Estonian Journal of Ecology, 2008, **57**, 1, 5–20 doi: 10.3176/eco.2008.1.01

Spatial distribution of macrofossil assemblages in surface sediments of two small lakes in Estonia

Tiiu Koff✉ and Egert Vandel

Institute of Ecology at Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia
✉ Corresponding author, tkoff@tlu.ee

Received 14 November 2007, in revised form 14 January 2008

Abstract. Surveys and mapping of macrophyte vegetation and its remains in the surface sediments of two Estonian lakes demonstrate that about 50% of the submerged and floating-leaved plants growing in the lake are represented as macrofossils in the sediment. Only one third of the helophyte taxa were found in the sediment, and they had a very limited distribution close to their growing place. Part of the macrofossils, such as fragments of *Nymphaea alba* seeds, were distributed over the entire lake bed and were not connected with the actual growing place. The bottom topography of the lake affects the distribution of macrofossils.

Key words: macrophytes, macrofossil analysis, lake sediments, Estonia.

INTRODUCTION

Macrophytes play an important role in the lake ecosystem as they are the primary source of organic matter to fresh waters (Wetzel, 1983; Jeppesen et al., 1998) and in carbon and nutrient cycling (Rooney & Kalff, 2000). The plant macrofossil assemblage in lake sediments consists of two main components: terrestrial macrofossils originating from the catchment and aquatic remains from the lake itself. Their distribution in lakes is determined by many parameters. Smith & Wallsten (1986) suggest that the percent cover of emergent macrophytes in Swedish lakes could be predicted from the mean depth and other morphometric parameters of the lake. Macrophyte data combined with lake water chemistry were used to devise a typology of Estonian lakes (Mäemets, 1974, 1991; Mäemets, 2005).

Analysis of plant remains in lake sediments provides information on these aspects through time and palaeoecological and palaeolimnological studies that involve macrofossil analysis could answer the questions about the development of the lake ecosystem in a longer perspective. Macrofossils have been widely used in past environment studies (e.g. Birks, 1973, 1980, 2001, 2007; Watts, 1978; Birks & Birks, 2000; Gaillard & Birks, 2007) and for reconstruction of vegetation (e.g. Väliranta, 2006; Väliranta et al., 2006). The method is widely used to reconstruct past lake-level changes (Digerfeldt, 1986; Ammann, 1989; Hannon & Gaillard, 1997; Lotter, 1999; Birks & Wright, 2000; Dieffenbacher-Krall &

Nurse, 2005; Koff et al., 2005) and anthropogenic impact (Rasmussen & Anderson, 2005). Application of the multiple core method will improve the reliability of results. As analysis of macrofossils is a time-consuming process, it is necessary to find the most representative set of cores. Before this selection it is necessary to consider various factors that may significantly affect the distribution of vegetation as well as the preservation of macrofossils in the course of sediment accumulation and diagenesis.

Information about the mechanism of macrofossil deposition in lake sediments can be obtained from surface sample studies (Birks, 1973; Davis et al., 1985; Dieffenbacher-Krall & Halteman, 2000; Zhao et al., 2006). It is important to know which plants will be represented by macrofossils in lake sediments, and whether it is informative to use these data to estimate the abundance of the plant in the past vegetation, lake trophy, or changes in the water level (e.g. Davidson et al., 2005; Dieffenbacher-Krall, 2007). The representation of macrofossils is not linearly or unimodally related to the variable (proportion of a species within the vegetation community) of interest. Many factors affect the relationship between macrofossil assemblages and plant communities, and studies of surface sediment samples may provide useful insights.

The aim of this study was to describe the present aquatic vegetation in two small lakes in Estonia and compare it with the macrofossil assemblages taken from the uppermost 10 cm of the lake sediment accumulated during the last decade. This was done in order to assess the relationship between macrophyte vegetation and the distribution and preservation of plant remains in sediments of lakes with different topography.

MATERIAL AND METHODS

Study sites

The study was performed in two lakes that are both small in size (Table 1) and characterized by quite stable macrophyte vegetation over the last decades, as shown by monitoring data (Ott & Kõiv, 1999).

Table 1. Selected morphological features of the investigated lakes

Main characteristic	L. Juusa	L. Viitna
Surface area, ha	3	3.8
Catchment area, ha	55	34
Maximum water depth, m	6.0	4.8
Mean water depth, m	3.9	1.8
Average slope inclination, %	8.7	4.5
Stratification depth, m	2.5–3.5	2.5–3.5
Area under macrophytes*, %	20	40

* Helophytes, floating-leaved, and submerged plants combined.

Lake Väike-Juusa (hereafter L. Juusa) is situated in the southern part of Estonia (Fig. 1a) (58°03′ N and 26°30′ E) on the Otepää Heights (Fig. 1b). The hillocks bordering the lake have steep slopes. The lake area is 3 ha, its maximum length 250 m, and width 160 m. The catchment area of L. Juusa is characterized by a semi-open cultural landscape. It is a meso-eutrophic dimictic lake with strong stratification during spring–summer. In summer the thermocline deepens from about 2.5 m in June to 3–3.5 m in July–August. The values of the pH were ca 7.7 in the epilimnion and 6.6 near the bottom during 2002–2003.

The lake bottom has a relatively regular shape; the near-shore zone deepens abruptly (Fig. 2a). The slope inclination is greatest (up to 20%) at depths from 0 to 3 m. The inclination of the deeper slope decreases rapidly and is on average only 2% at depths of 5–6 m (Terasmaa, 2005). The bottom sediments of L. Juusa are up to 12 m thick in the deepest point of the lake. The surface layers of

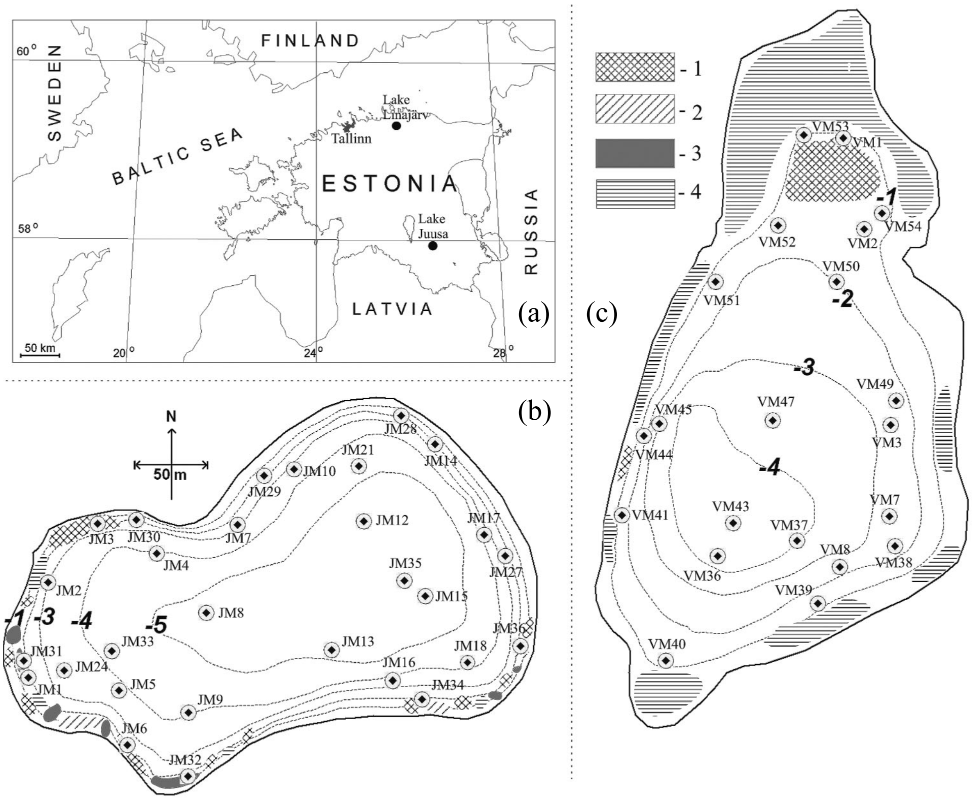

Fig. 1. Inset map of Estonia (a) showing the location of L. Juusa and L. Viitna. Water-depth contours at 1 m interval, vegetation map of the abundantly found floating leaved and submerged plants and sampling points are given for lakes Juusa (b) and Viitna (c). 1 – *Potamogeton* spp., 2 – *Nuphar lutea*, 3 – *Elodea canadensis*, 4 – *Nymphaea alba*.

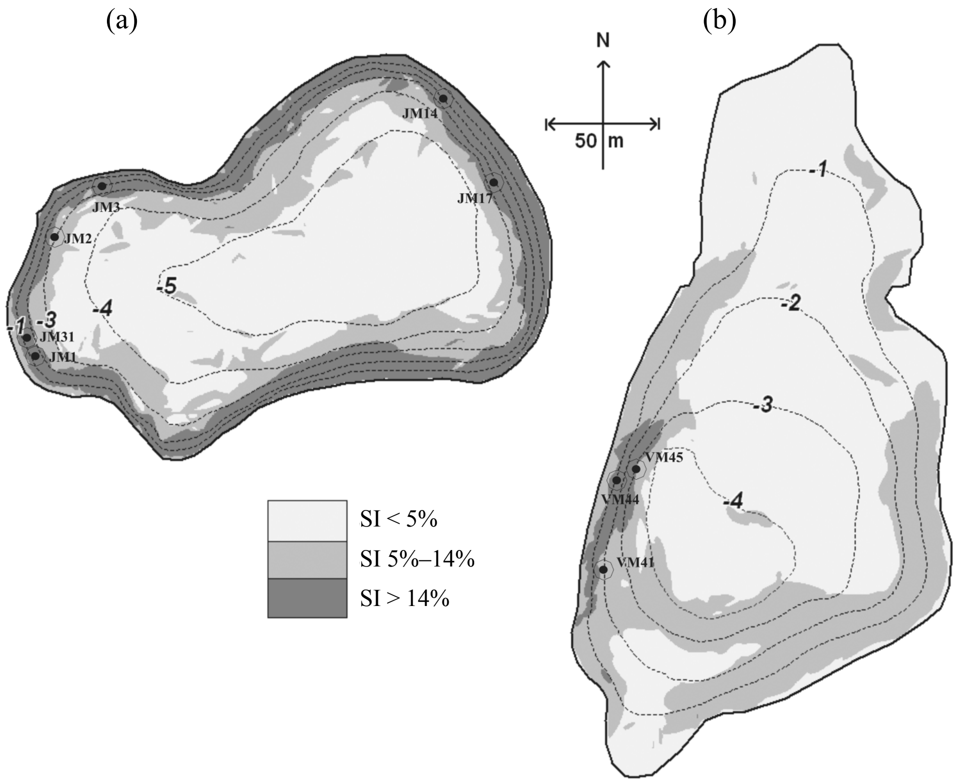

Fig. 2. Bathymetry, slope inclination (SI) (after Terasmaa, 2005), and selected sampling points in L. Juusa (a) and L. Viitna (b).

sediments are brownish gyttja with a high water (70–92%) and organic matter content. As estimated from the ^{210}Pb data, the uppermost 10 cm of the sediment in the deepest point accumulated during the last 10 years (Punning et al., 2005).

Lake Viitna Linajärv (hereafter L. Viitna) is situated in northern Estonia (59°40′ N, 25°45′ E) (Fig. 1c). It is a closed seepage lake with a small catchment (Table 1) underlain by limno- and fluvioglacial sediments. The lake is elongated from north to south. Steep-sloped eskers surround the lake from west and south. Regular studies here began already in 1972 (Simm et al., 1975) and therefore L. Viitna was used as the reference lake for the calibration of palaeoecological records with hydrobiological, hydrogeochemical, and hydrophysical data. In the epilimnion the pH values vary in the range from 6.5 to 7.5, while during the plankton bloom the pH values reach 9.1 (Punning & Leeben, 2003). The thermocline is at depths between 2.5 and 3.5 m during the stratification period (usually from May up to September).

The northern part of the lake is shallow with a mean depth of 1–2 m. It forms a relatively separate system from which matter fluxes to other parts of the lake are apparently not very large (Punning et al., 2004). The smallest slope inclinations in the south-western part of L. Viitna occur at depths of 4–5 m (Fig. 2b).

The bottom sediments of L. Viitna are up to 9.5 m thick in the deepest part of the lake. The surface layers of sediments are colloidal dark brownish gyttja with 97–98% water content. Estimated from the ^{210}Pb data the uppermost 10 cm of sediment in the deepest point accumulated during the last 10 years (Punning et al., 2003).

Vegetation mapping

The modern vegetation in the lakes was mapped in late August 2002. The whole littoral zone was traversed by boat and the species composition and depth limits of different plant groups were recorded. For submerged aquatic plants, which were not readily visible, five throws with a grapple were made in different directions around the boat. Abundances were estimated on a 5-point scale of Braun-Blanquet for the whole lake. The scores were dominant (5), abundant (4), frequent (3), occasional (2), and rare (1). The methods used are analogous with those of earlier investigations (Koff, 2004; Mäemets, 2005).

The distinction between an aquatic and a terrestrial plant is often blurred because of the tendency for many aquatic species to have both submersed and emerged forms, and because many terrestrial plants are able to tolerate periodic submersion (Wetzel, 1983). This is often the case for plants growing in habitats characterized by frequent flooding. We used the concept of helophytes – plants that tolerate extended periods of water logging around their roots, and even complete submersion under flood waters. In this study, we divided the macrophytes into three groups: helophytes, floating-leaved, and submerged plants.

Sediment sampling and macrofossil analyses

The surface samples (uppermost 10 cm) were taken with a gravity corer at 29 sampling points in L. Juusa and at 21 points in L. Viitna. The distribution of sampling points in both lakes is presented in Fig. 1b, c. The exact location of each sampling point was recorded by GPS Garmine 12 (maximum horizontal accuracy 3 m); distance to the shoreline (DS) and water depth (D) were measured. The morphometric characteristics of the lake and lithological composition of surface sediments of L. Viitna and L. Juusa are described in detail in Terasmaa (2005). The sediment samples were packed into hermetic PVC boxes in the field and refrigerated until analysis.

Sediment samples were dispersed in water and washed gently through a sieve with mesh size of 0.25 mm. Residues were dispersed in water and examined on a white plate at ×10–50 magnification under a binocular stereomicroscope. All seeds, fruit, and other plant remains were extracted and identified using the reference collection of the Institute of Ecology and manuals of seed descriptions (Beijerinck, 1947; Katz et al., 1977; Birks, 1980; Grosse-Brauckmann & Streitz, 1992; Cappers et al., 2006). The abundance of macrofossils was calculated as number per 100 cm^3 of sediment.

RESULTS

Modern vegetation in L. Juusa and L. Viitna

Table 2 presents the main taxa and abundances on a 5-point scale in the modern macrophyte vegetation and the presence of macrofossils in the sediment surface samples. The distribution of the more frequently found submerged and floating-leaved taxa is shown on the map (Fig. 1b, c).

In L. Juusa the most frequently found helophyte is *Phragmites australis*. *Juncus articulatus*, *Typha latifolia*, *Schoenoplectus lacustris*, and *Acorus calamus* were found occasionally and distributed evenly along the shoreline. *Sagittaria sagittifolia* and *Iris pseudacorus* were growing only along the western shore. *Calla palustris* and *Menyanthes trifoliata* occurred on the eastern paludified shore. All other species were distributed sporadically. Among the floating-leaved plants, *Nuphar lutea* and *Nymphaea alba* were most widely distributed along the western shore of L. Juusa (Fig. 1b). *Spirodela polyrhiza*, *Hydrocharis morsus-ranae*, and *Stratiotes aloides* were found rarely. Among the submerged plants *Utricularia vulgaris* was growing in a few places only, while *Potamogeton praelongus* and *Elodea canadensis* were found mainly close to the western shore. In comparison with the observations made in 1968 (H. Mäemets, pers. comm.), the composition and abundances of most taxa were similar, except for *Nymphaea alba*, which has decreased in abundance since then, and the moss *Warnstorfia fluitans* was not found any more.

In L. Viitna helophyte vegetation consisted of various rare taxa, but only the occurrence of *Phragmites australis* and *Typha latifolia* could be classified as occasional. *Equisetum fluviatile* was distributed along the southern shore of the lake, and *Lycopus europeaus* along the eastern and western shores. All other helophytes were rare. Among the floating-leaved plants *Nymphaea alba* was frequently found. In the northern part of the lake, where the water depth was less than 1 m, there was a zone of *Nymphaea alba* covering almost 80–90% of the area (Fig. 1c). To the south of this zone was a belt of *Potamogeton natans* and *Polygonum amphibium* plants. In the 1970s, the northern part of L. Viitna was described as overgrown by macrophytes (Simm et al., 1975). However, plants like *Sparganium gramineum* and *Acorus calamus* are currently missing.

Table 2. The DAFOR (dominant (5), abundant (4), frequent (3), occasional (2), rare (1)) scores for the main helophytes and submerged and floating-leaved plants recorded in the modern vegetation (M) and their representation by macrofossils (+) in surface sediments (F) of L. Viitna and L. Juusa; – not recorded

Taxon	L. Juusa		L. Viitna	
	M	F	M	F
EMERGENT HELOPHYTES				
Acorus calamus L.	2	–	–	–
Calla palustris L.	2	–	–	–
Sagittaria sagittifolia L.	2	–	–	–
Schoenoplectus lacustris (L.) Palla	2	+	–	–
Menyanthes trifoliata L.	2	–	–	–
Sparganium microcarpum (Neuman)	1	–	–	–
Thelypteris palustris Schott	1	–	–	–
Calamagrostis epigeios (L.) Roth.	1	–	–	–
Iris pseudacorus L.	1	+	–	–
Juncus articulatus L.	2	–	–	–
Rumex crispus L.	1	–	–	–
Eleocharis uniglumis (Link.) Schult.	–	–	1	–
Ranunculus reptans L.	–	–	1	+
Sparganium angustifolium Michx.	–	–	1	–
Scirpus sylvaticus L.	–	–	1	+
Juncus conglomeratus L.	–	–	1	–
Juncus effusus L.	–	–	1	–
Eleocharis palustris (L.) Roem. et Schult	1	+	1	–
Stellaria palustris Retz.	1	+	1	+
Carex spp.	1	+	1	+
Equisetum fluviatile L.	1	–	1	–
Lycopus europaeus L.	2	–	1	–
Lysimachia thyrsiflora L.	2	–	1	–
Phragmites australis (Cav.) Trin.	3	+	2	–
Typha latifolia L.	1	+	2	–
SUBMERGED AND FLOATING-LEAVED HYDROPHYTES				
Chara spp.	–	+	–	–
Ceratophyllum demersum L.	–	–	–	+
Isoetes lacustris L.	–	–	–	+
Spirodela polyrhiza (L.) Schleid.	1	–	–	–
Stratiotes aloides L.	1	–	–	–
Urticularia vulgaris L.	1	–	–	–
Hydrocharis morsus-ranae L.	1	–	–	–
Elodea canadensis Michx.	1	–	–	–
Nuphar lutea (L.) Sm.	2	+	–	–
Potamogeton praelongus Wulfen	1	+	–	–
Polygonum amphibium L.	–	–	1	–
Potamogeton natans L.	–	–	2	+
Nymphaea alba L.	1	+	3	+

Presence of macrofossils in the surface sediments

Altogether, only one third of the helophyte taxa were represented in surface samples of lake sediments as macrofossils (Table 2). The seeds of the widespread taxa such as *Phragmites* and *Typha* were found only in L. Juusa sediments, whereas the seeds of *Carex* species and *Stellaria palustris* were found in sediments of both lakes. In L. Viitna sediments *Scirpus sylvaticus* and *Ranunculus* spp. seeds were present as well, and in L. Juusa *Iris pseudacorus* and *Schoenoplectus lacustris* seeds were found (Table 2).

For the floating-leaved aquatics the macrofossil representation was better in the sediments of L. Viitna in which among the three frequently or occasionally distributed macrophyte taxa two were found as macrofossils, i.e. seed fragments of *Nymphaeae alba* and seeds of *Potamogeton natans* were extracted. In L. Juusa submerged and floating-leaved species consist of eight taxa, but only three were found as macrofossils in the surface sediments, i.e. *Nymphaea alba*, *Potamogeton praelongus*, and *Nuphar lutea* (Table 2).

Distribution of macrofossils over the lake surface sediments

The representation of macrofossils in certain sampling sites is presented in Figs 3 and 4. From the surface samples of L. Juusa a total of 28 plants were extracted and identified (Fig. 3).

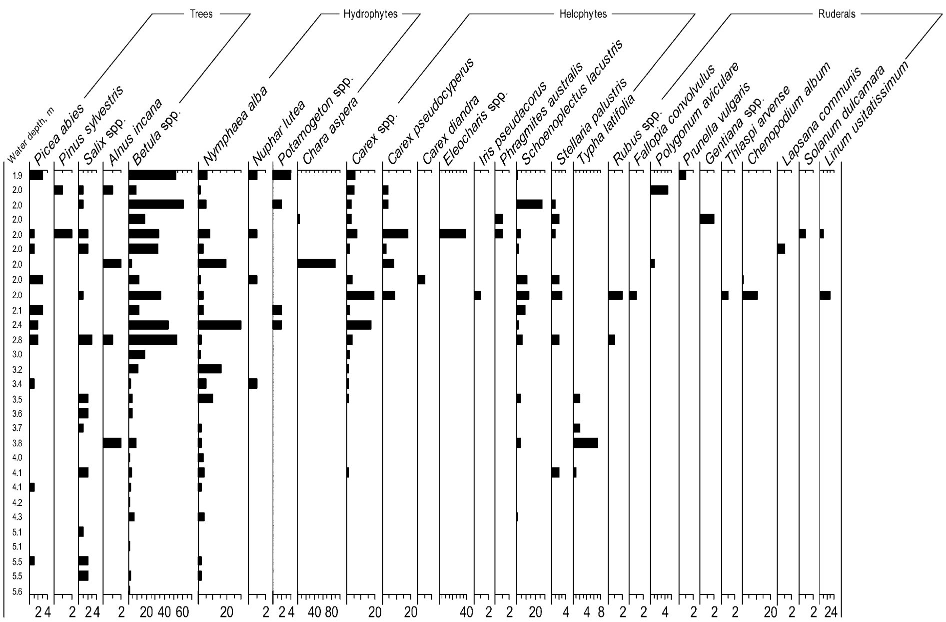

Fig. 3. Representation of macrofossils (number of macrofossils in 100 cm^3 of surface sediment) in sampling points (Fig. 1b) in L. Juusa.

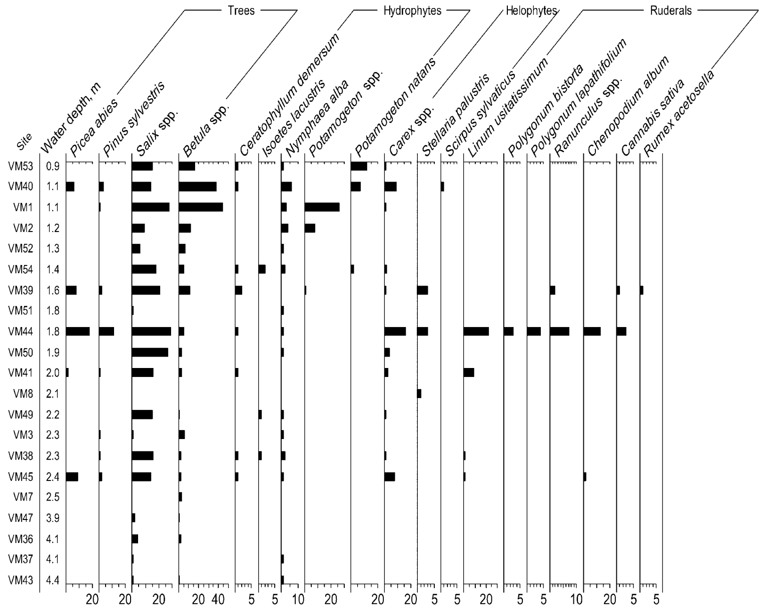

Fig. 4. Representation of macrofossils (number of macrofossils in 100 cm^3 of surface sediment) in sampling points (Fig. 1c) in L. Viitna.

Among the trees seeds and catkin scales of *Betula* (up to 60 per 100 cm^3 sediment) were most widely distributed in the surface sediments over the whole lake but most abundantly at nearshore points JM1 (D 1.9 m; DS 8.8 m), JM28 (D 2.0 m; DS 7.2 m), and JM14 (D 2.8 m; DS 7.4 m). *Salix* remains were found also at points JM12 (D 5.5 m; DS 58 m) and JM15 (D 5.5 m; DS 57.5 m), in the deepest part of the lake (Fig. 2b). The remains of *Alnus* and needles of *Pinus* and *Picea* were found in much lower numbers, and mostly in sampling sites close to the shore and the actual growing sites of these taxa (Fig. 3).

Among hydrophytes seed fragments of *Nymphaea alba* were most abundant at points JM2 (D 3.2 m; DS 12.7 m), JM3 (D 2.4 m; DS 7.0 m), and JM32 (D 2.0 m; DS 8.0 m), but some were found also in the deepest part of the lake at points JM12 (D 5.5 m; DS 58 m) and JM15 (D 5.5 m; DS 57.5 m) (Fig. 3). Only a few seeds of *Nuphar lutea* were found at three points: JM1 (D 1.9 m; DS 8.8 m), JM30 (D 2.0 m; DS 7.6 m), and JM34 (D 2.0 m; DS 9.5 m), all very close to the growing place of the respective plant (Fig. 1b). A similar pattern was observed also for *Potamogeton* spp. seeds. Among helophytes, seeds of *Carex*, distributed at sampling points JM3 (D 2.4 m; DS 7.0 m), JM30 (D 2.0 m; DS 7.6 m), and JM36 (D 2.0 m; DS 8.2 m) (Fig. 3), close to the shore (Fig. 1b), were the most abundant (up to 20 seeds). The same distribution pattern was also observed for *Schoenoplectus lacustris.* Up to 10 seeds of *Typha latifolia* were found at sampling point JM17 (D 3.8 m; DS 14.1 m). *Eleocharis* spp. seeds were found in high quantities (up to 40 seeds) at sampling point JM30 (D 2.0 m; DS 7.6 m). Despite the frequent modern distribution of *Phragmites australis*, its seeds were found only at points JM29 (D 2.0 m; DS 9.8 m) and JM30 (D 2.0 m; DS 7.6 m) (Fig. 3).

Most of the seeds from herbaceous species belong to ruderal plants related to agricultural activities around the lake. *Rubus* spp., *Fallopia convolvolus*, *Solanum dulcamara*, *Lapsana communis*, *Chenopodium album*, *Thlaspi arvense*, and *Prunella vulgaris* were found, although in quite low numbers, in eight samples collected at water depths less than 2 m and approximately 10 m from the lake shore. At sampling point JM36 (D 2.0 m; DS 8.2 m) as many as 15 seeds of *Chenopodium album* were found (Fig. 3).

Some plants were not present in the modern vegetation but were represented as macrofossils. For example, we extracted oogones of *Chara aspera* at sampling points JM29 (D 2.0 m; DS 9.8 m) and JM32 (D 2.0 m; DS 8.0 m) and *Linum usitatissimum* seeds at sampling points JM30 (D 2.0 m; DS 7.6 m) and JM36 (D 2.0 m; DS 8.2 m). *Linum* finds are interesting as there is no information about flax retting for the last 40 years.

A total of 19 different plants were found in L. Viitna surface sediment samples (Fig. 4) as macroremains. In the samples collected from sites where the water depth was more than 2.5 m there were only a few macrofossils (Fig. 4). Seeds and catkin scales of *Betula* spp. were most abundant (up to 40) at southern sampling point VM40 (D 1.1 m; DS 17 m) and at VM1 (D 1.1 m; DS 34 m) in the northern part of the lake (Fig. 2c). Seeds and needles of *Pinus* and *Picea* were found in much lower numbers and only at points VM39 (D 1.6 m; DS 18 m), VM40 (D 1.1 m; DS 17 m), VM44 (D 1.8 m; DS 8 m), and VM45 (D 2.35 m; DS 15 m), close to their actual growing place. *Salix* remains were quite abundant and evenly distributed over the lake sediment surface (Fig. 4).

The distribution of the helophytes is more sporadical; only *Carex* seeds were abundant (Fig. 4). We also found seeds of herbaceous species that are known as ruderals. Over 20 seeds of *Ranunculus* spp. and *Chenopodium album* were found at sampling point VM44 (D 1.8 m; DS 8 m).

Among the hydrophytes, seed fragments of *Nymphaea alba* were distributed evenly all over the lake, even at point VM43 with a water depth of 4.4 m and DS 59 m. Seeds of various *Potamogeton* species were found at sampling points from the northern part of the lake VM1, VM2, and VM53 (D 0.9 m; DS 36 m), in the area of their actual distribution (Fig. 1c).

In L. Viitna the number of the taxa not present in the modern aquatic vegetation but present in the surface sediments was much higher than in L. Juusa. For instance, seeds of *Ceratophyllum demersum* were represented in low numbers but uniformly. Spores of *Isoetes lacustris* were found at three sampling points from the eastern shore: VM38 (D 2.3 m; DS 19 m), VM49 (D 2.2 m; DS 31 m), and VM54 (D 1.35 m; DS 20 m). The presence of up to 20 seeds of *Linum usitatissimum* at point VM44 (D 1.8 m; DS 8 m) and 10 at VM41 (D 2.05 m; DS 11 m) is remarkable. It is known that L. Viitna was used for flax retting up to the 1950s.

DISCUSSION

Table 2 shows that representation of modern macrophytes as macroremains in surface sediments of the studied lakes is quite random. Certainly, a one-to-one relationship between the modern vegetation community and macrofossil assemblages is not to be expected. However, from palaeobotanical point of view it is important to understand which species tend to be over-, under-, or unrepresented in the macrofossil records.

The question of the poor macrofossil representation of certain macrophytes in lake sediments has been recently discussed in several papers. Zhao et al. (2006) studied the spatial representation of aquatic vegetation by macrofossils and pollen in a small and shallow lake. The authors concluded that the relationship between modern plants and their representation by different remains is highly complex and difficult to calibrate. Dieffenbacher-Krall (2007) summarized the main reasons for discrepancies between macrofossil : vegetation relationships such as macrofossil production, dispersal, loss, basin characteristics, and within-lake sample location.

As known, macrofossil production depends on reproductive strategies of species. Annual plants, which overwinter as seed, typically produce many times more seed per year than perennial species, and seed production may vary from year to year, depending on environmental conditions. Rare occurrence of helophyte plant seeds in both studied lakes may be related to their propagation peculiarities. For example, during a short and cold summer *Phragmites australis* very often has no chance for ripening. *Acorus calamus* is mainly reproducing vegetatively in boreal cool climatic conditions. As a result, only 33% of the modern helophyte species were represented as macroremains in the lake surface sediment samples from the two lakes.

Dispersal of potential macrofossils from source plants is influenced by species characteristics. Tiny seeds are likely to be more widely dispersed than large ones. For example, *Typha latifolia* is an anemophilous plant and its seeds are small – 1.2 mm in length (Cappers et al., 2006). Therefore its seeds can be found in the deeper part of lakes as it was the case in L. Juusa at sampling points JM4 (D 4.1 m; DS 17 m) and JM17 (D 3.8 m; DS 14 m) (Fig. 3). *Menyanthes trifoliata* seeds are bigger and round (length 2.6 mm and width 2.2 mm) (Cappers et al., 2006); its seed production is rather low and their distribution is very limited. This may explain the absence of findings in L. Juusa sediments although the species was occasionally recorded in the modern plant cover (Table 2). *Iris pseudacorus* seeds are rather large and round (length 8.7 mm), which explains their limited distribution. The finding of one seed at point JM36 (Fig. 3) is connected with the actual modern occurrence in L. Juusa.

Potential macrofossils may be lost as a consequence of decomposition, predation, and seed germination, although germinated seeds may still leave behind identifiable fragments of seed coats (Dieffenbacher-Krall, 2007). For example, *Nymphaea alba* seeds tend to break into smaller identifiable fragments. In the studied lakes *Nymphaea* seed tissues were found far from their actual place of growth. This sets limits to the precision of the method for palaeolimnological investigations. Davidson et al. (2005) studied historical, macrofossil, and pollen records of aquatic plants in a shallow lake, records spanning over the last 250 years. They concluded that approximately 40% of the historically recorded aquatic taxa are represented by macroremains. One reason might be that the fossil records of freshwater macrophytes are often based on fruit, seeds, and megaspores. However, much of the reproduction is asexual and vegetative parts usually lack cuticle and decay readily, so they are unlikely preserved as fossils (Collinson, 1988). This might be the reason why some submerged plants such as *Utricularia vulgaris*, *Spirodela polyrhiza*, *Hydrocharis morsus-ranae*, and *Elodea canadensis* present in the modern vegetation of L. Juusa were missing from fossil records (Table 2).

Zhao et al. (2006) suggested that macrofossils successfully reflect dominant components of aquatic vegetation, but underestimate species richness. Positive examples can be found in L. Viitna, where the macroremains effectively recorded the dominant floating-leaved plants like *Potamogeton natans* (Table 2). The spatial distribution of the macroremains of *P. natans* (Fig. 4) is in good correspondence with the distribution of these plants (Fig. 1c). Also in L. Juusa, the presence of *Nuphar lutea* and *Potamogeton praelongus* seeds agrees well with the distribution of these plants in the modern vegetation (Fig. 1b).

Macrofossil deposition depends on the location of the sediment core within a basin, where the nearshore sediment generally contains many more macrofossils than the sediment in the central part of lakes (Watts & Winter, 1966). In L. Juusa the number of *Betula* seeds was more than ten times higher in the nearshore points and most of the ruderals were found from points close to the lake shore. In L. Viitna these differences were not so clearly defined. Dieffenbacher-Krall & Halteman (2000) and Väliranta (2006) demonstrated that the abundance of plant remains can be used to infer water depth. In the current study the number of hydrophyte and helophyte plant macroremains in both lakes decreased below 2.5 m depth (Figs 3 and 4).

Numerous studies (e.g., Birks, 1973; Dieffenbacher-Krall & Halteman, 2000; Zhao et al., 2006) demonstrated that a macrofossil type may be abundant with no potential source plants in the near vicinity. Also in the current study seeds of plant species not occurring in a lake or the surrounding vegetation were detected. In L. Viitna, *Linum usitatissimum* together with the ruderals *Polygonum bistorta*, *P. lapathifolium*, *Ranunculus* spp., and *Chenopodium album* were present at sampling point VM44 (D 1.8 m; DS 8 m) (Fig. 4). The presence of allochthonous (i.e. originating from outside a lake system) seeds of *Linum usitatissimum* and some ruderal taxa in the sediments is a consequence of flax retting. A large amount of material was brought into the lake and later re-deposited in the steep slope area, where the inclination is more than 14% (Fig. 2b) or at sites with greater exposition to the prevailing wind directions (Punning et al., 2004). This may cause also redeposition of macrofossils. Lake-level changes may likewise enhance these processes. Therefore, when interpreting results of macrofossil analyses it is important to take into account the characteristics of the lake topography and sample location within the lake.

CONCLUSIONS

This study demonstrated that ca 50% of the species of submerged and floating-leaved plants are represented in the surface sediments of lakes. The low representation of individual plant macrofossils is affected by various factors. For some helophytes such as *Acorus calamus* and *Phragmites australis* the annual seed production depends on climatic conditions. In other cases individual characteristics of seeds explain the extent of the spatial distribution of macrofossils over the lake surface: tiny and wind-dispersed seeds of *Typha latifolia* are extensively distributed whereas limited distribution was observed for large seeds as in the case of *Menyanthes trifoliata* and *Iris pseudacorus*. Decomposition is intensive for macrophytes with soft tissues such as *Utricularia vulgaris*, *Spirodela polyrhiza*, *Hydrocharis morsus-ranae*, and *Elodea canadensis*; so they are unlikely to be preserved as fossils. The distribution of *Potamogeton* spp. was very strongly connected with the actual plant distribution and abundance in both lakes. In L. Juusa the presence of *Nuphar lutea* and *Potamogeton praelongus* seeds agreed well with the distribution of these plants in the modern vegetation. Therefore, the abundance of plant macrofossils may be used as an indicator of the water depth/distance to the shoreline.

The bottom topography of the lake should be taken into account when the research strategy is set up. Most representative places should be selected for multiple coring. Therefore steep slopes where the inclination is more than 14% or sites with greater exposition to the prevailing wind directions should be avoided as there post-sedimentational processes might have a stronger impact on the distribution and preservation of macrofossils than elsewhere.

ACKNOWLEDGEMENTS

Financial support of the Estonian Ministry of Education (No. 0282120s02) and Estonian Science Foundation (grants 5580 and 6679) is gratefully acknowledged. We thank H. Mäemets for help in vegetation mapping. We appreciate the assistance of colleagues from the Institute of Ecology. We are grateful to M.-J. Gaillard and M. Väliranta for critical comments on our manuscript.

REFERENCES

Ammann, B. 1989. Late-Quaternary palynology at Lobsigensee. Regional vegetation history and local lake development. *Diss. Bot.*, 137.

Beijerinck, W. 1947. *Zadenatlas der Nederlandische Flora*. H. Veenman and Zonen, Wageningen.

Birks, H. H. 1973. Modern macrofossil assemblages in lake sediments in Minnesota. In *Quaternary Plant Ecology* (Birks, H. J. B. & West, R. G., eds), pp. 173–189. Blackwell, Oxford.

Birks, H. H. 1980. Plant macrofossils in Quaternary lake sediments. *Arch. Hydrobiol.*, **15**, 1–60.

Birks, H. H. 2001. Plant macrofossils. In *Tracking Environmental Change Using Lake Sediments. Vol. 3. Terrestrial, Algal and Siliceous Indicators* (Smol, J. P. et al., eds), pp. 49–74. Kluwer Academic Publishers, Dordrecht.

Birks, H. H. 2007. Plant macrofossil introduction. In *Encyclopedia of Quaternary Science.* Vol. 3 (Scott, A. E., ed.), pp. 2266–2288. Elsevier, Amsterdam.

Birks, H. H. & Birks, H. J. B. 2000. Future uses of pollen analysis must include plant macrofossils. *J. Biogeogr.*, **27**, 31–35.

Birks, H. H. & Wright, H. E. 2000. Introduction to the reconstruction of the late-glacial and early-Holocene aquatic ecosystems at Kråkenes Lake, Norway. *J. Paleolimnol.*, **23**, 1–5.

Cappers, R. T. J., Bekker, R. M. & Jans, J. E. A. 2006. *Digitale Zadenatlas van Nederland*. Groningen Archaeological Studies, Vol. 4. Barkhuis Publishing & Groningen University Library.

Collinson, M. E. 1988. Freshwater macrophytes in paleolimnology. *Palaeogeogr*., *Palaeoclim*., *Palaeoecol.*, **62**(1–4), 317–342.

Davidson, T. A., Sayer, C. D., Bennion, H., David, C., Rose, N. & Wade, M. P. 2005. A 250 year comparison of historical, macrofossil and pollen records of aquatic plants in a shallow lake. *Freshwater Biol.*, **50**, 1671–1684.

Davis, B. M., Ford, M. S. & Moeller, R. E. 1985. Paleolimnology. In *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and Its Environment* (Likens, G. E., ed.), pp. 345–366. Springer Verlag, NewYork.

Dieffenbacher-Krall, A. C. 2007. Plant macrofossil methods and studies. Surface samples, taphonomy, representation. In *Encyclopedia of Quaternary Science.* Vol. 3 (Scott, A. E., ed.), pp. 2367–2374. Elsevier, Amsterdam.

Dieffenbacher-Krall, A. C. & Halteman, W. A. 2000. The relationship of modern plant remains to water depth in alkaline lakes in New England, USA. *J. Paleolimnol.*, **24**, 213–229.

Dieffenbacher-Krall, A. C. & Nurse, A. M. 2005. Late-Glacial and Holocene record of lake levels of Mathews Pond and Whitehead Lake, Northern Maine, USA. *J. Paleolimnol.*, **34**, 283–309.

Digerfeldt, G. 1986. Studies on past lake-level fluctuations. In *Handbook of Holocene Palaeoecology and Palaeohydrology* (Berglund, B. E., ed.), pp. 127–144. Wiley, New York.

Gaillard, M.-J. & Birks, H. H. 2007. Paleolimnological applications. In *Encyclopedia of Quaternary Science.* Vol. 3 (Scott, A. E., ed.), pp. 2337–2356. Elsevier, Amsterdam.

Grosse-Brauckmann, G. & Streitz, B. 1992. Pflanzliche Makrofossilien mittel-europäischer Torfe III. Früchte, Samen und einige Gewebe. *TELMA*, **22**, 53–102.

Hannon, G. E. & Gaillard, M.-J. 1997. The plant macrofossil record of past lake-level changes. *J. Paleolimnol.*, **18**, 15–28.

Jeppesen, E., Søndergaard, M., Søndergaard, M. & Christoffersen, K. 1998. *The Structuring Role of Submerged Macrophytes in Lakes*. Ecological Studies 131. Springer, New York.

Katz, N. J., Katz, S. V. & Skobeeva, E. I. 1977. *Atlas of Plant Remains in Peat*. Nedra, Moscow (in Russian).

Koff, T. 2004. Macrofossils in the sediments of L. Juusa (southern Estonia). In *Estonia. Geographical Studies 9* (Punning, J.-M. & Kaare, T., eds), pp. 30–40. Estonian Academy Publishers, Tallinn.

Koff, T., Punning, J.-M., Sarmaja-Korjonen, K. & Martma, T. 2005. Ecosystem response to early and late Holocene lake-level changes in Lake Juusa, southern Estonia. *Polish J. Ecol.*, **53**, 553–570.

Lotter, A. F. 1999. Late-glacial and Holocene vegetational history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland. *Veget. Hist. Archeobot.*, **8**, 165–184.

Mäemets, A. 1974. On Estonian lake types and main trends of their evolution. In *Estonian Wetlands and Their Life* (Kumari, E., ed.), pp. 29–62. Valgus, Tallinn.

Mäemets, A. 1991. Suurtaimestik kui järvede hindamise informatsiooniallikas. In *Inimene ja geograafiline keskkond* (Saarse, L., ed.), pp. 93–97. ENSV Teaduste Akadeemia, Eesti Geograafia Selts, Tallinn.

Mäemets, H. 2005. *Relationships of the Macrophyte Vegetation of Estonian Lakes with Environmental Conditions and Changes in the Course of Anthropogenic Eutrophication*. PhD thesis. Estonian Agricultural University, Tartu.

Ott, I. & Kõiv, T. 1999. *Estonian Small Lakes: Special Features and Changes*. Estonian Environment Information Centre, Tallinn.

Punning, J.-M. & Leeben, A. 2003. A comparison of sediment and monitoring data: implications for paleomonitoring a small lake. *Environ. Monit. Assess.*, **89**, 1–15.

Punning, J.-M., Kangur, M., Koff, T. & Possnert, G. 2003. Holocene lake-level changes and their reflection in the paleolimnological records of two lakes in northern Estonia. *J. Paleolimnol.*, **29**, 167–178.

Punning, J.-M., Alliksaar, T., Terasmaa, J. & Jevrejeva, S. 2004. Recent patterns of sediment accumulation in a small closed eutrophic lake revealed by the sediment records. *Hydrobiologia*, **529**, 71–81.

Punning, J.-M., Koff, T., Kadastik, E. & Mikomägi, A. 2005. Holocene lake level fluctuations recorded in the sediment composition of the small dimictic Lake Juusa (SE Estonia). *J. Paleolimnol.*, **34**, 377–390.

Rasmussen, P. & Anderson, N. J. 2005. Natural and anthropogenic forcing of aquatic macrophyte development in a shallow Danish lake during the last 7000 years. *J. Biogeogr.*, **32**, 1993–2005.

Rooney, N. & Kalff, J. 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry. *Aquat. Bot.*, **68**, 321–335.

Simm, H., Starast, H., Mälgi, U. & Lindpere, A. 1975. Viitna Linajärve vee keemiline koostis ja hüdrokeemiline režiim. *Eesti NSV TA Toim. Biol.*, **24**, 295–308.

Smith, V. H. & Wallsten, M. 1986. Prediction of emergent and floating-leaved macrophyte cover in Central Swedish lakes. *Can. J. Fish. Aquat. Sci.*, **43**, 2519–2523.

Terasmaa, J. 2005. Bottom topography and sediment lithology in two small lakes in Estonia. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **54**, 151–169.

Väliranta, M. 2006. Long term changes in aquatic plant species composition in north-eastern European Russia and Finnish Lapland, as evidenced by plant macrofossil analysis. *Aquat. Bot.*, **85**, 224–232.

Väliranta, M., Kultti, S. & Seppä, H. 2006. Vegetation dynamics during the Younger Dryas–Holocene transition in the extreme northern taiga zone, north-eastern European Russia. *Boreas*, **35**, 202–212.

Watts, W. A. 1978. Plant macrofossils and Quaternary paleoecology. In *Biology and Quaternary Environments* (Walker, D. & Guppy, J. C., eds), pp. 53–67. Australian Academy of Sciences, Canberra.

Watts, W. A. & Winter, T. C. 1966. Plant macrofossils from Kirchner Marsh, Minnesota – a paleoecological study. *Geol. Soc. Am. Bull.*, **77**, 1339–1360.

Wetzel, R. G. 1983. *Limnology*. Second edition. Saunders College Publishing, Philadephia.

Zhao, Y., Sayer, C. D., Birks, H. H., Hughes, M. & Peglar, S. 2006. Spatial representation of aquatic vegetation by macrofossils and pollen in a small and shallow lake. *J. Paleolimnol.*, **35**, 335–350.

Makrojäänuste ruumilisest jaotusest kahe Eesti väikejärve pindmistes setetes

Tiiu Koff ja Egert Vandel

Väike-Juusa järve ja Viitna-Linajärve suurtaimestiku leviku ning nende järvede pindmistes setetes sisalduvate makrojäänuste jaotuse võrdlev analüüs näitab, et kaldavööndis kasvavate taimede ja nende fikseeritud osiste (eelkõige seemnete) levikualade kattuvus sõltub liigist ning järve topograafiast. Liigiliselt on vaid 50% kasvavatest veesisestest ja ujulehtedega taimedest esindatud ka pindmistes järvesetetes makrojäänustena. Küllaltki rikkalikust kaldataimestikust on leitud vaid vahetult veepiiril kasvavate ja domineerivate liikide (*Carex* spp., *Typha latifolia*) makrojäänuseid. Samas on *Nymphaea alba* seemnete fragmendid levinud üle kogu järve ja neid võib leida ka järve sügavama osa setetes ning selle liigi indikatiivsus kasvukoha suhtes on madalam.