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Meiobenthos of some Estonian coastal lakes

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Abstract. Corer samples of zoobenthos were collected in 20 coastal water bodies of western Estonia including 2 inner parts of bays of the Baltic Sea, 5 lagoons weakly connected with the sea, and 13 freshwater lakes in August 2004. Reigi laht, an open bay, was the only site where brackish-water taxa dominated; in the same bay, eumeiobenthic small Nematoda were very abundant. At all other sites, the bulk of meiobenthos was formed of small, pseudomeiobenthic individuals of Chironomidae and Oligochaeta, while eumeiobenthos, consisting here mainly of Nematoda and Ostracoda, was outnumbered by the former. The near-bottom planktic Cladocera and Copepoda were also common. Freshwater taxa dominated in all lagoons and lakes, with scarce brackish-water species accompanying them in the lagoons as well as in some lakes. The abundance and biomass of pseudo- and eumeiobenthos, as well as of planktic crustaceans, were higher in the lagoons than in the fresh-water lakes.

Key words: fauna, zoobenthos, meiobenthos, abundance, biomass, halotrophic lakes, lagoons, Baltic Sea.

INTRODUCTION

Meiobenthos is a term to denote submicroscopic, multicellular bottom animals usually ignored in regular studies of macrozoobenthos. The word 'microbenthos' has been used with the same meaning to distinguish it from macrobenthos, i.e. bottom animals that are distinctly visible without any magnification (e.g., Stańczykowska, 1967; Mikhajlov, 1970; Babitskij, 1980). However, the term 'microbenthos' fits better the bottom-inhabiting unicellular Protoctista. Meiobenthos includes, besides several specific animal groups (eumeiobenthos), also numerous young submicroscopic stages of various macroscopic animals (pseudomeiobenthos), as well as representatives of zooplankton when they spend some time on bottom.

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Discrimination between macrozoobenthos and pseudomeiobenthos is conventional. A survey of the role of meiobenthos in freshwater lakes is given by Kurashov (1994, 2002).

Meiobenthos is poorly studied in Estonia. Short notes on the 'microbenthos' of Lake Peipsi–Pihkva, situated on the border between Estonia and Russia, were published by Mikhajlov (1970, 1973). Timm (2002) treated the meiobenthos of the transition zone between the deeper littoral and the profundal in 10 small Estonian lakes. A meiobenthic animal group, Ostracoda, was identified in the samples of macrozoobenthos from the Baltic Sea, and from the rivers and springs studied by Järvekülg (1979, pp. 91–92; 2001, p. 164; Timm & Järvekülg, 1975, p. 84).

The present study is part of a comprehensive research of the Estonian coastal halotrophic lakes, initiated by the Centre for Limnology of the Estonian University of Life Sciences. It is an attempt to give a preliminary survey of the submicroscopic bottom fauna of these lakes and its changes in the course of gradual isolation from the Baltic Sea due to isostatic land uplift.

STUDY AREA

Twenty brackish-water and freshwater bays, lagoons, and relic lakes were under study. These water bodies are located on the islands of Hiiumaa and Saaremaa and in the northwestern part of the Estonian mainland, between 58°10′–59°15′ N and 21°45′–23°45′ E. Many of them still bear a name indicating their recent marine nature, like *laht* (bay) or *mer*i (sea). Others are called *järv* (lake) or *lais* (coastal lake), while one lake is simply named *auk* (pit). Three hydrological categories can be distinguished under these sampling sites: 2 open bays, 5 lagoons receiving irregularly some brackish water from one or two canals, and 13 entirely freshwater lakes lying already above sea level. The lagoons and the lakes belong to different succession stages of the halotrophic lake type sensu Mäemets (1974) and Ott & Kõiv (1999). Their location is shown in Fig. 1. Most of them are very shallow, less than 1 m, while the depth of some others reaches 2–3 m. The bottom is usually sandy or clayey, often silted, seldom with a thick mud layer. The water is unstratified and rich in oxygen, mostly transparent to the bottom. The concentration of HCO_3^- in the lakes and lagoons fluctuated mostly between 61 and 348 mg L^{-1}, COD_{Cr} was 39–102 mg L^{-1}, pH 7.2–9.9, Ptot 0.010–0.039 mg L^{-1}, and Ntot 400–2748 mg L^{-1} (data of the Centre for Limnology).

Among the **open bays**, Reigi laht on the northwestern coast of Hiiumaa Island is a part of the open Baltic Sea, with a salinity of about 6–7‰. The sampling site is enriched by the effluent of a fish factory. The other bay, Rame laht, belongs to the Gulf of Riga and borders on the mainland. Its salinity is slightly lower (up to 5‰), and the water is unpolluted.

Of the **lagoons** Kirikulaht on Hiiumaa Island receives fresh water from a stream but is also connected with Reigi laht by a strait. The Käina laht on Hiiumaa Island is connected with the sea by two short ditches. The Laialepa laht on Saaremaa Island is connected with the sea by a short ditch. All three lagoons have extensive,

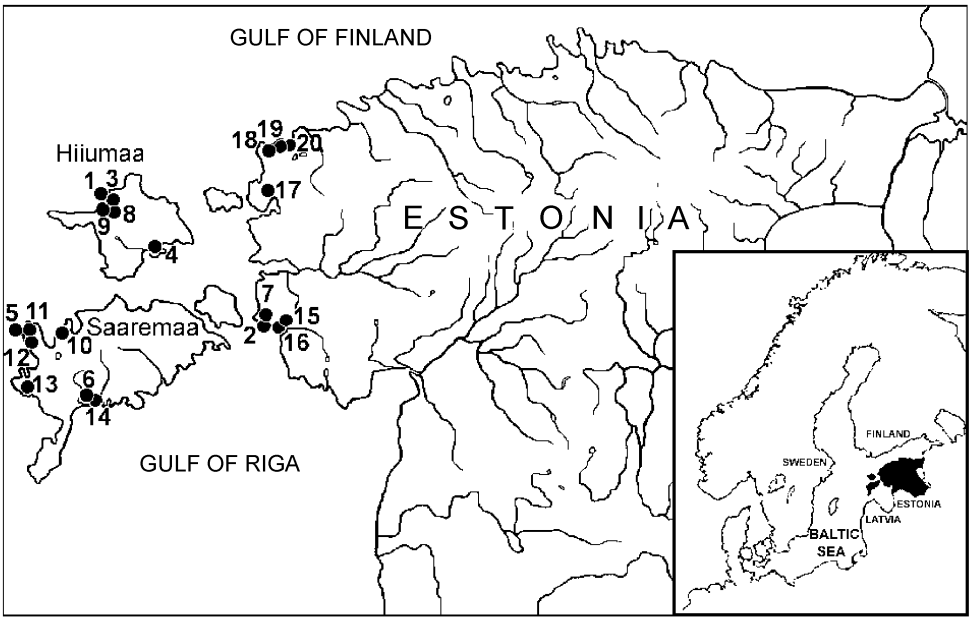

Fig. 1. Location of the water bodies under study. 1 – Reigi laht, 2 – Rame laht, 3 – Kirikulaht, 4 – Käina laht, 5 – Laialepa laht, 6 – Suurlaht, 7 – Mõisalaht, 8 – Tammelais, 9 – Veskilais, 10 – Kooru järv, 11 – Sarapiku järv, 12 – Kiljatu järv, 13 – Nonni järv, 14 – Linnulaht, 15 – Käomardi laht, 16 – Kiissa laht, 17 – Sutlepa meri, 18 – Pikane järv, 19 – Allikajärv, 20 – Lepaauk.

very shallow open water regions. The largest lagoon (area about 5 km^2, depth about 2 m), Suurlaht in Saaremaa has a 3 km outflow changing occasionally its direction. The Mõisalaht on the mainland is isolated from Rame laht with a half a kilometre long railway embankment; however, a small bridge enables some water exchange. The Mõisalaht is very muddy and mostly overgrown with reeds. The salinity of water varied mostly between 210 and 3380 mg L^{-1} Cl^- in different lagoons but was only 120–150 mg L^{-1} in the Suurlaht.

Among the conventional **freshwater lakes** (without direct contact with sea water, concentration of Cl^- 7–234 mg L^{-1}), Tammelais and Veskilais in Hiiumaa, and Kooru järv in Saaremaa are shallow and rich in vegetation. Sarapiku järv, Kiljatu järv, and Nonni järv in Saaremaa are shallow but mostly with open water. Linnulaht (*Bird Bay*), enriched by numerous nesting waterfowl, has a thick layer of watery mud, and is fringed with lush reed thickets. In the mainland, the shallow lakes of Käomardi laht and Kiissa laht are completely overgrown with reeds and dense *Chara*, while the lakes of Sutlepa meri and Pikane järv have also extensive but shallow open-water areas. Two of the mainland lakes, Allikajärv and Lepaauk, are most similar to small lakes of glacial origin, with a developed littoral vegetation zone well distinguished from the central deeper, profundal-like hollow. Their water is brownish, with HCO_3^- content ranging between 70 and 90 mg L^{-1}, and with a pH of about 7.

MATERIAL AND METHODS

Sampling was performed on 10–20 August 2004, always in shallow water (0.2–0.7 m). The sediment corer, made of a 48 cm long aluminium pipe with an inner diameter of 2.75 cm, took a core with a surface of 5.94 cm^2. Only the uppermost, soft sediment layer (2–10 cm thick) was sampled. One sample consisting of 5 replicate cores, randomly located several metres from each other, was taken from each water body. The whole material comprised 100 cores. They were fixed separately with a small amount of formalin, and were sieved later in the laboratory under tap water, on a double silk sieve with mesh sizes of about 400–500 and 60 µm. The sieving residues were studied using a Bogorov counting plate under ×20 magnification of a dissection microscope. The animals were picked out, measured, and the largest macrozoobenthic individuals were also weighed on a torsion balance with 1 mg accuracy. The weight of smaller animals was either calculated after their approximate body volume, particularly in the case of the cylindrical forms like Chironomidae and Oligochaeta (Smit et al., 1993; Timm, 2002), or by using standard tables (Kurashov, 1994). Application of a double sieve facilitated sorting but did not allow us to distinguish any size classes; thus both fractions were pooled in the calculations. Abundance and wet biomass were calculated per square metre.

In the calculations, all animals too small to belong to macrozoobenthos were divided into pseudomeiobenthos, eumeiobenthos, and plankton. Pseudomeiobenthos was limited to the individuals of Oligochaeta, Chironomidae, and other Insecta, as well as Malacostraca, etc., all shorter than 3 mm, while larger individuals were considered macrozoobenthic (as in Gusakov, 1993, 2005). Gastropoda, *Sphaerium*, and the adult Hydracarina as heavier animals were considered as macrozoobenthos regardless of their size. Eumeiobenthos was represented by Ostracoda, Harpacticoida, *Hydra* sp., and Nematoda without the large Mermithidae. All Copepoda (except Harpacticoida) and Cladocera were treated as planktic animals. Rotatoria were not detected with this method.

The animals were mounted on slides in glycerine and identified under a microscope using magnifications suitable for a particular taxonomic group. Most taxa were identified to the species level: Oligochaeta and some smaller groups, by Tarmo Timm; Chironomidae, by Margit Kumari; Cladocera and Copepoda, by Kaidi Kübar; Ostracoda, by Kadri Sohar; and Nematoda, by Walter Traunspurger.

RESULTS

Fauna

Altogether 122 taxa were found, among them 70 nominal species (Appendix). Part of the individuals remained undetermined to the species level due to their small size or poor preservation, but they may belong to some of the identified species. Most of the taxa, 69 of 103, are macrobenthic when reaching their full size but belong to pseudomeiobenthos when young. Nine more macrobenthic taxa (mostly molluscs, and a large polychaete) were never considered meiobenthic due to their high biomass. The diversity of eumeiobenthos was limited to 22 taxa. Plankton was represented with 22 taxa, too.

Oligochaeta was the most diverse group, with 28 taxa (24 of them identified to the species level). Most of them represented meiobenthos-sized Naididae. The Oligochaeta accounted for about 21% of the macrobenthic and 20% of the pseudo-meiobenthic specimens in the material. Four marine and brackish-water oligochaetes (*Heterochaeta costata*, *Paranais litoralis*, *Amphichaeta sannio*, and *Lumbricillus* sp.) were observed only in Reigi laht, the most typical marine site. A species usually limited to very slightly brackish water, *Potamothrix bavaricus*, was recorded from at least four lagoons and lakes. Besides it, immature *Potamothrix* sp. occurred in seven more lakes; they may belong either to *P. bavaricus*, or to its freshwater counterpart *P. hammoniensis* (Michaelsen, 1901); no mature individuals of the latter were found in this material. The rest of the oligochaetes live generally in fresh water, although some of them can tolerate also low salinity in the Baltic Sea bays (Järvekülg, 1979).

The larval Chironomidae were another dominant group of larger animals, with 19 taxa, among them 10 identified to the species or the larval form. They made up about 60% of the macrobenthic and 22% of the meiobenthic specimens. Many of the smallest individuals remained unidentified. Among the identified species, *Tanytarsus verralli* was the commonest, observed at 10 sites of 20. All of these chironomid taxa inhabit mostly fresh water, although some are slightly euryhaline. Chironomids were very scarce in the samples taken from both brackish water bays. On the other hand, their share was even higher in the lagoons than in the entirely separated lakes, both on the macrobenthic and pseudomeiobenthic levels.

Among the other macrobenthic and pseudomeiobenthic groups, three taxa were the most frequent in the samples: the crustacean *Asellus aquaticus* (8 sites, in the lagoons and lakes), the ephemeropteran *Caenis* sp. (6 sites, in the lagoons and lakes), and the bivalve mollusc *Sphaerium corneum* (6 sites, in the lakes only). Representatives of some other freshwater Insecta and Mollusca, as well as Hirudinea, Mermithidae, Hydracarina, *Gammarus*, and Bryozoa were observed seldom and as single individuals. In the cores taken from the bay of Reigi laht, a very large polychaete worm, *Hediste diversicolor*, was abundant, accompanied with an unidentified gastropod. *Hediste* was also observed in a qualitative sample from the lagoon of Kirikulaht, but was lacking in the cores. Another marine worm, the priapulid *Halicryptus spinulosus*, was found in Reigi laht.

The eumeiobenthic crustacean group of Ostracoda was represented with 8 species and with some unidentified individuals. *Darwinula stevensoni* was the most frequent species (6 sites), followed by *Cyprideis torosa* (5 sites) and *Candona candida* (4 sites). Most of them are known as euryhaline freshwater species but *Cyprideis torosa* prefers brackish water. In our material, these euryhaline ostracods were found both in the lakes and in the lagoons. *Cyprideis torosa* was the only ostracod at the most marine site, Reigi laht. The only true freshwater species in this list, *Cypria exsculpta*, was found once in the lake of Allikajärv. Ostracoda accounted for about 25% of the abundance of the meiobenthic animals both in the lagoons and in the lakes, but for much less in the open bays. The lagoon of Suurlaht and the lake of Kiissa laht were the richest in ostracods.

The small (non-mermithid) Nematoda, all in all 22 taxa, were observed at 13 sites of 20, most abundantly in the bay of Reigi laht and in the lagoon of Kirikulaht connected with each other. Owing to these two water bodies, the total share of Nematoda among meiobenthos was 39%. In the freshwater lakes, small nematodes were scarce, making up only 2.5% of the meiobenthos. Nine freshwater taxa were identified, among them *Dorylaimus stagnalis* and *Tobrilus* cf. *gracilis* being the commonest. Freshwater species were even found in the open bay of Rame laht and in the lagoon of Kirikulaht connected closely with the open bay of Reigi laht. At the same time, the highly abundant nematode fauna of Reigi laht itself consisted exclusively of marine taxa, 12 in number, but mostly not identified to the species level.

Two more eumeiobenthic taxa, *Hydra* sp. and unidentified Harpacticoda, were found only once and as single individuals.

Cladocera accounted for about 2/3 of the planktonic Crustacea in our samples, and about 6% of all meiobenthic animals. Nine taxa were registered, among them six identified to the species level. All of them are common freshwater species. *Alona costata* and *Sida crystallina* were the commonest, both registered from 6 sites – the former from the lagoons and lakes, and the latter only from the lakes.

Copepoda, another order of planktonic Crustacea, made up about 4% of the meiobenthos. Of the 13 taxa 4 belonged to the suborder Calanoida, and 9 to Cyclopoida (the third suborder, Harpacticoida, is eumeiobenthic). The cyclopoids were represented only with freshwater species, even in the open bays. *Megacyclops viridis* (7 sites) and *Mesocyclops leuckarti* (5 sites) were the most frequent. Among the three calanoids identified, two belong to the brackish-water fauna: *Limnocalanus grimaldii* (in two lagoons) and *Centropages* sp. (remarkably, in the freshwater lake of Allikajärv).

Abundance and biomass

The average abundance of all animals for all studied 100 cores was 53 973 ± 17 244 individuals per square metre, macrobenthos constituing about 15%, pseudomeiobenthos 30%, eumeiobenthos 47%, and plankton 9% (Table 1). The share of eumeiobenthos, mostly nematodes, was very high in the open bay of Reigi laht. Without the open bays, the percentage of eumeiobenthos was lower: 34% of all animals (or 41% of the meiobenthic animals) in the lagoons, and 20% (or 27%) in the freshwater lakes (Table 1). Nematoda accounted for about 39% of the meiobenthos-sized animals (but only 2.5% in the freshwater lakes); small Chironomidae, 23%; Ostracoda, 16%; Oligochaeta, 7%; Cladocera, 6%; and Copepoda, 4% (Table 2).

Table 1. Average abundance of animals, ind. m^{-2} (± standard error)

Water body	Macrozoo-benthos	Pseudomeio-benthos	Eumeio-benthos	Plankton	Total meiobenthos	All animals
1. Reigi laht	16 835	23 569	301 683	337	325 589	342 424
2. Rame laht	1 010	1 010	1 010	4 040	6 060	7 070
3. Kirikulaht	16 162	67 003	35 017	22 222	124 242	140 404
4. Käina laht	4 040	16 498	10 101	1 684	28 283	32 323
5. Laialepa laht	20 202	37 037	7 407	1 010	45 454	65 656
6. Suurlaht	11 448	30 303	69 360	17 508	117 171	128 619
7. Mõisalaht	11 784	8 754	17 172	673	26 599	38 383
8. Tammelais	4 714	15 825	2 694	21 549	40 068	44 782
9. Veskilais	3 030	8 080	3 704	1 684	13 468	16 498
10. Kooru järv	5 050	12 458	673	3 367	16 498	21 548
11. Sarapiku järv	3 367	24 242	337	0	24 579	27 946
12. Kiljatu järv	19 192	31 313	337	1 347	32 997	52 189
13. Nonni järv	1 010	10 438	0	0	10 438	11 448
14. Linnulaht	8 081	5 387	8 417	5 724	19 528	27 609
15. Käomardi laht	1 683	3 704	673	1 683	6 060	7 743
16. Kiissa laht	7 071	1 683	39 057	3 367	44 107	51 178
17. Sutlepa meri	12 121	8 417	0	0	8 417	20 538
18. Pikane järv	5 387	2 357	7 071	337	9 765	15 152
19. Allikajärv	4 040	5 387	2 357	2 694	10 438	14 478
20. Lepaauk	3 704	5 387	1 010	3 367	9 764	13 468
Open bays (1, 2)	8 922	12 289	151 346	2 188	165 824	174 747
	±7 912	±11 279	±150 336	±1 851	±159 764	±167 677
Lagoons (3–7)	12 727	31 919	27 811	8 619	68 350	81 077
	±2 699	±10 085	±11 449	±4 654	±21 657	±22 603
Lakes (8–20)	6 035	10 360	5 102	3 471	18 932	24 967
	±1 359	±2 445	±2 927	±1 580	±3 522	±4 204
Total (1–20)	7 997	15 943	25 404	4 630	45 976	53 973
	±1 379	±3 602	±15 067	±1 571	±16 472	±17 244

Total average biomass in all cores was calculated as 25 046±13 928 mg m^{-2}. However, 93% of it was formed of macrozoobenthos, particularly larger Chironomidae (but Polychaeta in Reigi laht). The remaining 1797±391 mg m^{-2} of meiobenthos consisted of pseudomeiobenthos (50%), eumeiobenthos (23%), and plankton (27%) (Table 3). Small chironomids and ostracods were the most important taxonomic groups in the biomass of meiobenthos, both accounting for 22%; Cladocera made up 17%, Copepoda 10%, and Oligochaeta 9%. The share of Nematoda in the biomass was negligible (Table 2).

Table 2. Percentage of animal groups in the abundance and biomass of meiobenthos

Type of water bodies	Oligo-chaeta	Chirono-midae	Other pseudomeio-benthos	Ostracoda	Nematoda	Other eumeio-benthos	Cladocera	Copepoda
Abundance:								
Open bays	6.90	0.20	0.30	1.22	90.05	0.00	0.10	1.22
Lagoons	3.74	33.20	9.75	24.83	15.57	0.30	6.40	6.21
Lakes	10.95	41.04	2.74	24.49	2.46	0.00	12.30	6.02
Total	6.81	23.40	4.47	16.22	38.90	0.11	5.71	4.36
Biomass:								
Open bays	43.48	0.67	9.48	26.42	9.92	0.00	0.00	10.03
Lagoons	6.02	23.55	24.09	20.55	0.22	1.19	12.20	12.18
Lakes	9.14	22.32	13.93	22.48	0.17	0.00	24.33	7.63
Total	9.27	21.89	18.93	21.66	0.67	0.61	16.86	10.11

Table 3. Average wet biomass of animals, mg m^{-2} (± standard error)

Water body	Macrozoo-benthos	Pseudomeio-benthos	Eumeio-benthos	Plankton	Total meiobenthos	All animals
1. Reigi laht	284 637	788	651	27	1 466	286 103
2. Rame laht	428	178	2	255	435	863
3. Kirikulaht	14 214	4 504	94	2 487	7 085	21 299
4. Käina laht	2 134	1 107	720	48	1 875	4 009
5. Laialepa laht	6 959	1 613	508	39	2 160	9 119
6. Suurlaht	14 523	922	2 175	1 933	5 030	19 553
7. Mõisalaht	40 664	1 790	569	10	2 369	43 033
8. Tammelais	6 104	1 263	21	1 072	2 356	8 460
9. Veskilais	6 871	446	138	79	663	7 540
10. Kooru järv	4 094	216	0	560	776	4 870
11. Sarapiku järv	11 656	1 082	20	0	1 102	12 758
12. Kiljatu järv	10 765	1 407	26	489	1 922	12 687
13. Nonni järv	740	255	0	0	255	995
14. Linnulaht	21 791	272	360	734	1 366	23 157
15. Käomardi laht	2 752	172	61	170	403	3 184
16. Kiissa laht	17 226	146	2 514	1 256	3 916	21 142
17. Sutlepa meri	7 561	548	0	0	548	8 109
18. Pikane järv	2 013	130	230	168	528	2 541
19. Allikajärv	7 319	879	144	151	1 174	8 493
20. Lepaauk	2 501	228	2	275	505	3 006
Open bays (1, 2)	142 532	483	326	247	950	143 483
	±142 104	±305	±324	±219	±515	±142 620
Lagoons (3–7)	15 699	1 987	813	903	3 704	19 403
	±6 660	±649	±356	±541	±1 017	±6 726
Lakes (8–20)	7 799	542	270	381	1 193	8 996
	±1 723	±127	±189	±116	±285	±1 914
Total (1–20)	23 247	897	411	498	1 797	25 046
	±13 891	±224	±157	±155	±391	±13 928

Succession of meio- and macrozoobenthos along the salinity gradient

A rich benthic fauna of animals typical of the Baltic Sea was found in the cores taken from the open bay of Reigi laht: the polychaete *Hediste diversicolor*, the oligochaetes *Heterochaeta costata*, *Paranais litoralis*, *Amphichaeta sannio*, and *Lumbricillus* sp., the priapulid *Halicryptus spinulosus*, a poorly preserved and hence unidentified prosobranchian gastropod, the meiobenthic ostracod *Cyprideis torosa*, and a number of marine nematodes. In another, more sheltered, bay of Rame laht, the fauna was very different: low in numbers and consisting mostly of freshwater animals including small chironomid larvae, nematodes, and planktonic cyclopoids.

Kirikulaht, a lagoon closely connected with the bay of Reigi laht, revealed a diverse freshwater fauna dominated by chironomid and ephemeropteran larvae, nematodes, and planktonic cladocerans. No brackish-water animals (except for a few nematodes), common with Reigi laht, were found in the cores, although some were recorded from the qualitative samples from the lagoon.

In the other four lagoons, too, the fauna consisted largely of diverse, and often abundant, freshwater animals. Besides, there occurred a few brackish-water species such as the oligochaete *Potamothrix bavaricus*, ostracod *Cyprideis torosa*, and calanoid *Limnocalanus grimaldii*.

The samples from the lakes contained some more freshwater animals not met in the lagoons, including several species of molluscs, oligochaetes, and cladocerans, as well as the ostracod *Cypria exsculpta*. However, also the brackish-water oligochaete *Potamothrix bavaricus* was repeatedly found here; the ostracod *Cyprideis torosa* and the calanoid *Centropages* sp., domestic in the Baltic Sea but not observed in the lagoons, were found on one occasion each. The average abundance and biomass of macro- and meiozoobenthos were higher in the lagoons than in the lakes (Tables 1 and 3).

DISCUSSION

There are no comparable data on the zoobenthos of small lakes on the Baltic coast. The best equivalent may be Lake Łebsko near Słupsk, Poland. This lake is much larger than the studied Estonian lakes (71.4 km^2, depth 6.3 m), and its water is slightly brackish (maximum salinity amplitude 0.021–2.574 g L^{-1} Cl$^-$ in different parts) like in the lagoon of Suurlaht in Saaremaa. The abundance of the littoral macrozoobenthos has been very similar (11 000 ind. m^{-2}) to that of Suurlaht while the biomass has been about twice higher, about 30 g m^{-2}. The bottom fauna consists exclusively of freshwater species, except for the single brackish-water oligochaete *Potamothrix bavaricus* common also in Suurlaht. Unfortunately, the meiobenthos of this Polish lake has not been studied (Dobrowolski, 1995).

Zhadin et al. (1972) studied the psammon of the largest lagoon of the Baltic, the Curonian Lagoon (Bay). The psammon here means the hygrophilous fauna of the moist sand in supralittoral and above the coastal groundwater. A rich fauna was found, consisting mostly of Aeolosomatida, Oligochaeta, Rotatoria, Nematoda, and Harpacticoida. No data on the true meiobenthos of this lagoon are available.

The open brackish-water bays of the Baltic Sea in Finland (Tvärminne Bay and the mouth of the Kyrojoki River) harbour a meiofauna consisting of a mixture of brackish- and freshwater species (Keynäs & Keynäs, 1978; Meriläinen, 1988). The bulk of the abundance is formed of small Nematoda; the brackish-water oligochaetes *Amphichaeta sannio* and *Paranais litoralis* were recorded as abundant in the Kyrojoki estuary, like in Estonian Reigi laht. However, the nematode species were different. The total abundance of meiobenthos in the Kyrojoki (38 300–2 398 800 ind. m^{-2}) was roughly comparable to that in Reigi laht, but much lower in Tvärminne Bay, evidently owing to the larger depth of the latter site.

The true brackish-water meiofauna typical of the Baltic Sea was investigated by Pallo et al. (1998) at 30 stations of the open Gulf of Riga, immediately near our study area, at depths of 13–54 m. The average abundance of metazoan meiobenthos was 4.8 million ind. m^{-2}; 86% of this was formed by Nematoda and 9% by Harpacticoida. This fauna was similar to that on the most 'marine' site in our material, Reigi laht, with a strong dominance of Nematoda. However, the abundance was even higher there, about by an order of magnitude. Shallowness of our sampling point can be a reason, but so can the difference in sample processing. Some part of the smallest nematodes may have been omitted during hand-sorting used by us while Pallo et al. (1998) practised elutriation of sieved samples in a denser solution.

Mikhajlov (1970, 1973) treated the 'microbenthos' (in fact, meiobenthos) of large unstratified Lake Pihkva (Pskovskoe) lying on the border of Russia and Estonia. A diverse fauna inhabited the sandy bottom, while small chironomids and oligochaetes prevailed on mud. The average abundance was 56 100 ind. m^{-2} for the whole lake in July 1967, which is comparable to the respective average figure for Estonian coastal lakes and lagoons. However, the average biomass of meiobenthos was about three times larger there, 5470 mg m^{-2}.

The data by Timm (2002) for ten small Estonian inland stratified lakes were collected in deeper muddy zones, which are lacking in the shallow coastal lakes and lagoons. These zones are expected to be quantitatively poorer in zoobenthos than the littoral. Indeed, the average abundance of macrozoobenthos + pseudo-meiobenthos was about three times lower there than in the coastal lakes (4937 versus 16 120 ind. m^{-2}, respectively), and nine times lower than in the lagoons (44 646 ind. m^{-2}). The abundance of eumeiobenthos + planktic animals in these stratified lakes was slightly higher (11 580 versus 8573 ind. m^{-2}), mostly due to Cyclopoida abundant in the deeper zones of the stratified lakes, but again three times lower than in the lagoons rich in Nematoda and Ostracoda (36 430 ind. m^{-2}).

The length of the taxon list for the inland lakes was similar to that for the coastal water bodies (120 versus 122), despite the lack of brackish-water species in the former. The major animal groups were the same, as were about 50 of the identified taxa.

Six small inland lakes in eastern Latvia (Kurashov & Belyakov, 1987) revealed high figures for the abundance and biomass of meiobenthos in the littoral, from 21 920 to 147 070 ind. m^{-2}, and from 0.75 to 5.43 g m^{-2}, with higher figures being registered for more eutrophied lakes. In the profundal mainly cyclopoids occurred, like in the small Estonian lakes studied by Timm (2002).

In deep mesotrophic Lake Verkhnee Vrevo in the Leningrad Region, Russia (Zakhodnova et al., 1984), high abundance and biomass figures, 160 000–900 000 ind. m^{-2} and 1.58–21.39 g m^{-2}, were recorded in different seasons, with a maximum in June. Nematoda formed an overwhelming majority of the meiobenthos there like in the Estonian bay of Reigi laht, with 142 000–730 000 ind. m^{-2} and 0.14–1.05 g m^{-2}. However, the nematode species were different from those found in the present study. Ostracods and cyclopoids were abundant too; oligochaetes, chironomids, and tardigrades were less numerous. Although it was not clearly indicated, the above study was limited to shallows like the present article.

In Finnish Lake Pääjärvi, 78 900–625 000 ind. m^{-2} of meiobenthic animals were found at different depths (Holopainen & Paasivirta, 1977). Nematoda formed the bulk of this amount, except at a depth of 2 m, where Ostracoda, particularly *Darwinula stevensoni*, which was also abundant in our material, dominated.

The average abundances and biomasses of meiobenthos for five small lakes on the Karelian Isthmus measured from 1200 to 14 900 ind. m^{-2} and from 0.15 to 0.92 g m^{-2} (Skvortsov, 1984). These figures are much smaller than those for Lake Vrevo, as well as for Estonian coastal water bodies. Yet they are rather similar to the corresponding figures for the deeper zones of small Estonian lakes (Timm, 2002); apparently, in the above study different depth zones were lumped. The author states that the share of meiobenthos in total benthos decreases with eutrophication of lakes.

Gusakov (1993) studied meiobenthos in a section of the Rybinsk Reservoir on the Volga River, northern Russia. In 26 cores taken seasonally from four unvegetated sites with depths of 2–12 m, 139 taxa (113 species) were registered – a number slightly higher than that based on our material. The species list included only freshwater taxa, among them several eumeiobenthic Harpacticoida and Tardigrada rare or lacking in our material, and much more species of Nematoda, while not all Oligochaeta were identified. However, the number of taxa registered from the shallow-water sites was only 87 – thus considerably less than registered from the Estonian coastal lakes and lagoons due to the higher ecological diversity of the latter. The average number of meiobenthic animals at these two shallow-water sites, 31 400 and 81 600 ind. m^{-2}, and the biomass, 480 and 1630 mg m^{-2}, were well comparable to the respective figures for the coastal lakes and lagoons studied here. For the deeper stations, the corresponding figures were markedly higher. Eumeiobenthos (together with planktonic animals) accounted for 85% and 78% of the number of individuals, and 40% and 19% of the biomass in the Rybinsk Reservoir. Nematoda were responsible for the bulk of total abundance, and Chironomidae, for the biomass.

Gusakov (2005) studied, using the same methods, also the Gor′kij Reservoir on the Volga River. The material was larger, 73 cores from ecologically different sections. Consequently, the species list was much longer, 223 taxa, including 170 taxa at the shallow-water sites of the river bed section. At these sites, best comparable to ours, the average abundance of meiobenthos fluctuated between 231 700 and 310 700 ind. m^{-2} and the biomass between 4900 and 7700 mg m^{-2} in different seasons, while eumeiobenthos (together with planktic animals) always made up more than 90% of the abundance and 50% of the biomass. Besides the Nematoda, also Oligochaeta, Cladocera, Cyclopoida, and Harpacticoida were abundant on the shallows of the Gor′kij Reservoir.

CONCLUSIONS

The meiobenthos of the Estonian coastal water bodies is comparable to that of many other shallow water bodies of neighbouring regions, regarding both quantity and diversity. The bulk of it is usually formed of the first stages of macrozoobenthic animals such as chironomids and oligochaetes; the near-bottom planktic crustaceans also build up its amount, while eumeiobenthic animal groups (mainly Ostracoda and Nematoda in this study) are outnumbered. The only site where small Nematoda gained an overwhelming majority, like in some inland freshwater lakes and in the Baltic Sea, was the brackish-water open bay of Reigi laht. This was also the only site where brackish-water taxa dominated, although their abundance remained considerably lower than in the open sea. At all other sites the fauna consisted of freshwater taxa, with a small addition of brackish-water species, mostly in the lagoons still weakly connected with the sea. The lagoons also revealed a significantly higher average abundance and biomass of meiobenthos than the coastal but entirely separated freshwater lakes.

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APPENDIX

LIST OF TAXA FOUND IN THE WATER BODIES STUDIED

Numbers of water bodies as in Fig. 1

Coelenterata
Hydra indet. – 5

Nematoda
Dorylaimus stagnalis Dujardin, 1845 – 2, 3, 4, 8, 9, 20
Paractinolaimus macrolaimus (DeMan, 1880) – 10, 16
Tobrilus cf. *gracilis* (Bastain, 1865) – 3, 7, 15, 16
Oncholaimus cf. *oxyuris* – 1
Adoncholaimus sp. – 1
Anoplostoma sp. – 1
Chromadorita sp. – 1, 3
Daptonema sp. – 1
Laimydorus sp. – 1
Laimydorus/Mesodorylaimus sp. – 3
Microlaimus sp. – 1
Oncholaimus sp. – 7
Plectus sp. – 3
Theristus sp. – 1, 3
Chromadoridae gen. sp. – 1
Mermithidae gen. sp. – 2, 6
Nematoda gen. sp. No 1 – 1 (marine)
Nematoda gen. sp. No 2 – 1 (marine)
Nematoda gen. sp. No 3 – 1 (marine)
Nematoda gen. sp. No 4 (cf. *Daptonema*, marine) – 1
Nematoda indet. – 4, 5, 6

Priapulida
Halicryptus spinulosus Siebold, 1894 – 1

Polychaeta
Hediste diversicolor (Müller, 1776) – 1

Oligochaeta
Stylaria lacustris (Linnaeus, 1767) – 3, 6, 10, 16, 19
Vejdovskyella comata (Vejdovský, 1884) – 8, 18
Slavina appendiculata (Udekem, 1855) – 6, 8, 19
Dero obtusa Udekem, 1855 – 8, 18
Nais communis Piguet, 1906 – 8, 15, 16
Nais pardalis Piguet, 1906 – 13, 14
Nais variabilis Piguet, 1906 – 6, 9, 17, 19
Nais simplex Piguet, 1906 – 6, 8
Nais pseudobtusa Piguet, 1906 – 6
Specaria josinae (Vejdovský, 1884) – 18, 19
Paranais litoralis (Müller, 1780) – 1
Chaetogaster diaphanus (Gruithuisen, 1828) – 3, 6, 19
Chaetogaster diastrophus (Gruithuisen, 1828) – 5, 20

Chaetogaster langi Bretscher, 1896 – 10
Amphichaeta sannio Kallstenius, 1892 – 1
Pristina longiseta Ehrenberg, 1828 – 6
Pristina aequiseta Bourne, 1891 forma *foreli* (Piguet, 1906) – 8, 20
Limnodrilus hoffmeisteri Claparède, 1862 – 20
Tubifex ignotus (Štolc, 1886) – 20
Heterochaeta costata Claparède, 1863 – 1
Psammoryctides barbatus (Grube, 1861) – 10, 11, 20
Potamothrix bavaricus (Oschmann, 1913) – 5, 14, 15, 16
Potamothrix sp. – 7, 11, 12, 13, 17, 18, 19
Tubificidae gen. sp. – 8, 20
Cognettia glandulosa (Michaelsen, 1888) – 20
Marionina argentea (Michaelsen, 1889) – 20
Marionina sp. – 8
Lumbricillus sp. – 1

Hirudinea
Helobdella stagnalis (Linnaeus, 1758) – 14

Chelicerata
Hydracarina indet. – 2, 9, 11, 17, 19

Cladocera
Alona costata Sars, 1862 – 3, 4, 8, 9, 10, 14
Acroperus elongatus (Sars, 1862) – 8
Daphnia longispina (Müller, 1776) – 3
Diaphanosoma brachyurum (Liévin, 1848) – 20
Sida crystallina (Müller, 1776) – 10, 12, 14, 18, 19, 20
Simocephalus exspinosus (Koch, 1841) – 14, 16
Camptocercus sp. – 20
Ceriodaphnia sp. – 19
Cladocera indet. – 12

Copepoda
Eudiaptomus gracilis (Sars, 1863) – 4
Limnocalanus grimaldii (De Guerne, 1886) – 5, 6
Centropages sp. – 19
Calanoida indet. – 2
Cyclops insignis Claus, 1857 – 14
Eucyclops serrulatus (Fischer, 1851) – 8
Megacyclops viridis (Jurine, 1820) – 2, 8, 9, 10, 12, 15, 16
Mesocyclops leuckarti (Claus, 1857) – 2, 3, 6, 14, 19
Mesocyclops oithonoides (Sars, 1863) – 20
Microcyclops gracilis (Lilljeborg, 1853) – 14
Paracyclops affinis (Sars, 1863) – 7
Paracyclops fimbriatus (Fischer, 1853) – 7, 20
Cyclopidae indet. – 1
Harpacticoida indet. – 5

Ostracoda
Candona angulata Müller, 1900 – 16
Candona candida (Müller, 1776) – 6, 15, 16, 18

Fabaeformicandona protzi (Hartwig, 1989) – 4, 6, 18
Cypria exsculpta (Fischer, 1855) – 19
Cypria ophthalmica (Jurine, 1820) – 3, 6, 16
Cyprideis torosa (Jones, 1850) – 1, 4, 5, 7, 16
Potamocypris unicaudata Schäfer, 1943 – 6
Darwinula stevensoni (Brady et Robertson, 1870) – 4, 5, 9, 11, 12, 19
Ostracoda indet. – 14

Malacostraca
Asellus aquaticus (Linnaeus, 1758) – 3, 4, 8, 10, 12, 14, 19, 20
Gammarus sp. – 2, 7, 17

Chironomidae
Chironomus plumosus (Linnaeus, 1758) – 6, 7, 14, 15
Chironomus sp. – 2, 4, 7, 15, 16
Glyptotendipes paripes (Edwards, 1929) – 4, 11
Glyptotendipes sp. – 5, 7, 11
Stictochironomus sticticus (Fabricius, 1781) – 20
Stictochironomus rosenschoeldi (Zetterstedt, 1838) – 3, 5
Einfeldia sp. – 10
Microchironomus sp. – 7
Chironomini indet. – 10
Tanytarsus verralli Goethgebuer, 1928 – 3, 4, 6, 8, 9, 11, 13, 14, 17, 20
Tanytarsus ex gr. *holochlorus* Edwards, 1929 – 15, 16
Tanytarsus sp. – 6, 19
Ablabesmyia phatta (Eggert, 1863) – 18
Ablabesmyia sp. – 2, 9, 17
Procladius ferrugineus (Kieffer, 1918) – 14, 17
Procladius sp. – 3, 6, 8, 16, 18
Cricotopus bicinctus (Meigen, 1818) – 4
Psectrocladius ex gr. *sordidellus* (Zetterstedt, 1838) – 4, 5, 9, 17
Chironomidae indet. – 1, 4, 5, 8, 9, 10, 11, 12, 13, 17, 18, 20

Insecta div.
Caenis sp. – 3, 5, 8, 9, 14, 19
Leptocerus tineiformis Curtis, 1834 – 15
Polycentropodidae gen. sp. – 3
Trichoptera indet. – 11
Sigara striata (Linnaeus, 1758) – 16
Corixidae gen. sp. – 3
Coleoptera indet. – 11
Ceratopogonidae indet. – 3, 5, 9, 10, 14, 16
Diptera indet. – 7

Mollusca
Bithynia tentaculata (Linnaeus, 1758) – 11, 12
Planorbidae indet. – 19, 20
Gastropoda indet. – 1
Sphaerium corneum (Linnaeus, 1758) – 8, 9, 14, 18, 19, 20
Pisidiidae indet. – 11, 17

Bryozoa
Bryozoa indet. – 7

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Mõnede Eesti rannikujärvede meiobentosest

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On uuritud submikroskoopilisi hulkrakseid põhjaselgrootuid 18 halotroofses, osalt veel merega seotud järves Eesti läänerannikul ja läänesaartel, võrdluseks ka kahes merelahes. Leitud 122 põhjaloomade taksoni seas on suures enamuses mageveeloomad. Ainult Reigi lahes valitsevad riimveeliigid; samas lahes on ka väga palju väikesi riimveelisi ümarusse. Kõigis teistes kohtades moodustavad põhilise osa meiobentosest suuremate loomade, peamiselt hironomiidivastsete ja väheharjasusside pisikesed noorvormid (pseudomeiobentos). Tõelised meiobentose organismid (eumeiobentos), siin peamiselt ümarussid ja karpvähilised, on vähemuses. Tihti on proovidest leitud ka põhja lähedal elavaid planktilisi vesikirpe ja aerjalgseid vähke. Üldiselt domineerivad nii merega seotud kui ka sellest eraldatud järvedes mageveeliigid; üksikuid riimveeliike esineb mõlemais. Nii pseudo- kui eumeiobentose arvukus ja biomass on merega seotud järvedes keskmiselt kõrgemad kui eraldiseisvais.