

Are fossil assemblages in a single sediment core from a small lake representative of total deposition of mite, chironomid, and plant macrofossil remains?

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Received: 3 October 2011 / Accepted: 28 July 2012 / Published online: 12 September 2012
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Abstract How representative of the whole-lake fossil assemblage are analyses from a single sediment core taken in the centre of a small lake? This question was addressed in five shallow Norwegian lakes that ranged in location from low-altitude, boreal-deciduous forest to mid-alpine environments. Surface-sediment samples were taken from the deepest part of each lake and in two transects running from the lake centre to shore, and analysed for mites, chironomids, and plant remains. Ordination techniques summarised patterns of variation between and within lakes. Correlations between whole-lake assemblages and water depth and sediment organic content (loss-on-ignition) were investigated. Representativeness of

each sample of the whole-lake assemblage was determined by comparing Principal Components Analysis scores of the original data with those of Monte Carlo-simulated data sets, using the actual data as constraints in the simulations. The majority of samples are representative of the whole-lake assemblages. Littoral samples, however, are most frequently unrepresentative or poorly representative samples. Water depth is an important controlling variable. A sediment core from the lake centre has the highest probability of representing the whole-lake assemblage. It may, however, also yield the lowest concentrations of terrestrial remains. A sediment core from the slope is slightly more likely to be unrepresentative of the total plant macrofossil assemblage, but generally has higher concentrations of terrestrial remains. These site differences should be considered when choosing a core location. Overall, the three fossil types

Electronic supplementary material The online version of this article (doi:10.1007/s10933-012-9637-y) contains supplementary material, which is available to authorized users.

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are deposited in similar patterns. Therefore they can be satisfactorily analysed using a single core.

Keywords Within-lake deposition patterns · Representativeness · Oribatid mites · Chironomids · Plant macrofossils · Modern sediment samples · Monte Carlo simulations

Introduction

Remains of plants and animals in lake-sediment sequences are used as proxies for biotic, ecological, and environmental change. Environmental aspects such as vegetation development or climatic factors are reconstructed from species assemblages and knowledge of their modern environmental tolerances (Erickson and Platt 2007; Birks 2007; Heiri 2007; Walker 2007).

Sub-fossil assemblages in lake sediments are influenced by a range of taphonomic processes, from initial production of plants and animals through to their final incorporation into lake sediment (Birks 1980; Birks and Birks 1980). Topography and vegetation around a lake can affect the flux of terrestrial remains to the lake. Transport into the lake by wind or water and processes within the lake can influence sub-fossil representation further. Floating remains may be expected to be deposited near the shore, whereas other remains may sink and be incorporated into sediments near the shore or the lake centre (Birks 1973; Glaser 1981; Erickson 1988).

For aquatic organisms, initial within-lake distribution is primarily influenced by their ecology. The distributions of living aquatic chironomid larvae are determined by the nature of the sediments and factors such as water depth, salinity, oxygen availability, and dissolved organic carbon (Walker 2007). After ecdysis, shed exuviae undergo a range of taphonomic processes. It is mainly the chitinised larval head capsules that are preserved (Walker 2007). Aquatic plant remains are usually deposited near their source (Birks 1973; Zhao et al. 2006).

Factors within the lake, such as morphometry, inlets and outlets, aquatic vegetation, waves, and prevailing wind direction, can all influence the initial point of deposition and possible re-sedimentation of sub-fossils. In combination, these taphonomic processes limit the preservation of fragile objects and can

cause differential influx of plant and animal remains. As a consequence of potential heterogeneous distribution caused by taphonomic processes, it is essential to choose the coring site for paleolimnological analyses that has the highest probability of providing answers to particular research questions of interest (Birks and Birks 2006). For general paleoecological studies, the aim is normally to find the site that best represents whole-lake sub-fossil assemblages. Samples from the deepest point in the lake are considered to provide a representative picture of chironomid assemblages (Schmäh 1993; Heiri 2004, van Hardenbroek et al. 2011). In general, macrofossils of aquatic and shore plants are best represented at intermediate depths, just below the zone of aquatic plant growth (Birks 1973; Dieffenbacher-Krall and Halteman 2000). Oribatid mites are often investigated from similar locations in a lake (Solhøy 2001). Taphonomy of plant macrofossils, mites, and chironomids was reviewed by Birks (1980, 2001), Dieffenbacher-Krall (2007), Erickson and Platt (2007), and Porinchi and MacDonald (2003).

Small sample size is often considered to be a limiting factor for making reconstructions (Heiri et al. 2003). Studies of 30-, 10-, and 5-g samples of lake sediment show that larger samples provide little additional information on aquatic oribatid mites, but that additional material might improve information about the terrestrial environment (Erickson 1988). Increased numbers of sub-fossil specimens, which may increase the potential detail of the results, can be obtained from larger samples obtained using wide-diameter corers or by taking multiple cores. The latter approach must be balanced against the expense and time involved in collecting, dating, analyzing and correlating multiple cores. Therefore, normally only one core is studied (Birks and Birks 2006) from a carefully selected location within the basin. The critical questions are (a) is there an optimal location and (b) where is it?

The aim of this study is to address these questions and determine if a single sediment core from a water body is likely to contain a fossil assemblage that is representative of the fauna and flora of the lake. We need to know if changes in a fossil sequence are due to real changes in the biota or if they are a result of changing taphonomic processes within the lake, related to environmental changes. Therefore, we analysed an array of surface sediment samples to

investigate within-lake distribution of sub-fossil mite, chironomid, and plant macrofossil remains in five shallow Norwegian lakes where Heiri (2004) had previously examined the distributions of recent chironomid remains. Water depth is a potentially important environmental and taphonomic variable. Percent loss-on-ignition (LOI) represents the organic content of the sediment and can reflect a variety of environmental variables such as organic productivity, minerogenic inwash, deposition of coarse organic material or sand near the shore, focusing of fine-grained organic material into deeper water, etc. The lakes were chosen to represent a range of environments along an altitudinal gradient from boreal-deciduous forest to coniferous forest, tree-line, and low-alpine situations, in the hope of making robust generalisations. The lakes are of similar size (>500 m diameter) and depth (9.2–7.3 m), but differ with respect to their surroundings and morphology (Table 1, Fig. 1). They are representative of the types of lakes that have been selected for paleo-studies in Norway. Selected water chemistry variables are presented in Heiri (2004). The lakes lie on acid bedrock, with the exception of some basic rock in the catchment of Råtåsjøen. The prevailing wind direction is from the west and southwest.

Heiri (2004) showed that the chironomid assemblages in these lakes varied with water depth, which influenced quantitative temperature reconstructions (Heiri et al. 2003). Today, many paleoecological investigations study multiple variables (Birks and Birks 2000, 2006; Lotter 2003) and differences in sedimentation patterns of these proxies may constrain the choice of coring site. It is thus important to expand the data from Heiri’s (2004) lakes to include additional proxies. Thus, plant macrofossils and mites were extracted from his material and analysed.

This is an exploratory study, which enables hypotheses to be generated concerning the origin and composition of fossil remains in a sediment core. These hypotheses can be addressed in future detailed studies. For now, our major concern is the representativeness of a single sediment core for paleoecological investigations. These are time-consuming and specialised activities, so it is highly desirable to know if results faithfully represent past biotic and environmental changes. Our information can help identify the optimal coring location within a lake, i.e. the site from which a single core will provide the best representation of all sub-fossil types being studied to answer research questions posed in the investigation.

Study sites

Characteristics of the lakes are described in Table 1. They differ with respect to their surrounding vegetation and position of inlets and outlets (Fig. 1), which are briefly described.

Histøl, 245 m asl, is in the middle boreal vegetation zone (Moen 1999). It is surrounded by marginal fens and possesses deciduous oak-dominated forest on the south-facing slope and pine-spruce dominated forest on the north-facing slope. There are two inlets on the west side and an outlet on the east side.

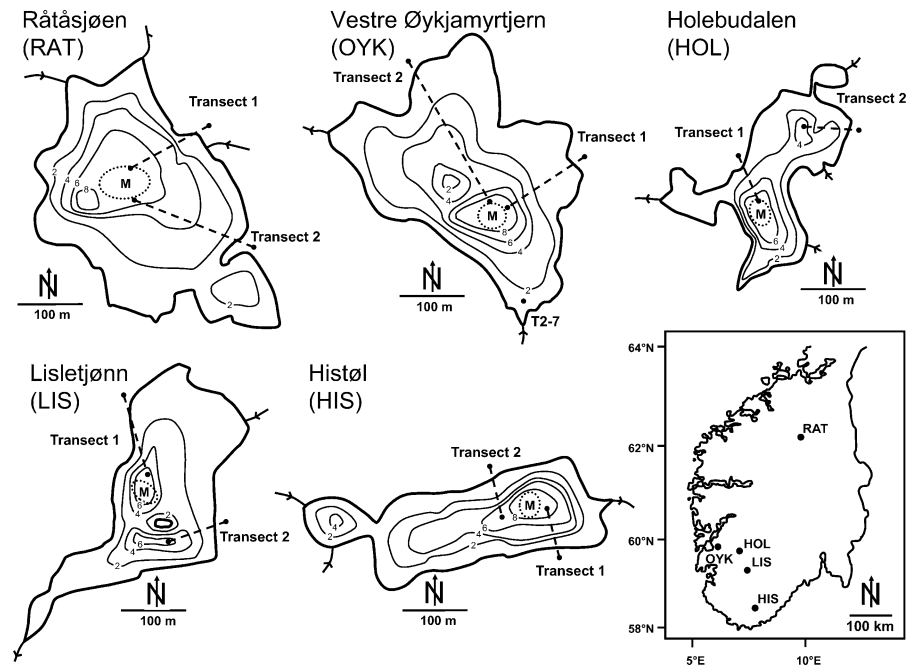
Lisletjønn, 518 m asl, is in the northern boreal vegetation zone (Moen 1999). It is surrounded by spruce-dominated forest, with scattered *Alnus incana* on south-facing slopes. It has one inlet at the northeast end, and an outlet at the southwest end. There is a small island in the southern part and transect 2 is south of the island (Fig. 1).

Vestre Øykjamyrtjern, 570 m asl, is in the boreo-nemoral vegetation zone (Moen 1999), close to the

Table 1 Altitude, geographical location, lake depth, and catchment vegetation for the five study lakes

	Histøl	Lisletjønn	Vestre Øykjamyrtjern	Holebudalen	Råtåsjøen
Abbreviation	HIS	LIS	OYK	HOL	RAT
Altitude, m asl	245	518	570	1,144	1,169
Latitude, °N	58°20′	59°21′	59°21′	59° 50′	62°16′
Longitude, °E	7°47′	7°18′	6°50′	6°59′	9°50′
Maximum lake depth, m	9.2	7.3	7.8	7.5	7.5
Catchment vegetation	Mixed coniferous-deciduous forest	Coniferous forest	Open subalpine woodland, scattered birch and rare pine	Alpine	Alpine

Fig. 1 Map of the five study lakes showing lake location, sampling scheme, and lake morphology. The location of the mid-lake samples is shown by *dotted lines*, and each transect is drawn with *dashed lines*. The inlets and outlets of the lakes are indicated by *arrows*. In OYK, sample T2-7 is taken close to the inlet of the lake, and not in line with the rest of the transect. Site abbreviations follow Table 1. Based on Heiri (2004)



tree-line formed by *Betula pubescens* and *Alnus incana* (Bjune 2005). It is surrounded by heath and grass vegetation, with scattered birch, pine, and willow trees (Bjune 2005). The inlet enters from the south and the outlet is in the northwest.

Holebudalen, 1,144 m asl, is in the low-alpine vegetation zone (Moen 1999). It is surrounded by grass-sedge-dominated tundra vegetation with *Salix herbacea* in snow-bed hollows (Eide et al. 2006). It has three inlets at the east side, one of them flowing from another small lake. The outlet is at the west side.

Råtåsjøen, 1,169 m asl, is in the low-alpine vegetation zone (Moen 1999) in a more continental area and receives less precipitation than the other lakes. It is surrounded by dwarf-shrub heath with abundant *Betula nana*, lichens, and drought-tolerant vegetation (Velle et al. 2005). The lake has two seasonal inlets, one from the east and one from the west (Velle et al. 2005). The outlet is at the north end.

Materials and methods

As described by Heiri et al. (2003), a bathymetric study was performed before short sediment–water interface cores were taken using a HON-Kajak corer (Renberg 1991). Twenty cores were collected from each lake, six from the deepest part of the lake

(M1–M6) and two transects of seven cores each from the lake centre to the shore in progressively shallower water (T1-1 to 7 and T2-1 to 7) (Fig. 1).

The top 1 cm of sediment in each core was used for analysis of chironomids and oribatid mites, following standard methods for chironomids (Heiri 2004). The sediment was rinsed through a 100- μm sieve and mite and chironomid remains were picked out under a stereomicroscope. The remains were dehydrated and mounted on permanent slides in Euparal mounting medium and identified at 400 \times magnification using a compound microscope. Unlike most paleoecological studies involving mites, not only the oribatids, but all mites were included in the analysis. The majority of the mites were, however, oribatids and only specimens within this group were identified to species, using comparisons with specimens from reference collections and drawings in the literature (Gilyarov 1975; Behan-Pelletier 1985, 1989; Weigmann 2006).

Plant macrofossils were analysed from the 2 cm of sediment directly below the chironomid/mite samples, using standard methods (Birks 2001). They were identified and counted, and remains that could not be counted, such as vegetative material, were recorded on an ordinal abundance scale (rare, occasional, frequent, and abundant). Chironomid head capsules were identified by OH, oribatid mites by MPH, and plant macrofossil remains by HHB and Wenche Eide.

Percent LOI at 550 °C for 6 h (Heiri et al. 2001; Heiri 2004) provides an estimate of the organic content of each sample from 1 to 2 cm depth.

Total concentrations of sub-fossils of each group of organisms (numbers per unit volume) are used as measures of abundance. Total numbers of sub-fossil taxa recorded in each group of organisms are used as measures of richness. Samples are divided into three categories: (1) samples closest to the lake shores, T1-7 and T2-7, are referred to as *littoral* samples, (2) the rest of the samples from the transects are called *slope* samples, and 3) mid-lake cores are referred to as *centre* samples.

Data analysis

Results are shown as concentrations per 50 cm³ of wet sediment in diagrams made with TILIA and TGView version 2.0.2 (Grimm 1993, 2004). Total concentrations, numbers of taxa, and concentrations of selected taxa are summarised in Figs. 3, 4, 5, 6, 7. Mite data are still relatively rare in proxy studies, and a full diagram presenting all the mite data is included in Fig. 8. For plant macrofossils and chironomids, the full diagrams are included as electronic supplementary material (Figs. S1–S10). For numerical analyses, the ordinal estimates of plant remains were transformed to 1, 2, 4, and 8, for the rare, occasional, frequent, and abundant categories.

Because we wished to analyse the absolute concentrations directly, we used principal components analysis (PCA) and its constrained relative redundancy analysis (RDA) (ter Braak and Šmilauer 2002), rather than techniques such as correspondence analysis in which relative abundances are implicitly analysed. The gradient lengths of compositional turnover of each proxy in each lake, as estimated by detrended correspondence analysis (DCA), are sometimes quite high (Table 2), suggesting that linear methods may not always be optimal statistically (ter Braak and Prentice 1988). We did not, however, observe any arch effect when using PCA and the null expectation in our study is that there are no differences between the different samples. Although rare species were downweighted, the longest gradient lengths found are probably a consequence of random outliers. DCA of Acari from Holebudalen and Lisletjonn show that the gradient length cannot be estimated because

these samples are poor in sub-fossil remains, with many species having only single occurrences.

The variance for each variable in each lake was estimated by PCA, as the total standard deviation in the biological data (TAU) (ter Braak and Šmilauer 2002). As the number of fossils varies greatly between groups, and TAU² is the total sum of squares divided by the number of taxa multiplied by the number of objects (ter Braak and Šmilauer 2002), we use TAU² as an estimate of the variance. Although TAU² considers sample size, it still depends on it. The chironomid samples range between 211 and 555 sub-fossils per sample, whereas mites range between 7 and 167 sub-fossils per sample (Table 2). To derive comparable variances, TAU² was also calculated from five sets of 100 chironomids randomly selected from each lake. The averages of these values for each lake were compared with the variance of the mites and the plant macrofossils, and are plotted in Fig. 10b.

Water depth and LOI may statistically explain parts of the distribution patterns. Their potential roles as explanatory environmental variables were examined by RDA of each taxonomic group in each lake. The total variance in the biological data sets was partitioned following Borcard et al. (1992). This method estimates the unique variance accounted for by each environmental variable alone, and the total amount of explained variance by water depth and LOI combined. We are not suggesting that LOI is a functional explanatory variable that directly determines the distribution and abundance of terrestrial sub-fossils such as many plant macrofossils, or oribatid mites. Rather, we are merely exploring the relationship between LOI and the sub-fossil assemblages because of its likely importance in influencing chironomid distributions and abundances within a lake (Heiri 2004).

To stabilise the variances, all biological data were square-root transformed prior to analysis in CANOCO version 4.5 (ter Braak and Šmilauer 2002). PCA and RDA results were scaled using inter-sample distances; otherwise, default settings were used. Statistical significances of the RDA results were assessed by 499 unrestricted Monte Carlo permutations (ter Braak and Šmilauer 2002).

The aim of many paleoecological studies is to obtain a sediment core that contains the most representative whole-lake sub-fossil assemblages. How well a sample represents the whole-lake assemblage

Table 2 Summary results of richness, gradient analyses, and representativeness for the five study lakes

	Histøil			Lisletjønn			Vestre Øykjamyrtjern			Holebudalen			Råtåsjøen		
	Ac	Chi	Plant mf	Ac	Chi	Plant mf	Ac	Chi	Plant mf	Ac	Chi	Plant mf	Ac	Chi	Plant mf
<i>Richness</i>															
Total number of sub-fossils	75	555	576	95	211	715	167	469	1030	73	279	250	5	403	1246
Concentration of sub-fossils, per 50 cm ³	5.8	171.5	450	7.4	239.3	558.6	13.0	159.2	804.7	5.8	209.3	195.3	0.6	180.0	973.4
Total number of taxa	16	68	52 (29)	25	50	36 (17)	39	54	42 (21)	15	32	23 (13)	4	49	36 (17)
Total number of taxa per sample	1–9	18–40	6–20	0–11	16–31	4–15	0–17	12–32	3–15	0–7	11–18	1–18	0–1	17–26	3–14
<i>Gradient analysis</i>															
DCA gradient length, SD units	3.90	1.29	3.46	NE	1.30	2.39	2.30	1.80	3.05	NE	1.20	1.76	1.40	2.37	
Total variance, TAU ²	0.250	0.619	0.255	0.238	0.823	0.221	0.288	0.527	0.691	0.120	0.711	0.132	0.566	0.551	
Independent contribution of water depth, %	15.8	9.1	14.3	11.9	13.6	25.2	8.4	12.7	4.0	8.5	13.2	8.5	15.3	10.4	
Independent contribution of LOI, %	15.0	2.9	8.3	7.7	8.7	4.7	12.6	6.3	20.3	13.7	4.0	7.3	4.4	1.5	
Total contribution of water depth and LOI	20.5	20.1	20.6	20.7	22.4	29.9	21.6	19.5	34.8	21.3	34.8	15.9	38.7	41.6	
<i>p</i> Value of water depth and LOI, (total RDA)	0.016	0.006	0.008	0.016	0.006	0.002	0.002	0.006	0.028	0.048	0.002	0.06	0.002	0.002	
<i>Representativeness</i>															
Unrepresentative samples	None	None	T2-7	None	T1-7	None	T2-7	T2-6	T1-6, T2-6	None	None	None	None	T1-7, T2-7	None
Poor representatives	T2-7	T1-7, MI	T2-3, T1-1	M4	None	T1-4	None	T2-7	T2-7	T1-5, T1-7	T1-5, T1-7, T2-7	None	None	T1-2, T1-3, T1-5, T1-7, T2-6, M5	

Because plant taxa often produce several different types of remains (e.g. seeds, leaves), the number of plant macrofossil taxa in parentheses represents the number of botanical species/genera. In Vestre Øykjamyrtjern, T1-6 and T2-6 are unrepresentative of the plant macrofossil community as they are dominated by *Isoetes lacustris*. For this lake TAU² is the estimated variance with and without (*) *I. lacustris* included in the data set. At Råtåsjøen, ordination results for oribatid mites are not available because of the low number of sub-fossils retrieved from the sediments. *Ac* Mites, *Chi* Chironomids, *Plant mf* Plant macrofossils, *NE* not estimatable, *SD* standard deviation units of compositional turnover, *p* probability, *DCA* detrended correspondence analysis

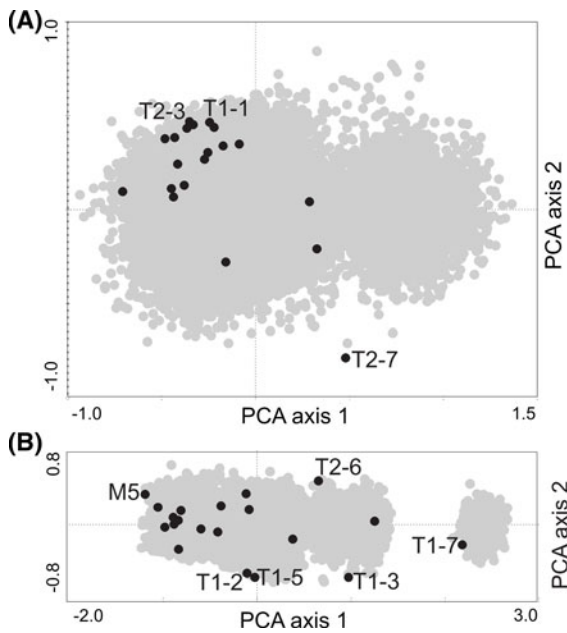


Fig. 2 An example of the PCA plots used for studying representativeness, showing plant macrofossil assemblages from **a** Histøl and **b** Råtåsjøen. The data are presented along the first and second PCA axes. The PCA was run on the simulated data (grey), and the original data were projected into the plot as supplementary data (black). The original data points with PCA scores outside the range of the simulated data sets are considered unrepresentative of the whole-lake assemblages. Samples close to the edge, or situated towards the edge and with high residuals, are considered poor representatives of the whole-lake assemblages. **a** The plot from Histøl shows that T2-7 is not representative, and both T1-1 and T2-3 are poor representatives of the sub-fossil assemblages because of their location on the plot and high residual values. **b** The plot from Råtåsjøen is included as an example of a more complicated pattern. This lake has a high concentration of *Ranunculus* sect. *Batrachium* in sample T1-7, splitting the cloud of the PCA scores for the simulated data into two parts. Additionally, this lake has many samples placed close to the edge of the representativeness, and consequently many samples are poor representatives of the total plant macrofossil assemblages in the lake (Table 2). The PCA plots for the other lakes and taxon groups are shown in Fig. 9

of a sub-fossil type is thus critically important and is the central aim of our analyses. In this study, representativeness of the samples was investigated by comparison of the surface samples with Monte Carlo-simulated sub-fossil assemblages from the same species pool. For each organism group in each lake, all individuals occurring in the lake were pooled. From this pooled data set, 1,000 new data sets were drawn at random, using R version 2.9.2 (R Development Core Team 2008). In these randomised data sets, each sample had the same numbers of specimens as the

original data set. For each lake and each group of organisms, a PCA was performed on each randomised data set separately. The PCA scores of the simulated data sets cluster together along the first and second axes, as shown in Fig. 2. The distributions of these randomised samples are used to detect representative species assemblages. The original data were projected onto the plane of the first two PCA axes as supplementary objects (ter Braak and Šmilauer 2002). The original samples falling outside the cloud of the simulated data are considered to be unrepresentative of the sub-fossil whole-lake assemblages, and these samples are referred to as *unrepresentative* (Fig. 2). Samples with PCA scores at the edge of the simulated distribution were considered to represent the within-lake assemblages poorly and are referred to as *poor representatives*. Samples close to the edges of the clouds may also poorly represent the whole-lake assemblages. To investigate these, the unexplained variance was estimated as the squared residual length of each data point, with the first two fitted PCA axes. Data points within the most extreme 5 % have poor fits to the plane of the first and second PCA axes (Birks et al. 1990). Samples with extreme residual values situated close to the edge of the clouds are also considered poor representatives of the whole-lake assemblages. Where the PCA scores of the simulated data sets are unevenly distributed, the original data points may sometimes occur between two clouds representing PCA scores of the simulated data sets. These points are also considered poor representatives of the sub-fossil assemblages.

The surface samples are unevenly distributed within the lakes, with 2 littoral samples, 12 slope samples, and 6 centre samples in each lake. Our approach does not consider sedimentation rates at each sample location. All PCA plots for representativeness and extreme residual values are presented in Fig. 9. Further information is presented in the online electronic supplementary material (Table S2).

Results

Results from the lakes are presented individually, in altitudinal order. The chironomid results were presented as percentage values and discussed previously (Heiri 2004). They are presented here as concentrations and new interpretations are outlined. The drying

process and mounting on permanent slides restricted identification of mites. Therefore, a relatively large number of specimens, 79 adult oribatids, could not be identified to species level.

Histøl, 245 m asl

Organic content is positively correlated with water depth, and LOI increases from ~32 % in shallow water to ~50 % in samples from the deepest water (Fig. 3). The two littoral samples have comparatively high LOI values, as the sediment includes coarse plant remains from the marginal fen. These samples also have the highest concentration of plant macrofossils. Water depth and LOI explain 20.1–20.6 % of the variance in the sub-fossil assemblages ($p < 0.016$, Table 2).

Sixteen sub-fossil mite taxa were found (Table 2, Fig. 8). Five of the six terrestrial oribatids are woodland or heathland species (Fig. 8). These are only present in the slope samples, whereas the aquatic oribatids are scattered over most of the lake. Mite distribution is correlated with both water depth and LOI.

There are 68 chironomid sub-fossil taxa (Table 2). Assemblage composition changes with water depth (Fig. 3), as shown by Heiri (2004), and concentrations are highest in slope samples, particularly of *Tanytarsus* spp. and *Zalutschia zalutschicola*-type, and lowest in the lake centre. The chironomid fauna includes taxa such as *Zalutschia zalutschicola*-type, *Ablabesmyia*, and *Psectrocladius sordidellus*-type and is typical of dystrophic lakes, which often develop an anoxic hypolimnion in summer. Hypolimnetic anoxia would explain the lower concentration of chironomid remains in the lake centre, which would be uninhabitable for chironomids (Fig. 3).

Fifty-two taxa of sub-fossil plant remains were found, representing 29 plant genera or species (botanical taxa) (Table 2). Like the mites, they reflect the surrounding woodlands and fens (Fig. 3). Whereas *Pinus* and *Betula pubescens* are well represented, no other tree taxa are recorded. Fern sporangia are only found in the lake centre. Aquatic taxa are most common near the shore, particularly *Isoetes*, where the plants are growing. Coarse material and moss are more abundant near the shores. Water depth explains the largest part of the variance of the plant macrofossils, 14.3 % (Table 2).

In the representativeness analysis, littoral sample T2-7 is unrepresentative of the total plant macrofossil assemblage, and a poor representative of the mite assemblages (Table 2, Fig. 9). M1 and T1-7 are poor representatives of the chironomid assemblages, and T1-1 and T2-3 are poor representatives of the plant macrofossil assemblages (Table 2).

Lisletjønn, 518 m asl

The LOI shows almost no correlation with water depth, with values ranging between 36 and 57 % (Fig. 4, Table 2). Together, water depth and LOI explain between 20.7 and 29.9 % of the variance in the sub-fossil assemblages of Lisletjønn ($p < 0.016$), with water depth being the most important (Table 2).

The sediments contain 25 mite taxa (Table 2, Fig. 8). *Hypothonius rufulus*, *Carabodes labyrinthicus*, and *Banksinoma lanceolata* reflect the surrounding woodland and *Malaconothrus monodactylus* and *Mucronothrus nasalis* represent the fen. Aquatic species are well represented, with several species of *Limnozetes* and *Hydrozetes* (Figs. 4, 8). Woodland and wetland species are commonest at the lake centre, whereas aquatic species are present in most of the lake.

Fifty chironomid taxa were found (Table 2). Many are most abundant in slope samples (e.g. *Microtendipes*, *Tanytarsus lugens/Corynocera oliveri*-type), whereas others are more abundant in the lake centre (e.g. *Ablabesmyia*, *Heterotrissocladius marcidus*-type) (Figs. 4, S2). Concentrations vary among samples, especially in the deeper parts of the lake. This might be a consequence of the complex bathymetry, as Lisletjønn has two basins separated by an island (Fig. 1). A single mid-lake sample, M1, contains particularly high values of *Heterotrissocladius marcidus*-type (Fig. 4).

The concentration and richness of plant macrofossils are lower than in Histøl, with 36 sub-fossil plant taxa representing 17 species or genera (Table 2). *Pinus sylvestris* bud scales are abundant, especially in the centre. *Betula* remains occur in low numbers in most samples, whereas *Picea* remains are restricted to shallow water (Fig. 4). *Sphagnum* is common, and appears in almost all samples. Large concentrations of *Isoetes* megaspores are limited to a few shallow samples.

Representativeness analysis shows that sample T1-7 is unrepresentative of the whole-lake chironomid

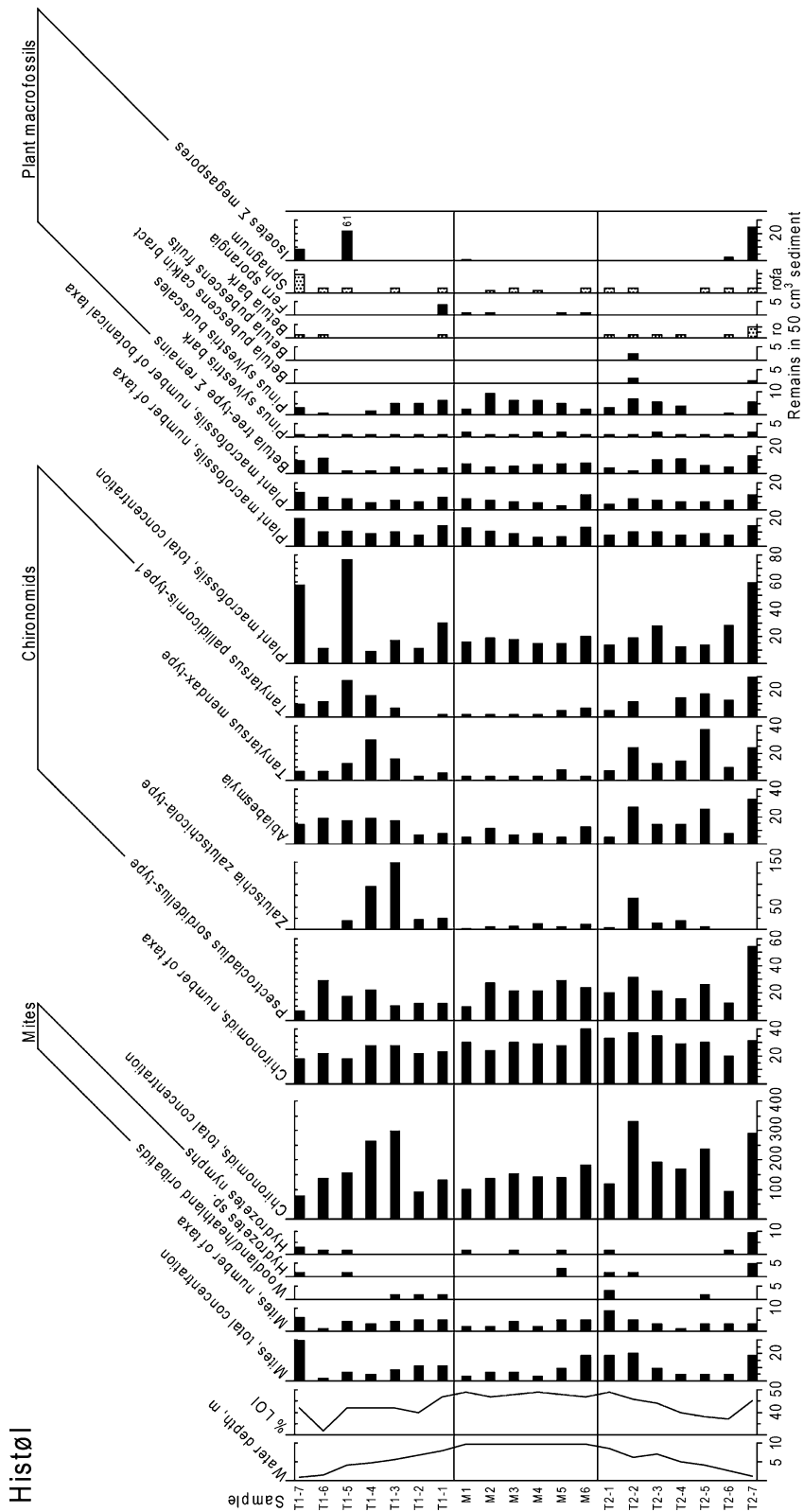


Fig. 3 Summary diagram of the sub-fossil remains from Histø. Water depth (m), percent organic content (LOI), concentrations, and number of taxa of mites, chironomids, and plant macrofossils are presented together with selected taxa from each group. Note the truncated LOI x-axis

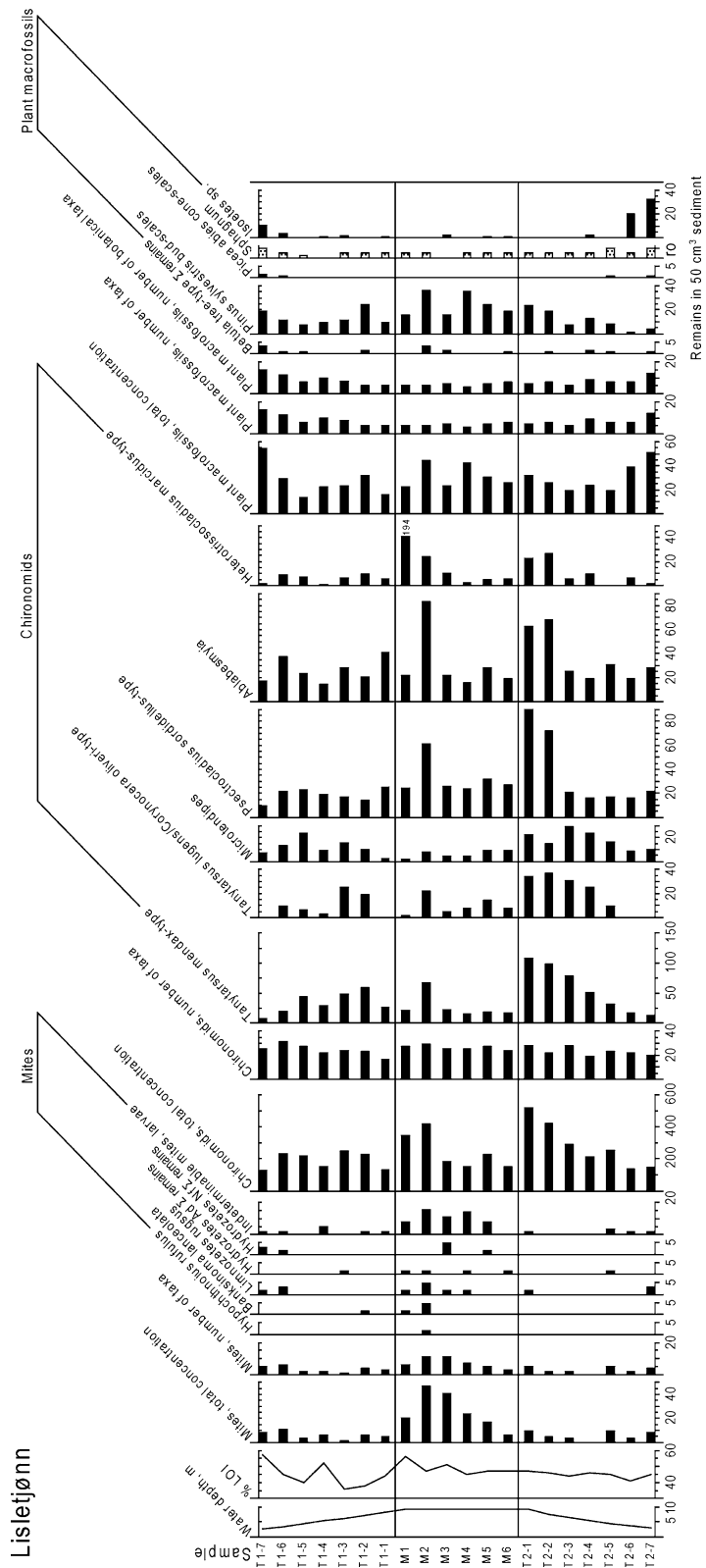


Fig. 4 Summary diagram of the sub-fossil remains from Lislefjøn. Water depth (m), percent organic content (LOI), concentrations, and number of taxa of mites, chironomids, and plant macrofossils are presented together with selected taxa from each group. Note the truncated LOI x-axis

assemblage. T1-4 is a poor representative of the plant macrofossil assemblages, and M4 is a poor representative of the mite assemblages (Table 2).

Vestre Øykjamyrtjern, 570 m asl

The littoral and centre samples have the highest LOI values, ~50–70 % (Fig. 5). Sample T2-7 has a much higher LOI than the rest of transect 2, but it was taken close to the inlet and not in line with the rest of the transect (Fig. 1). In samples T2-1 to T2-6, LOI increases with water depth. Water depth and LOI explain between 19.5 and 34.8 % of the total variance in the sub-fossil assemblages ($p < 0.028$, Table 2).

This lake has the greatest richness of mites, with 39 taxa including woodland, wetland, and aquatic species (Table 2, Figs. 5, 8). *Cosmochthonius lanatus* represents a genus that has not previously been reported from Norway. This species has a holarctic distribution and is normally found in dry moss, meadows, and forest floors (Weigmann 2006). Sub-fossil oribatids from all the main habitats are recorded throughout the lake. Interestingly, some taxa are most abundant in the centre and close to the edges of the lake, e.g. *Malaconothrus monodactylus* and aquatic taxa, particularly *Limnozetes*, whereas other wetland species have a tendency to be most abundant near the shores (Figs. 5, 8). Concentrations of mites are positively correlated with LOI (Table 2, Fig. 5).

Sub-fossil remains of 54 chironomid taxa were found (Table 2). Concentrations increase slightly with water depth (Fig. 5) and water depth alone explains 12.7 % of the variance in the data set (Table 2). Increased concentrations and richness are related to the increase in stream taxa in the middle of the lake and in sample T2-7, close to the inlet. The abundances of most lake-living chironomid taxa are not correlated with water depth (Figs. 5, S3).

The plant macrofossils have generally low concentrations, but high richness, and 42 fossil taxa and 21 botanical taxa are represented (Fig. 5). Numbers of taxa increase with LOI, which alone explains 20.3 % of the variance (Table 2). However, this relationship is probably influenced by sample T2-6, where LOI is only 3 %, and the plant macrofossils are completely dominated by *Isoetes lacustris* megasporae. *Isoetes lacustris* often grows in shallow water on a minerogenic substrate. Sample T1-6 also has large amounts of *I. lacustris*, but higher LOI (Fig. 5). Low numbers of

remains of *Pinus*, *Juniperus*, and *Betula*, together with species from dry-shrub heath, are scattered throughout (Fig. 5). *Sphagnum* occurs in all samples.

The littoral sample near the inlet, T2-7, is unrepresentative of the mite assemblages, and is a poor representative of the chironomid and plant macrofossil assemblages. T2-6 is unrepresentative of the chironomid assemblages. The unrepresentative plant macrofossil samples T1-6 and T2-6 are completely dominated by *I. lacustris* (Fig. 5).

Holebudalen, 1,144 m asl

The Holebudalen sediments have lower LOI than the lakes below the tree line, although LOI increases from 1.2 % close to the shore to about 40 % in deep water (Fig. 6). In alpine conditions, the proportion of minerogenic material in the sediment is often greater than in lakes within forests. Positive correlation of LOI with water depth is probably caused by near-shore deposition of minerogenic material derived from the catchment. The explanatory strength of water depth and LOI varies according to the sub-fossil groups (Table 2).

Although only 73 mite remains were found, the 15 taxa present represent heathland, wetland, aquatic, and generalist species (Table 2, Figs. 6, 8). The relative importance of generalists such as *Oppiella nova* and *Tectocephus velatus* reflects the alpine setting of the lake. Sample T1-7 has a particularly rich mite assemblage. For the mites, LOI explains 13.7 % of the variance, whereas water depth only explains 8.5 % (Table 2).

Holebudalen has the lowest richness of chironomid remains, with only 32 taxa (Table 2). The chironomid assemblages are related with water depth, which explains 13.2 % of the variance, whereas LOI only explains 4.0 % (Table 2, Fig. 6). Unlike the other groups of organisms, overall chironomid concentration increases with water depth, due largely to *Tanytarsus lugens/Corynocera oliveri*-type and *Zalutschia*-type A (Fig. 6) and *Cricotopus/Orthocladius*-type A, *Tanytarsus pallidicornis*-type, and *Psectrocladius sordidellus*-type (Fig. S4).

Plant macrofossil richness is also low at Holebudalen, with only 23 fossil taxa and 13 botanical taxa represented (Table 2). Like the mites, they reflect the alpine environment, with *Salix herbacea* and *Empetrum* remains (Fig. 6). *Salix* remains are most

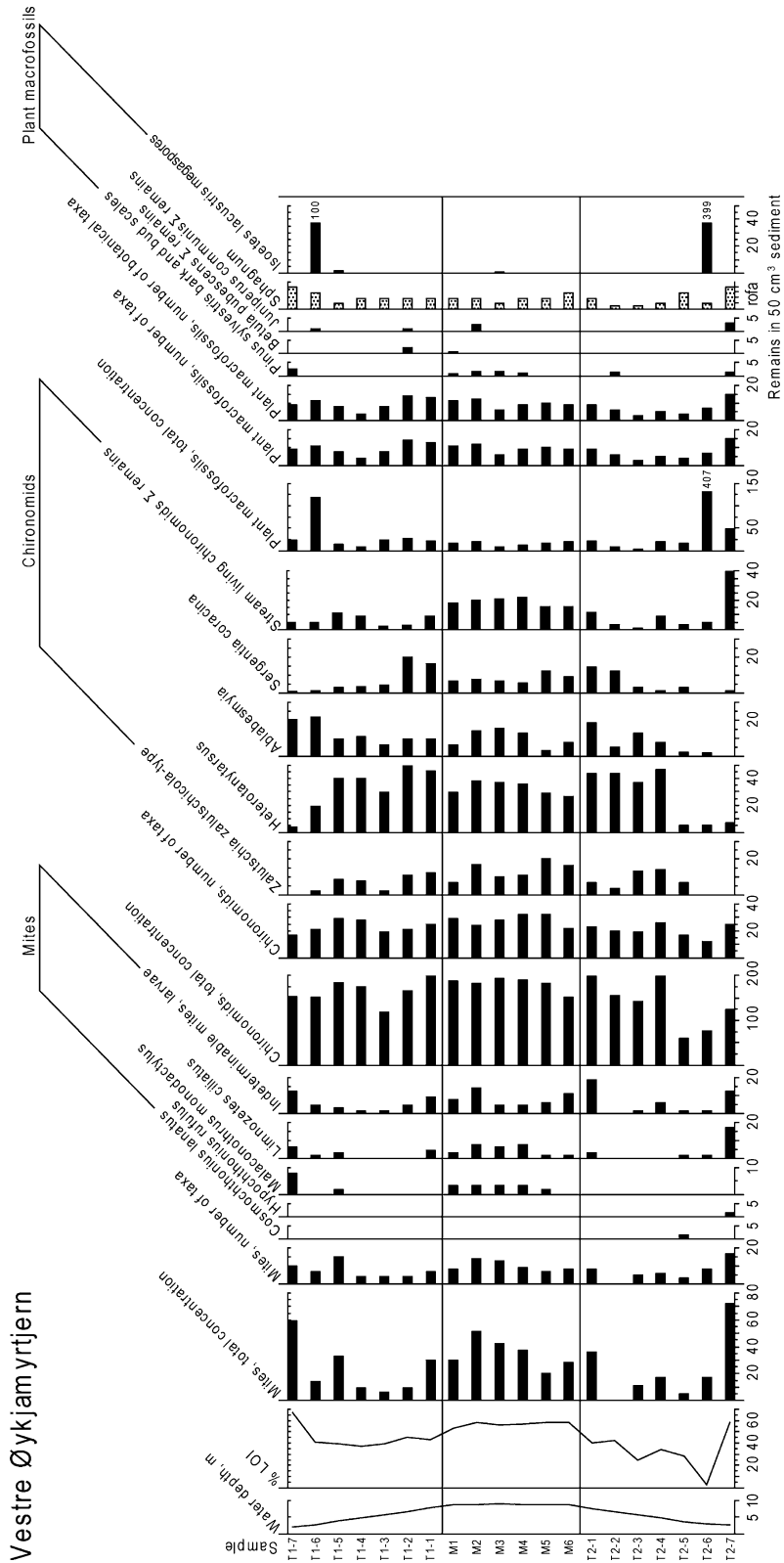


Fig. 5 Summary diagram of the sub-fossil remains from Vestre Øykjamyrtjern. Water depth (m), percent organic content (LOI), concentrations, and number of taxa of mites, chironomids, and plant macrofossils are presented together with selected taxa from each group

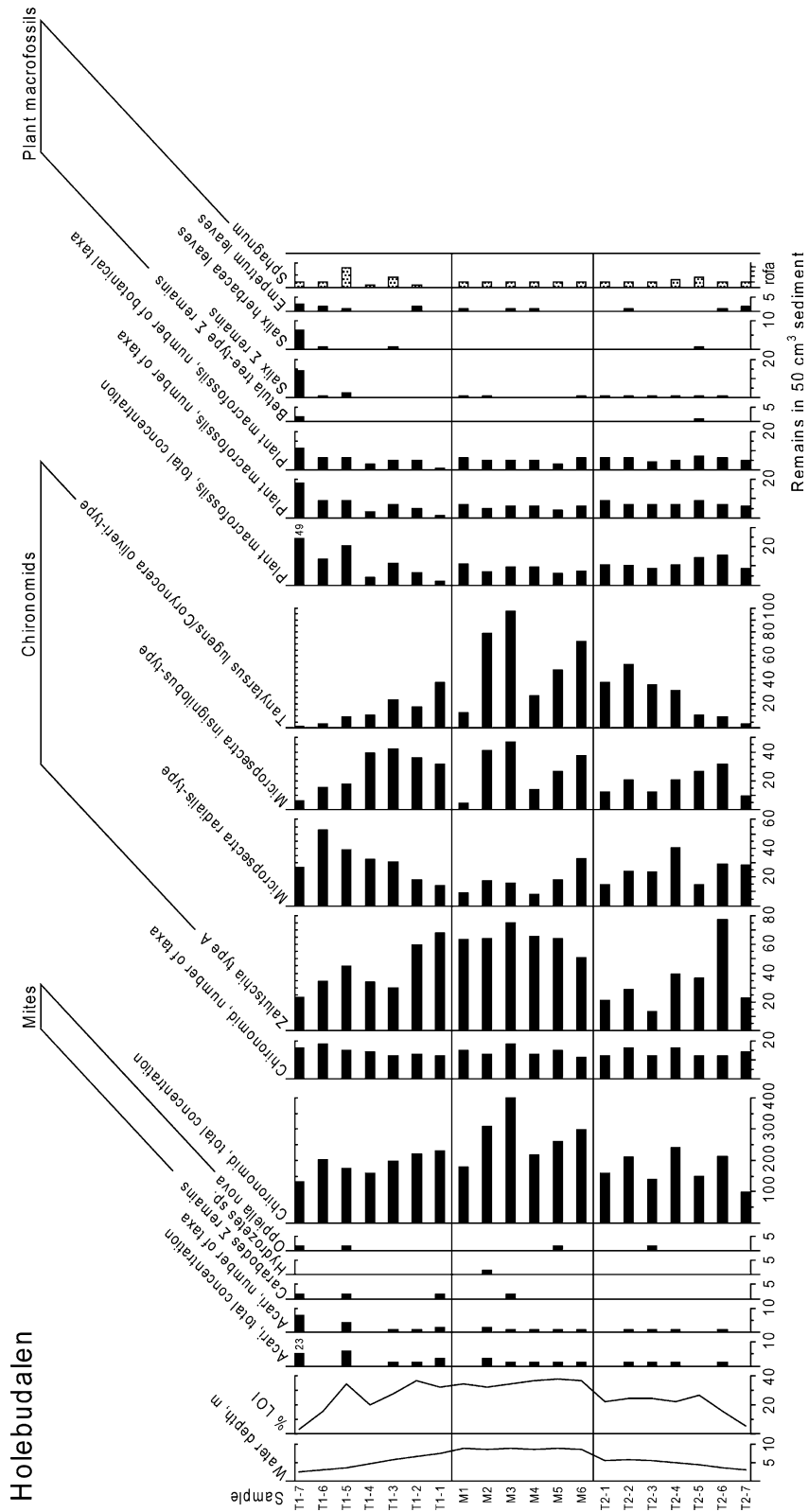


Fig. 6 Summary diagram of the sub-fossil remains from Hølebudalen. Water depth (m), percent organic content (LOI), concentrations, and number of taxa of mites, chironomids, and plant macrofossils are presented together with selected taxa from each group

abundant in sample T1-7. A few *Betula* remains are transported over long distances into the lake, from the birch forest below.

No samples are unrepresentative of the assemblages, but samples T1-5 and T1-7 are poor representatives of the mite and chironomid assemblages. Sample T2-7 is also a poor representative of the chironomid assemblage (Table 2).

Råtåsjøen, 1,169 m asl

Råtåsjøen is also a sub-alpine lake. The LOI of the sediments is generally low, increasing from 0.75 % close to the shore to ~30 % in the lake centre (Fig. 7). For both chironomids and plant macrofossils, water depth explains more variance than LOI (Table 2).

Only five remains, from four taxa of sub-fossil mites, were found (Table 2, Fig. 7). The only species that could be identified were the omnipresent *Oppiella nova* and *Tectocephus velatus*. No ordinations were performed on this limited material.

Chironomid remains from 49 taxa were found (Table 2). Water depth seems to affect the distribution of many (e.g. *Psectrocladius sordidellus*-type, *Microtendipes*, *Tanytarsus lugens/Corynocera oliveri*-type), but not all of these (Fig. 7). Their concentrations are positively related with water depth and LOI, but richness is constant (Fig. 7). The lake-living *Tanytarsus* spp. are among the taxa with highest abundances in the lake centre, whereas *Microtendipes* and *Paratanytarsus austriacus*-type are among those more abundant in slope samples (Fig. 7). Two stream-living taxa, *Heterotrissocladus grimshawi* and *Thienemannimyia*-type, have high abundances in shallow-water samples (Fig. S5). Water depth explains far more of the variance in the assemblages than LOI, and their combined influence is 38.7 % (Table 2).

The 36 plant macrofossil taxa (Table 2) reflect alpine vegetation, with *Betula nana*, *Salix herbacea*, *Empetrum*, and *Selaginella* megaspores (Fig. 7). The terrestrial *B. nana*, wetland *Selaginella*, and aquatic *Ranunculus* sect. *Batrachium* are most abundant in shallow-water samples, and the aquatic *Nitella* is most abundant in slope samples (Figs. 7, S10). The abundance and richness of plant macrofossils decrease with increasing depth and LOI. Water depth and the combined effects of water depth and LOI are most important, explaining 10.3 and 29.9 %, respectively, for the plant macrofossils (Table 2).

Representativeness analyses show that littoral samples T1-7 and T2-7 are unrepresentative of the overall chironomid assemblage in Råtåsjøen. T1-2, T1-3, T1-5, T1-7, M5, and T2-6 are poor representatives of the plant macrofossil assemblage (Table 2, Fig. 2).

Comparisons among lakes

The five lakes were chosen because they differ with respect to altitude and corresponding catchment vegetation. They also have contrasting morphologies that affect sedimentation patterns (Fig. 1). Differences among the lakes were investigated statistically by comparing the total variance of the taxon groups. Histøl, Lisletjønn, and Holebudalen have highest variances for chironomids and lowest for mites (Fig. 10a). In Vestre Øykjamyrtjern, the variance is highest for plant macrofossils. When *I. lacustris* is removed, however, the variance is lowered. In Råtåsjøen, the chironomids and plant macrofossils have similar variances (Table 2).

Discussion

Representativeness

Our main aim was to discover the place in a lake where the most representative fossil assemblages were deposited. Our results show that not all areas within the lakes have equally good representation of the whole-lake sub-fossil assemblages. Whereas some locations in a lake yield samples that represent a small part of the sub-fossil assemblages, others yield samples with a particularly good representation of the total investigated assemblage. Therefore, reasons why samples are unrepresentative should be further investigated so that these locations can be avoided when identifying coring sites, except for studying specific research goals (e.g. Davidson et al. 2005).

There are 30 littoral samples. Five of them are unrepresentative and eight are poor representatives (Table 2). Deposition sites of both terrestrial and aquatic organisms are known to depend on water depth (Birks 1973; Erickson 1988; Dieffenbacher-Krall and Halteman 2000). The high numbers of unrepresentative and poor representative samples among the littoral samples may not, however, be explained wholly by their proximity to the lake shore. Factors other than

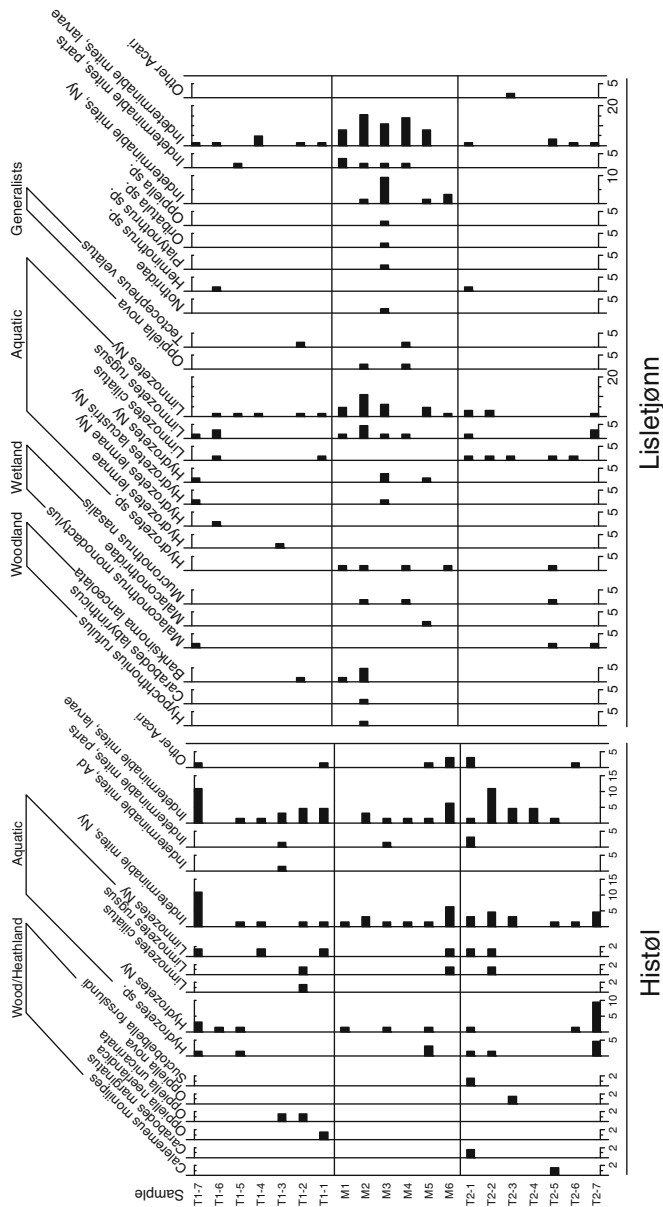


Fig. 8 Full diagram of the sub-fossil mite remains from all the five lakes. All recorded mite taxa are presented as concentrations in 50 cm³ wet sediment. For information on other aspects of the lakes, please refer to the summary diagrams (Figs. 3, 4, 5, 6, 7). Fig. 8 continues on the consecutive page

way down the slope. In Vestre Øykjamyrtjern, two shallow-water samples are unrepresentative as a consequence of the locally high amount of *Isoetes lacustris* megaspores (Fig. 5). In Råtåsjøen, T1-5 and T1-3 are poor representatives of the total plant-macrofossil assemblage. T1-5 is particularly rich in terrestrial species. T1-3 is dominated by *Nitella* oospores (Fig. S10), probably derived from locally growing *Nitella*. These samples may well be from within the submerged aquatic vegetation, although this was not recorded in this study. There is, however, high variability among all slope samples. Although unrepresentative samples are found in the shallowest water, poor representative samples are equally distributed among all slope samples (Table 2).

No samples from the lake centres are unrepresentative, and only three samples in the lake are poor representatives of the whole lake assemblages. One sample for mites, chironomids, and plant macrofossils from the lake centre is a poor representative of the respective assemblages in Lisletjønn, Histøl, and Råtåsjøen (Table 2). All these samples have relatively low fossil concentrations. The concentration of plant macrofossils and mites is often low at lake centres (Figs. 3, 4, 5, 6, 7), although the concentrations of mites are highest in the centre of Lisletjønn and Vestre Øykjamyrtjern (Figs. 4, 5). We conclude that a core taken from the deepest water or lower slopes to investigate environmental history and paleolimnology will contain representative assemblages.

Relations between sub-fossil assemblages and water depth and LOI

The roles of water depth and LOI in predicting the representativeness patterns were discerned using variance partitioning by RDA. Water depth and LOI together explain around 20 % of the variance ($p < 0.048$, Table 2), ranging between 15.9 and 41.6 % of the total. Water depth alone explains between 9.1 and 15.3 % of the variance in the chironomid assemblages, and is more important than LOI (Table 2). The good correlation with water depth is probably a result of the original habitat of the chironomid larvae, as the benthic invertebrate fauna changes with water depth (Brundin 1949; Bretschko 1974; Brinkhurst 1974; Gerstmeier 1989).

Covariances between mite and plant macrofossil assemblages and water depth and LOI are more

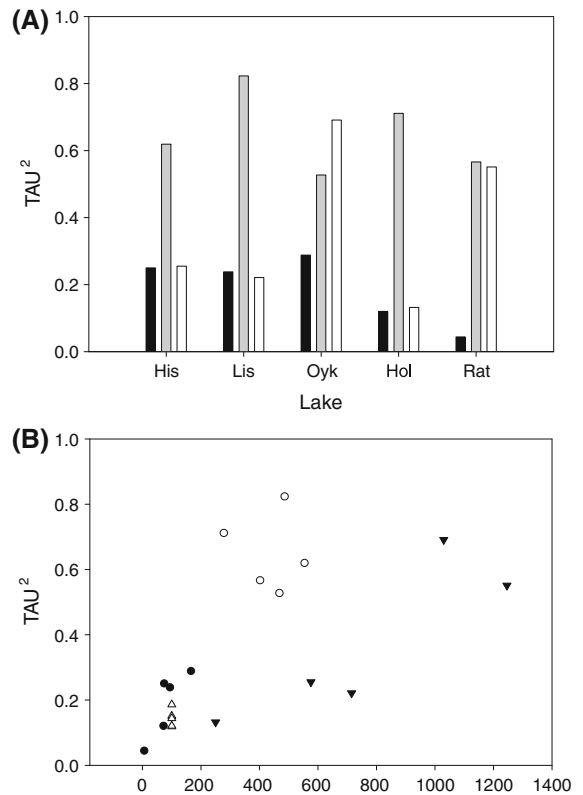


Fig. 10 **a** Estimated variance, TAU^2 , in the sub-fossil assemblages for each lake. Mites (black), chironomids (white), and plant macrofossils (grey). His Histøl, Lis Lisletjønn, Oyk Vestre Øykjamyrtjern, Hol Holebudalen, Rat Råtåsjøen. **b** Estimated variance in the sub-fossil assemblages, TAU^2 , plotted against the number of remains (n) for the three groups of organisms, mites (black circle), chironomids (circle) and plant macrofossils (inverted black triangle). Estimated TAU^2 of random subsamples with 100 chironomid remains is shown for each lake, as a mean of TAU^2 for 5 subsamples from each lake (triangle)

complex. The deposition patterns of mite and plant macrofossil remains are probably mainly dependent on water depth. The correlations with LOI are probably a result of common factors influencing both sub-fossil deposition and LOI. In all except Lisletjønn, LOI is correlated with water depth and is higher in deep water where fine organic material accumulates (Davis and Ford 1982). LOI can also be high in the littoral zone, due to macrophyte growth or derivation of plant material from marginal fens. In Lisletjønn, LOI is not correlated with water depth, and there mite and plant macrofossil assemblages are mainly correlated with water depth alone. Therefore the general correlation with LOI may be a result of the deposition of mite and plant macrofossil remains in the shallow macrophyte

zone or their coincidental deposition with other fine organic material in deep water (Figs. 3, 4, 5, 6, 7).

Other factors that may influence deposition patterns

The large amount of unexplained variance in the RDAs suggests that some important underlying factors were not considered in our analyses. Chironomids have the largest and mites the smallest variances (TAU^2) in all lakes except Vestre Øykjamyrtjern (Fig. 10a). For both these variables the differences of TAU^2 are larger between lakes than within each organism group. The variance estimates, however, increase with the number of remains (Fig. 10b), and chironomid and plant macrofossil remains are found in higher numbers than mites. Subsamples of chironomids with sample sizes of 100 show TAU^2 values similar to those of the mites (Fig. 10b). The plant macrofossils generally have a lower variance in relation to the number of remains. Different variances among the taxon groups suggest that some of the unexplained variance is due to their inherent characteristics. We propose alternative hypotheses to explain the observed distribution of sub-fossil remains. These hypotheses can be tested in future, detailed studies that take into account the original habitat, or the size, type, and morphological characters of the sub-fossil remains and specific lake features.

Hypothesis 1 Sedimentation processes: Taphonomic processes influence aquatic and terrestrial organisms differently, which should be reflected in observed deposition patterns. As terrestrial remains are brought into the lake by streams or wind, their deposition patterns are influenced by currents and high-energy processes. Subsequently, such remains, as well as those of aquatic organisms, are affected by sediment-resuspension processes, especially in shallow water, above the hypolimnion. Although resuspension is an important factor in the deposition and sorting of sediments, information on its occurrence and magnitude is limited. It varies with season and type of lake, and can account for around 85 % of the gross sediment flux (Evans 1994). Resuspension of fine sediment is influenced by lake morphology, slope steepness, and exposure to wave turbulence (Blais and Kalff 1995; Evans 1994). Fine particles are often resuspended and transported to and accumulated in

deep water by sediment focussing (Davis and Brubaker 1973). Resuspension is hence likely to be one of the determining factors of the deposition patterns of aquatic remains observed in our lakes. Heiri (2004), however, concluded that because the chironomid assemblages correlate with water depth, sediment-transport processes may be insufficient to obscure the pattern of the original habitats. Taphonomic processes such as sediment focussing may be more pronounced in deeper lakes. Therefore, surface sampling and sediment trapping programmes should be undertaken in both shallow and deep lakes, to test all aspects of this hypothesis.

Both oribatid and prostigmatic mites were recorded, although Acari remains from lake sediments are normally restricted to the well sclerotised oribatid mites (Solhøy 2001; Erickson and Platt 2007). Observation of prostigmatic mites, less sclerotised nymphs, and *Hypochthonius rufulus* and *Cosmochthonius lanatus*, is a result of the short period of time for decay to occur. After initial deposition and decay of fragile remains, continuing taphonomic processes are, however, not expected to change the chironomid, plant macrofossil, and oribatid mite assemblages significantly, and surface sediments are expected to be a good equivalent to assemblages in older sediments.

Hypothesis 2 Assemblage composition depends on proximity to local aquatic source areas, for example, the connection between original habitats and deposition sites of chironomids, and the relationship between plant macrofossil assemblages and the closest aquatic vegetation (Birks 1973; Zhao et al. 2006). The high abundances of *Isoetes lacustris* megaspores in Vestre Øykjamyrtjern and Histøl occur only in shallow-water samples (Figs. 3, 5) where the plant grows. Although aquatic vegetation was not recorded, it is likely that *I. lacustris* was growing in these sites. The megaspores are formed at the base of the leaves in the part of the rosette buried in mud (Lid and Lid 1994) and it is unlikely that they are dispersed far, except by an unusual event. Local macrofossil representation is also probably shown in Transect T1 in Råtåsjøen. The high concentrations of *Ranunculus* sect. *Batrachium* and *Nitella* remains in this transect probably reflect their growth at or near the sample sites. These high concentrations result in the unrepresentativeness of these samples (Table 2).

Hypothesis 3 Assemblage composition depends on the proximity to local terrestrial source areas: the original habitats near the shores may be reflected by remains of terrestrial species, as they are expected to be sedimented closest to their habitats (Spicer and Wolfe 1987). At Holebudalen, the mites have a slightly increased concentration in transect 1, but because of the low number of remains, this could be a result of stochastic processes (Fig. 6). Sample T2-7 near the inlet in Vestre Øykjamyrtjern has the highest number of woodland oribatids in the lake (Fig. 5). It is the only sample with an over-representation of any ecological group of mites, demonstrating the importance of stream flow for the dispersal of terrestrial mites into this lake. This sample also has a high concentration of stream-living chironomids, which are otherwise most abundant in the lake centres. There are few examples where forested terrestrial habitats seem to be reflected in the sub-fossil assemblages (Eide et al. 2006). In high-energy alpine environments, terrestrial remains can be dispersed in large numbers into deeper water, e.g. at Kråkenes, west Norway (Jonsgard and Birks (1995) and in Spitsbergen (Birks 1991). Lake size may play a role. Our lakes were small and taphonomic processes, particularly resuspension from shallow water, may obscure the original deposition pattern.

Hypothesis 4 Effects of morphology of remains: morphological characters influence the distribution of remains within a lake. Plant species may produce several types of remains, and therefore the numbers of botanical taxa are lower than the number of types of fossil remains (Table 2). As they have the same origins, the remains provide a good tool for investigating differential sedimentation. The six different types of remains of *Pinus sylvestris* recorded in Lisletjønn are distributed unevenly within the lake. Bark fragments are present in all samples, bud-scales are most abundant in deep water, anthers and needles are scattered in the slope samples, and floating seeds and wings are deposited in the littoral samples (Fig. S7). The *Pinus* bud-scales are small, thin, and have a large surface area. They remain suspended, and are transported into the centre of Lisletjønn, where they constitute the majority of the plant macrofossils (Fig. 4).

Regenerative parts are often morphologically adapted for spreading and deposition at favourable places. For example, fruits of *Ranunculus* sect.

Batrachium accumulate close to the shores of Råtåsjøen, where the plants grow (Fig. 7). *Nitella* oospores are also found in greatest numbers near source plants, as at Råtåsjøen (Fig. 7). Oospores, however, are small and light, with spiral flanges that decelerate sinking and they can be widely dispersed within a lake by water currents (Birks 1973; Diefenbacher-Krall and Halteman 2000).

Hypothesis 5 Size of remains: small remains are often deposited in the lake centre and larger and coarser remains accumulate near the shores. The presence of small fern sporangia in the middle of Histøl (Fig. 3) is an example, as they are transported to the middle of the lake prior to sedimentation. Body lengths of the oribatid mites were measured, but these did not correlate with location, water depth, or LOI. *Hydrozetes* nymphs may have long setae extending beyond their body. These long setae may prevent them from being transported away from their original habitats. The large amounts of *Hydrozetes* nymphs in T2-7 in Histøl (Fig. 3) may hence indicate that this was their original habitat.

Conclusions

For mites, chironomids, and plant macrofossils, the majority of the surface samples represent well the total sub-fossil assemblages in our five shallow lakes. Nearer the shores, the richness of terrestrial organisms is often high, but differences among samples in the littoral zone can be substantial (Fig. 6). Littoral samples are more often unrepresentative of the whole-lake assemblages than other samples. Terrestrial remains are often in highest concentrations in the slope samples, but this region can also be the area of a lake with the largest variability among samples (Figs. 3, 4, 5). The lake centre has the least number of samples that are poor representatives of the overall sub-fossil assemblages, but this is also the region that generally displays the lowest richness of terrestrial remains. Hence, in our five lakes, the choice is between coring in an area where there may be local differences over short distances and there is a risk of obtaining a core with lower abundance and richness, or coring in a deep-water region with high compositional stability, but possibly lower concentrations of remains.

The advantages and disadvantages of coring on the slopes versus the lake centre offset one another. If sediment depth is sufficient, then cores from the centre and slopes of small, shallow lakes are equally likely to contain representative assemblages of mites, chironomids, and plant macrofossils. We conclude from our study that these three fossil types can be reliably studied from the same core. We note, however, that our results are only applicable to small, shallow lakes. Similar studies in larger, deeper lakes are required before we can make general recommendations about 'ideal' coring locations for multi-proxy paleolimnological studies involving both aquatic and terrestrial organisms.

Acknowledgments Jan Berge, Aina Dahlø, Lapager Duorje, Jorunn Larsen, Endre Willassen, and Gaute Velle assisted with fieldwork. Mareile Andersson and Wenche Eide extracted the mites and plant macrofossils from the sediments, and assisted in the identification of the plant macrofossils. Arguitxu de la Riva Caballero, Torstein Solhøy, Ingelinn Aarnes, and Knut Helge Jensen provided valuable input regarding the analyses and interpretations. Oliver Heiri was financed by a Swiss National Science Foundation fellowship for prospective researchers (Fellowship 81BE-66224) and Marianne Presthus Heggen was financed by NORPEC, a NFR-funded Strategic University Program at the University of Bergen, co-ordinated by HJB Birks. NORPEC also financed the fieldwork.

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