Factors controlling recent diatom assemblages across a steep local nutrient gradient in central-eastern Finland

Mira Tammelin[1], Tommi Kauppila[2], Matias Viitasalo[3]

[1]Tammelin, Mira, University of Turku, Department of Geography and Geology, FI-20014 University of Turku, Finland
[2]Kauppila, Tommi, Geological Survey of Finland, P.O.Box 1237, FI-70211 Kuopio, Finland
[3]Viitasalo, Matias, Ramboll Finland Oy, Kirjastokatu 4, FI-70100 Kuopio, Finland

Abstract

The Iisalmi Route, a chain of lakes in central-eastern Finland, is more eutrophic than its surroundings. We used multivariate analyses to study the influence of selected environmental factors (water quality, basin characteristics, and subcatchment surficial geology) on the recent diatom assemblages across this steep local nutrient gradient. In addition to the spatial analysis of surface sediment diatom assemblages from 51 sampling sites (48 lakes), temporal changes in the total phosphorus (TP) concentrations of one Iisalmi Route lake (Lake Kirmanjärvi) were analyzed using weighted averaging partial least squares regression and 27 fossil diatom samples. Both TP and electrical conductivity (EC) showed statistically significant independent signals in the modern diatom data. The TP gradient was related to till grain size variation suggesting that geological factors affect the spatial TP variation directly or indirectly through differences in land use. Based on the temporal study, the direct effect of geology is most likely behind the steep nutrient gradient in the area because Lake Kirmanjärvi was found to be naturally eutrophic. EC, on the other hand, seems related to anthropogenic disturbance. Our study highlights the importance of taking the local geology into account when assessing past or present water quality or planning for lake management.

Keywords

Lakes, eutrophication, phosphorus, electrical conductivity, Quaternary deposits, multivariate analysis, transfer function

Introduction

Eutrophication remains one of the most persistent problems affecting lake water quality after a nearly half a century of mitigation practices (Ekholm & Mitikka, 2006; Schindler, 2006). Sediment-based paleolimnological techniques are widely used for assessing human-induced changes as well as for estimating the pre-disturbance conditions of lakes in order to set realistic management goals (Bennion et al., 2011a; Davidson & Jeppesen, 2013). Paleoecological methods utilize remains of micro-organisms preserved in sediment cores. These data are commonly studied with multivariate methods, suitable for revealing distribution patterns and the relationship between the species and environmental data, and transfer functions that enable the quantitative reconstruction of past water quality from the paleoecological data (Smol, 2008; Birks, 2010; Birks et al., 2012). Diatoms, in particular, are excellent biological indicators of environmental conditions (Battarbee et al., 2001).

Diatom assemblages are controlled by a multitude of environmental factors with complex relationships (Juggins, 2013; Rühland et al., 2015). These relationships tend to vary regionally as many characteristics of an individual lake system are defined by the local geological and land use histories as well as climate-related factors, such as vegetation, thermal properties, and insolation (Håkansson, 2005; Leavitt et al., 2009). The geological controls are based on basin morphology and watershed properties, such as topography, soil erodibility, and nutrient availability. For example, in regions where surficial geology is dominated by fine grained sediments, lake basins are typically shallow and the fertile, easily eroded watersheds have attracted agriculture early in their history (Sherratt, 1980; Taavitsainen et al., 1998).

The Iisalmi Route, a mosaic of interconnected lakes in central-eastern Finland (Fig. 1), is a prime example of a region where the relationship between environmental factors seems to differ from those in its surrounding areas. It has proven to be a challenging locality for water management, because models that seek to predict water quality and lake response to nutrient loading have performance issues, such as the underestimation of natural TP export (Dubrovin et al., 2016), when applied to the area. The Iisalmi Route has been suspected to be naturally nutrient rich and, indeed, its flanks were the first areas to be inhabited when central-eastern Finland was permanently populated in the 16th century (Soininen, 1961). Currently, it is characterized by conspicuously eutrophic lakes with generally poorer water quality than the lakes in its vicinity (Kauppila et al., 2012).

The main purpose of this study was to examine the diatom species gradient and the spatial relationship between surface sediment (recent) diatom assemblages and the environmental factors in the eutrophic Iisalmi Route and its nutrient poorer adjacent areas with ordination and regression methods. In addition to water quality and basin characteristics, we studied the influence of local geology (the composition of surficial sediments in the subcatchments of the lakes) to diatom assemblages. Our aims were to find the environmental variables with the strongest statistical total and independent effects on the diatom data, in other words the main drivers of the spatial diatom assemblage variation, and to study this spatial variation in the diatom, water quality, basin, and catchment geology characteristics between the Iisalmi route and its surrounding areas. Furthermore, we applied the found statistical connection between the modern diatom assemblages and total phosphorus (TP) as a tool to study the past TP conditions of one Iisalmi Route lake (Lake Kirmanjärvi) based on a previously published fossil diatom data set (Kauppila et al., 2012).

Materials and methods

Lake selection and study area

Lake selection for this study was done by first listing the lakes in the eutrophic Iisalmi Route and its nutrient poorer surroundings in central-eastern Finland according to their water quality and then qualitatively selecting lakes so that the different concentrations of the TP gradient from oligotrophic to hypertrophic were represented and that the variety of catchment geologies was captured as well. The selection process was restricted by the availability of suitable water quality observations, because the study area is remote and the water quality of many lakes is rather infrequently monitored. As many sites were selected as was possible with the available resources. Small and shallow lakes are typical in the area-of-interest (the Iisalmi Route) and, therefore, larger and deeper lakes were avoided in the lake selection process. Also low pH lakes in swampy areas and lakes next to anthropogenic point sources were left outside of this study.

The selected 48 lakes (51 sampling sites) are located between latitudes 62º 44´ N-63º 52´ N and longitudes 26º 18´ E-28º 96 04´ E (Fig. 1). Most sampling sites (26) belong to the Iisalmi Route, 12 to the Rautalampi Route, 8 to the Nilsiä Route, and 5 to the Kallavesi-Sorsavesi area. The Iisalmi Route is further divided into three subroutes (Kiuruvesi, Salahmi, and Sonkajärvi) that all drain into a central basin area. The Iisalmi and Nilsiä Routes drain into the Kallavesi-

Sorsavesi area, all located in the upper reaches of the Vuoksi drainage system that flows into Lake Ladoga in Russia. The Rautalampi Route, a headwater part of the Kymijoki drainage system, drains into the Gulf of Finland. The lakes are mostly small (surface area < 10 km^2) and shallow (average depth < 4 m) and the catchments vary in size from 0.1 to 5 600 km^2 (mean 605 km^2) and subcatchments from 0.1 to 336 km^2 (mean 39 km^2). The lakes are located at altitudes ranging 82-160 m.a.s.l. and their retention time varies from 4.5 days to 3.5 years (mean 221 days). The Iisalmi route, in particular, is characterized by small and shallow lakes that have high nutrient and humus concentrations (Table 1).

The bedrock in the area is characterized by the sheared Savo Belt that is located between the Archean Iisalmi complex and the Proterozoic central Finland granitoid complex (Vaasjoki et al., 2005). These are overlain by Quaternary tills, clays and other fine-grained sediments, eskers, and peat deposits. The tills covering Finland are typically coarse-grained, but fine-grained till is also common in the study area. The area belongs to the southern boreal vegetation zone (Ahti et al., 1968), but well-humified brown soils of the hemiboreal zone also exist in clayey and silty areas (Taavitsainen et al., 1998). The annual mean temperature, precipitation, and evaporation are 3.2 ˚C (Pirinen et al., 2012), 655 mm, and 464 mm, respectively (Korhonen & Haavanlammi, 2012).

The heaviest diffuse nutrient loading, mainly from grass cultivation, livestock husbandry, and forestry, is concentrated on the Iisalmi Route and the downstream parts of the Nilsiä Route (Vallinkoski et al., 2016). Livestock breeding, in particular, can lead to high amounts of easily available phosphorus (Järvenranta et al., 2014). In addition, many lakes have been lowered artificially and the water levels of the larger lakes are regulated (Tanskanen, 2002; Vallinkoski et al., 2016).

Sampling and data sets

Lake sediments were cored in late winter 2010 with a Limnos® gravity corer (Kansanen et al., 1991) that is designed for taking undisturbed surface sediments. The coring sites were located in the deepest parts of the lake basins, at or near pre-selected water quality monitoring sites of the environmental administration to provide a good match between water quality data and sediment diatom assemblages. Diatom slides were prepared from the surface sediments (0-1 cm) by using standard procedures described, for example, by Battarbee et al. (2001). A minimum of 400 valves were identified with a phase-contrast light microscope at 1000x final magnification and by using the nomenclature of Krammer &

Lange-Bertalot (1986-1991), Krammer (1992), Lange-Bertalot & Moser (1994) and Houk (2003). The taxonomical diversity of the diatom samples was calculated with Past software version 2.09 (Hammer et al., 2001) by using individual rarefaction (Hurlbert, 1971). In addition to diatoms, chrysophyte cysts were counted from the slides and transformed into cyst to diatom (CD) ratio (Werner & Smol, 2005).

Data for seven water quality variables and five lake basin characteristics were collected from the OIVA information service and from VEMALA (Huttunen et al., 2016), the national-scale nutrient loading model for Finnish watersheds of the Finnish Environment Institute (Table 1, see also Online Resource 1). When available, we calculated the medians of the growing season (~May – mid-Oct.) water quality observations of 2000-2009. Small and remote lakes, typical to the study area, are infrequently monitored, so 12 sampling sites lacked the desirable water quality data for one or more environmental variable. For these lakes, we used either near growing season observations (Apr./late Oct.) of 2000-2009 or growing season observations from the 1990s. In three cases, a mixture of whole year observations from the two decades had to be used. As TP was used for environmental reconstructions, we further ensured the applicability of the used TP observations by drawing plots from all the available observations in order to see possible temporal trends. Most lakes did not show any notable trend in TP during the last three decades and the variation of 2000-2009, in particular, was mainly dominated by seasonal variation. In addition to the water quality and basin characteristic data, the percentage of fields in each subcatchment was calculated based on the data available in VEMALA.

The distribution of surficial geology (Quaternary deposits) in the subcatchments of the study lakes (Table 2, see also Online Resource 2) were calculated using ArcGIS software and the Quaternary maps of Finland (Geological Survey of Finland, 2012). The most detailed (1:20 000) maps, covering approximately 50 % of the whole study area, were used when available. For areas lacking the detailed maps, the 1:1 000 000 map was used for calculating the percentages of fine-grained and coarse-grained till in the subcatchments and the 1:200 000 map (lacking a differentiation between the two till types) for the other deposits.

For the temporal study we used a previously published fossil diatom data set from Lake Kirmanjärvi (Kauppila et al., 2012) located in the Iisalmi Route (Fig. 1). The data set includes 27 core samples taken in 2006 with a downwards increasing interval reaching down to 150 cm in the sediment. Based on the age-depth model of Kauppila et al. (2012), the bottommost sample represents the mid-16th century at the latest.

Numerical methods

Prior to the ordination and regression analyses, the environmental data (excluding pH) were log-transformed to reduce skewness in the original distributions and the species data were square root transformed to stabilize the variance of the data (ter Braak & Šmilauer, 2002). Exploratory data analysis revealed one outlier sample (Lake Suo-Valkeinen) that differed from the other samples based on its water quality, low pH (5.5) in particular, as well as its benthic diatom community dominated by *Eunotia* spp., *Pinnularia* spp., and *Frustulia* spp, and a high CD ratio. Therefore, Lake Suo-Valkeinen was excluded from further analysis.

The structure of the diatom data, as well as the relationship between the species and the environmental data (water quality, basin characteristics, and Quaternary deposits), were examined with multivariate ordination methods by using Canoco 4.5 for Windows software (ter Braak & Šmilauer, 2002). Detrended Correspondence Analysis (DCA; Hill & Gauch, 1980) was first performed to examine the length of the species gradient and the properties of the unconstrained axes. The length of the species gradient exceeded 1.5 SD units allowing the use of unimodal methods (ter Braak & Prentice, 1988). Therefore, Canonical Correspondence Analysis (CCA; ter Braak, 1986) was used with Monte Carlo permutation test (999 permutations) to find out how well the supplied environmental data explained the observed variation in the species data and to discover the environmental factors with the strongest effects on the diatom data. CCA was run separately for water quality and Quaternary deposit data. The relationships between the diatom data and the water quality variables that had the strongest effects were further examined with partial, constrained CCA. In addition, the species gradient lengths in the direction of the different environmental factors were determined by using Detrended Canonical Correspondence Analysis (DCCA; ter Braak, 1986).

To further study the temporal changes in the nutrient concentrations of Lake Kirmanjärvi, we developed a diatom-TP transfer function based on weighted averaging partial least squares regression (WA-PLS; ter Braak & Juggins, 1993) and leave-one-out cross-validation (jack-knifing) with C2 software version 1.6.8 (Juggins, 2007). TP was chosen because it had a stronger independent signal in the diatom data than TN. Diatom taxa present in at least three samples and with a relative abundance of at least one percent, 110 in total, were included in the transfer function. The reconstructed values for the past water quality conditions in Lake Kirmanjärvi were compared to the annual averages of monitored values and LOESS smoothed annual averages, as well as to the sample scores of the first and second axes in Lake Kirmanjärvi DCA. The fossil samples were also plotted passively on top of a CCA ordination formed by the modern diatom and water quality data to see the trajectory of the lake during the last centuries in relation to modern water quality in the area.

Furthermore, the fossil samples were tested for good modern analogs in the modern data set by calculating the squared chord distances (SCD) between the fossil samples and their closest modern samples (Overpeck et al., 1985; Birks, 1995; Simpson, 2012) with Python programming language. These minimum SCDs between each fossil sample and the modern samples were compared to the 2.5th, 5th, and 10th percentiles of the distribution of the pairwise dissimilarities of the modern samples (Bennion et al., 2004; Bennion et al., 2011a, 2011b; Simpson, 2012). Fossil samples with a minimum SCD lower than the 2.5th percentile were considered to have very good modern analogs, whereas the 5th percentile was used as a critical value for good modern analogs (Simpson, 2012). Fossil samples with a minimum SCD exceeding the 10th percentile were regarded as having no modern analogs.

Results

Diatom assemblages

The diatom assemblages varied across the study area reflecting the variation in the environmental conditions between the lake routes. The central basin area of the Iisalmi Route and the Kiuruvesi Subroute showed the least diverse diatom communities with a high relative abundance of planktonic species and the lowest CD ratios (Fig. 2). Conversely, the Kallavesi-Sorsavesi area was characterized by the most diverse diatom assemblages with equally abundant benthic and planktonic taxa and a higher relative abundance of chrysophyte cysts than in the other areas.

From over 500 identified diatom taxa, the planktonic *Aulacoseira ambigua* (Grunow) Simonsen and *Aulacoseira subarctica* (Müller) Haworth were the most abundant, particularly in the Iisalmi route. Small *Fragilaria* spp., such as *F. construens* f. *venter* (Ehrenberg) Hustedt, *F. brevistriata* Grunow, and *F. exigua* Grunow, were the most abundant benthic taxa. Other common species occurring in the whole study area included *Cyclotella stelligera* Cleve & Grunow, *Asterionella formosa* Hassal, and *Aulacoseira lirata* (Ehrenberg) Ross. The areas surrounding the Iisalmi Route had also relatively high abundances of *Tabellaria flocculosa* (Roth) Kützing, *Achnantes minutissima* Kützing, *Aulacoseira distans* (Ehrenberg) Simonsen, *Aulacoseir*a *distans* var. *nivalis* (Smith) Haworth, *Aulacoseira alpigena* (Grunow) Krammer, *Cyclotella radiosa* Grunow, and *Cyclotella rossii* (Grunow) Håkansson. *C. rossii*, however, was only found in the Rautalampi Route and in the Kallavesi-Sorsavesi area.

Less abundant *Aulacoseira granulata* (Ehrenberg) Simonsen, *Aulacoseira islandica* (Müller) Simonsen, and *Fragilaria capucina* var.*gracilis* (Oestrup) Hustedt occurred primarily in the Iisalmi and Nilsiä Routes. *Cyclotella pseudostelligera* Hustedt favored only a few lakes in the Kiuruvesi Subroute and in the Rautalampi and Nilsiä Routes, whereas *Diatoma tenuis* Agardh was abundant only in Lake Kirmanjärvi and *Fragilaria nanana* Lange-Bertalot in Lake Saarisjärvi in the Iisalmi Route.

Ordination

Unimodal ordination methods were used as the species gradient length (2.32 SD units) of the square root transformed surface sediment diatom data (Lake Suo-Valkeinen excluded) was sufficient for their use. The results of the DCA based only on the surface sediment diatom data and the CCA constrained to all water quality and basin characteristic variables (Fig. 3) were very similar indicating that the selected variables were important in explaining the diatom data (Birks, 2010). The sum of all unconstrained DCA eigenvalues was 4.15, and the eigenvalues for the first and second axis were 0.26 and 0.16 explaining 6.3 % and 3.9 % of the variance in the species data, respectively. Correspondingly in the CCA constrained to all water quality and basin characteristics, the eigenvalues for the first and second axis were 0.25 and 0.16 explaining 5.9 % and 3.8 % of the variation in the diatom data. The species-environment correlations of the first and second CCA axes were 0.98 and 0.96. The CCA constrained to the Quaternary deposit data showed somewhat lower eigenvalues (0.21 and 0.11), species-environmental correlations (0.94 and 0.92), and variances explained (5.2 % and 2.7 %) for the first two axes than the water quality and basin characteristic data (Fig. 4). The sum of all canonical eigenvalues was also higher for the water quality and basin characteristic data (1.10) than for the Quaternary deposits (0.74).

The total effects of each environmental variable on the diatom data were studied with CCAs constrained to one environmental variable at a time combined with a Monte Carlo significance test of the first canonical axis (marginal testing). The relative explanatory power of a variable is often expressed as a λ_1/λ_2 ratio that is the ratio between the eigenvalues of the first (λ_1, constrained) and second (λ_2, unconstrained) ordination axes (Juggins, 2013). The marginal CCAs showed that all water quality factors, lake altitude, clay, fine- and coarse-grained tills, and other fine-grained sediments ($p = 0.001$), in addition to the other basin characteristics ($p < 0.02$), were statistically significant ($p < 0.05$). From these environmental variables, electrical conductivity (EC, $\lambda_1/\lambda_2 = 1.05$), total nitrogen (TN, $\lambda_1/\lambda_2 = 1.01$), lake altitude from sea surface ($\lambda_1/\lambda_2 = 0.99$), and total phosphorus (TP, $\lambda_1/\lambda_2 = 0.96$) had the highest explanatory power. Their species-environment correlation and explained variance in the species data were 0.94 and 5.1 % (EC), 0.93 and 4.8 % (TN), 0.90 and 4.4 % (altitude), and 0.95 and 4.9 % (TP). According to the DCCA, the gradient lengths in the direction of these four variables were 2.30 SD units (EC), 1.89 SD units (TN), 1.73 SD units (altitude), and 1.80 SD units (TP). The λ_1/λ_2 ratios, species-environment correlations, explained variances, and DCCA gradient lengths of the statistically significant Quaternary deposits ranged between 0.65-0.87, 0.86-0.88, 3.4-4.0 %, and 1.13-1.48 SD units, respectively.

The conditional or independent effects of the four variables with the highest λ_1/λ_2 ratios were further examined with partial CCAs and Monte Carlo testing. In the partial CCAs, each of these variables were tested by first taking the other three variables into account as covariables. All four tests were statistically significant ($p < 0.05$) but the independent effects of EC (71 % of its total effect) and TP (63 %) were the strongest ($p = 0.001$). The eigenvalue of the first axis was 0.134 for EC and 0.114 for TP, species-environment correlations were 0.95 and 0.97, and explanative percentages 3.6 % and 3.1 %, respectively.

Transfer function and reconstructions

The WA-PLS regression-based diatom-TP transfer function (with two components) had a coefficient of determination (r^2_{jack}) of 0.72 and a root mean squared error of prediction ($RMSEP_{jack}$) of 0.191 log µg l^{-1} (Online Resource 3). The diatom-inferred TP (DI-TP) of Lake Kirmanjärvi ranged mainly between 40-60 µg l^{-1} (Fig. 5a). Two samples representing the early 20th century showed elevated values up to 80 µg l^{-1}, but these samples lacked good modern analogs in the modern data set. The DCA sample scores of the first and second axis showed increased variation in the diatom assemblages since the late 19th century (Fig. 5a). The DI-TP correlated with the sample scores of the first DCA axis (0.72, $p < 0.001$), but not with the second ($p > 0.5$). The reconstructions of the last few decades also resembled the monitored TP values rather well (Fig. 5b) despite the 16th-19th century samples having better modern analogs than the more recent samples (Fig. 5a). The 2.5th, 5th, and 10th percentiles of the pairwise dissimilarity distribution of the modern samples in the transfer function training set (used in the analogue matching) were 0.35, 0.39, and 0.47, respectively. The trajectory of the fossil samples passively plotted on top of a CCA ordination of the modern data set displayed a recent increase in EC and pH in contrast to the rather similar nutrient conditions at the core ends (Fig. 6).

Discussion

Spatial variation in diatom assemblages and water quality

The spatial variation in the diatom assemblages is notable within our study area despite the limited geographical coverage, and the selected water quality variables are important in explaining this variance according to the ordination analysis. The Iisalmi Route samples, those in the Kiuruvesi Subroute and the central basin area in particular, plot to the high ends of the nutrient gradients in the CCA ordination (Fig. 3). These lakes are also humic, shallow, and have a low Secchi depth and TN:TP ratio. In contrast, the Kallavesi-Sorsavesi area and the Rautalampi Route samples plot to the opposite ends of these gradients. Correspondingly, the abundance of benthic diatom taxa, number of taxa, and CD ratio are lowest in the Kiuruvesi Subroute (25 %, 63, and 9, respectively) and in the central lake area of the Iisalmi Route (15 %, 48, and 7), whereas they are highest in the Kallavesi-Sorsavesi area (50 %, 81, and 29). The abundance of planktonic taxa in relation to benthic taxa, low species diversity, and a low CD ratio are often considered as indicators of eutrophy (e.g. Smol, 1985; Wetzel, 2001; Vadeboncoeur et al., 2003).

The variation in the diatom assemblages along the TP gradient is similar to that in the southern and eastern Finnish surface sediment data sets of Kauppila et al. (2002) and Miettinen (2003) that cover larger geographical areas than our data set and represent, in general, deeper and less humic lakes with lower nutrient concentrations and higher EC. *A. ambigua* and *A. subarctica*, that thrive in shallow, turbid, and eutrophic lakes (Gibson et al., 2003; Kangur et al., 2007; Heinsalu et al., 2008), as well as small, benthic *Fragilaria*, common in shallow lakes (Bennion, 1994; Sayer, 2001), are widespread and abundant in all three data sets. The upper ends of the TP gradients in these three data sets are characterized by eutrophic taxa, such as *A. granulata*, *Cyclostephanos dubius* (Fricke) Round, *Fragilaria ulna* (Nitzsch) Lange-Bertalot, and *Fragilaria crotonensis* Kitton (Van Dam et al., 1994; Bradshaw & Anderson, 2003; Bennion et al., 2015; Ventelä et al., 2016). *A. ambigua*, *A. subarctica*, *A. granulata*, *C. dubius*, and *Fragilaria* spp., in particular, are common taxa in the modern as well as background conditions of naturally eutrophic Finnish lakes (Räsänen et al., 2006). In contrast, oligo-mesotrophic species, such as *C. rossii*, *A. distans* with its subspecies, *T. flocculosa*, *C. radiosa*, and certain benthic taxa (e.g. *Brachysira* spp.) are common in the lower ends of the TP gradients in the three surface sediment data sets. The most striking difference between the data sets is in the abundance of *Stepahnodiscus hantzschii* Grunow that is infrequent in our data set but typical in the high TP and EC lakes of fertile clayey or silty areas (Miettinen, 2003), such as those in the southern Finnish data set of Kauppila et al. (2002).

According to the CCA variance partitioning, both TP and TN have a statistically significant independent effect on the diatoms but the independent fraction of TP (63 %) from the variance explained by the total effect of TP is higher than that of TN (58 %). The remaining fraction is shared with other confounding variables and can be either the result of a direct ecological effect or the environmental variable-of-interest acts as a surrogate for another, correlated environmental variable (Juggins et al., 2013). The λ_1/ λ_2 value of TP is below 1.5 in our data set, which suggests that it includes a mixture of taxa with responses to TP as well as to other confounding variables (Juggins, 2013). The λ_1/ λ_2 of TP is also slightly lower than the optimal value for reconstruction ($\lambda_1/ \lambda_2 \geq 1.0$; ter Braak, 1988), but the similarity in taxon responses along the TP gradient in our model and the two models that cover geographically larger areas suggest that TP is an ecologically important factor affecting the diatom assemblages (Juggins et al., 2013).

Indeed, most diatom taxa in our spatial data set appear to follow the TP gradient, but certain cyclotelloid, elongated pennate, and small *Fragilaria* taxa occur throughout the study area either in most lakes (e.g. *A. formosa*, *C. stelligera*, and *F. construens* f. *venter*) or sporadically in a few lakes (e.g. *D. tenuis*, *F. crotonensis*, and *C. pseudostelligera*) and are likely driven by factors other than TP. Small cyclotelloid and elongated pennate diatoms have been associated with a reduction in ice cover and an increase in thermal stability related to anthropogenic climate warming (Rühland et al., 2015), whereas small, benthic *Fragilaria* are common in shallow lakes and can be more sensitive to habitat availability than to TP (Bennion, 1994; Sayer, 2001). Anthropogenic climate warming in Finland exceeds the global warming trend and has led to earlier ice break-up, later freezing, and shorter ice cover duration in lakes (Korhonen, 2006; Tietäväinen et al., 2010; Mikkonen et al., 2015). In Lake Porovesi (a central basin of the Iisalmi Route), the period of permanent ice cover has shortened approximately by a month since the late 19th century. However, many of our lakes are colored and could, therefore, be less sensitive to climate warming than clear water lakes (Snucins & Gunn, 2000).

In addition to nutrients, EC has a statistically significant independent effect of 71 % on the diatom assemblages of our spatial data set, but it does not distinguish the lake routes as clearly as TP. The upper end of the EC (and pH) gradient is characterized by elongated pennate and small cyclotelloid taxa (e.g. *D. tenuis, C. dubius, C. pseudostelligera, F. ulna,* and *F. crotonensis*), whereas *Aulacoseira* taxa are typical in the lower gradient end. *D. tenuis* and *F. crotonensis*, in particular, are only or more commonly found in the recent sediments of naturally eutrophic Finnish lakes than in their pre-disturbance conditions suggesting that these taxa are influenced by anthropogenic activities (Räsänen et al., 2006). *D. tenuis*, for example, is most likely related to road de-icing in our study area. It is only abundant in the three lakes with the highest EC (Lake Siilinjärvi, Lake Kirmanjärvi, and Lake Pöljänjärvi) that are located next to a main road and groundwater areas with elevated chloride concentrations due to road salt (Vallinkoski et al., 2016). In addition, the supplementary variable of subcatchment field percentage resembles the EC gradient despite the EC values in our data set (mean 4.8 mS m^{-1}) being low compared to the typical Finnish values (5-10 mS m^{-1}) and especially to those increased by the intensive fertilization of fields (15-20 mS m^{-1}; Oravainen, 1999). Therefore, agriculture and other anthropogenic activities seem to influence the diatom assemblages in a way that is reflected in the EC gradient, whereas the TP gradient appears to be controlled by the underlying geology.

Spatial variation in Quaternary deposits

The occurrence of many diatom taxa in our data set follow the boundaries of the lake routes suggesting that the steep, local nutrient gradient is related to local geology either directly or indirectly through differences in land use (agriculture vs. forestry). Furthermore, the CCA sample and species biplots of the Quaternary deposits (Fig. 4) and water quality (Fig. 3) are strikingly similar. The subcatchments of the lakes in the eutrophic Iisalmi Route are characterized by a high percentage of fine-grained sediments including fine-grained till, clay and other fine-grained sediments, such as gyttja and silt. Due to these easily workable, fine-grained soils, the flanks of the Iisalmi Route were particularly attractive already for the early settlers of eastern Finland (Soininen, 1961; Orrman, 1991; Taavitsainen et al., 1998). In contrast, subcatchments in the least eutrophic Kallavesi-Sorsavesi area and the Rautalampi Route have high abundances of coarse-grained till, bedrock outcrops, and peat deposits.

The spatial distribution of the fine-grained and coarse-grained basal tills in the study area is the result of glacial dynamics during the retreat of the ice margin approximately 9 500 years ago. The fine-grained till, with a high clay fraction up to 30 % (Kukkonen & Sahala, 1988), forms a wedge-shaped area stretching from the Bothnian Bay coast across our study area in NW-SE direction. The fine fraction of the till originates from material eroded from interglacial fluvial sediments deposited in the Gulf of Bothnia (Lintinen, 1995). The fine-grained till deposited under a passive ice sheet in an interlobate area between two actively flowing, fan-shaped ice lobes, the North Karelian and the Lake District ice lobes (Punkari, 1997; Lunkka et al., 2004). The coarse-grained till areas, on the other hand, formed under these active ice lobes, where meltwater washed away the finest fractions from the till (Lintinen, 1995). Hence, there was net erosion in the active ice lobe areas and net accumulation in the interlobate area of passive ice (Punkari, 1997).

The abundance of clay in the subcatchments has a notably similar signal in the diatom data than the passively plotted subcatchment field percentage indicating that agriculture is still mostly located on the clayey flanks of the present-day lakes. These clays deposited on the bottom of the previous stages of the Baltic Sea and large lakes (ancient Great Lake Saimaa and Lake Päijänne) that formed after the Ancylus Lake drained. Kukkonen & Sahala (1988), for instance, found from Lake Porovesi (a lake collecting the waters from the three subroutes of the Iisalmi route) a complete sediment sequence since the deglaciation, spanning from Yoldia Sea varved clays and silts through Ancylus Lake clays and silts and Great Lake Saimaa clays to the present-day Lake Porovesi clays. The other fine-grained deposits in the area are most likely sediments of artificially lowered or dried lakes (Kukkonen & Sahala, 1988).

A comparison between the water quality and Quaternary deposit CCA plots (Fig. 3 & 4) also shows that the lakes with the lowest pH are situated on subcatchments that have the highest abundances of peatlands. The three lakes with the highest EC, on the other hand, are located next to an esker that formed between the active and passive ice lobes and runs in a NW-SE direction along the eastern flanks of the Iisalmi Route central basins. These three relatively small lakes appear to have been more susceptible to the effects of road salt from the de-icing of the main road than the larger central basins. However, the three lakes do not plot to the high end of the sand/gravel gradient, most likely because the esker with the main road is not the only sand and gravel formation in the area.

Temporal variation in Lake Kirmanjärvi

The fossil diatom assemblages, the DI-TP reconstructions, and the ordination analysis all indicate that Lake Kirmanjärvi has been eutrophic prior to intensive human impact in the area suggesting that the steep nutrient gradient in the study area is due to the direct effect of underlying geology. The mid-16th century core bottom sample most likely represents conditions close to the natural state of Lake Kirmanjärvi as permanent population spread into the area in the early 16th century (Soininen, 1961) and the first road was built in the late 18th century (Eskelinen, 1985). According to Kauppila et al. (2012), there are no major changes in the diatom assemblages of Lake Kirmanjärvi prior to 1836 CE (local diatom assemblage zone (LDZ) 3). The DCA sample scores (Fig. 5a) remain relatively steady until 1875 CE indicating a rather stable diatom assemblage. Therefore, the pre-1875 (or at least pre-1836) conditions could be considered as the reference conditions of Lake Kirmanjärvi. This is in accordance with the conclusion of Battarbee et al. (2011) that pre-1850 conditions are a suitable reference state for lake restoration in most European lakes. The pre-disturbance samples have also closer modern analogs in our spatial data set than the more recent samples (Fig. 5a). Lake Onkivesi, the central basin into which the Iisalmi Route drains, is the closest modern analog for most pre-1875 samples of Lake Kirmanjärvi, whereas Lake Nerkoonjärvi, the central basin that receives waters from Lake Kirmanjärvi and drains into Lake Onkivesi, is the closest modern analog for most post-1875 samples.

The pre-disturbance DI-TP of Lake Kirmanjärvi is high (average 52 µg l^{-1}), approximately 15-20 µg l^{-1} higher than with the southern Finnish transfer function of Kauppila et al. (2002) in which humic lakes, such as those in the Iisalmi Route, were excluded. However, it fits the upper end of the background concentration range in the previously studied naturally eutrophic southern Finnish lakes (median 35-40 µg l^{-1}; Räsänen et al., 2006) and is somewhat higher than the pre-disturbance DI-TP of Lake Onkivesi (40 µg l^{-1}; Miettinen, 2005). The diatom taxa common throughout the Lake Kirmanjärvi core as well as in the modern spatial data set, such as *A. ambigua*, *A. subarctica*, *A. islandica*, *A. granulata*, and *C. dubius* (Kauppila et al., 2012), also correspond to the taxa abundant in the background conditions of naturally nutrient rich Finnish lakes (Räsänen et al., 2006). The natural eutrophy of the lake is in accordance with the extremely high percentage (84 %) of fine-grained sediments in its subcatchment that have also led to the relatively high pre-disturbance EC and pH (Fig. 6).

The high correlation between the DI-TP record and the DCA sample scores of the first axis (Fig. 5a) suggests that TP has been an important factor affecting the Lake Kirmanjärvi diatom assemblages during the past centuries. The DI-TP ranges mostly between 40-60 µg l^{-1} throughout the core, but there are elevated concentrations up to 70-80 µg l^{-1} during the early 20th century simultaneously with elevated fine-grained mineral matter input levels that reflect increased erosion and sedimentation most likely related to modern agriculture and deforestation (Kauppila et al., 2012). Population growth led to the crisis of slash-and-burn cultivation in the end of the 19th century and to the subsequent transition to modern agriculture with mineral fertilizers, more effective ploughs, and the ditching of fields, forests, and peatlands (Soininen, 1974). The DI-TP returns to its background level during the 1960-1970s, whereas the diatom assemblage shows a shift from LDZ 2 into LDZ 1 during this time with a particularly notable increase in the abundance of *F. crotonensis* as well as *C. stelligeroides* (Fig. 5; Kauppila et al., 2012). The increase in the abundance of small cyclotelloids and elongated pennates suggests a possible link to anthropogenic climate warming as proposed by Rühland et al. (2015), but the area is also under the impact of modern agriculture. The field percent in the Lake Kirmanjärvi subcatchment is currently the highest of our spatial data set (33 %).

The temporal changes in Lake Kirmanjärvi support the interpretation that the relatively steady TP concentrations reflect the local geology (apart from the elevated values of the early 20th century), whereas a recent increase in EC and pH since the mid-1990s (Fig. 6, also seen in water quality monitoring) is most likely related to road salt and the location of the lake next to the main road. This increase in EC and pH is simultaneous with a further increase in the abundance of small cyclotelloids and elongated pennates, such as *D. tenuis* and *C. pseudostelligera* (Kauppila et al., 2012). The mid-1990s water quality change, as well as the lack of good modern analogs for certain post-disturbance samples, could confound the DI-TP reconstructions of the topmost samples, but the DI-TP values of the last few decades are of the same order of magnitude as the monitored values (Fig. 5b). Nevertheless, it needs to be taken into account that diatoms are more reliable indicators of long-term trends than short-term variation.

Conclusions

The conspicuously eutrophic Iisalmi Route in central-eastern Finland clearly differs from its surrounding areas based on the multivariate analyses of recent diatom assemblages, lake water quality and basin characteristics, and the surficial sediment distribution in the lake subcatchments. The Iisalmi Route is characterized by nutrient rich lakes, diatom taxa typically associated with eutrophic lakes, and a high abundance of fine-grained sediments (mainly fine-grained till and clay) in the subcatchments. Conversely, the least eutrophic neighboring catchments are located in the eastern and southern parts of our study area where coarse-grained till, bedrock outcrops, and peat are common. The lakes in these catchments have relatively low nutrient concentrations and the diatom assemblages are typical of oligo-mesotrophic lakes. The distribution of fine and coarse-grained tills in the area is the result of ice sheet dynamics during the deglaciation of the continental ice sheet c. 9 500 years ago.

The nutrient concentrations seem directly or indirectly affected by the variation in the local geology because the occurrence of many diatom taxa follows the boundaries of the lake routes and the nutrient gradients follow the distribution of fine-grained versus coarse-grained sediments. The indirect effect of geology is related to the better suitability of fine-grained sediments for cultivation (agriculture vs. forestry). However, the temporal study of Lake Kirmanjärvi indicates that the lake has been eutrophic already prior to intensive human impact suggesting that the diatom assemblages are, indeed, driven by the direct effect of the local geology. On the other hand, some diatom taxa occur throughout the spatial dataset suggesting that they could be influenced by other factors than the local geology and nutrients. In particular, certain small cyclotelloid and elongated pennate taxa, indicative of high electrical conductivity, pH, and nutrient conditions, seem to be related to anthropogenic actions, such as agriculture, road de-icing, or climate warming. Also the shallowness of the lakes is visible in the diatom data as relatively high abundances of small, benthic *Fragilaria* taxa.

This study highlights the importance of assessing the geology of an area, in addition to the typical examination of water quality, basin characteristics, and aquatic ecology, when evaluating the present or past conditions of a lake or planning for possible management measures. Our results indicate that the distribution of different Quaternary deposits in an area with a geographically limited coverage can lead to a steep local nutrient gradient. Because temporal changes in the fossil diatom assemblages and DI-TP were assessed in one lake, further studies are needed to verify whether the other currently nutrient rich lakes in the Iisalmi Route are also naturally eutrophic.

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Tables

Table 1 Summary statistics (minimum, average, and maximum values) for the lake water quality and basin characteristics in the whole study area and averages for the different lake routes

	Min	Av	Max	Av^{ir}	Av^{ks}	Av^{sa}	Av^{ss}	Av^{ic}	Av^{nr}	Av^{ka}	Av^{rr}
TP (µg l^{-1})	3.0	46	120	67	81	93	41	59	24	16	27
TN (µg l^{-1})	150	772	1750	980	1105	1160	756	922	574	464	583
TN/TP	9	24	88	16	14	13	19	16	31	42	30
pH	5.5	6.9	7.8	7.0	7.0	7.5	6.8	7.1	6.8	6.7	6.9
EC (mS m^{-1})	0.5	4.8	12	5.4	5.7	6.6	3.9	6.1	5.2	3.3	3.8
Color (mg Ptl^{-1})	5	117	340	156	185	58	144	146	73	59	87
Secchi depth (m)	0.4	1.5	8.0	0.9	0.7	1.1	1.1	0.9	2.3	2.0	2.1
Sampling depth (m)	1.2	8.2	25	6.5	5.1	3.4	10	6.0	8.2	15	9.2
Average depth (m)	0.7	2.8	6.9	2.3	2.0	1.1	2.9	2.8	3.5	4.0	2.8
Area (km^2)	0.039	9.0	110	13	6.6	0.78	2.9	49	4.0	0.56	6.2
Volume (10^6 m^3)	0.11	27	360	41	18	0.83	8.4	160	14	1.9	15
Altitude (m.a.s.l.)	82	109	160	99	101	86	101	96	109	138	120

TP = total phosphorus, TN = total nitrogen, EC = electrical conductivity

^{ir} = Iisalmi Route, ^{ks} = Kiuruvesi Subroute, ^{sa} = Salahmi Subroute, ^{ss} = Sonkajärvi Subroute, ^{ic} = Iisalmi Route central basin area, ^{nr} = Nilsiä Route, ^{ka} = Kallavesi-Sorsavesi area, ^{rr} = Rautalampi Route

Table 2 Summary statistics (minimum, average, and maximum values) for the Quaternary deposits and the percentage of fields in the study lake subcatchments of the whole study area and averages for the different lake route areas

	Min	Av	Max	Av^{ir}	Av^{ks}	Av^{sa}	Av^{ss}	Av^{ic}	Av^{nr}	Av^{ka}	Av^{rr}
F-g till (%)	0	29	77	38	51	46	12	42	26	23	15
Clay (%)	0	9.7	43	17	15	37	18	12	6.0	0	0.07
Other fines (%)	0	6.1	45	6.9	4.1	8.2	1.5	20	11	2.1	2.7
Sand/gravel (%)	0	3.9	26	1.9	1.6	1.7	1.3	3.5	5.2	7.1	6.0
Bedrock (%)	0	9.7	48	8.3	9.5	5.1	9.9	4.3	9.0	13	12
C-g till (%)	0	29	84	18	9.4	0.3	46	6.0	22	42	51
Peat (%)	0	12	77	8.9	8.1	2.6	11	11	20	11	13
Fields (%)	0	11	33	14	15	24	8.3	15	11	3.1	5.8

F-g till = fine-grained till, C-g till = coarse-grained till

^{ir} = Iisalmi Route, ^{ks} = Kiuruvesi Subroute, ^{sa} = Salahmi Subroute, ^{ss} = Sonkajärvi Subroute, ^{ic} = Iisalmi Route central basin area, ^{nr} = Nilsiä Route, ^{ka} = Kallavesi-Sorsavesi area, ^{rr} = Rautalampi Route

Figure captions

Fig. 1 Map of the study area in central-eastern Finland showing sampling sites, lake route catchments (thick lines), the subroute catchments of the Iisalmi Route (moderately thick lines), the subcatchments of individual lakes (thin lines), the drainage direction of the lake routes, agricultural land, and the location of Lake Kirmanjärvi (empty box) whose catchment area is shown in more detail in the inset

Fig. 2 Relative abundances of selected diatom taxa, rarefaction, and chrysophyte cyst to diatom (CD) ratio in 51 surface sediment samples grouped according to the lake routes

Fig. 3 CCA biplot of **a)** water quality variables and basin characteristics (arrows) with sampling sites in Kiuruvesi Subroute (squares), Salahmi Subroute (triangles), Sonkajärvi Subroute (filled diamonds), Iisalmi Route central basins (empty diamonds), Nilsiä Route (filled stars), Kallavesi-Sorsavesi area (empty stars), and Rautalampi Route (black circles) and **b)** diatom taxa (gray circles) and the environmental variables. The percentage of fields in a subcatchment (dashed arrow) is plotted passively on top of the ordinations. See Online Resource 1 for further information on the sampling sites and their water quality

Fig. 4 CCA biplot of **a)** Quaternary deposits (arrows) and sampling sites in Kiuruvesi Subroute (squares), Salahmi Subroute (triangles), Sonkajärvi Subroute (filled diamonds), Iisalmi Route central basins (empty diamonds), Nilsiä Route (filled stars), Kallavesi-Sorsavesi area (empty stars), and Rautalampi Route (black circles) and **b)** diatom taxa (gray circles) and Quaternary deposits. The percentage of fields in a subcatchment (dashed arrow) is plotted passively on top of the ordinations. See Online Resource 2 for further information on the sampling sites and the subcatchment Quaternary deposits

Fig. 5 a) Temporal changes in the diatom-inferred total phosphorus (DI-TP) concentrations of Lake Kirmanjärvi, DCA sample scores of the first and second ordination axes, and the minimum squared chord distances (SCD) between the fossil and modern samples. SCD values below the 2.5 % dashed line indicate that the fossil samples have very good modern analogs in the spatial surface sediment data set, whereas samples between the 2.5 % and 5 % dashed lines have good modern analogs. Samples over the 10 % dashed line are not considered to have modern analogs in the spatial data. The local diatom assemblage zones (LDZ), determined by Kauppila et al. (2012), refer to notable changes in the diatom community of the lake. **b)** Comparison between the reconstructed DI-TP (squares), monitored TP (solid line), and the LOESS smoothed annual averages of the monitored TP values (dashed line)

Fig. 6 Fossil Lake Kirmanjärvi samples (black circles) plotted passively on top of a CCA ordination of modern samples (grey circles), water quality and basin variables (arrows). The small diagram on the bottom right shows the trajectory of the fossil samples from the mid-16th century (square) to 2006 (triangle)

Electronic supplementary material captions

Online Resource 1 Lake water quality and coordinates at the sampling sites together with basin characteristics

Online Resource 2 Quaternary deposits in the subcatchments of the study lakes

Online Resource 3 Predicted versus observed values and a residual plot for the total phosphorus (TP) transfer function