

Macro- and meiozoobenthos in some small stratified lakes of Estonia

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Abstract. Macro- and meiozoobenthos (300 samples with a 225 cm² Boruckij grab and 180 with a 6.38 cm² corer) from unvegetated, soft-bottom areas in ten small stratified lakes were studied in July–August 1998–1999. The sampling sites were located just above, in the middle, and below the position of the metalimnion in each lake. Chironomidae and Oligochaeta were common in both macro- and meiozoobenthic samples but more abundant (by an order of magnitude) in the latter because the smallest individuals were included. The meiobenthic samples were dominated by planktonic crustaceans, particularly Cyclopoida, with respect to abundance while most of their biomass was formed by the macrobenthic animal groups. Eumeiobenthos *sensu stricto*, such as Nematoda, Ostracoda, etc., were scarce. Thirty-three variables (abundance, biomass, and number of taxa in different samples) were related to water layer (epi-, meta-, and hypolimnion), sampling depth, lake, year, and O₂ saturation %. Most variables depended on lake but not on year. Abundance and biomass of the studied taxa and the number of taxa of macrozoobenthos per sample decreased significantly from the epi- to hypolimnion, except for *Chaoborus flavicans*, which was more abundant in deeper layers of water. From the results of ANOVA, it was concluded that the biomass and abundance of *Chaoborus*, biomass of Hydrachnidia, abundance of Chironomidae and other ‘large’ animals in the meiobenthic samples, as well as the number of taxa of macrozoobenthos per sample did not follow the layers but only the depth. The distribution of the biomass of macrozoobenthic Chironomidae as well as the total biomass and abundance of macrozoobenthos without *Chaoborus* were more tied to separate layers. For the majority of individual taxa no dependence on depth was found. Discriminant analysis revealed a rather weak separation of the water layers in summer by the benthic characteristics. An index formed of 33 variables of zoobenthos with the highest statistical significance for testing the depth effect (Depth Index) revealed the most apparent changes in environmental conditions in the upper part of the metalimnion.

Key words: lakes, stratification, zoobenthos.

INTRODUCTION

Thermal and oxygen stratification of the water column is one of the most significant factors that influence the distribution of lake biota (Wetzel, 1983; Lampert & Sommer, 1997). According to water temperature, most stratified lakes in the temperate zone reveal two water layers with one transition area.

The uniformly warm, circulating, and fairly turbulent upper layer corresponding to the trophogenic zone forms the epilimnion. The region of greatest change in temperature and/or oxygen content below the epilimnion is called the metalimnion while the deepest, coldest, and relatively undisturbed region is the hypolimnion. During summer stratification, only the epilimnion can exchange gases with the atmosphere while the hypolimnion only consumes its supply of oxygen.

Hypolimnetic oxygen concentration, which is the main limiting factor for the profundal community, is not always related to the trophic state but can also depend on lake morphometry (Bazzanti & Seminara, 1985). Macrozoobenthos respond to a restricted oxygen content with a decreasing species number, abundance, and biomass (Kajak, 1988; Int Panis et al., 1995; Jónasson, 1996; Bazzanti et al., 1998). Summer oxygen content plays the main role among the factors that control the distribution of chironomid larvae on the bottom; it is more important than the concentration of nutrients (Kansanen et al., 1984).

Artificial oxygenation of the hypolimnion can lead to significant positive changes in hypolimnion benthic communities (Dinsmore & Prepas, 1993, 1997), while the autumn overturn alone cannot affect significantly anoxic deep-water communities (Bazzanti & Seminara, 1985; Bazzanti et al., 1998). Highly mobile taxa unable to tolerate hypoxia respond to a decline of the oxygen concentration by migrating upward in the water column. Episodes of hypoxia could have long-lasting effects on communities either by direct mortality or selective predation on less tolerant taxa (Kolar & Rahel, 1993). Few groups (some chironomids, oligochaetes, and sphaeriids) are able to utilize extremely low oxygen concentrations (Hamburger et al., 2000). Only *Chaoborus* larvae, although breathing the oxygen available in the epilimnion, use the anoxic hypolimnion as a refugium from fish predators (Wagner-Döbler, 1990; Voss & Mumm, 1999). In daytime, *Chaoborus* larvae do not penetrate into sediment but congregate in darkness above the maximum content of sulphids (redoxcline), where a dense population of bacteria occurs (Baker et al., 1985).

Very little is known about relations of freshwater meiozoobenthos to stratification, as meiobenthos studies have been performed either in lakes devoid of a distinct metalimnion (e.g. Stańczykowska & Przytoka-Jusiak, 1968; Kurashov, 1994; Särkkä, 1995), or without particular respect to the position of the metalimnion (e.g. Petukhov, 1999).

In most Estonian lakes stratification appears in June and lasts till October. Stratification became stronger and the anaerobic zone increased during the 1970s–1980s as a result of eutrophication (Mäemets et al., 1994; Ott et al., 1999).

We studied whether and how summer thermal stratification revealed the taxonomical composition and amount of macro- and meiozoobenthos in several Estonian lakes. Particularly, we were interested in whether changes in macro-invertebrate metrics followed water layers, or were caused rather by sampling depth.

The work was a part of the project ‘The influence of stratification on the biological matter circulation of the lake ecosystem’, carried out by the Võrtsjärv

Limnological Station of the Institute of Zoology and Botany at the Estonian Agricultural University (presently Estonian University of Life Sciences) in 1998–2000.

STUDY AREA

Ten dimictic lakes in South-East Estonia were studied (Fig. 1, Table 1). They are relatively small (mean area 5 ha) with the maximum depth between 10 and 30 m. Some of them belong to the deepest lakes in the area.

Two lakes, Nohipalo Valgõjärv and Kooraste Linajärv, lie in forests, Lake Vellavere Külajärv is surrounded mainly with arable lands, while Lake Verevi is partly in an urban area. Other lakes are situated in mixed landscapes. About 100 years ago, lakes Holstre Linajärv and Kooraste Linajärv were strongly affected by organic pollution from flax retting. Significant eutrophication in lakes Vellavere Külajärv and Verevi started in the 1970s. Except for Lake Nohipalo Valgõjärv, the content of PO₄-P in near-bottom water was typical of hypertrophic lakes (>100 mg/m³). Ammonium content was high in the hypolimnion in all lakes, but it decreased significantly in the lower boundary of the metalimnion (Tammert et al., 2009).

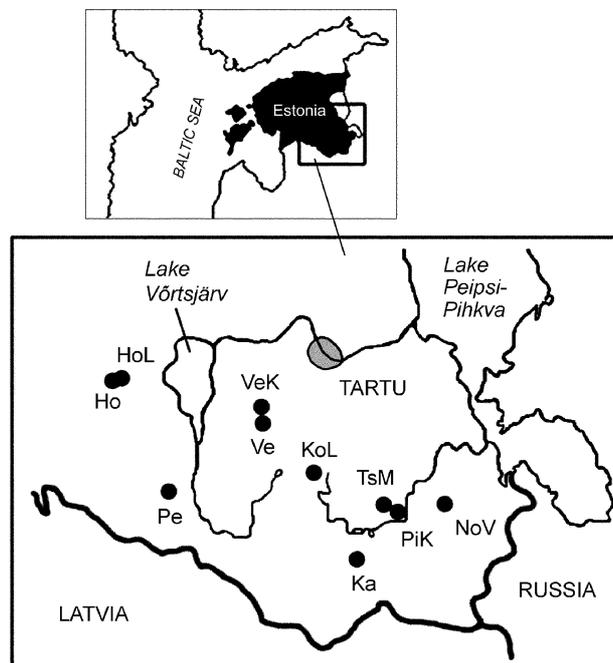


Fig. 1. Location of the lakes studied. Ho – Holstre, HoL – Holstre Linajärv, Pe – Petajärv, VeK – Vellavere Külajärv, Ve – Verevi, KoL – Kooraste Linajärv, Ka – Kaussjärv, TsM – Tsolgo Mustjärv, PiK – Pindi Kärnjärv, NoV – Nohipalo Valgõjärv.

Table 1. Description of the lakes studied. Temperature changes $> 1.5^{\circ}\text{C}/0.5\text{ m}$ were used as a criterion of the metalimnion

Lake	Approximate coordinates of sampling area, dd mm ss		Limnological type*	Area, ha*	Maximum depth, m*	Range and thickness (in brackets) of metalimnion, m**	
	Lat. (N)	Long. (E)				1998	1999
Holstre	58 16 43	25 41 21	Eutrophic, hardwater	2.9	16.3	3–5 (2)	2.5–4.5 (2)
Holstre Linajärv	58 17 28	26 42 20	Eutrophic, softwater	1.7	16.7	2.5–4 (1.5)	2.5–4 (1.5)
Kaussjärv	57 44 00	26 55 40	Eutrophic with mesotrophic features	1.9	22.0	5–6 (1)	4–5 (1)
Kooraste Linajärv	57 57 45	26 39 50	Hypertrophic, softwater	2.7	12.7	2.5–4.5 (2)	3–4.5 (1.5)
Nohipalo Valgöjärv	57 56 32	27 20 45	Oligotrophic, eutrophied	6.3	12.5	4–5.5 (1.5)	3.5–5.5 (2)
Petjärv	57 56 50	25 56 00	Eutrophic, softwater	3.6	25.0	3–4.5 (1.5)	2.5–4.5 (2)
Pindi Kärvjärv	57 54 00	27 09 50	Mixotrophic, hardwater	8.3	26.0	2.5–4 (1.5)	2.5–4 (1.5)
Tsolgo Mustjärv	57 55 33	27 06 50	Eutrophic, softwater	6.0	29.7	3–5 (2)	2.5–4.5 (2)
Vellavere Küljärv	58 15 33	26 24 24	Hypertrophic, hardwater	4.6	25.0	3–4.5 (1.5)	2.5–4.5 (2)
Verevi	58 13 58	26 24 45	Hypertrophic, hardwater	12.6	11.0	2.5–3.5 (1)	4–5.5 (1.5)
Mean						3.1–4.7 (1.6)	3.0–4.7 (1.7)

* After Mäemets, 1977. ** After Tammert et al., 2009.

MATERIAL AND METHODS

Sampling and identification

Benthic samples were taken from the soft unvegetated bottom on 15 July–5 August 1998 and 16 July–3 August 1999. Sampling was carried out in three zones: (1) at a depth corresponding to the epilimnion, near the upper boundary of the metalimnion; (2) in the middle part of the metalimnion; and (3) in the upper hypolimnion, near the lower boundary of the metalimnion (Fig. 2). Thus, epilimnetic areas with vegetation and/or hard bottom as well as deeper parts of the profundal hypolimnion were not sampled.

In 1998 the limits of the metalimnion and oxycline in the water column were established in each case before sampling by the team of hydrochemists involved in the same project (Tammert et al., 2009). The conditions above the bottom at each sampling site were considered to be equal to those observed at the same depth in the water column. In 1999 sampling was carried out at the same depths as in 1998, supposing that the location of benthic organisms was more stable than the possible small year-to-year variation in stratification (Table 1).

Macrozoobenthos was collected with a Boruckij-type sampler (a modification of the Ekman grab, grasp area 225 cm², box height 40 cm) and meiozoobenthos with a core sampler (6.38 cm², tube height 52 cm). In each lake five replicates of macrozoobenthos and three replicates of meiozoobenthos were taken in each zone and in both years. Thus a total of 150 samples of macrozoobenthos and 90 samples of meiozoobenthos were collected per year, except that three replicates of macrozoobenthos were missing in 1999 due to a sampling error. Macrozoobenthos samples were sieved in field (with a standard 0.4 mm mesh), sorted in laboratory alive, and then fixed in 70% ethanol.

Meiozoobenthos samples were fixed in situ in a weak formaldehyde solution, washed in the laboratory on sieves with mesh sizes of 0.4 and 0.15 mm, and sorted under $\times 16$ magnification in the Bogorov counting chamber. After the removal of the exterior moisture on blotting paper, wet biomass of macrozoobenthos and

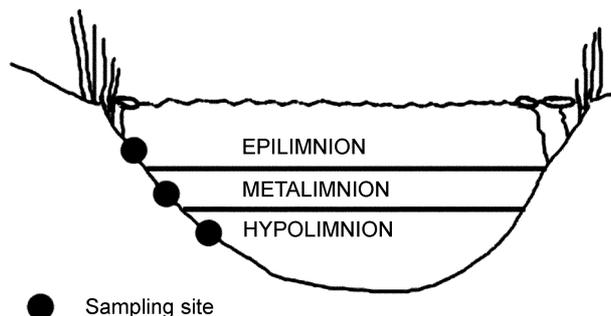


Fig. 2. Location of the sampling sites in the benthic zone.

of larger specimens of meiozoobenthos was estimated on torsion weights (with an accuracy of 1 mg). The wet weight of the smaller animals was calculated indirectly in different ways (see Timm, 2002). Identification was primarily carried out to family or higher taxonomic level following Bowman & Bailey (1997). As *Chaoborus* larvae are pelagic rather than benthic and thus they had a clearly different depth distribution than the other groups, their biomass and abundance were separated from the total counts where necessary.

Meiozoobenthos was divided into 'large' and 'small' animals, which corresponded respectively to young stages of macrozoobenthic groups (mostly chironomids and oligochaetes) and actual meiozoobenthos (small crustaceans, nematodes, etc.).

Data processing

We calculated the abundance and biomass of 20 taxa from macrozoobenthos samples and the abundance of 23 taxa from meiozoobenthos samples (these included also several 'macrozoobenthic' groups), as well as total abundance, total biomass, and number of taxa per sample.

All the studied benthic parameters were $\log(x + 1)$ transformed to obtain normality. The mean values and other statistics were calculated on transformed data and then converted back to the original scale. The distribution of 33 transformed variables was found similar to the normal curve. We used the SAS system (SAS, 1996) both for univariate and multivariate analyses. To estimate the impact of depth, layer, and oxygen saturation on benthic variables, and also to eliminate the disturbing effect of sampling years and lakes, we used type III ANOVA (analysis of variance), dividing the summary influence of all factors into independent parts related to separate factors. Results of this analysis were then presented through probabilities (*P*-values) that the observed value of the *F*- or *t*-statistic used in decision-making under null-hypothesis. In case of multiple decisions, the simplest form of the Bonferroni correction was applied. The conservativeness of this method can be taken as a penalty for a possible non-normality of $\log(x + 1)$ -transformed characteristics.

To test whether the depth changes of zoobenthos were due to depth rather than due to layers, we tested the effect of layer after elimination of the effect of depth (as presented by a second-order polynomial of depth). If the effect of layer then remained significant, the corresponding benthos variable was considered as tied to the layer.

The joint behaviour of benthic variables was analysed by parametric multivariate methods, mainly by MANOVA-option of the SAS/GLM procedure. The MANOVA option forces GLM procedure to calculate coefficients for the linear combination of variables, which can be best predicted by the sampling depth (in the sense of *F*-statistic's maximum). This combination is called below the Depth Index. Linear discriminant analysis of the SAS/STAT package was applied to test whether the zoobenthos community parameters enabled to determine the layer from which the sample was taken.

RESULTS

General data analysis

Chironomidae, Oligochaeta, and *Chaoborus flavicans* dominated both in the biomass and abundance in macrozoobenthos, while Cyclopoida, Chironomidae, and Oligochaeta were the most abundant in meiobenthos (Table 2). *Chironomus* larvae formed the majority of the chironomid biomass, especially in the meta- and

Table 2. Survey of data: *n*, number of observations; Gmean, geometric mean; MSD, multiplicative standard deviation; Max, maximum value. The minimal value for all variables is zero. All biomasses are given as g (wet weight) and abundances as number of individuals per haul (225 cm² for macro- and 6.38 cm² for meiozoobenthos)

Variable	<i>n</i>	GMean	MSD	Max
Macrozoobenthos				
Biomass of Chironomidae	297	6.71	6.13	878
Biomass of Oligochaeta	297	2.48	3.98	128
Biomass of Ceratopogonidae	297	1.20	1.68	36
Biomass of <i>Chaoborus</i>	297	2.07	3.25	68
Biomass of <i>Asellus</i>	297	1.06	1.42	18
Biomass of Hirudinea	297	1.03	1.37	152
Biomass of Hydrachnidia	297	1.04	1.25	6
Total biomass	297	19.48	6.29	2662
Total biomass without <i>Chaoborus</i>	297	13.87	7.67	2662
Number of taxa per sample	300	2.63	1.69	8
Abundance of Chironomidae	297	3.15	3.03	122
Abundance of Oligochaeta	297	1.78	2.65	130
Abundance of Ceratopogonidae	297	1.24	1.60	17
Abundance of <i>Chaoborus</i>	297	1.53	2.01	20
Abundance of Sphaeriidae	297	1.08	1.34	7
Abundance of Trichoptera	297	1.04	1.19	3
Abundance of <i>Sialis</i>	297	1.07	1.27	4
Abundance of <i>Asellus</i>	297	1.03	1.20	6
Abundance of Hirudinea	297	1.01	1.11	3
Total abundance	297	5.76	3.19	258
Total abundance without <i>Chaoborus</i>	297	4.61	3.50	258
Meiozoobenthos				
Abundance of Chironomidae	180	1.30	1.64	10
Abundance of Oligochaeta	180	1.76	2.33	90
Abundance of Sphaeriidae	180	1.05	1.25	5
Abundance of Nematoda	180	1.14	1.54	40
Abundance of Cyclopoida	180	2.60	3.12	90
Abundance of Calanoida	180	1.24	1.66	21
Abundance of Cladocera	180	1.21	1.58	9
Abundance of Ostracoda	180	1.15	1.51	8
Total abundance	180	6.92	3.26	144
Abundance of 'large animals'	180	2.19	2.50	96
Abundance of 'small animals'	180	3.58	3.26	96
Number of taxa per sample	180	2.70	1.78	9

hypolimnion. *Potamothenis hammoniensis* and *Limnodrilus hoffmeisteri* were the most common oligochaete species. Other groups (Ceratopogonidae, Hirudinea, Hydrachnidia, Sphaeriidae, *Asellus aquaticus*, *Sialis lutaria*, *Caenis* sp., various Trichoptera) were much rarer. In two lakes, a few specimens of megabenthic *Anodonta* occurred, which were not accounted in the calculations. In meiobenthos samples, *Mesocyclops leuckarti* and *M. oithonoides* dominated, often surprisingly in deeper zones together with *C. flavicans*. Zooplankton were scarce in the hypolimnion, and no peaks were observed there (Kübar et al., 2001; data of Lake Verevi). According to ANOVA, the majority of the variables depended on lake but not on year (Table 3). The influence of layers

Table 3. Results of Type III ANOVA of studied variables: *P*-values of factors. Boldface highlights *P*-values less than 0.0003, significant according to the Bonferroni correction at $\alpha = 0.05$

Dependent	Lake	Year	Layer	Year*Layer	O ₂ %
Macrozoobenthos					
Biomass of Chironomidae	<0.0001	0.0154	0.6355	0.0002	0.0524
Biomass of Oligochaeta	<0.0001	0.0447	0.8050	0.2096	0.5002
Biomass of Ceratopogonidae	0.0002	0.0012	0.8886	0.0992	0.0740
Biomass of <i>Chaoborus</i>	<0.0001	0.0010	<0.0001	0.7171	0.0004
Biomass of <i>Asellus</i>	0.1140	0.6325	0.0009	0.0202	<0.0001
Biomass of Hirudinea	0.1868	0.9301	0.5160	0.9590	0.0579
Biomass of Hydrachnidia	0.8230	0.4415	0.0135	0.8749	0.0684
Total biomass	<0.0001	0.0520	0.0050	0.0026	0.7423
Total biomass without <i>Chaoborus</i>	<0.0001	0.0287	0.0002	0.0025	0.3525
Number of taxa per sample	<0.0001	0.8805	0.0012	0.5127	0.4017
Abundance of Chironomidae	<0.0001	0.4370	0.7120	0.0162	0.0142
Abundance of Oligochaeta	<0.0001	0.0062	0.7600	0.2735	0.5145
Abundance of Ceratopogonidae	<0.0001	0.0168	0.8494	0.2718	0.0501
Abundance of <i>Chaoborus</i>	<0.0001	0.0040	<0.0001	0.7495	0.0009
Abundance of Sphaeriidae	<0.0001	0.0916	0.0015	0.6082	0.3164
Abundance of Trichoptera	0.0089	0.1101	0.2698	0.0942	0.1371
Abundance of <i>Sialis</i>	<0.0001	0.8788	<0.0001	0.2754	0.1132
Abundance of <i>Asellus</i>	0.1237	0.4305	0.0007	0.0566	0.0002
Abundance of Hirudinea	0.0052	0.8119	0.2954	0.3886	0.0032
Total abundance	<0.0001	0.3856	0.3823	0.0250	0.4701
Total abundance without <i>Chaoborus</i>	<0.0001	0.3513	0.1143	0.0116	0.1392
Meiozoobenthos					
Abundance of Chironomidae	<0.0001	0.0809	0.1150	0.9184	0.6081
Abundance of Oligochaeta	<0.0001	0.0059	0.0414	0.2586	0.8287
Abundance of Sphaeriidae	0.3049	0.5412	0.0258	0.3664	0.0123
Abundance of Nematoda	<0.0001	0.0117	0.3150	0.6664	0.4761
Abundance of Cyclopoida	<0.0001	0.0194	0.0227	0.7523	0.0514
Abundance of Calanoida	<0.0001	0.4330	0.1609	0.2341	0.0005
Abundance of Cladocera	0.0013	0.7394	0.0279	0.1443	0.0430
Abundance of Ostracoda	<0.0001	0.0233	<0.0001	0.0097	0.0109
Total abundance	<0.0001	0.0146	0.7180	0.9418	0.0051
Abundance of 'large animals'	<0.0001	0.0713	0.0093	0.4463	0.9563
Abundance of 'small animals'	<0.0001	0.0254	0.5821	0.7541	0.0007
Number of taxa per sample	<0.0001	0.6339	0.0252	0.9932	0.0055

on zoobenthos was clear in *Chaoborus* (both biomass and abundance) and in the abundance of *Sialis* and Ostracoda. As to total biomasses or abundances, only total biomass without *Chaoborus* was significantly connected to layers. As the summer of 1999 was much warmer than that of 1998, we assumed the dependence of chironomid biomass on the variable Year*Layer to be explained by phenological differences. A surprisingly low influence of oxygen saturation percentage in water to the variables studied was found (Table 3). A significant relationship was detected only in the case of *Asellus*, which is an 'oxyphile' taxon.

Correlation analysis demonstrated a good accordance between general macrozoobenthic variables except *Chaoborus* (Table 4). The abundance and biomass of *Chaoborus* were significantly positively correlated only to the total abundance of macrozoobenthos but not to their total biomass. In meiobenthos, the abundance of 'small animals' and the largest part of it, cyclopoids, were significantly correlated only to each other but not to other variables.

Analysis of zonal effects

In pairwise comparison of zones, significant differences between the epilimnion and the hypolimnion were the clearest: 10 of 21 variables in macrobenthos and 7 of 12 variables in meiobenthos (Table 5, Fig. 3). Between the epi- and metalimnion, eight variables of macrozoobenthos differed significantly, while significance was not confirmed for any of the meiobenthos variables. In the case of meta- and hypolimnion, only four significant differences of macrozoobenthic parameters were detected, while seven differences of meiozoobenthos occurred.

Type I ANOVA was used to ascertain whether effects of zones were caused by sampling depth. When the effect of sampling depth was removed, the following macrozoobenthic variables were found to respond to zones: biomass of Chironomidae and Oligochaeta; abundance of Chironomidae, Oligochaeta, and Sphaeriidae; total biomass without *Chaoborus*; total abundance without *Chaoborus*; total abundance (Table 6). No such significant relationships were observed for meiozoobenthos.

Discriminant analysis was used to predict zones on the basis of zoobenthic variables and to compare them with real zones based on water temperature. The level of misclassification was comparatively high and in some cases exceeded even 50%. Macrozoobenthic abundances gave the most consistent and meiozoobenthic abundances the least consistent results. Among zones, those corresponding to the metalimnion were the most complicated to predict (Table 7).

A specific linear combination (index) from all 33 benthic variables studied, called here Depth Index (DI), was constructed for all samples from the 10 lakes.

Table 4. Pearson's correlations between some studied variables. According to Bonferroni correction, a critical correlation is approximately 0.2. B, biomass; N, abundance; NTAX, number of taxa per sample; TOT, total; CHI, Chironomidae; OLL, Oligochaeta; CHA, *Chaoborus*; CYC, Cyclopoida. Boldface indicates significant results

	Macrozoobenthos										Meiozoobenthos					
	BCHI	BOLI	NTAX	BCHA	NCHI	NOLI	NCHA	BTOT- BCHA	NTOT- NCHA	BTOT	NTOT	Nsmall	Nlarge	NCYC	NTAX	
Macrozoobenthos																
benthos																
BCHI	1.000															
BOLI	0.395	1.000														
NTAX	0.563	0.589	1.000													
BCHA	0.023	-0.096	0.162	1.000												
NCHI	0.881	0.405	0.616	0.043	1.000											
NOLI	0.443	0.930	0.580	-0.076	0.465	1.000										
NCHA	0.027	-0.077	0.160	0.963	0.035	-0.071	1.000									
BTOT-BCHA	0.792	0.580	0.750	-0.099	0.731	0.570	-0.083	1.000								
NTOT-NCHA	0.805	0.653	0.779	-0.026	0.900	0.707	-0.030	0.853	1.000							
BTOT	0.747	0.544	0.786	0.159	0.696	0.540	0.162	0.935	0.800	1.000						
NTOT	0.767	0.616	0.810	0.241	0.856	0.674	0.257	0.783	0.935	0.847	1.000					
Meiozoobenthos																
benthos																
Nsmall	-0.030	-0.025	0.064	0.186	0.023	0.068	0.156	-0.023	0.031	0.018	0.063	1.000				
Nlarge	0.445	0.426	0.469	-0.101	0.509	0.541	-0.116	0.435	0.572	0.400	0.530	0.153	1.000			
NCYC	-0.047	-0.077	-0.009	0.143	-0.022	-0.011	0.109	-0.064	-0.044	-0.037	-0.035	0.914	0.041	1.000		
NTAX	0.201	0.191	0.315	0.090	0.286	0.299	0.064	0.219	0.346	0.229	0.346	0.588	0.665	0.402	1.000	

Table 5. Results of Type III ANOVA: estimated significant differences between the layers. Boldface indicates significant relationships ($P < 0.05$)

Dependent variable	Epilimnion– hypolimnion Diff. ±S.E.	<i>P</i> -value	Epilimnion– metalimnion Diff. ±S.E.	<i>P</i> -value	Metalimnion– hypolimnion Diff. ±S.E.	<i>P</i> -value
Macrozoobenthos						
Biomass of Chironomidae	0.235 ± 0.385	0.54140	0.002 ± 0.299	0.99364	0.233 ± 0.258	0.36669
Biomass of Oligochaeta	0.076 ± 0.245	0.75679	0.118 ± 0.190	0.53498	-0.042 ± 0.164	0.79709
Biomass of Ceratopogonidae	0.020 ± 0.124	0.87032	-0.024 ± 0.096	0.80250	0.044 ± 0.083	0.59345
Biomass of <i>Chaoborus</i>	-0.919 ± 0.226	0.00007	-0.069 ± 0.175	0.69305	-0.849 ± 0.151	0.00000
Biomass of <i>Asellus</i>	0.304 ± 0.082	0.00025	0.206 ± 0.063	0.00136	0.098 ± 0.054	0.07421
Biomass of Hirudinea	-0.024 ± 0.082	0.77242	0.035 ± 0.064	0.58525	-0.059 ± 0.055	0.28730
Biomass of Hydrachnidia	0.160 ± 0.058	0.00598	0.122 ± 0.045	0.00717	0.038 ± 0.038	0.31936
Total biomass	1.132 ± 0.417	0.00710	0.896 ± 0.324	0.00607	0.236 ± 0.279	0.39868
Total biomass without <i>Chaoborus</i>	1.654 ± 0.425	0.00013	0.913 ± 0.330	0.00607	0.740 ± 0.284	0.00981
Number of taxa per sample	0.378 ± 0.110	0.00070	0.286 ± 0.085	0.00090	0.092 ± 0.073	0.20746
Abundance of Chironomidae	0.071 ± 0.232	0.75922	-0.066 ± 0.180	0.71376	0.137 ± 0.155	0.37737
Abundance of Oligochaeta	-0.117 ± 0.156	0.45468	-0.049 ± 0.121	0.68640	-0.068 ± 0.104	0.51641
Abundance of Ceratopogonidae	-0.001 ± 0.109	0.98587	-0.041 ± 0.084	0.62936	0.039 ± 0.073	0.59384
Abundance of <i>Chaoborus</i>	-0.570 ± 0.134	0.00003	-0.021 ± 0.104	0.83748	-0.549 ± 0.089	0.00000
Abundance of Sphaeriidae	0.230 ± 0.067	0.00069	0.168 ± 0.052	0.00136	0.061 ± 0.044	0.16930
Abundance of Trichoptera	-0.005 ± 0.043	0.89538	-0.039 ± 0.033	0.24463	0.033 ± 0.029	0.24882
Abundance of <i>Stalix</i>	0.242 ± 0.054	0.00002	0.117 ± 0.042	0.00620	0.124 ± 0.036	0.00081

Table 5. Continued

Dependent variable	Epilimnion– hypolimnion Diff. ± S.E.	P-value	Epilimnion– metalimnion Diff. ± S.E.	P-value	Metalimnion– hypolimnion Diff. ± S.E.	P-value
Abundance of <i>Asellus</i>	0.159 ± 0.043	0.00028	0.122 ± 0.033	0.00035	0.037 ± 0.029	0.19557
Abundance of Hirudinea	-0.042 ± 0.027	0.12464	-0.023 ± 0.021	0.26436	-0.018 ± 0.018	0.31627
Total abundance	0.121 ± 0.245	0.62035	0.197 ± 0.190	0.30038	-0.075 ± 0.164	0.64403
Total abundance without <i>Chaoborus</i>	0.431 ± 0.241	0.07517	0.140 ± 0.187	0.45538	0.291 ± 0.161	0.07271
Meiozoobenthos						
Abundance of Chironomidae	0.300 ± 0.144	0.04006	0.152 ± 0.111	0.17526	0.147 ± 0.095	0.12534
Abundance of Oligochaeta	0.453 ± 0.230	0.05066	0.069 ± 0.177	0.69482	0.383 ± 0.152	0.01281
Abundance of Sphaeriidae	0.191 ± 0.072	0.00876	0.083 ± 0.055	0.13726	0.108 ± 0.047	0.02457
Abundance of Nematoda	-0.131 ± 0.129	0.31237	-0.002 ± 0.099	0.98009	-0.128 ± 0.085	0.13499
Abundance of Cyclopoida	-0.732 ± 0.301	0.01609	-0.212 ± 0.232	0.36111	-0.519 ± 0.199	0.00996
Abundance of Calanoida	0.158 ± 0.148	0.29028	-0.034 ± 0.114	0.76405	0.192 ± 0.098	0.05248
Abundance of Cladocera	0.334 ± 0.133	0.01314	0.129 ± 0.102	0.21212	0.205 ± 0.088	0.02106
Abundance of Ostracoda	0.344 ± 0.121	0.00528	-0.019 ± 0.094	0.83435	0.364 ± 0.080	0.00001
Total abundance	0.257 ± 0.310	0.40795	0.134 ± 0.239	0.57496	0.123 ± 0.205	0.55031
Abundance of 'large animals'	0.632 ± 0.249	0.01242	0.134 ± 0.192	0.48716	0.497 ± 0.165	0.00305
Abundance of 'small animals'	-0.315 ± 0.310	0.31174	-0.181 ± 0.239	0.45147	-0.134 ± 0.205	0.51447
Number of taxa per sample	0.381 ± 0.157	0.01666	0.113 ± 0.121	0.35282	0.268 ± 0.104	0.01108

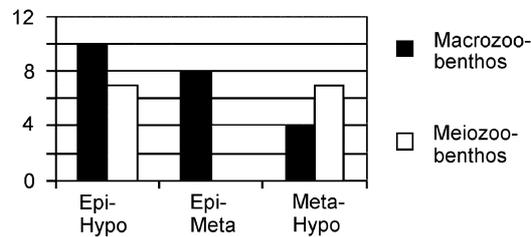


Fig. 3. The number of significant differences between different layers (Type III ANOVA; $P < 0.05$) among 21 variables of macrozoobenthos and among 12 variables of meiozoobenthos. Epi, epilimnion; meta, metalimnion; hypo, hypolimnion.

Table 6. P -values (0.05 level) from the Type I ANOVA of selected variables, using factors in the following order: lake, year, sampling depth, and Layer. When depth is significant but layer is not, the distribution of taxa is considered not connected to layers

Variable	Sampling depth	Zone	Comments
Macrozoobenthos			
Biomass of Chironomidae	0.1976	0.0013	Tied to zone
Biomass of Oligochaeta	0.0291	0.0164	Tied to zone?
Biomass of Ceratopogonidae	0.8013	0.4528	
Biomass of <i>Chaoborus</i>	<0.0001	0.3524	
Biomass of <i>Asellus</i>	0.1256	0.6473	
Biomass of Hirudinea	0.2010	0.6572	
Biomass of Hydrachnidia	0.0038	0.1078	Not tied to zone
Total biomass	0.0314	0.0967	Not tied to zone
Total biomass without <i>Chaoborus</i>	0.0003	0.0091	Tied to zone
Number of taxa per sample	0.0076	0.1412	Not tied to zone
Abundance of Chironomidae	0.0199	0.0003	Tied to zone
Abundance of Oligochaeta	0.1050	0.0070	Tied to zone
Abundance of Ceratopogonidae	0.4929	0.5450	
Abundance of <i>Chaoborus</i>	<0.0001	0.4034	Not tied to zone
Abundance of Sphaeriidae	0.0007	0.0145	Tied to zone?
Abundance of Trichoptera	0.7420	0.3157	
Abundance of <i>Sialis</i>	0.1193	0.5474	
Abundance of <i>Asellus</i>	0.0415	0.2389	
Abundance of Hirudinea	0.2651	0.8244	
Total abundance	0.0582	0.0058	Tied to zone
Total abundance without <i>Chaoborus</i>	0.0013	0.0004	Tied to zone
Meiozoobenthos			
Abundance of Chironomidae	0.0020	0.2945	Not tied to zone
Abundance of Oligochaeta	0.0482	0.3435	
Abundance of Sphaeriidae	0.1356	0.5346	
Abundance of Nematoda	0.0140	0.6498	Not tied to zone
Abundance of Cyclopoida	0.0181	0.0769	
Abundance of Calanoida	0.2520	0.3649	
Abundance of Cladocera	0.3301	0.2249	
Abundance of Ostracoda	0.2295	0.0928	
Total abundance	0.8047	0.7986	
Abundance of 'large animals'	0.0083	0.2368	Not tied to zone
Abundance of 'small animals'	0.1134	0.4501	
Number of taxa per sample	0.2802	0.5922	

Table 7. Discriminant analysis: misclassification (%) for different zones. Biomass of macrozoobenthos is presented by 7 variables, abundance by 10 variables, and meiobenthos by 9 variables

Zone	Macrobenthos: biomasses	Macrobenthos: abundances and number of taxa	Meiobenthos: abundances and number of taxa
Epilimnion	41.0	28.0	60.0
Metalimnion	48.5	46.4	70.0
Hypolimnion	37.0	35.0	40.0
Mean	42.2	36.5	56.7

This index has the highest statistical significance for testing the depth effect. Table 8 presents the coefficients of DI, and Fig. 4 the ordination of samples according to combination of DI and depth. The smooth line was fitted to data using a cubic spline routine of SAS/Graph package type SM65P. A sharp decline of the DI, registered between 3 and 4 m, corresponded to the upper part of the metalimnion estimated by temperature. According to the DI, the lower metalimnion (4–4.7 m) and the upper hypolimnion (deeper than 4.7 m) were similar down to the 5.7–5.8 m depth, where the curve started to fall again (Fig. 4), probably indicating worsening conditions.

Table 8. Coefficients of the Depth Index

Variable	Coefficient	Variable	Coefficient
Macrozoobenthos		Abundance of <i>Asellus</i>	-0.093
Biomass of Chironomidae	-0.015	Abundance of Hirudinea	-0.170
Biomass of Oligochaeta	-0.016	Total abundance	-0.241
Biomass of Ceratopogonidae	-0.038	Total abundance without <i>Chaoborus</i>	0.163
Biomass of <i>Chaoborus</i>	-0.022	Meiozoobenthos	
Biomass of <i>Asellus</i>	0.230	Abundance of Chironomidae	-0.026
Biomass of Hirudinea	-0.017	Abundance of Oligochaeta	-0.016
Biomass of Hydrachnidia	0.038	Abundance of Sphaeriidae	0.081
Total biomass without <i>Chaoborus</i>	-0.060	Abundance of Nematoda	-0.112
Total biomass	0.090	Abundance of Cyclopoida	-0.123
Number of taxa per sample	0.115	Abundance of Calanoida	-0.008
Abundance of Chironomidae	0.008	Abundance of Cladocera	0.056
Abundance of Oligochaeta	0.001	Abundance of Ostracoda	0.012
Abundance of Ceratopogonidae	0.023	Total abundance	0.045
Abundance of <i>Chaoborus</i>	0.006	Abundance of ‘large animals’	0.049
Abundance of Sphaeriidae	0.051	Abundance of ‘small animals’	0.066
Abundance of Trichoptera	-0.146	Number of taxa per sample	-0.017
Abundance of <i>Sialis</i>	0.064		

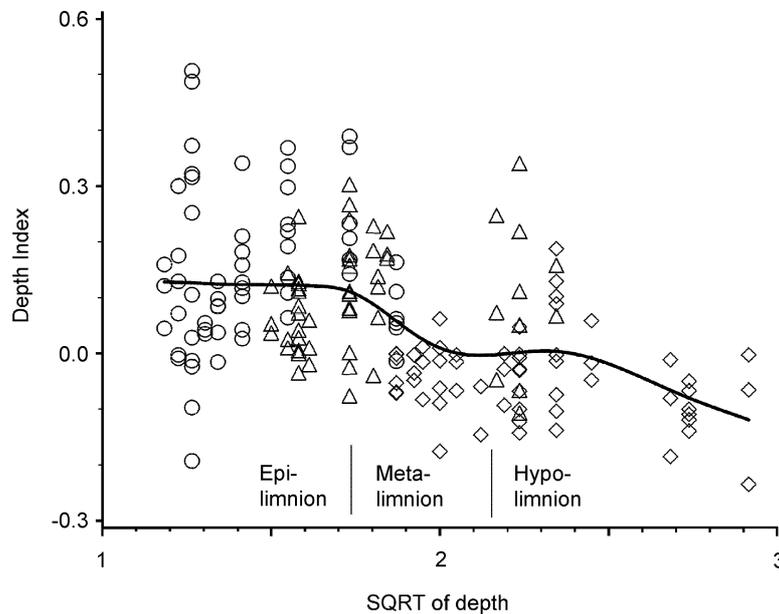


Fig. 4. Plot of the Depth Index against the square root of sampling depth. Rings indicate samples of the epilimnion, triangles those of the metalimnion, and diamonds those of the hypolimnion.

DISCUSSION

The study of the relation of macro- and meiozoobenthos to thermal stratification in 10 small lakes of South-East Estonia in summers of 1998 and 1999 revealed dependence of the majority of the variables on lake but not on year. The main similarity of the lakes studied was the presence of sharp stratification and a thick metalimnion. Major differences were in the lake area, lake type, maximum depth, and depth of the metalimnion. Therefore, like sampling depth, the location of the metalimnion in the water column had a different meaning for zoobenthos in different lakes. Although the position and extent of the metalimnion differed between the two study years due to the much warmer summer in 1999 than in 1998, the differences in the zonal distribution of zoobenthos between the two years were negligible or masked by other factors.

Correlation analysis demonstrated good accordance between general zoobenthic variables except *Chaoborus* and 'small' meiozoobenthos (mostly cyclopoids). These groups were not related to zones but to sampling depth (see also Timm & Möls, 2005). All meiobenthic variables showed much weaker relations to zones than macrozoobenthos, caused probably by the higher mobility of the former. Thus, like *Chaoborus*, the taxa forming the bulk of 'small meiozoobenthos' (two species of *Mesocyclops*) can and actively do migrate in the water column.

Zonal or depth distribution was clear in *Chaoborus* (both biomass and abundance), abundance of *Sialis* and Ostracoda, and total biomass without *Chaoborus*. The influence of oxygen saturation percentage in water on the variables studied was surprisingly low. The results show that for most zoobenthic variables in these lakes the metalimnion was an intermediate area rather than a sharp limit between oxygen-rich and oxygen-poor areas. The reason may be the annual variability of the metalimnion.

Not many authors have dealt with relationships between zoobenthos and lake stratification. Particularly scarce are references to meiozoobenthos. Heinis et al. (1989) described the behaviour of chironomid larvae (*Tanytarsus* sp.) adapted to the thermocline. In summer they leave the oxycline and migrate to the lower epilimnion. High hemoglobin concentration and weight both seem to contribute to an ability to cope with low oxygen concentrations, and determine the vertical distribution of chironomids in the sediment (Int Panis et al., 1996). *Procladius* larvae may not tolerate sharp summer stratification and move upwards (Berg et al., 1962; Bazzanti & Seminara, 1985). However, this behaviour may also be related to active emergence in summer. In winter, zoobenthic taxa intolerant to anoxia concentrate into littoral (Giziński, 1978). Further studies are needed to show such possible effects in Estonian lakes.

In pairwise comparison of the benthic zones corresponding to the water layers, significant differences between the epilimnion and hypolimnion were the most outstanding: 10 of 21 variables in macro- and 7 of 12 variables in meiobenthos, respectively. Between the epi- and metalimnion, eight variables of macrozoobenthos differed significantly, while no significant difference was confirmed for any meiobenthos variables. In the case of the meta- and hypolimnion, only four significant differences of macrozoobenthic parameters were detected, while seven differences occurred in meiozoobenthos. Thus, the difference in the effect of water layers on macrozoobenthos was greater between the epi- and metalimnion than between the meta- and hypolimnion. For meiozoobenthos, the epi- and metalimnion did not show great differences, while the meta- and hypolimnion differed significantly. This may be again explained by the 'planktonic' character of meiobenthos in these lakes. Perhaps cyclopoids, which form the majority of the meiobenthos, utterly avoid the littoral zone. Above the profundal, they can perform some diurnal migration to avoid fish predation, spending daytime near the bottom.

When the effect of sampling depth was removed, only a few macrozoobenthic variables (biomass of Chironomidae and Oligochaeta; abundance of Chironomidae, Oligochaeta, and Sphaeriidae; total biomass without *Chaoborus*; total abundance without *Chaoborus*; total abundance) were found to respond to layers. No such significant relationships were observed for any meiozoobenthic variables. In some West Canadian lakes, hypolimnetic dissolved oxygen was found to explain 37% of the variance in profundal macrozoobenthos, whereas water temperature explained 23% of variance (Dinsmore et al., 1999). In our case, predicting layers with discriminant analysis using zoobenthic variables gave a relatively high level of mismatching, exceeding 50% in some cases. Macrozoobenthic abundances gave the most consistent and meiozoobenthic abundances the least consistent results.

The Depth Index (DI) based on all 33 zoobenthic variables studied showed an abnormal decline between 3 and 4 m in an approximately linear curve against square rooted sampling depth. This depth interval corresponded to the upper part of the metalimnion estimated by water temperature. Thus the zoobenthos variables taken together revealed the most apparent changes in environmental conditions in the upper part of the metalimnion.

In conclusion, several macroinvertebrate metrics in small stratified lakes were significantly influenced by water layers but even more considerably by water depth. The difference between the epilimnion and the deeper areas was more important than the difference between the meta- and hypolimnion. As compared with macrozoobenthos, the differences in meiozoobenthos were less distinct. The depth of 3–4 m was considered an area where the characteristics of zoobenthos (macro- and meiozoobenthos) taken together changed most quickly.

The EU Water Framework Directive (Council of the European Communities, 2000) considers macroinvertebrates a required biological element indicating water quality of lakes. In European intercalibration of sampling, identification, and quality estimation, Estonia belongs to the Central Baltic group where main efforts are directed to the eulittoral zone (depth <1 m, vegetation included). Some other regions (such as Alpine or Nordic) have used macroinvertebrates effectively in bioindication of offshore areas. Historically, the offshore zoobenthos was used to indicate the quality of two Estonian large eutrophic lakes (Peipsi and Võrtsjärv) (Timm et al., 1996; Kangur et al., 2004), as well as in small lakes (Timm et al., 1982). We consider that the indicatory potential of macrozoobenthos in offshore areas of lakes in Estonia is not yet sufficiently used. The knowledge how zoobenthos is influenced by natural stratification is necessary in order not to confuse it with human influence.

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Makro- ja meiozoobentos mõnedes Eesti väikestes kihistunud järvedes

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1998. ja 1999. aasta suvel uuriti kümne väikese kihistunud järve taimedeta mudaste osade makro- ning meiozoobentost (kokku 300 prooviruutu Borutski 225 cm² põhjaammutiga ja 180 proovi 6,38 cm² toruammutiga). Proovikohad paigutati igas järves hüppekihist ehk metalimnionist kõrgemale (epilimnioni), selle keskele ja sellest sügavamale (hüpolimnioni). Nii makro- kui meiobentoses olid tavalisteks loomadeks surusääsklased ja väheharjasussid. Meiobentoses oli nende arvukus tillukeste isendite kaasamise tõttu suurusjärgu võrra kõrgem. Meiobentose arvukuses domineerisid planktonivähid, eriti aerjalgsed. Biomassist suurema osa moodustasid aga makrobentose loomad. “Päris” meiobentose loomi (näiteks ümarussid või karpvähilised) oli vähe.

Pärast log(x + 1) teisendusi uuriti 33 tunnuse (erinevad arvukused, biomassist ja taksonite arvud) seoseid veekihi (epi-, meta- ning hüpolimnion), proovi sügavuse, järve, aasta ja hapniku küllastusprotsendiga, kasutades variatsioonanalüüsi, mitmemõõtmelist variatsioonanalüüsi ning diskriminantanalüüsi.

Enamiku tunnuste väärtused ei sõltunud aastast, vaid järvest. Makrozoobentose arvukus, biomass ja taksonite arv vähenesid oluliselt suunas epilimnion-hüpolimnion, välja arvatud järve-klaasiksääse vastsetel, kelle arvukus oli sügavamal suurem.

Variatsioonanalüüs näitas, et klaasiksääskede biomass ja arvukus, vesilestade biomass, surusääsklaste ning muude makrobentiliste loomade arvukus meio-bentoses ja keskmine taksonite arv makrozoobentose proovis ei järginud veekihte, vaid sõltus sügavusest. Kihtidega olid kõige rohkem seotud makrozoobentose surusääsklaste biomass ja kogu makrozoobentose biomass ning arvukus. Enamiku üksikute taksonite puhul sõltuvust sügavusest ei avastatud.

Diskriminantanalüüs näitas, et põhjaloomade järgi erinesid kolm veekihti üsna nõrgalt. 33 tunnuse põhjal moodustatud indeks proovi sügavuse mõju uurimiseks näitas, et põhjaloomade jaoks toimub kõige olulisem muutus keskkonnatingimustes hüppekihi ülemises osas.