created in 1960. It is located in a similar sandy outwash plain. Kowalewski's research was based on aerial photographs and cartographic materials collected over time. He observed many hydrological consequences of the damming: (1) appearance of new water bodies and wetlands (resulting from paludification), (2) a rise in the water level of existing lakes, and (3) flooding of existing peatlands and their replacement by new water bodies. Such flooding was also observed in this study. Another effect described by Kowalewski was separation of the floating mats that previously were attached to the lakeshore. A similar process was observed around the Żur dam lake. The Żabicko kettle-hole lake (Fig. 1), located south of the Mukrza mire, has detached floating mats similar to those in the Koronowski Reservoir. We conclude that the same patterns

probably occurred in areas adjacent to the Koronowski and Żur reservoirs. Unfortunately, no palaeoecological study has yet been done near the Koronowski Reservoir for comparison with our study. We found no similar study done anywhere in the world.

The pattern of succession in the Mukrza mire can be a useful reference for rewetted *Sphagnum* mires, where processes of peat accumulation re-appear. We obtained data on a recent disturbance that led to a positive effect on peat accumulation. However, the present condition cannot be regarded as the pristine state of the peatland. The pattern of changes in testate amoebae might be useful to assess the results of restoration in cut-over peatlands (Mitchell et al. 2008a, b). Our data might be used to define a stable testate amoebae community in *Sphagnum*. Analysis of testate amoebae seems to be a good alternative approach for assessing restoration processes, in contrast to labour-intensive, repeated field measurements (Laggoun-Défarge et al. 2008). Short-core studies, covering the last 50–100 years, on restored sites might be key for choosing the best strategy for conservation or restoration efforts. In peatland ecology, an historical perspective on the present protozoan communities may help to predict their future stability.

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