

A quantitative ecological investigation of the littoral zoobenthos of an oligotrophic Finnish lake

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Bathymetric, monthly and intralacustrine variations in species composition of the macrozoobenthos and meiozoobenthos were investigated on soft and stony bottoms of lake Konnevesi. Regional differences were significant for many variables, although the lake was expected to be quite homogeneous. On soft bottom macrobenthos the numbers and biomasses were generally greater in spring than in late summer and the bathymetric maxima generally occurred at a depth of between 2 and 4 m. On stony bottoms, the variations were not as clear as on soft bottoms and the proportion of predator taxa was about half, as opposed to about one third on soft bottoms. The seasonal distribution in numbers of meiobenthos was opposite to that of macrobenthos, showing a maximum in late summer and not in spring. Soft bottom abundances were 3.3 times higher than stony bottom abundances for macrobenthos and 8 times higher for meiobenthos. Oligochaeta, Megaloptera and Chironomidae were more abundant on soft than on stony bottoms. Hirudinea, Trichoptera and Coleoptera were more abundant on stony than on soft bottoms. Insects formed about 3/4 of the abundances and 2/3 of the biomasses. It seems that, with regard to macrobenthos biomasses, if the investigating resources are limited, the sampling times ought to be reduced to one, rather than reducing the number of sampling depths or subareas.

The amounts of the merolimnic part of the zoobenthos were greater than the amounts of hololimnic zoobenthos on both kinds of bottom, and on stony bottoms the number of merolimnic fauna species was also greater than that of hololimnic fauna. On stony bottoms the number of species of merolimnic fauna increased with depth. The diversity and number of species were higher in spring than in late summer, which is not in agreement with the assumed food diversity. The bathymetric maximum of diversity occurred at depths of between 2 and 4 m and not in deeper zones, where the stability of environment ought to increase diversity. The quantitative proportion of predators on soft bottoms was lowest at the same depths at which the diversity was highest, which is in contrast with the predation hypothesis. However, examination of the numbers of species gave different results. On stony bottoms, the proportion of predators in the biomass was exceptionally high, which may indicate that the predators favour stones for habitation but gather food from the surrounding soft areas. A correlation analysis of the zoobenthos abundances coincided with certain niche overlap findings and certain correlation associations coincided with the results of factor analysis.

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1. Introduction

According to a very rough estimation, the total area of Finnish lakes covered by higher aquatic vegetation, and which can thus be understood as a littoral zone, may be about 7500 square km (Vaarama 1961). This is about a quarter of the total area of Finnish lakes or more than 2 % of the total area of Finland, showing the notable significance of the littoral zone, which probably usually has considerably higher production values per unit area than the pelagic zone (e.g. Pieczynska 1976). However, limnological approaches to entire water ecosystems frequently omit the existence of the littoral.

Knowledge of the littoral has also become more important because of the increasing human influence on the aquatic ecosystems. Moreover, the effect of pollution or even more the effect of the regulation of water level cannot be understood or even predicted without knowledge of the natural state of the littoral zone. The present study is an attempt to elucidate the composition of the littoral zoobenthos community of the oligotrophic, oligohumic, unregulated and nearly unpolluted lake Konnevesi, which has been the object of several other investigations, too (Särkkä 1972, Toivonen et al. 1982). The aim was also to find out the possible regional differences in the lake, which seems to be regionally quite homo-

Table 2. Numbers of individuals/m² of the taxa with a frequency $\geq 5/102$ in the soft bottom macrobenthos samples (Ekman and Dendy samplers, sieve 400 μm) as means for different subareas, months and depths. The significances of the regional, monthly and bathymetric differences according to 3-way ANOVA as follows: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

	Total	Subareas			Months			Depths, m									
	freq.	mean	North	West	East	p	Aug.	May	p	0.5	1	2	3	4	5	6	p
Nematoda	31	22.0	26.1	13.4	26.5	*	14.2	29.7	***	26.0	33.7	28.0	40.0	17.3	10.7	8.7	**
<i>Stylodrilus heringianus</i>	17	9.8	11.5	8.1	9.7	—	15.7	3.8	***	18.8	45.0	16.0	2.0	4.7	10.0	1.3	***
<i>Stylaria lacustris</i>	8	2.9	0.7	8.1	0	***	5.9	0	***	0	0	8.0	2.0	0	6.7	0	—
<i>Uncinails uncinata</i>	10	2.0	0.7	4.2	1.1	—	3.5	0.5	*	0	0	2.0	4.0	0.7	4.7	0	—
<i>Tubifex tubifex</i>	10	4.0	0.4	11.6	0	***	4.7	3.3	—	0	0	16.0	2.0	2.7	2.0	0	*
<i>Limnodrilus hoffmeisteri</i>	71	80.9	101	36.4	106	***	94.1	67.6	—	30.0	48.8	50.0	14.0	88.7	116	37.7	***
<i>Psammoryctides barbatus</i>	26	34.1	77.9	10.6	13.8	***	19.1	49.1	***	0	7.5	120	50.0	12.7	0	8.0	***
<i>P. albicola</i>	5	1.8	4.5	0	1.1	*	3.0	0.7	—	3.7	3.7	8.0	0	0	0	0	*
<i>Pelosclex ferox</i>	76	76.0	107	87.5	33.3	***	103	49.5	***	26.2	22.3	128	84.0	68.7	90.0	44.0	***
<i>Aulodrilus limnobius</i>	12	3.3	3.5	4.6	1.4	—	6.1	0.2	***	0	3.7	10.0	2.0	1.3	3.3	0	*
Enchytraeidae	6	2.9	1.3	0.4	7.0	***	1.1	4.6	***	18.8	22.3	2.0	0	0	0	0.7	***
<i>Helobdella stagnalis</i>	7	3.9	11.1	0	0.6	***	3.3	4.6	—	3.7	14.8	16.0	0	0	0	0	***
<i>Candona candida</i>	8	2.2	2.5	1.1	3.2	—	2.4	2.1	—	0	0	2.0	6.0	2.7	1.3	0.7	—
<i>Cyclops</i> spp.	6	2.2	0.7	2.8	3.2	—	0.2	4.2	**	0	0	0	2.0	4.0	1.3	5.3	—
<i>Acanthocyclops vernalis</i>	5	0.9	0.4	1.4	1.1	—	0.2	1.6	—	0	0	2.0	0	1.3	1.3	0.7	—
<i>Eurycerus lamellatus</i>	6	1.5	0	4.2	0.4	*	2.4	0.7	—	0	0	2.0	4.0	2.0	0.7	0	—
<i>Asellus aquaticus</i>	10	5.4	7.9	5.6	2.6	—	4.7	6.0	—	18.7	18.7	18.0	0	0	0	0	***
<i>Pallasea quadrispinosa</i>	12	1.8	1.1	3.2	1.1	—	1.4	2.1	—	0	0	0	2.0	0.7	2.0	5.3	—
<i>Ephemera vulgata</i>	61	31.8	30.7	25.8	38.8	—	26.1	37.4	—	0	0	36.0	76.0	34.7	24.7	8.7	***
<i>Caenis horaria</i>	15	4.8	3.5	3.1	7.6	—	1.6	7.9	**	3.7	7.3	12.0	4.0	4.7	2.0	0.7	—
Corixidae	10	2.5	4.2	0	3.2	—	0.2	4.7	*	0	0	2.0	6.0	2.0	2.0	2.0	—
<i>Sialis lutaria</i>	25	6.2	2.1	13.0	3.5	***	4.9	7.5	—	0	11.2	18.0	4.0	2.0	3.3	4.0	***
<i>S. sordida</i>	5	1.4	0.6	3.0	0.6	*	2.9	0	***	7.3	11.2	2.0	0	0	0	0	***
<i>Cyrmus flavidus</i>	7	2.3	4.5	1.8	0.6	—	2.7	1.9	—	3.7	7.5	2.0	6.0	0	0	1.3	—
<i>C. trimaculatus</i>	6	1.2	0.4	0.7	2.5	—	0	2.4	*	0	0	2.0	2.0	1.3	1.3	0	—
<i>Oecetis lacustris</i>	5	1.4	1.4	0.4	2.3	—	2.0	0.7	—	11.2	0	2.0	0	0.7	0.7	0.7	***
<i>Oxyethira flavicornis</i>	5	0.8	0	1.4	1.1	—	0	1.6	—	0	0	0	2.0	2.0	0.7	0	—
<i>Procladius</i> spp.	101	265	320	229	247	*	250	280	—	199	105	260	354	295	307	185	***
Tanypodinae, others	47	23.5	33.0	13.2	24.2	—	8.0	38.9	***	22.3	18.5	38.0	42.0	16.0	14.7	8.7	—
<i>Protonypus morio</i>	5	0.8	0	2.5	0	*	0.5	1.2	—	0	0	0	2.0	0	1.3	1.3	—
<i>Monodiamesa bathyphila</i>	20	9.3	18.0	9.9	0	***	12.0	6.6	—	0	0	0	10.0	3.3	16.7	22.7	***
<i>Heterotanytarsus apicalis</i>	62	126	223	69.0	85.4	***	9.4	242	***	7.5	18.5	138	220	203	78.7	64.0	*
<i>Heterotrissocladius marcidus</i>	21	10.1	6.4	19.4	4.6	***	17.6	2.6	***	0	0	2.0	18.0	14.7	22.0	0.7	***
<i>Parakiefferiella bathophila</i>	13	11.5	25.6	3.5	5.3	*	0	23.0	***	0	11.2	26.0	24.0	6.7	4.7	0	—
<i>P. smolandica</i>	34	36.6	56.8	24.9	28.2	—	3.5	69.7	***	3.7	18.7	46.0	60.0	62.7	30.7	0.7	—
<i>Psectrocladius medius</i> type	31	19.6	2.5	28.8	27.4	***	20.1	19.1	—	29.8	11.0	34.0	24.0	14.0	24.0	1.3	*
<i>P. psilopterus</i> type	37	17.6	11.2	35.4	6.2	***	10.8	24.4	***	3.7	33.7	30.0	28.0	16.7	12.0	0.7	***
<i>P. septentrionalis</i> type	6	1.3	0	2.8	1.1	—	0.7	1.8	—	0	3.7	2.0	0	2.7	1.3	0	—
<i>Zalutschia zalutschicola</i>	21	5.6	1.4	13.4	2.1	***	1.9	9.4	*	0	0	0	8.0	6.7	7.3	10.0	—
<i>Cladopelma viridula</i>	32	16.6	11.6	16.9	21.3	—	0.5	32.7	***	7.5	26.2	34.0	26.0	15.3	4.0	3.3	—
<i>Cryptochironomus defectus</i> type	7	2.5	5.6	0.4	1.4	—	0.5	4.5	*	0	0	10.0	2.0	0	0.7	1.3	*
<i>Demicryptochironomus vulneratus</i>	22	8.7	4.1	2.8	19.2	***	1.8	15.6	***	0	22.3	14.0	16.0	6.0	3.3	2.7	***
<i>Endochironomus intextus</i>	23	121	362	1.1	0	***	176	65.6	*	796	188	312	40.0	2.0	1.3	2.0	***
<i>Limnochironomus pulsus</i>	40	15.2	23.6	5.3	16.7	*	3.0	27.4	***	15.0	3.7	24.0	18.0	25.3	8.7	4.0	—
<i>Microtendipes chloris</i> type	19	6.0	6.6	8.4	3.0	—	8.1	3.9	—	14.8	7.3	14.0	4.0	2.7	4.0	2.0	—
<i>Pagastella orophila</i>	64	51.8	78.3	38.1	39.1	***	19.5	84.2	***	56.2	101	50.0	86.0	45.3	35.3	24.7	**
<i>Paracladopelma camptolabis</i>	19	10.0	16.5	11.3	2.1	—	3.5	16.4	—	0	3.7	2.0	42.0	4.7	2.0	4.7	**
<i>Polypedilum pullum</i>	46	75.1	138	25.7	61.1	***	3.0	147	***	7.3	14.8	38.0	104	34.0	54.0	188	***
<i>Pseudochironomus prasinatus</i>	60	52.5	44.3	84.7	28.6	—	42.2	62.8	—	45.0	26.2	38.0	132	64.0	35.3	4.7	—
<i>Tanytarsus</i> s. lat., indetermined	94	387	444	346	371	—	146	628	***	233	452	402	514	347	373	327	—
<i>Constempellina brevicosta</i>	15	4.5	4.2	2.8	6.4	—	0.2	8.7	***	0	3.7	10.0	8.0	3.3	1.3	1.3	—
<i>Stempellina bausei</i>	5	0.6	0	1.4	0.4	*	0	1.2	***	0	0	0	0	2.0	0	1.3	*
<i>Bezzia-Palpomia</i> type	32	17.1	17.4	9.9	25.9	*	2.7	32.6	***	33.7	18.5	40.0	24.0	10.7	4.0	4.0	***
<i>Culicoides</i> type	22	7.6	6.3	6.0	10.5	—	0.9	14.3	***	7.3	0	8.0	8.0	8.7	11.3	4.7	—
Tabanidae	10	3.2	5.6	1.8	2.4	—	1.1	5.4	—	7.5	3.7	4.0	8.0	1.3	0.7	0.7	—
Acari, total number	50	39.0	39.9	18.6	58.5	*	10.8	67.2	***	7.3	3.7	66.0	68.0	25.3	28.0	30.0	*
<i>Sphaerium corneum</i>	7	1.1	2.5	0.7	0	—	0.2	1.9	—	0	0	2.0	0	0	2.0	2.0	—
<i>Pisidium</i> spp. (total of <i>Pisidium</i>)	85	96.0	142	81.6	64.6	***	105	87.0	—	196	52.3	124	110	70.7	90.0	66.7	—
<i>P. amnicum</i>	6	2.2	5.6	0	1.1	—	0.9	3.5	—	0	0	8.0	0	2.0	0.7	2.0	—
<i>P. casertanum</i>	40	23.0	52.4	6.4	10.2	***	18.5	27.5	—	11.2	3.7	48.0	18.0	14.0	20.7	24.7	—
<i>P. henslowanum</i>	19	4.7	6.4	1.8	6.0	—	1.9	7.5	—	0	0	0	16.0	2.0	4.7	4.0	—
<i>P. hibernicum</i>	8	2.4	3.9	2.1	1.1	—	1.6	3.1	—	0	0	2.0	2.0	2.0	2.7	4.7	—
<i>P. liljeborgi</i>	40	15.7	29.5	7.4	10.1	***	11.9	19.4	—	7.5	14.8	10.0	14.0	12.0	24.0	21.3	—
<i>P. subtruncatum</i>	20	4.7	11.5	2.5	0	***	4.9	4.4	—	0	11.2	2.0	0	4.7	8.7	7.3	*
<i>Valvata macrostoma</i>	28	8.1	4.6	6.7	13.1	—	9.4	6.8	—	0	0	12.0	16.0	6.7	8.0	3.3	—
Total number	102	1821	2513	1431	1517	***	1227	2414	***	1921	1469	2348	2600	1618	1501	1119	***
n	102	102	34	34	34		51	51		6	6	18	18	18	18	18	

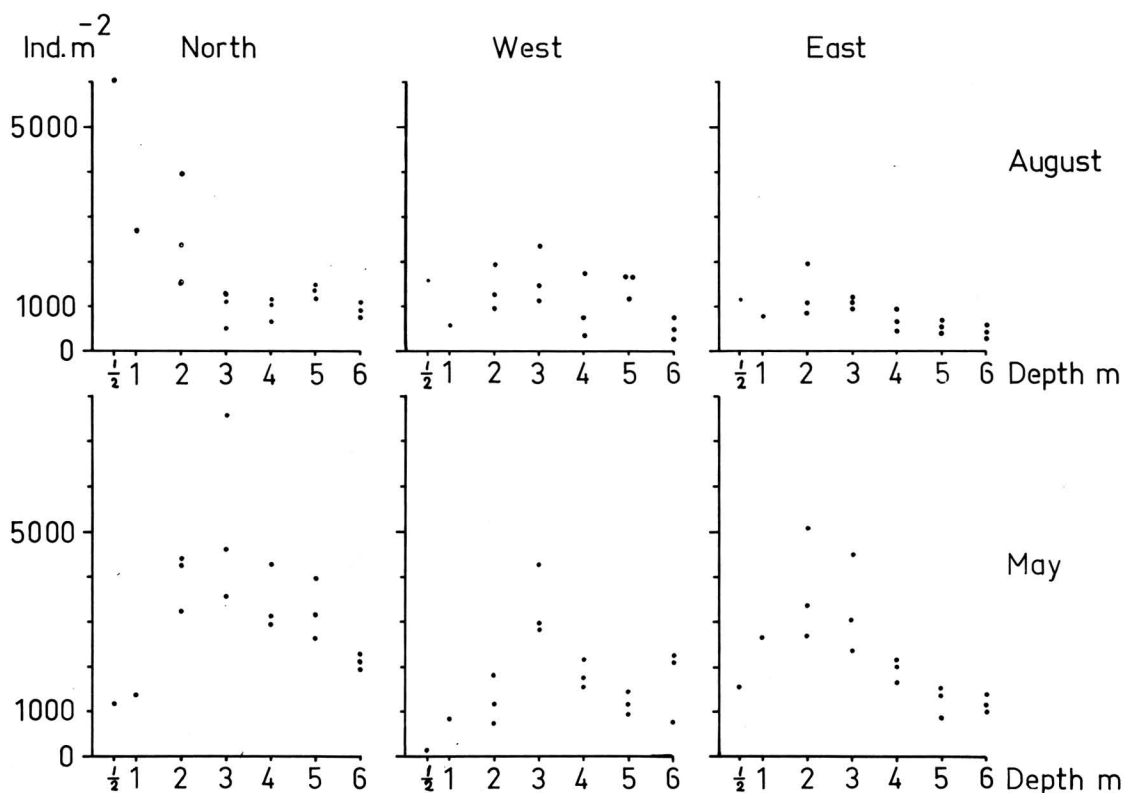


Fig. 2. Bathymetric distributions of the total abundances of the macrozoobenthos on the soft bottoms at the three subareas and on the two sampling occasions.

in 70 % ethanol. The picking of animals was made under a preparation microscope. The duration of preservation in formaldehyde was about 1 year, after which the duration of preservation in ethanol was from 1 to 3 years. The fresh weight biomasses were weighed from animals from which the excess ethanol was removed with a quick standard method and using a Mettler H 10 balance, and the biomasses were partially calculated using geometrical formulae, assuming the density to be 1.0. In order to preserve the material only fresh weights were determined, and dry weights were calculated from fresh weights using a general coefficient of 0.17. This was assumed to be representative of the most abundant taxa of the present study. Kajak & Dusoge (1975) and Kajak with other collaborators, Lundkvist (1978) and Morgan (1980) used 0.15 as the corresponding coefficient, whereas Howmiller (1972) and Wiederholm & Eriksson (1977) obtained somewhat lower values but Lappalainen & Kangas (1975) and Mölsä (1980) found values clearly higher than 0.15.

3. Macroenthos in soft bottoms

3.1. Abundances

Appendix 1 presents the frequencies of all taxa and Table 2 the regional, monthly and vertical

averages for taxa represented by ≥ 5 observations in soft bottoms (maximum frequency = 102). Table 2 also presents the significances of regional, monthly and vertical differences according to a 3-way analysis of variance.

Appendix 1 and Table 2 show that there were many more taxa with a significant May maximum than with a significant August maximum. Furthermore, there were several taxa whose only significant variation was the monthly variation and all such taxa had their maximum in May. However, within the oligochaetes there were more species with a maximum in August than in May. Most of the taxa with significant regional variation had their maximum in the northern sampling area. Most of the taxa with significant vertical variation had their maximum between depths of 2 and 3 m.

The regional variations were strongest in the abundances of Mollusca and large insect larvae (*Ephemera*, *Sialis*) and weakest in small Crustacea, and weaker in small insects than large. The monthly (= May/August) variations were strong-

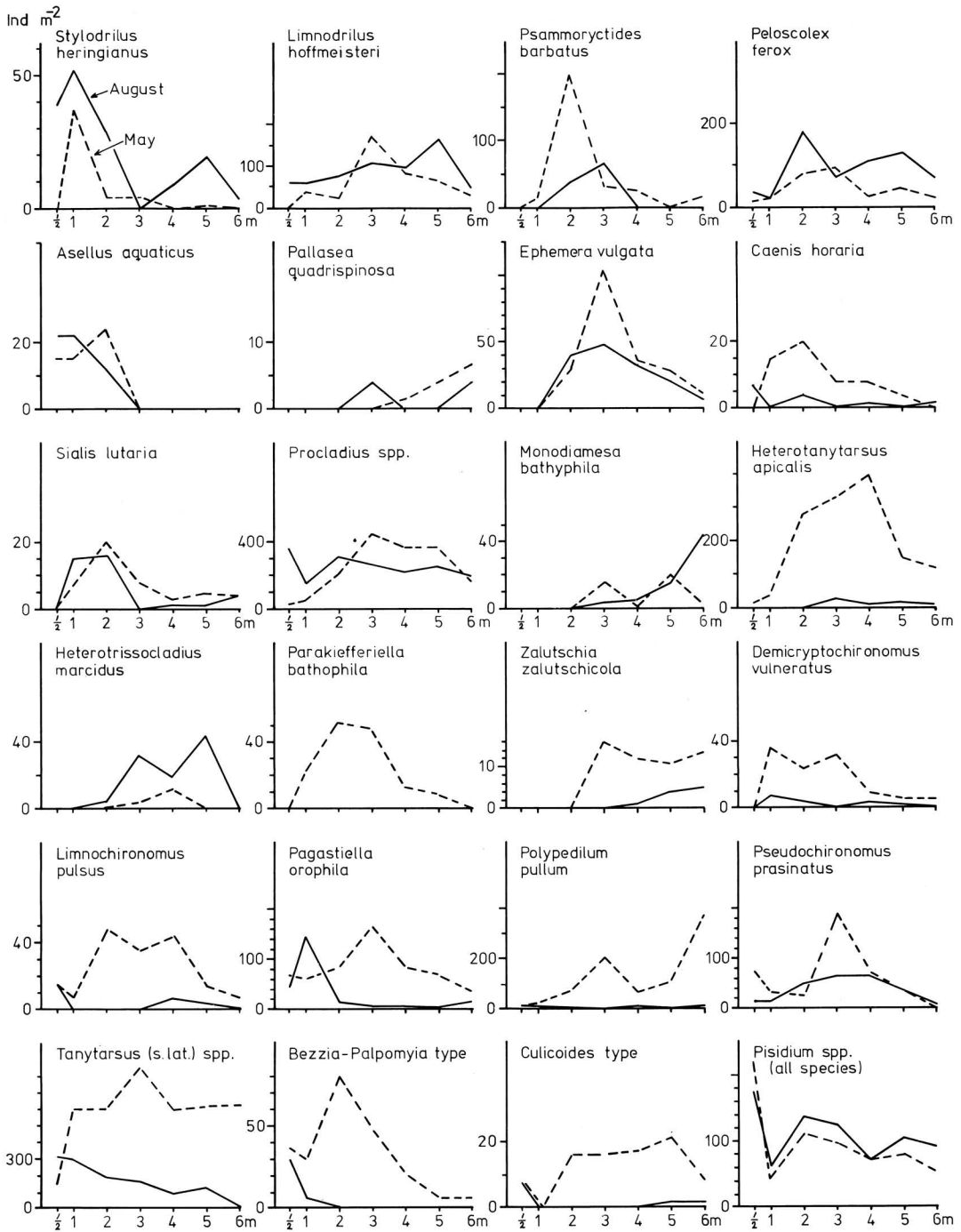


Fig. 3. Bathymetric distributions of the dominant macrobenthic taxa on the soft bottoms in August (solid curve) and in May (broken curve). The subareas and replicates pooled.

Table 3. Fresh-weight biomasses of the soft bottom macrobenthos (Ekman and Dendy samplers, sieve 400 μm) in mg/m^2 as means for different subareas, months and depths. The significances as in Table 2.

	Total		Subareas				Months			Depths, m								<i>p</i>
	Mean	<i>SD</i>	North	West	East	<i>p</i>	Aug.	May	<i>p</i>	0.5	1	2	3	4	5	6		
Herbivores and detritus feeding groups (mainly):																		
Oligochaeta	501	1000	1021	210	271	***	568	434	—	201	421	1389	515	305	288	134	**	
<i>Pisidium</i> spp.	120	130	167	103	89	*	149	90	—	199	76	136	137	102	139	74	—	
<i>Ephemera vulgata</i>	531	942	344	449	801	—	627	435	—	0	0	874	1293	421	364	59	***	
Trichoptera (herbivora)	26	172	62	11	4	—	12	40	—	37	1	9	113	5	5	2	—	
<i>Heterotanytarsus apicalis</i>	48	103	96	22	24	**	1	94	***	2	13	40	109	70	27	19	—	
Chironomini+Orthoclaadiinae	437	789	910	207	195	***	260	615	*	611	419	906	492	259	202	276	—	
Tanytarsini	118	153	162	68	123	*	44	192	***	76	165	166	121	108	110	85	—	
Herbivora, total	1858	1807	2932	1119	1524	***	1711	2006	—	1178	1108	3686	2719	1220	1327	817	***	
Predators (mainly):																		
Nematoda	3	12	6	1	2	—	3	3	—	5	14	6	2	1	1	1	—	
Hirudinea	120	711	346	0	14	—	54	185	—	1144	371	173	0	0	0	0	*	
<i>Sialis</i> spp.	120	288	77	212	69	—	159	80	—	140	359	327	22	5	55	103	**	
Polycentropidae	11	38	14	13	5	—	6	16	—	1	20	5	33	2	3	11	—	
Tanypodinae	331	236	442	228	323	***	368	295	—	309	124	392	329	348	378	285	—	
Ceratopogonidae	10	19	14	4	13	*	2	19	***	25	9	13	10	8	5	10	—	
Tabanidae	20	85	16	8	35	—	18	21	—	23	59	34	23	14	0	13	—	
Acari	49	96	50	21	78	*	17	82	***	16	3	66	101	40	29	38	—	
Predators, total	672	800	986	488	542	*	639	705	—	1663	989	1047	516	428	471	461	**	
Total fresh-weight biomass	2555	2056	3992	1607	2066	***	2350	2760	—	2773	2097	4734	3234	1649	1798	1441	***	
Total dry weight biomass	434	350	679	273	351	***	400	469	—	471	356	805	550	280	306	245	***	
Ratio predators/total %	31.4	22.1	24.9	32.5	36.8	—	33.7	29.1	—	49.2	43.5	29.6	17.4	28.3	30.4	41.1	**	
n	102		34	34	34		51	51		6	6	18	18	18	18	18		

est in large insects and in Oligochaeta, and weakest in Crustacea, especially in large species (*Asellus*, *Pallasea*). The vertical variations seemed to be strongest in the numbers of large insect larvae, large Crustacea and Oligochaeta, and weakest in small Crustacea. The vertical variations in abundances of Insecta and Mollusca were weaker than in those of Oligochaeta. About half of the species were, however, so rare that they were not included in the quantitative analysis. Comparatively strong regional, monthly and vertical variations could thus be seen, but they were not the same in different taxa. The present data show that the question raised by applied hydrobiology of what should be the best sampling time if only a single sampling is desired, cannot be answered on the basis of the present data; all that can be seen is that the differences in littoral zoobenthos abundances between May and August are comparatively large and different in different taxa, the numbers being on the average larger in May than in August. Another problem in the planning of routine investigations is how many sampling lines or stations should be used to represent a single lake. The present data show that, in a lake which is apparently regionally comparatively homogeneous, quite large differences between different subareas can still be found.

Fig. 2 shows that the vertical maximum of the total numbers is at a depth of 3 m in May and the abundances are higher in May than in August. However, the total numbers of individuals primarily represent a certain combination of

effects, because each of the species has its own vertical and seasonal distribution (Table 2), and there can also be several maxima or minima of particular species between May and August. Moreover, only individuals larger than a particular size have been included in the samples.

A multiple regression analysis was done for each of the dominant taxa (those presented in Table 2) in order to predict the abundances for a known depth and sampling time. For about two thirds of the taxa the depth and/or month had a significant effect but the degree of variation explained was comparatively weak (from 3.8 to 33.9%, average 11.7%). The sampling time had an effect significantly more often than the depth, which was the same result as from analyses of variance (Table 2).

Fig. 3 presents bathymetric distributions on the two sampling occasions and for the most abundant taxa. These graphs give a more detailed picture of the bathymetric distribution and monthly variation than Table 2 and the regression analysis. Fig. 3 shows that the vertical maximum for certain taxa is at very shallow depths (*Asellus aquaticus*, *Parakiefferiella bathophila*, *Bezzia* and *Palpomyia* type larvae), the maximum depth for most of the taxa is somewhere within the depth zone investigated, and the maximum depth for some species seems to be clearly deeper than the zone investigated (*Monodiamesa bathyphila*, *Polydillum pullum*, *Zalutschia zalutschicola*, *Pallasea quadrispinosa*). These observations mostly agree with some earlier observations on bathymetric

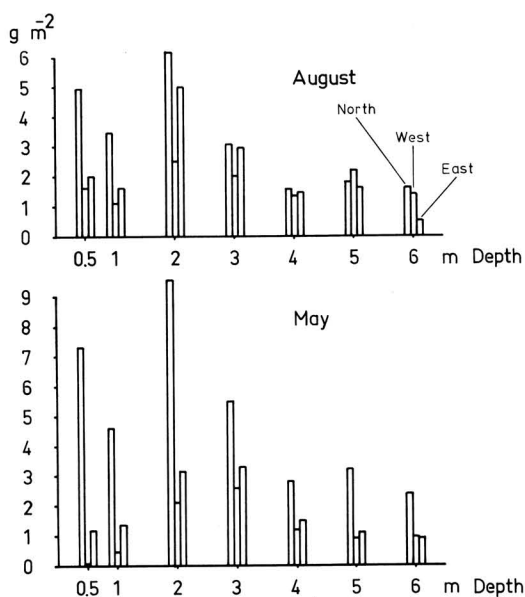


Fig. 4. Bathymetric distributions of the total fresh weight biomasses of the macrozoobenthos on the soft bottoms in different subareas and sampling occasions. The replicates pooled between depths of 2 and 6 m.

distribution (Grimås 1961, Paasivirta 1976).

It can be seen that the emergence of insects during the summer also makes the August values smaller. Certain oligochaete species, *Heterotrissocladius marcidus* and the peamussels (*Pisidium*), however, were somewhat more numerous in late summer. In oligochaetes and peamussels, this may be connected with the more permanent character of these groups as bottom animals. In late summer they are probably able to utilise at least some of the resources used by the chironomids in early summer, indicating the presence of temporal niches. However, it is also possible that the oligochaetes mostly feed in layers below the surface of the sediment whereas most chironomids feed on the sediment surface (Alsterberg 1925, Jonasson 1972). Furthermore, some of the species seem to live in a deeper zone in spring than in late summer, particularly *Asellus aquaticus*, *Sialis lutaria* and *Pagastiella orophila*. The two former species are large, mobile organisms and possibly tend to avoid the colder environment in the shallower depths in winter.

3.2. Biomasses

Regional differences were more common than bathymetric and monthly differences (Table 3).

On the other hand, the bathymetric differences were more common than those between the sampling months. This shows that even in faunal surveys in a lake which appears to be comparatively homogeneous, no conception of the biomasses of the littoral macrobenthos can be based on one sampling area only. If the investigating resources are limited, reduction of the sampling occasions is preferable to reduction of the number of the sampling depths or the number of subareas.

The regional variation in biomasses seems to be greater in small bottom animals (Oligochaeta, Chironomidae, Ceratopogonidae, Acari) than in large species (*Ephemera*, *Sialis*, Hirudinea). The difference between the two sampling months was also generally more significant in small taxa (*Heterotanytarsus*, Tanytarsini, Ceratopogonidae, Acari) than in large ones, which is evidently a consequence of the faster life cycles of the smaller species. The total biomasses did not show a significant seasonal difference, which may be partly a consequence of the alternation in the occurrence of the different size groups. This implies that the spatial and food resources (if they are assumed to be seasonally stable) are used fully during the time period.

The bathymetric differences (Tab. 3, Figs. 4 and 5) were significant for the total biomass, for herbivores and predators and for certain dominant taxonomic groups (Oligochaeta, *Ephemera*, Hirudinea, *Sialis* but not for Tanytarsini). The maximum of the total biomass (within the depth zone investigated) seems to be found at depths of 2–3 m (Fig. 4). The bathymetric distributions of certain groups (Fig. 5) show that Oligochaeta have clear biomass maximum at depth of 2 m, *Ephemera* between 2 and 5 m, subfamily Tanytarsini has a rather variable distribution and other chironomids and *Pisidium* have a comparatively even biomass distribution.

The proportion of predator taxa in the total biomass was an average of 31.4 % (Table 3), but it must be noted that the classification into predators and herbivores is crude and that there are very few monophagous species in the littoral zoobenthos (cf. e.g. Pieczynska 1976). With regard to the ratio predators/total, the regional and monthly differences were insignificant but the bathymetric differences were significant, showing a clear minimum at 3 m, where the total biomass reached its maximum. This is not in accordance with the ideas that herbivores are most often limited by predators or that predators are limited by the availability of food (Hairston et al. 1960). The average proportion of predators here is about the same as is usual in littoral macrobenthos according to Kajak (1980), who explains this high

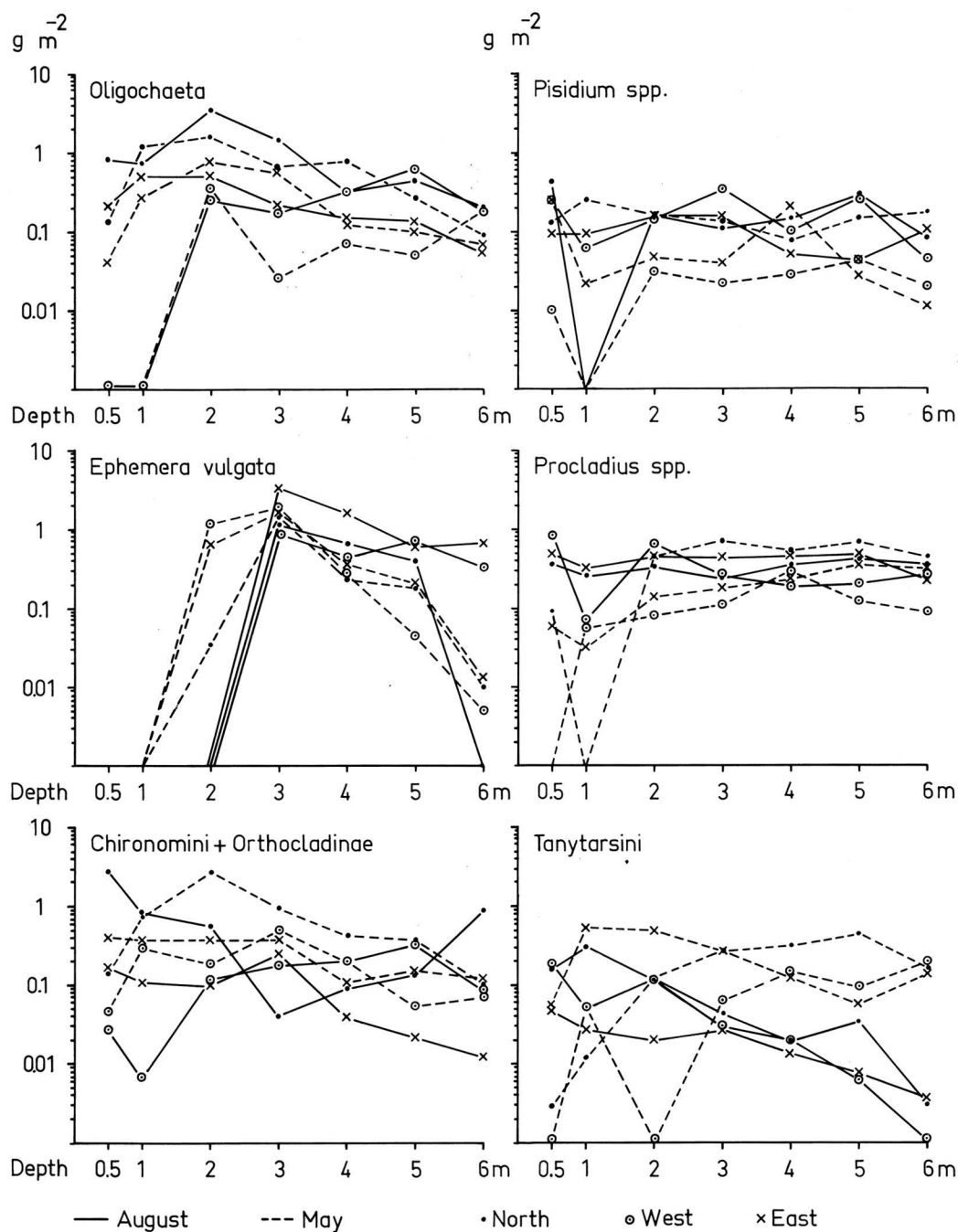


Fig. 5. Bathymetric distributions of the fresh weight biomasses of the main macrobenthic groups on the soft bottoms in different subareas and sampling occasions. The values for 0.5 and 1 m represent single samples, for 2–6 m three replicates.

Table 4. Numbers of individuals/m² of the taxa with a frequency $\geq 10/29$ in the stony bottom samples (SCUBA sampling, sieve 400 μm) as means for different subareas, months and depths. The significances of the regional, monthly and bathymetric differences according to one-way ANOVAs, significances as in Table 2.

	Total		Subareas				Months			Depths, m					
	freq.	mean	North	West	East	<i>p</i>	Aug.	May	<i>p</i>	0.2	1.0	1.5	2.2	3.0	<i>p</i>
<i>Asellus aquaticus</i>	24	37.2	29.3	51.6	29.9	—	58.2	17.6	*	14.0	37.6	81.2	22.1	29.9	—
<i>Caenis horaria</i>	13	7.4	1.7	7.6	12.4	—	7.0	7.9	—	6.7	11.2	7.4	6.7	4.6	—
<i>Cyrcus flavidus</i>	13	15.6	22.8	7.8	17.0	—	8.1	22.6	—	0	27.8	7.1	12.8	33.4	—
<i>C. trimaculatus</i>	13	17.9	12.6	12.1	28.6	—	0.7	34.0	**	0.8	6.1	17.2	35.2	32.9	—
<i>Enomus tenellus</i>	13	12.3	21.4	1.1	15.4	*	8.6	15.8	—	1.6	15.0	12.4	15.6	18.0	—
<i>Polycetropus flavomaculatus</i>	11	8.0	7.5	7.0	9.5	—	5.6	10.3	—	11.6	6.5	14.9	3.4	3.0	—
<i>Tinodes waeneri</i>	11	12.3	20.7	1.7	15.2	—	6.2	18.0	—	16.0	22.1	5.4	11.6	5.2	—
<i>Ablabesmyia</i> spp.	22	29.4	15.0	33.3	38.3	—	37.2	22.1	—	9.5	23.5	44.6	33.5	34.6	—
<i>Psectrocladius medius</i> type	18	32.1	18.7	35.3	40.8	—	26.4	37.2	—	33.4	26.4	31.0	43.3	25.0	—
<i>P. psilopterus</i> type	12	6.3	3.9	10.1	4.5	—	9.3	3.5	—	3.2	3.0	12.2	8.3	4.4	—
<i>Limnochironomus pulsus</i>	19	42.8	44.9	14.8	68.9	—	75.9	11.9	*	0	51.7	111	21.9	26.6	—
<i>Cladotanytarsus</i> spp.	10	27.2	62.3	18.4	4.3	—	54.5	1.6	*	0	43.4	41.8	32.5	16.3	—
<i>Oulimnius tuberculatus</i>	20	82.4	159	84.6	11.4	—	126	41.8	—	13.3	247	91.4	22.5	29.1	—
Total abundance	29	560	667	495	528	—	610	513	—	293	783	700	410	624	—
<i>n</i>	29		9	10	10		14	15		6	6	6	6	5	

proportion by the fact that many predators feed not only on macrobenthos but also on meiobenthos and microbenthos. The meiobenthos abundances of the present material, however, appeared to have no bathymetric differences (see section 5).

4. Macrobenthos on stony bottom

Appendix 1 and Table 4 show that the dominant taxa on stones were usually not those which were dominant in soft bottoms. Considering the taxa exceeding 10 ind./m² as dominants, only *Limnochironomus pulsus* and *Parakiefferiella bathophila* were dominant in both sets of samples. In stone samples, Trichoptera were represented by 21 taxa whereas in soft bottom samples there were only 16 taxa of caddis flies. *Asellus aquaticus* was much more abundant on stony (mean 37 ind./m²) than on soft bottoms (mean 5.4) and the larvae of *Oulimnius* (Elmidae, Coleoptera) were the most abundant group on stones but were absent from soft bottoms. Furthermore, Oligochaeta, *Ephemera vulgata*, *Procladius* spp., *Heterotanytarsus apicalis*, *Endochironomus in-textus*, *Pagastiella orophila*, *Polypedilum pullum*, *Pseudochironomus prasinatus*, Tanytarsini, Ceratopogonidae and *Pisidium* spp. were much more abundant on soft bottoms than on stones.

Tables 4 and 5 show that the regional, seasonal and bathymetric differences in abundances and biomasses were much weaker in stone samples than in soft bottom samples. This, however, is partly due to the smaller number of samples, because replicate sampling was not performed for stony bottoms. With regard to abundances, the regional variation was significant for only one dominant taxon, which was *Enomus tenellus*.

Monthly differences showed significant variation in numbers of *Cyrcus trimaculatus*, which were more numerous in spring than in late summer, and for *Limnochironomus pulsus*, which was more abundant in August. Bathymetric distribution was not significant for any group or species. With regard to biomasses, *Asellus aquaticus* was the only taxon showing significant monthly differences: the biomass was higher in late summer than in spring. Its bathymetric differences were also significant, showing a maximum at a depth of 1.5 m.

The proportion of predator groups on stony bottoms was on average higher (46.8 %) than in soft bottom material (31 %). This is a comparatively high proportion and may indicate that the predator species spend an appreciable proportion of their time on, between or below the stones, gathering their food from the more or less soft bottom in which the stones lie. This ratio differed significantly between the sampling months, being higher just after the thaw. This may indicate that the food of the predators has been consumed effectively during the winter. The bathymetric distribution was not significant.

5. Meiobenthos

Tables 6 and 7, which present regional, monthly and bathymetric averages and variation in individual numbers of the principal meiofaunal groups, show that only some of the monthly differences were significant. These indicated clearly higher abundances in late summer than in spring. This contrasts with the seasonal fluctuation in the macrofauna abundances (Tables 2 and 4), in which the vernal values were higher, but coincides with the meiofauna abundances in the profundal depths of lake Päijänne (Särkkä 1979,

Table 5. Biomasses (wet weight mg/m²) in the stony bottom samples (SCUBA sampling, sieve 400 µm) as means for the different subareas, months and depths. The significances of the regional, monthly and bathymetric differences according to one-way ANOVAs, significances as in Table 2.

	Total	Subareas				Months			Depths, m					
	mean	North	West	East	p	Aug.	May	p	0.2	1.0	1.5	2.2	3.0	p
Herbivores or detritus feeders (mainly)														
Oligochaeta	8.1	19.0	4.7	1.7	—	4.7	11.3	—	0.2	20.8	6.1	6.1	7.1	—
Cladocera	1.6	0.4	0.1	4.0	—	3.1	0.1	—	2.9	0.4	0.9	3.0	0.4	—
<i>Asellus aquaticus</i>	56.0	43.1	74.0	49.7	—	84.3	29.6	*	35.0	41.3	129	34.9	36.7	*
Ephemeroptera	8.3	3.4	14.3	6.7	—	11.2	5.5	—	18.6	9.9	6.1	4.0	1.6	—
Trichoptera, herbiv.	154	38.3	391	21.4	—	15.4	284	—	17.9	14.5	631	12.7	83.0	—
Chironomidae, herbiv.	102	75.5	53.2	174	—	120	84.9	—	31.4	94.5	120	50.4	234	—
<i>Pisidium</i> spp.	0.9	2.8	0	0	—	1.8	0	—	0	4.3	0	0	0	—
<i>Sphaerium corneum</i>	2.2	0	0	6.5	—	0	4.3	—	0	10.9	0	0	0	—
Gastropoda	77.7	202	28.2	15.7	—	150	10.4	—	148	197	8.5	21.5	1.2	—
Herbivores, total	411	384	566	279	—	390	430	—	254	393	902	133	364	—
Predators (mainly)														
Nematoda	0.6	0	1.8	0	—	1.3	0	—	0	3.0	0	0	0	—
Turbellaria	1.6	0	4.5	0	—	3.2	0	—	0	0	7.6	0	0	—
Hirudinea	135	6.1	342	44.0	—	31.7	231	—	147	111	56.3	310	33.5	—
Plecoptera	10.0	3.0	25.1	1.2	—	20.7	0	—	43.4	4.5	0	0.3	0	—
Trichoptera, carniv.	138	106	165	139	—	110	164	—	186	129	124	124	124	—
Tanypodinae	27.3	33.3	18.6	30.7	—	27.9	26.9	—	6.2	20.0	38.2	22.0	55.0	—
Ceratopogonidae	1.3	2.1	1.6	0.2	—	0.1	2.4	—	0.7	2.2	2.9	0.2	0.2	—
Tabanidae	0.6	1.8	0	0	—	0	1.1	—	0	2.0	0	0	0.9	—
<i>Oulimnius tuberculatus</i>	40.2	75.9	42.1	6.1	—	63.2	18.7	—	5.6	123	43.5	10.2	14.1	—
Acari	6.2	0	8.8	9.2	*	4.0	8.2	—	6.2	3.3	4.5	2.2	16.4	*
Predators, others	0.2	0.6	0	0	—	0	0.4	—	0	0	1.0	0	0	—
Predators, total	361	229	609	230	—	262	453	—	395	398	278	468	244	—
Total biomass	771	613	1175	509	—	652	882	—	649	791	1180	601	608	—
Ratio predators/total %	46.8	37.4	51.8	45.2	—	40.2	51.4	*	60.9	50.3	23.6	77.9	40.1	—
Total dry weight biomass	131	104	200	87	—	111	150	—	110	134	201	102	103	—
n	29	9	10	10		14	15		6	6	6	6	5	

Table 6. Numbers of individuals as thousands/m² of the main groups in the soft bottom meiobenthos samples (Kajak sampler, sieve 80 µm, 400 µm fraction omitted) as means for different subareas, months and depths. The significances of the regional and bathymetric differences according to one-way ANOVAs, those of monthly differences according to *t*-tests, significances as in Table 2.

	Total		Subareas				Months			Depths, m			
	mean	SD	North	West	East	p	Aug.	May	p	2	4	6	p
Nematoda	4.7	4.9	4.5	4.8	4.8	—	6.9	2.5	—	6.9	5.5	1.8	—
Oligochaeta	2.5	4.8	5.6	1.2	0.9	—	4.3	0.8	—	5.3	1.9	0.5	—
Cyclopoida	4.7	6.8	1.9	2.6	8.9	—	7.1	2.3	—	6.5	2.8	5.3	—
Harpacticoida	10.3	9.6	10.2	9.4	11.2	—	17.0	3.5	***	9.8	11.2	9.9	—
Chironomidae	14.0	10.8	17.8	8.5	14.0	—	16.1	11.9	—	18.9	13.8	9.3	—
Others	4.6	8.7	3.2	2.2	8.3	—	8.3	0.8	—	8.5	3.4	1.9	—
Total	41.1	33.8	44.9	29.7	48.6	—	60.0	22.1	*	56.1	38.2	28.9	—
n	18		6	6	6		9	9		6	6	6	

fig. 16). The increase in the meiofauna abundances during the summer could be due to the shorter life-cycle prevailing in the meiofauna, which thus appears to exploit the warmest season more efficiently. It seems to follow that for the insects which form the main part of the macrofauna early emergence is more important than the benefits of the warmest season in the water. This indicates that certain temporal niches can be found for the littoral zoobenthos: the merolimnic macrofauna uses more wintery and vernal resources whereas the meiofauna and hololimnic oligochaetes use the warmer period more efficiently. In August meiofauna numbers on the soft bottoms were about three times higher than in May, and on the stony bottoms about twice as

high as in May.
The following table shows certain ratios for meiofauna and macrofauna abundances:
Meiofauna on soft bottoms/
meiofauna on stones = 8.0
* Macrofauna on soft bottoms/
macrofauna on stones = 3.3
Meiofauna on soft bottoms/
macrofauna on soft bottoms = 22.5
Meiofauna on stones/
macrofauna on stones = 9.2
Thus the numbers of individuals are generally higher on soft bottoms than on stony bottoms, but the difference is still higher between the numbers of meiofauna and macrofauna.

Table 7. Numbers of individuals as thousands/m² of the main groups in the stony bottom meiobenthos samples (sieve 80 μ , 400 μ m fraction omitted) as means for different subareas, months and depths. The significances of the regional and bathymetric differences according to one-way ANOVAs, those of the monthly differences according to t-tests, significances as in Table 2.

	Total		Subareas				Months			Depths, m					
	mean	SD	North	West	East	<i>p</i>	Aug.	May	<i>p</i>	0.2	1.0	1.5	2.2	3.0	<i>p</i>
Nematoda	0.2	0.3	0.3	0.2	0.2	-	0.3	0.1	×	0.1	0.3	0.5	0.2	0.2	×
Oligochaeta	0.8	1.2	0.4	0.5	1.5	-	1.5	0.2	××	1.0	0.9	1.0	0.4	0.9	-
Cyclopoida	0.3	0.3	0.1	0.2	0.4	×	0.4	0.1	×	0.3	0.2	0.1	0.4	0.2	-
Harpacticoida	0.7	0.5	0.6	1.0	0.6	-	0.8	0.7	-	0.6	0.6	0.8	0.9	0.7	-
Chironomidae	2.6	1.5	2.7	2.4	2.8	-	3.2	2.1	-	3.2	2.8	2.8	2.1	2.1	-
Others	0.5	0.7	0.6	0.5	0.6	-	0.9	0.2	××	0.5	0.9	0.6	0.5	0.3	-
Total	5.2	3.2	8.3	4.7	6.2	-	7.0	3.4	××	5.6	5.6	5.7	4.4	4.3	-
n	29		9	10	10		14	15		6	6	6	6	5	

Table 8. Average proportions (%) of different taxonomic groups of abundances and fresh weight biomasses in macrobenthos of soft and stony bottoms.

	Soft bottoms		Stony bottoms	
	Abund.	Biomass	Abund.	Biomass
Nematoda	1.2	0.1	0.3	0.1
Oligochaeta	12.2	19.6	2.5	1.1
Hirudinea	0.4	4.7	2.5	17.5
Crustacea	0.9	1.0	7.6	7.5
Ephemeroptera	2.1	20.7	1.6	1.1
Plecoptera	-	-	0.4	1.3
Megaloptera	0.5	4.7	-	-
Trichoptera	0.5	1.4	16.9	37.9
Chironomidae	70.5	36.6	45.8	16.8
Ceratopogonidae	1.4	0.4	0.8	0.2
Tabanidae	0.2	0.8	0.3	0.1
Coleoptera	-	-	15.1	5.2
Acari	0.2	1.9	1.3	0.8
Mollusca	5.8	6.6	2.2	10.5
Other groups	4.1	1.5	2.7	0.1
Total	100	100	100	100

Table 9. Average bathymetric distributions of the merolimnic macrobenthos and its proportions (%) of total macrobenthos on soft and stony bottoms.

Depth m	Abundance		Biomass		Species	
	Ind./m ²	%	mg/m ²	%	s	%
Soft bottoms						
0.5	1514	78.8	1224	44.1	25	61.0
1	1128	76.8	1166	55.6	30	62.5
2	1652	70.4	2766	58.4	48	51.1
3	1922	73.9	2545	78.7	47	54.7
4	1261	77.9	1240	75.2	49	55.7
5	1094	72.9	1149	63.9	45	51.1
6	889	79.4	863	59.9	41	52.6
Total	1352	75.4	1565	66.5	69	50.7
Stony bottoms						
0.2	233	82.1	310	56.4	34	75.6
1.0	434	83.1	400	62.0	32	66.7
1.5	548	80.0	1011	73.3	41	73.2
2.2	348	82.6	223	63.0	43	76.8
3.0	541	85.6	512	78.6	47	81.0
Total	421	82.2	491	63.2	77	71.3

6. Discussion

6.1. Faunal groups

The comparison of the proportions of different taxonomic groups between soft and stony bottoms shows (Table 8) that Oligochaeta, Megaloptera (*Sialis*) and Chironomidae are much more dominant in soft than on stony bottoms with regard to both abundance and biomass, and the biomass of Ephemeroptera (mainly *Ephemera vulgata*) as well as the abundance of Mollusca (mainly *Pisidium*) are higher in soft than on stony bottoms. Stony bottom values are higher for abundances and biomasses of Hirudinea, Crustacea, Trichoptera and Coleoptera (mainly *Oulimnius*). Table 9 shows that the merolimnic fauna (= insects) forms more than 3/4 of the abundances and about 2/3 of the biomass in the littoral zone

investigated. The values of Table 8 can be used to produce indices for classifying the trophic state of lakes or in pollution studies (for instance the Oligochaeta/Chironomidae ratio of abundances and the proportion of Oligochaeta from total abundance by Wiederholm 1980). However, these indices have mainly been used in work on profundal depths.

It might be expected that the merolimnic fauna would be more adapted to life in the shallower depths and the hololimnic fauna in greater depths. There is, however, no clear bathymetric trend in the proportions of the merolimnic fauna within the depths studied, according to Table 9, but in absolute terms of numbers of species on stony bottoms the number of merolimnic species even increases with depth ($r = 0.91$, $p < 0.05$). With respect to the difference between soft and stony bottoms, the proportion of merolimnic taxa

Table 10. Regional, monthly and bathymetric averages of the Shannon diversity (\log_2 based) and number of species (s) in soft and stony bottoms and significances of differences according to one-way ANOVAs (values of probability of F with significances as in Table 2). For the soft bottoms the values are for the pooled replicates.

	Total		Station				Months			Depths, m							
	mean	SD	North	West	East	F	Aug.	May	F	0.5	1	2	3	4	5	6	F
Soft bottoms																	
diversity	3.36	0.66	3.33	3.31	3.45	0.848	3.15	3.57	0.035*	2.76	3.19	3.79	3.80	3.56	3.38	3.05	0.034*
s	28.6	11.9	30.4	27.0	28.4	0.764	22.0	35.1	0.000***	15.2	18.0	34.2	32.7	35.8	35.3	29.0	0.001**
Stony bottoms																	
diversity	3.33	0.70	2.93	3.31	3.71	0.046*	3.15	3.49	0.200								
s	17.2	6.2	13.6	16.4	21.4	0.013*	16.2	18.2	0.900								

is, except for biomasses, higher on stony bottoms (Table 9). Stony bottoms may resemble, in this respect, more or less lotic waters.

It can be assumed that the artificial regulation of the water level in a lake has a strong effect, particularly on the hololimnic fauna which is bound solely to the aquatic environment. However, the present study shows that the proportion of the hololimnic fauna in the littoral zone of an unregulated lake is smaller than that of the merolimnic fauna. This may decrease the influence of water level regulation on the entire littoral zoobenthos from what might otherwise be expected.

6.2. Diversity

The species diversity can be expected to increase with depth because of the increasing stability of the environment (cf. Sanders 1968). On the other hand, the diversity could be expected to be highest in the shallowest depths, where the habitat complexity or spatial heterogeneity is highest because of the many different kinds of microhabitats (cf. e.g. Simpson 1964, MacArthur & MacArthur 1961). The productivity factor (cf. Connell & Orias 1964) ought to move the bathymetric maximum to depths at which the biomass (and the productivity) are highest. If the seasonal fluctuation of the zoobenthos diversity follows the fluctuation in the diversity of the lower trophic levels, it could be expected that the zoobenthos diversity would be higher in late summer than in spring because this is what appears happen to the phytoplankton diversity (e.g. MacArthur 1965, Moss 1973, Eloranta 1976; cf. Margalef (1958) who assumes that the diversities of different trophic or taxonomic groups behave in the same manner). The predation factor (Paine 1966) is one of the possible causes of the differences in diversity, and the proportion of carnivore or predator species is at least partly indicative of the influence of predation (Fig. 7).

Table 10 presents the diversity values and numbers of species (s) for soft and stony bottom materials. The generally lower values of s for stony bottoms may indicate that the size of the sample was too small. On soft bottoms the regional differences were not significant, but the monthly and bathymetric differences were, showing higher values in May than in August. The bathymetric maxima were at depths of 2–4 m for diversity and at depths of 2–5 m for s . On stony bottoms only regional differences were significant.

Because of the small regional variation in the environmental conditions, regional differences were not anticipated. The manifestation of significant regional variation on stony bottoms may indicate that the stony bottom fauna in particular is sensitive to the small amount of eutrophication appearing in the eastern subarea, but it may be due to stronger aggregation in the distribution, too. The behaviour of the monthly differences is completely opposite to that expected on the basis of the phytoplankton diversity or the diversity of the benthic algae. However, conformity with food diversity applies principally to monophagous species, as stated by MacArthur (1965), and because there are not many monophagous species in the littoral zoobenthos (cf. e.g. Pieczynska 1976), there is probably no contradiction whatsoever between ingested food diversity and zoobenthos diversity. If the regular seasonal fluctuation is seen as a succession, it might be expected that the diversity increases during the succession (cf. e.g. Margalef 1963, 1968, Shafi & Yarranton 1973) from spring until autumn. However, as Cummins (1973) generalized, very significant amounts of feeding and growth of the benthic invertebrates occur during the autumn and winter, at least in running water which strongly resembles the littoral zone of lakes. It is thus possible that there is a succession from late summer until spring in the zoobenthos of a lake littoral as well as in that of running water, and not from spring until autumn; there should be no contradiction with the expected increasing diversity during succession. Furthermore, be-

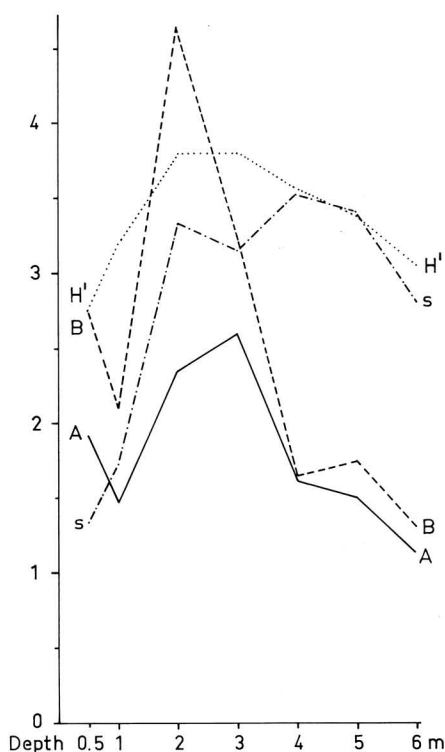


Fig. 6. Bathymetric distributions as means of the total material in the soft bottom macrozoobenthos for total abundance $\times 1000 \text{ ind. m}^{-2}$ ($=A$), total fresh weight biomass g m^{-2} ($=B$), the number of species $\times 10$ ($=s$) and Shannon diversity (\log_2 based, $=H'$).

cause living algae probably do not form as much food as detritus for zoobenthos (e.g. Pieczynska 1976), there is little contradiction with the diversity of the lower trophic levels.

The bathymetric distributions of diversity presented in Table 10 and also in Fig. 6, which includes the bathymetric distribution of abundance and biomass for soft bottom zoobenthos, show a maximum at depths of 2–4 m. For stony bottoms (Table 10) the diversity also seems to increase down to 3 m, below which the stony bottoms change to soft bottoms. It also seems that the diversity and number of species of zoobenthos generally decrease with depth from this littoral or sublittoral maximum (cf. e.g. Ruggiu & Saraceni 1972, Särkkä 1972, Paasivirta 1976, Sarvala et al. 1981). What, therefore, are the causes of the bathymetric distribution of the zoobenthos diversity in lakes?

Evolutionary causes or the adaptation of different species must determine the diversity of the zoobenthos together with biogeographical factors. If the biogeographical factors were

absent, the stability of the environment ought to cause an increase in the diversity from the littoral to the profundal. However, for example, the huge number of hololimnic species which form the main fauna of ancient lake Baikal (e.g. Kozhov 1963) is not found in postglacial lakes in which the majority of the fauna are merolimnic species (Table 9). At certain depths, which can be understood as an ecotone, where both merolimnic and hololimnic species live together, the diversity reaches its maximum. So the stability of the environment, which seems to be greater in the profundal than in the littoral, is not able to increase the diversity. It must also be noted that the profundal depth zone of the postglacial lakes has been a stable environment for only a short period of time.

Certain other factors generally conceived to have an effect on the diversity mostly agree with the bathymetric distribution of the diversity observed. The spatial heterogeneity of the environment is highest in the shallowest zone and ought to increase the diversity. However, the lability of the environment, caused by the changing wave-action, water level, temperature, illumination etc., together with the effect of the patchiness on the sampling result, decrease the diversity at the very shallowest depth zones. The productivity factor could be thought to have a positive correlation with diversity (Fig. 6) if biomass and abundance are accepted as representing production. It seems that productivity is the most important causative factor explaining the differences between the littoral and profundal diversity. The predation factor will be considered somewhat more deeply in the next section.

6.3. The proportion of predators

The proportion of the principally carnivore or predator species (as classified mainly by Merritt & Cummins 1978) of the total fresh weight biomass was 31.4 % in the whole soft bottom material (Table 3). Fig. 7 shows the variations between the subareas, depths and sampling occasions. The proportion of predators seems to have been higher in late summer than in spring but Table 3 shows that neither this difference nor the regional variation was significant. The bathymetric differences were significant and showed that this ratio was lowest at depths of about 2–5 m (Table 3). This is the same depth at which the diversity is highest (Table 10). This is in contrast to the predation hypothesis by Paine (1966) which assumes an increased proportion of predators in more diverse communities, although this hypothesis is based on numbers of species. Fig. 8 shows that in

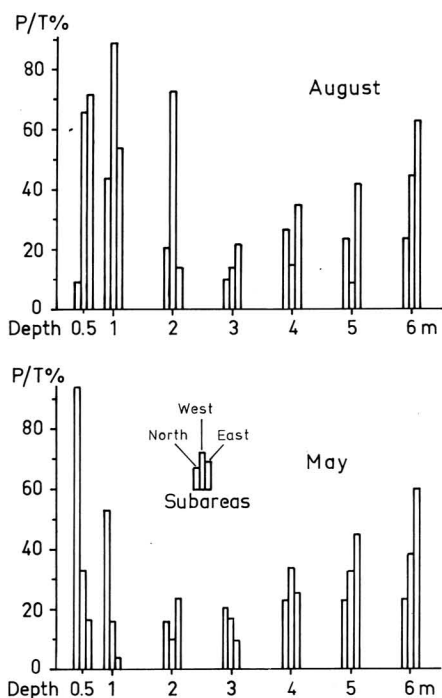


Fig. 7. Bathymetric distributions of the proportions of the mainly predator taxa (= P/T %) in the total biomass for the soft bottom macrozoobenthos in different subareas and sampling occasions.

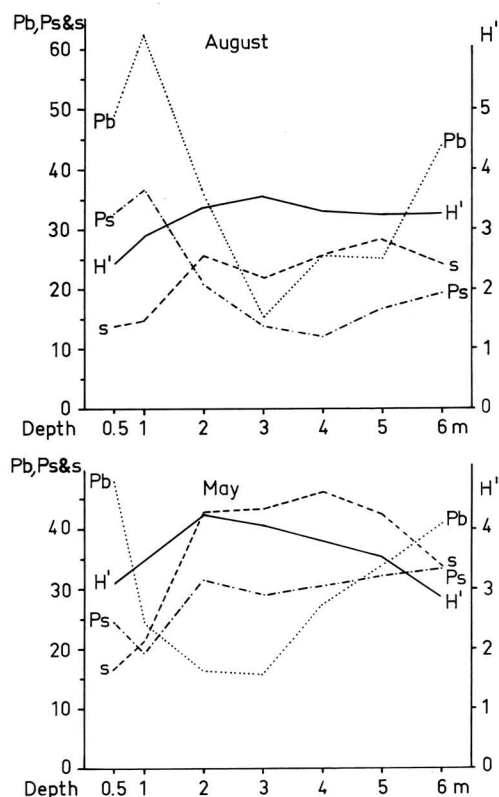


Fig. 8. Bathymetric distributions of Shannon diversity (\log_2 based, = H'), number of species (= s), proportion of the predators in the biomass as % (= P_b) and proportion of the predators in the number of species as % (= P_s) for the soft bottom macrozoobenthos on the two sampling occasions.

spring the proportion of predators based on numbers of species is positively correlated with the diversity (when the diversity is expressed as the number of species, $r = 0.51$, $p < 0.05$). Consequently, the predation hypothesis could be thought to be valid in spring but not in late summer when the correlations are even negative and significant (proportion of predator species number with Shannon diversity, $r = -0.54$, $p < 0.05$; proportion of predator species number with total number of species, $r = -0.72$, $p < 0.001$; proportion of predator biomass with total number of species, $r = -0.51$, $p < 0.05$). Why, then, are these proportions different in spring and late summer?

Fig. 9 shows that the absolute value of the herbivore biomass is at its maximum at depths of 2–3 m on both sampling occasions and thus probably during the whole year, while the predator biomass is highest at depths of 0.5–2 m, though in spring it is somewhat shallower than in late summer. There are several hypothetical explanations for these seasonal and vertical differences. It is possible that there are optimal conditions for the predator species in the most

illuminated depths in the shallow water. The predation on zoobenthos by fish is probably more important at somewhat greater depths, whereas the predation on zoobenthos by invertebrate carnivores may be stronger at shallower depths. The predation by fish is probably also weaker in winter when the fish do not generally consume much food, and the predation by fish may also be higher on the invertebrate predators at greater depths of the littoral zone than in shallow depths. The habitat diversity, which is highest in shallow depths, probably permits a more ample occurrence of the predators. It is also possible that the proportion of meiofaunal food increases with depth, which would mean that the ratios considered are not valid. However, the number of individuals of the meiofauna did not show any significant bathymetric differences within the zone investigated, as mentioned above (Tables 6 and 7). Furthermore, Paine's (1966) conclusions do not necessarily hold for habitats in which

Table 11. The most significant coefficients for the Pearson, Kendall and Spearman correlations between the abundances of different taxa of the soft bottom macrozoobenthos and niche overlap indices L according to equation by Hurlbert (1978). Significances as in Table 2.

	Pearson	Kendall	Spearman	Hurlbert L
Positive correlations				
<i>Protanypus morio</i> / <i>Zalutschia zalutschicola</i>	0.78***	0.45**	0.46**	7.43
<i>Cryptochironomus defectus</i> / <i>Pisidium amnicum</i>	0.72***	0.28**	0.29**	17.53
<i>Psammoryctides barbatus</i> / <i>Cryptochironomus defectus</i>	0.49***	0.09	0.10	12.25
<i>Stylaria lacustris</i> / <i>Uncinaxis uncinata</i>	0.56***	0.63**	0.64**	8.77
<i>Heterotanytarsus apicalis</i> / <i>Polypedilum pullum</i>	0.23*	0.52**	0.65**	1.41
<i>Cladopelma viridula</i> / <i>Bezzia-Palpomyia</i>	0.64***	0.52**	0.56**	4.39
<i>Parakiefferiella smolandica</i> / <i>Heterotanytarsus apicalis</i>	0.63***	0.47**	0.55**	3.81
<i>Heterotanytarsus apicalis</i> / <i>Limnochironomus pulsus</i>	0.54***	0.44**	0.52**	3.27
<i>Demicryptochironomus vulneratus</i> / <i>Bezzia-Palpomyia</i>	0.55***	0.40**	0.44**	4.52
Negative correlations				
<i>Sialis lutaria</i> / <i>Limnodrilus hoffmeisteri</i>	-0.34***	-0.38***	-0.45**	0.26
<i>Psectrocladius psilopterus</i> / <i>Limnodrilus hoffmeisteri</i>	-0.22*	-0.14	-0.18	0.68
<i>Heterotrissocladius marcidus</i> / <i>Pagastiella orophila</i>	-0.20*	-0.23**	-0.27**	0.33
Acari (total) / <i>Pisidium</i> (total)	-0.25*	-0.24**	-0.32**	0.56
<i>Helobdella stagnalis</i> / <i>Ephemera vulgata</i>	-0.18	-0.26**	-0.30**	0
<i>Sialis lutaria</i> / <i>Heterotrissocladius marcidus</i>	-0.19	-0.26**	-0.28**	0
<i>Asellus aquaticus</i> / <i>Ephemera vulgata</i>	-0.17	-0.24**	-0.28**	0.24
Others				
<i>Pseudochironomus prasinatus</i> / <i>Limnochironomus pulsus</i>	0.05	0.09	0.11	1.51

competition for space in less severe, and it is not certain whether there is in general any question of competition for space in benthic communities of the littoral soft bottom. The fact that neither simple food chains nor monophagous species come into question in the littoral ecosystem also means that the seasonal or vertical maxima do not necessarily conform to the maxima of the primary production, and that the predator maxima do not necessarily conform to the herbivore maxima. It must be noted that fresh weight biomasses have been considered in the present study, and dry weight values or calorific contents might give somewhat different but probably similar results. In addition, production values would give somewhat different results if the herbivores have shorter life-cycles than the mostly larger predators.

The predator biomass/total biomass ratio (46.8 %) was higher for stony bottoms than for soft bottoms, and the vertical and regional variations were not significant (Table 5). The difference between the sampling seasons was significant, showing a higher proportion of predators in May. The higher proportion of predators on stony than in soft bottoms, which in May comprises nearly half of the biomass, may also partly indicate that the predators favour the stones (and interstices and bases of the stones) as their living environment although they possibly prey on the benthic

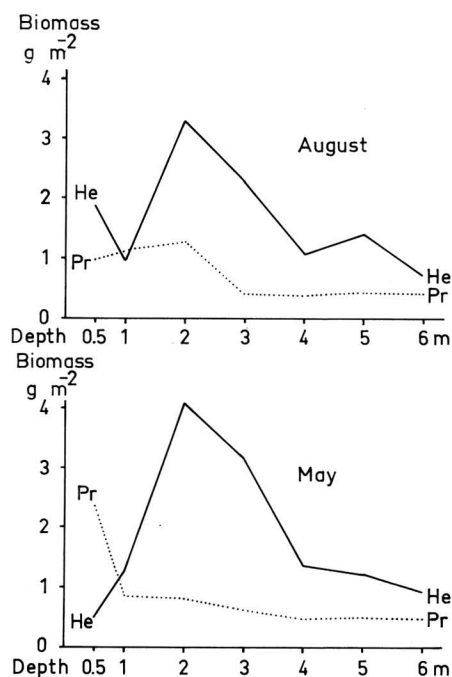


Fig. 9. Bathymetric distributions of the fresh weight biomasses of the (mainly) herbivores-detritivores (= He) and the (mainly) predators (= Pr) on the two sampling occasions for the soft bottom macrozoobenthos.

animals living on the surroundings of the stones. This seems especially probable at the greater depths of the stone samples (2–3 m), where the stones are found somewhat sporadically on the more or less soft bottom. The correlations of predator biomass/total biomass ratio were not significant with either diversity ($r = 0.11$, $df = 27$) or with the number of species ($r = -0.05$). The high proportion of predators in spring was due mainly to the higher numbers of Hirudinea which were also more common in spring on the soft bottom, although this seasonal difference was not significant.

6.4. Interrelationships between species

Correlation coefficients (Pearson, Kendall and Spearman correlations) calculated between the abundances of each pair of taxa exceeding the frequency 5/102, showed that the most common taxa (see Appendix 1) generally correlated most with the numbers of the other taxa. About one third of all of the correlations were significant ($p < 0.05$) and the nonparametric tests gave somewhat more significant correlations than the Pearson correlations (Kendall and Spearman 34.1 %, Pearson 32.7 %). The coefficients of the highest Pearson correlations were > 0.70 (Table 11). The nonparametric correlations showed the highest coefficients partly for other taxa than the Pearson correlation. Although the same mode of seasonal, bathymetric and regional distribution has a strong effect on the correlation coefficients, positive coefficients imply the co-occurrence and possible competition between pairs of species. A negative coefficient, however, may indicate different spatial and temporal distributions and the occurrence of the predator/prey relationship, although the correlations do not really reveal any causal relationships.

The Pearson correlations were significant ($p < 0.05$) and negative for four pairs of taxa only (Table 11), but the nonparametric correlations were negative and significant in many more cases (in 43 of 710 possible combinations). The highest negative correlations were found between the members of a pair consisting of a mainly predator taxon and another mainly herbivore or detritus feeding taxon, thus indicating a possible predator/prey relationship.

However, *Cryptochironomus*, which is known to be a predator on oligochaetes (Armitage 1968, Loden 1974, Titmus & Badcock 1981), showed no significant correlations with any of the oligochaete species in the present study. Armitage (1974), moreover, assumed that *P. prasinatus* fills the niche of *L. pulsus* in late summer, but these

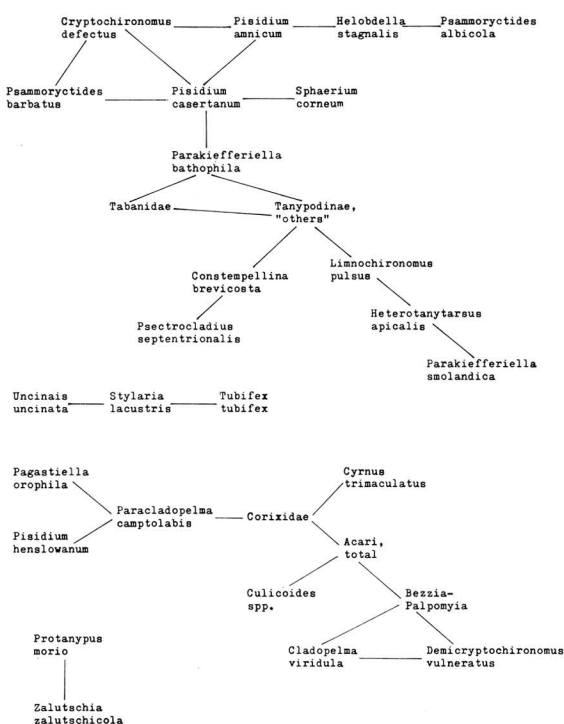


Fig. 10. Correlation associations for the soft bottom macrozoobenthos based on the numbers of individuals. Taxa exceeding the Pearson correlation coefficient $+0.50$ united into groups ($df = 100$).

species did not have any significant correlation in the present data, although both have higher numbers in May than in August (Fig. 3, Table 2) and nearly similar bathymetric distributions. However, it is clear that, for example, a weekly sampling might give a clearer picture of the possible seasonal niches. The niche overlap calculations performed according to equation L of Hurlbert (1978) for the pairs having the highest positive or negative correlation coefficients (Table 11) showed that the pairs of taxa with the highest positive correlations assumed values $L > 1.0$, which indicates that the utilization functions of the two species tend to coincide. Furthermore, all of the pairs with the strongest negative correlations assumed niche overlap values far below 1.0, which indicates that the resource states are weakly shared. However, the predator/prey relationship which possibly exists in some of the cases confuses the concept of niche overlap. To summarize, it seems that the significant negative correlations indicate the same as the low niche overlap values. The routine statistical computing programs thus seem to give nearly the same results as certain nichemetric measurements.

Table 12. Factor analyses for abundances of soft bottom macrozoobenthos. For each taxonomic group, the regional, seasonal and bathymetric maximum are also presented with significances according to ANOVA, significances as in Table 2. Factor 1 explains 43 %, factor 2 24 %, factor 3 19 % and factor 4 14 % of the total variance.

	Loading	Communi- nality	Regional maximum	Seasonal maximum	Bathymetric maximum
Factor 1					
Acari, total	0.75	0.66	East*	May***	2-3 m*
<i>Bezzia-Palpomyia</i>	0.69	0.55	East*	May***	0.5-3 m***
Tanypodinae, "others"	0.63	0.64	North	May***	0.5-3 m
<i>Limnochironomus pulsus</i>	0.61	0.51	North*	May***	0.5-4 m
Corixidae	0.59	0.47	North (+E)	May*	3 m
<i>Pagastiella orophila</i>	0.57	0.24	North***	May***	1-3 m**
Tanytarsini	0.55	0.53	North	May***	1-3 m
Factor 2					
<i>Pisidium casertanum</i>	0.82	0.76	North***	May	2 m
<i>Cryptochironomus defectus</i>	0.72	0.68	North	May*	2 m*
<i>Parakiefferiella bathophila</i>	0.69	0.73	North*	May***	2-3 m
<i>Psammoryctides barbatus</i>	0.68	0.58	North***	May***	2-3 m***
<i>Pisidium amnicum</i>	0.66	0.47	North	May	2 m
<i>Helobdella stagnalis</i>	0.63	0.50	North***	May	1-2 m***
Factor 3					
<i>Limnodrilus hoffmeisteri</i>	0.67	0.48	East(+N)***	Aug.	3-5 m***
<i>Pisidium lilljeborgi</i>	0.61	0.42	North***	May	-
<i>Procladius</i> spp.	0.51	0.39	North*	May	3-5 m***
Factor 4					
<i>Psectrocladius medius</i>	0.62	0.41	West(+E)***	-	0.5-5 m*
<i>P. psilopterus</i>	0.54	0.33	West***	May***	1-3 m***
<i>Portanyphus morio</i>	0.44	0.20	West*	May	3-6 m
<i>Zalutschia zalutschicola</i>	0.43	0.20	West***	May*	3-6 m
<i>Stalis lutaria</i>	0.41	0.22	West***	May	1-2 m***
<i>Constempellina brevicosta</i>	0.40	0.68	East	May***	2-3 m
<i>Psectrocladius septentrionalis</i>	0.37	0.15	West	May	1-5 m

Correlation coefficients can also be used to allot species into associations or guilds (e.g. Edwards 1975), or in other words, to divide the species or taxa into more or less homogeneous groups. Such a graphical grouping was done using the Pearson correlation matrix of soft bottom macrobenthos abundances as a basis. When all pairs of taxa which achieved a significance level of $p < 0.001$ (in which $r > 0.32$) were chosen, the associations were large and confused. The correlation coefficient used as limit was raised to 0.5 (see Fig. 10 in which two larger and some smaller associations of taxa can be seen). Here the taxa within the associations have more in common in their spatial and temporal distributions than with the taxa not belonging to the association.

Factor analysis, which also uses the Pearson correlation coefficients as its raw material, was performed, giving solutions consisting of different numbers of factors. Table 12 presents the taxa with the highest loadings in a four-factor solution using the abundance values. Each of the factors can be interpreted as a species association containing certain spatial and temporal affinity

between the taxa. Table 12 also gives a concise presentation of the spatial and temporal characteristics of each taxon. The taxa belonging to factor 1 have a somewhat larger depth distribution than those belonging to factor 2, and also a somewhat clearer vernal maximum. The regional maximum in the northern subarea is clearer in factor 2 than in factor 1. Both of these factors correspond clearly to the two correlation associations in Fig. 10. Factors 3 and 4 have lower loadings and communalities and the taxa do not have relationships with the subarea, season and depth as clear as those in factors 1 and 2. The taxa of factor 3 seem to live somewhat deeper, the regional maximum is still in the northern subarea and the seasonal differences are weak. The taxa of factor 4 have their regional maximum mostly in the western subarea. Because the relations with spatial and temporal environment are weaker within factors 3 and 4, the taxa of these factors possibly share more biotic reciprocal relations. However, it must be noted that the August maximum cannot be seen from this four-factor solution. In a ten-factor solution one factor

revealed several species with a monthly maximum in August (e.g. *Heterotrissocladius marcidus*, *Uncinaiis uncinata* and *Pelosclex ferox*).

A factor analysis was also done using only the soft bottom biomasses, and a five-factor solution showed that Ceratopogonidae, Tanytarsini, Acari and Chironomini-Orthoclaadiinae had the highest loadings in the first factor and particularly indicated the spring maximum. In the second factor the highest loadings were in Chironomini-Orthoclaadiinae, Oligochaeta and Tanypodinae, particularly indicating the regional maximum in the northern subarea. The third factor indicated the influence of depth, showing the concentration of Hirundinea and Nematoda on shallow and Tanypodinae on deep bottoms. The 4th and 5th factors were more difficult to interpret and the loadings and communalities were low.

A factor analysis was performed using the independent variables, viz. station, month and depth values, in addition to the abundance and biomass values, and this factor analysis resulted in a five-factor solution in which the environmental differences seemed to be exposed somewhat better than using only the abundances.

The "correlation associations" method and factor analysis thus produce at least partly corresponding groupings, and these groupings can be enlarged if the limiting correlation coefficient or loading in factor analysis is lowered; the number of factors in factor analysis can also be smaller or greater. It must be also noted that the nonparametric correlations do not wholly correspond with the parametric correlations, as seen earlier. Statistical and numerical procedures, however, naturally give only certain orientation from the functional affinities and differences which can be declared only with intensive autecological studies. However, an extensive study like this can give certain bases or ideas for more intensive studies, e.g. for answering the question of which species ought to be the objects of detailed autecological investigations for declaring the function of the littoral benthic ecosystem.

6.5. Other discussion

The littoral-sublittoral oligochaete fauna of lake Konnevesi partly includes the same species as those which are characteristic (Milbrink 1978) of the profundal depths of some lakes with the same total phosphorus/mean depth ratio (= 1). The Oligochaeta/Chironomidae ratio (Wiederholm 1980) also seems to correspond with that in oligotrophic profundals. However, *Limnodrilus hoffmeisteri* seems to be more abundant in the oligotrophic littoral zone investigated than was

expected (cf. Särkkä 1982).

The chironomid fauna of the lake studied, if compared with data of Saether (1979), corresponds mostly to that in other oligotrophic-mesotrophic lakes. Several species also living in mesohumic or polyhumic lakes were found in Konnevesi, which must be considered oligohumic (water colour < 40 mg Pt/l); these included *Zalutschia zalutschicola*, *Demicryptochironomus vulneratus*, *Heterotanytarsus apicalis* and *Protanypus morio*. The seasonal fluctuation of the chironomids showed mostly greater abundances in May than August (Table 2 and Appendix 1). Only a few species, such as *Monodiamesa bathyphila*, *Heterotrissocladius marcidus*, *Endochironomus intextus* and *Microtendipes chloris*, were more abundant in late summer than in spring. Of these *Monodiamesa* has been observed to emerge in August (Aagaard 1978), *Heterotrissocladius* in June and August (Aagaard 1978) or in August only (Paasivirta 1976) or just after the thaw (Bretschko 1974). Of the other chironomid species, most have been observed to emerge in spring or between the sampling times of the present investigation (Paasivirta 1976, Aagaard 1978), some species even being multivoltine, having several emergence times during the summer; these include *H. apicalis*, *Parakiefferiella bathyphila*, *Psectocladius* species and *Polypedilum pullum*. The emergence times can also be different at different depths, being earlier and more frequent in shallower depths (e.g. Paasivirta 1976). Some species, such as *Z. zalutschicola*, seem to emerge earlier in Konnevesi than in a small lake investigated by Armitage (1974).

It could be expected that the littoral zone, if understood to be equivalent to the illuminated zone of the bottom, extends deeper in oligotrophic lakes than in eutrophic or humic lakes. The bathymetric occurrence of the littoral species could also be expected to extend deeper in oligotrophic than in eutrophic or humic lakes and the profundal species to extend in humic or eutrophic lakes up to shallower depths than in oligotrophic lakes. The depths investigated reached to only 6 m, which means that the entire bathymetric distribution cannot be elucidated. Certain species, however, seem to be more characteristic in sublittoral than in littoral depths; e.g. *Monodiamesa bathyphila*, *Polypedilum pullum* and *Zalutschia zalutschicola*. *Heterotrissocladius marcidus* and *Protanypus morio*, however, seem to have about 3–5 m as the most characteristic depths, *Stempellinella minor* about 4 m, *Stempellinella bausei* 4–6 m and *Paralauterborniella nigrohalteralis* 3–5 m. These results mostly coincide with the observations by Paasivirta (1974, 1976), Aagaard (1978) and Lindegaard (1980), but some species seem,

contrary to expectations, to occur in oligohumic Konnevesi at somewhat shallower depths than in the mesohumic lakes studied by Paasivirta (1974, 1976): e.g. *Heterotanytarsus apicalis* and *Parakiefferiella bathophila*. Some species, in fact, seem to live at greater depths in Konnevesi than in mesohumic lakes: e.g. *Heterotrissocladius marcidus*, *Pseudochironomus prasinatus*, *Stempellina bausei* and *Stempellinella minor*. In the even more oligotrophic Norwegian lake Øvre Heimdalsvatn (Aagaard 1978) some species also seem to live at greater depths than in Konnevesi or deeper than was studied here: *P. morio* at 3–4 m, *H. apicalis*, *H. marcidus* and *Pagastiella orophila* at 1–9 m, *Cladopelma viridula* at 5–9 m, *Cryptochironomus defectus* at 1–9 m and *Endochironomus intextus* at 3–5 m.

Of the other taxa (see Fig. 3), *Asellus aquaticus* is clearly restricted to the upper two metres, and is clearly more abundant on stone bottoms than on soft bottoms, *Pallasea* has its maximum deeper than in the zone investigated, *Ephemera vulgata* has a clear maximum at 3 m and is lacking on stone bottoms, *Caenis horaria* has its maximum at 0.5–3 m, particularly in spring, *Sialis lutaria* (Fig. 3, Table 2) has its maximum somewhat deeper than *S. sordida*, and the *Sialis* species occur only on the soft bottoms.

With regard to the applied significance of the results of the present investigation, it must be noted that very little is generally known about the effects of artificial water level fluctuation on the littoral zoobenthos communities, or about the effects of eutrophication or pollution on the littoral zone. The present study can be considered to represent an investigation on the littoral zoobenthos in an oligotrophic, unregulated, boreal lake in which the natural water level fluctuation is only some dozens of cm during a year. Present knowledge of the effects of regulation mainly concerns the effects of a high degree (several metres) of regulation (Grimås

1961, 1965, Hakkari & Granberg 1977), but in Finland, for example, larger lakes are only "moderately" regulated (water level fluctuation in lake Puulavesi 1 m, Päijänne 1.4 m, Näsijärvi 1.6 m, Vanajavesi 1.8 m, Oulujärvi 2.7 m, and for the largest Finnish lake Saimaa mean regulation of within 0.95 m and maximum regulation of within 1.75 m is planned or already practically pursued (Vesihdistys 1980). The principal effects of moderate regulation are probably the following: drying and freezing destroy littoral benthic communities and fish spawn, the benthic communities move to deeper levels, their species and quantitative composition change and the abundances decrease, and the finer sediment moves and accumulates at deeper levels.

As was shown earlier, the depth zone between about 2 m and 4 m seems to be the most important depth when zoobenthos communities are considered. At these depths, the diversity, number of species and individuals as well as biomass are highest. Furthermore, if the regulated water level does not reach this most important depth, changes must occur. If the changed level extends down to this depth zone, the alteration is probably drastic. Because the littoral zone does not extend as deeply in eutrophic or polyhumic or smaller lakes as in oligotrophic or larger lakes, it is probable that the former are more sensitive to regulation than the latter. Because of this, it is probable that the eutrophication or pollution caused by human influence increases the possible effect of simultaneous water level fluctuation.

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References

- Aagaard, K. 1978: The Chironomidae of the exposed zone of Øvre Heimdalsvatn. — *Holarct. Ecol.* 1: 261–265.
- Alsterberg, G. 1925: Die Nahrungskirkulation einiger Binnenseetypen. — *Arch. Hydrobiol.* 15: 291–338.
- Armitage, P. D. 1968: Some notes on the food of the chironomid larvae of a shallow woodland lake in South Finland. — *Ann. Zool. Fennici* 5: 6–13.
- 1974: Some aspects of the ecology of the Tanypodinae and other less common species of Chironomidae in Lake Kuusjärvi, South Finland. — *Entomol. Tidskr.* 95 Suppl.: 13–17.
- Bretschko, G. 1974: The chironomid fauna of a high-mountain lake (Vorderer Finstertaler See, Tyrol, Austria, 2237 m asl). — *Entomol. Tidskr.* 95 Suppl.: 22–33.
- Connell, J. H. & Orias, E. 1964: The ecological regulation of species diversity. — *Amer. Nat.* 98: 399–414.
- Cummins, K. W. 1973: Trophic relations of aquatic insects. — *Ann. Rev. Entomol.* 18: 183–206.
- Dendy, J. S. 1944: The fate of animals in stream drift when carried into lakes. — *Ecol. Monogr.* 14: 334–357.
- Edwards, R. W. 1975: A strategy for the prediction and detection of effects of pollution on natural communities. — *Schweizerische Zeitschr. Hydrol.* 37: 135–143.
- Eloranta, P. 1976: Species diversity in the phytoplankton of some Finnish lakes. — *Ann. Bot. Fennici* 13: 42–48.
- Granberg, K. 1972: Konneveden kasviplankton ja perustuotanto vuonna 1970. (Summary: Phytoplankton

- and primary production of Lake Konnevesi, Central Finland, in 1970). — Suomen Kalatalous 46: 11-19.
- 1980: Rautalammin reitin tutkimus. (Summary: The effects of fish farming on the water quality of the water course of Rautalampi, Central Finland.) — Rep. Hydrobiol. Res. Centre 110: 1-71.
- Grimås, U. 1961: The bottom fauna of natural and impounded lakes in northern Sweden. — Rep. Inst. Freshwater Res. Drottningholm 42: 183-237.
- 1965: Effects of impoundment on the bottom fauna of high mountain lakes. — Acta Univ. Upsaliensis 51: 1-24.
- Hairton, N. G., Smith, F. E. & Slobodkin, L. B. 1960: Community structure, population control, and competition. — Amer. Nat. 94: 421-425.
- Hakkari, L. & Granberg, K. 1977: Säännöstelyn vaikutuksista eräiden Kainuun järvien limnologiasta. (Summary: On the effects of regulation on the limnology, fish stocks and the nutrition of fishes of some lakes in the water district of Kainuu, North-Eastern Finland.) — Rep. Hydrobiol. Res. Centre 90: 1-115.
- Howmiller, R. P. 1972: Effects of preservatives on weights of some common macrobenthic invertebrates. — Trans. Amer. Fish. Soc. 101: 743-746.
- Hurlbert, S. H. 1978: The measurement of niche overlap and some relatives. — Ecology 59: 67-77.
- Jónasson, P. M. 1972: Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. — Oikos, Suppl. 14: 1-148.
- Kajak, Z. 1980: Role of invertebrate predators (mainly *Procladius* sp.) in benthos. — Chironomidae, ecology, systematics, cytology and physiology. — Proc. 7th Internat. Symposium on Chironomidae, Dublin, August 1979: 339-348.
- Kajak, Z. & Dusoge, K. 1975: Macrobenthos of Mikolajskie Lake. — Ekol. Polska 23: 437-457.
- Kozhov, M. 1963: Lake Baikal and its life. — 344 pp., Dr. W. Junk Publ., The Hague.
- Lappalainen, A. & Kangas, P. 1975: Littoral benthos of the Northern Baltic Sea II. Interrelationships of wet, dry and ash-free dry weights of macrofauna in the Tvärminne area. — Int. Rev. Ges. Hydrobiol. 60: 297-312.
- Lindegaard, C. 1980: Bathymetric distribution of Chironomidae (Diptera) in the oligotrophic Lake Thingvallvatn, Iceland. — Chironomidae, ecology, systematics, cytology and physiology. — Proc. 7th Internat. Symposium on Chironomidae, Dublin, August 1979: 225-232.
- Loden, M. S. 1974: Predation by chironomid (Diptera) larvae on oligochaetes. — Limnol. Oceanogr. 19: 156-159.
- Lundkvist, H. 1978: A technique for determining individual fresh weights of live small animals, with special reference to Enchytraeidae. — Oecologia 35: 365-367.
- MacArthur, R. H. 1965: Patterns of species diversity. — Biol. Rev. 40: 510-533.
- MacArthur, R. H. R. & MacArthur, J. W. 1961: On bird species diversity. — Ecology 42: 594-598.
- Margalef, R. 1958: Temporal succession and spatial heterogeneity in natural phytoplankton. — In: E. Buzzati-Traverso (ed.), Perspectives in marine biology, Univ. California Press, Berkeley, pp. 323-349.
- 1963: Successions of populations. — Adv. Frontiers of Plant Sci., Inst. Adv. Sci. & Culture, New Delhi, pp. 137-188.
- 1968: Perspectives in ecological theory. — 111 pp. Univ. Chicago Press, London.
- Merritt, R. W. & Cummins, K. W. 1978: An introduction to the aquatic insects of North America. — 441 pp. Kendall/Hunt, Dubuque.
- Milbrink, G. 1978: Indicator communities of oligochaetes in Scandinavian lakes. — Verh. Internat. Verein. Limnol. 20: 2406-2411.
- Mölsä, H. 1980: Säkylän Pyhäjärven makroskooppisen pohjaeläimistön koostumus, biomassa ja tuotanto. — Manuscr., Univ. Turku, Dept. Biol., 79 pp.
- Morgan, N. C. 1980: Secondary production. — In: LeCren, E. D. & Lowe-McConnell, R. H. (eds.), The functioning of freshwater ecosystems. I.B.P. 22, pp. 247-340.
- Moss, B. 1973: Diversity in fresh-water phytoplankton. — Amer. Midland. Nat. 90: 341-355.
- Paasivirta, L. 1974: Abundance and production of the larval Chironomidae in the profundal of a deep, oligotrophic lake in Southern Finland. — Entomol. Tidskr. 95 Suppl.: 188-194.
- 1976: Suomunjärven (Lieksa) pohjaeläimistön koostumus, biomassa ja tuotanto. (Summary: The biomass, production and communities of the zoobenthos in the Lake Suomunjärvi, eastern Finland.) — Univ. Joensuu, Karelian Inst. Publ. 18: 1-17.
- Paine, R. T. 1966: Food web complexity and species diversity. — Amer. Nat. 100: 65-75.
- Pieczynska, E. 1976: Some regularities in the functioning of lake littoral. — In: E. Pieczynska (ed.), Selected problems of lake littoral ecology 211-228, Warszawa.
- Ruggiu, D. & Saraceni, C. 1972: A statistical study of the distribution and abundance of the bottom fauna of a lake undergoing accelerated eutrophication (Lake Mergozzo, N. Italy). — Mem. Ist. Ital. Idrobiol. 29: 169-187.
- Saether, O. 1979: Chironomid communities as water quality indicators. — Holart. Ecol. 2: 65-74.
- Sanders, H. L. 1968: Marine benthic diversity: a comparative study. — Amer. Nat. 102: 243-282.
- Särkkä, J. 1972: The bottom macrofauna of the oligotrophic Lake Konnevesi, Finland. — Ann. Zool. Fennici 9: 141-146.
- 1979: The zoobenthos of Lake Päijänne and its relations to some environmental factors. — Acta Zool. Fennica 160: 1-46.
- 1982: On the ecology of littoral Oligochaeta of an oligotrophic Finnish lake. — Holart. Ecol. 5: 396-404.
- Sarvala, J., Ilmavirta, V., Paasivirta, L. & Salonen, K. 1981: The ecosystem of the oligotrophic Lake Päijärvi 3. Secondary production and an ecological energy budget of the lake. — Verh. Internat. Verein. Limnol. 21: 454-459.
- Shafi, M. I. & Yarranton, G. A. 1973: Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. — Ecology 54: 897-902.
- Simpson, G. G. 1964: Species density of North American recent mammals. — Syst. Zool. 13: 57-73.
- Titmus, G. & Badcock, R. M. 1981: Distribution and feeding of larval Chironomidae in a gravel-pit lake. — Freshwater Biol. 11: 263-271.
- Toivonen, J., Auvinen, H. & Valkeajärvi, P. 1982: Fish stock assessments in Lake Konnevesi. — Hydrobiologia 86: 219-222.
- Tuunainen, P. 1972: Konneveden yleiskuvaus sekä veden fysikaaliset ja kemialliset ominaisuudet. (Summary: On the hydrological, physical and chemical conditions of Lake Konnevesi, Central Finland.) — Suomen Kalatalous 46: 3-10.
- Vaarama, A. 1961: Lake Finland and its lake types. — Arch. Soc. 'Vanamo' 16: suppl.: 33-38.
- Vesihdistys 1980: Säännöstely ja sen ympäristövaikutukset (Water Association, Finland: Water level regulation and its environmental effects). — 112 pp. Helsinki.
- Wiederholm, T. 1980: Use of benthos in lake monitoring. — J. Water Pollut. Control Feder. 52: 537-547.
- Wiederholm, T. & Eriksson, L. 1977: Effects of alcohol-preservation on the weight of some benthic invertebrates. — Zoon 5: 29-31.

Appendix 1. The taxa found in the soft and stony bottom macrofauna samples and the frequencies of their occurrence in August 1975 and May 1976.

	Soft bottoms		Stony bottoms			Soft bottoms		Stony bottoms	
	Aug.	May	Aug.	May		Aug.	May	Aug.	May
Porifera									
<i>Ephydatia mülleri</i> (Lieberkühn)	+		-	-	<i>Athripsodes aterrimus</i> (Stephens)	2	1	1	2
<i>Spongilla lacustris</i> (L.)	+	+	+	+	<i>A. cinereus</i> (Curtis)	1	1	1	6
Turbellaria	-	-	2	-	<i>A. excisus</i> Mort. (?)	-	-	-	1
Nematoda	24	31	1	1	<i>A. fulvus</i> Rambur (?)	-	-	1	-
Oligochaeta					<i>Ceraclea annulicornis</i> (Stephens)	-	-	1	1
<i>Stylodrilus heringianus</i> Claparède	12	5	2	-	<i>Cyrmus flavidus</i> McLachlan	4	3	3	10
<i>Lumbriculus variegatus</i> (Müller)	1	3	-	-	<i>C. insolutus</i> McLachlan	-	1	-	-
<i>Arcteonais lomondi</i> (Martin)	3	-	-	-	<i>C. trimaculatus</i> (Curtis)	-	6	1	12
<i>Dero digitata</i> (Müller)	-	1	-	-	<i>Ecnomus tenellus</i> (Rambur)	1	-	7	6
<i>Homochaeta</i> spp.	-	-	-	-	<i>Holocentropus dubius</i> (Rambur)	-	3	-	-
<i>Nais barbata</i> (Müller)	-	-	2	1	<i>Hydropsyche contubernalis</i> McLachlan	-	-	3	-
<i>N. pseudobuta</i> Piguet	1	1	1	2	<i>Hydroptila femoralis</i> (Eaton)	-	2	-	-
<i>Ripistia parvita</i> (Schmidt)	1	-	-	1	<i>Lepidostoma hirtum</i> Fabr.	-	-	-	1
<i>Specaria josinae</i> Vejdovsky	1	-	-	1	<i>Leptocerus</i> sp.	-	-	-	1
<i>Stylaria lacustris</i> (L.)	8	-	1	1	<i>Molanna angustata</i> Curtis	3	1	-	-
<i>Uncinaxis uncinata</i> (Ørsted)	8	2	-	-	<i>M. submarginalis</i> McLachlan	1	-	-	-
<i>Aulodrilus limnobius</i> Bretscher	11	1	-	-	<i>Mystacides azurea</i> (L.)	-	2	-	-
<i>A. pluriseta</i> (Piguet)	1	-	-	-	<i>Oecetis lacustris</i> (Pictet)	2	3	3	2
<i>Limnodrilus hoffmeisteri</i> Claparède	39	32	-	-	<i>Oecetis</i> sp.	-	-	-	5
<i>L. udekemianus</i> Claparède	2	1	-	-	<i>Oxyethira flavicornis</i> (Pictet)	-	5	-	1
<i>Pelosciolex ferox</i> (Eisen)	38	38	1	1	Phryganeidae	-	1	-	-
<i>Psammoryctides albicola</i> Michaelsen	4	1	-	-	<i>Polycentropus flavomaculatus</i> (Pictet)	-	1	3	8
<i>P. barbatus</i> (Grube)	8	18	1	-	<i>Sericostoma personatum</i> Spence	-	-	1	1
<i>Tubifex tubifex</i> (Müller)	5	5	-	-	<i>Tinodes waeneri</i> (L.)	1	-	1	10
Enchytraeidae	2	4	1	3					
Hirudinea					Diptera				
<i>Erbobdella octoculata</i> (L.)	-	3	4	5	Chironomidae				
<i>Glossiphonia complanata</i> (L.)	1	-	1	3	Indetermined pupae & imagines	18	32	14	10
<i>G. heteroclita</i> (L.)	-	-	-	1	Tanypodinae				
<i>Helobdella stagnalis</i> (L.)	3	4	3	5	<i>Ablabesmyia</i> spp.	-	-	11	11
<i>Piscicola geometra</i> (L.)	-	-	2	-	<i>Procladius</i> spp.	51	50	3	2
Ostracoda					Others	11	36	2	1
<i>Candona candida</i> (Müller)	5	3	-	-	Diametinae				
Copepoda					<i>Pothisia gædi</i> (Meigen)	-	-	-	1
<i>Cyclops</i> spp.	1	5	-	-	<i>Protanypus morio</i> (Zetterstedt)	2	3	-	-
<i>Acanthocyclops vernalis</i> (Fischer)	1	4	-	-	Prodiamesinae				
<i>Macrocyclus albidus</i> (Jurine)	-	2	-	-	<i>Monodiamesa bathyphila</i> (Kieffer)	13	7	-	-
<i>Megacyclops gigas</i> (Claus.)	-	4	-	-	Orthocladiinae				
<i>M. viridis</i> (Jurine)	-	1	-	-	<i>Corynoneura celeripes</i> Winnertz	-	-	-	1
Cladocera					<i>Corynoneura</i> sp.	-	-	4	2
<i>Alona affinis</i> Leydig	3	1	3	1	<i>Cricotopus sylvestris</i> type	-	4	1	7
<i>A. quadrangularis</i> (Müller)	-	-	1	-	<i>Epicocladus ephemeræ</i> (Kieffer)	-	2	-	-
<i>Camptocercus rectirostris</i> Schödler	-	-	-	1	<i>Heterotanytarsus apicalis</i> (Kieffer)	18	45	2	-
<i>Euryceus lamellatus</i> (Müller)	5	-	3	-	<i>Heterotrissocladius grimshawi</i> (Edwards)	-	1	-	-
<i>Sida crystallina</i> (Müller)	2	-	3	-	<i>H. marcidus</i> (Walker)	17	4	2	-
Isopoda					<i>H. subpilosus</i> (Kieffer)	-	1	-	-
<i>Asellus aquaticus</i> (L.)	5	5	12	12	<i>Orthocladus</i> spp.	-	3	-	-
Amphipoda					<i>Paracladius</i> spp.	1	-	-	-
<i>Pallasea quadrispinosa</i> Sars	4	8	-	-	<i>Parakiefferiella bathophila</i> (Kieffer)	-	13	3	4
<i>Pontoporeia affinis</i> Lindström	-	2	-	-	<i>P. smolandica</i> (Brundin)	6	28	-	-
Insecta, larvae					<i>Psectocladus medius</i> type	17	14	9	9
Plecoptera					<i>P. psilopterus</i> type	13	24	7	5
<i>Diura bicaudata</i> (L.)	-	-	3	-	<i>P. septentrionalis</i> type	2	4	2	2
Ephemeroptera					<i>P. sordidus</i> type	-	1	-	-
<i>Caenis horaria</i> (L.)	4	11	6	7	<i>Thienemanniella</i> spp.	-	-	4	1
<i>C. rivulorum</i> Eaton	1	-	-	-	<i>Zalutschia zalutschicola</i> Lipina	5	16	-	-
<i>Centroptilum luteolum</i> (Müller)	-	1	-	2	Chironomi				
<i>Ephemerula vulgata</i> L.	27	34	-	-	<i>Cladopelma viridula</i> (L.)	2	30	-	-
<i>Heptagenia dalecarlica</i> Bgtss.	-	-	2	1	<i>Cryptochironomus defectus</i> type	2	6	-	-
<i>Paraleptophlebia</i> sp.	-	-	-	1	<i>Demicyptochironomus vulneratus</i> (Zetterst.)	5	17	1	1
Siphonuridae	-	-	1	1	<i>Endochironomus intextus</i> (Walker)	14	9	1	-
Corixidae	1	9	-	-	<i>E. tendens</i> type	-	-	1	-
Megaloptera					<i>Glyptotendipes gripekoveni</i> Kieffer	-	1	4	5
<i>Stalis lutaria</i> L.	9	16	-	-	<i>Lauterborniella agrayloides</i> (Kieffer)	-	1	-	-
<i>S. sordida</i> Klingstedt	5	-	-	-	<i>Lenzia</i> (<i>Pentapedium</i>) type	2	1	-	-
<i>S. morio</i> Klingstedt	1	-	-	-	<i>Limnochironomus pulsus</i> (Walker)	8	32	9	10
Odonata					<i>Microtendipes chloris</i> type	12	7	5	2
<i>Enallagma cyathigerum</i> Charp.	-	1	-	-	<i>Pagastiella orophila</i> (Edwards)	18	46	-	2
Trichoptera					<i>Parachironomus arcuatus</i> (Goetghebuer)	-	1	-	-
<i>Agraylea multipunctata</i> Curtis	-	-	3	3	<i>Paraclopedelma camptolabis</i> (Kieffer)	10	9	1	-
<i>A. pallidula</i> McLachlan	-	-	-	1					
<i>Agrypnia pagetana</i> Curtis	-	-	1	1					
<i>Anabolia</i> sp.	-	-	-	1					

	Soft bottoms		Stony bottoms			Soft bottoms		Stony bottoms	
	Aug.	May	Aug.	May		Aug.	May	Aug.	May
<i>Paralauterborniella nigrohalteralis</i> (Mall.)	3	-	-	-	<i>Frontipoda musculus</i> (Müller)	1	3	-	1
<i>Polypedium pullum</i> (Zetterstedt)	6	40	-	3	<i>Hydrodroma despicens</i> (Müller)	-	11	-	-
<i>P. laetum</i> type	-	-	-	7	<i>Hygrobates longipalpis</i> Herm.	-	14	-	-
<i>Pseudochironomus prasinatus</i> (Staecker)	33	27	4	2	<i>Hygrobates longipalpis</i> Herm.	-	4	-	-
<i>Stenochironomus</i> sp.	-	-	1	-	<i>Lebertia</i> spp.	-	2	-	-
Tanytarsini	-	-	-	-	<i>Limnesia koenikei</i> Piers.	-	2	-	-
<i>Cladotanytarsus</i> spp.	-	-	9	1	<i>L. maculata</i> (Müller)	-	1	-	-
<i>Constempellina brevicosta</i> (Edwards)	1	14	-	-	<i>L. undulata</i> (Müller)	-	3	-	-
<i>Corynocera ambigua</i> Zetterstedt	-	1	-	-	<i>Limnochares aquatica</i> (L.)	-	3	-	-
<i>Paratanytarsus</i> spp.	-	-	1	6	<i>Mideopsis orbicularis</i> (Müller)	-	3	-	-
<i>Stempellina bausei</i> (Kieffer)	-	5	-	-	<i>Neumania callosa</i> (Koen.)	-	1	-	-
<i>Stempellinella minor</i> (Edwards)	1	-	-	-	<i>Oxus setosus</i> (Koen.)	-	3	-	-
<i>Tanytarsus</i> s. lat. sp. 1—sp. 7	-	-	1	8	<i>Piona pusilla</i> (Neum.)	-	2	-	-
<i>Tanytarsus</i> s. lat., indetermined	45	49	-	-	<i>P. longipalpis</i> (Krend.)	-	1	-	-
<i>Thienemanniola</i> sp.	-	-	-	1	Acari, total	12	38	3	10
Ceratopogonidae	-	-	-	-	Bryozoa	-	-	-	-
<i>Bezzia-Palpomyia</i> type	4	28	1	3	<i>Cristatella mucedo</i> Cuvier	+	+	+	+
<i>Culicoides</i> type	3	19	-	3	<i>Paludicella articulata</i> Ehrenberg	+	+	+	-
Tabanidae	2	8	-	2	<i>Plumatella</i> spp.	+	+	+	-
Syrphidae	-	-	-	1	Pelecypoda	-	-	-	-
Lepidoptera	-	-	-	-	<i>Sphaerium corneum</i> (L.)	1	6	-	1
<i>Nymphula nymphaeata</i> L.	-	1	-	-	<i>Pisidium amnicum</i> (Müller)	3	3	-	-
Coleoptera	-	-	-	-	<i>P. casertanum</i> (Poli)	19	21	-	-
<i>Oulimnius tuberculatus</i>	-	-	9	11	<i>P. conventus</i> Clessin	-	1	-	-
— " — imagines	-	-	1	4	<i>P. henslowianum</i> Sheppard	5	14	-	-
Dytiscidae	-	-	1	-	<i>P. hibernicum</i> Westerlund	3	5	-	-
Haliplidae	-	-	1	-	<i>P. lilljeborgi</i> Clessin	18	22	-	-
Helodidae (Scirtes sp.)	-	-	1	-	<i>P. obtusale</i> (Lamarck)	-	3	-	-
Hydrophilidae	-	-	1	1	<i>P. subtruncatum</i> Malm	11	9	-	-
Acari*	-	-	-	-	<i>Pisidium</i> , total	44	41	1	-
<i>Arrenurus albator</i> (Müller)	-	2	-	-	Gastropoda	-	-	-	-
<i>A. nobilis</i> Neum.	-	1	-	-	<i>Bithynia tentaculata</i> (L.)	-	-	1	-
<i>A. stjoerdalensis</i> Thor	-	1	-	-	<i>Lymnaea peregra</i> (Müller)	-	-	3	1
<i>Brachypoda versicolor</i> (Müller)	-	3	-	-	<i>Myxas glutinosa</i> (Müller)	-	-	1	-
<i>Forelia liliacea</i> (Müller)	-	5	-	-	<i>Valvata cristata</i> Müller	-	-	2	1
					<i>V. macrostoma</i> Mörch	16	12	3	-
					Total	51,	51	14	15

* Acari were determined only from soft bottom May material.

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