

Cladocera remains from the sediments of remote cold lakes: a study of 294 lakes across Europe

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With 9 figures and 6 tables

Abstract: Sediment cores were taken from 294 lakes in 12 different remote mountain areas in Europe (from Greenland to Finland in the north and from Spain to Bulgaria in the south) for the analyses of Cladocera remains. Surface samples (0 – 0.5 cm) were analysed to examine the contemporary distribution of Cladocera. These were compared with sub-samples from the pre-industrial period (depth > 15 cm) to assess changes in species composition over time. In total, the remains of 42 different Cladocera taxa were identified in the surface sediments. The number of taxa per lake decreased from north to south, which also corresponded to a gradient of increasing altitude. On average, 12 taxa per lake were found in northern regions (Scotland, North Finland = high-latitude lakes) and *ca.* 4 taxa in the southern regions (Romania, Bulgaria, Slovenia, Austria = high-altitude lakes). The most common taxa, occurring in the majority of lakes, were *Alona affinis*, *Chydorus sphaericus*, *Daphnia longispina* gr., *Alona quadrangularis* and *Acroperus harpae*. Most other species were also widely distributed across several of the lake districts, suggesting that all cold water lakes in Europe are equally favourable habitats for cladocerans. *Eurycerus glacialis* and *Eubosmina longispina* were the most abundant species restricted to specific regions, the former to Greenland and the latter to Northern Finland. Multivariate statistical analyses showed that the taxa assemblages were primarily determined by biogeographical factors. Dispersal limitations at high altitudes may be the most important factor for the differences in species diversity among districts. Physical, chemical and trophic conditions appeared to explain little of the variation independent of geographical location, though the potential role of fish predation is discussed. Comparisons between the top and the bottom section of the sediment cores revealed similar taxa numbers, but most cores, although only marginally, differed in taxa assemblage.

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Introduction

High-mountain and high-latitude lakes above the tree-line generally share a number common characteristics. Most of them are small and rather shallow, normally between 10 and 15 m deep, although some of them can be deeper than 100 m. These are systems whose functioning is highly influenced by physical variables such as light, temperature and duration of ice cover (AGUSTI-PANAREDA & THOMPSON, 2002). Winter is long and the water bodies are ice covered for several months and experience relatively low light penetration, a short open water season and low food supply. In most lakes, nutrient concentration and thus primary productivity are low. The limited taxa are organised in relatively simple food webs (GLIWICZ, 2003) and are highly sensitive to environmental change (WRONA et al., 2005). In this demanding environment, aquatic invertebrate communities can be stable and abundant.

Cladocera (Crustacea: Branchiopoda) are a major component of the planktonic and benthic crustacean fauna in high-latitude and high-altitude lakes (RAUTIO, 2001; O'BRIEN et al., 2004; BIGLER et al., 2006; TOLOTTI et al., 2006). They are tolerant to extreme environmental conditions and are one of few aquatic animal groups that are able to persist in remote lakes and build up viable populations. They include the primary herbivores in lakes and contribute to maintaining a low phytoplankton biomass, but they also play an important role in recycling nutrients in the water column. In addition, they form a large proportion of the diet of planktivorous fish and invertebrates. Their distribution, species numbers and abundance can vary substantially among lakes and reflect both the geological history of the area and the present-day conditions in the water body (CARTER et al., 1980; SHURIN et al., 2000). Most high-altitude and high-latitude lakes have been intensively affected by cold climate in the past. As recently as 8,000 – 20,000 years ago many were covered with glaciers in the form of ice sheets (northern Europe) or mountain glaciers (the Pyrenees, the Alps and the Tatras). Others (in south-east Europe - the Rila and the Retezat Mountains) were located on the edge of permanent ice cover where low temperatures prevailed and extended areas were covered with snow and ice for prolonged periods. While contemporary distributions of cladocerans may potentially reflect the species present during the pre-glacial period, they may also be highly affected by or entirely determined by more recent secondary colonisation.

Understanding cold arctic and alpine lakes is a major theme in current limnology, and recent studies have examined the influence of climate change and other anthropogenic impacts on lake biota and productivity (BATTARBEE, 1986; LOTTER et al., 1997; BATTARBEE et al., 2002; KORHOLA et al., 2002); however few extensive surveys of species composition have been undertaken. This study aims to describe the variations in community structure of cladocerans along a pan-European gradient of cold remote lakes based on analyses of sub-fossil remains recovered from the sediments. Physical and chemical variables from the lakes and their catchments, as well as trophic indicators, were used to select those important for structuring cladoceran communities and explaining taxa distribution for different lakes and regions. In addition, Cladocera communities of the pre-industrial period were reconstructed from sub-fossil remains deposited in deeper sediment, allowing a comparison with the present-day situation.

Materials and methods

Sampling and sample preparation

Sediment cores were collected at the deepest point in 294 remote lakes in 12 different areas (= lake districts) all over Europe (Greenland: 13 lakes, Finland – the Lapland province: 34 lakes, Central Norway: 19 lakes, Scotland: 29 lakes, Slovakia and Poland – the Tatra Mountains: 38 lakes, Austria – the Tyrol Alps: 29 lakes, Slovenia – the Julian Alps: 13 lakes, Italy and Switzerland – the Piedmont-Ticino: 28 lakes and the Central Swiss Alps: 11 lakes, Spain and France – the Pyrenees: 68 lakes, Romania – the Retezet Mountains: 4 lakes, Bulgaria – the Rila Mountains: 8 lakes) (Fig. 1). The lakes surveyed were situated above or at the local tree line (KERNAN et al., 2009). The mean altitude of the selected lake districts decreased towards the north (Fig. 2). Some slight deviation from this pattern occurred in Scotland and Greenland lakes where the observed altitudes were slightly below the altitude-latitude regression line.

From each sediment core the topmost sample (0 – 0.5 cm, representing the present-day period) and a sample from lower down, the ‘bottom’ (15 – 17 cm, representing the pre-industrial period) were used for qualitative analyses of Cladocera remains. An average sedimentation rate of 0.1 mm per year was assumed and analysis of spheroid carbonaceous particles (SCP) from each of 294 lakes was used to confirm that the bottom samples pre-dated the onset of industrialisation (ROSE 2001).

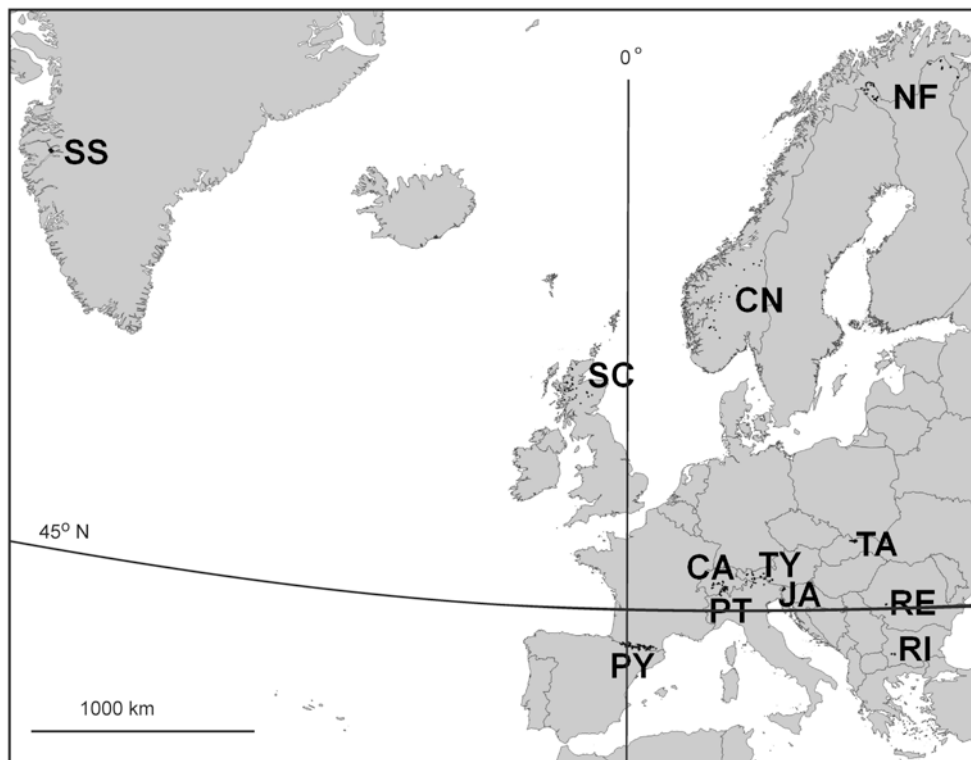


Fig. 1. Geographical position of the lake districts studied within the EMERGE project (CA – the Central Swiss Alps, CN – Central Norway, JA – the Julian Alps, NF – North Finland, PT – the Piedmont-Ticino, PY – the Pyrenees, RE – the Retezet Mountains; RI – the Rila Mountains, SC - Scotland, TA – the Tatra Mountains, TY- the Tyrolean Alps, SS - Greenland).

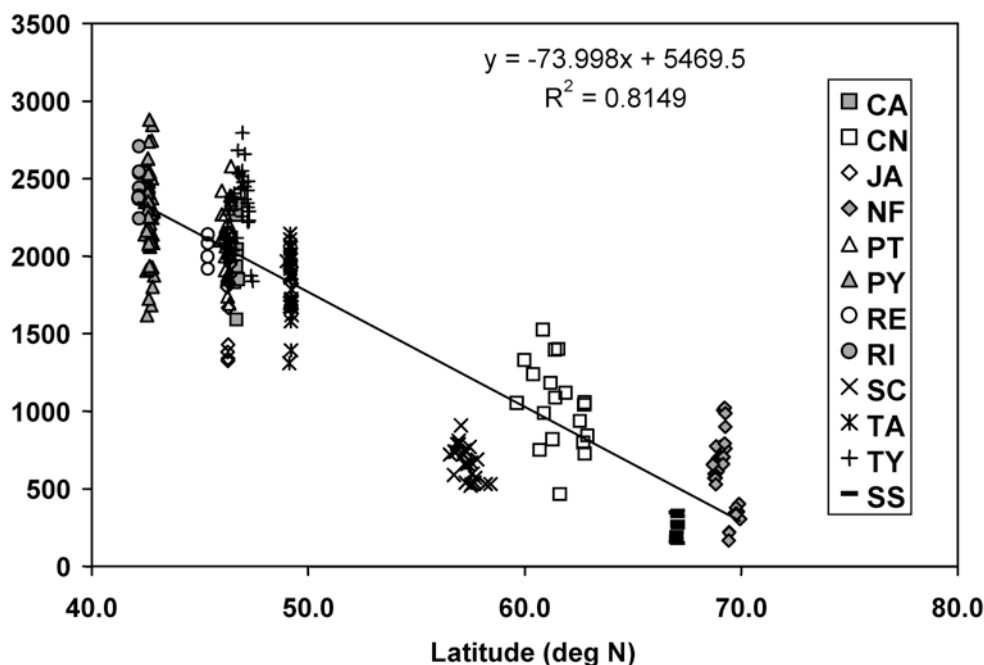


Fig. 2. Relationship between altitude and latitude for lakes within 12 EMERGE lake districts (n = 294).

About 1 g of wet sediment (weighed to 0.001 g) from both the bottom and top of the core was subsampled for cladoceran analysis, heated in 10% KOH and subsequently sieved through a net with a mesh size of 50 μm to remove fine mineral and organic particles. The material left on the mesh was transferred to a test tube, coloured with safranin-glycerin solution and microscopically analysed for Cladocera remains. For details on methods see KORHOLA & RAUTIO (2001). Characteristic body parts, such as head shields, valves, post-abdomens, end-claws, ephippia, tail spines, filters and mandibles, were used for taxa determination. Five taxa were determined to genus level and the rest to species level. For each body part, concentration was calculated as number per g DW⁻¹, but only the most numerous body part of each species was used for further analyses.

Taxonomic determination of the remains was undertaken by several specialists, each being responsible for one or more lake districts. The protocol and procedure on Cladocera remains determination were identical with those used in the MOLAR project (FOTT & HOFMANN, 1996), under whose auspices a workshop for the purpose of intercalibration was held. To avoid using synonyms in Cladocera nomenclature, a pre-prepared European species list was distributed to all specialists prior to analyses. In cases where determination to species level was not possible, only genus was recorded. These undetermined species all belonged to taxa recorded in only a few (up to 6) locations, normally one within each lake district. In the analyses, each of these genera were considered as one taxon (i.e. species). This potentially reduced the number of species found in the sediment as well as their geographical distribution. In the case of *Daphnia*, except for samples from the Pyrenees, the genus was separated into *Daphnia pulicaria* and *Daphnia longispina* gr. (including also records indicated as *Daphnia* sp.). In addition, all *Daphnia* in Northern Finland were categorised as *D. longispina* gr. although live *Daphnia* in most lakes have been identified as *D. umbra* (SCHWENK et al., 2004).

For each lake where Cladocera remains were sampled, a range of variables representing environmental conditions within the catchment was collated. Water chemistry samples were taken at each site (KERNAN et al., 2009). Each lake was also characterised according to a range of morphological attrib-

Table 1. Characteristics of lakes studied. Mean and standard deviation for depth, area and total phosphorus are shown for each Lake District. Secchi disc depth is presented as average depth and values in parenthesis indicate % of the lakes where transparency reaches lake bottom. Δ taxa indicates average differences in species assemblage per lake district in the top or bottom section of the sediment. For lake district abbreviations see Fig. 1.

Lake district	No. of lakes	Depth (m)	Area (ha)	Ptot ($\mu\text{g L}^{-1}$)	Secchi depth (m)	Δ taxa
RI	8	16.8 \pm 11.7	3.9 \pm 3.3	8.5 \pm 4.2	7.8 (25.0 %)	\pm 0.1
PY	64	22.1 \pm 20.6	8.2 \pm 8.9	4.8 \pm 4.9	9.7 (35.0 %)	\pm 2.2
RE	4	9.0 \pm 11.5	1.7 \pm 1.6	4.5 \pm 1.7	5.2 (100 %)	\pm 0.8
PT	29	17.1 \pm 18.0	4.2 \pm 4.6	4.8 \pm 4.2	7.3 (65.5 %)	\pm 2.3
JA	13	8.4 \pm 4.0	1.1 \pm 1.1	20.9 \pm 22.2	7.0 (78.6 %)	\pm 0.4
CA	10	15.4 \pm 12.5	8.8 \pm 12.15	20.3 \pm 33.4	4.9 (16.6 %)	\pm 1.1
TY	28	11.8 \pm 9.5	2.4 \pm 1.5	3.4 \pm 2.3	5.3 (35.5 %)	\pm 1.1
TA	36	17.5 \pm 19.0	4.6 \pm 7.9	2.7 \pm 2.4	8.0 (63.9 %)	\pm 1.6
SC	27	13.5 \pm 12.0	6.5 \pm 6.6	2.8 \pm 0.9	4.6 (13.8 %)	\pm 3.7
CN	22	19.0 \pm 9.1	76.8 \pm 54.1	2.2 \pm 1.1	15.3 (0 %)*	\pm 2.5
SS	13	11.7 \pm 7.5	14.2 \pm 9.2	7.2 \pm 4.8	3.6 (30.8 %)	\pm 2.3
NF	33	7.8 \pm 6.8	24.5 \pm 25.0	6.2 \pm 3.0	7.4 (60.9 %)	\pm 3.7

*Secchi depth available for 4 lakes only

utes (e.g. depth, area) (KERNAN et al., 2009). Information about the nature of the lake catchment was collated from a range of sources (e.g. GIS, maps), supplementing field observations. Output from climate models was also used to provide estimates for precipitation and ice cover duration. The geographical location of each site and its position relative to other lake districts were also considered. The environmental variables were split into three groups representing the proximal environment (i.e. conditions within the lake – this was further subdivided into chemical, trophic and physical environments), the catchment and the geographical location. Data on fish presence/absence and species composition were not available for all the lakes and fish were therefore omitted from the analyses. A summary of key variables is presented in Table 1 while more detailed information is provided elsewhere in this issue.

Data analyses

Similarity within and between lake districts was calculated using Jaccard's index based on presence/absence of taxa (DAVIS, 1973). To examine the differences in species assemblages between the surface sediment and the bottom sample (representing pre-industrial conditions) the Squared Chord Distance Analysis (SCDA) (OVERPECK et al., 1985), a dissimilarity coefficient between the two samples, was calculated summarised for each lake district by box and whisker plots. The box for each lake district represents the 25th and 75th percentiles with the bar indicating the median chord distance for that lake district, but there is no indication as to the 'direction' of change. Outliers are represented by circles and extremes by asterisk symbols.

Multivariate statistical analyses were used to identify species patterns. Two-way indicator species analysis (TWINSpan) (HILL, 1979) was used to classify sites according to their species or genera assemblages to examine inherent spatial patterns within the data.

Statistical analyses of species distribution and response to physical, chemical and catchment characteristics were undertaken using CANOCO, version 4.5 (TER BRAAK & ŠMILAUER 2002). After the Cladocera counts were transformed to percentages DCA was undertaken with rare species down-weighted and species data square root transformed. The primary gradient was 3.5 standard deviations, indicating that unimodal methods were the most appropriate to analyse the data (TER BRAAK 1995).

Canonical Correspondence Analysis (CCA) (TER BRAAK 1986) was used to examine the relationships between the Cladocera remains and each of the environmental data sets. This allows quantification of the proportion of species variance explained by the environmental data, highlighting the main gradients of variation and identifying key variables. CCA with forward selection and Monte Carlo permutation testing (MANLY 1991) enabled identification of a statistically significant subset of variables in each of the environmental data sets, thus reducing co-linearity between variables. Partial CCA (TER BRAAK 1988) was employed to decompose the species variation into that uniquely attributable to proximal, catchment and geographical factors.

Results

Distribution of taxa among lake districts and lakes

In total, remains of 46 Cladocera taxa were determined from the 294 lakes (Table 2). Thirty eight of these were found in both the top and bottom part of the cores. Twelve taxa belonged to planktonic or semi-planktonic species, the rest were strict bottom-dwellers or associated with plants (Table 2). The average number of taxa per lake varied among lake districts, ranging from ca. 4 (3.8 ± 2.2 and 4.0 ± 1.8 in the Tatra Mountains and in the Tyrol Alps) to ca. 11 (10.7 ± 3.0 and 11.7 ± 2.2 in Northern Finland and in Scotland) (Fig. 3).

The number of taxa per lake within each lake district tended to decrease with altitude, with the exception of the Greenland, Scotland and Retezet Lake Districts (Fig. 4). In Scotland altitude differences between the lakes were too small to detect any significant relationships, while in the Retezet Mountains all lakes had the same number of taxa. Regression analysis of the whole data set, though highly significant (at 95 % confidence level), may reflect the relationship between altitude and latitude (see Fig. 2). A decreasing trend, however, was also observed on a regional scale (i.e. within lake districts) and slopes of regression lines were negative in all but one lake district (Greenland) and significant in all but four districts.

Although relatively high numbers of Cladocera species were found in the surface sediment, only four species were present in all 12 lake districts (i.e. *Alonella excisa*, *Alona affinis*, *Chydorus sphaericus* and *Daphnia longispina* gr.) and four additional species occurred in 7 – 10 lake districts (*Alona rectangularis*, *Acroperus harpae*, *Alona quadrangularis* and *Alonella nana*). The remaining species were present in 6 or less lake districts (Table 2). *C. sphaericus* was the most common species, with sub-fossil remains found in 84 % of the lakes. It was followed by *A. affinis* (80 %) and *D. longispina* gr. (67 %). Other taxa were present in less than 50 % of the lakes. A relatively high number of species (25 % of the total) were found in a few lakes in only one lake district (most in < 10 lakes). *Eubosmina coregoni* was the only species widely distributed within only one lake district (Northern Finland) where it occurred in 88 % of the lakes sampled (Table 2).

In most lake districts, several taxa co-occurred regularly (Table 3). Co-occurring taxa are those found together in at least 50 % of the lakes within the same lake district. The three most common taxa present at most of the sites were *A. affinis*, *C. sphaericus* (replaced by *Paralona pigra* in some lakes in Scotland) and *D. longispina* gr. (replaced by *Bosmina/Eubosmina* taxa in Scotland, Central Norway and Northern Finland). In the south-eastern lake districts (the Rila Mountains, the Piemont-Ticino, the Julian Alps, the Central Swiss Alps, the Tyrol Alps), fewer taxa co-occurred (4 – 5 taxa) than in the northern ones (up to 7 taxa). Three taxa (out of 13 frequently co-occurring ones) were restricted to certain lake districts. *Eurycercus*

Table 2. List of taxa identified in the 12 lake districts (LD). Number of lake districts and lakes where taxa were present are given separately for top (0 - 0.5 cm) and bottom (> 15 cm) sections of the sediment. Taxa are arranged with decreasing frequency in the top section of the sediment core first. + = planktonic taxon, * - semi-planktonic species (usually in water column near shore, among the vegetation). The rest of taxa are benthic. ⁽¹⁾*Chydorus piger* was renamed to *Paralona pigra* recently.

Taxon	Author	Code	Top		Bottom	
			LD	Lakes	LD	Lakes
<i>Chydorus sphaericus</i>	(OF Müller, 1776)	CHYDOSPH	12	246	12	242
<i>Alona affinis</i>	(Leydig, 1860)	ALONAAFF	12	235	12	214
<i>Daphnia longispina</i> gr.+	OF Müller, 1776	DAPHNLON	12	177	12	172
<i>Alonella excisa</i>	(S Fischer, 1854)	ALONAEXC	12	89	12	82
<i>Alona quadrangularis</i>	(OF Müller, 1776)	ALONAQUA	10	148	10	146
<i>Acroperus harpae</i> *	(Baird, 1836)	ACROPHAR	10	138	10	132
<i>Alona rectangularis</i>	GO Sars, 1862	ALONAREC	8	28	9	29
<i>Alonella nana</i>	(Baird, 1843)	ALONENAN	7	83	7	80
<i>Eubosmina longispina</i> +	Leydig, 1860	EUBOSLON	6	86	6	79
<i>Eurycerus lamellatus</i>	(OF Müller, 1776)	EURYCLAM	6	84	7	75
<i>Macrothrix</i> sp.		MACROSP.	6	10	3	5
<i>Alona</i> sp.		ALONASP.	5	40	3	32
<i>Alona guttata</i>	GO Sars, 1862	ALONAGUT	5	36	6	32
<i>Ceriodaphnia</i> sp.+		CERIOSP.	5	18	3	10
<i>Daphnia pulex</i> +	Forbes, 1893	DAPHNPUL	5	13	3	18
<i>Alona intermedia</i>	GO Sars, 1862	ALONAINT	4	42	7	51
<i>Paralona pigra</i> ⁽¹⁾	(GO Sars, 1862)	CHYDOPIG	4	34	4	32
<i>Bosmina longirostris</i> +	(OF Müller, 1776)	BOSMILON	4	34	3	29
<i>Simocephalus vetulus</i> *	(OF Müller, 1776)	SIMOCVET	4	12	2	12
<i>Alonella exigua</i>	(Lilljeborg, 1855)	ALONEEXI	4	6	2	3
<i>Acroperus elongatus</i>	(Sars, 1864)	ACROPELO	3	53	4	54
<i>Alona rustica</i>	Scott, 1895	ALONARUS	3	38	4	41
<i>Graptoleberis testudinaria</i>	(S Fischer, 1848)	GRAPTRES	3	23	3	20
<i>Camptocercus rectirostris</i>	Schoedler, 1862	CAMPTREC	3	7	3	3
<i>Drepanothrix dentata</i>	(Euren, 1861)	DREPADEN	3	5	0	0
<i>Polyphemus pediculus</i> *	(Linne, 1758)	POLYPPED	2	11	2	7
<i>Ilyocryptus</i> sp.		ILYOCS.	2	6	1	1
<i>Sida crystallina</i> +	(OF Müller, 1776)	SIDA CRY	2	3	4	8
<i>Rhynchotalona falcata</i>	(GO Sars, 1862)	RHYNCFAL	2	3	2	3
<i>Pleuroxus truncates</i>	(OF Müller, 1776)	PLEURTRU	2	2	1	1
<i>Eubosmina coregoni</i> +	(Baird, 1857)	EUBOSCOR	1	30	1	31
<i>Eurycerus glacialis</i>	(Lilljeborg, 1887)	EURYCGLA	1	12	1	12
<i>Ophryoxus gracilis</i>	GO Sars 1862	OPHRYGRA	1	8	1	11
<i>Holopedium gibberum</i> +	Zaddach, 1855	HOLOPGIB	1	7	1	5
<i>Leydigia leydigii</i>	(Schoedler, 1858)	LEYDILEY	1	2	1	3
<i>Pleuroxus</i> sp.		PLEURSP.	1	2	1	3
<i>Alonopsis elongatus</i>	GO Sars, 1862	ALONOELO	1	2	0	0
<i>Alona costata</i>	GO Sars, 1862	ALONACOS	1	1	3	4
<i>Kurzia latissima</i>	(Kurz, 1874)	KURZILAT	1	1	2	2
<i>Simocephalus expinosus</i> *	(DeGeer, 1778)	SIMOCEXP	1	1	1	1
<i>Pleuroxus denticulatus</i>	(Birge, 1879)	PLEURDEN	1	1	0	0
<i>Bythotrephes longimanus</i> +	Leydig, 1860	BYTHOLON	1	1	0	0
<i>Pleuroxus aduncus</i>	(Jurine, 1820)	PLEURADU	0	0	1	1
<i>Oxyurella tenuicaudis</i>	(GO Sars, 1862)	OXYURTEN	0	0	1	1
<i>Chydorus latus</i>	GO Sars, 1862	CHYDOLAT	0	0	1	1
<i>Anchistropus emarginatus</i>	GO Sars, 1862	ANCHIEMA	0	0	1	1

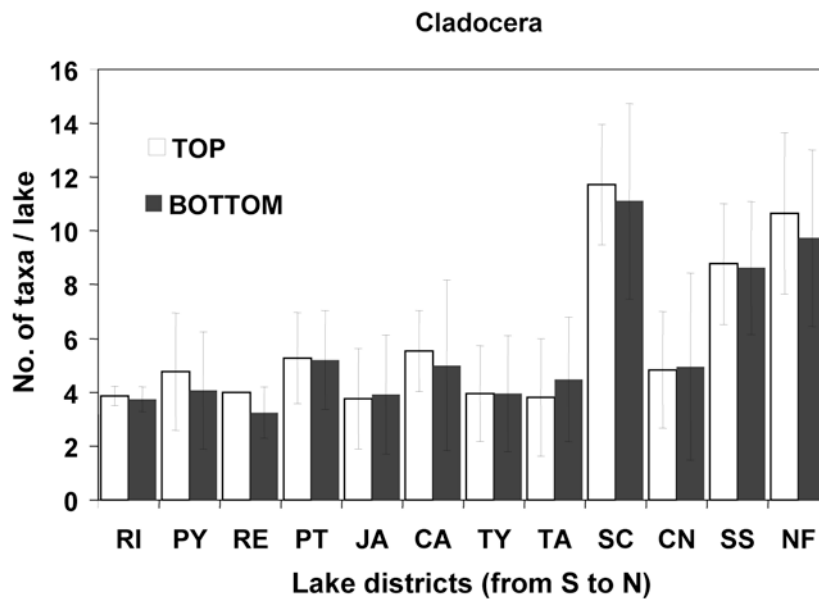


Fig. 3. Number of Cladocera taxa identified from subfossil remains (average, \pm st. dev.) in the top (0 – 0.5 cm) and bottom (> 15 cm) sections of sediment cores from 12 remote EMERGE lake districts (n = 294 /top/; n = 289 /bottom/).

glacialis and *Acroperus elongatus* in northern (i.e. Scotland, Greenland and North Finland) and *Alonella excisa* in southern (the Rila and the Retezet Mountains, the Tyrol Alps) lake districts.

Jaccard's index of similarity, based on presence / absence of taxa, separated the Northern Finland and Scotland districts from the others at the level of 51 % similarity. The other districts exhibited relatively high similarity in taxa composition. They were grouped in several clusters containing lakes from different lake districts and there was no clear relation between taxa and lake districts.

The similarity between and within lake districts was further tested using TWINSpan analysis. A dendrogram shows the hierarchical divisive classification of cluster sites and highlights the key indicator species for each division (Fig. 5). At the first level, the southern and eastern lake districts as well as Greenland (SS) (Group 2, 212 sites) were separated from Group 3 (82 sites) comprising the north-eastern European lake districts (Northern Finland – NF, Central Norway – CN and Scotland – SC). This split was driven by the presence of *Eubosmina longispina* and *Acroperus elongatus*, which were abundant in the northern lake districts but not found outside these. Group 3 was further divided into Group 6 (51 sites), comprising sites in Central Norway (CN) and Scotland (SC), and Group 7, which contains 31 sites, all from Northern Finland (NF). This division was driven by *Eubosmina coregoni* and other *Bosmina* sp., which were only observed in the Finnish lake district, but not in Scotland or Norway. Sites within group 2 were more widespread and lakes from Greenland (SS) were intermixed with sites from the Pyrenees, the Alps and in eastern Europe (the Tatra, the Retezet and the Rila Mountains). Group 2 was further split into two groups, one containing a mixture

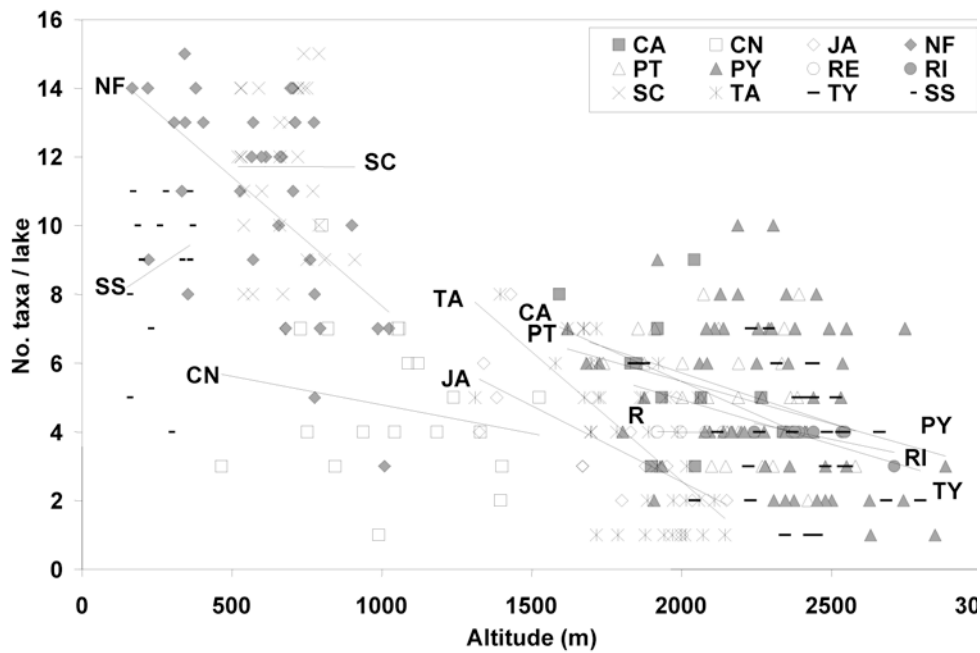


Fig. 4. Relationship between lake altitude and the number of Cladocera taxa (remains) in the top section of the sediment per lake within 12 remote EMERGE lake districts (n = 294).

Table 3. Co-occurrence of Cladocera within lake districts. Co-occurring species are present together in at least 50 % of the lakes within each lake district. For lake district abbreviations see Fig. 1.

No. of LD		Lake district											
		RI	PY	RE	PT	JA	CA	TY	TA	SC	CN	SS	NF
12	<i>Alona affinis</i>	X	X	X	X	X	X	X	X	X	X	X	X
11	<i>Chydorus sphaericus</i>	X	X	X	X	X	X	X	X		X	X	X
9	<i>Daphnia longispina</i> gr.	X	X	X	X	X	X	X	X			X	
6	<i>Acroperus harpae</i>						X		X	X	X	X	X
3	<i>Alonella excisa</i>	X		X						X			
3	<i>Alonella nana</i>									X		X	X
3	<i>Eubosmina / Bosmina</i>									X	X		X
2	<i>Acroperus elongatus</i>									X			X
2	<i>Alona quadrangula</i>				X							X	
2	<i>Eurycercus lamellatus</i>											X	X
1	<i>Alona</i> sp.								X				
1	<i>Paralona pigra</i>									X			
1	<i>Eurycercus glacialis</i>											X	
	Sum of taxa	4	3	4	4	3	4	3	5	7	4	7	7



Fig. 5. Two-way Species Indicator Analysis (TWINSPAN) based on Cladocera sub-fossil remains (species level) from top samples of sediment cores collected from sites ($n = 294$ lakes) within 12 EMERGE lake districts. For each group, the number of sites, the dominant lake districts and the indicator species are shown (For taxon abbreviations see Table 2).

of sites from southern and eastern Europe (Group 4, 93 sites) characterised by benthic / planktonic forms and another (Group 5, 119 sites) dominated by sites in the Central Swiss Alps (CA), the Pyrenees (PY), the Tyrol Alps (TY) and Greenland (SS). These were characterised by benthic and plant-associated forms of Cladocera.

Correspondence analysis (CA) was used to further explore the Cladocera data. The first CA Axis explained 17.7 % of the variation in species data, while Axis 1 and 2 combined accounted for 27.6 %. Fig. 6 and 7 show the distribution of samples (Fig. 6) and species (Fig. 7) plotted against CA Axis 1 and 2. The samples were classified according to lake districts, and the regional pattern suggested by the TWINSPAN analyses is confirmed. Samples were plotted according to species assemblages and species were plotted at the centroid of their distribution across samples. This showed which species characterise which groups of sites, reflecting the indicator species highlighted by TWINSPAN analyses. The initial separation was made along Axis 1 with sites in the northern lake districts (North Finland, Norway and Scotland) of the biplots plotting to the left and the others tending towards the right (Fig. 6) .

Species distribution in response to environmental variables

A series of Canonical Correspondence Analyses (CCA) (based on surface samples) was undertaken. The Greenland data were not included in this analysis as only a reduced environmental dataset was available for this Lake District. When separate analyses were undertaken on the combined proximal data, the catchment and the location data sets, the highest explanatory

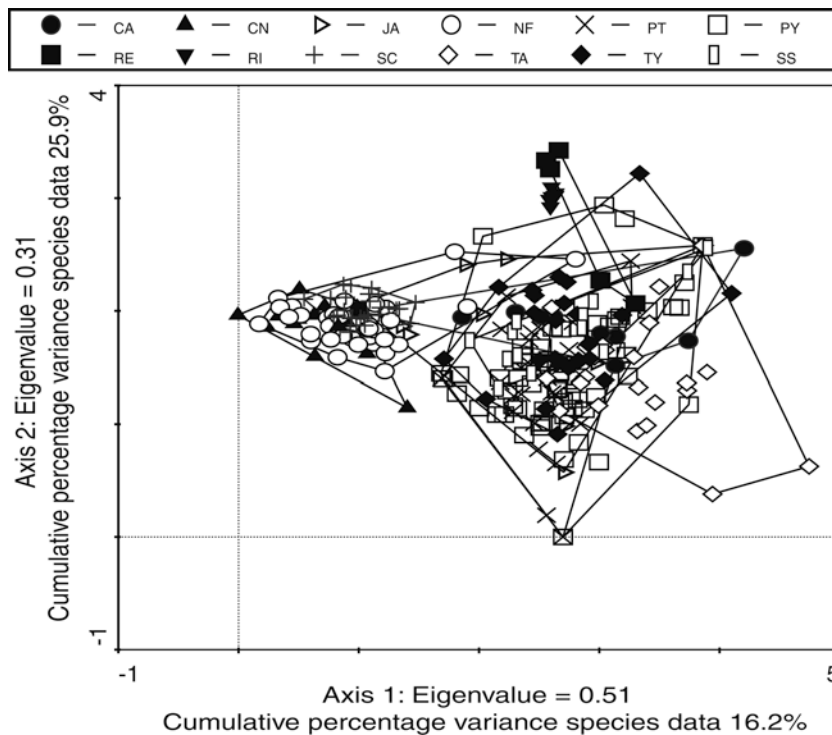


Fig. 6. Detrended Correspondence Analysis (DCA) biplot showing EMERGE sites classified according to 12 lake districts. Sites are positioned according to species assemblages (*Chydorus sphaericus* omitted) with sites exhibiting similar species composition plotted closely together. Envelopes have been drawn around each lake district to illustrate the geographical patterns of the Cladocera remains.

powers was exhibited by location (37.8 % of Cladocera variation explained), where altitude, distance to Scotland and distance to sea were the most important elements determining the Cladocera assemblage. Proximal characteristics explained 32.3 %) with chloride concentration (i.e. indication of the distance to sea and wind direction combined), ice cover duration and lake area explaining most of the variance. For catchment properties, which explained 19.4 % of variance, the most important variables explaining variance were land cover (% of moor/peat; % of glacial deposits and % of meadow/rural) (Table 4). Following variance partitioning, location provided the highest unique contribution to Cladocera assemblage variance (12.3 %), followed by proximal characteristics (5.7 %) and catchment properties (1.0 %) (Table 5).

CCA analyses of sedimentary Cladocera remains and in-lake physical and chemical attributes for 281 mountain lakes indicated that on Axis 1 the most important parameters determining the distribution of Cladocera were organic material (loss on ignition (LOI) and total organic carbon (TOC)), sea-salt (Na^+ and Cl^-), lake size (area), Ca^+ , nitrate and ammonia (Fig. 8) the latter three being negatively correlated with the others. The most important parameters on Axis 2 were the $\text{NO}_3^- / \text{NH}_4^+$ ratio and ice cover which exhibited an inverse relationship. Phosphorus (P_{tot} - as indicator of trophic level) was not statistically significant.

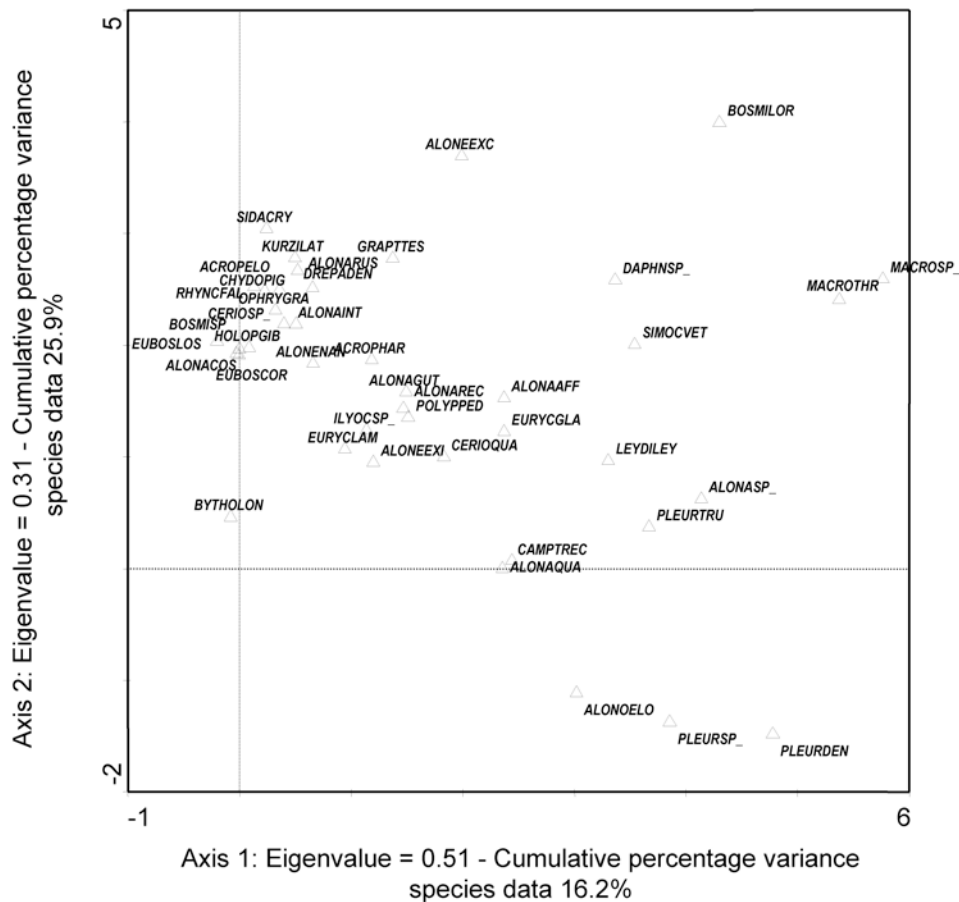


Fig. 7. Detrended Correspondence Analysis (DCA) biplot showing species distribution within EMERGE sites ($n = 294$) (*Chydorus sphaericus* omitted). This should be interpreted in conjunction with Fig. 7 showing distribution of sites (these were plotted separately for clarity). Species centroids are plotted closest to the sites where they occur with the greatest relative abundance. (For taxon abbreviations see Table 2).

Comparison of top and bottom sediment assemblages

The number of taxa in the top and bottom sections of the core was identical in 80 lakes. These were all located in the Julian Alps, the Central Alps and Rila and Retezet Mountains. In contrast, in Northern Finland and Greenland there were no lakes with identical species numbers in top and bottom cores.

In 99 lakes there were less taxa in the surface sediment samples. The decrease in species number ranged from one (in ca. 50 % of the lakes) up to 5 (one lake in Northern Finland). Increases in the number of taxa in the topmost section were observed in 109 lakes, in 50 % of the lakes the increase was represented by a single taxon and in 20 % of the lakes by two taxa. Substantial differences were observed in five lakes, where the increase exceeded 5 taxa (5,

Table 4. Results of partial Canonical Correspondence Analysis (CCA) using forward selection on proximal, catchment and location data from 294 EMERGE survey lakes

<i>Proximal</i>	<i>% extra fit</i>	<i>Catchment</i>	<i>% extra fit</i>	<i>Location</i>	<i>% extra fit</i>
Chloride	11.91	% moorland/peat	7.5	Altitude	13.3
Ice cover duration	5.10	% glacial deposits	4.4	Distance to Scotland	5.4
Lake area	3.06	% meadow/rural	2.7	Distance to sea	5.1
Max. lake depth	2.04	Catchment area	2.0	Distance to Rila	4.8
Water temperature	1.36	Relief (MaxAlt-Alt)	2.7	Distance to Norway	2.4
Potassium	1.36			Dist. to centr. of Alpine Lake Districts	2.0
Ammonium	1.02			Distance to N. Finland	2.0
Nitrate	1.0			Precipitation	0.7
Total carotenoids	1.0			Distance to Pyrenees	0.7
Seepage lake	1.0			Altitude relative to altitude of lowest lake in Lake District	0.7
Total phosphorus	0.7			Distance to western seaboard	0.7
Presence of outflow	0.7				
Calcium	0.7				
Conductivity	0.7				
Carbon to nitrogen ratio	0.7				
total variance explained	32.3		19.4		37.8

Table 5. The results of decomposing the variation in Cladocera assemblage into proximal, catchment and location data and their co-variation in 294 EMERGE survey lakes.

Component	% variation explained
Proximal	5.7
Catchment	1.0
Location	12.3
Proximal & Location	7.6
Catchment & Location	3.1
Proximal & Catchment	0.1
All three	15.3
total variance explained	45.1

6, 9 and 11 taxa, respectively). These lakes were located in Scotland and North Finland. However, a detailed analysis of the lakes from Scotland reveals no significant differences between lakes located close together. Data on the net number of taxa change between the top and bottom section of the sediment cores showed a weak trend towards an increase in the number of changes from south (= high-altitude lakes) to north (= high-latitude lakes).

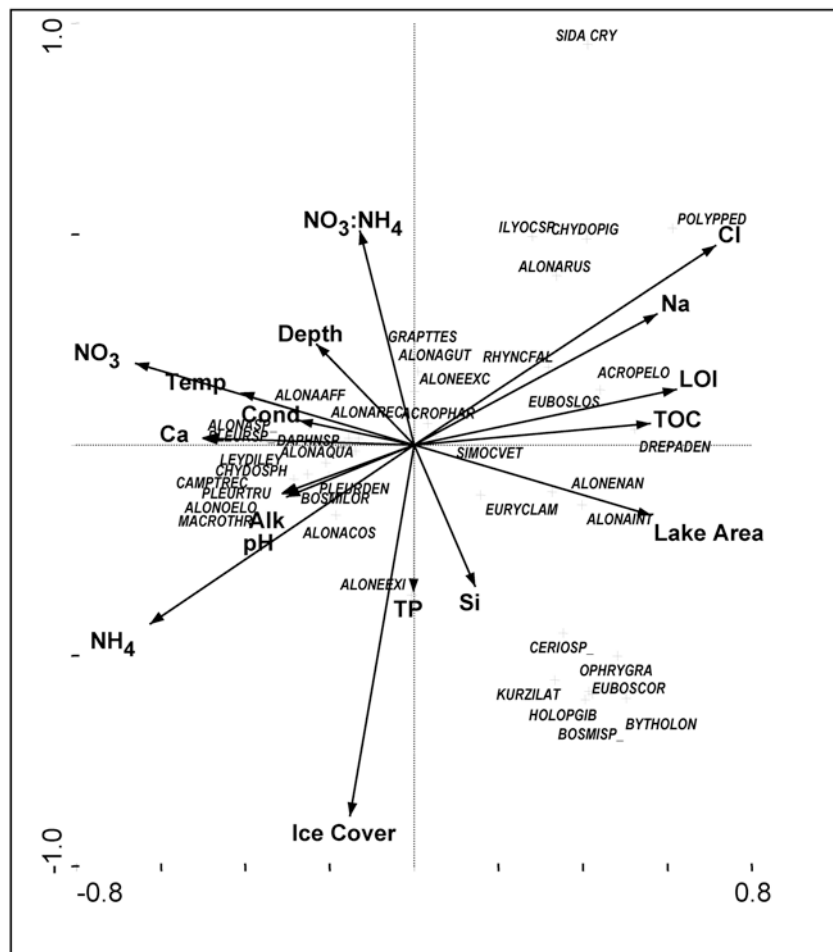


Fig. 8. Canonical Correspondence Analysis (CCA) biplot summarising the relationship between sedimentary Cladocera remains and in-lake physico-chemical attributes for 281 mountain lakes. Species centroids are shown by crosses and environmental variables are represented by vectors indicating the direction of variation. Projecting species centroids onto vectors provides an approximate ordering of species optima along the environmental gradient represented. (For taxon abbreviations see Table 2)

Species composition between the top and bottom samples was the same in 52 lakes while in the rest of the study lakes this varied between one and 17. In 68 lakes there was a single difference between the core top and bottom sections. In 53 lakes the top and bottom differ by two taxa (e.g.: two missing in the top section or added to top section or one missing in bottom section and another one added in top section of the core). In 94 lakes, 3 or 4 taxa were replaced. Five taxa or more were replaced in 20 lakes (5 taxa in 10 lakes, 6 in 6, 7 in 3, 9 and 17 taxa in one lake each).

There was no clear pattern between taxa being present only in the top or bottom section of the core. Each lake district had its own (specific) list of taxa being present either in the top or

bottom part of the core (Table 6). In some Lake Districts, a number species were present within the bottom sample only and in some lakes, only in the top part of the core and *vice versa* (e.g. Central Alps - *A. quadrangularis*; Tyrol Alps - *D. longispina* gr.; Central Norway - *C. sphaericus* & *E. longirostris*; North Finland - *Alona intermedia*). In the Tatra Mountains *D. longispina* gr. was the only species exclusively found in the bottom part of the core. Other taxa more frequently absent in the top layer were *A. quadrangularis* and *D. longispina* gr., which were absent in 30 lakes.

Species change between the samples of the pre-industrial period and those of the present time evaluated using SCDA is summarised in box plots for each lake district (Fig. 9). Squared chord distance values can range from 0.0 to 2.0, with 0.0 indicating identical proportions of species within the samples being compared (but with no indication as to 'direction' of change, however) and 2.0 indicating a completely different assemblage. If a value of 0.5 indicates substantial change, the majority of sites did not fall into this category and there was no significant difference between past and present fauna. This value is based on the 5th percentile value from SIMPSON et al. (2005). In this instance the 5th percentile lake has been chosen to represent substantial change contrary to SIMPSON et al. (2005) who used this value as a measure of similarity as they were investigating between-site differences rather than down core differences (see BENNION et al., 2005). In all lake districts median values were well below 0.3, and the top level of the 3rd quartile in 9 Lake Districts (out of 11) lay below 0.5; the remaining 2 lake districts were below 0.6. In most lake districts only few sites differing substantially with respect to the surface and bottom samples were found (in total 22 outliers/extremes). The lake district with the highest number of extremes was the Tyrol Alps (four extremes).

Discussion

Species richness of Cladocera across cold lakes in Europe

Today, about 170 freshwater Cladocera species are known to exist in Europe (HRBA EK et al., 1978; NEGREA, 1983; MARGARITORA, 1985; ALONSO, 1996; KORHOLA, 1999; FLÖSSNER, 2000) and 25 % of these (42 taxa) were found in the top section of the sediment in the remote lakes studied here. When comparing species richness at the Lake District level, the northern districts were most species rich. This is counter to the earlier observations which showed decreasing zooplankton species richness towards the north (PATALAS, 1990); for instance, in the cold, isolated expanses of Greenland 23 cladoceran taxa have been recorded (RØEN, 1997), while in smaller less remote and warmer Slovenia, 56 taxa are known to exist (A. BRANCELJ, unpubl.). However, these study lakes cannot be assumed to represent a south – north gradient because such comparison assumes a temperature difference or perhaps, as discussed below, a difference in age and accessibility since the last glaciation. All lakes in this study, regardless of latitude, had similar temperatures, and other environmental variables that usually change with latitude were comparable (duration of open water season, nutrient concentration etc). Taking this into account a latitude dependent geographical location ought not to have had a major effect on the species richness among lake districts.

The size of the district probably had the strongest influence on the number of taxa per lake district. In geographically small districts, like Retezet, Rila or individual districts in the Alps, the species number was low, but when considering the Alps as a unit, 27 taxa were found.

Table 6. Frequency of the two the most common Cladocera species being present in either in the bottom part of the sediment core (15-17 cm depth) only or in the top-most section (0-0.5 cm) only (number indicates number of lakes where taxon was present). "Bottom taxa" and "Top taxa" indicate a total number of taxa per lake district which were present only in the bottom/top part of the core. (For lake district abbreviations see Fig. 1 and for taxa Table 2.)

Lake District	Bottom taxon & frequency	Bottom taxa (sum)	Top taxon & frequency	Top taxa (sum)
RI	–	–	–	–
PY	ALONARUS – 10 ALONAINT – 8	15	DAPHNLON – 18 EURYCLAM – 12	20
RE	–	–	ALONAAFF – 2 DAPHNLON – 1	2
PT	ALONAREC – 5 EURYCLAM – 4	16	ACROPHAR – 5 CHYDOSPH – 4	17
JA	ACROPHAR – 1 ALONAQUA – 1	4	ALONAREC – 1 SIMOCEXP – 1	2
CA	ALONAINT – 1 ALONAQUA – 1	3	ALONAAFF – 2 ALONAQUA – 2	6
TY	DAPHNLON – 5 ALONAGUT – 3	6	DAPHNLON – 4 ACROPHAR – 2	11
TA	DAPHNLON – 10 DAPHNPUL – 9	10	ALONAAFF – 4 ALONAQUA – 3	7
SC	ALONAQUA – 7 CHYDOSPH – 5	17	ILYOCSF – 6 ALONARUS – 5	26
SN	ACROPELO – 1 ALONARUS – 1	4	ALONAQUA – 1 CHYDOPIG – 1	2
CN	CHYDOSPH – 17 EUBOSLOS – 15	15	EUBOSLOS – 20 CHYDOSPH – 14	14
SS	SIMOCVET – 3 ALONENAN – 2	9	CERIOSF. – 5 POLYPPED – 3	8
NF	OPHRYGRA – 6 ALONAINT – 4	20	ALONAAFF – 9 ALONAINT – 8	22

This number is similar to the taxa found in other large lake districts (North Finland: 25; Scotland: 26; the Pyrenees: 21) or even lower (Central Norway: 14) and suggests that the apparent increase in the species number towards north derived from the lake district size and less from the actual species number at different latitudes. Such similarity in species richness among equally sized areas is also common for lowland cladocerans in Europe. When comparing regional faunas in Spain, Romania and Italy, on average about 100 taxa per region are found (NEGREA, 1983; MARGARITORA, 1985; ALONSO, 1996).

Even with the similar number of species found in the southern, northern and western regions of Europe there were some substantial differences in species number in individual lakes among regions and between lakes in the northern and southern lake districts. The maximum number of taxa per lake never exceeded 16 and only 16 % of the lakes had 10 or more taxa. The lakes with the highest number of taxa were mostly situated in the northern part of

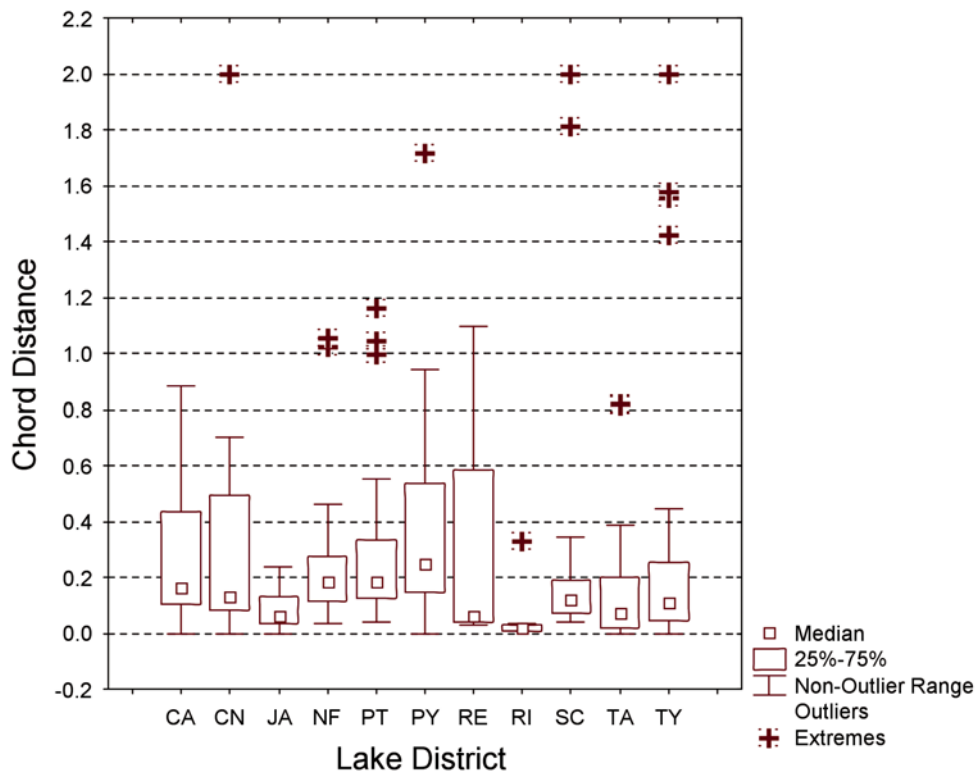


Fig. 9. Differences in species assemblages between the surface and bottom sediment. Box plots showing Squared Chord Distance distribution for eleven EMERGE lake districts (data from Greenland not included).

Europe (Scotland, North Finland, Greenland, Central Norway) at altitudes lower than 900 m. There were only two lakes in southern Europe, in the Pyrenees at altitude 2200 – 2300 m, with 10 or more taxa per lake. Similar species richness for European high-latitude lakes has been reported before. In the study of 53 subarctic Fennoscandian lakes, KORHOLA (1999) found up to 18 species of Cladocera per lake, however, the median number for all lakes was only 4.

Relatively few lakes (in total 14) hosted only one taxon (primarily *Chydorus sphaericus*). Most of these lakes were located in the southern lake districts (the Tatra Mountains, the Tyrol Alps and the Pyrenees), with only one representative from the northern groups (Central Norway). All the lakes were situated at 1700 – 2800 m altitude, except one lake in Central Norway, located at ca. 1000 m.

Some differences in species richness among lakes can be explained by their geological history, isolation and size. It is known that colonisation of freshly formed habitats after glacier retreat has been fast in high latitude but not in high altitude lakes (WILLIAMSON et al., 2001). Dispersal from a suitable habitat on one mountain top to another is more difficult than colonisation of sites in lowlands where suitable areas are often connected to each other. This is why high-altitude lakes (above the local tree line) exhibit such a paucity of Cladocera in the southern regions of Europe. Four out of eight significant regression slopes between taxa

richness and altitude were from high-altitude lakes, while most of the non-significant regression slopes were from high-latitude lakes. The positive relation between altitude and taxa richness in Greenland may be a reflection of the lower likelihood of lakes containing fish as altitude increases, as fish have large effects on species richness and abundance of cladocerans in Greenland lakes (JEPPESEN et al. 2001, LAURIDSEN et al. 2001). Other studies have also demonstrated that even small changes in altitude may alter the zooplankton species number. According to Patalas (1964) 5-8 mesozooplankton species are usually found at lakes situated at 1400-1700 m a.s.l. whereas at 2500-3200 m a.s.l. 2-8 species are found, and above 3200 m only 1-4. Without an altitude effect, the colonization potential of most cladocerans is high and their frequent dispersal events enhance richness (HOLLWEDEL 2002).

In a study of 128 lowland lakes across five different regions in Europe (Spain, Italy, the Netherlands, Scotland and Norway), HOBÆK et al. (2002) found a slight but significant positive effect of lake density and lake area on species richness of zooplankton. The more isolated the lake is, the smaller is the probability for species to colonize it, especially for species like cladocerans that disperse by passive means (MAGUIRE, 1963). Therefore, the small number of species in high mountain lakes can be partly explained by the isolation of the water body. The lakes in this study also varied in size. The lakes in Northern Finland, Greenland and Central Norway were, on average, an order of magnitude larger than the southern Europe lakes. This supports the finding of HOBÆK et al. (2002) that large lakes have a higher capacity to support a more species rich community.

Species distribution of Cladocera in different lakes

Although several species of cladocerans were found in each lake district, a single lake seldom contained more than a few species. The majority of taxa (i.e. 24) appeared in 2 – 8 lake districts where they inhabited between 5 to about 90 lakes. About 25 % of all species appeared only in a few lakes within a given lake district. This indicates a high variability in community structure and is frequently observed for zooplankton communities (HEBERT & HANN, 1986; RAUTIO 1998). However, three patterns could be highlighted as characteristics describing the cladoceran distribution in European cold lakes. These were; 1) the dominance of communities by the same few species in nearly all lakes; 2) the small number of species with limited geographical distribution; and 3) the strong separation in the distribution between large-bodied and small-bodied species.

Five taxa (*Alona affinis*, *Chydorus sphaericus*, *Daphnia longispina* gr., *Alona quadrangularis* and *Acroporus harpae*) were present in more than 50 % of the top sediment cores and can be considered as cosmopolitan or common cold-water species. Only two taxa, *Chydorus sphaericus* and *Alona affinis*, were found in the majority of the lakes (85 % and 81 % of lakes, respectively). In some lakes, *C. sphaericus* was the only species present, this phenomenon being most frequent in the Tatra Mountains (in 11 lakes out of 38) and most rare in Central Norway, the Julian Alps, the Pyrenees, and the Tyrol Alps). *C. sphaericus* is one of the most common and widespread Cladocera species, being present in a wide array of aquatic habitats, from temporary to permanent water bodies and from lowland to high-mountain lakes (ALONSO, 1996). Both *C. sphaericus* and *A. affinis* occur regularly in the earliest post-glacial assemblages in lakes in various parts of Europe (GOULDEN, 1964; HOFMANN, 1978; KORHOLA, 1992), indicating their cold water affinities and explaining their dominance in the lakes in this study.

Two taxa were found only in one lake district in which they were, however, quite common and could be described as typical regional species in the dataset. *Eubosmina coregoni* (30 lakes) and *Eurycerus glacialis* (12 lakes) were restricted to the northern group of the lake districts, *E. glacialis* to Greenland and *E. coregoni* to Northern Finland. Also KORHOLA (1999) and RAUTIO (2001) indicated *Bosmina sp.* to be the most abundant taxon in subarctic Finnish lakes and *E. glacialis* is endemic to the Arctic. Hence *E. glacialis* was the only taxon in the dataset showing strict cold-water affinity and it does not occur in lower latitude or lower altitude lakes in Europe. Three more benthic species, *Kurzia latissima*, *Holopedium gibberum* and *Ophryoxus gracilis*, were also restricted to Finnland sites. Finally, there is at least one planktonic taxon that is restricted to cold lakes, *Daphnia umbra* which occurs in many cold lakes and ponds in Europe (SCHWENK et al., 2004), but which in this study was considered as a species in the *Daphnia longispina* gr.

Although 25 % of all species in the top section of the sediment were planktonic, only *Daphnia longispina* gr. was widely distributed. The *Daphnia* genus was present in ca. 200 lakes, while three species of *Bosmina/Eubosmina* occurred in ca. 150 lakes (sometimes two species together in the same lake). In 328 locations both planktonic taxa combined were found. However, there was quite a strong separation in the distribution of the large-bodied daphnids and small-bodied bosminids. Together they were found only in relatively few lakes in 5 lake districts (Scotland – 12 lakes, the Tyrol Alps – 1; Central Norway – 3; Northern Finland – 11 and Greenland – 7).

TWINSPAN analyses at genus level also suggested major differences in the size distribution of Cladocera in different lakes. These included; a) small in Central Norway, Finland and Scotland and here dominated by bosminids; b) large in many of the central European lakes and Greenland, often with *Daphnia* as the dominant genus; and c) small again and dominated by *Chydorus* in some high mountain lakes in different areas. Several studies have shown that a shift from dominance of *Daphnia* to *Bosmina*, as evidenced both from contemporary samples and surface sediment, can be explained by enhanced predation pressure from fish in cold lakes (JEPPESEN et al., 2003a, b; DZIALOWSKI & O'BRIEN, 2004). This is also true for lakes from the same area of Greenland sampled in the present study (LAURIDSEN et al., 2001). An extensive study of lakes with and without fish in different parts of Greenland has shown that *Daphnia* only occur in lakes without fish. On the European continent, however, *Daphnia* may co-exist with fish, but usually the planktonic community will be dominated by small forms of *Daphnia* if fish are abundant (JEPPESEN et al., 2003a). The regular introduction of fish appeared to be responsible for the disappearance of *Daphnia* and the extreme impoverishment of zooplankton in Lake Paione Inferiore, a high altitude lake sensitive to acidification in the western Central Italian Alps (CAMMARANO & MANCA, 1997). The disappearance, which can be dated back to the beginning of the 19th century, coincides with the start of fish introduction. A similar effect was recorded in two lakes in the Julian Alps when large bodied Calanoida became extinct/disappeared after fish introduction in 1991 (BRANCELJ, 1999).

The strong separation between the bosminid sites in Central Norway, Finland and Scotland and the *Daphnia* dominated sites in lowland Greenland and mountain lakes in Central Europe therefore suggests major differences in fish predation. This makes sense as the lowland – highland lakes in northern Europe (except for Greenland) are usually inhabited by several fish species, while many mountain lakes and lakes in Greenland are devoid of fish or inhabited by one to a few species only. The shift to small chydorids at some alpine sites may also indicate enhanced fish predation as seen in north east Greenland (JEPPESEN et al., 2001), but may also be influenced by extreme cold/oligotrophic conditions or acidification. Unfortu-

nately, fish data in the present study are only qualitative and not detailed enough to test the role of fish further.

Change in number of species in time .

A qualitative comparison of Cladocera remains from the top and bottom section of the sediment cores (288 pairs of data sets) revealed less taxa per lake in the bottom sections. Exceptions were the lakes in the Tatra Mountains, the Julian Alps and in Central Norway (with one location only) (Fig. 3). Nevertheless, the differences at the level of lake district were not significant. However, in 120 lakes (out of 288) there was no change (52 lakes) or there was ± 1 taxon difference (68 lakes) in number of taxa in the top and bottom section of the sediment. A qualitative difference of five or more species between bottom and top of the core was recorded in 21 lakes (7.1 % of all lakes studied). On average, more than four species were replaced in less than 2 lakes per lake district. The biggest replacements were noticed in high-latitude lakes with a higher number of taxa per lake in comparison with high-altitude lakes.

This relatively high number of lakes with small or negligible qualitative changes and the paucity of lakes with large assemblage changes suggest that there was no specific trend in fauna changes in the last 150-200 years, which is somewhat contradictory to the expectations and results of several other studies. Both high altitude and high latitude ecosystems have been subject to considerable environmental changes in recent years as the result of climate warming (MAGNUSON et al., 2000; WRONA et al., 2005). Fossil records of cladocerans, diatoms and chironomids in lakes have revealed marked directional shifts in species assemblages in recent lake sediments (SMOL et al., 2005). These changes have been linked to longer growing seasons, decreased duration of ice cover, increased thermal stability and changes in limnological variables. In Subarctic Finnish Lapland, for instance, both diatom and cladoceran assemblages shifted from benthic to planktonic dominated taxa (RAUTIO et al., 2000; KORHOLA et al., 2002; SORVARI et al., 2002). Some studies on European high altitude lakes have also indicated shifts in species assemblages. In a study of 15 lakes from the southern Central Alps, MANCA & ARMIRAGLIO (2002) found that *A. quadrangularis* was replaced by the sibling species *A. affinis* in the surface sediments. In the Tatra Mountains, several lakes with only one species in the top section of the sediment core had remains of several taxa in the bottom section. In this instance we can relate the reduction of the present-day fauna to the effects of industrial pollution (PRAŽAKOVA & FOTT 1994) rather than to climate change. However, from some other parts of Europe it has been reported that *Daphnia* can survive in lakes with relatively low pH (CAMMARANO & MANCA 1997). The lack of change in the cladoceran assemblages here might partly derive from the qualitative nature of the data, as we focused on comparing the change of species number and shifts in species pairs rather than abundances.

Relationships between lake's environment and Cladocera community structure

The distribution of Cladocera in this study was shown to be most significantly correlated with a range of location variables, and especially with altitude. This result emphasizes the role of dispersal limitations in shaping high mountain lake communities and supports earlier observations (PATALAS, 1990; RAINA & VASS, 1993) and the discussion above. However, as

location and catchment variables were coupled with many in-lake variables and hence reflected in their values, we only included the in-lake physical and chemical attributes (proximal variables) in the analysis when identifying the role of single variables for each cladoceran taxon.

Environmental parameters often linked with cladoceran assemblages include various water chemistry parameters, such as pH and specific ions; physical parameters, such as temperature, lake area and depth, and UV radiation; and biological parameters, such as chl-*a* and fish (KORHOLA, 1999; JEPPESEN et al., 2001; RAUTIO & KORHOLA, 2002; AMSINCK et al., 2006; SWEETMAN & SMOL, 2006). Here, 19 variables were identified to which explained more than 1% of species variation. Different species clustered according to their affinities to different environmental variables and this indicated why they were more common in some lake districts than in the other. Axis 1 in the CCA is correlated positively with chloride, sodium, organic carbon, loss on ignition and lake area. These variables had their highest values in the Scotland and Central Norway lake districts where elevated sea-salt values reflect a significant marine influence. The peaty soils which are widespread in the catchments of many of the Scottish sites were likely to be responsible for the relatively high organic content of the lake waters. The species towards this end of the primary axis included common species in Scottish and/or Central Norwegian mountain lakes, such as *P. pigra*, *A. nana*, *E. longispina*, and *A. elongatus*. These taxa have earlier been reported to occur in all types of cold lakes, but being most frequent in large lakes with abundant littoral vegetation and in vegetation-filled ponds (NILSSEN & SANDØY, 1990; KORHOLA, 1992). The amount of vegetation was not evaluated in this study, but the peaty soils in the catchment and low altitude usually favor littoral vegetation. These species were less common in the central and southern European lake districts which are clustered (although not shown) towards the negative end of Axis 1, perhaps reflecting a rockier littoral zone in these lakes.

Several chemical variables exhibit a negative correlation with Axis 1, including nitrate, ammonium and calcium, which all tended to be higher in the central and southern lake districts. Nitrate and ammonium give a rough estimation of lake productivity and trophy, although P_{tot} and soluble reactive phosphorus are more commonly used. Species such as *C. sphaericus*, *A. affinis* and *D. longispina* gr., clustering towards the negative end of the Axis 1, were most abundant in these warmer lakes with higher nitrogen concentrations. All these species have a very wide ecological tolerance (HOFMANN, 1987; ALONSO, 1996). In this study *C. sphaericus* and *A. affinis* were the most widespread taxa occurring in all lakes districts. Calcium is an essential ion in the calcified exoskeletons of cladocerans and there is evidence that Ca deficiency acts as an important determinant of cladoceran community structure (HESSEN et al., 1995). Species without calcified exoskeleton (*H. gibberum*, *P. pediculus* and *B. longimanus*) were clustered towards the positive end of Axis 1 with the lowest values of Ca.

Axis 2 mirrors the results of the third TWINSpan division whereby sites in Norway and Scotland were grouped apart from sites in Northern Finland. This split was based on the abundance of *E. coregoni* and unidentified *Bosmina* species. These form a cluster of species centroids towards the negative end of Axis 2 with other species such as *Kurzia latissima*, *Holopedium gibberum* and *Ophryoxus gracilis* which occurred rarely and only in a small number of Finnish sites. The variable most closely associated with Axis 2 was ice cover duration; however, as these species also frequently occur in ponds with substantially shorter ice cover period in Northern Finland (RAUTIO, 1998) it is unlikely that ice cover directly determined their clustering; rather it reflects the limited high-latitude distribution of these taxa.

Some 'fundamental' ecological parameters, such as pH, alkalinity, conductivity and phosphorus (P_{tot} - as indicator of trophic level), were relatively unimportant for the distribution of Cladocera. This indicates a rather high ecological plasticity of this group of animals whose distribution is governed by other environmental factors. On the other hand, the range of many measured proxy variables was small in this study. All lakes had circum-neutral pH and were oligotrophic low-productive lakes. With larger chemical gradients these variables would most likely have played a more important role. The analyses indicated the importance of location in shaping cladoceran communities in European cold lakes, suggesting that the environmental gradients within the water bodies played a less significant role for species distribution patterns than location and hence altitude and isolation of the lake.

In conclusion, our detailed analyses showed four patterns in the Cladocera distribution in remote lakes on the pan-European scale. First, the clearest relation on a pan-European as well as on a local scale was the relation between species number and altitude, but not between altitude and specific taxon or assemblage. From this point of view, remote lakes could be considered as islands (*sensu* island biogeography theory, MACARTHUR & WILSON 2001) exposed to repeated attempts of colonisation. Successful colonisation depends not only on environmental (proxy) parameters, but also on the intensity and frequency of the transport of colonisers (i.e. Cladocera) and their competitive success (SHURIN et al. 2000). As the number of lakes decreases with altitude and as the distances between the lakes increase, the probability of colonisation of high-altitude lakes with additional new species is much lower than in high-latitude lakes. At the same time, lake size decreases with altitude, making them less probable targets for colonisation. Second, most species encountered showed wide distributions and occurred in several lake districts. This suggests that cold lakes in Europe provide habitats of equal quality for cladocerans with respect to their chemical and physical parameters. The few with limited distribution species (e.g. *E. glacialis*, *E. longispina*, *H. gibberum*) may have some restricted environmental requirements or poor dispersal abilities. Third, there was a difference in species size structure between the north-east and southern parts of Europe (including Greenland) that may in part be related to the presence and absence of size-selective fish predation. This last finding emphasises the trophic position of cladocerans in the middle of the food web and the importance of top-down control that has only recently been included in palaeolimnological studies (JEPPESEN et al. 2001, RAUTIO 2007, AMSINCK et al. 2007). Fourth, although some changes occurred in species composition from pre- to post industrialisation, the changes in cladoceran species composition was generally low.

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