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Diatom analysis of the Late Quaternary sediments from the area of the Czech Republic

Ph.D. Thesis

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Annotation

Diatom analysis performed on sediment profiles from several localities provided information on past changes in the aquatic environment related to climatic and artificial shifts since the Last Glacial-Interglacial Transition. The practicality of diatom analysis from fish guts of three European fish species in palaeolimnological studies was tested.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 23.4. 2014 ....
Tomáš Bešta

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List of papers and author’s contribution

The thesis is based on the following papers (listed chronologically):

I. **Bešta, T.**, Šafránková, J., Pouzar, M., Novák, J. & Nováková, K. 2009. Late Pleistocene–early Holocene transition recorded in the sediments of a former shallow lake in the Czech Republic. Hydrobiologia 631, 107–120 (IF = 1,99)
Tomáš Bešta was responsible for diatom analysis, LOI measurements, statistical processing and interpretation of multi-proxy data and writing the manuscript.

II. Pokorná, A., Houfková, P., Novák, J., **Bešta, T.**, Kovačiková, L., Nováková, K., Zavřel, J., Starec, P. The oldest Czech fishpond discovered? An interdisciplinary approach to reconstruction of local vegetation in medieval Prague suburbs. Hydrobiologia, accepted (IF = 1.99)
Tomáš Bešta was responsible for diatom analysis and participated in statistical processing of the multi-proxy data, reconstruction of the development of the aquatic environment and revision of the manuscript.

III. **Bešta, T.**, Muška, M., Juggins, S. & Těšitel, J. Comparison of diatom community structure from epilithon and fish guts for future palaeolimnological application. Submitted manuscript
Tomáš Bešta was responsible for design of the study, sampling, diatom analysis, part of statistical analysis, interpretation of results and writing the manuscript.

IV. **Bešta, T.,** Novák, J., Dreslerová, D., Jankovská, V., Lisá, L. & Valentová, D. Middle Holocene development in the infralittoral zone of a shallow lake, Lake Komořany, Czech Republic. Submitted manuscript
Tomáš Bešta was responsible for diatom analysis, LOI measurements, statistical processing, interpretation of multi-proxy data and writing the manuscript.

Contents

General introduction

The subject of the study

Diatoms are primarily autotrophic, unicellular organisms classified in the kingdom Eukaryota, division Chromophyta (Ochrophytes), class Bacillariophyceae (diatoms). They are spread worldwide inhabiting both marine and terrestrial habitats. They play a crucial role in the global cycles of silica and carbon. (e.g. Graham & Wilcox, 2000). The estimated number of living species is 10 - 12 000 (Norton et al., 1996), Guiry (2012) suggests 20 000, while Mann & Droop (1996) > 200 000 living species. Even estimates dealing with millions of still undescribed species are not rare (Norton et al., 1996). Such a wide range of the estimated total number of species is caused above all by the lack of a unified species concept (Guiry, 2012). The most obvious feature differentiating diatoms from other unicellular brown algae is a rigid silica (opal) cell wall commonly called a frustule. In a simplified view, it is composed of 2 valves connected with several girdle bands. The valves are the basic (and the sole) object of counting in diatom analysis (Battarbee, 2003).

Diatom analysis is one of the most widespread proxies (for further biological indicators see e.g. Smol et al., 2001a, b) in studies of past lacustrine environments (e.g. Battarbee 1986; Battarbee 2000, Smol & Cumming, 2000). Diatom community species structure has a strong relation to important physical (temperature, light conditions, turbulence, ice cover) and chemical (nutrients, pH, dissolved organic carbon, salinity) factors driving or characterizing the aquatic environment (Battarbee, 2003). Preservation of diatom frustules in sediments without considerable taphonomic degradation further enables reconstruction of important past aquatic characteristics.

Diatom analysis played a crucial role in the determination of the source of acidification in surface waters (e.g. Battarbee, 1990, Rengberg 1990; Ginn et al., 2007), and the tracking of both natural (e.g. Brüchmann & Negendank, 2004) and artificial (Anderson et al., 1990, Bennion et al., 1996; Fritz, 1989; Olli, 2007) lake eutrophication. Numerous studies focused on the changes in the diatom community according to generally accepted climatic events (e.g. Smol et al., 1995; Pientitz et al., 1995; Korhola et al., 1996; Weckström et al., 1997). The expected strong relation of diatom community structure to environment is also widely used in recent surface water policy, where diatoms play an important role as indicators of shifts in saprobity (e.g. Sládeček 1986, Rott et al. 1997), trophic state (e.g. Kelly & Whitton 1995, Rott et al. 1999) or water quality in general (e.g. Descy 1979, Dell'Uomo 2004).

The presented thesis deals with diatoms in terms of the Quaternary or Earth Sciences. In this context, diatoms are treated rather as lifeless particles carrying information about past environments than living organisms with a particular internal independence from external factors. Such an approach enables an undisturbed focus on the studied issue, but often at the price of excessive simplification and misleading interpretation of outputs.

Diatom analysis in the palaeolimnological context in the area of the Czech Republic

Diatom studies on past environments from the Czech Republic (further in the text as CR) have been relatively rare. Except for the pioneer taxonomical studies dealing with sediment deposits (e.g. Ehrenberg, 1854), palaeolomnological studies using diatom analysis were conducted by Zdeňka Řeháková in her studies from Komořany Lake (Řeháková, 1961, 1962, 1971, 1983, 1986) and quaternary diatomites from the Soos National Nature Reserve (Řeháková 1988). Studies on industrial lake acidification of Bohemian Forest glacial lakes were conducted by Arzet (1987, 1993). Recently, sediments of Plešné Lake in the Bohemian Forest were the subject of a multiproxy study (e.g. Jankovská, 2006; Pražáková et al., 2006; Kopáček et al., 2006) including diatom analysis (Štefková, 2008). Also a new study of the profile from the Soos National Nature Reserve (Rajdlová, 2011) and a rather unsuccessful investigation of the lake Švarcenberk sediments were conducted (Bešta, 2003). Diatom analysis performed by a Czech researcher (A. Bláhová) was recently conducted on sediments from Lake Baikal (Grygar et al., 2007).

Methods

Diatom analytical methods are described in more detail, since they are crucial for further interpretation of the results and the size of a standard paper does not allow for a deeper discussion of the meaning of diatom data.

Diatom classification

Contemporary classification of diatoms used in the context of the proposed thesis follows strictly the morphospecies concept and is still based on floras written by Krammer & Lange-Bertalot in the 1980s and early 1990s (Krammer & Lange-Beralot, 1986; 1988; 1991a; 1991b). within addition, information on local species was supplied from the book series Iconographia Diatomologica and Bibliotheca Diatomologica or international phycological journals (e.g. Diatom Research, Journal of Phycology). Harmonization of the taxonomy based on the determination literature with up to date classification can be obtained on the web pages of the Catalogue of Diatom Names or Algaebase. Determination of Quaternary fossil and subfossil diatoms can be done using literature on contemporary taxa due to their relatively slow evolution; recent taxa are morphologically often identical even with taxa from Tertiary deposits (e.g. Řeháková, 1980).

Diatom analysis

Diatom analysis in palaeolimnological studies means counting of diatom frustules on a permanent slide using a light microscope at the magnification of 1000x in order to obtain percentages of taxa present in the sample. Commonly, an exact volume of standard (usually polystyrene microspheres (Battarbee, 1982)) or lycopodium spores (Wolfe, 1997) added to the accurately weighed dry sediment enables estimation of valve concentration, often regarded as a measure of lake productivity (e.g. Wolfe, 1997). This information further serves as the basis for an estimation of local environmental conditions in the time of sediment deposition. An alternative to the quantification of valve concentration through counting is the chemical determination of the biogenic silica (e.g. Ohlendorf & Sturm, 2008), yet it is not without problems (e.g. biogenic silica originating from other organisms, analytical complications).

The obtained percentages follow a binomial distribution with uncertainty of the count of the given taxon dependent on the sum of all taxa found in the studied sample. The equation defined by Mosimann (1965) and adopted from Maher et al. (2012) is expressed in Formula 1. Confidence intervals for the obtained counts can be easy to calculated using functions in the package “PropCIs” in R (Scherer, 2013).

Formula 1 – Confidence limits based on the binomial distribution of percentage data (counts inside the sum)

$$p_{c_{limit}} = \frac{\hat{p} + Z/(2n_p) \pm Z\sqrt{\hat{p}(1-\hat{p})/n_p + Z^2/(4n_p^2)}}{1 + Z^2/n_p}$$

$p_{c\ limit}$ - approximate confidence limits of p

$\hat{p}$ - proportion of taxon counted in the sample

p - proportion of a taxon in the sample

Z - specified area under the normal curve (for confidence limits 0.95, $Z = 1.960$; for 0.99, $Z = 2.576$)

n_p – sum of all examined taxa

Usually, total counts between 300 – 600 valves are adequate for gathering diatom percentage data (Battarbee et al., 2003). This can be true in the cases where species dominants are crucial. Similarly, in studies where diatom percentage data are used as input for a model (transfer functions), uncertainties in counts are reflected in the model errors (usually also not discussed). But, sometimes also subdominants or rare taxa with a strong relation to a particular environment play important roles in the interpretations. However, increasing the total count over 500 valves does not improve the estimation of the real percentage even for the rare taxa (see difference between 100, 500 and 1000 total counts in Figure 1 - R script provided by S. Juggins).

The probability of the occurrence of rare taxa is dependent on the total count. This can be important e.g. for pollen analysis where a single find of a pollen grain can be crucial for further interpretations. Such formula can be found in Neustupný (1985).

Extraction of environmental information from diatom species data

The information on aquatic conditions hidden in the species spectra of the diatom community can be simply extracted through discussion of individual taxa preferences gained from the appropriate literature or through calculation of the required variable using a model connecting taxa percentage data with the studied variable. Such models can be divided into two types where so-called *transfer functions* are fully mathematical, whereas deriving of species optima for calculation of *diatom indices* is usually based on the experience of the researcher who introduces the particular index.

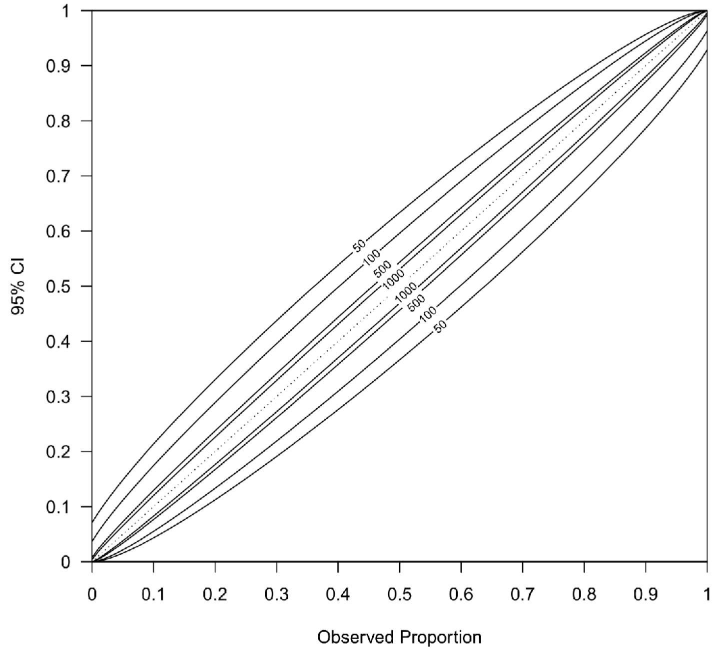

Fig. 1 Nomogram with confidence limits of gained taxa proportions for 50, 100, 500 and 1000 total counts. 95% CI – 95% Confidence Interval

Transfer functions

The methods used in modelling environmental variables from diatom community data are described in detail by Juggins & Birks (2012). The most widely used is Weighted Averaging (WA), since it provides robust results coming from relatively simple formulas. The first step is the WA regression (Formula 2) where optima of individual species are calculated on the basis of a "training set" consisting of instrumentally measured variables and diatom species spectra from tens of localities.

Formula 2 - WA regression

$$\hat{u_k} = \frac{\sum_{i=1}^{n} y_{ik} x_i}{\sum_{i=1}^{n} y_{ik}}$$

The second step, used also in calculation of *indices*, is WA calibration (Formula 3), where the value of the reconstructed variable is calculated using species spectra from a sediment sample and species optima gained from the WA regression.

Formula 3 – WA calibration

$$\hat{x_0} = \frac{\sum_{k=1}^{m} y_{ik} \hat{u_k}}{\sum_{k=1}^{m} y_{ik}}$$

n - number of samples
$\hat{u}_k$ - optimum of the taxon *k*
y_{ik} - abundance of taxon *k* in sample *i*
x_i - environmental variable in sample *i*
m - number of taxa
$\hat{x}_0$ - estimate of past environment (reconstructed variable)

These formulas were adopted from Juggins & Birks (2012). Other often used methods include modification of WA - e.g. LWWA – Locally Weighted - Weighted Averaging (Birks, 1998) constructed for larger datasets and WAPLS – Weighted Averaging – Partial Least Squares (ter Braak & Juggins, 1993), which partially solves the problem of multicollinearity. Further alternative methods, such as Inverse Calibration (Birks, 2012), Gaussian Logit Regression and Maximum Likelihood Calibration (GLRML, ter Braak & van Dam, 1989; Juggins 1992), Modern Analogue Technique (MAT, Prell, 1985) or Artificial Neural Networks (ANN, Næs et al., 1993), feature comparable accuracy in deriving past conditions. Current attempts in improving quantitative reconstructions are focused on Bayesian models (e.g Birks, 2010).

Development of various transfer functions is now possible using a number of software applications: package Rioja in R (Juggins, 2009) or software C2 (Juggins, 2007) for classical (mostly WA based) methods or PaleoNet for construction of models based on artificial neural networks (Racca et al., 2007).

Bias estimation in Transfer functions

A very important part of quantitative reconstructions is estimation of the model errors – ? preventing a too courageous interpretation of reconstructed variables. The model error is given by RMSE (Root Mean Square Error) in Formula 4:

Formula 4 – Root Mean Square Error

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(x_i - \hat{x}_i)^2}$$

$\hat{x}_i$ - model estimate of variable
x_i - measured value of variable
n - number of samples

The value of RMSE is regarded as an under-estimation since it is rather the model error than error of the value of the reconstructed variable. The error of prediction is given by the RMSEP (Root Mean Square Error of Prediction) of the training set. RMSEP is computed through cross-validation (k-fold leave-out or more commonly bootstrapping). The 95% confidence interval is then derived through multiplying of the RMSEP by the value from the Student's t-distribution with appropriate degrees of freedom. For common samples it is usually close to 2. The resulting error of estimation calculated for the reconstructed sample is then usually 2 x RMSEP of the training set (Næs et al 2002).

Such an approach supposes that there are no non-analogue problems - each reconstructed fossil sample has an analogous sample with a very similar species composition in the modern training data set - and the species relation to the reconstructed variable is perfectly described by the modern training data set. The non-analogical problem in the calculation can be eliminated using the sample specific error (Birks et al., 1990). Juggins & Birks (2012) argued that such errors can be too optimistic due to the inevitably (at least to some extent) different environmental conditions influencing the diatom community in the modern training data set and the situation determining the species composition in the fossil sample. Or they can also be too pessimistic if the modern training data set includes "noise" caused e.g. by errors in measurement of the reconstructed variable.

The reliability of the reconstructed environmental variable can also be assessed through calculation of the distance of the fossil sample (species composition) from the closest analogues in the training data-set. For example, the EDDi user guide (Juggins, 2001) suggests the value 150 of the squared chord distance using MAT analysis as a border beneath which the variable should be interpreted with particular prudence. Further, the accuracy of the model can be assessed through comparison with existing analytical measurements (e.g. pH). However, this approach is limited to a few cases in a short chronological section (starting from the 20th century). Comparison of outputs from models based on different statistical methods (WA, MAT, ANN) is also helpful, but it does not enable assessment of bias coming from the used training set. The most independent method is probably the multi-proxy approach where outputs from models based on different biota (diatoms, chironomids, cladocerans etc.) from one sample are compared. However, different biota are commonly related to different environmental variables (diatom - pH, TP; chironomids – temperature), therefore a simple averaging of outputs is not possible. For the future, a promising approach is the use of Bayesian models which combine the core multi proxy data into one model reconstructing the required variable (Juggins & Birks, 2012).

The limits of Transfer functions

Although transfer functions bring a quantitative dimension to palaeo reconstructions, they suffer from numerous limitations. Some of them were mentioned above in *Bias estimation in Transfer functions.* Juggins & Birks (2012) suggest a more critical consideration of uncertainties and weaker stress on the RMSEP. Further constrictions come from the basic assumptions of the models, as summarized in Juggins (2013). These assumptions were defined by Imbrie & Kipp (1971), Imbrie & Webb (1981), Birks et al. (1990) and Birks (1995, 2010). The following definitions of the assumptions were adopted from Juggins (2013):

1. The environmental variable(s) to be reconstructed is, or is linearly related to, an ecologically important determinant in the system of interest.

2. Environmental variables other than the one of interest have negligible influence, or their joint distribution with the environmental variable does not change with time.

Juggins (2013) clearly showed that the assumptions noted above often are not met and lead to a misleading interpretation of the core data. However, he concluded that such problems can be removed by careful selection of variables that directly drive the diatom community (e.g. pH, TP but not temperature or water depth). It is a question whether assumption 2 can be met in the real world at all.

3. The mathematical methods adequately model the biological responses to the environmental variable(s) of interest and yield numerical models that allow accurate and unbiased reconstructions.

Assumption 3 is widely discussed in Juggins & Birks (2012) and can be fulfilled by choosing the best model via model selections based on important criteria (e.g. RMSEP, goodness-of-fit and analogue measures, comparison of models based on different numerical techniques or proxies). However, the problems with estimation of errors thoroughly discussed in *Bias estimation in Transfer functions* suggests even this assumption is rarely fulfilled or at least its degree of fulfilment can hardly be assessed. We can choose the best model available, but cannot decide if it is good enough for our interpretations.

4. The taxa in the training set are the same biological entities as in the fossil data and their ecological responses to the environmental variable(s) of interest have not changed over time

Assumption 4 is not discussed in the above-mentioned literature with the remark that it “is based on the principle of uniformitarianism and is usually assumed to be met for studies covering the Holocene” (Juggins & Birks, 2012). However, the recent trend of algal species inhabiting polluted environments only several tens of years ago being considered as indicators of unpolluted conditions (e.g. *Lemanea* sp., *Batrachospermum moniliforme*, *Psammothidium subatomoides* etc.) suggests even assumption 4 must be seriously taken into consideration.

The largest limitation does not come from the statistical methods used, but from the unspecifity of diatoms, or other biota, to the reconstructed environmental variables. Direct ordination of TP or pH on species data usually explains less than 10% of the variability. With such results we can not expect better reconstructions even if an unproblematic model (fulfilling all assumptions) can be developed. We should accept the predicting limits of the diatoms themselves (and all other biota), interpret only substantial changes in the profiles and avoid the quest for finding shifts on the "appropriate" chronological locations (e.g. 8.2 cal yr BP event - supposed climatic shift, Neolithic or Bronze Age – supposed human induced change).

Also changes in the diatom community described by indirect ordination methods were suggested as the measure of changes in the environment (Legendre & Birks, 2012). This approach has a very important limitation: transfer functions were used, because variables such as TP or pH are expected to respond to external factors governing the lake environment (temperature, input of nutrients, acidification). If we remove such a consideration from our reasoning, the proportion of discussed variability increases, but the explained variability loses its meaning. Our interpretation then should be on the level of the statement "*Something happened*, *but we do not know why and what does it mean"*. Maybe this is the most straightforward approach to palaeolimnological research and a very good starting point to better understand our interpretations of past (recent) reality.

Indices

The second approach how to extract environmental information from diatom data is involvement of various indices primarily designed for water quality assessments of human-caused pollution in surface waters. Such an approach is not very extended in palaeolimnology, since the above-discussed transfer functions give the impression of greater exactness. Transfer functions are statistical models with defined errors and explained variability whereas water quality indices are based on the empirical approach of a single or few persons. While transfer functions reconstruct directly measurable physical or chemical variables (pH, TP, TOC etc.), indices are usually dimensionless expressions of water eutrophication (trophic indices), organic pollution (saprobic indices) and other phenomenon linked commonly with human disturbances.

Calculation of most indices is based on the weighted average formula often including an expression of species valence on the indices gradient – indicator weight (Zelinka & Marvan, 1961):

Formula 5 - WA calibration for index calculation

$$I = \frac{\sum_{k=1}^{m} h_k y_{ik} I_k}{\sum_{k=1}^{m} h_k y_{ik}}$$

h_k - indicator weight of the taxon *k*

I_k - indices value of the taxon k
m - number of taxa
y_{ik} - abundance of taxon k in sample i

There are many indices used usually in the monitoring of surface waters. Most European indices are incorporated in the program Omnidia 5.1. However, since numerous bugs are often present in programs having large lists, it is better to use original values for indices calculations. The Czech saprobic index is now counted using Marvan's update (unpublished) of values from Sládeček (1986). Other values of useful indices can be found in the following literature: Austrian trophic ind. (Rott et al., 1999), Austrian saprobic ind. (Rott et al., 1997), Diatom assemblage ind. for organic pollution (Watanabe et al., 1986), Leclerq & Maquet's ind. (Leclerq & Maquet, 1987), Eutrophication pollution ind. (Dell'Uomo, 2004), Trophic diatom ind. for UK (Kelly & Whitton, 1995), Diatom biological ind. (Lenoir & Coste, 1996), European diatom ind. (Descy & Coste, 1991), Swiss diatom ind. (Hurlimann & Niederhauser, 2006), Artois-picardie diatom ind. (Prygiel et al. , 1996), Descy's diatom ind. (Descy, 1979), Lobo's diatom ind. (Lobo et al., 2002), and Steinberg & Schiefele's diatom ind. (Steinberg & Schiefele, 1988).

Bias of estimation of Indices

Estimation of errors is complicated due to the partially empirical basis of the indices. The Standard Deviation of the Mean of the calculated weighted average can be then used as a measure of the homogeneity or reliability of the calculated indices (Horký, 2011). The lower it is, the more species with narrow valence on the indices gradient. In another words, more good indicators with respect to the calculated indices are present in the sample. The symbols used in the formula correspond with those used in formula 5. The limit value 0.2 was suggested as the border for use of the calculated saprobic index for assessment of water quality on a locality (prepared revision of the norm ČSN 75 7716, 1998).

Formula 6 - The Standard Deviation of the Mean of the index

$$I_s = \frac{\sqrt{\sum_{k=1}^{m}(I_k - I)^2 h_k y_{ik}}}{\sqrt{(m-1)\sum_{k=1}^{m} h_k y_{ik}}}$$

h_k - indicator weight of the taxon k
I_k - indices value of the taxon k
m - number of taxa
y_{ik} - abundance of taxon k in sample i

The limits of Indices

Although even indices are sometimes based on measurements of water characteristics of a locality (e.g. Rott et al., 1999), it is not the rule. What is missing is a formula analogical to WA regression (Formula 2) transforming diatom species data to a numerically expressed species optima (value of the index). This inexactness is the cause of much criticism. But, the transferring algorithm is based on hundreds and usually thousands of observations on various localities. In contrast, the largest training sets for transfer functions reach several hundreds of localities (EDDi combined pH training set – 627, combined salinity training set – 387, combined TP training set – 347, Juggins, 2001). The advantage of larger (although empirical) training sets for indices and uses of species specific weights taking into account a species indicative power (range of the species valence on the gradient of the index) compensate and sometimes probably outweigh the model exactness of transfer functions. Also, the disadvantage coming from the "unclear" term saprobity or trophic state according to "exact" values of TP or pH usually vanishes during interpretation of the data, where numerical values are also discussed in terms of qualities rather than quantities. The problematic determination of errors during indices calculation does not appear so crucial if the analogical problems for transfer functions are considered.

Brief outline of climatic development in the area of the Czech Republic since the Last Glacial-Interglacial Transition

The reaction of lacustrine environments to fluctuating climatic settings has been an essential theme for diatom analysis in the last century and remains crucial also in contemporary research. The conception of climate development since the Late Glacial-Interglacial Transition and especially for the Holocene is still a subject of discussion and is the major task of the presented thesis. Therefore, a brief summary is given, focusing on the supposed development in the CR used in the included papers. The referenced literature is not complete of course.

The Last Glacial-Interglacial Transition (LGIT)

is a transitional period of abruptly oscillating climate connecting the interval of the maximum glaciation in Earth's history - The Last Glacial Maximum (LGM: 26 500 – 19 000 yr BP; Clark et al., 2009) with the current interstadial - Holocene. This abruptly warmer period, in relation to the LGM, spans the interval of ca 15 000 – 11 500 yr BP. The LGIT has traditionally followed classification based on Danish biostratigraphical data (Iversen, 1942) later reinterpreted chronostratigraphically and climastratigraphically (Mangerud et al., 1973; Hoek, 2008; Lowe et al., 2008). An analogical approach proposed by Firbas (1954) has been widely used for central Europe and neighbouring areas (Hoek, 2008). As a result of the shift from a biostratigraphic to a clima- or chronostratigraphic understanding of the periods, it is very difficult to compare data from different proxies and different localities (in other words: a given period established on the basis of e.g. pollen data differs from a period defined by e.g. diatom data even from the same locality – diatom data usually reflects changes in aquatic environment potentially linked with climatic development whereas pollen data are more linked with succession and migration patterns). The chronological approach adopted here is primarily based on the event-stratigraphic concept proposed by the INTIMATE group (Walker et al., 2001), where division of the LGIT was constituted on the basis of cold and warm events in the δ^{18}O curve (supposed direct standard of palaeo changes in humidity and temperature) from the NGRIP ice core project (North Greenland Ice Core Project members, 2004). The LGIT division is further compared with the $\delta^{18}O$ GISP2 (Stuvier et al., 1995) and transformed to a classical Mangerud zonation (Mangerud et al., 1973) with appropriate time spans of periods (Benson et al., 1997 for GISP2; Hoek, 2008 for NGRIP). Walanus & Nalepka (2010) attempted to fix dating of the Mangerud boundaries.

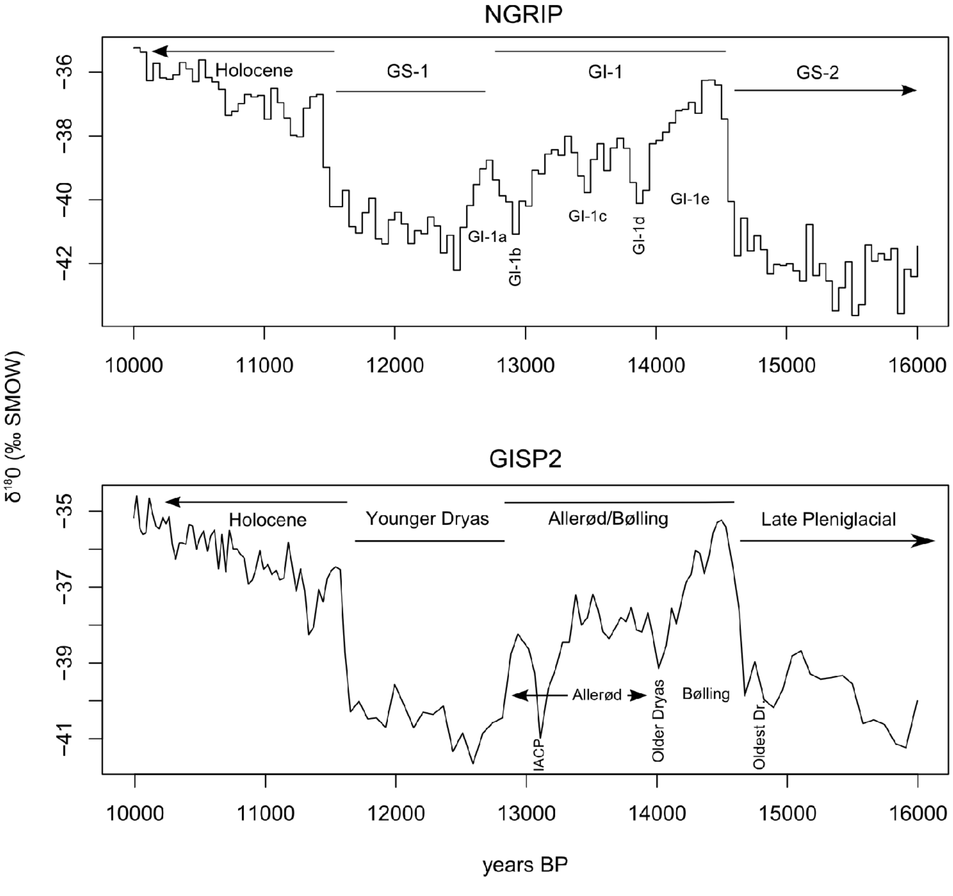

Fig. 2 Classification of the Late Glacial – Interglacial Transition following suggestions of the INTIMATE group (Walker et al., 2001; Lowe et al., 2008) where the NGRIP Greenland ice core $\delta^{18}O$ curve was established as a stratotype for the period. GS-1 – Greenland stadial 1, GI–1 – Greenland interstadial 1, GS-2 – Greenland stadial 2, GI-1a,GI-1c, GI-1-e correspond to warmer, whereas GI-b, GI-1d to colder intervals within GI-1. The oscillations on GISP2 Greenland ice core $\delta^{18}O$ curve are analogized with the classic Mangerud et al. (1974) zonation according to Benson et al. (1997). SMOW - Standard Mean Ocean Water

Their results are comparable (except e.g. the shifted start of the Holocene or shorter Allerød period), but the event stratigraphic approach is given priority here for the LGIT, since it has direct relation to climate changes which should drive the diatom community without any lag phases in contrast to vegetation changes reflected in pollen based zonation. The time frame of the zones is based on the Greenland Ice Core Chronology 2005 - GICC05 (Svenson et al., 2008) developed for the NGRIP ice core. The suggested chronological division is expressed in Figure 2.

LGIT division

Oldest Dryas, *DR1* (ca 15 000 – 14 640 GICC05 yr BP)
This period can probably be analogous with the DR1/DR2 (e.g. Jankovská, 2003) or pre-Allerød periods (Hošek et al., 2014). Jankovská (2003) interpreted the pollen spectra e.g. from Červené blato and Borkovická blata as a DR1/DR2 period. Pokorný et al. (2002) determined a DR1 oscillation on the basis of *Pinus* decline and expansion of heliophylous herbs in pollen in the sediment of Lake Švarcenberk.

Bølling, *GI-1e* (14 640 – 14 030 GICC05 yr BP)
A warmer period, first defined from Denmark (Iversen, 1942) was not recorded clearly in the CR, except as suggested from Lake Švarcenberk (Pokorný, 2002). Jankovská (2003) found this interstadial in Sivarna, Slovakia. The absence of the Bølling interstadial in the area of the CR is probably caused by a minor Older Dryas oscillation which prevents separation of Bølling from the Allerød interstadial.

Older Dryas, *DR2, GI-1d* (14 030 – 13 900 GICC05 yr BP) – Introduction of this short colder period results from distinction of the Bølling interstadial (Iversen, 1942). Pokorný et al. (2002, 2010) did not find any apparent changes attributable to DR2 in the detailed study from Lake Švarcenberk. Some suggestions of its occurrence were made from Sivarna (Jankovská, 2003). However, significant evidence of the Older Dryas is missing from the area of the CR.

Allerød, *GI-1c,a* (13 900 – 12 850 GICC05 yr BP) *including Intra Allerød Cold Period IACP, GI-1b* (13.26 -13.05 kyr BP)
This interstadial is clearly recognizable in the Czech palaeo records (e.g. Pokorný, 2002; Jankovská 2003; Svitavská, 2001; Svobodová et al., 2002). This period is in the data from the Greenland Ice core (e.g. Lowe et al., 2008) and continental data (e.g. Lotter et al., 1992). It is interrupted by the so-called Intra Allerød Cold period (IACP, GI-1b, Gerzensee Oscillation). This interruption has not been significantly determined in CR (except a suggestion in Hošek et al., 2014). It should be noted that the Allerød in the central European context often contains also Bølling and corresponds to an Allerød/Bølling resp. complete GI-1 period.

Younger Dryas, *GS-1* (ca 12 850 – 11 650 GICC05 yr BP)
This cold stadial is seen in the pollen records from numerous peat bogs and lakes (e.g. Pokorný, 2002; Jankovská 2003; Svitavská, 2001; Svobodová et al., 2002, Pražáková et al., 2006). This phase is the only one that could be probably fully analogous to the GS-1 and Younger Dryas in the NW Europe context. Some studies (e.g. Isarin & Bohncke, 1999; Berglund et al., 1994)

suggest the Younger Dryas had an initial, more severe phase and later warmer conditions arose. Results from the stable Greenland Ice cores are in agreement with these suggestions (e.g., Stuvier et al., 1995).

Problems with LGIT synchronization

In the division proposed here, the Oldest Dryas (DR1), Older Dryas (DR2) and Younger Dryas (DR3) represent colder phases (stadials) interrupted by the Bølling and Allerød (including intra Allerød cold period) warmer periods (interstadials). Such general trends in climatic settings of the LGIT periods are seen throughout North-Western Europe (Hoek, 2008). The $\delta^{18}O$ data suggest a high rate of synchronization of the outlined climatic shifts also between NW European and North American records (e.g. Benson et al, 1997). The Northern hemisphere synchronization of the LGIT climatic development encourages the search for a similar pattern also in central Europe including the area of the CR. Although the climate in the CR is less determined by changes in ocean circulation – the supposed main factor driving the changes (Broecker, 1998) - than maritime regions, it is still strongly influenced by the situation in NW Europe (Crumley, 1995). The current division of the LGIT based on sediments from the CR is less clear. Differentiation of the Bølling interstadial is almost impossible. This is probably the result of the weak and therefore undetectable colder oscillation of the Older Dryas (DR2). Among pollen analysts, the widely used DR1/DR2 zone (pre-Allerød, Firbas‘ zone I) therefore most probably corresponds to the Oldest Dryas (DR1). The Allerød must therefore have to be equivalent to the Allerød/Bølling period without the DR2 cold interruption – the GI-1 period. Analogously, the Allerød/Bølling interstadial without the colder interruption has been called the Windermere Interstadial (Hoek, 2008) in Britain or the Meindorf phase in Germany. The problems in making analogies of LGIT development between central and NW Europe is not so surprising, since even synchronization of Scandinavian and Netherlands' data is mildly problematic (Hoek, 2001) and probably points out to a general problem of synchronization between different localities (inaccuracy of ^{14}C dating, problematic definition of boundaries between periods etc.). Such discrepancies could be also partially attributed to application of strictly discrete thinking of the empirically (also) continuous universe (e.g. Einstein, 1916).

Holocene

(current interstadial) represents a period of climatic settings comparable and extending up to the present. It has been traditionally divided into three parts based on radiocarbon dating of pollen zones established for NW Europe - Early, Middle and Late Holocene (Mangerud et al., 1974). The dating of pollen zones enabled a switch from biostratigraphic to general palaeoclimatic usage of the zones without changing their local importance (Walker et al., 2012). This led to confusion resulting in the need for redefining the chronozone boundaries based on the event stratigraphic concept (Walker et al., 2001). Similarly to the Late Pleistocene-Interglacial transition, the NGRIP $\delta^{18}O$ curve was selected as the stratotype for the boundary between the Early and Middle Holocene (8.2 kyr BP event), while Mawmluh Cave, north-east India, was used for the 4.2 kyr BP event separating the middle from the Late Holocene (Walker et al., 2012). It is evident that establishment of intra Holocene period boundaries is more complicated than for the Late Pleistocene. This is probably caused by a lower amplitude of climtatic oscillations. The question remains why the 4.2 event is missing on the NGRIP $\delta^{18}O$ curve. In fact, interpretation of minor oscillations in the Holocene Greenland ice core data is at least problematic (Walker et al., 1999). Also, the major 8.2 kyr BP event was not found in most central European records. Therefore, division of the Holocene as Early (Preboreal, Boreal), Middle (Atlantic, Subboreal) and Late (Subatlantic) used here follows the recently radiocarbon dated Mangerud boundaries (Walanus & Nalepka, 2010) knowing that these reflect rather changes in vegetation cover than shifts in climatic settings and are more or less locally determined (e.g. Björck et al., 1998). An alternative division of the Holocene based primarily on the terrestrial record as suggested by Ložek (1997) is also discussed in the following text.

Holocene division

Early Holocene

Preboreal *(11 450 – 10 150 yr BP)* is also labelled as the transition from the Late Pleistocene to Holocene conditions and is characterized by unstable climatic settings. Climatic oscillations were determined in e.g. Netherlands and Belgium (Bohncke & Hoek, 2007; Bos et al., 2007): the humid Friesland phase (boreal forest with birch dominance) and dry Rammelbeek phase (prevailing grasses). Evidence for the so-called cold Preboreal Oscillation (11.2 kyr BP) was found also in the Greenland ice cores (e.g. Lowe et al., 2008). Attempts at synchronization of these events in NW Europe were partially successful (Bohncke & Hoek, 2007; Bos et al., 2007). Foraminiferan data from the Adriatic Sea also placed a dry event at ca 11.2 kyr BP (Favaretto et al., 2008). This suggests that the 11.2 kyr event was important over Europe and should be recorded also from the CR. There is a slight, but unproven, hint of a Preboreal Oscillation recorded in Lake Švarcenberk (Hošek et al., 2014). Pollen records are characterized by a regression of open vegetation (*Juniperus*) and the first continuous occurrence of *Quercus*, *Tilia* and *Fraxinus* (Pokorný, 2011). Jankovská (2000) characterizes the period by spread of *Betula* and enhanced percentages of *Corylus* in the surroundings of Lake Komořany

Boreal *(10 150 – 8 950 yr BP)* differs from the previous zone above all by having a more stable climatic settings (e.g. Davis et al. 2003). Ložek (1997) supposed a gradual warming of the climate within the period towards the following so-called Atlantic climatic optimum. The pollen records of lowland and upland sites are typified by increases in *Picea* (Pokorný, 2011) and *Corylus* (Jankovská 2000). Also mixed oak forests were abundant in lower altitudes (e.g Pokorný, 2011). The Greenland $\delta^{18}O$ curve is stable and no major events were determined there (Walker et al., 2012).

Middle Holocene

Atlantic *(8 950 – 5 750 yr BP)* is, in the area of the CR, determined by finds of "thermophilous" *Viscum* or *Hedera* pollen, which led to the assignation of the period as the so-called climatic optimum. A climax mixed oak forest dominated in the lowlands. *Fagus* and *Abies* firstly occurred continuously (e.g. Pokorný 2011). Jankovská (2000) stressed the dominance of *Quercus*, *Ulmus* and *Tilia* and *Fraxinus*. Žák et al. (2002) placed the start of the Atlantic ca 8.400 – 6.500 cal yr BP on the basis of thoroughly studied calcareous tufa accumulation in Svatý Jan pod Skalou. They further established a period of oscillations between dry and wet climate spanning ca 4.000 yrs after 6.500 cal yr BP, which they called the Epiatlantic. In fact, the Greenland $\delta^{18}O$ ice cores data (e.g. Stuvier et al., 1995) do not show any significant difference from the Boreal period (see also pollen temperature model in Davis et al., 2003) except the occurrence of the widely discussed 8.2 kyr BP event (e.g. Lowe et al., 2008). In contrast, temperature models based on accumulation rates revealed a climatic optimum with temperatures +2.5°C above present between ca 8 000 and 5000 yr BP (Dahl-Jensen et al., 1998). Suitable sites were settled by dense Neolithic cultures in the middle of the period from ca 7 500 cal yr BP (Pavlů & Zápotocká, 2007). From this point, the potential human influence of the aquatic environment has to be seriously taken into account (Kalis et al., 2003).

Subboreal *(5 750 – 2 550 yr BP)* is sometimes characterized by a decrease in temperature and precipitation (Ložek, 1997). The recently developed „Archaeoclimate" model (Dreslerová, 2012) suggests increased humidity and decreased temperature leading to considerably decreased evapotranspiration after ca 5 500 yr BP. Expansion of *Abies* and *Fagus* along with indicators of anthropogenic activity (cereal pollen) was typical for pollen spectra. The absence of *Hedera* and *Viscum* pollen points to a temperature decrease (Jankovská, 2000; Pokorný, 2011). Again, no major change occurred on the $\delta^{18}O$ curve in relation to the previous period (e.g. Stuvier et al., 1995)

Late Holocene

Subatlantic *(2 550 yr BP – present)* Anthropogenic influences on the landscape are huge (Pokorný, 2011, Jankovská, 2000) and complicate determination of a pure climatic signal in the sediment (pollen) record. The Little ice age (17th- first half of 19th century) was the major cold oscillation determined also from the Greenland ice core data (Fisher et al., 1998). Accumulation rates from the GRIP ice core places the cold oscillation between 1550 and 1850 yr AD (Dahl-Jensen et al., 1998). However, the response of the $\delta^{18}O$ curve was rather subtle (Stuvier et al., 1995).

Aims of the study

The primary aim of the presented study is to track changes in the aquatic environment of the studied sample locations in the context of chronological anchoring. The unique aims then also emerged during data processing and interpretation. Thus, the aim of Paper I was to study the reaction of the aquatic environment of a small lake, as recorded in diatom, plant macrofossil and geochemical data, to climatic development during the Last Glacial-Interglacial Transition. In paper II, the aim was to reconstruct the reactions of the aquatic environment in a small pond and surrounding vegetation in the medieval suburbs during the Middle Ages. Paper III aims to compare diatom assemblages from fish guts of three fish species with diatom epilithic samples from the same locality. The first reason for such a study was to assess the use of *Barbus barbus* (L.), *Chondrostoma nasus* (L.) and *Squalius cephalus* (L.) when researching past aquatic conditions or reconstructing reference conditions in rivers using specimens from museum collections. The second reason was to determine the most suitable diatom-based indices for such an application. Paper IV has the objective of reconstructing the aquatic conditions in a large shallow lake during the middle Holocene period. It aims also to track the development of the surrounding landscape and settlements. Another aim was to look for human influence on the lacustrine environment.

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Paper I

Late Pleistocene–early Holocene transition recorded in the sediments of a former shallow lake in the Czech Republic

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Hydrobiologia (2009) 631:107–120

Abstract

Quaternary limnic sediments from Velanská Cesta, a former lake in the Czech Republic, were investigated to document the response of an aquatic environment to global climatic shifts during the late Pleistocene–early Holocene transition. The obtained multi-proxy record, including subfossil diatoms, diatom-inferred variables (index of trophic state, halobic index, TP, and pH), plant macrofossils, and geochemical data, was compared with the $\delta^{18}O$ GISP2 curve. Diatom accumulation zones and subzones established on the basis of a ConSLink cluster analysis corresponded well with the boundaries of the Bölling, Older Dryas, Alleröd, Younger Dryas, and Preboreal periods. The diatom-inferred trophic state and salinity data showed increased values during the colder epochs, which were supported by the findings of low-temperature macrofossil indicators in the corresponding samples. The results of this study document a long-term forcing of a shallow lacustrine ecosystem in central Europe by climatic events of a global scale.

Keywords
Late Pleistocene–Holocene transition, Shallow lake, Diatoms, Macrofossils, Geochemistry

Následující pasáž o rozsahu 21 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originálu dizertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
Publikace vyšla tiskem v časopise Hydrobiologia.

Paper II

The oldest Czech fishpond discovered? An interdisciplinary approach to reconstruction of local vegetation in mediaeval Prague suburbs

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Hydrobiologia, accepted 13 February 2014

Abstract

Wet sediments of a former water reservoir were discovered during an archaeological rescue excavation. Vegetation and environmental changes taking place in the mediaeval suburbs of Prague, Czech Republic, from the tenth to the middle of the fourteenth century were investigated. The origin and function of the water reservoir was revealed using a multi-proxy approach that combined the results of macrofossil, pollen, diatom, antracological, archaeo-zoological and sedimentological analyses. Gradual changes of the surrounding vegetation were documented. Field indicators increased in time, whereas proportions of broadleaf trees and shrubs decreased; proportions of ruderal plants increased continually. A gradual decline of semi-natural hygrophilous vegetation was accompanied by an inverse tendency in trampled vegetation. All these trends indicate an intensification of human activity around the pool. A similar intensification of anthropogenic influence is clearly visible in the development of the aquatic environment. According to the diatom composition, the base of the profile is the result of sedimentation in considerably oligotrophic conditions. A successive deterioration of water quality was documented by various organisms (diatoms, green algae, water macrophyta, fishes and intestinal parasites). The high content of dissolved nutrients, probably connected with anoxia, could have caused the disappearance of both diatoms and fishes.

Keywords
Archaeobotany, Archaeozoology, Environmental changes, Human impact, Fishpond, Hydrobiology, Prague, The Middle Ages, Vegetation diversity

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Paper III

Comparison of diatom community structure from epilithon and fish guts for future palaeolimnological application

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Submitted manuscript

Abstract

The sampling skills of three common European fish species (*Barbus barbus, Chondrostoma nasus,* and *Squalius cephalus)* were tested to assess their potential as biomonitors of past changes in river water quality through the analysis of diatoms in fish guts from museum specimens. The study was performed on three rivers with different chemical and physical conditions. Comparison of similarity indices revealed rather low diatom assemblage resemblance between epilithic samples and samples collected from fish guts at the same locality. In contrast, a mixed-effect linear model identified significant differences between locations through comparison of diatom-based water quality indices. Among fish species, diatom indices calculated from gut samples of *Barbus barbus* and *Chondrostoma nasus* were in most cases not significantly different from those from epilithic samples while those from *Squalius cephalus* were often significantly different. The results of the study demonstrate that diatom analysis of fish guts provides a clear distinction between eutrophic and hypereutrophic rivers. Finer nutrient variations within hypereutrophic conditions were also found to be significant for some diatom indices. In this context, choice of appropriate diatom water quality index proved to be crucial in maximising the sensitivity of the method.

Key words
Diatoms, Fish guts, Palaeolimnology, Aquatic quality, Eutrophication

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Paper IV

Middle Holocene development in the infralittoral zone of a shallow lake, Lake Komořany, Czech Republic

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Submitted manuscript

Abstract

Paleolimnological reconstruction of the aquatic environment in Lake Komořany, based on sedimentology, geochemistry and diatom analysis in the infralittoral part of the basin reflects the history of the site from its origin ~ 7,200 cal yr BC to its transformation into an alder wood ~ 2,100 cal yr BC. The lake proved to be a shallow, meso-eutrophic water body with minor oscillations in the species structure of the diatom community and concentrations of elements associated with changes in its watershed. Diatom inferred total phosphorus concentrations varied from 50 – 80 $ug.l^{-1}$ and diatom inferred pH was ~ 7.6 through the studied limnic phase. A significant shift associated with decreased lake level and detected by most of the included methods occurred ~ 2,800 cal yr BC. Potential human impact was revealed through increases of *Corylus* and *Populus* pollen in the Neoliithic and a considerable shift in the microcharcoal curve in the Eneolithic. These changes in the lake surroundings had no detectable influence on the lacustrine environment. The outlined balanced development bounded by the occurrence of aquatic conditions (~ 7,200 cal yr BC) and the decreased lake level (~ 2,800 cal yr BC) probably reflects stable climatic settings corresponding to the Holocene climatic optimum.

Key words
Mid-Holocene, Shallow Lake, Diatoms, Geochemistry, Pollen, Archaeology

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General conclusions

Diatom analysis in an integral part of present palaeolimnological research. It commonly acts together with other analyses providing a complex, multi-proxy insight into the historical development of various environments. The presented study focuses on the lacustrine response to climatic changes during the Late Glacial – Interglacial Transition deduced from the sediments of Velanská Cesta Lake (Paper I). It was concluded that shifts in the aquatic environment faithfully followed the generally accepted climatic development outlined for northern Europe. These findings have to be treated with caution due to several limits of the study (imperfect depth-age model, low amplitude of detected shifts), but still it suggests that the changes outlined for high altitudes and maritime European regions played an important role also in the lower altitudes of central Europe including the Czech Republic. In contrast, the very stable diatom community and also steady outputs of other palaeolimnological analyses in the littoral profile of Lake Komořany (Paper IV) delineate an unprecedently long lasting (~ 4 400 years) period of aquatic stability within the middle Holocene interval. This makes it difficult to synchronize the situation across Europe and raises the question whether the lacustrine environment is always sensitive to climatic forces. The answer is not trivial, since it relativises results of all palaeolimnological research. The research combining numerous disciplines conducted on the sediments of a water reservoir existing from the 10th to the middle of the 14th century in the medieval suburbs of Prague (Paper II) reliably documented human-caused eutrophication of the primarily oligotrophic aquatic environment. Intensification of human impact was also evidenced through development of the surrounding vegetation. The study comparing diatom content of fish guts with epilithic diatom community composition (Paper III) proved the practicality of water quality indices calculated from gut samples of *Barbus barbus* (L.), *Chondrostoma nasus* (L.) and *Squalius cephalus* (L.) in reconstructing river aquatic quality development using museum specimens of the studied fish species. This points out that the shift in the aquatic environment has to be qualitative (eutrophic vs. hypereutrophic) to be clearly recognizable in the diatom community obtained from fish acquisitions. It further demonstrates the great differences in the sensitivity of the studied indices to aquatic changes.

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