Diatom response to mid-Holocene climate in three small Arctic lakes in northernmost Finnmark

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Abstract

Palaeoclimatic reconstructions from lake sediment biological records can be challenging, due to variation in non-climatic factors, which alter ecosystem responses. To consider this, it is important to replicate a study regionally, so as to gain information on spatial variability of ecosystem response and the influence of site-specific conditions. Previous pollen-based palaeoclimatic records from three well-dated Arctic lake sites highlight the response of regional Scots Pine (*Pinus sylvestris*) and Mountain Birch (*Betula pubescens* ssp. *czerepanovii*) forest-tundra transition to Holocene climatic variability, and suggest the northernmost Peninsulas of Finnmark to be climatically sensitive. This study analysed dated sediment sequences between c. 3,970 and c. 6,200 cal. yr BP from these three previously published shallow lakes: LitenCappesjavri (LCJ); over Gunnarsfjorden (OGF); and over Kobbkrokvatnet (OKV), for freshwater diatoms. Diatom assemblages showed an increase in the planktonic diatoms relative to benthic diatoms, with an onset towards higher abundances of small centric planktonic diatoms at OGF (between c. 5,270 and 5,350 cal. yr BP) and OKV (between c. 5,280 and 5,350 cal. yr BP). Additionally, a diatom compositional shift was detected at LCJ between c. 5,180 and 5,300 cal. yr BP. Trend analysis found the main diatom compositional change at all three sites to occur at 5,300 cal. yr BP. However, this synchronous diatom shift during the mid-Holocene varies in magnitude within the three Finnmark lakes. The abrupt planktonic:benthic diatom ratio changes are independent of the *Pinus*:*Betula* ratios, and are likely to be a result of lake ice-cover changes, allowing longer growing seasons, greater water column stability, and higher nutrient concentrations from surrounding catchments. This study highlights the significant differences in aquatic ecosystem and terrestrial vegetation response to climatic changes, with diatom assemblages at these sites either responding before the regional tree-line shift or to a separate climatic event within the mid-Holocene.

Key words: Diatoms; Finnmark; *Pinus:Betula* ratio; *Cyclotella*; Planktonic:benthic ratio; Ice-cover; mid Holocene

1. Introduction

Lake ecosystems clearly respond to changes in meteorological factors such as temperature, wind and precipitation, and these changes are recorded in lake sediments over a range of timescales (Battarbee, 2000; Adrian *et al.*, 2009). However, the challenge for palaeolimnologists remains to determine how, and to what degree, past climate is recorded in individual lake sediment records. In particular, the influences of non-climatic factors, and non-linear, and non-stationary responses mean that individual sites can produce quite different records resulting in spatial heterogeneity in the direction and timing of changes (Fritz, 2008). This problem is compounded by the scarcity of studies attempting to distinguish between local influences and regional patterns, and when such studies have been conducted dating uncertainties can make comparisons difficult. Studies recommend assembling sites from a large spatial distribution to help disentangle localised from regional variability (Fritz, 2008). This study represents an attempt to examine lake response to regional climate by using three previously published and well-dated, pollen-based palaeoclimate records from Arctic sites to determine the influence of a well-documented climate change on the lake ecosystems.

Lakes in the Arctic, free from direct human influence, are usually seen as being sensitive to changes in weather and climate (Smol *et al.*, 2005; Rühland *et al.*, 2008; Catalan *et al.*, 2013).

The effect of temperature has been shown to be important in Arctic limnology where air temperature controls ice-cover (formation, duration, and thickness), and affects the thermal stability within shallow lakes (Smol, 1988; Kilham *et al*., 1996; Battarbee, 2000; Post *et al*., 2009). Changes in temperature, wind and precipitation affect (directly and indirectly) aspects of lake ecosystem functioning, including growing season length, the extent of light penetration and lake-water mixing, along with nutrient availability within the benthos and water column (Findlay *et al*., 2001; Karlsson *et al*., 2009; Post *et al*., 2009). Furthermore climatic changes can also impact the complex lake-catchment feedbacks, changing lake metabolism, within-lake carbon processing and the export of catchment-derived dissolved organic carbon (Birks *et al*., 2000; Jones and Birks, 2004; Engstrom and Fritz, 2006; Heggen *et al*., 2010; Jones *et al*., 2011). As a result, the ecological consequences of these lake environmental changes on species composition and Arctic food-web structures are similarly complex (Jeppesen *et al*., 2003). Diatoms provide a useful proxy for assessing the impact of climatic change on Arctic lake ecosystems. Diatoms are unicellular siliceous algae, which can provide a unique insight into past lake environmental conditions through direct and indirect inferences of, for example, changes in lake-water pH, salinity and nutrients (Bigler and Hall, 2003; Jones, 2013). Diatoms respond indirectly to climate changes through alterations in lake water properties associated with warming, such as longer ice-free periods, changes in thermal structure and changes in resource availability of light and nutrients.

The assumption is often made that higher proportions of planktonic diatoms in relation to benthic diatoms indicate longer periods of ice-free conditions, turbulent waters, and more water column nutrients associated with warmer climatic conditions (Smol, 1988; Lotter and Bigler, 2000; Grönlund and Kauppila, 2002). In contrast, prolonged ice-cover is assumed strongly to inhibit planktonic growth and reduce lake productivity, with benthic diatoms (especially *Fragilaria sensu lato* spp.) dominating (Karlsson *et al*., 2009). In the Arctic much attention has been given to the dynamics of small centric *Cyclotella* populations which in some studies have been shown to be sensitive to effects of recent climatic warming (Catalan *et al*., 2002; Smol and Douglas, 2007; Rühland *et al*., 2008; Winder *et al*., 2009; Prowse *et al*., 2011), often displaying an increased abundance (at the expense of planktonic *Aulacoseira* and benthic *Fragilaria* populations) which has been related to their ability to thrive in lakes when the length of the growing season increases and there are longer periods of water-column stability (Catalan *et al*., 2013). These may be related to less summer ice-cover (Smol and Douglas 2007; Prowse *et al*., 2011). However, like other phytoplanktonic species, these diatoms respond directly to neither weather nor climate, but to proximal growing conditions (nutrients, light, temperature, mixing regimes, grazing), which are controlled by climate in a complex way (Smol 1988; Pienitz *et al*., 1995; Birks *et al*., 2000; Jones and Birks, 2004; Smol *et al*., 2005; Rühland *et al*., 2008; Adrian *et al*., 2009; Catalan *et al*., 2013; Rühland *et al*., 2013; Saros *et al*., 2013). This has been the premise for interpreting diatom changes in response to climate reported in many limnological and palaeolimnological studies. Experiments have successfully shown that nutrient concentrations and incubation depth (light availability) play important roles in the growth of centric diatoms (*Discostella stelligera*, *Cyclotella comensis* and *Cyclotella bodanica*) within Arctic lakes (Saros *et al*., 2013). Nethertheless fluctuations in past climate have induced changes similar to these recent *Cyclotella*-*Aulacoseira*-*Fragilaria* shifts (Wang *et al*., 2008; Wilson *et al*., 2008; Ampel *et al*., 2010; Huber *et al*., 2010; Lami *et al*., 2010), suggesting that these current taxon-specific changes are in response to an overriding effect of climate (Catalan *et al*., 2013), and that similar mechanisms may occur in the late mid-Holocene. However, at some Arctic and Alpine sites *Cyclotella* spp. dominate throughout the Holocene (Perren *et al*., 2009) and at others documented warming has not resulted in an increase in *Cyclotella* spp. (Koinig *et al*., 2002). Therefore it is not expected that all Arctic lakes will show an increase in planktonic *Cyclotella* species in response to warming, or their first appearance, as some lake sites have long had *Cyclotella* species present. Therefore it is important to consider the shift in the whole diatom assemblage, and not just within the *Cyclotella sensu lato* (*s.l.*) taxa.

Conditions of the last 6000 years are of particular interest to further our understanding of the Earth System because the boundary conditions of the climate system did not change dramatically (Wanner *et al*., 2008). How lake ecosystems responded to past changes in the late mid-Holocene may therefore give us clues on how they might respond in the future. The climate of the North Atlantic region has fluctuated on centennial to millennial timescales throughout the Holocene, as shown by palaeoclimatic studies from the Barents Sea (Duplessy *et al*., 2001; Voronina *et al*., 2001; Sarnthein *et al*., 2003; Risebrobakken *et al*., 2010) and Icelandic Sea (Bianchi and McCave, 1999; Rousse *et al*., 2006), as well as from Greenland (Bond *et al*., 1997; 2001; Hall *et al*., 2004; Mayewski *et al*., 2004) and Northern Fennoscandia (Korhola *et al*., 2000; Rosen *et* al., 2001; Korhola *et al*., 2002). Terrestrial sites from the Barents Sea margin also show evidence of climatic changes during the Holocene (Allen *et al*., 2007; Huntley *et al*., 2013) where the role of the Norwegian and North Cape currents (NCaC) are of critical importance. These are branches of the North Atlantic Current, which transport warm waters along the Norwegian coastline and around the North Cape region, into the Arctic basin of the southern Barents Sea (*Figure 1*) and control the regional temperatures around the Southern Barents Sea, driving sea ice-cover and sea-surface temperatures (Risebrobakken *et al.,* 2010).

Palaeovegetation research at three Arctic sites in Northern Finnmark situated along a West-East transect, adjacent to the southern shore of the Barents Sea, shows a regional response of the ecotone between *Pinus* forests and *Betula* woodlands to Holocene climatic changes (Allen *et al*., 2007; Huntley *et al*., 2013). Pollen analysis from tightly-chronologically constrained lake sediment cores was used to reconstruct spatial and temporal patterns in the Holocene position of this ecotone (Huntley *et al*., 2013). In a c. 2000 year period between c. 3970 and 6200 cal. yr BP the largest shifts in the *Pinus*:*Betula* ratio of the entire Holocene period were found at the three sites lying along a c. 170 km West-East transect (*Figure 1*). The *Pinus*:*Betula* ratios show two significant peaks at all three sites (*Figure 2*), which are short-lived at c. 5675 cal. yr BP (named peak (d) in *Figure 9* of Huntley *et al*., 2013; 95% age ranges at the sites ordered West-East 5450-5850, 5475-5875 and 5600-5850 cal. yr BP) and at c. 4525 cal. yr BP (peak (e) in Huntley *et al*., 2013; 95% age ranges at c. 4300-4675, 4350-4750 and 4100-4750 cal. yr BP). These suggest episodes of regional climatic warming, resulting in northerly shifts of the *Betula* treeline and *Pinus-Betula* ecotone, as inferred from higher ratio values associated with increased pollen accumulation rates (Allen *et al*., 2007; Huntley *et al*., 2013). Palaeoclimatic reconstructions suggest that in these warmer periods there was a higher mean annual thermal sum than currently experienced in Finnmark at present, and mean temperatures of the warmest month were 0.7-2.2^{o}C warmer than the present day (Huntley *et al*., 2013).

This study aims to establish the effect of these Holocene climatic fluctuations between c. 3970 and c. 6200 cal. yr BP on diatom community composition within the three Arctic lakes; LCJ, OGF and OKV. We hypothesise that if lake ecosystems are sensitive to climate, and if diatom assemblages reflect climatic changes, then diatom community composition should be driven by fluctuations in the strength and eastward penetration of the NCaC, and respond with the climatically-driven *Pinus-Betula* ecotone shifts. Although lake biota can respond to catchment vegetation shifts (Jones *et al*., 2011), in this case there have been no major shifts in catchment vegetation (Allen *et al*., 2007). As a result the aim is to examine biotic response to climatic changes in the absence of major catchment vegetation shifts. This study will investigate whether there are any synchronous diatom compositional changes in terms of planktonic:benthic diatom ratio shifts, between the three lakes located across a West-East gradient spanning a distance of ~170km. The West-East gradient will allow us to address potential spatial variability and site-specific differences in diatom responses to mid-Holocene climate change. We expect that higher planktonic:benthic diatom ratios will be observed during the *Pinus*:*Betula* ratio peaks (at c. 4,525 cal. yr BP and c. 5,675 cal yr BP), when regionally warmer climatic conditions are inferred.

2. Study sites

The vegetation of the northernmost peninsulas of Finnmark is especially sensitive to changes in the Atlantic meriodional overturning circulation (AMOC), and in particular to variations within the strength and eastward penetration of the NCaC (Huntley *et al*., 2013). Huntley *et al* (2013) propose that a stronger AMOC and a greater eastward penetration of the NCaC into the southern Barents Sea resulted in higher temperatures and a northerly shift of the *Pinus*-*Betula* ecotone, or increased pollen productivity within the *Pinus* forest, with higher *Pinus*:*Betula* ratios. In contrast, a weaker NCaC resulted in southward retreat or decreased pollen productivity of *Pinus*, with lower *Pinus*:*Betula* ratios, due to colder conditions. Today Scots Pine (*Pinus sylvestris*) forms the northernmost boreal forests within Fennoscandia, being situated south of the Mountain Birch (*Betula pubescens* ssp. *czerepanovii*) dominated sub-Arctic woodlands that extend to the Arctic treeline (Huntley *et al*., 2013).

Only brief site details are given here, further information is given in Huntley *et al*. (2013). The three small oligotrophic and shallow Arctic lake sites are situated beyond the *Pinus* and *Betula* limits, north of 70°N and adjacent to the southern Barents Sea shore (*Figure 1*; *Table 1*). They form a West-East transect (25°-29°E) across the northernmost Peninsulas of Finnmark, spanning a total distance of c. 170km. Liten Cap'pesjav'ri (LCJ) has a combined ice and water depth of 7m and is the most western site on the transect, situated on Magerøya. Situated in Nordkinhalvøya, the central site is over Gunnarsfjorden (OGF) with a combined ice and water depth of 4.8m, whilst the easternmost site is over Kobbkrokvatnet (OKV), situated in Varangerhalvøya with a combined ice and water depth of 2.3m (*Figure 1*). All sites lie outside the Younger Dryas ice limits of northern Scandinavian and are c. 100km and 70km north of the present-day *Pinus* treeline and *Betula* forest-tundra boundary respectively (*Table 1*) (Allen *et al*., 2007).

Northernmost Finnmark (70-71°N) experiences a relatively mild and wet climate compared to other Arctic regions at this latitude, as a result of the influence of the AMOC (Risebrobakken *et al*., 2010; Romundset *et al*., 2010). Warm oceanic waters around the Magerøya, Nordkinhalvøya and Varangerhalvøya regions from the NCaC are the cause of mild snowy winters and wet cool summers (Romundset *et al*., 2010). Two atmospheric pressure systems, the North Atlantic and Polar Arctic Fronts, control the regional climate. The coldest mean month temperatures at the three sites are -3.6^{o}C (LCJ), -5.4 ^{o}C (OGF) and -6.5 ^{o}C (OKV) in winter (October-March) (Huntley *et al*., 2013). In summer (April-September), the warmest month mean temperatures are 11.2^{o}C (LCJ), 9.5^{o}C (OGF) and 10.5^{o}C (OKV) (Huntley *et al*., 2013). Present-day catchment vegetation around the three lake sites consists predominantly of Arctic tundra dominated by dwarf-shrub species, including Crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) and Dwarf Birch (*Betula nana*) (Huntley *et al*., 2013).

3. Methods

3.1. Sediment coring, sub-sampling and chronology

A 7.5cm diameter square-rod piston corer was used from lake ice in the late winter to collect sediment core sections from the deepest points of the three lake basins (Huntley *et al*., 2013). OGF was sampled in April 2000, LCJ and OKV in April 2001. Two sets of consecutive 1 m core segments were collected from each lake with the second set covering the joints in the first. Only one set was used in subsequent analyses as no significant changes were found in the analyses across the joints. The cores were subsequently stored at 4^{o}C at Durham University, UK. Sediment cores comprised mainly of homogenous algal gyttja. AMS ^{14}C radiocarbon dates were obtained by ^{14}C measurements of terrestrial macrofossils. Radiocarbon ages were calibrated and age-depth models were constructed using a Bayesian method, Bchron (Parnell *et al*., 2008). This resulted in tightly-constrained chronologies at all three sites with 95% uncertainties of c. 200 years for the modelled dates for the majority of the Holocene (Huntley *et al*., 2013).

3.2. Diatom analysis

Wet sediment samples were prepared by conventional methods (H_2O_2, HCl) with a water bath (Battarbee, 1986; Renberg, 1990). Diatoms were identified to species level at 1000x magnification using a Zeiss light microscope and phase contrast under oil immersion. Published keys and guides (Krammer and Lange-Bertalot 1986; 1988; 1991a; 1991b; Camburn and Charles 2000) aided diatom taxonomy. Small centric diatoms (*Cyclotella* aff. *comensis* (Grunow) and *Cyclotella rossii* (H. Hakansson)) dominated the plankton; these had very variable valve morphologies and, because they were difficult to separate consistently, were grouped into a *Cyclotella rossii*-*comensis* complex (Hausmann *et al*., 2001, Cremer and Wagner, 2004). Diatom samples were taken at the same stratigraphic levels as the pollen samples, to enable sample-by-sample comparison between the diatom and *Pinus*:*Betula* ratio records for the chosen time interval.

3.3. Data analyses

Stratigraphic plots of diatom percentage abundances were drawn using C2 (Juggins, 2007). Discrete diatom assemblage zones were determined using Optimal Partitioning within the program ZONE (version 1.2) (Juggins, 1992). The broken stick model (Bennett, 1996) was applied to establish the number of statistically significant zones. Rate-of-change analysis (Grimm and Jacobson, 1992; Birks *et al*., 2000) was performed on the diatom species data to establish the amount of assemblage change in the stratigraphical profile. The statistical package, Bchron, was applied to test the synchronicity of events in the data sets (Haslett and Parnell, 2008).

4. Results

The diatom floras from the three Finnmark cores (*Figure 3*) were diverse with a total of 164 diatom species identified from the late mid-Holocene. The dominant benthic taxa were *Stauroforma exiguiformis*, *Brachysira vitrea*, *Achnanthidium minutissimum* and *Nitzschia fonticola*. At all three lakes benthic diatoms dominated the diatom assemblages, but planktonic diatoms were still an important component. The highest relative abundances of planktonic diatoms (16%) were found at OGF, and the other two lakes had notable abundances up to 7-10%. There was a sparse planktonic flora in OGF and OKV, contributing less than 20% of the total diatom assemblage at either site. The diatom valves were well preserved, with minimal amounts of valve breakage and dissolution.

4.1. LCJ (Liten Cap'pesjav'ri)

A summary diagram for LCJ is presented in *Figure 3a*. The *Cyclotella rossii-comensis* complex is present at low abundance throughout the section with no abrupt changes. *Stauroforma exiguiformis* and *Brachysira vitrea* dominate throughout the core sequence. Subtle changes in *S. exiguiformis* delineate the zones, along with declines in small benthic *Achnanthes* (*s.l.*), *Tabellaria, Nitzschia fonticola* and *Encyonema* taxa at the onset of Zone 3.

4.2. OGF (over Gunnarsfjorden)

A summary diagram for OGF is presented in *Figure 3b*. *Cyclotella rossii-comensis* complex reaches highest relative abundances in Zone 3. In Zones 1 and 2 (6,200 – 5,690 cal. yr BP and 5,690 – 5,310 cal. yr BP) planktonic taxa are sparse and there are high abundances of *Nitzschia fonticola* (11-26%) and *Achnanthes sensu lato* spp., mainly *Achnanthidium minutissimum* (11-23%). In Zone 3 (5,310 – 4,580 cal. yr BP) there are significant diatom floristic changes, as the *Cyclotella rossii-comensis* complex increases to relative abundances of 10-16% and *Nitzschia fonticola* declines to relative abundances of 5-11%. This results in a peak in planktonic:benthic ratios, between c. 5,310 and 4,580-4,700 cal. yr BP (*Figure 4*). In

Zone 4 (4,580 – 4,040 cal. yr BP); *Cyclotella* spp. decline to 7-3%, *Brachysira vitrea* increases to 12-21% abundance and plankton:benthic ratios remain low.

4.3. OKV (over Kobbkrokvatnet)

A summary diagram for OKV is presented in *Figure 3c*. Zones 1 and 2 (5,920 – 5,840 cal. yr BP and 5,840 – 5,790 cal. yr BP) mainly consist of benthic *Fragilaria sensu lato* spp. (33-37%), *Achnanthes sensu lato* spp. (22-23%) and *Nitzschia fonticola* (9-13%), with a rich diversity of pennate diatoms, including *Navicula radiosa*, *Brachysira vitrea* and *Cymbella descripta*. Planktonic taxa are sparse. In Zone 3 (5,790 – 5,320 cal. yr BP) there are increases in the abundances of *Fragilaria sensu lato* spp. (*Stauroforma exiguiformis*, *F. pseudoconstruens*, *F. elliptica*), and decreases in acidophilous *B. vitrea*, *Achnanthes sensu lato* and *Nitzschia* spp. Planktonic taxa are not abundant. The most notable diatom assemblage changes occur at the onset of Zone 4 (5,320 cal. yr BP). In Zone 4: (5,320 – 4,300 cal. yr BP); significant diatom floristic changes occur, with a rise in *Cyclotella rossii-comensis* complex species and large pennate diatoms, such as *N. radiosa*. *Fragilaria sensu lato* spp. subsequently decline from 64% to 11%. The plankton:benthic diatom ratio peaks within this zone (*Figure 4*). In Zone 5: (4,300 – 4,050 cal. yr BP) there is a return to higher *Fragilaria sensu lato* spp. abundances.

Rate-of-change analyses highlight the significant changes (95% confidence levels) in the three diatom records to be at 4,480 cal. yr BP (LCJ), 5,350 cal. yr BP (OGF) and 5,840 cal. yr BP (OKV) (*Figure 4*). The results from the Bchron statistical analyses suggest that a significant event in the diatom records at all three sites occurred synchronously and at 5,300 cal. yr BP. This diatom shift observed across the three sites occurs after the first *Pinus*:*Betula* peak at c. 5,675 cal. yr BP (LCJ: 5,450-5,850; OGF: 5,475-5,875; OKV: 5,600-5,850) and before the second *Pinus*:*Betula* peak at c. 4,525 cal. yr BP (LCJ: 4,300-4,675; OGF: 4,350-4,750; OKV: 4,100-4,750) (*Figure 3*).

5. Discussion

The diatom compositions within the three northern Finnmark lakes during the mid-Holocene show remarkable commonality, with a similar period of diatom change between c. 5,270 and 5,350 cal. yr BP. However, the synchronous diatom assemblage shifts in the mid-Holocene differ in their magnitude across the three sites. OGF and OKV show higher *Cyclotella* abundances within the late mid-Holocene, with changes centered around 5,300 cal. yr BP. At the central site, OGF, an abrupt taxonomic shift occurred after c. 5,350 cal. yr BP, with higher abundances of planktonic taxa (mainly *Cyclotella rossii-comensis* complex) together with a larger number of motile, large periphytic (attached to plants/mosses) diatoms, such as *Cymbella* spp., and fewer attached benthic forms. At the eastern-most site, OKV, the diatom record also exhibits this trend towards higher planktonic:benthic diatom ratios at c. 5,350 cal. yr BP, and more motile, larger periphytic pennate diatoms, such as *Navicula radiosa*. At LCJ, the most western site, the diatom composition changes are more subtle but there is an assemblage shift around c. 5,180 and 5,300 cal. yr BP (Zone 2 to Zone 3), which matches the timing of diatom changes observed at the other two sites. Therefore the diatom communities at all three sites react at a similar time, presumably due to regional climatic events.

Of interest is that higher planktonic:benthic ratios in the diatoms occurred between the timing of two significant peaks in *Pinus*:*Betula* ratio. This could be a result of leads and lags in the palaeoecological records not being fully accounted for, namely the time taken for *Pinus sylvestris* to migrate northwards, closer to the lake sites on the Barents Sea coast. In comparison to vegetation, diatoms respond rapidly to climate-driven changes of lake ecosystems, and their community assemblage is comprised of many different species. Within this diverse assemblage some species exhibit narrower ecological niches compared to terrestrial vegetation types (Birks and Birks, 2008). Freshwater diatoms are sensitive to both lake water and catchment changes, in particular temperature-associated changes in the water column, ice-cover dynamics and water chemistry changes. Thus, diatoms inherently respond indirectly to regional changes in wind patterns, air temperatures and precipitation fluctuations at a different rate and magnitude to terrestrial vegetation.

The maximum extent of the past *Pinus-Betula* forest ecotone for this region has been suggested to lie at the present-day *Betula*-tundra ecotone boundary (Seppä *et al*., 2002). Therefore the three lake sites on the northernmost Peninsulas of Finnmark would always have been significantly beyond the *Pinus sylvestris* limit, although at times close to or within the zone of *Betula pubescens* ssp. *czerepanovii* sub-Arctic woodlands (Allen *et al*., 2007). The catchments of these tundra lakes remained treeless throughout the Holocene. As a result, no significant lake catchment vegetation changes are likely to have affected the lake ecosystem directly through terrestrial inwash, as seen in Kharinei Lake in North Eastern European Russia where organic inwash occurs (Jones *et al*., 2011). *Pinus sylvestris* pollen grains preserved within lake sediments are wind transported over large distances from distant *Pinus sylvestris* dominated forests; for example, for lakes of similar size to those we studied MacDonald and Cwynar (1991) estimated that 20% of *Pinus* pollen was derived from beyond a radius of 100-200km.

5.1. *Cyclotella* increase and climatic change

The periods of higher *Cyclotella* abundances within OGF and OKV are likely to be a result of decreased summer ice-cover duration and increased growing season length. These climate driven changes are inter-related to the fundamental lake processes which affect algal production and composition; thermal stability and vertical mixing patterns, and availability of resources (light and nutrients) (Korhola *et al*., 2000; Sorvari *et al*., 2002; Smol *et al*., 2005; Rühland *et al*., 2008; Adrian *et al*., 2009; Rühland *et al*., 2013; Saros *et al*., 2013). Many remote Arctic lakes have provided evidence for global climatic change from palaeolimnological studies (Smol and Douglas, 2007; Rühland *et al*., 2008; Prowse *et al*., 2011; Catalan *et al*., 2013). These studies have reported increases in small planktonic *Cyclotella* spp. (*Cyclotella comensis* and *Discostella stelligera*) with climatic warming, due to onset of longer growing seasons with higher water column stability, resulting in increased nutrient availability. Studies have shown that climatic warming can result in abrupt changes within the diatom community and increased primary production, with appearances of small and more competitive *Cyclotella* spp. (*Cyclotella comensis* and *Discostella stelligera*) and of large benthic pennate diatoms (Catalan *et al*., 2013). Increases in the abundance of large pennate diatoms (*Navicula radiosa* and *Cymbella descripta*) are observed alongside the *Cyclotella* rise at OKV. Large complex pennate species require a longer growing season for development in harsh environments, and with warming the diatom assemblage richness can increase due to the availability of diverse aquatic habitats in near-shore environments, which large pennate diatoms exploit (Michelutti *et al*., 2003; Keatley *et al*., 2008; Paul *et al*., 2010). Therefore higher large pennate diatom abundances within high latitude lake ecosystems indicate longer ice-free periods and an increase in the availability of diverse littoral aquatic habitats. Within OKV (Zone 4), the abundances of the less motile benthic diatoms, which inhabit rock surfaces, such as *Fragilaria* spp., are significantly reduced. This substantial decrease in small benthic *Fragilaria* taxa and the concurrent increase in a more diverse planktonic and benthic assemblage suggest a change to greater littoral habitat availability with reduced ice-cover extent.

5.2. Spatial variability across the transect

The timing of the main diatom compositional change, inferred from the planktonic:benthic diatom ratios, appears to occur synchronously among the three lakes along the West-East transect and this is supported by trend analysis. Diatoms preserved within OGF sediments record the greatest assemblage change, with an abrupt shift in the planktonic:benthic ratios. This lake may have responded more to climatic change due to site-specific conditions, as OGF has the largest surface area (c. 5 ha) and no discrete inflows in comparison to the other sites (LCJ: c. 2.5ha, OKV: c. 1.7ha). OGF may be more sensitive to ice-cover changes, which drive changes in the diatom community, and wind may be playing a stronger role at this lake by making the ice-free period longer than at the other sites. Furthermore, the position of OGF along the coast may have influenced lake response; the site would have been affected by changes within the NCaC strength.

OKV, the easternmost site, exhibits notable changes in diatom community composition but has less *Cyclotella* species in comparison to OGF. This could possibly be a result of past ocean circulation dynamics around the Barents Sea region, as only a strong NCaC can transport warm waters as far eastwards as the Varangerhalvøya region. The diatom flora composition preserved within OKV suggests a weaker ocean circulation around Varangerhalvøya, as higher abundances of small benthic *Fragilaria* species were prevalent in Zone 3 of the diatom record. Then low abundances of large complex periphytic diatoms such as *Navicula radiosa* and *Cymbella descripta* appear in the warm period (Zone 4) when benthic *Fragilaria* species decline substantially.

Surprisingly the ecosystem response examined at the deepest lake in our study (LCJ) is more muted in comparison to the other two lakes, and shows the least amount of diatom change over the period examined. LCJ, the westernmost site, has the highest abundances of *Stauroforma exiguiformis* and no significant changes within the *Cyclotella rossii-comensis* complex, which might be a result of site-specific differences. The lack of substantial change in the LCJ diatom profile might be resulting from thermal inertia within this deeper lake, increasing the time taken for the onset of ice-free conditions. LCJ could possibly be less affected by wind driven ice dynamics and therefore takes longer to become ice-free and freezes up more readily at the end of the summer (Keatley *et al*., 2008).

5.3. Comparisons between diatom response and North Atlantic climatic proxies

Records of haematite-stained grain (HSG) percentages and sortable silt (SS) mean sizes (Bianchi and McCave, 1999) from North Atlantic marine sediments provide proxies for sea-ice rafting and the strength of the thermohaline circulation (THC) respectively. Comparing the diatom and *Pinus*:*Betula* ratio profiles to the HSG and SS records, over the period of interest, enables this study to examine if the three lake ecosystems and regional tree-line in Finnmark are responding to changes within the North Atlantic and Arctic air mass circulation. A shift to lower HSG percentages and higher SS mean sizes indicates less ice rafting and a stronger THC. Such a shift occurs at c. 5,130 cal. yr BP (*Figure 4*). Although the onset of higher planktonic:benthic values occurs earlier at c. 5,270-5,350 cal. yr BP at OGF and OKV, and thus may appear not to correlate with lower HSG percentages or higher SS mean sizes, dating constraints must be considered when making such comparisons. Even our well-dated terrestrial records generally have 95% uncertainty ranges of c. 200 yr, whilst age uncertainties in the marine record are considerably greater. Moreover, the relationship between the strength of the warm NCaC into the Southern Barents Sea and North Atlantic deep-water current strength is complex (Allen *et al*., 2007). Episodes of warmer and cooler sea surface temperatures (SST) detected from Barents Sea sediment records do not correspond to the diatom compositional changes (*Figure 4*). Although similar climatic patterns between 8.5-4.3 cal. kyr BP inferred from the *Pinus-Betula* ratio fluctuations are not consistently seen within the marine records (Hald *et al*., 2007; Huntley *et al*., 2013), the vegetation changes may nonetheless be reflecting episodic shut downs in the Barents Sea inflow (Semenov *et al*., 2009). The diatom responses observed at the three sites apparently reflect independent signals of climatic changes, and do not provide evidence of coupled ocean atmosphere forcing through linkages with the North Atlantic Bond Cycles (Ice-rafted debris (IRD) events 3 and 4).

6. Conclusion

Diatom flora shifts have been observed at three small Arctic lake sites located close to the Barents Sea Margin in northern Finnmark. The onset of the diatom assemblage shift is synchronous (within the errors of dating) between the three lake sites. It is likely that the species changes observed are indicative of fluctuations of the lakes' ice-cover duration and thickness, and thus microhabitat availability, lake-water nutrient concentrations and light availability, all driven by climatic changes. However, the diatom community shifts differ in magnitude across the West-East transect of study sites, due to site-specific environmental conditions. Small regional climatic changes, in particular temperature and wind, will exert a significant impact on these high-latitude lake ecosystems, as they only experience ice-free conditions for a short period each summer season. These climatic factors will influence lake ice cover dynamics, and in turn affect the lake-water column properties which are fundamental for algal production; thermal stability and vertical mixing, along with resource availability from light and nutrient distributions within the lake. Climate has played an important role in diatom compositional changes within shallow Arctic lakes throughout the Holocene, resulting in shifts within the planktonic and benthic diatom communities as lake systems change between ice-cover and ice-free conditions.

In comparison to regional North Atlantic palaeoclimatic data, the three lake sites on the Barents Sea margin do not appear sensitive to shifts between the North Atlantic and Arctic air masses within the mid-late Holocene (specifically between c. 3,970 and 6,200 cal. yr BP). This is because the synchronous period of diatom change at these three lake sites are not coeval with the decline in HSG percentages and rise in SS mean sizes at c. 5,130 cal. yr BP. However there are problems with correlating these events, as sample resolution for example can impact record comparison. The freshwater diatom assemblages changes can be assumed to be driven by climate-modulated changes in habitat and availabilities of nutrients and light, which are controlled by the length of the growing season, aquatic macrophyte coverage and extent of seasonal ice/snow cover (Pienitz *et al.*, 1995). OGF and OKV are the most sensitive to climate-driven ecosystem change, displaying the largest abundance shifts within both lake plankton and benthos. A more subdued diatom response is detected within LCJ sediments.

The diatom floristic shifts at c. 5,270 and 5,350 cal. yr BP within these three lake sites occur between two notable short-lived peaks in *Pinus*:*Betula* ratios. Pollen records from OGF and LCJ have higher *Pinus*:*Betula* ratios during the period examined, in comparison to OKV where the treeline response to climate appears more muted. The results highlight significant differences in the responses to climatic changes between aquatic ecosystems (freshwater diatoms) and terrestrial vegetation (tree limit fluctuations). There are clear similarities between the diatom records, however site-specific differences in the diatom response can make it more difficult to interpret a clear climate signal, as diatoms respond to a variety of environmental factors. Climatic signals from aquatic systems can be problematic, due to the complexity of climate-driven changes within high-latitude lake ecosystem functioning, with many factors affecting the diatom community composition. The diatom assemblage records from these lake sites appear to be responding to regional climatic changes, and are modulated by their catchment and lake site conditions. The abrupt diatom assemblage shifts found within these lakes between c. 5,270 and 5,350 cal. yr BP are indicative of the onset of warm conditions. This is where *Cyclotella* species and large pennate diatoms (*Navicula radiosa* and *Cymbella descripta*) increase in OGF and OKV. However, pollen data suggest that the warming trend did not occur until c. 4,525 cal. yr BP. This could be a result of lags in the response of trees to climatic changes, or it is possible that the diatoms within these three Arctic lakes are responding to a separate climatic event to which the vegetation was not sensitive. Thus, our results did not find synchronous responses of tree limits and diatom assemblages. Given, however, that these biological systems are experiencing and responding to different climatic or climate-related variables, such a result should perhaps not be a surprise, but should encourage further research that aims to clarify the climatic variables to which each proxy are responding (Huntley, 2012).

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Figure 1: (A) Location of study area in Northern Scandinavia and route of major surface currents. (B) Map showing the location of the three lake sites in Northern Finnmark, and the present-day tundra-*Betula* and *Pinus*:*Betula* ecotone positions (modified map from Allen *et al*., 2007). (LCJ: LitenCappesjavri; OGF: over Gunnarsfjorden; OKV: over Kobbkrokvatnet).

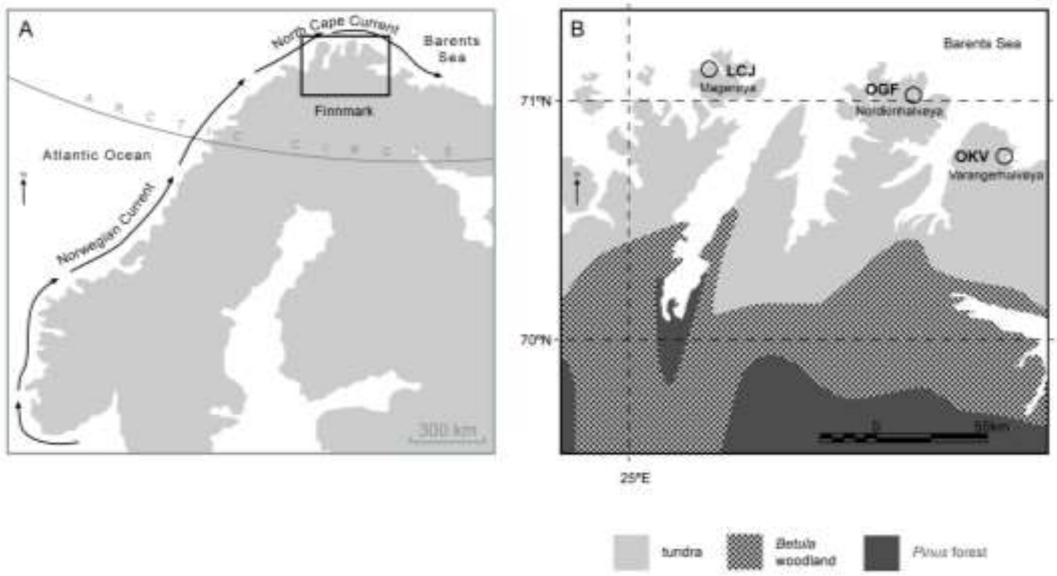


Figure 2: *Pinus*:*Betula* ratios at all three lake sites between c. 3970 and c. 6200 cal. yr BP (Data source: B. Huntley and J.R.M. Allen). The time intervals analysed for diatoms at each lake site are displayed underneath. (LCJ: LitenCappesjavri; OGF: over Gunnarsfjorden; OKV: over Kobbkrokvatnet).

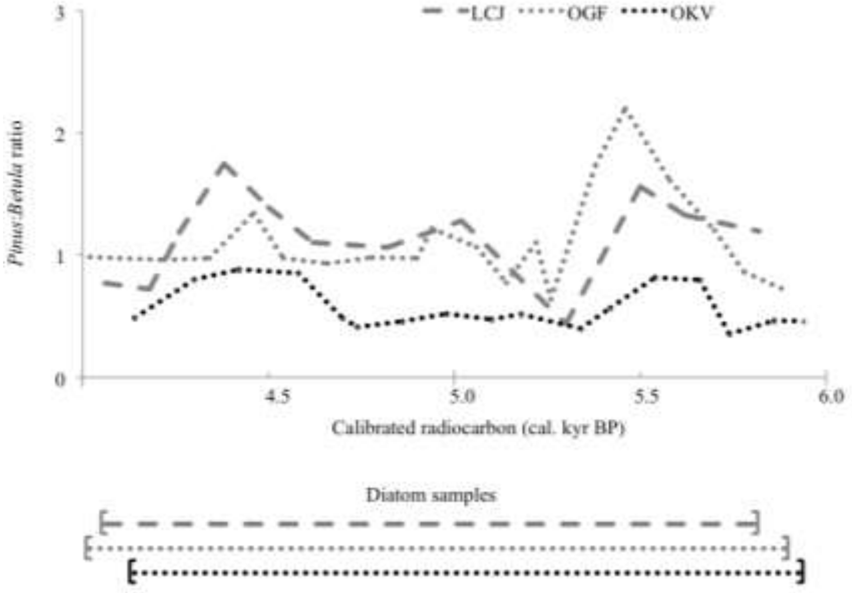
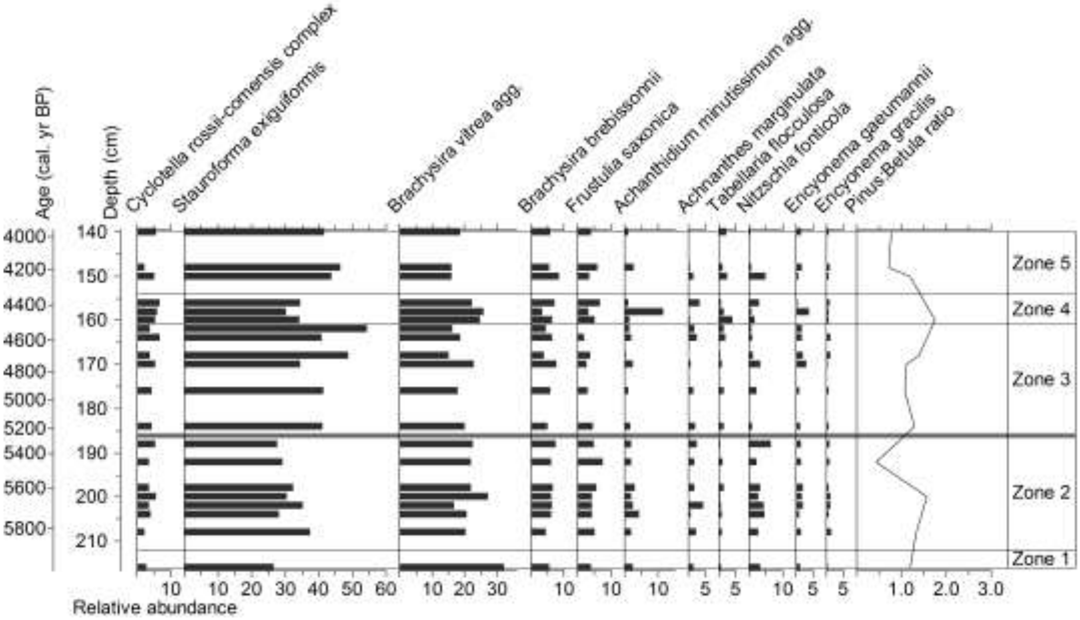
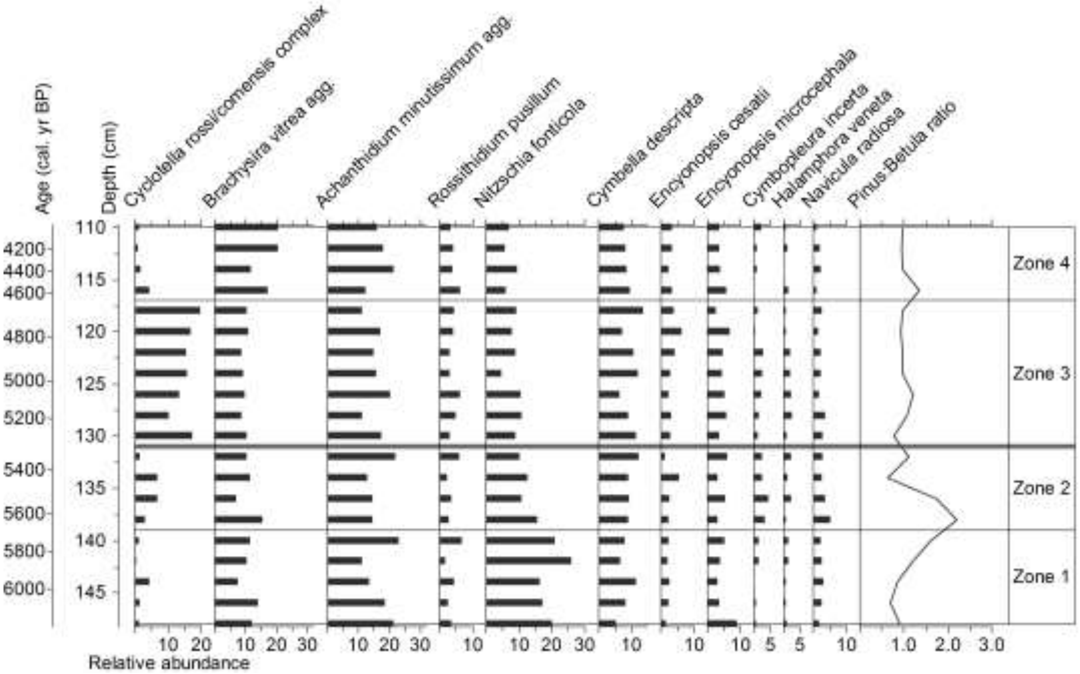


Figure 3: Summary stratigraphic profile of diatom percentage abundance of the most abundant diatom species (>2% relative abundance). Thick grey line highlights onset of diatom community change. (A) LCJ: LitenCappesjavri; (B) OGF: over Gunnarsfjorden; (C) OKV: over Kobbkrokvatnet).

(a)



(b)



(c)

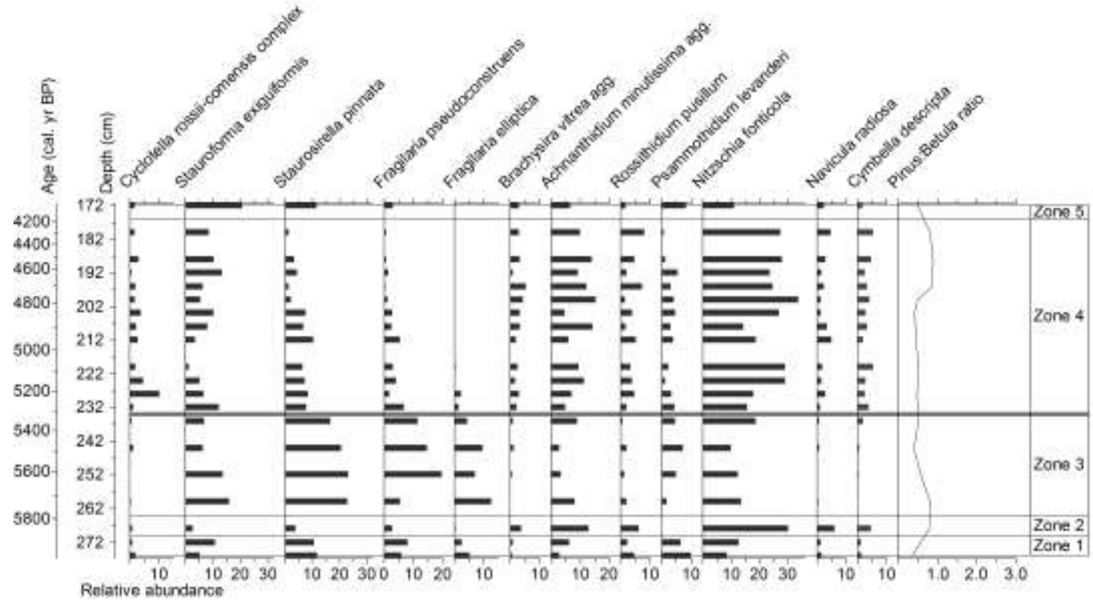


Figure 4: Summary diagram showing North Atlantic climatic proxy data; Haematite-stained grains (HSG) and sortable silt (SS) mean size (Bianchi and McCave, 1999), planktonic:benthic ratios, *Pinus*:*Betula* ratios and diatom assemblage rate-of-change data, including significant rate of change lines (95% confidence level). Figure includes the cold SST interval at 5,000 cal. yr. BP in S-E Barents Sea region (Voronina *et al*., 2001); warm SST interval at 5,500 cal. yr. BP in W Barents Sea region (Sarnthein *et al*., 2003); IRD event 3 (4.2 event) and IRD event 4 (5.8 event) (Bond *et al*., 1997; 2001); and period of diatom change between c. 5180-5350 cal. yr BP. (LCJ: LitenCappesjavri; OGF: over Gunnarsfjorden; OKV: over Kobbkrokvatnet).

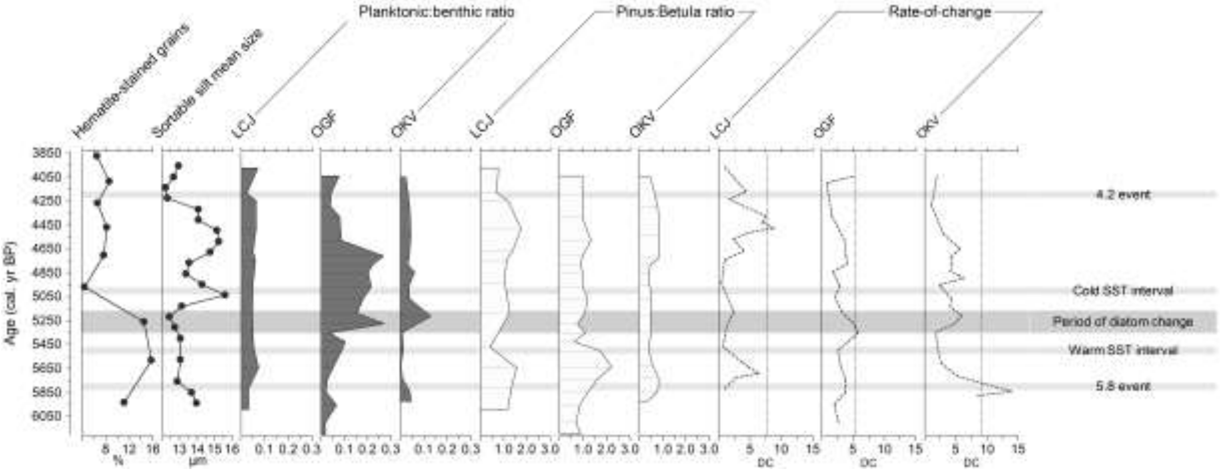


Table 1: Northern Finnmark lake sites (Data source: B. Huntley and J.R.M. Allen). (LCJ: LitenCappesjavri; OGF: over Gunnarsfjorden; OKV: over Kobbkrokvatnet).

Lake Site	Location	Combined ice and water depth (m)	Surface area (ha)	Distance north of present-day *Pinus* tree limit (km)	Distance north of present-day *Betula* forest-tundra boundary (km)
LCJ	71°04'28"N, 25°22'05"E	7	2.5	c. 100	c. 70
OGF	71°02'18"N, 28°10'6.6"E	4.8	5	c. 125	c. 75
OKV	70°41'57"N, 29°17'41"E	2.3	1.7	c. 100	c. 50