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Changes in the macrozoobenthos associations of polluted Lake Vanajavesi, Southern Finland, over a period of 50 years

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Long-term changes in the macrozoobenthos of Vanajavesi are described over 50 years from 1926, when the first benthic survey was made. This lake was then rather oligotrophic, but has become eutrophicated and polluted during the last two or three decades. Monitoring was started in 1965. The survey was repeated in 1971 and 1977 using identical methods. Some benthic stations were checked in 1966—1967 and 1974.

Between 1926 and 1965 the *Monodiamesa-Pontoporeia* community was replaced by a *Chironomus anthracinus* community in the profundal of the central basin of Vanajavesi. Regressive species were still present, especially in the sublittoral. Between 1965 and 1977 succession towards a *Chironomus plumosus* community was detected. *Pontoporeia* and *Monodiamesa* almost totally vanished. *C. plumosus* and oligochaetes became more abundant.

Changes in the macrozoobenthos of the other basins, which are heavily polluted by industrial or municipal effluents, were rather small during the period 1965—1977. A slight improvement was detected in 1977. This was indicated by a change in the bathymetric distribution of benthos. The profundal areas near the pollution outfall, which were totally desolate, were colonized by *C. plumosus* in 1977.

In general, the bottom faunal lake type system proposed by Brundin seems to be applicable in the large polluted lakes of the Finnish lake district. Besides the chironomid fauna *Pontoporeia affinis*, in particular, is one of the most useful organisms for analysing the degree of pollution in the lakes studied.

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1. Introduction

According to Odum (1971) pollution is now one of the most important limiting factors for man. In Finland the most serious environmental problems are caused by water pollution. The Finnish lakes are particularly sensitive to domestic sewage and industrial wastes. They are shallow, their water is poor in electrolytes and rich in humus substances, and the duration of ice cover is long (Ryhänen 1962a).

Another special feature of the pollution ecology of Finnish inland waters is that in most cases the pollution is directed into the large lakes, which usually constitute long chains of incompletely isolated basins. Therefore the influence of waste waters can extend as much as scores of kilometres downstream in the watercourse, as in rivers.

The object of this study, Lake Vanajavesi, is a typical system of such large lakes. For a hundred years the lake has been under pressure by waste water loading, but during the last two or three decades the serious ecological consequenses have developed rapidly. The first macrozoobenthos samples were collected as early as in 1926 (Järnefelt 1929), and are the oldest quantitative data reported from the large Finnish lakes.

Benthic fauna is generally regarded as one of the most suitable groups of organisms for studies concerning the ecology of water pollution in lakes (e.g. Thienemann 1920, Järnefelt 1953, Brundin 1956, Hynes 1960, Bagge & Jumppanen 1968, Warren 1971). The distribution and abundance of most benthic macroinvertebrates can be expected to reflect a general level of production or trophic status of a lake, because the processes of production directly alter the benthic environment. Eutrophication changes both the texture of the bottom sediments and their edible organic detritus content. The production of the benthic invertebrates increases to a certain limit, at which the lack of oxygen and other unfavourable consequences of the intensified microbial activity exceed their tolerance limits.

This fact has led to various lake typologies and to the use of indicator species. The evaluation of the trophic status on the basis of various indicator lists or indices has been criticized by several authors (e.g. Hynes 1960, Elster 1966, Harman 1974). In most cases these lists have been made up without sufficient knowledge of the ecological requirements and taxonomy of the indicator species. They also fail to accommodate the uniqueness of each body of water, each pollutant and each problem. Another evaluation method is to analyze macroinvertebrate associations and to take into account the complications caused by the physical complexities of each watercourse (cf. Johnson & Brinkhurst 1971).

The main object of most studies concerning bottom fauna and eutrophication is to classify different bodies of water according to their trophic status. However, eutrophication is a dynamic process. Relatively few benthos studies deal with lake succession caused by pollution over a long period of time. One of the best known examples is that of Lake Erie, where a 1930 survey was repeated in 1961 by Carr & Hiltunen (1965) using similar methods and sampling locations. In northern Europe Wiederholm (1974b, 1978) analysed the long-term changes in the profundal benthos of the largest Swedish lakes (Vänern, Mälaren and Vättern) since the beginning of this century. Morphometrically, however, the Finnish lakes are quite different and this kind of study is lacking in our hydrobiological and limnological literature. The aim of this paper is, therefore, to describe the changes in macroinverbrate benthos associations during the last fifty years in Vanajavesi.

2. Study area

2.1. Definition of the study area

The study area consists of four bodies of open water in the lake complex of Vanajavesi: Hattulanselkä, Vanajanselkä, Kärjenniemenselkä and Rauttunselkä (Fig. 1), and they are called sub-areas in this paper. They are a part of the drainage basin of the river Kokemäenjoki.

The limitation of the study area is mainly based on the results of Ryhänen (1962c-d). He pointed out that the central basin of the study area, Vanajanselkä, is under pressure by waste waters from two directions. Besides the wastes from the upper course it also receives impurities from the opposite direction, as a backward current near the lake bottom (Fig. 2). Therefore the study area must also include those bodies of open water which are situated just below the main source of waste waters (Hattulanselkä downstream from the town of Hämeenlinna and Kärjenniemenselkä from the town of Valkeakoski) as well as Rauttunselkä, which connects both the main branches of the watercourse (Fig. 1).

The directions of the waterflow in the Vanajavesi lake complex is indicated in Figs. 1 and 2.

2.2. Waste water load

The waste water load is principally directed to the study area from the settlement and industry of the towns of Hämeenlinna and Valkeakoski (Fig. 1). Hämeenlinna is the biggest centre of urban settlement, and had a population of 40 800 in 1976. Its municipal sewer network was taken into use in 1911. Valkeakoski is an industrial centre with 22 400 inhabitants. A paper factory and a wood pulp mill were founded there in 1871, a sulphate pulp mill in 1880 and a suplhite pulp mill in 1907. The scattered waste water loads of small villages and summer cottages have minor importance as sources of pollution.

The very high oxygen demand of the waste waters from Valkeakoski (Table 1) is mainly due to the wood-processing industry wastes. The nutrient content of these waters is rather low. There is also a chemical fibre factory in Valkeakoski. Its waste waters are highly toxic because of many sulphur compounds and heavy metals (cf. section 2.4).

The load from the Hämeenlinna area is characterized by a smaller amount of waste water with a lower oxygen demand, but a greater nutrient content than from Valkeakoski (Table 1). The waste waters of settlements and many small, chiefly foodstuffs factories have severely polluted the narrow chain of lakes (including Hattulanselkä) between Hämeenlinna and Vanajanselkä. The organic wastes have time to become mineralized before they reach Vanajanselkä. However, they still have a fertilizing effect.

The waste water load from Valkeakoski has increased strongly during the last 50 years. If the load is estimated using production numbers and pollution effect equivalents for various branches of industry (Imhoff 1956, Sierp 1959), the total load corresponds to a BOD load from the sewage of approximately 100 000 persons in 1924. Ryhänen (1962b) used the same method and estimated the total load in 1954 to be 480 000 persons. According to Jokinen et al. (1974) the measured total load of Valkeakoski had a BOD corresponding to that of 1 200 000 persons in 1974. Since then the waste water load has decreased, because the new washing plant and the chemicals recovery plant of the sulphite pulp mill and the new municipal sewage treatment plant of the town of Valkeakoski were taken into use in 1975. On the other hand, the international economic

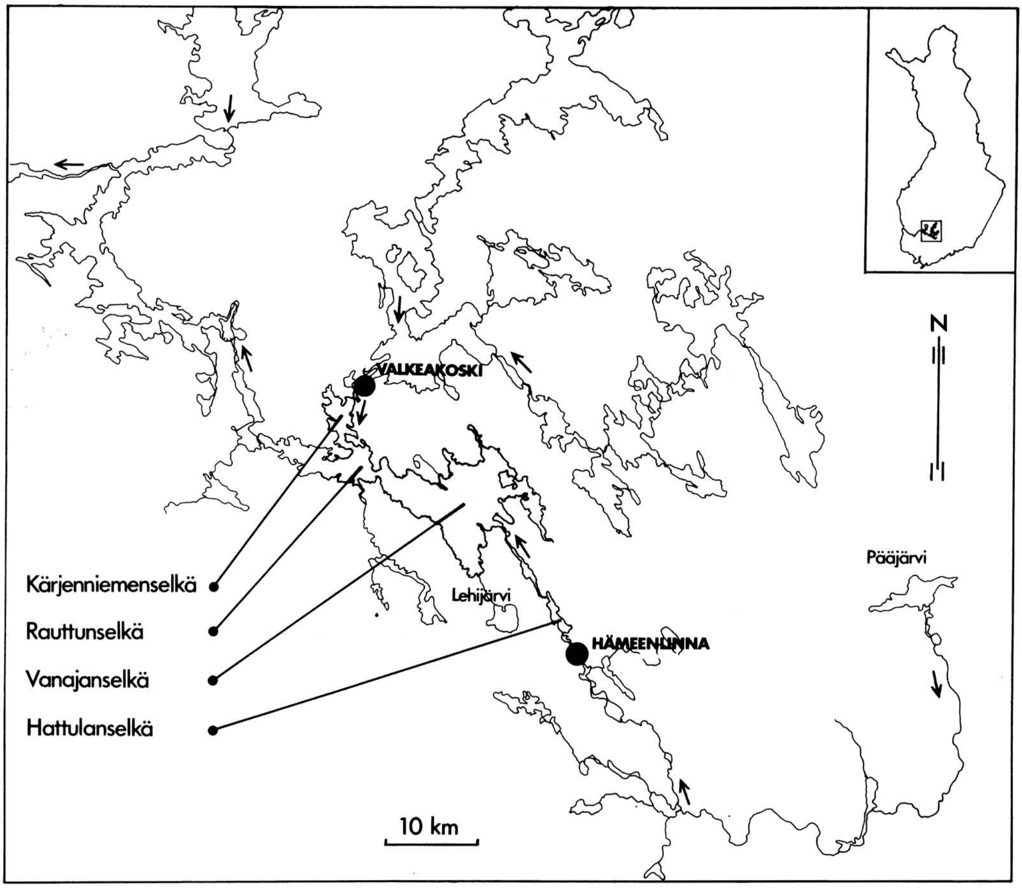


Fig. 1. The southern part of the drainage basin of the river Kokemäenjoki and location of the study area. Direction of the water flow is indicated by arrows.

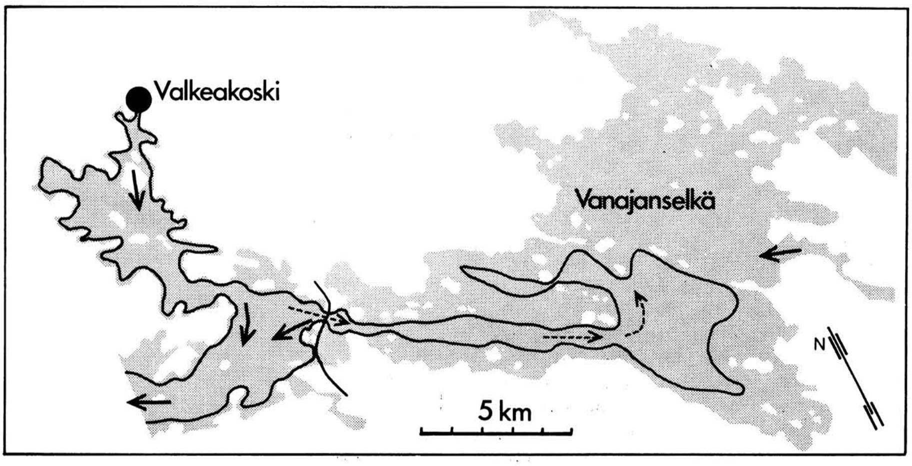


Fig. 2. The distribution of the effluents from the wood-processing industry 1.IV.1976. Delimited area = sodium lignosulphonate concentration of the water over 5 mg/l (measurements Kokemäenjoen vesistön vesiensuojeluyhdistys). For further explanation, see text.

Table 1. The waste water load (kg/day) directed into the study area and the upper course of Vanajavesi in 1977 (Oravainen 1978).

	BOD_7		Solid material		Phosphorus		Nitrogen	
From Valkeakoski	21 383	90 %	13 228	90 %	24.2	35 %	408	34 %
From Hämeenlinna area	2 450	10 %	1 405	10 %	44.2	65 %	810	66 %
Total load	23 833	100 %	14 633	100 %	68.4	100 %	1 218	100 %

recession during the second half of the 1970s caused a decrease in the industrial production and thus the waste water load, too.

2.3. Lake basins and their hydrology

Hattulanselkä and Kärjenniemenselkä, as the recipients of wastes, have the smallest area, mean depth and volume (Table 2). These bodies of open water are throughflow basins, their theoretical retention times being only 14—16 days because of the high mean discharge in relation to lake volume.

The most important detail in the morphometry and hydrology of the Vanajavesi lake complex is the Rauttunselkä basin, because part of the industrial wastes from Valkeakoski flow through it into Vanajanselkä, i.e. upwards in the watercourse. One of the main deeps of Rauttunselkä begins just at the point of the basin where the Kärjenniemenselkä water body empties into Rauttunselkä (Fig. 3). The valley in the lake bottom deepens quite evenly from 5 to 23 m straight towards the narrow sound which connects Rauttunselkä with Vanajanselkä. Behind the sound a chain of deeps continues quite a distance into Vanajanselkä. Downstream from the valley-like deep described above there is a sill across the basin of Rauttunselkä which reaches to 3—5 m below the surface.

Rauttunselkä receives heavily polluted water from Kärjenniemenselkä and purer water from Vanajanselkä. Mixing is incomplete, particularly in winter, and waste waters tend to sink to the bottom due to their greater density. Water from Vanajanselkä therefore forms a layer above the water from Kärjenniemenselkä (Ryhänen 1962c). The phenomenon is strengthened because both water masses discharge into Rauttunselkä from completely opposite directions (Fig. 2). In addition, the proportion of the mean discharge from heavily polluted Kärjenniemenselkä is 61 % of the total discharge into Rauttunselkä. The waste waters easily penetrate upstream into Vanajanselkä following the slope of the bottom (Fig. 2). The extent of this strange phenomenon varies greatly from year to year (Rautalahti-Miettinen 1977).

Vanajanselkä has the greatest area and mean depth (Table 2). Because of the high volume the theoretical retention time is much longer than in the other bodies of open water, 490 days. The basin is divided into two sub-basins by a submerged ridge running SE to NW (Fig. 3). The influence of waste waters from the Hämeenlinna area is mainly restricted to the north-eastern sub-basin. The penetration of the industrial wastes of Valkeakoski via Rauttunselkä into Vanajanselkä is limited to the south-western sub-basin, but during some winters (first in 1972) even the northeastern sub-basin has been affected by them.

Until 1959—1960 Vanajavesi was an unregulated lake. Since then the mean water level has been lowered c. 20 cm by running off considerable amounts of water during winter. This has largely eliminated spring flooding, while the summer level has remained somewhat higher than earlier.

On average, the duration of ice cover in Vanajavesi is 148 days, from 11th December to 8th May (Hydrologinen vuosikirja 1962).

2.4. Physical and chemical properties of lake water

The first detailed data of the physico-chemical properties of the water were reported by Ryhänen (1962a-d) from the 1950s. Some earlier information on hydrochemical characteristics has been published by Witting (1914) and Järnefelt (1929, 1956). In 1964 the local association for water protection (Hämeen vesiensuojeluyhdistys ry., later Kokemäenjoen vesistön vesiensuojeluyhdistys ry.) started an annual survey of the abiotic conditions in Vanajavesi together with the National Board of Waters, Finland (Hämeen vesiensuojeluyhdistys 1965a-b, 1967, 1968, Kokemäenjoen vesistön vesiensuojeluyhdistys 1969, 1970, 1971, 1972a-b, 1974, Keto 1975, Oravainen & Mankki 1976, Oravainen 1977, 1978).

Temperature

The summer stratification of each sub-area is unstable because they are rather open and shallow in proportion to

Table 2. Morphological and hydrological properties of the lake basins according to Kajosaari (1964).

	Kärjenniemenselkä	Rauttunselkä	Vanajanselkä	Hattulanselkä
Area (km^2)	11.8	27.8	119.2	8.4
Mean depth (m)	3.4	4.8	7.9	2.8
Max. depth (m)	15	24	24	13
Mean volume MC ($10^6 \times m^3$)	47.6	133.4	936.7	23.7
Mean discharge MQ (m^3/sec)	35	61	22	19
Theoretical retention time MT (days)	16	25	490	14

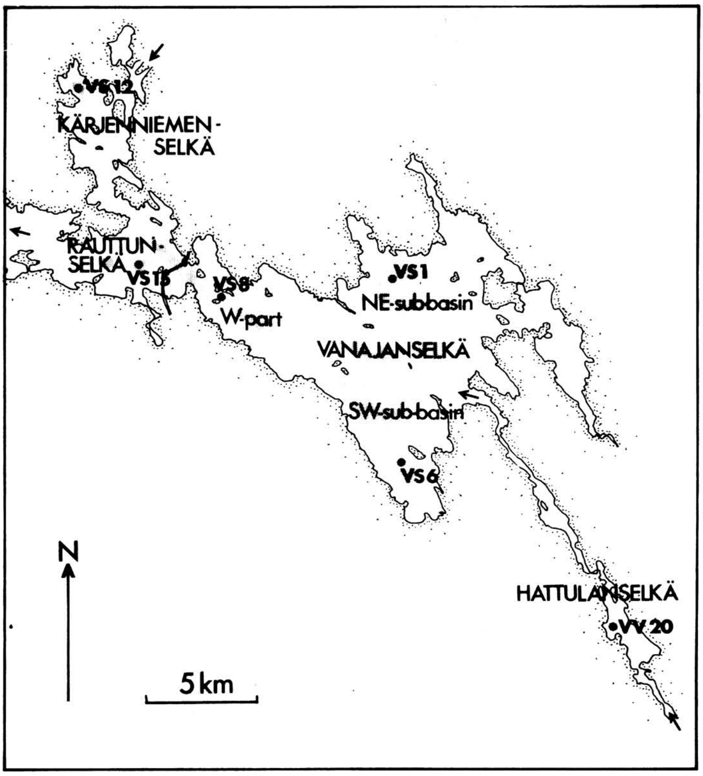


Fig. 3. The study area. Shaded area = depth over 12 m. The location of the hydrographic stations is indicated by black dots.

their area and/or because the water flow through the basins is quite fast. The duration and stability of the stratification depends on weather conditions. During a calm and warm summer the temperature difference between the surface and the bottom is clear and the thermocline usually lies at a depth of about 10 m (Fig. 4A). During a cold, windy summer the stratification can be totally absent (Fig. 4B). Because of the efficient mixing the bottom temperature can rise to 16—17 °C in late summer, even in the deepest places.

The physical conditions in winter are chiefly determined by the weather before the lake freezes (Ryhänen 1962c). In autumn, when the water has cooled down to about the temperature at which its density is greatest, the first spell of cold calm weather will cause the lake to freeze suddenly. In a windy autumn, on the other

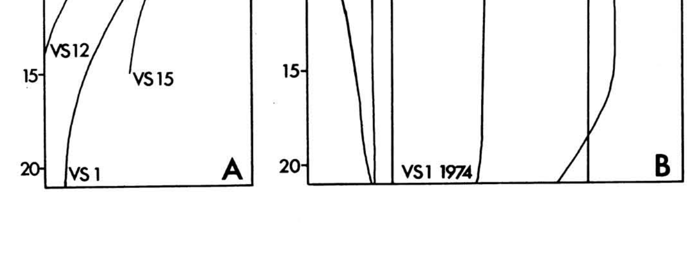


Fig. 4. a) Temperature curves for the three localities indicated in Fig. 3 during a warm summer. b) Temperature conditions in Vanajanselkä in 1974 (cool summer).

Table 3. Mean values of oxygen concentration (mg/l) and the oxygen saturation (%) in Kärjenniemenselkä (VS 12), Rauttunselkä (VS 15), Vanajanselkä, western part (VS 8), southwestern sub-basin (VS 6), northeastern sub-basin (VS 1) and Hattulanselkä (VV 20) derived from measurements made during March and April in 1970—1978, July and August in 1970—1977 (Kokemäenjoen vesistön vesiensuojeluyhdistys ry. and National Board of Waters). For location of sampling sites, see Fig. 3.

Depth	VS 12		VS 15		VS 8		VS 6		VS 1		VV 20	
m	mg/l	%	mg/l	%	mg/l	%	mg/l	%	mg/l	%	mg/l	%
March-April:												
1	4.6	34	9.5	69	11.1	80	10.3	74	11.2	81	6.3	45
5	1.5	11	2.8	27	10.3	74	10.2	75	10.8	79	4.2	31
10	0.3	3	0.5	8	2.9	16	4.8	36	8.5	62	1.1	8
15	0.3	3	0.2	4	1.2	9	2.3	17	3.8	29		
20					0.1	3	0.5	5	0.7	5		
July-August:												
1	3.5	39	6.7	74	8.0	93	9.0	96	8.7	95	8.7	96
5	2.1	23	5.9	65	—	83	8.4	85	8.0	83	5.4	58
10	0.1	1	4.8	51	6.5	65	7.8	82	7.0	72	0.4	4
15	0.0	0	3.0	32	5.6	49	6.2	62	3.5	35		
20					4.4	38	4.6	48	0.7	9		

hand, the water mass may become noticeably colder before the lake freezes. According to Aho (1978) Vanajanselkä effectively cools in autumn. The mean temperature of its water mass varied in 1964—1977 between 1.24 and 3.64 °C (mean 1.95 °C). This has an important influence on the oxygen consumption during winter. However, the duration of ice cover is a more important factor for the development of oxygen content in a heavily loaded lake such as Vanajavesi (Aho 1978).

Oxygen

Late winter is generally the most critical period in an ice covered and heavily loaded lake in Finland. In Vanajanselkä the regulation of water level renders the winter oxygen content still poorer because the volume of lake water is smallest in winter and therefore the dilution of waste waters is less effective.

The oxygen conditions during late winter at various depths and in different sub-areas are presented in Table 3. In Kärjenniemenselkä, in particular, but also in Hattulanselkä the oxygen concentration in the surface water just below the ice cover is very much lower than elsewhere in the study area (only 4.6 and 6.3 mg/l). The oxygen conditions in other sub-areas are good and the differences between them are small. At a depth of 5 m there is a notable oxygen deficit in Kärjenniemenselkä, and in Hattulanselkä and Rauttunselkä the conditions are almost as severe. There is no oxygen deficit at this depth in Vanajanselkä. The water layers between 10 and 15 m are almost totally de-oxygenated in Kärjenniemenselkä, Hattulanselkä and Rauttunselkä. The oxygen concentration also decreases rapidly in Vanajanselkä at this depth zone, especially in the western part which is situated near Rauttunselkä. At a depth of 20 m the oxygen deficit is severe in the whole of Vanajanselkä.

The oxygen conditions in Kärjenniemenselkä are even worse in summer than in winter (Table 3). In Hattulanselkä the oxygen concentration of the epilimnion is clearly higher in summer than in winter, but in the hypolimnion the conditions are as poor as in winter. Elsewhere they are, however, clearly better in summer, especially in the hypolimnion. This is mainly due to the instability of the thermal stratification. The influence of the heavy load from Valkeakoski can be seen in Rauttunselkä, where the

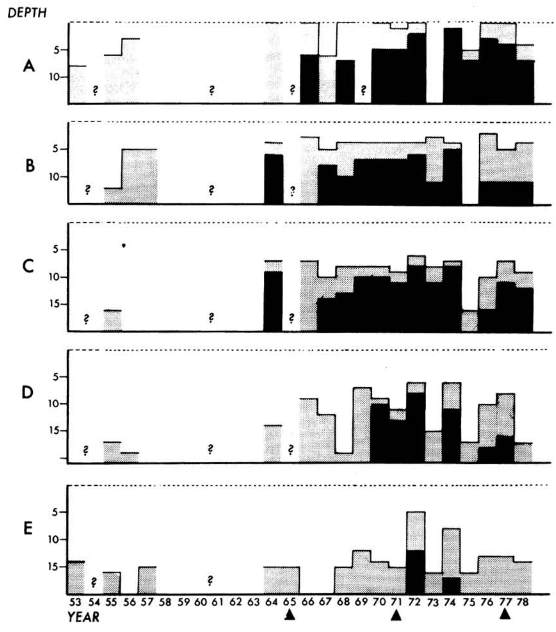


Fig. 5. The oxygen conditions in March-April 1953—1978 (Ryhänen 1962c, Kokemäenjoen vesistön vesiensuojeluyhdistys and Helsingin vesipiiri). Black = depth with no oxygen, shaded = oxygen concentration less than 5 mg/l, lightly shaded area = oxygen conc. greater than 5 mg/l. ? = results are lacking. A = Kärjenniemenselkä (VS 12), B = Rauttunselkä (VS 15), C = the western part of Vanajanselkä (VS 8), D = the south-western sub-basin (VS 6) and E = the northeastern sub-basin (VS 1).

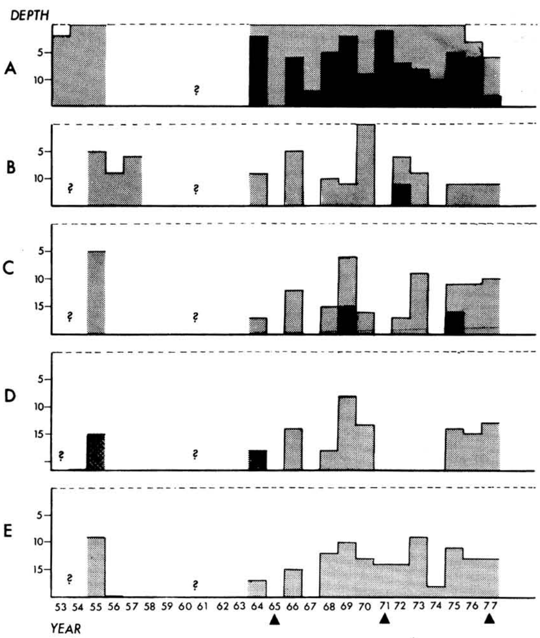


Fig. 6. The oxygen conditions in July-August 1953—1977 (Ryhänen 1962d, Kokemäenjoen vesistön vesiensuojeluyhdistys, Helsingin vesipiiri). For further explanation, see Fig. 5.

oxygen concentration at all depths (3—15 m) is lower than in Vanajanselkä. In summer the oxygen conditions in the hypolimnion of the northeastern sub-basin of Vanajanselkä are worse than in southwestern sub-basin and western part.

Comparable results of the oxygen concentration were first presented in the early 1950s by Ryhänen (1962c-d). Since then, however, there are gaps in our knowledge before the regular monitoring began in 1964 (Figs. 5 and 6). The great dispersal caused by different weather conditions makes it difficult to observe the long-term effects of the increasing waste water load.

No total oxygen deficit was observed in any sub-area in the 1950s, not even in Kärjenniemenselkä or in Hattulanselkä, where the conditions were, however, quite severe (Figs. 5 and 6). In Rauttunselkä and Vanajanselkä the oxygen conditions of the 1950's were fairly satisfactory when compared with those of 1964—1978, especially in winter. Between 1964 and 1978 the oxygen conditions were very poor in Kärjenniemenselkä (Figs. 5 and 6). The summer conditions have improved somewhat in 1976—1977, perhaps due to the reduction in the waste water load. In winter the oxygen concentration varied greatly with the mean discharge and the quantity of waste waters. It was sometimes "unnaturally" high because of the toxic inhibition of biogenic processes (Kokemäenjoen vesistön vesiensuojeluyhdistys 1974).

Total hypolimnic oxygen deficit was also an usual phenomenon in Rauttunselkä in the winters of 1964—1978. Since 1974 the thickness of the anaerobic water layer has decreased somewhat. During recent years the summer conditions have become a little better, too, and no total deficit, like that of 1972, has been observed.

The most evident long-term changes during the winters of 1964—1978 occurred in Vanajanselkä. The oxygen conditions in Vanajanselkä depend on how far the waste waters of Valkeakoski have penetrated each year. They mainly affect the western part of Vanajanselkä; a total oxygen deficit already occurred in 1964. Since then no clear deterioration or improvement has been observed. In the southwestern sub-basin the first total oxygen deficit was observed in winter 1970. Since then this has been repeated nearly every winter. During the last four years the conditions have been a little better than during 1970—1974. In the northeastern sub-basin total oxygen deficit has occurred only twice, during the winters of 1972 and 1974. These deficits were due to the fact that the sulphite wastes penetrated over the submerged ridge into the northeastern sub-basin, too. This had serious consequences on the fish stocks of Vanajanselkä. In both years thousands of kilograms of fish died, when the anaerobic wastes came welling up to the surface after the breaking up of the ice cover (Jokinen et al. 1972, 1974). No clear changes can be seen in the summer oxygen conditions in Vanajanselkä during 1964—1978.

Other properties of lake water

General information of some other physico-chemical properties of lake water is presented in Table 4.

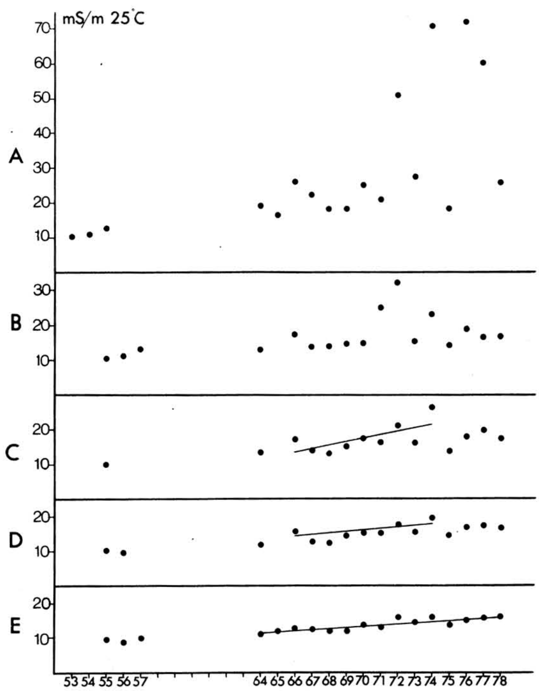


Fig. 7. The specific conductivity (mS/m + 25°C) of the water column in March-April 1953—1978. Trends at 95 % confidence level.

Table 4. Mean values of specific conductivity (mS/m +25 °C), chemical oxygen demand (mg O_2/l), pH, colour (mg Pt/l), total phosphorus (µg/l), total nitrogen (µg/l) and Secchi disc transparency (m) of the water based on measurements made during March and April in 1970—1978, July and August in 1970—1977.

	Depth (m)	March-April						July-August					
		VS 12	VS 15	VS 8	VS 6	VS 1	VV 20	VS 12	VS 15	VS 8	VS 6	VS 1	VV 20
mS/m	1	13	15	14	14	14	13	14	13	13	13	13	12
	5	39	20	14	14	14	16	15	13	13	13	14	12
	10	55	21	18	16	14	26	17	13	13	13	13	15
	15	57	24	22	18	15		39	13	13	13	14	
	20			23	21	17				14	14	14	
COD	1	32	14	14	13	12	12	23	15	14	13	13	15
	5	55	27	12	12	12	13	25	15	13	13	13	14
	10	63	37	35	23	12	14	30	14	13	13	13	15
	15	68	54	44	29	14		56	15	13	13	13	
	20			61	33	22				14	13	14	
pH	1	6.3	6.7	6.8	6.8	6.9	6.6	6.5	6.9	7.1	7.4	7.4	7.8
	5	4.8	6.3	6.8	6.8	6.9	6.6	6.4	6.9	7.1	7.1	7.1	7.2
	10	4.3	6.2	6.0	6.5	6.7	6.7	6.4	6.8	7.0	7.1	7.0	6.8
	15	4.4	6.5	5.9	6.4	6.6		6.4	6.8	6.9	7.0	6.8	
	20			6.6	6.8	6.7				6.8	7.0	6.8	
Colour	1	25	38	48	53	46	69*	34*	50	50	49	50	79
	5	42*	34	44	46	47	65*	26*	55	51	48	50	74
	10	44*	48	43*	49	46	77*	52*	52	56	50	50	111
	15	51*	131*	57*	62*	57		131*	62*	64*	52	63*	
	20			195*	109*	68				70*	72*	89*	
Total P	1	30	40	40	40	30	90	40	40	40	40	30	120
	10						440						770
	15	160	1070					300	70				
	20			580	220	90				80	80	100	
Total N	1	600	800	1100	1300	1000	1600	700	700	900	1100	1200	1200
	10						3800						2800
	15	1100	1800					2600	900				
	20			1800	1400	1000				1000	1100	1400	
Transparency		2.0	2.7	2.8	3.1	2.9	1.0	1.4	1.5	—	1.6	1.6	0.8

* Disturbing turbidity

A strange phenomenon is that the pH of the deep water can be very low (even below 4) in Kärjenniemenselkä in winter. This is due to the acid industrial effluents. Their influence can also be observed in Rauttunselkä and in the western part of Vanajanselkä, where the pH can be below 6 in winter.

Another noteworthy feature is the occurrence of zinc in the water and sediments of Vanajavesi. The following concentrations were analysed from the bottom sediments in the winter of 1978 (Helsingin yliopiston limnologian laitos 1979):

Kärjenniemenselkä	9.9—34.2 mg Zn/g (dry sediment)
Rauttunselkä	2.9— 3.3 mg Zn/g
Vanajanselkä	
western part	1.7— 1.8 mg Zn/g
southwestern sub-basin	0.6— 1.0 mg Zn/g
northeastern sub-basin	0.4— 0.9 mg Zn/g

These concentrations are much higher than the natural background concentrations, especially in Kärjenniemenselkä and Rauttunselkä.

Besides the oxygen content the specific conductivity is a useful parameter for comparison, because it gives a reliable picture of long-term changes. As shown in Fig. 7 the winter values have generally increased in each subarea since 1950s. The increase has been greatest in those parts of the study area, under the influence of Valkeakoski. In addition, the values indicate that the abiotic conditions in the Vanajavesi complex are most unstable in Kärjenniemenselkä and that the stability increases towards the northeastern sub-basin of Vanajanselkä.

3. Material and methods

Material was collected in 1965—1967, 1971, 1974 and 1977, between 25 July and 29 August. The number of sampling sites was 66 (Fig. 8). Fifty-nine of them were studied in 1965, 1971 and 1977; during other years only some of them were checked (11 in 1966, 7 in 1967, 16 in 1974). The 7 sampling sites of Hattulanselkä were sampled only in 1965. The samples were taken at the depths of 3, 5, 7, 10, 15 and 20 m. Some separate sites were placed in the deeps (15—20 m).

Each sample usually consisted of six hauls with an

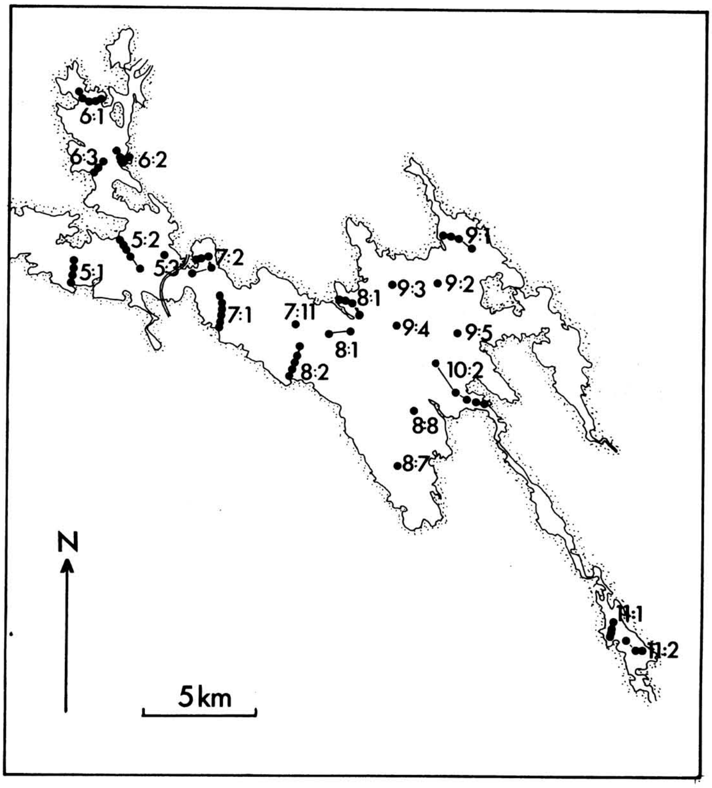


Fig. 8. The location of the benthic sampling stations.

Ekman-Birge grab (area 263 cm^2, height 23 cm, weight 6.7 kg). In some cases the number of hauls was reduced to 2—5 because large amounts of detritus or lake ochre interfered with sampling. The proportion of samples of reduced hauls made up 7.8 % of the total number of samples (N = 269). The total sample area in the whole study area was 39.8 m^2.

The samples were sieved through a 0.6 mm mesh. The sieving residues were examined as soon as was possible, mostly on the same day, on a white dish. The organisms were preserved in 80 % alcohol and weighed about 3—6 months later. The entire material consisted of about 41 000 individuals.

The sources of error and limitations of this widely used quantitative method are well known (e.g. Jonasson 1955, Kajak 1963). In this study the most important objective was to maintain the comparability of the results of different collections, not so much the exact quantitative estimation of the total benthos. The earliest study used in comparisons was made in 1926 (Järnefelt 1929). Järnefelt used an Ekman-Birge grab and 3—6 hauls, and the samples were taken in August just as in 1965—1977. The main point limiting the comparability was the mesh size; Järnefelt's was coarser (0.7—0.8 mm) than that used by the authors (0.6 mm). This caused greater sieving losses of oligochaetes and small insect larvae in the 1926 study. The sieving losses are, however, quite small or even negligible when dealing with large relict crustaceans, molluscs, *Chaoborus* larvae and those chironomid larvae whose head capsule is large enough to prevent them penetrating the mesh (cf. Jonasson 1955, Wiederholm 1974a). Järnefelt weighed the biomass after preservation, but there is no information about whether the preserving fluid was alcohol or formalin. The exact location of the 1926 sampling sites is also unknown.

There are also sources of error caused by temporal variablity in the distribution and abundance of benthic species. These vary from diurnal through seasonal to progressive changes (Brinkhurst 1974). Vertical diurnal migrations are known to occur in semipelagic *Chaoborus* and *Mysis relicta* populations, and the estimates of their population density are therefore unreliable when based on this method. The date of sampling is very important because of the great (up to 100-fold) seasonal variations in the abundance of bottom animals, especially of insects. It is known that there is a similarity in the character of the dynamics of abundance in different years and that it is specific for a given environment (Kajak 1963). When only one sampling is possible, it is best to choose the sampling time on the basis of knowledge of the dynamics of abundance in the given lake. All investigations in Vanajavesi have been made during late summer (25.VII—29.VIII). The variations were rather small during August (Kansanen, unpubl.). The concept of annual variation is not new. Halving or doubling of standing stocks in successive years has been reported by several authors (cf. Brinkhurst 1974). The causes of such variations are often little known. One possible cause of variations e.g. in chironomid populations is the failure of emergence because of unfavourable weather conditions.

4. Results

4.1. Vertical distribution of the macrozoobenthos as a whole

Vertical distribution of the total macrozoobenthos is a rough ecological measure, but it does, however, give a reliable picture of the general conditions of a lake (e.g. Brinkhurst 1974). The bathymetric distribution of the total number and biomass of animals in 1926, 1965, 1971 and 1977 is presented in Fig. 9.

In Vanajanselkä it is possible to compare the position of 1965—1977 that of 1926, when the abundance of bottom animals was quite low at all depths. However, there was a slight maximum in the deepest profundal (15—20 m), where the mean number of specimens was 282 ind./m^2 and the mean of biomass 0.98 g/m^2 (Järnefelt 1929). In 1965 the numbers of specimens were almost 11 times and the biomass values about 10 times greater than in 1926, viz. 2978 ind. and 9.53 g per m^2 in the profundal. In all surveys the maximum values of abundance were at the greatest depth (20 m). Although the bathymetric distribution has generally remained similar during 1965—1977, it is noteworthy that the abundance of animals seems to have decreased clearly in the deepest profundal since 1965. In the total biomass of 1977 there is even a slight decrease from 15 m to 20 m. In all cases the curves describing specimens and biomass run almost in parallel.

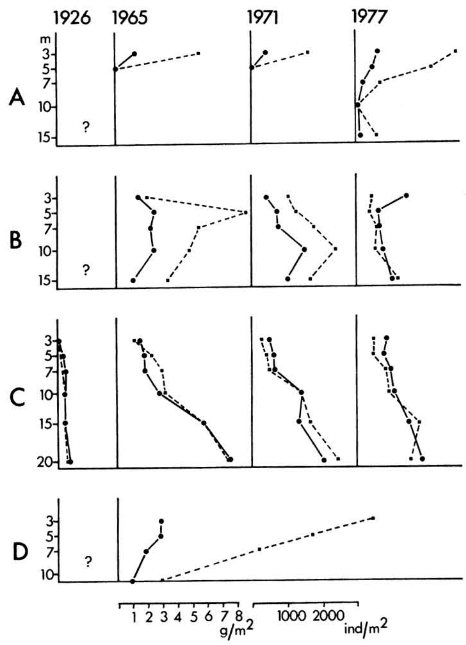


Fig. 9. The depth distribution of the number of individuals (solid line) and biomass (dotted line) of total benthos in Kärjenniemenselkä (A), Rauttunselkä (B), Vanajanselkä (C) in 1965, 1971, 1977 and in Hattulanselkä in 1965.

In Kärjenniemenselkä the situation is quite different. The occurrence of bottom animals was limited to the upper sublittoral (3—5 m) in 1965 and 1971. The biomass values were very high in samples from 3 m (in places more than 20 g/m^2). The anaerobic profundal and lower sublittoral were desolate. In 1977 the depth distribution had changed drastically; animals were found at every depth, but the clear maximum was still at 3 m. In the profundal (10—15 m) the abundance was very low when compared with Vanajanselkä and Rauttunselkä.

In Rauttunselkä the bathymetric distribution was, in principle, similar in 1965 and 1971. The maximum abundance was found at the depth zone of 5—10 m, where the biomass values especially were very high in 1965. Both the number and the biomass of animals were clearly lower at 15 m depth than in the depth zone of 5—10 m. A mass occurrence of *Chaoborus flavicans* larvae was found in the profundal of Rauttunselkä in 1971. This species has been excluded from the examination because of its semipelagic way of life (cf. Brundin 1949). In 1977 the bathymetric distribution of both abundance indices had changed and the biomass curve in particular was similar to that of Vanajanselkä, where the abundance increased with depth and reached its maximum in the lower profundal.

In Hattulanselkä a clear maximum of the biomass and the total number of animals was found in the upper sublittoral. The highest biomass values reached 20 g/m^2 as in Kärjenniemenselkä, but there was no clear inhibition of benthic production at any 3 m station of Hattulanselkä and animals were found deeper than in Kärjenniemenselkä, even in the profundal zone.

4.2. Delineation of profundal associations

Coefficient of community and percentage similarity of community

Two values are used here to delineate the profundal communities in 1965—1977; the coefficient of community (CC) and the percentage similarity of community (PS*c*) (Jaccard 1902, Renkonen 1938, Sanders 1960, Johnson and Brinkhurst 1971). The coefficient of community measures the percentage of species shared by two samples;

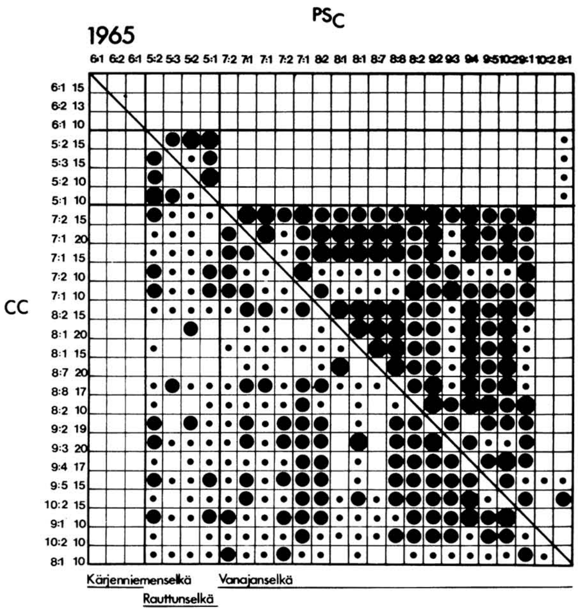
$$CC = \frac{c}{a + b - c} \cdot 100,$$

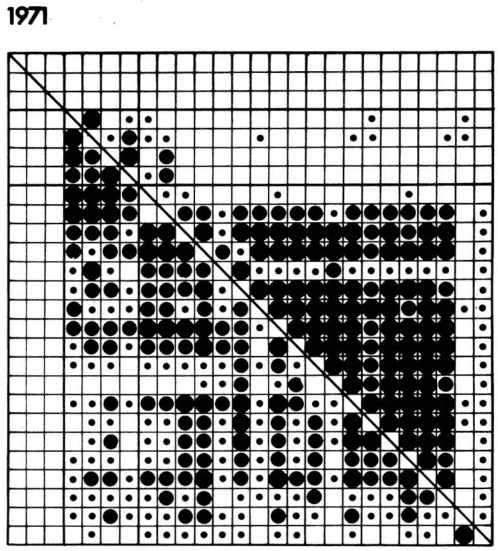
in which a and b are the numbers of species in samples A and B respectively and c is the number of species occurring in both. The percentage similarity of community takes into account the relative abundance of the species;

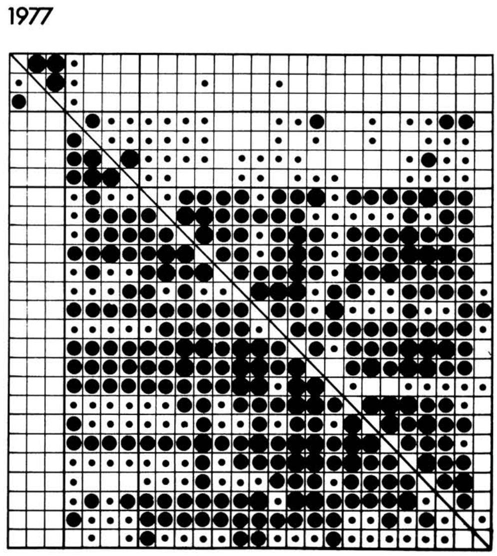
$$PS_C = \Sigma \min (a', b'),$$

in which a' and b' are, for each species the respective percentages of the total number of animals in samples A and B.

Each measurement has its advantages and limitations. The importance of minor species may







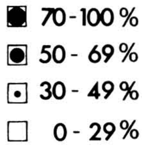


Fig. 10. Faunal affinity for profundal stations. Values of the coefficient of community (*CC*) in the lower left half, and percentage similarity of the community (*PSc*) in the upper right half.

be exaggerated by the coefficient of community (Whittaker & Fairbanks 1958) since differences in abundance are disregarded, while the percentage similarity of communities may depend too much on relative abundances. Used together the two indices show whether high affinity of samples is due not only to most species being present, but also to the occurrence of these species in about the same proportions.

The results of the comparisons of 26 profundal stations at a depth of 10—20 m are presented in the matrices of Fig. 10. The indices have been divided into four size classes.

The profundal of Kärjenniemenselkä differs from other areas very distinctly. As mentioned earlier it was totally desolate in 1965 and 1971. The affinity between its stations was very high in 1977, especially when measured with *PSc* (all comparisons > 90 %). The *CC* comparisons did not show as high affinity between these stations. This is mainly due to the small number of species in Kärjenniemenselkä (only 4). Of 69 comparisons between the stations of Kärjenniemenselkä and other areas only 5 values of *PSc* exceeded 30 % and none 50 %. No value of *CC* exceeded even 30 %.

The qualitative composition of the bottom fauna measured with *CC* seems to be quite similar in Rauttunselkä and Vanajanselkä. Of 253 comparisons within this rather uniform area, 214 exceeded 30 % (mean 43.5 %) in 1965. In 1971 and 1977 these values were 226 (mean 48.7 %) and 247 (mean 53.5 %), respectively. The affinity within individual stations of Rauttunselkä and Vanajanselkä has increased during 1965—1977.

If we take into account the percentage composition by means of a *PSc* index, there is a clear difference between Rauttunselkä and Vanajanselkä, especially in 1965. The affinity between stations of Rauttunselkä and between stations of Vanajanselkä was high in 1965. The mean of 6 comparisons within Rauttunselkä was 65.3 %. Only two stations of the northeastern subbasin (10:2 10 m and 8:1 10 m) were clearly different from other stations of Vanajanselkä. Of 76 comparisons between Rauttunselkä and Vanajanselkä only 4 exceeded 30 % (mean 10.7 %). Since then the affinity between these areas seems to have increased. In 1971, 11 of the comparisons between Rauttunselkä and Vanajanselkä exceeded 30 % and 2 of them 50 % (mean 18.8 %). Especially some stations in the western part of Vanajanselkä had become very similar to those of Rauttunselkä. In 1977, 41 comparisons between Rauttunselkä and Vanajanselkä were over 30 % and 4 over 50 % (mean 32.0 %). At the same time the affinity within Rauttunselkä seems to have decreased.

The relative abundance of the most frequent profundal species is presented in Table 5. The profundal association of Kärjenniemenselkä was dominated almost exclusively by *Chironomus plumosus* in 1977. The association of Rauttunselkä has been characterized by oligochaetes and *C. plumosus*, but also *Procladius* sp. c and *Chaoborus flavicans* have been important members of this association. The profundal of Vanajanselkä was dominated each year by *Chironomus anthracinus*. The profundal of Hattulanselkä was dominated in 1965 by *Chaoborus flavicans*, oligochaetes and *Chironomus plumosus*. The specific composition and its changes will be discussed later.

Table 5. Dominance (%) of the five most frequent species in the profundal of the main water bodies in 1965, 1971 and 1977. Dominance has been calculated for a given area as a mean of dominances at its sampling stations.

	Kärjenniemen-selkä			Rauttun-selkä			Vanajan-selkä			Hattulan-selkä
	1965	1971	1977	1965	1971	1977	1965	1971	1977	1965
Potamothrix hammoniensis				11	17	27	4	7	14	10
Chironomus plumosus			95	17	11	20			14	7
Chaoborus flavicans				5	30	7		9		72
Chironomus anthracinus					4		53	44	40	
Limnodrilus hoffmeisteri				38	36	13	3			
Chironomus ?corax							23	23	7	
Procladius sp. c			1	23		27				
Pontoporeia affinis							12	4		
Procladius sp. a									7	
Tanytarsus spp.			3							
Bezzia spp.										3
Cladopelma viridula			1							
Tanypus vilipennis										6

Table 6. Mean and range of the number of species per sample (S) and the diversity index H' for the sublittoral and profundal of the main water bodies in 1965, 1971 and 1977.

	N	S			H'		
		1965	1971	1977	1965	1971	1977
Kärjenniemenselkä							
3 — 7 m	9	0.8 (0— 4)	0.7 (0— 3)	4.0 (1— 9)	0.19 (0—1.37)	0.02 (0—0.17)	0.50 (0—1.76)
>10 m	3	0.0	0.0	2.0 (1— 3)	0.0	0.0	0.30 (0—0.50)
Rauttunselkä							
3 — 7 m	6	11.2 (8—15)	8.0 (5—11)	11.2 (8—16)	2.13 (1.75—2.97)	2.21 (1.91—2.88)	2.64 (2.26—3.21)
>10 m	4	7.8 (5— 9)	7.0 (5— 9)	6.8 (6— 8)	2.12 (1.87—2.49)	1.80 (1.48—2.36)	2.00 (1.74—2.15)
Vanajanselkä							
3 — 7 m	18	13.9 (7—21)	12.8 (7—19)	13.8 (8—19)	2.78 (1.46—3.68)	2.73 (1.78—3.51)	2.81 (1.85—3.40)
>10 m	19	10.5 (6—14)	8.3 (6—13)	9.8 (5—16)	1.66 (0.84—2.84)	1.80 (1.09—2.53)	2.24 (1.08—2.85)
Hattulanselkä							
3 — 7 m	6	9.5 (9—15)			2.27 (2.04—2.60)		
>10 m	1	6.0			1.43		

Diversity

Most diversity indices may be conveniently classified as either species diversity indices or dominance diversity indices (Whittaker 1965). Species diversity indices emphasize the number of taxa in a certain environment, and the index used in this paper is simply the number of species per sample (species richness). Dominance diversity indices employ the percentage composition by numbers of the various species, i.e. diversity increases as more species are represented by more equal relative abundances. The information statistic has been widely used as a diversity index in water pollution studies (Wilhm & Dorris 1968), too. The Shannon index is also used here:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i,$$

Table 6 gives the mean and range of the number of species (S) and the Shannon index (H') for the sublittoral and profundal stations of each main water body studied in 1965—1977. Diversity was generally higher in the sublittoral than in the profundal. Each year the lowest values of S and H' were found in Kärjenniemenselkä, where the diversity was also extremely low in the sublittoral zone in 1965 and 1971. Both S and H' show remarkable increases in 1977 at all depths, although also these values are distinctly smaller than in Vanajanselkä and Rauttunselkä.

According to both indices, the sublittoral and profundal bottom fauna of Vanajanselkä have each year been slightly more diverse than those of Rauttunselkä. No clear changes in the species richness are to be found in Rauttunselkä or in Vanajanselkä during 1965—1977. However, the values of H′ have increased from 1965 to 1977 in the sublittoral zone of Rauttunselkä and in the profundal of Vanajanselkä. The increase in profundal diversity in Vanajanselkä was mainly due to the very strong dominance of *Chironomus anthracinus* in 1965. The diversity seems to have increased in 1971 and 1977 at the same time as the importance of this species decreased in Vanajanselkä. The number of species remained, however, at the same level as earlier.

4.3. Distribution and abundance of species

Crustacea

The occurrence of crustaceans is totally limited to Vanajanselkä. Three relict species of Crustacea have been found: *Mysis relicta* Lovén, *Pontoporeia affinis* Lindström and *Pallasea quadrispinosa* Sars. *Pontoporeia affinis* is the species with quantitative importance in the benthos. *Pallasea quadrispinosa* has occurred only four times in samples. *M. relicta* is probably more common than *P. quadrispinosa*, but because of its pelagic way of life it appears only sporadically in samples (8 times). *Asellus aquaticus* L. belongs to the littoral fauna of Vanajavesi and it has been found only twice in the sublittoral samples.

The distribution and abundance of *P. affinis* changed quite a lot between 1926 and 1977. This species is a very suitable organism for studies of lake eutrophication, because its ecological requirements are well known and because it is large enough not to penetrate through the slightly different sieves used in 1926 and 1965—1977 (cf. p. 81). Therefore the comparability of our results with those of Järnefelt (1929) is good.

In 1926 *P. affinis* was a very abundant species in Vanajanselkä (Table 7). Its occurrence was

Table 7. Density (individuals per m², mean and range), dominance (%) and constancy (%) of *Pontoporeia affinis* in Vanajanselkä in 1926, 1965, 1971 and 1977. N = number of samples.

	N	Density	Dominance	Constancy
Sublittoral				
1926	20	65.3 (0—172)	34.2	85
1965	24	182.4 (0—710)	21.5	96
1971	34	87.6 (0—714)	11.1	65
1977	25	11.3 (0—129)	1.1	32
Profundal				
1926	11	140.5 (54—260)	49.8	100
1965	13	78.9 (0—482)	2.7	62
1971	15	0.8 (0— 6)	0.1	13
1977	13	1.4 (0— 12)	0.1	15

centred on the profundal, where the constancy was 100 % and the dominance 49.8 %. The corresponding values in the sublittoral samples were a little smaller (Table 7).

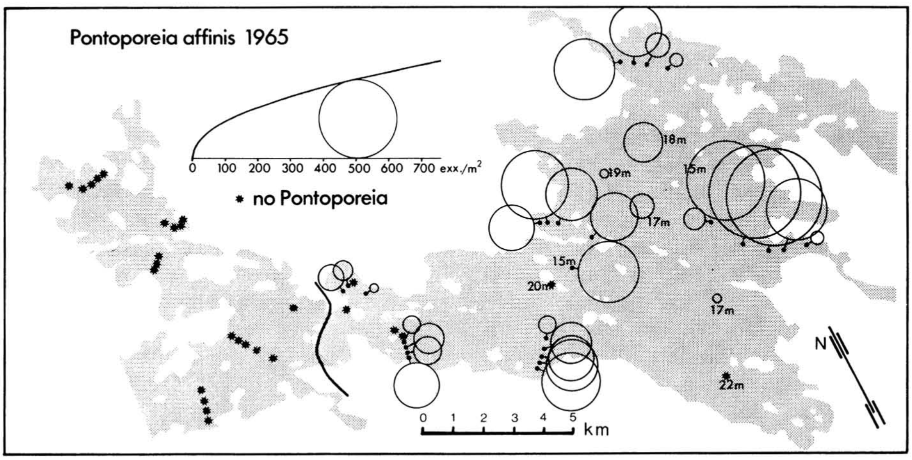
According to the observations of Toivonen (1960) the abundance of *P. affinis* in 1956 was about twice that of 1926 in Vanajanselkä. The oxygen concentration of the deepest profundal had already decreased in the 1950s to close to the tolerance limits of *P. affinis*. Toivonen (1960) predicted that this species will vanish from Vanajanselkä, if the deterioration in the oxygen conditions continues.

In 1965 *P. affinis* was, however, still common in the sublittoral, but in the profundal its relative abundance had decreased clearly (from 49.8 to 2.7 %; Table 7), especially in the southwestern sub-basin as a whole (Fig. 11). The decrease in constancy was not so drastic (from 100 to 65 %). In the profundal the maximum number of specimens was, however, as high as 482/m², which is about twice that of 1926. In the sublittoral zone *P. affinis* became rarer towards Rauttunselkä. The mean and maximum numbers of specimens from the sublittoral were 3—4 times greater than in 1926. The evenness of occurrence was a little higher, too (constancy 96 %).

In 1971 the abundance of *P. affinis* had further decreased, especially in the profundal and also in the sublittoral where it was only half of that in 1965 (Table 7). Its occurrence was practically limited to the northeastern sub-basin (Fig. 11), where it was very common in the sublittoral samples in places. Only a few individuals were found at the sublittoral stations elsewhere in Vanajanselkä.

In 1974, when only some of the sampling stations were checked, not a single specimen of *P. affinis* was found; not even in those stations of the northeastern sub-basin, where the maximum density three years earlier was over 700 individuals per m². In 1977 when all stations were checked again, the species was found at 11 sites, but its relative abundance was very low. The highest number of individuals was 129 per m² in a shallow, sheltered bay of the northeastern sub-basin (Fig. 11). Single individuals were found at two profundal stations.

In conclusion, the relative abundance of *P. affinis* decreased in the sublittoral from 34 % to 1 % and in the profundal from 50 % to about 0 % during 52 years. In 1926 the occurrence of *P. affinis* was centred on the profundal, and during later surveys on the sublittoral. The highest numbers of specimens were, however, found in 1965.



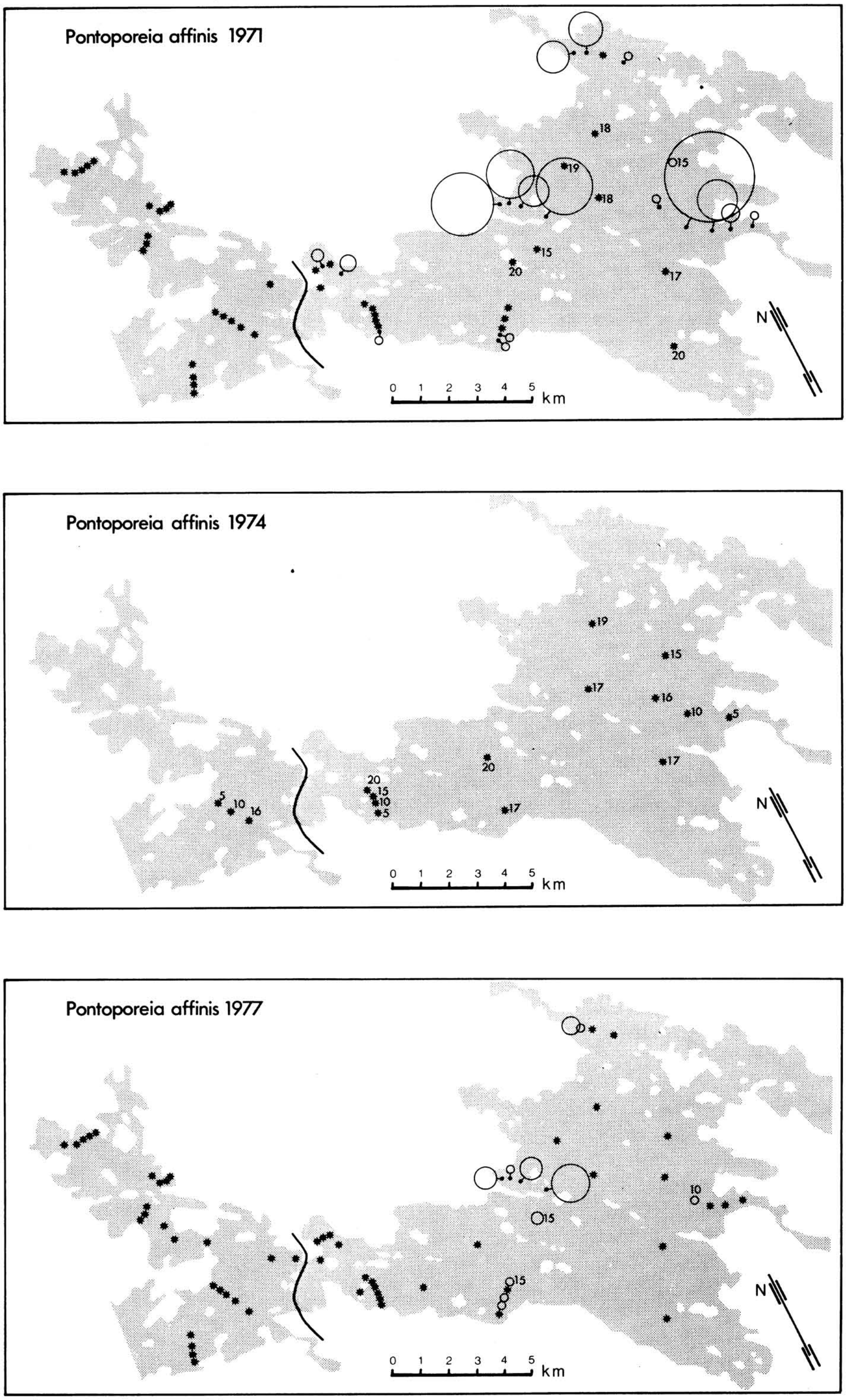


Fig. 11. The distribution and abundance of *Pontoporeia affinis* in 1965, 1971, 1974 and 1977.

Chironomidae

The very strong increase in total benthos since 1926 is mainly due to the midge larvae. In 1926 they comprised only 2.6 % of the total biomass in the sublittoral and 10 % in the profundal of Vanajanselkä. In 1965 these figures were 74 % and 90 % respectively. This increase is partly due to the fact that the sieve mesh was a little larger in 1926 than later.

There is no sense in making broad quantitative comparisons of the total chironomids between various years and areas, especially when based on only one sampling a year. The great differences in the seasonal variation pattern of various species make these comparisons very unreliable. It is better to compare the distribution and abundance of the common species which are large enough in August to appear quantitatively in samples. It is also important that the abundance of these species remain rather constant during the sampling period (no mass emergence in August). Of the profundal mass species, the most useful are *Chironomus anthracinus* Zett. and *C. plumosus* (L.), whose ecological requirements are also well known. A third *Chironomus* species, *C. ?corax* K. (larva of *salinarius* type, Lindeberg & Wiederholm 1979), has an emergence in August and the number of its larvae decreases distinctly during the sampling period used. Three *Procladius* species, which are very common in Vanajavesi, also have an emergence in August. In addition, their ecology is poorly known. The third useful species is *Monodiamesa bathyphila* (K.), which has earlier been important in the profundal of Vanajanselkä.

Monodiamesa bathyphila was the dominant chironomid species in the profundal of Vanajanselkä in 1926 (53.1 %; Järnefelt 1929). The other species belonged to the subfamily Tanypodinae. They were not identified to the species level by Järnefelt. *M. bathyphila* was not found in the sublittoral. The sublittoral fauna consisted of Tanypodinae larvae (43 %) and *Cryptochironomus* spp. (57 %). The chironomid fauna was also very poor quantitatively speaking.

In 1965 the importance of *M. bathyphila* had fallen in the profundal of Vanajanselkä. Its relative abundance was only 0.03 % and it was found in only one profundal sample from the northeastern sub-basin (Fig. 12). The depth distribution had changed, as it was generally found in the sublittoral. The densities were, however, quite low (max. 82 ind./m^2). The distribution of *M. bathyphila* in 1971 was similar to that in 1965. In 1977 it had also decreased in the sublittoral. It occurred at only two stations (7 and 10 m) and in low numbers (6—18 ind./m^2).

Chironomus larvae which were dominant chironomids in Vanajanselkä during 1965—1977, were not found there in 1926. In 1965, 72 % of the sublittoral and 97 % of the profundal chironomids were *Chironomus* larvae. *Chironomus anthracinus* was very abundant in the profundal of Vanajanselkä, with an average density of 2 025 ind./m^2 in 1965. In 1971 and 1977 this high abundance had decreased to 800—900 ind./m^2 (Table 8). No clear changes took place in the sublittoral. *C. plumosus* was scarce, especially in the profundal, in 1965 and 1971. In 1977 the number of *C. plumosus* larvae was notably higher in all depth zones. It was more abundant than *C. anthracinus* in the sublittoral (it is more eurybathic species than *C. anthracinus*). In the profundal *C. anthracinus* was still dominant, especially in the deeps of the northeastern sub-basin (Fig. 13).

The list of chironomid species found in the bottom samples during 1965—1977 (Table 9) shows that the fauna of Kärjenniemenselkä was richer in 1977 than in 1965 and 1971. *C. anthracinus* had been absent from Kärjenniemenselkä and very scarce in Rauttunselkä (Table 8). The depth distribution of *C. plumosus* had changed in Kärjenniemenselkä and Rauttunselkä in the same way as the depth distribution of the total benthos (cf. p. 82). In Rauttunselkä the number of larvae had decreased in the sublittoral and increased in the profundal (Table 8).

Table 8. The average abundance of *Chironomus anthracinus* and *C. plumosus* (ind/m^2) in the sub-areas and various depth zones.

	C. anthracinus/C. plumosus		
	1965	1971	1977
Kärjenniemenselkä			
3— 5 m	0 / 284	0 / 189	0 / 499
7 — 10 m	0 / 0	0 / 0	0 / 187
> 10 m	0 / 0	0 / 0	0 / 136
Rauttunselkä			
3— 5 m	0 / 411	0 / 137	0 / 39
7 — 10 m	0 / 425	0 / 238	2 / 136
> 10 m	0 / 38	53 / 123	0 / 224
Vanajanselkä			
3— 5 m	25 / 35	22 / 27	16 / 109
7 — 10 m	221 / 45	364 / 51	216 / 229
> 10 m	2025 / 41	880 / 12	810 / 241
Hattulanselkä			
3— 5 m	0 / 563		
7 — 10 m	0 / 217		

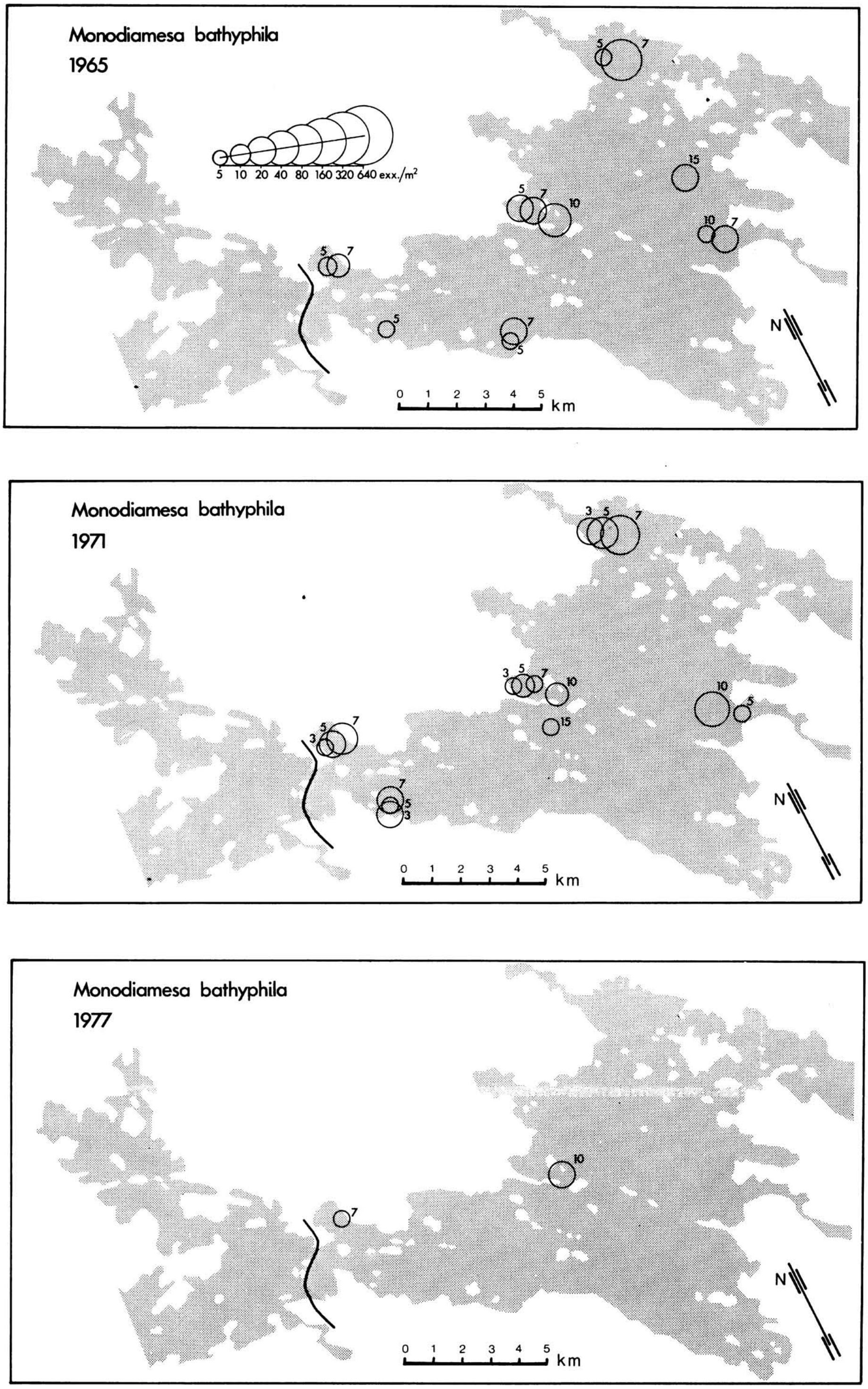


Fig. 12. The distribution and abundance of *Monodiamesa bathyphila* in 1965, 1971 and 1977.

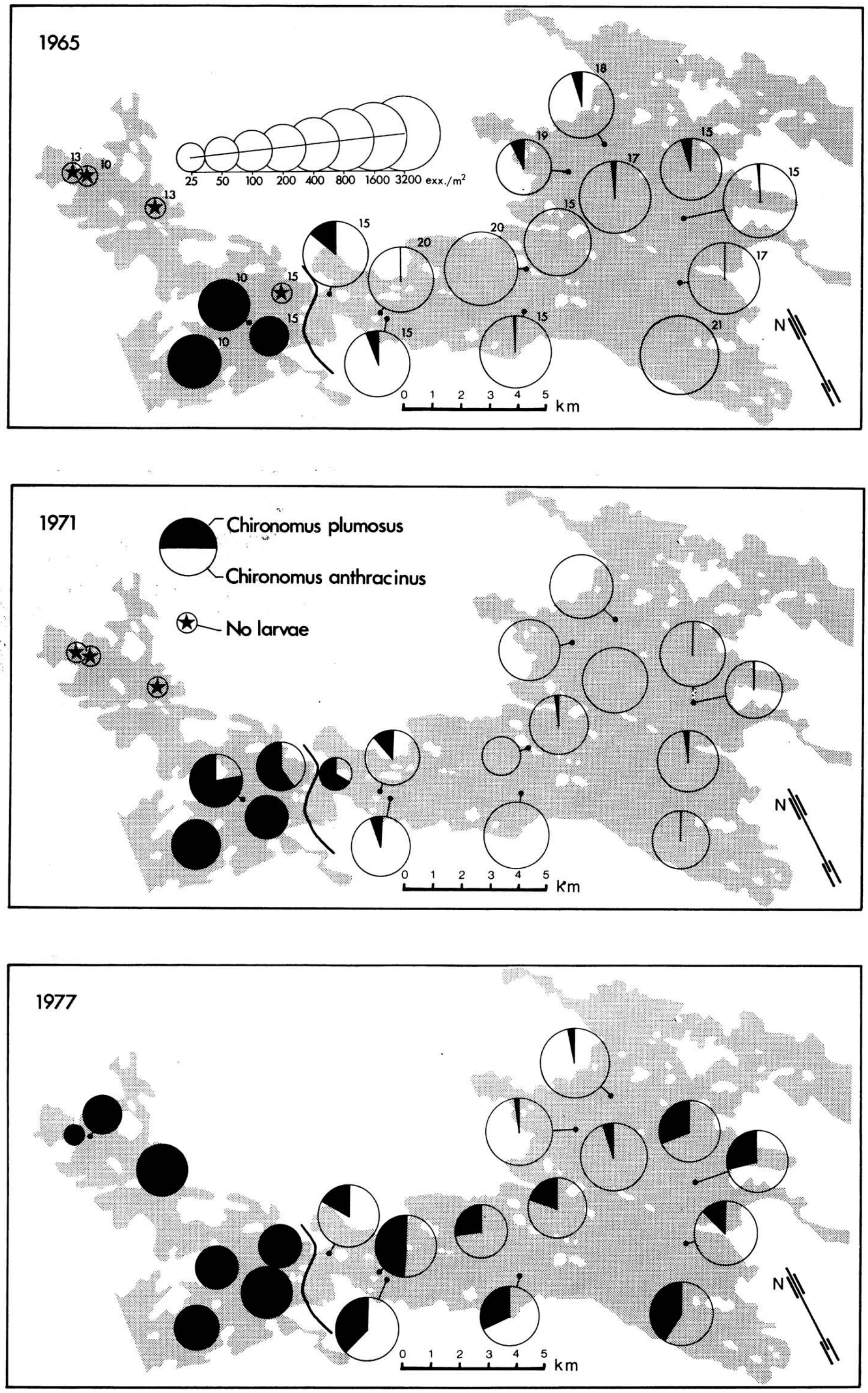


Fig. 13. The profundal distribution and relative abundances of *Chironomus plumosus* and *C. anthracinus* in 1965, 1971 and 1977.

Table 9. List of chironomid species found in the bottom samples in 1965—1977. S = found only in the sublittoral, X = found both in the sublittoral and profundal.

	Kärjenniemenselkä			Rauttunselkä			Vanajanselkä			Hattulanselkä
	1965	1971	1977	1965	1971	1977	1965	1971	1977	1965
Ablabesmyia longistyla Fitt.							S			
Ablabesmyia monilis-gr.									X	
Macropelopia sp.							S			
Procladius sp. a				X	S	X	X	X	X	X
Procladius sp. b				S			X	X	X	
Procladius sp. c			X	X	X	X	X	X	X	S
Psectrotanypus varius (Fabr.)										S
Tanypus kraatzi (K.)	S	S		S		S			S	S
Tanypus punctipennis Meig.						S				
Tanypus vilipennis Meig.			S	S	X	S				X
Potthastia longimanus K.							S			
Monodiamesa bathyphila (K.)							X	X	X	
Heterotrissocladius marcidus (Walk.)							S	S		
Orthocladius sp.								X		
Chironomus anthracinus Zett.					X	S	X	X	X	
Chironomus ?corax K.				X	X	X	X	X	X	
Chironomus plumosus (L.)	S	S	X	X	X	X	X	X	X	X
Cladopelma viridula (L.)			X	S	S	S				
Cryptochironomus defectus-gr.			S	S	X	S	X	X	S	S
Cryptochironomus ussouriensis G.			S	X	S	X		S	S	
Demicryptochironomus vulneratus (Zett.)							S	S		
Einfeldia dissidens (Walk.)						X			X	
Einfeldia sp. a							S			S
Glyptotendipes spp.						S				
Harnischia curtilamellata (Mall.)							S	S	S	
Limnochironomus spp.									S	
Microchironomus tener (K.)			S	X	S	X	X	X	X	S
Microtendipes spp.									S	
Nilothauma brayi (G.)							S	S	S	
Paracladopelma laminata (K.)								S		
Paralauterborniella nigrohalteralis (Mall.)							S		S	
Polypedium bicrenatum K.				X	S	S	X	S	X	
Polypedilum convictum-gr.							S		S	
Polypedilum nubeculosum (Mg.)				S	S	S		S	X	
Stictochironomus sticticus (Fabr.)						S	S	S	S	
Cladotanytarsus spp.							S	S	X	S
Stempellina spp.							S	S		
Stempellinella minor (Edw.)							X	S	S	
Tanytarsus bathophilus K.							X	X	X	
Tanytarsus spp.			X	S	S	S	X	X	X	S
Total number of species	2	2	8	14	13	18	26	24	26	11

Oligochaeta

The premises for the comparison of results from Oligochaeta are quite unfavourable. The Oligochaeta material was not identified to the species level in 1926. On the other hand the species composition remained rather constant in 1965—1977 (Table 10). Possible succession from an 'oligotrophic' fauna to the present 'eutrophic' fauna thus took place before 1965.

The quantitative comparison between 1926 and the current position is quite unreliable. This is due to the fact that the oligochaetes easily penetrate the 0.6 mm mesh (Jonasson 1955). The length of sieving time affects these losses, too. In any case, the oligochaetes were important members of the bottom fauna of Vanajanselkä in 1926 (over 60 % of the total biomass; Järnefelt 1926). The average density seems to have been lower (in the sublittoral 78 and in the profundal 106 ind./m^2) than in 1965 (148 and 263 ind./m^2, respectively). The biomass was, however, a little greater in 1926 than in 1965 in both depth zones. This might be due to a different species composition or a different method of biomass determination.

Comparisons between 1965, 1971 and 1977 are much more reliable, because the sieve was the same throughout. It should be borne in mind, however, that the horizontal distribution of the oligochaetes is uneven, especially on the sublittoral bottoms. Six Ekman hauls are not enough to give accurate estimates of the real population density of the oligochaetes. It is

Table 10. The percentage composition of the Oligochaeta fauna. Species are arranged into 7 groups according to their tolerance of unfavourable oxygen conditions: group 1 = very tolerant species, group 7 = very sensitive species (Milbrink 1973).

Group	Kärjenniemenselkä			Rauttunselkä			Vanajanselkä			Hattulanselkä
	1965	1971	1977	1965	1971	1977	1965	1971	1977	1965
1) *Limnodrilus hoffmeisteri* Claparede	67	—	75	61	67	33	47	34	19	49
2) *Potamothrix hammoniensis* (Michaelsen)	33	—	20	39	33	67	51	66	79	51
3) *Aulodrilus pluriseta* (Piguet) + *Limnodrilus claparedeanus* Ratzel	—	—	—	—	—	—	1	—	—	—
4) *Arcteonais lomondi* (Martin)	—	—	5	—	—	—	—	—	1	—
5) *Psammoryctes barbatus* (Grube)	—	—	—	—	—	—	—	+	—	—
6) *Peloscolex ferox* (Eisen)	—	—	—	—	—	—	1	+	1	—
7) *Stylodrilus heringianus* Claparede	—	—	—	—	—	—	+	—	—	—

therefore better to group together all samples in a given sub-area and depth zone and to pay attention to the gross scale quantitative differences.

Two tolerant species, *Limnodrilus hoffmeisteri* Claparede and *Potamothrix hammoniensis* (Michaelsen), clearly dominated in all three sub-areas. More oxygen demanding species were found in low numbers only in the sublittoral of Vanajanselkä (Table 10). The oligochaetes were surprisingly scarce in Kärjenniemenselkä (Fig. 14). In 1965 they were found at only two sublittoral stations (max. 25 ind./m^2). In 1971 they were totally absent. As a result of improvement of abiotic conditions the oligochaetes recovered in Kärjenniemenselkä in 1977, too, when they occurred at three stations, even in the most polluted northern part (max. 105 ind./m^2).

In 1965 there was a very clear difference between the Oligochaeta biomasses of Rauttunselkä and Vanajanselkä (Fig. 14). The highest biomasses were found in the profundal of Rauttunselkä. The regional differences within Vanajanselkä were quite small. The position was similar in 1971 except in the western part of Vanajanselkä, where the profundal abundance had increased near to the level of Rauttunselkä. In 1977 the differences between the subareas had also become smaller. On the one hand the abundances had increased in Vanajanselkä, especially in the western part, and on the other hand the numbers and biomasses had decreased in Rauttunselkä.

Mollusca

The comparability of the Mollusca results is good thanks to their large size. In 1926 molluscs were absent from the profundal samples of Vanajanselkä, but in the sublittoral they formed up to 13 % of the total number of individuals, the average density being 25 ind./m^2 and constancy 40 %. Of the molluscs 78 % belonged to the genus *Pisidium* and 22 % to *Valvata*. In 1965 their density had decreased in the sublittoral to only 6 ind./m^2. On the other hand they were also found in low numbers in the profundal (Fig. 15).

Molluscs were absent from Kärjenniemenselkä during 1965—1977 (Fig. 15), and in Rauttunselkä they were found only occasionally. They were not found in Hattulanselkä in 1965. In Vanajanselkä the molluscs had become scarcer. After 1965 they were not found deeper than 7 m. In 1977 they occurred at only 5 sublittoral stations, and the constancy of the commonest species had decreased (Table 11).

There is no information about unionids in 1926 (Järnefelt 1929). In 1965 the occurrence of unionids was centred on the sublittoral of Vanajanselkä, where their constancy was 33 % and mean biomass 19.3 % g/m^2. The unionids were absent from Kärjenniemenselkä and in the sublittoral of Rauttunselkä their constancy was 14 % and their mean biomass 18.8 g/m^2.

Other groups

Comparison of the abundances of *Chaoborus flavicans* (Meig.) can lead to erroneous conclusions. Because of their semipelagic way of life the number of individuals varies greatly in the bottom samples. *Chaoborus* larvae seemed to have become more abundant in 1965 than in 1926. They were found at only five sublittoral stations (Järnefelt 1929 sub *Sayomyia*) in 1926 (average density 15 ind./m^2). The maximum abundance was 86 ind./m^2. In 1965—1977 *C. flavicans* was one of the commonest species of Vanajanselkä, the maximum abundances were over 700 ind./m^2. They were even more abundant in Rauttun-

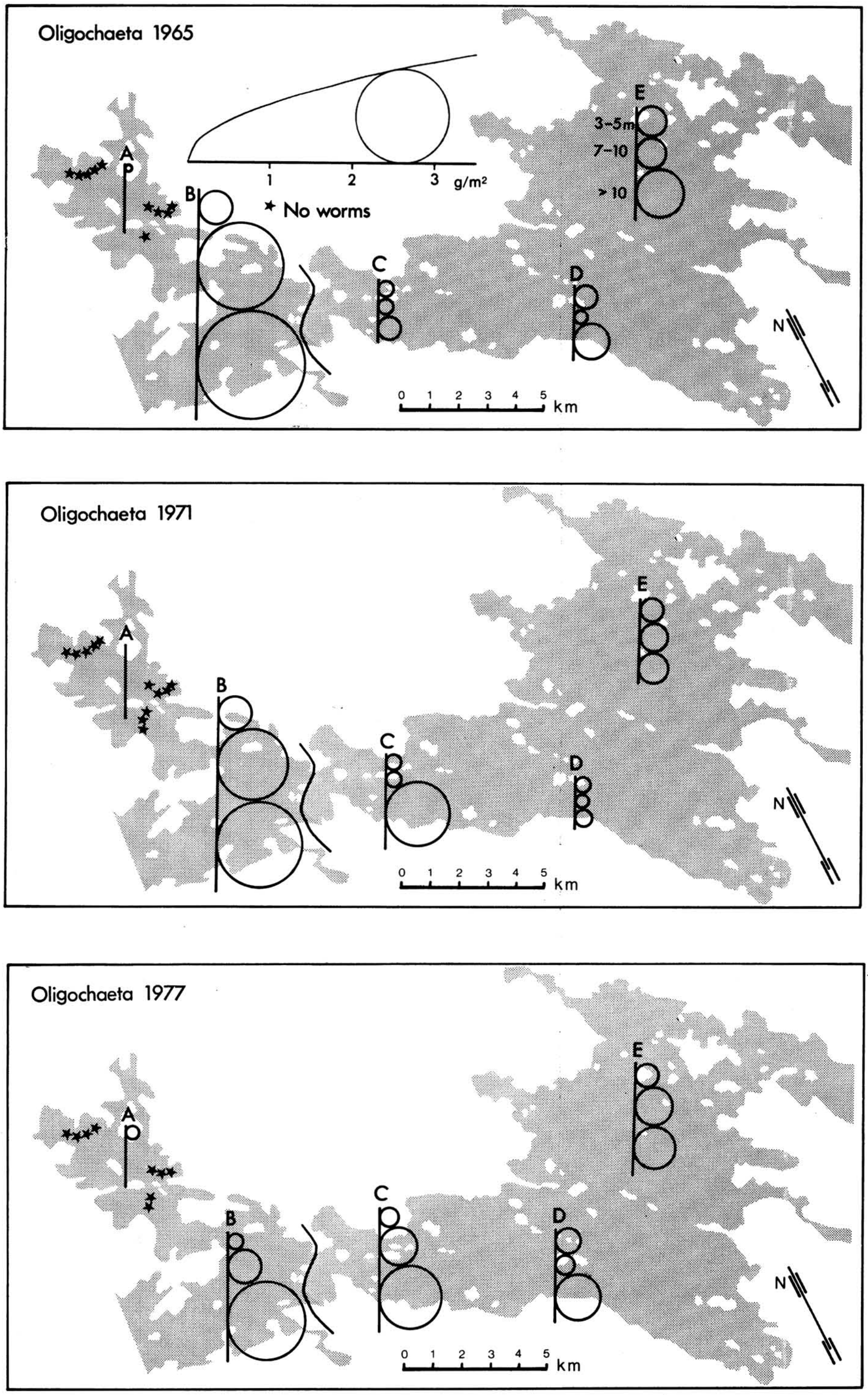


Fig. 14. The depth distribution of Oligochaeta biomasses in five sub-areas in 1965, 1971 and 1977.

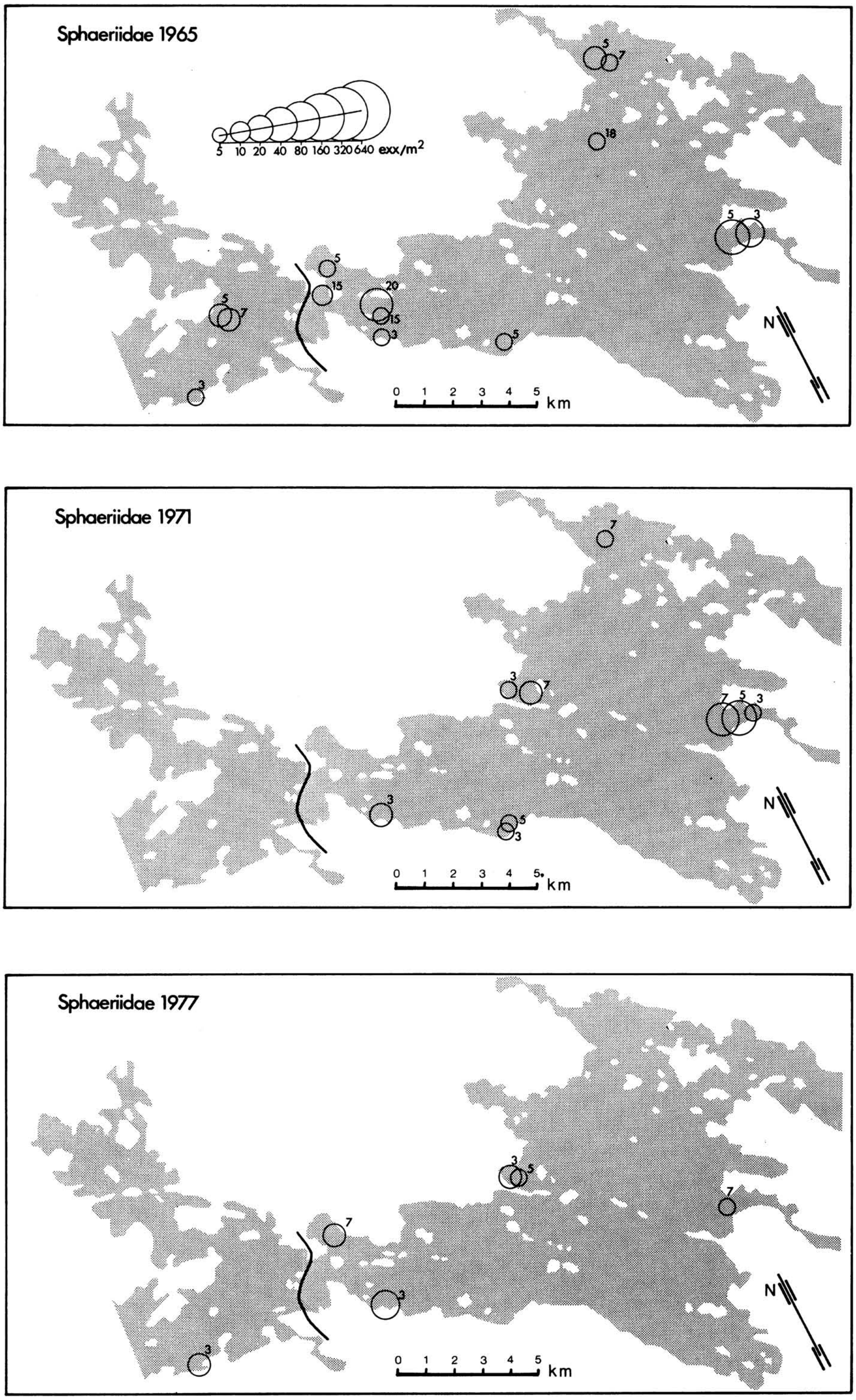


Fig. 15. The distribution and abundance of Sphaeriidae in 1965, 1971 and 1977.

Table 11. The occurrence of mollusc species found in the study area in 1965—1977 as expressed in terms of constancy (%). Number of sampling stations 59. Unionidae are excluded.

	1965	1971	1977
Valvata piscinalis Müller	2	5	0
Sphaerium corneum L.	5	5	3
Pisidium henslowanum Sheppard	8	10	2
Pisidium casertanum Poli	7	3	2
Pisidium amnicum Müller	0	2	0
Pisidium obtusale Lamarck	0	0	2
Pisidium moitessierianum Paladilhe	5	2	2

selkä (max. 2233 ind./m^2), but in Kärjenniemenselkä they were, surprisingly, never found.

The other groups (Ceratopogonidae, Turbellaria, Nematoda and Ephemeroptera) were scarce in samples and they have been excluded from these comparisons.

5. Discussion

5.1. Present benthic associations and the bottom faunal lake type system

Since Thienemann (1913, 1920) published his classical studies of the *Chironomus* and *Tanytarsus* lakes in Northern Germany, many investigators have presented lake typologies based on the bottom fauna. The chironomids have always played an important role in these classifications. Excellent historical reviews of the benthic lake typologies can be found in Brundin (1949) and Brinkhurst (1974). The lake typology of Brundin (1949, 1956, 1958) is regarded as the most precise in this field (Stahl 1959, Brinkhurst 1974). He proposes (1958) the following bottom faunal lake type system for Northern Europe:

- I *Heterotrissocladius subpilosus* lakes (ultra-oligotrophic)
- I/II *Tanytarsus-Heterotrissocladius* lakes (oligotrophic)
- II *Tanytarsus lugens* lakes (moderately oligotrophic)
- II/III *Stictochironomus-Sergentia* lakes (mesotrophic)
- III *Chironomus* lakes (eutrophic)
  - a) *Chironomus anthracinus* lakes (moderately eutrophic)
  - b) *Chironomus plumosus* lakes (more strongly eutrophic).

The ecological factors to which the composition of the profundal chironomid association is related are primarily the hypolimnetic oxygen concentration and secondarily the temperature and the nutrient value of the sediments. The classification is most valid for stably stratified lakes, since oxygen in their hypolimnion is not replenished during the summer stagnation period. The sublittoral and littoral zones do not characterize a lake as a whole in the same way as the profundal zone, but merely a local habitat of the lake.

When the bottom faunal lake type concept is applied to Vanajavesi, it should be taken into account that this lake is not stably stratified during the whole summer. In Vanajanselkä this is due to the large area, and in Kärjenniemenselkä and Rauttunselkä to the fast flow-through of water. Inspite of the instability of thermal stratification the bottom fauna below 10 m differs clearly from the sublittoral fauna. The profundal fauna of Vanajavesi consists at present of a few species which are able to tolerate low oxygen concentrations. The oxygen concentration is thus a primary limiting factor here as well. The main difference between Vanajavesi and the stably stratified lakes is the temperature, which is particularly high in the profundal of Vanajavesi. The cold-stenothermal deep-water species, which are important components of the oligotrophic fauna, have thus always been absent from the profundal of Vanajavesi.

The present profundal fauna of Vanajavesi mostly resembles the eutrophic *Chironomus* type. The profundal association of Rauttunselkä belongs to *C. plumosus* type and that of Vanajanselkä to the *C. anthracinus* type. Previously the profundal of Kärjenniemenselkä was a "dead" basin, but according to the last collection in 1977 it now belongs to the *C. plumosus* type, too. Both type species are eurythermal, for which the high hypolimnetic summer temperature is not a limiting factor.

The bottom faunal lake type concept of Brundin has been applied to Sweden's large lakes by Wiederholm (1974a, 1974b). Vanajavesi resembles the eutrophic basins of Lake Mälaren with regard to the hydrographical and hydrological conditions. This similarity is also evident in the bottom fauna. As many as 72 of the 97 chironomid species occurring in Vanajavesi (Kansanen, unpublished) have been found in Mälaren, 24 of them only or mainly in the eutrophicated basins.

The profundal of the *C. plumosus* areas of Mälaren is characterized, like Rauttunselkä, by a high abundance of *Procladius* larvae. Other *Chironomus* species are scarce. *Cryptochironomus* spp. and *Polypedilum nubeculosum*, which are common in the sublittoral of Rauttunselkä, are found in low numbers. The fauna is richer in the *C. anthracinus* areas, where *C. plumosus* is of minor importance. The *C. salinarius* group, *Monodiamesa, Procladius* spp., *Cryptochironomus* spp., *Demicryptochironomus vulneratus, Microchironomus tener, Harnischia, Polypedilum nubeculosum* and *Tanytarsus* spp. are typical species. The real identity of the *Chironomus salinarius* group is unknown in Mälaren, but it seems probable that it is identical to that of Vanajavesi, namely *Chironomus ?corax* K. (Lindeberg & Wiederholm 1979).

There is a high degree of similarity between these lakes among other groups, too. In both lakes the oligochaete fauna has two clearly dominant species in the *C. plumosus* and *C. anthracinus* areas: *Limnodrilus hoffmeisteri* and *Potamothrix hammoniensis*. In addition to these, some other rather tolerant species are found in *C. anthracinus* areas, e.g. *Aulodrilus pluriseta.* Although the fauna is qualitatively very similar, there is a clear difference in oligochaete abundances between *C. plumosus* and *C. anthracinus* areas. The biomass was significantly higher in *C. plumosus* areas than in *C. anthracinus* areas (as in Vanajavesi in 1965 and 1971; see Fig. 14). It is generally known that the abundance of oligochaetes, especially of tubificids, increases with organic enrichment and can rise to enormous numbers in grossly polluted watercourses (Milbrink 1973). In general, the quantity and quality of organic matter reaching the sediments appears to play a more important role in determining the qualitative composition and abundance of tubificids than do all of the commonly measured physical and chemical parameters of water or sediments (Brinkhurst and Cook 1974). Their ability to withstand considerable oxygen depletion is an essential adaptation to their niche.

Pontoporeia affinis is the most abundant relict crustacean in both Mälaren and Vanajavesi. This species is totally absent from the *C. plumosus* areas of both lakes. It occurs in rather low numbers in *C. anthracinus* associations. The highest numbers reported by Wiederholm (1974a) were 580 ind./m^2. In Vanajanselkä densities of over 700 ind./m^2 have been found. In the deep oligotrophic basins of Mälaren these can be as high as 5 000—10 000 ind./m^2. This species prefers cold water, but is not strictly cold-stenothermal (Järnefelt 1953). The oxygen demand is regarded as rather high by Järnefelt (1953): at least 4.7 mg/l.

In the profundal of Mälaren the genus *Pisidium* was quantitatively important. However, pisidia were quite scarce in eutrophicated *Chironomus*-areas, where the densities varied from zero to a few hundreds per m^2. The highest number of individuals in Vanajanselkä has been 38 ind./m^2 in the profundal zone. The species composition is mainly the same in Vanajavesi and in the *Chironomus* areas of Mälaren. The most important species were *Pisidium subtruncatum, P. casertanum* and *P. henslowanum* in Mälaren. *P. moitessierianum* also occurred in the profundal. The three last mentioned species have been the most abundant in Vanajanselkä, too. The sphaerids are often thought to be intolerant to pollution. In fact, in the southern part of Lake Saimaa they were totally absent from the areas loaded by the wood-processing industry (Koli and Turkia 1964), as in Kärjenniemenselkä in this study. Because of the scattered distribution and low abundances the molluscs are, however, not such useful species with regard to macrozoobenthos associations as some other benthic components.

In conclusion, the bottom faunal lake type system proposed by Brundin (1949, 1956, 1958) for Northern Europe seems to be applicable in the large polluted lakes of the Finnish lake district. In this connection, however, it was not possible to test the applicability of the oligotrophic and mesotrophic categories of the lake type system under consideration. But besides the chironomid fauna *Pontoporeia affinis* in particular is one of the most useful and valuable organisms when analysing the degree of pollution in the lakes studied.

5.2. Chironomid type associations and the trophic status of lakes

Wiederholm (1974a, b) gives a tentative schedule showing the relation between the type associations of chironomids and the range of some chemical and biological factors indicating the trophic degree. Only *C. anthracinus* and *C. plumosus* types are considered here.

Eutrophication is generally defined as a rise in the phytoplankton production rate and its consequences (Ohle 1965). According to the classification used by Oravainen (1978) the whole study area belonged in 1977 to the class "eutroph" on the basis of both the primary production capacity, the algal biomass and the chlorophyll — a content of the water. Regional differences between the subareas were small. The primary production capacity in Kärjenniemenselkä seems to have been a little lower than else-

Table 12. Chlorophyll-a, total phosphorus and primary production capacity in surface water for *Chironomus anthracinus* and *C. plumosus* areas. The values are averages for May-October in Mälaren and for June-August in Vanajavesi.

	C. anthracinus area		*C. plumosus* area	
	Mälaren	Vanajavesi	Mälaren	Vanajavesi
Chlorophyll-a (mg/m^3)	10—20	8.6	>20	10.4
Total phosphorus (µg/l)	30—60	32	>60	28
Primary production capacity (mg C/m^3/day)	500	350—380	700	350—400

where, especially in 1974, when the waste water load was higher than today. This is partly due to the toxic inhibition. The nutrient content of industrial effluents is also quite low after the treatment of wastes and lakes in the upper course are mainly oligotrophic.

The relationship between the benthic lake types and the trophic degree in Mälaren (Wiederholm 1974a, b) and Vanajavesi is indicated in Table 12.

The limit values between *C. anthracinus* and *C. plumosus* associations in Vanajavesi are at a lower level than in Mälaren. This is in accordance with results concerning the gastropod fauna (Aho 1966, 1978b). The fresh water gastropod species react differently to water quality in the lakes of Finland than in the lakes of southern Sweden. In Finland the gastropods as a whole are better able to tolerate extremely poor lake water. The corresponding adaptive difference in the whole macrozoobenthos fauna can be seen in Table 12. In Finland *C. anthracinus* associations become changed into *C. plumosus* associations at a less eutrophic level (about 30 µg P/l) than in Sweden. Thus, the benthic associations in the Finnish lakes seem to be more sensitive to pollution than in more southerly and luxuriant districts such as southern Sweden.

There is no clear difference in the trophic degree between the *C. anthracinus* area (Vanajanselkä) and *C. plumosus* area (Rauttunselkä). As shown earlier, the main difference is in the oxygen conditions, which are more severe in Rauttunselkä than in Vanajanselkä. In addition, these lakes are partly under pressure from different wastes. The annual hypolimnetic oxygen minimum was on average 4 % in Rauttunselkä and 18 % in Vanajanselkä (mean of values at 15 m in 1970—1977). The corresponding values in Mälaren were 10—20 % and 20—40 %. The oxygen conditions are better in both the *C. anthracinus* and *C. plumosus* areas of Mälaren than in those of Vanajavesi when measured with the annual hypolimnetic oxygen minimum. This minimum occurs, however, in Vanajavesi in winter and in Mälaren in summer. The summer oxygen conditions are at least as good in Vanajavesi as in Mälaren. In winter the bottom fauna of Vanajavesi even have to withstand anaerobic conditions. In Mälaren there is no complete oxygen depletion in these areas. The conclusion is that the oxygen deficiency in winter is not as fatal to the chironomids as it is in summer. This is partly due to the low oxygen consumption in winter (low temperature). In addition, Vanajanselkä cools very effectively before freezing, the mean temperature of the whole water mass being below 2 °C. Another possible factor can be found in the life cycles of *Chironomus* species. The critical phase in these cycles is the development of the first larval stages in summer. These small forms are not able to tolerate oxygen depletion as well as the large overwintering larvae of fourth degree (cf. Brundin 1951).

Although the composition of benthic associations is highly dependent on the trophic status, there are several factors which modify this relationship. According to Brundin (1949) the chironomids are not particularly good indicators of the trophic degree. The hypolimnic oxygen concentration which is the main limiting factor is usually, but not always, correlated with the trophic status. It is also dependent on the lake morphometry. The process of eutrophication and its effects on the bottom fauna are also dependent on the quality of waste water load directed into the lake. Municipal waste waters containing high concentrations of plant nutrients primarily cause secondary oxygen consumption. In the case of Vanajavesi the effluents of wood-processing industry have played an overwhelming role as a source of pollution. The effects of these effluents are characterized by a high primary oxygen consumption, allocthonous organic sedimentation and toxic substances which are of importance at least near the pollution outfall. The saprobic processes primarily determine the nature of the whole water body of Kärjenniemenselkä, which has been an extreme environment for all higher forms of life.

The slight difference in the variables describing the trophic status between the *C. anthracinus* and *C. plumosus* areas in Vanajavesi is logical because the *C. anthracinus* associations of Vanajanselkä were, during the 1970s, developing towards *C. plumosus* associations as shown on p. 84. While the pollution in Vanajavesi progresses, the homogeneity of the trophic status as well as of the benthic associations increases.

It seems to be evident that a certain general succession of the benthic associations occurs as a function of eutrophication, but the level of eutrophication where an association changes into something else may not be equal in different lakes and in different lake districts. The development of associations in relation to the trophic status depends on many different local factors such as the morphometry and hydrology of the lake basin, the physico-chemical properties of lake water, the quality of effluents, and also the genetic composition and physiological state of the benthic populations. Therefore the theoretical generalizations must be applied into each lake system separately and with special care.

5.3. Succession in the benthic communities

Vanajanselkä

According to Järnefelt (1929) Vanajanselkä was para-oligotrophic in 1926 and its bottom fauna belonged next to the mesohumic, oligotrophic Amphipoda type of Alm (1922). Later Järnefelt (1953) classified the benthos of Vanajanselkä in 1926 in his own typology, into the relict type or into the *Monodiamesa* type (when the system was based on chironomids). According to him both types were eutrophic, but the relation between his bottom faunal lake types and the trophic status is confused (Brinkhurst 1974). In any case, the productivity seems to have been remarkably lower than today.

Because the results of Järnefelt (1929) are quantitatively not fully comparable to our results, it is interesting to compare Vanajanselkä to other lakes of the same watercourse, which were studied by him using similar methods in 1926. Lake Lehijärvi (see Fig. 1), which was formerly connected with Vanajanselkä (Auer 1924), was already eutrophic in 1926. Lake Pääjärvi (see Fig. 1) was a dys-oligotrophic lake as it is today (Paasivirta 1974):

	Vanajanselkä	Lehijärvi	Pääjärvi
Average density of total fauna (ind./m^2)	223	738	117
Average biomass (g/m^2)	0.85	5.52	0.51
Dominant chironomid species	*Monodiamesa bathyphila*	*Chironomus semireductus*	*Monodiamesa bathyphila*

Although the abundance estimates are quite inaccurate and not fully comparable (Pääjärvi is very much deeper than other lakes), they give hints of the productivity (cf. Alley & Powers 1970). Lake Lehijärvi was faunally very similar to the Rauttunselkä of today. The abundance of oligochaetes was high (668 ind./m^2) and the dominant chironomid *Chironomus semireductus*-gr. is probably identical to *C. plumosus* (Saether 1975).

The bottom fauna of Vanajanselkä in 1926 is difficult to classify into any lake type of Brundin (1958). As pointed out earlier, Vanajanselkä is not stably stratified. On the other hand the small chironomid species must have penetrated the sieve mesh used by Järnefelt. *Monodiamesa bathyphila* was the dominant chironomid species in the profundal of Vanajanselkä in 1926 (p. 88) and according to Brundin (1949) it is a typical member of the *Tanytarsus lugens* community. In Pääjärvi, where the present profundal fauna belongs next to this community type, *Monodiamesa* was the only species found by Järnefelt in Pääjärvi in 1926. A paleolimnological method is the only way to establish more accurate by the chironomid succession in Vanajanselkä.

According to Järnefelt (1929) the productivity of Vanajanselkä was affected unfavourably by peatlands, which were left below the water level in the past (Auer 1924). Vanajanselkä already received eutrophicated waters from the upper course in the 1920s, but their effect was largely eliminated there.

After 1926 a rapid eutrophication took place in Vanajanselkä. The increasing pollution caused floral changes and also changed the zonation of water vegetation (Uotila 1971). The *Pontoporeia-Monodiamesa* community was replaced by a *Chironomus anthracinus* community up to 1965. The abundance of total benthos had increased. Regressive species were still present, but their abundance was lower than earlier in the profundal zone.

During 1965—1977 the increasing waste water load directed into Vanajanselkä caused serious deterioration of the oxygen conditions, which led to massive fish mortality in 1972 and 1974. In the bottom fauna, changes from the *Chironomus anthracinus* associations towards a *C. plumosus* association can be detected, especially after 1971. The faunal affinity measured with PSc and CC indices between Rauttunselkä and Vanajanselkä increased and the depth distribution became quite similar in both areas in 1977. The dominance and absolute numbers of *C. anthracinus* decreased and *C. plumosus* became more abundant in the profundal zone. The oligochaetes also became quantitatively more important near Rauttunselkä. The regressive species

Pontoporeia affinis, Monodiamesa bathyphila and molluscs decreased further and had totally disappeared at most stations in 1977. Changes in the diversity of the benthos were, in contrast, rather small. It seems obvious that the diversity indices are not very sensitive measures of eutrophication in lakes.

Changes in both vertical and horizontal distributions of *Pontoporeia affinis* are clearly related to the deterioration in oxygen conditions. It disappeared first in the deeps. On the other hand it became scarce first in the western part and the southwestern sub-basin. The collapse of *P. affinis* took place in the northwestern sub-basin between 1971 and 1974 (fish deaths in 1972 and 1974). The results of 1977 show that it was able to survive, although in low numbers, in the shallow bays of the northeastern sub-basin. Similar changes have been reported from other eutrophic lakes. *P. affinis* was abundant in the current *C. plumosus* areas of Mälaren in the beginning of this century, but has since vanished (Wiederholm 1974a). On the other hand it is known that other factors can also cause drastic changes in the population density of *P. affinis,* e.g. the predation pressure from fishes (Segerstråle 1937, Wiederholm 1978).

Rauttunselkä

Changes in the general state of Rauttunselkä were rather small after 1965, when the conditions were severe, especially in winter. A slight improvement has taken place during last few years. The composition of the *C. plumosus* community has remained constant. The improvement is best indicated by the bathymetric distribution of the benthos. In 1965 and 1971 a clear inhibition of the production of profundal benthos was detected. When the oxygen concentration increased, the high sublittoral biomasses decreased. This might have been due to the increased predation pressure from fishes.

Kärjenniemenselkä

The improvement in 1977 is clearly indicated by a change in the depth distribution and higher diversity of the bottom fauna. The very tolerant *Chironomus plumosus* is able to colonize the desolate profundal soon after oxygen concentration has increased there (Wiederholm 1975). The larvae are able to distribute horizontally in the free water (Yamagishi and Fukuhara 1971). The scarcity of oligochaetes and *Chaoborus flavicans* is due to toxic inhibition. These are known to be very tolerant to low oxygen concentrations. The oligochaetes are very sensitive to zinc (Hynes 1960), the concentrations of which are very high in the water and sediments of Kärjenniemenselkä. Recovery from this kind of pollution is a slow process.

Hattulanselkä

The benthos of this sub-area was quite similar to that of Rauttunselkä in 1965. The production was very high in the sublittoral. Although the oxygen conditions were bad in the profundal, animals were found even in the deepest places. No clear toxic inhibition of benthic production was detected in this area, which is under pressure from domestic waste waters in contrast to Kärjenniemenselkä, where the industrial effluents are highly toxic e.g. to oligochaetes.

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