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SUBFOSSIL CHYDORID TAXA AND ASSEMBLAGES FROM LAKE SEDIMENTS IN POLAND AND FINLAND WITH SPECIAL REFERENCE TO CLIMATE

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Abstract

In this study we compared chydorid cladoceran (Chydoridae) taxa and assemblages from sediments of 6 Polish and 6 Finnish lakes and investigated if the difference in climate of these two countries can be detected in the cladoceran data. The data were analysed in terms of 1) average relative proportions of chydorid taxa during the history of each lake and by 2) redundancy analysis (RDA) to explain the present effect of environmental variables (altitude, area, maximum depth, mean annual temperature, mean summer temperature and length of the growing season) on species abundances. The redundancy analysis (RDA) enabled us to distinguish groups of taxa 1) with a high thermal preference 2) associated with small, cold-water lakes and 3) associated with shallow lakes. There are clear differences in the dominant chydorid taxa and in the relative proportions of many other chydorid taxa between the two countries since the end of the last glaciation. Although these differences first of all appear to reflect the climatic difference, the influence of many other environmental factors, controlling the living conditions of particular chydorids have been raised and considered. Further studies with larger data are needed before the role of climate can be reliably separated from other elements of environment.

Key words: subfossil Cladocera, chydorids, Finnish lakes, Polish lakes, climate, redundancy analysis

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INTRODUCTION

Chydorids are littoral cladocerans (water-flees) of the family Chydoridae. The aim of the present study is to compare chydorid taxa and assemblages from lake sediments in Poland and Finland and to investigate if the difference in climate between the two countries can be detected using the cladoceran data. The geographical location of Poland (49°–55° N) is more southern than that of Finland (60°–70° N). There are also several other environmental differences, such as the bedrock, the soil type and the intensity of anthropogenic influence on lakes. Therefore it is possible that these differences are also reflected in the chydorid taxa and assemblages.

Modern cladoceran assemblages in water bodies are usually investigated by taking samples of living animals. The samples may be taken from different parts of a lake and several times during the open-water season to get as complete picture of the fauna as possible. David Frey, the initiator of analysis of subfossil cladoceran remains stated, however, that investigating cladoceran remains from sediments gives the most complete picture of the taxa (Frey 1987).

Because the remains of molting and dead animals are distributed all over the lake bottom before the ultimate deposition, one sample can contain the taxa from all the habitats, from the littoral to the pelagial zone. Unfortunately, preservation is selective and remains of many cladoceran families are lost. However, the outer body parts of chydorids preserve well.

In this study, data on subfossil chydorid Cladocera from 6 lakes in both countries were selected for the comparison. These data were studied in terms of 1) average relative proportions of taxa during the lake history to examine differences in species abundances and by 2) ordination against environmental variables to study the effect of present environmental differences on species abundances. The use of subfossil material enables comparison of the entire chydorid taxa in the lake and, on the other hand, comparison of relative abundances of individual taxa.

STUDY SITES

The precise location, size and depth of the lakes are listed in Table 1.

Finland

Aitajärvi (Sarmaja-Korjonen 1999) is a small, shallow lake, situated in subarctic northern Finnish Lapland (Fig. 1).

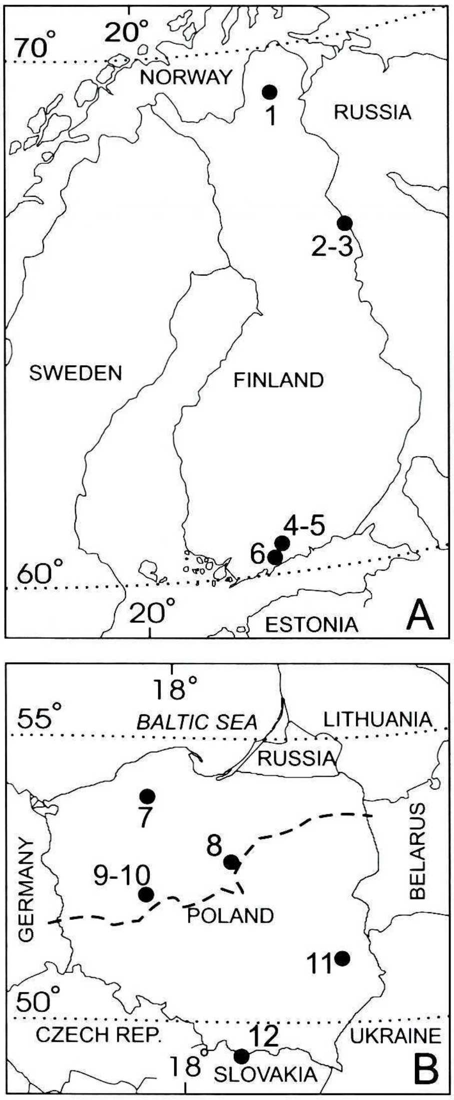

Fig. 1. Location of the studied lakes in Finland (**A**) and Poland (**B**). 1. Aitajärvi, 2. Putaanlampi, 3. Kuivajärvi, 4. Kaksoislammi, 5. Rutikka, 6. Iso Lehmälampi, 7. Ostrowite, 8. Gościąż, 9. Linie, 10. Lednickie, 11. Perespilno, 12. Przedni Staw. The broken line shows the southernmost limit of the Weichselian (Vistulian) Glaciation in Poland.

The lake was formed between 10,000 and 9500 BP when the Scandinavian Ice Sheet retreated from the area towards the SW. Aitajärvi lies near the northern limit of pine forests on sandy esker soil. The lake sediments (2 m) consist of gyttja above the initial silty clay layer. The lake trophy has not been quantified but it is probably low, judging by cladoceran taxa in the surface sediment sample (Sarmaja-Korjonen 1999).

Lake Putaanlampi and Lake Kuivajärvi (Ylimmäinen Kuivajärvi B) (Sarmaja-Korjonen, Hyvärinen 1999) are situated in Kuusamo, NE Finland, about 20 km south of the Arctic Circle (Fig. 1), close to the Russian border. The distance between the lakes is 10 km. The lakes have deposited calcareous sediments (lake marls) through the most of their history. The depth of the sediment at the coring point is 3 m in Putaanlampi and 2.85 m in Kuivajärvi. The present pH of the lake water (measured in November 1997) is 8.2 for Kuivajärvi and 7.9 for Putaanlampi. Despite the high pH, both lakes are ultraoligotrophic.

Rutikka (Sarmaja-Korjonen 2003) is a small lake in southern Finland (Fig. 1), near the transition of southern Boreal and Hemiboreal vegetation zones. It lies on the glaciofluvial deposits of the end moraine Salpausselkä I. Rutikka became isolated as an independent lake at the Pleistocene/Holocene transition (ca. 10,500–10,300 ^{14}C yr BP) when the water level in the Baltic basin fell by almost 30 m. The soil around the lake is glaciofluvial sand and the northern and eastern shores are paludified. The lake is dystrophic with a pH of 5.6 (November 2000). The sediments (3.5 m) consist of gyttja above the initial layer of silty gyttja.

Kaksoislammi (Sarmaja-Korjonen 2002, 2003) is a small humic lake (Fig. 1) situated 8 km southwest of Rutikka. Also Kaksoislammi became isolated from the Baltic basin at the Pleistocene/Holocene transition. The area is characterised by high bedrock outcrops surrounded by lower groves, many of them paludified. The soil between the outcrops is mainly till. The current pH is 4.9 (November 2000) and the trophic state probably low. The sediments (3 m) consist of gyttja above the initial layer of silty gyttja.

Iso Lehmälampi (Sarmaja-Korjonen, Alhonen 1999, Sarmaja-Korjonen 2001) is a small lake about 25 km north of the southern coast of Finland (Fig. 1). It lies on an elevated, rocky upland. Also this lake was isolated at the Late Pleistocene/Holocene transition. The topography is characterised by bedrock outcrops alternating with till layers. The lake is presently oligotrophic and acidic. The pH values frequently declined below 5.0 in the 1980's but they were 5.0–5.1 in early 1990's and increased to 5.4 in late October 1996. The sediments (2.5 m) consist of gyttja above the initial layer of silty gyttja.

Poland

Lake Ostrowite is located in the Pomeranian Lake District in northern Poland (Fig.1) and it is the largest lake in the "Bory Tucholskie" ("Tuchola Pinewoods") National Park. It lies on poor glaciofluvial sands, surrounded by pine forest of the Tuchola Forest complex. pH is ca. 8. The trophic state is presently at the transition from mesotrophy to eutrophy and, according to palaeobiological data (Milecka, Szeroczyńska 2003), it has not been higher during the lake history. In spite of this, as much as 13 m of sediment have accumulated during the Holocene. In the deepest part, where the core was taken, the sediments consist of fine-detritus gyttja with no or very low content of calcium carbonate. In the shallow northern part, the sediment contains more than 50% of calcium carbonate.

Lake Gościąż is a medium-size lake in central Poland, located in the Vistula Valley, 80 km NW from Warsaw (Fig. 1), where the river valley is broad. Annually laminated sediments accumulated in the lake during the Late Glacial and the Holocene and therefore the lake has been a subject of detailed studies (*e.g.* Goslar *et al.* 1993, Ralska-Jasiewiczowa *et al.* 1998, Szeroczyńska 1998c). It lies near the southern border of the Weichselian (Vistulian) Glaciation (Fig. 1). The bottom of the lake basin lies in Neogene (Miocene) sedimentary rocks (Churski 1998). At present it is surrounded by conifer

Table 1

Geographical and climatic parameters of the sites.
Mean temperature values from Finland represent an average from 1961 to 1990. The data were collected from climatological stations in Inari (Aitajärvi), in Oulanka (Kuivajärvi and Putaanlampi) and in Hyvinkää (Rutikka, Kaksoislammi and Iso Lehmälampi) (Finnish Meteorological Institute). The climatological data for Poland are after Leszczyński (1994).

Lake Name	Longitude °E	Latitude °N	Altitude m a.s.l.	Area ha	Max. Depth m	Mean annual temperature ° C	Mean summer temperature ° C	Growing season days
Finland								
Aitajärvi	27.23	69.13	250.0	6.4	2.0	-1.3	11.2	125
Putaanlampi	29.42	66.38	200.0	1.0	1.0	-0.9	12.7	130
Kuivajärvi	29.62	66.35	200.0	18.0	1.0	-0.9	12.7	130
Rutikka	24.88	60.73	130.0	2.8	2.0	3.9	15.0	175
Kaksoislammi	24.77	60.64	116.3	0.7	6.0	3.9	15.0	175
Iso Lehmälampi	24.60	60.35	91.7	2.8	8.1	3.9	15.0	175
Poland								
Ostrowite	17.60	53.80	124.2	280.7	43.0	6.8	16.5	210
Gościąż	19.35	52.59	64.2	45.5	23.6	7.9	18.1	215
Lednickie	17.38	52.54	109.8	339.1	15.1	8.0	18.0	220
Linie	17.40	52.55	110.0	5.8	8.5	8.0	18.0	220
Perespilno	23.57	51.43	165.1	24.3	6.2	7.3	17.8	215
Przedni Staw	20.05	49.21	1668.5	7.7	34.6	-1.1	7.0	150

forest. The lake is fed by groundwater (ca. 90% of inflow) and it is a dimictic, strongly thermally stratified eutrophic lake (Giziński *et al.* 1998). Most of the sediment sequence (ca. 20 m) is calcareous ferruginous gyttja.

The lakes Lednickie and Linie (Szeroczyńska 1998a, b) lie in the Great Poland Lowland Lake District, in a complex of lakes situated in the Lednica Landscape Park ca. 30 km from Poznań (Fig. 1). The lakes lie close to one another, in a glacial tunnel valley which was formed during the recession of the Scandinavian Ice Sheet after Poznań phase (ca. 17–18 ka BP). Lake Lednickie is a long and narrow basin, its lakeside area is deforested today and there has been intensive human activity for many centuries (Makohonienko 1991, Tobolski 1991). The lake is eutrophic and the sediments consist of carbonate detritus gyttja of varying thickness, accumulated since the Late Glacial. Lake Linie, ca. 1 km from the northern end of Lednickie, is a rather small and shallow lake. The lake shores are occupied by pine-birch woods. At present, Linie is eutrophic without any river inflow. The thickness of the Holocene sediments in the deepest part of the lake is ca. 13 m. The sediments consist mostly of homogenous gyttja with a fluctuating content of calcium carbonate (Filbrandt-Czaja 1993).

Lake Perespilno is located in the Łęczna-Włodawa Lake District (Fig. 1). It lies ca. 300 km out of the southern limit of the Scandinavian Ice Sheet (Goslar *et al.* 1999, Bałaga *et al.* 2002). As most water bodies located within the Włodawa depression, a tectonic unit of Precambrian origin, the origin of the lake is karstic/thermokarstic (Harasimiuk, Wojtanowicz, 1998). The lake consists of two shallow basins. Annually laminated sediments accumulated during the Late Glacial and the early Preboreal (Bałaga *et al.* 1998). The sediment (ca. 14 m) consists of an algal gyttja with or without carbonate. At present the lake is polymictic and eutrophic.

Przedni Staw (Szeroczyńska 1984) is a small, deep kettlehole lake in the granite massif of East Tatra Mountains in southern Poland (Fig. 1). The soil in the lake surrounding is *in situ* formed regolith. Przedni Staw lies above the present treeline and it is ultraoligotrophic. The very low trophic state has prevailed during the entire Holocene. The sediment is typical for oligotrophic lakes in Poland. Only 2 m of Holocene siliceous fine-detritus gyttja overlies a 1 m layer of Late Glacial silty-sandy gyttja (Krupiński 1983).

METHODS

Average abundances

Percent abundances of chydorid taxa in each subsample were calculated from the basic sum of total chydorids counted in the sample. Then an average of percent abundances of all samples was calculated for each taxon, showing its proportion of the chydorid fauna during the entire lake history. The lowermost, Younger Dryas spectra of Gościąż were excluded since the total number of chydorids was lower than 50 with only one or two species present.

Ordination methods

The spectra of chydorids in investigated sites were ordinated against environmental variables such as altitude, area, maximum depth, mean annual temperature, mean summer temperature and length of the growing season (Table 1). Because the past environmental conditions (*e.g.* lake area, the length of growing season and temperatures) were unknown,

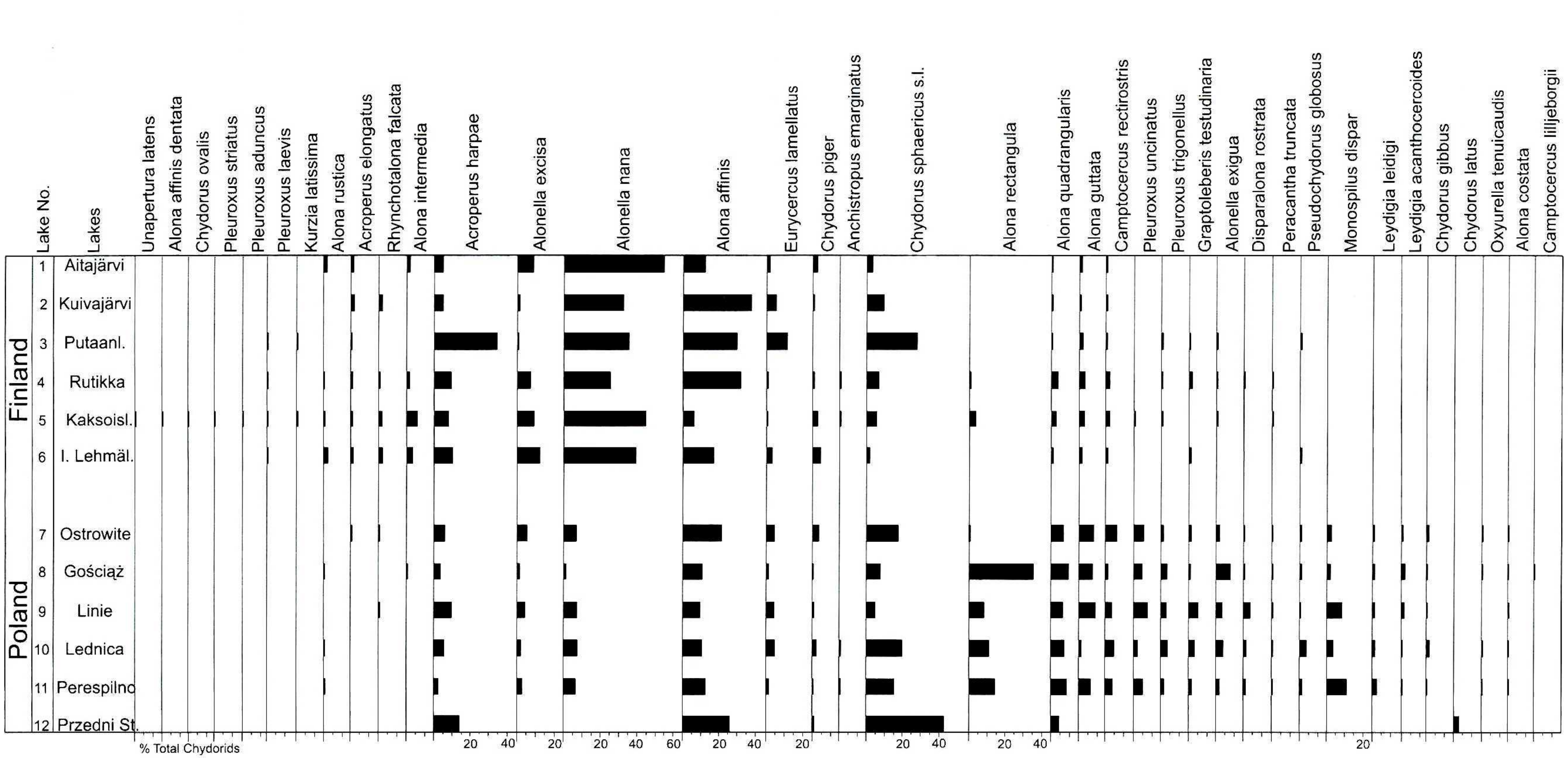

Fig. 2. Averages of percent abundances of chydorid taxa in the 12 studied lakes. First, percent abundances for chydorid taxa in each subsample were calculated with respect to the basic sum of total chydorids counted from the sample. Then an average of the percent abundances of all samples was calculated for each taxon, showing its proportion of the chydorid fauna during the entire lake history.

only the data from the topmost samples were used. An indirect ordination technique of detrended correspondence analysis (DCA) was applied first to determine whether linear or unimodal numerical techniques were more appropriate for the cladoceran data (ter Braak, Prentice 1988). The DCA results (detrending by segments, species data square-root transformed and rare species down-weighted) showed a clear linear response (length of gradient <2) and therefore redundancy analysis (RDA) was chosen. RDA can explain variation in community composition by a particular set of environmental variables. The methods have been described in detail by ter Braak & Prentice (1988) and ter Braak (1994). The calculations and triplot presentation were performed with Canoco 4.0 and CanoDraw 3.1 (ter Braak, Smilauer 1998).

RESULTS

Climate

In northern Finnish Lapland (ca. 70° N), the growing season (125 days) is very short (Table 1) compared to southern Finland (ca. 60° N – 175 days) or to Central Poland (50–53° N – 220 days). The difference is also reflected in the mean annual temperatures which vary from –1.3°C in Lapland to +8°C in central Poland, together with mean summer temperatures from +11.2°C in Lapland to +18°C in central Poland. Przedni Staw forms a clear exception as it represents alpine conditions high in the Tatra Mountains in southern Poland, where the growing season is only 150 days long and mean temperatures low.

Averages of chydorid proportions

Figure 2 shows average percentages of each taxon in all 12 lakes during the lake history. 30 taxa were found from Finland and 31 from Poland. In Finland *Alonella nana* and *Alona affinis* were clearly the dominants. *Acroperus harpae*, *Alonella excisa*, *Eurycercus lamellatus* and *Chydorus sphaericus* were also relatively abundant. *Alona intermedia*, *Alona rustica*, *Acroperus elongatus* and *Rhynchotalona falcata* are regularly found in Finnish lakes with small proportions, while in Poland they occur only sporadically.

Kurzia latissima, *Pleuroxus laevis*, *Pleuroxus aduncus*, *Pleuroxus striatus*, *Chydorus ovalis* and *Alona affinis dentata* were found in Finland (mainly in Kaksoislammi) but not in the Polish lakes under study. However, *Kurzia latissima* has been found occasionally in other Polish sites, *e.g.* it is relatively common (up to 10% of total Cladocera) in peat bogs of northeastern Poland (Szeroczyńska, Gąsiorowski 2002). *Pleuroxus laevis* has been found only in Przedni Staw mire in Poland (Szeroczyńska 1984).

Pleuroxus spp. are found sporadically in the mid-Holocene spectra of Finnish lakes. It is possible that *Alona affinis dentata* is more common in Russia than in Europe. It was found in the Holocene sediments of Lake Vankavad (Komi Republic, Russia) with proportions of 1–2% of total Cladocera (Sarmaja-Korjonen *et al.* in press). The subfossil finds from Lake Kaksoislammi were the first reported occurrences from Finland.

Unaperura latens is a recently found new species (Sarmaja-Korjonen *et al.* 2000) and known only from Finnish lake sediments so far. In Lake Njarga, northern Finnish Lapland, it was common and comprised up to 8% of Cladocera in the early and mid-Holocene (Sarmaja-Korjonen, unpublished data).

The dominants in Polish lakes are *Chydorus sphaericus*, *Alona rectangula* and *Alona affinis*. *Alonella nana*, *Alona excisa* and *Acroperus harpae* are found regularly, but in much smaller proportions than in Finnish lakes. *Chydorus piger* is equally common in both countries. In Finland the latter was often very abundant during the initial stages in newly formed lakes, together with *Alona intermedia*. Sporadic finds of *Anchistropus emarginatus* are regularly noted in sites of both countries.

Alona quadrangularis, *Alona guttata*, *Camptocercus rectirostris*, *Pleuroxus uncinatus*, *Pleuroxus trigonellus*, *Graptoleberis testudinaria* and *Pseudochydorus globosus* are more abundant and more regularly found in Poland than in Finland. *Monospilus dispar* is a common species in Poland, while in Finland it is very rare and was not found in the Finnish lakes under study. However, its subfossil headshields have been found at least in Lake Storträsk at the southern coast of Finland (Sarmaja-Korjonen, unpublished data) and in the sediments of the Ancylus Lake phase of the Baltic Sea (Sarmaja-Korjonen, Hyvärinen 2002), where *Pleuroxus uncinatus* was common too.

Leydigia leydigi and *Leydigia acanthocercoides* are regularly found in small numbers in Polish sediments. Presently *Leydigia acanthocercoides* appears to be absent from Finland. One postabdomen has been found in mid-Holocene sediments in southern Finland (Alhonen 1972). *Leydigia leydigi* is rare in Finland. Small proportions of *Chydorus gibbus*, *Chydorus latus* and *Camptocercus lilljeborgii* occur in Polish lakes but their subfossil remains have never been found in Finland.

Ordination analyses – control factors of modern species distribution

The results of the redundancy analysis (RDA) are shown in Fig. 3. The significance of all canonical axes was very high (Monte Carlo test significance $p<0.01$). The RDA triplot based on the two first axes explained 52.4% of the variance in the species data.

The distribution of species along axis 1 is most related to the lake area and the length of growing season and along axis 2 it is most related to the altitude and the mean summer temperature.

At least three groups of species can be distinguished. Firstly, there are species, which have a high thermal preference (*e.g. Alona quadrangularis*, *Alona rectangula*, *Camptocercus rectirostris*, *Graptoleberis testudinaria*, *Leydigia acanthocercoides*, *Pleuroxus trigonellus*, *Pleuroxus uncinatus*, *Monospilus dispar* and *Leydigia leydigi*). Secondly, there appear to be species of small, cold-water lakes (*Alonella nana*, *Alona affinis*, *Alona intermedia*, *Rhynchotalona falcata*, *Acroperus harpae* and *Acroperus elongatus*). Especially abundance of *Alona affinis* appears very negatively related to temperature. Thirdly, because taxa, such as *Alonella*

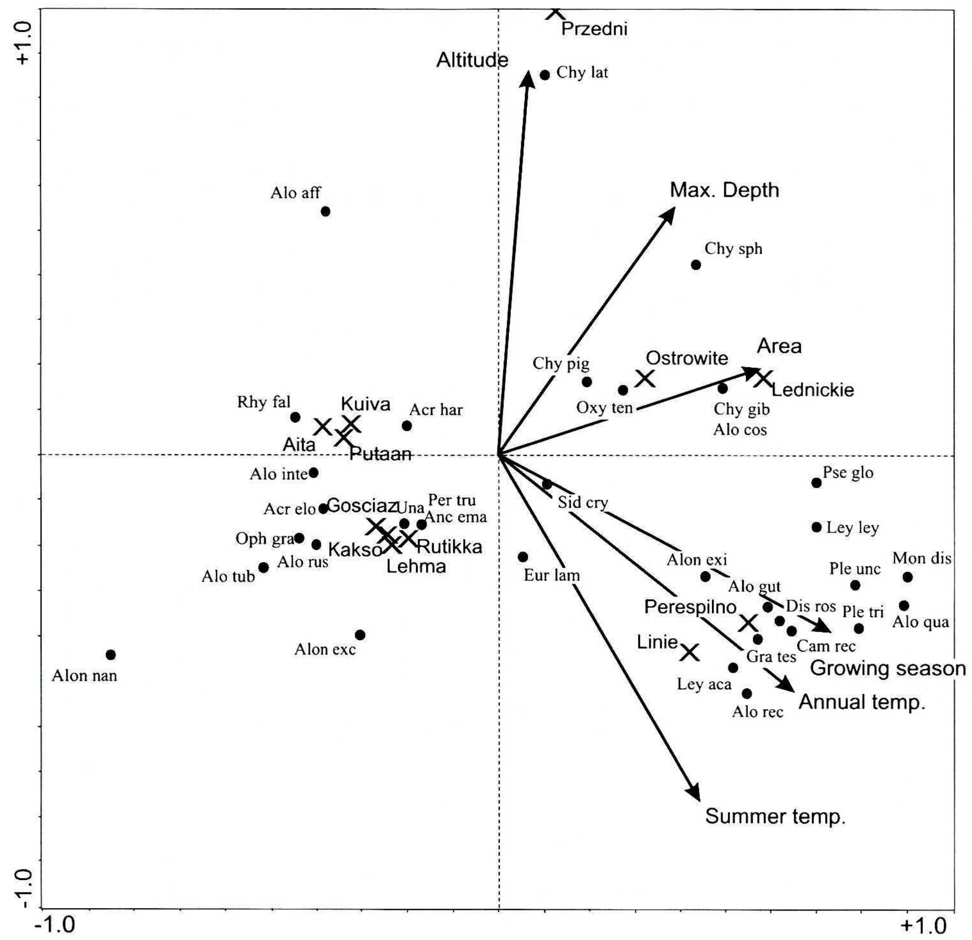

Fig. 3. Redundancy analysis (RDA) triplot displaying 52.4% (axis 1: 33.8% and axis 2: 18.6%) of the variance in the abundances. Species are indicated by points, sites are indicated by X-marks and quantitative environmental variables by arrows. The complete names of sites, chydorid taxa and variables are listed in Table 2.

nana, *Alona guttata* var. *tuberculata*, *Alonella excisa*, *Alona rustica* and *Ophryoxus gracilis*, have a strongly negative correlation to the maximum water depth they can be classified as shallow-lake taxa in the lakes of the present study.

Distribution of *Chydorus latus* is strongly related to altitude and maximum depth since this species was found only in Przedni Staw, which is a clear-water, deep mountain lake. *Acroperus harpae* and *Eurycercus lamellatus* are not sensitive to maximum depth and *Alona guttata tuberculata* and *Alona intermedia* to mean summer temperature. Surprisingly, abundance of *Chydorus sphaericus* appears to be related to maximum water depth.

Because 47.6% of variance in the species data remained unexplained, many other factors can also influence on distribution of chydorid Cladocera, *e.g.* pH, trophic state, composition of the macrophytic zone, etc.

Chydorid assemblages

Since only northern Poland was covered by the Scandinavian Ice Sheet during the Weichselian (Vistulian) Glaciation (Fig. 1) and the deglaciation took place already in the late Pleistocene, sediments of most Polish lakes cover a longer time span than the Finnish ones. The soils in many regions have a high content of carbonate. This results in a rather high productivity of lakes, reflected by the thickness of Holocene lake sediments (more than 10 m in Polish lakes while only 2.5–3 m in southern Finland). This does not concern Polish mountain regions (*e.g.* Tatra Mountains, Sudets), where acid metamorphic and plutonic rocks occur, and the lakes have low productivity.

Chydorus sphaericus s.l., *Alona affinis* and *Alonella nana* were typical pioneer species during the initial lake development in Poland. One exception is Lake Perespilno, where *Alona rectangula* was initially dominant (Bałaga *et al.* 2002). After this stage, each lake experienced its own individual succession of species and assemblages with a general trend of increasing species diversity during the Holocene. *Chydorus sphaericus*, *Alona affinis* and *Pleuroxus spp.* were the dominants in many lakes.

Since prehistoric times many Polish lakes have been significantly affected by human activities. Agriculture was introduced to Poland at the transition from the Mesolithic (*ca.* 7500–6500 BP) to the Neolithic Stone Age (*ca.* 6500–3700 BP). This stimulated erosion and was followed by an inflow of extra nutrients into lakes. The small initial settlements

Table 2

The list of complete names of sites, chydorid taxa and environmental variables coded in Figure 3

Name	Code
Chydorid taxa	
Acroperus elongatus	Acr elo
Acroperus harpae	Acr har
Alona affinis	Alo aff
Alona costata	Alo cos
Alona guttata	Alo gut
Alona guttata var. tuberculata	Alo tub
Alona intermedia	Alo inte
Alona quadrangularis	Alo qua
Alona rectangula	Alo rec
Alona rustica	Alo rus
Alonella excisa	Alon exc
Alonella exigua	Alon exi
Alonella nana	Alon nan
Anchistropus emarginatus	Anc ema
Camptocercus rectirostris	Cam rec
Chydorus gibbus	Chy gib
Chydorus latus	Chy lat
Chydorus piger	Chy pig
Chydorus sphaericus	Chy sph
Disparalona rostrata	Dis ros
Eurycercus lamellatus	Eur lam
Graptoleberis testudinaria	Gra tes
Leydigia acanthocercoides	Ley aca
Leydigia leydigi	Ley ley
Monospilus dispar	Mon dis
Ophryoxus gracilis	Oph gra
Oxyurella tenuicaudis	Oxy ten
Peracantha truncata	Per tru
Pleuroxus trigonellus	Ple tri
Pleuroxus uncinatus	Ple unc
Pseudochydorus globosus	Pse glo
Rhynchotalona falcata	Rhy fal
Sida crystallina	Sid cry
Unapertura latens	Una lat
Variables	
Altitude (m a.s.l.)	Altitude
Area (ha)	Area
Mean annual temperature (° C)	Annual temp.
Length of growing season (days)	Growing season
Maximum depth (m)	Max. Depth
Mean summer temperature (° C)	Summer temp.
Lakes	
Aitajärvi	Aita
Gościąż	Gosciaz
Iso Lehmälampi	Lehma
Kaksoislammi	Kakso
Kuivajärvi	Kuiva
Lednickie	Lednicki
Linie	Linie
Ostrowite	Ostrowit
Perespilno	Perespil
Przedni Staw	Przedni
Putaanlampi	Putaan
Rutikka	Rutikka

were not strongly reflected in the trophic state of lakes until the Bronze Age (3700–2700 BP), as is the case in Lednickie (Makohonienko 1991, Szeroczyńska 1998a, b) and Perespilno (Bałaga *et al.* 2002). In most Polish lakes a man-induced increase of trophy was clearly reflected by increases of *Chydorus sphaericus*, *Leydigia spp.* and *Alona rectangula* from the Middle Ages onward. In general, the signal is stronger in small lakes (Szeroczyńska 2002).

In southern Finland, large areas were submerged under the Baltic waters after the Scandinavian Ice Sheet retreat, and then emerged as a result of land uplift from the Pleistocene/Holocene transition onwards. In supra-aquatic areas the lake development began immediately after the deglaciation. In the areas of both types the typical pioneer fauna included *Alona intermedia*, *Alona guttata*, *Chydorus sphaericus* s.l., *Chydorus piger*, *Rhynchotalona falcata*, *Alona affinis* and *Alona quadrangularis*. At least *Chydorus piger* and *Rhynchotalona falcata* were bottom dwellers which were abundant before the macrophytic zone has developed.

Formed on the Precambrian bedrock of acidic rocks, the soils in many Finnish areas are unfertile and leaching of nutrients is very slow. Because of this, many Finnish lakes developed from mesotrophy/eutrophy in the early Holocene towards oligotrophy and low pH in the late Holocene (*e.g.* Tolonen *et al.* 1986). This is most probably reflected in the dominance of *Alonella nana*, *Acroperus harpae* and *Alonella excisa*, which appear to thrive in cold, acidic waters.

In Finnish lakes the number of species was the highest during the mid-Holocene, especially *Pleuroxus* spp., are present with small numbers, probably reflecting the milder climate at that period (*e.g.* Sarmaja-Korjonen 2003). Agriculture spread in Finland at the Late Stone Age/Early Bronze Age transition (*ca.* 3500 BP) (Vuorela 1998) but it was not strong until the early Iron Age (*ca.* 2000 BP onwards) when it became practised in a scale affecting the trophic state of lakes. Among the sites of the present study only Rutikka (Sarmaja-Korjonen 2003) experienced a slight rise of trophy at that period expressed by appearance of *Disparalona rostrata* and increase of *Chydorus sphaericus*.

DISCUSSION

According to the present results there are clear differences in the dominant chydorid taxa between Finland and Poland, first of all related to climate. Several authors have discussed the climatic tolerance of chydorids in Europe (*e.g.* Goulden 1964, Meijering 1983, Hofmann 1991, 2000). A classification of the European chydorid taxa according to their climatic tolerance was presented by Harmsworth (1968) but *e.g.* Hofmann (2000) found that Harmsworth's classification did not work in the Alps. According to Hofmann (2000) the species of cold conditions in the Alps were *e.g. Acroperus harpae*, *Alona affinis*, *Chydorus sphaericus*, *Acroperus elongatus* and *Alonella nana*. All these species, except *Chydorus sphaericus*, appeared more common in Finnish than in Polish lakes in the present study.

The results of the redundancy analysis (RDA) (Fig. 3) suggest that *e.g. Alona quadrangularis*, *Camptocercus rectirostris*, *Graptoleberis testudinaria, Leydigia acanthocercoides, Pleuroxus trigonellus, Monospilus dispar* and *Leydigia leydigi* are presently connected with higher temperatures. According to the averages of percentage abundances in the lake sediments (Fig. 2) these species were also more common in Poland than in Finland during the Late Pleistocene and the Holocene. Alternatively, *Alonella nana*, *Alona affinis*, *Rhynchotalona falcata*, *Acroperus harpae* and *Acroperus elongatus* which today prefer small, cold-water lakes (Fig. 3), were more common in Finland than in Poland (Fig. 2) during the Holocene. It is worth to note that *Leydigia acanthocercoides* which is usually regarded as a clearly southern species in Europe (Flössner 1972), showed a strong affinity to high temperatures also in our RDA analysis (Fig. 3).

The climate in Poland is clearly milder than in Finland. Although our results at first sight appear to reflect just this climatic difference, they should be interpreted with caution. For example, *Leydigia leydigi*, in agreement with its affinity to warmer climate suggested by RDA analysis, is rare in Finland. However, according to Mäemets (1961) and Røen (1995) living *Leydigia leydigi* adults can be found through the winter in Estonia and Denmark. This suggests that the species is cold-tolerant. It has also been found from the Holocene sediments of Lake Mezhgornoe, which is located at the modern tree-line in the pre-Polar Urals, northeastern European Russia (Kultti *et al.* 2003). Also it is present in sediments of Lake Kharbei, in the arctic tundra of northern European Russia (Sarmaja-Korjonen, unpublished data). It is therefore probable that its rarity in Finland is connected with factors other than climate, *e.g.* the content of calcium carbonate in soils.

There are many environmental factors other than the climate, that affect the living conditions of chydorids in lakes. For example, Polish soils have a higher carbonate content than soils in Finland. Also the trophic state of most lakes in Poland is increased by human activity, while almost all Finnish sites of the present study are oligotrophic. These differences are probably also reflected in the cladoceran assemblages. The present study is based on 12 lakes only and there is a large variation in their physical and chemical properties. For example the larger depth of Polish lakes chosen to the study is possibly the reason why *Chydorus sphaericus* s.l. appeared more common in Poland (compare Figs 2 and 3). Also the number of environmental variables considered in the RDA was small (6) and *e.g.* pH and trophy were not included because the relevant data were not available from all lakes. Therefore, the climatic difference should be studied on a larger set of lakes, and for such a study similar lakes should be chosen from both countries.

The present study is the first step to investigate how much the climate and other environmental variables influenced the chydorid compositions in lakes in Poland and Finland. These preliminary results show differences between these two countries and suggest several promising possibilities for further studies, *e.g.* the proportion and role of sexual reproduction indicating the length of the open-water season (Sarmaja-Korjonen 2003, Sarmaja-Korjonen in press) and collection of a larger data set from both countries. Further studies are needed before the role of climate can be more reliably separated from other environmental variables.

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