Studia Quaternaria, vol. 23: 37–45.

THE SIGNIFICANCE OF SUBFOSSIL CLADOCERA IN STRATIGRAPHY OF LATE GLACIAL AND HOLOCENE

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Abstract

This paper presents discussion on the results of subfossil Cladocera analyses from five lakes in Poland (Przedni Staw Lake, Perespilno Lake, Gościąż Lake, Imiołki-fossil lake and Ostrowite Lake). The Cladocera are represented in sediments by remains of planktonic (Bosminidae, Daphnidae) and littoral (Chydoridae) forms. Cladoceran assemblage phases ("ecostratigraphy") were determined on the basis of changes in dominance of indicator species and past ecological conditions were reconstructed. The results are being discussed from the viewpoint of climate change and anthropogenic activity and their role in the lake evolution. Moreover, an attempt to use the cladoceran phases for stratigraphic division of the Late Glacial and Holocene was made. During the Břlling/Allerřd interstadial, distinguished on the basis of pollen analysis, Cladocera indicated short phase of bad condition (dry or cold?), probably as the Old Dryas climate results. The beginning of Holocene is characterized, in mountain and lowland lakes, by high increase in the number of species and specimens of Cladocera. This described clear warming and marked the boundary Late Glacial/Holocene. It was indicated that the "ecostratigraphy" based on Cladocera can be useful for climatostratigraphy, if climate was the major factor controlling the development of freshwater lakes.

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Key words: stratigraphy, "ecostratigraphy" – biostratigraphy, climate, lakes, lacustrine sediments, subfossil Cladocera

INTRODUCTION

Freshwater lakes react intensely to climatic and environmental changes. Cladocera (Crustacea), which are a component of freshwater zooplankton, are a good tool for reconstructions of climatic and ecological changes. They react sensitively to changes in trophy, temperature and water level. Remains of these animals deposited in lacustrine sediments and especially changes of species composition and frequency enable reconstructing of past events. Analysis of subfossil Cladocera is one of the fundamental methods of paleolimnology (Frey 1986, Hann 1990, Korhola, Rautio 2001). The chitinous cladoceran remains have been used in investigations for several decades because they preserve well in gyttja, mud and peat sediments. The results obtained from Poland and from other countries indicate the usefulness of this method (Hofmann 1998, Korhola, Tikkanen 1991, Sarmaja-Korjonen, Alhonen 1999, Sarmaja-Korjonen *et al.* 2003, Szeroczyńska 2002). Past studies have mainly concentrated on lake and peat sediments deposited during the last 13,000 ^{14}C yr BP, but older sediments (*e.g.* Eemian) have also been studied (Mirosław-Grabowska, Niska 2005, Stankowski *et al.* 2003). Recently, many studies have used modern sediments. They enabled reconstruction of environmental preferences of the studied species in detail. The so-called surface sediment calibration-set approach is one of the best means of achieving information about the factors regulating the lake environments (Amsink *et al.* 2003, Korhola *et al.* 2000, Lotter *et al.* 1997).

The current paper presents discussion on results of subfossil Cladocera analyses of lacustrine sediments deposited during the Late Glacial and the Holocene in Poland and their usefulness to climatostratigraphy. The cladoceran analyses were accompanied by detailed analyses of pollen, chemistry and archaeology. Lakes whose development was mainly controlled by climate were chosen for this paper.

STUDY SITES

Lakes located in northern (Ostrowite Lake), central (Gościąż Lake, Imiołki-fossil Lake) and southern (Perespilno Lake, Przedni Staw Lake) Poland have been chosen for the discussion (Fig. 1). Sediments of these lakes were carefully studied by multi-proxy paleolimnological methods.

Ostrowite Lake

The lake is located in "Bory Tucholskie" National Park. It is one of the largest lakes in this region (280.7 ha in area and maximum depth of 48 m). 14 m thick sediments were deposited in the deepest part of the lake. The basal part of sediments has been dated to the Younger Dryas. Cladocera were analyzed from the entire sediment sequence (Gąsiorowski, Szeroczyńska 2004, Milecka, Szeroczyńska 2005).

Gościąż Lake

The lake is located in central Poland, in the Gostynin-Włocławek Landscape Park. The surface area of the lake is

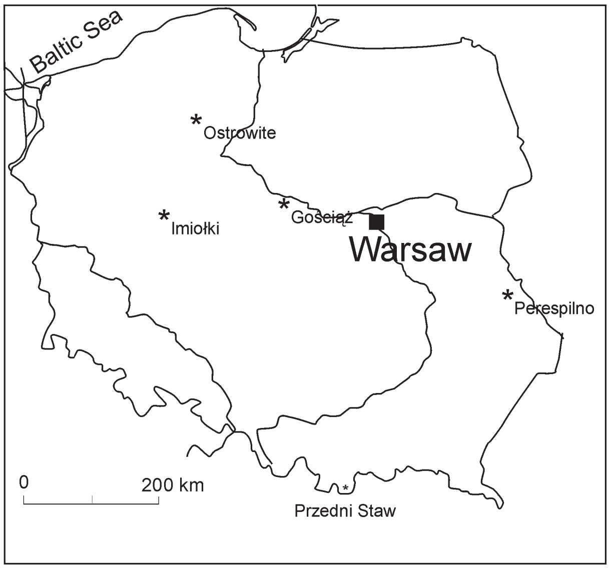

Fig. 1. Location of the lakes discussed in the paper.

45 ha and its maximum depth is *ca*. 28 m. The lake is unique since there is a continuous sequence of annually laminated sediments. The Cladocera were analyzed in several cores. The results obtain from the core T1/90 (Tobyłka Bay) were chosen for the discussion here. This sequence has a very clear record of environmental and climatic changes during the Late Glacial (Ralska-Jasiewiczowa *et al.* 1998, Goslar *et al.* 1998, Szeroczyńska, 1998a).

Imiołki-fossil lake

The site (5 ha in area) is located in the Lednica Landscape Park. It is located close to Lednickie Lake and is elevated 1 meter over its water level. The basin is filled up by sediments deposited only during the Late Glacial and is overgrown by meadows (Tobolski *et al.* 1998, Polcyn 1998).

Perespilno Lake

The lake is located in southeastern Poland, in the Łęczna-Włodawa Lake District. The lake has been intensively studied, since there are annually laminated sediments deposited during the Late Glacial. Only the Holocene part of the sediment sequence has been studied for cladoceran remains so far (Bałaga *et al.* 2002).

Przedni Staw Lake

This mountain tarn is located in the Tatra Mountains in the Polish Five Tarns Valley. The lake has a surface area of 7.7 ha and its maximum depth is 35 m. The Cladocera analysis was performed for mineral sediments of Late Glacial age and gyttja deposited during the Holocene (Krupiński 1983, Szeroczyńska 1984).

CLIMATE PERIODS AND CLADOCERAN STRATIGRAPHY – "ECOSTRATIGRAPHY"

The Cladocera – water temperature interactions have been studied for many years. One of the first researchers, who indicated the correlation between Cladocera frequency and climatic conditions, was DeCosta (1964). Harmsworth (1968) classified cladoceran species according to their temperature preferences into groups of arctic, species prefer cold-water and warm-water. Patalas (1990) who studied Canadian lakes, stated that climate was the most important factor controlling zooplankton development. In Polish studies, Cladocera analysis frequently has been used for climatic reconstructions (Sarmaja-Korjonen *et al.* 2003, Szeroczyńska 1998a, b, Szeroczyńska, Gąsiorowski 2002).

The Late Glacial

The Late Glacial period is represented in all cladoceran stratigraphies selected for this review. The cladoceran species composition changed many times during this period, indicating frequent changes in temperature. The cladoceran record was closely related to lake bathymetry and sedimentation rates and in layers rich in organic matter accumulated in a short time, a better resolution of the event was achieved by high sedimentation.

The lowland lakes, opposite to the mountain lakes, had relatively diverse zooplankton communities during the Late Glacial (Polcyn 1998, Szeroczyńska 1998a). High-resolution studies of Late Glacial sequences enabled discovering of short-term temperature fluctuations. Plant and animal remains were very well preserved in sediments of Gościąż Lake (Fig. 2) and Imiołki – fossil site (Fig. 3). The detailed analyses of these sequences enabled reconstructing of environmental changes since the Břlling to the Holocene. The Older Dryas, usually difficult to define by pollen analysis, is possibly reflected in the Cladocera remains. In Imiołki, during the Břlling/Allerřd interstadial distinguished on the basis of pollen analysis (Tobolski *et al.* 1998), a clear subphase of less favorable conditions for zooplankton (Fig. 3 – Cladocera zone 4a) is recorded (Polcyn 1998). Probably, this subphase reflects the cool Older Dryas period. A similar event (Fig. 2) was discovered in sediments of Gościąż Lake (Tobyłka Bay), where a significant decline of cladoceran frequency is also recorded between the Břlling and Allerřd periods (Szeroczyńska 1998a). It was studied also by Hofmann in Lobsigensee in Switzerland (Ammann *et al.* 1985) and by Bennike *et al.* (2004) in Břlling Sř in Denmark.

Moreover, species preferring warmer conditions (*Camptocercus rectirostris*, *Pleuroxus trigonellus*) occurred twice during the next cold period, the Younger Dryas. This may indicate that during the Younger Dryas there were short periods of milder climate conditions. Similar temperature fluc- tuations during the Younger Dryas have been recorded in others sites in Europe. During these events also cladoceran species composition varied (Hofmann 1983, 2000, Lotter *et al.* 1997, 2000).

The most distinct change in Cladocera taxa abundance and species composition was visible at the Late Glacial/Holocene transition in all lakes. The warm climate at the beginning of the Holocene induced increase in water temperature and favorable conditions for zooplankton. A rapid increase in species diversity and number of individuals was recorded in both, mountain and lowland lakes. The number of Cladocera species increased from 2 to 12 in Przedni Staw

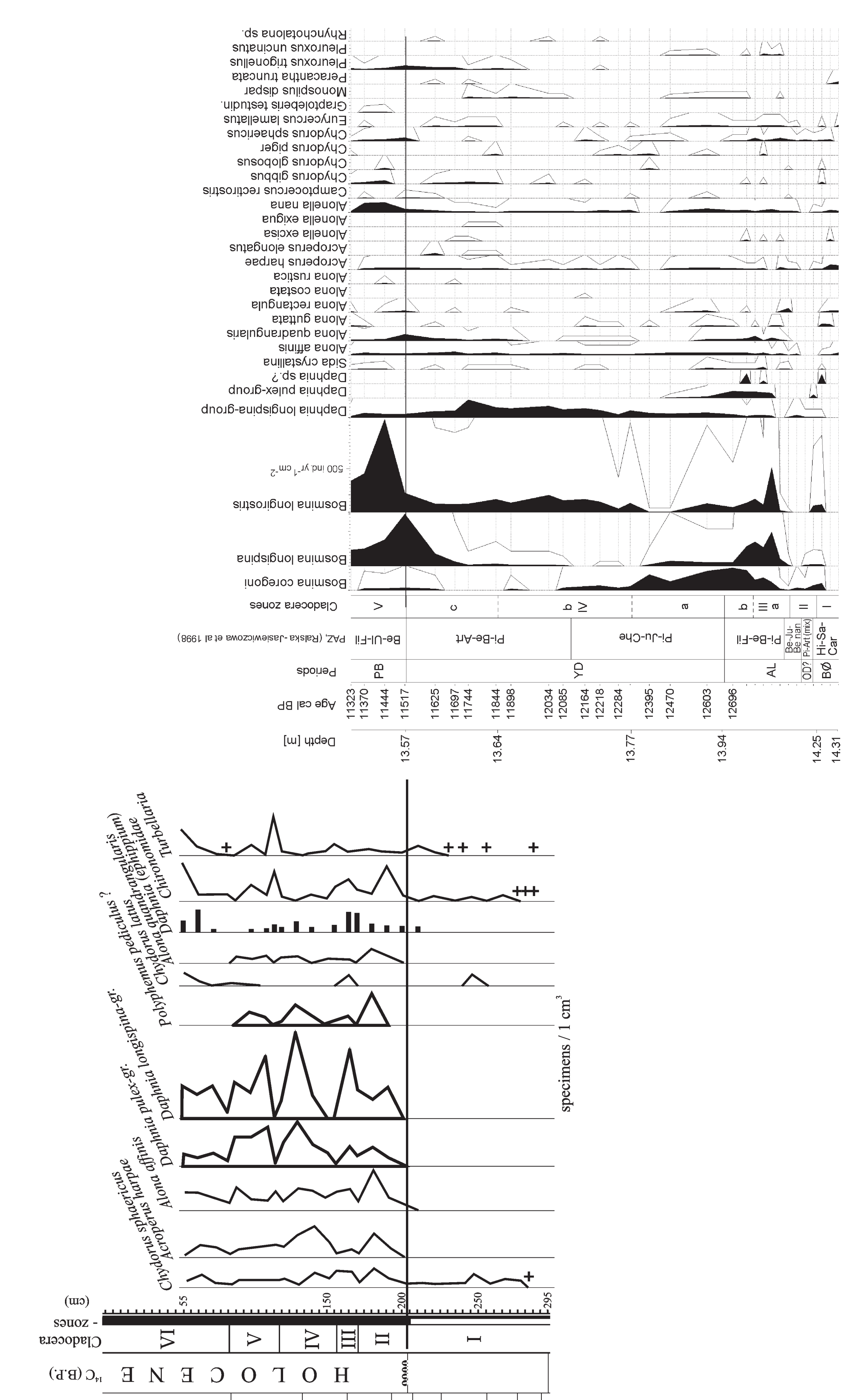

Fig. 2. Diagrams of number of Cladocera individuals in the sediments of lakes: Left – Przedni Staw (Tatra Mountains), Right – Gościąż – Tobyłka Bay T1/90 (central Poland), Late Glacial/Holocene boundary marked (after Krupiński 1983, Szeroczyńska 1984, 1998a, Ralska-Jasiewiczowa *et al.* 1998).

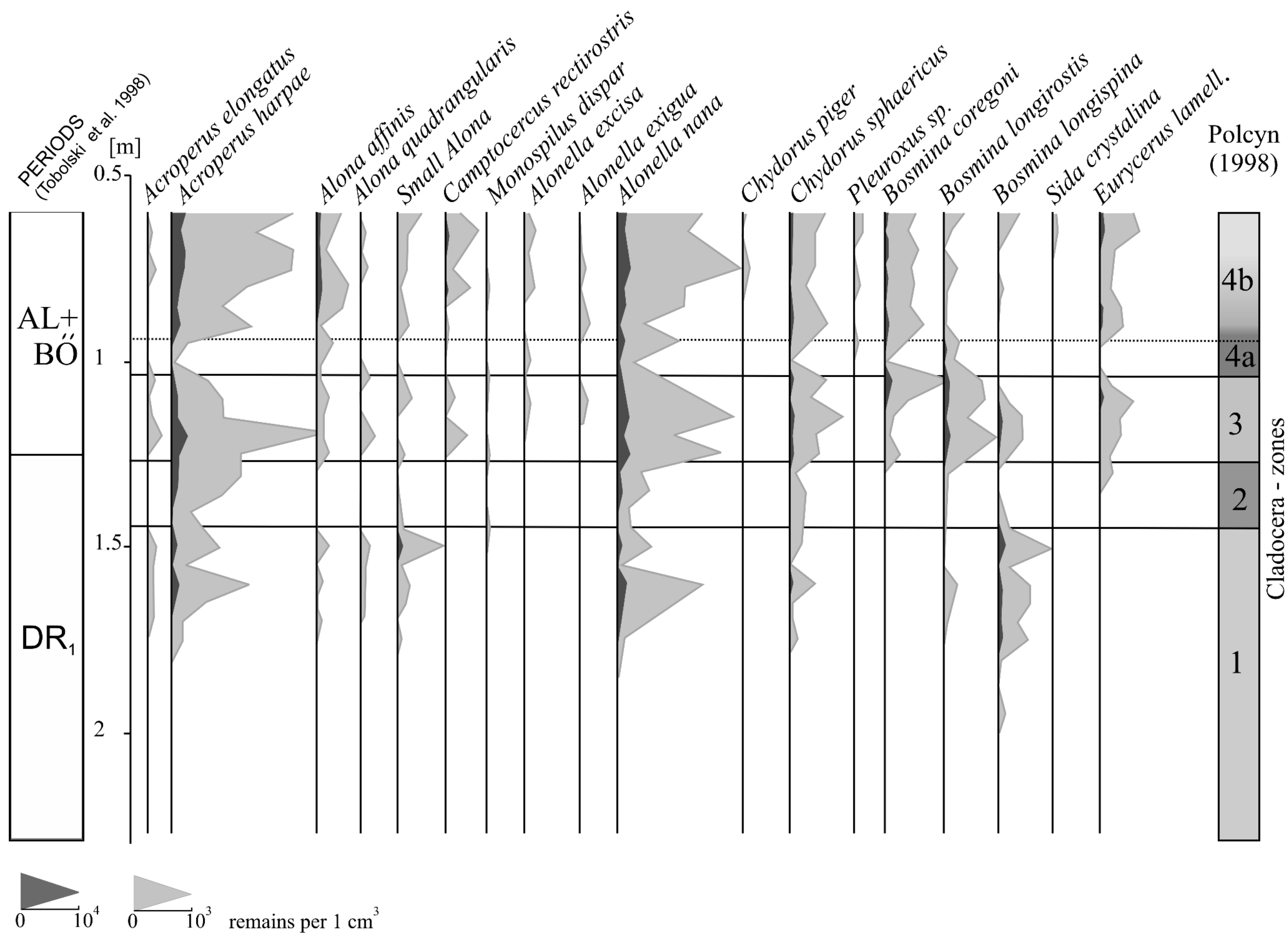

Fig. 3. Diagram of number of Cladocera individuals in the Late Glacial sediments of Imiołki – fossil lake (Lednica Lanscape Park) (after Tobolski *et al.* 1998, Polcyn 1998).

Lake (Tatra Mountains) and the number of individuals: *Bosmina longirostris, Bosmina (Eubosmina) coregoni* and *Alonella nana* increased from several hundreds to several thousands (indiv. yr^{-1}/cm^2 of sediment) in Gościąż Lake (Fig. 2). Similar changes in cladoceran assemblages at the Late Glacial to Holocene transition were discovered by Duigan and Birks (2000) in sediments of Krĺkenes Lake in Norway, and by Bennike *et al.* (2004) in Denmark. Such a distinguished change in cladoceran record can be used to distinguish a transition from a cool period to a warm period.

The Holocene

Preboreal period (10 000–9000 ^{14}C BP, chronozones after Mangerud et al. 1974)

Pollen and Cladocera records at the beginning of Holocene are characterized by an increase in the numbers of these microfossils. Moreover, species requiring better thermal conditions appeared and Late-Glacial species gradually disappeared (Ralska-Jasiewiczowa *et al.* 1998, Starkel 2002, Starkel *et al.* 1998). The warmer climate and the increase of water temperature are reflected by the appearance of not only numerous chydorids, but also of Bosminidae species. The taxa preferring higher trophic level, *i.e. Bosmina longirostris*, *Chydorus sphaericus* and *Alona rectangula* were numerous in shallow and in deeper lakes (Fig. 2, 4, 5). Pelagic species *Bosmina longispina* and *B. coregoni* as well littoral chydorids, which had been present since the Late Glacial, did also develop (Fig. 2, 5). The appearance of stenothermal species *i.e. Camptocercus rectirostris*, *Pleuroxus* sp. and *Alona quadrangularis* indicate the warming of climate.

Boreal (9000–8000 ^{14}C BP)

During the Boreal period a change of dominance occurred between *Bosmina* species, especially between forms of *Bosmina (Eubosmina) coregoni*-type, in some deeper lakes, mainly in northern Poland (*e.g.* Ostrowite Lake). Moreover, *Bosmina longirostris* (indicator of higher trophy), which, together with many littoral species, was the dominant during the Preboreal, gradually decreased. In late Boreal, the *Bosmina (Eubosmina)* taxa dominated, which preferred oligotrophic conditions (Flössner 1972, 2000), and lower pH (Nilssen, Sandřy 1986), suggesting altogether a decrease of trophic state, and perhaps an increase of water volume. Probably, inflow of nutrients into the lakes was low during this period and the trophic state decreased (Lotter, Boucherle 1984, Zawisza, Szeroczyńska 2005). The trophic state changed from meso- to oligotrophy in Ostrowite Lake and

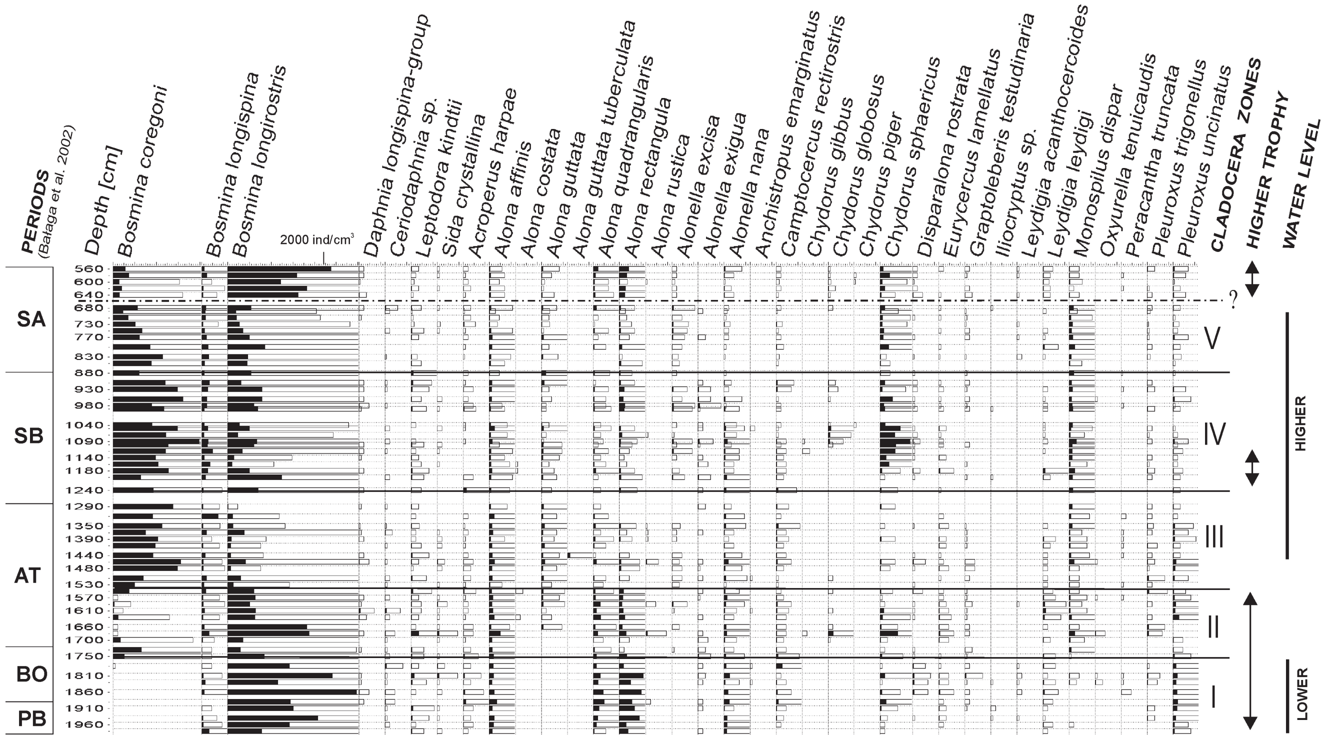

Fig. 4. Diagram of number of Cladocera individuals in the Holocene sediments of Perespilno Lake (Łęczna-Włodawa Lake District), with trophy and water level oscillations (after Bałaga *et al.* 2002).

from eutrophy to mesotrophy in Perespilno Lake at that time (Figs 4, 5). The lower trophic state in both lakes is also suggested by the lack of eutrophic *Pediastrum* (Bałaga *et al.* 2002, Milecka, Szeroczyńska 2005). The similar replacement species of *Bosmina longirostris* to *Eubosmina* were observed in this time in many other lakes in central Europe (Hofmann 1983, 1984).

Atlantic period (8000–5000 ^{14}C BP)

In Poland this period is often considered as a time of steady climatic conditions in the mesocratic stage of the glacial-interglacial cycle (Milecka, Szeroczyńska 2005). The cladoceran records suggest that during this period fluctuations in trophy and temperature of water were occurring (Gąsiorowski 2002, Gąsiorowski, Szeroczyńska 2004, Hofmann 1998, Sarmaja-Korjonen 2002). The ecological state of lakes in the early Atlantic appears to have been similar to that in the late Boreal. However, in more shallow lakes the early Atlantic was characterized by a great diversity of species, and increase in trophy (Fig. 4). During the late Atlantic the frequency of *Bosmina coregoni* and *B. longispina* individuals indicate development of the pelagic zone, and an increase in water volume. The high frequency of termophilous species indicates higher temperature. Simultaneously, higher proportions of meso/eutrophic species suggest increasing nutrient inflow. Climate was probably warm and humid, and therefore edaphic and climatic conditions were the most favorable for zooplankton during this period. In southern Finland and Sweden at the beginning of the Atlantic chronozone the rise of water level took place (Alhonen 1972, 1986).

During the Atlantic period, human activity was recorded in sediments of some lakes by the presence of pollen of synantropic plants (Ralska-Jasiewiczowa, van Geel 1998, Milecka, Szeroczyńska 2005, Noryśkiewicz 1995). Eutrophic Cladocera species appeared at that time, as a consequence of Neolithic human activities which causing higher nutrient input into the lakes. However, eutrophication at that time could be an effect of both warm climatic and anthropogenic factors (Gąsiorowski, Nalepka 2003). The human activity and its possible role in increasing nutrient inflow into lakes, makes climatic reconstructions based on Cladocera less reliable (Szeroczyńska, 2002, 1998b, Szeroczyńska, Polcyn 1998). However, the lakes chosen for this review were probably still only slightly influenced by human activity (Bałaga 2002, Milecka, Szeroczyńska 2005). Therefore, the increase in meso- and eutrophic species and the suggested changes of the trophic state, most probably were reflecting warmer and more favorable climatic conditions (Figs 4, 5). The warmer climate during the Atlantic caused overgrowing of many shallow lakes and their transformation into peat bogs (Szeroczyńska, Gąsiorowski 2002, Bałaga *et al.* 2003, Szeroczyńska 2003, Starkel *et al.* 1998, Pająkowski unpublished).

Subboreal period (5000–2500 ^{14}C BP)

A general change in cladoceran species composition was recorded in Ostrowite Lake and Perespilno Lake. A development to the maximum of eutrophic species characterized the beginning of the Subboreal. The rise of *Chydorus sphaericus*, *Bosmina longirostris* and replacement of forms *Bosmina*

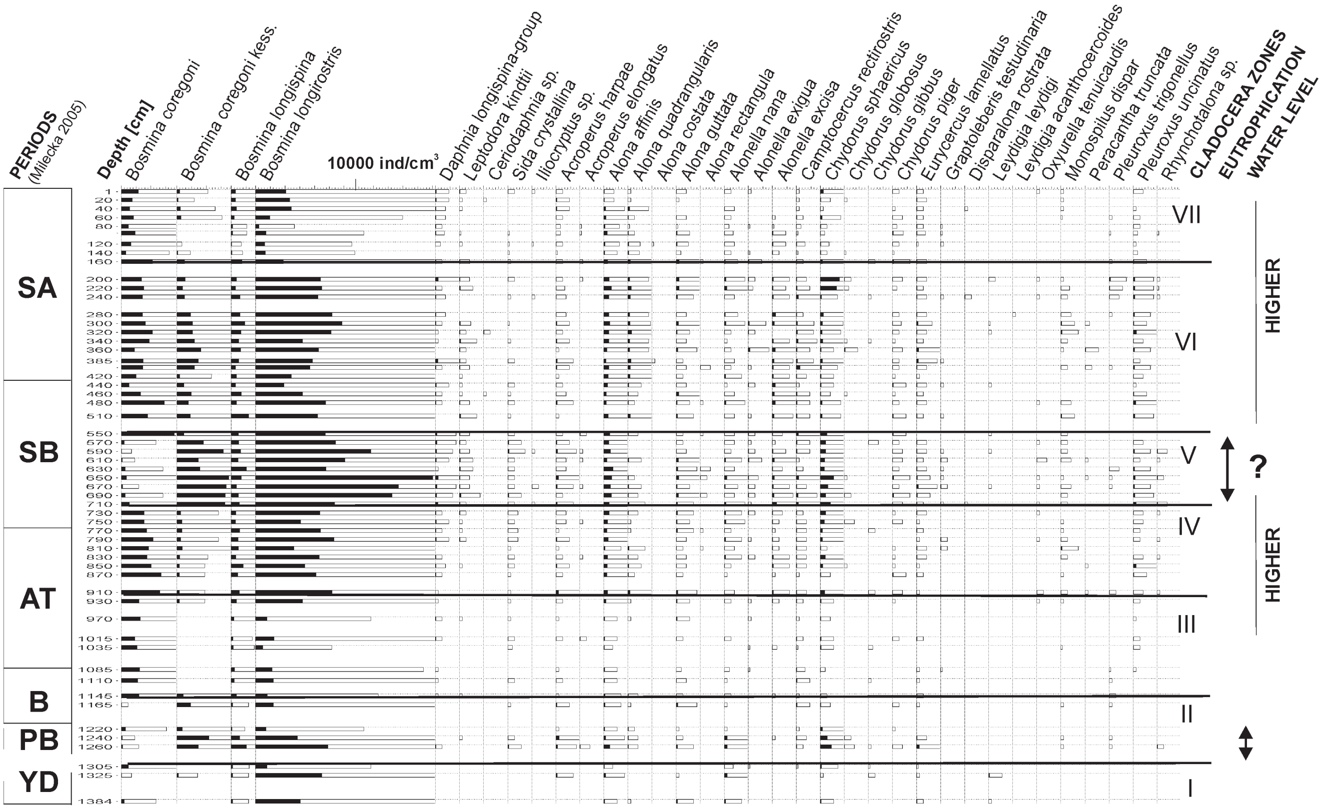

Fig. 5. Diagram of number of Cladocera individuals in the sediments of Ostrowite Lake ("Bory Tucholskie" National Park), with trophy and water level oscillations (after Milecka, Szeroczyńska 2005).

coregoni indicate higher trophy. *Daphnia longispina*-group was very abundant. An increase in *Pediastrum* curve also suggests high trophic state, but it is not possible to define whether it was influenced by climate or by human activities (Bałaga 2002, Milecka, Szeroczyńska 2005). A decrease in *Bosmina longirostris,* together with a repeated change of dominance between *Bosmina coregoni* – type as well as a decline in *Daphnia longispina* and *Chydorus sphaericus* in the early Subboreal suggest a decrease in the trophic state (Gąsiorowski, Szeroczyńska 2004). However, high proportions of pelagic and stenothermal species suggest a still mild climate and high water level. A decrease in many species occurred at the end of the Subboreal. It could have been a result of worse thermal conditions, indicated also by a decline in stenothermal species. Water levels were probably high during this period.

Subatlantic period (2500 ^{14}C BP – today)

The Bosminidae species dominated, and chydorids recorded during the Subboreal period were still present. The mesotrophic species *Monospilus dispar* had its maximum abundance during this period. Both the Perespilno Lake and the Ostrowite Lake were mesotrophic, and probably the climate was humid and temperate. Species associated with submerged vegetation, *e.g. Alona affinis*, *A. quadrangularis* and *Eurycercus lamellatus* increased gradually during the late Subatlantic period (Flössner 2000, Duigan, Birks 2000), probably indicating development of littoral zone (Fig. 4). Higher proportions of eutrophic species, *i.e. Bosmina longirostris* and *Chydorus sphaericus* in sediments of shallower lakes (*e.g.* Perespilno Lake), suggest increasing input of nutrients, probably related to human activity in the catchment. An entirely different development occurred in Ostrowite Lake during the early Subatlantic period (cladoceran phase 7b). At that time, littoral species decreased there and some eutrophic species (*i.e. Leydigia* sp., *Alona rectangula*) disappeared completely. The absence of these species and the decline of indicators of eutrophy (*Bosmina longirostris* and *Chydorus sphaericus*) suggest that (during the cladoceran phase 7b) water level dropped and the trophic state in Ostrowite Lake changed to oligotrophy/mesotrophy, the same as presently. The unchanged trophic state during the last millenium suggests that the lake has not been highly influenced by human activity and that the state of trophy was controlled by climate. Consequently, climate was cooler and more humid in northwestern Poland than in the southeastern part of the country, indicated by a difference in mire development. In the Łęczyca-Włodawa Lake District (southeastern Poland, Perespilno Lake) widespread, poor in water peat bogs were formed. In the peat bogs of the Tuchola Pine Forest (northwestern Poland, Ostrowite Lake) water level was frequently so high that cladoceran fauna recolonized the many peat bogs (Pająkowski, unpublished).

CONCLUSIONS

The species composition and frequency of Cladocera indicate that climate played a major role in the development of lakes during the Late Glacial and the Holocene. However, a different environmental setting and bathymetry of the studied lakes also controlled their development. Changes in subfossil Cladocera species composition and frequency reflected climatic conditions in mountain and lowland regions during the last 13,000 ^{14}C yr BP. This suggests a good correlation between zooplankton and climate and the usefulness of "ecostratigraphy", based on Cladocera analysis, in reconstructing past climate. Only high inflow of nutrients into lakes, resulting from human activities, may distort the interpretations. Generally, before the Middle Ages the influence of small settlements could not impact large lakes. The strong increase in the trophic state, visible in the uppermost sediments of the studied lakes was a result of the more intensive human activity since the Middle Ages. Therefore, the nutrient load-induced increase in eutrophic species prevents the use of Cladocera-based climate reconstruction for this period. In spite of this, the Cladocera seem very useful for climate reconstructions. The clear relationship between the relative proportion of planktonic and littoral Cladocera forms, in comparing with Late Glacial and Holocene climatic history, demonstrate water level oscillations correlated with dry and moist periods (Alhonen 1986).

To sum up, fluctuations in the cladoceran stratigraphy ("ecostratigraphy") can be correlated with the climate history. The species composition of Cladocera during the Late Glacial differentiated according to the temperature changes, and it was the richest during the period of Břlling and Allerřd. The dichotomy of the interstadial Břlling/Allerřd was marked in the majority of lakes by the collapse in the development of Cladocera species. A question remains open whether this record illustrates the cool or the drainage period. During the Late Glacial in the mountain lakes the species composition was very poor, there were present only the species considerably tolerant for the cold water (so called "artic species"). In the lakes situated at lower altitudes the species composition was richer and adequate to the morphologic lake type. The beginning of the Holocene, in lowland and mountain lakes, was characterized by high concentrations of Cladocera remains, suggesting warming of climate. During the Holocene, the development of Cladocera was characterized by distinct changes in planktonic and chydorid species diversity. The diversity increased in the Preboreal, slightly decreased in Boreal and increased to the high values in the late Atlantic, early Subboreal and late Subatlantic periods. Probably, good conditions for living zooplankton were influenced by mild, humid climate and nutrients inflow. A sudden increase of species indicating an excessive inflow of nutrients provoking rising trophy, might have been a result of human activity.

Recent studies indicate the significance of Cladocera in paleoclimatic investigation (Korhola *et al.* 2000, Lotter *et al.* 2000). Hofmann (Lotter *et al.* 2000) using linear-and unimodal-based inference models for the Late Glacial and the Holocene sediments of Gerzensee (Switzerland), stressed the important role of the cladoceran stratigraphy for reconstruction of mean summer temperatures. However, one should remember that Cladocera easily adapt to environmental conditions, and so the Cladocera analysis rather informs about trends in temperature changes than about past temperature values. Nevertheless, in Gerzensee the pollen and Cladocera transfer function results, cherish hopes of a relatively realistic model for climate reconstruction.

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