BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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URN:ISBN:978-951-39-9326-9
ISBN 978-951-39-9326-9 (PDF)
ISSN 0356-1062

Jyväskylän yliopisto, 2022

Jyväskylässä 1978 ● Oy Sisä-Suomen kirjapaino

Biol. Res. Rep. Univ. Jyväskylä 4: 3 - 87. 1977

On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland

LASSE HAKKARI

HAKKARI, L. 1977: On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. - Biol. Res. Rep. Univ. Jyväskylä 4: 3 - 87.

The study deals with the influence of some physical, chemical, and biotic factors upon the species composition, biomass, and production of zooplankton in several Finnish lakes.

Different groups of zooplankton species are separated according to their relation to eutrophication and pollution caused by sewage and wastes from pulp and paper mills. The zooplankton biomass, estimated with the mean volumes of different species and stages, is considered in relation to eutrophication and pollution, and also to the production of phytoplankton. Some comparisons are made between different methods of estimating production. The significance of vendace (Coregonus albula L.) and smelt (Osmerus eperlanus L.) as predators of zooplankton is discussed with reference to analyses of stomach contents and the gastric digestion rate.

Eutrophication seemed to increase the number of zooplankton taxa. Several taxa correlated so well with eutrophication and/or pollution that they can be used as indicators. The production of zooplankton followed the changes in the production of phytoplankton algae. In polluted areas bacteria seemed to form a large part of the energy source of zooplankton. Vendace and smelt fed mainly on zooplankters measuring more than 0.4 mm. Owing to the preference of for large zooplankton species, their production in oligotrophic waters was mainly consumed by fish. Consumption by fish thus affected the zooplankton composition.

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Contents

I Introduction

The aim of this study was to assess the role of the zooplankton in the biocoenosis, of Lakes Päijänne, Jyväsjärvi, Keitele, and Konnevesi, Central Finland, and to examine the effects of sewage and waste waters from the wood-processing industry on the zooplankton composition, biomass and production. Special attention was paid to:

1. Seasonal fluctuations in the species composition and biomass,
2. The occurrence, diversity, and biomass of zooplankton taxa in relation to pollution,
3. Zooplankton production,
4. The interrelationships between zooplankton and the organisms of other trophic levels in the lakes.

The study was carried out in the Hydrobiological Research Institute of Jyväskylä and in the Department of Biology of the University of Jyväskylä. The results for Päijänne were obtained during a larger limnological investigation, which is still in progress.

II Study area

A. Hydrographical and hydrological data

Päijänne is the central lake of the Kymijoki basin. Most of the inflowing water comes from the northern watercourses. Lake Keitele is the central lake of the Viitasaari watercourse, and Lake Konnevesi is the greatest lake in the Rautalampi watercourse. Päijänne is drained to the Gulf of Finland by the Kymijoki (Fig. 1).

Keitele is situated north of the town of Äänekoski (Fig. 1). The area of the lake is 526 km^2, the mean depth 6.3 m, and the mean discharge 51 m^3/s (AURA 1965 and Hydrological office 1970). The water colour is ca. 25-40 mg Pt/l, and the concentration of phosphorus in the middle part, where the sampling was done, is 10-12 µg/l (Hydrobiological Research Institute of Jyväskylä, unpubl.). The lake is thus oligotrophic except for the southernmost part, which is eutrophicated (GRANBERG *et al.* 1973). The water leaving Keitele is polluted by the effluents from sulphate and sulphite pulp mills in Äänekoski and flows via some smaller lakes to the northern end of Päijänne.

The area of Konnevesi is 184 km^2; the mean depth of the northern part is 7.6 m, that of the southern part 11.0 m (Central Finland Office of the National Board of Waters). The concentration of phosphorus was 10-13 µg/l, and the colour of the water 17-25 mg Pt/l (TUUNAINEN 1972). Thus, the lake is unproductive and in natural condition.

During the sampling in 1970, the temperature of the epilimnion was ca. 16 °C in the northern part and ca. 15 °C in the southern part. At St. K 1 (cf. Fig. 1) the metalimnion lay at 20-25 m, at St. K 2 at 10-15 m (TUUNAINEN 1972).

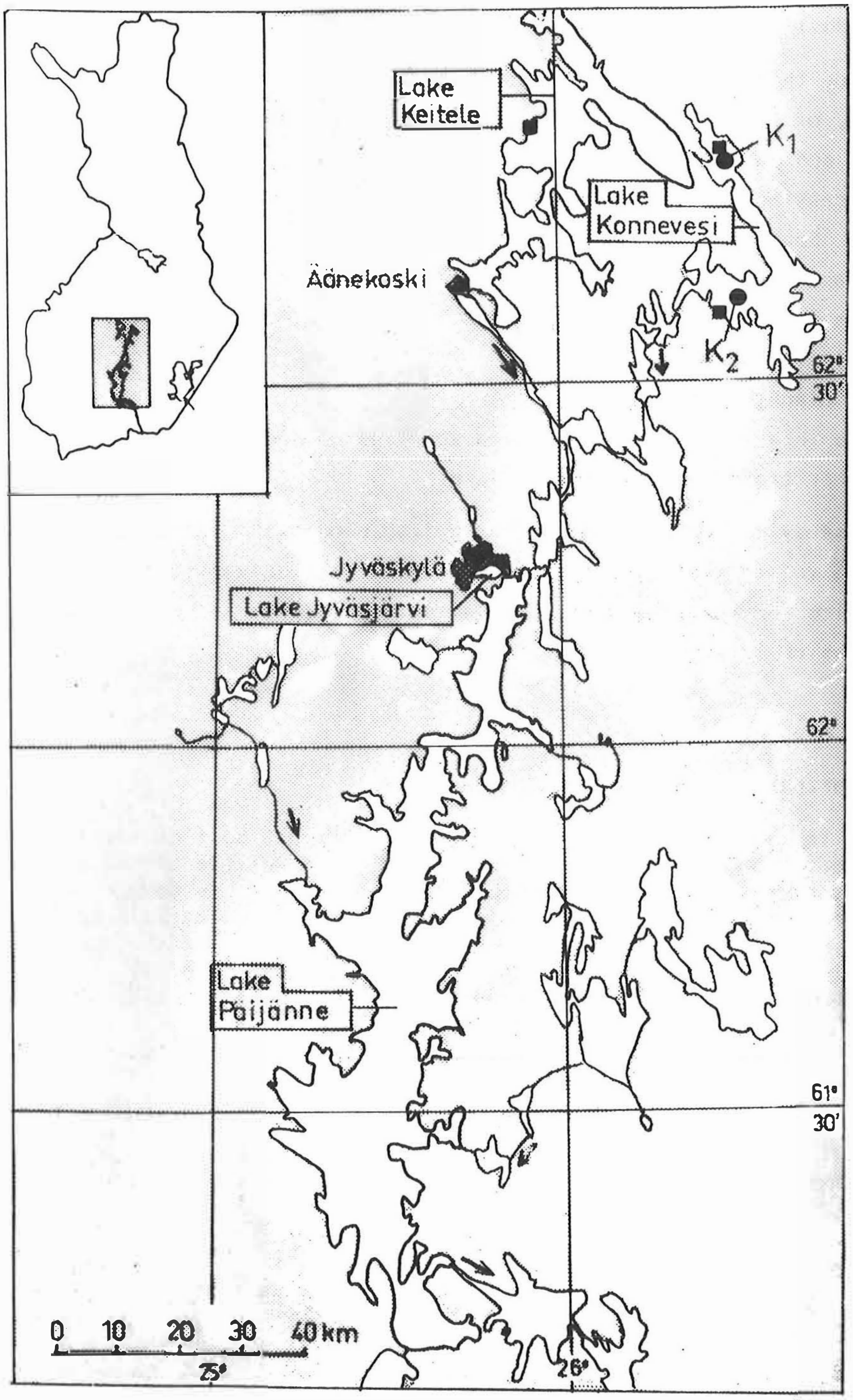

Fig. 1. The study area, the zooplankton sampling stations in Konnevesi, and the fishing places in Konnevesi and Keitele (● = zooplankton station, ■ = fishing place).

The mean discharge from the SW part of the lake is 53 m^3/s (TUUNAINEN 1972). Downstream, the water mixes with the polluted water from Äänekoski and flows to the northern end of Päijänne through the Haapakoski rapids, where the mean discharge is 139 m^3/s (Hydrological Office 1970).

The main physical characters of L. Päijänne are:

Maximum length	(km)	120
Maximum depth	(m)	104
Mean depth	(m)	17
Water area	(km^2)	1 090
Area of drainage basin	(km^2)	26 480
Water volume	(km^3)	17.8
Mean outflow	(m^3/sec)	209
Theoretical replenishment time	(days)	1 050

The mean temperature of the epilimnion in June-September is approximately 13-15 °C, and the maximum temperature is about 20 °C (investigations of the Hydrobiological Research Institute, Jyväskylä). The mean depth of the thermocline is 13-25 m (cf. MÄKINEN & KORTELAINEN 1974). In winter, the temperature of the near-bottom water layer is about 2-3 °C, and Päijänne is usually covered with ice from December to early May.

Päijänne consists of several water bodies (Fig. 2), which differ widely in their physical characters and waste loads. The lake receives waste waters from three main sources:

1. Waste waters from sulphite and sulphate pulp mills in Äänekoski, which flow through the Haapakoski rapids into the northernmost part of Päijänne.

2. Sewage from the town Jyväskylä (60 000 residents) and wastes from a paper mill, which flow into North Päijänne via Lake Jyväsjärvi, some kilometres SW of the Haapakoski rapids. The effect of these wastes can be seen throughout North Päijänne, downstream to Vanhanselkä (610, Fig. 2).

3. Wastes from a sulphite pulp mill and paper mills at Jämsänkoski and Jämsä, which flow into Tiirinselkä. The effect of these wastes is weakly seen in Tehinselkä (740-750). When the sulphite lye evaporating and burning plant started to operate in the sulphite pulp mill in 1969, the load of effluents decreased, which was clearly seen in both the hydrography and biology of Central Päijänne. The BOD_7 in the Jämsänjoki averaged 60 mg/l in 1962-1968, but was only 12 mg/l in 1970 (LAPPALAINEN 1972).

The waste waters cause differences in the hydrography of the different parts of Päijänne (cf. MÄKINEN & KORTELAINEN 1974, and Table 1).

The main direction of water flow is from north to south. The most rapid currents have been observed in the epilimnion, e.g. at a depth of 0-10 m in Poronselkä and Ristiselkä their rates are ca. 0.9 km/day in spring and ca. 0.5 km/day in winter (LAPPALAINEN 1972). The effluents from Äänekoski and Jyväskylä mainly affect the water area north of Vanhanselkä (610), but lignin compounds reach the southern part of the lake.

The currents are an important factor for the water quality in Central Päijänne. The wastes from the sulphite pulp mill and paper mills have polluted Tiirinselkä (655-657) and Lehtiselkä (675) (cf. Table 1), and slightly eutrophicated Souselkä (638) and Judinsalonselkä (715). In winter, a current of clean water flowing from Souselkä (638) to Lehtiselkä and Tiirinselkä improves the condition of these water bodies in the 0-5-m layer (LAPPALAINEN 1970). In spring, the water in the 0-10-m layer flows from Souselkä (638) to Tehinselkä (740-750) in ca. 30 days, averaging 0.9 km/day (LAPPALAINEN 1970).

The wastes mainly degrade and sediment in the area north of Tehinselkä (740-750). Only compounds that break down slowly (lignins) are observed in the water body of Asikkalanselkä (810), which is still in natural condition, apart from the slight regulation of the water level occurring since 1964; the concentration of oxygen is high and that of phosphorus low (Table 1).

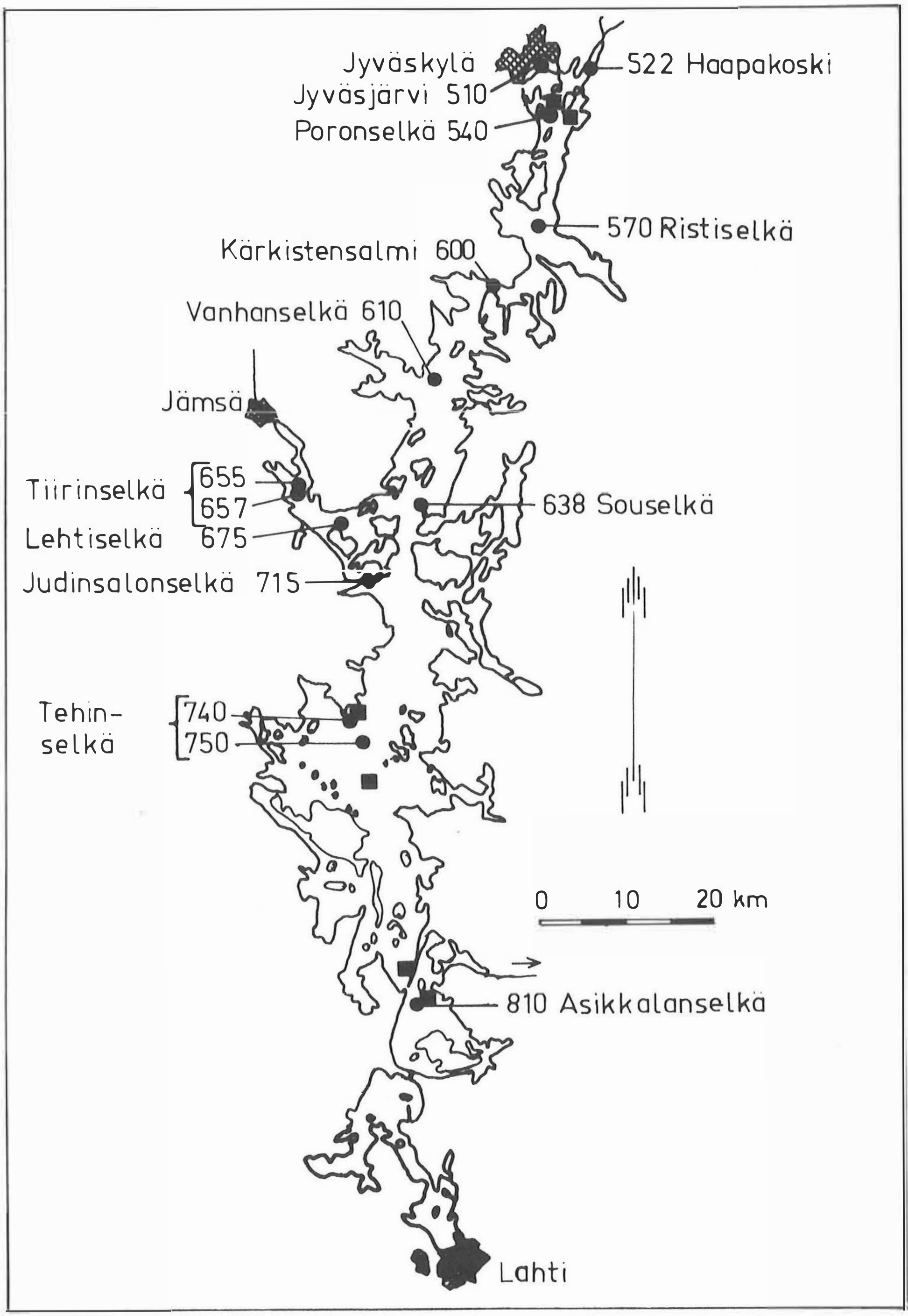

Fig. 2. The sampling stations in Jyväsjärvi and Päijänne (● = zooplankton station, ■ = fishing place).

Table 1. Total phosphorus (µg/l) in epilimnion (A), lignin (mg/l) in epilimnion (B), and oxygen (mg/l) in hypolimnion (C) in Jyväsjärvi (510), Päijänne (522-810) and Konnevesi (GRANBERG & LAPPALAINEN 1974, MÄKINEN & KORTELAINEN 1974 and TUUNAINEN 1972).

		LAKE JYVÄSJÄRVI	NORTHERN PÄIJÄNNE					CENTRAL PÄIJÄNNE				SOUTHERN PÄIJÄNNE		LAKE KONNEVESI	
	Station	510	522	540	570	600	610	638	655-657	675	715	740-750	810	1	2
	Season														
A	Winter	800	19	29	25	21	17	15	24	18	13	11	8	-	-
	Spring	420	27	48	26	22	20	20	45	35	20	15	9	11	12
	Summer	300	28	25	23	20	18	18	38	25	19	14	13	7	9
	Autumn	440	22	31	18	15	13	14	42	30	15	10	11	17	11
B	Winter	0.8	5.6	4.9	4.5	3.8	2.8	4.9	6.1	4.0	4.7	4.4	3.6	-	-
	Spring	0.9	5.2	3.8	2.9	2.7	2.7	4.7	6.2	7.4	6.6	5.9	3.1	0	0
	Summer	0.7	3.4	1.8	1.9	2.0	2.0	3.8	8.0	4.3	4.9	4.1	2.8	0	0
	Autumn	0.5	4.1	2.7	1.7	1.2	2.0	3.3	10.8	4.1	4.0	3.7	2.6	0	0
C	Winter	0.8		6.7	10.8	9.6	10.8	11.0	0.6	5.1	10.7	12.0	11.3	-	-
	Spring	3.5		7.2	7.9	9.3	9.2	10.3	2.0	4.3	10.7	11.8	11.0	-	-
	Summer	0.6		5.4	7.5	7.9	9.1	8.4	0.7	3.7	8.9	9.8	9.6	8.8	8.1
	Autumn	4.7		9.1	9.0	10.1	10.4	9.4	5.9	8.9	10.4	10.6	10.7	11.3	10.6

L. Jyväsjärvi, which has received the wastes of the town of Jyväskylä and the acid effluent of a paper mill, is a small polluted lake in Jyväskylä. Its area is 3.3 km^2, and its mean depth 7.2 m (Central Finland Office of the National Board of Waters). In summers 1969-1973 the concentration of total phosphorus in the epilimnion was ca. 300 µg/l (GRANBERG & LAPPALAINEN 1974). Lignin was almost lacking. In August, the pH of the epilimnion was usually ca. 5.0-6.0, but in the other summer months it could rise to 9.0 and more (cf. PIIPPONEN 1974). Oxygen was lacking in the hypolimnion in June-September and in December-April. In 1971, the maximum temperature in the epilimnion was ca. 20 ^oC (PIIPPONEN 1974).

B. Biological data

In Päijänne the dominant phytoplankton species are mostly *Cryptomonas* spp., *Rhodomonas minuta*, and Chrysomonadinae flagellates (GRANBERG 1973 and 1974). The main part of the phytoplankton biomass consists of small algae which are readily consumed by the zooplankton herbivores (cf. NAUWERCK 1963). In Jyväsjärvi, *Scenedesmus* spp. are dominant for long periods in the summer (GRANBERG & LAPPALAINEN 1974). Blue-green algae are not numerous in these lakes.

In the years 1969-1971, primary production was highest in Jyväsjärvi (ca. 700-2300 kg C_{ass}/ha x year) and in the water body of Poronselkä (540) in Northern Päijänne (ca. 150-300 kg C_{ass}/ha x year, cf. Fig. 7). In 1969-1970 the primary production in Tiirinselkä (655-657) and Lehtiselkä (675), Central Päijänne, was inhibited by effluents from the sulphite pulp mill in Jämsänkoski. When the evaporating and burning plant started to operate, the toxic effects decreased. In 1969 primary production was ca. 30 kg C_{ass}/ha x year in Tiirinselkä and ca 70 kg C_{ass}/ha x year in Lehtiselkä. GRANBERG reported a significant rising trend in primary production between

1969-1972, the values for 1972 being ca. 130 kg C_{ass}/ha x year in Tiirinselkä and ca. 150 kg C_{ass}/ha x year in Lehtiselkä. The lowest primary production was observed in Southern Päijänne; in Tehinselkä (740-750) it was ca. 50-80 kg/C_{ass}/ha x year and in Asikkalanselkä (810) ca. 30-60 kg C_{ass}/ha x year (cf. Fig. 7).

There is little information about the bacterial production. The provisional estimates of the production during the growing season in 1970 and 1972 are 900-1000 kg C/ha in Poronselkä, 600-800 kg C/ha in Tiirinselkä, 1000-1100 kg C/ha in Lehtiselkä, and 250-565 kg C/ha in Tehinselkä (GRANBERG 1975).

The semiplanktonic species *Chaoborus flavicans* may be a significant predator of the zooplankton (cf. RYLOV 1935, KAJAK & RANKE-BYBICKA 1970, FEDORENKO 1975). In Northern Päijänne (north of Vanhanselkä, 610), the mean abundance of *Chaoborus* varied between 0 and 119 exx/m^2, in Central Päijänne (Tiirinselkä, Lehtiselkä, Souselkä, and Judinsalonselkä) it was 6-73 exx/m^2, and in Southern Päijänne (Tehinselkä and Asikkalanselkä) 3-11 exx/m^2 (SÄRKKÄ & PAASIVIRTA 1972, TUUNAINEN *et al.* 1972).

The cyclopids belonging to the bottom meiofauna may also feed on zooplankton. In Northern Päijänne their abundance was ca. 27 000-207 000 exx/m^2 and in Southern Päijänne 6 000-9 000 exx/m^2 (SÄRKKÄ & PAASIVIRTA 1972).

Roach (*Rutilus rutilus* L.) and perch (*Perca fluviatilis* L.) are found regularly in the pelagic zone of the eutrophicated Poronselkä and Ristiselkä (NYRÖNEN & HAKKARI 1976), and may be important plankton feeders in this area. Vendace (*Coregonus albula* L.) and whitefish (*C. lavaretus* s. lat. L.) have decreased sharply in Poronselkä and Ristiselkä because of pulp mill and human effluents (TUUNAINEN 1970, 1971). In Tiirinselkä and Lehtiselkä, perch is an important species in the pelagial (TUUNAINEN 1970, 1971, HAKKARI 1975 b), and vendace and whitefish are almost lacking. The abundance of smelt (*Osmerus eperlanus* L.) does not appear to vary very much in the different parts of the lake. In 1969-1972 it was rarer than vendace in Southern Päijänne, but commoner than vendace in the central and northern parts of the lake. Vendace and smelt were important pelagial species in Tehinselkä, Asikkalanselkä, and Vanhaselkä. In 1970, during the maximum of vendace, its biomass in Southern Päijänne was estimated by P. TUUNAINEN at 40-60 kg/ha, but was only some kilograms/ha in Northern and Central Päijänne (cf. HAKKARI 1970 a). Small perch have also been found in the pelagial of Tehinselkä, and are known to feed abundantly on zooplankton (NYRÖNEN 1975).

III Material and methods

A. Zooplankton

1. Sampling

The water samples for zooplankton analyses were taken with a 7.4-litre Sormunen tube sampler (length 1 m, diameter 100 mm; Fig. 3). The tube was cast vertically into the water and closed at the desired depth by pulling a rope. The sampler usually descended fairly rapidly in the uppermost 10 m, 1-2 m/sec. Below this, the speed decreased to about 0.5-1 m/sec. Primary samples were taken at every metre in a water column of 0-20 m. These 20 samples were divided into three groups (0-5 m, 5-10 m, and 10-20 m) which

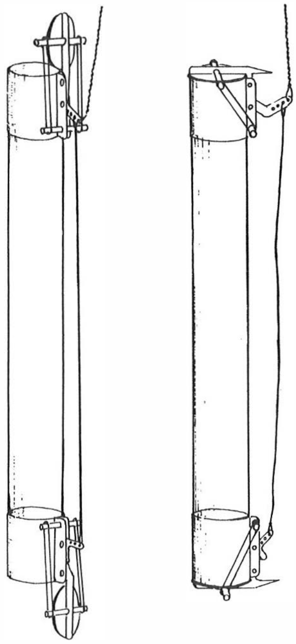

Fig. 3. The Sormunen tube sampler. Open - closed.

were poured separately through a plankton net with a mesh size of 50 µm. The material was preserved with 5 % formalin. In 1969 samples were also taken at a depth of 29-31 m.

The sampling was concentrated in the water layer of 0-20 m, because it represents the greater part of the water mass, e.g. ca. 80 % of the volume of Päijänne (Helsinki City Waterworks 1968), and contains an even greater proportion of the zooplankton production. Also, all the zooplankton species are found in this water layer. Because of the rapid descent of the sampler in the epilimnion, avoidance by the zooplankters was probably not significant, but it may have been more important in the deeper water layers. CLUTTER (1968), who also considered the results of other investigators, reported that more animals were generally taken with rapidly moving samplers. Though it is not necessarily the largest species that are best able to avoid the sampler, the strong species *Mysis relicta* (Lovén) and *Chaoborus flavicans* (Meigen) are especially likely to evade capture. About 3000 samples from the hypolimnion yielded only a few mysids. During the day, most *Chaoborus* individuals stay on the bottom, especially when the hypolimnion is oxygenated (NILSSEN 1974), and thus avoid sampling.

When the wind was not too hard, an attempt was made to decrease the error caused by the patchiness of the zooplankton by letting the boat drift.

There are many earlier studies on the patchiness or superdispersion of zooplankton. NAUWERCK (1963) found that in L. Erken, Sweden, the standard error in group I (14 samples taken from one place, depth 2 m) was half of that in group II (seven samples within a radius of 100 to 200 m). His values included counting errors, and since sampling was done only at 2 m, differences in the vertical distribution.

Discussing the results of several investigators, CASSIE (1963) observed that the coefficient of variation of a single plankton sample is most often in the range of 22-44 %, although much larger coefficients are not uncommon.

Various reasons have been suggested for superdispersion in the horizontal distribution of zooplankton: a hydrodynamic effect is supposed by HUTCHINSON (1967, p. 797); STAVN (1971) proposed a model of zooplankton distribution with Langmuir spirals (cf. HUTCHINSON 1957). *Daphnia magna* is carried towards the surface, but negative phototaxis causes it to orientate against the current, which leads to superdispersion. The same observation was made by GEORGE & EDWARDS (1974) in respect of *Daphnia hyalina*.

Schools of planktivorous fish may increase superdispersion by decreasing the abundance of a favoured zooplankton species in the area of feeding. The vendace, *Coregonus albula*, feeds in schools in summer (JÄRVI 1919, AIRAKSINEN 1967).

As the vertical distribution of zooplankton has been studied in many oligohumic and mesohumic lakes in Finland (see, e.g., HAKKARI 1967, 1969, GRANBERG 1970), the number of vertical samples was limited in this study.

The loss of zooplankton through a 50-µm mesh was investigated by PIIPPONEN (1974) in Jyväsjärvi. Her sampling method was the same as that used in the present study, though she sieved the water with a 25-µm net, as well. The proportion of the zooplankton specimens passing through a 50-µm mesh was about 27 %, and that of the biomass was 4 %. The greatest loss was observed with protozoans, but the rotifers *Anuraeopsis fissa* and *Keratella cochlearis* also often penetrated the net.

The sampling sites and the number of samples collected at the different stations are presented in Table 2 (cf. Figs. 1 and 2).

2. Counting and analysing

The zooplankton samples were divided with a Folsom sample splitter (McEWEN *et al.* 1954). The fraction generally used in summer was 1:8, which corresponded to an unsieved sample of 4.6 l at 0-5 m and 5-10 m and 9.2 l at a depth of 10-20 m; the fraction used in winter was 1:4. The fractions were allowed to settle for 6-12 hr and the sedimented sample was then counted with an inverted plankton microscope, Wild M 40, according to UTERMÖHL (1958).

The empirical model of PRESTON (1962) shows that the number of species is related to the number and size of the samples.

In Päijänne, the increase of the number of taxa with increasing water volume was small above ca. 2.3 l (Table 3, cf. HAKKARI 1970 b), although the numbers in 4.6 l and 9.2 l were apparently too small to give excessive concentration of zooplankton in the counting chambers. On average, the water

Table 2. Sampling stations and years, and number of samples taken during whole study and in June-September.

Area	Sampling sts.	Sampling years	Number of samples Whole study	June - Sept.
LAKE JYVÄSJÄRVI	510	1969 - 1970	67	43
NORTHERN PÄIJÄNNE				
Haapakoski	522	1969 - 1970	41	32
Poronselkä	540	1969 - 1971	83	56
Ristiselkä	570	1969 - 1971	70	48
Kärkistensalmi	600	1969 - 1970	59	38
Vanhanselkä	610	1969 - 1971	74	46
CENTRAL PÄIJÄNNE				
Souselkä	638	1969 - 1971	71	47
Tiirinselkä	655 - 657	1969 - 1972	104	68
Lehtiselkä	675	1969 - 1972	102	69
Judinsalonselkä	715	1969 - 1971	68	44
SOUTHERN PÄIJÄNNE				
Tehinselkä	740 - 750	1969 - 1971	138	105
Asikkalanselkä	810	1969 - 1971	66	48
LAKE KONNEVESI				
Northern part	1	1970	15	12
Southern part	2	1970	15	12
LAKE KEITELE				
Koivuselkä		1973	6	6
			Σ 979	674

Table 3. Numbers of taxa in different volumes of water from Kärkistensalmi (600) and Tehinselkä (740) in June-August. S.E. includes the difference between the eutrophicated and natural water bodies.

Water volume l	$\bar{x} \pm$ S.E. of the number of taxa	% of taxa in water volume of 18.5 l
0.3	13.5 ± 1.8	41.4 ± 2.4
0.6	18.0 ± 2.5	55.0 ± 1.1
1.2	20.8 ± 2.0	64.5 ± 2.5
2.3	27.3 ± 3.7	83.3 ± 1.5
4.6	26.8 ± 2.7	82.9 ± 1.8
9.3	27.8 ± 3.5	85.4 ± 1.8
18.5	32.5 ± 4.0	100.0

volumes investigated from eutrophicated water bodies were smaller than those from natural waters, and the error caused by this difference in size may have decreased the differences between the water bodies.

The precision of the dividing and counting of the samples was tested with four replicate counts (Table 4). The person who counted the samples did not know about the test.

The highest coefficients of variation (standard deviation/mean) were found in connection with very low numbers of individuals (*Leptodora*, *Limnocalanus*). The mean coefficient of variation was ca. 40 %, which includes the errors arising during the splitting of the samples and the counting of fractions, each containing the plankton of 4.6 l of water.

3. Volume and biomass

During the counts, measurements were made of the volumes of large species, such as *Leptodora kindti*, *Bythotrephes longimanus*, *Daphnia* spp. , *Holopedium gibberum*, *Limnocalanus macrurus*, *Heterocope* spp., *Asplanchna* spp., and

Table 4. The standard error and coefficient of variation in diving and countting of two different zooplankton samples.

	Sample I		Sample II	
	$\bar{x}$ ± S.E.	C.V. %	$\bar{x}$ ± S.E.	C.V. %
Tintinnopsis lacustris	12.3 ± 2.6	41.6	2.0 ± 0.4	20.5
Vorticella sp.	105.8 ± 23.9	45.2	39.8 ± 12.3	62.1
Keratella cochlearis	24.5 ± 3.0	24.2	26.3 ± 3.3	25.3
Kellicottia longispina	26.0 ± 3.7	28.8	12.5 ± 3.6	57.1
Gastropus stylifer	27.8 ± 2.7	19.1	22.0 ± 4.4	39.8
Polyarthra vulgaris	19.5 ± 1.4	14.8	55.3 ± 7.3	26.5
Conochilus unicornis	20.5 ± 1.7	18.1	33.3 ± 10.7	64.1
Limnosida frontosa	5.0 ± 1.7	69.2	0.8 ± 0.3	66.7
Holopedium gibberum	8.5 ± 0.3	6.8	7.0 ± 1.1	30.9
Daphnia cristata	53.0 ± 7.2	27.0	35.0 ± 1.1	6.2
Eubosmina spp.	15.8 ± 2.7	33.7	17.5 ± 2.1	24.0
Leptodora kindti	0.5 ± 0.3	116.0	0.0	
Limnocalanus macrurus	0.5 ± 0.3	116.0	5.5 ± 1.3	48.2
Eudiaptomus spp.	5.8 ± 1.3	43.1	9.5 ± 1.1	21.9
Cyclops spp.	34.3 ± 5.9	34.7	4.8 ± 1.1	46.7

Chaoborus flavicans. The values obtained correspond well with the mean volumes given by other investigators in North Europe (cf. NAUWERCK 1963, AASA 1970, ANDRONIKOVA 1971). The volumes of small species were taken from the tables of NAULAPÄÄ (1966). Since the specific gravity of zooplankton is usually ca. 1.0 (cf. RUTTNER 1962, HUTCHINSON 1967), the volume values µl/l can be converted to fresh weight biomass values.

The mean biomass of zooplankton in a certain volume or area of water was calculated by weighting the biomasses in vertical samples with the volumes of the corresponding water layers (cf. Helsinki City Waterworks 1968). The biomass beneath a depth of 20 m was estimated from the samples of 29-31 m. In summer 1969, the biomass at a depth of 29-31 m averaged 47 ± 13 % of the corresponding biomass at 10-20 m. In the calculations a value of 50 % was used.

4. Production

Rotifers

The production of rotifers was estimated by assuming that in June-September the daily P/B (production: biomass) coefficient was 0.16 for *Asplanchna* and 0.17 for other rotifers (GALKOVSKAYA 1965, cf. WINBERG 1971). Some comparisons were done by means of a method here called the "fluctuation method". The biomass maxima of different generation were summed, the life time of a generation being assumed to be 10 days (cf. HUTCHINSON 1967, p. 512). In the comparisons, the production of *Keratella cochlearis* and *Kellicottia longispina* was also calculated according to the formula of EDMONDSON (1960):

$$N_{t\ calc} = (B \times T \times N_0) + N_0,$$

where B is the rate of egg laying or the eggs laid per female per day,[1)] T is the time interval in days, and N_0 and N_t the initial and final number of individuals.

The estimates of rotifer production in Tehinselkä in 1969 made according to GALKOVSKAYA (1965) and EDMONDSON (1960) were very similar. The "fluctuation method" gave significantly lower estimates for the various rotifer species than the method of GALKOVSKAYA (Fig. 4:1). The coefficient of regression (b_{yx}), which gives information about the similarity of x and y, was 0.51. This low value is understandable because the "fluctuation method" does not take into consideration the production of young individuals that die before maturation, and the production of individuals that do not follow the fluctuations of the majority.

Cladocera and Copepoda

The production of Cladocera and Copepoda was estimated as follows.

1. In most cases by the graphical method proposed by WINBERG *et al.* (1965, cf. also WINBERG 1971, the first version, and EDMONDSON & WINBERG 1971).

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1) Not "biomass" as formerly

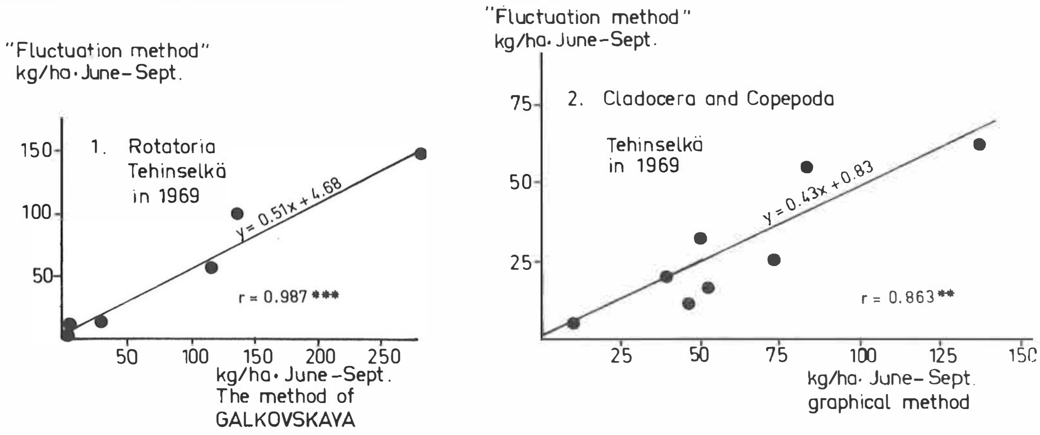


Fig. 4. The regression and correlation between different methods of estimating the production of Rotatoria, Cladocera, and Copepoda (cf. GALKOVSKAYA 1965, WINBERG *et al.* 1965).

The functions of time, the duration of development and the individual growth increment were obtained partly from the literature partly from empirical data (cf. Table 5).

2. By means of the formulae of PECHEN (1965) and SHUSHKINA (1966). PECHEN defines the relation of the monthly production (P) and the average monthly biomass (B, g/m^3) as follows:

Diaphanosoma $P = 4.43\ B^{0.90}$

Daphnia $P = 4.52\ B^{0.93}$

Bosmina $P = 2.61\ B^{0.82}$

Chydorus $P = 4.05\ B^{0.90}$

SHUSHKINA gives the following equations:

Diaptomus $P = 3.9\ B^{1.3}$

Cyclops $P = 3.2\ B^{1.4}$

3. By using the summer fluctuations of different species and summing the biomass maxima of the different generations (the "fluctuation method").

4. In the case of *Limnocalanus* and *Heterocope*, by the method recommended for estimating the production of planktonic monocyclic forms (WINBERG 1971):

$$P = N_2 \Delta \bar{w}_2 + N_e \Delta \bar{w}_e,$$

where $N_2 \Delta \bar{w}_2$ is the absolute growth increment for the period of individuals

Table 5. Average duration of development of different stages (in days). The values are for 13-18 °C, except in the case of *Limnocalanus macrurus* and *Heterocope appendiculata*.

Developmental stage / Species	Eggs	Nauplii	Copepodites or young Cladocera	Mature adults
Limnosida frontosa[1)]	3		6	4
Diaphanosoma brachyurum[2)]	3		6	4
Holopedium gibberum[3)]	3		8	5
Daphnia cristata[4)]	3		8	6
Eubosmina spp.[5)]	3		3	3
Limnocalanus macrurus[6)]	60	150	25	130
Heterocope appendiculata[7)]	(180)	60	20	105
Eudiaptomus spp.[8)]	5	11	10	7
Cyclops spp.[9)]	3	10	13	4

1) 2) 3) evaluated by HAKKARI 1970 b,

4) according to PETROWICH *et al.* 1961 and the present study

5) PETROWICH *et al.* 1961,

6) CARTER 1969, HAKKARI 1970 b,

7) according to ELSTER 1954 and the present study,

8) ELSTER 1954 and the present study

9) PETROWICH *et al.* 1961, WINBERG 1971 and the present study.

surviving to the end of the period, and $\Delta \overline{w}_e$ the mean absolute growth increment of those eliminated during the period. The individual growth and the population density curve are assumed to be linear.

5. In the case of *Bythotrephes longimanus*, *Leptodora kindti*, and *Eurytemora lacustris*, by assuming that the monthly P/B coefficient was 2 (cf. MORDUKHAI-BOLTOVSKAYA 1957).

With the individual-rich species of Cladocera and Copepoda in Tehinselkä, the estimate obtained by the "fluctuation method" was lower than that given by the graphical method (Fig. 4:2). The graphical method also gave higher estimates than the formulae of PECHEN (1965) and SHUSHKINA (1966; Fig. 5). The difference was usually small, the regression coefficient being 0.64-0.95, but with *Eudiaptomus* spp. the coefficient was only 0.52 (Fig. 5:6). It is possible that some small adult individuals of *Eudiaptomus* spp. were ident-

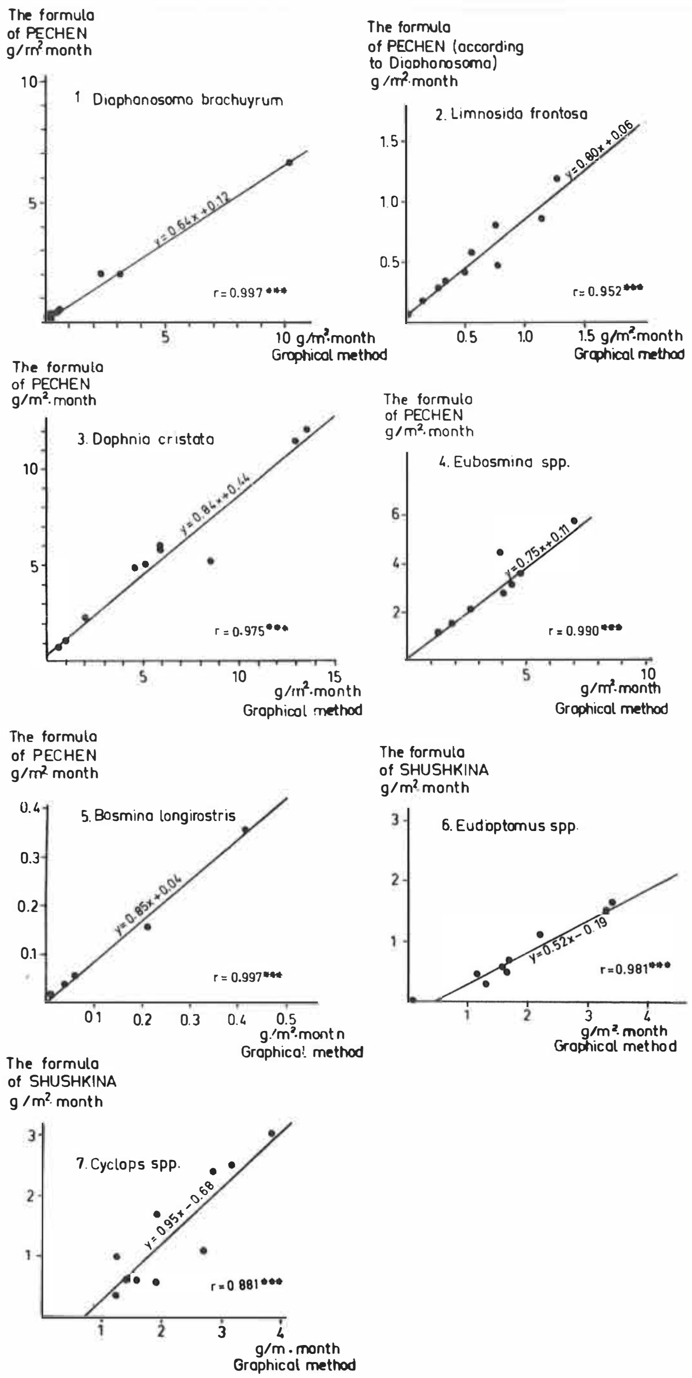


Fig. 5. The regression and correlation between different methods of estimating the production of some zooplankton taxa (cf. WINBERG *et al.* 1965, PECHEN 1965, SHUSHKINA 1966).

ified as young, which would increase the estimate given by the graphical method.

5. Relation of different taxa to eutrophication and pollution

The correlations were calculated between the frequencies of zooplankton taxa at the sampling stations in June-September and the means of the following variables in this season: oxygen concentration in the hypolimnion, $KMnO_4$ consumption, sodium lignosulphonate concentration (NALS) and total phosphorus in the epilimnion, and primary production. Calculations were also made of the regressions of the taxa frequencies on primary production and total phosphorus. The chemical values were obtained from the investigations of the Hydrobiological Research Institute of Jyväskylä (MÄKINEN & KORTELAINEN 1974) as were also those of the primary production (GRANBERG 1973, 1974).

Factor analysis was also applied to the taxa frequencies, using the Varimax solution (Computing Centre, University of Jyväskylä). In addition to the variables presented above, the following independent variables were used to describe the biotope and biocoenose: temperature in the epilimnion, and production of zooplankton herbivores and predators. The dependent variables were the zooplankton taxa. Their factor loadings were scrutinized. Very abundant and rare taxa were excluded because the distribution of their frequencies was skewed (level of significance 1 %; $-3.29 \leq Z \leq 3.29$).

The species preferring eutrophy or pollution and the species preferring oligotrophy were classified on the basis of the results of this and other investigations (BERZINS 1949, JÄRNEFELT 1952, JÄRNEFELT *et al.* 1963, MÄEMETS 1961, PEJLER 1957, 1964, PATALAS & PATALAS 1966, HAKKARI 1967). The E/O species ratio (E = the number of species preferring eutrophy or pollution, O = the number of species preferring oligotrophy) was calculated at every sampling time. Since the E and O species are most numerous in summer (e.g. PEJLER 1964, HAKKARI 1973), only the period June-September was taken into account.

6. Diversity

The diversity of the zooplankton was calculated with the information formula of Shannon and Wiener (HUTCHINSON 1967, p. 363):

$$D = - \sum_{i=1}^{m} p_i \log_2 p_i ,$$

where D is the diversity index, m is the number of taxa in a sample, p_i is the probability of occurrence of the i:th taxon. Diversity was calculated as the mean of the three vertical samples.

B. Planktivorous fish

1. Sampling

The material used to study the feeding of planktivorous fish, especially vendace (*Coregonus albula* L.) and smelt (*Osmerus eperlanus* L.), was collected with a seine, gill nets and a trawl in Konnevesi, Päijänne, and

Keitele in 1970-1973 (Table 6). The fishing grounds are presented in Figs. 1 and 2.

The fish were allowed to die, preserved with 5 % formalin and kept frozen.

2. Analysis

The fish were measured (total length) and weighed in the laboratory, and their age was determined from the ventral scales (cf. JÄRVI 1919). In the case of the material from Päijänne and Keitele, the contents of the stomach were weighed. The contents of the anterior part of the stomach were analysed, to permit comparison with the composition of the zooplankton, and some comparisons were made between the contents of the anterior and posterior parts of the stomach.

The differences in the composition of the food in the anterior and posterior parts of the stomach cause difficulties in comparing plankton composition and food composition. The food in the anterior part of the stomach is more comparable, but if the fish has just risen to the catching depth, the food composition and plankton composition at this depth may be absolutely different. In these cases comparison was made with the zooplankton composition of the hypolimnion.

The following average volumes were used for the prey items (cf. HAKKARI 1972 c):

	$10^6 \mu m^3$		$10^6 \mu m^3$
Limnosida and *Diaphanosoma*	30	*Leptodora*	500
Holopedium	35	*Eurytemora*	30
Daphnia cristata	30	*Heterocope*	70
D. galeata	40	*Eudiaptomus*	30
Eubosmina	15	*Cyclops*	10
Bythotrephes	400		

The length of *Limnocalanus*, and the larvae of *Chaoborus* and Chironomidae were measured. In the case of Keitele, the volumes of *Leptodora* individuals were determined according to the length of the fork.

The food weight was compared with the body weight, employing the index of stomach fullness (WINDELL 1971):

$$\text{Fullness index} = \frac{\text{weight of stomach contents} \times 10000}{\text{weight of fish}}$$

Table 6. Data on sampling of fish.

Fishing area	Date	Time	Depth m	Method	Investigated
LAKE KONNEVESI					
Northern Konnevesi	25. V.1970	20	5-15	seine	vendace, smelt
Southern Konnevesi	26. V.1970	19	5-10	"	vendace
Northern Konnevesi	1. VII.1970	20	10-25	"	"
Southern Konnevesi	2. VII.1970	16	5-15	"	"
Northern Konnevesi	28. VII.1970	21	10-25	"	"
Southern Konnevesi	28. VII.1970	16	5-10	"	"
"	7. IX.1970	15	5-15	"	"
LAKE PÄIJÄNNE					
Poronselkä	2. VI.1972	21	1- 5	"	smelt
"	6. VI.1972	24	3-10	"	" , whitefish
Tehinselkä	26. VI.1972	22	1- 6	trawl	vendace, smelt
"	28. VI.1972	22	1- 6	"	whitefish
Poronselkä	30. VI.1972	19	2-15	seine	smelt
Tehinselkä	11. VII.1972	21	3-15	"	"
"	11. VII.1972	23	1- 5	"	vendace, smelt
Asikkalanselkä	15. VII.1972	11	3-20	"	smelt, whitefish
Poronselkä	1.VIII.1972	18	2-14	"	smelt
Asikkalanselkä	18.VIII.1972	3	15-20	gill nets 19-20 mm	vendace, smelt
Tehinselkä	18.VIII.1972	6	11-16	gill nets 18-20 mm	vendace
"	15. IX.1972	8	20-25	gill nets 19-20 mm	"
Asikkalanselkä	20. IX.1972	6	16-20	gill nets 17-18 mm	"
Poronselkä	19. IX.1972	10	10-15	gill nets 17-21 mm	vendace, smelt
LAKE KEITELE					
Koivuselkä	19. VI.1973	23	2- 7	seine	vendace
"	26. VI.1973	23	2- 7	"	"
"	15.VIII.1973	22	4-15	"	"

3. Determination of the rate of gastric digestion of vendace

Eighty-one fish caught with a seine in Koivuselkä, Keitele, in June 1973 were immediately put into 80-l vessels, 5-6 individuals per vessel. The water in the vessels had been sieved through a plankton net (200 μm), which covered the vessel. Two control samples (15 fish) were taken immediately after the catch.

The incubation vessels were anchored at a depth of 5.5-6.0 m, where the temperature was 13.5-16.0 °C. The incubation times on 19-20 June were 1, 2, 3, 4, 5, and 6 hr, on 26-27 June 4, 7, 8, 9, 10, 11, and 12 hr. At the end of the incubation, the fish were taken out and preserved with formalin after death. The laboratory analysis was performed as with the other fish. The gastric digestion rate was taken as the change in stomach fullness during incubation.

4. Composition and digestibility of food

The proportions of the food components may change during digestion, since they are digested at different rates and chitinized items tend to accumulate (WINDELL 1971). Food digestibility was studied in connection the determination of gastric digestion, by comparing the food composition after different incubation times.

5. Selectivity of predators

The "electivity index" of IVLEV (1961) was used to measure predator selectivity:

$$E = \frac{s - b}{s + b},$$

where s is the percentage representation, by weight, of a food item in the stomach and b the percentage representation of the same item in the environment. The index yields E values between -1.0 and +1.0.

6. Food similarity

The index of food similarity proposed by SHORYGIN (1939) was calculated between the individuals of a sample and between the individuals of two fish species in order to study competition between different planktivorous species, especially vendace and smelt.

The percentages of total food were compared for each food item, and the lower values of each pair were summed.

IV Results

A. Zooplankton taxa

Altogether 107 taxa (genera, species, and subspecies) were identified in the material collected from Päijänne, Jyväsjärvi, Keitele, and Konnevesi. Ca.70 of these can be considered euplanktonic (Table 7). The scientific names and

Table 7. The zooplankton taxa identified in the material from Päijänne and Jyväsjärvi, their individual volumes (10^6 μm^3) and trophic level. Euplanktonic forms designated with +, herbivorous with h and carnivorous with c.

Taxon	Volume $10^6 \mu m^3$		
Protozoa:			
Arcella sp.	0.1		h
Difflugia limnetica Levander		+	h
D. hydrostatica Zacharias		+	h
D. curvicaulis Penard			h
D. oblonga Ehrenberg		+	h
Spathidium sp.			c
Paramecium sp.			h
Metopus sp.		+	
Caenomorpha sp.		+	h
Laboea sp.		+	h
Tintinnidium fluviatile S. Kent	0.05	+	h
Tintinnopsis lacustris Entz	0.05	+	h
Astylozoon sp.			h
Epistylis rotans Švec	1.0 (col.)	+	h
Vorticella sp.		+	h
Tokophrya sp.		+	h
Staurophrya sp.		+	c
Rotatoria:			
Cephalodella sp.			h/c
Trichocerca rousseleti (Voigt)			h
T. porcellus (Gosse)			h
T. similis (Wierzejski)		+	h
T. birostris (Mink)		+	h
T. rattus (Müller)			
T. pusilla (Lauterborn)	0.1	+	h
T. cylindrica (Imhof)		+	h
T. capucina (Wierzejski & Zacharias)		+	h
T. longiseta (Schrank)		+	h
Gastropus stylifer Imhof	0.1	+	h
Postclausa minor (Rousselet)		+	h
P. hyptopus (Ehrenberg)		+	h
Ascomoprha saltans Bartsch			h
A. ecaudis Perty			h
Chromogaster ovalis (Bergendahl)			h
Synchaeta spp.	0.1-3.0	+	h/c
Polyarthra vulgaris Carlin	0.4	+	h
P. dolichoptera Idelson	0.2	+	h
P. remata Skorikov	0.2	+	h
P. major Burckhardt	1.4	+	h
P. euryptera Wierzejski	2.0	+	h
Ploesoma triacanthum (Bergendahl)		(+)	c
P. hudsoni (Imhof)	4.0	+	c
Asplanchna herricki de Guerne	150	+	h/c
A. priodonta Gosse	50-100	+	h/c
A. cf. *brightwelli* Gosse		+	h/c
Lecane luna (Müller)			
L. lunaris (Ehrenberg)			
Lecane sp.			
Trichotria pocillum (Müller)			
Lepadella sp.			
Euchlanis dilatata Ehrenberg		(+)	h
Brachionus urceus (L.)			h
B. forficula Wierzejski			h
B. calyciflorus Pallas			h
Keratella cochlearis (Gosse)	0.1	+	h
K. cochlearis f. *tecta* (Gosse)	0.1	+	h
K. cochlearis f. *hispida* (Lauterborn)	0.1	+	h
K. serrulata (Ehrenberg)			h
K. ticinensis (Callerio)	0.1	(+)	h
K. hiemalis Carlin	0.2	+	h
K. quadrata (Müller)	0.2	+	h
Kellicottia longispina (Kellicott)	0.1	+	h
Notholca squamula (Müller)		+	h
N. caudata Carlin		+	h
Anuraeopsis fissa (Gosse)	0.2	(+)	h
Conochilus hippocrepis (Schrank)	1.0	+	h
C. unicornis Rousselet	0.5	+	h
Pompholyx complanata Gosse		+	h
P. sulcata Hudson		+	h
Filinia terminalis (Plate)	0.6	+	h
F. longiseta (Ehrenberg)	0.6	+	h
F. longiseta f. *limnetica* (Zacharias)		+	h
Collotheca sp. (spp.)			

Taxon		Volume $10^6 \mu m$		
Cladocera:				
Limnosida frontosa Sars	adult	30-50	+	h
	juv.	10		
Diaphanosoma brachyurum (Liévin)	adult	30-50	+	h
	juv.	10		
Holopedium gibberum Zaddach	adult	100	+	h
	juv.	10		
Daphnia pulex (de Geer)	adult	100-500	(+)	h
	juv.	50		
D. galeata Sars	adult	100(-300)	+	h
	juv.	20		
D. cristata Sars	adult	60	+	h
	juv.	10		
D. cucullata Sars	adult	60	+	h
	juv.	10		
Ceriodaphnia quadrangula (Müller)	adult	20	(+)	h
	juv.	5		
Bosmina longirostris Müller	adult	7	(+)	h
	juv.	2		
Eubosmina longispina longispina (Leydig)	adult	22	+	h
	juv.	5		
E. longispina obtusirostris (Lilljeborg)	adult	22	+	h
	juv.	5		
E. crassicornis (Lilljeborg)	adult	22	+	h
	juv.	5		
E. coregoni (Baird)	adult	22	+	h
	juv.	5		
E. mixta longicornis (Schoedler)	adult	22	+	h
	juv.	5		
E. mixta lilljeborgi Lilljeborg	adult	22	+	h
	juv.	5		
Chydorus sphaericus (Müller)	adult	15		h
	juv.	5		
Alona quadrangularis (Müller)				h
Alonella nana Baird				h
Alonopsis elongata Sars				h
Leydigia leydigi Schoedler				h
Camptocercus rectirostris Schoedler				h
Polyphemus pediculus Linné				h/c
Bythotrephes longimanus Leydig	adult	500-5000	+	c
	juv.	150		
Leptodora kindti (Focke)	adult	1000-10000	+	c
	juv.	200		
Copepoda:				
Limnocalanus macrurus Sars	adult	250	+	h
	copep.	50-100		
	naupl.	1-5		
Eudiaptomus gracilis (Sars)	adult	80	+	h
	copep.	10		
	naupl.	0.5		
Eudiaptomus graciloides (Lilljeborg)	adult	80	+	h
	copep.	10		
	naupl.	0.5		
Eurytemora lacustris (Poppe)	adult	80	+	h
	copep.	10		
	naupl.	0.5		
Heterocope borealis (Fischer)	adult	650	+	c
	copep.	200		h/c
H. appendiculata Sars	adult	170	+	c
	copep.	50-100		h/c
	naupl.	1.0		h
Cyclops strenuus s. lat. Fischer, *Mesocyclops leuckarti* (Claus), *Thermocyclops oithonoides* (Sars), *Cyclops* sp.	adult	15-25	+	c
	copep.	8		h
	naupl.	0.5-3		h
Insecta:				
Chaoborus flavicans (Meigen)	larva	500-15000	(+)	c
	pupa	15000	+	-

modes of life are mainly given according to GROSPIETSCH (1972), BICK (1972), KAHL (1930-1935), KUTIKOVA (1970), RUTTNER-KOLISKO (1972), VOIGT (1956-1957), RYLOV (1935), and HERBST (1962).

B. The variation in the number of taxa

The number of taxa was greatest in Northern Päijänne in summer (Table 8). The rotifers made up 2/3 of the total number of taxa in winter, and 1/2 in summer. The seasonal fluctuations in the numbers of taxa were mostly caused by other groups than rotifers, but rotifers were mainly responsible for the differences in numbers between the sampling areas.

In spring, the highest numbers of taxa were observed in Jyväsjärvi, Haapakoski and Tiirinselkä, evidently owing to the early warming of the water. In summer, the lowest numbers were found in Jyväsjärvi and Tiirinselkä, and the highest in the eutrophicated area of Northern Päijänne.

Table 8. Numbers of taxa in different seasons (PR = Protozoa, RO = Rotatoria, CL = Cladocera and CO = Copepoda). The numbers rounded to the nearest integer.

	Winter					Spring					Summer					Autumn				
Months	I - IV					V					VI - IX					X - XI				
	PR	RO	CL	CO	Σ	PR	RO	CL	CO	Σ	PR	RO	CL	CO	Σ	PR	RO	CL	CO	Σ
JYVÄSJÄRVI (510)	6	4	0	1	11	6	14	2	2	24	4	13	7	2	26	4	11	8	2	25
NORTHERN PÄIJÄNNE																				
Haapakoski (522)	1	13	0	3	17	3	14	2	3	22	6	19	9	3	37	6	18	4	3	31
Poronselkä (540)	1	14	2	3	20	2	12	2	3	19	6	19	9	4	38	6	19	5	3	33
Ristiselkä (570)	2	10	0	3	15	2	11	0	3	16	5	18	8	4	35	3	13	4	4	24
Kärkinen (600)	2	12	1	3	18	3	10	3	3	19	5	16	8	4	33	4	10	0	3	17
Vanhanselkä (610)	2	10	0	3	15	3	9	2	3	17	5	15	6	4	30	4	10	3	3	20
CENTRAL PÄIJÄNNE																				
Souselkä (638)	2	7	0	3	12	5	10	2	3	20	5	15	7	4	31	4	10	3	3	20
Tiirinselkä (655-57)	2	10	1	3	16	4	12	3	3	22	5	13	6	3	27	2	13	5	3	23
Lehtiselkä (675)	2	8	1	3	14	1	8	2	2	13	5	16	6	4	31	4	13	3	2	22
Judinsalonselkä (715)	1	5	0	3	9	3	10	3	3	19	5	13	7	4	29	3	9	1	3	16
SOUTHERN PÄIJÄNNE																				
Tehinselkä (740-50)	2	8	0	3	13	1	8	3	4	16	4	14	5	4	27	4	8	2	3	17
Asikkalanselkä (810)	1	12	0	3	16	1	4	3	3	11	4	14	7	4	29	5	13	3	3	24
KONNEVESI (1-2)											4	14	7	4	29	4	12	5	3	24

C. Frequency of species during different seasons

The following species or genera occurred evenly throughout the year: *Tintinnopsis lacustris*, *Synchaeta* spp., *Polyarthra vulgaris*, *Keratella cochlearis*, *Kellicottia longispina*, *Conochilus unicornis*, *Eudiaptomus* spp., and *Cyclops* spp. *Limnocalanus macrurus* was also generally found at most sampling stations in all seasons.

The frequencies of the following species were high in summer, but lower in other seasons: *Arcella* sp., *Difflugia limnetica*, *Tintinnidium fluviatile*, *Epistylis rotans*, *Polyarthra remata*, *Asplanchna priodonta*, *Conochilus hippocrepis*, *Holopedium gibberum*, and *Eubosmina longispina obtusirostris*.

The following species occurred mainly or solely in summer: *Trichocerca similis*, *T. pusilla*, *T. cylindrica*, *T. capucina*, *Polyarthra major*, *P. euryptera*, *Ploesoma hudsoni*, *Asplanchna herricki*, *Euchlanis dilatata*, *Limnosida frontosa*, *Diaphanosoma brachyurum*, *Ceriodaphnia quadrangula*, *Eubosmina longispina longispina*, *Chydorus sphaericus*, *Polyphemus pediculus*, *Bythotrephes longimanus*, and *Leptodora kindti*.

Less common in summer were cold-stenothermal species such as *Polyarthra dolichoptera*, *Keratella hiemalis*, *Notholca squamula*, and *N. caudata*.

D. Effects of eutrophication and pollution on the species composition

1. Areas of occurrence and correlations with some indices of the state of the lakes

The frequency of occurrence of most species was similar in the different parts of the main study area. However, differences were also found. The following species clearly preferred Jyväsjärvi (510) and polluted or eutrophicated areas in Päijänne: *Arcella* spp., *Brachionus* spp., *Keratella cochlearis hispida*, *K. cochlearis tecta*, *K. quadrata*, *Anuraeopsis fissa*, *Ceriodaphnia quadrangula*, *Bosmina longirostris*, and *Chydorus sphaericus*. The following species avoided Jyväsjärvi: *Epistylis rotans*, *Gastropus stylifer*, *Ploesoma hudsoni*, *Asplanchna herricki*, *Conochilus hippocrepis*, *C. unicornis*, *Collotheca* spp., *Holopedium gibberum*, *Eubosmina longispina longispina*, *Bythotrephes longimanus*, *Limnocalanus macrurus*, *Eurytemora lacustris*, and *Heterocope appendiculata*.

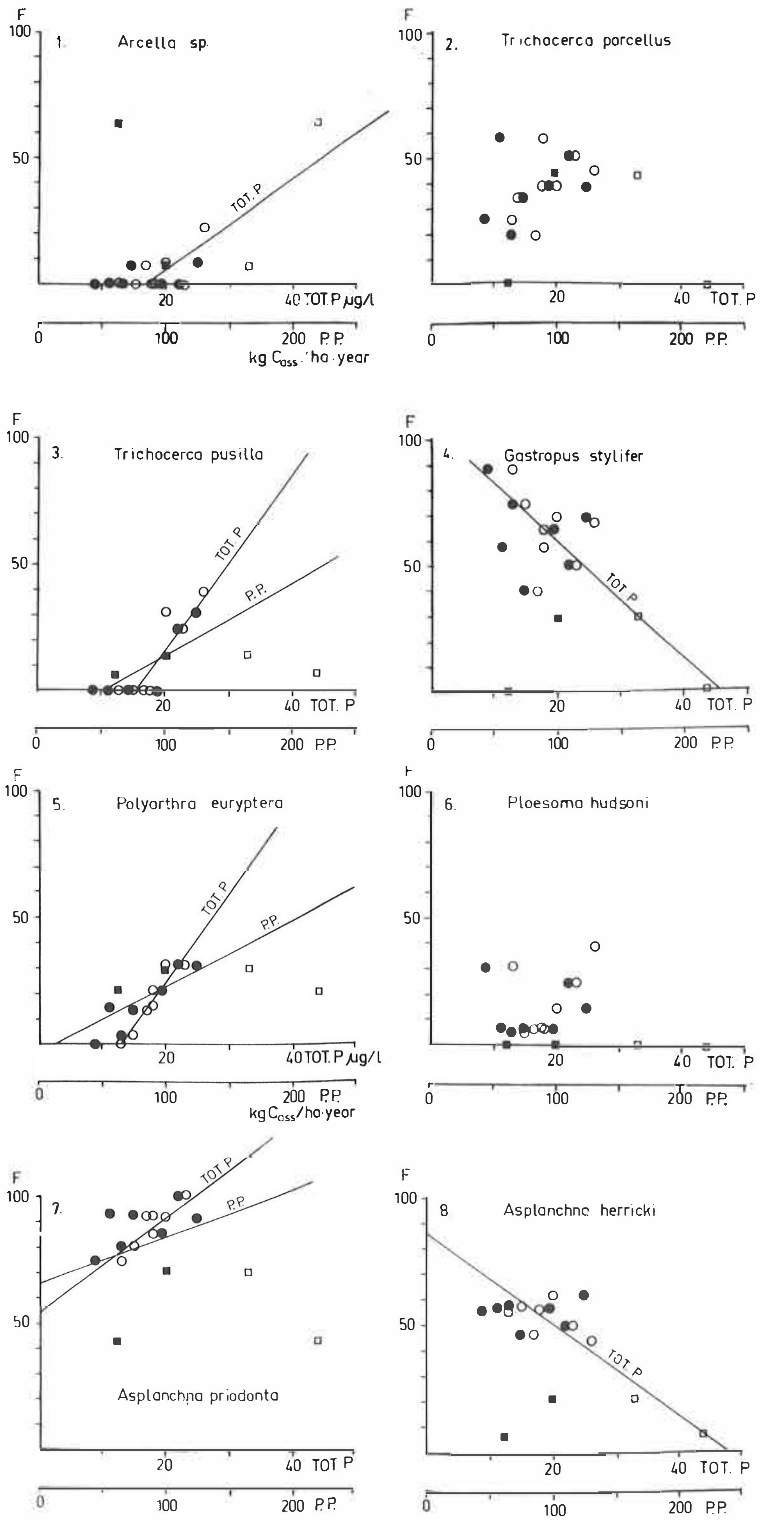
The correlations between the occurrence of different taxa and some environmental parameters are given in Table 9 (cf. also Fig. 6).

Arcella sp. (spp.) (Fig. 6:1). The frequency of *Arcella* showed a highly significant positive correlation with total phosphorus and a significant negative correlation with oxygen concentration. It thus seemed to prefer waters loaded with sewage, and pulp and paper mill effluents (Northern and Central Päijänne).

Table 9. Coefficients of correlation between the frequencies of zooplankton taxa and some environmental parameters (0 = no significant correlation).

	Prim. prod.	O_2(hypol.)	$KMnO_4$	Lignin	Tot. P
Arcella sp.	0	-0.552^{xx}	0	0	0.575^{xxx}
Tintinnidium fluviatile	0	0	0	-0.445^{xx}	0
Tintinnopsis lacustris	0	0.546^{xx}	-0.781^{xxx}	-0.857^{xxx}	-0.456^{xx}
Epistylis rotans	0.394^{x}	0	-0.503^{xx}	-0.540^{xx}	0
Trichocerca porcellus	0	0	-0.363^{x}	-0.428^{x}	0
T. pusilla	0.421^{x}	-0.362^{x}	0	0	0
Gastropus stylifer	0	0.620^{xxx}	-0.460^{x}	-0.407^{x}	-0.577^{xxx}
Polyarthra dolichoptera	0.375^{x}	0	0	0	0
P. major	0	0	0	0	0.364^{x}
P. euryptera	0.531^{xx}	0	0	0	0.368^{x}
Asplanchna priodonta	0.397^{x}	0.486^{xx}	-0.614^{xxx}	-0.566^{xx}	-0.428^{x}
A. herricki	0	0.500^{xx}	-0.401^{x}	-0.363^{x}	-0.483^{xx}
Keratella cochlearis tecta	0.743^{xx}	0	0	0	0
K. cochlearis hispida	0.494^{xx}	0	-0.364^{x}	-0.376^{x}	0
K. ticinensis	0	-0.855^{xxx}	0.802^{xxx}	0.735^{xxx}	0.731^{xxx}
K. quadrata	0.510^{xx}	0	0	0	0
K. hiemalis	0	-0.753^{xxx}	0.617^{xxx}	0.504^{xx}	0.775^{xxx}
Anuraeopsis fissa	0	-0.669^{xxx}	0	0	0.669^{xxx}
Conochilus hippocrepis	-0.368^{x}	0.487^{xx}	0	0	-0.413^{x}
Filinia longiseta	0	-0.812^{xxx}	0.655^{xxx}	0.558^{xx}	0.809^{xxx}
Diaphanosoma brachyurum	0	0	-0.411^{x}	-0.447^{x}	0
Holopedium gibberum	0	0.650^{xxx}	-0.532^{xx}	-0.531^{xx}	-0.649^{xxx}
Ceriodaphnia quadrangula	0	0	0	0	0.367^{x}
Bosmina longirostris	0	-0.445^{x}	0	0	0.588^{xxx}
Eubosmina coregoni	0	0.600^{xxx}	-0.697^{xxx}	-0.681^{xxx}	0.500^{xx}
E. mixta lilljeborgi	0	0.406^{x}	-0.601^{xxx}	-0.671^{xxx}	0
Chydorus sphaericus	0.625^{xxx}	0	-0.395^{x}	-0.419^{x}	0
Bythotrephes longimanus	0	0	0	0	-0.362^{x}
Leptodora kindti	0.519^{xx}	0	0	0	0
Limnocalanus macrurus	0	0.605^{xxx}	-0.392^{x}	0	-0.490^{xx}
Eurytemora lacustris	0	0.607^{xxx}	-0.364^{x}	0	-0.578^{xxx}
Chaoborus flavicans	0	-0.670^{xxx}	0.439^{x}	0	0.731^{xxx}

Fig. 6. Frequency (F,%) of zooplankton taxa considered to be indicators by BERZINS (1949), JÄRNEFELT (1952), JÄRNEFELT *et al.* (1963), PEJLER (1957, 1964), or PATALAS & PATALAS (1966), or in the present study, plotted versus mean total phosphorus concentration in epilimnion in June-Sept. (tot. P) and annual primary production (P.P.) (■ = primary production at stations 655-675, ● = primary production at other stations, □ = total phosphorus at stations 655-675, ○ = total phosphorus at other stations). The P.P. value of Poronselkä (540) in 1970, 303 kg C_{ass}/ha x year, not drawn but included in calculations. ⟶



F
100
50
1. Arcella sp.
TOT. P
20
40 TOT. P µg/l
0
100
200 P.P.
kg Cass./ha·year
2. Trichocerca porcellus
20
40 TOT. P
0
100
200 P.P.
3. Trichocerca pusilla
TOT. P
P.P.
20
40 TOT. P
0
100
200 P.P.
4. Gastropus stylifer
TOT. P
20
40 TOT. P
0
100
200 P.P.
5. Polyarthra euryptera
TOT. P
P.P.
20
40 TOT. P µg/l
0
100
200 P.P.
kg Cass/ha·year
6. Ploesoma hudsoni
20
40 TOT. P
0
100
200 P.P.
7.
TOT. P
P.P.
Asplanchna priodonta
20
40 TOT. P
0
100
200 P.P.
8 Asplanchna herricki
TOT. P
20
40 TOT. P
0
100
200 P.P.

Tintinnidium fluviatile. - A negative correlation with lignin concentration.

Tintinnopsis lacustris. - Avoided the polluted area of Central Päijänne.

Epistylis rotans. - A low positive correlation with primary production.

Vorticella spp. - No clear differences between the sampling stations in summer. In other seasons, high frequencies in eutrophicated and polluted areas.

Trichocerca porcellus. (Fig. 6:2). - Slight avoidance of sulphite pulp and paper mill effluents, but not clear positive correlation with primary production.

Trichocerca capucina, T. cylindrica, and *T. similis.* - Found occasionally, mainly in the eutrophicated part of Päijänne.

Trichocerca pusilla (Fig. 6:3). - A low positive correlation with primary production and oxygen concentration. Mainly observed in eutrophicated Northern Päijänne.

Gastropus stylifer (Fig. 6:4). - Clearly less frequent in polluted areas. Highly significant positive correlation with oxygen concentration, and negative correlations with total phosphorus, $KMnO_4$ consumption and lignin concentration. The species thus seemed to prefer natural water bodies.

Polyarthra dolichoptera. - A slight positive correlation with primary production.

Polyarthra major. - A slight positive correlation with total phosphorus but none with primary production.

Polyarthra euryptera (Fig. 6:5). - A significant correlation with primary production and a slightly significant correlation with total phophorus.

Ploesoma hudsoni (Fig. 6:6). - Seemed to avoid the polluted area of Central Päijänne. No clear correlation with eutrophy or oligotrophy.

Asplanchna priodonta (Fig. 6:7). - Highly significant negative correlation with $KMnO_4$ consumption and significant negative correlation with lignin concentration. Significant positive correlation with oxygen concentration, but only a slight positive correlation with primary production. Thus the species did not prefer clearly eutrophic water areas, but its frequency was high in both eutrophicated and oligotrophic waters.

Asplanchna herricki (Fig. 6:8). - Avoided polluted areas. In Päijänne, showed a negative correlation with $KMnO_4$ consumption, ligning concentration and total phosphorus. Significant positive correlation with oxygen concentration. Clearly prefers natural water bodies.

Keratella cochlearis f. *hispida* (Fig. 6:9). - A positive correlation with primary production, and a negative correlation with $KMnO_4$ consumption and lignin concentration.

Keratella cochlearis f. *tecta* (Fig. 6:10). - Not so common as *K. cochlearis* f. *hispida.* A highly significant positive correlation with primary production.

Keratella ticinensis (Fig. 6:11). - Preferred waters polluted by sulphite pulp and paper mill effluents in Central Päijänne (cf. HAKKARI 1972 a and 1972 b, under the name *K. curvicornis*). Highly significant positive correlations with $KMnO_4$ consumption, lignin concentration, and total phosphorus. No correlation with primary production. Also found in Lievestuoreenjärvi in Central Finland, which is strongly polluted by sulphite pulp mill effluents (HAKKARI 1967).

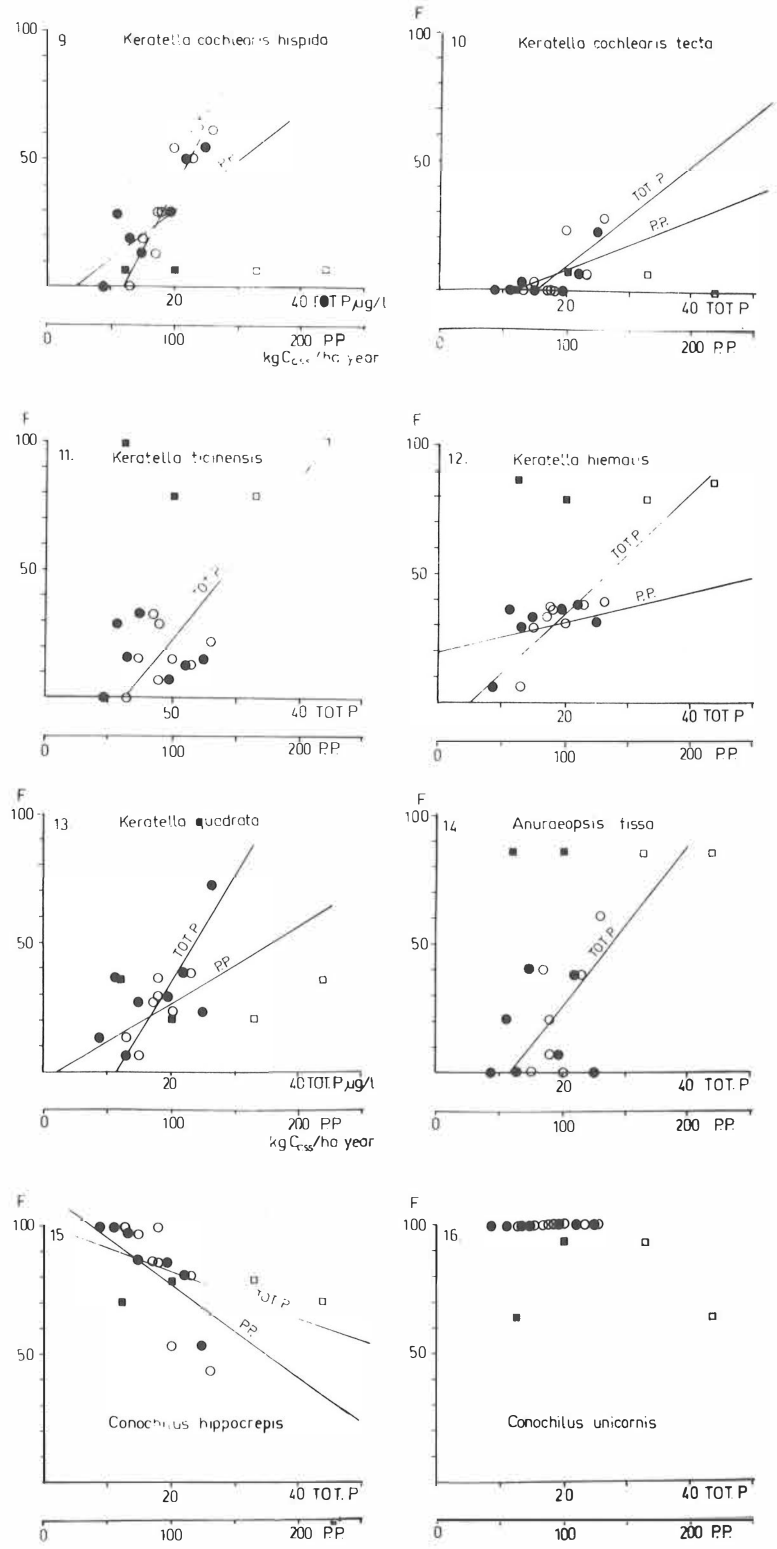

9 Keratella cochlearis hispida
10 Keratella cochlearis tecta
11. Keratella ticinensis
12. Keratella hiemalis
13 Keratella quadrata
14 Anuraeopsis fissa
15 Conochilus hippocrepis
16 Conochilus unicornis
F
100
50
20
40 TOT P µg/l
TOT P
P.P.
0
100
200 PP
kg Cass/ha year

Fig. 6 cont.

Keratella hiemalis (Fig. 6:12). - Unexpected, high significant correlation with phosphorus. No correlation with primary production. Preferred polluted Central Päijänne.

Keratella quadrata (Fig. 6:13). - Slight avoidance of pulp mill effluents but positive correlation with primary production.

Anuraeopsis fissa (Fig. 6:14). - Lacking in natural waters. Did not prefer only the polluted area of Central Päijänne, but also showed high frequencies in the northern part of the lake.

Conochilus hippocrepis (Fig. 6:15). - Significant positive correlation with oxygen concentration, which suggest a preference of clean waters, but no clear avoidance of areas with high concentrations of lignin.

Conochilus unicornis (Fig. 6:16). - Found in most samples in Päijänne, but scarce in polluted areas.

Pompholyx sulcata and *P. complanata*. - Found sometimes in Northern Päijänne.

Filinia terminalis. - Most frequent in Northern Päijänne, but no clear preference of eutrophy.

Filinia longiseta (Fig. 6:17). - Most frequent in Central Päijänne. Significant positive correlations with total phosphorus, $KMnO_4$ consumption and lignin concentration, but none with primary production.

Collotheca sp.(spp.) (Fig. 6:18). - No correlation with primary production but a significant negative correlation with total phosphorus. Found in all waters in Päijänne.

Limnosida frontosa (Fig. 6:19). - No clear preference of eutrophy or oligotrophy.

Diaphanosoma brachyurum. - Slight avoidance of the polluted area of Central Päijänne.

Holopedium gibberum (Fig. 6:20). - Significant negative correlation with primary production, if the values of Tiirinselkä and Lehtiselkä are excluded, and significant positive correlation with oxygen content. Negative correlations with total phosphorus, $KMnO_4$ consumption, and lignin. Evident preference of natural, oligotrophic waters.

Daphnia pulex (Fig. 6:21). - In Päijänne observed only in Tiirinselkä (655-657) and Lehtiselkä (675), but disappeared from Lehtiselkä in 1971, when the oxygen content increased in the hypolimnion.

Daphnia galeata (Fig. 6:22). - High frequencies in Northern Päijänne and in the polluted waters of Central Päijänne, very large individuals being found in the latter area. No correlations with environmental parameters.

Daphnia cristata (Fig. 6:23). - One of the most abundant Cladocera in Päijänne. Frequencies too high for calculation of correlations, but biomasses generally greatest in eutrophicated and polluted areas.

Ceriodaphinia quadrangula (Fig. 6:24). - Found mainly in Northern and Central Päijänne. Significant positive correlation with total phosphorus.

Bosmina longirostris (Fig. 6:25). - Highly significant positive correlation with total phosphorus. Avoided oligotrophic waters.

Eubosmina coregoni (= *Bosmina coregoni coregoni*, Fig. 6:26). - Avoided the polluted area of Central Päijänne. The correlations indicated strong avoidance of wood-processing effluents.

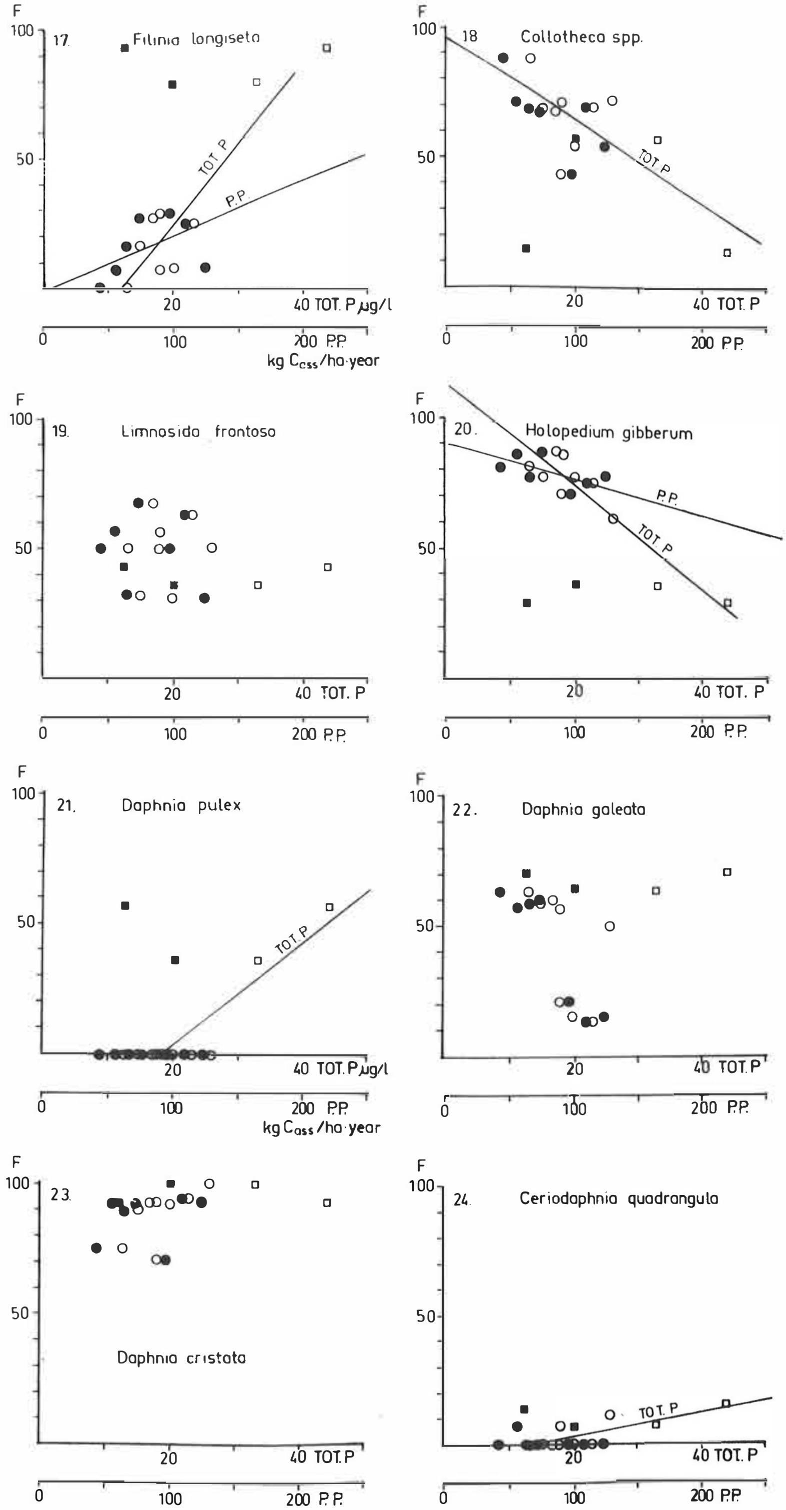

F
100
50
17. Filinia longiseta
TOT. P
P.P.
20
40 TOT. P µg/l
0
100
200 P.P.
kg C_{ass}/ha·year
18 Collotheca spp.
TOT. P
40 TOT. P
200 P.P.
19. Limnosida frontosa
40 TOT. P
200 P.P.
20. Holopedium gibberum
P.P.
TOT. P
21. Daphnia pulex
TOT. P
22. Daphnia galeata
23. Daphnia cristata
24. Ceriodaphnia quadrangula

Fig. 6 cont.

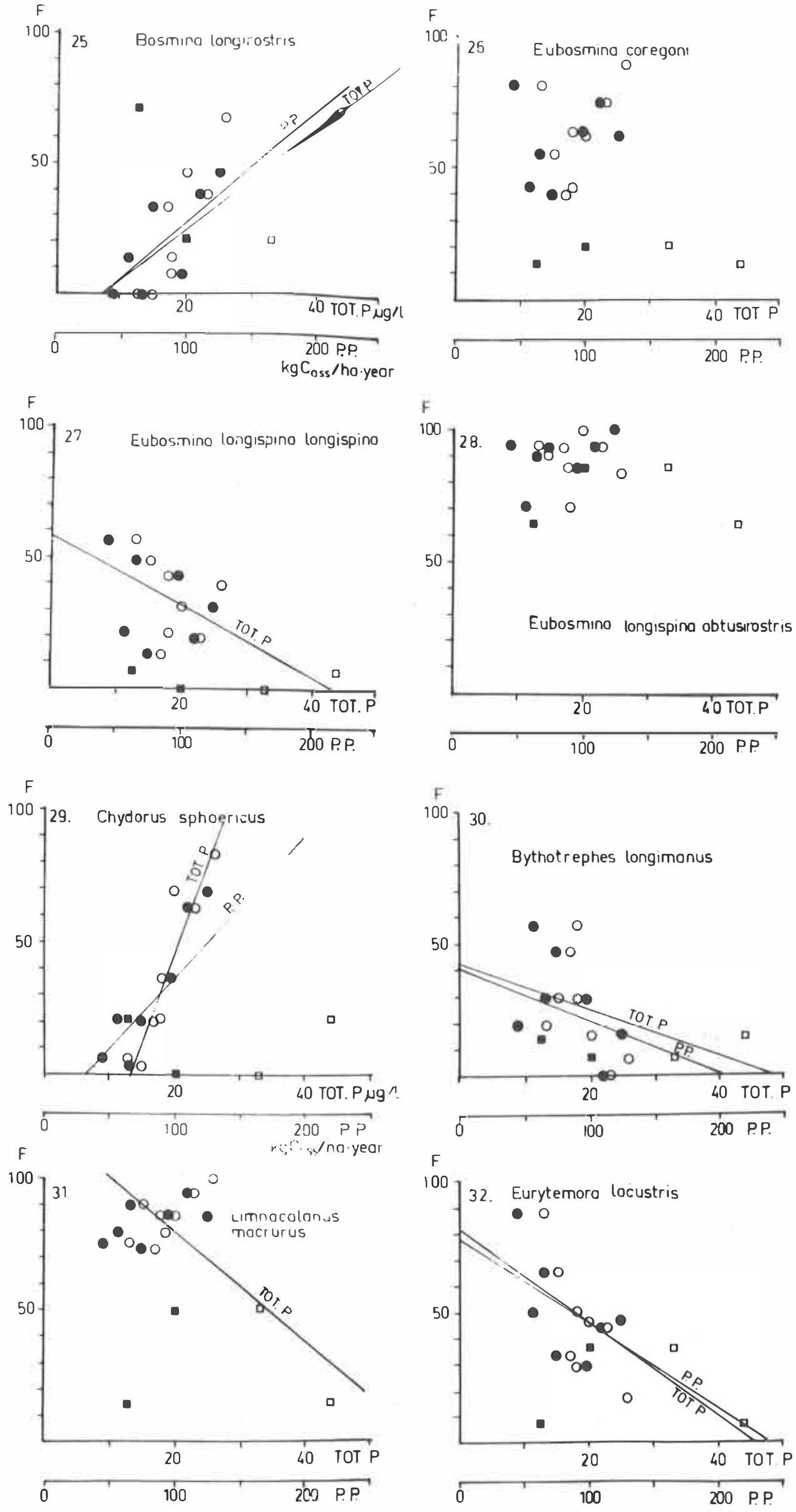

25 Bosmina longirostris
26 Eubosmina coregoni
27 Eubosmina longispina longispina
28. Eubosmina longispina obtusirostris
29. Chydorus sphaericus
30. Bythotrephes longimanus
31 Limnocalanus macrurus
32. Eurytemora lacustris
F
100
50
20
40 TOT. P µg/l
0
100
200 P.P.
kgC$_{ass}$/ha·year
TOT. P
P.P.

Fig. 6 cont.

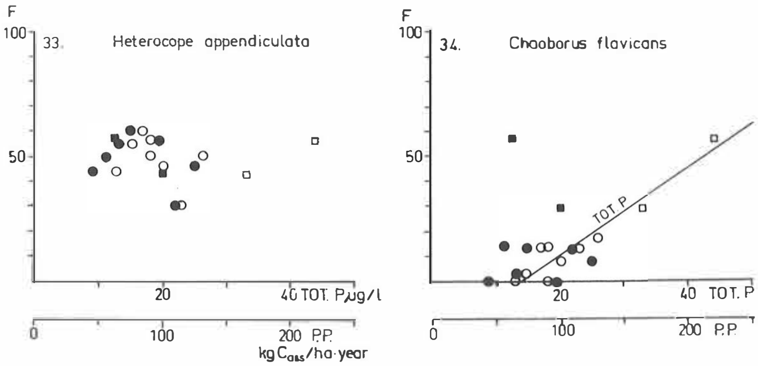


Fig. 6 cont.

Eubosmina longispina longispina (= *Bosmina coregoni longispina*, Fig. 6:27). - Avoided the polluted area of Tiirinselkä (655-657) and Lehtiselkä (675). But the negative correlations with $KMnO_4$ consumption and lignin were not significant.

Eubosmina longispina obtusirostris (= *Bosmina coregoni obtusirostris*, Fig. 6:28). - Abundant in Päijänne except in Tiirinselkä in 1969-1970. High frequencies at all stations.

Eubosmina mixta lilljeborgi (= *Bosmina coregoni lilljeborgi*). - Avoided the area polluted by pulp and paper mill effluents in Central Päijänne. Negative correlations with $KMnO_4$ consumption and lignin, and positive correlation with oxygen content.

Eubosmina crassicornis (= *Bosmina coregoni crassicornis*). - The colour of the water seemed to be an important factor in Päijänne, because this form was found only in Asikkalanselkä (810), which receives water from the oligo-humic and eutrophic lake Vesijärvi.

Chydorus sphaericus (Fig. 6:29). - Avoided the polluted waters of Tiirinselkä and Lehtiselkä. Highly significant positive correlation with primary production.

Bythotrephes longimanus (Fig. 6:30). - Correlated positively with oxygen content and negatively with total phosphorus. The species thus avoided strongly eutrophicated and polluted areas, but was common in slightly eutrophic areas.

Leptodora kindti. - Most common in Northern Päijänne, north of Poronselkä (540). Positive correlation with primary production.

Limnocalanus macrurus (Fig. 6:31). - Avoided polluted areas. In late summer and autumn *Limnocalanus* was most common in Poronselkä (540) and Ristiselkä (570), but during the spring overturn it was lacking at the station in Poronselkä. It was absent from Tiirinselkä (655-657) during June-September 1969-1970, but nauplii were found in the uppermost 5 m in winter (HAKKARI 1973). Nauplii are transported in the clean water layer flowing into Lehtiselkä and Tiirinselkä from Souselkä (cf. p. 7).

Eurytemora lacustris (Fig. 6:32). - Rather rare in Poronselkä (540) and almost lacking in Tiirinselkä (655-657). Correlations indicative of an oligotrophic species.

Heterocope appendiculata (Fig. 6:34). - No clear differencies between eutrophic and oligotrophic areas.

Chaoborus flavicans (Fig. 6:34). - Highly significant positive correlation with total phosphorus and negative correlation with oxygen content. A preference of polluted areas.

The mean values for primary production and total phosphorus at the different stations in Päijänne are given in Fig. 7.

2. Factor analysis of the occurrence of different taxa

With factor 1 of the Varimax solution total phosphorus had a high positive loading (.813) and the oxygen concentration in the hypolimnion a high negative loading (-.782) (Table 10). Primary production had a negative loading, while the loadings of $KMnO_4$ consumption and sodium lignosulphonate (NaLS) were positive and fairly high. Thus factor 1 can be called the "pollution factor", representing the effects of the wastes of the sulphite pulp mill and the paper mill.

With factor 2, primary production and herbivore production had positive loadings (.628 and .538). This factor can be named the "eutrophication factor".

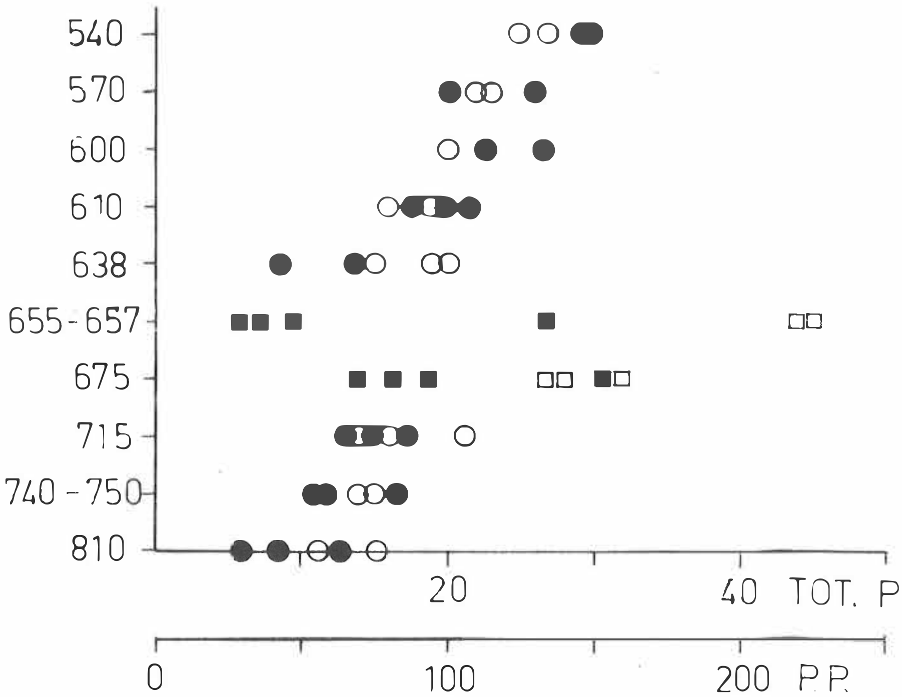


Fig. 7. Mean values of primary production (P.P.) and total phosphorus (tot. P) at different sampling stations in Päijänne during the growing seasons 1969-1972 (● or ■ primary production kg/ha x year, o or □ total phosphorus µg/l).

Table 10. The loadings of various taxa on different factors. Varimax solution.

Factors	1	2	3	4	5	6	Communality
Temperature (epilimn.)	-.005	.367	-.032	-.015	-.550	-.179	.470
Oxygen conc. (hypolimn.)	-.782	-.255	.448	-.151	.140	-.061	.923
$KMnO_4$ consumption	.543	-.087	-.765	.144	.009	.027	.910
NaLS	.454	-.091	-.829	.074	-.061	-.013	.910
Total phosphorus	.813	.319	-.241	.053	-.149	.001	.845
Primary production	-.043	.628	.307	.176	.000	.180	.554
Prod. of zoopl. herbiv.	.294	.538	.350	.370	.270	.107	.719
Prod. of zoopl. predators	.397	.331	.380	.317	-.447	.268	.784
Arcella sp.	.334	.601.	-.271	.092	-.229	-.231	.661
Difflugia limnetica	.024	.239	.131	.552	-.426	.082	.567
D. hydrostatica	.126	.263	.272	.560	.285	-.258	.621
Tintinnidium fluviatile	.090	-.224	.500	.067	.347	-.215	.480
Tintinnopsis lacustris	-.284	.128	.792	.093	.211	.213	.823
Epistylis rotans	-.044	.345	.688	.120	.065	.105	.624
Vorticella sp.	-.004	-.044	-.207	-.024	.073	-.717	.565
Trichocerca rousseleti	-.542	.241	-.190	.033	.031	.007	.390
T. porcellus	-.171	.036	.444	.151	.592	.101	.611
T. pusilla	.070	.618	-.343	.160	.233	.013	.585
T. capucina	-.166	.834	.193	-.100	-.077	.176	.808
Gastropus stylifer	-.705	.126	.136	.201	.013	-.477	.800
Polyarthra dolichoptera	.195	.146	.194	.701	.094	.130	.614
P. euryptera	.217	.598	.205	.195	.062	.325	.594
P. major	.488	.063	.323	.075	-.103	.014	.363
Asplanchna priodonta	-.536	.264	.409	.318	.065	.279	.708
A. herricki	-.643	-.075	.208	.209	-.343	.172	.653
Keratella cochl. tecta	.010	.772	.247	.228	-.139	-.022	.730
K. cochl. hispida	-.263	.662	.202	-.059	.006	.100	.562
K. ticinensis	.808	-.064	-.345	.301	-.099	-.064	.880
K. quadrata	.166	.658	.223	.362	.101	-.195	.690
K. hiemalis	.880	-.029	-.181	.067	.159	.138	.857
Anuraeopsis fissa	.755	.307	.109	.273	.017	.108	.763
Conochilus hippocrepsis	-.170	-.739	.213	-.187	.175	-.275	.762
Filinia terminalis	.059	.293	-.177	.521	.016	.282	.472
F. longiseta	.837	.130	-.243	.241	.089	-.122	.857
Limnosida frontosa	.104	.037	.535	-.443	-.044	-.087	.504
Diaphanosoma brachyurum	.046	.089	.583	.146	-.108	.214	.429
Holopedium gibberum	-.553	-.285	.348	.091	.137	-.035	.536
Daphnia cristata	.428	.117	.313	.027	.199	-.049	.337
D. galeata	.112	-.067	-.033	.105	-.609	.087	.408
Ceriodaphnia quadrangula	.242	.548	.020	.354	-.029	-.277	.563
Bosmina longirostris	.575	.543	.222	.017	-.083	.011	.682
Eubosmina coregoni	-.663	.384	.377	-.114	-.062	-.191	.782
E. mixta lilljeborgi	-.251	.309	.598	-.069	.092	.412	.700
E. longispina longispina	-.592	.258	-.153	.185	-.472	.175	.728
Chydorus sphaericus	-.019	.778	.405	.110	.059	-.087	.792
Bythotrephes longimanus	-.193	-.503	.243	.109	-.077	.182	.400
Leptodora kindti	-.097	.724	.020	.032	-.275	-.199	.651
Limnocalanus macrurus	-.642	-.049	.068	.127	.241	.156	.518
Heterercope appendiculata	-.047	-.010	-.087	.588	-.186	-.099	.400
H. borealis	.373	-.328	.186	.177	.074	.502	.570
Eurytemora lacustris	-.466	-.303	.106	-.348	.069	-.088	.453
Chaoborus flavicans	.826	-.073	.014	.086	-.198	.113	.748

$KMnO_4$ consumption and NaLS had high negative loadings (-.765 and -.829). For lack of a better name, it is called here the "wood-processing wastes avoidance factor".

The independent variables showed no high loadings on factors 4-6 of

Table 10, and these factors have not been named.

According to the results, a positive correlation with the effects of pollution, especially the waste waters of the wood-processing industry, was shown by the frequencies of:

Keratella hiemalis	*Filinia longiseta*
K. ticinensis	*Bosmina longirostris*
Anuraeopsis fissa	*Chaoborus flavicans*

The following taxa showed a significant preference for a eutrophicated environment:

Arcella sp. (spp.)	*Polyarthra euryptera*
Trichocerca capucina	*Ceriodaphnia quadrangula*
T. pusilla	*Bosmina longirostris*
Keratella cochlearis tecta	*Chydorus sphaericus*
K. cochlearis hispida	*Leptodora kindti*
K. quadrata	

Only one species showed a significant preference for both polluted and eutrophicated waters, *Bosmina longirostris*.

A eutrophicated environment was avoided by:

Conochilus hippocrepis
Bythotrephes longimanus

A negative correlation with the concentration of the waste waters of the wood-processing industry was shown by the frequencies of the following taxa:

Trichocerca rousseleti	*Holopedium gibberum*
Gastropus stylifer	*Eubosmina coregoni*
Asplanchna priodonta	*E. longispina longispina*
A. herricki	*Limnocalanus macrurus*

3. E/O species ratio in different areas

On the basis of the results of this work and other investigations (BERZINS 1949, JÄRNEFELT 1952, JÄRNEFELT *et al.* 1963, PEJLER 1957, 1964, PATALAS & PATALAS 1966, HAKKARI 1967), the following taxa were regarded as eutrophic (E) and oligotrophic (O) species.

E species:

Arcella sp. (spp.), *Trichocerca porcellus*, *T. pusilla*, *T. cylindrica*, *T. capucina, Polyarthra euryptera, Brachionus* spp., *Keratella cochlearis hispida, K. cochlearis tecta, K. ticinensis, K. hiemalis, K. quadrata, Anuraeopsis fissa, Pompholyx* spp., *Filinia longiseta, Daphnia pulex, Ceriodaphnia quadrangula, Bosmina longirostris, Chydorus sphaericus,* and *Chaoborus flavicans.*

0 species:

Gastropus stylifer, Ploesoma hudsoni, Asplanchna herricki, Conochilus hippocrepis, Holopedium gibberum, Eubosmina longispina longispina, Bythotrephes longimanus, Limnocalanus macrurus, Eurytemora lacustris, and *Heterocope appendiculata.*

The mean E/0 ratios were far higher in Jyväsjärvi than in the eutrophicated and polluted areas of Päijänne (Table 11). The ratio decreased from northernmost Päijänne (522) to Vanhanselkä (610) and from Tiirinselkä (655-657) to Asikkalanselkä (810).

The high E/0 ratios in Jyväsjärvi (510) were caused by the fact that 10 0 species were almost lacking in this sampling area (cf. p. 7), whereas most of the E species were present. Almost all the E species found in Jyväsjärvi were also observed in northernmost Päijänne (sts. 522-540), but the number of 0 species was higher there: all the 0 species were observed at sts. 522-540, except that *Bythotrephes longimanus* was lacking at st. 522. The decrease in the E/0 ratio from Poronselkä (540) to Vanhanselkä (610) was caused by the disappearance of E species.

The same species occurred in Tiirinselkä (655-657) and Lehtiselkä (675), but the E species were generally more frequent in Tiirinselkä and the 0 species in Lehtiselkä. The E/0 values of Tiirinselkä and Lehtiselkä declined during the study, which indicated that the sulphite lye evaporating and burning plant in Jämsänkoski was having a beneficial effect.

The species compositions and E/0 ratios of Souselkä (638) and Judinsalonselkä (715) were very similar. No clear decrease in the E/0 ratios was found in the years 1969-1971. In 1971 the E/0 ratios of Souselkä and Judinsalonselkä were significantly smaller than that of Lehtiselkä, and the value of Tehinselkä (740-750) differed significantly from those of Judinsalonselkä and Asikkalanselkä (810). The number and frequencies of E species decreased towards Southern Päijänne; they were almost lacking in Asikkalanselkä.

The following tabulation shows the relationship between the E/0 species ratios of the waters studied and the trophic status of the waters, as determined

Table 11. Mean E/O species ratios of zooplankton in Jyväsjärvi and Päijänne in June-Sept. in different years.

	Station	Year	n	$\bar{x} \pm$ S.E.	Range	C.V. %
LAKE JYVÄSJÄRVI	510	1969	4	7.75 ± 1.43	4.00 - 10.00	18
		1970	10	8.88 ± 0.39	7.00 - 11.00	14
		1971^x	16	9.06 ± 0.37	7.00 - 12.00	16
	522	1969	5	1.45 ± 0.14	1.14 - 2.00	22
		1970	6	1.45 ± 0.39	0.50 - 3.00	65
	540	1969	6	1.42 ± 0.29	0.71 - 2.29	51
		1970	7	1.24 ± 0.21	0.50 - 2.00	45
		1971	5	1.26 ± 0.35	0.33 - 2.50	63
NORTHERN PÄIJÄNNE	570	1969	3	0.92 ± 0.18	0.50 - 1.25	34
		1970	7	0.97 ± 0.10	0.60 - 1.40	28
		1971	5	0.67 ± 0.13	0.13 - 1.00	45
	600	1969	6	0.58 ± 0.06	0.38 - 0.75	26
		1970	7	0.61 ± 0.09	0.25 - 1.00	38
	610	1969	4	0.25 ± 0.11	0.00 - 0.57	84
		1970	5	0.26 ± 0.07	0.00 - 0.50	61
		1971	5	0.50 ± 0.09	0.17 - 0.75	42
	638	1969	4	0.40 ± 0.19	0.00 - 1.00	92
		1970	6	0.32 ± 0.05	0.09 - 0.50	41
		1971	4	0.50 ± 0.10	0.25 - 0.80	40
CENTRAL PÄIJÄNNE	655	1969	4	2.63 ± 0.41	2.00 - 4.00	31
		1970	6	3.84 ± 0.93	1.60 - 7.00	60
	657	1971	4	2.18 ± 0.39	1.40 - 3.50	36
		1972	9	1.76 ± 0.17	1.25 - 3.00	28
	675	1969	4	1.71 ± 0.40	0.83 - 3.00	47
		1970	6	1.38 ± 0.26	0.63 - 2.33	46
		1971	4	1.19 ± 0.21	0.60 - 1.67	35
		1972	9	0.72 ± 0.08	0.33 - 1.17	35
	715	1969	5	0.48 ± 0.12	0.29 - 1.00	54
		1970	5	0.55 ± 0.09	0.22 - 0.80	38
		1971	4	0.41 ± 0.18	0.00 - 1.00	90
SOUTHERN PÄIJÄNNE	740	1969	17	0.12 ± 0.06	0.00 - 0.75	200
	750	1970	9	0.21 ± 0.06	0.00 - 0.50	81
		1971	5	0.22 ± 0.05	0.00 - 0.33	54
	810	1969	5	0.00		
		1970	6	0.04 ± 0.02	0.00 - 0.13	150
		1971	5	0.07 ± 0.04	0.00 - 0.20	114

x) PIIPPONEN (1974)

according to the classification of LEHMUSLUOTO (1969 ; cf. GRANBERG 1973, 1974):

	Primary productivity mg C_{ass}/m^3 x 24 hr	Mean E/O species ratio of zooplankton
Highly eutrophic	more than 1000	more than 5.0
Eutrophic	200-1000	1.5-5.0

Moderately eutrophic	100-200	0.5-1.5
Oligotrophic	less than 100	less than 0.5

Owing to the inhibitory effect of pulp mill effluents primary productivity could not be used to classify the polluted areas. Instead, the degree of pollution of these waters was assessed from the oxygen concentration in the hypolimnion during August:

	O_2 mg/l in hypolimnion in August	Mean E/O species ratio of zooplankton
Highly polluted	less than 1	more than 1.5
Polluted	1-4	1.2-1.5
Moderately polluted	4-8	0.5-1.2
Unpolluted	more than 8	less than 0.5

The E/O ratios in the classification on pollution are lower than those for the trophic classes, since the polluted waters had a smaller number of E species.

E. Diversity index

1. Seasonal fluctuation

In 1969, eutrophicated Poronselkä (540) and oligotrophic Tehinselkä (740) had high diversity indices in the first half of June (Fig. 8). Polluted Lehtiselkä (675) had low values at this time, since the oxygen content was low. A slight minimum was evident in the first half of July, except in Lehtiselkä, and a maximum occurred from the second half of July to the first half of September. Diversity began to decrease at the end of September and was near the winter level by November.

In 1972, the minimum was observed in May-early June in Tiirinselkä (655-657) and Lehtiselkä (675) (Fig. 9), but in late June-July the level of diversity was the same as in other areas of Päijänne. The decline of diversity in autumn was especially clear in Tiirinselkä (Fig. 9).

2. Differences between areas

As is seen in Fig. 10, the mean diversity during June-September was lowest in Jyväsjärvi (510) and Tiirinselkä (655-657), i.e. in the most polluted areas. The greatest values were obtained from eutrophicated Northern Päijänne and from the oligotrophic parts of the lake, Tehinselkä (740-750) and Asikkalanselkä (810).

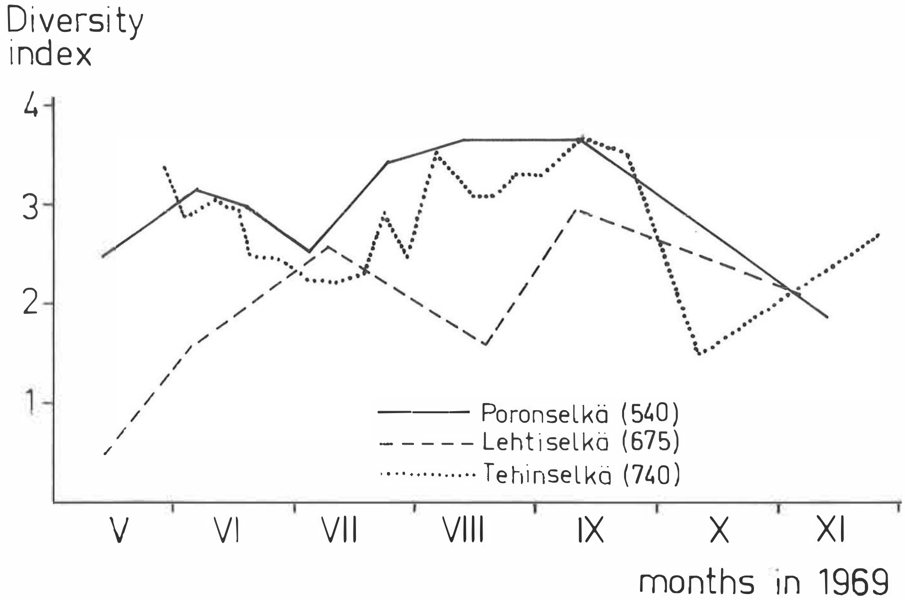


Fig. 8. The diversity index of zooplankton in Poronselkä (540), Lehtiselkä (675), and Tehinselkä (740), Päijänne, in May-November 1969.

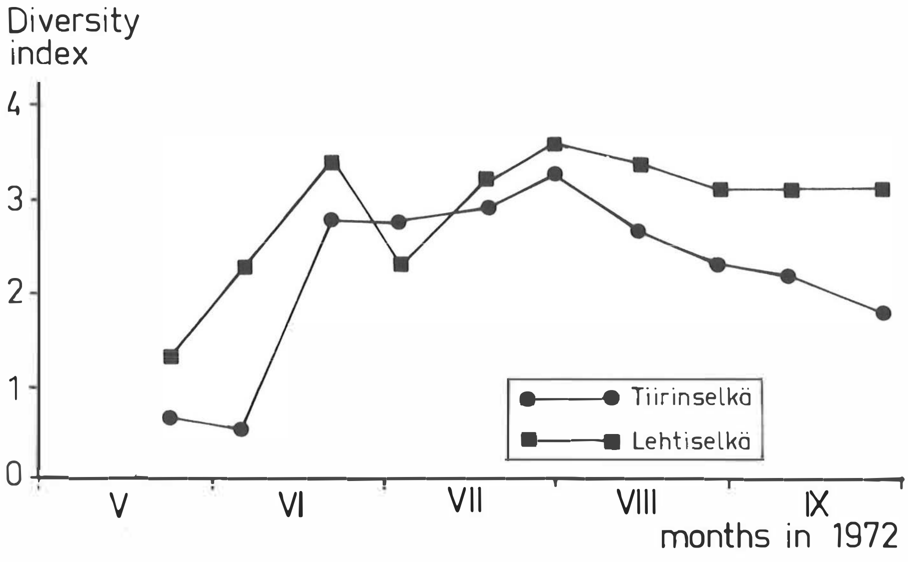


Fig. 9. The diversity index of zooplankton in Tiirinselkä (657), and Lehtiselkä (675), Päijänne, in May-Sept. 1972.

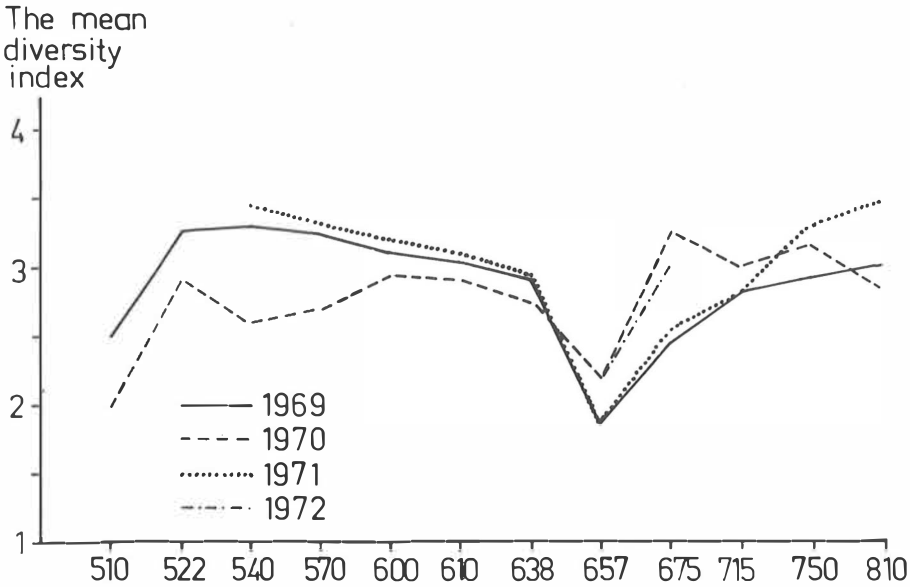


Fig. 10. The mean diversity of zooplankton at different stations in Jyväsjärvi (510) and Päijänne (522-810) in June-Sept. 1969-1972.

F. Seasonal fluctuation of zooplankton biomass

In northern lakes that are ice-covered in winter, zooplankton biomass fluctuates strongly with the season, the values for the winter months usually being only a small fraction of the summer biomass (HAKKARI 1969, 1973, GRANBERG 1970).

Tables 12-14 show mean monthly biomasses of different zooplankton taxa in Poronselkä, Tiirinselkä, and Tehinselkä.

Asplanchna priodonta and *A. herricki* usually composed most of the rotifer biomass. *A. priodonta* usually had a maximum in June, often followed by another in autumn. The summer maximum of *A. herricki* was in June-July; in the nearly natural Tehinselkä a clear autumn maximum was lacking. *Asplanchna herricki* was absent in winter.

Conochilus hippocrepis and *C. unicornis* made an important contribution to the biomass of the oligotrophic water bodies, having their maxima in June or July. In eutrophicated Poronselkä *C. unicornis* had an autumn maximum in all years. Their biomasses were low in winter and early spring.

In Poronselkä, *Synchaeta* spp. and *Polyarthra* spp. (mainly *P. vulgaris* and *P. major*) increased the rotifer biomass, especially in June-August. The same was observed in Tehinselkä. In Tiirinselkä, notable contributions to the rotifer biomass were made by *Keratella cochlearis, K. ticinensis, K. quadrata Filinia longiseta, Polyarthra vulgaris, P. major,* and *Anuraeopsis fissa.*

The Rotatoria biomass usually reached its maximum in June, after fluctuating during the first half of the month. In most cases the biomass sank

Table 12. Mean biomass (wet wt, mg/m^3, weighted mean from surface to bottom) of zooplankton taxa in different months in Poronselkä (540).

Year	1969						1970							1971							
Month	V	VI	VII	VIII	IX	XI	III	V	VI	VII	VIII	IX	XI	I	IV	V	VI	VII	VIII	IX	X
Asplanchna priodonta	3	89	36	23	10	86	-	-	80	10	464	331	94	20	3	-	559	27	13	246	128
A. herricki	-	-	22	-	10	-	-	-	-	13	10	58	-	-	-	-	-	-	-	64	-
Conochilus hippocrepis	-	-	+	2	+	-	-	-	-	+	-	-	-	+	+	+	4	1	+	1	1
C. unicornis	+	2	27	1	+	4	+	+	12	+	+	+	2	+	+	+	8	1	+	3	3
Other rotifers	15	47	23	15	17	8	1	4	7	60	71	16	19	5	2	1	15	14	4	15	8
ΣRotatoria	18	138	108	41	37	98	1	4	99	83	545	405	115	25	5	1	586	43	17	329	140
Limnosida frontosa	-	-	8	12	-	-	-	-	-	9	25	2	-	-	-	+	-	4	4	5	-
Diaphanosoma brachyurum	-	2	12	82	2	-	-	-	-	80	28	10	-	-	-	-	-	-	3	7	-
Holopedium gibberum	-	10	10	-	-	+	-	-	13	+	-	-	-	-	-	-	21	1	3	1	-
Daphnia cristata	1	39	214	270	153	24	2	1	61	583	108	279	163	16	2	2	23	417	24	314	180
D. galeata	-	-	-	-	-	-	-	-	4	9	5	17	3	3	3	-	-	-	3	33	18
Bosmina longirostris	+	1	3	-	1	1	-	-	5	1	2	5	8	-	-	-	+	1	-	+	3
Eubosmina spp.	+	12	79	88	36	1	-	-	22	69	11	51	3	+	-	1	47	40	12	193	47
Bythotrephes longimanus	-	-	-	-	-	-	-	-	-	90	-	-	-	-	-	-	-	-	-	-	-
Leptodora kindti	-	-	90	75	-	-	-	-	-	300	-	98	-	-	-	-	-	-	6	90	-
Other cladocerans	-	5	6	7	-	-	-	-	6	30	15	10	-	-	-	-	-	1	5	10	1
ΣCladocera	1	69	422	534	192	26	2	1	111	1171	194	472	177	19	5	3	91	46	460	653	249
Limnocalanus macrurus	+	11	14	20	15	3	2	-	40	43	63	28	-	3	+	+	6	15	7	7	15
Eurytemora lacustris	-	-	2	-	-	2	-	-	2	2	-	-	3	-	-	-	-	2	-	-	-
Heterocope appendiculata	-	11	16	5	-	-	-	-	2	10	-	-	-	-	-	-	10	5	-	-	-
H. borealis	-	-	1	-	-	-	-	-	-	-	19	-	-	-	-	-	-	-	-	-	-
Eudiaptomus spp.	4	10	54	23	26	44	10	7	11	123	24	110	13	7	13	7	18	34	3	39	138
Cyclops spp.	13	56	153	233	105	4	4	6	84	210	171	38	8	1	1	11	77	99	14	95	29
ΣCopepoda	17	88	240	281	146	53	16	13	139	388	277	176	24	11	14	18	111	155	24	141	182
ΣCrustacea	18	157	662	815	338	79	18	14	250	1559	471	648	201	30	19	21	202	619	84	794	431
Chaoborus flavicans	-	-	-	-	-	-	-	-	17	-	-	17	-	-	-	-	-	-	-	-	-
ΣZooplankton	36	295	770	856	375	117	19	18	366	1642	1016	1070	316	55	24	25	788	662	101	1123	571

during July and August. In oligotrophic waters, it decreased evenly to the winter level; in eutrophicated and polluted areas an autumn maximum could took place before November.

The taxa of Cladocera were mainly found in June-September. *Limnosida frontosa*, *Diaphanosoma brachyurum*, and *Leptodora kindti* occurred in the plankton only in those months, and are regarded as warm-stenothermal species. Their maxima were found in July or August. *Holopedium gibberum* appeared in the plankton at the end of May, when the water temperature was 3-5 °C (cf. HAKKARI 1970 b) and had its maximum in June, except in polluted Tiirinselkä, where the peak was found in June or July.

Daphnia cristata was the only cladoceran taxon that was sometimes abundant in winter (cf. HAKKARI 1973). This was observed especially in areas receiving sewage or wood-precessing effluent, particularly Poronselkä and Tiirinselkä. In oligotrophic areas, *D. cristata* was not found during winter, probably because of the scarcity of food. In May the biomass was still low, but it rose in the second half of June. Two maxima were usually found, occurring in July and autumn, mainly in polluted or eutrophicated areas.

Daphnia galeata was less significant in the zooplankton biomass than *D. cristata*. It was also found mainly in summer.

Bosmina longirostris was significant only in Poronselkä and Jyväsjärvi, having a maximum in July, and another usually in September and October.

Eubosmina spp. had their maximum in June-August, a second maximum being found in autumn in polluted or eutrophicated areas. Their proportion in the biomass of Cladocera was significant in oligotrophic waters. In

Table 13. Mean biomass (wet wt, mg/m^3, weighted mean from surface to bottom) of zooplankton taxa in Tiirinselkä (655-657) in different months.

Year	1969					1970							1971									1972					
Month	VI	VII	VIII	IX	XI	IV	V	VI	VII	VIII	IX	X	I	II	IV	V	VI	VII	VIII	IX	X	III	V	VI	VII	VIII	IX
Ciliata coll.	1	+	+	+	+	8	+	2	+	+	+	+	+	+	+	+	+	+	+	+	18	1	7	7	4	8	2
Asplanchna priodonta	-	-	-	3	67	8	3	1311	2	-	5	13	-	-	-	-	1626	-	-	-	4	-	-	793	13	4	12
A. herricki	-	-	51	-	-	-	-	-	3	-	12	-	-	-	-	-	22	-	-	-	-	-	-	-	-	-	64
Conochilus hippocrepis	-	+	+	-	-	-	-	1	3	+	-	-	+	-	-	-	1	1	1	+	-	-	-	1	22	1	+
C. unicornis	-	-	+	+	-	-	+	+	1	+	-	-	+	+	+	-	1	+	+	+	+	+	+	2	45	+	1
Other rotifers	5	271	63	40	203	1	2	18	16	16	6	15	2	1	1	1	20	8	8	9	8	+	1	44	45	41	26
Σ Rotatoria	5	271	114	43	270	9	5	1330	25	16	23	28	2	1	1	1	1670	9	9	9	12	+	1	840	125	46	103
Limnosida frontosa	-	-	20	+	-	-	-	-	10	-	-	-	-	-	-	+	-	14	-	+	-	-	-	-	23	24	2
Diaphanosoma brachyurum	-	-	-	1	-	-	-	-	7	2	+	-	-	-	-	-	-	1	1	1	-	-	-	-	9	8	2
Holopedium gibberum	-	-	-	+	-	-	-	4	5	-	-	6	-	-	-	-	3	-	-	-	-	-	-	10	46	-	-
Daphnia cristata	-	71	199	59	288	13	+	28	45	53	86	609	69	13	23	2	297	100	257	420	204	4	4	243	1026	383	141
D. galeata	-	-	34	20	26	-	-	-	20	300	263	212	3	-	-	-	-	4	73	32	-	-	-	-	9	59	43
Bosmina longirostris	-	-	-	+	1	-	+	5	3	+	3	1	-	+	-	-	3	1	2	-	+	-	-	-	1	+	1
Eubosmina spp.	-	-	-	+	-	-	-	8	3	-	1	1	-	-	-	1	20	19	1	2	+	-	1	38	20	10	6
Bythotrephes longimanus	-	-	-	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	110	-	-
Leptodora kindti	-	80	-	-	-	-	-	-	140	-	102	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99
Other cladocerans	-	-	-	-	44	-	-	2	3	13	106	175	-	-	-	+	+	+	-	+	+	-	-	-	-	4	+
Σ Cladocera	-	151	253	80	359	13	+	47	336	368	561	1004	72	13	23	3	323	139	334	455	204	4	5	291	1244	488	294
Limnocalanus macrurus	-	-	-	-	-	-	-	-	-	-	-	7	-	+	+	-	-	7	7	-	7	+	-	-	-	7	-
Eurytemora lacustris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Heterocope appendiculata	-	8	-	19	-	-	-	8	121	14	-	-	-	-	-	4	-	8	14	-	-	-	7	14	28	-	-
H. borealis	-	-	-	-	-	-	-	-	25	-	-	-	-	-	-	-	-	19	19	-	-	-	-	-	19	-	-
Eudiaptomus spp.	-	1	54	42	70	15	+	5	58	25	7	29	27	7	12	7	10	53	23	18	40	8	6	23	204	188	123
Cyclops spp.	-	22	107	80	16	23	16	50	134	186	72	41	6	2	4	17	103	155	125	166	30	7	48	138	179	240	170
Σ Copepoda	-	31	161	141	86	38	16	63	338	225	79	77	33	9	16	28	113	242	188	184	77	15	61	175	430	435	293
Σ Crustacea	-	182	414	221	445	51	16	110	674	593	640	1081	105	22	39	31	436	381	522	639	281	19	66	466	3197	923	587
Chaoborus flavicans	-	-	250	-	-	-	-	364	-	26	15	-	310	-	333	-	375	150	333	412	-	-	210	210	250	-	137
Σ Zooplankton	6	453	778	264	715	68	21	1806	699	635	678	1109	417	23	373	32	2481	540	864	1060	311	20	284	1523	3576	977	829

winter they were mainly absent.

Bythotrephes longimanus was usually seen for only short periods in summer and its biomass was generally low.

Daphnia pulex, included under "other Cladocera" in Table 13, formed a significant part of the zooplankton biomass of Tiirinselkä and Lehtiselkä during summer and autumn 1969-1970. Later, its biomass was smaller.

Limnocalanus macrurus had a low biomass during winter, when young individuals were found. Its maximum usually took place in June, when the individual growth had almost stopped (cf. HAKKARI 1970 b). The biomass sank during summer because of mortality, the decrease being faster in oligotrophic than in eutrophic areas.

Eurytemora lacustris had a low biomass in all the waters in Päijänne. It lacked a clear seasonal maximum, but most individuals were found during summer and autumn.

Heterocope appendiculata had a maximum in June or July; its biomass was mainly low.

Eudiaptomus spp. probably had three maxima during the year: a low first maximum in March-April, a second in July, and a third in October. Their biomass was relatively high in winter.

Cyclops spp. were important in the zooplankton biomass, with a maximum in July-August. The biomass was fairly high in winter, too.

The semiplanktonic *Chaoborus flavicans* did not show great seasonal fluctuation in biomass.

Table 14. Mean biomass (wet wt, mg/m^3, weighted mean from surface to bottom) of zooplankton taxa in Tehinselkä (740-750) in different months.

Year			1969							1970								1971			
Month	V	VI	VII	VIII	IX	X	XI	IV	VI	VII	VIII	IX	X	XI	I	IV	VI	VII	VIII	IX	X
Asplanchna priodonta	1	90	16	31	7	1	-	-	149	40	20	7	-	-	-	-	38	31	-	16	-
A. herricki	-	112	121	43	17	-	-	-	43	7	6	-	-	-	-	-	-	22	-	-	-
Conochilus hippocrepis	+	43	64	9	1	+	-	-	30	37	4	+	-	-	-	-	4	7	6	1	1
C. unicornis	+	5	9	11	5	+	+	+	15	12	4	+	-	+	+	-	3	6	6	1	+
Other rotifers	+	4	10	8	6	1	+	+	5	12	6	3	1	+	3	+	4	23	5	3	1
Σ Rotatoria	1	254	220	102	36	2	+	+	242	108	40	10	1	+	3	+	49	89	17	21	2
Limnosida frontosa	-	-	8	19	-	-	-	-	-	1	3	-	-	-	-	-	-	-	19	1	-
Diaphanosoma brachyurum	-	1	1	3	1	-	-	-	-	1	5	-	-	-	-	-	-	-	2	-	-
Holopedium gibberum	3	40	44	16	8	-	-	-	24	4	19	-	-	-	-	-	77	20	15	-	-
Daphnia cristata	+	24	10	1	3	-	-	-	12	16	35	6	2	-	-	-	+	83	112	22	6
D. galeata	2	14	14	16	7	-	-	-	1	9	3	-	-	-	-	-	-	11	10	1	1
Eubosmina spp.	+	4	4	13	18	4	-	-	15	35	11	3	1	1	-	-	4	29	9	7	3
Bythotrephes longimanus	5	15	15	5	-	-	-	-	2	-	22	-	-	-	-	-	-	-	20	-	-
Leptodora kindti	-	-	17	10	-	-	-	-	-	-	-	-	-	-	-	-	-	76	-	-	-
Other cladocerans	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
Σ Cladocera	10	98	113	83	37	4	-	-	54	66	98	9	3	1	-	-	81	219	187	31	10
Limnocalanus macrurus	20	105	40	23	32	-	-	5	94	23	18	5	10	-	16	2	5	-	7	7	-
Eurytemora lacustris	-	6	6	2	5	4	-	-	2	3	6	6	3	3	2	-	-	-	14	-	28
Heterocope appendiculata	1	24	27	17	-	-	-	-	7	9	3	5	-	-	-	-	23	-	2	-	-
H. borealis	-	2	6	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-
Eudiaptomus spp.	20	35	68	63	46	74	23	7	43	60	114	41	46	58	10	12	12	56	31	17	102
Cyclops spp.	13	55	48	59	56	27	1	3	25	27	84	38	24	1	+	2	32	44	80	32	25
Σ Copepoda	54	227	195	164	139	105	24	15	171	122	231	95	83	62	59	16	72	100	134	56	155
Σ Crustacea	64	325	308	247	176	109	24	15	225	188	329	104	86	63	59	16	153	319	321	87	165
Σ Zooplankton	65	579	528	349	212	111	24	15	467	296	369	114	87	63	62	16	202	189	338	108	167

Copepoda were dominant in the zooplankton biomass during winter and continued to be important until May. Rotatoria were dominant in June, Cladocera in July, Copepoda and Cladocera in August. In autumn Copepoda were dominant in oligotrophic water bodies, and Cladocera in Poronselkä and Tiirinselkä.

The zooplankton biomasses found at the sampling stations in the different months and seasons are given in Table 15. In winter, the biomass was usually less than 1.0 g/m^2, except in Tiirinselkä (655-657) and Lehtiselkä (675). Small differences in the sampling time affected the values, especially in May. The biomasses in May were not usually significantly higher than in winter. The increase in the zooplankton biomass in June was most rapid in Jyväsjärvi (510), Kärkistensalmi (600), Tiirinselkä (655-657), and Lehtiselkä (675). However, the biomass was low in Tiirinselkä and Lehtiselkä in June 1969, when the water was most polluted. The average biomass for June-September was highest at the stations in Jyväsjärvi, and Northern and Central Päijänne. Lack of oxygen in the hypolimnion in Tiirinselkä and Lehtiselkä lowered the weighted mean biomass.

Table 15. The zooplankton biomass (wet wt, g/m^2) at the sampling stations in different months and seasons. The values for Jyväsjärvi (510), Haapakoski (522) and Kärkistensalmi (600) are the means of 1969-1970, those for Tiirinselkä (655-657) and Lehtiselkä (675) the means of 1969-1972 and the values of the other stations in Päijänne the means of 1960-1971. The material for L. Konnevesi was taken during the period of open water in 1970.

	LAKE JYVÄSJÄRVI	NORTHERN PÄIJÄNNE					CENTRAL PÄIJÄNNE				SOUTHERN PÄIJÄNNE		LAKE KONNEVESI	
Station	510	522	540	570	600	610	638	655-657	675	715	740-750	810	K1	K2
Month														
I	0.3	-	0.6	-	-	1.6	1.2	4.8	1.6	0.4	0.7	0.3	-	-
II	-	-	-	-	-	-	-	0.2	1.6	-	-	-	-	-
III	0.0	1.0	0.3	0.6	-	0.6	0.7	-	-	1.3	-	-	-	-
IV	1.2	-	0.5	-	0.6	-	-	1.8	1.8	0.2	0.4	-	-	-
V	1.2	0.3	0.4	0.6	1.8	0.2	0.2	0.4	0.9	1.1	1.1	0.5	-	-
VI	64.9	6.8	8.4	8.9	27.5	4.5	3.9	10.9	13.4	12.0	9.1	5.5	2.5	0.6
VII	5.8	11.7	13.4	8.9	45.5	10.3	17.5	6.2	7.4	12.3	8.0	5.9	5.8	4.2
VIII	3.4	12.0	9.5	11.3	29.2	7.4	10.0	9.1	9.3	9.9	6.7	5.5	9.2	4.9
IX	18.5	10.1	10.7	6.8	9.0	3.9	6.6	7.5	7.2	5.8	2.5	2.7	4.6	3.5
X	5.2	-	8.3	-	-	1.8	3.2	12.2	4.2	1.7	2.4	2.4	5.9	2.2
XI	-	3.8	3.9	0.9	0.4	-	-	7.6	3.7	-	0.4	-	-	-
Winter (I-IV, XII)	0.5	1.0	0.5	0.6	0.6	1.2	1.0	2.3	1.6	0.6	0.5	0.3	-	-
Spring (V)	1.2	0.3	0.4	0.6	1.8	0.2	0.2	0.4	0.9	1.1	1.1	0.5	-	-
Summer (VI-IX)	23.2	10.2	10.5	8.9	27.7	6.6	9.5	8.4	9.3	10.1	6.5	4.9	5.5	3.3
Autumn (X-XI)	5.2	3.8	6.2	0.9	0.4	1.8	3.2	9.9	4.0	1.7	1.4	2.4	5.9	2.2
Whole year	8.8	4.5	4.8	3.4	9.6	3.0	4.1	5.5	4.5	4.0	2.7	2.2	-	-

values in these areas, but when expressed as g/m^3, the biomass in the epilimnion of Tiirinselkä was almost the same as in Poronselkä (Table 16). If we assume that the biomass value for 0-10 m in Asikkalanselkä (810) is the natural level of the zooplankton biomass (0.41 g/m^3), the biomass of Tehinselkä (740-750) has risen by 15 %, and that of Tiirinselkä (655, 657) and Poronselkä (540) by about 270 %.

In autumn, high biomass values were found in Poronselkä and Tiirinselkä. The zooplankton biomass rose in Jyväsjärvi as well during the autumn overturn, which took place at the end of September.

The biomasses in Konnevesi were quite low in summer (3.3-5.5 g/m^2) (cf. HAKKARI 1972 c).

G. Vertical distribution of zooplankton biomass

The vertical distribution of the mean zooplankton biomasses in different localities and study years is presented in Fig. 11. The differences between the biomasses of the surface layer and deeper layers were greatest in Jyväsjärvi (510) and in Northern Päijänne (540-600). Zooplankton was almost lacking in the deeper parts of Tiirinselkä (655) in 1969, but in the following years the biomasses increased at all depths in this area (cf. Table 16).

As we can see from Fig. 11 and Table 16, in June-September, the zooplankton biomass at a depth of 5-10 m was about half the biomass at 0-5 m, and

Table 16. The zooplankton biomass (wet wt, g/m^3) in different water layers in Jyväsjärvi, Päijänne and Konnevesi in June-Sept. (^{x} = according to PIIPPONEN 1974).

		LAKE JYVÄSJÄRVI	NORTHERN PÄIJÄNNE				CENTRAL PÄIJÄNNE					SOUTHERN PÄIJÄNNE		LAKE KONNEVESI	
Station		510	522	540	570	600	610	638	655 -57	675	715	740 -50	810	K1	K2
0 - 5 m	1969	5.26	0.82	1.54	1.63	2.37	1.31	1.13	0.71	0.68	1.28	1.00	0.54	-	-
	1970	3.40	0.97	2.01	0.95	1.38	0.50	1.11	1.22	1.34	1.05	0.44	0.60	0.95	0.44
	1971	5.21^x	-	1.19	0.70	-	0.51	0.76	1.42	0.67	1.29	0.36	0.35	-	-
	1972	-	-	-	-	-	-	-	1.80	0.82	-	-	-	-	-
5 - 10 m	1969	2.91	0.70	0.55	0.50	0.43	0.34	0.47	0.49	0.65	0.53	0.40	0.27	-	-
	1970	1.57	1.06	1.03	0.33	0.53	0.28	0.39	1.43	0.86	0.48	0.31	0.17	0.54	0.22
	1971	1.30^x	-	0.45	0.79	-	0.34	0.33	0.40	0.42	0.67	0.31	0.51	-	-
	1972	-	-	-	-	-	-	-	1.45	0.81	-	-	-	-	-
10 - 20 m	1969	0.26	0.96	0.21	0.22	0.51	0.27	0.33	0.08	0.19	0.44	0.22	0.31		
	1970	0.03	0.55	0.43	0.21	0.40	0.24	0.25	0.43	0.60	0.28	0.23	0.12	0.38	0.18
	1971	0.17^x	-	0.26	0.21	-	0.21	0.21	1.07	0.38	0.22	0.21	0.20		
	1972	-	-	-	-	-	-	-	1.10	0.41	-	-	-		

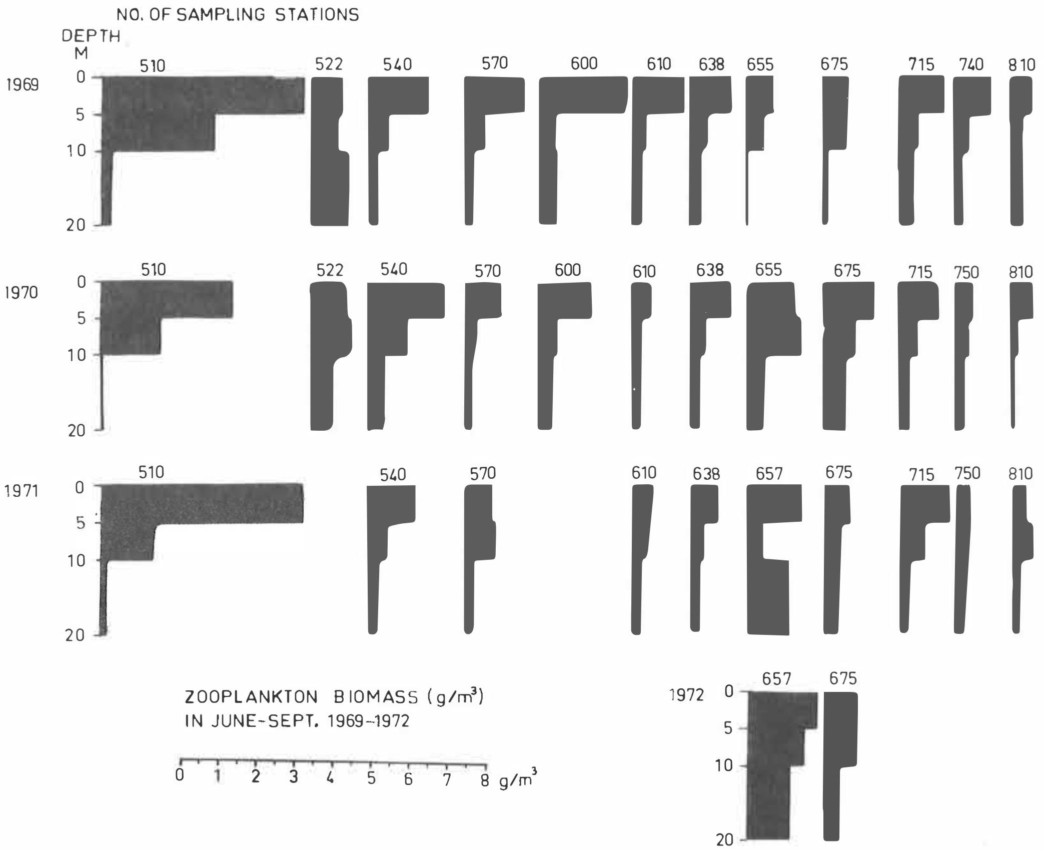


Fig. 11. The zooplankton biomass (wet wt, g/m^3) in different water layers in Jyväsjärvi (510) and Päijänne (522-810) in June-Sept. 1969-1972.

the biomass at 10-20 m about half that at 5-10 m. There were naturally exceptions to this general pattern. The vertical distribution was affected by the position of the metalimnion. In early June, the biomass at 5-10 m was low, near the biomass at 10-20 m and much smaller than that at 0-5 m. The differences disappeared in late September, when the autumn overturn was beginning.

The maximum tended to occur nearer the surface than in lakes with low colour (cf., e.g. HAKKARI 1972 c). In shallow lakes with a relatively small hypolimnion, large amounts of the cold-stenothermal *Limnocalanus* can cause a maximum in the hypolimnion (cf. ELORANTA 1975). This was not observed in the present study. In winter, the highest biomasses were found in the deep-water samples, which is a normal pattern (cf. ANDRONIKOVA 1971, HAKKARI 1969).

H. Zooplankton production

The most productive rotifer species were *Asplanchna priodonta* and *A. herricki* (Table 17). The most productive cladocerans were usually *Daphnia cristata* and *Eubosmina longispina obtusirostris*, but in Jyväsjärvi *Bosmina longirostris* (in "others" in Table 17) was more abundant than the latter. The main part of copepod production was made up by *Eudiaptomus* and *Cyclops* species.

In May, when the total production was rather low, the most productive species were eurythermal and cold-stenothermal rotifers, and some copepods. In June, the production of *Asplanchna priodonta* and *A. herricki* was most significant. The production of *Holopedium gibberum* also started early in June; eggs were found in the first week. The first maximum of *Holopedium* lasted to the end of July. Another maximum was observed in September or August.

Table 17. The mean production (wet wt, g/m^3) of some zooplankton taxa in June-Sept.

	LAKE JYVÄSJÄRVI	NORTHERN PÄIJÄNNE				CENTRAL PÄIJÄNNE				SOUTHERN PÄIJÄNNE	
Station	510	522	540	570	610	638	655-657	675	715	740-750	810
ROTATORIA											
Asplanchna priodonta	270.4	90.6	46.5	38.6	15.1	18.5	50.2	37.1	38.6	14.2	5.4
A. herricki	0.2	5.1	10.2	3.9	17.4	16.5	1.9	1.1	10.0	11.9	5.7
Conochilus hippocrepis	-	0.2	0.2	0.7	2.8	5.5	0.5	1.8	4.6	6.8	2.9
C. unicornis	0.4	0.2	1.1	1.0	3.0	3.0	0.7	0.8	3.7	2.5	1.1
Others	3.0	6.1	4.8	4.8	3.2	4.0	6.4	5.3	3.0	2.5	1.0
CLADOCERA											
Limnosida frontosa	0.3	1.1	2.6	1.5	0.9	1.8	2.0	0.9	3.1	3.6	2.0
Diaphanosoma brachyurum	0.5	5.8	8.8	16.8	5.3	2.9	1.0	2.6	2.2	1.0	1.3
Holopedium gibberum	-	0.6	2.5	1.0	3.3	8.8	1.1	1.4	7.0	10.4	5.8
Daphnia cristata	105.0	51.2	64.5	38.4	19.8	12.1	45.5	26.9	15.9	8.8	5.4
D. galeata	0.2	8.7	2.0	0.2	0.1	1.5	18.1	10.2	6.7	4.5	2.0
Eubosmina spp.	0.5	17.9	22.1	12.5	15.6	23.9	3.2	7.7	12.9	8.4	8.1
Bythotrephes longimanus	-	-	0.8	-	1.5	3.6	1.5	0.4	4.9	1.8	0.7
Leptodora kindti	1.2	4.6	6.2	0.6	0.5	1.8	3.3	1.0	0.1	1.1	0.2
Others	19.9	0.4	0.5	0.2	+	+	0.5	0.3	0.1	-	+
COPEPODA											
Limnocalanus macrurus	-	-	0.4	2.3	3.5	2.1	+	0.9	3.0	2.5	2.2
Eudiaptomus spp.	0.6	5.9	6.5	7.5	6.9	12.2	6.5	11.4	13.5	13.2	7.2
Heterocope appendiculata	0.5	0.4	0.3	0.3	0.4	0.4	0.7	1.2	0.8	0.8	0.5
Cyclops spp.	14.0	17.7	16.9	12.6	11.0	8.8	12.8	12.5	15.6	8.2	7.4
Others	+	0.4	0.2	0.8	0.3	1.0	0.4	1.5	1.1	0.5	1.1
INSECTA											
Chaoborus flavicans	-	-	+	0.1	-	+	2.3	2.0	0.3	-	-

The production of *Daphnia cristata* also started in the first half of June. It was greatest in July but quite small in August, and often had another maximum in September. *Eubosmina* species were mainly found in the plankton during the summer months, having maxima in June-July and sometimes another slight maximum in August or September.

The main part of the production of *Limnocalanus* and *Heterocope* occurred in June. At the end of June most individuals of both species were already adults (cf. HAKKARI 1970 b). This agrees with the results of CARTER (1969) in Georgian Bay, Canada. The adults of *Eudiaptomus* which had hatched in autumn reproduced in February-March and died off before May. The new generation reproduced in June. Altogether, the species had four summer generations in the study area, and thus five generations during the whole year, as NAUWERCK (1963) has observed in Lake Erken in Sweden.

According to some investigators (cf. NAUWERCK 1963), the copepodites of *Cyclops* species spend the winter in the bottom sediment, rising to the surface water and developing to adults in spring. In Tehinselkä they did not appear in the plankton till the end of May. The copepodites of *Thermocyclops oithonoides* developed to adults in mid-June, and those of *Mesocyclops leuckarti* at the end of this month. Four generations of these species were observed in Tehinselkä during summer 1969 (HAKKARI 1970 b). In winter, the plankton samples contained only a few specimens of *Cyclops strenuus* s. lat.

The zooplankton biomass in winter was usually less than 10 % of the summer biomass (Table 15). Since development takes at least three times as long time in winter as in summer (cf. MEDNIKOV 1962, ref. WINBERG 1971), the production in winter was less than 5 % of the summer production.

Table 18 shows the production values for the herbivore (H) and carnivore (C) zooplankton, and the mean ratios of these values. The H/C ratio averaged 3.1-6.7. It varied greatly between the sampling stations in the different years, but this was evidently caused by the smallness of the material, and no real differences were observed between the stations.

I. Feeding of planktivorous fish

1. Feeding of vendace

Food composition

Zooplankton is the basic food of vendace. Other items found were chironomid larvae and pupae, and very occasional fish.

Table 18. The production (wet wt, g/m^2) of herbivores and carnivores, and the ratio of these levels in the study area in June-Sept. (H = herbivores, C = carnivores).

	1969		1970		1971		1972		Mean
	H	C	H	C	H	C	H	C	H:C
LAKE JYVÄSJÄRVI (510)	372.5	127.9	303.6	28.8					6.7
NORTHERN PÄIJÄNNE									
Haapakoski (522)	155.4	27.6	185.2	65.6					4.2
Poronselkä (540)	155.1	38.1	160.3	50.3	145.3	22.5			4.6
Ristiselkä (570)	162.8	28.4	92.6	21.6	102.8	23.3			4.8
Vanhanselkä (610)	129.0	20.4	53.7	23.3	73.9	20.9			4.1
CENTRAL PÄIJÄNNE									
Souselkä (638)	124.1	14.8	117.5	33.1	72.3	17.7			5.3
Tiirinselkä (655-657)	54.2	11.7	143.1	51.4	126.4	37.0	173.5	35.1	3.9
Lehtiselkä (675)	70.6	17.4	107.5	44.5	59.3	18.7	83.8	30.1	3.1
Judinsalonselkä (715)	115.2	29.5	115.5	39.0	122.9	36.0			3.4
SOUTHERN PÄIJÄNNE									
Tehinselkä (740-750)	104.2	20.6	77.8	16.6	69.2	18.5			4.5
Asikkalanselkä (810)	54.8	9.3	53.4	16.5	35.2	10.4			4.2

If the percentage of fish containing a prey taxon is taken as the index of frequency, the most common food item in the whole material was *Eubosmina* spp; they were found in 85 % all of the dissected fish. Other common items were *Cyclops* spp. (71 %) and *Daphnia cristata* (63 %).

On the whole, the seasonal and spatial variation was very great (Table 19). The seasonal feeding pattern may differ between large bodies of water and shallow inlets, where the water warms earlier in spring. The fishing places used in Southern Konnevesi, and Koivuselkä, Keitele were shallow inlets of this kind, where only a few *Limnocalanus* were observed.

The selection of food organisms

The selection of zooplankters by vendace was investigated with the "electivity index" of IVLEV (1961) (Table 20). The following large food items were preferred: *Bythotrephes longimanus*, *Leptodora kindti*, *Limnocalanus macrurus*, and *Heterocope appendiculata*. No preference was noted for *Holopedium gibberum* or *Eubosmina* spp. Vendace of this size (total length 8.6-

Table 19. Percentage wet weights of different food items in the stomach of vendace.

	LAKE KONNEVESI								LAKE PÄIJÄNNE						LAKE KEITELE		
	Northern part			Southern part				Poronselkä	Tehinselkä				Asikkalanselkä		Koivuselkä		
Year	1970			1970				1972	1972				1972		1973		
Date	25.V.	1.VII.	28.VII.	26.V.	2.VII.	28.VII.	7.IX.	19.IX.	26.VI.	11.VII.	18.VIII.	15.IX.	18.VIII.	20.IX.	19.VI.	26.VI.	15.VIII.
Number of fish	9	3	9	9	9	9	9	10	12	2	10	10	10	10	8	7	10
Rotatoria		4.63															
Limnosida and *Diaphanosoma*			0.04	0.09	4.60	0.76	4.14		0.75						0.43	1.29	5.10
Holopedium		0.05				0.07			76.39		1.06	0.13			18.83	58.89	2.96
Daphnia		0.27	0.10	0.05	13.30	6.80	46.93	22.80	2.02		0.55	3.96	0.11	2.60	1.61	6.97	1.33
Eubosmina and *Bosmina*	57.64	0.36	0.37	26.74	35.74	1.09	6.50	16.70	13.83	1.66	0.40	1.38	0.48	0.92	67.45	14.74	5.83
Polyphemus					0.49												
Bythotrephes						8.22	0.93		6.15	98.34	96.82	92.30	98.96	95.79	0.94		80.76
Chydorus							2.00								0.02	+	
Leptodora					27.39	56.66	9.75	44.40			0.66	1.15	0.12	0.35	1.18		
Σ Cladocera	57.64	5.31	0.51	26.88	81.52	73.60	70.25	83.90	99.14	100.00	99.49	98.92	99.67	99.66	90.46	81.89	95.98
Limnocalanus	14.29	94.55	98.97	19.85	6.15	10.47	0.49	1.70			0.33	0.96	0.31				
Eurytemora			0.18			0.17	0.06										
Heterocope				0.28	0.95	1.56	21.43	4.30							2.45	10.29	1.86
Eudiaptomus		0.14	0.26	1.89	2.85	8.24	0.66		0.23		0.11			0.09	3.03	4.31	0.31
Cyclops	5.75	0.03	0.08	14.12	8.50	5.99	7.12	10.10	0.63		0.06	0.12	0.02	0.26	2.90	1.13	1.85
Σ Copepoda	20.04	94.72	99.49	36.14	18.45	26.43	29.76	16.10	0.86		0.50	1.08	0.33	0.34	8.38	15.73	4.02
Chaoborus				1.17													
Chironomidae	22.20			35.78											1.16	2.36	
Hydracarina	0.12																
Σ Others	22.32			36.95											1.16	2.36	

21.0 cm, $\bar{x}$ 15.1 $\pm$ 0.3 cm) showed pronounced avoidance of small zooplankters, rotifers and copepod nauplii, and less strong avoidance of adult *Limnosida* and *Diaphanosoma*, *Daphnia cristata*, *Eurytemora lacustris*, *Eudiaptomus* spp., and *Cyclops* spp.

Food composition in different seasons

The seasonal changes in food composition showed some common features in the different study places (Table 19). In May and sometimes early June, only a few cladocerans were hatched. The fish fed largely on chironomid larvae and pupae, young and adult *Cyclops*, and young *Limnocalanus*. Later in June, *Holopedium gibberum* and *Eubosmina longispina obtusirostris* seemed to be important food items during their maxima in the plankton (cf. Table 12-14).

In most cases *Bythotrephes* and *Leptodora* were dominant in the stomach contents during July-September. *Limnocalanus* also seemed to be important when available. It was numerous in the fishing place in Northern Konnevesi in July 1970 but scarce in Tehinselkä, Päijänne, in summer 1972. In spite of their fairly high biomasses in the plankton, *Daphnia cristata*, *Eudiaptomus* spp., and *Cyclops* spp. formed only a small part of the stomach contents in July-September.

Table 20. The "electivity index" of IVLEV (1961) in vendace.

			LAKE KONNEVESI								LAKE PÄIJÄNNE				LAKE KEITELE	
	Northern part				Southern part			Poron-selkä		Tehinselkä			Asikkalanselkä		Koivuselkä	
Date	25.V.	1.VII.	28.VII.	26.V.	2.VII.	28.VII.	7.IX.	19.IX.	26.VI.	11.VII.	18.VIII.	15.IX.	18.VIII.	20.IX.	26.VI.	15.VIII.
Number of fish	9	3	9	9	9	9	9	10	12	2	10	10	10	10	7	10
Limnosida and *Diaphanosoma*			-1.00		1.00	-0.12	0.24	-1.00	1.00		-1.00		-1.00	-1.00	-0.54	-0.66
Holopedium	-1.00	0.00	-0.99	-1.00	-1.00	1.00			0.82	-1.00	-0.73	1.00	-1.00		0.85	-0.55
Daphnia	-1.00	-0.84	-0.98	-0.90	0.21	-0.59	-0.14	-0.21	-0.31	-1.00	-0.89	-0.03	-0.99	0.92	-0.79	-0.81
Eubosmina	0.59	-0.76	-0.33	0.73	0.34	0.22	0.78	0.57	0.74	-0.39	-0.72	-0.68	-0.92	-0.69	0.17	0.30
Chydorus							0.82								0.38	-1.00
Bythotrephes						1.00	1.00		0.24	0.79	1.00	1.00	1.00	1.00		0.93
Leptodora					1.00	1.00	1.00	1.00			1.00	1.00	1.00	1.00	-1.00	-1.00
Limnocalanus	-0.27	0.06	0.46	-0.59	-0.16	1.00	1.00	1.00		-1.00	1.00	1.00	1.00			
Eurytemora		-1.00	-0.91			-0.86	-0.96		-1.00		-1.00		-1.00	-1.00		-1.00
Heterocope			-1.00	1.00	1.00	1.00	0.78	1.00	-1.00						0.94	0.48
Eudiaptomus	-1.00	-0.83	-0.88	0.00	0.09	0.10	-0.80	-1.00	-0.53	-1.00	-1.00	-0.99	-1.00	-0.99	-0.44	-0.98
Cyclops	-0.13	-1.00	-0.92	0.43	0.85	-0.67	-0.41	-0.25	-0.69	-1.00	-0.99	-0.99	-0.99	-0.99	-0.41	-0.86
Chaoborus				1.00												
Chironomidae	1.00			1.00												
Hydracarina	1.00															-1.00

Food composition and fish size

The differences in the food composition of vendace in different areas were partly caused by local variation in hydrological and biological features of the environment, partly by the size of the fish. The effects of these factors were difficult to separate. It seems that the conditions in the feeding area and depth at the moment of capture determined the food composition far more than the size of the fish. The only difference that might be caused by fish size was found in Southern Konnevesi, where the fish were small (total length 10.5±0.1 cm) contained larger proportions of *Daphnia* spp., *Eudiaptomus* spp., and *Cyclops* spp. than in other areas.

Gastric digestion rate

The time required for gastric digestion was determined from the change in stomach contents (wt of stomach contents as ‱ of fish wt) during incubation (cf. p. 22). At the beginning of the experiment the stomach content index averaged 65-72 ‱ (Fig 12). During 4-hr incubation, no clear changes in the index were observed. After 6-hr incubation, the food components (various Cladocera and Copepoda) could still be easily identified. After 10 hr, the stomach content index averaged less than 25 ‱.

In the samples incubated for 10-12 hr the food components were difficult to identify. The stomach contents mainly consisted of indigestible parts of crustaceans, parts of the carapace and cephalothorax, as well as spines and

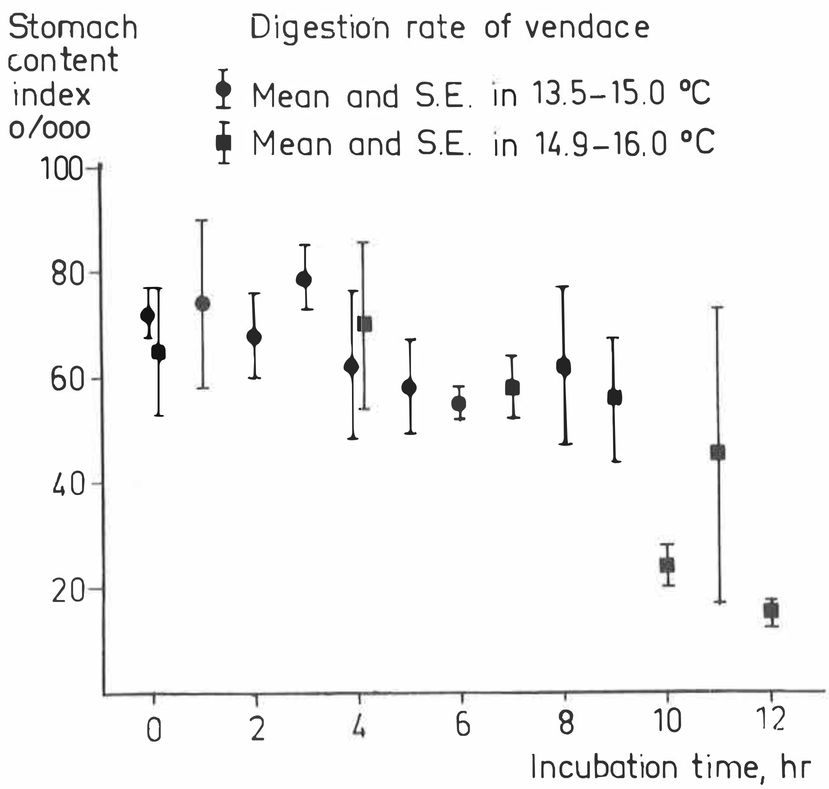


Fig. 12. The stomach content index of vendace (‰o , WINDELL 1971) after different incubation times *in situ* (cf. Table 21).

setae of different kinds. According to the results, the digestible portion of the stomach contents (ca. 80 %) was digested in 12 hr. The contents were red brown in "fresh" samples, but turned grey when the fish were kept several hours without food.

Composition and digestibility of food

Table 21 shows the percentage distribution of the individual items of food among the prey taxa after different incubation times. No clear differences exist in the percentage representation after digestion of a few or more hours. The material for the longer periods was rather small, however, and unfortunately *Bythotrephes longimanus* was lacking.

The seasonal variation in feeding

The index of stomach contents gives information on seasonal variation in feeding (cf. CHIKOVA 1970). The average index of stomach contents for vendace was as follows: May 0.01 ‰o, June 122 ± 13 ‰o, July 55 ± 2 ‰o, and

August 53 ± 7 ‰o. The samples were taken during or immediately after feeding in the evening. The index for fish caught in the early morning in August was 21 ± 5 ‰o and in September it was 16 ± 5 ‰o. Thus the intensity of feeding seemed to be highest during late June and to decrease towards autumn.

Table 21. Percentage distribution of individual food items among prey taxa in the stomach of vendace after different digestion times.

19.-20.VI.1973	Digestion, h						
	0	1	2	3	4	5	6
Limnosida	0.2	-	-	0.1	0.9	-	-
Diaphanosoma	0.1	-	-	-	-	-	-
Holopedium	10.2	10.5	9.3	6.7	7.7	8.8	11.3
Daphnia	1.1	2.3	1.5	1.9	1.2	2.0	0.5
Eubosmina	78.8	76.8	78.8	82.4	79.7	79.9	70.6
Chydorus	0.1	0.2	-	0.1	-	0.4	-
Leptodora	-	-	-	-	-	-	0.9
Heterocope	0.8	2.1	1.6	1.0	2.8	0.3	1.7
Eudiaptomus	2.2	1.3	2.2	1.0	1.2	2.7	4.8
Cyclops	6.6	6.9	6.5	6.8	6.5	5.9	10.2
	100	100	100	100	100	100	100
Number of fish	8	4	5	5	5	5	5

26.-27.VI.1973	Digestion, h							
	0	4	7	8	9	10	11	12
Limnosida	1.1	1.4	2.0	0.3	-	0.3	-	2.0
Diaphanosoma	0.1	0.8	0.5	-	0.7	-	-	1.5
Holopedium	50.7	46.4	62.0	36.7	36.5	44.4	43.0	59.5
Daphnia	6.9	2.8	5.2	4.7	2.4	0.2	1.0	5.5
Eubosmina	29.6	33.4	17.0	35.7	37.4	41.7	26.8	16.0
Chydorus	0.1	0.4	-	-	-	0.2	-	0.5
Leptodora	-	-	-	-	-	-	-	1.0
Limnocalanus	-	-	0.3	0.5	0.6	0.1	0.5	-
Heterocope	4.4	4.2	5.3	4.7	7.0	8.3	7.6	6.5
Eudiaptomus	3.7	3.4	4.3	8.3	12.3	2.3	9.6	3.5
Cyclops	3.4	7.2	3.5	9.0	3.0	2.3	11.6	4.0
	100	100	100	100	100	100	100	100
Number of fish	7	5	4	3	5	4	2	2

2. Feeding of smelt

Food composition

As with vendace, *Eubosmina* spp. and *Cyclops* spp. were the most frequent food items, being found in 72 % and 68 % of the fish dissected. Next in order of frequency were *Daphnia cristata* (56 %) and *Heterocope appendiculata* (47 %). *Leptodora kindti* and *Holopedium gibberum* were found in 28 % and 26 % of all the fish. *Mysis relicta*, which was not found in vendace, was observed in 8 % of the fish. Because of its large size, it seemed to be a rather important food item, as was also *Bythotrephes longimanus*, whose frequency was 18 %.

When *Mysis* was not present, zooplankton crustaceans usually composed more than 90 % of the stomach contents (Table 22). *Mysis* was not found in the stomachs of smelt in June, but during July-September it averaged 45 % of the stomach contents. This nektonic species was found in smelt measuring 12.2-15.7 cm and caught from the metalimnion.

Table 22. The percentages (by wet wt) of food items in the stomach contents of smelt.

	LAKE KONNEVESI	LAKE PÄIJÄNNE								
	Northern part	Poronselkä					Tehinselkä		Asikkalanselkä	
Date	25.V.	2.VI.	6.VI.	30.VI.	1.VIII.	19.IX.	26.VI.	11.VII.	15.VII.	18.VIII.
Number of fish	10	3	8	10	10	10	10	14	10	3
Limnosida and *Diaphanosoma*		0.03	2.86		6.44		0.17			
Holopedium		0.04	4.72	0.20			13.78		0.29	
Daphnia	2.18	0.03	2.38	6.56	2.36	0.72	0.48	1.16	35.42	
Eubosmina	7.26	0.03	4.76	4.51	0.17	0.18	19.02	3.83	31.57	0.08
Bythotrephes					4.43		22.79	3.31		5.26
Leptodora				75.48	66.50					
Σ Cladocera	9.44	0.13	14.72	86.75	79.90	0.90	56.24	28.55	67.28	5.34
Limnocalanus					9.82					
Eurytemora							0.22			
Heterocope				6.57	2.12	1.08	36.14	30.67	23.26	
Eudiaptomus	3.65	0.03	1.43							
Cyclops	9.44	1.60	58.47	0.56	0.10	0.22	7.41	3.49	1.16	
Σ Copepoda	13.07	1.63	59.90	7.13	11.74	1.30	43.77	34.16	24.42	-
Mysis						97.79		22.09	8.31	94.66
Chaoborus				6.12	8.06			15.19		
Chironomidae	77.48	73.38	25.39							
Pisces		24.84								
Σ Others	77.48	98.22	25.39	6.12	8.06	97.79	-	37.28	8.31	94.66

Seasonal differences in food composition

In spring the smelt fed on chironomid larvae and pupae, and *Cyclops* spp. also constituted a large proportion of the stomach contents. Cladocerans played a subordinate role, because of their small amount in the plankton.

The small smelt began to feed earlier in spring than the large fish, but by early summer (10.VI.) there were no significant differences between the indices of smelt of different sizes.

In summer, *Mysis*, cladocerans and *Heterocope appendiculata* formed the greater part of the smelt diet. Sometimes *Leptodora kindti* was dominant. Fish was found only seldom in the smelt stomachs.

Food selection

The "electivity index" of IVLEV (1961) (Table 23) shows a preference of chironomid larvae and pupae, *Daphnia cristata, Eudiaptomus* spp., and *Cyclops* spp. in spring. In summer, the crustacean plankters *Leptodora kindti* and *Heterocope appendiculata* seemed to be significantly favoured, as well as *Chaoborus flavicans* and *Mysis relicta*. *Bythotrephes longimanus* was only slightly preferred, and the fish showed significant avoidance of *Eudiaptomus* spp., *Cyclops* spp., and usually *Daphnia cristata*.

Table 23. The "electivity index" of IVLEV in smelt (see the text).

	KONNEVESI								
	Northern part	Poronselkä				Tehinselkä		Asikkalanselkä	
Date	25.V.	6.VI.	30.VI.	1.VIII.	19.IX.	26.VI.	11.VII.	15.VII.	18.VIII.
Number of fish	10	8	10	10	10	10	14	10	3
Limnosida and *Diaphanosoma*		1.00	-1.00	0.20	-1.00	1.00		-1.00	-1.00
Holopedium	-1.00	1.00	-0.87			0.30	-1.00	0.35	-1.00
Daphnia cristata	0.28	0.74	-0.72	-0.38	-0.97	-0.78	-0.61	0.30	-1.00
D. galeata			-0.90				-1.00	0.92	
Eubosmina	-0.41	0.38	-0.04	-0.69	-0.91	0.81	-0.84	-0.03	-0.99
Bythotrephes				1.00		0.72	-0.24	-1.00	1.00
Leptodora			1.00	0.00			1.00		
Limnocalanus	-1.00			0.15			-1.00	-1.00	
Eurytemora						-0.18		-1.00	-1.00
Heterocope			0.60	1.00	1.00	0.96	1.00	1.00	-1.00
Eudiaptomus	0.05	0.62	-1.00		-1.00	-1.00	-1.00	-1.00	-1.00
Cyclops	0.10	0.84	-0.90	-0.95	-0.96	-0.36	-0.27	-0.78	
Mysis					1.00		1.00	1.00	1.00
Chaoborus			1.00	1.00			1.00		
Chironomidae	1.00	1.00							

Stomach fullness

The fish were usually caught with a seine in the evening, and the results are thus comparable. The stomach content index in late May in Northern Konnevesi was 1.6 ± 0.7 ‱; thus feeding was just beginning. Sixty per cent of the stomachs were still empty. In early June (2.-6.VI.) the index in Poronselkä was 56 ± 12 ‱ and the proportion of empty stomachs was 9 %. At the end of June, when no empty stomachs were observed, the stomach content index was 101 ± 28 ‱. In early August, although empty stomachs were lacking, the index was only 34 ± 6 ‱. In September, most of the stomachs (> 70 %) were empty and the index of stomach contents was 7 ± 4 ‱. In Tehinselkä and Asikkalanselkä the trend was the same. In the sample taken in Asikkalanselkä on 15 July 1972, the index was 108 ± 23 ‱.

3. Similarity in the diets of smelt and vendace

The similarity of the food eaten by the fish in the same sample was tested with the index of SHORYGIN (1939). The results are given in Table 24. If there was one preferred food item (e.g. *Limnocalanus macrurus* in vendace from Northern Konnevesi in July 1970 or *Bythotrephes longimanus* in vendace from Tehinselkä and Asikkalanselkä in July-August 1972), the index of similarity was high, exceeding 90. But if there were many preferred species, e.g. in vendace from Southern Konnevesi in 1970, the individual fish had their own specialized diets and the similarity between them was rather low. In spring, when the amount of food was low, the diets were very dissimilar (cf. vendace in Northern Konnevesi 25.V.1970). The occasional occurrence of *Mysis relicta*

Table 24. The mean similarity indices, with their standard errors, for the diets of the fish (see the text).

	LAKE PÄIJÄNNE in 1972						LAKE KONNEVESI in 1970				LAKE KEITELE in 1973	
	Poronselkä		Tehinselkä		Asikkalanselkä		Northern part		Southern part		Koivuselkä	
	Date	$\bar{x}$ ± S.E.	Date	$\bar{x}$ ± S.E.	Date	$\bar{x}$ ± S.E.	Date	$\bar{x}$ ± S.E.	Date	$\bar{x}$ ± S.E.	Date	$\bar{x}$ ± S.E.
Vendace	19.IX.	62.0 ± 7.7	26.VI.	74.0 ± 2.3	18.VIII.	98.9 ± 0.9	25.V.	37.8 ± 13.8	26.V.	60.8 ± 3.3	19.VI.	74.3 ± 3.1
			11.VII.	97.5	20.IX.	84.8 ± 1.6	1.VII.	93.7 ± 3.5	2.VII.	69.3 ± 1.8	26.VI.	75.6 ± 2.2
			18.VIII.	92.5 ± 1.6			28.VII.	98.8 ± 0.1	28.VII.	67.6 ± 2.0	15.VIII.	86.7 ± 1.0
			15.IX.	70.0 ± 4.8					7.IX.	68.8 ± 2.3		
Smelt	2.VI	18.3 ± 18.3	26.VI.	65.2 ± 3.8	15.VII.	48.8 ± 3.3	25.V.	49.8 ± 7.2				
	6.VI.	60.3 ± 7.0	11.VII.	47.9 ± 3.1	18.VIII.	98.0						
	30.VI.	43.5 ± 4.4										
	1.VIII.	43.8 ± 5.1										
	19.IX.	66.0 ± 12.2										
Vendace -smelt	19.IX.	2.2	26.VI.	35.0	18.VIII.	5.3	25.V.	33.4				
			11.VII.	5.0								

in the stomachs of smelt also caused dissimilarity between individuals. Thus the similarity between the individuals of a sample was usually quite low, and the standard error was high.

The similarity index for the diets of smelt and vendace could be calculated from five samples (Table 24). The similarity was always low, the species having their own food items: vendace had *Bythotrephes*, *Holopedium*, *Eubosmina longispina obtusirostris* and *Limnocalanus*; smelt had *Mysis*, *Heterocope* and chironomous larvae and pupae in spring (cf. Table 25).

Some *Coregonus lavaretus* individuals (length 25.5-27.5 cm), caught during fishing for vendace and smelt, and also fed mainly on zooplankton (*Bythotrephes longimanus*, *Eubosmina longispina obtusirostris*, *Holopedium gibberum*, *Daphnia cristata* and *Cyclops* spp., in June-July), but partly also on adult insects (e.g. Culicidae, Hymenoptera, and Brachycera).

V. Discussion

A. Effects of eutrophication and pollution on the zooplankton

1. Species composition

Indicators of eutrophy and eurytopic species

PEJLER (1964) reported that the most eutrophic lakes are avoided by the majority of zooplankters, and only a few extremely eurytopic species and a number of typical indicators of eutrophy are found in them. This was observed in Jyväsjärvi (510). Of the eurytopic taxa, only *Tintinnopsis lacustris*, *Vorticella* spp., *Polyarthra remata*, *Keratella cochlearis*, *Daphnia cristata*, *Eubosmina mixta lilljeborgi*, and *Cyclops* spp. were encountered at most

Table 25. The most important food items in the samples of vendace and smelt.

LAKE PÄIJÄNNE				LAKE KONNEVESI
Poronselkä	Tehinselkä		Asikkalanselkä	Northern part
19.IX.1972	26.VI.1972	11.VII.1972	18.VIII.1972	25.V.1970
vendace: *Leptodora*, *Daphnia*	vendace: *Holopedium*	vendace: *Bythotrephes*	vendace: *Bythotrephes*	vendace: *Eubosmina*, *Limnocalanus*
smelt: *Mysis*	smelt: *Heterocope*	smelt: *Heterocope*, *Mysis*	smelt: *Mysis*	smelt: *chironomids*

sampling times (frequency > 80 %). In Poronselkä (540), the number of abundant eurytopic species was higher but the number of E species lower than in Jyväsjärvi:

Station	No. of taxa with frequency > 80 % in June-Sept.		
	E species	Eurytopic species	O species
Jyväsjärvi (510)	5	7	0
Tiirinselkä (655-657)	4	10	0
Poronselkä (540)	1	16	1
Asikkalanselkä (810)	0	14	3

In polluted Tiirinselkä the situation was like that in Jyväsjärvi. The number of eurytopic taxa was reduced and there were no abundant O species. On the other hand, only a few species were restricted to oligotrophic Asikkalanselkä, and only *Gastropus stylifer*, *Conochilus hippocrepis*, and *Eurytemora lacustris* were ± abundant there (frequency > 80 %). The total number of taxa in these waters also tended to be low (Table 9). This agrees well with PEJLER's (1964) observation: "The more extreme the character of a lake, the fewer species of zooplankters it usually contains".

The great complexity of the ecological links makes it difficult to identify the different environmental factors, but some of the most important can be presented.

Oxygen deficiency

The lack of oxygen was decisive in Jyväsjärvi in winter and during the spring overturn, when the lake was almost devoid of oxyphilous zooplankters. Similarly, after the spring overturn in 1969 in Tiirinselkä only a few living specimens were found. The hypolimnion of these waters was not inhabited by zooplankton in summer.

Cold-stenothermal species may be expected to avoid waters with an oxygenless hypolimnion. For instance, *Limnocalanus macrurus* and *Eurytemora lacustris*, which live in the meta- or hypolimnion in summer (cf. RYLOV 1935), avoided the polluted areas (cf. PATALAS & PATALAS 1966). However, the occurrence of these species seemed to be controlled by other factors as well; *Eurytemora* was rare in Poronselkä although the oxygen content was fairly good (ca. 3.8-7.0 mg/l in hypolimnion in summer), and the cold-stenothermal *Keratella hiemalis* was most abundant in polluted Tiirinselkä.

Some species seemed to benefit from a poor oxygen situation. *Arcella* spp. was common in areas where the oxygen concentration was low and the amount of dissolved iron was high (cf. JÄRNEFELT 1958). *Daphnia pulex* was abundant just above the oxygenless water layer in Lehtiselkä in 1969 and in Tiirinselkä in 1970, but disappeared when the oxygen content increased (cf. HAKKARI 1975 a).

The composition and amount of food

The selection of food is primarily based on the size of the food objects RUTTNER-KOLISKO 1972). The most common rotifers (e.g. *Keratella* , *Kellicottia*, *Conochilus*) eat mainly food particles under 12 µm in diameter (HUTCHINSON 1967); according to HILLBRICHT-ILKOWSKA *et al.* (1972), they generally feed on particles measuring 1-5 µm. *Polyarthra*, and *Synchaeta pectinata*, *and* sometimes also *Keratella* and *Kellicottia*, can feed on *Cryptomonas*, which may be 50 µm in diameter (POURRIOT & HILLBRICHT-ILKOWSKA 1969).

In Päijänne, small algal taxa, *Rhodomonas minuta*, *Cryptomonas* sp. and other flagellates, which are suitable food for herbivorous zooplankton, are dominant (GRANBERG 1973, 1974). Bacteria and allochthonous detritus, especially abundant in eutrophicated and polluted areas (cf. GRANBERG 1975), and fresh phytoplankton detritus, which is very valuable as food (cf. RODINA 1946, YESIPOVA 1969), are mainly available in Jyväsjärvi and Northern Päijänne.

It was difficult to find a direct connection between the food available and the species composition of the zooplankton. The wood-processing wastes were an important factor controlling the distribution of the species. *Trichocerca pusilla* found its best food conditions in Jyväsjärvi, as did also *Arcella* sp., *Brachionus* spp., *Keratella cochlearis hispida*, *K. cochlearis tecta*, *K. quadrata and Anuraeopsis fissa*. These species could tolerate the acid effluents from the paper mill. All but *Arcella* sp. are more or less reliable indicators of eutrophy (BERZINS 1949, JÄRNEFELT 1952, JÄRNEFELT *et al.* 1963, PEJLER 1957, 1964, RADWAN 1975).

Some other indicators of eutrophy (*Trichocerca capucina*, *T. cylindrica*, *Polyarthra euryptera*, *Pompholyx sulcata*, and *P. complanata*) found their most suitable environment in Northern Päijänne.

In Central Päijänne it seemed that the rotifers *Keratella ticinensis*, *K. hiemalis*, *Anuraeopsis fissa*, and *Filinia longiseta* had similar feeding requirements.

According to KUTIKOVA (1970), *K. ticinensis* is found in small, saprobic waters. CARLIN (1943) and PEJLER (1957) report that it lives only in polyhumic waters. It seems that it feeds on humic substances or bacteria breaking down detritus. Most herbivorous Cladocera prefer food particles measuring 3-20 µm (HILLBRICHT-ILKOWSKA *et al.* 1972). *Daphnia* spp., e.g. *D. magna* and *D. longispina*, may largely feed on detritus (YESIPOVA 1969, AKSENOVA *et al.* 1969).

NAUWERK (1963) supposed that the dahpnids in L. Erken, Sweden, feed mainly on detritus and bacteria. Similar observations were made in Central Päijänne. During the main production period in July-August, the maximum of *Daphnia cristata* was situated mainly at a depth of 10-20 m. The same tendency was observed in *D. galeata* and *D. pulex* (cf. HAKKARI 1975 a). In the deeper water layers only detritus and bacteria were available as food. As shown by AKSENOVA *et al.* (1969), algae and bacteria are qualitatively irreplaceable, since they contain the complete range of the main amino acids and several vitamins.

Ceriodaphnia quadrangula and *Bosmina longirostris* were found mainly in the metalimnion of Lievestuoreenjärvi, which is heavily polluted by the effluents of a sulphite pulp mill (HAKKARI 1967 and unpubl.). *Daphnia pulex* was also found there; besides ponds (cf. MÄEMETS 1961, HRBÁČKOVÁ-ESSLOVÁ 1963), it seems to prefer α-mesosaprobic and polysaprobic waters (HRBÁČEK 1962). In large lakes in Finland, it seems be a reliable indicator of pollution (cf. also SCHRÄDER 1958, JÄRNEFELT 1961).

Limnetic copepods filter all sizes of flagellates from 1-15 µm, but plankters in the size range 5-15 µm are most efficiently removed (HARGRAVE & GREEN 1970). Calanoida, except *Heterocope*, feed mainly on algae, bacteria, and detritus (e.g. HUTCHINSON 1967, NAUWERCK 1963, KIBBY & RIGLER 1973). The young stages (nauplii and early stages of copepodites) of *Heterocope* and cyclopids are herbivorous (McQUEEN 1969, DODSON 1975), and adults sometimes also feed on algae and bacteria (SAUNDERS 1969).

Several species were more abundant in eutrophicated Northern Päijänne than in oligotrophic Southern Päijänne. A good example was *Limnocalanus macrurus*, which avoided highly eutrophicated or polluted areas, but was more numerous in Poronselkä than in Tehinselkä (cf. p. 33), owing to the rich food supply. Heavy predation by planktivorous fish affected the abundance of large zooplankters in oligotrophic areas, and this was presumably one of the reasons why the carnivorous cladoceran *Leptodora kindti* had its maximum in northernmost Päijänne. According to MÄEMETS (1961), *Leptodora* is eurytopic. PEJLER (1964) has observed it in great numbers in heavily polluted lakes, but does not regard it as an indicator.

Effect of microbes

NAUMANN (1924) observed that the jelly enveloping zooplankters is easily attacked by bacteria and altogether very sensitive to outside influence. Study of the occurrence of the species enveloped in jelly (*Conochilus* spp., *Collotheca* spp. and *Holopedium gibberum*) showed that all of them avoided highly eutrophicated or polluted water areas.

Plankton as a resting substrate

Several authors (e.g. CARLIN 1943, MÄEMETS 1961, JÄRNEFELT *et al.* 1963, PEJLER 1964, and PATALAS & PATALAS 1966) have connected the plankton occurrence of *Chydorus sphaericus* with eutrophication, and this was also reported for *Trichocerca porcellus* (cf., e.g., CARLIN 1943). These species usually occur in periphyton, but in eutrophic lakes, where algal colonies provide suitable resting substrates, they are also found in plankton (CARLIN 1943).

2. Diversity

According to WILLIAMSON (1974), diversity increases with distance from toxic pollution. In some cases the same effect may be observed with pollutants that are not clearly toxic. Diversity may also increase with the stability of the environment; ODUM (1971) suggests that diversity correlates better with the stability than the productivity of communities.

Food chain relationships affect diversity in some communities. PAINE (1966) observed that if the predation on the dominant prey population increases, this increases diversity, because it prevents any species from becoming dominant. In communities where nutrient chains are long and form complex webs, there are no mass occurrences of any organisms, diversity is high. These communities are much more stable than communities with low diversity (cf. MARGALEF 1968).

The relation between the degree of eutrophication and zooplankton diversity was studied by comparing primary production and the mean diversity index (Fig. 13). According to GRANBERG (1973), after primary production has reached the level of 200-250 kg C_{ass}/ha x year, diversity begins to decrease. The same is evident in Fig. 13, which shows that the changes in the diversity of phyto- and zooplankton are very similar.

Zooplankton species diversity declined rapidly, when the E/O species ratio reached about 1.5-1.7 (Fig. 14). When pollution had exceeded this limit, the species composition seemed to change much more monotonically, to a community of polluted water. This E/O level was equivalent to a total P concentration of 32-35 µg/l, and primary production of 230-270 kg C_{ass}/ha x year (without inhibitory effects). GRANBERG (1973) has suggested that if the primary pro-

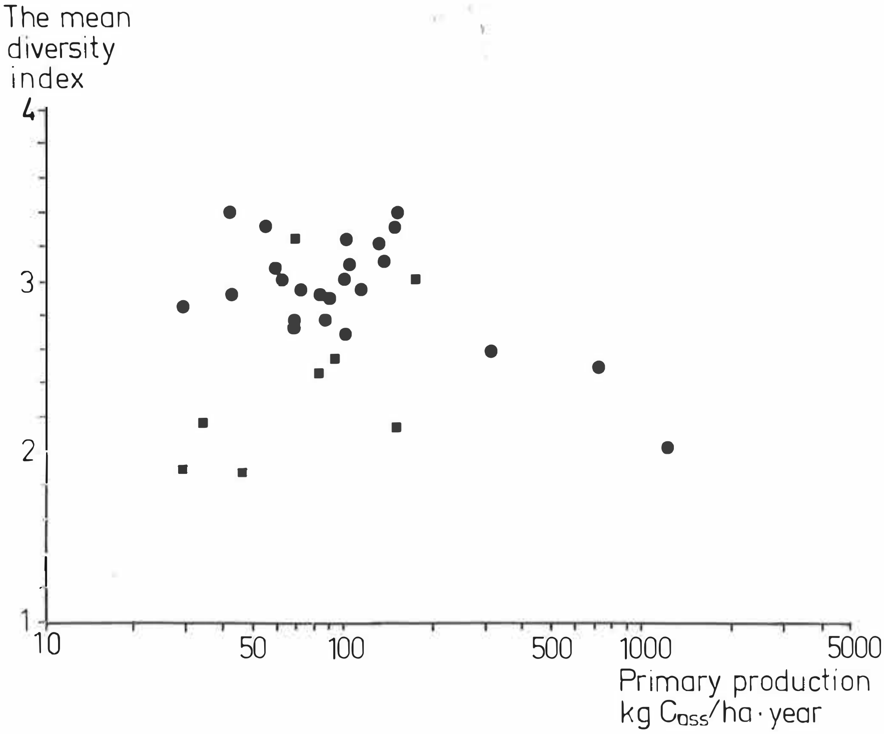


Fig. 13. The mean diversity index of zooplankton plotted versus primary production (■ = Tiirinselkä, 655-657, and Lehtiselkä, 675, ● = other stations).

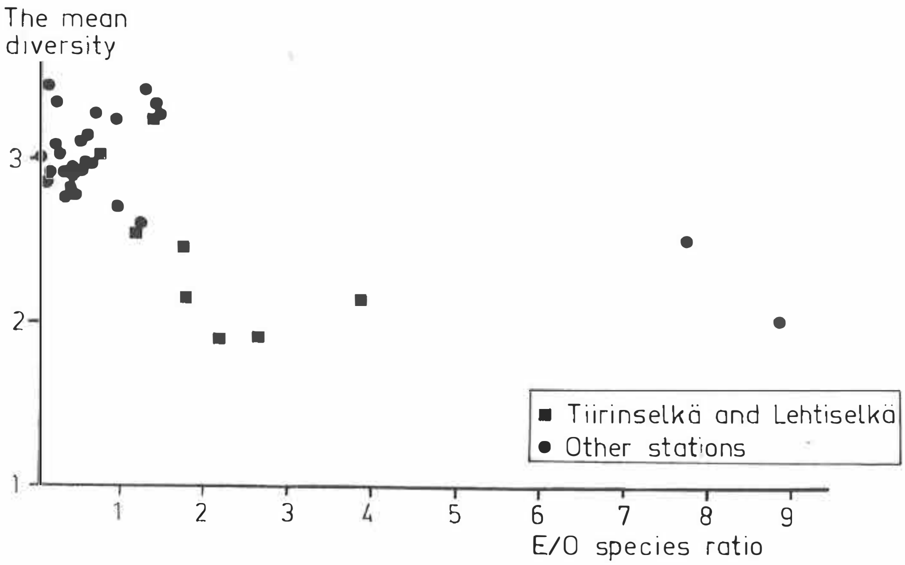


Fig. 14. The mean diversity index of zooplankton plotted versus the E/O species ratio in Jyväsjärvi and Päijänne in June-Sept. 1969-1972.

duction continues to grow over the limit of 250 kg C_{ass}, it may lead to "racing eutrophication". The zooplankton results seemed to support this opinion. A E/O species ratio of 1.5 to 1.7 represented the situation when the hypolimnion became oxygenless (see p.39) and phosphorus passed into solution from the sediment.

B. Effects of planktivorous fish on the zooplankton

Many studies have been made of the effects of predation by fish on zooplankton. In alewife (*Alosa pseudoharengus*) lakes in North America large prey species (e.g. *Daphnia galeata, D. retrocurva, Leptodora kindti, Limnocalanus macrurus, Epischura lacustris*) became very rare as a result of intense predation by *Alosa*, and small or medium sized planktonic crustaceans (*Bosmina longirostris, Ceriodaphnia*) increased in abundance (BROOKS & DODSON 1965, WELLS 1970, BROWN 1972, WARSHAW 1972).

In Southern Konnevesi, with a dense population of vendace, the relative frequency of large zooplankton species (e.g. *Leptodora kindti, Bythotrephes longimanus, Limnocalanus macrurus* and *Heterocope appendiculata*) was lower and that of small species (less than $10^6 \mu m^3$) was higher than in Northern Konnevesi, where the predation pressure of vendace was weaker (HAKKARI 1972 b, 1972 c).

The introduction of arctic char (*Salvelinus alpinus* (L.)) and whitefish (*Coregonus* sp.) into some North Swedish lakes caused the disappearance of large and easily available zooplankton species in a few years. Later, only small species were found in the fish stomachs (KARLSSON & NILSSON 1968, NILSSON & FILIPSSON 1971). In a North American lake, *Daphnia pulex* disappeared in four years after the introduction of *Osmerus mordax* (REIF & TAPPA 1966). According to KAJAK *et al.* (1972), stocking with carp and crucian carp lowered the proportion of large herbivores in the zooplankton, but increased the proportion of the rotifers, *Bosmina longirostris* and *Ceriodahpnia*.

Many authors have reported that predation by fish has marked effects on the zooplankton of fish ponds (e.g. GRYGIEREK 1962, HRBÁČEK & HRBÁČKOVA-ESSLOVÁ 1966, HAKKARI & DAHLSTRÖM 1969, HALL *et al.* 1972). All of them have made the same observation: Large zooplankters were removed and the relative frequency and production of rotifers, copepod nauplii and copepodids increased. HALL *et al.* (1972) observed that predation by sunfish affected zooplankton diversity but influenced production only at lower nutrient levels.

In 1970, the abundance of *Daphnia pulex* and large individuals of *Daphnia galeata* in Central Päijänne indicated that predation pressure was low. The reduction of these species in the following years may have been connected with the immigration of perch and other fishes, when the hypolimnion became oxygenated. According to test fishings, in 1973 perch was the most abundant fish in the pelagial of Lehtiselkä and Tiirinselkä (HAKKARI 1975 b). In Tiirinselkä, roach was also important. These species may shift to the pelagial if nutrient conditions are favourable (high zooplankton production) (cf. KRIEGSMANN 1955, NÜMANN 1964, ROTH & GEIGER 1972). However, *Limnocalanus macrurus* suffered more from pollution than from predation by fish; it became much commoner in Tiirinselkä and Lehtiselkä 1970-1972.

The increase in the population of vendace in 1969-1971 seemed to cause changes in the zooplankton composition and production in Tehinselkä (Table 26).

Naturally, the effect of other environmental factors besides predation e.g. competition for food, may cause deviations from the general (cf. WEGLENSKA 1971), but the presence of planktivorous fish was seen to cause an increase in the production of the avoided species *Holopedium gibberum*, *Daphnia cristata*, *Eubosmina* spp., and *Cyclops* spp., and a decrease in that of the preferred species *Daphnia galeata*, *Bythotrephes longimanus*, and *Limnocalanus macrurus*. The production values for *Leptodora kindti* are rough, owing to the small numbers of individuals. The production of highly preferred species (e.g. *Leptodora*, *Bythotrephes*, and *Limnocalanus*) was evidently nearly totally consumed by fish, which lowered the biomass of these species. The consumption of *Bythotrephes* was overestimated in scrutinizing the stomach contents, since the indigestible spines remained in the stomach longer than other food components. The use of a digestion time of 12 hr to calculate the consumption of *Bythotrephes* by vendace and smelt gives a value many times in excess of its production.

C. Relations between different trophic levels

1. Phytoplankton and zooplankton

Blue-green algae, which may have an inhibitory effect on zooplankton (cf.

Table 26. The productions(kg/ha, wet wt) of the most important plankton crustaceans compared with the "electivity index" of IVLEV (1961) + = preferred, - = avoided.

	Electivity	1969	1970	1971
Holopedium gibberum	-	91	64	142
Daphnia cristata	-	42	64	157
D. galeata	+	80	20	34
Eubosmina spp.	-	57	95	100
Bythotrephes longimanus	+	40	7	8
Leptodora kindti	+	4	-	30
Limnocalanus macrurus	+	44	22	9
Eudiaptomus spp.	-	150	162	86
Cyclops spp.	-	50	87	109
Σ of preferred species		168	49	81
Σ of avoided species		390	472	594

PEJLER 1964) were not important in the phytoplankton biomass in Jyväsjärvi and Päijänne. Thus, the correlation between primary production and zooplankton biomass was significant (r = 0.58^{xxx}; Fig. 15), when the values of Tiirinselkä and Lehtiselkä (pollution by pulp and paper mill wastes) were excluded. In those waters, the production of zooplankton was high, but primary production was generally inhibited by the wastes (e.g. GRANBERG 1975). The correlation between primary production and the production of herbivorous zooplankton was high (r = 0.70^{xxx}; Fig. 16).

According to GLIWICZ & HILLBRICHT-ILKOWSKA (1972) microfiltrators and sedimentators which consume mainly bacteria and detritus, are dominant in eutrophic lakes. In oligotrophic lakes, macrofiltrators are dominant, and they feed

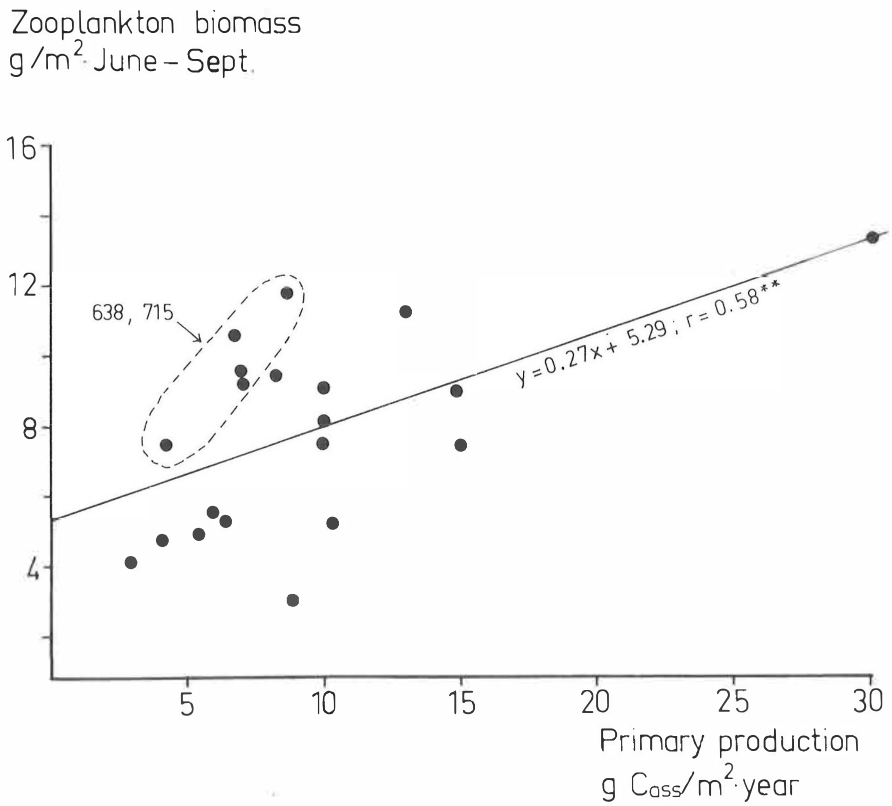


Fig. 15. The correlation between primary production and the mean zooplankton biomass in Päijänne. The values of Tiirinselkä (655-657) and Lehtiselkä (675) excluded. The effect of wastes from the sulphite pulp mill is evident in Souselkä (638) and Judinsalonselkä (715).

mainly on nannoplankton algae, in oligotrophic lakes, the nannoplankton production is chiefly limited by grazing zooplankters, while in eutrophic lakes other factors seem to be more important. In the eutrophic areas of Lake Päijänne the ratio of phytoplankton biomass to zooplankton biomass rose more rapidly during May-June than in the oligotrophic part of the lake. This agrees with the results of GLIWICZ & HILLBRICHT-ILKOWSKA.

According to SCHUMACHER (1958), a carbon content of 10 g C in plant cells can be assumed to represent about 20 g dry weight. The caloric value of this biomass of algae is ca. 100 kcal (cf. CUMMINS & WUYCHECK 1971). If we use the fuel value of carbon we obtain a caloric value of 94 kcal. A hundred grams of zooplankton (wet wt) is equivalent to 50-60 kcal (WINBERG 1966, SHERSTYUK 1971), and, thus, 170 g of zooplankton (wet wt) is equivalent to a plant C content of 10 g.

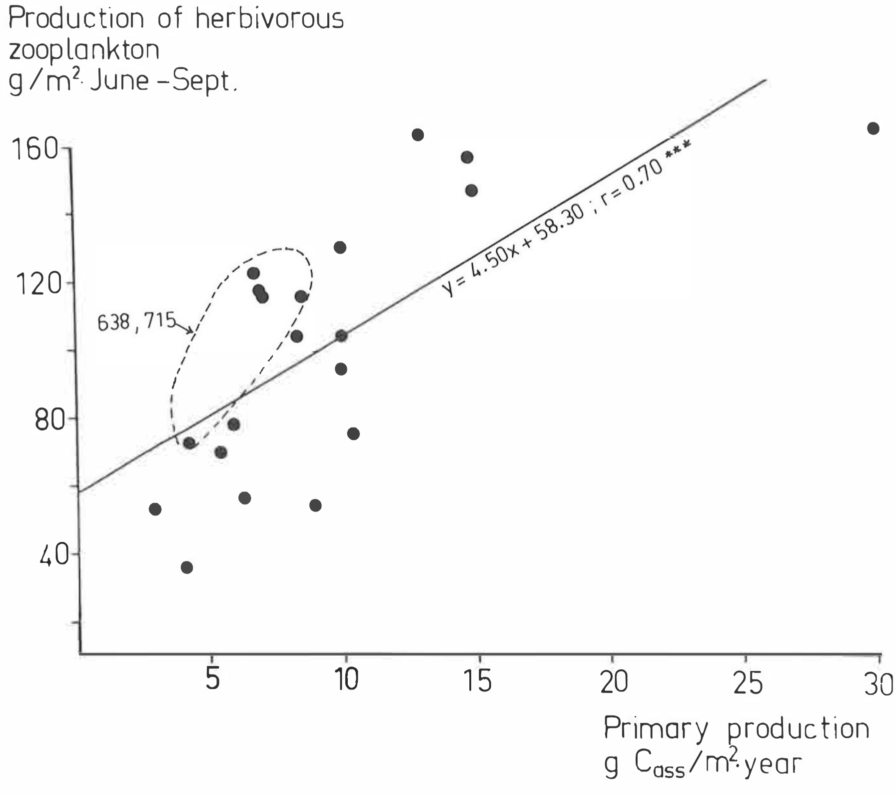


Fig. 16. The production of herbivorous zooplankton plotted versus primary production in Päijänne. The values of Tiirinselkä (655-657) and Lehtiselkä (675) excluded (see Fig. 14).

In most cases, the production of herbivorous zooplankton was ca. 50 % of the net primary production (Fig. 15). In Lake Pääjärvi, South Finland, the extracellular production of algae, which is not included in measurements made by the 14 C method, was ca. 5-20 % of the net primary production (ILMAVIRTA *et al.* 1974). If we take this into account in Päijänne, the production of herbivorous zooplankton was still at least 42 % of the net primary production. This is a surprisingly large percentage; BRYLINSKY & MANN (1973) reported that in the lakes studied for the International Biological Programme, the herbivorous zooplankton production averaged 13.7 % of the gross primary production. However, in oligotrophic Pääjärvi the production of herbivorous zooplankton was 49 % of the net primary production (SARVALA 1974).

If the assimilation of herbivorous zooplankton is 60-80 % of the food consumption and the net growth efficiency (production: assimilation) is 0.4 (WINBERG *et al.* 1972), the food consumption is about 3-4 times as great as the net production (HILLBRICHT-ILKOWSKA *et al.* 1972). Accordingly, in Päijänne the food consumed by the herbivorous zooplankton was about 150 % of the net primary production.

GRANBERG (1975) estimated the production of bacteria in different parts of Päijänne from dark assimilation measured by the 14 C method, (cf., e.g., KUZNETSOV & ROMANENKO 1967). Bacterial production was clearly higher than phytoplankton production throughout the lake, and especially in Tiirinselkä and Lehtiselkä. Thus, allochthonous detritus and bacteria form an important part of the diet of herbivorous zooplankton not only in the eutrophicated and polluted waters, but also in the oligotrophic parts of the lake. A rough estimate made from the vertical distribution of zooplankters indicates that in Tiirinselkä and Lehtiselkä detritus and bacteria may contribute up to 90 % of the energy intake of zooplankton (cf. HAKKARI 1975 a).

2. Herbivorous and carnivorous zooplankton

The nature of predation

Predation may be divided into active and passive predation (DODSON 1975). Active predation means the predation of species with griping limbs; passive predation is that practised by filtrators or sedimentators which use zooplankton food. As observed by DODSON (1975), zooplankton associations are not organized into a simple set of trophic levels. Most species eat plants, herbivores, and other predators, and are preyed upon in their turn.

The zooplankton predators that consume mostly Protozoa and Rotatoria serve as a link between the herbivorous zooplankton and fish (WINBERG 1966, SOROKIN 1972). The zooplankton that feeds on crustaceans suitable for planktivorous fish, "wastes" energy in the food chain between primary production and fish.

The predation by zooplankton may be highly selective, excluding certain populations. This favours the survival sub-optimal prey populations, which may be the preferred food of another predator (DODSON 1970). This interaction can also occur in complex communities including vertebrate planktivores.

The interaction in Päijänne

The correlation between the production of herbivores and carnivores in Päijänne was highly significant ($r = 0.73^{xxx}$; Fig. 17). The ratio of carnivore to herbivore production was 25 % in eutrophic areas, and 32 % in the oligotrophic part of the lake. Similar values have been reported from Lake Pääjärvi, southern Finland (22 %, SARVALA 1974). In Lakes Krivoe and Krugloe, in the northwestern part of the USSR, these ratios were 15 % and 18 % (ALIMOV & WINBERG 1972).

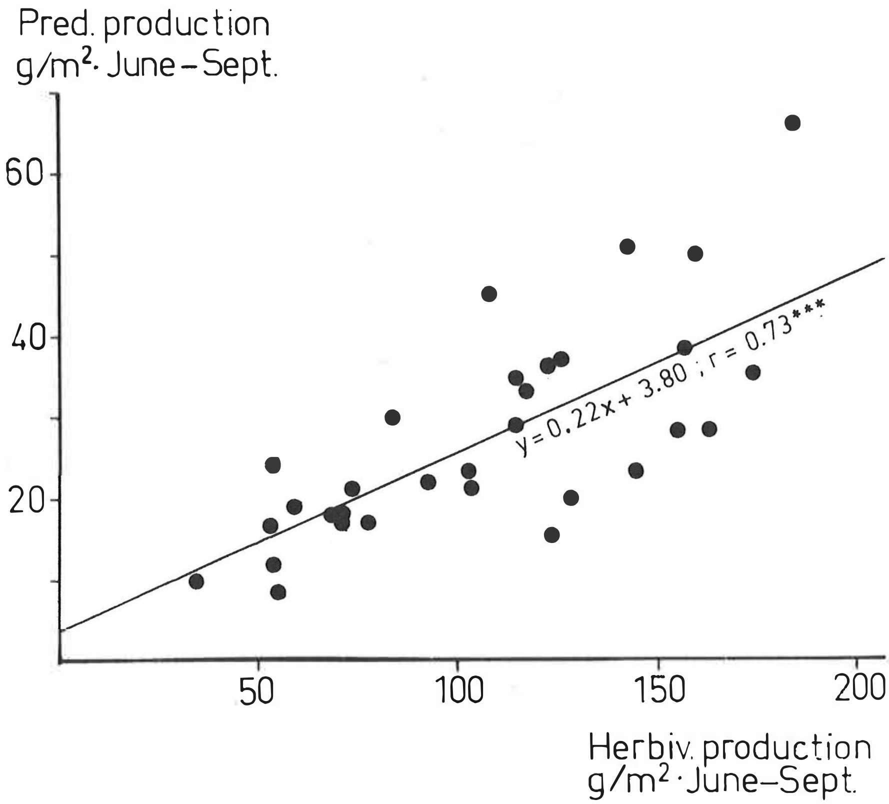


Fig. 17. The production of predaceous zooplankton plotted versus the production of herbivorous zooplankton in L. Päijänne.

ALIMOV & WINBERG (1972) calculated that in northern lakes the food consumed by zooplankton predators is ca. four times their production. According to this estimate, the herbivorous production in Päijänne is wholly consumed by zooplankton predators. However, the calculations did not include the production of protozoans.

3. Zooplankton fish

Feeding of planktivorous fish

A planktivorous fish eats food items that it can see (BROOKS 1968). SBIKIN (1974) demonstrated experimentally that in the plankton feeder *Leucaspius lineatus* (Heck.) vision was the only sense used in obtaining food. Individuals 40-70 mm long could feed on large *Daphnia* in illumination of some hundredths of a lux. In Lake Mälaren, Sweden, this illumination was measured by NORTHCOTE & RUNDBERG (1970) at a depth of 1-3 m at midnight in June and at ca. 20 m at midday.

Some investigators (e.g. JÄRVI 1919) have supposed that the migration of planktivorous fish to the near-surface water layer in the evening is connected with the movements of zooplankton. However, the most important prey species show little vertical diel migration, especially in humous water (JÄRNEFELT 1958). In the present study, vendace and smelt were observed to change their food items when they rose to the near-surface water layer in the evening. The changes in the diet of vendace are presented in Table 27.

Table 27. The food composition (% wet wt) in the anterior and posterior part of the stomach of vendace in Tehinselkä on 26.VI.1972.

Part of stomach	anterior		posterior	
Food items	$\bar{x}$	Range	$\bar{x}$	Range
Diaphanosoma	0.33	0.0 - 1.6	0.00	
Holopedium	67.05	35.0 - 89.2	18.09	4.7 - 40.9
Daphnia	1.83	0.0 - 4.7	1.91	0.0 - 4.5
Eubosmina	19.59	1.9 - 39.3	52.99	28.9 - 74.3
Bythotrephes	10.45	0.0 - 20.5	26.58	0.0 - 66.2
Eudiaptomus	0.11	0.0 - 0.7	0.00	
Cyclops	0.24	0.0 - 0.8	0.44	0.0 - 0.8

Holopedium gibberum, an epilimnetic species, had its maximum in Päijänne at a depth of 0-5 m. *Eubosmina longispina obtusirostris* has its maximum in the thermocline or hypolimnion (e.g. HAKKARI 1969, 1970 b). The fish in Table 27 fed mainly on *Eubosmina* in the afternoon and concentrated on *Holopedium* after rising to the surface layer. Similar observations were made on the feeding of smelt and whitefish. The reason for the migration of the fish is evidently the decrease in illumination before sunset; the vendace moved towards the surface in order to see the prey. This agrees well with the results of NORTHCOTE & RUNDBERG (1970).

AIRAKSINEN (1967) observed the importance of light, too. He reported the vendace in the Sound of Varmavirta, Eastern Finland, drove downstream by day, following the zooplankton, but swam against the current at night when they could no longer see their prey.

Food selection of planktivorous fish

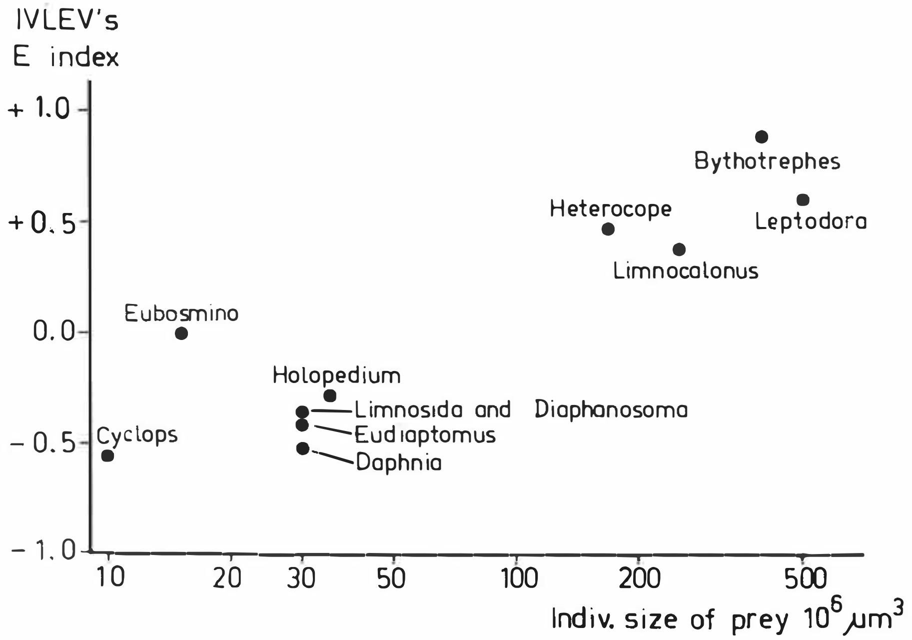
BROOKS & DODSON (1965) and HRBÁČEK & HRBÁČKOVA-ESSLOVÁ (1966) reported that planktivorous fish select large prey species (size-selectivity predation). This was also observed in Päijänne (Fig. 18). Vendace preferred the large species *Leptodora kindti* and *Bythotrephes longimanus*. In general, the only exception was *Eubosmina* spp. which, in spite of its small size, was preferred to *Holopedium*.

ZARET (1972) has given more information about the selection of prey. He observed that the size of the eye pigmentation area in *Ceriodaphnia cornuta* affected the chance of being eaten. When animals ingested particle of Indian ink, so that a pigmented area was produced in the area of the stomach and hepatic caecum, the fish ate them faster than other prey. Thus, in zooplankters with a transparent body, the size of pigmented areas is important.

The speed of movement of prey animals may also affect the diet of planktivorous fish. For instance, *Cyclops* is too agile a prey for *Chaoborus* and *Leptodora* (DODSON 1974 b), and possibly also for fish, judging from the small proportion of *Cyclops* in the diet of vendace, smelt and whitefish during summer. *Eudiaptomus* showed the same tendency. Both genera were rare in the stomachs of planktivorous fish but numerous in the plankton. *Eubosmina* moves more slowly and is easily caught by predators.

Food objects measuring less than 0.4 mm were not usually taken by the fish dissected in this study. Larger prey was chosen, according to its visibility (size), abundance, and agility.

Fig. 18. The dependence of IVLEV's "electivity index" on the size of zooplankton individuals eaten by vendace in Päijänne, Konnevesi, and Keitele.



Fish larvae naturally select small prey. Perch fingerlings under 7 mm long feed only on rotifers and copepod nauplii, and fingerlings measuring 7-20 mm prefer small Cladocera and Copepoda (FENYUK 1960, ref. CHIKOVA 1970). According to TSUNIKOVA (1970), the food of young Azov roach consisted of copepodid and naupliar stages of copepods, rotifers, small chironomid larvae (0.3 mm) and Ostracoda (0.2 mm). WONG & WARD (1972) noted that yellow perch fry smaller than 18 mm could not eat *Daphnia pulex* measuring more then 1.3 mm. GALBRAITH (1967) reported that adult yellow perch did not eat zooplankters smaller than 0.6 mm.

NYRÖNEN (1975) examined the diet of perch in Tehinselkä, Päijänne, on 26 June 1972. Of the fish measuring 12-17 cm, 20 % had fed on fish fingerlings and 80 % on crustaceans and insect larvae. The mean length of the fish which had fed on plankton and insect larvae was 13.8 $\pm$ 1.1 cm. *Bythotrephes longimanus* dominated in the stomach contents; its contribution to the wet weight of the food was 53.4 %, that of dipteran larvae was 23.6 %. *Eubosmina longispina obtusirostris* constituted 15.5 % of the stomach contents. *Bythotrephes* and *Eubosmina* were highly preferred. Similarly, CHIKOVA (1970) found that in the Kuybyshev Reservoir perch under 26 cm feed primarily on zooplankton. GRÖNBERG & WAHLBERG (1971) observed in Malingsbo-Kloten, Sweden, that zooplankton formed 62.7 % of the stomach contents of perch measuring 10-15 cm, and 45.9 % in the size class 15.5-20 cm.

In Varmavirta in November, vendace fingerlings fed primarily on rotifers, *Eubosmina*, and copepodids (AIRAKSINEN, 1967). The older age classes fed mainly on *Eubosmina* and copepods, the latter prey item being rather abundant in the stomach contents. This result seems to differ from the observations of the present study.

According to BERG & GRIMALDI (1966) and DE BERNARDI & GIUSSANI (1974), the principal food of whitefish in Lago Maggiore is cladocerans. Although apparently scarce in the lake, *Bythotrephes longimanus* and *Leptodora kindti* were very important food items during summer and autumn. Copepods were eaten mainly in winter. LAMPERT (1971) and NILSSON & PEJLER (1973) noted that small *Bosmina (Eubosmina)* and *Holopedium* were important as food for whitefish.

The present observations about the food chosen by whitefish agreed well with the reports in the literature. *Bythotrephes* was greatly preferred by *Coregonus lavaretus* in Tehinselkä and Asikkalanselkä. From the abundance of *Bythotrephes* in the plankton and the stomach, it was estimated that the whitefish must search a water volume of some tens of cubic meters in order to obtain the *Bythotrephes* consumed.

The diet of adult smelt in Lake Päijänne seemed to differ from that of the American smelt *Osmerus mordax*; PRICE (1963) and FERGUSON (1965) found that adult smelt feed mainly on young smelt. However, REIF & TAPPA (1966) observed that they also feed on zooplankton. Only one fish larva was found in a smelt stomach in the present material. Even large individuals (length 15-20 cm, investigated in addition to the material of this study) had mainly fed on other food items than fish, e.g. *Mysis relicta* and *Pallasea quadrispinosa*.

The similarity of diets of planktivorous fish

In spring, when the amount of food in the stomachs was small, the mean similarity values for the individuals in a sample were usually rather low (Table 24). The values were generally higher in vendace than in smelt, which seemed to be greater "specialists" in the selection of food.

The food similarity between vendace and smelt in the same catch was always low, never more than 35.2 %. The main food item shared by them was chironomous larvae. Since Chironomidae were not eaten in summer, their general significance as food for smelt and vendace was small. In the whole material, ca. a sixth of the food biomass was the same in vendace and smelt. The diets of both included *Bythotrephes longimanus*, *Holopedium gibberum*, *Eubosmina longispina obtusirostris*, *Daphnia cristata*, and *Leptodora kindti*. The main food items of vendace were *Bythotrephes*, *Holopedium*, *Eubosmina longispina obtusirostris*, and *Limnocalanus*, those of smelt *Mysis relicta*, *Heterocope appendiculata*, and *Eubosmina longispina obtusirostris*. This indicates a tendency to occupy different niches.

Evidence of this tendency was observed in Southern Päijänne in 1972, when vendace and smelt were fairly frequent. In Northern Päijänne, where vendace was scarce, the main food items of smelt in summer were *Leptodora kindti* and *Mysis relicta*. *Leptodora* formed a larger proportion of the plankton in Poronselkä than in Southern Päijänne. As vendace was caught only once, in September, it was difficult to study the similarity between the diets of vendace and smelt in Poronselkä. *Leptodora* may also be an important food item for vendace.

According to NYRÖNEN (1975), in Tehinselkä in Southern Päijänne, the index of food similarity between planktivorous perch and vendace was 25.1 %. The similarity was largely due to *Eubosmina longispina obtusirostris* and *Bythotrephes*. The similarity index between perch and smelt in the present study is as high as 42.2 %, mainly owing to *Bythotrephes* and *Eubosmina longispina obtusirostris*. Although the material is small, it suggests that perch may be a significant competitor of other planktivorous fish, since it is abundant throughout the lake.

If two planktivorous species have similar diets and consume all the available food, they must be competing for food. But, as NILSSON has pointed (e.g. NILSSON & PEJLER 1973), segregation into niches takes place as the species overgraze the food supply. Thus, even a low index of food similarity may mean competition for food. In Päijänne, vendace and smelt seemed to compete for zooplankton, but as vendace did not eat *Mysis relicta* in Lakes Keitele and Konnevesi, where the abundance of smelt was low, they were evidently not competing for *Mysis*.

Competition for food affects the size of the year classes mainly during the first months of the warm season, when all the species are eating rotifers and juvenile Crustacea (cf. LINDSTRÖM 1962, BRAUM 1967, ANDERSSON & SMITH 1971). If competition for food occurs later in the season, growth is slow and fingerlings are more likely to be included in the food of perch, etc. (LINDSTRÖM 1962).

Rate of food consumption

Among other factors, temperature and size of the fish affect the rate of gastric digestion. In pike-perch fry weighing 1.1 mg, digestion took 2 hr 25 min at 15-16 °C in fry weighing 8-25 mg it took 4 hr (TSUNIKOVA 1970). In perch measuring 12.5 cm, digestion took ca. 16 hr (CHIKOVA 1970).

The temperature used in this work, 13.5-16.0 °C, was close to the mean summer temperature of the epilimnion in large lakes in Central Finland, e.g. Päijänne (cf. MÄKINEN & KORTELAINEN 1974). According to the observations of, e.g., JÄRVI (1919) and NORTHCOTE & RUNDBERG (1970), in summer vendace live primarily in the metalimnion or close beneath it. In the evening they rise to the near-surface water layer to feed. The mean temperature of their summer biotope is thus only a little lower than that used in the present experiment.

Most of the vendace were caught during their feeding in the evening. The feeding seemed to have been interrupted because the stomach was not full. According to observations made in Lake Päijänne, the stomach fullness index was ca. 200‱ when the stomach was filled. CHIKOVA (1970) give an index of 233 ‱ for perch intensively in Kuybyshev Reservoir in July. The relation between the volume of the stomach and the weight of the fish thus seems to be approximately the same in vendace and perch.

The mean digestion time can be used to estimate the daily food consumption of a fish. If the stomach fullness index was constantly as great as was observed in this work (mean ca. 77 ‱ in Päijänne and Keitele), the daily food consumption in summer would be 2.5 times this volume. Thus the daily food consumption of a vendace in Keitele would be 1.9 % of body weight. This is smaller than the food consumption reported for perch by CHIKOVA (1970) - 3.1 % of body weight at 21.5 °C, and much smaller that that of 0 group herring, *Clupea harengus* (L.), off the west coast of Scotland in August - 5.3 % of body weight at 12.0 °C (DE SILVA 1973). According to DE SILVA & BALBONTIN (1974), the mean food intake of young herring varied between 8.1 and 12.6 % of body weight at 14.5 °C, and between 3.5 and 5.0 % at 6.5 °C. When fish were fed 1.3 % of body weight/day at 6.2 °C, growth was about 0.2 % of body weight/day. DE SILVA & BALBONTIN attribute the relatively high food intake to the active life of this pelagic fish.

Table 28. The growth of the 2+ and 1+ age classes of vendace in Poronselkä, Tehinselkä and Asikkalanselkä in summer 1972.

Age 2+	Length, mm		Length increase		Weight, g		Weight increase	
	May	Sept.	mm	%	May	Sept.	g	%
Poronselkä	156 ± 3	191 ± 4	35 ± 1	22.4 ± 0.9	28.2 ± 1.6	50.7 ± 3.3	22.5 ± 2.0	79.7 ± 5.9
Tehinselkä	157 ± 2	193 ± 2	36 ± 1	22.9 ± 0.6	28.2 ± 1.1	54.5 ± 1.3	26.3 ± 0.7	93.2 ± 3.9
Asikkalanselkä	148 ± 1	190 ± 1	42 ± 0.3	28.3 ± 0.2	24.0 ± 1.7	53.0 ± 1.7	29.0 ± 2.0	120.8 ± 13.8
Age 1+								
Poronselkä	119 ± 2	153 ± 2	34 ± 1	28.5 ± 1.0	11.0 ± 0.6	28.0 ± 1.1	17.0 ± 0.9	154.5 ± 11.4
Asikkalanselkä	124 ± 2	179 ± 1	55 ± 1	44.3 ± 1.3	12.3 ± 0.9	46.8 ± 1.1	34.5 ± 0.8	280.4 ± 15.1

Comparison of the results from Keitele with the growth of vendace in Päijänne shows that food intake was probably higher in Päijänne (Tables 28 and 29). If we use the food coefficient of 8 between zooplankton and fish (cf. PHILLIPS 1972, WINBERG *et al.* 1972), the daily food intake will be 5.8-7.7 % of body weight in 1+ group and 3.8-5.9 % in 2+ group vendace. The present material is small, but the observation that the food intake of the 1+ group was evidently greater than that of the 2+ group agrees with the results given by PHILLIPS (1972).

Relative growth was greatest in Asikkalanselkä and smallest in Poronselkä. This indicates that Asikkalanselkä had a low population density and little competition for food. The low growth rate in Poronselkä cannot be attributed to competition for food, because the biomass and production of prey species were high. The reason was apparently stress caused by low contents of oxy-

Table 29. The consumption of zooplankton by an individual in the age classes 1+ and 2+ in June-Sept. 1972 and the daily consumption of food as % of body weight in vendace in Päijänne.

	Age 1+		2+	
	g/June-Sept.	% of body weight/day	g/June-Sept.	% of body weight/day
Poronselkä	136	5.8	180	3.8
Tehinselkä	-	-	210	4.1
Asikkalanselkä	276	7.7	232	5.0

gen in the meta- and hypolimnion, and, perhaps, by substances released in wastes.

4. Problems encountered in evaluating the interrelationships in the pelagic biota

When biomass is determined from the average volumes of zooplankton species,it must be remembered that the size of individuals may vary with the lake and season (e.g. the volume of *Eudiaptomus graciloides*, see NAUWERCK 1963 and NAULAPÄÄ 1966). Further studies on the volumes of different stages are needed. The biomass can be measured best from the dry weight, a method which is generally used by American investigators (e.g. CUMMINS & WUYCHECK 1971), but needs a large material and is very laborious.

The development time of different stages in different temperatures needs further investigation. Since studies on zooplankton production are rather few in Finland (HAKKARI 1970 a, 1970 b, 1972 a, 1973, 1975 a, POIKOLAINEN 1970, TUUNAINEN *et al.* 1972, PIIPPONEN 1974, LATJA 1974, and ELORANTA 1975), estimates of the production of different zooplankton species must be partly based on data from the literature, obtained in conditions not always comparable with those in large lakes in Finland (cf. the development time of *Eudiaptomus* in Lake Esrom, Denmark, [BOSSELMANN 1975] and in Bodensee [ELSTER 1954]).

More information is needed about the production of Protozoa, since zooplankton predators feed on protozoans and change their energy to a form which is suitable for fish. Observations in the literature suggest that Protozoa may make an important contribution to the total production of zooplankton (cf. ALIMOV & WINBERG 1972).

The degree of predation by zooplankton species depends closely on the abundance of *Asplanchna* and *Cyclops*. As a result of the food selectivity of these predators, the production of zooplankton available for fish, can vary greatly.

Direct measurement of the carbon contents of different species and stages of zooplankton give the exact value of zooplankton as an energy source of fish. Such measurements, performed by a high temperature combustion method, will decrease the errors in regard to, e.g., *Asplanchna* spp. (cf. LATJA & SALONEN, in press).

The remains of plankton crustaceans in the stomach of fish may give an incorrect picture of the real food composition (e.g. *Bythotrephes*). But if this source of error can be eliminated, it will be possible to estimate, the relative predation by fish. The rate of food consumption by fish can be investigated be means of "in situ" incubations, which were used in this study, but this method is very laborious. Another possibility is to evaluate the predation from the zooplankton composition (large species/small species). This is best done in oligotrophic lakes, where eutrophication has not affected the species composition of the zooplankton.

VI. Summary

About 1000 zooplankton samples were collected from Lakes Päijänne and Jyväsjärvi in 1969-1972. The feeding of planktivorous fish was examined on 146 vendace, 88 smelt, and some whitefish taken from Lakes Päijänne, Keitele, and Konnevesi.

The zooplankton taxa identified in the material from Jyväsjärvi and Päijänne numbered 107. Ca. 70 of them can be considered euplanktonic. The number of taxa was greatest in June-September, smallest when the lakes were ice-covered. In all seasons, the majority of taxa were referred to Rotatoria. The number of taxa was greatest in eutrophicated Northern Päijänne, smallest in the polluted waters of Jyväsjärvi and Tiirinselkä, and in oligotrophic Southern Päijänne. The mean diversity index decreased repidly as the total phosphorus concentration rose above 32-25 µg/l.

The following taxa correlated positively and significantly with eutrophication: *Arcella* sp., *Trichocerca capucina*, *T. pusilla*, *Keratella cochlearis* f. *tecta*, *K. cochlearis* f. *hispida*, *K. quadrata*, *Polyarthra euryptera*, *Ceriodaphnia quadrangula*, *Bosmina longirostris*, *Chydorus sphaericus*, and *Leptodora kindti*. Eutrophicated waters were avoided by *Conochilus hippocrepis* and *Bythotrephes longimanus*. The following taxa showed a significant preference for water polluted by the wastes of a pulp mill and a paper mill: *Keratella hiemalis*, *K. ticinensis*, *Anuraeopsis fissa*, *Filinia longiseta*, *Bosmina longirostris*, and *Chaoborus flavicans*, and *Daphnia pulex* was found solely in polluted water. Significant avoidance of polluted water was shown by *Trichocerca rousseleti*, *Gastropus stylifer*, *Asplanchna priodonta*, *A. herricki*, *Holopedium gibberum*, *Eubosmina coregoni*, *E. longispina longispina*, and *Limnocalanus macrurus*.

The zooplankton biomass was greatest in Jyväsjärvi, and in Northern and Central Päijänne, lowest in Asikkalanselkä. The following biomasses were obtained for the 0-10 m layer in June-September: Asikkalanselkä 0.4 g/m^3, Tehinselkä 0.5 g/m^3, Tiirinselkä 1.2 g/m^3, Poronselkä 1.1 g/m^3, Jyväsjärvi 3.3 g/m^3. The differences were smaller between the weighted biomass means (g/m^2 x June-Sept.): Asikkalanselkä 4.9 g/m^2, Tehinselkä 6.5 g/m^2, Tiirinselkä 8.4 g/m^2, Poronselkä 10.5 g/m^2, Jyväsjärvi 23.2 g/m^2. The winter biomass was usually less than 10 % of the summer biomass, but in polluted Tiirinselkä it was 27 %.

The production of herbivores averaged 48 kg (Asikkalanselkä) - 338 kg (Jyväsjärvi) per ha in June-September, that of carnivores 12 kg (Asikkalanselkä) - 78 kg (Jyväsjärvi).

When the values for Tiirinselkä and Lehtiselkä were excluded because of pollution by sulphite pulp and paper mill wastes, a significant correlation was observed primary production and zooplankton biomass ($r = 0.58^{xx}$). The correlation between primary production and the production of herbivorous zooplankton was highly significant ($r = 0.70^{xxx}$). In most cases, the production of herbivorous zooplankton was ca. 50 % of the net primary production.

Bacteria seemed to form a surprisingly large proportion of the food consumed by zooplankton. A rough estimate suggests that in the polluted water bodies of Tiirinselkä and Lehtiselkä detritus and bacteria may contribute as much as 90 % of the energy intake of zooplankton. In the other basins this proportion was lower.

Planktivorous fish rarely took food items measuring less than 0.4 mm. Larger species chosen, depending on the visibility (size), abundance, and agility of the individuals. The large species *Leptodora kindti* and *Bythotrephes longimanus* were preferred in summer. Other plankters significant in the diet of vendace were *Limnocalanus, Holopedium, Eubosmina,* and, in some waters, *Heterocope appendiculata.* In spring chironomid larvae and Cyclopidae were also taken.

In Poronselkä in summer *Leptodora* and *Mysis relicta* were important food items of smelt. In other areas *Heterocope appendiculata* and *Eubosmina* spp. were important besides *Mysis.*

Vendace and smelt were observed to change their food items when they rose to the near-surface water in the evening. The reason for their upward migration seemed to be the decrease in light in the deeper water layers.

In addition to vendace and smelt, the fish feeding on zooplankton in the pelagial of Päijänne include whitefish, perch and evidently roach.

Some experiments were made on the duration of gastric digestion in vendace in Keitele. Eighty per cent of the stomach contents was digested in 12 hours. The fish thus consumed 1.9 % of their body weight per day. If the food coefficient between zooplankton and fish is assumed to be 8, the daily food consumption of vendace of group 2+ in Päijänne was 3.8-5.0 % of body weight. Consumption by fish affected the composition of the zooplankton. In Southern Päijänne in 1972, most of the production of *Leptodora, Bythotrephes,* and *Limnocalanus* was consumed by fish. In areas where vendace was lacking, the large species (*Daphnia pulex, D. galeata* and *Leptodora kindti,* sometimes *Limnocalanus macrurus* and *Bythotrephes longimanus*) were more numerous than in oligotrophic areas, where predation by vendace was heavy.

Acknowledgements. My sincere thanks are due to Professor Pauli Bagge, Doc. Pertti Eloranta, Dr. Kalle Purasjoki, and Dr. Pekka Tuunainen for valuable guidance and many suggestions for improving my manuscript. Valuable aid was given by the personnel of the Hydrobiological Research Institute of Jyväskylä and of the Hydrobiological Division, University of Jyväskylä. In particular, I want to thank Pirkko Selin and Tuula Pöntinen, who helped with the microscopy, Jukka Nyrönen, who performed part of the field and laboratory work in the fish food investigation, Mauno Väisänen for co-operation in the automatic computations, Matti Käppi and Markku Repo for help in sampling, and Helena Falck for typing the final text. My warmest thanks are due to my wife, Marjatta Hakkari, for drawing the figures and for all other help during this work. I am grateful to Mrs. Anna A. Damström, M.A., who checked the English of the manuscript.

This study was supported by grants from the Finnish Cultural Foundation (Suomen Kulttuurirahasto) and its Fund for Central Finland, as well as the State Committee of Natural Sciences. It was also financed by the Water Protection Association of Northern Päijänne and the Finnish Game and Fisheries Institute, Fisheries Division. I am much obliged for all this assistance.

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