



The Holocene environmental history of a small coastal lake on the north-eastern Kamchatka Peninsula



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ABSTRACT

A radiocarbon and tephra-dated sediment core from Lifebuoy Lake, located on the north-east coast of Kamchatka Peninsula, was analysed for pollen, spores, diatoms, chironomids and tephra in order to uncover regional environmental history.

The 6500-year environmental history of Lifebuoy Lake correlates with the broad regional patterns of vegetation development and climate dynamics with both diatoms and chironomids showing near-synchronous changes.

Between ca. 6300 and 3900 cal yr BP, the lake ecosystem was naturally enriched, with several *Stephanodiscus* species dominating the diatom plankton. This natural eutrophication state is likely to be due to a combination of the base-rich catchment geology, the fertilisation effect of several fires in the catchment, silica input from tephra layers and, possibly, nitrogen input from seabirds. The substantial tephra deposit at about 3850 cal yr BP might have stopped sedimentary phosphorus from entering the lake water thus decreasing the trophic state of the lake and facilitating the shift in diatom composition to a benthic Fragiliariaceae complex.

Both diatoms and chironomids showed simultaneous compositional changes, which are also reflected by statistically significant changes in their rates of change 300–400 years after the arrival of *Pinus pumila* in the lake catchment. The rapid increase in both total diatom concentration and the percentage abundance of the large heavy species, *Aulacoseira subarctica* might be a response to the change in timing and intensity of lake spring turn-over due to the changes in the patterns of North Pacific atmospheric circulation, most notably westward shift of the Aleutian Low.

The two highest peaks in *A. subarctica* abundance at Lifebuoy Lake occurred during opposite summer temperature inferences: the earlier peak (3500–2900 cal yr BP) coincided with warm summers and the latter peak (300 cal yr BP–present) occurred during the cold summer period. These imply that *A. subarctica* shows no direct response to the changes of summer air temperature. Instead, it appears to thrive during the periods of increased winter precipitation, thicker ice and late spring turn-over periods, i.e., shows indirect response to climate.

The clearest effect of tephra deposition on the lake ecosystem is above 908 cm (ca. 3800 cal yr BP) where the tephra deposit might have caused the shift from *Stephanodiscus*-dominated planktonic assemblages to the Fragiliariaceae complex of benthic species. Tephra deposits might have also contributed towards the development of eutrophic plankton from about 6300 cal yr BP. It is not certain if several tephra deposits influenced diatom and chironomid changes during the last 300 years.

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1. Introduction

There has been recent interest in the Holocene palaeoenvironmental history of the Kamchatka Peninsula with most studies largely focusing on lakes and peat deposits in the southern and central parts of the

peninsula (e.g., Dirksen et al., 2011, 2013; Hoff et al., 2012, 2014). The climate model experiments suggest that mid-Holocene climatic changes were time-transgressive in the Kamchatka Peninsula with the Holocene thermal maximum (HTM) being delayed in southern and central Kamchatka by about 2000 years in comparison with northern Kamchatka, Alaska and NE Siberia (e.g., see Fig. 3 in Renssen et al., 2009). It is therefore especially important to provide better insight into Holocene environmental and climate dynamics in northern Kamchatka since there is still little palaeoenvironmental evidence from this region, whereas the Holocene history of Alaska and NE Siberia are comparatively well-documented (e.g., Anderson et al., 2002; Edwards and Barker, 1994; Lozhkin et al., 2001, 2007).

In the last few decades, palaeoecological research in the Kamchatka Peninsula has largely comprised studies of vegetation history (Andreev and Pevzner, 2001; Dirksen et al., 2013), tephrochronology (e.g., Braitseva et al., 1993, 1997; Dirksen et al., 2011; Pevzner et al., 1998; Pevzner, 2006) and glacial dynamics (Savoskul, 1999; Barr and Solomina, 2014). A comprehensive study of the Holocene vegetation history of the Kamchatka Peninsula has been presented by A. Klimaschewski (2010). Climate history during the last 400 years was reconstructed using tree-rings by Solomina et al. (2007) and Sano et al. (2010) and is summarized by Jones and Solomina (2015-in this issue). Quaternary diatom records were studied by Braitseva et al. (1968).

Recently, a diatom sediment record from in the central Kamchatka was used to infer late-Holocene environmental changes (Hoff et al., 2012) and a diatom record from the Sokoch Lake in southern Kamchatka was used to reconstruct the past 9600 years of environmental history (Hoff et al., 2014). Hoff et al. (2011) also described a new diatom species (*Fragilaria flexura*) in Dvuyurtochnoe Lake. A recent paper by Nazarova et al. (2013) presents a chironomid-based climatic reconstruction from Dvuyurtochnoe Lake. Diatom phytoplankton, mainly *Aulacoseira subarctica*, has been studied in detail by Lepskaya et al. (2010) in the large and deep Kurilskoye Lake in southern Kamchatka.

This study presents the Holocene environmental history of the north-eastern coastal area of the Kamchatka Peninsula based on diatom, pollen and chironomid records from the sediment succession of a small coastal lake near the town of Ossora (Fig. 1a). The overall aims of this paper are (1) to qualitatively reconstruct the development of regional vegetation in north-eastern Kamchatka; (2) to assess its influence on the lake development (3) to compare environmental reconstructions with the Holocene environmental history of southern and central Kamchatka, north-eastern Siberia and Alaska and (4) to assess the importance of tephra on lake development.

2. Site description

Regional descriptions of northern Kamchatka Peninsula are presented in several papers in this volume, e.g., Self et al. and Andr en et al. Lifebuoy Lake (unofficial name; 59°06'593"N, 163°09'141"E) is a small lake (area is approximately 0.8 ha), which is located on a narrow peninsula between two coastal bays, Karaga Bay and Ossora Bay about 200 m from the Pacific coast, in north-eastern Kamchatka. It is situated about 20 km south of Pechora Lake (Andr en et al., 2015-in this issue), approximately 730 km to the north of Petropavlovsk and about one km from a small settlement of Karaga (Fig. 1a and b).

The lake lies about 6 km from the mountains to north-west, which reach altitudes of 385 m. The lake has an open hydrology with a well-defined outlet and at least one surface inlet with some diffuse leakage (recharge) through marginal fens. There are narrow peat margins around the lake, partly with small palsas (permafrost mounds). At the time of sampling the lake was stratified, with the thermocline occurring at about 3.5 m (the sampling depth was 5.1). It is likely that the lake is dimictic, with winter stratification occurring after the autumn ice sets in November–December. On the day of the sampling, in August 2005, the lake water was circum-neutral, with pH 7.82, conductivity 95.0 mS

and the surface water temperature 16.9 °C (Dan Hammarlund, pers. comm).

Sphagnum bogs prevail in the catchment, together with low-lying shrubby *Pinus pumila*, *Alnus fruticosa* and *Betula ermanii*, generally similar to the vegetation at Pechora Lake (Andr en et al., 2015-in this issue). Bushes of Siberian dwarf pine (*P. pumila*) grow on the higher ground near the lake. Birch (*B. ermanii*) covers the mountain slopes (Fig. 1c).

Summers are relatively cold (July mean T is about 12 °C) with a short growing season and cold winters (mean January T is about –17 °C) (meteorological data from Ossora weather station, 1983–2005, <http://kamchatka-meteo.ru/>).

The main bedrock type is of Eocene origin (Klimaschewski, 2010), the lake catchment is dominated by till with high peat coverage.

Shiveluch is the nearest active volcano, which is located approximately 300 km south of Lifebuoy Lake. Eight visible tephra layers, predominantly from Shiveluch, occur in the Lifebuoy Lake sediments (Plunkett et al., 2015-in this issue).

3. Materials and methods

3.1. Sampling techniques

The core segments were sampled with a 1-m long, 5 cm diameter piston corer (Wright et al., 1984), deployed from a rubber boat at the lake centre from 5.10 m of water in August 2005. Sediments were wrapped in plastic, aluminium foil, thick plastic and modified plastic drain pipes, and stored in wooden boxes in a cold room at 4 °C. The upper ca. 30 cm of the lake sequence was sampled with a gravity corer, subsampled at 1-cm intervals and stored in separate plastic bags.

3.2. Laboratory methods

Pollen slide preparation followed standard methods (F ægri and Iversen, 1993; Moore et al., 1991; Bennett and Willis, 2001); *Lycopodium* spores were used to enable quantitative analysis (Stockmarr, 1971). Where possible, a minimum of 500 pollen grains were counted. Pollen percentages are based on the total terrestrial pollen sum. Percentages of obligate aquatics, non-arboreal pollen and charcoal, *Pediastrum*, snow algae are based upon the total pollen sum plus the count of the taxon in question.

For identification, the pollen reference collection at the School of Geography, Archaeology and Palaeoecology, Queen's University Belfast was used together with Moore et al. (1991), Reille (1992), F ægri and Iversen (1993) and Beug (2004). The palynological nomenclature generally follows Beug (2004). *Betula nana* pollen was not separated from *Betula alba*. Pollen grains of *P. pumila* were identified using the handbook of Hesse et al. (2009). Fungi and algae remains were determined following van Geel (1976).

Diatom slide preparation followed standard methods (Battarbee et al., 2001) using the water-bath technique (Renberg, 1990). Slides were mounted using Naphrax®. The diatom concentration was estimated by adding microsphere markers (Battarbee and Kneen, 1982). Between 300 and 400 valves were counted where possible at 1000 times magnification. Diatom nomenclature followed Krammer and Lange-Bertalot (1986–1991). Counts of *Pseudostaurosira brevistriata* and *Staurosira construens v. venter* were combined into *Pseudostaurosira-Staurosira* group as these species are particularly difficult to separate, especially in girdle view. These taxa also show very similar stratigraphic changes within the Lake Lifebuoy sediment sequence.

Chironomid sub-fossils were prepared and slides mounted following standard techniques (Brooks et al., 2007) at sample intervals of between 2 and 14 cm. Chironomids were identified with reference to Wiederholm (1983), Rieradevall and Brooks (2001) and Brooks et al. (2007). Chironomids were absent or occurred at very low abundance at the base of the core (1204–1188 cm). These samples were excluded from the diagram and assemblages analysed at 3–8 cm intervals from

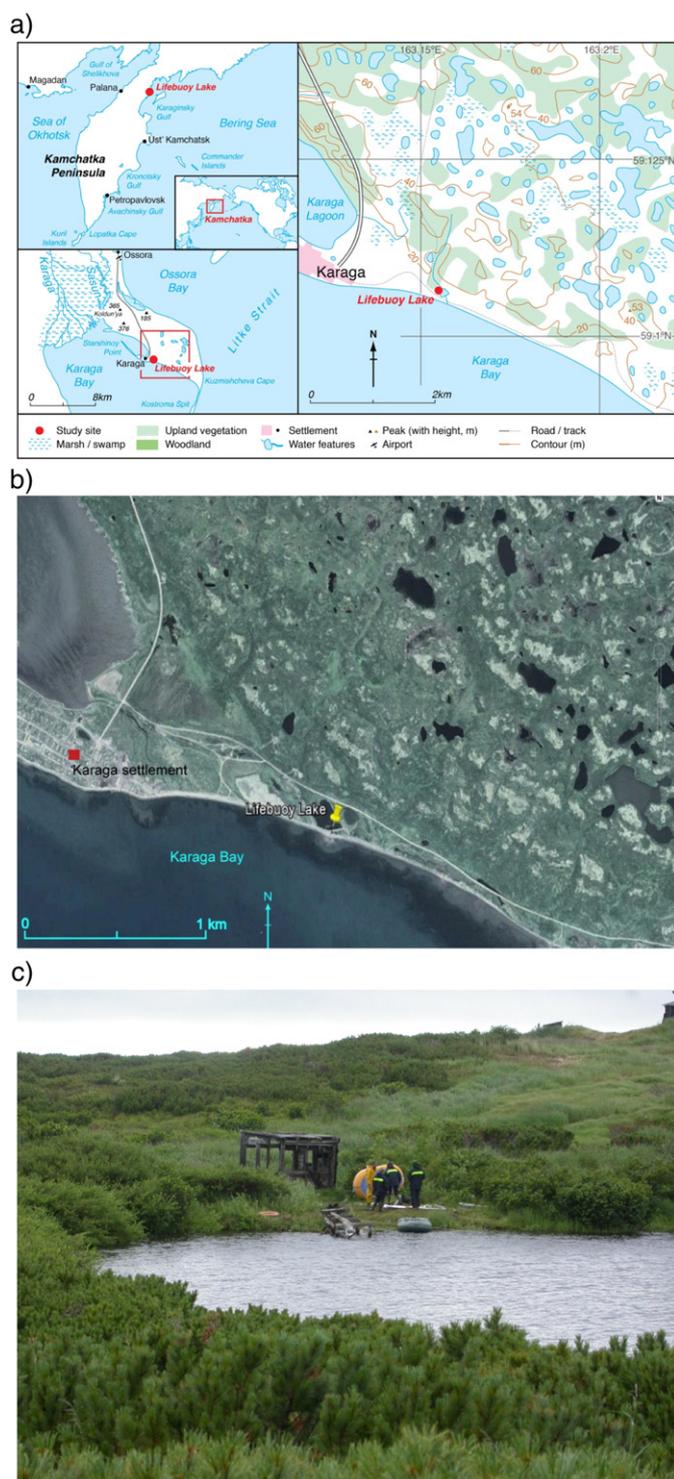


Fig. 1. a. Map of the study area and the location of Lifebuoy Lake. b. Google Earth image of Lifebuoy Lake and its surroundings. c. Lifebuoy Lake with surrounding *Pinus pumila* and *Betula ermanii* thickets.

1188 cm (6400 cal yr BP). Larger intervals between samples occurred where material had been lost from the ends of cores.

3.3. Numerical analysis

The programme 'psimpoll 4.27' (Bennett, 2009) was used for production of pollen diagrams and statistical analysis of the results,

including rate-of-change analysis, rarefaction analysis (palynological species richness) and principal component analysis (PCA).

Stratigraphic zonation of the pollen data was also performed using psimpoll 4.27. The following methods were used within the programme: divisive binary or optimal techniques (e.g., Gordon and Birks, 1972; Birks and Gordon, 1985); constrained cluster analysis by sum-of-squares (CONISS) developed by Grimm (1987) and CONIIC developed by Bennett (2009). Only taxa exceeding 5% abundance were included in the analysis. Eight bottommost samples (1226–1190 cm) were excluded from the analysis, as the pollen abundance was very low. Principal Component Analysis (PCA) was also used to assess the overall palynological change in the data. For details, see Klimaschewski (2010).

The programme ZONE version 1.2 (Juggins, 1991, unpubl. programme) was used to divide the diatom and chironomid data into stratigraphic zones. Within ZONE the following procedures were used: constrained single-link analysis (Gordon and Birks, 1972); constrained incremental sum-of-squares cluster analysis CONISS (Grimm, 1987); binary division using least squares (Gordon and Birks, 1972); binary division using information content (Gordon and Birks, 1972); and optimal division using least squares (Birks and Gordon, 1985). Zone boundaries were identified where there was a consensus between methods. The statistical significance of the stratigraphic zones in pollen, diatom and chironomid diagrams was assessed using a broken-stick-model (Bennett, 1996).

The diatom abundance in the three bottom samples (1188, 1184 and 1177 cm depth) was very low, so these samples were excluded from the analysis

Diatom and chironomid diversity were estimated by Hill's N2 effective number of occurrences (Hill, 1973).

Rate-of-change analysis (Birks et al., 2000) was used to quantify the total amount of biostratigraphical change in both the diatom and chironomid assemblages per unit time. Rates of change were estimated as chord distances per 50 years. Simple linear interpolation was used to produce time series at equally spaced time intervals (10 years). The analysis was carried out using the programme RATEPOL (Ratepol J.M. Line and H.J.B. Birks, unpublished programme). In order to identify rates of change that are greater than one would expect by chance, given the critical sampling density and inherent variance of each dataset, approximate significance values at 95% were obtained by a restricted Monte Carlo permutation test in CANOCO 4.5 for time series (ter Braak and Šmilauer, 2002).

Overall compositional change in all the diatom and chironomid data sets was estimated by Detrended Correspondence Analysis (DCA), since the length of the gradient in the data-sets is above 1.5 and thus requires the use of a unimodal method. Species data were square-root transformed, rare species were down-weighted, with nonlinear rescaling and detrending by segments. DCAs were carried out using CANOCO 4.5 (ter Braak and Šmilauer, 2002).

Total phosphorus (TP) concentration was inferred using the European Diatom Database, (EDDI, <http://craticula.ncl.ac.uk/Eddi/jsp/index.jsp>) using the combined TP dataset, which provided the best representation of the fossil diatom assemblages. The LWWA inverse model, was the most suitable in terms of its predictive performance (RMSEP = $1.990 \mu\text{g L}^{-1}$; R^2 0.718).

Mean July air temperatures were inferred using a chironomid-based temperature inference model (WA-PLS, 2 component, $R^2_{\text{boot}} = 0.81$, $\text{RMSEP}_{\text{boot}} = 1.43 \text{ }^\circ\text{C}$) (Nazarova et al., 2015-in this issue) based on a modern calibration data set of 88 lakes and 135 taxa from the Russian Far East (53–75°N, 141–163°E).

The following strategy was used to assess the reliability of the chironomid and diatom based reconstructions. Reconstruction results were treated with caution if fossil samples had (1) more than 5% taxa absent from the modern training set or (2) more than 5% taxa rare in modern data set (i.e., Hill's N2 less than 5) (Heiri and Lotter, 2001; Heiri et al., 2003). (3) Goodness-of-fit

to the inferred parameter was evaluated by passively positioning the fossil samples on a CCA of the modern training set constrained solely against the reconstructed value (i.e., total P or temperature). Fossil samples that had a squared residual distance value within the 10th percentile of values in the modern training set were considered to have a poor fit-to-temperature (Heiri and Lotter, 2001). (4) The modern analogue technique (MAT) was used to detect fossil samples that lacked good analogues in the modern calibration dataset using squared chord distance (chironomids) and squared chi-squared distance (diatoms) as measures of dissimilarity. Samples with dissimilarity larger than the 95% threshold in the modern data were considered as having no good analogues in the modern calibration dataset (Birks et al., 1990; Velle et al., 2005). (5) The significance of the reconstructions was also evaluated using the palaeoSig package (Telford, 2011) in R (R Development Core Team, 2013) with 999 random reconstructions. Following Telford and Birks (2011), a reconstruction is considered statistically significant if it explains more of the variance in the fossil data than 95% of reconstructions that are derived from random environmental variables. In addition, fossil samples which contained fewer than 50 chironomid head capsules were also regarded as unreliable.

MAT diagnostics and Hill's N2 values were calculated with the programme C2 version 1.7.4 (Juggins, 2005). DCA and CCA were performed using CANOCO 4.5 (ter Braak and Šmilauer, 2002). Species data were square-root transformed to stabilise species variance and rare species were downweighted. In the evaluation of goodness-of-fit (4) the CCA scaling focused on inter-sample distances with Hill's scaling selected to optimise inter-sample relationships (Velle et al., 2005).

All diagrams were plotted using the programme C2 (Juggins, 2005). In order to highlight the stratigraphic changes, diatom and chironomid species were sorted by their weighted averaging (WA) scores from bottom left to upper right in the stratigraphic diagrams (Figs. 4 and 5), which were calculated in C2.

4. Results and discussion

4.1. Chronology

The sediment sequence was dated using a combination of tephrochronology and ^{14}C analysis. In total, tephra layers were identified at eight levels in the Lifebuoy sequence: at 594, 597, 608, 610, 726, 906, 1061, 1172–1176 cm (Figs. 2–5).

Initially, 11 bulk sediment samples were ^{14}C dated. Subsequently, however, these dates were rejected as they exhibited consistent reservoir effects in the range of 200–1200 years when compared with four visible tephra layers, which were geochemically identified. Three of these layers were established on the basis of the age-modelled dates for their correlatives at the nearby Pechora Lake. Two additional dates, which were obtained from terrestrial macroscopic plant remains, confirmed the tephro-chronology dates (Fig. 2). The details of the chronological approach, which relies partially on tephra geochemistry data obtained at nearby sites, are provided by Plunkett et al. (2015-in this issue). All dates are given in calibrated years AD 1950 (cal yr BP). The model projected basal age of 7000 cal yr BP and sediment accumulation rates between 0.8 and 1.7 mm yr $^{-1}$ (Plunkett et al., 2015-in this issue).

Pollen analysis of the top piston core and the gravity core samples confirmed that both samples are, approximately, the same age.

4.2. Loss on ignition

The loss on ignition profile is shown together with the pollen sequence in Fig. 3. The low LOI is likely due to the thick tephra layer in the bottom of the core. The LOI values show little change until ca. 700 cm (1500 cal yr BP), fluctuating between 20 and 30% and then gently increasing towards the top of the core reaching ca. 40% in the surface sediments. Two sharp drops in the LOI values (at 982 and 946 cm) show no obvious correlation to any tephra layers, whereas the dips in the LOI

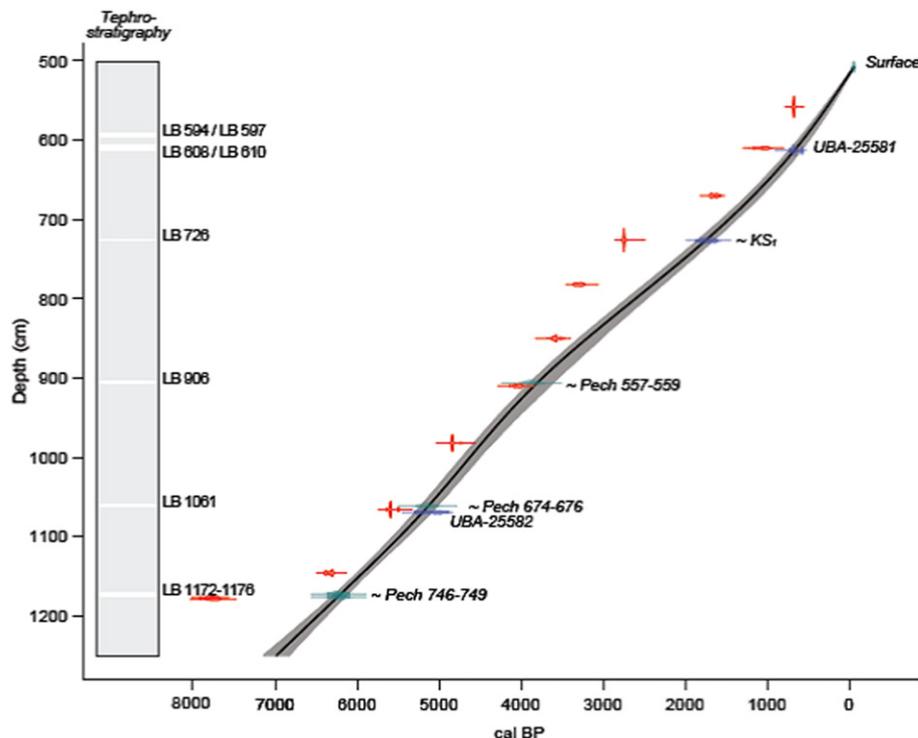


Fig. 2. Age–depth model of Lifebuoy and Pechora sediment sequences using ^{14}C dates and tephrochronology. Rejected bulk sediment dates are shown in red. For details please see Plunkett et al. (2015-in this issue).

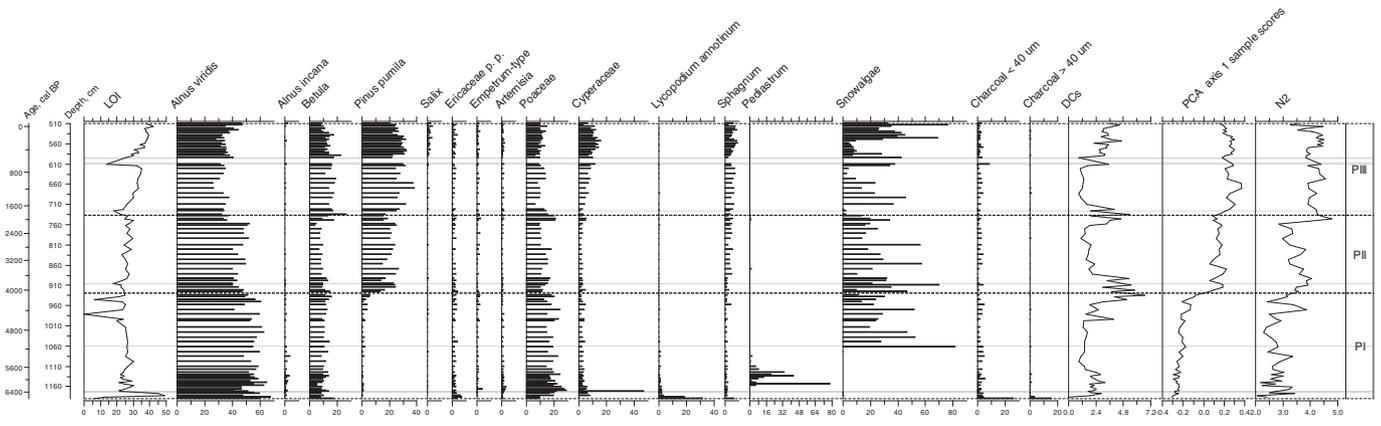


Fig. 3. Lifebuoy Lake pollen and spore stratigraphy. Selected pollen and spores, pollen local assemblage zones, % LOI at 550 °C, PCA axis 1 sample scores, number of effective occurrences of pollen taxa N2 and dissimilarity coefficients (DCs). Eight tephra layers are shown as grey lines.

curve at the bottom of the core and at 726, 608, 610 cm are related to the tephra layers.

4.3. Evaluation of diatom-based total phosphorus (TP) and chironomid-based July temperature reconstructions

Both reconstructed parameters showed good fit to reconstructed values. Diatom fossil samples were well represented by the modern training set, most of the fossil taxa were present and 88% of samples had good analogues. However, both reconstructed values should be regarded with caution, as both reconstructions failed the Telford test (Telford and Birks, 2011). Chironomid fossil samples had only few good modern analogues (17% of the fossil samples).

4.4. Pollen analysis

The pollen sequence was split into three local assemblage zones.

4.4.1. Zone PI (1190–934 cm; 6600–4050 cal yr BP)

The basal samples of zone PI are characterised by peaks of *Lycopodium annotinum* and *Cyperaceae* (Fig. 3). High abundances of the algae *Pediastrum* occur between 1074 cm and 1166 cm. From ca. 1000 cm (4650 cal yr BP) snow algae shows sharp increase to 60% then decreasing to ca. 25% and fluctuating between 25 and 55% with in the rest of PI. Throughout the whole sequence there are only low abundances of *P. pumila* pollen (<6%) which slightly increase towards the end of the zone. Filicales decrease from about 35% at the

base to ca. 20% at the upper boundary of the zone. Other taxa in this zone include *Betula*, which shows little change and *Alnus viridis*, which fluctuates between ca. 42% (970 cm, 4400 cal yr BP) and nearly 68% (1186 cm, 6500 cal yr BP) at its maximum.

The total pollen and spore concentration shows a peak of about 430,000 grains cm⁻³ at the beginning of sediment accumulation at Lifebuoy Lake, which is mainly derived from *A. viridis* pollen and spores of Filicales and *L. annotinum* (Klimaschewski, 2010). There is little fluctuation in the total pollen and spore concentration in PI with values ranging between 20,000 and 86,000 grains cm⁻³.

The rate-of-change in zone PI shows a distinct peak at ca. 1150 cm (6000 cal yr BP), above this level the values are relatively low. The N2 shows little change fluctuating around 3 (Fig. 3).

4.4.2. Zone PII (934–734 cm; ca. 4050–1800 cal yr BP)

The significant feature of this zone is the substantial increase in *P. pumila* from <5% at 946 cm (ca. 4200 cal yr BP, zone PI) to nearly 25% at ca. 914 cm, ca. 3900 cal yr BP (an interval of ca. 200 years). The *P. pumila* accumulation increases to above 600 g cm⁻² year⁻¹ (Klimaschewski, pers. comm). If its pollen production is similar to Scots pine (Seppä and Hicks, 2006), this suggests that *P. pumila* might already have been present in the catchment of the lake at this time. Snow algae show high abundance from ca. 1000 cm (4700 cal yr BP) suggesting long-lasting snow cover prior to the occurrence of *P. pumila* (Fig. 3)

A. viridis decrease slightly, whereas Poaceae and *Sphagnum* increases at the upper boundary of PII. *Betula* shows an increase from about <10%

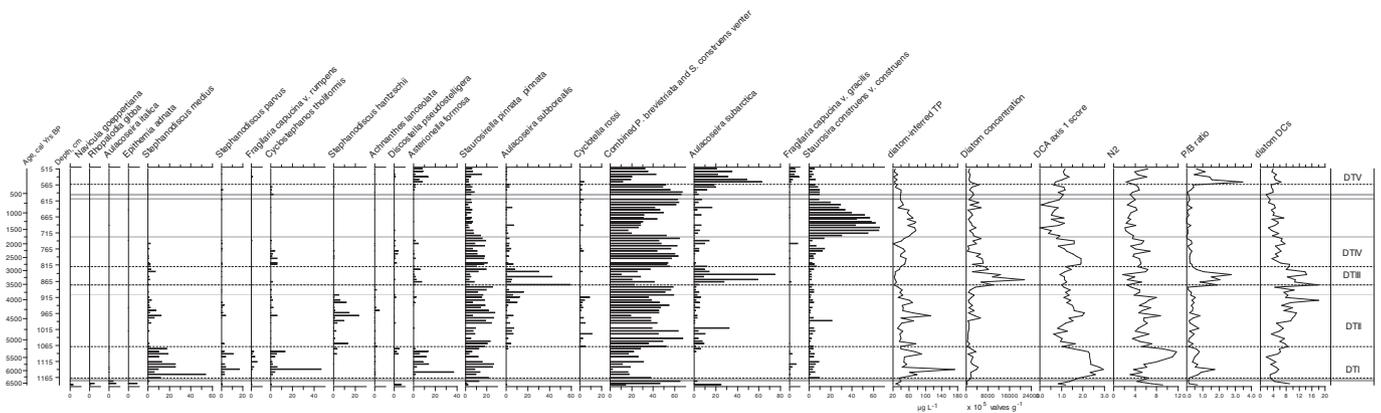


Fig. 4. Lifebuoy Lake diatom stratigraphy. Selected diatom species with abundance ≥ 2%, diatom local assemblage zones (dashed black lines), diatom-inferred total phosphorus (TP, μg L⁻¹), diatom concentrations (10⁶ valves g⁻¹), DCA axis 1 sample scores, number of effective occurrences of diatom taxa N2, planktonic/benthic ratio (P/B) and dissimilarity coefficients (DCs). Eight tephra layers are shown as grey lines. Solid black line shows statistically significant change in DCs.

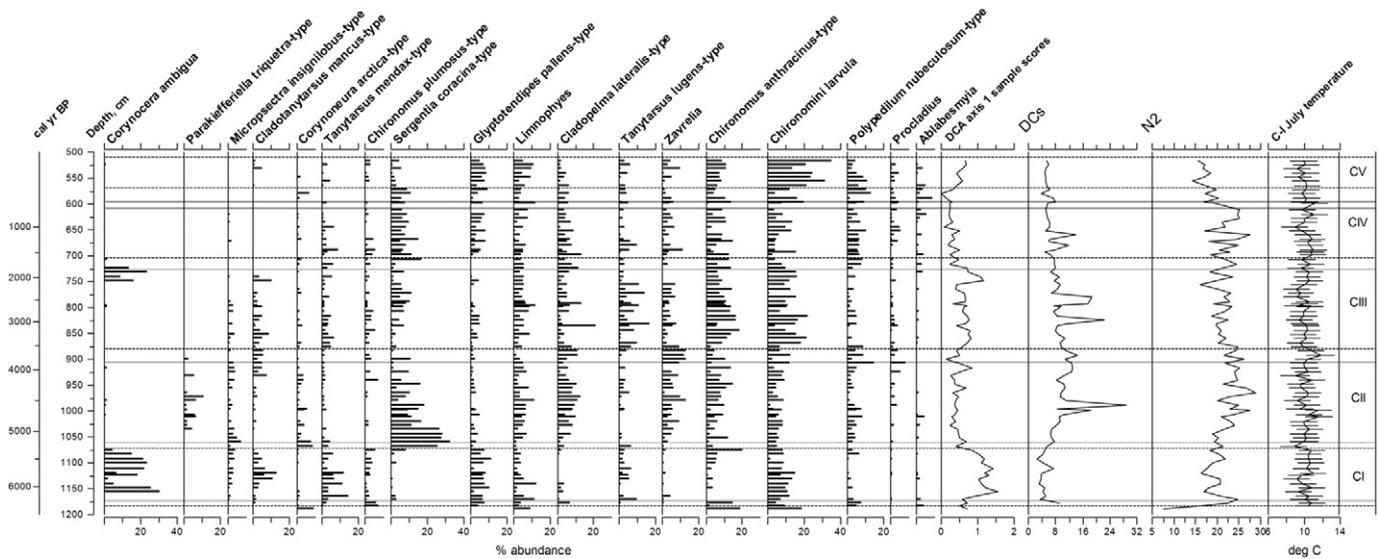


Fig. 5. Lifebuoy Lake chironomid stratigraphy. Selected chironomid species with abundance $\geq 2\%$, chironomid local assemblage zones (dashed black lines), DCA axis 1 sample scores, number of effective occurrences of chironomid taxa N2, dissimilarity coefficients (DCs) and chironomid-reconstructed July temperature. Eight tephra layers are shown as grey lines.

to nearly 20% above 760 cm. The percentages of Filicales decrease throughout the whole zone.

On average, N2 within zone PII is similar to zone PI.

4.4.3. Zone PIII (734–510 cm; 1800 cal yr BP–present)

This zone is characterised by increasing abundances of Cyperaceae from $<2\%$ to ca. 16% at about 554 cm. Also, *Betula* and *P. pumila* increase at the base of this zone and remain higher than in PII. A slight mid-zone peak of *P. pumila* pollen occurs at about 670 cm (39%) and *A. viridis* decreases at this depth (27%). The upper 40 cm of zone PIII are characterised by the increase in *A. viridis* pollen (to ca. 50%) as well as decreasing frequencies of *Betula* and *P. pumila*.

In comparison to the two lower zones, N2 shows an overall increase. The gradient of the dissimilarity measure (DCs) is low near the bottom part of PIII and constantly increases towards the top of the diagram.

4.5. Diatom analysis

In total, 163 diatom species and sub-species were identified in 83 samples from the Lifebuoy sediment core. Fig. 4 shows the diatom stratigraphy together with diatom concentration, diatom-inferred reconstructed total P, DCA Axis 1 scores, the planktonic to benthic ratio (P/B) and N2. Five diatom local assemblage zones DTI-DTV are also shown in Fig. 4.

Small Fragilariaceae, in particular the *Pseudostaurosira*–*Staurosira* group, *Staurosirella pinnata* and *S. construens* dominate the diatom assemblages throughout the core, reaching more than 60% abundance at some levels. Planktonic taxa, such as *A. subarctica*, *Stephanodiscus medius*, and *Stephanodiscus hantzschii* are also abundant at some levels. Overall, N2 shows its highest values in the lower part of the core, within the upper part of DTI and slowly decreases throughout the core.

Three bottom samples at 1204, 1200 and 1192 cm contain almost no diatoms making it impossible to analyse, and the diatom abundance from the next three levels (at 1188, 1184 and 1177 cm depth) is still comparatively low. The diatom composition of these samples is quite unusual compared to the rest of the sequence. Although these levels are dominated by the *Pseudostaurosira*–*Staurosira* group, large epiphytic *Epithemia adnata*, *Rhopalodia gibba* and rather rare *Navicula goeppertiana* reach 5–6% abundance. Planktonic *A. subarctica* reaches about 25% at the 1188 cm level, then decreases to 3% at 1177 cm; *Aulacoseira granulata* and *Aulacoseira italica* occur at abundance 3–6%. The reconstructed TP is about $80 \mu\text{g/L}$, which is near the average value

for the core; the diatom concentration is very low; P/B ratio decreases from about 0.7 to near 0 whereas N2 shows relatively high values.

4.5.1. Zone DTI (1167–1068 cm, ca. 6300–5150 cal yr BP)

In this zone, eutrophic planktonic diatoms (i.e., *S. medius*, *parvus* and *Cyclostephanos tholiformis*) prevail together with planktonic mesotrophic *Asterionella formosa*, and the benthic *Pseudostaurosira*–*Staurosira* group and *S. pinnata*.

S. medius fluctuates between ca. 13 and 25% reaching 54% at 1156 cm; *C. tholiformis* occurs between 6 and 10% abundance, but reaches 47% at 1140 cm. *S. parvus* is less abundant, occurring at 4% to 11% with a maximum of 17% at 1140 cm. *S. construens subsalina* reaches 8% at 1092 cm; *Fragilaria capucina rumpens* and *Fr. capucina gracilis* appear in the middle of the zone at 3 to 7% abundance.

Diatom-reconstructed TP reaches its highest values in the Lifebuoy sequence in DTI ($172 \mu\text{g L}^{-1}$ at 1140 cm, ca. $47.5 \mu\text{g L}^{-1}$ on average).

The diatom concentration in DTI increases slightly compared to the three lower-most samples, ranging between 1500 and 4500×10^5 valves g^{-1} . The P/B ratio remains at around 1, apart from one peak of 1.7 at 1140 cm depth. The DCA axis 1 sample scores increase as compared to the lower-most samples and reach their highest values for the core of 2.75 at 1132 cm depth.

4.5.2. Zone DTII (1068–876 cm; 5150–3500 cal yr BP)

Within this zone eutrophic *C. tholiformis* and *S. parvus* decrease, whereas *S. hantzschii* increases attaining a maximum abundance of 24% at 972 cm.

S. medius also declines overall, although there is a small peak between 980 and 956 cm. *A. formosa* disappears, and both forms of *A. subarctica* substantially increase with *A. subarctica* fo. *subborealis* rising to 23% in the middle of the zone above the tephra layer at 908 cm (ca. 3850 cal yr BP). The *Pseudostaurosira*–*Staurosira* group increases compared to DTI, varying from about 35 to 67%, whereas *S. construens* v *construens* remains at about 5%.

Diatom concentration remains relatively low, TP decreases compared to DTI with average inferences of about $48.0 \mu\text{g L}^{-1}$ and the P/B ratio decreases to about 0.5 on average. DCA sample scores also overall decrease to an average of 1.5, although there is an increase in values in the middle of the zone. The rate of diatom compositional change (as measured by DCs, Fig. 5) increases compared to DTI.

4.5.3. DTIII (876–820; ca. 3500–2850 cal yr BP)

The main feature of this zone is a dramatic increase in both *A. subarctica* and *A. subarctica* fo. *subborealis*. Interestingly, both forms do not show a simultaneous increase: instead, they increase at alternate levels. There is no clear ecological division between the two forms of *A. subarctica* in the literature; they co-occur in many lakes and have similar total phosphorus optimum (Gibson et al., 2003; Stevenson et al., 1991). However, *A. subarctica* fo. *subborealis* prefers slightly more acidic water as was demonstrated in Swedish modern water chemistry-diatom training set (Stevenson et al., 1991).

All other planktonic forms almost disappear except for *A. formosa* and *S. medius* (both taxa present at ca. 3–5% on average) and the *Pseudostaurosira* group decreases to about 25% on average.

Diatom concentration also reaches the highest values for the core within this zone (ca. $22,000 \times 10^5$ valves g^{-1}), whereas reconstructed TP decreases to $28.0 \mu g L^{-1}$ on average. The DCA sample scores also decrease slightly, while the P/B ratio increases substantially reaching 2.7 compared to DTII. Within this zone, the rate of change is both the highest for the whole core and statistically significant (at $p < 0.05$) at 876 cm (Fig. 4).

4.5.4. DT IV (820–564 cm, ca. 2850–300 cal yr BP)

S. construens v *construens* reaches its highest abundance in the core (65%) at the expense of the *Pseudostaurosira*/*Staurosira* group and this is the most striking aspect of DTIV. Both forms of *Aulacoseira* decrease: *A. subborealis* declines to 2–3% on average and *A. subarctica* averages 7%. While *A. formosa* declines, other planktonic species (*C. tholiformis* and *S. medius*) re-appear in the beginning of the zone at low abundance of 2–3%.

Diatom concentration declines and fluctuates between 800 and 5000×10^5 valves g^{-1} ; the P/B ratio and DCs also both decline, whereas the reconstructed TP slightly increases reaching about $52.0 \mu g L^{-1}$ on average.

4.5.5. DT V (564–515 cm, ca. 300 cal yr BP–present)

While *A. subarctica* increases up to 63% nearly matching its abundance in DTIII, *A. subarctica* fo. *subborealis* is present at low abundance and nearly disappears towards the end of the zone. *A. formosa* and *Fr. capucina* v *gracilis* also show a substantial increase, while *S. construens* v *construens* declines together with the *Pseudostaurosira*–*Staurosira* group.

Diatom concentration remains at the same level, reconstructed TP declines and the P/B ratio increases towards the end of the zone reaching the maximum for the core of 3.5. DCA axis 1 scores, DCs, and N2 show similar values to DTII.

4.6. Chironomid analysis

In total, 92 taxa and morphotypes were identified in 92 samples from the Lifebuoy sediment core. Fig. 5 shows the chironomid stratigraphy together with local assemblage zones, chironomid-inferred mean July air temperature, DCA axis 1 sample scores and Hill's N2.

Glyptotendipes pallens-type, *Polypedilum nubeculosum*-type and *Limnophyes* occurred throughout the core at up to 10% relative abundance. The chironomid assemblages are dominated by Chironominae, particularly *Sergentia coracina*-type and *Chironomus* spp. which reach relative abundances of approximately 30% at some levels.

Chironomids first appear at 1188 cm. It is dominated by *Chironomus anthracinus*-type and Chironomini larvula, which both occurred at 19% abundance. *Corynoneura arctica*-type and *Limnophyes* were also prevalent at approximately 10% abundance. Species richness is low, with 7 taxa recorded and a Hill's N2 of 6.8.

4.6.1. Zone CI (1184–1072 cm, 6500–5200 cal yr BP)

Species richness increased in this zone to between 26 and 38 taxa and Hill's N2 of 20 to 30 and remained at this level throughout the

remainder of the core. The relative abundances of *C. arctica*-type and *C. anthracinus*-type declined at the start of this zone while other taxa including *G. pallens*-type and *Tanytarsus mendax*-type appeared for the first time. A peak in the abundance of *Corynoneura ambigua* occurred between 1156 and 1084 cm when the taxon reached a maximum of 31%.

4.6.2. Zone CII (1072–880 cm, 5200–3550 cal yr BP)

G. pallens-type and *T. mendax*-type declined in this zone while *S. coracina*-type and *C. arctica*-type initially increased in relative abundances. *S. coracina*-type reached its maximum abundance of 33% at 1060 cm (5100 cal yr BP). From approximately 5.1 ka BP *S. coracina*-type and *C. arctica*-type declined, while other taxa, such as *Cladopelma lateralis*-type and *Zavrelia*, increased.

4.6.3. Zone CIII (880–703 cm, 3550–1500 cal yr BP)

S. coracina-type initially continued to decline in this zone before increasing to approximately 10% abundance between 756 and 792 cm. *C. lateralis*-type and *Zavrelia* also declined while *C. anthracinus*-type and Chironomini larvula increased in relative abundance. A *C. ambigua* peak occurred between 748 and 724 cm with a maximum abundance of 24%.

4.6.4. Zone CIV (703–568 cm, 1500–350 cal yr BP)

S. coracina-type increased in relative abundance and remained at approximately 5–15% abundance throughout this zone. *G. pallens*-type and *P. nubeculosum*-type also increased.

4.6.5. Zone CV (568–510 cm, 350–present)

S. coracina-type and *P. nubeculosum*-type declined in this zone. The abundance of Chironomini larvula increased to 22–32%, the abundance of *C. anthracinus*-type and *Chironomus plumosus*-type also increased, but to a lesser extent, suggesting high larvula mortality.

4.7. Chironomid-inferred July temperature

Chironomid-inferred July temperature profile (C-IT_{July}) shows almost no consistent trend fluctuating near its average value of 10.17 °C throughout ca. 6500 years of the lake history. The warmest phase in the reconstruction is between 5700 and 5300 cal yr BP when C-IT_{July} reconstruction were up to 1 °C above present (11 °C). Generally, C-IT_{July} reconstructions are slightly higher (10.24 °C) in the lower part of the core, between 1184 and 916 cm (ca. 6550 and 3900 cal yr BP), compared to the upper part (10.14 °C). However, this difference is within the error margin of the reconstruction.

5. Discussion. Environmental history of Lifebuoy Lake and regional climate patterns

5.1. Mid Holocene, ca. 6500–3900 cal yr BP

Basal sediments of Lifebuoy Lake have an age of 7000 cal yr BP (at 1230 cm), however, the eight bottommost samples contain very little pollen. The deposits at the core consist of brownish sediments with stones and gravels with very low organic content. Diatoms are present at very low abundance with most diatom frustules being broken and chironomids are totally absent from the lake sediments at this time. Although this might imply the beginning of lake development, sediment accumulation at nearby Pechora Lake started 3000 years earlier (Andrén et al., 2015-in this issue), which suggests that most likely the lake was formed before 7000 cal yr BP, but a tephra layer prevented the coring device from penetrating any deeper into the sediments (D. Hammarlund, pers. comm). However, broken diatom frustules and high mineral content of the sediment (LOI is at 5% at the bottommost layer) imply high catchment erosion and possibly murky waters between 1204 and 1190 cm.

The first unbroken diatoms appear at 1188 cm. The diatom flora of the three bottom layers is quite unusual, with large robust epipellic motile species e.g., *E. adnata* and *R. gibba* dominating the diatom assemblages. These species usually occur at high alkalinity fresh or brackish waters with low nutrient content (EDDI online diatom database). They also contain symbiotic Cyanophyta algae, which fix nitrogen enabling diatoms to thrive in low-nutrient environments. Motile diatoms were also shown to gain competitive advantage in lakes influenced by volcanic ash fallout (Harper et al., 1986). A planktonic taxon, *A. italica*, also appears early in the sequence indicating that the depth and water clarity was already sufficient to support plankton. High values of the algae *Pediastrum* between 1080 and 1160 cm also suggest expansion of permanent freshwater environment (Fig. 3). The first chironomids also appear at 1188 cm. The earliest sample is dominated by *C. anthracinus*-type and Chironomini larvula, which are typical early colonisers in lakes after significant environmental change (Brooks et al., 1997). *C. arctica*-type and *Limnophyes* are also common; these taxa are associated with aquatic macrophytes and their presence suggests the establishment of a relatively productive lake ecosystem. The first vegetation established in the surroundings of Lifebuoy Lake consisted mainly of shrub alder, birches, grasses and ferns. Abundances of *P. pumila* pollen grains are low (<5%), which suggests that the shrub was not yet established in the catchment area of Lifebuoy Lake at this time.

Several small Fragilaroid taxa (*Pseudostaurosira*/*Staurosira* group, *S. pinnata*, *S. construens v. construens*) are constantly present in the sediment record from about 7000 cal yr BP. These benthic diatoms are widespread in the Arctic and sub-Arctic and are considered pioneer species tolerating high energy environments of early Holocene and shallow windy waters. These taxa have wide total P tolerance occurring both in eutrophic ponds (e.g., Bennion, 1995; Bennion et al., 2010; Sayer et al., 2010) and in oligotrophic neutral to slightly alkaline arctic lakes in N America (e.g., Antoniadou et al., 2005; Bouchard et al., 2004; Douglas and Smol, 1995; Finkelstein and Gajewski, 2008), and Eurasia (e.g., Biskaborn et al., 2012; Laing et al., 1999; Solovieva et al., 2005, 2008; Wischniewski et al., 2011). They are also quite abundant throughout the Holocene in the nearby Pechora Lake (Andr n et al., 2015-in this issue), although at a slightly lower abundances compared to Lifebuoy Lake. Several Fragilariaceae species also occur at relatively high abundance at the southern Kamchatka lake Sokoch (Hoff et al., 2014).

From about 6300 cal yr BP the lake environment changes dramatically, both chironomid and diatom species diversity increases and the amount of organic matter increases sharply up to the highest levels for the core, with LOI reaching 45%. Diatom composition changes: the assemblages became dominated by the Fragilariaceae complex of species together with several eutrophic and mesotrophic planktonic taxa, i.e., *A. formosa*, *Cyclostephanos medius*, *C. tholiformis*, *S. parvus* until 5200 cal yr BP and *S. hantzschii* between ca. 5200 and 3850 cal yr BP. At present these species occur regularly in eutrophic ponds and reservoirs with a wide geographical distribution from the tropics to the sub-arctic covering Africa, Asia, N and S. America and Europe (e.g., Anderson, 1990; Genkal, 1993; Hakansson and Bailey-Watts, 1993; Bennion, 1995; Bennion et al., 2010; Sayer et al., 2010; Werner and Smol, 2005, EDDI online diatom database). The occurrence of the above eutrophic and mesotrophic taxa in Lifebuoy suggests high nutrient availability and high productivity from about 6200 cal yr BP and this is reflected by the high concentration of diatom-inferred TP values.

Relatively high productivity is often observed in recently deglaciated lakes where catchment minerals are readily available for use by algae and high temperatures facilitate nutrient cycling (e.g., Jones et al., 2011; Norton et al., 2011). For instance, *S. parvus* occurred in an Italian alpine lake during a short inter-stadial, Oxygen Isotope Stage 2 (Nimmergut et al., 1999). Several *Stephanodiscus* species also occurred in Ribains Maar lakes in France during the Eemian (Rioul et al., 2001). However, in sediment records of N America and NW Europe appearance of *Cyclostephanos* and *Stephanodiscus* taxa is often linked to

cultural eutrophication (e.g., Anderson, 1990; Battarbee, 1978; Bennion et al., 2010; Haworth, 1972; Sayer et al., 2010). In the case of Lifebuoy Lake the former explanation is more likely as there is no evidence of substantial anthropogenic influence on the lake at that time, although there is a Palaeolithic settlement at the Ushki Lake (about 300 km south from Lifebuoy Lake) dating back to ca. 13,000 cal yr BP (Dikov and Powers, 1968; Goebel et al., 2003). Another possible nutrient source is migrating and nesting sea birds, considerable numbers of which (up to 400,000 at present) are found on the nearby Karaginsky Island and a 2 km strip of coastal zone of Karaga Bay (Dan Hammarlund, pers. comm). Seabirds may contribute substantially to total nitrogen (N) concentrations in coastal lakes, although the diatom response to it is not always unequivocal (e.g., Keatley et al., 2011). Additional parameters, e.g., $\delta^{15}\text{N}$, may be required to confirm the source of total N in sediments.

The occurrence of various *Stephanodiscus* species, mainly *S. medius*, *S. minutulus* and *St. alpinus*, albeit at lower abundance, in lake sediment cores in the central and south Kamchatka is noted by Hoff et al. (2012, 2014) at around 5000–5500 cal yr BP. Several *Stephanodiscus* specimens also occurred in the nearby Pechora Lake (pers comm, Elinor Andr n, see this volume). At present, various *Stephanodiscus* taxa (e.g., *S. popovskaya*, *S. hantzschii*, *S. alpinus*) are found in several lakes from the southern Kamchatka (Genkal and Lepskaya, 2013).

Rapid increase in *C. ambigua* between 6150 and 5300 cal yr BP might also be an indication of enriched nutrient status of the lake during this period. Although this taxon occurs in various training sets as a cold stenotherm (Brooks and Birks, 2001; Larocque et al., 2006; Self et al., 2011), Brodersen and Lindegaard (1999) found it in warm, shallow eutrophic lakes in Denmark. They proposed that this chironomid prefers macrophyte-rich clear water environment to macrophyte-poor and turbid water with low light penetration. Therefore the peak in the abundance of *C. ambigua* may indicate the lake with water lake rich in macrophytes, which is also implied by the well-developed diatom phytoplankton assemblages occurring during the same time in Lifebuoy.

Interestingly, the chironomid assemblage changes are very similar to those of the diatoms, i.e., the zone boundaries in chironomid and diatom stratigraphic zones almost coincide, especially in lower part of the core, suggesting that both diatoms and chironomids respond to the same environmental triggers.

Tephra deposits might increase silica input to the lake (Telford et al., 2004) thus facilitating the development of diatom plankton, increase in diatom concentration and species diversity. A thick (1176.6–1172.5 cm, 6430–6390 cal yr BP) tephra layer occurs immediately beneath DTI (Fig. 4) and it is feasible that it might have caused some of the above changes in diatoms assemblages by supplying silica to the lake water (Telford et al., 2004). High amounts of charcoal occur at the same depth (Fig. 3) and this might imply fertilisation effect of forest fires and/or volcanic eruptions on Lifebuoy Lake, although the nearest volcano is located about 300 km away.

Tephra might also facilitate the increase in the *C. lateralis*-type and *Zavrelia* by providing favourable substrate for the development of their larvae (Ferrington, 1995; Pinder and Reiss, 1983). Abundance of these chironomids increased following deposition of the tephra layers at 1060 cm (5100 cal yr BP), 900 cm (3700 cal yr BP) and 724 cm (1700 cal yr BP).

5.1.1. Late-Holocene (3900 cal yr BP–present)

A dramatic increase in Siberian dwarf pine *P. pumila* from 1–2% to more than 20% took place at ca. 3900 cal yr BP, ca. 100 years later than the *P. pumila* increase at Pechora Lake (Andr n et al., 2015-in this issue) and Olive-backed Lake in central Kamchatka (Self et al., 2015-in this issue). In north eastern Siberia, at Smorodinovoye Lake (located west from Lifebuoy Lake across the Okhotskoe Sea) the peak of *P. pumila* occurs at about the same time although its spread started earlier, from about 5900 cal yr BP, which is typical for eastern Siberia

(Anderson et al., 2002). Generally, *P. pumila* is widespread in the Russian Far East even occurring above the alpine tree-line and limited by the 12 °C mean July isotherm (Andreev, 1980). In Japan, however, it occurs in sub-alpine zone with August temperature limit of 10 °C (Yanagimachi and Ohmori, 1991), which is comparable to the chironomid-inferred temperatures at Lifebuoy lake. The northward spread of *P. pumila* across the Kamchatka Peninsula appears to have been driven by an increase in the amount of winter snow and the duration of snow-cover (Hammarlund et al., this vol).

Major changes in both diatom and chironomid communities took place approximately 300 years after *P. pumila* arrival at the lake catchment as shown in Figs. 4 and 5. A dramatic increase in *A. subarctica* and *A. subarctica* fo. *subborealis*, together with the increase in diatom concentration and the P/B ratio occurs at the same time as the chironomid changes. From ca. 3500 cal yr BP chironomid taxa indicative of warm, productive lakes decline and are replaced by species typical of cooler summer temperatures such as *C. anthracinus*-type, *Tanytarsus lugens*-type and Chironomini larvula. Chironomid-inferred July temperatures decline slightly and are largely, between 9.5° and 10 °C (approximately 0.5 below present-day).

The rate of change measured in DCs (Fig. 4) in diatom assemblages shows a statistically significant increases at about 4000 and 3500 cal yr BP, the former peak coinciding with the *P. pumila* arrival in the catchment (Fig. 3). However, the statistically significant compositional change of the chironomid community occurs later, at about 3100 cal yr BP, and this coincides with another increase in the diatom rate of change (Fig. 4), albeit not statistically significant.

A. subarctica agg, which became the dominant planktonic taxon and almost totally replaced several *Stephanodiscus* species from 876 cm (3500 cal yr BP) is a meso-trophic planktonic taxon, and is commonly found across several biogeographical regions, including the Arctic, the Sub-Arctic and temperate zones. This heavily silicified diatom often occurs in the plankton of cold, large and turbulent lakes in western Europe, e.g., Lake District (e.g., Gibson et al., 2003), northern Ireland (Jewson et al., 1981), and north America (e.g., Kilham et al., 1996). It is also wide-spread in the sub-arctic and arctic Russia, e.g., the northern Urals (Solovieva et al., 2005, 2008), Siberia and in several lakes in Kamchatka (e.g., Andrén et al., 2015-in this issue; Hoff et al., 2012, 2014; Lepskaya et al., 2010). A similar increase of *A. subarctica* occurred about 700 years later than at Lifebuoy, at around 2800 cal yr BP, at a small lake in central Kamchatka (Hoff et al., 2012). At the nearby Pechora Lake *A. subarctica* largely dominates the diatom assemblages from about 6500 cal yr BP until present and shows no clear response to the arrival of *P. pumila* in the catchment.

In Yellowstone Lake *A. subarctica* thrived in years with longer cold winters and delayed spring turn-over period (Kilham et al., 1996) and its rapid increase in Ribains Maar coincided with the onset of the late Weichselian glaciation and *Pinus* expansion (Rioual et al., 2001). Its occurrence in the plankton is either associated with windy conditions, e.g., Lough Neagh (Jewson et al., 1981) or spring water turn-over in deeper lakes (e.g., Kilham et al., 1996; Lepskaya et al., 2010).

In Lifebuoy, the peak in *A. subarctica* (up to 80% abundance) coincides with the rapid increase in diatom concentration indicating the rise in diatom productivity. A similar period with high dominance of *A. subarctica* (up to 90% abundance) occurred about 1800 years earlier at Pechora Lake, (5200–3900 cal yrs BP, Andrén et al., 2015-in this issue).

The *A. subarctica* peak is unlikely to be related to the silica increase through tephra deposition (Barker et al., 2003; Telford et al., 2004), since the nearest tephra layer at 908 cm (ca. 3800 cal yr BP) was deposited almost 350 years before the rise in diatom productivity (Fig. 4). However, the abrupt disappearance of all *Stephanodiscus* and *Cyclotella/Discostella* taxa from the lake immediately above this tephra layer might be due to the tephra sealing the sediment and thus stopping phosphorus from re-entering the water column and therefore decreasing the nutrient status of the lake (Barker et al., 2003;

Telford et al., 2004) as the impact of tephra on lake ecosystem may vary.

The sudden increase in *A. subarctica* in Lifebuoy Lake might be a response to the changed climatic conditions, which also facilitated the spread of *P. pumila*: i.e., the late Holocene cooling, which led to cooler winters and the increase in winter precipitation and occurred at about 4200 yr cal BP in Kamchatka (Barr and Solomina, 2014 Hammarlund et al. this vol.). Recent chironomid-based reconstructions from the central Kamchatka suggest summer cooling between about 4500 and 3600 cal yr BP and then higher July temperatures between 3600 and 2800 cal yr BP (Nazarova et al., 2013). The warm summer phase almost exactly coincides with the peak in *A. subarctica* and the increase in diatom concentration in Lifebuoy Lake. On the regional scale, The North Pacific Index, which is a measure of the Aleutian Low Pressure system (AL), showed strengthening between 4500 and 3500 cal yr BP, which led to more intensive south-westerly winds (Anderson et al., 2005). After 3500 cal yr BP AL became weak again, thus leading to more moisture delivery and possibly higher levels of winter precipitation in the north Kamchatka and the delayed spring ice-melt and water turnover, which in turn created favourable conditions for *A. subarctica*.

From about 2900 cal yr BP both varieties of *A. subarctica* rapidly decrease and the lake is dominated by benthic Fragilariaceae, which again might indicate low light and high-energy conditions.

From ca. 1900 cal yr BP *P. pumila* and *Betula* pollen increase together with *Cyperaceae* and *Sphagnum* at the expense of *A. viridis* pollen grains and Filicales spores. This might be an indication of wetland expansion around the lake. From about 300 cal yr BP *A. subarctica* (long-valved form) again increases in Lifebuoy, whereas *A. subarctica* fo. *subborealis* (short-valved form) is almost absent from the lake.

The increase in *A. subarctica* during the last 300 years almost exactly coincides with the changes in chironomid community – the increase in Chironomini larvula and the corresponding decrease in *P. nubeculosum* and *S. coracina* type together with simultaneous changes in chironomid and diatom species diversity (chironomid N2 index declines whereas diatom N2 index increases) indicate again that the lake ecosystem responds to the same external triggers, most likely climatic. The C-IT_{July} reconstruction suggests the lowest July temperatures between ca. 600 and 100 cal yr BP in the whole Lifebuoy record. The cold summer phase during the late Holocene in central Kamchatka is also confirmed by other chironomid reconstructions (Nazarova et al., 2013) glacier advances (Savoskul, 1999; Barr and Solomina, 2014) on the Bering and Kurile Islands.

One period of the high abundance of *A. subarctica* in Lifebuoy Lake (between ca. 3500 and 2850 cal yr BP) coincides with generally warm summer phase in central Kamchatka, Kurile and Bering islands (although there is heavy winter precipitation and heavy snowfall) (e.g., Barr and Solomina, 2014; Nazarova et al., 2013), whereas the peak of *A. subarctica* during the last 300 years occurs at the period of low summer temperatures in both in Kamchatka and north Beringia (e.g., Dirksen et al., 2013; Barr and Solomina, 2014). This might imply that *A. subarctica* shows no direct response to changes in air temperature at Lifebuoy Lake. Instead, similarly to other planktonic diatom taxa, it is influenced by the amount of winter precipitation (prefers heavy snow fall and thick ice), the timing and intensity of the spring-turn over period and the length of ice-cover (thrives at the delayed spring turn-over period).

It is unlikely that synchronous changes in diatom and chironomid assemblages during the last 300 years could have been influenced by several underlying tephra layers, as they were deposited about 330 years earlier.

6. Conclusions

The reconstructed changes in pollen, spores, diatoms and chironomids from the Lifebuoy Lake sediment sequence reveal 7000 years of environmental history of the lake and its catchment. On the whole, the environmental history of Lifebuoy Lake follows the broad regional patterns of vegetation development and climate change. Throughout

the core, diatom and chironomid assemblages show synchronous changes, implying that both organisms were responding to the same triggers.

Between ca. 6300 and 3900 cal yr BP, the lake ecosystem was naturally enriched, with several *Stephanodiscus* species dominating diatom plankton. Most likely, the natural eutrophication state was brought about by a combination of catchment geology, the fertilisation effect of several fires in the catchment, silica input from underlying tephra and, possibly, nitrogen input from seabirds. A tephra deposit at 908 cm (3850 cal yr BP) changed the lake nutrient status by disrupting phosphorus sediment/water column cycling and led to an abrupt shift from a *Stephanodiscus*-dominated plankton to a benthic complex of taxa dominated by Fragilariaceae.

Both diatoms and chironomids showed coeval compositional changes, which are also reflected by statistically significant changes in the rates of change 300–400 years after the arrival of *P. pumila* in the lake catchment at ca. 3900 cal yr BP. The rapid increase in both diatom concentration and the abundance of large heavy *A. subarctica* was probably a response to the change in timing and intensity of lake spring turn-over of the lake as a result of heavier winter precipitation and thicker ice-cover due to the changes in the patterns of North Pacific atmospheric circulation, most notably the westward shift of Aleutian Low.

Interestingly, that the two highest peaks in *A. subarctica* abundance at Lifebouy Lake occurred during opposite summer temperature inferences: the earlier peak (3500–2900 cal yr BP) coincided with warm summers and the latter peak (300 cal yr BP–present) occurred during the coldest summers. This implies that in Lifebouy lake *A. subarctica* shows no direct response to changes in air temperature. Instead, climatic impact on diatom composition and abundance is indirect and is conveyed through either influence of erosion and leaching from catchment soils and/or changes in ice-cover regime and timing and intensity of period of water turn-over.

Tephra impacts on the Lifebouy lake ecosystem are not unequivocal. The clearest effect of tephra deposition is above 908 cm, where the tephra layer disrupted sediment/water column circulation. Tephra deposits might have contributed towards development of eutrophic plankton from about 6300 cal yr BP. It is not certain if several tephra deposits influenced diatom and chironomid changes during the last 300 years.

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