Comparison of Cladocera-based water-depth reconstruction against other types of proxy data in Finnish Lapland

Susanna Siitonen · Minna Väliranta ·
Jan Weckström · Sari Juutinen · Atte Korhola

Abstract Lake depth is an important limnological attribute defining the structure and function of freshwater aquatic ecosystems. Lake levels have fluctuated and lake depths changed through the Holocene reflecting regional climate variations and sediment accumulation. Cladoceran remains preserved in sediments have been widely used for qualitative (P/L ratio) and quantitative (inference models) lake-depth reconstructions. In addition to estimations of prediction errors for performance power of modern data sets, it is important also to evaluate the reliability of reconstructed environmental values and to ensure that they are ecologically and paleoclimatically meaningful. In this study, we reconstructed the Holocene lake-depth history of a northern boreal lake using the Cladocera P/L ratio and a Cladocera—lake-depth inference model. These results were evaluated by comparison with reconstructions based on other proxies (aquatic macrofossils, sediment composition and sedimentation pattern) derived from three radio-carbon-dated sediment cores from the same lake. Whilst the reconstructions based on Cladocera and on the combination of other proxies yielded similar long-term trends, the absolute water depth values derived from the quantitative cladoceran model deviated from what was indicated by the other proxies. Therefore, we strongly recommend that also other, independent methods should be used simultaneously when reconstructing past water depths using Cladocera remains.

Keywords Sub-fossil Cladocera · Quantitative water-depth reconstruction · P/L ratio · Holocene lake development · Aquatic macrophytes · Sediment properties · Finnish Lapland

S. Siitonen (✉) · M. Väliranta · J. Weckström ·
A. Korhola
Environmental Change Research Unit, Department of Environmental Sciences, University of Helsinki,
P.O. Box 65, 00014 Helsinki, Finland
e-mail: susanna.siitonen@helsinki.fi

S. Juutinen
Department of Forest Sciences, University of Helsinki,
P.O. Box 27, 00014 Helsinki, Finland

Introduction

Lake depth is a fundamental environmental variable, which defines the structure and function of freshwater aquatic ecosystems (Håkanson, 2005). Water-level changes have a direct impact on lake morphometry, which in turn affects essential physical, chemical and biological parameters in a lake (Wetzel, 2001). Various litho- and bio-stratigraphical evidence preserved in lake sediments can be used for investigating past water-levels. Long-term water-level fluctuations generally reflect the climatically controlled hydrological balance in a lake. However, in contrast to the

increasing amount of quantitative Holocene temperature reconstructions available from northern Fennoscandia (Korhola et al., 2000; Seppä & Birks, 2001; Weckström et al., 2006), water-level studies within this region lack the methodological consistency and geographical coverage needed for a reliable and comprehensive quantitative analysis of past changes in humidity (Hyvärinen & Alhonen, 1994; Barnekow, 2000; Korhola et al., 2005).

The most common methods for reconstructing past water levels in lakes include analyses of sediment properties that are largely controlled by water depth (e.g. organic content, water content and grain size) (Punning et al., 2005). Analysis of the sediment composition and the historical position of the sediment limit along a transect of dated sediment cores can give direct, and even quantitative, information on rising or falling water levels (Digerfeldt, 1988; Abbott et al., 2000; Barnekow, 2000; Almquist et al., 2001). Also changes in sediment macrofossil assemblages of aquatic and telmatic plant species (Hannon & Gaillard, 1997; Birks, 2001; see also Väliranta, 2006), and submerged megafossils, such as pine trunks preserved in the bottom of lakes (Eronen et al., 1999) have been used as indicators of past water level fluctuations. In addition, variation in the share of planktic and littoral cladoceran remains in the sediments (e.g. Hyvärinen & Alhonen, 1994; Sarmaja-Korjonen, 2001; Nevalainen et al., 2008 and references therein), and quantitative Cladocera—lake-depth inference models (Korhola et al., 2005; Amsinck et al., 2006; Nevalainen et al., 2011) have been commonly applied.

Cladoceran species dwell in planktic and littoral habitats and their remains in the sediments can originate from different parts of the lake (Whiteside & Swindoll, 1988). Historical variations in the ratio of "planktic" and "littoral" species (P/L ratio) in sub-fossil cladoceran assemblages have been used to infer changes in the extent of the littoral area and its proximity to the coring site, i.e. past changes in lake level (Alhonen, 1970; Hyvärinen & Alhonen, 1994; Sarmaja-Korjonen & Hyvärinen, 1999; Sarmaja-Korjonen, 2001; Gąsiorowski & Hercman, 2005). However, it is widely known that many other environmental variables in addition to lake depth affect the P/L ratio of sub-fossil cladoceran assemblages (Frey, 1986). Ecological concerns include difficulties in assigning species to certain habitats (littoral, planktic) (Lauridsen et al., 2001; Walseng et al., 2006), and the fact that planktic and littoral species can respond differently to environmental changes such as eutrophication (Hann et al., 1994). Also, the pressure and selectivity of predation, and changes in the diversity and abundance of habitats, especially submerged macrophytes, shape the cladoceran species composition (Brooks & Dodson, 1965; Jeppesen et al., 2003; Davidson et al., 2010). Taphonomical issues such as representativeness of a single sediment core taken from the deepest part of the lake (Kattel et al., 2007), and differential preservation of species (Frey, 1988) should also be taken into account. All of these factors can potentially be reflected in the P/L ratio of the sediment record without any changes in the lake depth. The ambiguity of the P/L method is further increased by the fact that, depending on the morphometry of a lake and its surroundings, the littoral area of a lake can either increase or decrease with rising lake level (Stone & Fritz, 2004). Thus, when interpreting a P/L ratio supporting evidence based on other proxy variables is of essential importance, as suggested by Hofmann (1998).

Quantitative Cladocera-based lake-depth inference models have been constructed in Canada (Bos et al., 1999), Finland (Korhola et al., 2000) and in Faroe Islands (Amsinck et al., 2006). In all cases lake depth significantly explained the cladoceran community structure. The advantage of the quantitative approach compared to the P/L ratio-approach is that it uses species-specific water-depth optima instead of groups of species with certain habitat preferences, making the results more easily interpretable (Bos et al., 1999).

In oligotrophic, high latitude lakes fish can exert strong predation pressure on planktic cladocera (Jeppesen et al., 2001). This is pronounced in shallow, clear-water lakes and in lakes with sparse and simple-structured aquatic vegetation that offers fewer refuges (Lauridsen et al., 2001; Jeppesen et al., 2003). Aquatic vegetation increases the heterogeneity of microhabitats and favours epiphytic algae, which is especially important for littoral cladocera (Whiteside, 1974; Rautio, 1998). Cladoceran communities in lakes are thus structured by multiple and often interacting forces which challenges the inference of single environmental variables, such as lake depth, from sub-fossil cladoceran assemblages (Davidson et al., 2010).

In this study, we reconstructed the Holocene lake-depth history of a northern boreal lake using a quantitative Cladocera—lake-depth inference model and the cladoceran P/L ratio. We then compared Cladocera-based reconstructions derived from one

single central core to a combination of other proxy evidence (aquatic macrofossils, sediment composition and sedimentation pattern) derived from a transect of three radiocarbon-dated sediment cores from the same lake and evaluated the suitability of Cladocera for water-depth reconstructions.

Materials and methods

Study site

Lake Kipojärvi is situated in a glacio-fluvial terrain at the northern border of the boreal vegetation zone in Finnish Lapland (69°11′N, 27°18′E) 159.4 m above sea level (Fig. 1). Mean annual and July air temperatures are −1 and 13.1°C, respectively, and annual precipitation is 395 mm. The lake is ice-covered from the end of October to the end of May. Lake Kipojärvi is bordered by an esker to the east whilst a large and open aapa mire skirts the lake to the north. Mineral soils that cover ∼50% of the catchment are dominated by pine-birch forest with abundant dwarf shrubs in the field layer. Fen vegetation is characterised by diverse brown moss cover (e.g. *Scorpidium* spp., *Warnstorfia* spp.), sedges (e.g. *Carex lasiocarpa*, *C. chordorrhiza*) and herbs (*Menyanthes trifoliata*, *Potentilla palustris*). The lake area is 11 ha, the catchment-lake ratio 7:1 and the

Fig. 1 a Location of Lake Kipojärvi. b The effective catchment area. The inlet and outlet are shown by *arrows*. c Spatial distribution of sediment thickness (cm). d Locations of the coring points KJ I, KJ II and KJ III along the transect *A–B*, lake depth contours and the lake sediment type
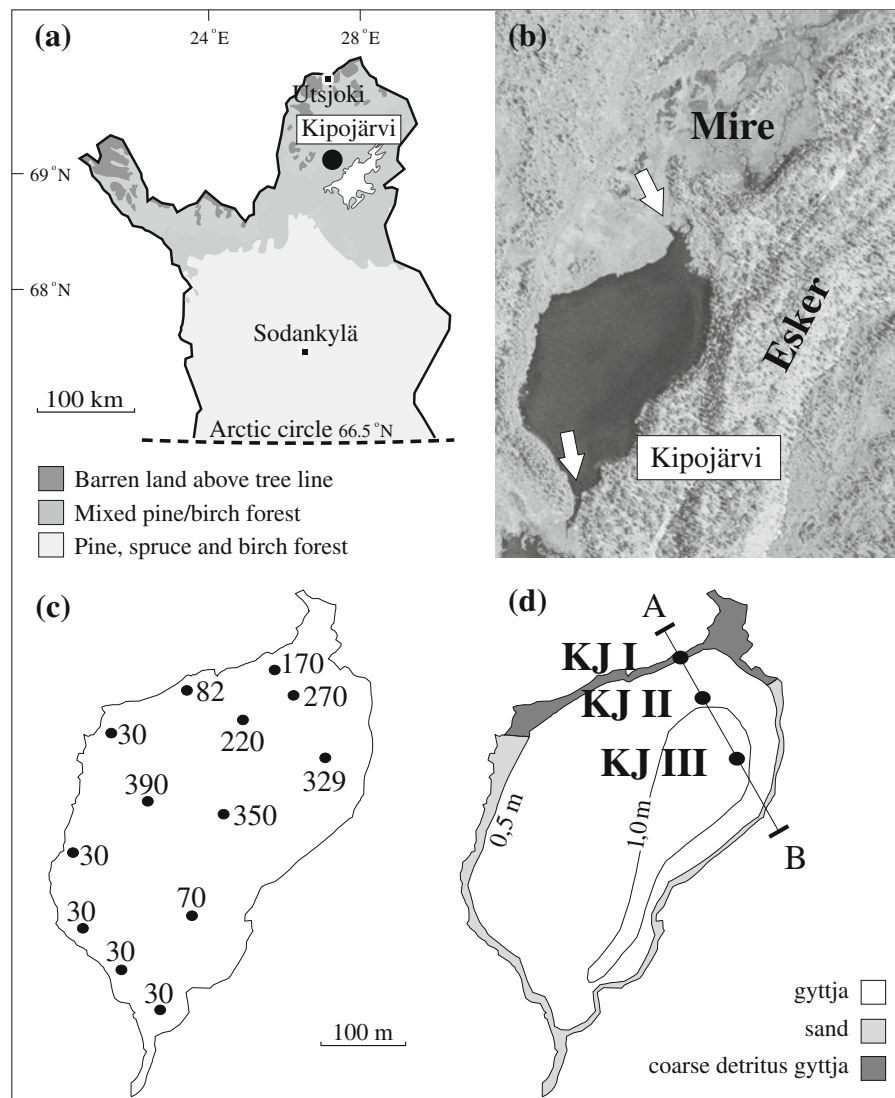
maximum water depth is 1.5 m. The lake has a small inlet that flows through the adjacent aapa mire and a narrow (∼1 m wide) and relatively shallow (∼0.5 m deep) stream as an outlet in the south. The bottom of the outlet threshold is minerogenic. The lake is oligotrophic and mesohumic with a pH of 7.3 and a mean total organic carbon (TOC) content of 7.5 mg l^{-1}. Modern aquatic macrophyte species include *Nuphar pumila* (Timm) DC., *Myriophyllum alterniflorum* DC., *Potamogeton alpinus* Balbis and *Sparganium* cf. *angustifolium* Michx. Their modern occurrence in the lake is patchy. Shoreline vegetation consists of *Utricularia intermedia* Hayne, *Carex rostrata* Stokes, *M. trifoliata* L., *Equisetum fluviatile* L. and *P. palustris* (L.) Scop.

Sampling

In winter 2006, three sediment cores [329 cm (KJ III), 276 cm (KJ II) and 108 cm (KJ I)] were derived along a transect from the deepest point to the shore using a Livingstone piston corer (Fig. 1). KJ III and KJ II both consisted of two overlapping cores, whilst KJ I consisted of only one core. The two cores overlap by 0.5 m and were correlated based on measurements of depth and organic content. Water depths at the coring sites were 1.4 m (KJ III), 1 m (KJ II) and 0.5 m (KJ I) and their distance from the shoreline ca. 50, 60 and 15 m, respectively. Plastic tubes were sealed immediately after the coring and stored intact in cold room

(+4°C). All cores were subsampled in 2-cm-thick slices. The longest sediment section, the central core KJ III, was assumed to cover the whole sedimentation history and was chosen for multi-proxy analyses. It was subsampled for plant macrofossil, Cladocera, diatom, pollen and organic matter analyses. Results of the biological multi-proxy study of KJ III have been published by Väliranta et al. (2011). Cores KJ I and KJ II were analysed for loss-on-ignition (LOI) and plant macrofossils. A survey of the sediment thickness in different parts of the lake was conducted in summer 2006 (Fig. 1).

Chronologies and sediment organic content

The sediment cores were Accelerator Mass Spectrometry (AMS) ^{14}C-dated at the Dating Laboratory of the University of Helsinki, Finland and the Ångström Laboratory, University of Uppsala, Sweden using terrestrial plant material. Radiocarbon dates (BP) were calibrated with the software CALIB 601 using the IntCal09 calibration curve (Stuiver & Reimer, 1993; Reimer et al., 2009). The calibrated date ranges are expressed as the total 1σ range and the single point estimates are based on the median probability (e.g. Telford et al., 2004) (Table 1). Age-depth models were created by fitting a second-order polynomial curve to the calibrated dates. Hela-1366 was a clear outlier and so an additional sample was dated (Hela-1606). However,

Table 1 Results of the radiocarbon analyses of Lake Kipojärvi sediment cores

Sample	Laboratory no.	Depth (cm)	Dated material	^{14}C age (yr BP)	Age (cal yr BP)	1σ range
KJ I	Hela-1941	30–32	Mixed, terrestrial plant remains	3275 ± 35	3505	3454–3557
KJ I	Hela-1940	54–60	Mixed, terrestrial plant remains	3415 ± 35	3666	3594–3703
KJ I	Hela-1939	100–104	Mixed, terrestrial plant remains	5270 ± 40	6058	5946–6176
KJ II	Hela-1944	124–132	Mixed, terrestrial plant remains	5985 ± 50	6825	6750–6886
KJ II	Hela-1943	180–182	Mixed, terrestrial plant remains	7745 ± 50	8519	8457–8583
KJ II	Hela-1942	270–276	Mixed, terrestrial plant remains	9785 ± 70	11208	11155–11262
KJ III	Hela-1361	28–30	Wood, bark	1065 ± 35	973	932–1048
KJ III	Hela-1362	76–78	Bark	2940 ± 35	3106	3008–3204
KJ III	Hela-1363	96–98	*Carex* seed, bark	3435 ± 35	3693	3637–3814
KJ III	Hela-1364	140–142	Mixed *Pinus* remains	5625 ± 65	6404	6317–6463
KJ III	Hela-1365	184–186	Mixed *Pinus* remains	6765 ± 50	7620	7586–7656
KJ III	**Hela-1366**	**234–236**	**Wood, bark**	**1790 ± 35**	**1719**	**1630–1811**
KJ III	**Hela-1606**	**236–246**	**Mixed *Pinus* remains**	**6135 ± 45**	**7040**	**6949–7156**
KJ III	Hela-1368	326–328	*Carex* seeds	8090 ± 60	9022	8798–9128

Bold entries were omitted

both samples from this sediment depth were too young and therefore omitted from the age-depth model.

Two consecutive 2-cm-thick sediment slices were combined, and subsamples of known volume were used for the approximation of organic matter content. The subsamples were dried at 70°C to a constant weight. The organic matter content was measured as LOI at 550°C and expressed as percentage of dry matter.

Plant macrofossil analysis

Macroscopic plant remains in KJ III were analysed from every second 2-cm subsample, whilst in cores KJ II and KJ I the interval was 8 cm. However, all three bottom sections were analysed contiguously. No chemical treatment was necessary. The volume of subsamples was determined by displacement of water in a measuring cylinder, and it varied from 10 to 25 cm^3, 20 cm^3 being the most common. The sediment was sieved with a 124 μm mesh, and the residue was systematically examined using a stereo-microscope and a high-magnification light microscope. The identification of vegetative remains of *Potamogeton* species was based on leaf tips. Narrow and pointed/blunt leaf tips with three veins are referred to as *P. berchtoldii* Fieb. */ P. pusillus* L. because reliable identification between these species is not possible. The plant nomenclature follows Hämet-Ahti et al. (1998). Only selected taxa are presented and discussed.

Cladocera

Cladocera were analysed from KJ III using 1 cm^3 subsamples with a resolution of 8 cm. The laboratory procedure, identification and nomenclature are mainly based on Szeroczyńska & Sarmaja-Korjonen (2007). The sediment was heated for 30 min in 10% KOH and sieved using a 38 μm mesh. Cladoceran remains were identified from permanent slides with a light microscope and 200× magnification. A minimum of 200 remains from each subsample was counted except for four samples, all older than 8500 cal yr BP, due to very low abundance of cladoceran remains. The number of individuals is based on the most common fragment of each species, and the results are expressed as relative abundances. Unidentified small and medium-sized *Alona*-type carapaces and head shields were grouped as small *Alona* spp. In addition to obvious *Bosmina* (*Eubosmina*) *coregoni* Baird, 1857 and *B.* (*E.*) *longispina* Leydig, 1860—types of head pores, intermediate forms were also common, and therefore these were grouped under a collective name *Eubosmina*. According to contemporary knowledge, *Chydorus sphaericus* is actually a complex of closely related species, and therefore it was considered here as *C. sphaericus* sensu lato (s. l.).

Data analysis and quantitative Cladocera lake-depth model

Cladoceran species diversity was calculated for each sample with Simpson's Index of Diversity (Simpson, 1949). It takes into account both species richness (number of species) and their relative abundance. For the planktic/littoral ratio, the cladoceran species were split into these categories as follows: *Eubosmina* spp., *Daphnia longispina* gr., *Daphnia pulex* gr., *Holopedium gibberum* Zaddach, 1855, *Bosmina longirostris* O.F. Müller, 1785 and *Leptodora kindti* Focke, 1844 were grouped as planktic, and the rest of the species, mostly Chydoridae, as littoral species (e.g. Hann, 1989). The division is somewhat artificial since many of the species are often found in both habitats. For example, *C. sphaericus* is usually considered a littoral species, but it is also frequently found in the pelagial (Nykänen et al., 2009), especially in eutrophic systems. We created three P/L ratios: one where *C. sphaericus* was classified as littoral, a second where it was classified as planktic, and a third, where *C. sphaericus* was excluded from the analysis. The cladoceran biostratigraphy was zoned using optimal partitioning, and the number of statistically significant zones was calculated using a broken-stick model as described in Bennett (1996). Optimal partitioning was performed using the program ZONE 1.2 (Lotter & Juggins, 1991). To assess if the fossil Cladocera have good analogues in the modern training set, squared chi-squared distance was used as a dissimilarity measure. Fossil samples were considered to have good analogues if they lay within the fifth percentile. The quantitative water-depth reconstruction is based on a calibration data set comprising 34 surface sediment Cladocera samples and an associated set of environmental data from northwest Finnish Lapland (Korhola et al., 2000, 2005). The water-depth gradient in the training set lakes varies between 1 and 17 m. A two-component Weighted Averaging Partial Least Squares (WA-PLSs) regression model (ter Braak & Juggins, 1993) was used to develop a transfer function.

After harmonisation of the cladoceran data between this study and Korhola et al. (2005), 21 taxa were included in the analyses. The fact that most of the physical and chemical variables of Lake Kipojärvi are within the ranges of the measured environmental variables of the training set lakes (in most cases close to the median values) lends support to the use of this training set for quantitative water-depth reconstructions of Lake Kipojärvi.

Results

Chronology and sediment organic content

KJ III

Although KJ III contains the longest sediment stratigraphy, it does not cover the entire Holocene. This fact is supported by the high basal LOI value (33%) (Fig. 2), and the diatom and pollen stratigraphies (see Väliranta et al., 2011). The dated basal age of KJ III (9200 cal yr BP) (Table 1) is thus too young. Based on comparisons of the KJ III pollen record (*Betula* and *Pinus* abundances, and a characteristic early-Holocene Ericaceae peak) with other pollen studies from the region (Seppä, 1996; Mäkelä, 1998), as well as on the variations in plant composition and LOI values between cores KJ III and KJ II, we propose a revised basal age (cf. Väliranta et al., 2011) of 10200 cal yr BP. Because the adopted age has an influence on the calculated sedimentation rates, and hence on the reconstructed lake basin development, which is one of the important scopes of our study, we apply an age-depth model where the bottom age is 10200 cal yr BP.

Organic content shows an increasing trend from the bottom towards the present and by ca. 8000 cal yr BP the value reaches ca. 70%. LOI remains high and relatively stable until ca. 4500 cal yr BP, when it decreases by more than 30%. After this decline, LOI remains stable for the rest of the Holocene with values around 35%. The sediment was homogenous gyttja along the entire length of the core, without any visually observable horizons.

KJ II

Although core KJ II is 53 cm shorter than KJ III, it contains the whole Holocene sediment stratigraphy.
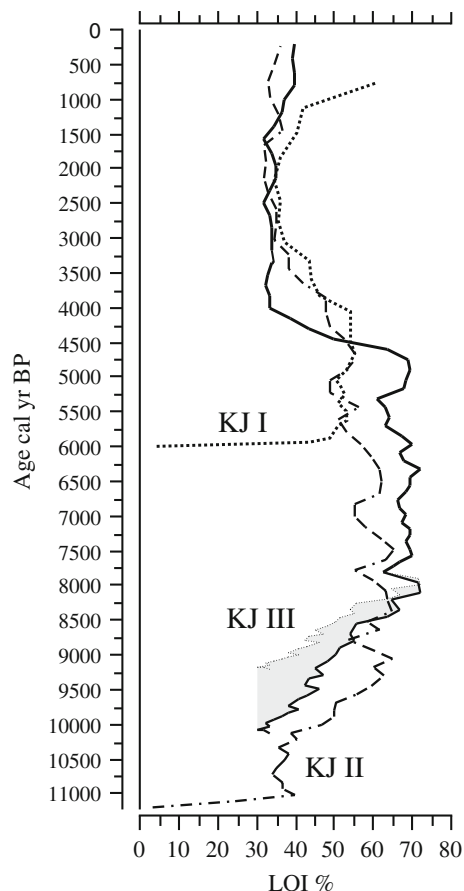

Fig. 2 Depth profiles of LOI from all three cores. The *bottom part* of KJ III was chronologically re-adjusted based on evidence provided by regional pollen and plant macrofossil data and LOI data from core KJ II. The original KJ III LOI curve (see Väliranta et al., 2011) is indicated as *dotted line*

This is supported by the initial low LOI values (<5%) (Fig. 2) and the bottom age of ca. 11200 cal yr BP (Table 1). LOI rises to ca. 60% by 9000 cal yr BP and remains relatively stable until ca. 6000 cal yr BP after which it starts to decrease. As in KJ III, a more pronounced decline in LOI begins around 4500 cal yr BP, after which LOI remains stable at around 35%. Above the minerogenic layer at the bottom, the core is composed of homogenous gyttja.

KJ I

According to the chronology, sedimentation started at KJ I ca. 5900 cal yr BP. After the initiation phase, the low LOI (<5%) increases rapidly above 50%, and after 4000 cal yr BP LOI declines to ca. 35%, as in other

cores (Fig. 2). The distinct rise in the surface LOI value after ca. 1000 cal yr BP towards the present reflects the increase of bryophytes (e.g. *Warnstorfia* spp.) in the sediment. These aquatic bryophyte species may have grown in situ at the site but their presence might also indicate the proximity of the coring point to the peaty shore line. Above the minerogenic bottom layers, the sediment consists of gyttja, overlaid by a 25-cm thick layer of coarse detritus gyttja.

Macrophytes

Early-Holocene (until ca. 8000 cal yr BP) macrophyte assemblages in cores KJ III and KJ II are characterized by the presence of a relatively diverse aquatic species community (Fig. 3). Several narrow-leaved *Potamogeton* species are present: *P. berchtoldii/pusillus*, *P. filiformis* Pers. and *P. compressus* L., occurring with *Callitriche hamulata* Kütz. ex Koch and *C. hermaphroditica* L., *Myriophyllum* sp. and Charales species *Nitella* C. Agardh. Remains of emergent species are scarce and only vegetative remains of

Equisetum and *Carex*/Cyperaceae remains are occasionally present. The aquatic macrophyte assemblage consists of submerged species with finely dissected leaves that can form dense beds under the water.

The Mid-Holocene (ca. 8000–4500 cal yr BP) represents a transition to a period with a low amount of remains and a lesser number of aquatic species. After ca. 8000 cal yr BP the submerged vegetation diminishes in the cores KJ III and KJ II to only two aquatic genera that were present earlier: unidentified remains of *Potamogeton* sp. at KJ III and *Myriophyllum* sp. at KJ II. Vegetative remains of floating-leaved taxa *Nuphar* and Nymphaeaceae appear in the central core KJ III. Otherwise, only *Equisetum* sp. remains (KJ III) and *M. trifoliata* (KJ II) are detected. Around 6000 cal yr BP the macrophyte remains in KJ I are scarce and small; the vegetation composition at the genus level is similar to the macrophyte remains in KJ III and II.

The Late-Holocene (ca. 4500–present) is characterized by the scarcity of macroscopic plant remains in all cores. The only aquatic plant taxa are
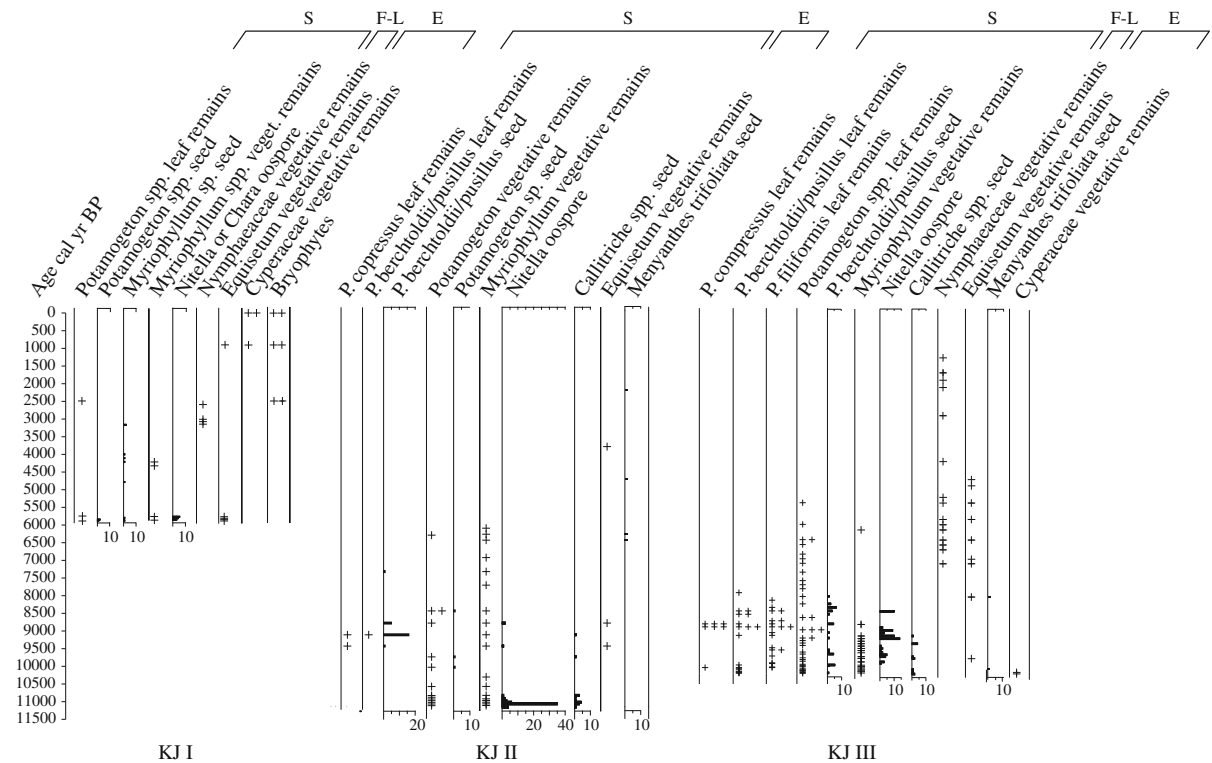

Fig. 3 Selected plant macrofossils. *Black bars* indicate the actual number of finds and a symbol (+) is used to describe the relative abundance of remains (+, rare; ++, occasional; and +++, abundant). *S* Submerged, *F-L* floating-leaved, *E* emergent

Nymphaeaceae in KJ III and *Myriophyllum* sp. and *Potamogeton* spp. in KJ I. After ca. 4250 cal yr BP *Equisetum* vegetative remains are no longer present in KJ III. During the past ca. 1000 years only the remains of emergent and terrestrial (not shown) taxa are found in the cores.

Cladocera

Altogether 34 species were identified from KJ III (Fig. 4). The cladoceran record was divided into three cladoceran assemblage zones (CAZ I–III).

CAZ I (ca. 10200–7500 cal yr BP) has the highest species richness (30 taxa) and diversity (Fig. 5f). The diverse assemblage is characterized by abundant occurrences of *Alona quadrangularis* O.F. Müller, 1860, *C. sphaericus*, and small *Alona* spp. together with some *Pleuroxus* (*P.*) *uncinatus* Baird, 1850 and *Grabtoleberis testudinaria* Fisher, 1848. Other species include *Alonella nana* Baird, 1843 and *Alona affinis* Leydig, 1860, and mostly planktic *B.* (*E.*) *coregoni* and *B.* (*E.*) *longispina*.

During CAZ II (ca. 7500–4500 cal yr BP), the number of taxa (24) and species diversity declines. The abundances of *A. quadrangularis* and *C. sphaericus* decrease, whereas the amount of *A. affinis* and *A. nana* increases. Towards the present *A. affinis* and *A. nana* eventually become the dominant species together with *Eubosmina* spp. Within this zone *P.* (*P.*) *uncinatus* disappears completely and *G. testudinaria* occurs only occasionally in low numbers.

At the beginning of CAZ III (ca. 4500 cal yr BP), *A. nana* becomes the dominant species at the expense of *A. affinis*. Abundances of other littoral species such as *Rhyncotalona falcata* Sars, 1903 and *Alonella excisa* Fisher, 1854 also increase. In general, the Late-Holocene cladoceran assemblages are less diverse, although the number of species (25) is similar to CAZ II.

Cladoceran P/L ratio and the reconstructed lake depth

Depending on whether *C. sphaericus* is included in littoral or planktic species or excluded from the analysis, it shapes the Holocene trend of the P/L ratio. The traditional P/L ratio with *C. sphaericus* as littoral species shows highest planktic percentages during the Mid-Holocene, peaking just before 6000 cal yr BP

(Fig. 5a). Including *C. sphaericus* as planktic, the highest percentages occur in the Early-Holocene with a pronounced peak at ca. 8000 cal yr BP (Fig. 5b). The peak around 8000 is also visible when excluding *C. sphaericus* from the analysis (Fig. 5c). After ca. 4500 cal yr BP, a decline in the share of planktic species towards present is visible in all three analyses.

A two-component WA-PLS model, with leave-one-out cross validation and without data transformations, performed best with a correlation coefficient (r^2) of 0.57 and a root mean square error of prediction (RMSEP) of 2.5 m (Fig. 6). The modelled water depth shows a general decreasing trend from the Early-Holocene to the present (Fig. 5d). During the Early-Holocene, the modelled water depth fluctuates notably, mainly between 3 and 4 m. According to the model, the lake was at its deepest (5 m) around ca. 9750 cal yr BP. A decreasing trend is visible during the Mid-Holocene (8000–4500 cal yr BP) when the highest water depths are ~4.5 m and the lowest ~2.5 m. The model indicates further decline in water depth in the Late-Holocene with depth variation of ~1.5 m. There is a slight increase in the modelled water depth from ca. 3000 cal yr BP to the present.

Discussion

Water-depth history based on sedimentation patterns and LOI

At present, sediments of Lake Kipojärvi that are deposited at depths greater than ca. 0.5 m consist of fine, homogenous gyttja. At shallower sites, above this sedimentation limit, the sediment is either sand (east side of the lake) or coarse, organic detritus along the shores surrounded by peatland. Thus, when homogenous gyttja is found in the Kipojärvi sediment cores, we assume that the water depth has been at least 0.5 m. Both KJ III and KJ II sediment cores consist of uninterrupted, homogenous gyttja without visually observable hiatuses and therefore we are relatively confident that they have been continuously under water during the entire Holocene.

According to the chronology, the littoral core KJ I did not start to accumulate limnic sediments until ca. 5900 cal yr BP. Hence we can assume that the water level remained below KJ I (ca. 1.5 m below modern water level) until ca. 5900. This means that the water
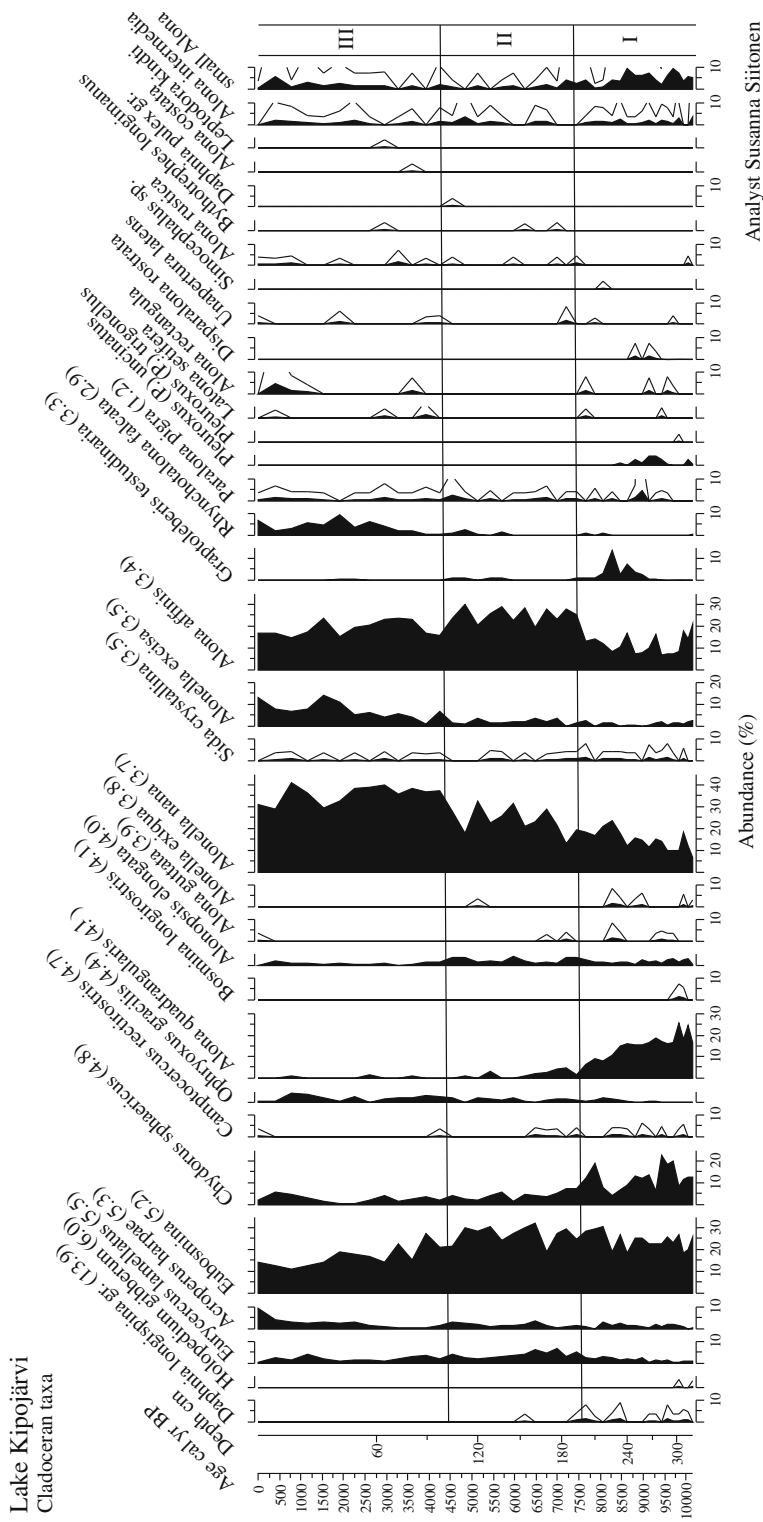
Fig. 4 Cladoceran percentage diagram of Lake Kipojärvi. *Open silhouettes* indicate the estimated weighted averaging (WA) water-depth optimum of that species in meters based on the 34 modern training set lakes. Species not included in the training set are missing these values

Fig. 5 Summary diagram showing **a** the percentage of planktic cladocera, *C. sphaericus* as littoral, **b** the percentage of planktic Cladocera, *C. sphaericus* as planktic, **c** the percentage of planktic Cladocera, *C. sphaericus* excluded from analysis, **d** quantitative Cladocera-based water-depth reconstruction in meters with *black squares* indicating samples which have poor analogues in the modern training set, **e** the reconstructed range of water depth based on sediment data, and **f** diversity of Cladocera assemblages
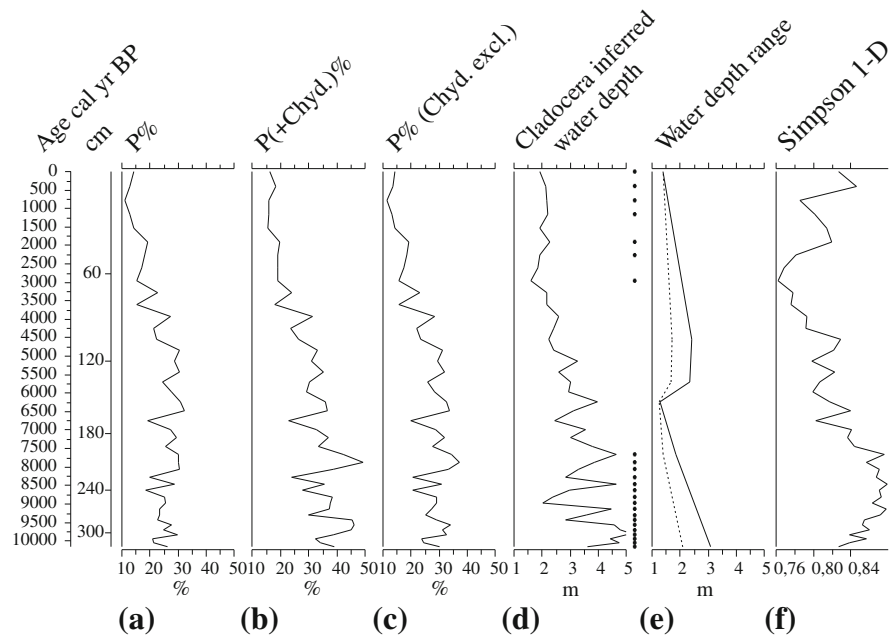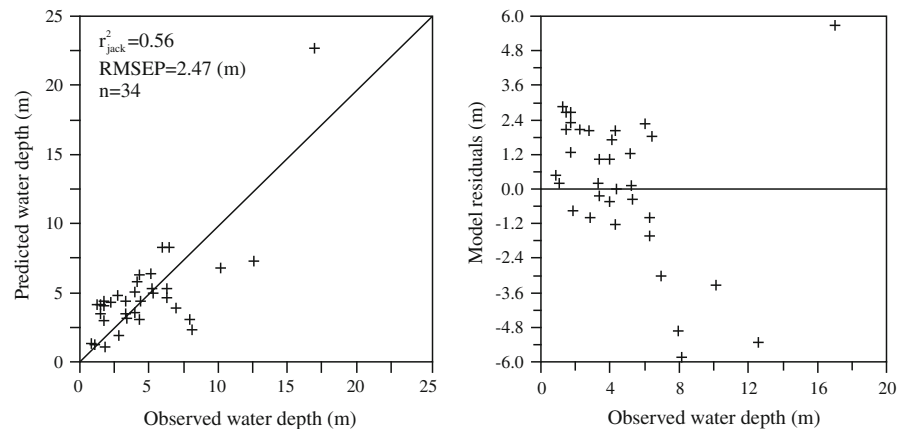

Fig. 6 Relationship between the observed and cladoceran-inferred water depth using a two-component WA-PLS model

level was also below the outflow threshold at least until this time and that the lake was a closed-basin lake during the Early- and Mid-Holocene.

Using the bottom sediment age of KJ I as a constraint of the maximum depth, 0.5 m as a minimum water depth for gyttja accumulation and the approximate sedimentation rates of KJ II and KJ III, we reconstructed a maximum water depth of ca. 3 m for the Early-Holocene (Fig. 7a) and a Mid-Holocene water depth decline to a maximum water depth of slightly above 1.0 m until 6000 cal yr BP (Fig. 7b).

Around 5900 cal yr BP, the site KJ I was inundated indicating a rise in water level. The lake became also deeper (~2.5 m) (Fig. 7c). Such a rise in the lake level would not have been possible if the lake had been

an open-basin lake. The increased inflow would have been compensated by increased discharge and hence the response of lake level to increased humidity would have been transient and muted. Around 4500 cal yr BP (Fig. 7d) (see below), the outflow threshold dynamics began to control the maximum lake level. During the Late-Holocene, Lake Kipojärvi became shallower due to continued sediment deposition (Fig. 7e).

LOI analyses support the lake depth reconstruction described above. The lake was formed in a glacifluvial depression where the bottom terrain was characterised by small holes formed after melting of dead ice blocks. The shape of the basin was initially more conical with steeper bottom slopes especially in the eastern part of the lake (Fig. 7a). The slightly higher sedimentation
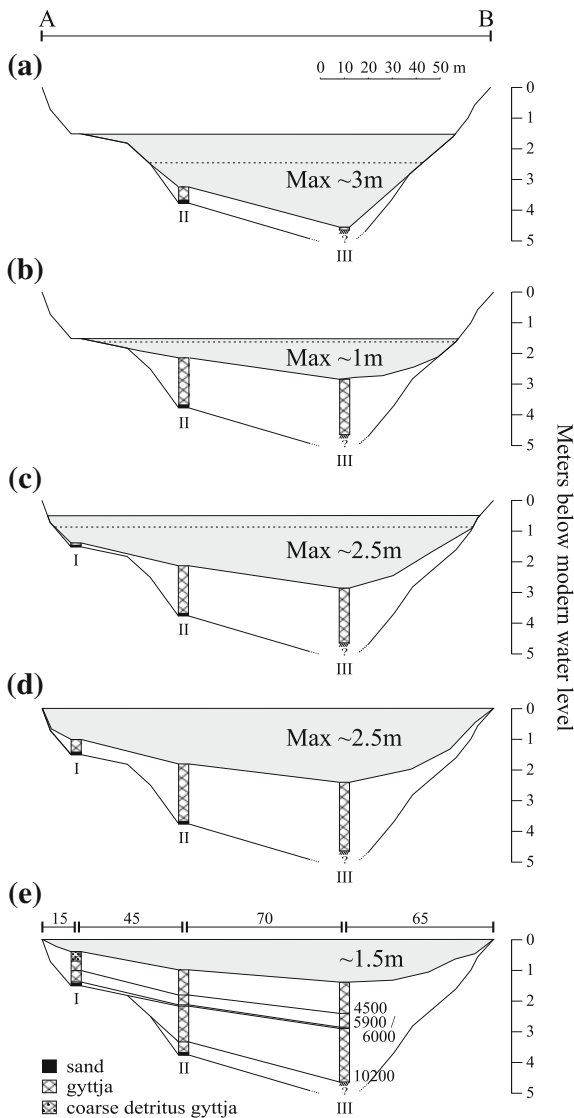
Fig. 7 A schematic overview of water depth, lake level and sedimentation succession in Lake Kipojärvi based on multi-proxy data derived from cores KJ III, KJ II and KJ I along the transect *A–B*. The *dash line* indicates contemporary minimum water level reconstructed using the 0.5 m limit for gyttja accumulation (see text). **a** The Early-Holocene (ca. 10200 cal yr BP) represents the deepest phase with a water depth of ca. 3 m. Only KJ II and KJ III accumulated sediment. **b** By 6000 cal yr BP KJ III had accumulated 2 m of sediment and the lake was at its shallowest phase. **c** At ca. 5900 core, KJ I started to accumulate limnic sediments as water level rose. **d** Around 4500 cal yr BP rising water level created an outlet to the south side of the lake and Lake Kipojärvi became an open system. **e** At present, Lake Kipojärvi is a shallow, open-basin lake. Also shown are distances in meters between the cores and to the lake shore

rate in KJ III compared to KJ II together with lower LOI values in the beginning of the Early-Holocene can be explained by the bathymetry of the lake and the steep relief of the catchment in the east (Shuman, 2003). Climate during this time enhanced the erosion and transportation of material from the catchment, especially from the mineral soils of the steep esker (Väliranta et al., 2011). Overall, the LOI values of KJ III and KJ II were highest during the Early-Holocene, reflecting the higher productivity within the lake (Väliranta et al., 2011). LOI values stayed high during the Mid-Holocene in KJ III and KJ II with a slight decreasing trend in both cores starting around 6000 cal yr BP, supporting the view of slowly rising water level. The slightly higher LOI values of KJ III at this time might result from more abundant aquatic vegetation at the site. The marked decline of LOI in all the cores starting around 4500 cal yr BP reflect differ-ent, but connected processes that shaped the compo-sition of the sediments (Shuman, 2003). First, the basin-wide LOI decrease could be attributed to shoreline erosion as the water level rose (Almquist et al., 2001). LOI decline was particularly pronounced in KJ III closest to the esker. Second, the declining LOI is also concurrent with a cooling climate that resulted in decreased production both in the catchment and in the lake (Väliranta et al., 2011). Thirdly, the decreased water residence time as the basin opened would alone cause a decline in sediment organic carbon (Whiteside, 1983).

Water-depth history based on macrophytes

Aquatic plant species occupy different sub- and eu-littoral niches and have specific preferences for water depth (Hannon & Gaillard, 1997). Due to the limited dispersal of especially vegetative parts of aquatic plants (Birks & Birks, 1980; Vance & Mathewes, 1993), sub-fossil remains represent contemporary, in situ habitat conditions. The depth distribution of macrophytes is, however, also controlled by other factors, most notably by water transparency, but a previous study from Lake Kipojärvi suggests that the water colour has not changed significantly over the Holocene (Väliranta et al., 2011). Thus, water depth can relatively reliably be inferred from the macrophyte composition.

Potamogeton compressus is mostly growing in 1–2 m deep water, *P. filiformis* prefers shallower depths (0.1–0.5 m), the maximum depth being around 3 m. *P. berchtoldii* remains could not be distinguished from those of *P. pusillus*. The former grows at shallow depths (0.2–0.5 m) and the latter in the sublittoral (0.4–1.5 m). Depending on the species, *Myriophyllum* has a wider depth distribution (1–5 m). *Callitriche* spp., on the other hand, grows mainly in less than 2 m depth. Charales oospores offer limited amount of information for depth reconstructions due to their wide depth distribution and effective spread of the oospores from the parent plant. The Early-Holocene macrophyte assemblages in KJ III and II suggest a shallow littoral environment with a water depth of ca. 1–2 (3) m, corresponding well with the depths inferred from the sediment data.

After ca. 8000 cal yr BP, the submerged macrophyte assemblages in KJ II and KJ III are reduced and *Nympheacea* sp. and *Equisetum* sp. appear in KJ III. The depth requirements of floating-leaved Nypheaceae and submerged *Potamogeton* spp./*Myriophyllum* sp./*Callitriche* spp. overlap, but this combination together with the presence of *Equisetum*, that grows at or very close to the water/air interface, suggests declined water depth (Hannon & Gaillard, 1997). Previous studies have observed a similar succession (*Myriophyllum–Equisetum*, *Nuphar*) pattern during decreasing lake levels (Hannon & Gaillard, 1997). The occurrence of *Equisetum* in KJ III during the Mid-Holocene supports the sedimentation data indicating that the lake was small and shallow (max ∼1 m) and that the lake shore was rather close to the coring point. *M. trifoliata* seeds are found from KJ II ca. 6300 cal yr BP. This species occurs on wetlands and lake shores up to a water depth of 1 m. The occurrence of seeds may indicate the proximity of the site KJ II to the shoreline. Vegetative remains of *Equisetum* are found in KJ III until 4750 cal yr BP, after which they are recorded only in the shallower core KJ II and later in the littoral core KJ I together with other shoreline vegetation (Cyperaceae). The disappearance of *Equisetum* from KJ III is roughly simultaneous with marked assemblage shifts observed in all biological proxies (Väliranta et al., 2011) as well as in LOI values, and supports the view that the modern extent of the lake and the outflow threshold was reached around this time due to a rising lake level.

Water-depth history of Lake Kipojärvi and Holocene climate

The water-depth reconstruction of Lake Kipojärvi, which combines the sedimentary and macrofossil data from three dated sediment cores, seems to agree well with paleoclimate and lake-level/water-depth reconstruction studies from northern Fennoscandia. In general, the Early-Holocene climate was humid, and warm and lakes were deeper than present (Seppä & Hammarlund, 2000; Korhola & Weckström, 2004; Korhola et al., 2005). Although the actual water level of Lake Kipojärvi was lower than today during the Early-Holocene, the lake was deeper than today (Fig. 7a). In northern Fennoscandia, the Mid-Holocene was dry and warm (Seppä & Birks, 2001) and the lake levels low (e.g. Hyvärinen & Alhonen, 1994; Eronen et al., 1999; Barnekow, 2000; Korhola & Weckström, 2004; Korhola et al., 2005; Väliranta et al., 2005; Sarmaja-Korjonen et al., 2006). According to these studies, water levels started to rise ca. 6000–4000 cal yr BP as a consequence of a cooler and more humid climate. Also Lake Kipojärvi became shallower during the Mid-Holocene due to a combination of sediment accumulation and drier climate, and the lake was at its shallowest before 6000 cal yr BP. After this the lake level rose and the lake became deeper and eventually an open-basin lake as the threshold was reached. Using macrofossils, pollen and multiple sediment cores derived from a small lake Badsjön in northern Sweden, Barnekow (2000) reconstructed a lake level lowering of roughly the same amplitude as in Lake Kipojärvi (1–1.5 m) during the warm and dry Mid-Holocene followed by a rise in lake level since ca. 4500 cal yr BP. Because the sediment- and macrophyte-based reconstructions, the long-term lake-level and water-depth trend and the amplitude of change in Lake Kipojärvi seem to be very comparable with the previous reconstructions in northern Fennoscandia, we feel confident to compare these data with the data derived from the cladoceran-based methods.

Lake Kipojärvi water-depth history based on Cladocera remains

Previous validations of quantitative Cladocera-based water-depth reconstructions are mainly based on other, indirect proxy methods, such as pollen, charcoal, geochemical variables and midge-based

inferences (Korhola et al., 2005; Nevalainen et al., 2011). In this study, the lake depth history of Lake Kipojärvi has been reconstructed using a combination of independent proxies that are directly affected by water depth changes. This reconstruction shows some similar trends with the results based on Cladocera methods, but also obvious discrepancies occur.

Qualitative Cladocera-based reconstruction

The cladoceran P/L ratio shows markedly different trends depending on whether *C. sphaericus* is included as littoral (P%), planktic (P(+C)%) or excluded (P%(CExcl)) from the analysis (Fig. 5). During the Early-Holocene (before 8000 cal yr BP), P% and P%(CExcl) remained rather constant indicating only minor fluctuations in water depth, whereas P(+C)% declined substantially, suggesting decreasing water depth. During the Mid-Holocene (8000 cal yr BP), both P% and P%(CExcl) show slightly higher values than during Early-Holocene, whereas P(+C)% has its highest values during the whole Holocene. None of the reconstructions capture the shallowest phase of the lake at ca. 6000 cal yr BP contradicting the sediment and macrophyte data. Changes in the ratio of planktic and littoral species should, in theory, reflect changes in the extent of these habitats in a lake. However, the rising water level starting at approximately 5900 cal yr BP and the related expansion of the littoral area is not distinguishable from any of the P/L curves. Before the lake level reached the outflow threshold at ca. 4500 cal yr BP, the actual water depth remained roughly the same. After the threshold was crossed and the lake became an open-basin lake, water depth gradually declined due to sediment accumulation without any large changes in the dimensions of the littoral area. At the same time, however, all three curves show a declining trend.

The decreasing percentages of planktic species in all three Cladocera records during the Late-Holocene could be related to the oligotrophication process of the lake favouring littoral species, as shallow, oligo-trophic lakes in high latitudes are usually dominated by benthic production (Vadeboncoeur et al., 2008). On the other hand, macrophyte vegetation continued to decline during the Late-Holocene. In shallow lakes, the biomass and production of zooplankton is lower compared to zoobenthos, and this has been largely attributed to the higher fish predation pressure on

zooplankton in shallow lakes (Jeppesen et al., 1997). After 4500 cal yr BP, fish were able to migrate to the lake, and the declining abundance of planktic species could be related to the increase of zooplanktivory, especially as the abundance and diversity of macrophytes, which offer refuge (Timms & Moss, 1984), were diminished. On the other hand, small-sized *Bosmina* spp. are known to be able to inhabit lakes with high fish densities (Ślusarczyk, 1997; Lauridsen et al., 2001; Siitonen, unpublished data), and even benefit from the presence of fish (Ślusarczyk, 1997).The interpretation of the P/L ratio is very complicated as there are several alternative explanations for the observed changes. In some paleolimno-logical studies from lakes with known eutrophication history, *C. sphaericus* has been excluded from the P/L analyses (Gąsiorowski & Hercman, 2005). Subjective categorising of species with uncertain habitat preference into either littoral or planktic, or excluding them from the analysis will likely, as shown here, result in substantially different P/L ratios. The requirement that the P/L ratio should only be used in lakes that have not experienced major changes in their food web, trophic state, or suffered from pollution (see e.g. Nevalainen et al., 2011) severely restricts the use of this method.

Quantitative Cladocera-based reconstruction

The quantitative Cladocera-based water-depth recon-struction consistently overestimates the Holocene water depths of Lake Kipojärvi (Fig. 5d). This is a common feature of inverse approaches such as WA-PLS (e.g. Birks, 1995) as they tend to overestimate higher values and underestimate lower values. For example, the modelled maximum depth of 5 m in the Early-Holocene would mean that KJ I was inundated and the lake level was higher than the current water level. Similarly, the maximum lake depths modelled for the Mid-Holocene indicate that the lake level would have been more than 1 m higher than at present. Also the minimum water depth reconstructed for the Mid-Holocene, i.e. ∼2.5 m around 6800 cal yr BP, would mean that KJ I was inundated and the threshold level was crossed. However, the overall trend of decreasing water depth during the Holocene is captured well by the model.

In addition to model uncertainties, also ecological, analogical and taphonomical issues affect the

reliability of quantitative reconstructions. Five taxa detected in the Lake Kipojärvi fossil record (*Eubosmina* sp., *A. nana*, *A. affinis*, *C. sphaericus*, and *E. lamellatus*) occurred in 30–34 out of the 34 modern training set lakes and they also have high Hill's N2 values (Hill, 1973), which indicates high abundance and even distribution across the sites. The Holocene cladoceran community changes in Lake Kipojärvi are mainly determined by these five species, which clearly dominate the species assemblages (60–90% of the total occurrence). These species seem to be common across a wide range of environmental variables. For example, Nevalainen et al. (2011) found these species in almost all 55 training set lakes extended across Finland, again with high Hill's N2 values, and Rautio (1998) found them to be amongst the most common species in a set of 17 small subarctic ponds from northwestern Finnish Lapland. The depth gradient of the 55 lakes is from 0.5 to 7 m, and that of the ponds 0.5–7.5 m (median 1.0 m). These species do not seem to show a distinct preference for water depth in these training sets nor in our modern lake set (Fig. 8). Instead, in our training set their distribution along both the depth and abundance axis appear very scattered (Fig. 8).

The analogues between the modern and fossil cladocera assemblages were good mainly between 7500 and 3000 cal yr BP (Fig. 5d). Poor analogues we recorded especially during the Early-Holocene and, surprisingly, also partly during the Late-Holocene. As quantitative reconstructions perform better under good analogue situations, water-depth reconstructions during the Early- and Late-Holocene should be interpreted with caution. The poor analogue situation during the Early-Holocene might be explained by the elevated nutrient concentration and diverse aquatic macrophyte community, as this environmental setting differs clearly from the modern training set lakes, which are oligotrophic with modest aquatic macrophyte populations. However, as squared Chi-squared distance is heavily affected by the proportional similarities/differences between taxa in modern and fossil samples, poor analogue situations may occur even if only one taxon is very abundant in the fossil sample but is not represented in the modern sample. This methodological bias might explain the poor analogue during the Late-Holocene.

Also taphonomical issues may affect the composition of cladoceran assemblages. For example, the surface sediment sample of the deepest lake in the training set (17 m) was dominated by *D. longispina* (75%), whereas it was rare in other lakes. Since *Daphnia* spp. are usually underrepresented in sediments (Rautio et al., 2000; Nykänen et al., 2009), their occurrence and variation in the sediment record may be sporadic. Moreover, the sediments taken from the deepest part of lakes may underestimate the actual abundance of littoral species, the remains of which deposit mainly in the littoral areas (Kattel et al., 2007).

Cladocera as water-depth indicators

In many previous training set studies lake depth seems to have been an important factor in explaining cladoceran distribution compared to other environmental variables (Bos et al., 1999; Korhola, 1999; Korhola et al., 2005; Amsinck et al., 2006; Nevalainen et al., 2011). Although the study of Amsinck et al. (2006) included fish data from Faroese lakes, lake depth proved to be more important than fish in explaining the composition of the cladoceran assemblages. This was attributed to the dominance of a less effective zooplanktivore, namely, brown trout. As mentioned earlier, *Bosmina* spp. might even benefit from the presence of fish, but the more visible *Daphnia* spp. are clearly controlled by zooplanktivorous fish abundance (Davidson et al., 2010). In the Faroese study, pelagic taxa (*B. longispina*, *Daphnia* spp.) were rare in lakes less than 5 m deep, but these species clearly dominated the sedimentary cladoceran composition of lakes deeper than 5 m. Lake depth can offer vertical refuge for large pelagic Cladocera against predators, and therefore the abundance distribution of these species could be seemingly controlled by depth. However, despite the importance of water depth, fish may often be the ultimate environmental variable controlling the distribution of cladoceran populations. For example, Bigler et al. (2006) showed that in Swiss lakes the abundance of *B. longispina* had no relationship with lake depth and speculated that its distribution was controlled by fish. Moreover, Rautio (1998) has found planktic cladocera species from shallow fishless ponds in subarctic Finland. These studies indicate that lake depth per se is not necessarily an important factor affecting cladoceran species distribution.

In small ponds, abundant macrophyte vegetation can protect Cladocera from predators. Especially littoral Cladocera species, which usually dominate the sedimentary assemblages, are greatly influenced

Fig. 8 Distribution of the five most common Cladoceran taxa along the water-depth gradient in the 34 lake training set and the number of lakes belonging to different depth categories. The *grey bars* highlight the random distribution of these species along both the depth and the relative abundance gradient
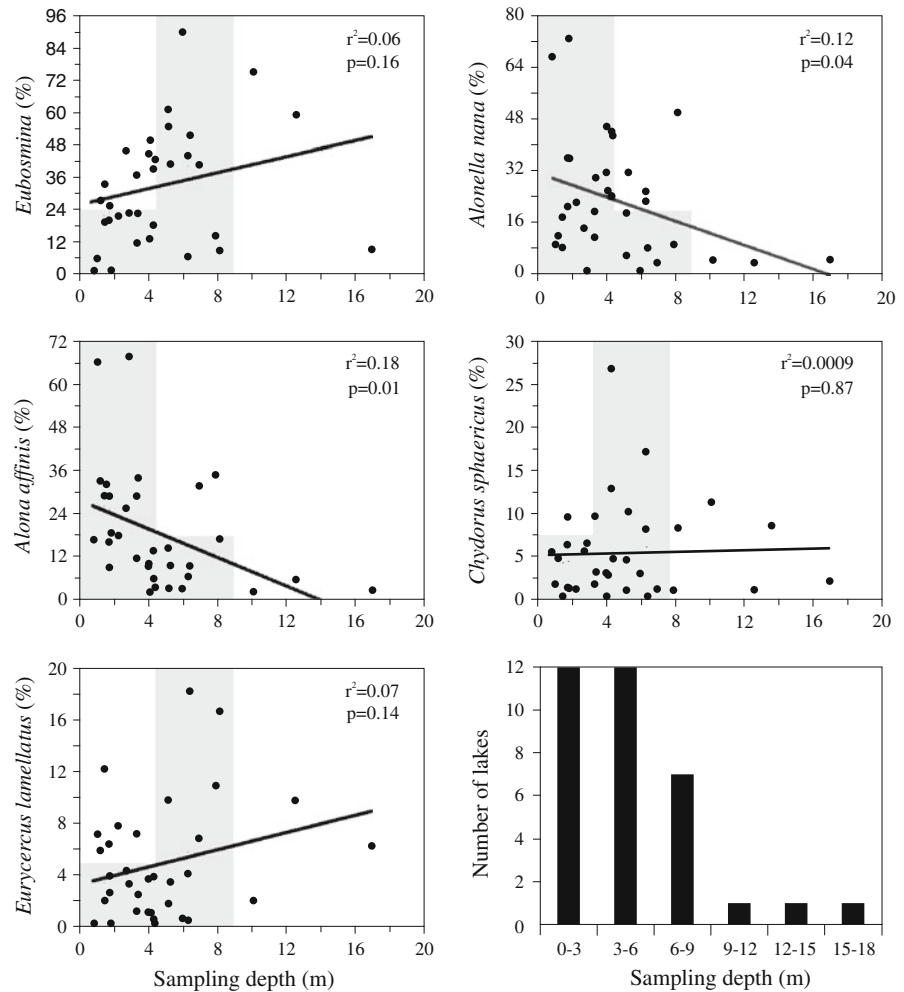
by the availability of protection and habitats. Holocene assemblage changes of Cladocera in Lake Kipojärvi seem to follow the aquatic macrophyte development (Väliranta et al., 2011). This is in agreement with previous studies showing the importance of macrophytes (density, type, structure and diversity) having an influence on cladoceran assemblage composition (Whiteside, 1970; Warner et al., 1984; Hann & Warner, 1987; Schriver et al., 1995). In Lake Kipojärvi, the cladoceran diversity is at its highest when abundant and diverse submerged vegetation is present in the lake, and coincidently with the dramatic disappearance of submerged macrophytes after 8000 cal yr BP their diversity declines. Finely lobed, submerged vegetation offers a large surface area for attached algae, and this provides an important food source for Cladocera (Hann & Turner, 1999). In Lake Kipojärvi, cladoceran diversity is lowest around

3000 cal yr BP when hardly any aquatic macrophyte remains are present. Later, when *Nympheacea* reappear in KJ III and when bryophytes appear in KJ I, the cladoceran diversity rises again. The vegetation development in Lake Kipojärvi was largely driven by changes in the lake trophic state, which was further linked to changes in hydrology (Väliranta et al., 2011).

Previous training set studies have rarely included macrophytes or fish as explanatory variables. As this violates against one basic assumption of the training set approach, namely that other environmental variables than the one being modelled have only negligible influence on the response variable (Birks et al., 2010), these reconstructions should be interpreted with caution. Also, the lack of strong linear relationships between lake depth and other factors controlling Cladocera communities probably also hampers the

applicability of the quantitative approach (Birks et al., 2010). However, despite these problems, quantitative Cladocera-based water-depth reconstructions seem to mimic well the overall long-term trends but are relatively unreliable in terms of absolute water-depth values. Therefore, to validate Cladocera-inferred lake-depth reconstructions the use of other independent proxy data is highly advisable.

Conclusions

Past lake water depths have been reconstructed using diverse methods, but after the introduction of quantitative paleolimnology Cladocera-based quantitative water-depth reconstructions have notably increased. Compared to the descriptive qualitative Cladocera-based water-depth reconstruction, the quantitative approach should provide exact depths of past water levels, and more easily interpretable results. To evaluate the performance of both Cladocera-based methods, independent reconstruction methods should be used.

In this study, we compared the Cladocera-based Holocene lake-depth reconstructions from a northern boreal Lake Kipojärvi with a combination of other proxy evidence (aquatic macrofossils, sediment composition and sedimentation pattern) derived from a transect of three radiocarbon-dated sediment cores. All Cladocera reconstructions revealed a similar long-term trend of decreasing water depth. However, the quantitative Cladocera-based water-depth reconstruction overestimated the water depth throughout the Holocene. None of the Cladocera-based reconstructions captured the water depth minimum that was evident in the sediment data and macrofossil records. Clear differences occurred also between the three qualitative water-depth reconstructions based on the P/L ratio depending on the classification of *C. sphaericus* as a littoral or planktic species or whether this species was excluded from the analysis.

This study suggests that multiple cores and a combination of proxies sensitive to changes in water depth should be used to reliably reconstruct past water-depth fluctuations. It further shows that modern and past information of aquatic macrophytes should be used together with Cladocera to describe historical aquatic ecosystem development and changes in water depth. We also demonstrate that currently open-basin lakes can provide information on past lake-level changes.

References

Abbott, M. B., B. P. Finney, M. E. Edwards & K. R. Kelts, 2000. Lake-level reconstruction and paleohydrology of Birch Lake, central Alaska, based on seismic reflection profiles and core transects. Quaternary Research 53: 154–166.

Alhonen, P., 1970. On the significance of the planktonic/littoral ratio in the cladoceran stratigraphy of lake sediments. Commentationes Biologicae 35: 1–9.

Almquist, H., A. C. Dieffenbacher-Krall, R. Flanagan-Brown & D. Sanger, 2001. The Holocene record of lake levels of Mansell Pond, central Maine, USA. The Holocene 11: 189–201.

Amsinck, S. L., A. Strzelczak, R. Bjerring, F. Landkildehus, T. L. Lauridsen, K. Christoffersen & E. Jeppesen, 2006. Lake depth rather than fish planktivory determines cladoceran community structure in Faroese lakes – evidence from contemporary data and sediments. Freshwater Biology 51: 2124–2142.

Barnekow, L., 2000. Holocene regional and local vegetation history and lake-level changes in the Torneträsk area, northern Sweden. Journal of Paleolimnology 23: 399–420.

Bennett, K. D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytologist 132: 155–170.

Bigler, C., O. Heiri, R. Krskova, A. Lotter & M. Sturm, 2006. Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south-eastern Switzerland. Aquatic Sciences – Research Across Boundaries 68: 154–171.

Birks, H. J. B., 1995. Quantitative palaeoenvironmental reconstructions. In Maddy, D. & J. S. Brew (eds), Statistical Modelling of Quaternary Science Data. Quaternary Research Association, Cambridge: 161–254.

Birks, H. H., 2001. Plant macrofossils. In Smol, J. P., H. J. B. Birks & W. M. Last (eds), Tracking Environmental Change using Lake Sediments. Kluwer Academic Publishers, Dordrecht: 49–74.

Birks, H. J. B. & H. H. Birks, 1980. Quaternary Palaeoecology. Edward Arnold, London.

Birks, H. J. B., O. Heiri, H. Seppä & A. E. Bjune, 2010. Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary biological proxies. The Open Ecology Journal 3: 68–110.

Bos, D., B. Cumming & J. Smol, 1999. Cladocera and Anostraca from the Interior Plateau of British Columbia, Canada, as paleolimnological indicators of salinity and lake level. Hydrobiologia 392: 129–141.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Davidson, T. A., C. D. Sayer, M. Perrow, M. Bramm & E. Jeppesen, 2010. The simultaneous inference of zooplanktivorous fish and macrophyte density from sub-fossil cladoceran assemblages: a multivariate regression tree approach. Freshwater Biology 55: 546–564.

Digerfeldt, G., 1988. Reconstruction and regional correlation of Holocene lake-level fluctuations in Lake Bysjön, South Sweden. Boreas 17: 165–182.

Eronen, M., H. Hyvärinen & P. Zetterberg, 1999. Holocene humidity changes in northern Finnish Lapland inferred from lake sediments and submerged Scots pines dated by tree-rings. The Holocene 9: 569–580.

Frey, D. G., 1986. The non-cosmopolitanism of chydorid Cladocera: implications for biogeography and evolution. In Gore, R. H. & K. L. Heck (eds), Crustacean Biogeography. Balkema, Rotterdam: 237–356.

Frey, D. G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. Journal of Paleolimnology 1: 179–191.

Gąsiorowski, M. & H. Hercman, 2005. Recent sedimentation and eutrophication of Kruklin Lake after artificial drop in water-level in the middle of 19th century. Studia Quaternaria 22: 17–25.

Håkanson, L., 2005. The importance of lake morphometry for the structure and function of lakes. International Review of Hydrobiology 90: 433–461.

Hämet-Ahti, L., J. Suominen, T. Ulvinen & P. Uotila, 1998. Retkeilykasvio. Forssan Kirjapaino Oy, Forssa, Finland.

Hann, B. J., 1989. Methods in quaternary ecology #6. Cladocera. Geoscience Canada 16: 17–26.

Hann, B. J. & M. A. Turner, 1999. Exploitation by microcrustacea of a new littoral habitat in an acidified lake. Hydrobiologia 416: 65–75.

Hann, B. J. & B. G. Warner, 1987. Late Quaternary Cladocera from coastal British Columbia, Canada: a record of climatic or limnologic change? Archiv fur Hydrobiologie 110: 161–177.

Hann, B. J., P. R. Leavitt & P. S. Chang, 1994. Cladocera community response to experimental eutrophication in Lake 227, Experimental Lakes Area, Ontario, as recorded in annually laminated sediments. Canadian Journal of Fisheries and Aquatic Sciences 51: 2312–2321.

Hannon, G. E. & M. Gaillard, 1997. The plant-macrofossil record of past lake-level changes. Journal of Paleolimnology 18: 15–28.

Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

Hofmann, W., 1998. Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. Journal of Paleolimnology 9: 55–62.

Hyvärinen, H. & P. Alhonen, 1994. Holocene lake-level changes in the Fennoscandian tree-line region, western Finnish Lapland: diatom and cladoceran evidence. The Holocene 4: 251–258.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen & L. Jensen, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342–343: 151–164.

Jeppesen, E., K. Christoffersen, F. Landkildehus, T. Lauridsen, S. L. Amsinck, F. Riget & M. Søndergaard, 2001. Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between Arctic charr (Salvelinus alpinus), Lepidurus arcticus and benthic chydorids. Hydrobiologia 442: 329–337.

Jeppesen, E., J. P. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. Lauridsen, P. Brettum & K. Christoffersen, 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. Ecosystems 6: 313–325.

Kattel, G., R. Battarbee, A. Mackay & H. J. B. Birks, 2007. Are cladoceran fossils in lake sediment samples a biased reflection of the communities from which they are derived? Journal of Paleolimnology 38: 157–181.

Korhola, A., 1999. Distribution patterns of Cladocera in subarctic Fennoscandian lakes and their potential in environmental reconstruction. Ecography 22: 357–373.

Korhola, A. & J. Weckström, 2004. Paleolimnological studies in arctic Fennoscandia and the Kola Peninsula (Russia). In Pienitz, R., M. S. V. Douglas & J. P. Smol (eds), Long-Term Environmental Change in Arctic and Antarctic Lakes. Kluwer Academic Publishers, Dordrecht: 381–418.

Korhola, A., H. Olander & T. Blom, 2000. Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. Journal of Paleolimnology 24: 43–54.

Korhola, A., M. Tikkanen & J. Weckström, 2005. Quantification of Holocene lake-level changes in Finnish Lapland using a cladocera – lake depth transfer model. Journal of Paleolimnology 34: 175–190.

Lauridsen, T., E. Jeppesen, F. Landkildehus & M. Søndergaard, 2001. Horizontal distribution of cladocerans in arctic Greenland lakes – impact of macrophytes and fish. Hydrobiologia 442: 107–116.

Lotter, A. F. & S. Juggins, 1991. POLPROF, TRAN and ZONE: programs for plotting, editing and zoning pollen and diatom data. INQUA-Subcommission for the Study of the Holocene Working Group on Data-Handling Methods, Newsletter 6: 4–6.

Mäkelä, E., 1998. The Holocene history of Betula at Lake Iilompolo, Inari Lapland, northeastern Finland. The Holocene 8: 55–67.

Nevalainen, L., T. P. Luoto & K. Sarmaja-Korjonen, 2008. Late-Holocene water-level changes in Lake Iso Lehmälampi, southern Finland, reflected in subfossil Cladocerans and Chironomids. Studia Quaternaria 25: 33–42.

Nevalainen, L., K. Sarmaja-Korjonen & T. P. Luoto, 2011. Sedimentary Cladocera as indicators of past water-level changes in shallow northern lakes. Quaternary Research (in press). doi:10.1016/j.yqres.2011.02.007.

Nykänen, M., K. Vakkilainen, M. Liukkonen & T. Kairesalo, 2009. Cladoceran remains in lake sediments: a comparison between plankton counts and sediment records. Journal of Paleolimnology 42: 551–570.

Punning, J., T. Koff, E. Kadastik & A. Mikomägi, 2005. Holocene lake level fluctuations recorded in the sediment composition of Lake Juusa, southeastern Estonia. Journal of Paleolimnology 34: 377–390.

Rautio, M., 1998. Community structure of crustacean zooplankton in subarctic ponds – effects of altitude and physical heterogeneity. Ecography 21: 327–335.

Rautio, M., S. Sorvari & A. Korhola, 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. Journal of Limnology 59(suppl. 1): 81–96.

Reimer, P. J., M. G. Baillie, E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, G. S. Burr, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, I. Hajdas, T. J. Heaton, A. G. Hogg, K. A. Hughen, K. F. Kaiser, B. Kromer, F. G. McCormac, S. W. Manning, R. W. Reimer, D. A. Richards, J. R. Southon, S. Talamo, C. S. Turney, J. van der Plicht & C. E. Weyhenmeyer, 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. Radiocarbon 51: 1111–1150.

Sarmaja-Korjonen, K., 2001. Correlation of fluctuations in cladoceran planktonic:littoral ratio between three cores from a small lake in southern Finland: Holocene water-level changes. The Holocene 11: 53–63.

Sarmaja-Korjonen, K. & H. Hyvärinen, 1999. Cladoceran and diatom stratigraphy of calcareous lake sediments from Kuusamo, NE Finland. Indications of Holocene lake-level changes. Fennia 177: 55–70.

Sarmaja-Korjonen, K., M. Nyman, S. Kultti & M. Väliranta, 2006. Palaeolimnological development of Lake Njargajavri, northern Finnish Lapland, in a changing Holocene climate and environment. Journal of Paleolimnology 35: 65–81.

Schriver, P., J. Bøgestrand, E. Jeppesen & M. Søndergaard, 1995. Impact of submerged macrophytes on fish–zooplankton–phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. Freshwater Biology 33: 255–270.

Seppä, H., 1996. Post-glacial dynamics of vegetation and tree-lines in the far north of Fennoscandia. Fennia 174: 1–96.

Seppä, H. & H. J. B. Birks, 2001. July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. The Holocene 11: 527–539.

Seppä, H. & D. Hammarlund, 2000. Pollen-stratigraphical evidence of Holocene hydrological change in northern Fennoscandia supported by independent isotopic data. Journal of Paleolimnology 24: 69–79.

Shuman, B., 2003. Controls on loss-on-ignition variation in cores from two shallow lakes in the northeastern United States. Journal of Paleolimnology 30: 371–385.

Simpson, E. H., 1949. Measurement of diversity. Nature 163: 688.

Ślusarczyk, M., 1997. Impact of fish predation on a small-bodied cladoceran: limitation or stimulation? Hydrobiologia 342–343: 215–221.

Stone, J. R. & S. C. Fritz, 2004. Three-dimensional modeling of lacustrine diatom habitat areas: improving paleolimnological interpretation of planktic:benthic ratios. Limnology and Oceanography 49: 1540–1548.

Stuiver, M. & J. Reimer, 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. Radiocarbon 35: 215–230.

Szeroczyńska, K. & K. Sarmaja-Korjonen, 2007. Atlas of Subfossil Cladocera from Central and Northern Europe. Friends of the Lower Vistula Society, Swiecie.

Telford, R. J., E. Heegaard & H. J. B. Birks, 2004. All age-depth models are wrong: but how badly? Quaternary Science Reviews 23: 1–5.

ter Braak, C. J. F. & S. Juggins, 1993. Weighted Averaging Partial Least Squares Regression (WA-PLS) – an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269: 485–502.

Timms, R. M. & B. Moss, 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnology and Oceanography 29: 472–486.

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden & J. Kalff, 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89: 2542–2552.

Väliranta, M., 2006. Terrestrial plant macrofossil records; possible indicators of past lake-level fluctuations in northeastern European Russia and Finnish Lapland? Acta Palaeobotanica 46: 235–243.

Väliranta, M., S. Kultti, M. Nyman & K. Sarmaja-Korjonen, 2005. Holocene development of aquatic vegetation in a shallow Lake Njargajavri, Finnish Lapland with evidence of water level fluctuations and drying. Journal of Paleolimnology 34: 203–215.

Väliranta, M., J. Weckström, S. Siitonen, H. Seppä, J. Alkio, S. Juutinen & E. Tuittila, 2011. Holocene aquatic ecosystem change in the boreal vegetation zone of northern Finland. Journal of Paleolimnology 45: 339–352.

Vance, R. E. & R. W. Mathewes, 1993. Deposition of modern pollen and plant macroremains in a hypersaline prairie lake basin. Canadian Journal of Botany 72: 539–548.

Walseng, B., D. O. Hessen, G. Halvorsen & A. K. Schartau, 2006. Major contribution from littoral crustaceans to zooplankton species richness in lakes. Limnology and Oceanography 51: 2600–2606.

Warner, B. G., R. J. Hebda & B. J. Hann, 1984. Postglacial paleoecological history of a cedar swamp, Manitoulin Island, Ontario, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 45: 301–345.

Weckström, J., A. Korhola, P. Erästö & L. Holmström, 2006. Temperature patterns over the past eight centuries in Northern Fennoscandia inferred from sedimentary diatoms. Quaternary Research 66: 78–86.

Wetzel, R., 2001. Limnology. Academic Press, San Diego.

Whiteside, M. C., 1970. Danish Chydorid Cladocera: modern ecology and core studies. Ecological Monographs 40: 79–118.

Whiteside, M. C., 1974. Chydorid (Cladocera) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. Ecology 55: 538–550.

Whiteside, M. C., 1983. The mythical concept of eutrophication. Hydrobiologia 103: 107–111.

Whiteside, M. C. & M. R. Swindoll, 1988. Guidelines and limitations to cladoceran paleoecological interpretations. Palaeogeography, Palaeoclimatology, Palaeoecology 62: 405–412.