

# Subfossil Cladocera from surface sediment in thermokarst lakes in northeastern Siberia, Russia, in relation to limnological and climatic variables

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**Abstract** Subfossil Cladocera were sampled and examined from the surface sediments of 35 thermokarst lakes along a temperature gradient crossing the tree line in the Anabar-river basin in northwestern Yakutia, northeastern Siberia. The lakes were distributed through three environmental zones: typical tundra, southern tundra and forest tundra. All lakes were situated within the continuous permafrost zone. Our investigation showed that the cladoceran communities in the lakes of the Anabar region are diverse and abundant, as reflected by taxonomic richness, and high diversity and evenness indices ( $H = 1.89 \pm 0.51$ ;  $I = 0.8 \pm 0.18$ ). CONISS cluster analysis indicated that the cladoceran communities in the three ecological zones (typical tundra, southern tundra and forest-tundra) differed in their taxonomic composition

and structure. Differences in the cladoceran assemblages were related to limnological features and geographical position, vegetation type, climate and water chemistry. The constrained redundancy analysis indicated that  $T_{\text{July}}$ , water depth and both sulphate ( $\text{SO}_4^{2-}$ ) and silica ( $\text{Si}^{4+}$ ) concentrations significantly ( $p \leq 0.05$ ) explained variance in the cladoceran assemblage.  $T_{\text{July}}$  featured the highest percentage (17.4 %) of explained variance in the distribution of subfossil Cladocera. One of the most significant changes in the structure of the cladoceran communities in the investigated transect was the replacement of closely related species along the latitudinal and vegetation gradient. The results demonstrate the potential for a regional cladoceran-based temperature model for the Arctic regions of Russia, and for and Yakutia in particular.

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## Introduction

Thermokarst lakes and ponds are the most common type of Arctic lake (ACIA 2005). These lakes most commonly form as a consequence of thawing of ice-rich permafrost, which forms depressions that subsequently fill with surface waters (Wetterich et al. 2008). Thermokarst lakes act as “hot spots” of biological

activity in northern regions with diverse and abundant microbial, plankton, benthic, aquatic plant, fish and bird communities (ACIA 2005). Climate change is emerging as the most far-reaching and significant stressor on Arctic biodiversity (Petersen 2010). Warming climate is expected to change or even reduce the distribution of animals living in Arctic regions.

Cladocera (Crustacea: Branchiopoda) are a key component of aquatic ecosystems; their community structure reflects a combination of the physical, chemical and biological characteristics of the ecosystem they inhabit (Davidson et al. 2007). Their chitinous exoskeletal components (shell, head shield, postabdomen, postabdominal claws, antennal segments and mandibles) are usually well preserved in sediments and most are identifiable to the species level (Korhola and Rautio 2001). Hence, cladoceran subfossils preserved in lake sediments contain valuable information about the climatic and environmental conditions prevailing during the lifetime of those organisms, which allows cladocerans to be used in palaeoecological studies (Korhola et al. 2000; Kienast et al. 2011).

The interpretation of subfossil cladoceran assemblages requires a detailed knowledge about their distribution and ecological preferences. Unfortunately, such information is still fragmentary and often restricted to calibration data sets from limited geographical areas (Lotter et al. 1997; Rautio 1998; Korhola 1999; Swadling et al. 2000; Sweetman et al. 2010). Very little is known about the biological and functional diversity of zooplankton taxa and communities that reside in the remote aquatic ecosystems of Arctic Russia. Scientifically documented knowledge on both the biological and functional diversity of the freshwater fauna in eastern Siberia and Beringia and the role of environmental factors in regulating cladoceran distribution is especially rare (Samchyshyna et al. 2008; Frolova et al. 2013) because of the difficulty accessing lakes in the Siberian Arctic.

Both the open-water and vegetation periods for the majority of aquatic organisms in the Arctic are limited to a short time interval of 1 or 2 months. Samples of zooplankton are usually collected using standard hydrobiological methods at one or two times per season so do not reflect the presence of all species. Therefore, the real species richness of such water bodies remains unknown because of the uncertain seasonal dynamics of their life cycles in Arctic water bodies. The top 0–1 cm

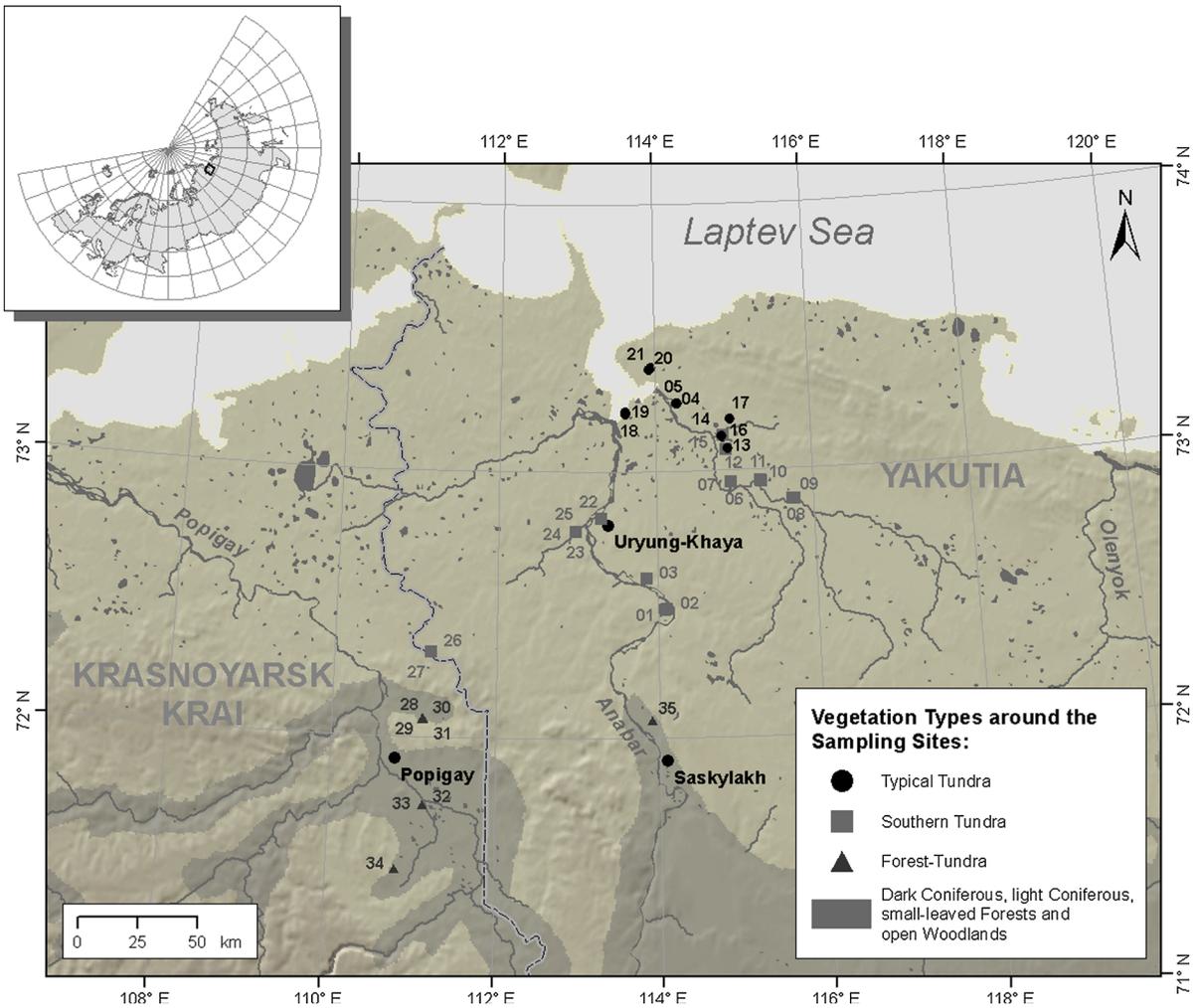
of sediment in a shallow lake is typically the accretion of material deposited over approximately 1–5 years depending upon the lake productivity (Anderson and Battarbee 1994). Therefore, palaeolimnological techniques can provide a better understanding of the taxonomic diversity for at least some selected families (Chydoridae, Bosminidae).

The aim of the present investigation was to examine subfossil cladoceran assemblages from northwestern Yakutia (northeastern Siberia, Russia), to document their distribution within the region, and to reveal the influence of environmental variables in structuring the cladoceran communities. To do this, we examined the surface sediments of 35 lakes that spanned a north–south transect across the modern treeline, and we related the cladoceran assemblages to the physical and chemical characteristics of these lakes.

#### Study site

The study lakes are located in the catchment area of the Anabar River in the northwestern part of Yakutia (Russia) west of the Lena River (Fig. 1). The river Anabar is situated north of the Arctic Circle, is 939 km long and has a catchment area of 104,461 km<sup>2</sup> (Chistyakov 1964). The climatic conditions of the Anabar region show extreme seasonal variations. Short, cool summers are followed by long and very cold winters. The coldest month is January with an average air temperature below  $-34$  °C and the lowest temperatures reaching  $-53$  °C. The mean July temperatures are 10–12 °C with maximum summer temperatures of 30–35 °C (Atlas Arktiki 1985). The mean annual air temperatures are between  $-10$  and  $-13$  °C (Gavrilova 1998). Consequently, shallow lakes are frozen to the bottom for 8–9 months of the year (Wetterich et al. 2008), which limits the annual period of active growth for aquatic organisms, such as Cladocera, in this region.

The mean annual precipitation in the Anabar region is low and varies from 140 to 350 mm. However, this still exceeds evaporation in most places (with  $\sim 100$  mm in the north and  $\sim 200$  mm in the south) because of the predominance of freezing temperatures for most of the year. Less than 30 % of the precipitation occurs in winter and most occurs during the summer months (Kirilov et al. 2007). The low precipitation in winter results in a shallow snow covering that ranges between 20 and 40 cm in the



**Fig. 1** Map of the study region showing the location of the sampled lakes and types of vegetation

lowlands (Atlas selskogo khozyaistva Yakutskoi 1989). The permafrost table in the region is 400–800 m thick. In summer, the upper 0.5–2.0 m of the ground is generally unfrozen (Gavrilova 1998). The thawing of the upper permafrost table and the soil–water content above the frozen ground provides the moisture necessary for vegetation. The formation of thawed lakes (Wetterich et al. 2008) is directly connected to permafrost processes such as ice wedge growth, thermokarst and thermoerosion as well as the fluvial dynamics of the Anabar River and its flood plain. These lakes are mostly shallow (1–5 m) and relatively small.

The study region is located within three different vegetation ecozones (typical tundra, southern tundra

and forest-tundra). The typical tundra is dominated by grasses, sedges and dwarf shrubs (<40 cm tall) such as *Vaccinium vitis-idea* L., *V. uliginosum* L. ssp., *Ledum palustris* L. (1753), *Betula nana* and small *Salix* L. taxa. In the southern tundra, the vegetation is dominated by shrub taxa that are often >40 cm (e.g., *Betula exilis* Sukaczew, *Salix pulchra* Cham., *S. lanata* L., *S. glauca* L., *Alnus fruticosa* Rupr.), dwarf shrubs and mosses (Walker 2000). The forest-tundra zone is characterised by patches of open larch forest (mostly *Larix dahurica* (Rupr.) Rupr. with the occasional occurrence of *Larix sibirica* Ledeb. (Karavaev and Skryabin 1971) and pure shrublands comparable to the southern tundra zone but with a higher *Alnus* component.

**Table 1** Location, elevation and size of the studied lakes

Lake No.	Latitude (°N)	Longitude (°E)	Elevation (m, a.s.l.)	Size <sup>a</sup> (m × m)
07-SA-01	72°29′02.5″	114°06′12.3″	10	2,000 × 1,000
07-SA-02	72°28′48.1″	114° 05′5.4″	6	30 × 30
07-SA-03	72°35′60.0″	113°51′25.2″	6	150 × 100
07-SA-04	73°15′10.0″	114°16′56.9″	3	500 × 300
07-SA-05	73°15′16.7″	114°16′19.8″	3	1,000 × 1,000
07-SA-06	72°57′20.4″	114°57′28.7″	0	300 × 200
07-SA-07	72°57′20.4″	114°57′28.7″	0	500 × 500
07-SA-08	72°53′09.6″	115°43′34.3″	4	2,000 × 2,000
07-SA-09	72°53′06.0″	115°45′18.0″	4	100 × 100
07-SA-10	72°57′23.1″	115°20′16.9″	11	2,000 × 2,000
07-SA-11	72°57′38.4″	115°19′50.4″	4	4,000 × 300
07-SA-12	73°04′44.5″	114°54′17.8″	0	2,000 × 2,000
07-SA-13	73°04′56.3″	114°55′23.3″	3	500 × 500
07-SA-14	73°07′32.2″	114°52′05.1″	1	300 × 300
07-SA-15	73°07′47.3″	114°51′54.9″	4	800 × 800
07-SA-16	73°07′45.8″	114°51′38.7″	4	800 × 800
07-SA-17	73°11′36.1″	114°57′48.1″	10	500 × 500
07-SA-18	73°12′56.2″	113°37′14.3″	8	500 × 300
07-SA-19	73°13′17.2″	113°37′10.4″	1	600 × 500
07-SA-20	73°22′53.9″	113°55′49.9″	4	700 × 300
07-SA-21	73°23′13.5″	113°56′56.3″	4	200 × 80
07-SA-22	72°49′32.2″	113°17′36.6″	8	300 × 200
07-SA-23	72°46′29.7″	112°58′39.5″	4	600 × 400
07-SA-24	72°46′35.5″	112°58′13.9″	1	200 × 200
07-SA-25	72°46′39.7″	112°58′13.0″	1	150 × 150
07-SA-26	72°19′12.0″	111°11′20.4″	86	400 × 400
07-SA-27	72°19′14.5″	111°11′13.8″	71	500 × 400
07-SA-28	72°04′16.9″	111°06′29.3″	41	500 × 300
07-SA-29	72°04′5.7″	111°06′25.3″	37	180 × 120
07-SA-30	72°04′7.0″	111°06′40.0″	36	200 × 180
07-SA-31	72°04′15.2″	111°07′3.4″	38	150 × 150
07-SA-32	71°44′51.7″	111°07′46.2″	50	100 × 100
07-SA-33	71°44′50.9″	111°07′55.2″	50	600 × 400
07-SA-34	71°30′10.8″	110°49′08.4″	80	400 × 150
07-SA-35	72°03′57.5″	113°54′49.3″	15	300 × 100

<sup>a</sup> Approximated by a circle or ellipse with these diameters

## Materials and methods

### Field work

Samples were collected during a joint Russian–German expedition in the summer of 2007. The study sites included 35 lakes distributed along a north–south

transect across the Anabar region (71°30′10.8″–73°23′13.5″N) (Fig. 1; Table 1). To avoid disturbances in the sediment deposition, we sampled only lakes that were over 0.9 m deep, not fed by large rivers, and were without anthropogenic impact. Most of the lakes were >2.5 m deep, but some shallow ponds in the Arctic tundra were included in the

**Table 2** Statistical summary for the limnological measurements of the study lakes in the Anabar region of Yakutia

Variable	Min	Max	Mean	Median	SD	Skew
T <sub>air July</sub> (°C)	10.2	12.1	11.2	11.0	0.51	0.09
Water depth (m)	0.90	8.00	3.90	3.35	2.39	0.27
Secchi depth (m)	0.50	4.50	1.59	1.50	0.85	1.44
Conductivity (µS cm <sup>-1</sup> )	16.00	277.00	51.10	33.00	49.20	3.25
HCO <sub>3</sub> <sup>-</sup> (mg L <sup>-1</sup> )	4.10	36.10	15.84	13.70	9.23	0.77
pH	4.85	7.55	7.00	7.18	0.58	-2.57
Cl <sup>-</sup> (mg L <sup>-1</sup> )	0.27	63.00	5.25	1.12	11.74	3.95
SO <sub>4</sub> <sup>2-</sup> (mg L <sup>-1</sup> )	0.11	9.94	0.73	0.22	1.84	4.63
Al <sup>3+</sup> (µg L <sup>-1</sup> )	21.10	200.00	59.55	30.30	57.79	1.73
Ca <sup>2+</sup> (mg L <sup>-1</sup> )	0.94	9.49	3.78	3.42	2.21	0.96
Fe <sub>total</sub> (µg L <sup>-1</sup> )	24.70	587.00	243.46	198.50	146.77	0.68
Mg <sup>2+</sup> (mg L <sup>-1</sup> )	0.67	4.96	1.77	1.73	1.00	1.04
Na <sup>+</sup> (mg L <sup>-1</sup> )	0.21	36.40	3.45	0.99	7.08	3.86
Si <sup>4+</sup> (mg L <sup>-1</sup> )	0.27	63.00	5.25	1.12	11.74	3.95
NO <sub>3</sub> <sup>-</sup> (mg L <sup>-1</sup> )	<0.15					
Mn <sup>2+</sup> (µg L <sup>-1</sup> )	<20					
TP (mg L <sup>-1</sup> )	<0.1					

The abbreviation SD refers to the standard deviation, Skew refers to skewedness (adjusted Fisher-Pearson standardized moment coefficient included in Excel). Concentrations of NO<sub>3</sub><sup>-</sup>, Mn<sup>2+</sup> and TP were mostly below the detection limits. Detection limits are given in the table.

investigation, to better represent this zone within the data set. The majority of the lakes were of medium size (area = 0.25–20 ha). Details are given in the Tables 1 and 2.

Hydrochemical samples and Secchi-disk measurements for each site were taken from the surface water layer (0.5–1 m) at the lake centre. Alkalinity and acidity were determined using titrimetric test kits (Macherey–Nagel, Visocolor series). We measured pH, water temperature, oxygen concentration and electrical conductivity (EC) using a handheld multi-parameter instrument (WTW 340i) equipped with appropriate sensors (pH: SenTix 41; Oxygen: CelloX 325; EC and temperature: Tetracon 325). Water samples for ion analysis were passed through a cellulose-acetate filter (pore size 0.45 µm) in the field. Samples for elemental (cation) analysis were acidified using HNO<sub>3</sub>. Samples for anion analysis and residue samples were stored cool. Surface sediments were collected from the deepest point of each lake using an Eckman–Birge dredge in modification of Lenz (Blomqvist 1990), which has an option to cut the sampled sediments horizontally in order to separate the upper 1-cm layer with no disturbance. The

sediments were stored in cold storage at 4 °C prior to analysis for invertebrate remains.

#### Laboratory methods. Analyses of water and subfossil Cladocera

Water samples were analysed at the Alfred Wegener Institute (Potsdam, Germany). The chemical analyses encompassed conductivity, pH, oxygen concentration, dissolved organic carbon (DOC), total phosphorus (TP), chloride (Cl<sup>-</sup>), sulphate (SO<sub>4</sub><sup>2-</sup>), nitrite (NO<sub>2</sub><sup>-</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), carbonate (HCO<sub>3</sub><sup>-</sup>), calcium (Ca<sup>2+</sup>), sodium (Na<sup>+</sup>), Si<sup>4+</sup>, Al<sup>3+</sup>, Fe<sub>total</sub>, Mg<sup>2+</sup>, Mn<sup>2+</sup>.

Only 31 of the initial 35 lakes contained sufficient cladoceran remains for analysis. The sample preparation method used for cladoceran analyses in our study was an adaptation of the subfossil preparation technique described by Korhola and Rautio (2001) and the method of Jeppesen et al. (2001). Between 4 and 8 g of fresh surface sediment sub-samples were heated in 10 % KOH at 75 °C for approximately 30 min. The sediments were then rinsed through 125 and 63 µm sieves in order to facilitate identification of remains. The material retained on sieves was transferred to

small vials containing distilled water and a few drops of ethanol to prevent fungal growth. Two to three drops of a safranin solution was added to stain any cladocerans remains. Sub-samples were analysed using a light microscope at 40–400 $\times$  magnification. The chitinous remains of cladoceran (post-abdomens, claws, mandibles, sections of antennae, ephippia and remains of carapaces) were identified with reference to Flössner (2000), Frey (1959, 1973), Smirnov (1974), Szeroczyńska and Sarmaja-Korjonen (2007).

At least 100 individuals per sample were counted from each sub-sample, both fractions were counted wholly, and if there were not enough remains, another subsample was prepared. All individuals were identified to the lowest taxonomic level possible. We had difficulty separating species of *Daphnia* based solely on postabdominal claws morphology. Most daphnid remains were divided into two broad groups as has been done in other investigations (Davidson et al. 2007; Sweetman et al. 2010). Remains containing teeth of middle pecten of the postabdominal claws that were significantly larger than teeth of proximal or distal pecten were classified as *Daphnia pulex* complex, whereas remains with teeth of middle pecten of similar size to the proximal and distal pectens were classified as *D. longispina* complex.

#### Data analyses

The environmental data included several physical, chemical and biological variables considered to be potentially important in structuring cladoceran communities. These included mean July air temperature, latitude, longitude, altitude, vegetation, water depth, Secchi depth, conductivity, pH, oxygen concentration, DOC,  $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{NO}_2^-$ ,  $\text{HCO}_3^-$ ,  $\text{Al}^{3+}$ ,  $\text{Si}^{4+}$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{Na}^+$  concentrations. TP,  $\text{Mn}^{2+}$  and  $\text{NO}_3^-$  were eliminated from the analysis because their concentrations were mostly below the detection limits (TP < 0.1 mg l<sup>-1</sup>,  $\text{Mn}^{2+}$  < 20  $\mu\text{g l}^{-1}$ ,  $\text{NO}_3^-$  < 0,15 mg l<sup>-1</sup>, Table 2). The mean July temperature ( $T_{\text{July}}$ ) for the sampled lakes was calculated from a gridded climate data set (New et al. 2002) measured 2 m above the ground using standard meteorological screens. Using these data, we estimated the mean air temperature at each lake via the spatial interpolation of elevation and distance from the coast. According to the calculation, the lakes are situated within a range

with mean July air temperatures from +10.2 to +12.1 °C (Table 2).

Normality of distribution of environmental parameters was tested using Fisher–Pearson standardized moment coefficient included in Excel. Values that exceeded two standard errors of skewness (regardless of sign) were identified as significantly skewed (Sokal and Rohlf 1995). Any environmental variables with a skewed distribution (altitude, conductivity, Secchi depth,  $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{NO}_2^-$ ,  $\text{Al}^{3+}$ ,  $\text{Fe}_{\text{total}}$ ) were  $\ln(x + 1)$  transformed, where x was the environmental variable under consideration. To reduce the variances across the cladoceran taxa, the percent abundances were square-root transformed prior to all numerical analyses.

A detrended correspondence analysis (DCA) was applied to the cladoceran data to calculate the sampled environmental gradient length. This was necessary to choose between unimodal or linear numerical techniques when estimating the relationship between the cladoceran assemblages and environmental variables (Birks 1995).

Variance inflation factors (VIF) were used to identify the intercorrelated variables. Variables with high VIFs (>20) were eliminated one at a time beginning with the highest until all of the VIFs were below 20 (ter Braak and Prentice 1988). The significance of the environmental variables was tested using a Monte Carlo test with 999 random permutations ( $p \leq 0.05$ ) (Hall and Smol 1996). To determine the relationships between the environmental variables and cladoceran taxa distribution and select those that best explained the cladoceran assemblage variation, a set of redundancy analysis (RDAs) separately constrained to each environmental variable was run and the ratios between the constrained axis ( $\lambda_1$ ) and the unconstrained axis ( $\lambda_2$ ) were calculated. Higher  $\lambda_1/\lambda_2$  show more relative strength of each environmental variable (Hall and Smol 1996; DeSellas et al. 2008).

Ordinations and estimation of VIFs were performed using CANOCO software, version 4.5 (ter Braak and Šmilauer 2002). TILIA version 2.0.b.4 was used to generate a cladoceran percentage diagram (Grimm 1993). The program CONISS was used to perform a stratigraphically constrained incremental sum-of-squares cluster analysis and identify the major groups in lake composition throughout the transect (Grimm 1987).

**Table 3** Characteristics of the cladoceran assemblages in lakes of groups I–III, separated by constrained cluster analysis (CONISS)

Variable	I	II	III
N taxa per lake	7.78	11.69	9.15
H (Shannon Index)	1.58	1.99	1.72
I (evenness)	0.78	0.82	0.78

Species diversity and evenness were calculated for each sample using the Shannon Index of Diversity (H) (Shannon and Weaver 1963) and Pielou Index (I) (Pielou 1966), respectively.

## Results

General composition of subfossil cladocerans from the Anabar region

The investigated lakes were slightly acidic to neutral and generally dilute. Analysis of the ion composition showed that  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  dominated the cations with  $\text{HCO}_3^-$  the primary anion. The original hydrochemical data will be presented and discussed elsewhere.

The cladoceran assemblages were quite rich and diverse in all lakes with relatively stable structures, as reflected by the high evenness indices (Table 3). A total of 28 cladoceran taxa belonging mostly to the family Chydoridae were identified in these lakes. None of the taxa occurred in all lakes. The most common cladoceran taxa were *Chydorus sphaericus* (O.F. Müller, 1785), *Eurycercus* spp., *Alona rectangularis* Sars, 1861, *Acroperus harpae* (Baird 1834) and *D. pulex* agg. (frequency of occurrence >50 %). The species richness (the total number of taxa per lake) ranged between 5 (lakes 05, 14, 18) and 20 (lake 24) with a median of nine which was not significantly correlated to any of the environmental variables measured. The most abundant cladoceran taxon in the modern samples was *C. sphaericus*, which had a mean relative abundance of 44.6 % ( $\sigma = \pm 4.5$  %) across all lakes and reached an abundance of over 50 % in 13 of the 31 lakes (Fig. 2).

Constrained cluster analysis (CONISS), based on the structure of the cladoceran community, revealed three groups of lakes in the investigated area (Fig. 2).

The clusters show a clear geographic pattern reflecting vegetation zonation into typical tundra, southern tundra and forest-tundra (Fig. 1). However, the cladoceran assemblage from lake 27 was clustered with the forest-tundra lakes, although this lake is situated in the tundra zone (30 km north of the tree line observed from the helicopter in field) (Fig. 2).

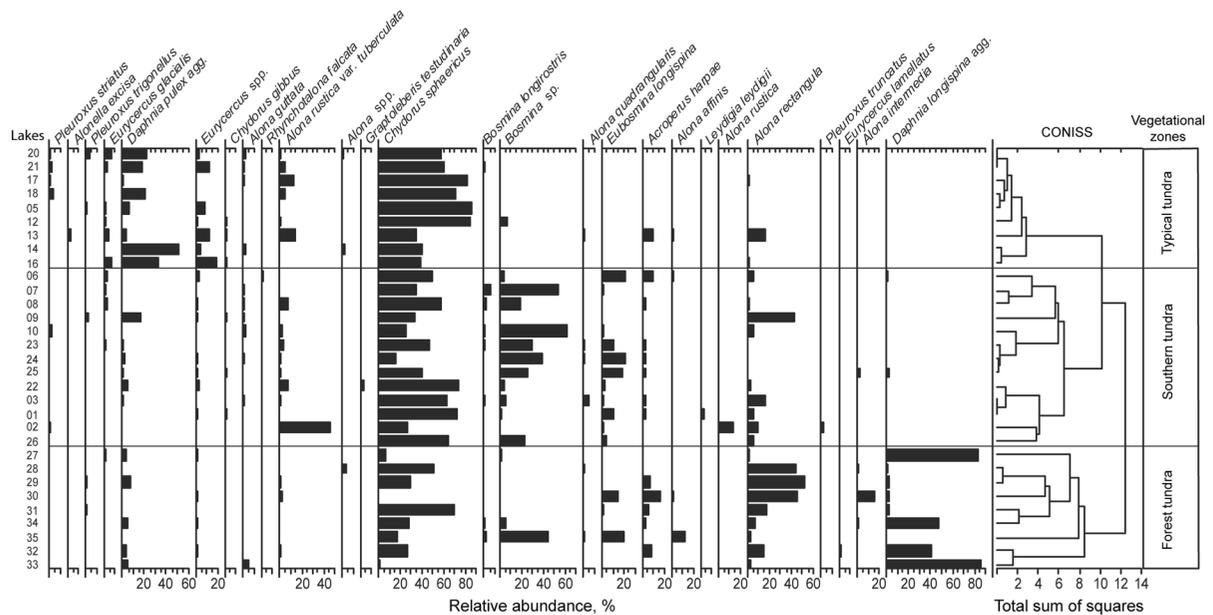
The first cluster revealed by CONISS was formed by 9 northern lakes located in the typical tundra zone (mean  $T_{\text{July}} = 10.6$  °C, range between 10.2 and 10.9 °C). Several littoral taxa, including *C. sphaericus*, *Alona rustica* var. *tuberculata*, *Eurycercus* spp. and *D. pulex* agg. were the most abundant in this environment (Fig. 2). The species richness (N) and Shannon Diversity Index (H) in this group of lakes was lower than for southern tundra lakes, however the evenness, which reflects the structural stability of the cladoceran communities, was at the same level, or higher than in southern lakes (Table 3).

Lakes from the southern tundra (cluster II; mean  $T_{\text{July}} = 11.2$  °C, range 11.0–11.7 °C) were dominated by diverse littoral and pelagic cladoceran assemblages (*C. sphaericus*, *Bosmina longirostris* (O. F. Müller, 1785), *Eubosmina longispina* Leydig, 1860, *Bosmina* sp., *A. rectangularis* Sars, 1862). The Shannon Index and evenness for this group of lakes were higher than for group I and II (Table 3).

All of the lakes in cluster III, except lake 27 were located in the forest-tundra zone (mean  $T_{\text{July}} = 11.8$  °C, range 11.7–12.1 °C). The most common taxa were *C. sphaericus*, *A. rectangularis* and *Daphnia longispina* agg. Interestingly, a dominant taxon in the northern part of the transect from the family Daphnidae, *D. pulex* agg., was replaced in the forest-tundra zone lakes by *D. longispina* agg. (Fig. 3). Cladoceran assemblages in this cluster were more diverse and had a higher evenness than in lakes in the typical tundra zone (Table 3).

## Multivariate analysis

The DCA revealed a gradient length of 2.971 SD units, which is an intermediate gradient length and suggests either linear or unimodal ordination methods might be appropriate (ter Braak and Šmilauer 2002). RDA axis 1 ( $\lambda = 0.174$ ) and axis 2 ( $\lambda = 0.157$ ) were both significant ( $p \leq 0.05$ ) and explained 33.1 % of variance of species data (Table 4). Constrained RDA on individual environmental variables with Monte Carlo



**Fig. 2** Distribution of the most common cladoceran taxa found in the studied lakes based on the occurrence of their remains in the lake sediments. Lakes are ordered by  $T_{\text{July}}$  with vegetational/ecoclimatic zones indicated to the right of the diagram

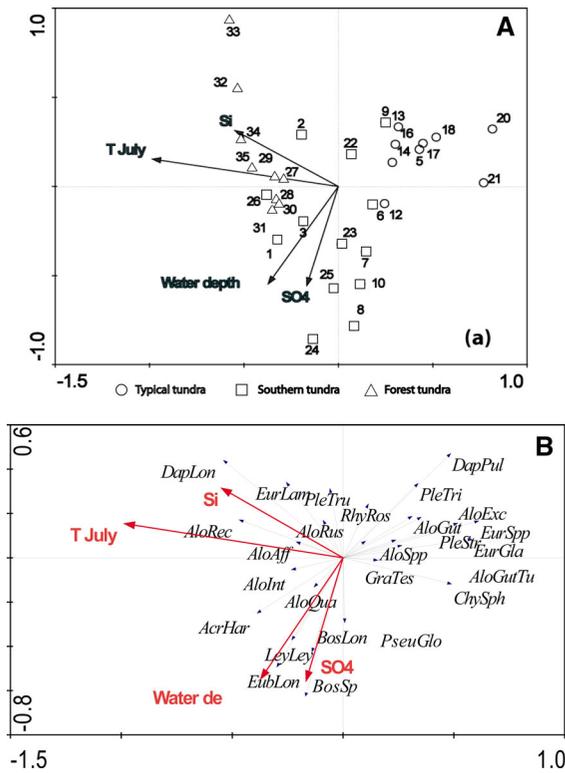
permutation tests (999 permutations) identified environmental variables that significantly ( $p \leq 0.05$ ) explained the taxonomic data variation:  $T_{\text{July}}$ , water depth,  $\text{SO}_4^{2-}$  and  $\text{Si}^{4+}$  (Fig. 3).  $T_{\text{July}}$  and  $\text{Si}^{4+}$  correlated to RDA axis 1, while water depth and  $\text{SO}_4^{2-}$  correlated to RDA axis 2.

Of the four identified significant environmental variables,  $T_{\text{July}}$  featured the highest percentage (17.4 %) of explained variance and had the highest  $\lambda_1/\lambda_2$  ratio (0.66) if tested in an RDA with only a single constraining environmental variable (Table 4). The latter measure in particular indicates how effectively the variance in the species data was captured by a particular gradient (Korhola et al. 2000). The results suggest that the relationship between the cladoceran distribution in this data-set and  $T_{\text{July}}$  is sufficiently strong to be promising for the future development of a regional transfer function to reconstruct past mean July temperatures from cladoceran data in palaeoenvironmental investigations. The sites with high axis 1 scores were clustered in the top right portion of the biplot. These lakes are located in the typical tundra zone in the North at low elevation and were shallower than the more southern lakes (water depth: mean 3.17 m, range 1.0–7.4 m). Lakes with low axis 2 scores are relatively deep (mean > 6.5 m, range

0.9–>10.0 m) and most are located in the southern tundra and characterised by diverse littoral and pelagic cladoceran assemblages (*C. sphaericus*, *B. longirostris*, *E. longispina*, *Bosmina* sp. and *A. rectangula*) (Fig. 3a,3b). Lakes with high axis 2 and low axis 1 scores also came from the southern part of the transect, though mostly from the forest-tundra zones with higher elevations and had high  $\text{Si}^{4+}$  ion concentrations (Fig. 3b).

There was a separation of littoral and pelagic cladocerans along the second RDA axis that was related with lake depth. Littoral cladocerans generally occurred in shallow lakes (Fig. 3a: different taxa of the genera *Pleuroxus*, *Eurycercus* and *Alona*), whereas some pelagic cladocerans occurred in higher relative abundances in relatively deep, clear lakes (Fig. 3a: e.g., *Bosmina* sp. and *B. longirostris*). A typical profundal cladoceran species found in the deep lakes was *Leydigia leydigii* (Leydig 1860). Only one pelagic taxon, the *D. pulex* complex, was abundant in the shallow coloured lakes (Fig. 3a).

Overall, the ordination results supported the classification of the lakes made on the basis of CONISS (Fig. 2). Cladoceran assemblages have the strongest relationship to the climate related parameters ( $T_{\text{July}}$ , vegetation type) and lake water depth.



**Fig. 3** Redundancy analysis ordination plot illustrating the relationship between the most significant ecological factors and both **a** the sites and **b** the most frequent cladoceran taxa. The taxon codes are given in Table 1

**Discussion**

Abundance and habitat characteristics of cladoceran taxa

It is unfortunately impossible to make an intra-regional comparison of subfossil Cladocera communities because of the total absence of such data for the

Siberian North. A comparison of our data to the data sets from other regions indicate the species richness and total number of taxa in our investigation was similar to that of Cladocera in thermokarst lakes from permafrost zones along the tree line in Alaska, where 27 Cladocera taxa were identified from the study lakes (Sweetman and Smol 2006), in Canada, where twenty-nine cladoceran taxa were identified (Sweetman et al. 2010) and Fennoscandia, where a total of 29 cladoceran taxa representing 19 genera were identified (Korhola 1999).

The most abundant taxa in our investigation can be classified as subarctic taxa according to their latitudinal affinities, such as *E. longispina*, *Alona affinis* (Leydig 1860), *A. harpae* and *Eurycercus lamellatus* (O. F. M., 1776) (Rautio 1998; Korhola 1999) (Table 5). Many of these taxa are cold-tolerant, tolerant of nutrient deficits and adapted to the oligotrophic conditions characteristic of the majority of the investigated lakes (concentration of TP in all of the investigated lakes was below 0.10  $\mu\text{g l}^{-1}$ ).

Subfossil cladoceran assemblages in Anabar basin included planktonic and benthic taxa. The true planktonic taxa in the studied lakes were *D. pulex* agg., *D. longispina* agg. and taxa from the family Bosminidae. The most characteristic benthic profundal taxon was *L. leydigii*.

Most of the cladocerans in our investigation belonged to littoral species, which occur among macrophytes and in muddy substrate within the macrophyte zone at the lake margins. The littoral component was represented by *C. sphaericus*, *A. rectangula* and other taxa from the family Chydoridae. The dominant taxon, *C. sphaericus*, is probably a complex of species that comprise several ecologically and geographically distinct species (Belyaeva and

**Table 4** The results of DCA and RDA of the cladoceran data from North Siberia

	DCA		RDA		RDA	RDA	RDA	RDA
	Axis 1	Axis 2	Axis 1	Axis 2	T <sub>July</sub>	WD	Si <sup>4+</sup>	SO <sub>4</sub> <sup>2-</sup>
					$\lambda_1/\lambda_2$	$\lambda_1/\lambda_2$	$\lambda_1/\lambda_2$	$\lambda_1/\lambda_2$
Eigenvalue	0.672	0.333	0.174	0.157	0.172/0.258	0.085/0.267	0.082/0.250	0.074/0.263
Gradient length (SD)	2.971	2.914	–	–	–	–	–	–
% of variance explained	26.5	13.1	17.4	15.7	17.4	8.5	8.2	7.4
p value					0.001	0.010	0.018	0.028

p values were assessed by 999 unrestricted Monte Carlo permutation tests

WD water depth

**Table 5** List of non-rare cladoceran taxa (relative abundance of at least 2 % in at least one study lake) from the studied lakes and their zoogeographic characteristics in north Yakutian lakes

Taxon	Note	# Occ	Geographical range <sup>a</sup>
<i>Acroperus harpae</i>	AcrHar	19	H
<i>Alona affinis</i>	AloAff	12	K
<i>Alona guttata</i>	AloGut	11	K
<i>Alona intermedia</i>	AloInt	4	K
<i>Alona quadrangularis</i>	AloQua	6	H
<i>Alona rectangula</i>	AloRec	24	K
<i>Alona rustica</i>	AloRus	2	H
<i>Alona rustica</i> var. <i>tuberculata</i>	AloRusTub	17	P
<i>Alona</i> spp.	AloSpp	9	
<i>Alonella excisa</i>	AloExc	3	K
<i>Bosmina longirostris</i>	BosLon	8	K
<i>Bosmina</i> sp.	BosSp	17	
<i>Chydorus sphaericus</i>	ChySph	33	K
<i>Daphnia longispina</i> agg.	DapLon	10	
<i>Daphnia pulex</i> agg.	DapPul	19	
<i>Eubosmina longispina</i>	EubLon	15	P
<i>Eurycerus glacialis</i>	EurGla	13	A
<i>Eurycerus lamellatus</i>	EurLam	5	K
<i>Eurycerus</i> spp.	EurSpp	25	
<i>Graptoleberis testudinaria</i>	GraTes	3	K
<i>Leydigia leydigi</i>	LeyLey	6	H
<i>Pleuroxus striatus</i>	PleStr	7	H
<i>Pleuroxus trigonellus</i>	PleTri	5	P
<i>Pleuroxus truncatus</i>	PleTru	1	H
<i>Pseudochydorus globosus</i>	PseuGlo	8	H
<i>Rhynchotalona falcata</i>	Rhyfal	1	H

Occ number of occurrences, A arctic, K cosmopolite, H holarctic, P palearctic

<sup>a</sup> Information about zoogeography was taken from Flößner (2000), Manuilova (1964), Smirnov (1974, 1996)

Taylor 2009). *Chydorus sphaericus* is a nearshore and littoral ubiquitous taxon that may be abundant in eutrophic conditions as well as oligotrophic conditions, but an increase in this taxon is typical sign of increased levels of nutrients and of eutrophication processes (Flößner 2000; Nevalainen and Luoto 2013; Table 5).

Taxa in this data set that are typical for deep lakes were mostly planktonic, such as *B. longirostris*, *E.*

*longispina* and *Bosmina* sp. Typical benthic profundal species included *L. leydigii*, whereas *A. harpae* was the only littoral taxon with preference for deeper sites. *Alonella excisa* (Fischer 1854), *A. affinis*, *Pleuroxus trigonellus* (O. F. Müller, 1776) and other littoral species were distinctly associated with shallow lakes. These results are in agreement with other studies on the present-day cladoceran distribution for lakes in Finnish Lapland (Rautio 1998; Korhola et al. 2000).

Some Cladocera taxa have wide ecological tolerance and are able to colonise various types of aquatic environment, whereas other taxa are more restricted to particular conditions and narrower ecological niches (Flößner 2000). Therefore, despite most of the taxa appearing to be widely distributed and present in lakes from all three ecozones, some cladoceran groups are more specifically affiliated to a certain ecozone.

The most abundant Cladocera taxa in the typical tundra zone were *C. sphaericus*, *Eurycerus glacialis*, *D. pulex* agg. and *Alona guttata* var. *tuberculata*. *E. glacialis*, one of the largest species of cladocerans, inhabits ponds and pools in both Arctic and subarctic regions and has been observed at lower latitudes in Europe and North America (Frey 1973). *Eurycerus glacialis* is one of few Arctic cladoceran species with a circumpolar distribution and is almost completely limited to tundra zones (Smirnov 1996). Minakawa et al. (2006) reported that on Sakhalin *E. glacialis* was primarily found in shallow waters (10–30 cm deep) with sandy substrates. Closely related species, *E. lamellatus* demonstrates a marked preference for the cold, deep, clear and organic-poor waters in the far North (Korhola 1999). This taxon is cold-tolerant Arctic-subarctic according to the classification of Harmsworth (1968). According to Flößner (2000), *E. glacialis* and the more widely distributed *E. lamellatus* occupy different water bodies: *lamellatus* inhabits small ponds and *glacialis* inhabits lakes. However, populations of both species were found in lakes during our investigations and those of Duigan and Frey (1987).

Another relatively abundant taxa in the tundra zone was *Alona guttata* var. *tuberculata*. Daphnidae were represented by *D. pulex* complex, which most likely included *Daphnia middendorffiana*. According to Reed (1959), this species dominated in 170 water bodies in the Arctic North American tundra. Flößner (2000) stated that the distribution of this species was restricted to tundra regions. Similar to our findings,

DeSellas et al. (2008) reported that *D. pulex* agg. preferred shallow, coloured lakes in south-central Ontario (Canada).

The lakes in the southern tundra zone were deeper than those from the typical tundra zone. Therefore, more planktonic taxa, such as *E. longispina* and *Bosmina* sp. were found there. *E. longispina*, a taxon typically associated with oligotrophic conditions (Flössner 2000) rather than harsh climatic conditions (Hofmann 1978), was frequently identified.

One of the most significant changes in the structure of cladoceran communities along the investigated transect was the replacement of closely related species along the latitudinal gradient. In the forest tundra *E. glacialis* was replaced by the subarctic species *E. lamellatus*. The dominant species in the tundra and south tundra zones, *D. pulex* complex, was replaced in forest tundra by *Daphnia longispina* agg.

#### Relationships between subfossil cladoceran assemblages and environmental factors

Temperature has been identified as an important factor in the structuring of cladoceran assemblages in Finnish Lapland (Korhola 1999; Sarmaja-Korjonen et al. 2006), Norway (Hessen et al. 2006) and the Yukon and Northwest Territories, Canada (Swadling et al. 2000; Sweetman et al. 2010). This is in agreement with our data. We found that  $T_{\text{July}}$  was significantly correlated with the distribution of subfossil Cladocera in the lakes of the northwestern Yakutia, and 17.4 % of the variance in the taxa data was explained by this variable. This finding implies that cladocerans can not only provide important insight into the impact of changing temperature conditions in northern aquatic ecosystems, but are also likely to be susceptible to future warming.

A second environmental factor that was identified as important for the cladoceran distribution in our lakes was water depth. Several previous studies have recognised the importance of lake depth in influencing cladoceran communities (Korhola 1999; Korhola et al. 2000; Sarmaja-Korjonen and Alhonen 1999). In addition, subfossil cladoceran remains have been previously used by palaeolimnologists to reconstruct changes in the lake depth (Sarmaja-Korjonen and Alhonen 1999). Shallower lakes are typically smaller and more homogeneous but have a larger proportion of littoral habitats relative to deeper lakes (Keller and

Conlon 1994). Accordingly, the abundance of littoral taxa in shallow lakes is higher, while a relatively high pelagic cladoceran abundance was found in deeper lakes.

The correlation between the  $\text{Si}^{4+}$  ion concentration and structure of subfossil Cladocera communities found in the lakes of the Anabar region can be indirectly explained by the trophic relationships between cladocerans and diatoms. Diatoms are often the dominant group of phytoplankton in Arctic and subarctic lakes. This also was shown for the region of our investigation, the Anabar river basin (Gabyshev and Gabysheva 2010). It is known that there is a direct link between the seasonal diatom dynamics and changes in the dissolved silica and phosphorus content of the water (Rossolimo 1971). Silica can be a limiting factor for the development of diatom algae that use Si to produce siliceous frustules. The quantity of diatom algae influences the grazing conditions for some Cladocera species that use them as their primary diet component. For example, the diet of *Eurycerus* spp. consists primarily of diatoms (*Gomphonema* spp. Ehrenberg (1832), *Tabellaria* spp. Grunow (1868)) according to Frey (1973). A similar interrelation between the Si concentration and Cladocera community structures was found in the small, high-mountain lakes of Switzerland, which have similar ecological conditions to Arctic and subarctic lakes (Lotter et al. 1997). In our investigation, lake conditions were favourable for the development of, and in certain cases, the dominance of diatom production despite the low content of Si in the water (0.09–1.29 mg L<sup>-1</sup>, Table 1) (Gabyshev and Gabysheva 2010). Thus, with the shortage of biogenic elements in northern water bodies, the indirect influence of Si concentrations on hydrobiont communities can be expected.

The sulphate ( $\text{SO}_4^{2-}$ ) concentrations show relationships with distribution of the Cladocera in our study. The same was found in south-central Ontario (Canada) (DeSellas et al. 2008). Our finding could be connected to the negative water balance in the region and requires further investigations.

We found essential changes in the subfossil Cladocera communities across the small temperature gradient, which is two degrees, crossing the tree line in northwestern Yakutia. Assuming temperatures will rise within the range forecasted by the IPCC (2007), the biological communities of the subarctic tundra are likely to move northward and the northern most

communities of the Arctic tundra are likely to be lost. Thus the Arctic cladoceran communities will undergo significant changes and species with strict circumpolar distribution (*E. glacialis*) might disappear from this territory entirely.

The investigation of cladoceran assemblages in northwestern Yakutian lakes has demonstrated the potential of this group of hydrobionts as an indicator of the ecological state of both water bodies and of the changes caused by climate change occurring in the ecosystem. The results obtained encourage further work to create a regional cladoceran-based temperature model appropriate for the Arctic regions of Russia as a whole and Yakutia in particular.

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