

Diatom assemblage dynamics during abrupt climate change: the response of lacustrine diatoms to Dansgaard–Oeschger cycles during the last glacial period

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Abstract The sedimentary record from the paleo-lake at Les Echets in eastern France allowed a reconstruction of the lacustrine response to several abrupt climate shifts during the last glacial period referred to as Dansgaard–Oeschger (DO) cycles. The high-resolution diatom stratigraphy has revealed distinct species turnover events and large fluctuations in stable oxygen isotope values in diatom frustules, as a response to DO climate variability. More or less identical species compositions became re-established during each DO stadial and interstadial phases, respectively. However, the relative abundance of

the most dominant species within these assemblages varies and might indicate differences in climatic conditions. Interstadial phases are characterized by identical species successions. Transitions from stadial to interstadial conditions show a distinct *Fragilaria–Cyclotella* succession, which resembles the diatom regime shifts that have been recognized in some lakes in the Northern Hemisphere since the mid-nineteenth century.

Keywords Diatoms · Oxygen Isotopes · Les Echets · Dansgaard–Oeschger cycles

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Introduction

The response of ecosystems to abrupt climate change has attracted significant interest since the realization of rapid temperature changes in the twentieth century. Floras and faunas can experience considerable rearrangements as a consequence of warming (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006; Lenoir et al. 2008). One such example are the arctic and subarctic freshwater ecosystems in the Northern Hemisphere, which show widespread limnological changes and distinct diatom community turnovers as a result of the temperature increase during the last 150–200 years (Smol et al. 2005; Rühland et al. 2008). Knowledge about the response of aquatic and terrestrial ecosystems to rapid

shifts in climate is therefore important to better understand the extent of these regime shifts.

The study of the diatom record from the former lake Les Echets in France revealed the response to a repeated series of rapid climate shifts, referred to as Dansgaard–Oeschger (DO) cycles, during the last glacial period (Ampel et al. 2008). Here we explore the different DO stadial and interstadial assemblages in more detail and focus on successional developments within and transitions between assemblages as well as changes in oxygen isotope values in diatoms ($\delta^{18}\text{O}_{\text{Si}}$).

Study site

Les Echets (45°54'N, 4°56'E) is situated at 267 m a.s.l on the Dombes Plateau, ~15 km northeast of Lyon in eastern France (Fig. 1). The basin was formed during the retreat of the Rhône glacier at the end of the penultimate glaciation. During the last glaciation (ca. 115–11.5 kyr BP), Alpine glaciers terminated in the valley to the east of the plateau. Consequently, the Dombes Plateau was never

glaciated during the last glaciation and the lake at Les Echets has accumulated sediments since the end of the last pleniglacial (ca. 130 kyr BP). The basin was filled in by the early Holocene and an extensive peat bog developed which was drained and excavated in the mid-fifteenth century (de Beaulieu and Reille 1984).

Materials and methods

In 2001 a 44 m long core (EC1) was retrieved from the central part of the Les Echets basin (Fig. 1). The diatom stratigraphy between 30.07 and 3.30 m has been discussed in Ampel et al. (2008). Here we focus in more detail on the section between 27.47 and 22.52 m of the record which corresponds to an age of ca 36.2 to 31.7 thousand years (kyr) before present (BP). The age-depth curve was established using AMS ^{14}C measurements and infrared luminescence dates (see Wohlfarth et al. (2008) for more details).

Samples for diatom analysis (0.5–1 cm³) were prepared according to standard methods (Battarbee et al. 2001). Diatoms were identified and counted

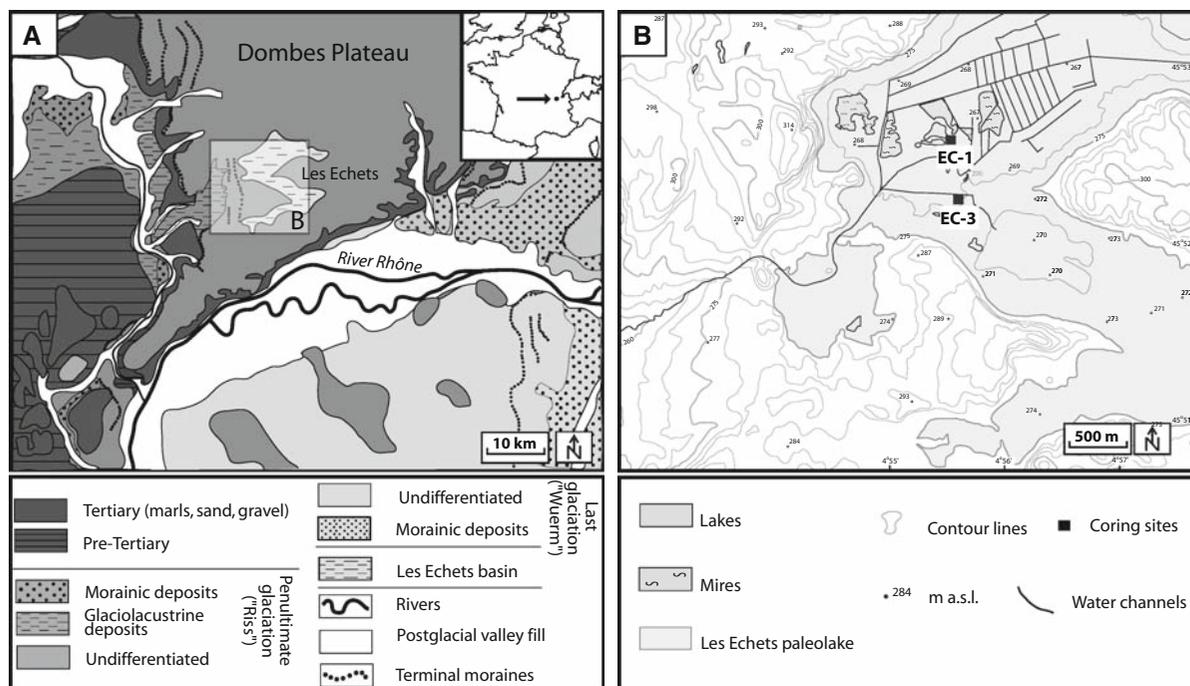


Fig. 1 **a** Geological map of the area surrounding Les Echets and the location of the site in France. **b** Topographic map over the paleobasin at Les Echets. The coring location of core EC1 is indicated

across transects under $1260 \times$ magnification with oil immersion using a Zeiss Axiophot light microscope. Taxonomic identifications are based on Cleve-Euler (1951, 1952, 1953a, b, 1955) and Krammer and Lange-Bertalot (1997, 1999, 2004a, b). A minimum of 400 diatom valves was identified at most levels.

Diatom stratigraphical zone boundaries were originally established by Ampel et al. (2008). To evaluate the difference between zones, the stratigraphical diatom data expressed in relative abundances were analysed by correspondence analyses using the program CANOCO (version 4.5) (ter Braak and Smilauer 2002). An initial Detrended Correspondence Analysis (DCA) resulted in a gradient length of 3.25 SD units, indicating that numerical methods based on a unimodal response model were most appropriate (ter Braak and Prentice 1988). For the final analysis, a regular Correspondence Analysis (CA) without detrending was applied, as the first CA axis did not show any arch effect.

Nine samples were prepared for $\delta^{18}\text{O}_{\text{Si}}$ analysis following a separation method modified after Morley et al. (2004) and Leng and Barker (2006). The oxygen was disassociated from the silicon by a three stepped fluorination technique (Leng and Barker 2006). Oxygen yields were monitored by comparison with the calculated theoretical yield for SiO_2 . The oxygen isotope composition of diatom silica is expressed on the delta scale in terms of per mil (‰). For diatom oxygen the reference is VSMOW (Vienna Standard Mean Ocean Water). The samples were measured against NBS27 and a laboratory standard diatomite. Standard deviation is typically $\pm 0.3\text{‰}$ (1 SD).

Results

Eight diatom zones (DZ 2–9) were assigned between 27.47 and 22.52 m in EC1 (Ampel et al. 2008). The most dominant taxa in these zones (Fig. 2) reveal distinct assemblage turnovers coinciding with changes in TOC and $\delta^{18}\text{O}_{\text{Si}}$. DZ-2, 4, 6, and 8 are characterised by the presence of planktonic *Cyclotella* spp. (*C. delicatula* Hustedt, *C. comensis* Grunow, *C. ocellata* Pantocsek, *C. rossii* Håkansson, *C. krammeri* Håkansson, *C. bodanica* v. *lemanica* (O. Müller) Bachmann) together with the benthic species; *Diploneis elliptica* (Kützing) Cleve, *Navicula rhyncocephala* Kützing, *Navicula pupula* Kützing, *Navicula*

radiosa Kützing, *Stauroneis anceps* Ehrenberg and *Stauroneis phoenicenteron* (Nitzsch) Ehrenberg. DZ-3, 5, 7, and 9 are distinguished by a *Fragilaria* spp. dominated assemblage (*F. pinnata* Ehrenberg, *F. construens* *F. venter* (Ehrenberg) Grunow, *F. construens* *F. construens* (Ehrenberg) Grunow, *F. brevistriata* Grunow) together with *Amphora inarzensis* Krammer, *Navicula jentzschii* Grunow, *Navicula scutelloides* W. Smith, and *Navicula jaernefeltii* Hustedt (Fig. 2).

DZ-2, 4, 6 and 8 and DZ-3, 5, 7 and 9 are clearly separated on CA1 (Fig. 3), while CA2 shows that there are also differences within the two types of assemblages. DZ-8, together with the five lowest levels in DZ-2 cluster in the lower left quadrant, which diverges significantly from DZ-4 and 6. DZ-4 shows some vertical spread along CA2 in the upper left quadrant (Fig. 3). DZ-3, 5 and 7 appear more homogenous as they cluster together in the upper right quadrant while DZ-9 plots on the negative range of CA2.

DZ-2, 4, 6 and 8 display a distinct successional pattern in the fossil diatom assemblages (Fig. 2). The succession begins with a significant increase of *Cyclotella* spp. with peak abundances occurring in the lower part of the zone. The most dominant benthic species reveal a succession pattern in which *D. elliptica* increases slightly but abruptly at the zone boundary and then remains at a stable abundance throughout the zone. Subsequently, *N. rhyncocephala* increases, followed by *N. pupula*, *N. radiosa*, *S. anceps* and *S. phoenicenteron*. This successional increase is followed by a reversed successional decrease of the five benthic species, i.e., first *S. phoenicenteron*, *S. anceps*, *N. radiosa*, *N. pupula*, and *N. rhyncocephala* and finally a small decline in the abundance of *D. elliptica*. At the same time as *N. radiosa*, *N. pupula*, *S. anceps* and *S. phoenicenteron* start to decrease, *Cyclotella* spp. increase again, with peak abundances in the upper part of the zone. DZ-2, however, diverts somewhat from this pattern, since this interstadial lacks the abrupt increase of planktonic taxa within the lower part of the zone. Instead, benthic assemblages typical of interstadial conditions increase abruptly and are succeeded by *Cyclotella* spp. which increase during the second part of the interstadial.

The $\delta^{18}\text{O}_{\text{Si}}$ values show changes coinciding with the diatom assemblage shifts. DZ-2, 4, 6, and 8 have

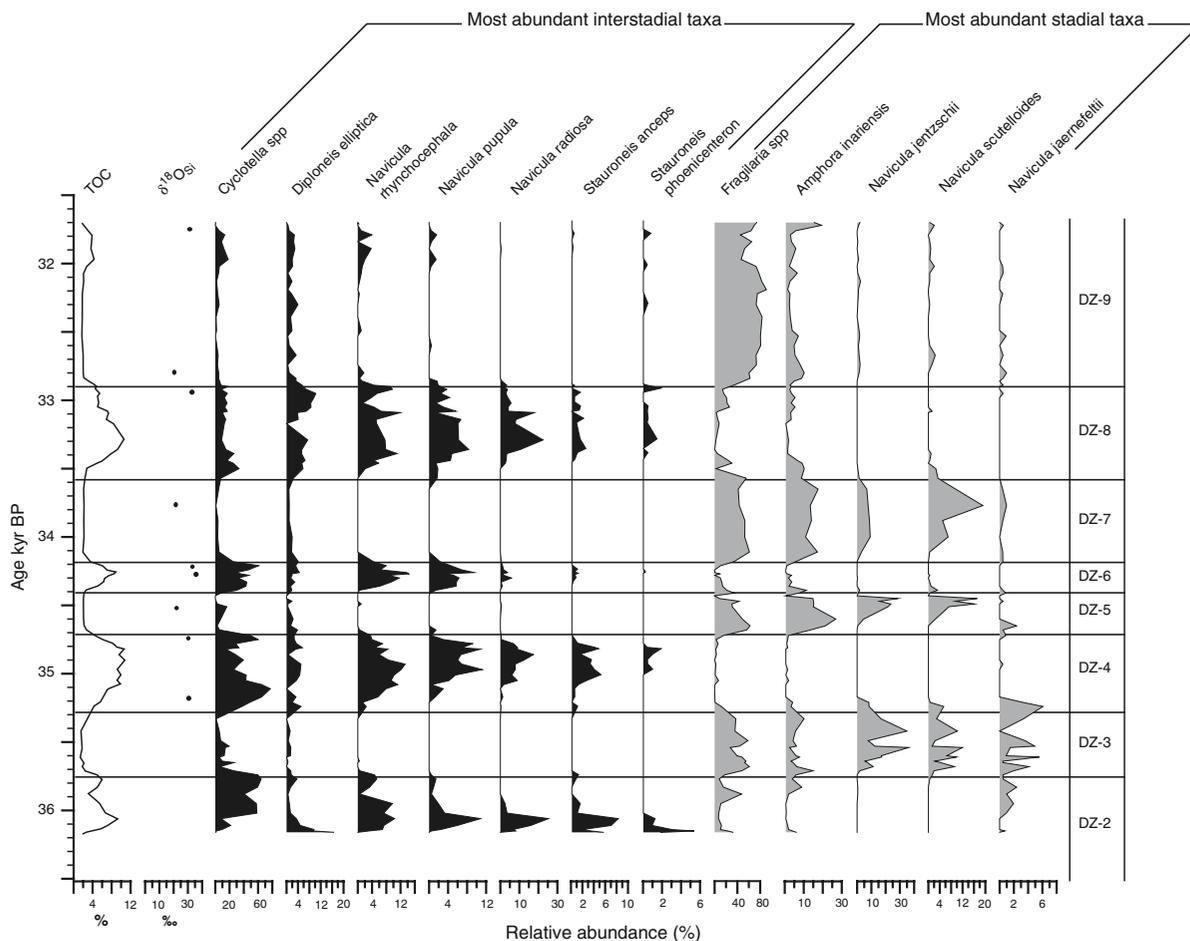


Fig. 2 The most dominant diatom species in EC1 between 36.2 and 31.7 kyr BP (27.47–22.52 m) together with the profiles of $\delta^{18}\text{O}$ and TOC

values between +30.1 and +36.9‰, while DZ-3, 5, 7 and 9 show values that range between +19.5 and +22.1‰ (Fig. 2).

Discussion

In Ampel et al. (2008) we suggested that the synchronous phasing of diatom assemblages and organic productivity between 36.2 and 31.7 kyr BP (Fig. 2) occurred as a response to DO climate variability. DZ-2, 4, 6 and 8 which are characterized by higher organic productivity, increased diatom productivity and more diverse assemblages suggest DO interstadial conditions, while DZ-3, 5, 7 and 9, which are distinguished by low organic productivity, decreased diatom productivity and less diverse

assemblages were interpreted as a response to the stadial phase of a DO cycle (Ampel et al. 2008).

Oxygen isotopes in diatom silica $\delta^{18}\text{O}_{\text{Si}}$

The result of the $\delta^{18}\text{O}_{\text{Si}}$ analyses demonstrates significant shifts in conjunction with the diatom assemblage changes (Fig. 2). Changes in $\geq 10\text{‰}$ are difficult to account for by other means than a modification in the precipitation to evaporation balance. A large shift from approximately +20‰ during stadials to $> +30\text{‰}$ during interstadials therefore suggests that the basin was subjected to large changes in effective moisture (Leng and Marshall 2004). During interstadials, which have higher $\delta^{18}\text{O}_{\text{Si}}$ values the evaporation rates were probably much higher than during stadials, which have lower $\delta^{18}\text{O}_{\text{Si}}$ values.

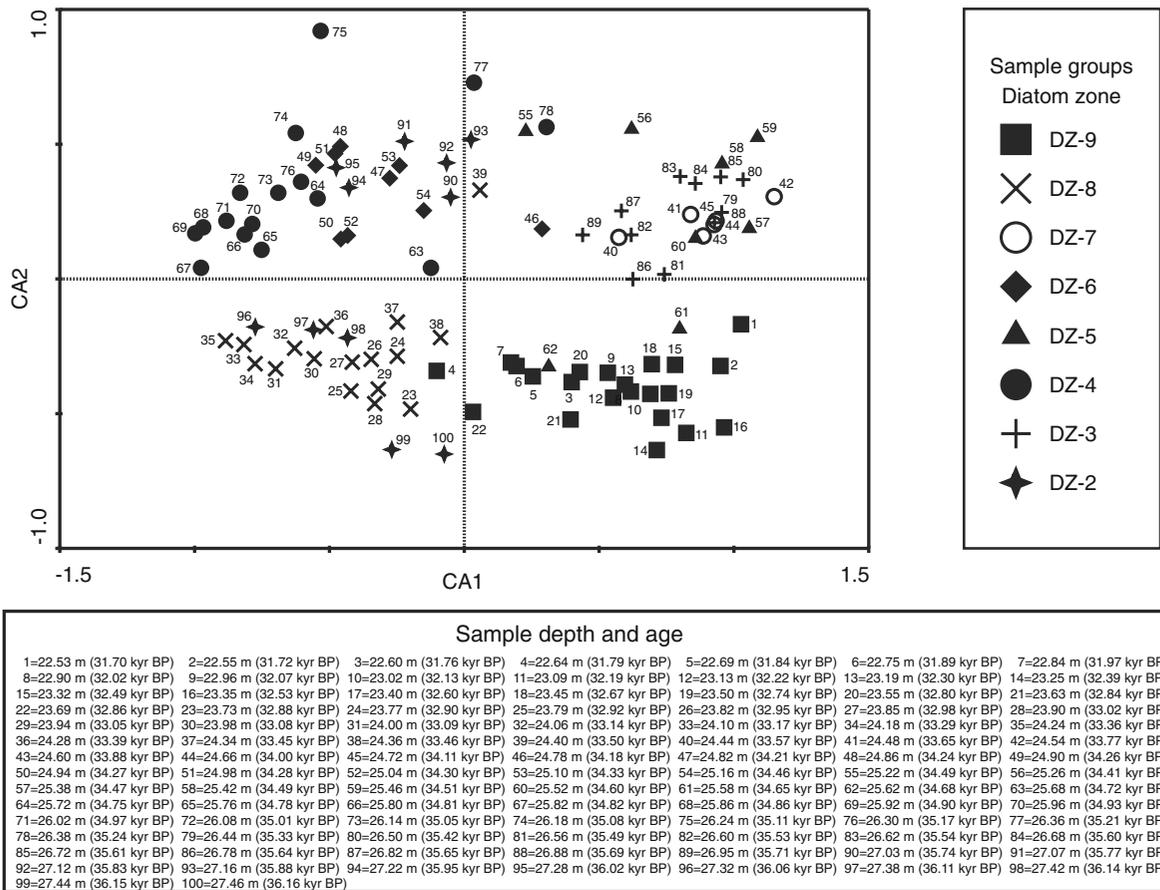


Fig. 3 The distribution of samples from each zone in the Correspondence Analysis (CA)

However, differences in evaporation rates at Les Echets are unlikely to have been the consequence of atmospheric aridity/humidity changes, since this would contradict the climatic conditions described for DO cycles at this latitude in Europe, i.e. cold and dry stadial conditions and warmer and more humid interstadials (Rousseau et al. 2002; Sánchez Goñi et al. 2008). We, therefore, interpret variations in $\delta^{18}\text{O}_{\text{Si}}$ as an expression of changes in the duration of seasonal ice-cover and water-stratification patterns, discussed in Ampel et al. (2008), on potential evaporation. During DO stadials shorter open-water periods meant that the lake experienced less evaporation, which resulted in more depleted $\delta^{18}\text{O}_{\text{Si}}$ values. In contrast, interstadial phases were characterised by shorter ice-cover periods and stratified lake water during the open-water season. A longer open-water season would have facilitated greater evaporation producing higher $\delta^{18}\text{O}_{\text{Si}}$ in diatom frustules,

especially in the epilimnion, where diatoms commonly grow.

Differences and similarities between individual interstadial and stadial assemblages

The most intriguing features of the diatom stratigraphy between 36.2 and 31.7 kyr BP are the regular alternations between two types of dominant assemblages (Fig. 2). The consistency in species composition during each interstadial and stadial interval suggests that taxa, within the respective assemblages, most likely endured in small populations during those phases of the DO cycle that did not favour their growth. These repeated species alternations also suggest that the paleolake at Les Echets had two stable limnological states during this time interval.

The CA moreover indicates slight differences in the assemblages between individual interstadials and

individual stadials. The spread of DZ-4, together with the clear separation of DZ-8 and the early part of DZ-2 from the other interstadials along CA2 and their distinct association with an abundance in planktonic taxa, suggest that the relative abundance of *Cyclotella* spp. is an important factor for differentiating interstadials. Except for this feature, the assemblages from the first three interstadials (DZ-2, 4 and 6) are rather similar, clustering together in the upper left quadrant (Fig. 3). The relationship between *C. comensis* and *C. delicatula* and lake water stratification (Scheffler et al. 2005; Kiss et al. 2007) might indicate variations in climatic conditions between different interstadials. Slightly lower temperatures and/or increased wind intensities might have been enough to delay the establishment of a stratified water column. Consequently, the period during which the planktonic taxa could thrive would have become shorter and would have resulted in decreased relative abundances (Lotter and Bigler 2000). Such conditions probably would not have influenced the overall length of the growing season or other parameters important for the benthic assemblage and therefore did not influence the size or composition of the benthic population.

The stadal assemblages in DZ-3, 5 and 7 appear rather similar as they cluster together in the upper right quadrant of the CA, while DZ-9 plot on the negative range of CA2 (Fig. 3). This divergence is explained by the relative abundance of *Fragilaria* spp., *A. inariensis*, *N. jentzschii* and *N. scutelloides*, which are present in more or less equal abundances in DZ 3, 5, and 7. Because *Fragilaria* species are considered to be rather competitive during extreme conditions (Denys 1990; Lotter et al. 1999) the dominance of these species during DZ-9 might imply that this stadal was much colder in comparison to the former three stadials. Suggestively, the environmental conditions became too harsh even for *N. jentzschii* and *N. scutelloides* to grow although they might be considered as cold adapted taxa in large lakes with reference to their abundance in the Ancylus Lake stage of the Baltic Sea (Risberg et al. 1996; Hedenström and Risberg 1999).

Succession patterns in interstadial assemblages

DZ-4, 6 and 8 are characterized by a successional development of the interstadial assemblages starting with a large and rapid increase in *Cyclotella* spp. and a slight increase in *D. elliptica* followed by

N. rhynchocephala, *N. pupula*, *N. radiosa*, *S. anceps* and *S. phoenicenteron*. Because *C. comensis* and *C. delicatula* are dependent on water column stratification, the abrupt increase of *Cyclotella* spp. at the beginning of interstadials might indicate that climatic changes associated with the commencement of a DO interstadial occurred rather rapidly. Thus, the thresholds for the physical conditions important for *Cyclotella* spp. to compete for nutrients, were probably reached in less than 100 years, according to the age-depth model (Wohlfarth et al. 2008). *N. pupula*, *N. radiosa*, *S. anceps* and *S. phoenicenteron*, show changes in relative abundance that correspond to changes in TOC, and occur only in significant abundances coincident with peaks in TOC (Fig. 2). In some cases *N. radiosa*, *S. anceps* and *S. phoenicenteron* are common during elevated nutrient levels (Krammer and Lange-Bertalot 1999; Rühland et al. 2003). We therefore speculate that these four species may have required stable nutrient cycling before they could compete for nutrients. The increase in TOC usually lagged ~100–200 years behind the increase of planktonic taxa, suggesting that the surrounding catchment may have taken a while to adapt and stabilize after the climatic change.

Planktonic taxa also tend to increase at the end of the interstadial zones, just as several benthic species and TOC values begin to decrease, suggesting that nutrient cycling may have been disrupted by climate changes that influenced the catchment and lake productivity. As a result the benthic flora decreased in abundance, and the relative abundance of the planktonic flora increased; but as soon as the planktonic taxa had decreased they were followed by a rather abrupt increase of *Fragilaria* spp. and *A. inariensis*. Some successional patterns may exist during stadal periods as well, but factors that might have been important for these transitions are difficult to discuss since the ecological information for these species is limited.

Transition from stadal to interstadial conditions

Interestingly, the repeated rapid shift from *Fragilaria*-dominated assemblages to *Cyclotella*-dominated assemblages associated with the interstadial warming at Les Echets resembles some of the reorganisations of diatom assemblages in lakes across a latitudinal gradient from mid-latitude to the high arctic since the

mid-nineteenth century (Smol et al. 2005; Rühland et al. 2008). A synthesis of more than 200 diatom records from non-acidified/non-enriched lakes indicates a consistent pattern of climate-driven taxon-specific changes across vast regions in the Northern Hemisphere. These changes are at some locations characterised by a significant increase in the relative abundance of *Cyclotella* taxa, while *Fragilaria* species had decreased considerably, most likely as a consequence of the recent temperature rise resulting in longer ice-free periods. These community reorganisations were initiated in Arctic and alpine regions during the mid-nineteenth century, but extended to mid-latitude regions of North America and Europe during the mid-twentieth century. Freshwater ecosystems in the Northern Hemisphere might thus already have crossed a significant ecological threshold as a consequence of anthropogenic warming (Rühland et al. 2008). Although, caution should be applied when comparing the glacial record of Les Echets with recent conditions of lakes in North America and Europe, due to different glacial boundary conditions, the taxonomic similarity suggests that the limnological and catchment settings might have been rather similar in many respects. The study by Rühland et al. (2008) and the present study of Les Echets show that the observed diatom assemblage changes are/were probably driven by climate. Our findings suggest that the *Fragilaria*–*Cyclotella* transition seen in mid-latitude and high Arctic lakes during the nineteenth and twentieth centuries might only represent a first threshold in a succession of ecosystem responses to climate change in settings typical for these taxa. Much larger reorganisations and additional thresholds may be crossed if average global temperatures continue to increase as many predictive climate models suggest.

Conclusions

- The diatom stratigraphy from the paleolake Les Echets has revealed distinct shifts in diatom assemblage composition between 36.2 and 31.7 kyr BP, as a response to DO climate variability.
 - Differences in the relative abundance of specific taxa might indicate variations in climatic conditions during individual DO cycles.
 - Interstadial assemblages, as opposed to stadial assemblages, display a more complex successional

assemblage build up and retraction, which might be related to catchment development and nutrient cycling.

- Transitions from stadial to interstadial conditions occurred in two steps: a *Fragilaria* dominated assemblage is succeeded by an abrupt and significant increase of *Cyclotella* species; thereafter the subsequent increase of the most abundant interstadial benthic taxa started.

- The results of the oxygen isotope analysis show large fluctuations in $\delta^{18}\text{O}_{\text{Si}}$ values between stadials and interstadials. This indicates changes in the precipitation to evaporation balance and is most likely an expression of the duration of seasonal ice cover versus open water.

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