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Effects of spatial heterogeneity on the estimation of diatom assemblage composition: an example of Lake Imbradas (NE Lithuania)

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Abstract. High spatial resolution diatom and loss-on-ignition analyses were carried out on the surface sediments of a shallow, medium-sized lake in north-eastern Lithuania to examine the degree of spatial heterogeneity of diatom assemblages in the lake, as well as the influence of water depth on diatom compositions. The compositional properties of sediments and diatom assemblages show a strong relationship with water depth; some less prominent changes were attributed to the tributary catchment. Diatom assemblage compositions are rather homogenous throughout the lake (Morisita-Horn similarity indices make >0.9 in most locations of the lake, in relation to others), especially in its deeper parts. Our case shows that the most representative point does not lie in the centre of the lake, as it is assumed in most of fossil studies. Studies of spatial heterogeneity of modern diatoms can facilitate site selection and fossil diatom data interpretation.

Keywords*: modern diatoms; lake sediments; Principal Component Analysis; spatial analysis*

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INTRODUCTION

Diatoms are important indicators of lacustrine environmental parameters due to their abundance in palaeorecords, taxonomic richness, sensitivity to a range of ecological variables, as well as good preservation of their frustules in sediments. Thus, diatom analysis is one of the most efficient tools for the reconstruction of the palaeoenvironmental conditions of a water basin (Smol, Stoermer 2010). Unlike fossil diatom studies, modern diatom studies can leverage plenty of environmental information that is usually available for comparison with the diatom analysis results (e.g., Kato *et al.* 2003; Poulíčková *et al.* 2004; Pan *et al.* 2006; Reed *et al.* 2012; Liu *et al.* 2015; Wang *et al.* 2018). This enables a much better understanding of the relationship between diatom assemblages and environmental parameters that can be later used for the interpretation of fossil diatom records, as well as quantitative palaeoenvironmental reconstructions (Birks 1998, 2010). However, due to the scarcity of studies of modern diatom distributions (Lotter, Bigler 2000; Kienel, Kumke 2002; Adler, Hübener 2007; Biskaborn *et al.* 2019) in different water bodies, the knowledge of quantitative relationships between diatom records and various environmental variables is not universal. More studies are necessary from lakes of different shapes and sizes, as well as a range of climatic and environmental settings (Birks 2010; Soininen, Teittinen 2019).

Lakes with simple shapes and bottom morphologies, and without significant inflows, present a more effective source of general information on ecological factors, influencing the spatial heterogeneity of diatom assemblages. Large, deep lakes usually are complex sedimentation systems, having diatom assemblages affected by a large number of factors (e.g., large, complex catchment area, inflow from tributaries, hydrodynamic activity, water stratification, complex bottom morphology, and diverse sediment types) that are often difficult to evaluate and quantify (Davydova *et al.* 1999; Cocquyt, Scharm 2000; Moss *et al.* 2005; Pla *et al.* 2005; Kireta *et al.* 2007; Kingsbury *et al.* 2012; Wang *et al.* 2015; Pla-Rabés, Catalan 2018). In relatively small, shallow, sub-circular lakes, having saucer-shaped bottoms and insignificant inflow, the effect of the above-mentioned factors is usually minimized. Therefore, such lakes are more sensitive to local natural, as well as anthropogenic environmental changes and these changes can be better represented in diatom assemblages of the bottom sediments. Shallow lakes are usually rich in macrophytes, which provide a specific habitat for a large variety of diatom species, thus allowing diverse diatom assemblages from different habitats (both planktonic and benthic) to accumulate in sediments. Diatom species in sediments provide information on the environment of different parts of the lake ranging from pelagic to shallow littoral zones. However, diatom assemblages accumulated in the bottom sediments can be influenced by various environmental factors characteristic of a shallow lake – re-suspension, erosion, biological and chemical activity (Bennion *et al.* 2010; Liu *et al.* 2012), which should be considered when interpreting diatom data.

The aim of this study is to provide a detailed examination of the diatom species' spatial distribution in the surface layer of organic bottom sediments in a shallow, medium-sized lake with the surroundings of weak human impact. These data should provide means to evaluate the influence of natural processes on the spatial distribution of diatoms in the bottom sediments of a shallow lake that can later be used for the interpretation of fossil diatom data.

STUDY AREA

Lake Imbradas (Fig. 1A) is situated in the Baltic highlands, in north-eastern Lithuania (N 55°46'00'', E 26°7'20'', elevation 154.35 a.s.l.), in a depression formed by the glacial advances of the last (Weichselian) glaciation (Guobytė, Satkūnas 2011). The surface sediments around the lake are dominated by glaciofluvial sand from the northern and eastern sides, and Holocene peat from the southern and western sides. The lake is 1.4 km long, almost 0.7 km wide, with an average depth of 2.6 m, and maximum depth of 4.3 m. The lake occupies a 0.6 km^2 area, and the shoreline length is ca. 4 km. Lake Imbradas is surrounded by a hilly landscape covered by forests. The average wind speed of 2.5–3.0 m/s is observed in January, and of 2.0–2.5 m/s in July (LHMT 2021); indeed, this part of Lithuania is characterised by mild winds. The prevailing direction of the wind is westerly (LHMT 2021). The largest tributary (75 l/s, as measured during fieldwork in May 2019) inflows from the north-east, while the tributary inflowing from the north-west brings only 1l/s of water to the lake.

The surroundings of the studied lake are dominated by pastures and meadows, with limited patches of arable land. The territory between Imbradas and Avilys lakes (south-west from Lake Imbradas) is a fen, overgrown with birch and alder trees. A smaller woodland with a similar vegetation composition is situated on the eastern shore of the lake. The south-eastern and north-western parts of the lake contain abundant aquatic vegetation and are slightly overgrown with peat. The Imbradas village, with a population of 224 (Population and Housing Census 2011) is situated ca. 500 m from the north-western shore of the lake. The extent of human economic activity in the area is low. No large farms, industrial facilities, or other significant sources of pollution are located in the watershed of Lake Imbradas.

MATERIALS AND METHODS

Fieldwork

The sampling sites (Fig. 1B) were arranged in a 110 × 110 m rectangular grid pattern to uniformly cover the entire lake area. The surface sediment samples were collected for loss-on-ignition analysis from a boat using *Kajak Model B* sediment sampler in September 2017. The top 10 cm of the lake bottom sediments were collected for loss-on-ignition analysis. The exact timespan, represented by the surface samples is unknown, as ^{210}Pb or ^{137}Cs dating for estimating their absolute ages has not been carried out. However, sedimentation rates of 0.5–1.2 mm per year have been reported from eastern Lithuania (Mažeika, Taminskas 2005; Šeirienė *et al.* 2009). Therefore, 10 cm samples can represent roughly 80–200 years. The surface sediment samples were collected for diatom analysis from the same sampling locations as those collected for loss-on-ignition analysis in March 2018. The top 2 cm of bottom sediments that could accordingly be considered to represent the last 15–40 years (Mažeika, Taminskas 2005; Šeirienė *et al.* 2009) were sampled for diatom analysis. Some sediment samples could not be obtained due to the dense vegetation on the lake bottom: samples 2, 30, 38, 45, and 48 from the 2017 fieldwork, as well as samples 3, 4, 18, and 45 from the 2018 fieldwork.

Loss-on-ignition

The loss-on-ignition methodology followed Heiri *et al.* (2001). A total of 44 fresh samples were air-dried for three days prior to furnace drying, then dried in the furnace for 48 hours at a temperature of 105°C to estimate water loss from the samples. The dry sample weight (D_{105}) was calculated by excluding water loss from the primary sample weight. The dry samples were heated in a muffle furnace at 550°C for four hours to eliminate organic components from the sediment and estimate the remaining sample weight (D_{550}). During the last stage, samples were burned at 900°C for two hours to eliminate carbonate matter and estimate the weight of the minerogenic components.

Diatom analysis

Diatoms were analysed in 45 surface sediment samples. The collected samples consisted of very soft organic mud. Small amounts of mollusk shell detritus and remnants of macrophytes were present in some samples from the littoral zone. In the laboratory, sediments were removed from plastic bags (using distilled water for the cleaning of bags) for diatom analysis. Ten ml of the watery suspension of each sediment sample was prepared following the techniques described by Battarbee (1986). At first, the sediments were processed with 10% of HCl to remove carbonates. After rinsing with distilled water (six times) the sediments were treated with 30% hydrogen peroxide (gently heating) to oxidise organic matter. After reaction, the sediments were rinsed with distilled water once again. The amount of residual sediments was very small (heavy liquid was not used because of the small content of minerogenic matter). The slides for microscopic analysis were made using the mounting medium *Naphrax* (refractive index 1.73). Diatom species were identified using a light microscope '*Nikon Eclipse 200*', at ×1,000 magnification. Diatom valves were counted in the main (central) part of the slide. Different numbers of valves were identified in samples (from 370 to 1,330) due to the differences in relative diatom abundance.

Diatoms were identified to the species level using primarily European (Krammer, Lange-Bertalot 1986, 1988, 1991a, b) and North American (Diatoms of North America 2021) sources. Diatom species names were verified and updated according to the *AlgaeBase* database taxonomic nomenclature (Guiry, Guiry 2020).

The *TILIA* software (Grimm 2011) was used to present diatom data. Taxa that constituted at least 2% of the relative abundance in samples were presented in the diatom diagram. Species percentages (relative abundance) were calculated from the total sum of all counted valves in the sample. It should be noted that the percentage data that we used in all our calculations were not sensitive to absolute abundances, and therefore, variations in the sample size of the diatom valve counts were highly unlikely to impact the quality of the results. Constrained cluster analysis (CONISS; Grimm 1987) results are also presented in the diatom diagram.

Diatom habitats are usually related to different depth zones in the lake. The species were classified according to habitats into planktonic and benthic (including the unattached as well as attached to various surfaces in the lake) to highlight the relationship between the lake depth and diatom assemblages in surface sediments. The diatom checklists of Denys (1991), van Dam *et al.* (1994), Barinova *et al.* (2006), and the internet source for diatom identification and ecology "Diatoms of North America" (Diatoms of North America 2021) were mainly consulted for the information on diatom species habitat requirements.

Data analysis and visualization

To quantify the significance of lake tributaries, hydrological modelling was carried out using *ArcHydro* software (Jenson, Dominique 1988) based on the 10 m digital elevation model (DEM) provided by the National Land Service of Lithuania. A stream network in the area was constructed, stream segments were ranked, and catchment areas of tributaries were delineated as a result (Fig. 1C). A 2,000 m^2 drainage area threshold was used to define a stream.

The similarity of diatom assemblages was compared using Morisita-Horn taxonomic overlap index (Morisita 1959) modified by Horn (1966). Morisita-Horn is a classical index of taxonomic overlap, which compares two communities in compositional space (Horn 1966). In this manner it is a measure which is non-sensitive to the absolute sample sizes, unlike classical Euclidean distance, for example, which measures the divergence between samples as measured by absolute abundances (therefore it needs additional transformations before the analysis). An increase in sample size will only increase the precision of the measured proportions, and a lower sample size would not cause any directional bias or decrease in accuracy of between-sample comparisons. This index scales between zero (no similarity between compared pair of assemblages) and one (assemblages are identical). The average values of Morisita-Horn index were calculated between each location and its neighbouring locations in order to evaluate the heterogeneity of diatom assemblages. Neighbourhoods of 150 m (covering four nearest neighbouring locations) and 200 m (covering eight nearest neighbouring locations) were used as two alternative approaches.

Principal Component Analysis (PCA) was carried out using the *ggbiplot* package in the *R* software to reveal the main factors influencing diatom assemblages. All diatom species with maximum values of at least 2%, as well as amounts of carbonate, organic, and minerogenic matter contents were included. To stabilise the variance between diatom and LOI data, an arcsine transformation (Warton, Hui 2011) was applied to the proportion data prior to PCA analysis.

All estimates acquired by diatom and loss-on-ignition analyses, as well as further calculations are expressed as interpolated maps. Raster surfaces, comprising these maps, were interpolated using the Inverse Distance Weighted algorithm (Watson, Philip 1985), in the ArcGIS Spatial Analyst software (power = 3, number of points = 8).

RESULTS

Hydrological modelling

The lake catchment area, calculated using hydrological modelling, occupies approximately 14.3 km^2 (Fig. 1C). More than half of this area (8.8 km^2) is oc-

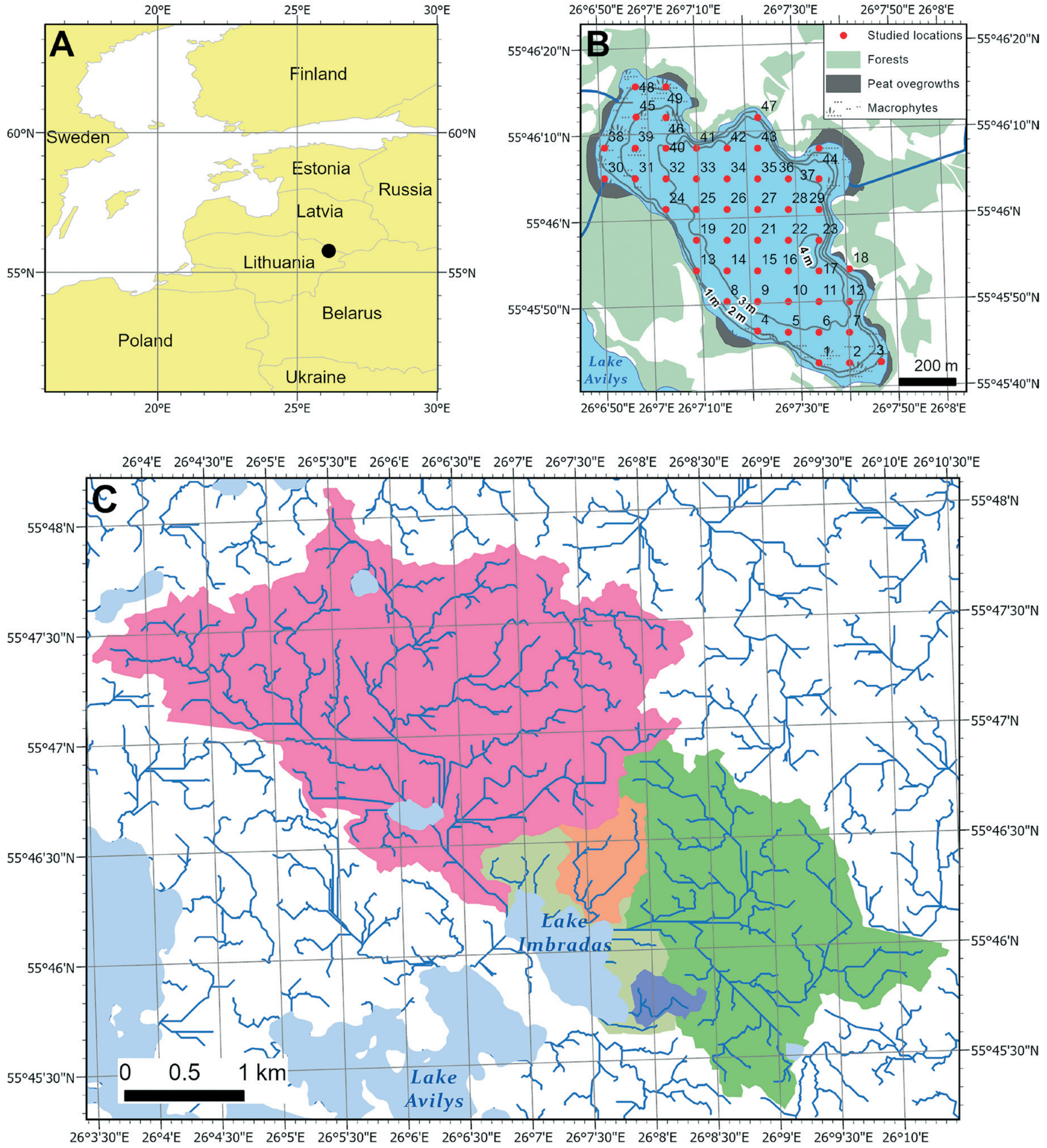

Fig. 1 Locations of Lake Imbradas (A), sampling points (B), modelled stream network and catchment areas of Lake Imbradas tributaries (C)

cupied by the catchment of the tributary flowing into the lake from the north-west. Discharge from this tributary, according to measurements made in May 2019, is only 5 l/s. Significantly greater discharge (75 l/s) is generated by the tributary flowing in from the east, despite its smaller catchment area (4.2 km^2), probably due to the higher gradients in this area, as well as the higher degree of flow concentration.

Loss-on-ignition analysis

Loss-on-ignition analyses revealed that organic sediments are dominant in the central (relatively deep) part of the lake, where they comprise 50–64% of the total sample mass (Fig. 2A). Carbonate material (predominantly mollusk shell detritus) is the most significant (20–45%) at <2 m depths, though the amounts of it rapidly decrease towards the lake centre at the locations of the highest slopes (Fig. 2B). The amount of the minerogenic matter makes up 23–38% in the middle part of the lake (Fig. 2C). Although more minerogenic matter would be expected around the lake shore, due to the extremely high carbonate contents in this area, the percentages of minerogenic matter are often even lower here than in the central part of the lake. In some single samples (especially 46, 47, 7), however, minerogenic components prevail.

Diatom analysis

A total of 82 diatom species (including varieties) were identified during the study, 18 of which exceeded 2% in at least one sample (these species are presented in the diatom diagram in Fig. 3). According to CONISS analysis, the most significant change between the shallow and deep diatom assemblages occurs at water depth between 2.49 and 2.8 m.

Variations in the proportion of planktonic/benthic diatoms detected in surface-sediments typically reflect different depth zones in the lake. Diatom analysis of the Lake Imbradas sediments revealed that the planktonic group comprises 30% to 78% of the total diatom valves and is represented mainly by *Aulacoseira ambigua* (Grunow) Simonsen and *Aulacoseira granulata* (Ehrenberg) Simonsen. The former is the most abundant planktonic taxa; it was identified in every sample with percentages between 22% and 67%. Significantly lower percentages (0.1–4%) of the planktonic group are characteristic of *Lindavia radiosa* (Grunow) De Toni & Forti and *Cyclotella distinguenda* Hustedt. Planktonic species are not distributed uniformly in the deepest part of the lacustrine bottom sediments. The most abundant planktonic group (mainly *Aulacoseira ambigua* and *Aulacoseira granulata)* comprises >50% of the total sum mostly in sediments accumulated at depths >3 m. Less numerous planktonic *Cyclotella distinguenda* and *Lindavia radiosa* were found mainly at depths <2.46 m. Generally, planktonic taxa were extremely abundant (70–78%) at locations 8, 40, 10, 17, 27, 28, 40, which were sampled at depths >3 m and are laid out along the central part of the lake. An exception was sample 8, which was collected from a depth of 2.49 m, near the south-western shore of the lake. Planktonic taxa are abundant in some limited shallow (depth 2–2.5 m) areas (sites 1, 2, 31, 39) along the southern and north-western shores, though benthic species are rather numerous here as well.

The percentages of benthic diatoms vary between 22% and 70% of the total diatom valve sum. This group is mostly represented by *Staurosira construens* Ehrenberg, *Navicula oblonga* (Kützing) Kützing, *Epithemia adnata* (Kützing) Brébisson, *Eunotia arcus* Ehrenberg, *Gyrosigma attenuatum* (Kützing) Rabenhorst, *Gomphonema pumilum* (Grunow) E.Reichardt & Lange-Bertalot, and *Staurosirella martyi* (Hériboud) E.A.Morales & K.M.Manoylov. The most abundant and common species is *Staurosira construens*. It was found in all samples and its percentages varied in a range of 10–41%. The benthic group predominates (>50% of the total sum) mostly at depths <2 m in the northern and eastern parts of the lake (samples 30,

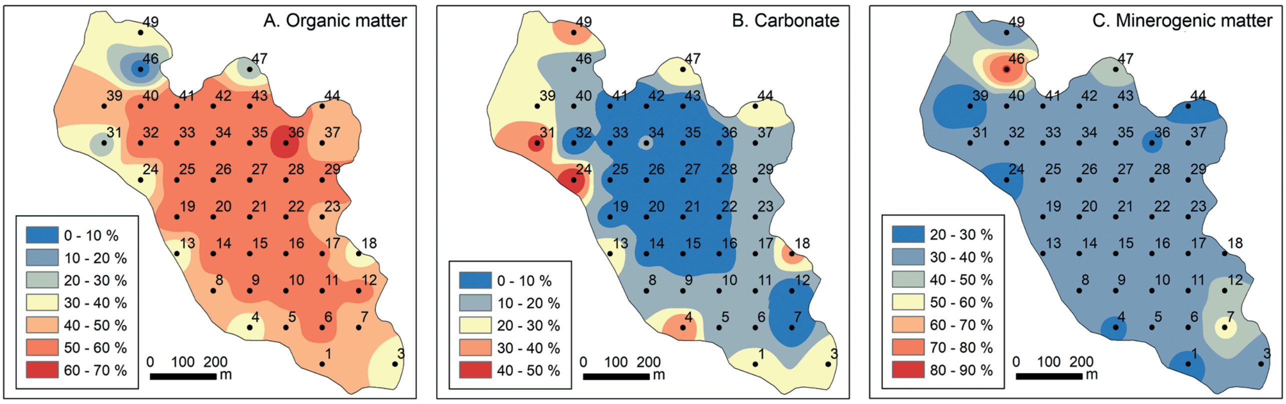

Fig. 2 Results of the loss-on-ignition analysis: organic matter (A), carbonate (B) and minerogenic matter (C) content in the surface sediments of Lake Imbradas

44, 49, 48, 38, 13). However, it can be noticed that benthic taxa occasionally exceeded 50% at depths of 2.8–3 m (samples 7, 12, 41, 32). Increased percentages of benthic species were found in a few samples of the deep-water (>3 m) area of the lake (samples 14, 15, 23). The above-mentioned sampling locations are scattered throughout the eastern and western parts of the lake.

Diatom assemblage similarity

The average Morisita-Horn indices (Fig. 4) show significant similarity between samples in the central part of the lake (up to 0.983 for 200 m neighbourhood, and 0.991 for the 150 m neighbourhood). Smaller clusters of similar diatom assemblages are situated in the north-western and south-eastern ends of the lake. Location 40 can be characterised by its increased contents of planktonic species, while location 32 contains larger amounts of benthic species. The causes of such differences are difficult to determine, as both locations are at a similar depth, and distance to the shore, as well as to the nearest tributaries. The locations 14 and 15, separating the southern cluster from the main body of similar assemblages have untypically low contents of planktonic taxa (and a higher proportion of the benthic group) for depths ca. 3.5 m, at which they are both situated.

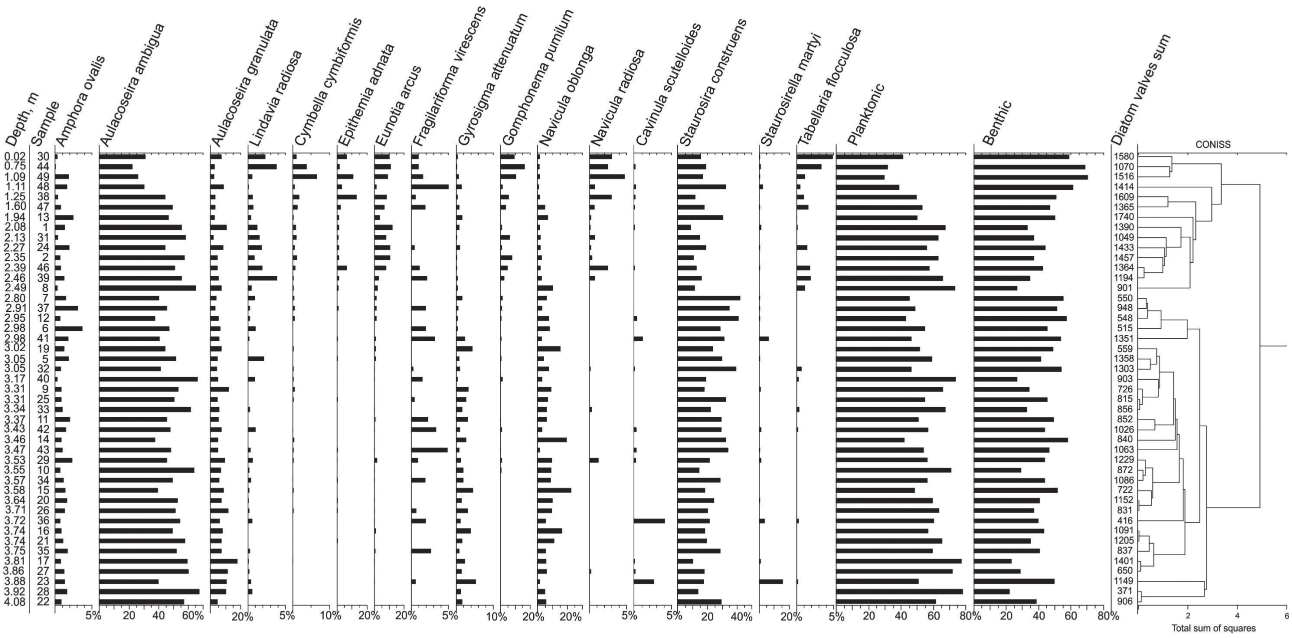

Fig. 3 Diatom diagram of the Imbradas lake bottom surface sediments

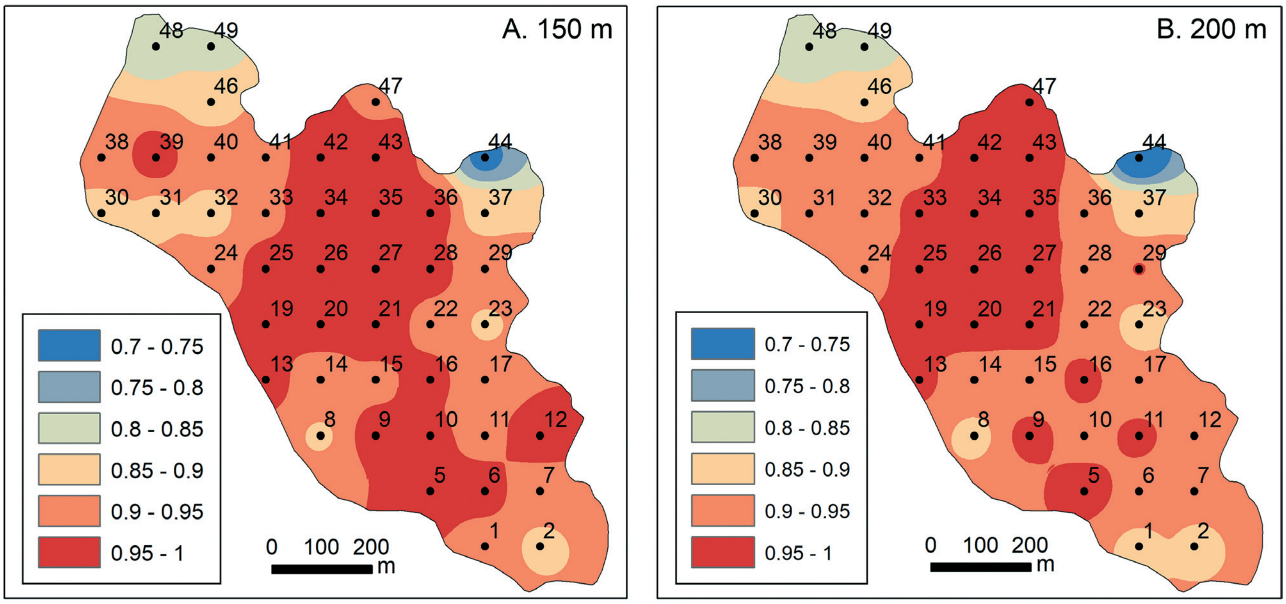

Fig. 4 Morisita-Horn overlap index averages within 150 m (A) and 200 m (B) neighbourhoods

The above-mentioned locations separating clusters of similar locations represent anomalous assemblages rather than transitions from one type of environment to another, since the above-mentioned clusters are similar not only to each other, but to the central part of the lake as well.

Principal component analysis (PCA)

PC1 explains 44.4% of the total variation in diatom composition (Fig. 5). The highest values of this component are characteristic of the species identified in shallow environments (*Gomphonema pumilum, Epithemia adnata, Eunotia arcus*) as well as carbonate matter, characteristic to the relatively shallow areas. On the negative side of this axis are benthic *Navicula oblonga,* and planktonic *Aulacoseira granulata* and *Aulacoseira ambigua*, as well as organic matter, characteristic of the central part of the lake. The occurrences of *Staurosira construens, Fragilariforma virescens* (Ralfs) D.M.Williams & Round*, Amphora ovalis* (Kützing) Kützing, and *Gyrosigma attenuatum* seem to be largely unrelated to depth. All these species, however, have high PC2 values, while *Aulacoseira granulata* and *Aulacoseira ambigua* have low PC2 values. 14.1% of the total variation is explained by PC2.

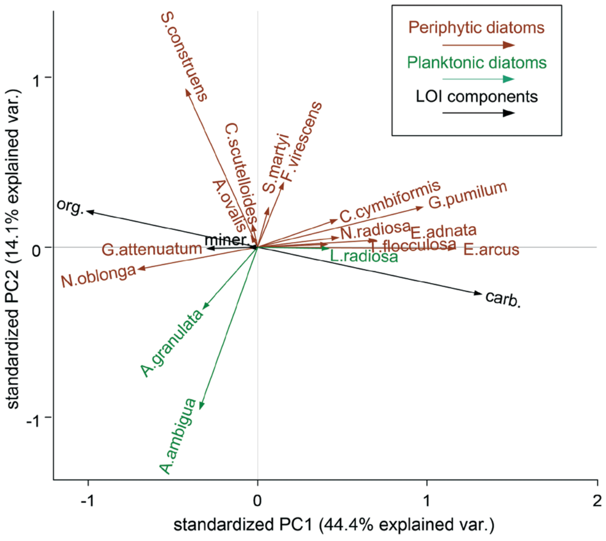

Fig. 5 Results of Principal Component Analysis (PCA)

Fig. 6 shows the loadings of PC1 and PC2. It is evident from the figure that PC1 can be rather confidently related to depth. The distribution of PC2 is not that straightforward. It is noticeable that the highest PC2 loadings are more characteristic of the north-eastern side of the lake, including the vicinities of the mouths of the main tributaries. However, PC2 is also high in some locations further from the tributary mouths (e.g., 14, 32, 41). Therefore, PC2 cannot be reliably related to any single factor. Indeed, it is possible that it is somewhat related to the proximity to the tributary mouths, although this is not a strong relationship.

DISCUSSION

Factors influencing differences in diatom assemblages

PCA shows that the main factor influencing the formation of diatom assemblages in the bottom sediments of Lake Imbradas is water depth. Almost half (44.4%) of the total variation is explained by PC1 (this component can be confidently related to depth), which is extremely significant, considering the complex nature of possible factors influencing changes in

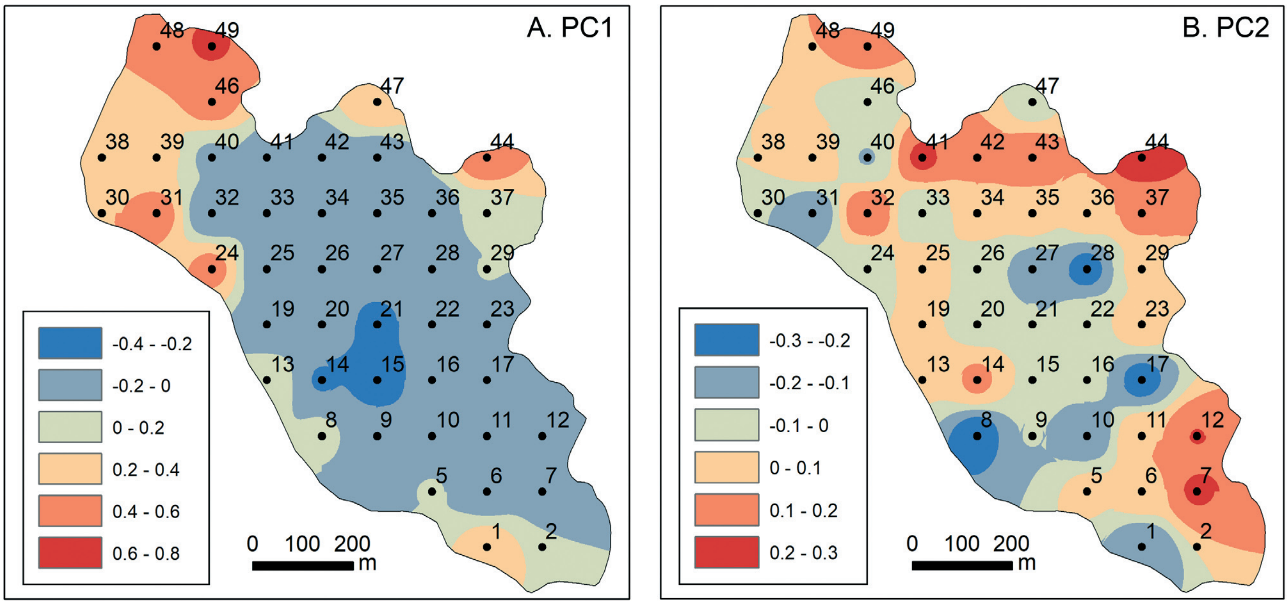

Fig. 6 Interpolated distribution of loadings of PC1 (A) and PC2 (B)

diatom assemblages. Although depth is often an important factor in determining the composition of diatoms in sediments (Moss *et al.* 2005; Adler, Hübener 2007; Punning, Puussepp 2007; Wang *et al.* 2012; Pla-Rabés, Catalan 2018), in Lake Imbradas this influence seems to be dominating. A more pronounced dominance of depth among the factors influencing diatom assemblages in Lake Imbradas, compared to many other lakes, could be caused by the low discharge from tributaries (considering the size of the lake) and flat-saucer bottom morphology that results in a relatively even trophic status and the availability of light throughout the lake. The most obvious impact of depth on the diatom assemblages is the dominance of planktonic species in the main part of the deep-water zone of the lake. They comprise 50–70% in most parts of the Lake Imbradas' bed (>3 m depth), though values drop significantly towards the lake shore (Fig. 7A). Predominant non-planktonic diatom species (*Fragilaria* spp., *Achnanthes* spp., *Amphora* spp., *Navicula* spp.) are usually characteristic of shallow areas of the lake (Moss *et al.* 2005; Punning, Puusepp 2007; Bennion *et al.* 2010). This is noticeable in Lake Imbradas as well. However, deep-water locations with increased percentages of benthic taxa, as well as shallow-water zones with lower percentages of benthic taxa indicate a possible influence of other factors, characteristic of shallow lacustrine environments, such as complex sediment accumulation processes, hydrological activity, and biological effects observed in different types of lakes (Davydova *et al.* 1999; Moss *et al.* 2005; Bennion *et al.* 2010). The role of these phenomena in Lake Imbradas is also confirmed by the distribution of planktonic *Aulacoseira ambigua* (Fig. 7B) and *Aulacoeseira granulata*. They predominate mostly in the deep-water central area of the Lake Imbradas bottom sediments but are also abundant in limited, relatively shallow areas, possibly due to water mixing caused by the wind and re-suspension of the bottom sediments. These two species have very similar ecological requirements and thrive in nutrient rich lakes where active water mixing, caused by strong winds, takes place (Wang *et al.* 2008; Puusepp, Punning 2011; Liu *et al.* 2012; Bicudo *et al.* 2016; Biskaborn *et al.* 2019).

The Lake Imbradas tributaries do not add significant amounts of discharge to the lake. Small drainage ditches inflow from the eastern and northern parts of the lake. An increased percentage (up to 16%) of *Gomphonema pumilum* is observed in these areas (Fig. 7C; locations 44, 46, and 49). This species is characterised as being tolerant to a wide range of trophic status environments (van Dam *et al.* 1994) and has been recorded in unpolluted streams (Wojtal 2003; Hafner *et al.* 2013; Biskaborn *et al.* 2019). Small amounts of this species in most sites indicate weak currents in the local littoral zones of the lake, as can be expected considering the low discharge rates of the tributaries. Similarly to *Gomphonema pumilum*, increased percentages of benthic *Eunotia arcus* are observed at the same locations as well (Fig. 7D). *Eunotia arcus* is known as a cosmopolitan taxa, occurring in slightly acidic to circumneutral water and can be found in wet places outside water bodies (Denys 1991; van Dam *et al.* 1994; Hafner *et al.* 2013; Biskaborn *et al.* 2019). Another acidophilous diatom species, occurring in moist places outside water bodies, is *Tabellaria flocculosa* (Roth) Kützing, which reaches up to 3% at the same locations (Fig. 7E). These two acidophilous taxa indicate slightly increased water acidity in the littoral zone close to tributary areas. This probably indicates the transport of organic matter from the surrounding wetlands, as the surroundings lack intensive economic and agricultural activities which could generate significant pollutants, increasing acidity. Relatively low abundances of the mentioned species also confirm the negligible influence of water flows from tributaries, which do not have a great impact on the redistribution of sediments in the areas of tributary mouths (Cocquyt, Scharm 2000). Therefore, if any water mixing or sediment redistribution took place in the lake, it must have been caused by the wind-initiated waves rather than inflowing currents.

Most of the predominant species belong to the eutrophic and meso-eutrophic groups (van Dam *et al.* 1994). In the deep-water area, planktonic eutrophic *Aulacoseira ambigua* and *Aulacoseira granulata* prevail, whereas meso-eutrophic epiphytic *Staurosira construens* (Fig. 7F) is the dominant species in the benthic group. Thus, according to the diatom data, Lake Imbradas can be considered a freshwater eutrophic/meso-eutrophic lake. Higher abundances of meso-eutrophic species near the shore might indicate the increasing amount of nutrients towards the shore of the lake, which might be related to the abundant macrophyte outgrowths in the littoral zone. On the other hand, such a distribution could be explained by habitat changes, as many of the meso-eutrophic species are associated with lower depths at the same time (van Dam *et al.* 1994). Periphytic Fragilaria (*sensu lato*) diatoms are sensitive to light conditions and usually thrive in shallow littoral zones of the lake (Lotter, Bigler 2000; Bennion *et al.* 2010).

According to earlier studies, shallow lakes are usually very sensitive to various sources of pollution (Janssen *et al.* 2014; Ferencz *et al.* 2018). In most cases eutrophic planktonic diatoms are dominant, while periphytic taxa, related to macrophytes, are reduced in polluted lakes (Bennion *et al.* 2010). However, Lake Imbradas is surrounded by forest in the east and in the west. Human economic activity is not significant near the lake; land use in the lake surroundings is

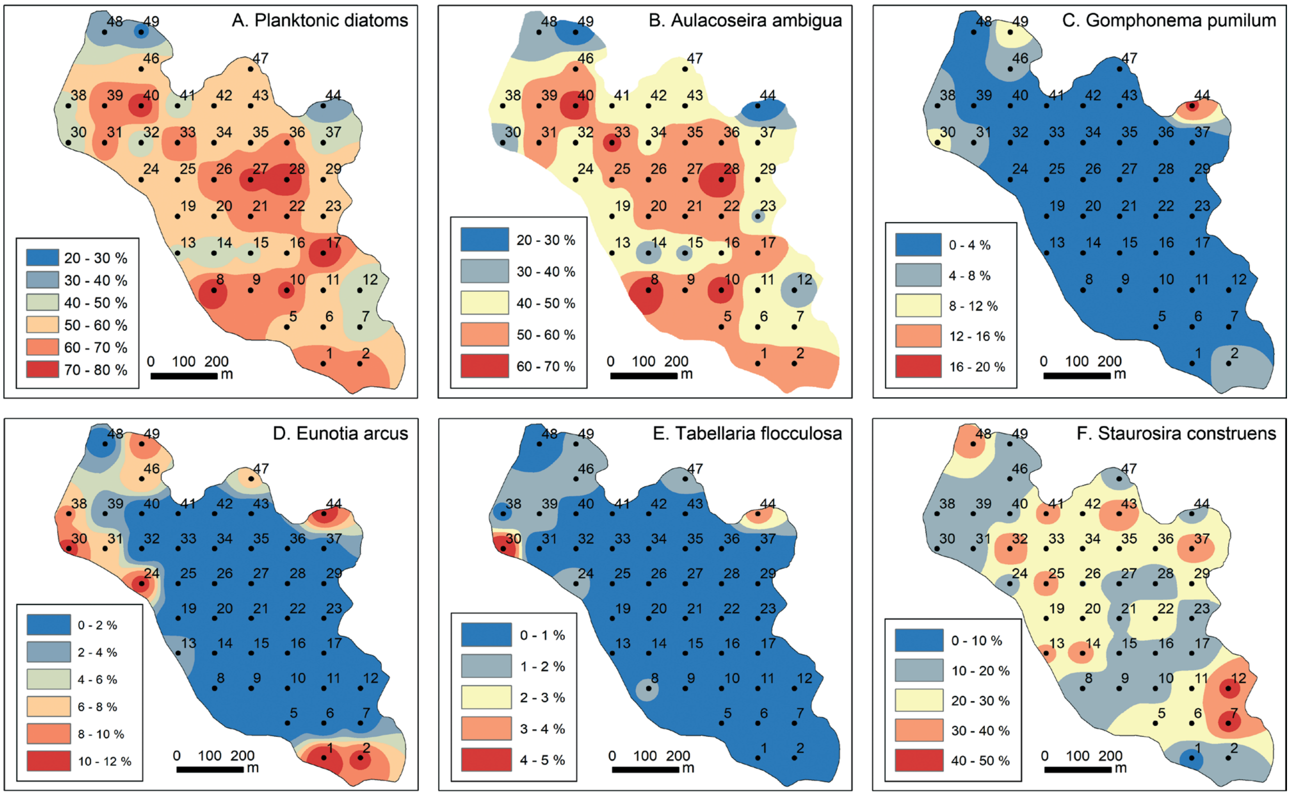

Fig. 7 Distribution of the selected diatom species and indicators in surface sediments of Lake Imbradas: planktonic diatoms (A), *Aulacoseira ambigua* (Grunow) Simonsen (B), *Gomphonema pumilum* (Grunow) (C)*, Eunotia arcus* Ehrenberg (D), *Tabellaria flocculosa* (Roth) Kützing (E)*, Staurosira construens* Ehrenberg (F)

limited to mainly pastures and meadows, without the presence of any industrial facilities or larger farms. Thus, eutrophication in the lake is most likely caused by the natural lake cycle.

Implication of spatial variability for site selection

When carrying out fossil paleoecological studies, it is generally accepted that sediment sampling should be carried out in the central part of the lake. The reason palaeolimnologists core in the centre of a basin is that this location is likely to contain the longest and undisturbed core sequence (Kingsbury *et al.* 2012). Although the assumption that the whole basin is best represented by the central location is not always correct (Berglund 1986; Whitmore *et al.* 1996), it is usually the safest approach to follow when lacking knowledge about the lake bottom's morphology, hydrodynamics, and ecology, which is the case in most studies, at least in their early stages. A high-resolution surface sediment survey, on the other hand, such as the one presented in this paper, enables using a more precise methodology for selecting an investigation site since it provides possible ranges of variability within and between different depth zones (Kienel, Kumke, 2002).

Our results show a general similarity of 0.9 or higher of the Morisita-Horn index anywhere beyond a 125 m distance. Therefore, any point in the central part of the lake is fairly representative of the whole lake, while areas closer to the shore should be avoided in cases where studies encompass only one fossil study site.

The farthest point from the shore is situated roughly between locations 21 and 27. The average Morisita-Horn values, however, suggest location 20 as the most similar to all other lake samples and therefore being better as representative of the whole lake diatom assemblage. It should be noted that the ongoing pollen analyses of the same samples show that the highest pollen concentrations are observed at location 20, gradually decreasing in all directions from this location (Balakauskas *et al.*, in preparation), which suggests that this location represents a pollen focussing point. It is likely that diatoms tend to focus at the above-mentioned location, thus reducing differences in diatom compositions between this location and the surrounding ones. Location 20 is dominated by the most common diatom species found in the bottom samples: planktonic eutrophic *Aulacoseira ambigua* (52%) and *Aulacoseira granulata* (7%), and benthic *Navicula oblonga* (10%) and *Staurosira construens* (24%). To consider this location as an optimal location for fossil studies, an assumption has to be made that it has remained unchanged throughout the investigated period. This could be true, for instance, if sedimentological and stratigraphic evidence indicated that the lake did not experience any significant morphological and hydrodynamical changes over the studied time period. Surface sediment studies should be especially useful in the case of complex, irregular-shaped lakes. Preferably, diatom assemblages should be also investigated in the littoral zone, as it is more complex and sensitive to environmental changes (Bennion *et al.* 2010). Our results also suggest that changes in the littoral zone can supplement the data acquired from the central location with valuable information. The most distinct diatom species complexes were found in the relatively shallow (depth <3 m) eastern-northern-western littoral zone of the lake, which is likely to be influenced by several factors, significantly differing from the central part of the lake; the nearshore zone is rich in macrophytes, small amount of water inflows from the tributaries, overgrowth occurs on parts of the shore. Cores from the littoral zone would be more sensitive to such factors, thus revealing more details on the basin environment. Although shallow areas tend to be prone to erosion and there is a risk of sediment loss from the profiles, this can often be assessed by examining the ^{210}Pb inventories in core sections (Whitmore *et al.* 1996).

A similar approach of high-resolution surface sediment studies can be adopted to evaluate the effect of spatial heterogeneity in the lake and delineate the representative locations for the investigated phenomena. Naturally, the depth and location of the sediments are dynamic and might change over time, and therefore, an assumption has to be made that such changes did not take place. In the case of simple lakes, when significant human impact can also be rejected, such an assumption should be more or less valid for an extended amount of time in the past.

CONCLUSIONS

The bottom sediments of Lake Imbradas are predominated by organic sediments (gyttja) and planktonic diatoms in deep-water areas. Sediments in the shallow areas have higher carbonate and minerogenic contents. Benthic diatoms are relatively more significant in these areas of the lake.

The dominant factor that determines the spatial heterogeneity within the studied lake is water depth. Water mixing probably plays an important role in reducing heterogeneity as well. The effect of inflow from tributaries is insignificant throughout most of the lake, with the exception of the distinct vicinity of tributary mouths. Thus, Lake Imbradas represents a rather uncomplicated case of a water basin, which allows generalisations that can be transferred throughout the region. Certainly, lake size, bottom morphology, as well as local environmental parameters should be considered when making such generalisations, and they would be the most appropriate to similar lakes. On the other hand, further modern diatom studies in lakes from different environments, should broaden the understanding of factors influencing diatom assemblages, thus improving the capabilities to predict diatom distribution, potentially within any lake.

The central part of the lake (>125 m from the lake shore) demonstrates a high similarity between modern diatom assemblages in the bottom sediments. Based on the assumption that the lake morphology and hydrodynamics have remained stable during the investigated period, any point in this area could be considered to be representative of the whole lake.

The optimal location for fossil studies, can be determined using a set of modern surface samples by comparing their heterogeneity and testing for overall representativeness. This conclusion can be extrapolated to similar lakes, situated in comparable environments. Ideally, high-resolution diatom studies could be carried out in a lake prior to fossil studies to delineate areas or sampling points which would likely most effectively represent the overall conditions of a lake.

Modern diatom studies can benefit from the delineation of the most representative areas in the basin and the selection of fossil study sites.

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Supporting Online Material