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Kalataloudellinen tutkimustoimisto

LANTBRUKSSTYRELSEN
Byrån för fiskeriundersökningar

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44

TUUNAINEN, PEKKA: Relations between the benthic fauna and two species of trout in some small Finnish lakes treated with rotenone

HELSINKI 1970

SUOMEN KALATALOUS 44 FINLANDS FISKERIER

RELATIONS BETWEEN THE BENTHIC FAUNA AND TWO SPECIES OF TROUT IN SOME SMALL FINNISH LAKES TREATED WITH ROTENONE

PEKKA TUUNAINEN
Hydrobiological Research Institute
Jyväskylä, Finland

Maataloushallitus Kalataloudellinen tutkimustoimisto
Lantbruksstyrelsen Byrån för fiskeriundersökningar
Board of Agriculture Bureau of Fisheries Investigation

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Relations between the benthic fauna and two species of trout in some small Finnish lakes treated with rotenone

PEKKA TUUNAINEN[1]

TUUNAINEN, P. 1970: Relations between the benthic fauna and two species of trout in some small Finnish lakes treated with rotenone. – Ann. Zool. Fennici 7: 67 – 120.

The influence of some physical, chemical and biotic factors upon the growth and survival of brown trout (*Salmo trutta* L.) and rainbow trout (*S. gairdneri* Richardson) introduced into nine small lakes in southern and central Finland is described. The lakes had been treated with rotenone before being stocked with trout. Attention was especially paid to the interrelations between the fish and the benthic fauna, the selective feeding of the fish, and the biological productivity of the benthic fauna and fish populations.

In most respects the lakes were found to be suitable habitats for trout. Scarcity of food and the small size of the food organisms were the most important factors limiting the growth of the fish. The fish stock had a considerable influence upon the abundance of the benthic fauna. Clear selective feeding was observed; animals living on submerged vegetation as well as freely in water were preferred to benthic organisms. Factors affecting the productivity of the benthic fauna and fish stock are discussed in detail.

I. Introduction

The aim of this study was to ascertain the habitat requirements, growth, food, and mortality of brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*) reared in small lakes that had been treated with rotenone. Attention was also paid to interspecific competition between the fish, the interrelationships beween the fish and the benthic fauna, and the productivity of the lakes.

After the establishment of Evo fish hatchery in 1892, brown trout were introduced into numerous small waters in the Evo district. Eggs of rainbow trout were obtained by

[1] Present address: Hydrobiological Research Institute, Jyväskylä, Finland

the hatchery for the first time from Germany in 1897, and fry and older fish were released into small lakes and ponds (BROFELDT 1920). ERICSSON (1904) reported that rainbow trout 11 – 25 cm long were caught in the Majakoski rapids, in the Evo district, in the autumn of 1904. In Valkea-Mustajärvi, a lake without any outlet, they grew to considerable size, the largest being 33 – 35 cm long and 300 – 400 g (BROFELDT 1920). From the other lakes they migrated when they grew larger. These experiments revealed that the rainbow trout is able to live in the pools of hatcheries and may in some cases be suited to natural waters as well.

Attempts were also made to introduce rainbow trout into some of the larger watercourses. Near Savonlinna, a rainbow trout weighing 3.8 kg was caught, which probably originated from one of these introductions (H-o 1908, SUOMALAINEN 1909).

Similar introductions were made elsewhere in Europe. In Yugoslavia (MRŠIĆ 1935) and Austria (NERESHEIMER 1937) stocks of rainbow trout are known to have reproduced in natural watercourses. In England such stocks have also been observed (WORTHINGTON 1940, 1941). The northernmost European stock of the rainbow trout which has been observed to reproduce in natural watercourses is in Ångermanland, Sweden (TÄGSTRÖM 1958).

Not until recently has attention again been paid to the possibility of growing salmonids in small Finnish lakes and ponds (HALME 1962, 1963, TOIVONEN 1962, 1964). Attempts have been made to kill the natural fish stocks in some lakes by exploding charges, and brown trout were then released in them (DAHLSTRÖM 1964), but the original fish stocks were not completely exterminated. A newer method for getting rid of the original fish population is to use rotenone. Rotenone has been used for killing fish in North America, but only on a large scale during the past twenty years (SVÄRDSON 1955, ALMQUIST 1959, ÖBERG 1964). In Finland the first rotenone treatment was carried out in 1960 on Ulpasjärvi, Pielavesi. The rotenone emulsion used here was a Swedish preparation (25 g rotenone + 25 g sulphoxide + 50 g other cube extracts per litre) (Suomen Kalastusyhdistys 1961, TOIVONEN 1962). In 1961 a small lake was treated in Ahvenanmaa (WIKGREN 1963) and in the years 1962 – 1967 several treatments were performed (cf. TOIVONEN 1962, 1964). Nowadays over a hundred lakes have been treated with rotenone in Finland by the Bureau of Fisheries Investigation, Board of Agriculture, and others.

The ecology of brown trout and rainbow trout in lakes treated with rotenone has already been investigated in Sweden and Ireland (e. g. NILSSON & SVÄRDSON 1962, O'RIORDAN & KENNEDY 1964).

There is a voluminous literature dealing with the toxic effects of rotenone on plankton, bottom animals and fish (e.g. DANIELS 1905, SCHEURING & HEUSCHMANN 1935, HAMILTON 1941, SMITH 1941, BROWN & BALL 1943, KRUMHOLZ 1948, BĒRZINS 1958, 1961, ALMQUIST 1959, Suomen Kalastusyhdistys 1961, TOIVONEN 1962, 1964, ÖBERG 1964). Rotenone is a substance that dissolves readily in organic solvents but weakly in water. Its solubility in fats is of great physiological importance, because this property enables it to enter the cells easily and quickly (ÖBERG 1964).

In Sweden experiments have shown that humus and layers of sludge adsorb rotenone and render it ineffective (BĒRZINS 1958, LINDGREN 1960). Oxygen from the photosynthesis of aquatic plants also inactivates rotenone. According to LINDGREN (1960), a micro-gradient of oxygen near the bottom and the presence of aquatic plants increase the chances that many animals will survive.

The fish may escape rotenone if protected by aquatic plants (SVÄRDSON 1955, ENROS & MOLIN 1956).

For various groups and species of plankton and bottom animals the lethal doses are very different because the toxic effects of rotenone depend on so many different factors, such as composition of the preparation, pH, temperature, presence of organic substances (e.g. humus), density of plankton, the nature of the bottom, and the aquatic vegetation (e.g. ÖBERG 1956, BĒRZINS 1958, ALMQUIST 1959, LINDGREN 1960). A very commonly used concentration of rotenone, 0.5 – 0.6 mg/l, kills the zooplankton almost completely and a great number of bottom animals and phytoplankton (ALMQUIST 1959). The most resistant groups of zooplankton are Rotatoria and Ciliata, but the mortality of the species varies very much even within the same genus.

A renewal of phytoplankton begins a few weeks after treatment but the renewal of zooplankton usually takes 1 ½ – 3 (5) months (ALMQUIST 1959, BĒRZINS 1963).

GÖNCZI (1964) made a theoretical study of the influences of rotenone on food chains of fish and concluded that the selective toxic effect of rotenone plays an important role in the development of predator-prey relationships after poisoning.

Benthic animals, among which the destruction was not total, reached equilibrium a few months after the treatment (BĒRZINS 1958). In many cases the most resistant species reproduce at a very high rate after poisoning. This is the situation, for example, in Oligochaeta (HOOPER 1948, CUSHING & OLIVE 1956), Amphipoda and Gastropoda (SMITH 1941). When the ecosystem of a lake attains a balanced state after poisoning, the numbers of specimens of the groups mentioned above decrease again and remain at normal levels (LINDGREN 1960, LELLÁK 1965).

II. Methods and technique

1. Chemical and physical samples

A vertical series of water samples were taken by the Bureau of Fisheries Investigation, Board of Agriculture, and local agricultural societies from the lakes treated in the years 1960 and 1962 (Fig. 1). They were taken with a Ruttner sampler (cf. KAARTOTIE & RYHÄNEN 1957) from the deepest part of the lake. Samples were collected on 102 different dates. Temperature, pH, oxygen content, and usually conductivity as well, were determined in the field. Other analyses were carried out in the laboratory.

Temperature was read instantaneously to the nearest 0.1 °C from a mercury thermometer mounted in the sampler.

pH was determined with a pH meter Radiometer Model PHM 24.

Electrolytic conductivity ($\varkappa_{18}$) was determined with a Normameter conductivity-measuring bridge. Results are given as µS.

The colour of the water was determined with a Hellige comparator and the data are given as Pt mg/l.

Transparency was measured by using the white lid of the Ruttner sampler.

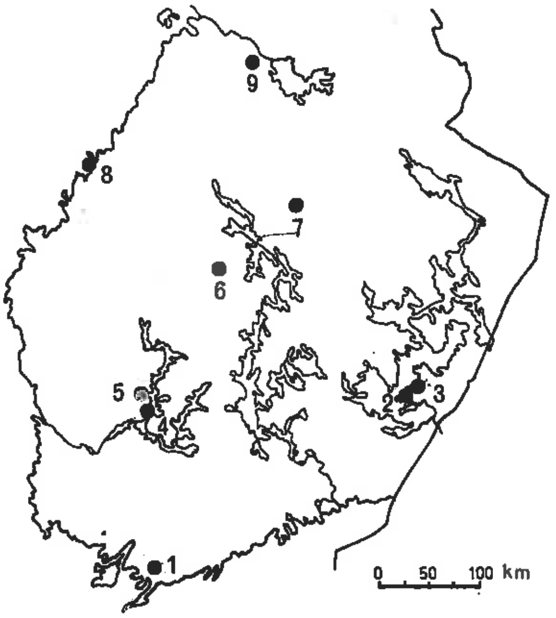

Fig. 1. Location of the lakes studied. 1 = Sahalampi, 2 = Ahvenlampi, 3 = Pien-Valkealampi, 4 = Julkujärvi, 5 = Satimuslampi, 6 = Särkilampi, 7 = Ulpasjärvi, 8 = Långviken, 9 = Kivi-Ahveroinen.

The amount of dissolved oxygen was determined by Winkler's method. The results are expressed as O_2 mg/l and O_2 %.

$KMnO_4$ consumption was titrated from 100 ml of water by a standard method.

Alkalinity was titrated with 0.1 N HCl, with methyl orange as indicator. The results are expressed as mval/l.

Total hardness was determined by titration by the complexon method. The results are expressed as °dH.

The concentration of Fe salts was determined colorimetrically from an unfiltered sample with a rodanide method. The results are expressed as Fe mg/l.

The physical and chemical analyses were carried out according to instructions given by Gesellschaft Deutscher Chemiker (1960) and Elintarviketutkijain seura r.y. (1962).

2. Sampling of plankton, benthic fauna, fish, and fish food

Plankton samples were collected as a vertical series (two samples per m) with a Ruttner sampler and filtered through a 50 μ mesh sieving apparatus constructed by T. Nissinen (Fig. 2). From the sieving bottle the sample was washed into a 200 ml bottle and preserved in 5 % formalin. For counting, the 200 ml sample was filtered through a 25 μ mesh filter and then put into a bowl with a small amount of glycerin and a lattice of lines on the bottom (cf. Purasjoki 1958).

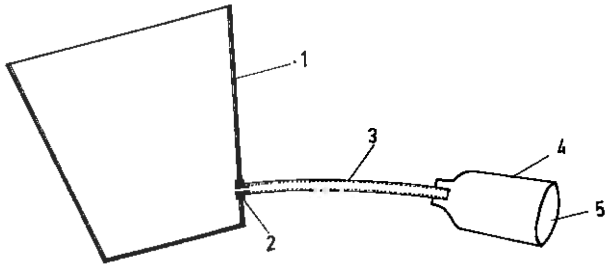

Fig. 2. Sieving apparatus for filtration of plankton samples. Design by fishery biologist T. Nissinen. 1 = plastic pail, 2 = brass socket, 3 = plastic tube, 4 = plastic bottle (detachable), 5 = plankton net (50 μ).

A total of 898 bottom samples (24.9 m^2) were collected with an Ekman – Birge grab 1/36 m^2 in area; as a rule, 6 (1 – 9) samples were taken from each sampling depth. The samples were sifted through two sieves with 2.5 and 0.75 mm mesh, and the bottom animals were picked from the sieves and preserved in 5 % formalin. The animal samples were weighed wet in a closed bowl to the nearest 0.1 mg.

The nature of the bottom affects the results. If the bottom is sandy or muddy, almost all bottom particles are washed away and the animals are easy to find. In the small lakes studied, however, the bottom was often of mud with a profusion of cones, needles and other plant remains, which reduced the chances of finding all the specimens.

The mesh size of the sieve affects the results. According to Jónasson (1955), the numbers of animals obtained with a 0.2 mm mesh were 100 – 600 % greater than with a mesh of 0.6 mm. For example, all the Chironomid larvae less than 10 mm were lost if the mesh was 0.6 mm. A high proportion of the Chironomid larvae and young *Pisidium* as well as other small bottom animals thus probably escaped attention. However, all the large animals important as fish food were sampled effectively.

Fish samples were collected mainly in May – June and in September – December, but some fish were caught in July – August, too. Their total length was measured to the nearest millimetre and they were weighed to the nearest gram. The average growth of the fish was estimated from a material comprising 555 brown trout and 405 rainbow trout. The total numbers of fish caught were 741 brown trout and 743 rainbow trout. Earlier data about the growth of fish released in Ulpasjärvi were published by Jahnsson (1963).

Because the fish populations studied usually originated from a single introduction of fish of the same age, there is less variation in the size of the fish than in a natural population, where all age classes are represented. A suitable selection of nets will thus give a sample which is representative of the whole fish population, even if quite small samples are taken.

To eliminate the selective effect of gill nets, a series of nets with mesh sizes of 12, 17, 20, 25, 30, 35, and 45 mm was used simultaneously (cf. LAGLER 1968). Some fish were caught by angling, too.

Samples of food eaten were collected from 200 brown trout and 167 rainbow trout. Earlier data about the food of three rainbow trout from Ulpasjärvi were published by JAHNSSON (1963).

Food is digested all the time while the fish is in the net. According to REIMERS (1957), the rate of digestion is temperature-dependent. In brown trout the digestion of soft-bodied food organisms (e.g. *Helodrilus*) takes about 12 hours at 10°C, whilst that of medium hard-bodied ones (e.g. *Gammarus*) takes about 13 hours and that of hard-bodied ones (e.g. *Arctopsyche*) about 16 hours at the same temperature. At 2°C the times are 25, 26, and 44 hours, respectively. To diminish this source of error the nets were examined at intervals of $^1/_2$ – 2 hours in summertime and at intervals of about 12 hours in the period of cold water. If the fish are caught by angling or by spinning, this source of error is eliminated. Every fish caught was killed immediately and its whole digestive tract was preserved in formalin (cf. WINDELL 1968).

The volume of the food samples was determined to the nearest 0.1 ml.

III. The lakes studied and their environmental factors

1. Kivi-Ahveroinen, Utajärvi

General description

64° 35′ 16″ N, 26° 27′ E, 130 m above sea level. Area 4.3 hectares, maximum depth 11.0 m, volume 215 000 m³ (TOIVONEN 1962). About 80 % of the shore-line is sandy and the rest more or less marshy. Bottom sand or mud, springs in places (TUUNAINEN 1966a, 1966b). No inlet and no outlet. Fig. 3.

Aquatic vegetation rather scanty. The belt of emergent vegetation consists of sedges, *Phragmites communis* at the southeast end, and *Lobelia dortmanna* on the sandy shores. The floating vegetation consists of *Nuphar luteum*, which grows to 3 – 3.5 m depth, especially where the bottom is soft. At a depth of 7 – 10 m aquatic mosses in places.

Kivi-Ahveroinen is a dimictic lake of the type that is normal in the temperate zone, with stratification both in summer and in winter, and normal spring and autumn turnover.

In winter the oxygen content of the water was high in the upper five metres, but lower towards the bottom. During the summer stratification it was high in the epilimnion, but in the hypolimnion it was found to vary from year to year. Usually there was a considerable oxygen deficit in late summer. The pH was near the neutral point, usually a little on the acid side. Electrical conductivity and $KMnO_4$ consumption were very low; there are almost no humous substances to increase the consumption. According to JÄRNEFELT's (1953) classification, Kivi-Ahveroinen is an oligohumous lake. The alkalinity, total hardness, and Fe content of the water were very low.

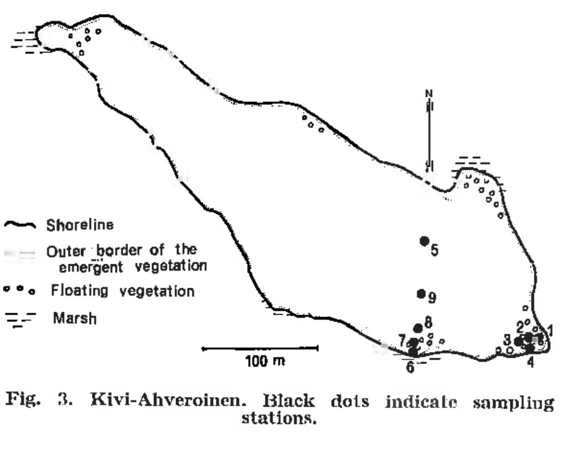

Fig. 3. Kivi-Ahveroinen. Black dots indicate sampling stations.

Some physical and chemical data (according to TUUNAINEN 1968) are listed below:

	Depth m	t °C	n	
VII. – VIII. 1959 – 1966	0.3 – 1	15.0 – 19.7	9	Maximum on 8. VIII. 1963
	~5 – 8		9	Metalimnion
	9.5 – 10	8.3 – 12.7	9	
IV. 1961 – 1966	1	0.8 – 1.0	6	
	9 – 10	4.0 – 4.9	6	

Days without ice: 177 – 195 days per year (TUUNAINEN 1966a, 1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VII. – VIII. 1959 – 1966	0.3 – 1	8.9 – 11.0	94 – 114	8	6.0 – 7.0	7
	4 – 5	8.9 – 11.0	94 – 112	8	6.3 – 7.0	6
	9 – 11	0.0 – 9.9	0 – 90	8	5.7 – 6.5	7
IV. 1961 – 1966	1	9.4 – 14.4	68 – 106	6	5.5 – 6.8	5
	4 – 5	5.8 – 9.4	46 – 72	6	5.5 – 6.8	5
	9 – 10	0.3 – 2.3	~0 – 18	6	6.5 – 6.8	5

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
VII. – VIII. 1959 – 1966	0.3 – 1	14 – 20	7	6.6 – 13.3	7
	4 – 5	11 – 16	6	7.8 – 14.5	6
	9 – 11	14 – 23	7	6.1 – 15.8	8
IV. 1961 – 1966	1	15 – 19	5	5.7 – 9.5	6
	4 – 5	14 – 18	5	3.5 – 9.5	6
	9 – 10	21 – 34	5	6.0 – 13.3	6

	Depth m	Range	Colour Pt mg/l x̄	n	Transparency m Range	x̄	n
5. VII. 1959 –	0.3 – 1	0 – 10	6.2	11	3.9 – 10.0	6.6	13
2. VIII. 1966	7.0 – 11	5 – 60	22.1	11			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n	Fe mg/l	n
VII. – VIII.	1 – 3	0.08 – 0.14	2	0.14 – 0.28	5	0.00 – 0.07	4
1959 – 1966	7 – 11	0.08 – 0.16	2	0.16 – 0.32	5	0.02 – 0.23	4
IV.	3	–	–	0.28 – 0.30	3	0.00 – 0.12	3
1962 – 1965	7	–	–	0.30 – 0.34	3	0.03 – 0.13	3

Benthic fauna and zooplankton

The sampling stations are seen in Fig. 3. *Pisidium* spp., *Asellus aquaticus* and Chironomid larvae were the most frequent groups in the samples of bottom animals, but larvae of *Sialis*, Trichoptera and Ephemerids were also abundant (Tuunainen 1968). Fig. 4 shows that there were considerable differences between the biomass values of bottom animals at different seasons, partly because of the emergence of Ephemerids, *Sialis*, Trichoptera and Chironomids.

On 4. VII. 1963 a series of 60 plankton samples of 1.4 l each had the following composition (specimens per 10 l):

Rotatoria	50
Daphnia sp.	+
Bosmina sp.	100
Chydorus sp.	+
Hydracarina	+
	Total 150

Fish population

At the time of the poisoning (6. IX. 1962), the fish population of Kivi-Ahveroinen consisted of small perch, according to Toivonen (1962) about 24.1 kg per hectare.

On 30. V. 1963, 7 000 specimens (1 628 per hectare) of brown trout fry were released into the lake. The fry were from Montta fish hatchery, Muhos, and according to Mr. O. Niinimäki (personal communication) they belonged to a race living in the Oulujoki watercourse. This race may have been partly hybridized with trout from Indalsälven, Sweden.

Data on the growth of these trout are presented in Figs. 28 – 29. Except during the first growth period the growth rate was higher than in the other lakes, although the density in these was lower. Some of the data on the growth of brown trout in Kivi-Ahveroinen have been published already (Tuunainen 1966a, 1966b, 1968).

Food of the fish released

The diet of the brown trout was found to consist mainly of *Asellus aquaticus* as well as

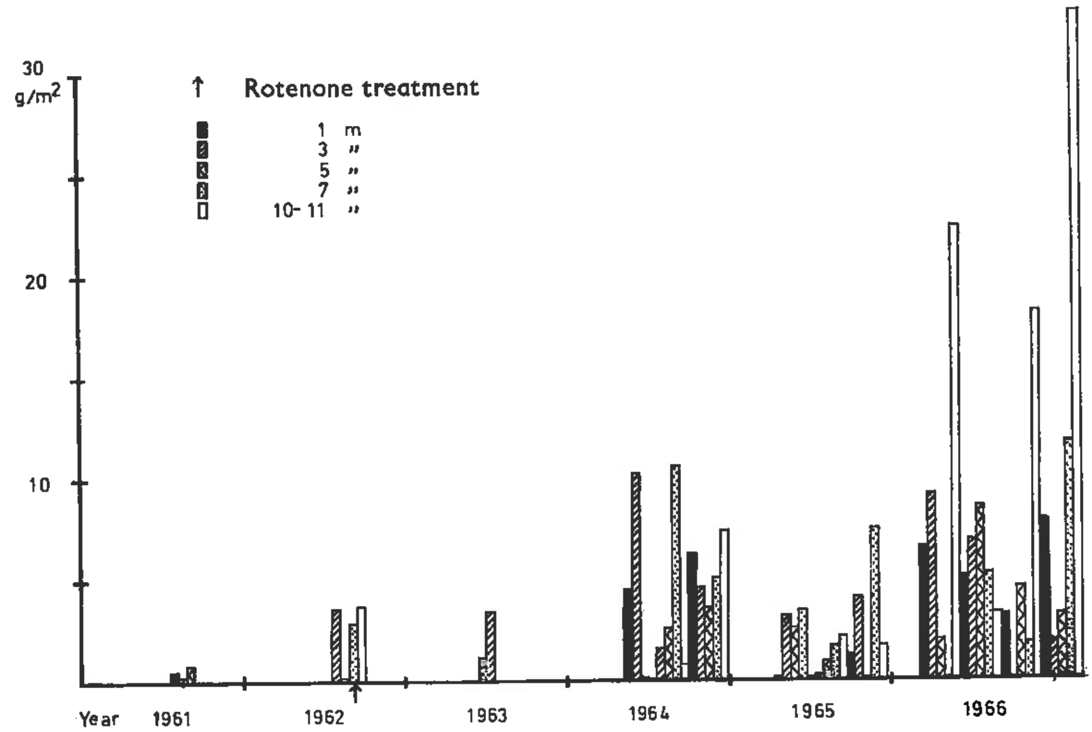

Fig. 4. Biomass of benthic fauna in Kivi-Ahveroinen.

Table 1. Food of brown trout in Kivi-Ahveroinen. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
7. – 8. VI. 1964	1 +	7	388	2.1	Chironomid pupae 50/47 %, terr. insects 22/13 %, *Asellus* 21/21 %
4. XI. 1964	1 +	10	149	2.9	*Asellus* 96/84 %, Trichopterous larvae 3/16 %
19. V. 1965	2 +	10	112	3.0	*Asellus* 87/84 %, Chironomid pupae 12/7 %
6. – 7. VIII. 1965	2 +	10	104	2.4	*Asellus* 75/60 %, Corixid larvae 9/5 %, Trichopterous larvae 4/4 %
3. XI. 1965	2 +	10	108	2.7	*Asellus* 70/56 %, Trichopterous larvae 28/38 %
27. V. 1966	3 +	10	176	7.3	*Asellus* 95/84 %, Trichopterous larvae 2/4 %
2. – 6. VIII. 1966	3 +	5	142	6.4	*Asellus* 49/45 %, Corixid adults and larvae 44/44 %, Trichopterous larvae 2/5 %

larvae of Corixids, Trichoptera and Chironomids (Table 1). Aerial food was less important (cf. TUUNAINEN 1966b); the most important of these were Chironomids and Trichoptera.

HESS & SWARTZ (1941) proposed the term forage ratio, which means the ratio of the percentage of an organism in the stomach contents of the fish to the percentage of the same organism in the total benthic population.

Table 2 shows the forage ratios of the bottom animals. The accuracy of the figure depends, of course, upon the reliability of the measuring technique used. The only bottom animal samples taken into consideration were those which were collected from places where the fish fed during the time of sampling.

Table 3 shows the frequencies of the bottom animals in the bottom samples and in some stomach analyses.

Table 2. Forage ratios for brown trout in Kivi-Ahveroinen

	7. – 8. VI. 1964	3. – 4. XI. 1964	19. V. 1965	6. – 7. VIII. 1965	3. XI. 1965	27. V. 1966	2. – 6. VIII. 1966	15. VII – 2. – 6. VIII. 1966
Hirudinea	–	–	0.09	–	–	0.33	–	–
Pisidium sp.	–	0.09	–	–	–	0.67	–	0.02
Asellus aquaticus	0.72	2.65	1.21	1.69	–	4.41	2.05	3.70
Hydracarina	4.17	–	–	–	–	–	–	–
Corixid adults	–	–	–	–	–	–	24.50	52.60
Dytiscid larvae	2.70	–	–	–	–	–	–	0.27
Sialis larvae	–	–	–	0.09	–	–	–	–
Trichopterous larvae	0.21	1.62	0.09	–	36.20	0.45	–	–
Chironomid larvae	0.07	0.05	0.01	0.04	0.01	0.004	0.05	0.17
Chironomid pupae	–	–	–	–	–	0.33		

Table 3. Frequency (%) of occurrence of benthic animals in bottom samples taken on thirteen different dates (A), in stomachs of brown trout caught on eight different dates (B), and in eight samples taken simultaneously with bottom samples (C).

	A	B	C
Nematoda	7	–	–
Oligochaeta	46	–	–
Hirudinea	23	29	25
Glossosiphonia sp.	15	–	–
Planorbids	31	43	–
Pisidium sp.	54	71	38
Asellus aquaticus	100	86	88
Hydracarina	15	14	13
Ephemerid larvae	15	43	–
Agrionid »	–	29	–
Aeschnid »	15	29	–
Corixid »	–	29	–
» adults	23	71	25
Dytiscid larvae	23	43	25
» adults	7	57	–
Sialis larvae	77	43	13
Trichopterous larvae	62	100	63
Chaoborus »	7	14	–
Chironomid »	100	100	100
» pupae	15	57	13
Tabanid larvae	54	–	–
Other Dipterous larvae	7	–	–

Reactions of the benthic fauna

Fig. 4 shows the changes in the biomass of the bottom fauna after the rotenone treatment. The slight effect of the poisoning of the fish population upon the bottom fauna is perhaps due to the smallness of the perch population; the numbers of bottom animals were near the upper limit because of weak predation. The decrease of the bottom fauna at 1 – 3 m depth noted on 14. VIII. 1964 may have been the result of predation by brown trout. When the fish stock decreased during the following years, a corresponding increase in the bottom fauna was observed.

2. Satimuslampi, Viljakkala

General description

61° 50′ 27″ N, 23° 31′ 12″ E, 152 m above sea level. Area 2.0 hectares, maximum depth 4.8 m, volume 50 000 m^3 (TOIVONEN 1962). The shores are slightly paludified. Bottom mud, with plankton debris (TUUNAINEN 1966a, 1966b).

No inlet and no outlet. No emergent vegetation. *Nuphar luteum* grows quite scantily at depths of 2 m or less. Fig. 5.

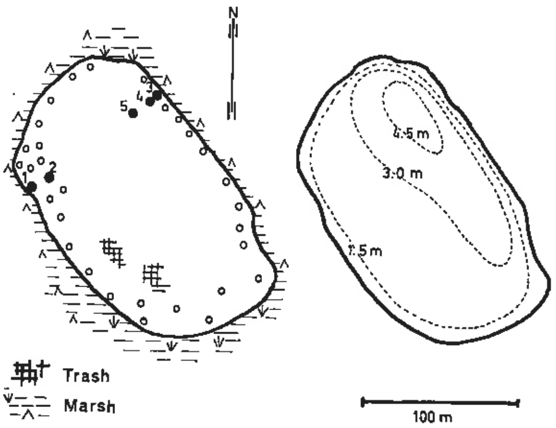

Fig. 5. Satimuslampi. Black dots indicate sampling stations. Other explanations: see Fig. 3.

The temperature was quite uniform in summertime; there was no clear stratification. The oxygen content was suitable for fish in the upper layers in winter, but near the bottom there was a greater deficit of oxygen. In summer the oxygen content of all the water layers was good, because the lake was not stratified.

Originally, Satimuslampi was quite acid, pH 4.7 on the surface at the time of the poisoning, 18. IX. 1962 (Toivonen 1962). To diminish the acidity, about 10 000 kg of crushed limestone was sprinkled into the lake in late winter 1963. The effect of this treatment was visible in the water samples collected afterwards.

Electrical conductivity, $KMnO_4$ consumption and Fe content were very low. Humous substances were practically absent. According to Järnefelt's (1953) classification, Satimuslampi is an oligohumous lake.

Some chemical and physical data (according to Tuunainen 1968) are listed below:

	Depth m	t°C	n	
VI. – IX. 1962 – 1965	0.5 – 1	10.5 – 19.7	4	Maximum on 7. VI. 1963
	4	10.4 – 19.1	4	No stratification in summer
II. – III. 1963	1	0.9 – 1.0	2	
	3 – 4	4.0	2	

Days without ice: 194 – 200 days per year (Tuunainen 1966a, 1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VI. – IX. 1962 – 1965	0.5 – 1	9.6 – 10.4	90 – 115	2	4.8 – 7.3	3
	3 – 4	9.9 – 10.9	92 – 111	2	5.3 – 6.8	2
II. – III. 1963	1	7.0 – 11.0	52 – 86	2	4.5 – 4.7	2
	3 – 4	1.2 – 2.6	9 – 21	2	4.7	2

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n	Fe mg/l	n
VI. – IX. 1962 – 1965	0.5 – 1	18	1	11.0	1	–	–
	3 – 4	18	1	21.0	1	–	–
II. – III. 1963	1	22	2	6.3 – 11.4	2	0.01	1
	3 – 4	17 – 18	2	11.1 – 13.3	2	0.15	1

	Depth m	Colour Pt mg/l	n	Transparency m	n
18. IX. 1962 –	1.0	5	1	> 4.8 (bottom)	2
10. VI. 1965	4.0	25	1		

Benthic fauna and zooplankton

The bottom fauna was very poor both in species and in numbers (Fig. 6) (cf. Tuunainen 1968). Its main constituents were *Sialis* larvae and, to a lesser degree, larvae of Chironomids.

The tabulation below shows the composition of the zooplankton (specimens per 10 l) in the early summer of 1963, when the brown trout and rainbow trout fry were released. The tabulation is based on 27 samples of 1.4 l each.

Rotatoria	16
Daphnia sp.	+
Bosmina sp.	789
Holopedium gibberum	10
Cladocerous embr.	72
Calanids	1
Ceriodaphnia sp.	7
Hydracarina	+
Total	895

Fish population

At the time of the poisoning (18. IX. 1962), the fish population consisted of small perch, according to Toivonen (1962) 18.2 kg per hectare.

In June 1963, brown trout and rainbow trout fry (1 000 specimens per hectare of each species) were released into the lake. The fry was from Myllypuro fish hatchery, Ylöjärvi. The rainbow trout were of the spring-spawning Danish race (Tuunainen 1966b). The brown trout were of the same origin as those released into Julkujärvi (p. 86).

In spring 1964, smelt were released into the lake as food for the trout (Tuunainen 1966b). These fish were probably all eaten by the trout.

Except for the initial growth of the rainbow trout, the growth rate of both species was very low (Figs. 28 – 31) (Tuunainen 1968), probably because of too high an introduction density in relation to the food available. Interspecific

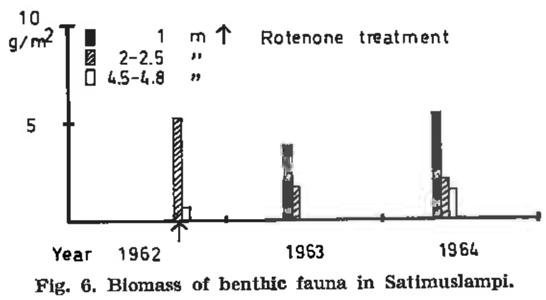

Fig. 6. Biomass of benthic fauna in Satimuslampi.

competition between the trout species probably also retarded their growth; the quotient of similarity of the food, for instance, was found to be 87 % in a sample taken on 3. VI. 1964 (TUUNAINEN 1966b).

Food of the fish released

Larvae and pupae of Chironomids were important food organisms for brown trout (Table 4). One-year-old young also took some zooplankton (Cladocera) in early summer. Adults of *Hygrotus* and *Hyphydrus* as well as larvae of Trichoptera were also important.

The food of the rainbow trout was similar at the end of their second growth period; in addition they utilized a notable amount of aerial food (Table 4).

The forage ratios for brown trout and rainbow trout estimated on 3. VI. 1964 were as follows:

	Brown trout	Rainbow trout
Sialis larvae	–	0.03
Chironomid larvae	0.66	0.12

Table 4. Food of brown trout and rainbow trout in Satimuslampi. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
Brown trout:					
3. VI. 1964	1 +	2	65	0.3	Chironomid pupae 59/75 %, Cladocera 29/9 %, Chironomid larvae 8/1 %
17. X. 1964	1 +	1	6	1.2	Trichopterous larvae 49/80 %, Dytiscid adults 17/8 %, *Sialis* larvae 17/8 %
Rainbow trout:					
3. VI. 1964	1 +	10	76	0.3	Chironomid pupae 58/51 %, Cladocera 23/3 %, Dytiscid adults 7/17 %
17. X. 1964	1 +	8	8	0.8	Chironomid larvae 38/14 %, terr. insects 32/19 %, Trichopterous larvae 17/21 %

Table 5. Frequency (%) of occurrence of benthic animals in bottom samples taken from Satimuslampi on three different dates (A), in stomachs of brown trout (B) and rainbow trout (C) taken on two different dates, and in one sample (D = brown trout, E = rainbow trout) taken simultaneously with bottom samples.

	A	B	C	D	E
Eurycercus sp.	33	–	–	–	–
Hydracarina	33	–	50	–	–
Libellulid larvae	33	–	–	–	–
Other Odonatous larvae	–	–	50	–	–
Dytiscid adults	–	100	50	–	–
Donacia pupae	33	–	–	–	–
Sialis larvae	100	50	50	–	(100)
Trichopterous larvae	–	50	50	–	–
Chironomid »	33	100	100	(100)	(100)
» pupae	–	50	50	–	–
Ceratopogonid larvae	–	50	100	–	–

Table 5 shows the frequencies of animals in the bottom samples and in some stomach analyses.

Reactions of the benthic fauna

Rotenone treatment had no clear effect upon the bottom fauna. The slight increase in biomass and density at 1 and 2 – 2.5 m depth from 1963 to 1964 (Fig. 6) was mainly due to the increase in the numbers of *Sialis* larvae, which were eaten by the trout very ineffectively.

3. Pien-Valkealampi, Puumala

General description

61° 28′ 10″ N, 28° 38′ 30″ E, about 80 m above sea level. Area 1.0 hectares, maximum depth 11.3 m and volume 70 000 m³ (TOIVONEN 1962). All shores are marshy. Bottom mud, with some springs (TUUNAINEN 1966a, 1966b); No inlet and no outlet. Aquatic vegetation scanty, no emergent vegetation. Floating vegetation represented by *Nuphar luteum*. Water mosses at 5 m depth. Fig. 7.

The lake is clearly stratified in summer, with an oxygen deficit in the hypolimnion and almost complete lack of oxygen near the bottom. From spring 1965 on, the rainbow trout were fed with pellets which caused secondary eutrophy and decrease of the oxygen content in the winters of 1965/1966 and 1966/1967. Attempts were made to improve the oxygen conditions by pumping air into the lake with a compressor.

At the time of the poisoning (11. IX. 1962), the pH was 5.5 on the surface (TOIVONEN 1962). About 1 000 kg of waste lime (mainly $CaCO_3$) was scattered into the lake on 10. XI. 1962. This caused a rise in the pH, which then remained elevated up to the year 1966.

Pien-Valkealampi is very poor in electrolytes in spite of treatment with waste lime, but the conductivity rose from 1965 to 1966 because of secondary eutrophy caused by feeding the fish. The $KMnO_4$ consumption was originally low, but increased owing to the secondary eutrophy (cf. TUUNAINEN 1968). The values of alkalinity and total hardness

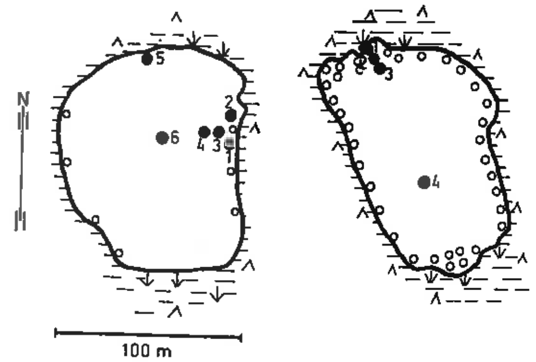

Fig. 7. Pien-Valkealampi (left) and Ahvenlampi (right). Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

were very low. According to JÄRNEFELT's (1953) classification, the lake is an oligohumous lake.

Some physical and chemical data (according to TUUNAINEN 1968) are listed below:

	Depth m	t°C	n	
V. – IX. 1962 – 1966	0.2 – 1	12.7 – 23.6	7	Maximum on 26. VII. 1966
	~ 4 – 9		7	Metalimnion
VII. 1964 – 1966	10 – 11	4.9 – 7.3	3	

Days without ice: 205 – 213 days per year (TUUNAINEN 1966a, 1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
V. – IX.	0.2 – 1	9.4 – 13.1	94 – 141	5	5.5 – 7.2	5
1962 – 1966	6 – 7	2.8 – 9.4	24 – 95	5	5.6 – 6.3	5
	10 – 10.5	0.1 – 4.8	0 – 39	5	5.7 – 6.6	2

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
V. – IX.	0.2 – 1	8 – 20	5	6.0 – 25.6	3
1962 – 1966	6 – 7	9	1	6.0	1
	10 – 10.5	12 – 27	5	19.7 – 33.0	3

	Depth m	Colour Pt mg/l Range	$\bar{x}$	n	Transparency m Range	$\bar{x}$	n
1. IX. 1962 –	0.2 – 1	5 – 20	15.0	3	2.0 – 8.0	4.1	4
26. VII. 1966	10	5 – 20	15.0	3			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n
V. – VII.	0.2 – 0.5	0.07 – 0.17	4	0.04 – 0.22	3
1965 – 1966	10 – 10.5	0.12 – 0.17	4	0.22 – 0.39	3

Benthic fauna and zooplankton

The bottom fauna mostly consisted of Chironomid larvae, *Sialis* and Trichopterous larvae being the next. As a whole, the bottom fauna was quite sparse (Fig. 8).

In the spring, at the time when the brown trout fry were released, the zooplankton was rather poor. The mean of 66 samples from 0 – 11 m depth (1.4 l each) was only 14 specimens per 10 l, the majority consisting of Rotaria.

Fish population

The fish population consisted exclusively of perch at the time of the poisoning (11. IX. 1962), according to TOIVONEN (1962) 26.6 kg/hectare.

On 21. V. 1963, 2 000 specimens (2 000 per hectare) of brown trout fry from Savitaipale fish hatchery were released into the lake. On 22. IX. 1963, 150 one-summer-old rainbow trout (150 per hectare) from Simunankoski fish hatchery, Laukaa, were released (TUUNAINEN 1966b).

In the first growth period the growth rate was quite high. During this time the food of the brown trout fry consisted mainly of zooplankton and aerial food. In the third growth period the growth of brown trout was found to be slow in Pien-Valkealampi compared with the other lakes studied. In the rainbow trout the growth rate was already quite low by the second growth period, and these fish also grew more slowly than in the other lakes (Figs. 28 – 31). The low growth rate may have been due to very keen food competition caused by high density combined with scarcity of bottom animals.

Food of the fish released

The diet of the brown trout was found to be quite varied (Table 6). Larvae and pupae of Chironomids were the predominant food organisms, but larvae of Ceratopogonids, Ephemerids and Trichoptera as well as adult Dytiscids and aerial food were also important. In late summer 1964, some stomach samples contained zooplankton too.

The diet of the rainbow trout was also quite varied (Table 6), the predominant food organisms being larvae and pupae of Chironomids and Ceratopogonids, as well as Hydracarina, zooplankton and terrestrial insects. The food selection of the fish released is shown in Tables 7 and 8.

Table 6. Food of brown trout and rainbow trout in Pien-Valkealampi. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
Brown trout:					
2. VII. 1964	1 +	3	824	0.8	Chironomid larvae 77/63 %, Chironomid pupae 22/24 %
24. IX. 1964	1 +	7	10	0.3	Ceratopogonid larvae 36/11 %, terr. insects 22/22 %, *Argyroneta aquatica* 15/24 %
8. VI. 1966	3 +	3	26	0.9	Ephemerid larvae 37/12 %, Chironomid larvae 28/9 %, terr. insects 18/15 %
Rainbow trout:					
2. VII. 1964	1 +	9	978	1.0	Hydracarina 48/8 %, Chironomid larvae 39/59 %, Chironomid pupae 6/10 %
24. IX. 1964	1 +	3	10	0.3	Terr. insects 45/46 %, Chironomid pupae 31/29 % Ceratopogonid larvae 24/15 %

Table 7. Forage ratios for brown trout and rainbow trout in Pien-Valkealampi.

	Brown trout 1. – 2. VII. 1964	Brown trout 8. VI. 1966		Rainbow trout 1. – 2. VII. 1964
Ephemerid larvae	–	14.50	Trichopterous larvae	0.19
Trichopterous »	–	0.33	*Chaoborus* »	0.05
Chaoborus »	0.02	–	Chironomid »	0.65
Chironomid »	1.28	1.08		
Ceratopogonid larvae	–	1.98		

Table 8. Frequency (%) of occurrence of benthic animals in bottom samples taken from Pien-Valkealampi on six different dates (A), in stomachs of brown trout (B) and rainbow trout (C) caught on three and two different dates, respectively, and in two samples of brown trout (D) and one sample of rainbow trout (E) taken simultaneously with bottom samples.

	A	B	C	D	E
Nematoda	17	–	–	–	–
Oligochaeta	67	–	–	–	–
Argyroneta aquatica	17	33	–	–	–
Hydracarina	17	–	50	–	–
Ephemerid larvae	33	33	–	50	–
Agrionid »	–	–	50	–	–
Aeschnid »	–	–	50	–	–
Libellulid »	17	33	–	–	–
Other Odonatous larvae	17	–	–	–	–
Corixid larvae	17	–	50	–	–
Dytiscid »	17	–	–	–	–
» adults	17	67	–	–	–
Donacia pupae	67	–	–	–	–
Other Coleopterous larvae	33	–	–	–	–
Sialis larvae	50	–	–	–	–
Trichopterous larvae	67	67	50	100	(100)
Chaoborus »	50	33	50	50	(100)
Chironomid »	100	67	50	–	(100)
» pupae	33	67	100	100	–
Ceratopogonid larvae	33	100	100	50	–

Reactions of the benthic fauna

The density of the bottom animals and particularly of the Chironomid larvae, was found to decrease continuously from 1963 to 1965. From 1965 to 1966, there was an increase of bottom animal density, presumably owing to the decrease of the fish stock combined with eutrophication of the lake (cf. p. 74).

4. Ahvenlampi, Ruokolahti

General description

61° 27′ 20″ N, 28° 30′ E, about 80 m above sea level. Area 0.93 hectares, maximum depth 5 m, volume 30 000 m³ (Toivonen 1962). The shores are paludified and the bottom is mud (Tuunainen 1966a, 1966b). No inlet and no outlet.

No belt of emergent vegetation. *Nuphar luteum* grows down to 2 – 3 m depth. At 3 – 5 m depth aquatic mosses grow on the bottom. Fig. 7.

Usually no temperature stratification. In summer the oxygen content was high throughout the lake; this was probably also the case in the winters of 1964/1965 and 1965/1966, because the rainbow trout survived the winter.

At the time of the poisoning, the water was quite acid (pH 4.3) (Toivonen 1962). In November 1962, about 800 kg of waste lime was scattered into the lake, and this treatment clearly affected the electrolytic conductivity, which was higher after the treatment (cf. Tuunainen 1968). $KMnO_4$ consumption, alkalinity and total hardness were quite low. According to Järnefelt's (1953) classification, the lake is an oligohumous lake.

Some physical and chemical data (according to Tuunainen 1968) are listed below:

	Depth m	t°C	n	
VI. – IX. 1962 – 1966	0.2 – 1	14.2 – 22.7	7	Maximum on 26. VII. 1966
	4 – 5	8.2 – 17.0	7	No stratification in summer

Days without ice: 200 – 209 days per year (Tuunainen 1966a, .1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VI. – IX.	0.2 – 1	8.7 – 11.6	88 – 125	5	4.7 – 7.3	5
1962 – 1966	4 – 5	8.7 – 12.4	88 – 131	5	4.0 – 7.3	5

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
IV. – IX.	0.2 – 1	15 – 31	5	19.0 – 23.4	3
1962 – 1966	4 – 5	13 – 34	5	17.0 – 23.7	3

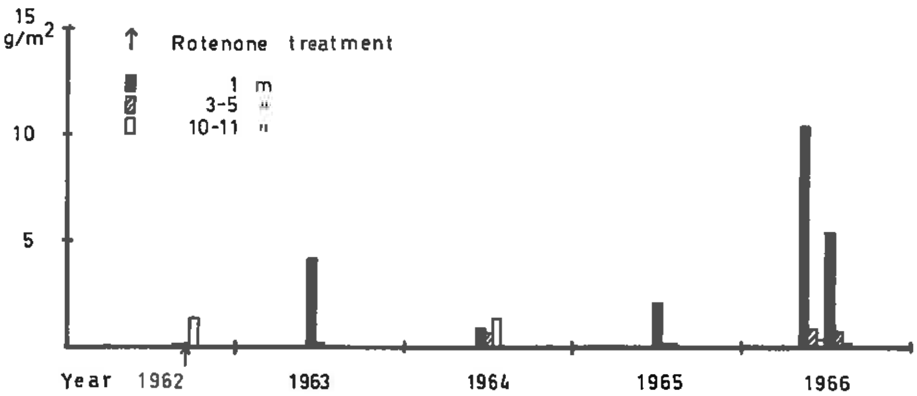

Fig. 8. Biomass of benthic fauna in Pien-Valkealampi.

	Depth m	Colour Pt mg/l Range	$\bar{x}$	n	Transparency m Range	$\bar{x}$	n
10. IX. 1962 –	0.2 – 1	7 – 20	15.7	3	3.5 – 4.0	3.7	4
26. VII. 1966	4 – 5	10 – 25	17.5	3			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n
VI. – VII.	0.2 – 0.5	0.17 – 0.32	4	0.08 – 0.39	3
1965 – 1966	4 – 4.5	0.21 – 0.36	4	0.06 – 0.48	3

Benthic fauna and zooplankton

Sampling stations are marked in Fig. 7. The bottom fauna (Fig. 9) mostly consisted of Chironomid larvae. Of the other groups Oligochaeta as well as larvae of *Sialis* and Ceratopogonids were important (Tuunainen 1968).

In spring 1963, the zooplankton was found to be quite poor; Rotatoria was the predominating group, and the average number of specimens obtained from 27 samples (1.4 l each) was only 28 specimens per 10 l.

Fish population

At the time of the poisoning (10. IX. 1962), the fish population consisted solely of perch, 30.6 kg/hectare (Toivonen 1962).

In the spring after the poisoning 1 500 specimens of brown trout fry were released into the lake, but the introduction failed, probably because rotenone had persisted over the winter. On 30. XI. 1964, 300 specimens (322 per hectare) of two-summer-old rainbow trout (average size 20 – 21 cm and 90.3 g) were released into the lake. The trout were from the fish hatchery of Mr. K. Peltoniemi, Espoo (Tuunainen 1966b).

The growth rate of these rainbow trout (Figs. 30 – 31) was quite high in 1965 and 1966. In the summer of 1966 the fish were fed with pellets once or twice a week.

One brown trout (3-year-old, 31.6 cm, 320 g), presumably introduced into the lake accidentally with the rainbow trout, and caught on 26. VII. 1966, had grown a little less than the rainbow trout.

Food of the fish released

The diet of the rainbow trout consisted mainly of larvae and pupae of Chironomids, but larvae of Odonata and aerial food were also frequently found (Table 9).

The forage ratios for rainbow trout are presented in Table 10. The percentages of bottom animals were calculated from samples taken at 1 – 5 metres. In Table 11 those organisms which

Table 9. Food of rainbow trout and brown trout in Ahvenlampi. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
Rainbow trout:					
1. VI. 1965	2+	10	72	2.5	Chironomid larvae 50/19 %, Ephemerid larvae 11/5 %, terr. insects 9/11 %
12. VII. 1965	2+	5	120	2.4	Chironomid pupae 44/19 %, Chironomid larvae 31/7 %, terr. insects 18/26 %
7. VI. 1966	3+	6	728	8.5	Chironomid pupae 97/60 %, Libellulid larvae 0.1/2 %
26. VII. 1966	3+	3	227	2.1	Chironomid larvae 73/26 %, Chironomid pupae 25/9 %, Libellulid larvae 0.4/6 %
Brown trout:					
26. VII. 1966	3+	1	19	0.6	Chironomid larvae 48/9 %, Ephemerid larvae 37/18 %, Libellulid larvae 5/36 %, Trichopterous larvae 5/36 %

Table 10. Forage ratios for rainbow trout in Ahvenlampi.

	12. VII. 1965	7. VI. 1966	25. – 26. VII. 1966
Hydracarina	–	–	0.88
Libellulid larvae	0.22	0.83	0.26
Sialis »	–	0.42	–
Chironomid »	0.47	0.01	0.83
» pupae	–	270.00	–
Ceratopogonid larvae	3.03	0.83	–

Table 11. Frequency (%) of occurrence of benthic animals in bottom samples taken from Ahvenlampi on six different dates (A), in stomachs of brown trout (B) and rainbow trout (C) caught on one and four different dates, respectively, and in one sample of brown trout (D) and three samples of rainbow trout (E) taken simultaneously with bottom samples.

	A	B	C	D	E
Gordius sp.	–	–	50	–	–
Oligochaeta	83	–	–	–	–
Hydracarina	50	–	25	–	33
Ephemerid larvae	17	(100)	25	(100)	–
Agrionid »	–	–	75	–	–
Aeschnid »	–	–	25	–	–
Libellulid »	50	(100)	100	(100)	100
Other Odonatous larvae	–	–	50	–	–
Notonecta »	33	–	25	–	–
Corixid »	33	–	25	–	–
» adults	–	–	50	–	–
Dytiscid larvae	17	–	–	–	–
» adults	17	–	50	–	–
Donacia pupae	50	–	–	–	–
Other Coleopterous adults	17	–	–	–	–
Sialis larvae	100	–	25	–	33
Trichopterous larvae	17	(100)	25	(100)	–
Lepidopterous »	–	–	25	–	–
Chaoborus »	50	–	–	–	67
» pupae	–	–	50	–	–
Chironomid larvae	83	(100)	100	(100)	100
» pupae	17	(100)	100	(100)	33
Ceratopogonid larvae	67	–	75	–	67
Tabanid »	–	–	25	–	–
Other Dipterous pupae	17	–	–	–	–

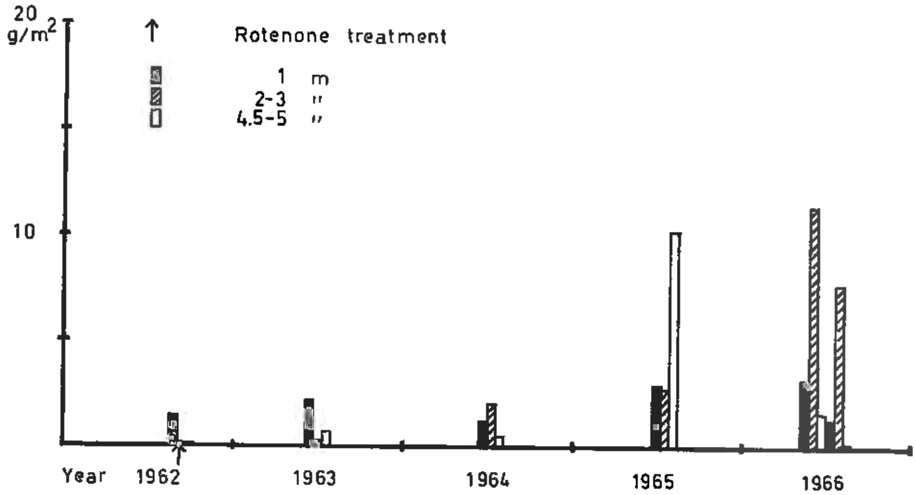

Fig. 9. Biomass of benthic fauna in Ahvenlampi.

were found solely in either bottom animal samples or the fish stomach are also listed.

Reactions of the benthic fauna

The average density and biomass of the benthic animals increased from 1963 to 1966 (Fig. 9), mainly because of the increase in the numbers of Chironomid larvae (cf. Tuunainen 1968). In the fish food (Table 9) both the relative and absolute numbers of larvae and pupae of Chironomids also increased in 1966 compared with 1965.

5. Ulpasjärvi, Pielavesi

General description

63° 14′ 30″ N, 27° 01′ 26″ E, about 150 m above sea level. Area 3.7 hectares, maximum depth 19.5 m, volume 200 000 m^3 (Suomen Kalastusyhdistys 1961). 40 % of the shore-line is stony, 20 % is slightly paludified and 40 % is boggy. The bottom is mainly mud, but there are gravelly patches (Tuunainen 1966a, 1966b). No inlet and no outlet.

The narrow belt of emergent vegetation consists mainly of *Carex* spp. The belt of floating vegetation contains scattered *Sparganium* spp., *Nuphar luteum* and *Nymphaea candida*. Aquatic mosses grow in places at 4 – 5 depth. Fig. 10.

The lake was clearly stratified in summer. In winter the oxygen conditions were satisfactory down to 10 m depth, but in the deeper layers there was a sharp decrease of the oxygen content. During the summer stratification the oxygen content was high in the epilimnion, but there was a total lack of oxygen at depths below 15 – 17 m.

The water was clearly acid; its electrolytic conductivity and $KMnO_4$ consumption were quite low. At the deepest place the $KMnO_4$ consumption was occasionally quite high near the bottom. According to Järnefelt's (1953) classification, the lake must be included among the oligohumous lakes, but it has features nearer to the mesohumous type. Alkalinity, total hardness and Fe content were also low.

Some physical and chemical data (according to Tuunainen 1968) are listed below:

	Depth m	t°C	n	
VI. – IX. 1960 – 1966	0.2 – 1	12.6 – 21.5	10	Maximum on 2. VIII. 1960
	~ 3 – 15		10	Metalimnion
	18.5 – 19.5	3.2 – 4.6	11	
III. – IV. 1962 – 1966	1	0.6 – 0.8	3	
	10	4.0 – 4.2	3	
	19	4.1 – 4.3	3	

Days without ice: 180 – 205 days per year (Tuunainen 1966a, 1966b)

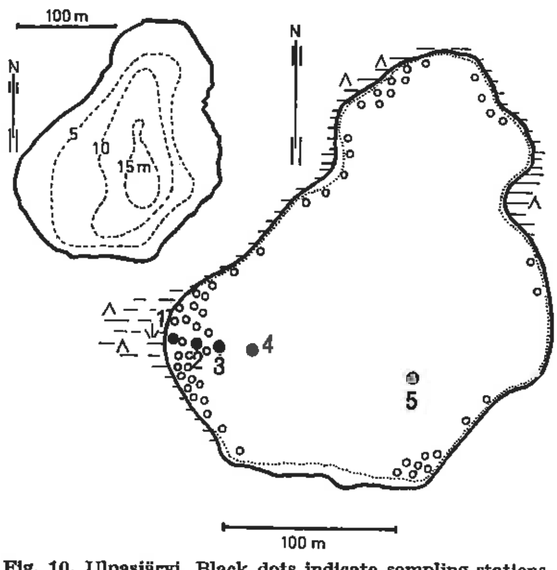

Fig. 10. Ulpasjärvi. Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VI. – X.	0.2 – 3	8.6 – 11.1	96 – 122	9	5.8 – 6.1	5
1960 – 1966	9 – 15	1.4 – 8.6	12 – 75	9	4.6 – 5.5	5
	17 – 19	0.0 – 0.3	0	8	4.3 – 6.1	6
III. – IV.	1 – 4	8.0 – 10.1	62 – 74	4	5.5 – 6.3	3
1962 – 1966	10 – 15	0.9 – 6.8	7 – 54	4	5.3 – 5.8	3
	19	0.0	0	3	5.3 – 5.5	2

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
VI. – X.	0.2 – 3	10 – 16	7	15.2 – 39.5	10
1960 – 1966	9 – 15	11 – 16	7	15.2 – 53.5	9
	17 – 19	12 – 17	2	27.1 – 63.5	4
III. – IV.	1 – 4	12 – 15	2	20.2 – 24.9	4
1962 – 1966	10 – 15	13 – 15	2	23.0 – 26.7	4
	19	–	–	25.7 – 29.7	2

	Depth m	Colour Pt mg/l Range	x̄	n	Transparency m Range	x̄	n
2. VIII. 1960	3	15 – 35	23.2	11	3.0 – 4.3	3.9	6
27. VII. 1966	1 – 15	15 – 40	30.0	10			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n	Fe mg/l	n
VII. – IX.	0.2 – 3	0.09	1	0.17 – 0.31	6	0.00 – 0.06	5
1960 – 1966	10 – 19	0.10	1	0.16 – 0.32	6	0.05 – 0.32	5
IV.	1 – 4	–	–	0.20 – 0.22	2	0.06 – 0.11	2
1962 – 1965	10 – 15	–	–	0.22 – 0.46	2	0.03 – 0.21	2

Benthic fauna and plankton

Sampling stations are seen in Fig. 10. The most important constituents of the bottom fauna were *Pisidium* spp., *Asellus aquaticus*, and larvae of *Sialis*, Trichoptera and Chironomids (TUUNAINEN 1968).

The average biomass values are quite low (Fig. 11). At the time of poisoning (2. VIII. 1960), the bottom fauna was very poor and bottom animals were found only in 1-metre samples (Suomen Kalastusyhdistys 1961).

Plankton samples collected at the time of the poisoning contained an average of 130 specimens of zooplankton per 10 l. The most abundant phytoplankton species were *Anabaena flos-aquae* and *Tetrastrum luteracantrum*, the most abundant zooplankton species *Daphnia cristata*.

Fish population

At the time of the poisoning, the natural fish population consisted of roach, perch and ruff, altogether about 500 specimens or 27.5 kg per hectare (Suomen Kalastusyhdistys 1961).

On 8. – 9. VI. 1961, 1 500 specimens of brown trout fry and 1 500 specimens of rainbow trout fry (405 per hectare of each species) were released into the lake. The brown trout were from Simunankoski fish hatchery, Laukaa, and the rainbow trout from Kontiolahti fish hatchery. In addition, 2 000 specimens of brown trout fry (540 per hectare) from Kontiolahti fish hatchery were released into the lake on 25. V. 1964, but not one of them was caught later. In the spring of 1963, 5 000 – 10 000 specimens of vendace (*Coregonus albula* L.) fry an dabout 100 specimens of older vendace were released into the lake to provide food for the trout (TUUNAINEN 1966b).

The growth rates of both brown trout and rainbow trout in the first growth period were higher than the means of the values in the other lakes studied, whilst the growth rates for the second, third and fourth growth periods agree fairly well with the means of the values obtained from other lakes (Figs. 28 – 31).

Food of the fish released

Larvae of Trichoptera as well as *Asellus aquaticus*, and larvae of Ephemerids, Agrionids,

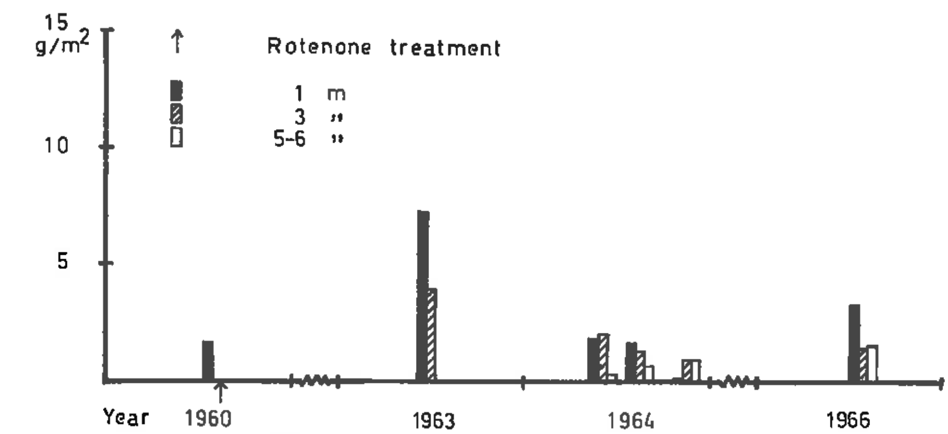

Fig. 11. Biomass of benthic fauna in Ulpasjärvi.

Aeschnids and Libellulids constituted the main food of the brown trout, whilst the proportion of Chironomid larvae and pupae was quite low (TUUNAINEN 1966b). The proportion of aerial food was considerable during the period of open water (Table 12).

The food of the rainbow trout was similar, although the numbers of larvae of Aeschnids and Libellulids were clearly lower (Table 12). Zooplankton also made an important contribution to the food of two-year-old rainbow trout.

Tables 13 and 14 show the selective feeding of the two trout species.

Table 12. Food of brown trout and rainbow trout in Ulpasjärvi. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
Brown trout:					
12. – 13. XII. 1962	1 +	2	16	2.4	Trichopterous larvae 92/91 %, Chironomid larvae 6/0.5 %
18. – 20. VI. 1963	2 +	20	62	4.0	Terr. insects 56/32 %, Trichopterous larvae 22/35 %, Libellulid larvae 6/15 %
4. – 5. XII. 1963	2 +	9	19	3.6	Trichopterous larvae 78/84 %, Libellulid larvae 4/10 %, Aeschnid larvae 2/11 %
9. – 11. VI. 1964	3 +	11	90	2.1	Trichopterous larvae 29/45 %, terr. insects 40/28 %, *Asellus* 27/20 %
18. – 23. XI. 1964	3 +	6	61	6.1	Trichopterous larvae 48/47 %, Agrionid larvae 39/20 %, Libellulid larvae 3/8 %
19. VI. 1965	4 +	9	35	3.6	Trichopterous larvae 46/29 %, *Asellus* 22/18 %, terr. insects 24/11 %
30. XI. 1965	4 +	2	46	8.0	Trichopterous larvae 54/42 %, Dytiscid adults 8/51 %, *Asellus* 20/2 %
Rainbow trout:					
13. XII. 1962	1 +	16	16	1.6	Trichopterous larvae 42/66 %, *Asellus* 28/9 %, Dytiscid adults 6/6 %
18. – 20. VI. 1963	2 +	12	172	2.1	Cladocera 50/33 %, terr. insects 36/39 %
4. – 5. XII. 1963	2 +	4	6	2.0	Trichopterous larvae 83/82 %, Ephemerid larvae 10/2 %
9. – 11. VI. 1964	3 +	8	143	2.9	*Asellus* 63/38 %, Trichopterous larvae 9/38 %, terr. insects 14/11 %
18. – 23. XI. 1964	3 +	2	73	5.4	Trichopterous larvae 29/30 %, *Asellus* 58/11 %, Agrionid larvae 3/3 %
19. VI. 1965	4 +	13	62	3.3	*Asellus* 50/27 %, terr. insects 39/17 %, Trichopterous larvae 5/6 %
30. XI. 1965	4 +	2	7	0.1	*Asellus* 54/41 %, Trichopterous larvae 26/42 %, Ephemerid larvae 20/6 %

Table 13. Forage ratios for brown trout and rainbow trout in Ulpasjärvi.

	18. – 20. VI. 1963	9. – 11. VI. 1964	18. – 23. XI. 1964
Brown trout:			
Asellus aquaticus	0.26	1.16	0.03
Ephemerid larvae	6.15	–	–
Odonatous »	3.26	–	–
Sialis »	1.54	0.02	–
Trichopterous »	27.05	5.15	1.76
Lepidopterous »	0.46	–	–
Chironomid »	0.88	0.39	–
» pupae	6.15	–	–
Rainbow trout:			
Asellus aquaticus	1.46	1.89	1.60
Hydracarina	7.24	–	–
Ephemerid larvae	12.60	–	–
Odonatous »	0.80	–	–
Trichopterous »	2.41	1.10	1.06
Chironomid »	1.80	0.14	–
» pupae	25.05	–	–

Table 14. Frequency (%) of occurrence of benthic animals in bottom samples taken from Ulpasjärvi on seven different dates (A), in stomachs of brown trout (B) and rainbow trout (C) caught on seven different dates and in three samples of brown trout (D) and rainbow trout (E) taken simultaneously with bottom samples.

	A	B	C	D	E
Oligochaeta	29	–	–	–	–
Mollusca [1]	–	–	29	–	–
Pisidium sp.	71	–	14	–	–
Asellus aquaticus	100	86	100	100	100
Argyroneta aquatica	–	29	–	–	–
Hydracarina	43	–	29	–	33
Ephemerid larvae	14	57	100	33	33
Agrionid »	–	14	29	–	–
Aeschnid »	–	43	–	–	–
Libellulid »	–	57	29	–	–
Other Odonatous larvae	14	14	14	33	33
Corixid »	–	–	14	–	–
» adults	14	100	71	–	–
Dytiscid larvae	–	14	14	–	–
» adults	–	71	29	–	–
Sialis larvae	86	43	14	67	–
Trichopterous larvae	57	100	100	100	100
Lepidopterous »	14	14	–	33	–
Chaoborus »	–	–	14	–	–
Chironomid larvae	86	43	57	67	67
» pupae	14	29	43	33	33
Ceratopogonid larvae	14	–	14	–	–
Other Dipterous »	–	14	–	–	–

[1] according to JAHNSSON (1963)

Reactions of the benthic fauna

The bottom animal density increased after the poisoning, but in June and August 1964 it decreased again. The increase of biomass values after 1964 is presumably due to the decrease of the fish stock.

6. Sahalampi, Pohja

General description

60° 17′ N, 23° 30′ E, 54 m above sea level. Area 0.8 hectares, maximum depth 3.0 m, volume 16 000 m³ (TOIVO-

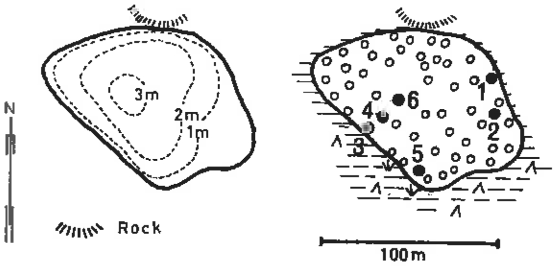

Fig. 12. Sahalampi. Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

NEN 1962). About 99 % of the shoreline is swampy and 1 % is rocky. The bottom is mud (TUUNAINEN 1966a, 1966b). No inlet and no outlet.

No emergent vegetation. *Nuphar luteum* grows sparsely everywhere except in a small area at the deepest place. Near the southeast shore there is some *Nymphaea candida*. Aquatic mosses at 2 – 3 m depth, Fig. 12.

The temperature of the whole water mass was quite high in summer, and there was no clear stratification.

In winter the oxygen content was very low, the minimum being observed on 5. IV. 1965 (TUUNAINEN 1968). Intensive seine fishing of trout carried out on 5. – 6. X. 1964 may be one reason for the decrease of the oxygen content in winter 1964/1965, because oxygen-consuming sediments were disturbed and mixed with the water mass. In the late winter of 1964/1965, some of the trout died of oxygen deficiency and two brown trout and one rainbow trout were found dead in the spring after the melting of the ice. However, many of the fish survived the winter (TUUNAINEN 1966 b). Less intensive seine fishing in the autumn of 1963 did not cause a similar effect.

Sahalampi is quite acid; during the period of observations there was a fluctuation of pH 4.8 – 7.1. This is a consequence of the low hydrocarbonate content (cf. e.g. JÄRNEFELT 1958, ALM 1960).

The electrolytic conductivity and $KMnO_4$ consumption were quite low, but there were great fluctuations in the latter. Very great fluctuations were found in colour and transparency. In the Fe content considerable fluctuations were also found. Iron may be the main factor producing the colour of the water; this is indicated by the analytic data. Because of the great fluctuation of colour and transparency, the lake is difficult to classify; the present author (TUUNAINEN 1966a, 1966b) regarded it as a poly-mesohumous lake in the sense of ALM (1960), but the data collected in 1962 – 1967 show that it belongs to JÄRNEFELT's (1953) oligohumous type. The values of methyl orange alkalinity and total hardness were quite low. Some physical and chemical data (according to TUUNAINEN 1968) are listed below:

	Depth m	t °C	n	
VI. – IX. 1962 – 1967	0.2 – 1	16.6 – 24.3	10	Maximum on 5. VII. 1966
	2.5 – 3	10.1 – 22.6	10	No stratification in summer
II. – IV. 1962 – 1966	0.5 – 1	0.6 – 1.3	5	
	2.5 – 3	3.2 – 4.0	5	

Days without ice: 210 – 227 days per year (Atlas of Finland 1960)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VI. – X. 1962 – 1967	0.2 – 1	6.6 – 10.6	70 – 120	8	5.2 – 7.1	8
	2.5 – 3	3.2 – 10.8	30 – 120	8	5.3 – 6.3	8
II. – IV. 1962 – 1966	0.5 – 1	1.5 – 9.4	11 – 69	5	4.8 – 5.9	5
	2.5 – 3	0.0 – 1.8	0 – 14	5	5.5 – 6.4	5

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
VI. – X. 1962 – 1967	0.2 – 1	20 – 30	6	13.9 – 33.0	4
	2.5 – 3	20 – 31	6	15.5 – 39.0	4
II. – IV. 1962 – 1966	0.5 – 1	25 – 39	5	25.4 – 31.0	4
	2.5 – 3	25 – 38	5	26.0 – 59.0	4

	Depth m	Colour Pt mg/l Range	x̄	n	Transparency m Range	x̄	n
27. II. 1962 – 24. X. 1967	0.2 – 1	5 – 40	22.2	18	1.5 – > 3.0 (bottom)	> 3.0	12
	2.5 – 3	5 – 100	35.4	18			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n	Fe mg/l	n
VI. – X. 1963 – 1967	0.2 – 0.5	0.07 – 0.10	10	0.30 – 0.50	8	0.00 – 0.41	7
	2.5 – 3.0	0.05 – 0.14	10	0.28 – 0.42	8	0.00 – 0.88	7
II. – IV. 1964 – 1966	0.5 – 0.7	0.12	1	–	–	0.19 – 0.39	2
	2.5 – 3.0	0.26	1	–	–	1.19 – 3.34	2

Benthic fauna and zooplankton

The bottom fauna mostly consisted of *Pisidium* spp., but larvae of Libellulids, *Sialis*, Chironomids and Ceratopogonids were also important (TUUNAINEN 1968).

The biomass was high compared with other lakes of the same type. In winter 1962/1963 it remained unchanged, but during summer 1963 a rapid increase was observed, chiefly owing to a marked increase in the numbers of *Pisidium* after the poisoning. Peaks in biomass values were again found in the autumns of 1965 and 1967 (Figs. 13 – 14).

In spring 1963, when the brown trout and rainbow trout fry was released, zooplankton was found to be quite plentiful in Sahalampi.

The composition of 14 samples (1.4 l each) taken on 11. VI. 1963 was as follows (specimens per 10 l):

Rotatoria	222
Bosmina sp.	1
Cladocerous embr.	2
Diaphanosoma brachyurum	68
Ceriodaphnia sp.	175
Hydracarina	1
Total	469

Fish population

At the time of the poisoning (27. VIII. 1962) the fish population consisted of perch and ruff, about 70 kg/hectare (TOIVONEN 1962).

On 25. V. 1963, 1 500 specimens of brown trout fry and 500 specimens of rainbow trout fry (2 500 specimens per hectare), both 3 – 5 cm in

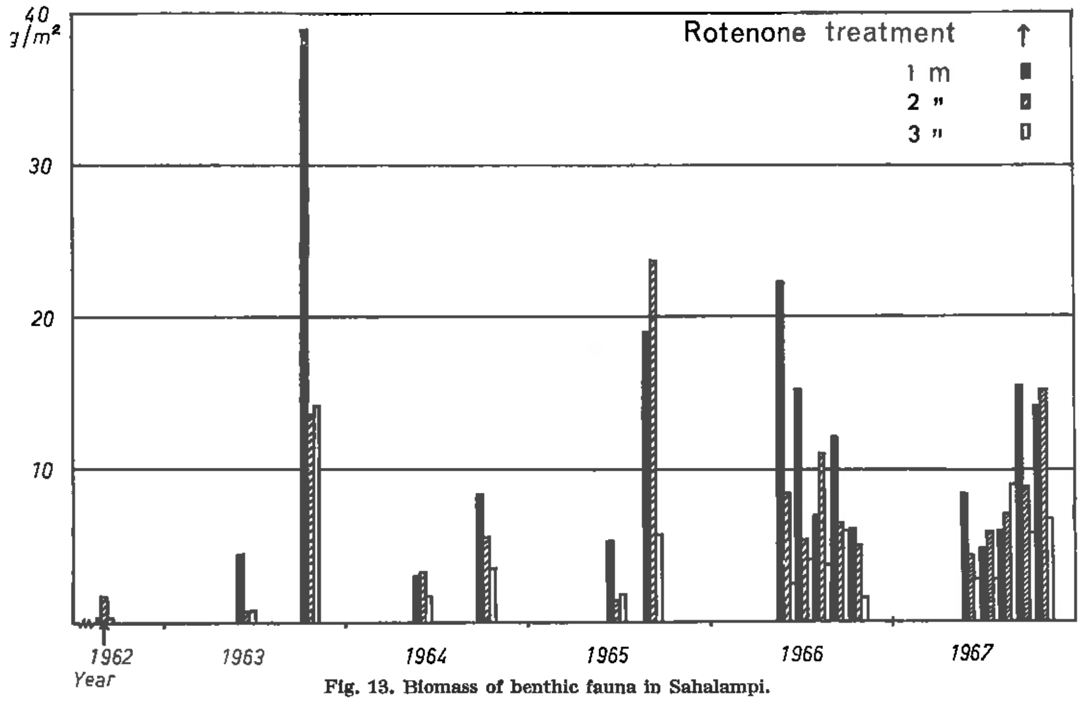

Fig. 13. Biomass of benthic fauna in Sahalampi.

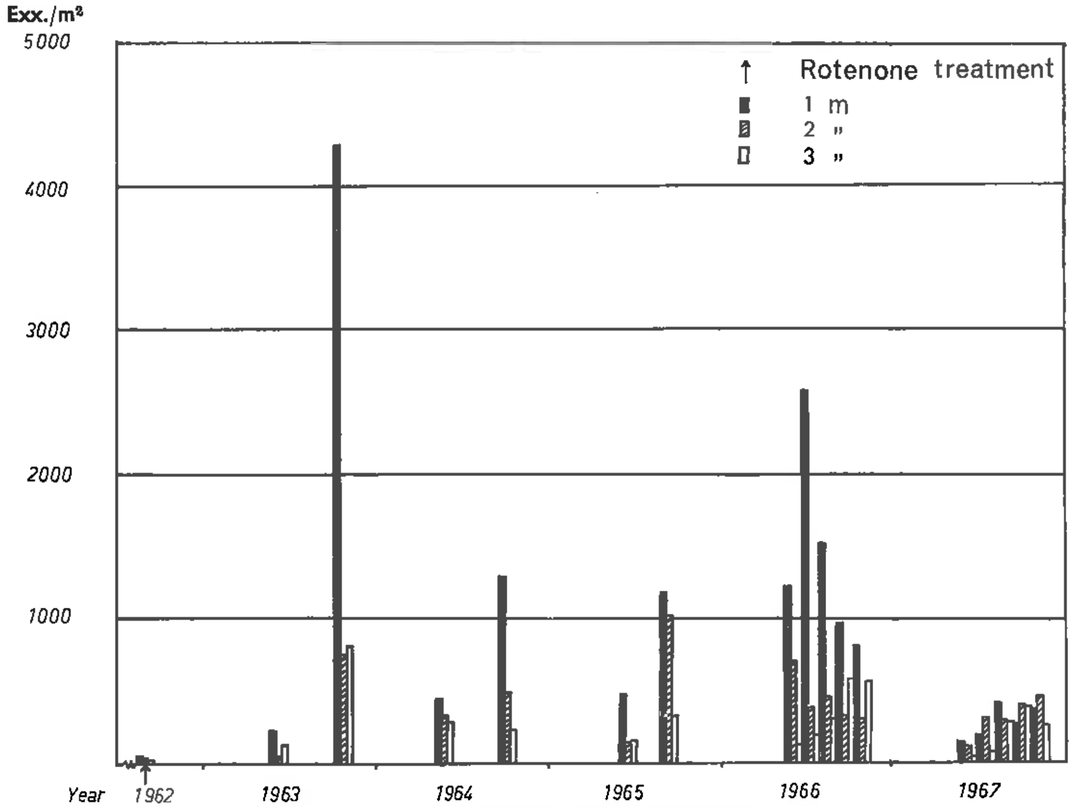

Fig. 14. Density of benthic fauna in Sahalampi.

length, were released into the lake. The fry was from Porla fish hatchery, Lohja. Data on the growth of the trout are presented in Figs. 28 – 31. The growth rates of both species were high in the first year, and even later were higher than average (cf. TUUNAINEN 1968).

Food of the fish released

Larvae of Agrionids, Aeschnids, Libellulids and Trichoptera, as well as larvae and pupae of Chironomids, were important food of both trout species (Table 15). In addition, zooplankton, aerial food, and parts of plants were observed. A quotient of similarity of 63 – 87 % was calculated (TUUNAINEN 1966b).

Tables 16 – 17 show the selective feeding of brown trout and rainbow trout. The diet of the latter was less variable than that of the brown trout.

Table 15. Food of brown trout and rainbow trout in Sahalampi, A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), D = main food items as percentages (number/volume).

	A	B	C	D	E
Brown trout:					
17. X. 1963	0 +	3	19	0.6	Agrionid larvae 25/27 %, Libellulid larvae 13/28 %, Trichopterous larvae 3/33 %
28. – 29. V. 1964	1 +	10	186	1.1	Chironomid larvae 61/41 %, » pupae 27/20 %, Libellulid larvae 8/12 %
5. – 6. X. 1964	1 +	11	5	1.0	Trichopterous larvae 39/41 %, Libellulid larvae 28/32 %, Agrionid larvae 16/12 %
16. V. 1965	2 +	4	126	3.8	Libellulid larvae 13/46 %, Chironomid larvae 37/7 %, *Sialis* larvae 16/14 %
22. VI. 1965	2 +	1	41	1.0	Corixid larvae 68/15 %, Libellulid larvae 2/50 %, terr. insects 13/25 %
9. IX. 1965	2 +	5	49	1.5	Cladocera 44/13 %, *Chaoborus* larvae 26/11 %, Trichopterous larvae 10/24 %
1. VI. 1966	3 +	4	68	5.4	Libellulid larvae 22/41 %, Chironomid larvae 28/2 %, Corixid adults 20/8 %
2. IX. 1966	3 +	6	63	5.5	Libellulid larvae 22/56 %, Trichopterous larvae 23/22 %, Agrionid larvae 12/5 %
14. – 15. X. 1966	3 +	7	41	4.2	Agrionid larvae 54/25 %, Trichopterous larvae 22/17 %, Aeschnid larvae 3/17 %
Rainbow trout:					
28. – 29. V. 1964	1 +	5	91	2.0	Chironomid pupae 62/22 %, Chironomid larvae 30/5 %, Aeschnid larvae 2/26 %
5. – 6. X. 1964	1 +		13	4.7	Trichopterous larvae 69/66 %, Libellulid larvae 23/28, terr. Arachnids 8/6 %

Table 16. Forage ratios for brown trout and rainbow trout in Sahalampi.

	16. – 17. X. 1963	28. – 29. V. 1964	5. – 6. X. 1964	21. – 22. VI. 1965	9. IX. 1965	1. – 2. VI. 1966	2. IX. 1966	14. – 15. X. 1966
Brown trout:								
Pisidium sp.	–	–	–	–	–	0.03	–	–
Asellus aquaticus	6.75	–	–	–	–	0.71	–	0.48
Agrionid larvae	–	0.41	–	–	0.20	19.34	5.30	32.70
Aeschnid »	–	–	–	–	–	25.20	–	–
Libellulid »	5.77	5.97	39.10	1.35	0.42	4.41	4.80	3.16
Sialis »	–	–	0.04	0.46	–	1.93	0.07	0.34
Trichopterous »	–	1.38	65.40	1.73	6.64	14.20	5.56	12.58
Chaoborus »	–	0.38	–	–	–	–	42.70	–
Chironomid »	0.61	2.07	0.20	–	0.13	1.85	–	0.04
» pupae	–	119.40	–	8.70	–	–	–	–
Ceratopogonid larvae	–	0.24	0.72	–	–	–	–	–
Rainbow trout:								
Hydracarina	–	0.69	–	–	–	–	–	–
Agrionid larvae	–	0.41	–	–	–	–	–	–
Libellulid »	–	1.49	30.50	–	–	–	–	–
Trichopterous »	–	1.38	111.20	–	–	–	–	–
Chaoborus »	–	0.38	–	–	–	–	–	–
Chironomid »	–	1.02	–	–	–	–	–	–
» pupae	–	233.00	–	–	–	–	–	–
Ceratopogonid larvae	–	0.25	–	–	–	–	–	–

Table 17. Frequency (%) of occurrence of benthic animals in bottom samples taken from Sahalampi on twelve different dates (A), in stomachs of brown trout (B) and rainbow trout (C) caught on nine and two different dates, respectively, and in eight samples of brown trout (D) and two samples of rainbow trout (E) taken simultaneously with bottom samples.

	A	B	C	D	E
Oligochaeta	25	–	–	–	–
Pisidium sp.	100	33	–	13	–
Asellus aquaticus	58	44	–	38	–
Argyroneta aquatica	17	–	–	–	–
Hydracarina	83	–	50	–	50
Ephemerid larvae	–	11	–	–	–
Agrionid »	50	100	50	63	50
Aeschnid »	17	44	50	13	–
Libellulid »	92	100	100	100	100
Notonecta »	8	11	–	–	–
Corixid »	8	22	50	–	–
» adults	–	67	–	–	–
Dytiscid larvae	8	–	–	–	–
» adults	–	44	50	–	–
Other Coleopterous larvae	17	–	–	–	–
Sialis larvae	92	67	–	63	–
Trichopterous larvae	75	100	100	88	100
Lepidopterous »	17	–	–	–	–
Chaoborus »	50	33	50	–	50
» pupae	8	11	–	25	–
Chironomid larvae	100	78	50	75	50
» pupae	42	33	50	25	50
Ceratopogonid larvae	92	33	50	25	50
Other Dipterous »	8	–	–	–	–
» » pupae	8	–	–	–	–

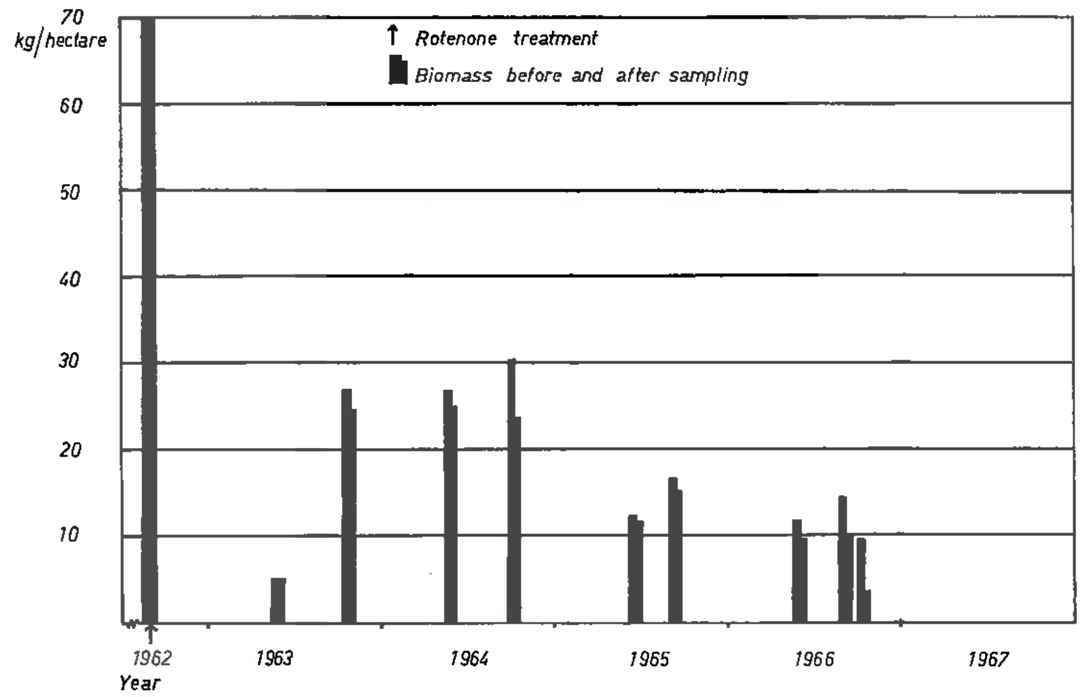

Fig. 15. Biomass of fish stock in Sahalampi

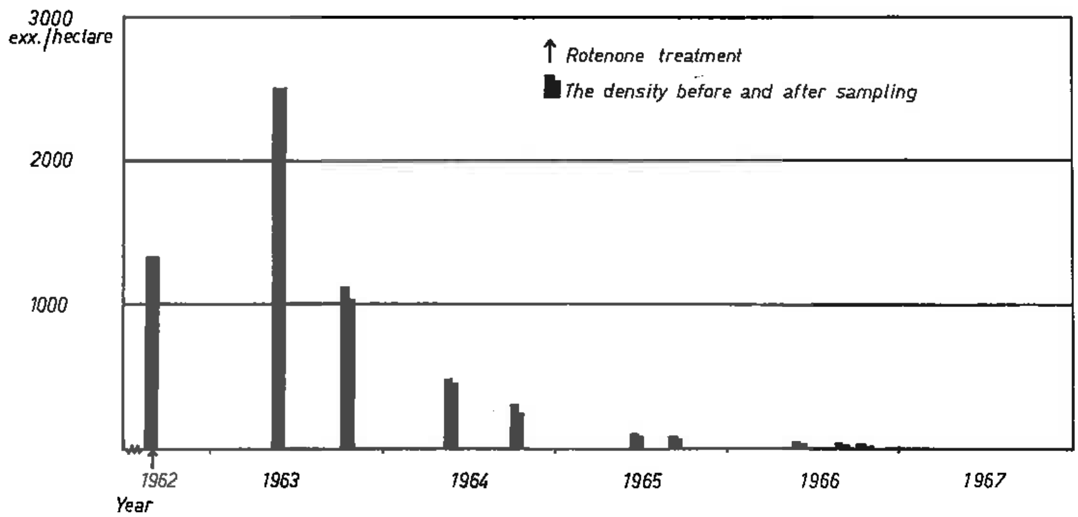

Fig. 16. Density of fish stock in Sahalampi

Reactions of the benthic fauna

As reported earlier (Tuunainen 1966a, 1966b), a clear interaction was discernible, both in densities and in biomass values, between the fish stock and the bottom fauna. This interaction is seen in Figs. 13 – 17. The bottom fauna was originally very poor, but after the killing of the fish, a rapid increase occurred. The observations (Table 15) indicate that the brown trout fed on bottom animals toward the end of their first growth period. The decrease of the fish stock is here again reflected in higher average biomass values of the bottom fauna in 1965 – 1967.

7. Julkujärvi, Ylöjärvi

General description

61° 33′ 36″ N, 23° 31′ 20″ E, 143 m above sea level. Area 3.2 hectares, maximum depth 9.8 m, volume 100 000 m^3 (Toivonen 1962). Of the shoreline 55 % is stony, 33 % sandy and 12 % paludified. Bottom mainly mud, part of the littoral stony and sandy. Springs in places (Tuunainen 1966a, 1966b). No inlet and no outlet.

The belt of emergent vegetation consists of high sedges, which are absent on stony shores. *Nuphar luteum* grows to a depth of 1.5 – 2 m. Fig. 17.

The lake is clearly stratified in summertime.

The oxygen content was quite low in many winters. At least in the late winter of 1964/1965 some of the trout died of lack of oxygen; after the melting of the ice about 20 rainbow trout were found dead, but most of the trout survived (Tuunainen 1966b). During the summer stratification, the oxygen content was high only from the surface to 3 m depth, and there was a marked deficiency in the deeper layers. The lake is slightly acid, and its electrolytic conductivity and $KMnO_4$ consumption are quite low.

According to Järnefelt's (1953) classification, the lake is intermediate between the oligo- and mesohumous types. The transparency is as in mesohumous lakes.

Some chemical and physical data (according to Tuunainen 1968) are listed below:

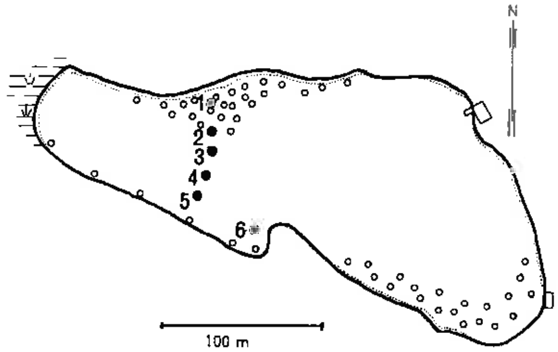

Fig. 17. Julkujärvi. Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

	Depth m	t °C	n	
VI. – IX. 1961 – 1966	0.5 – 1	10.4 – 19.8	7	Maximum on 9. VI. 1965
	~ 3 – 7		6	Metalimnion
	7.0 – 9.8	5.7 – 10.2	7	
III. – IV. 1963 – 1966	0.5 – 1	0.4 – 1.0	6	
	3	0.9 – 3.5	5	
	7	4.2 – 4.5	2	

Days without ice: 194 – 200 days per year (Tuunainen 1966a, 1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VI. – IX. 1961 – 1966	0.5 – 1	9.5 – 10.6	89 – 120	5	5.8 – 7.2	4
	3	8.9 – 9.4	88 – 95	3	5.7 – 7.1	4
	5 – 7	0.1 – 9.3	0 – 81	5	5.6 – 7.1	4
III. – IV. 1962 – 1966	0.5 – 1	1.8 – 10.0	13 – 74	6	5.8 – 6.1	3
	3	0.7 – 5.4	5 – 25	5	5.6 – 5.8	3
	5 – 7	0.2 – 0.6	0 – 5	4	5.8 – 6.0	3

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
VI. – IX. 1961 – 1966	0.5 – 1	12 – 15	3	20 – 29	3
	3	11 – 14	3	20 – 26	3
	5 – 7	11 – 26	3	21 – 32	3
III. – IV. 1962 – 1966	0.5 – 1	14	1	22 – 42	2
	3	15	1	24 – 38	2
	5 – 7	21	1	30 – 51	2

	Depth m	Colour Pt mg/l Range	$\bar{x}$	n	Transparency m	n
17. IX. 1962 – 22. VIII. 1966	1.0	15 – 35	26.6	3	2.8	1
	7.0	20 – 45	33.3	3		

Benthic fauna and zooplankton

Pisidium spp., *Asellus aquaticus* and Chironomid larvae were important constituents of the bottom fauna. The increase of the biomass from 1963 to 1964 (Fig. 18) is chiefly

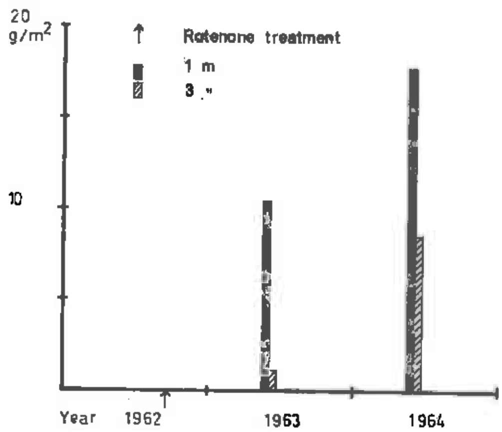

Fig. 18. Biomass of benthic fauna in Julkujärvi.

due to the increase of *Pisidium* and *Asellus aquaticus* (cf. TUUNAINEN 1968).

At the time of release of brown trout and rainbow trout into the lake, the zooplankton consisted mainly of Rotatoria. The composition (specimens per 10 l) of 54 samples (1.4 l each) taken on 6. – 7. VI. 1963 was as follows:

Rotatoria	127
Daphnia sp.	1
Bosmina sp.	5
Holopedium gibberum	+
Calanids	1
Cyclopids	+
Ceriodaphnia	+
Hydracarina	+
Total	134

Fish population

At the time of the poisoning (17. IX. 1962), the natural fish stock consisted of perch and crucian carp, their total biomass being 36.3 kg/hectare (TOIVONEN 1962). An introduction of brown trout and rainbow trout fry on 29. V. 1963 failed because rotenone had persisted over the winter.

According to TOIVONEN (1962), 0.8 mg/l rotenone was used to kill the very resistant crucian carp. On 6. VI. 1963, 50 kg crystalline $KMnO_4$ or 0.5 mg/l was used to eliminate the poisonous effect of the rotenone. On 26. VI. 1963, 250 specimens of brown trout fry and 350 specimens of rainbow trout fry (a total of 187 per hectare) were released into the lake. On 30. X. 1963, 400 specimens of one-summer-old brown trout and 600 rainbow trout of the same age were released into the lake. After the second introduction the total density was 499 specimens per hectare. Both batches of rainbow trout originated from Myllypuro hatchery, Ylöjärvi. The brown trout originated from Indalsälven, Sweden (Mr. I. Vuorinen, personal communication).

The growth rate of the brown trout was low during the first two growth periods but considerably higher during the third growth period. The four-summer-old brown trout were of nearly the same size as brown trout of the same age in Kivi-Ahveroinen (Figs. 28 – 29). It was impossible to tell whether these were trout introduced in the spring or in the autumn, because the first growth area of the scales was quite small in both batches.

In the rainbow trout the growth rate from the very beginning was higher than in the other lakes investigated. The fish that had been introduced in the spring were easy to distinguish from those released in the autumn, because in the former the first growth area in the scales was clearly larger than in those which were kept in the hatchery until autumn. Figs. 30 – 31 show that the size difference between these groups persisted, because their growth rates were about equal.

Table 18. Food of rainbow trout in Julkujärvi. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
2. VI. 1964	1+	11	971	4.4	Chironomid pupae 81/78 %, *Asellus* 9/10 %, terr. insects 9/9 %
20. X. 1964	1+	14	192	2.5	*Asellus* 82/72 %, Trichopterous larvae 3/22 %, Chironomid larvae 11/3 %

Table 19. Frequency (%) of occurrence of benthic animals in bottom samples taken from Julkujärvi on two different dates (A), in stomachs of brown trout (B) and rainbow trout (C) caught on one and two different dates, respectively, and in one sample of rainbow trout (D) taken simultaneously with bottom samples.

	A	B	C	D
Pisidium sp.	100	–	50	–
Asellus aquaticus	100	(100)	100	(100)
Nepa sp.	–	–	50	–
Corixid adults	50	(100)	100	(100)
Dytiscid larvae	50	–	100	–
» adults	–	–	50	–
Donacia pupae	100	–	–	–
Sialis larvae	50	–	–	–
Trichopterous larvae	50	–	100	–
Chironomid »	100	–	100	(100)
» pupae	50	–	50	–

Food of the fish released

The diet of rainbow trout was found to consist mainly of *Asellus aquaticus* as well as larvae and pupae of Chironomids. Food items are listed in Tables 18 and 19.

The forage ratios for eleven rainbow trout collected on 2. VI. 1964 were as follows:

Asellus aquaticus	0.25
Corixid adults	1.00
Chironomid larvae	0.02

Reactions of the benthic fauna

After the poisoning there was a marked increase in both the density and the biomass of the bottom fauna (Fig. 18). Because of the small fish population the bottom fauna increased more than in the natural state.

8. Särkilampi, Saarijärvi

General description

62° 45′ N, 25° 09′ E, 145 m above sea level. Area 2.5 hectares, maximum depth 5.5 m volume 75 000 m³ (Toivonen 1962). The shores are slightly paludified. Bottom mud (Tuunainen 1966a, 1966b). No inlet and no outlet.

A belt of sedges on the shore. *Nuphar luteum* and *Nymphaea candida* grow to a depth of 1.5 m. Aquatic mosses at a depth of 3 metres. Fig. 19.

Thermal stratification is incomplete in summer, with the hypolimnion either partly or completely lacking.

In March 1966 the oxygen content was quite low. Death of trout in the winters 1963/1964 and 1964/1965 was presumably caused by lack of oxygen in the ice-covered lake or at the time of the spring circulation as in polluted lakes. In summer the oxygen content was high down to two metres, whilst it was temporarily low in the deeper water even in summer.

The water is slightly acid. Electrolytic conductivity, $KMnO_4$ consumption, alkalinity, total hardness and Fe content are low. According to Järnefelt's (1953) classification, the lake is mesohumous but in the colour of the water it resembles the oligohumous type.

Some physical and chemical data (according to Tuunainen 1968) are given below:

	Depth m	t °C	n	
VI. – VIII. 1962 – 1966	0.2 – 1	13.1 – 21.4	7	Maximum on 20. VII. 1965
	~ 4 – 5.5			Metalimnion
	4.5 – 5.5	6.3 – 14.6	7	
III. 1966	1	1.0	1	
	3	3.3	1	
	5.3	4.0	1	

Days without ice: 192 – 196 days per year (Atlas of Finland 1960)

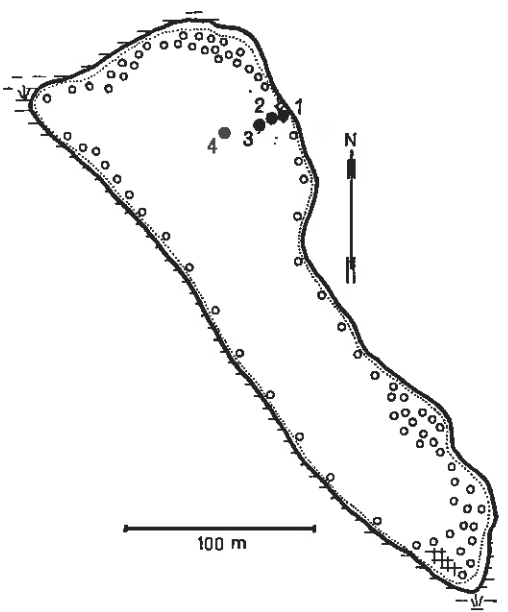

Fig. 19. Särkilampi. Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

	Depth m	O_2 mg/l	O_2 %	n	pH	n
VII. – VIII. 1962 – 1966	0.2 – 1	6.8 – 11.0	72 – 126	5	5.9 – 6.7	4
	3	0.9 – 11.8	10 – 127	5	5.8 – 6.7	3
	4.5 – 5	0.0 – 8.2	0 – 83	5	5.8 – 6.4	4
III. 1966	1	5.9	43	1	5.0	1
	3	1.6	13	1	5.8	1
	5	0.8	7	1	5.9	1

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n
VII. – VIII. 1962 – 1966	0.2 – 1	19 – 24	5	25.3 – 30.0	4
	3	18 – 31	2	26.0 – 29.9	3
	4.5 – 5	18 – 36	5	26.0 – 34.0	4
III. 1966	1	26	1	29.6	1
	3	32	1	29.6	1
	5	30	1	33.1	1

	Depth m	Colour Pt mg/l Range	$\bar{x}$	n	Transparency m Range	$\bar{x}$	n
7. VIII. 1962 – 23. VIII. 1966	0.2 – 1	20 – 30	25.7	4	2.0 – 3.7	2.8	5
	4.5 – 5	30 – 60	45.0	4			

	Depth m	Alkalinity mval/l	n	Total hardness °dH	n	Fe mg/l	n
VII. 1965 – 1966	0.2 – 0.5	0.08 – 0.17	2	0.33 – 0.38	2	–	–
	4.5 – 5	0.17 – 0.19	2	0.48 – 0.49	2	–	–
III. 1966	2	0.16	1	0.24	1	0.14	1
	5	0.27	1	0.36	1	0.60	1

Benthic fauna and zooplankton

The bottom fauna consisted mainly of *Pisidium* spp., *Asellus aquaticus*, and larvae of *Sialis*, *Chaoborus* and Chironomids (Tuunainen 1968). In comparison with the other lakes investigated, the biomass of the benthic fauna was

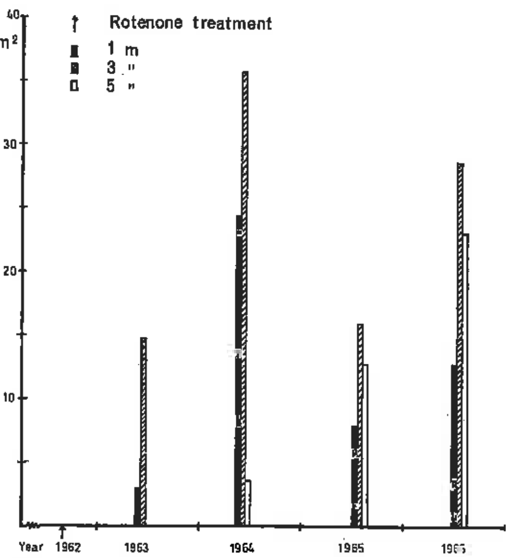

Fig. 20. Biomass of benthic fauna in Särkilampi.

quite high. The increase in the biomass of the bottom fauna from 1963 to 1964 was mainly due to the increase in the numbers of *Asellus aquaticus* and *Pisidium* spp., and the subsequent decrease from 4. VI. 1964 to 20. VII. 1965 was mainly due to the decline in the numbers of *Asellus*. In addition, the brown trout and rainbow trout released in summer 1964 may also have reduced the numbers of the bottom fauna. A further increase in the benthic fauna was observed after the fish stock decreased (Fig. 20). On 6. VII. 1963 the composition of 30 zooplankton samples (1.4 l each) was as follows (specimens per 10 l):

Rotatoria	7
Bosmina sp.	+
Cladocerous embr.	1
Ceriodaphnia sp.	17
Chydorus sp.	8
Diaphanosoma brachyurum	+
Chaoborus sp.	+
	Total 33

Fish population

At the time of the poisoning (30. VIII. 1962), the fish population consisted of perch, roach, ruff, pike and burbot, in total 79.6 kg per hectare (Toivonen 1962).

Brown trout fry and rainbow trout fry (5 000 specimens each) were released into the lake in spring 1963. These fish died during the following winter owing to the lack of oxygen.

On 19. V. 1964, 500 one-year-old (10 cm, 10 – 15 g) brown trout and, on 10. VII. 1964, 500 one-year-old (10 – 15 cm, 15 – 25 g) rainbow trout (a total of 400 per hectare) were introduced into the lake (Tuunainen 1966b). By 28. VIII. 1964, the average length of 24 brown trout was 18.6 ± 0.5 cm and their average weight 73 ± 6 g, and that of 32 rainbow trout 19.7 ± 0.3 cm and 86 ± 4 g, respectively. Although these fish had grown well, this introduction also failed and no more fish were caught.

Reactions of the benthic fauna

A rapid increase in the bottom fauna occurred in the summer following the poisoning. The trout released in 1964 were so large that they could immediately feed on the bottom fauna. The effect of the predation of these fish can be clearly seen. After the death of the fish in winter 1964/1965 the biomass of bottom fauna increased again in 1966.

9. Långviken, Kaarlela (Öja)

General description

63° 46′ 30″ N, 23° 01′ E, at about sea level. Area 2.2 hectares, volume 70 000 m³ (Toivonen 1962). Maximum depth 5.0 m. Of the shores 45 % are stony and 55 % peatland. Bottom mud (Tuunainen 1966a, 1966b). A small outlet but no inlet.

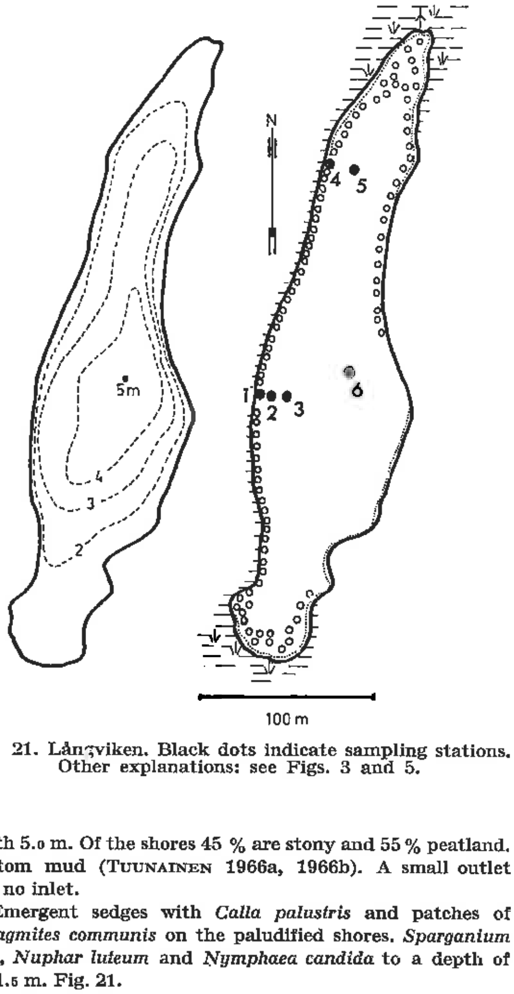

Fig. 21. Långviken. Black dots indicate sampling stations. Other explanations: see Figs. 3 and 5.

Emergent sedges with *Calla palustris* and patches of *Phragmites communis* on the paludified shores. *Sparganium* spp., *Nuphar luteum* and *Nymphaea candida* to a depth of 1 – 1.5 m. Fig. 21.

The lake is thermally stratified in summer, although the volume of the hypolimnion is small.

On 25. II. 1964, the oxygen content was quite low, but no death of fish due to lack of oxygen was observed. In summer there was an oxygen deficit in the deepest water layer only.

The lake is slightly acid, the electrolytic conductivity is higher than in the other lakes studied, the $KMnO_4$ consumption is quite high and the Fe content low. According to Järnefelt's (1953) classification, the lake is polyhumous. In transparency it is intermediate between meso- and polyhumous lakes.

Some physical and chemical data (according to Tuunainen 1968) are listed below:

	Depth m	t °C	n	
VI. – IX. 1962 – 1964	0.5 – 1	13.0 – 18.2	3	Maximum on 3. VII. 1963
	~ 3 – 5		3	Metalimnion
	4 – 4.5	6.8 – 12.2	4	
II. 1964	1	0.5	1	
	3	3.0	1	

Days without ice: 153 – 167 days per year (Tuunainen 1966a, 1966b)

	Depth m	O_2 mg/l	O_2 %	n	pH	n
IX. 1962 – 1963	1	7.3	72	1	6.3	1
	4.5	5.4	52	1	6.6	1
XII. – II. 1963 – 1964	1	3.8 – 9.7	28 – 70	2	6.6	1
	3	2.7	21	1	–	–
	4	6.1	–	1	–	–

	Depth m	Conductivity µS	n	$KMnO_4$ mg/l	n	Fe mg/l	n
IX. 1962 – 1963	1	60	1	67.0	1	–	–
	4.5	68 – 95	2	131.0	1	0.33	1
XII. – II. 1963 – 1964	1	136	1	71.0	1	–	–
	3	110	1	70.0	1	–	–
	4	–	–	–	–	–	–

	Depth m	Colour Pt mg/l Range	$\bar{x}$	n	Transparency m	n
3. IX. 1962 – 25. II. 1964	1	90 – 110	100	2	1.3	1
		300	300	1		

Table 20. Food of brown trout and rainbow trout in Långviken. A = age of the fish (years), B = number of fish studied, C = average number of food organisms per stomach, D = average volume of food (ml), E = main food items as percentages (number/volume).

	A	B	C	D	E
Brown trout:					
2. – 3. IX. 1963	0 +	8	28	1.5	Chironomid larvae 62/53 %, *Asellus* 37/42 %
6. VI. 1964	1 +	4	78	1.1	Terr. insects 44/30 %, Chironomid pupae 38/12 %, *Asellus* 12/22 %
25. VII. 1964	1 +	2	11	0.7	*Asellus* 66/32 %, Aeschnid larvae 7/22 %, Trichopterous larvae 6/18 %
Rainbow trout:					
2. – 3. IX. 1963	0 +	10	243	1.1	Cladocera + Copepoda 54/32 %, *Asellus* 17/18 Lymnaeids 12/16 %
6. VI. 1964	1 +	10	147	0.8	Chironomid pupae 61/53 %, terr. insects 27/27 %, Trichopterous larvae 0.7/10 %
25. VII. 1964	1 +	5	43	5.4	Cladocera 55/42 %, terr. insects 22/19 %, *Asellus* 12/7 %

Table 21. Forage ratios for brown trout and rainbow trout in Långviken

	Brown trout		Rainbow trout	
	2. – 3. IX. 1963	6. – 7. VI. 1964	2. – 3. IX. 1963	6. VI. 1964
Hirudinea	–	–	–	1.41
Pisidium sp.	–	0.01	0.06	–
Asellus aquaticus	1.80	1.57	2.00	0.44
Trichopterous larvae	–	11.11	–	5.55
Chaoborus »	–	–	0.17	–
Chironomid »	1.24	0.12	0.48	0.12
» pupae	–	204.50	–	254.50
Ceratopogonid larvae	0.04	7.55	0.14	15.10

Table 22. Frequency (%) of occurrence of benthic animals in bottom samples taken from Långviken on four different dates (A), in stomachs of brown trout (B) and rainbow trout (C) taken on three different dates and in two samples of brown trout (D) and rainbow trout (E) taken simultaneously with bottom samples.

	A	B	C	D	E
Nematoda	25	–	–	–	–
Gordius sp.	–	–	33	–	–
Oligochaeta	100	–	–	–	–
Hirudinea	–	–	33	–	50
Glossosiphonia sp.	50	–	–	–	–
Helobdella sp.	75	–	–	–	–
Valvata sp.	25	67	67	–	–
Lymnaeids	–	–	67	–	–
Pisidium sp.	75	33	33	50	50
Asellus aquaticus	100	100	100	100	100
Hydracarina	–	–	33	–	–
Ephemerid larvae	–	–	33	–	–
Aeschnid »	25	33	33	–	–
Libellulid »	50	–	–	–	–
Corixid adults	50	33	67	–	–
Dytiscid larvae	–	–	33	–	–
» adults	–	33	100	–	–
Other Coleopterous larvae	25	–	33	–	–
Sialis larvae	50	–	–	–	–
Trichopterous larvae	50	67	33	50	50
Lepidopterous »	–	33	–	–	–
Chaoborus »	75	–	67	–	50
Chironomid »	100	67	100	100	100
» pupae	50	100	100	50	50
Ceratopogonid larvae	75	67	67	100	100
Other Dipterous »	50	–	–	–	–

Benthic fauna and zooplankton

The bottom fauna (Fig. 22) consisted mainly of Oligochaeta, *Pisidium* spp., *Asellus aquaticus* and larvae of Chironomids (Tuunainen 1968).

The composition of the zooplankton (specimens per 10 l) on 3. VII. 1963 (27 samples, 1.4 l each) was as follows:

Rotatoria	16
Daphnia sp.	62
Polyphemus pediculus	+
Cladocerous embr.	2
Calanids	1
Cyclopids	21
Copepod nauplii	2
Hydracarina	+
Chaoborus sp.	1
Total	105

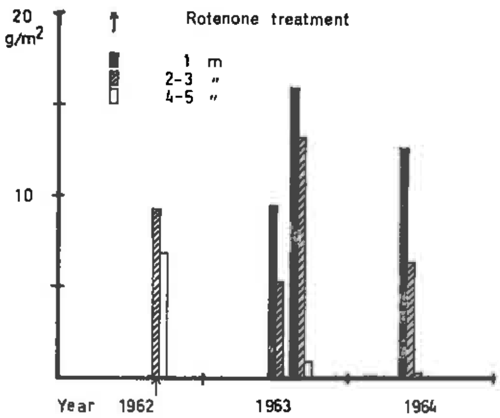

Fig. 22. Biomass of benthic fauna in Långviken.

Fish population

At the time of the poisoning the natural fish stock consisted of roach, pike and rather large crucian carp, in total 17.6 kg/hectare (TOIVONEN 1962).

On 15. VI. 1963, 2 500 specimens of brown trout fry and 2 500 specimens of rainbow trout fry (a total of 2 272 per hectare) were released into the lake. The brown trout were from Huopana fish hatchery, Viitasaari, and the rainbow trout from Kontiolahti fish hatchery (TUUNAINEN 1966a, 1966b).

In the brown trout the growth rate was a little below the average (Figs. 28 – 29), whilst it was near the average in the rainbow trout (Figs. 30 – 31).

During the first two growth periods the brown trout were smaller than the rainbow trout but after the fourth growth period they were slightly larger than the rainbow trout (cf. TUUNAINEN 1968).

Food of the fish released

Larvae and pupae of Chironomids, *Asellus aquaticus*, larvae of Trichoptera and surface organisms comprised the bulk of the brown trout's food (Table 20). Zooplankton and terrestrial invertebrates were important constituents, and of the bottom fauna *Asellus aquaticus*, larvae and pupae of Chironomids, *Valvata* and Lymnaeids were utilized.

As can be seen from Tables 21 – 22, the food of the rainbow trout was more variable than that of the brown trout.

Reactions of the benthic fauna

Because the natural fish stock was too small to utilize the bottom animals efficiently, the biomass of the bottom fauna was quite high at the time of the poisoning in summer 1962, except at 1 m depth. After the treatment, the bottom fauna at 1 – 3 m increased in 1963 and even in 1964, although the trout were already feeding on bottom animals in late summer 1963, but decreased at 4 – 5 m owing to a decrease of larvae of *Chaoborus* and Chironomids (Fig. 22, Table 20; TUUNAINEN 1968).

IV. Biological production[1]

After the natural fish stock has been killed, the biomass of the benthic fauna increases according to Pearl – Verhulst's formula. The maximum growth rate (r_m) of a population (P) is obtained from the formula

$$\frac{\Delta P}{\Delta t} = r_m P \left(1 - \frac{P}{K}\right)$$

where K is the maximum biomass of a population observed and t = time (cf. e.g. HAYNE & BALL 1956).

The bottom animal production (net production) in Sahalampi in the summers of 1963 – 1967 was calculated from the data of TUUNAINEN (1968):

	11. – 12. VI – 16. – 17. X. 1963	29. V – 6. X. 1964	21. VI – 9. IX. 1965	2. VI – 2. IX. 1966	6. – 7. VI. – 24. X. 1967
P g/m²	13.730	4.635	10.521	11.297	8.150
ΔP »	22.770	3.528	14.803	–4.765	7.535
K »	25.115	6.399	17.922	8.914	13.417
Δt days	128	131	81	93	141
r_m	0.0287	0.0210	0.0404	–0.0285	0.0167

By using conversion coefficients (pp. 92 – 93) and values of maximum growth rate (r_m), the bottom animal production between 29. V – 6. X. 1964 can be calculated as follows. If the conversion coefficient of 5.03 or 12.66 is used, the amount of bottom fauna eaten by the fish in that period is 4.68 or 11.78 g/m², respectively. According to bottom animal samples, the increase in the bottom animal biomass was 3.53 g/m² at the same time. The whole production (gross production) is thus 8.21 – 15.31 g/m² or, generalized to represent the whole lake, 82.1 – 153.1 kg/hectare. The increase is thus 2.9- to 5.3-fold during 131 days. These values are a little too low on account of sources of error discussed later.

[1] Some of the terms used in this paper are defined as follows:
Production = actual increase in biomass
Productivity = production capacity
Net production = biomass at the end of a growth period – biomass in the beginning of the same period
Gross production = net production + predation (caused by fish or by man)

Year	Initial biomass g/m²	Gross production g/m²	Gross production $\bar{x}$ g/m²	Gross production 100 g/m/day	Length of observation period (days)
1963	2.345	22.770	22.770	17.79	128
1964	2.871	8.205 – 15.305	11.755	8.97	131
1965	3.119	17.318 – 21.133	19.226	23.74	81
1966	13.679	– 2.552 – 0.805	– 0.874	– 0.87	93
1967	5.882	7.535	7.535	5.34	141

The bottom animal production in the other four summers 1963, 1965, 1966, 1967 can be calculated in the same way. The above tabulation based on the data from Sahalampi shows that it depends clearly on the initial biomass of benthic animals in the spring.

An attempt was made to calculate the rate of increase of the biomass of bottom animals during the growth period, as the initial biomass value was known. The growth rate is highest with optimal initial biomass and slows up if there is no new source of energy and if the species composition remains unchanged. Ultimately, a situation is reached where the growth rate is zero. The perishing part of the biomass is replaced, but there is no increase. If the initial biomass value is still higher, the growth rate is negative and the biomass returns to the level where the growth rate is zero (Fig. 23). In spring 1966, the initial biomass value of the over-dense

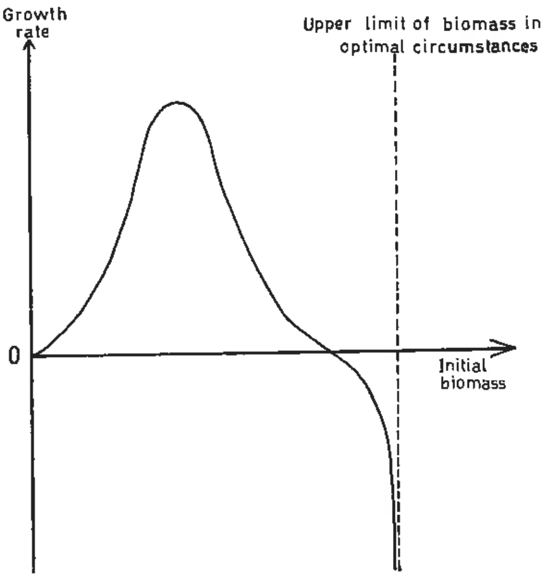

Fig. 23. Dependence of the increase of the biomass on its initial size in the case of the benthic fauna.

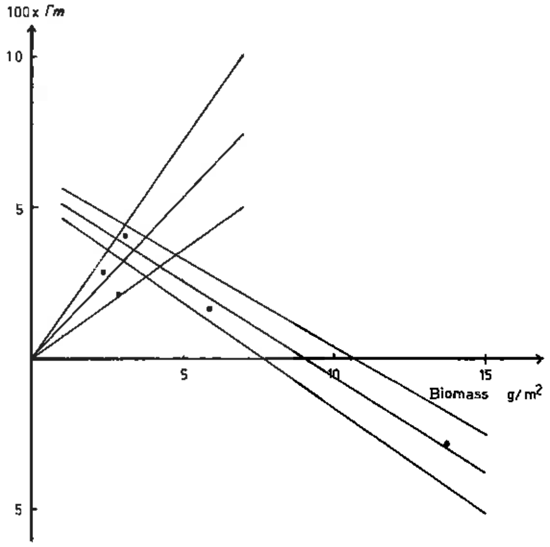

Fig. 24. Dependence of the rate of increase of the biomass on its initial size in the case of the benthic fauna. The effect of predation by fish is excluded. The correlation coefficient (r) for the ascending part = + 0.905 (0.10 > P > 0.05). Regression line $y = 1.079\,x$. $b \pm s_b = 1.079 \pm 0.358$. The number of degrees of freedom is 2. The correlation coefficient (r) for the descending part = – 0.996 (0.10 > P > 0.05). Regression line $y = -0.637\,x + 5.766$. $b \pm s_b = -0.637 \pm 0.058$. The number of degrees of freedom is 1.

stock was so high that it decreased towards the autumn.

Fig. 24 shows regression lines for the rate of

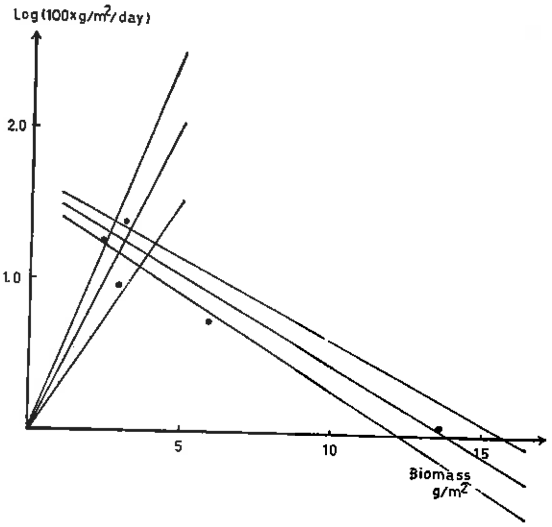

Fig. 25. Dependence of the increase of the biomass on its initial size in the case of the benthic fauna. The effect of predation by fish is taken into consideration. The correlation coefficient (r) for the ascending part = + 0.939 (0.10 > P > 0.05). Regression line $\log y = 0.410\,x$. $b \pm s_b = 0.410 \pm 0.106$. The number of degrees of freedom is 2. The correlation coefficient (r) for the descending part = – 0.968 (P > 0.10). Regression line $\log y = -0.116\,x + 1.802$. $b \pm s_b = -0.116 \pm 0.010$. The number of degrees of freedom is 1.

Table 23. Frequency distribution (%) of the benthic fauna on the basis of samples collected in the springs of 1963 – 1967 (cf. TUUNAINEN 1968), and similarity of the samples calculated from the percentages according to SØRENSEN's (1948) method based on the quotient of similarity.

	1963	1964	1965	1966	1967
Oligochaeta	2	–	–	+	–
Pisidium sp.	3	51	52	64	33
Asellus aquaticus	2	–	–	4	8
Argyroneta aquatica	3	–	1	–	–
Hydracarina	3	1	1	1	–
Agrionid larvae	–	1	–	+	–
Aeschnid »	–	–	–	+	–
Libellulid »	3	1	2	4	10
Notonecta »	2	–	–	–	–
Corixid »	5	–	–	–	–
Dytiscid »	2	–	–	–	2
Other Coleopterous larvae	9	–	–	–	–
Sialis larvae	–	2	6	6	47
Trichopterous »	–	1	2	+	2
Lepidopterous »	–	–	1	–	–
Chaoborus »	–	2	–	–	–
Chironomid »	58	41	31	19	
» pupae	–	1	1	1	
Ceratopogonid larvae	2	1	3	–	–
Other Dipterous larvae	2	–	–	–	–
» » pupae	2	–	–	–	–
Total	98	102	100	99	102

	1963	1964	1965	1966	1967
1963	–	47	40	28	10
1964	–	–	89	75	37
1965	–	–	–	81	43
1966	–	–	–	–	47
1967	–	–	–	–	–

increase of the bottom animal biomass. In this calculation the influence of the fish stock has been ignored. The growth rate, $r_m = 0.0363$, was found to be optimal if the initial value was 3.36 g/m², and zero if the initial biomass was 9.05 g/m². In Fig. 25 the effect of the fish stock has also been taken into consideration. The growth rate was optimal, 0.18 g/m²/day, if the initial value was 3.05 g/m², and zero if it was 13.79 g/m².

The initial value of the benthic animal biomass is almost the same in the two calculations. If the second method is employed, the biomass value at which the growth rate is zero is clearly greater. The second calculation, in which fish are included, is more correct.

Temperature conditions and other environmental factors were rather uniform during the period of study (cf. TUUNAINEN 1968). The differences in growth rates cannot be due to differences in the composition of the fauna, because in 1964, 1965, and 1966, for instance, the increase of the biomass was very different in spite of great similarity of the bottom fauna composition (Table 23). These differences were thus in all probability caused by the different initial biomass values of the bottom fauna.

Since the trout feed mainly on bottom organisms and those living on submerged vegetation, the increase of the biomass of fish depends essentially on the abundance of these. Calculations concerning growth of fish population were based on catches, mean weights (TUUNAINEN 1968) and data included in Fig. 34. An attempt was also made to estimate the increase in the biomass of the fish stock from that of the bottom fauna.

The growth rate (r_m) of the fish biomass was calculated in the same way as that of the bottom fauna (p. 90). The value of K was obtained by adding to the biomass at the end of a growth period the catch in the same period.

	25. V – 16. X. 1963	29. V – 5. X. 1964	21. VI – 9. IX. 1965	1. VI – 15. X. 1966
P kg/ha	15.9	29.5	14.1	11.8
ΔP »	21.7	9.2	5.0	4.4
K »	26.7	34.1	16.6	14.0
Δt days	145	130	81	137
r_m	0.0233	0.0178	0.0291	0.0172

The growth rates (r_m) of the bottom fauna and the fish stock were as follows:

Year	Bottom fauna	Fish stock
1963	0.0287	0.0233
1964	0.0210	0.0178
1965	0.0404	0.0291
1966	−0.0285	0.0172
1967	0.0167	0.0000

Except in 1966, the growth rate of the bottom fauna was higher than that of the fish stock.

Assuming that the biomass of the bottom fauna is equal at the same season of the various years (autumn—winter) if there is no predation by fish, one can calculate the bottom animal biomass which will be converted into fish flesh and serve as a source of energy for the fish.

Growth of the fish biomass was 9.2 kg/hectare/130 days (0.0071 g/m²/day) during the summer of 1964. For this growth an average of (0.0077 × 4.635 g/m²/day =) 0.0357 g/m²/day of bottom animals was needed. 4.635 is the average biomass of bottom animals (P) in summer 1964, 0.0077 is the difference between the mean growth rates (r_m) in 1963 and 1964 (cf. HAYNE & BALL 1956). The difference, 0.0357 g/m²/day − 0.0071 g/m²/day = 0.0286 g/m²/day, represents the proportion of the increase of bottom animal biomass used for the energy requirements of the fish. The average conversion coefficient (food eaten by fish per unit of fish flesh produced) for the fish population in Sahalampi in the summer of 1964 was thus

$$\frac{0.0357 \text{ g/m}^2\text{/day}}{0.0071 \text{ g/m}^2\text{/day}} = 5.03$$

In 1965, the r_m of the bottom animal biomass was 0.0404 instead of 0.0210 in 1964; the difference is 0.0194. Assuming that the growth rate of the bottom fauna would have been the same in 1965 inas 1964 if the fish had not been present, it is estimated that the fish must have used (0.0194 × 1.635 g/m²/day =) 0.0899 g/m²/day of the bottom fauna in 1964. The conversion coefficient is higher than that above:

$$\frac{0.0899\ \text{g/m}^2/\text{day}}{0.0071\ \text{g/m}^2/\text{day}} = 12.66$$

However, the correct conversion coefficients are slightly higher than these, because part of the bottom animal biomass was consumed by fish both in 1963 and in 1965, to which the values of 1964 were compared. Another source of error is the fact that the fish also fed on plankton and terrestrial insects to some degree. (During the period 29. V – 6. X. 1964 the average volume of the food of the fish in Sahalampi consisted of 93.7 % bottom fauna, 6.0 % aerial food and 0.3 % zooplankton.)

The mean value of the conversion coefficient (8.85) estimated for Sahalampi is a little higher than those obtained in some other experiments. According to PHILLIPS *et al.* (1954), conversion coefficients for brown trout fed with natural food varied for 2.5 to 7.1. The lowest values were obtained with fresh fish and the highest ones with *Gammarus* (6.8) and house-fly maggots (7.1). SCHÄPERCLAUS (1967) investigated the effect of temperature. If rainbow trout are kept under the same circumstances and fed with the same food, the conversion coefficient is 2.9 at 10°C and 6.0 at 17°C. A high O_2 content of the water decreased the conversion coefficient. In experiments carried out in aquaria at 9 – 12°C the conversion coefficient was 4.4 for rainbow trout fed with larvae of Chironomids and 5 – 8 for those fed with fresh fish. For fish living in natural waters higher conversion coefficients are obtained than for fish kept in pools and aquaria, probably because hunting for food may demand more energy in natural waters than if the fish are fed regularly.

Table 24 shows that the smaller the proportion of the total biomass constituted by the fish stock, the greater is the sum of the biomass values of the bottom-feeding fish and the bottom fauna.

In a study of the correlation between fish stock and bottom fauna (Fig. 26), observations made during the period 27. VIII – 16. X of the years 1962 – 1966 were used to avoid errors inherent in spring or summer samples (emergence of Ephemerids, Odonata, Trichoptera, *Sialis* and Chironomids, for instance). The negative correlation between the biomass values was significant.

Table 24. Fish stock and bottom fauna (kg/hectare) in Sahalampi.

	Fish stock	Bottom fauna	Total
27. VIII. 1962	70.0[1]	7.40	77.4
25. V – 12. VI. 1963	5.0[2]	23.45	28.5
16. X. 1963	26.7	251.15	277.9
29. V. 1964	26.6	28.71	55.3
5. – 6. X. 1964	30.3	63.99	94.3
21. VI. 1965	12.4	31.19	43.6
9. IX. 1965	16.6	179.22	195.8
1. – 2. VI. 1966	11.6	136.79	148.4
2. IX. 1966	14.4	89.14	103.5
6. – 7. VI. 1967	0.0	58.82	58.8
24. X. 1967	0.0	134.17	134.2

[1] TOIVONEN (1962).
[2] Fry of brown trout and rainbow trout.

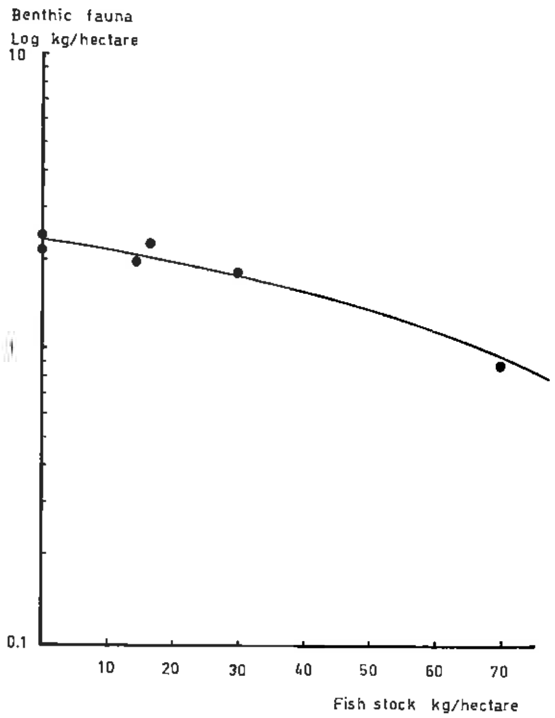

Fig. 26. Correlation between benthic fauna and fish stock in Sahalampi. The correlation coefficient (r) was – 0.956 (0.01]> P > 0.001). Regression line log y = – 0.020 x + 2.339. $b \pm s_{b_a}$ = – 0.020 ± 0.003. The number of degrees of freedom is 4.

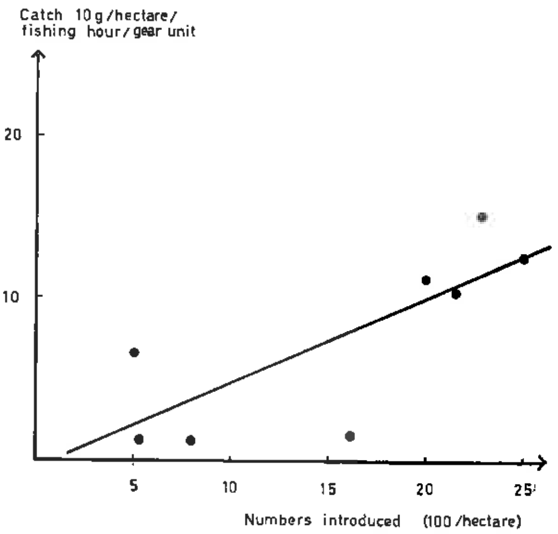

Fig. 27. Dependence of catch on stocking density. The correlation coefficient (r) was + 0.719 (0.05 > P > 0.01). Regression line $y = 0.516\,x - 0.370$. $b \pm s_b = 0.516 \pm 0.223$. The number of degrees of freedom is 6. For the calculations catch values from Table 27 were used except for Kivi-Ahveroinen, where only catches up to 17. IX. 1966 (47.5 kg and 794 fishing hours) were used. All the fish in question were released as fry.

In the lakes studied the fishing efficiency was 34 – 398 hours per gear unit per hectare (Table 25). Catches from Satimuslampi and Julkujärvi were quite large in spite of a considerably lower fishing intensity.

Fig. 27 shows that the catch per unit of fishing gear per unit of time is within certain limits dependent on the numbers of fish introduced.

In most of the lakes the fishing intensity was low and the total catches quite small (1.3 – 10.6 kg/hectare/year.) (Tables 25 – 27). The catches from Sahalampi and Långviken are exceptional. The catch from Sahalampi consisted mainly of brown trout and 85 % of the fishing was done with nets. In Långviken about two thirds of the catch was rainbow trout and 97 % of the fishing was angling. According to SØMME (1954), trout production in large and medium-sized Norwegian trout lakes is 2 – 4 kg/hectare/year, while small lakes can produce up to 8 kg of trout/hectare/year.

The percentage recapture of rainbow trout was statistically very significantly greater than that of brown trout in four lakes out of seven

Table 25. Fishing intensity expressed as fishing hours.

Lake	In the whole lake				Per hectare				Per hectare per year			
	Fishing with net	Angling	Fishing with seine	Total	Fishing with net	Angling	Fishing with seine	Total	Fishing with net	Angling	Fishing with seine	Total
Kivi-Ahveroinen	1708.0	4.0	–	1712.0	397.2	0.9	–	398.1	99.3	0.2	–	99.5
Satimuslampi	52.5	16.0	–	68.5	26.3	8.0	–	34.3	6.6	2.0	–	8.6
Pien-Valkealampi	–	50.0	–	50.0	–	50.0	–	50.0	–	12.5	–	12.5
Ahvenlampi	52.0	3.0	–	55.0	55.9	3.2	–	59.1	27.9	1.6	–	29.5
Ulpasjärvi	948.0	37.0	–	1021.0	265.5	10.0	–	275.5	53.0	2.0	–	55.0
Sahalampi	197.0	26.5	9.0	232.5	246.0	33.1	11.3	290.4	61.5	8.3	2.8	72.6
Julkujärvi	113.5	24.0	–	137.5	35.4	7.5	–	42.9	8.9	1.9	–	10.8
Långviken	9.5	270.0	–	279.5	4.3	122.7	–	127.0	1.1	30.6	–	31.7

Table 26. Recapture of brown trout and rainbow trout. The t-value is for the difference in percentage recapture between brown trout and rainbow trout.

Lake	Brown trout			Rainbow trout			Total			t-value
	Numbers introduced	Catch exx.	Recapture per cent ± S.E.	Numbers introduced	Catch exx.	Recapture per cent ± S.E.	Numbers introduced	Catch exx.	Recapture per cent ± S.E.	
Kivi-Ahveroinen	7 000	141	2.01 ± 0.16	–	–	–	–	–	–	–
Satimuslampi	2 000	57	2.85 ± 0.38	2 000	60	3.00 ± 0.38	4 000	117	2.93 ± 0.27	0.283
Pien-Valkealampi	2 000	63	3.15 ± 0.39	150	25	16.67 ± 3.05	2 150	88	4.09 ± 0.43	8.048***
Ahvenlampi	–	–	–	300	24	8.00 ± 1.57	–	–	–	–
Ulpasjärvi	1 500	85	5.66 ± 0.60	1 500	144	9.60 ± 0.76	3 000	229	7.64 ± 0.48	4.064***
Sahalampi	1 500	186	12.40 ± 0.85	500	15	3.00 ± 0.76	2 000	201	10.05 ± 0.67	6.026***
Julkujärvi	650	10	1.54 ± 0.48	950	78	8.20 ± 0.72	1 600	88	5.50 ± 0.57	5.776***
Särkilampi	500	24	4.80 ± 0.96	500	32	6.40 ± 1.00	1 000	56	5.60 ± 0.73	1.103
Långviken	2 500	174	6.96 ± 0.51	2 500	365	14.60 ± 0.71	5 000	539	10.80 ± 0.43	8.711***

Table 27. Catch of the introduced fish. In the right column a (+) means that introduced fish were still left after the sampling in the autumn of 1966. The figures for total catch (kg/hectare/year) refer to the time since introduction.

Lake	Number of			Kg					Per fishing hour per gear unit				
	brown trout	rain-bow trout	total	brown trout	rain-bow trout	total	per hec-tare	per hec-tare per year	exx.	kg	kg per hec-tare	Mean weight of fish caught g	Fish left
Kivi-Ahveroinen	141	–	141	60.6	–	60.6	14.1	3.5	0.082	0.035	0.008	429.8	+
Satimuslampi	57	60	117	7.7	7.6	15.3	7.7	1.9	1.708	0.223	0.112	130.8	+
Pien-Valkealampi	63	25	88	3.5	1.7	5.2	5.2	1.3	1.760	0.104	0.104	59.1	+
Ahvenlampi	1	24	25	0.3	5.8	6.1	6.6	3.3	0.455	0.111	0.120	244.0	+
Ulpasjärvi	85	144	229	22.2	23.3	45.5	12.3	2.5	0.224	0.045	0.012	198.7	–
Sahalampi	186	15	201	22.3	1.2	23.5	29.4	7.4	0.865	0.101	0.126	116.9	–
Julkujärvi	10	78	88	7.1	22.1	29.2	9.1	2.3	0.640	0.212	0.066	331.8	+
Särkilampi	24	32	56	1.8	2.8	4.6	1.8	1.8	–	–	–	82.1	–
Långviken	174	365	539	28.1	65.4	93.5	42.5	10.6	1.932	0.335	0.152	173.5	+
Total	741	743	1 484	153.6	129.0	283.6							

(Table 26). Monten (1964) observed the same feature in the natural waters in Sweden, and pointed out that rainbow trout reach fishing size sooner. In Särkilampi the difference between the recapture percentages of brown trout and rainbow trout was small, and the size of the two species at the time of recapture was the same. The introduction of rainbow trout into Sahalampi failed because of the acidity of the water, but the exceptional result for Satimuslampi remains unexplained.

If both rainbow trout and brown trout were released into the same lake, the percentage of rainbow trout in the catches of the growth periods I – III was usually greater than that of brown trout, but later the brown trout were in the majority.

Recently, very much attention has been paid to the possibility of calculating the productivity of the waters (e.g. Carlander 1955, Paloheimo & Dickie 1965, 1966a, 1966b, Ryder 1965, Ivlev 1966). Ivlev (1966) presented a general equation for estimating the unknown production of any population of heterotrophic organisms from information on the production of its food populations and appropriate coefficients. In this equation

$$W = K \sum_{i=1}^{t} v_i e_i$$

where W is the production of some group of organisms (a population) for a time interval from $i = 1$ to $i = t$ (i = the initial time step) and K the energy coefficient of growth (energy used for growth divided by the quantity of energy that an organism obtains in its food), v_i is the production of food populations and e_i the so-called ecotrophic coefficient. The »dynamic» ecotrophic coefficient is obtained from the equation

$$e_i = \frac{\sum_{i=1}^{t} r_i}{\sum_{i=1}^{t} \Delta B_i}$$

where e_i is the unknown ecotrophic coefficient for a time interval from $i = 1$ to $i = t$, which will in general be a rather long time interval, typically a year, r_i is the daily ration, and ΔB_i the daily increment of the food. This »dynamic» ecotrophic coefficient by Ivlev (1966) is the ratio of a predator's consumption to the production of its prey.

To calculate the growth of fish populations, Paloheimo & Dickie (1965, 1966a, 1966b) described a method based on knowledge of the water temperature and the energy metabolism per fish. This method and those presented by Ivlev (1966), Davis & Warren (1968) and Ricker (1968) are in general very similar, even though the initial values are somewhat different.

An attempt was made to calculate the trophic step between bottom fauna and fish stock in Sahalampi on the basis of Ivlev's (1966) method and that presented by Hayne & Ball (1956).

At optimum density and composition the average growth rate of the bottom animal biomass in Sahalampi was 0.18 g/m^2/day (p. 92). If the conditions for bottom animal production remained optimal throughout the growth period, and if all the new biomass produced by the bottom fauna were consumed by the fish, the productivity of the fish stock can be calculated from IVLEV's (1966) equation. (Length of growth period in Sahalampi is regarded as 150 days per year and a conversion coefficient of 8.85 is used.)

$$e_i = \frac{150 \times 0.18 \text{ g/m}^2\text{/day}}{150 \times 0.18 \text{ g/m}^2\text{/day}} = 1$$

$$K = \frac{1}{8.85} = 0.11$$

$$v_i = 0.18 \text{ g/m}^2\text{/day}$$

$$\sum_{i=1}^{t} v_i e_i = 150 \times 0.18 \times 1 \text{ g/m}^2$$

$$t = 150 \text{ days}$$

These data give, from the equation

$$W = K \sum_{i=1}^{t} v_i e_i,$$

$$W = 0.11 \times 150 \times 0.18 \text{ g/m}^2 = 2.97 \text{ g/m}^2$$

The productivity was thus 2.97 g/m²/growth period or 29.7 kg/hectare/growth period.

The actual fish production (gross production) in Sahalampi was calculated to be as follows:

1963	0.015 g/m²/day
1964	0.007 »
1965	0.008 »
1966	0.003 »

The average productivity of the fish stock was $K \times 0.18$ g/m²/day or 0.02 g/m²/day. In various years the fish production was actually 15 – 75 % of this. The apparently high efficiency percentage (75 %) in the first growth period is chiefly due to the facts that besides the benthic fauna the fish also utilized plankton in their first growth period, and that the conversion coefficient for the young fish is lower than that for older stages. In the second (35 %), third (30 %) and fourth (15 %) growth periods the efficiency percentages almost always depended on consumption of bottom fauna.

V. Growth of the fish released

1. Growth and the coefficient of condition

The growth of the brown trout and rainbow trout was checked by sampling, mainly with gill nets, and in some lakes (Table 25) also with reel and seine fishing. Attempts were made to eliminate the selective effect of the gill nets (cf. McCOMBIE & FRY 1960, McCOMBIE 1961) by using nets of appropriate mesh sizes (12, 17, 20, 25, 30, 35 and 40 mm) simultaneously. In reel fishing there is always the possibility that the tackle exerts a selective effect.

The mean lengths and weights of the fish caught were reported by TUUNAINEN (1968). The differences in the growth of the fish of the same species in different lakes were considerable, except during the first growth period (Figs. 28 – 31). The most important limiting factor was too high a density, with resulting competition for food. As can be seen from Table 28, in rainbow trout the increase in weight was nearly 2 – 3 times as great as that of brown trout in the first and second growth periods, and only in the third growth period was the increase in weight greater in brown trout than in rainbow trout.

Table 28. Growth in length and weight during the growth periods I – III of brown trout and rainbow trout introduced into the same lakes.

	I		II		III	
	x̄	R	x̄	R	x̄	R
Brown trout:						
cm	15.4	13.2 – 17.5	8.0	5.4 – 11.9	5.2	0.8 – 8.5
g	25.3	15 – 43	71.3	35 – 117	132.0	3 – 333
Rainbow trout:						
cm	21.6	20.0 – 22.6	7.4	1.7 – 17.2	3.4	1.8 – 7.2
g	77.0	68 – 93	150.7	41 – 526	111.0	3 – 414

With a few exceptions, the length : weight ratios of salmonids fit Fulton's formula (cf. e.g. SØMME 1954, BROWN 1957);

$$W = \frac{L^3}{100} \times K$$

The coefficient of condition (K) is determined with the aid of the following formula

$$K = \frac{100\,W}{L^3}$$

where W = weight of fish in grams and L = total length in centimetres.

Many sources of error have to be taken into account if the coefficient of condition are used to compare different populations. For example, the stage of maturity and the amount of food in the stomach of the fish affect the values of the coefficient.

In Table 29 the average coefficients of condition for the trout are presented. One-summer-old brown trout in Kivi-Ahveroinen had the

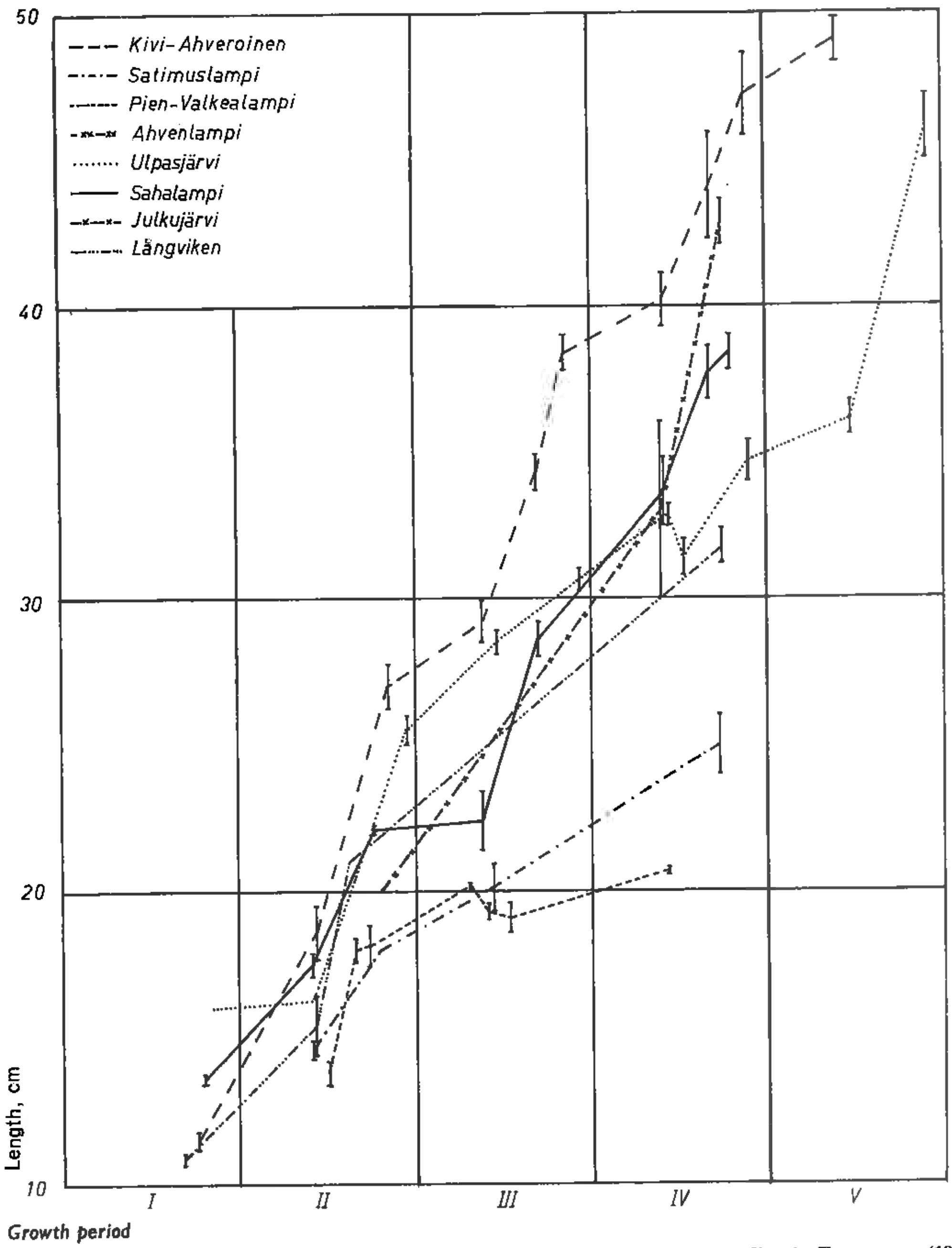

Fig. 28. Growth of brown trout. Mean values and standard errors for catches are according to TUUNAINEN (1968).

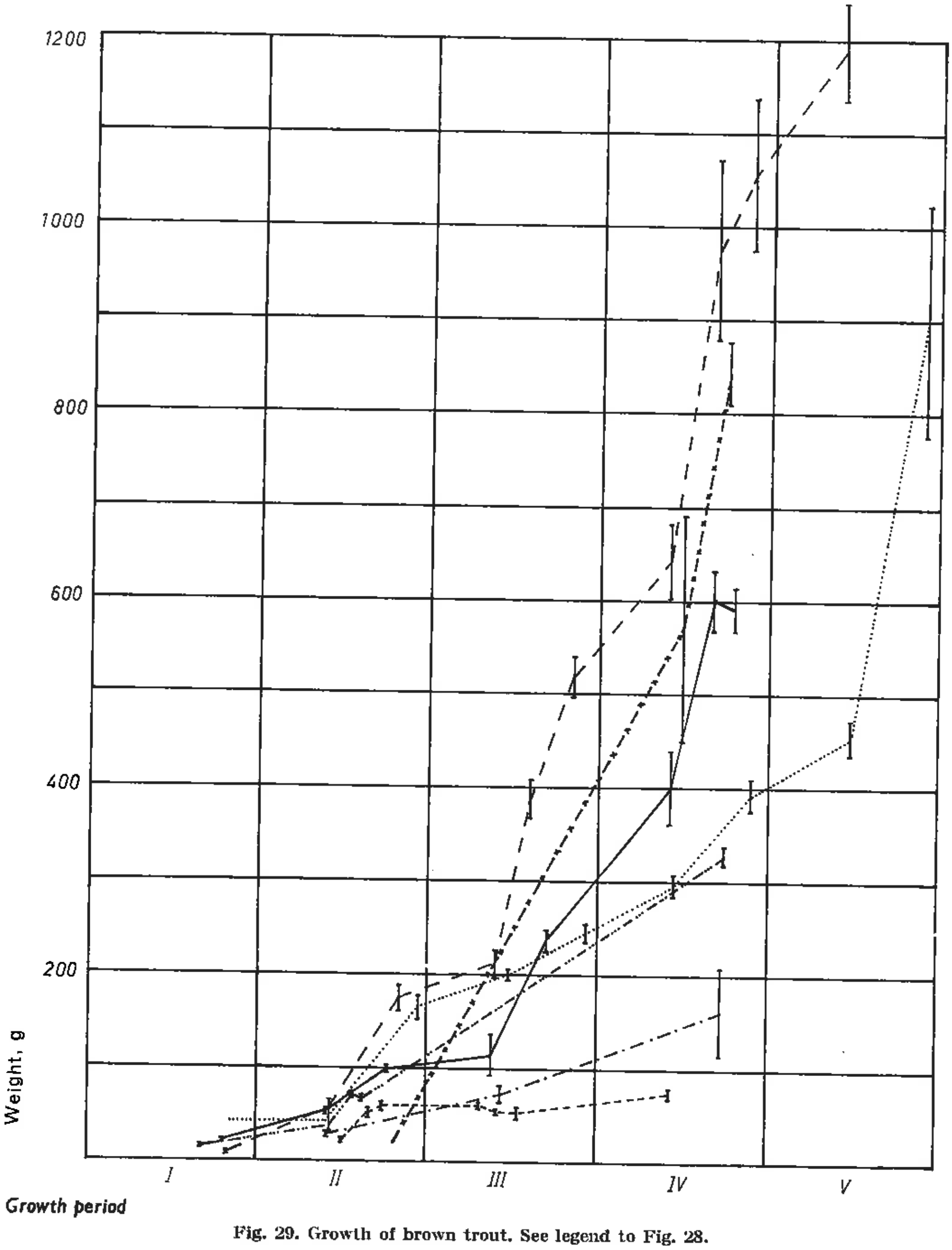

Fig. 29. Growth of brown trout. See legend to Fig. 28.

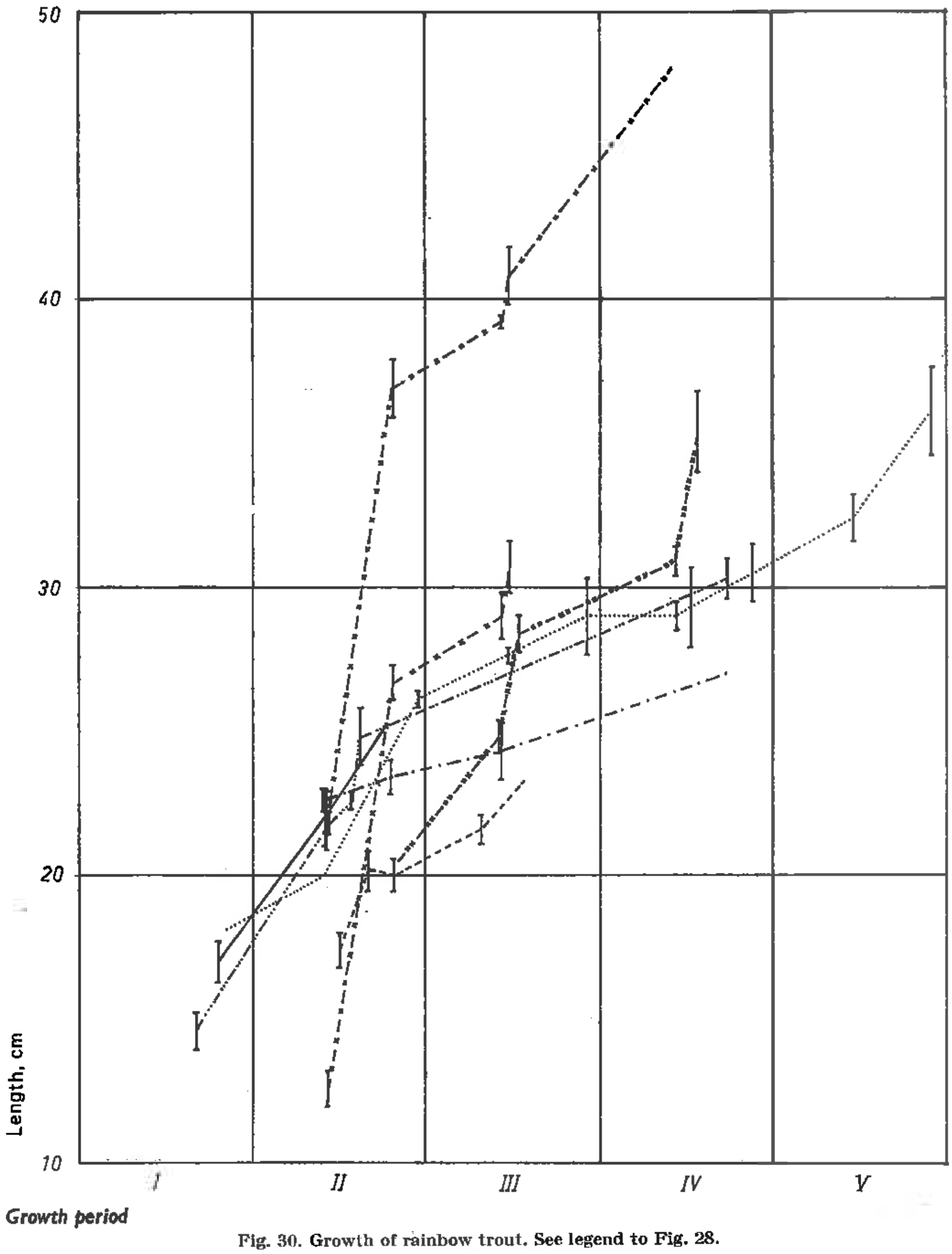

Fig. 30. Growth of rainbow trout. See legend to Fig. 28.

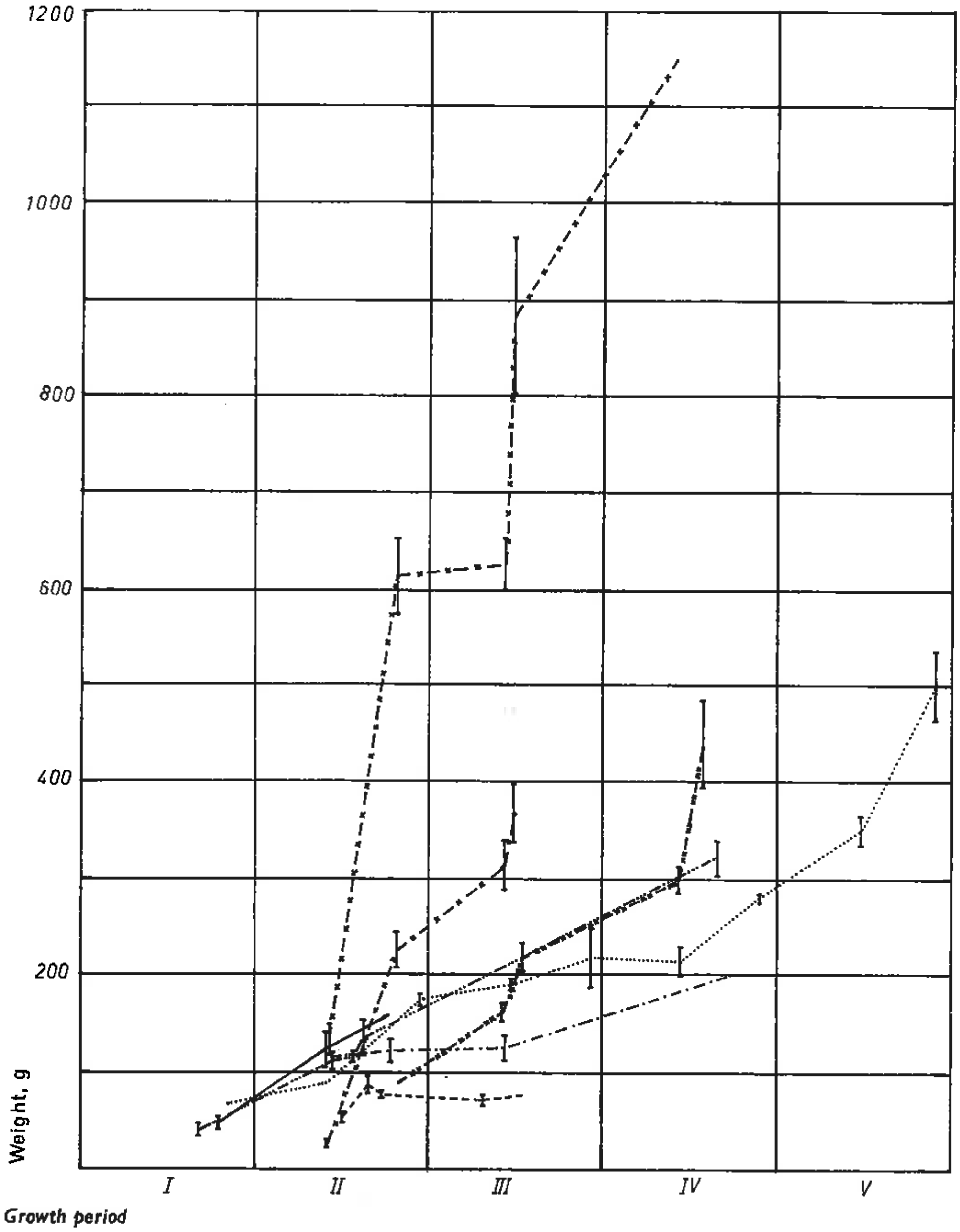

Fig. 31. Growth of rainbow trout. See legend to Fig. 28.

Table 29. Coefficient of condition in brown trout and rainbow trout.

	Age in years	0+		1+			2+		3+		4+	
	Lake	Summer	Autumn	Spring	Summer	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn
Brown trout	Kivi-Ahveroinen	–	0.60	0.91	–	0.88	0.85	0.91	0.99	1.00	1.01	–
	Satimuslampi	–	–	0.92	–	0.86	0.90	–	–	1.04	–	–
	Pien-Valkealampi	–	–	1.00	0.91	0.93	0.75	0.76	–	0.84	–	–
	Ulpasjärvi	–	1.10	1.04	–	0.99	0.86	0.85	0.85	0.98	0.97	0.92
	Sahalampi	–	0.85	1.02	–	0.93	1.00	1.01	1.05	1.05	–	–
	Julkujärvi	–	–	–	–	1.06	–	–	1.60	1.07	–	–
	Särkilampi	–	–	–	1.14	–	–	–	–	–	–	–
	Långviken	0.99	–	1.08	0.93	–	–	–	–	1.02	–	–
Rainbow trout	Satimuslampi	–	–	1.00	–	0.95	0.87	–	–	1.01	–	–
	Pien-Valkealampi	–	–	1.02	0.94	0.95	0.71	0.62	–	–	–	–
	Ahvenlampi	–	–	–	–	–	1.06	0.97	1.01	0.98	–	–
	Ulpasjärvi	–	1.10	1.12	–	0.97	0.91	0.90	0.88	0.98	1.03	1.06
	Sahalampi	–	0.98	1.16	–	1.00	–	–	–	–	–	–
	Julkujärvi	–	–	1.29	–	1.21	1.03[1]	–	1.04	–	–	–
	»	–	–	–	–	–	1.30[1]	–	–	–	–	–
	»	–	–	–	–	–	1.29[2]	–	–	–	–	–
	»	–	–	–	–	–	1.27[2]	–	–	–	–	–
	Särkilampi	–	–	–	–	1.14	–	–	–	–	–	–
	Långviken	1.29	–	1.08	0.96	–	–	–	–	1.16	–	–

[1] Introduced in spring
[2] Introduced in autumn

lowest value (0.60), and it was highest in the three-year-old brown trout in Julkujärvi (1.60).

2. Factors affecting growth and survival

Genetic factors

Immature stages of different stocks of brown trout have a tendency to show a similar growth pattern in similar conditions. Alm (1939, 1949, 1959) reported that there were no differences in the growth rates of the young of *Salmo trutta* morpha *fario* and *S. trutta* morpha *lacustris* kept under similar conditions. Brown trout inhabiting a brook were already mature at the age of three years instead of five years, the usual time for a lake population; the fishes which inhabited a brook also remained smaller than those living in a lake.

According to Brown (1957), it is hard to prove that genetic factors have a direct effect on growth, but they may considerably affect the growth pattern of young fish, the time of maturation and, in connexion with the latter, also the maximum size. She also showed that in a dense population of brown trout there were no differences in growth even if the quality of the food was different, whilst in a sparse population with abundant food supply there will be differences caused by food and genetic factors. From this point of view, the origin of the fish is of minor importance if the amount of food is the limiting factor, as was the case in the lakes studied by the present author. This is true at least up to the time when the fish become mature.

In rainbow trout there are great differences in the adaptability of different stocks to life in natural waters (e.g. Mršić 1935, Neresheimer 1937, Nilsson & Svärdson 1962, Jensen 1964). In our waters a Danish spring-spawning race of rainbow trout was used.

Quality and quantity of food

The availability of suitable food for each size group is important for the growth of brown trout and rainbow trout (e.g. Rayner 1953, Nilsson 1955, Johannes & Larkin 1961). Fish which feed on insects, plankton and other small-sized food remain smaller than those which feed on larger animals such as Mollusca, larvae of Trichoptera, *Asellus*, *Gammarus*, and fish. This is true even if the small-sized food is abundant (e.g. Dahl 1917, Alm 1939, Sømme 1954, Seppovaara 1962).

Young brown trout and rainbow trout feed mainly on zooplankton (Cladocera, Copepoda). The plankton diet of older brown trout and rainbow trout consists mainly of Cladocera, whilst the amount of Copepoda eaten is almost nil (Lindström 1955, Johannes & Larkin 1961).

Table 30. Dependence of growth of brown trout and rainbow trout on the abundance of zooplankton and benthic fauna. In the table the correlation coefficients (*r*) together with the t-values and corresponding probabilities (P) of the population regression coefficient (*b*) being equal to zero are presented.

		Growth	*r*	|t|	P	D.f.
Density of zooplankton (exx./10 l) in the first growth period	brown trout	cm	+ 0.038	0.076	> 0.30	4
	rainbow trout		+ 0.907*	3.059	0.10 > > 0.05	2
	brown trout	g	− 0.348	0.744	> 0.30	4
	rainbow trout		− 0.082	0.117	> 0.30	2
Density of zooplankton (exx./10 l) in the first growth period/ introduction density (exx./hectare)	brown trout	cm	− 0.092	0.187	> 0.30	4
	rainbow trout		+ 0.490	0.795	> 0.30	2
	brown trout	g	+ 0.385	0.837	> 0.30	4
	rainbow trout		+ 0.986*	8.387	0.02 > > 0.01	2
Abundance of benthic fauna (g/m^2) in the first growth period	brown trout	cm	− 0.172	0.351	> 0.30	4
	rainbow trout		− 0.780	1.768	0.30 > > 0.20	2
	brown trout	g	+ 0.375	0.809	> 0.30	4
	rainbow trout		+ 0.018	0.026	> 0.30	2
Abundance of benthic fauna (g/m^2) in the second growth period	brown trout	cm	+ 0.676	1.838	0.20 > > 0.10	4
	rainbow trout		+ 0.787	2.215	0.20 > > 0.10	3
	brown trout	g	+ 0.263	0.547	> 0.30	4
	rainbow trout [1]		+ 0.928*	4.334	0.05 > > 0.02	3
Abundance of benthic fauna (10 g/m^2) in the first growth period/ introduction density (exx./hectare)	brown trout	cm	− 0.116	0.235	> 0.30	4
	rainbow trout		− 0.115	0.164	> 0.30	2
	brown trout	g	+ 0.385	0.837	> 0.30	4
	rainbow trout		+ 0.986*	8.387	0.02 > > 0.01	2
Abundance of benthic fauna (10 g/m^2) in the second growth period/ introduction density (exx./hectare)	brown trout	cm	+ 0.430	0.954	> 0.30	4
	rainbow trout		+ 0.947*	5.150	0.02 > > 0.01	3
	brown trout	g	+ 0.023	0.047	> 0.30	4
	rainbow trout [1]		+ 0.946*	5.071	0.02 > > 0.01	3

[1] For calculation, a log-transformation of growth was used.

According to JOHANNES & LARKIN (1961), NILSSON & SVÄRDSON (1962), and TUUNAINEN (1966b), rainbow trout continue to feed on plankton and aerial food to a larger size than brown trout.

As the size of the fish increases, their diet changes from plankton to bottom fauna. In two-and-a-half-month-old rainbow trout from Långviken the volume of plankton eaten was only 32 % in fish whose mean length was 14.6 cm. Brown trout whose mean length was 10.9 cm had already begun to feed on bottom fauna and aerial food. In Sahalampi, 97 % of the diet of one-summer-old brown trout (mean length 13.8 cm) consisted of bottom fauna, the volume of zooplankton being only 1 % and that of aerial food 2 %.

In those lakes (e.g. Julkujärvi, Kivi-Ahveroinen and Sahalampi) where the bottom fauna was abundant and the organisms relatively large, the growth rate of the fish was high. In this respect *Asellus* as well as larvae of Trichoptera and Odonata were obviously important. The relations between the growth of fish and the amount of plankton and bottom fauna were studied on the basis of plankton and bottom animal samples collected in early summer (cf. TUUNAINEN 1968). The results are seen in Table 30.

The results show that the growth of rainbow trout is more dependent on the amount of plankton and bottom fauna than that of brown trout, because the potential growth rate of rainbow trout is probably higher during the first and second growth periods than that of brown trout. Therefore it is likely that the amount of food will earlier become a limiting factor for rainbow trout.

Some physical and chemical properties of the water

Oxygen content. During the period of open water the oxygen content of the epilimnion is usually sufficient. In winter the oxygen content was satisfactory in all lakes except Sahalampi (1.5 – 9.4 mg/l, 11 – 69 %), Julkujärvi (1.8 – 10.0 mg/l, 13 – 74 %) and Långviken (3.8 – 9.7 mg/l, 28 – 70 %).

In the periods of full circulation, all the bottom areas are available as feeding areas for the fish, whilst at the time of the summer and winter stagnation only a part of the bottom area is available, because of the oxygen deficit. This directly affects the growth of the fish and their productivity. In the stagnation periods the percentages of the bottom areas above the given levels of oxygen content were as follows:

	Summer		Winter	
	period of observation	% of bottom area above 5 mg/l O_2	period of observation	% of bottom area above 2 mg/l O_2
Kivi-Ahveroinen	1959 – 1966	80 – 100	1961 – 1966	90 – 100
Satimuslampi	1962 – 1965	100	1963	90
Pien-Valkealampi	1962 – 1966	70 – 100	–	–
Ahvenlampi	1962 – 1966	100	–	–
Ulpasjärvi	1960 – 1966	65 – 85	1962 – 1966	90 – 100
Sahalampi	1962 – 1967	85 – 100	1962 – 1966	0 – 80
Julkujärvi	1961 – 1966	80 – 95	1963 – 1966	0 – 80
Särkilampi	1962 – 1966	50 – 100	1966	80
Långviken	1962 – 1964	100	1964	75

According to SCHÄPERCLAUS (1961), the oxygen requirements of salmonids in summertime are as follows:

5 – 5.5 mg/l	critical
4 »	respiration becomes difficult
3 »	insufficient during long exposure
1.5 – 2 »	lethal even during short exposure

According to WIKGREN (1963), the lowest tolerable oxygen content for brown trout in summertime is 3 – 4 mg/l and 1.2 mg/l at 2 – 3 °C. Two-year-old rainbow trout survived in a lake at + 2 °C when the oxygen content was 1.4 mg/l (10 – 11 %).

With rising temperature the oxygen consumption of fish increases according to van't Hoff's rule. In steelhead trout (*Salmo gairdneri*) it is about 50 cm^3 O_2/g/h at 5 °C, about 70 cm^3 at 10 °C and about 180 cm^3 at 15 °C (MACAN 1963).

FRY (1957) studied the effect of temperature and oxygen content on the basic and active metabolism of brook trout. At higher temperatures (20 °C), the basic metabolism increases in relation to the active metabolism in large fish proportionally more than in small ones. Therefore small fish tolerate warm water better than large ones. A fish is also able to regulate its oxygen consumption within certain limits. The lethal limit of temperature and oxygen content is the level at which the oxygen required for basic metabolism exceeds that needed for active metabolism. At different temperatures the lethal limit is thus different. According to VARLEY (1967), rainbow trout tolerate higher temperatures and lower oxygen contents than brown trout.

pH and Fe. Great and abrupt changes in water quality are characteristic of small lakes and ponds. If the calcium content is low (buffer value small), both seasonal and daily fluctuations of pH are considerable.

The influence of pH upon the growth of fish cannot be verified exactly. In those lakes where the growth rate of the fish was low, a low pH was usually associated with low production of bottom fauna and high introduction density of fish. Low production of bottom fauna is often caused by low pH. According to FROST (1945), lower growth rates of brown trout in rivers with low pH values were mainly due to scarcity of food (cf. also SEPPOVAARA 1962).

The pH also affects the fish itself. According to MACAN (1963), the breathing intensity of steelhead trout increases by 21 % as the pH changes from 8 to 5.4. The energy requirement of a fish is thus considerably greater in acid than in neutral water; this causes a decrease of the growth rate in acid water, where the food supply is also usually smaller.

Low pH may also affect the tissues of fish (e.g. SCHÄPERCLAUS 1954). But there was no damage of the type reported, for instance, by RYHÄNEN (1961) for some fish species in a lake where the pH was temporarily as low as 4 – 5.

The CO_2 content of the water depends, within certain limits, on pH and calcium content. If the Ca content and pH are quite low, the bulk of the CO_2 is free and only a small part is in the form of bicarbonate (e.g. RUTTNER 1962). Many species of fish tolerate carbon dioxide quite well, but according to FRY (1957) many salmonids are very sensitive to it. An increase of blood carbon dioxide increases the respiration rate and thus the energy consumption of fish.

A low pH together with a high Fe content of the water is injurious to fish (e.g. OTTERSTRØM 1938, SEPPOVAARA 1962). Iron is deposited on the gill, because the pH of the fish is higher than that of the surrounding acid water, and may cause death by suffocation.

An Fe content as high as 1.92 mg/l was found in Sahalampi on 26. II. 1964 at 2.5 m depth with pH 5.9, and 3.34 mg/l on 9. IV. 1966 with pH 6.4. On both occasions the oxygen content was so low (1.8 and 0.0 mg/l) that the fish lived in the upper layers where the oxygen content was higher and the Fe content lower (0.19 – 0.39 mg/l Fe at 0.5 – 0.7 m). A high Fe content of water was caused by absence or deficit of oxygen (e.g. OHLE 1934, EINSELE 1936, MORTIMER

1941). However, no Fe deposits were found on the gills of any brown trout or rainbow trout in Sahalampi. In the other lakes investigated, the Fe content of the water was not higher than the average reported by JÄRNEFELT (1958) for Finnish waters.

The tabulation below, based on the data by BĒRZINS (1962), shows that in all the other lakes except Sahalampi and Ulpasjärvi the rainbow trout lived at the pH optimum of the species. For brown trout the quality of the water in all the lakes investigated was suitable in this respect.

	Lethal limits		Satisfactory		Optimum
Brown trout	5.0	9.2	5.0 – 5.6	8.0 – 9.2	5.6 – 8.0
Rainbow trout	5.5	9.2	5.5 – 6.2	8.4 – 9.2	6.2 – 8.4

Temperature and length of growth period. In the lakes studied no correlation was found between the growth of the fish and the length of the open water period. According to SEPPOVAARA (1962), the difference in growth between the brown trout of Lake Inari and Lake Päijänne is caused by a difference in the length of the growth period, which is 3 – 4 months shorter in the former lake. In the lakes studied now, the difference is much smaller (1 – 2 months).

In not one of the lakes was temperature found to be a lethal factor, but it was one of the factors limiting the growth rate, especially in winter.

During the open water period the increases in length and weight of both brown trout and rainbow trout were clearly greater than in winter time (Figs. 28 – 31).

As can be seen from the coefficients of condition (Table 29) the increase of weight compared with that of length was greater in winter than in summer. According to ELLIS & GOWING (1957), a rapid increase in the value of the coefficient of condition (i.e. a rapid increase of weight) occurs right at the beginning of a growth period, in May and June. The growth rate of brown trout is highest at about + 12 °C, according to SWIFT (1961), and at temperatures above and below this the growth rate decreases. Thus, there are two maxima in the growth of brown trout, the spring maximum being higher than the autumn one. In winter and in midsummer the growth rate is lower. According to BROWN (1957), the food intake of brown trout is maximal at 10 – 19° C.

In the rainbow trout the optimal temperature range is greater than in the brown trout (NERESHEIMER 1937). According to JENSEN (1964), the optimal temperature for rainbow trout is 10 – 18 °C. JOHNSON & HASLER (1954) demonstrated that in lakes with a long open water period and high mid-summer temperature the growth rate of rainbow trout is lower than in lakes where the temperature is lower. The highest growth rate was observed at 14 – 18 °C. The latter authors concluded that if the biomass of fish was low, the factors regulating the growth rate of rainbow trout were length of open water period and temperature, but with increasing biomass of fish the amount of food also became a factor limiting growth.

Sexual maturity

The stage of sexual maturity of brown trout and rainbow trout was estimated both in the field and in the laboratory from gonads collected at the same time as samples of alimentary tracts. No natural reproduction was observed in any of the lakes investigated. The nature of the bottoms, mainly soft mud, limits the possibilities of successful reproduction.

Table 31 presents the observations on the attainment of sexual maturity in the fish in the lakes investigated. Only one specimen of brown trout became sexually mature in Sahalampi during the second summer. In Ulpasjärvi the brown trout became sexually mature roughly according to the pattern described by SEPPOVAARA (1962) for brown trout living in brooks.

Some sexually mature one-year-old male rainbow trout were found in Sahalampi, Satimuslampi and Långviken. Of the females, only the largest fish in Julkujärvi reached sexual maturity at two years of age.

The smallest sexually mature brown trout

Table 31. Observations on sexual maturation in brown trout and rainbow trout

	Sex	Age years	cm	g	n
Sahalampi					
brown trout	♂	1 +	22.0	99	1
rainbow trout	♂	1	19.9 – 25.0	87 – 190	3
Julkujärvi					
rainbow trout	♀	2	35.0 – 38.4	550 – 685	3
Satimuslampi					
rainbow trout	♂	1	19.2 – 22.3	66 – 109	4
Ulpasjärvi					
brown trout	♂	2 +	24.8	153	1
» »	♀	2 +	25.0	145	1
rainbow trout	♂	2	26.2 – 26.5	154 – 170	2
» »	♂	3	29.9	257	1
» »	♂	3	29.5 – 31.5	275 – 280	2
Långviken					
rainbow trout	♂	1	19.7 – 20.4	86 – 104	3

Table 32. Correlation coefficient (*r*) between growth and introduction density in brown trout and in rainbow trout, together with t-values and corresponding probabilities (P) of the population regression coefficient (*b*) being equal to zero. The data in Table 33 were used.

Growth period		Growth	*r*	|t|	P	D.f.
I	brown trout	cm	+ 0.006	0.015	> 0.30	5
	rainbow trout		+ 0.371	0.693	> 0.30	3
	brown trout	g	− 0.590	1.638	0.20 > > 0.10	5
	rainbow trout		− 0.743	1.928	0.20 > > 0.10	3
II	brown trout	cm	− 0.650	1.914	0.20 > > 0.10	5
	rainbow trout		− 0.800	2.317	0.20 > > 0.10	4
	brown trout	g	− 0.311	0.733	> 0.30	5
	rainbow trout[1]		− 0.716	2.055	0.20 > > 0.10	4
III	brown trout	cm	− 0.209	0.480	> 0.30	5
	rainbow trout		− 0.725	1.828	0.20 > > 0.10	3
	brown trout	g	− 0.372	0.897	> 0.30	5
	rainbow trout[1]		− 0.653	1.497	0.30 > > 0.20	3

[1] For calculation, a log-transformation of growth was used.

were from Sahalampi (♂ 22.0 cm) and Ulpasjärvi (♂ 24.8 cm, ♀ 25.0 cm). SEPPOVAARA (1962) reported that some male brown trout were sexually mature when 16.3 – 32.5 cm in length. The smallest mature female found by him was 25 cm long.

In the lakes treated with rotenone the length of one-year-old sexually mature male rainbow trout was 19.7 – 25.0 and that of two-year-old females 35.0 – 38.4 cm. According to ALM (1959), the length at the time of maturation is > 17 cm in male rainbow trout (2 to 3 years old) and > 27 cm in females (3 to 4 years old). The values obtained here are slightly greater than ALM's (1959), although the fish were younger. According to SCHÄPERCLAUS (1961), rainbow trout become sexually mature earlier than brown trout, some males already at the end of their first year, i.e. as in the lakes of the present study.

Sexual maturation is mainly regulated by genetic factors, but temperature, quantity and quality of food, stream flow and photoperiodism are also important (ALM 1939, 1959, SCHÄPERCLAUS 1961, HAZARD & EDDY 1951). In warm and/or running water the fish mature at a younger age than in cold and/or still water. The amount of food available has an indirect influence upon this, because early maturation is correlated with a high growth rate and good condition.

Male fish usually become sexually mature at a younger age than females (e.g. DAHL 1917, ALM 1939, 1959, SCHÄPERCLAUS 1961, SEPPOVAARA 1962). Specimens of the *Salmo trutta* group which live in brooks reach sexual maturity at an average age of 3 – 4 years, whilst those which live in lakes mature at an age of 4 – 6 years (ALM 1939, SEPPOVAARA 1962).

Brown trout inhabiting a brook also spawn more often than those inhabiting a lake; this influences the growth rate too.

According to RAYNER (1953), the growth rate of rainbow trout slows down after maturation. The loss of weight caused by spawning, and the growth of the gonads for the following year have to be compensated by food. In those lakes where the food organisms are small, the weight of rainbow trout did not increase after they reached maturity, even if food was available. It is thus obvious that the growth rate of rainbow trout slows down or, according to RAYNER (1953), the

Table 33. Dependence of increase of length and weight of brown trout and rainbow trout in age classes I – III on the introduction density.

Introduction exx./hectare	Length cm I	II	III	Weight g I	II	III
Brown trout:						
187	15.3	–	–	36	–	–
499	–	9.6	8.1	–	72	333
810	16.3	11.9	5.1	43	117	81
1628	18.4	11.2	11.2	23	162	366
2000	13.2	–	–	20	–	–
2150	–	6.1	3.5	–	35	57
2000	14.6	5.4	0.8	15	45	3
2272	15.3	9.7	5.0	25	87	120
2500	17.5	5.6	8.5	33	72	198
$\bar{x}$	15.8	8.5	6.0	25.0	84.3	165.3
Rainbow trout:						
187	22.0	–	–	93	–	–
499	–	17.2	7.2	–	526	414
810	20.0	7.5	2.7	73	103	42
2000	22.6	1.7	1.8	79	44	36
2150	–	5.9	2.6	–	41	3
2272	21.6	5.2	2.7	68	102	60
2500	22.0	5.9	–	72	88	–
$\bar{x}$	21.6	7.4	3.4	77.0	150.7	111.0

fish may even die after spawning. There is no reliable information, however, as to whether the fish spawn even if there is no suitable spawning ground. It is also not known what happens if the mature fish do not spawn owing to lack of a releasing stimulus.

Density of fish stock

The influence of introduction density upon the growth of fish in the lakes investigated could be studied only during the first few growth periods, because in the later years the differences caused by different natural mortality and fishing become so great that a comparison of growth and introduction density was no longer warranted (Table 32).

Table 33 shows the length and weight increase of the fish. In rainbow trout growth seems to be more clearly dependent on the introduction density than in brown trout, in the range 187 – 2 500 fry/hectare.

VI. Food of the fish released

1. Composition

Terrestrial and aerial food. The number was 0 – 47 % and the volume 0 – 30 % in the brown trout. The corresponding figures were 0 – 45 % and 0 – 46 % in the rainbow trout. The numbers of Chironomids, Ephemerids, Trichoptera and Formicids were relatively high during the periods of emergence and swarming of these insects (Tuunainen 1966b). Both species of trout fed on the most abundant food organisms (cf. Frost & Smyly 1952).

Plankton. The zooplankton amounted to 0 – 29 % of all food specimens and 0 – 9 % of the volume in the brown trout (except in Julkujärvi), and 0 – 55 % and 0 – 42 %, respectively, in the rainbow trout. Cladocera were the most important, whilst the numbers of Copepoda were insignificant in the diet of the older fish (cf. Lindström 1955, Johannes & Larkin 1961). In Ulpasjärvi about 50 % of the food of rainbow trout 27 – 28 cm in length consisted of plankton, mainly *Leptodora kindti*. For small-sized fish in Satimuslampi, *Eurycercus lamellatus* was an important food item.

Benthic fauna. This group was the most important both for brown trout and for rainbow trout in the lakes studied. In brown trout the number of benthic animals was usually 53 – 100 % and their volume 36 – 100 %; only in some young fish was their proportion < 10 %. In rainbow trout both these values were 18 – 100 %.

Other food items. Traces of vertebrates (other fish, frogs, etc.) were found in the diet of five fish.

Some needles, leaves and other litter, together with aquatic moss and pieces of roots of some aquatic plants, were also occasionally found in the stomachs of the fish.

2. Variations in food and food competition

Seasonal variation in food consumption is presented in Figs. 32 and 33.

The quotients of similarity in the food of brown trout and rainbow trout were calculated using Sørensen's equation (e.g. Sørensen 1948, Jalas 1962). Samples collected at the same time in August are lacking. As can be seen below, in this material the quotient of similarity was lowest in July.

Month	V	VI	VII	VIII	IX	X	XI	XII
Frequency %	98	80	54	–	63	89	100	100
Volume %	91	89	55	–	61	90	73	89

There was also a clear daily variation in the food of the brown trout and rainbow trout. The similarity of food samples collected from the same lake in the different years was very great. If the fish stock was dense (e.g. Sahalampi), the similarity in the food of brown trout and rainbow trout was greater than if the density was lower (e.g. Ulpasjärvi). In those lakes where brown trout and rainbow trout fed on the same organisms, predation usually occurred at least partly at different times of day or year (Tuunainen 1966b).

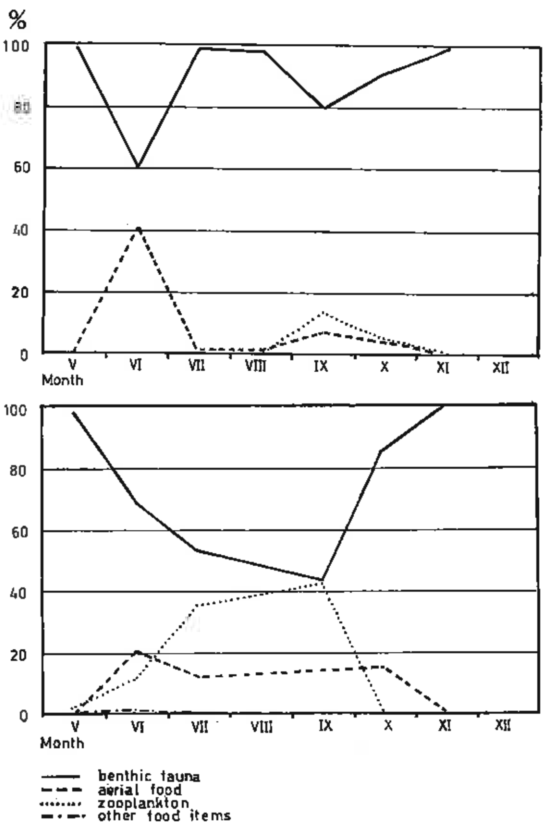

Fig. 32. Food of brown trout (above, n = 200) and rainbow trout (below, n = 167) expressed as frequencies of occurrence. For further details see text.

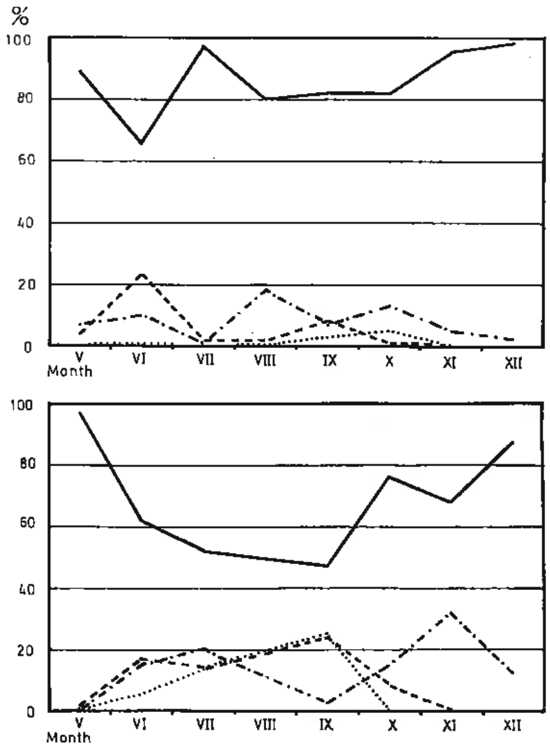

Fig. 33. Food of brown trout (above, n = 200) and rainbow trout (below, n = 167) expressed as percentage composition of food items by volume. For further details see text.

Table 34. Forage ratios for brown trout calculated from all data. n = number of samples in which the food organism in question was found in the stomachs of the fish caught.

	n	$\bar{x} \pm s_{\bar{x}}$	R
Hirudinea	2	0.21 ± 0.12	0.09 – 0.33
Pisidium sp.	5	0.16 ± 0.13	0.01 – 0.67
Asellus aquaticus	15	1.94 ± 0.47	0.03 – 6.75
Hydracarina	1	4.17	
Ephemerid larvae	2	10.33	6.15 – 14.50
Agrionid »	5	11.60 ± 6.32	0.20 – 32.70
Aeschnid »	1	25.20	
Libellulid »	9	7.70 ± 4.36	1.35 – 39.10
Other Odonatous larvae	1	3.26	
Corixid adults	2	38.50	24.50 – 52.60
Dytiscid larvae	2	1.49	0.27 – 2.70
Sialis »	8	0.56 ± 0.26	0.02 – 1.93
Trichopterous larvae	18	10.87 ± 3.96	0.09 – 65.40
Lepidopterous »	1	0.46	
Chaoborus »	3	14.35 ± 14.17	0.02 – 42.70
Chironomid »	21	0.52 ± 0.15	0.004 – 2.07
» pupae	5	67.80 ± 40.70	0.33 – 204.50
Ceratopogonid larvae	5	2.11 ± 1.40	0.04 – 7.55

Table 35. Forage ratios for rainbow trout calculated from all data. n = number of samples in which the food organism in question was found in the stomachs of the fish caught.

	n	$\bar{x} \pm s_{\bar{x}}$	R
Hirudinea	1	1.41	
Pisidium sp.	1	0.06	
Asellus aquaticus	6	1.27 ± 0.24	0.44 – 2.00
Hydracarina	3	2.93 ± 2.15	0.69 – 7.24
Ephemerid larvae	1	12.60	
Agrionid »	1	0.41	
Libellulid »	5	6.65 ± 3.16	0.22 – 30.50
Other Odonatous larvae	1	0.80	
Corixid adults	1	1.00	
Sialis larvae	2	0.23	0.03 – 0.42
Trichopterous larvae	7	17.55 ± 16.06	0.19 – 111.20
Chaoborus »	3	0.20 ± 0.10	0.05 – 0.38
Chironomid »	11	0.52 ± 0.52	0.01 – 1.80
» pupae	4	195.50 ± 57.36	25.05 – 270.00
Ceratopogonid larvae	5	3.86 ± 2.86	0.14 – 15.10

3. Selective feeding of fish

The mean values of forage ratios from all the lakes are presented in Tables 34 and 35. In Table 36, in addition, a summary of the occurrence of organisms or groups of organisms in the food and in bottom animal samples collected at the same time is presented. This information is supplementary in those groups of bottom organisms which do not occur at the same time in both samples.

Both brown trout and rainbow trout had a forage ratio > 1 in respect of the following groups: *Asellus*, Hydracarina, larvae of Ephemerids, Libellulids, Trichoptera, and Ceratopogonids, as well as pupae of Chironomids.

A value < 1 was found for *Pisidium* sp., larvae of *Sialis* and larvae of Chironomids.

In other groups the results for brown trout and rainbow trout were different.

Brown trout and/or rainbow trout clearly also selected larvae of Agrionids and Aeschnids as well as adults of Corixids and Dytiscids.

The following groups were avoided: Nematoda, Oligochaeta, Hirudinea, larvae of Coleoptera, Dytiscids, and Diptera, as well as pupae of *Donacia* and Diptera. As regards Hydracarina and larvae of Libellulids, the results included in Tables 34 and 35 differ from those in Table 36.

Table 36. Occurrence of benthic animals in the food samples and bottom samples collected at the same time (brown trout in eight lakes, rainbow trout in seven lakes). A = found in food, not in bottom samples, B = found in bottom samples, not in food.

	A		B		Total	
	brown trout	rain-bow trout	brown trout	rain-bow trout	A	B
Nematoda	–	–	3/8	2/7	–	5/15
Gordius sp.	–	2/7	–	–	2/15	–
Oligochaeta	–	–	6/8	5/7	–	11/15
Hirudinea	–	1/7	–	–	1/15	–
Glossosiphonia sp.	–	–	2/8	1/7	–	3/15
Helobdella sp.	–	–	1/8	1/7	–	2/15
Lymnaeids	–	1/7	–	–	1/15	–
Pisidium sp.	–	–	2/8	1/7	–	3/15
Other Mollusca	–	1/7	–	–	1/15	–
Asellus aquaticus	–	–	–	1/7	–	1/15
Argyroneta aquatica	1/8	–	1/8	2/7	1/15	3/15
Hydracarina	–	1/7	5/8	–	1/15	5/15
Ephemerid larvae	2/8	1/7	–	2/7	3/15	2/15
Agrionid »	2/8	3/7	–	–	5/15	–
Aeschnid »	1/8	2/7	–	–	3/15	–
Libellulid »	1/8	1/7	2/8	3/7	2/15	5/15
Other Odonatous larvae	–	2/7	1/8	1/7	2/15	2/15
Nepa sp.	–	1/7	1/8	–	1/15	1/15
Notonecta sp.	–	–	1/8	1/7	–	2/15
Corixids	2/8	2/7	2/8	–	4/15	2/15
Dytiscid larvae	1/8	2/7	4/8	3/7	3/15	7/15
» adults	4/8	5/7	2/8	1/7	9/15	3/15
Donacia sp. pupae	–	–	4/8	4/7	–	8/15
Other Coleopterous larvae	–	–	4/8	2/7	–	6/15
» » adults	–	–	–	1/7	–	1/15
Sialis larvae	–	–	4/8	4/7	–	8/15
Trichopterous larvae	1/8	1/7	1/8	–	2/15	1/15
Lepidopterous »	1/8	1/7	1/8	2/7	2/15	3/15
Chaoborus larvae	–	1/7	2/8	–	1/15	2/15
» pupae	–	1/7	–	–	1/15	–
Chironomid larvae	–	–	1/8	1/7	–	2/15
» pupae	1/8	1/7	1/8	1/7	2/15	2/15
Ceratopogonid larvae	1/8	1/7	2/8	–	2/15	2/15
Tabanid larvae	–	1/7	1/8	–	1/15	1/15
Other Dipterous larvae	–	–	3/8	2/7	–	5/15
» » pupae	–	–	2/8	2/7	–	4/15

VII. Mortality

The mortality rate of the fish in Sahalampi was studied with the aid of the marking—recapture method (cf. ROUNSEFELL & EVERHART 1960).

A total of 60 fish (59 brown trout and 1 rainbow trout) were caught on 5. X. 1964, measured, weighed, marked by fin clipping and then released into the lake. On 6. X. 1964, 52 fish were caught, of which 12 brown trout and 1 rainbow trout bore marks and the remaining 39 specimens of brown trout were unmarked.

The total fish stock was reckoned to consist of 240 specimens on 6. X. 1964. The proportion of marked fish in the catch was 25 %. The standard deviation of the marked group in the catch is 3. At the probability level of 95 % the number of marked fish in the catch is 13 ± 6. Estimated from these data, the number of fish on 6. X. 1964 was from 162 to 464, nearly all of which were brown trout. The rainbow trout caught on 5. X and 6. X. 1964 may have been the last specimens, since not one was caught later. In Fig. 34 an estimate of the number of brown trout and rainbow trout in the lake during the period 25. V. 1963 – 15. X. 1966 is presented. The number of fish in Sahalampi after 15. X. 1966 is hard to estimate accurately, but because the last sampling was very intensive, only a few specimens of brown trout could have remained after that. In summer 1967 no further fish were caught.

The natural mortality rates of the age classes were estimated from Fig. 34 and Table 37. The natural mortality may be a little lower than if there had been no fishing, because the remaining fish were in a better position than they would have been if there had been no fishing. Thus fishing will reduce the density-dependent mortality (e.g. MILLER 1958, LE CREN 1965). Table 38 shows the natural mortality rates of the age classes I – III in Sahalampi. The low value in the age class II in the rainbow trout may be a

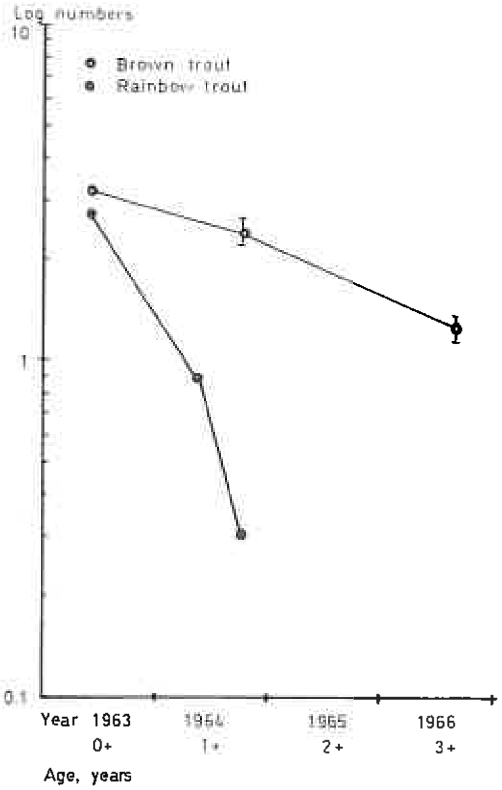

Fig. 34. Size of fish stock in Sahalampi

Table 37. Observations on the size of the fish stock in Sahalampi.

Date	Species	Before sampling Exx./hectare	Before sampling Total Exx./hectare	Before sampling Total kg/hectare	After sampling Total Exx./hectare	After sampling Total kg/hectare
27. VII. 1962 [1]	perch ruff	– 1330	– 1330	– 70.0	– 0.0	– 0.0
25. V. 1963 [2]	brown trout rainbow trout	1875 625	2500	5.0	2500	5.0
16. X. 1963	brown trout rainbow trout	1040 70	1110	26.7	1026	24.5
29. V. 1964	brown trout rainbow trout	465 9	474	26.6	450	24.9
5. X. 1964	brown trout rainbow trout	298 2	300	30.3	235	23.7
21. VI. 1965	brown trout	95	95	12.4	87	11.6
9. IX. 1965	brown trout	70	70	16.6	64	15.1
1. VI. 1966	brown trout	29	29	11.6	24	9.6
2. IX. 1966	brown trout	24	24	14.4	16	9.9
15. X. 1966	brown trout	16	16	9.5	6	3.6

[1] Toivonen (1962)
[2] Introduction

Table 38. Natural mortality rates in various age classes of brown trout and rainbow trout in Sahalampi

Age class	Species	Size of the stock at the beginning of each age class exx./hectare	Mortality exx./hectare	Percentage mortality in each age class
I	brown trout rainbow trout	1875 625	1337.5 604.7	71.3 96.8
II	brown trout rainbow trout	465 9	235.0 1.3	50.5 14.4
III	brown trout	95	53.5	56.3

result of the high efficiency of fishing (85.6 % of the total decrease of rainbow trout stock).

In the various age classes of the brown trout and rainbow trout the natural mortality rate is not constant. It is highest in the first age classes and diminishes with increasing size of the fish (e.g. Alm 1939, Johnson & Hasler 1954, Halme & Orpana 1963). The natural percentage mortalities in the two trout species in Sahalampi were in general higher than those reported by the above investigators (p. 117).

VIII. Discussion

1. General

The lakes dealt with in this study represent special environments in both limnological and biological respects. Small lakes or ponds with quite a small water volume are more susceptible to environmental changes than larger ones. The killing of the natural fish stocks with rotenone also affected a great number of other animal groups and thus increased the special features of these lakes.

Of the nine lakes studied, the natural fish stock was totally exterminated in all except Ulpasjärvi. During a sampling carried out in

Ulpasjärvi on 4. – 5. XII. 1963, twelve roach were caught. The ages of these fish were 2+ years according to determinations made by the scales, so at the time of the poisoning (5. VIII. 1960) they were about two months old. At the temperature prevailing at the time of the treatment (surface +21.5 °C) (Suomen Kalastusyhdistys 1961), the toxin disappears from the surface water in about two weeks (cf. Bērzins 1961).

Samples of zooplankton collected ten days after the poisoning showed that in the cold hypolimnion the zooplankton survived quite well, whilst only very few specimens were found in the epilimnion; 4 1/2 months after the treatment no zooplankton were found (Suomen Kalastusyhdistys 1961). In Julkujärvi, where 0.8 mg/l rotenone was used, the zooplankton was composed almost entirely of Rotatoria. The same was found in Ahvenlampi and Pien-Valkealampi, too. The poison did not disappear from Julkujärvi during the following winter, as was shown not only by the zooplankton but also by the fact that the brown trout and rainbow trout released the following spring all died. The toxic effect of rotenone on the zooplankton lasted for about eight to nine months in Julkujärvi; then it was inactivated with $KMnO_4$.

After the natural fish stocks had been killed, all the lakes were without fish for at least one winter. New fish were released into most of the lakes in the summer following the poisoning: brown trout, rainbow trout or both as fry or as older fish. The new stocks were in many respects exceptional. The species were in by no means a natural state, and the age class composition differed from that of natural stocks, because the fish released represented only one age class (cf. Toivonen 1962, 1964). This diminished intraspecific predation and lowered fish production. If the age composition of the fish is normal, the different steps in the food chains are more efficiently utilized by fish than if the age composition is uniform. In their lenitic conditions, small lakes differ from the normal environment of trout fry; for instance, active hunting for food is necessary. The absence of a current may cause changes in territoriality and other behavioural activities (cf. Kalleberg 1958). The lack of suitable spawning grounds in small lakes means that additional introductions must be carried out at suitable intervals.

2. Limnological features

All the lakes studied lie between 60° 17' – 64° 35' N and 23° 01' – 28° 38' E and 0 – 152 m above sea level. The areas of the lakes are 0.8 – 4.3 hectares, maximum depths 3.0 – 19.5 m and volumes 16 000 – 215 000 m³ (Toivonen 1962, Tuunainen 1966a, 1966b). The shores of the lakes are in general marshy or paludified. The bottom is mainly mud with plankton debris.

Aquatic vegetation is quite scanty. The belt of emergent vegetation consists mainly of sedges and is generally narrow, at most some metres broad. The belt of floating vegetation usually grows to a depth of 1 – 3 metres. This belt is very abundant in Sahalampi, Julkujärvi and Långviken. The submerged vegetation consists chiefly of various species of aquatic mosses. This belt is abundant in oligo- and mesohumous lakes, especially in Kivi-Ahveroinen, Pien-Valkealampi, Ahvenlampi, Ulpasjärvi, Sahalampi and Särkilampi.

Temperature

Several factors affect the thermal stratification of the lakes in summer. The stratification is clear in Kivi-Ahveroinen, Pien-Valkealampi, Ulpasjärvi and Julkujärvi. In Långviken and Särkilampi the stratification is usually incomplete or absent. In Satimuslampi, Ahvenlampi and Sahalampi there is no thermal stratification in summer, or it is temporary in spring if the weather rapidly becomes warm. Maximum temperatures were 18.2 – 24.8 °C.

In winter the temperature of the water near the bottom was about +4 °C.

The length of the open-water period is different in different lakes. It is longest (200 – 227 days/year) in the southernmost lakes, Sahalampi, Pien-Valkealampi and Ahvenlampi, but only 153 – 205 days per year in the northern lakes, Ulpasjärvi, Långviken and Kivi-Ahveroinen (cf. Tuunainen 1966b).

Oxygen

Oxygen conditions were clearly better in the oligohumous lakes than in the meso- or polyhumous ones. In Sahalampi and Julkujärvi some of the fish died as a result of the oxygen deficit, and in Långviken the oxygen content was also very low. Humous substances cause oxygen consumption during the winter, especially if sufficient nutrients for microbial activity are present (e.g. HYVÄRINEN 1965, SORMUNEN 1965, RYHÄNEN 1966). In Julkujärvi both humous substances and pollution cause increased oxygen consumption in winter.

During the open season the oxygen content was sufficient for fish in the epilimnion. In the hypolimnion, however, there was occasionally an oxygen deficit in Kivi-Ahveroinen, Pien-Valkealampi, Ulpasjärvi, Julkujärvi, Särkilampi and Långviken.

pH

Great and rapid fluctuations of pH are typical of small lakes, especially of those surrounded by marshland.

In the epilimnion the pH was 4.8 – 7.3 during the time of observation. In the same lake the fluctuation was usually about 1 – 2 pH units. In some small lakes in the Kälarne district, Sweden, the fluctuation of pH was found to be as much as 1.5 – 2.5 pH units (ALM 1960).

Ahvenlampi, Pien-Valkealampi and Satimuslampi were more acid before the poisoning than during the time when trout were present. Ahvenlampi and Pien-Valkealampi were treated with waste lime before the trout were introduced, and Satimuslampi with crushed limestone (TUUNAINEN 1966b).

Conductivity

Though the electrical conductivity of the water is mostly correlated with the total amount of dissolved inorganic substances, colloidal humous substances also affect the conductivity (e.g. OHLE 1934, JAMES 1941, RYHÄNEN 1961, HYVÄRINEN 1965).

In the lakes studied, the limits for conductivity were 6 – 136 μS. The highest value was for Långviken, the lowest for Pien-Valkealampi. In 24 lakes treated with rotenone in 1963 the conductivity was 6 – 40 μS (TOIVONEN 1964), so eight of the nine lakes studied, i.e. all except Långviken, had values that fell within these limits.

$KMnO_4$ consumption

The $KMnO_4$ consumption in the lakes studied ranged from 3.5 to 131.0 mg/l. The lowest value was for Kivi-Ahveroinen, the highest for Långviken, which is rich in humous substances.

Colour and transparency

Apart from humous substances, dissolved Fe and Mn compounds may also colour the water if present in high enough concentrations. In Sahalampi there is an oxygen deficit in winter in the water layers near the bottom, and then Fe from the sediment dissolves into the water (cf. e.g. OHLE 1934, EINSELE 1936, MORTIMER 1941) and increases its colour.

On the basis of colour and transparency JÄRNEFELT (1953) classified lakes as oligohumous (transparency $\geqq$ 3.5 m, colour $<$ 40 Pt mg/l), mesohumous (transparency $>$ 1.25 m, but $<$ 3.5 m, colour 40 – 80 Pt mg/l) and polyhumous (transparency $\leqq$ 1.25 m, colour $>$ 80 Pt mg/l). If classified according to colour, Långviken is polyhumous, but all the other lakes included in this study are oligohumous. On the basis of the average value of transparency, Kivi-Ahveroinen, Satimuslampi, Pien-Valkealampi, Ahvenlampi, Ulpasjärvi and Sahalampi are oligohumous, whilst Julkujärvi and Särkilampi are mesohumous. Långviken is intermediate between meso- and polyhumous lakes (transparency 1.3 m).

The observed colour range was 0 – 300 Pt mg/l and the transparency range 1.3 – 10 m. The lowest value for colour and the highest value for transparency were found in Kivi-Ahveroinen and the brownest water and lowest value for transparency in Långviken.

Alkalinity, hardness, and Fe

The values for alkalinity were 0.05 – 0.36 mval/l, the lowest value being for Sahalampi and the highest for Ahvenlampi.

Total hardness covered a range of 0.04 – 0.50 °dH. Both extremes were for Pien-Valkealampi.

In Kivi-Ahveroinen, Satimuslampi, Ulpasjärvi, Sahalampi, Särkilampi and Långviken the Fe content was 0 – 3.34 mg/l. The lower limit was for Ulpasjärvi and Sahalampi, the upper for Sahalampi. A low value for pH combined with a high Fe content is harmful to fish, because iron is deposited on the more alkaline gills of fish and in the extreme case causes them to suffocate (e.g. OTTERSTRØM 1938, SEPPOVAARA 1962, SCHÄPERCLAUS 1967). SEPPOVAARA (1962) found that brown trout were able to live and reproduce well in a brook where the pH was 5.7 and the Fe content of the water 0.76 mg/l. SCHÄPERCLAUS (1967) reported that a concentration of 0.9 mg/l was lethal to fish at a level of pH 6.5 – 7.5. Even in Sahalampi, where the Fe concentration was highest, there were no deposits of Fe on the gills of the fish. However, the physiological and ecological effects of the Fe – humus complex on fish are unknown.

3. Variations in the abundance of the benthic fauna

That several species of the bottom fauna are subject to seasonal fluctuations in numbers is well known (e.g. BRUNDIN 1949, PALMÉN 1958, SERNOW 1958, GRIMÅS 1961, JÓNASSON 1961, 1965, MACAN 1963, 1964, 1965, REYNOLDSON & YOUNG 1965, PALMÉN & AHO 1966). The emergence of Ephemerids, Odonata, *Sialis*, Trichoptera and Chironomids and the appearance of new generations cause great fluctuations in the density and biomass of the bottom fauna. Because of differences in climatic and other ecological factors in different lakes, emergence of these insects does not occur simultaneously in most of the lakes. This partly invalidates comparison of samples collected from different lakes at the same time or from one lake in different years. The most comparable samples are those taken in late autumn or early spring.

After the poisoning, the bottom animal density increased in all the lakes for which data are available. In Julkujärvi and Särkilampi, however, no bottom animal samples were collected before the lakes were treated. The increase in biomass was usually most obvious in the year following the poisoning. After release of the new fish stock the biomass of the bottom fauna decreased again, and a decrease in the fish biomass was followed by an increase in the bottom fauna.

LELLÁK (1965) suggested that the increase of bottom fauna after poisoning is caused both by the elimination of direct predation of fish and by the indirect influence of the fish on the food chains of the bottom fauna. Rotenone kills most of the phyto- and zooplankton which then sediment and form a new supply of food for the benthic fauna. This, according to LELLÁK (1965), is the most important factor increasing bottom animal production, elimination of predation being less important. This investigator showed that if a bottom area was protected from fish, the biomass of the bottom fauna was twice that of the unprotected areas. In ponds treated with poisons the density and biomass of the benthic fauna increased about 50 – 70-fold, or definitely more than could be expected as a result of removing the fish.

WIKGREN's (1963) observations on Strömma Tjenan in Ahvenanmaa, Finland, also show that some eutrophication occurs as a sequel of poisoning. However, this did not occur after treatment in the winter. Rotenone probably caused an almost »dead» state in the lake, with quite a high oxygen content of the water. The abrupt increase of nutrients during the following spring circulation afforded better conditions for the growth of phytoplankton than before and the breaking up of the organic substances consumed more oxygen in the following winter than did the previous smaller amount of organic substances.

In Sahalampi and Kivi-Ahveroinen the oxygen conditions were better during the winter after the poisoning than in the previous winters. On the other hand, no unusual consumption of oxygen was observed during the second winter after the poisoning (cf. TUUNAINEN 1968), presumably owing to the more oligotrophic nature of the lakes.

In Sahalampi and Julkujärvi the oxygen conditions were worse than usual in the winter of 1964/1965. Seine fishing in Sahalampi in the autumn of 1964 caused the bottom sediment to whirl in the water, and the following winter this material led to an abnormally high consumption of oxygen. In winter 1965/1966 the oxygen conditions were »normal» again. In Julkujärvi the main cause of the oxygen deficit was sewage from houses around the lake.

The lakes studied by LELLÁK (1965) and WIKGREN (1963) represent a eutrophic type, whilst the lakes treated with rotenone in 1960 and 1962 were considerably more oligotrophic. The facts presented above indicate that in food chains of oligotrophic lakes the consequences of rotenone treatment are different from those in eutrophic waters and the effect of fish upon the benthic fauna is also greater than in eutrophic lakes. This is supported by the fact that the density and biomass of the benthic fauna increased again after the trout had disappeared, in some cases even more than just after the treatment. In the lakes studied by LELLÁK (1965) the bottom fauna returned to the original density level after some time, and there was no second increase afterwards.

Several studies have shown that the zooplankton is more sensitive to rotenone than larger animals are (e.g. Brown & Ball 1943, Cushing & Olive 1956, Almquist 1959, Lindgren 1960, Andreasson 1963, Bērzins 1963). Of the benthic fauna *Astacus* and Molluscs are less sensitive. Chironomids, some Oligochaeta, Hirudinea, *Asellus*, as well as larvae of some Trichoptera and Ephemerids are the most sensitive. Many of the least sensitive species or groups of the benthic fauna (e.g. many Oligochaeta, Amphipoda and Gastropoda) increase considerably after poisoning (e.g. Smith 1941, Hooper 1948, Cushing & Olive 1956, Bērzins 1958, Lindgren 1960). Lellák (1965) observed an initial increase of Chironomid larvae and after their disappearance a general increase in the numbers of benthic worms, especially Tubificids, which consumed the increased quantity of food and then disappeared. After this, both the abundance and the biomass of the bottom fauna stabilized within the normal limits.

Differences from this pattern in more oligotrophic waters may be caused not only by the lower trophic level but also by differences in the composition of the species. For example, in the lakes included in the present study, the bottom fauna consists of a larger number of groups and species than those studied by Lellák (1965).

No group or species originally present in the lakes studied was actually exterminated by the rotenone treatment. An increase in most groups after the poisoning was a general feature. This was especially clear in *Pisidium*, *Asellus* and larvae of Chironomids in Kivi-Ahveroinen, and in *Pisidium* as well as in larvae of Odonata, *Sialis* and Chironomids in Sahalampi, whilst in Satimuslampi, Ahvenlampi and Pien-Valkealampi most of the groups showed only a slight increase, which was clearest in Oligochaeta and larvae of Chironomids. In Ulpasjärvi there was an increase of *Pisidium*, *Asellus* and larvae of *Sialis*, in Långviken a similar increase of Oligochaeta, *Pisidium*, and *Asellus* as well as larvae of Chironomids and Ceratopogonids. In Julkujärvi and Särkilampi there was an increase of *Pisidium* and *Asellus*, in Särkilampi also in Hydracarina and larvae of *Sialis* and Chironomids.

The influence of the fish stock on the benthic fauna has been studied by many different authors (e.g. Alm 1922, 1960, Olstad 1925, Lundbeck 1926, Pentland 1930, Hayne & Ball 1956, Macan & Mackereth 1957, Reimers 1957, 1958, Svärdson 1957, Ruggles 1959, Ivlev 1961, Macan 1962, Tuunainen 1964, 1966b, Lellák 1965, Straškraba 1965). This influence depends greatly on the habits of the species in question, on the reproductive capacity and other specific factors. It has been pointed out that it is hard to find a logical relation between the biomass values of fish and bottom fauna (e.g. Alm 1922, 1960, Tuunainen 1964). The lakes where observations are made are often so variable in ecological respects that it is impossible to draw general conclusions. Continuous observations on the same lake are better suited for an analysis of quantitative relationships. Such observations were carried out on Sahalampi.

4. Production and productivity

Production may be measured in terms of wet weight, dry weight, nitrogen content or energy content. Of these units, energy is the most flexible, universal and realistic. On the other hand, nearly all production studies are based on measurements of wet weight in the first instance, and energy contents are computed secondarily if at all (Chapman 1968). For this study, equipment for analyses of the caloric values for organisms was not available. Therefore, the more conventional method based on wet weights was employed.

In the lakes included in the study, the growth of the populations of brown trout and rainbow trout after their first summer depends directly on the production of the benthic animals.

The bottom animal production (net and gross production) was calculated from a series of observations on biomass values, but predation by fish was also taken into account. From Pearl–Verhulst's formula (e.g. Hayne & Ball 1956) the growth rate of the biomass can be calculated, presuming that the initial and highest values of the biomass are known.

In Sahalampi the initial biomass in the beginning of the first summer after the treatment with rotenone was small (2.3 g/m^2) and the production of new biomass during 128 days was 9.7-fold compared with the initial value. As the biomass of the benthic animals grew, the growth rate of the biomass diminished and reached zero in the summer of 1966. For the benthic fauna of the lake (cf. Tuunainen 1968) a maximum growth rate of 0.18 g/m^2/day was found if the initial value of the biomass was 3.05 g/m^2. If the initial value of the biomass was 13.79 g/m^2 the growth rate of the biomass was zero. The estimate of the maximum growth rate is too low on account of errors included in the conversion coefficient and the fact that the effects of natural mortality and emergence are excluded.

The highest growth rate of the biomass of benthic animals in Sahalampi was considerably lower than that reported by LELLÁK (1965) from some eutrophic waters in Bohemia, Czechoslovakia, where the biomass of the benthic fauna increased 55-fold in two months after poisoning. According to HAYNE & BALL (1956), in some small lakes in south Michigan, U.S.A., the biomass of bottom animals rose 7.3-fold within one and a half months after the fish were removed. The lower growth rate in Sahalampi reflects the oligotrophy of this lake.

The growth rate of the bottom fauna in Sahalampi was greater than that of the fish stock except in summer 1966. In 1963 – 1966, the calculated fish production (gross production) was 4.4 – 21.7 kg per hectare per growth period, the value being highest for the first year the fish were in the lake.

The productivity of the trout population in relation to bottom animal productivity was calculated using IVLEV's (1966) equation. If the biomass of the bottom fauna stayed at the optimum level during the whole growth period and if the fish stock consumed the whole biomass produced, the productivity of the fish stock would be 29.7 kg per hectare per year (conversion coefficient = 8.85). Here again, the estimate is too low on account of errors discussed above. The actual trout production (gross production) during the second, third and fourth growth periods, however, was only 15 – 35 % of the productivity, i.e. the fish utilized the resources of the lake quite ineffectively.

Fishing carried out in the lakes was not very effective and the catches were rather small, only 1.3 – 10.6 kg per hectare per year. In most cases it would have been possible to increase the catches by more effective fishing timed in a suitable way. If the whole fish stock of Sahalampi had been caught in autumn 1964, the catch would have been 1.6-fold of the weight actually caught, but the average size of the fish would have been considerably smaller. The maximum biomass of trout in Sahalampi (in autumn 1964) was 30.3 kg /hectare or 43 % of the biomass of the original fish population before rotenone treatment. The average weight of the trout was then about twice that of the original perch. This biomass value is about half that reported for rainbow trout by JOHNSSON & HASLER (1954) for small dystrophic lakes in Wisconsin, U.S.A., probably because of the superior productivity of the latter lakes. The actual catches are only about 25 – 34 % of the catches from small Finnish eutrophic lakes, whilst the annual catches from small oligotrophic lakes are about the same (cf. Maatalous-hallituksen kalataloudellinen tutkimustoimisto 1963, 1964, 1965, 1966).

5. Growth of the fish and factors influencing this

The maximum size of a fish in a certain environment is determined by the interaction of food and population density within the limits of genetic factors (ALM 1939).

In the present experiments, the effects of physical and chemical factors upon the growth of fish could not be distinguished from the influence of biotic factors. In the first and second growth periods the growth of rainbow trout was more clearly dependent on the amount of the plankton and bottom fauna than that of brown trout. When densities of 187 – 2 500 fry per hectare were used, growth was independent of density in the first growth period. In the second growth period, however, there was a tendency to a lower growth rate if the introduction densities were high. In the third growth period the influence of introduction density could still be observed in the rainbow trout, but it was less clear in the brown trout.

In the Finnish waters the weight gain of rainbow trout was about 1- to 3-fold in the first, about the same in the second and less in the third growth period compared with the values found by LUNDGREN (1962) in Swedish lakes treated with rotenone, if the densities were equal. LUNDGREN (1962) suggested introduction densities of 500 fry or 200 one-summer-old brook trout or rainbow trout per hectare in small lakes treated with rotenone. If introduction densities of 500 – 5 000 fry per hectare were used, the one-summer-old fish were 75.0 – 11.3 g, respectively. In the small Finnish lakes treated with rotenone, with introduction densities of 187 – 2 500 fry per hectare, one-summer-old brown trout were about 45 – 9 g and rainbow trout about 90 – 50 g, respectively.

In the first two growth periods in the small lakes studied the growth rate of brown trout was in all cases better than that of wild brown trout in the watercourses of southern and central Finland studied by SEPPOVAARA (1962).

The growth rate of the rainbow trout was highest in Julkujärvi, where the average size of two-summer-old fish was 36.9 cm and 613 g, i.e. about the same as that of rainbow trout of Seattle stock (37.4 cm) in Lake Halmsjön, Sweden, reported by NILSSON & SVÄRDSON (1962). The average size of two-summer-old rainbow trout (25.6 cm) calculated from all the data, however, was considerably smaller than that of the Seattle stock and somewhat smaller than that observed in small Irish lakes treated with rotenone (cf. O'RIORDAN & KENNEDY 1964).

The highest average weight of four-year-old rainbow trout (886.7 g) was from Julkujärvi. LUNDGREN (1962) reported 840 g as the highest average weight observed in Jämtland, Sweden. Apart from the less favourable quality of the water and the feeding conditions, the lower growth rate in Finnish waters may be due to the hardness of the climate. The possible effect of the different origin of the fish cannot be entirely ruled out, either.

In lakes where brown trout and rainbow trout occurred simultaneously (Sahalampi, Satimuslampi, Pien-Valkealampi, Ulpasjärvi, Julkujärvi, Särkilampi and Långviken), there were some differences in the growth rates of these species. In all cases the average size of the rainbow trout was greater than that of the brown trout at the end of the first and second growth periods. In Satimuslampi and Julkujärvi this was also observed at the end of the third and fourth growth periods. In the other lakes the rainbow trout, if present, were of the same size as or smaller than the brown trout during the third growth period and subsequently.

In England, according to VARLEY (1967), rainbow trout grow a little more rapidly than brown trout in the same environment. If the two species were grown as a mixed population in aquaria, fry of rainbow trout were more aggressive than those of brown trout; the growth rate of the latter decreased and some even died.

The coefficient of condition (K) was 0.60 – 1.60 in brown trout and 0.62 – 1.30 in rainbow trout in the whole material. Compared with the range of the coefficient reported by REIMERS (1957, 1963), the condition of one-summer-old brown trout in Kivi-Ahveroinen and that of three-summer-old rainbow trout in Pien-Valkealampi was very poor. The maximum average coefficient of condition, 1.60, was found in three-year-old brown trout in Julkujärvi. In Julkujärvi and Långviken the coefficient of condition of rainbow trout was at times quite high (1.27 – 1.30).

According to REIMERS (1957), brown trout kept without food in a river in California died when the coefficient fell below 0.55 – 0.60. From this it appears that the condition of the brown trout in these Finnish lakes has usually been good. The low value for one-summer-old brown trout in Kivi-Ahveroinen may be due to scarcity of food suitable for the fry.

According to BROWN (1957), in brown trout high values of the coefficient (K) were always connected with a high growth rate. At 11.5 °C K tends to reach the value of 1.08. If $K < 1.08$, the relative weight gain is greater than the gain in length, whilst $K > 1.08$ indicates the opposite situation.

On the average, coefficients of condition were found to be a little higher in rainbow trout than in brown trout. The lowest value (0.62) was observed in a three-summer-old rainbow trout from Pien-Valkealampi. According to REIMERS (1963), the condition of steelhead trout was normal at the K values of 0.80 – 0.90; 0.60 – 0.70 is at the limit of survival, and the test animals died if the coefficient dropped to 0.55 – 0.62.

The coefficient of condition was generally higher in spring than in autumn. In mature rainbow trout this is almost entirely due to the large size of the gonads in spring. In Ulpasjärvi the coefficient of condition of both trout species decreased successively up to the beginning of the fourth growth period, probably owing to scarcity of food. During the fourth growth period the population had become considerably less dense and so the conditions of the surviving fish were improved. This is reflected in the higher values of K. In all the lakes studied the same trend could be observed during the fourth and fifth growth periods in both trout species.

6. Food of the fish released

As the trout grow, the proportion of plankton in their diet decreases. Rainbow trout feed on plankton longer than brown trout, but they then select the largest plankton crustaceans for food (e.g. NEAVE & BAJKOV 1929, LINDSTRÖM 1955, JOHANNES & LARKIN 1961, NILSSON & SVÄRDSON 1962, TUUNAINEN 1966b, GALBRAITH 1967). The transition from plankton to bottom fauna is gradual. Aerial food is taken at any size during the whole open water period (TUUNAINEN 1966b).

It is important that suitable food for each size class should be available. Changing from benthic fauna to a fish diet depends on the quantity and quality of the food available. Nilsson (1955) reported that brown trout began to feed on fish at a size of 35 – 40 cm (400 g). Brown trout living in mountain brooks already fed on fish at a size of 75 g (Crisp 1963). In the lakes of British Columbia studied by Johannes & Larkin (1961), 60 % of the food of the rainbow trout < 25 cm consisted of *Daphnia*, but rainbow trout 25 – 35 cm long had also eaten fish to some degree, and in rainbow trout > 35 cm long 70 % of the food consisted of fish. In the lakes of the present study there was no fish continuously suitable as food for trout. This may be the most important reason for the rapid decrease in growth rate after the fish had grown to 25 – 30 cm. In Julkujärvi growth did not decrease so soon, because bottom animals were available in abundance.

In some lakes treated with rotenone and then stocked with brown trout or rainbow trout these began to feed on *Pungitius pungitius* at a size of about 200 g (Fürst 1964). In the lakes where stickleback were released as food for trout, the growth rate of the brown trout increased considerably (Nordin 1964). Fürst (1964) regarded stickleback as the best food for brown trout and rainbow trout, because this fish remained abundant enough in spite of predation. A permanent stock had been introduced into waters where there was a permanent stock of trout. This measure has not yet been considered in Finland.

Interspecific competition for food is to be expected, because the similarity of the diet of brown trout and rainbow trout may be as high as 73 – 100 % throughout the year, except in July–September. Competition will not be weakened by the fact that the same food organisms or groups of organisms are at least partly utilized at different times of the day or year, because the total production of food organisms persists unchanged (Tuunainen 1966b). From July to September the similarity of the diet of brown trout and rainbow trout was 54 – 63 %; thus the competition for food may be weaker during this period.

Differences in diets between the two trout species may, at least partly, be caused by their different habits. The rainbow trout live mainly in the upper water layers, are more mobile and show less territoriality than the brown trout. If rainbow trout, brown trout and brook trout live together in the same lake, the brown trout is a very local and territorial species (Lindhe 1961, Tägström 1965). The relationship between brown trout and rainbow trout very much resembles that between brown trout and arctic char studied by Nilsson (1955, 1963).

A clear selective feeding was observed. In general, the value of the forage ratio varies considerably even for the same group of organisms. Frost (1945) reported that brown trout living in rivers selected larvae of Chironomids, Ephemerids, Trichoptera and Plecoptera, but avoided larvae of Coleoptera, which occurred abundantly. Animals living on submerged vegetation as well as freely in water were preferred to benthic organisms. In the waters studied by Frost & Smyly (1952), however, *Pisidium* and larvae of *Sialis*, which live on bottom mud, were utilized considerably more than in the lakes studied here, where Dytiscid larvae were likewise utilized to a lesser extent than reported by Macan (1965). In some cases there were great individual differences in the food of fish caught at the same time.

7. Mortality

Most investigations on the factors regulating the size of fish populations concern economically important species, such as salmon and trout (cf. e.g. Johnson 1965, Le Cren 1965, Lindroth 1965). The factors causing mortality in salmonids change with the age of the fish. However, at all ages the mortality of the fish is to a certain extent dependent on the population density (Le Cren 1958, 1965, Watt 1959).

Several methods have been developed for calculating the mortality rate (e.g. Ricker 1958, Regier 1962, Robson & Regier 1968). Information about the various causes of mortality, apart from the population density, is very inadequate (cf. Paling 1968). Only occasionally have epidemics and other pathological causes been shown to be important factors (e.g. Bardach 1951). As regards introductions into lakes treated with rotenone the main causes for the rapid disappearance of rainbow trout and brown trout from such lakes may be extreme physical, chemical and biotic conditions as well as mortality connected with the attainment of sexual maturity (cf. e.g. Rayner 1953, O'Riordan & Kennedy 1964, Tuunainen 1966b).

In Sahalampi the rainbow trout disappeared exceptionally rapidly, about one and a half years after release, probably owing to the extreme physical and chemical factors, whilst brown trout were still caught at the end of the fourth growth period. In the other lakes the rainbow trout survived for 3 – 5 growth periods and the brown trout for 4 – 5. LUNDGREN (1962) reported that rainbow trout disappeared from lakes treated with rotenone in Jämtland, Sweden, after four years on an average.

In Sahalampi the mortality percentages are considerably higher than those reported by ALM (1939) for some populations of brown trout, and by JOHNSON & HASLER (1954) for rainbow trout. ALM (1939) reported that natural mortality of brown trout in a brook where there were no other fish species was 30 % in the first, 20 % in the second, 10 % in the third and 5 % in the fourth year. In the natural waters the natural mortality of rainbow trout introduced at a size of 15 – 18 cm was 32 – 60 % in the first year and 15 – 19 % in the second (JOHNSON & HASLER 1954). On the contrary, JOHNSON (1955) reported that 88.3 % of the rainbow trout released into a lake in Minnesota, U.S.A., were dead in one year, 98.3 % in two years, and 99.8 % in three years. HALME & ORPANA (1963) reported that in ponds with no other fish the natural mortality of young salmonids fed entirely on natural food was 70 – 90 % in the first summer. In the best cases 50 % of the young survived the first year. These data fit quite well with those obtained from Sahalampi.

Summary

Nine small lakes in southern and central Finland were treated with rotenone, and brown trout and rainbow trout were introduced, mainly as fry, into these lakes where the original fish populations had been killed. The influence of some physical, chemical and biotic factors upon the growth and survival of the introduced fish were then studied. Attention was also paid to the food and selective feeding of the fish, as well as to the biological production of the benthic fauna and fish stocks.

The lakes studied are situated at 60° 17' – 64° 35' N and 23° 01' – 28° 38' E and 0 – 152 m above sea level. The areas of the lakes are 0.8 – 4.3 hectares and the maximum depths 3.0 – 19.5 m. The bottoms are mainly organic mud. The shores of most of the lakes are paludified. Eight of them have no outlet.

In winter the oxygen content of the water was low in four of the lakes, and as a result some fish died in two of them. The acidity of the water probably contributed to the rapid disappearance of rainbow trout from one of the lakes.

The catches of brown trout and/or rainbow trout were 1.3 – 10.6 kg per hectare per year. The productivity, based on the productivity of the bottom fauna, was calculated to be 29.7 kg per hectare per year in one of the oligotrophic lakes. In the same lake the maximum growth rate of the benthic fauna (0.18 g/m²/day) was observed if the initial value of the biomass in spring was 3.05 g/m². If the initial value was 13.79 g/m² the growth rate of the biomass was found to be zero. Factors affecting the growth rate of the benthic fauna and the validity of the estimates are discussed in detail.

The scarcity of food and small size of the food organisms were the most important factors limiting the growth of the fish. The growth rate was independent of introduction density in the first growth period in the density range 187 – 2500 fry per hectare. In the second growth period a tendency to a lower growth rate in dense stocks was observed. In rainbow trout this tendency was even more pronounced in the third growth period than in brown trout.

In all the lakes where both brown trout and rainbow trout were introduced the size of the rainbow trout was greater than that of the brown trout at the end of the first and second growth periods. Later, the brown trout grew larger than the rainbow trout in some of the lakes.

Similarity of food between brown trout and rainbow trout was 54 – 63 % in July – September and 73 – 100 % at other times. Brown trout and rainbow trout preferred animals living on submerged plants as well as larger free-living aquatic invertebrates.

The influence of the fish stock on the abundance of the benthic fauna was found to be important. The quantitative relationship between the biomass values of the fish stock and the benthic fauna was determined in one of the lakes.

Studies on the mortality rate of the trout were carried out in one of the lakes.

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