



Sedimentary Cladocera as indicators of past water-level changes in shallow northern lakes

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ABSTRACT

The usability of subfossil Cladocera assemblages in reconstructing long-term changes in lake level was examined by testing the relationship between Cladocera-based planktonic/littoral (P/L) ratio and water-level inference model in a surface-sediment dataset and in a 2000-yr sediment record in Finland. The relationships between measured and inferred water levels and P/L ratios were significant in the dataset, implying that littoral taxa are primarily deposited in shallow littoral areas, while planktonic cladocerans accumulate abundantly mainly in deepwater locations. The 2000-yr water-level reconstructions based on the water-level inference model and P/L ratio corresponded closely with each other and with a previously available midge-inferred water-level reconstruction from the same core, showing a period of lower water level around AD 300–1000 and suggesting that the methods are valid for paleolimnological and -climatological use.

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Introduction

The understanding of past natural climate variability and its influence on ecosystems, e.g. in freshwater lakes, is important because knowledge of the magnitude and consequences of past climate changes will provide invaluable information for the presently occurring changes. Freshwater lakes are excellent indicators of climate change because their long-term water-level fluctuations mostly reflect changes in effective moisture, i.e. precipitation minus evapotranspiration, and therefore they can be used to observe changes in climatic moisture balance. Currently the anthropogenic climate change scenarios project dramatically higher frequency of heavy precipitation and generally increasing precipitation in northern Europe (Christensen et al., 2001) along with rapidly increasing temperatures (Benestad, 2004). These changes will shift the long-term patterns in effective moisture and thus in water levels that are regulated by the atmospheric circulation patterns (North Atlantic Oscillation, NAO) (Lamb and Pepler, 1987; Hurrell, 1995; Yu and Harrison, 1995). The predicted changes in the climate of northern Europe are considerable for Finland (Benestad, 2004; Jylhä et al., 2004).

Paleolimnological lake-sediment research has provided various methods to investigate long-term variability in lake levels that have been mostly driven by changes in effective moisture. In addition to reconstructing hydroclimatic changes through isotope tracers (Heikkilä et al., 2010), microfossil assemblages of aquatic

invertebrates such as Cladocera (Crustacea) and Chironomidae (Nematocera) have provided proxy data on past lake-level changes (Alhonen, 1970a; Hofmann, 1998; Korhola et al., 2000; Sarmaja-Korjonen, 2001; Luoto, 2009). The use of fossil invertebrates in lake-level research is due to assumption that under changes in effective moisture, water level in shallow and enclosed basins varies according to changes in precipitation and evapotranspiration and is consequently reflected in the area and volume of littoral and pelagic zones. As a result, the changes in littoral and pelagic habitats will affect abundance and distribution of littoral, profundal and pelagic invertebrates (Frey, 1988).

Surface sediment assemblages of Cladocera are well known to be regulated by water depth, because the distribution and accumulation of these organisms in lakes are dependent on their pelagic (planktonic) or littoral habitats (Korhola, 1999; Sweetman and Smol, 2006; Amsinck et al., 2006; DeSellas et al., 2008). This perspective has been applied in various semi-quantitative and quantitative water level reconstructions of the Holocene period in southern and northern Finland. Alhonen (1970a, 1970b, 1971) pioneered this research with his investigations on Holocene lake level changes based on planktonic/littoral (P/L) ratio of Cladocera. The P/L ratio was applied later for many paleoclimatic studies (Hyvärinen and Alhonen, 1994; Sarmaja-Korjonen and Alhonen, 1999; Sarmaja-Korjonen and Hyvärinen, 1999; Sarmaja-Korjonen, 2001). Later, due to developments in numerical techniques, in addition to Cladocera-based temperature inference models (Lotter et al., 1997; Korhola, 1999), a quantitative regional Cladocera-based transfer function for water-level inferences in northern Finnish Lapland was developed by Korhola et al. (2000) and applied to quantify the changes in past lake levels (Korhola et al., 2005).

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The previous studies have examined the relationship between Cladocera assemblages and maximum lake depth (Korhola, 1999; Sweetman and Smol, 2006; Amsinck et al., 2006; DeSellas et al., 2008) based on an assumption that the deepest points of lakes provide integrated microfossil assemblages from littoral and offshore communities *sensu* Frey (1988). Recent studies on faunal microfossil assemblages (Kattel et al., 2007; Kurek and Cwynar, 2009; Luoto, 2009, 2010a) have provided data which suggests that invertebrate taxa accumulate primarily to shallow or deep water areas according to their ecological preferences. In the current study we aimed to test how water depth is reflected in Cladocera assemblages and proportions of littoral and planktonic taxa. For this, we investigated 55 surface sediment samples collected mainly from the sublittoral zone of shallow lakes across boreal zone (ca. 1000 km south–north transect) for their subfossil Cladocera assemblages to develop a Cladocera-based water-level transfer function. In addition, we examined the relationship between the P/L ratio and the transfer function inferences in the surface sediment dataset and in a sediment core and compared the inferred results with a previously available midge-based water-level reconstruction from the same sediment core (Luoto, 2009) for validation of our results.

Methods

The surface sediment dataset includes 55 lakes across a ca. 1000 km transect in Finland (60–70°N, 22–30°E) within different vegetation zones from the southern spruce (*Picea*), pine (*Pinus*) and birch (*Betula*) forests to the northern mountain birch (*Betula pubescens* ssp. *czerepanovii*) woodland (Fig. 1). The lakes are small (<1 km²) and shallow (<7 m) with different climatic and limnological conditions (Table 1). The sites in the current dataset are mostly the same pristine lakes as in Luoto (2009), except for the deletion of lakes with extremely low pH and a lake with extreme climate located in barren tundra to better focus the study on lakes with distinct and well-developed littoral zones. The case study site, Lake Iso Lehmälampi (60°20'N, 24°36'E) is an oligotrophic forest lake with a wide littoral zone of submerged and floated-leaved aquatic vegetation (*Sphagnum* spp., *Carex* spp., *Nuphar lutea*, *Nymphaea alba*) in the northern part of the basin and deeper pelagic areas in the southern part of the basin (Fig. 1). The catchment is characterized by

Table 1

Environmental variability among the 55 study lakes across Finland.

	Minimum	Mean	Maximum
Mean air, T_{jul} (°C)	12.0	14.6	16.7
Elevation (m a.s.l.)	8	144	274
Surface area (km ²)	0.003	0.031	0.988
Sampling depth (m)	0.5	2.6	7.0
pH (units)	5.6	5.9	7.0
Conductivity ($\mu\text{S cm}^{-1}$)	9	53	97

the presence of bedrock outcrops, coniferous forests, and paludified areas. There is a small outlet from the northern part of the basin draining towards the west (Fig. 1).

Surface sediment (topmost 1–2 cm) sampling from the 55 lakes was performed with a Limnos-type gravity corer (Kansanen et al., 1991) in late winter 2005 mainly from the sublittoral zone (between profundal and littoral) from water depths of 0.5–7.0 m, rather than the deepest points of the basins. This was done to include the littoral taxa in analyses better. A short sediment sequence of 24 cm was cored from the northern and shallower part of Lake Iso Lehmälampi with the Limnos-type corer in late winter 2005 from a water depth of 4.1 m (Fig. 1). The sediment was sliced at 1-cm intervals into subsamples and dated from the depths of 13, 18 and 24 cm using AMS radiocarbon dating to gain a chronology (Nevalainen et al., 2008).

Environmental data (Table 1) for water depth, conductivity and pH for the 55 study lakes was collected during the sediment sampling in late winter 2005. Water depth was measured from the surface sediment sampling site and conductivity and pH were measured on sampling site as single measurements from the epilimnion prior to sediment sampling. Mean July air temperature for the studied lakes was estimated using a geographical information system-based method where the temperature data from meteorological stations based on climate normals (years 1971–2000, provided by Finnish Meteorological Institute) was interpolated to a 50 × 50-km grid (Seija Kultti, personal communication). Elevation and surface area of the study lakes were estimated from maps.

The laboratory procedure of subfossil Cladocera analysis followed the standard methods described in Szeroczyńska and Sarmaja-Korjonen (2007). Wet sediment was treated with warm 10% KOH for 20 min and sieved and washed through a 44- μm mesh. The residue was concentrated by centrifuging (4000 rpm, 10 min) and mounted in safranine-stained glycerine jelly on preparation slides. The slides were examined with a light microscope and a minimum of 400 cladoceran remains were counted from the samples. The most common body part (headshield, carapace, ephippium, postabdomen, claw) of each taxon was chosen to represent the number of individuals. The percentage abundances of each taxon were calculated from the total sums of all individuals. The cladoceran nomenclature follows Szeroczyńska and Sarmaja-Korjonen (2007).

All numerical analyses were performed without species or environmental transformations using relative abundances. Detrended correspondence analysis (DCA) was applied to choose between linear- or unimodal-based methods in further numerical analyses by estimating the lengths of compositional gradients (DCA axes 1 and 2). DCA is an indirect ordination method that summarizes the variation in species assemblages along the DCA axes (ter Braak, 2003). DCA of subfossil Cladocera assemblages in the dataset showed gradient lengths of 2.212 SD units for axis 1 and 1.393 SD for axis 2. Due to these relatively short gradients (<2), redundancy analysis (RDA) was chosen for further analyses. RDA was chosen to explore relationships between Cladocera assemblages and environmental variables available from the study lakes; water depth, elevation, surface area, mean July air temperature (T_{jul}), conductivity and pH. RDA is a linear technique that can be used to identify environmental variables that are significantly related to the species assemblages. RDAs were run

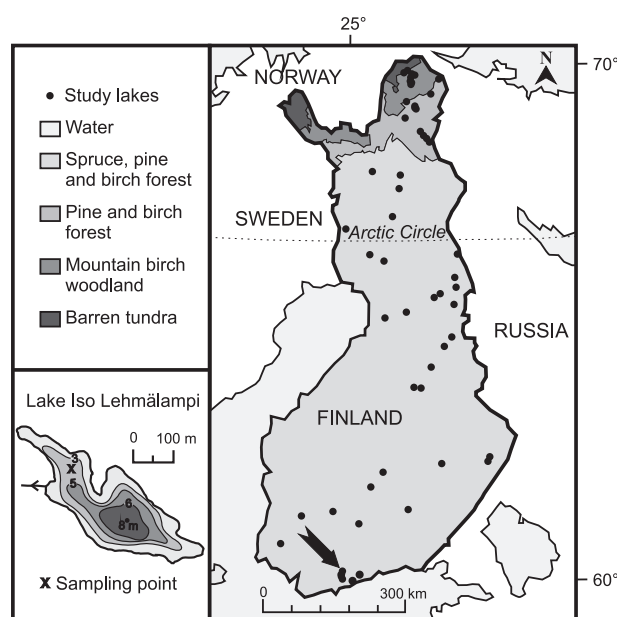


Figure 1. Location of the study lakes across Finland, with an arrow pointing the location of Lake Iso Lehmälampi and the basin bathymetry (in meters) of Lake Iso Lehmälampi.

with only one environmental variable at a time to test the significance of the variables related to Cladocera assemblages. The significance of each variable was tested with a Monte Carlo permutation test (999 unrestricted permutations) and variables were considered significant if the permutation test value was $P \leq 0.05$. When only one environmental variable is used, the ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) indicates the relative significance of the specific variable in explaining the cumulative variance in the species data. Explanatory variables having high $\lambda_1:\lambda_2$ ratios can be used in quantitative inference models (ter Braak, 2003). For RDA ordination, the data was run with the most significant environmental variables (water depth, elevation, T_{Jul} , and conductivity). DCA and RDAs were performed using CANOCO, version 4.52 (ter Braak, 2003).

Several techniques were tested to develop the best paleoenvironmental inference model (transfer function) for water level including weighted averaging (WA), weighted averaging-partial least squares (WA-PLS), PLS, Gaussian logit model (i.e. maximum likelihood) and modern analogue technique (MAT) (Juggins, 2007). The best model was considered to have the highest cross-validated coefficient of determination (r_{jack}^2) and lowest prediction error (RMSEP) and mean and maximum biases in jackknife residuals.

Results

In the surface sediment samples the most frequently occurring taxa in the dataset included planktonic *Bosmina* (*Eubosmina*) and *Polyphemus pediculus* and littoral *Alonella nana*, *A. excisa*, *Alona affinis* and *Acroperus harpae* (Table 2). Proportionally most abundant taxa included planktonic *Bosmina* (*Eubosmina*), *B. longirostris* and *Daphnia* spp. and littoral species *A. nana*, *A. affinis*, *A. excisa* and *A. harpae* (Fig. 2). Also *Chydorus sphaericus* s.l. occurred frequently and with high proportions (Table 2, Fig. 2). In the sediment core samples of Lake Iso Lehmälampi the most abundant planktonic taxon was

Bosmina (*Eubosmina*). Of the littoral species, *Chydorus piger*, *A. excisa*, *A. affinis* and *A. harpae* were most abundant (Table 2). The relative proportions of Cladocera taxa in Lake Iso Lehmälampi sediment core are originally presented by Nevalainen et al. (2008).

The RDAs for each environmental variable separately and Monte Carlo permutation tests showed that water depth at the sampling site was most significant variable in explaining the subfossil Cladocera assemblages ($\lambda_1:\lambda_2 = 0.43$, $P = 0.001$) and accounted for 14% of the cumulative variance of the taxon data (Table 3). The RDA, run with the most significant environmental variables (sampling depth, T_{Jul} elevation and conductivity), is presented in Fig. 3. The first RDA axis explained 15.6% of the variance of the species data and the second RDA axis explained 12.3%, with total variance explained by both axes being 27.9%. The RDA biplot for taxa and environmental variables showed that e.g. *Eubosmina*, *Alona rustica*, and *Diaphanosoma brachyurum* had intermediate scores for axis 1 and low scores for axis 2. *Chydorus sphaericus* s.l., *Sida crystallina*, *Graptoleberis testudinaria*, and *Bosmina longirostris* had slightly positive or negative values for axis 1 and low values for axis 2. Species such as *Alonella nana*, *Alona affinis*, *Alonopsis elongata*, and *Eurycercus* spp. scored negative values for axis 1 and intermediate values for axis 2.

The best Cladocera–water level transfer function was obtained using a MAT. The best statistics were obtained when using the squared chi-square distance and the number of closest analogues was set to ten. The best model yielded performance statistic of $r_{jack}^2 = 0.58$ and RMSEP = 1.1 m and mean and maximum biases in the model were 0.05 and 2.86 m, respectively (Fig. 4).

In the surface sediment dataset the relationships between observed water depth and P/L ratio showed high and significant Pearson's correlation ($r = 0.36$, $P = 0.006$, Fig. 5a) and the inferred water depth and P/L ratio similar correlations ($r = 0.43$, $P = 0.001$, Fig. 5b). In the sediment core of Lake Iso Lehmälampi the relationship between the Cladocera-inferred water level and P/L ratio, measured as Pearson's correlation, was strong and significant ($r = 0.88$, $P < 0.001$).

Table 2

Number of occurrences (N), maximum abundance (Max %), and Hill's (1973) N2 diversity of the most common (>10 occurrences) Cladocera in the 55 surface sediment samples across Finland and in the sediment core from Lake Iso Lehmälampi. The species codes are used in Figure 3.

	Codes	Life form	Surface sediment dataset			Sediment core samples		
			N	Max %	N2	N	Max %	N2
<i>Bosmina</i> (<i>Eubosmina</i>)	Euboid	Plankton	52	70.6	34.7	25	23.9	47.7
<i>Bosmina longirostris</i>	Bosm lon	Plankton	22	74.7	11.9			
<i>Daphnia</i> spp.	Daphind	Plankton	23	18.4	7.4			
<i>Polyphemus pediculus</i>	Poly ped	Plankton	39	2.6	26.9	3	3.0	0.3
<i>Diaphanosoma brachyurum</i>	Diap bra	Plankton	12	7.0	2.6	2	2.0	0.3
<i>Ceriodaphnia</i>	Ceriind	Plankton	35	2.5	22.1	2	2.0	0.3
<i>Ophryoxus gracilis</i>	Ophr gra	Littoral	41	7.9	18.8	23	14.2	2.1
<i>Sida crystallina</i>	Sida cry	Littoral	38	3.4	18.4	13	9.7	1.0
<i>Chydorus sphaericus</i> s.l.	Chyd sph	Littoral	54	43.7	20.4	25	19.0	1.5
<i>Chydorus piger</i>	Chyd pig	Littoral	36	3.0	22.3	25	20.1	6.8
<i>Alonella nana</i>	Alon nan	Littoral	55	72.3	31.8	25	20.9	51.6
<i>Alonella excisa</i>	Alon exc	Littoral	53	35.4	21.7	25	22.8	13.3
<i>Alonella exigua</i>	Alon exi	Littoral	15	2.1	8.5	5	5.0	0.3
<i>Graptoleberis testudinaria</i>	Grap tes	Littoral	22	4.7	10.4	9	8.3	0.5
<i>Alona affinis</i>	Alon aff	Littoral	53	57.7	27.9	25	22.7	13.7
<i>Alona quadrangularis</i>	Alon gua	Littoral	25	14.1	11.9	25	5.2	15.4
<i>Alona intermedia</i>	Alon int	Littoral	44	6.1	26.0	25	20.7	3.0
<i>Alona rustica</i>	Alon rus	Littoral	38	15.7	15.5	25	18.6	5.5
<i>Alona guttata</i>	Alon gut	Littoral	21	2.1	13.6	9	8.9	0.4
<i>Alona guttata tuberculata</i>	Alon tub	Littoral	36	8.8	16.3	23	19.9	2.7
<i>Alona rectangula</i>	Alon rec	Littoral	10	8.2	5.2			
<i>Acroperus harpae</i>	Acro har	Littoral	54	22.7	31.2	25	19.8	16.1
<i>Alonopsis elongata</i>	Alon elo	Littoral	35	3.8	19.1	25	18.3	2.2
<i>Eurycercus</i> spp.	Eurycind	Littoral	45	6.5	19.4	25	20.3	1.4
<i>Camptocercus rectirostris</i>	Camp rec	Littoral	36	5.0	17.0	22	18.5	1.4
<i>Rhynchotalona falcata</i>	Rhyn fal	Littoral	24	11.4	8.6	25	17.4	3.0
<i>Pleuroxus trigonellus</i>	Pleu tri	Littoral	10	2.0	5.7			
<i>Unapertura latens</i>	Unap lat	Littoral	21	18.5	3.8			
<i>Acantholeberis curvirostris</i>	Acan cur	Littoral	16	4.8	7.1			

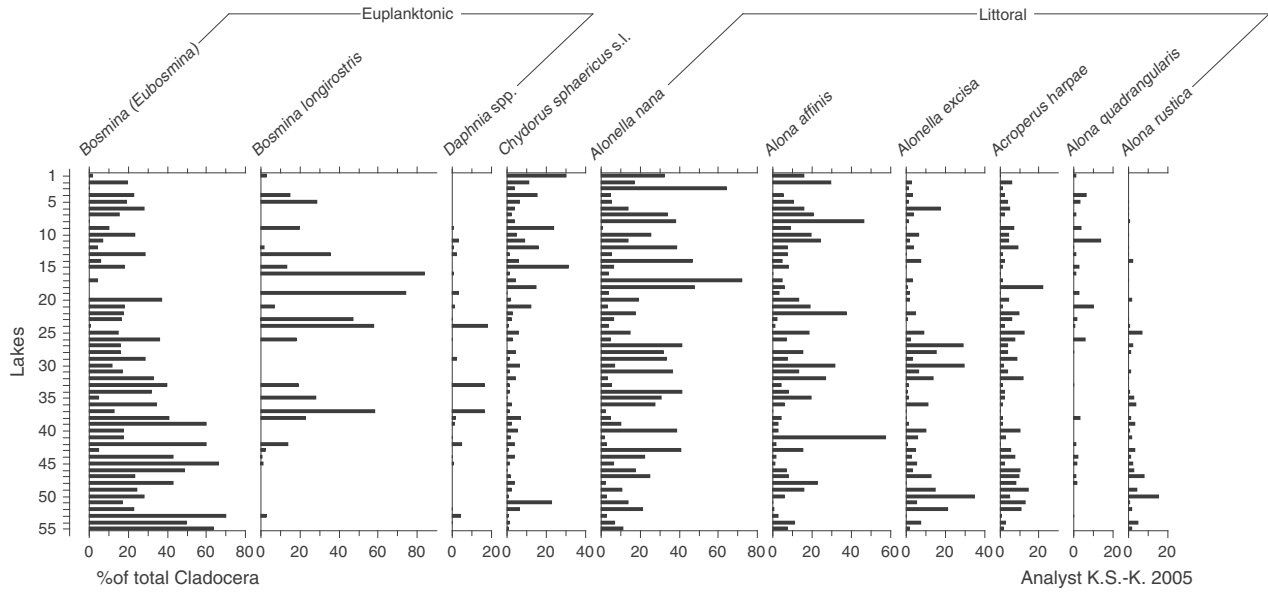


Figure 2. Distribution of the most abundant Cladocera taxa (mean proportion in the dataset >1.5%) in 55 lakes in Finland according to water depth gradient from the shallowest to the deepest.

Cladocera-inferred water level reconstruction and P/L showed simultaneously lowering lake level during ca. AD 300–1000 (Fig. 6), closely corresponding with the previously available midge-inferred water depth by Luoto (2009). The Pearson’s correlations between Cladocera-inferred and chironomid-inferred water level ($r = 0.46, P = 0.021$) and P/L ratio and chironomid-inferred water level ($r = 0.50, P = 0.012$) were strong and significant.

Discussion

Bosmina (Eubosmina) was an abundant taxon in the majority of the training set assemblages, whereas other planktonic Cladocera were rarer (Table 2, Fig. 2). *Bosmina longirostris* was very abundant in some of the lakes, but it did not occur in such high frequencies as *Eubosmina*. Of the chydorids, *Alonella nana* and *Chydorus sphaericus* s.l., the two ubiquitous species (or *C. sphaericus* being a species group *sensu* Frey, 1986) together with *Alona affinis*, *Acroperus harpae* and *Alonella excisa*, were frequent and abundant inhabiting almost all of the 55 lakes. In the present study, water depth had strongest influence on Cladocera assemblages in the dataset (Table 3, Fig. 3), being presumably related to their littoral or planktonic habitat preferences. However, cladocerans are not a homogenous group in respect to their habitats, feeding, or positions at the food-webs and, in addition to water depth, there are several environmental variables; ionic concentrations, dissolved organic carbon, summer water temperature, fish predation, macrophytes, nutrients, and sediment properties that have been recorded to

be important forcing factors behind Cladocera assemblages (Korhola, 1999; Jeppesen et al., 2003; Amsinck et al., 2005; Sweetman and Smol, 2006; Davidson et al., 2007; DeSellas et al., 2008; Kattel et al., 2008).

In addition to the environmental variables listed above, water depth, as stated previously, has also been recorded as a major explanatory variable of the community structure. Cladoceran taxa such as *Eubosmina*, *Alona rustica*, *Chydorus sphaericus* s.l., and *Ophryoxus gracilis* were distributed in the RDA ordination diagram according to the water depth gradient (Fig. 3). In the current results, water depth explained 14% of the cumulative variance in the assemblages and showed high correlation of the eigenvalues suggesting that this variable can be used to develop a transfer function for deducing past water level changes (ter Braak, 2003; Table 3). Although water depth has been indicated to affect strongly

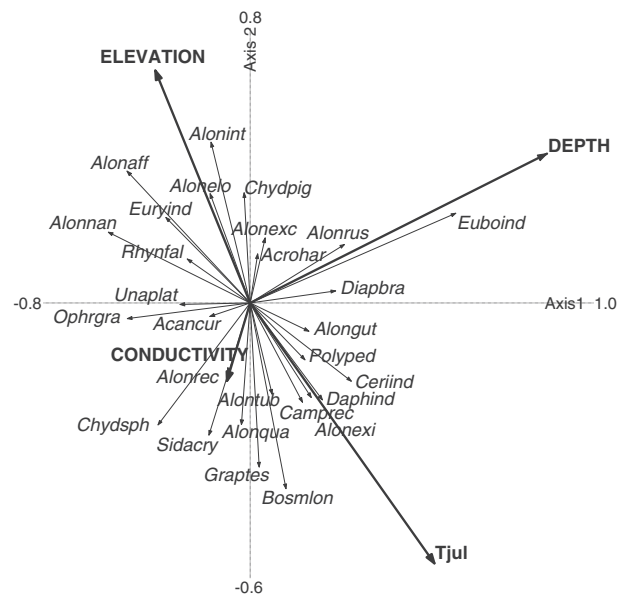


Figure 3. RDA ordination for the significant environmental variables; sampling depth, conductivity, mean July air temperature (T_{jul}), and elevation and most common Cladocera taxa (occurrences >10 and maximum proportions >2% in the dataset).

Table 3
Summary of redundancy analyses (RDA) of Cladocera assemblages and environmental variables in the 55 study lakes. Shown are the ratio of the first eigenvalue to the second unconstrained eigenvalue ($\lambda_1:\lambda_2$), species–environment correlations, variance explained as percentage of each variable and significance level of the Monte Carlo permutation tests (P).

Variable	$\lambda_1:\lambda_2$	Species environment correlation	Variance explained (%)	P
Sampling depth	0.430	0.695	14.0	0.001
Conductivity	0.416	0.559	12.8	0.002
Mean air, T_{jul}	0.367	0.610	13.0	0.002
Elevation	0.202	0.480	7.6	0.002
pH	0.084	0.316	3.4	0.060
Surface area	0.055	0.345	2.3	0.158

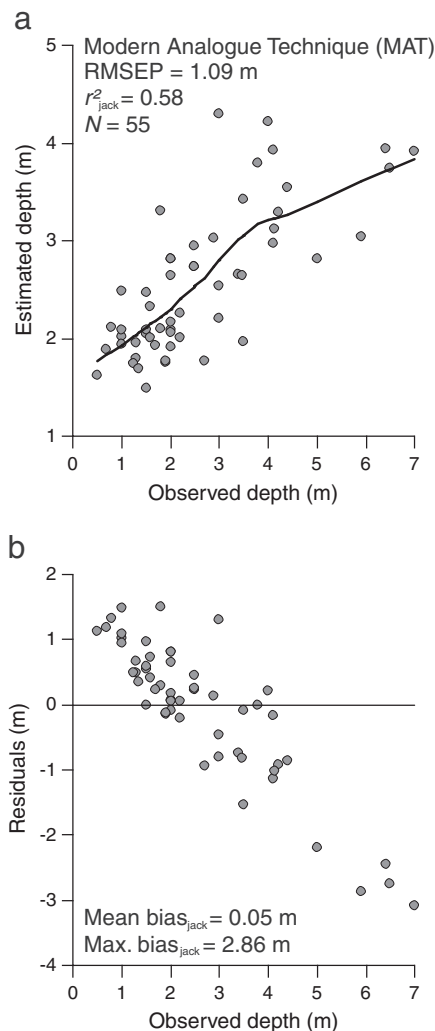


Figure 4. Cladocera-based inference model for water level in 55 lakes in Finland: a) relationship between observed and estimated water levels, using a MAT model and b) residuals along the water level gradient with a locally weighted scatterplot smooth (span 0.75) indicated by black line.

the community structure of Cladocera (Table 3; Korhola, 1999; Amsinck et al., 2006; Sweetman and Smol, 2006; DeSellas et al., 2008), it is probable that the forcing factor is not the water depth *per se* but the environmental conditions (e.g. macrophytes and substrata) associated with the depth. The currently developed transfer function for water depth inferences yielded relatively good performance, although having a quite large maximum bias (Fig. 4).

Korhola et al. (2000) developed a regional Cladocera-based quantitative inference model for maximum lake depth in subarctic Finnish Lapland using a dataset of 53 lakes, in which maximum depth varied from 0.85 to 27.0 m. Their PLS-based two-component model with log-transformed maximum lake depth had better explanatory power ($r^2_{\text{jack}} = 0.70$) than the current model, most likely due to a longer depth gradient in their training set. Unfortunately, it is difficult to compare the present RMSEP with that of Korhola et al. (2000), because they used log-transformed depth. Furthermore, since the depth measurements in this study are based on the depth at the sampling sites and not the maximum lake depth as in Korhola et al. (2000), the results are not straightforwardly comparable.

When comparing the present geographically wide, but environmentally relatively short-gradient training set (Fig. 4) with the geographically restricted, but wide-gradient training set by Korhola

et al. (2000) an analogous inclination was observed in the inferred values and residuals, which cause overestimation of the shallow sites and underestimation of the deeper sites. This type of “edge-effect” suggests that these Cladocera-based inference models can perform reliable quantifications of past water level changes in sampling sites of intermediate depths relative to the training set depth gradient. A similar problem apparently exists with midge-based inference model for water depth by Luoto (2009), which is also based on measurements of water level at the sampling site. The nonlinear distortions at the ends of the gradients are an inherent problem in all unimodal-based calibration methods (ter Braak and Juggins, 1993; Lotter et al., 1997) and can possibly be reduced only by increasing the number of samples representing the ends of the gradients (evenly distributed samples) without increasing the gradient itself (Luoto, 2009). In addition, the tendency of the inferences toward average depths in the present model (Fig. 4) can be related to taphonomic processes because planktonic taxa also occur in the open waters of the littoral zone and accumulate into littoral and offshore surface sediments (Fig. 5).

Quantitative paleolimnology has been based on single-factor transfer functions, such as the present Cladocera–water depth transfer function (Fig. 4), although these models produce inferences, which do not evaluate multiple controls on biological assemblages. To tackle this, Davidson et al. (2010a, 2010b) recently applied a new

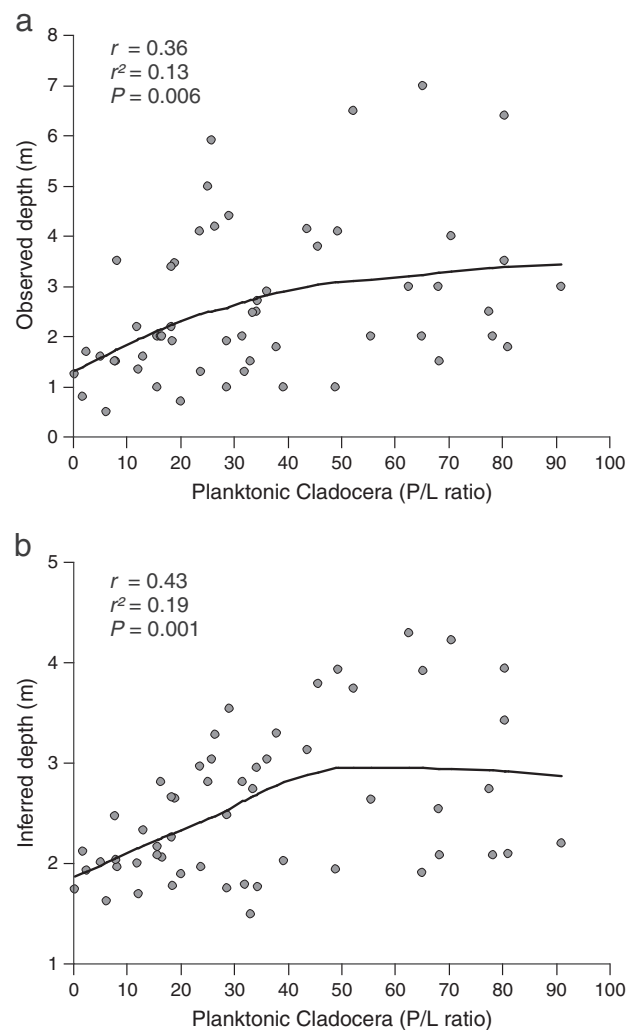


Figure 5. Relationships between a) observed water depth and P/L ratio of Cladocera and b) Cladocera-inferred water depth and P/L ratio in the 55 study lakes in Finland.

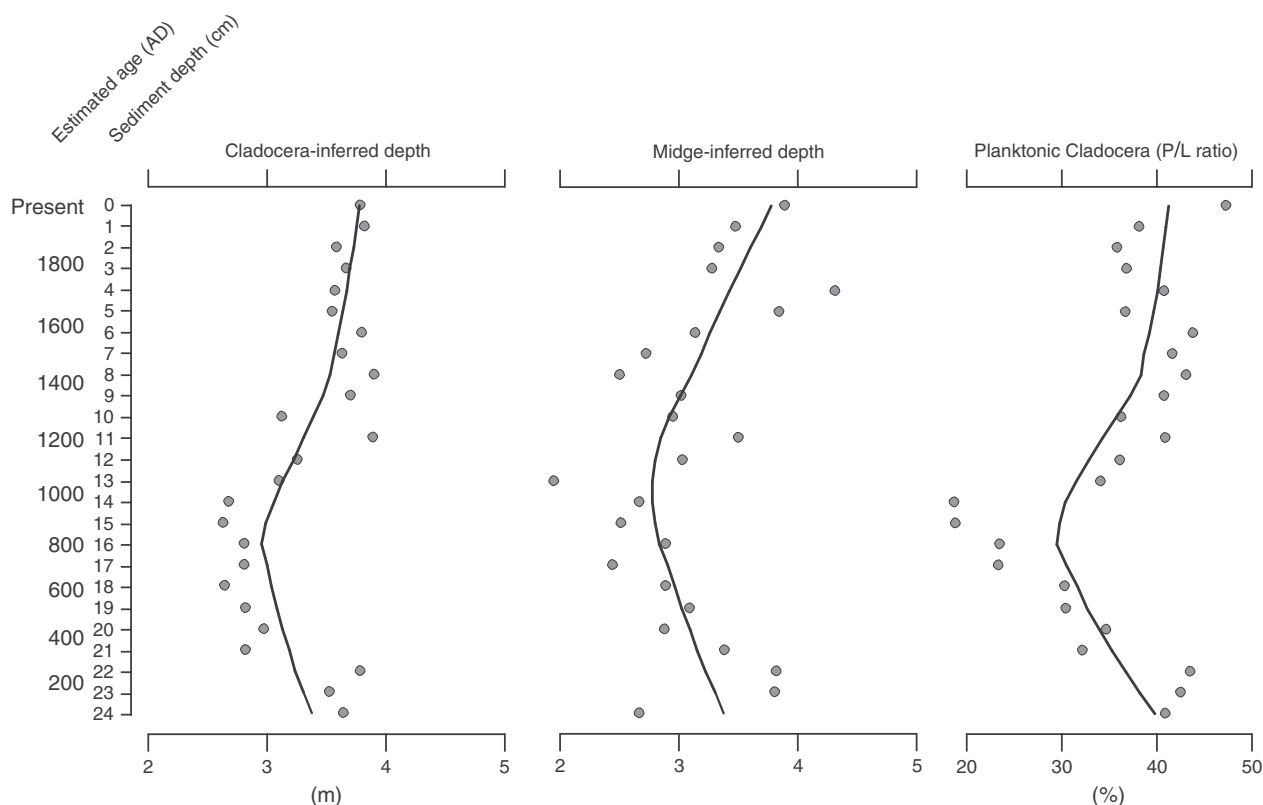


Figure 6. Cladocera- and midge-based water level reconstructions together with P/L ratio of the Cladocera from Lake Iso Lehmälampi, southern Finland. A locally weighted scatterplot smooth (span 0.75) is applied to indicate the general trends.

multivariate regression tree approach to develop a Cladocera-based model for assessing past changes in both fish and macrophyte abundance. In addition, Luoto (2010b) indicated that different single-factor midge-based transfer functions can be constructed to infer multiple environmental parameters in the same lake using a spatial scaling approach in the development of training sets. This is because the communities are unique in a particular spatiotemporal environment and the presence and proportions of taxa in a unique community thus reflects a particular environment, which consists of multiple forcing factors (Luoto, 2010b). Therefore, quantitative paleolimnology probably further develops in the near future toward the use of several transfer functions or models that can infer multiple variables.

The Cladocera-based water level reconstruction of the past 2000 yr from the sediment core of Lake Iso Lehmälampi is in accordance with the previously available quantitative independent midge-based water level inference from the same lake (Fig. 6; Luoto, 2009) showing a clear decrease from AD 300 onward until ca. AD 1000. During AD 1300 onward both of the inferences indicate elevated water level. The similar reconstruction trend was indicated also by the P/L ratio, which had strong relationships between Cladocera-based and midge-based water-level reconstructions (Fig. 6). The clear signal of water-level changes detected from Lake Iso Lehmälampi (Fig. 6) was probably due to the selection of the sublittoral sampling site from an area with wide littoral zone (Fig. 1), hence reflecting clearly fluctuations in the water level and volume of littoral and pelagic habitats relative to the coring point. However, the Cladocera-based reconstruction may have been affected by other independent parameters affecting the communities and changing thus the results of the inference. For example, changes in the food-web might cause a shift in planktonic communities from large species dominance toward smaller taxa. This would change the inferred water level in the transfer function but not necessarily in the P/L ratio water-level inference. Nevertheless, this problem exists in all

types of proxy-based reconstructions. In the present study the independent quantitative midge-based reconstruction showed similar trends in water level as the Cladocera-based reconstruction, providing evidence for actual water-level changes in the lake (Fig. 6).

Prior to the present results, the only quantitative water-level reconstructions from southern Finland are by Luoto (2009) and Luoto et al. (2010). In northern Finland, Seppä and Birks (2001) and Korhola et al. (2005) have quantified precipitation/lake levels and provided evidence of elevated effective moisture during late Holocene, possibly associated with long-term fluctuations in NAO (Yu and Harrison, 1995; Seppä and Hammarlund, 2000). Since lake-level changes are mostly regulated by the effective moisture balance, the lowering lake levels prior to AD 1300 may indicate dryer climatic conditions (Fig. 6). Helama et al. (2009) showed that northern Europe underwent a severe precipitation deficit during the Medieval Climate Anomaly, which corresponds to low lake levels reconstructed by Luoto (2009) and Luoto et al. (2010). The lowering lake level from our reconstruction (Fig. 6) also corresponded roughly to the period of this multicentennial megadrought reported by Helama et al. (2009).

Prior to quantitative paleolimnology, semi-quantitative records of lake level changes were often based on the P/L ratio of Cladocera providing evidence of water level fluctuations derived by climate development during the Holocene (Alhonen, 1970a, 1970b, 1971, 1972; Sarmaja-Korjonen and Hyvärinen, 1999; Sarmaja-Korjonen, 2001). The current results (Fig. 5), which compare the measured and inferred water level and P/L ratio in the surface sediment dataset suggest that relative abundances of planktonic and littoral taxa in these cases are linked to water depth, although not completely straightforwardly since high proportions of planktonic taxa were also observed in shallow sites (Fig. 5). However, the use of the P/L method requires lakes that have not experienced major changes in food web, e.g. in predation or trophic state (Sarmaja-Korjonen, 2001), and/or severe pollution (Manca and Comoli, 1995). Although in lake bottoms

constant resuspension and transportation can be suspected, our results may indicate that littoral taxa are primarily deposited close to their shallow habitats while planktonic cladocerans accumulate mostly in deepwater locations (Fig. 5), but also in shallower locations due to available open waters in littoral zones. These results may suggest that subfossil cladoceran remains are not always transported far from their original habitats and therefore whole-lake assemblages are not necessarily focused to the deepest point of a lake basin. As stated above, this approach is supported by Kattel et al. (2007), Kurek and Cwynar (2009), and Luoto (2010a) who indicated that intralake assemblages of Cladocera and Chironomidae may be very heterogeneous. Nevertheless, this perspective should be studied in more detailed using several intralake datasets of Cladocera assemblages together with modern sampling.

Conclusions

The present results show that cladocerans can be used in quantitative inferences of past water level fluctuations, whereas the P/L ratio provides a reliable alternative reconstruction method if a regional transfer function is not available. In basins with heterogeneous bathymetry, the water level signal from littoral and planktonic Cladocera will probably appear stronger, because the well-developed littoral zone with various substrata for habitats enables the development of true littoral communities. The results suggest that planktonic cladocerans accumulate in high proportions into surface sediments primarily in deep water sites whereas littoral taxa are more abundant in shallow sites. This perspective may offer interesting possibilities in the future to examine habitat-specificity of divergent taxa and to develop lake-specific paleolimnological models.

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