



# Climate controls on the Holocene development of a subarctic lake in northern Fennoscandia



Marttiina V. Rantala <sup>a,\*</sup>, Tomi P. Luoto <sup>a</sup>, Jan Weckström <sup>b</sup>, Marie-Elodie Perga <sup>c</sup>,  
Milla Rautio <sup>d</sup>, Liisa Nevalainen <sup>e</sup>

<sup>a</sup> University of Helsinki, Department of Geosciences and Geography, P.O. Box 64 (Gustaf Hållströmin katu 2), 00014, Finland

<sup>b</sup> University of Helsinki, Department of Environmental Sciences, Environmental Change Research Unit (ECRU), P.O. Box 65 (Viikinkaari 1), 00014, Finland

<sup>c</sup> French National Institute for Agronomical Research (INRA), 75 Avenue de Corzent, BP 511, 74203, Thonon les Bains, France

<sup>d</sup> Université du Québec à Chicoutimi, Département des Sciences Fondamentales, Centre for Northern Studies (CEN) and Groupe de Recherche Interuniversitaire en Limnologie (GRIL), 555 boulevard de l'Université Chicoutimi, Québec G7H 2B1, Canada

<sup>e</sup> University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35 (Survontie 9), 40014, Finland

## ARTICLE INFO

### Article history:

Received 10 February 2015

Received in revised form

27 August 2015

Accepted 31 August 2015

Available online 11 September 2015

### Keywords:

Holocene climate

Subarctic lakes

Paleohydrology

Organic carbon

Stable isotopes

Diatoms

Cladocera

## ABSTRACT

Climate exerts strong control over the functioning of northern freshwater ecosystems, yet their resilience and responses to climate forcing may vary. We examined postglacial development patterns in subarctic Lake Vårdöaijävri to discern the impact of direct climate controls, catchment influence, and ontogenic processes on the ecological functioning of the lake over the Holocene. Subfossil diatom assemblages together with the elemental and stable isotopic ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) composition of sediment organic matter were used to examine climate-induced changes in the structure of the phototrophic community and transport of terrestrial organic matter from the catchment. Stable isotopic composition ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of subfossil Cladocera (Crustacea) was further used to assess how the changes were reflected higher up the food web. The diatom assemblages and sediment geochemistry closely mirrored the established climate patterns of the Holocene, confirming the strong climate coupling evidenced by earlier studies from lakes across the circumpolar Arctic. Our record indicates overarching influence of moisture fluctuations, superimposing the impact of light limitation by terrestrial organic carbon and temperature-driven alterations to lake physical regimes, which have been emphasized by recent research. The millennial changes in humidity were reflected as shifting dominance between planktonic and benthic diatom life forms, related to changes in the depth of the water column, vertical mixing patterns, and underwater light conditions. Despite the marked regime shifts at the base of the food web, zooplankton carbon utilization was little changed over the Holocene, likely attributable to selective feeding strategies. Overall, our results propose that the projected increases in precipitation in high-latitude regions may have marked impact on the structure and functioning of aquatic communities in shallow subarctic lakes.

© 2015 Elsevier Ltd. All rights reserved.

## 1. Introduction

A key feature of subarctic landscapes across the Northern Hemisphere is the myriad of small lakes and ponds that are characteristically oligotrophic, dilute and shallow (Rautio et al., 2011). In relation to these attributes, the lakes are distinct in their sensitivity

to climate fluctuations, and in their close connection to terrestrial processes via strong catchment-lake coupling. The functioning of the northern aquatic ecosystems is often strongly regulated by direct climate influences on the length of the growing season, hydrological conditions, and the thermal properties of the water column. Recent studies have emphasized the influence of temperature on high-latitude lakes that are covered by ice through much of the year (Smol et al., 2005; Weckström et al., 2014). Even small changes in the timing and duration of the ice free period may induce notable changes in the ecological structure of the lakes through altered light and nutrient availability, and thermal regimes. Widespread shifts from benthic and/or heavy

\* Corresponding author.

E-mail addresses: [marttiina.rantala@helsinki.fi](mailto:marttiina.rantala@helsinki.fi) (M.V. Rantala), [tomi.luoto@helsinki.fi](mailto:tomi.luoto@helsinki.fi) (T.P. Luoto), [jan.weckstrom@helsinki.fi](mailto:jan.weckstrom@helsinki.fi) (J. Weckström), [marie-elodie.perga@thonon.inra.fr](mailto:marie-elodie.perga@thonon.inra.fr) (M.-E. Perga), [Milla.Rautio@uqac.ca](mailto:Milla.Rautio@uqac.ca) (M. Rautio), [liisa.nevalainen@jyu.fi](mailto:liisa.nevalainen@jyu.fi) (L. Nevalainen).

tychoplanktonic diatom taxa to small planktonic life forms have been observed in association with warming temperatures and increased thermal stability (Rühland et al., 2015). Similarly, changes in humidity affect the physical properties of lakes, including depth, mixing conditions, and solar radiation attenuation in the water column (e.g., Moser et al., 2000; Korhola and Weckström, 2004; Korhola et al., 2005), although the resultant alterations to aquatic ecosystem functioning have been less extensively investigated.

In addition to their susceptibility to direct climate impacts, the small and shallow northern freshwater ecosystems are sensitive to climate influences mediated through the catchment. Here, terrestrial (allochthonous) organic carbon plays a key role as it governs light attenuation and thermal properties of the water column, depth of the photic layer, and exposure to harmful ultraviolet (UV) radiation in lakes (Laurion et al., 1997; Pienitz and Vincent, 2000; Karlsson et al., 2009; Nevalainen et al., 2014). Consequently, organic carbon exerts strong control over lake productivity (Karlsson et al., 2009), community structure and food web dynamics (Rautio and Vincent, 2007; Rosén et al., 2009), as well as lake metabolic balance (Jansson et al., 2008; Tranvik et al., 2009). The input of terrestrial carbon into subarctic lakes situated above the tree line is generally low because the barren landscapes provide few carbon sources. However, the often dilute, benthic-dominated ecosystems (Rautio et al., 2011) are sensitive to even small variations in allochthonous carbon input (Laurion et al., 1997; Snucins and Gunn, 2000). Moreover, lakes in ecotonal regions affected by tree line oscillations, or those surrounded by extensive wetlands, may undergo marked fluctuations in the export of terrestrial organic matter (e.g., Seppä and Weckström, 1999; Rosén, 2005; Reuss et al., 2010; Jones et al., 2011). Associated changes in the spectral attenuation of solar radiation in the water column and in the balance between aquatic autotrophic and heterotrophic production may significantly alter the ecological structure of the lakes, and their carbon balance (Jansson et al., 2008; Karlsson et al., 2009; Rautio et al., 2011).

Recent studies have already evidenced changes in the length of the growing season and thermal stratification (Smol et al., 2005; Rühland et al., 2015) driven by the 20th century warming, and the proposed increases in precipitation in high-latitude regions may similarly affect the physical regimes in lakes. Moreover, enhanced surface runoff, raised ground water levels, and expansion of wetland areas related to increased humidity are likely to increase the input of terrestrial organic matter into lakes (Forsberg, 1992). Increasing temperatures are also projected to advance the limits of vegetation zones north- and upwards along latitudinal and altitudinal gradients (Pienitz and Vincent, 2000), with potential major impacts on subarctic lake ecosystems, particularly on those influenced by the advancing northern tree line. Although their effects may be displayed in a number of ways, it seems evident that the increasing warmth and moisture in high-latitude regions will affect the functioning of the sensitive northern lakes. Comprehensive long-term postglacial records provide us tools to better understand the magnitude, pace and mechanisms of climate-induced change on aquatic ecosystem functioning.

Here, several biogeochemical proxies were used to decipher the ecological development of subarctic Lake Várddoaijávri since the late Quaternary glaciation. With this study, we aim to address the differential roles of direct climate influences and those mediated through catchment-lake coupling in controlling ecosystem functioning and carbon dynamics in shallow subarctic lakes above the tree line. Carbon and nitrogen content in the sediment organic matter, C/N ratio, and the isotopic composition of bulk organic matter ( $\delta^{13}\text{C}_{\text{OM}}$ ,  $\delta^{15}\text{N}_{\text{OM}}$ ) were investigated to assess changes in the quantity and origins of organic carbon. Subfossil diatom assemblages were used to study changes in the phototrophic community

structure and to quantitatively infer variations in lake-water dissolved organic carbon (DOC). The isotopic composition of subfossil cladoceran exoskeletons ( $\delta^{13}\text{C}_{\text{ZOO}}$ ,  $\delta^{15}\text{N}_{\text{ZOO}}$ ) was examined to identify changes in zooplankton feeding patterns. We hypothesise that the climate oscillations of the Holocene have largely shaped the postglacial development of Lake Várddoaijávri. Moreover, it is presumed that direct climate impacts, related to millennial variations in temperature and precipitation, have exerted fundamental control over the ecological development of the lake by altering the physical properties (ice cover, depth, vertical mixing, solar radiation attenuation) of the lake. It is further hypothesized that climate-driven changes in the transport of terrestrial organic carbon have influenced underwater light regimes and, consequently, resource availability for the diatom and zooplankton communities. The results may provide valuable information for the prediction of future development patterns of similar shallow oligotrophic lakes that are widespread in the subarctic regions of the Northern Hemisphere.

## 2. Material and methods

### 2.1. Study site

Lake Várddoaijávri is located in the northernmost part of the Finnish Lapland (Fig. 1) in the rocky outcrops of the barren tundra. The lake was formed some 11,500 years ago following the retreat of the late Weichselian ice sheet (Lundqvist, 1986), and presently lies at an elevation of ca. 400 m.a.s.l. The catchment is situated on a granulite belt and the thin soil cover, where present, supports patches of moss, lichen and small-sized shrubs. The tree line, indicated by the growth of Scots pine (*Pinus sylvestris*), lies approximately 300 m below the surface of Lake Várddoaijávri. The limit for mountain birch (*Betula pubescens* spp. *czerepanovii*), commonly found in Lapland, is located some 200 m below the surface of the lake. The lake has a surface area of ca. 26 ha and a maximum depth of ca. 5 m. The catchment area is relatively small (ca. 150 ha) compared to the lake area and there are couple of minor streams flowing into the lake, with no evident outlets. The soil is paludified around the north-eastern corner of the lake, probably indicating a seasonal floodway. Limnological measurements performed in 2005 indicate a pH of 6.3 and the lake is characterized as ultraoligotrophic. The region is featured by sub-arctic climate, with an annual mean temperature of ca. 2.6 °C and a mean July temperature of ca. 11.3 °C in the area near the lake extrapolated from measurements at the Kevo meteorological station. More detailed description of the limnology of the lake and features of the catchment can be found in Luoto and Sarmaja-Korjonen (2011) and Luoto et al. (2014).

### 2.2. Sediment core collection

The 296-cm sediment profile was obtained from Lake Várddoaijávri in April 2005 using a Russian peat corer. Six sequential sediment cores were retrieved and correlated chronologically based on sediment magnetic properties and visual assessment of the lithology of the partly overlapping cores. The sediment cores were subsampled at 1-cm intervals. The sediment profile was AMS  $^{14}\text{C}$  dated using bulk sediment organic matter as terrestrial macrofossils were absent. Based on high minerogenic content of the lowermost section of the sediment sequence, it is presumed that the lake was likely formed following the retreat of the Weichselian ice sheet from the area ca. 11,500 cal yr BP (Lundqvist, 1986). However, the Early Holocene chronology of the sediment core should be considered cautiously due to uncertainties in the exact timing of the ice retreat in the area, and as it cannot be affirmed that the lake was formed during the deglaciation period,

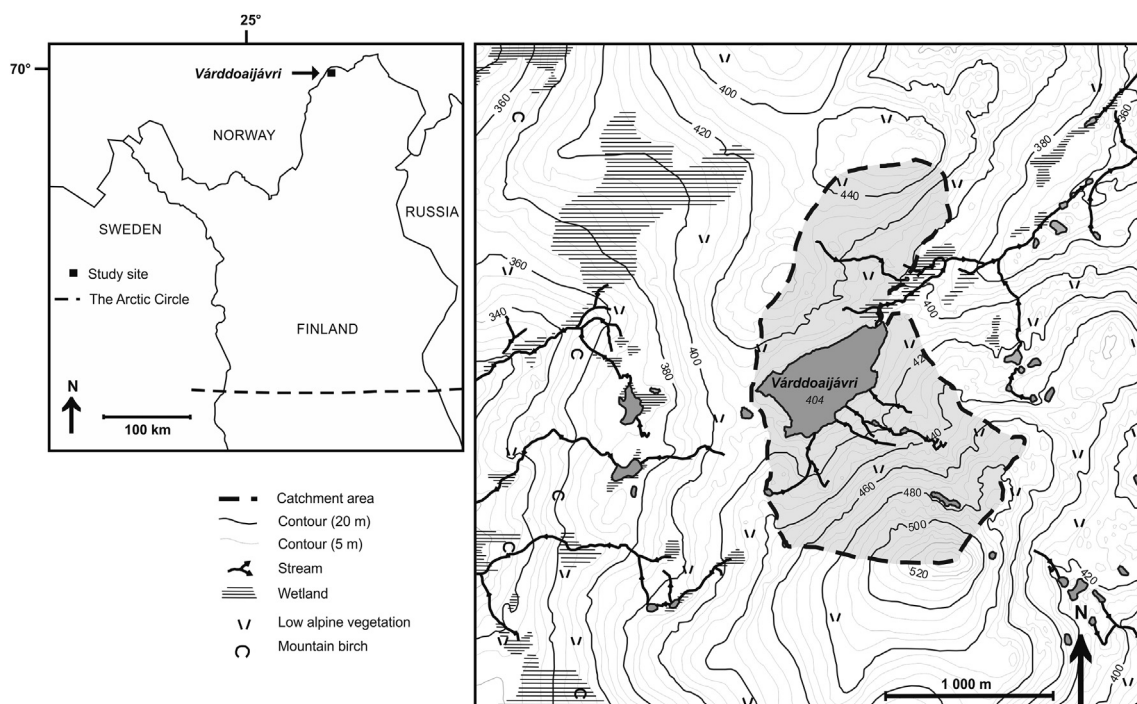


Fig. 1. Location of Lake Várddoaijávri in the Finnish Lapland and catchment characteristics.

as discussed in [Luoto and Sarmaja-Korjonen \(2011\)](#). For more detailed description of sampling procedures, core lithology and radiocarbon analysis, please see [Luoto and Sarmaja-Korjonen \(2011\)](#). In this study, every fifth sample was analysed for diatom assemblages and the elemental and isotopic composition of sediment organic matter. Stable isotopic analyses using subfossil cladoceran exoskeletons were performed with a sample interval of 15 cm.

### 2.3. Diatom analysis

Samples for diatom analysis were prepared following [Battarbee et al. \(2001\)](#). Organic matter was removed by oxidizing freeze-dried samples with water/hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) solution, and mineral matter was cleaned using physical techniques. Fine minerogenic fraction was reduced by allowing the diatom valves and the coarse matter to settle for 2 h in 1 L beakers (~15 cm), after which the supernatant containing the clayey particles was carefully decanted. The washing procedure was repeated, reducing the settling time to 1 h for visibly clear samples. Subsequently, coarse minerogenic matter was removed by swirling the sample suspension in a beaker in order to centre the large grains at the bottom of the beaker, followed by collecting the supernatant containing the diatom valves. Small amounts of the cleaned diatom-water suspensions were dried and mounted with Naphrax® on microscope slides. From each sample a minimum of 300 diatom valves were counted and identified with Olympus CX31 at 1000× magnification. Identification was mainly based on the diatom flora of [Krammer and Lange-Bertalot \(1986, 1988, 1991a, 1991b\)](#).

The diatom data were used to reconstruct past variability in lake-water total organic carbon (TOC) using a calibration dataset from northern Finland ([Seppä and Weckström, 1999](#)). The dataset comprises 98 lakes and has a TOC gradient of 1.3–12.6  $\text{mg L}^{-1}$  with a mean value of 5.4  $\text{mg L}^{-1}$ . The reconstruction was carried out with C2 data analysis program ([Juggins, 2003](#)) using partial least squares (PLS) regression. The model had a jack-knifed coefficient of

determination ( $R^2_{\text{jack}}$ ) of 0.37 and root mean squared error of prediction (RMSEP) of 2.3  $\text{mg L}^{-1}$ . The inferred TOC concentrations were converted to DOC by multiplying the obtained values by 0.9 (e.g. [Sobek et al., 2007](#)). Rare taxa approach was used to assess the fit between the calibration data set and the fossil assemblages. Taxa having a Hill's  $N_2$  value below 5 are considered 'rare' in the calibration set, and fossil samples containing more than 15% rare taxa are considered poorly represented by the calibration data set.

Principal component analysis (PCA) was used to identify temporal patterns in the diatom community for comparison with the diatom-inferred DOC and other studied variables. Taxa present in less than 5 samples with a mean abundance <1% were excluded from the analysis. The analysis was run using Canoco 5 ([Šmilauer and Lepš 2014](#)). Additionally, the ratio between planktonic and benthic taxa was calculated to depict changes in the community structure.

### 2.4. Stable isotope analyses

Prior to the carbon and nitrogen isotope analyses from sediment bulk organic matter ( $\delta^{13}\text{C}_{\text{OM}}$  and  $\delta^{15}\text{N}_{\text{OM}}$ ), the fresh sediment was subjected to acid fumigation to remove carbonates. Subsamples of ca. 10 mg of the freeze-dried, homogenized sediments were weighed into silver (Ag) capsules, moistened by adding ca. 50  $\mu\text{L}$  of Milli-Q® water to each sample, and placed inside a vacuum desiccator. The desiccator was vacuum-sealed and the samples were exposed to HCl (12 M) vapour for 6 h, after which the samples were dried at 60 °C for 4 h. The analysis was performed at the University of California, Davis, Stable Isotope Facility (USA) using an Elementar Vario elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The results are expressed as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) described as  $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ , where R equals  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ , respectively, and the standards used were Vienna Pee Dee Belemnite for carbon and atmospheric nitrogen for nitrogen. Additionally, the analysis

yielded the proportions of carbon (C%) and nitrogen (N%) in organic matter allowing also the calculation of the carbon-to-nitrogen ratio (C/N ratio) that can be used as an indicator of organic matter sources (Meyers and Teranes, 2001). The results are expressed as C/N atomic ratios (Meyers and Teranes, 2001).

Preparation of cladoceran samples for stable carbon and nitrogen isotope analyses ( $\delta^{13}\text{C}_{200}$  and  $\delta^{15}\text{N}_{200}$ ) was performed following Perga (2010). Freeze-dried sediment samples were heated for 30 min in KOH (10%) solution to remove organic material, after which the sediment was retained on a 100  $\mu\text{m}$  filter cup and rinsed thoroughly with deionized water. Additionally, the samples were treated with 1 M HCl to remove possible carbonate coating, and mineral matter was removed by centrifugation. Approximately 1000 bosminid (mostly *Eubosmina longispina*) headshields and carapaces were picked under stereomicroscope into Milli-Q® water from each sample in order to reach a minimum of 0.2 mg weight for the analysis. The bosminid-water solutions were filtered onto 25 mm GF/F filters, dried and weighted to ensure adequate sample mass. The remains were scraped from the filters into Sn-capsules that were compressed to suitable size. The analysis was carried out at the Stable Isotope Laboratory of the Department of Biological and Environmental Science, University of Jyväskylä, with a FlashEA 1112 elemental analyser coupled with a Thermo Finnigan DELTA plus Advantage mass spectrometer (Thermo Electron Corporation, Waltham, MA, USA). The results are expressed as delta notations as described above.

### 3. Results

#### 3.1. Diatom community composition and lake-water DOC

The diatom flora identified from the sediment core comprised a total of 138 taxa. The most abundant genera were *Frustulia*, *Aulacoseira* and *Pinnularia*. The lowermost sequence of the profile was characterized by few dominant species of Fragilariaceae and *Aulacoseira* with major fluctuations in their relative abundances (Fig. 2).

*Staurosira construens* and *Staurosirella pinnata* dominated the two lowermost samples, and were soon replaced first by *Aulacoseira italica* var. *valida* and shortly after by *Stauroforma exiguiformis*. From ca. 9000 cal yr BP onwards, the above species nearly vanished from the record and the community became more diverse as several species of *Frustulia*, *Brachysira*, *Eunotia* and *Nitzschia*, among other benthic forms (Fig. 3), emerged. The community was stable during the following five millennia, with particularly high abundance of *Frustulia rhomboides* var. *saxonica* f. *undulata* and *Brachysira brebissonii* f. *brebissonii*. Around 4000 cal yr BP, the diatom community underwent major changes as *Aulacoseira italica* var. *valida* began to increase in abundance, along with few other *Aulacoseira* species, while *Frustulia*, *Brachysira*, *Eunotia*, *Cymbella* and *Nitzschia* declined. Other distinct features were a sudden emergence of *Pinnularia viridis* around 4500 cal yr BP and a brief increase in *Achnanthes* and *Navicula* at ca. 2000 cal yr BP. In the topmost sequence (ca. 1000 cal yr BP–present), the relative abundance of benthic taxa began to increase.

The diatom-inferred DOC varied between 3.6 and 5.9 mg L<sup>-1</sup> in the record (Fig. 3). Elevated concentrations were inferred for the bottom-most sequence and for the upper half of the profile (ca. 4000 cal yr BP onwards), while the period between ca. 10,000–4000 cal yr BP showed generally slightly lower values. Rare taxa analysis identified 13 samples (Fig. 3) containing more than 15% of taxa that were rare (Hill's N2 < 5) in the calibration data set, suggesting that the respective DOC values should be considered with particular caution.

The first two PCA axes explained 31% and 23% of the variation, respectively. The PCA axis 1 values showed a pattern very similar to that of the ratio between planktonic and benthic diatom taxa (Fig. 3), with elevated values in the bottom-most samples and in the upper half of the profile.

#### 3.2. Carbon, nitrogen and C/N ratio

The variation in the relative proportions (%) of carbon (C) and

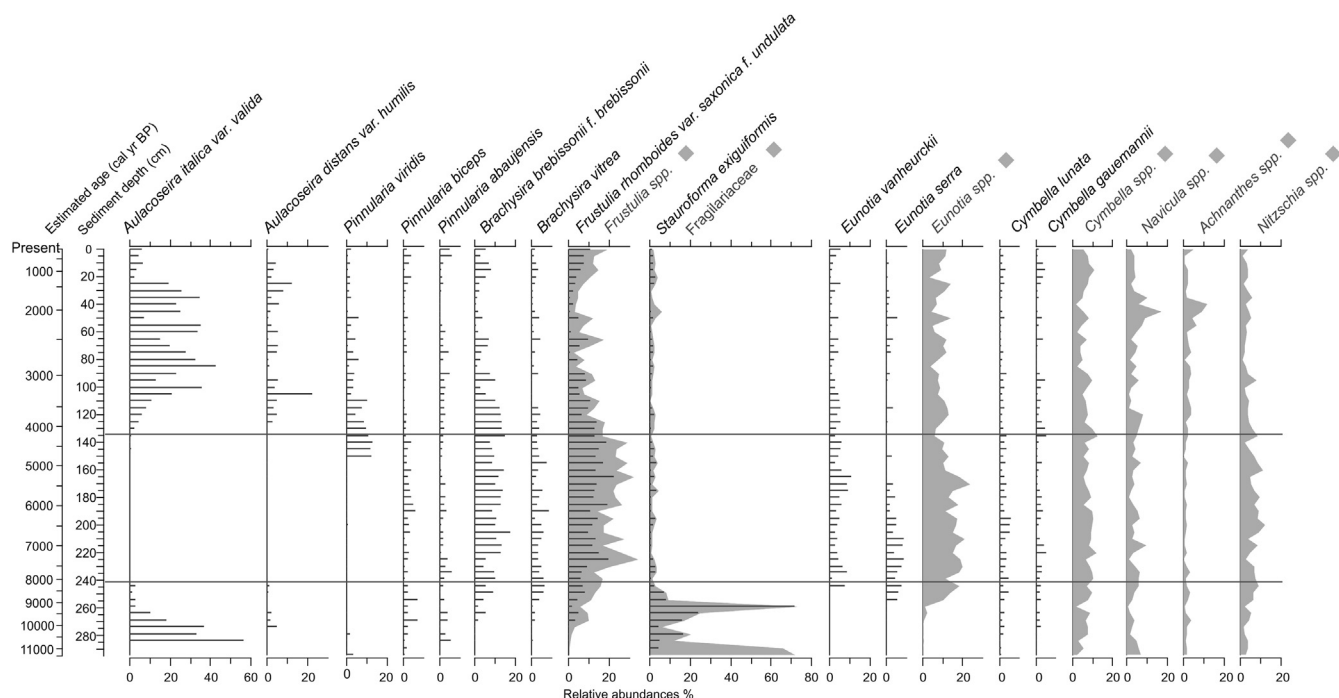
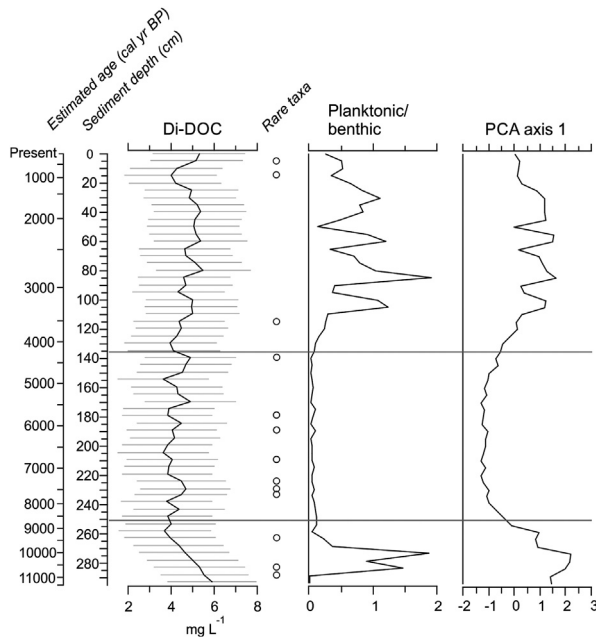


Fig. 2. Diatom stratigraphy of Lake Värddoajärvi showing the relative abundances of the most common taxa ( $N > 30$ , mean % abundance  $> 2$ ). The horizontal lines divide the stratigraphy into Early (ca. 11,700–8200 cal yr BP), Middle (8200–4200 cal yr BP) and Late Holocene (4200 cal yr BP–present), following Walker et al. (2012).





**Fig. 3.** Diatom-inferred lake-water dissolved organic carbon (DOC) with sample-specific errors, ratio between planktonic and benthic diatom taxa, and principal component analysis (PCA) axis 1 scores for the diatom stratigraphy in Lake Várddoajávri. Based on rare taxa analysis, samples with more than 15% of taxa that are rare in the calibration data set are indicated with open circles. The horizontal lines divide the stratigraphy into Early (ca. 11,700–8200 cal yr BP), Middle (8200–4200 cal yr BP) and Late Holocene (4200 cal yr BP–present), following Walker et al. (2012).

nitrogen (N) in the sediment sequence (Fig. 4) followed a very similar pattern. Lowest values were found at the bottom of the profile, followed by a rapid increase around 9500 cal yr BP, and subsequent long-term decline. The decline was replaced by a gradually increasing trend around 3000 cal yr BP. The C/N ratio

(Fig. 4) varied between 10.3 and 13.3 and showed an overall gradual decline in the sediment profile. Minimum values were reached ca. 2500 cal yr BP, followed by a minor increase towards the surface.

### 3.3. Stable carbon and nitrogen isotopes in bulk organic matter

$\delta^{13}\text{C}_{\text{OM}}$  values varied between  $-19.1\text{‰}$  and  $-23.5\text{‰}$  (Fig. 4). The values were declining in the lowermost samples until around 9500 cal yr BP, followed by relatively constant values until ca. 4000 cal yr BP. Then, a declining trend occurred until ca. 1500 cal yr BP when values rose by approximately one per mill and remained nearly constant in the topmost sequence.

The  $\delta^{15}\text{N}_{\text{OM}}$  values (Fig. 4) were relatively high in the lower end of the profile. Between ca. 8500 and 5000 cal yr BP, the values remained consistent at around 1‰, then declined to the minimum of ca. 0.5‰ at 55 cm (ca. 2300 cal yr BP), followed by a marked increase towards the surface.

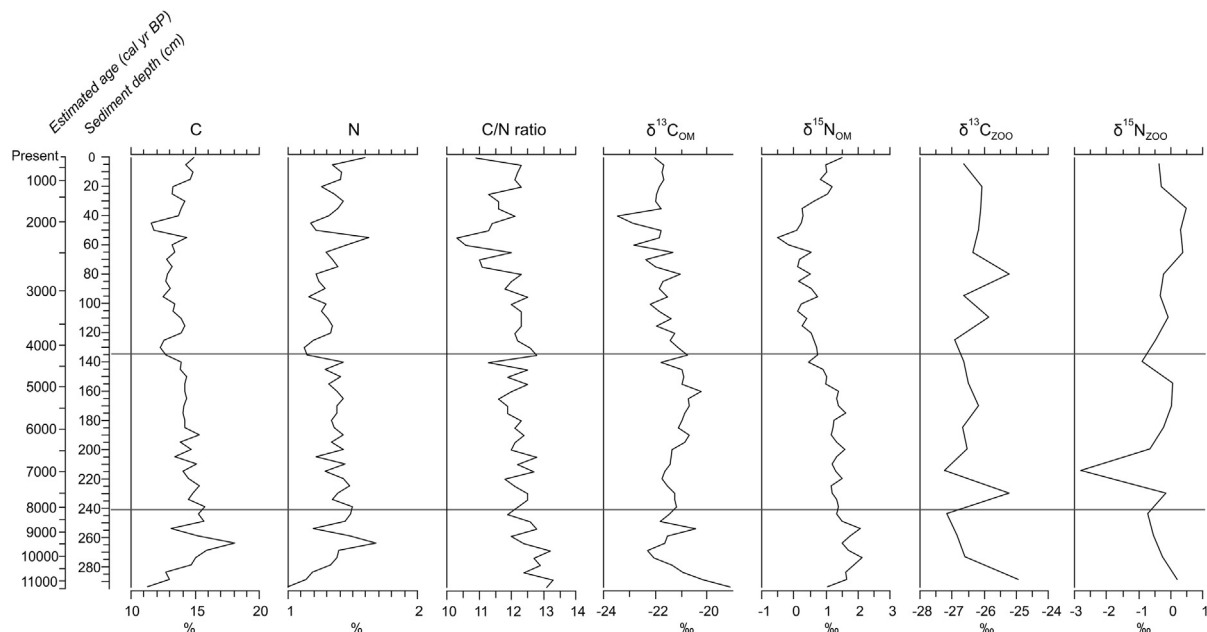
### 3.4. Stable carbon and nitrogen isotopes from subfossil cladoceran exoskeletons

The  $\delta^{13}\text{C}_{\text{ZOO}}$  values varied between  $-24.9$  and  $-27.2\text{‰}$ , both the lowest and the highest values occurred in the bottom half of the core (Fig. 4). Overall, the variation was small, with no conspicuous trends. The values between ca. 4000–1500 cal yr BP, were generally slightly higher than in the lower end of the profile.

The  $\delta^{15}\text{N}_{\text{ZOO}}$  profile showed also little variability (Fig. 4), the values ranging between 0.5 and  $-2.8\text{‰}$ . The minimum value, distinct from the rest of the variability, was recorded for the sample at 215 cm ( $\sim 7000$  cal yr BP). Slightly elevated values were inferred between ca. 3500–1500 cal yr BP.

## 4. Discussion

Numerous studies have demonstrated the importance of climate in shaping the development of northern aquatic ecosystems, although the susceptibility and responses of individual ecosystems



**Fig. 4.** Sediment geochemistry in Lake Várddoajávri, including carbon (C) and nitrogen (N) contents expressed as percent of dry sediment mass, C/N atomic ratio, stable carbon and nitrogen isotopic composition of bulk organic matter ( $\delta^{13}\text{C}_{\text{OM}}$  and  $\delta^{15}\text{N}_{\text{OM}}$ ) and of subfossil cladoceran remains ( $\delta^{13}\text{C}_{\text{ZOO}}$  and  $\delta^{15}\text{N}_{\text{ZOO}}$ ). The horizontal lines divide the stratigraphy into Early (ca. 11,700–8200 cal yr BP), Middle (8200–4200 cal yr BP) and Late Holocene (4200 cal yr BP–present), following Walker et al. (2012).

to climate forcing may vary considerably (e.g., Smol et al., 2005; Fritz and Anderson, 2013). In particular, temperature influence on the length of the growing season and the multitude of related physical and chemical changes (Rühland et al., 2015), and climate impact via light limitation by terrestrial organic matter (Karlsson et al., 2009) have been emphasized in recent years. Our record confirms the pivotal role of climate, yet stresses in particular the influence of humidity and associated variation in the physical properties of the lake. The most distinct regime shifts in Lake Várddoaijávri took place roughly in accordance with the major Holocene climate transformations and are discussed within the context of the established climate patterns of the Early, Middle and Late Holocene.

#### 4.1. Early Holocene (ca. 11,700–8200 cal yr BP)

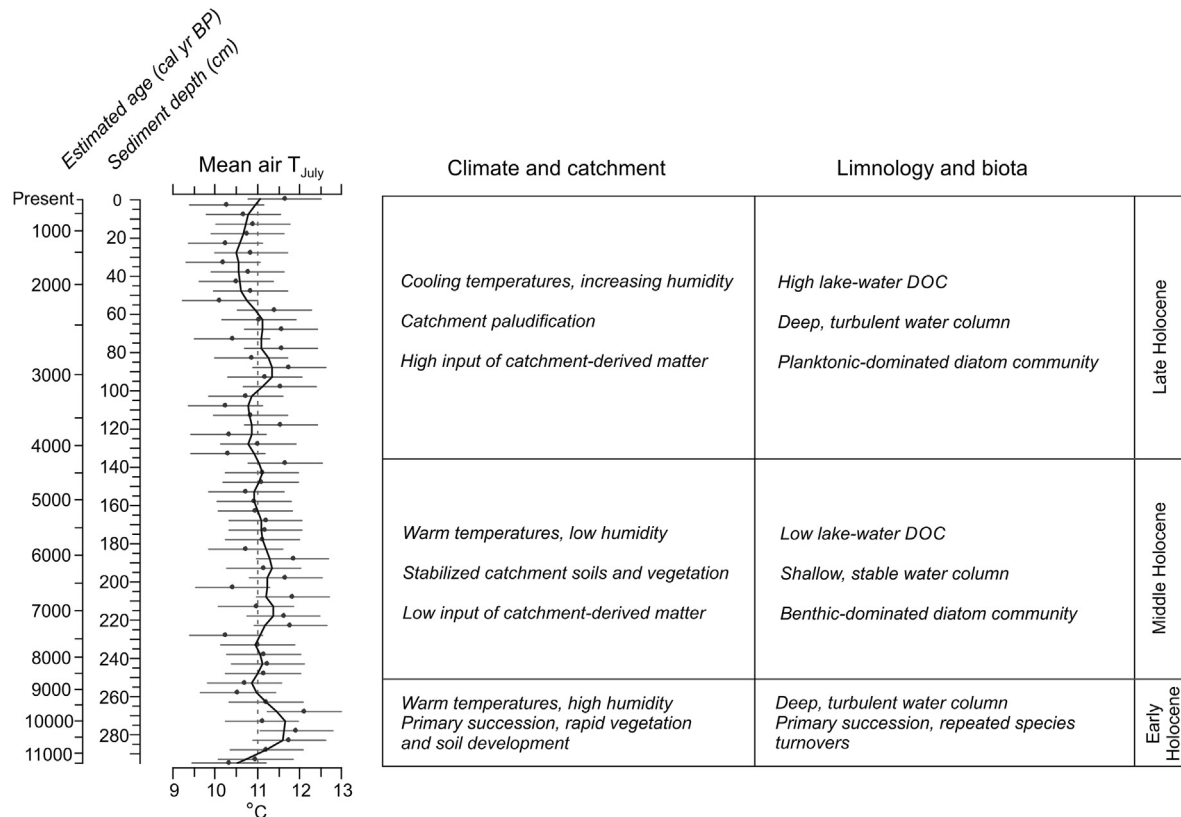
The early development patterns in Lake Várddoaijávri resemble those commonly inferred from lake records in glaciated regions, reflecting the terrestrial and aquatic primary succession initiated by the glacial retreat and the rapid postglacial climate transition (Engstrom et al., 2000; Fritz and Anderson, 2013). The initial low carbon and nitrogen contents at the bottom of the sediment sequence (Fig. 4) reflect high mineral erosion from the deglaciated terrain (Luoto and Sarmaja-Korjonen, 2011), while the subsequent increases imply rapid catchment development at the base of the profile. Progressive accretion of organic matter in the catchment (Engstrom et al., 2000) may have contributed to the rise in sediment carbon and nitrogen contents, yet the sharp increasing patterns are probably largely driven by improved binding of mineral soils by catchment vegetation. Previous studies from the Eurasian subarctic have suggested relatively high algal production during the early postglacial period (Reuss et al., 2010; Jones et al., 2011; Fritz and Anderson, 2013), attributed to the enhanced nutrient flux from the newly exposed soils (Engstrom et al., 2000). In contrast, the elevated C/N values at the bottom of the profile in Lake Várddoaijávri (Fig. 4) indicate high relative share of catchment-derived matter, probably reflecting relatively low production in the lake rather than high input of organic matter from the barren catchment. The distinction between the sites is likely attributable to the infertile landscape surrounding Lake Várddoaijávri (Fig. 1).

In common with the sediment geochemistry, the diatom assemblages indicate rapid community succession during the Early Holocene (Fig. 2) mirroring the early postglacial climate and catchment conditions. The initial dominance of typical pioneering taxa of Fragilariaceae reflects the extreme and instable environmental conditions following the glacial retreat (Seppä and Weckström, 1999; Bigler et al., 2002; Korhola and Weckström, 2004). Diatom communities dominated by few benthic fragilarioids have also been associated with cool temperatures and extensive ice cover periods in lakes across the Northern Hemisphere (Smol et al., 2005; Rühland et al., 2015), and may similarly in the present record reflect the cool early postglacial climate that limited the establishment of algal habitats. Several records from glacial lakes in the circumpolar Arctic indicate elevated lake-water pH during the early lake ontogeny, related to readily available base cations in the exposed soils and low availability of organic acids (Seppä and Weckström, 1999; Engstrom et al., 2000; Korhola and Weckström, 2004). As lake-water pH commonly has a strong control over diatom community succession, the transient alkaline period and subsequent decline related to progressive catchment leaching may have influenced the diatom assemblages. However, studies from Fennoscandian tundra show that the overall change in lake-water pH during the Holocene is commonly gradual and small in scale (Korhola and Weckström, 2004), underlining the role of other environmental factors driving the floral succession. Most

likely the cool climate together with the strong mineral erosion from the catchment, associated high water turbidity, and scarcity of organic substrate constrained habitat availability during the early development of the lake, allowing the emergence of few resilient species. In accordance with recent studies investigating the ontogenic trajectories of glacial lakes (Engstrom et al., 2000; Fritz and Anderson, 2013), our record thus supports the notion of strong catchment influence during early lake development.

A previous chironomid-inferred temperature reconstruction from Lake Várddoaijávri (Luoto et al., 2014) showed that the initial cold phase following the glacial retreat was rapidly followed by a temperature increase with Holocene maxima reached between ca. 11,000–10,000 cal yr BP (Fig. 5). Similarly, warm Early Holocene temperatures have been inferred from other northern Eurasian sites (Kultti et al., 2004; Jones et al., 2011; Engels et al., 2014). The abrupt increase and brief dominance of the planktonic *Aulacoseira italica* var. *valida* between ca. 10,500–9500 cal yr BP (Fig. 2) coincides with the period of inferred maximum temperatures (Fig. 5) and may indicate a connection with the climate transition. In support, recent studies examining the influence of the 19th century global warming on freshwater ecosystems (e.g., Smol et al., 2005; Rühland et al., 2015) have emphasized the importance of temperature in controlling the ecology of northern lake ecosystems. Temperature-driven changes in the physical properties of the water column, particularly the timing and duration of the ice free period and associated changes in resource and habitat availability, have been shown to exert fundamental control over aquatic communities in high-latitude regions, and are often sensitively reflected in diatom communities. On the other hand, these studies also highlight the heterogeneity of ecosystem responses to environmental forcing, dependent on the characteristics of the lake basin and catchment, as well as species life history traits.

In Lake Várddoaijávri, the overall variation in the diatom community was related to the fluctuating dominance between large planktonic *Aulacoseira italica* var. *valida* (English and Potapova, 2010) and diverse benthic taxa (Figs. 2 and 3). Adequate depth and vertical mixing of the water column are fundamental prerequisites for the heavy planktonic species to flourish, allowing buoyancy and adequate nutrient supply (e.g., Bigler et al., 2002; Rosén et al., 2009; Rühland et al., 2015). These functional traits thus imply that the diatom regimes shifts in Lake Várddoaijávri are related to changes in the thermal structure and turbulence of the water column. Owing to the relatively shallow depth and transparency, the lake has likely remained isothermal even during periods of elevated lake level or increased DOC concentrations (Snucins and Gunn, 2000). Regardless, enhanced living conditions in the pelagic zone would have provided competitive advantage for the planktonic species. In accordance, a study from northwestern Finnish Lapland by Sorvari et al. (2002) showed that in isothermal lakes temperature-driven regime shifts may take place between *Aulacoseira* and benthic algae, the latter becoming more dominant with increasing temperatures and thermal stability. In Lake Várddoaijávri, the elevated Early Holocene temperatures were accompanied by thriving pelagic habitats, which suggests overriding influence by other environmental factors that govern thermal structure and mixing in the water column. In addition to the warm temperatures, lake records from northern Fennoscandia indicate elevated water levels during the Early Holocene (Korhola and Weckström, 2004; Korhola et al., 2005; Luoto et al., 2014). It is likely that the emergence of the heavily silicified *Aulacoseira italica* var. *valida* in Lake Várddoaijávri thus reflects Early Holocene moisture conditions rather than temperature, as the heavily silicified frustules of the species depend on sufficient water column depth and high turbulence. Lower water retention capacity of the exposed catchment, and strong winds and spring snowmelt may



**Fig. 5.** Summary of the climatic and limnecological shifts in Lake Värddoajávri and the catchment, and a chironomid-based mean July air temperature reconstruction from Lake Värddoajávri (Luoto et al., 2014). The black curve indicates a locally weighted scatter plot smooth (lowess, span 0.1) and the dashed vertical line marks the mean inferred temperature over the Holocene.

have reinforced efficient vertical mixing of the water column. Moreover, extended ice-free period likely provided competitive advantage for the planktonic species (Weckström et al., 2014; Rühland et al., 2015). While the elevated C/N values (Fig. 4) implied relatively low primary production in the lake, enhanced nutrient input from the deglaciated catchment (Engstrom et al., 2000) may have promoted the emergence of the planktonic taxa, although the relative influence of possible nutrient enrichment cannot be traced with the data available.

The overall low species diversity during the Early Holocene, with communities dominated by benthic *Fragilariaceae* and *Aulacoseira italica* var. *valida*, probably also reflects the ability of these common species to find suitable ecological niches in the lake that was providing few growth substrate for algae. Similarly, the establishment of the diverse benthic community at the end of the Early Holocene (Figs. 2 and 3) may reflect natural diversification of habitats related to reduced mineral erosion and accretion of organic substrate in the lake. The benthic habitats are also restricted by light limitation, as highlighted by recent studies (e.g., Karlsson et al., 2009), which could have been induced by high water column turbidity or elevated DOC concentrations. High turbidity has been inferred from various sites in northern Fennoscandia related to high catchment erosion and strong winds during the early postglacial period (Korhola and Weckström, 2004), whereas increased loading of allochthonous coloured humic substances could have been induced by wetland development which has been shown to be intensive in subarctic Fennoscandia during the Early Holocene (Weckström et al., 2010). The timing of the elevated diatom-inferred DOC, between ca. 11,500–10,500 cal yr BP (Fig. 3), however implies that the diatom communities were governed by

confounding environmental factors during the early lake development, as it is improbable that the barren catchment would have produced high quantities of organic matter. Any changes in the underwater optical environment were thus likely superimposed on the primary aquatic succession, catchment processes and climate-driven changes in hydrological conditions. The rare taxa analysis identified three samples within the Early Holocene period that may have biased DOC values due to poor fit with between the modern calibration data set and the fossil samples (Fig. 3). Quantitative inferences should always be considered with certain caution due to potential distortion caused by confounding environmental variables and possible inaccuracies related to the use of the model to predict environmental conditions far back in time (Juggins, 2013). Yet, diatom assemblages have been used successfully to reconstruct variations in lake-water organic carbon (Pienitz et al., 1999; Pienitz and Vincent, 2000; Rantala et al., 2014), and previous studies suggest unique, independent relationship between organic carbon and diatom assemblages (Seppä and Weckström, 1999; Rosén et al., 2000).

The organic matter content of lake sediments in northern Fennoscandia is also commonly controlled by climate via changes in erosion rates and the accumulation and transport of terrestrial organic matter (Korhola and Weckström, 2004). In Lake Värddoajávri, the C/N values (mean ratio of ~12) suggests that the sediment organic matter is largely of autochthonous origin (Meyers and Teranes, 2001), with minor decline in the allochthonous component towards the present (Fig. 4). Additionally, the  $\delta^{13}\text{C}_{\text{COM}}$  values in the sediment organic matter (Fig. 4) resemble those typically associated with benthic primary production and related diffusion-limited  $\text{CO}_2$  uptake (Hecky and Hesslein, 1995),

supporting dominance of autochthonous sources. Lack of clear connection between the diatom community shifts (Figs. 2 and 3) and the elemental sediment geochemistry (Fig. 4) throughout the Holocene implies that, despite their strong influence on the algal community, the climate variations have not induced marked changes in the accumulation and sources of organic matter in the lake. The carbon isotopic signature of sediment organic matter (Fig. 4), on the other hand, seems to mirror the changing balance between different diatom life forms (Figs. 2 and 3) in the sediment profile. Though the patterns are not entirely synchronous, increases in  $\delta^{13}\text{C}_{\text{OM}}$  are clearly associated with benthic dominance and *vice versa*, with significant negative correlation ( $R = -0.64$ ,  $p < 0.001$ ) between the planktonic/benthic ratio and the  $\delta^{13}\text{C}_{\text{OM}}$ . Similar relationship has been observed from other subarctic sites in relation to climate-driven changes in water transparency and planktonic/benthic production (Rosén et al., 2009), and to tree line oscillation driving changes in terrestrial inputs (Wolfe et al., 1999). The overall range of  $\delta^{13}\text{C}_{\text{OM}}$  values implies that even during periods of higher phytoplankton production, as suggested by the diatom assemblages, benthic habitats have dominated the biomass production in Lake Várddoajávri. This notion is in agreement with the commonly observed benthic dominance of primary production in the shallow oligotrophic lakes of the circumpolar Arctic (Rautio et al., 2011). Overall, the differential responses of the elemental and isotopic sediment geochemistry suggests that the former reflects the relative contribution of allochthonous and autochthonous carbon sources for the sediment organic matter, whereas the isotopic sediment geochemistry seems to mirror in more detail the internal dynamics of the autotrophic community.

The  $\delta^{15}\text{N}$  of autochthonous organic matter in nitrogen-poor lakes not interfered by anoxia or high alkalinity is typically close to that of the original source, as all of the nitrogen is eventually consumed by the biota (Talbot, 2001; Leng et al., 2006). Owing to the limnological and catchment characteristics of Lake Várddoajávri, the observed  $\delta^{15}\text{N}_{\text{OM}}$  values are presumed to reflect primarily the balance between atmospheric and terrestrial nitrogen sources. The values showed small variability and fell mostly within the range of 0–2‰ (Fig. 4) suggesting dominance of light atmospheric nitrogen ( $\delta^{15}\text{N} = 0\text{‰}$ ) fixed by cyanobacteria (Talbot, 2001; Meyers, 2003), consistent with the scarcity of allochthonous inputs to the lake. In support, elevated  $\delta^{15}\text{N}$  values are associated with higher C/N ratio in the sediment profile ( $R = 0.55$ ,  $p < 0.001$ ), likely indicating minor increases in light soil-derived nitrogen that may exhibit variable but generally positive  $\delta^{15}\text{N}$  values (Talbot, 2001; Meyers, 2003; Leng et al., 2006).

#### 4.2. Middle Holocene (ca. 8200–4200 cal yr BP)

While there is some variation in the inferred patterns of Early Holocene temperatures in northern Europe (e.g., Luoto et al., 2014; Weckström et al., 2014), the climate conditions of the Middle Holocene, between ca. 8200–4200 cal yr BP (Walker et al., 2012), have been relatively well established. The period is generally considered to have been warm (e.g., Salonen et al., 2011; Luoto et al., 2014) and previous paleolimnological records based on microfossil and physicochemical proxy data suggest also low humidity in the subarctic Fennoscandia (Barnekow, 2000; Seppä and Birks, 2001; Korhola and Weckström, 2004; Korhola et al., 2005). The gradual development patterns in Lake Várddoajávri during the Middle Holocene similarly imply warm and dry climate conditions (Fig. 5), as well as overall climatic stability.

The diatom regime shift in Lake Várddoajávri (Figs. 2 and 3) suggest that the combination of warm and dry climate coupled with stabilized catchment conditions affected the availability of algal habitats in the lake. The nature of the shift, from heavy

planktonic diatom life forms (dependent on high turbulence and adequate nutrient supply) to light-limited benthic flora, implies changes in the physical and chemical properties of the water column (Bigler et al., 2002; Sorvari et al., 2002; Rühland et al., 2015). Temperature seems an unlikely cause due to the persisting warmth of the Middle Holocene, however, earlier records from the region have illustrated declined lake levels driven by the dry climate conditions (Barnekow, 2000; Korhola and Weckström, 2004). The collapse in the planktonic diatom community in Lake Várddoajávri (Figs. 2 and 3) may similarly reflect reduced water level, concurrently increasing the relative proportion of shallow habitats for benthic autotrophs. Nutrient deficiency may further have hampered the phytoplankton communities, driven by the gradual leaching of the catchment soils (Engstrom et al., 2000; Reuss et al., 2010; Fritz and Anderson, 2013), decreased catchment inputs (Figs. 4 and 5) and reduced nutrient cycling in the lake. Many of the benthic taxa present during the Middle Holocene have also been associated with slightly acidic waters in the calibration data set (Seppä and Weckström, 1999), which may imply that gradual acidification (Engstrom et al., 2000; Bigler et al., 2002) further promoted the effects of the hydrological changes. While the gradual natural oligotrophication and acidification may have played a part, the moisture-driven hydrological changes seem the most prominent environmental force behind the observed diatom community changes, as suggested also by the subsequent regime shift discussed below in relation to Late Holocene.

Along with reduced water levels, the emergence of the benthic flora may have been promoted by high water transparency. The subtle decline in the carbon and nitrogen contents and the C/N ratio (Fig. 4), likely reflecting the prolonged dry climate conditions and progressive catchment stabilization, suggest low input of terrestrial organic matter, including coloured organic substances that stain the water. The diatom-based DOC reconstruction, displaying generally lower concentrations (Fig. 3), also suggests low catchment inputs and high water transparency. In contrast, several paleolimnological records from the subarctic region display major changes in water chemistry and aquatic communities during the Middle Holocene climatic optimum, driven by tree line advance (e.g., Seppä and Weckström, 1999; Pienitz et al., 1999; Rosén, 2005; Jones et al., 2011). In common with the Lake Várddoajávri record, stable DOC concentrations during the Middle Holocene have been inferred from high-altitude (e.g., Nevalainen et al., 2014) and high-latitude (e.g., Rosén, 2005) sites not affected by the oscillating forest boundary, suggesting that the boreal forest never reached the catchment of Lake Várddoajávri. In the absence of marked temperature and catchment vegetation change, the floral assemblages and geochemical features of the sediment thus seem to reflect predominantly the moisture conditions of the Middle Holocene, influencing the depth and stability of the water column, and underwater light regimes.

#### 4.3. Late Holocene (ca. 4200 cal yr BP – present)

Several earlier studies suggest unanimously that air temperatures began to decline in northern Fennoscandia from around 5000 cal yr BP onwards, and that this was accompanied by increased effective precipitation (e.g., Seppä and Birks, 2001; Salonen et al., 2011; Luoto et al., 2014). The shift from the warm and dry Middle Holocene to the cool and humid Late Holocene is particularly visible in paleolimnological records from the subarctic tree line, associated with forest retreat and related changes in catchment-lake coupling (Pienitz et al. 1999, Seppä and Weckström, 1999; Kultti et al., 2004; Reuss et al., 2010). Vegetation degradation in the already barren catchment of Lake Várddoajávri was likely of relatively little influence, yet the



climatic transition was reflected distinctly in the biogeochemical features of the sediment.

The diatom regime shift in Lake Vårdöajävi, demonstrated as the re-emergence of the planktonic *Aulacoseira italica* var. *valida* at around 4000 cal yr BP (Figs. 2 and 3), likely reflects another climate-mediated change in the physical properties of the water column. Diatom-based records from northern Fennoscandia suggest that the Neoglacial cooling was reflected as shortened open water season in the shallow subarctic lakes of the region (Weckström et al., 2014). Extended ice cover period generally favours benthic rather than planktonic growth, although recent studies have shown that the associated reorganizations in diatom assemblages generally occur between small planktonic taxa (commonly cyclotelloids), and small benthic life forms together with large tychoplanktonic/planktonic *Aulacoseira* (Smol et al., 2005; Weckström et al., 2014; Rühland et al., 2015). The heavy *Aulacoseira* species may thus thrive also in colder climate provided adequate depth and turbulence of the water column, as also suggested by the present record. A similar species shift has been observed from subarctic Sweden (Reuss et al., 2010), with an increase in planktonic over benthic forms attributed to more turbulent waters, and from the arctic Russia (Jones et al., 2011) related to improved nutrient cycling in the pelagic zone. Moreover, several records from Finnish Lapland (Korhola and Weckström, 2004; Korhola et al., 2005) and Sweden (Barnekow, 2000) indicate elevated lake levels during the Late Holocene. It seems probable that increased precipitation and runoff from the catchment altered the depth and stability of the water column in Lake Vårdöajävi, resulting in larger relative proportion of planktonic habitats, improved mixing conditions, and enhanced nutrient cycling. Elevated water depth would also have diminished living condition in the benthic habitats, although diverse periphyton persisted in the lake throughout the Late Holocene despite the decline in their relative abundance. This may be attributed to expansion of the lake area resulting in increased abundance of shallow littoral habitats that, in contrast to the early postglacial period, were rich in growth substrate for periphytic taxa. Rühland et al. (2015) presented a contrasting pattern, with lower benthic community diversity associated with degradation of the littoral habitats under extended ice cover period. However, this discrepancy likely merely reflects the overriding influence of humidity (rather than temperature) in Lake Vårdöajävi.

The diatom-inferred DOC (Fig. 3) showed generally elevated concentrations during the Late Holocene, which may have been driven by a combination of climate-related mechanisms increasing the transport of terrestrial organic matter into the lake. For one, the cool and moist climate conditions promoted wetland expansion in northern Fennoscandia, particularly at the beginning of the Late Holocene (Weckström et al., 2010). Associated increases in lake-water DOC have been inferred from earlier lake records in the region (e.g., Seppä and Weckström, 1999; Rosén, 2005), and wetland cover has been shown to exert strong control over DOC concentrations in northern Finnish lakes (Korhola et al., 2002). Inundation of catchment soils may also have increased concentrations of dissolved organic matter in the lake. Additionally, permafrost aggradation associated with the declining temperatures (e.g., Kultti et al., 2004; Jones et al., 2011) may have increased the input of terrestrial DOC with enhanced surface runoff. The barely discernible upward trend in the C/N ratio, between ca. 4200–3000 cal yr BP (Fig. 4), may indicate a small increase in allochthonous inputs at the beginning of the Late Holocene. However, the overall gradual decline in C/N values gives no evidence of major increase in the relative share of terrestrial organic matter. The discrepancy between the C/N ratio and diatom-inferred DOC may reflect the changes in the volume and areal extent of the lake, i.e., decreasing relative importance of allochthonous matter in the sediment along

with increasing distance from the shore (Talbot, 2001).

The clear decline in the  $\delta^{13}\text{C}_{\text{COM}}$  profile initiated at around 4000 cal yr BP (Fig. 4) could partly be related to increased input of  $^{13}\text{C}$ -depleted terrestrial organic matter. However, lack of significant correlation between the carbon isotopic signature and C/N ratio in the sediment profile, and the synchronous increase in planktonic diatoms (Figs. 2 and 3) suggests that the  $\delta^{13}\text{C}_{\text{COM}}$  values reflect primarily the increase in pelagic over benthic production. Rosén et al. (2009) showed that temporal patterns in  $\delta^{13}\text{C}_{\text{COM}}$  values in a subarctic lake in northern Sweden were connected to both factors, i.e., increase in terrestrial inputs reduced benthic production through light limitation, which was reflected as  $^{13}\text{C}$ -depletion in the carbon isotopic signature of the sediment. The structure of the benthic substrata and changes in water turbulence may also have influenced the  $\delta^{13}\text{C}_{\text{COM}}$  values in Lake Vårdöajävi. Higher water turbulence and more loosely structured benthos during the Early and Late Holocene could have caused enhanced  $^{13}\text{C}$  depletion related to reduced boundary layer effect and subsequent enhanced diffusion (Rautio and Vincent, 2007).

In contrast to the fluctuating diatom assemblages, the variations in the stable isotopic composition of cladoceran remains were small (Fig. 4), suggesting little change in the carbon utilization of the zooplankton during the Holocene. Carbon enrichment between trophic levels is generally assumed low and thus the  $\delta^{13}\text{C}_{\text{ZOO}}$  in the sediment may be considered an approximate of the  $\delta^{13}\text{C}$  of zooplankton diet. The  $\delta^{13}\text{C}_{\text{ZOO}}$  values (mean  $-26 \pm 0.6\text{‰}$ ) were consistently more  $^{13}\text{C}$ -depleted than the  $\delta^{13}\text{C}$  of bulk organic matter (mean  $-21 \pm 0.7\text{‰}$ ), and resemble those often associated with terrestrial organic matter (e.g., Grey et al., 2000; Rosén et al., 2009; Jones et al., 2011). Considering the dominant role of autochthonous production for the organic matter pool in Lake Vårdöajävi, it seems however likely that the bosminids rely on autotrophic production as a primary food source. Recent studies have shown that benthic production may comprise an important energy source for zooplankton in unproductive lakes with limited phytoplankton growth (Grey et al., 2000; Rautio and Vincent, 2007; Mariash et al., 2014). In Lake Vårdöajävi, the depleted  $\delta^{13}\text{C}_{\text{ZOO}}$  values (compared with the benthic  $\delta^{13}\text{C}_{\text{COM}}$  signal), and their stability in contrasts to the algal planktonic/benthic shifts (Figs. 3 and 4) suggest that the bosminids have been selectively feeding on phytoplankton. Additionally, the diatom-inferred DOC (Fig. 3) shows significant correlation with the  $\delta^{13}\text{C}_{\text{ZOO}}$  ( $R = 0.65$ ,  $p < 0.01$ ) and  $\delta^{15}\text{N}_{\text{ZOO}}$  ( $R = 0.45$ ,  $p < 0.05$ ), which may imply that allochthonous organic matter has provided an important supplementary food source for the zooplankton, either via heterotrophic energy mobilization or through direct utilization of terrestrial detritus (Grey et al., 2000; Rautio and Vincent, 2007). Differentiating the exact contributions of each source is difficult, as phytoplankton may exhibit highly variable isotopic signatures that may overlap with the terrestrial signal (Grey et al., 2000). Assuming a trophic fractionation of around  $+3.4\text{‰}$  for nitrogen (Cabana and Rasmussen, 1996) and  $^{15}\text{N}$  depletion by ca. 2–4‰ from the original signature (Perga, 2011), the  $\delta^{15}\text{N}$  of the zooplankton diet is close to 0‰ or slightly negative in Lake Vårdöajävi. The  $\delta^{15}\text{N}_{\text{ZOO}}$  values thus suggest that the small, filter-feeding bosminids utilize nitrogen-fixing cyanobacteria as a food source, consistent with the  $\delta^{15}\text{N}_{\text{OM}}$  values that indicate abundant cyanobacterial communities.

The data may suggest a minor shift in the carbon utilization of the zooplankton in association with the Late Holocene cooling, as the  $\delta^{13}\text{C}_{\text{ZOO}}$  values between ca. 4000–1500 cal yr BP, and the  $\delta^{15}\text{N}_{\text{ZOO}}$  values between ca. 3500–1500 cal yr BP, were slightly elevated in comparison with the lower end of the core. This could imply that during the Late Holocene, in association with the elevated DOC-concentrations and increased phytoplankton production in the lake (Figs. 2 and 3), the zooplankton had improved

access to their preferred planktonic and heterotrophic food sources. The deviation between  $\delta^{13}\text{C}_{\text{ZOO}}$  and  $\delta^{15}\text{N}_{\text{ZOO}}$  and  $\delta^{13}\text{C}_{\text{COM}}$  and  $\delta^{15}\text{N}_{\text{COM}}$  values is lowest in the upper half of the core, reflecting proximity between cladoceran diet and the source of bulk organic matter during higher phytoplankton production and increased terrestrial DOC inputs. Overall, the stable isotopic record from subfossil Cladocera shows marked stability in comparison with the altering diatom community structure, which is likely related to selective feeding strategies diminishing the effects of the diatom regime shifts. As yet, there are no comparable records of long-term natural variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of zooplankton in the subarctic region, which prevents extending the present findings to a broader context. Our record however suggests that the long-term patterns in the stable isotopic composition of zooplankton may provide a valuable tool to assess how climate-induced changes at the base of the food web are reflected to higher trophic levels.

#### 4.4. Implications on climate controls on shallow subarctic lakes ecosystems

Our understanding of the hierarchy of environmental controls shaping aquatic ecosystem development over a range of spatial and temporal gradients has been much improved during recent years (e.g., Smol et al., 2005; Karlsson et al., 2009; Fritz and Anderson, 2013; Rühland et al., 2015). The spatial heterogeneity of ecosystem responses to environmental forcing however continues to pose challenges. As emphasized by Rühland et al. (2015), context provides the key to assessing mechanisms and drivers of ecosystem change. Earlier studies have evidenced the sensitivity of shallow freshwater ecosystems in the circumpolar Arctic to climate variability, confirmed also by our study. The importance of direct temperature influence generally increases along latitudinal gradients (Smol et al., 2005; Rühland et al., 2015) owing to the dilute and oligotrophic nature of the aquatic ecosystems in the subarctic and arctic regions, their short growing season, and scarcity of direct human influences. On the other hand, the development of lakes situated close to the tree line or in the proximity of wetlands may be governed by fluctuations in the input of terrestrial organic matter (Karlsson et al., 2009). While Lake Värddoajävi may be considered susceptible to both environmental forcing mechanisms, our record underlines the importance of long-term moisture variability, controlling both the structure of the diatom community and the geochemical features of the sediment. The life traits of the fluctuating planktonic and benthic diatom taxa imply that long-term changes in humidity have altered the physical regimes in the water column, i.e., depth, mixing conditions, and light attenuation, with effects on habitat and resource availability for the algae. In support, several studies from the region have demonstrated changes in lake physical regimes driven by the Holocene climate oscillations (e.g., Barnekow, 2000; Korhola and Weckström, 2004; Korhola et al., 2005). While the sediment geochemistry and diatom-inferred DOC both imply relatively small catchment influence, apart from the early postglacial period, the moisture-driven changes in the input of terrestrial organic carbon may have subsidised the physical controls by affecting light availability to periphytic taxa. The overall range of variation in the diatom-inferred DOC values in Lake Värddoajävi is small, yet may be considered ecologically significant due to the sensitivity of shallow, clear-water subarctic lake ecosystems to DOC-driven changes in the spectral attenuation of solar radiation (Laurion et al., 1997; Snucins and Gunn, 2000; Karlsson et al., 2009).

Overall, our record shows that the relatively small-scale environmental variability of the Holocene has been adequate to fundamentally and repeatedly alter the ecosystem at the base of the food web. This proposes that the projected enhanced precipitation

in high-latitude regions and associated changes in physical regimes may result in marked ecological changes in Lake Värddoajävi, and in similar shallow freshwater ecosystems distributed widely across the subarctic region. The hydrological changes are also anticipated to increase the transport of terrestrial organic matter into lakes (Tranvik et al., 2009; Weckström et al., 2010), which may reinforce the influence of the physical controls on habitat availability and associated aquatic community reorganizations. As the carbon balance in lakes is connected to the structure of the aquatic community (Jansson et al., 2008; Tranvik et al., 2009), such prospects could have implications also for the global carbon cycle. Our results however imply that for a thorough community turnover to take place, the magnitude of the future climate changes should exceed those of the past eleven millennia.

#### Acknowledgements

This study was funded by the Doctoral Program in Geosciences of the University of Helsinki, and Academy of Finland (VIOLET project, #287547). We are grateful to Kaarina Sarmaja-Korjonen for providing the sediment material and to Sakari Salonen for assistance with sample preparation. We wish to express our gratitude for the two anonymous reviewers for their constructive feedback on the manuscript.

#### References

- Barnekow, L., 2000. Holocene regional and local vegetation history and lake-level changes in the Torneträsk area, northern Sweden. *J. Paleolimnol.* 23, 399–420.
- Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.C., Bennion, H., Carvalho, L., Juggins, S., 2001. Diatoms. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments, Terrestrial, Algal, and Siliceous Indicators*, vol. 3. Kluwer Academic Publishers, Dordrecht, pp. 155–202.
- Bigler, C., Larocque, I., Peglar, S.M., Birks, H.J.B., Hall, R.L., 2002. Quantitative multiproxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. *Holocene* 12, 481–496.
- Cabana, G., Rasmussen, J.B., 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proc. Natl. Acad. Sci. U S A* 93, 10844–10847.
- Engels, S., Self, A.E., Luoto, T.P., Brooks, S.J., Helmens, K.F., 2014. A comparison of three Eurasian chironomid-climate calibration datasets on a W-E continentality gradient and the implications for quantitative temperature reconstructions. *J. Paleolimnol.* 51, 529–547.
- English, J., Potapova, M., 2010. *Aulacoseira Valida*. In: *Diatoms of the United States*. Retrieved May 28, 2015, from: [http://westerndiatoms.colorado.edu/taxa/species/aulacoseira\\_valida](http://westerndiatoms.colorado.edu/taxa/species/aulacoseira_valida).
- Engstrom, D.R., Fritz, S.C., Almendinger, J.E., Juggins, S., 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature* 408, 161–166.
- Forsberg, C., 1992. Will an increased greenhouse impact in Fennoscandia give rise to more humic and colored lakes? *Hydrobiologia* 229, 51–58.
- Fritz, S.C., Anderson, J.J., 2013. The Relative Influence of Climate and Catchment Processes on the Holocene Lake Development in Glaciated Regions. *Papers in the Earth and Atmospheric Sciences*, Paper 381.
- Grey, J., Jones, R.L., Sleep, D., 2000. Stable isotope analysis of the origins of zooplankton carbon in lakes of differing trophic state. *Oecologia* 123, 232–240.
- Hecky, R.E., Hesslein, R.H., 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J. North. Am. Benthol. Soc.* 14, 631–653.
- Jansson, M., Hickler, T., Jonsson, A., Karlsson, J., 2008. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. *Ecosystems* 11, 367–376.
- Jones, V.J., Solovieva, N., Self, A.E., McGowan, S., Rosén, P., Salonen, J.S., Seppä, H., Välranta, M., Parrott, E., Brooks, S.J., 2011. The influence of Holocene tree-line advance and retreat on an arctic lake ecosystem: a multi-proxy study from Kharine Lake, North Eastern European Russia. *J. Paleolimnol.* 46, 123–137.
- Juggins, S., 2003. C2 Software for Ecological and Paleoecological Data Analysis and Visualization. User Guide Version 1.3. University of Newcastle, Newcastle.
- Juggins, S., 2013. Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quat. Sci. Rev.* 64, 20–32.
- Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems. *Nature* 460, 506–509.
- Korhola, A., Weckström, J., 2004. Paleolimnological studies in arctic fennoscandia and the Kola Peninsula (Russia). In: Pienitz, R., Douglas, M.S.V., Smol, J.P. (Eds.), *Long-term Environmental Change in Arctic and Antarctic Lakes*. Springer, Dordrecht, The Netherlands, pp. 381–418.
- Korhola, A., Weckström, J. and Blom, T., 2002. Relationship between lake and land-cover features along latitudinal vegetation ecotones in arctic Fennoscandia. *Archiv für Hydrobiologie. Suppl.* 139/2, Monogr. Stud., 203–235.

- Korhola, A., Tikkanen, M., Weckström, J., 2005. Quantification of Holocene lake-level changes in Finnish Lapland using a cladocera – lake depth transfer model. *J. Paleolimnol.* 34, 175–190.
- Kultti, S., Oksanen, P., Väliaranta, M., 2004. Holocene tree line, permafrost, and climate dynamics in the Nenets region, East European Arctic. *Can. J. Earth Sci.* 41, 1141–1158.
- Krammer, K., Lange-Bertalot, H., 1986. Bacillariophyceae. 1. Teil: Naviculaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), *Süsswasserflora von Mitteleuropa*. Band 2/1. Gustav Fischer Verlag, Stuttgart, p. 875.
- Krammer, K., Lange-Bertalot, H., 1988. Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), *Süsswasserflora von Mitteleuropa*. Band 2/2. Gustav Fischer Verlag, Stuttgart, p. 596.
- Krammer, K., Lange-Bertalot, H., 1991a. Bacillariophyceae. 3. Teil: Centrales, fragilariaceae, Eunotiaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), *Süsswasserflora von Mitteleuropa*. Band 2/3. Gustav Fischer Verlag, Stuttgart, p. 576.
- Krammer, K., Lange-Bertalot, H., 1991b. Bacillariophyceae. 4. Teil: Achnanthaceae, Kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema, Gesamt-literaturverzeichnis. In: Ettl, H., Gärtner, G., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), *Süsswasserflora von Mitteleuropa*. Band 2/4. Gustav Fischer Verlag, Stuttgart, p. 437.
- Laurion, I., Warwick, F.V., Lean, D.R.S., 1997. Underwater ultraviolet radiation: development of spectral models for northern high latitude lakes. *Photochem. Photobiol.* 65, 107–114.
- Leng, M.J., Lamb, A.L., Heaton, T.H.E., Marshall, J.D., Wolfe, B.B., Jones, M.D., Holmes, J.A., Arrowsmith, C., 2006. Isotopes in lake sediments. In: Leng, M.J. (Ed.), *Isotopes in Palaeoenvironmental Research*. Springer, Dordrecht, pp. 147–184.
- Lundqvist, J., 1986. Late Weichselian glaciation and deglaciation in Scandinavia. *Quat. Sci. Rev.* 5, 269–292.
- Luoto, T.P., Kaukolehto, M., Weckström, J., Korhola, A., Väliaranta, M., 2014. New evidence of warm early-Holocene summers in subarctic Finland based on an enhanced regional chironomid-based temperature calibration model. *Quat. Res.* 81, 50–62.
- Luoto, T.P., Sarmaja-Korjonen, K., 2011. Midge-inferred Holocene effective moisture fluctuations in a subarctic lake, northern Lapland. *Boreas* 40, 650–659.
- Mariash, H.L., Devlin, S.P., Forström, L., Jones, R.I., Rautio, M., 2014. Benthic mats offer a potential subsidy to pelagic consumers in tundra pond food webs. *Limnol. Oceanogr.* 59, 733–744.
- Meyers, P.A., 2003. Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. *Org. Geochem.* 34, 261–289.
- Meyers, P.A., Teranes, J.L., 2001. Sediment organic matter. In: Last, W.M., Smol, J.P. (Eds.), *Tracking Environmental Change Using Lake Sediments, Physical and Geochemical Techniques*, vol. 2. Kluwer Academic Publisher, Dordrecht, The Netherlands, pp. 239–269.
- Moser, K.A., Korhola, A., Weckström, J., Blom, T., Pienitz, R., Smol, J.P., Douglas, M.S.V., Hay, M.B., 2000. Paleohydrology inferred from diatoms in northern latitude regions. *J. Paleolimnol.* 24, 93–107.
- Nevalainen, L., Rantala, M.V., Luoto, T.P., Rautio, M., Ojala, A.E.K., 2014. Ultraviolet radiation exposure of a high arctic lake in Svalbard during the Holocene. *Boreas*. <http://dx.doi.org/10.1111/bor.12108>.
- Perga, M., 2011. Taphonomic and early diagenetic effects on the C and N stable isotope composition of cladoceran remains: Implications for paleoecological studies. *J. Paleolimnol.* 46, 203–213.
- Perga, M., 2010. Potential of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of cladoceran subfossil exoskeletons for paleo-ecological studies. *J. Paleolimnol.* 44, 387–395.
- Pienitz, R., Vincent, W.F., 2000. Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* 404, 484–487.
- Pienitz, R., Smol, J.P., MacDonald, G.M., 1999. Paleolimnological reconstruction of Holocene climatic trends from two boreal treeline lakes, Northwest Territories, Canada. *Arc. Ant. Alp. Res.* 31, 82–93.
- Rantala, M.V., Luoto, T.P., Nevalainen, L., 2014. Holocene changes in the humic state of a boreal lake and their associations with organic matter transport and climate dynamics. *Biogeochemistry*. <http://dx.doi.org/10.1007/s10533-014-0053-4>.
- Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W.F., Christoffersen, K.S., 2011. Shallow freshwater ecosystems of the circumpolar arctic. *Écoscience* 18, 204–222.
- Rautio, M., Vincent, W.F., 2007. Isotopic analysis of the sources of organic carbon for zooplankton in shallow subarctic and arctic waters. *Ecography* 30, 77–87.
- Reuss, N.S., Hammarlund, D., Rundgren, M., Segerström, U., Eriksson, L., Rosén, P., 2010. Lake ecosystem responses to Holocene climatic change at the subarctic tree-line in northern Sweden. *Ecosystems* 13, 393–409.
- Rosén, P., 2005. Total organic carbon (TOC) of lake water during the Holocene inferred from lake sediments and near-infrared spectroscopy (NIRS) in eight lakes from northern Sweden. *Biogeochemistry* 76, 503–516.
- Rosén, P., Hall, R., Korsman, T., Renberg, I., 2000. Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentrations from lakes in northern Sweden. *J. Paleolimnol.* 24, 109–123.
- Rosén, P., Cunningham, L., Vonk, J., Karlsson, J., 2009. Effects of climate on organic carbon and the ratio of planktonic to benthic primary producers in a subarctic lake during the past 45 years. *Limnol. Oceanogr.* 54, 1723–1732.
- Rühland, K.M., Paterson, A.M., Smol, J.P., 2015. Lake diatom responses to warming: reviewing the evidence. *J. Paleolimnol.* 54, 1–35.
- Salonen, S.J., Seppä, H., Väliaranta, M., Jones, V.J., Self, A.E., Heikkilä, M., Kultti, S., Yang, H., 2011. The Holocene thermal maximum and late-Holocene cooling in the tundra of NE European Russia. *Quat. Res.* 75, 501–511.
- Seppä, H., Weckström, J., 1999. Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from Lake Tsuolbmajavri, Finland. *Écoscience* 6, 621–635.
- Seppä, H., Birks, H.J.B., 2001. July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. *Holocene* 11, 527–539.
- Šmilauer, P., Lepš, J., 2014. *Multivariate Analysis of Ecological Data Using CANOCO 5*, second ed. Cambridge University Press, Cambridge. Cambridge Books Online. Web. 20 May 2015. <http://dx.doi.org/10.1017/CBO9781139627061>.
- Smol, J.P., Wolfe, A.P., Birks, H.J.B., et al., 2005. Climate-driven regime shifts in the biological communities of arctic lakes. *Proc. Natl. Acad. Sci. U S A* 102, 4397–4402.
- Snucins, E., Gunn, J., 2000. Interannual variation in the thermal structure of clear and colored lakes. *Limnol. Oceanogr.* 45, 1639–1646.
- Sobek, S., Tranvik, L.J., Prairie, Y.T., Kortelainen, P., Cole, J.J., 2007. Patterns and regulation of dissolved organic carbon: an analysis of 7,500 widely distributed lakes. *Limnol. Oceanogr.* 52, 1208–1219.
- Sorvari, S., Korhola, A., Thompson, R., 2002. Lake diatom responses to recent arctic warming in Finnish Lapland. *Glob. Change Biol.* 8, 171–181.
- Talbot, M.R., 2001. Nitrogen isotopes in palaeolimnology. In: Last, W.M., Smol, J.P. (Eds.), *Tracking Environmental Change Using Lake Sediments, Physical and Geochemical Methods*, vol. 2. Kluwer Academic Press, Dordrecht, pp. 401–439.
- Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., Dillon, P., Finlay, K., Fortino, K., Knoll, L.B., et al., 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol. Oceanogr.* 54, 2298–2314.
- Walker, M.J.C., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., Weiss, H., 2012. Formal subdivision of the Holocene Series/Epoch: a discussion paper by a working group of INTIMATE (integration of ice-core, marine and terrestrial records) and the sub-commission on quaternary stratigraphy (international commission on stratigraphy). *J. Quat. Sci.* 27, 649–659.
- Weckström, J., Seppä, H., Korhola, A., 2010. Climatic influence on peatland formation and lateral expansion in sub-arctic Fennoscandia. *Boreas* 39, 761–769.
- Weckström, J., Hanhijärvi, S., Forsström, L., Kuusisto, E., Korhola, A., 2014. Reconstructing lake ice cover in subarctic lakes using a diatom-based inference model. *Geophys. Res. Lett.* <http://dx.doi.org/10.1002/2014GL059474>.
- Wolfe, B.B., Edwards, T.W.D., Aravena, R., 1999. Changes in carbon and nitrogen cycling during tree-line retreat recorded in the isotopic content of lacustrine organic matter, Western Taimyr peninsula, Russia. *Holocene* 9, 215–222.