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PRIMARY RESEARCH PAPER

Zooplankton (Cladocera) in assessments of biologic integrity and reference conditions: application of sedimentary assemblages from shallow boreal lakes

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Abstract Zooplankton are potentially powerful proxies for the assessments of biologic integrity. The paleolimnological perspective and use of fossil Cladocera also provide the means to reconstruct reference conditions and natural long-term community dynamics. Unfortunately, the use of zooplankton in lake quality assessments is currently underexploited. We studied a surface sediment dataset of 41 lakes in Finland to examine the relationship between Cladocera remains and environmental variables. Of the examined environmental variables, total phosphorus availability was found to be the most important variable in explaining the Cladocera community composition. Following the tests on species environment relations, we selected a lake trophic typology as the most suitable environmental variable for developing a new tool for limnoecological quality assessments. A test of the model on a modern and historic sample from a eutrophied lake showed that the test lake has proceeded from "mesotrophic/poor" to "eutrophic/bad" limnoecological state in agreement with previous independent evidence. The model developed here showed favorable performance that can be used to provide reliable estimates of ecological and environmental state of lakes.

Keywords Baseline condition · Cladocera · Ecological state · Eutrophication · Paleolimnology · Trophic state

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Introduction

Eutrophication is the most serious water quality problem in the world (UNEP, 1999; Schindler, 2006) causing problems for humans through contaminated water supplies and for the ecological quality (i.e. ecosystem heath) of lakes, also in boreal lakes (Räike et al., 2003). The bioindicators in contemporary ecological water quality assessments include several plant, algal, and animal groups. Of the animals, benthic macroinvertebrates (Sæther, 1979) and zooplankton, such as crustaceans and rotifers (Gannon & Stemberger, 1978; Kane et al., 2009; Louette et al., 2009), have been used in lake monitoring and in assessments of ecological quality and in estimations of the success of restoration efforts. Zooplankton occupy a key role in the structure and functioning of lake ecosystems through grazing, recycling nutrients, and as food items (Makarewicz & Likens, 1979). The success of secondary producers, such as zooplankton, is dependent upon algal production, which is limited by phosphorus availability (Hessen et al., 2006).

For conservation and preservation of ecological quality in lakes, long-term data are essential for understanding the baseline conditions of the natural state and ecosystem dynamics. Using the paleolimnological approach, remains of zooplankton in lake sediments provide means to reconstruct past community compositions (Frey, 1960; Eggermont & Martens, 2011). Of the zooplankton, remains of Cladocera preserve well and can be identified mostly to species level (Szeroczyńska & Sarmaja-Korjonen, 2007). Fossil Cladocera analysis has been shown to be a potential tool in reconstructing past ecological and limnological status of lakes (Jeppesen et al., 2001a; Chen et al., 2010; Nykänen et al., 2010; Davidson et al., 2011) and, instead of single indicator species, community structure has been judged to be the most reliable predictor of lake status (Korhola & Rautio, 2001).

Numerical techniques enable the use of Cladocera as quantitative indicators of environmental conditions. Previously, Cladocera have been used to reconstruct changes in water quality parameters, including pH (Krause-Dellin & Steinberg, 1986), total phosphorus (TP) (Brodersen et al., 1998; Lotter et al., 1998), and water color (Huttunen et al., 1988). However, multiple stressors affect the Cladocera assemblages (DeSellas et al., 2011; Korosi & Smol, 2011; Nevalainen et al., 2011a), and may therefore confound the reconstruction of a single variable (Luoto et al., 2011; Nevalainen et al., 2012). For example, the presence or density of fish (Jeppesen et al., 1996; Amsinck et al., 2005; Nevalainen & Luoto, 2010) and macrophyte coverage (Bjerring et al., 2009; Nevalainen, 2011) can cause distinctive patterns in Cladocera community assemblages. Therefore, trophic indices or methods, which can simultaneously infer multiple environmental variables, may sometimes be more applicable (Davidson et al., 2010a, b). Furthermore, single factor assessments of reference conditions may be problematic as targets in the actual lake management acts (Luoto & Nevalainen, 2011). It is, however, clear that paleolimnological methods are needed to reliably assess lake reference conditions and holistic understanding of the "pristine" state are invaluable for the implementation of the European Union Water Framework Directive (WFD) (Bennion & Battarbee, 2007). The principal goal of the WFD, which emphasizes the structure and function of aquatic ecosystems with biologic elements, is to achieve "good ecological quality" in relevant waters by the years 2015–2027 (European Commission, 2000, 2003).

Recently, Jeppesen et al. (2011) wrote a scientific-based plea for including zooplankton in the ecological quality assessments of lakes according to the WFD, from which it had been omitted without a scientifically sound reason. As Jeppesen et al. (2011) wrote: "It was a matter of some surprise to lake ecologists that zooplankton were not included as a biologic quality element (BQE) despite their being considered to be an important and integrated component of the pelagic food web." In their study, Jeppesen et al. (2011) showed that zooplankton have a strong indicator value, which cannot be covered by sampling fish and phytoplankton without a very comprehensive and costly effort. In this study, we aim to provide further support and demonstrate the usefulness of Cladocera as indicators of lake limnoecological quality through testing the influence of various environmental factors on the composition of fossil cladocera assemblages in surface sediment samples from 41 shallow lakes in Finland. We hope to identify indicator taxa for key environmental variables and to develop a new tool, which can be used in the environmental assessments of ecological and environmental quality and in tracking lake reference conditions.

Materials and methods

A total of 41 lakes were cored during late-winter 2005 for surface sediment samples (topmost 0–1 cm) representing the present (recent years of sedimentation) using a Limnos gravity corer (Kansanen et al., 1991). The cores were collected approximately from the midway of the shoreline and the center of each lake to better include both planktonic and littoral taxa. The lakes are located in Finland between 60°13′ and 69°53′N (Fig. 1). The lakes are mostly the same as in the chironomid-based study by Luoto (2011) where the study sites are described in more detail. These sites were selected based on the availability of measured limnological data, which were provided by the Finnish Environment Centre. Of the 51 lakes in the original dataset, 10 were not analyzed for Cladocera due to rareness of sedimentary remains. The used bottom water hypolimnetic dissolved oxygen (DO) measurements reflect late-winter conditions, whereas the other limnological variables are based on measurements performed from the epilimnion during autumn. The lakes range from ultraoligotrophic (TP = 1.5 $\mu g\ l^{-1}$)

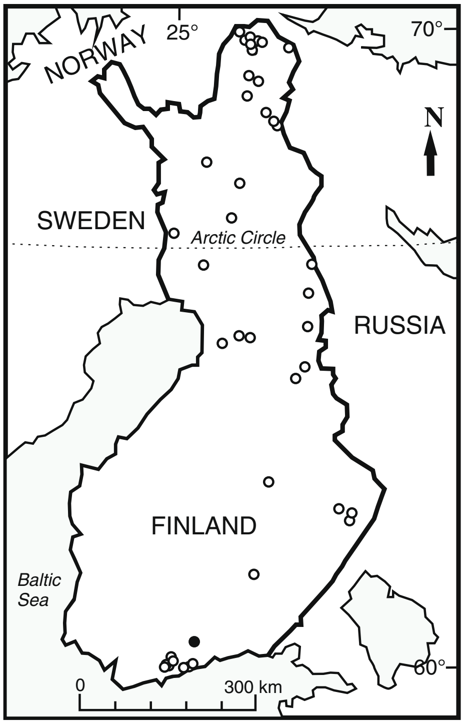

Fig. 1 Location of the 41 study lakes (*open circles*) in Finland. Lake Mallusjärvi is marked with a *solid circle*

Table 1 Environmental characteristics of the 41 lakes in Finland

	Minimum	Mean	Median	Maximum
DO (mg l^{-1})	0	6.9	7.7	14
TP (μg l^{-1})	1.5	16.7	10	76
TN (μg l^{-1})	110	425	370	1400
pH	4.5	6.4	6.5	7.3
Conductivity (μS cm^{-1})	8	35	26	158
Color (mg Pt l^{-1})	2.5	47	30	180
Mean air T_{Jul} (°C)	11.3	14.8	15.2	17.1
Water depth (m)	0.7	2.9	2.2	7.0

to eutrophic (TP = 76 μg l^{-1}) sites, from anoxic (O_2 = 0 mg l^{-1}) to hypersaturated (14 mg l^{-1}) oxygen conditions, and from acidic (4.5) to mildly alkaline (7.3) pH conditions (Table 1). The temperature range (mean air T_{Jul} = 11.3–17.1°C) in the dataset is primarily forced by the latitudinal transect. For more detailed use of the environmental data, see Kultti et al. (2011) and Luoto (2011). For this study, the lakes were assigned to eutrophic, mesotrophic, dystrophic, oligotophic, and ultraoligotrophic groups (Groups I–V, respectively) according to (Forsberg & Ryding, 1980) and we also considered the sites in the context of the pan-European typology and ecological classification system for shallow lakes (ECOFRAME, Moss et al., 2003) that has been tested for Finnish lakes by Nykänen et al. (2005).

The surface sediment samples were processed for fossil Cladocera applying the standard methods described by Korhola & Rautio (2001) and the specimens were identified according to Szeroczyńska & Sarmaja-Korjonen (2007), which the nomenclature follows. A minimum of 200 individuals were counted from each of the samples. This count sum describes well the Cladocera species composition for community analysis (Nevalainen, 2010). Numerical analyses were performed by relative species abundances and square-root transformation of species data and down-weighting of rare species to stabilize the variance. To select between unimodal and linear-based methods, detrended correspondence analysis (DCA) was used and, consequently, redundancy analysis (RDA) was used for the ordination analysis and to identify environmental variables which are strongly related to the species assemblages. The RDAs were run for each of the variables with and without co-variables to test the strength of specific variables against other environmental factors. The statistical significance was tested by Monte Carlo permutations using 999 unrestricted permutations. The obvious multicollinear variables were identified by studying the variance of their regression coefficients as depicted by the Variance Inflation Factors (VIF) and variables yielding VIFs higher than 20 were omitted. The DCA and RDAs were run with the program CANOCO, version 4.52 (ter Braak & Šmilauer, 2002).

For the environmental data, Pearson correlation was used to test the relationships between the environmental variables at levels of statistical significance of $P \leq 0.05$ and $P \leq 0.01$. For spatial analysis, Mantel non-parametric test (Mantel, 1967; Mantel & Valand, 1970) was used on the Cladocera assemblages to determine the influence of spatial autocorrelation. The Manter correlogram has recently been shown to be a powerful enough method to successfully detect spatial correlation (Borcard & Legendre, 2012). A Bray-Curtis distance was used for the biologic distance matrix and geographic distance (coordinates) between the sites for the spatial distance matrix (1,000 randomizations). The Mantel test was performed using the program PAST (Hammer et al., 2001).

To identify significant relationships between species and environmental variables, generalized linear models (GLM) were constructed. The GLMs were set to quadratic degree and Poisson distribution. The GLMs were run with CanoDraw, a component of CANOCO. Two-way indicator species analysis (TWINSPAN) was used as a divisive technique to classify the 41 lakes and to identify indicator taxa. Pseudospecies cut levels were set to 0, 2, 5, 10, and 20%. TWINSPAN was performed by the program WinTWINS, version 2.3 (Hill & Šmilauer, 2005). Maximum likelihood (Gaussian logit model) method was used for the construction of a Cladocera-based inference model for environmental assessments. The model was developed to infer lake limnoecological quality, i.e., the limnological group (Group 1 = eutrophic, Group II = mesotrophic, Group III = dystrophic, Group IV = oligotrophic, Group V = ultraoligotrophic). Model performance was evaluated based on the squared correlation between jackknife-predicted and observed values (R^2_{jack}), root mean squared error of prediction (RMSEP), and mean and maximum biases. The model was developed by the program C2 Data Analysis (Juggins, 2007). The performance of the model was tested on a modern (surface sediment sample 0–1 cm) and a reference sample (21–22 cm) from currently eutrophic Lake Mallusjärvi (60°44′N, 25°38′E), southern Finland (Fig. 1). The modern (years 2007–2010) observed autumn epilimnetic TP in Lake Mallusjärvi varies between 74 and 103 μg l^{-1}, which is in the upper limit of the present dataset. The lake in a cultural landscape (cultivation and pasture) is known to suffer from wintertime anoxia (Luoto & Nevalainen, 2011) and it has been mesotrophic in the past (Luoto & Raunio, 2011). Lake Mallusjärvi is not included in the calibration set. The sediment sampling matches the methods used in the dataset as the core was taken from the sublittoral at water depth of 3.5 m. Detailed site descriptions are available for Lake Mallusjärvi in Luoto & Nevalainen (2011). The reference sample is previously AMS ^{14}C dated to be of age 210–431 cal BP (Luoto & Nevalainen, 2011). The performance of the Cladocera-based model in Lake Mallusjärvi was compared with results derived from the same samples using a chironomid-based inference model of TP (Luoto & Raunio, 2011).

Results

In the dataset of 41 lakes in Finland, several environmental factors had intercorrelations (Table 2). Most of the water quality parameters correlated with each other, with the exception of pH, which correlated with climatic and morphometric variables. Mean July air temperature (T_{Jul}) had positive correlation with TP, TN, and water color and negative correlation with DO and pH. The mantel test showed spatial autocorrelation in the dataset that was statistically significant ($P = 0.031$), but very weak ($R = 0.11$). Owing to the weakness of the correlation, we do not interpret this further, but reject modern analog technique (MAT) as a potential model type between Cladocera and the

Table 2 Correlation matrix of the environmental variables in the dataset from Finland

	DO	TP	TN	pH	Conductivity	Color	T_{Jul}	Depth
TP	<u>**−0.51**</u>	<u>1</u>						
TN	<u>**−0.58**</u>	<u>**0.80**</u>	<u>1</u>					
pH	−0.05	0.10	0.18	<u>1</u>				
Conductivity	−0.30	<u>**0.57**</u>	<u>**0.58**</u>	**0.39**	<u>1</u>			
Color	<u>**−0.54**</u>	<u>**0.51**</u>	<u>**0.59**</u>	0.10	0.24	<u>1</u>		
T_{Jul}	**−0.37**	<u>**0.57**</u>	<u>**0.48**</u>	<u>**−0.49**</u>	0.19	<u>**0.46**</u>	<u>1</u>	
Depth	−0.00	−0.06	−0.04	<u>**−0.54**</u>	−0.18	−0.13	0.23	<u>1</u>
Latitude	0.27	<u>**−0.54**</u>	**−0.36**	<u>**0.54**</u>	−0.14	**−0.36**	<u>**−0.94**</u>	−0.24

Relationships significant at the level of $P \leq 0.05$ are marked in bold type and relationships significant at the level of $P \leq 0.01$ are underlined

Table 3 Results from RDA between Cladocera assemblages and environmental variables in 41 Finnish lakes

	Effect	Species environment correlation	Variance explained (%)	*P*	VIF
TP	Marginal	0.769	16.9	0.001	16.7
	Conditional	0.621	7.3	0.001	
T_{Jul}	Marginal	0.756	13.5	0.001	14.8
	Conditional	0.722	6.0	0.020	
pH	Marginal	0.700	7.6	0.007	6.4
	Conditional	0.765	16.8	0.001	
Depth	Marginal	0.659	5.8	0.029	2.9
	Conditional	0.607	5.6	0.042	
DO	Marginal	0.574	8.3	0.002	6.9
	Conditional	0.511	2.4	>0.05	
Color	Marginal	0.720	16.0	0.001	46.6
TN	Marginal	0.708	14.5	0.001	424.6
Conductivity	Marginal	0.528	7.7	0.004	34.9

Variables having high VIFs were excluded from the partial RDA analyses

selected environmental variable. This is due to the tendency of MAT producing an overoptimistic estimation of its performance in a spatially structured dataset where "local datasets" within the true dataset may enhance autocorrelation (Telford & Birks, 2005; Luoto, 2012).

The DCA based on the Cladocera assemblages showed gradient lengths of 1.6 SD for axis 1 and 1.3 SD for axis 2 indicating that RDA would be most appropriate for these relatively short gradient lengths. The initial RDA showed high VIFs for color, TN, and conductivity (Table 3) and these variables were thus removed from further analyses because such highly collinear variables do not warrant the usage of their canonical coefficients (ter Braak & Šmilauer, 2002). Of the remaining variables TP (16.9%), pH (16.8%), and mean T_{Jul} (13.5%) explained most of the variance. When tested against covariables (variables with VIFs < 20), TP, mean T_{Jul}, water depth, and DO suffered from the conditional effects with the other forward-selected variables, whereas pH gained from the covariance. More specifically, pH and the covariables together explained more than the sum of individual effects of these two groups and the intersection of their linear effects was negative (Legendre & Legendre, 1998).

The RDA was also used to ordinate samples, species, and the most important environmental variables on a triplot (Fig. 2). The first axis explained 18.6% and the second axis 7.1% of the total variance. Of the taxa having significant relationship with TP, T_{Jul}, or water depth, *Graptoleberis testudinaria*, *Chydorus sphaericus* s.l., *Bosmina longirostris*, *Alona quadrangularis*, and *Sida crystallina* were associated with elevated TP, whereas *Alona rustica*, *Bosmina (Eubosmina)*, and *Alonella excisa* were associated with deeper lakes. Taxa associated with warm lakes included *Alona guttata* var. *tuberculata*, *Ceriodaphnia* spp., and *Alonella exigua*, whereas *Alona affinis*, *Eurycercus* spp., *Ophryoxus gracilis*, and *Alona intermedia* were associated with cold lakes.

The TWINSPAN divided the lakes into five groups which were identified to reflect eutrophic, mesotrophic, dystrophic, oligotrophic, and ultraoligotrophic lakes (Table 4). The indicator taxa for the eutrophic Group I included *Daphnia longispina* group, *G. testudinaria*, *B. longirostris*, *A. quadrangularis*, *Alona rectangula*, *Disparalona rostrata*, *Pleuroxus uncinatus*, and *C. sphaericus* s.l. and the indicators for the mesotrophic Group II were *Ceriodaphnia* spp., *S. crystallina*, and *Holopedium gibberum*. The indicators of the dystrophic Group III included *Unapertura latens*, *A. rustica*, *A. excisa*, *Acantholeberis curvirostris*, *Rynchotalona falcata*, *Eurycercus* spp., *A. affinis*, *A. intermedia*, and *O. gracilis*. The indicator species of the oligotrophic Group IV were *Acroperus harpae*, *Alona guttata*, and *Alonella nana*, whereas the indicator of the ultraoligotrophic Group V was *Diaphanosoma brachyurum*. All the common and most abundant taxa had significant relationship with TP,

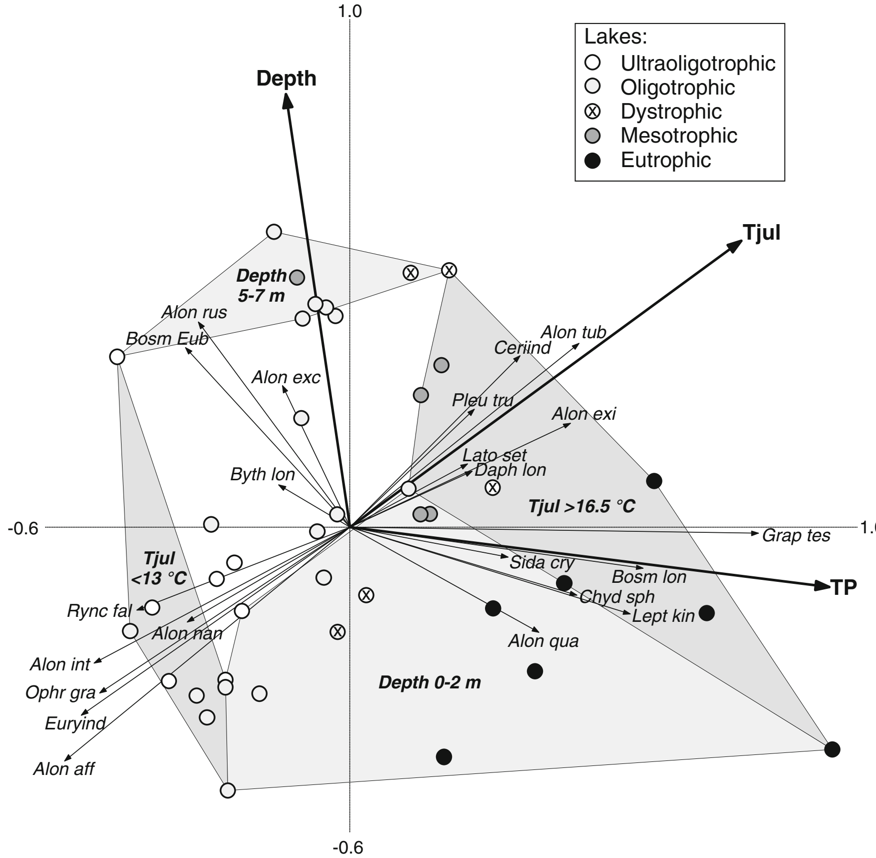

Fig. 2 Results from RDA of fossil Cladocera in 41 lakes in Finland in relation to environmental variables. Only the common taxa having significant relationship statistically (assessed using GLM) with at least one of the environmental variables are shown. The taxa codes are abbreviated from the first *four letters* of the genus names and first *three letters* of species names. The *first axis* explains 19% and the *second axis* 7% of the total variance. The drawn envelopes represent the warmest/coldest lakes and the deepest/shallowest lakes

T_{Jul}, or water depth assessed using GLMs (Table 5). 84% of the taxa were significantly related to TP, 52% to T_{Jul}, and 12% to water depth.

Clustered lake groups (lake typology) were selected as the modeled variable for assessments of lake limnoecological quality. Using this variable, the ratio between the first constrained eigenvalue (λ_1) and the second unconstrained eigenvalue (λ_2) in RDA, that expresses the relative strength of the variable in the species variation, was 1.021. Variables with such high λ_1:λ_2 ratios can be considered suitable for environmental reconstructions. With the lake group as constraining variable, the species environment correlation was 0.819 and it explained 19.8% of the total variance at a significance level of $P = 0.001$. The developed model using the maximum likelihood method had an R^2 of 0.89, R^2_{jack} of 0.81, RMSE of 0.50, RMSEP of 0.63, mean bias of -0.17, and maximum bias of 0.47 (Fig. 3). The number of taxa in the model was 56. Logistic regression failed for six species, which were hence omitted from the model, but all these taxa were rare in the samples. Although the developed model predicted the limnological groups generally correctly, some of the samples had such high residuals that the samples were misclassified to the neighboring group (Fig. 4).

In the test site of the model, Lake Mallusjärvi, the "modern" surface sample was dominated by *Bosmina longirostris* (relative abundance 34.2%), *Chydorus sphaericus*-type (32.1%), and *Bosmina (Eubosmina)* (21.8%), whereas the reference sample was dominated by *Bosmina (Eubosmina)* (47.3%) followed by *Leptodora kindti* (18.2%), and *Daphnia longispina*-type (9.1%). All the taxa in Lake Mallusjärvi were well represented in the calibration set. The test of the model on the surface sample from Lake Mallusjärvi yielded a value of 1.3 representing "eutrophic/bad" limnoecological conditions corresponding well with the chironomid-inferred TP of 91.5 μg l^{-1} and modern measured TP of 103 μg l^{-1}. The reference sample yielded a value of 2.3, which represents "mesotrophic/poor" conditions. This result is in agreement with the lower

Table 4 Grouping of 41 Finnish lakes according to two-way indicator species analysis (TWINSPAN) based on Cladocera assemblages

Group	I	II	III	IV	V
Trophic status	"Eutrophic"	"Mesotrophic"	"Dystrophic"	"Oligotrophic"	"Ultraoligotrophic"
Ecological quality	"Bad"	"Poor"	"Moderate"	"Good"	"High"
Number of sites	14	8	5	9	5
Mean TP (μg l^{-1})	42	27	17	12	5
Mean pH	6.9	6.7	5.2	6.1	6.7
Mean DO (mg l^{-1})	3.5	6.2	5.3	6.9	9.0
Mean color (mg Pt l^{-1})	91	80	60	47	18
Mean TN (μg l^{-1})	815	654	413	346	246
Mean conductivity (μS cm^{-1})	67	47	19	40	24
Mean T_{Jul} (°C)	15.6	16.2	16.2	14.9	13.2
Mean depth (m)	1.7	2.7	4.6	2.7	2.8
Indicator species	*Daph lon*	*Ceriind*	*Unap lat*	*Acro har*	*Diap bra*
	Grap tes	*Sida cry*	*Alon rus*	*Alon gut*	
	Bosm lon	*Holo gib*	*Alon exc*	*Alon nan*	
	Alon qua		*Acan cur*		
	Alon rec		*Rync fal*		
	Disp ros		*Euryind*		
	Pleu unc		*Alon aff*		
	Chyd sph		*Alon int*		
			Ophr gra		

The taxa codes are abbreviated from the first four letters of the genus names and first three letters of species names

chironomid-inferred value of 57.2 μg l^{-1} for the reference sample.

Discussion

It is well known that water quality parameters are closely connected to each other and lake trophic status can change along climate gradients (Catalan et al., 2009). In the present dataset, significant correlations were found among most of the examined water quality parameters and also latitude and mean air T_{Jul} correlated significantly with lake trophic conditions (Table 1). In addition, pH was found to correlate with sampling depth. These intercorrelations obviously hamper general assessments of lake water quality in different lakes. Of the examined variables, water color, TN, and conductivity did not have unique contribution to the regression equation having high VIFs (Table 3), and were thus removed from further analyses. Of the remaining variables, pH was strongly affected by the conditional effects of covariables, and therefore its influence on the Cladocera assemblages was not independent. In addition, DO correlated very strongly with nutrients, but its influence was not as important; for that reason, it was rejected. Hence, the remaining variables, TP, mean air T_{Jul}, and sampling depth, were selected for further examination. Of these, TP had the highest species environment correlation and percentage of variance explained. Previous studies from the Finnish lakes have also identified the importance of temperature and depth in structuring Cladocera communities (Korhola, 1999; Luoto et al., 2011; Nevalainen et al., 2011b; Siitonen et al., 2011), but the influence of TP was not tested in any of these studies. However, studies from elsewhere in Europe have shown that TP is in fact a key variable in explaining Cladocera distribution (Brodersen et al., 1998; Lotter et al., 1998; de Eyto et al., 2002; Kamenik et al., 2007).

According to the RDA and TWINSPAN, eutrophic lakes (Group I) were characterized by *Daphnia longispina* group, *Graptoleberis testudinaria*, *Bosmina longirostris*, *Alona quadrangularis*, *Alona rectangula*, and *Chydorus sphaericus* s.l., mesotrophic

Table 5 The 25 most common ($N2 \geq 3$, maximum abundance $\geq$1%) Cladocera taxa in the 41 study lakes and their indicator value assessed by generalized linear modeling to determine significant (x = significant at $P \leq 0.05$; X = significant at $P \leq 0.01$) relationships between species and environmental variables

	*N*2	Number of occurrences	Mean%	Min.%	Max.%	TP	T_{Jul}	Depth	Limn. group
Bosmina (Eubosmina)	27.1	39	24.7	0	70.6			X	IV
Acroperus harpae	25.7	39	5.7	0	17.1	x			IV
Alonella nana	24.4	41	17.8	1.0	72.3	X	x		IV
Alona affinis	20.5	41	12.5	0.3	57.7	X	X		III
Alona intermedia	20.2	31	1.1	0	4.1	X	X		III
Alonella excisa	18.5	41	6.5	0.3	35.4	X			III
Ophryoxus gracilis	18.4	30	0.8	0	3.0	X	X		III
Ceriodaphnia spp.	15.5	27	0.5	0	2.5	X	X		II
Alona guttata var. *tub.*	13.0	27	1.3	0	8.8		X		III
Alonopsis elongata	12.9	25	0.6	0	3.7	x			IV
Eurycercus spp.	12.8	32	1.2	0	9.3	x	X		III
Chydorus sphaericus	12.7	41	7.8	0.7	60.1	x	x		I
Sida crystallina	11.9	25	0.4	0	3.4	x			II
Alona rustica	11.6	30	1.9	0	15.7			X	III
Unapertura latens	10.3	15	0.3	0	2.5	x			III
Rynchotalona falcata	8.1	20	0.8	0	8.7	x	X		III
Graptoleberis testudinaria	7.8	17	0.4	0	4.7	X	X		I
Bosmina longirostris	7.2	13	8.6	0	74.7	X			I
Alonella exigua	6.6	12	0.2	0	2.1		x		II
Daphnia longispina group	6.0	18	1.2	0	16.9	X			I
Alona quadrangularis	5.4	14	1.1	0	14.1	X			I
Disparalona rostrata	4.5	6	0.1	0	1.5	X	x	x	I
Alona rectangula	4.3	8	0.8	0	8.2	x			I
Pleuroxus laevis	3.7	7	0.1	0	1.6	X	x		I
Pleuroxus trigonellus	3.0	6	0.1	0	2.0	X			I
Total number of indicators						21	13	3	

In addition, the assigned limnoecological group is given for each taxa (I = eutrophic/bad, II = mesotrophic/poor, III = dystrophic/moderate, IV = oligotrophic/good, V = ultraoligotrophic/high)

lakes (Group II) by *Ceriodaphnia* spp., and *Sida crystallina*, dystrophic lakes (Group III) by *Alona rustica*, *Rynchotalona falcata*, *Eurycercus* spp., *Alona affinis*, *A. intermedia*, and *Ophryoxus gracilis*, oligotrophic lakes (Group IV) by *Acroperus harpae*, *Alona guttata*, and *Alonella nana*, and the ultraoligotrophic group (Group V) by *Diaphanosoma brachyurum* (Fig. 2; Table 4). These observations are in good general agreement with previous descriptions on their trophic associations (Gannon & Stemberger, 1978; Lotter et al., 1998; de Eyto et al., 2003; Kamenik et al., 2007). However, particular attention should be directed to *C. sphaericus*, which was found as an indicator of eutrophic lakes in the current dataset. This is partly because it dominated also in some of the dystrophic lakes. In addition, the indicator value of this species is questionable because it often increases its dominance in other extreme conditions besides eutrophication, such as under cold climate or ultraoligotrophic conditions (Manca & Armiaglio, 2002; Kamenik et al., 2007; Luoto & Nevalainen, 2012). In general, *C. sphaericus* s.l. is a cryptic taxon and its taxonomy remains very puzzling (Szeroczyńska & Sarmaja-Korjonen, 2007). Also, *Daphnia longispina* group consists of several species, which may have differing ecological requirements. Furthermore,

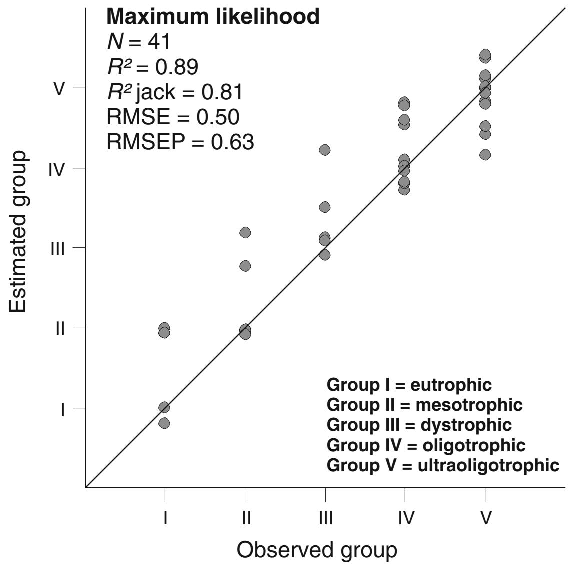

Fig. 3 Relationship (1:1) between observed and estimated limnoecological groups based on Cladocera assemblages from 41 Finnish lakes

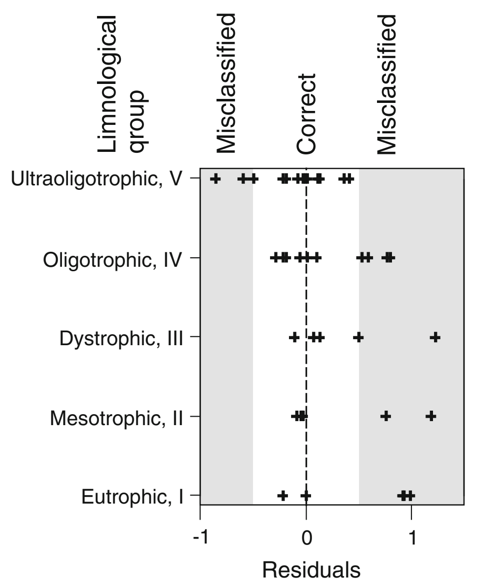

Fig. 4 The risk of misclassifying the limnological group based on the residuals of the Cladocera-based Gaussian logit model

Daphnia species are known to be very sensitive to fish predation (Jeppesen et al., 2001b) which may cause ambiguity when determining its trophic relationships.

The ECOFRAME typology by Moss et al. (2003) is based on four climate categories, where Finland belongs to the group "cool" with ice cover over >2 months and mean temperature of the warmest month >10°C. In addition, all the lakes in the present dataset were shallow. Therefore, neither temperature nor depth was considered in the lake typology. *Alona rustica*, *Bosmina (Eubosmina)*, and *Alonella excisa* were associated with "deeper" lakes and taxa associated to warm lakes included *Alona guttata* var. *tuberculata*, *Ceriodaphnia* spp., and *Alonella exigua*, whereas *Alona affinis*, *Eurycercus* spp., *Ophryoxus gracilis*, and *Alona intermedia* were associated with cold lakes (Fig. 2). Among these taxa, particular care should be taken when applying the present limnoecological results in deeper lakes or in different climate zones. In addition, *Acroperus harpae* has been found to dominate in cold Alpine lakes (Kamenik et al., 2007; Nevalainen & Luoto, 2012) that suggest it may benefit from reduced temperatures. Despite the influence of multiple stressors, most of the taxa were significantly related to TP (Table 5). *Bosmina (Eubosmina)*, *A. guttata* var. *tuberculata*, *A. rustica*, and *A. exigua* were the only common species that did not have statistically significant relationship with TP, but they had significant relationship with either temperature or water depth (Table 5). Comparable to our results, de Eyto et al. (2002) failed to find correlation between these particular *Alona* and *Alonella* species and TP. *Alona rustica* was assigned as an indicator species of the dystrophic lake group by the TWINSPAN (Table 4) and it has previously been found to be acidophilic in Fennoscandian lakes (Walseng et al., 2001). Because dystrophic lakes can have differences in phosphorus availability, the preference of *A. rustica* for acidic humic lakes may lead to its unresponsiveness to TP. Although *Bosmina (Eubosmina)* did not have significant relationship with TP, it preferred oligotrophic lakes in the present dataset (Fig. 2), which is in agreement with previous records (Gannon & Stemberger, 1978).

The TWINSPAN showed that zooplankton assemblages in the present dataset can be used to classify the lakes into five groups, which were identified roughly as eutrophic, mesotrophic, dystrophic, oligotrophic, and ultraoligotrophic (Table 4). Therefore, the observed lake classification (Hertta database of the Finnish Environment Centre), taking into account the measured trophic status of each lake, was examined against Cladocera-inferred lake type. The developed maximum likelihood model with an R^2_{jack} of 0.81 and an RMSEP of 0.63 showed good performance and ability to estimate the lake type generally correctly (Fig. 3).

As implied by the RMSEP and the residuals (Fig. 4), there is, however, a risk of misclassifying the lake type to the neighboring group. In general, the risk is for overoptimistic estimations of limnoecological quality, except in the ultraoligotrophic lakes, which may become estimated as oligotrophic (Table 4). However, the prediction power of the model was strong that confirms the fact that Cladocera can be used as indicators of lake water quality in environmental assessments, such as those related to the WFD or local lake management.

Simpson et al. (2005) used the modern analog technique (MAT) in defining the reference condition of acidified lakes based on diatoms and Cladocera. However, the use of MAT may be problematic because it assumes no model and it is very sensitive to no-analog situations and spatial autocorrelation. An advantage of the present typology and the maximum likelihood method is that it is able to distinguish dystrophic lakes and zooplankters associated with them using a Gaussian logit model. Because dystrophic lakes tend to have "moderate" TP concentrations, there is a general risk of misinterpretation of the lake type or its reference conditions if dystrophy is not accounted for in the calibration data. In any case, lake reference conditions are always unique and should be carefully assessed to avoid forcing a lake with naturally elevated TP into a higher quality group.

The test of the Cladocera-based model of biologic integrity on sediment samples from Lake Mallusjärvi indicated a decline from a value of 2.3 in the reference sample to 1.3 in the modern sample. This decline corresponds well with the decreased chironomid-inferred TP in the same samples. The present biologic integrity value reflected "eutrophic/bad" limnoecological status that is confirmed also by the observed TP. The value of the reference sample reflected "mesotrophic/poor" conditions in agreement with the similar trend of lower, although still relatively high, chironomid-inferred TP. Although the top/bottom-approach using single samples can be used in the current model testing, we stress that due to the age of the reference sample of ~1700 AD potential climate-related problems may arise when assessing the true baseline conditions. This is because at around 1700 AD, the cold climate episode known as the Little Ice Age was at its coldest in southern Finland (Luoto et al., 2009) and this cold event resulted as naturally "improved" limnological conditions in lakes in southern Finland (Luoto & Salonen, 2010). Therefore, we recommend that in assessments of lake reference conditions using a model such as the one presented in this study, more samples should be used to estimate the lake development more reliably and to detect the natural variability in community structure. It should also be noted that the current autumnal TP in Lake Mallusjärvi is higher than the maximum in the calibration set causing a potential bias to the results. However, the estimation of "eutrophic/bad" modern limnoecological status was correct when compared to the observed data, suggesting that the model can also be applied to lakes with higher TP concentrations. This may be possible whenever the species are well represented in the calibration set, as was in the assemblages from Lake Mallusjärvi.

In the future, Cladocera-based models of limnological conditions can be refined by constructing more local models that would minimize the effects of climate. In addition, more reduced gradients in other variables than those related to water quality would improve the species environment relation, however, with the side affect that invaluable ecological information on secondary variables, such as lake depth or abundance of macrophytes, would be lost. The present dataset suffers from the absence of data on macrophytes and fish that have a major role in determining zooplankton community composition in lakes (Willby et al., 2000; Adamczuk, 2012). For future efforts, as the intralake variability of the fossil remains of Cladocera is strongly correlated to the species actual habitats (Nevalainen, 2011, 2012), it may be more beneficial to take samples from the sublittoral areas instead of the profundal, which may be underrepresented by littoral taxa. Previous studies based on fossil chironomids and Cladocera have indicated that sublittoral samples better represent the lake communities and provide the most reliable results in quantitative environmental reconstructions (Luoto, 2010; Luoto et al., 2011). However, owing to within-lake taphonomic features and differences in sediment accumulation, care should be taken in interpretations when sampling sites are chosen differently between a surface sediment dataset and a downcore. It is also necessary to combine contemporary ecology and paleolimnology to better understand shallow lake ecosystem change (Saros, 2009; Nevalainen, 2010; Sayer et al., 2010; Luoto & Raunio, 2011). The present model can be used in assessments of contemporary limnoecological quality of lakes using lake surface sediment samples and in assessments of reference conditions using the fossil records from downcore sediment samples. This can be especially valuable when aiming for the goals set by the WFD in assessments of the ecological status of European surface waters (Nõges et al., 2009). Because multiple stressors affect lake ecosystems (Smol, 2010), the multiproxy approach is recommended for characterizing the ecological state reliably.

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