https://doi.org/10.3176/eco.2007.2.05

Proc. Estonian Acad. Sci. Biol. Ecol., 2007, **56**, 2, 141–153

Variation of macrozoobenthos communities in the reed *Phragmites australis* belt of two large shallow lakes

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Received 16 June 2006, in revised form 22 March 2007

Abstract. This paper investigates macrozoobenthos communities of the reed belts in the two largest lakes of the Baltic region: Peipsi (3555 km^2) and Võrtsjärv (270 km^2). Although both are shallow and unstratified water bodies, their trophic states differ slightly in physico-chemical aspects and primary production. The reed *Phragmites australis* (Cav.) is a dominant species in the macrophyte communities, which has increased drastically in both lakes during the last 30 years. Although the bottom fauna of the two large Estonian lakes has been studied for several decades, investigations of the macrozoobenthos communities of the reed belt are scarce. The aims of this study were to describe the macrozoobenthos communities of the reed belt, to find out the main factors affecting the structure of the communities, and to compare these communities in the two lakes. The material for this study was collected from 13 profiles of L. Peipsi and from 9 profiles of L. Võrtsjärv at depths between 0.1 and 0.6 m in the reed belt from August to October 2002 and 2003. The benthic fauna of the reed belt was statistically different in the two large lakes of Estonia. Chironomids were dominating in the macrophyte zone of L. Võrtsjärv. In L. Peipsi, the gammaridean amphipod *Gmelinoides fasciatus* (Stebbing), introduced from L. Baikal into the lake at the beginning of the 1970s, was strongly dominating in the littoral zoobenthic communities. This amphipod has explosively increased in the lake, while the native gammarids have been virtually superseded by this invader during recent decades. Substrate type and vegetation significantly influence the macrozoobenthos communities. The results of the present study show that the abundance and taxon richness of macrozoobenthos were the highest on gravel bottom.

Key words: macrozoobenthos, littoral zone, Lake Peipsi, Lake Võrtsjärv.

INTRODUCTION

Benthic communities are structured both by abiotic and biotic factors along the spatial and the temporal scales (Jonasson, 1969). Littoral macroinvertebrate communities are first influenced by factors like habitat type and substrate quality,

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water depth, vegetation, hydrodynamic stress and exposure to wind fetch in large lakes, and winter ice conditions (Meriläinen & Hamina, 1993; Weatherhead & James, 2001). Owing to differences in bottom sediments and presence of macrophyte aggregations, but also as a result of wave action, littoral habitats are highly variable in different parts of lakes. The species richness and abundance of macroinvertebrates are generally much higher in littoral compared to profundal habitats, and are particularly high in macrophyte beds (Saether, 1979; Timm et al., 2001; Schmieder, 2004). The bottom fauna of L. Peipsi and L. Võrtsjärv has been studied for several decades (Timm et al., 2001; Kangur et al., 2004). However, data on the macrozoobenthos communities of the reed belt of L. Peipsi and L. Võrtsjärv are scarce.

The reed *Phragmites australis* (Cav.) is dominant in the macrophyte communities of both lakes. The reeds of L. Peipsi and L. Võrtsjärv have increased drastically over the last 30 years. The main reasons for the expansion of the reed could be eutrophication, low-water periods, and the decline in cattle breeding in the shore areas (Mäemets & Freiberg, 2004). The expansion of reeds has changed significantly the habitat for macroinvertebrate communities in the littoral of both lakes.

Introduction of non-indigenous species has become one of the most serious threats to biological diversity (Ojaveer et al., 2003; Lévêque et al., 2005). Two invasions of bottom animals have played an important role in L. Peipsi. In the 1930s, the zebra mussel *Dreissena polymorpha* (Pallas) appeared in the lake (Mikelsaar & Voore, 1936). In 1970–1975, the amphipod *Gmelinoides fasciatus* was introduced into L. Peipsi (Timm & Timm, 1993; Panov et al., 2000). This invasive species is not yet found in L. Võrtsjärv (Kangur et al., 2004).

The aims of this study were to describe macrozoobenthos communities in the reed belt, to find out the main factors affecting the structure of the communities, and to compare these littoral communities of the two lakes.

STUDY SITE

Lake Peipsi is situated on the border of Estonia and Russia (Fig. 1). Its surface area is 3555 km^2, mean depth 7.1 m, and maximum depth 15.3 m (Jaani, 2001) (Table 1). Lake Peipsi is the fourth largest lake in Europe. The lake consists of three parts: the largest and deepest northern part L. Peipsi *s.s.*, the middle strait-like part L. Lämmijärv, and the southern part L. Pihkva. Lake Peipsi *s.s.* belongs to unstratified eutrophic lakes with mesotrophic features, L. Lämmijärv has some dyseutrophic features, and L. Pihkva is strongly eutrophic (Milius et al., 2005). The volume of the whole lake is 25 km^3 and the residence time of water is about two years. The only outflow is through the Narva River into the Gulf of Finland.

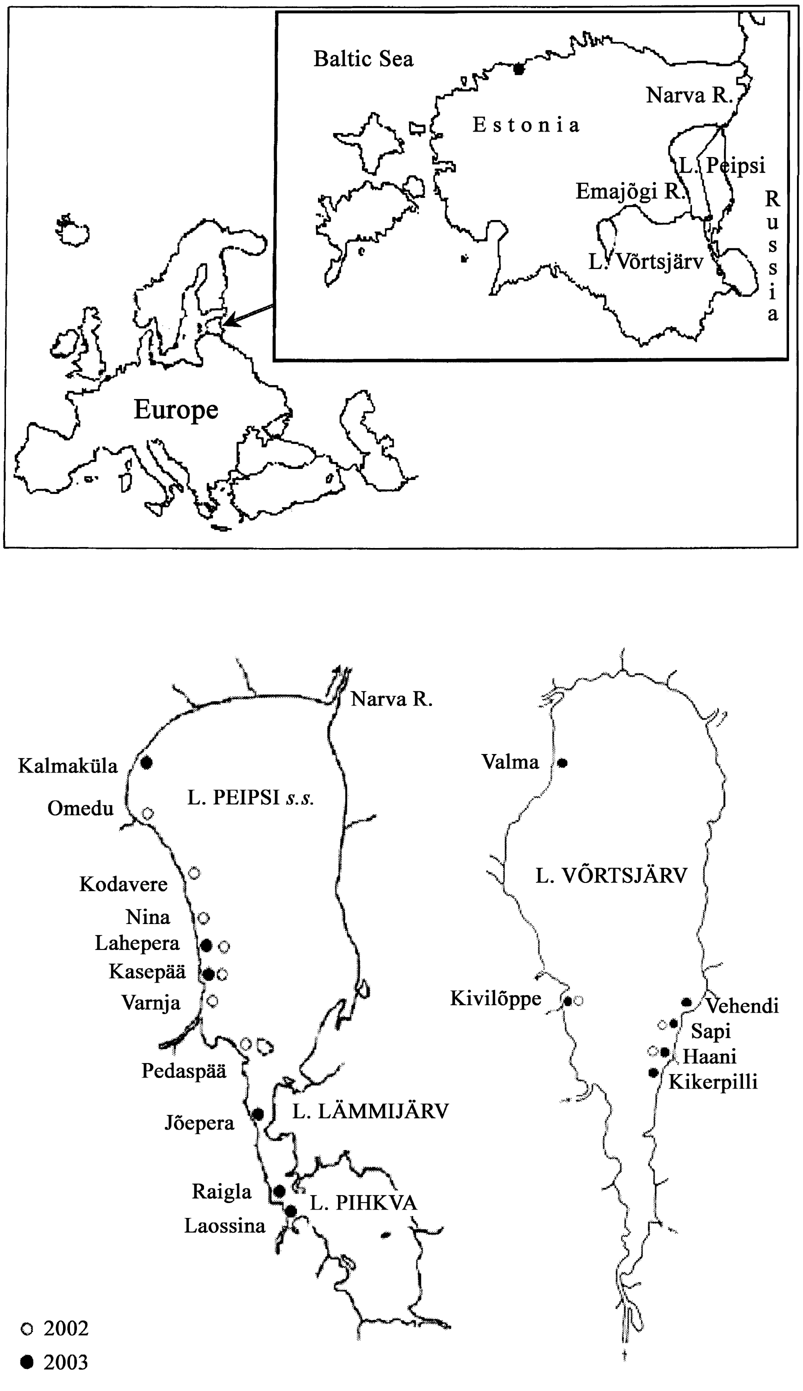

Fig. 1. Map of the study area and location of transects on L. Peipsi and L. Võrtsjärv.

Table 1. Morphometric and physico-chemical characteristics of L. Peipsi and its parts and L. Võrtsjärv (according to Jaani, 2001; Järvet et al., 2004; Tuvikene et al., 2004; Milius et al., 2005)

Characteristic	L. Peipsi *s.s.*	L. Lämmijärv	L. Pihkva	L. Peipsi *s.l.*	L. Võrtsjärv
Surface area, km^2	2611	236	708	3555	270
Volume, km^3	21.79	0.60	2.68	25.07	0.75
Mean depth, m	8.3	2.5	3.8	7.1	2.8
Maximum depth, m	12.9	15.3	5.3	15.3	6
Length of shoreline, km	260	83	177	520	109
Total P, mgP m^{-3}	35	63	65	41	53
Total N, mgN m^{-3}	664	907	982	739	1600

Water-level fluctuations in L. Peipsi are considerable and cause changes in both the surface area and volume of the lake. During the course of the last 80 years, a maximal amplitude of 3.04 m was registered (Eipre, 1983), the average annual range of water-level fluctuations is 1.15 m (Jaani & Kullus, 1999).

Bottom deposits near the coast consist mainly of aleurite sand or sandy aleurite, while the deep central regions are mostly covered with silt (Miidel & Raukas, 1999). Lake Peipsi provides a great variety of biotopes with a diverse trophic state, which support water organisms with different ecological requirements. As a result of this, the flora and fauna of this lake are quite rich both in the number of species and in their abundance. The number of plant species is large, altogether 128 taxa have been found there (Mäemets & Mäemets, 2001). The mean (with ±SE) abundance and biomass of macrozoobenthos in L. Peipsi in June 1964–1998 were 2671 ± 132 ind. m^{-2} and 12.95 ± 0.71 g m^{-2}, respectively (Timm et al., 2001). Altogether 33 fish species and one lamprey species inhabit permanently L. Peipsi together with the lower reaches of its tributaries (Pihu & Kangur, 2001). With respect to biomass, pikeperch predominates in L. Peipsi, while the share of benthivorous fishes is low (Kangur, 2003).

Lake Võrtsjärv is situated in central Estonia (Fig. 1). Its surface area is 270 km^2, mean depth 2.8 m, and maximum depth 6 m (Järvet et al., 2004) (Table 1). Lake Võrtsjärv is connected with L. Peipsi by the Emajõgi River. Lake Võrtsjärv is strongly eutrophic, its southern part being even hypertrophic (Tuvikene et al., 2004).

The shallowness of the lake and the wave-induced resuspension of bottom sediments contribute to the formation of a high seston (detritus) concentration and high turbidity in summer. Approximately 2/3 of the bottom is covered with lake silt (sapropel) lying on marl (Raukas, 2004). In the northern part of the lake and along the shoreline, the bottom is mostly covered by sand, silty sand, or clay and stony ridges, which occur in some of these areas.

In L. Võrtsjärv, the mean (±SE) macrozoobenthos abundance and biomass (without big molluscs) were 804 ± 56 ind. m^{-2} and 6.5 ± 0.9 g m^{-2} in 1973–2003, respectively (Kangur et al., 2004). As the number of benthophagous fish (mainly bream, ruffe, and eel) is large, the effect of predation by fish is one of the most significant factors causing reduction in the biomass of macroinvertebrates in L. Võrtsjärv (Kangur et al., 2004).

MATERIAL AND METHODS

Sampling and analysis

The material for this study was collected in the reed belt at different depths (0.1 and 0.6 m) of L. Peipsi and L. Võrtsjärv from August to October 2002 and 2003. Quantitative samples were taken from 7 profiles of L. Peipsi and from 3 profiles of L. Võrtsjärv in the first year and from 6 profiles of both lakes in the second year. At every station three replicate samples were taken. Altogether 78 quantitative samples from L. Peipsi and 54 samples from L. Võrtsjärv were analysed.

The samples were taken with bottom grabs of two different types: the Zabolotskij sampler (grasp area 225 cm^2) for sandy or stony substrates, and the cylindrical Mordukhaj-Boltovskoj corer for reed (grasp area 100 cm^2). The samples were washed on a silk sieve of about 0.3 mm mesh size, the animals were sorted alive by the eye, and fixed in 70% ethanol in four separate vials (for Chironomidae, Oligochaeta, small Mollusca, and other small animals – Varia). Large molluscs (*Dreissena*, Unionidae, and *Viviparus*) were fixed separately and were not included in the total figures of macrozoobenthos abundance and biomass due to their much bigger individual weight compared with all other animals. Ethanol-fixed animals were dried on filter paper for absorption of external moisture and weighed with a torsion balance with an accuracy of 1 mg. Large molluscs were weighed with a laboratory balance with an accuracy of 0.1 g.

Data treatment

Main statistical analysis was carried out with a general linear model technique provided by the SAS System, Release 8.2 (SAS Institute Inc., 1999). In the statistical processing of the data (2002 and 2003), dispersion analysis was employed. The mixed analysis of variance was carried out with lake, substrate, and vegetation as factors on the abundance and biomass of macrozoobenthos groups (command "estimate" in the procedure MIXED).

The substrate was represented by five different types: 1 – silt; 2 – silty sand; 3 – sand, clay; 4 – gravel; 5 – stones. Macrophytes were represented by two different macrophyte community types: only reed and mixed macrophytes (reed and other macrophyte species, e.g. *Potamogeton* spp., *Nuphar* sp.).

RESULTS

Abundance and biomass

The mean abundance and biomass of macrozoobenthos (without big molluscs) in the reed zone of L. Peipsi were about twice higher than in L. Võrtsjärv (Fig. 2, Table 2). Also the abundance and biomass of various animal groups were higher

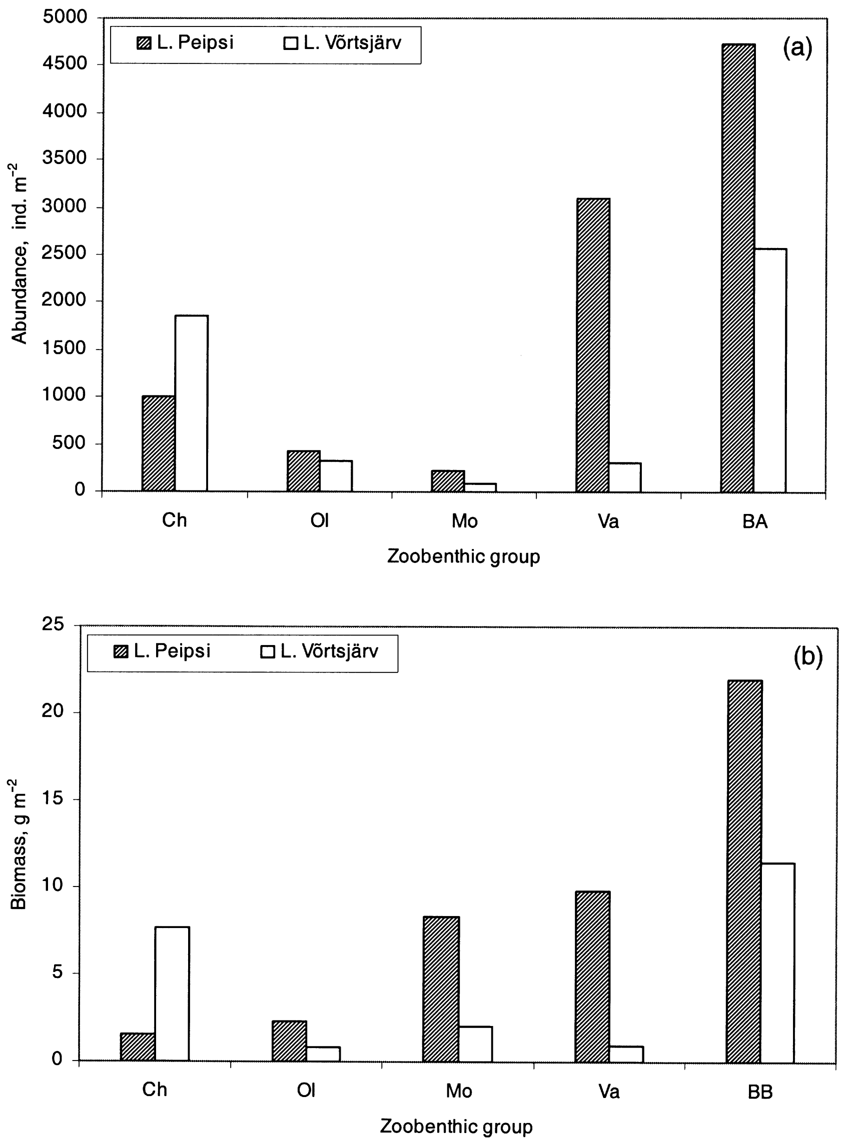

Fig. 2. Abundance (a) and biomass (b) of zoobenthic groups (Ch – Chironomidae, Ol – Oligochaeta, Mo – Mollusca (small), Va – Varia (other groups)) in the reed zone of L. Peipsi (Estonian part) and L. Võrtsjärv.

Table 2. Statistically significant differences ($\alpha \leq 0.05$) in the abundance (A) and biomass (B) of macrozoobenthic groups in the reed belt between L. Peipsi and L. Võrtsjärv

Zoobenthic group	Parameter, unit	L. Peipsi	L. Võrtsjärv	Statistically significant differences, *p*-value
Total zoobenthos	A, ind. m^{-2}	4648	2451	0.049
	B, g m^{-2}	22.19	10.35	0.016
Varia	A, ind. m^{-2}	3002	343	0.013
	B, g m^{-2}	9.5	1.07	0.007
Gammaridae	A, ind. m^{-2}	2802	0	0.000
	B, g m^{-2}	8.26	0	0.002
Ceratopogonidae	A, ind. m^{-2}	38	109	0.008
	B, g m^{-2}	0.03	0.10	0.001

in L. Peipsi, except for chironomids. The mean abundance of big molluscs was also higher in L. Peipsi.

The most significant differences between the zoobenthic communities in the lakes were revealed in the abundance and biomass of the whole Varia group, Gammaridae, and Ceratopogonidae (Table 2). The abundance of Gammaridae (*G. fasciatus*) was high in L. Peipsi, while this group was absent from our samples from L. Võrtsjärv. Ceratopogonidae were more abundant in L. Võrtsjärv than in L. Peipsi.

Taxonomic composition and dominants

The dominants in the zoobenthic communities of the reed belt of the large lakes of Estonia appeared to be different. *Gmelinoides fasciatus* was strongly dominating in the littoral of L. Peipsi, while chironomids were the most abundant group in the macrophyte zone of L. Võrtsjärv.

The benthic fauna of the reed belt in the two lakes was also different. In the reed zone of L. Peipsi 64 taxa of macrozoobenthos were found. Larvae of *Einfeldia carbonaria* (Meigen), *Polypedilum tetracrenatum* Hirv., and *Stictochironomus rosenscholdi* (Zett) were most abundant among the chironomids. The dominating species of oligochaetes were *Lumbriculus variegatus* (Müller), *Limnodrilus udekemianus* Clap., and *Limnodrilus hoffmeisteri* Clap. *Sphaerium* spp. and *Pisidium* spp. were abundant among the small molluscs (Table 3).

In the reed zone of L. Võrtsjärv 45 taxa of macrozoobenthos were found. Among the chironomids *Einfeldia carbonaria*, *Endochironomus albipennis*, *S. rosenchoeldi*, and *Glyptotendipes paripes* (Edwards) were abundant; among the oligohaetes, *Psammoryctides barbatus* (Grube) and *L. hoffmeisteri*; among the small molluscs

Table 3. Dominants of macrozoobenthos abundance in the reed zone of L. Peipsi and L. Võrtsjärv

Taxon	L. Peipsi (number of ind. in samples)		L. Võrtsjärv (number of ind. in samples)	
	2002	2003	2002	2003
Einfeldia carbonaria	95		177	
Glyptotendipes paripes		297		87
Polypedilum tetracrenatum	54			
Stictochironomus rosenschoeldi	49		298	
Endochironomus albipennis				121
Lumbriculus variegatus	76			
Limnodrilus hoffmeisteri	75			32
Limnodrilus udekemianus		117		
Psammoryctides barbatus			33	
Sphaerium spp.	98			
Pisidium spp.	71		6	
Valvata spp.				22
Gmelinoides fasciatus	928	1472		
Ceratopogonidae			30	51

Pisidium spp., and among the Varia group, Ceratopogonidae were the most abundant (Table 3). Only one species of big molluscs, *Anodonta* sp., was found in L. Võrtsjärv.

Factors influencing macrozoobenthos communities

The results of statistical analysis demonstrated that substrate type and vegetation as well as differences in the studied lakes influenced the macrozoobenthos communities of the reed belt. The abundance of the varia group was the highest in L. Peipsi (Table 2). This high value can be ascribed largely to one species, *Gmelinoides fasciatus*. Among the substrate types, the total abundance of macrozoobenthos, especially of *G. fasciatus* and oligochaetes, was the highest on gravel bottom (Table 4). Silty bottom in the reed belt was the most sparsely populated by macroinvertebrates, although Hirudinea preferred the silty substrate. The abundance and biomass of macrozoobenthos were mostly highest in the zone of macrovegetation where various plant species occur (Table 5). Two macrozoobenthic groups were most significantly influenced by macrovegetation type: *Asellus aquaticus* L. among the Isopoda and *Valvata* spp. among the small molluscs. *Asellus aquaticus* was abundant in the mixed vegetation zone, whereas the abundance of *Valvata* spp. was higher in the reed belt.

Table 4. Statistically significant differences ($\alpha \leq 0.05$) in the abundance (A) and biomass (B) of macrozoobenthic groups in the reed belt between different sediment types (1 – silt; 2 – silty sand; 3 – sand, clay; 4 – gravel)

Zoobenthic groups	Parameter, unit	Parameter values on the different substrate types				Statistically significant differences, *p*-value					
		1	2	3	4	1–2	1–3	1–4	2–3	2–4	3–4
Total zoobenthos	A, ind. m^{-2}	1550			7256			0.032			
Total zoobenthos	A, ind. m^{-2}		2521		7256					0.027	
Total zoobenthos	A, ind. m^{-2}			3137	7256						0.005
Total zoobenthos	B, g m^{-2}			9.18	32.67						0.004
Oligohaeta	A, ind. m^{-2}		215		803					0.009	
Oligohaeta	A, ind. m^{-2}			192	803						0.005
Oligohaeta	B, g m^{-2}			0.43	4.47						0.020
Varia	A, ind. m^{-2}		508		5002					0.027	
Varia	A, ind. m^{-2}			1715	5002						0.028
Gammaridae	A, ind. m^{-2}	133			4765			0.037			
Gammaridae	A, ind. m^{-2}		243		4765					0.026	
Gammaridae	A, ind. m			1470	4765						0.015
Hirudinea	A, ind. m	250	12			0.028					
Valvata	A, ind. m		43		0					0.006	
Valvata	A, ind. m			19	0						0.037
Valvata	B, g m^{-2}		0.58		0					0.007	
Valvata	B, g m^{-2}			0.37	0						0.043

Table 5. Statistically significant differences ($\alpha \leq 0.05$) in the abundance (A) and biomass (B) of macrozoobenthic groups between different macrophyte types

Zoobenthic group	Parameter, unit	Reed	Mixed macrophytes	Statistically significant differences, *p*-value
Asellus	A, ind. m^{-2}	8	92	0.018
Asellus	B, g m^{-2}	0	0.79	0.019
Valvata	A, ind. m^{-2}	29	0	0.013
Valvata	B, g m^{-2}	0	0	0.015

DISCUSSION

The littoral zone accounts for about 5% of the bottom of Lake Peipsi (Timm et al., 2001). The abundance of macrozoobenthos in the littoral zone is associated with the exceptionally high heterogeneity of biotopes (hard substrates, macrophytic vegetation, sediments), combined with good oxygen conditions and a variety of food sources, thus forming suitable habitats for numerous species (Lods-Crozet & Lachavanne, 1994). The results of our study indicate that the macrozoobenthos communities in the macrophyte zone of L. Peipsi and L. Võrtsjärv are diverse with a large number of taxa. According to a pilot study of six shallow lakes (Van de Meutter et al., 2005), the number of organisms and taxon richness are also higher among reed than in other microhabitats. In comparison with the open water area of L. Peipsi and L. Võrtsjärv, usually a limited number of individuals from two groups, Chironomidae and Oligochaeta, have occurred in recent decades (Kangur et al., 2004). The abundance of macrozoobenthos was higher in the reed belt than in the profundal of the investigated lakes (Timm et al., 2001; Kangur et al., 2004). According to the present study, substrate type and vegetation as well as the lake are the main factors that determine the variations of macrozoobenthos communities in the littoral zone. Our results show that the abundance and taxon richness of macrozoobenthos were the highest on gravel bottom. Most macrozoobenthos may have found refuge on the gravel bottom from predators.

The high abundance and biomass of chironomids probably reflects the eutrophic status of L. Võrtsjärv. Some authors assess eutrophication of lakes using chironomids (Brodersen & Lindegaard, 1999; Langdon et al., 2006). Some chironomid-based eutrophication studies have shown that chironomid communities respond to a decrease in dissolved oxygen caused by the decomposition of increased amounts of sedimentary organic matter (Meriläinen et al., 2000). Brodersen & Lindegaard (1999), however, examined the response of the chironomid community in shallow, largely unstratified lakes and found that chironomid assemblages are most strongly related to the chlorophyll *a* content, reflecting more immediate benthic–pelagic coupling in shallow lakes (i.e. food quantity and quality).

Most chironomid taxa living in L. Võrtsjärv are limited to various littoral habitats. Larvae of *Stictochironomus rosenschoeldi*, *Cladotanytarsus* gr. *mancus*, *Polypedilum tetracrenatum*, and *P. bicrenatum* prevail on sand. On silty sand or silt the phytophilous species *Endochironomus*, *Polypedilum*, *Glyptotendipes*, and *Pseudochironomus* are common among the macrovegetation. *Glyptotendipes paripes* and *Microtendipes pedellus* occur abundantly on stones (Kangur et al., 2004).

The results of the present study indicate that *G. fasciatus* was the most abundant macroinvertebrate species in the reed belt of L. Peipsi. This newcomer was introduced from L. Baikal into the NE part of L. Peipsi at the beginning of the 1970s (Timm & Timm, 1993) and has explosively increased in the lake. At present, this gammarid species has a strong effect on the benthic communities of the littoral zone in L. Peipsi. These communities have been irreversibly altered by *G. fasciatus*, while the native gammarids *Gammarus lacustris* Sars and *Pallasea quadrispinosa* Sars were not found in our samples. In L. Peipsi *G. fasciatus* is the most abundant in shallow water and prefers a hard substrate, especially gravel bottom. In such habitats the benthic fauna is very monotonous, being strongly dominated by Gmelinoides. The spread of non-indigenous species and the decline in autochthonous species lead to the homogenization of the freshwater fauna in terms of systematic units; however, the functional consequences are poorly documented (Devin et al., 2005). The decrease in oligochaetes in shallow water can be accounted for by an increase in predatory *G. fasciatus* (Timm et al., 1996).

ACKNOWLEDGEMENTS

This research was supported by the Estonian Science Foundation grant No. 6820 and target financed project No. 0362483s03. Many thanks are due to Tarmo Timm for identifying the Oligochaeta.

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Makrozoobentose koosluste varieeruvus kahe madala suurjärve roostikus

Margit Kumari, Külli Kangur ja Marina Haldna

On antud ülevaade makrozoobentose kooslustest roostikuvööndis kahes madalas suurjärves: Peipsi (3555 km^2) ja Võrtsjärves (270 km^2), mis erinevad oluliselt toitelisuse (biogeenide sisalduse) poolest. Pilliroog *Phragmites australis* (Cav.) on mõlema järve kaldaveetaimestikus dominant, olles viimase 30 aastaga tugevasti laienenud. Kuna roostikuvööndi põhjaloomastiku kohta on andmeid vähe, on artikli eesmärgiks anda ülevaade seal elavatest põhjaloomastiku kooslustest, võrrelda nende erinevusi kahes järves ja uurida, millised faktorid mõjutavad põhjaloomastiku kooslusi roostikus kõige enam. Uuringu tulemused näitavad, et Peipsi ja Võrtsjärve roostikuvööndis on zoobentose dominandid erinevad. Peipsis on dominandiks *Gmelinoides fasciatus* ja Võrtsjärves erinevad hironomiidiliigid. *G. fasciatus* sattus Peipsi järve 1970. aastatel ja muutus seal massiliseks, põhjustades kohaliku põhjaloomastiku koosluse muutusi. Kõige enam mõjutavad põhjaloomastikku substraat ja taimestik. Eelistatuim substraadi tüüp on kruus. Põhjaloomastiku arvukus on kõrgem sellisel kaldalähedasel alal, kus peale pilliroo esineb ka teisi taimeliike.