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LATE-GLACIAL CLADOCERAN SUCCESSION IN THREE LAKES OF THE CHEŁM HILLS REGION (ŁĘCZNA-WŁODAWA LAKE GROUP, SE POLAND)

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Abstract

High resolution studies on subfossil Cladocera from three closely located lakes of the Chełm Hills Region – Lake Słone, Syczyńskie, and Pniówno, evidenced a strong zooplankton response to the well-known climatic changes of the Late-Glacial and early-Holocene. The general changes in the cladoceran community structure resemble those described from other Polish and European lakes. Certain important differences were identified, however, which can be attributed to the peculiarity of the environmental conditions of the region, regarding: the deep character of the lakes studied already in the initial phase of their development (Older Dryas), an intensive eutrophication process induced by the Alleröd climate warming with a periodical lowering of the trophic status, and the character of the Younger Dryas cooling less severe than in some other regions. The chronology of the palaeoenvironmental changes identified by means of subfossil Cladocera analysis was based on the results of palaeobotanical analysis, and confirmed by radiocarbon dating available for two profiles. Taking advantage of the close location of the study sites, their morphometric and geological similarities, and the high resolution of sampling, an attempt was made to use cladoceran succession in order to establish the stratigraphic division for Lake Pniówno, lacking palynological and radiocarbon data.

Key words: Late-Glacial, subfossil Cladocera, Chełm Hills, Łęczna-Włodawa Lake Group

INTRODUCTION

Within the last decades, a lot of scientific attention has been paid to the rapid climatic fluctuations occurring at the end of the Last Glaciation (Walker 1995, Ammann *et al.* 2000, Duigan, Birks 2000, Stančikaitė *et al.* 2009). The climatic changes of the period between approximately 14 ka and 10 ka BP are therefore considered to be quite well recognised. Results of palaeogeographic research show the diversified character of climatically-driven environmental changes in different regions of Europe (Ammann, Lotter 1989, Björck *et al.* 1996, Litt, Stebich 1999, Birks, Ammann 2000, Litt *et al.* 2001). The environmental response to the climate change largely depended on the local and regional factors such as geology, elevation, distance from the sea or from plant refuges.

One of the most commonly used archives for Late-Quaternary palaeoclimatic reconstructions are lacustrine sediments. They are examined by means of a wide range of palaeolimnological methods. Among those, in the context of the present study, the palaeoecological methods should be highlighted. The ecological response of aquatic ecosystems to climatic oscillations provides valuable information concerning not only past temperature and humidity, but also lake trophic status, water depth, productivity of ecosystems, terrestrial erosion, etc. By applying different proxies (different groups of organisms storing information on past environmental changes), this and a lot of other information can be obtained. In this paper, the subfossil cladoceran community is used as a proxy for tracking the response of the aquatic environment to climatic factors.

Cladocera are known for their sensitivity to climatic conditions (deCosta 1964, Harmsworth 1968). Their response to climatic change is detectable as a change in the cladoceran species composition, total abundance, or the number of Chydoridae ephippia (Bennike *et al.* 2004, Nevalainen, Luoto 2010). Moreover, due to their short reproduction cycle, these organisms react quickly to environmental changes, and respond to different drivers than terrestrial vegetation, e.g. the length of the open-water season, lake nutrient status, and water temperature (Sarmaja-Korjonen *et al.* 2003).

As show the maps of subfossil Cladocera sites which have been studied during the last decade (Szeroczyńska 1998c, Szeroczyńska, Zawisza 2007), the region of southeast Poland have gained recently much scientific attention. The reason for this was an attempt to identify sediment sequences covering longer time period that in case the northern part of Poland. Important was the discovery of laminated sediments in Lake Perespilno, which provided valuable data covering Late-Glacial to early-Preboreal period (Bałaga *et al.* 1999, Goslar *et al.* 1999, Litt *et al.* 2001, Bałaga 2004). Other significant cause for intensive paleolimnological research in the region was, as widely discussed in literature (Wilgat 1954, Maruszczak 1966a, Buraczyński, Wojtanowicz 1974, Woj-

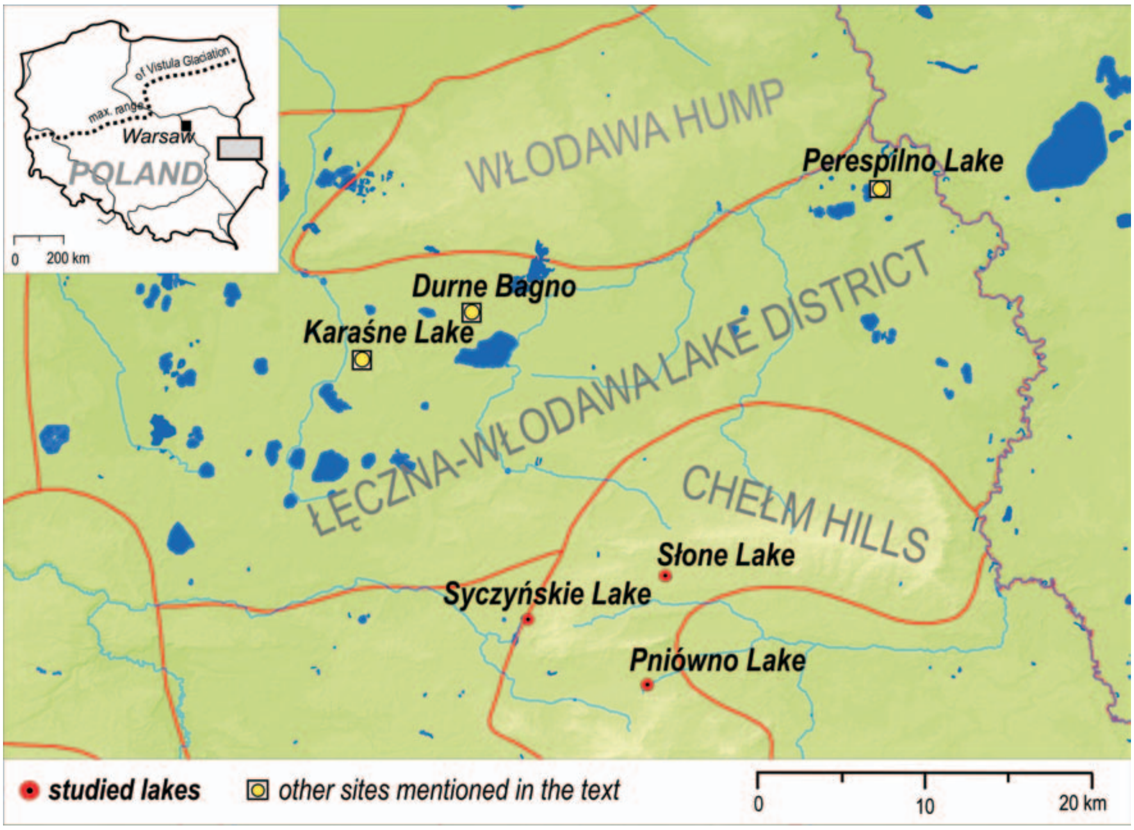


Fig. 1. Location of the lakes discussed in the paper on the background of physiographic division (regional division after Chałubińska, Wilgat 1954).

tanowicz 1994, Bałaga *et al.* 1995, Dobrowolski 2006), the problem concerning the genesis of a group of over 60 lakes (Łęczna-Włodawa Lake Group) situated far from the range of Last Glaciation. As the lakes are diversified in terms of geology and morphometry only the detailed studies of many sites representing different types of lakes among this group may lead to final conclusion of this issue.

One type of lakes that can be distinguished within the Łęczna-Włodawa Lake Group are small, regular-shaped lakes with calcareous rocks present in the mineral bottom. Studies of three such lakes, situated in northern part of Chełm Hills Region, are presented in this paper.

In the scope of this study, closely located lakes: Słone, Syczyńskie and Pniówno were analysed with the purpose of (1) investigating the response of the cladoceran community to well-known climatic changes of the Late-Glacial and early-Holocene. Due to careful selection of the study sites, providing their similarities in terms of morphological and geological conditions, the influence of external factors, which might have differentiated the cladoceran composition, was minimised. As a consequence, it was possible to (2) track the Late-Glacial environmental changes in their vicinity at the regional scale, with a particular focus on the peculiarity of the Chełm Hills Region, mostly involving the presence of carbonate bedrock. The chronology of the palaeoenvironmental changes, identified by means of subfossil Cladocera analysis, was based on the results of palaeobotanical analysis, and confirmed by radiocarbon dating. A palynology-based correlation with the laminated sediments of Lake Perespilno (Bałaga 2004) was also performed (Kulesza *et al.* 2011). Unfortunately, the radiocarbon dating and palynological analyses were only performed for sediments from two lakes: Słone and Syczyńskie. Taking advantage of the close location of the study sites, their morphometric and geological similarities, and high resolution of sampling, an attempt was made (3) to apply cladoceran-based stratigraphy (ecostratigraphy) in order to establish the stratigraphic division for Lake Pniówno, lacking palynological data.

MATERIAL AND METHODS

Description of study sites

The lakes studied belong to the Łęczna-Włodawa Lake Group – a unique group of 67 lakes in south-eastern Poland, located outside the range of the last ice sheet (Fig. 1). The external location in relation to the Weichselian ice-sheet, and geological contact with karst-liable Upper-Cretaceous bedrock, provoked a discussion concerning the genesis and early development of those waterbodies (Wilgat 1954, Maruszczak 1966a, Buraczyński, Wojtanowicz 1974, Wojtanowicz 1994, Bałaga *et al.* 1995, Dobrowolski 2006). The issue was complicated, because those lakes represent high internal heterogeneity, concerning their size, geological setting, trophic status, water chemistry, etc. Due to this, it was difficult to develop a general model of the evolution of these ecosystems, as well as the reconstruction of some components of the palaeoenvironmental conditions in their vicinity (Bałaga 2002).

Table 1

Basic morphometric and hydrobiological characteristics of studied lakes (after Harasimiuk *et al.* 1998)

Parameter	Słone	Syczyńskie	Pniówno
absolute height of water surface [m a.s.l.]	185.6	179.6	189.6
area [ha]	3.4	5.6	4.5
max. water depth [m]*	7.6	3.0	3.0
water mixing	dimictic	polymictic	polymictic
trophy	eutrophic	hypertrophic	eutrophic

*measurement taken by author in the date of coring (between 2008-2010)

In spite of belonging to the Łęczna-Włodawa Lake Group (Wilgat 1954, Wilgat *et al.* 1991), all of the lakes studied are located outside the physiographic region of the Łęczna-Włodawa Lakeland (Fig. 1). They belong to the geographical region of Chełm Hills. The specific character of the Chełm Hills Region, worth highlighting in the context of the present paper, is mostly related to the shallow occurrence of carbonate rocks of different facies. Among their soft types, chalk karst phenomena developed (Maruszczak 1966b, Dobrowolski 1998).

Lakes Słone, Syczyńskie, and Pniówno are small and shallow waterbodies (Table 1), with regular-shaped basins developed entirely in Upper-Cretaceous carbonate bedrock, formed in chalk facies. Multiple sediment corings also revealed the dominance of carbonate bedrock in the catchment areas (Kulesza *et al.* 2008). The geological factors largely determine the chemical composition of the lake waters. The total dissolved salts (TDS) in studied lakes exceed 500 mg/l, which is a value rarely found in freshwaters (Dawidek 1998). The maximum distance between the sites varied from 6 to 8 km (Fig. 1).

Coring and dating

One sediment core was collected from the deepest point of each lake basin with an Instorf corer (Lakes: Słone and Pniówno) and with a Więckowski's piston corer (Lake Syczyńskie) in the years 2008–2010. The coordinates of the coring sites, total lengths of sediment sequences, and the water depth at the coring sites are presented in Table 2.

The radiocarbon dating (AMS-method) was performed in the Poznań ^{14}C Radiocarbon Laboratory. When possible, macrofossils of terrestrial plants were selected for dating purposes. Only in the case of profile JS-c, due to the lack of suitable macrofossil material, bulk sediments were dated. The results were calibrated with OxCal v 3.9 software (Bronk Ramsey 2001).

Cladocera analysis

For the Cladocera analysis, 1 cm^3 of fresh sediment was taken for each sample. Samples were analyzed at regular intervals of 5 cm (Lakes Słone and Syczyńskie) and 10 cm (Lake Pniówno). Cores were sliced into 1-cm thick segments, and 1 cm^3 samples from every fifth, or in the case of Pni-1 every tenth slice were analyzed. Additionally, if a distinct change in the character of the sediments occurred, the sample spacing was tightened (a sample was collected below and above the lithological boundary). Samples were prepared in accordance with the standard methodology (Frey 1986, Szeroczyńska 1998a). Each sample was treated with 10% HCl to eliminate carbonates, and boiled for 30 minutes in 10% KOH to remove humic matter. At each stage of chemical preparation, the fossils were washed on a 40-µm mesh. All residue was transferred to a scaled test tube, and filled up with distilled water to the fixed volume of 10 ml. Quantitative slides were prepared by pipetting of a volume of 0.1 ml from a well-stirred sample. Before counting, cladoceran remains were coloured by adding 2–3 drops of safranin-glycerin solution. Depending on the frequency of remains, 2–6 slides were prepared, so that the total number of remains was more than 400. All identifiable elements of the chitinous cladoceran exoskeleton were counted: head shields, valves, postabdomens, postabdominal claws, and ephippia. The identification of remains followed Szeroczyńska, Sarmaja-Korjonen (2007). The most abundant body part was chosen for each species to represent the number of individuals. Ecological preferences of species followed mainly Harmsworth (1968), Fryer (1968), Whiteside (1970), Flössner (1972) and Duigan (1992). The percentages for all cladoceran species were calculated from the total sum of individuals. Cladocera diagrams were prepared using the POLPAL software (Walanus, Nalepka 1999). Also graphs of absolute cladoceran abundance (counted as number of specimens for 1 cm^3 of fresh sediment) were added to the diagrams.

The species diversity for Cladocera was estimated with the application of the Shannon-Weaver species diversity index (Shannon, Weaver 1949). The cladoceran stratigraphy was divided into local faunal zones – cladoceran assemblages were grouped by cluster analysis using PAST software (Hammer *et al.* 2001) with the paired group algorithm as a linkage rule, and the Euclidean distance as a distance measure.

Table 2.

Geographic coordinates of drilling points and basic characteristics of sediment cores

Site	Symbol	Coordinates	Water depth at drilling point [m]	Total length of sediment core [m]
Lake Słone	JS-c	51°18'15"; 23°21'55"	7.60	5.00
Lake Syczyńskie	Sycz-1	51°17'13"; 23°14'15"	3.00	12.50
Lake Pniówno	Pni-1	51°14'46"; 23°20'32"	2.50	16.40

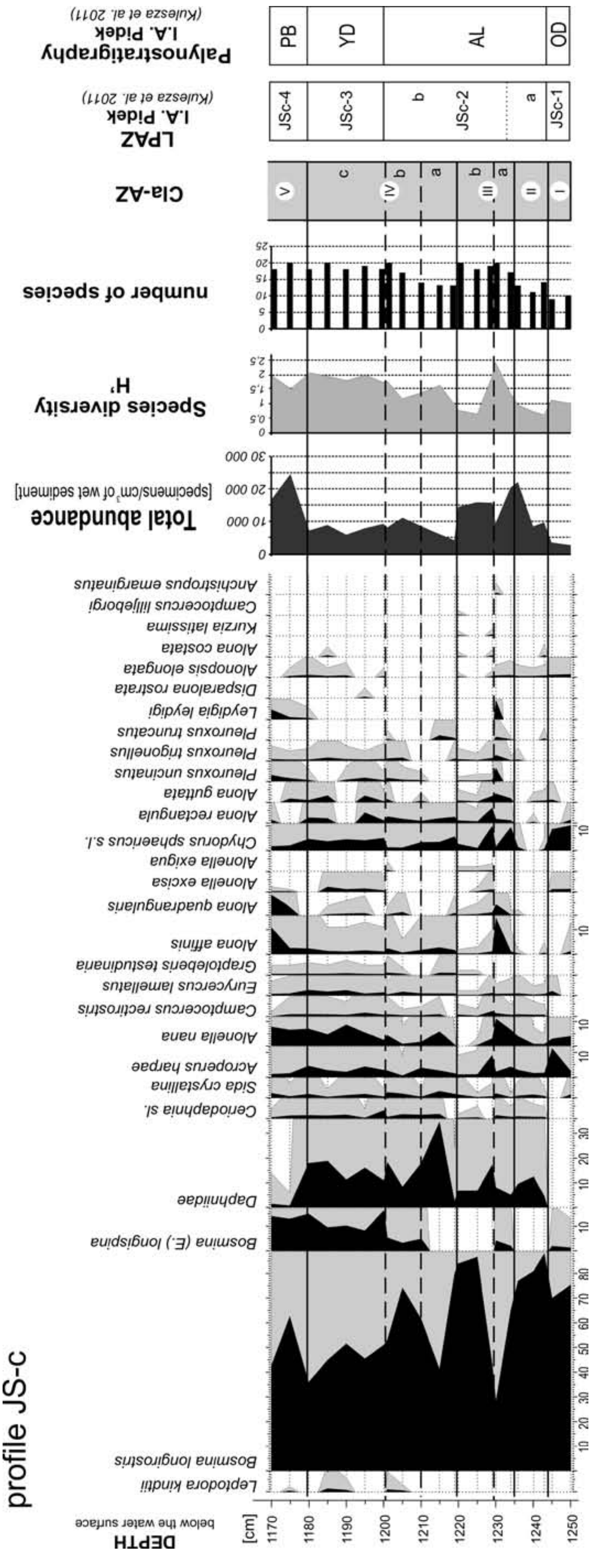


Fig. 2. Percentage diagram of cladoceran species composition for Słone Lake – JS-c profile.

RESULTS

A total of 33 taxa were identified in the lakes studied for the Late-Glacial – early-Holocene (early Preboreal) period. In the case of Lake Słone, 28 taxa were identified, in Lake Syczyńskie 31, and 28 in Lake Pniówno. Based on the species composition and the total abundance of cladoceran remains, Cladocera assemblage zones (Cla-AZ) were distinguished.

Lake Słone

In the studied section of profile JS-c, covering the Late-Glacial and the onset of the Holocene (early Preboreal period), 5 Cladocera assemblage phases were distinguished (Fig. 2).

Phase I (1250–1244 cm) was distinguished by a low number of Cladocera species (9–10) and low (2,600–3,400 spec. cm^{-3}) frequency of individuals. Relative abundance of open-water cladocerans exceeded 70%. Planktonic communities were represented by *Bosmina longirostris* and *Bosmina (E.) longispina*. Littoral communities were dominated by *Acroperus harpae*, *Chydorus* cf. *sphaericus*, and *Alonella nana*. Species *Alonopsis elongata*, *Alona rectangula*, *Alona guttata*, *Alonella excisa*, and *Alona affinis* were only found in low numbers.

Phase II (1244–1235 cm) showed an increase in the total abundance of Cladocera. The proportion of planktonic forms (over 88%), clearly predominating in the subfossil community, increased mostly due to the growing abundance of *B. longirostris*. In addition, *Daphnia* sp. replaced *B. (E.) longispina*. Littoral, plant-associated species *Camptocercus rectirostris* and *Eurycercus lamellatus* appeared.

Phase III (1235–1220 cm) – in this phase a significant increase in the number of species (19–21) as well as in the frequency of individuals (from 9,200 to 15,800 spec. cm^{-3}) suggested favourable conditions for the development of cladoceran fauna. Based on the disappearance of *B. (E.) longispina* and a distinctive change in diversity, two sub-phases were distinguished:

Sub-phase III a (1235–1229 cm) – with the occurrence of *B. (E.) longispina*; certain bottom-dweller species (*Alona quadrangularis*, *Pleuroxus uncinatus*, and *Leydigia leydigi*), as well as plant-associated *Pleuroxus truncatus* and *Pleuroxus trigonellus* appeared. Only *A. elongata* disappeared from the chydorid community. At a depth of 1230 cm, a significant decrease in the proportion of planktonic species was observed (down to approx. 55%), mainly resulting from the declining abundance of *B. longirostris* and, to a smaller extent, *Daphnia* sp.

Sub-phase III b (1229–1220 cm) showed no occurrence of *B. (E.) longispina*, and a major increase in the numbers of *B. longirostris*. Chydorid species such as *Graptoleberis testudinaria*, *Alonella exigua*, and *Kurzia latissima* appeared in the lake. After a temporal absence in phase II and sub-phase IIIa, *A. rectangula* and *A. excisa* reappeared.

Phase IV (1219–1180 cm) was distinguished by low frequency of individuals (4,000–11,000 spec. cm^{-3}) and a decreasing share of *B. longirostris* in the cladoceran population.

Sub-phase IV a (1219–1210 cm) was characterized by a low number of species (13–14), a drastic decline in *B. longirostris*, and the disappearance of *A. quadrangularis*, *A. excisa*, *A. exigua*, *P. trigonellus*, and *P. uncinatus*. The only new species absent in the previous sub-phase (III b) was *Pleuroxus truncatus*.

Sub-phase IV b (1210–1201 cm) showed an increase in the number of species to the level of 17–20, and an increase in the total abundance to approximately 10,000 specimens cm^{-3}. The planktonic species *B. (E.) longispina* appeared again, in numbers indicating permanent population. *Alona quadrangularis*, *Pleuroxus trigonellus*, and *P. uncinatus*, which had disappeared during the previous sub-phase, reappeared, but in much smaller proportions than before. The frequency of *B. longirostris* increased slightly.

Sub-phase IV c (1201–1180 cm) during this sub-phase, the number of species ranged from 18 to 21. The relative and absolute abundance of *A. nana*, as well as *A. guttata* and *Chydorus* cf. *sphaericus* increased substantially. *A. elongata* and *A. excisa* reappeared.

Phase V (above 1180 cm) was distinguished by an increase in total Cladocera abundance with a simultaneous decrease in *Daphnia* sp. Among chydorids, the highest increase was recorded in the case of *A. nana, A. affinis, A. quadrangularis*, and *P. uncinatus*. After a long absence (since sub-phase III b), *Leydigia leydigi* reappeared in the sediment.

Lake Syczyńskie

For the studied section of profile Sycz-1, covering the Late-Glacial and the onset of the Holocene (early Preboreal period), 5 Cladocera assemblage phases were distinguished (Fig 3).

Phase I (1550–1523 cm) – based on the change in the species composition, two sub-phases were distinguished:

Sub-phase I a (1550–1538 cm) – was the initial phase of cladoceran zooplankton development with a typical low number of species (9) and low cladoceran abundance (2,500–9,100 spec. cm^{-3}). With regard to ecological groups, the most numerous were the representatives of open-water taxa (over 70%). Initially, *Bosmina longirostris* predominated in the open-water community, with a

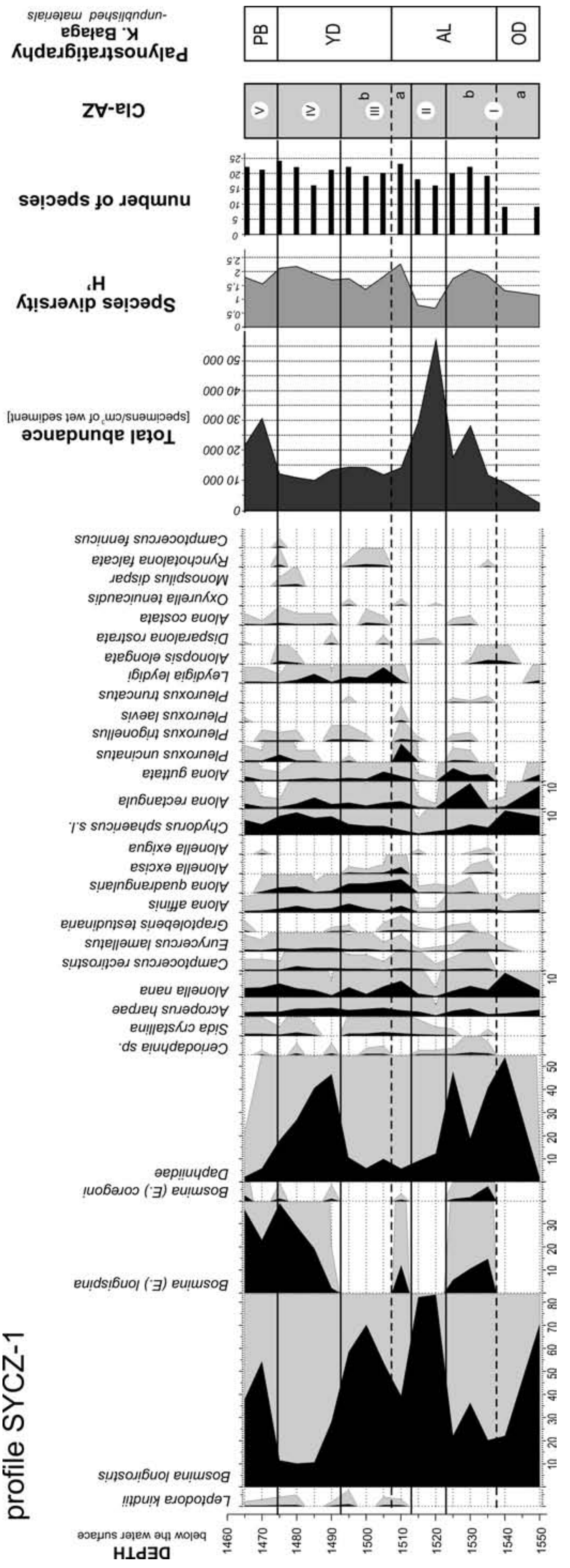


Fig. 3. Percentage diagram of cladoceran species composition for Syczyńskie Lake – Sycz-1 profile.

further increase in the abundance of Daphniidae. Among littoral cladocerans, pioneer, cold-tolerant taxa dominated: *Chydorus* cf. *sphaericus*, *Acroperus harpae*, and *Alonella nana*. Less abundant were *Alona rectangula* and *Alona guttata*. *Leydigia leydigi* – a species rarely reported in the early history of lake development – was also present.

Sub-phase I b (1538–1523 cm) – in this sub-phase, the cladoceran abundance increased (over 11,000 spec. cm^{-3}), as well as the number of species (19–22). Within this phase, new open-water taxa appeared in the fossil community: *Bosmina (E.) longispina* and *Bosmina (E.) coregoni*, but the predominance of Daphniidae remains (with the exception of sample 1530 cm) was sustained. Among littoral taxa, plant-associated species *Pleuroxus truncatus*, *Graptoleberis testudinaria*, *Eurycercus lamellatus*, and *Camptocercus rectirostris* started to play a significant role.

Phase II (1523–1513 cm) – in this phase, cladoceran abundance increased considerably, and then decreased. Despite this marked fluctuation, total cladoceran abundance remained high (29,200–57,200 spec. cm^{-3}). The number of taxa decreased to 16–18. The structure of subfossil assemblage was clearly dominated by *B. longirostris*, while Daphniidae remains decreased, and *B. (E.) longispina* disappeared completely. For the first time in the lake's history, *Oxyurella tenuicaudis* emerged in the population. The species is commonly regarded as typical of elevated trophy (Duigan 1992, Bjerring *et al.* 2009). A profound decline in species diversity (H'< 0.8) occurred as a consequence of the expansion of *B. longirostris* and a drop in the number of species.

Phase III (1513–1493 cm) – a further decline in total cladoceran abundance occurred. In comparison to the previous phase, the declining proportion of *B. longirostris* and Daphniidae was remarkable. At the same time, the total and relative abundance of many Chydoridae species increased (*A. quadrangularis*, *A. guttata*) or remained similar to that in phase II (*A. harpae*, *A. nana*). Taxa which reappeared in the assemblage after a temporary decline included: *Leydigia leydigi*, *Alonella excisa*, and *Rynchotalona falcata*. Also the predatory species *Leptodora kindtii* appeared for the first time. In this phase, from 19 to 23 taxa were identified. Based on differences in species diversity, two sub-phases were distinguished.

Sub-phase III a (1513–1508 cm) – in this sub-phase, oligotrophic *B. (E.) longispina* reappeared. Consequently, due to a further decrease in *B. longirostris* and a simultaneous increase in the abundance of species such as *A. quadrangularis*, *P. uncinatus*, *A. nana*, and *A. excisa*, the species diversity index increased (H' = 2.2). In terms of ecological groups, the proportion of plant-associated and sediment-associated chydorids increased.

Sub-phase III b (1508–1493 cm) – in this sub-phase, the planktonic taxa composition changed distinctively. *B. (E.) longispina* disappeared and *B. longirostris* increased in abundance. Among benthic cladocerans, *Pleuroxus uncinatus* disappeared from the assemblage, while *Rynchotalona falcata* – a taxon typical of sandy substrate and clear water (Duigan 1992), appeared. The species diversity index (H') ranged from 1.4 to 1.8.

Phase IV (1493–1473 cm) – in this phase low abundance of Cladocera continued (10,000– 13,000 spec. cm^{-3}). *B. (E.) longispina* reappeared in the open-water community, whereas the share of *B. longirostris* decreased significantly. Also the share of Daphniidae rose. Among the littoral species, *Graptoleberis testudinaria* reappeared. Despite its low abundance, the presence of *Monospilus dispar* is worth mentioning. This taxon, preferring sandy substrate and waters with a lower trophic status, appeared in the lake for the first and the only time.

Phase V (above 1473 cm) – during this phase, a distinctive, almost twofold increase in total cladoceran abundance occurred (more than 20,000 spec. cm^{-3}). The frequency of majority of pelagic species increased (*B. longirostris, B. (E.) longispina*, *Leptodora kindtii*). Only the numbers of *Daphnia* sp. remains decreased. Among the chydorids, the highest increase in total abundance was observed for *A. nana* and *A. guttata*. Due to an overwhelming growth of open-water species, however, the increase is poorly demonstrated in the percentage diagram. Species *Alonopsis elongata*, *Monospilus dispar*, and *Rynchotalona falcata* disappeared from the population, and *Graptoleberis testudinaria* appeared.

Lake Pniówno

Due to the lack of palynological and ^{14}C analysis for the bottom section of core Pni-1, the selection of a depth range representing the Late-Glacial was made based on a distinctive increase in total cladoceran abundance (Szeroczyńska 2006, Szeroczyńska, Zawisza 2007). Based on similarities in cladoceran assemblages between the two previously described sites, an attempt to use the cladoceran proxy for stratigraphic division of the Late Glacial was made. Such an approach has been successfully applied before (Szeroczyńska 1985, 2006).

For the studied section of profile Pni-1, 4 Cladocera assemblage phases were distinguished (Fig. 4):

Phase I (1890–1865 cm) – this phase was distinguished by low cladoceran abundance (600–2,240 spec. cm^{-3}) and low number of species (8–11). Pelagic species were dominated by *Daphnia* sp. remains, constituting from 24 to 73% of total cladoceran abundance. Another pelagic species, *Bosmina longirostris* was less abundant (4–9%). The most abundant littoral species were: *Acroperus harpae*, *Alonella nana*, *Alonopsis elongata*, *Chydorus* cf. *sphaericus*, *Alona affinis*, *Alona quadrangularis*, and *Alona rectangula*. Attention should be paid to the presence of *Leydigia leydigi*, as well as – very rare in the lakes studied – *Monospilus dispar*.

Phase II (1865–1825 cm) – during this phase, an increase in abundance occurred (13,400–29,900 spec. cm^{-3}), as well as a gradual increase in the number of species (8–21). In the littoral zone, taxa preferring warmer conditions appeared – *Camptocercus rectirostris* and *Pleuroxus trigonellus*. Planktonic cladocerans became dominated by *B. longirostris* (68–76%), with a less dynamic increase in absolute number of *Daphnia* sp. Consequently, the relative abundance of *Daphnia* sp. decreased (12–18%) as compared to the previous phase. Based on the presence of *B. (E.) longispina*, two sub-phases were distinguished:

Sub-phase II a (1865–1845 cm) – with increasing total

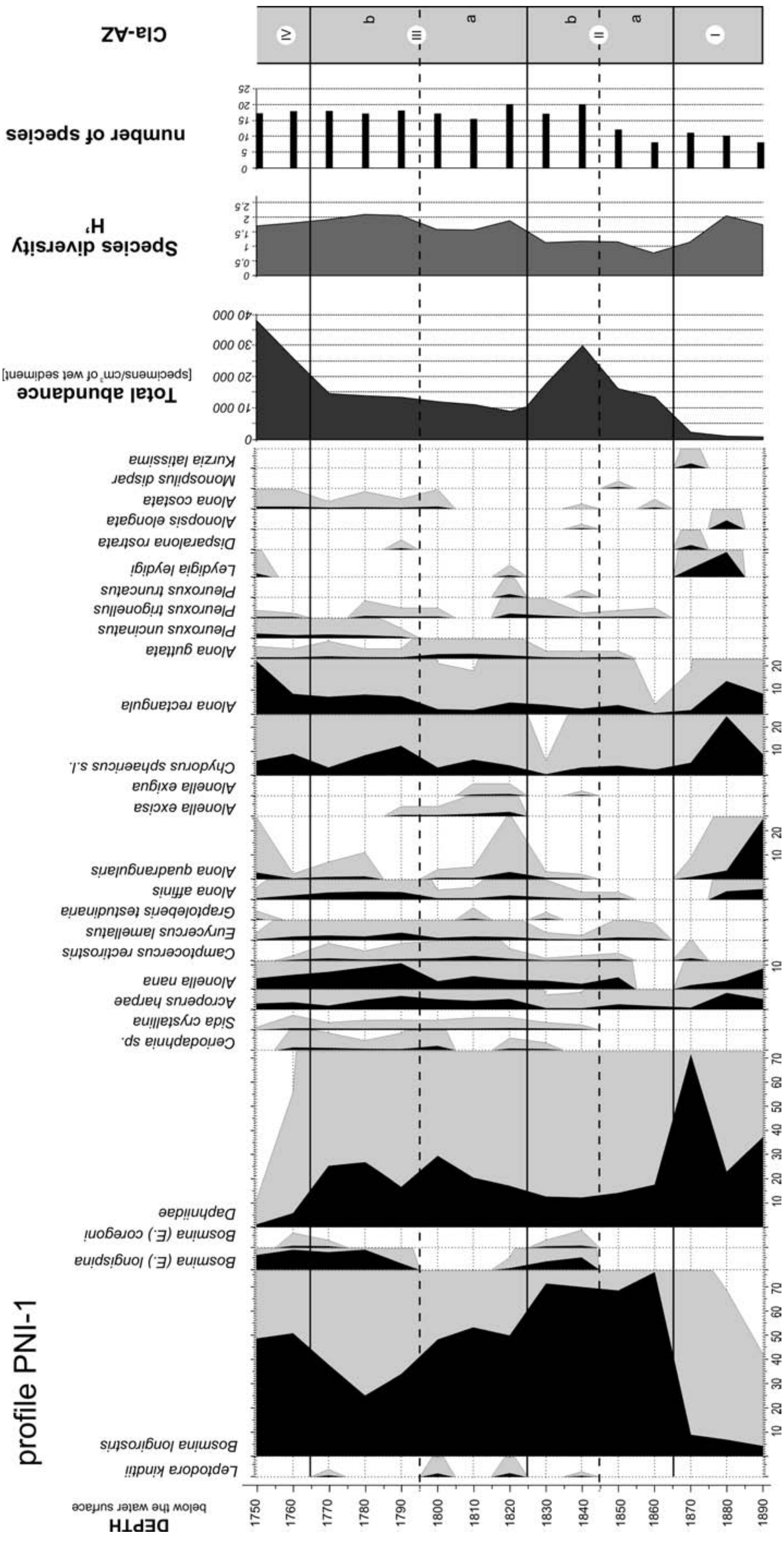


Fig. 4. Percentage diagram of cladoceran species composition for Pniówno Lake – Pni-1 profile.

abundance, but still low number of species (8–12). In the group of littoral cladocerans, *Alona quadrangularis* vanished temporarily from the population.

Sub-phase II b (1845–1825 cm) – with higher number of species (17–21). *Bosmina (E.) longispina* was found here for the first time, as well as several littoral species: *Sida crystallina*, *Graptoleberis testudinaria*, *Alonella exigua*, and *Pleuroxus truncatus*. *Alona quadrangularis* reappeared.

Phase III (1825–1765 cm) – distinguished by low total abundance (9,100–14,100 spec. cm^{-3}). The absolute number of species ranged from 16 to 21. A major change in the percentage structure of planktonic cladocerans occurred, involving: a clear decline in *B. longirostris*, a temporary vanish of *B. (E.) longispina* (sub-phase III a), and an increase in *Daphnia* sp. remains.

Sub-phase III a (1825–1795 cm) – in addition to the vanishing of *B. (E.) longispina*, in this sub-phase, *Alonella excisa* appeared in the lake for the first time. The number of species declined from 20 (at the beginning of the sub-phase) to 15–16.

Sub-phase III b (1795–1765 cm) – the planktonic species *Bosmina (E.) longispina* was present again. Among Chydoridae, the relative abundance of *A. harpae*, *A. nana*, *E. lamellatus*, *A. affinis*, and *A. rectangula* increased. *Pleuroxus uncinatus* was found in the sediments for the first time. Since then, the species established a stable population.

Phase IV (above 1765 cm) – distinguished by distinctively higher total cladoceran abundance (25,700–38,000 spec. cm^{-3}), regarding both planktonic and littoral species. The only taxon noticeably decreasing in numbers was *Daphnia* sp. In the group of littoral species, the highest increase was observed for *A. nana*, *A. quadrangularis*, *A. rectangula*, *C.* cf. *sphaericus*, and *P. uncinatus*. After a long absence, *L. leydigi* and *G. testudinaria* reappeared.

Radiocarbon dating results. The issue of chronology

For the profiles studied, five samples were radiocarbon dated. All dates confirm the Late-Glacial age of the deposits (Table 3). However, when confronted with the palynological data, the results obtained seem overestimated (Kulesza *et al.* 2011). The most probable reason for such an inconsistency is the reservoir effect (Walanus, Goslar 2004) resulting from the closeness of calcareous bedrock. A very similar inconsistency was found in Late-Glacial sediments from Lake Karaśne (Bałaga 2007) and Perespilno (Bałaga 2004), located in the Łęczna-Włodawa Lakeland. This effect is also commonly observed in majority of lake sediments of western and central Europe. Also Litt *et al.* (2003) stressed that the radiocarbon method is problematic in terms of establishing the Late Glacial time scale. Because of the ^{14}C plateaux, it is very difficult to define the duration of Late-Glacial biozones. A possible solution providing reliable chronology for palaeoecological changes in the Late-Glacial period is the application of correlation with well-dated annually laminated sediment sequences (Litt *et al.* 2001). Due to the good correlation of palynological data between the two lakes studied: Lake Słone (Kulesza *et al.* 2011) and Lake Syczyńskie (Bałaga – unpublished) with the record from laminated sediments of Lake Perespilno (Bałaga 2004), changes in the cladoceran assemblage could be referred to the Late-Glacial time scale.

DISCUSSION

Cladocera-based ecostratigraphy for lakes of the Chełm Hills Region

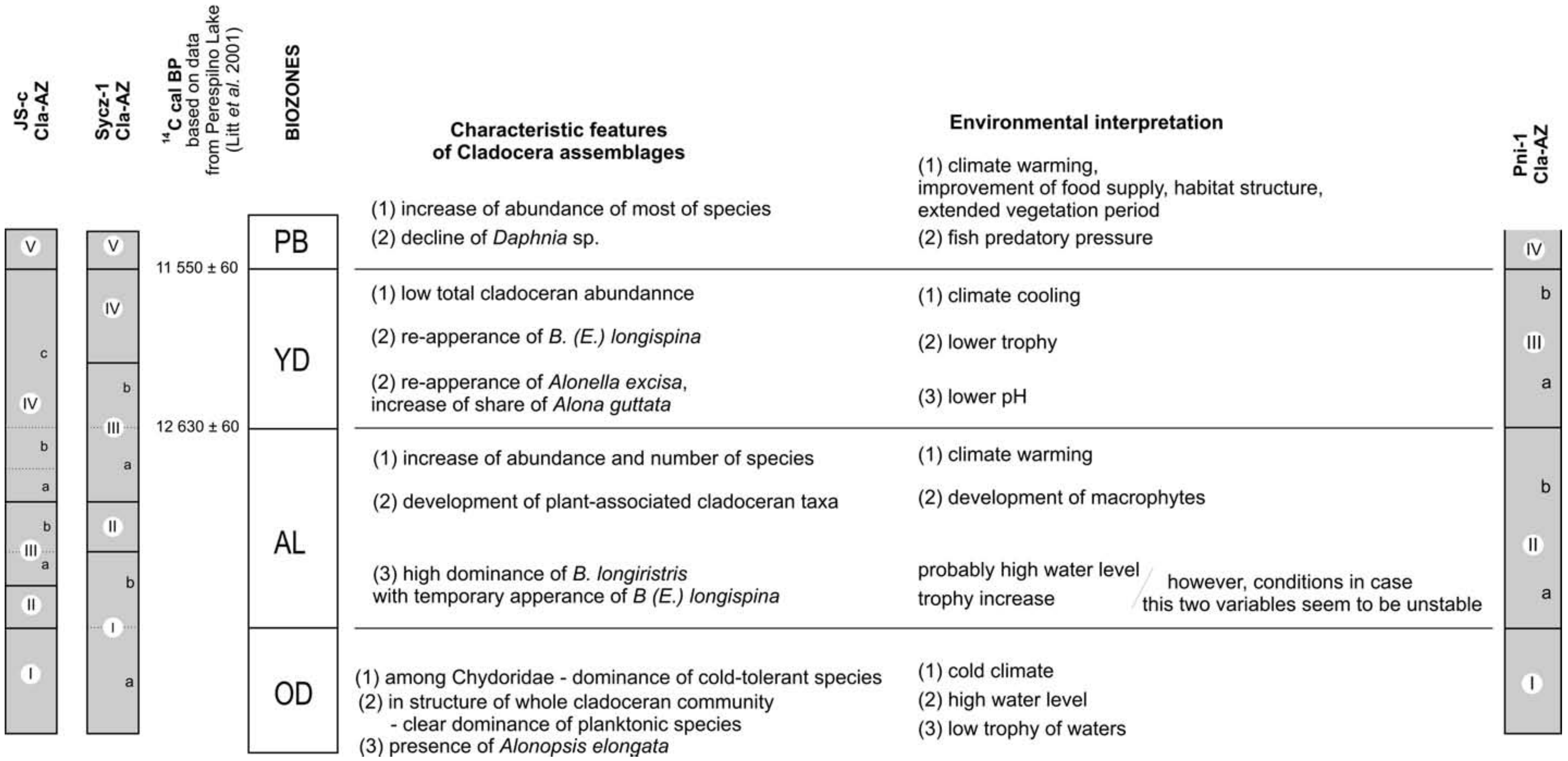
Based on results of detailed palynological research, the correlation between Cla-AZ from profiles JS-c and Sycz-1 was performed. Due to the fact that the study confirmed a strong zooplankton response to the climate-driven environmental factors of the Late Glacial, the authors could apply cladoceran-based "ecostratigraphy" for those closely located sites of similar character in order to distinguish the stratigraphic units of the Late Glacial. Based on common features of cladoceran assemblages confirmed for the two previous cores, the ecostratigraphic division for profile Pni-1 was proposed (Fig. 5), and used in the final discussion.

In the case of application of this method, attention should be paid to the accurate sampling resolution. Due to the low sedimentation rate, sediment compaction, and high dynamics of Cladocera population typical of the Late-Glacial, too low sampling resolution may result in missing the characteristic spots, crucial for the accurate correlation of the profiles. The sampling resolution applied to profile Pni-1, lower than in the case of the other two sites, but sufficient for the correlation of profiles, resulted in a lower number of Cladocera phases distinguished for this site.

Table 3

Results of radiocarbon dating

^{14}C lab. no.	Profile	Depth [cm]	^{14}C age (BP)	14C age (cal. BP, 2σ)		Material dated
				68.2%	95.4%	
Poz-32148	JS-c	1185	10 930±60	12 885 - 12 696	13 054 (1.4%) 13 027 12 973 (94.0%) 12 628	gyttja
Poz-32149	JS-c	1230	13 120±70	16 333 - 15 599	16 492 (95.4%) 15 234	gyttja
Poz-35971	Sycz-1	1498	11 420±60	13 362 - 13 224	13 416 - 13 147 cal BP	plant macrofossils
Poz-35972	Sycz-1	1523	11 630±60	13 578 - 13 384	13 668 - 13 316 cal BP	plant macrofossils
Poz-35973	Sycz-1	1527	11 840±60	13 794 - 13 611	13 838 - 13 472 cal BP	plant macrofossils



BIOZONES	Characteristic features of Cladocera assemblages	Environmental interpretation
PB	(1) increase of abundance of most of species (2) decline of *Daphnia* sp.	(1) climate warming, improvement of food supply, habitat structure, extended vegetation period (2) fish predatory pressure
YD	(1) low total cladoceran abundannce (2) re-apperance of *B. (E.) longispina* (2) re-apperance of *Alonella excisa*, increase of share of *Alona guttata*	(1) climate cooling (2) lower trophy (3) lower pH
AL	(1) increase of abundance and number of species (2) development of plant-associated cladoceran taxa (3) high dominance of *B. longiristris* with temporary apperance of *B (E.) longispina*	(1) climate warming (2) development of macrophytes probably high water level / trophy increase – however, conditions in case this two variables seem to be unstable
OD	(1) among Chydoridae - dominance of cold-tolerant species (2) in structure of whole cladoceran community - clear dominance of planktonic species (3) presence of *Alonopsis elongata*	(1) cold climate (2) high water level (3) low trophy of waters

Fig. 5. Correlation of Cladocera phases for profiles JS-c, Sycz-1 and Pni-1 supplied with main characteristics of cladoceran assemblages, and their environmental interpretation.

Cladoceran fauna succession in the Chełm Hills Region in view of literature data

Older Dryas (before 13 700 cal BP)

The beginning of limnic accumulation in all of the three lakes studied dates back to the Older Dryas. In the case of each of the sites, this biozone is represented by only one cladoceran phase or – in the case of Lake Syczyńskie – sub-phase (Fig. 5). A low number of species (8–11) and low frequency of individuals were typical. Total cladoceran abundance ranged from 600 to 9,100 spec. cm^{-3}. In all of the lakes, cold climate conditions were reflected in the species composition by an almost exclusive presence of cold-tolerant, pioneer chydorid species such as *Acroperus harpae*, *Alonella nana*, *Chydorus* cf. *sphaericus*, and *Alona affinis* (Harmsworth 1968, Whiteside 1970). The presence of less abundant *Alona guttata* and *Alonopsis elongata*, species preferring low conductivity and slightly acidic waters (Fryer 1968, Duigan 1992), might be related to the occurrence of bogs in the vicinity of the lakes (Kulesza *et al.* 2011). Because majority of studied Polish lakes have not been developed until the Alleröd, sites with the record of Older Dryas cladoceran succession are relatively rare (Szeroczyńska 1985, 1998b, 2006, Pawłowski 2012). More examples of such records are known from Europe (Hofmann 2001, Bennike *et al.* 2004), but due to their geographical remoteness or hydrological specificity, not all of them can be considered as reference sites.

High relative abundance of planktonic cladocerans (oscillating around 70–80%) is typical of cladoceran succession in lakes of the Chełm Hills Region. Such a high proportion of planktonic cladocerans in the early phase of lake development has not been recorded for other studied sites from the Łęczna-Włodawa Lake Group, namely Lakes Karaśne and Durne Bagno (Szeroczyńska 2003). This suggests the deep-water character of the lakes studied already in the early stage of their development.

Alleröd (13,700–12,700 cal BP)

The Alleröd period was definitely the most diverse stage of cladoceran community development. Depending on the site, from 3 to 5 phases (sub-phases) of fauna development were distinguished for the period (Fig. 5).

The response of cladocerans to the Early Alleröd climate warming involved an increase in their frequency. Maximum abundances and numbers of the species in the Late-Glacial were observed for this biozone. In the littoral zones of all of the lakes, stenothermal chydorid species (*Camptocercus rectirostris*, *Pleuroxus* spp., *Alona quadrangularis*) were present. Also macrophyte-associated chydorid species *Eurycercus lamellatus*, *Pleuroxus trigonellus*, *Pleuroxus truncatus*, and *Graptoleberis testudinaria* (Fryer 1969) appeared. This suggested intensive development of aquatic vegetation. Such a change in zooplankton composition must have been related to the improvement of climatic but also edaphic conditions. The development of chydorid species representing different ecological groups should be attributed to the diversification of lake habitats.

In addition to changes observed for littoral cladocerans, also the composition of the planktonic community, and particularly Bosminidae, was very informative. The temporal presence of *Bosmina (E.) longispina*, a species considered as an indicator of oligotrophic conditions (Flössner 1972, Frey 1988), suggested low water trophic status. The sub-phases involving the presence of this taxon, however, seem to be an exception rather than a rule. Phases with predomination of *B. longirostris* as the major planktonic species generally prevailed. The presence of *B. longirostris* as the only representative of Bosminidae suggests high water trophic status (Szeroczyńska 1998a). The periods with lower trophic status, reflected in the presence of *B. (E.) longispina*, might have resulted from intensive groundwater supply. Activation of groundwater circulation has been evidenced to be crucial in the Late-Glacial morphogenesis of lakes in the Polesie Region with calcareous sediments in the bedrock (Dobrowolski 2006).

Within the palynologically distinguished Alleröd period, the total Cladocera abundance declined (sub-phases JS-c: IVa-b; Sycz-1: III a, Pni-1: IIIa). This phenomenon, known from a number of central and north-eastern European lakes (Szeroczyńska 1998b, Hofmann 2000, Bennike *et al.* 2004), is an example of a response of zooplankton to the signal of climate cooling faster than that of terrestrial vegetation. The factors causing lower abundance may include: a shorter vegetation period during which cladocerans can reproduce effectively, as well as the slower growth and reproduction rate of zooplankton in cooler climate conditions.

Younger Dryas (12,700–11,560 cal BP)

This period has been widely discussed due to the availability of results of Cladocera analyses from numerous geographical locations all over Europe, representing different lake types (Goulden 1964, Harmsworth 1968, Hofmann 1986, 1996, Szeroczyńska 1998a, Duigan, Birks 2000, Zawisza, Szeroczyńska 2007, Milecka *et al.* 2011). The opinion on the occurrence of a secondary climatic fluctuation during the cold and dry Younger Dryas is common. It is mostly based on studies on small lakes, responding to environmental changes in a more visible manner. In those lakes, more demanding cladoceran species were present during warmer periods of the Younger Dryas. The lakes analysed in the scope of the present study should also become a subject of the discussion.

During the palynogically distinguished Younger Dryas, the littoral zone of the lakes studied was again dominated by the cold-tolerant chydorid species *Acroperus harpae*, *Alonella nana*, *Chydorus* cf. *sphaericus*, and *Alona affinis*. During this cooling period, however, the species diversity remained high, and after a short decline, also stenothermal species (*Camptocercus retirostris*, *Pleuroxus* spp.) were present. This suggests the occurrence of short periods of ameliorated climate conditions during the Younger Dryas. A change in the trophic status was possibly equally important for the lakes studied as the direct influence of the climate. Clear-water species, represented by *Alonella nana*, as well as species preferring lower-pH, acidic, low conductive lakes – *Alona guttata*, *Alonopsis elongata*, and *Alonella excisa* (Whiteside 1970, Bjerring *et al.* 2009) appeared. A tendency common to all of the sites studied was a decrease in the proportion of *Bosmina longirostris*, whereas *Bosmina (E.) longispina* reappeared in the assemblage. Again, such a change has been observed at other sites (e.g. Hofmann 2001), and may be interpreted as the oligotrophication of lake waters, or a response to decreasing pH. According to Flössner (1972), *Bosmina (E.) longispina* is more tolerant to low pH conditions than *B. longirostris*. A decrease in pH was also suggested by the presence of species *Alonella excisa* and *Alonopsis elongata*, and an increase in *Alona guttata* in all of the three lakes.

Early Preboreal (from 11,560 cal BP)

The cladoceran fauna responded to the Holocene warming with an overall increase in abundance. This is a well-known response reported from majority of sites (Duigan, Birks 2000, Hofmann 2000, Bennike *et al.* 2004), regardless of their size or geographical location (Szeroczyńska, Zawisza 2007).

Because almost all temperate species (*sensu* Harmsworth 1968) were already present in the lakes studied during the Younger Dryas, the absolute number of species did not increase. In the case of Lake Syczyńskie, it even decreased as a result of a decline of low-trophy species such as *Alonopsis elongata*, *Monospilus dispar*, *Rynhotalona falcata*, or *Camptocercus fennicus*. In the case of chydorids, the overall proportion of the cold-tolerant species decreased, whereas those typical of warmer waters (*Pleuroxus uncinatus*, *Alona quadrangularis* and *Leydigia leydigii*) were present, or even expanded. The littoral community changed only slightly. Changes in the plankton composition were more profound. The most noticeable was a decrease in the abundance of *Daphnia* sp., most probably related to an intensification of size-selective fish predation at the onset of the Holocene warming. Such a change was also observed in Lake Gościąż (Szeroczyńska 1998b), as well as in Lake Lake Bølling Sø (Bennike *et al.* 2004). Another change involved the expansion of *B. longirostris*, resulting in a slight decrease in species diversity in spite of a high number of species.

Environmental changes at the turn of the Younger Dryas and the Preboreal must have been very abrupt. This is suggested by a clear correlation between the phases of cladoceran development (Cla-AZ) and palynology (Fig. 5).

CONCLUSIONS

As a conclusion, the following remarks should be emphasised:

– In the case of all of the study sites, cladoceran fauna responded to climatic changes of the Late-Glacial and Early-Preboreal.

– The high relative proportion of planktonic to littoral taxa suggested the deep-water character of the newly-formed waterbodies. The general domination of planktonic cladoceran taxa throughout the Late-Glacial history of the lakes studied suggested the continuous presence of an extensive pelagic zone in these lakes.

– The number of phases distinguished in the case of all of the lakes for the Alleröd and Younger Dryas periods points to the high changeability of climatic and trophic conditions at that time. The sensitivity of records may result from higher vulnerability of small lakes to environmental signals.

– In the case of the lakes studied, the Younger Dryas/Preboreal boundary was marked by (1) an increase in total cladoceran abundance and (2) a decrease in Daphniidae remains.

– Due to common patterns identified in the species composition and total abundance of cladoceran remains for particular periods of the Late-Glacial, the description of the subfossil fauna composition can be used as a basis for correlation in further studies.

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