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Chrysophyte cyst-inferred variability of warm season lake water chemistry and climate in northern Poland: training set and downcore reconstruction

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Abstract

Chrysophyte cyst assemblages from sediment trap and surface sediment samples of 50 lakes in northern Poland were related to environmental variables using multivariate numerical analyses (DCA, CCA). Water electric conductivity, total nitrogen, total phosphorous, turbidity, and cation and anion compositions (Ca^{2+}, HCO_3^-) accounted for significant and independent variations in the chrysophyte cyst assemblages. The first canonical axis was related to the gradient of Ca^{2+} while the second axis was correlated with total nitrogen. A quantitative transfer function was then developed to estimate Ca^{2+} (log_{10} transformed) from modern chrysophyte cyst assemblages using weighted-averaging regression (WA) with classical deshrinking. The bootstrapped regression coefficient (R^2_{boot}) was 0.68, with a root-mean square error of prediction (RMSEP) of 0.143 (log_{10} units). The calibration model was applied to a varved sedimentary sequence (AD 1898-2010) from Lake Żabińskie, Masurian Lakeland (NE Poland). Observational data from this lake show that the Ca^{2+} variability in the epilimnion depends on the efficiency of Ca^{2+} scavenging by $CaCO_3$ precipitation in early summer, which in turn is a function of water column stratification, temperature and the wind regime from late spring to early fall. The spring-fall wind regime drives the water column mixing. In Lake Żabińskie, cyst-inferred warm-season lake water Ca^{2+} concentrations are significantly negatively correlated with calcite precipitation ($CaCO_3$ concentrations in sediments; R = -0.49, p_{adj}<0.001; AD 1898-2010; 3-year filtered), and cyst-inferred lake water Ca^{2+} concentrations are significantly correlated with zonal wind speed ($m \cdot s^{-1}$) (R=0.50; p_{adj}<0.001; AD 1898-2010; 3-year filtered). This study demonstrates that chrysophyte cyst assemblages in Polish lakes respond to hydrochemical factors driven by climate variability.

Introduction

Long-term environmental and quantitative climate reconstructions for the last millennium are fundamental to understanding modern trends in climate variables and distinguishing between natural and anthropogenic variability and forcing (IPCC 2007). Regional reconstructions are particularly important since regional climate change and extremes exhibit much larger amplitudes than hemispheric and global reconstructions (PAGES 2k Consortium 2013). Lake sediments are excellent natural archives to reconstruct long-term climate and environmental fluctuations (Williamson et al. 2009). In this sense, the project 'Climate of northern Poland during the last 1000 years: Constraining the future with the past' (CLIMPOL) aims to develop quantitative climate reconstruction in northern Poland during the last millennium using lake sediments. Recent studies combining instrumental, documentary, dendrochronological and borehole data from Poland have demonstrated that climatic variability in this region accurately represents climate conditions in Central Europe (Przybylak 2010). Given the high number of varved lake sediments in Poland (Tylmann et al. 2013b), this region is ideal for the study of European climate variability.

The golden algae or chrysophytes (classes Chrysophyceae and Synurophyceae) produce siliceous resting stages (cysts). These cysts are usually well preserved in the sedimentary record as microfossils. Although they are quite common and widely distributed in lakes, their use in modern and paleoecological studies has been hindered by a lack of detailed specific ecological data (Sandgren et al. 1995). As this group forms a high percentage of the phytoplanktonic biomass in lakes, it is necessary to better understand the relative importance of each environmental variable in controlling the occurrence and distribution of different species. Developments of chrysophyte-based training sets have overcome these limitations, providing precise tolerance information along different environmental gradients required for their use in paleolimnological reconstructions (Duff and Smol 1991; Kamenik and Schmidt 2005; Lotter et al. 1997; Pla and Anderson 2005; Pla et al. 2003; Siver 1995; Wilkinson et al. 1997). It has been demonstrated that chrysophyte cyst assemblages record temperature variability, mainly in alpine and subalpine lakes (De Jong and Kamenik 2011; De Jong et al. 2013; Pla 2001; Pla and

Catalan 2005), while in low-altitude lakes factors related to water chemistry (i.e., conductivity, salinity, trace metals, nutrients, pH or alkalinity) seem to be more important (Betts-Piper et al. 2004; Duff et al. 1997; Pla et al. 2003; 2009; Rybak et al. 1991; Siver and Hamer 1992; Zeeb and Smol 1995; Zeeb et al. 1994). The consistency of chrysophyte cyst records showing past hydrochemical changes is promising, and can be also potentially used as a tool for quantitative climate reconstructions. These data contribute to our understanding of chrysophyte biogeography and its implications for regional reconstructions in these climatically and environmentally sensitive regions. In this paper we present a new data set of the relationship between chrysophyte cysts and environmental and climate variables from a regional training set of Polish lakes. The goals of this study were to (a) identify the environmental gradients influencing the chrysophyte cyst assemblages in northern Poland; (b) develop a calibration model to relate environmental variables to the chrysophyte cyst assemblages; (c) investigate the quantitative relationship with present-day climate in northern Poland; and (d) present a chrysophyte cyst-based reconstruction for Lake Żabińskie (NE Poland) that can be verified with observational data. Lake Żabińskie was selected for the downcore reconstruction because sediments in the deepest basin are continuously varved, and the high sedimentation rates allow subsampling with annual resolution. Seasonal sediment production yields distinct light (spring/summer) and dark (late summer/autumn/winter) laminations (varves) that are preserved in the anoxic bottom of Lake Żabińskie. We show that changes in chrysophyte cyst communities from Polish lakes are mainly driven by fluctuations in dissolved Ca^{2+}, which is related to changes in the photic depth and the lake mixing regime driven by westerly winds. Therefore, reconstructed Ca^{2+} can be used as an indirect tracer of May-October zonal circulation (W-E) in northern Poland.

Study area

The Great Poland, Pomeranian, and Masurian Lakelands form an east-west belt of moraines that counts more than 7000 lakes (Fig. 1A). In the Masurian Lakeland, the surface covered by lakes reaches up to 20%. This region is characterized by the postglacial landscape, and is dominated by glaciofluvial sediments deposited during

the maximum stage of the Vistulian glaciation (~ 21ka; Marks 2002). The climate in northeast Poland is characterized by strong continentality (warm summers and cold winters). Mean annual air temperature (1971-2005) is about 6.5°C, with the lowest air temperature in January and highest in July. Mean annual precipitation totals range from 550 to 600 mm (Lorenc 2005). The snow cover lasts from 1.5 to 3 months in winter. Lake Żabińskie (54°07'54.5'' N, 21°59'01.1'' E; 120 m a. s. l) is a eutrophic, hardwater, 41.6-ha area, 44.4-m deep, postglacial lake situated in the northern part of the Masurian Lakeland (Fig. 1A). The catchment surface is dominated by glacial and fluvioglacial sediments. The most common landforms in the catchment are moraine plateaus, outwash plains and kame terraces (Szumański 2000). Precipitation and temperature are higher during the summer months (up to 90 mm and 17°C, respectively) and lower during winter (Fig. 2A). The atmospheric circulation over this region is dominated by zonal circulation (W-E). The Westerlies are the strongest and most frequent winds as depicted by the analyses of the wind components for the 20th century (Compo et al. 2011; Fig. 2B).

Lake Żabińskie has one inflow that comes from Lake Purwin in the north-eastern part and two inflows from the south (Fig. 1B). The outflow that connects Lake Żabińskie to the much larger Lake Gołdopiwo is in the south-western part. Limnological measurements indicate that, during stratification, the hypolimnion of Lake Żabińskie extends over the water depth range from 10 to 44 m and is anoxic during most of the year. The lake is thermally stratified between May to October, and it mixes twice a year (dimictic), in early spring and late fall. Conductivity through the water column varies from 350 to 450 µS/cm and the pH ranges from 6.9 to 8.0. In Lake Żabińskie $Ca^{2+}$and HCO_3^- predominate over potassium, sodium, magnesium, chloride and sulphate. Between late spring and early fall (May-October), higher water temperature reduces the solubility of calcite and biological productivity causes higher carbon fixation in the epilimnion, resulting in a greater calcite precipitation and thus a decrease in conductivity (and dissolved Ca^{2+} and HCO_3^-) (Fig. 2C-D).

The village of Żabinka (0.5 km south of the lake) was established in AD 1713. From the 19th century until the Second World War it had about 200-250 inhabitants. The first buildings near the northern shore were built between 1910 and 1920, for recreational use. After being used for military operations during the war, the location was abandoned until the mid-1950s, when recreational activities were re-established

again. New infrastructures were built in the early 1970s and during 1980s due to the increase of activities related to tourism.

The chronology of the Lake Żabińskie sediment core has been performed by microscopic analyses of thin sections and varve counting. A regular succession of two types of laminae was identified; light autochthonous calcite layers and dark organic-rich layers composed mainly of diatoms, chrysophyte cysts and other organic remains. Although more complex structures including multiple calcite laminae were also identified, this microstratigraphy is identical to the biochemical varves as defined by Zolitschka (2007) and was found in many lakes in northeast Poland (Tylmann et al. 2013b; Zolitschka 2007). Annual nature of these laminations was confirmed in nearby Lake Łazduny (Tylmann et al. 2013a) and at Lake Żabińskiehe varve counting has been verified by additional dating methods (^{210}Pb, ^{137}Cs) .

Methods

Training set, monitoring and sediment analysis

Morphological, physical and chemical data (longitude, latitude, altitude, surface area, volume, max. depth, mean depth, length, width, shoreline length, shoreline development, exposure index (ratio between lake surface area and mean depth), conductivity, pH, chemical oxygen demand, calcium, sulphate, and chloride) from a total of 2913 lowland lakes available in Jańczak et al. (1996) were used to design a training set and select 50 lakes to calibrate chrysophyte assemblages against environmental and climatic variables. Quantitative reconstructions for last millennium are likely to be most reliable if modern transfer functions are developed from training sets in regions where anthropogenic effects are minimal. Human impact can interfere in the realtionships between biological indicators and environment/climate (Anderson 1993). By selecting the most unaltered lakes, we aim to find good analogues of past climatic and natural environmental conditions. The outlier detection was made using box-plots comparing the distribution of chemical and morphological features. From the origininal dataset of 2913 lakes, 1666 were removed. Lakes closer than 20 km to

the Baltic coast and 10 km to any of the 45 biggest cities were removed to reduce potential effects of sea-spray or pollution. In the same way, lakes with unusual pH (dystrophic lakes), shore-line development, dissolved oxygen values, ion concentration, or with missing physical or chemical observations were removed as well.

Among the 1247 remaining lakes, 50 lakes representing mean values and standard deviations of the 19 environmental variables were selected for the training set using stratified balanced sampling. Strata were defined to represent ten equidistant blocks along longitude and latitude, which corresponds to two major climatic gradients: mean annual temperature (W-E, 8.5-6°C) and precipitation (N-S, 700-550 mm $year^{-1}$), respectively (Lorenc, 2005) and several environmental variables related to lake morphometrics and water chemistry to spread a broad range of physical and chemical characteristics. The spatial extension of the study area is large (52º31'- 54º19' N, 14º37'- 22º53'E), covering about 600 km from the westernmost to the easternmost lake. The selected lakes are below 260 m.a.s.l., deeper than 6 m, and slightly alkaline (pH ranging 6.5-9), with moderate agricultural activity and/or forestry in the catchments.

Integrating sediment traps equipped with thermistors were deployed in the deepest parts of the 50 lakes during the field campaign of October-December 2011. A simple Bloesch-type (PVC-liners with a length of 80 cm and a diameter of 9 cm, 2 tubes per trap) was used (Bloesch and Burns 1980), with the openings of the traps approximately 1.5 m above the lake bottom. After one year of sediment-trap exposure, 37 traps were found and recovered, and 15 were lost. In order to maintain the original size of the training set, the first cm of the surface sediment, which was approximately one-year deposition (based on observations of varve thickness in other lakes), or the first varve when it was visible, was sampled with an Uwitec corer in those 15 lakes.

Measurements of physical and chemical variables in the water column (temperature, conductivity, oxygen, pH and turbidity) were taken in all lakes at 3-month intervals during the time of sediment trap exposure at 2-m below the lake surface (Table 1). At the same time, water transparency was determined using a Secchi disc and surface and bottom water samples were collected (1 m below the surface and 1 m above the bottom). The concentrations of major ions (Ca^{2+}, Mg^{2+},

Na^+, K^+, SO_4^-, fluorides, Cl^-) were determined by ion chromatography (ICS 1100, Dionex, USA) equipped with an IonPack AS22 column for anions and an IonPack CS16 column for cations. Nutrient (total P and N) analyses were performed after sample mineralization (CrakSet20, Merck), using the colorimetric method and a Spectroquant NOVA 400 spectrophotometer (Merck). For the case study Lake Żabińskie, these measurements were made at monthly intervals.

Surface sediment and sediment trap samples for chrysophytes analyses (0.2 g wet sediment) were prepared following the standard diatom procedures with HCl and H_2O_2, and repeated washing with distilled water (Battarbee 1986). To remove particles outside the potential size range of cysts (mainly large diatoms), we filtered the samples with Milipore nylon-filters (60 μm). Cysts were analysed using a scanning electron microscope (Carl-Zeiss EVO40). A minimum of 300 modern cysts were counted per sample. For the downcore sediment samples from Lake Żabińskie for the period AD 1898-2010, we sampled annual layers, counted 80 cysts per sample and then applied a 3-year filter (240 observations per data point) to have a significant number of cyst per sample (Fatela and Taborda 2002). Our cyst identification criteria follow that of PEARL (Paleoecological Environmental Assessment and Research Laboratory) Duff et al. (1995), Wilkinson et al. (2002).The unpublished new cysts were assigned a new number using the code 'ZAB', for the fossil samples and Żabińskie modern samples, and 'TSP' for the modern samples.

Numerical methods

Multivariate numerical analyses were used to evaluate the distribution of chrysophyte assemblages present in the training set and to identify the major environmental gradients that explained interdependent portions of the variance in the biotic data.

Annual values of all environmental variables calculated from the seasonal measurements, were $\log_{10}$-transformed (excluding pH) to avoid skewed distributions. A principal component analyses (PCA) was performed to investigate the main patterns of variability in the environmental data set. Numerical analyses excluded taxa with maximum abundances below 1% and appears only in one lake, following

criteria used in another chrysophyte training set (Kamenik and Schmidt 2005). To standardize variances among taxa, percentage abundances were transformed using the square root transformation prior to all numerical analyses.

Modern chrysophyte cyst assemblages were analysed by detrended correspondence analyses (DCA) to determine whether linear or unimodal based numerical techniques should be used (Birks 1995; ter Braak 1987). The data set has a compositional gradient length of 2.4 Standard Deviation (SD) units, suggesting a unimodal response model (Birks 1995; ter Braak 1987).

Canonical correspondence analysis (CCA) was used to analyse the relationship between chrysophyte cyst assemblages and environmental variables, and to identify unusual values of environmental variables or unusual cyst assemblages (ter Braak 1987). As the original environmental data set contains 19 variables, there is a high risk of finding multi-collinearity in the environmental information. The redundancy of the environmental information was determined with weighted correlations and variance inflation factors (VIF) (ter Braak 1987). Variables with VIF > 25 have unstable canonical coefficients and do not merit interpretation, and were removed from the subsequent CCA. Forward selection using a Bonferroni adjustment identified significant variables (p <0.05). A series of partial CCA were performed on the forward selected variables to determine which one explained significant variation in the cyst assemblages. This step was followed by CCAs of individual environmental variables with the remainders as covariables to determine which ones independently explained more variation in the species data. Finally, the ratio of eigenvalues of first (constrained) and second (unconstrained) DCCA axes (λ_1/λ_2) for each of these variables provided a measure of the predictive power of the inference models (Birks 1998; ter Braak 1992).

To establish transfer functions, the following models were tested: Weighted averaging (WA) classical and inverse deshrinking, weighted averaging – partial least squares (WA-PLS), partial least squares (PLS), and a modern analog technique (MAT) as implemented in the computer program C2 (Juggins 2003). The minimal adequate model was developed using weighted averaging (WA) with classic deshrinking,. This model produced the lowest root mean squared error of prediction (RMSEP) assessed by cross-validation (bootstrapped, 999 permutation cyldes; Birks 1995), the highest $R^2_{\text{cross-validated}}$ and low mean and maximum bias (Birks 1995).

The reconstruction of $\log_{10} Ca^{2+}$ was performed applying the calibration model to the downcore chrysophyte cyst assemblages from Lake Żabińskie. As this variable is not directly related with climate, we correlated the Ca^{2+} reconstruction (AD 1898-2010, 3-year triangular filtered) with the dominant wind component in the region (zonal winds) from 20th century reanalysis data (Compo et al. 2011). Ca^{2+} scavenging (and electric conductivity) of the surface lake water depends on calcite precipitation in the epilimnion of hardwater lakes (Stabel 1986). Calcite precipitation is driven by temperature and primary productivity, which is strongly influence by wind, that is the controlling factor for the thickness of the epilimnion (Boehrer and Schultze 2008).

The zonal wind time series was also filtered at 3 years to make it comparable with the resolution of the cyst assemblage data downcore. To find the optimal correlation between the chrysophyte cyst-Ca^{2+} reconstruction and the zonal wind, both time series were compared using a multiple correlation. With this test we are able to find the combination of months that shows highest correlation, accounting for lagged responses (De Jong and Kamenik 2011). Regressions were performed including corrections for serial autocorrelation. All ordinations and calculations were performed using the open software PAST 2.17 (Hammer et al. 2001) and R (R Development Core Team 2009) with the add-on packages VEGAN (Oksanen et al. 2006).

Results

Training set and chrysophyte cyst transfer function

The summary statistics of the environmental variables from the 50 lakes included in the Polish training set are outlined in Table 2. The two first axis of PCA performed on the environmental data were significant, according to the ‘broken-stick’ model, and explained 53% of the variance (Fig. 3A). The variation along the first axis was explained by conductivity and ion concentration, while the variation along the second axis was explained by nutrients (total N and P).

A total of 78 chrysophyte cyst types occurring with maximum abundance >1% and at least in two sediment traps were found in the 50 lakes. Cysts were well preserved and abundant in the sediment traps. Small unornamented cysts (<5.9 μm) without collar (Pearl 1) were excluded from the analyses, because they were correlated with high nitrogen content in the training set. This species have been found in great abundances after nutrient (P and N) additions to a manipulated lake (Zeeb et al. 1994). Lake Sumile (53º15'38.0" N, 16º19'30.4" E) was also removed from the training set due to the unusually high nitrogen values (4.4 mg L^{-1}).

In a first CCA, conductivity, magnesium, dissolved oxygen, sulphates, fluorides, longitude and latitude were highly correlated with other variables and VIF > 25. Ca^{2+} was the dominant cation in water samples from the majority of the lakes. There is a clear relationship between conductivity and dominant ions, and longitude, latitude, and dissolved oxygen with other variables. This multicollinearity can cause problems of inflated variance. Because these variables act as surrogates for other variables, they were removed.

In the second CCA, the remaining 12 variables explained 45% of the variation in the chrysophyte cyst assemblage (Fig. 3B). A subset of two significant environment variables (p = 0.001), Ca^{2+} and total N, explained independent portions of the variance in the chrysophyte data, as determined by forward selection with a Bonferroni adjustment. Variance partitioning (individual CCA for each variable with the others as conditional variable) indicated that 11.93% of the variation in the chrysophyte data was due to the combination of these two variables. Ca^{2+} had the highest unique contribution to variance (7.46%) and total N (4.03%), with only 0.44% of variance shared (Table 2). Finally, λ_1/λ_2 for Ca^{2+} was the highest and greater than 1.0 (1.09), indicating that Ca^{2+} is the most suitable variable for transfer function development since it represents an important ecological gradient in the training set. The transfer function, based on weighted-averaging (WA) using classical deshrinking had a high coefficient of determination of R^2_{boot} = 0.68 and a RMSEP= 0.143 (log_{10} units) (Fig. 4).

Downcore Ca^{2+} reconstruction and correlation with wind data (AD 1898 – 2010)

Chrysophyte cysts observed in the sediment (annual layers AD 1898 – 2010) were abundant, well preserved and generally without corrosion. More than 160 types were identified in 114 downcore samples from lake Żabińskie, but only 42 cyst types with abundance > 2% and present at least in four samples were used for the reconstruction. Sediment-core cyst assemblages were poorly represented in the training set (<10%). The sediment-core assemblages comprised 5% to 22% (mean 8%) of cyst types absent in the training set.

The multiple correlation test indicates that May-October zonal winds are most highly correlated with reconstructed chrysophyte-based Ca^{2+} lake water concentrations (time series 3-year triangular filtered; R= 0.50; p_{adj} <0.001; Fig. 5A). Reconstructed $\log_{10}$ Ca^{2+} fluctuated between 1.4 and 2.1, whereby higher Ca^{2+} values in the lake water are observed during periods of stronger westerly wind speed (Fig. 5A). The 31-year running correlation between $\log_{10}$ Ca^{2+} and May-October zonal winds shows higher and significant (p_{adj} < 0.001) correlations until 1970. Afterwards, correlations decreased, which coincided with an abrupt increase in the mass accumulation rates (MAR) (Fig. 5B-C). In addition, reconstructed Ca^{2+} in the lake water and detrended $CaCO_3$% in the downcore sediment samples are negatively correlated (time series 3-year triangular filtered; R= -0.49; p_{adj} <0.001; Fig. 5D).

The reconstructed zonal wind speed for the period (AD 1898-2010) shows pronounced decadal and interdecadal variability. Between AD 1898-1910, there is a progressive decrease in the zonal circulation, which is followed by a period of relatively strong westerlies (AD 1910-1938), interrupted abruptly by a sudden fall in the zonal circulation at AD 1938-1940. From 1940 onwards, there is a slight increase in the zonal winds, followed by a period of high inter-annual variability but without any apparent trend until AD 2010.

Discussion

The chrysophyte-Ca^{2+} transfer function

Chrysophyte cyst distributions are strongly correlated with ion concentrations in waters and related variables (e.g. salinity, alkalinity, conductivity). In the present dataset, inference models for $\log_{10}$ Ca^{2+} showed high predictive performance (R^2_{boot} = 0.68). Although the influence of this variable on chrysophyte species distributions is well known from correlation-based studies (Cumming et al. 1993; Duff et al. 1997), the mechanisms by which it affects chrysophyte distributions have not been well understood. The effect of ionic concentrations on chrysophytes is thought to be related to the ability of algal cells to adjust to changes in the external osmotic pressure (Cumming et al. 1993). In addition, taxon-specific responses to conductivity could be related to lake water concentrations of major ions which may be toxic to some chrysophyte species (Sandgren 1988).

In the Polish training set, Ca^{2+} in the epilimnion explained more variability (7.46%) in the chrysophyte cyst assemblages found in the 49 lakes studied in Poland than any other of the 19 environmental variables considered. Values of the ratio λ_1/λ_2 > 1 (Table 2) are typical for training sets where the majority of the taxa have a response only to the gradient of interest, and thus are useful for reconstructions (ter Braak 1992). Other studies have found similar results, with environmental variables related to ion concentration explaining the highest amount of variation in the chrysophyte cysts assemblages. Duff et al. (1997) developed a transfer function for conductivity (R^2= 0.78; non-cross-validation) based on a training set of 221 lakes in Adirondacks, Siberia, and British Columbia. Siver (1993), using 28 lakes from the Connecticut area, developed a model to reconstruct lake water electric conductivity (R^2= 0.87; non-cross-validation). Pla et al. (2003) used surface sediments from 105 mountain lakes in the Pyrenees to reconstruct alkalinity (R^2= 0.75; cross-validation), although the variance explained was very low (λ_1/λ_2= 0.80). Pla and Anderson (2005) also found that Ca^{2+} was one of the strongest environmental gradients along 70 lakes located southwest Greenland and explained significant amounts of variability of the cyst data. In their dataset, Ca^{2+} was highly correlated with conductivity which was the variable finally reconstructed (R^2= 0.86; cross-validation). Zeeb and Smol (1995) developed a chrysophyte cyst-inferred salinity model using assemblages in 60 lakes located on the Interior Plateau of British Columbia (R^2= 0.80; non-cross-validation). In this study, Ca^{2+} was a major ion highly correlated with salinity, and also explained a significant proportion of the variance in the chrysophyte cyst assemblage. In a similar way, Smol et al. (1984) found a significant response of siliceous scales from 38 lakes

in New York to lake water pH (R^2 = 0.63) and related factors (log_{10} alkalinity, R^2 = 0.66; Ca^{2+}, R^2 = 0.39).

Ca^{2+} explained a significant amount of variation even when the other important environmental variable that remained after forward selection was removed (total N). The partial CCA indicates that, besides the chemical composition of water (Ca^{2+}), cyst assemblages are driven by factors related with productivity in the lake, such as nutrients. This indicates that changes in nutrients (total N) might modify chrysophyte assemblages, as it has been observed in some studies (Pla et al. 2003). Although the influence of total N was minimized in this study (all lakes were located far from cities; see section Training set, monitoring and sediment analysis), changes in the nutrient levels might be attributed to fertilization by atmospheric nitrogen deposition or local agricultural and industrial sources (Saros et al. 2003).

The residuals from the regression model (WA classical deshrinking; Fig. 4B) suggest that low log_{10} Ca^{2+} contents are overestimated. As all WA-based models, our prediction shows a tendency to systematically overestimate values at the low end of the gradient and underestimate values at the high end of the gradient (Birks 1998). In under-sampled portions of the gradient the uncertainty can be much larger than the RMSEP as there are only few available analogues. Conversely, in over-sampled portions of the gradient, the uncertainty can be smaller than the overall RMSEP. This residual structure might be related to the uneven sampling of the environmental gradient (Fig. 4B). Including more lakes with low Ca^{2+} concentration in our training set would help to develop a more robust model. We selected the WA model regardless of the distinct bias occurring at low log_{10} Ca^{2+} because our reconstructed log_{10} Ca^{2+} were never that low (Fig.5A).

The influence of Ca^{2+} on the composition of the chrysophyte cyst assemblages from the Polish lakes may be explained by changing occurrences of specific cyst types. Typically during late spring to autumn calcite precipitates in the epilimnion and cyst types living in waters with low dissolved Ca^{2+} and conductivity is reduced (Fig. 2C-D). However, during early spring-winter season, when temperatures are lower, calcite precipitation decreases, epilimnetic waters have higher Ca^{2+} concentration, and cysts typical of high-conductivity waters are found.

Epilimnion, lake water Ca^{2+} concentrations and wind

From the results of the previous section it appears that chrysophytes are very sensitive to Ca^{2+} concentration in the epilimnion. The interpretation of oscillations in Ca^{2+} concentration is directly related to the biogeochemical cycle that controls calcite precipitation. In hardwater lakes the process that changes alkalinity and hence dissolved Ca^{2+} in the water is driven by the seasonal hydrochemical cycle related to calcite equilibrium in the epilimnion, which in turn varies with pH, alkalinity, and total dissolved inorganic carbon (DIC) (Stabel 1986). Commonly inorganic calcite precipitation begins only after a lake water has reached a high level of supersaturation. In lakes the calcium ion mainly derives from river or groundwater input and sediment refluxing, whereas carbonate ions may also be derived from direct atmospheric equilibria, respiration, and bacterial reduction of organic matter. The prepitation of calcite in hard water lakes is believed to be mediated by biogenic changes (photosynthesis) and by physical-chemical (temperature) (Effler and Johnson 1987; Kelts and Hsü 1978b). High water temperature reduces the solubility of calcite and biological productivity increases the pH of epilimnetic waters, **d**ecreases CO_2 (aq), and shifts the carbonate equilibrium and favouring calcite precipitation (Kelts and Hsü 1978a). In turn, temperature can directly affect the rate of primary productivity by setting the maximum potential growth rate of phytoplankton (Cuhel and Lean 1987). Maximum disequilibrium and precipitation occurs in the warmer and more productive months, during the onset of water column stratification (Effler and Johnson 1987; Hodell et al. 1998; Reynolds 1989). The onset of water column stratification in late spring and depth of the mixing layer in turn depends on regional weather conditions such as air temperature and wind speed. Relatively high temperatures and low wind speeds between spring to early fall promote strong stratification (Gaedke et al. 1998; Tirok and Gaedke 2007) and thus boosts phytoplankton production and calcite precipitation. In contrast, high mixing rates in the epilimnion imply lower surface temperatures and reduced primary productivity. Rybak (1985) demonstrated the inhibiting effect of water masses mixing on the development of algae by producing artificial destratification in Lake Mutek, in the Masurian Lakeland.

Wind is a key factor controlling the mixing of surface lake waters. When a lake is stratified, the wind induced currents are confined to the thermocline, leaving the hypolimnion unaffected (Octavio 1977). Wind induced mixing contributes to the formation and maintenance of a cool and mixed upper layer. If the temperature in the epilimnion drops below the temperature of the water just beneath, the water column is unstable and the thermocline descends, decreasing the temperature (Gorham and Boyce 1989; Octavio 1977). Modelling studies in Lake Belau, in Germany, underline the sensitivity of the processes within the lake, like thermal stratification and calcite precipitation to wind mixing (Schernewski et al. 1994). Westerlies (positive values in zonal wind components) are the prevailing winds in mid-latitude Europe (Slonosky et al. 2000) and, as is shown in the wind rose (Fig. 2B), are the dominant wind direction blowing over Lake Żabińskie. The fact that reconstructed chrysophyte-based lake water Ca^{2+} concentrations are correlated with May-October zonal winds at Lake Żabińskie (Fig. 5A) reflects the important role of water column stability and volume of the epilimnion on calcite precipitation (Ca^{2+} scavenging) during the productive period (late spring-early fall). The lake is frozen in winter. Warm season wind mixing interferes equally in the calcite precipitation by changing the water temperatures in the epilimnion by mixing and decreasing primary productivity (Bluszcz et al. 2008; Hodell et al. 1998; Schelske and Hodell 1991; Stabel 1986). Small decreases in the stability of the epilimnion by wind mixing during this period translate into less net removal of Ca^{2+} from the epilimnion and thus greater Ca^{2+} concentration in surface waters during summer (Groleau et al. 2000). Since the correlation between reconstructed $\log_{10}$ Ca^{2+} and zonal wind is 0.5 ($p_{adj}<0.001$; 3-year filtered), it is evident that other environmental factors (e.g. temperature, precipitation) may have influenced on the epilimnetic Ca^{2+}. Other factors that may potentially control Ca^{2+} supply to the lake are inflowing surface water or groundwater. However, interannual variability showed by downcore $\log_{10}$ Ca^{2+} (Fig. 5A) can not be explained by groundwater changes, because the recharge time for water to reach the groundwater is quite high (MacDonald et al. 2003), and the downcore Ca^{2+} would show strong interannual autcorrelation.

Evidence supporting this interpretation is also seen in profiles of temperature and conductivity of Lake Żabińskie measured in monthly intervals during the period between October 2011 and July 2013. Conductivity and Ca^{2+} in surface waters are strongly correlated (R^2= 0.89). Thus changes in conductivity reflect changes in the

Ca^{2+} concentration in the lake. Figures 2C-D show the spatio-temporal pattern of conductivity and temperature corroborating that conductivity (and dissolved Ca^{2+}) decrease mainly during period of stratification between late spring and early fall (May-October). This is the period when calcite precipitates from the epilimnion.

In summary, because mixing depth governs both the light climate and the temperature regime in the mixed surface layer, we propose that wind-driven changes in the timing and depth of water column mixing may have a larger control on concentrations of Ca^{2+}, and thus on chrysophyte assemblages that respond to this variable.

Downcore reconstruction

Reconstructed Ca^{2+} captured a significant amount of variation in the May to October zonal winds (Fig. 5A). Westerly winds dominate the wind regime at Lake Żabińskie, being more frequent and stronger than winds blowing from the east, or than meridional circulation (N-S). Moreover, westerly winds have stronger impact in Lake Żabińskie due to its morphology and location. Long axis (max. wind fetch) of the lake basin is exactly along W-E direction and Lake Żabińskie is 'open' to wind action from the western side (it is on this side that Lake Gołdopiwo is located). Large open and flat areas on the western side of Lake Żabińskie enhance the potential of westerly winds to mix waters of Lake Żabińskie effectively (Fig. 1B).

During episodes of strong westerlies during May-October, epilimnion mixing and the reduction in phytoplankton and temperature lead to a lower calcite precipitation. With more intense zonal circulation, stratification of the epilimnion is broken, which in turn leads to lower calcite precipitation and hence higher concentration of Ca^{2+} in waters. The good inverse agreement between reconstructed lake water Ca^{2+} and downcore variations in sedimentary $CaCO_3$ (R=-0.49, 3-year filter, detrended) provides independent validation of the mechanism proposed here to explain the downcore changes in reconstructed Ca^{2+}. Calcite precipitation reflects the removal of dissolved Ca^{2+} from the lake water (Fig. 5D).

Poor fits of low chrysophyte cyst-inferred Ca^{2+} values make the reconstruction of very low values of Ca^{2+} less reliable. However, Lake Żabińskie is today a hardwater lake, and it is very unlikely that Ca^{2+} concentration reached low values close to those where our transfer function is less reliable. As we are reconstructing the part of the gradient with higher Ca^{2+}, we consider that the irregular sampling is not biasing our reconstruction (Fig. 3A).

Running correlations (31-year) between downcore Ca^{2+} and zonal circulation show high and significant values during the period AD 1898–2010. The running correlation remains higher than 0.6 until 1970 and decreases subsequently. The disagreement between reconstructed Ca^{2+} and zonal circulation in the last 40 years may be attributed to a change in the trophic status in the lake (Fig. 5B). Existing buildings near the lake were actively used as holiday resort since the late 1950s, which was later expanded at around 1970. Higher MAR are recorded during this period indicating an anthropogenic impact on the lake (Fig. 5C). Increased nutrient input may have had a profound effect on the relationship between chrysophytes and lake-water alkalinity. However, the correlation between reconstructed Ca^{2+} and zonal circulation remained high despite this anomalous period indicating that the transfer function is robust for the calibration period, particularly for the period before the anthropogenic impact around 1970.

While proxy data for temperature and precipitation are available for Europe, reconstructions of past atmospheric conditions are rare. Confidence in future changes in windiness is relatively low, but it seems more likely that in general, summer wind-speeds are projected to increase in north Europe (Räisänen et al. 2004). It has been showed that the atmospheric circulation is able to explains up to 77% and 44% of air temperature and precipitation variance (Degirmendžić et al. 2004). In periods of a negative North Atlantic Oscillation, weaker westerly winds allow a stronger influence of cold and dry continental air masses in central and eastern Europe, including Poland (Luterbacher et al. 2010). Therefore, our local wind reconstructions can potentially help to produce more skillful large-scale reconstructions and improve the understanding of atmospheric circulation indices in Europe.

Conclusions

Our study indicates that chrysophyte assemblages from Polish lakes respond to epilimnetic dissolved Ca^{2+}, and are potential tools for estimating quantitative changes in lake water. Changes in soluble Ca^{2+} in the surface waters during summer are likely related to calcite precipitation, which is controlled by the structure of the epilimnion and phytoplanktonic productivity. We suggest that these changes in calcite precipitation in Lake Żabińskie depend on the lake mixing regime, driven by westerly winds. The application of a chrysophyte cyst-based Ca^{2+} model to a varved sedimentary core from Lake Żabińskie indicate good agreement between reconstructed lake water Ca^{2+} and downcore variations in sedimentary $CaCO_3$. Reconstructed Ca^{2+} are correlated with May-October zonal circulation AD 1898-2010, and hence show the control of wind-mixing on calcite precipitation at Lake Żabińskie. Low correlations between reconstructed Ca^{2+} and wind after 1970 are in agreement with changes in the lake conditions (anthropogenic impact), indicating that the cyst assemblages are also sensitive to other factors apart from water chemistry.

Acknowledgements

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Figures

Figure 1. A) Map showing the distribution of the 50 lakes included in the training set across northern Poland. The lake used in the reconstruction (Lake Żabińskie, 54°07'54.5'' N; 21°59'01.1'' E) is indicated with a yellow star. B) Map showing the bathymetry of Lake Żabińskie and the coring site.

Figure 2. A) Average monthly temperature (lines) and rainfall (bars) at Lake Żabińskie between AD 1898-2010. B) Wind rose showing frequency and direction from which the wind (at 1000 hPa) is blowing and wind speed ($m \cdot s^{-1}$) at the same location between AD 1898-2010, based on 20^{th} century Reanalysis data (Compo et al. 2011). Isopleths of C) lake water temperature; D) electric conductivity from October 2011 until October 2013.

Figure 3. A) Principal Component Analysis (PCA) of all the measured environmental variables at the 50 lakes in Poland. B) Canonical Correspondence Analysis (CCA)

based on 49 sites (black circles) and 78 cyst types (white circles), with environmental variables with VIF < 25.

Figure 4. Plots of the A) observed versus predicted $\log_{10}$ Ca^{2+} and B) observed versus residual $\log_{10}$ Ca^{2+} based on WA regression with classical deshrinking. The black dot represents Lake Żabińskie, used in the reconstruction.

Figure 5. A) Bootstrapped estimates of $\log_{10}$ Ca^{2+} reconstructed from the sedimentary chrysophyte cyst assemblages at Lake Żabińskie based on the WA prediction model for the period AD 1898-2010. Log_{10} Ca^{2+} was highest correlated with the mean May-October zonal winds speed ($m \cdot s^{-1}$; 1000 hPa) (grey line). B) 31-year running correlation coefficients between $\log_{10}$ Ca^{2+} and zonal winds May-Oct. C) Mass accumulation rates (MAR) at Lake Żabińskie, indicating increased MAR between 1970-90. D) Correlation between reconstructed $\log_{10}$ Ca^{2+} and $CaCO_3$% (detrended) (R=-0.49, 3-year filter, note the inverted y axis for $CaCO_3$%).

Table 1. Summary statistics of measured environmental variables at the 50 Polish lakes included in the transfer function.

Table 2. Eigenvalues of axis 1 (**λ_1**), ratio between eigenvalues (λ_1/λ_2), and percent variance of species explained by the variables that remained after forward selection.

Supplementary material. Downcore stratigraphy of the 16 most abundant chrysophyte cysts identified at Lake Żabińskie. Chrysophyte cyst percentage diagram of the 16 most abundant species at Lake Żabińskie, spanning the AD 1898-2010 interval. Cyst types numbered with 'Pearl' code refers to Duff et al. (1995) and Wilkinson et al. (2002). New cysts identified at Lake Żabińskie are numbered with 'ZAB' code.

Figure 1
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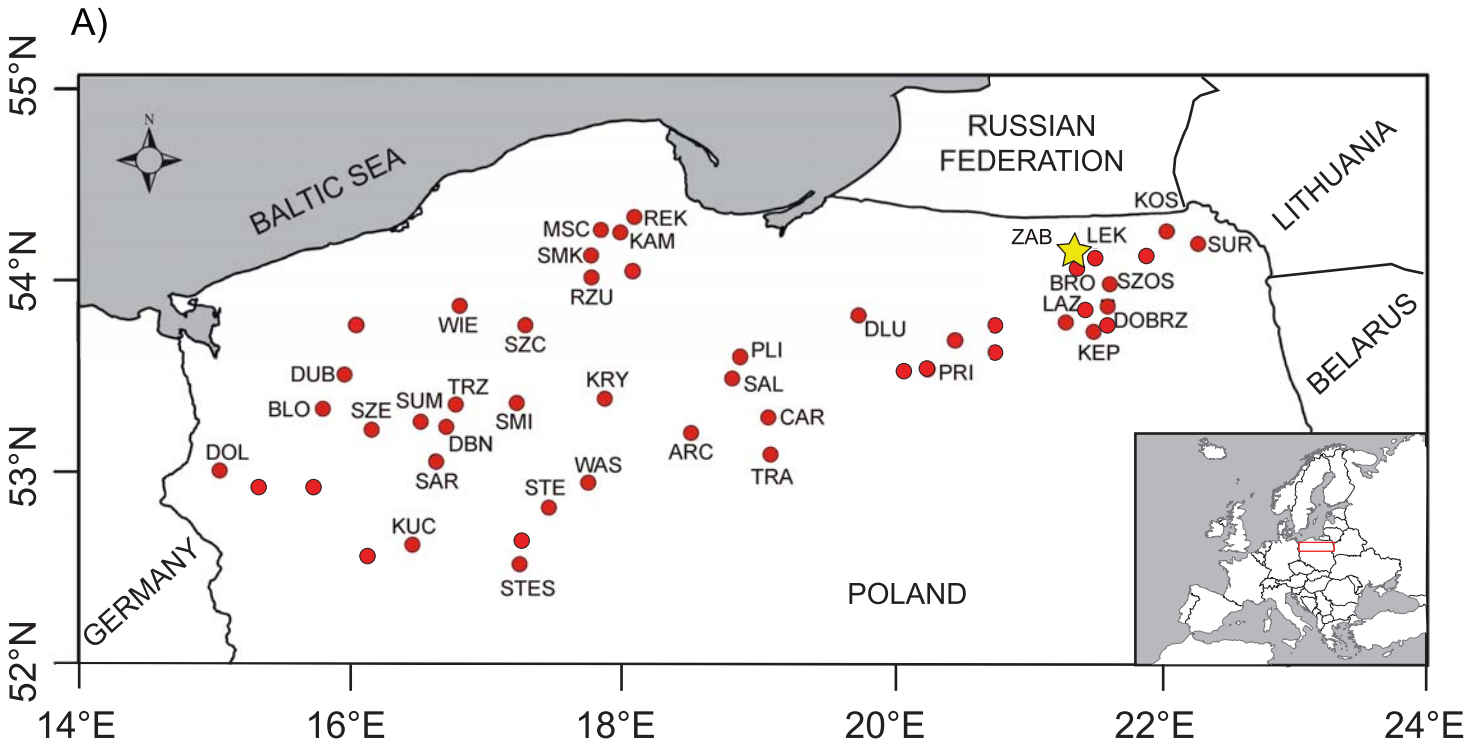

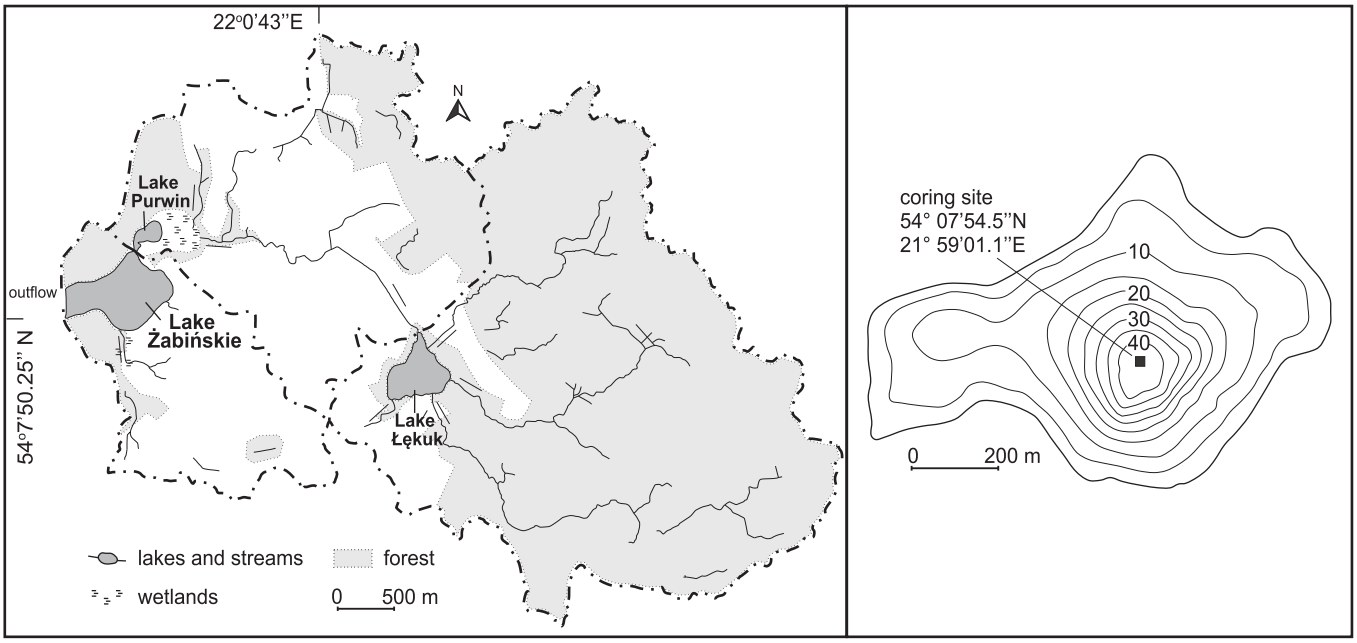

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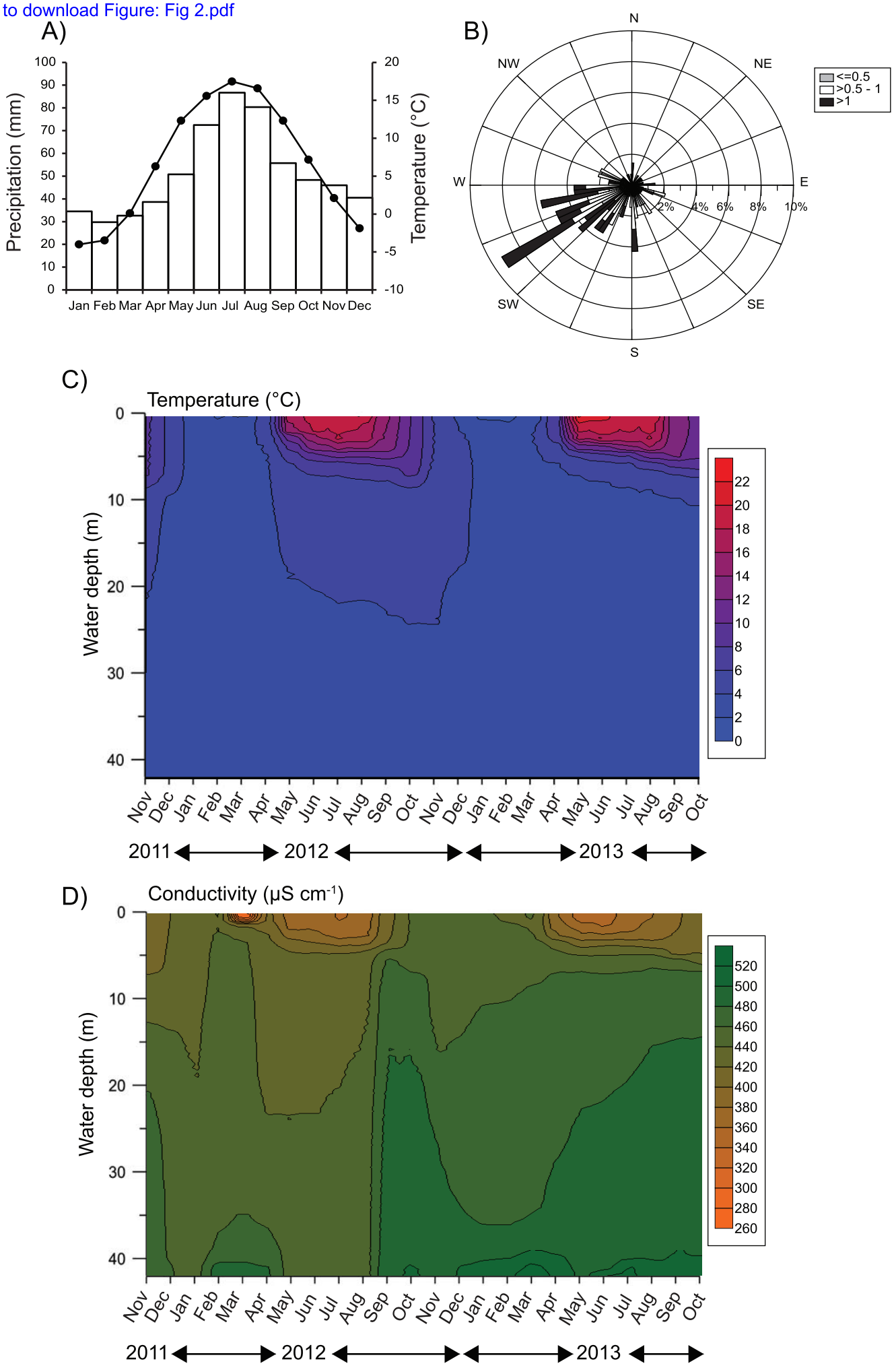

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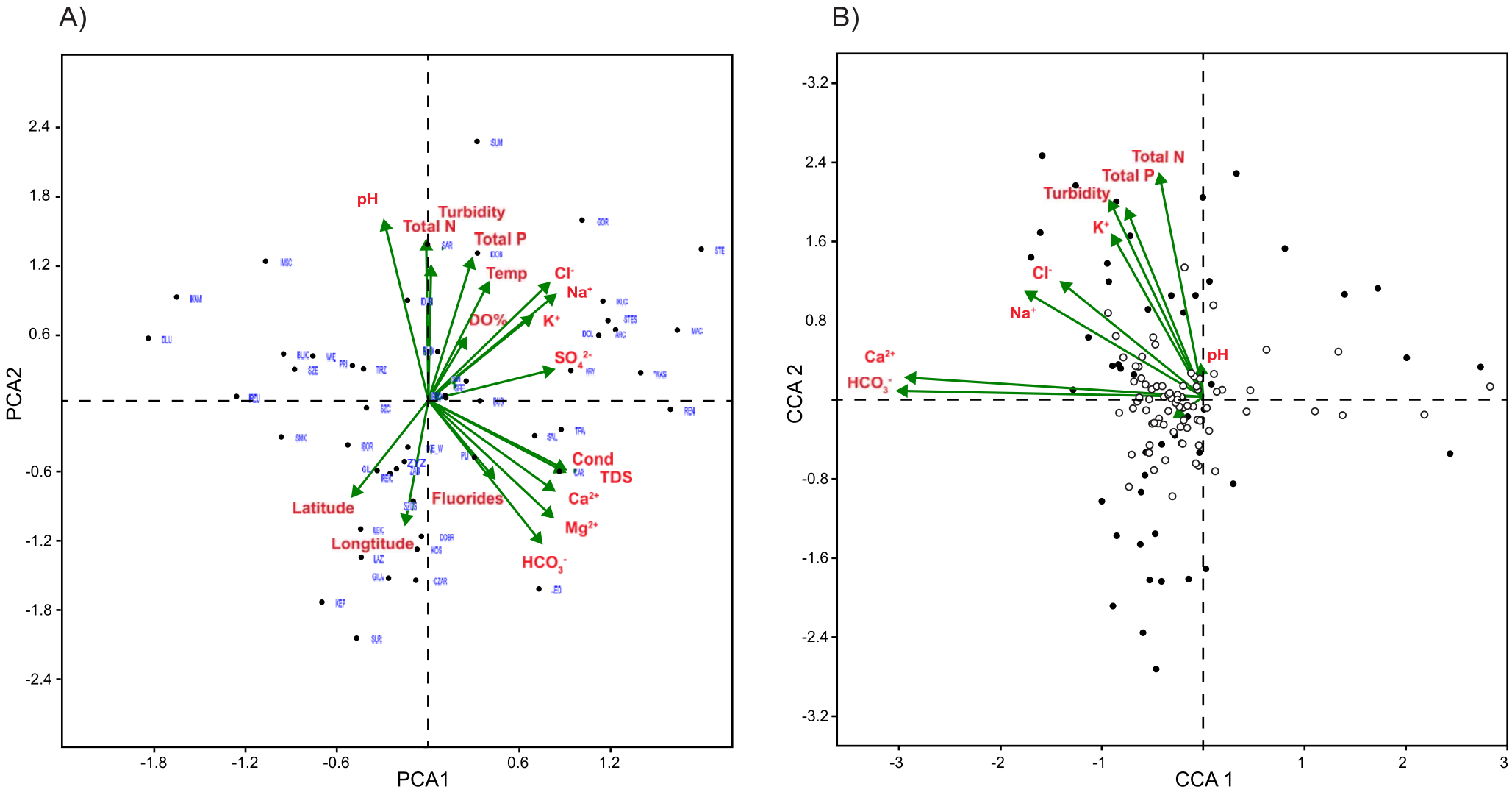

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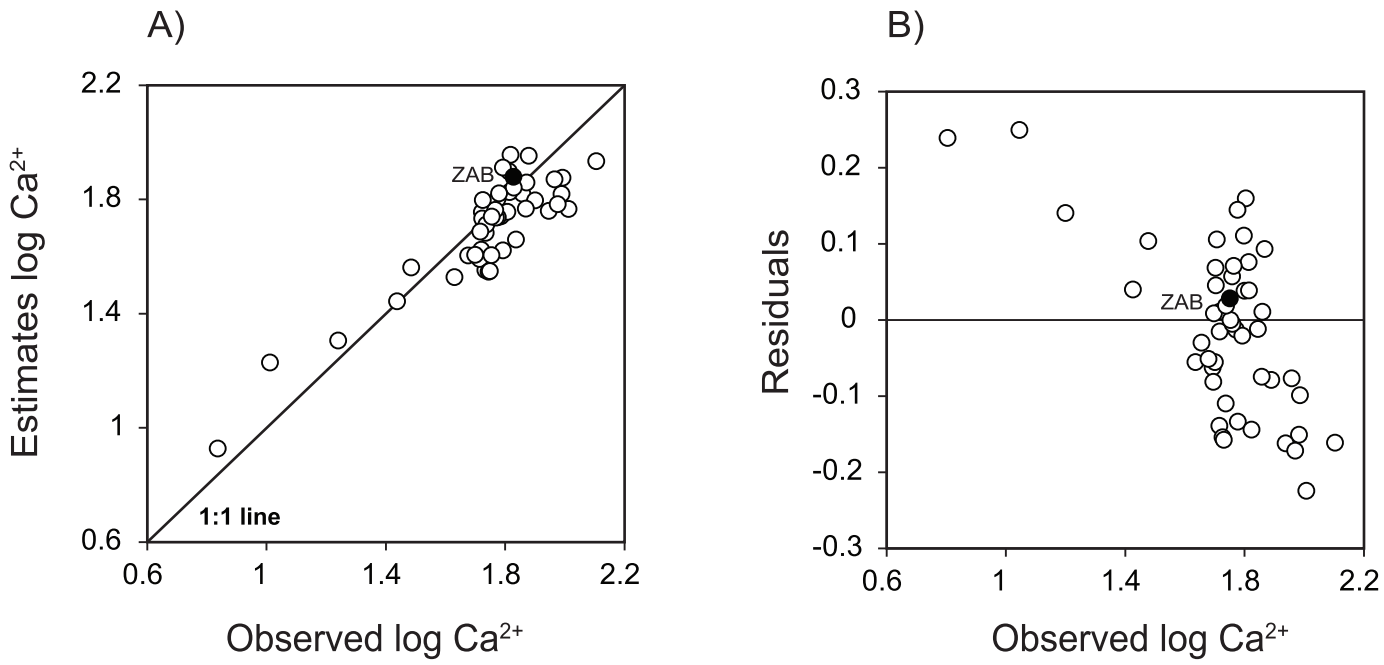

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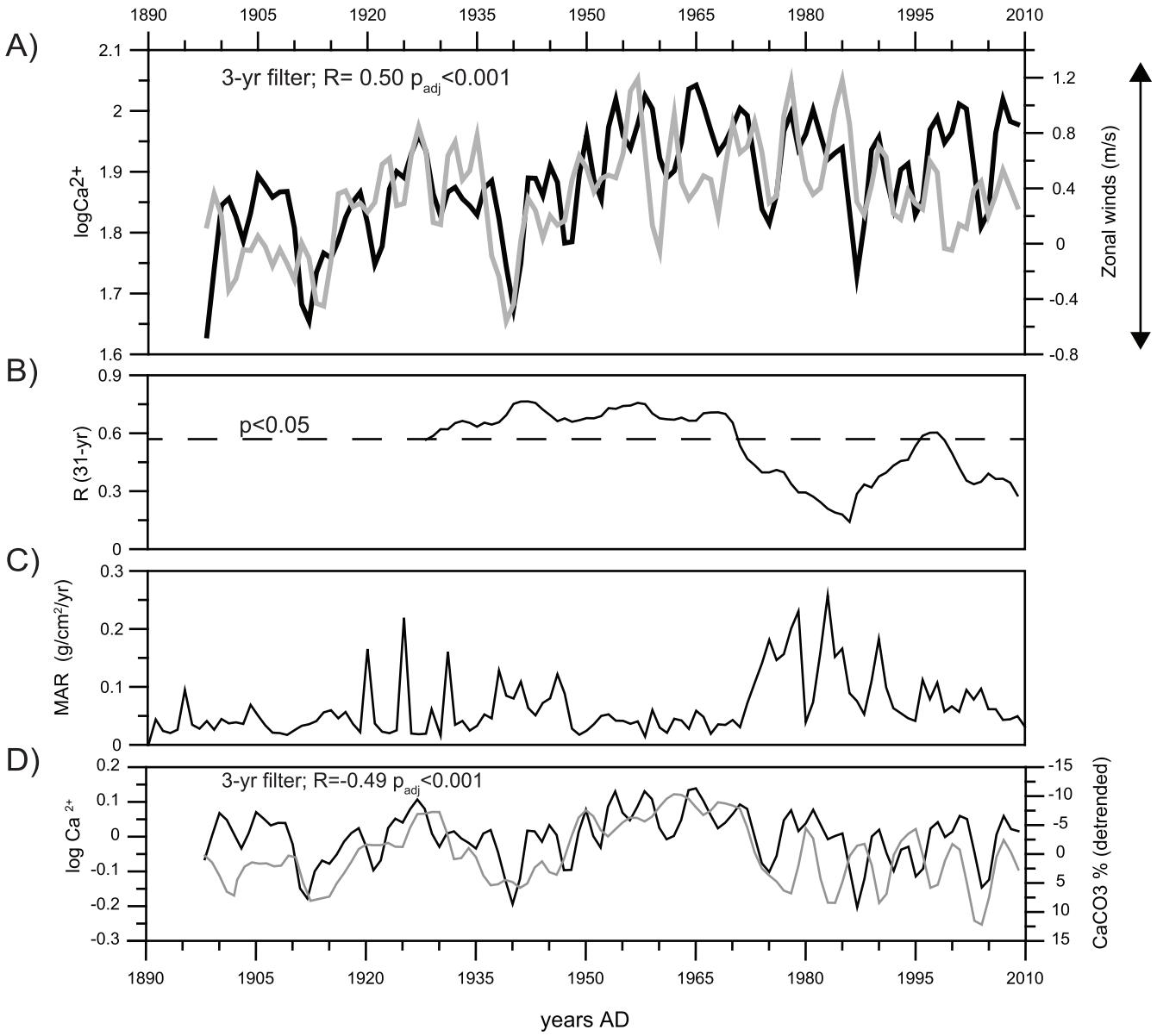

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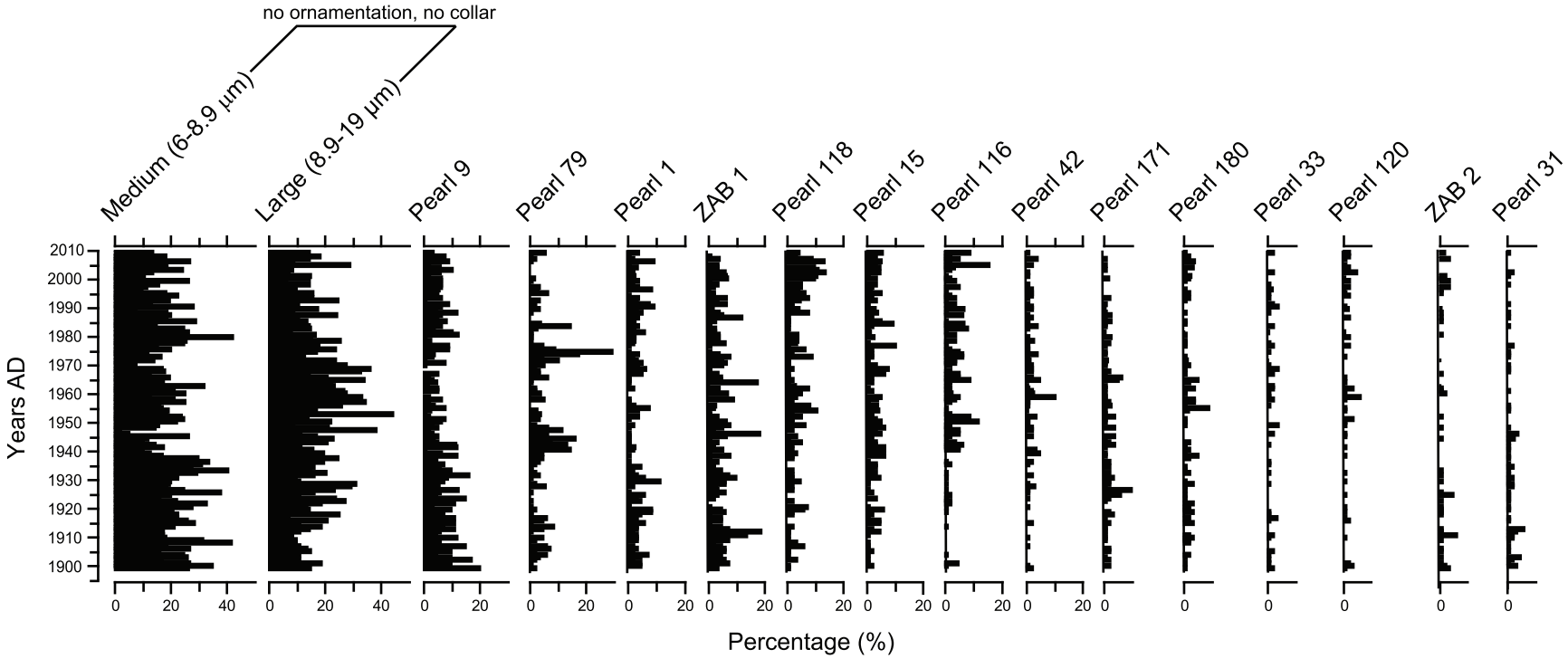

Table 1
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Table 1

Variable	Min	Max	Median	Mean
Latitude (dec°)	52.5	54.3	53.6	53.6
Longtitude (dec°)	14.6	22.9	18.1	18.7
Temperature (°C)	9.9	14.6	11.1	11.3
pH	7.7	8.2	7.9	7.9
DOC (mg L^{-1})	7.5	12.7	10.0	9.9
Turbidity (NTU)	1.7	23.0	4.1	5.3
Conductivity (µS cm^{-1})	53.5	770.8	364.4	384.6
Na^{+} (mg L^{-1})	1.7	23.9	5.5	7.3
K^{+} (mg L^{-1})	0.5	16.2	3.1	3.8
Mg^{2+} (mg L^{-1})	0.9	24.6	8.7	9.3
Ca^{2+}(mg L^{-1})	6.0	127.0	57.0	59.6
HCO_3^{-} (mg L^{-1})	0.3	5.3	2.8	2.7
SO_4^{2-} (mg L^{-1})	4.0	136.0	18.7	29.0
Fluorides (mg L^{-1})	0.1	18.9	0.1	0.5
Cl^{-} (mg L^{-1})	2.4	74.2	8.0	15.0
Total N (mg L^{-1})	0.3	4.4	1.1	1.3
Total P (mg L^{-1})	0.0	0.3	0.1	0.1

Table 2
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Table 2

	λ_1	λ_1/λ_2	% variance explained
Ca	0.093	1.09	7.46
Total N	0.080	0.89	4.03