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ORIGINAL PAPER

Intra-lake patterns of aquatic insect and mite remains

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Abstract Surface sediment samples from Lake Moaralmsee in the Austrian Alps were examined for fossil remains of aquatic insects and mites. This study investigated the influence of water depth on the fauna, to explore the possibility of using such fossil remains in sediment cores to reconstruct past water level changes. In addition, instar-specific patterns of chironomid (Diptera: Chironomidae) head capsule accumulation were examined to evaluate whether the smaller, lighter-weight early instars are more easily transported within the lake basin, creating a potential source of error for paleolimnological inferences. Results showed that intra-lake distribution of these zoological remains is closely related to water depth and suggested that the fossils accumulate near each species' habitat. In addition, the ratio between exoskeletons of oribatid mites (Acari: Oribatida) and chironomid head capsules was strongly related to water depth. Examination of instar-specific accumulation patterns of all chironomid remains showed no significant relationship between specific instars and water depth, though littoral samples consisted only of the 3rd and 4th instars. A taxon-specific examination revealed that the early instars of *Paracladius* are significantly focused to the deeper parts of the basin. Because most taxa displayed significant relations with water depth, a transfer function was developed, relating fossil chironomids to water depth. This model has a high coefficient of determination and a low estimate of prediction error. In this study, *Paracladius* was found to prefer shallow and intermediate water depths, hence enhanced offshore transport of early instar head capsules may weaken model performance statistics. Results indicate that intra-lake calibration sets of invertebrate remains have great potential in paleolimnological research, though there is a possible risk of spatial autocorrelation. Such datasets also contribute to the understanding of the modern ecology of the fauna because fossil assemblages in surface deposits provide habitat-specific autecological information. More effort should be directed at evaluating how remains of different instars are transported within other lake basins, because selective offshore transport of head capsules of different larval stages can potentially cause bias in environmental reconstructions.

Keywords Austrian Alps · Chironomidae · Instars · Spatial autocorrelation · Taphonomy · Water depth

Introduction

Midges (Diptera: Nematocera) are holometabolic insects that go through four life stages: egg, larva,

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pupa, and imago (adult) (Tokeshi 1995). Of these stages, the aquatic larval stage is the longest. It is divided into four stages, each of which ends with moulting and leaves behind the old exoskeleton and head capsule (Pinder 1986). Chitinized head capsules preserve well in lake sediments and can be recovered for paleolimnological purposes and used as proxies for a variety of environmental variables (Walker 2001; Brooks et al. 2007). Although traditional use of midges as environmental indicators has focused on lake productivity (Wiederholm and Eriksson 1979), more recent studies have used them for climate reconstruction (Brooks 2006; Walker and Cwynar 2006). Another recent application of fossil midge analysis has been for lake-level reconstruction. Training sets, using multi-lake datasets (Korhola et al. 2000; Barley et al. 2006; Luoto 2009a) and intra-lake and local datasets (Kurek and Cwynar 2009a; Luoto 2010), have been collected to reconstruct past water level fluctuations, which probably reflect effective moisture dynamics (Mason et al. 1994). Long-term patterns in effective moisture provide invaluable information on past precipitation changes (Luoto and Sarmaja-Korjonen 2011; Nevalainen et al. 2011).

Intra-lake datasets of fossil midge (mostly Chironomidae) and other invertebrate assemblages are often collected assuming that the animal remains accumulate in sediments near the species' habitat (Kurek and Cwynar 2009b; Engels and Cwynar 2011; Nevalainen 2011a, b). These datasets are used to better understand species autecology and to select optimal coring sites for paleolimnological studies (Luoto 2010; Engels and Cwynar 2011; Luoto et al. 2011; Nevalainen 2011a, b). Use of intra-lake invertebrate assemblages in paleoenvironmental calibration sets is still relatively new and needs further examination and testing. For example, taphonomy of fossil midge head capsules is relatively poorly known and patterns of specific instar deposition are not established. Kauppila (2002) showed that small, light diatom frustules are easily transported after initial deposition, but larger, heavier midge head capsules show significant within-lake heterogeneity, suggesting they accumulate close to the habitats in which they live (Eggermont et al. 2007; Engels and Cwynar 2011). It could, however, be hypothesized that small, light-weight head capsules of early instars and broken (split) head capsules, might display evidence of offshore transport and accumulation in deeper water. Van Hardenbroek et al. (2011) demonstrated that fossil head capsules were transported well beyond the location of living chironomids in a lake with a steeply sloped bottom, which suggests there may be differences in taphonomic processes among lakes of different morphometry. It is also notable that within-lake variability in chironomid fossil assemblages can cause systematic offsets when inferring temperatures paleolimnologically (Heiri et al. 2003).

In this study, I selected a lake with minimum human impact and minimized effects of gradients in other factors to investigate the influence of water depth on within-lake distribution of fossil insect and mite assemblages. The first goal was to investigate whether the fossil assemblages correlate with water depth. Second, I evaluated whether early instar or broken head capsules of midges are easily transported after initial deposition. Third, I developed a chironomid-based calibration model that could be used to infer past lake water depth.

Study site

The study lake, Moaralmsee, is located in the Niedere (Schladminger) Tauern Alps in Austria (Fig. 1). The Niedere Tauern forms a compact, but imposing massif of crystalline and limestone bedrock. Moaralmsee is separated from the corrie (i.e. cirque) back-wall to the south by an upper basin and a moraine field, making the basin mostly groundwater fed. The near-pristine oligotrophic lake lies at an altitude of 1825 m a.s.l. The lake has a maximum length of 232 m, maximum width of 127 m, and maximum depth of 6–7 m. The water temperature in Moaralmsee is cold compared to other lakes at similar altitude in the region due to slower snowmelt, and has thus been judged to be ultra-sensitive to climate warming (Thompson et al. 2005).

Materials and methods

Water temperature and sediment sampling

Water temperature between July 2009 and July 2010 was measured at water depths of ~1 and 3 m (Fig. 1) using 8-bit MINILOG-TR thermistors (Vemco Ltd., Halifax, Nova Scotia, Canada). Limnological variability within the water column on 17 August 2010 is

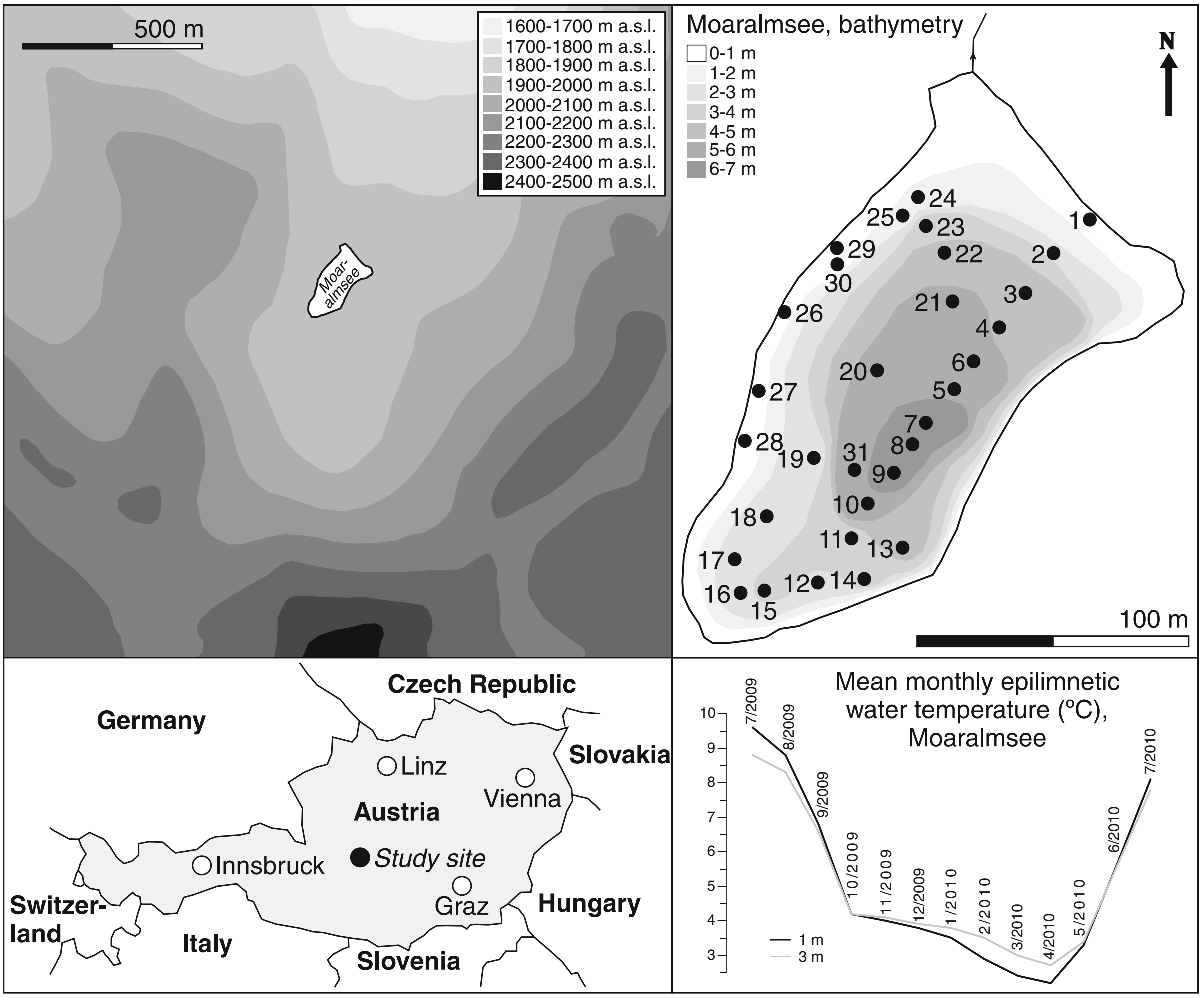

Fig. 1 Location of the study site, Lake Moaralmsee, in the Niedere Tauern Alps, Austria, and distribution of the surface sediment samples along the depth gradient in the basin. The mean monthly epilimnetic water temperatures in Moaralmsee were measured at depths of ~1 and 3 m

illustrated in Fig. 2. These measurements were taken in the center of the lake using a multisonde 6600V2 (YSI Inc., Yellow Springs, Ohio, USA), which measures multiple water variables simultaneously.

Surface sediment samples from Lake Moaralmsee were obtained from a small boat with a Kajak gravity corer on 17 August 2010. The study lake was chosen because it is nearly pristine and has a homogenous bottom type (i.e. habitat). The lake lacks dense littoral vegetation and input streams, the latter fact making it suitable for water-depth studies and investigations of effective moisture fluctuations (Mason et al. 1994). Thirty-one samples were collected along a water-depth gradient. Water depth was measured using an echosounder. Samples 26 and 29 (Fig. 1) contained aquatic macrophytes. Surface sediment samples used in this study (topmost 0–1 cm) represent recent accumulation, but may encompass slightly different time spans due to sediment focusing. Fossil faunal assemblages in surface sediment samples can be considered analogues of modern relative abundances (Frey 1960; Nykänen et al. 2009) for purposes of characterizing the lake environment for paleoenvironmental calibration studies (Bunbury and Gajewski 2008). Samples were stored in plastic bags in a cold room at +4°C.

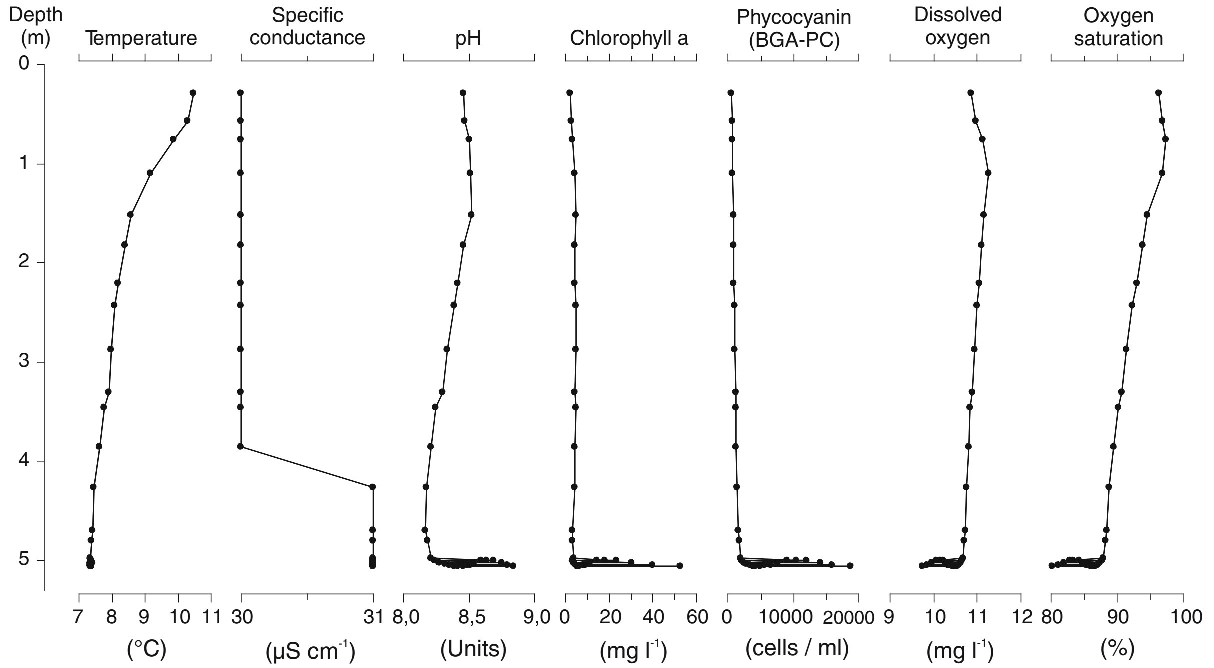

Fig. 2 Limnological measurements (17 August 2010) from Lake Moaralmsee, along the water depth gradient

Zoological fossils and loss-on-ignition analysis

Sediment samples for fossil insect and mite analysis were prepared applying standard methods for fossil chironomid analysis described in Brooks et al. (2007), but without pretreatment in KOH, which was not required. Volumetric subsamples were used to enable calculation of concentrations. Sediments were sieved through a 100-µm sieve and the residue was examined using a Bogorov counting chamber (Gannon 1971) under a binocular microscope to extract the remains with fine forceps (40× magnification was used to better detect 1st instars). Fossil remains were permanently mounted on microscope slides in Euparal® and identified to the best taxonomic resolution possible under a light microscope at 400× magnification.

Identification of chironomids was done using Wiederholm (1983) and Brooks et al. (2007). Biting midges (Nematocera: Ceratopogonidae), mayflies (Insecta: Ephemeroptera), and oribatids (Acari: Oribatida) were identified according to Luoto (2009b), water mites (Acari: Hydrachnida/Hydracarina) according to Rumes et al. (2005), black fungus gnats (Nematocera: Sciaridae) according to Heiri and Lotter (2007), and black flies (Nematocera: Simuliidae) according to Currie and Walker (1992). Nomenclature follows the above-mentioned literature. Different larval stages (instars 1–4) were identified according to their head capsule size and chitin formation. Because clear distinction between the 1st and 2nd and between the 3rd and 4th instars was difficult, at times, results are presented as early (1st and 2nd) and late (3rd and 4th) instars. A minimum of 50 head capsules was counted (Quinlan and Smol 2001a).

Loss-on-ignition (LOI) (Dean 1974) was determined on sediment samples (~10 g) that were dried at 105°C for 12 h. Dry samples were combusted in an oven at 550°C for 2 h. The LOI is considered to be a good estimate of the organic content of the sediment. LOI analysis was not conducted on samples 1, 4, 27, and 28, because there was not enough sediment available after fossils were analysed.

Numerical analyses

Data analyses were performed using relative abundances without any taxa deletions. Detrended correspondence analysis (DCA) was used to test whether a unimodal relationship existed between the taxa data and the primary ordination axis (Lepš and Šmilauer 2003). Consequently, direct relationships between midge taxa and environmental data were investigated by unimodal CCA, using biplot scaling with emphasis on interspecies distances. CCA can be used to identify environmental variables that are strongly related to the species assemblages (ter Braak and Šmilauer 2002). The CCA was run with water depth as the sole constraining environmental variable. The statistical significance ($p \leq 0.05$) was tested with a Monte Carlo permutation test (999 unrestricted permutations). When only one environmental variable is used, the ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) indicates the relative importance of the specific variable in explaining the cumulative variance in the species data (ter Braak and Šmilauer 2002). Explanatory variables that have high λ_1:λ_2 ratios may be useful for quantitative inference models. A similar test was also performed between the midge taxa and LOI, using only the 27 samples for which LOI was analyzed. Due to the different number of samples, LOI was not used as a co-variable to test the influence of water depth against substrate properties. The DCA and CCAs were performed using downweighting of rare species and were run with the program CANOCO, version 4.52 (Plant Research International, Wageningen, The Netherlands) (ter Braak and Šmilauer 2002).

Taxa optima and tolerances were calculated using weighted-averaging (WA), applying the computer program C2 Data Analysis, version 1.6.6 (Juggins 2007). Taxa response models were constructed using generalized linear models (GLM) to identify relationships significant at levels $p \leq 0.05$ and $p \leq 0.01$, between taxa and water depth. The GLMs were set to quadratic degree and Poisson distribution (Rees et al. 2008) and run with CanoDraw, a component of CANOCO. Sample-specific midge diversity was assessed using taxon richness (number of taxa in samples, *S*) and Shannon diversity (*H*). Relationships between chironomid instar deposition patterns and water depth, and between broken head capsules and water depth, were evaluated using Pearson's correlation (*r*), coefficient of determination (R^2), and level of statistical significance (*p*). In addition, the relationship between water depth and LOI was tested using linear correlation. To examine whether split Orthocladiinae (Chironomidae) head capsules are more easily transported after their initial deposition because they are lighter in weight, the split head capsules were calculated separately from the rest of the Moaralmsee data.

Spatial analyses were performed using Mantel non-parametric tests (Mantel 1967; Mantel and Valand 1970) on the midge assemblages to determine if spatial autocorrelation existed in the intra-lake dataset, which may be considered to come from a strongly spatially structured environment. A Bray-Curtis distance was used for the biological distance matrix and geographic distance between the sites for the spatial distance matrix (1000 randomizations), following the example of Quinlan et al. (2003) and Nevalainen (2011a). Geographic distances between sampling points were derived using a map tool, because exact coordinates were not measured during sediment sampling. The Mantel test was performed using the program PAST (Hammer et al. 2001). The Mantel test is a permutation test for correlation between two distance or similarity matrices and very suitable for examining spatial autocorrelation (Legendre and Legendre 1998). In addition to the Mantel test, performed on the whole assemblages, autocorrelation tests (Davis 1986) were carried out separately for each taxon. Lags up to *n*/2, where *n* is the number of values in the vector, are fitted along the x-axis (the autocorrelation function is symmetrical around zero). A predominantly zero autocorrelation signifies random data and periodicities turn up as peaks. The "95% confidence interval" (Davis 1986) is the confidence interval for random, independent points (white noise). White noise is an unrealistic null model and the confidence interval is only strictly valid at each individual lag. The one-dimensional (longest direction, NE-SW, in Fig. 1) autocorrelation test is suitable for relatively evenly distributed samples, such as in the present dataset.

For developing the water-depth inference model, several calibration techniques were used to select the method that performed best, i.e. that which yields a high squared correlation between jackknife-predicted and observed values (R^2_{jack}), low prediction error (RMSEP), and low mean and maximum biases in jackknife residuals. The methods used were simple WA with an inverse de-shrinking regression, WA with taxon tolerance weighting (WAtol) and an inverse de-shrinking regression, simple WA with a classical de-shrinking regression, WA with WAtol and a classical de-shrinking regression, locally weighted WA (LWWA), partial least squares (PLS), WA-PLS, a Gaussian logit model (i.e. maximum likelihood), and the modern analogue technique (MAT) (Juggins

2007). The inference models were developed and tested with the program C2.

Results

Midges dominated in Lake Moaralmsee, mayflies occurred infrequently, and oribatid mites were more common than hydrachnid mites (Fig. 3). *Paracladius* was the most abundant midge taxon (30 occurrences, mean abundance 34.1%), followed by *Tanytarsus lugens*-type (23, 25.8%), *Psectrocladius sordidellus*-type (25, 14.2%), and *Paratanytarsus austriacus*-type (29, 7.7%) (Fig. 4). Most of the 28 midge taxa encountered, of which eight were common ($N2 \geq 5$), showed a linear response to water depth, but *Paracladius* and *Heterotrissocladius marcidus*-type had unimodal responses. Instead of having common faunal break points, the taxa showed gradual shifts from the littoral towards offshore assemblages. About 75% of the taxa displayed a statistically significant relationship ($p \leq 0.001$) with water depth, assessed using GLMs. Of the most abundant taxa, *Corynoneura arctica*-type and *P. sordidellus*-type had shallow optima, *Paracladius* and *H. marcidus*-type had intermediate optima, and *Procladius* and *Tanytarsus lugens*-type had deep optima, relative to the depth gradient in the dataset (Fig. 5). Among the common taxa, *P. austriacus*-type ($N2 = 19.6$), *Cricotopus cylindraceus*-type ($N2 = 7.9$), and *Zavrelimyia*

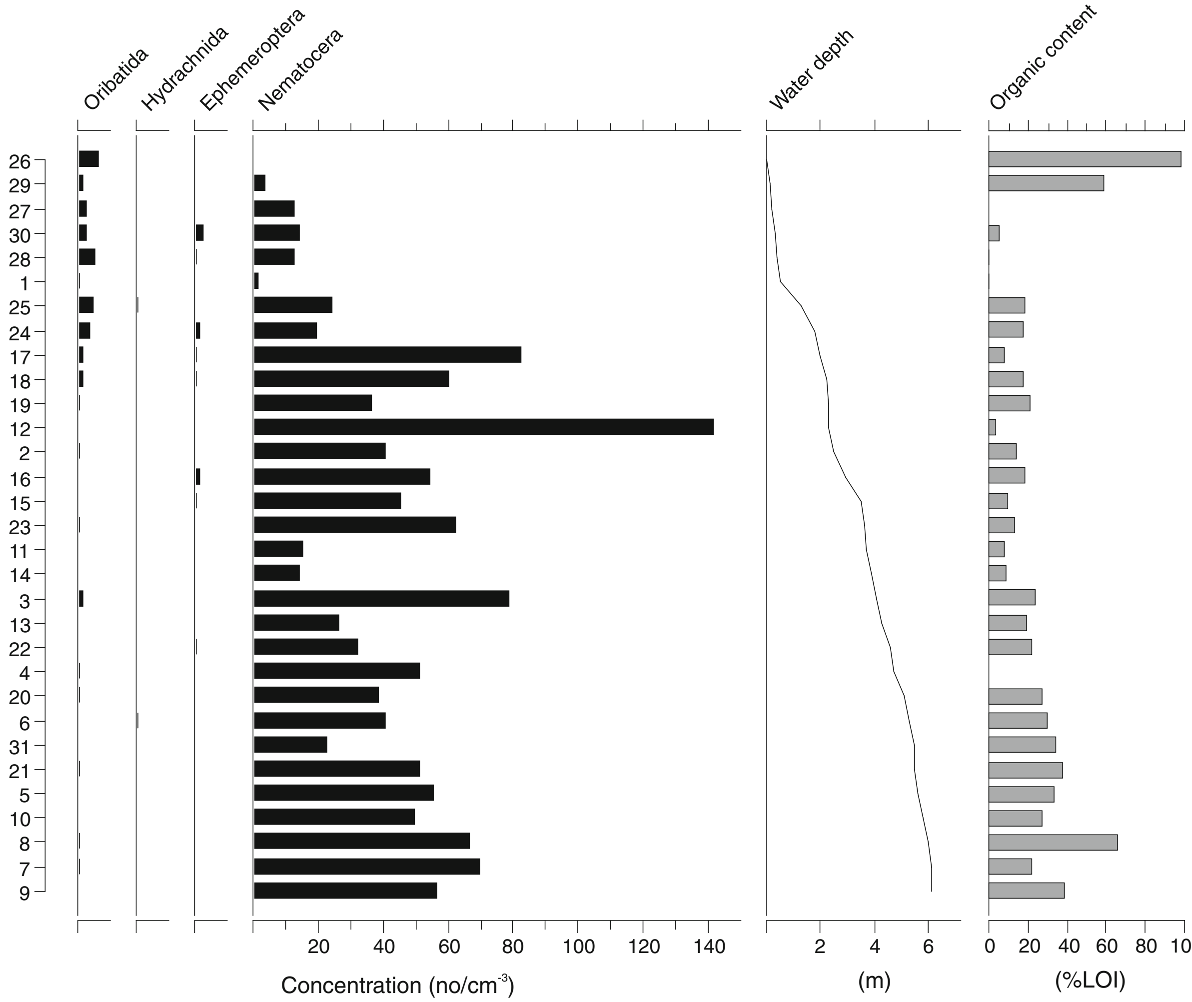

Fig. 3 Concentration per cm^3 of aquatic mites (Oribatida and Hydrachnida), mayflies (Ephemeroptera), and midges (Nematocera) along the water depth transect and organic content of the sediment (measured as loss-on-ignition, LOI) in Lake Moaralmsee

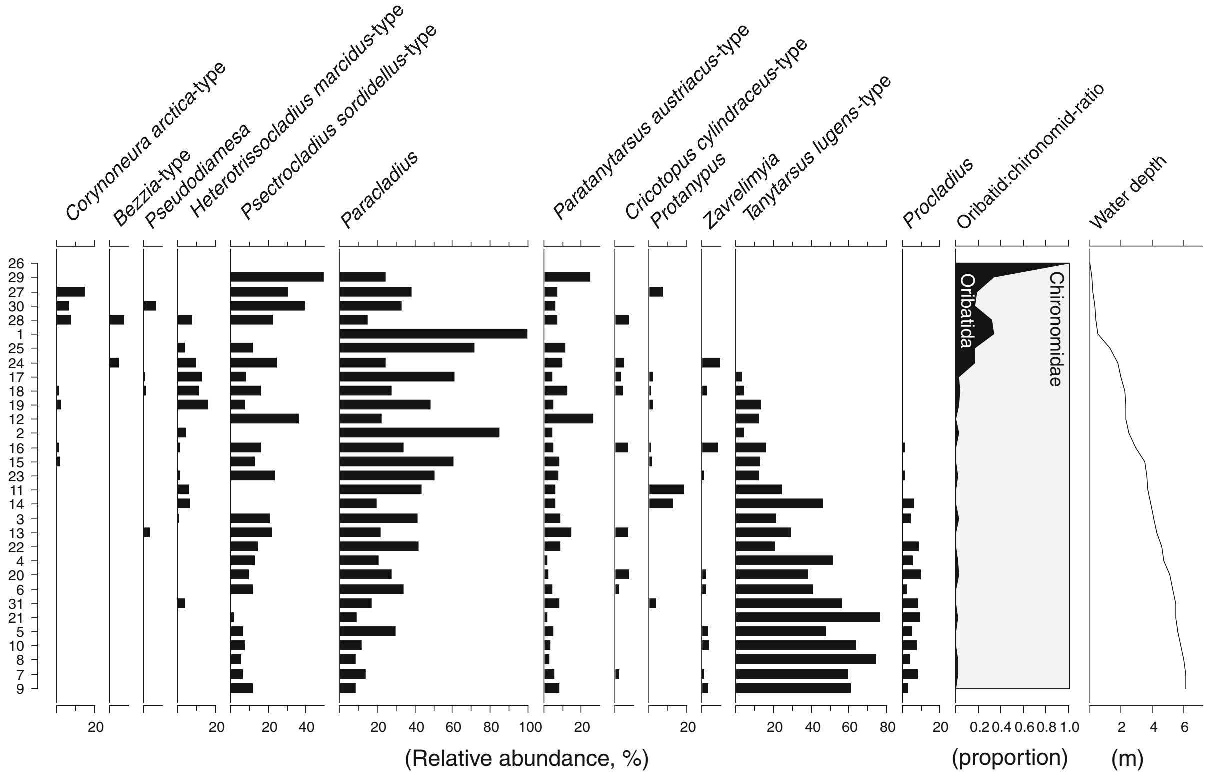

Fig. 4 Relative abundances of the most common midge taxa in Lake Moaralmsee. The taxa are arranged according to their water depth optima (weighted averaging) from the shallowest (*left*) to the deepest (*right*) and the samples are arranged according to their depth from the shallowest (*top*) to the deepest (*bottom*). The oribatid:chironomid ratio along the water depth gradient is also shown

(N2 = 6.8) did not have a significant relationship with water depth. The ratio between oribatid exoskeletons and chironomid head capsules showed that oribatids dominate near the land–water interface and remain common in littoral samples (Fig. 4). Samples retrieved from sites with depth >2 m were almost completely dominated by chironomids.

The highest number of taxa in the volumetric samples was found in some samples from intermediate depths (maximum $S = 17$ at 2.2 m) and lowest in littoral samples (minimum $S = 0$ at 0 cm), whereas the deeper-water samples (>3 m) were characterized by 5–7 taxa (Fig. 6a). The Shannon diversity index was more variable in samples from <3 m depth, but there was a general decline in diversity of samples from depths >3 m (Fig. 6b).

Few chironomid head capsules belonging to the 1st larval stage were found in surface sediments of Moaralmsee, but 2nd instars were more frequent. The majority of the head capsules were those of 3rd and 4th instars. Early instar chironomid head capsules, belonging to 1st and 2nd larval stages, were very limited in the littoral samples, but were more abundant in samples taken from depths >1 m (Fig. 7a). Overall, the relationship between the proportion of early instar head capsules and depth was weak ($r = 0.33$, $R^2 = 0.11$) and insignificant statistically ($p = 0.072$). A clear trend, in which a larger proportion of early instar head capsules was deposited in deeper water, was apparent for accumulation of instars of the most common taxon, *Paracladius* ($r = 0.48$, $R^2 = 0.23$, $p = 0.007$) (Fig. 7b). In addition, a significant trend ($r = 0.52$, $R^2 = 0.27$, $p = 0.004$) was found for the broken (split up) head capsules of the subfamily Orthocladiinae, for which the number of split head capsules was clearly higher in littoral samples (Fig. 7c).

The DCA showed gradient lengths of 2.3 SD (variance explained 33.4%) for axis 1 and 1.5 SD (11.1%) for axis 2, and indicated that both CCA and

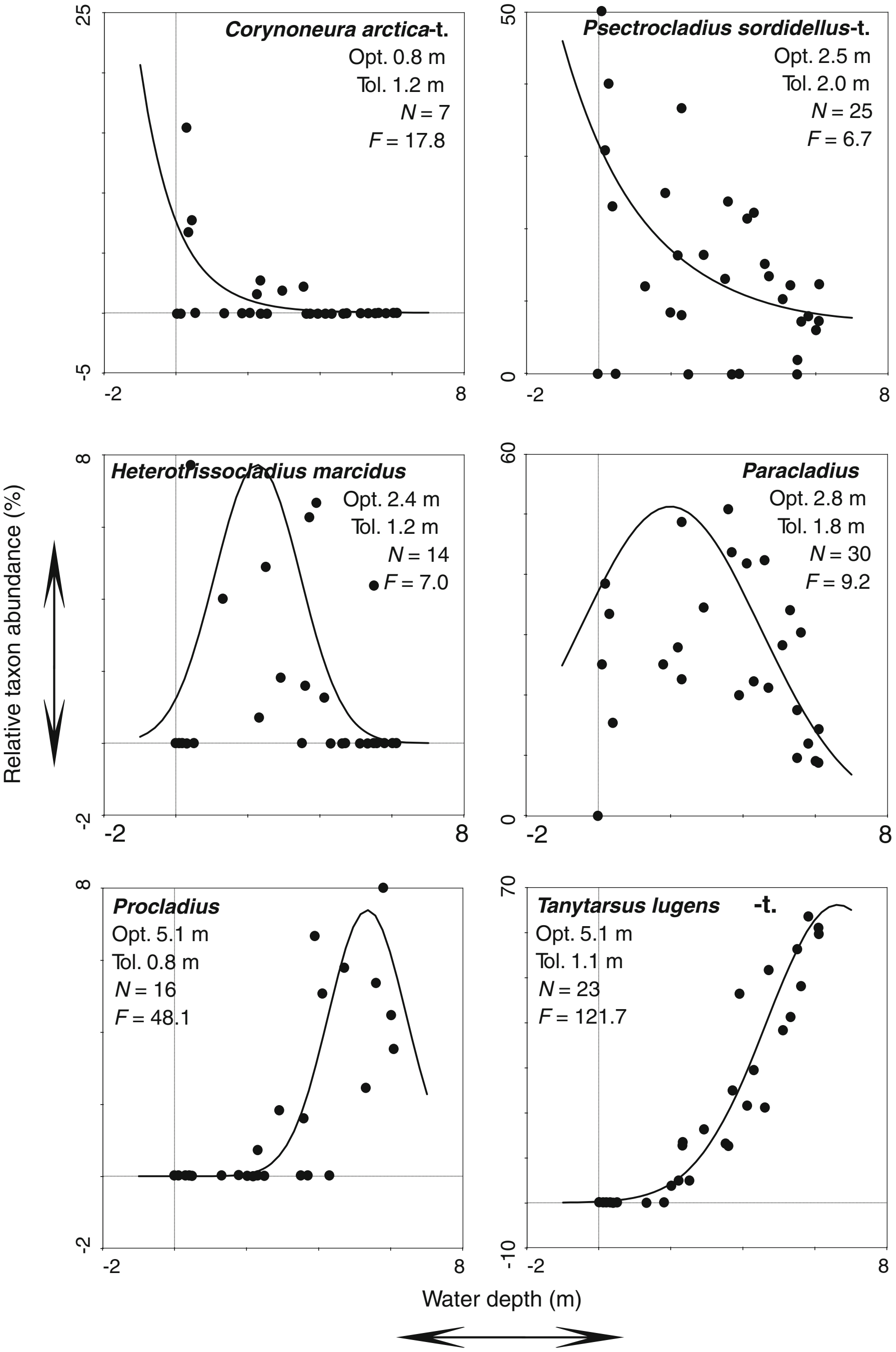

Fig. 5 Taxa response curves (generalized linear models) to water depth for the most common taxa that display a significant relationship ($p \leq 0.001$) with water depth in Lake Moaralmsee. The estimated optima and tolerances using weighted averaging, number of occurrences (*N*), and *F* statistics for testing model significance relative to null model are given for these taxa

redundancy analysis (RDA) would be appropriate methods for further numerical analyses. The CCA, which was selected, showed that chironomid distribution in the lake basin is strongly related to water depth because the level of statistical significance was $p < 0.001$, the λ_1:λ_2 ratio 1.662, the species environmental correlation (r) 0.928, and the variance explained by the species data 28.6%. In the case of the relationship between midge assemblages and LOI, the λ_1:λ_2 ratio was 0.518, p was 0.002, r was 0.689, and the variance explained by the species data 10.2%. These results showed that water depth was more important in explaining midge distribution than was LOI. No significant relationship was found

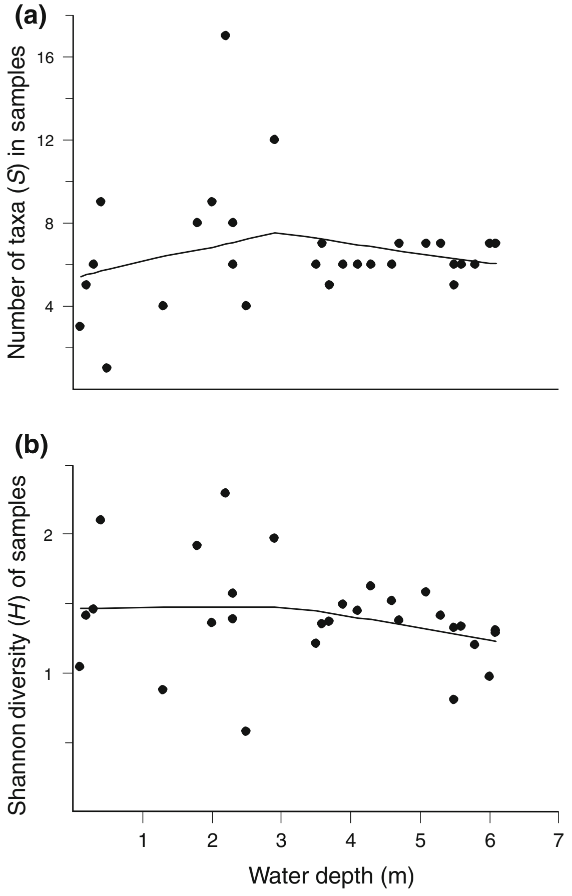

Fig. 6 Fossil remains of midges in surface sediments, reported as **a** number of taxa per sample (*S*) and **b** Shannon diversity index of samples (*H*), along the water-depth gradient in Lake Moaralmsee. A locally weighted scatterplot smooth is applied to the figures using a span of 0.9 to illustrate general trends

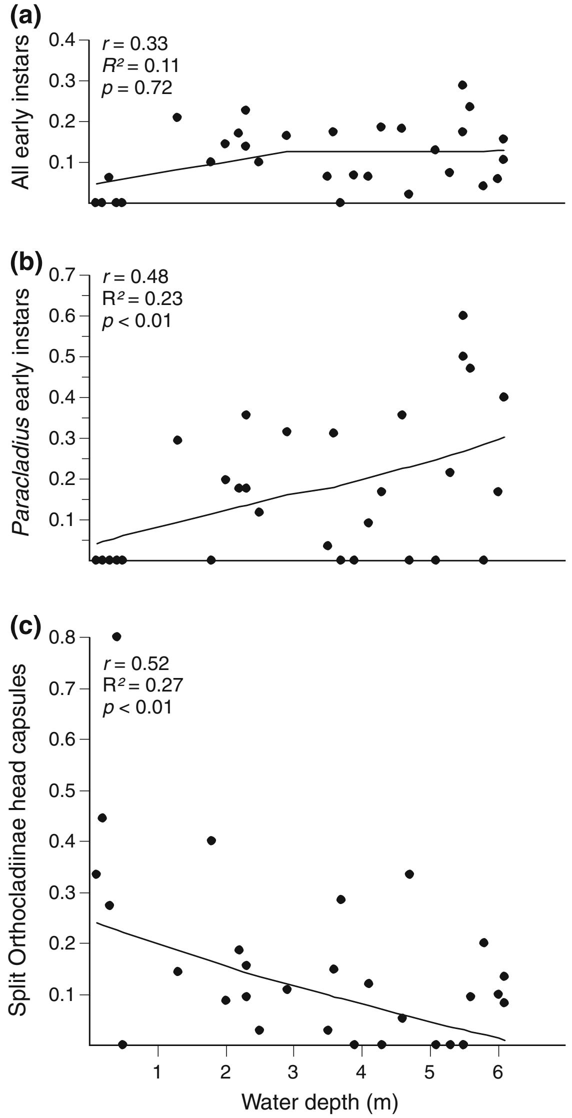

Fig. 7 Proportion of **a** early instar chironomid head capsules, **b** early instar *Paracladius* head capsules, and **c** broken (*split*) head capsules of Orthocladiinae along the water-depth gradient in Lake Moaralmsee. A locally weighted scatterplot smooth is applied to the figures using a span of 0.9 to illustrate general trends

between water depth and LOI ($r = 0.12$, $R^2 = 0.01$, $p = 0.546$), which might otherwise increase model ambiguity. Of the different water-depth inference model types tested (Table 1), WA using classical de-shrinking regression and down-weighting of taxon tolerances showed the best performance statistics, with an R^2_{jack} of 0.905, RMSEP of 0.621 m (9.8% of the training set gradient), and mean and maximum biases of −0.137 and 0.876 m, respectively (Fig. 8a). The littoral samples had residuals with a tendency towards higher inferred depths, but otherwise the residuals were quite evenly distributed within the residual plot (Fig. 8b).

The Mantel test revealed only minor spatial autocorrelation in the dataset with an *r* of 0.17 and *p* of 0.028. This correlation was significant at $p \leq 0.05$, but insignificant at $p \leq 0.01$. Autocorrelation tests run separately for each taxon (Fig. 9) revealed that the distribution of head capsules of *Tanytarsus lugens*-type suffered most from autocorrelation. When the Mantel test was rerun for the taxa assemblages by excluding *Tanytarsus lugens*-type, spatial autocorrelation weakened ($r = 0.11$) and became insignificant ($p = 0.064$).

Table 1 Performance statistics for the different midge-based water-depth calibration models

Technique	R^2_{jack}	Mean bias	Maximum bias	RMSEP
$\text{WA}_{\text{inverse}}$	0.81	−0.10	1.36	0.86
$\text{WA}_{\text{classical}}$	0.81	−0.12	1.21	0.87 (−0.3%)
$\text{WAtol}_{\text{inverse}}$	0.90	−0.12	1.07	0.66
$\text{WAtol}_{\text{classical}}$	**0.91**	**−0.14**	**0.88**	**0.62 (+6.3%)**
$\text{WA-PLS}_{\text{comp. 1}}$	0.80	−0.13	1.50	0.89
$\text{WA-PLS}_{\text{comp. 2}}$	0.76	−0.12	1.46	0.96 (−7.5%)
$\text{WA-PLS}_{\text{comp. 3}}$	0.72	−0.17	1.56	1.05 (−9.7%)
$\text{PLS}_{\text{comp.1}}$	0.71	−0.05	1.65	1.05
$\text{PLS}_{\text{comp.2}}$	0.76	−0.06	1.41	0.96 (+8.0%)
$\text{PLS}_{\text{comp.3}}$	0.74	−0.10	1.59	0.99 (−3.0%)
$\text{MAT}_{\text{average of 10}}$	0.84	−0.42	2.00	1.01
$\text{MAT}_{\text{weighted average of 10}}$	0.88	−0.41	1.78	0.91
Maximum likelihood	0.87	−0.15	1.77	0.72
$\text{LWWA}_{\text{inverse}}$	0.81	−0.12	1.40	0.87
$\text{LWWA}_{\text{classical}}$	0.81	−0.14	1.23	0.88

The methods used were simple WA with an inverse de-shrinking regression, WA with taxon tolerance weighting (WAtol) and an inverse de-shrinking regression, simple WA with a classical de-shrinking regression, WA with WAtol and a classical de-shrinking regression, locally weighted WA (LWWA), partial least squares (PLS), WA-PLS, a Gaussian logit model (i.e. maximum likelihood), and the modern analogue technique (MAT). The best model (i.e. highest coefficient of determination, lowest error of prediction, and mean and maximum biases) was developed using $\text{WAtol}_{\text{classical}}$ (in bold type). The brackets behind the RMSEPs indicate the change in error compared to the simplest model

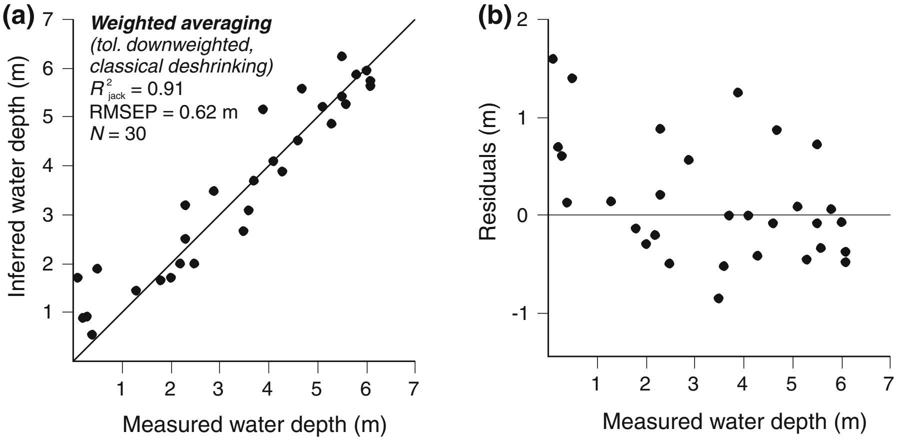

Fig. 8 Weighted averaging (tolerance downweighted/classical de-shrinking) chironomid-based intra-lake inference model of water depth from Lake Moaralmsee, illustrated as **a** the 1:1 relationship between measured and inferred water depth, and **b** the residuals along the water depth gradient

Discussion

Distribution of aquatic mites and insects along the water-depth gradient

Within-lake variability in limnological characteristics is strongly determined by water depth in lakes with homogenous catchment characteristics, such as Lake Moaralmsee. Autumnal limnological measurements from Moaralmsee showed that temperature and oxygen content decrease with increasing water depth (Fig. 2). Midges are known to be sensitive to both temperature and oxygen (Bryce and Hobart 1972; Walker 2001; Brooks et al. 2007) and have hence been used to reconstruct past changes in air/water temperature (Heiri and Lotter 2005) and hypolimnetic oxygen (Quinlan and Smol 2001b; Luoto and Salonen 2010). Furthermore, other limnological factors also

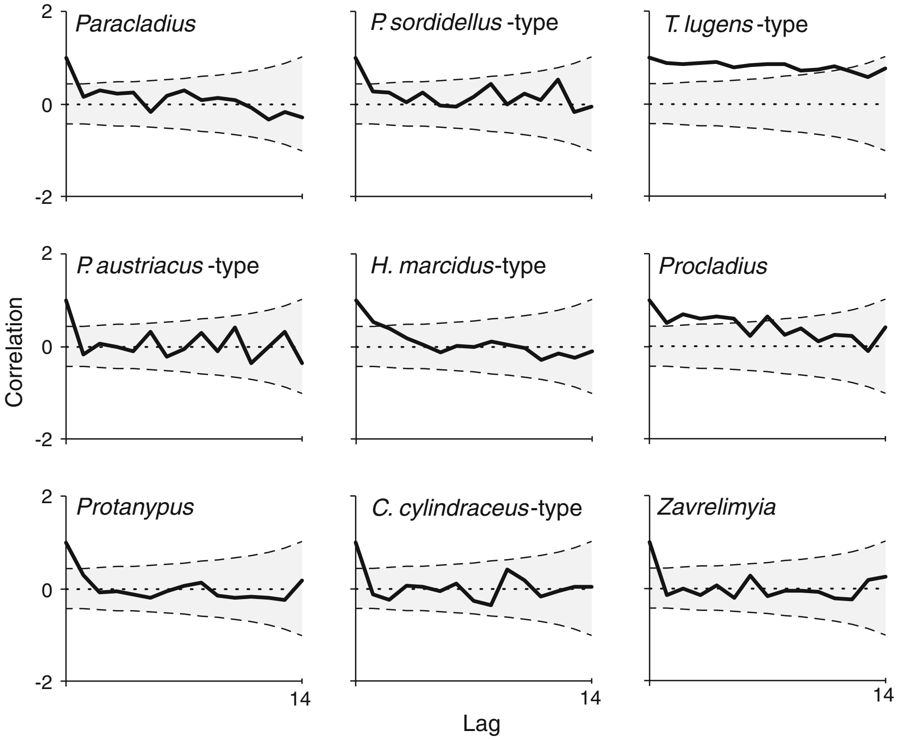

Fig. 9 Autocorrelation tests for the most common taxa in Lake Moaralmsee. Lags up to *n*/2, where *n* is the number of values in the vector, are shown along the x-axis. The autocorrelation function is symmetrical around zero. A predominantly zero autocorrelation signifies random data, while periodicities show up as peaks. The "95% confidence intervals" (*gray area*) follow Davis (1986) and represent the confidence intervals for random, independent points (*white noise*). White noise is an unrealistic null model and the confidence interval is only strictly valid at each individual lag

control midge distribution (Ruse 2010; Raunio et al. 2010) and it is possible to reconstruct past total phosphorus concentrations, chlorophyll *a*, and pH from lake sediments using fossil midge assemblages (Brooks et al. 2001; Langdon et al. 2006; Rees and Cwynar 2010; Luoto 2011). These limnological characters change, along with water depth, as the autumnal pH and chlorophyll *a* were elevated at depths >5 m in Moaralmsee (Fig. 2).

Results from Moaralmsee show that the distribution of midge larvae is strongly determined by water depth, which has been noted in many studies that examined fossil data (Korhola et al. 2000; Heiri 2004; Barley et al. 2006; Kurek and Cwynar 2009b; Engels and Cwynar 2011) and living larvae (Mousavi 2002; Jyväsjärvi et al. 2009). Therefore, because many environmental variables are linked to depth, a critical question in midge-based paleoenvironmental reconstructions arises—what is the ultimate variable(s) that is being inferred if changes in lake depth and other environmental variables occur simultaneously over time? A potential approach to tackle this question is to reconstruct water depth alongside the inferred environmental variable of interest, e.g. temperature (Luoto et al. 2010). It may not always be possible to separate the signals of the two variables, but may provide insights into whether lake level changes have occurred. In addition, identification of indicator taxa for inferred variables can be helpful when trying to separate the signals of these variables (Luoto et al. 2010). Midge-based calibration models of water depth, however, are not available for every region, and taxon-specific responses to water depth (direct or indirect) can vary between geographic regions, thus reducing the applicability of models constructed elsewhere. Nevertheless, if a regional calibration set is not available for a particular study site, local or site-specific models (Kurek and Cwynar 2009a) can be constructed relatively easily. Unfortunately, fossil midge assemblages can be mixed if steep or wind exposed lake basins are examined (Holmes et al. 2009; van Hardenbroek et al. 2011), thereby ruining the possibility for developing intra-lake, midge-based water depth models.

Of the remains of aquatic mites and insects, midges were most abundant in Moaralmsee (Fig. 3). The sample taken near the land/water interface (sample 26 at 0.05 m), however, consisted completely of oribatids, possibly representing a mixture of limnic, limnotelmatic, and terrestrial species. They were present in all samples taken from depths <2 m (Fig. 4). Hence, the oribatid:chironomid-ratio may be useful as a simple tool in downcore paleolimnological studies to detect changes in past lake level, which may influence midge-based reconstructions of other variables. Oribatids can be found from the tropics to the Arctic (Solhøy 2001) and consequently, provide an approach that can be widely applied. The reliability of the oribatid:chironomid-ratio as an indication of a water depth must, however, be further assessed in other regions. Furthermore, the method may only work well in relatively shallow coring sites and when there have been relatively large shifts in lake level, as oribatids seem to be common only in water depths <2 m (Fig. 3).

Fossil midge assemblages in Moaralmsee showed a distinct gradient along the water-depth transect (Fig. 4) and this relationship was statistically significant. Among the most common taxa, *Corynoneura arctica*-type and *Psectrocladius sordidellus*-type were identified as indicators of shallow water, *Heterotrissocladius marcidus*-type and *Paracladius* were indicators of intermediate depths, and *Procladius* and *Tanytarsus lugens*-type were found in deep water sites (Fig. 5). Although not all of these taxa were identified in every previous intra-lake dataset, the observations are consistent with those of previous studies in western Alaska, USA (Kurek and Cwynar 2009b), northeastern USA (Engels and Cwynar 2011) and eastern Finland (Luoto 2010), providing evidence of a rather uniform response of these taxa to water depth. Midge response to water depth is mostly indirect and mediated through changes in water chemistry, substrate type, and macrophytes (Figs. 2, 4; Hofmann 1998; Brodersen and Quinlan 2006; Luoto 2010). Consequently, many littoral taxa (e.g. *P. sordidellus*-type) are associated with macrophytes (sample 29 in this dataset) and warmer temperatures, and deep-water taxa (e.g. *T. lugens*-type) are associated with soft sediments and cold temperatures (Figs. 2, 4; Luoto 2009c, 2010). This makes it difficult to identify the most important factor influencing specific taxa. It also confounds single-variable paleoenvironmental reconstructions and makes the multi-proxy approach essential.

Results from Moaralmsee do not indicate any particularly distinct change in midge taxon richness along the water-depth gradient, although intermediate samples generally had the highest number of taxa (Fig. 6a). The Shannon diversity of samples was more variable in shallow and intermediate samples, but showed a slight general decline in the deepest sites (Fig. 6b). Intermediate depths also displayed the highest number of midge taxa in a lake in eastern Finland, which had an abundance of habitat types, including different littoral vegetation stands, lentic and lotic environments, and highly variable substrate properties (Luoto 2010), but Engels and Cwynar (2011) found uniform taxon richness throughout several lakes in the northeastern USA. This implies that intra-lake midge diversity patterns are not uniform among lakes and that such patterns are probably related to lake type and habitat diversity.

Instar-specific variability in fossil midge assemblages

According to Walker (2001), the most common chironomid remains in lake sediments are the head capsules of 3rd and 4th instars. For some chironomids, however, the 4th instar head capsules can remain attached to the larval exuviae, hence head capsules are found beyond the larval habitat. Furthermore, early instar larvae are frequently found in fossil samples regardless of the fact that 1st instar head capsules easily pass through sieves of ~100 μm, and that chitin of the 1st and 2nd instar head capsules may be resorbed prior to ecdysis (Iovino 1975). The taphonomy of midge head capsules belonging to different instars is not well established, although it may be important for the reliability of paleoenvironmental reconstructions. An individual organism may be represented in lake sediments by one to four head capsules (Luoto and Raunio 2011), thus selective deposition patterns or preservation can distort the assemblages. Carter (1977) included only the 4th instars in a down-core analysis, but instar separation is not widely done in chironomid analysis. Carter (2001) also tested whether the interpretation of down-core results is affected by identification of some taxa to the instar level and found that proportions of 3rd and 4th instars were not constant throughout the examined sediment cores, suggesting there was differential preservation of instars. Although including only one instar in fossil analysis has the advantage of avoiding duplicate counting of a single individual, it has the drawback that more sediment material is needed (Carter 2001).

In this study, larval stages were separated on the basis of head capsule morphology, i.e. size and thickness of the cuticle. The accumulation patterns showed a trend in which littoral samples consisted almost solely of capsules of late instar larvae, and the intermediate and deep-water sites had a larger proportion of early instar capsules (Fig. 7a). The relationship between the proportion of early instar remains and depth, however, was not significant. When the proportion of early instar capsules belonging to the most abundant taxon, *Paracladius*, was examined, there was a significant trend of greater early instar deposition in deep water (Fig. 7b), but no noticeable pattern was found for other common taxa such as *P. sordidellus*-type and *T. lugens*-type. This may indicate that patterns in instar taphonomy may be taxon-specific. Furthermore, these deposition patterns may indicate niche separation of the different larval stages. For instance, most of the 1st instar larvae are planktonic and only settle to the bottom for ecdysis (Walker 2001). Because there can be significant variability in the accumulation of different fossil instars (Fig. 7b) and because no living larvae were sampled in the present study, future efforts should investigate the possibility of taxon-specific habitat differences between larval stages and related taphonomy.

Midge head capsules belonging to the subfamily Orthocladiinae are often found broken in two pieces as they easily split down the middle. Some of this damage is caused by laboratory treatment (mostly the sieving), but samples often contain specimens containing only half a head capsule, implying that the head capsule broke in two prior to sampling. This may indicate transport following initial deposition. Split head capsules from Moaralmsee were assessed separately to examine whether split Orthocladiinae head capsules are transported more easily after initial deposition. Results showed a significant negative relationship between split head capsules and water depth (Fig. 7c). Surprisingly, more split head capsules were found in littoral samples. This is most likely because the littoral samples contained more coarse mineral material, causing greater in situ and laboratory breakage of head capsules. Sample 29 had coarse mineral composition (large grain size), though the LOI analysis indicated higher organic content (Fig. 4) due to the presence of aquatic macrophytes. Because more broken Orthocladiinae remains were found in littoral samples, it seems that split head capsules are not preferentially transported to the deepest part of the basin. It should also be noted that head capsules of Orthocladinae often split during moulting, thus a split head capsule is not necessarily a sign of redeposition.

Although the present results suggest some within-lake variability in instar-specific head capsule distribution and in the occurrence of split head capsules, the results do not show an immediate reason why future studies should identify chironomids into instar-specific pseudotaxa. However, the results do stress the need for more research on taphonomy-related subjects. The most problematic situation in midge stratigraphy would probably arise if the processes responsible for the differences in head capsule accumulation had changed through time.

Chironomid-based inference model for water depth

Of the 31 samples analyzed, 30 included chironomids. The strong relationship between chirononomid distribution and water depth in Lake Moaralmsee, with a λ_1:λ_2 ratio of 1.66 and r of 0.93, indicated that it was possible to develop a valid water-depth transfer function. Of the tested model types, WA models outperformed the others in their R^2_{jack}s, RMSEPs, and maximum biases (Table 1). In addition, the maximum likelihood method provided favorable performance statistics. The best performance statistics were derived using WA with classical de-shrinking regression and tolerance downweighting. This model had an R^2_{jack} of 0.91, RMSEP of 0.62 m, and mean and maximum biases of −0.14 and 0.88 m, respectively (Fig. 8a). The maximum biases (Fig. 8b) were found in two littoral samples (samples 2 and 9), one of which was dominated by *Paracladius* (100%) and the other by *P. sordidellus*-type (~50%) (Fig. 4). The sample dominated by *P. sordidellus*-type contained abundant aquatic mosses. The relatively poor water-depth estimates for these samples is probably related to the fact that they were dominated by these particular taxa and that species richness ($S = 1$ and 3) was lowest in these samples (Fig. 6a). Nevertheless, because the number of samples in the model was relatively low (30) and the water-depth estimates of these two samples seemed to fit in with the overall trend of the inferred *vs.* measured relationship (Fig. 8a), all samples were included in the final model.

In principle, it should be possible to construct a chironomid-based calibration model of water depth, taking into account the observed patterns in instar taphonomy (Fig. 7a, b). These patterns can potentially cause autocorrelation in reconstruction results and influence the model performance statistics. Because the autecology of different larval stages remains to be adequately established, however, it is not possible to conclude that the patterns found in fossil instar taphonomy are explained solely by transport after initial deposition. In fact, fossil distribution patterns, considering all instars (Fig. 4) and the calculated taxa response curves (Fig. 5), may represent the habitats of these taxa through all their life stages in Moaralmsee. Furthermore, if a model separating the instars were to be developed, it would require that fossil midge instars be identified.

In this study, the strongest relationship between instar accumulation patterns and water depth was found with *Paracladius*, which was the most abundant taxon, but no significant relationship was found using the total instar deposition or instar patterns of e.g. *T. lugens*-type or *P. sordidellus*-type. Because the water-depth optimum of *Paracladius* (2.8 m) was slightly shallower than the mean depth of Moaralmsee (3.1 m), and early *Paracladius* instars seem to have a tendency to deposit in intermediate and deep-water sediments, the model performance statistics may be weakened. Nevertheless, even with this potential bias, the present chironomid-based inference model for water depth has very favorable performance statistics compared to previous midge/water-depth models (Korhola et al. 2000; Barley et al. 2006; Kurek and Cwynar 2009a; Luoto 2009a, 2010), indicating that it is ready to be used in a downcore study. Because of possible lake-specific discrepancies in modern distributions, the model is most suitable for use in the training set lake itself, but may be applicable to nearby lakes if similar assemblages are present. It remains to be shown how different a lake must be for the model to break down. Another factor that may determine the wider applicability of the model, besides a match in taxonomic composition, could be the range of variables that co-vary with water depth, such as temperature and dissolved oxygen.

There are inevitable taphonomy-related model autocorrelations involved with intra-lake calibration sets, as fossil remains can be transported (postmortem) downslope, but probably not in the opposite direction. Spatial autocorrelation, the tendency of closely located sites to resemble one another, is not solely a problem in intra-lake models, but is a common factor in other training set types and in ecological data, as well (Legendre 1993). It may lead to inappropriate model choice and misleading, over-optimistic estimates of model performance (Telford and Birks 2005, 2009). In particular, the modern analogue technique (MAT) can be sensitive to autocorrelation (Telford and Birks 2005). Similar to MAT, the locally weighted weighted-averaging (LWWA) technique creates "local" datasets within the true dataset and may suffer from autocorrelation more easily than other WA-based methods that use data from the whole training set. Therefore, if a MAT- or LWWA-based model suffers from spatial autocorrelation, other WA-based methods may be more appropriate. There are various techniques and tests to assess autocorrelation in ecological and paleoecological data (Legendre 1993; Quinlan et al. 2003; Telford and Birks 2005, 2009; Laird et al. 2010; Moberg and Brattström 2011; Naimi et al. 2011; Nevalainen 2011). Assessment of how well the inferred estimates correspond to the main direction in variation of the species assemblages (i.e. CA or PCA axis scores) can also be used to determine the most appropriate model for downcore application (Laird et al. 2010). The performance of the MAT approach is more sensitive to poor analogues, which have a low correspondence to the main direction in variation. In spatially autocorrelated training sets, the MAT usually provides superior performance statistics compared to other model types (Telford and Birks 2005) as a consequence of the cumulative influence that autocorrelation has on MAT model performance statistics. This, in turn, is a result of the influence of the "local" datasets (usually 10 closest analogues) that feed the autocorrelation. Therefore, unrealistically superior performance of the MAT can be used as a test to examine whether spatial autocorrelation exists in a training set. It has been shown, however, that most of the results published with MAT over the last three decades are statistically sound (Guiot and de Vernal 2011), hence there is no reason to abandon the technique.

In the present training set, MAT showed poorer performance statistics compared to the WA-based methods, suggesting no considerable spatial autocorrelation. The Mantel test, however, indicated that the midge assemblages exhibited statistically significant spatial autocorrelation ($p = 0.028$), but this relationship was very weak ($r = 0.17$). The separate autocorrelation tests for each taxon showed that the most problematic taxon was *Tanytarsus lugens*-type (Fig. 9). When the Mantel test was rerun for the assemblages with *T. lugens*-type removed, the autocorrelation became insignificant. These tests suggest that *T. lugens*-type may cause problems in downcore reconstructions of water depth and may also improve the model's performance statistics unrealistically. Previous studies, however, confirmed that *T. lugens*-type is a characteristic taxon of deep-water communities (Brundin 1949; Luoto 2009a, 2010; Engels and Cwynar 2011), hence it is very likely that its estimated water-depth optimum in Lake Moaralmsee (Fig. 5) is realistic and there should be no particular risk (compared to the other taxa) involved in using *T. lugens*-type in downcore water-depth reconstructions, especially if the MAT is not used.

Conclusions

Aquatic mite and insect distributions in Lake Moaralmsee, Austria were strongly related to water depth, which mostly determines in-lake variability in temperature, substrate, and water chemistry. Because fossil midges are often used to infer past changes in temperature and water chemistry, simultaneous changes in lake depth can potentially confound inference of these variables. Enumeration of oribatid mites along with chironomids, and utilization of the oribatid:chironomid-ratio, can be used as a rough proxy for lake level changes.

There was an apparent trend in accumulation of head capsules of different instars. Early instars showed greater deposition in intermediate and deep-water sites. This trend was clearest in the most common taxon, *Paracladius*. Because this study did not distinguish whether this pattern in instar deposition was caused by transport after initial deposition or by different niche requirements of living larval stages, the chironomid-based inference model for water depth was developed using all instars. Accumulation variability among instars can potentially influence water-depth reconstructions, and habitat patterns for living larvae must be assessed further.

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