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Dystrophication of lake Suchar IV (NE Poland): an alternative way of lake development

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ABSTRACT

Dystrophication of lake Suchar IV (NE Poland): an alternative way of lake development

The long-term dynamics of a lake development and the role of the catchment and climate change in the dystrophication process were studied. Lacustrine sediments from Lake Suchar IV, NE Poland (880 cm long core), were selected for paleolimnological studies. The paleoecological reconstruction was based on pollen, subfossil cladocerans, diatoms, macrofossils and chemical analyses. Sediment chronology was based on the results of ^{14}C dating and palynological analysis. The obtained data showed that the lacustrine sedimentation at Lake Suchar IV began in the Late Glacial and continues to this day. The plant succession indicates that sedimentation processes started as early as the Oldest Dryas ~ over 15 000 cal yr BP ago. Important changes in the pollen spectrum of aquatic plants were noted from the mid-Atlantic period. At that time, communities of *Nymphaea* and most species of green algae disappeared from the lake, which indicates a significant ecological transformation in the aquatic environment. This transformation is also manifested in the subfossil Cladocera and diatom communities. The Cladocera community in the sediments of Lake Suchar IV was represented by 37 species, mostly littoral ones. From the transition time (7200–5600 cal yr BP), Cladocera communities were dominated by taxa tolerant of acidification such as *Alonella excisa*, *Acroperus harpae*, *Alona affinis* and *Alonella nana*. A total of 193 diatom taxa (species and varieties) were identified in the sediment, including 172 belonging to *Pennales* and 21 to *Centrales*. In general, the diatom community was dominated by alkaliphilous – on average 45 % of the species composition. In terms of trophic preferences, the largest group of diatoms was represented by oligotraphentic, meso-eutraphentic and eutraphentic taxa. No diatoms were present during about 6000 cal yr BP from the transition stage. Sediment geochemistry and macrofossils also indicate the limnological development and climate trends.

The obtained paleolimnological results indicate that Lake Suchar IV has undergone an ecological transformation from a harmonic to disharmonious ecosystem. During the Late Glacial and the early Holocene, Lake Suchar IV was a typical harmonic lake that transformed into a dystrophic state at the end of the Atlantic period. Sediments of Lake Suchar IV also show a very interesting sequence of trophic changes, from oligotrophic to mesotrophic and to dystrophic conditions.

Key words: Suchar IV, Lake history, Dystrophy, Harmonic/disharmonic state, Paleolimnology studies, Wigry National Park, NE Poland

RESUMEN

Distrofización del lago Suchar IV (NE Polonia): Un camino alternativo del desarrollo de un lago

Se estudiaron la dinámica a largo plazo del desarrollo del lago y el papel de la cuenca de captación y el cambio climático en el proceso de distrofia. Se realizó un análisis paleolimnológico de los sedimentos del lago Suchar IV, NE Polonia (core de 880 cm de largo). La reconstrucción paleoecológica se basó en el análisis del polen, los cladóceros subfósiles, las diatomeas, los macrofósiles y el análisis químico. La cronología de los sedimentos se basó en los resultados de la datación de ^{14}C *y el análisis palinológico. Los datos obtenidos mostraron que la sedimentación lacustre en el lago Suchar IV comenzó en el período Glacial tardío y continúa hasta ahora. La sucesión de plantas indica que los procesos de sedimentación comenzaron hace 15 000 cal años AP en el periodo Dryas primitivo. Se observaron cambios importantes en el espectro del polen de las plantas acuáticas a partir del período Atlántico Medio. En ese momento, las comunidades de* Nymphaea *y la mayoría de las especies de algas verdes desaparecieron del lago, lo que indica una transformación ecológica significativa en el medio acuático. Esta transformación también se manifiesta en las comunidades de cladóceros subfósiles y en las diatomeas. La comunidad de cladóceros en los sedimentos del lago Suchar IV estuvo representada por 37 especies, en su mayoría litorales. A partir del tiempo de transición (7200-5600 años cal BP), las comunidades de cladóceros estuvieron dominadas por taxones tolerantes a la acidificación como* Alonella excisa*,* Acroperus harpae*,* Alona affinis *y* Alonella nana*. Se identificaron un total de 193 taxones de diatomeas (especies y variedades) en el sedimento, incluyendo 172 pertenecientes a Pennales y 21 a Centrales. En general, la comunidad de diatomeas estaba dominada por especies alcalófilas, en promedio el 45 % de la composición de las especies. En términos de preferencias tróficas, el grupo más abundante de diatomeas estaba representado por taxones* oligotrafénticos, meso-eutrafénticos *y* eutrafénticos*. No se encontraron diatomeas durante 6000 años cal BP desde la etapa de transición. La geoquímica de los sedimentos y los macrofósiles también indican el desarrollo limnológico y las tendencias climáticas.*
Los resultados paleolimnológicos obtenidos indican que el lago Suchar IV ha sufrido una transformación ecológica de un ecosistema armónico a uno disarmónico. Durante el Glaciar Tardío y el Holoceno temprano, el lago Suchar IV era un lago armónico típico que se transformó en un estado distrófico al final del período Atlántico. Los sedimentos del lago Suchar IV también muestran una secuencia muy interesante de cambios tróficos, desde condiciones oligotróficas a mesotróficas y distróficas.

Palabras clave: *Suchar IV, historia lacustre, distrofia, estado armónico y disarmónico, estudios paleolimnológicos, Parque Nacional Wigry, NE Polonia*

INTRODUCTION

At the middle and upper attitudes of the northern hemisphere (North America, Europe, Asia), a large number of lakes can be found in areas that were covered by ice during the Last Glaciation (Vistulian, Würm, Wisconsin). Over time, from the deglaciation to modern times, these lakes have witnessed environmental and climatic changes (Smol, 1992; Kernan *et al.*, 2009). Thus, sediments that are progressively deposited in lakes by diverse agents are a natural archive of the changes occurring at regional and local geographic scales (Smol, 2002; Rosen *et al.*, 2009). Given continuous sediment deposition through time, the composition of lake sediments reflects the regional climatic history, and also more local factors such as human activities (Battarbe & Benion, 2012). In areas where human activities have been absent or of limited extent (e.g. Scandinavia, Poland, Russia, Canada), lake sediments reflect an environmental history that can be almost entirely attributable to natural variability (Bos & Cumming, 2003; Luoto *et al.*, 2012; Korosi & Smol, 2012; Zawisza *et al.*, 2016). In NE Poland, a region characterized by low human population densities, lake sediments represent archives of the natural climatic and ecological conditions that have prevailed through the last several thousand years. Numerous paleolimnological studies from the region (e.g. lakes: Wigry (Zawisza & Szeroczyńska, 2007), Linówek (Gałka *et al.*, 2014), Romoty (Mirosław-Grabowska *et al.*, 2015), Suchar II (Drzymulska *et al.*, 2014), Czarne Lake (Karpińska – Kolaczek *et al.*, 2016) and from Central and Northern Europe e.g. Arapisto (Luoto *et al.*, 2012); Abisko (Bigler *et al.*, 2002); Tsulbmajarvi (Seppä & Wechström, 1999) have shown that lakes have mostly developed under natural climatic regimes, and only the youngest sediments (from the Middle Ages or industrial revolution) have been affected by human activities (Korsman *et al.*, 1994; Ott *et al.*, 2017).

Paleolimnological reconstructions of the lakes that formed during the Last Glaciation in the area of N Poland usually shows typical harmonic development (Kajak, 1998; Kupryjanowicz, 2007; Zawisza & Szeroczyńska, 2007), represented by one of the following steps of the lake successions: (1) from oligotrophy through mesotrophy to eutrophy and encroachment of vegetation or transformation to peat bogs; (2) from oligotrophy to dystrophy; and (3) from oligotrophy to a lake overgrown with vegetation. These harmonic changes are reflected in the composition of flora and fauna and in the chemical composition of lake deposits, reflecting ecological and climatic changes that occurred during the Late Glacial and the Holocene. Contrary to harmonic lakes, disharmonic lakes (e.g. lobelia and polyhumic lakes) are oligotrophic from their origin, with high limitation of Ca^{+2} ions, and are later transformed into polyhumic and/or dystrophic due to high allochtonous organic matter input (Sobek *et al.*, 2007; Rosen *et al.*, 2009; Weyhenmeyer & Karlsson, 2009). Although the definition of dystrophy is still unclear and the process of dystrophication is not well understood, paleolimnological studies of these lakes enable us to follow and reconstruct the natural dystrophication process. Very low primary production based on the allochthonous matter is a characteristic feature of dystrophic (polyhumic) lakes, with the water characterized by high contents of Total Organic Carbon (TOC), which distinguishes them from oligotrophic lakes (Hessen, 1992; Kulberg *et al.*, 1993; Porcal *et al.*, 2009).

Dystrophic lakes in the Central European Lowlands are usually considered natural relicts of past environmental conditions. Therefore, these humic lakes are believed to have undergone minor changes over the last thousand years (Górniak, 1996; Drzymuska *et al.*, 2013). Indeed, because of their extraordinary nature, dystrophic lakes are protected by national and international laws (e.g. EU Habitat Directive) as National Parks, Nature Reserves, or Natura 2000 sites. Nevertheless, some studies have demonstrated

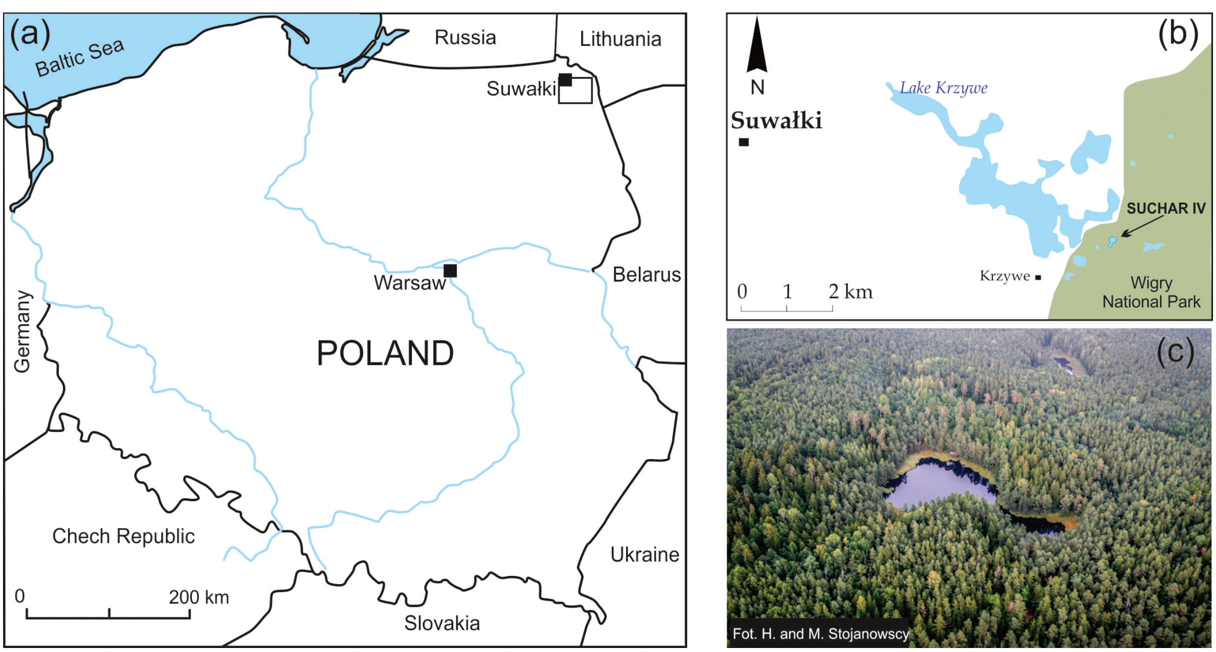

Figure 1. Location map of Lake Suchar IV: (a) location in Poland; (b) location of Lake Suchar IV in Suwalki region, green colour on the map indicated area of Wigry National Park; (c) photography of Lake Suchar IV surrounded by *Pinus* forest (photo by www.sudawcy.blogspot.com). *Mapa de la localización del Lago Suchar IV: (a) localización en Polonia; (b) Localización del lago Suchar IV en la región de Suwalki; el color verde en el mapa indica el Parque Nacional Wigry; (c) fotografía del lago Suchar IV rodeado por un bosque de* Pinus *(fotografía por www.sudawcy.blogspot.com).*

that even dystrophic lakes can shift from dystrophy to eutrophy because of anthropogenic nutrients input (Zawiska *et al.*, 2013; Drzymulska *et al.*, 2014; Rantala *et al.*, 2015). Regional climate changes derived from global human activities represent an additional threat to these unique ecosystems (Curtis, 1998).

The main objective of this study was to determine whether dystrophic lakes are hyper-stable ecosystems. We use a continuous sediment sequence from Lake Suchar IV (NE Poland) covering from the Oldest Dryas to present to study the stability of the lake, aiming to find out if its dystrophic state is derived from climate changes during the Late Glacial and the Holocene. Thus, our study sheds light on the nature of the dystrophication process reconstructing at the same time the changes experience by the local and regional flora and fauna. A natural byproduct of this study is therefore the description of the typical flora and fauna association of dystrophic environments.

MATERIAL AND METHODS

Study site

Lake Suchar IV is located in NE Poland, in the area of Wigry National Park (Fig. 1), at an altitude of 155 m a.s.l. Wigry National Park is situated in the range of the Pomeranian Phase of

Table 1. ^{14}C dates from Lake Suchar IV sediments, bls - below lake surface. Age years cal BP determined by program online CalPal (http://www.calpal-online.de). *Fechas* ^{14}*C procedentes de los sedimentos del lago Sucher IV, bls – por debajo de la superficie del lago. Edad en años* cal BP *determinados con el programa* CalPal *(http://www.calpal-online.de).*

samples number	depth (cm bls)	type of dating	laboratory number	^{14}C yr BP	age cal yr BP
1	860-865	conv.	MKL-1190	3250 ± 80	3493 ± 85
2	947.5-952.5	conv.	MKL-1191	3405 ± 70	3772 ± 98
3	1145-1050	conv.	MKL-1192	4750 ± 70	5767 ± 99
4	1160-1165	conv.	MKL-1193	5370 ± 85	6046 ± 109
5	1275-1280	conv.	MKL-1194	7920 ± 70	8795 ± 134
6	1335-1340	conv.	MKL-1196	8890 ± 90	9976 ± 161
7	1380-1385	conv.	MKL-1197	8980 ± 110	10065 ± 154
8	1425-1430	conv.	MKL-1201	9480 ± 100	10826 ± 199
9	1470-1475	conv.	MKL-1202	10820 ± 110	12213 ± 108
10	1535	AMS	Poz-46264	12150 ± 80	13526 ± 245
11	1545	AMS	Poz-46268	12150 ± 60	13788 ± 236
12	1560	AMS	Poz-46265	11880 ± 70	13998 ± 150
13	1620	AMS	Poz-46267	12580 ± 70	14928 ± 301

the Last Glaciation – Weichselian (Marks, 2002), within the Lithuanian Lakeland region (Kondracki, 1994). Within the Polish lowlands, the NE region represents the most severe climatic regime with a mean annual air temperature and precipitation of 5.3 °C and 593 mm, respectively (Grabowska-Bajkiewicz, 1997). The winter lasts about four and a half months, with a mean temperature ranging from -6.7 to -2.7 °C, and the ice cover lasting approximately 3 months, from the end of December until the end of March. The vegetation resembles the boreal zone and is characterized by coniferous forests with a growing season of approximately 190 days per year (Grabowska-Bajkiewicz, 1997).

With a kettle shape, Lake Suchar IV is a small water body (approximate area of 0.95 ha and z_{max} of 8.0 m) of glacial origin (Górniak, 2006). With a dystrophy index (HDI) of 104.2 (Górniak, 2006), one of the highest for the Polish area, Lake Suchar IV represents a clear example of dystrophic lake. The water pH is around 4.6, conductivity is 27 µS/cm, and dissolved oxygen is 12.0 mg/L. The entire catchment of the lake is occupied by coniferous forests. The shoreline is overgrown with floating vegetation mats, composed mostly of *Vaccinio uliginosi-Pinetum* and *Sphagno girgensohnii-Piceetum* (Górniak, 2006; Zawiska *et al.*, 2013).

Sampling

In summer 2010, an 855-cm-long sediment core was retrieved from Lake Suchar IV, using a Livingstone-type corer from the deepest part of the lake (54° 05' 23" N 23° 01' 30" E, water depth ~8.0 m). After coring, the core was packed and transported to the laboratory for a lithological description and sediment subsampling at 5-to-10-cm intervals. Subsamples were taken for pollen, subfossil cladocerans, diatoms, macrofossils and basic geochemistry.

Chronology

The chronology was constructed using thirteen ^{14}C dates distributed along the core. Whereas nine dates were based on bulk sediment analyzed by ^{14}C conventional method at the Laboratory of Absolute Dating in Cianowice, the other four were based on terrestrial plant macrofossils analyzed though ^{14}C AMS at Poznań Radiocarbon Laboratory (Table 1). ^{14}C dates were calibrated using the curve IntCal13 (Reimer *et al.*, 2013) and selected calibrated age-depth data pairs were used to fit a Bayesian age-depth model (Fig. 2) though Bacon (Blaauw & Christen, 2011). An alternative chronological model was built incorporating the appearance depth of biostratigraphic markers of the Central European chronostratigraphy in the sediments of Lake Suchar IV (Mangerud *et al.*, 1974; Walanus & Nalepka, 2010).

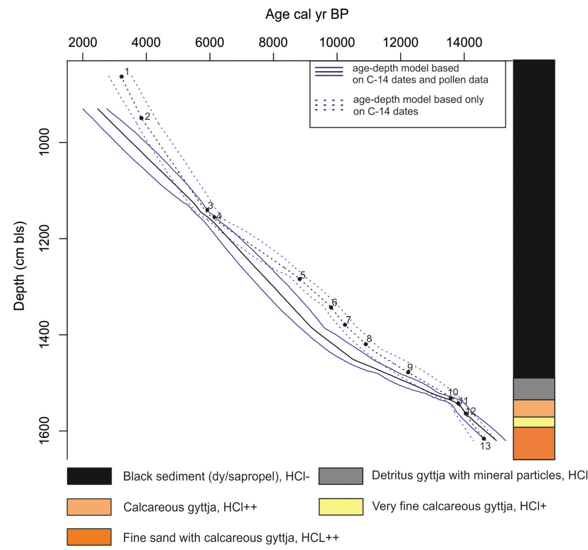

Figure 2. Age-depth model based on the ^{14}C dating of Lake Suchar IV sediments, showing sediment accumulation from Late Glacial to current times. Black dots (from 1 to 13) on diagram indicates ^{14}C date (see Table 1). Dashed lines represent age-depth model based only on ^{14}C dates and solid lines represent age-depth model based on ^{14}C dates and chronostratigraphical (pollen) borders according to Mangerud *et al.* (1974) and Walanus & Nalepka (2010). Right column is shows schematic lithology of sediment profile of Lake Suchar IV. *Modelo de edad-profundidad de los sedimentos del lago Suchar IV basado en la datación* ^{14}C*, indicando la acumulación de sedimentos desde el Glacial tardío hasta la actualidad. Los puntos negros (desde 1 hasta 13) en el diagrama, indican la fecha* ^{14}C *(ver tabla 1). La línea discontinua representa el modelo edad-profundidad basado únicamente en fechas* ^{14}C*, y la línea continua representa el modelo edad-profundidad basado en fechas* ^{14}C *y fronteras cronoestratigráficas de acuerdo con Mangerud* et al. *(1974) y Walanus & Nalepka (2010). La columna derecha muestra la litología esquemática del perfil de sedimento del lago Suchar IV.*

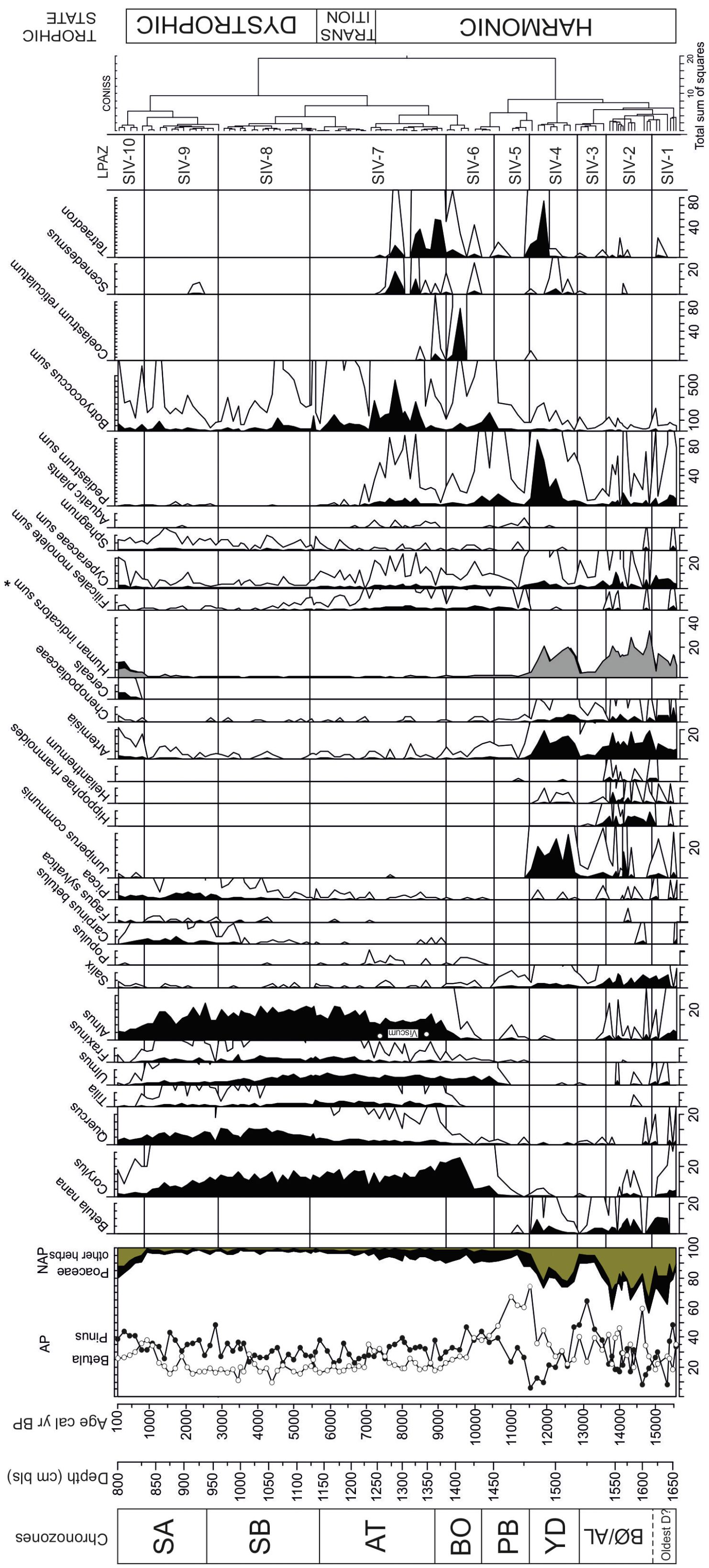

Figure 3. Percentage pollen diagram with selected taxa. Asterisk indicates species present in the environment of Lake Suchar IV before human activity due to climatic condition. *Diagrama del porcentaje de polen con taxones seleccionados. Los asteriscos indican la presencia de especies en el medio del lago Suchar IV antes de la actividad humana debido a condiciones climáticas.*

Pollen analysis

Palynological analyses were conducted on 104 sediment subsamples, accounting for a resolution of 5–10 cm. Palynological samples (1 cm^3 of sediment per sample) were prepared and analyzed using standard methods according to Berglund & Ralska-Jasiewiczowa (1986). Treated samples were stained with safranin and immersed in glycerine, and sporomorphs were counted under a Zeiss microscope at magnifications of 400x and 1000x (immersion oil). At least 500 pollen grains were counted from each sample, with total pollen counts being lower only in bottom samples because of very low pollen concentrations in the deepest part of the core. Identification of pollen grains and spores was based on Faegri & Iversen (1989), Moore *et al.* (1991), Reille (1992), and Beug (2004). Regional pollen assemblages reported as markers of chronostratigraphic units for the studied time period were used to refine the chronology (Fig. 2). The pollen record of LPAZ was divided into zones using CONISS cluster analysis (Grimm, 1987), aiming to facilitate the report of results. During the analysis, non-pollen palynomorphs (green algae) were identified too. The pollen percentage diagram (Fig. 3) was constructed using Tilia and TiliaGraph (Grimm, 1991/2011).

Subfossil Cladocera analysis

Subfossil Cladocera analysis was conducted on 169 sediment subsamples (1 cm^3) that were processed according to Frey (1986). Samples were heated and stirred in a 10 % solution of KOH for 20 min and washed through a 38 µm mesh. The final residue was dissolved in 10 ml distilled water. Aliquots of 0.1 ml of the final solution were mounted on microscope slides that were in turn use to identify cladoceran's remains at magnifications of 100x, 200x, and 400x, using an OLYMPUS BX40 transmitted-light microscope. Two to four slides (minimum of 200 remains) were counted from each sample. All cladoceran remains were counted (head shields, shells, ephippia, postabdomens), and complete individuals were put together from different parts of the body. The identification of Cladocera was based on Szeroczyńska & Sarmaja-Korjonen (2007) and Flössner (2000). The results were plotted as a relative abundance diagram (Fig. 4), using the C2 software (Juggins, 2007). The total number of Cladocera indicated in the diagram (Fig. 4) were standardized to concentration (Cladocera individuals per gram of dry sediment).

Diatom analysis

Diatom analysis was conducted on 85 sediment subsamples (1 cm^3) according to Battarbee (1986). A 10 % solution of HCl was used to remove calcium carbonate and distilled water was used to wash the samples several times. Afterwards, samples were boiled in 30 % H_2O_2 to oxidize organic matter. Permanent microscope slides were mounted in Naphrax®. The identification of diatoms was performed using a Nikon Eclipse E-200 light microscope at a magnification of ×1000. At least 500 frustules of diatoms were counted on each slide to estimate the relative abundance of each taxon, which were identified according to Krammer & Lange-Bertalot (1986, 1988, 1991a,b), Denys (1991), van Dam *et al.* (1994), Lange-Bertalot & Metzeltin (1996), Lange-Bertalot (1999), Lange-Bertalot & Genkal (1999), Krammer (2002), and Hoffmann *et al.*, (2011). AlgaeBase (Guiry & Guiry 2016) dataset was used for homogenizing taxonomy to the more recent diatom nomenclature. The classification of diatoms into environmental affinities (trophic state, pH), was based on the OMNIDIA database (Lecointe *et al.*, 1993). Also, diatom taxa were grouped according to their lifeform following Round classification (Denys, 1991). The diatom percentages diagram (Fig. 5) was constructed using Tilia and TiliaGraph (Grimm, 1991/2011).

Macrofossils analysis

For macrofossil analysis, 156 samples were washed and sieved through a 125-µm-size mesh and analyzed according to Birks (2007). All macrofossil counts were standardized to concentration (number of individuals per 50 cm^3). Identification of subfossil remains was based on the available literature (Birks, 2007; Mauquoy & van

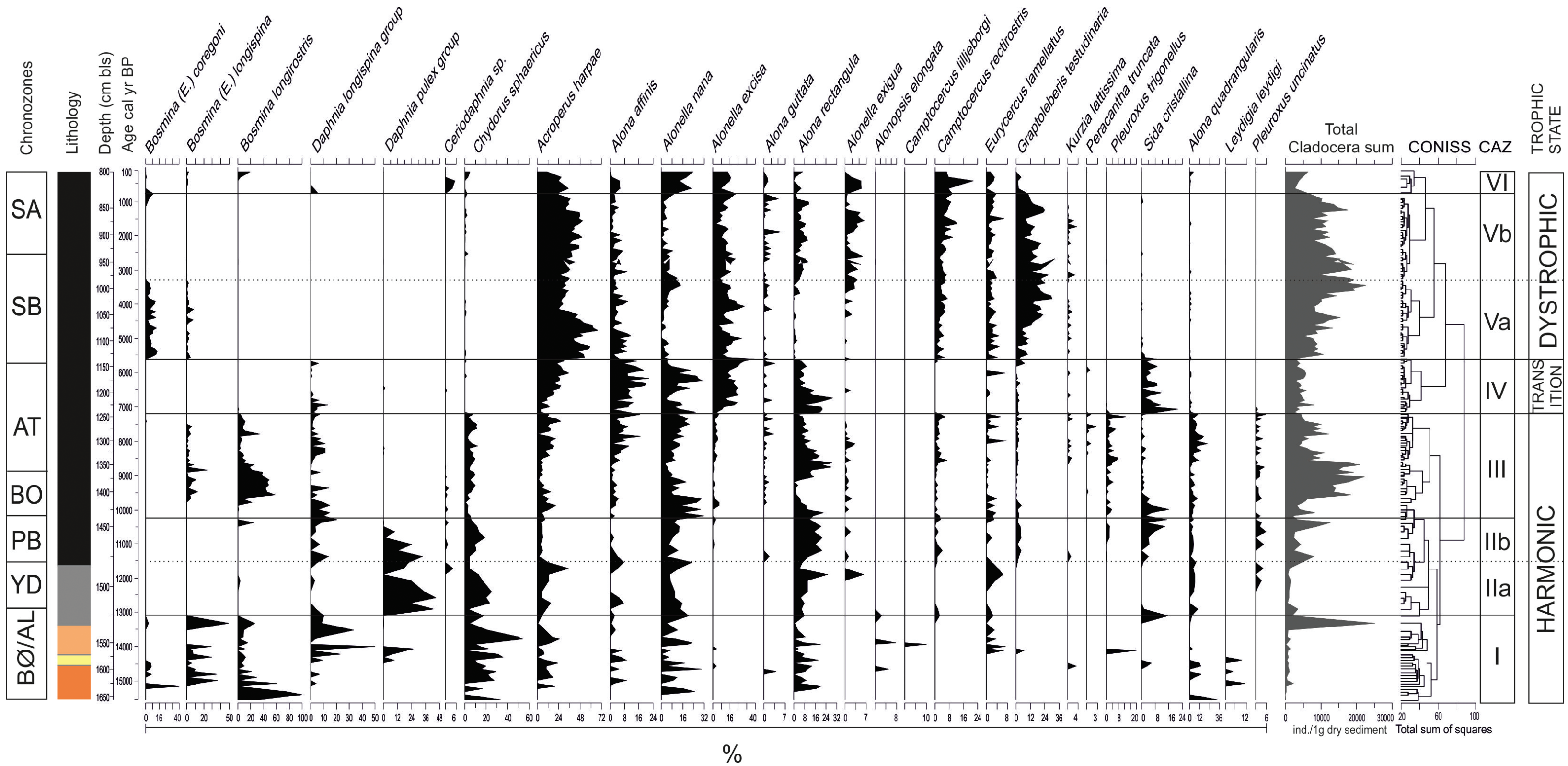

Figure 4. Relative abundance (%) diagram of subfossil cladoceran taxa identified in the sediments core from Lake Suchar IV, including the CONISS dendrogram on which zonation was based. *Diagrama de la abundancia relativa (%) de los taxones de cladóceros subfósiles identificados en los sedimentos del lago Suchar IV, incluyendo el dendrograma CONISS en el que se basa la zonación.*

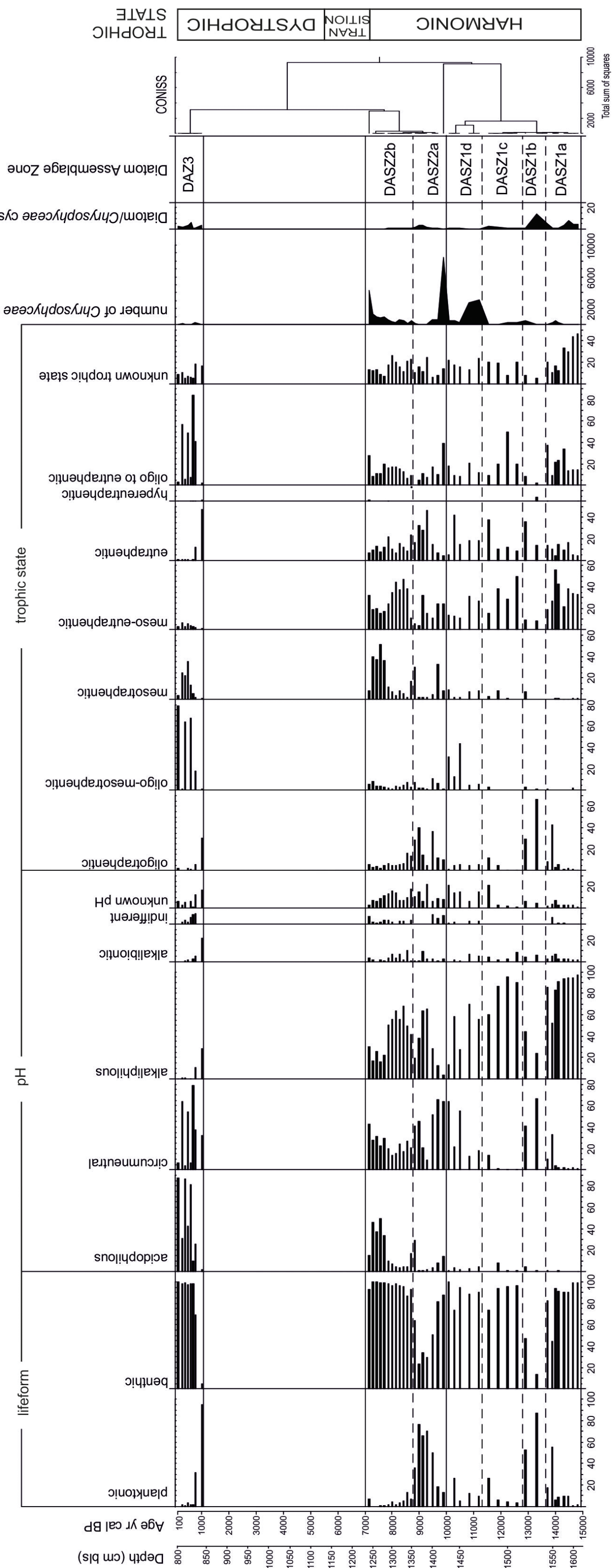

Figure 5. Relative abundance (%) diagram for the diatoms: lifeforms, pH groups, trophic state and Chrysophyceae cysts in the sediments core from Lake Suchar IV including the CONISS dendrogram on which zonation was based. *Diagrama de la abundancia relativa (%) para las diatomeas: formas de vida, grupos según pH, estado trófico y quistes de Chrysophyceae en los sedimentos del core del lago Suchar IV, incluyendo el dendrograma CONISS en el que se basa la zonación.*

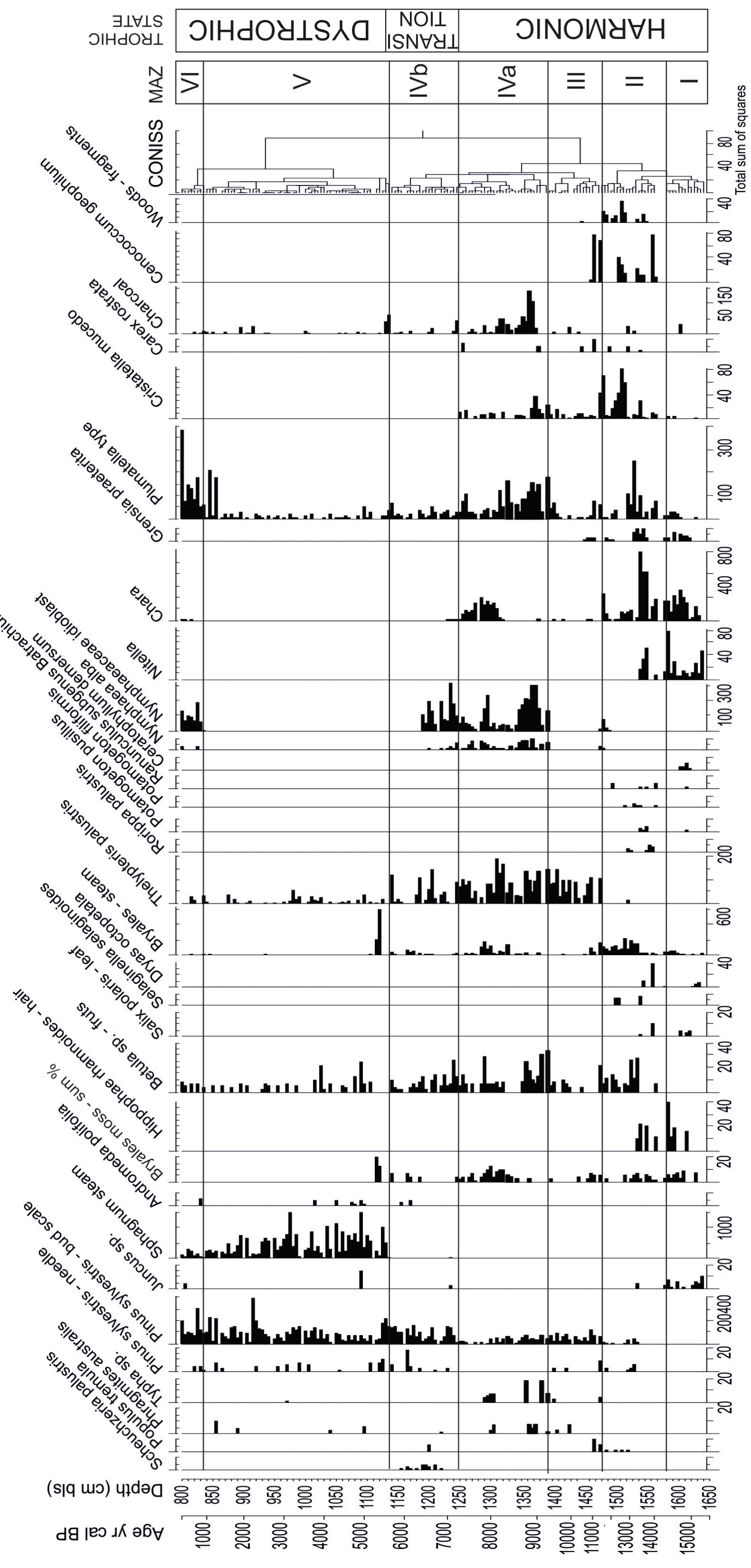

Figure 6. Absolute abundance diagram for macrofossils in the sediments core from Lake Suchar IV including the CONISS dendrogram on which zonation was based. *Diagrama de abundancias absolutas para macrofósiles en los sedimentos del core del lago Suchar IV, incluyendo el dendrograma CONISS en el que se basa la zonación.*

Geel 2007; Velichkevich & Zastawniak 2006; Velichkevich & Zastawniak 2008). The results were plotted using the C2 software (Juggins, 2007) (Fig. 6).

Geochemical analysis

Total carbon (TC), total nitrogen (TN) and total sulfur (TS) were determined in 155 sediment subsamples by Elemental Analysis (EA) (Elementar VarioMax CNS). Total organic carbon (TOC) was determined by analyzing TC in the samples treated with 1 M HCl to remove carbonates. The total inorganic carbon (TIC) was calculated as TIC [wt. %] = TC-TOC. The TOC/N ratio was calculated on a molar basis. All samples were analyzed in duplicate. The quality control was performed using certified reference materials for peaty, chalky and sandy soils, provided by Elementar. The results were plotted (Fig. 7) using the C2 software (Juggins, 2007).

Statistical analysis

A Principal Component Analysis (PCA) was performed based on the correlation matrix of the dataset biological components (algae, cladocerans, and pollen), aiming at generalizing the ecological and environmental information contained in the sedimentary sequence of Lake Suchar IV (Legendre & Legendre, 2012). Before the analysis, the dataset was logarithmically transformed to meet the normality assumption of the method (Borcard *et al.*, 2011). Taxon scores in the correlation biplot were used to interpret the potential relationship among the biological attributes of the dataset. The distance biplot was used to interpret the ecological and environmental meaning of the

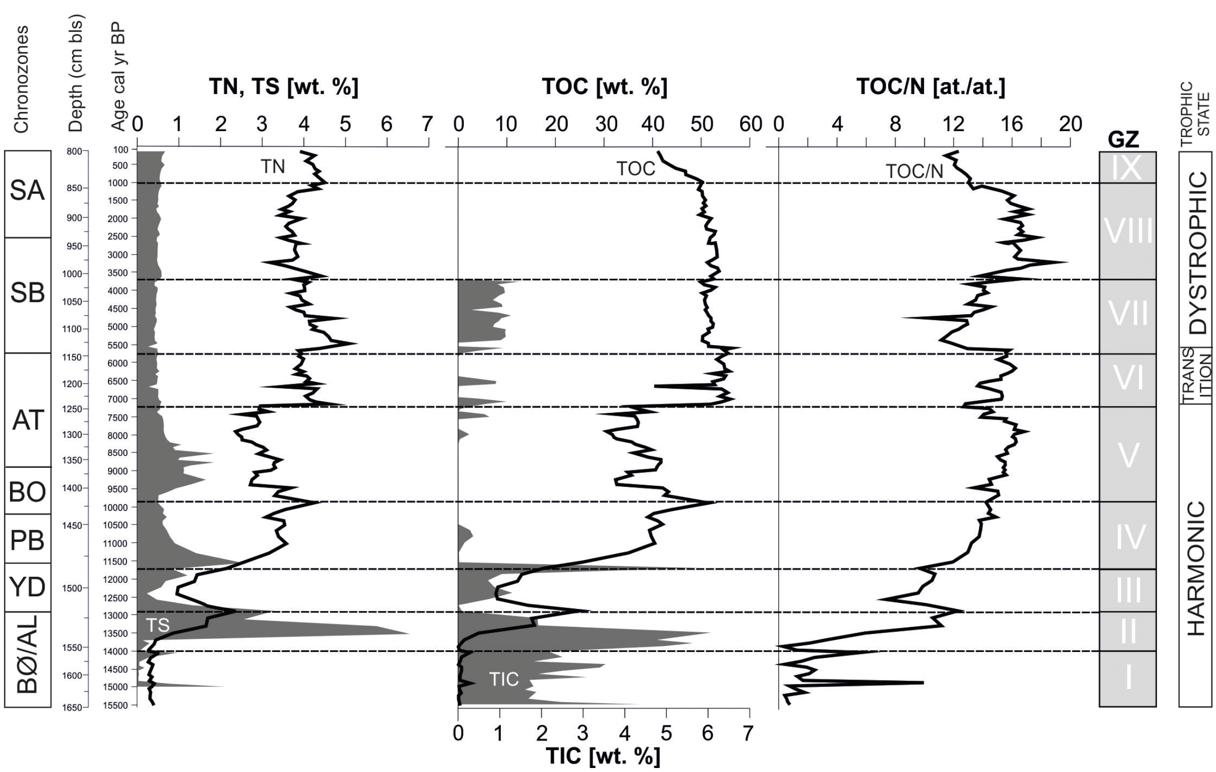

Figure 7. Chemical composition of the sediments of Lake Suchar IV: TN- total nitrogen, TS – total sulphur, TOC- total organic carbon and TIC –total inorganic carbon. *Composición química de los sedimentos del lago Suchar IV: TN - nitrógeno total, TS - sulfuro total, TOC carbono orgánico total y TIC – carbono inorgánico total.*

principal components, whose significance was tested using a broken-stick model.

RESULTS

Sediment lithology

The sediments of Lake Suchar IV were mainly composed of black highly organic sediment probably dy/sapropel (Hansen, 1959). The sediment floor, 1655 cm below lake surface (bls), was composed of sand, with the overlaying layer (1655–1587 cm bls) consisting of fine sand with layers of silt and calcareous gyttja. From 1587 to 1570 cm bls, the sediment was dominated by grey silt gyttja with fine sand. From 1570 to 1530 cm bls, the sediment was composed of beige-grey detritus-calcareous gyttja. From 1530 to 1480 cm bls, the sediment was dark brown detritus gyttja and from 1480 to 800 cm bls, black detritus, unconsolidated “jelly” deposits (dy/sapropel) was identified.

Chronology

Both age-depth models constructed for the sediments of Lake Suchar IV (Table 1) yielded a basal age of ~15 000 cal yr BP. Nevertheless, the models showed inconsistencies in the age of the sediments for the early and late Holocene. Between ~11 000 and 8000 cal yr BP and from 4000 cal yr BP to present, the model based on ^{14}C dates produced ages that were between 100 and 1000 years younger than the model that incorporated chrono-stratigraphic markers. We decided to use the model based on the combination of ^{14}C dates and stratigraphic markers given that the latter have been consistently identified though changes in the region and therefore represent a more parsimonious temporal contextualization for our results.

Pollen

A total of 91 taxa of pollen and spores were identified through the sedimentary sequence of Lake Suchar IV. Based on the results of the palynological analysis, the sediments from Lake Suchar IV have continuously accumulated since the Late Glacial to present. Pollen assemblages suggest that the sediment started accumulating during the Oldest Dryas. Ten local pollen assemblage zones (LPAZ SIV) were distinguished in the percentage pollen diagram, reflecting the stages of vegetation history (Fig. 3). Changes in the occurrence and abundance of green algae and aquatic plants corresponded with the distinguished pollen zones.

LPAZ SIV-1 NAP-*Betula* (The oldest samples before 15 000 cal yr B; 1650÷1615 cm)

High percentage of NAP (above 20 % with max 37 %); *Betula* between 18 and 37 %, *Betula nana* type 10 %. The upper limit marked by the beginning of the continuous curve of *Hippophae rhamnoides*. The presence of *Pediastrum and Botryococcus* colonies and single coenobia of *Tetratedron*.

LPAZ SIV-2 NAP-*Betula-Hippophae* (ca. 15 000–13 500 cal yr BP; 1615 ÷1535 cm)

Betula between 30 and 60 %. The continuous curve of *Hippophae rhamnoides* (max 9 %). High percentage of NAP (21–44 %) with *Artemisia* dominance (8–19 %). Significant contribution of *Helianthemum* pollen grains (max 7 %). The upper limit marked by a decline in NAP and *Hippophae*. The presence of green algae without changes. Only single coenobia of *Scenedesmus* present.

LPAZ SIV-3 *Pinus* (ca. 13 500–12 900 cal yr BP; 1535÷1520 cm)

Rapid growth of *Pinus* till max 67 %. Decline of NAP (< 10 %). Decline of *Salix* (3–1 %). The *Helianthemum* curve disappeared. The upper limit marked by an increase of *Juniperus* and NAP curves. Very low percentage of all chlorophytes.

LPAZ SIV-4 NAP-*Juniperus* (ca. 12 900–11 500 cal yr BP; 1520÷ 1480 cm)

High percentage of *Juniperus* (max 26 %). Increase in NAP (> 20 %) and *Salix* (up to 3 %). *Pinus* declined from 47 to 20 %. Return of the *Helianthemum* curve. The upper limit marked by a rapid decline of *Juniperus* and *Betula nana* t. PAZ with the highest percentage of *Pediastrum* (max 89 %) and *Tetraedron* (75 %). The curve of *Scenedesmus* present.

LPAZ SIV-5 *Betula* (ca. 11 500–10 600 cal yr BP; 1480÷1455 cm)

Increase of *Betula* up to 60 % (max 75 %). Disappearance of *Juniperus* and *Betula nana* t. curves. Decline of NAP below 10 %. The beginning of *Corylus* and *Ulmus* continuous curves. The upper limit marked by an increase in *Corylus* above 5 %. Decline of all green algae.

LPAZ SIV-6 *Corylus* (ca. 10 600–9200 cal yr BP; 1455÷1385 cm)

Pinus and *Betula* below 50 %. Rapid growth of *Corylus* (max 26 %). NAP below 3 %. Poaceae about 7 %. The upper limit marked by the beginning of the continuous curves of *Quercus*, *Tilia*, *Fraxinus* and *Alnus*. Increase of *Pediastrum* and *Botryococcus*. Varying contribution of *Tetraedron* and *Scenedesmus*. High percentage of *Coelastrum reticulatum* in the upper part of LPAZ.

LPAZ SIV-7 *Ulmus* (ca. 9200–5450 cal yr BP 1385÷1125 cm)

AP above 90 %. Pollen grains of the main component of mixed deciduous forest dominate (*Corylus*, *Quercus*, *Tilia*, *Fraxinus*, *Ulmus*, *Alnus*). *Ulmus* between 4 and 8 %. The beginning of the *Picea* curve. The upper limit marked by a decline of *Tilia* and *Ulmus* and increase of *Quercus*. LPAZ with the highest percentage of *Botryococcus*. *Coelastrum reticulatum* disappeared in the bottom part of PAZ. *Pediastrum*, *Scenedesmus* and *Tetraedron* colonies were present till the middle part of the zone and then disappeared

LPAZ SIV-8 *Corylus-Quercus* (5450–2900 cal yr BP; 1125÷960 cm)

Significant growth of *Quercus* (from 5 % to max 11 %.). Decline of *Tilia* and *Ulmus*. The beginning of the continuous curve of *Carpinus*. The upper limit marked by an increase of *Picea* and *Carpinus* curves. Only *Botryococcus* occurred in the water.

LPAZ SIV-9 *Picea-Carpinus* (2900–800 cal yr BP; 960÷830cm)

The growth of *Picea* (up to 6 %) and *Carpinus* (up to 5 %). Small increase in the percentage of *Pinus*. Gradual decline of *Corylus*. The upper limit marked by an increase in NAP. Small contribution of *Botryococcus* and single appearance of *Pediastrum* and *Scenedesmus*

LPAZ SIV-10 *Pinus*-NAP (ca. 800–100 cal yr BP; 830÷800 cm)

Significant growth of NAP (9–20 %). Human indicators present, e.g. pollen grains of cereals. Decline of deciduous tree curves. Low percentage of *Botryococcus* and single coenobia of *Pediastrum*.

Subfossil Cladocera

A total of 36 Cladocera species belonging to five families were identified in the sedimentary sequence of Lake Suchar IV. Planktonic species were represented by the families of Bosminidae and Daphniidae, and littoral species by Chydoridae, Holopedidae and Sididae. Littoral species represented the major (~60 %) component of the Cladocera assemblages, especially through the last 7000 years (Fig. 4). Cladocera assemblages composition and structure allowed the identification of six Cladocera assemblage zones (CAZ) that summarize the main stages of Cladocera development in Lake Suchar IV (Fig. 4). Cladocera concentrations during the Late Glacial was very low (except for the Allerød), increasing substantially during the Holocene.

CAZ I (The oldest samples from origin till 13 100 cal yr BP; 1655÷1525 cm)

Twenty-one species were identified in the sediments. The total number of Cladocera individuals per 1 g of dry sediment was ca. 1700. Planktonic species from Bosminidae and Daphniidae dominated. *Chydorus sphaericus*, *Acroperus harpae* and *Alonella nana* dominated in the littoral.

CAZ II (ca. 13 100–10 300 cal yr BP; 1525÷1440 cm)

Twenty Cladocera species were identified. The number of Cladocera individuals increased to 3400. Specimens from the Daphniidae family dominated (on average 22 %) among planktonic species: the *Daphnia longispina* group and the *Daphnia pulex* group. Bosminidae almost completely disappeared. *Alona rectangula* (on average 12 %), *Chydorus sphaericus* (on average 11 %) and *Alonella nana* (on average 11 %) were most abundant in the littoral.

CAZ III (ca. 10 300–7200 cal yr BP; 1440÷1245 cm)

The number of Cladocera individuals (average 10 000; max 22 000) and the number of species (23) significantly increased. Planktonic species accounted for 25 % on average. *Bosmina longirostris* (max 58 %) was the most abundant one. Littoral species were dominated by *Alonella nana* and *Alona rectangula*.

CAZ IV (ca. 7200–5600 cal yr BP; 1245÷1135 cm)

The number of Cladocera individuals (4300) and the number of species (16) decreased. The percentage of littoral species (~98 %) significantly increased; *Acroperus harpae*, *Alona affinis*, *Alona rectangula*, *Alonella nana* and *Alonella excisa* dominated. *Chydorus sphaericus* completely disappeared. Among planktonic species, only the *Daphnia longispina* group was present but with very low percentage – on average 2 %.

CAZ V (ca. 5600–750 cal yr BP; 1135÷830 cm)

The number of Cladocera individuals significantly increased (average 11 800). Littoral taxa dominated, especially species associated with macrophytes: *Acroperus harpae* (41 %), *Graptoleberis testudinaria* (15 %) and acidophilous *Alonella excisa* (14 %). Planktonic species occurred again (average 5 %): *Bosmina (E.) coregoni* and *Bosmina (E.) longispina*.

CAZ VI (ca. 750–100 cal yr BP; 830÷800 cm)

The number of Cladocera individuals decreased (average 4800). The importance of planktonic species slightly increased: Bosminidae and Daphniidae (mean 10 %). *Acroperus harpae*, *Alonella nana* dominated in the littoral.

Diatoms

A total of 193 diatom taxa (species and varieties) were identified. The sequence was divided into 3 diatom assemblage zones (DAZ), two of which were subsequently divided into subzones (DASZ) (Fig. 5). The diatom zones were defined using CONISS – the cluster analysis software (Grimm 1991/2011).

DASZ 1a (The oldest samples from origin till 13 700 cal yr BP; 1655÷1540cm)

Absolute dominance of benthic diatoms (*Fragilaria lapponica*, *Pseudostaurosira brevistriata*, *Staurosira construens*, *Staurosirella pinnata*). Dominance of alkaliphilous species; high proportion of oligotraphentic and eutraphentic species. Increase in contribution of diatoms/Chrysophyceae cysts (D/Ch) indicator from 0.4 to 7.8.

DASZ 1b (ca. 13 700–12 900 cal yr B; 1540÷1520 cm)

Abundance of planktonic species increased and then declined (*Lindavia comensis*, *Cyclotella ocellata* and *Puncticulata radiosa*). Dominance of circumneutral species; high proportion of oligotraphentic taxa. The content of D/Ch indicator increased up to 14.

DASZ 1c (ca. 12 900–11 500 cal yr BP; 1520÷1480 cm)

Decline of planktonic taxa; increase in benthic species, mainly *Fragilaria lapponica*, *Pseudostaurosira brevistriata*, *Staurosira construens*, *Staurosirella pinnata*. Dominance of pH alkaliphilous. Dominance of meso-eutraphentic taxa; high values of eutraphentic taxa. Decrease in D/Ch indicator (average 1.6).

DASZ 1d (ca. 11 500–10 000 cal yr BP; 1480÷1430 cm)

Dominance of benthic diatoms, mainly *Staurosira construens*, *Navicula cryptocephala*, *Navicula radiosa*. Dominance of pH circumneutral, followed by alkaliphilous taxa. High values of meso-eutraphentic, eutraphentic and mesotraphentic taxa. First and large increase of Chrysophyceae cysts. D/Ch indicator values decrease to 0.3.

DASZ 2a (ca. 10 000–8800 cal yr BP; 1430÷1360 cm)

Decline of benthic taxa; increase in planktonic species (*Lindavia comensis*, *Cyclotella ocellata*, *C. meneghiniana* and *Puncticulata radiosa*). Dominance of pH alkaliphilous; low proportion of circumneutral diatoms. High contribution of taxa with a wide range of tolerance (oligo- to eutraphentic). The largest increase in the number of Chrysophyceae cysts. The D/Ch indicator was rather low.

DASZ 2b (ca. 8800–7100 cal yr BP; 1360÷1240 cm)

Decline of planktonic taxa; increase in the number of benthic species, mainly *Staurosira construens*, *Navicula radiosa*, *Pinnularia gibba*, *Stauroneis phoenicenteron*. Dominance of circumneutral taxa and alkaliphilous; increase in acidophilous taxa. High values of mesotraphentic, meso-eutraphentic and eutraphentic taxa.

Lack of diatoms (ca. 7100–1100 cal yr BP; 1240÷845 cm)

DAZ 3 (ca. 1100–100 cal yr BP; 840÷800 cm)

Dominance of planktonic and then benthic species (*Pinnularia subcapitata* var *elongata*, *Pinnularia gibba*, *Tabellaria flocculosa*, *Stau-*

roneis phoenicenteron). Increase in acidophilous taxa; large number of circumneutral species. Dominance of oligo-mesotraphentic taxa; large numbers of mesotraphentic, meso-eutraphentic and eutraphentic taxa. High contribution of diatoms/Chrysopohyceae cysts: 0.6–6.4.

Macrofossil

In the studied sediment, were identified macrofossil remains of 48 taxa and were dominated mostly by water plant species (submerged and floating plants) and wetlands species connected with overgrowing mats. Results allowed to distinguish six macrofossil assemblage zones (MAZ) which are shown by an absolute frequency composition diagram (Fig. 6).

MAZ I (the oldest samples ~15 000- 14 400 cal yr BP; 1640÷1585 cm)

Algae from the family Characeae (*Chara sp.* and *Nitella sp.*) dominated in the open water zone. *Ceratophyllum demersum*, *Potamogeton pusillus*, *Ranunculus sect. Batrachium* occurred in the littoral zone. Reed beds occurred in the shore zone and they were dominated by *Juncus sp.* and *Bryales* sp. The vegetation development was accompanied by increased abundance of the bryozoans: *Plumatella type* and *Cristetella mucedo*. *Salix polris*, *Hippophae rhamnoides*, *Betula nana*, *Dryas octopetala* grew in the nearest vicinity of the lake.

MAZ II (ca. 14 400–11 500 cal yr BP; 1585÷1480 cm

Nitella sp. and *Chara* sp. co-occurred in the form of underwater meadows. *Nitella* sp. disappeared in the middle of this period, along with species from the *Potamogeton* genus. The relative abundance of the *Plumatella* type and *Cristetella mucedo* increased. The arrival of pine and birch was followed by the withdrawal of *Juncus sp.*, *Salix polris*, *Selaginella selaginoides*, *Hippophae rhamnoides*, *Betula nana*, *Dryas octopetala*. The amount of charcoal and the abundance of *Cenococcum geophilum* increased. *Populus tremula*, *Rorippa palustris* occurred and Nymphaeaceae in the planktonic zone.

MAZ III (ca. 11 500-9300 cal yr BP; 1480÷1390 cm)

The decline or lack of some aquatic species (e.g.*Chara* sp) was accompanied by a decline of *Plumatella* sp. and *Cristatella mucedo*. The littoral zone was dominated by *Thelypteris* sp. The percentage of birch decreased, *Typha* sp. and *Phragmites australis* occurred.

MAZ IVa (ca. 9300-7100 cal yr BP; 1390÷1240 cm)

Dominance of Nymphaeaceae (*Nymphaea alba*). *Chara* sp. occurred again in the second part of this phase and was accompanied by *Plumatella* sp. *Cristetella mucedo* disappeared at the end of this zone. The amount of wood charcoal increased.

MAZ IVb (ca. 7100-5700 cal yr BP; 1240÷1135cm)

The increased content of Nymphaeaceae was accompanied by disappearance of *Chara* sp. and *Cristetella mucedo*. The percentage of pine increased. The amount of charcoal and the content of *Bryales* sp. macrofossils decreased.

MAZ V (ca. 5700-1000 cal yr BP; 1135÷840 cm)

Floating mats of *Sphagnum* developed in the littoral zone, which was accompanied by the disappearance of *Bryales* sp. and Nymphaeaceae.

MAZ VI (ca. 1000-100 cal yr BP; 840÷800 cm)

The decline of *Sphagnum* and the return of Nymphaeaceae in the near-shore zone. The increased abundance of *Plumatella* sp.

Geochemistry

Nine geochemical zones (GZ) were identified on the basis of changes in TS, TN, TOC, TIC and TOC/N. The highest content of nitrogen was identified in the second half of the Holocene – from the transition state (ca. 7200 cal yr BP), accompanied by the maximum content of Total Organic Carbon (TOC). The highest content of sulfur was recorded during the Allerød (GZ II), along with the maximum content of Total Inorganic Carbon (TIC). Since the transition time, the content of sulfur remained below 1 %. A high content of TIC (up to 10 %) was also found in the early Subboreal period (GZ VII) (Fig. 7). Based on the observed changes in TOC, TIC and TN and TS, nine Geochemical zones (GZ) were distinguished:

GZ I (The oldest samples before 15 000 – 14

000 cal yr BP; 1655÷1565 cm)

Sediments are predominantly mineral with very low TOC and considerable carbonate content (2–3 % TIC). Low TOC/N indicates autochthonous organic matter.

GZ II (ca. 14 000–12 900 cal yr BP 1565÷1520 cm)

Sediments are distinguished by the high TIC (up to ca. 6 %) and TS (up to 6.5 %). TOC and TOC/N are increasing toward the top of the zone. Increasing TOC/N (up to 12) indicates the increasing contribution from terrestrial (soil-derived, macrophytes) organic matter.

GZ III (ca. 12 900–11 700 cal yr BP; 1520÷1485 cm)

Sediments are characterized by low TOC and TIC, but increasing toward the upper layer. TS content is low < 1 %. The reduced TOC/N ratio indicates the predominance of phytoplankton-derived organic matter.

GZ IV (ca. 11 700–9900 cal yr BP; 1485÷1420 cm)

Sediments are characterized by steeply increasing TOC and decreasing TS. TIC is depleted, except for the bottommost section of the zone. TOC/N gradually increases to ca. 15.

GZ V (ca. 9900–7200 cal yr BP; 1420÷1245 cm)

TOC decreases sharply and TIC is completely absent. TS shows enrichment between 9500–8200 cal yr BP. TOC/N is high and increases throughout the zone, except for the top section.

GZ VI (ca. 7200–5700 cal yr BP; 1245÷1145 cm)

TOC shows maximum values throughout the core and increases sharply at the base of the zone. TOC/N is high and TIC is absent.

GZ VII (ca. 5700–3800 cal yr BP; 1145÷1015 cm)

TOC/N shows a decline from ca. 16 to ca. 8. This coincides with a slight increase in TIC to ca. 1 %. TS is low (< 1 %). TOC is high (ca. 50 %).

GZ VIII (ca. 3800–1000 cal yr BP;1015÷840 cm)

The zone is characterized by high and invariant TOC (ca. 50 %). TIC is absent, TS is low and TOC/N shows the highest values throughout the core (14–20).

GZ IX (ca.1000–100 cal yr BP; 840÷800 cm)

TOC and TOC/N decrease. TIC is absent and TS is low.

Principal components analysis

The dataset used for the ordination contained a total of 154 taxa that yielded a log-transformed variance of 31.41 units. PCA 1 and 2 axes explained 33.3 and 15.5 % of the total variance, respectively, and resulted significant according to the broken-stick model. Extreme scores in the correlation biplot were obtained by algae and cladocerans (Fig. 8), reflecting the higher variability inherently linked with indicators derived from short-lived organisms. PCA 1 axis sample scores were around -1.0 between the bottom of the record and ~11 500 cal yr BP (Fig. 8). From ~10 500 to 5500 cal yr BP, PCA 1 axis sample scores progressively raised to reach scores of ~0.8, which in turn prevailed up to present. PCA 2 axis sample scores progressively fell from ~2.0 at the bottom of the sequence to ~1.5 at ~7500, when they started increasing up to ~0.3 at ~5500 cal yr BP. From ~5500 to present, Axis 2 sample scores remained relatively stable around 0.3.

DISCUSSION

With a basal age that goes back to the Oldest Dryas, the sedimentary sequence of Lake Suchar IV enabled us to reconstruct climatic and ecological changes occurred in the lake and its catchment through the last ~15 000 years. Paleolimnological studies enabled us detailed tracing of transformation processes from the harmonic into disharmonic (dystrophic) state, a change pattern that has been the focus of limnological and paleolimnological studies (e.g. Sayer *et al.*, 2010; Smol, 1992). Although the concept and the state of dystrophy remain ambiguous and controversial (e.g. Alhonen, 1987; Havens, 1991; Marek, 1992; Carpenter & Pace, 1997), most researchers understand dystrophic lakes as low-primary-production oligotrophic water bodies. The high contents of organic carbon and humic acids in these lakes make the water acid and dark brown (Alhonen, 1987; Marek, 1992; Górniak, 2006).

The lithological variability of the sedimentary sequence (gyttja, calcareous gyttja, dy/sapropel)

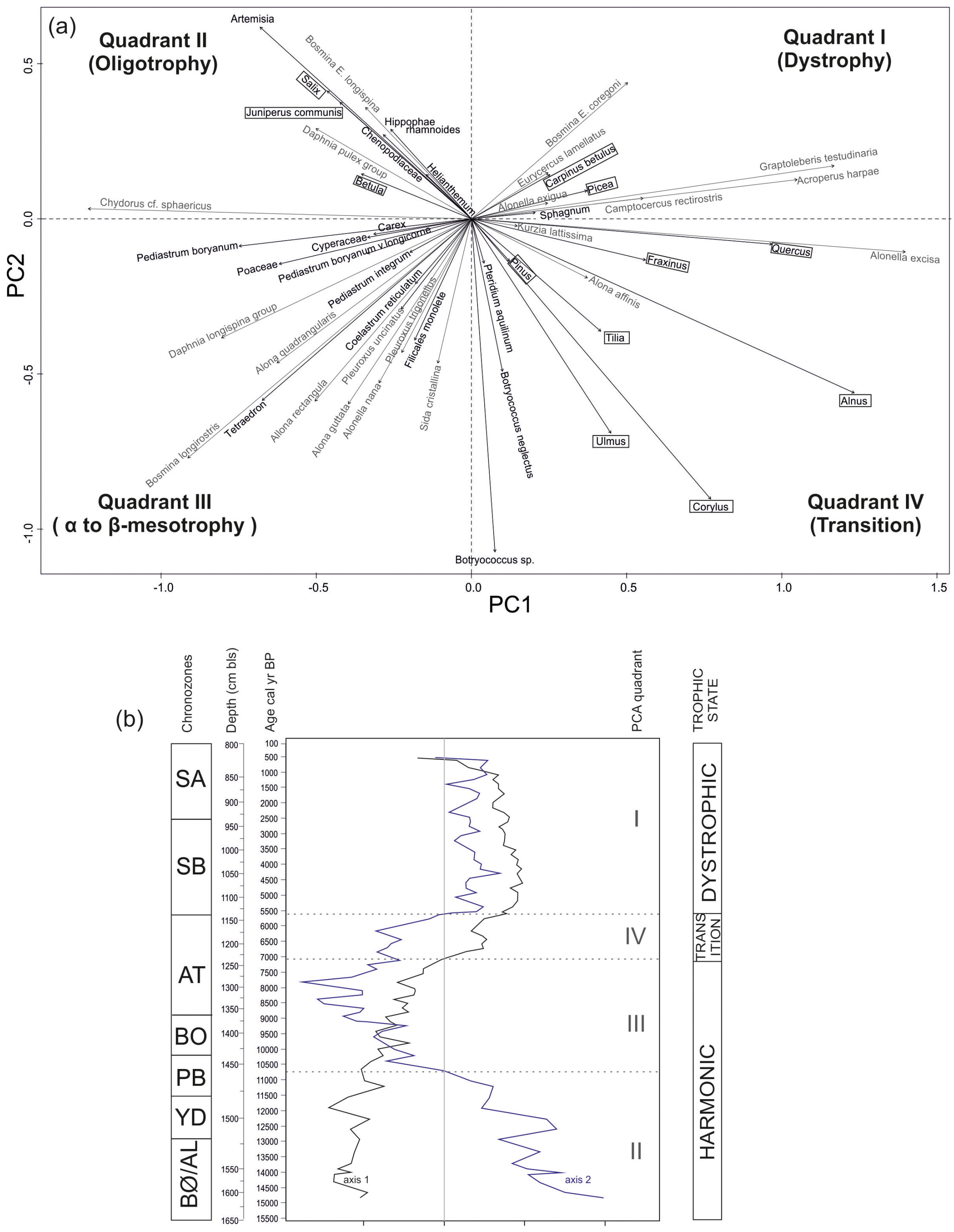

Figure 8. a) Principal component analysis (PCA) biplot of biological components (green algae, cladocerans, pollen) in the sediment core of Lake Suchar IV; b) PCA axis 1 and axis 2 scores for samples following either their algae, cladoceran and pollen assemblages (percentages) in the sediment core of Lake Suchar IV. *a) Análisis de componentes principales, PCA biplot, de los componentes biológicos (algas verdes, cladóceros y polen) en los sedimentos del core del lago Suchar IV; b) valores del eje 1 y eje 2 del PCA para muestras que siguen cualquier asociación (porcentaje) de algas, cladóceros y polen en los sedimentos del core del lago Suchar IV.*

and changes in its chemical composition (TN, TS, TIC, TOC, TC/N), demonstrate that the history of Lake Suchar IV has been intimately linked to regional environmental conditions. The inflow of biogenic and humic substances from the catchment determined both the type of sediments and the trophic conditions of the water body. Substantial changes in the proportions of major plant types and species composition of cladocerans and diatoms suggest a successional pattern that reflect the changes in the lake. Both phyto- and zooplankton responded not only to changes in water temperature and trophic state (oligotrophy → α-mesotrophy →β-mesotrophy →dystrophy) (Fig. 9) associated with the deglaciation, but also to the degree of humification of the water body (pH and color of water). Today, the high content of humic substances in the water of Lake Suchar IV results in water with a dark brown coloration that reduces the penetration of sunlight into deeper water layers (0.65 m Secchi disk). According to the fossil evidence, the lake acquired this attribute at ~5600 cal BP. The changes of Lake Suchar IV could be broadly summarized in three stages marked by significant changes of fauna and flora. From the bottom of the record up to 7200 cal yr BP the evidence reflects a harmonic development of the lake. Significant ecological changes occurred in Lake Suchar IV during the second part of the Atlantic period (7200–5600 cal yr BP) that transformed the lake into the modern disharmonic (dystrophic) state (5600 cal yr BP to present).

PCA sample scores show changes in the lake and the regional system that describe the sequence of dystrophication. Samples from the bottom of the sequence up to 11 500 cal yr BP resulted ordinated obtained negative and positive scores in PCA 1 and 2 axes, respectively (PCA quadrant II, Fig. 8). This quadrant was occupied by vegetation taxa typical of the deglaciation and pioneer cladocerans species typical of oligotrophic lakes. From 11 500 to 7200 cal yr BP, samples were ordinated in quadrant III of the PCA (negative scores for both axes, Fig. 8), which was char-

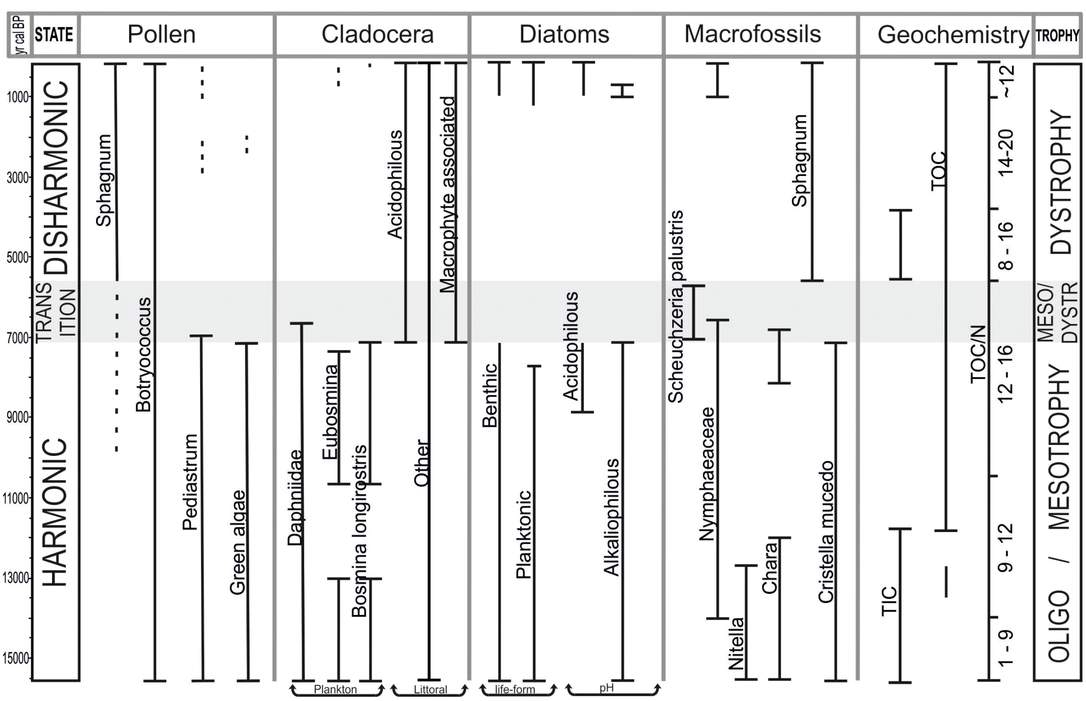

Figure 9. A Comparison of selected sequences of: pollen, Cladocera, diatoms, macrofossils and geochemistry, in the sediment core from Lake Suchar IV. *Una comparación de secuencias seleccionadas de: polen, Cladócera, diatomeas, macrofósiles y geoquímica, en los sedimentos del core del lago Sucher IV.*

acterized by algae and cladocerans typical of α to β-mesotrophic environments. This phase coincides with the development of a more thermophilous system at local and regional scales. From 7200 to 5600 cal yr BP, sample scores in both axes increased rapidly, although remained mostly within quadrant IV of the ordination. The rapid pace at which these changes took place suggest a transitional state of the lake that led to positive scores in both axes (PCA quadrant I, Fig. 8) from ~5600 cal yr BP and present. This quadrant was dominated by algae and cladoceran species typical of dystrophic environments in regional forests appeared Picea, and a water body with abundant floating mats of *Sphagnum*. Overall, the PCA suggests a sequence from oligotrophic to α- to β-mesotrophic to dystrophic. The initial changes from oligotrophic to mesotrophic is considered a harmonic sequence, whereas the dystrophic zone is considered disharmonic. Although there was an evident change in the local and regional conditions at the Pleistocene-Holocene transition, our interest is focused on the dystrophication process, and therefore our discussion is structured in three phases articulated around the transition that took place between 7200 and 5600 yr cal BP.

Harmonic stage (*from the initial time to 7200 cal yr BP*)

From the Oldest Dryas to ~7200 cal yr BP (i.e. till the mid-Atlantic period), Lake Suchar IV was apparently characterized by a harmonic development (Fig. 9). Sediments deposited during the Late Glacial significantly varied in terms of lithology (sand, calcareous gyttja) and the content of TIC and TOC, indicating relatively frequent fluctuations related to climate change (Ralska-Jasiewiczowa *et al.*, 1998). High concentration of TIC during the Late Glacial suggest that the sediments were mostly allochthonous. In slightly warmer periods (the Bølling and the Allerød), the content of TOC was higher, while during the colder periods (the Oldest, Old and Younger Dryas) –TIC and TS contents increased. The species composition of flora and fauna deposited during colder periods indicates that the lake was shallow at that time and its waters were oligotrophic. *Chrysophyceae* cysts, charophytes and diatoms occurred at that time, especially alkaliphilous species (*Pseudostaurosira brevistriata* and *Stauroneis construens*). The cladocerans were represented both by littoral and planktonic species. In warmer periods (the Bølling and the Allerød), the content of oligo/mesotrophic taxa (e.g. Daphniidae, *Chydorus sphaericus*, *Pleuroxus*), in the plankton slightly increased. Aquatic vegetation was represented mainly by *Potamogeton* and reed beds in the shoreline zone of the lake. During the Late Glacial, the most favorable temperature and edaphic conditions for the development of plankton prevailed in the lake during the late Allerød when the zooplankton frequency reached the maximum value (Total Cladocera sum; Fig. 4). In the PCA, these conditions are reflected by low and relatively stable scores of Axis 1, and declining and highly variable scores in Axes 2 (Fig. 8). A similar sequence of changes was determined by Drzymulska *et al.* (2014) in Suchar Wielki located in Wigry National Park. In general, the recorded sequence of changes in sediments of Suchar IV in the Late Glacial period is typical of oligotrophic lakes of N Poland, formed after the ice sheet melting (Zawisza & Szeroczyńska, 2007; Filoc *et al.*, 2017). As evidenced by other studies from the late post-glacial areas of N Poland (e.g. Ralska-Jasiewiczowa *et al.*, 1998; Zawisza & Szeroczyńska, 2007), small water bodies formed in depressions after melting of dead-ice blocks were initially oligotrophic and gradually evolved following the climate fluctuations toward mesotrophy representing the harmonic development.

The beginning of the Holocene is reflected in the significant change of arboreal pollen spectra. The open plant communities with the juniper shrubs and light demanding species (e.g. *Helianthemum*, *Artemisia*) began to replace by forest communities. At first with *Betula*, than *Pinus* and new spreading deciduous trees (*Corylus*, *Ulmus*, *Alnus*). In the area around the lake developed the local communities of *Thelypteris palustris* that caused a significant inflow of nitrogen (TN) and organic carbon (TOC) into the lake. This vegetation cover change is clearly reflected in the lowest scores of PCA 2 axis. Such changes probably resulted in the gradual increase in the trophic status of the lake. Diatoms were increasingly represented by meso-eutraphentic and eutraphentic species such as *Staurosira construens*, *Navicula radiosa*, *Pinnularia gibba* and *Stauroneis phoenicenteron*. The harmonic development of the lake continued, with a species composition of cladocerans and green algae similar to that determined in the Late Glacial, although taxon abundances were much higher (Figs. 3 and 4). At the beginning of the Holocene, *Nitella* and *Chara* disappeared from the lake, indicating that waters of the lake changes of water trophy transparency or water depth (Hannon & Gillard, 1997). The harmonic development of the lake, from the oligotrophic state through α-mesotrophy to β-mesotrophy continued until the mid-Holocene Climate Optimum (Atlantic), when abundances of both phyto- and zooplankton specimens reached the highest values. A gradual reduction in the phyto- and zooplankton species in Lake Suchar IV occurred in the second half of the Atlantic period (Figs. 3 and 4). The observed sequence of changes during the Late Glacial period and the first half of the Holocene in Lake Suchar IV is typical of shallow lakes in Poland. During the climate optimum, these lakes were usually meso- and eutrophic, and were often transformed into land or peat bogs (Żurek, 1994; Kowalewski, 2014). Significant changes in the aquatic ecosystem of Lake Suchar IV occurred also at the end of the Atlantic period, when the development of the lake changed from harmonic into disharmonic. The occurrence of acidophilous diatoms, *Sphagnum moss* (Fig. 3) and the gradual increase in the frequency of *Alona guttata* and *Alonella excisa* were indicative of the changing water pH and a harbinger of significant ecological changes. These changes are reflected in the progressive increasing of PCA 1 scores and decreasing PCA 2 scores (Fig. 8).

Transitional stage (*7200–5600 cal yr BP*)

Major changes occurred in the lake during this period (Fig. 9), while the vegetation and climate remained relatively stable (Fig. 3). Species such as *Nymphaea alba*, *Chara*, *Typha*, algae (*Scenedesmus*, *Tetraedron*) and *Pediastrum* completely disappeared from the lake. The species composition of phyto- and zooplankton changed significantly. Frequency of Cladocera specimens was very low and planktonic species were replaced by littoral ones (Fig. 4). The littoral species were dominated by acid-tolerant *Alonella excisa* and species occurring among vegetation (*Alona affinis*, *Sida crystallina*). At that time diatoms totally disappeared. The periphytic fauna (creeping on surface), i.e. *Cristatella mucedo* also completely disappeared during that period. The content of *Bryales* was minor, while the interesting fact is that *Scheuchzeria palustris* occurred only during the transition state. Probably, this species was involved in the creation of mire on the lake shore, which characterize wet conditions (Słowiński *et al.*, 2016). The sediments deposited during the transition state are characterized by an increased content of TN, while TIC and TOC fluctuated significantly. The TOC/N ratio increased to a value of 16. This indicates a change in the trophic conditions of the lake toward dystrophy (Rosen, 2005; Rantala *et al.*, 2015). It is likely that the lake in the transition period (7200–5600 cal yr BP) was relatively shallow, and its waters were characterized by lower pH, reduced transparency and a low content of nutrients. These changes were reflected by increasing trends in the scores of the two first PCA axes (Fig. 8).

Disharmonic (Dystrophy) stage (*5600 cal yr BP to present*)

The end of the Atlantic and the beginning of the Subboreal periods was marked by major climatic changes (cooler weather and increased moisture content) that were clearly reflected in the sediments of Lake Suchar IV. At the beginning of the Subboreal period, the water level of lake Suchar IV likely increased, enabling the re-colonization of the lake by planktonic cladocerans from the family of Bosminidae. The littoral zone of the lake was inhabited by Cladocera species living in associations with aquatic vegetation and tolerant of reduced water pH (mainly Alonidae, *Acroperus harpae*, and *Graptoleberis testudinaria*) (Fig. 4). Zooplankton reached the maximum development at that time, and fluctuations in the TOC/N ratio (8 - 20) indicate that both allochthonous and autochthonous materials were important sources of material to the lake (Figs. 7 and 9). The sediments deposited in the first half of the Subboreal period contained approximately 10 % TIC, indicating a significant inflow of allochthonous material from the catchment (Alhonen, 1987). Climate conditions and the continued development of *Sphagnum* intensified the initiated change in phyto- and zooplankton succession. The conditions in the lake were becoming polyhumic. A similar picture of changes and humic conditions in boreal (Polish and Finnish) lakes was recorded by Drzymulska *et al.* (2015), Luoto *et al.* (2013) and Rantala *et al.* (2015). The intensive development of *Sphagnum* mat on the shore and *Botryococcus* brought about a consistent systematic change in the structure of Lake Suchar IV. The invasion by *Sphagnum* created surface platforms in the form of floating mats which affected the regular development of the lake, especially in the open water zone. From about 3000 to ca 500 cal yr BP, only the littoral zone was inhabited by oligo and/or acid-tolerant species of phytoplankton (pioneer diatoms: *Lindavia comensis*, *Cyclotella planktonica*, *Puncticulata radiosa*) and zooplankton (Alonidae e.g. *Alona guttata*, *Alonella exigua*; *Acroperus harpae*). The development of *Botryococcus* and the inflow of humus from the catchment caused a significant reduction in the penetration of light in the water column, and thus inhibited the development of life in the planktonic zone. The youngest sediments in Lake Suchar IV showed another change in the lake ecosystem. The smaller content of *Sphagnum* and the appearance of *Nymphaea*, as well as the presence of *Plumatella* specimens is indicative of declining dystrophic conditions. This situation is also reflected in the reduced content of littoral specimens and the arrival of Cladocera and diatom species living in the open water zone. Palynological analysis showed the presence of human indicators. It appears that the observed changes in the youngest sediments are most likely induced by human impact.

Our results demonstrate that dystrophy is a fairly unstable (disharmonic) state and is subject to fluctuations because of regional climatic and anthropogenic changes. The encroachment of vegetation on the water bodies may proceed from the shores toward the central part of a reservoir or from the water surface toward the bottom (formation of *Sphagnum* mats). The process is primarily determined by the type of catchment, i.e. catchment vegetation and the availability and the type of allochthonous material. The catchment area around Lake Suchar IV was dominated by forest of *Pinus*, so the supply of nutrients into the water body was insignificant. Researchers studying the history of Scandinavian boreal lakes also found large fluctuations during the transformations of oligotrophic lakes into dystrophic ones (Alhonen, 1987; Korsman *et al.*, 1994; Rantala *et al.*, 2015). They showed that the main cause of dystrophication of lakes were climate changes as a result of which humic acids were washed away from the drainage basin.

CONCLUSIONS

1. The results of the interdisciplinary sediment study introduced here showed that Lake Suchar IV has continuously developed from the Late Glacial to the present day.
2. The lake acquired its modern dystrophic nature at the beginning of the second half of the Atlantic period and was preceded by an unstable period of transition.
3. Given the biological and chemical composition and lithology of sediments, the development of the lake and its trophic state was affected mainly by regional factors such as climate and the conditions and quality of the drainage basin.
4. The harmonic development (oligo-, α-meso-, β-mesotrophic) was disturbed by an excessive influx of humic substances at the end of Atlantic period, the growth of *Sphagnum* and *Botryococcus* (especially in Subatlantic period), which resulted in the reduced light availability, thus changing the species composition of flora and fauna as well as pH of water, and consequently changing the trophic state into the dystrophic one.
5. The harmonic development of the lake and the increasing trophic conditions reflected regional climate changes. Warmer and colder periods were manifested through the species composition and frequency of phyto- and zooplankton.
6. During the disharmonic development period, the lake was dominated by acidophilous

species, indicative of low water pH and the trophic status at the level of dystrophy.
7. The transition between the harmonic and disharmonic development was preceded by a transitional period that was characterized by considerable fluctuations, especially in the phyto- and zooplankton structure.

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