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ZOOBENTHOS OF SOME ESTONIAN BROWN-WATER LAKES

Abstract. Fifteen small dystrophic and dyseutrophic lakes were studied in 1966—1991, two of them seasonally, five repeatedly after long intervals. An impoverished bottom fauna was found which consisted altogether of 136 taxa, mainly various insects, including a few species specific to this kind of lakes. Molluscs and worms were scantily represented. The profundal zone was usually very poor in animals or azoic. The average abundance and biomass of zoobenthos were very low in closed bog lakes but increased gradually together with the trophic condition, up to a very high level in one dyseutrophic lake. A tendency towards the increase of biomass during several decades is evident.

Introduction

There are about 1,150 lakes in Estonia. Since 1951, some 500 of them have been investigated hydrobiologically by the Institute of Zoology and Botany, about 300 lakes also with respect to the bottom fauna. A considerable part of the lakes are humified with allochtonous substances from bogs and forests. They belong to the dystrophic type sensu Naumann (1931). A detailed limnological typology for Estonian lakes was elaborated by Mäemets (1974) on the basis of the accumulation type, biogeochemical circulation and water circulation. A guide for the identification of these lake types was given by Mäemets and Mäemets (Мяэметс, Мяэметс, 1991). According to this, Estonian humified brown-water lakes are divided into semidystrophic (soft-water, with a moderate accumulation of humic substances), dystrophic (strongly humified), and dyseutrophic types (accumulating simultaneously mineral, humic and biogenic substances), each with several subtypes. As the bottom invertebrates of Estonian semidystrophic lakes studied during the last decades were already treated elsewhere (Тимм et al., 1991), only 15 lakes belonging to dystrophic and dyseutrophic types are included in this paper. Their main limnological characteristics are presented in Table 1, their geographic location in the Figure.

The lakes under consideration are small (1.2—78.7 ha, with the maximum depth 2.4—18 m), with strongly coloured (reddish to yellowish brown) water, mostly poor in macrovegetation. Their common hydrochemical features are low total alkalinity (usually <30 mg/l HCO_3', often zero) and pH (<7) combined with high dichromate oxidability (usually >35 mg/l O) due to allochtonous humic substances. Profundal sediments are represented by brown dy, sometimes with a blackish surface layer, while various peaty, sandy and muddy bottoms can occur in the littoral. The water can be rich in biogenic substances but eutrophication phenomena are less apparent than in clear-water lakes.

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Four of the lakes are shallow and polymictic-dystrophic, situated in or near *Sphagnum* bogs (limnological subtype D^3 by Mäemets, 1974). Seven more lakes belong to strongly stratified subtype D^2; they are located on sandy soils and accumulate humified water from pine forests. Finally, four dyseutrophic lakes represent the soft-water subtype DE^1 which differs from D^2 only by a somewhat higher concentration of mineral compounds (Table 1).

Material and methods

The material was collected during limnological expeditions of the Institute of Zoology and Botany in 1966—1991. In case there exists comparable material from an earlier period (1953—1963), it is considered after Mäemets (1968). Quantitative zoobenthos samples were taken mostly in summer, in lakes Pakasjärv and Nohipalu Mustjärv also seasonally. One to five sampling spots were chosen at the characteristic depths and

Table 1

Some limnological features of the lakes studied, after Mäemets (1968), Kask (1964), Mäemets (1974), and unpublished data

Lake	Surface area, ha	Maximal depth, m	Date	pH	Dichromate oxydability, O mg/l	Total alkalinity, mg/l	Total P, mg/m³	Total N, mg/m³	Limnological subtype
Loosalu	34.1	5.0	2.7.56	4.0	50.7	0			D^3
			9.8.77	<6	34	0			
Pakasjärv	17.8	2.4	6.7.72	4.55	48.6	0			D^3
Nigula	17.9	3.1	6.8.54	<6	38.1	6.1			D^3
			17.7.83	6.4	37	9.2			
Meelva	78.7	3.2	5.9.58	5.2	46.4	0			D^3
			10.7.91	6	74.5	12.2	119	1250	
Viroste	10.4	10.0	30.6.63	4.7	75.2	0			D^2
			10.7.91	~6	100	12.2	74	2230	
Holvandi Kivijärv	5.9	18	6.7.83	<6	72	0			D^2
			10.7.91	6.25	83.6	12.2	49	1500	
Pikamäe	6.7	11.7	5.7.83	<6	80	12.2			D^2
			10.7.91	5.6	100	12.2	172	1260	
Partsi Saarjärv	11.8	11.9	5.7.83	<6	85	7.3			D^2
			11.7.91	5.5	111	6.1	42	2050	
Koolma	6.1	6.0	5.7.83	<6	53	0			D^2
Nohipalu Mustjärv	21.9	8.9	8.7.83	<6	80	3.6			D^2
			12.7.90	4.1	110	0	21	3260	
Suur-Kaksjärv	2.2	4.0	27.6.66	5.8	80	0			D^2
Piigandi Mustjärv	14.8	14.3	23.7.73	6.0	47	0			DE^1
			8.7.91	6.9	65.4	6.1	47	1620	
Orava Mustjärv	5.1	9.2	25.6.54	<6	65.4	0			DE^1
			9.7.83	6.8	76	24			
Orava Kõverajärv	11.1	15.0	9.7.83	6.6	39	7.3			DE^1
Neeruti Sinijärv	1.2	4.8	29.6.88	6.0	60	36	70	947	DE^1

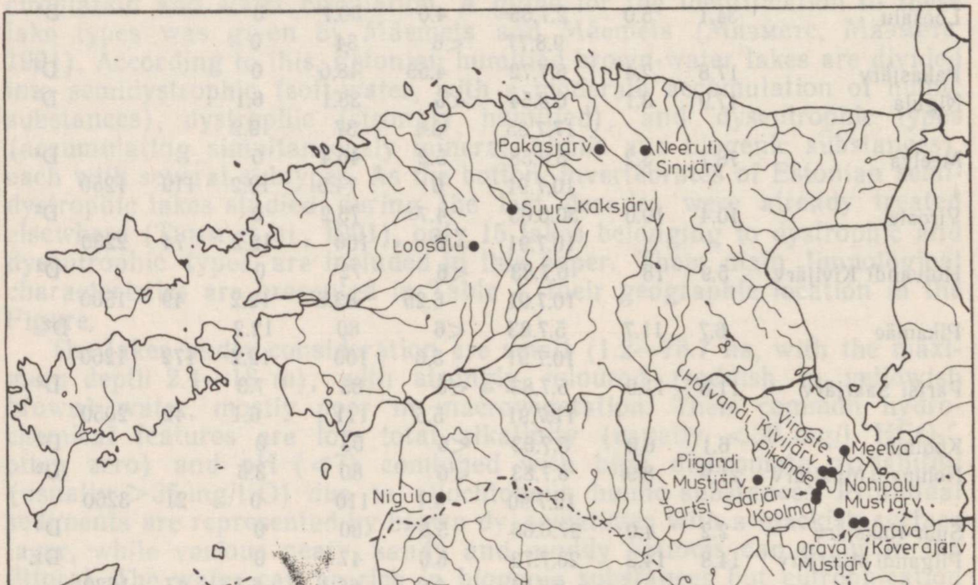
vegetation zones of every lake. Usually, three hauls with the Borutski or Zabolotski bottom grab (modifications of the Ekman grab, 225 cm^2) were taken at every spot; in 1966 there was only one haul. The samples were sieved on a gauze net (14 threads per cm), macroscopic bottom invertebrates were picked out alive and preserved in 70% ethanol. Their wet weight was established on a torsion balance with 1 mg precision. Altogether 62 quantitative samples (most of them triple) were collected and treated, besides several qualitative ones.

The *Chironomidae* larvae were identified mostly by K. Kangur (by Õ. Tõlp in 1966—1972), *Oligochaeta* and *Hirudinea* by T. Timm, *Mollusca* by V. Timm, *Hydracarina* by I. Lissenko, *Ephemeroptera* and *Odonata* by E. Remm, and *Trichoptera* by O. Kachalova.

Results

Composition of the fauna. 131 taxa were identified, among them 58 species and larval forms of *Chironomidae*, 24 species of *Oligochaeta*, 12 of *Mollusca*, and 37 species and groups of other animals (Table 2).

Chironomidae were common in all the lakes studied. The number of taxa met with in different lakes fluctuated from 3 (Suur-Kaksjärv) to 19 (Nohipalu Mustjärv), depending also on the number of samples. *Procladius choreus* was the most widely distributed species (found in 12 lakes), followed by *Sergentia* gr. *longiventris*, *Endochironomus albipennis* (both in 8 lakes), and *Microtendipes pedellus* (7). *Sergentia longiventris* (specific to the profundal of polyhumose lakes after Brundin, 1949) and sometimes *Procladius* spp. were frequent but not numerous in the profundal, either. *Chironomus solitus* was abundant in the profundal of Lake Koolma, various forms of *Procladius* and *Chironomus* were in the unstratified Lake Pakasjärv. *Chironomidae* were lacking in the anaerobic profundal of several strongly stratified lakes (Table 4). The littoral fauna



Location of the lakes studied.

of *Chironomidae* was more diverse; sometimes a mass development of *Tribelos intextus* (in Orava Kõverajärv, Koolma, and Meelva) or *Chironomus* spp. (Neeruti Sinijärv) occurred. *Zalutschia zalutschicola*, specific to brown-water lakes, was found in four lakes only (Table 2); it was numerous in the bog lake Loosalu but lacking in the similar Lake Pakasjärv. The same species was common in Lake Nohipalu Mustjärv in 1971—1972 but lacking in 1983.

Oligochaeta occurred in the samples of seven lakes only. In Lake Meelva (after repeated qualitative collecting) 21 species were found, in the other lakes only 2—6. *Limnodrilus hoffmeisteri* (found in six lakes) and *Lumbriculus variegatus* (in four) were most frequent. The profundal of these lakes was almost devoid of *Oligochaeta*, except Lake Piigandi Mustjärv which maintained a regular profundal population of *Potamothrix hammoniensis*. In the littoral of Lake Meelva a very rare arctoalpine species *Tatriella slovenica* was observed up to 1969 but not later on. Another oxyphilous species *Stylodrilus heringianus* was met with in the littoral of three lakes.

Mollusca seem to be entirely lacking in most of the lakes studied. In five lakes a few *Pisidiidae* were found (most frequently *Euglesa nitida*), in Lake Orava Mustjärv also *Sphaerium corneum* and two species of *Planorbidae* snails. *Pisidiidae* were abundant only in lakes Nigula and Pikamäe, while in the former even the profundal supports numerous *Euglesa nitida* and *E. milium*.

Among the other animals, the larvae of the ghost midge *Chaoborus flavicans* were widely distributed and often dominating in the poorly oxygenated or anaerobic profundal. They were found in 14 lakes, except the shallow, well-mixed Lake Pakasjärv. *Asellus aquaticus* (in 10 lakes), larvae of *Sialis* sp. (10), various *Hydracarina* (11), *Trichoptera* (10), and *Ceratopogonidae* (9) occurred rather frequently but mostly in the littoral only.

Abundance and biomass. The average midsummer abundance and biomass fluctuated from 296 ind./m^2 and 0.46 g/m^2 in Lake Pakasjärv to 7,955 ind./m^2 and 34.88 g/m^2 in Lake Neeruti Sinijärv, hence 27 and 76×, respectively. Usually *Chironomidae* dominated, sometimes *Chaoborus*, rarely other groups (Table 3).

Shallow dystrophic bog lakes with peaty shores devoid of any macrovegetation zone (Loosalu and Pakasjärv) were the poorest: on the average 359 ind./m^2, 0.98 g/m^2. *Chironomidae* formed the bulk of zoobenthos. Neither *Oligochaeta* nor *Mollusca* were found. Lakes Nigula and Meelva belong to the same limnological subtype D^3 but lie on the bog edge, have stretches of sandy littoral and somewhat harder water. Their zoobenthos is more diverse, with the average abundance and biomass (978 ind./m^2, 3.62 g/m^2) about three times higher than in genuine bog lakes.

The strongly stratified dystrophic lakes on sandy soil (subtype D^2: Viroste, Holvandi Kivijärv, Pikamäe, Partsi Saarjärv, Koolma, Nohipalu Mustjärv, Suur-Kaksjärv) appeared to be rather variable, with a tenfold difference in the abundance and biomass. However, the average parameters of the whole set (1223 ind./m^2, 3.54 g/m^2) were comparable with those of lakes Nigula and Meelva, while the lowest ones (415 ind./m^2 in Lake Nohipalu Mustjärv, and 1.11 g/m^2 in Lake Partsi Saarjärv) were rather close to those of true bog lakes. The faunal composition appeared poor, too.

The three deeper dyseutrophic lakes (DE^1) Piigandi Mustjärv, Orava Mustjärv and Orava Kõverajärv were, in their turn, twice as rich as the previous group: on the average 2,214 ind./m^2 and 6.03 g/m^2. All main animal groups were represented here.

List of the taxa and their finding-places in the lakes studied

Abbreviations: HK — Holvandi Kivijärv, K — Koolma, L — Loosalu, M — Meelva, N — Nigula, NM — Nohipalu Mustjärv, NS — Neeruti Sinijärv, OK — Orava Kõverajärv, OM — Orava Mustjärv, Pa — Pakasjärv, Pi — Pikamäe, PM — Piigandi Mustjärv, PS — Partsi Saarjärv, SK — Suur-Kaksjärv, V — Viroste

Chironomidae:

Ablabesmyia annulata (Say) — PM
A. longistyla Fittkau — OK
A. gr. *monilis* L. — M, NM, SK
A. phatta (Eggert) — M
Ablabesmyia sp. — NM
Larsia curticalcar (Kieffer) — NM, Pa
Procladius choreus (Meigen) — HK, K, L, M, N, NS, OK, OM, Pi, PM, PS, V
P. ferrugineus (Kieffer) — HK, L, M, N, OK
P. nigriventris (Kieffer) — M, PM
Procladius sp. — NM, Pa, PM, SK
Corynoneura scutellata Winn. — M
Nanocladius bicolor (Zett.) — PM
Psectrocladius gr. *psilopterus* Kieffer — NM
P. simulans (Johan.) — NM, OK, Pi
Zalutschia zalutschicola Lipina — L, N, NM, PM
Allochironomus Kieffer? — NM, Pa
Camptochironomus pallidivittatus (Malloch) — OM, V
Chaetolabis macani Freeman — L
Chironomus annularius sensu Keyl & Keyl, 1959 — PM
C. cingulatus Meigen — NS
C. commutatus Keyl complex — NS, PM
C. pilicornis (Fabr.) — K, OM, V
C. plumosus (L.) — N, NM, OM, Pa
C. pseudothummi Strenzke complex — NS
C. solitus Lin. et Erb. — K, M, N, V
Chironomus sp. — L, NM, Pa
Cladopelma viridula (L.) — M, OK, Pa
Demicryptochironomus vulneratus (Zett.) — M, OK
Dicrotendipes gr. *nervosus* Staeger — SK
D. pulsus (Walker) — OK
D. tritomus (Kieffer) — PS
Dicrotendipes sp. — K
Einfeldia sp. — NS
Endochironomus albipennis (Meigen) — M, N, NM, NS, OK, OM, Pi, PM
E. impar (Walker) — NM
Endochironomus sp. — M, NM
Glyptotendipes glaucus (Meigen) — L, NS, OK, PM
G. gripekoveni (Kieffer) — NM, NS, OM, PM
G. paripes (Edw.) — N
Microtendipes pedellus (De Geer) — M, NM, OK, OM, Pi, PM, PS
Pagastiella orophila (Edw.) — Pa
Parachironomus arcuatus (Goetgh.) — PM
Pentapedilum sordens (v. d. Wulp) — PM
Phaenopsectra sp. — K
Polypedilum bicrenatum Kieffer — M, N
P. gr. *convictum* Walker — NM
Pseudochironomus prasinatus (Staeger) — N, NM, OK

Sergentia gr. *longiventris* Kieffer — HK, L, M, OK, OM, Pi, PS, V
Stenochironomus sp. — NM
Tribelos intextus (Walker) — HK, K, M, OK, PM
Tribelos sp. — OM
Cladotanytarsus gr. *mancus* Walker — N, PM
Micropsectra gr. *praecox* Meigen — Pa

Tanytarsus excavatus Edw. + *T. nemorosus* Edw. complex — OM, PM
T. gregarius Kieffer — NM, Pa
T. holochlorus Edw. + *T. occultus* Brundin + *T. volgensis* Miseiko complex — HK, M, N, OK
T. medius Reiss et Fittkau — HK, OK, OM, PS
T. verralli Goetgh. — HK, OK, PS

Oligochaeta:

Stylaria lacustris (L.) — M, OK, PM
Ripistes parasita (Schmidt) — M, OM
Vejdovskyella comata (Vejdovský) — M, OM
Slavina appendiculata (d'Udekem) — M
Nais communis Piguet — M
N. variabilis Piguet — N, OM
Uncinais uncinata (Oersted) — M
Chaetogaster diastrophus (Gruith.) — M, SK
C. langi Bretscher — M
Pristina aequiseta f. *foreli* (Piguet) — M
P. rosea (Piguet) — M
Tubifex tubifex (Müller) — M, Pi
T. ignotus (Štolc) — M, OM, SK
Spirosperma ferox Eisen — M, OK
Limnodrilus hoffmeisteri (Clap.) — M, N, OK, OM, Pi, PM
L. udekemianus Clap. — M
Potamothrix hammoniensis (Mich.) — PM
Psammoryctides barbatus (Grube) — PM
Cernosvitoviella sp. — M
Cognettia sp. — M
Marionina riparia Bretscher — M
Lumbriculus variegatus (Müller) — M, N, OK, PM
Stylodrilus heringianus Clap. — M, N, OM
Tatriella slovenica Hrabě — M

Mollusca:

Euglesa fedderseni (West.) — OM
E. milium (Held) — N, OM
E. nitida (Jenyns) — N, OK, OM, Pi
E. pulchella (Jenyns) — OK
E. rivularis (Clessin) — N, OM
E. scholtzi (Clessin) — M, OM
E. tanuga Timm — OK
Neopisidium alpinum (Odhner) — N
N. stelfoxi Pir. et Star. — Pi
Sphaerium corneum (L.) — OM
Planorbis planorbis (L.) — OM
Anisus albus (Müller) — OM

Turbellaria indet. — L

Hirudinea indet. — NM

Table 2 (continued)

Isopoda:

Asellus aquaticus L. — L, M, N, NM, OK, OM, Pi, PS, SK, V

Aranei:

Argyroneta aquatica (L.) — M, PM

Hydracarina:

Lebertia sp. — Pa
Forelia liliacea (Müller) — NM
Piona coccinea (Koch) — Pa
Mideopsis orbicularis (Müller) — NM
Arrhenurus affinis Koen. — NM
A. forcipatus Neuman — NM
A. neumani Piersig — NM
Hydrodroma despiciens (Müller) — NM
Hydracarina indet. — HK, K, M, N, NM, OK, OM, Pa, Pi, PS, V

Ephemeroptera:

Leptophlebia marginata (L.) — NM
L. vespertina (L.) — NM

Odonata:

Cordulia aenea L. — NM, OK
Coenagrion sp. — SK
Sympetrum danae Sulz — NM
S. flaveolum (L.) — M
Somatochlora metallica Vand. — M
Enallagma cyathigerum Charp. — NM
Leucorrhinia rubicunda L. — NM
Aeshna sp. — OK

Heteroptera:

Micronecta sp. — NM, V
Corixidae indet. — NM

Coleoptera:

Donacia sp. — K, M, V
Coleoptera indet. — L, M, N, NM, SK

Megaloptera:

Sialis sp. — K, L, N, NM, OK, OM, Pi, PS, SK, V

Trichoptera:

Cyrnus flavidus McLachlan — NM
Agrypnia obsoleta McLachlan — NM
Phryganea bipunctata Retzius — NM
Holocentropus sp. — NM
Trichoptera indet. — K, L, N, NM, OK, OM, Pi, PM, SK, V

Lepidoptera indet. — NM

Diptera (excl. Chironomidae):

Chaoborus flavicans Meigen — HK, K, L, M, N, NM, NS, OK, OM, Pi, PM, PS, SK, V
Ceratopogonidae indet. — K, M, N, NM, NS, OK, OM, PM, SK
Diptera indet. — M

Average abundance (A, ind./m²) and biomass (B, g/m²) of zoobenthos in the lakes studied, after Mäemets (1968) and original data

Taxon	Loosalu						Pakasjärv		Nigula			
	28. 6. 53		22. 7. 55		9. 8. 77		6. 7. 72		6. 8. 54		17. 7. 83	
	A	B	A	B	A	B	A	B	A	B	A	B
Chironom.	504	0.40	74	0.07	326	0.81	281	0.42	130	0.09	267	2.16
Oligoch.	—	—	—	—	—	—	—	—	4	0.01	168	0.34
Pisid.	—	—	—	—	—	—	—	—	252	0.60	222	0.53
Turbell.	—	—	—	—	7	0.01	—	—	—	—	—	—
Asellus	7	0.04	52	0.17	45	0.30	15	0.04	—	—	119	0.20
Hydracar.	52	0.11	22	—	—	—	—	—	7	0.01	10	0.01
Insecta?	7	0.01	—	—	—	—	—	—	—	—	—	—
Coleopt.	15	0.06	7	0.02	—	—	—	—	—	—	5	0.01
Sialis	7	0.12	7	—	37	0.36	—	—	18	0.60	5	0.02
Trichopt.	7	0.10	15	0.31	—	—	—	—	—	—	5	—
Chaoborus	22	0.13	—	—	7	0.04	—	—	7	0.02	—	—
Ceratop.	—	—	—	—	—	—	—	—	—	—	20	0.02
Total	621	0.97	178	0.58	422	1.51	296	0.46	418	1.33	821	3.28

Table 3 (continued)

Taxon	Meelva		Viroste				Holvandi Kivijärv		Pikamäe		Partsi Saarjärv	
	7. 7. 83		10. 6. 63		8. 7. 83		6. 7. 83		6. 7. 83		5. 7. 83	
	A	B	A	B	A	B	A	B	A	B	A	B
Chironom.	572	0.80	156		760	5.43	449	0.66	124	0.20	212	0.36
Oligoch.	202	1.28	—		—	—	5	0.01	39	0.05	—	—
Pisid.	63	0.26	—		—	—	—	—	538	0.88	—	—
Asellus	112	0.36	+		—	—	40	0.12	138	0.15	30	0.03
Argyroneta	15	0.22	—		—	—	—	—	—	—	—	—
Hydracar.	55	0.03	—		10	0.01	143	0.08	74	0.05	10	0.01
Odonata	6	0.15	—		—	—	5	0.03	—	—	—	—
Micronecta	—	—	—		5	—	—	—	—	—	—	—
Coleopt.	12	0.17	—		—	—	—	—	—	—	—	—
Donacia	—	—	—		5	0.35	—	—	—	—	—	—
Sialis	—	—	—		15	0.58	—	—	10	0.36	10	0.12
Trichopt.	6	0.11	—		—	—	—	—	10	1.36	—	—
Diptera?	24	0.49	—		—	—	—	—	—	—	—	—
Chaoborus	45	0.09	+		449	1.61	148	0.45	50	0.25	252	0.59
Ceratop.	24	0.02	—		—	—	—	—	—	—	—	—
Total	1136	3.97	289		1244	7.98	790	1.35	983	3.30	513	1.11

Table 3 (continued)

Taxon	Koolma		Nohipalu Mustjärv						Suur-Kaksjärv	
	5. 7. 83		14. 7. 60		14. 7. 72		8. 7. 83		27. 6. 66	
	A	B	A	B	A	B	A	B	A	B
Chironom.	3393	5.36	140	0.19	607	0.62	257	0.90	233	0.21
Oligoch.	5	0.01	—	—	—	—	—	—	11	0.01
Asellus	—	—	—	—	—	—	—	—	222	0.80
Hydracar.	25	0.02	4	—	—	—	—	—	22	0.01
Odonata	—	—	15	0.32	—	—	5	1.30	—	—
Corixidae	—	—	7	0.03	7	0.02	—	—	—	—
Micronecta	—	—	—	—	—	—	5	—	—	—
Coleopt.	—	—	—	—	7	0.02	5	0.06	11	—
Donacia	5	0.15	—	—	—	—	—	—	—	—
Sialis	10	0.13	4	0.09	37	0.11	—	—	11	0.03
Trichopt.	10	0.23	67	0.46	44	0.07	—	—	11	0.19
Lepidopt.	—	—	4	0.04	—	—	—	—	—	—
Chaoborus	553	0.76	256	0.66	156	0.45	124	0.66	55	0.16
Ceratop.	10	0.01	4	—	15	0.02	20	0.01	33	0.02
Total	4010	6.66	500	1.78	873	1.31	415	2.94	610	1.43

Table 3 (continued)

Taxon	Piigandi Mustjärv		Orava Mustjärv				Orava Kõverajärv		Neeruti Sinijärv	
	10. 7. 91		24. 6. 54		9. 7. 83		9. 7. 83		30. 6. 88	
	A	B	A	B	A	B	A	B	A	B
Chironom.	1130	3.98	256	0.68	445	0.98	1832	0.78	7652	29.84
Oligoch.	100	0.34	148	0.21	30	0.06	208	0.82	—	—
Pisid.	—	—	—	—	69	0.31	20	0.13	—	—
Sphaerium	—	—	—	—	59	3.05	—	—	—	—
Planorb.	—	—	—	—	25	0.08	—	—	—	—
Asellus	685	0.96	52	0.26	—	—	257	0.36	222	0.86
Argyroneta	11	0.02	—	—	—	—	—	—	—	—
Hydracar.	33	0.11	—	—	—	—	64	0.06	—	—
Odonata	—	—	30	0.21	10	0.40	5	0.12	15	3.96
Coleopt.	4	0.01	29	1.95	—	—	—	—	—	—
Sialis	—	—	15	0.63	—	—	34	0.59	—	—
Trichopt.	81	0.66	15	0.27	5	0.02	25	0.64	—	—
Chaoborus	22	0.07	15	0.06	1254	3.16	74	0.31	59	0.22
Ceratop.	8	0.02	7	0.04	—	—	153	0.06	7	—
Total	2074	6.16	837	4.31	1897	8.06	2672	3.88	7955	34.88

The small shallow but strongly stratified dyseutrophic Lake Neeruti Sinijärv revealed exceptionally high average figures of zoobenthos (Table 3), mostly of various *Chironomus* larvae which are very abundant in shallow water.

The profundal zoobenthos is always poor in species, consisting usually of the larvae of *Chaoborus* and some *Chironomidae* (*Chironomus*, *Procladius*, or *Sergentia*), sometimes with a few *Oligochaeta*, *Sialis*, etc.; in Lake Nigula also with *Pisidiidae*. It revealed a comparatively low level of abundance and biomass, too (Table 4). Only in two cases (lakes Nigula and Koolma) did biomass appear higher in the profundal than in the littoral due to the presence of big larvae of *Chironomus solitus* and *C. plumosus*. In two lakes devoid of any vegetation zone, namely Loosalu and Pakasjärv, the profundal represented the whole lake bottom.

Table 4

Profundal zoobenthos of the lakes studied

Lake	Date	Abundance		Biomass	
		ind./m²	Dominant group (>50%)	g/m²	Dominant group (>50%)
Loosalu	9. 8. 77	422	*Chironomidae*	1.51	*Chironomidae*
Pakasjärv	6. 7. 72	296	*Chironomidae*	0.46	*Chironomidae*
	11. 9. 71—9. 10. 72 (6×)	802	*Chironomidae*	2.59	*Chironomidae*
Nigula	17. 7. 83	697	*Pisidiidae*	4.93	*Chironomidae*
Meelva	7. 7. 83	148	*Chironomidae*	0.37	*Chironomidae*
Viroste	8. 7. 83	326	*Chaoborus**	0.96	*Chaoborus**
Holvandi Kivijärv	6. 7. 83	104	*Chaoborus*	0.22	*Chaoborus*
Pikamäe	6. 7. 83	163	*Chaoborus*	0.71	*Chaoborus*
Partsi Saarjärv	5. 7. 83	341	*Chaoborus**	0.99	*Chaoborus**
Koolma	5. 7. 83	2845	*Chaoborus*	13.39	*Chironomidae*
Nohipalu Mustjärv	17. 9. 71—4. 10. 72 (6×)	2025	*Chaoborus*	5.14	*Chaoborus*
	8. 7. 83	371	*Chaoborus*	1.78	*Chaoborus*
Suur-Kaksjärv	27. 6. 66	111	*Chaoborus**	0.31	*Chaoborus**
Piigandi Mustjärv	10. 7. 91	830	*Chironomidae*	3.23	*Chironomidae*
Orava Mustjärv	9. 7. 83	193	*Chaoborus*	0.52	*Chaoborus*
Orava Kõverajärv	9. 7. 83	237	*Chaoborus*	0.99	*Chaoborus*
Neeruti Sinijärv	30. 6. 88	89	*Chaoborus*	0.28	*Chaoborus*

* The only group in the profundal of this lake.

Seasonal changes of zoobenthos were studied in lakes Pakasjärv and Nohipalu Mustjärv only (Table 5). A clear summer minimum was observed, apparently caused by the emergence of heterotopic insects. The abundance and biomass were 2—6× lower in July in comparison with the annual average. This probably applies to other lakes, too.

Table 5

Seasonal fluctuations of the zoobenthos in two lakes studied

Lake	Date	Abundance, ind./m²	Biomass, g/m²	Lake	Date	Abundance, ind./m²	Biomass, g/m²
Pakasjärv	11. 9. 71	355	1.53	Nohipalu	17. 9. 71	2940	18.46
(one station)	11. 11. 71	548	1.56	Mustjärv	17. 11. 71	2363	8.84
	16. 3. 72	1200	1.84	(two stations)	9. 3. 72	2151	11.80
	17. 5. 72	474	1.11		20. 5. 72	1355	4.12
	6. 7. 72	296	0.46		14. 7. 72	873	1.31
	9. 10. 72	1941	9.07		4. 10. 72	1370	7.43
	Average	802	2.60		Average	1842	8.66

Long-time changes. Five lakes were repeatedly studied with intervals of many years (Table 3). The last investigation showed that in all of them the biomass of zoobenthos and in three lakes also its abundance appeared the highest. In lakes Loosalu and Nohipalu Mustjärv the abundance has been higher at some earlier time. A tendency towards the increase of the amount of zoobenthos in the lakes is evident, which is probably caused by the general eutrophication of all the lakes.

Discussion

The 15 brown-water lakes studied cover the whole scale of abundance and biomass of zoobenthos in Estonian lakes (according to Eesti järved, 1968). They reveal examples of both very low (<600 ind./m², <1.5 g/m², as in lakes Loosalu and Pakasjärv) and very high level (>7,000 ind./m², >16 g/m², as in Lake Neeruti Sinijärv), with an intermediate gradation. The quantity of zoobenthos seems to increase together with the trophic level of the lakes.

The authors have described the bottom invertebrate fauna of 53 Estonian lakes with soft and lighter water (Тимм et al., 1991). A comparison shows dystrophic bog lakes (subtype D³) as being quantitatively the poorest in zoobenthos among the Estonian lakes. Dystrophic lakes on mineral soil (subtype D²) are on the same level with semidystrophic and eutrophized oligotrophic lakes, while the lakes of the dyseutrophic type treated in both papers do not differ essentially from one another.

291 taxa were identified in soft light-water lakes, that is, over twice more than in brown-water ones. This is partially caused by the larger number of the lakes and samples. However, several dystrophic lakes lack many species and whole groups of animals (*Mollusca*, *Oligochaeta*, *Hirudinea*, etc.). The main cause lies in the acidic water of these lakes and not directly in humic substances (Салазкин, 1971, 1976). Some animals are typical of humified lakes (e. g., chironomids *Zalutschia zalutschicola*, *Sergentia* gr. *longiventris* and probably also *Tribelos intextus*), some oxyphilous or stenotherm relicts have also remained here. However, most bottom invertebrate species living in brown-water lakes are common in light-water ones. Besides, the dominants are changed. In soft light-water lakes *Polypedilum bicrenatum* (especially in oligotrophic and semidystrophic lakes), *Ablabesmyia* gr. *monilis* and *Tanytarsus* spp. were the

most common among chironomids, but not so in brown-water lakes. The decrease of *Tanytarsus* spp. in humified lakes was noted also by Brundin (1949). In the profundal of light-water lakes *Chironomus plumosus* (replaced by *C. cingulatus* in several oligotrophic lakes), the worm *Potamothrix hammoniensis*, and often *Pisidiidae* occur as the commonest. The profundal of brown-water lakes is usually inhabited neither by worms nor molluscs, while *C. plumosus* can be replaced by *C. solitus* or by some other species of the genus. *Procladius* spp. and *Chaoborus flavicans* are common in the profundal of all lake types mentioned, the last species being abundant in the case of oxygen deficiency.

One of the characteristics of dystrophic lakes after Naumann (1931) is their low concentration of biogenic elements. Now, all brown-water lakes appear to be eutrophized to some degree. The concentration of total phosphorus in the water of eight lakes given in Table 1 corresponds to the hypertrophic level >54 mg/m³ after Milius et al. (1991) in four lakes, to the eutrophic level 20—56 mg/m³ in three lakes, and to the mesotrophic level only in Lake Nohipalu Mustjärv. The biological phenomena of eutrophization are comparatively weak in brown-water lakes, where they are evidently inhibited by humic substances in some way. This is indirectly confirmed by the occurrence of some oxyphilous relicts in several brown-water lakes, e.g. the chironomid *Sergentia* gr. *longiventris* in the profundal and the oligochaete *Stylodrilus heringianus* in the littoral.

Brundin (1949) described the bottom fauna of three polyhumose (dystrophic) lakes in southern Sweden. He counted several thousands of ind./m² in the littoral and about one thousand in the profundal. These figures are considerably greater than ours, which comes from taking into account also submicroscopic animals disregarded in our samples. In the profundal *Chironomidae*, *Oligochaeta*, *Pisidiidae*, and *Chaoborus* were found regularly, among chironomids *Sergentia longiventris*, *Chironomus tenuistylus*, and *Orthocladius naumanni* (= *Zalutschia zalutschicola*) were numerous, while the last two were described by Brundin as new species peculiar to polyhumose lakes.

Another species-rich bottom fauna of similar abundance was found by Berg and Petersen (1956) in the polyhumose Lake Gribsö, Denmark. The average biomass there fluctuated between 1.6 and 29.5 g/m² (in sublittoral and in the upper littoral, respectively). *Sergentia longiventris* and *Orthocladius naumanni* dominated in the upper profundal while *Corethra* (= *Chaoborus*) *flavicans* was the main inhabitant of the deepest region.

It seems that these Swedish and Danish lakes studied in the 1940s were then more typical dystrophic lakes than our 15 lakes are now; probably, they were less disturbed by human activity.

The zoobenthos of 27 dystrophic lakes in Latvia has been summarized by Vadzis et al. (Вадзис et al., 1976). They give even lower values of biomass than there is in our lakes: 0.06—1.3 (average 0.6) g/m² in bog lakes, and 0.2—3.0 (1.5) g/m² in the case of a developed littoral. The profundal fauna is stated to consist of a few species occurring also in eutrophic lakes: *Ilyodrilus hammoniensis* (=*Potamothrix hammoniensis*), *Procladius*, *Chironomus* f. l. *plumosus*, *Chironomus* sp., and *Chaoborus flavicans.*

Eastwards, in the Leningrad Region of Russia, the zoobenthos of two mesohumose lakes was very poor according to Salazkin (Салазкин, 1968): only 170—360 ind./m², 0.53—0.80 g/m². The fishery cadastre of the small lakes of the region (Рыбохозяйственный кадастр . . . , 1977, 1980) gives 0.12—2.7 g/m² for brown-water lakes, only in the case of one vegetation-rich lake as much as 5 g/m². The bottom fauna consisted mainly of *Chironomidae*, often also of other insects, oligochaetes and molluscs, in the profundal of stratified lakes mostly or exclusively of *Chaoborus*.

A monograph on the Karelian lakes (Озера Карелии, 1959) gives 0.07—1.12 g/m² for the zoobenthos biomasses of five larger oligotrophic polyhumose lakes. Gordeyev and Russanova (Гордеев, Русанова, 1964) found 0.26—2.93 g/m² in four small forest lakes near Konchozero. Aleksandrov (Александров, 1968) confirms that in 21 dystrophic lakes of southern Karelia the biomass of zoobenthos rarely exceeded 1 g/m², reaching exceptionally 2.5 g/m². The fauna consisted mainly of insect larvae, usually with *Chironomidae* and *Chaoborus* or neither in the profundal. Hence, Karelian dystrophic lakes seem to be even poorer in zoobenthos than those in Estonia.

In general, Estonian brown-water (dystrophic and dyseutrophic) lakes resemble those of the neighbouring countries lying at the same latitudes, but all are eutrophized to a different extent. Some of them can reveal a high biomass of zoobenthos, while the qualitative composition of their fauna is poor. They have no complete primeval bottom fauna consisting of oxyphilous soft-water species, but its single relicts occur frequently together with more tolerant animals. The profundal of several brown-water lakes is anaerobic during stagnation periods and therefore devoid of any macroscopic animals. Closed bog lakes have preserved best of all.

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MÕNEDE EESTI PRUUNIVEELISTE JÄRVEDE PÕHJALOOMASTIK

Aastail 1966—1991 uuriti 15 väikest düstroofset ja düseutroofset järve. Põhjaloomastiku liigiline koosseis on neis suhteliselt vaene. Leitud 136 taksonist kuulus enamik putukate, eriti hironomiidivastsete hulka; limuseid ja usse kohati vähe. Ainult väga üksikud liigid olid pruuniveelistele järvedele spetsiifilised. Profundaal oli hapnikunappuse tõttu eriti loomavaene või hoopis loomadeta. Põhjaloomade keskmine arvukus ja biomass kõikusid järvedes laiades piirides: väga madalast tasemest ehtsates düstroofsetes rabajärvedes kuni väga kõrge tasemeni düseutroofses Neeruti Sinijärves. Kahte järve (Pakasjärv ja Nohipalu Mustjärv) uuriti 1971.—1972. aastal sesoonselt; täheldati selget suvist, putukate väljalennust tingitud põhjaloomastiku miinimumi. Viies paljuaastaste vaheaegade järel uuritud järves ilmnes tendents loomade kogubiomassi kasvu suunas. Klassikaliste Skandinaavia huumusjärvedega võrreldes on meie pruuniveeliste, suhteliselt eutrofeerunud järvede põhjaloomastik vormi- ja ka isendivaesem, kuid Läti, Karjala ja Leningradi oblasti omadega üsna sarnane.

Тармо ТИММ, Кюлли КАНГУР, Вийви ТИММ

ЗООБЕНТОС НЕКОТОРЫХ БУРОВОДНЫХ ОЗЕР ЭСТОНИИ

В 1966—1991 гг. были исследованы 15 малых дистрофных и дисэвтрофных озер Эстонии. Видовой состав зообентоса оказался относительно бедным. Найдено 136 таксонов, в основном насекомых, особенно личинок хирономид; моллюсков и червей было мало. Лишь единичные виды оказались специфичными для буроводных озер. Профундаль озер была особенно бедна или совсем лишена животных вследствие недостатка кислорода. Средняя численность и биомасса зообентоса в отдельных озерах колебались в широких пределах, от очень низких в типичных дистрофных озерах на верховых болотах до очень высокого уровня в одном дисэвтрофном озере. В двух посезонно исследованных озерах наблюдался четкий летний минимум зообентоса, обусловленный вылетом насекомых. Пять озер были изучены повторно через многие годы; в них наблюдалась тенденция к росту биомассы. По сравнению с донным населением классических гумифицированных озер Скандинавии, донное население наших, довольно эвтрофированных буроводных озер качественно и количественно беднее. Данные о буроводных озерах Латвии, Карелии и Ленинградской области близки нашим данным.