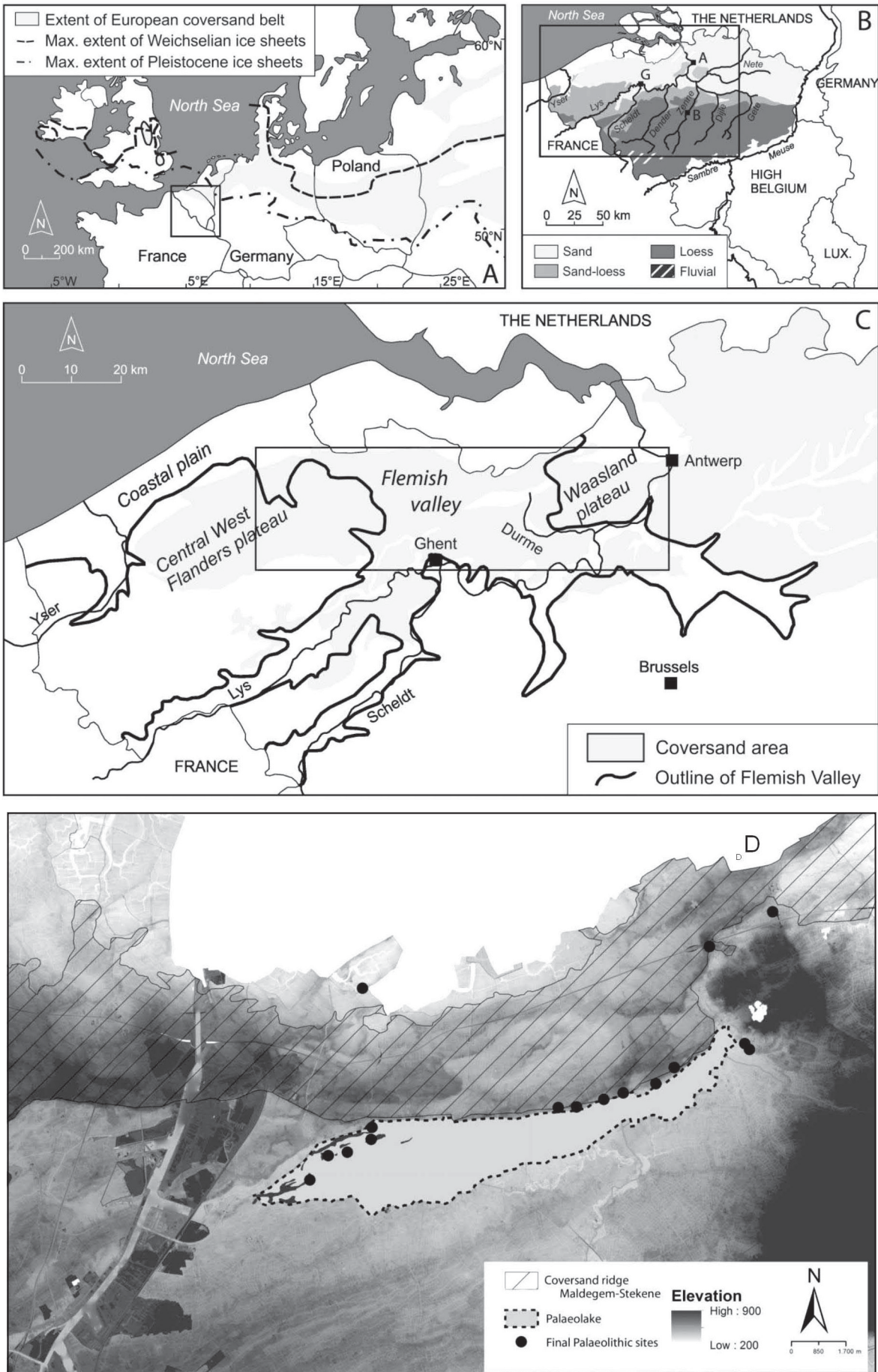# Diatom-based palaeoecology of a late-glacial palaeolake in the Moervaart area (northwestern Belgium) in relation to its prehistoric occupation

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1. Introduction

Assessing past climate-human-environment interactions at local and regional scales is particularly relevant in the evaluation of factors controlling the behaviour and mobility of prehistoric human societies. To gain new insight about the variability of the nature of these complex interactions, we need to tackle issues concerning simple causation, scale mismatch between social and ecological processes and conflicting conclusions about the effects of environmental change on human adaptation (Dearing, 2006). The reliable assessment of environmental change itself, with adequate reference to spatial entities such as lakes and other landscape elements, is then of paramount importance. All over northwestern Europe, lake sediment archives from the Late Pleistocene and Holocene have provided a large number of proxy records, which enable reconstructions of past climatic conditions and processes (e.g., Harrison & Digerfeldt, 1993; Digerfeldt, 1998; Rühland *et al.*, 2008). However, lakes with sediments suitable for climate change reconstruction may vary strongly according to differences in age, in origin, in biotic composition (e.g., local and regional species pool), in chemistry and in the climate events encompassed by each biological proxy (e.g., cyanobacteria, diatoms, chironomids, cladocera and ostracods) (Battarbee, 2000). Moreover, only few lake-sediment archives (e.g., Bos & Janssen, 1996; Bos *et al.*, 2013) originate from a locality and time period of archaeological interest (Charles, 1985; Demiddele & Ervynck, 1993; Denys, 1992; Dean *et al.*, 1984; Digerfeldt, 1986; Lotter, 1988). Due to the high variability in natural landscape elements (e.g., topography, hydrology, soil conditions, and food resources) and human occupation patterns, the Moervaart area in northwestern Belgium is a very suitable region from which to assess the response of hunter-gatherers to abrupt climate change. Over the past 20 years, archaeological fieldwork has yielded numerous prehistoric sites, dating back to different chronological stages (Crombé & Sergant, 2008; Crombé & Verbruggen, 2002; Crombé *et al.*, 2011; Crombé *et al.*, 2013). Given the temporal and spatial gradients of prehistoric settlements on a large cover sand ridge across the area, it seems that local hunter-gatherers strongly depended on the resources provided by a large palaeo-lake, bordering the slightly elevated cover sand ridge to the south (Heyse, 1979; Bats *et al.*, 2009, 2010; Crombé *et al.*, 2012).

A recently recovered high-quality sediment sequence from the deepest part of the palaeo-lake offered the opportunity to collect valuable proxy data concerning the climate and palaeoenvironment in this region and to -ultimately- assess more comprehensively human response to climate-driven ecosystem shifts. Among biological proxy indicators studied in lake sediments, diatoms have proven to be good indicators for reconstructing past changes in salinity, water depth and water quality (Battarbee, 2000; Cumming & Smol, 1993). Shifts in moisture regimes from closed-basin lakes in arid and semi-arid regions can lead to the concentration or dilution of dissolved salts and oxygen, visible through changes in the composition of fossil diatom assemblages. However, reconstructing precipitation-evaporation changes in open drainage freshwater lakes from temperate and high-latitude regions is far more difficult due to basin-related thresholds and ground-

water outlets (Battarbee, 2000). As a result, the use of regionally-developed diatom-based regression and calibration models may considerably enhance the reconstruction of past environmental conditions and facilitate bio-chronological correlation of fossil diatom assemblages. In this paper, we report on a new high-resolution, late-glacial record of lake ecosystem responses to natural climate variability in the Moervaart area (northwestern Belgium). We studied shifts in the composition of the diatom community occupying the late-glacial palaeolake to elucidate its development. Compared to other organism groups, the potential of diatoms as palaeoclimatic and palaeoenvironmental indicators is hardly investigated within archaeology. However, particularly in arctic regions, diatoms have shown to be a valuable proxy for past climatic shifts. The objective of the research was therefore to identify the potential of diatoms as palaeoclimatic indicators in an area that now has a temperate climate.

2. Geomorphological and archaeological setting

The Moervaart area is situated in a long-stretched palaeovalley, known as the Flemish Valley, which laterally extends from the coastal plain and polder areas in the west to the clayey cuestas of Boom and Waasland in the east (Tavernier, 1946; De Moor, 1963; Tavernier & De Moor, 1974; Fig. 1a-c). This palaeovalley developed during several periods of fluvial incision and infilling, caused by extreme climatic fluctuations and corresponding sea level changes in the (Late) Pleistocene (De Moor, 1963; De Moor & Van De Velde, 1995). The largest fluvio-periglacial infilling occurred during the Last Glacial, the Weichselian (115-11.5 ka ago) (De Moor & Heyse, 1973), which resulted in a ~25 m-high accumulation of mainly sandy sediments in the central part of the valley. From the Late Pleniglacial (ca 27-11.5 ka ago) onwards, drier climatic conditions followed by increased aeolian activity in this sandy area resulted in the development of east-west oriented coversand ridges, of which the sand ridge extending from Maldegem to Stekene is the most apparent (De Moor & Heyse 1973; Heyse 1979) (Fig. 1d). This coversand ridge (length: ~80 km, width: 1.5 to 3 km, height: ~5 m on average above present sea level) is characterised by a complex microrelief of small dunes and irregularly elongated depressions and dune slacks. During the late-glacial, a large palaeolake (length: ~15 km, width: ~2.5 km) was formed in the low-lying Moervaart depression, located to the south of the coversand ridge Maldegem-Stekene (De Moor & Heyse, 1973; Verbruggen, 1971, 2005) (Fig. 1d). The depression itself has an asymmetrical north-south profile, and currently consists of a ~2 m-high moderately sloping northern edge, bordering the coversand ridge, and a more gently sloping southern edge.

Numerous prehistoric sites, dating from the late-glacial (Final Palaeolithic) and the (early) Holocene (Mesolithic), have been discovered in the Moervaart area. Most typical for the late-glacial period is the high density of *Federmesser* occupation patterns (Crombé & Verbruggen, 2002; Crombé *et al.*, 2011), forming an almost continuous site-complex stretching along the coversand ridge Maldegem-Stekene (over ca 15 km) and some small interfluvial levees on the northern side of the depression (Fig. 1d). The site-clustering and uniformity between the lithic assemblages (e.g., backed points, bladelets and burins) throughout the study area may indicate that temporary campsites were frequently (re-)occupied by small groups of hunter-gatherers. Probably, the contemporaneous presence of a large water resource in the Moervaart depression formed a principal component in the subsistence strategies of hunter-gatherers communities in Sandy Flanders (Sergant *et al.*, 2009; Crombé *et al.*, 2011).

Fig. 1 - (opposite page) Location of the Moervaart depression in Europe (A), Belgium (B), Sandy Flanders (C) and on a digital elevation model (cm above reference sea level TAW) with indication of Final Palaeolithic *Federmesser* sites (D).

3. Materials and methods

3.1. Fieldwork

During 2008, several longitudinal transects of boreholes (468 boreholes in total) were drilled along the Moervaart depression, permitting a preliminary documentation of the lateral and vertical sedimentological properties of the study area (Bats *et al.*, 2009; Crombé *et al.*, 2013). Based on the results of this survey, in 2009 (Bats *et al.*, 2010) a 70-m long trench was excavated across the deepest part of the depression, which allowed us to study the lateral variation in sediment composition and morphology in more detail (Fig. 2). The different sedimentary units were macroscopically/visually described with the following parameters: (i) lithology (including colour and grain-size determination), (ii) sedimentological features and post-depositional formation, (iii) thickness and form, and (iv) lower and upper boundaries of sediment horizons, and the presence of internal ravination surfaces. The lithological sequence (Fig. 3) described in this paper has been selected because it represents the most complete and best preserved section of the trench profile at Moerbeke.

3.2. Diatom sampling and analysis

A master sequence, consisting of two subsequent sample sections, P3 (for microscopic analyses) and M3 (for macroscopic analyses; Fig. 3), was selected for further palaeoecological research.

The sediment profile P3 was subsampled for quantitative diatom analysis at 2 cm interval, resulting in a total of 80 contiguous depth increments. The wet sediment samples (1 g)

Fig. 2 - Sampled trench in Moervaart depression (overview). Photo P. Crombé, UGent.

were prepared according to the standard diatom extraction technique described by Battarbee *et al.* (2001). Diatom counting was performed at 1000 x magnification with an oil immersion objective of 100 x, using an Optika B 500 Tpl. light microscope equipped with a CMEX 5000 digital USB camera. Diatoms were identified with reference to the identification guides of Krammer and Lange-Bertalot (1997a-b, 2004a-b), Spaulding *et al.* (2010), Hofmann *et al.* (2013). Although long pennate diatoms were often broken and fragmented, particularly in the upper layers, the diatoms were in general abundant and well-preserved (Counting procedure broken valves after Schrader & Gersonde, 1978). Per stratigraphic level more than 500 valves were counted, except for the levels: 1.98 m (293), 1.96 m (396), 1.9 m (409) 1.88 m (289), 1.86 m (447) and 1.84 m (289). When a single taxon (mainly *Fragilaria*, *Staurosira*, *Pseudostaurosira*) dominated the diatom assemblage, we continued counting until 700 to 900 valves were identified.

3.3. Explorative data analysis

Diversity indices were employed to explore how diatom community structure has changed throughout the lakes history. Diatom counts were first transformed to relative abundances. The diatom assemblages from the Moervaart section were stratigraphically plotted using C2 version 1.5 software (Juggins, 2007). Biological communities are often characterised by their diversity, abundance and ecological groups. Diversity measurements play an important role in bio assessment because it relates to environmental characteristics. To compare the different assemblages, we calculate for each depth interval the species richness and Berger-Parker Dominance (Hammer & Harper, 2006). Diversity indices can be plotted as a function of time in order to identify events and trends (Hammer & Harper, 2006). Diversity can also be used to characterize different types of communities.

The Berger-Parker index is not totally independent of species richness (S) because the minimum value of the index (at minimal dominance) is $1/S$. It only takes into account the abundance of the single most dominant species. Still the Berger-Parker index is attractive because of its simplicity. Zonation of the diatom profile is based on the results of a constrained incremental sum of squares (Grimm, 1987; Grimm, 2004) cluster analysis.

Because of the appearance of some abundant diatom species (ie. *Fragilaria spp.*, *Pseudostaurosira spp.*, *Staurosira spp.*, *Mastogloia spp.*) and a large number of uncommon taxa in the diatom set, a square root transformation was applied. If diatom species show a strong relation to a particular environmental vari-
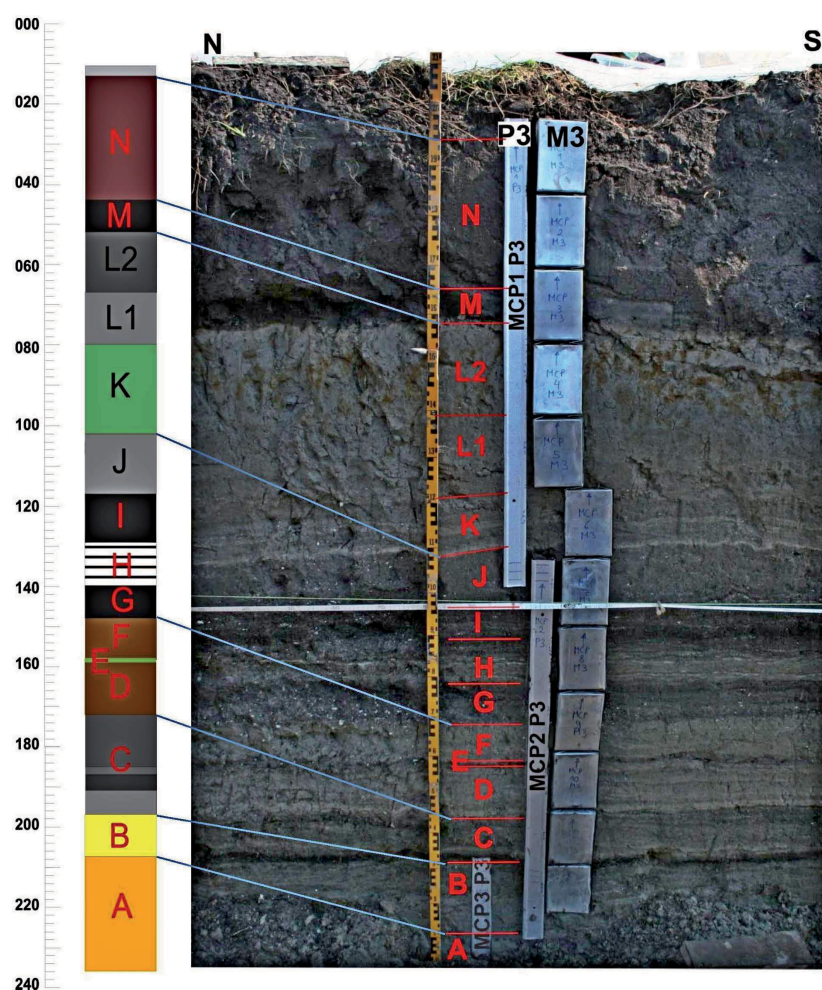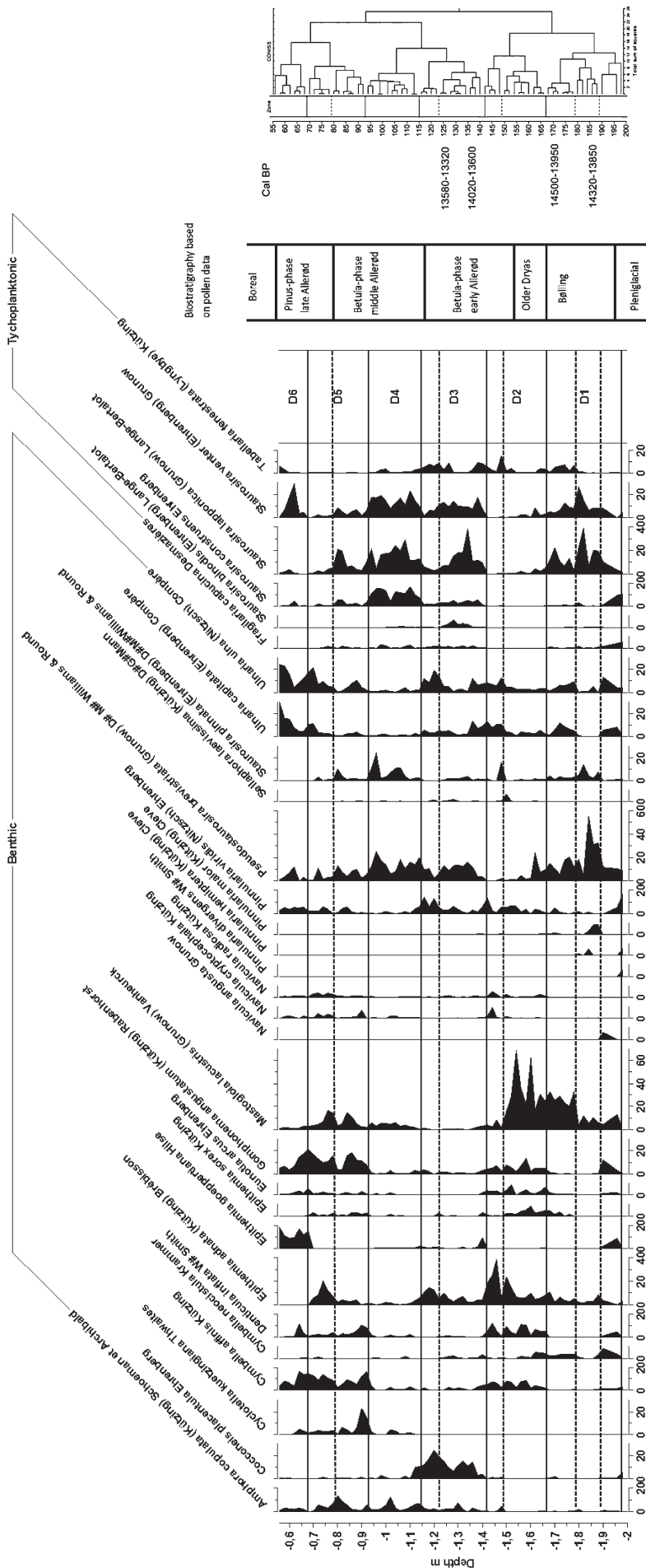

Fig. 3 - Detail of sampled strata indicating profiles P3 and M3. Depths in cm below surface. Photo P. Crombé, UGent.

able, then realistic inferences should be possible from diatom assemblages preserved in a sediment sequence.

3.4. Ecological indicators

The sampled section was quantitatively expressed using values of ecological indicators (their apparent ecological requirements) for all diatom species observed. Species-specific optimum values for these indicators were taken from Denys (1991) and van Dam *et al.* (1994). Denys (1991) defined the auto ecology of 980 fossil diatom taxa based on 800 samples taken mainly from cores and also from some outcrops of Holocene deposits along the western Belgian coastal plain. The recent diatom flora of the area, however, was not considered, while reworked diatoms derived from older deposits were included. van Dam *et al.* (1994) on the other hand used for his check-list all recent and fossil freshwater diatoms, which have been encountered in the Netherlands, with ecological indicator values for those environmental variables which are considered to be the most important ones in aquatic and wetland ecosystems in the Netherlands.

For each sample an average value of each ecological indicator was calculated using observed species abundances as weights (Bijkerk, 2010). We applied weighted averaging, as it is one of the most used and most effective methods for the development of diatom indicators (Roberts & Mc Minn, 1998; Denys, 2006). The diatom zones are not considered as chronozones, but are based on the main qualitative changes of the diatom taxa. For the current

Fig. 4 - Depth distributions (left, m relative to surface) of the counts of the most important taxa grouped by habitat; pollen biozones (Bos *et al.*, submitted), ^{14}C-dates (Crombé *et al.*, 2014) and CONISS clusters (right). Calibration of the radiocarbon dates according to Reimer *et al.*, 2013.

study, we assumed that the characteristics of a species in the fossil record are the same as for that species today. Denys (1991) and van Dam *et al.* (1994) have proposed ranges in salinity, trophic conditions, pH, nutrient availability, saprobity, oxygen requirement, habitat or moisture, and lifeform for diatoms found in Belgium and the Netherlands. Van Dam *et al.* (1994) estimated pH, nitrogen, oxygen, salinity, saprobity preferences and trophic state of 948 diatom taxa of fresh and weakly brackish water in the Netherlands. In the diatom diagrams curves for the respectively ecological parameters were plotted in accordance with the diatom taxa used by Denys (1991) and van Dam *et al.* (1994). Many extant diatoms only occur in a restricted range of environmental conditions. Equations for inferring lake water pH were derived from the EDDI database (The European Diatom Database).

4. Results

4.1. Lithostratigraphy and chronology

The sampled sequence (Fig. 3) starts at the base with a ca 0.25 m thick stratified layer (C) of humic calcareous gyttja with intercalated thin organic to peaty lenses. This layer is followed by two deposits of laminated lake marl (D and F), separated by a thin humic to peaty horizon (E). These lower lake marls are covered by two layers of (highly) organic calcareous gyttja (G and I); in between these, a layer of white sands is present (layer H), which increases in thickness towards the eastern part of the palaeolake. Micromorphological analyses suggest an aeolian origin for these sands, which were most likely blown into the palaeolake from the adjacent Great Sand Ridge by northern winds. The roundness, size and mineralogy (dominance of quartz and some calcium carbonate) of the sand grains are very similar to the deeper, non-decalcified sand layers of the ridge. Most likely these sediments were deposited as lake infill beds on the lake surface during episodes of freezing (Crombé *et al.*, 2013). The gyttja layer I is followed by a second horizon of lake marl deposits (J-L), varying from organic (J) over clayey (K) to finely laminated with traces of oxidation (L). At the top of the sequence the lake sediments are covered by peat (M). The latter is relatively thin and discontinuously preserved at the sampled site. Further east in the palaeolake, however, it is much thicker (ca. 0.5 m) and better preserved, thanks to the deposition of overlying sediments dating back to the Medieval period (13th-14th century). Elsewhere in the Moervaart depression the upper peat has disappeared almost entirely due to extraction and subsequent ploughing (Jongepier *et al.*, 2011).

According to the pollen (Bos *et al.*, submitted) and radiocarbon evidence (Crombé *et al.*, 2013; 2014) the Moervaart sequence represents a contineous sedimentation from the Bølling or Greenland Interstadial 1e (GI-1e) till the late Allerød or GI-1a/b. Ultimately at the onset of the Younger Dryas or GS-1 the lake dried out and disappeared permanently.

4.2. Diatom counts and diversity

A total of 107 species and intra-specific taxa were identified[1]. Figure 4 shows depth distributions of the (square root-transformed) counts of the most common taxa, classified into two groups by lifeform: tychoplanktonic and benthic. Figure 5 shows the species counts and the diversity indices. Taxa that could not be identified to the species level were excluded in the analysis of diversity. Species counts and diversity indices show distinct variations over depth, but an increasing trend is observable in diatom community diversity with time. Furthermore, changes in the diatom assemblages indicate that the lake has undergone environmental changes.

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1 A detailed list of all found taxa is available on demand to the corresponding author.

4.3. Diatom zonation

The cluster analysis with CONISS revealed 6 clusters at a threshold value of 14 for the total sum of squares (Fig. 4, solid horizontal lines). These clusters are firmly related to lithostratigraphic units and therefore served as strata in the diatom zonation D1-D2-D3-D4-D5-D6. A further division (Fig. 4, dotted horizontal lines) can be made following the threshold value of 8; this leads to sub-zones within D1, D2, D3 and D5.

In general (Fig. 5), the species count and the species diversity are less in diatom zones D1 and D2 than in D3-D4-D5 and D6. Below follows a brief summary of species composition of the diatom zones. Based on the available pollen evidence (Bos et al., submitted) these can be roughly attributed to the biozones Bølling (D1), the Older Dryas (lower part of D2), the early Allerød (upper part of D2 and D3), the *Betula*-phase of the middle Allerød (D4 and lower part of D5) and the *Pinus*-phase of the late Allerød (upper part of D5 and D6).

Diatom zone D1 198-167 cm: the diatom composition of this zone is dominated by benthic and tychoplanktonic taxa *Staurosira* and *Pseudostaurosira*. Limited presence was observed of *Cymbella*, *Epithemia* taxa, *Denticula inflata* and *Ulnaria*. At the end of D1 *Mastagloia lacustris* strongly increases, a trend which continues into D2.

Diatom zone D2 167-142 cm: in this biozone nearly all benthic and tychoplanktonic Staurosira taxa disappear after the start of D2. Besides *Mastogloia lacustris*, other benthic species like *Cymbella affinis*, *Denticula inflata*, *Epithemia adnata*, *E. sorex*, *Eunotia arcus* and *Gomphonema angustatum* dominate.

Diatom zone D3 142-115 cm: at the start of D3 there is a remarkable increase in benthic and tychoplanktonic *Staurosira* and *Staurosirella* taxa, *Cocconeis placentula* and *Epithemia adnata*. *Mastogloia lacustris* completely disappears, a process which started already at the end of D2. Benthic and tychoplanktonic *Staurosira s.l.* taxa are highly abundant throughout this zone.
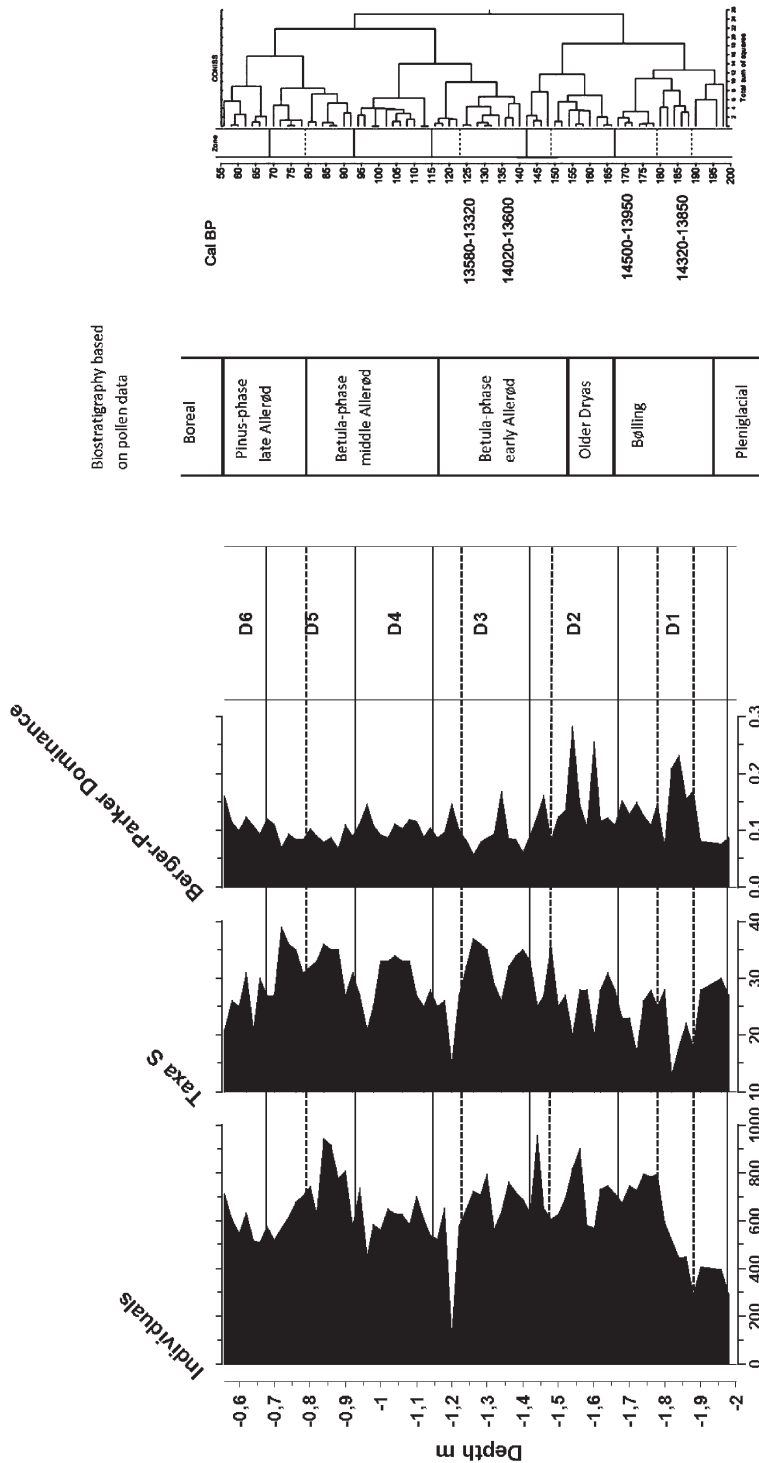

Fig. 5 - Results of species counts (individuals), diversity indices (number of taxa and Berger-Parker index). Results of cluster analysis (CONISS) in biozones and ^{14}C-dates are added for reference. Depths in m below surface.

Diatom zone D4 115-93 cm: from the start of D4, the benthic and tychoplanktonic *Staurosira* and *Staurosirella* taxa further increases after a short but abrupt dip in the top of D3. *Mastogloia lacustris* reappears at 111 cm though at much lower abundance than in D2.

Diatom zone D5 93-68 cm: from 92 cm onwards benthic species dominate (*Cymbella affinis*, *Epithemia adnata*, *Pinnularia viridis*, *Ulnaria ulna*, *Ulnaria capitata*, *Gomphonema angustatum*, *Epithemia goepertiana*). At 90 cm there is a maximum in *Cyclotella kuetzingiana* as well as in cold-resistant *Cymbella affinis*.

Diatom zone D6 68-55 cm: cold-resistant forms as *Cymbella affinis* persist and dominate D6. At a depth of 62 cm *Staurosira* taxa reappears. At a depth of 58 cm a strong decrease of the *Staurosira* taxa occurs. The diatom concentration values are very low throughout the end of diatom zone D6 sediments. The very few diatoms found in this section were well preserved so their absence cannot be explained by dissolution but maybe due to a higher sedimentation rate. This is also corroborated by the massive abundance of *Ulnaria* species at the transition from D5 to D6.

5. Discussion

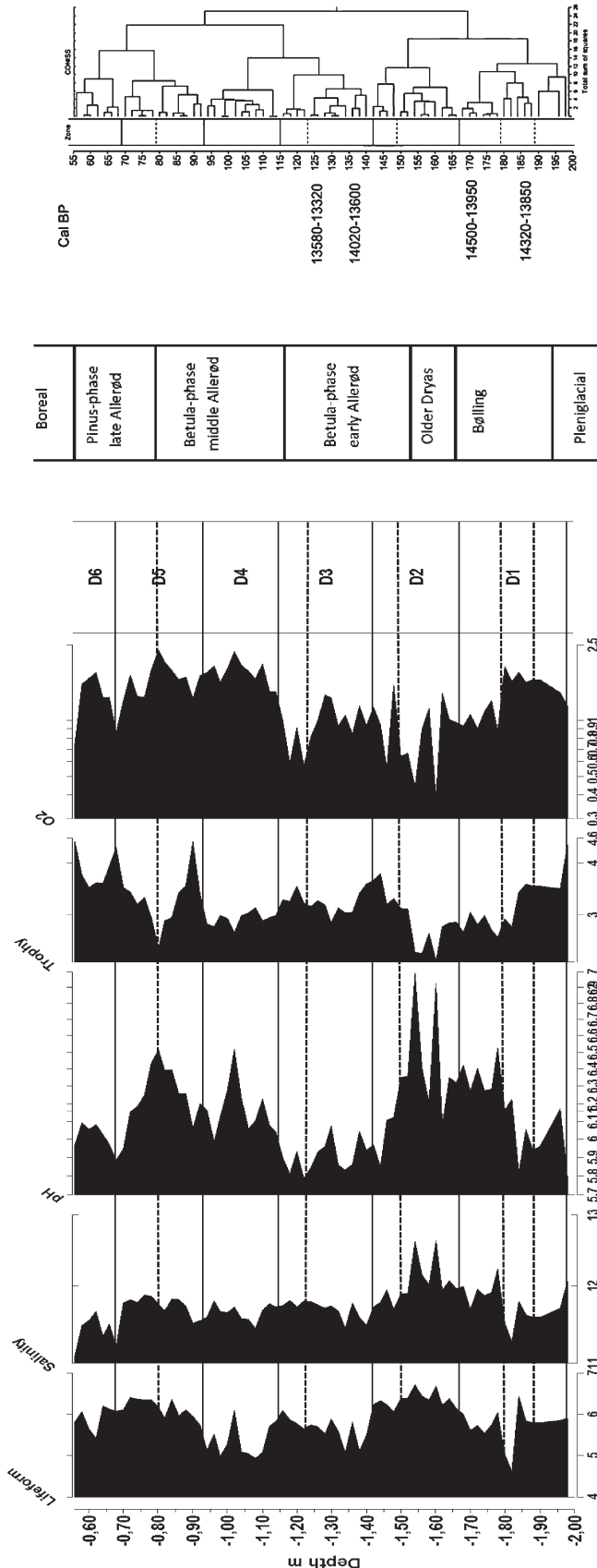### 5.1. Ecological characterization of the diatom zones

Diatom zone D1: the values of the ecological variables (Fig. 6) indicate high oxygen levels in a mesotrophic environment, especially in the early part of D1. Species are predominantly benthic and tychoplanktonic (*Staurosira* and *Staurosirella*). Tychoplanktonic species are free-living or attached benthic organisms, that are carried into the plankton through a disturbance of their benthic habitat, or by winds and currents. This can occur by direct turbulence or by disruption of the substrate and subsequent entrainment in the water column. Tychoplankton are, therefore, a primary subdivision for sorting planktonic diatoms by duration of lifecycle spent in the plankton, as neither their entire lives nor particular reproductive portions are confined to planktonic existence. The small benthic and tychoplanktonic taxa are known to be competitive in shallow, mesotrophic, alkalic and cold environments with possible periods of ice-cover (Pienitz & Smol, 1993; Lotter & Bigler, 2000). This fits with the Bølling age deduced from the pollen biozonation and radiocarbon dates (Fig. 4).

Diatom zone D2: the ecological variables indicate a clear change in salinity starting at the end of D1 and continuing throughout D2. At the same time, oxygen levels decrease, the water becomes more eutrophic and the lifeform becomes epontic (taxa that normally live firmly attached to any kind of substratum [macrophytes, rocks, sand grains...]). The higher salinity is indicated by an increase of the BF-FB species like *Mastogloia lacustris* (salinity according to van Dam *et al.* (1994) of Cl 1000-5000 mg dm^{-3}, 1.8-9 ‰). Biozone D2 is dominated by brackish fresh-brackish taxa (particularly *Mastogloia lacustris*).

In closed basins like the Moervaart, an evolution towards a lower precipitation surplus or even a deficit causes salinization to occur in carbonate-rich waters. The leaching of the still calcareous coversands in the Moervaart area produced these carbonate-rich waters, which is also indicated by the higher values for the ecological variable pH (Fig. 6) when salinity is high. The shallowness and the shape (shoreline length) of the lake will cause its volume and extension to respond strongly to changes in the precipitation-evaporation regime, which is supported by fairly strong pH-fluctuations starting in D1 and continuing over D2. The same phenomenon was also observed in inland lakes in the Netherlands (Hoek & Bohncke, 2002; Bohncke *et al.*, 1988). A decreasing precipitation surplus will have caused increased salinity by increased salt concentration and decreased lake vol-

ume with associated shore line changes. In Switzerland this mechanism was identified as well. Several studies (Straub, 1993; Gasse *et al.*, 1997; Roberts *et al.*, 2006) therefore used salinity and electrical conductivity as proxies for climate change. In summary, the increase in salinity indicated by *Mastogloia lacustris* likely corresponds to a shallower lake (or swamp) during D2 caused by drying (see also Cumming *et al.*, 1995; Laird *et al.*, 1998; Pienitz *et al.*, 2000). This might be caused by a cooling event, as indicated by the presence in D2 of the cold-resistant species *Cymbella affinis*. This corresponds perfectly with the Older Dryas attribution of the lower part of D2. As a consequence of a shallower lake, the turbidity will have increased (Nõges *et al.*, 1999). At the onset of the Allerød (top part of D2) the abrupt decrease of *Mastogloia lacustris* likely indicates the onset of a water level rise.

Diatom zone D3: relative to D2, this zone is characterized by a lower salinity, a tychoplanktonic lifeform and more bentic species, a fairly constant but more mesotrophic regime and a higher but varying oxygen status (Fig. 6). D3 shows a strong likeliness to D1, except for the almost entire absence of *Mastogloia lacustris*. However, the species richness and the number of individuals is higher compared to D1 (Fig. 5). This is mainly caused by tychoplanktonic species and probably relates to increasing habitat diversity in the lake. A shallow lake under the warming climate of the early Allerød will have increased colonization of shoreline plants. According to the available pollen evidence (Bos *et al.*, submitted) these plants strongly increased at the onset of D3, pro-

Fig. 6 - Result values for environmental variables. Depths (left) are in m relative to surface. Scales of lifeform, salinity, trophic level, oxygen demand variables.
Lifeform: 4 = tychplanktonic, benthic origin; 5 = tychoplanktonic, both epontic and benthic origin; 6 = epontic; 7 = epontic and benthic.
Salinity: 14 = BF to FB (Cl 500-1000 mg/L); 13 = FB (Cl<500 mg/L); 12 = FB-F (Cl 100-500 mg/L); 11 = Cl<100 mg/L).
pH: pH 5, *acidobiontic*; pH 6, *acidophilous*; pH 7, *circumneutral*.
Trophic level: 2 = eutrophic (P 35-200 µg/L); 3 = eutrophic to mesotrophic; 4 = mesotrophic (P 10-35 µg/L).
Oxygen demand: 1 = irrelevant; 2 = high (above 75 % saturation).

viding habitats for epiphytic diatom taxa and possibly increasing the relative abundance of acidophillic diatoms. The strong decrease in salinity and the strong increase of tychoplanktonic species (like *Staurosira*, *Pseudostaurosira* and *Staurosirella*) at the beginning of D3 indicate a clearly increasing lake depth during that period. *Staurosira* taxa are fast-growing highly adaptable species associated to disturbances or strongly varying environments (Denys *et al.*, 1990), and are often dominating lake environments in the early Holocene and late-glacial (Pienitz *et al.*, 1991; Lotter *et al.*, 1997; Seppä & Weckström, 1999; Bigler *et al.*, 2002; Solovieva & Jones, 2002; Rosén *et al.*, 2004). Another abundant (143-110 cm) opportunistic species is Cocconeis placentula, whose abundance is likely due to biotic interactions (Veres *et al.*, 1995) such as its preference for substrates rich in macrophytes. The presence of *Cocconeis placentula* is connected with the presence of macrophytes, probably *Nymphea* and *Nuphar*. Leaves of these plants probably supported diverse epiphytic diatoms, which are usually very abundant during the plant growing seasons. *C. placentula* is found throughout the year, however, it is most abundant in summer when it can form one of the most abundant individuals present in an epilithic sample. Furthermore, it is tolerant to moderate, but not severe organic pollution.

In the top of D3 a temporal decrease in the tychoplanktonic species *Staurosira*, *Pseudostaurosira* and *Staurosirella* is clearly observable. This might indicate a temporal lowering of the lake level at the transition from the early to the middle Allerød, as shown also by other proxies (Bos *et al.*, submitted).

Diatom zone D4: during D4, lake deposits change from humic, calcareous gyttja (Layer J) into clayey, calcareous gyttja (Layer K). This change in lithology is also reflected in a decrease in the organic matter values. The disappearance of the diatom *Cocconeis placentula* is probably connected with a decrease of these macrophytes.

Diatom zone D5: relative to zone D4, changes in trophic level and salinity are minor. The oxygen levels gradually decrease towards the end of D5. Both the number of individuals and species initially increase but this is temporal (Fig. 5). *C. placentula* gradually disappears. This phase is mainly characterized by an increase of cold resistant species like *Cymbella*, which continues into D6. This lets us presume that D5 corresponds to a colder stage at the transition between the middle and late Allerød, probably before the expansion of *Pinus*. This is also corroborated by the abundance of *Ulnaria* species at the transition from D5 to D6. *Ulnaria* species need a high Si value and a low P value (van Dam, 1994). Such species match with the cyclic bloom in the lake. *Ulnaria* growth (bloom) peaks under the ice. An increase of the oligotrophication at the end of this zone, is deduced from the increased waterplants from a shallow eutrophic and carbon rich water, also plants that live with a low P value. This is also the reason for the high abundance of the *Ulnaria* taxa in this layer. When the ice has disappeared, nutrients like Phosphor and Silica, released during winter, are used during the short productivity pulse of the planktonic algae. In absence of radiocarbon dates it remains unclear whether this colder event can be correlated with the Intra Allerød Cold Period or GI-1b (Donnelly *et al.*, 2005), as reflected in the oxygen isotope record of the Greenland ice-cores (GI 1b; Blockley *et al.*, 2012).

Synchronic with this increase of cold species, the reappearance of *Mastogloia lacustris* and the strong reduction of tychoplanktonic species *Staurosira*, *Pseudostaurosira* and *Staurosirella* at the onset of D5 suggest a decrease in water level. The increase of *Cymbella affinis* also indicates a more shallower lake.

Diatom zone D6: in zone D6 *Epithemia goeppertiana*, a more aquatic species, appears abruptly. At the same level there is a sharp peak in *Staurosira venter*. Together these might indicate a short but weak increase of the lake level during the *Pinus* stage of the Allerød. This is also suggested by the pollen evidence, which indicates a temporary re-occurrence

of aquatics, such as *Potamogeton natans*, *Nymphaea*, *Nuphar* and *Characeae* (Bos *et al.*, submitted).

Near the end of D6, species richness decreases and above 56 cm no more diatoms were found. This indicates that water levels went down and the lake probably disappeared altogether or became a swamp.

5.2. Lake evolution in relation to the human occupation

Earlier archaeological studies (Crombé & Verbruggen, 2002; Crombé *et al.*, 2011) have pointed out a much denser site distribution during the late-glacial around the Moervaart palaeolake compared to other areas within Sandy Flanders. This is most apparent for the Allerød, when the northern border of the Moervaart palaeolake was intensively occupied by hunter-gatherers belonging to the *Federmesser* Culture (Fig. 1d). The Moervaart landscape with its dry soils adjacent to one of the largest lakes in Sandy Flanders must have offered a great diversity and density of resources, such as game, waterplants and drinking water. The diatom proxy data show that certainly from the early Allerød (end of D2) onwards the Moervaart depression evolved into a shallow lake until at least the middle Allerød (D4), with a possible temporal lowering at the transition from early to middle Allerød. Afterwards (D5-D6) the lake level fluctuated probably in response to changing climate but most likely never reached the same level as before. It finally disappeared permanently towards the end of the Allerød or the start of the Younger Dryas. The scarcity of archaeological evidence related to the Younger Dryas (Crombé & Robinson, in press) indicates that the area was much less attractive for hunter-gatherers probably due to a lack of open water and the prevailing cold conditions. It is not until the start of the Boreal that man returned to the former Moervaart lake area, now settling along the dry banks of a meandering river called the Kale/Durme (Crombé *et al.*, 2011).

The lack of human activity prior to the Allerød probably results from the too shallow character of the lake during the Bølling (D1) and the Older Dryas (D2). During the latter a drop of temperature and a lowering of the water level occurred albeit not leading to a total desiccation of the lake.

6. Conclusions

The diatom stratigraphy of the palaeolake Moervaart shows a clear shift in diatom composition during the late-glacial. The differences in relative abundance of specific taxa show a variation in climatological conditions during this period. The different zones show a complex composition due to changing environmental factors. It seems that the diatom assemblages were most strongly regulated by physical factors, such as the influence of high rates of minerogenic erosion and abundant supply of epontic habitats and corresponding low light availability.

The changes in life-form (benthic vs tychoplanktonic diatoms) likely reflect changes in water depth. Lake water transparency and species diversity increases with the occurrence of macrophytes. In the diatom assemblage, one can clearly see a connection between the eutrophy, lifeforms, acidity and saprobity in zones with no or few macrophytes. Zones with predominantly benthic species are more turbid and more eutrophic and this in more extreme environmental conditions. The acidity points to a fluctuating level as well (especially in zone D2). Inland lakes often have lots of archaeological remains. Results of the investigation help to resolve some of the uncertainties about the water level and climatic circumstances of the Moervaart depression. The prehistoric development can be explained by the changing environment shown in the different bio zones. The intense

exploitation of the area by hunter-gatherers of the *Federmesser* Culture clearly coincides with a high water level of the Moervaart lake during the Allerød, making the area highly attractive for both animals and humans. The absence of deep open water before and after the Allerød most likely hindered prehistoric man to settle along the Moervaart depression. The patterns of limnological and environmental change reconstructed from fossil diatoms demonstrate the important links between aquatic and terrestrial environments.

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Abstract

Although climate fluctuations during the late-glacial are well-known for northwestern Europe, better knowledge of past lake ecosystem responses to natural climate variability is prerequisite to assess more comprehensively direct and indirect linkages between climate change and lake water properties (e.g., primary production, nutrient cycling and water-column pH). These insights are also important for understanding the climate forcing processes at the spatial and temporal resolution required to determine the role of environmental factors in past human adaptation. Here, we analyse fossil diatom assemblages recorded in a sediment sequence of a late-glacial palaeolake in the Moervaart area (northwestern Belgium) to reconstruct distinct climate-driven changes in lake productivity and water-level fluctuations and to evaluate the effects of these changes on the lake's ecosystem services for local hunter-gatherer communities. The diatom analysis from the Moervaart palaeolake shows sensitive climate-related paleolimnological responses, and most of all the species shifts are caused by changes in temperature and water level fluctuation. Starting as a large swamp during the Bølling, the Moervaart depression gradually evolved into a shallow lake which reached its highest level in the early and start of middle Allerød. These conditions were favorable for settling by groups of migrating hunter-gatherers belonging to the *Federmesser* Culture.

Keywords: Biozonation, Ecological characterization, Hunter-gatherers, Late-glacial, Diatoms.

Samenvatting

In deze paper worden de resultaten van een gedetailleerde analyse van diatomeeën uit wellicht het grootste laatglaciale paleomeer in Vlaanderen, de Moervaart (ca. 25 km²), besproken. In totaal werden 80 stalen afkomstig van een ca. 2 m lange sequentie bestudeerd. De resultaten wijzen op een fluctuerende waterpeil doorheen het grootste deel van het Laat-Glaciaal veroorzaakt door verschillende klimaatveranderingen. Tijdens het Bølling was wellicht nog geen sprake van open water, maar veeleer van een drassige depressie. Na een kort interval van grondwaterverlaging tijdens de Oude Dryas, evolueerde de Moervaart tot een uitgestrekt maar ondiep meer, dat zijn hoogste peil bereikte tijdens het vroege en midden-Allerød. Dit is wellicht ook de periode waarin mens en dier zich aangetrokken voelden tot de Moervaart. Tientallen *Federmesser* sites bevinden zich geclusterd langsheen de noordelijke rand van dit immense meer. In de tweede helft van het Allerød daalde het waterpeil, mogelijk onder invloed van een korte afkoeling, de *Intra Allerød Cold Period* of GI-1b. Aan het einde van het Allerød of het begin van de Jonge Dryas droogde de Moervaart depressie uiteindelijk volledig uit en kende de menselijke bewoning een forse terugval.

Trefwoorden: Laat-Glaciaal, diatomeeën, jagers-verzamelaars, *Federmesser* cultuur, paleomeer, klimaatverandering.

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