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

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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 Várddoaijávri 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 ($\delta^{13}C$, $\delta^{15}N$) 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 ($\delta^{13}C$, $\delta^{15}N$) 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.

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

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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 ($\delta^{13}C_{OM}$, $\delta^{15}N_{OM}$) 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 ($\delta^{13}C_{ZOO}$, $\delta^{15}N_{ZOO}$) 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 sylvesteris*), 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}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,