Ann. Zool. Fennici 14:124—134. 1977

Abundance and biomass of the meiozoobenthos in the oligotrophic and mesohumic lake Pääjärvi, southern Finland[1]

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HOLOPAINEN, I. J. & PAASIVIRTA, L. 1977: Abundance and biomass of the meiozoobenthos in the oligotrophic and mesohumic lake Pääjärvi, southern Finland. — Ann. Zool. Fennici 14: 124—134.

The abundance, biomass and species composition of the meiozoobenthos in the littoral and profundal of a deep, oligotrophic lake in southern Finland were studied for two years. Single and multiple Kajak-type corers were used and the meiofauna was defined as animals retained between sieves with 0.1- and 0.4-mm meshes.

The total numbers of the meiozoobenthos were 80 000—230 000 ind./m^2 in the profundal and 400 000—630 000 in the littoral, and it consisted mainly of Nematoda, Cyclopoida, Harpacticoida, Ostracoda and Chironomidae.

Other groups were Turbellaria, Rotatoria, Oligochaeta, Cladocera, Ephemeroptera, Ceratopogonidae, Oribatei, Hydrachnellae, Halacaridae and Tardigrada, but their contribution to the total numbers was only c. 8 % in the littoral and c. 6 % in the profundal.

The total biomasses (ash-free dry wt.) of the meiozoobenthos were 0.1—0.3 and 0.6—0.8 g/m^2 in the profundal and littoral, respectively. More than 95 % of the meiobenthic animals lived in the uppermost 2 cm of the sediment.

The seasonal variation in total numbers was most pronounced in the littoral, and the maximum abundances were reached in early autumn after a slight minimum in early summer.

The ratio between the numbers of meiofauna and macrofauna was 10—19:1 in the littoral and 41—52 : 1 in the profundal. The ratio between their biomasses was 0.5 : 1 in the littoral, 3 : 1 in the littoriprofundal and upper profundal and 2:1 in the deep profundal.

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1. Introduction

The word "meiobenthos" was introduced by MARE (1942) for organisms intermediate in size between "macrobenthos" and "microbenthos". Earlier, the term microbenthos was generally used for meiobenthic animals as well, and it is still so used by some authors (e.g. STANCZYKOWSKA & PRZYTOCKA-JUSIAK 1968, SAKHAROVA 1970, PREJS & STANCZYKOWSKA 1972). The term "mesobenthos" is apparently synonymous with "meiobenthos" (ENCKELL 1968, GURVICH 1969), but is not so widely used.

The meiofauna is most usually defined as the fraction of the zoobenthos retained between 0.5-mm and 0.1-mm sieves (MCINTYRE 1969). The first studies on meiofauna were qualitative but by now the quantitative work, especially that on marine meiofauna, has become quite voluminous (cf. MCINTYRE 1969, GERLACH 1971, HULINGS & GRAY 1971 and THIEL 1975).

The quantitative ecology of freshwater meiozoobenthos, somewhat neglected after the papers of MOORE (1939), PENNAK (1940, 1951) and COLE (1955), has recently attracted more research (e.g. KAJAK & RYBAK 1966, STANCZYKOWSKA 1966, PREJS 1969, SAKHAROVA 1970,

[1] This paper is part of Project No. 2 supported by the Academy of Finland.

SÄRKKÄ & PAASIVIRTA 1972, PREJS & STANCZYKOWSKA 1972, BRETSCHKO 1973, PAASIVIRTA 1974 and 1975, SÄRKKÄ 1976).

Although the quantitative importance of meiozoobentos has often been emphasized (e.g. STANCZYKOWSKA & PRZYTOCKA-JUSIAK 1968, EDMONDSON & WINBERG 1971, ELMGREN 1973) its contribution to the production of lake bottoms is still almost unknown. In connexion with the research project on the ecosystem of Lake Pääjärvi, the production and seasonal variation in the abundance and biomass of the macro- and meiofauna were studied for over two years. This paper presents the major results for the meiozoobenthos. The species were identified by the author L. P. if not otherwise stated.

2. Study area

Pääjärvi is a mesohumic, oligotrophic lake situated in southern Finland (61° 04'N, 25° 08' E). It has an area of 13.42 km^2, a mean depth of 14.4 m and a maximum depth of 87 m. The water is mixed completely twice a year and no oxygen deficit occurs in the water column. The transparency of the water is only 2 to 2.5 m. The ice cover normally lasts from December to the beginning of May and stable thermal stratification occurs during the summer. Some mean values of the chemical and physical properties of the water, and of the surface layer (0—2 cm) of the profundal sediment are listed below:

Water:	
Conductivity (μS)	68
pH	6.9
Colour (mg Pt/l)	60
Inorganic carbon (mg/l)	2.8
Tot. phosphorus "	0.012
Tot. nitrogen "	0.950
$KMnO_4$ consumption "	38
Sediment:	
Ignition loss (%)	7
Organic matter (mg/g dry sed.)	108±1.7($\bar{x}$±SE, n = 36)
Total phosphorus "	1.4
Total nitrogen "	3.0±0.3($\bar{x}$±SE, n = 35)
Redox potential, Eh_7 (mV)	+200

For more detailed information on the lake, see RUUHIJÄRVI (1974).

3. Sampling sites

The littoral (0—2.5 m) and littoriprofundal (2.5—5.5 m) samples were taken from a permanent sampling transect in the western arm of the lake (PAASIVIRTA 1975). The 1-m station has isoetid vegetation and the mineral content of the sediment is relatively high. At the 2-m and 3-m stations the sediment is softer and covered by algae, mainly *Oscillatoria* and diatoms. The algal vegetation is, however, rather sparse at 3 m and the lower limit of living algae is 4.5 m.

At the 8-m station, the surface sediment is coarser and contains more mineral particles than at the other five profundal stations (PAASIVIRTA 1975), which have a 2—3 cm thick surface layer of reddish brown gyttja (or dygyttja) underlain by a hard, red, ca. 0.5 cm thick layer of lake ochre (iron hydroxide), below which is gray or dark gray ooze. However, at the 13-m station in the eastern arm of the lake there is a thin brown surface layer (1—2 cm) overlying yellowish clay. For the redox potential, organic content, etc., in the profundal sediment, see Fig. 1.

4. Material and methods

The material from the profundal was mostly collected in 1971, and that from the littoral and littoriprofundal in 1972. In 1971, four hauls with a three-unit multiple corer (one core 15.2 cm^2, HAKALA 1971) were made monthly at all the six profundal stations. In addition, in May 1971 a series of samples was taken from 25 squares (200 × 200 m) randomly distributed throughout the profundal, each sample consisting of one haul with the three-unit corer. The topmost 5—6 cm of each core was taken to the laboratory, sieved and counted separately.

In 1972 the profundal stations were sampled in June, August—September and November and in 1973 in February-March. Three hauls were made with the multiple corer and all the nine cores were combined to form one sample.

The littoral and littoriprofundal were sampled in 1972 during the same months as the profundal and the samples from the depths of 1, 2 and 3 m mostly consisted of one 54.6 cm^2 core, the corer being mounted on a pole. At the depth of 5 m, all the samples consisted of three hauls with the multiple corer and all the cores were combined. In the laboratory all the samples were sieved with a water jet through a 0.1-mm mesh nylon net, and in 1972 an additional sieve with a 0.4-mm mesh was used to eliminate the macrofauna.

The combined samples were divided with a modified Folsom sample splitter (HOLOPAINEN & SARVALA 1975) into 8—32 subsamples, depending on the abundance of the animals. Five of these subsamples were then chosen systematically for counting. The animals were counted alive with a grooved disc under a stereo-microscope with × 12 magnification.

The vertical distribution of animals in the sediment was examined by cutting some cores into 1-cm slices with a piston-operated slicing device (HAKALA 1971).

The biomasses were calculated from mean individual ash-free dry weights worked out for different animal groups and size classes. Some 50 to 200 individuals of one species or group were placed in pre-ignited and weighed aluminium foil cups and oven-dried at +60 °C

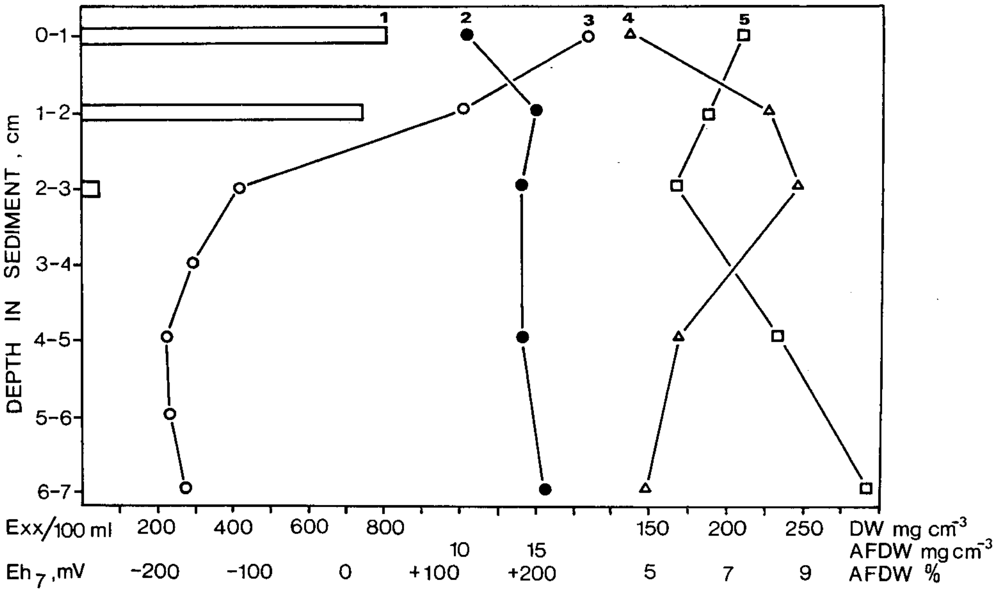

Fig. 1. The vertical distribution of some properties of the sediment at 14 m in the western arm of Pääjärvi. 1: numbers of meiozoobenthos (ind./100 ml), 2: organic matter (ash-free dry wt., mg/cm^3), 3: redox potential, 4: dry weight (mg/cm^3), 5: percentage of organic matter.

for at least 12 hours to obtain the dry weight. The ash content was determined by combusting the samples at 500 °C in a muffle furnace for three hours. The weighing accurary of the electronic microbalance used was reported to be $\pm$ 1 μg.

The 90 % confidence limits for the numbers of different meiofauna groups were calculated according to the recommendations of Elliot (1971). When dispersion was random the formula $\bar{x} \pm t \sqrt{\frac{\bar{x}}{n}}$ was used and when it was contagious, a logarithmic transformation was chosen. The mean numbers given by the three cores in the multiple corer were treated as statistical units in the samples from 1971. The confidence limits in the 1972 material refer to the variation of the subsamples.

The redox potential of the profundal sediment was measured from an undisturbed core sample with an area of 15.2 cm^2. A pre-ignited platinum sheet electrode and an Orion digital pH- and mV-meter were used. The values were corrected to those obtained with the normal hydrogen electrode and to pH 7.0. The organic matter of the sediment was measured as ignition loss at + 500 °C for 3 hours.

Sources of error. The sampling efficiency of the multiple corer is here considered to be comparable to that of the single corer with a tube of same size. This efficiency is c. 80 % in the conditions prevailing in the profundal of Pääjärvi and so the figures given may be slightly underestimated. The larger corer gives true values, especially when attached to a pole (Holopainen & Sarvala 1975).

In 1971 the macrofauna was not removed with an additional sieve. However, members of *Pisidium* were afterwards excluded from the counts and biomass calculations, since all of them are retained on the 0.4-mm sieve. In 1972 the numbers of macrofauna in the littoral and profundal regions were, respectively, 5—11 % and 2—3 % of those of meiofauna. So the effect of the macrofauna on the numbers and biomasses is negligible, particularly as the biomasses were calculated from the mean individual weights of the meiofauna.

In the sieving procedure, the water jet and the duration of sieving were kept as stable as possible in order to obtain comparable results. The amount of animals broken or going through the sieve was not tested. The early copepodid stages of some cyclopoids, for example, are likely to suffer in the sieving. In general, however, the meiobenthic animals seemed to stand sieving with a water jet fairly well and most were still alive when picked out. Storing the sieved samples up to ten days in a cool place (+3 °C) before picking out the animals did not affect the results, either.

The samples splitting is a possible source of error, if the distribution of subsample counts is biased. From the 8 to 32 subsamples five were chosen systematically for counting. These five always included the opposite ends of the division series and two others were both from one of the last divisions. At least no systematic error was caused by the splitter, because the left end of the division series (sample always coming from splitter compartment A) gave a higher estimate of the total fauna in 14 cases and the right (one compartment B) gave a higher estimate in 11 cases, this difference not being statistically significant (sign test). Further tests also showed the subsample counts to be unbiased (Holopainen & Sarvala 1975).

All the counting was done by the authors and checks revealed no significant differences between persons. Still, there may have been some variation in the counting efficiency during the two study years.

5. Results and comments

A. Representativeness of the permanent profundal stations

The maximum deviations of the densities of the meiofauna at the permanent stations from the mean densities of the random squares in the corresponding depth zones were 47.4 % and 39.7 % at 25 m and 65 m, respectively (Table 1). Most of the differences in total numbers were not statistically significant. The deviation at 25 m is mostly due to the great numbers of Ostracods at the permanent station and the low abundance of Nematodes in the random squares. The difference at 65 m is due to the greater abundance of Nematodes in the random squares. The spatial distribution of Nematodes is random at all the permanent stations but clearly contagious in the corresponding depth zones, so that there are great differences in abundance between larger areas in the same depth zone.

In spite of the differences noted above, the permanent stations of the profundal seem to represent the corresponding depth zones relatively well. The random square material is, however, too meagre for further discussion.

Table 1. The percentage deviations of the densities of the meiozoobenthos at the permanent sampling stations from the mean densities of the random samples from the corresponding depth zones in May 1971. ** = $P < 0.01$.

Permanent station (m)	Random samples depth (m)	n	Deviation (%)	Mann-Whitney U-value
8	5—10	6	7.6	10
14	10—20	5	23.9	8
25	20—30	6	47.4	0**
40	30—50	5	7.7	8
65	over 50	3	39.7	0

B. Vertical distribution in the sediment

More than 95 % of the meiobenthic animals live in the uppermost 2 cm of the profundal sediment and practically none lower than 3 cm, which agrees well with the vertical variation in the redox potential of the sediment. In the profundal of the unpolluted areas of Lake Päijänne the meiofauna goes a few cm deeper, though 95 % of the animals still occur in the topmost 4 cm. The oxidized zone of the sediment is thicker there than in Pääjärvi (Särkkä & Paasivirta 1972). According to Bretschko (1973), the Nematodes in Vorderer Finstertalersee also live in the top 4 cm of the sediment, which have a high water content. In three Mazurian lakes, Stanczykowska (1966) found that more than 90 % of the meio- and microbenthic animals dwelt in the uppermost 4 cm. In Lake Mälaren, Milbrink (1969) reported Cyclopoids and Nematodes from sediment layers deeper than 10 cm, but he used a different kind of sampler.

Thus it seems that the meiofauna most often inhabits only the loose, more or less oxidized, uppermost 2—4 cm of the sediment. Some of the exceptions reported may be due to invalid sampling methods. Obviously the vertical distribution of the micro- and meiofauna depends on the physical and chemical properties of the sediment (e.g. Kirchner 1975). Before starting any major quantitative study on meiozoobenthos it is therefore useful to work out the vertical distribution and limit laborious counting to this layer.

C. Abundance and biomass of the total meiozoobenthos

The mean annual population density of the meiozoobenthos in Lake Pääjärvi is between 80 000 and 230 000 ind./m² in the profundal and littoriprofundal and between 400 000 and 630 000 ind./m² in the littoral (Table 2). The corresponding biomasses (ash-free dry wt.) are 0.1—0.3 and 0.6—0.8 g/m². The highest values recorded for the profundal and littoriprofundal were 270 000 ind. and 0.34 g/m² (in late August at 13 m) and for the littoral 890 000 ind. and 1.08 g/m² mid-September at 2 m). At 13 m in the eastern bay the density is much higher than at the same depth in the western bay (Table 2). This is mostly due to the greater density of Nematodes and Harpacticoids at the former station. This may be caused by the greater inflow of water and thus also of allochthonous organic matter into the eastern bay (Ruuhijärvi 1974).

Forty per cent of the total biomass of the meiozoobenthos lies in the littoral and 20 %

Table 2. The mean annual numbers of the meiozoobenthos (thousands per m²) at different depths and the mean individual ash-free dry weights used.

		Permanent stations, depth (m)									
	μg/ind.	1	2	3	5	8	13	14	25	40	65
Turbellaria	2.5	1.2	6.0	4.1	2.7	1.2	3.2	3.8	3.3	2.1	2.7
Nematoda	1.3	178.2	186.0	50.0	5.70	6.79	135.5	107.0	94.0	53.4	34.2
Rotatoria	0.1	1.2	1.0	1.0	3.6	—	—	0.7	0.5	0.2	0.2
Oligochaeta	1.0	6.9	6.0	0.9	0.5	0.1	—	—	+	0.1	0.1
Cladocera		2.6	9.3	3.2	4.2	1.8	0.9	3.4	0.3	—	1.2
μg/ind.		2.3	2.3	2.5	2.7	2.3	3.0	2.7	2.0	—	2.8
Ostracoda		48.1	230.0	3.8	1.2	0.1	3.7	9.0	10.0	1.1	0.3
μg/ind.		2.9	0.8	1.9	6.8	1.7	1.7	2.1	2.1	1.7	1.3
Cyclopoida	1.0	90.0	75.0	49.1	26.7	16.1	19.1	25.2	17.2	30.0	19.7
Harpacticoida	1.0	45.1	58.6	19.1	17.1	23.2	59.1	13.0	7.7	21.6	19.5
Ephemeroptera	5.0	1.0	—	0.1	—	—	—	—	—	—	—
Ceratopogonidae	10.0	1.8	0.7	—	0.1	0.1	—	—	—	—	—
Chironomidae	4.0	16.2	45.2	14.8	8.6	5.8	2.7	2.8	0.6	0.3	0.3
Oribatei	7.5	2.6	0.2	0.3	0.4	—	—	—	—	—	—
Hydrachnellae		0.2	0.2	+	0.8	0.9	0.1	0.1	0.1	—	—
μg/ind.		11.0	7.6	10.0	14.1	11.5	12.0	10.0	10.0	—	—
Halacaridae		9.1	4.8	1.0	4.1	5.9	1.2	0.9	2.5	0.3	0.1
μg/ind.		0.5	0.4	0.5	0.5	0.4	0.5	0.5	0.4	0.3	0.1
Tardigrada	0.1	0.6	2.0	0.2	—	+	0.1	1.0	5.2	3.2	0.6
Total		404.8	625.0	147.6	127.0	123.1	225.6	166.9	141.4	112.3	78.9
Total g/m²		0.630	0.795	0.221	0.196	0.172	0.284	0.228	0.182	0.131	0.096

in the littoriprofundal, these zones themselves making up 15 and 27 % of the whole lake area, respectively.

The abundance of the meiozoobenthos is high compared with that in the unpolluted profundal areas of Lake Päijänne (17 000—44 000 ind./m², SÄRKKÄ & PAASIVIRTA 1972) or in the dystrophic and oligotrophic Polish lakes (STANCZYKOWSKA 1966). Data on the population densities of the freshwater meiobenthic animals have also been reported by MOORE (1939), GREZE (1951), COLE (1955), TSVETKOV (1959), STANCZYKOWSKA & PRZYTOCKA-JUSIAK (1968), MILBRINK (1969), SCHIEMER *et al.* (1969), SAKHAROVA (1970) and PREJS & STANCZYKOWSKA (1972), but comparison of the values is invalidated by the heterogeneity of the methods, e.g. different mesh sizes of sieves. High densities of the meiozoobenthos have been found in the sublittoral mud bottoms of the northern Baltic (1.5—2.7 × 10⁶ ind./m² with 0.1-mm sieve, ELMGREN 1973).

The bathymetric curve of the biomass of the meiozoobenthos follows that of the macrozoobenthos, having a steep decline between 2 and 3 m, a depression at 5—8 m and a slight peak at 13—14 m (Fig. 4). However, the difference between the littoral and profundal is not so pronounced as with the macrozoobenthos. The main factors affecting the bathymetric distribution pattern are evidently the steep decrease of the primary production at depths greater than 2 m, the widely fluctuating temperature and relatively low sedimentation rate at 5—8 m and the decreasing mean annual temperature below 20 m. The contents of organic matter and nitrogen in the surface sediment vary only slightly and their effect on the abundance of the meiozoobenthos is thus small.

The seasonal variation of density values is more pronounced in the littoral than in the profundal. The maximum abundance is reached at most sites in early autumn and the minimum in early summer. In eutrophic or polluted lakes the autumnal maximum is more marked because of the greater abundance of dormant Cyclopoids (SÄRKKÄ 1976).

D. Bathymetric and seasonal variation in the occurrence of the groups and species

The mean annual population densities and individual weights of the meiozoobenthos groups at different depths are shown in Table 2. The mean individual weights for Rotatoria, Halacaridae and Tardigrada are based on estimates made according to body size but for Turbellaria, Nematoda, Oligochaeta, Cyclopoida, Harpacticoida and Chironomidae they are the means of values obtained with a micro-balance for animals picked at random. It should be noted that the following survey is based only on the material obtained when an additional 0.4-mm sieve was used to remove the macrofauna. This technique has not commonly been used in earlier meiofauna studies.

Turbellaria

Found fairly evenly in the lake, a slight maximum at 2—3 m. Proportion of total biomass 0.5 (1 m) — 7 % (65 m). Maximum abundance in autumn. Except at 1 m, all the animals are *Gyratrix h. hermaphroditus*, whose eggs are abundant on the shells of *Pisidium*.

Nematoda

The most abundant group except at 2 m, where the Ostracods are dominant. The bathymetric distribution pattern resembles that of the total meiozoobenthos. Represents one third of the total biomass of meiofauna in the littoral and littoriprofundal, and about half in the profundal areas, the maximum proportion being 67 % (25 m). About 30 % of the specimens pass through the 0.1-mm sieve. The seasonal variation in numbers is not significant in the littoriprofundal and profundal, but there is a pronounced peak in September at 1 m and in November at 2 m (Fig. 2). The year-to-year variation in numbers is not significant (Fig. 3).

Thirty-seven species have been identified in the lake by Mrs. Eeva Ikonen (Haka *et al.* 1974). Abundant species in the littoral are *Tobrilus grandipapilloides*, *Ironus ignavus*, *Tripyla glomerans*, *Paraphanolaimus behningi*, Dorylaiminae spp., *Mononchus maduei* and *M. truncatus*, and in the profundal *Ironus tenuicaudatus* (30—70 % of the specimens), *Tobrilus grandipapilloides*, *Eudorylaimus carteri*, Dorylaiminae spp. and *Mononchus maduei*.

The abundance values presented here are much greater than in the profundal of Lake Päijänne, where particularly low values are recorded in the most eutrophic area (Särkkä & Paasivirta 1972). Some very high density values (300—2300 × 10^3 ind./m^2) have been reported in the sublittoral mud bottoms of the northern Baltic (Ankar & Jansson 1973, Elmgren 1973).

Rotatoria

The scarce occurrence may be partly due to the small size of the animals, which allows them to pass through the sieve. A slight maximum can be observed at 5 m. Nearly all the animals belong to sessile *Dissotrocha* species.

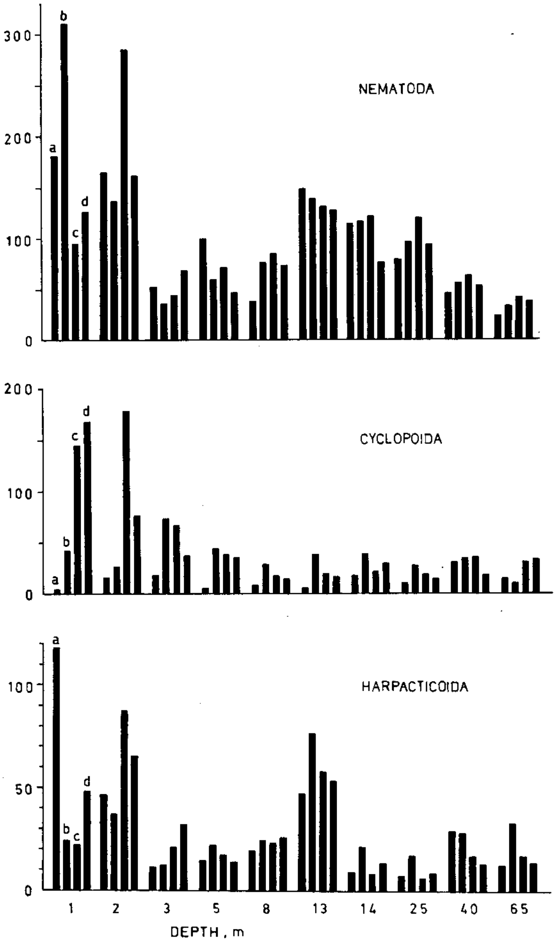

Fig. 2. The seasonal variation (numbers in thousands per m^2) in the numbers of three meiobenthic groups at different depths. a: June 1972, b: September 1972, c: November 1972, d: February-March 1973.

Oligochaeta

Meiobenthic animals are fairly abundant in the littoral, but very scarce in the littoriprofundal and profundal. In the littoral abundance peaches a peak in September, when small Naidids predominate. The densities in the profundal of the eutrophic part of Lake Päijänne are much greater than in the profundal of Pääjärvi (Särkkä & Paasivirta 1972).

Cladocera

The maximum is at 2 m, but they occur fairly evenly down to 14 m, although rather scarce at 13 m in the eastern bay. Their maximum proportion of the biomass is 6 %. The peak in abundance is mostly in early autumn in both the littoral and profundal. The occurrence of the meiofaunal species is presented in Table 3.

Table 3. Occurrence of the meiobenthic Cladocera in Pääjärvi.

	Sites of occurrence					Maximum occurrence	
	Macro-phytes	Stony belt	1—2 m	3—5 m	over 5 m	depth m	month
Sida crystallina	+	—	—	—	—		
Ceriodaphnia pulchella	+	+	+	—	—	2	VI
Daphnia spp.	—	—	—	+	+		
Scapholeberis mucronata	+	—	—	—	—		
Bosmina spp.	—	+	+	+	+		
Ilyocryptus acutifrons	—	—	—	+	+	14	VIII
I. sordidus	—	—	+	+	—	3	VI
Ophryoxus gracilis	—	—	+	—	—	1	IX
Acroperus harpae	+	+	+	—	—	1	IX
Alona affinis	+	+	+	+	+	1	IX
A. quadrangularis	—	—	+	+	+	2	IX
A. rectangula	—	+	+	—	—	1—2	VI
Alonella excisa	—	—	+	—	—	1	VI
A. nana	—	+	—	—	—		
Alonopsis elongata	—	+	—	—	—		
Camptocercus rectirostris	+	—	+	—	—		
Chydorus spp.	+	+	+	—	—		
Eurycercus lamellatus	+	—	+	—	—		
Graptoleberis testudinaria	+	—	—	—	—		
Monospilus dispar	—	+	+	—	—		
Peracantha truncata	+	+	—	—	—		
Pleuroxus laevis	+	—	—	—	—		
P. trigonellus	—	+	+	+	+	1	IX
P. uncinatus	—	—	+	—	—		
Polyphemus pediculus	—	+	—	—	—		

Ostracoda

The Ostracoda are the most abundant group at 2 m, and reach a lower peak at 14—25 m. This group is also rarer in the eastern bay, Unlike the abundance, the proportion of the biomass is nearly the same at 1 m and 2 m (about 23 %) going down to 12 % at 25 m and not exceeding 10 % at the other depths. The seasonal fluctuation in numbers is pronounced only in the littoral, where the peak lies in June (1 m) and in September (2 m).

The abundance is greater at corresponding depths in the semi-polluted profundal areas of Päijänne (SÄRKKÄ & PAASIVIRTA 1972) as well as in the more eutrophic Lake Mälaren in central Sweden (MILBRINK 1969). Much higher values have also been reported in the sublittoral mud bottoms of the northern Baltic (18—73 × 10^3 ind. / m^2, ANKAR & JANSSON 1973, ELMGREN 1973). Most mature individuals (excluding *Darwinula*) are retained on the 0.4-mm sieve.

Darwinula stevensoni. Found only at 1—3 m; the highest density observed is 566 000 ind./m^2 at 2 m, but there were only 66 000 ind./m^2 at 1 m and 3500 ind./m^2 at 3 m. These values were all recorded in September, when the population mainly consisted of young individuals. About 97 % of the Octracods at 2 m belong to this species.

Candona spp. Permanent member of the benthos down to 14 m, the maximum being reached in June, when the majority of the *candida* group consists of younger animals, and the population density is 2000 (14 m) — 80 000 ind. / m^2 (1 m). The seasonal and bathymetric variation in occurrence reflects the partitioning of food supplies with the previous species. The stony belt has its own species.

Cytherissa lacustris. A permanent inhabitant of the depth zone of 13—65 m, but found up to 2 m. The highest density was recorded at 25 m (16 000 ind./m^2) in late August, but the value was nearly as high at 14 m in November. The mean individual weight is lowest in winter or early summer.

Cypridopsis vidua. Restricted to the uppermost 1 m, maximally 1200 ind./m^2. Frequent in the stony belt as well.

Cyclocypris spp. Occurs sparsely in the depth zone of 0—5 m, the maximum being 1600 ind. / m^2 at 2 m.

Cyclopoida

The mean densities do not exceed 100 000 ind. / m^2 in the littoral and 30 000 ind./m^2 in the profundal. The proportion of the biomass is between 7 % (13 m) and 23 % (3 and 40 m). The densities are much higher in autumn and winter, especially in the littoral and littoriprofundal (Fig. 2). This is evidently due to the greater proportion of pelagic animals lying dormant

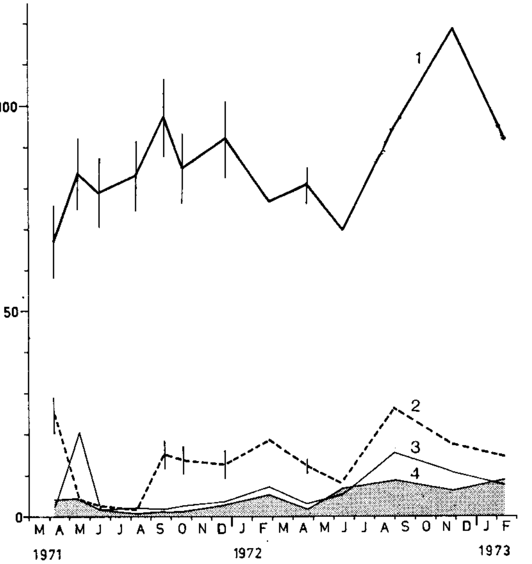

Fig. 3. The year-to-year variation in the numbers (thousands per m²) of the main meiobenthic animal groups at a depth of 25 m. 1: Nematoda, 2: Cyclopoida, 3: Ostracoda and 4: Harpacticoida. The vertical lines represent 90 % confidence limits.

on the bottom in wintertime. According to SARVALA (unpubl.), in winter some 70—80 % of the benthic Cyclopoids in Pääjärvi are of pelagic origin. Similar seasonal variation in numbers has been found earlier in many studies (e.g. SMYLY 1961, STANCZYKOWSKA & PRZYTOCKA-JUSIAK 1968, SAKHAROVA 1970, PREJS & STANCZYKOWSKA 1972, SÄRKKÄ 1976). The abundance on the bottom is greatly influenced by the Cyclopoid production in the water above (SÄRKKÄ & PAASIVIRTA 1972).

The main true meiobenthic species are *Paracyclops fimbriatus* and *Diacyclops nanus* in the littoral and littoriprofundal, *Diacyclops abyssicola* throughout the profundal and *D. nanus* (identified by Dr. J. Sarvala) in the upper profundal (HAKA *et al.* 1974).

Harpacticoida

Two peaks of abundance (about 55 000 ind./m²), at 1—2 m and at 13 m. The density at 14 m in the western bay is only one quarter of that at 13 m in the eastern bay, where the surface sediment bears evidence of water currents near the bottom. Harpacticoids constitute 7—9 % of the biomass in the littoral and littoriprofundal, and about 20 % at 13 m and 65 m. Density reaches a maximum in early summer at 1 m, in wintertime at 2—3 m and in early autumn at most deeper sites (Fig. 2).

The abundance of hypoprofundal Harpacticoids in Lake Päijänne is much lower than in Pääjärvi (SÄRKKÄ & PAASIVIRTA 1972). The group seems to be rather sensitive to oxygen deficits, thus suffering from eutrophication (MILBRINK 1969, ANKAR & JANSSON 1973). In the northern Baltic, the corresponding density values are 13—129 × 10³ ind./m² (ANKAR & JANSSON 1973, ELMGREN 1973).

According to J. Sarvala (HAKA *et al.* 1974), the main littoral species in Pääjärvi, in sequence of decreasing biomass, are *Attheyella crassa*, *Paracamptus schmeili*, *Moraria brevipes* and *M. mrazeki* and the main profundal species are *Bryocamptus echinatus*, *P. schmeili*, *M. brevipes* and *A. crassa.*

Ephemeroptera

The only meiobenthic animals found are young individuals of *Caenis horaria*, which occur constantly at 1 m, being most abundant in autumn and winter.

Ceratopogonidae

Young larvae of two species of the *Palpomyia* — *Bezzia* group are frequently found at 1—2 m and occasionally down to 8 m.

Chironomidae

Abundance has a pronounced peak at 2 m and decreases sharply below 8 m. Chironomids make up about 25 % of the total biomass at 2—3 m, about 15 % at 1 m and 5—8 m, and less than 5 % below 8 m. Seasonal variation in numbers is apparent only in the littoral, where the maximum occurs in September. The meiofaunal species most often found in the littoral samples are *Parakiefferiella bathophila*, *P. coronata*, *Pseudosmittia smolandica*, *Cryptocladopelma viridula*, *Paralauterborniella nigrohalteralis*, *Cladotanytarsus* spp., *Constempellina brevicosta*, *Stempellina bausei*, *S. subglabripennis*, *Stempellinella minor* and *Tanytarsus* spp.; the most frequent species in the profundal are *Mesocricotopus thienemanni*, *Micropsectra* sp., *Stempellinella minor* and *Tanytarsus* spp.

The profundal meiobenthic Chironomids have been shortly dealt with in an earlier paper (PAASIVIRTA 1974) and the littoral ones will be treated in the near future.

Oribatei

Concentrated in the uppermost 1 m, but occasionally found down to 5 m. Most numerous just near the water's edge in algal and stony areas, but very rare on macrophytes.

Hydrachnellae

The meiobenthic animals are most abundant at 5—8 m and are lacking at depths greater than 25 m. Their proportion of the biomass is nowhere more than 6 %. The commonest species are *Limnesia connata*, which has its main occurrence at 5—8 m, and *Hygrobates nigromaculatus*, which is restricted to 5 m. Other species in the littoral and littoriprofundal are *Piona* spp., *Forelia liliacea*, *Brachypoda versicolor* and *Midea orbiculata*, mostly immature individuals, and in the profundal *Acalyptonotus violaceus*, which in Fennoscandia has earlier been reported only from some subarctic lakes in Sweden and Lake Siljan in central Sweden (LUNDBLAD 1962).

Halacaridae

Maximum at 1 m but fairly abundant down to 25 m. Not constituting more than 2 % of the total biomass. The occurrence of the species in Pääjärvi has been described earlier (Paasivirta 1975).

Tardigrada

Most abundant at 25 m, with a minor peak at 2 m. Some animals presumably pass through the 0.1-mm sieve. Abundance shows seasonal variation in the profundal, reaching a maximum in winter. The profundal species is *Macrobiotus dispar* (identified by T. Hallas, Copenhagen).

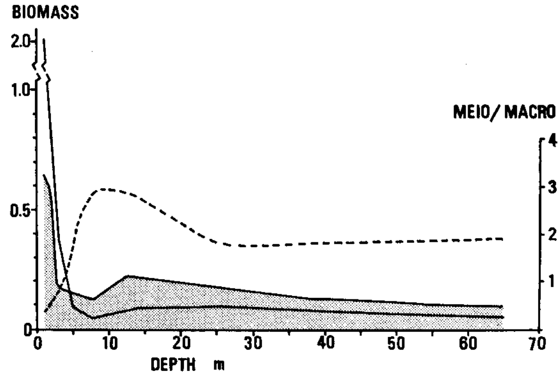

Fig. 4. The mean annual biomasses of the meiozoobenthos (shaded area) and macrozoobenthos (solid line), and the meio : macro ratio (broken line) at different depths in Pääjärvi.

E. The quantitative relationship between the meio- and macrofauna

The ratio between the densities of the meiofauna and macrofauna (retained on 0.1- and 0.4-mm sieves) respectively is 10—19 : 1 in the littoral and 41—52 : 1 in the profundal. The corresponding biomass ratios of the main animal groups occurring in both the macro- and meiofauna are shown in Table 4. The relationship of the mean annual biomasses at different depths is illustrated in Fig. 4. The proportion of meiofauna in the profundal areas is high compared with the figures reported earlier from other lakes. In the studies of Shcherbakov (1955), Tseeb (1958), Sakharova (1965) and Kajak & Rybak (1966), the biomass of the meiofauna did not exceed that of the macrofauna in the profundal, the biomass ratio thus being closer to that in the littoral area of Pääjärvi. The density ratios of the marine meio- and macrofauna are in most cases between 30 and 180 : 1 (McIntyre 1969), being higher in soft mud and comparatively deep water.

Table 4. Ratios between the meiofauna and macrofauna biomasses at different depths in the main animal groups belonging to both the meio- and macrofauna.

Depth zone	1—2 m	5—65 m
Turbellaria	2.1	7.1
Nematoda	4.4	19.4
Cladocera	0.6	10.0
Ostracoda	1.7	3.5
Cyclopoida	3.7	7.4
Chironomidae	0.2	0.3
Hydrachnellae	0.1	0.6

6. General discussion

The animals passing though the 0.1-mm sieve — and thus belonging to the microfauna — are apparently numerous. In the profundal c. 70 % of the Nematodes and only a few of the Rotatoria and Protozoa are retained. The densities of the microfauna may be high compared with those of the meio- and macrofauna, and the biomasses may also be considerable (e.g. Goulder 1974, Fenchel 1974, Thiel 1975).

In terms of production and assimilation, the relative importance of these smaller animals is evidently still more pronounced. In the profundal of Pääjärvi the production: biomass coefficient for the total macrofauna is c. 2 and if we assume a coefficient of 4 for the meiofauna (Gerlach 1971, Bretschko 1973, Haka *et al.* 1974) the meio : macro production ratio will be 4 : 1. Thus in an oligotrophic, mesohumic lake like Pääjärvi, the macrofaunal percentage of the total zoobenthic production in the profundal may be only 15—25, depending on the magnitude of the microfaunal production. In the littoral, the corresponding percentage may be 40—55, if we assume the P/B coefficients for the macro- and meiofauna to be 3 and 5, respectively.

Owing to the scantiness of basic biological information on the smallest size classes of animals, the role of the animals of the various size classes and their mutual relationships in the benthic systems of lakes is poorly understood.

Together with bacteria, yeast and fungi, the smallest animals play an important role in the recycling of nutrients but they may also make a significant contribution to the production of biomass and the consumption of oxygen in the benthic community.

Many crucial methodological and taxonomical difficulties must be solved before we can hope to elucidate the trophic relationships and structure of the various benthic communities. The great abundance and microdistributional patchiness of different species populations makes these systems extremely complex but interesting subjects for a community approach.

Acknowledgements. We wish to thank Associate Prof. RAUNO RUUHIJÄRVI, Ph.D., Head of the Lammi Biological Station, for excellent working facilities at the station. Our sincere thanks are also due to other members of the Pääjärvi project, especially Mr. ILPO HAKALA, M.Sc., Mrs. EEVA IKONEN, B.Sc., Miss ANJA LEISMA, M.Sc., Mr. PERTTI SAARISTO and Mr. JOUKO SARVALA, Ph.D., for their help in collecting the material. This work was supported financially by the Academy of Finland and the University of Helsinki.

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Received 16. V. 1976
Printed 15. IX. 1977