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DROTTNINGHOLM

Report No 44

LUND 1962
CARL BLOMS BOKTRYCKERI A.-B.

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Gunnar Alm

29.9 1889—9.2 1962

Founder of the Institute of Freshwater Research, Drottningholm and its inspiring and respected director 1932—1948

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The effect of increased water level fluctuation upon the bottom fauna in Lake Blåsjön, northern Sweden

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Contents

I. Introduction

Investigations into the composition and distribution of the bottom fauna of Lake Blåsjön prior to its regulation have been carried out by A. MÄÄR. His material is, however, only in part available in published form (BRUNDIN 1949, BRINCK 1949, NILSSON 1955).

MÄÄR's investigations were concentrated to areas near the inlets, and part of his material is derived from the time after the regulation. On account of the unstable environmental conditions prevailing in the regions near the inlets and also of the fact that even minor deviations from the natural water-level can influence the bottom fauna, his material can not without reservation be considered significant for the normal conditions in the lakes within the region. This remark refers especially to the distribution of the fauna in the littoral. For this reason complementary investigations have been carried out in the unregulated Lake Ankarvattnet (Fig. 1), situated within the same drainage system, 3 km. above Lake Blåsjön (GRIMÅS 1961).

On the basis of the combined experience from Lake Blåsjön before the regulation and from Lake Ankarvattnet the effect of the regulation upon the bottom fauna in Blåsjön has been estimated (GRIMÅS op. cit.).

The present paper deals mainly with the effects produced upon the fauna by a relatively brief period, (since 1958), with increased amplitude of water level fluctuation.

II. The Lake

1. General conditions

Lake Blåsjön is situated in the subarctic region of Jämtland, northern Sweden, at the altitude of 435 metres above sea level.

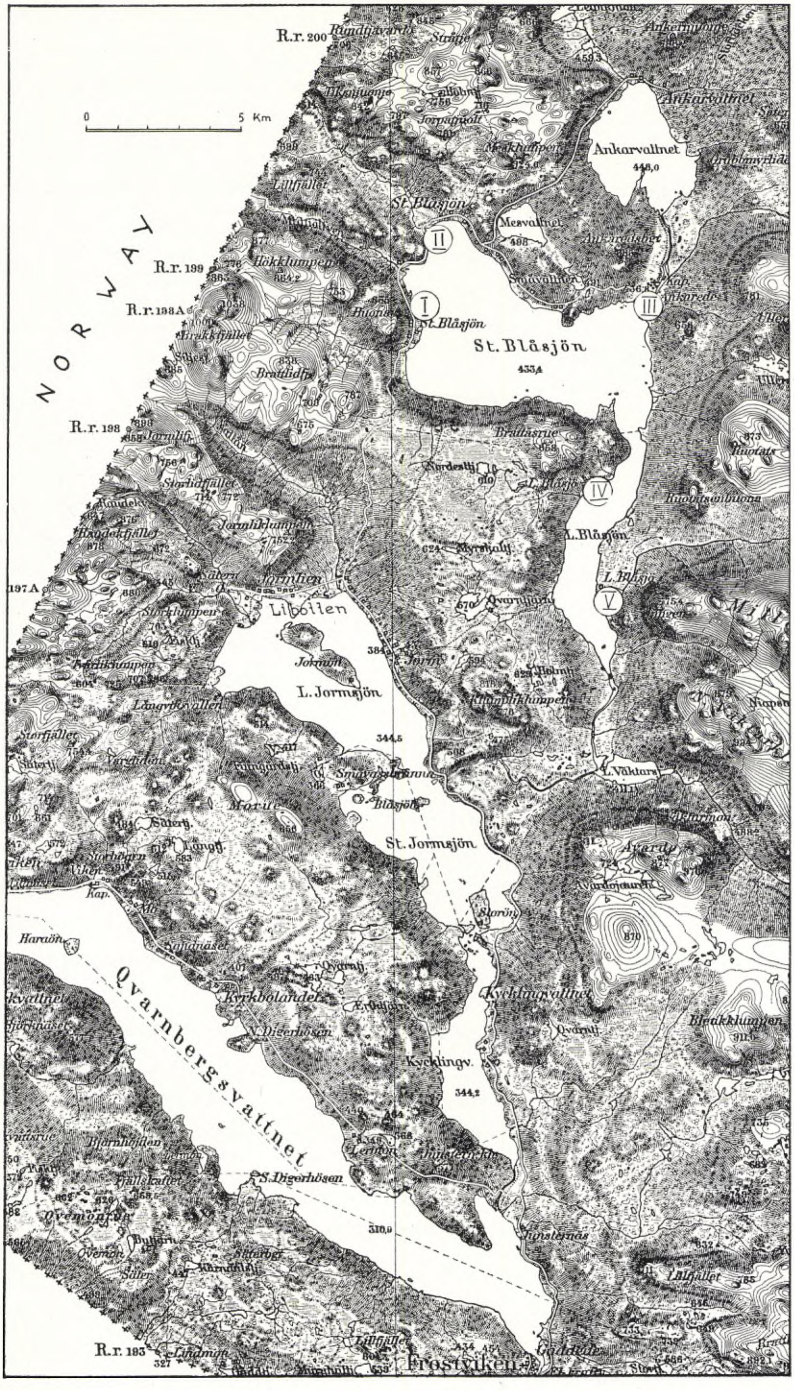

Fig. 1. Map of the lake region.

The basin of the lake as well as the drainage area is situated upon a bedrock which is dominated by schists, represented by phyllites in the west and mica schists in the east (ÄNGEBY 1947). The western basin of St. Blåsjön with a greatest depth of 145 m. is separated from the remainder of the lake by a threshold of, amongst others, granite and with a maximal depth of 35 m.

Since the year 1947 the lake has been influenced by an artificial water level fluctuation. During the first two years this water regulation was restricted to a damming-up. Between the years 1949 and 1957 the annual amplitude of the water level amounted to 6 vertical metres, being composed of a rise of 2 metres and a drop of 4 metres in relation to the normal water level in summer before the regulation.

Since the winter 1957—58 the amplitude is increased by an additional draw down of 7 metres, resulting in an annual amplitude of 13 metres.

During the period of the 6 metres' amplitude, about 11 per cent of the whole bottom area, 40 sq.km., was affected by drainage. The increased amplitude covers a bottom area of about 8.8 sq.km., i.e. 22 per cent of the total bottom area of the lake. During the year 1958 this draw down limit at 13 metres was reached, but during the winter 1959 the fluctuation amounted to 9 vertical metres only.

2. Temperature conditions

As a result of the extended regulation the entire littoral of the lake, 0—13 metres, is laid dry during the winter. This brings about a freezing of the sediments and fauna within the littoral, only the regions immediately above the draw down limit, that are drained during the spring, remaining unaffected.

Owing to the relatively fast, artificial lowering of the water surface the drop of temperature in the draining zone takes place within a short period of time (cf. GRIMÅS 1961).

Bottom areas below the draw down limit, i.e. parts of the profundal, come under the influence of abnormally low winter temperatures. These areas are, however, excepted from a fast warming-up during spring, since at this time the surface of the water has risen to the damming-up limit.

3. Transparency

The transparency of the water before and after the extended regulation is represented in Fig. 2. The course of the curves for 1956 and 1957 indicates that after the first period of regulation a certain stabilization has taken place in the lake. Erosion of loose sediments does occur, but is restricted mainly to fairly coarse minerogenic material that does not influence the transparency of the water to any considerable extent. Most of the fine sediments of the old

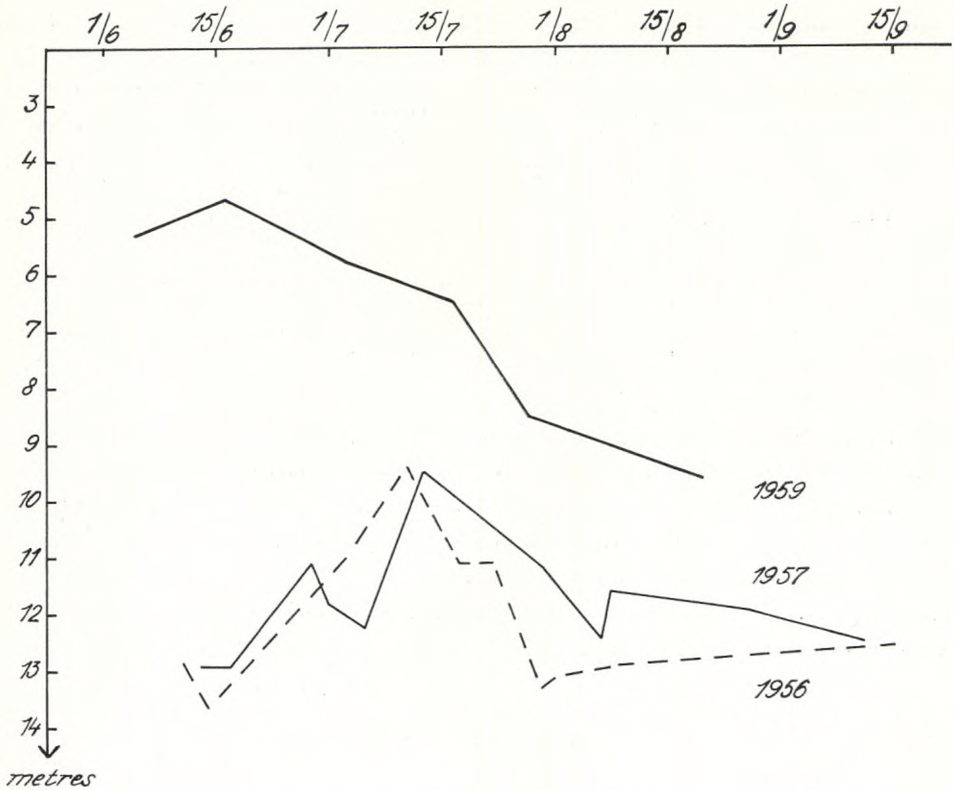

Fig. 2. Transparency in Lake Blåsjön before and after the extended regulation.

area of regulation has been transported to areas below its draw down limit, and the transparency conditions are determined mainly by the autochthonous production of planktonic organisms. There exists thus a great similarity with the conditions before the regulation. The highest values for transparency (16.6 and 17 m.) have been recorded by MÄÄR immediately after the breaking-up of the ice, while the minimum (about 9 m.) falls into July. Subsequently the transparency of the water increases again towards autumn (11—12 m.).

The extended regulation brings about a redisposition of the fine sediments within the new register of regulation, which can be assumed to cause the altered transparency of the water in the lake (Fig. 2.). Now the minimum value (4.5 m.) falls in during spring, the water becoming slowly clearer and reaching its greatest transparency (9 m.) in late summer. In autumn a new minimum can be expected during the final lowering of the water.

In Lake L. Blåsjön special conditions exist. In 1958 and 1959 extensive excavations were carried out in order to deepen the narrow sound between

Table 1. Data on the chemistry of the water in Blåsjön, Ankarvattnet, and feeders of these lakes on June 16, 1959.

	Blåsjön 0 and 50 metres, mean value	Ankarvattnet 0 and 50 metres, mean value	Eight feeders, mean value
PO_4 .... µg/l	0.9	0.3	0.3
Tot-P .... µg/l	4.4	3.8	4.1
% PO_4/P	20.5	7.9	7.3
NO_3 .... µg/l	36.9	28.3	12.9
Tot-N .... µg/l	101	92	68
% NO_3/N	36.5	30.8	19.0
Si .... mg/l	0.61_6	0.54_7	0.58_0

St. and L. Blåsjön. Nearly all feeders discharge their water into St. Blåsjön. On this account L. Blåsjön gives the impression of a widened outlet in which the current is always directed away from St. Blåsjön and the turbulence caused by the excavations in the sound is supposed to be without decisive importance for the transparency in the great western basin of St. Blåsjön. Lake L. Blåsjön on the other hand becomes strongly turbid with the ensuing deposition of new sediments upon the bottoms.

4. Chemical conditions

Lake Blåsjön can be characterized as oligotrophic and oligohumous with a high oxygen content in the hypolimnion throughout the year. The analytical values obtained for the different chemical components during the final phase of the first period of regulation do not differ from the values obtained for the lake before the regulation (MÄÄR, in manuscript, BRUNDIN 1949, LÖFFLER 1949, NILSSON 1955, GRIMÅS 1961). After the extended regulation no great changes can be established for the major components in the greater portion of the waters. Between the surface and the depth of 50 metres the content of elektrolytes varied on June 16, 1959 between 24.3 and 24.5 $\varkappa_{20} \cdot 10^6$ and Ca+Mg between 90 and 94 mmol/l. The minor constitutents, viz. nitrogen, phosphorus, and silica, exhibit, however, without exception values that are higher in Lake Blåsjön than in other waters in this region at the same time which might be an effect of the regulation (cf. RODHE et alii, 1957, RODHE 1962). Table 1 contains a comparison of the mean values for the depths of 0 and 50 metres in Blåsjön and Ankarvattnet and for 8 feeders of these lakes on June 16, 1959. Both lakes have recently been filled by the spring flood, and are near the termination of the spring circulation. Some of the feeders drain neighbouring lakes.

Attention should be paid to the high percentage of free phosphate-P in the surface water of Blåsjön, viz. 22.2 per cent compared with 13.9 per cent in

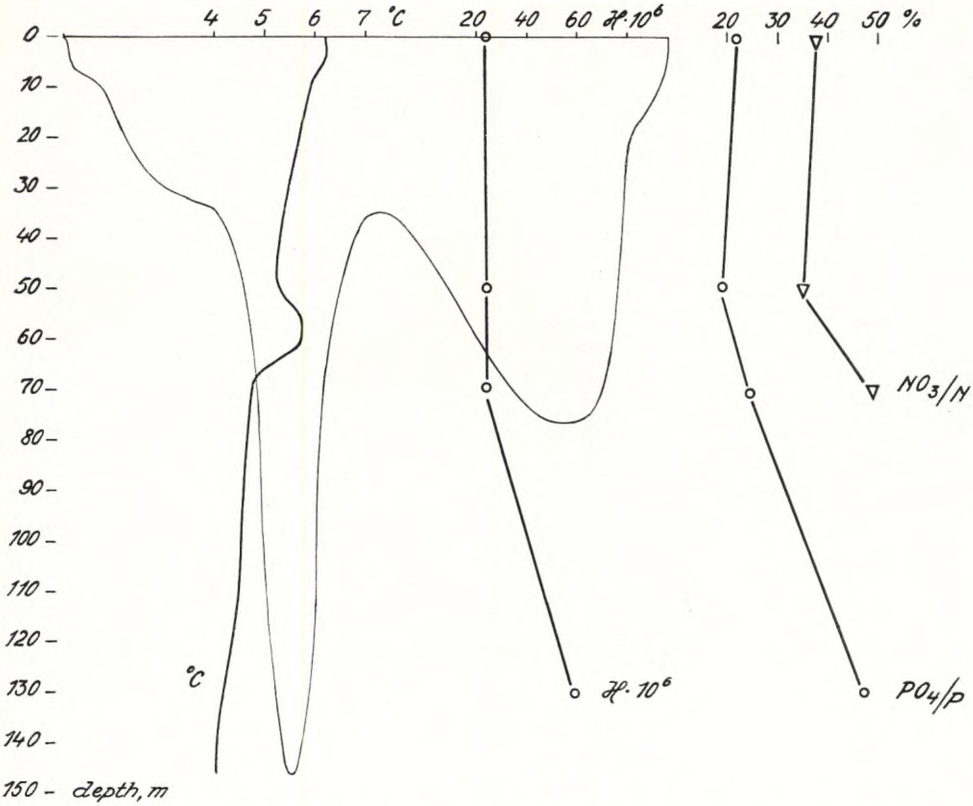

Fig. 3. Section through Lake Blåsjön from west to east and some chemical and physical conditions at the maximum depth on June 16, 1959.

Ankarvattnet. This difference can probably be ascribed to the turbidity in Blåsjön due to the regulation.

Special conditions seem to exist in the central deep area of Blåsjön. The transverse section through St. Blåsjön in Fig. 3 includes in the west a ridge rising from the bottom. The deep cavity, extending to a maximum of 145 m., is for the rest limited by flats at a depth of about 70—80 m. To judge from the topographical conditions this deep can easily be isolated from the movements in the rest of the waters. This is supported by observations made on June 16, 1959. Anomalies in the course of the temperature curve conditioned by an interfoliated layer of warmer water appear at the mouth of the deep cavity, roughly at the level of the surrounding bottom flat (Fig. 3). Below this layer major changes take place, amongst others in the percentage of PO_4 and NO_3 in the total phosphorus and total nitrogen. At the same time a heavy turbidity of the water can be observed at the depth of 130 m. This water has a conductivity of 60.6 $\varkappa_{20} \cdot 10^6$ and a total content of phosphorus of 773 µg/l

Fig. 4. Lake Blåsjön. The eroding effect of melting water in spring upon loose bottom sediments of the regulated area.

of which not less than 48 per cent are constituted by free phosphate-P. It is possible that this deep water is brought into circulation in the remaining parts of the hypolimnion at times of very strong winds that are common in the region. The threshold that separates the western basin from the other parts of the lake is covered by relatively shallow water. This circumstance can contribute to a retention of these turbidifying fine sediments in the western basin.

5. Bottom conditions

As a result of the increased amplitude of the water the new areas in the depth zone 6—13 m. are exposed to powerful erosion, especially when the water-level in the lake is low, i.e. during the lowering of the water in autumn and winter, and when the lake is filled in spring. During summer the water level remains relatively constant near the damming limit, which results in the clearing-up of the lake.

An important eroding factor is represented by the melting water which in spring along the shores forms a layer between the ice and the bottom. The erosive force of this water grows towards deeper areas concordantly with the concentration of the water into major runlets (Fig. 4). In this way also

Table 2. Distribution in per cent of the bottom samples upon different types of loose sediments in Blåsjön before and after the extended regulation.

Depth zone	Bottom area	year	sand	silty sand	sandy gyttja	gyttja
0— 6 m	4 1/2 km^2	1956—57	71	29	—	—
		1959	46	54	—	—
6— 13 m	4 1/2 km^2	1956—57	—	10	45	45
		1959	5	23	38	34
13— 30 m	10 km^2	1956—57	—	—	7	93
		1959	—	—	26	74
30—145 m	21 km^2	1956—57	—	—	—	100
		1959	—	—	—	100

relatively coarse minerogenic material in the sediments is affected and transported to regions beyond the draw down limit.

The distribution in per cent of the bottom samples upon the different types of loose sediments can in a general way illustrate the changes within the different depth zones after the extended regulation (Table 2).

The redisposition of the bottom sediments thus causes 1) an addition of fine sediments upon the old register of regulation, 2) an impoverishment of the fine sediments in the new area of regulation, and 3) an exportation of, amongst others, minerogenic material unto the gyttja bottoms below the draw down limit.

In 1956—57 the bottom sediments in a belt along the eastern parts of St. Blåsjön and in the whole of L. Blåsjön were characterized by a high content of coarse allochthonous detritus which had been deposited by the great feeders Ankarälven and Lejaren. In L. Blåsjön the greater part of these organogenic bottoms has been covered by minerogenic material which has been washed out by the excavations in the sound between St. and L. Blåsjön. These important transformations of the superficial layer of the bottoms thus hide in L. Blåsjön changes that could be attributed to the increased amplitude of the water.

In the winter 1957—58 the increased draw down of the water has produced within limited regions around Blåsjön bottom slides, causing portions of loose sedimentary layers to descend towards deeper areas. This ought to be responsible for a greater turbidity of the water in Blåsjön especially in the summer of 1958. Fig. 5 shows one of the more extensive sliding areas immediately in front of Sörälven.

The thin streak of *Nitella* within the depth zone 6—7 m. which after the first regulation step was the last remnant of macrovegetation in the bottoms has entirely disappeared.

Fig. 5. Lake Blåsjön. Bottom slides provoked by the additional draw down of the water level.

III. Material and methods

The sampling period during the year 1959 in Lake Blåsjön includes the months June—August. Only these months have been taken into account in the material from Blåsjön 1956—57 and from lake Ankarvattnet.

The quantitative material has been collected by a bottom sampler, type EKMAN-BIRGE, and emergence funnels according to BRUNDIN. The sifting of the bottom samples has been carried out with 0.6 mm mesh. The quantitative material comprises in all about 32,000 animals, obtained from 471 bottom samples, covering a total bottom area of 10.7 sq.m. and 363 emergence samples.

The qualitative material contains benthic organisms, including aquatic insects in stages of emergence, swarming, and deposition of eggs.

The zero point for the fixation of comparable depth zones has been the average level of the water during the summer, which in the regulated lake means a water level near to the damming-up limit.

The determination of transparency has been made by a SECCHI-disk. The water has been chemically analysed by T. AHL at the Limnological Institute of the University of Uppsala.

IV. The bottom fauna

All calculations concerning the total fauna comprise *Insecta, Crustacea, Hydracarina, Mollusca, Oligochaeta, Hirudinea, Turbellaria, Nematoda,* and *Hydrozoa.* Small species or developmental stages of species of which an appreciable percentage can be expected to be lost in sifting have been excluded, e.g. newly hatched individuals of chironomids and oligochaetes and small species among oligochaetes, nematodes, and cladoceres.

1. Quantity

In Lake Blåsjön both steps of the regulation have brought about a reduction of bottom animals. The average density of animals can be calculated in Ankarvattnet at 5,095, in Blåsjön (1956—57) at 2,696, and in the same lake (1959) at 1,526 individuals per sq.m., which indicates an approximate reduction of 50 and 40 per cent, respectively.

The diagrams in Fig. 6. express the distribution in per cent of the bottom samples upon areas with various density of animals. A synopsis of the results is given also in Table 3.

The sampling in Lake Ankarvattnet comprises bottom areas with up to 16,000 ind. per sq.m. The majority of the samples or 80 per cent of the total number represent bottom areas with an abundance between 2,000 and 8,000 ind. per sq.m.

The sampling method being the same in both lakes the results permit a comparison between the two waters. Thus the diagrams for Blåsjön express general reduction of bottoms with high density of individuals in the lake. 50 per cent of the bottom samples in 1956—57 refer to regions in the lake with an abundance below 2,000 ind. per sq.m. An abundance greater than 9,000 ind. per sq.m. is preserved only in regions having close connection with feeders (in the diagram represented by white parts of the piles).

The diagram for Lake Blåsjön in 1959 shows a further limitation in this respect. Of the bottom samples 75 per cent refer to areas with less than 2,000 ind. per sq.m. More than 4,000 ind. per sq.m. have been encountered mainly in connection with inlets.

The regulation affects above all the biotic community within the area of drainage, which explains the above development. The bathymetric distribu-

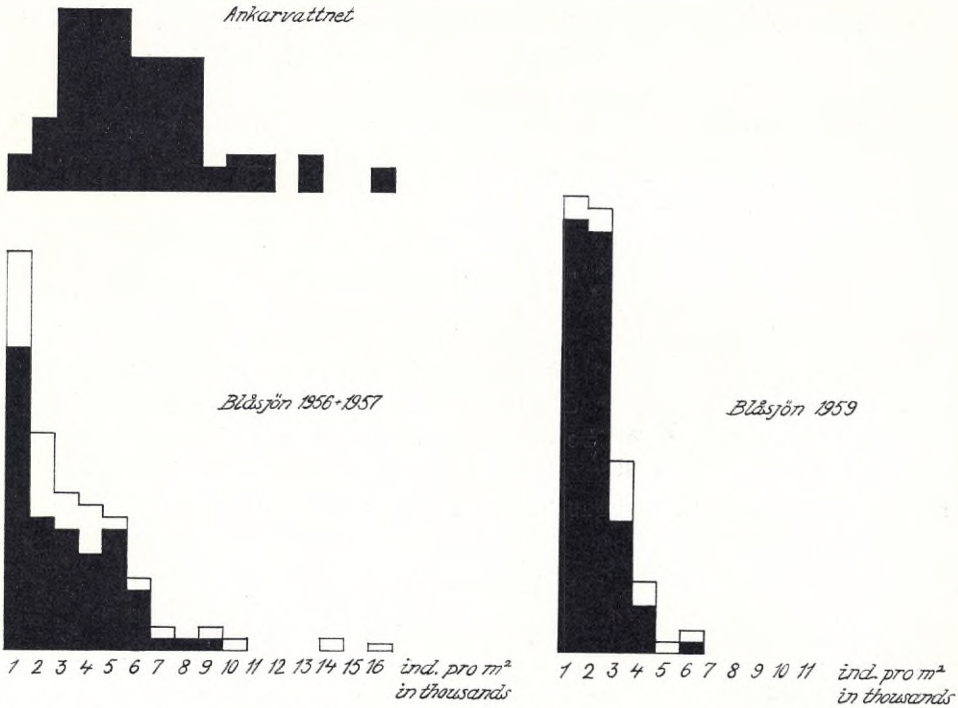

Fig. 6. Lakes Ankarvattnet and Blåsjön. The percentual distribution of bottom samples upon areas with various density of animals.

tion of the bottom fauna can be gathered from Table 4. The values of this Table form the basis of the distribution diagrams in Fig. 7.

The first regulation step in Lake Blåsjön brought about an inverted bathymetric distribution within the regulation zone 0—6 metres in comparison with the unregulated Ankarvattnet. The extended regulation causes further reductions, especially within the new register 6—13 metres, leading to increasingly pronounced deviations from natural conditions. The result is a heavy reduction in density and frequency of animals within the most important faunal region of the lake, viz. the littoral.

Owing to a direct modification of the environment and a disturbance of

Table 3. Distribution in per cent of the samples upon bottoms with different animal abundance in the lakes Blåsjön and Ankarvattnet.

Animal abundance in ind. per sq.m.	< 2,000	2,000–6,000	6,000–10,000	10,000–16,000
Ankarvattnet	8	58	27	7
Blåsjön 1956—57	50	43	6	1
Blåsjön 1959	75	25	—	—

Table 4. Bathymetrical distribution of bottom animals during June—August in the Lakes Blåsjön and Ankarvattnet: individuals/sq.m.

Depth zone	Blåsjön 1959	Blåsjön 1956–57	Ankarvattnet
0— 2 metres	198	1,308	7,597
2— 4 „	924	1,196	7,358
4— 6 „	2,135	3,112	5,578
6— 8 „	2,513	5,358	4,673
8— 10 „	2,518	4,369	4,714
10— 13 „	1,346	3,004	3,828
13— 20 „	1,073	1,555	2,871
20— 30 „	914	689	1,672
30— 70 „	983	733	1,309
70—140 „	704	869	—

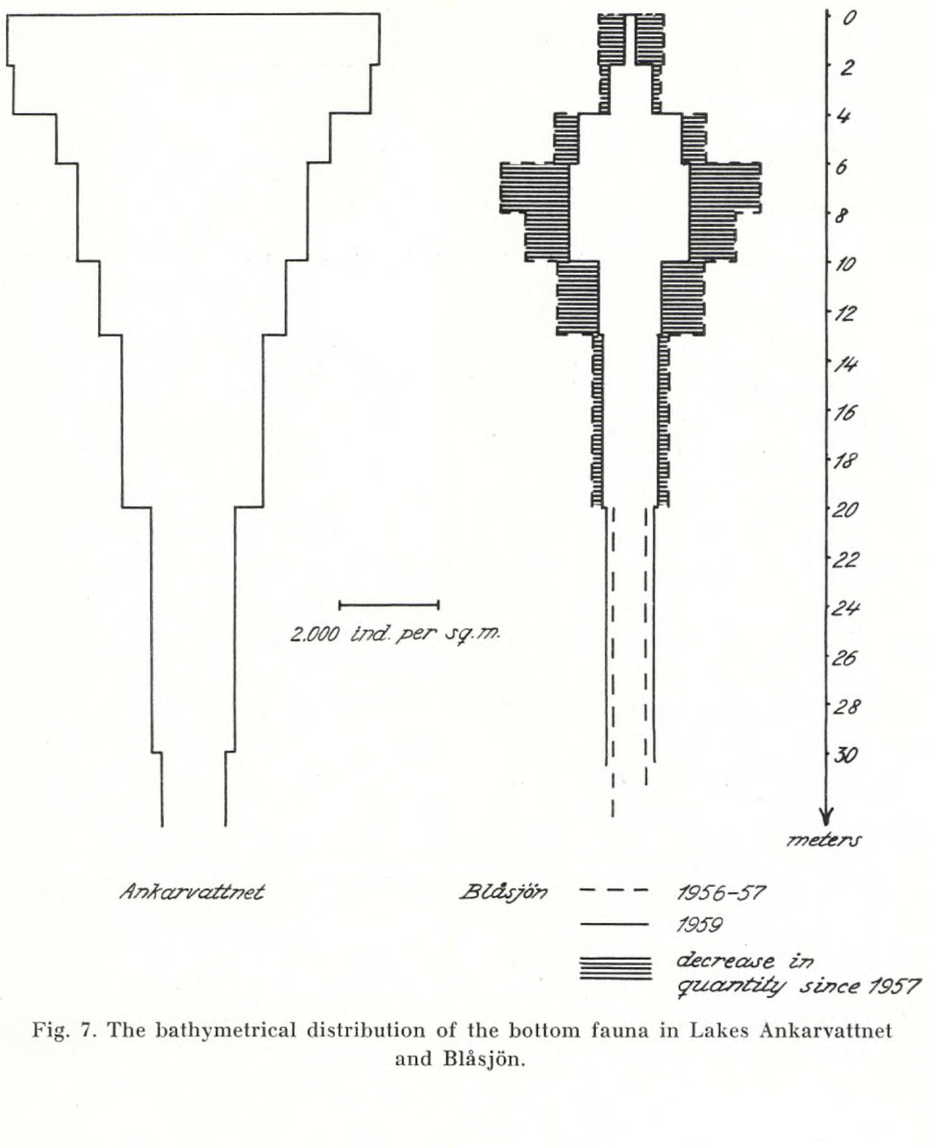

Fig. 7. The bathymetrical distribution of the bottom fauna in Lakes Ankarvattnet and Blåsjön.

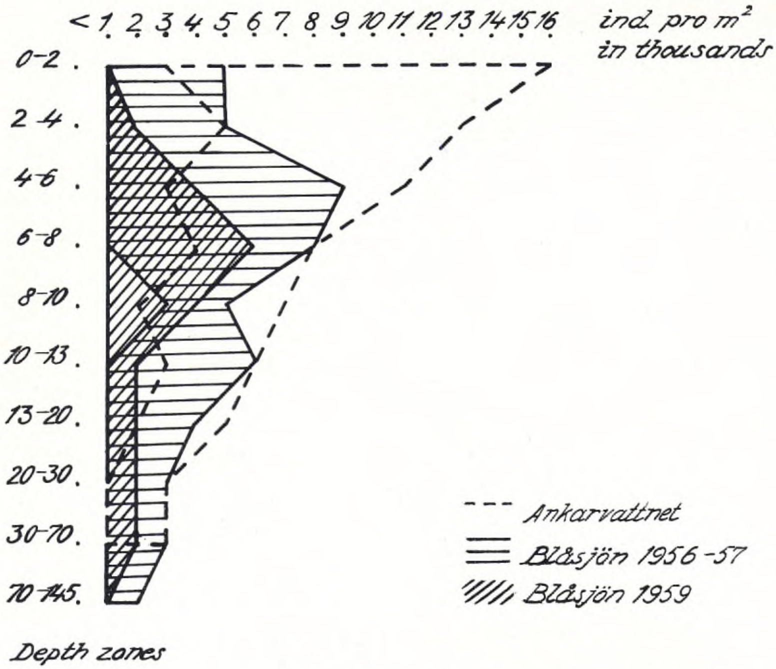

Fig. 8. The upper and lower limits of the variations in abundance with regard to depth zones and lakes.

the normal interaction between littoral and profundal within the ecosystem of the lake the effect of the regulation extends even to the animal community of the profundal region.

In response to the environment every depth zone has its own pattern of distribution. The diagrams in Fig. 8 give the upper and lower limits of the variation in abundance of animals with regard to depth zone and lake. The regions near inlets are not included in the diagrams.

In Ankarvattnet the range of variation in animal abundance is greatest in the upper littoral. Hand in hand with the decreasing average density of animals the range of this variation gradually decreases towards deeper regions.

In Lake Blåsjön there is a gradual shifting of the zone with the maximum range of variation in abundance towards deeper regions. There exists, however, no direct agreement with the average density of animals (cf. Fig. 7). In 1956—57 the maximum average abundance occurs immediately below the draw down limit in the depth zone 6—8 metres, while the maximum range of variation in abundance falls into the depth zone 4—6 metres. The conditions after the extended regulation are less clear partly on account of the different amplitudes of the water level in 1958 and 1959. The region with

Table 5. The average abundance of bottom animals during June—August in Lake Ankarvattnet and Lake Blåsjön 1956—57 and 1959. Individuals pro sq.m.

	Blåsjön 1959	Blåsjön 1956–57	Ankarvattnet
Chironomidae	557	1,387	1,778
Cladocera	357	396	1,321
Oligochaeta	295	384	724
Pisidae	120	188	301
Nematoda	87	108	180
Copepoda	64	89	222
Turbellaria	15	36	60
Hydracarina	14	49	33
Hydrozoa	14	20	100
Insecta excl. *Chir.*	2	17	106
Ostracoda	1	11	13
Gastropoda	1	13	47
Gammarus lacustris	0	7	208
Hirudinaea	0	1	2
Total	1,526	2,696	5,095

the maximum range of variation in abundance has, however, descended to the depth zone 6—8 metres.

The material from Lake Blåsjön contains within almost all depth zones areas with an abundance below 1,000 ind. per sq.m. (Fig. 8). A comparison between the mean value and the variation in animal density within every depth zone shows in fact that the main part of the material from Lake Blåsjön, especially within the regulated region, centres around areas with low abundance, in spite of the relatively wide limits of variation. The distribution of the material within these zones, indicates a tendency towards a clumped distribution of animals.

2. Quality

The extended regulation causes a quantitative reduction within all groups of animals. With the exception of the *Hydracarina* this is similar to the effect of the first step of regulation (Table 5).

Common to the lakes is the fact that chironomids, cladoceres, oligochaetes, and pisidians occupy a dominant position in the total fauna of the bottoms, and that their mutual position is retained also after the regulating interferences. The reduction of individuals is, however, not evenly distributed over the different groups of animals, which results in an altered balance between the different main groups of the total fauna.

Comparing the effect of the two regulation steps in this respect we find that some groups of animals react upon the two interferences in the same way, i.e. either decrease or increase their respective quota in the total mate-

Table 6. The relative abundance of some bottom animals in Lakes Blåsjön and Ankarvattnet, calculated as percentage of the total number of animals.

	Blåsjön 1959	Blåsjön 1956–57	Ankarvattnet
Gammarus lacustris	—	0.2	4.1
Big insect larvae	0.1	0.6	2.1
Gastropoda	< 0.1	0.5	0.9
Total	< 0.2	1.3	7.1
Oligochaeta	19.3	14.3	14.2
Pisidae	7.9	7.0	5.9
Nematoda	5.7	4.0	3.5
Total	32.9	25.3	23.6
Chironomidae	36.5	51.1	34.9
Cladocera	23.4	14.7	25.9
Copepoda	4.2	3.3	4.4
Total	64.1	69.1	65.2

rial. Other groups of animals show incongruent reactions to the two interferences.

A comparison between the situation in Lake Blåsjön immediately after the extended regulation (1959) and the conditions in Lake Ankarvattnet points to the following alterations in Blåsjön (Table 6).

Consistently with the above referred effect upon the animal community in the littoral region typical littoral forms like *Gammarus lacustris*, bigger insect larvae, and gastropods decrease in relative abundance in the lake.

Animal groups with wide bathymetrical limits, viz. species of oligochaetes, pisidians, and nematodes, show the opposite tendency.

The results from the years 1956—57 indicate that these courses of development will continue even as a long term effect of the regulation.

The relative abundances of chironomids and cladoceres in Lake Blåsjön 1959 do not diverge essentially from those in Ankarvattnet. This state of equilibrium seems, however, not to be stable, and can be interpreted merely as a short term effect, provoked by the extended regulation. The chironomids and the cladoceres present a heterogeneous response to the two different regulation steps in the lake, and a divergent mutual reaction (Table 6). To judge from the conditions in Blåsjön 1956—57, a longer period with the uniform artificial water level fluctuation will result in an increased relative abundance of chironomids and a decrease of small crustaceans.

In lakes with water level fluctuations similar to that in Blåsjön the reduction of littoral animals has been established by several authors (cf. DAHL 1926, 1931, HUITFELDT-KAAS 1935, HAEMPEL and STUNDL 1943, RUNNSTRÖM 1946, 1951, 1955, CUERRIER 1954, RAWSON 1958, NILSSON 1958, 1962, MILLER and PAETZ 1959, AASS 1957, 1961, GRIMÅS 1960, HYNES 1961, GRIMÅS and NILSSON 1962). An equivalent supression of littoral animals in alpine lakes with natural wide limits of water level fluctuations has been reported by ZSCHOKKE (1894) and SCHMASSMANN (1920).

The damage to the original littoral fauna caused by a damming-up (STUBE 1958, SHADIN 1961) or by a steady lowering of the water-limit in a lake (MESCHKOWA 1961) underline the general sensitivity of these animals to artificial changes of the environment.

The small fraction of the *Gammarus lacustris*-population which could be connected with the remaining water vegetation immediately below the draw down limit in Lake Blåsjön before the extended regulation is now eliminated. The results are confirmed by the analysis of the feeding habits of trout and char in the lake (NILSSON 1961).

Siphlonurus lacustris EAT., which of all ephemeropteran species seems best to endure the conditions of regulation (cf. GRIMÅS and NILSSON 1962), is found in small numbers in the bottom samples. *Ameletus inopinatus* EAT. is missing in the quantitative material, but is found sparsely as subimago in June, and is supposed to be bound to the block bottoms.

Among the trichoptera can be mentioned small larvae of *Apatania* sp. and *Agraylea cognatella* MC LACHL., especially in the vicinity of inflows.

The gastropods are represented by only one species, *Limnea peregrea* MÜLL. which is found in small numbers within the depth zone 10—13 metres.

The natural consequence of the transformation of the littoral zone is the altered equilibrium within the animal community of the lake to the benefit of animals of the profundal zone. Sometimes the losses are balanced by a corresponding gain within the regulated zone of probably littoral forms. HYNES (op. cit.) reports amongst others a great proliferation of oligochaetes in bottoms affected by the drainage. This might be interpreted as a short term effect due to the modification of the bottom deposits. The slightly increased abundance of oligochaetes in the topmost 6-metre zone of Lake Blåsjön after the extended regulation (Fig. 9) is supposed to be of short duration, and might be connected with the deposition of fine sediments upon the old register of regulation (cf. page 21).

The pervading increase in numbers of oligochaetes, mainly naids in bottoms below the draw down limit seems to be more stable (Fig. 9), and counterbalances part of the losses in the regulation zone. A similar increase in abundance below the draw down limit applies to the nematodes. Calculations comprising the otherwise excluded small species of oligochaetes and nematodes confirm these observed conditions.

The flourishing — temporary or sustained — of small, half pelagian as well as planctonic crustaceans has been established as an effect of the damming-up of a lake (DAHL, RUNNSTRÖM op. cit., AXELSSON 1961).

According to NILSSON (1955) there are reasons to believe in a similar increasing standing crop of littoral cladocerans in Lake Blåsjön after the damming up. The short duration of this effect is obvious (GRIMÅS 1961) and

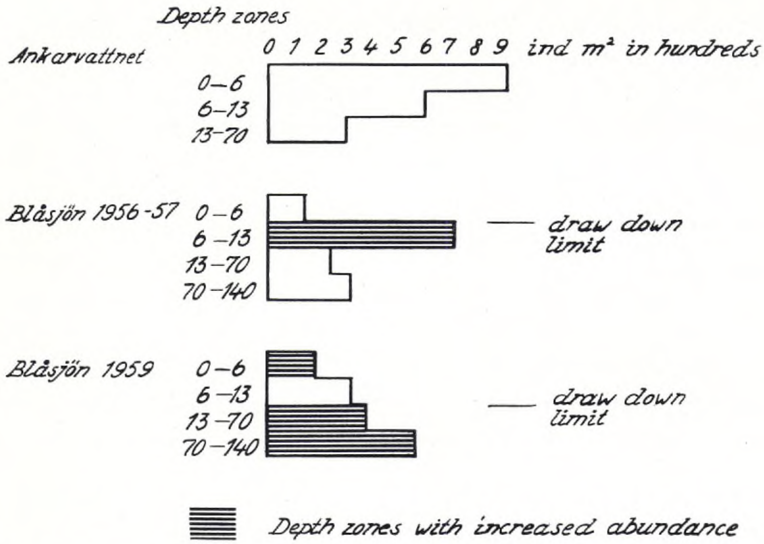

Fig. 9. The altered abundance of oligochaetes in various depth zones of Lake Blåsjön after the two regulation steps.

agrees with observations in other lakes (HUITFELDT-KAAS, RUNNSTRÖM, op. cit.).

The extended regulation seems, however, to retard the observed reduction of small crustaceans. In fact some species like *Holopedium gibberum* ZADD. and *Ophryoxus gracilis* SARS increase in abundance. *Eurycercus lamellatus* MÜLL. maintains its dominant position, comprising 38 per cent of the total number of cladoceres in the material. Smaller, eurybathic species with a tendency to maximum abundance in the upper littoral like *Alona quadrangularis* MÜLL. and *Iliocryptus acutifrons* SARS (GRIMÅS 1959) decrease in abundance. *Diaphanosoma brachyurum* LIEV., which is the predominant cladocere in the unregulated Lake Ankarvattnet with definite orientation towards the upper littoral, was almost eliminated by the first step of regulation and shows no tendency to increase in abundance.

The findings of RAWSON for Lake Minnewanka (1958) show, after a fairly long period of regulation, an increasing relative abundance, viz. from 52.5 to 93.5 per cent, of chironomids in the lake. This development fits also Lake Blåsjön after the first regulating step (Table 6).

The chironomid fauna in Lake Blåsjön in 1956—57 can be characterized by 1) a reduced number of species especially among the *Chironomini* to the benefit of *Orthocladiini* and *Tanytarsini,* 2) a tendency towards a stenobathic distribution of the species with some few or only a single "specialist" within every depth zone of the littoral, and 3) isolated, brief emergence periods, rich in individuals, especially within the regulated area and an elimination of spring emergence throughout the entire littoral.

Table 7. The percentage of the four main groups of chironomids in the littoral of Lake Blåsjön after and before the extended regulation. (Emerging results.)

Species %	1959	1956–57
Tanypodinae	6	12
Orthocaldiinae	55	52
Chironomini	6	4
Tanytarsini	33	32
Number of species	18	25
Individuals %		
Tanypodinae	1	1
Orthocladiinae	34	32
Chironomini	< 1	< 1
Tanytarsini	65	63
unidentified material	—	4
Number of individuals	631	1,037

The dominant species are: in the depth zone 2—4 m. *Parakiefferiella bathophila* KIEFF., 4—6 m. *Tanytarsus gregarius* EDW., 6—10 m. *Acricotopus thienemanni* GOETGH., and in zone 10—13 m. *Microspectra groenlandica*. The two last-named species dominate also in the upper profundal. In addition to the above we can establish an increased abundance of *Constempellina brevicosta* EDW. in the whole lake and of the parthenogenetic species *Abiscomyia virgo* EDW. in the regions near inlets.

The extended regulation brings about a further reduction in species without, however, altering the balance between the species of the four main groups in any appreciable degree (Table 7). More than half of the species still belong to the *Orthocladiinae*. With regard to the wealth in individuals the material is dominated by *Tanytarsini*, constituting more than 60 per cent of the chironomids of the littoral, which indicates an impoverishment of the environment (cf. NURSALL 1952).

The main course of emergence is still characterized by few, concentrated peaks and no spring emergence occurs in the littoral (Fig. 10).

The above described pattern caused by the different species dominating in their respective depth zones has been altered. In the major part of the littoral *Constempellina brevicosta* is now the species represented beyond comparison by the greatest number of individuals, and constitutes there 61 per cent of the hatching insects (Table 8). Only in the deepest parts, 10—13 metres it is superseded by *Acricotopus thienemanni*. A considerable increase of *Constempellina* in the fish food has been established by NILSSON (1958) in Lake Vojmsjön, Sweden, which might point to a similar increased abundance of the species.

The earlier tendency of many species towards stenobathic distribution is

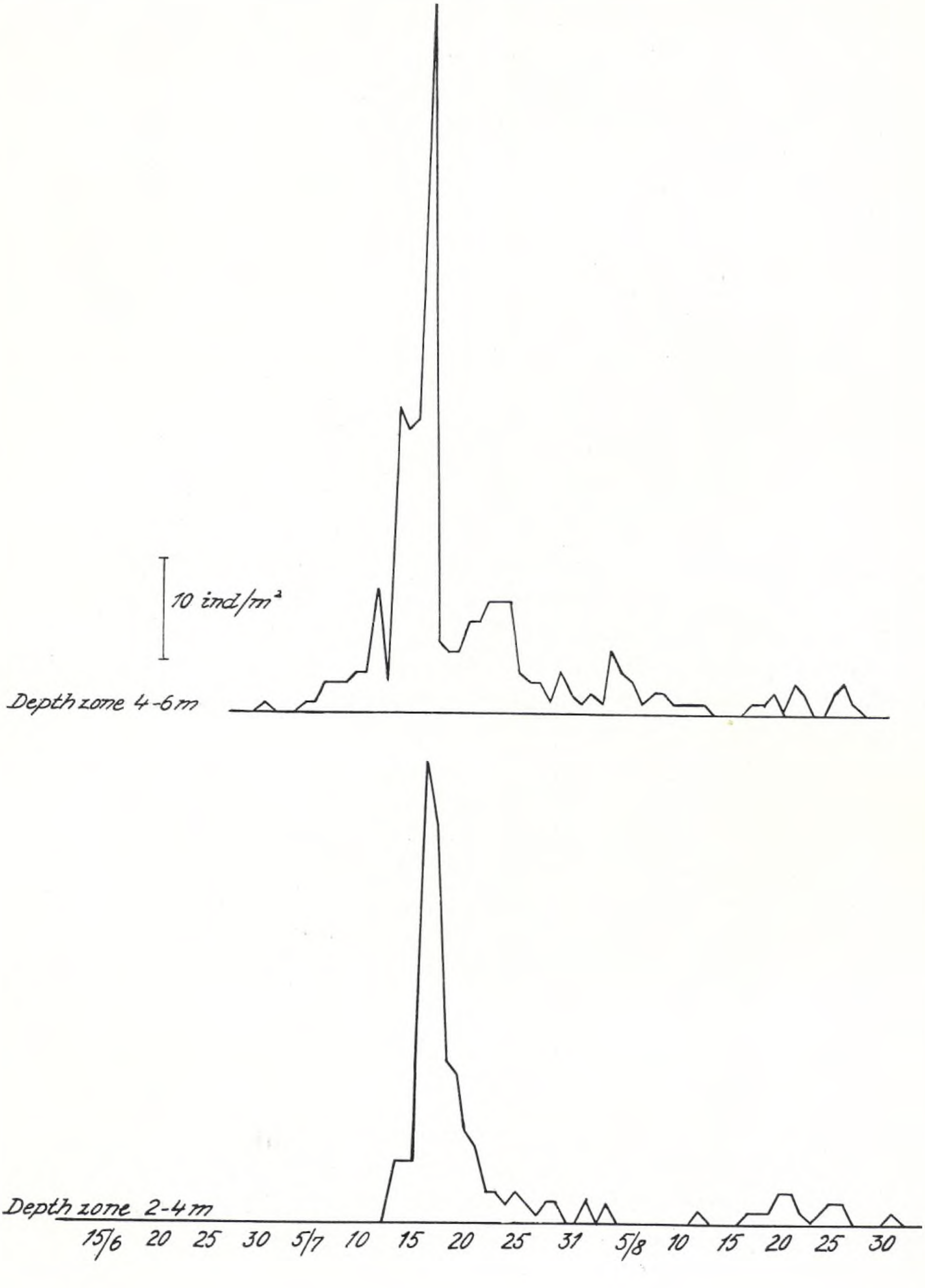

Fig. 10. Seasonal changes in emergence of chironomids in the upper littoral of Lake Blåsjön, 1959.

Table 8. The percentages of different species of emerging chironomids in the littoral of Lake Blåsjön 1959 and 1956—57.

1959	%
Constempellina brevicosta Edw.	61
Cricotopus lacuum Edw.	14
Acricotopus thienemanni Goetgh.	11
Parakiefferiella bathophila Kieff.	5
Paratanytarsus hyperboreus Brund.	2
Heterotrissocladius määri Brund.	1
Psectrocladius fennicus Storå	1
Heterotrissocladius subpilosus Edw.	1
Procladius barbatus Brund.	1
Corynoneura cleripes Winn.	1
Heterotrissocladius grimshawi Edw.	< 1
Paratanytarsus penicillatus Goetgh.	< 1
Tanytarsus gregarius Edw.	< 1
Tanytarsus heusdensis Goetgh.	< 1
Paracladopelma obscura Brund.	< 1
Protanypus caudatus Edw.	< 1
Stempellinella brevis Edw.	< 1
Orthocladiinae sp.	< 1
	100

1956–57	%
Tanytarsus gregarius Edw.	34
Parakiefferiella bathophila Kieff.	12
Paratanytarsus hyperboreus Brund.	11
Acricotopus thienemanni Goetgh.	8
Paratanytarsus penicillatus Goetgh.	7
Constempellina brevicosta Edw.	6
Psectrocladius fennicus Storå	5
Microspectra groenlandica Anders.	3
Heterotrissocladius grimshawi Edw.	2
Cricotopus alpicola Zett.	2
Cricotopus lacuum-group	1
Tanytarsus heusdensis Goetgh.	1
Procladius barbatus Brund.	1
Heterotrissocladius määri Brund.	< 1
Paracladopelma obscura Brund.	< 1
Diamesa sp.	< 1
Ablabesmyia spp.	< 1
Stempellinella minor Edw.	< 1
Abiskomyia virgo Edw.	< 1
Tanytarsus curticornis Kieff.	< 1
Protanypus caudatus Edw.	< 1
Monodiamesa bathyphila Pag.	< 1
Protanypus morio Zett.	< 1
Heterotanytarsus apicalis Kieff.	< 1
unidentified material	4
	100

modified. By the way of example can be mentioned that representatives of *Tanypodinae* and *Chironomini* now appear within the old register of regulation, which has not been the case previously. *Heterotrissocladius subpilosus,* the characteristic profundal species of the lake, which prior to the regulation richly occurred also in the lower littoral (Brundin 1949), and which by the first regulating step has been depressed to about 20 metres' depth, appears now again in the lower littoral of the lake.

V. Discussion

The effect of the water level fluctuation upon the animal community of the bottoms depends on a combination of a direct agency upon the individuals and an indirect action by the transformation of the benthic environment. The extraction of single agents out of the complexity of active factors responsible for the alterations is not possible with desirable certainty.

The most obvious direct effects of the regulation are the freezing-in and the drying-up of bottoms and animals within the regulated area. The low water level during winter means an abnormal cooling-down of the fauna even below the draw down limit, i.e. in the upper profundal (cf. page 16).

The altered standard of temperature in the bottoms of the lake can be taken to be of great importance for the specific composition of the fauna. Probably these drastic and annually recurrent conditions in the environment are responsible for the reduction of numerous littoral species, and contribute also to the continued development within the *Chironomidae* towards an extreme sub-arctic to arctic assemblage of species (cf. THIENEMANN 1942, BRUNDIN 1949, 1956, GRIMÅS 1961).

On the other hand drying-up and refrigeration ought not to have a decisive influence upon the quantitative distribution of the animals. The drying-up has a favourable effect in some isolated cases only. The considerably increased area of bottoms between high water and low water seems to lead to an increase in the numbers of tipulids in and near the lake, due to the semi-aquatic orientation of these animals.

Literature contains numerous references to species among bottom animals that resist freezing and drying-up (ROEDEL 1886, MAYENNE 1933, SCHÄPERCLAUS 1943, ANDERSEN 1946, RUNNSTRÖM 1946, 1955, SCHOLANDER et al. 1953, KANWISHER 1955, GRESE 1960, GRIMÅS 1961, LEADER 1961). The experiments as well as observations in the field point, i.a., towards great resistence of many chironomid species which might be capable to develop populations rich in individuals within the regulated area. It is therefore reasonable to suppose that the size of such populations within this region is determined by other factors. In this connection the strongly reduced supply of food ought to be of importance.

The regulation brings about a complete extinction of the macrovegetation in the lake (cf. QUENNERSTEDT 1958). Prior to the regulation this vegetation was characterized mainly by submerged carpets of *Isoetes lacustris* and the great alga *Nitella opaca*. QUENNERSTEDT's investigations (1959) in Lake Blåsjön establish great changes also in the benthic microvegetation which is strongly reduced. There exists in the lake no resemblance to the close permanent microvegetation of the littoral in Lake Ankarvattnet.

For this reason the reduction in numbers of littoral animals that depend directly upon the vegetation appears natural, e.g. herbivorous bigger insect larvae, *Gammarus* which seems to be bound to the dead, not yet decomposed plant substance (cf. WUNDSCH 1922, SEGERSTRÅLE 1954), and gastropods which to a large extent exploit the microvegetation (cf. ALSTERBERG 1930).

The loss of the aquatic vegetation implies a reduction of the supply of organogenic material to the bottom sediments. This affects first of all the littoral which is furthermore deprived of organic deposits by the eroding agencies. Consequently the long-term effect of the regulation will amount to a reduction within this zone also of the bottom animals feeding on detritus.

The transportation of the sediments towards deeper parts of the lake implies a contribution of organogenic as well as minerogenic material to the bottoms of the profundal. The reaction of the different species upon this increased supply is determined, amongst others, by the feeding habits of the species. In general it seems that species embedded in the sediment with unspecialized feeding habits, e.g. oligochaetes and nematodes, were favourably influenced by this contribution.

Upon filtering animals, like pisidians, a strongly increased descent of particles with a high percentage of minerogenic material can produce a negative effect. This is distinctly proved by the results in Lake L. Blåsjön, where the pisidians are practically eliminated. The gradual leaching-out of the register of regulation produces, however, more favourable conditions, especially if the long-term effect of the regulation implies an increased production of planktonic organisms.

The extension of the regulation produces a relatively favourable effect upon smaller crustaceans, as littoral cladoceres, adequate to the immediate effect of a damming-up. The connection ought to lie in the redisposition of the bottom deposits resulting in an intensified production of suitable algae (Rodhe 1962) and an increased availability of fine detritus which might serve as food for the cladoceres (cf. SCHERER 1961). The temporary nature of this positive effect has already been noticed.

The reaction of the chironomids is opposite to that of the littoral cladoceres. Many of the previously dominating chironomid species within the littoral, which ought to be able to utilize the available type of food, have in connection with the extended regulation suffered a considerable reduction and have in part been replaced by *Constempellina brevicosta*. The explanation might be found in the strong mechanical disturbances in the habitat of most species, i.e. in the superficial layers of the sediment, where the new interference was followed immediately by very unstable conditions. These disturbances ought to affect the larvae of *Constempellina* to a lesser extent since they move freely upon the sediments. It is remarkable that the abundance of *Abiskomyia virgo* with its similar biology of the larva increased in the regions of the inlets.

As already mentioned a gradual increasing relative abundance of chironomids is to be expected in the total fauna of the lake hand in hand with the leaching-out of the new register of regulation and a stabilization of the environment. It is premature to tell, whether or not this long-term effect of the regulation will result in a return to a wider specific spectrum.

Some observations regarding Lake Jormsjön

The importance of the composition of the bottom sediments and of the access to organogenic material can be illustrated by some results from the regulated Lake Jormsjön situated within the same lake region as Lake Blåsjön and with an annual water-level fluctuation of 5 metres (Fig. 1). The main part of shores and bottoms within the regulation zone can be described as influenced by the regulation in a normal way, exhibiting a structural change of the sediments towards sand-gravel-blocks combined with an extreme scarcity of food. Within these areas the fauna has undergone an impoverishment which in a high degree coincides with the development in Lake Blåsjön up to 1956—57. The average density of the fauna, composed of chironomids, oligochaetes, and minor crustaceans, in the upper littoral amounts to about 700 individuals per sq.m.

A wide and shallow bottom area, "Libotten", which is drained during the lowering of the water in winter exhibits, however, an essential difference in the composition of the sediments. Against the remaining part of the lake this area is in part bordered by an submerged ridge. This has damped the effect of the eroding forces, and contributed to the preservation of the organogenic material in the bottoms. The qualitative as well as the quantitative results stress the character of the area as a refuge for faunal elements which in response to a regulation easily incline towards reduction or extinction.

The average density of animals within this area is 6,000 individuals per sq.m., i.e. ten times that of corresponding deep regions under the normal influence of regulation. Gastropods and larvae of ephemerids and trichopters constitute noticeable faunal elements, and isolated specimens of *Gammarus lacustris* have been encountered. Also the high concentration of oligochaetes immediately below the draw down limit outside this area is worthy of notice.

A similar expression for the reaction of the fauna is found in those parts of Lake Blåsjön that are situated near the inlets, where the average density of individuals is higher than in other regions. This depends to some extent upon outdrifted rheophile forms, but can be connected mainly with the floating-in of allochthonous organic matter, suitable as food for bottom animals.

The regulation has caused an altered interaction between the species.

In connection with the rise of the water level in spring and early summer it might be expected that several species, coming from regions below the draw down limit, would invade the bottoms of the regulation zone. This invasion seems, however, to be limited, It can be observed that a hibernating or early immigrating chironomid species prevents an occupation of the regulated area by other chironomids until it leaves the bottoms during the emergence (GRIMÅS 1961). This might be a function of the gradual growth of the population in the course of the summer and the limited food supply. This form of blocking in connection with the extreme properties of the environment ought to contribute to the stenobathic appearance of chironomid species in Lake Blåsjön in 1956—57.

The tendency towards stenobathy is found to be modified by the extended regulation. In addition to the previously given examples (cf. page 31) we can mention that in 1959 11 species of chironomids emerged in the depth zone 2—4 metres against altogether 4 species in 1956 and 1957. In spite of the predominant position of *Constempellina brevicosta* which forms about 85 per cent of the chironomids emerging in this zone, and the larvae of which hibernate within the area, the extended regulation seems to bring about a modification of the chironomid fauna of the old register of regulation. Here a connection can exist with the introduction into the area of fine sediments by the redisposition of new bottom deposits. (Cf. the effect upon the oligochaete fauna, page 29.)

In contrast to the conditions in the unregulated Lake Ankarvattnet the quantity of emerging chironomids in Lake Blåsjön is no measure of the quantitative distribution of larvae and pupae in the bottoms. During 1956—57 the standing crop was considerably larger below the draw down limit, while the emergence was most numerous in the regulation zone. This disproportion between chironomids available in the bottoms and the quantity of emerging chironomids in the depth zones persisted during the year 1959. The most abundant emergence in relation to the standing crop exists in the old register of regulation. This may in part be due to a change in the balance between producers and consumers within the area. Active predators ought to be favoured by a rich fauna of chironomids the individuals of which are represented by many succeeding species. Conditions of this kind do not exist in the regulation zone which during part of the year is exposed, and which furthermore contains a chironomid fauna consisting of relatively few individuals and dominated by some few species. The examinations of the bottoms indicate also that there exist few predators among the invertebrates.

The importance of the fish predators upon the production of bottom animals is attested (cf. BALL and HAYNE 1952, LELLAK 1957, HRUSKA 1961). HAYNE and BALL (1956) established that "in the absence of fish the apparent production rate of fish food organisms decreased and finally stopped at a higher level of standing crop". The conditions in Lake Blåsjön suggest that the fish predation has decreased in the regulated zone. The investigations by NILSSON (1955, 1961) show that the chironomids are available as fish food for the population of trout and char mainly in the form of pupae and imagos. This predation probably takes place in connection with the emergence and the deposition of eggs of the chironomids. The investigations show that on account of the new pattern of emergence the chironomids can not be exploited by fish to an extent corresponding to the number of emerging individuals. The relatively higher intensity of emergence, especially within the regulation area, thereby increases the losses of bound energy in the food chain of the lake.

In the discussion of the fish-prey relationship the availability of food organisms is of the greatest importance (cf. DEMOLL 1930, ALLEN 1941, 1942, NILSSON 1955). The results of this investigation indicate that the new conditions within the benthic environment favour organisms which normally are not available as food to char and trout. There is a positive short-term effect only upon small littoral crustaceans. The long-term effect implies an increasing relative abundance of oligochaetes, nematodes, and pisidians. The increasing relative abundance of chironomids is counteracted by a reduced availability as fish food, conditioned by the regulation.

VI. Summary

1. The material from Lake Blåsjön before and after the extended regulation and from Lake Ankarvattnet includes about 30,000 animals from quantitative bottom samples and about 2,000 insects from the emergence experiments.

2. The water-level fluctuations have caused a reduction of the bottom fauna which can be estimated at 50 per cent for the 10-year period of 6 metres annual amplitude and 40 per cent for the following 2-year period of 13 metres annual amplitude of the water-level.

3. The regulation affects above all the fauna within the regulation zone, viz. the littoral, which means a general reduction of bottom areas in the lake with higher density of animals (Figs. 6 and 7).

4. The regulation results in an altered balance between the different main groups of the bottom fauna (Table 6). There is a decrease in the relative abundance of typical littoral forms as *Gammarus lacustris*, bigger insect larvae and gastropods and an increase of oligochaetes, nematodes, and pisidians. This course of development is suggested to be applicable as a short term as well as a long term effect of the regulation. The chironomids and the cladoceres present an incongruent response to the two different regulation steps in the lake and a divergent mutual reaction. A long period with uniform artificial water level fluctuation is supposed to result in an increased relative abundance of chironomids and a decrease of small littoral crustaceans.

5. The changed balance between species, e.g. within the chironomids, indicates an arctification of the bottom environment and a sharpening of the oligotrophic character of the lake (Table 7).

6. There is an altered interaction between species caused by the regulation, including amongst others an altered fish-prey relationship. There is a positive short term effect only upon small littoral crustaceans among the fish food organisms. The long term effect of the regulation favours 1) organisms which normally are not available as food to char and trout, 2) chironomids, which by the changed pattern of emergence seem to get less available as fish food organisms (Fig. 10).

7. The direct freezing-in and drying-up of the regulation zone is supposed to be responsible mainly for the qualitative changes in the bottom fauna.

8. The elimination of the bottom vegetation and the heavy losses of organic deposits in the bottoms of the littoral owing to the eroding forces seem to be the important limiting factors dimensioning the quantity of animals.

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The growth of the roach (*Leuciscus rutilus* L.) in some Swedish lakes

By Olof Kempe

Contents

Introduction

This investigation was undertaken, since there existed at the Institute for Freshwater Research of the Fishery Board of Sweden a desire to obtain a widened knowledge of the roach and its growth in different environments, partly natural ones and partly in those that, caused by human interference, were known or believed to have undergone major deviations from normal conditions. This was the reason, why in the course of years a fairly large material of scales has been collected from many lakes so as to supply a possibility of obtaining a deeper knowledge about the roach in our waters. The interferences and alterations in the Swedish lakes are carried out in connection with the construction of water-power plants, and the major part of the material of roach scales (more than 20,000 samples) kept at the Institute has for this reason been taken in lakes of northern Sweden, where the Institute has the task of examining and estimating the effect of a regulation or of the erection of a dam upon the fish population and the fauna in general of the lake or river. One of the lakes examined in this paper is a water power reservoir with a population of immigrated roach. As in many other countries rotenone preparations have been used also in Sweden in the interest of fishing, and in connection with the unsuccessful treatment of an eutrophic lake with a population of stunted fish the growth before and after the poisoning has been studied. Into a couple of lakes in central Sweden a mining company has released water containing large amounts of phosphates and nitrates derived from the washing of the ore. This has evidently had a fertilizing effect upon the water that previously had been poor in nutrition, and there the growth of the roach, for instance, has risen far above what is normal for lakes of this type. Finally the growth of the population of roach in two, so far intact lakes has been studied by way of comparison. One of them is a large eutrophic lake on the same level as the Baltic, the other a long and narrow oligotrophic lake of the type occurring in river valleys, where the roach lives at an altitude that is near its natural upper limit. This limit seems to lie at ca. 400—450 m in this country. For these two last-mentioned lakes a number of hydrological and meteorological data are available, permitting a correlation of the variations of growth with temperature, insolation, precipitation, and water-level.

The growth has been calculated with the methods for the interpretation of scales and backward calculation as they have been used at the Institute during the last decade. More about the methods in page 44.

The roach is of common occurrence in Sweden with the exception of the higher mountainous regions. It is found in lakes as well as in slowly running water, and occurs likewise in the Baltic as far south as Öre Sound. Contrary to what is the case in European countries farther eastward, in Sweden the roach is of no importance whatsoever as human food. Its importance is of an indirect nature, positive in that it forms an important food of economically more valuable fish, and negative by its competition for the available food with these species. In this competition the roach on account of its wide distribution seems to have good possibilities.

A species of such wide spreading and often dominating like the roach has of course been the subject of numerous investigations, especially in the countries, where it is of importance as human food, but also in this country it has been studied, although here mainly with regard to its growth and its choice of food in uninfluenced lakes. Many papers deal with the growth in a lake only to the extent that its size at certain ages is established and then compared with the corresponding figures from other lakes. The growth is then assessed as "good, normal or poor", no attempt being made to establish or discuss the reasons of the observed rates of growth. In other papers again the investigation has been supplemented by an analysis of the contents of the stomach of the roaches, and in this connection it has frequently been shown that populations feeding on molluscs grew in general at a faster rate than those that were reduced to algae and plankton for their subsistence. Also within one and the same population a change to mollusc diet has proved to effect another and faster growth in comparison with other individuals. This change seems to be possible, when the fish have reached a certain size. In the fry the differences in the choice of food seem to be very small, and analyses from different parts of Europe show that during the first year of life plankton, both phytoplankton and zooplankton, consisting of roughly identical species and genera furnishes the main food.

The growth of the roach in lakes formed by the damming-up of running water has been dealt with only rather summarily in literature, and, as far as the present author is aware, no examinations of the conditions before and after the damming-up have been made. The author is, however, forced to admit that his unacquaintance with the Russian language is responsible for his very restricted acquaintance with the results obtained in Eastern Europe and the Sovjet Union on the biology of fish.

As far as the present author knows, no analysis of the growth of the roach has been carried out in connection with the fertilizing of the water courses. Very frequently, however, the results of the rearing of fish in ponds and the measures taken in this connection for the improvement of growth, e.g. the use of fertilizing substances, are accounted for together with exact examinations of the chemistry of the water and the production of food organisms. Fertilizing of lakes on a major scale has, however, been carried out in several countries, and the conditions in the lake before and after the introduction of the nutritive substances have been studied with greater or lesser precision.

Also the change of the rate of growth subsequent to a reduction of the population of fish has been studied, and in some isolated cases mention has been made of the result of the death of fish due to suffocation during winter on account of lack of oxygen. This has, amongst others, caused a reduction of the population of roach, followed in the ensuing summer by a distinct increase in the rate of growth.

The important influence upon growth of climatic factors has been studied for different species in an immense number of papers, but, as far as the roach is concerned, there exist only some few, rather general references to the connection between warm summers and a faster than normal growth and the appearance of good year classes.

Materials and methods

The scale material comprises almost 4000 scales of roach the age of which is known. The fish have been caught with gill nets and fyke nets, both types of gear being selective, but in different ways. Gill nets catch the faster growing individuals in the younger year classes of the population and the more slowly growing among the older and oldest fish. Use of different size

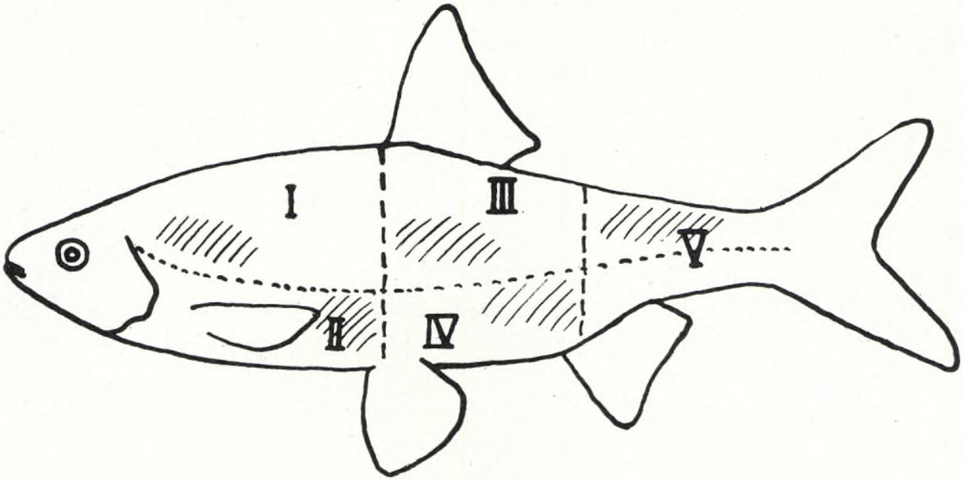

Fig. 1. Body regions of the roach, referred to on page 45.

of mesh shows to influence the sex ratio, sales dominating in the catch with small mesh and *vice versa.* For fishing at spawning time fyke nets have been used in Lake Mälaren only, where the material of roach exhibits an extremely marked dominance of males with a sprinkling of mostly very large females, the ratio of males to females being 15: 1. Once the fishing tackle starts to become full, the size of mesh does no longer seem to be of any greater importance, since it was observed that many of the smaller males might have escaped provided they had not lain flat against the net. No attempts have been made to correct the possible influence of different sex ratios in different parts of the material.

The scales have been taken on the left side below the lateral line between the ventral and the anal fin, yet as close to the lateral line as possible. An examination of the variation of the values for the radius upon the scale along which the distances between the annuli have been measured has shown that among the five regions examined (see Fig. 1) that with No. III exhibited the smallest variations for the radius in question (for the choice of the radius, see page 46), and that No. IV provided the highest values. The differences between the five regions were, however, not particularly great. The roach from which the material had been taken was a female of 10 years with a length of 232 mm (total length). From every region 12—15 scales were taken. This number is rather small for an investigation of this kind, but the result points nevertheless in the right direction, since several other authors have taken their scale samples from region No. III. That the same has not been done here is due to the fact that a great number of the scales had been taken long before the present author was given the opportunity of studying the samples and of continuing the investigation. Thus, for con-

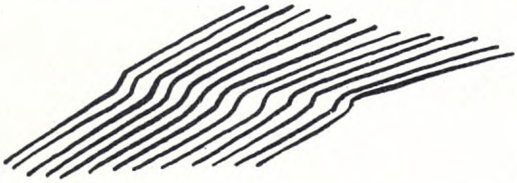

Fig. 2. Interruption of the pattern of the striae on the roach scale, used as a criteria for the validity of the annual rings.

tinuity's sake, it was deemed preferable to take the scales from region IV.

The ensuing impression, i.e. the production of an imprint of the scale in a plastic material, is done at our laboratory between rollers, distance of the rollers and pressure being adjustable.

Among the impressions of the scales on the sheet of plastic the one is chosen that in the collection is of medium size, has an undamaged centre, and a radius which is not overduly curved, and which does not run from the part covered by neighbouring scales to the exposed part of the scale. The choice was in general determined by a compromise between these demands, undamaged centre and straight radius being considered the most important points. Exclusively for reasons connected with the technique of reading the radius was chosen that runs obliquely backward and upward from the focus. This radius is here called the caudo-dorsal radius. This choice has been dictated by the circumstance that this radius has as a rule a rather straight course as long as it does not run from the unexposed to the exposed part. Here a natural radius is found upon the scale in most cases. A minor examination of the spreading of the values for different radii in different regions (see Fig. 1 and what has been said on page 45 about the spreading of the values for the caudo-dorsal radius within different regions) has shown that the directly caudally pointing radius in region III contained the best, i.e. the lowest, values, and that the use of this radius would be the most suitable for the reading of the scales. In the roach, especially in older individuals, it is, however, very difficult distinctly to determine the position of the annual rings, since some striae assume such a coarse aspect that in the caudal part of the scale they remind very much of the whole annual ring. In addition to the fact of being the most distinct even on older individuals the caudo-dorsal radius has also the advantage of rarely being placed so that marginal resorption, which is a fairly common phenomenon in the older roaches, truncates the part of the margin, where the radius runs out. Scales with resorbed margins have been excluded, whenever possible, or, if no scales with intact margin could be found, that with the smallest damage has been selected.

As annual rings have been considered:

a) striae that traverse striae nearer the centre, and do so in a perfectly distinct way around the whole scale,

Table 1. Lake *Glaningen,* see p. 47 for explanations.

Yearclass	Year of capture	1955	1957	1960
1950		6 years	8 years	11 years

b) an interruption of the pattern according to Fig. 2 which can be traced round or which replaces or completes a traversing stria.

As criteria for the validity of the annual rings have been used:

Scales from roach reared in ponds, kindly put at the author's disposal by the late Prof. GUNNAR ALM, showed that the age as determined by the reading of the scales agrees up to the age of 10—12 years with the entries kept on file.

Scales of known age from a natural environment, in this case from Lake Halmsjön that had twice been treated with rotenone, where the number of annual rings agrees with the number that could be expected to have been formed between the two poisonings.

Rich year class that is followed up during several years, here from Lake Glaningen and the reservoir of Storfinnsjön.

In Lake Glaningen only year class 1950 succeeded to survive, and first towards the end of fifties new year classes came into existence which survived several summers. In the reservoir of Storfinnsjön, e.g. the year class 1953 can be followed in the material during a number of years, when it is distinctly dominant every time.

Table 2. The *Storfinnsjön* reservoir, see p. 47 of explanations.

Yearclass	Year of capture					
	1955	1956	1957	1958	1959	1960
1934	1	—	—	—	—	—
1937	1	—	—	—	—	—
1939	3	—	—	—	—	—
1940	—	—	—	—	—	—
1941	—	—	2	—	—	—
1942	—	—	—	—	—	—
1943	4	—	4	—	—	—
1944	8	—	3	1	—	—
1945	8	—	11	—	—	1
1946	14	—	15	2	—	—
1947	21	2	15	2	—	—
1948	—	1	3	4	—	—
1949	2	1	5	1	—	—
1950	6	8	30	11	7	1
1951	7	14	14	27	6	9
1952	2	—	3	17	4	7
1953	18	11	87	127	149	175
1954	—	—	—	5	21	6
1955	—	—	—	—	—	—
Total	95	37	192	197	187	199

Table 3. Calculation of relative growth, see p. 48 for explanations.

Age group	Number of fish	Mean lengths at age 1	2	3	4	5	6	7 years etc.
III	34	41	79	113				
IV	95	45	76	111	138			
V	191	39	75	111	139	159		
Total and means	320	41	76	111	139	159		
Standard of growth		41	35	35	28	20		

The backward calculation has been carried out with the aid of a "Eichkurve" (standard curve) constructed along the same lines as that described in 1942 by Einsele for whitefish. The base of the roach curve is formed by scales of fish of all dimensions, from one and two year-old to the biggest, altogether 839 individuals caught between November and May 1957—59 in Lake Mälaren, in all cases during the season of arrested growth. In order to facilitate work a gauge of this curve has been prepared in acrylic plastic. This gauge was then made to swivel round an axis at the point of intersection of the extrapolated curve and the abscissa.

For different calendar years the growth has been calculated according to a new method first described by Svärdson in 1961. As his paper has been published in the Swedish language, a brief description of the method will be given here. The backward calculated material is first grouped as usual according to mean values for the different years of age for age groups and year classes during all years of capture. Then what is called by Svärdson "the relative growth during the calendar year" is calculated as follows. (See also Table 3).

From the entire material to be treated a "*standard of growth*" for the *yearly increment* has to be calculated for all different age groups. In doing so all fish considered during the years of capture to belong, e.g., to age group III are lumped together into a single age group III. The average lengths for the first, second, third, etc. year of age are calculated. The same procedure is then applied to all age groups in the material. After this of all these average lengths for the different years of age mean values are calculated, and from these the standard of growth is calculated as yearly increments. (See Table 3.) On the basis of this norm it is now possible to calculate the relative growth for different calendar years and, if desired, for year classes. The procedure in the calculation of the growth for the calendar year is the following (see Table 4):

For all year classes represented within the material the average of the growth is calculated for every year in the year class, the growth of the different years of age being then calculated as percentage of the norm for every year class. The growth calculated above in Table 4 at 103 per cent

Table 4. Relative growth of year classes. See p. 48 for explanations.

Standard of growth	41	35	35	28	20		
Year class	Growth of the year class at age						
	1	2	3	4	5	6	7
1953	42	33	36	25	21	millimetres	
	102	94	103	89	105	% of standard	
1954	40	37	33	28	17	mm	
	98	106	94	100	85	%	

for the third year of age of year class 1953 and at 106 per cent for the second year of age for year class 1954 has accrued in the course of the calendar year 1955, and thus the percentages can be used for obtaining a measure of the growth in different calendar years. After weighing the percentages against the values of the standard in order to give added weight to the values derived from relatively young fish, of which the underlying material is greatest, the relative growth for the years is obtained as

Calendar year	1953	1954	1955	1956	1957	1958
Relative growth %	102	96	105	92	192	85

In this way the adult growth (from the fourth to the seventh or to the tenth year of age, all inclusive) has been calculated. It has been kept apart from the growth of the young comprising the first and second, and possibly also part of the third year in the life of the roach. In the following the growth of the young has comprised the one-year lengths only that had been obtained from the mean values for the one-year lengths of the year classes. No comparisons with the norm have been carried out. Later on the reasons for the choice of the one-year length as representative for the growth of the young will be discussed.

By means of a method described by SVÄRDSON in 1961 also the strength of a year class has been obtained, here without the graphic adjustment (see SVÄRDSON). In its general principles the method resembles very much that for the calculation of the growth. Here the procedure is as follows (see Table 5):

First in the capture of one year the number of fish in every age group is calculated, and the number in the age group is expressed as percentage of the capture of the year (e.g. 5 % in 1958). According to Table 5 the standard then becomes for age group II $\frac{5+6+2+33}{4}$, for age group III $\frac{26+31+27+14}{4}$, etc. With the standard as point of departure the relative strength of the year class is then calculated. The representation of the year classes in the entire material is obtained from Table 5 by considering that e.g. year class 1956

Table 5. Calculations of year class strengths. Explanations: —56=yearclass 1956; 7=number of fish caught in 1958 belonging to age group II (and year class 1956); 5 %=7 as percentage of 132 (the total number of fish caught in 1958).

Age group	II	III	IV	V	Sum
Year of capture					
	—56	—55	—54	—53	
1958	7	34	22	69	132
	5 %	26	17	52	100 %
	—57	—56	—55	—54	
1959	11	55	78	32	176
	6	31	45	18	100 %
	—58	—57	—56	—55	
1960	3	40	35	69	147
	2	27	24	47	100 %
	—59	—58	—57	—56	
1961	48	20	41	34	143
	33	14	29	24	100 %
Standard (%)	$\frac{5+6+2+33}{4}$	$\frac{26+31+27+14}{4}$	etc.		

is found as age group II in 1958, as III in 1959, as IV in 1960, and as V in 1961, and that altogether 131 roaches born in 1956 have been caught.

Thus the strength of the year classes is obtained by expressing the sum of the percentages found (e.g. for year class 1956 5, 31, 24, and 24 %) as percentage of the sum of the corresponding norms, $\frac{5+6+2+33}{4}$ $+ \frac{26+31+27+14}{4}$, etc. This gives for every year class a figure expressing the relation of the class to a normal value for the entire material. In this constructed example the relative strength of the year class for the years 1953—59 becomes the following:

1953	149	1957	96
1954	55	1958	44
1955	133	1959	285
1956	84		

In order that the above described method should give tolerably representative values for the strength relations existing in nature between the year classes it is, amongst others, necessary that the scale material should have been taken from fish caught with the same type of gear under conditions permitting the assumption that the fishing should have taken place in a part of the population which is comparable from year to year. The best that can be expected of this method is a result pointing towards a tendency in the strength relation, and that this tendency does not imply too great errors.

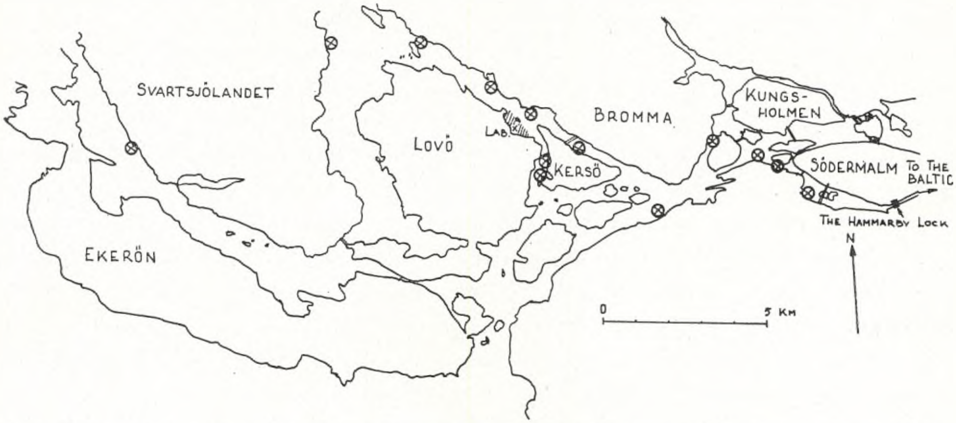

Fig. 3. Map of the eastern part of Lake Mälaren, showing the recaptures of roach marked at the laboratory, and those at 'Kungsholmen' and 'Södermalm' are situated in the middle of Stockholm, the capital.

The method has been considered to have certain advantages over that described by HILE in 1941. The method for the calculation of the strength of year classes which is based upon statistics at capture has not been considered applicable here, since in Sweden the roach is not caught for economic purposes.

Growth in the different lakes

A. Under natural conditions

1. *In Lake Mälaren at 0.5 m altitude*

Lake Mälaren (Fig. 3) is a large lake, covering 1140 sq.km, with great deep fjords, some of them almost 60 m deep, alternating with narrow sounds and shallow regions. The lake is eutrophic, and in the regions near dense habitation under the influence of their sewage. This influence has, however, as yet produced no distinct effects in any larger part of the lake. The height above sea-level amounts to only 0.5 metres, and before sluice-gates had been erected at the outlets towards the Baltic, salt water could at high water enter Lake Mälaren. At that time there also existed considerable fluctuations of the water-level which are now eliminated since the vernal flood is regulated, and its high water is not allowed to persist far into the summer. The previous normal water-level of 4.10 metres above the threshold of the sluice within the town of Stockholm is now, as the result of the regulation, often the normal level in June, whereas it was previously reached perhaps not before late summer. To its present extent the regulation was carried out mainly in 1943, and can only be considered a very moderate interference with the natural conditions, intended mainly to prevent the previously fairly common inundations of low-lying pasture lands. It does not imply any increased variation of the water-level in Lake Mälaren. In spite of the regulation or, rather, drainage the lake has to be considered as uninfluenced by man, and was for this reason deemed a suitable object for the study of the growth of the roach in natural environment. In addition to the usual analysis of age and size attempts have been made to correlate growth and strength of year classes with some climatic factors, viz. temperature, insolation, precipitation, and water-level. The correlations have been calculated on the basis of BONNIER and TEDIN (1940), from where formulae and methods were obtained. Growth (divided into one-year length and adult growth) and strength of year classes have been calculated according to the methods indicated in the foregoing. Data on the climatic factors have been taken from the SMHI yearbooks (Meteorological and Hydrological Institute of Sweden). The daily information about the temperature of the water, read off by the Port Authorities of Stockholm, are made accessible by SMHI. The temperature of the water is read at the sluice-gate of Hammarby, in the middle of the town of Stockholm. But, as far as recaptures of roach marked in 1960 and 1961 have shown, also this station for the observation of the temperature far up in the town has with certainty supplied temperature values that are relevant for the growth of the roach, three of the recaptures reported so far having been made in the same narrow bay, where the sluice is situated, and less than 500 m from the sluice-gates.

The recaptures have furthermore shown that the roach caught off the Institute do not form part of a stationary population, but that they migrate in the easternmost parts of Lake Mälaren (see Fig. 3), and that the fish which up to the spring of 1962 had been found at the greatest distance had covered at least 17 kilometres. Altogether 1130 roach have been marked of which not quite 40 have been recaptured so far. Fourteen of them had been taken by private persons, while the rest had been caught immediately off the landing stage at the Institute for Freshwater Research. As the marking experiment is still not considered terminated, a detailed account will be published elsewhere. Previously markings of roach had been carried out in England (FRIDRIKSSON 1952), but no results have been published. In Germany STEINMANN, KOCH, and SCHEURING (1937) have accounted for the migrations of cyprinids in running water, and the scanty informations available about the roach only tell that it has as a rule migrated downstream, in some cases covering a distance of almost 70 kilometres.

The roach have been taken just off the Institute in a shallow region with a dense zone of *Phragmites* and a rich occurrence of *Cladophora aegagropila* upon the bottom down to a depth of about 4—5 metres. Here in the shallow water the roach can be caught all the year round, and there does not seem to exist in this species a distinct tendency to move towards deeper water as the bream often do in winter.

Table 6. Captures of roach from Lake Mälaren, number of scales that have been analysed.

Year	Number of fish				Fishing gear	Date
	♂♂	♀♀	?	Σ		
1946	14	48	1	63	Gill nets	Oct. 10—Dec. 12
1947	24	104	1	129	Gill nets	Mar. 1—Nov. 29
1948	8	52	8	68	Gill nets	Feb. 11—Dec. 10
1949	4	33	9	46	Gill nets	Feb. 11—Nov. 25
1956	72	16	2	90	Fyke nets?	May 31
1957	261	19	375	655	Fyke nets	May (Spawning)
1958	—	—	27	27	Gill nets	Nov. 12—26
1959	62	150	59	271	Gill- and fyke nets	Feb. 12—June 9; Sept. 3—24; Dec. 22—29
1960	31	136	6	173	Gill nets	Aug. 25; Nov. 3
Total	476	558	488	1,522		

The roach have been caught partly with gill nets and partly with fyke nets at the dates and in the years given in Table 6.

A minor part of the scale material collected in 1959 and all collected in 1957 has been taken from spawning roach which are very easily caught in fyke nets. The occurrence of so many males in fyke nets has to be attributed to the division, observed by SVÄRDSON (1952), of the spawning area into a male and a female belt, the latter being situated outside the former, and to the circumstance that a female that by chance has got into a fyke net will in a short time attract a great number of males. There exists no record of the gear used in 1956, but date and distribution of the sexes point to fishing with fyke nets at the time of spawning.

The average growth of 1522 roach in Lake Mälaren is tabulated in Table 7. If use is made of the older terminology, the rate of growth might be characterized as normal.

This average growth is of some interest only in connection with the comparison between different lakes, but in this case it is necessary that all factors influencing the growth are known, and that they can be rendered in a comparable form before the growth can be used as a scale for the properties of different lakes as producers of roach. At the present state of limnology and the biology of fishery such comparisons are absolutely impossible. Curves or tables illustrating the growth of roach are found in, amongst others, the following papers: ALM 1917, 1918, 1919, 1920, 1922; BALON 1955; FRANK 1959; GEYER 1939; GRAF VON WESTPHALEN 1956; HUITFELDT-KAAS

Table 7. Growth of roach in Lake Mälaren. Length in relation to age.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13 years
Mean length (mm)	42	76	111	140	161	178	191	199	206	213	220	229	234

Table 8. Lake Mälaren. Correlations between lengths of age groups during successive calendar years. (r=correlation coefficient; P=probability=001 means probability less than one permille.)

Age group	2 years		3		4		5		6		7	
	r	P	r	P	r	P	r	P	r	P	r	P
1 year	.945	.001	.644		.169		.262					
2	—		.627		.063		.063					
3	—		—		.718	.02	.713	.05	.524		.541	
4	—		—		—		.891	.001	.818	.01	.817	.02
5	—		—		—		—		.959	.001	.850	.01
6	—		—		—		—		—		.902	.001

1917, 1927; Jones 1953; Järnefelt 1921; Karpińska-Waluś 1961; Neuhaus 1936; Otterstrøm 1930—31; Schilde 1936; Stangenberg 1953, 1956, 1958; Wagler 1949.

If it is intended to deal with the growth in different calendar years and with the reasons for these variations, the investigation assumes an entirely different aspect. It then becomes necessary to divide growth into two phases, viz. growth of the young and adult growth. On account of the fact that as young the roach has a biotope which differs completely from that of the adult it is impossible that the young should be influenced by the environment in the same way as the adult. It may not even be the same factors that are in play, and many investigations have shown that young and adult do not as a rule live on the same kind of food. The choice of food of the roach as young and adult will be discussed in a later part of this paper (p. 76). The difference in the growth during a calendar year between young and adult becomes obvious also from a comparison of one-year or two-year lengths with that at four years or later as has been done in Table 8. Here the lengths of the different age groups have been correlated with each other, the smallest number correlated being seven, the greatest ten, all being derived from an uninterrupted series of calendar years. Quite obviously one and two year-old show the same fluctuations, but after this age there exist no certain similarities with older fish. The latter, on the other hand, have mutually a very high positive significance, and the limit between the growth of young and adult seems to lie between the ages of two and four years. This is the reason, why in this paper a consistent distinction has been made between the growth of young and adult in such a way that the growth of the young is represented by the one-year lengths, while the adult growth has been calculated on the basis of the lengths of individuals of from 4 to 7 years, inclusive.

The *growth of the young* i.e. the one-year lengths, have been correlated with temperature, insolation, precipitation, and water-level. In consideration of the fact that the scale material had been collected in two periods, viz. 1946—49 and 1956—60, it has been split into two groups, the first covering

Table 9. Calculated first-year lengths in millimetres of roach for different calendar years in Lake Mälaren.

Group	Calendar years and first-year lengths (means in mm)										
	1934	—35	—36	—37	—38	—39	—40	—41	—42	—43	—44
1	45	41	43	44	46	46	46	44	41	44	43
	1945	—46	—47	—48	—49	—50	—51	—52	—53	—54	—55
2	40	40	43	45	40	43	39	38	45	41	46

the years 1934—44, the other 1945—55. The scale material contained in the first group is rather small, amounting to about 300 pieces. On this account less weight has been attributed to it. The other group, consisting of about 1200 scales, is probably more representative. The backward calculated lengths have been tabulated in Table 9.

The correlations of one-year lengths and climatic factors have thus been made with the series, called group 2.

The *temperature* has been considered under two headings, viz.

a) temperature of the air.

This exhibits good agreement with the number of degree-days above 16°C. (degree-days calculated from the temperature of the water at the Hammarby sluice), if the temperature of the air has been calculated as the mean for the month and the degree-days as the sum for the month. For this reason no correlation between the temperature of the air and the one-year length has been carried out.

For the number of degree-days, see p. 57.

b) temperature of the water as the mean at the Hammarby sluice.

Here the temperature has been expressed as the mean for the month or for a period of ten days. Since the spawning takes place during the latter half of the month of May, no correlations over periods of ten days have been carried out for this month, hatching of the fry at this early season being considered rather unusual. The temperature of the water at the Hammarby sluice has been determined in epilimnic water, and on this account the objection might of course be raised that these series do not apply to the young of roach, while they stay in the shore zone. To this can only be answered that the temperature curves from Hammarby and those obtained in surface water at the Institute exhibit the same tendency, although there exist of course slight differences in the actual values. Since the course of the curves is similar, the values from Hammarby must be usable for the above discussed type of correlation.

As can be seen from Table 10, the later part of the summer (in the Stockholm region counted to include the months June—August) seems to be of the greatest importance for the attained one-year lengths. The correlation coefficient is of course positive.

Table 10. Correlation between first-year lengths and mean temperature of the water for months and ten-day periods. Roach in Lake Mälaren. J. J. A. = June, July, and August; Jun.A. = June and August; Jul. A. = July and August.

Period	May	June	July	Aug.	Sept.	J. J. A.	Jun. A.	Jul. A.
r	.043	.133	.373	.743	.325	.705	.653	.747
P	—	—	—	.01	—	.02	.05	.01

Period	June 1—10	June 11—20	June 21—30	July 1—10	July 11—20	July 21—31	Aug. 1—10	Aug. 11—20	Aug. 21—31	Sept. 1—10	Sept. 11—20
r	−.030	−.027	.370	.274	−.125	.422	.477	.770	.723	.402	.326
P	—	—	—	—	—	—	—	.01	.02	—	—

The latter half of August seems to have the greatest influence upon the length. In the course of a season of growth with normal temperature as well as during a summer with a temperature deficit the young of roach reach a "normal length" or nearly so, while in a year with an excess of temperature in the latter half of August the lengths of the young will exceed the normal. The circumstance that the young of roach attain or almost attain "normal length" also in spite of a coolish summer must constitute an advantage in the struggle for continued existence, since the growing size gradually makes them secure from an increasing number of enemies that no longer dare an attack. And in the case of a late summer with higher than normal temperature the roach will grow still bigger and perhaps escape some additional predators.

The few available data on *observed* (not calculated) mean lengths of roach of one year seem to suggest that a length of about 40 mm is common in lakes of "natural" type. Thus ALM (1922) has found roach of one year to be 40—45 mm long, BALON (1955) found (?) the length of young of roach to be 45—50 mm, FRANK (1959) obtained for the same age group almost 40 mm, while the present author has found in the Storfinnsjön reservoir young of roach of one year (41 individuals on June 8, 1961) that measured 48.2 mm, and in Lake Mälaren, on May 8, 1962, 398 roach, likewise of one year's age, with a mean length of 39.6 mm. In the two last-mentioned lakes the roach had been taken with rotenone, so that the method of capture has probably not exerted a more important selective influence upon the size of the individuals.

The apparent growth obtained in one-year young during winter also on capture with rotenone is certainly due to the fact that in autumn also the smallest individuals are still alive. When they have succumbed to the severities of the winter, the reduced population of fry, consisting only of the bigger, more resistant individuals, exhibits a greater mean length.

In the course of their investigations on largemouth bass also KRAMER and SMITH (1960) have clearly proved the temperature in the later part of the growing season to have a decisive influence upon the final length of the one-year young. They found, however, also that the temperature conditions of the very first time after hatching were decisive for the rate of growth during this period. In the case of the roach the method used does not permit to establish a dependence of the rate of growth immediately after the hatching upon the temperature, unless the attained one-year length should in some way be influenced by the temperature reigning so far back in time. Another necessary condition for the discovery of such a dependence on temperature would be exact information about the time of spawning for every calendar year covered by the investigation about roach. In this case the ten-day periods used now should be made to start not from a fixed date (June 1st), but from the time of spawning increased by the time for hatching. The figures in Table 10 for the periods June 21 —30 and July 1—10 might perhaps indicate an influence of temperature upon the one-year length during this period. But this would first to have been corroborated by continuous measurement during the season of the growth of the young and of the temperature as taken by KRAMER and SMITH.

c) temperature of the water expressed as accumulated degree-days (values from Hammarby).

Against the background of the above (p. 55) discussion about mean temperatures these temperature values ought to be representative.

On correlation with the one-year lengths also the accumulated degree-days show that especially the month of August (see Table 11), but to a still higher degree the combination June+August exerts great influence upon the one-year lengths. Singly, June and July do not exert any interpretable influence, neither does September, nor the combination June+July. The entire season (May to September, both inclusive) shows lower values than the combination June+July+August which in turn has lower coefficients than June+August. The one-year length seems to depend upon the temperature mainly of the earlier and the later part of the summer, while the temperature of the intervening time might be of smaller importance. This might depend upon the circumstance that in the middle of the summer, i.e. the month of July, conditions for growth are always at an optimum. It is then the temperature might exceed the optimum level during the middle of the sumof the one-year length. Or (according to KRAMER and SMITH) the influence of the mean temperature might be overshadowed by other factors, or the temperature might exceed the optimum level during the middle of the summer. For rock bass HILE (1941) found no distinct dependence of the one-year lengths upon temperature. Concerning brown trout RUNNSTRÖM (1957) reports a certain connection between the one-year lengths and temperature in June and July.

If the relations between the temperature of the water at Hammarby and that near the shore were known, a table like Table 11 might permit conclusions on the number of degrees which has the greatest importance for the

Table 11. First-year lengths of roach compared with accumulated degree-days of water-temperature. Different periods during growth season in Lake Mälaren.

Degree-days above	Period											
	June		July		Aug.		Sept.		Season		Jun.+Jul.	
	r	P	r	P	r	P	r	P	r	P	r	P
15°C	.417		.365		.749	.01	.083		.818	.01	.555	
16°C	.494		.348		.743	.01	.127		.803	.01	.511	
17°C	—		.380		.739	.01	—		.779	.01	—	
18°C	—		.345		.695	.02	—		.687	.02	—	

Degree-days above	Period					
	J+J+A		June+A		July+A	
	r	P	r	P	r	P
15°C	.873	.001	.886	.001	.736	.01
16°C	.827	.01	.908	.001	.724	.02
17°C	.791	.01	.880	.001	.732	.02
18°C	—		—		—	

one-year length, and which ought to be considered the optimum temperature. As far as Lake Mälaren is concerned the minimum temperature lies presumably at about or just above 17°C. as shown by SVÄRDSON (1952) and the author's own measurements at spawning time, since it is hardly probable that the roach should spawn at this temperature provided the young should not be able to grow at it.

Insolation has been measured in grammcalories/cm², and in the correlations with the one-year lengths it has been expressed as the sums for the periods in question. These periods have been months or periods of ten days or combinations within each category. No significant coefficient has been obtained, but for the combination June 11—30+August 11—31 the value very closely approaches the five per cent level (r=0.623, n=10). Thus we have also here to do with two periods, viz. one at the beginning, the other at the end of the season of growth, which, combined, might play an important rôle. KRAMER and SMITH, who also studied the insolation, found no connection between it and growth.

Precipitation exerts no interpretable influence upon the growth of the young of roach. It has been correlated in the shape of sums for months or periods of ten days, and attempts have also been made to establish, whether or not the precipitation of the preceding year might have had any influence, but neither that of the current nor the preceding year seems to be of any importance for the one-year length.

The *water-level* has not been examined for group 2, but for group 1 the coefficient was negative and high (—0.586) without, however, being signi-

Table 12. Adult growth of roach in Lake Mälaren expressed as relative growth for the calendar year.

Calendar year	1948	—49	—50	—51	—52	—53	—54	—55	—56	—57	—58	—59
Relative growt	97	92	79	83	96	114	114	80	113	175	73	163

ficant for the combination of the months June+August. High water-levels in summer prior to the regulation of Lake Mälaren were due to copious precipitation and, in connection with it, also low temperatures in summer.

The one-year lengths have been correlated also with the strength of the year classes, but no connection could be found between the two. No information about a connection of this kind has been found for the roach, neither has HILE (1941) observed it for rock bass. RUNNSTRÖM (1957) arrived at the same result for brown trout.

On account of the above-mentioned composition of the material of two batches also the *adult growth* (understood here to cover the fourth to the seventh year, inclusive) has been split so as to cover two periods, viz. 1937—48 and 1948—59. Only the latter series will be discussed here in any detail, the reasons being the same as those given previously for the choice of the one-year lengths. The growth as tabulated in Table 12 has been calculated by the method devised by SVÄRDSON (see p. 49 pp.).

As for the one-year lengths correlations have been set up between the adult growth and climatic factors, these being again temperature, insolation, precipitation, and water-level.

Temperature has been split into:

a) temperature of the air (mean values)

For the period from June 11—20 and July 16—31 (see Table 13) the significance for the connection between adult growth and temperature of the air lies at the five per cent level. Only periods of ten days and combinations of such have been studied.

b) temperature of the water (mean values at the Hammarby sluice).

Here the first attempt aimed at the discovery of a possibly existing connection between the mean for the months and the growth. When this had

Table 13. Adult growth compared with mean temperature of the air for ten-day periods in Lake Mälaren, years 1948—59.

	Period								
	June 1—10	June 11—20	June 21—30	July 1—10	July 11—20	July 21—31	Aug. 1—10	July 16—31	June 11—20 and July 16—31
r	—.053	.364	—.100	.008	.150	.447	—.161	.466	.588
P	—	—	—	—	—	—	—	—	.05

Table 14. Adult growth of roach compared with means of temperature of the water for months and ten-day periods in Lake Mälaren, years 1948—59.

	Period				
	May	June	July	Aug.	Sept.
r	.020	.122	.446	.153	—.459
P	—	—	—	—	—

	Period									
	June 1—10	June 11—20	June 21—30	July 1—10	July 11—20	July 21—31	Aug. 1—10	Aug. 11—20	July 16—31	June 11—20 and July 16—31
r	—.188	.370	.175	.187	.328	.450	.052	.143	.488	.607
P	—	—	—	—	—	—	—	—	—	.05

proved unsucessful, attempts were made also with periods of ten days and combinations of such. Precisely as in the case of the temperature of the air the only significant value obtained came from correlation with the periods June 11—20 and July 16—31, but as can be seen from Table 14 the significance lay at the value of five per cent only.

c) temperature of the water (accumulated degree-days, at Hammarby sluice).

LeCren (1958) found that the perch (the adult) was dependent for its growth upon the number of degree-days above 14°C., or as he himself points out, upon a temperature immediately below 14°C. This made it advisable to examine, whether or not also the roach was dependent upon the same temperature limits. For these reasons a start was made with a correlation of the number of degree-days above 14°C. during the whole season from May to September, both inclusive, with the adult growth. This examination was then extended so as to comprise months and periods of ten days. No connection could be traced between the number of degree-days and the growth either for the whole season or for months, while the combination of the periods June 11—20 and July 16—31 exhibited a feeble significance between 0°C. and 13°C., but no longer at a number of degree-days above 14°C. or higher temperatures. See Tables 15 and 16. Also the combination June 11—20 and July 11—31 shows a feeble significance, whereas none could be observed for June 11—20 and July 21—31.

Table 17 has been derived from Table 16, and shows, how the significant connection at the interval 13—14°C. gives way to non-significance. This agrees fairly well with the temperature (somewhat below 14°C.) presumed by LeCren as the limit for the best agreement betwen number of degree-days and adult growth. In the case of the roach this limit seems to lie between 12 and 13°C.

Table 15. Growth of adult roach compared with accumulated degree-days for months and the whole season (season=May to September, both inclusive) in Lake Mälaren.

Above		Period					
		June	July	Aug.	Sept.	Season	June+July
14°C	r	—	.420	—	—	.067	—
	P	—	—	—	—	—	—
15°C	r	.067	.429	.119	—.444	.028	.331
	P	—	—	—	—	—	—
16°C	r	—	.421	—	—	—	—
	P	—	—	—	—	—	—
17°C	r	—	.417	—	—	—	—
	P	—	—	—	—	—	—
18°C	r	—	.447	—	—	—	—
	P	—	—	—	—	—	—

Insolation, precipitation, and *water-level* show no significant connection with the adult growth of the roach, either for months or for periods of ten days. Also the precipitation has been studied partly for months of the preceding year, partly for combinations with months of the current year. In neither case a distinct connection with growth could be traced.

Already in 1932 SEGERSTRÅLE found that the fluctuations in the growth of the bream and also of the roach were in good agreement with the temperature of the water (mean values) and still more so with the mean temperature of the air in the time from July to September, the best agreement falling into July—August. SCHILDE (1936) observed in North-German lakes an influence of the annual mean temperature (April to April) of the surface water upon the growth of two age groups of roach, but no such influence upon a feebly growing strain in STRAUSEE. GEYER (1939), studying the growth of the roach, found no direct influence of temperature (air) and water-level upon the growth of the age groups. About rock bass HILE (1941) tells that during certain limited periods weather conditions can exert an important influence upon the annual fluctuations of growth and strength of year class. A high temperature in June often results in good growth. He also found the combination June+September to give a good growth, and assumes this to be due to the extended growing season. STROUD (1948) points out that adult of basses and black crappie grow at a slower rate in the middle of the summer, but faster at its beginning and end. SVÄRDSON (1957) showed that warmth in May and June favours the growth of whitefish; the later part of May being perhaps of the greatest importance. The results arrived at by LECREN (1958) have just been discussed.

According to this and other investigations it thus has the appearance as if there existed during the season of growth one or several critical periods,

Table 16. Growth of adult roach compared with accumulated degree-days for ten-day periods and their combinations in Lake Mälaren 1948—59.

Period		June 1—10	June 11—20	June 21—30	July 1—10	July 11—20	July 21—31	Aug. 1—10	Aug. 11—20	June 11—July 10	June 11—July 31	June 11—Aug. 10	June 21—July 10	June 21—July 20	June 21—July 31	June 21—Aug. 10	July 11—31	July 16—31	June 1—20+ July 11—31	June 11—20+ July 11—31	June 11—20+ July 16—31	June 11—20+ July 21—31	June 11—30+ July 11—31	June 11—30+ July 21—Aug. 10
Above 0°C	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.608	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.05	—	—	—
10	r	—	.370	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.466	—	—	.609	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.05	—	—	—
11	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.609	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.05	—	—	—
12	r	—.120	.373	.171	.183	.345	.447	.020	—	—	—	—	—	—	—	—	.481	.469	—	.594	.609	.554	.487	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.05	.05	—	—	—
13	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.469	—	—	.553	.587	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.05	—	—	—
14	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.470	—	—	—	.519	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	r	—	—	.037	.195	.328	.443	.066	.027	.318	.292	.318	.126	.223	.352	.323	.471	—	.449	.478	.467	—	—	.261
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	.474	—	—	.432	—	—	—
	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 17. Growth of adult roach compared with accumulated degree-days above certain temperatures, for the combined periods June 11—20 and July 16—31.

	Above degrees C							
	0.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0
r	.609	.609	.609	.609	.587	.519	.467	.432
P	.05	.05	.05	.05	.05	—	—	—

when temperature is of great importance and will determine, whether the annual growth in length will be great or small or perhaps nil. If in the case of the roach two periods in combination are of importance for the growth in length, and if these two periods are separated by a time interval without noticeable importance for growth, the explanation is probably found in the circumstance that during the intervening time the temperature is either higher than the one most favourable to growth and in this case of minor importance, or that the influence of the temperature is overshadowed by other factors, or, finally, that perhaps no growth in length worth mention takes place in the course of this time.

Between younger and older adults there exists a sliding transition between the importance of growth in length and growth in weight. For the younger animals length is still of great importance, since a specimen that is able to grow somewhat more than others becomes fitter for competition, and perhaps at an earlier date can turn to other and less sought-after food (partly from SVÄRDSON 1962). These younger animals need a relatively smaller deposit of fat as reserve for the coming winter. The older animals on the other hand have to accumulate a deposit of fat which in proportion to the volume of the body is much greater, and thus tends mainly towards an increase in weight. It neither can be or is of advantage to them to grow in length, once they have reached the maximum size as determined either by heredity or by the conditions in the lake. It is perfectly natural that in the admittedly not adult one year-olds growth in length depends upon much longer periods. They also differ distinctly from the adults with respect to the length of the periods during which they depend upon temperature.

The growth in length begins after spawning, and the annulus, as observed also by WALLIN (1957) in his paper about the roach, is formed simultaneously with the beginning of growth. In this paper these two facts have been established in the following way:

1. None of the 655 roach in the material of spawning fish of 1957 showed an unmistakable sign of possessing a newly formed stria at the extreme edge of the scales.
2. The spawning has been studied in the three years 1960, 1961, and 1962,

and in none of them has here, in this part of Lake Mälaren, spawning taken place at a temperature of the water off the spawning place of 11—12°C. at the bottom in a depth of 1.5—2 metres.

3. As has been shown above, the growth in length seems to depend to the greatest extent upon temperatures above a limit somewhere between 12 and 13°C.

Since temperature conditions are not the same upon different spawning places and in different lakes or water courses, point 2 requires some comments. The roach is known to spawn both in running and stagnant water, and there exists information about spawning temperatures varying from 7—9 to 16—18°C. (ALM 1922). Also GRAF VON WESTPHALEN (1956) points out that spawning takes place at very different temperatures. Both these two authors must mean temperatures at the spawning-place, not on the depths discussed in point 2.

In one and the same locality it takes, however, place at fairly constant temperature year after year, and a superficial examination shows that the time can be quite distinct in two lakes in close vicinity of each other and of the same character, but distinguished by different size and different depth conditions. In a small and relatively shallow former bay of Lake Mälaren the roach spawn at a temperature of about 12°C., but 2—4 weeks earlier than the roach spawning off the Institute.

Also the *strength of the year classes* has been put into relation with the above-mentioned environmental factors, but the results of the numerous correlations furnish a picture the interpretation of which is very difficult, and as yet few indications point in the direction that the time immediately after spawning and hatching should be the most critical for the dimensioning of the year classes. It was especially MONTÉN's paper of 1948 on the fry and young of pike that induced the expectation of a connection between environmental factors and strength of year classes also for the roach during their very earliest life. KEMPE (1961) who had found that in the autumn of 1961 about 25 per cent of the year class 1959 were infested with the parasitic *Ligula intestinalis* L. has shown that the dimension of a year class can be altered even after having reached the age of one or several years, since it must be expected that the major part of the infested fishes will not survive the infection, but succumb to it.

2. *In Lake Särnasjön at 422 m altitude*

Lake Särnasjön (Fig. 4) is a widening of the river Österdalälven and covers 9.5 sq.km. Its maximum depth is smaller than 30 m. It is, of course, of oligotrophic type. Roach dominates in company with perch, but in addition there occur also whitefish, pike, burbot, and trout. In the course of 11 fishing periods in the years 1952—57 the roach represented on the average

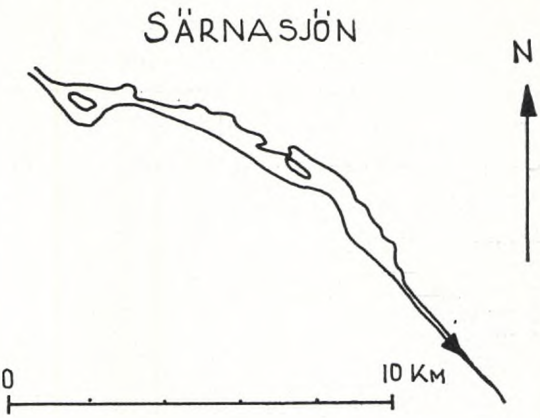

Fig. 4. Lake Särnasjön, at an altitude of 422 metres.

53 per cent of the number of fish caught. Available climatological data refer to temperature of the air and precipitation only. They have been derived from the SMHI yearbooks and have been obtained at the meteorological station at Särna.

During a number of years the Institute for Freshwater Research has been carrying on test fishing in the lake in order to get an idea of the conditions in the lake before the begin of its regulation in connection with the erection of a power plant farther down in the river. This was the reason, why from 1952 to 1960, inclusive, scale samples of roach have regularly been taken according to Table 18. It is expected that the regulation will begin to affect the lake in the course of 1962, and for this reason the present analysis refers to the natural, i.e. unaffected conditions. The procedure has been the same

Table 18. Number of fish caught in Lake Särnasjön for calendar years. It should be observed that in this case the figures mean number of fish that have been analysed for age, and that these represent only about half the total number of investigated scales, the rest being undecipherable on account of their high ages.

Year	Number of fish				Fishing gear	Date
	♂♂	♀♀	?	Σ		
1952	—	5	—	5	Gill nets	July 16—29
1953	9	29	3	41	» »	June 26—July 2
1954 ...	21	14	—	35	» »	June 10—11
1955	14	49	1	64	» »	June 30—July 4
1956	27	49	—	76	» »	June 15—26
1957	48	83	—	131	» »	June 14—18
1958	14	13	—	27	» »	Aug. 6—7
1959	29	55	—	84	» »	May 24—28
1960	2	19	—	21	» »	June 12—24
Total ...	164	316	4	484		

Table 19. Lengths of different age groups compared with each other. Roach from Lake Särnasjön.

Age groups	2		3		4		5		6		7		8	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P
1	.128		.146		—		—		—		—		—	
2	—		.272		.132		—		—		—		—	
3	—		—		.840	.02	.915	.02	—		—		—	
4	—		—		—		.943	.01	—		—		—	
5	—		—		—		—		.831	.05	.574		—	
6	—		—		—		—		—		.949	.01	.361	
7	—		—		—		—		—		—		.622	

as for the analysis of the material from Lake Mälaren. The growth has been split into one-year lengths (growth of the young) and adult growth (growth during the fourth to tenth year of life). This splitting was effected after a comparison of the growth of the different age groupe (See Table 19). This table produces the impression as if, contrary to conditions in Lake Mälaren, the growth in the first and second year should not be subjected to the same variations, but since in Lake Särnasjön no analyses of the stomach content of these two age groups have been carried out, it is impossible to theorize about the causes of the differences. As in Lake Mälaren the growth of the age groups above three years exhibits good agreement. Here the adult growth has been made to include the years from four to ten, inclusive. This was possible, because the average age of the material, the age of which had been analysed, was so high that it contained a number of individuals of up to ten years' age sufficient for the inclusion of this year in the calculation of the relative growth for the calendar year.

Here the *growth of the young* has, perhaps somewhat incorrectly, been identified with the one-year lengths. (For correctness sake of course also the two-year lengths should be analysed by themselves, since in Lake Särnasjön they might represent a second phase of the growth before the latter turns into the "stanza" of the adult). To start with the one-year lengths have been correlated with the mean values for the temperature of the air of the month, but no significant connection was found to exist either for individual months or combinations of months. The investigation covered the years 1941—48.

Later the connection between growth of young and precipitation has been examined, and here (see Table 20) the combination May + September was significant on the five per cent-level. The negative sign must imply that abundant precipitation produces small one-year lengths. This can be explained by the fact that rain is linked with coolish weather and produces on account of the fast drainage a lowering of the temperature of the water, and perhaps also by greater difficulty, following from the higher water-level

Table 20. Correlations between first-year lengths and precipitation in Lake Särnasjön.

Period	March	April	May	June	July	Aug.	Sept.	May+ Sept.
r	—.442	—.373	—.572	—.026	.278	.071	—.614	—.712
P.........	—	—	—	—	—	—	—	.05

and the turbidity, encountered by the young of roach in searching for and finding their food. In Lake Särnasjön, situated in a narrow river valley the precipitation must have implications which are entirely different from those e.g. in Lake Mälaren. Also here the period covered extended from 1941 to 1948.

The one-year lengths have been correlated also with the strength of the year classes in Lake Särnasjön. No significant connection has been found.

Also *the growth of the adult* has been put into relation with the temperature of the air and with precipitation, but only the former has proved to have a distinct influence upon growth; see Table 21.

The precipitation has been studied for months and combination of months, the period comprised being the same as for the temperature, viz. the series 1944—57.

It appears rather peculiar that the dependence upon climatic factors should be so different for young and adults. The one year-old have not been influenced by temperature to any noticeable degree, while the adult did not exhibit any dependence upon precipitation. In case these differences have any real significance, the latter might depend upon the different choice of the dwelling place. The examination of young of roach from Lake Mälaren has shown the temperature of the air to have a very distinct connection with the number of degree-days (temperature of the water) above 16°C., and then the relations ought to be the same in Lake Särnasjön also.

The *strength of the year classes* will be given a fuller treatment here, than when the roach from Lake Mälaren was under discussion. Fishing in Lake Särnasjön has been carried out all the time exclusively with nets, admittedly at first with cotton nets which in the later years were replaced by nets of nylon, and in his investigation of 1962 STEINBERG proves the visibility of the

Table 21. Adult growth compared with means of air-temperature. Roach from Lake Särnasjön.

Period	May	June	July	Aug.	Sept.	May+ June	June+ July	June+ Aug.	July+ Aug.	June+ July+ Aug.
r	.263	.417	.358	.257	—.008	.431	.633	.654	.402	.560
P.........	—	—	—	—	—	—	.02	.02	—	.05

Table 22. Strength of year classes compared with mean temperatures of the air for the years 1941—48. Roach from Lake Särnasjön.

Period	May	June	July	Aug.	Sept.	May+ June	May+ Aug.	Aug.+ Sept.	May+ Aug.+ Sept.
r	.726	.619	—.374	.643	.688	.837	.374	.756	.878
P	.05	—	—	—	—	.01	—	.05	.01

material of the net to be the most important catching property of gill-nets, contrasting nets giving poorer catches, while hardness and cross-section of the net material are of minor importance. MOLIN (1953) found that nylon nets, twined as well as monofilament, caught more fish than cotton nets, and that the nylon nets on account of the superior stretching in the meshes had a tendency of catching fish with a wider spreading in length than cotton nets of the same size of mesh. In spite of the skewness that might attach to the material on account of the use of nets of different materials, the strength of the year classes in Lake Särnasjön has nevertheless been correlated with the available environmental factors. That this has been done in spite of everything had its reason in the circumstance that the fishing had been carried on in the same places year after year and, with some few exceptions, with nets with the same size of meshes. Thus the material varies less on account of selection due to the tackle than in Lake Mälaren.

The temperature of the air partly during the earlier and partly during the later part of the season proves to exert the greatest influence upon the dimensioning of the year classes (See Table 22). For the pike (*Esox lucius* L.) MONTÉN (1948) has found that the greatest relative loss of fry takes place during the earliest time of their life, and it appears probable that the essential dimensioning occurs at this time, even if considerable reduction in the number of individuals can take place up to the age of three years as has already been pointed out (p. 64). HILE (1941) found the conditions of temperature and precipitation during the early part of the season, especially the month of June, to exert a great influence upon the strength of the year classes, the correlation being positive for both temperature and precipitation. SVÄRDSON has repeatedly (e.g. 1957 and 1961) stressed the great importance

Table 23. Strength of year classes compared with sums of precipitation for the years 1941—48. Roach from Lake Särnasjön.

Period	March	April	May	June	July	Aug.	Sept.	May+ Aug.
r	.206	.455	—.368	.021	.455	—.883	—.298	—.949
P	—	—	—	—	—	.01	—	.001

Table 24. Relative strength of year classes for calendar years in Lake Mälaren and Särnasjön.

Lake	1941	–42	–43	–44	–45	–46	–47	–48	–49	–50	–51	–52	–53	–54	–55
Särnasjön	45	154	106	50	128	113	307	81	—	—	—	—	—	—	—
Mälaren	—	—	—	—	30	122	149	90	40	26	65	119	110	92	66

of higher than normal temperatures during the earlier part of the season of growth, especially in June, for the formation of rich year classes, and also RUNNSTRÖM (1957) has shown that in the years leading to rich year classes the temperature in June has been above normal. The importance of the temperature in early summer evidently expresses a general tendency, but that, as in the case of the roach, also the late summer is of importance has not been stated for any other species, and it is difficult to understand in what way the temperatures of August and September could be of importance, unless by the connection between greater length of the fish and their increased chance of survival.

The precipitation (Table 23) also plays an important rôle for the formation of the year classes, but contrary to the findings of HILE (1941) the influence is here towards the negative side, i.e. years with poor year classes are mostly those in which much rain has fallen during the combination of months May + August.

Here in Sweden the examination of the year classes of different species has been carried out mainly by RUNNSTRÖM and SVÄRDSON. These examinations deal with brown trout, char, species of whitefish, and cisco, and have shown that rich year classes had been formed in many places, but not everywhere, in the years 1943, 1947, and 1953. As can be seen in Table 24 the roach of Lake Särnasjön had a strong year class in 1942. 1943 produced a year class somewhat above normal, while 1947 gave a strong year class. Also in Lake Mälaren the year class of 1947 was rich, that of 1953 was above normal, yet somewhat feebler than that of the preceeding year. (In Lake Mälaren the strength relations may and probably have, however, been distored by the selective effect of the fishing gear used). Thus the tendency towards the formation of rich year classes in certain calendar years is on the whole the same for the roach as for the other examined Swedish species.

There exist indications for the formation of a new rich year class in Lake Mälaren in 1959, and in this year the three months June, July, and August had higher than normal temperatures of the air as well as of the water.

Comparison between Lake Mälaren and Lake Särnasjön together with some other lakes at great altitude.

Growth of the young. The absolute figures are rather similar, and the means for the series so far examined from the two lakes are for Lake Mälaren 42

Table 25. Growth of roach expressed as mean lengths for age in Lake Mälaren and in Lake Särnasjön.

Lake	Mean lengths at age													
	1	2	3	4	5	6	7	8	9	10	11	12	13	years
Mälaren	42	76	111	140	161	178	191	199	206	213	220	229	234	mm
Särnasjön ...	41	70	89	104	114	124	135	144	153	161	169	178	190	mm

and for Lake Särnasjön 41 millimetres. The differences of the amplitude within the year series are somewhat greater, the maximum and the minimum being for the former lake 46 and 38, for the latter 44 and 40 mm, respectively.

The coefficient of correlation is without significance for the comparison of the two series. In Lake Mälaren the one-year lengths were obviously dependent upon the temperature of the air as well as of the water. This was, however, not the case in Lake Särnasjön, where these lengths were instead dependent upon precipitation which they were not for the roach of Lake Mälaren.

It seems as if the young in the two lakes were not living under the same environmental conditions. They might not even inhabit localities of the same type. If it be true that in Lake Särnasjön temperature does not influence the roach in the same way as in Lake Mälaren, there must necessarily exist another very important factor that carries still greater weight than temperature which is generally recognized as important. In spite of the great difference in altitude the young has reached almost identical lengths during the sequence of years covered by the investigation.

Also *the adult growth* exhibits both similarities and differences in the two lakes. The similarities are found in the dependence upon the temperature (growth dependent mainly upon an earlier and a later period of the season) and also in the non-existing dependence upon precipitation. With respect to Lake Särnasjön the latter appears somewhat peculiar. A similarity is likewise found, if the relative growth during the calendar years is compared. Then the coefficient of correlation becomes positive and significant at the level of five per cent. All this indicates that as adult the roach is influenced by the same environmental factors in the same way in the two lakes, but that a comparison of the growth represented by the size attained in a certain year of life nevertheless gives a different results. As can be seen from Table 25, the roach in Lake Mälaren grow faster, i.e., attain a certain given length at a lower age. In Lake Mälaren roach of six years are already as big as twelve year-old roach in Lake Särnasjön.

Since no small roach have been available for examination in Lake Särnasjön, no comparison between the sexes in the two lakes is possible, but with regard to Lake Mälaren it can be stated that many of the males are sexually mature already at the age of three years, some isolated individuals already at two years, while the sexual development of the females seems to be completed one or several years later.

The great similarity of the physiology and the climatic variations in the region of Stockholm and Särna at a distance of about 360 km, measured in a straight line, is proved by the fact that the differences in the reaction to the environment as far as variations within the season are concerned are not great. The average length attained at a certain age indicates, however, that there must exist a decisive difference somewhere, and that this difference influences the rate of growth in Lake Särnasjön, when the fish have reached the age of two years. The so far examined samples of the stomach content seem to point to a fairly distinct difference in the food of the adult of the two lakes. In Lake Mälaren they feed mainly on plants, especially filamentous algae, while in Lake Särnasjön their food consists to an overwhelming part of animalic substances. With regard to the different character of the lakes it is possible that in Lake Särnasjön the roach meet with a keener competition for food than in Lake Mälaren. There exists still another essential difference between the lakes, viz. the difference of the mean temperature of the water. Lake Särnasjön is the colder of the two, and it appears possible that there the roach would not grow much faster, even if the competition for food by the other species were removed. WAGLER (1949) reports that the roach occurs as high up as 1000 m, but that at this altitude the growth is poor. From a lake at the altitude of 1138 m fish of four years had not reached a length of 100 mm. For this reason we can be sure that the poorer growth in Lake Särnasjön is due partly to the lower mean temperature and partly to the keener competition for food.

The fact that there exist no greater differences in the one and two-year lengths is probably to be explained by the circumstance that the choice of food of the young is on the whole the same, i.e. planktonic organisms, for the first two years of life in both lakes.

The *strength of the year classes* has already been discussed, and also been compared to some extent for the two lakes.

B. Growth following upon an increase of the space accessible to roach

1. *After reduction of population density, in Lake Halmsjön*

Lake Halmsjön has twice, in 1956 and 1958, been treated with rotenone with the intention of eliminating the existing species and of replacing them by salmonids. At the first attempt at poisoning the lake proved to contain great populations of small-sized roach, bream, perch, normal-sized pike, and in smaller numbers rudd, crucian carp, nine-spined stickleback, tench, ruffle and burbot. The concentration of the poison was about 0.5 ppm, the treatment taking place on July 10, 1956. In 1958 certain signs indicated that

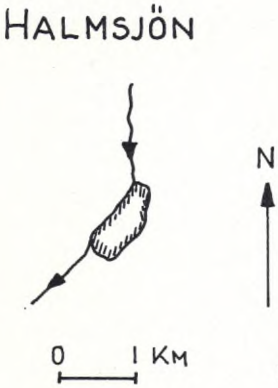

Fig. 5. Lake Halmsjön. The dots mark zones of reeds.

something had gone amiss. Reports were received to the effect that considerable numbers of small fish occurred along the shore, and in the autumn of 1958, on Nov. 11, the whole procedure was repeated, now with a concentration of 0.5—0.6 ppm of rotenone. The result was rather unexpected. Of the species previously existing in Lake Halmsjön roach, perch, pike, crucian, and nine-spined stickleback were found to have survived the treatment, and the remaining fish proved to belong to two year classes of fry and, in comparison with the fry, rather few "parents". The latter were all of a size which, as far as roach and perch are concerned, had been decidedly uncommon prior to the first poisoning.

Lake Halmsjön (fig. 5) is a shallow, eutrophic lake covering a surface of 0.38 sq.km. The greatest depth is 5.5 m. Both inlets and outlets are small. The lake is one of the larger Swedish lakes which has been poisoned with rotenone. Also the other attempt in 1958 does not seem to have been a complete success, since crucian and stickleback were found to have survived. One of the main causes of the failure lies probably in the very rich occurrence of rushes, *Phragmites communis,* that has prevented the free and efficient spreading of the poison. Inlet and outlet could be carefully checked, and are hardly responsible for the failure.

Prior to the first treatment the roach were of very small size, and belonged to the type of population, discussed by ALM (1946) in his paper about stunted fish populations. Of the fishes killed on this occasion (1956) 319 scale samples have been taken, and their age has been analysed with the method described above. The reading of these scales soon proved ticklish, the uncertainty resulting in the establishment of two alternatives, below called 'I' and 'II', respectively. 'I' implies that all annual rings or structures resembling them have been taken into account in the determination of the age. 'I' can thus be said to be the unadjusted alternative. In the other alternative the reading was carried out with exclusion of all ring-like structures

Table 26. Mean lengths in millimetres at different ages for roach in Lake Halmsjön, calculated from the scales taken at the first rotenone treatment on July 10, 1956. For explanation of alternatives, see the text, p. 72.

Alternative	Mean length in mm at age									
	1	2	3	4	5	6	7	8	9	10 years
I	37	56	73	89	98	106	124	136	144	158
II	37	62	81	96	109	122	130	143	149	—

that were not considered to belong to the picture. This adjusted alternative 'II' is perhaps very subjectively coloured. Personally the present author has more confidence in alternative 'II'.

On account of ALM's paper of 1946 the population of roach in Lake Halmsjön requires some commentaries. It has already been pointed out that the roach were of small size (see Table 26), and ALM explains the small size of his perch partly by lack of food and partly by an unsuitable environment in some tarns, with unfavourable values for oxygen, temperature of the water, and pH. In Lake Halmsjön the environment need not be considered unsuitable. There it was merely the availability of food that determined the process of growth.

Age and growth of the other species in Lake Halmsjön have not been subjected to any more detailed examination so far, but it can nevertheless be of interest to compare the strength of the year classes of roach with ALM's ideas of 1946. Fig. 6 shows that 'I' gives a picture of the year classes that seems to represent some kind of normal distribution, after the strengths have been expressed as percentages of the total number of examined roach, while 'II' gives the same picture as that given by ALM for perch in stunted populations, viz. a very strong year class surrounded by next to nothing. In the case of the roach in Lake Halmsjön the strong year class forms almost 50 per cent of the entire population. It is conceivable that in either case, that treated by ALM and Lake Halmsjön, the perch, and to a certain extent of course also other rapacious fishes, are responsible for these conditions, since in Lake Halmsjön also the perch, though no analysis of their age hade been made, appeared to be of the stunted type, and since, typically enough, some isolated, but comparatively much bigger individuals of the same species have been found among all the small fish. If it should be so that also the perch were stunted, then in addition to their own fry also that of the remaining species is endangered by the food requirements of the thousand, and the result will then be a distribution of the strength of the year classes of the roach in Lake Halmsjön which is identical with that demonstrated by ALM (1946) for the perch. It appears rather improbable that the roach should be cannibalistic towards their own fry, and no information pointing in this

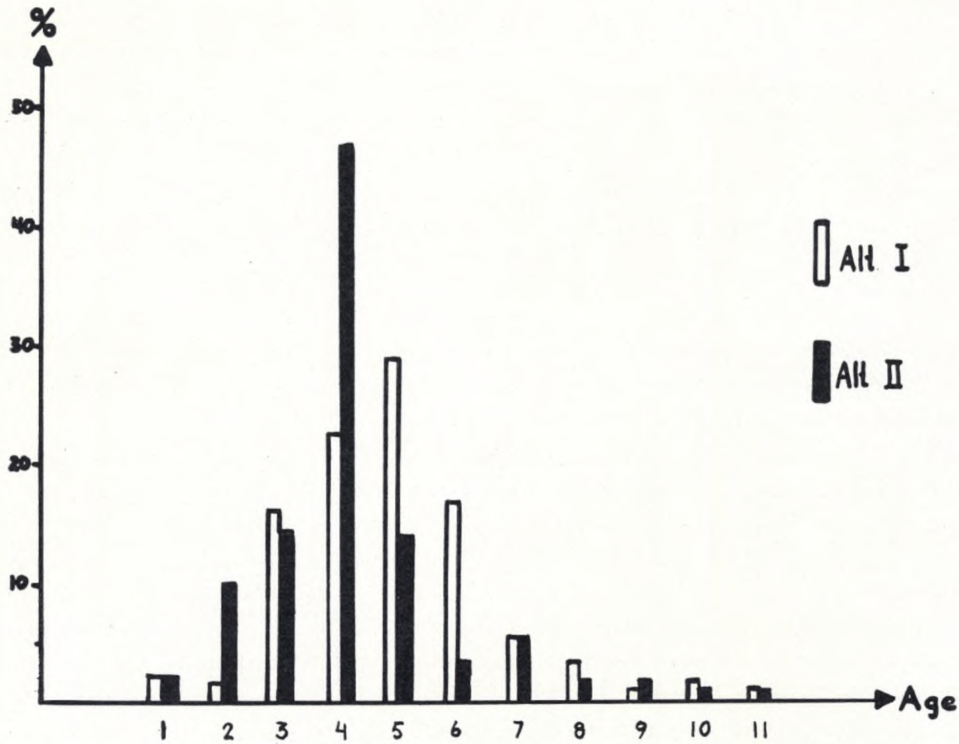

Fig. 6. Distribution of age groups in Lake Halmsjön after age analyses of 319 scale samples. For explanation of alternatives, see p. 44.

direction has ever been found in the literature dealing with the results of analyses of samples of the content of the stomach.

In connection with the poisoning of 1956 no attempts at estimating the quantity or the weight of the populations of the different species have been made.

At the poisoning of 1958 roach, perch, and pike, together with small quantities of crucian and nine-spined stickle back's, were found to have survived the first poisoning in 1956. This was probably due to the fact that they could remain hidden within the zone of rushes. It must also be kept in mind that the treatment took place in the middle of the summer, when the poison soon looses its efficiency. On this occasion altogether 201 samples were taken of the scales of roach the age of all of which was determined. The roach that were newly poisoned and floated upon the surface were dominated by young. These were easily separable into two size groups, and quite obviously belonged to two different year classes. In addition there existed among all the small fish also some isolated large roach, evidently the parents of the young. The method employed for the collecting of the roach for the taking

Table 27. Growth of roach in Lake Halmsjön between the two rotenone treatments of 1956 and 1958. The sign '—' is placed in front of the figure that refers to the growth of the year 1957, i.e. the year after the first treatment. Figures within brackets refer to the growth of the year 1958. The lengths have been calculated from scales taken on Nov. 17, 1958.

Age group	n	Mean length in mm at age													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14 years
0	88	(48)	—	—	—	—	—	—	—	—	—	—	—	—	—
I	60	—70	(93)	—	—	—	—	—	—	—	—	—	—	—	—
V	2	—	—	—	109	—174	(202)	—	—	—	—	—	—	—	—
VI	10	—	—	—	—	115	—190	(217)	—	—	—	—	—	—	—
VII	5	—	—	—	—	—	122	—202	(233)	—	—	—	—	—	—
VIII	14	—	—	—	—	—	—	142	—218	(243)	—	—	—	—	—
IX	12	—	—	—	—	—	—	—	153	—223	(246)	—	—	—	—
X	3	—	—	—	—	—	—	—	—	164	—223	(247)	—	—	—
XI	2	—	—	—	—	—	—	—	—	—	171	—222	(261)	—	—
XII	4	—	—	—	—	—	—	—	—	—	—	168	—233	(258)	—
XIII	1	—	—	—	—	—	—	—	—	—	—	—	186	—258	(285)

of the samples of scales permits no conclusions whatsoever about the strength relation existing between the two year classes of young.

Provided that ALMQUIST's conclusions (1959) about the effect of the rotenone treatment of Lake Halmsjön and other lakes are universally applicable, the first poisoning led to the more or less complete extinction of the greater part of the zooplankton, of most of the epiphytic animals and those living upon the bottom, and part of the phytoplankton. In spite of this the newly formed young of roach have survived very well already in the following summer and have reached a very good size (see Table 27). This suggests that the effects of the rotenone upon the above-mentioned small organisms have been of a very passing nature, and that the latter could reproduce already to the ensuing spring.

In 1957 the *young* exibit a better than normal growth (one-year length 70 mm), while the young of the following year were of the more normal size of 48 mm. In 1958 the year class 1957 reached a mean length of 93 mm. For 1957 the one-year size is not normal, the observed one-year length being usually about 40—50 mm as pointed out already. There is therefore all reason to believe that one of the causes of this high value has to be looked for in the relation between the size of the population and the available amount of food, since there is no doubt that after the first poisoning the population of roach has been essentially reduced. This fact must have resulted in an increased supply of food for the remaining or newly hatched fish. This increase of available food is, however, probably not the only factor working in positive direction, but also the climatic factors must be given attention. In the region of Stockholm the summer of 1957 was on the whole nearly

Table 28. Length increments for the year 1957 expressed as percentage of lengths from 1956.

Age............	4	5	6	7	8	9	10	11	12	years
Increment......	60	65	66	54	46	42	30	33	39	%

normal with regard to temperature, while in the months of July and August precipitation was greater than normal. The summer of 1958 was cool and rainy with temperature below and precipitation greater than normal for this season. The normal summer of 1957 has had a favourable influence upon the growth of the young of this year, and has probably not had the effect it should have produced, if the competition for food had been the same as before the poisoning. The summer of 1958 was one of the worst in the course of the last decades, and in this year the one-year length did not exceed 48 mm, while at the same time the length of the young of the preceding year grew from 70 to 93 mm only. Thus also in this year we must count with at least two causes of the short lengths, viz. the cool summer, as mentioned just now, and the appearance of a new year class of roach, in addition to the year classes of all other species which perhaps also have influenced the growth of the roach, which feeds on the same substances as the roach that are one year older. For both years it can thus be imagined that the effect upon the growth of decreasing and increasing population, respectively, can have been intensified by climatic factors. There is no doubt that the summer of 1957 produced a much smaller effect upon the growth of the calendar year than the summer of 1958 upon the growth of this year.

The *adult roach* have shown a very great increase in length already during the first season of growth after the rotenone treatment. The increase during the year 1957 has been calculated as percentage of the length before the poisoning (Table 28). Prior to 1956 the normal growth for one calendar year was about 10 per cent or less for fish of more than four years, but in 1957 the growth reached, in the course of this single calendar year, values as high a 60—65 per cent. It is remarkable that fish as old as 12 years and as long as 186 mm are capable of growing 72 mm or by 39 per cent in the course of a single year of growth (see Tables 27 and 28). This again proves that small size is not hereditarily determined for the roach either, as it had been shown earlier by FRANK (1959). This has been known rather long ago for e.g. the perch and different species of whitefish. Table 28 shows furthermore that with increasing age and size the annual increase in length decreases in comparison with that attained by younger fish.

Also in adult fish the growth of 1958 is poorer than that of 1957. This is perhaps due mainly to the worse summer and perhaps also to the fact that with the growth of the preceding year the roach had already to a fairly

Table 29. Length increments for the year 1958 for adult roach expressed as percentages of the lengths of 1956 and 1957, and expressed as absolute values (mm).

Increment	Age								
	4	5	6	7	8	9	10	11	12 years
% of 1956	26	23	25	18	15	15	17	15	15
% of 1957	16	14	15	11	10	11	13	11	10
mm	28	27	31	25	23	24	29	25	27

large extent compensated their previous small size, and that it was for this reason that in this year the increase was nearer to what is normal for the lengths of fish that are in question here. Table 31 shows the uniformity in the increase in size of both older and younger individuals among the examined fish. Only the youngest and smallest fish are clearly separated from the rest by a distinctly better growth, when the percentages are considered, while the absolute increase in length does not permit the establishment of the distinction between younger and older roach. In the latter case the increase seems to lie between about two and a half and three centimetres for all of them. Probably at this time no competition of any importance for food has made itself felt in the case of the older roach, since such a competition is excluded by the choice of food eaten by the other species which then (in 1958) were found in Lake Halmsjön in greater number, especially perch and pike. Thus the roach, the older individuals, were still at most as numerous as in the preceding year. The reduced growth of 1958 in comparison with 1957 has thus to be attributed mainly to the influence of the climate and an hereditary reduced ability, accentuated with age, of growing in length.

Information about the effect of a reduction of the population upon the growth of the roach are very scant, and so far only FRANK (1959) has related the changes in the rate of growth after a rotenone treatment to the decrease of the population, while KARPIŃSKA-WALUŚ (1961), who observed an increase of growth after a winterkill, denies the importance of the density of the population for the rate of growth.

MARRE (1932) tells that "Spitzplötzen" feeds on plankton and is of small size, while "Palmplötzen" consumes molluscs and grows at a fast rate, and that the former "through inheriting its bad features forms a uniform, slowly growing strain" (translated by the author of this paper), while NEUHAUS (1936) almost quite correctly points out that "Palmplötzen" (of small size) are nothing than juvenile forms of "Spitzplötzen" (of large size). In spite of the confused ideas of these two authors about the forms of roach, they nevertheless agree on which of them spawns at the earlier date. It should be

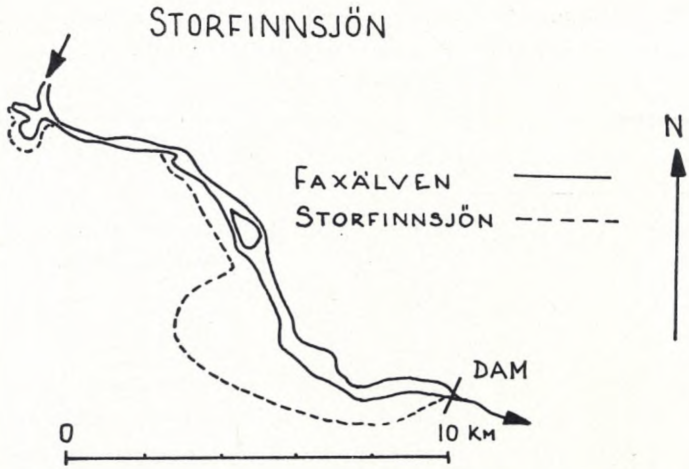

Fig. 7. The Storfinnsjön reservoir. The solid line represents the Faxälven, viz. the river before damming-up, and the dotted line the approximate size of the reservoir.

the smaller one. According to ALM (1922) the larger roach spawn earlier than the smaller. MARRE's and NEUHAUS' opinions might be attributable to the simple fact described by SVÄRDSON (1952) of the division of the spawning places into a "male belt" and a "female belt", and to the circumstance that at the spawning of the roach the males are smaller than the females, and also can create the impression of spawning before the latter, since they have established their stations already at the beginning of the spawning and therefore are discovered with greater ease.

It might be added that MARRE and other adherents of the conception of a hereditarily determined poor rate of growth might at least have examined what happens, if badly growing roach are transferred into a lake without roach.

2. *After the damming-up of the Storfinnsjön reservoir*

In the case of Lake Halmsjön the space available to roach remained altogether unattered and a real reduction of the population has taken place instead. The population of roach in the Storfinnsjön reservoir is not known to have undergone any considerable change in size, but here the available space has been greatly increased in connection with the inauguration of the dam for the power plant.

Originally the Storfinnsjön reservoir was a valley with a river running in it, but now there has been formed in connection with the erection of the power plant a typical "talsperre" (Fig 7) with a surface of 27 sq.km. and a depth which varies somewhat with the amount of the damming-up, but attains at most little less than 30 metres. The water is oligotrophic, and of

Table 30. The scale material collected from the Storfinnsjön reservoir.

Year	Number of fish				Fishing gear	Date
	♂♂	♀♀	?	Σ		
1955	60	35	—	95	Gill nets	Sept. 1—10
1956	18	19	—	37	,,	Sept. 5—13
1957	116	76	—	192	,,	Aug. 21—24
1958	94	103	—	197	,,	Sept. 2—11
1959	156	16	15	187	,,	May 12—14 (Spawning)
1960	188	11	—	199	,,	May 30 ,,
Total	632	260	15	907		

the original species perch and roach have found the new environment to their taste as could be expected, while grayling, trout, and also whitefish have been considerably reduced in numbers. The influence on burbot and ide is not known. The possibilities for the spawning of the roach appear to be rather small, if it should be absolutely necessary that spawning take place in the shore vegetation, since so far any kind of grass or sedge vegetation has made its appearance in only a few, very limited areas. The coastal region seems to be extremely sterile. There exist otherwise several shallow regions which are suitable for roach, and there the greatest numbers are regularly obtained in test fishing.

The Storfinnsjön is one of the so-called type lakes of the Institute for Freshwater Research. This implies that the Institute has a long-term program for its examination aiming at the study of the results of the regulation of a water, in this case the damming of a valley transforming it into a great reservoir. Only lakes which have been or will be regulated are considered as type lakes. In the case of the Storfinnsjön the program foresees a continuation of the sampling for some years to come, since there exists no doubt that the situation is still far from stabilized, but belongs perhaps still to the so-called damming-up phase or to the following that usually implies a decrease in the rate of growth of the fish, created by a population which is too large in relation to the available amount of food.

Up to now 907 scale samples have been taken and analysed in the lake. The capture has taken place with gill nets in the years 1955—60 (see Table 30), and in the course of the last two years spawning fish have been caught.

The damming-up of the reservoir had the following course:

1953	1st April	243.20	metres	(unregulated, damming-up started)
	1st May	258.73	,,	
	1st June	266.72	,,	
	1st July	272.10	,,	
1954	1st April	272.40	,,	
	1st May	272.11	,,	
	1st June	272.74	,,	(damming-up essentially terminated)

The above shows that already in July 1953 the damming-up had reached the level which since then is the normal one, with small deviations caused by the drawing down in the course of the day which only implies a lowering of the surface of the water by some metre. In contrast to what is the usage in German "talsperren" the surface of the water is never lowered enough so as to expose large parts of the bottom of the lake, but only the very topmost part of the shore zone is exposed.

The damming-up drowned great areas of forest with the smaller lakes and tarns situated in them. In this case two minor tarns have been entirely covered by the dammed-up water. The subsequent analyses of the age of the fish proved that at least one of these tarns must have contained a population of roach which later formed part of the population of this fish in the Storfinnsjön reservoir. It is likewise known that roach occurred in the highest, quietly running reaches of the former river, and that nothing could have prevented these roach to invade the reservoir.

The analysis of the scales very soon showed that the scales could be referred to three categories, in the following called A, B, and C. There existed one type in which the rate of growth had been very poor, of the same type as in the stunted population of Lake Halmsjön prior to the first poisoning, and another with as a rule great age and good growth, entirely unlike that of the stunted fish. At last there existed a third type which, after being scantily represented at the beginning, became increasingly dominant. It comprised the year classes 1953 and 1954, and must according to all indications, be the result of spawning in the new reservoir. By its good rate of growth from the first year of life onwards the last type differed entirely from the other two. The three types are thus:

A = small-sized, of the type of stunted populations, presumably derived from one of the tarns,

B = large-sized and old, from the river in the upper part of the present reservoir, and

C = fast-growing, born 1953 and 1954, presumably resulting from spawning in the reservoir itself, parents A and/or B.

Fig. 8 represents the quantities of the three types of roach in different years of catch, expressed as percentages of the total catch. During the later years, when A and B had gradually died out or in some other way been eliminated from the total population of roach in the Storfinnsjön reservoir, C has occupied an increasingly dominant place in the catches. If the aberrant year 1956 be disregarded, the tendency in Fig. 8 is quite obvious. The course of the curves for 1956 can probably be explained in the following way. In this year altogether only 37 scale samples have been taken, and in spite of the fact that they have been taken in the same places as all the rest, but in this year exclusively with the two greatest sizes of mesh (12 and 16 v/a), the

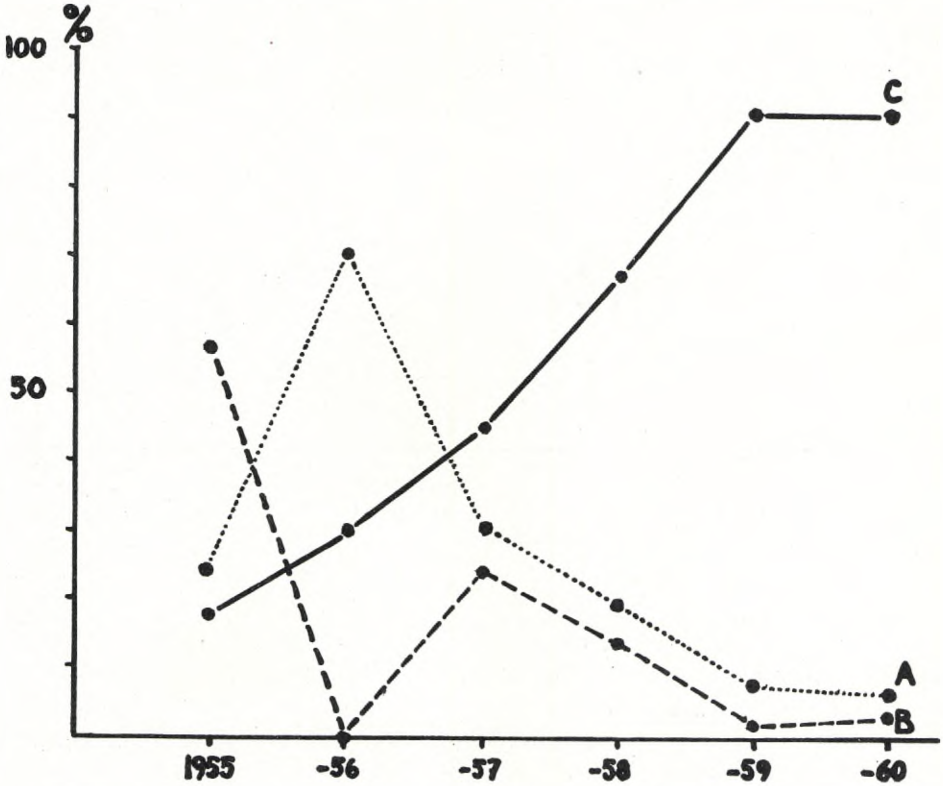

Fig. 8. Percentage representation for different years of catch in the Storfinnsjön reservoir of the three types of roach, A the stunted type, B the large-sized river type, and C the fish born in the reservoir.

uneven distribution is nevertheless most likely the product of chance. The following size of mesh, viz. 18 v/a, catches roach of the size that is in question here. Fig. 8 likewise tells that at the beginning the C-fish represent the fastest-growing individuals, and that selection has decreased some years later only.

Fig. 9 shows the percentages of the different year classes of A, B, and C-fish in the catches of these types. The development of an extremely strong year class in the first year of the damming-up is very characteristic. In this case this class represented 95 per cent of the total number of C-fish, while those of 1954 occurred in an entirely different percentage. As far as can be judged from the analyses of the scales no new year classes have come into existence after these two, but in June 1961 the catching with rotenone and subsequent examination of young proved the existence in the reservoir of year classes that are younger than the two mentioned above, but also the

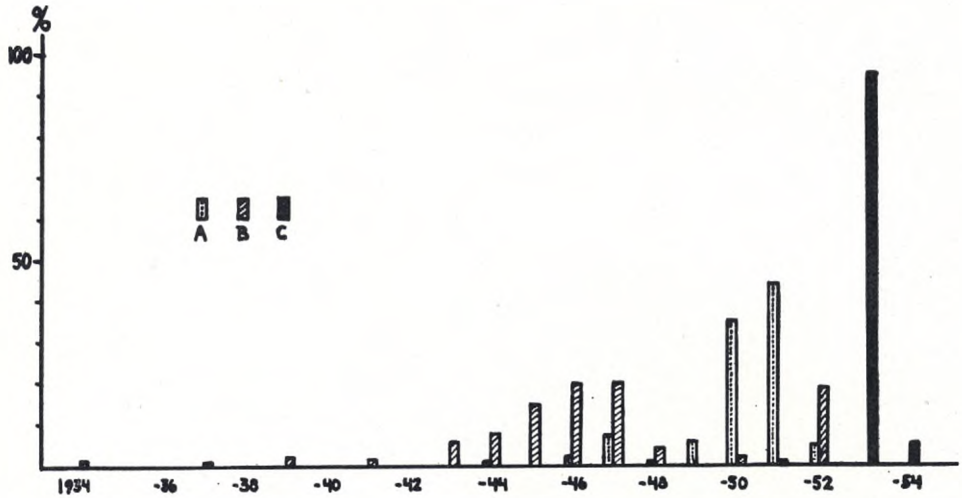

Fig. 9. Percentage of the different year classes of A, B, and C-fish in the catches of these types.

existence of a gap between the earlier and the later year classes. This gap can be explained either by the non-formation or the non-survival of the intervening year classes. The catches of other species, perch and pike, point to similar conditions also in their case. The following reasons could be suggested:

a) The diurnal variation of the water-level, resulting from drawing down at the power plant, which exposed great portions of the shallow bottoms in the shore zone, where the newly deposited roe of the three species, roach, perch, and pike, can not do without water, but certainly dies to the greatest extent. In the most favourable case the year classes will become almost exterminated.

b) The, in the years 1955 to 1957—58, both inclusive, still very numerous representatives of the year class for the damming-up (1953) oppress by their predation the remainders of new year classes that might have succeeded in surviving the variation of water-level, and perhaps exterminate them completely. Presumably the perch are responsible for the greatest share in this predation, but also the pike have certainly been of great importance. The smallest young of the roach have probably become the victims of the perch, while the pike took what was left.

c) The variation of the water-level produces furthermore a sterilized "tidal zone" that is devoid of the protective vegetation which is so essential for the young of the roach. For this reason the environment is always rendered more or less unsuitable to the young of roach, and will remain so. This must exert its influence upon the dimensioning of the year classes as well as upon the growth, wherever the young of roach are rependent upon this unaccessible environment.

If the development of year classes has followed these lines, the tendency in the continuation will be the following. With the increasing dying-out of the year class of the damming-up — this applies to all the three species discussed above — an annually increasing number of representatives of the newly formed year classes will survive, and within a limited number of years the distribution of the year classes of every species will not differ from that found in any other lake. To express it differently, conditions will have become stabilized. But the important diurnal variation of the water-level will continue as long as the power plant is needed, and future will have to show, what will be the effect upon the development of the fish populations. It is imaginable that the dimensioning influence of the changes of the water-level will lead to a population of big and old, but relatively few roach. When the great number of perch and pike have reached more normal proportions perhaps this reservoir, after having been what WUNDSCH (1949) calls a "Weißfischfrage", will develop into a type of lake, where planktonic species find the best conditions or at least are not completely subdued by that terrible couple, perch and pike. It has to be kept in mind that occasionally isolated whitefish are still caught, and it is imaginable that some species requiring a relatively low temperature of the water might develop a population in the downstream situated part of the reservoir, i.e. near the dam. The problem of introducing another, maybe new species has actuality, since the inhabitants of the region, thinking even pike to be a fish of not much value, do not fish at all in the lake. (In case the Storfinnsjön were situated in the neighbourhood of a bigger town in southern Sweden it would soon be completely invaded by eager amateur fishermen). The choice of a new species has perhaps to be determined also by considerations about the future development of the fish population existing in the reservoir at the present time. It has already been mentioned that there exists no certainty that the roach will be equally numerous also in the future. In this case it will not serve as the standard food of a new species which perhaps will have to share these roach also with perch and pike. Therefore the new species ought to be able to act as predator at least towards the perch, and also to seek food at the bottom. Its spawning should take place preferably in regions that do not form part of the customary stations of the perch.

If only the first developmental phase is considered, this reservoir ought therefore to be termed a "Cyprinidensperr", but might later on turn into a "Salmonidensperr", since it can never become an eutrophic lake as long as no new measures for the improvement of the trophic level are taken. It might be said that the reservoir has been eutrophic during a very short time immediately after its formation, but this eutrophism was false and temporary. The explosive increase of roach, perch, and pike was no unnatural

Table 31. Length increments of the year 1953 expressed as percentage of the total lengths of the year 1952. Roach of the two types A and B (for explanations see p. 80) from the Storfinnsjön reservoir.

Type	Length increment (%) at age									
	1	2	3	4	5	6	7	8	9	10 years
A	(65)	98	71	57	34	43	33	—	—	—
B	(112)	—	40	—	13	14	10	8	6	7

phenomenon, but a natural transition towards the natural population of fish in the "lake" as WUNDSCH says in his paper about German dams of 1949. (The expressions "Cyprinidensperre" and "Salmonidensperre" have been coined by SCHRÄDER, 1956). The final cause of the explosive development of the different species lies in the reduced intraspecific competition between the newly introduced (newly hatched) fry which of course are not as numerous as the fry in a stable population of fish (SVÄRDSON 1949 p. 115). The fact that the explosion has yielded not more than one large year class is due not only to the keen competition for food of the classes of 1953 and 1954, but also to a certainly very heavy predation on the later year class from the year class 1953 of perch that also was very strong. (The pike hunted both roach and perch in unknown proportions). Presumably perch as well as pike have influenced both the own species and each other in exactly the same way so that their occurrence as damming-up class is the same as for the roach.

When the growth of the three groups is taken into consideration, the greatest interest attaches itself to the change in the rate of growth in A and B in connection with the erection of the dam, and as far as C is concerned to an attempt at comparison in order to find out, whether the growth of the group has been exceptionally good or more normal.

Fig. 10 shows that the small-sized A-roach have undergone a very strong change of the yearly increments. Starting with 1953 a distinct raise of the curve for the growth of every year class occurs, and this better growth continues for some, before the curve begins to fall again. Table 31 illustrates the increase of growth for the calendar year 1953 in percentages. As has been the case in Lake Halmsjön (see Table 28) also here the youngest year classes account quite naturally for the greatest increase.

During the year of the damming-up, 1953, also the big-sized B-roach (Fig. 11) exhibit an increased rate of growth, which is, however, not at all as marked as for the A-type. For the next years to follow the growth curve show a feeble rise which is, however, of shorter duration than for the small-sized, and since the B's were old and large-sized already at the beginning, it would have been more peculiar, if the amelioration of the growth had

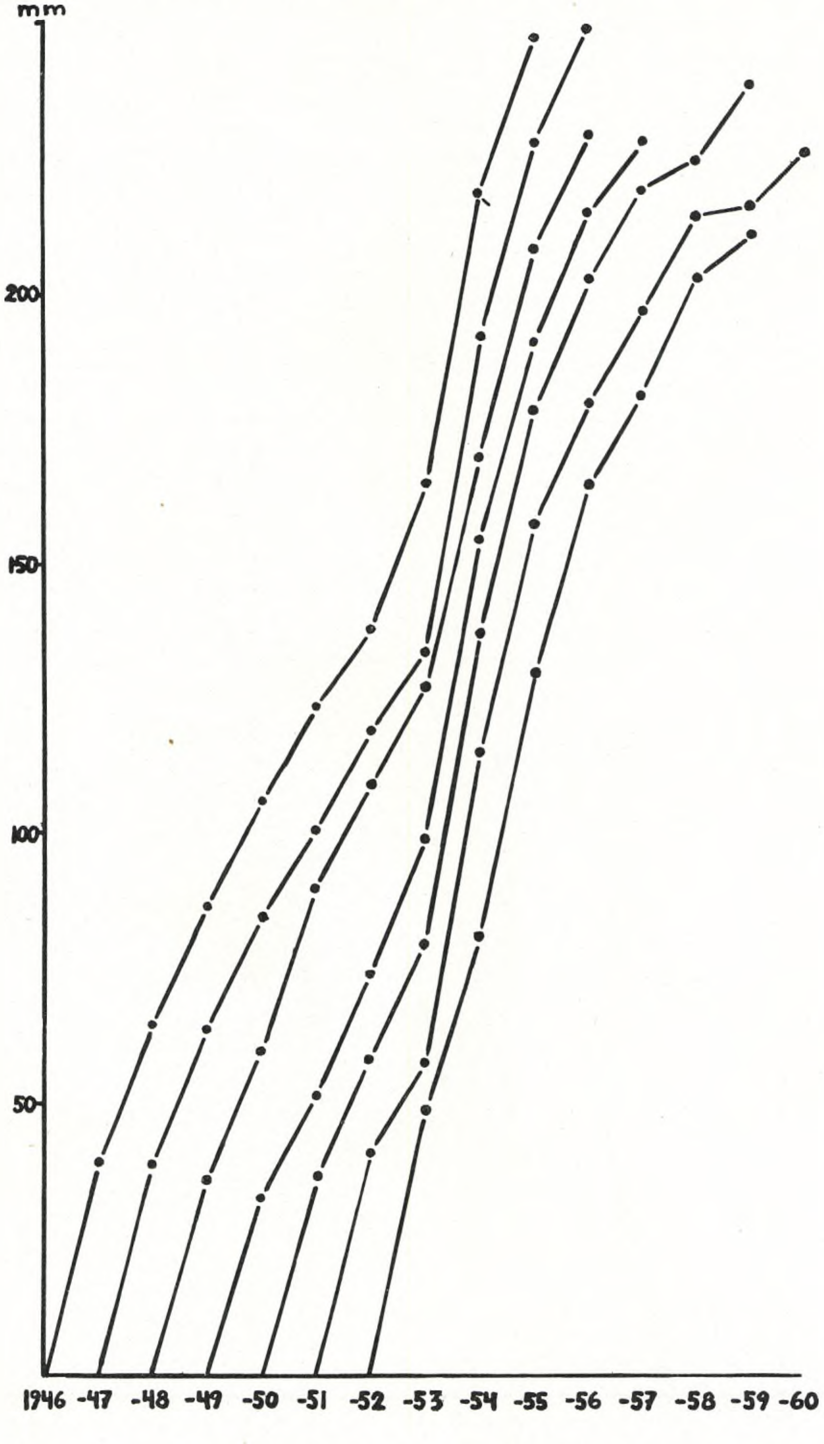

Fig. 10. Growth curves of the year classes of roach of the A-type, viz. the stunted population, showing the marked increase of growth rate in the year 1953.

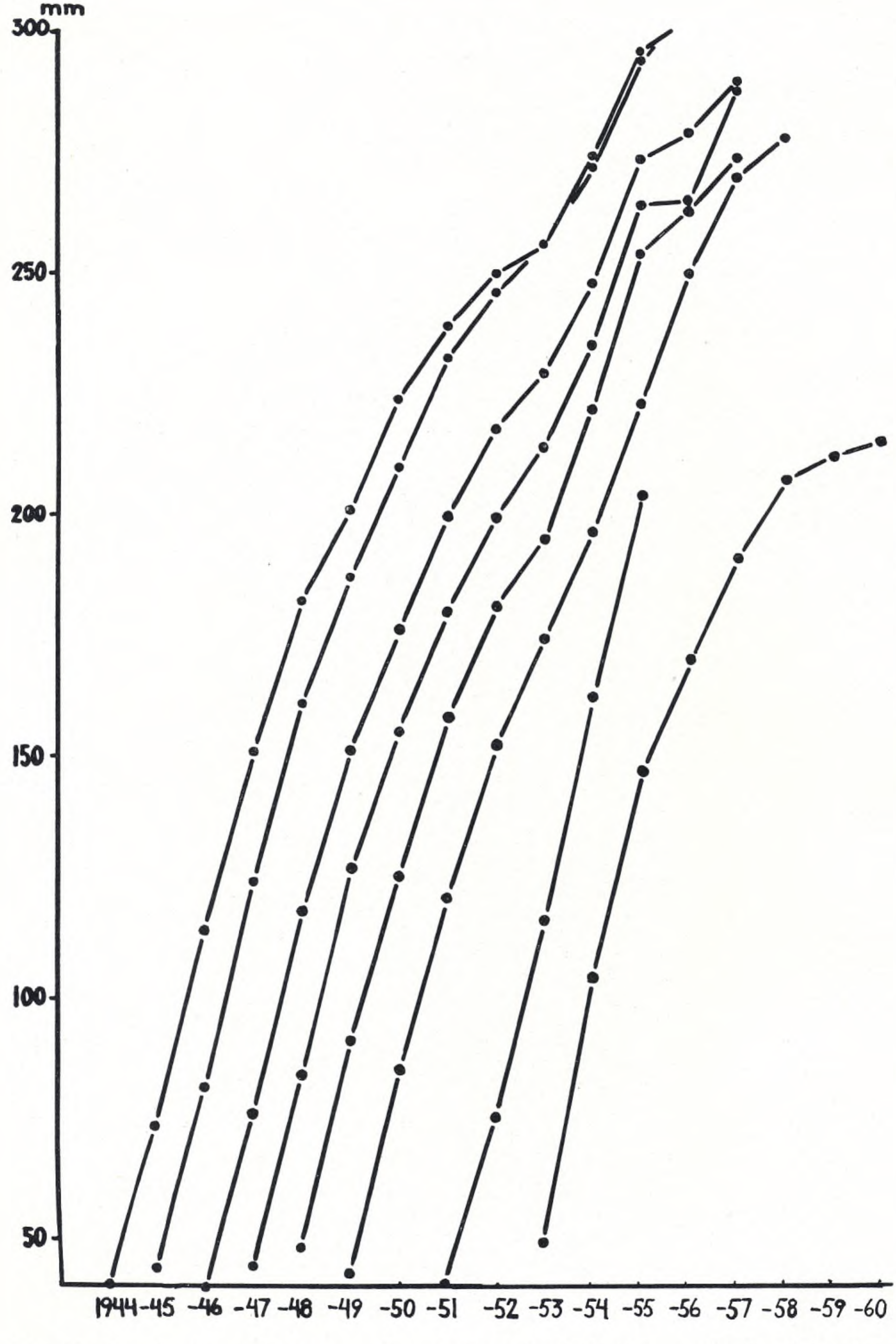

Fig. 11. Growth curves of the year classes of roach of the B-type, viz. the fishes from the river, showing no distinct increase of growth rate in the year 1953.

Table 32. Growth of the three types of roach in the Storfinnsjön reservoir. Growth as mean lengths at age. It should be observed that for the types A and B the growth is calculated from the time before the damming-up of the reservoir.

Type	Mean lengths in millimeters at age									
	1	2	3	4	5	6	7	8	9	10 years
A	39	59	81	101	120	134	156	—	—	—
B	44	83	122	155	180	199	220	236	254	263
C	51	90	117	137	155	166	190	—	—	—

continued for many years. Table 31 also shows that the increase in the percentages of which the B-type was capable differs essentially from that of the A-type. The explanation of this fact must have its base in the circumstance that for the B-roach the establishment of the reservoir did not imply any marked amelioration, of the food conditions, the youngest members of the B-group not exhibiting the same good increase as A-roach of the same age. In this case the food conditions perhaps comprise both the type of available food and the competition for it.

During the very first years the C-roach born in the reservoir grew faster than the B's, but later (Table 32) they soon began to lag behind, and at the age of seven years their length amounts to an average of the lengths of A and B at the same age (prior to the construction of the reservoir). The growth is very good in C especially during the first two years, but at the age of four years it is B that has a much steeper curve indicative of better growth. The probable explanation is that the originally not overlarge population (C) by the increasing impoverishment of the littoral after some years, without an increase in numbers, has become increasingly larger in relation to the available amount of food, and that this has caused the curve of growth to become increasingly flatter.

The material of the A- and B-fish did unfortunately not permit the following-up of the variations of growth during several calendar year before and after the damming, and with the existing distribution of the year classes of the C-roach no relative growth can be calculated here, neither is it possible to study the changes in the rate of growth. If this had been feasable, interesting comparisons between the growth of the fish in the Storfinnsjön reservoir and lakes that have been dammed-up and are used as sources of water power could with certainty have been made. The effect of damming upon char and brown trout has been discussed especially by Runnström (1951, 1952). He has found an initial increase in the rate of growth which later gives way to a decrease. This decrease has led to dwarfing in the case of the char, while the populations of brown trout have been markedly reduced in numbers. This effect of the damming-up can be traced also in the Stor-

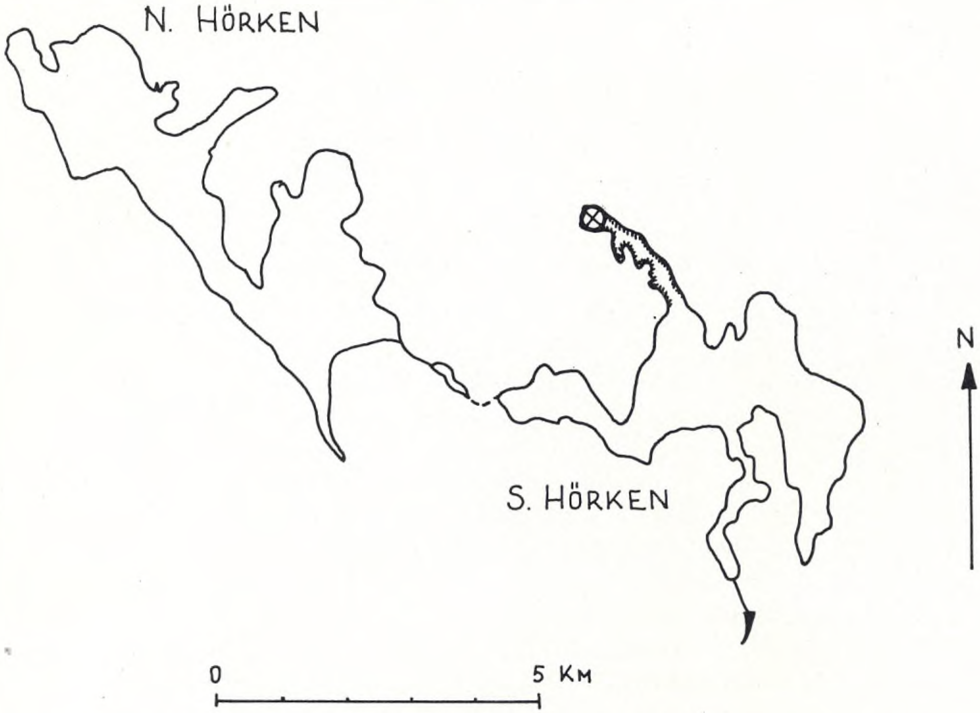

Fig. 12. Lakes N. and S. Hörken. The circle with a cross within it marks the place where the sewage is let out. The dots mark zones of reeds.

finnsjön reservoir, at least as far as the first momentary increase of the growth of the B-fish is concerned. It is still too early to express an opinion about the future development of the population of roach, but, as pointed out above, it is imaginable that the destruction of the uppermost parts of the littoral will result in a relatively small population of big roach with fairly good growth. (Remark the parallel with the brown trout which is also tied to the littoral, and for which it is known that regulations of the water cause damage of the bottoms with suitable food animals and of its spawning places.)

It is thus obvious that this damming-up of the reservoir has initially created a situation which considerably improved the conditions regulating the growth of the roach, but the examined scale material does not yet permit any assertions concerning the interaction between the impoverishment of the topmost bottoms of the littoral, and the destruction of the localities for spawning and fry will lead towards a minor population of relatively big roach.

Also the causes of the development of a very dominant year class from the year of the damming-up is discussed together with those responsible

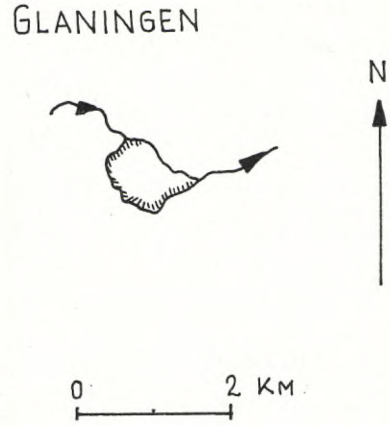

Fig. 13. Lake Glaningen. The dots mark zones of reeds.

for the fact that no new year classes have been formed during several years. It is most likely that among the three fishes, viz. roach, perch, and pike, the perch will get the upper hand, both on account of its ability to spawn also in deeper water, and the great rapacity of the species. To this must be added the circumstance that the young of perch is less dependent than that of roach and pike upon the cover provided by an overgrown coastal zone during the earliest part of its life.

C. In two heavily fertilized lakes, the Södra Hörken and the Glaningen

The Södra Hörken covers an area of ca. 9 sq.km., has a depth of a little more than 20 m, and has originally been oligotrophic. The neighbouring Lake Norra Hörken is oligotrophic, and has up to very recent times been connected with Lake Södra Hörken by a channel permitting free passage of the fish (Fig. 12). The small Lake Glaningen (Fig. 13), without any connection with the Hörken lakes, covers an area of 0.72 sq.km. and has a depth of less than 5 metres. Its earlier trophic level is unknown. Lakes Södra Hörken and Glaningen have been heavily fertilized by industrial sewage containing nitrates and phosphates, and deriving from the handling of ore at Grängesberg. Table 33 gives the amounts of fertilizing salts released into the different lakes in the course of the seven years during which such release has taken place. All data except those referring to the roach have been taken from VALLIN (1960).

VALLIN's analyses of the chemistry of the water as well as of the biological conditions in the lakes show that in Lake Södra Hörken a considerable accumulation of nutritive salts takes place also rather far off shore. (In this lake the release is effected inside the sign of cross and circle in Fig. 12.) Even farther towards the centre of the lake the concentrations decrease rather

Table 33. The approximate release of the sewage-water containing nitrogen calculated as HNO_3 and phosphate as P into the Lake Glaningen and the Lake Södra Hörken.

Year	To Lake Glaningen		To Lake S. Hörken	
	Acid in tons HNO_3	Phosphate in tons P	Acid in tons HNO_3	Phosphate in tons P
1949—50	691	41.4	340	20.4
1951	350	21.0	437	26.3
1952	645	38.7	805	48.3
1953	765	45.8	955	57.2
1:st halfyear 1954	2128	127.8	304	18.2
2:d ,, 1954			—	—
1955	3185	191	—	—
1956	3379	203	—	—
1:st quarter 1957	1300	78	—	—
2—4 ,, 1957			627	38
1958	2353	141	124	7.5
1—3 quarter 1959	585	35.2	31	1.8
Calculated for 1959	950	57	50	3.0
,, 1960	950	57	50	3.0

slowly, but there occurred a noticeable drop during the interruption of the release in the years 1955—56 (Tab. 33). The decrease of the value for NO_3 is, however, less pronounced, and in 1956 the contents were still 2—3 mg against 7—12 mg in July 1959. For the water in an uninfluenced lake the probable value lies in the neighbourhood of 1.0 mg. The salts are accumulated especially in the water near the bottom. During interruptions or reduction of the release of sewage-water into the lake the production of algae has diminished very quickly and thoroughly, this reduction being indicated by the values for pH and O_2 in the surface water, and the transparency. On several occasions in the course of spring and summer very high pH, sometimes exceeding 10.0, have been measured in the surface water in connection with an intense production of algae, the amount of oxygen rising simultaneously to 200 per cent of saturation. The transparency is great in late autumn and winter, while in spring and summer of years with more abundant release low values of 1 metre and less have been recorded both in the open water and in the bay, where the sewage was discharged. During the interruption of 1955—56 high values for the transparency have been measured. Subsequently it again decreased strongly and quickly all over the lake, indicating an intense algal production. No critical values for the content of oxygen have been obtained in the open water, but well in the inner part of the bay, where the release takes place.

The examination of a great number of qualitative as well as quantitative samples has shown a distinct effect of the over-fertilization with nutritive salts upon the composition of the plankton. Some of the original forms have disappeared completely or almost completely, while others have increased. Some forms which are typical for over-fertilized waters, in part forms from ponds, appeared dominant even in the open water. The rich production of algae has produced also an algal gyttja rich in nutrition and, in combination with it, a greatly increased production of the bottom fauna. A small mussel, *Sphaerium,* has appeared in great masses in the littoral and different larvae of chironomids also at greater depths, both types being of importance as fish food.

In Lake Glaningen extremely high values for PO_4 and NO_3, up to 20 and 530 mg/l, respectively, have been obtained, especially in the years 1955 and 1956, when the release into this lake was at a maximum. The plankton has been dominated all the time by types which are characteristic for very strongly fertilized waters, e.g. duck ponds, etc. At the time of sampling the pH exceeded 10 in the summers of 1953, 1956, and 1957.

The higher vegetation shows that fertilizing has occurred in the inner parts of the bay of discharge in Lake Södra Hörken and in Lake Glaningen, while in the open water of Lake Södra Hörken no more noticeable effect upon the higher vegetation could be observed.

The population of fish prior to the fertilization was in Lake Södra Hörken: pike, perch, pike-perch, whitefish, cisco, smelt, roach, and burbot, in Lake Glaningen: pike, perch, and roach together with crayfish. Lake Glaningen contained very numerous pike and large roach already in the 1940's before the start of the release of sewage-waters. The roach in Lake Södra Hörken is said to have been rather scarce 30 years ago, but has gradually increased in numbers, and is now considered to dominate the fish population.

By means of the introduction of lime and neutralization in addition to aeration it has been possible to preserve in Lake Glaningen a population of fish in the winters, when critical oxygen values started to appear.

VALLIN is of the opinion that the great production of algae in Lake Södra Hörken and Lake Glaningen is attributable to an essential degree to the released industrial sewage-water with its high contents of nitrates and phosphates. He likewise believes that the introduction of nutritive salts has brought about a great increase of the fish population in Lake Södra Hörken which is of great importance for the domestic fishing carried on by numerous persons. For this reason he is of the opinion that the release of nutritive salts ought to be continued, let be on a reduced scale, so as to prevent a more inconvenient production of algae. With regard to Lake Glaningen he suggests that the release of sewage-water should cease altogether, the fish population of the lake with its complete dominance of roach being without any value whatsoever from the fisherman's point of view.

The fertilizing of lakes has been carried on in several continents with varying results. The following discussion of the results obtained by the introduction of fertilizing substances into a water will keep no account of all the papers dealing with the rearing of fish in ponds, where it could be hoped to control the development of the process of fertilizing in a much more efficient way.

As a rule in the attempts at the fertilizing of lakes some type of trade fertilizer, i.e. artificial substances has been used. Although the results have been varying, at least a plankton bloom has in general been obtained.

In one of the fertilized lakes BALL (1950) obtained a plankton bloom and says: "From these experiments it appears that by artificial enrichment a trout lake can be so altered that its characteristics approach those of a eutrophic, or a warm-water fish lake."

BALL and TANNER (1951) have studied the effect of fertilizing substances upon a warm-water lake, and have found a distinct increase of the plankton after every fertilization and, probably a great increase of the bottom fauna, no figures being available for the time before the fertilization. No difference could, however, be detected in alkalinity or pH, neither a lack of oxygen either in summer or winter. In the summer after the fertilization no plankton bloom, comparable with that of the preceding year, was found.

EGUCHI, KUROHAGI, YOSHZUMI, and SASAKI (1954) found the plankton to increase soon after fertilization with superphosphatet and ammonium sulphate.

MACIOLEK (1954) studied the existing literature up to 1953, and concluded with the statement that in most cases the fertilizing agents produced an obvious and distinct effect upon lower organisms and also upon plants. In several cases a winterkill resulted from a powerful increase of the phytoplankton, and he was not sure that the fertilization has actually increased the yield of fishing. Frequently unsatisfactory examinations into the status of the fertilized lake before fertilization.

NELSON and EDMONDSON (1955) found a fast decrease of transparency after the fertilization, though there had been no such decrease prior to it. Phosphate and nitrate disappeared very quickly due probably to the greatest extent to absorption by the phytoplankton, higher plants, and bottom sediments. Compared with the ten days preceding the fertilization photosynthesis was found to increase 2.7—7 times during the ten days after the treatment. Also the population of phytoplankton increased by many times after every fertilization, the transparency dropped from 6 m to less than 2 m, the lake being situated far north in Alaska, the pH increased from 7 to more than 9, and phosphate and nitrate sunk within a few days so much that their presence could no longer be detected!

Weatherley and NICHOLLS (1955) studied a fertilized lake with low natural productivity in Tasmania, and found a very strong increase of the zooplankton, mostly copepods. Myriophyllum became high and also the phytoplankton increased as well as the epiphytic fauna. They assume that the stimulating effect upon plants and plankton was due to the phosphorus.

Table 34. Number of age-analysed scales of roach from the two fertilized lakes S. Hörken and Glaningen and the non-fertilized Lake N. Hörken.

Year of capture	Lakes and number of investigated scales		
	N. Hörken	S. Hörken	Glaningen
1955	7	44	111
1957	6	71	18
1961	—	111	71
Total	13	226	200

The examinations into the growth of the roach are based upon material from the two fertilized lakes Lake Södra Hörken and Lake Glaningen, and from Lake Norra Hörken (Table 34).

For the reading of the scales, etc. the methods have been used that have been accounted for above (p. 44) in connection with the age-analyses of roach in Lake Mälaren.

The scale material from *Lake Norra Hörken* is exceedingly small, and the conclusions obtainable from the results of the age-analyses supply information only about the general rate of growth of the examined fish (Table 35). It seems to be rather normal for a lake of this character, and poorer than in Lake Mälaren. The scale material from Lake Norra Hörken has been collected exclusively in order to permit comparisons with the growth of the roach in Lake Södra Hörken, since at an earlier date the populations of roach in the two lakes have probably had very similar rates of growth.

Some of the scale samples from *Lake Södra Hörken* show that the roach have grown very fast (Table 36), but there exist also scales indicating a rate of growth which is closer to that found in the roach of the neighbouring Lake Norra Hörken that had been connected with Lake Södra Hörken. At last there exist scales which prove that some of the fish have experienced a strong increase in the rate of growth. These fish are in the following termed immigrants. On account of the small quantity of the scale material it has not been possible to calculate the relative growth in the course of the calendar year. Such a calculation would have been very desirable as it would have permitted the establishment of a correlation between the growth and the quantity of the released nutritive salts. It would, e.g., have been interesting to find out how, or whether or not, growth has been influenced by the

Table 35. Mean lengths at age of capture for roach from Lake Norra Hörken.

Age	4	5	6	7	8	9	10	11	years
Mean lenghts	140	145	155	160	170	195	183	205	mm
Number	1	2	2	1	1	1	3	2	

Table 36. Mean lengths at age of the three types of growth exhibited by roach from Lake Södra Hörken. The sign '=' means the first great growth-increment that differs clearly from the earlier growth.

Type of growt	Year class	Num ber	Mean length in millimetres at age											Year of capture
			1	2	3	4	5	6	7	8	9	10	11 years	
Fast	1953	32	62	118	(184)	—	—	—	—	—	—	—	—	1955
	1953	33	62	110	164	198	(234)	—	—	—	—	—	—	1957
	1954	15	50	108	155	(193)	—	—	—	—	—	—	—	1957
	1955	17	64	114	(157)	—	—	—	—	—	—	—	—	1957
	1955	1	63	106	155	187	239	260	(—)	—	—	—	—	1961
	1958	103	53	117	141	(—)	—	—	—	—	—	—	—	1961
Slow (for example)	1953	1	39	62	103	122	131	136	149	152	(—)	—	—	1961
"Immi-grants"	1945	1	45	75	101	126	139=	195	250	282	316	344	(360)	1955
	1949	1	41	62	82	99	121=	206	(280)	—	—	—	—	1955

reduced quantity of sewage-water released in the years 1955 and 1956, and by the soon after following reduction of the production of algae. Under the existing conditions interest is restricted to the rate of growth which could be calculated from the analyses of the scales. Compared with the fish which had a good rate of growth those with poor growth, but caught in Lake Södra Hörken constitute a clear minority, representing only 10 per cent of the total number of analysed samples. To them have to be added 3 individuals of immigrants.

Table 36 does not permit to discover, in the course of the years, when the release of nitrates and phosphates has been large or small, among the roach which have been placed under the "heading" "fast" any tendency towards better or poorer growth. The 103 roach from year class 1958 are somewhat smaller than the rest, and in the course of the immediately preceding years the release (Table 33) had been nil or inferior to that of the introductory period. In the course of the following year the quantity of nutritive salts has been relatively very small. According to Vallin (1960) also for perch and pike, the growth has been very good in the lake, but only very young fish have been caught throughout, 3, 4, and 5 years old, and this is less common with roach with a normal rate of growth.

The fishing has been carried out with the assortment of mesh sizes commonly used in test fishing at our Institute. For this reason we are probably not facing a problem of selection only, as in this case the catches also of the later year 1961 ought to have contained representatives for the older year classes. It seems as if the year classes 1953, 1954, and 1955 had disappeared from the lake at a relatively low age, connected possibly with their fast growth. In any case no organized fishing for roach has taken place in Lake Södra Hörken, and the sample fishing of the Institute has yielded no more roach than are accounted for in this paper.

The occurrence of the few specimens belonging to the "slow" group is somewhat peculiar, and can hardly be explained otherwise than by the assumption that they have, in the year of capture, migrated from Lake Norra Hörken into Lake Södra Hörken, passing through the above-mentioned channel, and that on this account they had not yet had time to adjust their rate of growth to what it ought to be in the new environment. On account of the great increase of the plankton everywhere in the lake as established by VALLIN (1960) it seems less probable that these slowly growing roach should have come from some of the most distant parts of Lake Södra Hörken.

Those roach at last which have been termed immigrants exhibit exactly the great increase in the rate of growth to be expected of fish which quite suddenly enter an environment that differs widely from the previous one in the amount of available food. For the younger roach the increase amounts to 70 per cent, for the older to 40 per cent, both figures being fully comparable with the increases shown by roach of the same ages in Lake Halmsjön and the Storfinnsjön reservoir at the transition to a reduced density of population.

In *Lake Glaningen,* at last, roach has been represented up to the very last years by a single year class only, viz. that of 1950. In the course of the intervening years no representatives of possibly formed year classes have survived. Not before 1958 there appears a greater number of individuals which are found in the catches of 1961, like those of 1959. On the occasion of his visit to Lake Glaningen in the spring of 1961 for the purpose of collecting material the author of this paper observed a very great number of small fish which must have been young of roach of the preceding year, i.e. of the year class 1960. It also seems as if in the course of the last years new year classes should have come into existence, and in this case this must be due to the altered environmental conditions. As already mentioned, pH had a very high value in the summers, and has most probably been responsible for the non-appearance of year classes. On July 15, 1958 a pH of 9.8 has been measured. According to the figures given by VALLIN the highest value for pH in 1959 was 8.0 (one May 15), while on July 14 7.4 has been recorded. According to a verbal communication by VALLIN the values observed in the course of sampling in May—July 1960 were at most 8.0, while in June 1961 a pH of 10.0 has been recorded. It has proved impossible to visit Lake Glaningen in the spring of 1962 in order to find out, how especially the year classes 1960 and 1961 had survived this high pH which occurred simultaneously with an intense plankton bloom, a transparency of 0.4 m and saturation values for oxygen of about 180 per cent.

It is not very probable that the non-appearance of the year classes is due to the extremely small numbers of perch and pike.

The older roach of the year class 1950 have at all events survived as long as to the spring of 1961, and if the mortality of the young should have been

Table 37. Growth of roach from Lake Glaningen.

Year class	Year of capture	Number	Mean length at age											
			1	2	3	4	5	6	7	8	9	10	11	12 years
1950	1955	111	61	113	169	207	255	(281)	—	—	—	—	—	—
1950	1957	17	61	117	175	200	259	286	308	(327)	—	—	—	—
1950	1961	22	58	108	164	208	257	288	310	330	340	352	364	(—)
1956	1957	1	59	(120)	—	—	—	—	—	—	—	—	—	—
1958	1961	23	54	143	190	(—)	—	—	—	—	—	—	—	—
1959	1961	25	90	135	(—)	—	—	—	—	—	—	—	—	—

caused by the high pH, it seems as if adult roach should have different limits of tolerance or at least be less sensitive instantaneously and capable of surviving a short period. (The turnover of the water in Lake Glaningen being fast, these extremely high values for pH may not last very long.) Previously the growth of these now very big roach has been very good, but has dropped gradually in the course of the last years (Table 37). Among the 22 roach caught in 1961 the biggest was 394 mm long, the smallest measured 323 mm, the heaviest specimen weighing almost 1 kg. These big roach did not seem to be rare, since they have been caught during a single night in two nets only. For all ages of the roach growth in this lake has been far above normal. The reduced rate of growth of the older roach is certainly due to the circumstance that they approached the genetically determined upper limit for the size of roach which seems to lie in the neighbourhood of 400 mm. MARRE (1932) gives some information about and references to big roaches, and also OTTERSTRØM (1930) has reported about roach of this size. These large fish in Lake Glaningen have presumably not suffered from any keener competition for food, since, with the exception of an extremely small number of perch and pike, there exist no other species, and since the population of roach has increased during the very last years only. These young roach have not yet changed over to the diet of the big ones. It thus seems probable that the decrease in the rate of growth should be due to an approach to the maximum size of the species. On account of the feeble competition for food it is not easy to state with certainty that the good growth at least in earlier life depended wholly or in part upon the rich production of food organisms in Lake Glaningen.

With regard to VALLIN's information about the earlier occurrence of big roach in the lake, prior to the introduction of nutritive salts, but also to the high production of algae, etc. which has been established, it is perhaps most correct to conclude that the growth of the roach has at all events been favoured by the fertilization, but it must also be pointed out as extremely probable that the possibly occurring absence of intra- and interspecific competition for food has in this case had a considerable share in the favourable result.

Table 38. Calculated or attained lengths at the ages of 5 and 8 years in the different lakes treated in this work.

Lake	Mean length in millimetres at age	
	5 years	8 years
Södra Hörken	234	— (282 for an immigrant)
Glaningen	255	327
Norra Hörken	137	165
Mälaren	161	199
Storfinnsjön reservoir	152	(200)
Särnasjön	114	148
Halmsjön	99	135

Table 38 contains a comparison between the sizes of fish of 5 and 8 years in the lakes treated in this paper. In the two fertilized lakes the rate of growth very much exceeds that in the others.

The previously quoted papers on experiments with fertilization on a large scale contain of course also information about the results with regard to the growth of the fish, etc.

BALL (1950) found that before the winterkills that followed upon fertilization during two summers the fertilization had a favourable influence upon the growth of the fish. He mentions, however, the possibility that reproduction was unfavourably affected, obviously first of all by the increased production of filamentous algae which hindered the fish (amongst others *Salomonidae*) in spawning.

BALL and TANNER (1951) are inclined closely to connect the intensely significant increase in the rate of growth with the great increase of the bottom fauna forming the food of the fish. The summer after the fertilization produced no plankton bloom comparable with that of the preceding year, but the fast growth of the fish introduced after the winterkill is ascribed to the good supply of food. The increase in the rate of growth applied to all gamefish with the exception of the one-year lengths of two species.

In the lake in Alaska examined by NELSON and EDMONSON (1955) these authors found that during a sequence of years the emigrating salmon became bigger, presumably in response to an increased store of food.

After the introduction of a trade fertilizer SMITH (1955) found a significant increase of the rate of growth of *Salmo fontinalis* MITCHILL, and that this increase lasted for 2—3 years after the fertilization. After control of predators, renewed fertilization, and fresh implantations the catches per hectare increased, while at the same time the increased density of population brought about a slowing-up of growth.

Also WEATHERLEY and NICHOLLS (1955) affirm the increase in the rate of growth of the fish. Also fish implanted later shows the same reaction, but they suppose that the expected, but non-appearing rise in the rate of growth is due to the increased density of population. At all events a distinct increase.

For the same lake in Alaska NELSON (1959) found as the most important result of the fertilization an increase in the size of the smolt, and that this increase was perhaps the reason of an increased return of the emigrated fish. No similar increases were observed in a nearby, unfertilized lake during the period of the experiment.

In the case of Lake Södra Hörken there is no doubt that the increased rate of growth is the result of the fertilization. This receives additional support by the reaction of the immigrants on confrontation with the new environment. In Lake Glaningen, however, the real reason is certainly to be found not merely in an increased production of fish food, but perhaps also, and in an equally high degree, in a size of population which had not formed the least obstacle to the very fast growth.

In many of the fertilizing experiments in foreign countries no influence upon the fish could be traced (MACIOLEK 1954). In several of these experiments the fertilizers have been introduced once only, and for this reason the non-appearance of any reaction on the part of the fish might possibly be ascribed to an insufficient quantity of fertilizer. In all cases referred to here the plankton has increased, but it has also been shown that this increase is of very brief duration and can not be observed in the season following that of the fertilization. A single fertilization in one year thus produces no noticeable effect upon the fish provided the latter has not succeeded in benefitting from the increased production of this single year, especially if only a small quantity of fertilizer has been introduced. The distinct increase of the rate of growth in Lake Södra Hörken is certainly the result of a powerful fertilization with very great quantities of nutritive salts together with their introduction during many years.

The "experiment", accounted for here, and others referred to show that the effect of the fertilizing substance is of brief duration, even if, as in Lake Södra Hörken and Lake Glaningen the amount of nutritive salts has been immense in comparison with the economic possibilities of the usual measures taken in the interest of fishing, and that for obtaining a lasting effect upon the growth of the fish we shall have to calculate with fertilization as a regularly repeated procedure as it is the case in agriculture. Even if it should be possible to obtain from the mining industry great quantities of sewage-water rich in nutritive salts, the high cost of transport would prevent the refundment of even a small part of the invested capital, since at the present moment the fishing in the Swedish inland lakes is practically without economic importance.

Diet-dependent growth, a summary of other investigations

There exists a great number of investigations into the dietary habits of the roach. This summary makes no pretension of being a complete reference to the contents of all these papers, since there existed no possibility of exploiting even a small part of the literature of Eastern Europe and Asia, when published in the native languages. Thus the following authors' papers contain information about the choice of food of the roach:

ALM 1917, 1921, 1922; BALON 1956; HUITFELDT-KAAS 1927; JÄRNEFELDT 1921; KARPIŃSKA-WALUŚ 1961; MARRE 1932; NEUHAUS 1936; NORDQVIST 1914; OTTERSTRØM 1930—31; PASCHALSKI 1958; RADFORTH 1940; SCHIEMENZ 1924, 1934; SCHNEIDER 1908; SEEMANN 1960; STANGENBERG 1958; STANKOWITCH 1921; GRAF VON WESTPHALEN 1956.

According to all information the young chooses during the first and second year of life plankton, both zooplankton and phytoplankton, for its food. Particularly among the zooplankton are cladoceres. rotifers, and copepods, represented by forms living in the shallow water of the littoral, and among the phytoplankton epiphytic and planktonic diatoms, *Chlorophyceae* and *Protococcales,* together with threads of *Enteromorpha* and *Ulothrix.* STANKOWITCH has carefully examined the choice of food of the young of cyprinids with sizes of up to 50 mm, and has found rotifers to play the most important rôle for all stages below 16 mm. Later *Cladocera* and also *Copepoda* assume an increasing importance, while that of the *Rotatoria* diminishes.

With increasing size the young afterwards change more and more to vegetable food in the form of filamentous algae, even if especially zooplankton still plays an important rôle. At a size growing above 100—120 mm a gradual transition takes place towards an increasing intermixtion of bottom animals (chironomids, gammarids, trichopters, etc) and detritus, and it seems, as if roughly at this size the roach could start to eat what the locality has to offer. To express it differently, they can exploit the greater part of the lake, and are no longer bound to the shore regions for their survival. According to numerous reports (ALM 1922, JÄRNEFELT, NEUHAUS, SEEMAN, STANGENBERG, and GRAF VON WESTPHALEN) at or above the length of 150 mm the roach are capable of consuming *Mollusca.* In the lakes, where molluscs occur in greater number, this seems to imply a minor revolution for part of the roach. Expressed in general terms the roach that are capable of feeding on molluscs obtain in comparison with the rest an essentially increased rate of growth, and it has been shown that lakes with populations of very big roach always contain a large amount of molluscs. Analyses of the contents of the stomach have shown that the big roach, where occasion existed, had lived almost exclusively on snails and mussels, the genera *Valvata, Bythinia, Dreissenia,* and *Pisidium* being commonly found. The existence of this possibility to change over to another diet certainly furnishes the explanation of the peculiar size distributions that can often be observed in a stunted population of roach, where very small individuals of uniform size form 99.9 per cent of the population, while the remaining 0.1 per cent are of perfectly normal size or even very big. This size distribution can certainly be explained in the following way. First of all the quantity of food available in the lake is too small, and on this account the roach attain in general roughly the same size. Some of these small-sized roach, however, have a genetically determined faster rate of growth, and reach sooner or later the size, when they can suddenly change to an entirely new type of food. viz. molluscs, and since the majority of the roach are unable or will not be able to utilize this new type of food, the competition for it is almost non-existent. This results in a noticeably increased rate of growth of these isolated individuals. The material from Lake Halmsjön that has been dealt with in an earlier part of this paper contained unfortunately only two individuals of roach which had begun to feed on molluscs, but their rate of growth seems to have improved after they had reached a size of 14—16 cm. In lakes with a better supply of food suitable for the smaller fish the entire population normally reaches the limit for the transition to mollusc diet, most of them obtaining a better rate of growth, and attaining in some lakes very great lengths and weights, depending perhaps upon the size of the population of molluscs. In some papers (e.g. NEUHAUS and SEEMANN) the occurrence of very big-sized roach has been reported from the Baltic, and NEUHAUS insists upon that *Mollusca* are eaten not on account of properties inherent in the species, but by reason of their abundant occurrence.

Thus a differentiation in the choice of food, accentuated with growing size, takes place in the fish, and in some lakes the attainment of the limit of 150 mm implies that small fractions of the populations of roach obtain access to a rich and almost unexploited store of food, with obvious consequences for the rate of growth.

Many lakes also exhibit a frequently attested connection between a rich occurrence of Mollusca and very big-sized populations of roach.

Summary

After the examination of some 4.000 scales from roach and using of a new method for the calculation of adult relative growth and relative year class strength, the one-year lengths representing the growth of the young, the growth and the year class strength have been related to some climatic factors, two of which (the temperature and the precipitation) have been shown to exert some influence on the roach. The dependence on density of population, type and amount of accessible food is also discussed. The investigated lakes have been of the following types:

Two natural (not interfered with) lakes, one oligotrophic the other eutrophic and at different altitudes.

Two, where the density of the population has been altered by means of rotenone managment (small eutrophic lake) and damming-up (water power reservoir).

Finally two, which have been the subject of a large-scale fertilizing treatment because of the release of sewage water containing large amounts of nitrates and phosphates, derived from the washing of ore.

There is a positive correlation between temperature and growth, and a negative one for precipitation (found only for the young in the natural oligotrophic lake.

With decreasing population density or increasing area of the biotop of roach the individual fish will grow faster than under former conditions for at least a short period, a few years.

The fertilizing has at least with certainty in one of the lakes given a faster growth not being the normal rate before the treatment, but in the other lake the size of the population might have been responsible for some part of the good growth.

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Baltic salmon fluctuations 2: Porpoise and salmon

By ARNE LINDROTH

Introduction

The populations of Atlantic salmon, enclosed in the brackish water Baltic Sea(see map, Fig. 1) exhibit simultaneous abundancy fluctuations not only of the ordinary year to year type but also of a long-term type with periods of bad catches alternating with periods of good catches as evident from historical documents and, for the last 150 years, statistical records (ALM 1924; LINDROTH 1950, 1957; BERG 1957). These long-term fluctuations seem to be in some way correlated with climatic changes as reflected in, for instance, extent of ice cover in the Baltic (LINDROTH 1950, 1957; SVÄRDSON 1955). The hypothesis has been put forward that the causative agent should be the porpoise (*Phocaena phocaena* L.) proved under certain conditions to suffer from an extensive ice cover and, as presupposed, predating upon the salmon (LINDROTH 1950; SVÄRDSON 1955). As SVÄRDSON put the hypothesis in ultimate wording supplementing it with a pretended effect of the periodical porpoise hunting in the Danish sounds and as he proposed the hunting to be revived on a large scale in order to prove the hypothesis (SVÄRDSON 1955, 1957 a and b) I have suggested investigations on the food of this whale (LINDROTH 1957).

Material and methods

Not until now I have succeeded in obtaining porpoise stomachs for analysis of their contents. By the ready help of fishery officers and fishermen getting drowned porpoises in their gear (mostly drift net for salmon), now 50 porpoise stomachs have been placed at my disposal, one from the year 1960 all others taken in spring, summer and autumn of 1961. Place of capture is indicated on the map, Fig. 1, by serial numbers. Month of capture is as follows.

Nr.	Month
1	1960, Nov.
2—3	1961, March
4—9	April
10—16	May—June
17	July
18—47	Aug.—Sept.
48—50	Oct.

Size and sex were recorded only occasionally. Mean estimated weight of 17 specimens was 60 kg (range 40—100 kg).

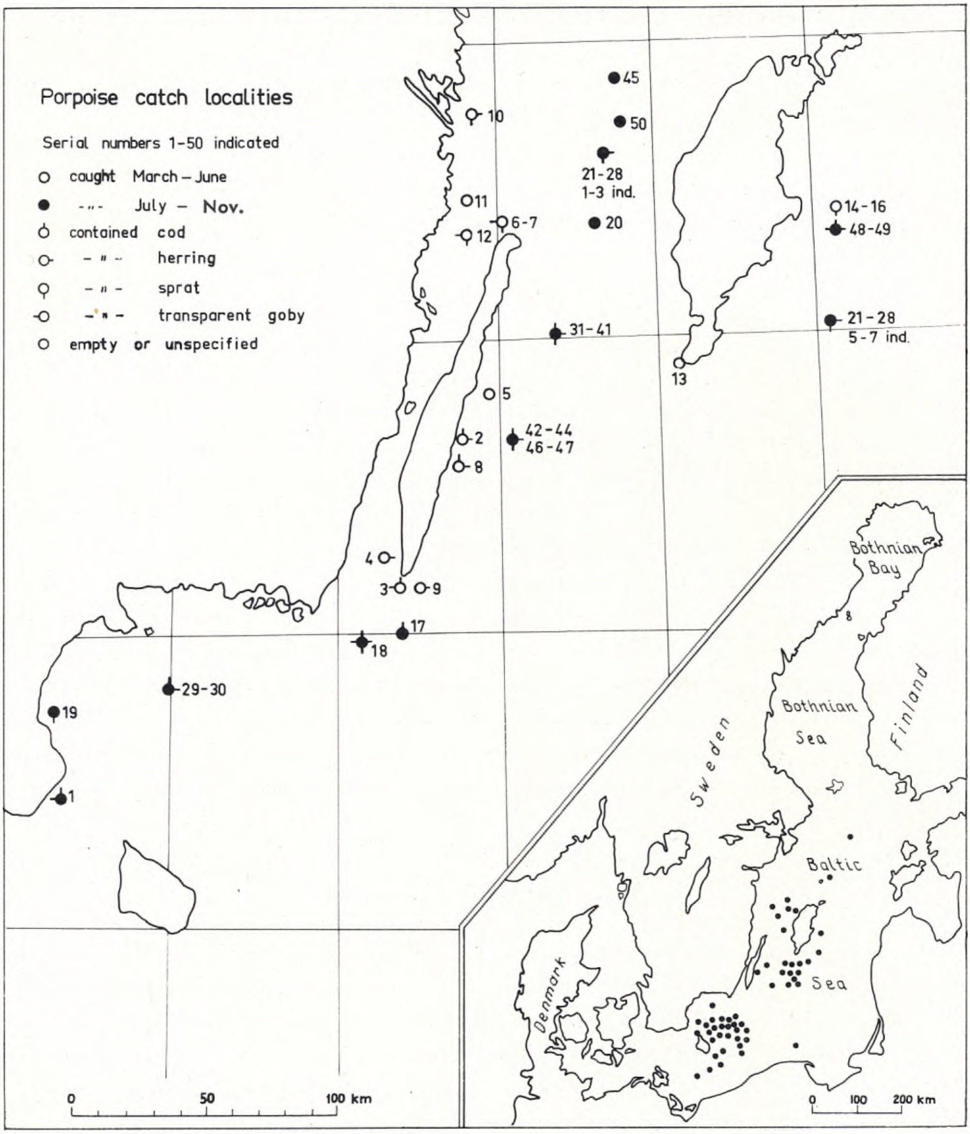

Fig. 1. Porpoise catch localities, season of catch and food fishes. The small scale map indicates place of recapture during the year 1959 of salmon in the Baltic proper, tagged as smolts this year and liberated in spring in the river Indalsälven emptying into the Bothnian Sea (informations by courtesy of the Salmon Research Institute).

The stomachs were dissected by fishery assistant L. ÖSTERDAHL, fishery officer G. CHRISTIERNSSON or myself. The volume of the content varied from nothing to about 1 litre. After thorough rinsing and decanting of soft tissues there remained backbones, bones, eye lenses and otoliths. In a few cases undigested food fishes could be specified but ordinarily the specification and enumeration were made by means of the otoliths. Not seldom bodies and eye lenses indicated more food specimens than did the otoliths, in the first case this was considered when giving the number, in the last case not as specification of eye lenses was not attempted.

Otoliths of some 20 Baltic fish species were studied from known specimens and after some difficulties regarding *Aphya minuta* (the transparent goby) hesitation remains only for 2 types of otoliths, the one assigned provisionally to *Ammodytes sp.* the other so far unspecified (two specimens). The sprat and the goby food specimens may vary in size but do not exceed about 12 and 6 cm respectively. For the larger herring and cod it is of some interest to know the size preyed upon by the porpoise and for these species size is roughly estimated by means of a provisional body/otolith relationship based on the assumption, not true but permissible in this connection, of proportionate growth. Conversion factors used for transforming otolith length into fish length (total length) were 26 for cod and 56 for herring.

Results

Table 1 gives the food items of the porpoise stomachs investigated.

Four stomachs were empty. Eight more stomachs contained only sparse remains of fish, not identified.

The 38 remaining stomachs contained the following fish species.

	Total nr. of fish	Nr. of stomachs	P.c. of 38 stomachs
Cod (*Gadus callarias*)	62	13	34
Herring (*Clupea harengus*)	110	21	55
Sprat (*Clupea sprattus*)	1,400	24	63
Transparent goby (*Aphya minuta*)	200	7	18
Sandeel (*Ammodytes sp.*)?	4	2	5

The occurrence of the four main food species is indicated by symbols on the map, Fig. 1.

Cod was found in 13 stomachs all over the area of porpoise catch. Of the 62 cod identified 48 have been estimated to be 12 cm or less, 6 have been 13—30 cm and 8 over 30 cm with c. 38 cm at most.

Herring and sprat were identified over the whole area in 21 and 24 porpoises respectively in total numbers of c. 110 and c. 1,400 specimens as estimated by means of otoliths or bodies. In many cases the number of eyelenses have greatly exceeded the number of otoliths.

The transparent goby is not normally recorded for the Baltic. For the fishing year 1961, however, there exist reports of mass-invasions into the Baltic and this occurrence of a pelagic fish is immediately taken advantage of by the porpoises, 7 of which contained c. 200 gobies. The southernmost

Table 1. Stomach contents of 50 porpoises from the Baltic. Approximate numbers of food fishes and — for cod and herring — estimated size in cm.

Nr	Date	Cod		Herring		Sprat	Goby	Sand-eel	Sp?	Remains of fish	Remarks
		Nr	Size	Nr	Size	Nr	Nr	Nr	Nr		
1	1960, 20.XI	11	6—12, 29, 31	—	—	—	3	—	—	—	
2	1961, c. 10.III	30	5—12	1 (?)	?	—	17	—	—	—	
3	c. 18.III	1	8	—	—	—	> 50	—	—	—	
4	13.IV	—	—	15	c. 20—25	—	—	—	—	—	
5	c. 15.IV	—	—	—	—	—	—	—	—	+	
6	20.IV	—	—	—	—	40	—	—	—	—	
7	20.IV	—	—	—	—	35	9	1?	—	—	
8	24.IV	1	32	20	c. 20	—	—	—	—	—	
9	27.IV	—	—	1	19	—	—	3?	—	—	
10	4.V	—	—	1	17	> 6	—	—	—	—	
1	18.V	—	—	—	—	—	—	—	—	+	
2	27.V	—	—	—	—	2	50	—	—	—	
3	V—VI	—	—	—	—	—	—	—	—	—	Empty, found dead
4	V—VI	—	—	—	—	1	—	—	—	—	
5	V—VI	—	—	—	—	—	—	—	—	+	
6	V—VI	—	—	—	—	> 50	—	—	—	—	
7	18.VII	1	32	—	—	—	—	—	—	—	
8	14.VIII	1	8	1	19	10	> 50	—	—	—	
9	17.VIII	—	—	—	—	1	—	—	—	—	
20	29.VIII	—	—	—	—	—	—	—	—	—	Empty
1	25.VIII—11.IX	—	—	—	—	7	—	—	—	—	
2	25.VIII—11.IX	—	—	—	—	50	—	—	—	—	
3	25.VIII—11.IX	—	—	5	13—16	110	—	—	—	—	
4	25.VIII—11.IX	—	—	2	14, 16	—	—	—	—	—	
5	25.VIII—11.IX	—	—	7	17—25	8	—	—	—	—	
6	25.VIII—11.IX	—	—	15	13—18	220	—	—	—	—	
7	25.VIII—11.IX	—	—	—	—	—	—	—	—	—	Empty
8	25.VIII—11.IX	—	—	2	13, 15	—	—	—	—	—	
9	4.IX	2	30. 34	>30	11—21	—	—	—	1	—	
30	4.IX	—	—	—	—	—	—	—	—	—	Empty
1	11—16.IX	—	—	—	—	—	—	—	—	+	
2	11—16.IX	—	—	2	14, 16	35	—	—	—	—	
3	11—16.IX	—	—	—	—	1	—	—	—	—	
4	11—16.IX	4	23, 33, 36, 38	2	17, 18	30	—	—	—	—	
5	11—16.IX	—	—	—	—	1 (?)	—	—	—	—	
6	11—16.IX	—	—	—	—	5	—	—	—	—	
7	11—16.IX	1	36	—	—	200	—	—	—	—	
8	11—16.IX	1	24	3	14—17	100	—	—	—	—	
9	11—16.IX	—	—	2	13	100	—	—	—	—	
40	11—16.IX	—	—	8	13—18	300	—	—	—	—	
1	11—16.IX	—	—	—	—	—	—	—	1	+	
2	18.IX	—	—	5	24—27	—	—	—	—	—	
3	19.IX	2	24, 30	—	—	10 (?)	—	—	—	—	
4	21.IX	—	—	2	14, 15	75	—	—	—	—	
5	22.IX	—	—	—	—	—	—	—	—	+	
6	24.IX	—	—	1	?	—	—	—	—	—	
7	26.IX	—	—	—	—	—	—	—	—	+	
8	6—8.X	2	8, 13	5	17—20	—	—	—	—	—	
9	6—8.X	5	2—4	—	—	—	20	—	—	—	
50	12.X	—	—	—	—	—	—	—	—	+	
Sum of porpoises		13		21		24	7	2		8	4
Sum of fish		62		110		1,400	200	4			

find of a goby was done in the first porpoise taken (Nov. 1960) and the northernmost find in one of the last porpoises (Oct. 1961). This may reflect the course of invasion.

No salmon was found.

Discussion

The main argument for the porpoise hypothesis of salmon fluctuations has been the apparent coincidence between these fluctuations on the one hand and, on the other hand, extent of ice cover of the Baltic, some of the recorded winter kills of porpoise, and porpoise hunting in the Danish sounds (SVÄRDSON 1955, 1957).

In this connection it may only be pointed out firstly that the statistical correlation between ice cover of the Baltic and the salmon yield is rather low (r about 0.4, $P < 0.001$, LINDROTH 1957) and in itself telling us nothing but a highly probable covariation between climate and salmon and nothing about operating factors, secondly that porpoise mortality due to ice, of unknown extent, it is true, has been recorded without subsequent rise in salmon catch (1924, 1947), and thirdly, that the porpoise hunting has always been practised at times when strong ice winters have also occurred. The effect of porpoise hunting on salmon can not be separated out from the effect of strong winters who have been suspected to act by means of a porpoise mortality. The comparison of time-series, though admittedly suggestive, yields no evidence of an interaction between porpoise and salmon.[1] (See further LINDROTH 1957.)

As complementary argument SVÄRDSON (1957) has advanced the elimination method. He states that predation is the most likely agent determining the abundance of salmon and, one by one, eliminates all possible predators except the toothed whales. Even if the eliminations seem rather plausible as far as present knowledge reaches they can not be regarded as positive evidence of the guilt of the porpoise. Such evidence is still lacking. Reports on porpoise preying upon large salmon exist but may be based upon suppositions or observations of chasing, not of real feeding. (TAUBER 1892, MAC INTYRE 1934, BERRY 1935; see also BENNET 1960 who does not attach importance to the porpoise as predator on salmon).

A preliminary report on the beluga whale (*Delphinapterus leucas*) in Bristol bay, Alaska, states that this whale feeds upon fingerling red salmon (sockeye, *Oncorhynchus nerka*) leaving the rivers in June, and adult salmon of various species during the remainder of the season, but that they "vary their diet in accordance with varying abundance and availability of different fishes" (BROOKS 1954). Further records of the food of toothed whales strengthen

[1] The general warning against a "time-series correlation danger" (RICKER 1958, p. 233) is especially appropriate in cases like this. See also ODUM 1953, p. 141.

this statement (VLADYKOV 1940, WILKE, TONIWAKI and KURODA 1953, NICHOLSON 1954, WILKE and NICHOLSON 1958, FINK 1959).

Summing up the arguments in favour of the porpoise hypothesis it may be stated that they are just arguments and constitute no evidence, one by one or together, of the validity of the hypothesis.

Against the hypothesis the following is to be said.

Of 50 porpoises now investigated from the Baltic proper 38 contained specified food. No salmon was found in the stomach contents which consisted of *Clupeidæ* (herring and sprat), cod, and transparent goby to mention the main constituents. All sizes of cod were encountered up to about 38 cm. This would be the largest fish taken by a porpoise which seems not to cut its prey up before swallowing it.

The salmon smolts leave the rivers about June and grow beyond prey size during their first half year in the sea. In this period of the year the smolts, calculated to an order of 5 millions annual recruitment to the sea (KÄNDLER 1958, in agreement with own estimations) gradually migrate southwards into the Baltic proper. No avoidance of the present area of porpoise catch is to be traced in the few recaptures of salmon of the year made in the Baltic proper in the course of the extensive tagging operations by the Salmon Research Institute (informations by courtesy of Dr B. CARLIN, see map). In the Baltic the survivors of the 5 millions young salmon are mixed up with some 300,000 millions of herring, 100,000 millions of sprat and 1,000 millions of cod (very rough estimates, LINDROTH 1961) shown to constitute the bulk of the food of the porpoise. At present, until contrary evidence is produced, we have to base our estimates upon the supposition that the porpoise feeds without selecting its food fishes, that salmon contributes to the food only in the very slight proportion indicated by its sparse occurrence as compared with the common Baltic fishes. Only few salmon would be eaten by every porpoise. Should the porpoise under these circumstances be responsible for any considerable share of the sea mortality of the salmon, now about 80—90 p.c., this would mean a very large porpoise population, in the order of 1 million probably. A recent inquiry among sea fishermen did not indicate any large population though no figures can be produced. For the main mortality, and fluctuations thereof, other causes are to be sought for.

The possibility of the porpoises following the example of the beluga gathering in the estuaries of salmon rivers in May—June to prey on smolts is out of question as the porpoise has never been seen in numbers in the Bothnian Bay (see map) where the most important salmon rivers debouch all displaying the typical long-term fluctuations of their salmon populations.

The only remaining chance of any significant interference between porpoise and salmon would lie in a hypothetical meeting of postsmolts and porpoises in the Bothnian Sea (see map) in the summer in periods of porpoise abundance in this part of the Baltic where the smolts could be thought to be delayed and a little less diluted with other fish. This possibility is mentioned here only for the sake of completeness, not for its likelihood.

The arguments against the porpoise hypothesis are, shortly, that salmon of prey size constitutes only an exceedingly small fraction of the fishes shown here to be eaten by the porpoise; that salmon has not been found in the porpoise stomachs examined; and that predation in salmon river estuaries at time of smolt migration is out of question. At this state of things it would at present be safe to conclude that the porpoise, though probably catching also small salmon, has no important influence upon the size of the Baltic salmon stock or its fluctuations.

Acknowledgement

My thanks are due to fishery officers and fishermen who have been helpful in collecting the porpoise stomachs and to the Salmon Research Institute for paying rewards to the fishermen.

Summary

1. Of 50 Baltic porpoise stomachs investigated 38 contained identifiable food fishes: cod, herring, sprat, transparent goby. No salmon was found.
2. The arguments for and against the hypothesis of Baltic salmon fluctuations as caused by porpoise predation are discussed. The hypothesis seems to lack adequate foundations.

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Life history of whitefish young (*Coregonus*) in two lake reservoirs

By THOROLF LINDSTRÖM

Contents

Introduction

The life history of whitefish young has been studied by, e.g., SCHEFFELT (1926), BAJKOV (1930), HART (1931), PRITCHARD (1931), WAGLER (1933), FREIDENFELT (1934), LINDROTH (1957).

In lake reservoirs, where the water level is regulated for the benefit of power plants in the river further downstream, the recruitment of the fish populations is probably controlled by mortality factors operating during the first year of life after the egg deposition, lake reservoirs not forming an exception from other lakes in this respect. As life history studies precede quantitative population estimates — a subject discussed e.g. in the Durham symposium on page 381 (LE CREN & HOLDGATE 1962) — the present study of the first year of life of whitefish contributes necessary preliminary data for an understanding of recruitment in lake reservoirs.

The present paper presents material and discussions from a series of paper in Swedish, mostly mimeographed, from 1955 to 1962. It has also in part been published in English by LINDSTRÖM & NILSSON (1962).

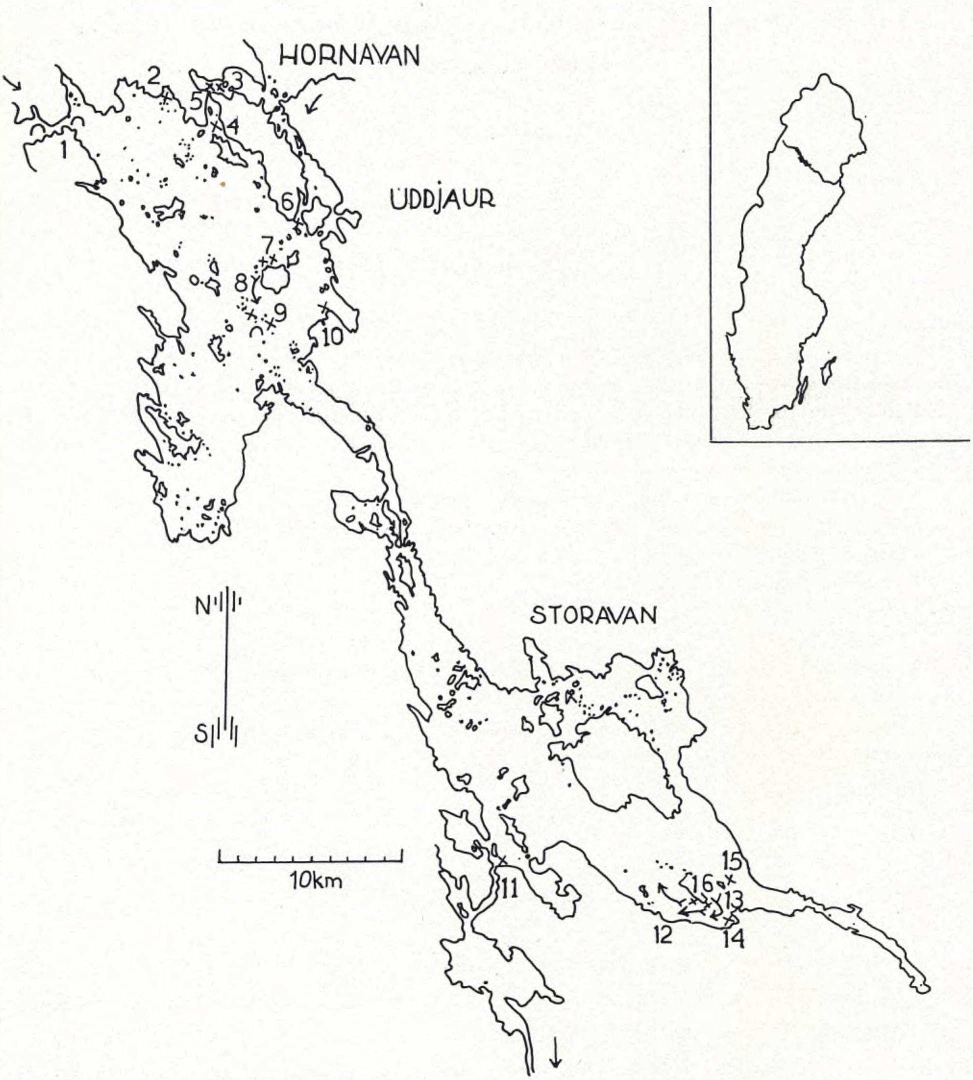


Fig. 1. Map of Lakes Uddjaur and Storavan with Stations 1—16. The dam is close to Station 11.

>→ = tow net
× = inspection from the shores
⌒ = seine 27

1. Localities, catch methods and field observations on whitefish young of the year

This investigation has been carried out in Lakes Uddjaur and Storavan and mainly in the Välbma-Doljaur section, Figs. 1 and 2. The level of Lake Storavan was regulated between 1936 and 1957 within the amplitude of the

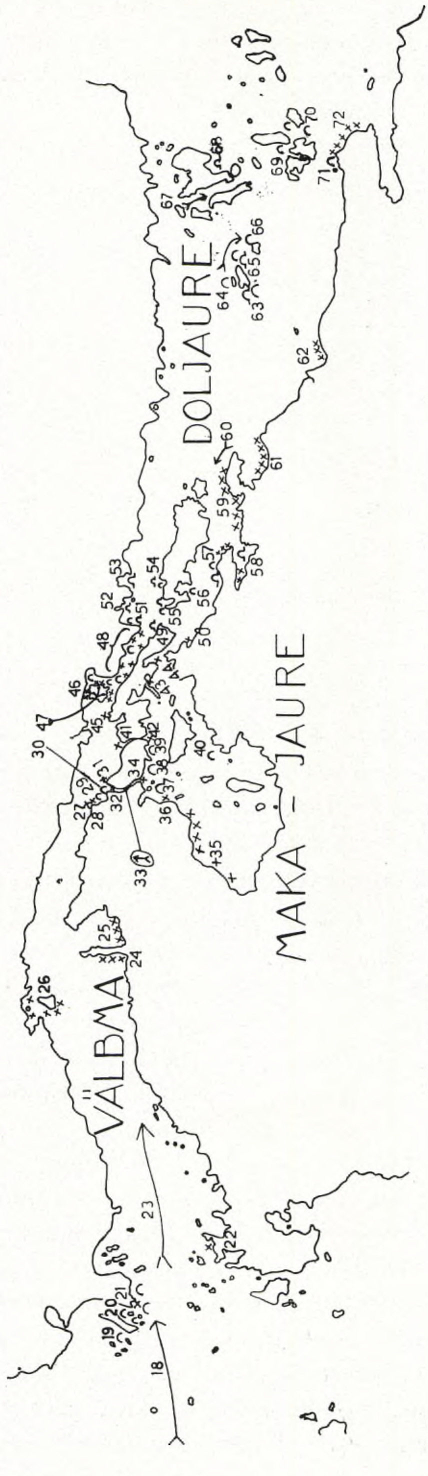


Fig. 2. Map of the central parts in Fig. 1 with Stations 18—72.

>→ = tow net
× = inspection
∩ = seine 27
–∩– = bait seine

Table 1. Fishing for whitefish young. Station numbers refer to the map, Fig. 1. *Methods* are described in the text. *Results*: observation of young is only recorded if the observation was made in June and was not followed by a catch of young.

Station	Method	Date	Results
Lake Uddjaur			
1	Seine 27	July 20, 1954	0
2, 3, 4	Inspection	June 13, 1955	0
5	,,	June 17, 1955	Observation of whitefish young
6	,,	June 13, 1955	0
7	,,	July 18, 1954	0
8	Tow net	July 18, 1954	0
9	Inspection	June 9, 1954, June 19 and July 1, 1955	Catch of whitefish young
9	,,	July 18, 1954	0
9	Seine 27	Oct. 9, 1954	0
10	Inspection	June 10, 1954	0
Lake Storavan			
11	Inspection	June 8, 1954	0
12	Tow net	June 3, 1954, June 9, 1960	0
13	,, ,,	June 8, 1960	0
14, 15, 16	Inspection	June 9, 1960	0

natural fluctuations. The level of Lake Uddjaur was — secondarily — slightly affected through the regulation in Lake Storavan. Since 1958 the damming in Lake Storavan has been increased by $1/2$ metre and the effect on Lake Uddjaur is now greater, so that the level fluctuations of this lake too have adopted the typical year rhytm of a regulated lake (Fig. 15).

Tow nets. Different kinds of fine-meshed nets were towed after motor boats (Tables 1 and 2). Net openings not more than 1 m. diam., quadrangular mesh apertures with 1 $1/2$ mm side. Newly hatched whitefish fry could pass through the meshes. No catch was obtained.

Inspection. From the shores of the lakes the closest water region was inspected on the days and at the places referred to in Tables 1 and 2 and Figs. 1 and 2. Whitefish young were caught with hand nets. It is not possible to estimate their density — from catch per hour or otherwise — as observation is, of course, highly dependent on weather condition. Besides, the young react early with escape movements from observer and net.

Stations 46 and 47 (Fig. 2) were often inspected, as a spawning place was situated in this stream. Whitefish young were observed there at the first visit each year. They still remained there in the middle of July in 1955, when summer came late, but normally minnows, small pikes and grayling young but no whitefish young are observed from the banks of this stream in July. In this and other examined streams whitefish young appeared in

Table 2. Fishing for whitefish young. Station numbers refer to the map, Fig 2. Methods are described in the text. Observation of young is only recorded (under the heading "Results") if the observation was made in June and was not followed by a catch of young.

Station	Method	Date	Results
Lake Uddjaur			
18	Tow net	June 9, 1954	0
19	Seine 27	Oct. 9, 1954	0
20	,,	July 24, 1954	Catch
20	,,	Oct. 9, 1954	0
21	,,	July 24, 1954	0
21	Inspection	July 1, 1955	Catch
22	,,	July 18, 1954	0
23	Tow net	June 9, 1954	0
24	Inspection	June 11, 1954	Catch
24	,,	June 16, 1955	0
25	,,	June 11, 1954	0
26	,,	June 13, 1955	0
27	,,	June 15, 1954, June 18, 1955	Catch
27	,,	July 16 and 19, 1954	0
28	,,	June 18, 1955	0
29	Seine 27	July 16, 1954, July 10, 1957, July 19, 1958, Aug. 15, 1959	0
The streams and Lake Makajaur			
30	Seine 27	July 16, 1954, July 19, 1958	0
30	,,	July 19, 1954	Catch
31	Inspection	June 4, 1954	0
32	,,	June 15, 1954, June 15, 1955	Catch
33	Tow net	July 19, 1954	0
34	Inspection	June 7, 1954	0
35	,,	June 18, 1955	0
36	,,	June 18, 1955	Catch
37	Seine 27	July 19, 1958	0
38, 39, 40	,,	July 16, 1954	0
41, 42	Inspection	June 4, 1954	0
43	,,	June 6, 1954	0
44	,,	June 13 and 14, 1955	Catch and observation
45	,,	June 1, 4 and 7, 1954	0
46	,,	June 7, 1954, June 12 and 16 and July 1 and 14, 1955, July 3, 1958	Catch
46	,,	June 12, 1954, June 13, 1955	Observation
46	,,	July 19 and 22, 1954, July 11, 12, 13, 17, and 18, 1958, June 11 and 12, 1960	0
47	,,	June 12, 1954, June 18, 1955	Observation
47	,,	June 13, 1960	Catch
47	,,	July 17, 19 and 22, 1954, July 11, 12, 13, 17 and 18, 1958, June 27 and 28, 1959, June 11 and 12, 1960	0
47	Seine 27	July 23, 1954	0
48	,,	July 23, 1954	0
48	Inspection	June 12, 1960	Catch
49	Bait seine	Aug. 14, 1959	0
Lake Storavan			
50	Inspection	June 6, 1954	0
51	Seine 27	July 23, 1958	0
51	Bait seine	July 13, 1958	0
52	,, ,,	Aug. 12, 1959	Catch

Station	Method	Date	Results
53	Bait seine	July 13, 1958, Aug. 12, 1959	0
54	Seine 27	July 13, 1958, July 18, 1959	Catch
54	,,	July 20, 1958, Aug. 11, 1959	0
54	Bait seine	July 13, 1958, Aug. 12, 1959	0
55	Seine 27	Aug. 11, 1959	Catch
55	Bait seine	Aug. 12, 1959	0
56	Seine 27	July 23, 1958	Catch
56	,,	July 18 and Aug. 11, 1959	0
57	Inspection	June 18 1955	0
57	Seine 27	July 23, 1954, July 14, 1955, July 9, 1957	Catch
57	,,	July 12, 13, 20 and 23, 1958	0
57	Bait seine	Aug. 14, 1959	0
58	Inspection	June 6, 1954	0
58	Bait seine	Aug. 14, 1959	0
59	Inspection	June 13, 1955	0
60	Tow net	June 2, 1954	0
61	Inspection	June 14, 1954	(Catch)
61	,,	June 19, 1955	0
62	,,	June 12, 1954	(Catch)
63	Bait seine	July 22, 1954, July 18 and 21, 1958	0
63	,, ,,	Aug. 4 and Oct. 10, 1954, Oct. 9, 1959	Catch
63, 65	Seine 27	Aug. 16 and 17, 1959	0
64, 66	,,	Aug. 16 and 17, 1959	Catch
65	Bait seine	July 21, 1958	0
64—66	Tow net	June 2, 1954	0
67	,, ,,	June 2, 1954	0
68	Bait seine	July 22, 1954, July 21, 1958	0
69	Seine 27	Aug. 18, 1959	0
70	,,	July 21, 1954	0
71	,,	Aug. 16 and 18, 1959	0
71	Kakuami	Aug. 7, 1958	Catch
72	Inspection	June 12, 1955	0

water of a few decimetres' depth in backwaters behind boulders and logs or in larger eddies, sometimes out in direct current.

The typical habitat of whitefish young in the lakes during June appears to be places where the depth rapidly increases to one metre or more. In shallower water, minnows are often observed but seldom whitefish young. During 1955 whitefish young were for the first time observed in the middle of June in the lakes after appropriate places had been inspected for some days without result. In July whitefish young are not observed from the shores of the lakes within reach of a hand net.

Both the characteristics of the individuals and the schools can be used to distinguish between young of whitefish and one-year-old minnows, both species appearing close to the shore in June. Only the whitefish young swim with undulating movements of the whole body (NURSALL 1958). When excited, they still keep together, the school making evasive movements horizontally, whereas excited minnow schools finally break up, the individuals searching for cover between the bottom stones.

Seining. Older whitefish young were caught with seines. One seine had an inner mesh perimeter of 27 mm in the bag, a total length of 30 metres and a

Table 3. Number of hauls without and with catch in seine 27, July and August 1954—59 (Cf. BONN 1953).

	Without catch	With catch
Day haul	29	2
Evening and night haul (after 5 p.m.)	33	14

maximum depth of 2 metres at the bag while working. Normally the depth is less, especially towards the end of a haul. This seine was used floating, except during the period July 16—21, 1954. Seining started each year in July while the whitefish young could still pass through the meshes of this "seine 27". Seines with the double depth and a total length of more than 100 metres were also used from July to October with the aim of reducing the opportunities for the fish young to swim away from the gear. In October they could still pass through the meshes, which had an inner perimeter of 59—65 mm at the bag in these "bait seines". The bait seines were only used as bottom seines. As the investigation proceeded, the seine fishing passed into a purposeful search for whitefish young at localities and times which had proved favourable.

Influence of wheather condition and diurnal rhythm on catch is suggested by the following material. During 1958 the fine-meshed seine was hauled 11 times in the evenings of the 12th and 20th July without catch and four times in the evenings of the 13th and 23rd July with two successful hauls. The air temperature at Arjeplog at 7.00 p.m. on the 12th, 20th, 13th and 23rd July was 8.3, 11.2, 13.2, and 14.6°C, respectively according to the Meteorological and hydrological institute of Sweden.

The density of whitefish young can hardly be estimated with the present material, but important habitats for whitefish young are identified (Tables 1 and 2). This is verified e.g. by observations on warm and calm July evenings: whitefish young rose to the surface and jumped frequently during 1954 and 1955 at Stations 33 and 34 (Fig. 2) and each year in the district around stations 48, 49 and 54—57. The schools could also be observed through the water surface. Merganser fished at these localities.

2. Spawning place and spawning time

An account of whitefish spawning from this district is published in Swedish (mimeographed). The systematic of whitefish follows SVÄRDSON (1957, 1958). *Coregonus peled* spawns in the streams, e.g. Stations 5, 11 and 45—47 in Figs. 1 and 2. Spawning *Coregonus pidschian* and *lavaretus* have not been observed when fishing after spawning *peled* at Stations 46—48. The nearest spawning places of those two species are more than one kilometre

Table 4. Size of eggs and new-hatched fry.

Year	1959		1961		
Lake Species	Storavan C. lavaretus	Storavan C. pidschian	Hornavan C. lavaretus	Hornavan C. pidschian	Uddjaur C. peled
Mean egg diameter, mm	2.3	3.3	2.7	2.9	3.2
Mean fry length, mm	10.5	12.3	10.6	11.3	12.5

away. They spawn in the lakes during December and January, after the spawning of *peled* is over. The spawning of *pidschian* and that of *lavaretus* are very close in space and time.

Further material from Northern Sweden on general spawning ecology and spawning ethology of whitefish and mechanisms preventing hybridization is presented by FABRICIUS (1950), SVÄRDSON (1951, 1953), FABRICIUS & LINDROTH (1954) and LINDROTH (1957).

3. Ecology of the hatching period

The small importance of spawn in the food of whitefish from the spawning time in these lakes (LINDSTRÖM & NILSSON 1962) and the relations between egg diameter and bottom structure may have a bearing on the discussion of survival and ecological isolation between the three whitefish species during the winter, but otherwise the material for a discussion of these subjects is very incomplete.

Egg size varies with the size of the spawning fish (for whitefish in Hornavan and Uddjaur cf. TOOTS, 1951; "*blåsik*" = *C. lavaretus*). Fry size at hatching varies with egg size. Table 4 gives egg and fry sizes in batches of hatching eggs from spawning fish of ordinary catch size.

The means for fry length are significantly different in these samples, p less than 0.001. The material from Lake Hornavan is presented to illustrate the local variation somewhat, as it has not been possible to present data from Välbma—Doljaure (Fig. 2) where most whitefish young are captured. Hornavan is separated from Lake Uddjaur only by a short stream. The Sella hatchery is situated in this stream and the water passing the hatchery is not heated. A spawning place for *C. peled* is situated in this stream and the temperature in the hatchery cannot deviate much from the temperature at the spawning place. The hatching time in the hatchery should give a fair estimate of the hatching time for *peled* in the streams, Table 5.

The spawning time of *peled* is one month ahead of that of the other two species, but in the uniform hatchery environment the hatching times differ much less. JOHN & HASLER (1956) have shown that the hatching time for ciscoe is governed by the spring temperature rising over a threshold value.

Table 5. Hatching time in the Sella hatchery.

Year	1954	1955	1958	1961
C. peled	May 12—22	May 26—June 6	—	May 12—31
C. lavaretus	—	—	—	May 28—June 3
C. pidschian	May 12—22	May 26—June 10	June 9—20	May 25—June 1

In Lakes Uddjaur and Storavan the spawning streams of *peled* get rid of the ice cover first and there have always been whitefish young at the first visit each year (Tables 1 and 2). The hatching time of *peled* in 1955 can be estimated from Table 5. The ice breaks up later over the spawning places of *lavaretus* and *pidschian* and the critical temperature threshold is therefore reached later. Whitefish fry were not observed in the lakes until the middle of June 1955, the only year with an appropriate observation series. The spring was very late in 1955.

4. Period I, the first weeks, identification

There are differences in pigmentation of young from different whitefish species in these lakes (cf. THIENEMANN 1950, KOLLER 1934). The variation of this character in different environments should be studied more closely. In the present study young from the *peled* spawning place, Stations 46—48, Fig. 2, are tentatively recorded as *peled* young during the first weeks and those from the lakes as *pidschian-lavaretus*. In July the *peled* young move down in the lake below and in stage F the three species can be distinguished by their gillrakers.

Table 7 shows that the development of the whitefish young in the stream is ahead of the development of the whitefish young in the lakes.

Table 6. Description of stages. All data refer to studies with magnification 8 ×. Cf. SCHEFFELT 1926, SCHNAKENBECK 1936.

Stage A. The yolk sac still protruding in the ventral profile of the body.
Limit A/B. The pelvic fins protude from the body surface.
Stage B. Fin rays visible at the bases of the dorsal, anal and caudal fins.
Limit B/C. The unpaired dorsal fin fold is divided into the dorsal and the adipose fin. Finrays now visible in the whole length of the caudal fin.
Stage C. The alimentary canal is still a straight tube.
Limit C/D. The canal begins to bend in the cranial part of the visceral cavity. The hind end of the air bladder reaches the cranial part of the dorsal fin.
Stage D. The adipose fin dwindles and becomes smaller than the anal fin. The caudal fin is still clearly asymmetrical. Fin rays visible in the pelvic fins.
Limit D/E. The caudal fin becomes secondarily symmetrical externally.
Stage E. All fins have the adult appearance but the adipose fin is still fairly large.
Limit E/F. The first scales appear.

Table 7. Stages of whitefish young in the *peled* spawning stream and in the lakes (*pidschian-lavaretus*).

Year	1954	1954	1954	1954	1954	1955
Date	June 7	June 9	June 11	June 12—14	July 19—24	June 12
Stream, stages	B	—	—	—	}F	B
Lakes, stages	—	A	B	B		—

Year	1955	1955	1955	1955	1957	1958
Date	June 16	June 18—19	July 1	July 14	July 9	July 3
Stream, stages	A—B	—	D	}(D) E	E	D
Lakes, stages	—	A	B			—

Year	1958	1958	1959	1960
Date	July 13	July 23	July 18	June 12—13
Stream, stages	}E	F	F	(B) C
Lakes, stages				—

5. Period I, food of whitefish young

In the earliest stage, the alimentary canal of whitefish young from Uddjaur and Storavan is ordinarily empty (Table 8, stage A). When food is observed for the first time in young from the lakes, it consists of small zooplankton forms, in some cases though an undefined mass. The access of zooplankton in the lakes can be judged from Table 9 from a period when the young had not yet started to feed in the lakes. (For further development of the zooplankton populations, see Table 10.) Whitefish young from the *peled* spawning stream had also fed on zooplankton. Plankton is carried from the lake to the stream in spite of the mechanisms reducing the loss of zooplankton from the lakes (LINDSTRÖM 1957, AXELSON 1961), but the low

Table 9. Plankton density, June 1955. Mean for five samples with 5.3 litre plankton sampler ($\bar{x}$) and mean square (s^2). Stations where whitefish young are caught. Total depth $\leq$ 1 m.

Station	27		27		27		46		47	
Date	June 19		June 20		June 20		June 16		June 16	
Time	20^{30}—21^{30}		7—8		14—15		13—15		13—15	
	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2
Nauplii	31	117	28	136	20	274	5.6	2.3	34	464
Cyclopoida, copepodites I–III	5.4	13	10	51	5.6	10	0.8	0.7	6.2	64
,, ,, IV	0.2	0.2	1.2	2.7	0.4	0.3	0.2	0.2	0.6	1.8
,, ,, V	3.0	10	—	—	0.4	0.3	0.6	0.8	2.8	1.7
Cyclops adults	0.4	0.3	0.2	0.2	—	—	0.2	0.2	—	—
Daphnia, juv.	0.2	0.2	0.2	0.2	—	—	—	—	—	—
Bosmina	4.4	12	5.2	9.2	0.6	0.3	1.2	2.7	19	242
Holopedium, juv.	3.6	2.3	2.0	2.5	0.2	0.2	1.2	0.7	1.4	2.8
Polyphemus, juv.	—	—	—	—	0.6	0.8	—	—	—	—
Other Cladoceres	—	—	—	—	—	—	0.4	0.3	—	—
Rotifers, solitary	28	99	18	313	5.4	3.8	2.8	1.7	7.8	44
Hydracarina	—	—	—	—	0.2	0.2	0.2	0.2	0.2	0.2
Insects	—	—	—	—	—	—	0.4	0.3	0.2	0.2

Table 8. Food and growth of whitefish young. Identification of whitefish: see text.

⊕=number not counted. +=counted, but very few (< 0.5 for plankton, <0.05 for other items). The total stomach content is analysed unless otherwise stated in "Notes" column.

Year	Date	Station	Species	Stage	Mean total length, mm	Number	Mean number of identified food organisms per fish																			Number of young. Grouping according to food forming more than half the food volume				Time at capture	Stomach contents mean weight, mg	Weight proportion plankton : insects	Notes
							Bosmina	Daphnia	Holopedium	Polyphemus	Chydoridae (not Eurycercus)	Other Cladoceres	Nauplii	Cyclopoida, copepodites & adults	Calanoida, copepodites & adults	Copepods	Conochilus	Other Rotiferes	Diptera, larvae	Diptera, pupae & imagines	Hemiptera, i.	Hymenoptera, i.	Other insects	Hydracarina	Other invertebrates	Plankton crust.	Insects	Empty	Not classified				
1954	June 7	46	C. peled	B	16	20	15	—	+	—	+	—	1	2	—	—	—	—	0.4	—	—	—	—	—	—	15	3	1	1	—	—	—	The entire digestive tract analysed
	June 9	9	C. lavaretus - C. pidschian	A	11	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	,, ,, ,, ,, ,,
	June 11	24	C. lavaretus - C. pidschian	B	12	16	—	—	—	—	—	—	3	1	—	—	—	+	—	—	—	—	—	—	—	3	—	1	12	11—12	—	—	,, ,, ,, ,, ,,
	June 12 & 14	61, 62	C. lavaretus - C. pidschian	B	14	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	
	July 19	30	C. lavaretus	F	(57)	13	140	4	20	5	—	—	—	—	—	—	⊕	—	—	—	—	—	0.1	—	—	12 1/2	1/2	—	—	17	—	—	
	,,	,,	C. lavaretus - C. peled	F	51	16	150	4	25	3	+	—	—	—	—	1	⊕	—	—	—	—	—	—	—	—	16	—	—	—	17	—	—	
	,,	,,	C. peled	F	(63)	1	350	10	25	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	17	—	—	
	,,	,,	C. pidschian	F	56	3	200	1	6	6	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—	—	2	1	—	—	17	—	—	
	July 23	57	C. lavaretus	F	62	10	1,200	—	—	25	+	—	—	—	—	—	—	—			⊕			—	0.1	8 1/2	1 1/2	—	—	20—21	—	—	Insects often in the hind part of the stomach
	,,	,,	C. lavaretus - C. peled	F	64	1	1,000	—	—	—	—	—	—	—	—	—	—	—			—			—	—	1	—	—	—	20—21	—	—	
	,,	,,	C. peled	F	65	34	1,100	+	—	40	—	+	—	6	—	—	—	—			⊕			+	0.1	29 1/2	4 1/2	—	—	20—21	—	—	Insects often in the hind part of the stomach
	,,	,,	C. pidschian	F	59	1	240	1	—	132	1	—	—	—	—	—	—	—			⊕			—	—	1	—	—	—	20—21	—	—	
	July 24	20	C. lavaretus	F	(60)	10	42	—	—	—	+	—	—	—	—	—	—	—			⊕			1.3	—	—	10	—	—	8	—	—	
	,,	,,	C. lavaretus - C. peled	F	56	4	47	1	—	1	1	—	—	—	—	—	—	—			⊕			—	—	1 1/2	2 1/2	—	—	8	—	—	
	,,	,,	C. peled	F	56	1	40	—	—	—	—	—	—	—	—	—	—	—			⊕			—	—	1/2	1/2	—	—	8	—	—	
	Aug. 4	63	C. lavaretus	F	67	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	—	—	—	
	,,	,,	C. lavaretus - C. peled	F	68	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	
	,,	,,	C. peled	F	74	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	
	Oct. 10	63	C. lavaretus	F	98	21	⊕	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	—	—	—	Noon	—	—	
	,,	,,	C. peled	F	105	10	⊕	—	—	+	—	—	—	—	—	+	—	—	0.1	—	—	—	—	—	—	10	—	—	—	,,	—	—	
	,,	,,	C. pidschian	F	96	2	⊕	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	,,	—	—	
1955	June 12	46	C. peled	B	17	23	6	+	+	—	—	—	5	5	—	—	—	—	0.3	—	—	—	—	—	—	17	1	—	5	15	—	—	The entire digestive tract analysed
	June 13	44		—	14	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	—	—	—	
	June 15	32		A	11	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	The entire digestive tract analysed
	June 16	46	C. peled	A/B	15	21	2	—	—	—	—	—	—	+	—	—	—	—	0.5	—	—	—	0.1	—	—	7 1/2	7 1/2	6	—	—	—	—	,, ,, ,, ,, ,,
	June 18	36	C. lavaretus - C. pidschian	A	12	18	—	+	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	2	—	16	—	17	—	—	,, ,, ,, ,, ,,
	June 18	27	C. lavaretus - C. pidschian	A	12	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	8	—	—	,, ,, ,, ,, ,,
	June 19	9	C. lavaretus - C. pidschian	A	12	38	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	38	—	—	—	—	,, ,, ,, ,, ,,
	July 1	9	C. lavaretus - C. pidschian	B	16	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	10	—	—	
	July 1	21	C. lavaretus - C. pidschian	B	14	13	2	—	—	—	+	+	2	+	+	—	—	2	—	—	—	—	—	—	—	11	—	2	—	9	—	—	The entire digestive tract analysed
	July 1	46	C. peled	D	23	20	47	+	5	—	—	—	+	1	—	—	—	+	—	0.1	—	—	—	—	—	20	—	—	—	5—6	—	—	,, ,, ,, ,, ,,
	July 14	46	C. peled	D/E	27	17	2	—	7	—	—	+	—	—	12	—	—	+	—	0.1	—	0.1	0.2	—	—	15	2	—	—	16	—	—	Calanoida mostly Heterocope
	July 14	57		E	32	66	61	+	4	1	+	+	+	+	+	—	⊕	+	—	5.3	—	—	1.3	—	0.1	39	27	—	—	20—21	3	—	The values 5.3, 1.3 and 0.1 from a sample, n=37
1957	July 9	57		E	33	87	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	87	21—22	—	—	
1958	July 3	46	C. peled	D	21	32	17	+	7	—	+	+	+	1	—	—	—	—	0.7	0.4	—	—	0.1	—	—	25 1/2	6 1/2	—	—	—	—	—	The entire digestive tract analysed
	July 13	54		E	37	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	21	—	—	
	July 23	56	C. lavaretus	F	(53)	7	787	+	1	+	+	+	—	1	—	—	—	—	—	3.9	—	—	0.3	—	—	7	—	—	—	16^{30}	17	12 : 1	
	,,	,,	C. lavaretus - C. peled	F	47	56	570	+	2	1	1	+	—	+	+	—	—	—	+	6.5	+	0.1	0.1	+	—	50 1/2	5 1/2	—	—	16^{30}	15	5.9 : 1	
	,,	,,	C. peled	F	(51)	24	840	—	2	+	+	+	—	—	—	—	—	—	—	10.0	—	0.1	0.2	1.0	+	21	3	—	—	16^{30}	21	4.6 : 1	
	,,	,,	C. pidschian	F	56	2	910	—	1	—	—	—	—	—	—	—	—	—	—	2.5	—	—	—	—	—	2	—	—	—	16^{30}	20	10 : 1	
	Aug. 7	71	C. lavaretus	F	60	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—	Bosmina dominates the stomach contents
	,,	,,	C. lavaretus - C. peled	F	58	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	,, ,, ,, ,, ,,
	,,	,,	C. peled	F	62	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	1	—	—	—	—	—	,, ,, ,, ,, ,,
1959	July 18	54	C. lavaretus	F	55	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	19	—	—	
	,,	,,	C. lavaretus - C. peled	F	54	8	+	—	23	133	—	+	—	—	—	—	—	—	0.1	15.9	0.1	—	—	0.4	0.1	2 1/2	5 1/2	—	—	19	—	—	
	,,	,,	C. peled	F	55	19	+	—	18	44	+	+	—	—	—	—	—	—	0.1	16.5	0.3	0.1	—	0.4	0.1	3 1/2	15 1/2	—	—	19	—	—	
	,,	,,	C. pidschian	F	57	1	—	—	—	—	—	—	—	—	—	—	—	—	—	18	1	—	—	—	—	—	1	—	—	19	—	—	
	Aug. 11	55	C. lavaretus	F	86	1	529	2	7	47	—	—	—	2	2	—	—	—	—	—	—	—	—	—	—	1	—	—	—	20	—	—	
	,,	,,	C. peled	F	89	19	367	+	74	97	2	+	—	7	+	—	—	—	0.2	5.0	0.5	0.3	—	0.1	—	14	5	—	—	20	37	2.6 : 1	Insects in the hind part of the stomach
	,,	,,	C. pidschian	F	90	1	87	—	4	39	—	—	—	—	—	—	—	—	—	37	1	2	1	1	—	—	1	—	—	20	—	—	
	Aug. 12	52	C. peled	F	89	15	55	—	+	37	1	+	—	+	8	—	—	—	0.3	5.7	1.1	0.3	0.5	0.5	—	5 1/2	9 1/2	—	—	14^{30}	23	0.3 : 1	The Calanoida are Heterocope
	Aug. 16—17	64, 66	C. lavaretus	F	85	15	511	—	1	16	1	1	—	110	—	—	—	—	—	12.4	3.0	2.6	—	0.1	0.1	10	5	—	—	22—24	37	2.9 : 1	Insects in the anterior part of the stomach
	,,	,,	C. peled	F	96	3	60	—	—	8	2	4	—	742	—	—	—	—	0.3	21.0	7.0	2.7	—	2.7	0.7	2	1	—	—	22—24	78	1.2 : 1	,, ,, ,, ,, ,, ,, ,, ,,
	,,	,,	C. pidschian	F	92	2	672	—	—	3	—	—	—	—	—	—	—	—	—	84.0	21.5	4.5	1	1	—	1	1	—	—	22—24	77	0.2 : 1	,, ,, ,, ,, ,, ,, ,, ,,
	Oct. 9	63	C. peled	F	113	20	492	17	38	1	+	—	—	1	23	—	—	—	0.1	—	—	—	—	—	—	20	—	—	—	12	—	—	Only the anterior part of the stomach analysed
1960	June 12—13	46, 48	C. peled	B/C	18	29	+	—	—	—	+	+	+	4	—	—	—	—	0.5	0.3	—	—	0.1	—	—	8	6	15	—	—	—	—	

Table 10. The state of the plankton population July 15, 1955, at 7—8 p.m. Mean for three samples with 5.3 l. plankton sampler ($\bar{x}$) and mean square (s^2). Southern Välbma (outside stations 30—31), total depth 9 m.

Depth of sample, m	Surface		2		5		8	
	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2
Heterecope, copepodites	2.0	3.0	4.3	8.4	2.7	5.4	0.33	0.33
Diaptomus, copepodites	—	—	1.0	1.0	1.7	1.3	0.67	0.33
„ adults	0.33	0.33	1.7	0.33	1.0	1.0	—	—
Nauplii	16	64	21	57	16	57	17	122
Cyclopoida, copepodites I–III	4.0	1.0	4.0	7.0	1.3	0.33	0.67	0.33
„ „ IV	1.0	0	0.67	1.3	0.33	0.33	1.0	1.0
„ „ V	—	—	0.67	0.33	1.7	2.3	—	—
Cyclops adults	0.67	0.33	1.7	1.3	2.7	6.3	2.0	3.0
Daphnia cristata	—	—	—	—	1.3	1.3	1.0	1.0
Bosmina	6.0	19	14	4.0	11	48	32	50
Holopedium	2.7	1.3	10	2.3	6.3	14.3	3.3	1.3
Polyfemus	1.0	1.0	—	—	—	—	—	—
Other Crustacea	—	—	—	—	0.33	0.33	0.33	0.33
Rotifers, solitary	90	2281	106	1021	96	1444	71	272

plankton density at Station 46, June 16 (Table 9) should exemplify those variations in plankton density that could be expected in a water area without zooplankton production and where physical factors and predators can act with greater effect on the plankton density than in the lakes. The whitefish young from this station on June 16 had eaten less plankton than on June 12 (Table 8). In July the plankton consumption had again increased at this station; the diet varies strongly with the food offered.

Whitefish young can early manage to catch food animals 2—3 mm in length (*Diptera,* Table 8) and of course the plankton Crustacea, $^1/_2$—$1^1/_2$ mm in length, too (*Bosmina, Cyclops* adults and larvae). The only sign of a change in size of food animal with length of predator in this material is the fact that nauplii and rotifers disappear from the diet during the first year.

With such a plasticity in feeding habits, the diet should vary with differences in habitats, provoked by the choice of spawning sites of the parent fish.

6. Period I, habitat and school behaviour

Between young *peled* and young of the group *pidschian-lavaretus* such differences as those mentioned above exist during the first weeks after hatching, judging from the known spawning places. The spawning places of *pidschian* and *lavaretus* are, however, so intermingled that compound schools of fry must result at hatching. PRITCHARD (1931) has observed compound schools of whitefish and ciscoe young and KEENLEYSIDE (1955) has discussed compound schools. Observations referred to in Chapter 1 show that whitefish young behave like true pelagic fish — the school is the shelter of a pelagic fish (ATZ 1953) — and their primary reaction should be an unspecified attraction to other whitefish young, without regard to species.

It is not known when those reactions mature in young whitefish that cause a mixed school to break up into one-species schools (cf. KEENLEYSIDE 1955).

LINDROTH (1959) has studied the rather varied behaviour of the young of two whitefish species in relation to the environmental details of a rearing pond, without finding any differences between species.

7. Observations on whitefish young in ponds and aquaria

Experiments that have been described in more detail in the mimeographed version (in Swedish) further illustrate how whitefish young can vary their diet. No difference between species in feeding behaviour was observed. Adult *Daphnia* was attacked and often ejected again from the mouth (cf. WAGLER 1937, BLAXTER & HOLLIDAY 1958, LINDROTH 1959). It did not seem to be effectively used as food until the young reached a length of about 3 cm. Newly hatched *Artemia* were taken not from the aquarium bottom but when whirled up from it. They were eaten and often also rejected in swarms, but in contrast to *Daphnia* they ended up in the alimentary canals of small whitefish young too.

8. Period II, identification

The variation in gill raker number of adult *peled, lavaretus* and *pidschian* in Uddjaur and Storavan is illustrated in Fig. 3 and SVÄRDSON 1957. The range of *peled* and *lavaretus* overlap to a slight degree, and single individuals may be wrongly classified. The same applies to the delimiting of a fourth whitefish form, preliminarily called "älvsik", from *lavaretus* and *pidschian.* "Älvsik" are only caught in small numbers where they exists in regular populations, i.e., around Station 12, and are very rare in the Välbma—Doljaure district where the majority of whitefish young are caught.

The uncertainty in the classification of younger individuals is greater, the greater is the overlap (Fig. 3).

In Fig. 3 A is presented all material from Uddjaur and Storavan on the relation body length—number of gillrakers of young. The points gather in three diverging bundles which at the end of the first year almost reach the levels of the definite numbers of gillrakers for *peled, lavaretus* and *pidschian.* A tentative delimitation of *peled* from *lavaretus* young has been worked out. assuming a variation of 8—11 gillrakers for each species. Only the lower limit of *peled* and the upper limit of *lavaretus* are of any importance and these are set forth in Fig. 3 B. As the regions of variation overlap, those two limits

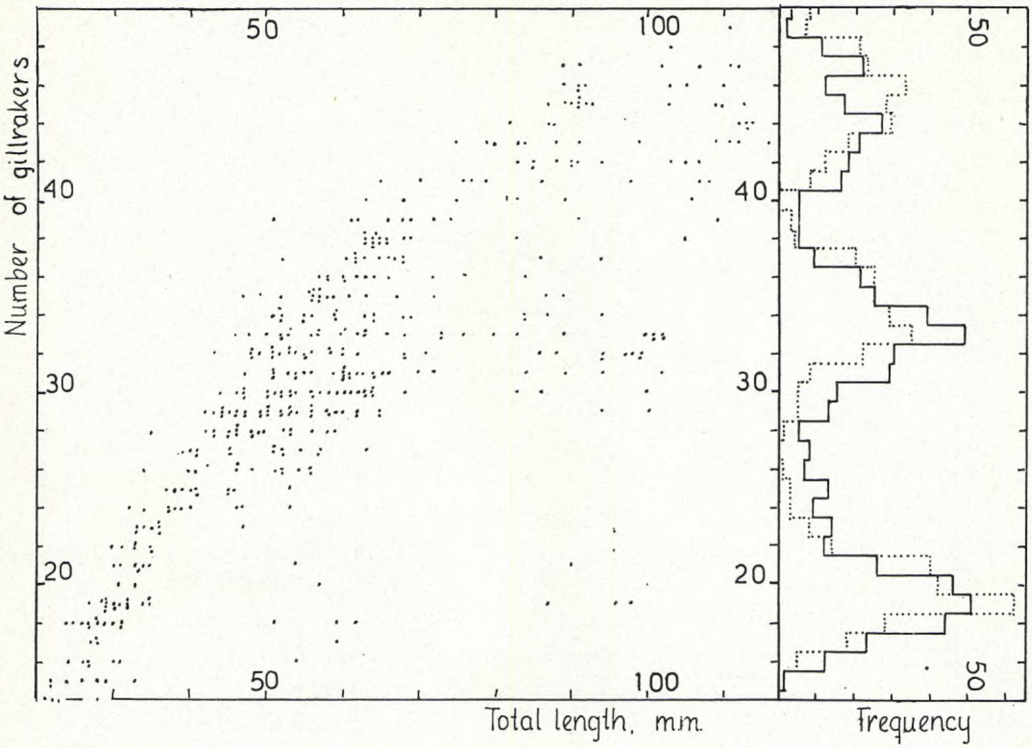


Fig. 3 A. Identification of whitefish young. All analysed material from Lakes Uddjaur and Storavan on the relation between total length and number of gillrakers (left). In the right-hand part of the figure the frequency distribution of gillrakers of adult whitefish caught 1954—59 is represented. Dotted line=Uddjaur, continuous line=Storavan. *C. peled* at the top, *C. lavaretus* in the middle and *C. pidschian* at the bottom.

include between them a number of unclassified young (either *peled* or *lavaretus*). This classification method can be tested against the gillrakers-body length relation of *lavaretus* young that had been reared in ponds and where offspring of well-identified parent fish (Fig. 4) .

9. Period II, habitat

The existence of whitefish young of more than one species in the same habitat is illustrated by Figs. 5—8. Single *pidschian* young are caught in many of the successful hauls with the seine together with other species. Catches from the district covered by Stations 52—71 contain both *peled* and *lavaretus* young in 1954 and 1958. It is not shown that they existed in one school, only that they existed within the region the small seine could cover.

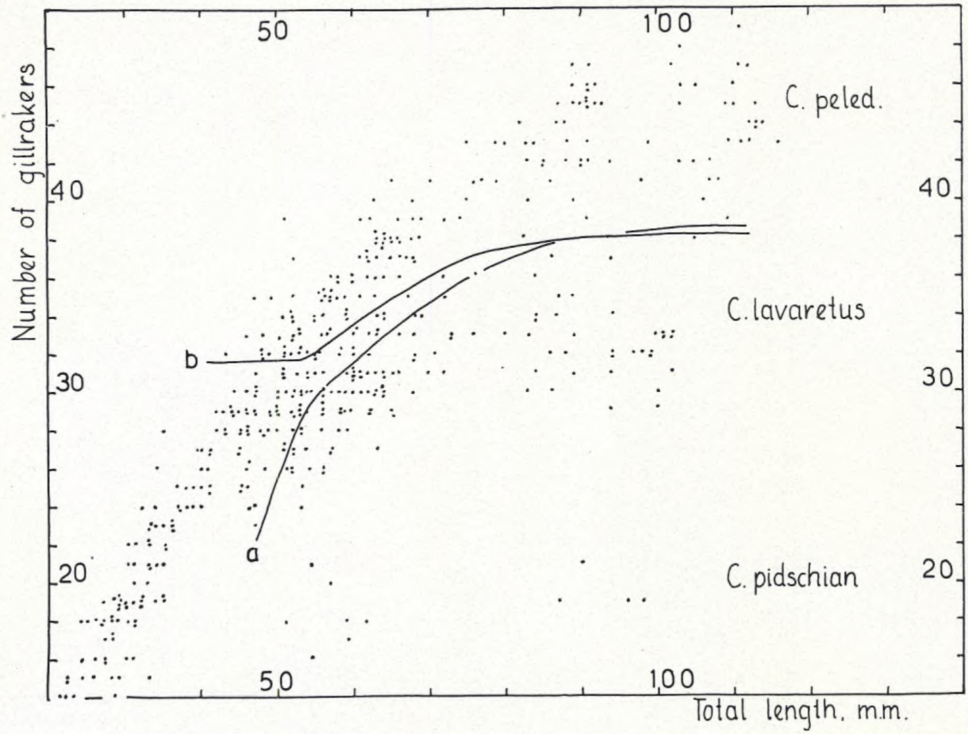


Fig. 3 B. The same material as in the left-hand part of Fig. 3 A. a=lower limit of *C. peled,* b=upper limit of *C. lavaretus.*

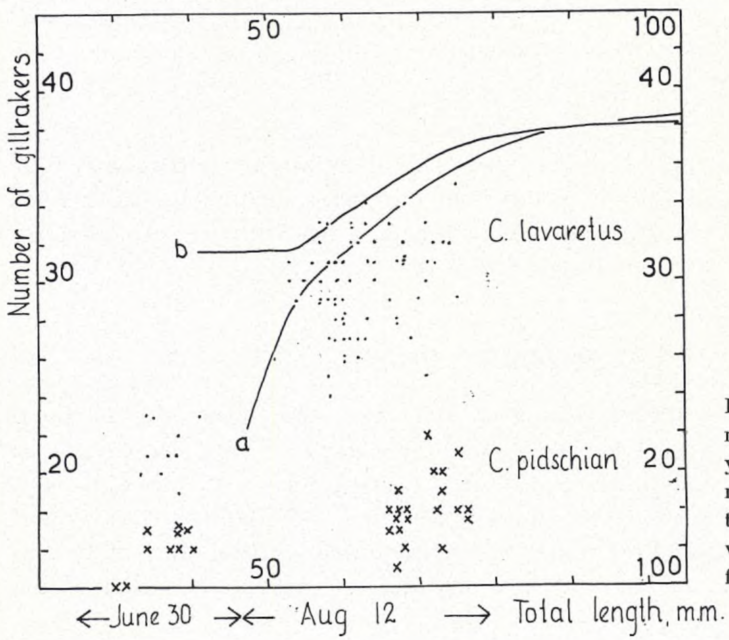
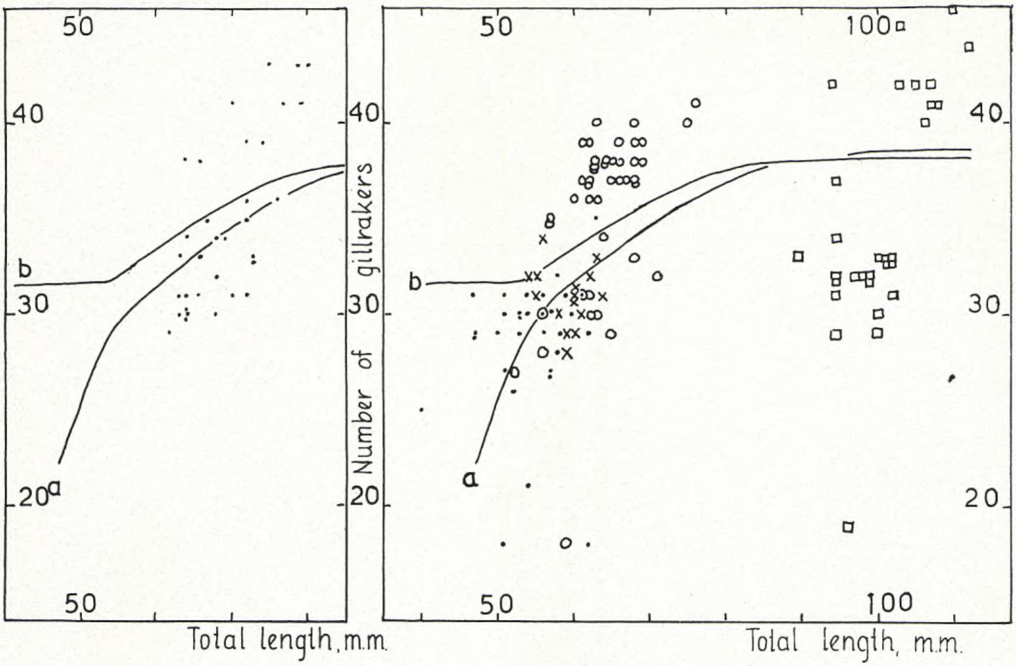


Fig. 4. Total length and number of gillrakers of young that had been reared in ponds and that were offspring of well-identified parent fish.



Figs. 5—8. Details from Fig. 3 B, different species at the same station. Limits a and b have the same meaning as in Fig. 3 B.

Legend: Fig. 5. · sample from Station 63, August 4, 1954
Fig. 6. · " " " 30, July 19, 1954
○ " " " 57, July 23, 1954
× " " " 20, July 24, 1954
□ " " " 63, October 10, 1954

No typical habitats for *pidschian* young have been found. The proportions between adult *pidschian* and other species in Table 11 do not agree very well with the proportions in Fig. 3.

10. Period II, food

Methods. Before weighing, preserved material is washed in accordance with a fixed scheme. Incomplete classification of stomach contents in insects and plankton before weighing introduces a source of error. So also does counting of individual food items, as only those are counted that are not too far digested. If the two methods are used together the reliability of the results is increased.

Consumption of food. The increase in the consumption of food is illustrated in Table 8, but the data cannot be converted into amounts of fresh food.

Variation in feeding habits. The variation in feeding habits with place and

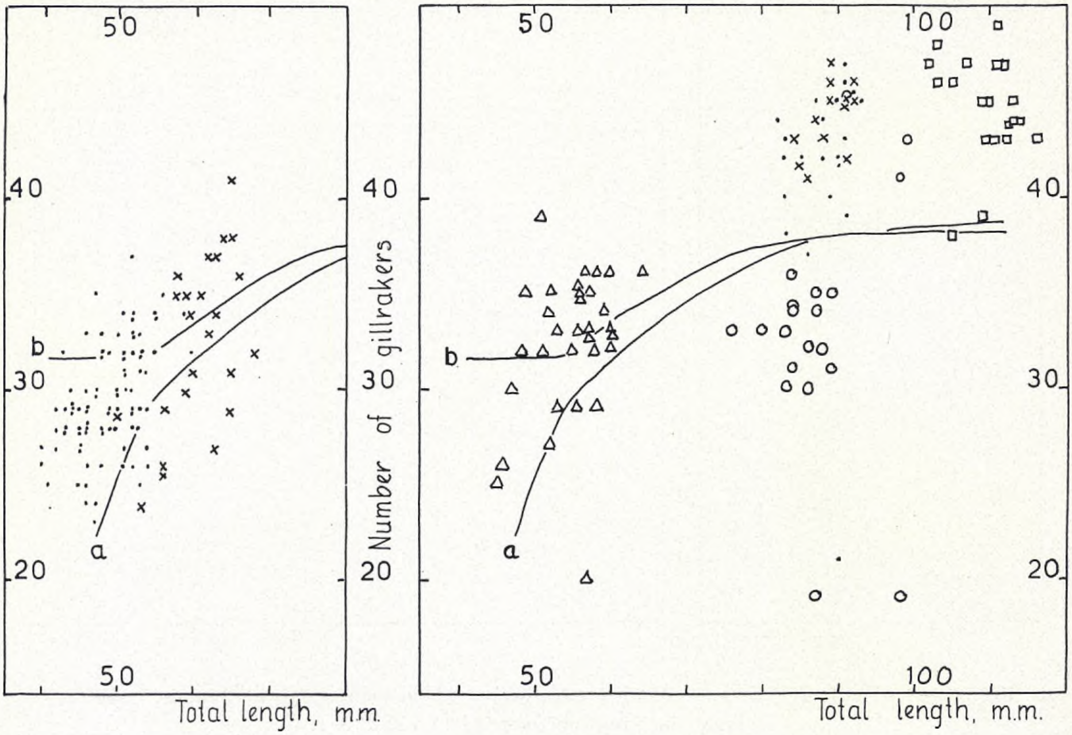


Fig. 7. · sample from station 56, July 23, 1958
× ,, ,, ,, 71, August 7, 1958
Fig. 8. △ ,, ,, ,, 54, July 18, 1959
· ,, ,, ,, 55, August 11, 1959
× ,, ,, ,, 52, August 12, 1959
○ ,, ,, ,, 64, 66, August 16 and 17, 1959
□ ,, ,, ,, 63, October 9, 1959

diurnal rhythm is illustrated by the food of *lavaretus* young in July 1954 (Figs. 9—10), and the diurnal rhythm is also illustrated by the food of *peled* young in August 1959. Those young that were caught in daytime on July 24, 1954, and August 12, 1959, had relatively more insects in the stomach contents than those caught in the evenings of July 19, 1954, and August 11, 1959. The diurnal rhythm can be observed in other ways too. Plankton was found in the fore end of the stomachs of the young caught in the evenings of July 23, 1954, and July 18 and August 11, 1959. In catches made at midnight on August 16 and 17, 1959, the young had insects in the fore end of their stomachs. (In other respects the sample of July 18 forms an exception from the general tendency, and in samples from period I the diurnal rhythm is not manifest at all.)

The variation in feeding habits which can be referred to place and diurnal rhythm is strong enough to disguise such variation between species as may exist (Figs. 9 and 10).

Table 11. Catches of adult whitefish

Gear	Station (Figs. 1 & 2)	Date	Numbers of		
			C. peled	*C. pidschian*	*C. lavaretus*
Seine, mesh perimeter 120 mm	29, 49—55	June and July, 1955, 1957	51	28	—
Bait seine, mesh perimeter 59—65 mm	Doljaure	July 1958, Aug. 1959	49	31	37
Gill nets, mesh size 33—100 mm, stretched mesh	Storavan	July—Aug. 1957	15	22	76
Gill nets as specified above	Uddjaur	Aug. 1957	26	30	45
Gill nets as specified above	Storavan	July—Sept. 1958	10	111	Not noted

11. Period II, growth

Effect of preservation When dealing with preserved material a correction factor of 1.016 is used for formol-preserved and 1.01 for alchohol-preserved fish to calculate the length of fresh fish (VAN OOSTEN 1929, HILE 1941).

Tearing of the caudal fin. For correction of total length when the caudal fins are torn, the total length is checked against standard length on undamaged specimens. In the length range 4—10 cm the total length approximately equals 1.21 times the standard length minus 2 mm.

Gear selection. Observations referred to in Chapter 1 show that whitefish young at certain stages can pass through the meshes of the seines. The mesh selection of a seine is difficult to estimate, as it only works during the brief final stage of a haule. If biassed, the mean length of a seine-caught sample would be too high.

Back calculation. During the 1950s scale samples were taken laterally of the midventral line of the whitefish, behind the pelvic fins. Scale radius — body length relations for *peled* and *lavaretus* have been worked out with the material presented in Table 12 and Fig. 11. Total fresh body length and cranial scale radius of dried scales of average size enter the relations. In those few cases when preserved material is used, body length is corrected as stated above and the radius length of dried and formol-preserved scales is multiplied by 1.05. The straight regression line for *lavaretus* is drawn in Fig. 11. For *peled* the lower part of the graph is drawn freehand and the upper part is a straight regression line. Values for young of 5 cm body length are also presented in Fig. 11, as they increase the validity of the graph. Back calculation of length at the end of the first year is made with the graph in fixed position. The scale interpretations imply that scale growth starts in July in most years.

Back-calculated body length at the end of the first year is tabulated in Table 13 by catch year and age group and in Fig. 12 a straight regression line

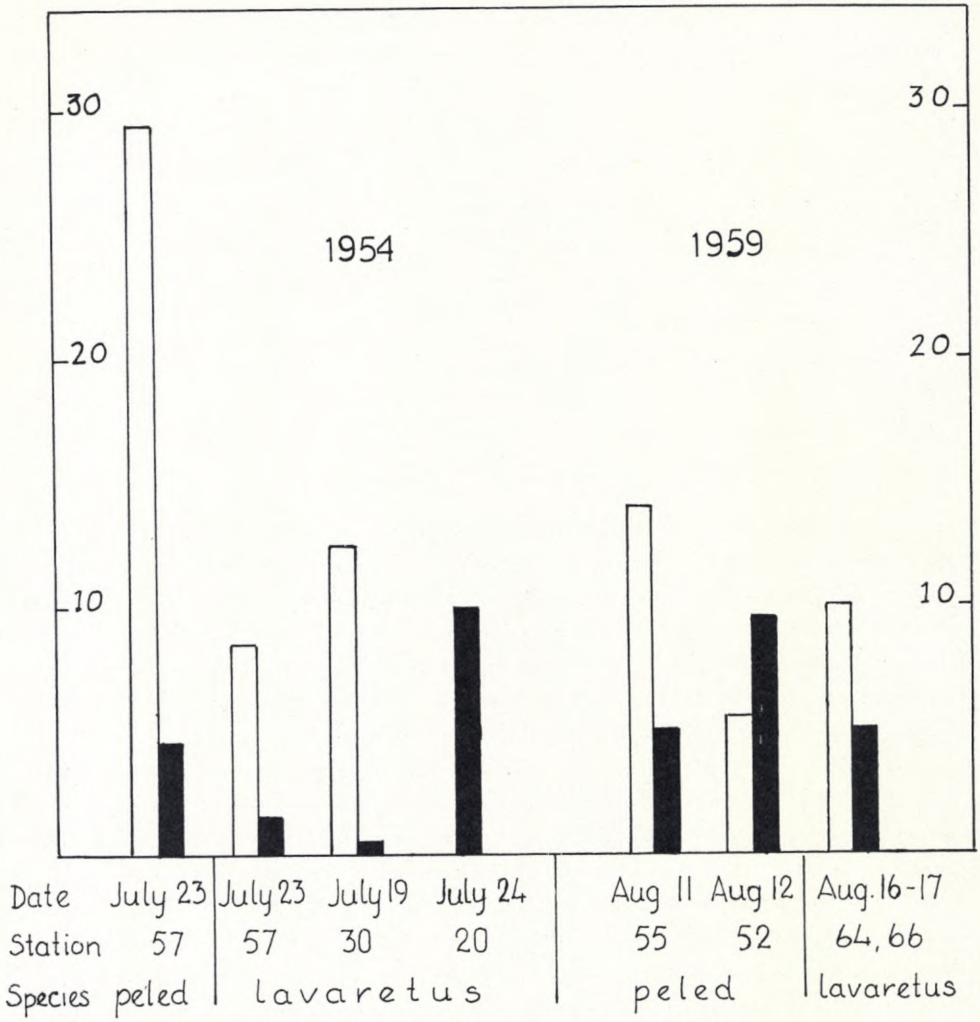
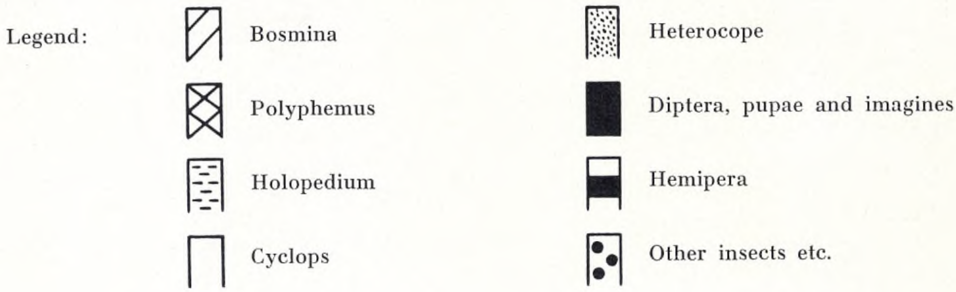


Fig. 9. Food of *C. peled* and *lavaretus* young, number of stomachs with plankton (white columns) or insects (black columns) forming more than half the stomach contents.



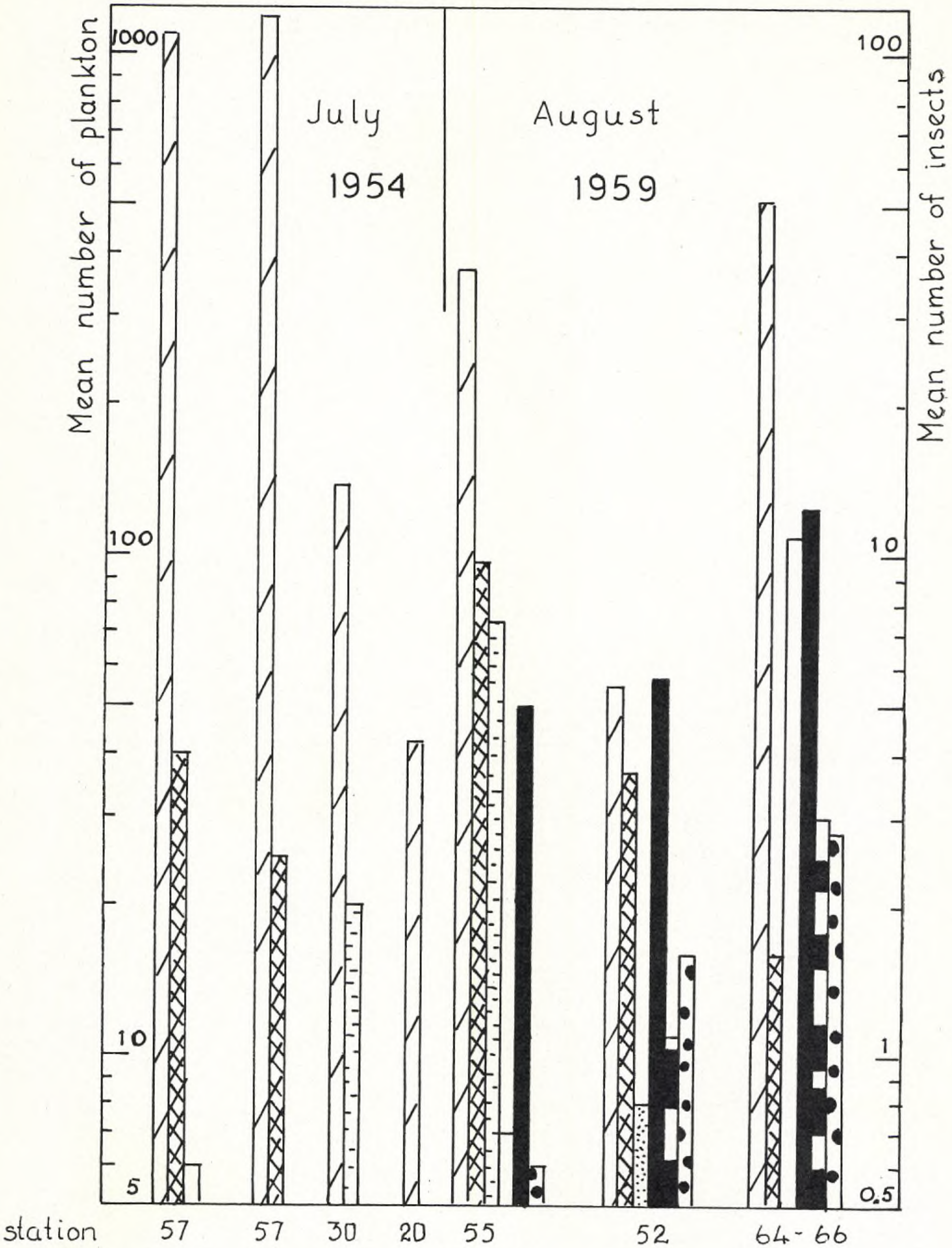


Fig. 10. Food of *C. peled* and *lavaretus,* particulars from the material presented in Fig. 9. Mean number of different food items per stomach. In the left part (1954) only plankton is represented though insects also existed in the food (cf. Table 8). Note: the log. scales differ. Fig.text continued on p. 130.

Table 12. Relation between total body length and anterior scale radius. Catches from Lake Storavan 1954—1958 with seine, gill nets and "kakuami".

$\bar{l}$=mean total length, measured on fresh fish, cm.

$\bar{s}$=mean length of anterior scale radius, measured on dried scales of average size, taken latero-ventrally behind the pelvic fins, mm., magnification $30^1/_2$ ×.

Length group	*C, lavaretus*			*C. peled*		
	n	$\bar{l}$	$\bar{s}$	n	$\bar{l}$	$\bar{s}$
9—11	44	10.3	19.8	10	10.5	17.0
11.5—13.5	11	13.3	26.9	6	12.7	19.3
14—16	29	15.3	38.8	—	—	—
16.5—18.5	69	17.3	43.1	1	16.8	34
19—21	16	19.9	48.3	4	20.1	42.0
21.5—23.5	—	—	—	12	22.4	50.1
24—26	—	—	—	12	25.1	66.4
26.5—28.5	—	—	—	17	27.6	80.5
29—31	—	—	—	32	30.0	89.5
31.5—33.5	—	—	—	26	32.4	94.9
34—36	—	—	—	31	34.8	107.8
36.5—38.5	—	—	—	9	37.7	135.1
39—41	—	—	—	4	39.5	145.5

is calculated for those means in Table 13 representing five or more specimens in the series from catch years 1957 and 1958 (*peled*) and 1954, 1957 and 1958 (*lavaretus*).

Certain year classes are specially marked off in Fig. 12. The deviation from the regression line indicates whether a year class had a bad or a good growth during the first year of life, and the best estimate of the first-year body length should lie in the vicinity of the intercept between the regression line and the body-length axis, corrected upwards or downwards for the individual year class.

According to this method, 1954 was a normal year and the first year length of the 1954 year class is estimated at $10^1/_2$—11 cm for *peled* and $9^1/_2$—10 cm for *lavaretus*.

During 1959 the scale samples were taken midventrally as indicated by EINSELE (1943) and his relation for body length and scale radius is used for back calculation (graph in fixed position). The first-year length of the 1953 and 1954 year classes acquires a slightly lower estimate with this method (Fig. 11, Tab. 16, Fig. 12).

Observed length of young in October has been discussed above (error, if any, an over-estimation, but then the growth is perhaps not quite completed in October). Table 8 gives a length of 10 $^1/_2$ cm for *peled* and 10 for *lavaretus* in 1954.

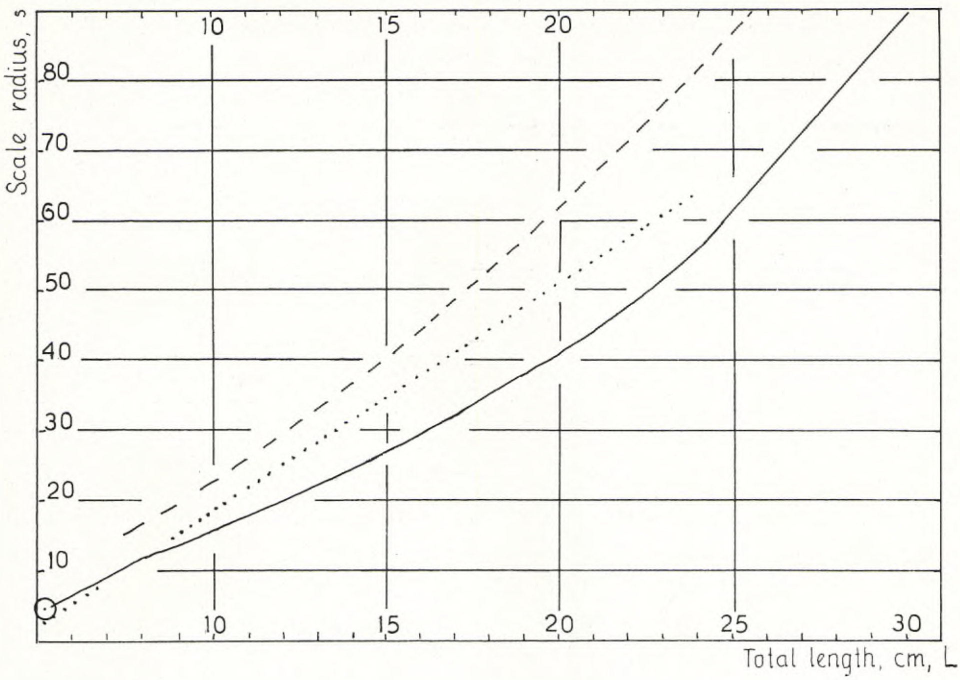


Fig. 11. Total body length in cm and anterior scale radius magnified 30 ½ ×, mm.

Broken line: the relation according to EINSELE.

Dotted line: *C. lavaretus*, lateroventral scales. s=3.26 L—14.2.

Continuous line: *C. peled*, lateroventral scales. s=5.56 L—77.6 for the straight regression part.

⊙ the relation for a sample of young caught in July.

Table 13. Length of one-year-old whitefish young from Lakes Uddjaur and Storavan, back-calculated from scales of older fish. Mean total length=$\bar{l}_1$ number=n.

Species	*C. peled*								*C. lavaretus*							
Catch year...	1954		1955		1957		1958		1954		1955		1957		1958	
Age at Capture	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n
I + ...	9.3	4	—	—	—	—	10.7	6	10.0	4	9.0	25	10.2	2	—	—
II + ...	—	—	—	—	9.7	5	8.5	1	8.7	22	10.0	8	10.0	8	9.6	7
III + ...	—	—	8	1	9.5	2	10.1	22	9.5	15	—	—	10.3	25	9.6	17
IV + ...	—	—	8.9	4	11.2	16	10.3	31	9.1	9	—	—	9.7	52	9.5	26
V + ...	—	—	8.4	18	9.8	7	10.8	27	8.9	2	—	—	9.6	27	9.6	23
VI + ...	—	—	8.5	11	9.8	6	10.5	8	—	—	—	—	9.0	8	9.0	6
VII + ...	—	—	9.8	3	8.6	9	10.6	10	—	—	—	—	—	—	9.7	4
VIII + ...	—	—	9.8	3	7.8	2	8.6	7	—	—	—	—	—	—	—	—
IX + ...	—	—	—	—	10.6	4	9.5	3	—	—	—	—	—	—	7.5	1

Table 14. Back-calculated first-year length, variation between Lakes Uddjaur and Storavan (Cf. Table 16, catch after increased impoundment). $\bar{l}_1$=mean total length, n=number.

Species		*C. peled*				*C. lavaretus*							
Catch, year		1955				1954				1957			
Lake		Storavan		Uddjaur		Storavan		Uddjaur		Storavan		Uddjaur	
		$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$	n
Age at capture	II +	—	—	—	—	8.9	8	8.6	14	—	—	—	—
	III +	—	—	—	—	9.6	10	9.2	5	10.3	19	10.2	6
	IV +	—	—	—	—	—	—	—	—	9.7	28	9.8	24
	V +	8.3	7	8.5	11	—	—	—	—	9.2	12	9.9	15
	VI +	8.8	6	8.0	5	—	—	—	—	—	—	—	—
Mean		8.5	13	8.2	16	9.2	18	8.9	19	9.7	59	10.0	45

Table 15. Back-calculated first-year length of *C. peled* from Lake Storavan, variation between estimates from different scales of the same fish. Fish caught summer 1957 and (No. 13) Nov. 22, 1958.

Fish no	Age	First year length from estimate no: 1	2	3	4	5
1	II+	9 1/2	10	—	—	—
2	II+	10	10	—	—	—
3	V+	10	10 1/2	—	—	—
4	V+	9 1/2	8 1/2	—	—	—
5	V+	9	8	—	—	—
6	VI+	9	9 1/2	—	—	—
7	VII+	8 1/2	8 1/2	—	—	—
8	VII+	8 1/2	9 1/2	—	—	—
9	VII+	8	10	—	—	—
10	VII+	8 1/2	9	—	—	—
11	IX+	9 1/2	10	—	—	—
12	IX+	10 1/2	12 1/2	—	—	—
13	IV+	12	11	10.5	12	11.5

Table 16. Back-calculated first-year length of *C. peled* from Lakes Storavan and Uddjaur. Scales from the midventral part, between the pelvics. Catch year 1959. $\bar{l}_1$=mean length, cm., n=number.

Lake		Uddjaur		Storavan		Storavan +Uddjaur
		$\bar{l}_1$	n	$\bar{l}_1$	n	$\bar{l}_1$
Age at capture	I+	—	—	9.6	33	9.6
	II+	9.7	37	9.7	5	9.7
	III+	9.0	10	9.2	5	9.1
	IV+	8.7	13	10.4	5	9.2
	V+	9.5	15	9.8	18	9.7
	VI+	9.1	8	9.6	7	9.3
	VII+	—	—	9.1	12	9.1
	VIII+	—	—	8.7	8	8.7

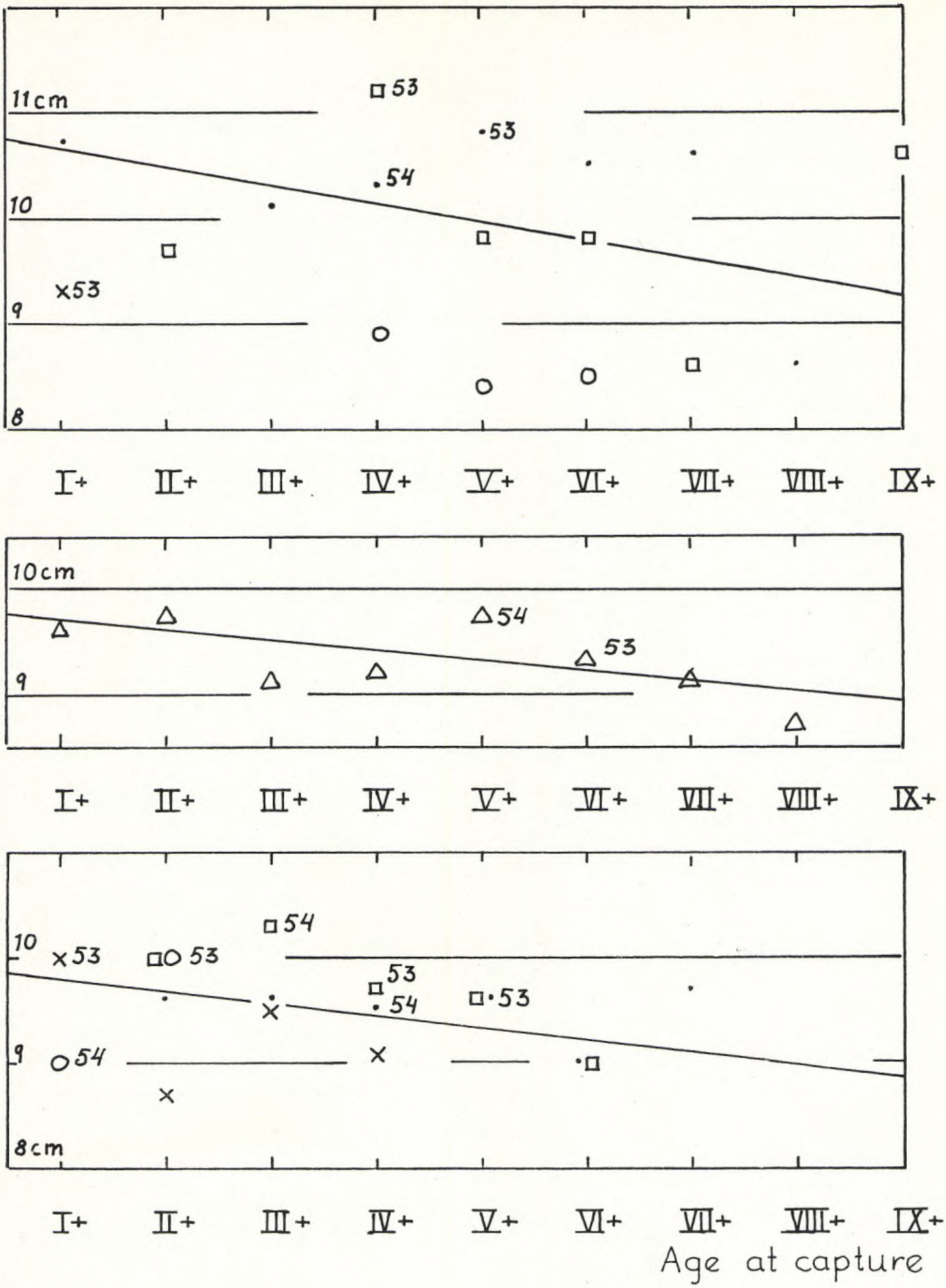


Fig. 12. Length of whitefish young at the end of the first year, back-calculation from scales of older fish. *C. peled* at the top (scales taken lateroventrally) and in the middle (scales taken midventrally). *C. lavaretus* at the bottom (lateroventral scales). 53 and 54 indicates the year classes 1953 and 1954.

Catch year is indicated according to the following legend:

× 1954 · 1958

○ 1955 △ 1959

□ 1957

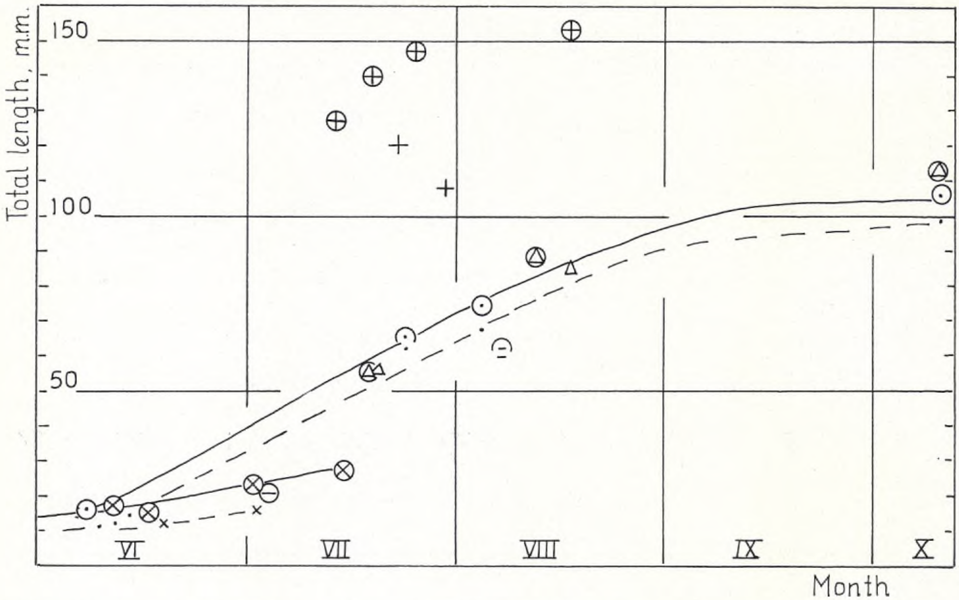


Fig. 13. Growth of whitefish young during their first year and some observations from their second summer. The growth curves for 1954 and 1955 are drawn freehand, continuous line=*C. peled*, broken line=*C. lavaretus*.[1]

C. peled	C. lavaretus [1]	
⊙	·	Year class 1954 during 1954
⊗	×	„ „ 1955 „ 1955
⊖	—	„ „ 1958 „ 1958
◬	△	„ „ 1959 „ 1959
⊕	+	Several year classes during their second summer

[1] In June and at the beginning of July: *C. lavaretus*+*C. pidschian*, cf. Chap. 4, identification.

Observations on the growth during the first year are presented in Fig. 13 together with some observations on the body length of whitefish during their second summer.

The growth of older whitefish is calculated for the 1958 catch in Storavan (Fig. 14). Method: EINSELE's relation of body length and scale radius, the graph movable round the intercept with the body-length axis.

12. Ecological isolation and interaction between whitefish young of different species

The material does not permit a full treatment of interaction and ecological isolation between the young of the three whitefish species during winter. Judging from the spawning places of the parent fish and from the behaviour

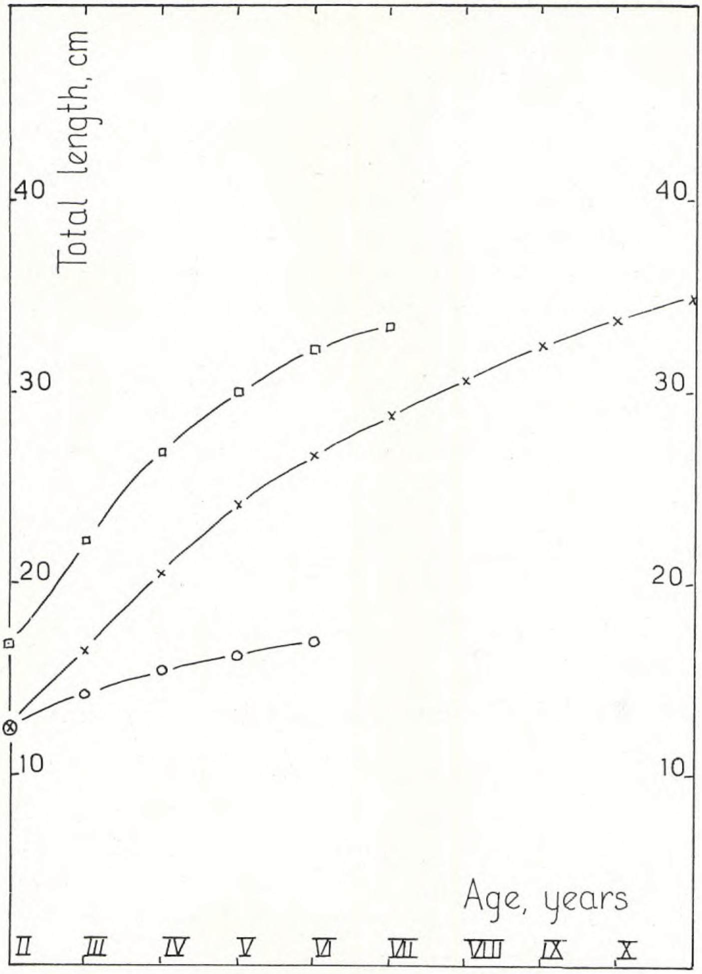


Fig. 14. Growth of *C. peled* (at the top), *C. pidschian* (in the middle) and *C. lavaretus* (at the bottom). Catch from Storavan in 1958.

of fry one can infer that, after hatching, the whitefish young appear in two groups with different habitats and probably also different food. The groups consist of *C. peled* and *C. pidschian*+*lavaretus*. The water that the hatching fry enter can be in intense motion during the spring — the water of the *peled* stream, of course, always is in this state — and the spreading resulting from this motion and the movements of the young themselves overrule the after effects of the choice of spawning places of the parent fish and new patterns for ecological isolation and interaction is established. *C. peled* and *lavaretus* now appear to a certain extent in the same habitat, and the influence of habitat choice and diurnal rhythm cause such variation in the diet that it has not been possible to show any differences in feeding habits between the young of those two whitefish species.

Interaction and ecological isolation between whitefish young of these species has been discussed in a paper by LINDSTRÖM & NILSSON in the Durham symposium 1960. It was commented that the most effective segregating mechanisms were to be expected during the early stages when the size of the populations are decided, but that the ecological isolation seemed more difficult to reveal during these stages than with the adult fish. It is true that the main isolating mechanism is likely to be differences in their ability to escape predators in different situations, but as there is a very complex series of events responsible for young fish mortality the isolating mechanism is bound to be correspondingly complex. Finally it was remarked that the measure of the similarity as regards choice of food and habitat of whitefish young in Uddjaur and Storavan may be crude. Starting from experiences of studies of adult fish and working with methods worked out therein, an investigater of young fish ecology may be inclined to overlook small but essential differences in the first year ecology.

13. Whitefish young and lake-level regulations

The main topic of the present paper is the life history of whitefish young in lake reservoirs. For this purpose the problem of species identification within the whitefish group (Ch. 4 and 8) is not equally important. There is a substantial amount of knowledge about the effect of lake regulations but the main predators on whitefish young are not even known with certainty. Until further investigations have disclosed those predators and a closer analysis has shown differences in choice of food and habitats between the young of different whitefish species, whitefish young can be treated as one heterogeneous group.

Much of the material in Chaps. 3—6 has been obtained from Lake Uddjaur, where the artificial changes in level fluctuations were slight up to 1957/1958, or from the streams between the lakes. This material cannot be expected to reveal any specific traits of a lake reservoir. Nor has it been possible to show any clear differences during period II between the three stages: Uddjaur up to 1957/1958, Storavan after the old regulation and Storavan after the increased damming in 1958 (with one possible exception, see next Chapter). The material still permits some general conclusions about the effect of lake regulations. Interest in the effect of a lake regulation is at present ultimately centred on the effect on individual growth and population density, Chaps. 14 and 15, and fish fauna composition.

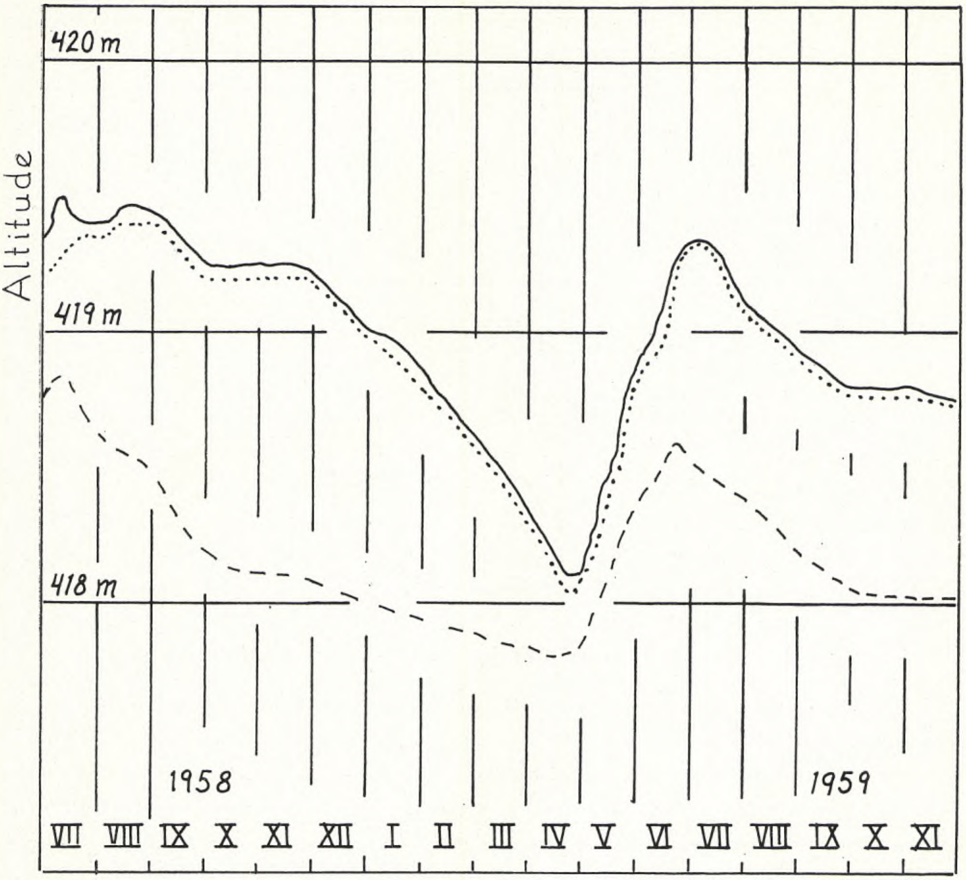


Fig. 15. Water-level fluctuations in Uddjaur (continuous line) and Storavan (dotted line) after the increased damming of Storavan and natural fluctuations in Storavan (reconstruction). Based on data from *Skellefteälvens Regleringsförening.*

14. The "damming effect" and the first year growth

The most advanced results in Scandinavian fisheries investigations of lake reservoirs are concerned with growth changes and changes in the food-organism populations and feeding habits (for a recapitulation, cf. NILSSON 1961). If fish young are in any way dependent on those food organisms that react with an increase on the damming during the first years, they could possibly show a better growth. Char young do not show such an increased growth (RUNNSTRÖM 1951). It remains to investigate whether their food habits differ from those of young whitefish in any essential way, and whether the slight indications of a better growth of whitefish young in 1959 in Lake Storavan can be connected with the increased damming (Fig. 13). The data in Figs. 12 and 13 and Tables 17 and 18 suggest that the good growth in 1959 is not only a temperature effect.

Table 17. Mean water temperature in the outflow from Storavan according to SMHI (the Metereological and hydrological institute of Sweden).

	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean June—Sept.	Mean May—Sept.
1953	—	—	—	—	—	13.08	16.23	14.61	9.03	4.45	0.98	0.37	13.22	—
1954	0.28	0.26	0.28	0.84	4.02	10.04	16.02	13.87	9.55	2.60	0.83	0.71	12.37	10.79
1955	0.14	0.79	0.65	0.83	2.50	6.93	14.10	14.22	10.09	2.93	0.63	0.92	11.44	9.57
1956	0.98	0.95	0.92	1.16	3.98	9.31	15.30	12.55	7.63	1.94	0.28	0.39	11.20	9.75
1957	0.46	0.55	0.57	1.15	2.96	9.03	13.81	14.19	8.49	1.95	0.42	0.39	11.38	9.70
1958	0.37	0.35	0.40	0.58	2.18	7.74	12.70	13.67	10.50	3.73	0.36	0.19	11.15	9.36
1959	0.21	0.24	0.39	0.94	5.08	10.86	14.59	13.90	7.43	3.52	0.40	0.46	11.70	10.37
1960	0.45	0.40	0.53	0.84	5.02	12.66	15.60	15.49	9.54	2.74	1.45	1.50	13.32	11.66
1961	1.23	1.04	0.78	1.18	—	—	—	—	—	—	—	—	—	—

The importance of temperature is evident from e.g. the retarded growth in 1955 and 1958 when summer came late (Fig. 13 and Tables 17 and 18).

15. Size of year classes in a lake reservoir

Though fishing statistics from test fishing and from the fishermen around the lakes have been gathered ever since the investigation on lake reservoirs began, the methodical problems of this approach have not been satisfactorily solved (discussed in the Swedish version). There is another approach to population density: a study of young fish mortality.

The idea of a short critical stage with high mortality caused by one factor during the development of fish young is nowadays replaced by the idea of a longer critical period with several operating mortality factors for pelagic young of marine fish (SIMPSON 1956, MARR 1956, BRIDGER 1961, PEARCY 1962; the length of the period and the use of the word "period" is under discussion). Investigations on freshwater young mortality are not easy to summarize. There are many factors making a fish's first year of life hazardous (cf. LE CREN 1959). The pattern certainly is not the same in all lakes and in all species. Both MONTÉN (1949, pike) and KRAMER & SMITH (1962, largemouth bass) report a short critical period, but the most important mortality factor is predators in one case and temperature and wind in the other. The examples of divergences could be multiplied.

BRETT (1958) has described how several factors can cooperate in producing a stress state. Predators belong to the group "discriminate, lethal stresses" in his terminology unless they only act as a potential lethal stress by chasing the fish young around without actually consuming the prey. RICKER & FOERSTER (1948) point out that a rapid growth of fish young means a decrease in the time during which the young are vulnerable to

Table 18. Dates for the breaking up of ice and the formation of a new ice-cover according to SMHI.

	Storavan		Uddjaur	
1950	June 5	Nov. 9	May 30	Nov. 11
1951	June 9	Nov. 14	June 7	Nov. 11
1952	June 4	Oct. 20	May 31	Oct. 27
1953	May 28	Nov. 21	May 23	Nov. 16
1954	May 30	Oct. 25	May 31	Oct. 25
1955	June 16	Oct. 20	June 14	Oct. 29
1956	June 4	Oct. 29	June 3	Oct. 30
1957	June 1	Nov. 2	June 1	Nov. 10
1958	June 14	Nov. 19	June 14	Nov. 19
1959	May 23	Oct. 29	May 17	Nov. 5
1960	May 30	Oct. 23	May 28	Oct. 25

predation. From the interaction between the young of whitefish species (LINDSTRÖM & NILSSON 1962) it was concluded that there is a rapid, optimal growth during the first year in the sense of RICKER & FOERSTER. The critical period, however, seems to be rather long — cf. Fig. 13. As often seems to be the case, the presumed predators are not known with certainty in Lakes Uddjaur and Storavan, and still less is known about the effect of the lake-level regulation on these predators. From the exposition above it is obvious that there is every reason to search for other mortality factors too.

The connection between degree of the winter draw down and size of the year class has been studied in lake reservoirs in Scandinavia with the following results. RUNNSTRÖM (1951) has shown that a maximal draw down in winter did not result in smaller year classes of char in Lake Torrön than in the years with a smaller draw down. In Lake Pålsbufjorden, on the contrary, very rich year classes of char come from years when the draw down did not approach the maximal limit according to AASS (1960), but the winter draw down of this lake ordinarily reaches the considerable value of 22—23 metres. Such comparisons show what draw down is needed in order to give a smaller year class as result in a lake that is already regulated, but they do not give an estimate of the changes in the average year class size that follow the lake-level regulation.

The present investigation has shown that whitefish young do not feed only on plankton — as is sometimes postulated — and this applies both to Uddjaur in 1954, before the lake level was distinctly influenced by the dam of Lake Storavan below, and to Storavan before and after the increased damming. *Diptera,* mainly pupae and imagines of chironomids, hymenopters and hemipteres, mainly *Aphididae,* all of small size, are consumed. With such a diet, a reduction of the bottom animals in the upper littoral zone where the habitats of whitefish young are found may influence the mortality rate of the young. GRIMÅS (1961) has shown that such a reduction takes place when a lake is converted into a lake reservoir. It is not yet established whether the species selected by the whitefish young in the present investigation are actually reduced, but with the plasticity in feeding habits typical of whitefish young any reduction of hatching insects of small size may affect the mortality of the young. The periods is that of rapid growth during the first year and thus a critical period according to RICKER & FOERSTER (1948). The possible effect of a decrease in the food animal populations is not food shortage and starvation in the old sense of these words, but a reduction of rich food animal accumulations is likely to affect the number of whitefish young that can grow fast enough to escape the effect of predators, whether these produce a lethal or potentially lethal stress in the sense of BRETT (1958).

Summary

Hatching time, length at hatching, growth, feeding habits and habitats of whitefish young of the year in two lake reservoirs are described. Differences between species are pointed out if observed; identification of species in Chaps. 4 and 8.

Notes on behaviour on pp. 118 and 124.

The plasticity in feeding habits is considerable and the variation which can be referred to place or diurnal rhythm is strong enough to disguise such variation as may exist between species or between the studied lakes (with different degree of lake-level regulation).

Variation between different estimates of length at the end of the first growth year is studied. No difference in growth is as yet observed between different lakes but the growth is retarded when summer comes late.

The effect of lake-level regulations is discussed.

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