6700 years of diatom changes related to land use and climatic fluctuations in the Lake Aydat catchment (Auvergne, France): Coupling with cyanobacteria akinetes, pollen and non-pollen palynomorphs data

Aude Beauger, Karen Serieyssol, Benjamin Legrand, Delphine Latour, Vincent Berthon, Marlène Lavrieux, Yannick Miras

Quaternary International xxx (xxxx) xxx

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

6700 years of diatom changes related to land use and climatic fluctuations in the Lake Aydat catchment (Auvergne, France): Coupling with cyanobacteria akinetes, pollen and non-pollen palynomorphs data

Aude Beauger[a,*], Karen Serieyssol[b], Benjamin Legrand[c], Delphine Latour[c], Vincent Berthon[a,d], Marlène Lavrieux[e,f,g], Yannick Miras[a,h]

[a] University Clermont Auvergne, French National Centre for Scientific Research (CNRS), Laboratory of Physical and Environmental Geography (GEOLAB), F-63000, Clermont-Ferrand, France
[b] University of Lyon, University Jean Monnet de Saint-Etienne, French National Centre for Scientific Research (CNRS), Environment City Society (EVS), 6 rue Basse des Rives, F-42023, Saint-Etienne cedex 2, France
[c] University Clermont Auvergne, French National Centre for Scientific Research (CNRS), Microorganisms: Genome and Environment Laboratory (LMGE), F-63000, Clermont–Ferrand, France
[d] AQUABIO Design Office, ZA du Grand Bois Est, Route de Créon, 33750, St Germain du Puch, France
[e] University of Basel, Department of Environmental Sciences, 4056, Basel, Switzerland
[f] University of Orléans, French National Centre for Scientific Research (CNRS), Office of Geological and Mining Research (BRGM), Institute of Earth Sciences in Orléans (ISTO), F-45071, Orléans, France
[g] University François-Rabelais of Tours, Continental GeoHydrostems Laboratory (GéHCo), F-37200, Tours, France
[h] French National Centre for Scientific Research (CNRS), National Museum of Natural History (MNHN), Natural History of the Prehistoric Human (HNHP), F-75013, Paris, France

A R T I C L E I N F O

Keywords:
Palaeoenvironment
Lake
Multidisciplinary
Multi-proxies
Eutrophication

A B S T R A C T

Nowadays Lake Aydat is an important site for tourism activities but blooms of cyanobacteria induced some restriction for aquatic activities by humans and their livestock. Thus, it was important to understand the lake's history as it should help in the development of restoration strategies to improve water quality in the future. Lake Aydat had a complex history affected by climatic changes and human influences. Two different sedimentary periods of deposition were observed (6700 ± 200–3180 ± 90, and 1770 ± 60 cal. BP – nowadays) separated by a mass wasting deposit. The lower unit was dominated by Stephanodiscus diatom species (*S. medius*, *S. minutulus* and *S. parvus*) and two Aulacoseira species (*A. pusilla* and *A. subarctica*) and the upper layer by *Aulacoseira subarctica* and its form *recta* along with *Lindavia radiosa* and a series of "Fragilariod" taxa. The eutrophic diatom species increase, associated with the lower layer, was most likely related to prehistorical human activities within the watershed (progressive change from a wooded landscape to an agricultural patchy landscape). The Middle Bronze Age degradation was noted as a period with a rise in planktonic and tychoplanktonic diatom species. The lower diatom zone in the upper unit marked the final transition to a domination of agricultural practices and high human pressure and a whole new set of environmental factors affecting the lake since 1750 cal. BP. Increased nutrient enrichment was observed and the *Lindavia radiosa* presence in the lake was associated with the beginning of hemp (*Cannabis sativa*) cultivation and an increase in agricultural pressure. High concentrations of cyanobacteria akinetes were associated with the final transition and the maximum of hemp cultivation, when the lake became very eutrophic. For future restoration strategies, improving the water quality will be a challenge as high concentrations of akinetes and nutrients are observed since the Antiquity in the lake.

1. Introduction

Since the second of July 2018, the "Faille de Limagne and Chaîne des Puys" (Limagne & Chaîne des Puys fault) is registered on UNESCO's World heritage list and socio-economic development is occurring in the area. To guarantee environmental quality and guide future

* Corresponding author.
E-mail address: aude.beauger@uca.fr (A. Beauger).

https://doi.org/10.1016/j.quaint.2022.01.013
Received 15 March 2019; Received in revised form 27 January 2022; Accepted 27 January 2022

developments such as touristic activities, it is important to understand the region's environmental heritage. Thus, palaeoecological investigations aim at developing retrospective and prospective models of ecosystem functioning and landscape evolution.

As diatom valves have been the mainstay of many palaeolimnological investigations, they are a powerful tool in biomonitoring of environmental changes, as they have siliceous cell walls which are resistant to chemical dissolution and are often preserved in lake or peat sediments. Moreover, there are thousands of diatom species that live in different environments with different optima and tolerances (Smol, 2008). In the Massif Central, only a few palaeoecological studies have focused on diatoms. The earliest diatom studies were the study of Frère Héribaud with the study of diatomite deposits and travertines in many areas of the Massif Central (1883, 1902, 1903, 1908). Some other studies were done in fenlands (Cubizolle et al., 2005; Serieyssol et al., 2012) and peat bogs (Gandouin et al., 2016). In lakes, diatom studies have pertained mainly to Lake Pavin. Manguin (1954) studied material dragged from the sublittoral zone of Lake Pavin. Gasse (1969), later, studied a small core from Lac Pavin taken from 23 m depth and gave a systematic and repartition list of the diatoms within 8 samples. In 2000, Rioual examined surface sediments from 25 lakes and developed a surface sediment training set and then constructed a transfer function and, in 2007, the Ribains Maar was also studied (Rioual et al., 2007). For Lake Pavin, Stebich et al. (2005) analyzed a 182 cm long sediment core taken from the center of the lake. This material corresponded to the top diatom zones identified in a recent investigation of a more than 12 m long core by K. Serieyssol and A. Beauger in which seven zones were identified (Serieyssol et al. unpublished). For Lake Aydat, only three articles have been published (Lavrieux et al., 2013a, b; Miras et al., 2015) mainly on sedimentological features and pollen. New articles focusing on sedimentology present the last knowledge on lacustrine records in the Massif Central (Chapron & Chassiot, This issue; Chassiot et al., This issue). Thus, Massif Central lakes, particularly Lake Aydat, part of the Chaîne de Puys, Auvergne, has had limited palaeo-environmental studies and none combined an analysis of diatom, pollen and cyanobacteria akinetes data.

Lake Aydat has been strongly developed as a touristic hotspot (fishing, residential areas, etc.). The lake has been and is being affected by human influences (Miras et al., 2015) that cause high eutrophication levels, often resulting in the prohibition of swimming during the summer due to *Anabaena* (cyanobacteria) blooms. Indeed, during the second half of the 20th century studies underlined that in the epilimnion, the summer inorganic nitrogen concentration was about 70 μmol l^{-1} N and the soluble inorganic phosphorus concentration between 10 and 40 μg l^{-1} P (Millérioux, 1976; Jamet Planche, 1995; Mallet et al., 1998). The bloom of cyanobacterias is not compatible with socio-economic development. Thus, our palaeoecological investigation aims to provide fresh insights into the functioning of the lake in order to develop a better understanding on how to restore and preserve it for future use. Local and regional authorities are therefore particularly interested in lake restoration while allowing ecotourism.

For Lake Aydat, Lavrieux et al. (2013b) studied one chemical compound, cannabinol, detected in the sediments for approximately 600 years (since ca. AD 1260 until ca. AD 1850), which revealed the history of hemp retting around the lake. But using pollen, the beginning of the hemp cultivation, possibly associated to retting, must have started somewhere around AD 870. The hemp cultivation and retting peaked during the 17th and 18th centuries. A multiproxy dataset, including sedimentological features, age-depth model and accumulation rates, recurrent floor deposits and pollen data, was presented along with a preliminary discussion of climate and anthropogenic influences (Lavrieux et al., 2013a). Later, Miras et al. (2015) gave a detailed discussion of long-term vegetation changes and land use history that lead to trophic change. Indeed, even Neolithic and Bronze Age human activities (between ca. 4600 and 4300 cal. BP (2650–2350 BC) and between ca. 3900 and 3500 cal. BP (1950–1550 BC)) appeared to have had a discernible influence on catchment vegetation and lacustrine trophic dynamics of the lake. Grazing activities, but also land use practices, such as hemp cultivation and retting lead to phases of water nutrient over-enrichment. Preliminary results on diatoms and water quality were given in this study using inferred total phosphorus concentrations. The reconstruction showed that total phosphorous concentrations were significantly higher between 1400 and 100 cal. BP, with total epilimnetic phosphorus concentration varying between 2 and 37 μg.L^{-1}. Moreover, in Legrand et al. (2016) akinetes from cyanobacterial strains were characterized from Lake Aydat. Given their resilience over time, akinetes are emerging as markers of toxic cyanobacterial proliferations in palaeoenvironmental studies.

The present study focuses on Lake Aydat that is under constant pressure between keeping environmental quality of the water and the socio-economic development around the lake. This article presents a multi-proxy approach based on diatom research, unique for the Auvergne. The purpose of this study was to explore the lacustrine ecosystem dynamics with climatic variations and human activities that changed through time in the watershed using diatoms and making correlation with the first studies that have focused on pollen and sediment analyses (Lavrieux et al., 2013a, b; Miras et al., 2015). Detailed information on diatom sequences and their relationship to land use changes and water quality is presented along with the cyanobacteria akinete results. The main objectives are to: 1) use diatoms to establish a reference condition for the lake during the Mid-Holocene when climate was the strongest influencing factor, as the anthropogenic impacts were still weak, 2) identify the chemical evolution over time in terms of trophic state, saprobity, lifeforms, nitrogen, oxygenation, pH and moisture in order to evaluate if the system is resilient or if there was a gradual degradation due to accumulation of impacts over time, and 3) identify the main forcing to these changes (climatic and/or land use changes).

2. Regional settings

Lake Aydat (2°59.106′E, 45°39.809′ N, 845 m a.s.l.) is located 25 km south from the city of Clermont-Ferrand in the southern section of the volcanic Chaîne des Puys range (Fig. 1). The climate is characterized as oceanic-montane with a mean annual temperature of ca. 12 °C, and an annual mean rainfall of ca. 800 mm. The lake, which originated by damming of the Veyre River with basaltic lava flows (dated to 8551 ± 400 cal. BP) issuing from the Puy de la Vache and Puy de Lassolas volcanoes (Boivin et al., 2004). The lake has a surface area of 60 ha with a volume of ca. 4.1 hm^3 (Direction Régionale de l'Environnement, de l'Aménagement et du Logement, 2017) and an average depth of 7 m, and a maximum depth of 15 m (Lavrieux et al., 2013a). The catchment area has a surface area of ca. 30 km^2 and is situated between 837 m and 1300 m a.s.l. The eutrophic lake is fed by the Veyre River which is also the main outlet for water, however, some infiltration occurs through the basalt flows. Granodiorites composes mainly the basement rock that is partially covered by Late-Glacial to Holocene volcanic deposits and recent colluvium and alluvium (Boivin et al., 2004). Nowadays, the catchment is mainly covered with grassland and pastures, and with secondary forests (dominated by coniferous) reforested on volcanic summits (Lavrieux et al., 2013a). A detailed description of the Lake Aydat features (e.g. geological and geomorphological settings) is given in Lavrieux et al. (2013b).

3. Material and methods

3.1. Diatom and cyanobacteria akinete analyses

A continuous, 16 m long stratigraphical sequence was retrieved (in 2 and 3 m sections) from the deepest part of Lake Aydat at a water depth of 14.5 m near the Veyre River delta. The core was later divided into two main units (6700 ± 200 to 3180 ± 90 cal. BP, and 1770 ± 60 cal. BP to present) based on sedimentary features separated by a mass wasting deposit triggered ca. 1770 ± 60 cal. BP. Age-depth model correlation for

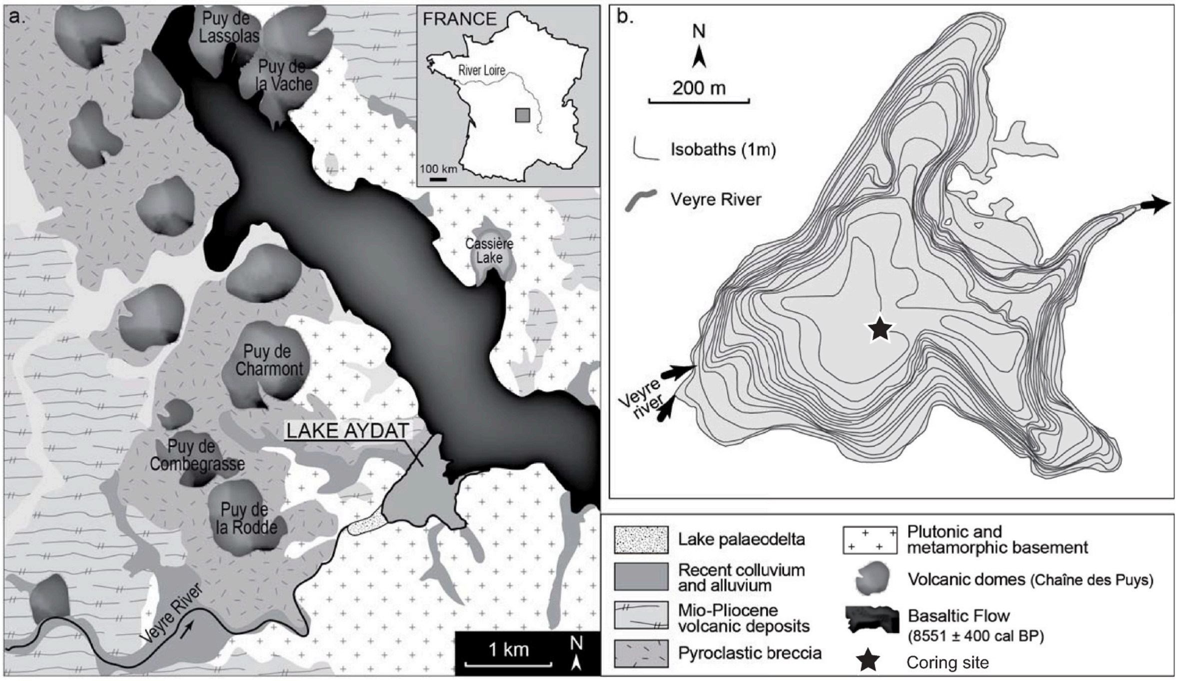

Fig. 1. a. Location of Lake Aydat in the Massif Central (France). b. Coring location in Lake Aydat with bathymetric contour lines.

Lake Aydat was given in Lavrieux et al. (2013a). Diatom samples were taken on average every 30 mm (varying between 16 and 40 mm) and processed following Serieyssol et al. (2010/11) and mounted in Naphrax. No diatom analysis was performed on the mass wasting deposit. A minimum of 300 but more often 400 individuals were counted per sample. They were identified using either an Axioskop 2 or Leica® DM2700M microscope with 100x oil immersion objective. Diatoms were identified using the following literature: Germain (1981), Camburn and Kingston (1986), Krammer (2002, 2003), Krammer and Lange-Bertalot (1997–2004), Lange-Bertalot (2001), Buczkó et al. (2010), Houk et al. (2010). The interpretation of the ecology was based on van Dam et al. (1994) and the ecological preferences (trophic state, saprobity, nitrogen uptake, oxygen & pH requirements and moisture) were calculated using OMNIDIA 6.0.6 (Lecointe et al., 1993). Moreover, the information given by Rioual (2000) and Kauppila (2006) were used for the ecology of *Aulacoseira subarctica* and its f. *recta* respectively. Indeed, Rioual considered this diatom species as meso-eutrophic, while van Dam et al. (1994) consider it as oligo-mesotrophic. For the form *recta*, it must be eutrophic, contrary to van Dam et al. (1994) that estimate it as oligo-mesotrophic. Ecological preferences were modified related to this information. For the trophic state, oligotrophic and oligo-mesotrophic data were associated. The same was done for meso- and meso-eutrophic data. At last, the facultative N-heterotrophic diatom taxa were associated with the obligatory N-heterotrophic diatom taxa. Moreover, related to the ecological knowledge of diatom species, they were divided into: planktonic, tychoplanktonic and periphytic.

Cyanobacteria akinete extraction and enumeration protocols are described in Legrand et al. (2016). Between 0.25 and 0.5 g of fresh sediment was diluted in 5 mL distilled water. Then, 4 mL of ludox (Sigma-Aldrich, Saint- Louis, USA) is added. Solutions were sonicated (40 s, frequency: 50%, power: 80 W, Sonoplus, Bandelin, Berlin, Germany) and centrifuged at 9000 g for 20 min at 4 °C. The first 4 mL of supernatant were pipetted, homogenized and divided in two replicates. For each sample, 2 extractions corresponding to 4 replicates were performed. Each replicate was filtered using an 8 μm filter (TEPT filters Merck Milipore, Tullagreen, Ireland). Cyanobacteria akinetes were counted under an epifluorescence microscope (microscope Zeiss Axiovert 200 M; 200x magnification, Oberkochen, Germany) and forty fields on each filter were counted.

3.2. Statistics

Diatom zones were determined using Psimpoll 4.26 (Bennett, 2002) using a constrained cluster analysis by sum-of-squares (CONISS) on diatom species having a relative abundance greater than 1% in at least one sample. Principle Components Analysis (PCA) was performed on diatom species having a relative abundance greater than 1% to minimize the influence of rare diatom taxa, and by using PC-Ord 6.0 (McCune and Mefford, 2011) with variance/covariance, distance-based biplot, and randomization options.

Mean pH was reconstructed from a diatom inference model based on 622 surface sediment samples collected from lakes in Europe (European Diatom Database – EDDI – web site: http://craticula.ncl.ac.uk/Eddi/jsp/index.jsp). The model was calibrated using pH data. The selected model was then applied to the diatom biostratigraphy of each lake section. The Diatom-inferred pH (DipH) reconstructions were performed using the C2 software (Juggins, 2007). Several models were tested: weighted averaging with classical deshrinking (WAcla regression), weighted averaging with inverse deshrinking (WAinv regression) (ter Braak and van Dam, 1989), weighted averaging partial least squares regression (WAPLS) (ter Braak and Juggins, 1993) and the Modern analog technique: weighted average pH of 10 closest analogues (WMAT) (Overpeck et al., 1985). Their relative performances were estimated using r^2 and the root mean square error of prediction (RMSEP) calculated using a cross validation method (bootstrapping, 1000 permutations) on the calibration dataset. The same bootstrapping procedure was used to calculate the standard error of the prediction of the core samples.

Diatom and cyanobacteria akinete data were compared with the palynological data (pollen, cryptogam spores and non-pollen palynomorphs (NPPs)) already published in Miras et al. (2015). Then, pollen, cryptogam spores, NPPs and diatom data were reanalysed using a correlation matrix using the diatom species with a relative abundance >1% in at least one sample. The absolute abundances of diatom species were log-transformed ($x = \log(n + 1)$) to normalize the data. Then, co-inertia analyses (COIA) were performed on the PCAs to analyse the co-structure of the two pairs of matrixes (Dray et al., 2003). The statistical significance of the analyses was tested through a Monte Carlo random re-sampling test using 1000 random permutations (p-value ≤0.05). The Monte Carlo permutation test where the rows of one matrix are randomly permutated and followed by a re-computation of the total inertia, was used to check the significance of co-structure of this co-inertia. ADE4 in R 3.3.1 provided the software for these calculations (R Development Core Team, 2006).

4. Results

4.1. Diatom and cyanobacteria communities

For this study, 56 samples were studied and among them, 179 different taxa were observed. A first PCA (using this database) was performed on the more abundant taxa (>1%). A clear separation between the lower and upper units was observed. This separation was statistically underlined, with the first two axes explaining 72% of the total inertia (axis 1–48%, axis 2–24%; p = 0.001).

Therefore, two new PCAs were performed on each unit individually (Fig. 2). For the lower unit, the PCA explained 80% of the total inertia (axis 1–52%, axis 2–28%, p = 0.036) while the upper unit explained 88% (axis 1–81%, axis 2–7%, p = 0.001).

For the lower unit, the lower right part of the first factorial plan (Group 1) was dominated by *Aulacoseira pusilla* (Meister) Tuji et Houki. This diatom species is associated with the deepest samples and also with the highest samples for this unit (813, 837 and 869 cm). The upper half part was determined by three *Stephanodiscus* (*S. medius* Håkansson, *S. minutulus* (Kützing) Cleve & Moller, *S. parvus* Stoermer & Hakansson) and grouped together samples between 1444 cm and 1140 cm with the samples 946, 929, 913 and 893 cm. *Aulacoseira subarctica* (O. Müller) Haworth is associated with the lower left part (group 3) and grouped together for the samples between 1108 cm and 1010 cm, and with the samples of 1224 and 1200 cm. Sample 789 cm occurs just below the unconformity and was associated with this last group.

For the upper unit, the upper half part of the first factorial plan (Group 1) is controlled by *A. formosa*, *S. parvus*, and *Discotella pseudostelligera* combined with its f. *diminuta*. These diatom species are associated with the deepest samples and with some more recent samples (85 and 30 cm). For the lower right part (group 2) *Lindavia radiosa* (Grunow) De Toni & Forti was linked to the samples between 482 and 234 cm corresponding to the hemp-retting phase and, at last, the lower left part (Group 3) is controlled by *A. subarctica* combined with its f. *recta*. These diatom species and forms are associated with six different samples corresponding to different levels (between 728 cm and 50 cm).

On the stratigraphical diagram, a total of seven diatom zones (Fig. 3) were determined: four in the lower lake unit and three in the upper

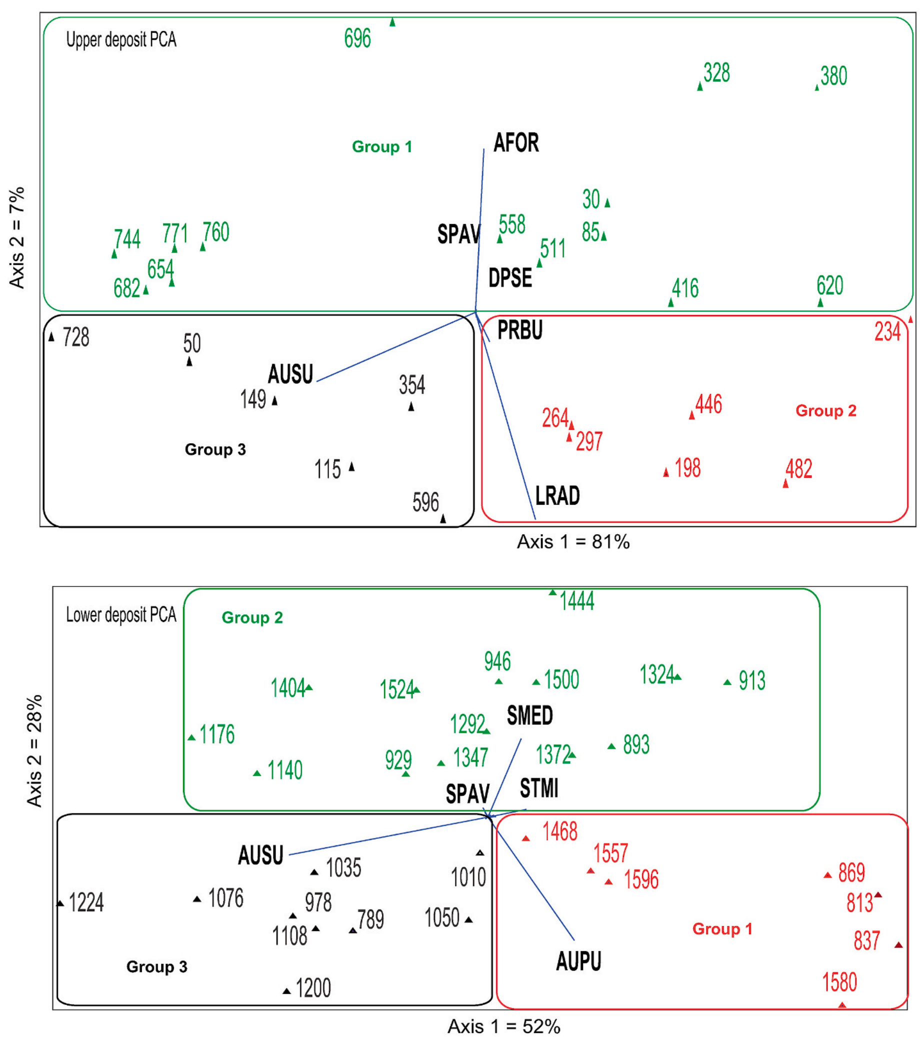

Fig. 2. Principle component analyses for diatom data performed on the stratigraphy extracted from Lake Aydat in the Massif Central (France) and for the two separated diatom units (Upper and Lower sediment deposits). The main diatom species were *Aulacoseira subarctica* (AUSU), *Asterionella formosa* (AFOR), *A. pusilla* (AUPU), *Discostella pseudostelligera* (DPST), *Lindavia radiosa* (LRAD), *Pseudostaurosira robusta* (PRBU), *Stephanodiscus medius* (SMED), *S. minutulus* (STMI), and *S. parvus* (SPAV).

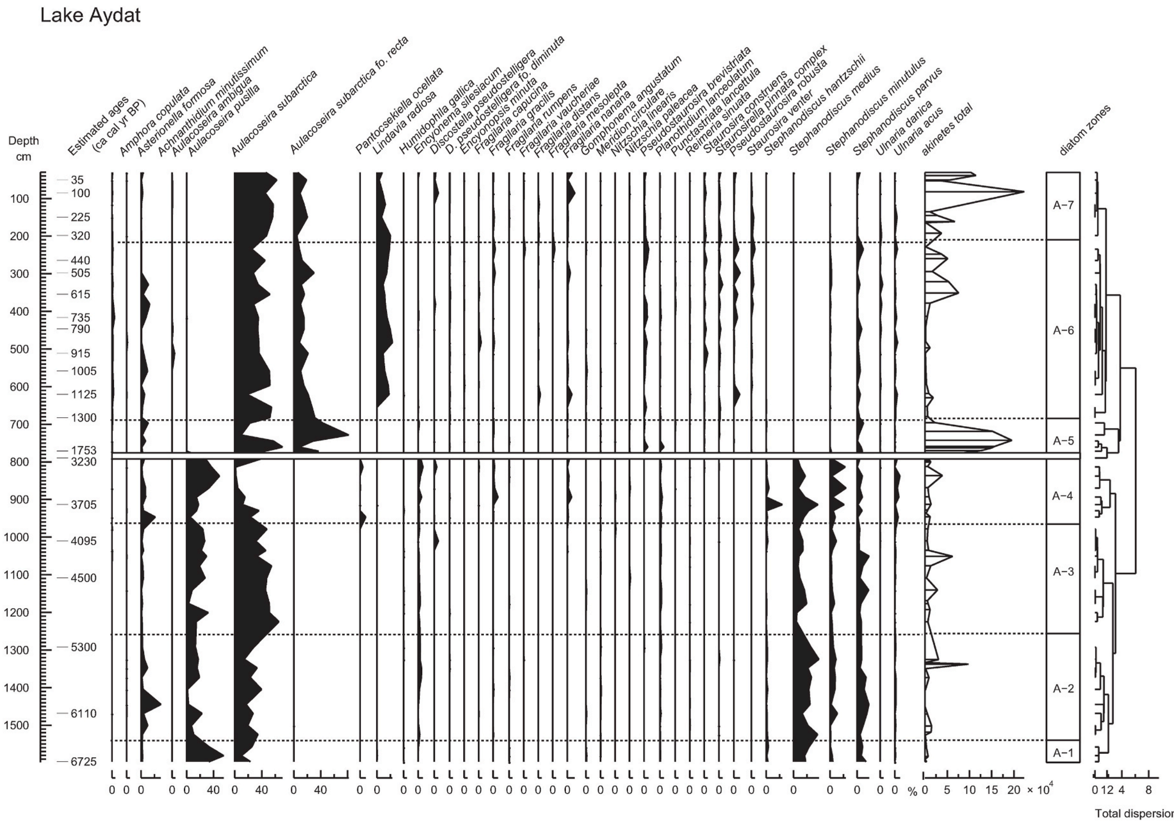

Fig. 3. Stratigraphic diatom zonation for Lake Aydat in the Massif Central (France) together with the associated cyanobacteria akinetes total. Zonation determined using Psimpoll 4.26. The double line marks a mass-wasting event.

deposits, with the mass-wasting event found between zone 4 of the lower unit and zone 5 of the upper unit. In Fig. 3 the counts of cyanobacteria akinetes were added. For the lower unit four zones were recorded. Zone A-1 (1596–1557 cm; 6720–6530 cal. BP) represents the beginning of the functioning of the lake. The community is dominated by *Aulacoseira pusilla* and *A. subarctica* with some *Stephanodiscus* species (*S. hantzshii* Grunow, *S. medius* Hakansson, *S. minutulus* and *S. parvus*). Cyanobacteria akinetes are present in very small concentrations. Then, in Zone A-2 (1557–1292 cm; 6530–5300 cal. BP) *A. pusilla* decreases with an increase in *Asterionella formosa* and *S. minutulus* while *Encyonema silesiacum* (Bleisch in Rabh.) D.G. Mann, *Planothidium lanceolatum* (Brebisson ex Kützing) Lange-Bertalot and *D. pseudostelligera* combined making a continue appearance, along with cyanobacteria akinetes. Noticeable higher concentrations of cyanobacteria akinetes are observed at the end of the zone. Zone A-3 (1292–978 cm; 5300–3950 cal. BP) is dominated by *A. subarctica* and *A. pusilla* with a decrease in the *Stephanodiscus* species and *A. formosa*. *D. pseudostelligera*, found in small concentration in previous zones, now becomes more important in this zone. Higher values of cyanobacteria akinetes are regularly registered except at the end of the zone where a slight decline is observed. At last, in Zone A-4, there is an important decrease in *A. subarctica* (978–789 cm; 3950–3230 cal. BP) with an increase in *A. formosa*, *A. pusilla, S. medius* and *S. minutulus*, while *S. hantzschii* reached its maximum. *Pantocsekiella ocellata* (Pantocsek) K.T. Kiss et Ács, *D. pseudostelligera*, *Fragilaria gracilis* Oestrup, *Fragilaria nanana* Lange-Bertalot and *Ulnaria ulna* (Nitzsch.) Compère var. *acus* (Kütz.) Lange-Bertalot are common in the community. Cyanobacteria akinete concentrations were similar to the end of the previous zone. Sample 789 cm shows a large increase in *A. subarctica*. This sample is maybe affected by the reworking from the mass-wasting event.

Above the mass-wasting event three zones were recorded. In Zone A-5 (771–696 cm, 1750–1380 cal. BP) *A. pusilla* and certain *Stephanodiscus* species (*S. hantzschii, S. medius,* and *S. minutulus*) disappear and *A. subarctica* its f. *recta* appears. It was combined with *A. subarctica. Aulacoseira subarctica* combined becomes the dominant member of the community. Both *A. formosa and S. parvus* remain common. A series of "*Fragilaria*" species became prevalent: (*Fragilaria capucina* complex (includes *F. gracilis* Østrup, *F. rumpens* (Kutzing) Lange-Bertalot, *F. vaucheriae* (Kutzing) Lange-Bertalot), *Pseudostaurosira brevistriata* (Grun. in Van Heurck) Williams & Round, *Staurosira construens* Ehrenberg, and *Staurosirella pinnata* complex Ehrenberg). A large amount of cyanobacteria akinetes were observed. Then, in Zone A-6 (696–234 cm, 1380–385 cal. BP) *Lindavia radiosa* appears in the lake sediments along with more "*Fragilaria*" species (*Fragilaria capucina* complex, *Fragilaria distans* (Grunow in Van Heurck) Bukhtiyarova and *Fragilaria nanana*. Throughout this period, *A. subarctica* and its f. *recta* are present. Moreover, *Pseudostaurosira robusta* (Fusey) Lange-Bertalot and *Staurosira venter* (Ehr.) Cleve & Möller) also appear. A first peak of *P. robusta,* observed at 1125 ± 50 cal. BP, is associated with higher concentration of cyanobacteria akinetes. At the end of the period (upper part of the zone) *P. robusta* and *S. venter* increase again, associated with high concentration of cyanobacteria akinetes. At the same time *A. formosa* practically disappears. The last zone A-7 (234–30 cm; 385–(-5) cal. BP) is marked by decreases in *A. formosa, L. radiosa* and *S. parvus*. *A. subarctica* combined dominates this zone. Globally, above the mass-wasting event (since 1497 cal. BP) an increasing trend in the amount of cyanobacteria akinetes is observed throughout the zone with maximal values at ca. 110 ± 40 cal. BP.

4.2. *Palaeocological significance*

4.2.1. *The lower sedimentary unit of Lake Aydat (1596–789 cm; 6720–3230 cal. BP)*

Below the mass-wasting event, in the lower sedimentary zones, certain ecological indicator values were higher than in the upper sedimentary zones. Higher nutrient enrichment in the lake was observed with: 1) greater amounts of hypereutrophic diatom taxa (Fig. 4), 2) higher amounts of organic matter and 3) larger amounts of nitrogen-autotrophic diatom taxa that tolerate elevated concentrations of the organic bound nitrogen and facultatively nitrogen-heterotrophic diatom taxa needing periodic elevated concentrations of organic bound nitrogen. Higher pH was observed in the lower level with a large percentage of alkalibiontic diatom taxa (optima always >7) along with high percentage of planktonic diatom taxa. Zone A-4 just below the mass-wasting event, is characterized by an increase in "aquatic, sometimes subaerial" diatom species along with increased nutrient enrichment.

4.2.2. The upper sedimentary unit of Lake Aydat (771–30 cm, 1750–(-5) cal. BP)

Above the mass-wasting event, major changes occurred in the lake chemistry with an increase in diatom species being eutrophication indicators, because of more nutrient-rich lake waters (increase in trophic state, saprobity and nitrogen) (Fig. 4). The water had an increase in oxygen saturation with more aquatic and tychoplanktonic diatom taxa, along with a change in pH with a decrease in alkalibiontic diatom taxa and an increase in circumneutral diatom taxa.

4.2.3. Diatom inferred pH of the Lake Aydat water

There were no relevant differences between WAcla, WAinv and WAPLS model performances. Only the WMAT model had higher performance. The RMSEP of the models compared well with the standard error of the prediction (SEP) calculated on the core samples (Table 1). Results presented in Fig. 5 are those obtained using the MAT model. The reconstruction showed that the total epilimnetic pH in Lake Aydat varied between 6.74 and 7.43.

Using this diatom-inferred epilimnetic pH, the differences between the lower and upper part were small. When considering the lower unit, periods of increases occurred. The last sample of the lower unit, with the increase in *A. subarctica*, could explain the peak observed. For the upper unit, fluctuations occurred but a slight increase was observed during the zone A-6 compared to the zone A-5.

4.3. Coupling diatom communities with palynological observations

The pollen and NPP study allowed estimation of long-term vegetation changes and land use history observed for Lake Aydat (Miras et al., 2015). The pollen, cryptogam spore and NPP results were associated with those obtained with diatoms using a co-inertia analysis.

The co-inertia analyses (Fig. 6) linking pollen, cryptogam spores and NPPs with diatoms indicated that the first two axes (total inertia = 193.2 and 102.5 respectively) explained 92% and 80% respectively of the total variance and thus present a good initial summary of the co-structure between the two data sets. Permutation analysis showed that the observed inertia was much greater than that of the simulated data sets. The probability of obtaining a total inertia equal to that observed, using the hypothesis of independence between the proxy data sets, was less than 0.001. This underlines that the two tables are significantly related and a co-structure exists.

Table 1
Performance of the different tested transfer function models (r2: Bootstrapped Squared correlation between inferred and observed values, model RMSEP: root mean squared error of prediction evaluated through bootstrap, deeper slices SEP: standard error of the prediction in the deepest slices of each core).

Reconstruction model	r^2	RMSEP	Deepest slices SEP
WMAT	0.83	0.41	0.41
WAPLS	0.76	0.46	0.53
WACla	0.76	0.51	0.47
WAInv	0.76	0.47	0.44

In the COIA linking pollen to diatoms (Fig. 6 a & b), four groups of samples (A–D) can be distinguished in the COIA factorial plan. In Fig. 6a, the position of the samples on the first factorial plan is presented, whereas on Fig. 6b the diatom, pollen and cryptogam taxa are shown in association. Samples within these groups are arranged according to core depth. COIA axis 1 separated both tree pollen taxa (groups A & B) i.e. *Quercus*, *Tilia*, *Ulmus*, *Fagus sylvatica*, *Corylus avellana*, *Betula* and *Abies alba* on the positive side of the axis from herb communities and anthropogenic pollen indicators (group C & D) i.e. Poaceae, Caryophyllaceae, Cichorioideae, Cyperaceae, *Secale* cereale, *Cannabis*-type, *Cannabis-Humulus*-type on the negative side.

When each group is considered independently, an evolution from the lower right to the upper right and then to the upper left and finally to the lower left of the first factorial plan was observed. Group A, situated in the lower right of the first factorial plan includes samples from the bottom of the core (1596–1200 cm, + 1076 cm, 728 cm) corresponding to the zones A-1 and A-2 (with some more samples). *Quercus*, *Tilia* and *Fraxinus* pollen-types are associated with planktonic and hypereutrophic and eutrophic diatoms such as *S. minutulus*, *S. parvus*, *S. hantzschii* and *A. pusilla*. Then, Group B, situated in the upper right of the first factorial plan, grouped samples (1176–744 cm) corresponding to the zones A-3 and A-4 (with some more samples of the upper unit A-5). Eutrophic diatoms such as *A. formosa*, *P. ocellata*, *D. pseudostelligera*, *G. parvulum*, *N. paleacea*, *N. linearis* and *P. lanceolatum* are linked with *Fagus sylvatica, Abies alba, Betula* (that replaced *Quercus*) and the decrease of *Corylus*

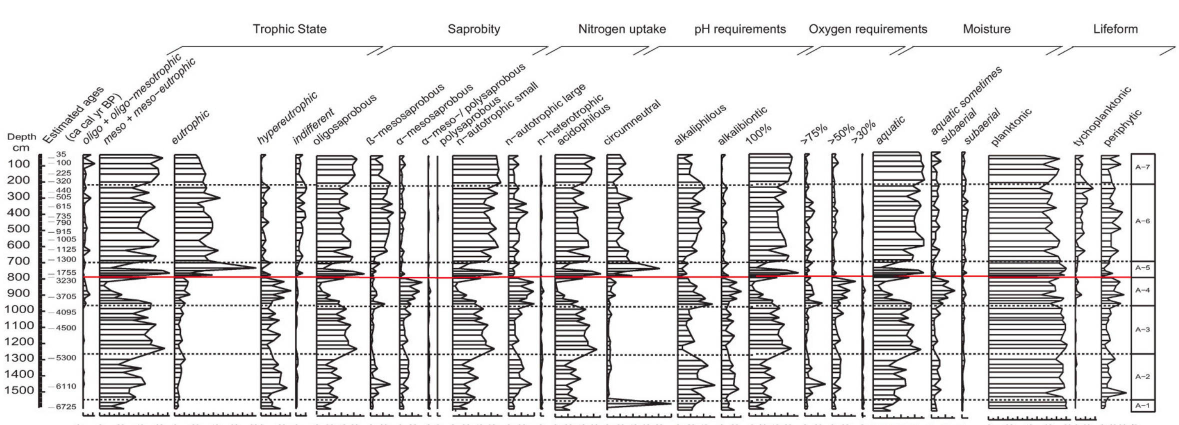

Fig. 4. The different ecological indicator values based on the percentage of diatom species belonging to an indicator category as observed along the sediment core of Lake Aydat in the Massif Central (France): Trophic State, Saprobity, Nitrogen uptake metabolism (autotrophic small diatom taxa, tolerating very small concentrations of organic bound nitrogen, autotrophic large diatom taxa, tolerating elevated concentrations), pH and Oxygen (percent of water saturation) requirements, moisture and lifeforms reduced to planktonic, tychoplanktonic or periphytic. See text for discussion about the ecology of *Aulacoseira subarctica* and *A. subarctica* f. *recta*.

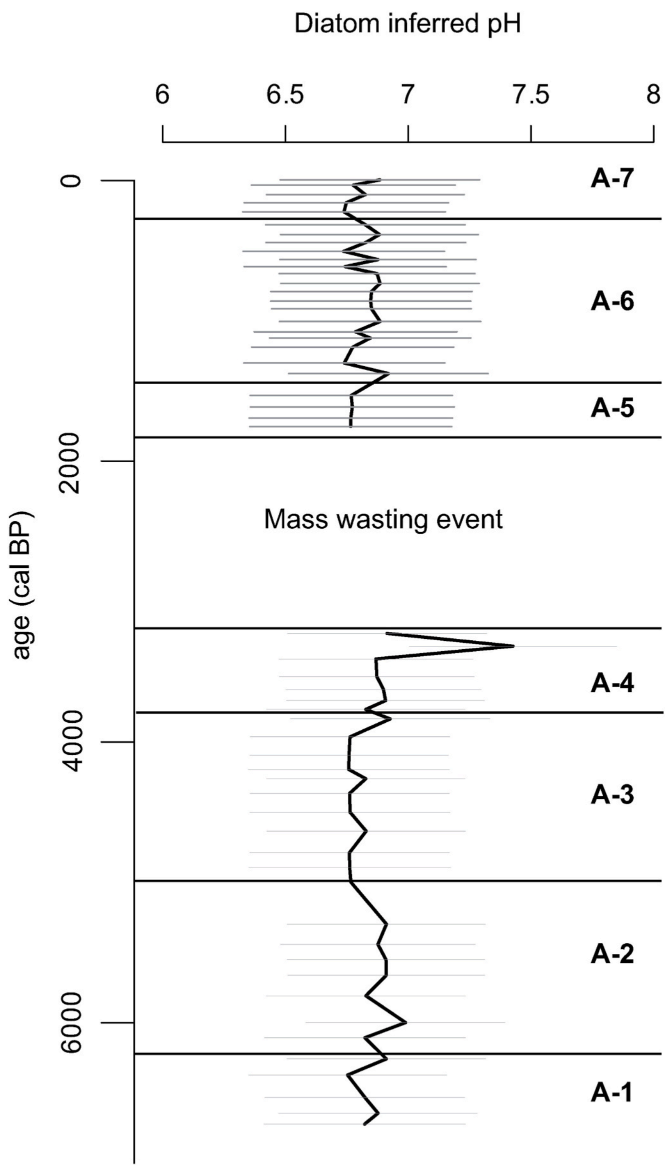

Fig. 5. Diatom-inferred epilimnetic pH values for the water of Lake Aydat in the Massif Central (France) since the Mid-Holocene (black line; grey bars indicate bootstrap estimated standard error for prediction).

avellana and aquatic macrophytes, such as *Myriophyllum spicatum*. For Group C, situated in the upper left of the first factorial plan, the samples from 700 cm to 400 cm are grouped corresponding to the deepest part of zone A-6. Meso- to eutrophic diatoms such as *Aulacoseira ambigua* (Grunow) Simonsen, *A. subarctica* f. *recta*, *Sellaphora nigri* (De Not.) C.E. Wetzel et Ector, *Navicula radiosa* Kützing, *P. brevistriata*, *S. construens* (a mixture of planktonic and littoral diatom species) and are associated with grass and cropland pollen types (Poaceae, Cerealia-type, etc.). At last, Group D, situated in the lower left of the first factorial plan grouped the samples from the uppermost part of the core (400–0 cm, corresponding to the second part of A-6 and A-7). Different meso- to eutrophic diatoms as *A. subarctica*, *L. radiosa*, *F. vaucheriae* and *S. venter* are associated with hemp cultivation and retting along with the introduction of certain trees to the area (i.e. *Juglans regia*, *Castanea sativa*).

A second COIA linking NPPs and diatoms (Fig. 6c) found three groups of samples (A–C) that can be distinguished in the COIA factorial plan. COIA discriminates samples related to land use changes, separating woodland domination from mainly agricultural use. The positive side containing the oldest samples were characterized by fewer NPPs than the negative side. This axis reflects a gradient of grazing pressure, separating groups B and C from taxa standing for week grazing in group A. Groups B and C, situated on the negative side of the factorial plan are characterized mainly by: 1) the presence of dung-related fungal spores (i.e. *Sporormiella*-type and *Sordaria*), 2) rotifers such as *Conochilus hippocrepis* and *Diporotheca rhizophila*, 3) diatoms such as *A. subarctica* and *A. subarctica* f. *recta*. Thus, four groups were recorded. Group A (right half of the factorial plan) corresponds to the lower unit (1596−780 cm) along with the upper unit zone A-5 (771–728 cm, except sample 696 cm). It is characterized by the presence of meso- to (hyper-) eutrophic diatoms i.e. *S. minutulus*, *S. parvus*, *S. hantzschii* along with *A. formosa*, *P. ocellata, A. pusilla* and different NPPs as *Triposporium elegans* and *Keratella*. Group B, situated in the upper left of the first factorial plan grouped samples from 700 cm to 440 cm + 380 cm, and 198 cm corresponding to a part of zone A-6. Planktonic diatom taxa (*A. ambigua*, *A. subarctica* f. *recta*) and many periphytic diatom species (i.e. *Achnanthidium minutissimum* (Kütz.) Czarnecki*, Encyonopsis minuta* Krammer & Reichardt*, E. silesiacum, Reimeria sinuata* (Gregory) Kociolek & Stoermer) and also tychoplanktonic fragilarioid diatom taxa (*Fragilaria distans, F. gracilis, F. nanana, Staurosira construens, S. construens* Ehr. var. *binodis* (Ehr.) Hamilton and *S. pinnata* complex) are linked to different rotifers and coprophilous fungi such as *Conochilus hippocrepis* and *Sordaria*. At last, Group C, situated in the lower left of the first factorial plan grouped samples mainly from the upper section of the core (354–0 cm + 596 cm, and 416.5 cm, corresponding to the second part of A-6 and A-7). Planktonic diatoms as *A. subarctica* and *L. radiosa* and different tychoplanktonic fragilarioid diatoms (i.e. *F. vaucheriae*, *P. brevistriata,* and *S. venter*) are associated with the cyanobacteria *Anabaena* and the fungal spores of *Sporormiella*.

5. Discussion

This study illustrates the impact of human influence on the long-term evolution of the diatom communities and the water quality in Lake Aydat. Fritz and Anderson (2013) working on examples from arctic, boreal and temperate regions found that catchment processes, the strength of the lake turnover, and changes in the trophic status depend on the basin history. These conclusions therefore explain the evolution of diatom communities also for Lake Aydat.

The PCA and COIA breaks down the samples differently; the PCA clearly separates the samples below the mass-wasting deposit from the upper units, while with COIA the samples just before and after the event are associated. Interestingly, the COIA of pollen and of NPPs put the diatom zone (A-5) with the lower units (A-1–A-4) as tree pollen dominated that zone. In the same way, the Psimpol contrained cluster analysis put the lower unit sample from 789 cm depth with the upper unit A-5. This is most likely caused by reworking of sediments from the lower unit, causing a mixing of fossil diatoms with those developing in the lake after the mass-wasting event. Changes appear from a diversified oak woodland (A-1) followed by woodland mainly composed by *Fagus sylvatica* (and a noticeable presence of *Betula* and *Alnus*) (Fig. 6) to the gradual increase in agro-pastoral indicators, implying major human impact on the landscape in Zone A-6. The woodland zones, A-1 through A-5, had very few NPP taxa. Major taxa changes occurred between the lower units (A-1 to A-4) and upper units (A-5 to A-7) (Fig. 7).

5.1. Palaeoecological reconstruction for the lake and landscape status 6720–3230 cal. BP

The dominant diatom species in zones A-1 through A-4 were *S. hantzschii, S. medius, S. minutulus, A. pusilla* and *A. subarctica*, the latter one being still dominant today in some of the deepest crater lakes of the region such as Lake Pavin (Amblard and Bourdier, 1990). Classically, *A. subarctica* is considered as oligo-mesotrophic for diatomologists (van Dam et al., 1994; Roy, 2012). However, in European palaeoenvironmental studies the ecology is interpreted differently. Indeed,

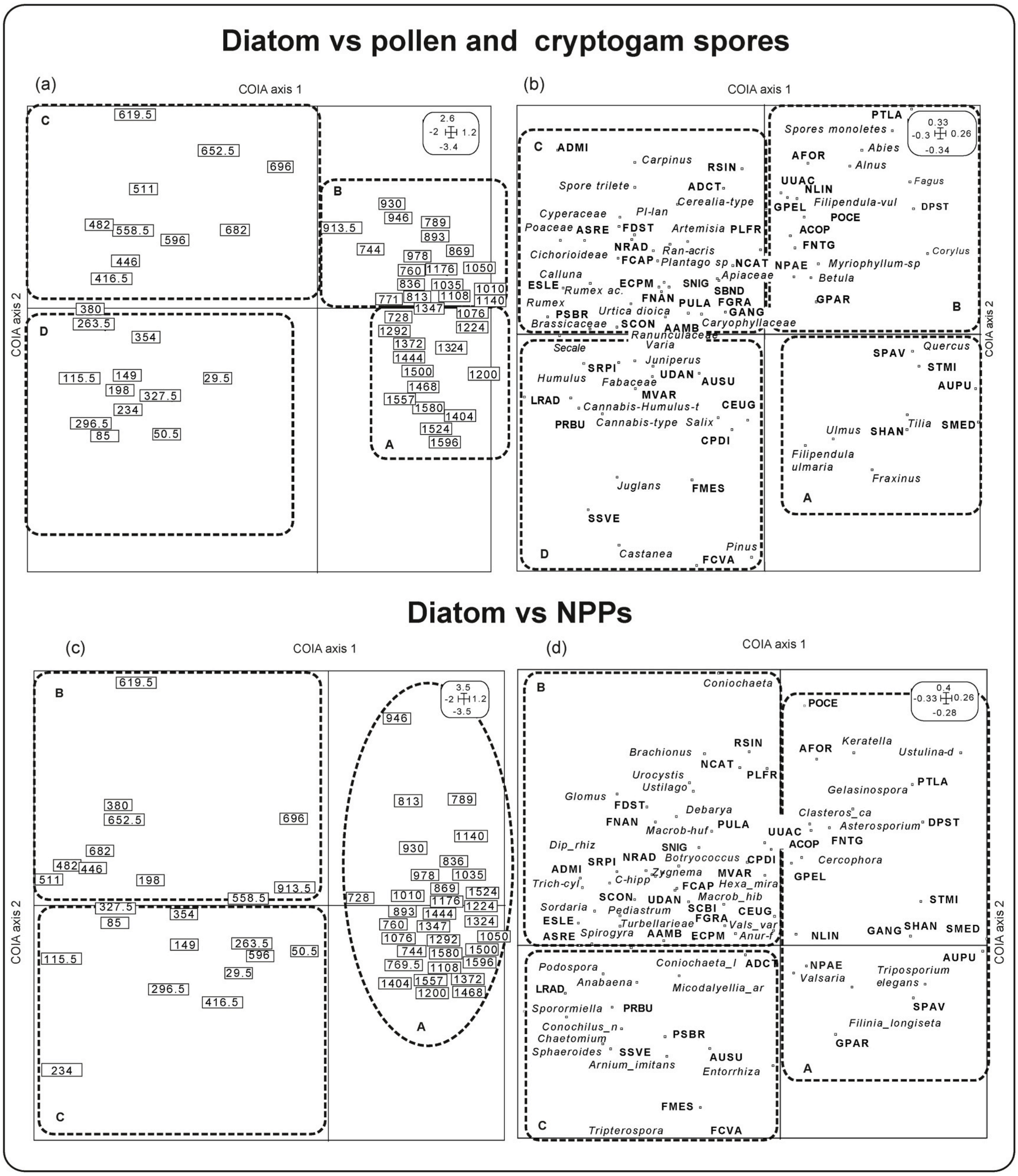

Fig. 6. Co-inertia analysis (COIA) biplots showing the relationship between selected pollen, cryptogam spores and diatom taxa (Fig. 6a and b) from the stratigraphy of Lake Aydat in the Massif Central (France), and the relationship between non-pollen palynomorphs and diatom taxa (Fig. 6c and d). In biplot b selected pollen and diatom taxa are shown (respectively in italics and capitalized abbreviations). Biplot d shows the relationship between non-pollen palynomorphs and diatom taxa. Abbreviation used on the chart are:

Pollen – *Cerealia* type = Cerealia-type; *Secale* = Secale-; *Cannabis* type = Cannabis-type; *Cannabis Humulus* type = *Cannabis-Humulus*-t; *Humulus* type = *Humulus*; *Plantago lanceolata* = *Pl-lan*; *Rumex acetosella*-type = *Rumex ac.*; *Ranunculus acris*-t = *Ran-acris*; *Filipendula vulgaris* = *Filipendula_vul*; *Myriophyllum spicatum*-type = *Myriophyllum* sp.;

Non pollen palynomorphs – *Coniochaeta ligniaria* = *Coniochaeta_l; Arnium imitans* = *Arnium_imitans; Diporotheca rhizophila* = *Dip_rhiz; Valsaria variospora* = *Vals_var; Ustulina deusta* = *Ustulina_d; Clasterosporium caricinum* = *Clasteros_ca; Triposporium elegans* = *Triposporium_elegans; Conochilus hippocrepis* = *C_hipp; Conochilus natans* = *Conochilus_n; Trichocerca cylindrica* = *Trych_cyl; Anuraeopsis fissa* = *Anur_f; Keratella; Filinia longiseta* = *Filinia_longiseta; Hexarthra mira* = *Hexa_mira; Macrobiotus hufelandi* = *Macrob_huf; Macrobiotus hibernicus* = *Macrob_hib; Micodalyellia armigera* = *Micodalyellia_ar;*

Diatoms – ADCT = *Achnanthidium catenatum* ADMI = *Achnanthidium minutissimum*; ACOP = *Amphora copulata*; AFOR = *Asterionella formosa*; AAMB = *Aulacoseira ambigua*; AUPU = *Aulacoseira pusilla*; AUSU = *Aulacoseira subarctica*; ASRE = *Aulacoseira subarctica* f. *recta*; CEUG = *Cocconeis euglypta*; POCE = *Pantocsekiella ocellata*; CPDI = *Cyclotella pseudostelligera* f. *diminuta*; LRAD = *Lindavia radiosa*; DPST = *Discostella pseudostelligera*; ELSE = *Encyonema silesiacum*; ECPM = *Encyonopsis minuta*; FCAP = *Fragilaria capucina* var. *capucina*; FGRA = *Fragilaria gracilis*; FCVA = *Fragilaria vaucheriae*; FDST = *Fragilaria distans*; FMES = *Fragilaria mesolepta* Rabenhorst; FNAN = *Fragilaria nanana*; FNTG = *Fragilaria nanana* abnormal form; GANG = *Gomphonema angustatum*; GPAR = *Gomphonema parvulum* var. *parvulum* f. *parvulum*; GPEL = *Gomphonema pumilum* var. *elegans*; MVAR = *Melosira varians*; NCAT = *Navicula catalanogermanica*; NRAD = *Navicula radiosa*; NLIN = *Nitzschia linearis* var. *linearis*; NPAE = *Nitzschia paleacea*; PLFR = *Planothidium frequentissimum*; PTLA = *Planothidium lanceolatum*; PSBR = *Pseudostaurosira brevistriata*; PULA = *Punctastriata lancettula*; RSIN = *Reimeria sinuata*; SNIG = *Sellaphora nigri*; SCON = *Staurosira construens*; SBND = *Staurosira binodis*; SRPI = *Staurosirella pinnata* complex; PRBU = *Pseudostaurosira robusta*; SSVE = *Staurosira venter*; SHAN = *Stephanodiscus hantzschii*; SMED = *Stephanodiscus medius*; STMI = *Stephanodiscus minutulus*; SPAV = *Stephanodiscus parvus*; UDAN = *Ulnaria danica*; UUAC = *Ulnaria acus*.

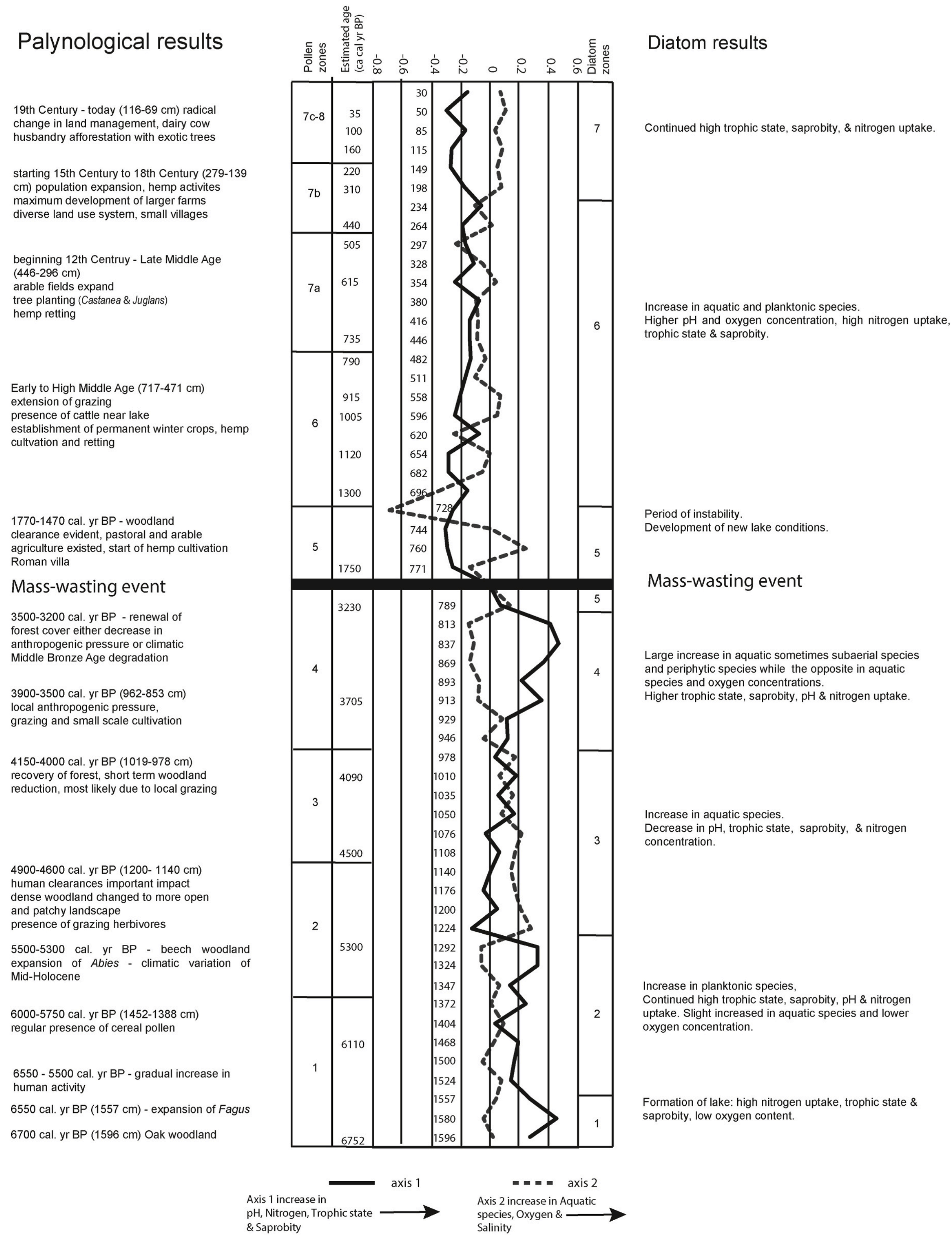

Fig. 7. Comparison of pollen and diatom zones resulting from the stratigraphy of Lake Aydat in the Massif Central (France) using the PCA results done on diatoms using all samples (PCA sample scores for axes 1 and 2).

for Rioual (2000), who studied lakes in the same area as Lake Aydat, and Sienkiewicz and Gąsiorowski (2014), this diatom species requires high phosphorus, silicon and nitrogen concentrations and is linked to more meso-eutrophic conditions with a strong overturn period. *Aulacoseira* species, in general, need wind-driven turbulence to remain in suspension within the water column. *Planothidium lanceolatum* was also observed and is found to be frequent in forested areas (Antonelli et al., 2017). Throughout the lower unit, the concentration in cyanobacteria akinetes were low with only three small peaks revealing three short events in the lake's history. However, due to the age of the sediments and the fact that few palaeoenvironmental studies have been done on cyanobacteria akinetes, this leads to a gap in information and taphonomic problems.

The diatom zones A-1 through A-3 are marked by an increase in *A. subarctica* and the presence of several *Stephanodiscus* species, which typically are encountered in lakes with elevated nutrient concentrations, i.e. in eutrophic or hypertrophic conditions (Kirilova et al., 2009) along with *Aulacoseira pusilla* that also tolerates large concentrations of nutrients and grows in winter (Roy, 2012). Since 6000 cal. BP the anthropogenic impact increased when humans gradually opened the forest (Miras et al., 2015). A peak in the phosphorus concentrations, as reconstructed from the diatom inference model, appeared and reinforced the human impact (Miras et al., 2015). This impact is superimposed by a climatic forcing and a phase of high background detrital input (between 6000 and 5750 cal. BP) synchronous to a period of cooler and more humid conditions due to lower solar activity (Miras et al., 2015) that as a result could favoured soil erosion in the catchment. This double forcing was underlined by the presence of cyanobacteria akinetes in the sediments and could explain the quick development of eutrophic and hypereutrophic diatom species in Lake Aydat. At the same time (zone A-2) the diatom-inferred epilimnetic pH increase lead to more circumneutral conditions (Fig. 5), also corresponding to the increase in alkaliphilous diatom species (Fig. 4) in relation with the eutrophication. Indeed, algae covered the lake surface, and the chemical by-products of the photosynthesis processes increased the pH of the water, making it so more alkaline conditions (Chislock et al., 2013).

An increase in *Asterionella formosa* was observed during zone A-2. This diatom species has a higher light requirement and favours late-spring overturn after a long period of ice cover (Rioual et al., 2001; Garibaldi et al., 2004; Voigt et al., 2008). The dominance of *A. subartica* and *A. formosa* could suggest colder spring conditions during zone A-2 than during zone A-1 as noted in observations of Rioual et al. (2007) on the Ribains maar in the Massif Central. Moreover, Rioual (2000) found in other lakes of the Massif Central, that: 1) *S. parvus* bloomed earlier than *S. minutulus*, and that 2) *S. medius* had a lower temperature optimum than *S. parvus* within these planktonic diatom species being associated with the late winter/spring period of mixing. Moreover, *S. minutulus* also likes low light conditions (Rioual et al., 2007; Baier et al., 2004). Since zone A-2, an increase in aquatic diatom species appeared. At the end of the period, the trophic status remained high, even if there was an increase in meso-eutrophic diatom species; no real recovery was observed.

With Zone A-4, there is a radical decrease in *A. subarctica* between the beginning of the zone (3950 cal. BP) and 3300 cal. BP, marked by increases in *A. pusilla, A. formosa, Stephanodiscus hantzschii, S. medius,* and *S. minutulus*, and with the continued appearance of *S. parvus*, suggesting hypereutrophic conditions (van Dam et al., 1994; Rioual et al., 2007; Roy, 2012) as underlined on Fig. 4. Moreover *U. acus, F. gracilis* and *F. nanana* appeared. *F. nanana* require high phosphorus and nitrogen concentrations and is linked to meso-eutrophic conditions (Gąsiorowski and Sienkiewicz, 2010; Sienkiewicz and Gąsiorowski, 2014). A peak of S. *hantzschii* was observed at 3500 cal. BP during an enrichment phase (ca. 3900–3500 cal. BP) as underlined by Miras et al. (2015). However, two peaks of oligo-mesotrophic diatom species such as from *F. gracilis* appeared, and could have been linked to small periods of resilience. During this period, the conditions were also alpha-mesosaprobous and alpha-mesopolysaprobous with less oxygenated water (Fig. 4). Linked to this eutrophication, the pH increased leading to an increase in alkaliphilous diatom species (Figs. 4 and 5). At the end of this period, the observed peak of the diatom-inferred pH could be due to the increase of *A. subarctica*. Indeed, a higher abundance of a species, compared to the abundances of the same diatom species in the calibration dataset, could lead to an overestimate of the ecological trait associated (pH in this case) (Marchetto et al., 2004).

Aulacoseira pusilla grows in winter (Roy, 2012), followed by spring upwelling and inwash from melt waters that permit development of spring blooming diatom taxa such as *Asterionella formosa*, which needs high Si, moderate to high P and N (Hausmann and Pienitz, 2009; Rioual et al., 2007) occurring in spring blooms (Rioual, 2000; Voigt et al., 2008). The highest percentage of *S. minutulus* suggested that intense mixing in the water-column took place during the spring. It was followed by summer stratification with reduce nutrient content that permitted the development of "*Cyclotella*" taxa. Indeed, *P. ocellata*, *D. pseudostelligera* and its form *diminuta* are favoured by lower Si and P concentrations and typically occur with stable light and temperature conditions (Stoermer, 1993; Voigt et al., 2008). This combination of diatom species may be the result of seasonal changes but also the intensification of anthropogenic activities. During this period, there is an intensification of the local anthropogenic pressure related to the landscape management marked by grazing, but also small-scale areas of crop cultivation (Miras et al., 2015) (Fig. 6b A).

With the beginning of the zone A-4 and 3300 cal. BP, a decrease in aquatic diatom species (Fig. 4) with an increase in "aquatic, sometimes subaerial" diatom species (as *S. hantzschii*, Fig. 4) were observed. Moreover, there is an increase in tychoplanktonic and periphytic diatom taxa, such as "*Fragilaria*" taxa like *Ulnaria acus*, that could suggest inwash of diatom species from other habitats (Selby and Brown, 2007) with the development of aquatic plants in the littoral zone or more turbid conditions (Selby and Brown, 2007; Baier et al., 2004). Miras et al. (2015) confirmed the presence of aquatic plants by observing that algae (*Pediastrum*, *Spirogyra*) progress, parallel to a rise in the presence of rotifer resting eggs. Moreover, at this period, the maximal values of *Myriophyllum spicatum* are present (Miras et al., 2015). This last species is statistically associated with zone A-4 in the COIA (Fig. 6bB).

Even if the upper part of zone A-4 coincides with the climatic degradation of the Middle Bronze Age, with cooling temperatures and increasing precipitation between 3500 and 2800 cal. BP (Magny et al., 2009, Miras et al., 2015), this lead to a renewal of the forest cover concomitant with a decrease in anthropogenic indicators and the dung related fungi (Miras et al., 2015) (Fig. 7). In addition, this period is always characterized by eutrophic and alpha-mesosaprobous diatom species. However, may be linked to this degradation, there was a slight decrease in hypereutrophic diatom species (mainly in the upper part of the zone) with an important decrease of *S. hantzschii* (Fig. 3). However, no recovery in water quality occurred, if we consider the trophic state.

When comparing Lake Aydat to Lake Holzmaar (West-Eifel, Germany) the upper Bronze Age (3000 cal. BP) showed a high trophic status until the upper Iron Age (~2150 cal. BP) when there was a decrease (Baier et al., 2004). However, there is no sedimentary record from the Iron Age in Lake Aydat due to the lack of sediments of this period. Therefore, no information could be given about this period. Lake Aydat could also be compared with Lake Jues (Harz Mountains, Germany; Voigt et al., 2008). The two records have many diatom species in common such as: *L. radiosa, P. ocellata, S. minutulus, A. formosa*, and *F. gracilis*. Between 6750 and 5700 cal. BP, which corresponds to the Aydat zone A-1 and the lower part of zone A-2, Lake Jues recorded warm summers and may be decreased precipitation, causing lower lake levels, but for Lake Aydat, this interval is characterized by a relative increase in aquatic diatom species, and may be by a rise in lake levels. A more humid phase was recorded between 5700 and 5250 cal. BP for Lake Jues, while for Lake Aydat it happened between 6000 and 5750 cal. BP. This was followed between 5250 and 4750 cal. BP by a warmer summer phase with lowered lake levels as registered in Lake Jues. The human occupation around Lake Jues started again during the Early Bronze Age and continued with almost no interruption for the following two millennia, while in Lake Aydat, human impact started more than 6000 years ago.

5.2. Palaeoecological reconstruction for the lake and landscape status 1750 cal. BP–(-5) cal. BP

With zone A-5 (1750–1380 cal. BP) *Aulacoseira subarctica* and its f. *recta,* considered as eutrophic diatom species (Kauppila, 2006), were the dominant diatom species, together with *S. parvus, A. formosa* and *P. brevistriata,* becoming regular components of the upper unit. The highest percentages of *A. subarctica* f. *recta* indicate higher phosphorous concentrations than for *A. subarctica* (Kauppila, 2006; Hoff et al., 2015), and coincides with a major increase in cyanobacteria akinetes. After and before the mass wasting event, the phosphorus concentrations, reconstructed from a diatom inference model, higher (Miras et al., 2015). During this period, woodland clearances with pastoral and arable activities became evident (Miras et al., 2015). However, pollen from woodland plants still dominates the palynological picture (Fig. 6bB & 7).

A new set of lake environmental conditions were developing within the lake. Planktonic and aquatic diatom species increased, as *Aulacoseira subarctica* and its f. *recta.* There is also a change in the oxygenation with more diatom species living in water (>100%) that could may be due to the increase in wind that caused mixing of the upper water layers, and produced more oxygen rich conditions. During this period, there was an increase in agricultural activities and the first evidence of hemp (*Cannabis sativa*) cultivation started at the top of this zone. Compared to Lake Holzmaar (Germany), both lakes are characterized by an increase in the trophic status particularly marked in the German lake toward the end of the Roman Empire (~1600 cal. BP; Baier et al., 2004).

In Zone A-6 the dominant diatom species were eutrophic ones, such as *A. subarctica*, *A. subarctica* f. *recta* and *A. formosa.* This zone marked the appearance of *L. radiosa* and a series of "*Fragilaria*" taxa (*S. construens*, *S. pinnata* complex, *P. robusta,* and *S. venter*) that vary in percentage throughout this zone. Eutrophic and β-mesosaprobous diatoms increased all along this zone, as did tychoplanktonic "*Fragilaria"* diatoms. However, some peaks of oligo-mesotrophic diatom species appeared that could be linked to small periods of resilience. Moreover, using the ecological preference, an increase of alkaliphilous diatom species occurred, that could be linked to the eutrophication corresponding to the slight increase of diatom-inferred epilimnetic pH.

Interestingly, this zone was divided using the COIAs. The first part (up to 400 cm) was associated with the agricultural activities (*Cerealia*), ruderal indicators (*Rumex*), with dung-related fungal spores (as *Sordaria*), rotifers such as *Conochilus hippocrepis* associated to soil disturbance, and *Diporotheca rhizophila* (related to human activities and presence of cattle) and also algae (*Botryococcus*, *Spirogyra*) that could grow on the littoral area. In response to these human and livestock impacts, different planktonic and periphytic diatom taxa were present such as the eutrophic species *A. subarctica* f. *recta* (ASRE), and also *Fragilaria* (e.g. *Fragilaria nanana* FNAN) and *Staurosira* (e.g. *Staurosira binodis* Lange-Bertalot in Hofmann Werum & Lange-Bertalot SBND). Epiphytic diatom taxa were also observed such as *Achnanthidium minutissimum* (Kützing) Czarnecki (ADMI). During this period, the concentration of cyanobacteria akinetes was low. This could be due to taphonomic problems or a change in the nutrient enrichment.

The second part of zone A-6 related to COIA was associated with the hemp cultivation and retting (*Cannabis sativa*) and arboriculture (*Castanea sativa* and *Juglans regia*; Miras et al., 2015). Different "*Fragilaria*" were associated to these activities, such as *L. radiosa*. Moreover, the cyanobacteria *Anabaena* was also present (COIA NPP group C, Fig. 6d; Miras et al., 2015), so their akinetes became an important component (COIA NNP group C; Fig. 6dC). *Anabaena*, a nitrogen fixer, is responsible for blooms in very eutrophic water (van Geel et al., 1994). A large increase in total akinetes was noted in the upper part of the zone, confirming the increased nutrient enrichment in the upper unit. This concentration is comparable to the one observed during the Antiquity. The increase of cyanobacteria akinetes blooms limits light penetration and could be responsible for the decrease in *A. formosa*, a high light requirement diatom species, while *A. subarctica* (associated with low light conditions, Rioual, 2000) is given an advantage over other diatom taxa. Related to the PCA (Fig. 2) a large part of the samples belonging to this period are statistically associated with *L. radiosa* confirming the observations. So, *L. radiosa* appeared at the same time as the palynological signals for hemp cultivation and retting (Lavrieux et al., 2013b; Miras et al., 2015). This diatom species blooms in summer/late summer in mesotrophic condition at the onset of the autumn circulation period (Morabito et al., 2002; Kienel et al., 2005; López-Merino et al., 2011) but is also common in eutrophic lakes with warm temperatures (Baier et al., 2004) and prefers dry summers (Rioual et al., 2007). With the retting of hemp, the chemistry of the lake could have permitted the development of *L. radiosa.* Hemp cultivation requires nitrogen fertilisation and is well known to cause degradation of lake waters (van Geel et al., 1994).

In summary, during this period (A-6: 1380–385 cal. BP), the anthropogenic impacts on the lake were due to: 1) the change from a woodland-dominated landscape to grassland and croplands (COIA pollen groups C, Fig. 6b) in the lower part of this zone leading to an extension of grazing near the lake and soil disturbances (presence of dung-related fungal spores as from *Sordaria*, Fig. 6dB) and, 2) the development of hemp cultivation and retting with an increase in detrital material into the lake (presence of NPPs associated to soil disturbance as *Diporotheca rhizophila*) (Miras et al., 2015). The different uses exercised by man on the catchment could explain the increase in tychoplanktonic "*Fragilaria"* diatoms that could be linked with possible inwash of surrounding soil-derived material (Baier et al., 2004; Selby and Brown, 2007). This increase could also be linked to the hemp cultivation. Indeed, Finsinger et al. (2006) found that percentages of "*Fragilaria*" spp. increased during the period of hemp-retting in the sediment record from Lago Grande di Avigliana (Piedmont, Italy). They concluded that retting had an influence on the abundance of the "*Fragilaria*" spp. and that these diatom species probably grew on the hemp fibres during the retting. Moreover, some periphytic diatom taxa, such as *Ulnaria acus* and *Gomphonema angustatum*, were represented and could be associated with the retting but also to the development of aquatic plants such as *Spirogyra* and Cyperaceae.

The upper part of the diatom zone A-6 corresponds to the Little Ice Age. The noted increase in small "*Fragilaria"* taxa (*P. brevistriata*, *S. construens*, *S. pinnata* complex, and *S. venter*) could be related to this cooling. Lotter et al. (2010) noted, "*Fragilaria*" spp. are commonly associated with high environmental instability and poor light conditions. As the palynological data do not indicate that a climatic fluctuation had any repercussions on the landscape evolution or any negative impact on the increase exploitation of upland areas (Miras et al., 2015), this increase could be linked to the hemp cultivation.

In zone A-7, the dominant taxa were eutrophic diatom species such as *A. subarctica*, *A. subarctica* f. *recta*. At the same time *Lindavia radiosa* and planktonic diatom taxa decreased. This could be linked to the hemp pollen maximum that was followed by a rapid decrease. There was an increase in periphytic diatom taxa such as *Ulnaria acus* and "aquatic, sometimes subaerial" diatom species such as *F. nanana*, may be due to the fact that the lake was slowly filling up. Shallower water is more easily stirred, so allowing for better oxygenation with surface mixing by winds. At last, the concentrations in cyanobacteria akinetes were among the highest, and cyanobacteria, in general, are still a water quality and environmental problem in Lake Aydat, today.

6. Conclusions

In Lake Aydat, the two different units contained different diatom assemblages, and showed a major change in the communities occurring after the mass wasting event since 1750 cal. BP. The study underlined how rapidly the lake developed a meso-eutrophic diatom community and allowed for a better understanding of Lake Aydat's complex history. The eutrophication of the lake is – in part at least – due to successive phases of the human activities and climatic changes. Related to our results, the main forcings of these changes were the anthropogenic influences that occurred all along the history of Lake Aydat, and lead to eutrophic or even hyper-eutrophic water conditions. Indeed, the prehistorical forest openings, agricultural activities, crop cultivation, hemp retting, and actually, touristic and agro-pastoral activities, fishing, as well as the impact of people from residential areas, have profoundly changed the water quality. Even if resilience phases occurred in the past, human activities have affected the lake since 6000 cal. BP and have had their greatest impact since the Middle Ages on the catchment and the lake's water quality. This lead to eutrophication and its consequences such as the presence of cyanobacteria akinetes blooms that are still observed in the todays summers.

With the highest concentrations of cyanobacteria akinetes recorded during the Antiquity (zone A-5) and actually, the management of the lake and its catchment to clean up the waters will be difficult due to the long history of eutrophication and the loss of water resilience. The results obtained during this study do also explain why the summer inorganic nitrogen concentration was about 70 μmol l^{-1} N and the soluble inorganic phosphorus concentration was between 10 and 40 μg l^{-1} P during the second half of the 20th century. Therefore, our study gives a better understanding of the lake's history and should help in the development of restoration strategies that improve water quality in the future.

Author contributions

Aude Beauger: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing - Original Draft, Review & Editing, Visualization, Supervision. Karen Serieyssol: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing - Original Draft, Review & Editing, Visualization. Benjamin Legrand: Data Curation, Writing - Original Draft, Review & Editing. Delphine Latour: Data Curation, Writing - Original Draft, Review & Editing. Vincent Berthon: Data Curation, Writing - Original Draft, Review & Editing, Visualization. Marlène Lavrieux: Data Curation, Writing - Original Draft, Review & Editing, Visualization. Yannick Miras: Data Curation, Writing - Original Draft, Review & Editing.

Data availability

The datasets used or analyzed during this study are available from the corresponding author on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Two anonymous reviewers are thanked for their valuable comments. The authors acknowledge the DIPEE (DIspositif de Partenariat Écologie Environnement) of the National Ecology and Environment Institute (INEE), CNRS.

References

Amblard, C., Bourdier, G., 1990. The spring bloom of the diatom *Melosira italica* subsp. subarctica in Lake Pavin: biochemical, energetic and metabolic aspects during sedimentation. J. Plankton Res. 12, 645–660.

Antonelli, M., Wetzel, C.E., Ector, L., Teuling, A.J., Pfister, L., 2017. On the potential for terrestrial diatom communities and diatom indices to identify anthropic disturbance in soils. Ecol. Indicat. 75, 73–81.

Baier, J., Lücke, A., Negendank, J.F.W., Schleser, G.-H., Zolitschka, B., 2004. Diatom and geochemical evidence of mid- to late Holocene climatic changes at Lake Holzmaar, West-Eifel (Germany). Quat. Int. 113, 81–96.

Bennett, K.D., 2002. PSIMPOLL: plotting and analysis program. http://www.kv.geo.uu.se/psimpoll.html.

Boivin, P., Besson, J.C., Briot, D., Gourgaud, A., 2004. Volcanologie de la Chaîne des Puys. Aydat. Editions du Parc Naturel Régional des Volcans d'Auvergne.

Buczkó, K., Ognjanova-Rumenova, N., Magyari, E., 2010. Taxonomy, morphology and distribution of some *Aulacoseira* taxa in glacial lakes in the south Carpathian Region. Pol. Bot. J. 55, 149–163.

Camburn, K.E., Kingston, J.C., 1986. The genus *Melosira* from soft-water lakes with special reference to northern Michigan, Wisconsin and Minnesota. In: Smol, J.P., Battarbee, R.W., Davis, R.B., Meriläinen, J. (Eds.), Diatoms and Lake Acidity. Dr. W. Junk Publishers, Dordrecht, pp. 17–34.

Chapron, E., Chassiot, L., This Issue. Tracking Exposure of French Massif Central to Holocene Environmental Changes and Natural Hazards from Lake Sediments Based on a Multidisciplinary and Regional Limnogeological Approach.

Chassiot, L., Chapron, E., Simonneau, A., Di Giovanni, C. This issue. Lacustrine records of sediment yield in the French Massif Central: anthropogenic vs. natural forcings.

Chislock, M.F., Doster, E., Zitomer, R.A., Wilson, A.E., 2013. Eutrophication: causes, consequences, and controls in aquatic ecosystems. Nat. Educ. Knowl. 4 (4), 10.

Cubizolle, H., Serieyssol, K.K., Argant, J., 2005. Diatom and pollen evidence of Holocene vegetation dynamics and human impact on the Virennes fenland (French Massif Central). Diatom Res. 20, 257–273.

Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological data tables. Ecology 84, 3078–3089.

Direction Régionale de l'Environnement, de l'Aménagement et du Logement, 2017. Surveillance des plans d'eau de la région Auvergne-Rhône-Alpes. Bilan 2004-2014, p. 52.

Finsinger, W., Bigler, C., Krähenbühl, U., Lotter, A.F., Ammann, B., 2006. Human impacts and eutrophication patterns during the past 200 years at Lago Grande di Avigliana (N. Italy). J. Paleolimnol. 36, 55–67.

Fritz, S.C., Anderson, N.J., 2013. The relative influences of climate and catchment processes on Holocene lake development in glaciated regions. J. Paleolimnol. 49, 349–362.

Gandouin, E., Rioual, P., Pailles, C., Brooks, S.J., Ponel, P., Guiter, F., Djamali, M., Andrieu-Ponel, V., Birks, H.J.B., Leydet, M., Belkacem, D., Haas, J.N., Van der Putten, N., de Beaulieu, J.-L., 2016. Environmental and climate reconstruction of the late-glacial-Holocene transition from a lake sediment sequence in Aubrac, French Massif Central: chironomid and diatom evidence. Palaeogeogr. Palaeoclimatol. Palaeoecol. 461, 292–309.

Garibaldi, L., Anzani, A., Marieni, A., Leoni, B., Mosello, R., 2004. Studies on the phytoplankton of the deep subalpine Lake Iseo. J. Limnol. 62, 177–189.

Gąsiorowski, M., Sienkiewicz, E., 2010. 20th century acidification and warming as recorded in two alpine lakes in the Tatra Mountains (South Poland, Europe). Sci. Total Environ. 408, 1091–1101.

Gasse, F., 1969. Les sédiments à diatomées du Lac Pavin (Auvergne). Ann. Stn. Biol. Besse-En-Chandesse 4, 221–237.

Germain, H., 1981. Flore des diatomées diatomophycées: eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe occidentale. Collection Faunes et Flores Actuelles. Société Nouvelle des Editions Boubée, Paris.

Hausmann, S., Pienitz, R., 2009. Seasonal water chemistry and diatom changes in six boreal lakes of the Laurentian Mountains (Québec, Canada): impacts of climate and timber harvesting. Hydrobiologia 635, 1–14.

Héribaud, J., 1883. Les diatomées d'Auvergne. In: Libraire des Sciences naturelles. Clermont-Ferrand.

Héribaud, J., 1902. Les diatomées fossiles d'Auvergne. In: Libraire des Sciences naturelles. Clermont-Ferrand.

Héribaud, J., 1903. Les diatomées fossiles d'Auvergne (second Mémoire). In: Libraire des Sciences naturelles. Clermont-Ferrand.

Héribaud, J., 1908. Les diatomées fossiles d'Auvergne (Troisième Mémoire). In: Libraire des Sciences naturelles. Clermont-Ferrand.

Hoff, U., Biskaborn, B.K., Dirksen, V.G., Dirksen, O., Kuhn, G., Meyer, H., Nazarova, L., Roth, A., Diekmann, B., 2015. Holocene environment of central Kamchatka, Russia: implications from a multi-proxy record of two-Yurts lake. Global Planet. Change 134, 101–117.

Houk, V., Klee, R., Tanaka, H., 2010. Atlas of freshwater centric diatoms III. *Cyclotella, Tertiarius, Discostella*. Fottea 10 (Supplement), 1–498.

Jamet Planche, D., 1995. Variations temporelles et verticales de l'activité phosphatase alcaline associée à différentes classes de taille du matériel particulaire au sein de trois lacs du massif central de degrés trophiques différents (lac Pavin, lac d'Aydat, retenue de Villerest). Unpublished Ph.D. Thesis, University Clermont II.

Juggins, S., 2007. C2. Version 1.7.2 User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation. Newcastle University, Newcastle upon Tyne, UK, pp. 1–73.

Kauppila, T., 2006. Sediment-based study of the effects of decreasing mine water pollution on a heavily modified, nutrient enriched lake. J. Paleolimnol. 35, 25–37.

Kienel, U., Schwab, M.J., Schettler, G., 2005. Distinguishing climatic from direct anthropogenic influences during the past 400 years in varved sediments from Lake Holzmaar (Eifel, Germany). J. Paleolimnol. 33, 327–347.

Kirilova, E., Heiri, O., Enters, D., Cremer, H., Lotter, A.F., Zolitschka, B., Hüvener, T., 2009. Climate-induced changes in the trophic status of a central European lake. J. Limnol. 68, 71–82.

Krammer, K., 2002. Cymbella. In: Lange-Bertalot, H. (Ed.), Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats, vol. 3. A.R.G. Gantner Verlag K.G.

Krammer, K., 2003. Cymbopleura, Delicata, Navicymbula, Gomphocymbellopsis, Afrocymbella. In: Lange-Bertalot, H. (Ed.), Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats, vol. 4. A.R.G. Gantner Verlag K. G.

Krammer, K., Lange-Bertalot, H., 1997a. Bacillariophyceae. 1. Teil: Naviculaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süsswasserflora von Mitteleuropa, vol. 2. Gustav Fischer Verlag, Stuttgart, 1.

Krammer, K., Lange-Bertalot, H., 1997b. Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süsswasserflora von Mitteleuropa, vol. 2. Gustav Fischer Verlag, Stuttgart, 2.

Krammer, K., Lange-Bertalot, H., 2000a. Bacillariophyceae. 3. Teil: centrales, Fragilariaceae, Eunotiae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süsswasserflora von Mitteleuropa, vol. 2. Gustav Fischer Verlag, Stuttgart, 3.

Krammer, K., Lange-Bertalot, H., 2000b. Bacillariophyceae. 5. Teil: English and French translation of the keys. In: Büdel, B., Gärtner, G., Krienitz, L., Lokhorst, G.M. (Eds.), Süsswasserflora von Mitteleuropa, vol. 2. Spektrum Akademischer Verlag, Heidelberg, 5.

Krammer, K., Lange-Bertalot, H., 2004. Bacillariophyceae. 4. Teil: Achnanthaceae, kritische Ergänzungen zu *Navicula* (Lineoatae) und *Gomphonema*. In: Ettl, H., Gärtner, G., Heynig, H., Mollenhauer, D. (Eds.), Süsswasserflora von Mitteleuropa, vol. 2. Spektrum Akademischer Verlag, Heidelberg, 4.

Lange-Bertalot, H., 2001. *Navicula* sensu stricto, 10 Genera separated from *Navicula* sensu lato Frustulia. In: Lange-Bertalot, H. (Ed.), Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats, ume 2. A.R.G. Gantner Verlag K. G.

Lavrieux, M., Disner, J.-R., Chapron, E., Beéheret, J.-G., Jacob, J., Miras, Y., Reyss, J.-L., Andrieu-Ponel, V., Arnaud, F., 2013a. 6700 yr sedimentary record of climatic and anthropogenic signals in Lake Aydat (French Massif Central). Holocene 23, 1317–1328.

Lavrieux, M., Jacob, J., Disnar, J.-R., Bréheret, J.-G., Le Milbeau, C., Miras, Y., Andrieu-Ponel, V., 2013b. Sedimentary cannabinol tracks the history of hemp retting. Geology 41, 751–754.

Lecointe, C., Coste, M., Prygiel, J., 1993. OMNIDIA: software for taxonomy, calculation of diatom indices and inventories management. Hydrobiologia 269/270, 509–513.

Legrand, B., Lamarque, A., Sabart, M., Latour, D., 2016. Characterization of akinetes from cyanobacterial strains and lake sediment: a study of their resistance and toxic potential. Harmful Algae 59, 42–50.

Lotter, A.F., Pienitz, R., Schmidt, R., 2010. Diatoms as indicators of environmental change in subarctic and alpine regions. In: Smol, J.P., Stoermer, E.F. (Eds.), The Diatoms Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge, pp. 231–248.

López-Merino, L., Moreno, A., Leira, M., Sigró, J., González-Sampériz, P., Valero-Garcés, B.L., López-Sáez, J., Brunet, M., Aguilar, E., 2011. Two hundred years of environmental change in Picos de Europa National Park inferred from sediment of Lago Enol, northern Iberia. J. Paleolimnol. 46, 453–467.

Magny, M., Peyron, O., Gauthier, E., Rouèche, Y., Bordon, A., Billaud, Y., Chapron, E., Marguet, A., Pétrequin, P., Vannière, B., 2009. Quantitative reconstruction of climatic variations during the Bronze and early Iron Ages based on pollen and lake-level data in the NW Alps, France. Quat. Int. 200, 102–110.

Mallet, C., Charpin, M.F., Devaux, J., 1998. Nitrate reductase activity of phytoplankton populations in eutrophic Lake Aydat and meso-oligotrophic Lake Pavin: a comparison. Hydrobiologia 373/374, 135–148.

Manguin, E., 1954. Contribution à la connaissance biologique des boues lacustres. Lac Pavin (Puy-de-Dôme). Annales de l'Ecole Nationale des Eaux et Forêts et de la Station de Recherches et Expériences 14, 69–90.

Marchetto, A., Lami, A., Musazzi, S., Massaferro, J., Langone, L., Guilizzoni, P., 2004. Lake Maggiore (N. Italy) trophic history: fossil diatom, plant pigments, and chironomids, and comparison with long-term limnological data. Quat. Int. 113, 97–110.

McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6 M jM software. Gleneden Beach, Oregon U.S.A.

Millérioux, G., 1976. Contribution à l'étude du lac d'Aydat (Puy de Dôme). Unpublished Ph.D. Thesis. University Clermont II.

Miras, Y., Beauger, A., Lavrieux, M., Berthon, V., Serieyssol, K., Andrieu-Ponel, V., Ledger, M.P., 2015. Tracking long-term human impacts on landscape, vegetal biodiversity and water quality in the Lake Aydat catchment (Auvergne, France) using pollen, non-pollen palynomorphs and diatom assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 424, 76–90.

Morabito, G., Ruggie, D., Panzani, P., 2002. Recent dynamics (1995-1999) of the phytoplankton assemblage patterns in the Italian deep lakes. J. Limnol. 61, 129–145.

Overpeck, J.T., Webb III, T., Prentice, I.C., 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. Quat. Res. 23, 87–108.

R Development Core Team, 2006. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-projetct.org.

Rioual, P., 2000. Diatom Assemblages and Water Chemistry of Lakes in the French Massif Central: a Methodology for Reconstruction of Past Limnological and Climate FLuctuations during the Eemian Period. Unpublished Ph.D. Thesis. University College London, London.

Rioual, P., Andrieu-Ponel, V., de Beaulieu, J.-L., Reille, M., Svobodova, H., Battarbee, R. W., 2007. Diatom responses to limnological and climatic changes at Ribains maar (French Massif central) during the Eemian and early Würm. Quat. Sci. Rev. 26, 1557–1609.

Rioual, P., Andrieu-Ponel, V., Rietti-Shati, M., Battarbee, R.W., de Beaulieu, J.-L., Cheddadi, R., Reille, M., Svobodova, H., Shemesh, A., 2001. High-resolution record of climate stability in France during the last interglacial period. Nature 413, 293–296.

Roy, A.-J., 2012. Reconstitution de l'état trophique du lac Nairne, Charlevoix, QC. Mémoire présenté à la Faculté des études supérieures et postdoctorales de l'Université Laval dans le cadre du programme de maîtrise en sciences géographiques pour l'obtention du grade de Maître en sciences géographiques.

Selby, K.A., Brown, A.G., 2007. Holocene development and anthropogenic disturbance of a shallow lake system in Central Ireland recorded by diatoms. J. Paleolimnol. 38, 419–440.

Serieyssol, K., Chatelard, S., Cubizolle, H., 2010/11. Diatom fossils in mires: a protocol for extraction preparation and analysis in palaeoenvironmental studies. Mires Peat 12, 1–11.

Serieyssol, K., Cubizolle, H., Tourman, A., Latour-Argant, C., 2012. Holocene evolution of two ponds on the Devès plateau in the Frecnch Massif central. Diatom Res. 27, 189–211.

Sienkiewicz, E., Gąsiorowski, M., 2014. Changes in the trophic status of three mountain lakes – Natural or anthropogenic process? Pol. J. Environ. Stud. 23, 875–892.

Smol, J.P., 2008. Pollution of Lakes and Rivers. A Paleoenvironmnetal Perspective. Blackwell Publishing.

Stebich, M., Brüchmann, C., Kulbe, T., Negendank, J.F.W., 2005. Vegetation history, human impact and climate change during the last 700 years recorded in annually laminated sediments of Lac Pavin, France. Rev. Palaeobot. Palynol. 133, 115–133.

Stoermer, E.F., 1993. Evaluating diatom succession: some peculiarities of the Great Lakes case. J. Paleolimnol. 8, 71–83.

ter Braak, C.J.F., Juggins, S., 1993. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269/270, 485–502.

ter Braak, C.J.F., van Dam, H., 1989. Inferring pH from diatoms: a comparison of old and new methods. Hydrobiologia 178, 209–223.

van Dam, H., Mertens, A., Sinkeldam, J., 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Neth. J. Aquat. Ecol. 28, 117–133.

van Geel, B., Mur, L.R., Ralska-Jasiewiczowa, M., Goslar, T., 1994. Fossil akinetes of *Aphanizomenon* and *Anabaena* as indicators for medieval phosphate-eutrophication of lake Gosciaz (Central Poland). Rev. Palaeobot. Palynol. 83, 97–105.

Voigt, R., Grüger, E., Baier, J., Meischner, D., 2008. Seasonal variability of Holocene climate: a palaeolimnological study on varved sediments in Lake Jues (Harz Mountains, Germany). J. Paleolimnol. 40, 1021–1052.